Exxon Valdez Oil Spill
Restoration Project Annual report

APEX Project:

Alaska Predator Ecosystem Experiment in Prince William Sound and the Gulf of Alaska

Restoration Project 98163
Annual Report

This annual report has been prepared for peer review as part of the Exxon Valdez Oil Spill Trustee Council Restoration Program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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Study History: The research project APEX (the Alaska Predator Ecosystem Experiment) was initiated under Restoration Project 95163, merging together a group of existing bird and forage fish investigations and proposals to provide an integrated research approach that examines the interactions of seabirds and their prey, the reasons that changes in prey might have occurred, and the consequences for seabirds. The primary hypothesis to be tested is that several seabird species have failed to recover from the *Exxon Valdez* oil spill because of shifts in food supply that may have occurred independently in the marine ecosystem of Prince William Sound and the northern Gulf of Alaska. This annual report (98163) covers the 1998 field season, the fourth of five seasons planned for the project.

Abstract:

The Alaska Predator Ecosystem Experiment (APEX) is a five-year study of the effect of food resources on seabirds from the *Exxon Valdez* oil spill (EVOS) in Prince William Sound and Cook Inlet. The study examines historical data, forage fish resources, seabird reproduction and colony and population dynamics to address this issue. Research to date strongly suggests a basic shift in ecosystem structure occurred after the late 1970's, with a decrease in species nutritious to seabirds and an increase in species less rich in lipids. This resulted in population declines for several forage species and may help explain the subsequent failure of seabird species to recover from EVOS mortality. Current work aims at extending and refining these conclusions, understanding the factors that may trigger such major shifts, identifying critical areas in Prince William Sound for fish and seabird interactions, and developing a means of monitoring the Northern Gulf of Alaska.

Key Words: *Ammodytes*, *Brachyramphus*, Capelin, *Clupea,* Cook Inlet, *Fratercula*, Guillemot, Gulf of Alaska, Herring, Kittiwake, *Mallotus*, Murre, Murrelet, pollock, Prince William Sound, puffin, *Rissa*, sandlance.

Project Data: (will be addressed in the final report)

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Executive Summary

The APEX Project is a five-year study to determine if food has limited the recovery of seabirds in the Northern Gulf of Alaska area affected by the oil spill of the *Exxon Valdez*. The project has three interconnected components that study fish ecology, seabird foraging at sea, and seabird reproductive success and colony dynamics on land.

Historical analysis of fisheries research trawls shows a strong shift in the marine ecosystem from a shrimp/capelin/sandlance system to one dominated by pollock since the late 1970's and early 1980's. The change is associated with an increase in ocean temperature which may have altered recruitment strength and patterns or changed the distributions of predators.

Analysis of data from APEX and previous studies suggest that Pigeon Guillemot breeding numbers in Prince William Sound declined in response to decreases in sandlance, a major prey. Similarly, Black-legged Kittiwake populations in northern Prince William Sound that have depended more on herring have been more stable than southern populations, which may have formerly been more capelin-dependent.

Pigeon Guillemot and Black-legged Kittiwake reproductive success reflect lipid levels in prey, delivery rates by adults, meal size, and--for kittiwakes-- foraging trip length and energy expenditure. Other factors such as predation can obscure such relationships. By using multiple sites over a number of years, we can begin to weigh the relative influence of different forces.

Because of the complexity of the interplay of forces affecting seabird and fish populations, we use models to test the importance of different factors that affect seabirds. These products will identify the environmental measurements that should be most useful for longterm monitoring of the Sound. They will also identify critical areas that should be protected either in the event of another oil spill or as development occurs, especially in the western part of Prince William Sound.

INTRODUCTION

The spill from the oil tanker *Exxon Valdez* resulted in significant mortality of several seabirds and in acute massive damage to Prince William Sound (PWS), Lower Cook Inlet (LCI) and the Gulf of Alaska (GOA) (Piatt *et al.* 1990). Seven years following the spill in 1996, several species have not recovered. This may be the result of lingering effects of the oil spill (toxicity of prey or sublethal effects of oil exposure to organisms) or inertia in population response. However, other non-oil factors may also be involved, such as predation, climate-driven ecosystem changes (Duffy 1993), or even 'random' perturbations (Wolfe and Kjerfve 1986).

Numerous seabird species have declined between surveys in the 1970's and the 1990's in Prince William Sound: cormorants (*Phalacrocorax* spp.), Black-legged Kittiwake, Glaucous-winged Gull (*Larus glaucescens*), Arctic Tern (*Sterna paradisaea*), Kittlitz's and Marbled murrelets (*Brachyramphus brevirostris* and *B. marmoratus*), Tufted (*Lunda cirrhata*) and Horned (*F. corniculata*) puffins, and Pigeon Guillemot (*Cepphus columba*) (Agler *et al.* 1994 a,b; Klosiewski and Laing 1994).

Colony trends for kittiwakes in Prince William Sound have been inconsistent, with colonies decreasing in the southern portion and increasing in the north (Irons and Suryan, APEX unpubl. data). The population of Pigeon Guillemots in PWS decreased from about 15,000 in the 1970's to about 3,000 in 1993 (Isleib and Kessel 1973; Sanger and Cody 1993). Based on censuses taken around the Naked Island complex, pre-spill counts were roughly twice as high as post-spill counts

(Oakley and Kuletz 1993). Pigeon Guillemots are listed as "Not recovering" in the 1994 *Exxon Valdez* Oil Spill Restoration Plan.

Common Murres (*Uria aalge*) in Cook Inlet were among the species most damaged by the oil spill (Piatt *et al.* 1990). Murres were also listed as "Not recovering" in the 1994 *Exxon Valdez* Oil Spill Restoration Plan, but have been upgraded to "recovering" because productivity has been normal since 1993 (Roseneau *et al.* 1995, 1996).

The best evidence for a shift in trophic resources for seabirds within Prince William Sound comes from Pigeon Guillemots (Hayes and Kuletz 1996). In 1994, sandlance (*Ammodytes hexapterus*) accounted for only about 1% of prey items fed to guillemot chicks at Jackpot Island and about 8% at Naked Island. In contrast, in 1979 the sandlance component at Naked Island was about 55% (Kuletz 1983; Oakley and Kuletz 1993). Gadids were much more prevalent in the diet of guillemot chicks on Naked Island in the 1990's than they were in 1979-1981 (< 7%) (Hayes and Kuletz 1996).

The decline in the prevalence of sandlance in the diet of guillemots breeding at Naked Island might be a key element in the failure of this species to recover from the oil spill. The schooling behavior of sandlance, coupled with its high lipid content relative to that of gadids and nearshore bottom fish, might make this species a particularly high-quality forage resource for guillemots. This is consistent with the observation that other seabird species (e.g., puffins, murres, kittiwakes) experience enhanced reproductive success when sandlance are available (Pearson 1968; Harris and Hislop 1978; Vermeer 1979, 1980; Monaghan *et al.* 1989) .

In addition, the carrying capacity of the forage environment for guillemots in the absence of pelagic forage species such as sandlance or herring is probably low, restricted to benthic fish. The more pelagic fish present, the greater the carrying capacity. Hayes and Kuletz (1996) found a strong correlation between total numbers of adult guillemots and active nests and the annual percentage of sandlance in chick diets at Naked Island, supporting this hypothesis.

There is considerable evidence of shifts in forage species from shrimp and lipid-rich capelin to low-lipid wall-eye pollock (*Theragra chalcogramma*) and bottomfish (Springer 1993; Piatt and Anderson 1995; Anderson *et al.* 1996; Bechtol 1996; Hansen 1996).

Mechanisms that could cause a reduction in energy-rich forage fish populations remain unknown. Major oceanographic shifts in the northern Gulf of Alaska and North Pacific (Springer 1993; Piatt and Anderson 1995) may have favored pollock, one of the most abundant forage fish species currently available to seabirds (Parks and Zenger 1979; Springer and Byrd 1989; Brodeur and Merati 1993). Pollock may also be an important competitor or predator of other forage fish species and may suppress populations of these species. Similarly, other species-pairs may overlap in diet, such as herring and sandlance (McGurk and Warburton 1992) or pink salmon (*Oncorhynchus gorbuscha*) and sandlance (Sturtevant 1995 and unpubl.), raising the possibility that reductions in abundance of one species may 'release' others from competition for food.

Both to aid in the recovery of injured resources and to safeguard the long-term health of Prince William Sound, Cook Inlet, and the upper Gulf of Alaska, we need to understand the ecological processes that control the ecosystem. This project focuses on the trophic interactions of seabirds and the forage species they depend on. We chose food as the focus because:

1) much of seabird population theory and several empirical field tests have identified food as an important limiting factor (Ashmole 1963; Furness and Birkhead 1984; Birt *et al.* 1987; Cairns 1989);

2) seabird/fish researchers in the PWS/GOA complex have concluded that major changes in food have occurred during the period (Springer 1993; Piatt and Anderson 1995; Anderson *et al.* 1994);

3) other factors such as oil toxicity and climate change might express themselves through the food supply; and

4) knowledge of the forage prey base is critical for other apex predators, such as marine mammals and predatory fish (Pitcher 1980, 1981; Lowry *et al.* 1989), as well as for any larger effort to manage the marine resources of Prince William Sound and the Gulf of Alaska in a sustainable manner.

This report documents progress in the study of the distribution and abundance of prey species through acoustic and net sampling in relation to food, environmental conditions and possible competitors, then proceeds to examine the physical, behavioral and competitive factors that limit access to these forage species for seabirds. We examine the reproductive consequences of such limitations for Pigeon Guillemots, Black-legged Kittiwakes, Tufted Puffins, Common Murres, and cormorants at the chick and colony level.

The study uses between-year comparisons within sites and within-year comparisons between sites in Prince William Sound and Lower Cook Inlet, areas that have a range of different food-availabilities. The comparisons between years allow us to assess the degree of variability of different food regimes, while the between-site comparisons allow us to assess the responses of seabird communities to these same regimes. We use models to relate oceanographic and spatial features of estuaries in the Northern Gulf of Alaska to changes in seabird diet and population trends. We hope to build up a picture of the forage base for the entire seabird community, setting the stage for a long-term, low-cost monitoring program.

Objectives

The APEX Project has as its objective the testing of a general hypothesis:

A shift in the Prince William Sound marine trophic structure has prevented recovery of injured resources.

This is approached through research testing several more specific hypotheses:

1. The trophic structure of PWS and GOA have changed at the decadal scale.
2. Planktivory is the factor determining abundance of the preferred forage species of seabirds.
3. Forage fish species differ in their spatial responses to oceanographic processes.
4. Productivity and size of forage species change the energy potentially available for seabirds.
5. Forage fish characteristics and interactions among seabirds limit availability of seabird prey.
6. Seabird foraging group size and species composition reflect prey patch size.
7. Seabird diet composition and amount reflect changes in the relative abundance and distribution of forage fish at relevant scales around colonies.
8. Changes in seabird productivity reflect differences in forage fish abundance. as measured in adult seabird foraging trips, chick meal-size and chick provisioning-rates.

9. Seabird productivity is determined by differences in forage fish nutritional quality.
10. Seabird species within a community react predictably to different prey bases.
11. Continuing damage from oiling is restricting recovery of some forage fish species.

By testing these hypotheses, we hope to understand how past effects of changes at the ecosystem level continue to affect seabird populations at present. We also hope to determine which environmental measures will be most effective for future monitoring, to help managers take the pulse of the estuaries of the Northern Gulf of Alaska.

Methods and Results

APEX is a complex project, with fifteen subprojects and three main lines of investigation. In many cases, a single project may contribute to two or more such lines. In addition, data flow is equally complex: a project may contribute some of its data to a second project for analysis, while performing analysis and synthesis of its own data, combined with that of a third project. Several projects provide technical support (Project C, I, O).

There are three main field components of APEX:

1. studying the fish community (Projects A, B, K, L, M),
2. studying fish /bird (Projects B, E, F) and harbor seal/fish (Project I) interactions at sea,
3. those studying the effects of food supply on colony size and reproductive success (Projects E, F, G, J, M).

In addition, Project Q is modelling the fish/forage/colony interaction and Projects B and I are modelling spatial aspects of the prey. Project O provides statistical and modelling advice to a range of projects.

Methods and results may be found in the detailed project descriptions for each subproject.

Discussion

Four years into APEX, we have a good picture of how seabirds respond to prey differences. We also know what prey are best for higher seabird reproductive success. We know that these prey are in short supply regionally or annually, compared to the pre-1970's. We know that this change is associated with warmer ocean temperatures. We also known that some species like Black-legged Kittiwake exhibit considerable ecological inertia, continuing to breed in regions where food has become consistently unavailable.

Response to the 1970's changes may in fact still be occurring, as many colonies fail to produce enough young to sustain themselves and others need time to become established in food-rich areas. The breeding adults are highly competent; they have simply evolved to remain attached to a single colony, a somewhere where food has become rare. We also know that the Northern Gulf of Alaska has a core cool area, associated with upwelling between the Barrens and Kachemak Bay. This area appears to have consistently hgih reproduction compared to outlying, wamer areas, such as Prince William Sound.

We also know that food supply for breeding has two or three different and distinct periods: all three have to be favorable for breeding to be successful The first is winter food that provides the energy with which birds return to breed. If, as in spring 1998, winter food is in short supply, breeding is delayed. The second period, associated with year 1 sandlance and herring occurs during incubation, If these prey are absent, whether because of current environmental conditions or because their year-classes failed the year before, breeding may again be late, may not occur, or clutch size may be reduced. Finally in July and August, an influx of spent capelin, young herring and sand lance offer food for fledging young birds. Again, if these are absent, the birds may fail.

We also know that, far from there being any substance to the "dumb kittiwake" hypothesis of two years ago, kittiwakes are skilled fishers, specializing by location and even down to tide stage. We also know that murrelets are essential to driving prey to the surface and that flock foraging may actually be a sign of limited food, at least for some species. Unfortunately we lack data on how many of these species forage and interact under conditions of food abundance and we can only guess how the recent retreat of many glaciers has affected murrelets and kittiwakes that may have spent much of their ecological history at the glaciers' edge.

Because we chose to divert our limited resources to the study of bird-fish interactions, we had to short-change our studies of fish ecology in relation to environmental conditions. We had hoped to be able to predict the link from climate to food to fish to birds. We have instead had to settle on the "tactical" response of fish to environmental conditions at small scales and short periods. We had just begun to be able to follow cohorts of fish from year to year, as they interact with environmental conditions at different life stages. This is a rich field for further one and an essential one if Alaska's marine resources are to be properly managed.

For sandlance, we have an emerging picture of a species usually tied to a narrow range of substrates in limited supply in the Sound; for capelin, we see a species marginalized from our study area by its need for cool waters. Herring appear to be especially sensitive to overwintering in their first winter, so that summer conditions may be less critical to their ecology.

It is my own belief that the key to the APEX question rests with the capelin, a cool-water species that was common in seabird diets before the climatic regime shift in the 1970s. Capelin are now found breeding primarily in a cool-water core area around the Barren Islands. In cooler years, this core extends outwards to Kodiak, Middleton Island and Prince William Sound, producing a summer of increased netsing success as in 1996. Usually, however, these three areas have seabird populations that consistently exhibit failure at a regional level, although individual colonies continue to produce young because of local conditions.

If a long-term monitoring program continues to give us an index of the three species' abundances, as well as of environmental conditions, this may prove to be the key to understanding these critical prey species. If we can understand them, and their response to environmental change, then we will finally be able to be predictive, not just reactive, about the response of seabirds and other apex predators to environmental change.

Acknowledgments

This project is the result of the work of a large number of investigators, field workers, technicians, and support staff. These are recognized and acknowledged in the individual sections. They worked under often miserable conditions of cold and rain, but they had fun and they did an amazing job. Finally, this project is very much the creation of an exceptional set of principal investigators. As APEX ends and many of these people disperse in a few years, we can expect them to make a wider mark on marine science. At the overall program level, S. Senner, R. Spies, and B. Wright have been extremely helpful in providing moral support, insights, and critical suggestions that have

greatly improved the project. The EVOS Scientific Reviewers have also helped greatly with their commentary.

Literature Cited

Agler, B. A., P. E. Seiser, S. J. Kendall, and D. B. Irons. 1994 a. Marine bird and sea otter population abundance of Prince William Sound, Alaska: trends following the T/V *Exxon Valdez* oil spill, 1989-93. *Exxon Valdez* oil spill restoration final reports, Restoration Project 93045. U.S. Fish and Wildlife Society, Anchorage.

Agler, B. A., P. E. Seiser, S. J. Kendall, and D. B. Irons. 1994 b. Winter marine bird and sea otter population abundance of Prince William Sound, Alaska: trends following the T/V *Exxon Valdez* oil spill, 1989-94. *Exxon Valdez* oil spill restoration final reports, Restoration Project 94159. U.S. Fish and Wildlife Society, Anchorage.

Anderson, P. J., J. E. Blackburn and B. A. Johnson. 1996. Declines of forage species in the Gulf of Alaska, 1972-1995, as an indicator of regime shift. pp. 531-544. In. Forage Fishes in Marine Ecosystems. University of Alaska Sea Grant, Anchorage.

Anthony, J. A., D. D. Roby, and K. R. Turco. submitted. Lipid content and energy density of forage fishes from the northern Gulf of Alaska.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103 b: 458-473.

Bechtol, W. R. 1996. Changes in forage fish populations in Kachemak Bay, Alaska, 1976-1995. pp. 441-456 In. Forage Fishes in Marine Ecosystems. University of Alaska Sea Grant, Anchorage.

Birt, V. L., T. P. Birt, D. Goulet, D. K. Cairns, and W. A. Montevecchi. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Marine Ecology Progress Series 40: 205-208.

Brodeur, R. D. and N. Merati 1993. Predation on walleye pollock *(Theragra chalcogramma)* eggs in the western Gulf of Alaska: the roles of vertebrate and invertebrate predators. Marine Biology 117: 483-493.

Cairns, D. K. 1989. The regulation of seabird colony size: a hinterland model. American Naturalist 134: 141-146.

Duffy, D. C. 1993. Stalking the Southern Oscillation: environmental uncertainty, climate change, and North Pacific seabirds. pp. 61-67 In. K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey (eds.). The status, ecology, and conservation of marine birds of the North Pacific. Special Publication, Canadian Wildlife Service, Environment Canada, Ottawa.

Francis, R. C. and S. R. Hare. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. Fisheries Oceanography 3: 279-291.

Furness, R. W. and T. R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311: 655-656.

Hansen, D. J. 1996. Shrimp fishery and capelin decline may influence decline of Harbor Sea (*Phoca vitulina*) and Northern Sea Lion (*Eumetopias jubatus*) in western Gulf of Alaska. pp. 197-208. In. Forage Fishes in Marine Ecosystems. University of Alaska Sea Grant, Anchorage.

Harris, M. P., and J. R. G. Hislop. 1978. The food of young puffins *Fratercula arctica.* J. Zool. Lond. 85:213-236.

Hatch, S. A., G. V. Byrd, D. B. Irons, and G. L. Hunt, Jr. 1993. Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. pp. 140-153 In. K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey (eds.). The status, ecology, and conservation of marine birds of the North Pacific. Special Publication, Canadian Wildlife Service, Environment Canada, Ottawa.

Hayes, D. L. and K. J. Kuletz. 1996. Decline of Pigeon Guillemot populations in Prince William Sound, Alaska and apparent changes in distribution and abundance of their prey. pp. 699-702. In. Forage Fishes in Marine Ecosystems. University of Alaska Sea Grant, Anchorage.

Heincke, F. (1913). Untersuchungen über die Scholle, Generalbericht I. Schollenfischerei und Schonmassregeln. Vorläufige Kurze Übersicht über die wichtigsten Ergebnisse des Berichts. Rapp. Proces-Ver. Con. int. Explor. Mer, 16: 1-70.

Isleib, M.E. and B. Kessel. 1973. Birds of the north Gulf Coast -- Prince William Sound region, Alaska. Biol. Pap. Univ. of Alaska 14:1-149.

Klosiewski, S. P. and K. K. Laing. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the Exxon Valdez oil spill. NRDA Bird Study Number 2. Unpubl. Rep., U.S. Fish and Wild. Serv., Anchorage.

Kuletz, K. J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding Pigeon Guillemots. Unpublished M.S. Thesis. Univ. of California, Irvine. 79 pp.

Lowry, L. F., K. J. Frost, and T. R. Loughlin. 1989. Importance of walleye pollock in the diets of marine mammals in the Gulf of Alaska and Bering Sea, and implications for fishery management. pp. 701-726 In. Proceedings of the International Symposium on the Biology and Management of Walleye Pollock. University of Alaska Sea Grant Report 89-01.

McGurk, M. D. and H. D. Warburton. 1992. Fisheries oceanography of the Southeast Bering Sea: relationships of growth, dispersion and mortality of sand lance larvae to environmental conditions in the Port Moller estuary. OCS Study MMS 92-0019, Marine Management Service. Anchorage.

Monaghan, P., J. D. Uttley, M. Burns, C. Thane, and J. Blackwood. 1989. The relationship between food supply, reproductive effort, and breeding success in Arctic Terns *Sterna paradisea.* Journal of Animal Ecology 58:261–274.

Oakley, K.L., and K.J. Kuletz. 1993. Population, Reproduction and Foraging ecology of Pigeon Guillemots at Naked Island, Prince William Sound, Alaska, Before and After the *Exxon Valdez* Oil Spill. Bird Study Number 9.

Parks, N. B. and H. Zenger. 1979. Trawl survey of demersal fish and shellfish resources in Prince William Sound, Alaska. NWAFC Process Report 79-2. NOAA, NMFS, Seattle.

Pearson, T. H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.

Piatt, J. F. and P. Anderson. 1995. Response of Common Murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem. In. S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright (eds.). *Exxon Valdez* Oil Spill Symposium Proceedings. American Fisheries Society Symposium No. 18.

Piatt, J. F., C. J. Lensink, W. Butler, M. Kendziorek, and D. R. Nysewander. 1990. Immediate impact of the "Exxon Valdez" oil spill on marine birds. Auk 107: 387-397.

Pitcher, K. W. 1980. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Fisheries Bulletin 78: 544-549.

Pitcher, K. W. 1981. Prey of the Steller sea lion, *Eumetopias jubatus,* in the Gulf of Alaska. Fisheries Bulletin 79: 467-472.

Roemmich, D. and J. McGowan. 1995. Climatic warming and the decline of zooplankton in the California Current. Science 267: 1324-1326.

Roseneau, D. G., A. B. Kettle, and G. V. Byrd. 1995. Common murre restoration monitoring in the Barren Islands, 1993. Restoration Project No. 93049. Annual. report. by the U.S. Fish Wildl. Serv., Homer, AK.

Roseneau, D. G., A. B. Kettle, and G. V. Byrd. 1996. Common murre restoration monitoring in the Barren Islands, 1994. Restoration Project No. 94039. *In Preparation.* Annual. report. by the U.S. Fish Wildl. Serv., Homer, AK.

Sanger, G. A. and M. B. Cody. 1993. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. Draft Final Report, Restoration Project 93034, U. S. Fish and Wildlife Service. Anchorage.

Springer, A. M. (compiler). 1993. Report of the seabird working group. pp. 14-29 In. Workshop Summary: Is it food? Addressing marine mammal and seabird declines. Alaska Sea Grant College Program, Fairbanks.

Springer, A. M. and G. V. Byrd. 1989. Seabird dependence on walleye pollock in the southeastern Bering Sea. In. Proceedings of the International Symposium on the Biology and Management of Walleye Pollock. University of Alaska Sea Grant Report 89-01.

Sturdevant, M. V. 1995. 1994 forage fish diet study: progress and preliminary data report of stomach analysis by Auke Bay Laboratory. Auke Bay Laboratory, NMFS, Alaska (unpubl.).

Trenberth, K. E. and J. W. Hurrell. 1995. Decadal coupled atmosphere--ocean variations in the North Pacific Ocean. Canadian Special Publication Fisheries and Aquatic Science 121: 15 - 24.

Vermeer, K. 1979. Nesting requirements, food and breeding distribution of Rhinoceros Auklets, *Cerorhinca monocerata,* and Tufted Puffins, *Lunda cirrhata.* Ardea 67: 101-110.

Vermeer, K. 1980. The importance of timing and type of prey to reproductive success of Rhinoceros Auklets *(Cerorhinca monocerata).* Ibis 122: 343-354.

Wolfe, D. A. and B. Kjerfve. 1986. Estuarine variability: an overview. pp. 3-15 In. D. A. Wolfe (ed.). Estuarine Variability. Academic Press. New York

APPENDIX

REPORTS OF INDIVIDUAL SUBPROJECTS

A Forage Fish Assessment

Exxon Valdez Oil Spill
Restoration Project Annual Report

Forage Species Studies in Prince William Sound, 1998

Restoration Project 98163 A

Annual Report

Lewis Haldorson
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...........Screaming, the gulls watch,
Wild with envy and malice, cursing and snatching, what
hysterical greed!
What a filling of pouches! the mob
Hysteria is nearly human - these decent birds! - as if
they were finding
Gold in the street. It is better than gold,
It can be eaten: and which one in all this fury of wild-
fowl pities the fish?
....

from Birds and Fishes by Robinson Jeffers

INTRODUCTION

Prince William Sound (PWS) is one of the largest areas of protected waters bordering the Gulf of Alaska (GOA). It, and the nearby open waters of the Gulf, provide foraging areas for populations of apex predators including piscivorous seabirds and marine mammals. These surface-dependent predators were adversely impacted by the EXXON VALDEZ oil spill (EVOS); and many experienced declines from which they have not recovered. Piscivorous seabirds and marine mammals in PWS are near the apex of food webs based on pelagic production of small fishes, including Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes hexapterus*), walleye pollock (*Theragra chalcogramma*), capelin (*Mallotus villosus*) and eulachon (*Thaleichthys pacificus*); and macroinvertebrates, especially euphausiids, commonly called krill. The lack of recovery by some seabirds may be due to long-term changes in forage species abundance. In this report we describe abundance and distribution patterns of small pelagic fishes in Prince William Sound, based on acoustic surveys.

OBJECTIVES

1. Provide an estimate of the distribution and abundance of forage species in study areas of Prince William Sound.

2. Describe species composition of the forage base and size distributions of the most abundant forage species in the three survey areas.

3. Gather basic oceanographic data describing salinity, temperature, and chlorophyll profiles of the water column in the three study areas.

FIELD METHODS

Sampling was conducted 13 - 31 July 1998. The research cruise objectives were:

1. Conduct a hydroacoustic survey of three survey areas within PWS

2. Collect samples of acoustic targets to describe species composition and size distributions.

3. Describe and quantify zooplankton and zooplanktivorous species at three process study sites.

Acoustic Survey:

We conducted a series of acoustic transects in four areas (Figure 1), using a Biosonics DT 4000, 120 kHz down-looking system. The transects were in a pattern of zigzags within 12 km segments of shoreline. The 12 km segments were laid out sequentially along the shoreline within each area. The number of 12 km segments within each study area were: North - 26, Central - 8, South - 21, Montague - 2. Within each 12 km segment there was a series of 20 transects (10 zigs and 10 zags). Each transect was about 1.2 km long. The subset of segments sampled in each area were:

North	1, 3, 5, 7, 9, 13, 15, 17, 19
Central	1-3, 6-8
South	2, 4, 6, 8, 10, 14, 16, 20
Montague	1

Field calibration of the acoustic equipment was done in the evening of July 24 using a standard target suspended under the transducer.

Acoustic targets found by the survey vessel were sampled using a fry seine, purse seine, dip net, jigging or ROV (Remote Operated Video).

CTD profiles were collected at 3 offshore sites in each survey area (Table 1, Figure 1). The water column was sampled to a depth of 150 m or within 20 m of the bottom.

PROCESS STUDIES:

Plankton samples were collected in three process study areas (Figure 2), with eight sampling locations per area (24 total). Plankton were sampled at night (1030 - 0430) with a 1 m^2 NIO/Tucker trawl with 500 micron mesh towed in a double oblique trajectory to a depth of 60 m or to 10 m above the bottom at shallower stations, and with a 20 cm Bongo net with 243 micron mesh towed vertically from 60 m (or 10 m above bottom) to the surface (Table 2). CTD measurements of temperature, salinity and chlorophyll were collected at all stations (Table 1).

Jellyfish were sampled to estimate their abundance in the North, Central and South process study areas by randomly setting a purse seine at each station in each area (Table 3). Jellyfish were also collected for digestion experiments and dip netted out of the process study area for analysis of gut contents.

SAMPLE PROCESSING:

Plankton samples were preserved in 5% buffered formalin. Fishes larger than about 50 mm were identified in the field and sorted to species. All fish were measured (fork length) unless net hauls contain large numbers of individuals of some species. Large catches were randomly subsampled by splitting the catch down to 100 - 200 individuals for measurement. Subsamples of all forage fish species were frozen and/or preserved in 10% buffered formalin.

ACOUSTIC DATA ANALYSES

Each data record consisted of 1 m depth increments from 1 m below the transducer to the bottom or about 115 m depth, whichever was greater. Averaging was done using geometric means. The program returned volume scattering, depth, and latitude and longitude for each record. Various parameters in the bottom tracking software were modified to avoid integrating through the bottom. The bottom window was varied from 20 to 40 m, with larger values for files with steeper slopes. A cross-section of the volume scattering for each transect was plotted using visual basic software. Cross-sectional plots were scanned visually, and estimates of species identification and size class were made for all substantial acoustic targets. The files were edited to remove any bottom integration left in the data. The portion of the total transect abundance or biomass value contributed by each integration was estimated by multiplying the integrated value by the integration distance divided by the total transect length. The volume scattering was corrected for calibration by the standard target.

The default sound scattering was assumed to be plankton with a target strength of -70 dB/g. For identified fish targets, estimates of the number of individual fish per cubic meter were determined by equations relating acoustic target strength to fish length.

Herring: TS = 20*log10(length(cm)) - 71.9

Pollock: TS = 20*log10(length(cm)) - 66

Capelin: TS = 20*log10(length(cm)) - 74.6

Rockfish: TS = 20*log10(length(cm)) - 67.5

Sand lance: TS = 20*log10(length(cm)) - 85

Estimates of fish numbers were converted to an estimate of biomass per cubic meter using the length-weight relationship for the dominant species. Equations to compute biomass (W - in grams, L - in mm) were:

pollock	$W = (1.89 \times 10^{-6})\ L^{3.272}$
herring	$W = (5.007 \times 10^{-6})\ L^{3.196}$
sand lance	$W = (4.81 \times 10^{-7})\ L^{3.451}$
capelin	$W = (2.40 \times 10^{-6})\ L^{3.213}$
rockfish	$W = (7.5 \times 10^{-3})\ L^{3.2}$ (length in cm)

Biomass per cubic meter estimates were converted to biomass per square meter of surface (biomass density) by integrating the results over the depth of the sampled water column. Biomass density for each transect was calculated by partitioning each transect into sections based on the targets present. Biomass density was estimated for each 12 km sampling segment by calculating the mean for all transects in the segment. Biomass density in each of the three study areas (North, Central, and South) was estimated by averaging all transects in the area. Geographic distributions of forage species were assessed with area plots of biomass density gradients determined through a kriging routine.

The procedures used to estimate biomass density in 1998 were similar to those used in 1997; however, the target-strength models used in 1998 were changed for several species. In order to make the estimates from 1996 and 1997 comparable to 1998 we reanalyzed the 1996 and 1997 acoustic data using the new target-strength models.

The 1996 data were collected with two BioSonics acoustic systems: a DT6000 130 kHz digital system and a 120 kHz ESP system. The DT6000 system was used for the South and Central surveys, but failed in the North survey two days before the end of the cruise. Therefore, the last two days of transecting in the North area were done with the 120 kHz ESP system. When tank calibrations were made on the DT6000 system following repair, changes in source level and receive sensitivity decreased the resulting volume scattering by about 5 dB from that computed by receive sensitivity and source level values read from the EEPROM (the system software program). Since no standard target calibration was done on this system prior to its field deployment, it was unclear which values were correct. In 1997 we ran standard target calibrations on the DT4000 system during field collections. In comparing the DT data from the two years, we found that the 1997 integrated volume scattering was very similar to that observed in the 1996 data, if the original 1996 data were corrected to incorporate the 5 dB decrease in volume scattering indicated in the 1996 post-season tank calibrations. Consequently we adjusted the 1996 DT6000 data by the 5 db increment indicated in the 1996 post-repair calibration. Also, for the 1996 North area data, direct comparison of the ESP data with the DT data is complicated by the fact that the DT systems are much quieter. When integrating the ESP data, the noise is summed as well as the actual acoustic backscatter, producing inflated estimates of volume scattering per unit area relative to estimates by the DT systems. Similar integrated volume scattering plots could be generated for data from the DT and ESP systems if the noise level for the ESP system were set to -60 dB in contrast to -80 dB for the DT systems. When this correction is applied to estimates of biomass using the ESP system, estimates for fish school biomass remains similar but plankton estimates drop. Comparison of plankton estimates obtained with the DT and corrected ESP data suggest that the -60 dB noise floor is more appropriate for the ESP system than the -80 dB noise floor used by the DT systems; therefore we used the -60 dB value in our calculations of the ESP data from 1996.

RESULTS

Physical and Biological Conditions

In July 1998 temperature and salinity were generally similar to patterns observed in the preceding three years (Figures 3, 4). Summer stratification is maintained largely by lower salinity in upper 30 m. Near-surface water in the central area was typically more saline than in the north and south. In 1996, salinity tended to be higher in the upper 30 m, especially in the North and South areas. Temperature was somewhat higher at many stations in 1997. In all years there is considerable variability in temperature and salinity within the Sound, largely due to localized inputs of fresh waters from rainwater run-off and melting of tidewater glaciers. For example, stations N1 and S2 are in channels near tidewater glaciers and were quite variable relative to stations in open-water parts of the Sound.

We measured chlorophyll and the abundance of euphausiids in the three process study areas. Chlorophyll was lowest in the South and highest in the Central area (Figure 5), although differences were not pronounced and were not significant. Euphausiid density did vary significantly among study areas (Figure 5). Density of euphausiids exceeded 50 m-2 in the South, but was less than 20 m-2 in the Central and North.

Acoustic Biomass Density - Within and Among Year Patterns

Acoustic target verification was conducted in all study areas. As in prior years, herring were by far the most abundant species identified as acoustic targets (Table 4).

In 1998 the South survey area had very high biomass density relative to the other areas. (Table 5). The exceptionally high value in the south was due to large and very dense schools of adult herring in the channels on the southwest side of the Sound, especially in Prince of Wales Passage. A division of overall biomass density into target category gives a more accurate estimate of the foraging environment available to avian predators, as several important species or species size groups are not vulnerable to birds (e.g. rockfish and adult herring). Of the seven categories of acoustic targets we analyzed, sandlance, YOY herring and 1+ herring are the Avian Vulnerable Energy Sources (AVES).

In 1998 the abundance of AVES was highest in the South and lowest in the North (Table 6). In all areas 1+ herring were the dominant prey category present on acoustic transects. The distribution in 1998 differed from 1997 when the highest AVES biomass density occurred in the North survey area, and was comprised mainly of YOY herring. Comparison with 1996 is tenuous due to the complications identified in the acoustic methods section.

In the North there has been a steady decline in AVES availability from 1996 - 1998, and substantial differences among years in the prey categories within AVES. In 1996, the North area had high density of 1+ herring, and relatively large concentrations of sandlance, especially in Port Gravina. In 1997, there was a large decline in density of 1+ herring and sandlance; however, those losses were partially offset by relatively high density of YOY herring. In 1998 the only AVES component in the North were relatively scarce 1+ herring.

The Central survey area appears to have experienced increasing abundance of AVES from 1996 to 1998; due mainly to increased abundance of sandlance, especially in 1997, and the occurrence of 1+ herring in 1998.

In 1998 the South survey area had high abundance of 1+ herring that were responsible for a sharp increase over 1997, when both sandlance and YOY herring were present in modest numbers.

In all years, YOY and 1+ herring were the dominant prey categories in AVES biomass density estimates. A strong year-class of herring within PWS will appear as exceptionally abundant YOY herring in the summer after spring hatching, with subsequent high abundance of 1+ herring in the following summer; although it is possible that overwinter mortality of YOY fish could result in low abundance of 1+ herring even when the preceding summer had high abundance of YOY herring. In our surveys, 1996 had relatively high abundance of 1+ herring, but few YOY herring. In 1997, as expected, there were almost no 1+ herring, but substantial numbers of YOY fish were present, indicating a relatively strong 1997 year class. That 1997 year class produced the 1+ herring that dominated AVES biomass density in 1998.

The distributions of YOY and 1+ herring within the Sound appear to differ. YOY fish were always most abundant in the North study area, whereas 1+ herring appear more abundant in Central and South study areas. This shift is consistent with our observation that herring adults are concentrated in the South study area, where they occur in the narrow channels in the Southwest part of Prince William Sound. There may be an ontogenetic shift in distribution of herring within PWS during the first few years of life.

Geographic Distribution of Forage Fishes in PWS

In the North survey area the distribution of forage fishes has shifted markedly in the period 1996 through 1998 (Figures 6 - 8). In 1996 most schools of small fishes were encountered in the southern sections of the North survey area, with many schools of sandlance and herring in Port Gravina and Port Fidalgo (Figure 8). The pattern changed in 1997, as very few fish schools were encountered in Port Gravina, and the number of schools in Port Fidalgo was reduced (Figure 7). This trend continued in 1998, when relatively few schools were found in the North survey area, and the southern sections of Port Fidalgo and Port Gravina had very few fish schools present (Figure 6).

In the Central survey area the distributions of forage fishes have remained similar from 1996 - 1998 (Figures 9 - 11). The Naked Island complex consistently had schools of sandlance on the west side, with schools of rockfish present around that island group. In 1997, substantial schools of adult herring were found in the eastern parts of the Naked Island group (Figure 10); unfortunately, both the 1996 and 1998 surveys missed that area due to equipment malfunction and rough weather, respectively.

The South survey area has consistently had concentrations of age 1+ and adult herring in the channels that lead out of PWS to the southwest, especially Prince of Wales Passage (Figures 12 - 14). In 1998 those schools were notably larger and had dense concentrations of herring (Figure 12). Other schools of fishes have typically occurred on both sides of Dangerous Passage.

ACKNOWLEDGEMENTS

We were assisted in field, laboratory and data analyses by University of Alaska Fairbanks graduate students, Jill Mooney and Julia Mabry. Jennifer Purcell and Kim Black from the University of Maryland were valued participants in our field collections.

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Figure 12. Geographic distribution of acoustic biomass in the South study area in 1998

Figure 13. Geographic distribution of acoustic biomass in the South study area in 1997

Figure 14. Geographic distribution of acoustic biomass in the South study area in 1996

Table 1. CTD casts collected in July 1998 on cruise 98-1.

Date	Time	Station #	Location	Lat.		Long.		Bottom Depth (m)	Gear Depth (m)
14/7	1640	2	N7	60	41.04	146	18.07	39	128
14/7	1733	4	N8	60	41.72	146	14.01	45	146
14/7	1910	6	N4	60	42.28	146	19.81	19	150
14/7	1940	7	N5	60	43.82	146	19.84	9	25
15/7	920	9	N3	60	40.66	146	23.48	13	40
15/7	110	12	N6	60	38.35	146	22.24	40	125
15/7	1230	14	N2	60	38.78	146	26	14	40
16/7	1600	17	N1	60	39.49	146	35.07	11	30
16/7	840	23	C5	60	43.43	147	15.15	47	150
16/7	955	25	C6	60	41.26	147	13.55	51	150
16/7	1110	27	C7	60	39.66	147	12.66	51	150
16/7	1240	28	C8	60	37.93	147	15.58	55	150
17/7	820	33	C4	60	36.76	147	36.29	167	150
17/7	910	34	C3	60	38.87	147	37.89	186	150
17/7	1117	37	C2	60	41.1	147	33.04	186	150
17/7	1630	41	OFFSHORE C1	60	42.13	147	34.17	93	150
17/7	1830	43	C1	60	44.29	147	34.24	149	150
18/7	940	44	S1	60	19.44	148	9.82	72	150
18/7	1050	46	S2	60	16.95	148	10.87	79	150
18/7	1235	48	OFFSHORE S2	60	14.54	148	9.93	93	150
18/7	1300	49	S4	60	13.62	148	10.57	93	150
18/7	1845	53	S3	60	16.24	148	7.73	76	150
19/7	715	55	S5	60	15.6	148	2.47	93	150
19/7	820	57	S7	60	13.95	147	59.59	93	150
19/7	1445	60	S8	60	9.32	147	59.6	557	150
19/7	1645	63	S6	60	12.08	148	4.84	73	150
19/7	1700	64	S6	60	12.08	148	4.84	73	150
21/7	1255	67	OFFSHORE N2	60	45.47	146	38.62	13	35
22/7	1020	77	OFFSHORE N3	60	56.54	146	42.5	62	150
22/7	1300	82		60	57.78	146	45.31	19	40
22/7	1545	84	REEF IS.	60	51.61	146	49.23	10	40
22/7	1625	85	OFFSHORE N1	60	50.42	146	56.44	53	150
23/7	900	88	N. NAKED IS.	60	41.33	147	27.78	7	20
23/7	1035	91	NW OF NAKED	60	41.27	147	28.99	7	20
23/7	1330	95	OUTSIDE BAY	60	38.85	147	26.4	8	20
23/7	1430	98		60	37.93	147	28.18	11	30
24/7	1425	105	NE INGOT IS	60	31.52	147	37.12	6	20
24/7	1810	109	BAY OF ISLES	60	25.02	147	37.58	40	35
25/7	1430	114	GREEN ISLAND	60	14.58	147	25.81	18	16
26/7	1600	119	FOX FARM	59	58.43	148	10.39	40	35
27/7	1248	122	N. EVANS ISLAND	60	7.17	147	53.38	35	30
29/7	1320	127	KNIGHT IS. PASS; OFFSHORE S1	60	12.84	148	59.87	350	150
29/7	1110	130	DANGEROUS PASSAGE	60		148			
29/7	1120	131	DAN. PASS. OFFSHORE S3	60	18.5	148	10.54	300	150

Table 2. Plankton samples collected in APEX process studies, cruise 98-1.
Gear codes: N = NIO/Tucker Trawl G = Bongo

Date	Time	Station #	Gear	Location	Lat. In	Long In.	Bottom Depth (m)	Gear Depth (m)
14/7	2327	1	G	981N8	60 41.873	146 14.372	146	60
14/7	2337	1	N	981N8	60 41.924	146 14.187	146	53
15/7	35	2	G	981N7	60 40.722	146 17.962	132	60
15/7	53	2	N	981N7	60 40.68	146 13.219	131	?
15/7	325	2	N	981N7	60 40.897	146 18.247	101	52
15/7	405	3	G	981N4	60 42.167	146 19.883	56	55
15/7	417	3	N	981N4	60 42.223	146 19.811	41	43
15/7	2242	4	G	981N5	60 43.976	146 19.777	25	22
15/7	2250	4	N	981N5	60 43.946	146 19.685	31	21
15/7	2327	5	G	981N3	60 41.622	146 23.026	41	35
15/7	2340	5	N	981N3	60 40.957	146 23.374	35	44
16/7	10	6	G	981N6	60 39.117	146 22.336	118	60
16/7	21	6	N	981N6	60 39.1	146 22.349	118	49
16/7	45	6	N	981N6	60 38.79	146 22.555	124	49
16/7	146	7	G	981N2	60 38.908	146 27.075	43	40
16/7	230	7	N	981N2	60 38.849	146 26.822	45	23
16/7	318	8	G	981N1	60 39.639	146 35.287	37	30
16/7	330	8	N	981N1	60 39.787	146 35.292	37	18
16/7	2252	9	G	981C8	60 37.829	147 17.273	105	60
16/7	2305	9	N	981C8	60 37.845	147 17.121	112	49
16/7	2325	9	N	981C8	60 37.944	147 16.280	156	46
16/7	2343	9	G	981C8	60 38.03	147 15.495	173	60
17/7	11	10	G	981C7	60 39.773	147 14.837	140	60
17/7	25	10	N	981C7	60 39.811	147 14.208	155	56
17/7	49	10	N	981C7	60 39.891	147 13.527	155	61
17/7	123	11	G	981C6	60 41.161	147 14.620	161	60
17/7	137	11	N	981C6	60 41.193	147 14.291	162	52
17/7	157	11	N	981C6	60 41.297	147 13.556	170	67
17/7	239	12	G	981C5	60 43.29	147 15.446	170	60
17/7	250	12	N	981C5	60 43.3	147 15.590	180	64
17/7	311	12	N	981C5	60 43.289	147 16.290	98	73
17/7	328	12	N	981C5	60 43.256	147 17.087	145	57
17/7	349	12	N	981C5	60 43.226	147 17.644	158	61
17/7	2255	13	G	981C1	60 43.92	147 33.803	592	60
17/7	2305	13	N	981C1	60 43.919	147 34.152	592	53
17/7	2326	13	N	981C1	60 43.94	147 33.235	>560	50
18/7	13	14	G	981C2	60 40.816	147 33.253	>275	60
18/7	23	14	N	981C2	60 40.82	147 33.066	>275	50
18/7	43	14	N	981C2	60 40.873	147 32.292	153	62
18/7	125	15	G	981C3	60 38.787	147 36.651	560	60
18/7	135	15	N	981C3	60 38.785	147 36.682	560	67
18/7	153	15	N	981C3	60 38.653	147 37.566	560	67
18/7	235	16	G	981C4	60 36.791	147 36.734	585	60
18/7	244	16	N	981C4	60 36.82	147 36.708	585	56
18/7	303	16	N	981C4	60 36.806	147 37.302	585	67
18/7	2234	17	G	981S2	60 16.808	148 11.346	151	60
18/7	2250	17	N	981S2	60 16.711	148 11.256	195	59
18/7	2325	18	G	981S1	60 18.934	148 10.219	181	60

Table 2 (cont).

Date	Time In	Station #	Gear	Location	Lat. In	Long In.	Depth (m)	Depth (m)
18/7	2335	18	N	981S1	60 18.934	148 10.219	181	67
18/7	2352	18	N	981S1	60 19.329	148 10.161	181	64
19/7	35	19	G	981S3	60 17.184	148 7.824	94	60
19/7	46	19	N	981S3	60 17.107	148 7.880	86	64
19/7	107	19	N	981S3	60 16.561	148 8.198	137	55
19/7	152	20	G	981S4	60 13.362	148 9.920	108	60
19/7	206	20	N	981S4	60 13.317	148 9.928	114	49
19/7	224	20	N	981S4	60 13.229	148 10.649	137	55
19/7	243	20	N	981S4	60 13.448	148 10.957	238	70
19/7	303	20	N	981S4	60 13.749	148 11.552	238	66
19/7	2235	21	G	981S6	60 11.759	148 5.482	238	60
19/7	2246	21	N	981S6	60 11.817	148 5.413	238	53
19/7	2303	21	N	981S6	60 12.133	148 5.093	238	70
19/7	2345	22	G	981S5	60 15.604	148 3.635	485	60
19/7	2350	22	N	981S5	60 15.621	148 3.778	485	52
20/7	13	22	N	981S5	60 15.845	148 3.325	183	67
20/7	50	23	G	981S7	60 14.925	147 58.993	640	60
20/7	100	23	N	981S7	60 14.672	147 59.222	647	47
20/7	134	23	N	981S7	60 13.972	147 59.388	640	50
20/7	219	24	G	981S8	60 9.296	147 59.507	256	60
20/7	228	24	N	981S8	60 9.265	147 59.665	256	46

Table 3. Purse Seine sets in cruise 98-1 for jellyfish collection

Date	Time	Station #	Location	Lat.		Long.		Bottom Depth (m)
14/7	1520	1	N7	60	40.96	146	18.07	90
14/7	1715	3	N8	60		146		147
14/7	1845	5	N4	60	42.26	146	19.99	63
14/7	1947	8	N5	60	43.74	146	20	26
15/7	935	10	N3	60	40.54	146	23.61	43
15/7	1035	11	N6	60	38.4	146	22.98	129
15/7	1150	13	N2	60	38.89	146	27.69	41
16/7	1525	16	N1	60	39.54	146	36.03	40
16/7	808	22	C5	60	43.33	147	15.17	191
16/7	940	24	C6	60	41.21	147	13.34	174
16/7	1035	26	C7	60	39.7	147	12.55	179
16/7	1255	29	C8	60	37.92	147	15.57	175
17/7	745	32	C4	60	36.48	147	37.1	549
17/7	925	35	C3	60	38.85	147	37.87	610
17/7	1035	36	C2	60	40.9	147	33.09	610
17/7	1700	42	C1	60	44	147	34.06	4877
18/7	950	45	S1	60	19.48	148	10	235
18/7	1130	47	S2	60	16.87	148	10.61	274
18/7	1310	50	S4	60	13.61	148	10.57	305
18/7	1905	54	S3	60	16.22	148	7.66	244
19/7	730	56	S5	60	15.72	148	2.8	305
19/7	830	58	S7	60	13.99	147	59.57	305
19/7	1455	61	S8	60	9.43	147	59.35	244
19/7	1705	65	S6	60	12.06	148	4.75	241

Table 4. Samples to identify acoustic targets in cruise 98-1

Gear Types: V=Video, J=Herring Jig, D=Dip Net, B=Beach Seine, F=Fry Seine

Date	Time	Gear	Lat.		Long.		Bottom Depth (m)	Gear Depth (m)	ID
18/7	1710	V	60	19.55	148	9.2	21	5	jellyfish
19/7	1520	V	60	9.31	147	59.87	305	20	jellyfish
21/7	1015	V	60	44.04	146	43.99	27	21	herring ad
21/7	1350	V	60	49.21	146	39.09	46	14	herring
21/7	1440	V	60	48.69	146	42.29	30	9	herring
21/7	1620	V	60	49.71	146	19.54	0	6	jellyfish
22/7	935	V	60	56.24	146	37.81	107	14	salmon
22/7	1115	V	60	57.73	146	44.58	53	12	herring
23/7	1125	V	60	39.56	147	29.83		3	
28/7	945	V	60	3.34	148	7.79	200	40-60	
29/7	800	V	60	20.22	148	16.17	15	1-5	jellyfish
29/7	1045	V	60	19.06	148	11.68	25	10	herring
30/7	1030	V	60	16.51	147	20.06	25	50	herring YOY
21/7	1400	J	60	49.21	146	39.09	45	14	herring ad
22/7	1130	J	60	57.73	146	44.58	50	12	
27/7	1745	J	60	59.19	148	6.23	100	40	herring ad
27/7	1900	J	60	0.84	148	10.52	100	2	black cod
28/7	2015	J	60	1.81	148	8.87	125	20	herring ad
28/7	950	J	60	3.34	147	7.79	200	40-60	herring ad
24/7	1555	D	60	29.82	147	37.9	10	1	herring YOY
25/7	1320	D	60	15,25	147	24.46	5	3	herring YOY
26/7	955	D	60	4.44	147	50.53	10	1	herring YOY
30/7	1045	D	60	17.87	147	19.16	70	1	herring YOY
30/7	830	B	60	42.62	147	29.58	1	1	herring YOY
22/7	840	F	60	55.46	146	37.22			herring
22/7	1430	F	60	54	146	47.92			herring YOY
25/7	1300	F	60	15.25	147	24.46	5	3	herring YOY
26/7	1115	F	60	6.91	147	53.33	4	3	herring YOY

Table 5. Biomass density (g/m2) estimated in three study areas of PWS in July 1998.

CATEGORY	BIOMASS DENSITY (G/M2) NORTH	 CENTRAL	 SOUTH
ROCKFISH	0.008	0.075	1.116
SANDLANCE	0.001	0.011	0.000
YOY HERRING	0.000	0.000	0.000
1+HERRING	0.139	0.192	0.331
ADULT HERRING	0.009	0.000	19.063
POLLOCK	0.002	0.000	0.000
PLANKTON	0.047	0.081	0.064
TOTAL	0.206	0.358	20.573

Table 6. Biomass density (g/m2) of Avian Vulnerable Energy Sources (AVES) estimated in three study areas of PWS in July 1998

	BIOMASS DENSITY (G/M2)		
1996	NORTH	CENTRAL	SOUTH
SANDLANCE	0.087	0.002	0.001
YOY HERRING	0.027		0.003
1+HERRING	0.948		1.046
TOTAL	1.062	0.002	1.050
1997			
SANDLANCE		0.029	0.023
YOY HERRING	0.313	0.019	0.039
1+HERRING	0.005		
TOTAL	0.318	0.048	0.062
1998			
SANDLANCE	0.001	0.011	
YOY HERRING			
1+HERRING	0.139	0.192	0.331
TOTAL	0.140	0.202	0.331

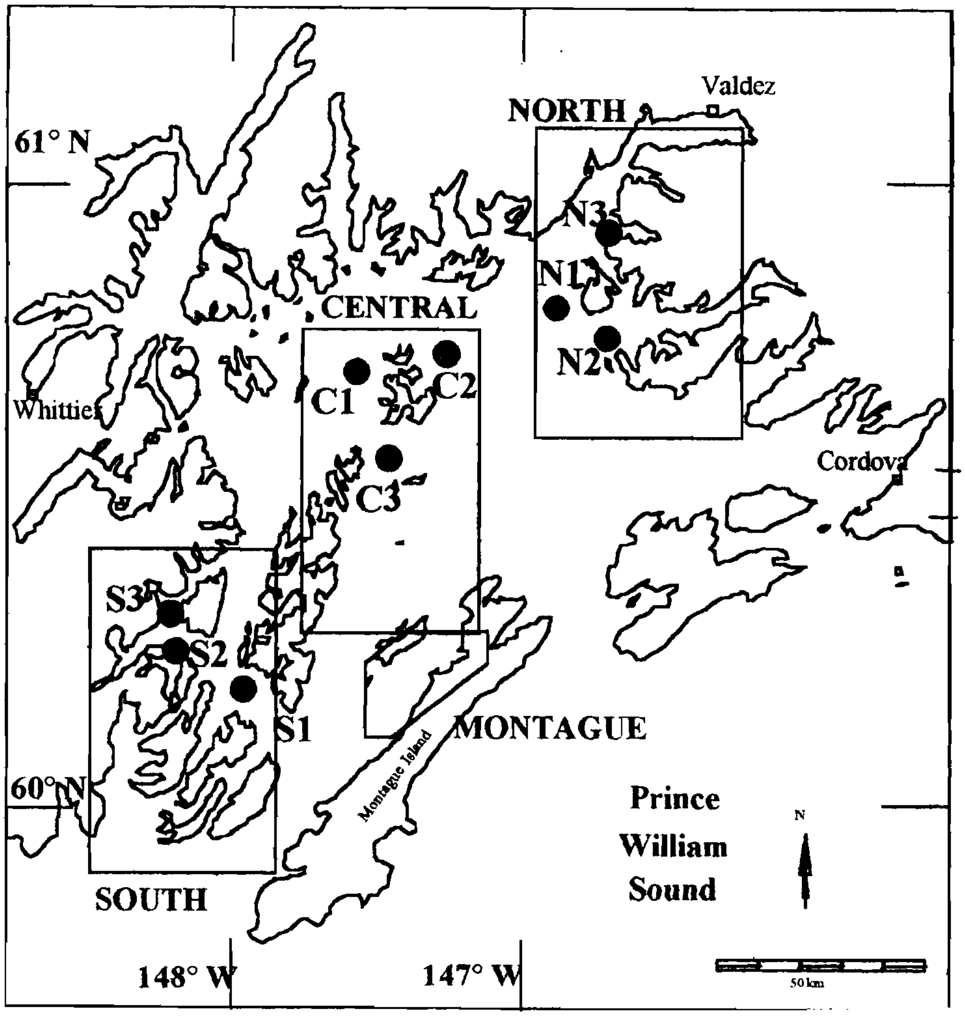

Figure 1. Locations of acoustic survey areas for the APEX project, with locations of CTD casts, 1995 - 1998.

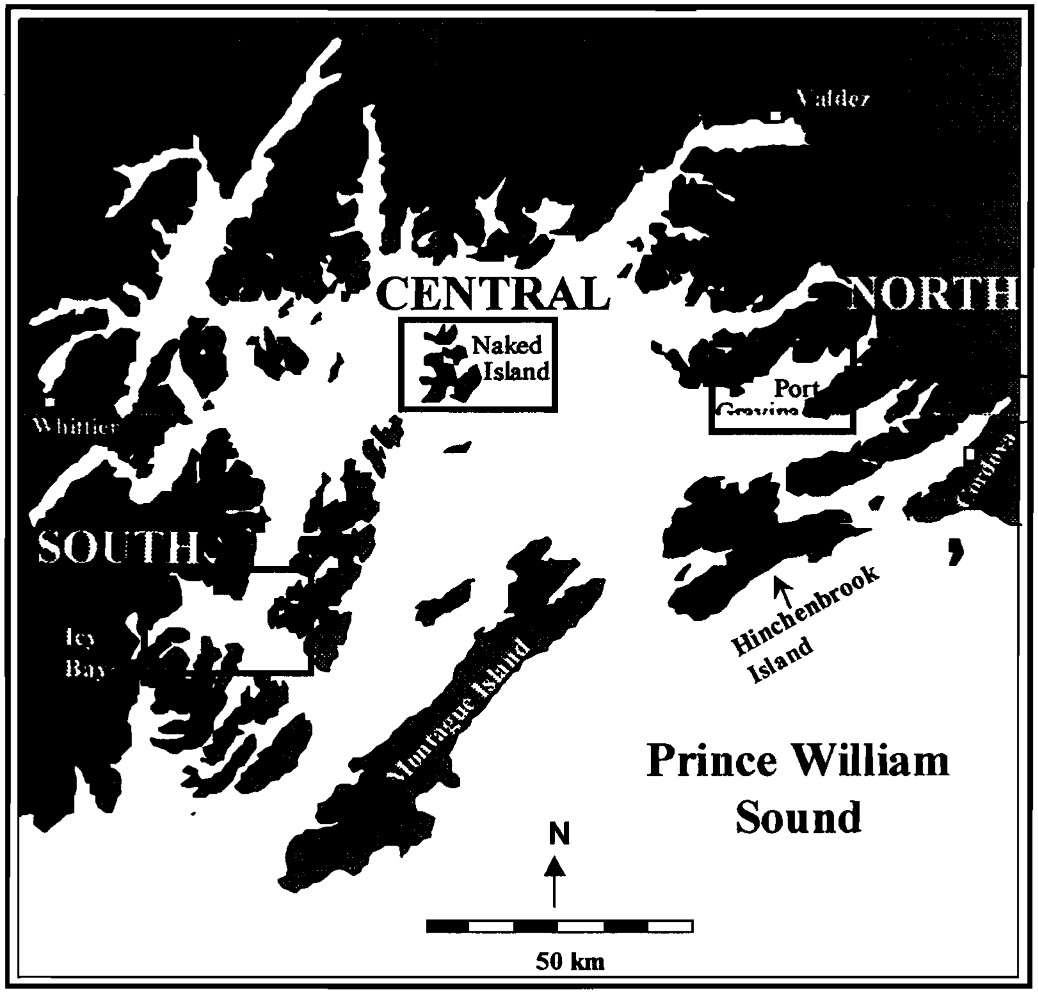

Figure 2. Location of process study areas in Prince William Sound.

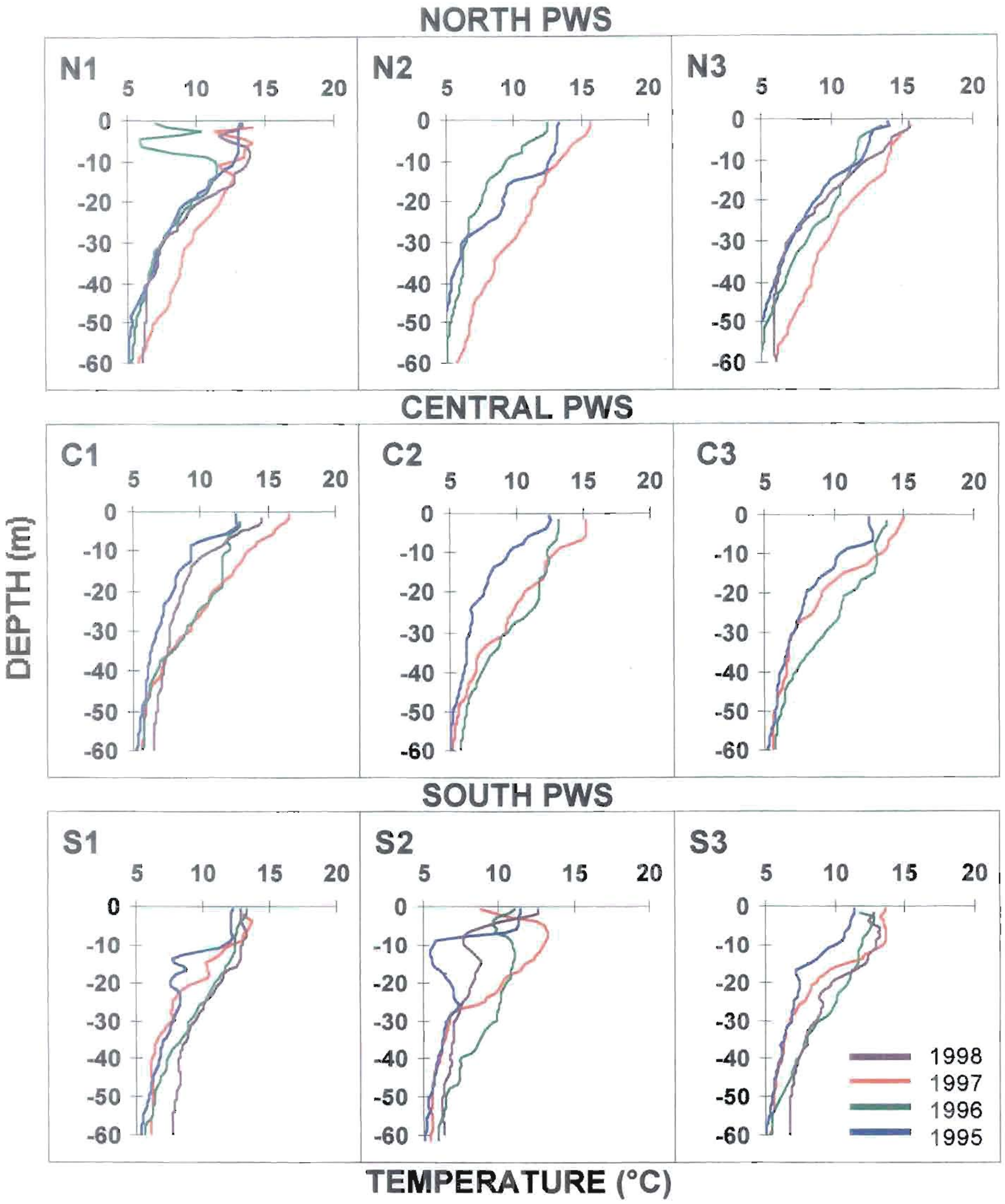

Figure 3. Temperature profiles for three stations in north, central, an south PWS taken between July 15 and August 1, 1995-98 (Fig. 1 shows station locations).

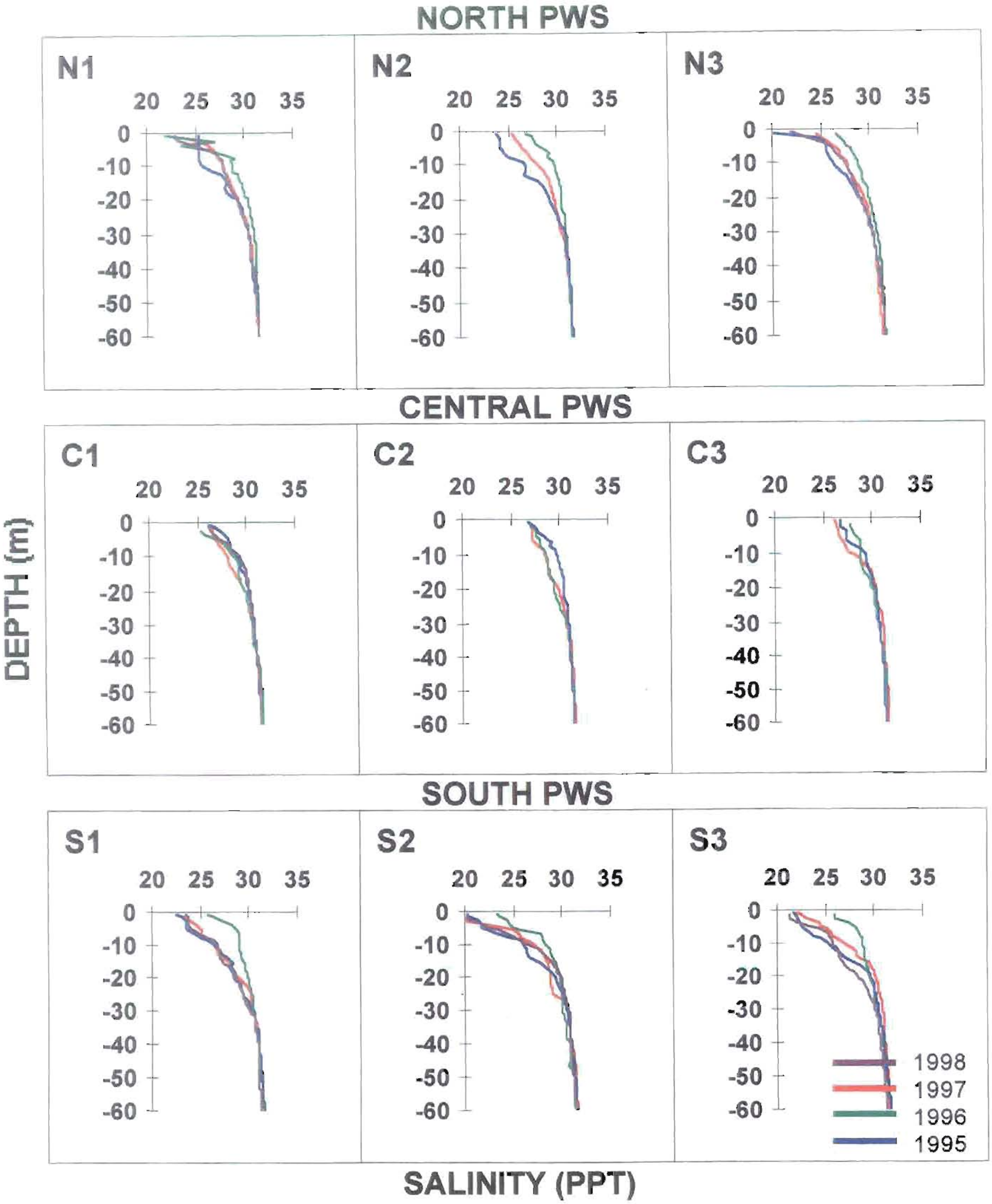

Figure 4. Salinity profiles for three stations in north, central, and south PWS taken between July 15 and August 1, 1995-98 (Fig. 1 shows station locations).

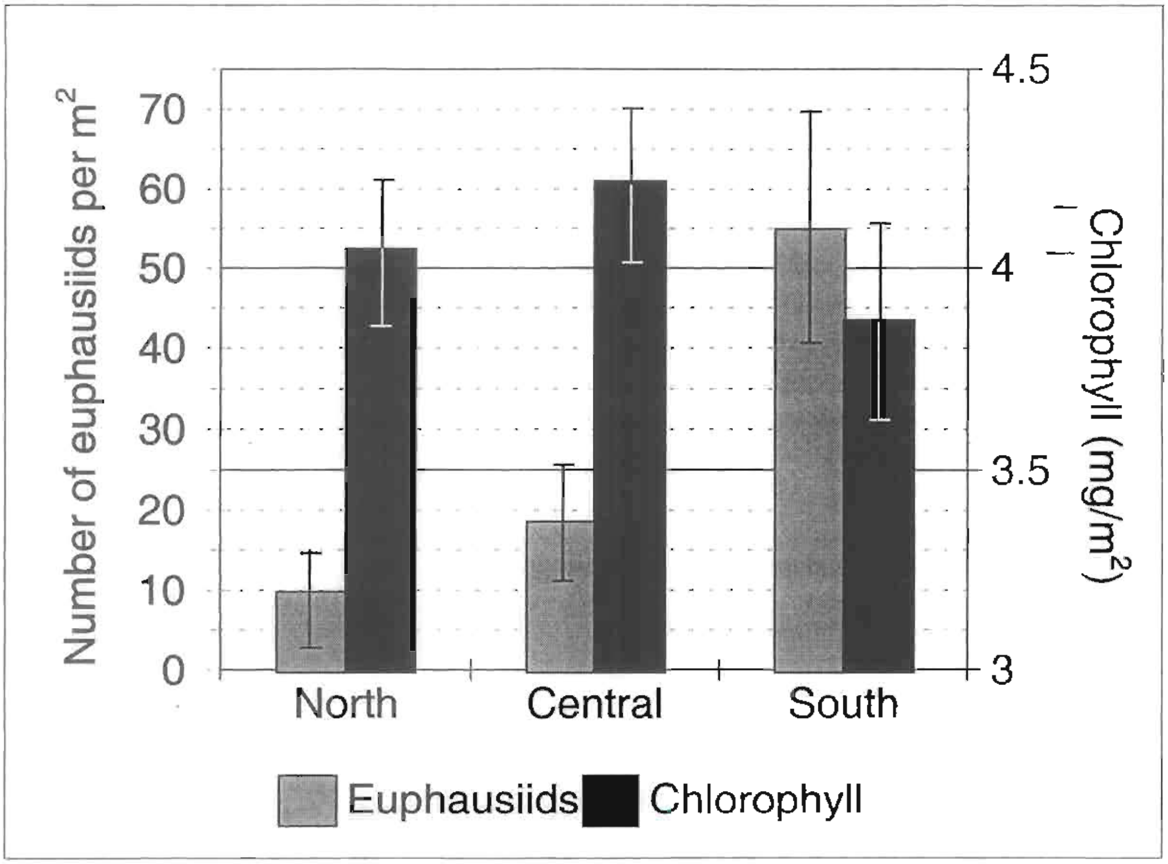

Figure 5. Density of adult euphausiids (*Euphausia pacifica*, *Thysanoessa inermis*, *T. longipes*, *T. raschi* and *T. spinifera*) per m^2 and chlorophyll concentration (mg/m^2) integrated to 50 m or the deepest depth at shallower stations in the North, Central and South study areas. Vertical bars represent ± one standard error.

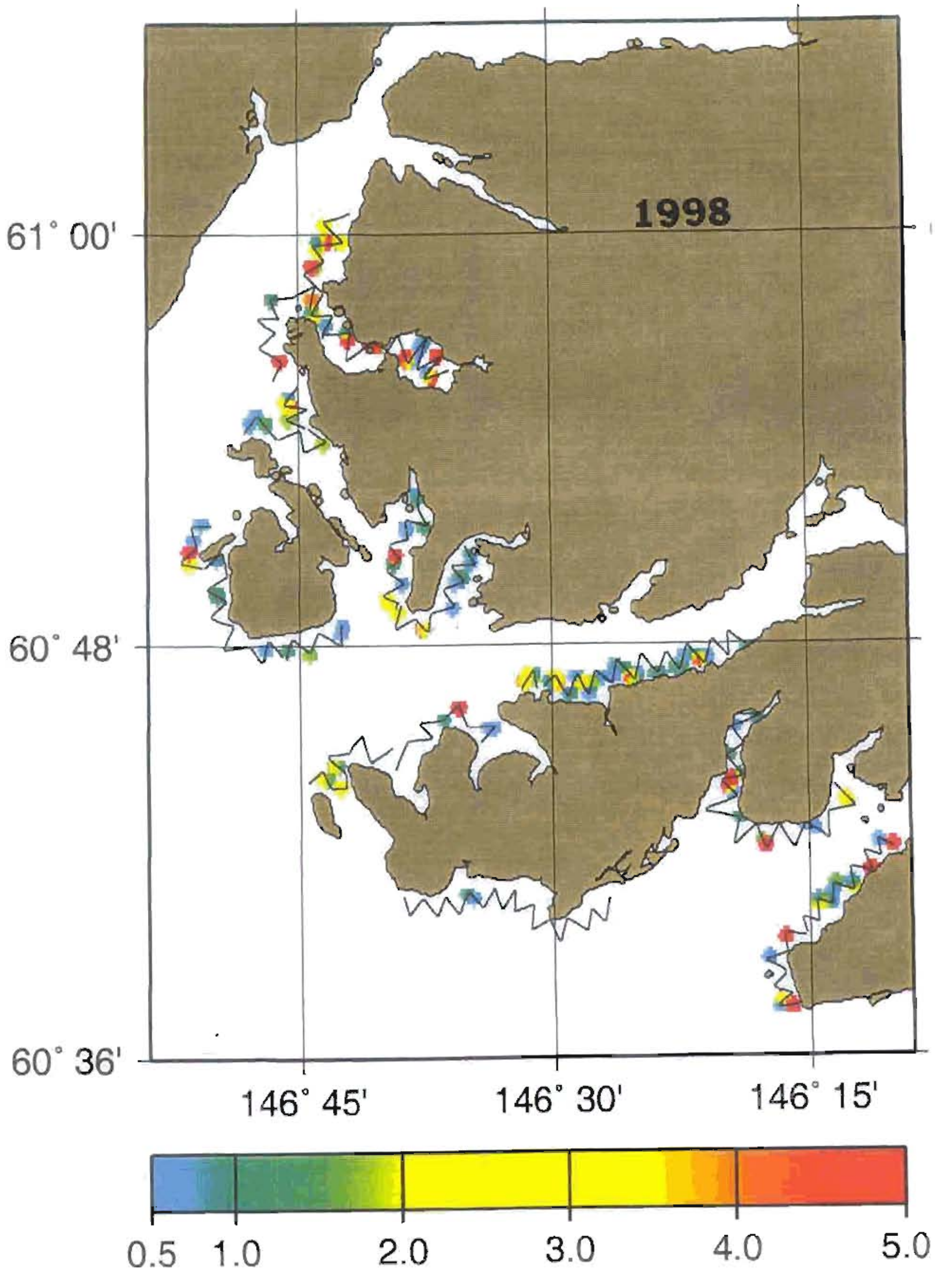

Figure 6. Geographic distribution of acoustic biomass in the North study area in 1998. Color scale units are grams/m^2. Codes for species are H - herring, Sn - sandlance, R - rockfish.

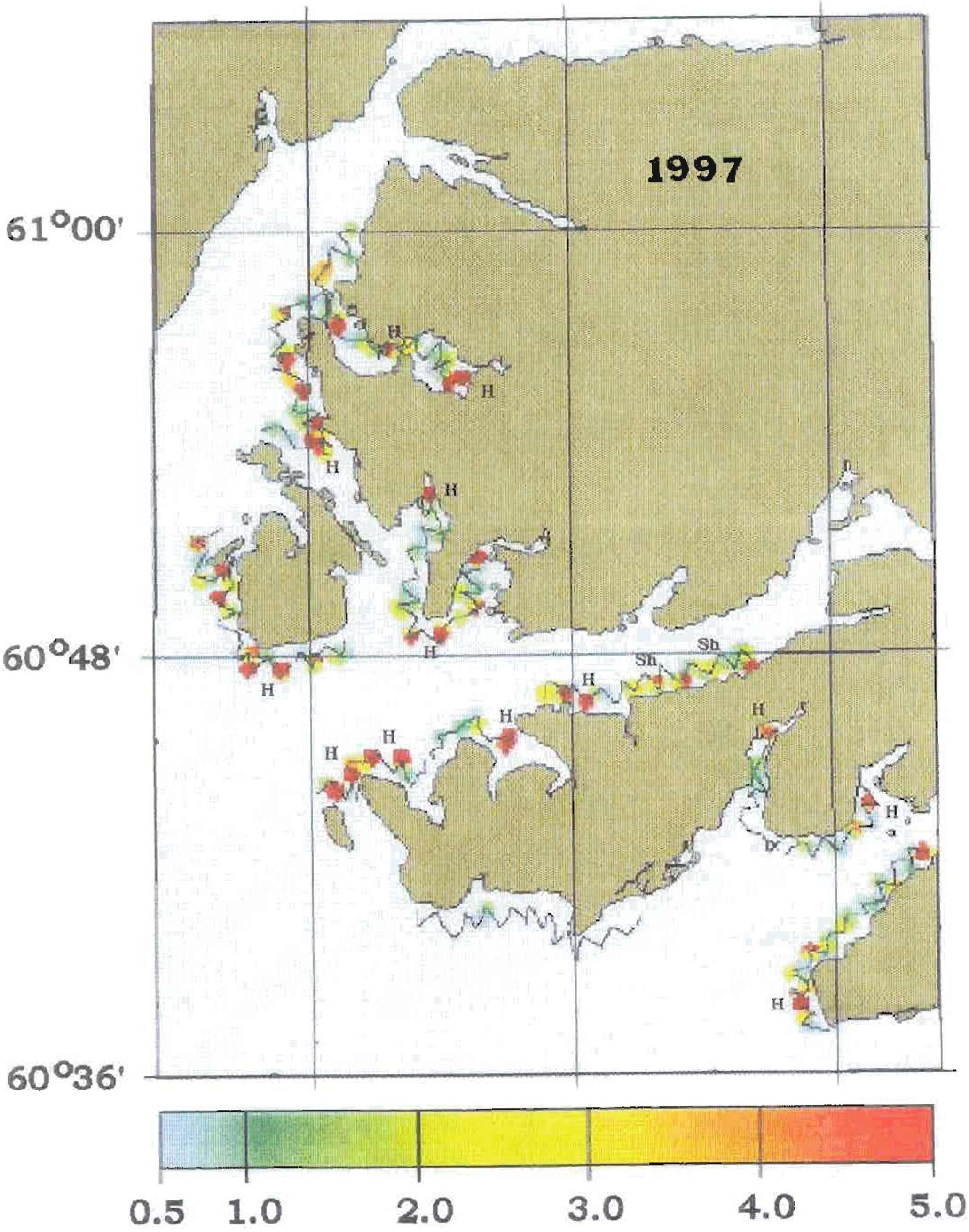

Figure 7. Geographic distribution of acoustic biomass in the North study area in 1997. Color scale units are grams/m^2. Codes for species are H - herring, Sn - sandlance, R - rockfish.

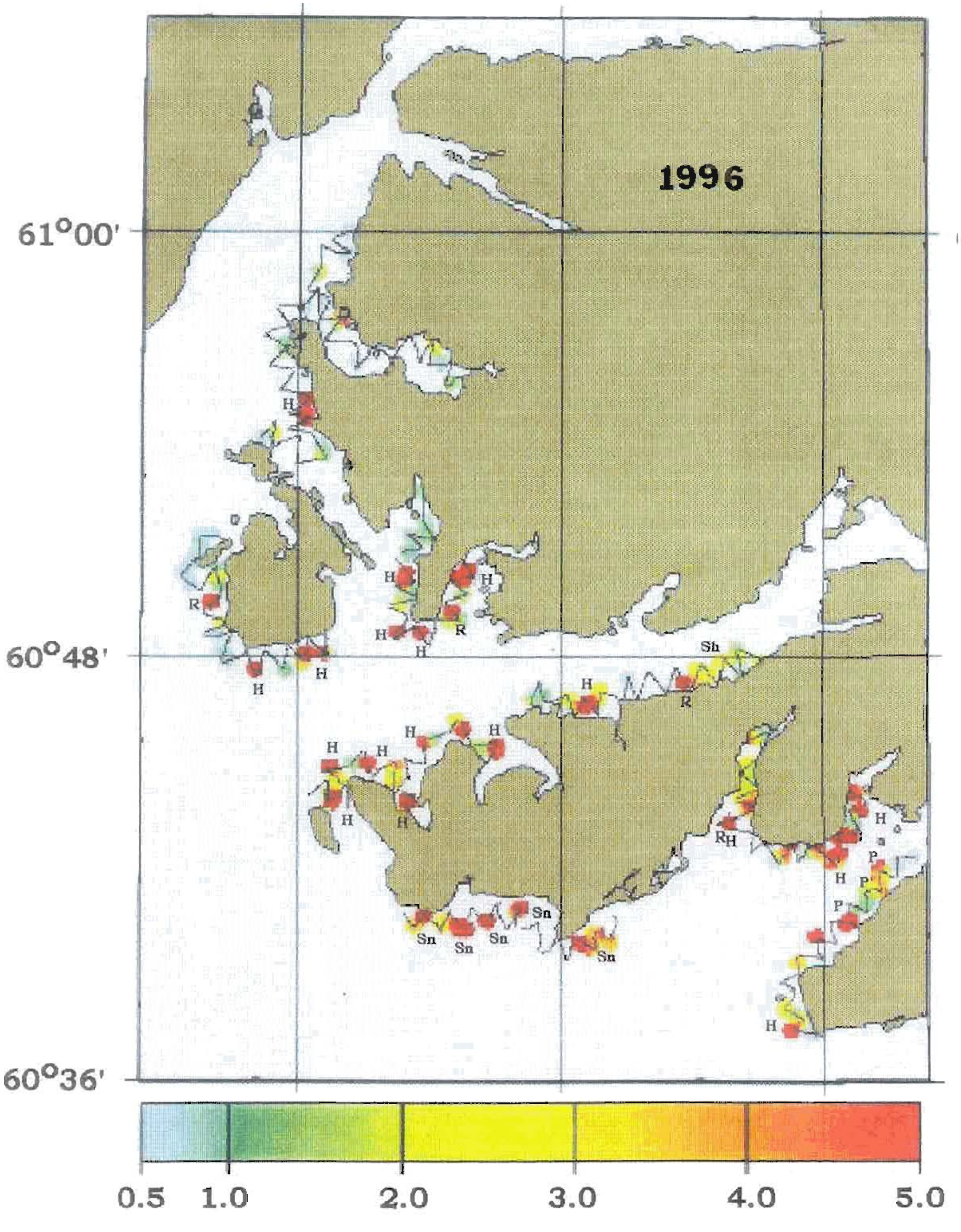

Figure 8. Geographic distribution of acoustic biomass in the North study area in 1996. Color scale units are grams/m^2. Codes for species are H - herring, Sn - sandlance, R - rockfish.

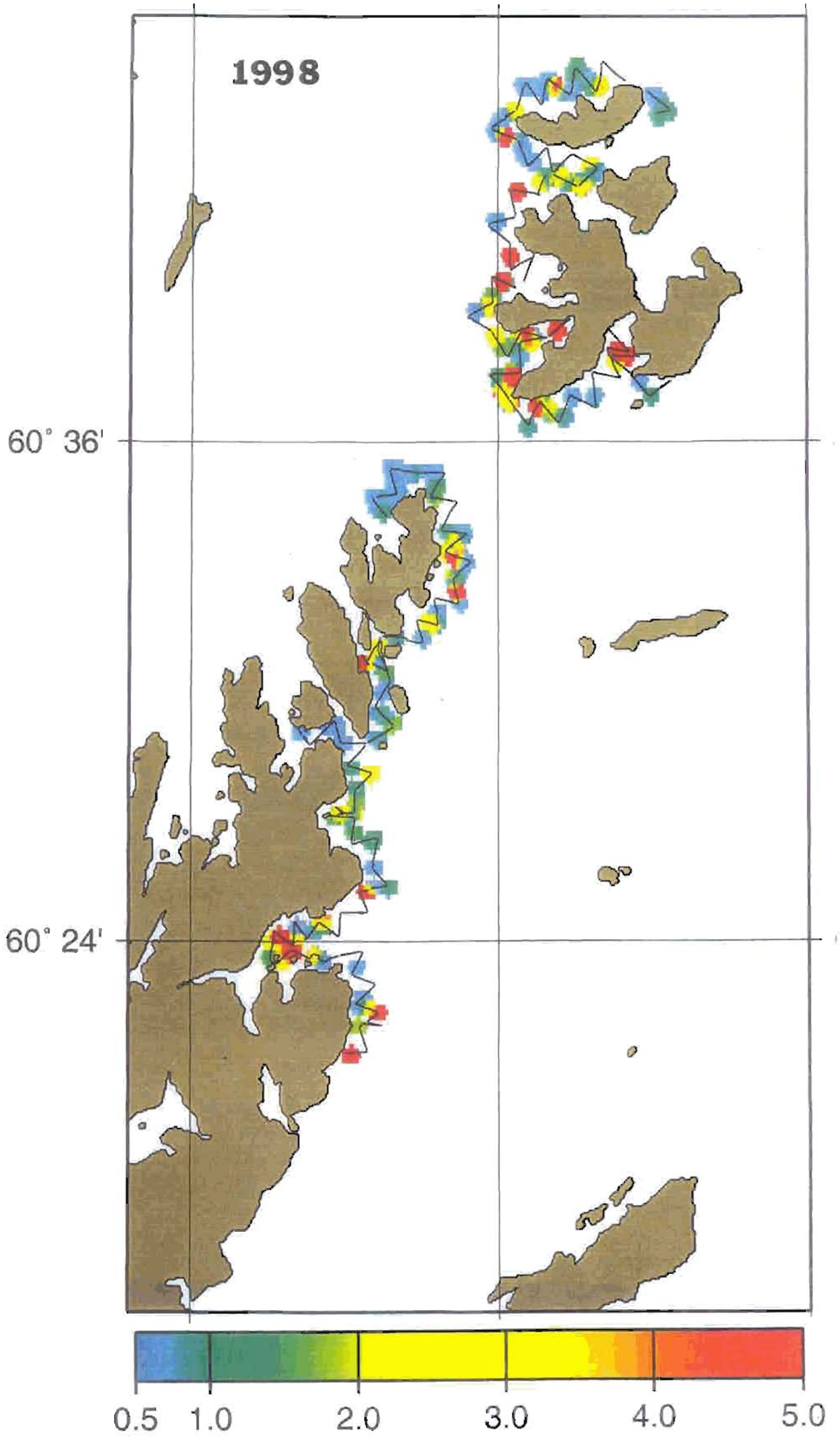

Figure 9. Geographic distribution of acoustic biomass in the Central study area in 1998. Color scale units are grams/m^2. Codes for species are H - herring, Sn - sandlance, R - rockfish.

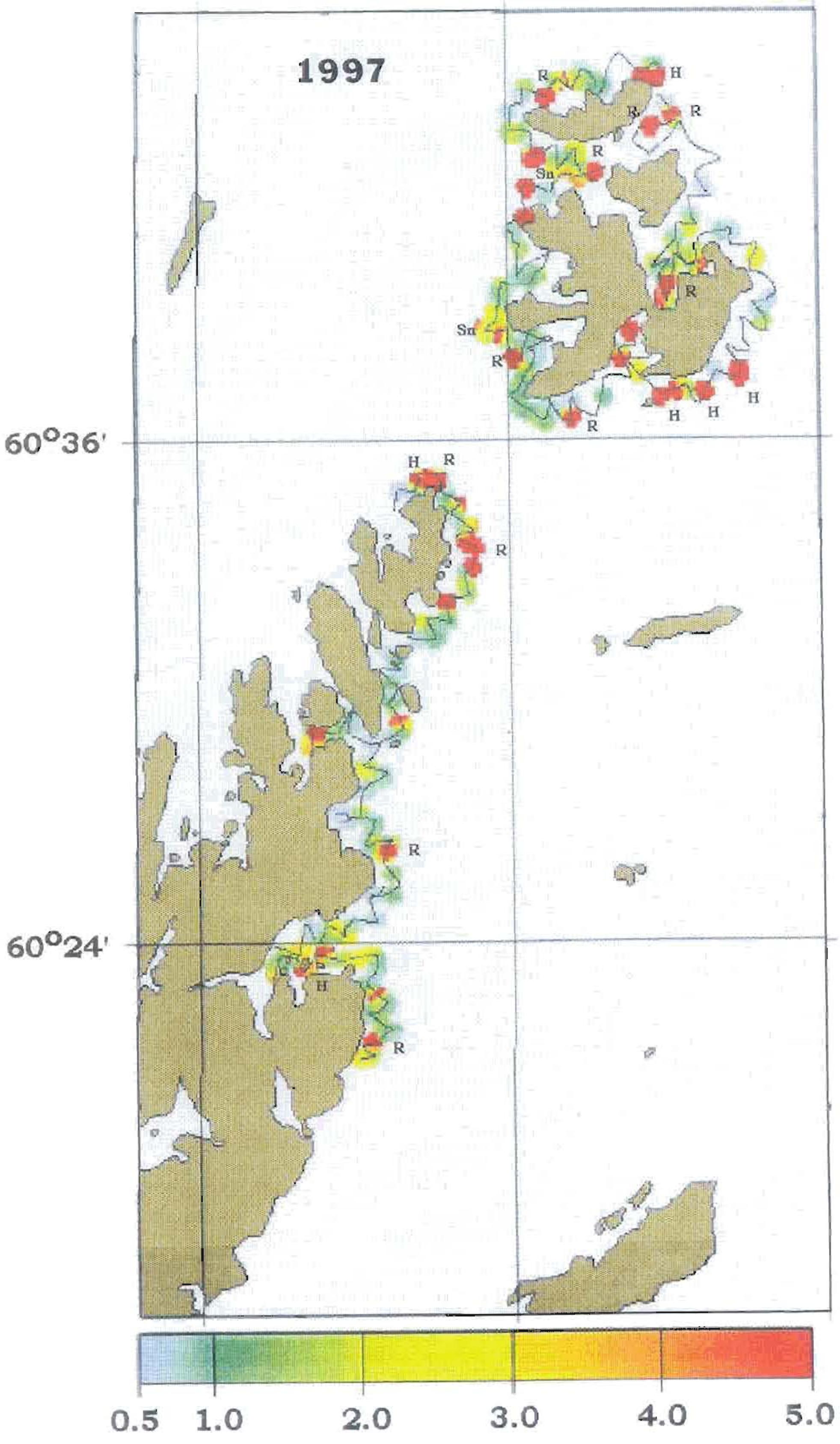

Figure 10. Geographic distribution of acoustic biomass in the Central study area in 1997. Color scale units are grams/m^2. Codes for species are H - herring, Sn - sandlance, R - rockfish.

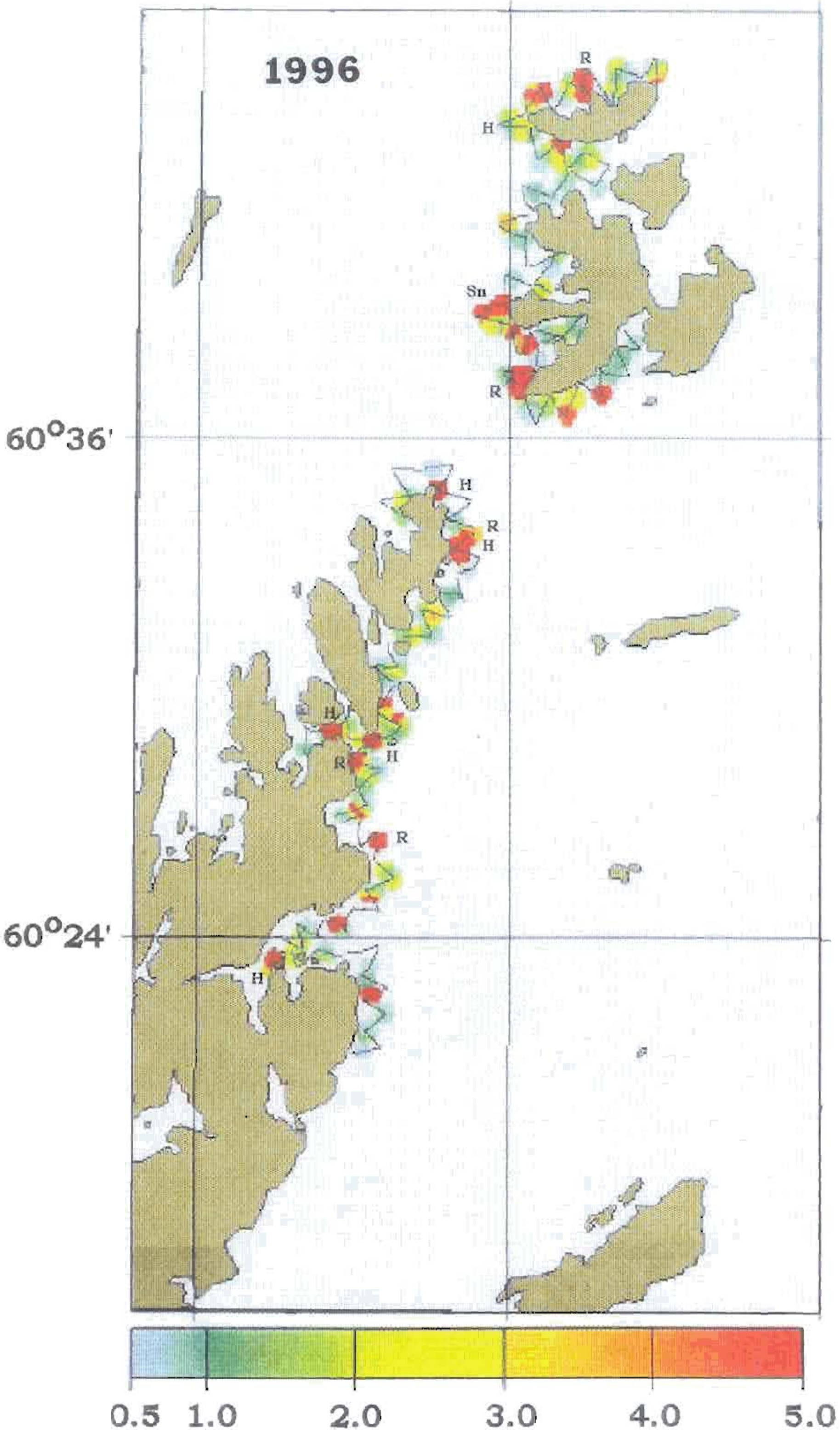

Figure 11. Geographic distribution of acoustic biomass in the Central study area in 1996. Color scale units are grams/m^2. Codes for species are H - herring, Sn - sandlance, R - rockfish.

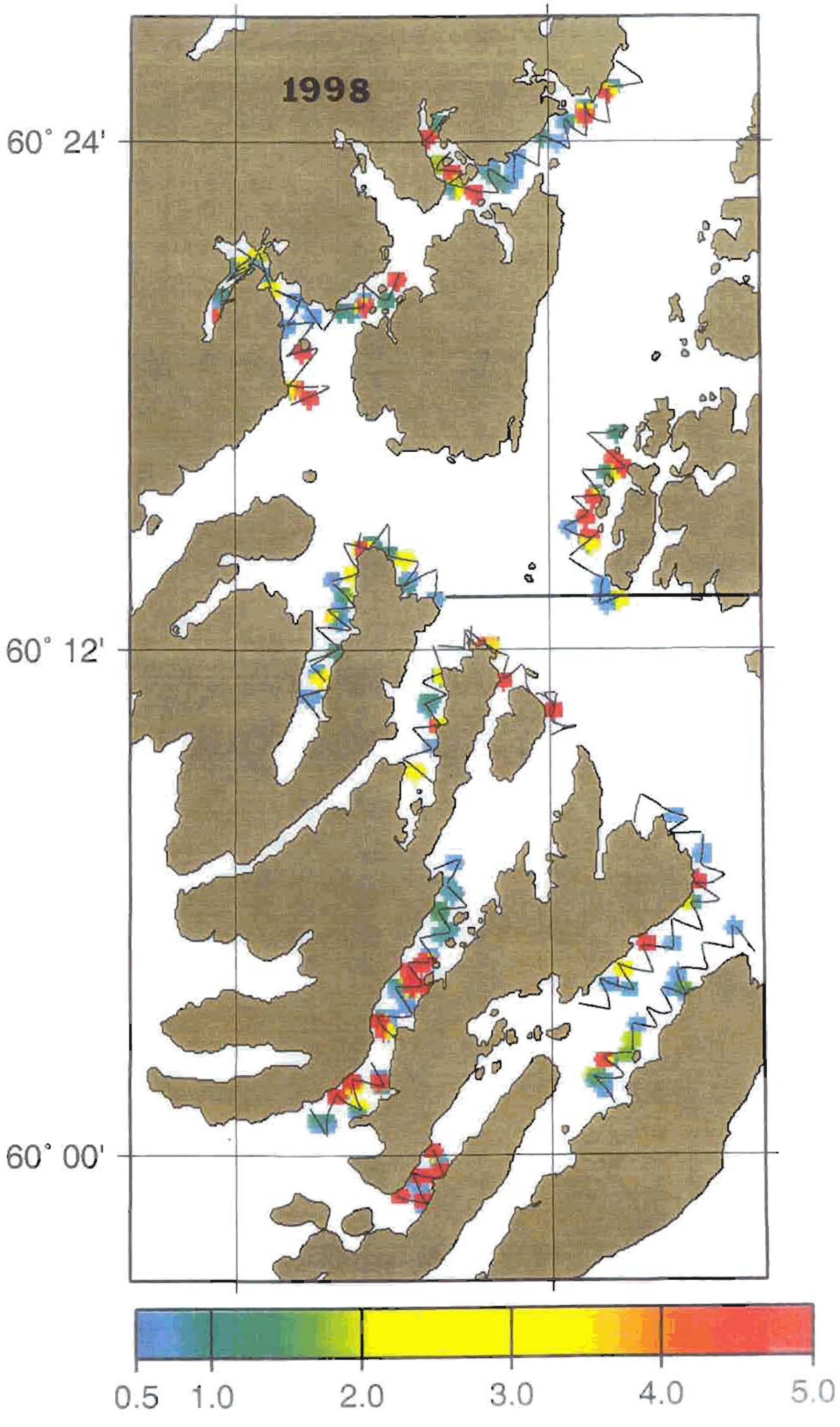

Figure 12. Geographic distribution of acoustic biomass in the South study area in 1998. Color scale units are grams/m^2. Codes for species are H - herring, Sn - sandlance, R - rockfish.

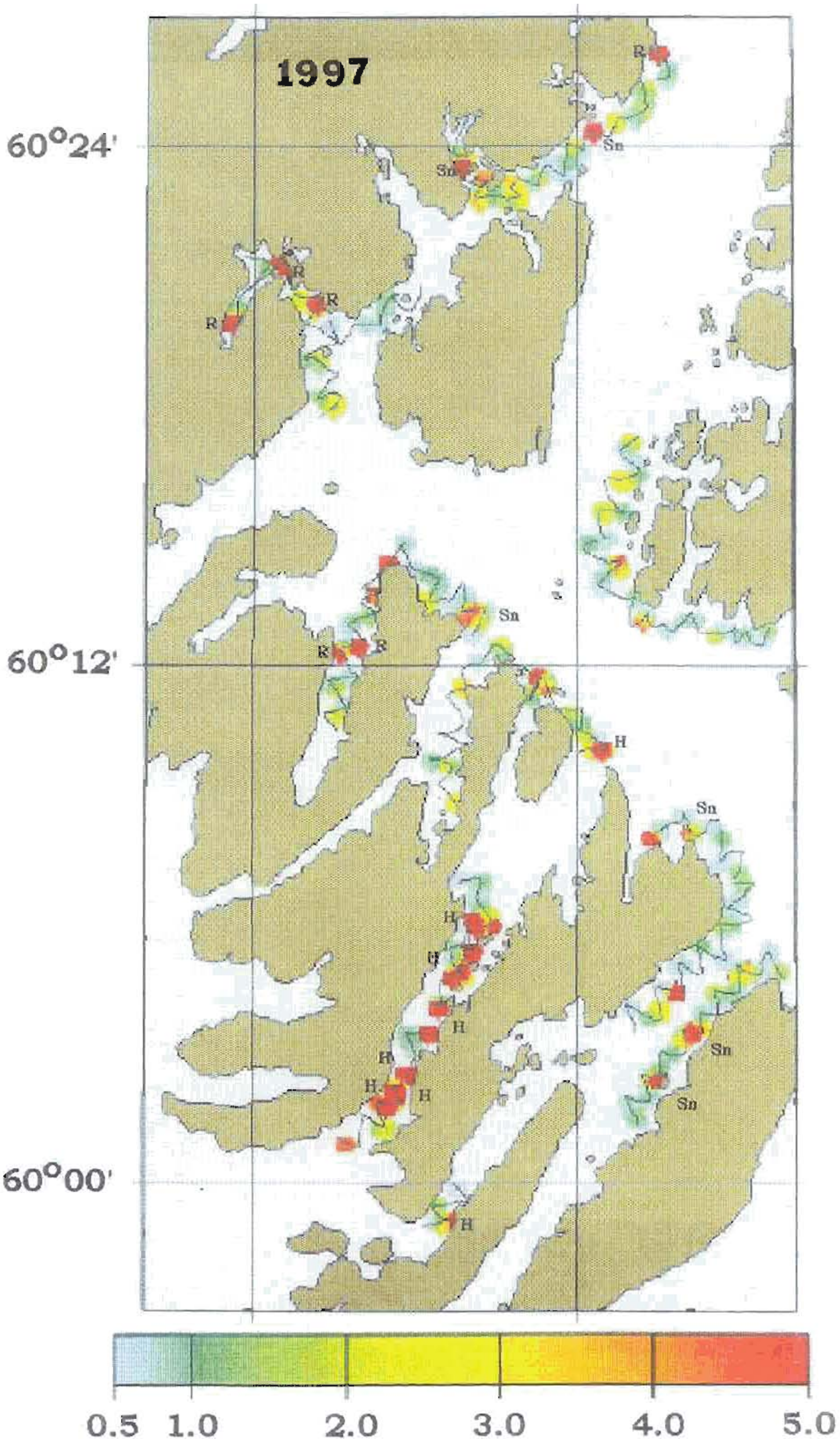

Figure 13. Geographic distribution of acoustic biomass in the South study area in 1997. Color scale units are grams/m^2. Codes for species are H - herring, Sn - sandlance, R - rockfish.

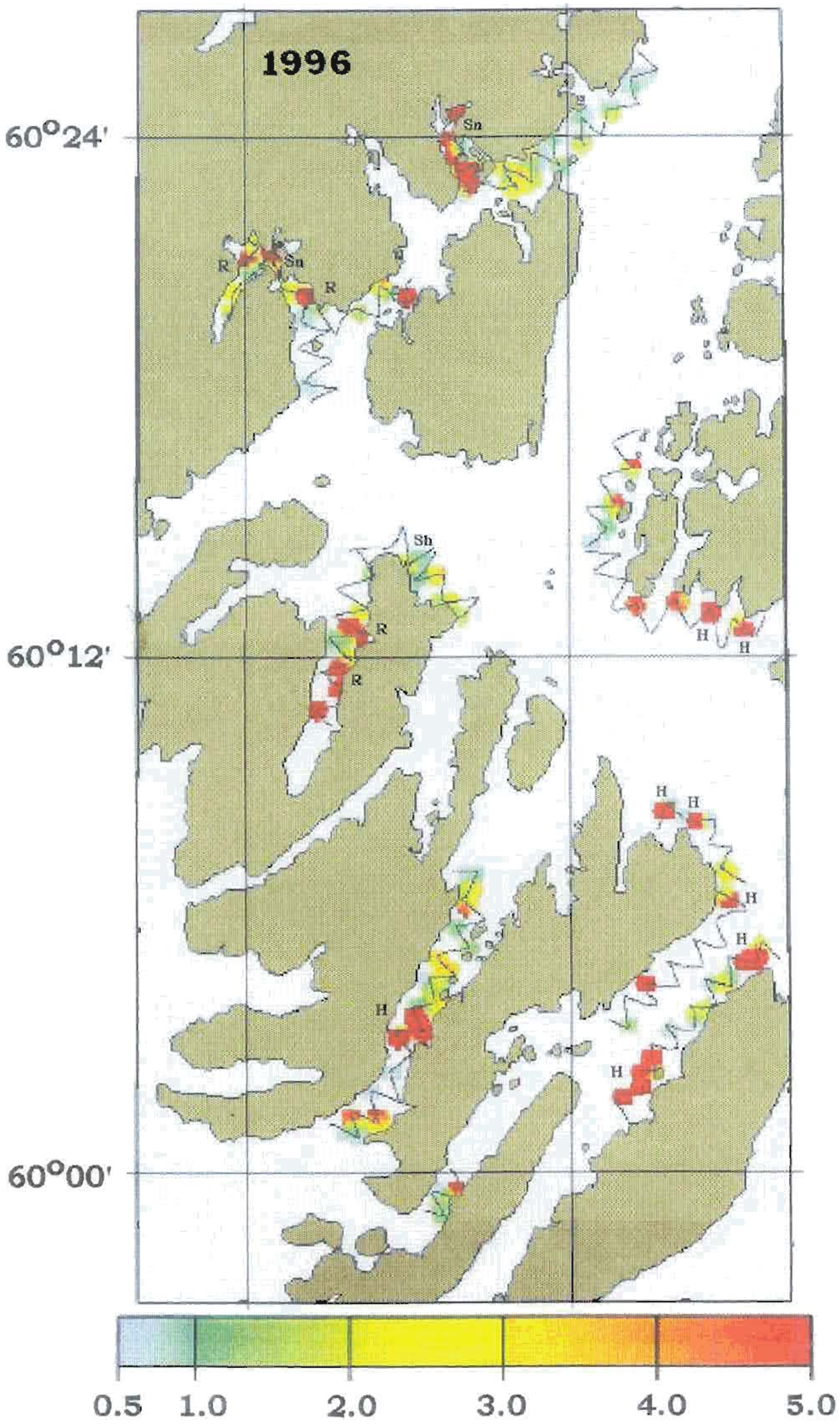

Figure 14. Geographic distribution of acoustic biomass in the South study area in 1996. Color scale units are grams/m^2. Codes for species are H - herring, Sn - sandlance, R - rockfish.

B Bird/Fish Interactions

Exxon Valdez Oil Spill
Restoration Project Annual Report

Seabird/Forage Fish Interactions Component
APEX

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

William D. Ostrand
Tracey Gotthardt
John M. Maniscalco
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April 1999

Seabird/Forage Fish Interactions Component
APEX

Restoration Project Component 97163B
Annual Report

Study History: This is an ongoing study which began with a pilot effort in 1994 to test field methods. In 1995, the study was expanded to look at seabird foraging in several habitats in 3 study sites within Prince William Sound. Data collected in 1994 and 1995 indicated that seabird activity was concentrated in shallow water nearshore. In response to these findings, data collection in 1996 and 1997 was focused on nearshore habitats. During 1998 we began an effort to model habitat selection by Pacific sand lance (*Ammondytes hexapterus*). In past years we have directed much of our time to the comparisons of hydroacoustic data and the distribution of seabirds. Due to concerns about target strength values of forage fish, we suspended work that involved the use of fish abundance data and focused our efforts on developing a habitat selection model for sand lance and preparing manuscripts on the behavioral interactions of seabirds at feeding flocks.

Abstract:

Our preliminary investigations of bottom typing software, conducted in 1998, determined substrates associated with sand lance were significantly different from locations selected randomly. Encouraged by these results we have preceded to develop a model of habitat selection by sand lance. During 1999 we have collected and processed bottom samples for the purpose of calibrating bottom typing software. We have also completed the analysis of bottom-typing the hydroacoustic data. We intend to continue this effort and ultimately will develop geographic information system coverages of bathymetry, bottom type, and the probability of encountering sand lance. Our behavioral studies determined that Marbled Murrelets (*Brachyramphus marmoratus*) initiated most feeding flocks that we observed and, at flocks, the rate at which Black-legged Kittiwakes (*Rissa tridactyla*) attempted to feed was inversely related to the abundance of Glaucous-winged Gulls (*Larus glaucescens*).

Key Words: *Ammodytes*, *Brachyramphus*, forage fish, foraging, habitat selection, *Larus*, marbled murrelets, Prince William Sound, *Rissa*. seabirds.

Project Data: (will be addressed in the final report)

Citation: Ostrand, W. D., Tracey Gotthardt, John M. Maniscalco, and Lisa A. Joyal. 1999. Seabird/forage fish interactions. Appendix B *in* D. C. Duffy, compiler. APEX Project: Alaska Predator Ecosystem Experiment in Prince William Sound and the Gulf of Alaska. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 99163), Alaska Natural Heritage Program and Department of Biology, University of Alaska Anchorage, Anchorage, Alaska.

TABLE OF CONTENTS

INTRODUCTION

This report for component 99163B is composed of three chapters that represent two manuscripts and a work in progress. Chapter one is a manuscript on the initiation of feeding flocks in Prince William Sound that has been submitted to the journal *Waterbirds* for review. Chapter two is a manuscript on competative interactions between Black-legged Kittiwakes and Glaucous-winged Gulls that is under internal review. Chapter three presents the status of the developement of a habitat selection model for sand lance and bottom typing of our study areas. We antipate that our manuscripts will be accepted for publication this year and that the work described in Chapter 3 will be completed early in 2000.

17 March 1998

MARBLED MURRELETS AS INITIATORS OF FEEDING FLOCKS IN PRINCE WILLIAM SOUND, ALASKA

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RH: Murrelets as Feeding Flock Initiators

Abstract. I sought to determine which seabird species initiated small, ephemeral, multispecies feeding flocks in Prince William Sound, AK (PWS), by observing the formation of flocks at sites known to have frequent feeding aggregations. I observed 43 feeding flocks at 5 sites during June 1996 and determined the initiating species at 34. All of the latter flocks were initiated by pursuit divers, of which 76.5 % were Marbled Murrelets (*Brachyramphus marmoratus*), the most abundant seabird in PWS. Formation of feeding flocks followed either of 2 scenarios: 1) larids were attracted to a feeding location by the presence or activity of Marbled Murrelets or 2) both larids and murrelets were present and flock feeding began after the murrelets dove from the surface. Of the observed flocks, 26.9 % and 50.0 % were initiated under scenarios 1 and 2, respectively. Other principal participants were Black-legged Kittiwakes (*Rissa tridactyla*) and Glaucous-winged Gulls (*Larus glaucescens*). I observed an apparent commensal relationship between murrelets and larids at feeding flocks with larids being the beneficiary.

Key words: *Black-legged Kittiwakes*, Brachyramphus marmoratus, *foraging*, *feeding flocks*, *Glaucous-winged Gulls*, Larus glaucescens, *Marbled Murrelets, Prince William Sound, AK,* Rissa tridactyla.

INTRODUCTION

Worldwide, seabirds commonly form mixed-species feeding flocks in pursuit of plankton or nekton (Hoffman et al. 1981, Duffy 1983), which may be a response to the aggregation of their prey (Ainley and Boekelheide 1990) and enhanced feeding success when participating in flocks (Götmark et al. 1986). In Prince William Sound, Alaska (PWS), Tufted Puffins (*Fratercula cirrhata*), Marbled Murrelets (*Brachyramphus marmoratus*) (Ostrand et al. 1996), and Black-legged Kittiwakes (*Rissa tridactyla*) (Irons 1998) feed more frequently as individuals or in pairs than in flocks. However, kittiwakes and Glaucous-winged Gulls (*Larus glaucescens*) have high foraging efficiency rates when feeding in flocks (Mansicalco and Ostrand 1997) and during years of lower food availability, they fed more frequently in flocks than during years of greater food abundance (D. B. Irons, R. M. Suryan, and W. D. Ostrand, U.S. Fish and Wildl. Serv., Anchorage, AK, unpubl. data). These findings suggest that although flock feeding is not the exclusive foraging strategy of seabirds in PWS, it does retain a great importance, particularly during times of food stress.

Hoffman et al. (1981) grouped seabird feeding flocks into three classes: Type I, ephemeral flocks associated with tightly aggregated prey; Type II, large and persistent flocks associated with dispersed prey; and Type III, flocks associated with prey concentrated by downwelling. Of these, Type I are the most common in PWS (Maniscalco and Ostrand 1997). Due to the short duration of these flocks, birds must frequently find new food sources by either locating their own prey or joining others. Hence, those species that function as flock initiators within PWS serve an important ecological function by locating available prey for themselves and in doing so, benefit other species.

Studies conducted in the North Pacific report equivocal findings as to which species initiate feeding flocks. Most of these indicate that larids are the principle initiators of feeding flocks (Sealy 1973, Hoffman et al. 1981, Porter and Sealy 1982). However, Chilton and Sealy (1987) reported that both alcids and larids initiated flocks and, in a more recent investigation, all the flocks observed were initiated by Marbled Murrelets (Mahon et al. 1992). This disparity in the literature results in an uncertainty concerning the ecological roles of seabirds and how they interact during foraging. Here, I report on my effort to determine which seabird species initiate Type I flocks within PWS.

STUDY AREA AND METHODS

I conducted this study in PWS, an embayment of ca.10,000 km^2, located on the southcentral coast of Alaska (Fig. 1). The climate is maritime with a mean annual precipitation of 1.6 m and moderate temperatures for the subarctic. The coastline of PWS is rugged, with mountains up to 4,000 m in elevation and numerous fjords and tidewater glaciers. The avia-fauna of PWS is diverse collection species with Marbled Murrelets the most abundant seabird (Agler and Kendall 1997).

I preselected seven locations where I and others had consistently observed feeding flocks (Fig. 1). At each location, observations were made from 7:00 to 19:00 h (Alaska standard time), between 14-29 June 1996, by 2 individuals who alternated 2-h watches. Two observation days were terminated early, at 14:40 and 11:10, to respond to a Mayday call and adverse weather; respectively. Data collected during shortened days were included in the analysis. The observations were made from the deck of a 7.3-m boat at sea level with the aid of 8 x 42 or 10 x 42 binoculars. Data were collected on flocks within 500 m of the boat. If flocks were forming >100 m away, we motored closer without disturbing feeding activities. We recorded the initiating species when possible and noted whether other seabird species were present (within 100 m) at the moment of initiation. A count of each species participating (actively feeding) in each flock was made at 10-min intervals begining at initiation. These counts were averaged to determine a representative value for each flock. I defined a flock as a mixed species feeding group of ≥ 3 individuals; mono-specific aggregations were not considered. Location, depth of water, and distance from shore were obtained for each flock using a commercial global positioning system device, fathometer, and radar, respectively.

At each of the observation sites, measurements of depth and distance to shore may have been spatially correlated and different flocks may have contained some of the same individual birds. Therefore, to avoid pseudoreplication, I used the observation site, rather than the flocks, as the sample unit in analyzing data. To determine mean values for each variable presented (Table 1), I determined the mean value for each location and then calculated the grand mean and standard error for all locations.

To quantify feeding flock participation for each species I converted the composition of each 10-min flock count to proportions. Next I averaged the 10-min proportions to determine participation composition of each flock. I then determined the mean proportions for each species at each observation site. Lastly I calculated grand means and standard errors for all observation sites. Because observation sites were not selected randomly, statistical inference was limited to the locations sampled.

RESULTS

I observed Type I flocks from initiation to dispersal at 5 of the 7 observation sites, 3 of which were located near Naked Island (Fig. 1). Of 43 flocks detected, I was able to determine the initiating species at 34. Pursuit divers initiated all of the observed flocks, primarily Marbled Murrelets (Table 1). Of the non-murrelet initiated flocks, one was initiated by Pacific Loons (*Gavia adamsii*), at Graveyard Point, one by a Red-throated Loon (*Gavia stellata*) at Cabin Bay, and Tufted Puffins (*Fratercula corniculata*) initiated 2 flocks observed at South Naked Island. The puffin-initiated flocks were located within 1 km of a Tufted Puffin colony.

The initiation of feeding flocks by murrelets generally followed either of 2 scenarios: 1) larids were attracted to a feeding location by the presence or activity of Marbled Murrelets or 2) both larids and murrelets were observed together, either both on the water or larids resting on rocks nearby, and flock feeding began after the murrelets dove from the surface. Of the observed flocks, 26.9 ± 11.0 % and 50.0 ± 15.6 % were initiated under scenarios 1 and 2, respectively.

The mean depth and distance to shore at flock locations was 15.1 ± 3.1 m and 161.7 ± 37.6 m, respectively. Twelve species were observed in feeding flocks; however, composition was dominated by 3 species, Marbled Murrelets, Glaucous-winged Gulls, and Black-legged Kittiwakes (Table 2).

DISCUSSION

The sites that I chose to observe feeding flocks were located near shore and over shallow water as were the feeding flocks sampled by Maniscalco and Ostrand (1997) on a systematic survey of PWS during the previous summer. These similarities suggest that our findings did not differ greatly from what could have been obtained from a systematic or random sample.

In their survey of feeding flocks in Alaskan waters, Hoffman et al. (1981) recorded much larger Type I feeding flocks than observed during this study, 88.1 vs 24.9 ± 8.8 birds. However, their observations of mixed species flocks containing the numerically dominant PWS species were similar in size to our overall mean value; 30.1, 26.0, and 24.5 individuals for their flocks containing Glaucous-winged Gulls, Black-legged Kittiwakes, and Tufted Puffins, respectively. These similarities suggest that Type I feeding flocks in PWS are comparable in size to those observed elsewhere in Alaskan waters.

My findings that pursuit divers initiated all of the observed Type I flocks differs from studies conducted in the North Pacific which reported larids as initiators (Sealy 1973, Hoffman et al. 1981, Porter and Sealy 1982, Chilton and Sealy 1987). Results consistent with mine have been reported by Mahon et al. (1992), who observed murrelets as initiators, and Grover and Olla (1983) who describe another pursuit diver, the Rhinoceros Auklet (*Cerorhinca monocerata*), as behaving as described in initiation scenario 2 (Table 3). These disparities may be the result of differences in the response of seabirds to local conditions. Hoffman et al. (1981) observed Marbled Murrelets in only one feeding flock, which may have been a consequence of conducting his study outside of areas where murrelets are abundant (Piatt and Ford 1993, Agler et al. 1998). In both Mahon et al.'s (1992) and my study area, Marbled Murrelets were a numerically dominant species (Piatt and Ford 1993) and in PWS there were few other alcids that could have competed with them for forage (Agler and Kendall 1997). These attributes may have facilitated the murrelets role in the formation of Type I flocks. Also, in the Galapagos Archipelago, Mills (1998) determined that pursuit-divers played an important role in prolonging the duration of feeding flocks in nearshore habitats where the mechanisms that keep prey near the surface and available to seabirds differed from those of flocks on the open ocean. It is possible that such differences also occur between inshore and offshore feeding flocks of northern latitudes. Ostrand et al. (1998) observed that Marbled Murrelets in PWS selected fish schools which occurred in shallow water, which suggests that murrelets would have a limited role in pelagic flocks and a greater role in shallow, nearshore, waters as was observed by Porter and Sealy (1981). Disparity may also have resulted from differences among study designs. Grover and Olla (1983), Chilton and Sealy (1987), and Mahon et al. (1992) had the specific objective to observe the initiation of feeding flocks. That Chilton and Sealy (1987) made their observations from land at distances up to 1 km and were not able to approach flocks may be problematic. During the collection of the data for this study I observed that murrelets on the water were difficult to detect >100 m distant and data collected at greater distances my be suspect.

My findings suggest a commensal relationship between larids and Marbled Murrelets of PWS, with larids being the benificiary species. Murrelets locate fish schools, then force schools into tight balls and drive them to the surface where they become available to larids (Mahon et al. 1992, Hunt 1995, Maniscalco and Ostrand 1997). I did not observe any benefits to murrelets that resulted from their roll in feeding flocks and there may be a negative effect due to kleptoparasitism by larids (Maniscalco and Ostrand 1997). However, Hunt (1995) speculated that the foraging activity of larids may aid murrelets by driving fish from their protective balls.

Mahon et al. (1992) and I have demonstrated that in at least two locations within their range, murrelets functioned as initiators of Type I feeding flocks. As such, murrelets may be viewed as a catalyst in the transfer of energy from the marine system to other avian predators within PWS. Elucidation of their role in seabird foraging ecology raises questions about the impacts of murrelet population declines on other species. Do murrelet population declines result in less forage available to other seabirds? To what extent have Marbled Murrelet declines within PWS (Klosiewski and Laing 1994) impacted other picivorous predators? Likewise, if Marbled Murrelets fill a similar roll throughout their range, then are their continuing population declines (Beissinger 1995) having broader impacts on other marine communities? These questions merit further discussion and investigation within the context of the management and conservation of seabirds of the North Pacific.

ACKNOWLEDGMENTS

The research described in this paper was supported by the *Exxon Valdez* Oil Spill Trustee Council and the U. S. Fish and Wildlife Service. However, the findings and conclusions presented are mine and do not necessarily reflect the views or position of the Trustee Council and the Service. I thank individuals who provided assistance throughout this study. J. M. Maniscalco assisted with data collection and study design. L L. McDonald and J. Kern of Western EcoSystems Technology, Inc. provided advice and assistance with statistical analysis. T. A. Gotthardt developed maps. The suggestions of D. G. Ainley, G. S. Drew, D. C. Duffy, T. A. Gotthardt, D. B. Irons, K. J. Kuletz, B. K. Lance, and R. M. Suryan significantly improved this paper.

LITERATURE CITED

Agler, B. A. and S. J. Kendall. 1997. Marine bird and sea otter population abundance of Prince William Sound, Alaska: trends following the T/V *Exxon Valdez* oil spill, 1989-1996. *Exxon Valdez* oil spill restoration final reports, Restoration Project 96159. U. S. Fish and Wildl. Serv., Anchorage AK.

Agler, B. A., S. J. Kendall, and D. B. Irons. 1998. Abundance and distribution of Marbled and Kittiltz's Murrelets in Southcentral and Southeast Alaska. Condor 100:254-265.

Ainley, D. G. and R. J. Boekelheide. 1990. Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community. Stanford Univ. Press, Stanford, CA.

Beissinger, S. R. 1995. Population trends of the Marbled Murrelet projected from demographic analyses, p. 385-393. *In*: C. J. Ralph, G.L. Hunt, M. G. Raphael, and J. F. Piatt (eds.), Ecology and conservation of the Marbled Murrelet. Pacific Southwest Res. Sta. Albany, CA.

Chilton, G. and S. G. Sealy. 1987. Species roles in mixed-species feeding flocks of seabirds. J. Field Ornithol. 58:456-463.

Duffy, D. C. 1983. The foraging ecology of Peruvian Seabirds. Auk 100: 800-810.

Götmark, F., D. W. Winkler, and M. Andersson. 1986. Flock-feeding on fish schools increases individual success in gulls. Nature 310:589-591.

Grover, J. J. and B. L. Olla. 1983. The role of Rhinoceros Auklet (*Cerorhinca monocerata*) in mixed-species feeding assemblages of seabirds in the Strait of Juan de Fuca, Washington. Auk 100:979-982.

Hunt, G. L. Jr. 1995. Monspecific and mixed species foraging associations of Marbled Murrelets, p. 255-256. *In*: C. J. Ralph, G.L. Hunt, M. G. Raphael, and J. F. Piatt (eds.), Ecology and conservation of the Marbled Murrelet. Pacific Southwest Res. Sta. Albany, CA.

Hoffman, W. D., D. Heinemann, and J. A. Wiens. 1981. The ecology of seabird feeding flocks in Alaska. Auk 98:437-456.

Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79:647-655.

Klosiewski, S. P. and K. K. Laing. 1994. Marine bird populations of Prince William Sound, Alaska before and after the *Exxon Valdez* oil spill. NRDA Bird Study Number 2. Unpubl. Rep., U.S. Fish and Wildl. Serv., Anchorage, AK.

Mahon, T. E., G. W. Kaiser, and A. E. Burger. 1992. The role of Marbled Murrelets in mixed-species feeding flocks in British Columbia. Wilson Bull. 104:783-743.

Maniscalco, J. M. and W. D. Ostrand. 1997. Seabird behaviors at forage fish schools in Prince William Sound, Alaska. Proceedings - Forage Fishes in Marine Ecosystems, Alaska Sea Grant College Program, AK-SG-97-01, Anchorage, AK.

Mills, K. L. 1998. Multispecies seabird feeding flocks in the Galápagos Islands. Condor 100:277-285.

Ostrand, W. D., K. O. Coyle, G. S. Drew, J. M. Maniscalco, and D. B. Irons. 1998. Selection of forage-fish schools by murrelets and Tufted Puffins in Prince William Sound, Alaska. Condor 100:286-297.

Piatt, J. F. and R. G. Ford. 1993. Distribution and abundance of Marbled Murrelets in Alaska. Condor 95:662-669.

Porter, J. M. and S. G. Sealy. 1981. Dynamics of seabird multispecies feeding flocks: chronology of flocking in Barkley Sound, British Columbia, in 1979. Colonial Waterbirds 4:104-113.

Porter, J. M. and S. G. Sealy. 1982. Dynamics of seabird multispecies feeding flocks: age-related feeding behaviour. Behaviour 81:91-109.

Sealy, S. G. 1973. Interspecific feeding assemblages of marine birds off British Columbia. Auk 90:792-802.

Table 1. Mean values for feeding flocks observed at 5 sites in Prince William Sound, Alaska during June 1996.

Location	Duration of observations (d)	No. flocks observed	% initiated by murrelets	$\bar{x}$ flock size (bird no.)	$\bar{x}$ no. murrelets	$\bar{x}$ no. kittiwakes	$\bar{x}$ no. gulls	$\bar{x}$ flock duration (min.)
Graveyard Point	2.6	10	88.9	5.5	2.7	2.4	0.1	5.4
NW Naked Is.	2	2	100.0	14.2	6.5	0.6	11.5	18.0
Cabin Bay	1.4	21	93.8	13.9	4.8	4.6	3.7	19.9
Disk Is.	2	9	100.0	38.7	25.8	2.5	10.6	20.2
S Naked Is.	1	2	0.0	52.3	0.0	0.7	19.5	21.5
Mean ± SE	1.8 ± 0.3	8.8 ± 3.5	76.5 ± 19.2	24.9 ± 8.8	7.9 ± 4.6	2.2 ± 0.7	9.1 ± 3.4	17.0 ± 3.0

TABLE 2. The proportional composition of feeding flocks at 5 study sites by species. See text for method of calculation of mean values. Data were collected in Prince William Sound, Alaska during June 1996.

Species	Mean percentage for all locations
Marbled Murrelet	39.0 ± 8.7
Glaucous-winged Gull	34.9 ± 12.9
Black-legged Kittiwakes	17.8 ± 8.7
Tufted Puffin	9.6 ± 9.5
Horned Puffin	2.7 ± 2.7
Pacific Loon	2.2 ± 1.7
Pigeon Guillemot	0.9 ± 0.9
Mew Gull	0.4 ± 0.4
Pelagic Cormorant	0.2 ± 0.2
Red-throated Loon	< 0.1 ± 0.1
Common Murre	< 0.1 ± 0.1
Arctic Tern	< 0.1 ± 0.1

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TABLE 3. Summary of the findings of studies conducted in the Northeast Pacific that report on initiators of seabird feeding flocks.

Study	Location	Initiators of feeding flocks
Sealy (1973)	Queen Charlotte Islands, British Columbia, Canada	72 % kittiwakes (surface-feeders) and 14 % alcids (pursuit-divers)
Hoffman et al. (1981)	Northern Gulf of Alaska and Destruction Is., Washington, USA	76% kittiwakes (surface-feeders) (Gulf of Alaska), 77 % gulls (surface-feeders) (Washington)
Porter and Sealy (1982)	Barkley Sound, Vancouver Is., British Columbia, Canada	96 % gulls (surface-feeders)
Grover and Olla (1983)	Strait of Juan de Fuca, Washington, USA	100 % Rhioceros Auklets (pursuit-divers)
Chilton and Sealy (1987)	Barkley Sound, Vancouver Is., British Columbia, Canada	57.1 % gulls (surface-feeders) and 39.7 % alcids (pursuit-divers)
Mahon et al. (1992)	Okeover Inlet, SW British Columbia, Canada	100 % murrelets (pursuit-divers)
Ostrand (this study)	Prince William Sound, Alaska, USA	100 % pursuit-divers, of which 76.5 % were murrelets

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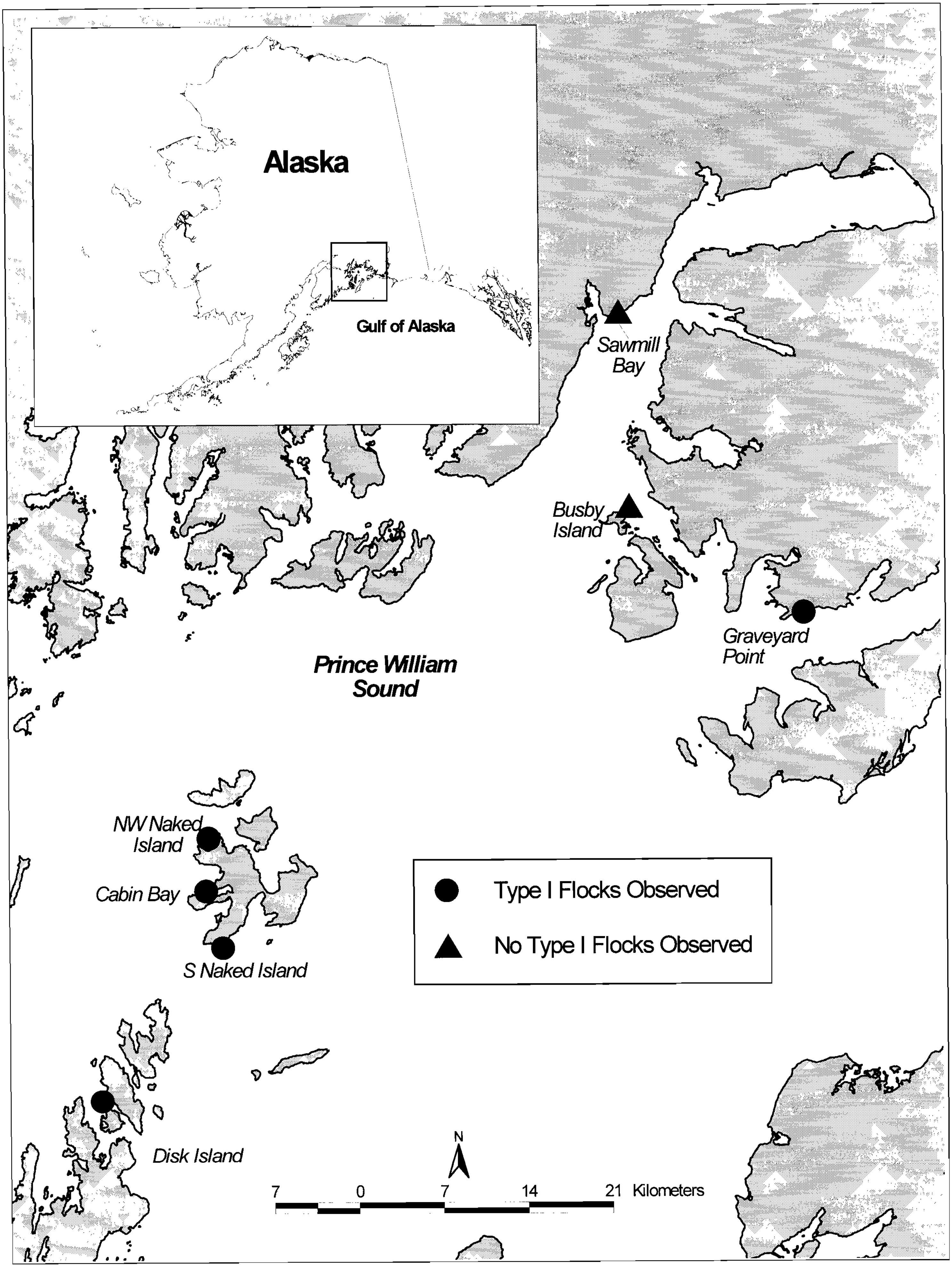
Ostrand (this study)	Prince William Sound, Alaska, USA	100 % pursuit-divers, of which 76.5 % were murrelets

FIGURE 1. Map of the study area depicting observation sites where data were collected on the initiation of feeding flocks in Prince William Sound, Alaska, 14 June-29 June 1996


Alaska
Gulf of Alaska
Sawmill Bay
Busby Island
Graveyard Point
Prince William Sound
NW Naked Island
Cabin Bay
S Naked Island
Disk Island
● Type I Flocks Observed
▲ No Type I Flocks Observed
N
7 0 7 14 21 Kilometers

LRH: J. M. Maniscalco et al.

RRH: Passive Interference of Kittiwakes

Passive Interference Competition of Black-legged Kittiwakes by Glaucous-winged Gulls in Prince William Sound, Alaska.

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Abstract – We studied mixed species feeding flocks during 1995 and 1996 and analyzed data from an independent radio-tracking study of Black-legged kittiwakes from 1997, both in Prince William Sound, Alaska. Our purpose was to determine if Glaucous-winged Gulls hinder prey capture by kittiwakes by examining their foraging and feeding behaviors. At tightly aggregated feeding flocks, gulls sat on the water directly over the prey source and maintained their position by making brief hop-plunges or surface-seizing. Kittiwakes, on the other hand, fed by looking for an open spot in the flock and plunging from the air. Data from both studies indicated that kittiwakes made significantly fewer feeding attempts in flocks that had greater numbers of gulls. However, kittiwakes were no more successful at feeding when gulls were absent. Kittiwakes were also more likely to join flocks that had fewer Glaucous-winged Gulls. Our findings are evidence of interference competition between these two species and suggest that increased populations of large gulls in PWS cause additional stress on Black-legged Kittiwakes especially when prey is scarce.

INTRODUCTION

Central place foraging theory attempts to predict which and how much of a particular food patch will be used by a predator dependent upon factors such as travel time and food density (Orians and Pearson 1979). Interference, which reduces the rate of food intake by the inferior competitor, is essentially the same as a decrease in food density for that competitor. Thus, increased interference by a superior competitor at a prey patch should result in a decrease in the optimal food load and an increase in search times for alternative patches by the inferior competitor (Ydenberg et al. 1986).

Interference competition is commonly divided into two major categories: active (Schoener 1983) and passive (Charnov et al. 1976). Passive interference competition in which one species obstructs the availability of a resource to another species by non-aggressive behaviors is often difficult to detect (Maurer 1984). However, in surface feeding seabirds it may be more readily observed due to their highly viewable habits of feeding on a nearly two-dimensional surface in localized areas. For example, Shealer and Burger (1993) have shown that Brown Noddies (Anous Stolidus) interfere with Roseate Terns (Sterna dougalli) by blocking access to prey and hence reducing the number of feeding attempts by terns. Also, in the feeding guild of dabbling ducks, evidence exists of the passive exclusion of Northern Shovelers (Anas clypeata) by Green-winged Teals (A. crecca; Poysa 1985).

The purpose of this study was to determine if passive interference exists among surface feeding seabirds in Prince William Sound (PWS), Alaska. We examined data from two different and independent studies in PWS with emphasis on the feeding strategies of Black-legged Kittiwakes (Rissa tridactyla) and Glaucous-winged Gulls (Larus glaucescens). Glaucous-winged Gulls are large (66 cm in length) compared to kittiwakes (43 cm) and recent changes in their relative abundance in PWS have been estimated (Data provided by Brian Lance, USFWS). In many cases, larger species outcompete smaller ones (Persson 1985) and thus can monopolize a greater proportion of resources as their numbers increase and/or food supply decreases. We briefly discuss the potential impact that interference competition might have on kittiwakes in PWS.

STUDY AREA AND METHODS

Prince William Sound is a large estuarine embayment of the northern Gulf of Alaska which provides important foraging and breeding habitat for many seabirds (Isleib and Kessel 1973, Irons et al. 1988). During the summers of 1995 and 1996 we examined the behaviors of seabirds at feeding flocks encountered along systematically run transects in PWS from vessels averaging 18 m in length using 7 x 40 and 10 x 42 binoculars. During 1995 we ran a combination of offshore and nearshore transects (See Ostrand et al. 1998 for details). However, in 1996, we concentrated our efforts on nearshore transects in randomly selected 12 x 1 km blocks (Haldorson et al. 1998) because feeding flocks were found to be close to shore (Maniscalco et al. 1999).

A feeding flock was defined as an aggregation of three or more seabirds actively feeding as observed by diving alcids surfacing with fish in their bills or larids plunging or dipping into the water. Flock types were loosely classified following Hoffman et al. (1981): (I) small, short duration flocks over tightly clumped prey; (II) large, persistent flocks over more broadly dispersed prey; and (III) flocks associated with sites where forage was concentrated by downwelling or other hydrophysical influence, determined by a subjective evaluation of oceanographic features. For this part of the study we concentrated our analyses on Type I flocks where gulls and kittiwakes fed in close proximity.

Upon encountering a feeding flock we noted species composition and their positions in the flock and quantified the frequencies and types of feeding strategies for Glaucous-winged Gulls and Black-legged Kittiwakes using a voice recorder or videotape. Feeding was categorized as plunge-diving, surface-seizing, piracy (Ashmole 1971) and hop-plunging (Hoffman et al. 1981) and compared between the two species with reference to their position in the flock. We did not record aborted dives or swoops because of uncertainty to their cause. We did record feeding frequency and success of kittiwakes when our position and the prey type facilitated those observations. We remained with each flock until it broke up naturally or became disturbed by our presence.

We also examined 1997 radio-tracking data of several kittiwakes from Shoup Bay, a large colony in Northeastern PWS (see Suryan et al. 1998 for methodology). Fish abundances in that region were low in 1997 compared to the previous year (Haldorson et al. 1998). Furthermore, Suryan et al. (1998) reported that kittiwakes foraged more often in flocks in 1997 as opposed to 1995 and 1996 although only the 1997 data were suitable for our analyses here. With those data we compare the species composition of flocks joined with those passed by using individual kittiwakes as the sample unit and averaging the data collected for each individual bird. We also examined the ratio of Glaucous-winged Gulls to kittiwakes in relation to the number of feeding attempts by kittiwakes and their success as averaged by flock. We did not use data from flocks formed by fish processors spewing offal into the waters because they were intermittent and artificial in nature.

Changes in the relative abundance of Glaucous-winged Gulls and Black-legged Kittiwakes are displayed graphically from data provided by U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Anchorage, Alaska.

RESULTS

Feeding Flock as the Sampling Unit

The majority of feeding flocks encountered (14 of 22 in 1995 and 20 of 22 in 1996) were tightly aggregated Type I flocks. Sixteen of those flocks had both Black-legged Kittiwakes and Glaucous-winged Gulls participating. Other members of the Laridae, comprising less than 5% of the flocks, included Mew Gulls (Larus canus), Bonaparte's Gulls (L. philadelphia), Arctic Terns (Sterna paradisaea), and Parasitic (Stercorarius parasiticus) and Pomarine (S. pomarinus) Jaegers. Marbled Murrelets (Brachyramphus marmoratus), Tufted Puffins (Fratercula cirrhata), and Pigeon Guillemots (Cepphus columba) also commonly took part in the flocks.

At Type I feeding flocks, Glaucous-winged Gulls often sat on the water over the center of a concentrated prey source while kittiwakes typically circled or hovered above the flock. Glaucous-winged Gulls maintained their position in the flocks by hop-plunging and surface-seizing for their prey 86.9% of the time; they also plunge-dived 6.6%, and pirated 6.5% of the time. Conversely, kittiwakes hop-plunged and surface-seized 13.9%, plunge-dived 80.1%, and pirated 6.0% of the time. These feeding strategies were drastically different ($P^2 = 962.9$, df = 2, $P < 0.001$). Fish schools held in tight balls near the water surface by alcids (Maniscalco and Ostrand 1997) were easily monopolized by gulls on the water which virtually blocked access to plunge-diving kittiwakes. On two occasions kittiwakes were denied any feeding opportunities at flocks where several gulls were centralized over the prey.

In Type I flocks that contained both kittiwakes and Glaucous-winged gulls kittiwakes made more feeding attempts in flocks when there was a smaller ratio of gulls to kittiwakes (Spearman rank correlation, $r_s = 0.547$, df = 14, $P = 0.002$, Fig. 1a). There was not a significant difference in the feeding success of kittiwakes in flocks without Glaucous-winged Gulls (27/30.97 min) as opposed to those with (30/28.55 min, $P^2 = 0.496$, df = 1, $P = 0.479$).

Black-legged Kittiwake as the Sampling Unit

During 1997, we radio-tracked 20 Black-legged kittiwakes from Shoup Bay colony. Data from 16 of those birds contained enough information for our analysis here. Kittiwakes joined feeding flocks that had a mean of 4.7 (SE = 1.61, n = 16) Glaucous-winged Gulls as opposed to 9.8 (SE = 1.79, n = 13) gulls in flocks that were passed by ($P^2 = 10.462$, df = 1, $P = 0.001$).

In flocks that were joined, kittiwakes made fewer feeding attempts in the presence of greater ratios of Glaucous-winged Gulls to kittiwakes (Spearman rank correlation, $r_s = 0.332$, df = 15, $P = 0.019$, fig. 1b). There was no relationship between the feeding success of kittiwakes and the relative number of Glaucous-winged Gulls in the flock (Spearman rank correlation, $r_s = 0.002$, df = 22, $P = 0.824$). We did not examine the feeding methods during this portion of the study.

The relative abundance of Glaucous-winged Gulls to kittiwakes has increased steadily in PWS since 1991 (Figure 2). Data from 1989 and 1990 were available but not included due to possible biases from disturbances caused by the Exxon Valdez oil spill and clean-up operations.

DISCUSSION

Unlike active interference, which more likely occurs when resources are abundant and concentrated, passive interference may occur more often when resources are rare and concentrated (Maurer 1984). In the former situation the predator will gain enough energy for active resource defense. The prey availability of seabirds feeding in flocks, although at times abundant, may be quite ephemeral in nature due to rapid dispersion below the birds' diving ability. In that case it may be prudent for birds to devote more time to feeding and limit other activities. Therefore, passive interference would likely be the major aspect of competition at feeding flocks of seabirds. This is what we observed at the tightly aggregated Type I feeding flocks where Glaucous-winged Gulls maintained their position over the prey source by hop-plunging and surface-seizing. In doing so, the large gulls were able to block access to prey from kittiwakes by expending little or no extra energy.

In other studies (e.g. Duffy 1986, Shealer and Burger 1993) larger seabirds flew in circles or hovered close to the water between the prey and their smaller competitors and fed by plunge-diving or dipping. Those feeding methods are advantageous when prey is highly mobile and the dominant competitor must change its position frequently to track it. However, when prey is held in one location such as by feeding alcids (Hoffman et al. 1981, Mahon et al. 1992, Maniscalco and Ostrand 1997), it makes better economic sense for the superior competitor to sit over the patch and not make movements by which it could lose an advantageous position.

We posit that passive interference induced by Glaucous-winged Gulls' location in the flock and feeding behaviors resulted in the reduced number of feeding attempts by Black-legged Kittiwakes as evidenced here by two independent studies. Both studies also revealed no significant difference in the feeding success of kittiwakes with the presence of gulls indicating that reduced feeding rates also reduce overall capture rates by kittiwakes. Further, during 1997 kittiwakes joined flocks that had fewer gulls. The biomass of kittiwakes' favored prey in Northeastern PWS (age 1+ Pacific herring and sand lance) was greatly reduced in 1997 compared to 1996 (Haldorson et al. 1998) effecting an increase in predator aggregation where prey was available (Hassell and May 1974). Thus, kittiwakes were obligated to feed at flocks more often, but chose flocks that had fewer gulls because interference at those flocks was diminished. During 1996, when prey was more abundant and therefore easier to locate, kittiwakes frequently fed alone (Suryan et al. 1998).

The results presented here are similar to those found by Shealer and Burger (1993) who state that the effects of passive interference on Roseate Tern survival may be insignificant. Although active interference can have obvious and serious detrimental effects on the inferior species (e.g. Kennedy and White 1996), no such evidence exists in regard to passive interference, to our knowledge. At Shoup Bay colony in Northeastern PWS greatly reduced productivity of kittiwakes in 1997 compared to 1996 (Roby et al. 1998) may be attributed primarily to lower prey abundance. We could not ascertain potential negative effects on the survival of kittiwakes due to interference competition. However, our study indicates that the presence of large gulls may confer additional stresses on kittiwakes during times of food shortage.

Populations of Glaucous-winged Gulls may not be significantly increasing in PWS but data presented here suggests an increasing trend when taken in relation to kittiwake numbers. Additional growth in the relative abundance of large gulls may compound kittiwakes ability to obtain food with or without changes in prey abundance.

LITERATURE CITED

Ashmole, N. P. 1971. Sea bird ecology and the marine environment. Pp. 223-286 in D. S. Farner and J. R. King, eds. Avian Biology Vol. 1. Academic Press, New York.

Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. Am. Nat. 110:247-259.

Duffy, D. C. 1986. Foraging at patches: interactions between common and roseate terns. Ornis Scand. 17:47-52.

Haldorson, L., T. Shirley, and K. Coyle. 1998. Forage species studies in Prince William Sound. Pp. A1-10 in D.C. Duffy, compiler. Exxon Valdez Oil Spill Restoration Project Annual Report. Restoration Project 97163 A-Q. Anchorage, AK.

Hassell, M. P. and R. M. May. 1974. Aggregations of predators and insect parasites and its bearing on stability. J. Anim. Ecol. 43:567-594.

Hoffman, W., D. Heinemann, and J. A. Wiens. 1981. The ecology of seabird feeding flocks in Alaska. Auk 98:437-456.

Kennedy, D. E., and D. W. White. 1996. Interference competition from house wrens as a factor in the decline of Bewick's wrens. Conserv. Biol. 10:281-284.

Mahon, T. E., G. W. Kaiser, and A. E. Burger. 1992. The role of marbled murrelets in mixed-species feeding flocks in British Columbia. Wilson Bull. 104:738-743.

Maniscalco, J. M. and W. D. Ostrand. 1997. Seabird behaviors at forage fish schools in Prince William Sound, Alaska. Pp. 175-189 in Forage fishes in marine ecosystems. Alaska Sea Grant College Program, AK-SG-97-01, University of Alaska Fairbanks.

Maniscalco, J. M., W. D. Ostrand, and K. O. Coyle. 1999. Selection of fish schools by flocking seabirds in Prince William Sound, Alaska. Col. Waterbirds in press.

Maurer, B. A. 1984. Interference and exploitation in bird communities. Wilson Bull. 96:380-395.

Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pp. 154-177, in D. J. Horn, R. D. Mitchell, and G. R. Stairs, eds. Analysis of ecological systems. Ohio State University Press, Columbus.

Ostrand, W. D., K. O. Coyle, G. S. Drew, J. M. Maniscalco, and D. B. Irons. 1998. Selection of forage-fish schools by murrelets and tufted puffins in Prince William Sound, Alaska. Condor 100:286-297.

Perrson, L. 1985. Asymmetrical competition: are larger animals competitively superior? Am. Nat. 126:261-266.

Poysa, H. 1985. Circumstantial evidence of foraging interference between two species of dabbling ducks. Wilson Bull. 97:541-543.

Roby, D. D., K. R. Turco, and J. A. Anthony. 1998. Diet composition, reproductive energetics, and productivity of seabirds damaged by the Exxon Valdez oil spill. Pp. G1-23 in D. C.

Duffy, compiler. Exxon Valdez Oil Spill Restoration Project Annual Report. Restoration Project 97163 A-Q. Anchorage, AK.

Schoener, T. W. 1983. Field experiments on interspecific competition. Am. Nat. 122:240-285.

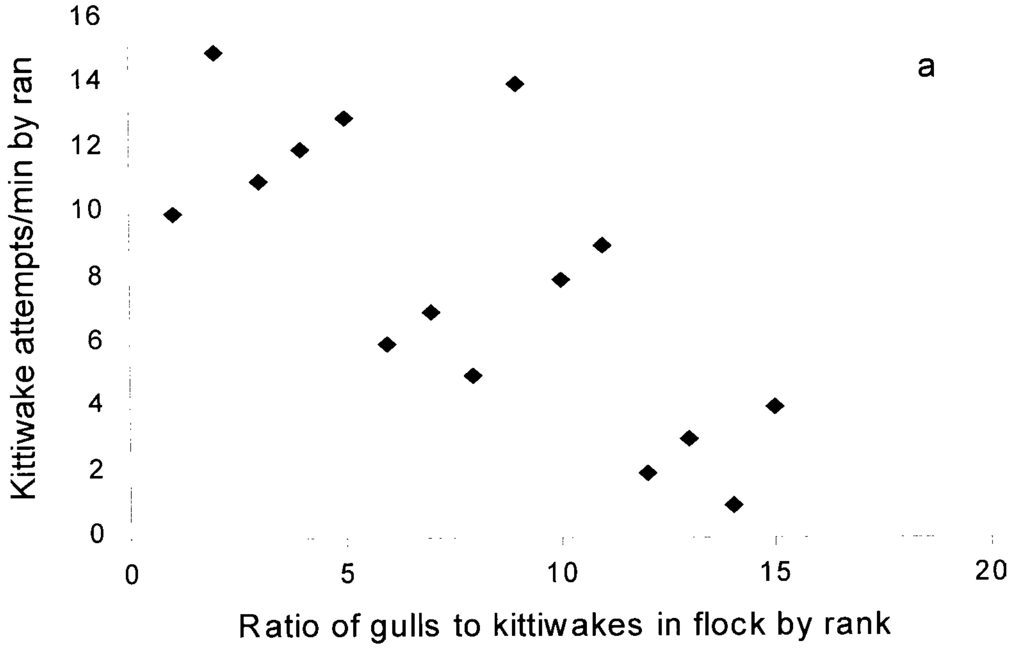
Shealer, D. A., and J. Burger. 1993. Effects of interference competition on the foraging activity of tropical roseate terns. Condor. 95:322-329.

Suryan R. M., D. B. Irons, and J. E. Benson. 1998. Interannual variation in diet and foraging effort of kittiwakes in relation to prey abundnace. Pp. E1-15 in D. C. Duffy, compiler. Exxon Valdez Oil Spill Restoration Project Annual Report. Restoration Project 97163 A-Q. Anchorage, AK.

Ydenberg, R. C., L-A. Giraldeau, and D. L. Kramer. 1986. Interference competition, payoff asymmetries, and social relationships of central place foragers. Theor. Popul. Biol. 30:26-44.

Figure 1. Relationship between the number of feeding attempts by Black-legged Kittiwakes and the ratio of Glaucous-winged Gulls to kittiwakes in the feeding flock; a) feeding flocks as the sample unit (1995 and 96) and b) Black-legged Kittiwake as the sample unit (1997).

Figure 2. Relative abundances of Glaucous-winged Gulls to Black-legged Kittiwakes in PWS since 1991 with trend line.


a
Kittiwake attempts/min by ran
Ratio of gulls to kittiwakes in flock by rank
0
2
4
6
8
10
12
14
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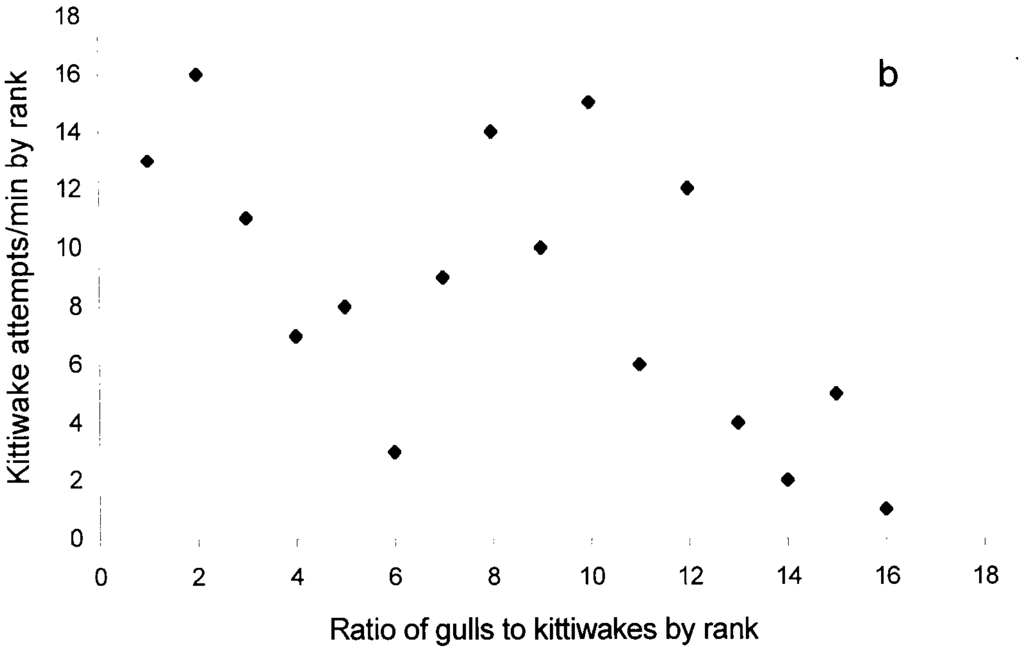
5
10
15
20


b
Kittiwake attempts/min by rank
Ratio of gulls to kittiwakes by rank
0
2
4
6
8
10
12
14
16
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0
2
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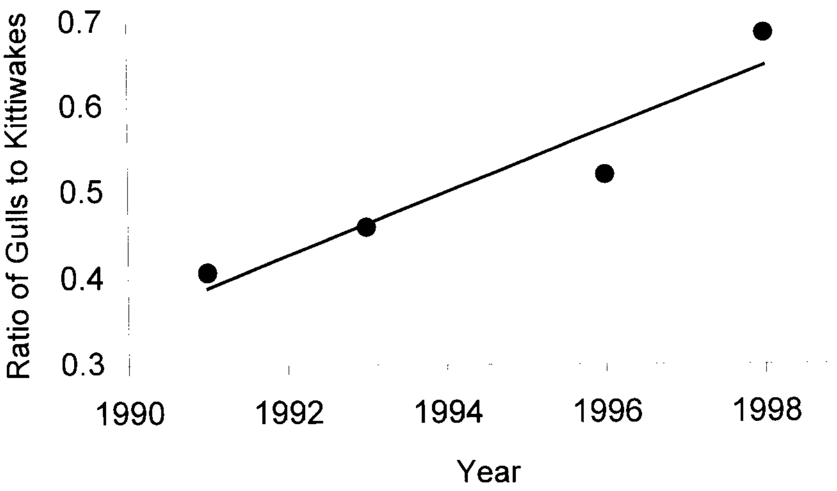


Ratio of Gulls to Kittiwakes
0.7
0.6
0.5
0.4
0.3
1990
1992
1994
1996
1998
Year

Sand Lance Habitat Determination Through Hydroacoustic Sampling

Ostrand, W., T. A. Gotthardt, and L. A. Joyal. Migratory Bird Management, U. S. Fish and Wildlife Service, Anchorage, AK

Pacific sand lance (*Ammodytes hexapterus*) play an important ecological role as energy-rich prey for seabirds, marine mammals, and predatory fishes in Prince William Sound, Alaska (PWS). However, due to lack in commercial interest, the biology and habitat requirements of this species are poorly understood (McGurk and Warburton 1992). Sand lance are commonly found in shallow nearshore habitats where they burrow in sandy substrates while not foraging, to avoid predation, and during overwintering, thereby linking this species distribution to habitats with distinct sediment grain sizes (Pinto et al. 1984). Sand lance are generally found in association with sandy bottoms, and avoid rocky, muddy, and coarse gravel bottoms (Reay 1970).

Sand lance population dynamics may play an important role in regulating apex predator populations and are a potential indicator of marine pollution in areas at risk to oil spills. For example, the reproductive success of at least 10 avian species has been correlated with sand lance availability, including: great skuas, parasitic jaegers, shags, black-legged kittiwakes, Arctic terns, common terns, Atlantic puffins tufted puffins, and rhinoceros auklets (Wilson et al., In prep.). In addition, the distribution of kittiwake breeding colonies has been shown to reflect sand lance distribution and abundance (Lock 1986 *in* Wilson et al., In prep.). The life history of sand lance, as both a schooling and a semi-demersal species, places them at risk to oil slicks, soluble toxins within the water column, and long term impacts due to sediment contamination. In planning development in marine environments and in identification of critical habitats to protect in the event of oil spills, we suggest that sand lance burrowing habitat should be of a primary concern.

Sand lance habitat may be broadly distributed (Penttila 1997), making the identification of critical habitat problematic. Dedicated surveys are expensive and time consuming. The development of accurate and inexpensive methods of identifying sand lance habitat are desirable both for research and environmental protection. Recently, software has been developed that can classify bottom type by interpreting narrow beam, quantitative hydroacoustic data. In other words, this software can determine the bottom type by interpreting data that may have been previously collected during fisheries (hydroacoustic) surveys. The use of acoustic methods to retrieve information from the acoustic bottom echo has advantages over other methods (i.e. geological cores) as being non-invasive, more cost effective, and faster (Lubniewski and Stepnowski 1997). Due to the strong linkage of sand lance to a narrow range of sediment types (Reay 1970), the classification of substrates through the use of bottom typing software is a potential tool in determining the distribution of sand lance burrowing habitat.

Objectives

1. Develop an inexpensive method to predict the distribution of sand lance burrowing habitat.

2. Develop GIS coverages that indicate the probability of encountering sand lance at all locations within our study areas using results derived from sand lance resource selection function.

Data collection and analysis completed and in progress:

During 17-27 July 1997 (in collaboration with the School of Fisheries and Ocean Sciences, University of Alaska, Fairbanks, Project 98163A) we hydroacoustically sampled nearshore transects in PWS arranged within 27 study blocks. Blocks followed the contour of 12 km of shoreline with a width of 1 km and contained 20 continuous, 1.2 km transects, that were laid out in a zigzag pattern for a total of 530 transects (Figure 1). Hydroacoustic data were collected with a single beam 120 kHz BioSonics DT4000 system that emitted a 6° beam.

To model forage fish habitat selection we have developed a set of sand lance locations that were collected by numerous APEX studies in PWS during 1997 and 1998 (Figure 2). Techniques used to determine the presence of sand lance included cast, dip, and seine nets; fish traps; under rocks and by stomping; visual identification; video cameras; and aerial surveys.

To calibrate bottom typing software, sediment samples were collected with a Ponar grab at 53 randomly selected locations within the APEX study area during the summer of 1998 . Due to the roughness and/or rockiness of the bottom substrate, successful samples (i.e. ≥ 50 g) were only obtained at 26 of 53 random sites (Figure 1). Samples were frozen and then oven dried (150^0 C for three hours) prior to laboratory analysis. Grain size analysis was performed on sediment samples using a sieve/hydrometer procedure (Day 1965) which determined percentage gravel, sand, silt, and clay for each sample following the USDA scale (Gee and Bauder 1986).

To model habitat selection by sand lance we began by performing cluster analysis, Ward's minimum variance method (SAS Institute Inc., 1996), of sediment sample data with the variables percent gravel, sand, and mud (silt/clay). Clusters were assigned a sediment code (gravel, sand, sandy mud, and mud) taken from Folk (1980) (Table 1; Figure 3). We added an unknown category to account for all substrate types that we did not sample.

Next, we analyzed hydroacoustic data collected during the 1997 forage fish survey with bottom typing software (VBT Seabed Classifier™, BioSonics, Inc., Seattle, WA). This process produced several variables that described the characteristics of the bottom signal. We adjusted the software to average the characteristics of the bottom and produce an output at 30-m intervals. We found the calibration feature of the software to be ineffective and are proceeding to develop our own methods to calibrate and categorize the programs output. First we will import the bottom typing output into GIS. A separate coverage will be developed for each variable of the output to which we will apply a krigging algorithm (surface interpolation function) to create a 1-km wide buffer along the survey routes (Figure 4). Next we will categorize sediments by comparing the characteristics of the bottom signal at locations at which grabs were taken to all locations through the use of compositional analysis (SAS Institute Inc., 1996). Each location within the buffers will be assigned the bottom type to which its bottom signal is most similar. We will also develop a krigged bathymetry coverage from the hydroacoustic data for the buffered survey lines. These coverages will be used to determine the depth, distance from shore, and bottom type at known sand lance and an equal number of randomly selected locations. We will utilize these data to develop a sand lance resource selection function, based upon logistic regression (Manly et al. 1993). Finally the resource selection function will be utilized to develop a GIS coverage that displays the probability of encountering sand lance along the buffered survey routes.

Literature Cited

Day, P. R. 1965. Particle fractionation and particle-size analysis, hydrometer method. *In* Methods of Soil Analysis, Part I. Agronomy 9:562-66. Amer. Soc. of Agron., Madison, Wis.

Folk, F. L. 1980. Petrology of sedimentary rocks. Hemphill Publishing Co., Austin, T., pp 182.

Gee, G. W. and J. W. Bauder. 1986. Particle-size analysis. Chapter 15 *in* Methods of Soil Analysis, Part I. Physical and Mineralogical Methods. Agronomy Monograph no. 9, pp. 383 – 411.

Lubniewski, Z. and A. Stepnowski. 1997. Sea bottom typing using fractal dimensions. Pages 12 – 16 *in* International Symposium on Hydroacoustics and Ultrasonics. Gdansk-Jurata, Poland.

Manly, B. F. J., L.L. McDonald, and D. L. Thomas. 1993. Resource selection by animals, statistical design analysis for field studies. Chapman and Hall, London.

McGurk, M. D. and H. D. Warburton. 1992. Pacific sand lance of the Port Moller estuary, southeastern Bering Sea: an estuarine-dependent early life history. Fisheries Oceanography 1(4):306-320.

Penttila, D. E. 1997. Investigations of intertidal spawning habitats of surf smelt and Pacific sand lance in Puget Sound, Washington. Pages 395 – 408 *in* Forage Fishes in Marine Ecosystems: Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program, AK-SG-97-01, Anchorage, AK.

Pinto, J M, W.H. Pearson and J. W. Anderson. 1984. Sediment preferences and oil contamination in the Pacific sand lance *Ammodytes hexapterus.* Marine Biology 83: 193-204.

SAS Institute Inc., 1996. SAS/STAT User's Guide: Volume 1, Version 6, Fourth Edition. SAS Institute Inc., Cary, N.C., pp. 535 – 536.

Wilson, M. F., R. H. Armstrong, M. D. Robards, and J. F. Piatt. In prep. Sand lance as cornerstone prey for predator populations. Res. Pap. PNW-RP-XXX, Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest research Station, pp. 48.

Table 1. Results of cluster analysis of sediment types for 26 samples using four variables: gravel, sand, silt, and clay.

Cluster	1	2	3	4
Sediment	S	SM	G	M
N of Samples	4	11	7	3
min%S	0.8	0.38	0.05	0.13
max%S	0.92	0.62	0.31	0.39
min%M	0.06	0.01	0.05	0.49
max%M	0.2	0.47	0.29	0.55
Description	Sand >80%	Sandy Mud	Gravel >50%	Mud (Silt/Clay) >50%

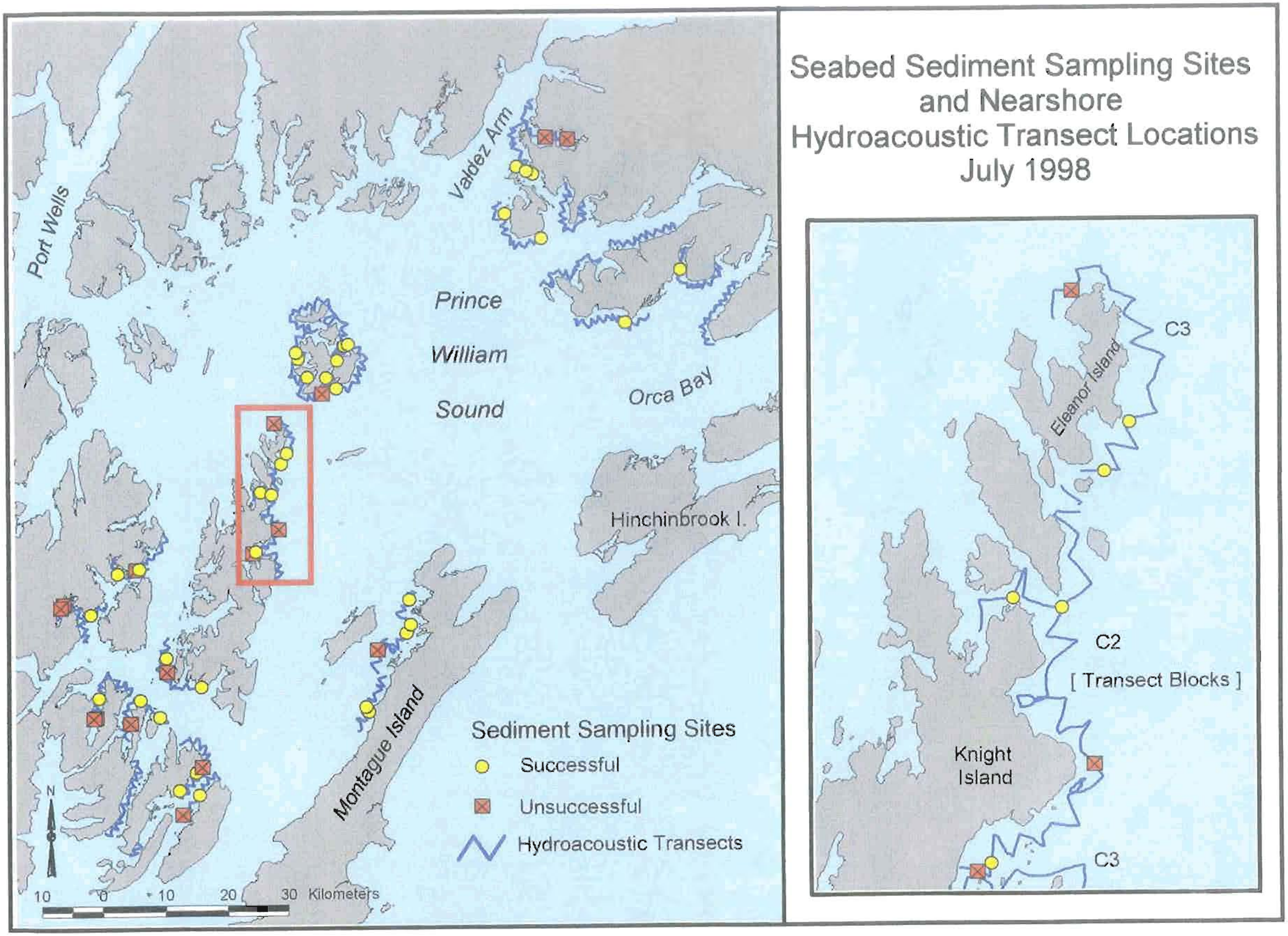
Figures

FIGURE 1. Location of nearshore hydroacoustic transects during summer 1997 and location of seabed sediment sampling sites during summer 1998.

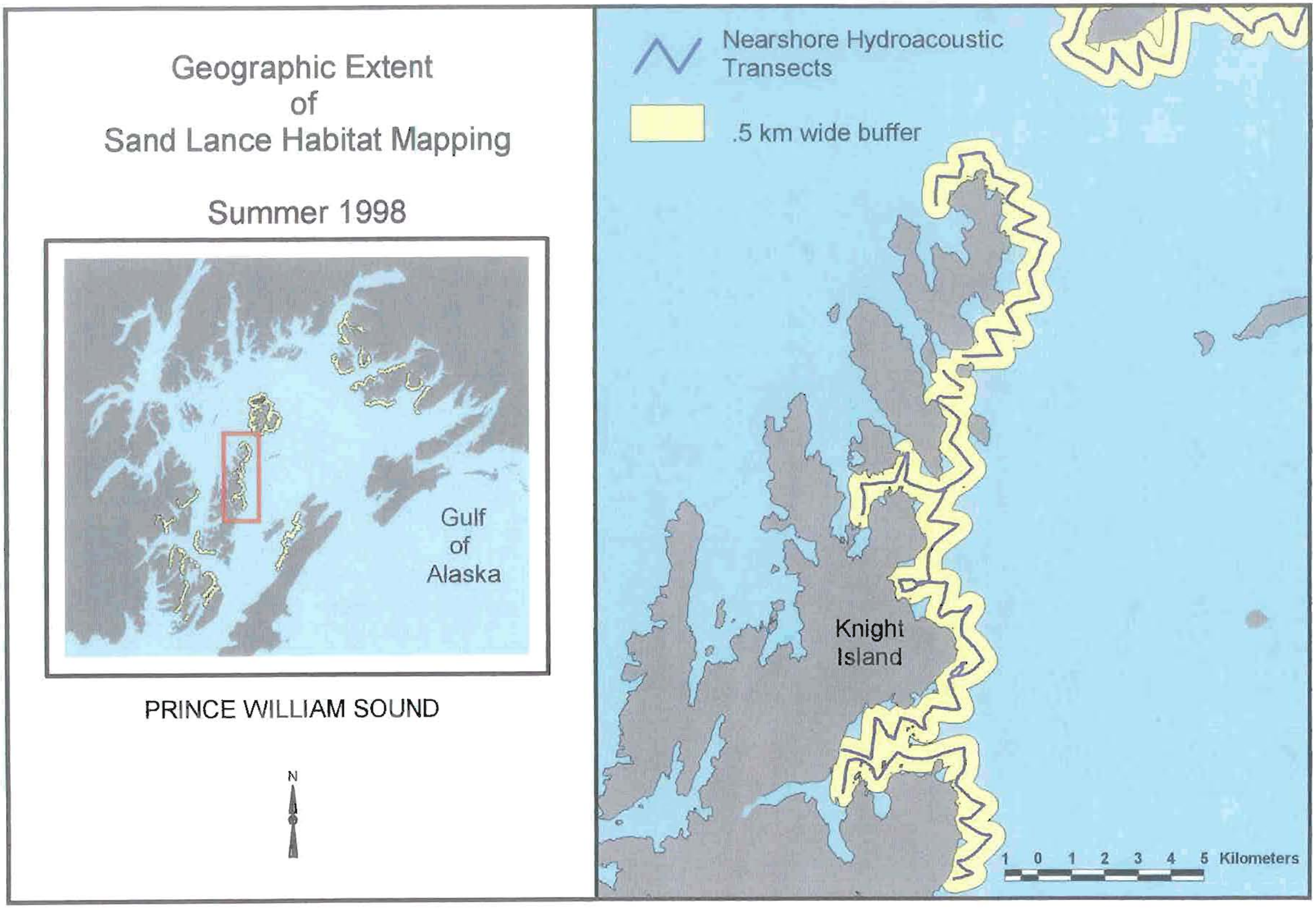
FIGURE 2. Locations where sand lance were observed during summer 1997.

FIGURE 3. Particle size analysis results for 26 sediment samples.

FIGURE 4. The geographic extent of sand lance habitat mapping. To determine this extent we generated a 1 km wide buffer around nearshore transects. Kriging analysis will be performed only within buffered areas.

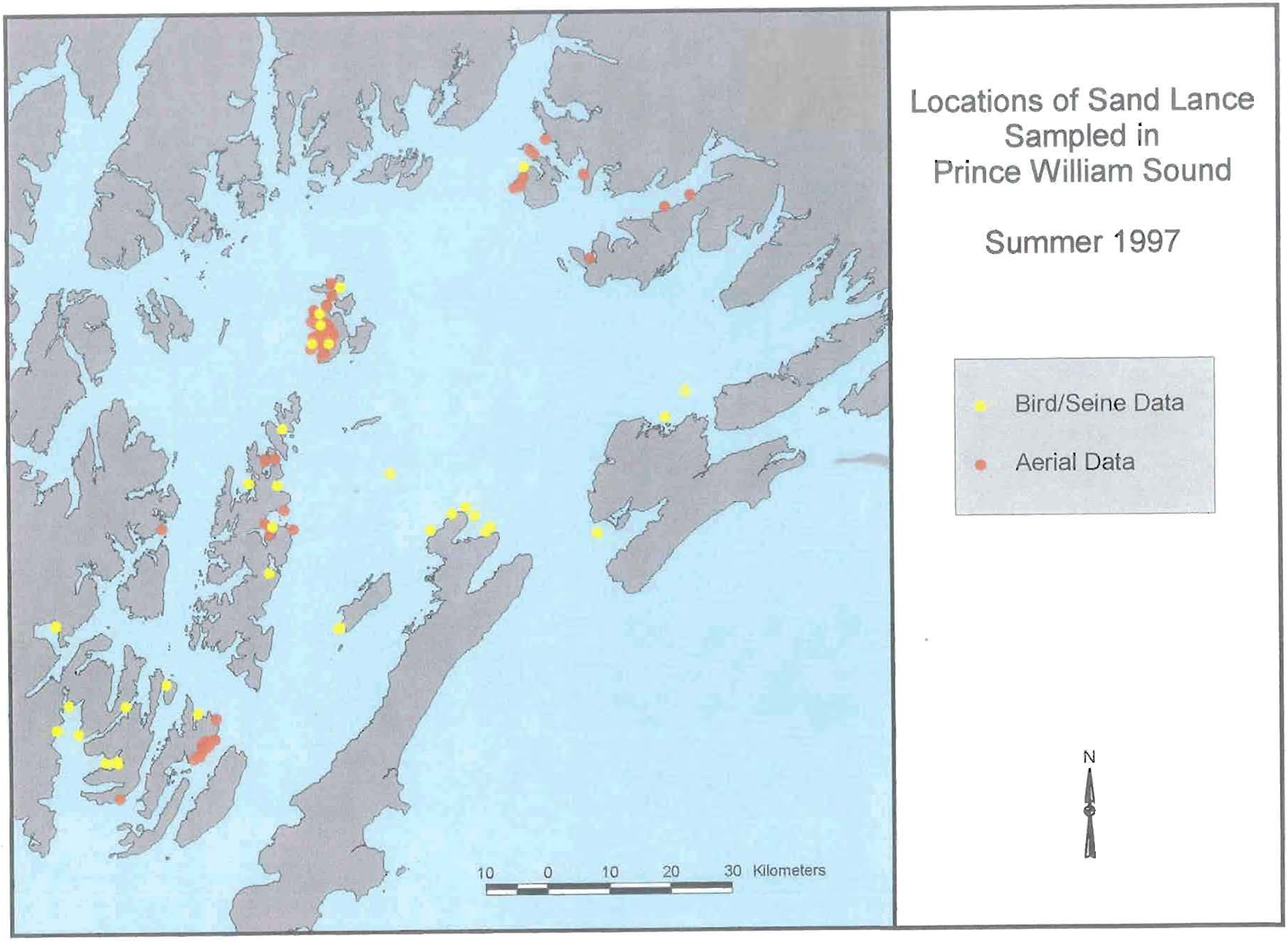


Seabed Sediment Sampling Sites and Nearshore Hydroacoustic Transect Locations July 1998



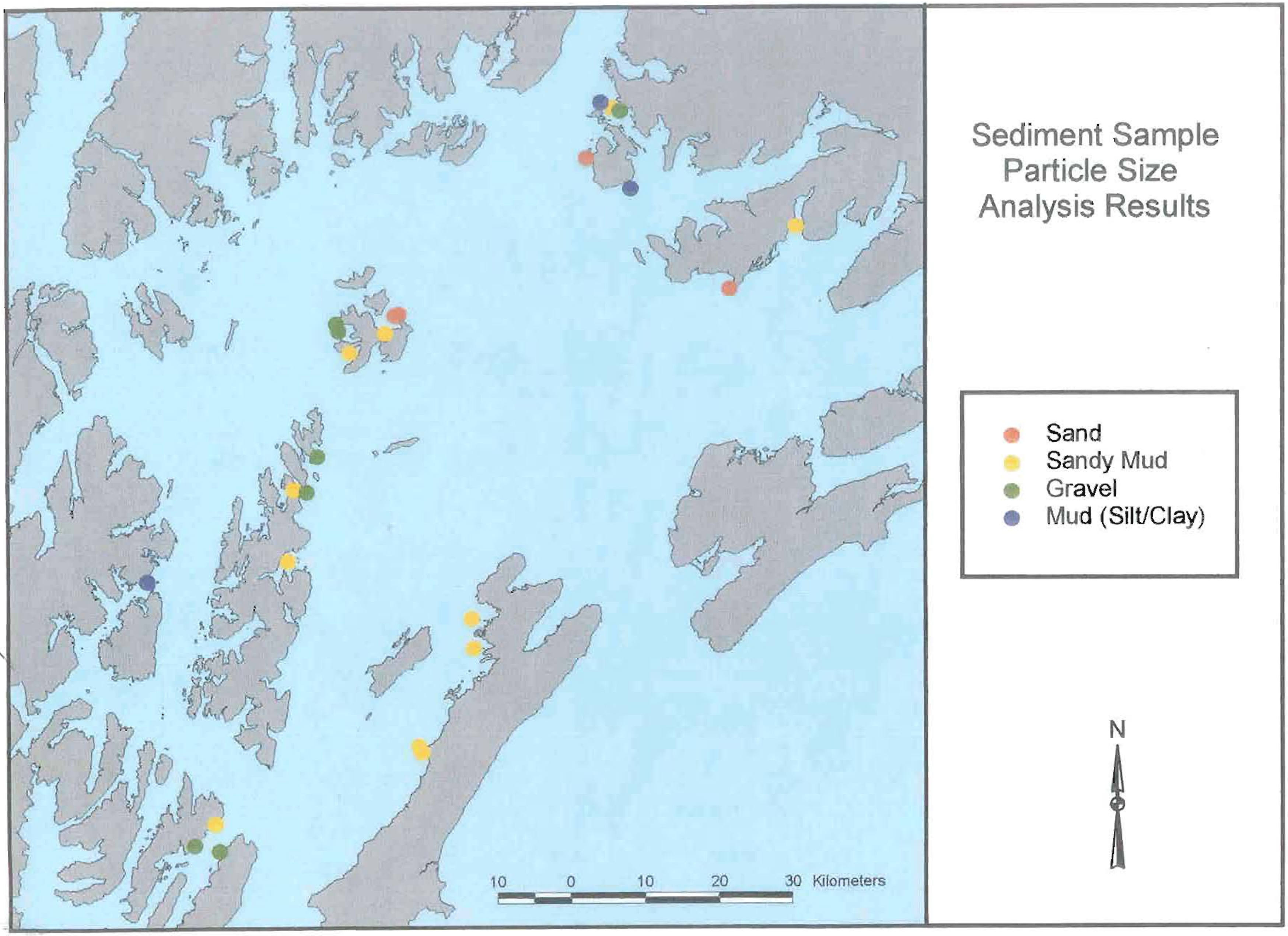
Geographic Extent of Sand Lance Habitat Mapping

Summer 1998



Locations of Sand Lance Sampled in Prince William Sound

Summer 1997


Sediment Sample
Particle Size
Analysis Results
● Sand
● Sandy Mud
● Gravel
● Mud (Silt/Clay)
N
10
0
10
20
30 Kilometers

E Kittiwake Studies

Exxon Valdez Oil Spill
Restoration Project Annual Report

KITTIWAKES AS INDICATORS OF FORAGE FISH AVAILABILITY

Restoration Project 98163E
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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March 1999

Study History: Field work for project 163E began during the summer of 1995 and consisted of detailed studies of the reproductive biology and foraging ecology of Black-Legged Kittiwakes (*Rissa tridactyla*) in Prince William Sound (PWS), Alaska. In 1995, studies were conducted at one colony in northeastern (Shoup Bay) and two colonies (Eleanor Island and Seal Island) in central PWS. Research at Shoup Bay was conducted in conjunction with ongoing studies funded by the U.S. Fish and Wildlife Service (USFWS). Since 1996, we have expanded the study to include North Icy Bay rather than Seal Island, thereby having sites representing northeastern (Shoup Bay), central (Eleanor Island), and southwestern (North Icy Bay) PWS. Additionally, we can make comparisons with long-term demographic (Shoup Bay) and population studies (all of PWS) conducted by the USFWS. This allows us to more accurately address relationships of variation in prey and decadal trends in populations. In 1998, we conducted work at the same three sites as in 1996 and 1997.

Abstract and Summary:

Progress of Manuscript Preparation and Analyses

Within the past year, we revised and submitted two manuscripts that were presented in draft form in last year's annual report (FY97). The first paper (Suryan and Irons, in review) involved a population analysis of Black-legged Kittiwakes in PWS using data from 1972 to 1997. We discussed temporal and regional differences in population dynamics of kittiwakes in PWS and concluded populations were regulated by both prey availability and predation, depending on colony location and size. We also noted that breeding success and population trends of colonies in southern PWS were more similar to colonies in the Gulf of Alaska (GOA) then colonies in northern PWS. Our results were discussed in regards to current theories concerning the regulation of seabird populations. This paper was submitted to the Auk in November 1998.

The second manuscript (Suryan et al., in review) concerned the diets and foraging effort of Black-legged Kittiwakes from the Shoup Bay and Eleanor Island colonies in years of varying prey abundance (data from 1989 to 1997). Years of low prey abundance were associated with declines primarily in the availability of age-one Pacific herring (*Clupea pallasi*). Years of low prey abundance resulted in increased foraging effort (trip duration and distance) of adult kittiwakes (supporting Cairns' 1987 hypothesis) and prey switching. The ability to prey switch, however, was limited for kittiwakes at Shoup Bay (northern PWS), where few alternatives to reduced herring abundance existed in close proximity to the colony. In contrast, kittiwakes at Eleanor Island (central PWS) were able to take advantage of Pacific sand lance (*Ammodytes hexapterus*) in relatively close proximity to the colony and capelin (*Mallotus villosus*) schools associated with GOA waters.

Four manuscripts that are currently in progress are attached to this annual report. These manuscripts are in various stages of completion, nonetheless, they provide good summaries of our recent efforts. The first paper (Kaufman *et al.*) addresses the response of adult kittiwakes to within-season changes in prey availability. Using data collection computers, we were able to determine daily foraging trip durations of radio-tagged birds. This allowed us to quantify daily changes in foraging effort of kittiwakes in relation to increased energy requirements of nestlings and changes in the availability and species composition (detected in nestling diets) of their prey. In the latter three papers we address methods of data analysis and collection. One of these papers (Suryan *et al.*) involves an evaluation of methods used in determining nestling growth rates. Several methods for determining nestling growth have been used in past years by APEX and other investigators and results of this paper will determine which method is best to use in various situations (particularly valuable for APEX synthesis papers). A second "method" paper (Benson *et al.*) addresses the application of multivariate analyses for comparing nestling development when repeated measures of individual nestlings are not feasible (e.g. birds are intolerant of human disturbance or nestlings are difficult to access). These multivariate analyses will be particularly valuable for species such as Common Murres (*Uria aalge*) and Tufted Puffins (*Fratercula cirrhata*). In a third paper (Benson and Suryan, in review) we present a technique that was developed for capturing adult kittiwakes. This capture design has proven invaluable in recapturing kittiwakes for doubly-labeled water experiments, attaching radio transmitters, and determining body condition.

Preliminary Results of the 1998 Field Season

The breeding chronology of kittiwakes throughout PWS can be synchronous or asynchronous among regions, depending on environmental conditions. Timing of nesting at individual colonies relies, in-part, on over-wintering conditions for adults and local conditions during the month(s) prior to egg laying. With the winter of 1997-98 being one of the strongest El Ninos recorded in the North Pacific Ocean, it was possible that the 1998 breeding season for seabirds in the GOA would be affected. The strongest indication of possible El Nino effects in PWS was late hatch dates and reduced clutch sizes at Eleanor Island and N. Icy Bay colonies (Fig. 1). Our observations of delayed breeding in central and southern PWS were consistent with reports from colonies in Lower Cook Inlet (APEX component M). This was not the case, however, for kittiwakes at Shoup Bay in northwestern PWS. Median hatch date and clutch size was consistent with previous years, with no initial indication of delayed or disrupted breeding (Fig. 1). It is plausible that conditions in the Gulf of Alaska affected initial stages of breeding, but local conditions in northern PWS buffered kittiwakes from this disruption.

These conditions and trends, however, did not persist throughout the breeding season. In fact, the regional trends described for early breeding season (May and June) reversed during the chick-rearing period (July to early August). At Shoup Bay foraging conditions became poor during chick-rearing, resulting in increased foraging trip duration, increased brood reduction, decreased nestling growth, and decreased fledgling mass compared to years of moderate to high reproductive success (Fig. 2). In contrast, foraging conditions during the chick-rearing period at Eleanor Island and N. Icy Bay were equal to or above average compared to Shoup Bay in 1998 and other years at these two colonies (Fig. 2). This regional discordance between reproductive success within PWS is likely explained by mechanisms described above (Suryan et al., in review). The abundance of age class 0 and 1 herring in northeastern PWS appeared to be low in July and August, resulting in reduced reproductive success of kittiwakes at Shoup Bay (where limited prey alternatives to herring existed in close proximity to the colony). Whereas prey availability appeared greater in central and southwestern PWS where kittiwakes at Eleanor Island and N. Icy Bay obtained herring (N. Icy Bay only), sand lance and capelin in relatively close proximity to the colonies and Gulf of Alaska waters (Fig. 3).

We are approaching a point of effectively describing causes and mechanisms for observed variation in prey abundance, breeding success, and population dynamics of kittiwakes in PWS. These relationships can then be incorporated into a long-term monitoring program and to model the effect of environmental perturbations on kittiwake populations in PWS; with applications throughout the range of this species and to seabird ecology and predator-prey relationships in general.

Key Words: Black-legged Kittiwake, Rissa tridactyla, foraging effort, Pacific herring, Pacific sand lance, capelin, prey abundance, reproductive success, regional concordance, Prince William Sound, Alaska.

Project Data: (will be addressed in the final report)

Citation: Irons, D. B., R. M. Suryan, J. Benson, and M. Kaufman. 1999. Kittiwakes as indicators of forage fish availability. *Exxon Valdez* Oil Spill Restoration Project Annual Report, (Restoration Project 98163E), U.S. Fish and Wildlife Service, Anchorage, Alaska.

In addition to the summary of 1998 data presented, this report is comprised of four draft manuscripts.

Kaufman, M., R.M. Suryan, D.B. Irons and J. Benson. Detecting intra- and inter-annual variation in prey availability using daily foraging trip durations.

Suryan, R.M., D.D. Roby, D.B. Irons and J.F. Piatt. An evaluation of methods for determining growth rates of nestling seabirds.

Benson, J., R.M. Suryan and J.F. Piatt. A multivariate approach to assessing nestling growth from one-time measurements. Will be submitted to Condor.

Benson, J. and R.M. Suryan. In review. A leg-noose for capturing adult kittiwakes on the nest site. J. Field Ornithology.

Literature Cited

Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5:261-267.

Suryan, R. M. and D. B. Irons. In review. Black-legged kittiwakes in Prince William Sound, Alaska: Population dynamics in a heterogeneous environment. Auk.

Suryan, R. M., D. B. Irons, and J. Benson. In review. Interannual variation in diet and foraging effort of kittiwakes in relation to prey abundance. Ibis

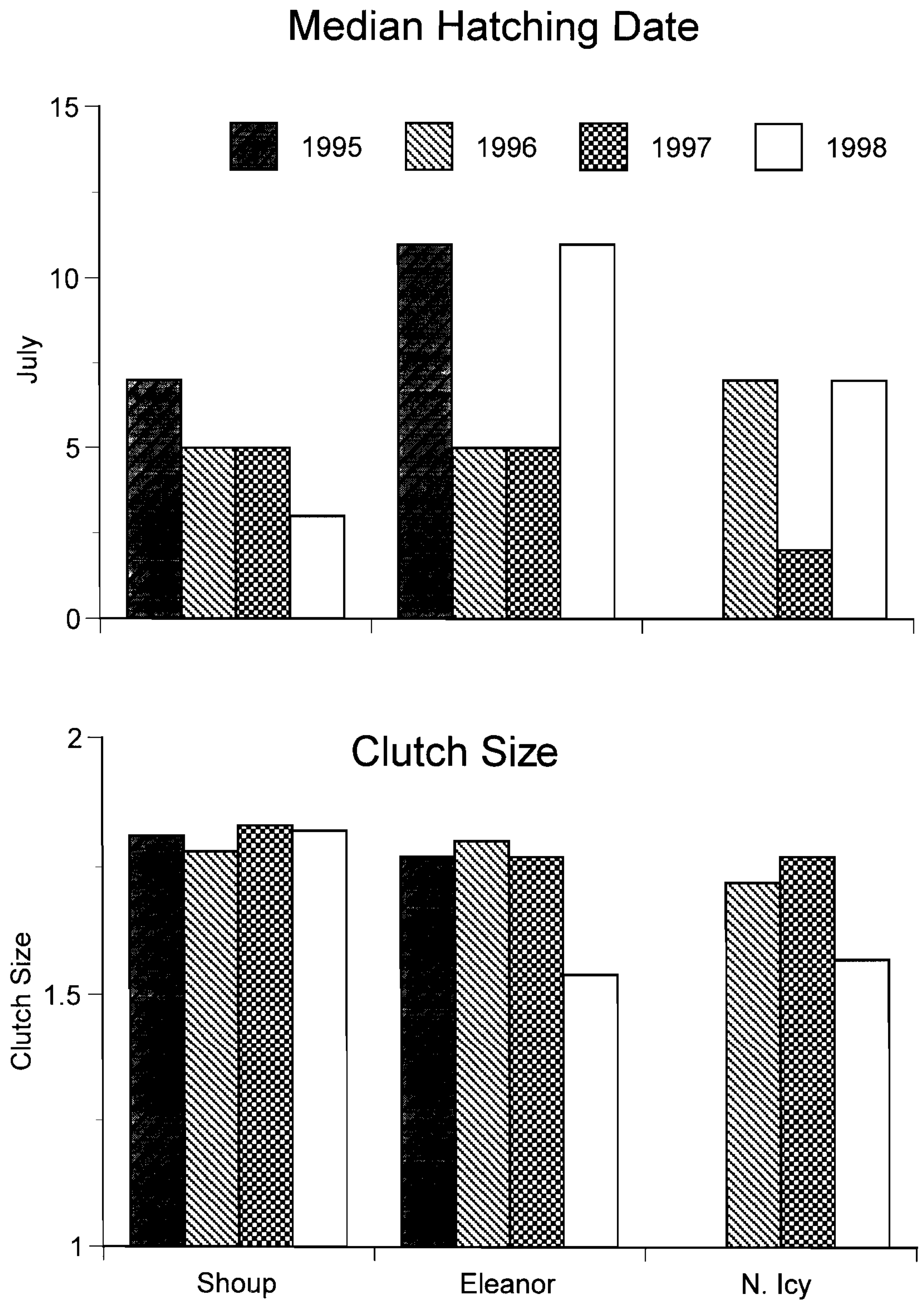

Figure 1. Median hatching date and clutch size of Black-legged Kittiwakes nesting in Prince William Sound, Alaska 1995-1998

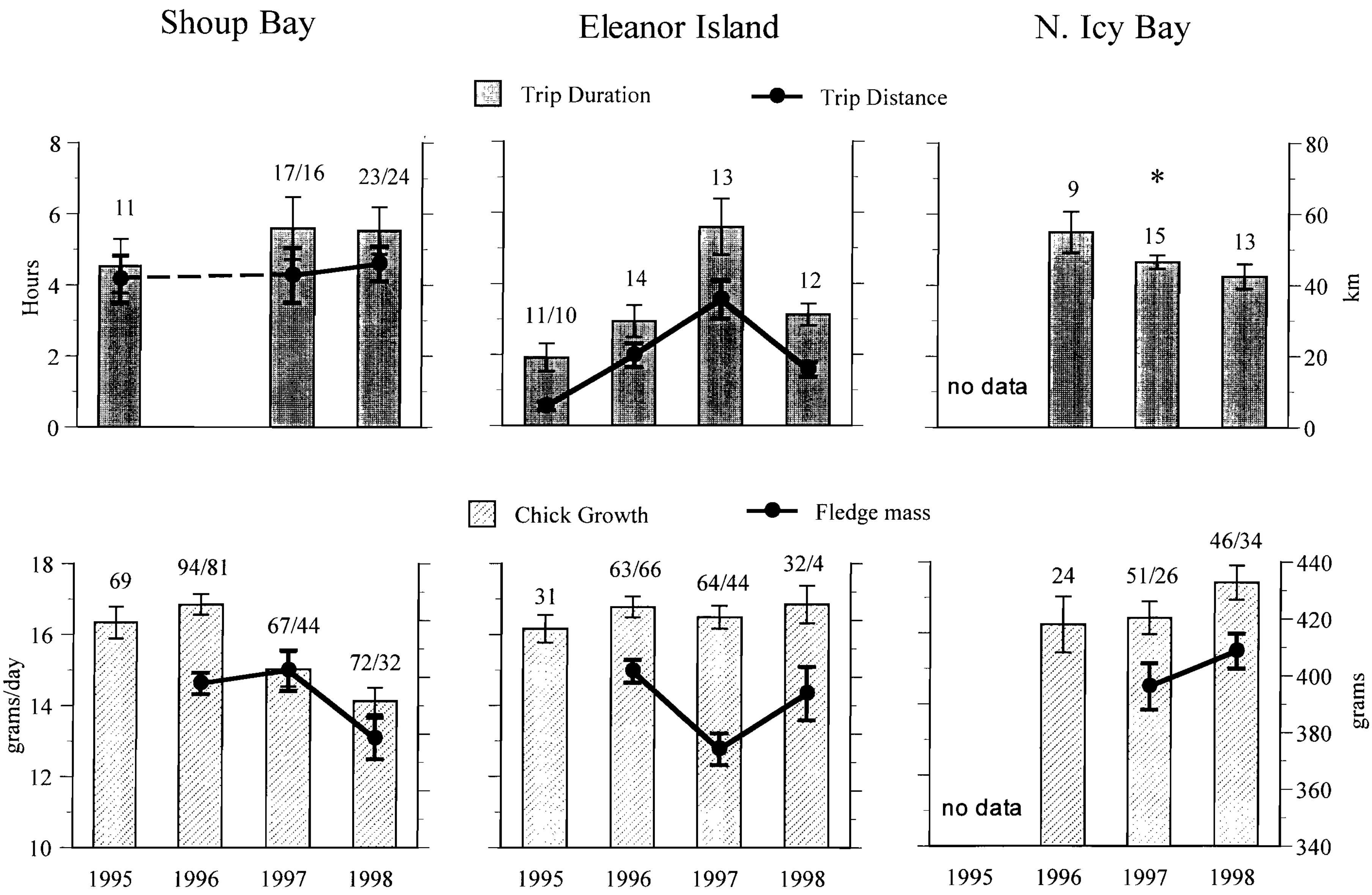

Figure 2. Foraging effort of adult kittiwakes (trip duration and distance) and nestling development (growth rate and near-fledging mass) for birds nesting at the Shoup bay, Eleanor Island, and N. Iorth Icy Bay colonies, Prince William Sound 1995-1998. Note (*) that trip duration for North Icy bay is reported from data collection computers which are typically greater on average than those determined by radio tracking (as for Shoup Bay and Eleanor Island).

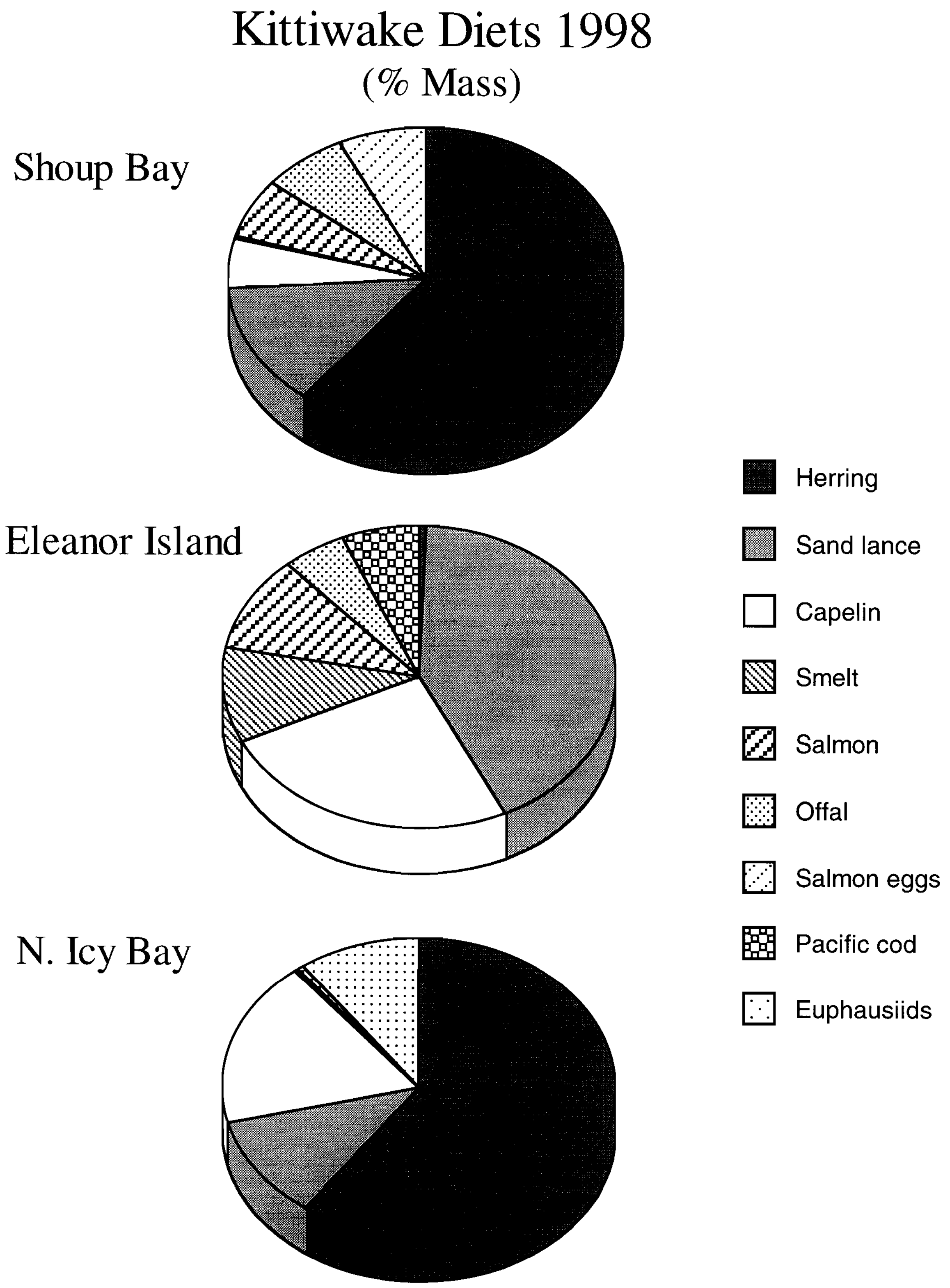

Figure 3. Diets (% mass) of Black-legged Kittiwakes at our three study colonies in Prince William Sound, Alaska, in 1998

DETECTING INTRA- AND INTER-ANNUAL VARIATION IN PREY AVAILABILITY USING DAILY FORAGING TRIP DURATIONS.

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22 March 1999

Running head: Kittiwake Foraging Trip Duration and Prey Availability

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INTRODUCTION AND OBJECTIVES

The daily energy expenditure (kj/day) of Black-legged Kittiwake nestlings steadily increases until 23 days of age (Gabrielsen et al. 1992). Response in foraging activities of adult kittiwakes to increasing energetic requirements of their nestlings should differ in three predictable ways depending on prey availability. A) If prey are easily obtained and the distribution is unchanged throughout nestling development, then negligible effort is required to obtain additional prey and foraging trip duration should remain relatively constant throughout the chick rearing period (Fig. 1, A). B) If prey are difficult to obtain and availability does not change, then we would predict a steady increase in foraging trip duration and an asymptote when nestlings reach 23 days old (Fig. 1, B). The slope of the curve should reflect the relative difficulty of obtaining prey. C) If there is within season variation in prey availability, then we should observe an unexpected change in foraging trip duration that is inconsistent with response A or B (Fig. 1, C).

Analysis of mean daily trip durations provided examples of the three responses described above. Abrupt or otherwise unexpected changes in trip duration (response C) typically corresponded with changes in species and/or quantities of prey consumed. Preliminary results indicated that comparing daily foraging trip durations to our three hypothetical responses may provide valuable information about intra- and inter-annual variation in prey availability.

METHODS

Three kittiwake colonies in Prince William Sound (PWS) were selected for study. The Shoup Bay colony is the largest (ca. 8000 breeding pairs) in PWS and is located in a fjord in the northeastern region. The Eleanor Island colony is much smaller (ca. 300 breeding pairs) and located among the islands of central PWS. The north Icy Bay colony (ca. 2400 breeding pairs) is located in the southwestern region of PWS, closer to the Gulf of Alaska.

Adult Black-legged Kittiwakes were captured at their nests, usually during incubation, using a noose-pole (Hogan 1985) or leg-noose (Benson and Suryan unpubl. ms.). Radio transmitters (164 - 167 MHZ, 9 g Advanced Telemetry Systems, Inc (ATS), Isanti, Minnesota, USA) were attached to 15 - 40 birds at each colony per year. Transmitters were secured ventrally to the base of the tail feathers (Anderson and Ricklefs 1987; Irons 1992) with two nylon cable ties and Loctite 494 instant adhesive (Loctite Corporation, Rocky Hill, Connecticut, USA). Nest contents of radio-tagged birds were observed every three days.

An automated data logging system recorded the daily colony attendance of radio-tagged kittiwakes through the breeding season. The receiving stations consisted of an ATS data collection computer (DCC II) linked to an ATS R4000 receiver with a limited-range H or dipole antenna. The system drew power from a 12 v deep cycle marine battery charged by a 3.3 amp photovoltaic panel. For each transmittered bird, the DCC was programmed to listen for an optimal frequency, and two “bracket” frequencies 2 kHz to either side: this prevented reception problems caused by possible frequency drift. A reference transmitter was deployed to later assess the continuity of the record and “dummy” frequencies were programmed in to monitor noise levels. The DCC scanned through 15 to 40 birds three times every 17 to 42 minutes (20 seconds each frequency).

Data were downloaded to laptop computer in the field and processed using Paradox (Borland International, Inc., Scotts Valley, CA USA) and Quattro Pro (Corel Corp., Ottawa, Ontario, Canada) software. Absences over 45 minutes were counted as foraging trips. For this study we included only foraging trips of adults provisioning nestlings. Our sampling unit was individual birds; therefore, an average trip duration was calculated for each adult kittiwake initiating foraging trips on a particular day. Daily mean trip durations were then determined by calculating a mean among birds for each day of the chick rearing period. Only daily means derived from the records of five or more kittiwakes were used.

Diet samples (regurgitations) were collected opportunistically from nestlings throughout the colony, not specifically from the young of radio-tagged birds. Samples were collected while handling chicks and frozen for later analysis. Typically, no more than one sample was collected per nestling. Prey were identified using otoliths, morphological characteristics, scales, and bones. To relate foraging trip duration and diet we were interested in the week to week changes in occurrence of various prey types, therefore diet data are presented as percent occurrence.

DATA ANALYSIS AND PRESENTATION

Figures 2 through 4 are records of mean daily foraging trip durations of adult kittiwakes from three study colonies in PWS during 1995 to 1997. Each figure contains trip duration records that represent a particular response described above. The assignment of a trip duration record to a response category was based on simple visual (qualitative) comparisons. We are working with APEX component O to develop methods for statistically quantifying which hypothetical response best fits a particular record.

RESULTS

Mean daily trip duration and chick diet data were used to illustrate three ways we predicted black-legged kittiwakes would respond to variation in the distribution and availability of prey.

Response A: Eleanor Island trip duration records from 1995 (Fig. 2a) and 1997 (Fig. 2b) are examples of the response to a prey supply that is abundant and easily obtained and whose distribution remains relatively unchanged throughout chick rearing.

- The flat to very low slopes of the mean daily trip duration lines indicate food was readily available and that, through time, minimal additional foraging effort was required to meet the increasing energy demands of growing chicks.

- The percent occurrence of different prey species remained fairly constant indicating prey species composition remained steady through the period.

- A comparison of Y-intercepts of the two figures yields an interesting insight. In 1995, short durations indicated food was readily available near the colony. In 1997greater mean trip durations (double those of 1995) indicated the foraging areas were farther away. Diets and radio tracking support this (Suryan et al, in review).

Response B: The records of Eleanor Island 1996 (Fig. 3a) and North Icy Bay 1996 (Fig. 3b) illustrate a kittiwake foraging response to a prey supply that was stable in its availability (as response A) but was relatively <u>more difficult to obtain</u>. In this case, additional energy required by growing chicks required detectable increases in effort by the adult.

- The steeper slopes of figures 3a and 3b show that through time, foraging adult kittiwakes were forced to stay out progressively longer to collect the additional prey required by their young.

- As in figures 2a and 2b, there were no consistent changes in nestling diets in 1996 at Eleanor Island (Fig. 3a). The prey availability and species composition remained relatively constant.

- Trip durations at N. Icy Bay 1996 (Fig. 3b) were longer, in the first two weeks, than those of Eleanor Island 1996 (Fig. 3a), indicating prey was more difficult to obtain for kittiwakes at N. Icy Bay.

Response C: Within season changes in forage fish availability are predicted to cause unexpected or sudden shifts in mean daily foraging trip duration inconsistent with responses A and B. Plots of mean daily foraging trip duration from Shoup Bay contain slope breaks which often correspond to significant changes in the species composition of kittiwake diets.

- Shoup Bay 1995: A sharp rise in trip duration coincides with a reversal in the relative abundance of sandlance and herring in the diets (Fig. 4a). The sandlance were relatively close and easy to obtain while the herring may have been further away or more difficult to obtain.

- Shoup Bay 1997: Figure 4b is an example of a sudden change in mean daily trip duration that is directly linked to a change in both availability and distribution of different prey species. Average trip durations started high in July 1997 and climbed to higher values, indicating prey was difficult to obtain (Fig. 4b). A sudden reduction in trip duration on 23 July corresponded to a reversal in the proportions of herring and sandlance in the nestling diets.

CONCLUSION

A comprehensive record of colony attendance and trip duration is a useful component of a long term monitoring program, especially where diet, nestling growth and breeding success are also being tracked.

- In conjunction with chick diet data, trip duration records let us a track changes in the availability of forage species at a colony within the same season. This can help explain changes in reproductive parameters. This method provides a more complete record of changes in trip duration than relatively infrequent direct or video observation sampling techniques.

- The plots also clearly demonstrate there are marked differences in trip duration within and between years at the same colony. These differences reflect the predator's response to weekly and year-to-year fluctuations in the abundance and distribution of prey. Multi-year records are crucial to obtaining more than a "snapshot" view of these long lived seabirds' interaction with their complex and changeable environment.

Is low variance in trip durations a sign of a predictabile food supply?

- When radio-tagged BLKI make trips of similar average duration each day, variability (SE) is small (e.g. Figs. 2a, 3b). We predict this happens when food is abundant and consistently found in one area or at a given distance from the colony. Large variability (e.g. Figs. 3a, 4b) indicates birds are traveling a variety of distances, employing a range of individual foraging strategies to search for a more patchy, unpredictable distribution of prey. Assessment of relative variability among years may provide another indication of relative "difficulty" in obtaining prey and the predictability of food resources. Due to intra-specific competition, within colony variation in foraging strategies may be accentuated at large colonies (e.g. Shoup Bay) when food becomes less available.

LITERATURE CITED

Gabrielsen, G. W., M. Klassen, and F. Mehlum. 1992. Energetics of black-legged kittiwake *Rissa tridactyla* chicks. Ardea 80: 29-40.

Suryan, R.M., D.B. Irons, and J. Benson. In review. Interannual variation in diet and foraging effort of kittiwakes in relation to prey abundance. Ibis.

List of Figures

Fig. 1. Three hypothetical responses in foraging effort (trip duration) of adult kittiwakes to increasing energy requirement of nestlings - which peaks at 23 days old.

Fig. 2. a) Plot of mean daily trip duration (hours ± SE) from adult kittiwakes (n=5-7 birds/day) at the Eleanor Island colony in 1995. Bars indicate percent occurrence of prey species for three weeks beginning 22 July (n=3-13 samples/week).

b) Plot of mean daily trip duration (hours ± SE) from adult kittiwakes (n=8-17 birds/day) at the Eleanor Island colony in 1997. Bars indicate percent occurrence of prey species for five weeks beginning 1 July (n=9-29 samples/week).

Figures 2a, 2b are examples of predicted kittiwake foraging response (A): prey availability remains constant, prey is easily obtained, and negligible effort is required to obtain sufficient additional prey.

Fig. 3. a) Plot of mean daily trip duration (hours ± SE) from adult kittiwakes (n=5-8 birds/day) at the North Icy Bay colony in 1996. Bars indicate percent occurrence of prey species for one week beginning 29 July (n=4 samples).

b) Plot of mean daily trip duration (hours ± SE) from adult kittiwakes (n=5-16 birds/day) at the Eleanor Island colony in 1996. Bars indicate percent occurrence of prey species for four weeks beginning 08 July (n=7-19 samples/week).

Figures 3a, 3b are examples of predicted kittiwake foraging response (B): prey availability is constant, but prey is difficult to obtain. Note the large variability in Fig. 3a in comparison to Fig. 2a (similar sample size). Increased variability may be a sign of a less predictable food supply.

Fig. 4. a) Plot of mean daily trip duration (hours ± SE) from adult kittiwakes (n=8-11 birds/day) at the Shoup Bay colony in 1995. Bars indicate percent occurrence of prey species for two weeks beginning 15 July (n=51-73 samples/week).

b) Plot of mean daily trip duration (hours ± SE) from adult kittiwakes (n=5-24 birds/day) at the Shoup Bay colony in 1997. Bars indicate percent occurrence of prey species for four weeks beginning 08 July (n=256 total samples).

Figures 4a, 4b are examples of the predicted kittiwake foraging response (C) to change(s) in the distribution and/or availability of prey. Sudden changes in mean trip duration were concurrent with changes in diet composition.

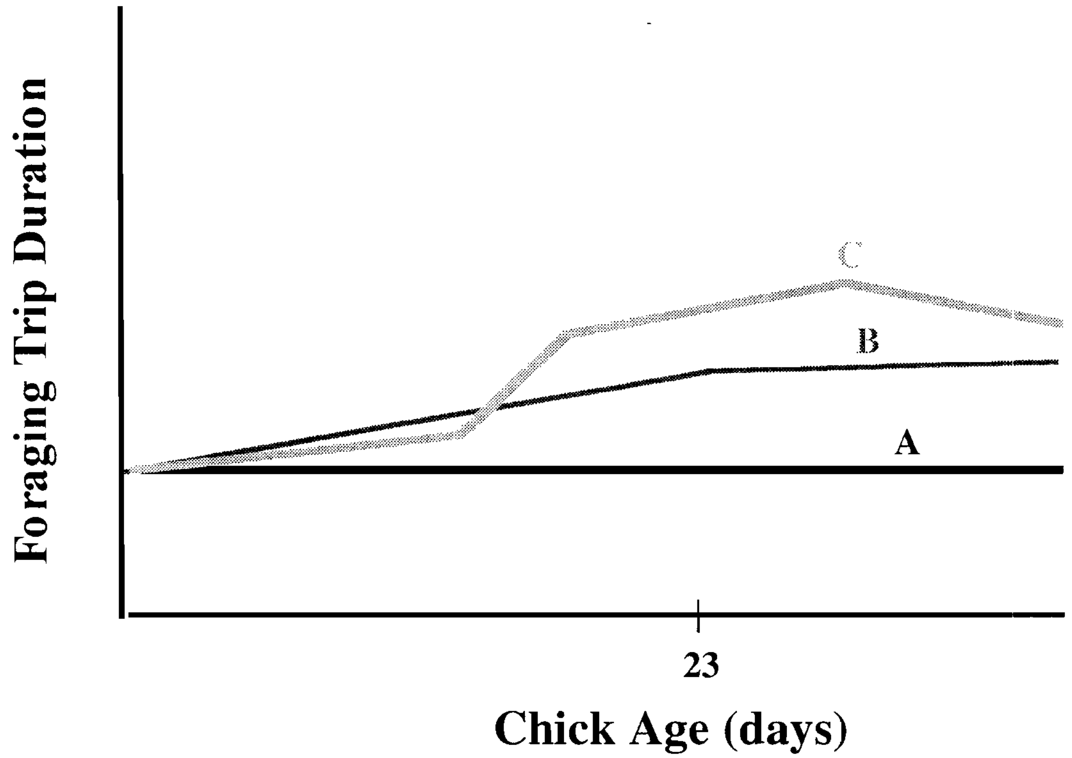


Figure 1. Hypothetical responses in foraging effort (trip duration) of adult kittiwakes to increasing energy requirements of nestlings - which peak at 23 days old.

A) Prey is easily obtained and negligible effort is required to obtain sufficient additional prey.

B) Prey is difficult to obtain and availability does not change.

C) Within season variation in prey availability causes changes in foraging effort that are inconsistent with A or B.

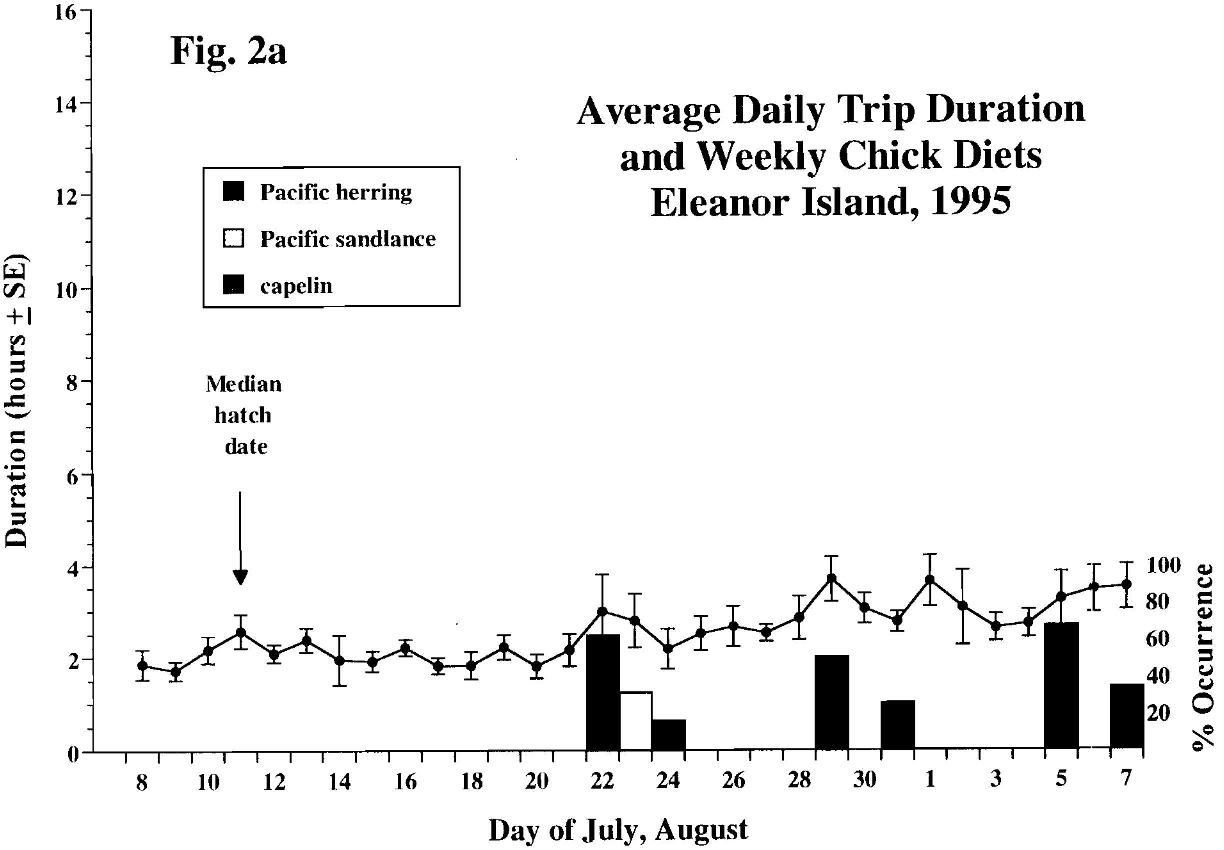


Fig. 2a

Average Daily Trip Duration and Weekly Chick Diets Eleanor Island, 1995

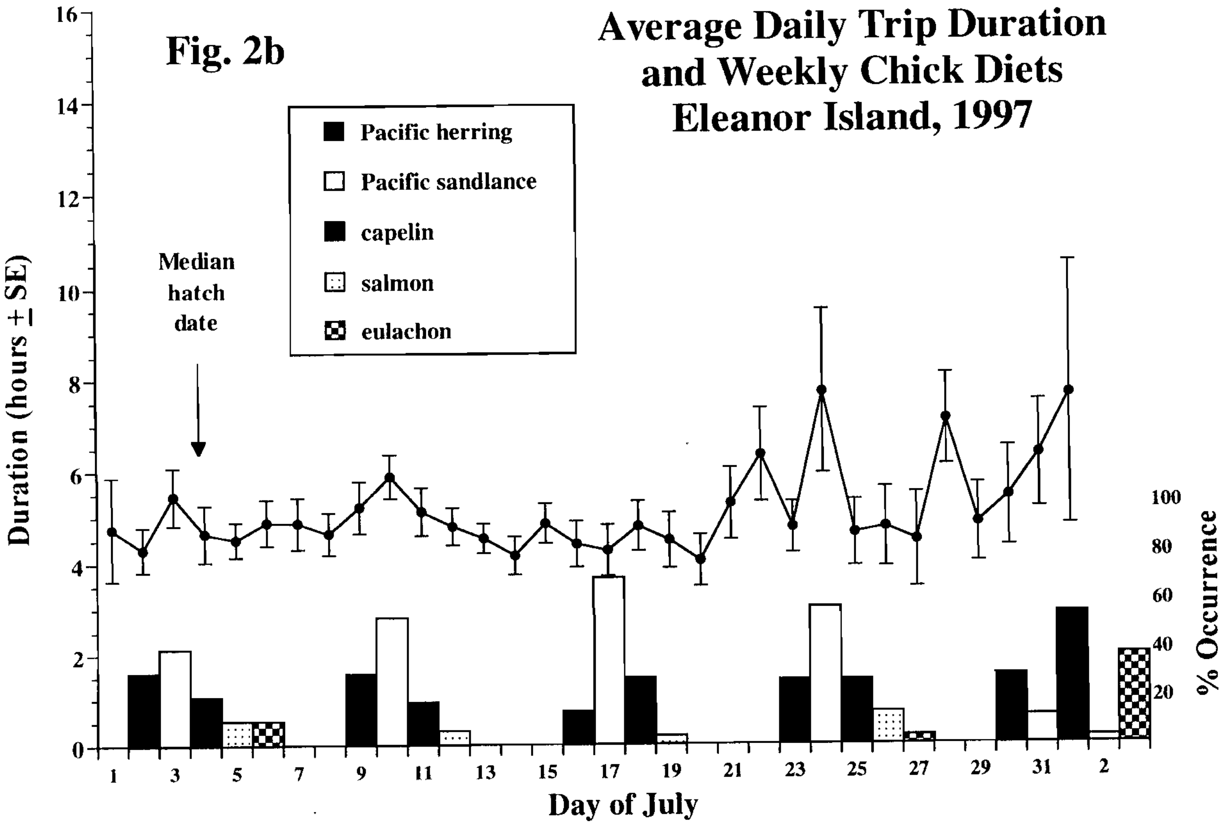
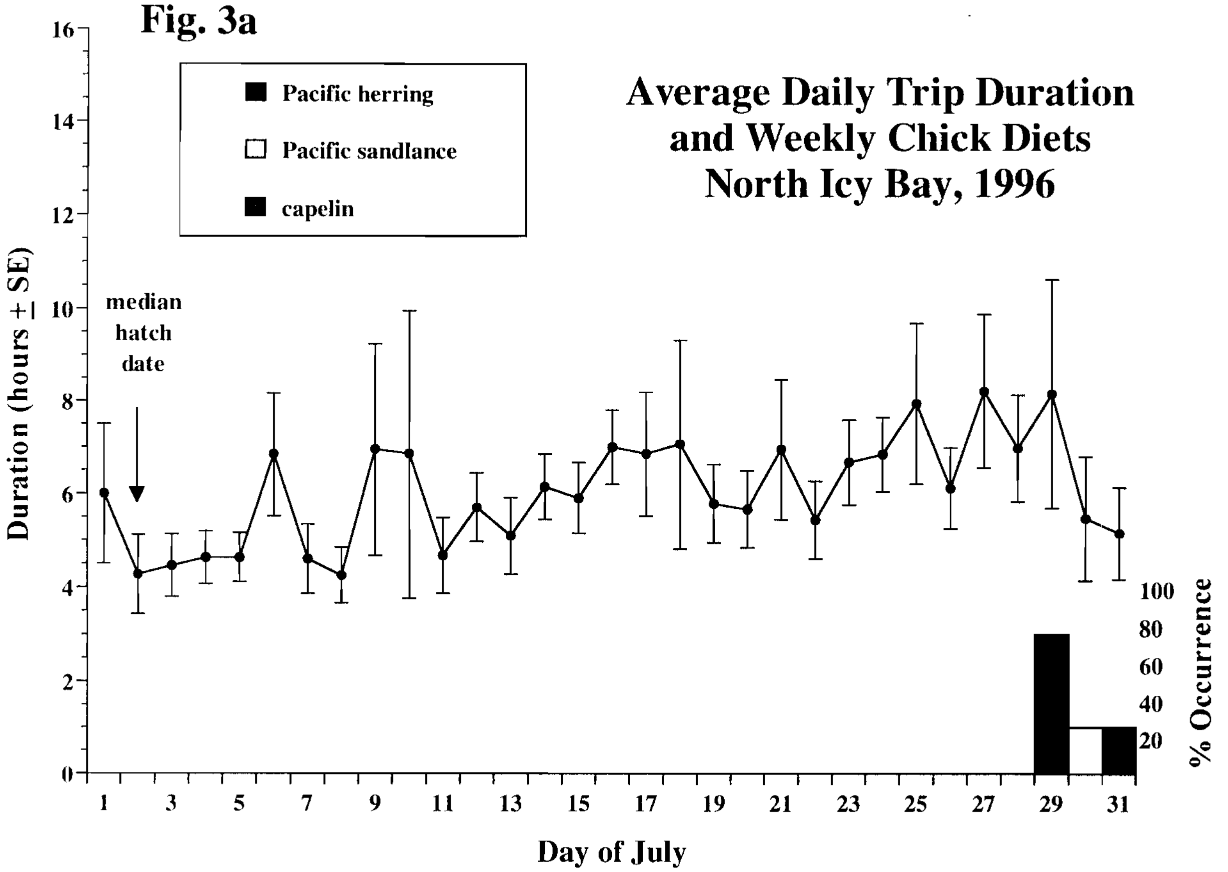


Fig. 2b

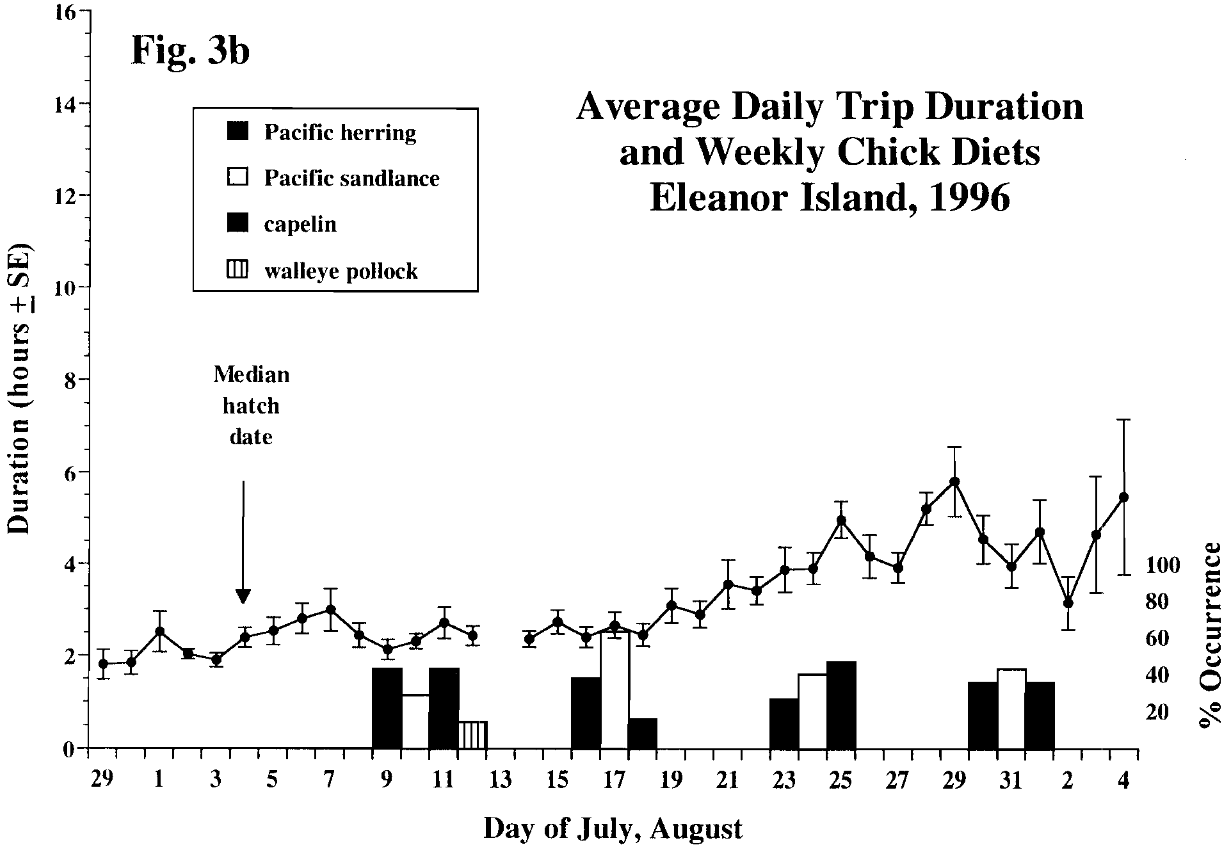
Average Daily Trip Duration and Weekly Chick Diets Eleanor Island, 1997

Fig. 3a



Average Daily Trip Duration and Weekly Chick Diets North Icy Bay, 1996

Fig. 3b



Average Daily Trip Duration and Weekly Chick Diets Eleanor Island, 1996

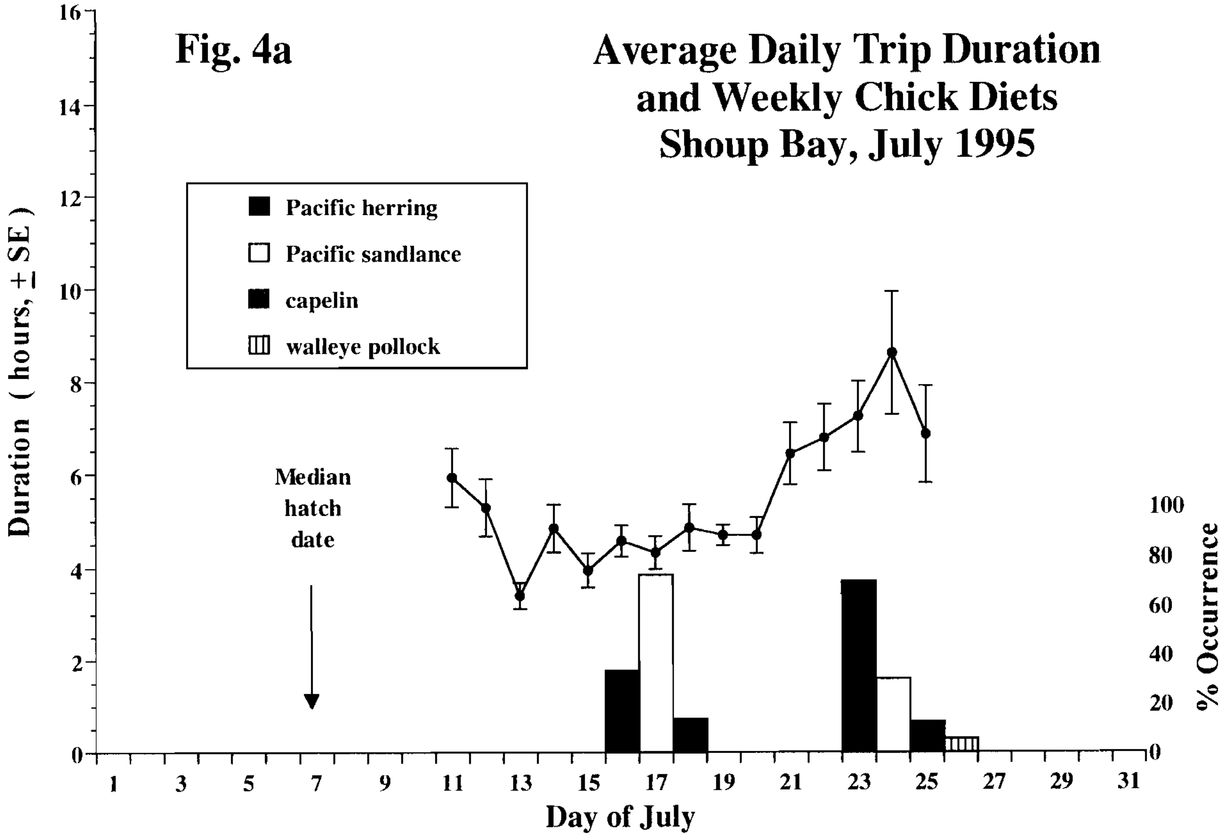


Fig. 4a

Average Daily Trip Duration and Weekly Chick Diets Shoup Bay, July 1995

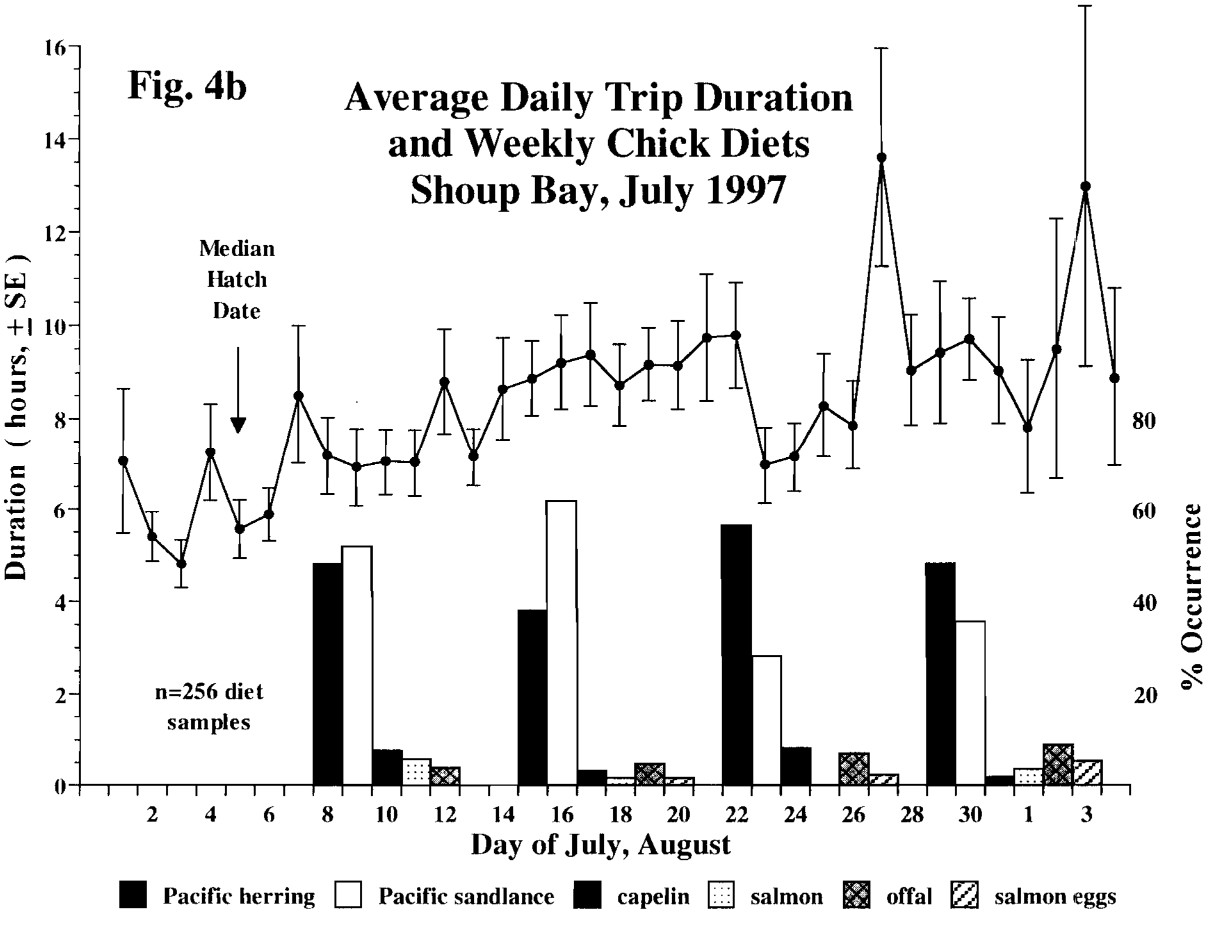


Fig. 4b

Average Daily Trip Duration and Weekly Chick Diets Shoup Bay, July 1997

AN EVALUATION OF METHODS FOR DETERMINING GROWTH RATES OF NESTLING SEABIRDS

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INTRODUCTION AND OBJECTIVES

The primary factor controlling the development of nestling seabirds is energy intake (KJ/day, which can be defined as meal quality (KJ/g)*meal size (g)*meal provisioning rate (#/day)). The ability for adult seabirds to meet the energetic demands of nestlings is primarily controlled by the availability and quality of their prey. The availability and quality of prey can be affected by naturally occurring processes or anthropogenic influences. Nestling growth rate, therefore, can be a sensitive indicator of natural factors influencing prey (Boersma and Parrish 1998) or serve as a biomarker of exposure to anthropogenic-originated contaminants (Fendley and Brisbin 1977); both are conditions that affect the integral health of the parent-offspring relationship. Nestling growth is also one measure of reproductive success that is, for the most part, independent of forces that confound the assessment of prey quality and availability (e.g. measures such as hatching success and fledging success can be strongly affected by predation, disturbance, or weather).

Comparisons of nestling growth within species have provided details of foraging conditions among geographic regions (Barrett and Runde 1980, Pettit et al. 1984) or among years at a given colony (Pettit et al. 1984). A persistent problem in the calculation of nestling growth rates, however, is the inconsistent use of methods among investigators. Some investigators have used non-linear models fitted to complete records of growth (from day 1 to near-fledging age; Ricklefs 1983, Pettit et al. 1984), while others have focused on certain portions of the development period (e.g. the near-linear phase; Coulson and Porter 1985, Coulson and Thomas 1985). Unfortunately, growth rate values calculated by these different methods are not directly comparable and, to the best of our knowledge, there has not been a rigorous comparison of accuracy and sensitivity of these methods at detecting differences in growth rates among years and among populations.

In this paper we selected measures of Black-legged Kittiwake (*Rissa tridactyla*) nestlings from several years and colonies that exhibited various patterns of growth (e.g. rapid growth but low fledging mass, slow growth but high fledging mass, etc.). We then compared the performance of three commonly used methods for determining the rate of mass increase (nonlinear, linear based on mass, and linear based on age) and one new method, an index of growth based on the relationship between transformed wing and mass values.

METHODS

The shape of the three commonly used nonlinear model (logistic, Gompertz, and Von Bertalanffy) is determined by three parameters; the asymptote (A), the growth rate constant (K), and the inflection point (I; Ricklefs 1983). Calculating the first derivative (i.e. slope of the tangent at the inflection point) of either curve provides the maximum instantaneous growth rate with units of g/day (e.g. AK/4 for the logistic model). For most seabird species, the logistic equation provides the best fit to nestling growth data.

When comparing the "linear" growth rate of nestlings, nestling mass is plotted against age for a given age or mass range, then regression analysis is used to calculate the slope or growth rate (g/day). Investigators have used varying criteria for defining the "linear" range of the growth curve. For kittiwake nestlings Coulson and Thomas used 100 to 300 g, while Coulson and Porter (1985) used 60 to 300 g to represent the near-linear phase of growth. It is reasonable to expect that defining the upper and lower bounds of the near-linear phase would vary depending the shape of the growth curve. Other investigators have used nestling age to define the bounds of the "linear" phase of growth. The upper and lower bounds are commonly set by plotting the mean mass versus nestling age and visually defining the limits of near-linear growth. Investigators have also used quantitative means for defining these age limits (Lance 199?). In our analyses of kittiwakes we used age ranges of 6 - 22 days and 5 - 25 days to represent the near-linear phase of nestling growth.

The third method we evaluated was the growth performance index (GPI). The GPI is a regression of the square root of mass vs. square root of the natural log of wing length. Slopes of this relationship can be compared among "populations" of interest, similar to slopes or growth rates determined using "linear" methods above. The benefits of this method are that all nestling measurements are used in the analysis (as with non-linear methods) and nestling age can be unknown.

We first tested results of the various methods by applying them to basic growth curves. We generated two logistic and two Gompertz growth curves that represented observed growth patterns of Black-legged Kittiwake (*Rissa tridactyla*) nestlings. The first logistic and Gompertz curves represented a normal growth pattern and possessed equal initial masses (at day zero) and asymptotic weights (Figure 1). The second logistic and Gompertz curves represented a reduced growth pattern (similar to that of undernourished young reported by Romano et al. (1998) while also having equal initial masses and asymptotic weights (Figure 1). Logistic and Gompertz curves were also generated for wing length measures corresponding to normal and low growth (Figure 2). These wing length values were used in calculating the GPI. Parameters of these generated curves are provided in Table 1. We then calculated the linear approximation of these curves using the methods described above.

To evaluate the sensitivity of detecting differences in growth with the various measures, we ran two comparisons using four sets of data collected at kittiwake colonies in PWS. The data sets represented several different growth patterns. The first comparison was between data representing a high growth rate with high fledging mass (from alpha nestlings) and low growth rate with low fledging mass (from beta nestlings; Figure 3). The second comparison included nestlings exhibiting a high rate of growth that could not be maintained, resulting in reduced fledging masses (from alpha and beta nestlings). These nestlings were compared to a group showing an opposite effect, a lower rate of growth that was maintained for a longer period resulting in a greater fledging mass (Figure 4).

PRELIMINARY RESULTS

Model Data

All methods for calculating growth rate (g/day) responded as expected when comparing the normal versus low growth patterns of the model curves; rates during normal growth were greater than those during low growth (Table 2). There were, however, differences in values among methods. For the logistic curve, rate determined by KA/4 produced the highest value followed by rate based on age; with rates based on age increasing as the age range of each method decreased (Table 2). The effect of age range on rate was due to narrowing age ranges representing steeper portions of the growth curve, thereby approaching the maximum instantaneous growth rate or AK/4 (for the logistic curve). Rate based on linear approximation delimited by mass was comparable to other methods for normal growth, but was biased low when applied to the curve of reduced growth. This bias resulted from the asymptotic mass of the curve representing poor growth being slightly above 300g, therefore, the 6 - 300 g range included ages of nestlings that were well beyond the "near-linear" phase of growth.

When applied to the Gompertz curves, the relative performance of the various methods were similar to that described for the logistic model. The GPI produced results that depicted conditions of fast and slow growth. A more thorough evaluation of the GPI was possible with the use of empirical data sets.

Comparisons using empirical data sets: high rate and high fledging mass versus low rate and low fledging mass.

For the non-linear method, the logistic curve best fit the data presented in Figure 3. Significant differences between the two data sets were detected using three of the methods; logistic (AK/4), linear by mass, and GPI (Table 3). The greatest difference between high and low growth and the most significant result occurred with the linear by mass method. However, the linear by mass method may have exaggerated the slow growth of the beta chicks, as described with the model data, resulting in a greater effect size and the greatest significant result. The linear by age method did not produce significant results using either age range.

Comparisons using empirical data sets: high rate and low fledging mass versus low rate and high fledging mass.

The logistic growth curve (Figure 4) was the only method that detected significantly different trends between these two sets of data (Table 4). For the logistic curve, these differences were evident in the maximum instantaneous growth rate (AK/4) and the fledging mass (asymptote). The linear by mass and linear by age (6 - 22 days) methods produced means supporting the observed trends of fast and slow growth, but the differences were not significant. The linear by age (5 - 25 days) and GPI methods produced very similar means, respectively, for the two data sets. These latter two methods likely failed to detect the differences because they averaged or "smoothed over" the opposing changes in growth the two groups of nestlings exhibited.

Additional Analyses

To provide a complete evaluation of these various methods, we will include several more empirical data sets representing additional growth scenarios of nestling seabirds.

DISCUSSION

................see Table 5 for now.............

LITERATURE CITED

Barret, R. T. and O. J. Runde. 1980. Growth and survival of nestling Kittiwakes *Rissa tridactyla* in Norway. Ornis. Scand. 11:228-235.

Boersma, P. D. and J. K. Parrish. 1998. Flexible growth in fork-tailed storm-petrels: a response to environmental variability. Auk 115(1):67-75.

Coulson, J. C. and J. M. Porter. 1985. Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size , chick growth rates and parental quality. Ibis 127:450-466.

Coulson, J. C. and C. S. Thomas. 1985. Changes in the biology of the kittiwake Rissa tridactyla: a 31-year study of a breeding colony. J. Anim. Ecol. 54:9-26.

Fendley, T. T. and I. L. Brisbin, Jr. 1977. Growth curve analyses, a potential measure of the effects of environmental stress upon wildlife populations. Int. Congr. Game Biol. 13:337-350.

Pettit, T. N., G. V. Byrd, G. C. Whittow, and M. P. Seki. 1984. Growth of the wedge-tailed shearwater in the Hawaiian Islands. Auk 101:103-109.

Romano, M. D., D. D. Roby, and J. F. Piatt. 1998. Effects of diet quality on post-natal growth of seabirds: captive feeding trials. *In* D. C. Duffy, compiler, APEX project: Alaska predator ecosystem experiment in Prince William Sound and the Gulf of Alaska. *Exxon Valdez* oil spill restoration project annual report (project 96163N). Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon.

Ricklefs, R. E. 1983. Avian postnatal development. Avian Biology, Vol VII. pp 1-83.

Table 1. Parameters of model curves.

	Mass		Wing	
	normal	low	normal	low
Logistic				
A	417	310	255	210
K	0.1844	0.165	0.1411	0.132
I	11.65	10.5	17.82	17.2
Gompertz				
A	417	310	255	210
K	0.13	0.13	0.09	0.086
I	6.3	4.8	10.5	9.8

Table 2. Growth rates determined from model curves

	KA/4			by Age				by Weight				GPI		
	normal	low	age range (days)	normal	age range (days)	low	age range (days)	normal	age range (days)	low	age range (days)	normal	low	age range (days)
Logistic	19.22	12.09	(1 - 30)	17.93	(5 - 17)	12.21	(5 - 16)	16.93	(2 - 16)	9.15	(2 - 30)	24.41	20.24	(1 - 30)
				16.65	(6 - 22)	10.97	(6 - 22)							
				15.43	(5 - 25)	10.21	(5 - 25)							
Gompertz			(1 - 30)	19.53	(3 - 9)	14.42	(3 - 9)	18.19	(2 - 14)	8.23	(1 - 30)	24.70	20.57	(1 - 30)
				13.74	(6 - 22)	9.14	(6 - 22)							
				12.76	(5 - 25)	8.48	(5 - 25)							

Table 3. Comparisons using empirical data sets with high rate and high fledging mass versus low rate and low fledging mass

	N. Icy Bay (alpha's)			Shoup Bay (beta's)			Mann-Whitney		
	X	SE	n	X	SE	n	Chi-Sqr Approx.	P	Power
Measure									
A	439.19	9.17	15	401.40	19.87	14	1.9505	0.1625	
AK/4	20.50	0.58	15	16.92	0.85	14	8.5500	0.0035	
Linear (Mass)	18.81	0.56	15	12.88	1.09	14	14.0880	0.0002	
Linear (Age)									
6 - 22 days	16.34	0.73	15	14.14	1.06	14	2.2019	0.1378	In Progress
5 - 25 days	15.88	0.58	15	14.26	0.72	14	1.9505	0.1625	
GPI	24.74	0.34	15	22.81	0.84	14	4.0305	0.0447	

Table 4. Comparisons using empirical data sets with high rate and low fledging mass versus low rate and high fledging mass.

	Eleanor Island			Shoup Bay					
	X	SE	n	X	SE	n	t	P	Power
Measure									
A	396.23	5.54	50	434.06	10.10	46	-3.355	0.001	
AK/4	19.5465	0.3108	50	18.3977	0.3713	46	2.386	0.019	
Linear (Mass)	16.60	0.36	50	15.83	0.55	46	1.178	0.242	In
Linear (Age)									
6 - 22 days	16.13	0.27	50	15.58	0.42	46	1.137	0.258	Progress
5 - 25 days	14.96	0.23	50	14.95	0.33	46	0.011	0.991	
GPI	23.28	0.28	50	23.69	0.28	46	-1.029	0.306	

Table 5.

Method	Accuracy	Known-age Nestling?	Sensitivity	Comments
Logistic	Good in all situations	yes	high	Requires frequent measurements of nestlings. Nestlings that die or are without a complete growth record cannot be included in analyses (although see discussion section and Ricklefs 1983).
Linear by mass (60 - 300 g)	Good for normal growth Poor for slow growth with asymptote at or near 300 g	no	low	Requires relatively few measures of nestlings. Nestlings that die prematurely can still be included if two or more data points are obtained within the specified range.
Linear by age (6 - 22 days)	Good in most situations Some concern for situations of slow growth when asymptote occurs at an early age	yes	low	Same as linear by mass method.
Linear by age (5 - 25 days)	Good in most situations Definite concern for situations of slow growth when asymptote occurs at an early age	yes	low	Same as linear by mass method.
GPI	Good in most situations Poor at detecting situations where growth changes within a season (e.g. high rate, low asymptote)	no	moderate	Requires relatively few measures of nestlings. It is best that measurements are throughout the entire growth period, but they could be restricted to a defined range of wing lengths. A primary concern of this method is that the calculated rate is not in commonly used units (e.g. g/day) for comparison with other studies.

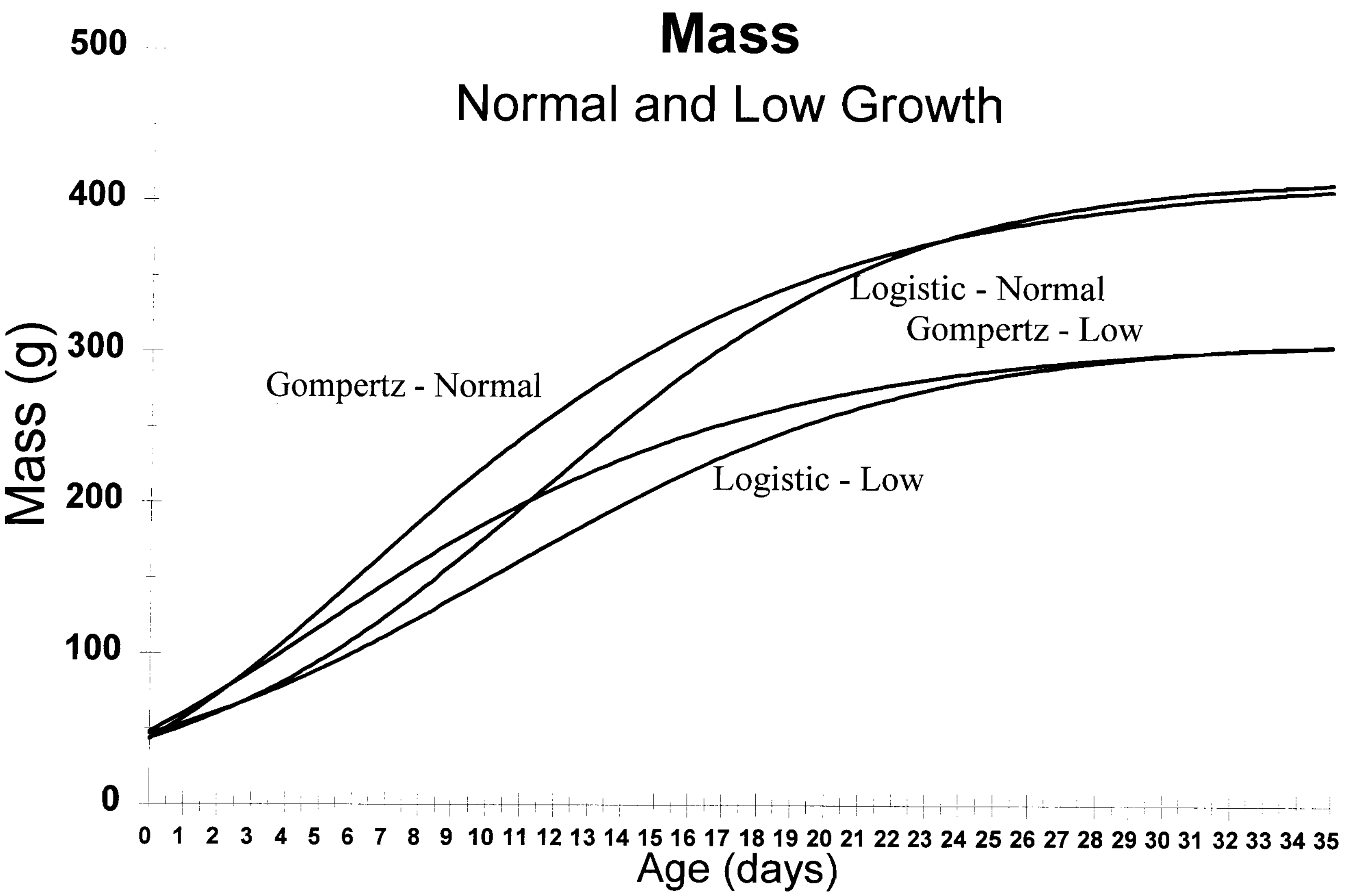
Mass
Normal and Low Growth
Mass (g)
500
400
300
200
100
0
Age (days)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35
Gompertz - Normal
Logistic - Normal
Gompertz - Low
Logistic - Low

Figure 1.

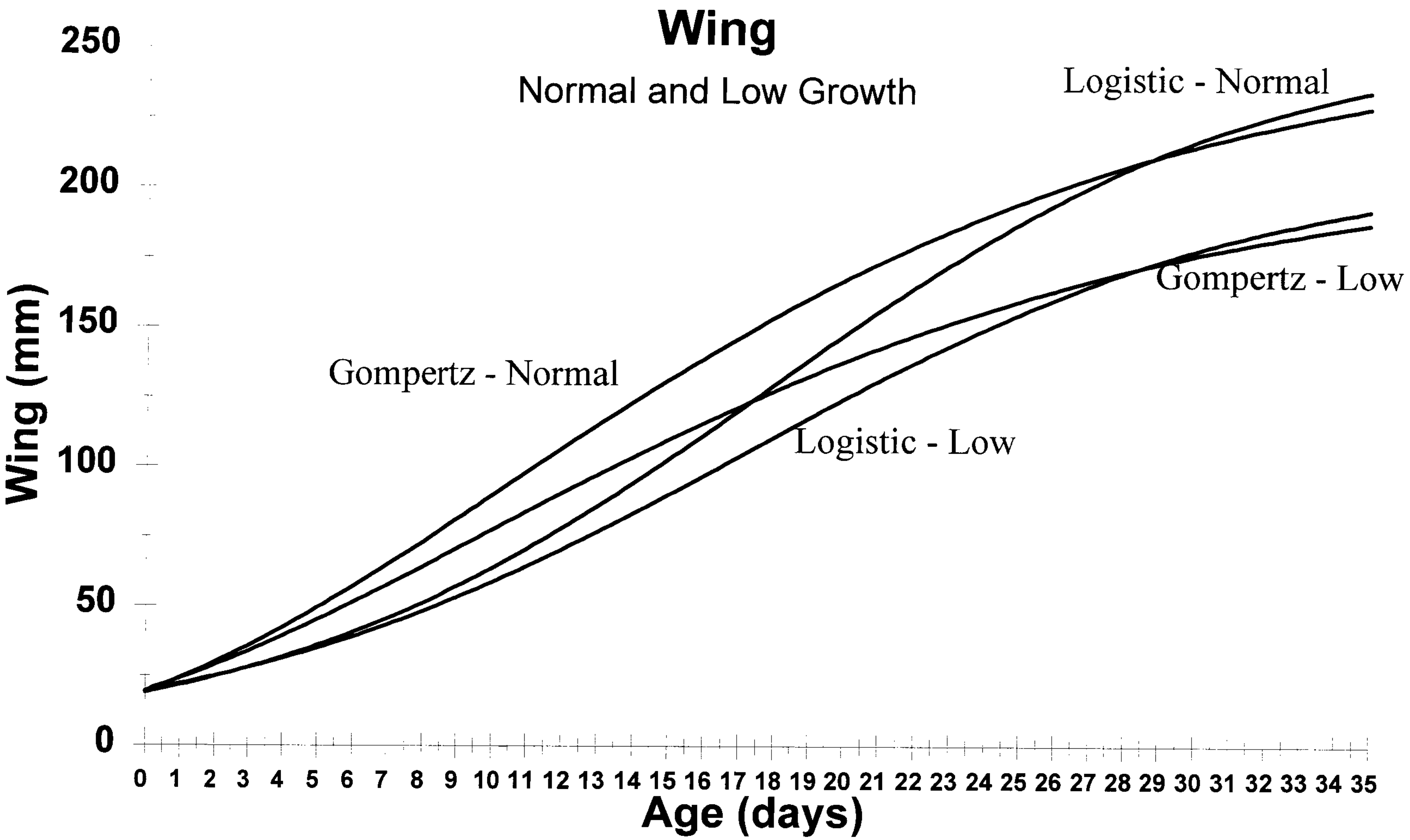
Wing
Normal and Low Growth
Logistic - Normal
Gompertz - Low
Gompertz - Normal
Logistic - Low
Wing (mm)
250
200
150
100
50
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35
Age (days)

Figure 2.

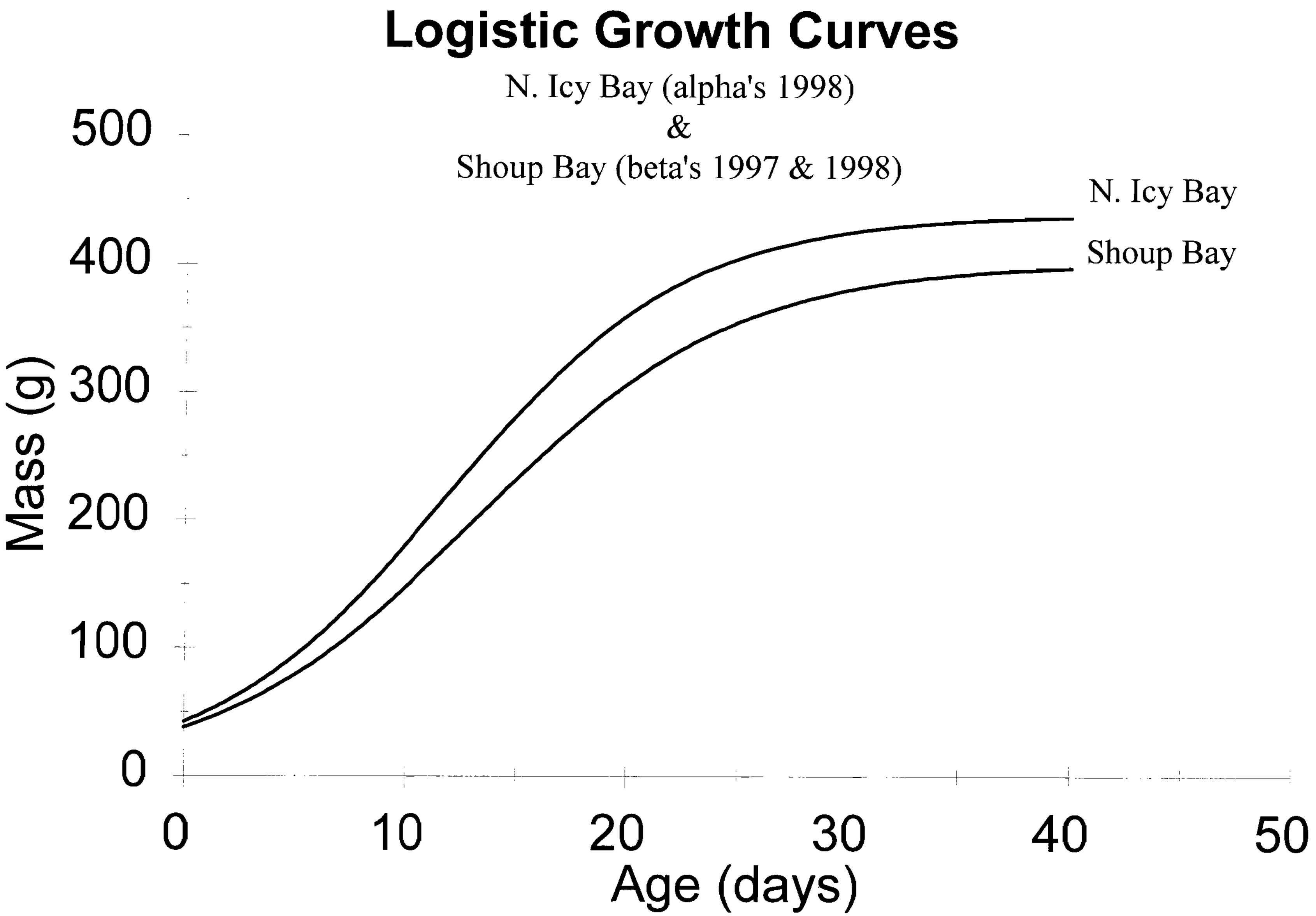
Logistic Growth Curves
N. Icy Bay (alpha's 1998)
&
Shoup Bay (beta's 1997 & 1998)
N. Icy Bay
Shoup Bay
Mass (g)
500
400
300
200
100
0
0
10
20
30
40
50
Age (days)

Figure 3.

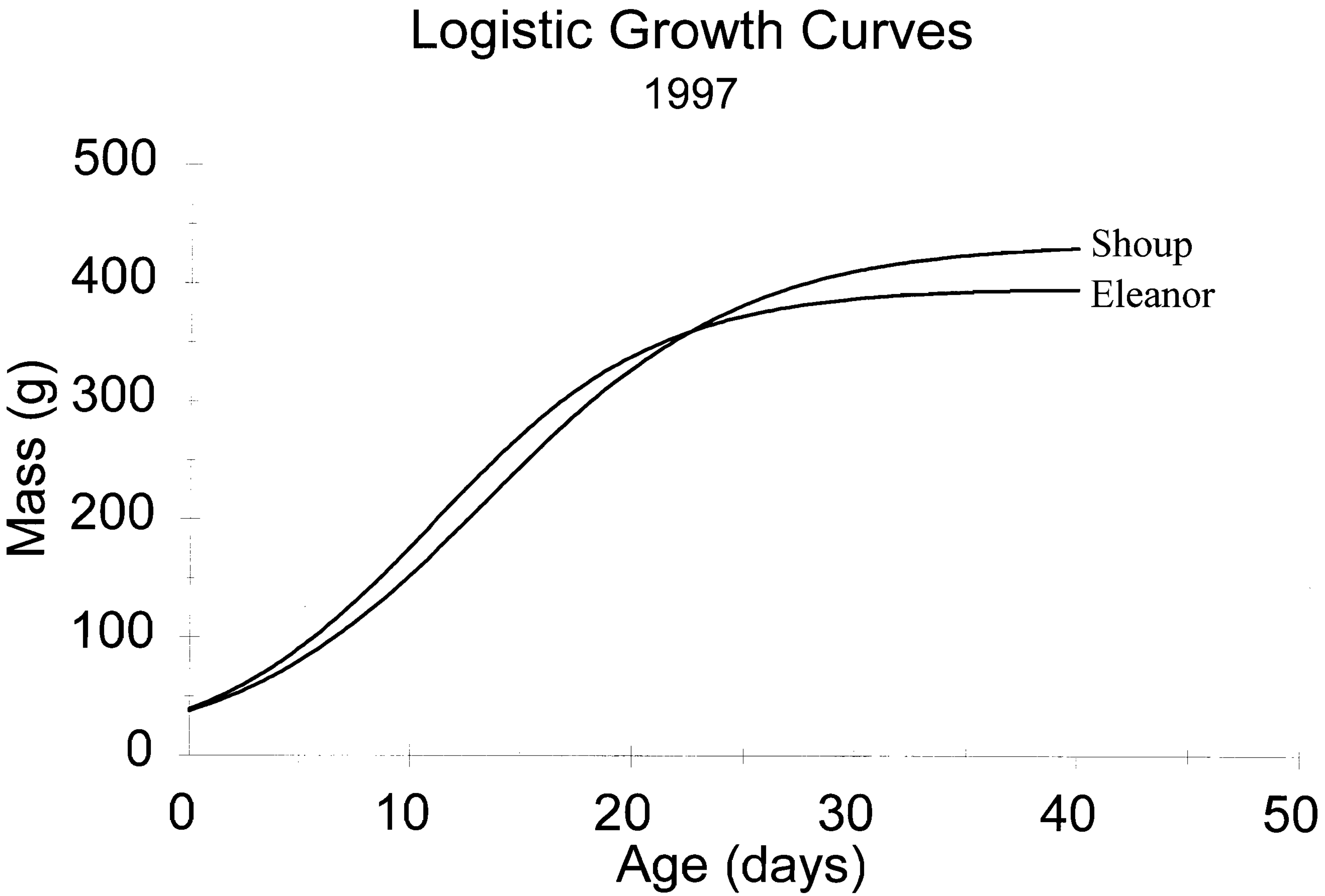
Logistic Growth Curves
1997
Mass (g)
0
100
200
300
400
500
Age (days)
0
10
20
30
40
50
Shoup
Eleanor

Figure 4.

A MULTIVARIATE APPROACH TO ASSESSING GROWTH OF SEABIRD NESTLINGS FROM ONE-TIME MEASUREMENTS

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Abstract. The collection of growth data from nestling seabirds can be logistically difficult, and may take up to 3 months, depending on the species, to measure from hatching to fledging. We evaluated the feasibility of a simpler approach, which utilizes a one-time sampling of nestling measurements obtained during a single visit to a seabird colony, to assess nestling growth. To simulate a one-time visit to a colony, we used a sub-sample of nestling measures that were obtained during a single day at four Black-legged Kittiwake (*Rissa tridactyla*) breeding colonies in Alaska. We used principal components analysis to create a body-size index. In this approach, body-size becomes a proxy for age and the residuals from a regression of mass on body-size can be used to assess relative body-condition. We compared results from analysis of one-time measurements by utilizing repeated measurements of the same individual nestlings to calculate a linear growth rate. One-time measurements revealed differences and similarities in chick growth as effectively as repeated measurements. Thus, we recommend them as a useful tool for monitoring seabirds at colonies where multiple visits and/or repeated measurements of individual nestlings are impractical.

Key words: Alaska, Black-legged Kittiwake, body-condition, nestling growth, principal components analysis, Rissa tridactyla, *seabird monitoring.*

INTRODUCTION

There are many ways to measure and contrast nestling growth data (Ricklefs 1983). The applicability of any given technique depends on the extent of data collected. Repeated measurement of known-age individuals throughout development is the most useful and informative approach to studying chick growth (Ricklefs 1983). However, collection of these data for seabird nestlings, which may require 1-3 months, is often prohibited by logistic and time constraints.

Investigators may use simpler methods to estimate growth rates. For example, Ricklefs and White (1975) used two measurements of a single body part (e.g., wing) taken at a 10 day interval as a proxy for age in order to construct an average growth curve for nestlings at a seabird colony. However, this still requires an initial visit to measure and band individual nestlings, and a return visit to find and measure the same individuals. Further, differential growth of body parts (Øyan and Anker-Nilssen 1996) may lead to biased results. Multivariate analyses incorporating several anatomical measures provides a more complete assessment of size and growth (Ricklefs 1968b).

Studies of adult birds are often limited to one-time measurements taken during capture. Given this constraint, some investigators have used principal components analysis (PCA; Manly 1994) with a residual index (Jakob et al 1996) to compare relative body-condition among adult birds (Hamer et al. 1993, Golet et al. 1998). In this approach, PCA is used to score birds by relative body-size based on several morphological measurements. This creates an index for size, and thus the residuals from a regression of mass on body-size can be used to compare body-condition among individuals and/or treatment groups.

We evaluated the feasibility of using one-time measurements for detecting differences in body-condition of nestling Black-legged Kittiwakes (*Rissa tridactyla*) at four different breeding colonies in Alaska. In this approach, the body-size index generated by PCA becomes a proxy for age. We reviewed these results by utilizing repeated measurements of the same individual nestlings to calculate a linear growth rate for comparison.

METHODS

We measured and weighed kittiwake nestlings at four breeding colonies in the northern Gulf of Alaska: Gull Island and Chisik Island in lower Cook Inlet during 1996, and Shoup Bay, in 1996, and North Icy Bay, in 1998, in Prince William Sound. We checked a sample of representative nests daily to determine hatch dates. When the first chick hatched, we began collecting measurements every four days, including new nestlings as they hatched. We recorded measurements of nestlings from hatching to near-fledging (30 days ± 1 day). Recorded measurements included right tarsus (± 0.1 mm; excluding Chisik Island), head-plus-bill (± 0.1 mm; Shoup Bay and North Icy Bay only), culmen (± 0.1 mm; Gull Island

and Chisik Island only), wing (± 1 mm; from the wrist region to the tip of the longest primary), tenth primary (± 1 mm; from skin to tip of the developing primary; excluding Chisik Island), and body-mass (± 1 g). We banded nestlings with United States Fish and Wildlife Service stainless steel bands and individual color band combinations for identification.

We regressed mass versus age to calculate growth rates (g/day) of individual nestlings during the linear growth phase of 60 to 300 g (Coulson and Porter 1985). We made comparisons using a two-sample t-test. To assess effort, we calculated mean number of measurements that were made per nestling during linear growth and the mean number of days we measured nestlings over the range of linear growth. We calculated mean age of chicks at the end of its observed linear growth phase (i.e., last day recorded where mass was under 300 g). We included all individual nestlings used to calculate linear growth rates in the sub-samples described below.

To simulate a one-time visit to each breeding colony we used a sub-sample of nestling measures that were obtained on a single day at Gull Island (July 22) and Shoup Bay (July 21) in 1996, and N. Icy Bay in 1998 (July 23). A limited number of nestling measures were present in the Chisik Island data on any single day, and therefore we took a sample of unique nestling measurements from several days (July 9,13,18,22). We calculated mean age of nestlings for each sub-sample.

We pooled data for comparisons based on the anatomical measures conducted at each site. At Chisik Island, only culmen and wing were measured. To conduct multivariate analyses we paired these data with Gull Island, the only other site where culmen was measured. Head-plus-bill, tarsus, wing, and tenth primary were measured at Shoup Bay and North Icy Bay, and therefore we paired these data and included all four variables in analyses. We standardized variables to means of zero and standard deviations of one (Manly 1994). We conducted PCA to create an index of body-size using the PRINCOMP procedure in SAS (SAS 1989). We regressed body-mass on body-size and used the residuals, expressed as a percentage of predicted body-mass, to assess relative body-condition. We made comparisons using a two sample t-test after evaluating distribution and homoscedasticity of the data.

RESULTS

Nestlings at Gull Island and Chisik Island exhibited significantly different linear growth rates ($t_{30} = 4.2$, $P < 0.0005$), but nestlings at Shoup Bay and North Icy Bay did not ($t_{76} = 1.1$, $P > 0.05$; Table 1). All data were normally distributed and homoscedastic.

For nestlings at Gull Island and Chisik Island, body-mass was related to body-size index scores (first principal component) by the equation $mass$ (g) = 60.4$size$ + 243.7 (Fig. 1a). Based on residuals from this regression, nestlings at Gull Island were 20% heavier for their body-size than Chisik Island nestlings ($t_{30} = 3.4$, $P < 0.005$; Table 1). Based upon residuals from a regression equation for Shoup Bay and North Icy Bay, *mass* (g) = 34.2*size* + 292.6 (Fig. 1b), nestlings did not differ in body-condition ($t_{76} = 0.7$, $P > 0.05$; Table 1). Nestlings selected for one-time measurements from Shoup Bay were older than those from North Icy Bay ($t_{76} = 2.4$, $P < 0.05$; Table 1).

DISCUSSION

Our results suggest that a one-time sampling of nestling mass and body-size can be used to detect differences (or a lack of differences) in growth among seabird populations. Compared to the effort required to calculate linear growth rates for nestlings at Shoup Bay and North Icy Bay, the average number of measurements per nestling and the total number of days required at the colony for one-time measurements were reduced by 70% and 90%, respectively (Table 1). In addition, it appears that residuals of mass on relative overall body-size can be compared among groups of unequal age.

We extracted sub-samples of equal *n* to generate unbiased statistical comparisons, but other investigators may opt to avoid culling data. An unequal *n* will bias the regression line towards the higher *n*, but conclusions should be similar when sample sizes are approximately equal. Otherwise, separate regressions could be calculated for each sample group and their relative elevations compared (Zar 1984).

We selected days from mid-July to simulate a one-time visit to each colony for two reasons. First, for kittiwakes in the northern Gulf of Alaska, this is typically a period of optimal growth leading up to peak energetic demand for kittiwake nestlings (Gabrielsen et al. 1992), and therefore variation in chick development will most likely be expressed here. Second, we wanted to use simple linear regression to analyze residual body-mass, and we found body-size related linearly to body-mass during the linear growth phase. Measurements of nestlings should be made prior to pre-fledging weight recession (common among seabirds; Ricklefs 1968a,b) because body-mass would decline while body-size continued to increase; creating misleading results. We do not recommend applying this method to very young nestlings because they are relatively homogeneous in body-size and mass in early development.

This snapshot approach to assessing variation in nestling growth is not recommended as a substitute for measuring complete growth curves. Variations in food supply or environment at different stages of chick-rearing can alter the growth rate, duration of growth, and asymptotic mass of nestlings so that birds growing at a slower rate may complete growth at a higher mass and vice-versa (Ricklefs 1968b). This flexibility warrants caution when interpreting results from one-time measurements. On the other hand, because one-time measurements can be collected relatively easily at different seabird colonies over a span of many years, we recommend them as a useful monitoring tool.

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LITERATURE CITED

Coulson, J. C. and J. M. Porter. 1985. Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. Ibis 127:450-466.

Gabrielsen, G. W., M. Klassen, and F. Mehlum. 1992. Energetics of black-legged kittiwake *Rissa tridactyla* chicks. Ardea 80: 29-40.

Golet, G. H., D. B. Irons, and J. A. Estes. 1998. Survival costs of chick rearing in Black-legged Kittiwakes. J. Anim. Ecol. 67:827-841.

Hamer, K. C., P. Monaghan, J. D. Uttley, P Walton, and M. D. Burns. 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. Ibis 135:255-263.

Jakob, E. M., S. D. Marshall, and G. W. Uetz. Estimating fitness: a comparison of body condition indices. Oikos 77:61-67.

Manly, B. F. J. 1994. Multivariate statistical methods: a primer. 2nd ed. London: Chapman & Hall. Chap. 6, Principal components analysis; p 76-92.

Øyan, H. S. and T. Anker-Nilssen. 1996. Allocation of growth in food-stressed Atlantic Puffin chicks. Auk 113:830-841.

Ricklefs, R. E. 1968a. Weight recession in nestling birds. Auk 85:30-35.

Ricklefs, R. E. 1968b. Patterns of growth in birds. Ibis 110: 419-451.

Ricklefs, R. E. and S. C. White. 1975. A method for constructing nestling growth curves from brief visits to seabird colonies. Bird-Banding 46:135-140.

Ricklefs, R. E. 1983. Avian postnatal development. Stud. Avian Biol 7:1-83.

SAS. 1989. SAS/STAT user's guide. Version 6. SAS Institute, Cary, North Carolina, USA.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. p 292-304.

TABLE 1. Results from two methods of analysis used to compare growth of known-age kittiwake nestlings from Gull Island versus Chisik Island and Shoup Bay versus North Icy Bay. Results are presented as means ± SE.

	Gull Island	Chisik Island	Shoup Bay	North Icy Bay
Repeated measurements, *n*	14[a]	11[a]	39	39
Measurements per nestling	2.4 (± 0.3)	2.1 (± 0.5)	3.7 (± 0.1)	3.5 (± 0.1)
Measurement days per nestling[b]	7.3 (± 1.1)	5.5 (± 1.3)	10.3 (± 0.4)	10.2 (± 0.4)
Age (days)[c]	16.4 (± 0.7)	16.1 (± 1.2)	14.1 (± 0.5)	14.7 (± 0.4)
Linear growth rate (g/day)	18.6 (± 1.1)	11.8 (± 1.3)	16.7 (± 0.5)	17.5 (± 0.5)
One-time measurements, *n*	16	16	39	39
Age (days)	15.6 (± 1.0)	16.5 (± 1.7)	17.8 (± 0.5)	15.9 (± 0.6)
Body-condition (%)	8.9 (± 3.6)	-10.9 (± 4.7)	0.7 (± 1.2)	-0.8 (± 1.5)

[a] We did not have enough measurements within the linear growth phase to calculate a growth rate for all of the nestlings used in the sub-sample of one-time measurements.

[b] The total number of days that mass was within the 60 to 300g linear phase, measured at 4 day intervals.

[c] Mean age of chicks at the end of the linear growth phase.

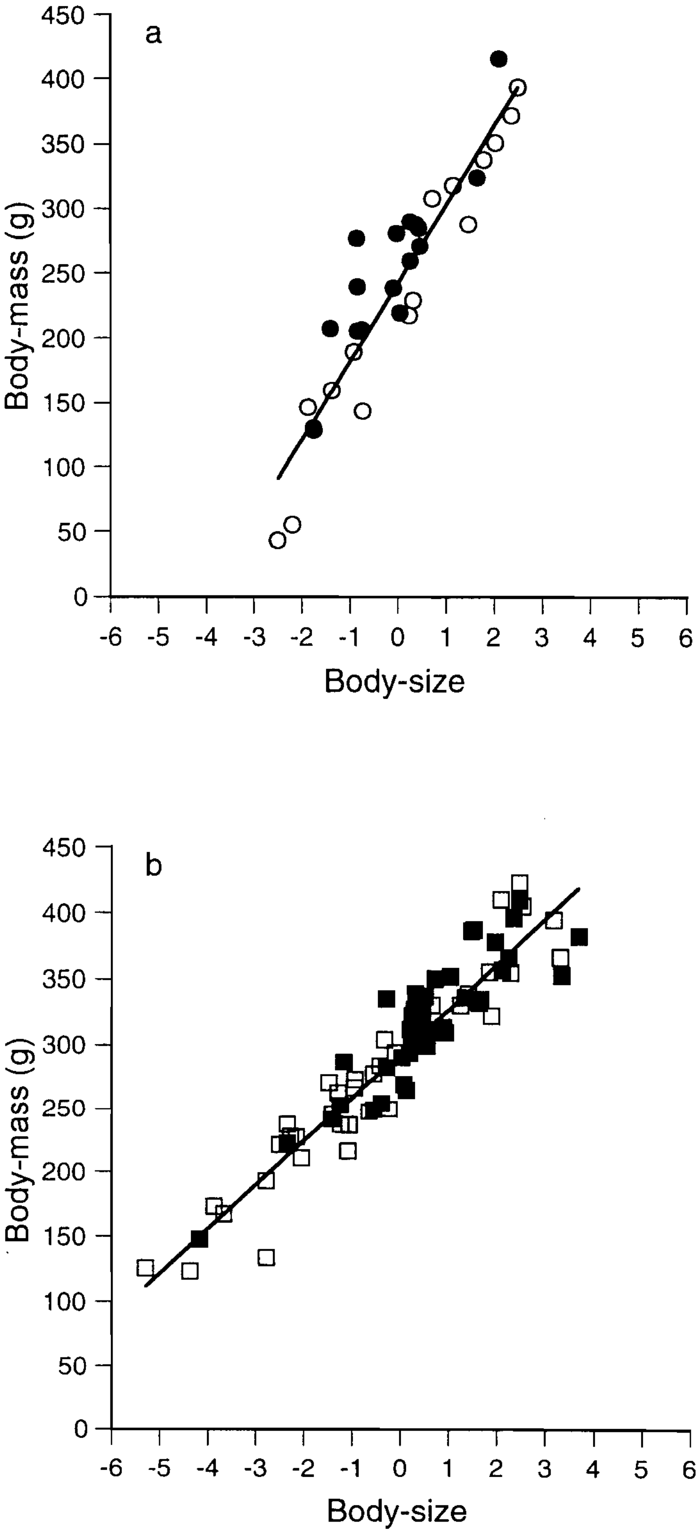

FIGURE 1. Regression of body-mass on body-size (first principal component) for kittiwake nestlings at the a) Gull Island (closed circles) and Chisik Island (open circles; $r^2 = 0.87$, $P < 0.0001$) and b) Shoup Bay (closed squares) and North Icy Bay (open squares; $r^2 = 0.88$, $P < 0.0001$).

A LEG-NOOSE FOR CAPTURING ADULT KITTIWAKES AT THE NEST

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Abstract.—We developed a leg-noose for capturing adult Black-legged Kittiwakes (Rissa tridactyla), a cliff-nesting, colonial seabird. The capture device consisted of an adjustable wire base secured to the rim of the nest. The base is simple to construct, and we describe three design options. The base held open a circular noose that was used to snare a kittiwake around the tarsometatarsi. A spool of line attached to the noose permitted the capturer to move away from the colony, encouraging the birds' return. Using this device, we captured 75 kittiwakes in 1996 and 1997. In particular, the leg-noose proved invaluable in the safe capture and recapture of specific individuals for our study that could not be captured by noose-pole. This leg-noose concept is versatile and could be adapted for capture of other nesting avian species.

INTRODUCTION

The study of avian ecology increasingly demands that birds be captured and handled for banding, measurement, blood or tissue sampling, and instrument attachment. Because seabirds are long-lived, philopatric, often accessible and present in great numbers at a breeding colony, their capture offers excellent opportunities for long-term ecological research and monitoring. Cliff-nesting seabirds have been captured in previous studies using a noose-pole (Hogan 1985, Jacobsen et al. 1995, Irons 1998), rocket-net (Hatch et al. 1993, Golet et al. 1998), mist-net (Roberts and Hatch 1993), and noose-mat (Roberts and Hatch 1993). However, noose-poles tend to flush most birds in the area, leaving available for capture only those individuals tolerant of such a disturbance, rocket-nets and mist-nets are indiscriminate, and noose-mats require that a bird snare itself.

Certain studies require that either specific birds or birds in specific areas be captured. As part of a study of the reproductive and foraging ecology of Black-legged Kittiwakes (Rissa tridactyla), we captured adult birds at several breeding colonies in Prince William Sound, Alaska during 1996 and 1997. To facilitate capture of specific birds, we created a leg-noose trap that fits on the rim of a kittiwake nest and can be remotely triggered.

TRAP DESIGN AND OPERATION

The leg-noose consists of two basic parts, the base and the noose (Fig. 1). The base has several noose-supports that keep the noose open and anchors that secure the trap in place. The end of the noose passes through a line-guide and is attached with a swivel to a line wound on a spool or reel.

We created three different leg-noose designs, described below in the order that they were developed. We assembled the prototype using galvanized steel wire (2-mm diameter), foam pieces (from Pelican Case® products), lag-bolts (8 mm x 51 mm), and duct-tape. We constructed a base by shaping the wire into spring-like coils so that a three-dimensional circle was formed (Fig. 1a). We made rectangular noose-supports from foam, with a slit on the top running one-third its length, and attached these to the base simply by running the wire through the foam so that the noose-supports were free to slide along the base. For a line-guide, we formed two eyelets at opposite ends of a 5-cm long steel wire attached to the base by a loop in the middle of the wire, which we taped to a piece of foam for stability. We used wire to attach four lag-bolts to the base for anchoring the trap to the nest. We used braided Dacron® line (Western Filament®; 36 kg test) for the noose and tied this to a swivel (prevented line from twisting) and leader clip, which allowed attachment to either clear monofilament line (9 kg test) or buoyant line (9 kg test).

In the second design, we constructed a simple adjustable base (Fig. 1b) out of wire by forming a circle with overlapping ends, held in place by two nylon cable ties (127 mm X 3.2 mm; 13.5-kg pull). The cable ties were tight enough to keep the ends from slipping and expanding the circle, but loose enough to allow adjustment. The noose-supports and line-guide were fashioned and attached as described above, with the exception that the foam pieces were T-shaped. We attached four wire loops around the base, which allowed us to position the anchors before affixing the base to the nest with lag-bolts.

The third, less conspicuous design requires several noose-supports, a single anchor/line-guide, and a fishing rod and reel (Fig. 1c). There is no base in this design and the noose-supports are made of wire so that they can be inserted directly into the nest material. The line-guide is attached to the only anchor. The fishing gear is used to set the noose and the bird should be held to the nest by the anchor/line-guide. If the bird breaks away from the nest it can be controlled by rod and reel as it glides to the water.

To set the leg-noose, the base should be attached to the nest bowl using the anchors. The noose is held in position by leading it through the line-guide (oriented toward the direction of pull), expanding it to the width of the base, and gently placing in the noose-supports. The line is then spooled out to a suitable location. Once the bird has landed within the noose, the line should be quickly, but steadily, reeled in until the noose closes around the legs (tarsometatarsi). Gaining control of the bird should be swift and immediate and, once in hand, the noose may be loosened and removed.

FIELD RESULTS AND DISCUSSION

Kittiwakes construct nests on small ledges of oceanside cliffs from mud and vegetation. Accessibility and structure varied widely among nests, requiring the leg-noose setup to vary accordingly. To allow use of the trap, nests must be: accessible by foot, ladder, boat, or other means; strong enough to support the leg-noose anchors; and visible from a nearby, but inconspicuous location.

In 1996 and 1997 we captured 75 adult kittiwakes at three breeding colonies with the leg-noose. Adult birds were captured from 37 nests containing eggs, 18 nests containing chicks or chicks and eggs, and 20 empty nests. None of the captured birds appeared to have been injured, and there were no observed differences between the post-capture behavior of those birds captured by leg-noose versus birds captured by noose-pole or uncaptured birds. We did not see any evidence of destroyed or damaged nests in 1996, but in 1997 we damaged two nests, destroying four eggs (described below).

We recorded capture effort as attempts per successful capture in 1997 and calculated means for each method. We did not monitor capture effort in 1996. Capture effort using the leg-noose (1.4 attempts/capture, $n = 57$) was similar to effort using the noose-pole (1.6 attempts/capture, $n = 179$). The noose-pole was a more efficient method to capture many kittiwakes in a limited amount of time, thus we used it to capture large numbers of previously uncaptured adults and to recapture adults that did not exhibit trap shyness.

Our studies required the capture and attachment of radio-transmitters to previously radio-tagged adults and/or banded individuals of known-age. We observed birds becoming trap weary after successive capture attempts within and among years. This progressed until nearly all birds in certain sections of the colonies would flush at the sight of a noose-pole, preventing capture. In these situations the leg-noose proved invaluable. For example, we recorded six individuals in which repeated capture attempts ($\bar{x} = 3.3$) with the noose-pole failed and success was achieved in fewer attempts ($\bar{x} = 1.7$) by immediately employing the leg-noose. Even with the leg-noose some kittiwakes acquired trap shyness, hence the development of lower profile designs. Of the 75 adult capture events using the leg-noose in 1996 and 1997, 51 were recaptures from previous years. It would have been near impossible to safely capture and/or recapture those specific birds that we targeted with any other method, especially in as few attempts. Thus, we feel the leg-noose was less disturbing to the colony than any other available methods.

The leg-noose was also used extensively during a 1998 study of the metabolic requirements of breeding kittiwake adults. The investigators employed doubly-labeled water techniques that required the capture and recapture of individuals within a 48-h period. Inherently, the recapture process and the potential disturbance that is involved (kittiwakes will usually either maintain vigilant flight or raft in the water until the disturbance ends) must be relatively quick so that the metabolic rates of the experimental birds are not artificially raised. Of 42 adults recaptured, it was estimated that 13 were caught by leg-noose. The leg-noose proved to be a reliable alternative for birds that had been captured with the noose-pole less than 48 hours previous.

Trapping technique varied depending on site-specific requirements and individual birds. Access to nests with suitable blinds far enough from the nest to encourage landing, but close enough to allow an efficient capture and retrieval, was the foremost difficulty encountered while working on land. Some captures required a third individual to watch the nest from a boat and relay signals or radio messages to the capturers hiding out of view of the nest. When calm seas allowed, we successfully used inflatable boats to access nests and capture birds. While waiting for the birds to return, tension on the line caused by the drifting boat created difficulties. To alleviate this problem, we used buoyant line and maneuvered the boat against the current and/or wind. When capturing by boat at a large active colony, we unintentionally captured two birds that flew into and became entangled in the monofilament line. Movement of the trigger line occasionally frightened birds and successful attempts were made to conceal the line in natural crevices on the colony. It also was helpful to keep the line taught so there was minimal line movement when tightening the noose during capture.

After the noose is reeled in and the bird has fallen just over the edge of the nest, the force created by the weight of the bird and the tension on the line is transferred to the anchors holding the base on the nest. Therefore, the nest must be strong and the base must be securely anchored. When possible we used irregular features in the rock to help hold the trap in place. Sometimes nests were too thin or fragile to secure the leg-noose. In this case, modifications to the third design allowed the bird to be snared and fly from the nest with little or no stress on the nest structure. It was also important that tension on the line be sustained either by the individual who reeled in the line while a coworker gained control of the bird, or by a weighted object placed on the line, if a person was capturing alone. This minimized the chance that a struggling bird would damage either itself or its nest. It is important that the noose cinches around both legs, otherwise the adult may remain upright on one leg and create enough force with its wings to lift either the trap off the nest or both the trap and the nest off the cliff. This was how we damaged the two nests mentioned above.

The three leg-noose designs performed with distinct advantages and trade-offs. All designs showed increased success if: the base was adjusted to fit on the outside top edge of the nest bowl, giving the bird an area to land; the noose-supports positioned the noose high on the legs and clear of nest material; attempts were made to camouflage the trap with nest material and/or paints; efforts were made to conceal the movement of the line being pulled by the capturer from the view of birds in vicinity of the trap. The second and third trap designs proved highly adjustable and inconspicuous, and even non-breeding adults frequently returned to the nest when the leg noose was in place. However, these designs were not as strong or efficient for capturing birds compared to the original design, likely because the noose was positioned higher on the legs atop the coiled base, and due to the easier nest setup of this design. Preference varied among capturers and both technique and efficiency improved with increased familiarity of each design.

It was easier to capture incubating birds than birds rearing chicks with the leg-noose. If present, we left eggs in the nest during capture but removed chicks before capture. We observed that adult birds returned more often to nests with the eggs than nests where chicks had been removed. To capture birds on failed nests we placed an egg in the nest bowl, which caused some birds whom were previously trap wary to return to their nest. We sometimes replaced live eggs with a decoy egg while the leg-noose was set to reduce the potential of destroying eggs. We achieved limited success by placing a chick decoy in the nest.

We recommend the leg-noose as a reliable method for capturing kittiwakes that can not be captured with a noose-pole or other methods, and where nest structure and location permit traps to be set. Using the leg-noose allowed us to select a nest, set the trap, and move out of view and/or direct influence from the colony. As other kittiwakes returned to their nests, the selected bird usually returned with them and landed within the noose. It was invaluable in the capture and recapture of specific birds for radio-telemetry, behavioral observation, and doubly-labeled water experiments.

This leg-noose design may prove effective for capturing other avian species where conditions permit. Among seabirds, cliff-nesting cormorants and fulmars, and ground-nesting gulls and terns would seem likely candidates for the leg-noose. This method, however, could be adapted for any bird with an accessible nesting platform. Kittiwakes are relatively small birds and have little strength when suspended upside down by the leg-noose. Stronger anchoring and materials would be required for larger seabirds that prove too heavy or powerful for the leg-noose described here, especially for capturing ground-nesting birds that may remain upright after the noose is tightened.

ACKNOWLEDGMENTS

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LITERATURE CITED

GOLET, G.H., D.B. IRONS, AND J.A. ESTES. 1998. Survival costs of chick rearing in Black-legged Kittiwakes. J. Anim. Ecol. 67:827-841.

HATCH, S.A., B.D. ROBERTS, AND B.S. FADELY. 1993. Adult survival of Black-legged Kittiwakes Rissa tridactyla in a Pacific colony. Ibis 135: 247-254.

HOGAN, G. G. 1985. Noosing adult cormorants for banding. N. Am. Bird Bander 10:76-77.

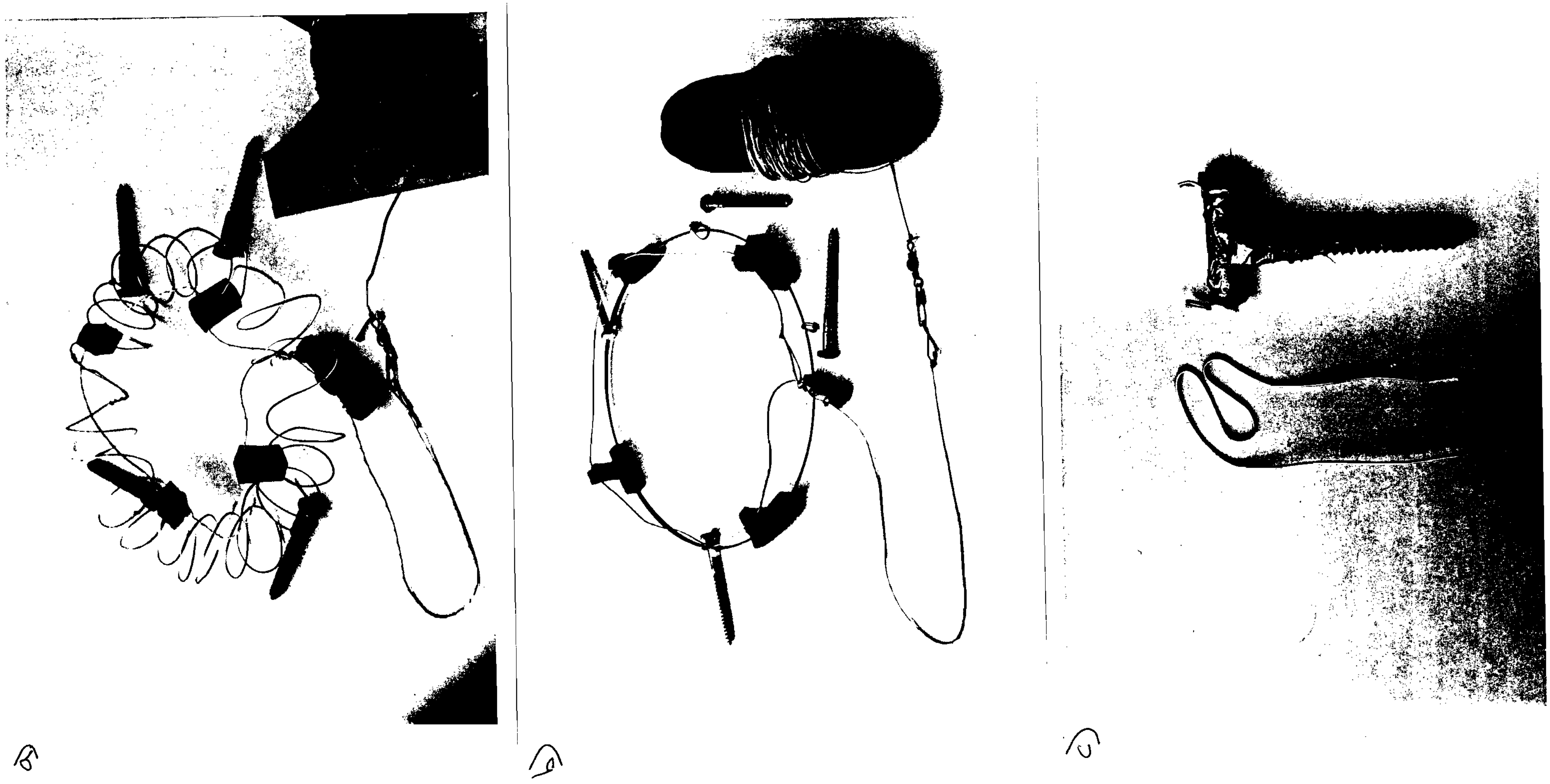
IRONS, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79: 647-655.

JACOBSEN, K. O., K.E. ERIKSTAD, AND B.E. SAETHER. 1995. An experimental study of the costs of reproduction in the kittiwake Rissa tridactyla. Ecology 76: 1636-1642.

MCNICHOLL, M. K. 1983. Use of a noosing pole to capture Common Nighthawks. N. Am. Bird Bander 8:104-105.

ROBERTS, B. M., AND S.A. HATCH. 1993. Behavioral ecology of Black-legged Kittiwakes during chick rearing in a failing colony. Condor 95: 330-342.

FIGURE 1. Three leg-noose designs used to capture Black-legged Kittiwakes on their nests. The trap concept remained the same, although the base designs varied from (a) coiled, (b) flat, and (c) no base in order to reduce the conspicuousness of the trap.



F Guillemot Studies

Exxon Valdez Oil Spill
Restoration Project Annual Report

THE BREEDING AND FEEDING ECOLOGY OF PIGEON GUILLEMOTS AT NAKED ISLAND, PRINCE WILLIAM SOUND, ALASKA

Restoration Project 98163F
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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March 1999

Study History: The field work for APEX subproject 98163F was conducted during the summer of 1998. Previous related field work was conducted during the summer of 1995-7 as part of APEX subprojects 95163 F and 96-97163. A study of similar scope took place in 1994 as Project 94173. Previous related projects have been funded by the Trustee Council. Oakley and Kuletz (1996) undertook a study in 1989-1990 to compare various population and reproductive parameters of pigeon guillemots before (Oakley and Kuletz 1979, Kuletz 1981, 1983, Oakley 1981) and after the spill. Also, Project 93034, an extensive survey of pigeon guillemot colonies throughout Prince William Sound, was conducted during the summer of 1993 (Sanger and Cody 1994).

Abstract: see attached manuscript.

Key Words: see attached manuscript.

Project data: to be addressed in the final report.

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DRAFT

SEABIRD POPULATION DECLINE LINKED TO CHANGES IN PREY TYPES

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Seabird population decline linked to changes in prey types

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Population sizes and distributions of seabirds are believed ultimately to be limited by food, but the mechanisms responsible remain unclear [1-4]. Food stress may be highest when birds concentrate at colonies and feed chicks in addition to themselves [2-4]. The polyphagous pigeon guillemot (*Cepphus columba*) should be less subject to prey fluctuations than other seabirds [5, 7]. From 1979-1997, however, guillemot populations in Prince William Sound (PWS) fluctuated, apparently in response to changes in the relative abundance of two prey types that occupy different habitats and have differing degrees of aggregation. Demersal fishes are more predictable and constant [6] but spatially limited, and appear to support only a limited number of guillemot pairs. The surface-schooling fishes are patchy and variable in abundance over time [7,8], but their use by guillemots results in high chick growth rates [9]. The decline in guillemots in PWS tracked a decline in the proportion of surface-schooling fishes in chick diets. Despite advantages to raising chicks on high-lipid schooling fish [9, 10], those guillemots using demersal fishes now comprise the majority that breed in this area.

During 1972 to 1997, the total PWS population of pigeon guillemots declined from 15,000 to <3,500 today [11, 12, & unpubl.]. Although the guillemot population was affected by the 1989 *Exxon Valdez* Oil Spill, the decline began prior to the spill [11], and its magnitude suggests a pervasive environmental factor. To examine the reasons for this decline and subsequent lack of recovery, we examined long-term data from Naked Island, where nearly one-fourth of PWS pigeon guillemots nest. We studied population trends, foraging, productivity, and chick diet at this island for nine years.

Guillemots usually lay two eggs, forage <4 km from their nest [13, 14], and bring their chicks single, whole fish, which can be visually identified. In most of their range, (California to the Bering Strait), guillemots feed themselves and their chicks primarily benthic fishes [13-17] such as blennies (gunnels [Pholidae] and pricklebacks [Stichaeidae]), sculpin (Cottidae), and juvenile cod and pollock (Gadidae). Although typically less common in the diet, guillemots also eat surface-schooling fishes such as Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea pallasi*), and smelts (*Osmeridae*) [13-17].

In the years 1979-81 sand lance was the largest component of chick diet ($\bar{x} = 42.1\%$, SD= 17.3%) at Naked Is., with decreasing percentages of sand lance in following years (Fig. 1). In the six years during 1989-90 and 1994-97, sand lance was a much smaller fraction of chick diet ($\bar{x} = 14.5\%$, SD = 5.0%), as the use of blennies, sculpin, and gadids increased. Herring were prominent in 1981 and 1989.

The principal surface-schooling fish at Naked was sand lance and the annual percentage of sand lance in the chick diet was positively related to both the total number of guillemots at the colonies ($r = 0.66$, $P = 0.014$; Fig. 2) and to the number of active nests ($r = 0.69$, $P = 0.010$). We did not, however, find a relationship between sand lance in the diet and the proportion of birds breeding at the colonies, suggesting population decline as opposed to higher instances of nonbreeding.

We expected annual reproductive success to be higher in years with more sand lance in the chick diet. Although overall productivity did not differ significantly among years, there have been confounding factors such as nest predation and disturbances related to the oil spill [11]. For years where both diet and substantial numbers of chicks were measured (1989-1997), there was a positive relation between the proportion of schooling fishes brought to the nest and chick growth rate and nestling survival [9]. These direct measures of productivity reflect the higher energy densities of most pelagic fishes compared to most demersal fishes [10, 18], and indicate advantages to foraging on surface-schooling fishes.

Marked individuals at Naked Is. displayed prey specialization in the food delivered to chicks[9, 14, unpublished data]. Individual adults tended to bring their chicks either surface-schooling fishes (sand lance, herring, smelt) or demersal fishes (blennies, sculpin, flatfish, cod)[14]. Between 1979-1981, 12 of 23 marked individuals specialized in sand lance (>50% of deliveries), whereas in 1989-1996, only 3 of 22 individuals were sand lance specialists.

Colony size is hypothesized to be determined by the abundance of food within foraging distance from the colony [2, 4, 19]. For pigeon guillemots, which have small dispersed colonies [5, 13], local demersal fish abundance is likely an important limiting factor. However, a sustained influx of pelagic prey such as sand lance through the colony forage area during chick rearing could greatly increase local carrying capacity [4, 20]. Like most seabirds, guillemots are highly tenacious in choice of breeding site [13]. For polyphagous guillemots, a numerical response at breeding colonies resulting from changes in local prey might only be evident over many years. Prey preferences of guillemots have been associated with habitat use [14, 21] and demersal fishes tend to show greater predictability in abundance within their preferred habitats [6-8]. A decline in sand lance could have changed the profitability of forage habitats, thus generating an ideal-free distribution among breeding birds [22].

The mechanism for reallocation of diet preferences among guillemots feeding chicks at Naked Is. is not clear. Both the pigeon guillemot and its congener, the black guillemot (*C. grylle*), demonstrate individual specialization in prey within a season [9, 13,14,15, 21]. Evidence for diet preferences across years is less conclusive, but the link in utilization of the nearshore pelagic sand lance, herring and smelts suggests learned foraging behaviors [14]. Individuals may have difficulty switching between prey guilds, and guillemots that are demersal feeders may dominate the population now because they are successful. The present guillemot population at Naked is half what it was in 1979-1980, which is consistent with the decline in sand lance specialists among marked individuals.

Regardless of the mechanism, the influx of high-quality pelagic fishes, and of sand lance in particular, is apparently important for maintaining large colonies of guillemots in Alaska. The high proportion of sand lance use by guillemots at Naked Is. is not typical of guillemot diet throughout its range, and may partly explain the higher chick growth rates at Naked, compared to populations where chicks are fed primarily demersal fishes [9]. We propose that the biomass of demersal fishes alone is not sufficient to support the PWS guillemot population at the numbers observed in the 1970s.

Numerous sources indicate that there has been a change in the Gulf of Alaska that began in the late 1970s, which has probably affected marine bird populations [23-25]. In PWS, seabird diets suggest a decrease in sand lance availability, with corresponding population changes in many piscivorous birds and mammals [26]. We demonstrate population changes in response to those ecosystem changes and suggest potential mechanisms leading to the population changes. Our data also suggest that since 1996, sand lance use has begun to increase (Fig. 1), and we will be able to determine if the guillemot population increases in the coming years.

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References

1. Lack, D. *Ecological adaptations for breeding in birds.* (Lond., Methuen & Co. Ltd., England, 1968).

2. Ashmole, N.P. The regulation of numbers of tropical oceanic birds. *Ibis* **103b**, 458-473 (1963).

3. Furness, R.W., & Birkhead, T.R. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* **311**, 655-656 (1984).

4. Cairns, D.K. The regulation of seabird colony size: a hinterland model. *Am. Natur.* **134**,141-146 (1989).

5. Storer, R.W. A comparison of variation, behavior and evolution in the seabird genera *Uria* and *Cepphus*. *Univ. Calif. Publ. Zool.* **52**, 121-222 (1952).

6. Rosenthal, R. J. *Shallow water fish communities in the northeast Gulf of Alaska: habitat, evaluation, temporal distribution, relative abundance and trophic interactions.* (EAACS An. Rep., NOAA/BLM, Boulder, CO, 1979).

7. Cairns, D. K. The ecology and energetics of chick provisioning by Black Guillemots. *Condor* **89**,627-635 (1987).

8. Blackburn, J.E. in Rep. 6, *Outer Continental Shelf Environ. Assess. Progr.* 727-852 (NOAA/BLM, Boulder, CO, 1979).

9. Golet, G.H., Kuletz, K.J., Roby, D.D., & Irons, D.B. Adult prey choice affects chick growth and reproductive success of pigeon guillemots. *Auk* (in press).

10. Anthony, J.A. & Roby, D.D. Variation in lipid content of forage fishes and its effect on energy provisioning rates to seabird nestlings, in *Forage Fishes In Marine Ecosystems: Proc. Internat. Symp. on Role of Forage Fishes in Marine Systems.* (Alaska Sea Grant) **97-01**, 725-729. (Univ. of Alaska Fairbanks, 1997).

11. Oakley, K.L., & Kuletz, K.J. Population, reproduction, and foraging of pigeon guillemots at Naked Island, Alaska, before and after the *Exxon Valdez* oil spill. *Am. Fish. Soc. Symp.* **18**,759-769 (1996).

12. Agler, B.A., Seiser, P.E.,Kendall, S.J., & Irons, D.B. *Marine bird and sea otter population abundance of Prince William Sound, Alaska: population trends following the T/V Exxon Valdez oil spill, 1989-93. (*Oil Spill Restoration Rep., U.S.F.W.S., Anchorage, AK, 1994).

13. Ewins, P.J. in *The birds of North America* (eds Poole, A., and Gill, F.) **49** (The Academy of Natural Sciences, Washington, D.C., 1993)

14. Kuletz, K.J. *Mechanisms and consequences of foraging behavior in a population of breeding pigeon guillemots*. Thesis, Univ. of Calif., Irvine (1983).

15. Drent, R.H. Breeding biology of the Pigeon Guillemot, *Cepphus columba. Ardea* **53**:99-160 (1965).

16. Follett, W.I. & Ainley, D.G. Fishes collected by Pigeon Guillemots nesting on southeast Farallon Island, California. *Calif. Fish & Game* **62**, 28-31 (1976).

17. Ainley, D.G. & Boekelheide, R.J. *Seabirds of the Farallon Islands* (Stanford Univ. Press, Stanford, CA,1990).

18. Van Pelt, T.I., Piatt, J.F., Lance, B.K., and Roby, D.D. Proximate composition and energy density of some North Pacific forage fishes. *Comp. Biochem. & Physiol.* **119A**,

1-6 (1997).

19. Diamond, A.W. Feeding strategies and population size in tropical seabirds. *Am. Natur.* **112**, 215-223 (1978).

20. Cairns, D.K. & Schneider, D.C. Hot spots in cold water: feeding habitat selection by Thick-billed Murres. *Stud. in Avian Biol.* **14**, 52-60 (1990).

21. Slater, E.B. & Slater, P.J. Behavior of the Tystie during feeding of the young. *Bird Study* **19**, 105-113 (1972).

22. Fretwell, S. D., & Lucas, H.L. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**, 16-36 (1970).

23. Hayward, T.L. Pacific Ocean climate change: atmospheric forcing, ocean circulation and ecosystem response. *TREE* **12(4)**, 150-154 (1997).

24. McGowan, J.A., Cayan, D.R., & Dorman, L.M. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* **281**, 210-217 (1998).

25. Piatt, J.F., & Anderson, P. Response of common murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska Marine Ecosystem. *Am. Fish. Soc.* **18**,

720-737 (1996).

26. Kuletz, K.J., Irons, D.B., Agler, B.A., Piatt, J.F., & Duffy, D.C. Long-term changes in diets and populations of piscivorous birds and mammals in Prince William Sound, Alaska. In *Forage fishes in marine ecosystems, Proc. Internat. Symp. on Role of Forage Fishes in Marine Systems.* (Alaska Sea Grant) **97-01**, 703-706 (Univ. of Alaska Fairbanks, 1997).

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FIGURE CAPTIONS

Figure 1. Prey types and their relative proportions in the diet of pigeon guillemot chicks on Naked Island, Prince William Sound, Alaska in 1979-81, 1989-90 and 1994-97. Blennies included primarily Pholidae and Stichaidae. Sample sizes are above bars. We used binoculars and spotting scopes to monitor guillemot chick provisioning at five sub-colonies on Naked Island. From blinds, we identified prey items to the nearest possible taxon. Prey items were periodically verified by taking delivered items from chicks and adults, and via minnow traps and beach seining.

Figure 2. Pigeon guillemot population at Naked Island, Prince William Sound, Alaska as a function of proportion of sand lance in diet of chicks. Data from 1979-1980, 1989-1990, and 1994-1997 (in 1981 there was no population census). The total population was counted by circumnavigating Naked Island during morning high tides in early June, when colony attendance was highest.

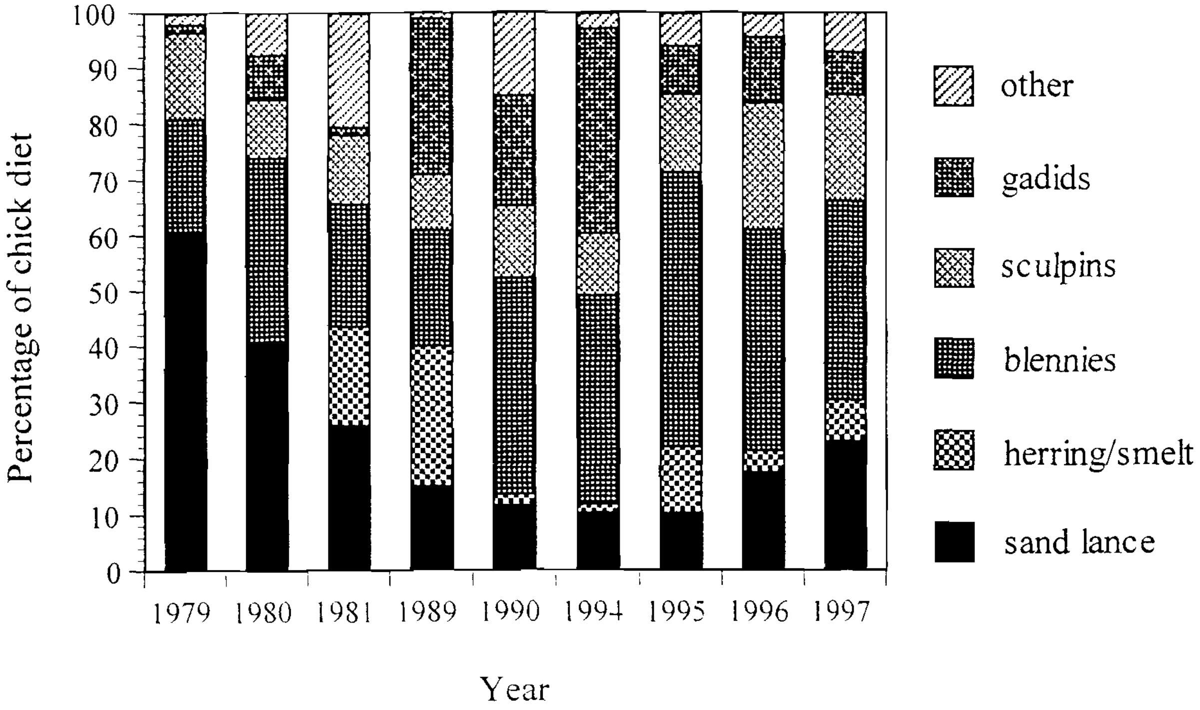

Fig. 2
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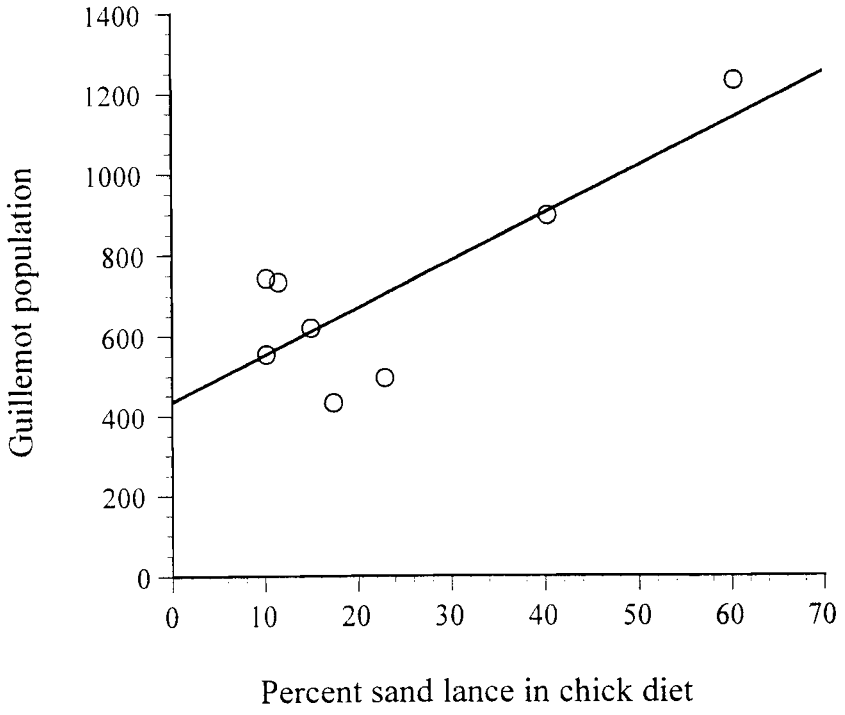

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RRH: *Prey Choice in Guillemots*

ADULT PREY CHOICE AFFECTS CHICK GROWTH AND REPRODUCTIVE SUCCESS OF PIGEON GUILLEMOTS

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ABSTRACT.--Pigeon Guillemots, *Cepphus columba*, are diving seabirds that forage near shore and feed their chicks both demersal and schooling fishes. During nine years between 1979 and 1997, we studied chick diet, chick growth rate, and reproductive success of Pigeon Guillemots at Naked Island, Prince William Sound, Alaska, to determine factors limiting guillemot breeding populations. We found evidence for prey specialization among guillemot breeding pairs, and detected differences in reproductive success between specialists and generalists. Pairs that specialized in particular prey types when foraging for their chicks fledged more chicks than those that generalized, apparently because they delivered larger individual prey items. Reproductive performance also varied among guillemot pairs as a function of the proportion of high-lipid schooling fishes fed to the chicks. Pairs that delivered primarily high-lipid fishes (Pacific sand lance, *Ammodytes hexapterus,* and Pacific herring, *Clupea pallasii*) attained higher overall reproductive success than pairs that delivered primarily low-lipid demersal fishes (e.g., sculpins, Cottidae spp., blennies, Stichaeidae and Pholididae spp.) and gadids (Gadidae spp.). The proportion of high-lipid fishes in the diet was positively related to chick growth, suggesting that piscivorous seabird chicks benefit from diets with high energy densities during early stages of development. Pigeon Guillemot chick diet showed high annual variation from 1979 to 1997, presumably because of fluctuations in abundance of Pacific sand lance, a high-lipid schooling fish. Regression analyses suggest that, at the population level, the percent occurrence of high-lipid fishes in the diet affected chick growth rate. We conclude that Pigeon Guillemots benefit by specializing when selecting prey for their chicks, and that high-lipid schooling fishes promote higher chick growth and reproductive success than low-lipid demersal fishes.

Within both marine and terrestrial populations of generalist predators, individuals have been identified that demonstrate high degrees of prey specialization (Tinbergen 1960, West 1988, Werner and Sherry 1987, Wendeln et al. 1994). Differences in patterns of prey choice between individuals within populations are of interest from an ecological standpoint because they represent alternate strategies to the general life history challenge of maximizing lifetime reproductive success. Despite this, relatively few studies have compared the reproductive performance of adults within a population that specialize on different prey types (but see Trillmich 1978, Trivelpiece et al. 1980, Pierotti and Annett 1991, Spear 1993). Much more common are studies that relate intra-annual or inter-colony differences in diet to reproductive performance (e.g. Harris and Hislop 1978, Monaghan et al. 1989, Hamer et al. 1991).

Cepphus guillemots eat a wide range of prey types (Bradstreet and Brown 1985, Ewins 1993). Individuals are often highly specialized, however, with adult prey selection patterns differing markedly among conspecifics within the same breeding colony (*C. columba*: Drent 1965, Koelink 1972, Kuletz 1983, Emms and Verbeek 1991; *C. grylle*: Slater and Slater 1972, Cairns 1981, 1984). Guillemot colonies thus present valuable opportunities for studies relating foraging ecology to reproductive performance. Because adults with differing prey selection patterns are found within the same breeding colony, chick growth and reproductive success can be related to adult prey selection patterns without having to account for confounding variables present in inter-annual or inter-colony comparisons.

The guillemot foraging strategy differs from that of other piscivorous alcids. Guillemots often forage solitarily, or in small groups, and primarily select nearshore demersal fishes (e.g., sculpins Cottidae spp., blennies Stichaeidae and Pholididae spp.) for their chicks (Winn 1950, Drent 1965, Cairns 1987a, Ewins 1993). These prey tend to be dispersed, but may be predictable in time and space (Rosenthal 1979, Cairns 1987a). In contrast, most other piscivorous alcids, (e.g., murres *Uria* spp., puffins *Fratercula* spp.) feed in foraging flocks on dense aggregations of pelagic schooling fishes (e.g., Pacific sand lance *Ammodytes hexapterus*, Capelin *Mallotus villosus*, Pacific herring *Clupea pallasii*, Gadidae spp.) (Barrett et al. 1987, Piatt 1990, Hatch and Sanger 1992). Given that many pelagic schooling fishes have higher lipid content (gadids are an exception), and consequently higher energy density, than demersal fishes (Montevecchi et al. 1984, Barrett et al. 1987, Hislop et al. 1991, Martensson et al. 1996, Van Pelt et al. 1997, Anthony and Roby 1997), it is perhaps surprising that guillemots do not prey on schooling fishes more extensively. At times high-lipid schooling fishes are available to guillemots, as instances of individual birds specializing in them demonstrate (Slater and Slater 1972, Cairns 1981, Kuletz 1983). Only rarely, however, has it been reported that guillemots exploit schooling fishes to a large degree (see Kuletz 1983).

To better understand the foraging ecology of guillemots we studied chick diet, chick growth, and reproductive success. We tested two main hypotheses, the first being that adults that are highly specialized when selecting prey items for their chicks have higher reproductive success than adults that are less specialized. This might be expected if specializing increases foraging efficiency by reducing prey handling time or enabling adults to select larger or more nutrient-rich prey (Slobodkin and Sanders 1969, Futuyma and Moreno 1988). The second hypothesis is that reproductive success varies as a function of the percent of high-lipid prey items in the chick diet. Adults that select high-lipid prey for their chicks may be expected to have higher reproductive success than those that select low-lipid prey for a number of reasons. Field and laboratory studies of seabird nestling growth suggest that chicks fed high-lipid prey grow faster than chicks fed low-lipid prey because lipids are energy-rich (Harris and Hislop 1978, Massias and Becker 1990, Roby 1991). Because lipids tend to replace water and not protein, high-lipid prey fishes are not typically lacking in other nutrients (Harris and Hislop 1978). A further benefit of high-lipid prey for seabirds is that they generally yield higher assimilation efficiencies than low-lipid prey (Massias and Becker 1990, Brekke and Gabrielsen 1994). By investigating how prey selection habits relate to reproductive performance in Pigeon Guillemots, we gain a better understanding of the selective forces that have shaped the foraging patterns of this unique seabird.

METHODS

Study site.--We studied Pigeon Guillemots during nine years (from 1979 to 1981, 1989 to 1990, and 1994 to 1997) at Naked Island, Alaska (Fig. 1). Naked Island (ca. 3,862 ha) is located in central Prince William Sound (PWS), and is part of a three-island complex. The near shore habitat of this region is characterized by numerous bays and passages with shallow shelf habitat (<30 m) radiating about one kilometer from shore. Naked Island is forested to its 371 m summit, mostly with sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*). Guillemots nest semi-colonially along the island's rocky shorelines. They nest in cavities beneath tree roots overhanging crumbling cliffs, in rock crevices, or among boulders on talus slopes. From 1979 to 1997 the guillemot population at the Naked Island complex declined from 1,871 to 670 birds (Oakley and Kuletz 1996, Golet *unpublished data*). Other members of the Alcidae breeding on these islands include Marbled Murrelets (*Brachyramphus marmoratus*), Parakeet Auklets (*Cyclorrhynchus psittacula*), Tufted Puffins (*Fratercula cirrhata*), and Horned

Puffins (*F. corniculata*). Populations of these species have also declined appreciably in PWS since the 1970's (Irons *unpubl. data*).

Chick diet and prey specialization.--We determined chick diet composition and delivery rates by observing prey items held crosswise in the bills of adults guillemots as they provisioned their chicks. Feeding observations were made with binoculars and spotting scopes from land-based blinds at five colonies. We watched from each blind for an average of four full days, alternating our observations among colonies to ensure that the diet of chicks aged 8 to 30 days was well documented. Because guillemots often pause on the water or on rocks in front of their nests before making deliveries to their chicks, we were usually able to identify the prey items they carried in their bills. Prey items were identified to the lowest possible taxon that we could visually distinguish, and then grouped into the six categories listed in Table 1. Lengths of prey items were estimated visually as multiples of guillemot bill lengths. Because chick diet composition was determined through observation alone, adult behavior and chick growth were not negatively affected.

Guillemot pairs were classified as generalists or one of five specialist types. We classified pairs rather than individual birds because we usually could not distinguish among mates. This classification was appropriate, however, because the reproductive parameters we studied were dependant upon both adult's prey deliveries. We included pairs in our analyses only if ≥10 deliveries were observed in which prey items were identified (as per Pierotti and Annett (1991)), although, on average, 29.3 (max = 148) deliveries were identified per pair. Pairs were classified as specialists (SPEC) when particular prey items or classes of prey items (as defined in Table 1) comprised > 50% of their deliveries, and as generalists (GEN) when they did not meet this criterion. Based on these classifications we examined the distribution of specialist types among colonies and years.

To examine the effects of the proportion of high-lipid fishes in the diet on chick growth and reproductive success, we pooled specialist types according to the energy density of their prey. Sand lance specialists were grouped with herring/smelt specialists because these prey typically are energy-rich (energy densities range from 6 to 8 kJ/g fresh mass, Anthony and Roby 1997). The non-schooling fishes, the gadids (which school, but have low lipid content in the size classes that guillemots select), were combined to form the low-lipid category (energy densities typically < 5 kJ/g fresh mass, Anthony and Roby 1997). Generalists were also included in this category because they delivered only 25.3 % high-lipid fishes, on average.

Data from 1979-1981 were excluded in these analyses because there were few nests in which chick diet, nestling growth and productivity were simultaneously studied. We report diet data from these early years (see Table 1), however, because they relate to the population level effects that we describe between diet and growth rate (see Discussion).

Chick growth and reproductive success.--We determined chick growth and reproductive success at guillemot nests to examine the effects of prey choice on reproductive performance. At hatching we recorded brood size and hatching order. We marked the web of the foot of alpha (the first to hatch, or larger chick, of two-chick nests), and beta (the second to hatch, or smaller chick, of two-chick nests) chicks with a permanent pen to distinguish them from one another until they were old enough for banding. Chicks were weighed and measured at least once every five days from hatching until fledging. Growth rate was calculated as the slope of the regression of mass on age for chicks between 8 and 18 days, the linear phase of the growth cycle (Emms and

Verbeek 1991, Ewins 1993). Because this growth measure is not influenced by the particular asymptote that individual chicks attain (Hussel 1972, Gaston 1985), it has the advantage of being independent of peak and fledging mass, which we also report. We define peak mass as the highest mass measured, and fledging mass as the last mass measured prior to fledging. Peak and fledging mass have been shown to affect fledgling success and subsequent survival, and may well represent the condition of nestlings at their time of highest energetic demand (Perrins et al. 1973). Based on observations made during nest visits we determined hatching success (eggs hatched per egg laid), nestling survival (chicks fledged per egg hatched), and productivity (chicks fledged per egg laid).

Statistics.--General linear models (GLMs) were used to test for effects of prey specialization and the proportion of high-lipid prey in the diet on reproductive performance. We determined the degree of specialization of guillemot pairs with the modified Hill's ratio, $F_{2,1}$ (Alatalo 1981):

$$F_{2,1} = \frac{\dfrac{1}{\sum_{i=1}^{n} p_i^2} - 1}{\exp\left(-\sum_{i=1}^{n} \ln p_i\right) - 1}$$

In this equation, p_i is defined as the number of prey type *i* delivered by the pair in a season divided by the total number of all prey types delivered by that pair in that season, and *n* equals the total number of prey types ($n = 6$, see Table 1). This diversity index has the advantage of not requiring an independent assessment of species richness, which is often a function of sample size (Alatalo 1981). We incorporated this diversity index as an independent variable into our GLMs to test for effects of specialization on reproductive performance. To examine the effects of the proportion of high-lipid prey in the diet on reproductive performance we calculated a high-lipid prey index, which we also included in our GLMs. This was defined as the proportion of prey items observed delivered to each nest that were sand lance or herring/smelt. We also included "year" as a categorical random factor in all GLMs. For binomially distributed data we compared multiple logistic regression models, and tested for significance by assessing the deviance (expressed as a likelihood ratio statistic) of saturated models and models lacking particular effects (Agresti 1990, 1996). We used the Lilliefors test to assess normality with variables having continuous frequency distributions, and compared variables identified as non-parametric with the Kruskal Wallis test or the Mann Whitney *U*- test. The remainder were contrasted with ANOVAs or *t*-tests assuming equal or unequal variance as appropriate. For contingency table analyses, we used loglinear models (SYSTAT 1996), log-likelihood ratio tests (*G*-tests) (Fienberg 1970, Bishop et al. 1975), and Fisher's exact test. For *G*-tests involving only two classes, the Williams correction was applied to reduce the likelihood of type 1 errors (Sokal and Rohlf 1995). Means are presented ± 1 SE. All tests are two-tailed.

RESULTS

Effects of specialization and high-lipid diet on reproductive performance.--Dietary diversity (degree of specialization) and proportion of high-lipid prey in the diet both affected reproductive performance of adult guillemots (Table 2). Dietary diversity was negatively related to overall productivity, suggesting that adults that specialize when selecting prey items for their chicks can raise more young than those that generalize. The difference in reproductive output between specialists and generalists resulted largely from differences in nestling survival, suggesting that the benefits of specializing came during the later part of the nestling stage. Dietary diversity was not found to affect hatching success, chick growth rate, peak or fledge mass. Differences in nestling survival apparently resulted from differences in the size of prey items delivered to chicks, as dietary diversity was negatively related to prey size ($F_{1,79} = 4.57$, $P = 0.036$), but not prey delivery rate ($F_{1,70} = 0.09$, $P = 0.77$).

The percent of high-lipid prey items in the diet was positively related to both nestling survival and overall productivity (Fig. 2). Benefits of feeding chicks high-lipid prey fishes appeared early in the chick-rearing phase, when a significant effect was detected on chick growth rate. The growth rate difference appeared pronounced only among two-chick nests (Fig. 3). In nests with single chicks, growth did not differ according to diet. In two-chick nests, the difference was most apparent among beta chicks, although alpha chicks also had lower mean growth rates when fed mostly low-lipid fishes. Chicks fed more high-lipid fishes did not, however, attain higher peak or fledging masses than chicks fed low-lipid fishes. The higher reproductive performance found among adults that delivered more high-lipid prey apparently resulted from the differences in the nutritional status of the prey, as neither prey size ($F_{1,79} = 1.42$, $P = 0.24$), nor prey delivery rate ($F_{1,70} = 1.6$, $P = 0.22$) varied according to the percent of high-lipid prey delivered by adults.

Prey specialization patterns.--Adult guillemots demonstrated preferences when selecting prey items for their chicks. From 1989 to 1990 and 1994 to 1997, 59% of nests had a particular prey type that comprised >50% of the observed deliveries (Table 3). The actual proportion of individuals specializing was likely greater than this, however, because mates within a given nest sometimes differed in their prey selection habits. Guillemots clearly differed in the diversity of prey items that they delivered to their chicks. In 1995 there was even a flatfish specialist (*n* = 34 identified deliveries, 62% flatfish Bothidae spp.), although this prey item comprised < 5% of the diet in the population that year. The proportion of pairs that delivered primarily high-lipid fishes did not differ significantly among the three main colony areas between 1989 and 1997 (*n* = 95 pairs, *G* = 2.00, *P* = 0.59). Thus the availability of high-lipid fishes did not appear to vary among the Naked Island guillemot colonies. We did, however, find significant variability in the relative abundances of particular specialist types from year to year (*n* = 114 identified specialists, *G* = 37.9, *P* = 0.009; Table 3). This variability appeared to be influenced by the overall abundance of particular prey items in the diet (compare Table 1 with Table 3). Because guillemots have strong nest site fidelity (Drent 1965), consistency in prey specialization may be examined by comparing prey selection patterns at individual nests over multiple years. Among nests classified as a particular specialist type in one year, 50% were classified as the same specialist type in the subsequent year. This level of consistency is substantially greater than what would be expected at random (20%). Interannual consistency appeared strongest among blenny specialists (73%) and generalists (55%).

Differences among Years.--On average 82 ± 4% of the prey items observed delivered to the chicks were identified each year. Significant variability was found among years in the items delivered (*n* = 5,534 prey deliveries, *G* = 1908, *P* < 0.001; Table 1), with schooling fishes fluctuating most in their percent occurrence. Pacific sand lance declined steadily from a high of 60% of the prey deliveries in 1979 to a low of 10% in 1994 & 1995. Variability was also high in the herring/smelt category (0 - 25%), and among the gadids (1 - 37%). In contrast, demersal fishes, such as blennies and sculpins, remained relatively constant in the chick diet among years.

DISCUSSION

Benefits of prey specialization in guillemots.--Adults that specialized when selecting prey items for their chicks had higher reproductive success than those that generalized, apparently due to differences in foraging efficiency. This finding is important, as empirical support for a trade-off between foraging efficiency and dietary diversity has seldom been found (Leigh 1990, Cockburn 1991).

To forage efficiently, organisms must develop and maintain accurate environmental representations of prey distribution and abundance (Dall and Cuthill 1997). Such representations are always incomplete, however, because individuals are limited in terms of the time, energy, and cognitive resources that they can allocate to prey sampling (Real 1992). Moreover, for generalists, representations of particular prey are expected to be less accurate than for specialists, due to differences in prey sampling frequency (Dall and Cuthill 1997). Apparently this was the case for guillemots in our study, although the particular mechanism whereby specialization led to increased foraging efficiency deserves further explanation.

Specialists did better than generalists not because they selected more energy-rich prey (this effect was factored out in the GLM), nor because they delivered prey more frequently, but rather because they selected larger prey for their chicks. In guillemots, which deliver prey items one at a time to their chicks, it may be more advantageous to modify the size of the prey items delivered than their rate of delivery. Although both modifications may increase the rate at which energy is provisioned to the nestlings, delivering larger prey likely entails lesser increases in energy expenditure than delivering prey more frequently, since it does not require additional trips to and from the foraging grounds. A further benefit of increasing the size of the prey delivered is that it does not necessarily increase the exposure of the nestlings to predators, as more frequent nest visitation might. The main benefit of specializing appeared to be increased nestling survival. Specialization did not affect chick growth rates, suggesting that during the early stages of nestling development prey quantity may be less important than prey quality (see below).

Patterns of prey choice in generalist predators.--Benefits of a high-lipid diet were evident early in the nestling period. Chick growth rates were positively related to the percent of high-lipid prey in the diet, and this effect was especially pronounced among beta chicks. This finding supports the prediction of Kuletz (1983), who suggested that adults that deliver primarily low-lipid fishes are less likely to fledge a second chick. High-lipid fishes may be a better food source for guillemot chicks because they tend to be more energy-rich, yield higher assimilation efficiencies (Massias and Becker 1990, Brekke and Gabrielsen 1994), and have less cartilaginous and bony parts than their low-lipid counterparts.

In other studies that demonstrated effects of diet choice on reproductive performance, the advantages of foraging on particular prey types varied. Delivery rates appeared important in several studies that attributed high reproductive success of particular groups of birds to close proximity of reliable prey. For example, South Polar (*Catharacta maccormicki*) and Brown (*C. lonnbergi*) skuas that specialized on nearby penguin eggs and chicks were more successful raising chicks than those that fed mainly at sea on fish (Trillmich 1978, Trivelpiece et al. 1980). Similarly, Western Gulls (*Larus occidentalis*) that exploited nearby Common Murres (*Uria aalge*) or Brandt's Cormorants (*Phalacrocorax penicillatus*) had higher breeding success than gulls from the same colony that foraged elsewhere (Spear 1993). Among Herring Gulls (*Larus* *argentatus*), however, adults specializing in mussels had higher reproductive success than those specializing on petrels or human refuse not because of differences in energy densities or delivery rates of their prey, but instead because mussels contained a more complete complement of the nutrients required for laying viable eggs (Pierotti and Annett 1991). Thus the mechanisms by which particular prey items benefit individuals appear to vary, supporting the view of Futuyma and Moreno (1988) that there are many sources of natural selection that may favor one foraging strategy or another.

Population level effects.--At the population level the percent of high-lipid fishes in the diet also appears to have affected chick growth rates at Naked Island (Fig. 4). Chicks grew faster from 1979 to 1981, when high-lipid fishes comprised 40 to 60% of their diet, than in 1990 and 1994, when high-lipid fishes comprised only about 10% of their diet. Other studies of guillemots similarly suggest that chicks grow slowly when there are few high-lipid fishes in the diet (Fig. 4). At Mandarte Island, chick growth was 15.6 g/day (linear slope analysis of chick measurements in Drent (1965)) when *Ammodytes* (a high-lipid schooling fish) comprised 4.7% of the diet. At Mitlenatch Island, Emms and Verbeek (1991) measured a growth rate of 14.5 g/day when chicks received 4.6% *Ammodytes* and 1% *Clupea*, and at Skidegate Inlet, Vermeer et al. (1993) measured a growth rate of 15.5 g/day when *Ammodytes* comprised 10% of the chick diet (although their sample size for chick diet was small, $n = 20$). These growth measurements are comparable to the values we recorded at Naked Island when the percent of high-lipid fishes in the chick diet was lowest in nine years of study.

Studies of Black Guillemots in the North Atlantic Ocean further suggest that the proportion of high-lipid fishes in the diet affects chick growth. In Shetland, Black Guillemot growth rates were among the highest recorded for this species (16.9 g/day) when *Ammodytes* was 52% of the chick diet (Ewins 1990, 1992). This contrasts the relatively low growth rate (14.2 g/day) measured for Black Guillemots in Hudson Bay when *Ammodytes* was < 1% of the chick diet (Cairns 1987a).

An effect of diet on reproductive performance was also found in guillemots at the Farallon Islands (Ainley et al. 1990). In cold water years, when rockfish (*Sebastes* spp.) comprised a large portion of the chick diet, fledging weights and reproductive success were higher than in warm water years when rockfish were less often fed to chicks. Although growth rates of chicks were not affected by the percent rockfish in the diet, chicks grew slowly in all years at the Farallons (16.5 g/day, $n = 6$ years), relative to what we observed at Naked Island (19.1 g/day, $n = 9$ years). Perhaps chicks grew more slowly at the Farallons because high-lipid fishes were lacking in their diet. Rockfish tend to have lower lipid content, and hence lower energy density (kJ/g wet mass) than *Ammodytes*, *Clupea*, or *Mallotus* (Van Pelt et al. 1997). Rockfish may also be less easily digested and assimilated than high-lipid fishes due to their numerous spines and thick scales (Eschmeyer and Herald 1983).

Cairns (1987b) hypothesized that among polyphagous seabirds, the availability of a principle prey item may vary considerably before changes occur in parameters such as chick growth rates. Our findings, however, suggest otherwise: In years when the proportion of high-lipid fishes was low in the chick diet, growth rates were also low (Fig. 4). Similar results were found in a 15-year study of the Great Skua (*Catharacta skua*), in Shetland (Hamer et al. 1991). Sandeels (*Ammodytes marinus*), a high-lipid fish, varied from 5 to 95% of the skua chick diet, and their use was positively correlated with chick growth rate. Apparently, for some generalist foragers, there are no suitable replacements for high-lipid fishes in years when they are absent from the chick diet. These results suggest that chick growth may be sensitive to the percent occurrence of a principle prey item in the diet, particularly when there are pervasive differences in prey quality.

Foraging strategies of guillemots.--Our comparisons among years, and among studies, suggest that guillemot chick growth and productivity is maximized when high-lipid fishes comprise a major portion of the prey fed to chicks. Nonetheless, low-lipid fishes (e.g., blennies and sculpins) form the staple of the chick diet for most guillemot populations. These findings present an interesting question to the evolutionary ecologist: Given the apparent selective advantage of foraging on high-lipid schooling fishes, why haven't guillemots evolved (as other piscivorous alcids have) to become more highly specialized in feeding on these prey? The explanation may lie in the relative predictability of prey types. In Prince William Sound, high-lipid fishes, such as *Ammodytes*, have a distribution that is temporally and spatially variable (Blackburn 1979). Low-lipid fishes, by contrast, are predictable; they do not show marked movements during the breeding season (Rosenthal 1979). As a result, low-lipid fishes are probably easier for guillemots to specialize in than high-lipid fishes. Because there are benefits in specialization per se (e.g., increased prey size), foraging on predictable, low-lipid fishes may present a viable alternative to the more common alcid strategy of foraging on ephemeral high-lipid schooling prey.

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LITERATURE CITED

AGRESTI, A. 1990. Categorical data analysis. Wiley, New York.

AGRESTI, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, New York.

AINLEY, D. G ., R. J. BOEKELHEIDE, S. H. MORRELL, AND C. S. STRONG. 1990. Pigeon Guillemot. Pages 276-305 *in* Seabirds of the Farallon Islands (D. G. Ainley and R. J. Boekelheide, Eds.). Stanford University Press, Stanford, California.

ALATALO, R. V. 1981. Problems in the measurement of evenness in ecology. Oikos 37:199-204.

ANTHONY, J. A., AND D. D. ROBY. 1997. Variation in lipid content of forage fishes and its effect on energy provisioning rates to seabird nestlings. Pages 725-729 *in* Forage fishes in marine ecosystems. Proceedings of the international symposium on the role of forage fishes in marine ecosystems. Report no. 97-01, Alaska sea grant college program, University of Alaska Fairbanks.

BARRETT, R. T., T. ANKER-NILSSEN, F. RIKARDSEN, K. VALDE, N. ROV, AND W. VADER. 1987. The food, growth and fledging success of Norwegian puffin chicks *Fratercula arctica* in 1980-83. Ornis Scandinavica 18:73-83.

BISHOP, Y. M., S. E. FIENBERG, AND P. W. HOLLAND. 1975. Discrete multi variate analysis: theory and practice. MIT Press, Cambridge, Massachusetts.

BLACKBURN, J. E. 1979. Demersal fish and shellfish assessment in selected estuary systems of Kodiak Island. Pages 727-852 *in* Principal investigators' final reports, Vol. 6, Outer continental shelf environmental assessment program. National Oceanic and Atmospheric Administration/Bureau of Land Management, Boulder, Colorado.

BRADSTREET, M.. S. W., AND R. G. B. BROWN. 1985. Feeding ecology of the Atlantic alcidae. Pages 263-318 *in* The Atlantic alcidae: The evolution, distribution and biology of the auks inhabiting the Atlantic Ocean and adjacent water areas (D. N. Birkhead and T. R. Nettleship, Eds.). Academic Press, San Diego.

BREKKE, B., AND G. W. GABRIELSEN. 1994. Assimilation efficiency of adult Kittiwakes and Brünnich's Guillemots fed Capelin and Arctic Cod. Polar Biology 14:279-284.

CAIRNS, D. K. 1981. Breeding, feeding, and chick growth of the Black Guillemot (*Cepphus grylle*) in southern Quebec. Canadian Field-Naturalist 95:312-18.

CAIRNS, D. K. 1984. The foraging ecology of the Black Guillemot (*Cepphus grylle*). Ph.D. dissertation, Carleton University, Ottawa, Ontario.

CAIRNS, D. K. 1987a. The ecology and energetics of chick provisioning by Black Guillemots. Condor 89:627-35.

CAIRNS, D. K. 1987b. Seabirds as indicators of marine food supplies. Biological Oceanography

5:261-71.

COCKBURN, A. 1991. An introduction to evolutonary ecology. Blackwell, Oxford.

DALL, S. R. X., AND I. C. CUTHILL. 1997. The information costs of generalism. Oikos 80:197-202.

DRENT, R. H. 1965. Breeding biology of the Pigeon Guillemot, *Cepphus columba.* Ardea 53:99-160.

EMMS, S. K., AND N. A. M. VERBEEK. 1991. Brood size, food provisioning and chick growth in the Pigeon Guillemot *Cepphus columba.* Condor 93:943-51.

ESCHMEYER, W. N., AND E. S. HERALD. 1983. A field guide to Pacific coast fishes: North America. Houghton Mifflin, Boston.

EWINS, P. J. 1990. The diet of Black Guillemots *Cepphus grylle* in Shetland. Holarctic Ecology 13:90-97.

EWINS, P. J. 1992. Growth of Black Guillemot *Cepphus grylle* chicks in Shetland in 1983-84. Seabird 14:3-14.

EWINS, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). *In* The birds of North America, no. 49 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington D.C.

FIENBERG, S. E. 1970. The analysis of multi-dimensional contingency tables. Ecology 51:419-433.

FUTUYMA, D. J., AND G. MORENO. 1988. The evolution of ecological specialization. Annual Review of Ecological Systems 19:207-233.

GASTON, A. J. 1985. Development of the young in the Atlantic alcidae. Pages 319-354 *in* The

Atlantic alcidae: The evolution, distribution and biology of the auks inhabiting the Atlantic Ocean and adjacent water areas (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, San Diego.

HAMER, K. C., R. W. FURNESS, AND R. W. G. CALDOW. 1991. The effects of changes in food availability on the breeding ecology of Great Skuas *Catharacta skua* in Shetland. Journal of Zoology (London) 223:175-88.

HARRIS, M. P., AND J. R. G. HISLOP. 1978. The food of young puffins *Fratercula arctica.* Journal of Zoology (London) 185:213-36.

HATCH, S. A., AND G. A. SANGER. 1992. Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Marine Ecology Progress Series 80:1-14.

HISLOP, J. R. G., M. P. HARRIS, AND J. G. M. SMITH. 1991. Variation in the calorific value and total energy content of the Lesser Sandeel (*Amodytes marinus*) and other fish preyed on by seabirds. Journal of Zoology (London) 224:502-527.

HUSSEL, D. J. T. 1972. Factors regulating clutch size in arctic passerines. Ecological Monographs 42:317-364.

KOELINK, A. F. 1972. Bioenergetics of growth in the Pigeon Guillemot, *Cepphus columba.* M.S. thesis, University of British Columbia, Vancouver.

KULETZ, K. J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding Pigeon Guillemots. M.S. thesis, University of California, Irvine.

LEIGH, E. G. JR. 1990. Community diversity and environmental stability: A re-examination. Trends in Ecology and Evolution 5:340-344.

MARTENSSON, P. E., A. R. LAGER-GOTAAS, E. S. NORDOY, AND A. S. BLIX. 1996. Seasonal changes in energy density of prey on northeast Atlantic seals and whales. Marine Mammal Science 12:635-40.

MASSIAS A., AND P. H. BECKER. 1990. Nutritive value of food and growth in Common Tern *Sterna hirundo* chicks. Ornis Scandinavica 21:187-194.

MONAGHAN, P., J. D. UTTLEY, M. D. BURNS, C. THAINE, AND J. BLACKWOOD. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns *Sterna paradisaea*. Journal of Animal Ecology 58:261-274.

MONTEVECCHI, W. A., R. E. RICKLEFS, I. R. KIRKHAM, AND D. GABALDON. 1984. Growth energetics of nestling Northern Gannets (*Sula bassanus*). Auk 101:334-41.

OAKLEY, K. L., AND K. J. KULETZ. 1996. Population, reproduction, and foraging of Pigeon Guillemots at Naked Island, Alaska, before and after the *Exxon Valdez* Oil Spill. American Fisheries Society Symposium 18:759-69.

PERRINS, C. M., M. P. HARRIS, AND C. K. BRITTON. 1973. Survival of Manx Shearwaters *Puffinus puffinus*. Ibis 115:535-48.

PIATT, J. F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of Capelin. Pages 36-51 *in* Studies in Avian Biology, no. 14 (S. G. Sealy Ed.). Allen Press, Lawrence, Kansas.

PIEROTTI, R., AND C. A. ANNETT. 1991. Diet choice in the Herring Gull: Constraints imposed by reproductive and ecological factors. Ecology 72:319-28.

REAL, L.A. 1992. Information processing and the evolutionary ecology of cognitive architecture. American Naturalist 140:S108-S145.

ROBY, D. D. 1991. Diet and postnatal energetics in convergent taxa of plankton-feeding seabirds.

Auk 108:131-146.

ROSENTHAL, R. J. 1979. EAACS annual report: Shallow water fish communities in the northeast Gulf of Alaska: habitat, evaluation, temporal distribution, relative abundance and trophic interactions. National Oceanic and Atmospheric Administration/Bureau of Land Management.

SLATER, P. J. B., AND E. P. SLATER. 1972. Behaviour of the Tystie during feeding of the young. Bird Study 13:105-113.

SLOBODKIN, L. B., AND H. L. SANDERS. 1969. Brookhaven Symposia in Biology 22:82-95.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. W. H. Freeman, New York.

SPEAR, L. B. 1993. Dynamics and effect of Western Gulls feeding in a colony of guillemots and Brandt's Cormorants. Journal of Animal Ecology 62:399-414.

SYSTAT. 1996. Statistics, SYSTAT 6.0 for Windows. SPSS, Chicago.

TINBERGEN, N. 1960. The Herring Gull's world. Harper Torchbooks, Boston.

TRILLMICH, F. 1978. Feeding territories and breeding success of South Polar Skuas. Auk 95:23-33.

TRIVELPIECE, W., R. G. BUTLER, AND N. J. VOLKMAN. 1980. Feeding territories of Brown Skuas (*Catharacta lonnbergi*). Auk 97:669-676.

VAN PELT, T. I., J. F. PIATT, B. K. LANCE, AND D. D. ROBY. 1997. Proximate composition and energy density of some North Pacific forage fishes. Comparative Biochemistry and Physiology 119A:1-6.

VERMEER, K., K. H. MORGAN, AND G. E. J. SMITH. 1993. Nesting biology and predation of Pigeon Guillemots in the Queen Charlotte Islands, British Columbia. Colonial Waterbirds

16:119-29.

WENDELN, V. H., S. MICKSTEIN, AND P. H. BECKER. 1994. Auswirkungen individueller ernährungsstrategien von flußseeschwalben (*Sterna hirundo*) auf die anwesenheit am koloniestandort. Die Vogelwarte 37:290-303.

WERNER, T. K., AND T. W. SHERRY. 1987 Behavioral niche variation in *Pinaroloxias inornata*, the "Darwin's Finch" of Cocos Island, Costa Rica. Proceedings of the National Academy of Sciences 84:5506-5510.

WEST, L. 1988. Prey selection by the tropical snail *Thais melones:* A study of interindividual variation. Ecology 69:6.

WINN, H. E. 1950. The Black Guillemots of Kent Island, Bay of Fundy. Auk 67:477-485.

TABLE 1. Diet of Pigeon Guillemot chicks at Naked Island, PWS, Alaska. Values reported are percents of the identified deliveries, which averaged 81.5 ± 3.5% of the total deliveries. Prey specialization was studied from 1989-1997.

Year	*n*	Blennies[a]	Gadids[b]	Herring/smelt[c]	Sand lance[d]	Sculpins[e]	Other[f]
1979	525	20.6	1.5	0	60.4	15.4	2.1
1980	622	33.8	7.9	0	40.4	10.3	7.7
1981	431	22.3	1.4	17.6	25.8	12.3	20.7
1989	508	21.1	27.8	25.0	15.0	10.0	1.2
1990	646	38.7	19.7	2.2	11.5	13.0	15.4
1994	927	37.3	36.7	1.6	10.1	11.2	3.0
1995	689	49.3	8.7	11.8	10.2	13.9	6.1
1996	645	39.8	11.8	3.9	17.4	22.6	4.5
1997	541	35.9	7.6	7.0	22.9	19.0	7.6
mean	5,534	33.2	13.7	7.7	23.7	14.2	7.5

[a] crescent gunnel *Pholis laeta*, slender eelblenny *Lumpenus fabricii*, snake prickleback *L.sagitta*, daubed shanny *L. maculatus,* black prickleback *Xiphister atropurpureus*, y-prickleback *Allolumpenus hypochromus*, high cockscomb *Anoplarchus purpurescens*, penpoint gunnel *Apodichthys flavidus*, northern ronquil *Ronquilis jordani*, searcher *Bathymaster signatus*, arctic shanny *Stichaeus punctatus,* snailfish *Liparis* spp.

[b] Pacific cod *Gadus macrocephalus*, Pacific tomcod *Microgadus proximus*, walleye pollock *Theragra chalcogramma.*

[c] Pacific herring *Clupea pallasii*, smelt Osmeridae, including capelin *Mallotus villosus.*

[d] Pacific sand lance *Ammodytes hexapterus.*

[e] ribbed sculpin *Triglops pingelii*, slim sculpin *Radulinus asperllus*, tidepool sculpin *Oligocottus maculosus*, plain sculpin *Myoxocephalus jaok,* roughspine sculpin *Triglops macellus*, armorhead sculpin *Gymnocanthus galeatus*, grunt sculpin *Rhamphocottus richardsonii*, red irish lord *Hemilepidotus hemilepidotus.*

[f] flatfish Bothidae, including rex sole *Glyptocephalus zachirus*, slender sole *Lyopsetta exilis*, dover sole *Microstomus pacificus*, rockfish *Sebastes* spp., Pacific sandfish *Trichodon trichodon*, greenling *Hexagrammos* spp., lingcod *Ophiodon elongatus*, salmon Salmonidae, invertebrates (shrimp *Pandalus* spp., squid *Rossia pacifica*, and crabs).

TABLE 2. Results of general linear model analyses testing for effects of dietary diversity and % high-lipid fishes in the chick diet on Pigeon Guillemot reproductive parameters at Naked Island, PWS, Alaska (1989-1990 and 1994-1997). Multiple logistic regression models[a] of the following type were constructed: Parameter = diversity index (Hill's ratio $F_{2,1}$) + % high-lipid fish (SAN and H/S) in the diet + year. The G statistic is a measure of deviance between the fully saturated model and the model lacking a particular effect. Improved reproductive performance was associated with *reduced* dietary diversity (increased specialization) and *increased* selection of high-lipid prey. Significant P values are in bold face type.

Parameter	Effect[b]	Test statistic	n	P value
Chick growth rate (g/day)	diversity	$F = 0.00$	41	0.99
	% high-lipid	$F = 5.7$	41	**0.023**
Peak mass[c] (g)	diversity	$F = 1.1$	62	0.31
	% high-lipid	$F = 1.1$	62	0.24
Fledge mass[c] (g)	diversity	$F = 2.6$	63	0.12
	% high-lipid	$F = 1.6$	63	0.21
Hatching success (eggs hatched per egg laid)	diversity	$G = 0.77$	65	0.68
	% high-lipid	$G = 3.7$	65	0.16
Nestling survival (chicks fledged per egg hatched)	diversity	$G = 4.5$	58	**0.034**
	% high-lipid	$G = 4.2$	58	**0.041**
Productivity (chicks fledged per egg laid)	diversity	$G = 6.7$	58	**0.01**
	% high-lipid	$G = 8.8$	58	**0.003**

[a] Diversity and proportion high-lipid prey were not autocorrelated (Pearson correlation coefficient = 0.096, Bonferroni probability $P = 0.32$).

[b] The interaction term, diversity x % high-lipid, was nonsignificant in all cases.

[c] Year effect was also significant.

TABLE 3. Percent of guillemot pairs that specialized in particular prey items at Naked Island, PWS, Alaska (1989-1990 and 1994-1997). Values listed are percents of total pairs classified in that year.

Year	*n*	Sand lance	Herring /smelt	Blennies	Gadids	Sculpins	Total specialists	Generalists
1989	28	5.9	23.5	17.7	11.8	0	58.9	41.1
1990	25	5.6	0	22.2	5.6	5.6	39.0	61.0
1994	55	9.4	0	34.4	25.0	3.1	71.9	28.1
1995	29	11.8	11.8	41.2	0	5.9	76.5[a]	23.5
1996	18	0	0	38.5	0	7.7	46.2	53.8
1997	29	11.1	0	38.9	0	11.1	61.1	38.9
All	184	8.8	5.8	32.2	7.1	5.6	58.9	41.1

[a] In addition to the specialists listed, one flatfish specialist was identified in 1995.

FIGURE LEGENDS

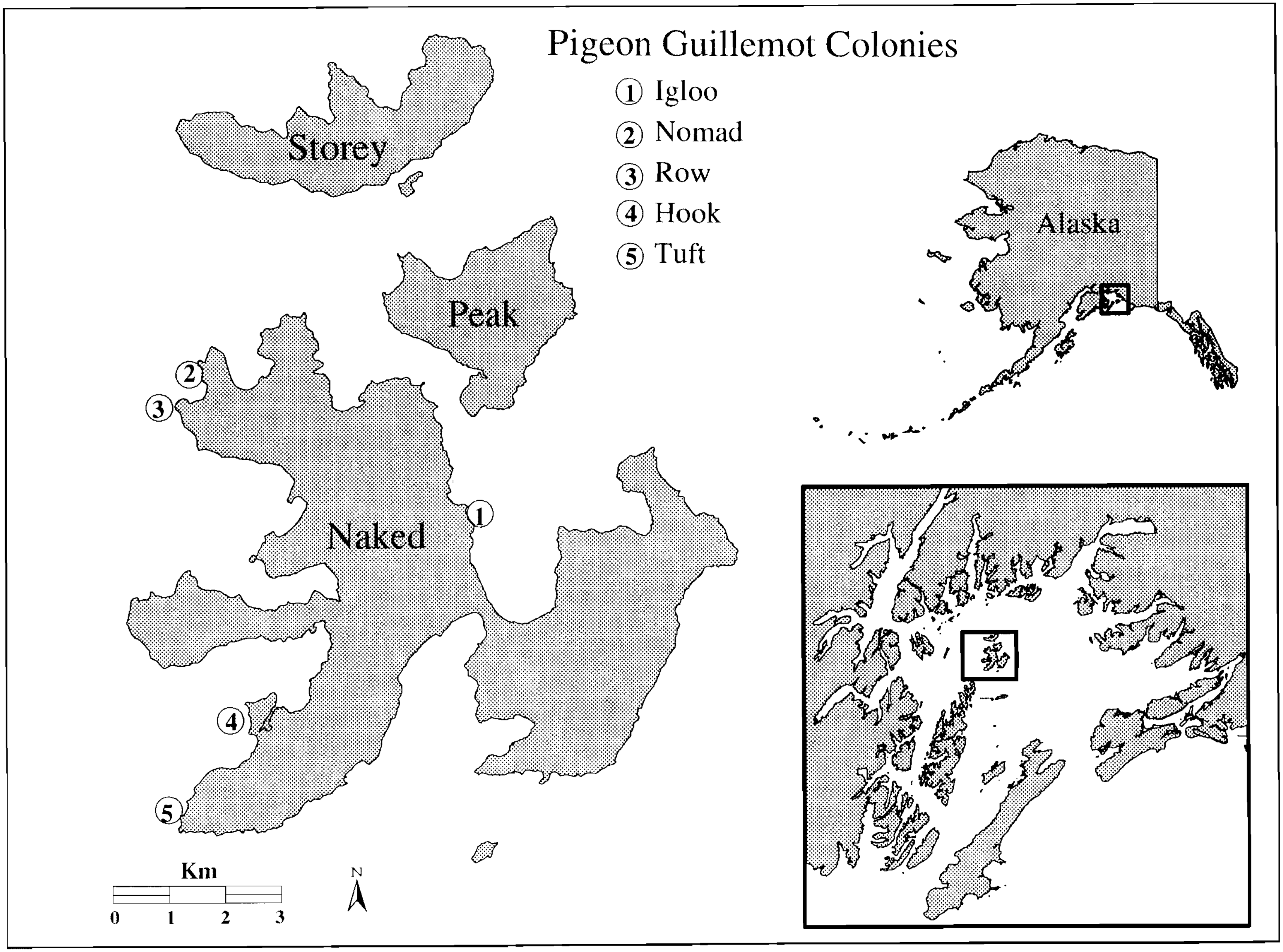
FIG. 1. The Naked Island group with the locations of the five Pigeon Guillemot study colonies indicated by numbered circles. Inset maps show the location of the Naked Island group within Prince William Sound (PWS), and the location of PWS within Alaska.

FIG. 2. Hatching success (eggs hatched per egg laid), nestling survival (chicks fledged per egg hatched), and productivity (chicks fledged per egg laid), at nests with adults specializing in either high-lipid or low-lipid fishes at Naked Island, PWS, Alaska, 1989-1990, and 1994-1997.

FIG. 3. Growth rates (g/day) of Pigeon Guillemot chicks 8-18 days post-hatch fed by adults specializing in either high-lipid or low-lipid fishes at Naked Island, PWS, Alaska, 1989-1990, and 1994-1997.

FIG. 4. Regression of Pigeon Guillemot average chick growth rate on average percent high-lipid fishes in the diet ($Y = 1.17X + 15.1$, $n = 13$ colony-years, $r^2 = 0.70$, $P < 0.001$). The significant regression indicates that a high proportion of high-lipid fishes in the diet has a beneficial effect on chick growth. In all studies the primary high-lipid fish was Pacific Sand lance, *Ammodytes hexapterus*. This figure incorporates data from 5 studies [Naked Island, PWS, Alaska, this study; Mandarte Island, Haro Straight, BC, Drent (1965); Mitlenatch Island, Straight of Georgia, BC, Emms and Verbeek (1991); Skidegate Inlet, Queen Charlotte Islands, BC, Vermeer et al. (1993); and Farallon Islands, CA, Ainley et al. (1990)]. The regression is significant for Naked Island alone, as well ($n = 9$ years, $r^2 = 0.53$, $P = 0.026$). Growth rate values presented were calculated with the linear slope method (Emms and Verbeek 1991, Ewins 1993)

by the original authors, except for Mandarte Island, where values were derived from our analyses of Drent's (1965) chick mass measurements.


Pigeon Guillemot Colonies
① Igloo
② Nomad
③ Row
④ Hook
⑤ Tuft
Storey
Peak
Naked
Alaska
1
2
3
4
5
Km
0
1
2
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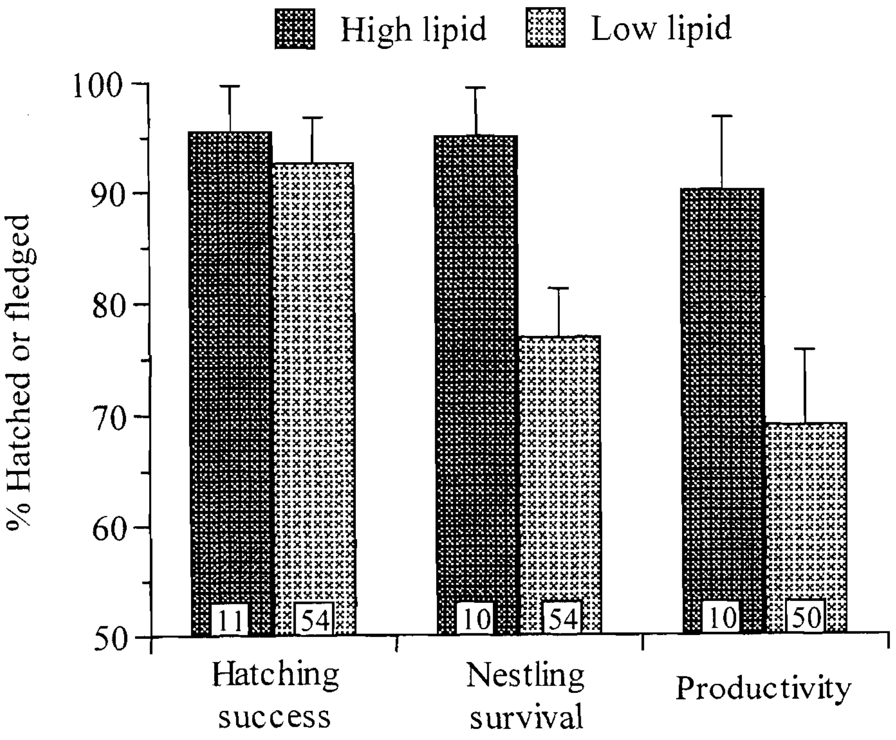
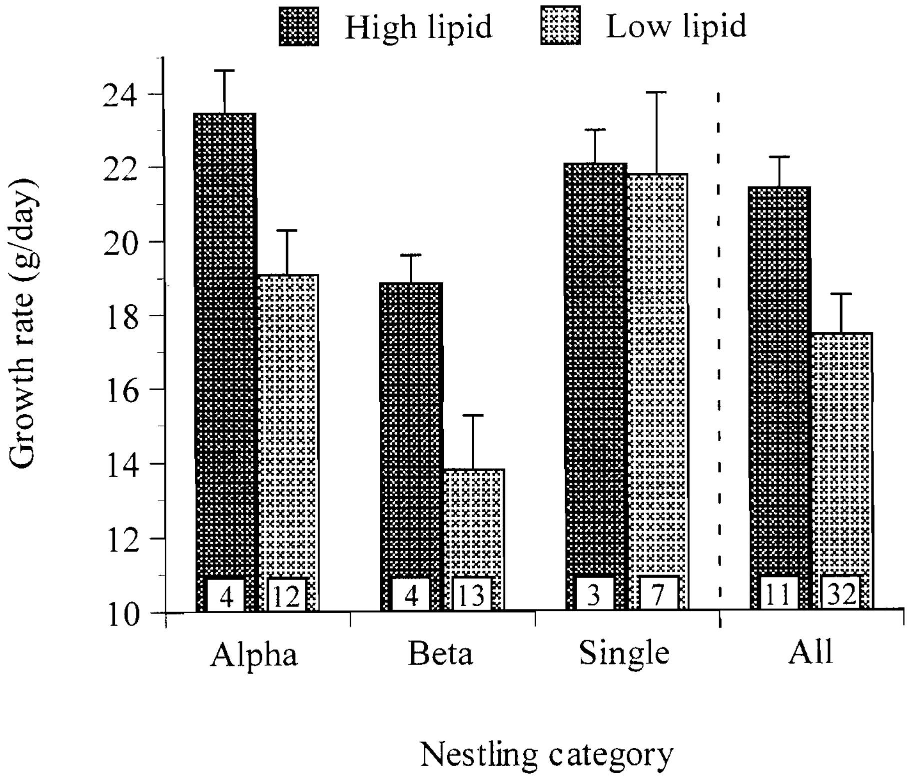
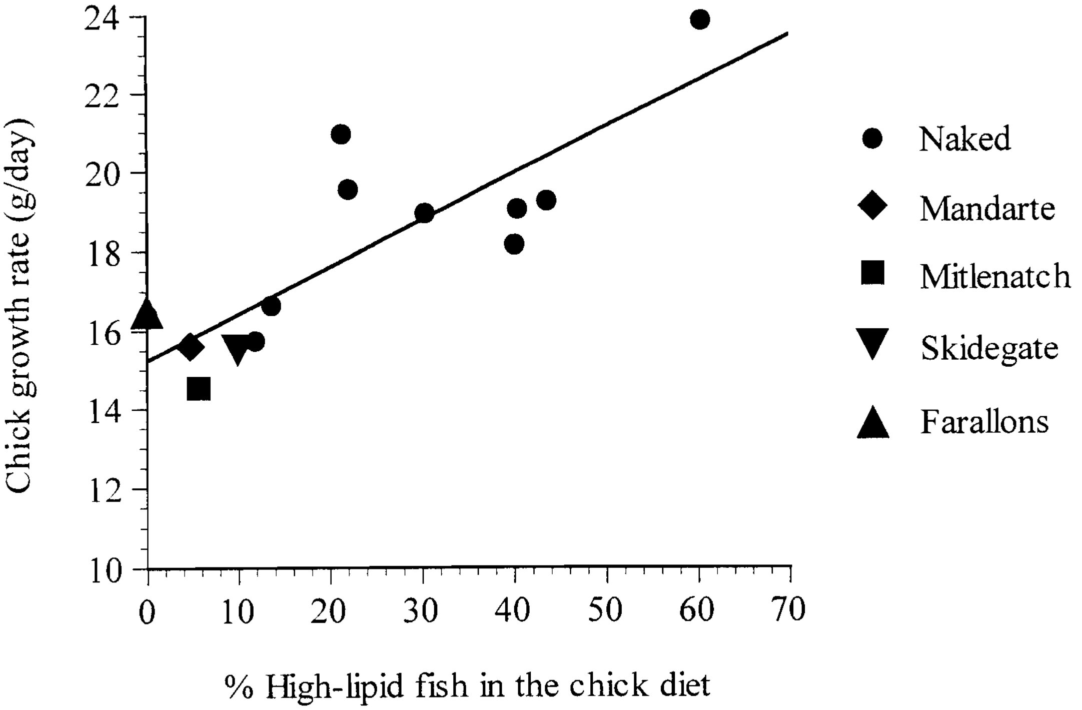

High lipid
Low lipid
% Hatched or fledged
100
90
80
70
60
50
11
54
10
54
10
50
Hatching success
Nestling survival
Productivity


High lipid
Low lipid
Growth rate (g/day)
24
22
20
18
16
14
12
10
4
12
4
13
3
7
11
32
Alpha
Beta
Single
All
Nestling category



Chick growth rate (g/day)
24
22
20
18
16
14
12
10
0
10
20
30
40
50
60
70
% High-lipid fish in the chick diet
● Naked
◆ Mandarte
■ Mitlenatch
▼ Skidegate
▲ Farallons

G Energetics

Exxon Valdez Oil Spill
Restoration Project Annual Report

Diet Composition, Reproductive Energetics, and Productivity of Seabirds Damaged by the *Exxon Valdez* Oil Spill

Restoration Project 98163 G

Annual Report

Start-up Date: May 1, 1998

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

Daniel D. Roby
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March 1999

Study History: Restoration Project 98163 G is similar to the research described in the original proposal submitted as 95118-BAA. It is a component of the Alaska Predator Ecosystem Experiment Project (APEX), for which funding was first approved by the EVOS Trustee Council in April 1995. This research examines the effects of diet composition on the reproductive energetics and productivity of piscivorous seabirds in the northern Gulf of Alaska, using Pigeon Guillemots and Black-legged Kittiwakes as models. Component G works closely with other colony-based research that is part of APEX, including components E, F, J, and M, and provides data for Component Q of APEX (modeling factors limiting seabird recovery). In 1995, study sites for kittiwakes were breeding colonies at Shoup Bay, Eleanor Island, and Seal Island in Prince William Sound, and Gull Island, Chisik Island, and the Barren Islands in Lower Cook Inlet; study sites for guillemots were at Naked Island and Jackpot Island in PWS, and Kachemak Bay in Lower Cook Inlet. In 1996, field research continued with a shift in kittiwake study sites from Seal Island to North Icy Bay. In 1998, all study sites remained the same as in 1996 and 1997 with the exception of adding a Black-legged Kittiwake reference study site at Middleton Island in the northern Gulf of Alaska.

Abstract: A shift in marine trophic structure in the area affected by the *Exxon Valdez* oil spill (EVOS) may have hindered or prevented recovery of injured seabird resources, especially Pigeon Guillemots, Common Murres, and Marbled Murrelets. We studied energetic factors (diet composition, diet quality, meal size, meal delivery rate, adult daily energy expenditure) potentially constraining seabird productivity in the EVOS area, focusing on Pigeon Guillemots and Black-legged Kittiwakes as models of fish-eating seabirds. Energy density (kJ/g wet mass) varied widely within and between species of forage fish; schooling pelagic fishes had relatively high or low values, whereas nearshore demersal fishes were intermediate. Seabirds and other fish-eating predators can experience multi-fold differences in energy intake rates based solely on the types of fish consumed.

1998 was a mediocre or poor year for kittiwake nesting success at most APEX study colonies despite an apparent increase in proportion of after hatching year herring, capelin, and sand lance in the diets at most colonies. Low kittiwake productivity within the study area appeared to be linked to low availability of these species of forage fish within foraging range of nesting colonies early in the breeding season, but was not reflected in poor chick growth later in the breeding season. Similarly, 1998 also was a poor year for Pigeon Guillemot nesting success. Availability of high-quality schooling forage fish within foraging distance of guillemot colonies continues to be positively correlated with energy provisioning rates to guillemot nests, nestling growth rates, and overall productivity.

Key Words: energetics, energy, *Exxon Valdez* oil spill, fish, lipid, proximate composition, seabird, reproduction, trophic.

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EXECUTIVE SUMMARY

This restoration research project is a component of the APEX Project (Alaska Predator Ecosystem Experiment), which is investigating whether low food availability and quality contribute to the failure of some seabird and marine mammal populations to recover from the *Exxon Valdez* Oil Spill (EVOS). The basic premise of APEX is that a shift in marine trophic structure of the EVOS area has prevented recovery of injured seabird resources. Specifically, this research component of APEX addresses whether changes in diet quality may have constrained reproduction in Pigeon Guillemots (*Cepphus columba*), Common Murres (*Uria aalge*), and Marbled Murrelets (*Brachyramphus marmoratus*), all resources injured by the spill. The major hypothesis tested is that differences in the nutritional quality of forage fishes are a primary determinant of energy provisioning rates to seabird nestlings, which influence not only the growth and survival of young, but also other factors that regulate seabird populations (e.g., post-fledging survival and recruitment rates).

Pigeon Guillemots and Black-legged Kittiwakes (*Rissa tridactyla*) were the focal piscivorous seabirds studied during the 1998 breeding season. In cooperation with other APEX projects, we collected samples of nestling diets and measured nestling provisioning rates, growth rates, and nesting success in relation to diet. The two guillemot study sites in Prince William Sound (PWS) were located at Naked Island (an oiled site) and Jackpot Island (a non-oiled site), and were compared with guillemots nesting in Kachemak Bay (a reference site). The three study sites for kittiwakes in PWS were Eleanor Island (an oiled site), North Icy Bay (a non-oiled site), and Shoup Bay (a non-oiled site). The three kittiwake study sites for Lower Cook Inlet (LCI) were at Gull Island, Chisik Island, and the Barren Islands (all reference sites). Black-legged Kittiwakes also were studied on Middleton Island in the northern Gulf of Alaska where USGS biologists have been studying reproduction and behavior using a controlled experimental approach since 1996. In addition, forage fishes were collected using a variety of methods and analyzed in the lab to determine quality as seabird prey.

Forage fish exhibited a ten-fold difference in lipid content (% dry mass) and a five-fold difference in energy density (kJ/g wet mass) among individuals, such that predators could potentially experience large differences in foraging efficiency depending on prey choice (Anthony et al. unpubl. ms.). Schooling pelagic fishes tended to have either relatively high lipid content and energy density (e.g., Pacific herring *Clupea harengus*, capelin *Mallotus villosus*, and juvenile Pacific sand lance *Ammodytes hexapterus*) or low lipid content and energy density (e.g., juvenile walleye pollock *Theragra chalcogramma*, juvenile Pacific cod *Gadus macrocephalus*, and juvenile Pacific tomcod *Microgadus proximus*), whereas nearshore demersal fishes (e.g., blennies, gunnels, sculpins) had intermediate values. Interspecific variation in lipid content was the primary factor influencing energy density of forage fish, with variation in water content also contributing. Lipid content (% dry mass) was negatively correlated with water content (% wet mass) and positively correlated with protein content (% lean dry mass). Thus, in addition to higher energy density, high-lipid fish had higher nutritional value than low-lipid fish in part because of lower water content and higher protein content. Intraspecific differences

in lipid content and energy density of forage fishes were related to size, sex, month, reproductive status, location, and year. Pelagic species maturing at a smaller size (e.g., capelin, sand lance, lanternfish (Myctophidae)) had higher and more variable energy densities than did pelagic or nearshore species maturing at a larger size (e.g., gadids, salmonids). Diet quality for some piscivorous seabirds in the EVOS area is sufficiently variable to affect prey selection.

The diets of Pigeon Guillemots at Naked Island and Kachemak Bay in 1998 were similar to each other but differed from that at Jackpot Island. As in recent years, near-shore demersal fishes were the dominant prey at Naked Island. Sand lance constituted ≤ 25% of prey items delivered at Kachemak Bay for the second year in a row in marked contrast to 1994 - 96 when sand lance dominated the diet. Pigeon Guillemot diets at Jackpot Island in 1998 contained a substantial proportion of Pacific herring, similar to 1994 - 1996 but in sharp contrast to 1997 when herring were notably absent from the diet.

In 1998, energy provisioning rates to Pigeon Guillemot nestlings were highest at Jackpot Island, intermediate at Naked Island, and lowest at Kachemak Bay. Naked Island experienced high nest predation in 1998 and so it is difficult to expand upon relationships among food resources, energy provisioning rates, and productivity at this site. Productivity and energy provisioning rates at Kachemak Bay were poor in 1998, reflecting the continued decline in the proportion of sand lance in the diet. Productivity and energy provisioning rates at Jackpot Island each increased slightly from 1997. Both productivity and energy provisioning rates, however, were still less than values measured in 1995. Energetics and productivity data from all three study sites continue to support the concept that Pigeon Guillemots require high energy provisioning rates to maintain productivity, and that all three components of energy provisioning rate (i.e., meal delivery rate, meal size, and energy density) are critical to their success.

Diets of Black-legged Kittiwakes in 1998 differed from those observed in 1997. The relative biomass of young-of-the-year (YOY) sand lance in the diet of Black-legged Kittiwakes decreased dramatically at all colonies except Eleanor. At the Shoup and Icy bay colonies, YOY sand lance was replaced by 1+ Pacific herring. In contrast the relative biomass of YOY sand lance increased in kittiwake diets at Eleanor Island, whereas the proportion of 1+ capelin declined markedly. Sand lance continued to be a primary prey item at all colonies in Lower Cook Inlet. The proportion of YOY sand lance declined and 1+ sand lance increased in the diet at each LCI colony in 1998 compared with 1997. Other notable diet shifts included a modest increase in the proportion of 1+ capelin and other osmeriids in the diet at the Barren Islands and Chisik Island.

Energy provisioning rates to Black-legged Kittiwake broods at Shoup and Icy bays in 1998 were similar to those observed in 1997. However, energy provisioning rates at Eleanor Island in 1998 decreased appreciably from the previous year. This decrease appeared to be due predominantly to a decline in average meal size. High levels of Peregrine Falcon predation at Eleanor Island in 1998 interfered with collection of chick meals later in the nesting season, when larger meals would have been more prevalent.

Productivity at Shoup Bay in 1998 was similar to 1997, reflecting the similarity in energy provisioning rates, while productivity at Icy Bay improved. In 1998, Icy Bay was the only kittiwake colony where energy provisioning rates exceeded 400 kJ / nest day. Energy provisioning rates at kittiwake colonies in LCI in 1998 were similar to those observed in 1997 and none of these colonies showed an improvement in productivity compared to 1997.

Despite the occurrence of prey items in the diet with relatively high energy density, energy provisioning rates and productivity only improved at Icy Bay in 1998 compared with 1997. Black-legged Kittiwakes in LCI initiated nesting later than usual and this may have been due to a lack of sufficient food resources early in the season. Black-legged Kittiwakes at Shoup Bay in 1998 continued to exhibit low meal delivery rates compared to years of higher productivity, suggesting individuals may have been travelling farther and allocating more time and energy to foraging to obtain prey. In contrast, Black-legged Kittiwakes at Icy Bay had higher feeding frequencies, higher energy provisioning rates, and higher productivity, despite similar diet composition to 1997. These data from LCI and PWS suggest that spatial and temporal availability of forage fish with high energy density may limit productivity of Black-legged Kittiwakes in the EVOS area.

INTRODUCTION

Reproductive success in seabirds is largely dependent on foraging constraints experienced by breeding adults. Previous studies on the reproductive energetics of seabirds have indicated that productivity is energy-limited, particularly during brood-rearing (Roby 1991). Also, the young of most seabird species accumulate substantial fat stores prior to fledging, an energy reserve that can be crucial for post-fledging survival in those species without post-fledging parental care (Perrins et al. 1973; but see Schreiber 1994). Data on foraging habitats, prey availability, and diet composition are critical for understanding the effects of changes in the distribution and abundance of forage fish resources on the productivity and dynamics of seabird populations.

The composition of forage fish is particularly relevant to reproductive success because it is the primary determinant of the energy density of meals delivered to nestlings. Parent seabirds that transport chick meals in their stomachs (e.g., kittiwakes) normally transport meals that are close to the maximum load. Seabirds that transport chick meals as single prey items held in the bill (e.g., guillemots, murres, and murrelets) experience additional constraints on meal size if optimal-sized prey are not readily available. Consequently, seabird parents that provision their young with fish high in lipids are able to support faster growing chicks that fledge earlier and with larger fat reserves (see annual report for APEX Component 98163 N). This is because the energy density of lipid is approximately twice that of protein and carbohydrate. Also, forage fish are generally very low in carbohydrate, and metabolism of protein as an energy source requires the energetically expensive process of excreting the resultant nitrogenous waste. Consequently, the metabolizable energy coefficient (proportion of ingested food energy that is usable by the bird) for diets high in lipids is significantly higher than low-lipid diets (see Annual report for APEX 98163N).

While breeding adults can afford to consume prey that are low quality (i.e., low-lipid) but abundant, reproductive success may depend on provisioning young with high quality (i.e., high-lipid) food items. If prey of adequate quality to support normal nestling growth and development are not available, nestlings either starve in the nest or prolong the nestling period and fledge with low fat reserves.

Forage fish vary considerably in lipid content, lipid:protein ratio, energy density, and nutritional quality. In some seabird prey, such as lanternfishes and eulachon (*Thaleichthys pacificus*), lipids may constitute over 50% of dry mass (Van Pelt et al. 1997; S. Payne, unpubl. data, Anthony et al., unpubl. ms.); while in other prey, such as juvenile walleye pollock and Pacific cod, lipids are frequently less than 5% of dry mass (J. Wejak, unpubl. data; Van Pelt et al. 1997; Anthony et al., unpubl. ms.). This means that a given fresh mass of lanternfish or eulachon may have 3-4 times the energy content of the same mass of juvenile pollock or Pacific cod. By increasing the proportion of high-lipid fish in chick diets, parents can increase the energy density of chick meals in order to compensate for the low frequency of chick feeding (Ricklefs 1984, Ricklefs et al. 1985; Lance and Roby, unpubl. ms.).

Three seabird species that were damaged by the *Exxon Valdez* oil spill (EVOS) are failing to recover at an acceptable rate: Pigeon Guillemot, Common Murre, and Marbled Murrelet. Damage from the spill to a fourth species of seabird, Black-legged Kittiwake, is equivocal, but recent reproductive failures of kittiwakes within the spill area may be due to longer term ecosystem perturbation related to the spill (D. B. Irons, pers. comm.). The status of Pigeon Guillemots and Marbled Murrelets in PWS and Lower Cook Inlet (LCI) has been of concern for nearly a decade due to declines in numbers of adults observed on survey routes (Laing and Klosiewski 1993, D. Zwiefelhofer, pers. comm.). All of these damaged or potentially damaged seabirds are piscivorous and rely to a greater or lesser extent on pelagic schooling fishes during the breeding season.

One prevalent hypothesis for the failure of these seabirds to recover is that changes in the abundance and species composition of forage fish resources within the spill area has resulted in reduced availability and quality of food for breeding seabirds. Concurrent population declines in some marine mammals, particularly harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubata*) have also been blamed on food limitation. Seabirds, unlike marine mammals, offer the possibility of directly measuring diet composition and feeding rates, and their relation to productivity. Thus the piscivorous seabirds breeding in PWS and LCI present an opportunity to assess the relationship between the relative availability of various forage fishes and the productivity of apex predators. Whether these changes in forage fish availability are related to or have been exacerbated by EVOS is unknown.

This study is relevant to EVOS Restoration Work because it is designed to develop a better understanding of how shifts in the diet of seabirds breeding in the EVOS area affect reproductive success. By monitoring the composition and provisioning rates of seabird nestling diets, prey preferences can be assessed. Measuring provisioning rates is crucial because even very poor quality prey may constitute an acceptable diet if it can be supplied at a high rate without substantially increased parental investment. Understanding the diet composition, foraging niche, and energetic constraints on seabirds breeding within the spill area will be crucial for designing management initiatives to enhance productivity in species that are failing to recover from EVOS. If forage fish that are high in lipids are an essential resource for successful reproduction, then efforts can be focused on assessing stocks of preferred forage fish and the factors that impinge on the availability of these resources within foraging distance of breeding colonies in the EVOS area. As long as the significance of diet composition is not understood, it will be difficult to interpret shifts in the utilization of forage fishes and develop a management plan for effective recovery of damaged species.

Guillemots are the most neritic members of the marine bird family Alcidae (i.e., murres, puffins, and auks), and like the other members of the family, capture prey during pursuit-dives. Pigeon guillemots are a well-suited species for monitoring forage fish availability for several reasons: (1) they are a common and widespread seabird species breeding in the EVOS area (Sowls et al. 1978); (2) they primarily forage within 5 km of the nest site (Drent 1965); (3) they raise their young almost entirely on fish; (4) they prey on a wide variety of fishes, including schooling forage fishes (e.g., sand lance, herring, pollock) and subtidal/nearshore demersal fishes (e.g., blennies, gunnels, sculpins; Drent 1965, Kuletz 1983); and (5) the one- or two-chick broods are fed in the nest until the young reach adult body size. Guillemots carry whole fish in their bills to the nest-site crevice to feed their young. Thus individual prey items can be identified, weighed, measured, and collected for composition analyses. In addition, there is strong evidence of a major shift in diet composition of guillemot pairs breeding at Naked Island. Sand lance were the predominant prey fed to young in the late 1970s (Kuletz 1983), but currently sand lance is a minor component of the diet (see annual report for APEX 98168 F). In contrast, guillemots breeding in Kachemak Bay provisioned their young predominately with sand lance in 1994 and 1995, and sand lance is particularly prevalent in the diet at breeding sites that support high densities of nesting guillemots (Prichard 1997).

Black-legged kittiwakes also breed abundantly in the spill area and rely largely on forage fish during reproduction. Unlike guillemots, kittiwakes are efficient fliers, forage at considerable distances from the nest, and capture prey at or near the surface. Although kittiwakes are highly colonial, cliff-nesting seabirds, they construct nests and can be readily studied at the breeding colony without causing substantial egg loss and chick mortality. Like guillemots, kittiwakes can raise one- or two-chick broods, and chicks remain in the nest until nearly adult size. Kittiwake breeding colonies at Shoup Bay, Eleanor Island, and North Icy Bay in PWS are easily accessible so that chicks can be weighed regularly without resorting to technical climbing. Kittiwake colonies at Gull Island, Chisik Island, and the Barren Islands in LCI are not as accessible as the PWS colonies, but acquiring sufficient data on reproductive performance for comparison with PWS colonies is feasible.

This study is component G of the Alaska Predator Ecosystem Experiment (APEX) Project (EVOS Projects 98163 A-T), whose goal is to test the general hypothesis that a shift in the marine trophic structure of the EVOS area has prevented recovery of injured resources.

APEX addresses 10 more specific working hypotheses, 5 of which (hypotheses 4, 7, 8, 9, 10) this component helps test and two of which are the focus of this study:

APEX Hypothesis 8: Changes in seabird productivity reflect differences in forage fish abundance, as measured in adult seabird foraging trips, chick meal-size, and chick meal delivery rates.

APEX Hypothesis 9: Seabird productivity is determined by differences in forage fish nutritional quality.

These two hypotheses address the two primary determinants of energy provisioning rates to nestling seabirds, which in turn have a direct bearing on fitness through variation in reproductive output. Another variable, parental investment, was assumed to remain constant among breeding sites and years. This assumption was tested for kittiwakes in 1997 and 1998 at Shoup Bay and North Icy Bay colonies by measuring parental energy expenditure rates during chick-rearing.

OBJECTIVES

The overall objective of this research is to determine the energy content and nutritional value of various forage fishes used by seabirds breeding in the EVOS area, and to relate differences in prey quality and availability to nestling growth performance and productivity of breeding adults. The research in 1998 emphasized Pigeon Guillemots and Black-legged Kittiwakes.

Objective 1. To determine the proximate composition of various forage fish species consumed by seabirds in the EVOS area as a function of size, sex, age class, and reproductive status, including:

a) lipid content
b) water content
c) ash-free lean dry matter (protein) content
d) energy density (kJ/g wet mass)

Objective 2. To determine dietary parameters of Pigeon Guillemot and Black-legged Kittiwake chicks in the EVOS area, including:

a) provisioning rate (meal size X meal delivery rate)
b) taxonomic composition of diets
c) biochemical composition of diets
d) energy density of diets

Objective 3. To determine the relationship between diet and the growth, development, and survival of seabird nestlings. Variables measured will include:

a) growth rates of total body mass
b) rates and patterns of wing and flight feather growth
c) fledgling body mass
d) fledging age

Objective 4. To determine the contribution of specific forage fish resources to the overall productivity of seabird breeding pairs and populations, including:

- a) relative contribution of each forage fish species to overall energy intake of nestlings
- b) gross foraging efficiency of parents
- c) conversion efficiency of food to biomass in chicks
- d) net production efficiency of the parent/offspring unit
- e) estimates of population-level requirements for forage fish resources during brood-rearing

STUDY AREAS

Data collection from the field occurred in PWS (Naked, Jackpot, and Eleanor islands, and Shoup and North Icy bays), LCI (south shore of Kachemak Bay, Gull, Chisik, and the Barren islands), and Middleton Island during the 1998 breeding season. These sites, with the exception of Middleton Island, were identical to those seabird breeding sites that were used in 1996 and 1997 and by other components of APEX.

Field work on Pigeon Guillemots was conducted at breeding colonies on Naked Island (oiled area), Jackpot Island (non-oiled area, both in PWS), and in Kachemak Bay (reference site). Approximately 500 guillemots nest along the shores of Naked Island (Sanger and Cody 1993), supporting a large proportion of the total breeding population of guillemots in PWS. The field camp in Cabin Bay served as the base camp for field studies of guillemots nesting on the western and northern shorelines of Naked Island (see annual report for APEX Component 98163 F by G. Golet). Naked Island has been the site of long term studies of guillemot reproductive ecology since 1979 by the U.S. Fish and Wildlife Service (Kuletz 1983).

Jackpot Island is a small island in southwestern PWS that supports the highest known breeding density of guillemots in the Sound (G. Sanger, D. L. Hayes, pers. comm.). Jackpot Island has been the site of intensive studies of guillemot nesting success since the 1994 field season and is located in a non-oiled portion of PWS. Kachemak Bay served as a third study site for guillemots. The breeding population of guillemots on the south shore of Kachemak Bay between Mallard Bay and Seldovia has been the site of intensive studies of guillemot breeding biology, diet, and productivity since 1994, first by UAF graduate student A. Prichard, and then by M. Litzow and J. Piatt. Results in 1994-96 suggested that the guillemot prey base in parts of Kachemak Bay is largely sand lance, and is perhaps similar to the prey base at Naked Island 15-20 years ago. Consequently, the Kachemak Bay guillemot study site provides an excellent reference site for guillemot studies in PWS.

Field work on Black-legged Kittiwakes in PWS was conducted at three breeding colonies: (1) Shoup Bay in Port Valdez (non-oiled area), the largest kittiwake colony in PWS consisting of c. 8000 breeding pairs, (2) Eleanor Island in central PWS near Knight Island (oiled area), with ca. 200 breeding pairs, and (3) North Icy Bay in south western PWS (non-oiled area), with ca. 500 breeding pairs. The Shoup Bay colony is the site of continuing long-term studies of kittiwake nesting ecology in PWS by the U.S. Fish and Wildlife Service. Eleanor Island and North Icy Bay have been selected as sites for intensive study for comparison purposes (see annual report for APEX Component 98163 E by R. M. Suryan and D. B. Irons). In Lower Cook Inlet, kittiwake breeding colonies at the Barren Islands, Gull Island, and Chisik Island were monitored for diet and reproductive success (see annual reports for APEX Component 98163 J by D. G. Roseneau, A. B. Kettle, and G. V. Byrd and APEX Component 98163 M by J. Piatt et al.) In addition, a kittiwake colony on Middleton Island in the northern Gulf of Alaska was chosen to directly examine the effects of food availability on daily energy expenditure. Approximately 250 pairs of kittiwakes nest on an artificial structure on Middleton Island and have been under the influence of a supplementary feeding experiment since 1996 (Hatch pers. comm.).

METHODS

Field Data Collection

The research approach utilized a combination of sample/data collection in the field (in conjunction with other APEX components in PWS and LCI) and laboratory analyses of seabird diet and forage fish samples. A minimum of 40 active and accessible nests of each species were located and marked prior to hatching at each of the study colonies, and these nests were closely-monitored until the young fledged or the nesting attempt failed. Samples of forage fishes were collected concurrently with data on seabird reproduction during the 1998 breeding season.

Fresh samples of forage fishes used by guillemots were collected for determination of species composition and proximate composition of the diet. Guillemot diet samples were collected opportunistically when dropped fish were encountered during nest checks or by capturing adults in scraps of mist net as they entered the nest crevice with a chick meal held in their bill. Supplemental samples of fishes fed to guillemot chicks were collected using beach seines and minnow traps deployed in guillemot foraging areas and by netting specimens at low tide during spring tide series.

Adult kittiwakes transport chick meals in the foregut, so chick diet samples consist of semi-digested food. Most kittiwake diet samples were collected when chicks regurgitated during routine weighing and measuring. Additional diet samples were collected by capturing adult kittiwakes as they returned to feed their young and encouraging them to regurgitate the contents of their esophagus. Fresh specimens of forage fishes used by kittiwakes were provided by trawl, cast net, dip net, and other methods through the cooperation of APEX Component 98163 A and others.

Guillemot chick meals, kittiwake regurgitations, and fresh fish samples were weighed (± 0.1 g) in the field on battery-powered, top-loading balances, placed in whirl-paks, and immediately frozen in small, propane-powered freezers that were maintained at each of the study sites. Samples of fresh forage fish, guillemot chick meals, and kittiwake regurgitations were shipped frozen to the lab of Dr. Alan Springer and Kathy Turco at the Institute of Marine Science, UAF, where the third author (KRT) sorted, identified, sexed, aged, measured, and determined reproductive status of specimens in preparation for proximate analysis.

Proximate analysis of all samples was conducted in the lab of the first author (DDR) under the direction of the second author (PGRJ) at the Department of Fisheries and Wildlife, Oregon State University. Forage fish specimens and chick meals were reweighed on an analytical balance (± 0.1 mg) and dried to constant mass in a convection oven at 60^{o}C to determine water content. Lipid content of dried samples was determined by solvent extraction for a minimum of ten hours using a soxhlet apparatus and hexane/isopropyl alcohol 7:2 (v:v) as the solvent system. Lean dry samples were then transferred from extraction thimbles to glass scintillation vials and ashed in a muffle furnace at 600°C for 12 hours in order to calculate ash-free lean dry mass (ca. 94 % protein) by subtraction. Energy density (kJ/g wet mass) and energy content of forage fishes and chick meals were calculated from their composition (% water, lipid, ash-free lean dry matter, and ash), using published energy equivalents of these fractions (Schmidt-Nielsen 1997: 171).

Chick provisioning rates for Pigeon Guillemots and Black-legged Kittiwakes at each of the study sites were determined by monitoring active nests to determine meal delivery rates (meals/day) throughout the 24 h period (dawn to dusk watches). Average meal mass was determined for guillemots using the sample of individual prey items collected at nest sites. Average meal mass for Black-legged Kittiwakes was estimated from average mass of regurgitations recovered from chicks that had just been fed and from adults that had just returned to the colony from foraging trips. These data were supplemented with data on meal size from a few colonies using the periodic weighing technique. Nestlings were weighed in a sample of nests at 2-hour intervals during concurrent watches to determine meal delivery rates. The mass increment between weighings of chicks that were fed was corrected for mass loss between weighings and feedings by adding the average of mass loss in the previous 2-hour period and mass loss in the subsequent 2-hour period to the observed mass increment. This corrected mass increment was used as an estimate of meal size. The product of average meal size (g) and average meal delivery rate (meals/day) was used as an estimate of average quantity of food delivered to a nest daily by a pair of adults (g/(nest day)). The taxonomic and proximate composition of the diet was used to calculate average energy density of chick diets for each species at each site. Finally, the product of average energy density of chick diets (kJ/g wet mass) and average quantity of food delivered (g/(nest day)) was used as an estimate of energy provisioning rates (kJ/(nest day)) for each species at each site.

Active guillemot and kittiwake nests were checked every few days during the hatching period in order to determine hatching date. In the case of two-chick broods, siblings were marked soon after hatching so that individual growth rates could be monitored throughout the nestling period. Nestling growth rates were determined by weighing and measuring chicks on a regular basis (every 3-5 days) throughout the nestling period. Nestling survival rates were calculated from the results of periodic nest checks, using the Mayfield method.

During the fledging period, we attempted to check nests and weigh nestlings more frequently in order to more precisely determine fledging mass and age. Data on nestling body mass, wing chord, and primary feather length were separated by colony for each species.

Parental investment by adult kittiwakes raising broods was assessed by measuring daily energy expenditure (DEE) of breeding adults during the chick-rearing period. DEE was determined by measuring CO_2 production using the doubly-labeled water (DLW) technique (Lifson and McClintock 1966, Nagy 1980, Roby and Ricklefs 1986, Speakman 1997). DEE of adult kittiwakes was measured at the Shoup Bay and North Icy Bay colonies in 1997 and 1998, as representative of kittiwake colonies of different size, productivity, and food availability. Twenty-five nesting adults were injected with doubly-labeled water during the chick-rearing period at each of these colonies. DEE of adult kittiwakes feeding young also was measured at Middleton Island in 1998. Eighty kittiwakes were injected with DLW over 6 days; 40 were birds that received ad libidum supplemental feeding three times / day and 40 were birds that did not receive supplemental feeding.

Parent kittiwakes were captured at the nest with a noose pole and injected intraperitoneally with 0.9 ml (Shoup and Icy bays) or 0.4 ml (Middleton Island) of a mixture of deuterated (99.8 atom %) and oxygen-18 labeled (90 atom %) water ($D_2{}^{18}O$). These two isotopes are stable, so no permits for use of radioactive materials were necessary. Following injection, each adult was banded, weighed, measured, and marked with dye on the plumage for easy recognition on the colony. One hour after injection, when injected DLW had equilibrated with body water, a blood sample was collected from each adult by puncturing the brachial vein and collecting about 100 ul of blood in non-heparinized microhematocrit tubes, which were subsequently flame-sealed and kept refrigerated. Injected adults were then released and an attempt was made to recapture each adult at least once in the subsequent 48-hour period at Shoup and Icy bays or once in the subsequent 24-hour period at Middleton Island. Once recaptured, injected adults were reweighed and a second blood sample collected as described above. Isotope enrichments of blood samples were measured using mass spectrometry in the laboratory of Dr. Henk Visser (Centre for Isotope Research, University of Groningen, The Netherlands). Carbon dioxide production of each adult during each measurement interval was calculated using the equations of Speakman (1997). DEE was calculated from CO_2 production using an assumed RQ of 0.8 and an energetic equivalent of respired CO_2 of 27.3 kJ/liter (Gessamen and Nagy 1988).

RESULTS AND DISCUSSION

Objective 1: Proximate Composition of Forage Fishes

Analysis of proximate composition of forage fishes continued during 1998. Approximately 63 Pigeon Guillemot and 178 Black-legged Kittiwake chick meals were collected and analyzed for the 1998 field season. Notable additions to the prey species analyzed include surf smelt (*Hypomesus pretiosus*) from Chisik Island, euphausiid spp. from Icy Bay, salmon eggs from PWS Black-legged Kittiwake colonies, and a time series of surf smelt from LCI. Results and discussion from analyses completed prior to the

1998 field season represent the majority of these analyses and are presented in the manuscript attached to last years annual report: "Lipid content and energy density of forage fishes from the northern Gulf of Alaska" by J.A. Anthony, D.D. Roby, and K.R. Turco. This manuscript has been submitted to the peer-reviewed Journal of Experimental Marine Biology and Ecology.

Objective 2: Dietary Parameters of Nestling Seabirds

Pigeon Guillemots

Sixty-three Pigeon Guillemot chick meals were collected from the colonies at Jackpot Island, Naked Island, and Kachemak Bay during 1998 (Table 1). Nineteen fish species were identified in the diet and the number of prey species collected at each study area appeared similar (Table 2). However, 13 prey species were unique to a single study area and only two prey species (slender eelblenny *Lumpenus fabricii* and ribbed sculpin *Triglops pingeli*) were collected at all three Pigeon Guillemot study sites. Tables 3-5 show the taxonomic composition, average item mass, and the percent of the total biomass for each prey species at each site.

Pigeon Guillemot nestling diets assessed during day-long nest watches are used to determine the proportion of the total deliveries represented by each prey species or forage-fish group. These are hereafter referred to as meal delivery rate (MDR) diets and appear in Figure 1. MDR diets differed from chick meal collection diets at two sites in 1998 (compare Tables 3-5 with Figure 1). For example, at Jackpot Island, Pacific herring were under-represented and gadids over-represented in the collection diet. Similarly, at Kachemak Bay, gadids and blennies were under-represented and sculpins over-represented in the collection diet. However, as all meals collected at Kachemak Bay were discards, the collection diet may not be entirely accurate. Diet as determined from collections and MDR appeared similar at Naked Island in 1998. These differences demonstrate the importance of collecting both types of diet data.

As in previous years, blennies, crescent gunnels (*Pholis laeta*), and various sculpins (Cottidae) continued to comprise a large proportion of the number of items delivered to the nests of Pigeon Guillemots at all three study areas (Figure 1). This consistent pattern among years at all study areas likely reflects the relative availability of these items near nest sites. Despite the relative importance of these nearshore demersal fishes to nestling diets at all nesting areas in 1998, some differences in diet composition among the three study areas did occur this year. For example, Naked Island and Kachemak Bay diets were the most similar, consisting primarily of nearshore demersal fishes. Sand lance continued to comprise a smaller proportion of the diet at these two sites. However, the Jackpot Island diet differed from these two locations; here, Pacific herring was the most dominant prey item numerically, although nearshore demersals continued to be important. Annual shifts in diets within nesting areas were inconsistent. Diet composition at Kachemak Bay and Naked Island in 1998 was similar to that observed in 1997. The most notable aspect of each of these diets is the relatively low proportion of schooling fish in the diet, especially at Kachemak Bay where sand lance were more prevalent in 1994 - 1996. In contrast, the diet at Jackpot Island in 1998 differed substantially from that of 1997. Pacific herring, which were an important item in the diet of Jackpot Island guillemots in 1994 and 1995, rebounded considerably.

The average mass of chick meals collected at each of the three sites in 1998 appeared similar to values obtained in 1997 (Table 6). Chick meals at Jackpot Island tended to be the largest while those at Kachemak Bay and Naked Island were somewhat smaller (about half the mass of those at Jackpot Island) and similar to each other. Meal size at Jackpot Island and Kachemak Bay in 1998 appeared similar to previous years. Meals collected at Naked Island in 1998, although similar to 1997 in size, still showed an approximate 35% decrease from the first two years of the study.

Feeding frequency also appeared similar among the three study sites, ranging from 11.1 to 13.1 meals delivered per nest day (Table 6). These values and their ranking among sites were similar to 1997. The total amount of food delivered to nests, however, did not appear to be similar among the three study sites in 1998. As in previous years, higher food delivery rates to nests were observed at Jackpot Island (237 g/day) than at Naked Island (130 g/day) or Kachemak Bay (117 g/day). Furthermore, the amount of food delivered to Kachemak Bay nests in 1998 appeared to decrease from 1997 (197 g/day), and although the daily amount of food delivered to Naked Island increased between 1997 and 1998, it was still less than the amount measured in 1995 and 1996 (~165 g/day).

Diet quality in 1998 (as determined by average energy density of collected prey items) was similar among study sites (Table 6). Compared to 1997, however, the average energy density decreased slightly at Kachemak Bay, increased slightly at Naked Island, and remained similar at Jackpot Island. Energy provisioning rates also increased at Jackpot Island and Naked Island but decreased substantially at Kachemak Bay. The increase at Jackpot Island appears to be due to an increase in mean meal size (possibly due to more herring being delivered as opposed to blennies; Table 3) while at Naked Island it appears due to increases in both delivery rate and increased energy density of food. The decrease in EPR at Kachemak Bay was due primarily to a decrease in delivery rate. However, as all of the meals collected at Kachemak Bay nests in 1998 were discards, it is difficult to assess the reliability of the average energy density value used to calculate energy provisioning rate.

Black-legged Kittiwakes

A total of 118 adult and 60 whole chick meals were collected from the six Black-legged kittiwake colonies in PWS and LCI (Table 7). The average number of species / meal ranged from 1.0 to 1.4 at all colonies (Table 8). As in previous years, Pacific herring, Pacific sand lance, and capelin made up the majority of the diet and accounted for 41.1%, 27.3%, and 19.0% of the biomass, respectively, when data were pooled among all six colonies. Pacific herring were more common in meals collected at PWS colonies while at LCI colonies sand lance and capelin were more common (Figure 2). Sand lance, Pacific herring, and capelin combined for the lowest proportion of biomass in the diet

(79%) at Shoup Bay. Shoup Bay kittiwake diets also had the greatest number of species in collected meals.

Diets at each colony in 1998 appeared to shift from those observed in 1997 (Figure 3). In general, PWS colonies experienced an increase in the proportion of 1+ Pacific herring and a decrease in the proportion of YOY sand lance in the diet. The proportion of older sand lance in the diets at Shoup and Icy bays appeared to remain similar in 1998, however. Unlike Shoup and Icy bays, the kittiwakes at Eleanor Island experienced a large increase in the proportion of YOY sand lance in the diet while the proportion of 1+ capelin decreased dramatically. In LCI, all colonies experienced a dramatic decrease in the proportion of YOY sand lance in the diet. Chisik and the Barrens had substantial increases in the proportion of 1+ osmeriids (i.e., capelin and unidentified osmeriids, the latter appears in the 'other' category of Fig. 3), while kittiwakes at Gull Island experienced a dramatic increase in 1+ sand lance. Euphausiid spp., which appeared to be an important part of the diet at the Barrens in 1997, did not occur in the diet in 1998 at any colonies in LCI. Adult meals containing euphausiid spp. were, however, collected at Icy Bay. Additionally, one regurgitation with longfin smelt (*Spirinchus dilatus*) were collected from both Icy Bay and Eleanor Island.

Average nestling meal sizes at all six Black-legged Kittiwake colonies were estimated from the average mass of whole chick and adult regurgitations (Table 9). Unlike 1997, mean meal size in PWS varied more than in LCI. Chick meals collected in 1998 compared with 1997 appeared to decrease in size at Eleanor, the Barrens, and Gull and appeared to remain similar at the other three colonies. Meals at Shoup Bay (24.4 g, n = 59) appeared to be larger than at all other colonies, while meals at Eleanor (~ 10.0g, n =15) appeared to be smaller than those at other colonies. This pattern may have been due to the prevalence of 1+ herring in the diet at Shoup Bay and YOY sand lance in the diet at Eleanor Island (Figure 3). Meal sizes at the other four colonies appeared similar (range 15.6 g - 18.9 g).

As in 1997, feeding frequencies in 1998 appeared to be higher at Icy Bay than at any of the other colonies (Table 9). Additionally, the feeding frequency at Icy Bay appeared to be slightly higher in 1998 than in 1997 while average meal sizes at Icy Bay were similar in 1997 and 1998, resulting in a slight increase in the amount of food delivered to nestlings to ~ 90 g / nest day. Feeding frequencies appeared to be similar between kittiwakes nesting at Eleanor and Gull islands during 1998. Because of differences in average meal sizes at each colony, however, the amount of food delivered to nestlings differed (~ 45g / nest day at Eleanor and ~ 65 g / nest day at Gull). Amount of food delivered to kittiwake nests in the barrens remained similar between 1997 and 1998 (~ 65 g / day) as feeding frequency increased but meal size decreased. The decrease in meal size may be due in part to small sample sizes of meals in 1997 (n = 11) and two meals in 1997 with large amounts of euphausiids (37 g and 40 g). None the less, it still appears that meal size decreased in 1998. Feeding frequency for kittiwakes at Shoup Bay did not change from 1997. These birds had the lowest feeding frequency of any colony during 1998, although lower feeding frequencies may have been partially offset by larger meal sizes. This resulted in ~ 75 g of food being delivered / nest day at Shoup, a slightly higher value than observed in LCI but lower than observed at Icy Bay.

Diet quality (as determined from energy density of collected meals) at Shoup and Icy bays during 1998 remained similar to values observed in 1997 (Table 9). Energy density of meals at Eleanor Island, however, appeared to decrease from 1997. This led to a greater range in mean energy density values at the three PWS colonies. At LCI colonies, energy density values appeared to be less divergent than in 1997.

Energy provisioning rates appeared to remain similar at 4 colonies (Shoup Bay, Icy Bay, Barren Islands, and Gull Island) and decrease at one (Eleanor Island; Table 9). Energy provisioning rates were not available for Chisik Island due to total colony failure. As in 1997, the energy provisioning rate was highest at Icy Bay. All 1998 energy provisioning rate values are, however, still lower than those observed during 1995 and 1996 at Shoup Bay. Feeding frequencies appear to be limiting energy provisioning rates at Shoup Bay and the Barrens, while meal size appears to have limited energy provisioning rates at Gull this year. The extreme drop in energy provisioning rate at Eleanor was due to smaller meal sizes which were likely due to wide-spread nest predation and a decrease in sampling effort during the latter portions of the breeding season, when larger meals and a shift in diet to capelin likely would have been observed. In 1998, energy provisioning rate was > 400 kJ/nest day only at Icy Bay.

Objective 3: Diet and Productivity

Pigeon Guillemots

Nesting productivity of Pigeon Guillemots in 1998 was mediocre to poor at all three study sites. Mink nest predation was the primary cause of poor productivity at Naked Island, although prior to much of the predation chick growth rates appeared to be poor also. These results are in agreement with the low energy provisioning rates observed at Naked Island in 1998. In fact, energy provisioning rates at Naked Island were substantially lower in 1997 and 1998 when compared to 1995 and 1996, although even those energy provisioning rates were low compared to 1995 at Jackpot Island. Productivity of Pigeon Guillemots at Kachemak Bay also was low in 1998, continuing a trend of lowered productivity over the past two years. Similarly, energy provisioning rate at Kachemak Bay in 1998 also was substantially lower than that observed in 1997 and slightly lower than that observed in 1996. Productivity and chick growth rates of Pigeon Guillemots at Jackpot Island in 1998 were similar to those observed in 1997 and greater than those observed at Kachemak Bay and Naked Island in 1998. Similarly, energy provisioning rates at Jackpot Island in 1998 were similar to those observed in 1997 yet substantially higher than those observed at the other two study sites in 1998. Neither productivity nor energy provisioning rates at Jackpot Island have returned to levels observed in 1995 or 1994.

Black-legged Kittiwakes

The productivity of Black-legged Kittiwakes in 1998 was poor at all colonies except Icy Bay despite the prevalence of older Pacific herring, sand lance, and capelin in the diet at each colony. Productivity at Icy Bay in 1998 was the highest recorded over the past few years at any of the study colonies and energy provisioning rates there appear slightly higher than last year. In contrast, productivity at the other five colonies in 1998 was similar to or lower than 1997 levels, although predation was at least partly responsible for lower productivity at Eleanor Island. Similarly, energy provisioning rates at these five colonies also were similar to or lower than those observed in 1996 or 1997, suggesting food resources may be limiting productivity despite the presence of high quality prey in the diet at each colony (Table 9, Figure 3). Delayed nest initiation at Gull Island and the Barren Islands, longer foraging trips at Shoup Bay, lower feeding frequencies at Shoup Bay and Chisik Island, lower meal sizes at Eleanor, Gull, and Chisik islands, and lower forage fish densities from surveys all suggest that availability of high quality prey items may have been limited temporally and spatially in 1998. Furthermore, a comparison of energy provisioning rates and productivity at Black-legged Kittiwakes colonies in PWS and LCI since 1995 suggest a positive correlation between the two metrics and indicate that productivity usually appears to be poor for Black-legged Kittiwakes at these colonies when energy provisioning rates drop below 400 kJ / nest day.

Objective 4: Contribution of Forage Fish Resources to Seabird Productivity

As in 1997, the average Pigeon Guillemot prey size at Jackpot Island in 1998 continued to be higher than at Naked Island or Kachemak Bay. Diet quality appeared to improve at Naked Island and Jackpot Island in 1998; unfortunately, a small sample size of collected meals from Kachemak Bay in 1998 prohibits a sound comparison of energy density values among all colonies. An increased proportion of 1+ Pacific herring in the diet at Jackpot Island compared to last year contributed to the increase in energy density and energy provisioning rates at that colony in 1998. The importance of schooling fish in the diet is further supported by the return of 1+ Pacific herring in the diets of Black-legged Kittiwakes at Shoup and Icy bays. Furthermore, Black-legged Kittiwakes in LCI appeared to be opportunistic and continued to make use of a variety of high energy osmeriids as well as 1+ sand lance. It appears that although such high quality prey items are essential for good/high productivity, mere presence of these items in the diet does not insure high productivity. Other factors, such as sufficient availability near colonies early in the breeding season, affect productivity via the interaction with breeding phenology and feeding frequency. These relationships continue to highlight the importance of collecting an array of data at multiple time and space scales.

In an effort to further improve our understanding of relationships between foraging and breeding biology of seabirds in the northern Gulf of Alaska, we investigated daily energy expenditure (DEE) of Black-legged Kittiwakes in 1997 and 1998. We used doubly-labeled water to measure field metabolic rates of adults with chicks at Shoup and Icy bays in 1997 and 1998. Our objective was to determine if DEE varied among colonies within years or within colonies among years. We also sought to determine if there was a relationship between DEE and either productivity or energy provisioning rate. Furthermore, we examined DEE of Black-legged Kittiwakes at Middleton Island in 1998. Although not located in PWS, Middleton Island provides a unique opportunity to directly examine the role of food availability on DEE. Here, a manipulative experiment has been underway since 1996 with a treatment group of nests receiving ad libidum supplemental food three times / day and a control group of nests receiving no supplemental food each day. We hypothesized that the treatment group would exhibit lower DEE than the control group. We also hypothesized that the treatment group at Middleton would exhibit lower DEE than Black-legged Kittiwakes at Shoup or Icy bays.

Figure 4 shows the distribution of DEE values for Black-legged Kittiwakes at each colony. Despite having only half of the DEE analyses completed from Shoup and Icy bays in 1998, an ANOVA still revealed a significant difference among many of the colony-by-year groups. Kittiwakes at Icy Bay in 1998 had a higher mean DEE than kittiwakes in any of the other groupings and the fed kittiwakes at Middleton Island had a lower mean DEE than kittiwakes in any of the other groupings. There were no other pairwise comparisons that were significantly different. This pattern suggests a convex relationship where DEE and productivity are lower when food availability is low (Shoup Bay 1997 & 1998, Icy Bay 1997), DEE and productivity rise as food availability improves (Icy Bay 1998), and DEE decreases but productivity remains stable or increases as food becomes super abundant (Middleton fed birds). These relationships may become clearer in 1999 when we plan on measuring DEE in conjunction with direct observations of foraging behavior.

CONCLUSIONS

Objective 1: Proximate Composition of Forage Fishes

- Please see manuscript "Lipid content and energy density of forage fishes from the northern Gulf of Alaska" attached to the 1997 annual report.

Objective 2: Dietary Parameters of Nestling Seabirds

Pigeon Guillemots

- As in 1997, nearshore demersal fishes (blennies, gunnels, and sculpins) provided the majority of the biomass in Pigeon Guillemot diets at all three study sites.

- Herring rebounded at Jackpot Island in 1998, with the overall diet appearing more similar to that observed in 1994 - 1996.

- Sand lance did not rebound at Kachemak Bay and continued to comprise a smaller proportion of the diet than observed in 1994 - 1996.

- Energy provisioning rates increased at Jackpot Island (due mostly to an increase in Pacific herring and average energy density of prey) and Naked Island (increase in feeding frequency and energy density). In contrast, energy provisioning rates decreased drastically at Kachemak Bay (sharp drop in feeding frequency).

Black-legged Kittiwakes

- In 1998, 1+ Pacific herring rebounded at Shoup and Icy bays while the proportion of 1+ capelin and osmeriids increased at Chisik Island and the Barrens.

- Young of the year sand lance accounted for less biomass in the diets at all colonies in 1998 compared with 1997, except at Eleanor Island. Despite the relatively high availability of young of the year sand lance at most colonies in 1997, there was not an increase in the biomass of 1+ sand lance in the diets at most colonies in 1998 (with the exception of Gull Island).

- At each colony except Icy Bay, energy provisioning rates in 1998 did not improve and remained < 400 kJ/day. As in 1997, Icy Bay had higher EPRs than all other colonies. EPR at Icy Bay was still less than that observed in 1996 at Shoup Bay, however.

- The diets observed in 1998 appeared to differ from those observed in 1997 at all colonies. Most colonies saw an increase in 1+ schooling fish (Pacific herring in PWS, capelin, unidentified osmeriids, and sand lance in LCI). The exception to this was Eleanor Island, where young of the year sand lance dominated the diet.

Objective 3: Diet and Productivity

Pigeon Guillemots

- Productivity was similar at Jackpot Island in 1998 compared to 1997, in agreement with similar energy provisioning rates between the two years. Productivity was still substantially lower, however, than that observed in 1994.
- Productivity at Kachemak Bay was lower in 1998 than 1997, in agreement with lower energy provisioning rates in 1998.
- Productivity at Naked Island was poor in 1998 due to nest predation by mink.

Black-legged Kittiwakes

- Only at Icy Bay was productivity high in 1998 and improved compared to 1997; energy provisioning rates continued to be > 400 kJ / nest day at Icy Bay.
- Productivity in 1998 at Eleanor Island was low due to nest predation by peregrine falcons.
- Productivity in 1998 at all other colonies was lower than in 1997, in agreement with declines in energy provisioning rates at each colony.

Objective 4: Contribution of Forage Fish Resources to Seabird Productivity

Pigeon Guillemots

- Diet quality improved at Jackpot Island in 1998 concurrent with a return of Pacific herring to the diet; this forage fish species was noticeably absent in 1997.
- Diet quality remained similar at Kachemak Bay and Naked Island, with low proportions of schooling fish in the diet at both sites. The proportion of sand lance in the diets at Kachemak Bay guillemots remained lower than 1994 - 1996.
- Higher proportions of schooling forage fish in the diet was associated with higher energy provisioning rates to chicks.

Black-legged Kittiwakes

- Despite the appearance of generally high quality fish in the diet at each colony, productivity in 1998 remained low at all colonies but Icy Bay. Young of the year sand lance comprised smaller proportions of the diet at each colony in 1998, except at Eleanor Island.
- A variety of other data suggest that, although present in the diet, sufficient quantities of high quality prey may not have been available early enough in the season or near enough to most colonies (with the exception of Icy Bay) to maintain high productivity. This was supported by higher nest failure rates during incubation
- Colonies in LCI relied on capelin and unidentified osmeriids to compliment sand lance in the diet.
- As with last year, the trend in the early years of APEX of higher Black-legged Kittiwake productivity associated with increasing availability of sand lance, capelin, and Pacific herring was not restored, with productivity remaining poor at all colonies except Icy Bay.
- Doubly-labeled water studies of adult kittiwake energetics from PWS and Middleton Island indicated that DEE of Black-legged Kittiwakes may be highest at intermediate levels of food availability.

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LITERATURE CITED

Asbirk, S. 1979. The adaptive significance of the reproductive pattern in the black guillemot, *Cepphus grylle*. Vidensk. Meddr. dansk naturh. Foren. 141:29-80.

Anthony, J.A., D. D. Roby, and K. R. Turco. Unpubl. ms. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Sumitted to J. Exp. Mar. Biol. Ecol.

Ashmole, N. P. 1971. Seabird ecology and the marine environment. Pp. 223-286 in D. S. Farner and J. R. King (eds.), Avian Biology, Vol. 1. Academic Press, New York.

Barrett, R. T., T. Anker-Nilssen, F. Rikardsen, K. Valde, N. Rov, and W. Vader. 1987. The food, growth and fledging success of Norwegian puffin chicks *Fratercula arctica* in 1980-1983. Ornis Scand. 18: 73-83.

Birt-Friesen, V. L., W. A. Montevecchi, D. K. Cairns, and S. A. Macko. 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. Ecology 70:357-367.

Bligh, E. G., and W. J. Dyer. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911-917.

Clarke, A. in press. Seabirds. in R. G. Ackman (ed.), Marine Biogenic Lipids. Chemical Rubber Co.

Dick, M. H., and I. M. Warner. 1982. Pacific sand lance, *Ammodytes hexapterus* Pallas, in the Kodiak island group, Alaska. Syesis 15:43-50.

Dragoo, D. E. 1991. Food habits and productivity of kittiwakes and murres at St. George Island, Alaska. Unpubl. M.S. thesis, University of Alaska, Fairbanks. 104 pp.

Drent, R. H. 1965. Breeding biology of the pigeon guillemot, *Cepphus columba*. Ardea 53:99-159.

Ellis, H. I. 1984. Energetics of free-ranging seabirds. Pp. 203-234 in G. C. Whittow and H. Rahn (eds.), Seabird Energetics. Plenum Press, New York.

Flint, E. N., G. L. Hunt, Jr., and M. A. Rubega. 1990. Time allocation and field metabolic rate in two sympatric kittiwake species. Acta XX Congressus Internationalis Ornithologici, Supplement, pp. 426-427. (Abstract).

Hatch, S. A., G. V. Byrd, D. B. Irons, and G. L. Hunt, Jr. In press. Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. In The status, ecology and conservation of marine birds of the North Pacific, K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey (eds.). Can. Wildl. Serv. Spec. Pub., Ottawa.

Hislop, J. R. G., M. P. Harris, and J. G. M. Smith. 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. J. Zool., Lond. 224: 501-517.

Hunt, G. L., Jr., B. Burgeson, and G. A. Sanger. 1981a. Feeding ecology of seabirds in the eastern Bering Sea. Pp. 629-647 in D. W. Wood and J. A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources. Vol. 1, U.S. Gov. Printing Office, Washington, D.C.

Hunt, G. L., Jr., Z. Eppley, B. Burgeson, and R. Squibb. 1981b. Reproductive ecology, foods and foraging areas of seabirds nesting on the Pribilof Islands, 1975-1979. Environ. Assess. Alaskan Contin. Shelf, Ann. Rep. Princ. Investig. NOAA Environ. Res Lab., Boulder, CO 12: 1-258.

Kuletz, K. J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding pigeon guillemots. M.S. Thesis, Univ. of California, Irvine. 79 pp.

Laing, K. K., and S. P. Klosiewski. 1993. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. Bird Study No. 2. Final Report. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska.

Lance, B. K., and D. D. Roby. Unpubl. ms. Diet and postnatal growth in Red-legged and Black-legged Kittiwakes: an interspecies fostering experiemnt. Submitted to The Auk.

Massias, A., and P. H. Becker. 1990. Nutritive value of food and growth in common tern *Sterna hirundo* chicks. Ornis Scand. 21: 187-194.

Montevecchi, W. A., and J. Piatt. 1984. Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. Comp. Biochem. Physiol. 78A: 15-20.

Montevecchi, W. A., R. E. Ricklefs, I. R. Kirkham, and D. Gabaldon. 1984. Growth energetics of nestling gannets (*Sula bassanus*). Auk 101: 334-341.

Oakley, K. 1981. Determinants of the population size and distribution of the pigeon guillemot (*Cepphus columba*) at Naked Island, Prince William Sound, Alaska. M.S. Thesis, Univ. of Alaska, Fairbanks. 65 pp.

Oakley, K., and K. J. Kuletz. ms. Population, reproduction and foraging ecology of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. Bird Study Number 9. Final Report. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska.

Obst, B. S., K. A. Nagy, and R. E. Ricklefs. 1987. Energy utilization in Wilson's Storm-petrel (*Oceanites oceanicus*). Physiol. Zool.

Prichard, A.K. 1997. Evaluation of Pigeon Guillemots as bioindicators of nearshore ecosystem health. Unpubl. M.S. thesis, Univ. Alaska Fairbanks. 93p.

Prince, P. A., and C. Ricketts. 1981. Relationships between food supply and growth in albatrosses: an interspecies chick fostering experiment. Ornis Scand. 12: 207-210.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pp. 152-292 in R. A. Paynter (ed.), Avian Energetics. Publ. Nuttall Ornithol. Club, No. 15.

Ricklefs, R. E. 1979. Adaptation, constraint, and compromise in avian postnatal development. Biol. Rev. 54: 269-290.

Ricklefs, R. E. 1983a. Some considerations on the reproductive energetics of pelagic seabirds. Studies in Avian Biology No. 8: 84-94.

Ricklefs, R. E. 1983b. Avian postnatal development. Pp. 1-83 in D. S. Farner, J. R. King, and K. C. Parkes (eds.), Avian Biology, Vol. 7. Academic Press, New York.

Ricklefs, R. E. 1984. Meal sizes and feeding rates of Christmas Shearwaters and Phoenix Petrels on Christmas Island, Central Pacific Ocean. Ornis Scand. 15: 16-22.

Ricklefs, R. E., S. C. White, and J. Cullen. 1980a. Postnatal development of Leach's Storm-petrel. Auk 97: 768-781.

Ricklefs, R. E., S. C. White, and J. Cullen. 1980b. Energetics of postnatal growth in Leach's Storm-petrel. Auk 97: 566-575.

Ricklefs, R. E., C. H. Day, C. E. Huntington and J. B. Williams. 1985. Variability in feeding rate and meal size of Leach's Storm-petrel at Kent Island, New Brunswick. J. Anim. Ecol. 54: 883-898.

Ricklefs, R. E., A. R. Place, and D. J. Anderson. 1987. An experimental investigation of the influence of diet quality on growth in Leach's Storm-Petrel. Am. Nat. 130: 300-305.

Roby, D. D. 1989. Chick feeding in the diving petrels *Pelecanoides georgicus* and *P. urinatrix exsul*. Antarctic Science 1: 337-342.

Roby, D. D. 1991a. Diet and postnatal energetics in two convergent taxa of plankton-feeding seabirds. Auk 108: 131-146.

Roby, D. D., and R. E. Ricklefs. 1986. Energy expenditure in adult Least Auklets and diving petrels during the chick-rearing period. Physiol. Zool. 59: 661- 678.

Sanger, G. A., and M. B. Cody. 1993. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. Draft Final Report, Restoration Project 93034, U.S. Fish and Wildlife Service, Anchorage, AK.

Sargent, J. R. 1976. The structure, metabolism and function of lipids in marine organisms. Pp. 149-212 in D. C. Malins and J. R. Sargent (eds.), Biochemical and Biophysical Perspectives in Marine Biology, Vol. 3. Academic Press, London.

Shea, R. E., and R. E. Ricklefs. 1985. An experimental test of the idea that food supply limits growth in a tropical pelagic seabird. Am. Nat. 126: 116-122.

Simons, T. R., and G. C. Whittow. 1984. Energetics of breeding Dark-rumped Petrels. Pp. 159-181 in G. C. Whittow and H. Rahn (eds.), Seabird Energetics. Plenum Press, New York.

Sowls, A. L., S. A. Hatch, and C. J. Lensink. 1978. Catalog of Alaskan seabird colonies. U.S. Dept. Interior, Fish and Wildlife Service, FWS/OBS-78/78.

Speakman, J.R. 1997. Doubly Labelled Water. Theory and Practice. Chapman and Hall, London.

Springer, A. M. 1992. A review: walleye pollock in the North Pacific--how much difference do they really make? Fish. Oceanogr. 1: 80-96.

Springer, A. M., and G. V. Byrd. 1988. Seabird dependence on walleye pollock in the southeastern Bering Sea. Pp. 667-677 in International symposium on the biology and management of walleye pollock. Lowell Wakefield Fish. Symp. 7, Alaska Sea Grant Rep. 89-1.

Van Pelt, T. I., J. F. Piatt, B. K. Lance, and D. D. Roby. 1997. Proximate composition and energy density of some north Pacific forage fishes. Comp. Biochem. Physiol. 118A: 1393-1398.

Walsberg, G. E. 1983. Avian ecological energetics. Pp. 161-220 in D. S. Farner and J. R. King (eds.), Avian biology, Vol. 7. Academic Press, New York.

Wanless, S., and M. P. Harris. 1992. Activity budgets, diet and breeding success of kittiwakes *Rissa tridactyla* on the Isle of May. Bird-Study 39: 145-154.

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Table 1. Number of meals collected at Pigeon Guillemot nests from adults, chicks, and discards at three study sites in the northern Gulf of Alaska, July - August 1998.

	Jackpot Island	Kachemak Bay	Naked Island	All sites
Sampling Effort				
No. nests	20	4	12	36
Collection days	17	3	12	32
Dates	7/15 - 8/10	7/10 - 8/01	7/07 - 8/03	7/07 - 8/10
Meals Collected				
No. adult meals	12	0	6	18
No. chick meals	5	0	0	5
No. discard meals	14	13	13	40
Total meals	31	13	19	63

Table 2. Number of items of each prey species collected at Pigeon Guillemot nests at three study sites in the northern Gulf of Alaska, July - August 1998.

Species	# sites	Jackpot Island	Kachemak Bay	Naked Island
Crested Sculpin	1	1	0	0
Great Sculpin	1	0	3	0
Ribbed Sculpin	3	1	1	2
Rough-spined Sculpin	1	2	0	0
Unknown Sculpin	1	0	1	0
Red Irish Lord	1	0	2	0
Northern Ronquil	2	5	0	1
Crescent Gunnel	2	4	0	3
Arctic Shanny	1	0	2	0
Daubed Shanny	1	0	0	2
Snake Prickleback	1	2	0	0
Slender Eelblenny	3	1	1	1
Flatfish	1	0	0	1
Rock Sole	1	0	0	1
Ling Cod	1	0	0	3
Pacific Cod	1	3	0	0
Walleye Pollock	1	4	0	0
Pacific Herring	2	8	0	1
Sand Lance	2	0	3	4
Species richness	19	10	7	10

Table 3. Taxonomic composition, individual mass, and proportion of total prey mass of each prey type delivered to Pigeon Guillemot broods at Jackpot Island, Prince William Sound, Alaska, July - August 1998.

Species	Number of prey items	Average mass g	% Total biomass of prey
Pacific Herring	8	18.19	23.75
Walleye Pollock	4	35.13	22.93
Pacific Cod	3	41.38	20.26
Northern Ronquil	5	12.29	10.03
Rough-spined Sculpin	2	21.50	7.02
Snake Prickleback	2	15.10	4.93
Crescent Gunnel	4	6.82	4.45
Crested Sculpin	1	26.75	4.36
Ribbed Sculpin	1	7.47	1.22
Slender Eelblenny	1	6.42	1.05

Table 4. Taxonomic composition, individual mass, and proportion of total prey mass of each prey type delivered to Pigeon Guillemot broods at Kachemak Bay, lower Cook Inlet, Alaska, July - August 1998.

Species	Number of prey items	Average mass (g)	% Total biomass of prey
Red Irish Lord	2	17.66	25.80
Great Sculpin	3	11.76	25.78
Pacific Sand Lance	3	6.61	14.48
Slender Eelblenny	1	18.90	13.81
Ribbed Sculpin	1	16.72	12.21
Unknown Sculpin	1	6.25	4.57
Arctic Shanny	2	2.28	3.34

Table 5. Taxonomic composition, individual mass, and proportion of total prey mass of each prey type delivered to Pigeon Guillemot broods at Naked Island, Prince William Sound, Alaska, July - August 1998.

Species	Number of prey items	Average mass (g)	% Total biomass of prey
Crescent Gunnel	3	11.90	18.96
Pacific Sand Lance	4	8.11	17.24
Ribbed Sculpin	2	13.78	14.64
Daubed Shanny	2	11.62	12.34
Ling Cod	3	5.97	9.52
Slender Eelblenny	1	15.89	8.44
Pacific Herring	1	14.33	7.61
Rock Sole	1	14.17	7.52
Flatfish	1	5.99	3.18
Northern Ronquil	1	1.03	0.55

Table 6. Average feeding frequency, meal size, energy density, and energy provisioning rates to Pigeon Guillemot broods at three study sites in the northern Gulf of Alaska, 1995 - 1998.

Location / Year	Feeding frequency (meals/nest day)[1]	Meal size (g)	Energy density (kJ / g wet mass)	Energy provisioning rate (kJ / nest day)[2]
Jackpot Island				
1995	13.8	20.0	4.2	1158
1996	?	?	?	?
1997	12.7	17.1	4.1	890
1998	12.0	19.8	4.2	997
Kachemak Bay				
1995	?	?	5.2	?
1996	10.9	11.4	5.1	634
1997	16.2	12.2	5.0	989
1998	11.1	10.5	4.5	532
Naked Island				
1995	11.4	14.7	4.4	737
1996	11.6	14.2	4.4	725
1997	11.2	9.7	4.0	434
1998	13.1	9.9	4.4	570

[1] Nest days are 16 hour observation periods.

[2] Energy provisioning rate = feeding frequency * meal size * energy density.

Table 7. Number of regurgitated meals collected at Black-legged Kittiwake nests from adults and chicks (whole = complete chick meals, random = partial chick meals) at six colonies in the northern Gulf of Alaska, June - August 1998.

	Adult	Whole	Random	Total
Eleanor Island	10	5	18	33
Icy Bay	25	11	50	86
Shoup Bay	17	42	182	241
Barren Islands	23	2	0	25
Chisik Island	16	0	0	16
Gull Island	27	0	76	103
Total	118	60	326	514

Table 8. Mean (± 1 s.e.) number of prey species / chick meal in regurgitations collected from Black-legged Kittiwakes at six colonies in the northern Gulf of Alaska, June - August 1998.

	Adult	Chick
Eleanor	1.4 (0.16)	1.2 (0.20)
Icy	1.2 (0.52)	1.2 (0.40)
Shoup	1.1 (0.24)	1.4 (0.54)
Barrens	1.3 (0.66)	1.0 (0.00)
Chisik	1.4 (0.81)	--
Gull	1.1 (0.42)	--

Table 9. Average feeding frequency, meal size, energy density, and energy provisioning rates to Black-legged Kittiwake broods at six colonies in the northern Gulf of Alaska, 1995 - 1998.

Location / Year	Feeding frequency (meals/nest day)	Meal size (g)	Energy density (kJ / g wet mass)	Energy provisioning rate (kJ / nest day)
Shoup Bay				
1995	3.3	29.0	4.8	463
1996	4.3	30.6	4.7	618
1997	3.0	22.7	4.9	337
1998	3.0	24.4	4.7	344
Eleanor Island				
1995	4.9	21.3	4.2	441
1996	4.6	23.1	3.8	404
1997	3.9	17.6	4.5	312
1998	4.6	10.5	4.0	193
North Icy Bay				
1996	?	24.5	4.5	?
1997	4.5	19.7	4.6	410
1998	5.1	20.5	4.4	460
Barren Islands				
1996	3.2	20.8	4.0	266
1997	2.2	30.6	4.0	269
1998	3.5	18.9	4.5	297
Gull Island				
1996	4.7	17.2	4.9	396
1997	3.5	23.0	4.6	373
1998	4.1	15.6	5.4	345
Chisik Island				
1996	2.8	24.4	3.4	232
1997	2.7	11.0	5.1	154
1998	Failed	15.9	4.5	?

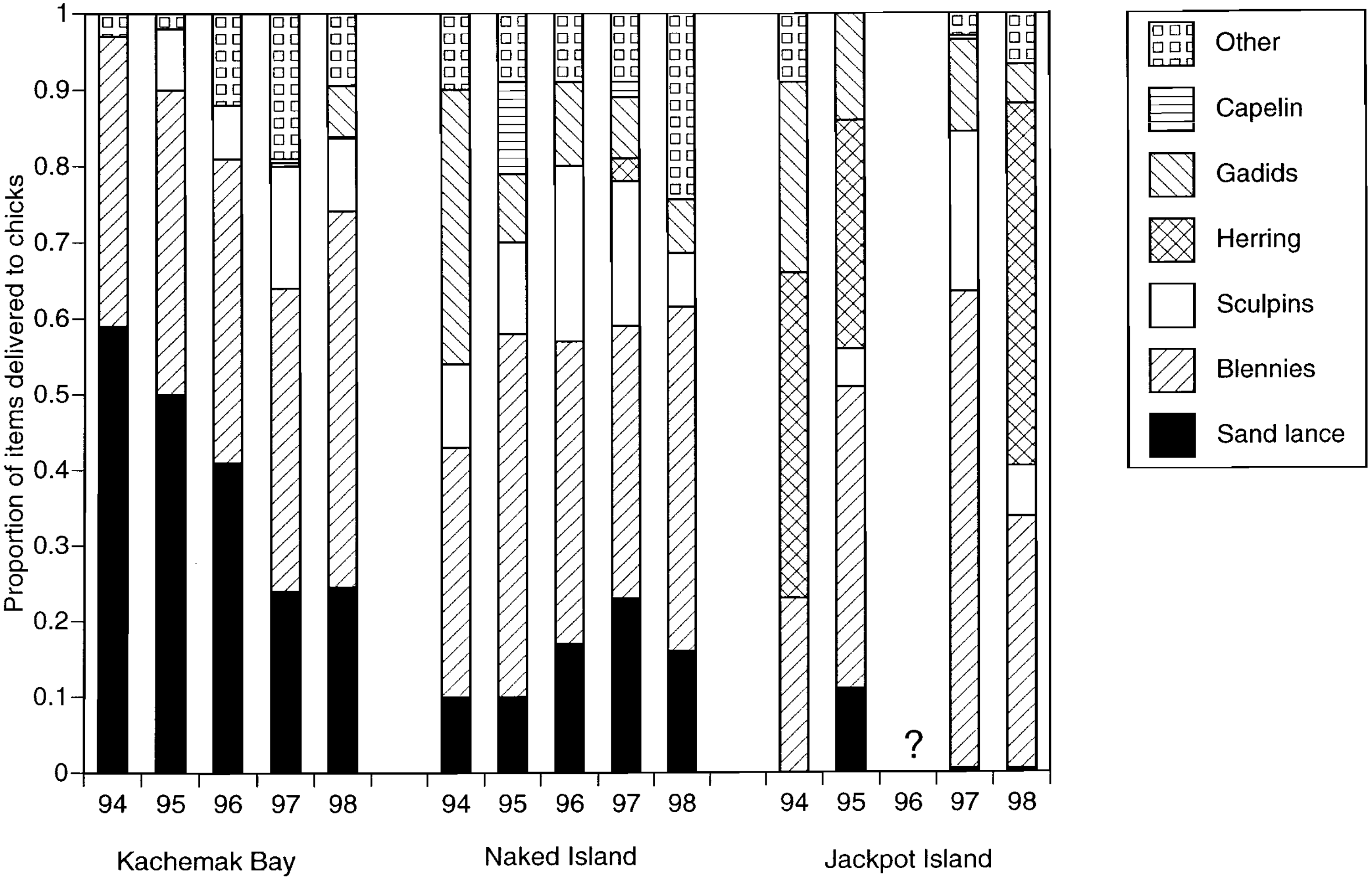
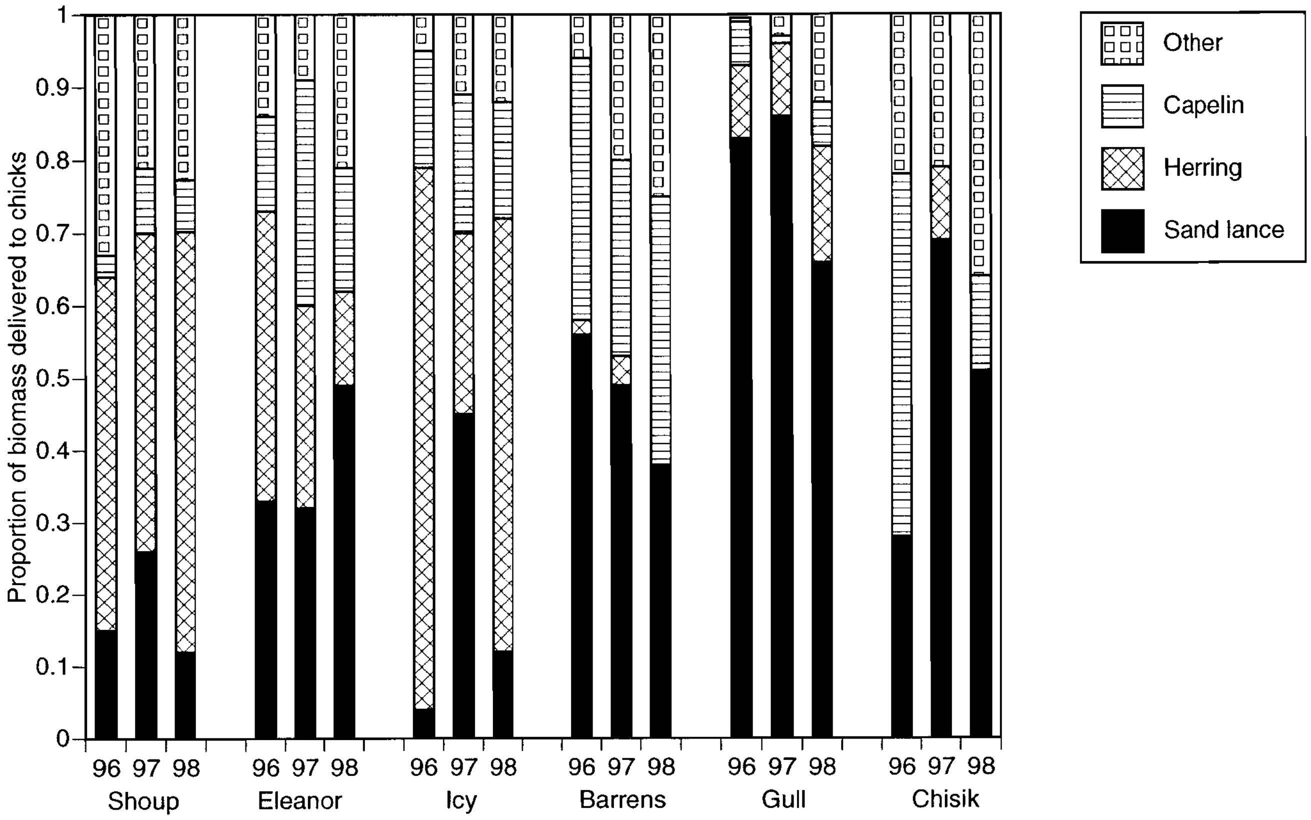

Proportion of items delivered to chicks
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
94
95
96
97
98
94
95
96
97
98
94
95
96
97
98
?
Kachemak Bay
Naked Island
Jackpot Island
Other
Capelin
Gadids
Herring
Sculpins
Blennies
Sand lance

Figure 1



Proportion of biomass delivered to chicks
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
96 97 98
Shoup
96 97 98
Eleanor
96 97 98
Icy
96 97 98
Barrens
96 97 98
Gull
96 97 98
Chisik
Other
Capelin
Herring
Sand lance

Figure 2

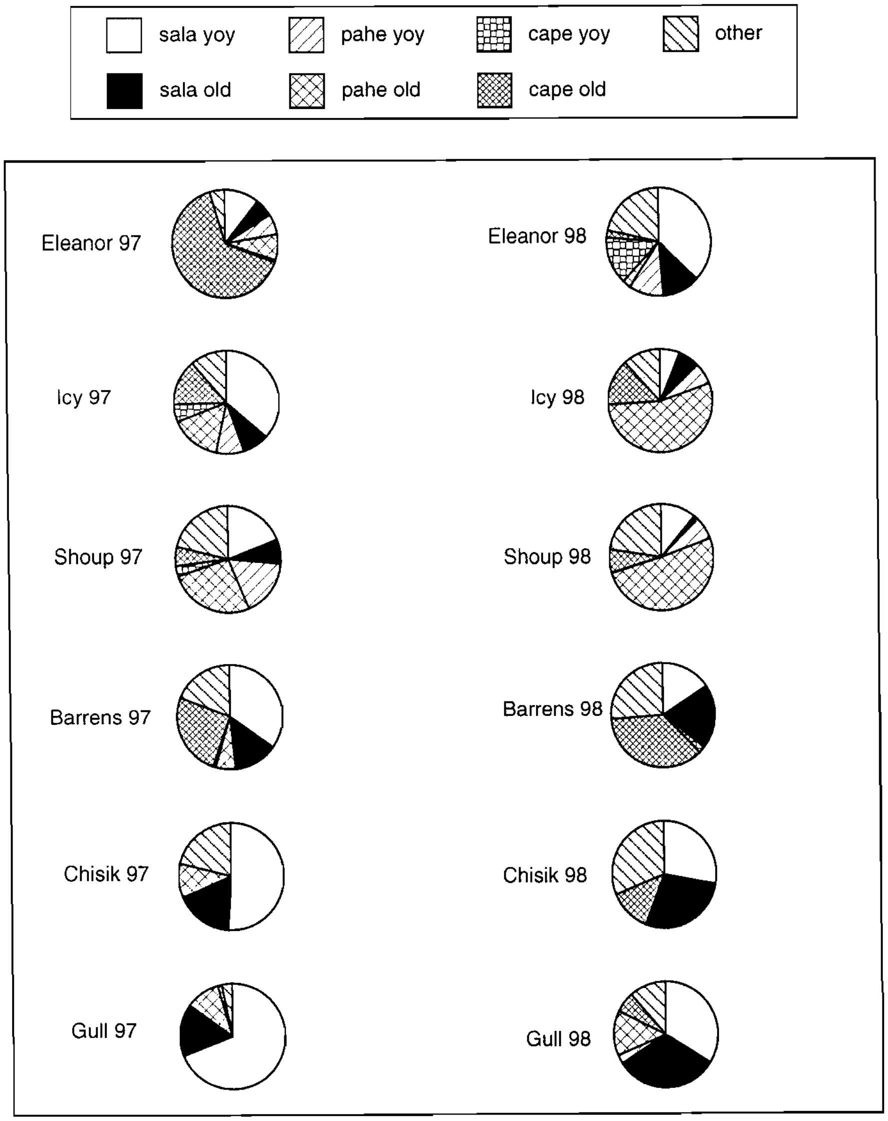

sala yoy
pahe yoy
cape yoy
other
sala old
pahe old
cape old
Eleanor 97
Eleanor 98
Icy 97
Icy 98
Shoup 97
Shoup 98
Barrens 97
Barrens 98
Chisik 97
Chisik 98
Gull 97
Gull 98

Figure 3

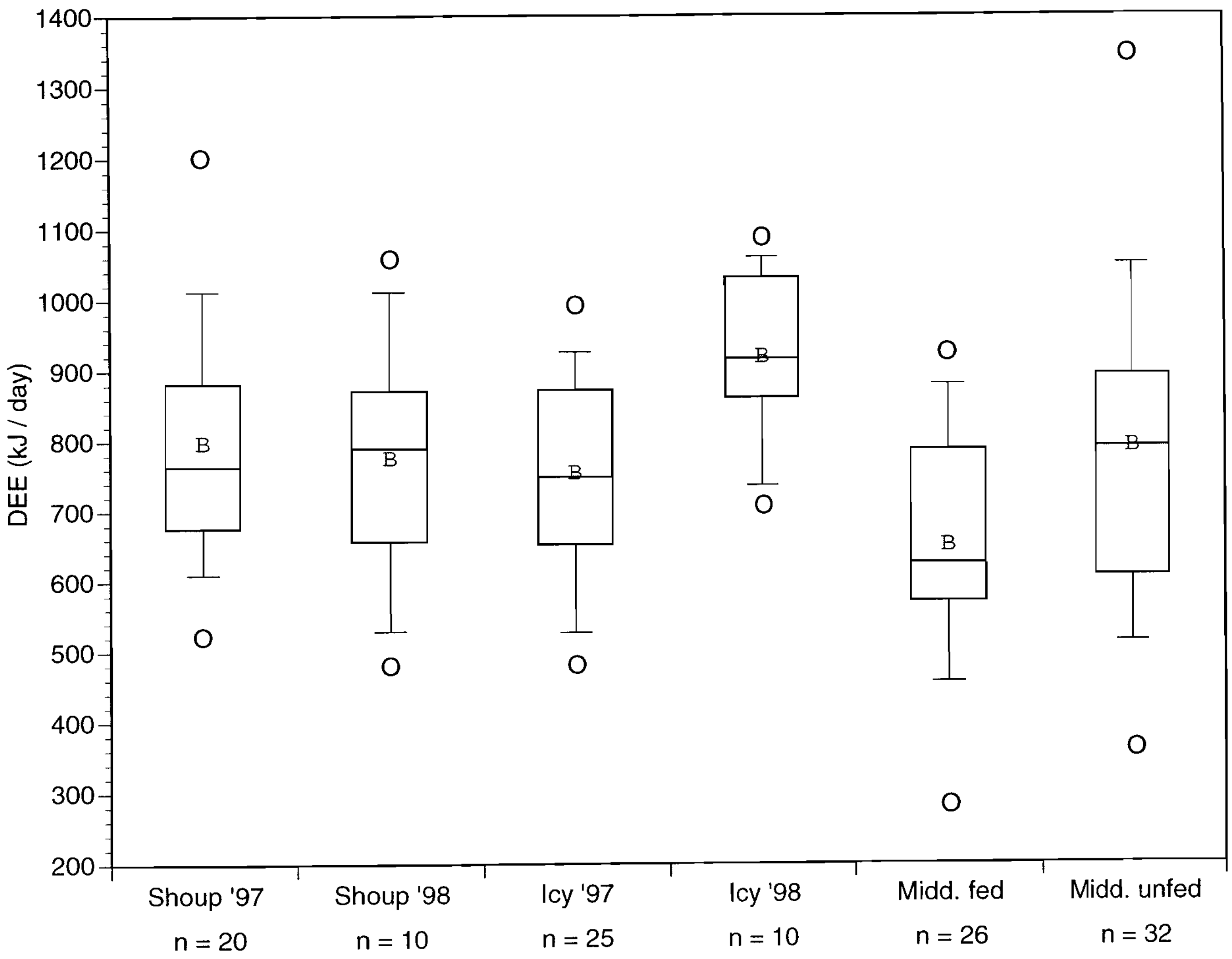

1400
1300
1200
1100
1000
900
800
700
600
500
400
300
200
DEE (kJ / day)
B
O
Shoup '97
n = 20
Shoup '98
n = 10
Icy '97
n = 25
Icy '98
n = 10
Midd. fed
n = 26
Midd. unfed
n = 32

Figure 4.

I Project Leader

Project Number 98163 I Project Leader

This project provides coordination and scientific oversight for the APEX project. It produces the summary document for the APEX annual report and the detailed project description each year. It also identifies research needs or gaps within APEX and liases with other EVOS projects and marine research programs with interests similar to those of APEX.

Project 98163 I does not directly conduct field work. It is involved in three projects, a collaborative one with 98064 to compare forage fish distribution with dive distribution and behavior of harbor seals (details of this may be found under 98064) through a graduate student Tracey Gotthardt, and a project developing electronic cover layers of the distribution of seabird colonies and fish abundance, based on historical data in Prince William Sound, for an ArcInfo Geographic Information Systems, for modelling. Finally, Project 98163 I has developed an APEX web page which can be found at: http://www.uaa.alaska.edu/enri/apex/index.html. A number of other topics have been spun off to other subprojects. 98163 I also coordinated an international Internet effort to document the 1997-98 El Niño, to evaluate how changes in the APEX study area related to changes elsewhere in birds and fish.

J Barren Islands Study

Exxon Valdez Oil Spill
Restoration Project Annual Report

Barren Islands Seabird Studies, 1998

Restoration Project 98163J
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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March 1999

Barren Islands Seabird Studies, 1998

Restoration Project 98163J
Annual Report

Study History: Barren Islands APEX seabird studies began in 1995 (Project 95163J; see Roseneau *et al.* 1996a) and continued through 1996 (Project 96163J; see Roseneau, *et al.* 1997), 1997 (Project 97163J; see Roseneau, *et al.* 1998), and 1998 (Project 98163J).

Abstract: We monitored breeding and foraging parameters of common murres, black-legged kittiwakes, and tufted puffins at the Barren Islands, Alaska, and compared the results with those from studies in 1995-1997. Breeding parameters included productivity, nesting chronology, and chick growth rate; foraging parameters were adult nest attendance, foraging trip duration, chick feeding frequency, and chick meal size. We monitored the prey base by examining chick diets and by beach seining.

During 1998 nesting was late and productivity declined for all three species. Many murres lost first eggs and some relaid. Kittiwakes produced few eggs. Nest attendance by murres during the incubation period was lower than during 1996-1997. Attendance during the nestling period by murres and kittiwakes was similar to that of other years, and kittiwake chicks grew at normal rates. Puffin chicks grew slowly.

The Gulf of Alaska warmed during the late winter-early spring of 1998 and many murres died in the gulf during this period. Foraging conditions may have been poor before the breeding season and during the early part of the nesting period.

Murre chicks were fed almost exclusively capelin, as in 1995-1997. Kittiwake chick diet was similar to that of 1996-1997; it was composed mainly of sand lance and capelin. The proportion of capelin in puffin chick diets increased during 1995-1998.

Results presented in this report are preliminary. Data will be analyzed in greater detail in the Final Report.

Key Words: Barren Islands, black-legged kittiwake, common murre, East Amatuli Island, *Exxon Valdez*, forage fish, *Fratercula cirrhata*, oil spill, Prince William Sound, *Rissa tridactyla*, tufted puffin, *Uria aalge*.

Project Data: (To be addressed in the final report)

Citation: Roseneau, D.G., A.B. Kettle, and G.V. Byrd. 1999. Barren Islands seabird studies, 1998, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 98163J), U.S. Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge, Homer, Alaska.

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INTRODUCTION

This study is a component of the Alaska Predator Ecosystem Experiment (APEX). The APEX Project, initiated in 1995, is composed of 16 related studies designed to determine whether forage fish availability and quality are limiting the recovery of seabird populations injured by the T/V *Exxon Valdez* oil spill. Over the course of the 5-year project, seabird breeding parameters and the distribution, abundance, and energy content of forage fish are being compared among species, years, and study sites in Prince William Sound and lower Cook Inlet-Kachemak Bay to help determine how ecosystem processes affect populations of seabirds nesting in the spill area.

The Barren Islands support some of the largest nesting concentrations of black-legged kittiwakes (*Rissa tridactyla*), common murres (*Uria aalge*), and tufted puffins (*Fratercula cirrhata*) in the spill area. Information on several productivity and population parameters for these species is available from past Barren Islands studies (e.g., Bailey 1975*a,b*, 1976; Manuwal 1978, 1980; Manuwal and Boersma 1978; Nysewander and Dippel 1990, 1991; Dippel and Nysewander 1992; Nysewander *et al.* 1993; Dragoo *et al.* 1995; Boersma *et al.* 1995; Erikson 1995; Roseneau *et al.* 1995, 1996*a,b*, 1997, 1998). The islands' offshore location provides opportunities to compare data from an oceanic environment with results from APEX studies in Prince William Sound and with Minerals Management Service (MMS) and other APEX research in lower Cook Inlet-Kachemak Bay.

Data collected at the Barren Islands are being used to help test 3 APEX hypotheses:

Hypothesis 7: Composition and amount of prey in seabird diets reflect changes in the relative abundance and distribution of forage fish near nesting colonies.

Hypothesis 8: Changes in seabird productivity reflect differences in forage fish abundance as measured by the amount of time adult birds spend foraging for food, amount of food fed to chicks, and provisioning rates of chicks.

Hypothesis 9: Seabird productivity is determined by differences in forage fish nutritional quality.

In 1998 we monitored murre, kittiwake, and puffin productivity and nesting chronology; type and amount of prey fed to chicks; growth rate of kittiwake and puffin chicks; feeding frequency of chicks; and time-activity budgets of kittiwake and murre adults. We counted adults on productivity study plots as one index of population size for each of the 3 species. We also made 30 beach seine sets during the 1998 field season, using methods employed by the Gull and Chisik island studies (Project 98163M).

Data were compared with results from the 1993-1994 EVOS-sponsored Barren Islands common murre restoration monitoring projects (Projects 93049 and 94039; see Roseneau *et al.* 1995, 1996b) and the 1995-1997 APEX Barren Islands seabird studies (see Roseneau *et al.* 1996a, 1997, 1998). Information was shared with other APEX investigators for among-colony comparisons (e.g., Projects 98163E, 98163M, and 98163G).

OBJECTIVES

Objectives of the 1998 Barren Islands seabird studies were to:

1. Determine the productivity of common murres (fledglings/eggs laid), black-legged kittiwakes (fledglings/nests), and tufted puffins (percent of occupied burrows containing chicks).
2. Determine the nesting chronology of common murres, black-legged kittiwakes, and tufted puffins (median hatch date).
3. Determine the fledging size of murre chicks (grams) and growth rate of black-legged kittiwake and tufted puffin chicks (grams/day).
4. Determine the types of prey fed to common murre chicks (composition by number) and to black-legged kittiwake and tufted puffin chicks (composition by number and weight).
5. Determine provisioning rate for common murre and black-legged kittiwake chicks (feedings/nest/hour), and tufted puffin chicks (feedings/nest/day).
6. Obtain an index of the amount of food fed to black-legged kittiwake and tufted puffin chicks (grams/chick regurgitation and grams/nest screen, respectively).
7. Calculate activity budgets for common murre and black-legged kittiwake adults (time spent attending the nest, duration of foraging trips).
8. Measure body condition of adult kittiwakes.
9. Sample near-shore forage fish populations throughout the season with regular beach seine sets using Project 97163M methods.
10. Collect forage fish samples from kittiwake regurgitations, tufted puffin burrow screens, and beach seines for proximate and isotope analyses by other investigators.

METHODS

Study Area

The Barren Islands are located at about 58° 55' N, 152° 10' W, between the Kodiak archipelago and the Kenai Peninsula (Fig. 1). The study was conducted at East and West Amatuli islands, and Amatuli Cove camp served as base of operations (Fig. 2). Data were collected during 10 June-12 September by a team of 4-5 people. Team members commuted to murre and kittiwake study sites in outboard-powered, 4.8-m-long, rigid-hulled inflatable boats, and to puffin study areas by boating and hiking.

Productivity

Murres: Murre productivity data were collected at 10 East Amatuli Island - Light Rock plots established for this purpose in 1993 (see Roseneau *et al.* 1995). Plots contained 19-42 nest sites (sites with eggs) each (1998 nest site total = 286) and were viewed through 7 x 42 binoculars and 15-60 power spotting scopes from land-based observation posts as often as weather permitted (range = 1-5 days). Viewing distances varied from about 50 to 150 m, and each observer was assigned specific plots for the field season. Nest sites were mapped using photographs and sketches, and data were recorded for each site using previously established codes. Plot checks consisted of noting whether nests contained eggs, chicks, or adults in incubation or brooding posture, and counting adults. Plots were checked at least 35 times during 13 June - 4 September, from before eggs were laid until almost all chicks had gone to sea. Plots were treated as sample units and productivity was calculated as fledglings/nest sites. Hatching and fledging success were also calculated. Differences among 1993-1998 results were tested by Analysis of Variance (ANOVA). *Additional information on APEX murre monitoring methods is provided in Appendix 1 of Roseneau et al. 1997.*

Kittiwakes: Kittiwake productivity data were collected from 11 East Amatuli Island plots (5 were established 1993 and 6 in 1995) located on the headlands that contained the murre productivity plots. Plots contained 13-27 nests (1998 nest total = 210; 60 contained eggs). Methods for collecting and analyzing data were similar to those used for murres and for Projects 96163E and 96163M. Nest checks consisted of searching for eggs and chicks (adult postures were not used to determine the content of kittiwake nests) and counting adults. Plots were checked at least 35 times during 13 June - 4 September, from the start of egg-laying until most chicks had fledged. Plots were treated as sample units and productivity was calculated as fledglings/nests. Differences among 1993-1998 results were tested by ANOVA.

Puffins: Puffin productivity data were obtained from 3 study plots established in 1990 by University of Washington personnel for measurement of chick growth rate (see Growth Rates below) and 4 transects totaling 270 m^2 established in 1986 by FWS crews for monitoring numbers and occupancy of burrows (see Nishimoto 1990). Burrows in the growth study plots were first searched for signs of activity (trampled and cleared vegetation, guano from adults and chicks, fresh digging) and nestlings during 30 July - 4 August, when most chicks were about 1 week old. A 35-cm-long flexible scoop was used to help search burrows for nestlings. After the initial visit, burrows containing chicks were checked every 5 days until 11 September. Active burrows, inactive burrows, and nestlings in the 4 transects were counted on 03 September, just prior to fledging.

Data from burrows in the plots and transects were pooled for analysis. Productivity was calculated as: (number of active burrows containing chicks just prior to fledging) / (number of active burrows). The differences among 1995-1998 results were compared with Pearson's Chi-square test.

Hatching success was measured in 5 plots that contained a total of 55 burrows with eggs. Burrows were checked 3 times during the nesting season: just before hatching, just after hatching, and just before most chicks fledged. We calculated hatching success for each plot and then calculated the mean among plots.

Nesting Chronology

Murres: Median hatch date was the measure of murre nesting chronology (see Roseneau *et al.* 1995, 1996*a*,*b*, 1997). The median date was calculated for each of the productivity plots, and the average of these median dates was the annual index for the timing of nesting events. Because laying and hatching of eggs and fledging of chicks were rarely observed, the date that nest sites changed status (i.e., from eggs to chicks) was estimated to be the midpoint between the closest pre- and post-event observation dates. Two methods were used to maintain precision during analysis. First, for nest sites with closer pre- and post-egg-lay observations than pre- and post-hatch observations, the hatch date was calculated by adding 32 days to the lay date (32 days is the average incubation time—see Byrd 1986, 1989; Roseneau *et al.* 1995, 1996*a*,*b*, 1997). Second, nest sites with data gaps of more than 7 days surrounding both laying and hatching were excluded from the data set. Plots were treated as sample units and differences among 1993-1998 results were tested by ANOVA.

Kittiwakes: Median hatch date was also used to measure kittiwake nesting chronology (see Roseneau *et al.* 1996a, 1997). Methods were identical to those described above for murres, except that 27 days (rather than 32) were added when hatch dates were calculated from lay dates (see Byrd 1986, 1989). Because few nests had fledglings in 1998, we grouped some plots to increase the number of nests in the samples. The resulting 6 plots were treated as sample units for 1998; differences among 1994-1998 results were tested by ANOVA.

Puffins: Mean hatch date was the measure of puffin nesting chronology. Because burrows were not visited until puffin chicks were about 1 week old (visiting burrows prior to this time can result in abandonment of eggs or chicks), hatch date was calculated from wing measurements rather than nest status observations. We used a growth equation reported by Amaral (1977) to estimate the age at first wing measurement of each of 41 growth study chicks, and then calculated hatch dates. The chicks' mean hatch date was the index for the season; differences among 1994-1998 results were tested by ANOVA.

Chick Growth Rate

Murres: During 1996 and 1997 we were able to dip-net and measure a sample of murre chicks as they left the cliffs. Because sea conditions were rough during most of the 1998 fledging period, we were able to capture only 3 chicks.

Kittiwakes: Fourteen kittiwake chicks from 13 broods were weighed (to 1 g) and measured (e.g., wing chord, culmen, tarsus, and back of head to tip of bill to 0.1 mm) every 4-7 days, from just after hatching until they were about 30 days old, unless they died at a younger age (6 chicks reached 30 days). Growth rate calculations followed Project 95163E protocol: average daily increase in weight was calculated for each chick for the most linear section of the growth curve (60-300 g) by dividing the difference in weight between the first and last measurements within this range by the number of days between measurements. We averaged these results for 'A' chicks (chicks in single-chick nests plus first-to-hatch chicks in 2-chick nests; *n* = 13) and 'B' chicks (the second-hatched chicks in 2-chick nests; *n* = 1). Using chicks as sample units, differences among 1995-1997 'A' chick growth rates were tested by ANOVA.

Puffins: Thirty-eight puffin chicks in the 3 growth study plots and the FWS transects (see Productivity above) were weighed (to 1 g) and measured (culmen, wing chord, and tarsus to 0.1 mm) every 5 days, from the time they were about 1 week old until they fledged. Weight gain was used as the primary indicator of growth. The rate of increase was calculated for each chick by fitting a simple linear model to the 150-450 g section of the growth curve (the portion that is nearly linear); then the rates were averaged. Among-year differences in growth rate during 1995-1998 were tested by ANOVA.

Chick Diet

Murres: Prey items delivered to murre chicks were identified in parents' bills as they returned to nest sites. Observations were made with 7 x 42 binoculars from a blind located 1-10 meters from nest sites. On 9 days during 9 August - 8 September, 408 prey items were observed. Four hundred-four (99%) of these were identified to species or family groups (e.g. Gadidae) using color and shape of the body and fins (e.g., caudal, anal, adipose fins). We calculated percentages of the total number for 6 categories of prey: capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), Cods (Gadidae), prowfish (*Zapora silenus*), pink salmon (*Oncorhynchus gorbuscha*), and squid (Cephalopoda).

Kittiwakes: Samples of prey brought to kittiwake nestlings were obtained from growth study chicks (*n* = 24 samples), incubating adults (*n* = 10), and adults with chicks (*n* = 14) when they regurgitated while being handled. Chick regurgitations were obtained on 9 days during 18 July - 21 August, when nestlings were about 1-4 weeks old. Samples were weighed (to 0.01 g) and frozen in the field. Prey items were identified, measured, and weighed by K. R. Turco and A. M. Springer, FALCO. Percent composition of the total number and weight were calculated for 11 categories of prey: capelin, Pacific sand lance, Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theregra chalcogramma*), Pacific herring (*Clupea harengus pallasi*), salmonids (*Onchorynchus* spp.), greenlings (*Hexagrammos* spp.), unidentified smelt (Osmeridae), euphausiids (*Thyssanoessa* spp.), squid, and unidentified.

Puffins: Samples of prey brought to puffin chicks by adults were collected by blocking nesting burrows for 3 hours with squares of hardware cloth. When bill loads were collected, they were replaced with freshly-thawed fish caught during beach seining operations; these replacement meals were placed inside the burrows, close to the nest bowl (Wehle 1983 supplemented the diet of tufted puffin chicks with this method). Forty-one bill loads containing 77 prey items were obtained on 7 days at East Amatuli Island and 4 at West Amatuli Island during 13 August - 8 September. Prey items were identified in the field using taxonomic keys and field guides and then cleaned, weighed (to 0.01 g), measured (fork length to 0.1 mm), and frozen. Percentages of the total number and weight were calculated for 9 categories of prey: capelin, Pacific sand lance, Pacific cod, walleye pollock, prowfish, pink salmon, larval fish, squid, and euphausiids.

Amount Fed to Chicks

Murres: Because it would have caused high levels of disturbance to many birds we did not weigh or measure prey brought to murre chicks.

Kittiwakes: We used the weight of regurgitated samples (see Chick Diet, above) as the measure of kittiwake meal size. Because mean meal size increased with the age of chicks until they were about 20 days old, we used as the annual index the average weight of regurgitations collected from chicks 20 days or more of age ($n = 7$). Using regurgitations as sample units, we tested differences among 1995-1998 results by ANOVA.

Puffins: We used the average weight of screen samples ($n = 41$; see Chick Diet, above) as the index for puffin chick meal size. Using each screened bill-loads as sample units, differences among 1995-1998 results were tested by ANOVA.

Chick Provisioning Rate

Murres: Murre chick provisioning rate data were collected on 8 days (9, 11, 14, 15, 20, 22, 27, and 30 Aug) from a plot of 9 nest sites near one of the productivity observation posts. Activities at the nests were recorded with a video camera and a time-lapse recorder set at 5 frames/sec. Frames were labeled with dates and times. Each day's record began before dawn and ended after dusk. Tapes were viewed with a variable-speed player; times of all adult arrivals, chick feedings, departures, and exchanges of brooding duties were entered on a spreadsheet for later analysis. During tape playback it appeared that all recordings started before birds began delivering food to chicks and ended after deliveries had stopped.

During several occasions in 1996-1997, we recorded events on video tape while simultaneously collecting these data by hand with binoculars. Results from the two methods did not differ for feeding frequency, attendance, and times of day when nest activities were first and last visible.

To analyze the data, for each observation day we calculated the average number of feedings/hr for each of the 9 nests, and then averaged the 9 nest-day values. This daily mean was the value used for among-year and among-site comparisons. Data collection times common to the 4 study years were 0700-1959 hr. Results from this interval were tested for among-year differences with ANOVA.

Kittiwakes: Data on kittiwake chick provisioning rate were collected on 28 July and 3, 11, and 14 August from nests containing 10- to 32-day-old chicks. A new plot of 5-7 nests was used each day. At least one adult from each nest was marked with a magic marker and/or leg-banded. Nests were observed with binoculars during 0600-2300 hr. We recorded adult arrival and departure times, and the times that chicks were fed.

Only the first regurgitation to a chick after a parent returned from a trip was scored as a 'feeding', and then only if it occurred within 30 min of an adult's return from a trip of at least 30 min duration. In accordance with Project 97163E protocol, we used the number of feedings per nest per day as the value for comparison among years and project sites. Because there were significant differences in feeding frequency between 1- and 2-chick nests (n = 17 and 5, respectively), we analyzed data from the 2 nest types separately.

In 1995 observations ended at 1959 hr and in 1996 observations began at 0700 hr (instead of encompassing all daylight hours as in 1997-1998). Results from the 4 study years were compared using the block of time common to all years: 0700-1959 hr. Differences among 1995-1998 results were tested with ANOVA.

Puffins: We collected data to measure provisioning rate of tufted puffin chicks by observing adults returning to 8 marked nest burrows in one of the chick growth rate study plots during 4 all-day watches (0600-2230 hr on 19, 23, and 24 Aug and 0600-2200 hr on 30 Aug). Observations began at first light, before adults returned with bill loads, and ended after dusk, when deliveries had ceased. Observations were made with 7 x 42 binoculars from a blind located about 20 m from the burrows. We recorded the times adult returned and departed, and whether returning adults carried bill loads. These observations and those made in 1996-1997 were intended as preliminary investigations of this parameter, and results will be discussed in the Final Report.

Activity Budgets of Adults

Murres: Using data from the all-day observations during the nestling period (see Feeding Rates, above) and 9 days during the incubation period (9, 11, 13, 15, 18, 27, 29, and 31 July and 6 Aug), we calculated the amount of time adult murres spent at their nest sites. Bird-minutes/hour was used to measure nest attendance. For example, if 1 adult was present for the entire hour and its mate was present for 30 min, nest attendance was 90 bird-min for that nest, that hour. For each observation day we averaged bird-minutes-per-hour values for each nest. The average among nests for the day was the value used for comparisons among years and project sites. We analyzed data from the incubation and nestling periods separately. Differences among 1995-1998 results were tested with ANOVA.

We also calculated the duration of foraging trips made by adults. Only trips that concluded with chick feedings were used in the analysis (n = 192 trips). The average of all trips was used as the annual index. Differences among 1995-1998 indices were tested by ANOVA, and frequencies of trips in the first two 2-hr blocks of time (0-2 and 2-4 hr) were compared among years with Pearson's Chi-square test.

Kittiwakes: Using data from the all-day observations (see Feeding Rates, above), we calculated the amount of time 1, 2, and no adult kittiwakes attended each nest during the nestling period. Bird-minutes/hour was used to measure nest attendance. Since adults rarely attended the nest together, bird-minutes/hour rarely exceeded 60; fewer than 60 bird-minutes indicated that the nest were unattended for some portion of the hour. The average number of bird-minutes/hour for all hours of the day was calculated for each nest, each day (the 'nest-day'), and the annual index was the average of the nest-day values for the season. Differences among 1995-1998 results were tested with ANOVA.

We also calculated the duration of foraging trips made by adults. Only trips that concluded with chick feedings ($n = 57$ trips) were used in the analysis. Mean trip time was used as the annual index. Differences among 1995-1998 results were tested with ANOVA.

Puffins: Adult puffins did not stay at their nests during the 4 all-day observation periods; they usually spent less than 15 seconds in the burrow to deliver bill loads to chicks before flying off. Because both adults were gone at the same time and were unmarked, it was not possible to determine the duration of foraging trips made by individual birds.

Population Counts

Murres: Murre adults were counted on the 10 productivity plots on 16 days between the peak of egg-laying and the first sea-going of chicks. Methods for collecting and analyzing data were the same as those used by the 1993-1994 and 1996 Barren Islands murre population monitoring studies (see Roseneau *et al.* 1995, 1996b, 1997) and the 1995-1997 Barren Islands APEX seabird projects (see Roseneau *et al.* 1996a, 1997). Differences among the 1993-1998 indices were tested with ANOVA.

Kittiwakes: Adult kittiwakes were counted on the 11 productivity plots on 21 days. Counts from the 11 plots were summed for each day, then sums were averaged for the portion of the nesting season with stable counts. In 1998 counts were most stable between the median hatch date and the first fledging of chicks. Because we counted kittiwakes on only 4 plots in 1993, we used these plots to compare 1993-1998 results. Differences among years were tested with ANOVA.

Individual kittiwakes and nests were counted repetitively on a larger set of plots from a boat. Results from these data and the larger set of productivity plots will be presented and discussed in the Final Report.

Puffins: The number of active puffin burrows on the 3 chick growth rate study plots and 4 transects was used as an annual index of population size. Differences among 1995-1997 results were compared with the Friedman test.

Sea Temperature

We recorded sea temperature at Amatuli Cove during 11 June-8 September and at Lonesome Cove during 15 June-14 July and 2 August-7 September with Onset Optic Stowaway Temp data loggers anchored about 5 m deep (the Lonesome Cove logger failed to self-start after an in-field download on 14 July; in 1999 we will use 2 loggers at each location). Temperatures were recorded every 12 minutes. These data were graphed and will be discussed in the Final Report.

Other Data

Kittiwake adult body condition: We weighed (to 1 g) adult kittiwakes and measured the length of the head-bill (to 0.1 mm), tarsus (to 0.1 mm), wing chord (to 1 mm), and 10th primary feather (to 1 mm), using APEX protocol. We measured 25 incubating adults, 24 brooding adults, and 12 adults without chicks during the nestling period. We also measured adults in 1997. Results will be presented and discussed in the Final Report.

Beach seine sets: We made 30 beach seine sets and processed catches according to Appendix 1 and Project 98163M protocol. Similar methods were used during 1996-1997. Results will be presented and discussed in the Final Report.

RESULTS

Productivity

Murres: Murre productivity was 0.59 fledglings/nest sites [standard deviation (*s*) = 0.31; (Fig. 3a)], hatching success was 0.74 chicks/eggs (*s* = 0.26), and fledging success was 0.71 fledglings/chicks (*s* = 0.34); productivity was not significantly different from 1993-1997 values (0.47, 0.72, 0.73, 0.74, and 0.81 fledglings/nest sites, respectively).

Kittiwakes: Productivity of kittiwakes was very low (0.04 fledglings/nests, *s* = 0.06; Fig. 3b) and significantly lower than 1994-1997 values (0.67, 0.81, 0.71, and 0.29; *P* <0.001, <0.001, <0.001, and = 0.008, respectively), but similar to 1993, when there were no eggs or chicks on study plots.

Puffins: Just before fledging 0.22 (*s* = 0.02; Fig. 4) tufted puffin chicks/occupied burrows were found in the 3 growth rate plots and group of 4 transects. This was lower than the 1997 and 1995 values (0.34 and 0.53; *P* = 0.30 and <0.001) and similar to the 1996 value (0.31). Hatching success in the 5 plots established to measure this parameter was 0.34 (*s* = 0.20) chicks/eggs.

Nesting Chronology

Murres: The median hatch date of murre chicks was 7 August (*s* = 2.6; Fig. 5a), 5 days later than in 1997 [2 August; this difference was marginally significant (*P* = 0.087)]. The 1998 date was significantly earlier than in 1993 (16 August, *P* <0.001) but was not different from dates in 1994-1996 (10, 8, and 4 August).

Kittiwakes: The median hatch date for kittiwake chicks was 28 July (*s* = 5.9; Fig. 5b). This was significantly later than hatch dates in 1994-1997 (11, 7, 7, and 17 July; *P* <0.001 in each case).

Puffins: The mean hatch date for puffins was 31 July (*s* = 3.4; Fig. 6). This was significantly later than in 1995-1997 (22, 18, and 30 July, *P* <0.001 in each case).

Chick Growth Rate

Kittiwakes: The average growth rate of kittiwake 'A' chicks (chicks in single-chick nests plus first chicks to hatch in 2-chick nests) was 17.3 g/day (*s* = 2.6; Fig. 7a). This result was similar to 1995-1997 values (18.7, 17.6, and 16.7 g/day). There was only one 'B' chick.

Puffins: Puffin chicks in the 3 main study plots gained an average of 3.5 g/day (*s* = 2.51; Fig. 7b). This was significantly slower than in 1995 and 1997 (11.5 and 6.7 g/day; *P* <0.001 in both cases) and similar to growth rates in 1996 (3.2 g/day).

Chick Diet

Murres: Most prey items delivered to murre chick were capelin (94% by number, Fig. 8). Adults also fed nestlings Pacific sand lance (2%), Gadidae (2%), and salmonids (2%). Four fish (<1%) could not be identified to group or species. Results were similar in 1995-1997: capelin was the predominant prey fed to chicks (86%, 91%, and 91% in 1995-1997).

Kittiwakes: By weight, kittiwake chick regurgitation samples (*n* = 17) were composed of 54% Pacific sand lance, 27% capelin, 16% salmonids, 3% herring, and 1% pollock (Fig. 9). Regurgitation samples from brooding adults (*n* = 15) contained 42% Pacific sand lance, 37% capelin, 17% unidentified smelt, and 4% Pacific cod. Samples from incubating adults (*n* = 9) contained 78% sand lance, 15 % capelin, and 6% greenling.

Puffins: By weight, puffin screen samples contained 60% capelin, 11% pollock, 11% pink salmon, 8% sand lance, 4% Pacific cod, 4% squid, and less than 1% each of euphausiids, octopus, and larval fish (Fig. 10). While the diversity and type of prey species in puffin chick diets remained fairly consistent during 1995-1998, the proportion of capelin gradually increased over the period.

Amount Fed to Chicks

Kittiwakes: Kittiwake chick regurgitation samples collected from chicks 20 or more days old averaged 12.9 g (*s* = 10.4, *n* = 7). This value was significantly lower than that of 1995 (27.7 g, *P* <0.001) and did not differ from values in 1996-1997 (20.8 g and 14.1 g).

Puffins: The average weight of 41 screen samples collected during the nestling period was 8.2 g (*s* = 7.3). This was not significantly different from values in 1995-1997 (10.6 g, 6.9 g, and 7.4 g).

Chick Provisioning Rate

Murres: During the 8 all-day observation periods, murre chicks averaged 0.22 feedings/hr (*s* = 0.06; Fig. 11a), and during 0700-1959 hr (the time period used for among-year comparisons), they averaged 0.23 feedings/hr (*s* = 0.06). In 1995-1997, the averages for this time period were 0.29, 0.26, and 0.27 feedings/hr. Differences among years were not significant.

Kittiwakes: During the 4 all-day observation periods single-chick kittiwake nests averaged 0.19 feedings/hr (*s* = 0.09, *n*= 17 nest-days; Fig. 11b); nests containing 2 chicks averaged 0.25 feedings/hr (*s*= 0.09, *n* = 5 nest-days). During the block of time used for among-year comparisons (0700-1959 hr) single-chick nests averaged 0.18 feedings/hr (*s* = 0.11) and 2-chick nests averaged 0.26 (*s* = 0.13). Feeding rates in 1-chick nests in 1997 were significantly lower in 1997 than in 1995, 1996, and 1998 (*P* = 0.004, 0.01, and 0.002, respectively). There were no significant among-year differences in attendance of 2-chick nests.

Puffins: It is apparent from the 1996-1998 results (Fig. 12) that to measure provisioning rate in tufted puffins we must increase the number of days that we sample. In 1999 we will attempt to do so.

Activity Budgets of Adults

Murres: *(Nest Attendance)* -- During the incubation period, at least 1 adult murre always attended each nest site, and both pair members were present an average of 12.7 min/hr (72.7 bird-min/hr, s = 4.2, *n* = 12 days; Fig. 13). During the 0700-1959 hr block of time the average was 73.7. This result was lower than the 1996 and 1997 values (80.3 and 83.8, *P* = 0.074 and 0.003).

During the nestling period at least 1 adult always attended each site; both birds were present an average of 8.9 min/hr (68.9 bird-min/hr, *s* = 5.1; Fig. 14a). During the 0700-1959 hr block of time, the result (69.2 bird-min/hr, *s* = 5.7) was similar to the 1995-1997 values (65.8, 69.1, and 73.1 bird-min/hr).

(Duration of Foraging Trips) -- During the nestling period, murre foraging trips averaged 157.9 min (*s* = 119.5; Fig. 15). This did not differ significantly from 1995-1997 values (157.7, 170.6, and 157.4 min). In 1998 the proportion of 0-to-2-hr trips to 2-to-4-hr trips in 1998 (94 trips vs. 83 trips, respectively) was significantly higher than in 1996 (22 vs. 51 trips, *P* <0.001) but similar to that of 1995 (39 vs. 29 trips) and 1997 (65 vs. 55 trips).

Kittiwakes: *(Nest Attendance)* -- Single kittiwake chicks were left alone an average of 1.5 min/hr (bird-min/hr= 58.5, *s* = 5.5, *n* = 1; Fig. 14b) and 2-chick broods were always attended by adults (60.3 bird-min/nest/hr, *s* = 0.3, *n* = 5). During the 0700-1959 hr block of time, results for 1- and 2-chick nests were 58.7 (*s* = 5.8) and 60.3 (*s* = 0.4) bird-min/nest/hr, respectively. Results for 1998 were not significantly different from those of 1995-1997 for 1-chick nests (57.1, 57.7, and 50.9 bird-min/hr) or for 2-chick nests (55.3, 54.6, and 43.6 bird-min./hr), although the 1997 value was lower than the 1998 value at a marginally significant level (*P* = 0.078).

(Duration of Foraging Trips)-- Kittiwake foraging trips averaged 289.2 min (*s* = 176.0 min; Fig. 16). This was not significantly different from 1995-1997 values (236.6, 325.9, and 332.1 min).

Population Counts

Murres: Counts of murres on the productivity plots averaged 455 birds (*s* = 38.1; Fig. 17a). This was significantly higher than the 1994-1996 counts (412, 392 and 406 birds; *P* = 0.002, <0.001, and <0.001, respectively) but similar to the 1993 and 1997 values (429 and 436 birds, respectively).

Kittiwakes: Kittiwake counts on the 4 productivity plots that could be compared among the years 1993-1998 averaged 145 birds (*s* = 27.4; Fig. 17b). This was similar to 1994-1997 averages (192, 201, 183, and 196). Counts in each of these years were higher than counts made in 1993 (average = 120 birds, *P* <0.001 in each case).

Puffins: The number of occupied puffin burrows on the 3 growth rate study plots and group of 4 transects was similar during 1995-1998 (125, 142, 127, and 93 burrows; Fig. 18).

Sea Temperature

Sea temperature was warmer at the beginning of the 1998 season than at the start of the 1996-1997 seasons (Fig. 19). These data will be discussed in the Final Report.

DISCUSSION

Results from the 1998 season will be discussed in the Final Report, which will be submitted in September 2000.

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LITERATURE CITED

Amaral, M.J. 1977. A comparative breeding biology of the tufted and horned puffin in the Barren Islands, Alaska. M.S. thesis. Univ. of Washington. 98 pp.

Bailey, E.P. 1975a. Barren Islands survey notes, 1974-1975. Unpubl. field notes, 1974-1975. U.S. Fish Wildl. Serv., Homer, AK.

_____. 1975b. Breeding bird distribution and abundance in the Barren Islands Alaska. Unpubl. rept., 1975. U.S. Fish Wildl. Serv., Homer, AK.

_____. 1976. Breeding bird distribution and abundance in the Barren Islands, Alaska. Murrelet 57:2-12.

Boersma, P.D., J.K. Parrish, and A.B. Kettle. 1995. Common murre abundance, phenology, and productivity on the Barren Islands, Alaska: The *Exxon Valdez* oil spill and long-term environmental change. Pp. 820-853 *in Exxon Valdez* Oil Spill: Fate and effects in Alaskan waters, ASTM STP 1219, P.G. Wells, J.N. Butler, and J.S. Hughes (eds.), Amer. Soc. for Testing and Materials, Philadelphia, PA.

Byrd, G.V. 1986. Results of seabird monitoring in the Pribilof Islands in 1986. Unpubl. U.S. Fish Wildl. Serv., Homer, AK. 74 pp.

_____. 1989. Seabirds in the Pribilof Islands, Alaska: Trends and monitoring methods. M.S. thesis. Univ. of Idaho.

Dipple, C. and D. Nysewander. 1992. Marine bird and mammal censuses in the Barren Islands, 1989 and 1990, with specific emphasis on species potentially impacted by the 1989 *Exxon Valdez*, including supplemental appendices for 1991 murre data. Unpubl. rept., U.S. Fish Wildl. Serv., Homer, AK. 71 pp.

Dragoo, D.E., G.V. Byrd, D.G. Roseneau, D.A. Dewhurst, J.A. Cooper, and J.H. McCarthy. 1995. Effects of the T/V *Exxon Valdez* oil spill on murres: A perspective from observations at breeding colonies four years after the spill. Final rept., Restoration Proj. No. 11, U.S. Fish Wildl. Serv., Homer, AK.

Erikson, D.E. 1995. Surveys of murre colony attendance in the northern Gulf of Alaska following the *Exxon Valdez* oil spill. Pp. 780-819 *in Exxon Valdez* oil spill: Fate and effects in Alaskan waters, ASTM STP 1219, P.G. Wells, J.N. Butler, and J.S. Hughes (eds.), Amer. Soc. for Testing and Materials, Philadelphia, PA.

Manuwal, D. A. 1978. Dynamics of marine bird populations on the Barren Islands, Alaska. Unpubl. Environ. Assess. Alaska Contin. Shelf, Annu. Repts. Princ. Invest. Minerals Manage. Serv., Anchorage, AK. 97 pp.

_____. 1980. Breeding biology of seabirds on the Barren Islands, Alaska. Unpubl. rept., U.S. Fish Wildl. Serv., Off. Biol. Serv., Anchorage, AK. 195 pp.

_____ and D. Boersma. 1978. Dynamics of marine bird populations on the Barren Islands, Alaska. Pp. 575-679 in Environ. Assess. Alaska Contin. Shelf, Annu. Repts. Princ. Invest., Vol. 3. NOAA Environ. Res. Lab, Boulder, CO.

Nishimoto, M. 1990. Status of fork-tailed storm-petrels at East Amatuli Island during the summer of 1989. Unpubl. rept., U.S. Fish Wildl. Serv., Homer, AK. 25 pp.

Nysewander, D. and C. Dipple. 1990. Population surveys of seabird nesting colonies in Prince William Sound, the outside coast of the Kenai Peninsula, Barren Islands, and other nearby colonies, with emphasis on changes in numbers and reproduction of murres. Bird Study No. 3. Unpubl. prog. rept., U.S. Fish Wildl. Serv., Homer, AK. 48 pp.

_____ and _____. 1991. Population surveys of seabird nesting colonies in Prince William Sound, the outside coast of the Kenai Peninsula, Barren Islands, and other nearby colonies, with emphasis on changes of numbers and reproduction of murres. Bird Study No. 3. Unpubl. prog. rept., U.S. Fish Wildl. Serv., Homer, AK. 70 pp.

_____, C.H. Dipple, G.V. Byrd, and E.P. Knudtson. 1993. Effects of the T/V *Exxon Valdez* oil spill on murres: A perspective from observations at breeding colonies. Bird Study No. 3. Final rept., U.S. Fish Wildl. Serv., Homer, AK. 40 pp.

Roseneau, D.G., A.B. Kettle, and G.V. Byrd, 1995. Common murre restoration monitoring in the Barren Islands, Alaska, 1993. Unpubl. final rept. by the Alaska Maritime National Wildlife Refuge, Homer, Alaska for the *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK. (Restoration Project 93049). 71 pp.

_____, _____, and _____. 1996a. Barren Islands seabird studies, 1995. Unpubl. annual rept. by the Alaska Maritime National Wildlife Refuge, Homer, Alaska for the *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK. (APEX Project 96163J). 34 pp.

_____, _____, and _____. 1996b. Common murre restoration monitoring in the Barren Islands, Alaska, 1994. Unpubl. final rept. by the Alaska Maritime National Wildlife Refuge, Homer, Alaska for the *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK. (Restoration Project 94039). 76 pp.

_____, _____, and _____. 1997. Barren Islands seabird studies, 1996. Unpubl. annual rept. by the Alaska Maritime National Wildlife Refuge, Homer, Alaska for the *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK. (APEX Project 96163J).

_____, _____, and _____. 1998. Barren Islands seabird studies, 1997. Unpubl. annual rept. by the Alaska Maritime National Wildlife Refuge, Homer, Alaska for the *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK. (APEX Project 97163J).

Wehle, D. H. S., 1983. The food, feeding, and development of young tufted and horned puffins in Alaska. Condor 85:427-442.

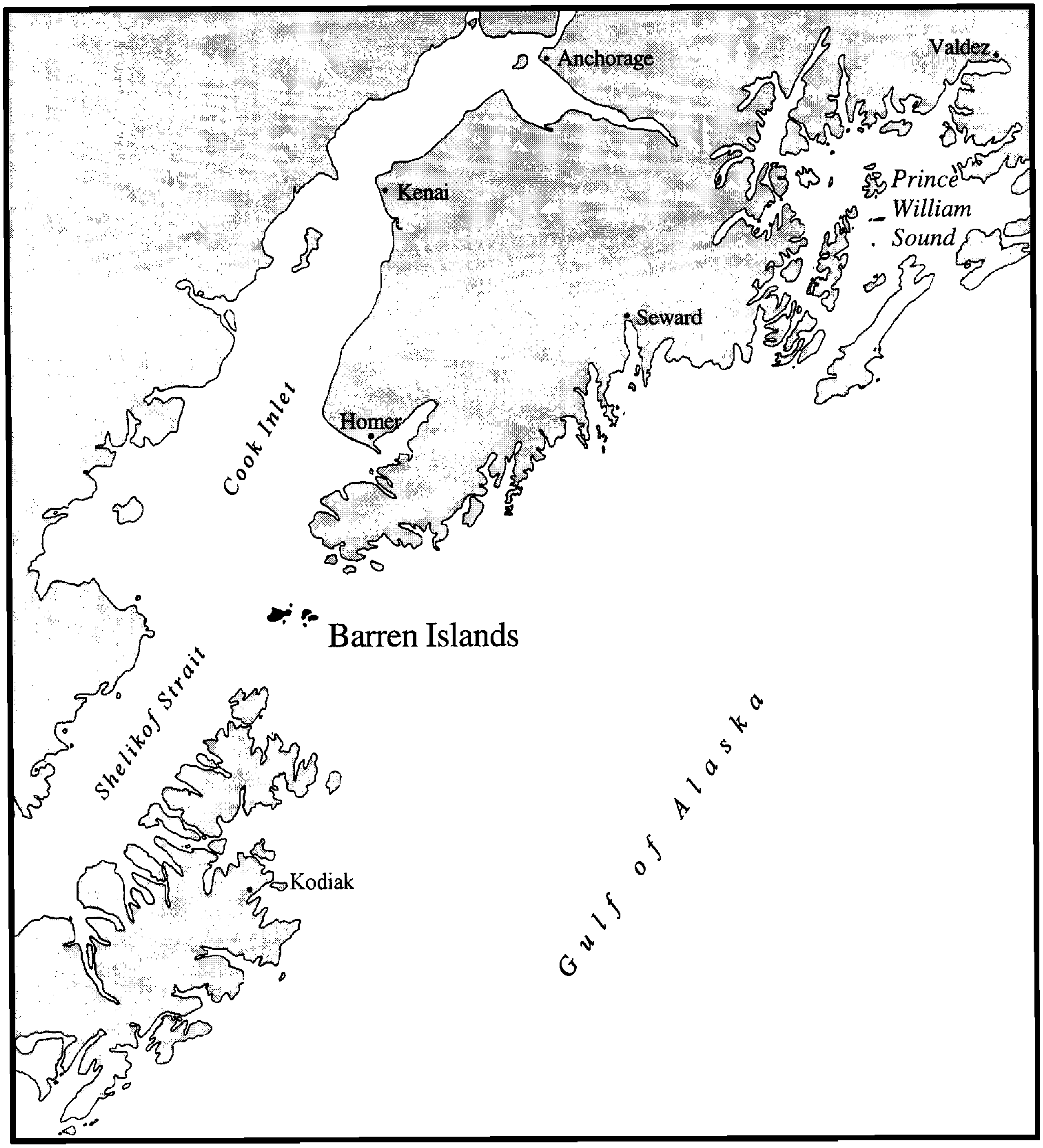


Figure 1. Location of the Barren Islands, Alaska.

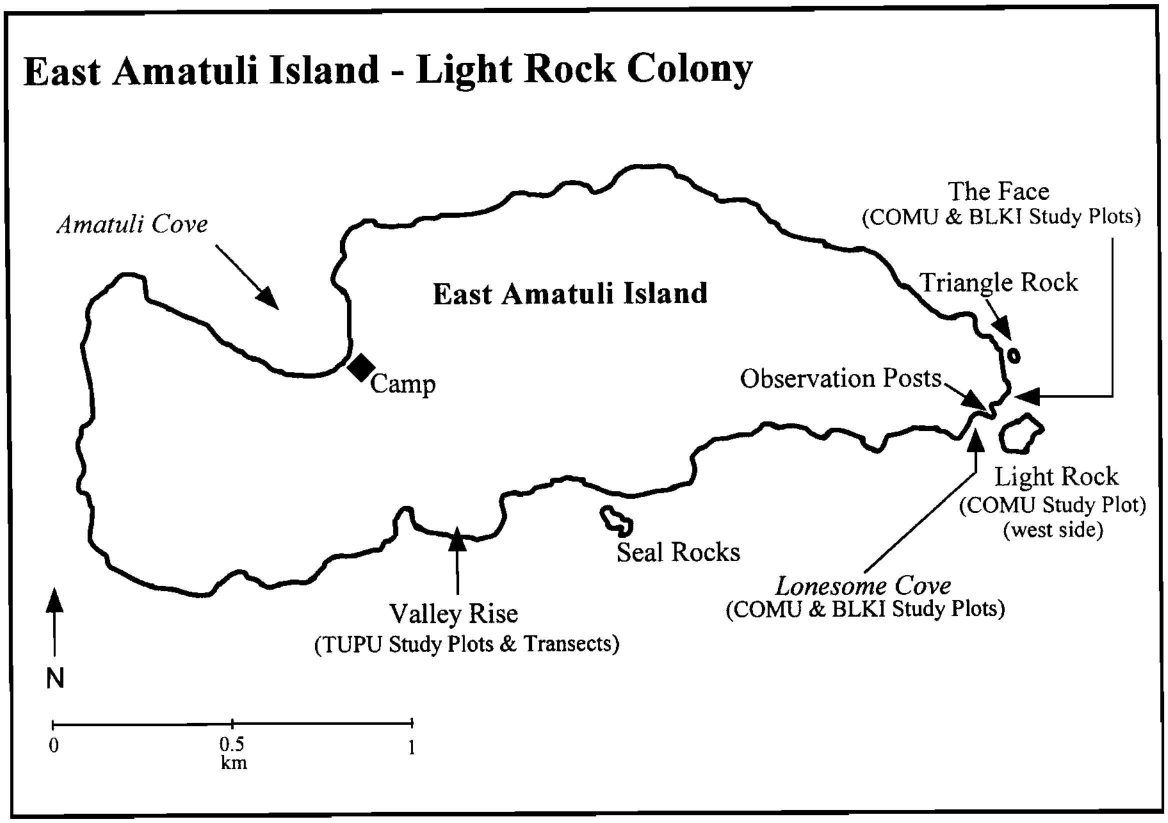
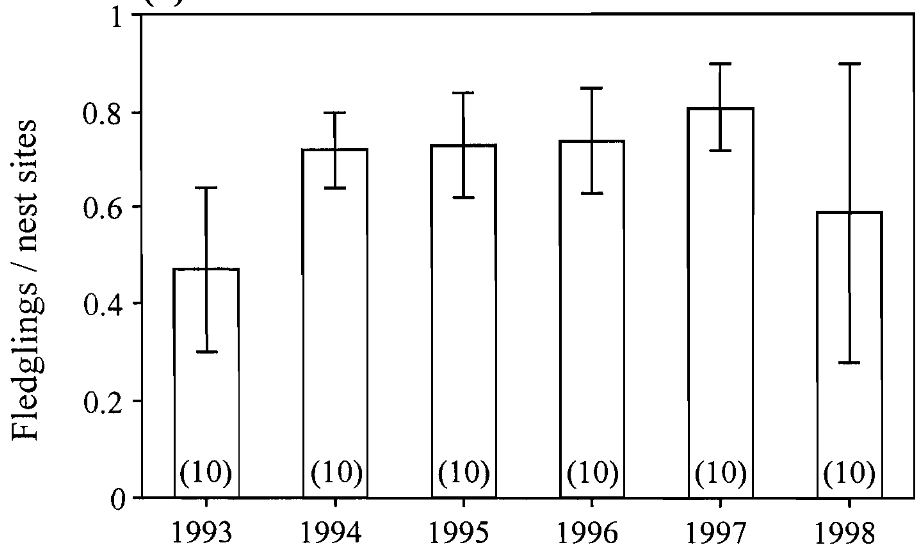


Figure 2. The East Amatuli Island study area, showing the general locations of common murre (COMU), black-legged kittiwake (BLKI), and tufted puffin (TUPU) study sites.

Productivity

(a) Common murre



(a) Black-legged kittiwake

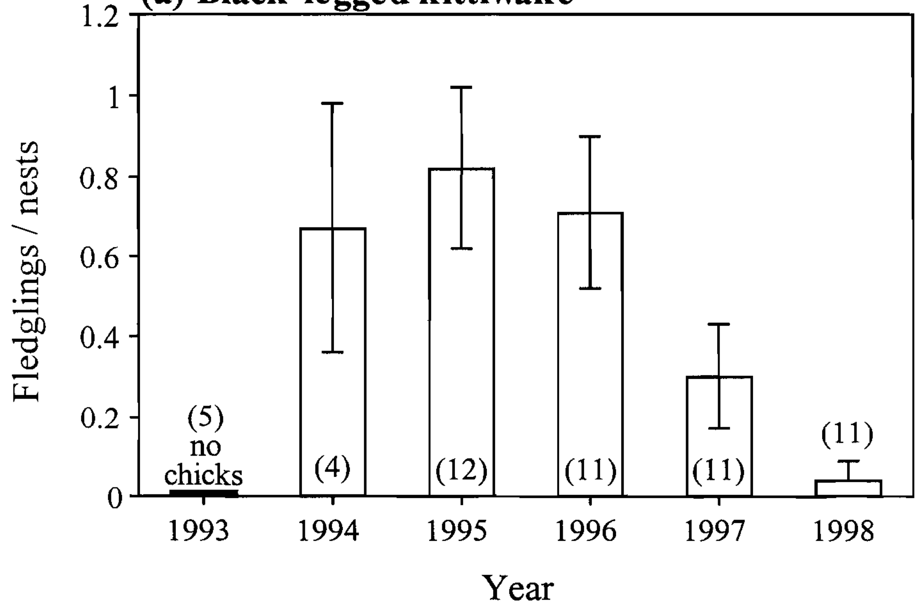


Figure 3. Productivity of (a) common murres (fledglings per nest site) and (b) black-legged kittiwakes (fledglings per nest) at East Amatuli Island, Barren Islands, Alaska, 1993-1998. Number of plots in parentheses; error bars = standard deviation.

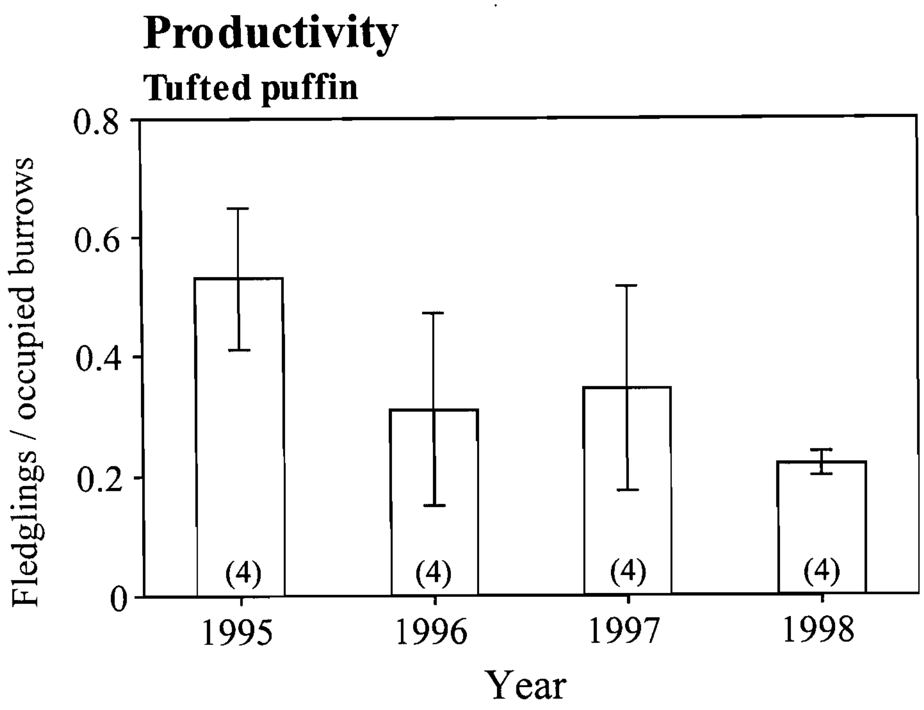
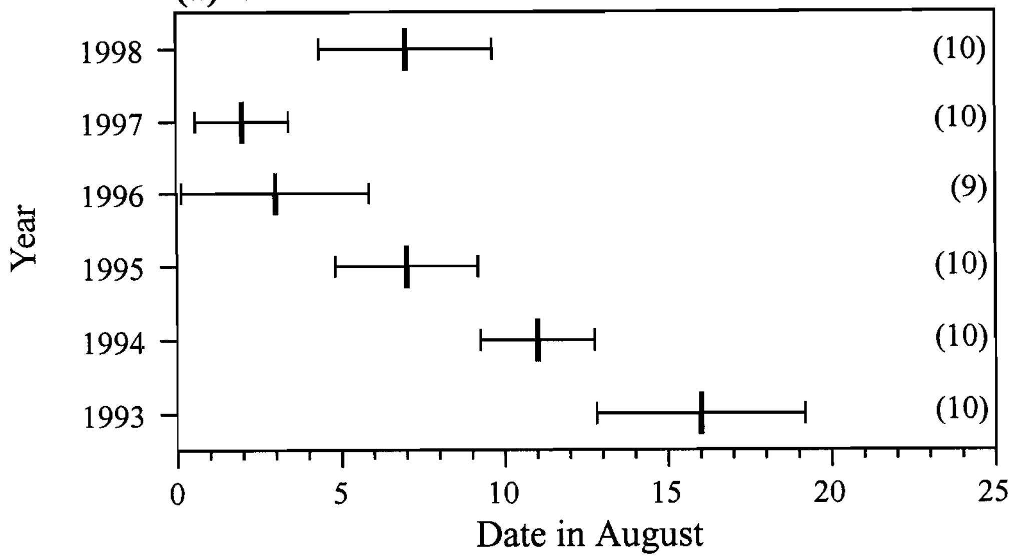


Figure 4. Productivity (fledglings per occupied burrow) of tufted puffins at East Amatuli Island, Barren Islands, Alaska, 1995-1998. Number of plots in parentheses; error bars = standard deviation.

Nesting chronology

(a) Common murre



(b) Black-legged kittiwake

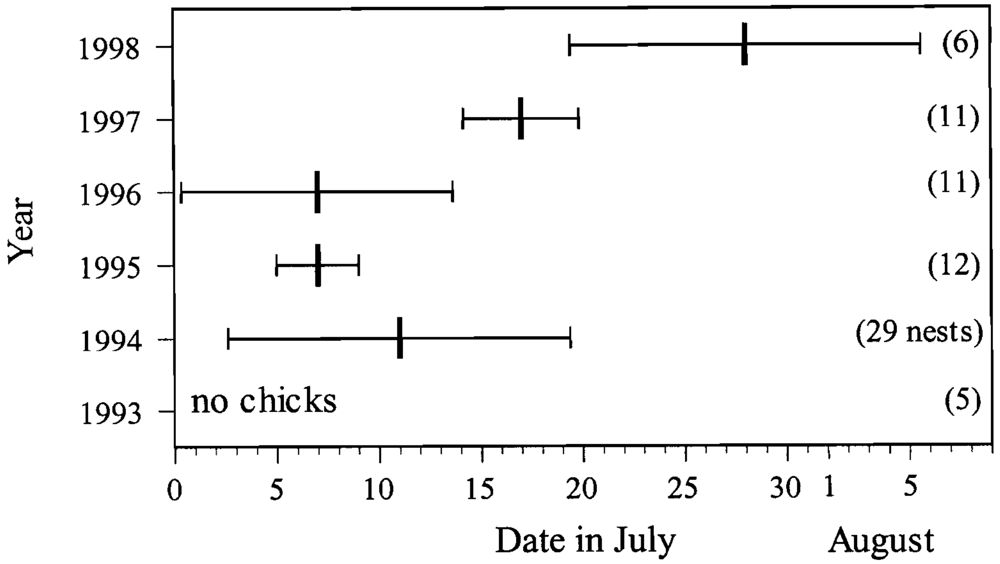


Figure 5. Nesting chronology (median hatch date) of (a) common murres and (b) black-legged kittiwakes at East Amatuli Island, Alaska, 1993-1998. Number of plots in parentheses; error bars = standard deviation.

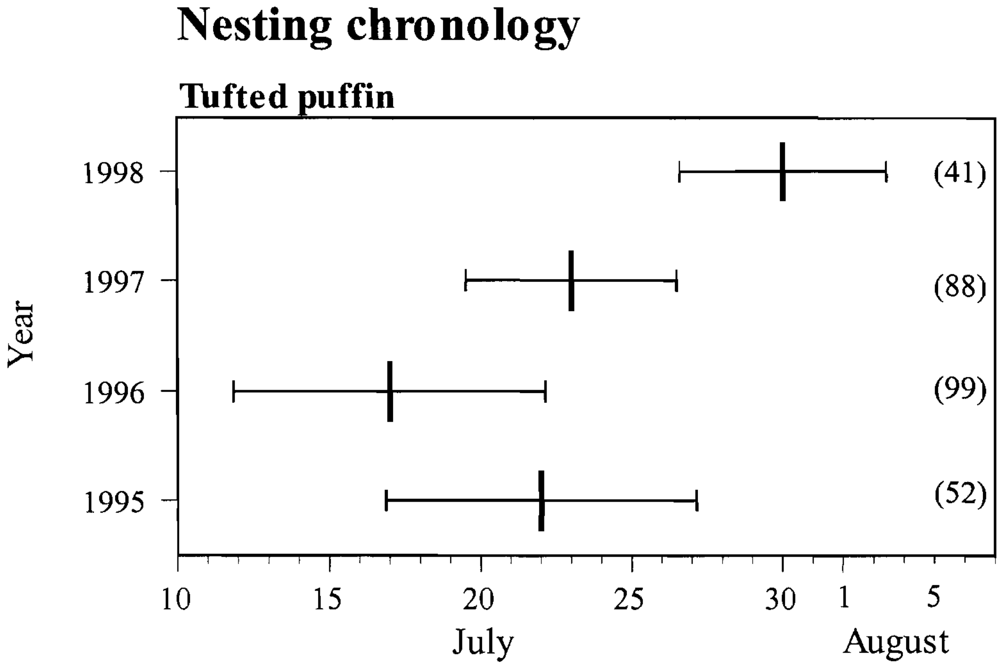
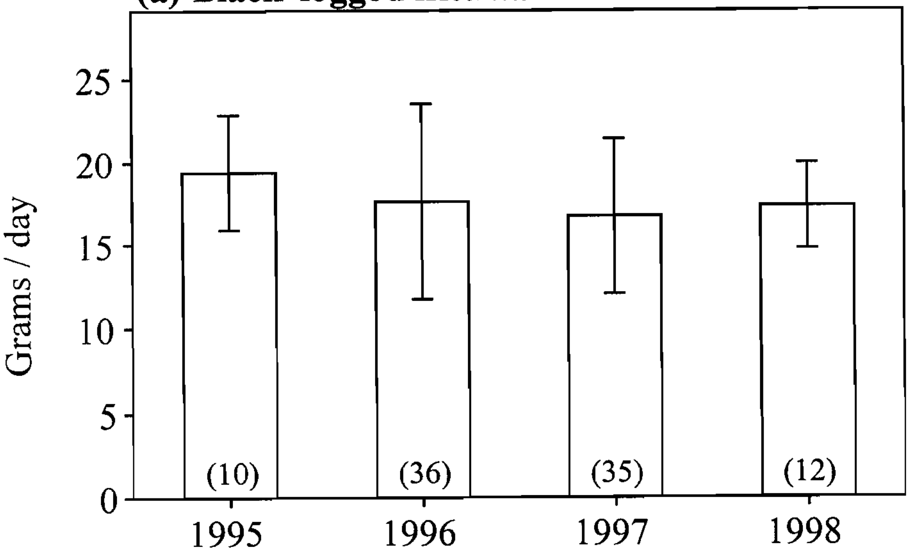


Figure 6. Nesting chronology (mean hatch date) of tufted puffins at East Amatuli Island, Alaska, 1994-1998. Number of chicks in parentheses; error bars = standard deviation.

Chick growth rate

(a) Black-legged kittiwake



(b) Tufted puffin

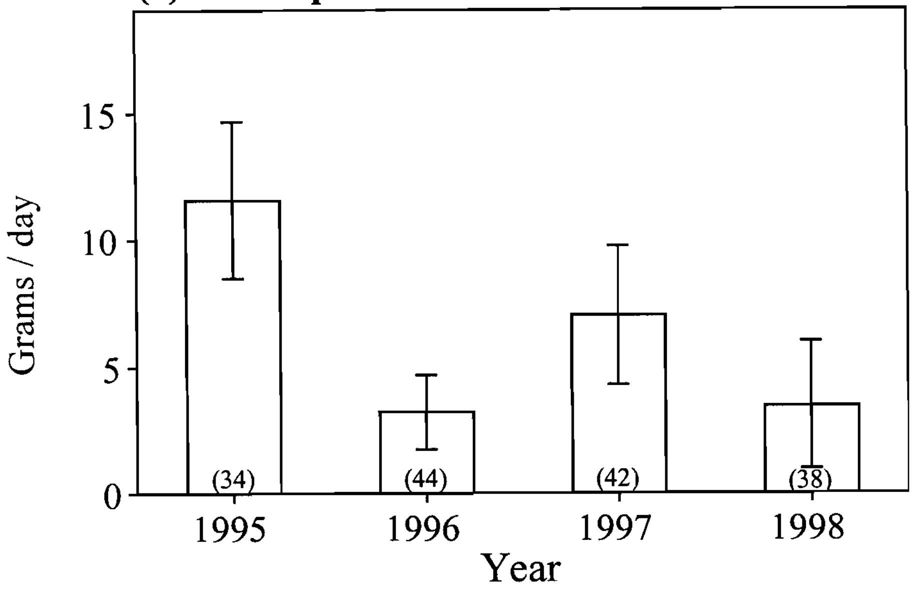


Figure 7. Growth rate of (a) black-legged kittiwake chicks and (b) tufted puffin chicks at East Amatuli Island, Barren Islands, Alaska, 1995-1998. Number of chicks in parentheses; error bars = standard deviation.

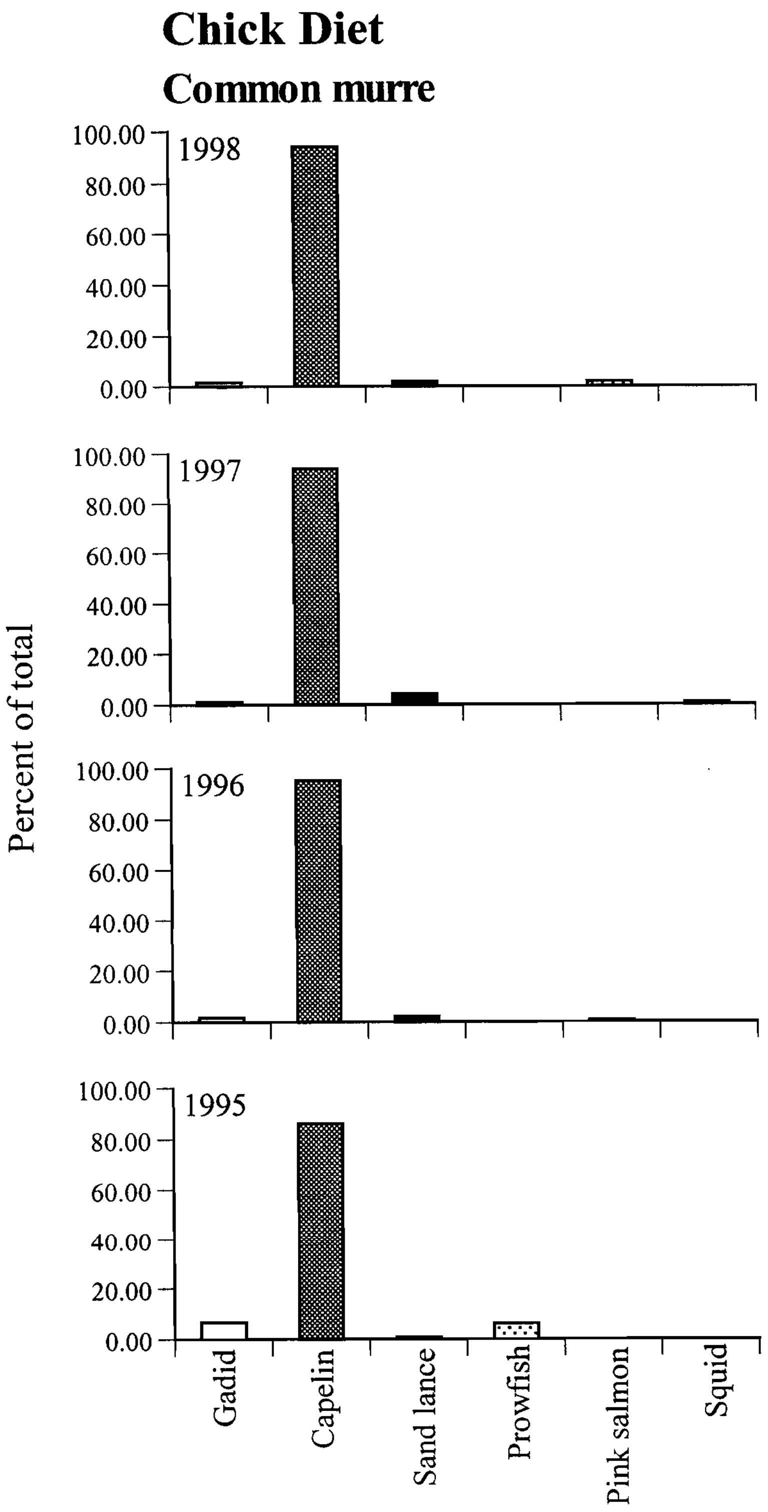


Figure 8. Types of prey fed to common murre chicks at East Amatuli Island, Barren Islands, Alaska, 1995-1998. Percent of total, by number of prey items, of each prey type.

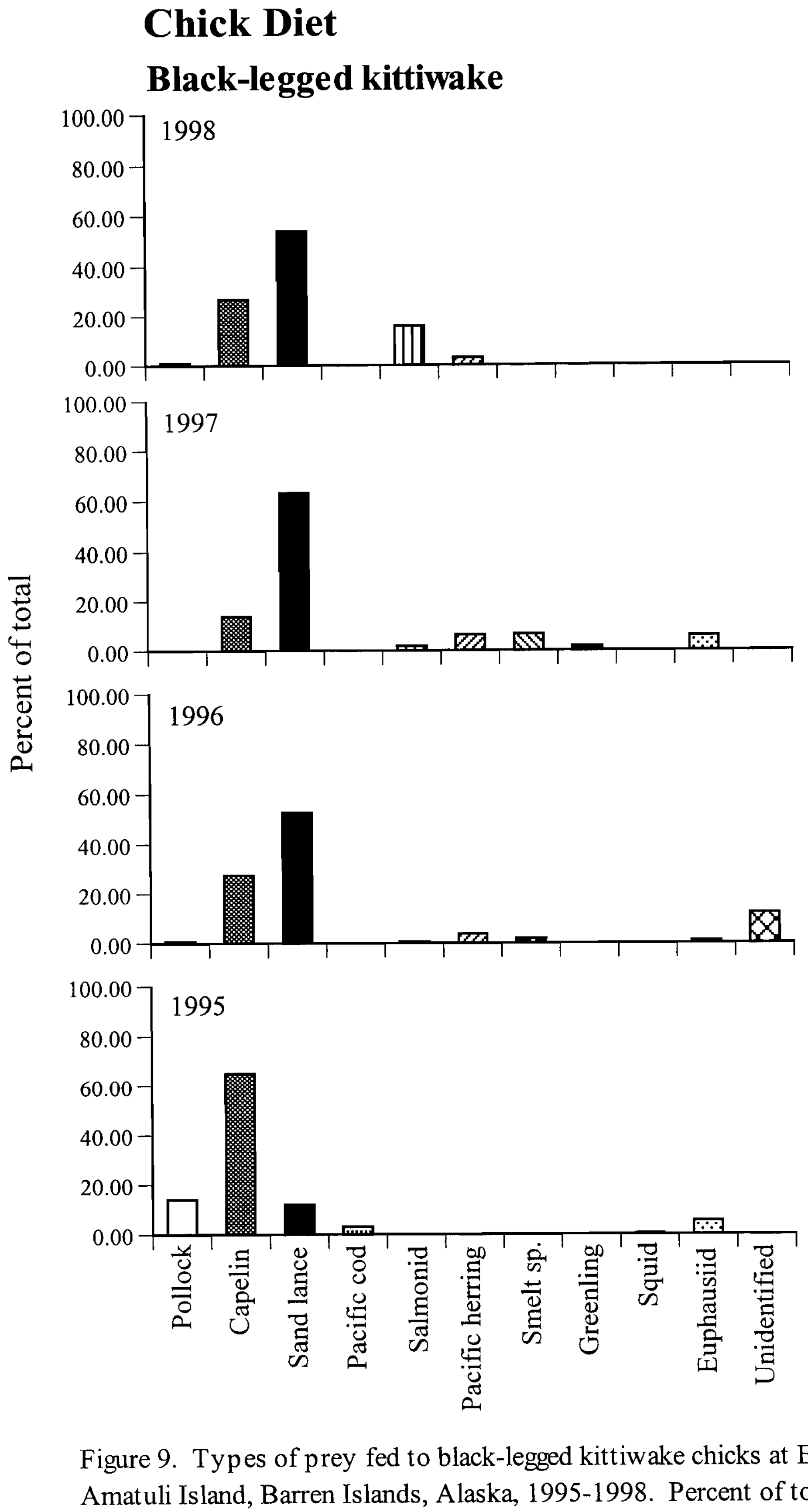


Figure 9. Types of prey fed to black-legged kittiwake chicks at East Amatuli Island, Barren Islands, Alaska, 1995-1998. Percent of total, by weight, of each prey type.

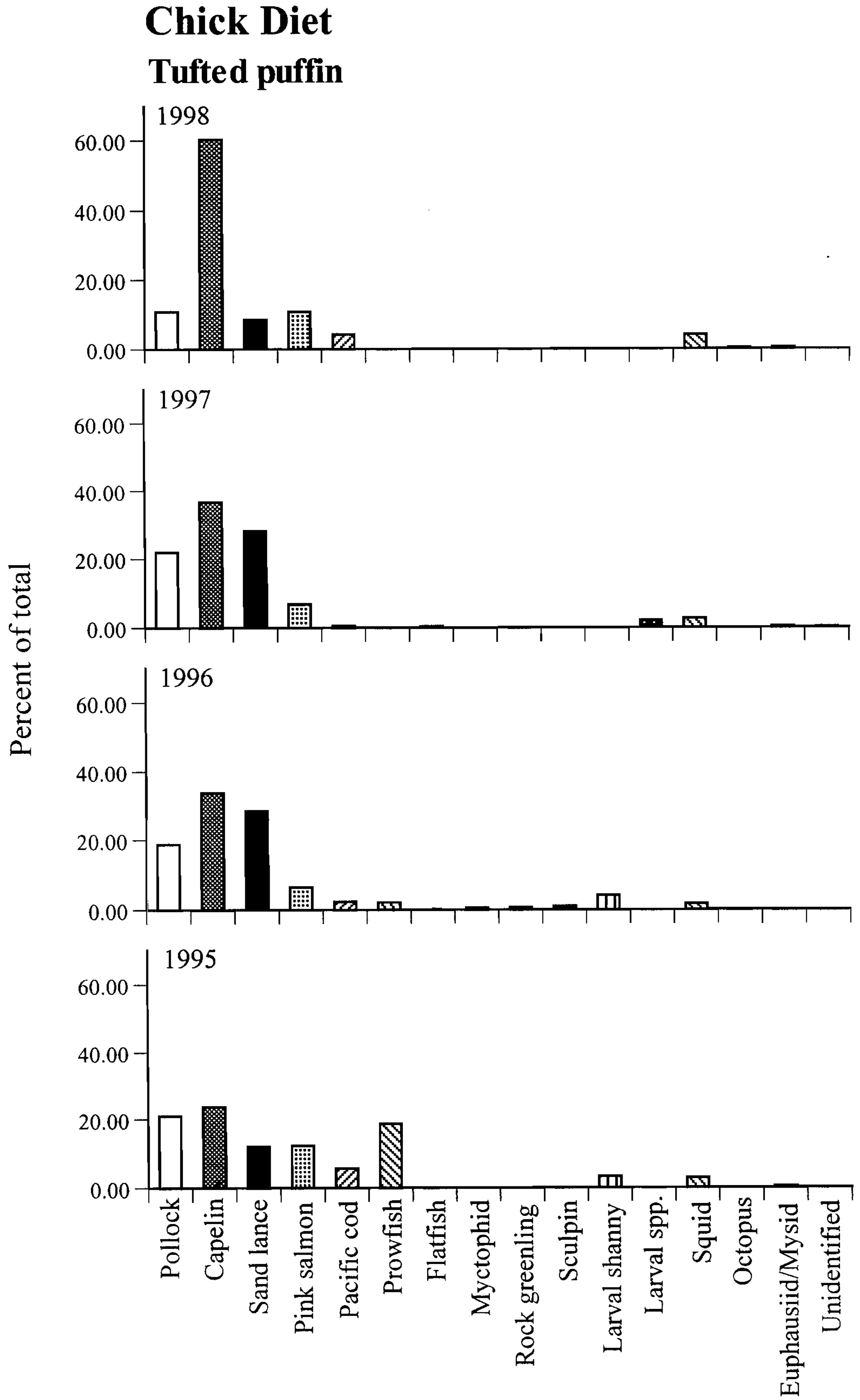
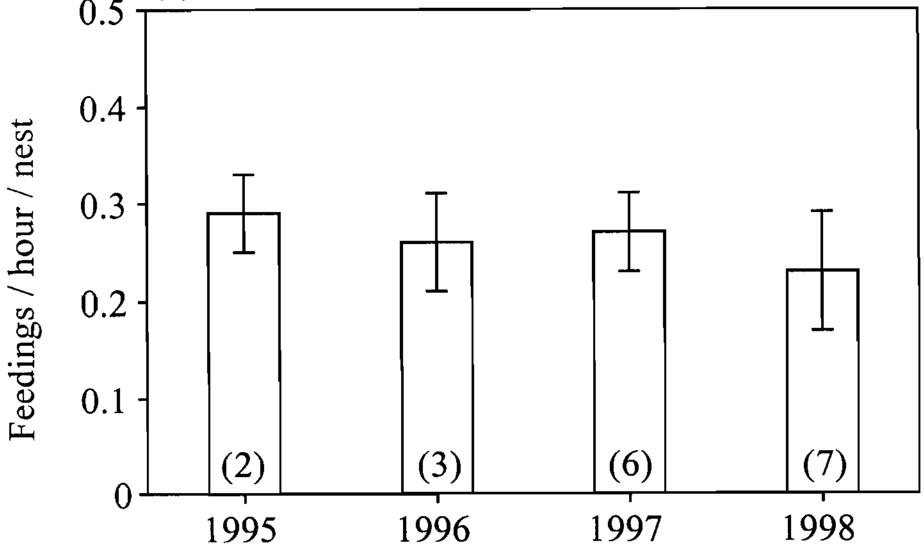


Figure 10. Types of prey fed to tufted puffin chicks at East Amatuli Island, Barren Islands, Alaska, 1995-1998. Percent of total, by weight, of each prey type.

Chick provisioning rate

(a) Common murre



(b) Black-legged kittiwake

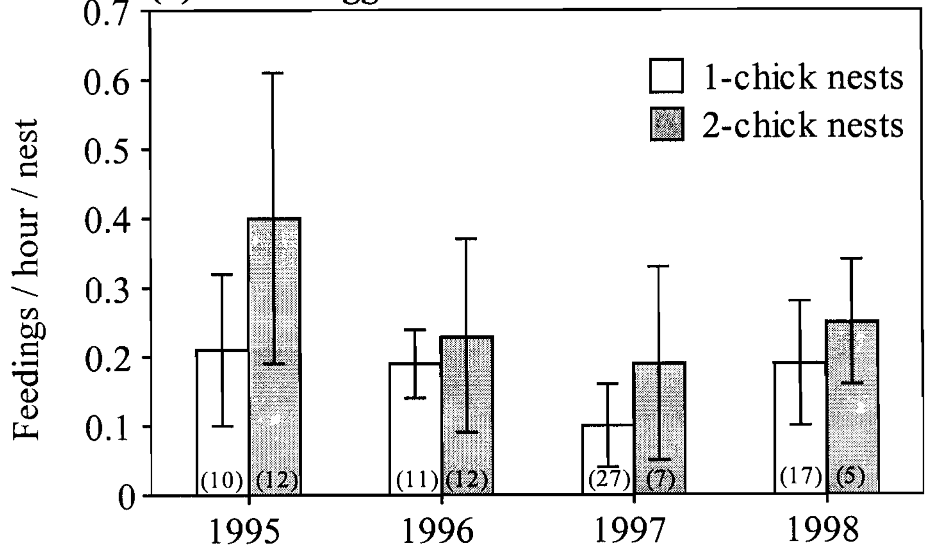


Figure 11. Provisioning rate of (a) common murre (number of days in parentheses) and (b) black-legged kittiwake (number of nest-days in parentheses) chicks at East Amatuli Island, Barren Islands, Alaska, 1995-1998. Error bars = standard deviation.

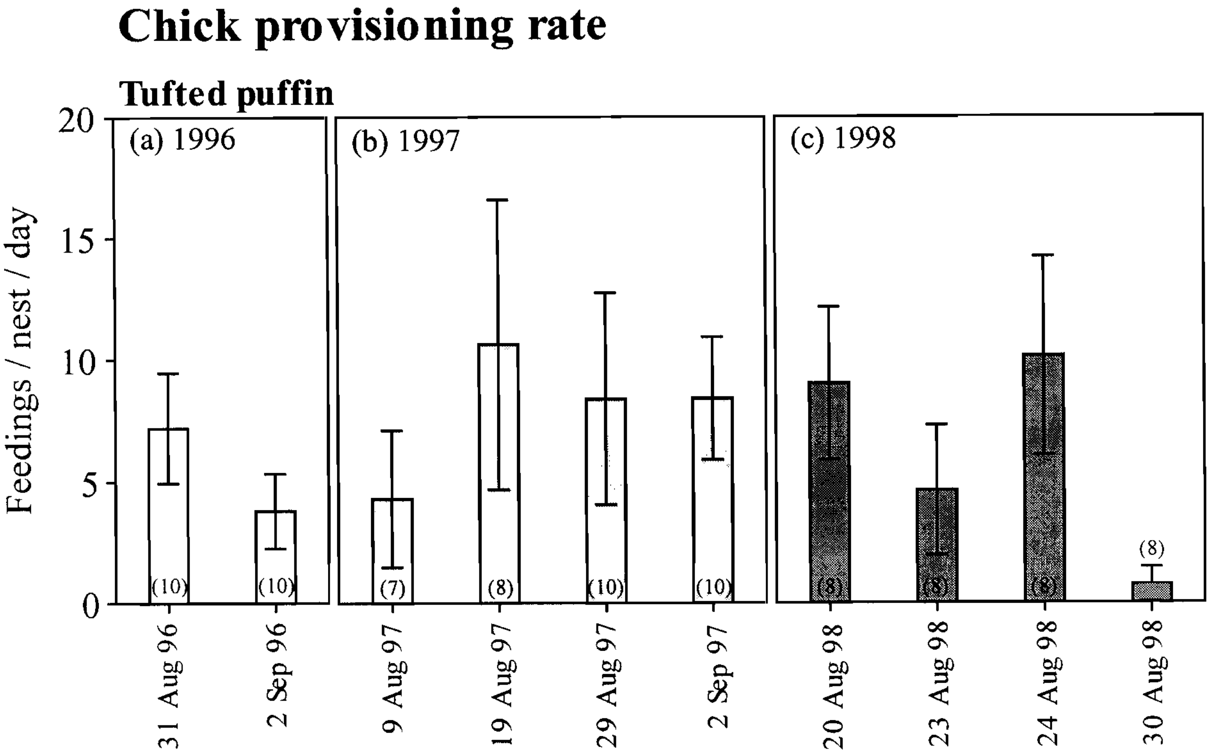


Figure 12. Provisioning rate of tufted puffin chicks at East Amatuli Island, Barren Islands, Alaska during (a) 1996, (b) 1997, and (c) 1998. Number of nests in parentheses; error bars = standard deviation.

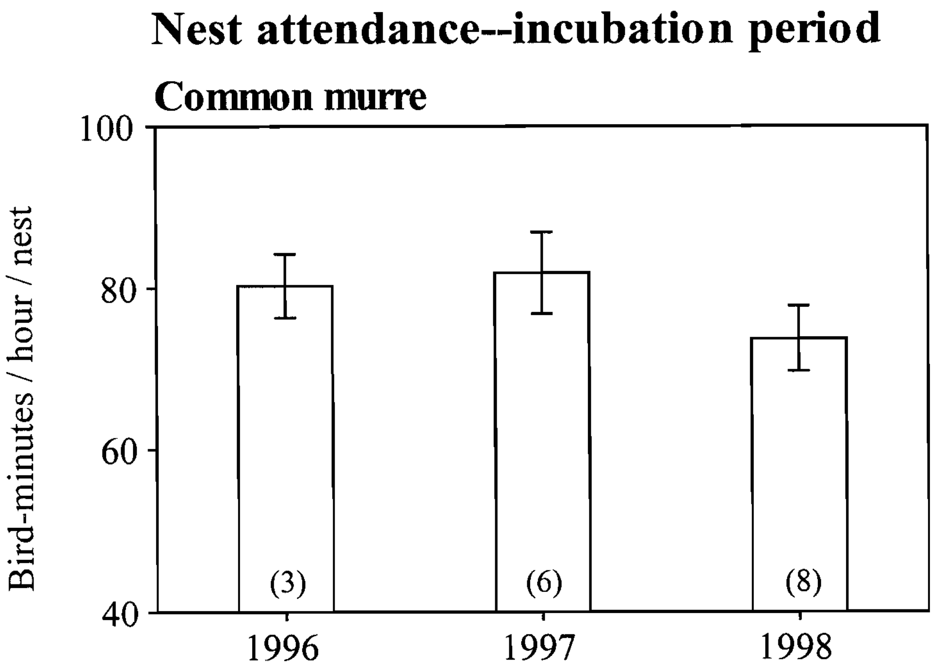
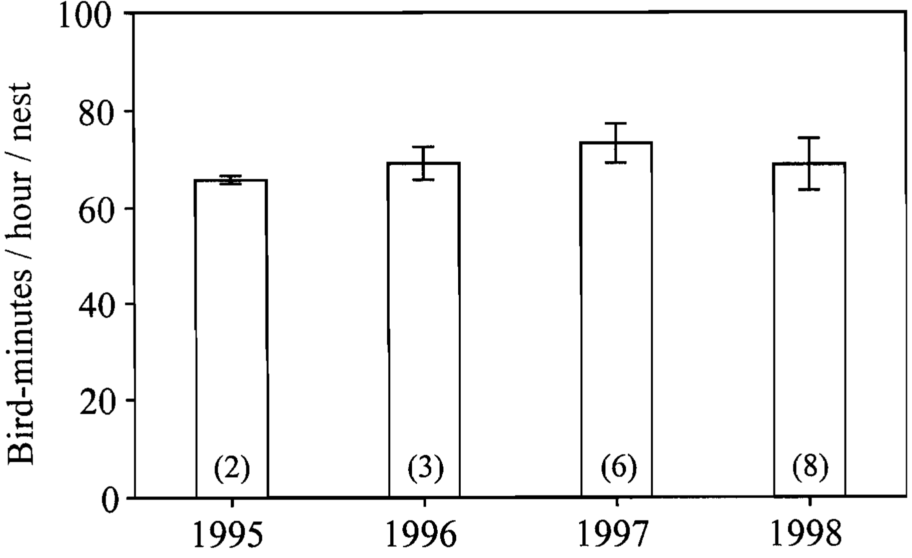


Figure 13. Number of minutes per hour spent at nests by common murres (number of days in parentheses) during the incubation period at East Amatuli Island, Barren Islands, Alaska, 1995-1998. Error bars = standard deviation.

Nest attendance--nestling period

(a) Common murre



(b) Black-legged kittiwake

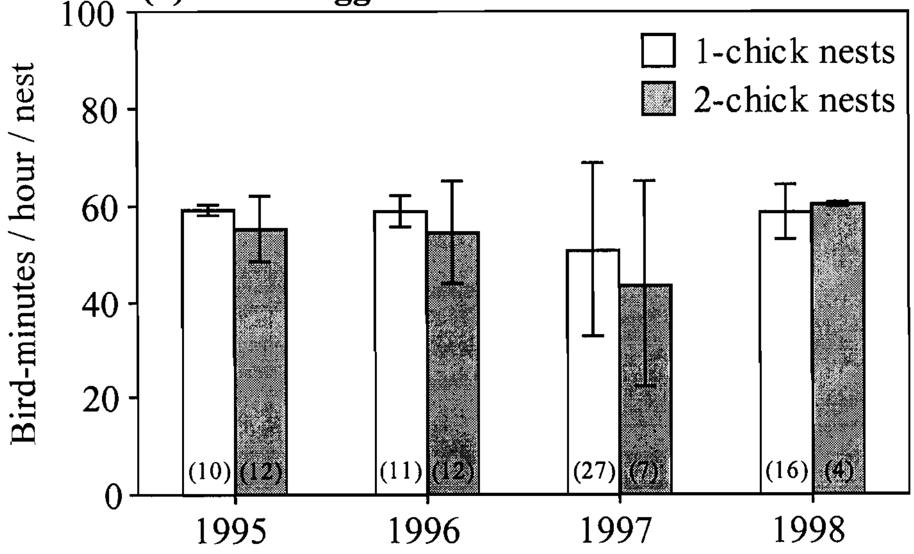


Figure 14. Number of minutes per hour spent at nests by (a) common murre (number of days in parentheses) and (b) black-legged kittiwake (number of nest-days in parentheses) parents during the chick-rearing period at East Amatuli Island, Barren Islands, Alaska, 1995-1998. Error bars = standard deviation.

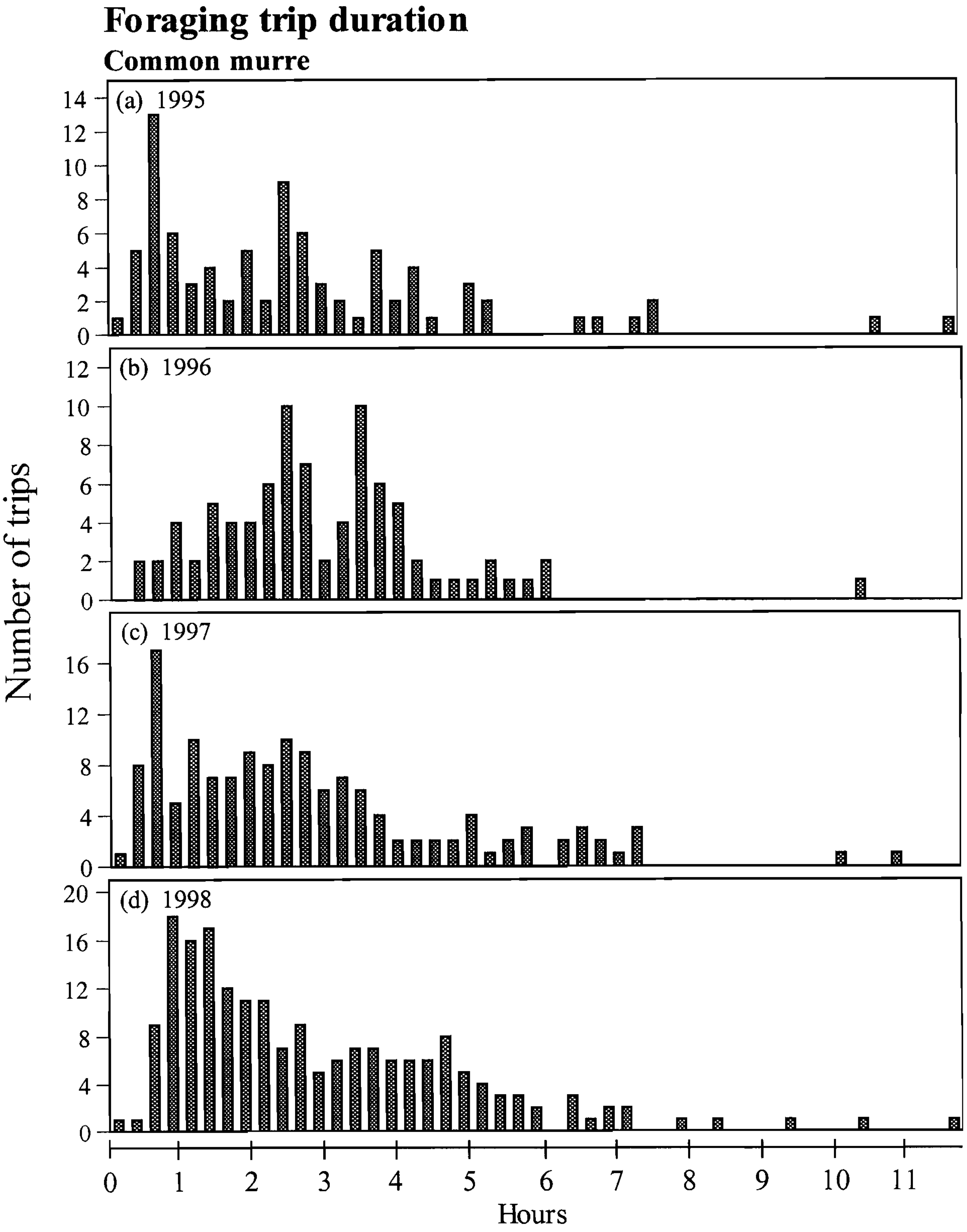


Figure 15. Duration of foraging trips by common murres at East Amatuli Island, Barren Islands, Alaska during (a) 1995, (b) 1996, (c) 1997, and (d) 1998.

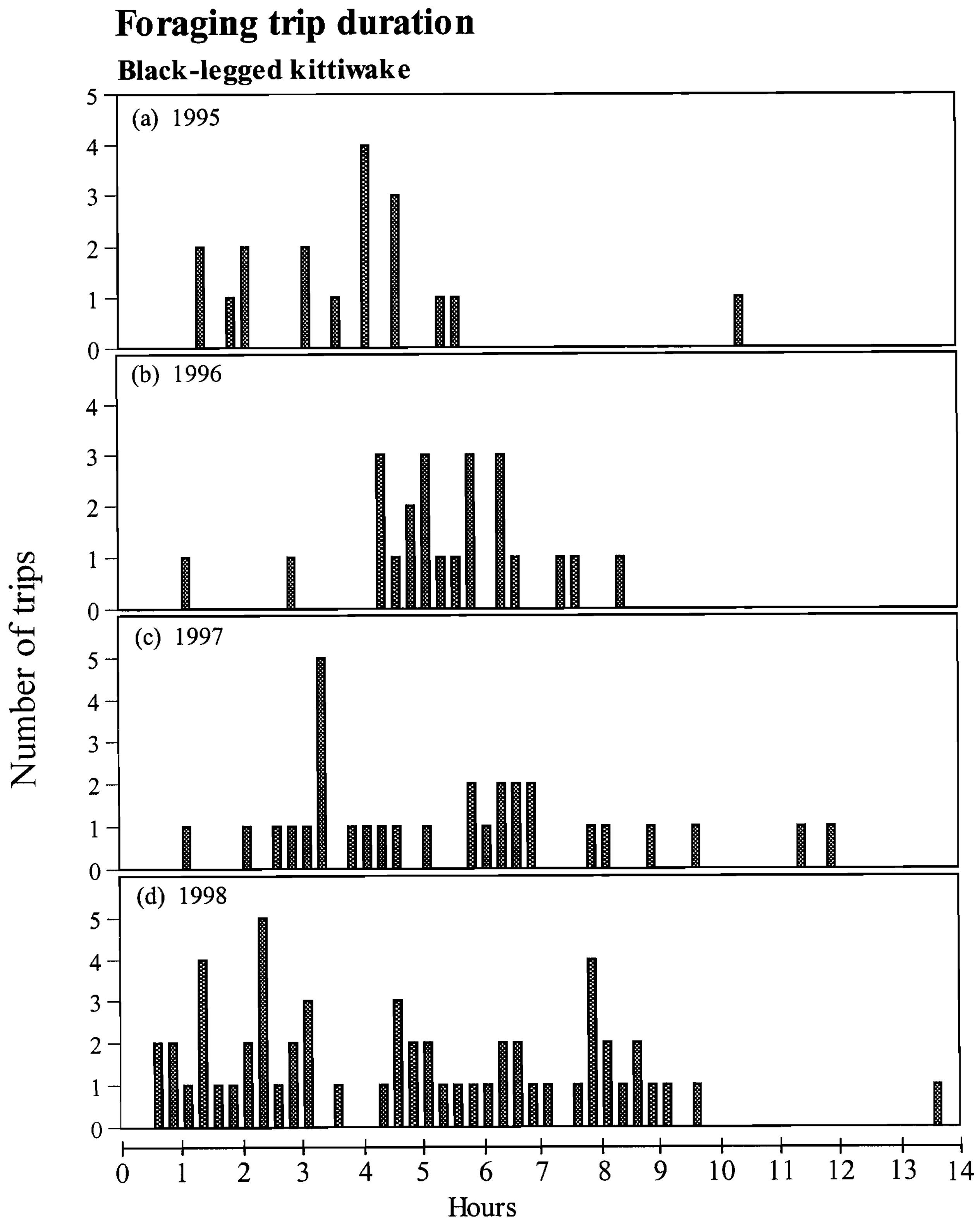


Figure 16. Duration of foraging trips by black-legged kittiwakes at East Amatuli Island, Barren Islands, Alaska during (a) 1995, (b) 1996, (c) 1997, and (d) 1998.

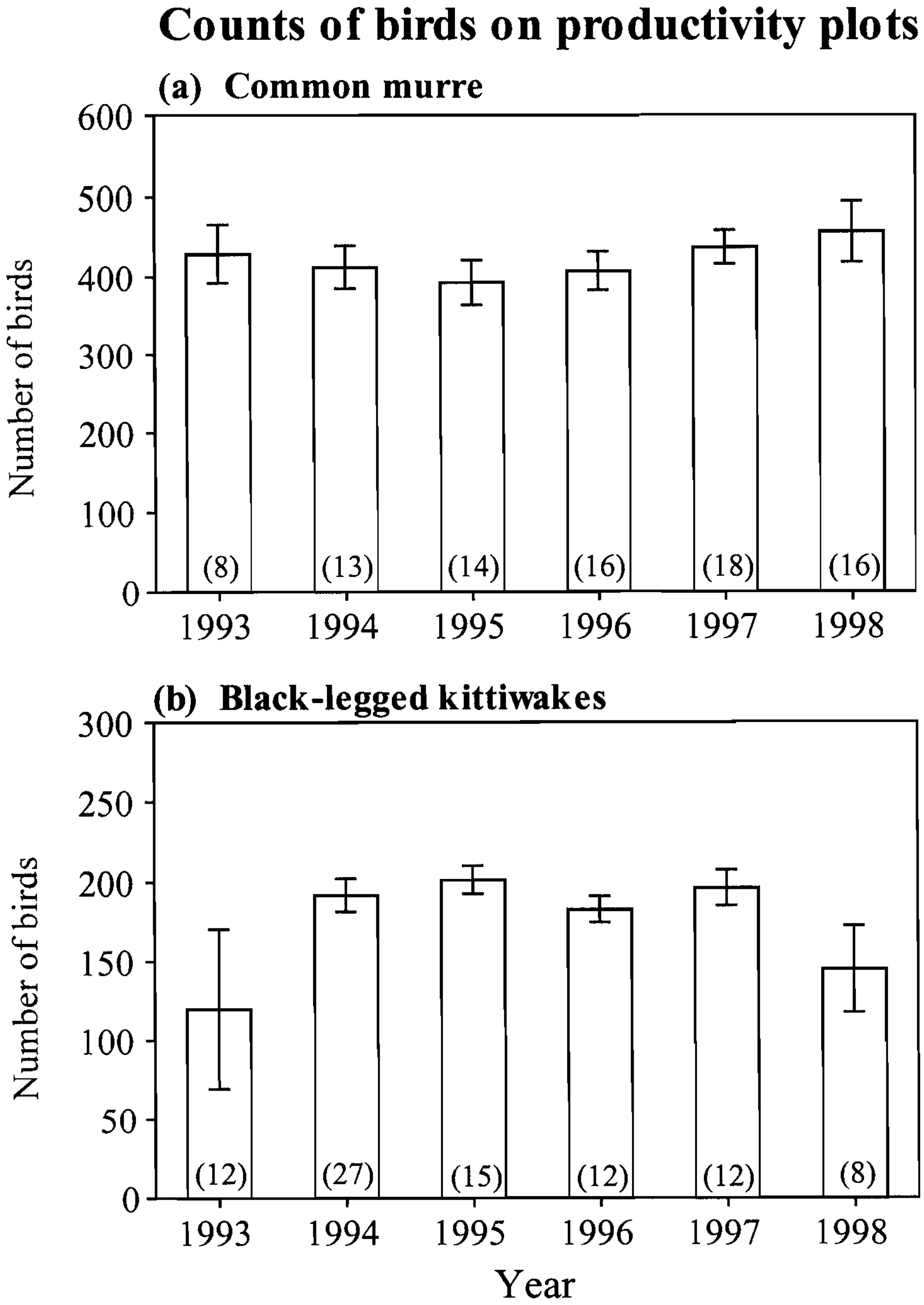


Figure 17. Counts of adult birds on productivity plots of (a) common murres and (b) black-legged kittiwakes at East Amatuli Island, Barren Islands, Alaska, 1993-1998. Number of counts in parentheses; error bars = standard deviation.

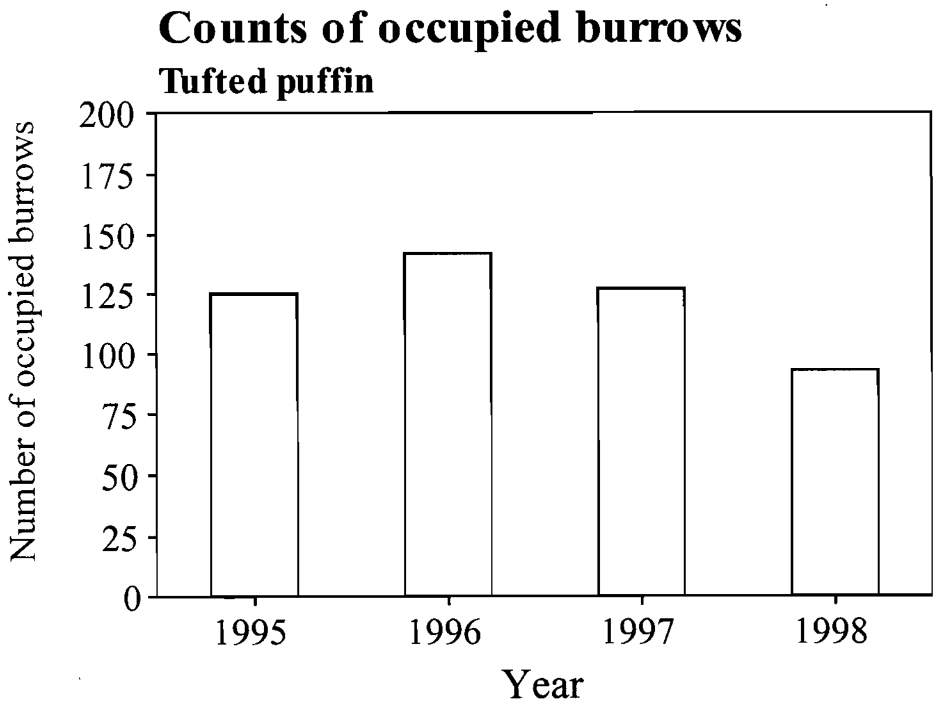


Figure 18. Number of occupied tufted puffin burrows in 7 plots at East Amatuli Island, Barren Islands, Alaska, 1995-1998.

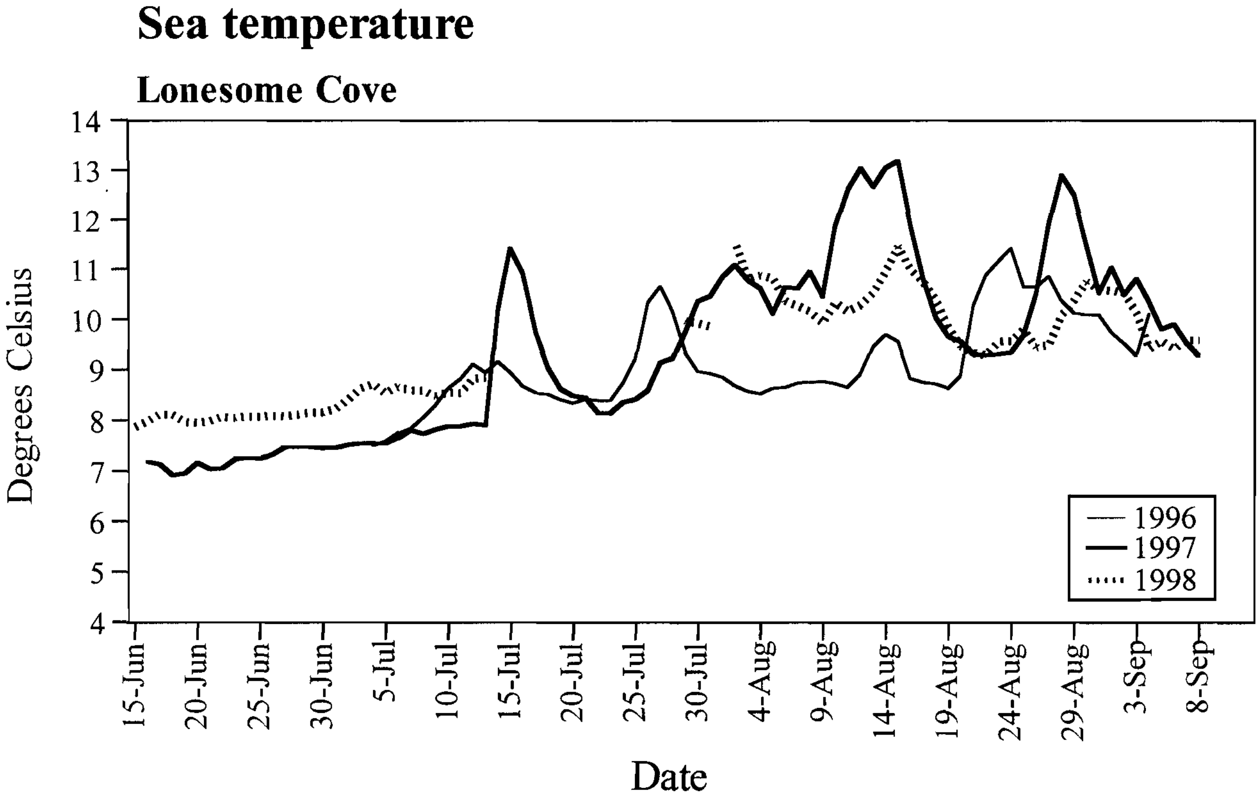


Figure 19. Sea temperature at Lonesome Cove, East Amatuli Island, Barren Islands, Alaska in 1996-1998. Daily averages of measurements taken at 12-minute intervals.

Appendix 1. Schedule for small-mesh beach seine sets at the Barren Islands, Alaska, 1998.

Locations:

--Amatuli Cove at East Amatuli Island
--Cove at NW side of West Amatuli Island (1 day only)

Duration:

16 June - 8 September

Frequency:

Every two weeks, during maximum tidal range: two adjacent sets during low tide and two during high tide.

Disposition:

When catches were small (less than about 2 liters of fish) we sampled the entire catch. Larger catches were subsampled and the remainder was returned to the sea as quickly as possible. Fish longer than 150 mm were measured and returned to the sea. Samples were processed and those not collected and frozen were dumped into nearby deep water.

Processing of samples:

Every set:
--All individuals were identified.
--Individuals were grouped by species. Each group was weighed and individuals were counted. When sets were subsampled, whole-set weights and counts for each species were extrapolated.

Every two weeks:
--100 randomly-chosen sand lance of each age class were weighed to 0.01 g with an electronic balance and measured to 0.1 mm with vernier calipers.

--50 randomly-chosen individuals of each age class of each other species were weighed (to 0.01 g) and measured (to 0.1 mm).

Every month:
We collected and froze in individually-labeled bags:
--50 sand lance 100 mm or less
--50 sand lance >100 mm
--50 of each other forage fish species
--50 larval spp. individuals

Per season:
We collected and froze 50 individuals of each other (non forage-fish) species caught.

K Fish as Samplers Study

Exxon Valdez Oil Spill
APEX Project Annual Report

Using Predatory Fish to Sample Forage Fishes, 1998

APEX Project 98163K
Annual Report

David G. Roseneau
G. Vernon Byrd

U.S. Fish and Wildlife Service
Alaska Maritime National Wildlife Refuge
2355 Kachemak Bay Drive (Suite 101)
Homer, Alaska 99603-8021

March 1999

Using Predatory Fish to Sample Forage Fishes, 1998

APEX Project 98163K
Annual Report

Study History: This project was initiated as part of the *Exxon Valdez* Oil Spill Trustee Council-sponsored Alaska Predator Experiment (APEX) in 1995 (Project 95163K). One annual report and one publication were written at the conclusion of the first year of work (see Roseneau and Byrd 1996, Using predatory fish to sample forage fishes, 1995; and Roseneau and Byrd 1997, Using Pacific halibut to sample the availability of forage fishes to seabirds). Additional data were collected in 1996 and 1997 with support from the Alaska Maritime National Wildlife Refuge and the Trustee Council, respectively, and this information was combined with 1995 data in another annual report (see Roseneau and Byrd 1998, Using predatory fish to sample forage fishes, 1997; Project 97163K). In 1998, the study continued as APEX Project 98163K.

Abstract: Evaluating the influence of fluctuating prey populations (e.g., forage fish) is critical to understanding the recovery of seabirds injured by the T/V *Exxon Valdez* oil spill; however, it is expensive to conduct annual hydroacoustic and trawl surveys to assess forage fish stocks over broad regions. As part of the 1995 *Exxon Valdez* Oil Spill Trustee Council-sponsored Alaska Predator Ecosystem Experiment (APEX), we began to test the feasibility and effectiveness of using stomach contents from sport-caught Pacific halibut *(Hippoglossus stenolepis)* to obtain spatial and temporal data on capelin *(Mallotus villosus)* and Pacific sand lance *(Ammodytes hexapterus)*, two forage fish important to piscivorous seabirds. Because initial efforts provided valuable information on both species of fish in Kachemak Bay - lower Cook Inlet, we collected additional data from this region in 1996-1997 with support from the Alaska Maritime National Wildlife Refuge and Trustee Council, respectively. In 1998, we analyzed another 951 halibut stomachs from the study area. Results from these analyses continued to suggest that this relatively simple sampling technique can supply low-cost relative abundance data on Kachemak Bay - lower Cook Inlet forage fish populations that can be utilized to help monitor seasonal and interannual variations in forage fish stocks and seabird prey bases near nesting colonies.

Key Words: *Ammodytes hexapterus*, Barren Islands, capelin, Cook Inlet, forage fish, halibut, *Hippoglossus stenolepis*, Kachemak Bay, *Mallotus villosus*, Pacific halibut, Pacific sand lance, sand eels, sand lance.

Project Data: (To be addressed in the final report).

Citation: Roseneau, D.G. and G.V. Byrd. 1999. Using predatory fish to sample forage fishes, 1998. Unpubl. annual rept. by the Alaska Maritime National Wildlife Refuge, Homer, Alaska for the *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska (APEX Project 95163K). 15 pp.

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INTRODUCTION

Evaluating the influence of fluctuating prey populations (e.g., forage fish) is critical to understanding the recovery of seabirds injured by the T/V *Exxon Valdez* oil spill; however, it is expensive to conduct annual hydroacoustic and trawl surveys to assess forage fish stocks over broad regions. As part of the 1995 *Exxon Valdez* Oil Spill Trustee Council-sponsored Alaska Predator Ecosystem Experiment (APEX), we began to test the feasibility and effectiveness of using stomach contents from sport-caught Pacific halibut *(Hippoglossus stenolepis)* to obtain spatial and temporal data on capelin *(Mallotus villosus)* and Pacific sand lance *(Ammodytes hexapterus)*, two forage fish important to piscivorous seabirds (APEX Project 95163K; see Roseneau and Byrd 1996, 1997, 1998). Because initial efforts provided valuable information both species of fish in Kachemak Bay - lower Cook Inlet, we collected additional data from this region in 1996-1997 with support from the Alaska Maritime National Wildlife Refuge and Trustee Council, respectively. In 1998, we analyzed another 951 halibut stomachs from the study area for the ongoing APEX ecological processes project. Results from these analyses continued to suggest that this relatively simple sampling technique can supply low-cost relative abundance data on Kachemak Bay - lower Cook Inlet forage fish populations that can be utilized to help monitor seasonal and interannual variations in forage fish stocks and seabird prey bases near nesting colonies.

OBJECTIVES

Objectives were to test the feasibility of using stomach contents from sport-caught halibut to sample forage fish stocks in the Kachemak Bay - lower Cook Inlet region, and evaluate the effectiveness of the technique in obtaining information useful to APEX seabird and forage fish studies in the spill area (e.g., studies of common murres, *Uria aalge*; black-legged kittiwakes, *Rissa tridactyla*; tufted puffins *(Fratercula cirrhata)*, sand lance, capelin).

METHODS

Halibut were chosen as potential samplers of forage fish populations because they opportunistically take a wide range of both fish and invertebrate prey, including sand lance and capelin (see Yang 1990; Roseneau and Byrd 1996, 1997, 1998). They were also selected as sampling tools because a large, 100-150 vessel sport charter boat fleet fishes for them in Kachemak Bay - lower Cook Inlet throughout May-August in several of same areas utilized by foraging seabirds nesting at the Barren Islands and Gull and Chisik islands colonies (see Roseneau and Byrd 1996, 1997).

The Kachemak Bay - lower Cook Inlet study area was set up and divided into 12 sampling subunits in May 1995 (Fig. 1, Appendix 1; see Roseneau and Byrd 1996, 1997, 1998). During late May - early September 1995-1998, we obtained 586, 778, 1,433, and 951 halibut stomachs from 7-8 of these areas, respectively (Appendix 2)[1]. Most stomachs were acquired when charter boat operators filleted fish for customers at public and private fish-cleaning facilities on the Homer Spit. However, Lake Clark National Park and Alaska Department of Fish and Game (ADF&G) biologists collected 173 stomachs from lodge owners and sport fishermen in Areas 1-2 in 1996, and ADF&G fisheries personnel also obtained 324 and 282 stomachs from these areas in 1997 and 1998, respectively.

Catch dates, locations, and fish lengths were usually obtained when stomachs were removed from carcasses; however, in some cases, these data were attached to bagged frozen samples saved for the project by participating fishermen. Stomach contents were identified using taxonomic keys,

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[1] During 1995-1998, halibut lengths averaged 99 cm (n = 586, range = 71-213 cm), 111 cm (n = 778, range = 64-160 cm), 87 cm (n = 433, range = 57-141 cm), and 88 cm (n = 280, range =45-147 cm), respectively.

photographs, and voucher specimens (see Roseneau and Byrd 1996, 1997, 1998). Whole and partly digested, but still recognizable fish and invertebrates were sorted into several categories, including capelin, sand lance, flatfish, sculpin, cod, crabs, shrimp, squid, octopus, mollusks, and other fish and invertebrate species. Empty stomachs were weighed to obtain estimates of content weight, and undigested capelin and sand lance were weighed and measured to obtain size data for other investigators (e.g., J. Piatt, Project 98163M). Some whole capelin and sand lance were also frozen, or preserved in 10% buffered formaldehyde and 75% ethanol - 2% glycerin solutions for later analysis by other researchers.

Data were entered stomach-by-stomach into computer spreadsheets. Analysis consisted of eliminating all potential bait items from the data base (e.g., cod and salmon heads; Pacific herring, *Clupea harengus pallasi*); sorting remaining information by dates, areas, and species; and calculating numbers and frequencies of occurrence of fish and invertebrates in different geographic areas and time periods (see Roseneau and Byrd 1996, 1997, 1998).

RESULTS

We limited preliminary multiyear analyses to Areas 2, 4, 6, 8, and 10 (see Fig 1). Data from Areas 1 and 12 will be incorporated into the final FY 99 report. *[Samples were not obtained from Areas 3, 5, 7, 9, and 11 during 1995-1998, because these areas are rarely fished by the sport charter fleet].*

In 1998, fish were present in 39% of the stomachs, compared to 49% in 1995, 55% in 1996, and 32% in 1997 (Fig. 2). Occurrence of fish also varied in stomachs containing prey over the 4-year interval (Fig. 3). The percentage of stomachs containing sand lance tended to increase from 1995 to 1998 (11%, 6%, 17%, and 20%, respectively). In contrast, the percentage containing capelin declined during 1995-1997 and then rebounded to a point between 1995 and 1996 levels in 1998 (33%, 11%, 8%, and 20%, respectively). The proportion of other forage fish (17%, 30%, 28%, and 5%) and non-forage fish (24%, 31%, 34%, and 24%) species was lowest in 1995 and 1998, years when percentages of capelin were highest.

Numbers of fish in stomachs containing prey followed a pattern similar to occurrence of capelin: they declined markedly during 1995-1997 (79%, 45%, and 36%, respectively) and then rebounded in 1998 (50%; Fig 4). Although capelin and sand lance dominated the fish component by number every year (83%, 56%, 68%, and 87 in 1995-1998, respectively), combined percentages of these fish were lowest in 1996-1997, when non-forage fish numbers were highest (22% and 25%, respectively). Capelin and sand lance also clearly switched roles between 1995 and 1997 (60% and 23% in 1995 *vs* 19% and 49% in 1997, respectively; see Fig. 4).

When fish numbers were compared among areas and years, numbers of capelin were consistently lowest in Area 2 (Fig. 5a; mean 3%, range 0-7%) and highest in Areas 6 (Fig. 5b; mean 62%, range 47-74%) and 10 (Fig. 5c; mean 60%, range 28-82%). Data from these areas and Areas 4 and 8 also provided evidence that capelin stocks declined and sand lance populations increased between 1995 and 1997; for the five areas combined, capelin averaged 45% (range 0-82%) and 18% (range 2-47%), and sand lance averaged 23% (range 0-57%) and 47% (range 33-74%), respectively (see Figs. 5a, 5b, and 5c). Combined data from the five areas also suggested that sand lance and capelin stocks were both high in 1998; sand lance averaged 41%, a value only 6% below the 1997 level, and capelin averaged 44%, a figure 26% higher than the 1997 value and identical to the 1995-1996 levels (45% and 44%, respectively; see Figs. 5a, 5b, and 5c).

DISCUSSION

The consistently small number of capelin found in halibut stomachs from Area 2 was probably related to the less saline, more turbid water conditions typically found north of Anchor Point, and the consistently high percentage of these forage fish in Area 6 and 10 stomachs was probably associated with cold water upwellings that occur in the Point Adam and Barren Islands vicinities (J. Piatt, pers. comm.).

Study results indicated that forage fish stocks were higher in 1995 and 1998 than during 1996-1997. They also suggested that sand lance populations increased while capelin stocks declined and rebounded during this 4-year period. These changes were consistent with observations from other studies and charter boat skippers. For example, in 1993-1995, tens of thousands seabirds, including sooty shearwaters *(Puffinus griseus)*, black-legged kittiwakes, tufted puffins, murres, and cormorants *(Phalacrocorax* spp.*)*, and up to 200 humpback whales *(Megaptera novaeangliae)* were regularly observed feeding on large post-spawning schools of capelin in the Barren Islands area during late June - late August (see Roseneau *et al.* 1995, 1996; Roseneau and Byrd 1996, 1997). Capelin schools and associated concentrations of feeding seabirds and whales were scarce in this area during mid-July - mid-August 1996, and almost entirely absent from it during the same interval in 1997 (seabirds primarily consisted of tufted puffins and kittiwakes in groups of fewer than 500 individuals in 1996, and fewer than 100 birds the following year, and the highest daily whale counts in these years were 12 and 4 individuals, respectively; D.G. Roseneau, pers. obs., Projects 96144 and 97144). In 1998, large schools of capelin that attracted as many as 40-100 humpback whales, 20-45 killer whales *(Orcinus orca)*, and thousands of seabirds were common in the Barren Islands, Kennedy Entrance, and Point Adam areas after mid-July (Capt. R. Swenson, Homer Ocean Charters, pers. comm.).

The apparent shift from a capelin dominated food web in 1995 to one containing large numbers of sand lance in 1997 that was suggested by the multiyear halibut stomach data paralleled 1995-1997 changes in Barren Islands kittiwake chick diets. During these three years, kittiwake chicks reared at the East Amatuli Island - Light Rock colony were fed about 64%, 28%, and 14% capelin, and 13%, 53%, and 63% sand lance by weight, respectively (see Roseneau *et al.* 1998). In 1998, when halibut stomachs contained high percentages of both forage fish species, chick diets reflected the change: regurgitation's from nestlings contained about 32% capelin and 50% sand lance, and regurgitation's from adult kittiwakes delivering food to chicks consisted of about 29% capelin and 38% sand lance (Roseneau *et al.*, unpubl. data). *Note: 1998 chick and adult regurgitation s also contained about 5% and 33% unidentified smelt, respectively; most of these fish were probably capelin.*

Preliminary analyses of beach seine data collected by APEX Projects 96163J, 97163J, 96163M, and 97163M also indicated that sand lance were more numerous than capelin in the Kachemak Bay - lower Cook Inlet region in 1997 (M. Robards, pers. comm.). More comprehensive analyses that incorporate halibut stomach information from Areas 1 and 2, and beach seine, trawl, and seabird chick diet data from the Barren Islands and Gull and Chisik islands colonies will be included in the FY 99 final report.

CONCLUSIONS

1. Results from the third year of study helped confirm that analyzing stomach contents from sport-caught halibut can supply low-cost relative abundance data on forage fish populations in Kachemak Bay - lower Cook Inlet that are needed to help monitor and assess seasonal and interannual variations in forage fish stocks and seabird prey bases.

2. Results also indicated that the sampling method can be used to monitor seasonal changes in relative abundance of capelin and sand lance in certain circumstances. When data were sufficient to be divided into two-week time blocks, we were able to detect within-season variation in these species (e.g., Area 6 in 1995; see Roseneau and Byrd 1996, 1997, 1998). Based on these data, we believe that this relatively simple cost-effective technique can provide a variety of useful information on forage fish stocks in areas where seabird foraging areas and regular sport fishing activities overlap (e.g., Barren Islands, Gull and Chisik island vicinities).

RECOMMENDATIONS

Based on 1995-1998 results, including similarities between halibut stomach contents and kittiwake chick diets, we recommend continuing this relatively inexpensive forage fish sampling study in Kachemak Bay - lower Cook Inlet during the last field season of the APEX project in FY 99.

ACKNOWLEDGMENTS

We would like to thank our volunteers, Jill Aho (1995-1998), Daniel Boone (1995-1996), and Martin Robards (1996-1998), for their help during the study. Jill and Dan made arrangements to obtain samples from halibut charter boat operators, met returning vessels, recorded catch dates and locations, and processed stomach contents. Martin single-handedly identified contents from over 2,500 stomachs in 1996-1998. We also thank Scott Meyer and Willy Dunn of the Homer office of the Alaska Department of Fish and Game for collecting stomachs from fishermen in the Ninilchik -Deep Creek vicinities in 1996-1998; Alan Bennet, Lake Clark National Park and Preserve, for providing data from stomachs collected by National Park Service staff along the western side of Cook Inlet in 1996; Captain Rick Swenson, Homer Ocean Charters, for letting us sample carcasses at his Homer Spit facilities in 1995-1998, and for contributing valuable observations of forage fish schools and feeding seabirds and whales to the study; and all of the other charter boat operators and vessel captains who provided samples and information to the project. Bruce Wright, National Marine Fisheries Service, and John Piatt, U.S.Geological Survey Biological Resources Division, made helpful suggestions during the work. The study was funded by the *Exxon Valdez* Oil Spill Trustee Council in 1995 and 1997-1998, as part of the ongoing Alaska Predator Ecosystem Experiment (APEX Project 98163); additional support was provided by the Alaska Maritime National Wildlife Refuge and APEX Project 97163M in 1996 (J. Piatt).

LITERATURE CITED

Roseneau, D.G., and G.V. Byrd. 1996. Using predatory fish to sample forage fishes, 1995. Appendix K (13 pp.) *in* APEX: Alaska Predator Ecosystem Experiment (D.C. Duffy, Compiler), *Exxon Valdez* Oil Spill Restoration Proj. Annual rept. (Restoration Proj. 95163), Alaska Natural Heritage Program, Univ. of Alaska - Anchorage, Anchorage, AK.

_____. 1997. Using Pacific halibut to sample the availability of forage fishes to seabirds. Pp. 231-241 *in* Forage Fishes in Marine Ecosystems, Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, University of Alaska Sea Grant College Program Report No. 97-01, University of Alaska-Fairbanks, Fairbanks, AK.

_____. 1998. Using predatory fish to sample forage fishes, 1997. Appendix K (14 pp.) *in* APEX: Alaska Predator Ecosystem Experiment (D.C. Duffy, Compiler), *Exxon Valdez* Oil Spill Restoration Proj. Annual rept. (Restoration Proj. 95163), Alaska Natural Heritage Program, Univ. of Alaska - Anchorage, Anchorage, AK.

Roseneau, D.G., A.B. Kettle, and G.V. Byrd. 1995. Common murre restoration monitoring in the Barren Islands, Alaska, 1993. Unpubl. final rept. by the Alaska Maritime National Wildlife Refuge, Homer, Alaska for the *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK (Restoration Project 93049). 71 pp.

_____. 1996. Common murre restoration monitoring in the Barren Islands, Alaska, 1994. Unpubl. final rept. by the Alaska Maritime National Wildlife Refuge, Homer, Alaska for the *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK (Restoration Project 94039). 73 pp.

_____. 1998. Barren Islands seabird studies, 1997. Appendix J *in* Apex: Alaska Predator Ecosystem Experiment (D.C. Duffy, Compiler), *Exxon Valdez* Oil Spill Restoration Proj. Annual rept. (Restoration Proj. 97163), Alaska Natural Heritage Program, Univ. of Alaska, Anchorage, AK.

_____. 1999. Barren Islands seabird studies, 1998. Appendix J *in* Apex: Alaska Predator Ecosystem Experiment (D.C. Duffy, Compiler), *Exxon Valdez* Oil Spill Restoration Proj. Annual rept. (Restoration Proj. 98163), Alaska Natural Heritage Program, Univ. of Alaska, Anchorage, AK.

Yang, M-S. 1990. Food habits of the commercially important groundfishes in the Gulf of Alaska in 1990. NOAA Tech. Memorandum NMFS-AFSC-22, NTIS, Springfield, VA.

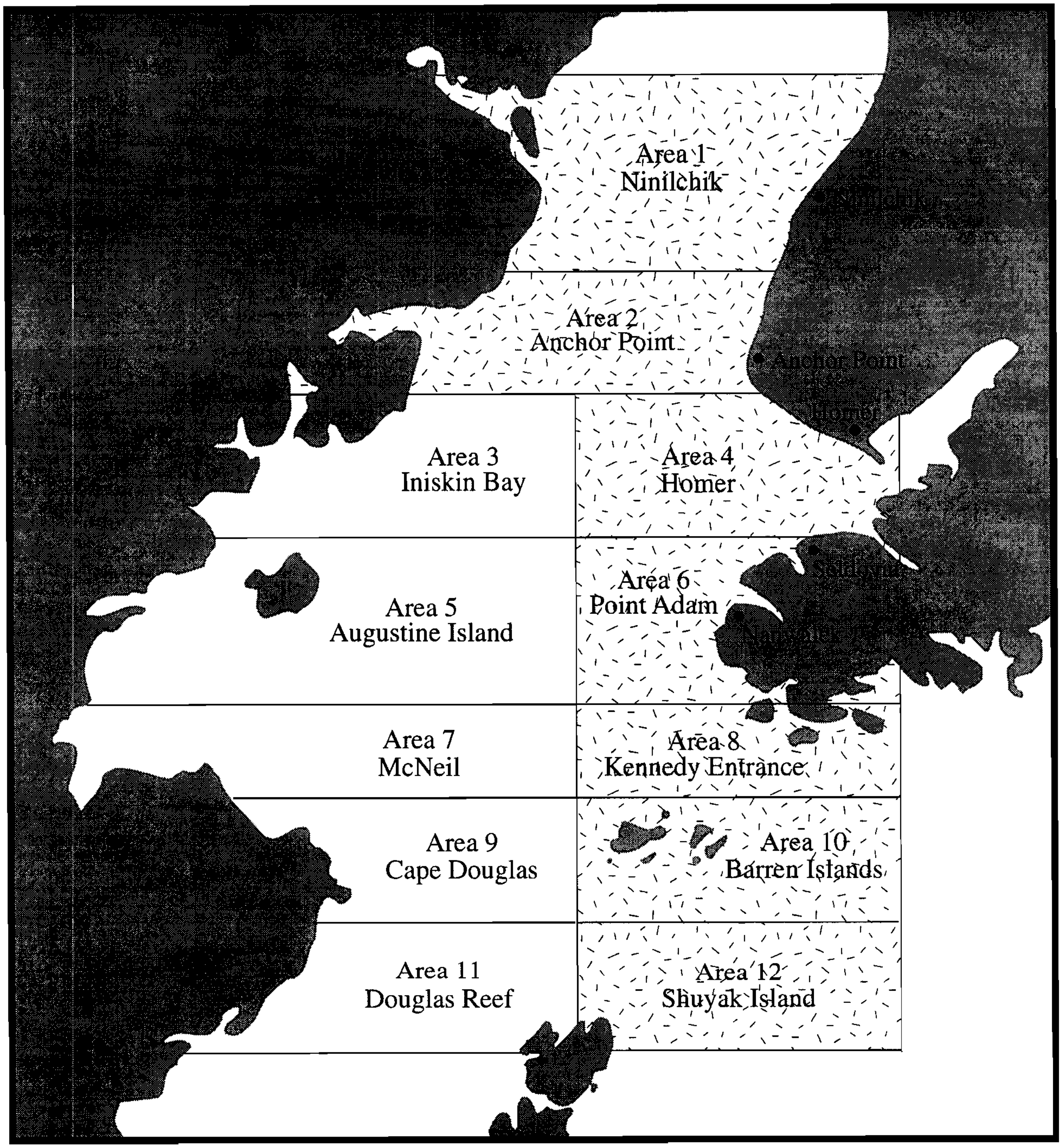


Figure 1. The Kachemak Bay - lower Cook Inlet study area (all samples were obtained from stippled areas).

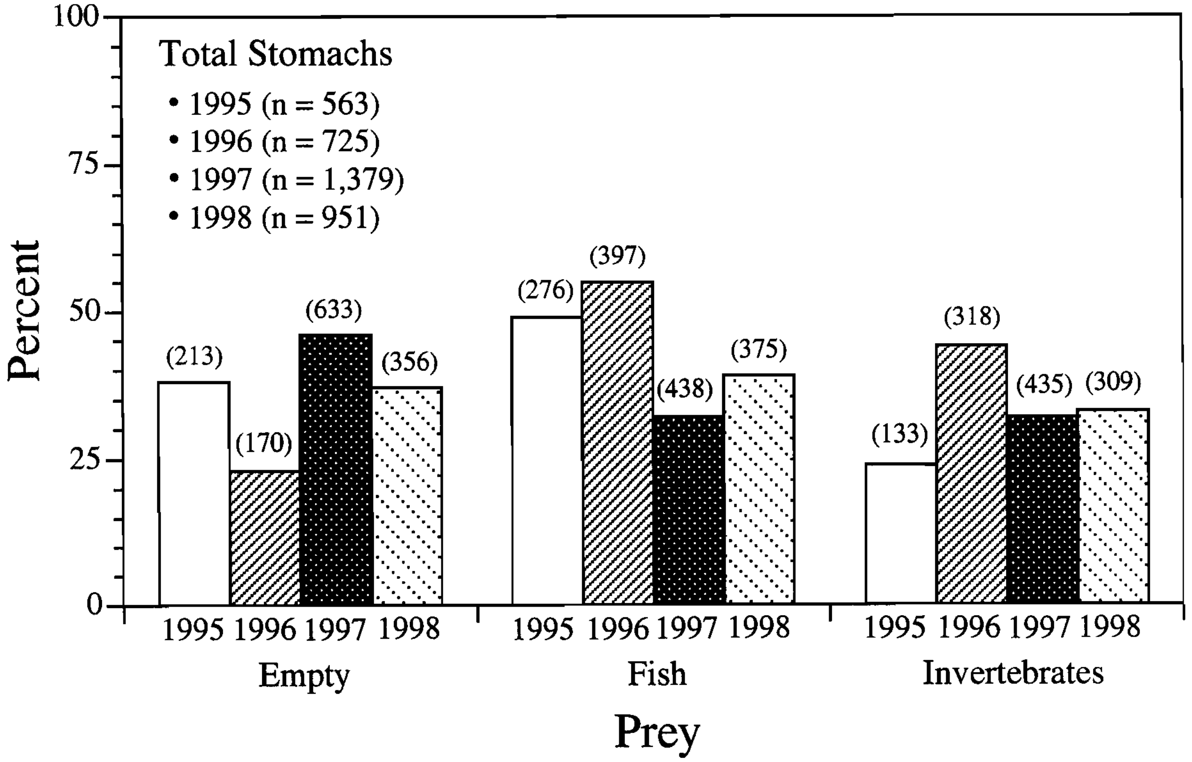
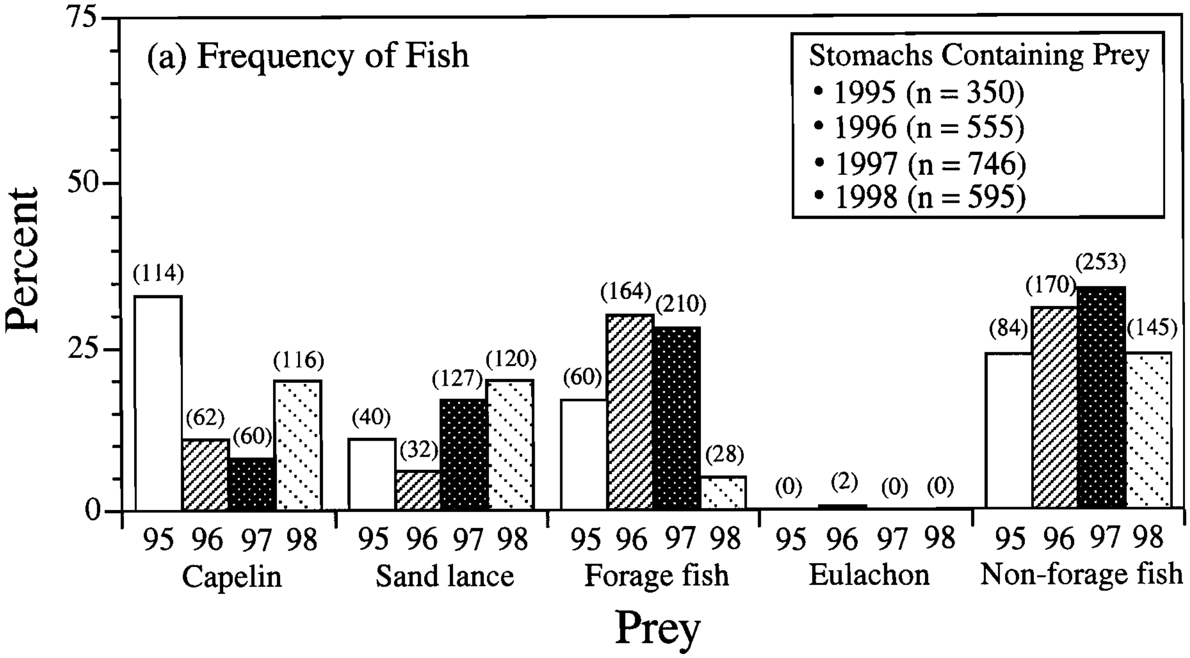


Figure 2. Frequency of occurrence of fish and invertebrates in halibut stomachs from Areas 2, 4, 6, 8, and 10 in Kachemak Bay - lower Cook Inlet, 1995-1998 (numbers of stomachs shown in parentheses).



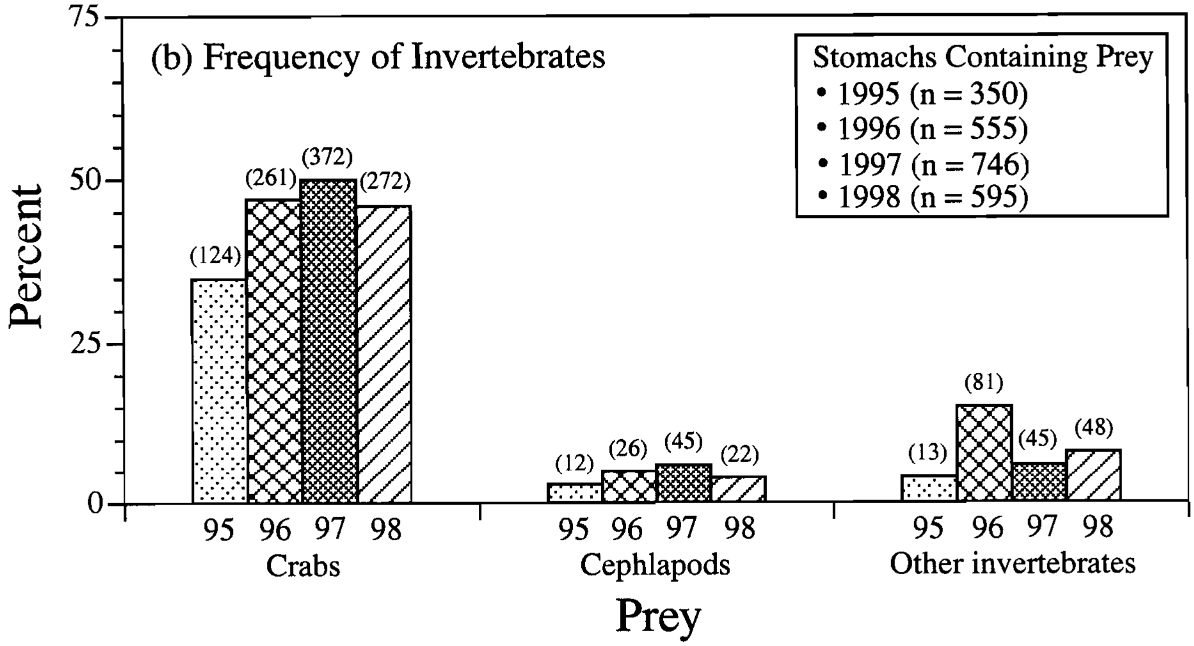


Figure 3. Frequencies of occurrence of (a) fishes and (b) invertebrates in halibut stomachs from Areas 2, 4, 6, 8, and 10 in Kachemak Bay - lower Cook Inlet that contained prey, 1995-1998 (numbers of stomachs shown in parentheses).

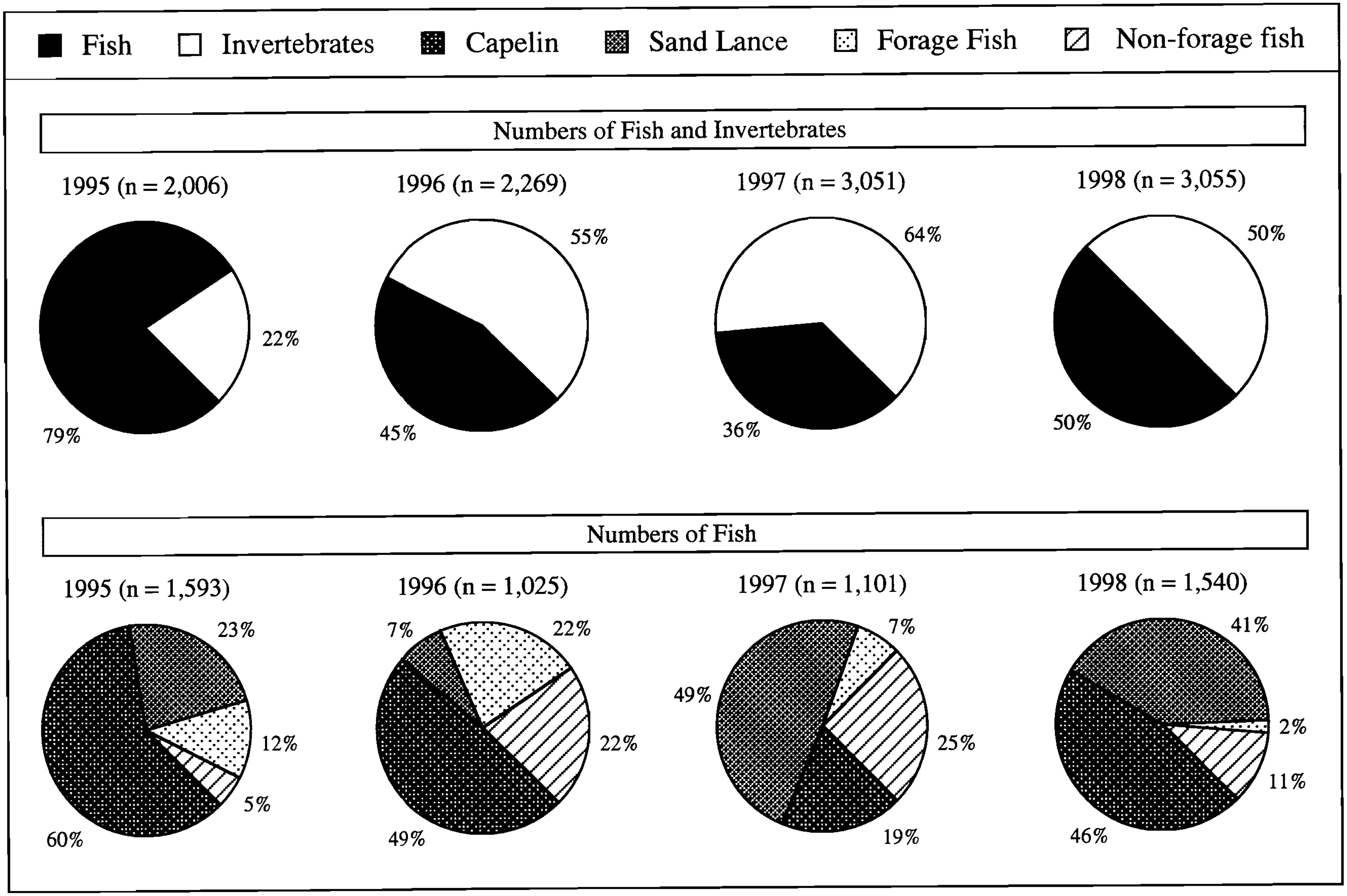


Figure 4. Numbers of fish and invertebrates in halibut stomachs from Areas 2, 4, 6, 8, and 10 in Kachemak Bay - lower Cook Inlet that contained prey, 1995-1998.

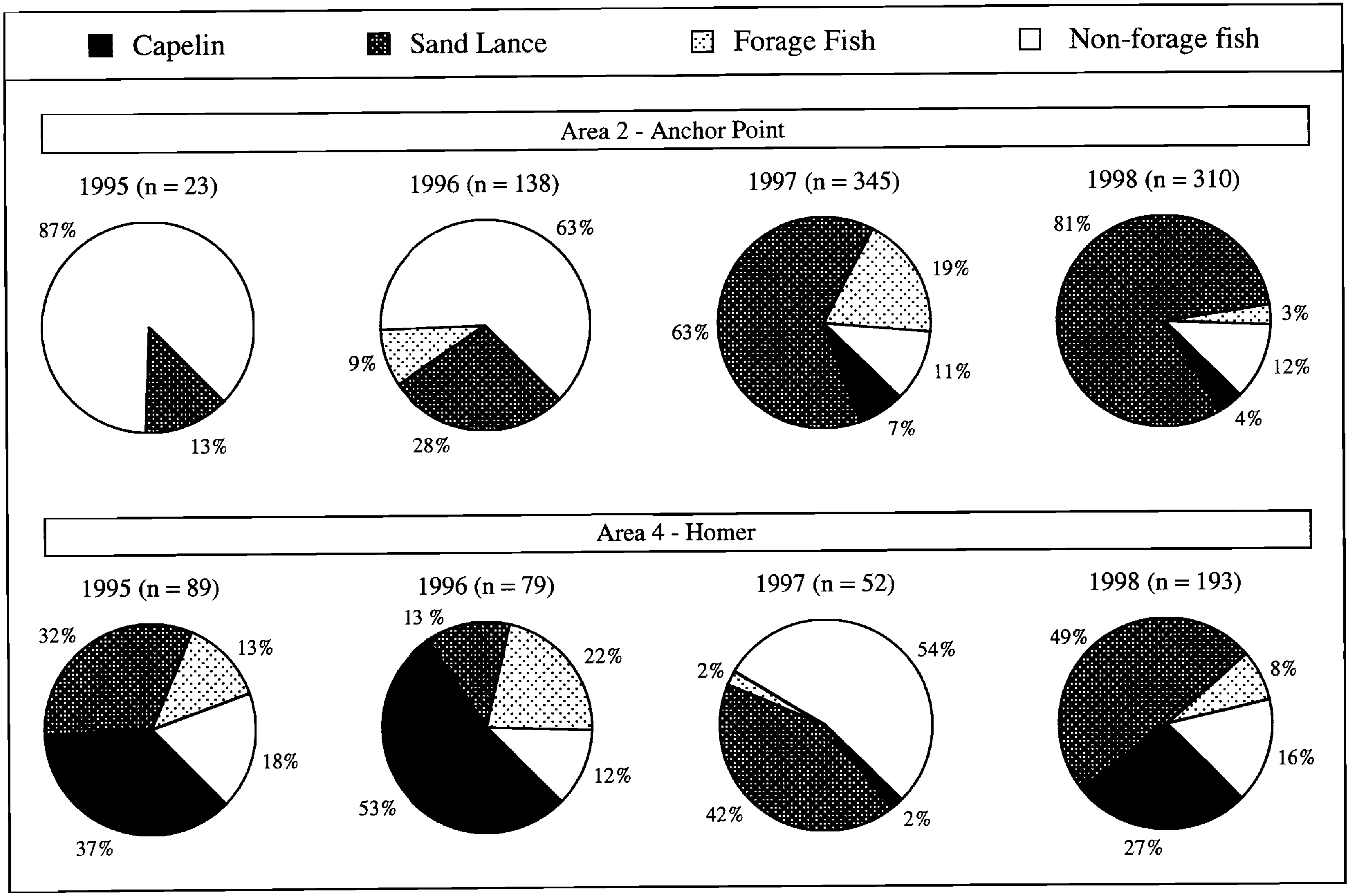


Figure 5a. Numbers of fish in halibut stomachs from Areas 2 and 4 in Kachemak Bay - lower Cook Inlet that contained prey, 1995-1998.

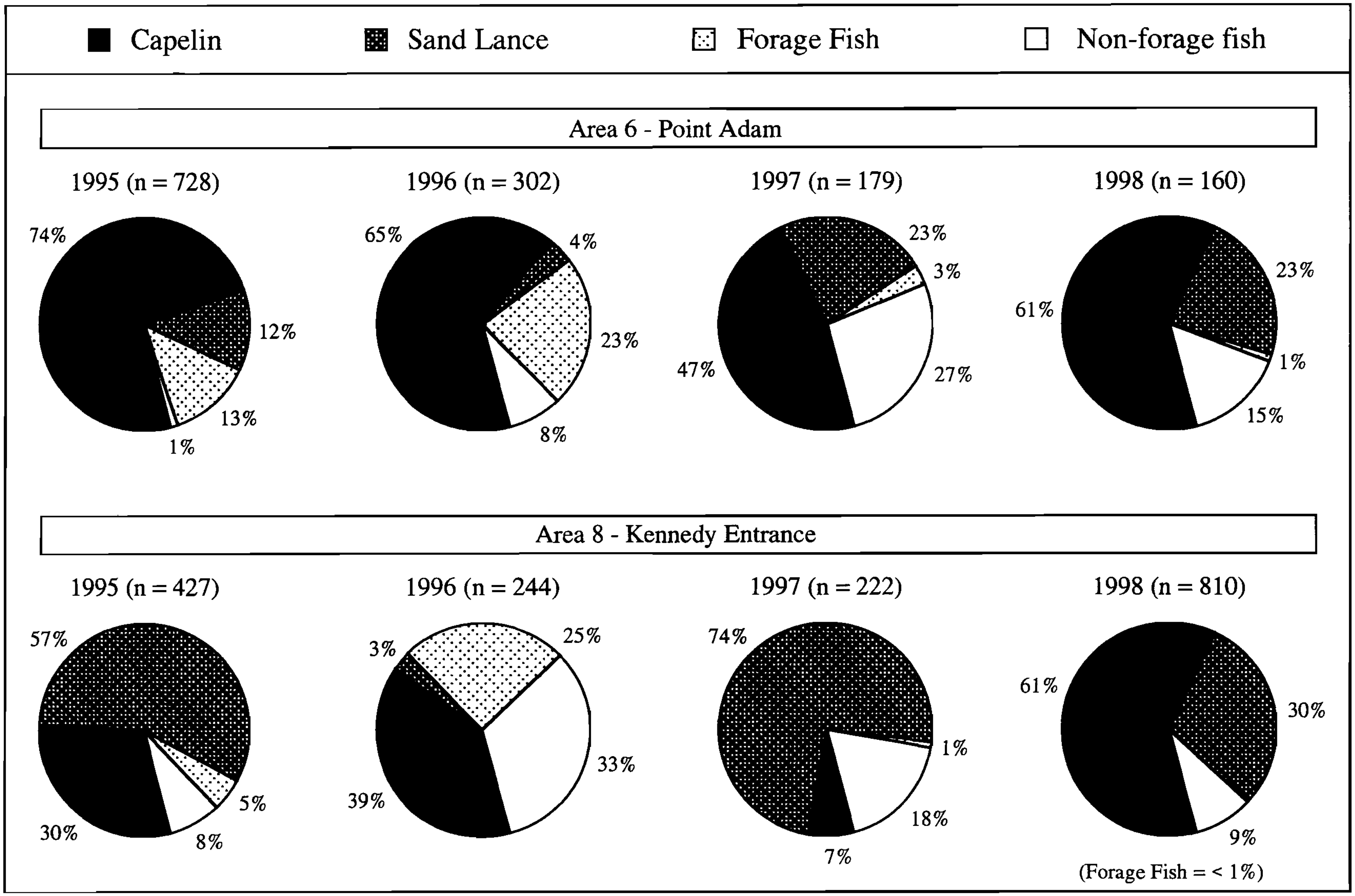


Figure 5b. Numbers of fish in halibut stomachs from Areas 6 and 8 in Kachemak Bay - lower Cook Inlet that contained prey, 1995-1998.

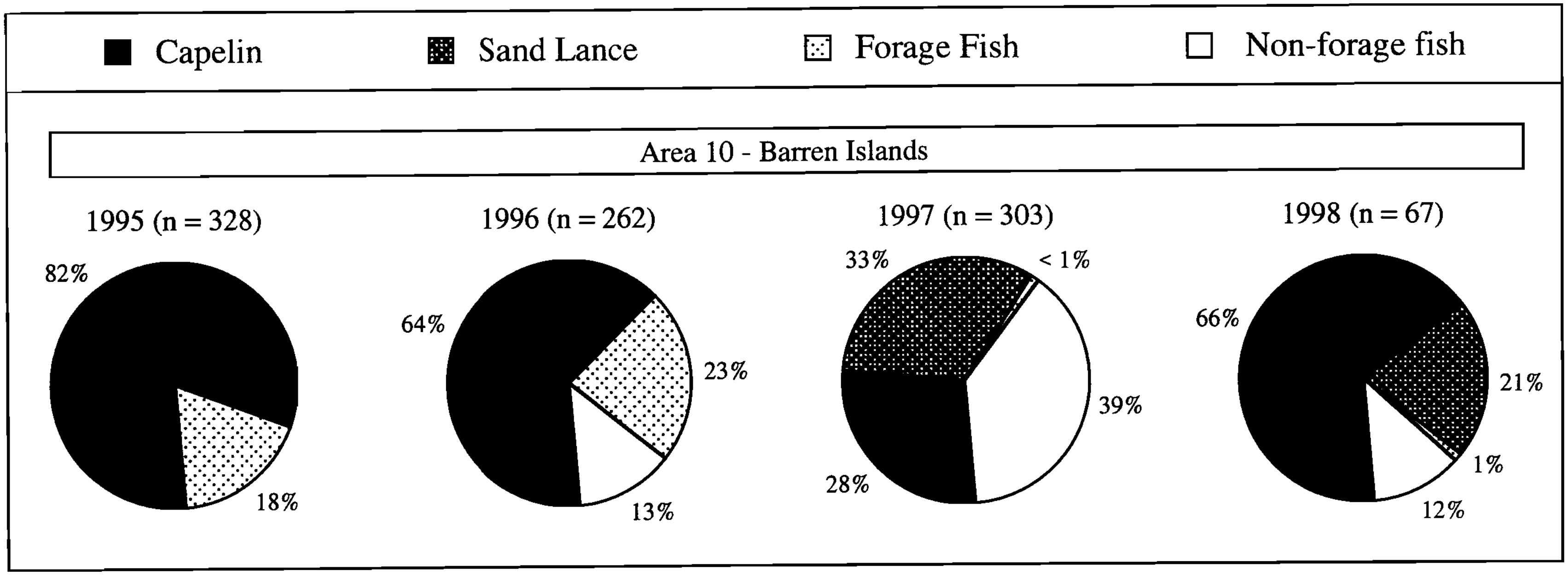


Figure 5c. Numbers of fish in halibut stomachs from Area 10 in Kachemak Bay - lower Cook Inlet that contained prey, 1995-1998.

Appendix 1. Boundaries of the 1995-1998 Kachemak Bay - lower Cook Inlet halibut stomach sampling areas (latitudes and longitudes in hundredths of minutes and degrees and minutes).

Area 1 (Ninilchik): The northern boundary is 60.23 N (60° 14' N), the southern boundary is 59.92 N (59° 55' N), and the western and eastern boundaries are the shorelines of Cook Inlet.

Area 2 (Anchor Point): The northern boundary is 59.92 N (59° 55' N), the southern boundary is 59.72 N (59° 43' N), and the western and eastern boundaries are the shorelines of Cook Inlet.

Area 3 (Iniskin Bay): The northern boundary is 59.72 N (59° 43' N), the southern boundary is 59.45 N (59° 27' N), the western boundary is the shoreline of Cook Inlet, and the eastern boundary is 152.50 W (152° 30' W).

Area 4 (Homer): The northern boundary is 59.72 N (59° 43' N), the southern boundary is 59.45 N (59° 27' N), the western boundary is 152.50 W (152° 30' W), and the eastern boundary is 151.42 W (152° 25' W).

Area 5 (Augustine): The northern boundary is 59.45 N (59° 27' N), the southern boundary is 59.17 N (59° 10' N), the western boundary is the shoreline of Cook Inlet, and the eastern boundary is 152.50 W (152° 30' W).

Area 6 (Point Adam): The northern boundary is 59.45 N (59° 27' N), the southern boundary is 59.17 N (59° 10' N), the western boundary is 152.50 W (152° 30' W), and the eastern boundary is 151.42 W (152° 25' W).

Area 7 (McNeil): The northern boundary is 59.17 N (59° 10' N), the southern boundary is 59.02 N (59° 01' N), the western boundary is the shoreline of Cook Inlet, and the eastern boundary is 152.50 W (152° 30' W).

Area 8 (Kennedy Entrance): The northern boundary is 59.17 N (59° 10' N), the southern boundary is 59.02 N (59° 01' N), the western boundary is 152.50 W (152° 30' W), and the eastern boundary is 151.42 W (152° 25' W).

Area 9 (Cape Douglas): The northern boundary is 59.02 N (59° 01' N), the southern boundary is 58.80 N (58° 48' N), the western boundary is the shoreline of Cook Inlet, and the eastern boundary is 152.50 W (152° 30' W).

Area 10 (Barren Islands): The northern boundary is 59.02 N (59° 01' N), the southern boundary is 58.80 N (58° 48' N), the western boundary is 152.50 W (152° 30' W), and the eastern boundary is 151.58 W (151° 35' W).

Area 11 (Douglas Reef): The northern boundary is 58.80 N (58° 48' N), the southern boundary is 58.58 N (58° 35' N), the western boundary is the shoreline of Cook Inlet, and the eastern boundary is 152.50 W (152° 30' W).

Area 12 (Shuyak Island): The northern boundary is 58.80 N (58° 48' N), the southern boundary is 58.58 N (58° 35' N), the western boundary is 152.50 W (152° 30' W), and the eastern boundary is 151.58 W (151° 35' W).

Appendix 2. Summary of 1995-1998 Kachemak Bay - lower Cook Inlet halibut stomach collections by sample area (samples were not obtained from Areas 3, 5, 7, 9, and 11; see Fig. 1 and Appendix 1).

Area 1 (Ninilchik)

Total stomachs sampled: (1995) n = 10, number empty = 5 (50%), number with prey = 5 (50%); (1996) n = 52, number empty = 7 (13%), number with prey = 45 (87%); (1997) n = 53, number empty = 18 (34%), number with prey = 35 (66%); (1998) n = 70, number empty = 18, number with prey = 52.

Sample dates: (1995) 1 Jul; (1996) 1 Jun, 4 Jun, 5 Jun, 6 Jun, 8 Jun, 10 Jun, 18 Jun, 19 Jun, 20 Jun, 24 Jun, 26 Jun, 25 Jul, & 28 Jul; (1997) 12 Jun, 20 Jun, 21 Jun, 29 Jun, 2 Jul, 16 Jul, 27 Jul, & 28 Jul; (1998) 5 Jun, 8 Jun, 15 Jun, 19 Jun, 20 Jun, 22 Jun, 30 Jun, 8 Jul, 11 Jul, 19 Jul, 28 Jul, & 1 Aug.

Area 2 (Anchor Point)

Total stomachs sampled: (1995) n = 45, number empty = 10 (22%), number with prey = 35 (78%); (1996) n = 130, number empty = 29 (22%), number with prey = 101 (78%); (1997) n = 270, number empty = 67 (25%), number with prey = 203 (75%); (1998) n = 212, number empty = 45, number with prey = 167.

Sample dates: (1995) 27 May, 31 May, 28 Jun, 29 Jun, & 8 Jul; (1996) 1 Jun, 5 Jun,8 Jun, 9 Jun, 10 Jun, 11 Jun, 13 Jun, 20 Jun, 24 Jun, 27 Jun, 9 Jul, 15 Jul, 16 Jul, 21 Jul, 2 Jul, 14 Jul, 25 Jul, & 27 Jul; (1997) 5 Jun, 12 Jun, 14 Jun, 20 Jun, 21 Jun, 29 Jun, 2 Jul, 6 Jul, 8 Jul, 15 Jul, 16 Jul, 17 Jul, 19 Jul, 24 Jul, 28 Jul, 29 Jul, 2 Aug, 5 Aug, 6 Aug, 10 Aug, 17 Aug, 18 Aug, & 22 Aug; (1998) 5 Jun, 15 Jun, 20 Jun, 22 Jun, 28 Jun, 29 Jun, 30 Jun, 4 Jul, 8 Jul, 10 Jul, 11 Jul, 16 Jul, 18 Jul, 19 Jul, 25 Jul, 28 Jul, 1 Aug, & 9 Aug.

Area 4 (Homer)

Total stomachs sampled: (1995) n = 96, number empty = 41 (43%), number with prey = 55 (57%); (1996) n = 60, number empty = 11 (18%), number with prey = 49 (82%); (1997) n = 92, number empty = 42 (46%), number with prey = 50 (54%); (1998) n =153, number empty = 55, number with prey = 98.

Sample dates: (1995) 27 May, 9 Jun, 28 Jun, 7 Jul, 10 Jul, 17 Jul, 18 Jul, 12 Aug, 18 Aug, & 19 Aug; (1996) 24 Jun, 27 Jul, 19 Aug, & 20 Aug; (1997) 5 Jun, 13 Jun, 15 Jun, 14 Jul, 16 Jul, 2 Aug, 14 Aug, & 16 Aug; (1998) 17 Jun, 18 Jun, 19 Jun, 22 Jun, 23 Jun, 18 Jul, 31 Jul, & 14 Aug.

Area 6 (Point Adam)

Total stomachs sampled: (1995) n = 199, number empty = 54 (27%), number with prey = 145 (73%); (1996) n = 177, number empty = 30 (17%), number with prey = 147 (83%); (1997) n = 246, number empty = 93 (38%), number with prey = 153 (62%); (1998) n 136, number empty = 50, number with prey = 86.

Sample dates: (1995) 1 Jun, 3 Jun, 8 Jun, 14 Jun, 16 Jun, 26 Jun, 27 Jun, 8 Jul, 11 Jul, 15 Jul, 21 Jul, 23 Jul, 27 Jul, 31 Jul, 5 Aug, 6 Aug, 9 Aug, & 14 Aug; (1996) 8 Jun, 13 Jun, 14 Jun, 15 Jun, 18 Jun, 19 Jun, 26 Jun, 30 Jun, 5 Jul, 6 Jul, 8 Jul, 9 Jul, 12 Jul, 22 Jul, 23 Jul, 10 Aug, &

Area 6 (Point Adam)

11 Aug; (1997) 26 May, 5 Jun, 6 Jun, 14 Jun, 18 Jun, 1 Jul, 7 Jul, 16 Jul, 31 Jul, 10 Aug, 18 Aug, & 23 Aug; (1998) 20 Jun, 25 Jun, 3 Jul, 7 Jul, 20 Jul, 29 Jul, 7 Aug, & 14 Aug.

Area 8 (Kennedy Entrance)

Total stomachs sampled: (1995) n = 145, number empty = 61 (42%), number with prey = 84 (58%); (1996) n = 175, number empty = 50 (29%), number with prey = 125 (71%); (1997) n = 288, number empty = 173 (60%), number with prey = 115 (40%); (1998) n =374, number empty = 164, number with prey = 210.

Sample dates: (1995) 1 Jun, 2 Jun, 10 Jun, 14 Jun, 21 Jun, 22 Jun, 3 Jul, 5 Jul, 16 Jul, 20 Jul, 24 Jul, 3 Aug, 21 Aug, 1 Sep, & 3 Sep; (1996) 21 Jun, 22 Jun, 27 Jun, 7 Jul, 8 Jul, 16 Jul, 18 Jul, 23 Jul, 7 Aug, 8 Aug, 9 Aug, 13 Aug, 14 Aug, & 18 Aug; (1997) 1 Jun, 8 Jun, 15 Jun, 20 Jun, 21 Jun, 22 Jun, 28 Jun, 4 Jul, 5 Jul, 14 Jul, 21 Jul, 21 Jul, 26 Jul, 28 Jul, 12 Aug, 16 Aug, & 27 Aug; (1998) 17 Jun, 22 Jun, 4 Jul, 6 Jul, 8 Jul, 12 Jul, 17 Jul, 19 Jul, 22 Jul, 23 Jul, 25 Jul, 27 Jul, 30 Jul, 1 Aug, 3 Aug, 4 Aug, 10 Aug, 12 Aug, 17 Aug, 19 Aug, & 21 Aug.

Area 10 (Barren Islands)

Total stomachs sampled: (1995) n = 80, number empty = 33 (41%), number with prey = 47 (59%); (1996) n = 184, number empty = 49 (27%), number with prey = 135 (73%); (1997) n = 483, number empty =258 (53%), number with prey = 225 (47%); (1998) n = 76, number empty = 42, number with prey = 34.

Sample dates: (1995) 17 Jun, 18 Jun, 23 Jun, 24 Jun, 25 Jun, 2 Jul, 26 Aug, & 30 Aug; (1996) 6 Jun, 7 Jun, 16 Jun, 21 Jun, 28 Jun, 29 Jun, 7 Jul, 14 Jul, 19 Jul, 22 Jul, 24 Jul, 26 Jul, 28 Jul, 3 3 Aug, & 8 Aug; (1997) 4 Jun, 8 Jun, 11 Jun, 15 Jun, 16 Jun, 20 Jun, 21 Jun, 26 Jun, 27 Jun, 28 Jun, 29 Jun, 7 Jul, 10 Jul, 12 Jul, 19 Jul, 27 Jul, 3 Aug, 4 Aug, 6 Aug, 7 Aug, 14 Aug, & 25 Aug; (1998) 26 Jun, 6 Jul, 9 Jul, & 10 Jul.

Area 12 (Shuyak Island)

Total stomachs sampled: (1995) n = 11, number empty = 2 (18%), number with prey = 9 (82%); (1996) n = 0, no data; (1997) n = 0, no data; (1998) n = 29, number empty = 6, number with prey = 23.

Sample dates: (1995) 20 Jun; (1996) none; (1997) none; (1998) 20 Jul & 25 Jul.

L Historical Data Review

Synthesis and Analysis Gulf of Alaska of Small-Mesh Trawl Data
1953 to 1998

by
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Prepared for: *EXXON VALDEZ* oil spill restoration Trustees under
APEX project 98163L -Annual Report- March 15, 1999.

Abstract

Large declines of apex predator populations (murres, kittiwakes, harbor seals, and Steller sea lion) have occurred in the Gulf of Alaska since the 1970s. Changes in composition and abundance of forage species may be responsible for the decline of these predator populations and their chronic low population levels. In an effort to delineate changes in forage species and a trophic regime shift over the last several decades, we have gathered together historical fishery-independent scientific survey data to address this question. Nearly 10,000 individual sampling tows are in the current database of the two agencies. Recent analysis of the 1998 trawl survey data has indicated that the fundamental trophic shift in the ecosystem is still in place. No evidence suggests that the shift is reversing itself. Recent results are discussed and future analysis strategy is discussed. There clearly is a need for moving the survey portion of this project into a long-term monitoring program to keep a time series reference intact. Additionally there is need to integrate oceanographic observations with those from the trawl survey database in order to understand the driving mechanisms that control changes in the community structure of the ecosystem. This will play an increasingly important role in future studies. This report includes several abstracts from recently prepared presentations and manuscripts resulting from project-funded studies.

Introduction

This project pursues analysis of small-mesh trawl sampling results from near-shore surveys in the Gulf of Alaska conducted by the National Marine Fisheries Service (NMFS) and the Alaska Department of Fish and Game (ADF&G). The data for analysis was collected starting in 1953 and continues through 1998. Only general background material concerning this part of the project will be discussed in this section. The reader is referred to the two recently published manuscripts (Anderson et al., 1997 and Bechtol, 1997) for details of the methodology and analysis used with this portion of the data.

Recently there has been information presented that the Gulf of Alaska ecosystem has undergone some abrupt and significant changes (Piatt and Anderson, 1996; Anderson et al., 1997). The extent and degree of these changes are poorly documented and is important in determining future strategies for management of the marine ecosystem. Analysis of the historic data is a first step in gaining an appreciation for the rapid and abrupt changes that have occurred in the marine species complex in the last five decades. The data from small-mesh shrimp trawl cruises provides an opportunity to review changes in the composition of forage species that occurred through time in the Gulf of Alaska.

Historically, there is evidence of major abundance changes in the fish/crustacean community in the western Gulf of Alaska. Fluctuation in Pacific cod availability on a generational scale was reported for coastal Aleutian communities by Turner (1886). Similarly, landings from the near-shore Shumagin Islands cod fishery (Cobb, 1927) showed definite periods of high and low catches with the fishery peaking in late 1870s. King crab commercial catches in the Gulf of Alaska show two major peaks of landings, one in the mid 1960s and another in 1978-1980 (Blau, 1986). All of the area was closed to fishing in response to low population levels in 1983 (Blau, 1986) and has yet to reopen. By the 1960s there was evidence of high Pandalid shrimp abundance in these same areas (Ronholt 1963). One of the highest densities of Pandalid shrimp known in the world was to spur the development of a major shrimp fishery (Anderson and Gaffney, 1977). By the late 1970s the shrimp population density had declined radically and was accompanied by a closure of the shrimp fishery and the return of cod to inshore areas (Albers and Anderson, 1985). Catches of almost all salmon stocks of Alaskan origin suddenly increased to unprecedented levels in the 1980's (Francis and Hare, 1994, Hare and Francis, 1995). These changes, witnessed over the last century, imply dynamic fluctuations in abundance of commercially fished species. Managers, fisherman, and processors should be aware of these dynamics and their impacts on the ecology and economy.

Results From 1998 Surveys

Late summer surveys continued in the Pavlof Bay study area in 1998. Although this area is outside the EVOS spill zone, it has been the site for the longest annual trawl survey sampling in the entire Gulf of Alaska during the last 27 years. Changes in the trophic structure were first observed in this area which led to expanded analysis of trawl survey data from other areas of the Central and Western Gulf of Alaska. This long-term study has been the impetus toward a better understanding of the degree and magnitude of the trophic shift that has occurred and continuing impacts on the marine ecosystem.

Twenty-two tows were completed in the Pavlof Bay study area. This same survey location has been sampled in the same manner and at the same relative time each year for the past 27 years. It is anticipated that we will again complete this survey again in late summer of 1999, thus keeping this valuable time series continuous.

Osmerids and Pandalid shrimps continue to remain at historic low levels. Pandalid shrimps are at their lowest levels ever during the entire survey series. Shrimp were recorded at 7.47, 2.11, and 2.38 kg/km during 1996, 1997, and 1998 respectively. Cod and pollock remained the major component of catches in each year averaging 212.89, 379.66, and 493.9 kg/km in 1996, 1997, and 1998 respectively. Pleuronectid fish populations have apparently stabilized, and they averaged 144.45, 158.21, and 265.5 kg/km for 1996-98. The relative abundance of Pacific cod declined in survey catches (126.18 kg/km in 1997 and 42.0 kg/km in 1998); observed shrimp density increased slightly from that seen in 1997 2.11 versus 2.38 kg/km. The trend of cod abundance being negatively correlated with observed shrimp abundance seems to support the "predator forcing" hypothesis for adult populations of Pandalid shrimps.

Interesting life history table changes are also being observed for shrimp and fish species. Change in sex transformation of Pandalid shrimp in response to density dependant population levels was first reported by Charnov and Anderson, 1989. The continuing survey results continue to support the hypothesis, that shrimp are transforming earlier as first presented in the earlier preliminary analysis. This will lead to important future work not supported by project funding that will improve our understanding of the dynamics of Pandalid shrimp in Alaskan waters.

It is interesting to note that this was the first year since the survey series began that spiny dogfish shark (*Squalus acanthias*) was encountered in survey samples. They were also present in survey samples taken around Kodiak Island in the ADFG triennial trawl strata. Despite this unusual occurrence recently, historical fish survey records indicate that spiny dogfish were once common locally in inshore waters during the later part of the 1880s (Tanner, 1890). Maintaining accurate and published accounts from surveys that have taken place in the past is one important means of maintaining the proper perspective on survey results.

Papers and Presentations

1. Title: Community reorganization in the Gulf of Alaska following ocean climate regime shift.

Authors: Paul J. Anderson and John F. Piatt

Submitted to: Marine Ecology Progress Series. Status: In Review

ABSTRACT: A shift in ocean climate during the late 1970s triggered a reorganization of community structure in the Gulf of Alaska ecosystem, as evidenced in changing catch composition on long-term (1953-1997) small-mesh trawl surveys. Forage species such as pandalid shrimp and capelin declined and never recovered because of recruitment failure and predator forcing. Total trawl catch biomass declined > 50% and remained low through the 1980s. In contrast, recruitment of high trophic-level groundfish improved during the 1980s, yielding a > 250% increase in catch biomass during the 1990s. This trophic reorganization apparently occurred at the expense of piscivorus sea birds and marine mammals.

2.Title: Accessing Forty-five Years of Trawl Survey Data from the Gulf of Alaska with a GIS.

Authors: Sharon D. Loy and Paul J. Anderson

Presented: First International Symposium on GIS in Fishery Sciences; Seattle, WA March 2 - 4, 1999.

Abstract:

The Gulf of Alaska is a vitally important region containing a great wealth and variety of marine organisms. Questions regarding the driving mechanisms behind recent spatial and temporal changes in distribution and abundance of many species have resulted in a need for access to long-term data. The National Marine Fisheries Service (NMFS) has collected small-mesh research trawl data from the Gulf of Alaska since 1953. This data includes spatial data (locations of each haul in lat/long), parameters of each haul(date, time, distance, duration, depth, etc.), and environmental data (surface and near-bottom temperatures). The species composition of each haul (by both numbers and mass) is in an associated "Catch" data file .

This data is integrated into a GIS using ArcInfo and Arcview (Environmental Systems Research Institute, Redlands CA) software (1) to make the data accessible and easy to query for a broad audience, (2) to enable spatial and temporal analysis of the data to identify long-term patterns in distribution and density both between and within species, and (3) to create visual representations of these spatial and temporal patterns. The GIS project contains themes showing the Alaska Coastline, bathymetry contours, spatial locations of the start of each trawl survey haul, and an area of interest theme which outlines regions in the Gulf of Alaska. The user chooses an area

of interest to view, the GIS zooms into that view, and the user selects survey trawl data to view from that area. The user is given the choice to select data by species, by location (bay), or by user-selected points.

This GIS will increase the accessibility and application of past and current research survey trawl data, and will be maintained for future surveys as well. The system can be queried for simple and complex relationships such as species distributions and how they change over time, changes in species density over time, or changes in spatial relationships between species. This type of analysis improves understanding of the spatial interdependence between organisms and their environment.

3. Title: Distribution Shift of Pacific Cod in Crab Pot Surveys in the Kodiak Area 1971 Through 1986.

Author: James E. Blackburn

Abstract: Catches of Pacific cod were recorded from 26,995 pots during red king crab surveys in the Kodiak area of the Gulf of Alaska from 1971 through 1986. The abundance of cod increased through out the area during this time period. The inshore areas had a higher inter-annual coefficient of variation than offshore areas. The inshore areas were largely devoid of cod prior to about 1982 and cod were common in these same areas in 1982 through 1986. The inshore waters are where juveniles of many species commonly are found. Cod is a major component of the marine community, and a significant predator on some species. The inter annual variability of cod predation in the nursery habitat is identified as a potentially significant source of variability in recruitment of some stocks. Similarly, the inter decadal variability described is likely a source of long term changes in abundance of some species. The warming of waters that seems to be associated with the distribution shift of cod likely affected other species also, generalizing this impact.

4. Patterns in Space and Time; Small-mesh Trawl Surveys in the Gulf of Alaska 1953-98.

Author: Paul J. Anderson

Seminar Presented at the Alaska Fisheries Science Center, Seattle WA and Kodiak, AK on February 6 and 16, 1999.

Abstract: Recognition of changing patterns in species composition from annual small-mesh surveys in the Gulf of Alaska was first realized from the long-term data collected from Pavlof Bay. One of the first criticisms was that this represented a small area. How was it related to the wider Gulf of Alaska? Further studies combined long-term survey data from Alaska Department of Fish and Game with data from NMFS surveys to explore the patterns in the central and western Gulf. These studies 1972-97 showed that at least with the same gear, trends that were first evident in Pavlof were found over a broad area of the Gulf. Since there is broad temporal coherence in the observed patterns, there is probably not a need to conduct extensive annual surveys. Study results suggest selecting representative areas that are logistically capable of producing a reliable time series is more important than trying to provide coverage over a broad area. Analysis success of current survey data demonstrates the importance of maintaining a stable sampling protocol. Sampling gear has remained unchanged throughout the data series, as well as time of day and methodology.

5. Web Page on APEX Project 98163L : www.fakr.noaa.gov/trawl/index.htm

Authors: Sharon Loy, Paul Anderson, John Piatt, and Jim Blackburn.

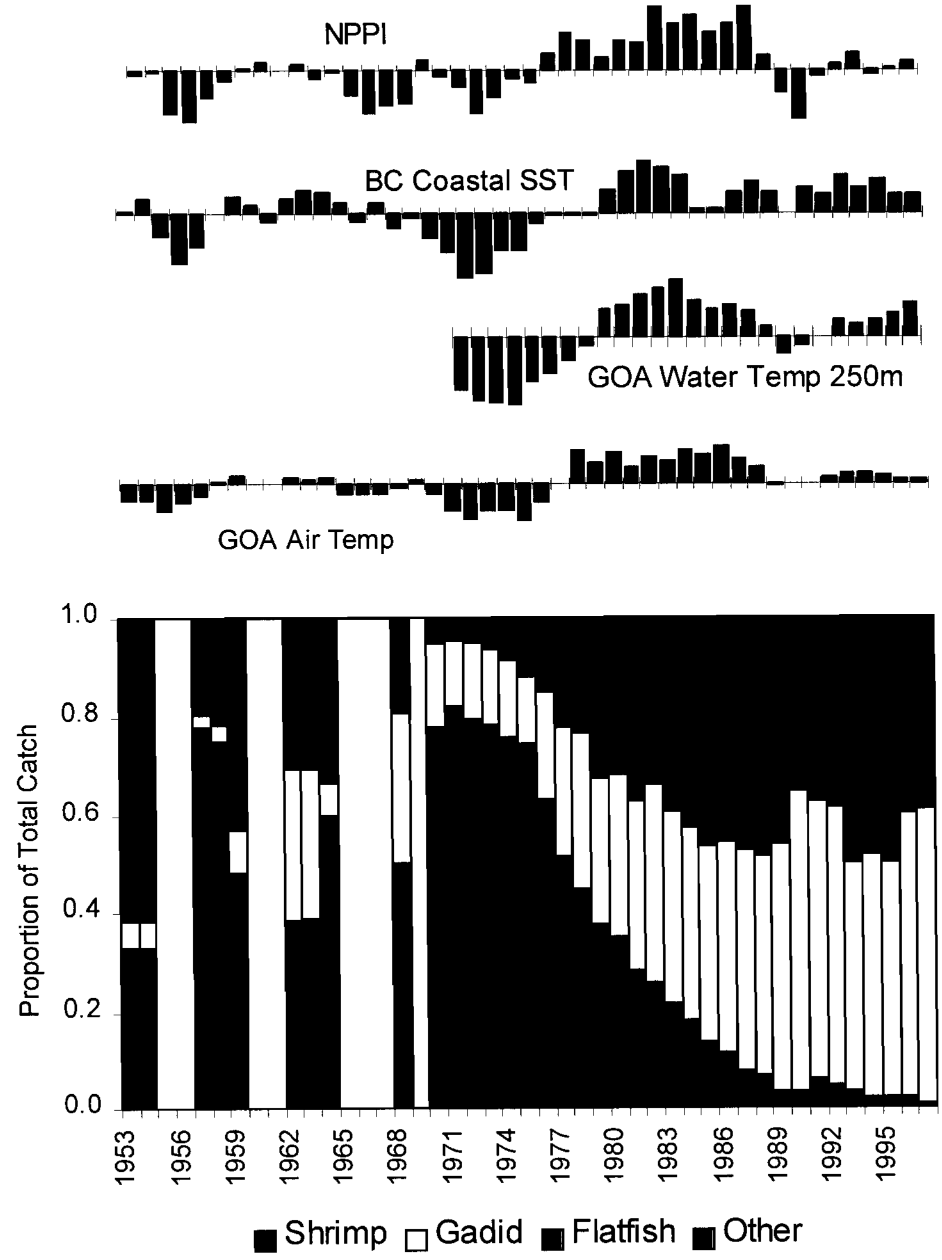

Figure 1. Composition of small-mesh trawl catches in the Gulf of Alaska between 1953 and 1997 in relation to climate indices. Climate data expressed as normalized anomalies NPPI is the North Pacific Pressure Index. Trends smoothed by taking 3-year running averages.

LITERATURE CITED

Albers, W. D., and P. J. Anderson 1985. Diet of the Pacific cod, *Gadus macrocephalus*, and predation on the Northern pink shrimp, *Pandalus borealis*, in Pavlof Bay, Alaska. Fish. Bull., U.S. 83:601-610.

Alverson, D.L., A. T. Pruter and L. L. Ronholt. 1964. Study of Demersal Fishes and Fisheries of the northeastern Pacific Ocean. H. R. MacMillan Lectures in Fisheries, Inst. Fish., Univ. British Columbia, Vancouver, B.C. 190p.

Anderson, P.J. 1991. Age, growth, and mortality of the northern shrimp Pandalus borealis Kröyer in Pavlof Bay, Alaska. Fish Bull. 89:541-553.

Anderson, P. J., J. E. Blackburn, and B. A. Johnson. 1997. Declines of Forage Species in the Gulf of Alaska, 1972-1995, as an Indicator of Regime Shift. In: Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01 p.531-544.

Anderson, P. J. and F. Gaffney. 1977. Shrimp of the Gulf of Alaska. Alaska Seas and Coasts 5(3):1-3.

Blackburn, James E. and Paul J. Anderson. 1997. Pacific Sand Lance Growth, Seasonal Availability, Movements, Catch Variability, and Food in the Kodiak-Cook Inlet Area of Alaska. In: Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01 p.409-426.

Blau, S. F. (1986). Recent Declines of Red King Crab (*Paralithodes camtshatica*) Populations and Reproductive Conditions Around the Kodiak Archipelago, Alaska, p. 360-369. In G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates.

Bechtol, William R. 1997. Changes in Forage Fish Populations in Kachemak Bay, Alaska, 1976-1995. In: Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01 p.441-455.

Bertram, D. F. and G. W. Kaiser. 1993. Rhinoceros Auklet (*Cerorhinca monocerata*) Nestling Diet May Gauge Pacific Sand Lance (Ammodytes hexapterus) Recruitment. Can. J. Fish. Aquat. Sci. 50:1908-1915.

Charnov, Eric L. and Paul J. Anderson 1989. Sex Change and Population Fluctuations in Pandalid Shrimp. Am. Nat. Vol. 134 pp. 824-827.

Cobb, J. N. (1927). Pacific Cod Fisheries. Report U.S. Comm. of Fisheries for 1926, Appendix VII (Doc. No. 1014) p. 385-499.

Favorite, F., A. J. Dodimead, and K. Nasu. 1976. Oceanography of the subarctic Pacific region, 1960-71. International North Pacific Fisheries Commission Bulletin No. 33. 187 pp.

Francis, R. C. and S. R. Hare. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. Fish. Oceanogr. 3:4, 279-291.

Gerasimova, O. V. Peculiarities of spring feeding by capelin (Mallotus villosus) on the Grand Bank in 1987-90. J. Northw. Atl. Fish. Sci., Vol. 17:59-67.

Hare, S. R. and R. C. Francis. 1995. Climate change and salmon production in the Northeast Pacific Ocean. In: R. J. Beamish (ed.) Climate change and Northern Fish Populations. Can. spec. Publ. Fish. Aquat. Sci. 121.

Harriman, E. H. 1910. Harriman Alaska Expedition 1899. Volume I (Narrative) C. H. Merriam (Ed.) Smithsonian Inst. 389pp.

Hood, D. W. and S. T. Zimmerman. 1986. The Gulf of Alaska; Physical Environment and Biological Resources. US GPO 655p.

Hughes, S. E. 1976. System for sampling large trawl catches of research vessels. J. Fish. Res. Bd. Can., 33:833-839.

Jackson, P. B., L. J. Watson, and J. A. McCrary. 1983. The westward region shrimp fishery and shrimp research program, 1968-1981. Infl. Leafl. 216, Alaska Dep. Fish Game, Div. Commer. Fish., Juneau.

Macy, P.T., J.M. Wall, N.D. Lampsakis, and J.E. Mason. 1978. Resources of nonsalmonid pelagic fishes of the Gulf of Alaska and eastern Bering Sea. NOAA, NMFS, Northwest and Alaska Fish. Ctr., Final Rep. OCSEAP Task A-7, RU 64/354. Part I. 355 pp.

Mangel, M., and P. E. Smith. 1990. Presence-Absence Sampling for Fisheries Management. Can. J. Fish. Aquat. Sci. 47:1875-1887.

Piatt, J. F. and P. Anderson. 1996. p.720-737 *In* Rice, S. D., Spies, R. B., and Wolfe, D. A., and B.A. Wright (Eds.). 1996. *Exxon Valdez* Oil Spill Symposium Proceedings. American Fisheries Symposium No.18.

Posgay, R. K. and R. R. Marak, 1980. The MARMAP bongo zooplankton sampler. J. Northw. Atl. Fish. Sci. 1:91-99.

Reed, R. K. and J. D. Schumacher. 1986. p. 57-75. Physical Oceanography *In*: Hood, D. W. and S. T. Zimmerman (Eds.) The Gulf of Alaska; Physical Environment and Biological Resources. US GPO.

Ronholt, L. L. 1963. Distribution and Relative Abundance of Commercially Important Pandalid Shrimps in the Northeastern Pacific Ocean. U.S. Fish Wildl. Ser., Spec. Scient. Rept., 449, 28p.

Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1978. Demersal Fish and Shellfish Resources of the Gulf of Alaska from Cape Spencer to Unimak Pass 1948 - 1976 (A Historical Review). Vol 1 - 3. Northwest and Alaska Fisheries Center Processed Report 871 pp.

Rugen, W. C. 1990. Spatial and Temporal Distribution of Larval Fish in the Western Gulg of Alaska, with Emphasis on the Peak Period of Abundance of Walleye Pollock (Theragra chalcogramma) Larvae. Unpublished Data Report, Northwest and Alaska Fisheries Center Processed Report 90-01, Seattle.

Sameoto, D. D. and L. O. Jaroszynski 1969. Otter surface trawl: a new neuston net. J. Fish. Res. Board Can. 26:2240-2244.

Tanner, Z. L., 1890. Explorations of the fishing grounds of Alaska, Washington territory, and Oregon, during 1888, by the U.S. Fish Commission steamer Albatross. Bulletin of the United States Fish Commission Vol. VIII, for 1888. pp 5-92.

Turner, L. M. 1886. Contributions to the Natural History of Alaska. No. II. Arctic Series of Publications Issued in Connection with the Signal Service, U. S. Army. Gov. Printing Office 226 p.

Wathne, F. 1977. Performance of trawls used in resource assessment. Mar. Fish. Rev. 39:16-23.

M Lower Cook Inlet

Exxon Valdez Oil Spill
Restoration Project Report

Cook Inlet Seabird and Forage Fish Studies

Restoration Project (APEX) 98163M
Annual Report

John Piatt, Alisa Abookire. Gary Drew
Mike Litzow, Alexander Kitaysky, April Nielsen
Tom Van Pelt, Martin Robards, Suzann Speckman, Stephani Zador

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1011 E. Tudor Rd.
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April 1999

Cook Inlet Seabird and Forage Fish Studies

Restoration Project (APEX) 98163M
Annual Report

Study History: Since the late 1970's, seabirds in the Gulf of Alaska have shown signs of food stress: population declines, decreased productivity, changes in diet, and large-scale die-offs. Small-mesh fishing trawls conducted during the past 30 years reveal that a major shift in fish community composition occurred in the late 1970's: some forage species (e.g., capelin) virtually disappeared, while predatory fish (e.g., pollock) populations increased markedly. Restoration Project 98163M was initiated as part of APEX in 1995 to characterize relationships between seabird population dynamics, foraging behavior, and forage fish densities in lower Cook Inlet--the area in which most seabirds were killed by the EVOS. CISeaFFS is a collaborative project of the Alaska Biological Science Center and the Alaska Maritime National Wildlife Refuge, with major funding and logistic support from the EVOS Trustees (APEX), the MMS, USGS, USFWS, ADF&G, the University of Alaska, Fairbanks and the University of Washington.

Abstract: Water temperatures through the summers of 1995-1997 were similar and near the long-term average, but temperatures in winter of 1997/98 were about 1-2 C higher than in previous years owing to warming from El Niño. Breeding success in all seabird species was lower in 1998 than in previous years. Murres on Chisik Island had a complete reproductive failure-- the first time we have observed a murre failure at any colony since studies began in 1995. Measures of baseline corticosteroid levels suggest that murres on Chisik were highly stressed even before they attempted to lay eggs in July. A large die-off of murres was observed in Cook Inlet in April and May, foreshadowing the poor breeding season for murres during summer of 1998. Over all years of study, seabird parameters (breeding success, foraging effort, diets, etc.) varied most between islands and least between years. We attribute this regional stability in biological responses to distinct oceanographic regimes around each colony that tend to strongly influence the biology of birds within those areas. Thus, all measured seabird parameters varied some between years, but, for example, murres at Gull Island always fared better than those at Chisik. While each colony responded differently to the ENSO perturbation of 1997/98, responses were commensurate with the underlying physical and biological regime observed in each area. As predicted, the numerical and functional responses of seabirds to food density is non-linear. Based on response curves of breeding success, foraging effort, attendance, etc., to prey density, it appears that food supplies at Gull and Barren islands— but not at Chisik— are presently adequate to support recovery of losses from the Exxon Valdez oil spill.

Key Words: Cook Inlet, murre, kittiwake, guillemot, forage fish, diet, pollock, capelin, sandlance, reproduction, growth rate, hydroacoustic, trawl, seine, *Exxon Valdez*, Kachemak Bay.

Citation: John Piatt, Alisa Abookire, Gary Drew, Mike Litzow, Alexander Kitaysky, April Nielsen, Tom Van Pelt, Martin Robards, Suzann Speckman, & Stephani Zador. 1998. Cook Inlet Seabird and Forage Fish Studies. Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 98163M), Biological Resources Division, U.S. Geological Survey, Anchorage, Alaska.

In lieu of a report, we have attached a copy of a manuscript published by the North Pacific Marine Science Organization (PICES) in the "Proceedings of the 1998 Science Board Symposium on the Impacts of the 1997/98 El Nino Event on the North Pacific Ocean and its Marginal Seas" entitled:

Piatt, J.F., G. Drew, T.Van Pelt, A. Abookire, A. Nielsen, M. Shultz, and A. Kitaysky. 1999. Biological effects of the 1997/1998 ENSO event in lower Cook Inlet, Alaska. PICES Scientific Report No. 10:93-100.

This report contains many of the significant findings on seabirds and forage fish in lower Cook Inlet that we observed in summer, 1998. In addition, progress was also made on the following papers.

Manuscripts published or accepted since FY98 annual report:

Anderson, P.J., and J.F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series. *Accepted.*

Zador, S., and J.F. Piatt. 1998. Time-budgets of Common Murres at a declining and increasing colony in Alaska. Condor 101:149-152.

Robards, M.R., and J.F. Piatt. 1999. Biology of the Genus *Ammodytes* - The Sand Lances. U.S. Forest Service Technical Report Series. *In Press.*

Kitaysky, A.S., J.C. Wingfield, and J.F. Piatt. 1999. Dynamics of food availability, body condition and physiological stress response in breeding Black-legged kittiwakes. Functional Ecology. *Accepted.*

Robards, M.D., J.F. Piatt, and G.A. Rose. 1999. Maturation, fecundity and intertidal spawning of Pacific Sand Lance (*Ammodytes hexapterus*) in the northern Gulf of Alaska. Journal of Fish Biology. *In press.*

Kitaysky, A.S., J.F. Piatt, J.C. Wingfield, and M. Romano. 1999. The adreno-cortical stress-response of Black-legged Kittiwake chicks in relation to dietary restrictions. Journal of Comparative Physiology (B). *Accepted*

Robards, M., J.F. Piatt, A. Kettle, and A. Abookire. 1999. Temporal and geographic variation in fish populations in nearshore and shelf areas of lower Cook Inlet, Alaska. Fishery Bulletin. *In Press.*

Kuletz, K. and J.F. Piatt. 1999. Juvenile Marbled Murrelet nurseries and the productivity index. Wilson Bulletin. *In press.*

Piatt, J.F., N.L. Naslund, and T.I. van Pelt. 1999. Nesting habitat selection and nest-site fidelity in the Kittlitz's Murrelet (*Brachyramphus brevirostris*). Northwestern Naturalist *In Press.*

Litzow, M.A., J.F. Piatt, and J.D. Figurski. 1998. Hermit crabs in the diet of Pigeon Guillemots at Kachemak Bay, Alaska. Colonial Waterbirds. 21:242-244.

Abookire, A.A. and B.L. Norcross. 1998. Depth and substrate as determinants of distribution of juvenile flathead sole (*Hippoglossoides elassodon*) and rock sole (*Pleuronectes bilineatus*) in southcentral Alaska. Journal Sea Research 39:113-123.

Van Pelt, T.I., J.F. Piatt, and G.B. van Vliet. 1999. Vocalizations of the Kittlitz's Murrelet. Condor. *In press.*

Piatt, J.F., D.D. Roby, L. Henkel, and K. Neuman. 1998. Habitat use, diet, and breeding biology of Tufted Puffins in Prince William Sound, Alaska. Northwestern Naturalist 78:102-109.

Cook Inlet related manuscripts in progress in FY99.

Benson, J., R.M. Suryan, and J.F. Piatt. A multivariate approach to assessing growth of seabird nestlings from one-time measurements. Submitted to Condor.

Robards, M.D., J. Anthony, J.F. Piatt, G. Rose, and J.F. Piatt. 1999. Seasonal and regional variation in proximate composition of Pacific sand lance (*Ammodytes hexapterus*) in lower Cook Inlet, Alaska. Mss. submitted to Journal of Experimental Marine Ecology.

Zador, S.G., J.F. Piatt, A. Kettle, A. Abookire, and Alan Springer. 1999. Can the diet of Common Murres be used to assess forage fish stocks? Submitted to Marine Ecology Progress Series.

Norcross, B.L., A.A. Abookire, and S.C. Dressel. 1999. Essential fish habitat requirements of juvenile groundfishes in southcentral Alaska. Submitted to Bulletin of Marine Science.

Robards, M.D., G.A. Rose, and J.F. Piatt. 1999. Somatic growth and otolith development of Pacific sand lance (*Ammodytes hexapterus*) under different oceanographic regimes. Mss. submitted to Fisheries Oceanography.

Abookire, A.A., J.F. Piatt and M. Robards. 1999. Stratification and small-scale thermohaline differences influence nearshore fish distributions in an Alaskan estuary. Mss. under final revision for submission to Estuarine, Coastal and Shelf Science.

Kitaysky, A., J. Wingfield, and J. Piatt. 1999. Parent-offspring feeding interactions in food-stressed Black-legged Kittiwakes. Mss. under final revision for submission to Behavioural Ecology.

Harding, A., J.F. Piatt, T. Van Pelt and A. Kitaysky. 1999. Parental Flexibility: An experimental reduction of provisioning effort in response to chick nutritional status in the Horned Puffin (*Fratercula corniculata*). Mss. under revision for submission to Behavioural Ecology and Sociobiology.

Zador, S., A. Nielsen, J.F. Piatt, A. Kettle, and Tom van Pelt. 1999. Diets of Black-legged Kittiwakes in relation to prey availability in Cook Inlet, Alaska. Mss. under revision for submission to Polar Biology.

Litzow, M.A., J.F. Piatt, A.A. Abookire, A.K. Prichard and M.D. Robards. 1999. Pigeon Guillemot Nestling Diets as Monitors of Nearshore Fish Communities. Mss. Under final review for submission to Marine Ecology Progress Series.

Zador, S., J.F. Piatt, and A.S. Kitaysky. 1999. Prey selectivity in breeding common murres. Mss. under revision for submission to Journal of Avian Biology

Biological Effects of the 1997/98 ENSO in Cook Inlet, Alaska

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SUMMARY

We have been conducting detailed studies of the biology of seabirds in relation to oceanography and forage fish ecology in lower Cook Inlet, Alaska, since 1995. This fortuitously allowed us to document biological effects of the 1997/98 ENSO in this region. Anomalously warm sea surface temperatures (SST's) were observed in the Gulf of Alaska (GOA) beginning in June of 1997, but not in Cook Inlet until September, 1997. Warm temperature anomalies at the surface and at depth persisted until May of 1998, when temperatures returned to average in the GOA and Cook Inlet. Thus, temperature anomalies occurred outside the core window of productivity (June-August) for forage fish and seabirds in both 1997 and 1998. Abundance or production of phytoplankton, zooplankton, fish, and seabirds in lower Cook Inlet varied among years, and overall appeared to be depressed in 1998. We observed a few biological anomalies that might be attributed to ENSO effects: 1) a significant die-off of Common Murres occurred in March-May of 1998, 2) murres and Black-legged Kittiwakes were physiologically stressed during the 1998 breeding season, 3) murres failed to reproduce at one colony in 1998, 4) kittiwake breeding success was lower than usual at colonies in 1998, and 5) phenology of breeding was later in 1998 for both murres and kittiwakes. We presume that seabird die-offs, reduced productivity and delayed phenology were linked to a reduction or delay in food availability, but the mechanism by which anomalously warm water temperatures in winter reduce forage fish availability during the summer breeding season for seabirds is not known.

OCEANOGRAPHY

The 1997/98 ENSO was well developed at the equator by July of 1997. Anomalously warm sea surface temperatures (SST's) developed rapidly during June in the Gulf of Alaska (GOA) and Bering Sea, presumably via atmospheric tele-connection with the tropics. SST anomalies of 2+ C in the GOA persisted throughout summer of 1997 (Fig. 1), diminished to ~1 C in October; and persisted until May/June of 1998. Water temperatures at depth (0-250 m) differed markedly from surface temperatures during summer of 1997. Warming of deeper waters started much later (September) and peaked in February/ March of 1998.

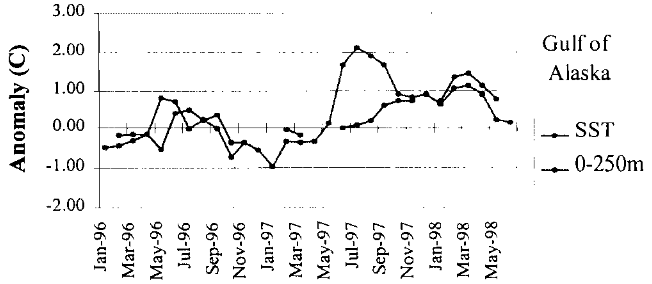

Figure 1. Temperature anomalies at the surface and over the entire water column in the Gulf of Alaska from January 1996 to May 1998.

In lower Cook Inlet, effects of the 1997/98 ENSO were ameliorated by upwelling and tidal mixing at the entrance to Cook Inlet. Whereas the northern GOA was well-stratified during summer of 1997 and capped by warm surface layers, strong upwelling occurs around the Kodiak Archipelago and at the entrance to Cook Inlet, leading to complete mixing of the water column and reduced surface temperatures in these areas (Fig. 2). Cold, mixed waters are carried north by prevailing currents far into Cook Inlet. Strong tidal mixing limits stratification to protected areas such as Kachemak Bay where river outflows create shallow lenses of warm, low-salinity water at the surface. On the west side of Cook Inlet, currents flow south and waters are weakly stratified, warmer and less saline. Although they differ slightly in absolute temperature, SST's from Kachemak Bay, Chisik (on the west side, Fig. 2) and the Barren Islands (entrance to Cook Inlet) show similar seasonal and annual SST trends.

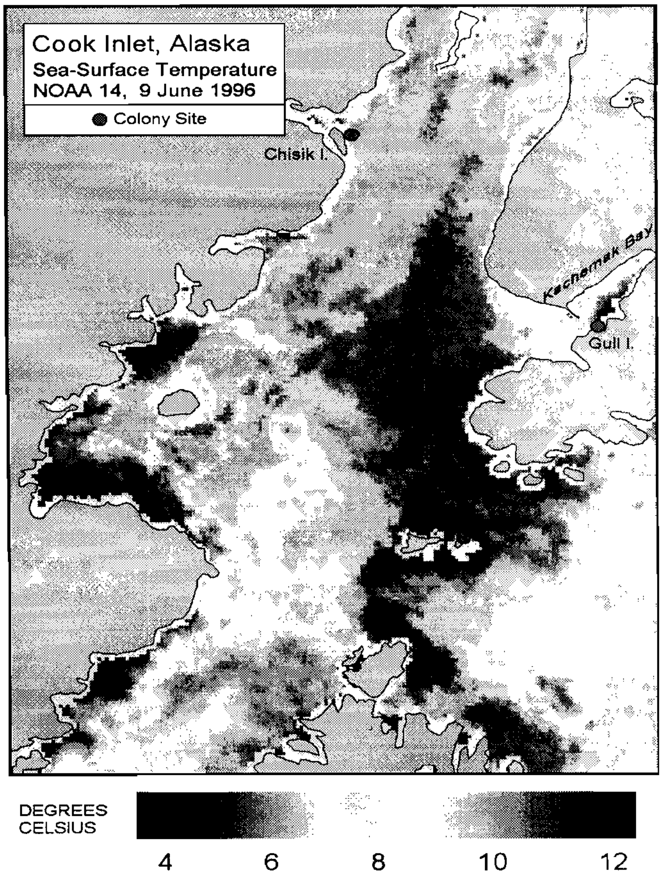

Figure 2. AVHRR image showing sea surface temperatures in Cook Inlet and seabird colonies under investigation.

As a consequence of this oceanographic regime, SST's in Kachemak Bay (Fig. 3) do not reflect SST's in the outer GOA; instead they reflect temperature fluctuations of the entire GOA water column (Fig. 1). SST's in Kachemak Bay and the GOA during 1996 were about average most of the year. The large SST anomaly observed in the GOA during June-August of 1997 (Fig. 1) was not observed in Kachemak Bay (Fig. 3) or at Chisik and Barren islands. SST's in Kachemak Bay began to increase in August 1997 and were 1-2 C higher than average throughout fall and winter; returning to average in May of 1998. As for GOA temperatures at 0-250 m depth, SST's in Kachemak diverged most from average values during February and March of 1998 (Fig. 3).

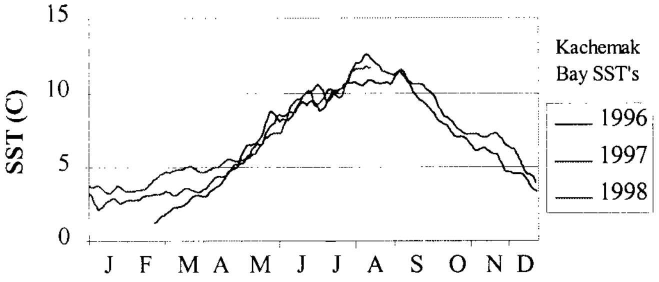

Figure 3. Sea surface temperatures (5 m below low-low tide) in Kachemak Bay, Cook Inlet, Feb. 1996 to Aug. 1998. Mean daily temperatures smoothed with 7-day running average.

BIOLOGICAL EFFECTS

Plankton: We began monitoring phytoplankton and zooplankton abundance in 1997. Phytoplankton concentrations were measured using a CTD with attached fluorometer. Zooplankton were collected seasonally at a single station in Kachemak Bay, and we measured settled volumes to estimate abundance (Fig. 4). Primary and secondary production in Kachemak Bay varied among and between seasons, but with only two years of data we can only conclude that there was no indication of any dramatic ENSO effects (e.g., total production failure) in either year. However, maximum zooplankton volumes in 1998 were about a third of those observed in 1997.

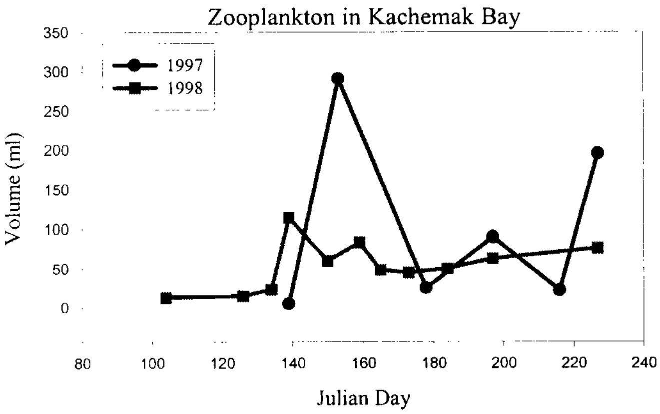

Figure 4. Seasonal variation in zooplankton volume in Kachemak Bay during 1997 and 1998. Zooplankton were collected using a 1-m ring net with 505 micron mesh.

Fish: Fish were sampled in both Kachemak Bay and around Chisik Island using a modified herring mid-water trawl (July) and beach seines (June-Aug.), and in Kachemak Bay using a small bottom trawl (Aug.). The same gear and methods were used in all years of study. We targeted small forage fishes consumed by seabirds. More than 300,000 fish comprising over 60 species have been caught on these surveys. Dominant taxa include juvenile pollock, sand lance, osmerids, and herring. In general, fish catches are much higher in Kachemak Bay (Fig. 5a) than around Chisik Island (Fig. 5b) owing to regional differences in productivity. Catches of forage fish increased in Kachemak Bay, but decreased around Chisik Island, between 1997 and 1998. Catches in both areas in 1997/98 were higher or similar to those observed in 1996. However, trawl catches are highly variable and biased because we conduct trawls only where hydroacoustic signals indicate the presence of fish. Analyses of hydroacoustic data (in prep.) suggest that biomass of fish was reduced in most areas of Cook Inlet in 1998. Beach seines suggest that fish were delayed in arriving nearshore in 1998.

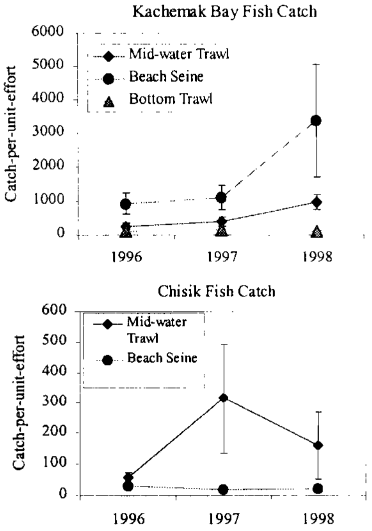

Figure 5. Catches of fish in mid-water trawls, beach seines and bottom trawls: a) in Kachemak Bay , and, b) around Chisik Island, 1996-1998.

Seabird Productivity: Here we consider two species (Common Murres and Black-legged Kittiwakes) from colonies at Chisik Island and Gull Island. Murres maintained relatively high productivity among all years of study at Gull Island in Kachemak Bay (Fig. 6). Diets were similar among years, and analyses of time budgets (foraging trip duration, "loafing time") suggest that murres had no difficulty finding food in 1997 or 1998. At Chisik Island, however, murres experienced a complete breeding failure in 1998 (Fig. 6). They started breeding later than usual (Fig. 7), displayed erratic attendance, and had significantly higher levels of stress hormones in their blood plasma in 1998

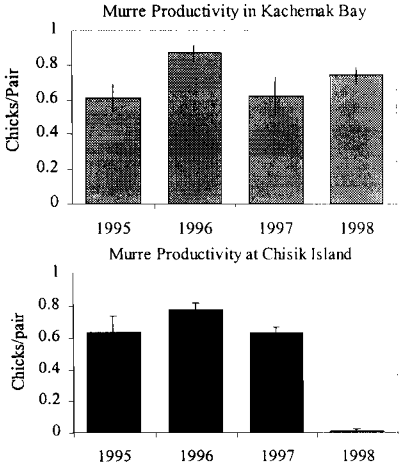

Figure 6. Breeding success of Common Murres in 1995-1998.

than in 1997 (Fig. 8). Complete breeding failure is rare in murres because they can compensate for wide fluctuations in food supply by adjusting their time budgets-- which is why they usually manage to produce chicks at Chisik despite poor food supplies. We therefore view the delayed phenology and subsequent breeding failure of murres at Chisik in 1998 as particularly significant.

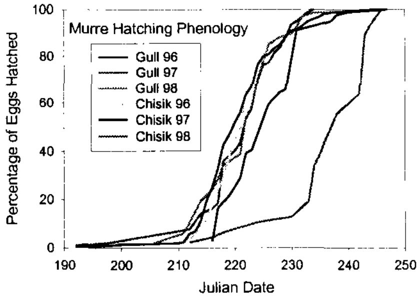

Figure 7. Phenology of egg hatching in murres at Gull and Chisik islands, 1996--1998.

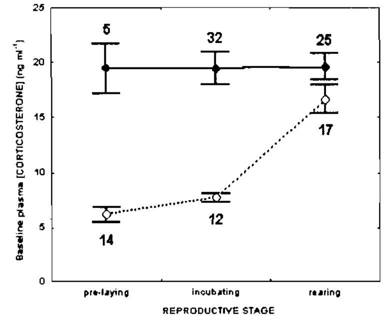

Figure 8. Stress hormone levels in murres at Chisik during a 'normal' year (1997, open circles) with seasonal increase in food stress, and ENSO year (1998, closed circles) with high stress load at beginning of the breeding season.

In contrast, kittiwake breeding success is typically more variable and sensitive to fluctuations in food supply. In Kachemak Bay, kittiwake breeding success was much reduced in 1998 compared to 1996/1997-- but fell within range of variability observed in previous years of study (Fig. 9a). However, notable low production events in the past also correspond to years with moderate ENSO warming of winter water temperatures in Alaska (1987, 1993, 1994). Low production in 1998 was largely due to low laying and hatching success, which was about 3 weeks later than usual (Fig. 10). Once hatched, chick survival was high. At Chisik Island, kittiwakes have always done poorly in recent years (Fig. 9b).

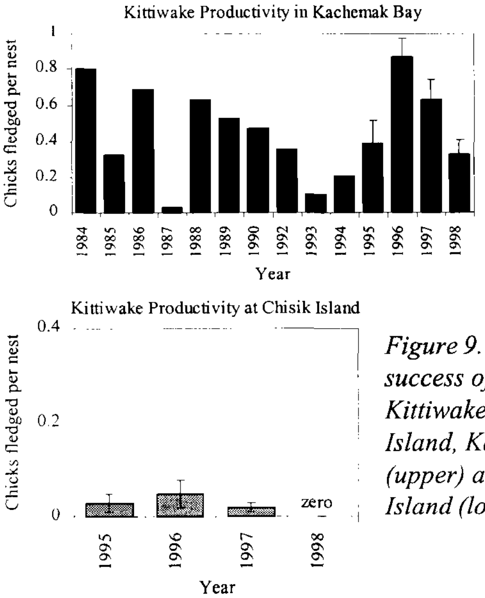

Figure 9. Breeding success of Black-legged Kittiwakes at a) Gull Island, Kachemak Bay (upper) and b) Chisik Island (lower).

Evidence suggests this is because of generally poor food supplies around Chisik and because, in contrast to murres, kittiwakes cannot adjust their time budgets to deal with fluctuations in food supply, nor can they range as far to find food. The 1998 breeding season at Chisik was notable because birds failed much earlier than usual (during incubation), phenology of egg-laying was about 2-3 weeks later than usual, and adults produced absolutely zero chicks.

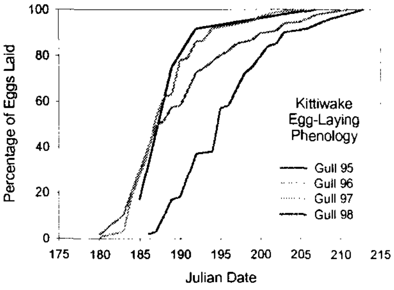

Figure 10. Phenology of kittiwake egg-laying on Gull Is., 1995-1998.

Seabird Die-offs:

A large and extensive seabird die-off was observed in Alaska during summer 1997; largely confined to the southern Bering Sea and Aleutians. Surface-feeding species such as shearwaters (and much lesser numbers of kittiwakes) died *en masse* from apparent starvation. Some hundreds of thousands of birds were probably affected, and peak mortality occurred in August when SST anomalies were highest. Smaller die-offs of murres were also reported from the northern Bering Sea, mostly in May and June. Although SST anomalies were also high in the GOA during the summer of 1997, no die-offs were reported there. In 1998, however, a moderate die-off of Common Murres was observed in the northern GOA. Dead murres were reported over a wide area (Fig. 11) from about March through May, with peak mortality occurring in mid-April. This followed a long period of anomalously warm water temperatures in the GOA (Fig. 1). Most murres were apparently subadult (non-breeders) and died of starvation. A preliminary tally indicates that at least 1300 dead murres were observed on beaches in the GOA. Previous studies indicate this would be a small fraction of the total mortality, which probably numbered in the tens of thousands. The most recent large seabird die-off observed in the GOA occurred during late winter of 1993 following a prolonged period of anomalously warm SST's associated with the 1992/93 ENSO. In that die-off, about 120,000 murres died from starvation in the northern GOA.

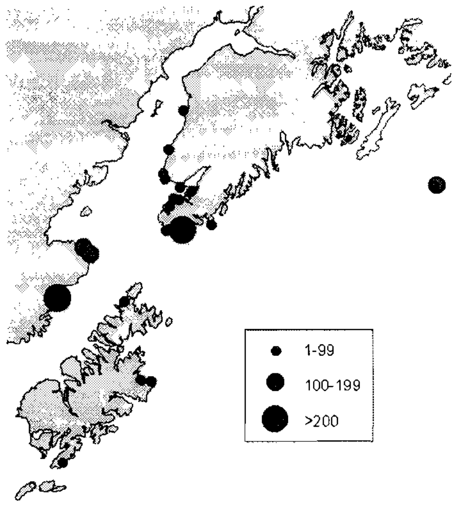

Figure 11. Distribution of dead murres recovered from beaches in the northern Gulf of Alaska during March-May, 1998.

O Statistical review

Alaska Predator Ecosystem Experiment: Annual Project Report

Project Number 99163 O Statistical Review

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March 17, 1999

WEST biometricians have been involved in a range of consulting activities from March 1998 through March 1999. Activities have included collaborations with William Ostrand developing statistical sampling designs for ground truthing hydroacoustic surveys for bottom type classification at 25 near shore sites in Prince William Sound and development of a bootstrapping technique for analyzing resource selection data. These hydroacoustic data are also being used to estimate biomass density and total biomass over the same 25 near shore areas. In addition to statistical design, WEST used discriminant analysis techniques to develop a classification scheme based on indices developed from biosonics visual bottom typing software. Additionally, WEST consulted with William Ostrand and Tracey Gotthardt on geostatistical methods for development of maps of bottom type within the 25 nearshore sampling areas in Prince William Sound. Additional work in the upcoming year will include development of geostatistical models of bottom type for use in investigations of resource selection by sandlance.

WEST finalized a manuscript with Kenneth Coyle (Kern and Coyle 1999) documenting development of new statistical methods for analysis of non-randomly sampled hydroacoustic data. These methods will be presented in a poster session at the 10th anniversary symposium of the Exxon Valdez Oil Spill. The new methods will be used to make estimates of biomass density in the nearshore areas and to investigate temporal trends and to compare total biomass These methods were based on the geostatistical methods known as Kriging but were modified to allow analysis of large data sets common to hydroacoustic surveys. The new methods allow statistically valid comparisons of mean biomass densities over spatial and temporal ranges.

WEST also worked with Dave Roseneau and Arthur Kettle at the Alaska Maritime Refuge in Homer Alaska reviewing existing monitoring protocols and discussing statistical analysis of those data. Additional consultations with APEX principal investigators has included interactions with: Greg Golet regarding diagnostic measures in logistic regression and analysis of capture-recapture data, Robert Suryan developing preliminary design of analyses to investigate the influence of prey availability on nest attendance for Black-legged Kittiwakes, Kathy Kuletz in analysis of marbled murrelet distribution data, and David Irons for general analysis of seabird data arising from the APEX program.

WEST has attended and participated in the Annual EVOS Symposia.

References

Kern, J.W., K. O. Coyle. 1999. Estimation of the global block kriging mean with large sample sizes on irregular polygonal regions: Applications to acoustic surveys for zooplankton in the Western Aleutian Islands. Canadian Journal of Fisheries and Aquatic Sciences (Submitted).

Q Modelling

Exxon Valdez Oil Spill
Restoration Project Annual Report

The Factors that Limit Seabird Recovery in the EVOS Study Area: A Modeling Approach

Restoration Project 98163Q
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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June 1999

The Factors that Limit Seabird Recovery in the EVOS Study Area: A Modeling Approach

Restoration Project 98163Q
Annual Report

Study History: The project effort was initiated in February 1997 as a new project. Field work has not been a direct component of this project, which relies on the data gathered by all other APEX projects as well as data in the literature. In a sense, many APEX principle investigators are part of Restoration Project 98163Q. By the nature of our work --- inter-relating the data gathered by other investigators in APEX --- we, generally, are at least one year behind the other APEX projects.

Abstract: We use mathematical models to assess the degree to which food supply could be affecting recovery of seabirds in the EVOS study area, indicate the mechanisms by which this could come about, and identify the scale at which interactions are occurring between food availability and the species and colonies being studied by APEX. In the first two years of effort we concentrated on acquiring and formatting data, and developing initial models to tie food supply to seabird demography; a significant relationship was detected for Black-legged Kittiwakes. We explored the feasibility of working with Pigeon Guillemots, as well, but the available data proved to be inadequate, although in the future this is likely to change. The models that we were successful in developing compared kittiwake foraging effort, using data gathered by APEX component B, G and E, and prey availability, from APEX component A and a SEA component. Best correspondence existed between kittiwake foraging and aerial spotting of fish schools. Logistic regression models indicated the temporal, physical and biological habitat features that brought closest correspondence between kittiwake foraging and fish availability. A foraging model linked kittiwake foraging behavior and effort to the density and distribution of prey schools.

Key Words: Black-legged Kittiwake, capelin, eulachon, *Exxon Valdez*, foraging behavior, foraging model, herring, prey availability, prey selection, sandlance, mathematical modeling.

Project Data: (will be addressed in the final report)

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EXECUTIVE SUMMARY

We used mathematical models to assess ways in which food supply could be affecting recovery of seabirds in the EVOS study area. Thus, we addressed the main APEX (Alaska Predator Experiment) hypothesis that food supply is limiting recovery of certain avian populations from the *Exxon Valdez* oil spill. Data inputs comprised information from the field components of APEX supplemented with data published elsewhere. We confined our effort in 1998 to the Black-legged Kittiwake *Rissa tridactyla*, the species in Prince William Sound for which data were sufficient for analysis. We found that foraging activity was affected by food availability, as determined from fish school assessments (aerial spotting 1996, 1997, 1998). Herring *Clupea pallasi* and sandlance *Ammodytes hexapterus* schools were the most common prey over which kittiwakes foraged; capelin *Mallotus villosus* and eulachon *Thaleichthys pacificus* schools were much less common but appeared to be favored. The link between foraging and prey was affected by such factors as prey species, school density, year, time of day, tide state and distance from the colony, as well as other factors. A foraging model successfully linked kittiwake searching behavior to localities where the presence of prey schools was most predictable.

INTRODUCTION

The general hypothesis of the APEX project is that a change in the relative abundance of forage fish species has prevented recovery of injured avian populations in Prince William Sound; within this general hypothesis a series of 10 working hypotheses are being investigated by the various APEX components (see Duffy 1996, p. 6-7). The data being collected to test these hypotheses differ in temporal and spatial scale. Some additional data at the time scale of decades exist. However, most of the data are at much smaller scales than the general hypothesis, which is at the scale of decades (time for recovery in long-lived species) and at the spatial scale of the entire sound. Statistical inference can be used to bridge some but not the entire gap. We discussed how this task would be undertaken, in a conceptual way, in a previous Annual Report (Ainley et al. 1997). Our approach integrates the available information, bridges the gap from data to the hypothesis, and identifies variables that need to be linked. The model output allows avian recovery rates to be evaluated in relation to prey availability, using data and knowledge gathered for this ecosystem (Ford et al. 1998).

After exploring the data available to us, i.e. those from the 1996, 1997 and 1998 field seasons, it became clear that the formulation of our models would be most successful for the Black-legged Kittiwake *Rissa tridactyla* in Prince William Sound (PWS). We sought to relate the kittiwake data — reproductive success as well as foraging effort — to the availability of forage fish. We discussed preliminary findings in regard to prey availability, foraging behavior and breeding success previously (Ford et al. 1998). Here we report results from more intensive investigation between foraging behavior and prey availability.

OBJECTIVES

Hypotheses to be evaluated by mathematical modeling using existing data, under the null hypothesis:

1. Kittiwake foraging behavior and occurrence patterns in Prince William Sound can not be explained by the abundance and distribution of prey schools.

2. No differences in 1 will be evident in pre- and post-spill comparisons, where possible.

METHODS

Kittiwake Foraging Effort

We began with the foraging effort data compiled by APEX Project 163E (David Irons, Robert Suryan and Jeb Benson). Data were available for 1995-1998, for 3 kittiwake colonies: Icy Bay, Eleanor Is and Shoup Bay, but not for all years and all colonies. As fish availability data were not obtained in 1995 (see below), we did not consider the kittiwake data acquired for that year. Useable data were available for Eleanor and Icy in 1996, and all three in 1997 and 1998. The data were collected by following radio-tagged individuals in a boat; positions and behavior, as well as other data, were then recorded regularly. More details on data collection are contained in Irons (1992) and Irons et al. (1997). In the present report, we consider 1996 -1998 data. Data acquisition occurred from about 3 July through 10 August each year.

The data were provided to us in ASCII format. These were processed and loaded into CAMRIS by computing the rate of movement (km/hr) between each pair of sequential observations of kittiwakes and assigning that rate to the latitude/longitude midpoint of the pair. Points representing intervals of slow movement were overlaid on a map of Prince William Sound. Slow movement was considered to be foraging. We placed a 1 km grid over the sound and counted the number of slow-movement points occurring in each grid cell. A binary search procedure was then used to find the density isopleths that would contain 85%, 90% and 95% of these points. In other words, for example, the 90% isopleth contained the minimum area of 90% of the foraging activity. These regions were termed "foraging grounds" and were assumed to be equivalent to "patches" in the traditional sense of optimal foraging theory. Note that we could have used the actual foraging observations to define the foraging grounds and would have gotten similar results. Using the movement rates instead of the observations helped to compensate for areas where the kittiwakes search for food but actually find nothing on which to feed, and also allows us to compute the feeding rate, i.e. the number of feeding behaviors per unit time while in the patch. Using speed to define the patch and then using behavioral observations to define feeding rates avoids circularity.

Fish Abundance

We had found previously that fish schools spotted from the air correlated much more closely with kittiwakes than schools identified by hydroacoustics (Ford et al. 1998).

Therefore, we confined our subsequent effort to aerial spotting data, obtained by Evelyn Brown, working in the SEA program (until joining APEX in 1998). Flights were conducted at low level (200 m elevation) from 10 June to 11 August 1996-1998. Length of survey tracks in 1996, 1997, and 1998 were 6,729; 7,358; and 21,256 km, respectively, for a total on 35,343 km (Figure 1). All shorelines in the Sound were over-flown, as we had determined earlier that kittiwakes rarely forage in deep waters (see also Ostrand and Flint 1995, Ostrand and Maniscalco 1996). This was at least one of the reasons we found little correspondence between kittiwakes and hydroacoustic data (collected in deeper water owing to logistical constraints).

Fish schools were spotted and identified from the air, and each school was measured to determine major and minor axis lengths using a calibrated cylinder. The product of the axis lengths provided an index of school size. However, a preliminary analysis found no relationship of kittiwake occurrence to the size of schools. Forage fish were identified as herring *Clupea harengus*, capelin *Mallotus vilosus*, sandlance *Ammodytes hexapterus*, eulachon *Thaleichthys pacificus*, salmon *Onchorhyncus* spp., walleye pollock *Theragra chalcogramma*, or unidentified forage fish. Some ground truthing of schools was conducted, but results (positive) are not reported on herein. Besides fish schools also recorded were number of Black-legged Kittiwakes, Humpback Whales *Megaptera novaeangliae*, Glaucous-winged Gulls *Larus glaucescens* and unidentified gulls. For each sighting of a bird, the following behaviors were recorded: 1) resting on shore, 2) flying in a steady direction (traveling), 3) resting on the water, 4) milling, or 5) actively feeding (plunging, dipping).

Data collected during aerial transects were logged directly into a laptop computer using dLOG software (Ford, 1997). A GPS unit was linked to the computer so that geographic position was recorded at 5 second intervals or whenever the observer entered an observation. The resultant ASCII files were checked for accuracy and transmitted to us for post processing.

Kittiwake Foraging Grounds Versus Fish Abundance.

We determined the minimum spatial scale in which we could see relationships between kittiwake foraging behaviors and fish school density. In a preliminary analysis, we found that foraging bird occurrence patterns were related only to herring, sandlance, eulachon and capelin. Therefore, in all further analyses we confine our efforts only to these forage fish species. We found that strong statistical relationships resulted when data were binned into blocks 1.5 nm (2.8 km) on a side (= 7.7 km^2). These we called survey blocks.

Regression Analyses

We used forward and backward step-wise multiple regression analyses (CRC 1995) to model density of feeding kittiwakes (the dependent variable) in relation to physical, temporal (year and date), and biological variables (Table 1). The sample unit for these analyses was one survey block sampled on a particular day. All independent variables were analyzed as continuous except tide phase and year, analyzed as categorical.

Variables — For each block for each day we assigned values for ocean depth, distance to shore, and an index of distance to kittiwake colonies weighted by colony size.

Initially, we grouped all the colonies in Prince William Sound into 7 colony clusters (Figure 2). The clusters were defined by spatial proximity, overlap in foraging area (Suryan et al. Ms), and observations that in some years certain colonies changed in size but in a direction that was reciprocal to that of colonies in the immediate area (R. Suryan pers. comm.). Therefore, some sort of "meta-colony" is included in each cluster. We then determined the coordinates for the mid-point for these clusters (Figure 2). For a given block, colony index was the sum of values ($n = 7$) for the distance between clusters divided by the number of kittiwakes composing that cluster.

The counts of kittiwakes and schools of herring, sandlance, eulachon, and capelin were summed for each survey block. We calculated "densities" per block for each species as the number of birds or schools divided by the *length* of survey transects per block per day. In this way, we corrected for survey effort block by block. Transect lengths per survey block/day averaged 3.47 km, SD = 2.71 (range = 0.01 - 35.98 km; n = 10,181 blocks/day). Tide stage at the time of survey for each block was grouped into three phases: ebb, slack, and flood, as 1, 2, and 3, respectively.

We grouped the kittiwake behaviors including resting on the water, milling, and actively feeding as representing "feeding" birds (birds that were sitting on shore or flying in a steady direction were excluded). We included birds resting on the water under the feeding category because satiated birds often rest on the water just after feeding, and therefore usually represent feeding activity in the area.

Analyses — We log-transformed density to satisfy assumptions of normality (Skewness/Kurtosis Test for Normality of residuals, $P > 0.05$). Because densities included values of zero, transformations were calculated as the log (density $\pm$ 0.05; 0.056 was the lowest density > 0). All regressions were of the log-transformed counts, and to facility presentation of data in graphs we used the log of bird density per 100 km (i.e., density was multiplied by 100 prior to log-transformation). Normality was not achieved, but least-squares regression analyses are considered to be very robust with respect to non-normality (Seber 1977, Kleinbaum et al. 1988). Although regression analyses yield the Best Linear Unbiased Estimator relating density to independent variables, even in the absence of normally distributed residuals, P-values at the lower levels of significance must be regarded with caution (Seber 1977). Therefore, to reduce the chances of Type I error we assumed significance at $P \leq 0.02$.

Second- and third-order polynomials as well as all possible interactions were tested for and between independent variables. We also used one-way ANOVAs, followed by Sidak multiple comparison tests (an improved Bonferroni test [SAS Institute, Inc. 1985]), to statistically compare each habitat variable among years and tide phases. Unless noted otherwise, variance is reported as the standard error.

All variables except 'tide phase' and 'year' (analyzed as categorical [= cat.] in the model reported) were analyzed as continuous. Main effects were calculated before interaction terms were introduced into the model. The terms 'tide phase' and 'Julian date' were included in the model as main effects when testing interaction relationships.

FORAGING BY BLACK-LEGGED KITTIWAKES IN PRINCE WILLIAM SOUND, ALASKA: I, PHYSICAL, TEMPORAL AND BIOLOGICAL FACTORS AFFECTING TEMPORAL AND SPATIAL VARIATION IN FORAGING DENSITY

RESULTS

The regression analyses are based on counts of 59,101 Black-legged Kittiwakes, 176 Glaucous-winged Gulls, and 75 Humpback Whales; 3,379, 2,481, 54, and 48 schools of herring, sandlance, eulachon, and capelin, respectively. We found no negative or positive relationships of kittiwakes to either whales or to gulls. The latter will not be considered further.

Abundance of Prey Species

Overall, herring schools were significantly more abundant than those of sandlance (0.096 ± 0.0033 and 0.070 ± 0.0037 schools km^{-1}, respectively, $n = 10,181$ survey segments), a difference that was highly significant (Sidak tests, $P < 0.0001$; Figure 3). Abundance of eulachon and capelin schools was significantly lower than that of herring and sandlance ($0.0015 \pm .0006$ and 0.0014 ± 0.0005 schools km^{-1}, respectively, $P < 0.0001$), being about 65 and 45 times lower than that of the former two species, respectively. Abundance of eulachon and capelin did not differ significantly ($P = 0.9$).

Sandlance abundance was higher, and herring abundance lower, in 1996 compared to 1997 and 1998 (Figure 3; Sidak tests, both $P < 0.0001$). Abundance of both species differed insignificantly between 1997 and 1998 (both $P > 0.3$). Abundance of eulachon and capelin differed insignificantly between the three years (all $P > 0.1$).

Within a year, the abundance of herring, eulachon and capelin decreased with Julian date (Table 2, Figure 4). In the case of herring, the relationship was quadratic because the decrease leveled off after 10 July. Sandlance, on the other hand, increased over time, peaking 20-30 July, and decreasing slightly thereafter.

Temporal, Spatial and Biological Variables: Main Effects

The regression model, including all significant main effects and interactions, explained 18.8% of the variance in log-transformed abundance of feeding kittiwakes during the three years (Table 1; $F[50,10130] = 48.77$). Each of the terms, including ocean depth, distance from shore, colony distance index; and counts of herring, sandlance, eulachon, and capelin schools, had significant linear relationships with kittiwake density (Figures 4, 5). Although Julian date and tidal phase were not significant as main effects, they were retained in the model because they had significant interactions with other independent terms (see below). Thus, few of the covariates were rejected from the final model.

Kittiwake density increased with year (see Table 1: continuous effect; Figure 5) and with number of schools of herring, sandlance, eulachon, and capelin (Figure 6). Kittiwake density decreased with ocean depth, distance from shore, and colony distance index (Figure 5). Kittiwake density also was related to number of herring, sandlance, and capelin schools in a curvilinear (quadratic) fashion (Table 1). These latter effects were due to a steep increase in kittiwake density from blocks having zero fish schools to those having one fish school, followed by leveling or slight decline in blocks having more than one school (Figure 6).

Temporal and Spatial Variables: Interactions

Five interactions existed between temporal and/or spatial variables and their relationship with kittiwake density (Table 1, Figure 7). These interactions included those of year with Julian date, distance from shore, colony distance index, and tide phase; and an interaction between Julian date and tide phase. There were no interactions between ocean depth and other covariates.

First, densities of feeding kittiwakes were highest early in the study period during 1996 and 1998, and highest late in the period during 1997. Statistically, an interaction between year and Julian date affected kittiwake density positively in 1997, compared to significant negative relationships in 1996 and 1998 (all $P < 0.0001$).

Second, the tendency for kittiwakes to feed closer to shore increased with year. That is, the interaction between year and distance from shore became increasingly negative from 1996 to 1998 ($P < 0.0001$).

Third, assuming that colony sizes did not vary much (which was true), density of feeding kittiwakes increased with increase in distance from the colony, but varied by year. The interaction between kittiwake density and the distance index were significantly negative in both 1997 and 1998, compared to a significant positive relationship in 1996.

Fourth, the relationship of feeding densities relative to tide phase changed by year. There was a significant association between feeding kittiwakes and flood tides (i.e., a positive relationship; see Methods for numerical coding of tide phase) during 1996, a significant association with ebb tides in 1997, and lack of an association with any tide phase in 1998.

Finally, there was a curvilinear interaction between Julian date and tidal phase. Feeding kittiwakes were associated with ebb tides during late-June and July (i.e., a negative relationship), followed by a significant relationship with flood tides during early August. The relationship was quadratic.

Biological Variables: Interactions

No interactions between pairs of fish species affected the density of foraging kittiwakes (Table 1). That is, the relationship between kittiwake density and a given species of fish was not dependent on the presence or absence of another fish species. On the other hand, spatial or temporal variables affected the density of kittiwakes foraging over herring (3 interactions), sandlance (4), and eulachon (3). These interactions are as follows, by fish species:

Pacific herring — Year, distance from shore, and tide phase interacted with the density of herring schools to affect kittiwake density (Table 1). First, in regard to year, a more positive association existed between feeding kittiwakes and herring abundance in 1997 compared to 1996 and 1998 (all three relationships significant, $P < 0.01$, Figure 8. Thus, the strength of the relationship between feeding kittiwakes and herring abundance did not track the annual abundance of herring, the schools of which were far more prevalent in 1996 than in the next two years (cf. Figure 2).

Second, the density of foraging kittiwakes and of herring schools increased with distance from shore (Figure 8). Only the relationship at 250 m from shore (the nearest category) was insignificant. Recall, however, that density of foraging kittiwakes and forage-fish schools showed no relationships farther from shore (at least as determined from hydroacoustic data). Thus, the category '>2000 m' (see Figure 8) does not extend indefinitely to greater and greater distances. Rather, it is near to the limit of kittiwake and fish school associations.

Third, a positive relationship existed between kittiwake density and herring abundance at each tide phase ($P < 0.0001$). The most positive association occurred between kittiwakes and herring schools during flood tides, and the least positive relationship occurred during slack tide (Figure 8).

Sandlance — The same variables as for herring, with the addition of date, interacted with the density of sandlance schools to affect density of foraging kittiwakes (Table 1). First, in regard to year, sandlance abundance and density of feeding kittiwakes were positively associated in both 1997 and 1998, but not so in 1998 (Figure 9). Thus, the strength of the relationship between feeding kittiwakes and sandlance abundance tracked the annual abundance of this species in the study area (cf. Figure 2).

Second, within a year, the association between densities of feeding kittiwakes and sandlance schools declined with date (Figure 9). Regardless, the association with date was significant for each of the five date categories (all $P < 0.01$).

Third, the interaction between density of foraging kittiwakes and sandlance schools as a function of distance from shore was similar to that shown for herring: higher densities of both with greater distance (Figure 9). The positive relationship between densities of feeding kittiwakes and sandlance school abundance was significant at each of the five distance categories except 750 m.

Finally, as with herring, kittiwake and sandlance density exhibited a strong association at flood tides compared to ebb tides, but also such an association at slack tide (Figure 9). Unlike herring, a strong association existed at slack tides, too. Overall, there was a significant positive relationship between density of feeding kittiwakes during each of the three tide phases (all $P < 0.02$).

Eulachon — Three environmental variables had significant interactions with kittiwake and eulachon associations. First, as with herring and sandlance, distance from shore and tide phase were important, but also important was distance from colony (Table 1). In regard to distance from shore, the relationship was the same as for the other two prey species (Figure 10). The relationship was significant only at distances of 1,250 and, especially, at distances > 2,000 m from shore.

Second, the interaction between eulachon and kittiwake density with tide phase was similar to that shown by sandlance. The interaction reflected a highly significant relationship at flood tides ($P < 0.0001$), a slightly less significant association during slack tides ($P < 0.01$), and no relationship during ebb tides ($P = 0.8$; Figure 10).

Finally, the strength of the association between densities of foraging kittiwakes and eulachon abundance increased with distance from the colony (Figure 10). The relationship was quadratic because the relationship between kittiwakes and eulachon was insignificant at indices of 225 to 325 (no eulachon schools were seen at the colony index of 375), compared to the highly significant relationship recorded at indices > 400.

Prey Species Preference by Kittiwakes

Densities of feeding kittiwakes, to a highly significant degree, were greater when associated with eulachon and capelin than when associated with herring and sandlance (Sidak tests, both $P < 0.0001$, Figure 11). Densities of feeding kittiwakes associated with herring schools did not differ significantly from those associated with sandlance ($P > 0.1$): and densities of kittiwakes feeding on eulachon did not differ from those feeding on capelin ($P > 0.5$).

Densities of feeding kittiwakes increased significantly, in increasing order, when schools of herring, sandlance, capelin, and eulachon were present (see above, Main effects). Thus, although kittiwakes were seen in association with herring and sandlance schools greater than 40 and 20 times more often, respectively, than with schools of eulachon and capelin, densities of feeding kittiwakes were much greater when associated with eulachon and capelin. Therefore, although herring and sandlance contributed more to the diet, kittiwakes may prefer eulachon and capelin when available.

DISCUSSION

A large number of factors contributed to the explanation of where and when kittiwakes foraged in Prince William Sound during the summers of 1996-1998. The regression model explained 18.8% of the variance, which is not a remarkable value, but a substantial one considering that in single-year models (1996, 1997 or 1998, alone) the variance explained increased to as high as 40%. In other words, when year was added as a variable it became a surrogate for many other mostly unknown factors that affect kittiwake foraging and, of course, were not measured in our study.

In the case of most, but not all, significant variables, the relationship between kittiwake occurrence and that of fish schools is understandable in the context of current knowledge. Here we will review these relationships.

Differences in composition of the diet fed to kittiwake chicks at Shoup Bay and Eleanor Island colonies in 1996 and 1997 (Suryan et al. Ms; 1998 data not yet available), both sites being within our study area, were consistent with variation in prevalence of fish schools. The latter was assessed (and reported herein) also during the chick-feeding period. For instance, our results showed herring schools to be more prevalent in the study area in 1996 than in 1997, and sandlance schools to be more prevalent in 1997 than 1996. Accordingly, herring were more prevalent in the kittiwake diet in 1996 than 1997, and vice versa for sandlance. Similarly, eulachon schools were much more prevalent in the Sound in 1997 compared to 1996, and eulachon were evident in the diet at Eleanor Island in 1997, but not 1996. Thus, variation in diet reflected variation in prey availability to a substantial degree.

What was not supported by our study was a reflection of diet composition relative to the abundance of one fish species relative to others. In other words, our results showed herring schools to be about twice as abundant as sandlance schools, which was borne out in the diet only at Shoup Bay in 1996. In that year, herring contributed 60% and sandlance 30% to overall diet (Suryan et al. Ms). On the other hand, at Shoup Bay in 1997 and at Eleanor Island in both years, sandlance was more prevalent in the diet by 20-50% compared to herring. The elevated importance of herring to Shoup Bay parents in 1996 may have been related to the greater availability that year of age class 1+ herring; or, at least, those were the fish that dominated diets in 1996 (but not 1997). Older herring are much more energy-rich compared to the age 0 herring taken in 1997 (Anthony et al. 1998). This pattern was not perfect, however, because at Eleanor the age composition of herring fed to chicks showed the same pattern, but sandlance nevertheless were the more commonly taken prey (Suryan et al. Ms). That is, sandlance were taken over age 1+ herring.

Our data did show an actual preference of kittiwakes for capelin and, especially, eulachon, if the density of kittiwakes foraging over schools of these species, versus those of other prey species, is an indication. Not surprising, the energy density of eulachon is double that of the other forage fish (Anthony et al. 1998). Eulachon, therefore, appear to be a much-sought prey. Why kittiwakes would select capelin over herring and sandlance is not readily clear on the basis of our data. Capelin, sandlance and, to a lesser extent, herring were much more available during the early summer. Capelin, too, captured early in the summer would be much more valuable energetically than herring or sandlance (Anthony et al. 1998). Sandlance also decrease in energy density over the course of the summer. These relationships may explain, therefore, the decreasing interaction of date with kittiwake and sandlance school density; kittiwakes are much more abundant over sandlance schools early than later in the summer.

In regard to the density of kittiwakes as a function of the density of prey schools, the response of kittiwakes was similar regardless of prey species. That is, few, if any, kittiwakes occurred in areas where no prey schools were evident, but appreciable numbers were present in the company of at least one prey school. The fact that kittiwake density did not increase as a function of the number of schools, once at least one prey school was present, could be an argument supporting a relationship to an avoidance of (or, the result of) interference competition. When kittiwakes descend upon a school, the school responds immediately to become less available to surface-foraging predators. Thus, if foraging kittiwakes move from one school to a more-susceptible nearby school, which they do if given the chance, having more schools in a local area would not necessarily encourage more kittiwakes to accumulate (and have an equal chance of foraging success). In fact, Irons (1992) noted that kittiwakes on their flights out to secure food for chicks commonly over-flew foraging conspecifics (see below).

The fact that kittiwakes tended to feed as close as possible to the colony, at least most of the time (see below), is not surprising, nor hard to explain in terms of reducing foraging and reproductive effort. Foraging over shallow water, close to shore must have to do with foraging effort, too, by way of exploiting increased prey availability or susceptibility of prey to capture. That fact that the shallow water is offshore, i.e. not immediately adjacent to the beach, but over shoals and reefs (i.e., tendency to feed in shallow water) has to be a factor related to prey behavior and availability/susceptibility. Foraging by kittiwakes over shoals and reefs in Prince William Sound has been noted previously (Irons 1992). The various relationships to tide stage are support for taking advantage of an increased susceptibility of prey as a foraging strategy (see, too, Irons 1992). Sandlance burrow in the sand at low tides and, thus, would be available to a surface-foraging predator only at flood and high slack tides. The behavior of eulachon, too, explains their availability at flood and high slack tides compared to ebb tides. The species is anadromous and moves into spawning rivers on flood tides. Herring, on the other hand, are taken at any moving tide, either ebb or flood (but not slack). Predatory fish feed at that time, too, if the success rate of human fishermen is a good indication (we're saying, yes, it is).

Therefore, forage fish must be more susceptible to capture at that time. Tidal currents flowing around and over reefs, and the turbulence generated in the process, might increase susceptibility of forage fish to surface predators as well.

That kittiwake density over eulachon schools increases with greater distance from the colony is a complex issue to explain. Eulachon are more prevalent in the southern portion of the Sound (see below, Part II), and the total of kittiwake pairs at colony clusters in the northern part of the Sound (12,500 pairs) are twice as great as the total nesting in the south. Thus, the northern colonies would dominate the index (see Methods, for the way the index was calculated). The result would show foraging for eulachon at greater distances from colonies; certainly true for northern colonies but not for the smaller southern colonies. Similar arguments might help to explain why kittiwakes tended to feed farther from colonies in 1997, the year when sandlance were so prevalent. Sandlance, too, are found much more in the southern part of Prince William Sound than they are in the north.

Here we have attempted to explain some of the relationships between kittiwake foraging and various temporal, spatial and biological variables. The fact that adding years to our study (3 instead of any 1) reduced our power to explain relationships, at the least, would support an argument for additional years of investigation if the objective was to understand even better the foraging ecology of kittiwakes in Prince William Sound. As it is, a significant portion of unexplained variance could be related to the way that individual kittiwakes respond to various factors as a result of their short-term and long-term experience. For instance, Irons (1992) discovered that individual kittiwakes have habitual foraging areas that they visit repeatedly regardless of near-future foraging success. We will explore some of these experiential factors in the development of a foraging model based on kittiwake search behavior (see below).

FORAGING BY BLACK-LEGGED KITTIWAKES IN PRINCE WILLIAM SOUND, ALASKA: II, PROVISIONAL MODEL TO DESCRIBE PREY-SEARCHING STRATEGIES

RESULTS

Relationship between Kittiwake Behavior and Fish Distribution

We explored the statistical relationships between types of kittiwake behavior and forage-fish school abundance. Our goal was to predict kittiwake foraging behavior from the distribution of forage-fish schools (Figure 12). Our first effort was to determine whether the frequency of various behaviors was related to the presence of forage-fish schools. We calculated the frequency of the most common behaviors in areas where schools were and were not observed (see Results of Part I, above). For this analysis, we partitioned the data set into the first (6 June to 20 June) and second (21 June to 11 August) halves of the breeding season.

Results showed that behavior frequency was significantly different in areas where forage-fish schools were observed than would be expected if behavior was random (Chi-square, $P<0.01$, Figure 13). In areas where aerial transects indicated the presence of forage-fish schools, kittiwakes were less likely to engage in straight flight and more likely to engage in back-and-forth flight, resting on water, and plunge diving.

The plunge-dive rate was chosen as the best indicator of successful foraging, since a high percentage of plunge dives result in the capture of prey items (pers. obs.). The regression of the plunge-dive rate on the density of forage-fish schools showed a strong non-linear relationship between the two variables (Figure 14), indicating that the density of forage-fish schools is a good predictor of foraging behavior. The non-linearity of the relationship suggests that the behavioral response to the density of schools is asymptotic (see above, Part I), and that a doubling of school density results in a constant increment in the rate of plunge diving.

Previous analysis of behavioral data (Ford et al. 1998) showed that plunge diving and other feeding-related behaviors are associated with relatively slow rates of linear movement. In general, when the movement rate of a kittiwake drops below 25 km/hr, it is usually either searching for food, diving, or waiting for a fish school to come near enough to the surface to be accessible. Areas where a high density of foraging behaviors occur, called foraging grounds, can be easily delineated using behavioral data by plotting the locations of all observations where the rate of movement is 25 km/hr or less and then generating isopleths of the density of these slow movements.

Foraging grounds for the Shoup Bay and Eleanor Island colonies in 1996, 1997, and 1998 are shown in Figure 15. Different years are associated with distinct differences in the location of foraging areas. For the Eleanor Island colony, Smith Island was a very active feeding area in 1998, but not in 1996 or 1997. By comparison, the Green Island vicinity and the northwest side of Montague Island were much more active in 1997 than in 1996 and 1998. Birds from the Shoup Bay colony were not tracked in 1996, but their foraging areas also shifted somewhat between 1997 and 1998. In 1997, the principle focus of activity was the southern side of Glacier Island. In 1998, the focus shifted to the northern side of Glacier Island and to Columbia Bay and to Long Bay. It is likely that these shifts in foraging grounds reflect a shift in the distribution of forage-fish schools, but data describing forage fish distribution prior to 1998 cannot be used to resolve these fine scale differences. Comparison of Figure 15 (foraging grounds) with Figure 12 (distribution of forage-fish schools) shows that, as would be expected, there is a strong correspondence between foraging grounds and areas with high densities of forage-fish schools (see Discussion).

Modeling Kittiwake Foraging Behavior

Kittiwakes foraging bouts consist of intervals of straight flight interspersed with sporadic searching behaviors alternating with intervals of intense searching and plunging behavior. These sequences for Eleanor Island and Shoup Bay in 1998 are illustrated in Figure 16. Kittiwakes appear to engage in a low level of search activity even during intervals of straight flight, so that even commutes are punctuated by occasional searching behaviors and plunge dives.

Our basic model of kittiwake foraging behavior makes the classical optimal foraging assumption that individuals are attempting to maximize their food uptake rate (see for example Orians and Pearson 1979). Assuming that completed plunge dives are a good index of foraging success, and knowing that the plunge-dive rate can be predicted by the density of forage fish, birds should select travel itineraries that maximize their expected foraging rate. The quality of such an itinerary is dependent not just on the endpoint of the journey, but on the quality of the intervening habitat. Our model finds the optimal foraging path using the following algorithm based in part on the model presented in Ford (1983):

1. Divide the study area into a grid and calculate the density of forage-fish schools in each cell;
2. Create a candidate itinerary consisting of a series of adjacent grid cells ("rook's move" only);
3. Compute the mean expected foraging rate over the entire candidate itinerary;
4. Repeat steps 2 and 3 until all possible itineraries have been examined; and
5. Output the itinerary with the greatest expected foraging rate.

This model predicts that an optimally foraging kittiwake starting from Shoup Bay should move down the western side of Valdez Arm, turn west at Point Freemantle into the channel between Glacier Island and the mainland, and pass first into Columbia Bay and then into Long Bay. Based on radio-tracked kittiwakes from the Shoup Bay colony, this is the most common itinerary.

In this form, the foraging model predicts only a single optimal path, yet kittiwakes select a variety of different paths. It is likely that this results from unpredictability in the abundance of fish schools. In Part I, above, we found that certain factors did help to predict the occurrence of forage-fish schools, and certainly these factors are likely used by kittiwakes. However, a high degree of unpredictability still remained. We examined predictability by calculating the degree to which a kittiwake could use the density of forage fish cell in one area (1.5-nm cell) related to the density of forage fish nearby (other 1.5-nm cells) for various times and distances between cells. Figure 17 shows the resultant correlation coefficient as a function of time and distance. Using this measure of variability, the knowledge of the density of forage-fish schools at one point in space and time is of almost no use in predicting the density of schools more than about 20 miles away or 5 days in the future.

DISCUSSION

Based on these results, we assume that the variation in the kittiwakes' solution to the optimal-foraging problem results from uncertainty on the part of a kittiwake's as to the distribution of forage-fish schools and their availability. For one thing, as noted above, the location of foraging areas differed among years; for another, as noted in Part I, while a number of factors can be used to predict fish availability to kittiwakes, additional and (at least to us) unknown factors remain. The extent to which a kittiwake is aware of these other factors remains to be determined. Following the 1999 field season, we will be able to determine whether annual changes in foraging-ground locations track annual changes in the distribution of forage-fish schools.

To simulate the effect of uncertainty in predicting the availability of forage fish, we ran the foraging model many times, each time perturbing the value of the density of forage-fish schools in each of the grid cells around the mean value using a normally-distributed random deviate. This resulted in the distribution of simulated foraging paths for the Shoup Bay colony shown in Figure 18. As would be expected, the itinerary that passes down the west side of Valdez Arm and into Columbia Bay remains the most popular. The stochastic version of the foraging model, however, results in a family of foraging-trip itineraries that mimic most of the itineraries followed by radio-tagged kittiwakes leaving the Shoup Bay colony. At this point, we consider the correspondence between the observed and the predicted behaviors to be highly promising, and will continue to develop it as a means for predicting foraging success and colony productivity.

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LITERATURE CITED

Ainley, D.G., R.G. Ford and D.C. Schneider. 1997. The factors that limit seabird recovery in the EVOS study area: a modeling approach., *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 97163Q), Anchorage, Alaska. Volume II.

Anthony, J.A., D.D. Roby, and K.R. Turco. 1998. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 97163G), Anchorage, Alaska. Volume II.

CRC. 1995. STATA reference manual: Release 3.1, 6th Ed. Stata Corp., College Station, TX.

Duffy, D.C. (compiler) 1997. APEX Project: Alaska Predator Ecosystem Experiment in Prince William Sound and the Gulf of Alaska. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 96163 A-Q). Alaska Natural Heritage Program, University of Alaska Anchorage, Alaska. Volumes I & II.

Ford, R. G. 1983. Foraging in a patchy environment. American Zoologist 23:315-326.

Ford, R.G., D.C. Schneider and D.G. Ainley. 1998. The factors that limit seabird recovery in the EVOS study area: a modeling approach., *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 98163Q), Anchorage, Alaska. Volume II

Haldorson, L., T. Shirely, K. Coyle and R. Thorne. 1997. Forage species studies in Prince William Sound. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 97163A), Anchorage, Alaska. Volume I.

Irons, D.B. 1992. Aspects of foraging behavior and reproductive biology of the Black-legged Kittiwake. Unpubl. PhD Dissertation. Univ. Calif., Irvine.

Irons, D.B., R.M. Suryan and J. Benson. 1997. Kittiwakes as indicators of forage fish availability. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 97163E), Anchorage, Alaska. Volume II.

Kleinbaum, D.G., L.L. Kupper, and K.E. Muller. 1988. Applied regression analysis and other multivariable methods. PWS-KENT Publishing Co., Boston, MA.

Orians, G. H. and N. E. Pearson 1979. On the theory of central place foraging. Pp. 155-177 *in* D. J. Horn, R. D. Mitchell and G. R. Stairs (eds.), Analysis of ecological systems. Ohio State University Press, Columbus, OH.

Ostrand, W.D., and D.A. Flint. 1995. Forage fish project – seabird/forage fish interactions. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 94163B), Anchorage, Alaska. Volume I.

Ostrand, W.D, and J.M. Maniscalco. 1996. Seabird/forage fish interactions. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 96163B), Anchorage, Alaska. Volume I.

SAS, Inc. 1985. SAS user's guide: Statisics. 5th Ed., SAS Institute Inc., Cary, NC.

Seber, G.A.F. 1977. Linear regression analysis. John Wiley & Sons, New York.

Sowls, A.L., S.A. Hatch, and C.J. Lensink. 1978. Catalog of Alaskan seabird colonies. U.S. Fish and Wildlife Service, Biological Services Program. FWS/OBS 78/78. Anchorage.

Suryan, R.M., and D.B. Irons. Ms. Population dynamics of kittiwakes in Prince William Sound, Alaska: Productivity of individual colonies and population trends. U.S. Fish & Wildlife Service, Anchorage.

Suryan, R.M., D.B. Irons, and J. Benson. Ms. Inter-annual variation in diet and foraging effort of the Black-legged Kittiwake (*Rissa tridactyla*) in relation to prey abundance. Ibis, submitted.

Table 1. Results of multiple regression analyses indicating relationships between kittiwake density (log-birds per 100 km) and temporal, spatial, and biological variables in Prince William Sound, Alaska, 1996-1998. The analysis was weighted by the kilometers surveyed per transect block surveyed per day.

	Regression coefficient sign	*F*-value	*P*-value	df
Main effects:				
Year (continuous)	+	486.13	<0.0001	1
Year (categorical)	(cat.)	190.23	<0.0001	2
Depth	-	18.97	<0.0001	1
Distance from shore	-	85.77	<0.0001	1
Colony index	-	29.16	0.001	1
Herring	+	204.09	<0.0001	1
Herring^2	-	60.88	<0.0001	1
Sandlance	+	63.95	<0.0001	1
Sandlance^2	-	14.16	0.0001	1
Sandlance3	+	11.90	0.001	1
Eulachon	+	8.09	0.01	1
Capelin	+	18.34	<0.0001	1
Capelin^2	-	31.72	<0.0001	1
Rejected terms:				
Julian date	ns	5.21	0.023	1
Latitude	ns	4.47	0.035	1
Tide phase	(cat.)	3.01	0.044	2

Table 1 continued

	Regression coefficient sign	F-value	P-value	df
Interactions:				
Year x Julian date	(cat.)	7.39	0.001	2
Year x Distance from shore	(cat.)	6.31	0.01	2
Year x Colony index	(cat.)	6.78	0.001	2
Year x Tide phase	(cat.)	9.45	<0.0001	4
Tide phase x Julian date	(cat.)	6.83	0.001	2
Tide phase x Julian date^2	(cat.)	4.67	0.01	3
Tide phase x Julian date^3	(cat.)	5.59	0.001	3
Herring x Year	(cat.)	31.22	<0.0001	2
Herring x Distance from shore	+	7.32	0.01	1
Herring x Tide phase	(cat.)	8.66	0.01	2
Sandlance x Year	(cat.)	5.84	0.01	2
Sandlance x Julian date	-	16.74	<0.0001	1
Sandlance x Distance from shore	+	5.64	0.02	1
Sandlance x Tide phase	(cat.)	14.72	0.0001	2
Eulachon x Distance from shore	+	16.31	<0.0001	1
Eulachon x Colony index	+	22.29	<0.0001	1
Eulachon x Colony index^2	+	6.44	0.01	1
Eulachon x Tide phase	(cat.)	26.13	<0.0001	2

Table 2. Regression models for the relationship between school abundance and date for four species of kittiwake forage fishes in Prince William Sound, Alaska. Data grouped across years 1996, 1997, and 1998.

	Regression coefficient ± SE	P-value
Herring		
Date	-0.00087 ± 0.00021	<0.0001
Date^2	-0.000026 ± 0.000012	0.02
Date^3	$6.58e^{-06} \pm 2.25e^{-06}$	0.01
Sandlance		
Date	0.00052 ± 0.00020	0.01
Date^2	0.000058 ± 0.000011	<0.0001
Date^3	$-5.04e^{-06} \pm 1.56e^{-06}$	0.001
Eulachon		
Date	-0.00010 ± 0.000040	0.01
Capelin		
Date	-0.000065 ± 0.000029	0.01

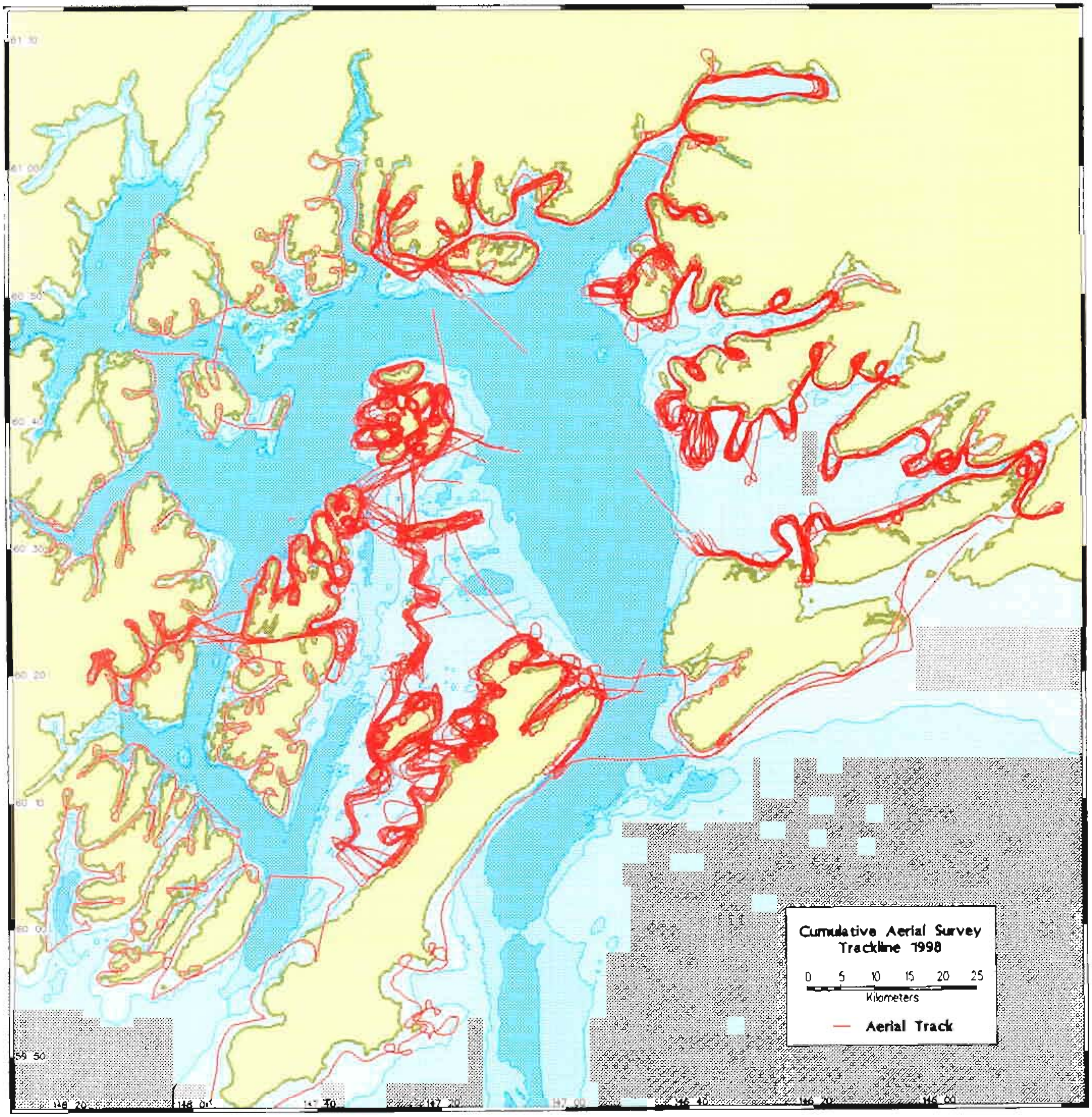

Figure 1. Prince William Sound showing aerial survey tracks for 1998; tracks for 1996 and 1997 were similar to these. Tracks are based on automated logging of aircraft position at 5 sec intervals using a GPS unit.

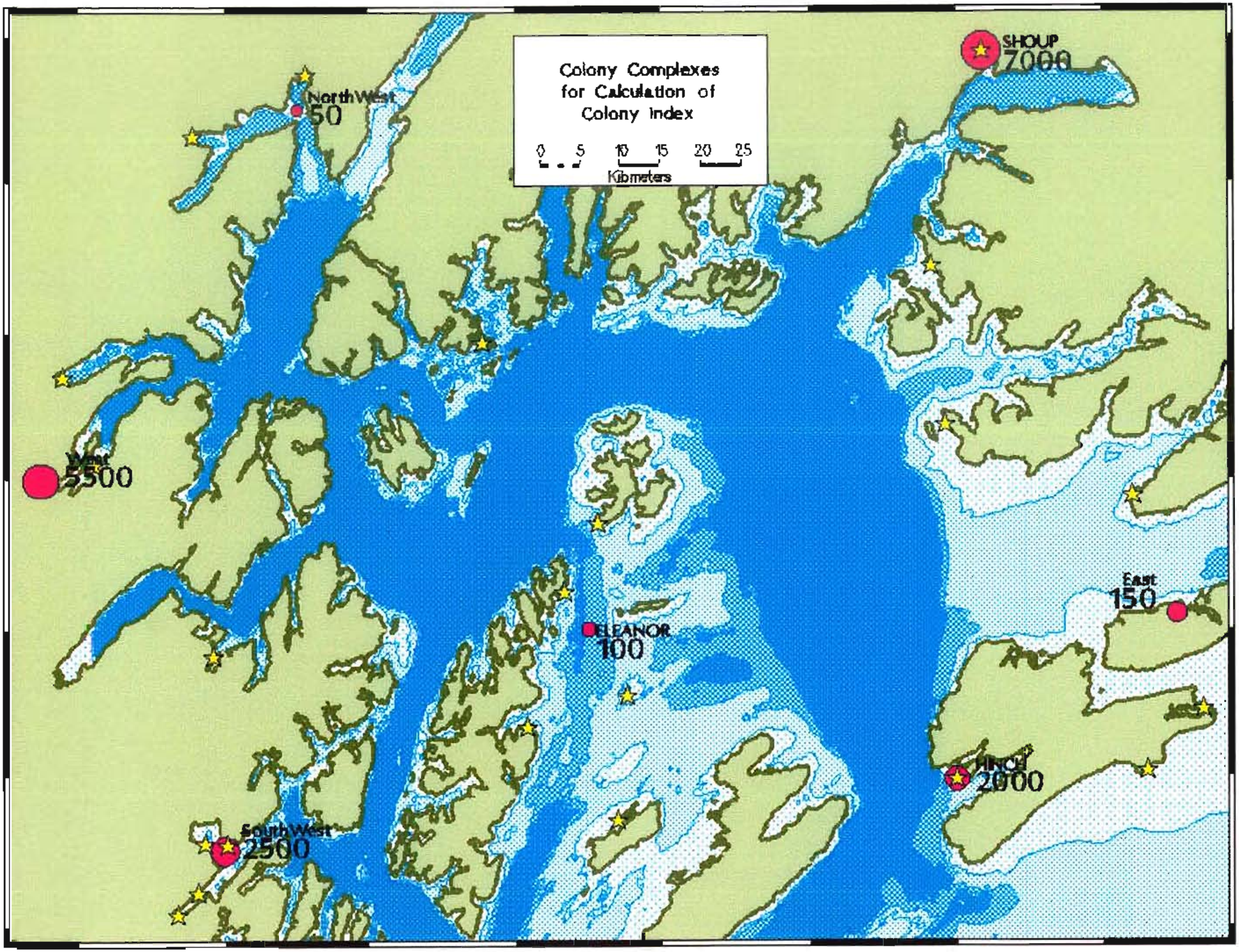

Figure 2 Prince William Sound and the locations of Black-legged Kittiwake colonies (stars). Red dots indicate the location of the position used to calculate distance to the 7 colony clusters Colony sizes from Sowls et al. (1978), with updates from Irons, Suryan et al (pers.comm.)

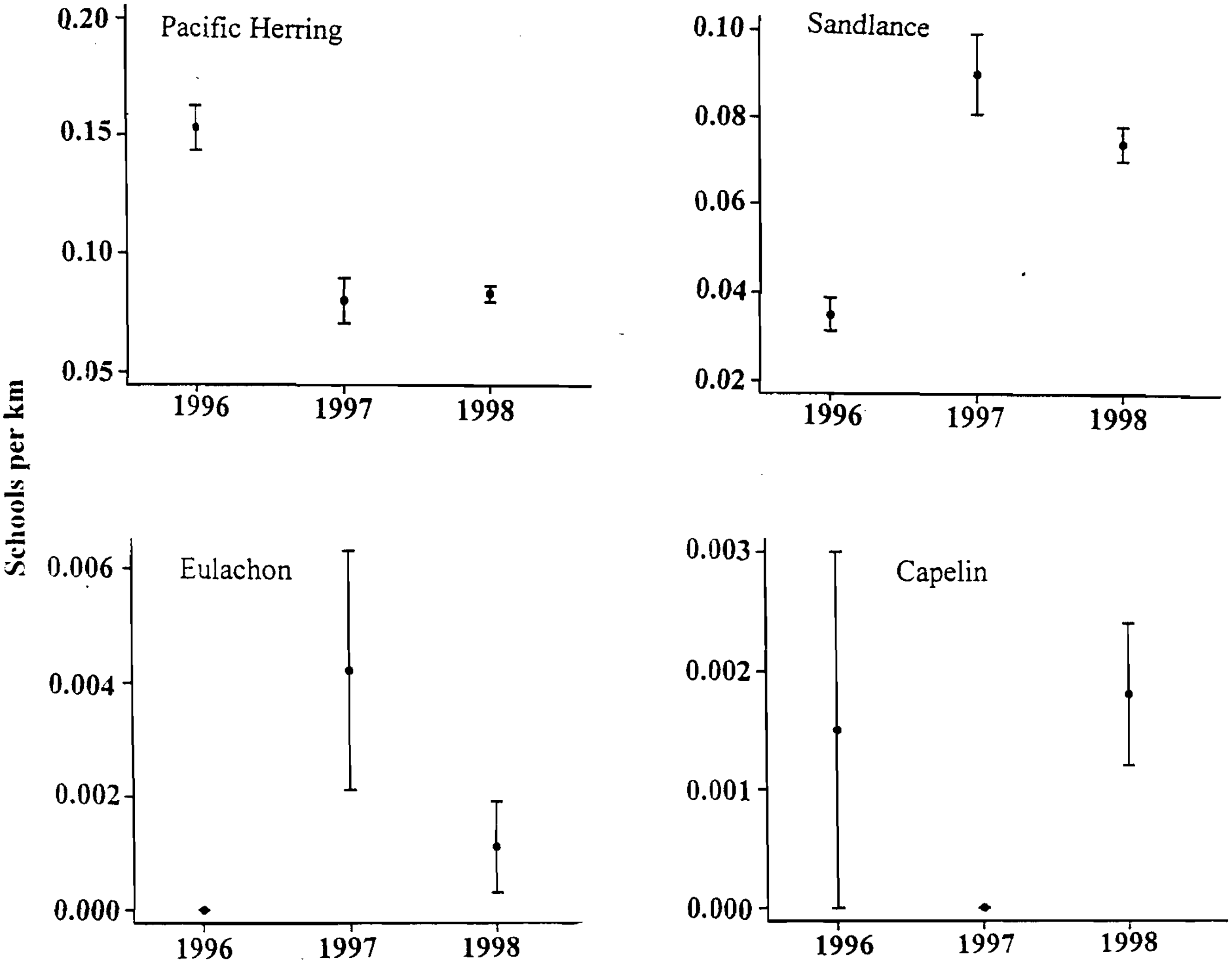

Figure 3. Densities of schools by year of four species of fish preyed upon by Black-legged Kittiwakes in Prince William Sound, Alaska. Densities are number of schools per km for each survey block sample (n = 10,181). Calculations were weighted by the kilometers of track line surveyed per sample.

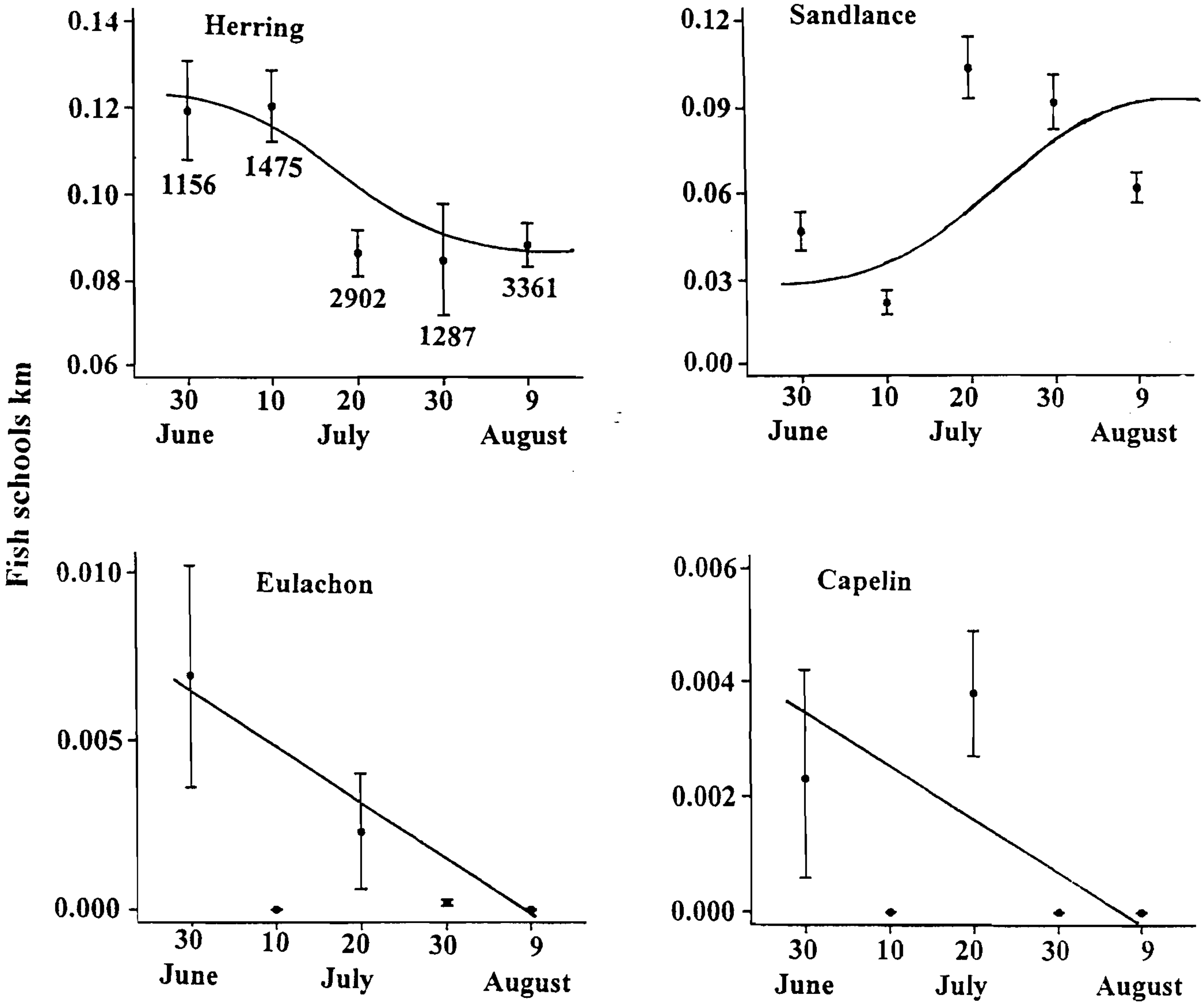

Figure 4. Density by date within year of schools of fish preyed upon by Black-legged Kittiwakes in Prince William Sound, Alaska. Densities are number of schools per kilometer for each survey block sample (n = 10,181). Calculations were weighted by the kilometer of track line surveyed per sample.

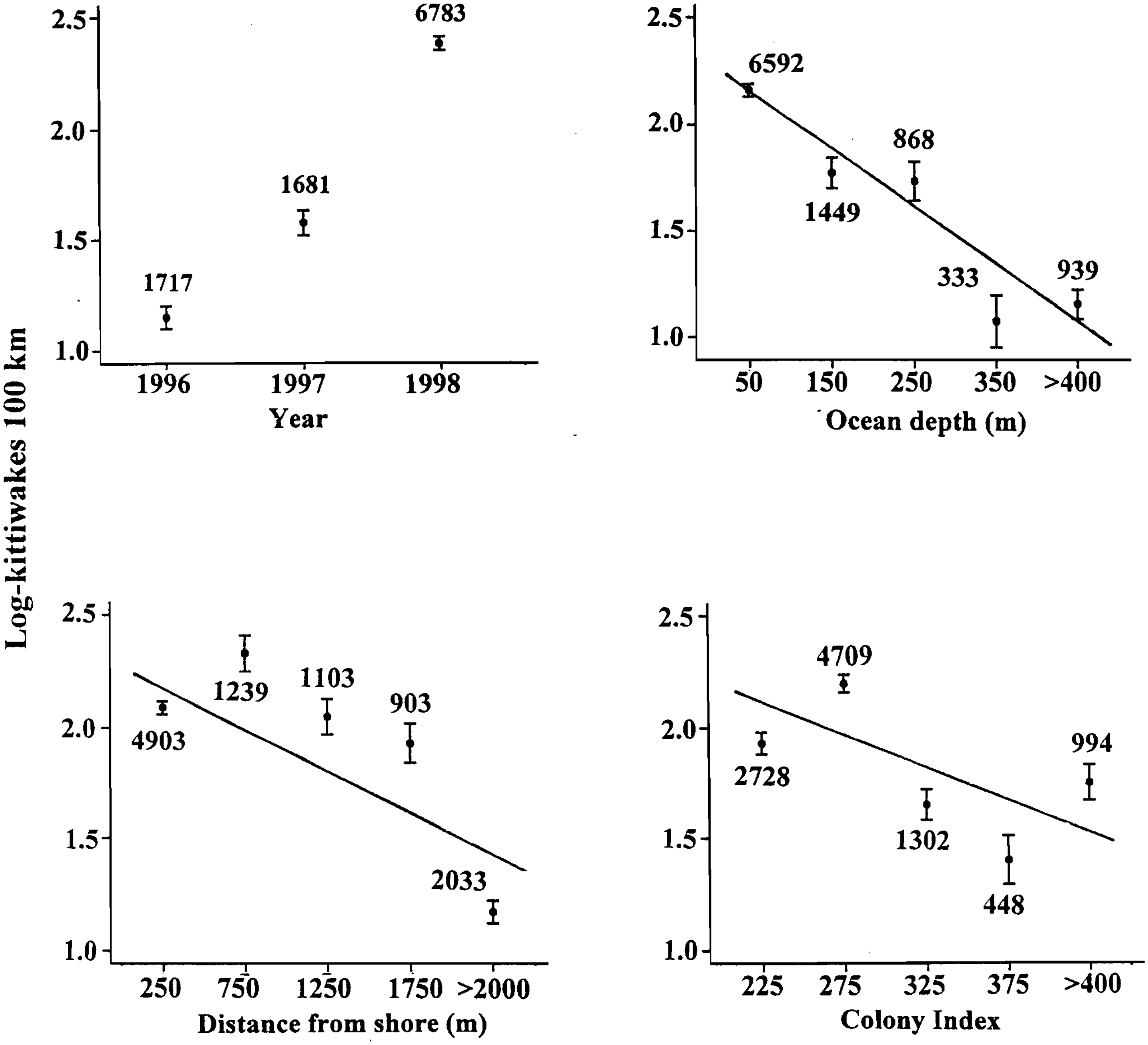

Figure 5. Densities (log-transformed) of feeding Black-legged Kittiwakes with respect to four environmental variables. Shown are the means, SE, and the sample sizes (numbers adjacent to means = the number of blocks sampled). Lines of best fit are shown for the variables that were analyzed as continuous.

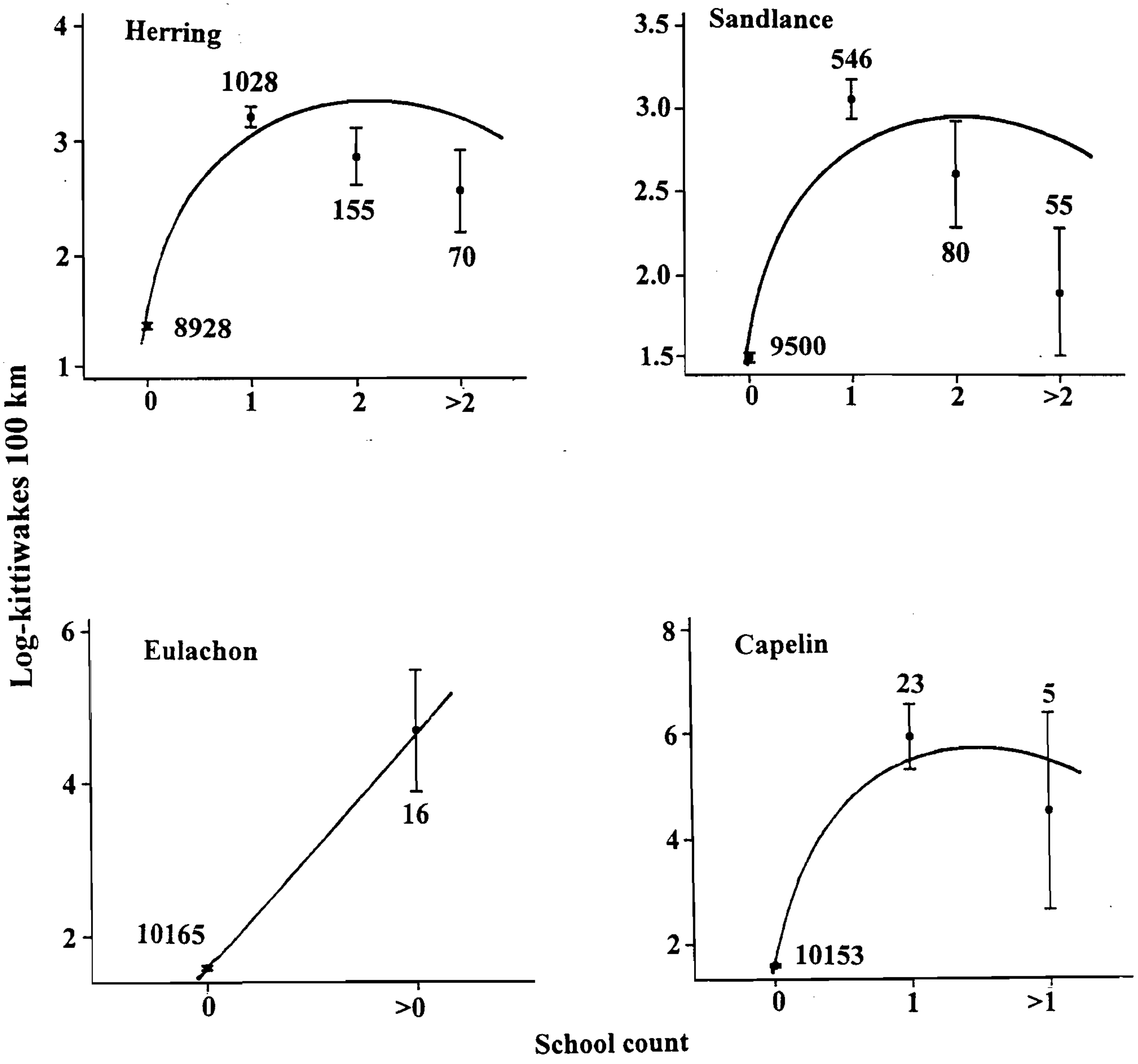

Figure 6. Densities (log-transformed) of feeding Black-legged Kittiwakes with respect to abundance of four species of forage fishes. Shown are the means, SE, sample sizes (numbers adjacent to means = the number of blocks sampled), and lines of best fit.

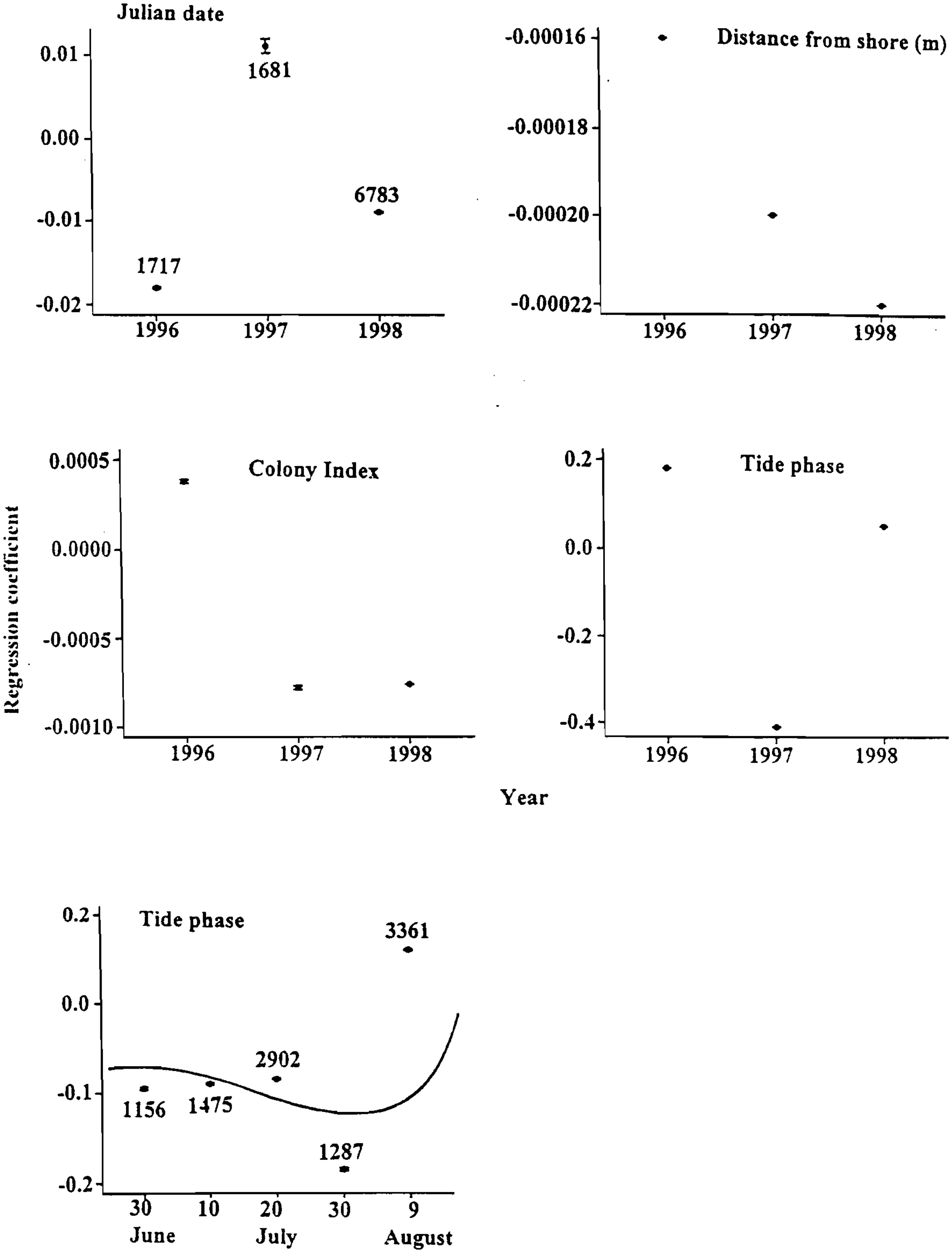

Figure 7. Regression coefficients for the relationship between log-transformed densities of feeding Black-legged Kittiwakes and environmental variables (given at the top of each graph) with respect to temporal period (year and date; x-axis). Shown are the coefficient means and SE. Sample sizes (numbers adjacent to means = the number of blocks sampled) are shown adjacent to means for date. Sample sizes for year -- 1996, 1997, and 1998 -- were 1717, 1681, and 6783, respectively. Line of best fit is shown for date, analyzed as a continuous term.

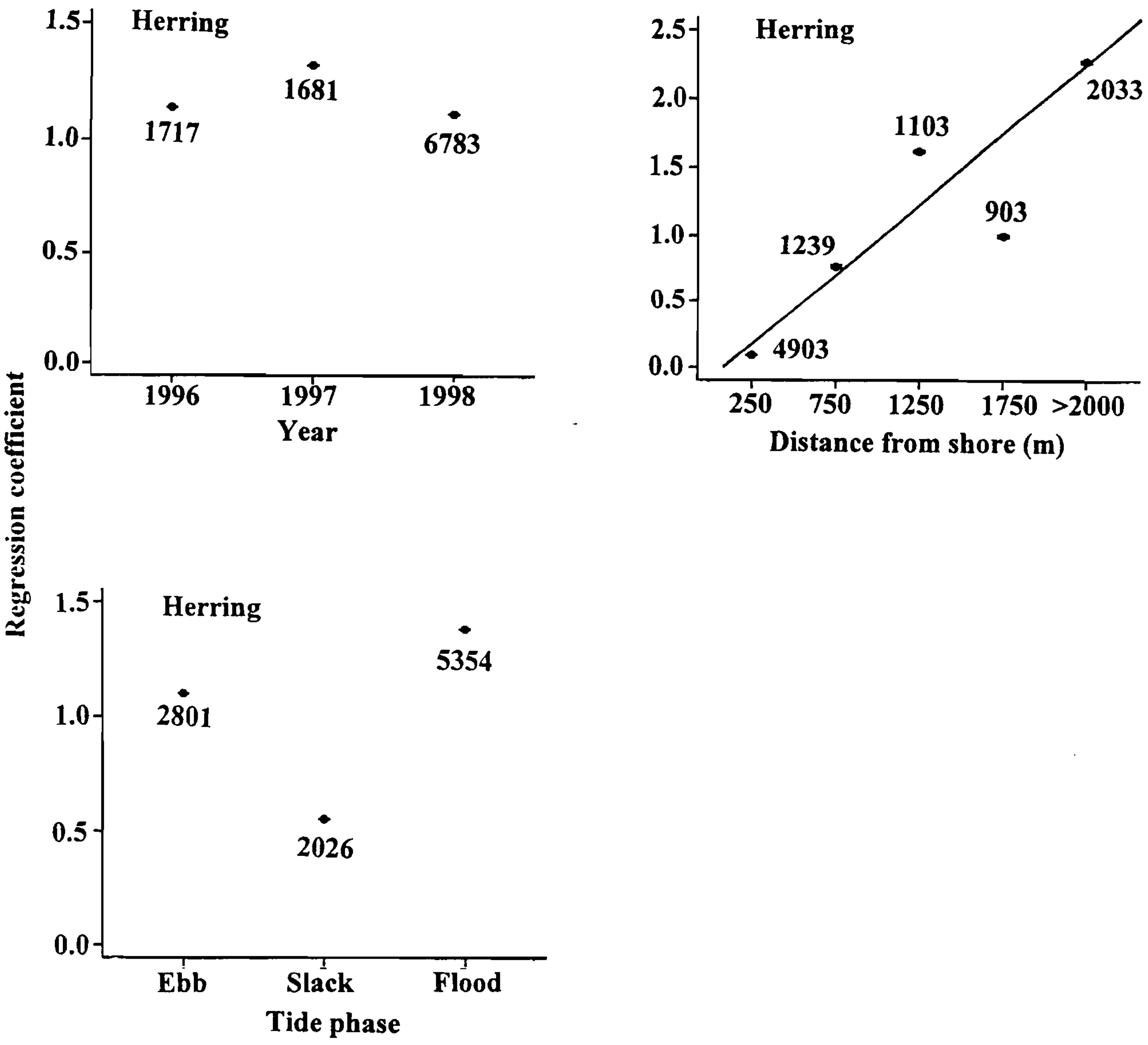

Figure 8. Regression coefficients for the relationship between log-transformed densities of feeding Black-legged Kittiwakes and abundance of herring schools, shown with respect to year, increments of distance from shore, and tide phase (x-axis). Shown are the coefficient means, SE, and sample sizes (numbers adjacent to means = the number of blocks sampled). Line of best fit is shown for distance from shore, analyzed as a continuous term.

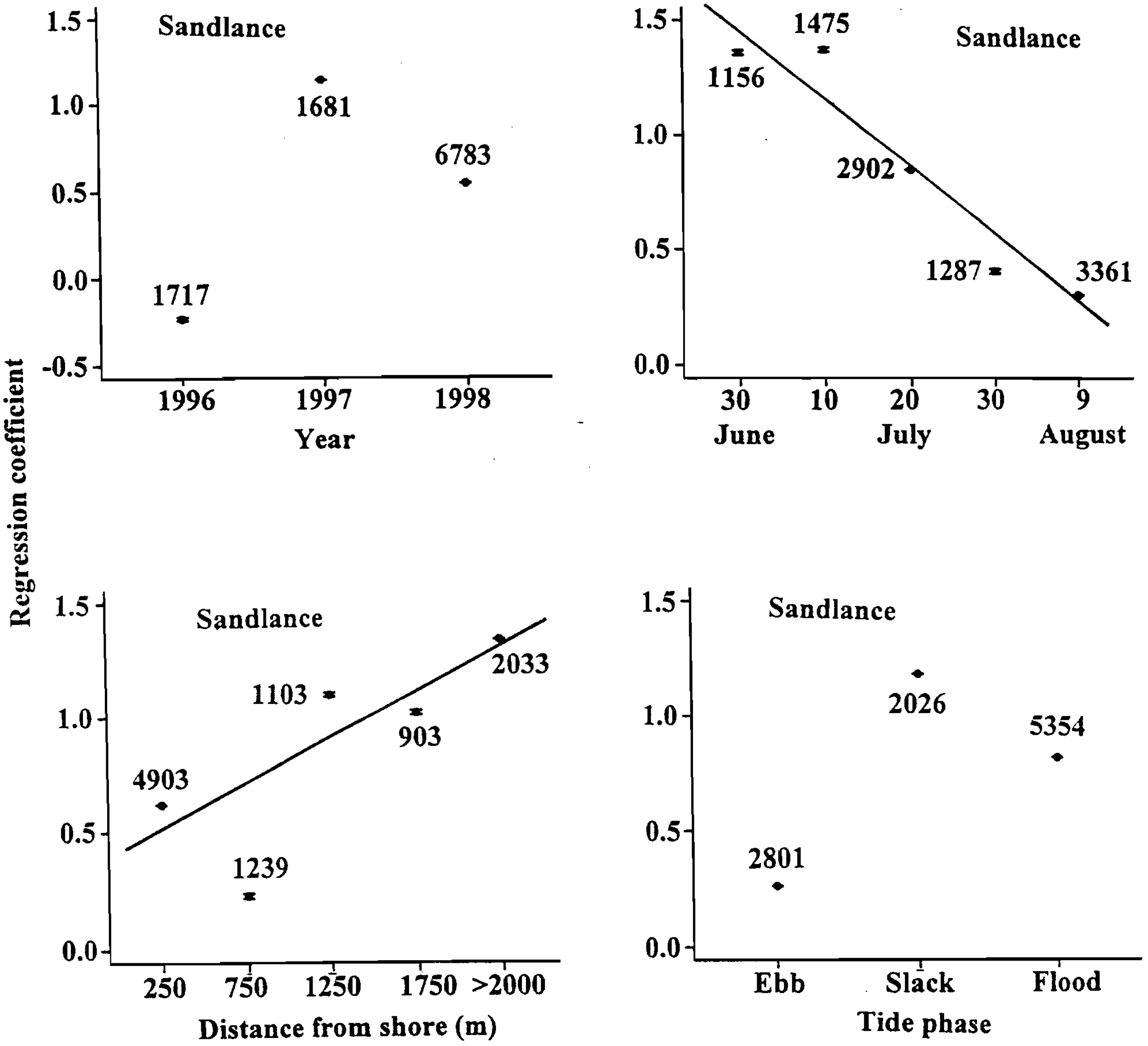

Figure 9. Regression coefficients for the relationship between log-transformed densities of feeding Black-legged Kittiwakes and abundance of sandlance schools, shown with respect to year and increments of date, distance from shore, and tide phase (x-axis). Shown are the coefficient means, SE, and sample sizes (numbers adjacent to means = the number of blocks sampled). Lines of best fit are shown for date and distance from shore, analyzed as a continuous terms.

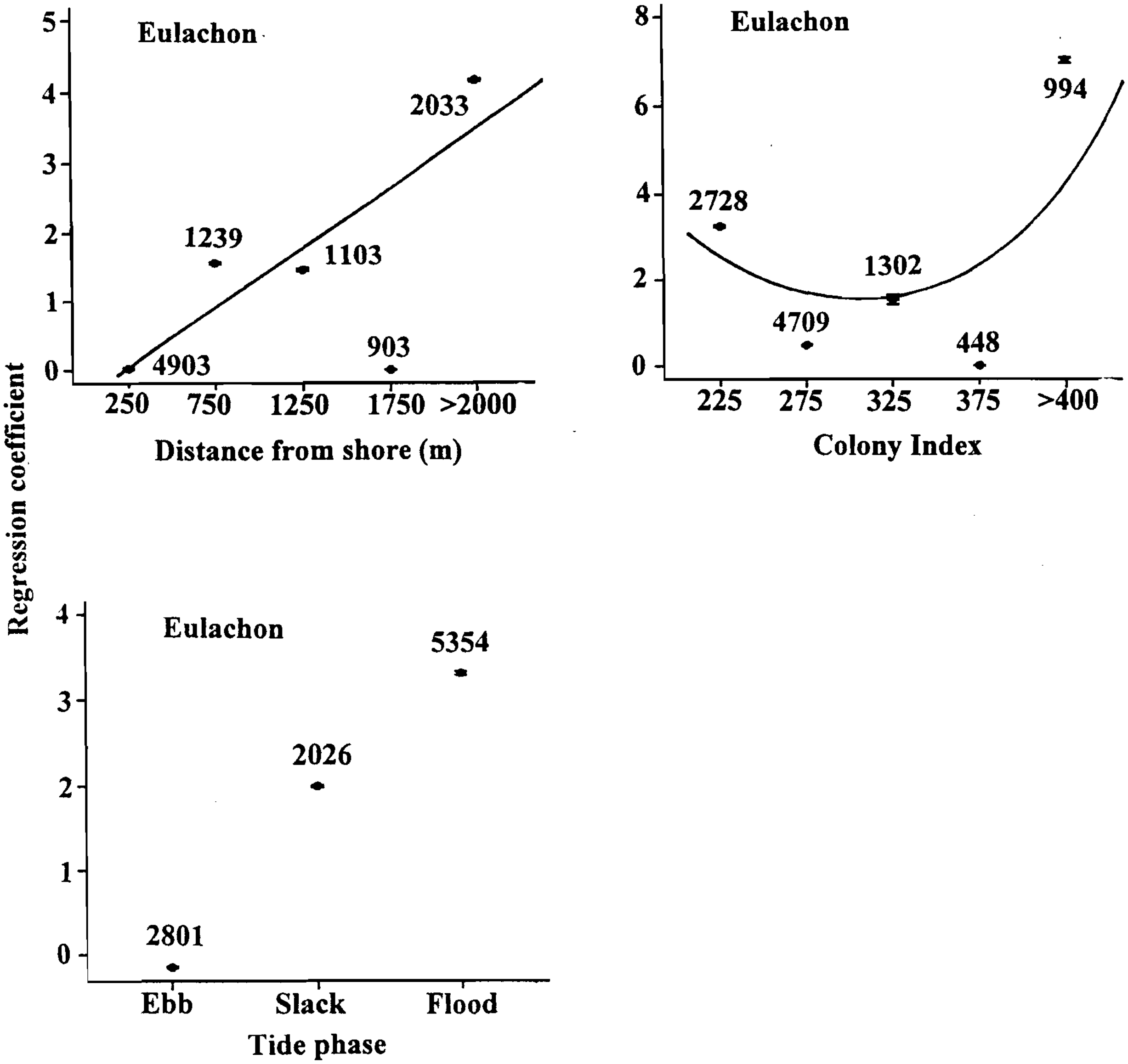

Figure 10. Regression coefficients for the relationship between log-transformed densities of feeding Black-legged Kittiwakes and abundance of eulachon schools, shown with respect to distance from shore, colony index and tide phase (x-axis). Shown are the coefficient means, SE, and sample sizes (numbers adjacent to means = the number of blocks sampled). Lines of best fit are shown for distance from shore and colony index, analyzed as a continuous terms.

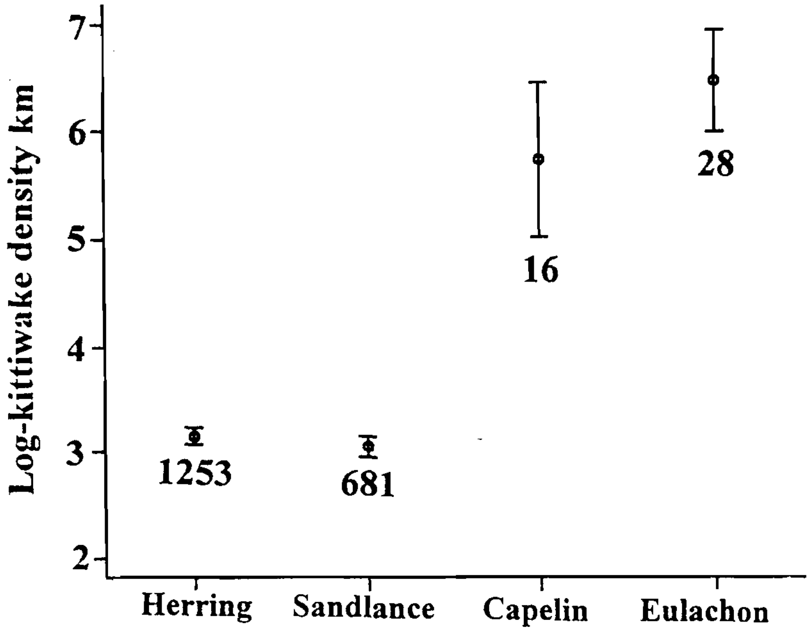

Figure 11. Density (log-transformed) of feeding Black-legged Kittiwakes observed within survey blocks in which at least one school of a given species of fish was observed. Shown are the means, SE, and sample sizes (numbers adjacent to means = the number of blocks sampled in which a school was seen).

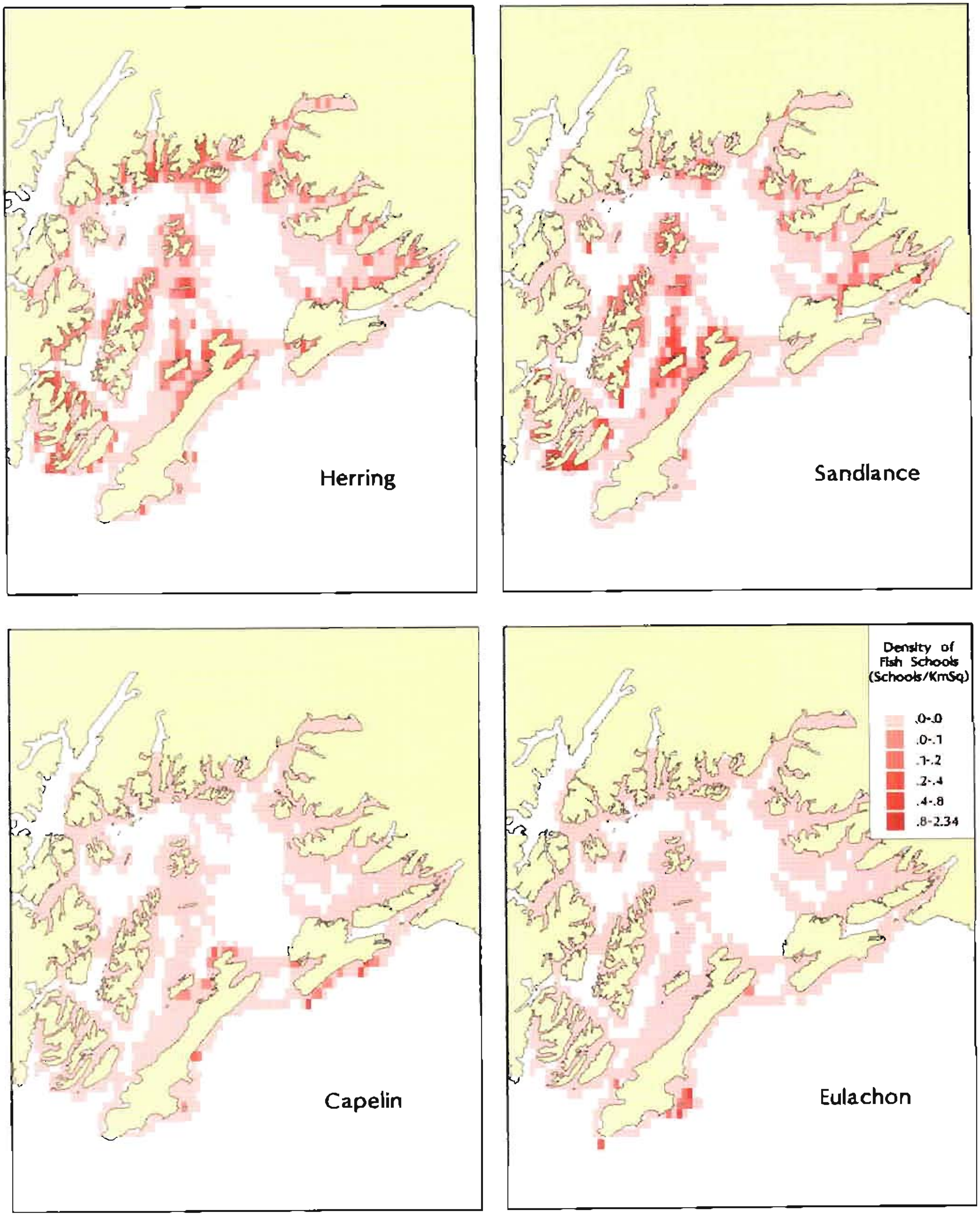

Figure 12. The density of schools of forage fish in 1998 based on aerial survey data. Density of fish schools was estimated as the number of schools in a 1.5-nm2 block divided by the product of the length of trackline within that block and the effective transect width for fish school spotting. Effective transect width was estimated as 1/f0 using program DISTANCE.

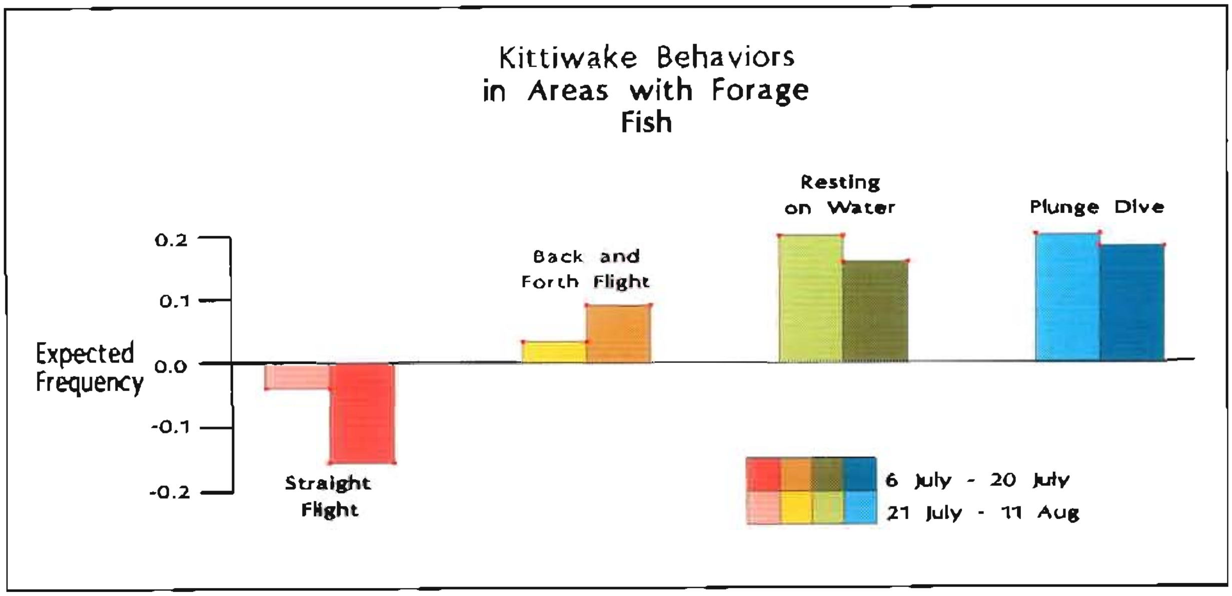

Figure 13. The frequency of various behaviors in 1.5-nm blocks where fish schools were observed. Bars above the line and below the line, respectively, indicate behaviors that occur more or occur less frequently than expected if behaviors were independent of fish density.

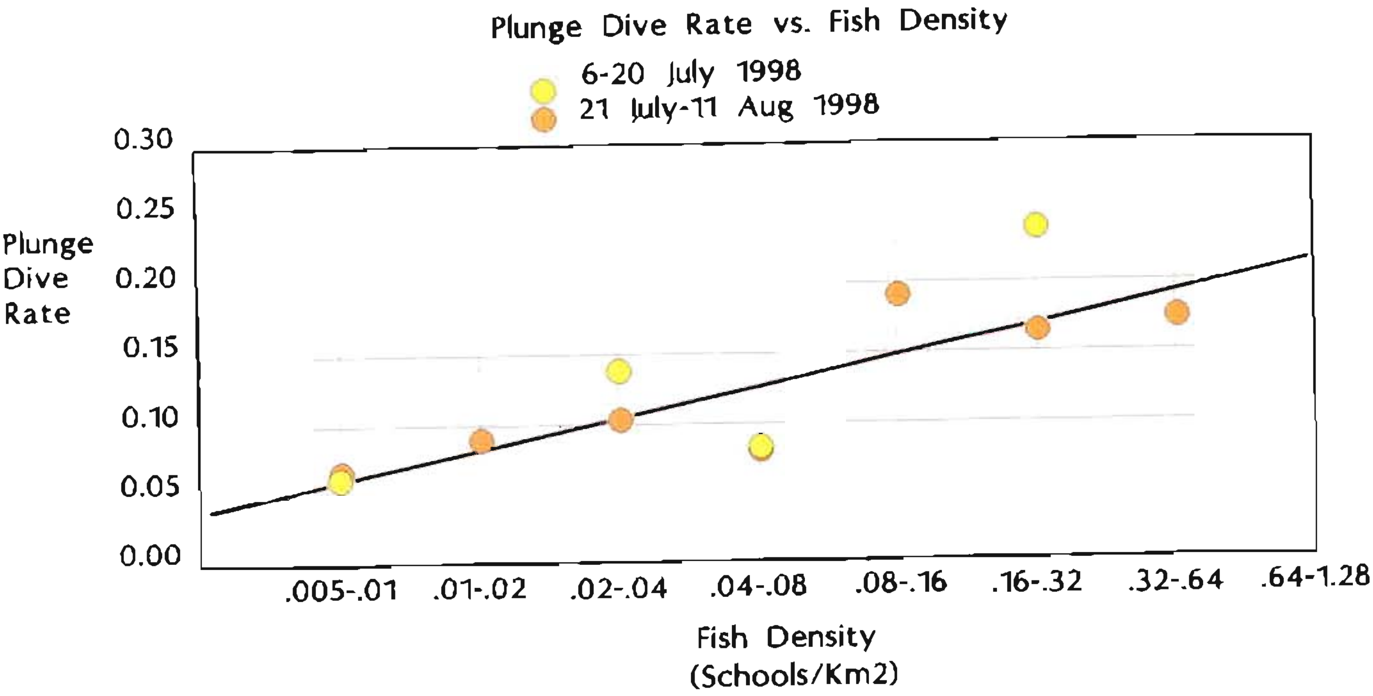

Figure 14. The regression of plunge-dive rate on the density of forage-fish schools in 1998. All observed behaviors initially were binned into seven spatial categories based on the density of forage-fish schools in the 1.5-nm block where kittiwakes occurred. Plunge-dive rate is the proportion of all behaviors that were plunge dives.

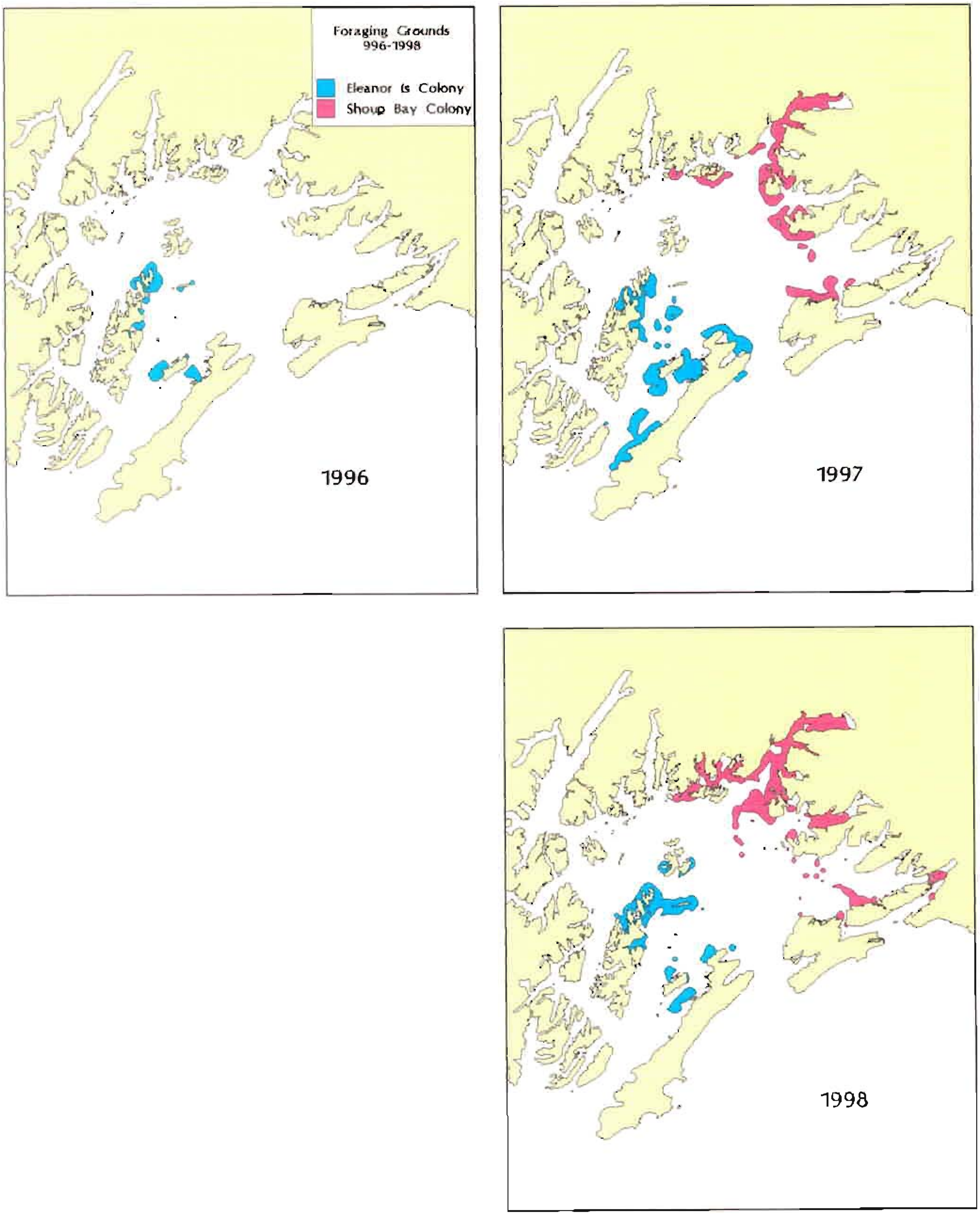

Figure 15. Foraging grounds for the Eleanor Island and Shoup Bay colonies in 1996, 1997, and 1998. Foraging grounds are defined as the minimum areas containing 95% of all observations where the movement rate was less than 25 nm/hr.

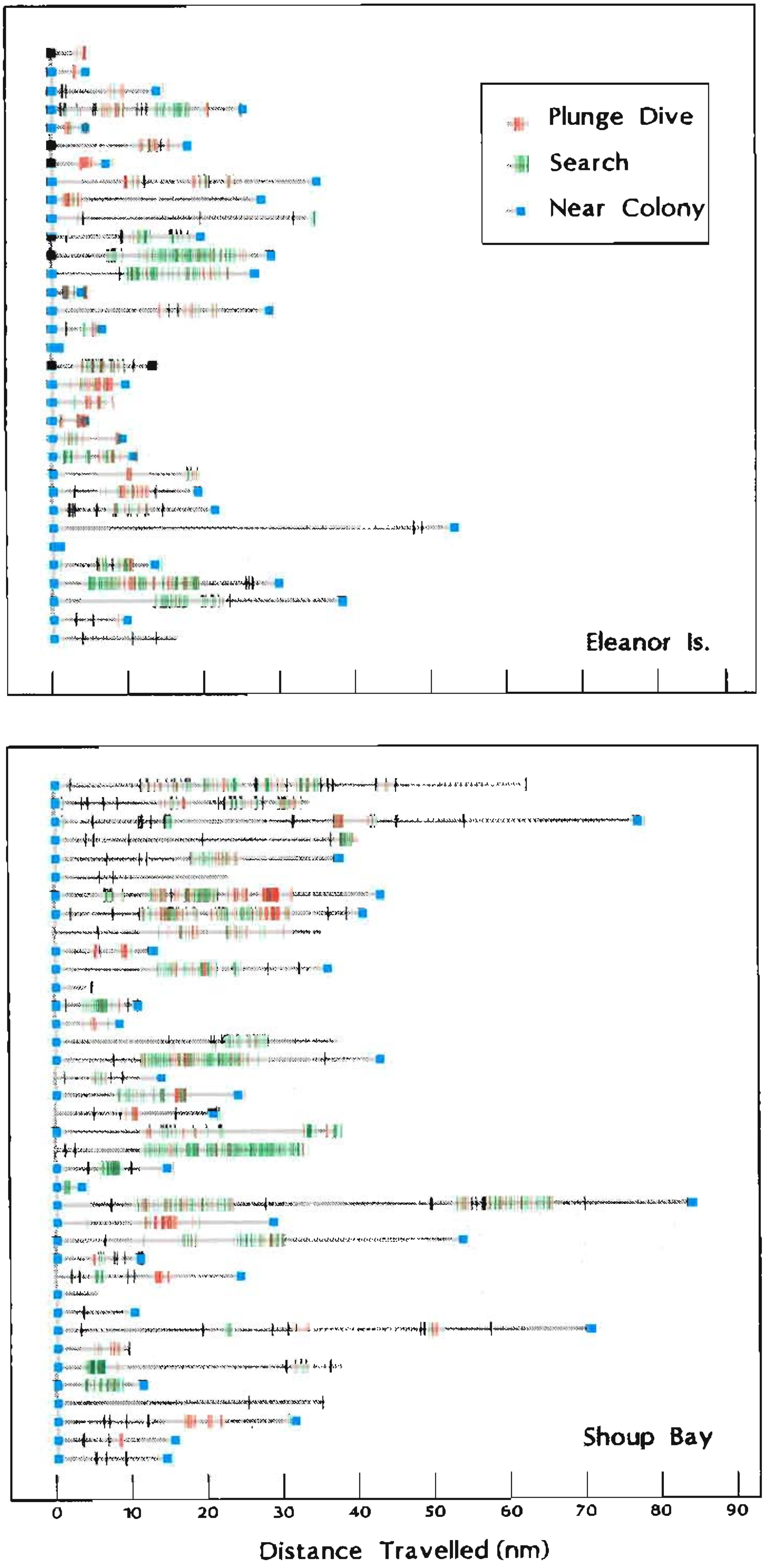

Figure 16. Searching and plunging behaviors displayed as a function of total distance moved on a foraging trip. Data for individual birds from Eleanor Island and Shoup Bay are displayed in the upper and lower panels, respectively. Distance is calculated as the sum of the straight-line distance between one observation and the next.

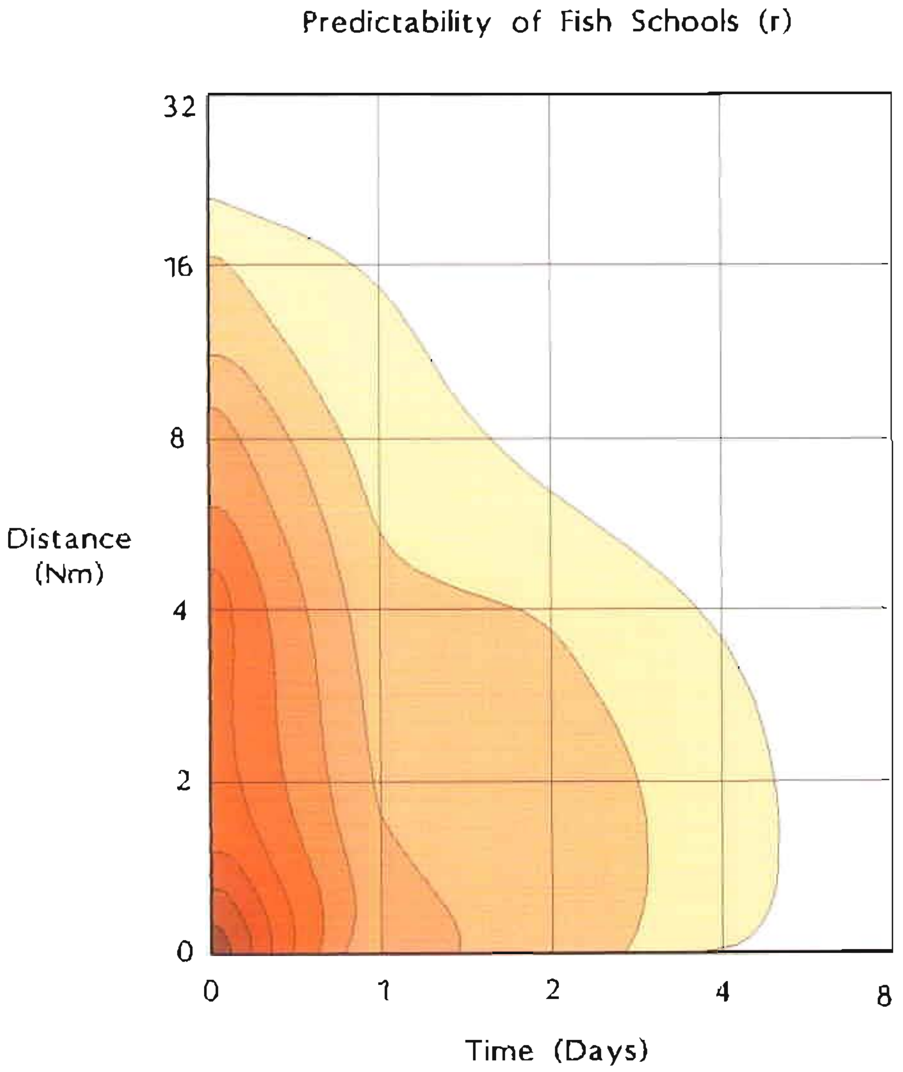

Figure 17. The spatial and temporal; predictability of forage-fish schools. The height of the surface represents the correlation coefficient for the density of forage-fish schools for all pairs of cells separated by a given distance and time.

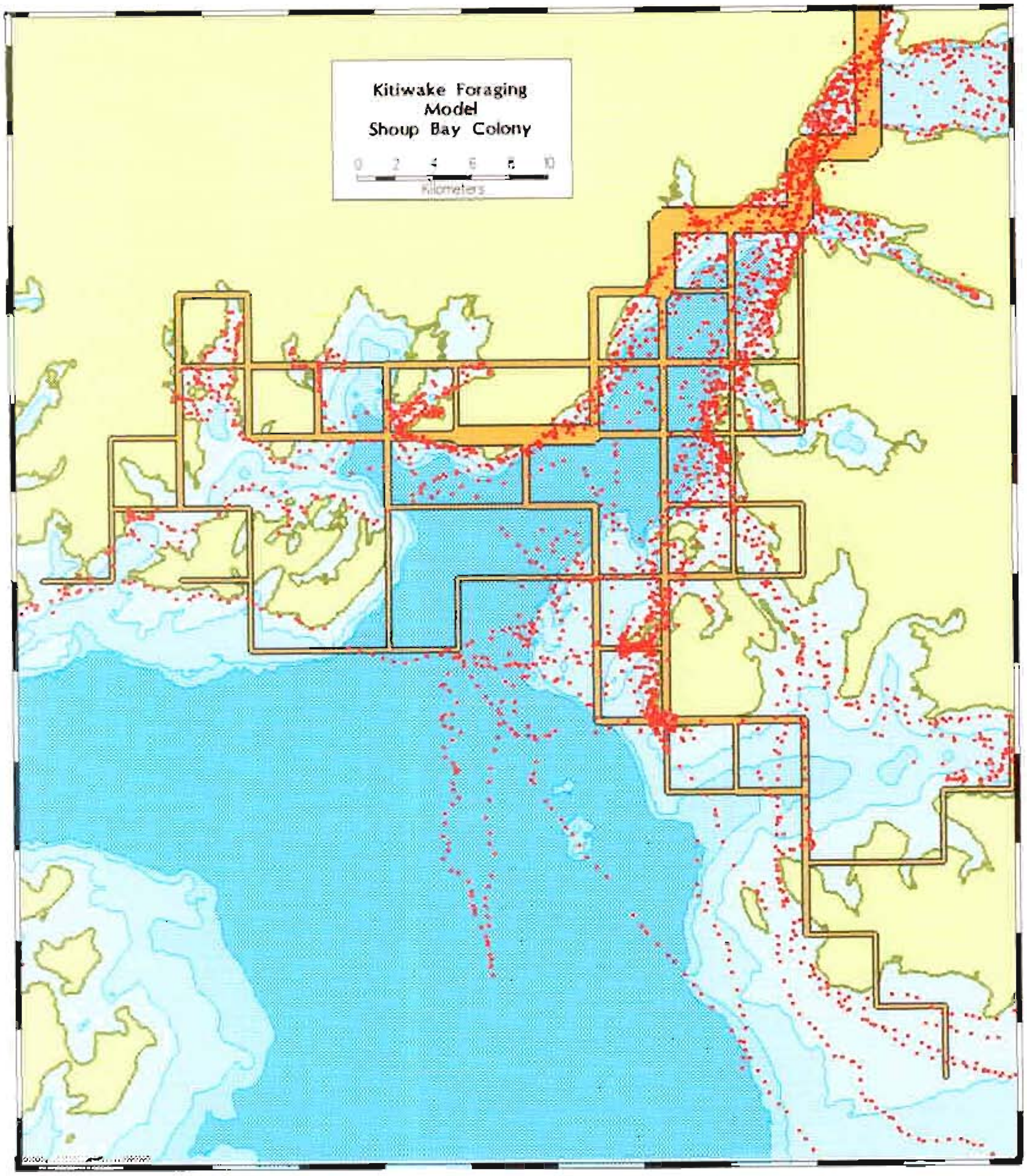

Figure 18. Observed and predicted foraging-trip itineraries for kittiwakes from the Shoup Bay colony. Data points represent sightings of individual birds; lines represent predicted itineraries. The thickness of a line segment is proportional to the predicted frequency of that line segment in the predicted family of itineraries. Predicted itineraries were generated by using "rook's moves" on a square grid.

R Marbled Murrelet

Exxon Valdez Oil Spill
Restoration Project Annual Report

Marbled Murrelet Productivity Relative to Forage Fish Abundance and Chick Diet

Restoration Project 98163R
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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March 1999

Marbled Murrelet Productivity Relative to Forage Fish Abundance and Chick Diet

Restoration Project 98163R
Annual Report

Study History: This project was originally funded in 1997 as a separate restoration project that was coordinated with the APEX study and is currently part of APEX as 98163R. Therefore, 1997 results are incorporated into the 1998 APEX annual report. Project 98163R follows a study that developed the murrelet productivity index (Project 95031; see also Kuletz and Kendall 1998a). Some analyses presented in this report include data from the 1995 project. A pilot murrelet productivity study was presented in Project 94102. Previous murrelet restoration studies, which will be incorporated in the final synthesis for this project, pertained to murrelet nesting habitat; these include Trustee reports 93051B, R15, and various publications.

Abstract:. In Prince William Sound (PWS), Alaska, marbled murrelets (*Brachyramphus marmoratus*) are the most abundant and widely dispersed seabird, but they have not shown recovery since the 1989 oil spill. To determine if food availability is limiting murrelet recovery, we tested for spatial and temporal differences in murrelet productivity in PWS relative to diet and fish abundance. We conducted at-sea surveys to determine juvenile murrelet densities. Forage fish abundance was measured by hydroacoustic surveys (Project 98163A) and aerial counts of fish schools (98163T). In 1995-97 average juvenile murrelet densities at sites were positively correlated with both fish abundance and numbers of fish schools. Data will be reanalyzed with 1998 murrelet data when target strength studies are completed. As in 1997, chicks at Naked were fed primarily Pacific sand lance (88%) and juveniles appeared earlier in the season and were more abundant there ($1.53/km^2$) than at Jackpot ($0.49/km^2$), where chicks received 88% Pacific herring. Galena continued to have the lowest juvenile density ($0.21/km^2$). Fish caught below foraging adults at Naked (N=14 net samples) showed equal amounts of herring and sand lance, however, herring (20-60 mm) were smaller than sand lance (60-90 mm) and may not have been adequate for chick-feeding. The single catch at Jackpot had large herring (120-130 mm), similar to those caught by murrelets at twilight for their chicks. Relative measures of productivity remained consistent among the 3 sites. Peak fledging was later in 1998 than in 1997 and may not have occurred until early September at Jackpot, which was beyond our survey window. Although juvenile murrelet density has not shown extreme fluctuations over 3-5 years (depending on site), it has been sensitive to changes in average fish biomass within a narrow range of approximately 0.4-1.7 g/m^2.

Key Words: *Ammodytes*, *Brachyramphus*, *Clupiedae*, diet, *Gadidae*, forage fishes, foraging patterns, hydroacoustics, juveniles, marbled murrelet, marine surveys, Prince William Sound, productivity.

Project Data: To be addressed in the final report.

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INTRODUCTION

Marbled murrelets (*Brachyramphus marmoratus*) suffered high mortality in the 1989 spill (Piatt et al. 1990, Kuletz 1996), but the spill cannot account for the 67% reduction in numbers observed in post-spill years. The population has not increased since 1989 (Agler et al. 1994) and has shown a downward trend since 1993, with the 1998 population estimate lower than that for 1989 (D. Irons, unpubl. data). Recovery of the PWS marbled murrelet population may be inhibited by an apparent shift in the marine ecosystem of southcentral Alaska that began in the late 1970s (Piatt and Anderson 1997, Kuletz et al. 1997). Seabird productivity is generally acknowledged to be linked to prey abundance, but it is not known if or how the reproductive success of birds in PWS has been restricted by the abundance of forage fish. The goal of this project is to examine the relation between marbled murrelet productivity, diet, and forage fish abundance.

The adaptiveness of seabird behavior, including the implications of central-place foraging and population regulation, have largely been examined through studies of highly colonial seabirds (Furness and Monaghan 1987, Wittenberger and Hunt 1985) . Little is known about how these results apply to non-colonial seabirds such as the marbled murrelet. The low density of marbled murrelet nests and the scattered distribution of murrelets at sea suggest a species that exploits spatially dispersed prey, perhaps at prey densities unsuitable for colonial seabirds. Selection of habitat (Kuletz and Kendall, ms) and fish schools (Ostrand et al. 1998) support this premise, although the implications to murrrelet reproductive success remain speculative. In addition to the relation between murrelets and prey abundance, this study examines murrelet diet and its possible effects on murrelet chronology and productivity. These questions will be examined at spatial and temporal scales within PWS, and will ultimately be compared to other areas of the spill zone.

Preliminary analyses found a significant positive relationship between fish abundance and murrelet productivity (Kuletz and Kendall 1998a). We also found concordance between murrelet chick diet, chronology and productivity in 1997 and 1998. These results are preliminary, however, and await final data on fish biomass for further analysis.

METHODS

Study Area

All study sites were in Prince William Sound (PWS), Alaska, a 10,000 km^2 embayment along the north coast of the Gulf of Alaska. In 1998 we continued monitoring the 3 study sites used in 1997 and in previous murrelet studies. The sites, each approximately 50 km of shoreline, were in the northeast, central and southwest portions of PWS (Fig.1). In 1995 the murrelet study included 3 additional study sites. These were Unakwik Bay (Unakwik), northern Knight Island (Knight) and Port Nellie Juan (PNJ) (Fig. 1). Of these, only Knight overlapped with the hydroacoustic surveys. In 1996, no field work was funded for the murrelet project, but the U.S. Fish and Wildlife Service conducted limited surveys at Naked. Thus, comparisons between murrelets and fish biomass were available for 4 sites in 1995, 1 site in 1996, and 3 sites in 1997. For the 1998 annual report, the only fish data available was the number of fish schools observed during aerial surveys.

The boundaries of the Galena and Naked sites were adjusted in 1997 from those of the 1995 surveys to accommodate changes in nearshore coverage by the hydroacoustic surveys (Galena) or time constraints (Naked). At Galena, we surveyed Galena Bay and shorelines south of Galena, whereas in 1995 we had surveyed Galena Bay and north along Valdez Arm. We treat 1995 and 1997-98 boundaries for the northern area as the same site, because habitats are similar and preliminary analyses showed no significant difference in murrelet abundance or distribution. At Naked, the entire island had been surveyed in previous years (1994-1996) and the east side of Naked, which was not surveyed in 1997-98, had consistently low numbers of murrelets and no juveniles. To avoid bias in among-year comparisons we equalized 1995 and 1996 data by recalculating murrelet densities without the 3 east side transects. At Jackpot, boundaries have remained the same.

Methods

Murrelet productivity

Because marbled murrelet nests are hard to find, we use an index of productivity based on at-sea surveys to obtain juvenile densities and the ratio of juveniles-to-adults (see Kuletz and Kendall 1998b). Because adult murrelets leave breeding areas in August, we counted adults in early June (incubation) and both adults and juveniles in July-August (fledging period). There is a positive correlation between the early June counts and the numbers of fledglings at a site (Kuletz and Kendall 1998a,b)

In 1997 we surveyed each of the 3 study sites 3 times during 31 May-15 June, and 6-8 times during 25 July - 26 August. Each survey took a full day (0700 - 1600 h). We surveyed from 7.5 m vessels traveling 100 m from shoreline. A boat operator and 2 observers recorded all birds and marine mammals 100 m either side of and ahead of the boat. In 1997 and 1998 we entered observations into a laptop computer using the program DLOG (Ecological Consulting, Inc.). The program was integrated with a Global Positioning System, so that every observation had a corresponding latitude and longitude. We also entered behavior codes for each entry indicating if the bird was diving, on water, flying or part of a forage flock.

For murrelets we also recorded plumage, ranging from full breeding to black-and-white in four categories. When we encountered potential juvenile murrelets (black-and-white plumage) we paused to identify the age class and record behavior of the bird, marine and shoreline habitat, and water depth. We assumed that most juveniles observed at a site originated there or nearby. Current information suggests that in PWS the assumption is reasonable during July-August (see Kuletz and Marks 1997, Kuletz and Kendall 1998a). We used the changes in daily numbers of juveniles counted during the July-August surveys as a measure of nesting chronology. Another means of estimating hatching and egg-laying (by backdating) was the numbers of birds holding fish earlier in the summer (see Diet, below).

Fish abundance and species composition

Prior to 1998, we examined fish biomass within specific murrelet study sites by extracting nearshore hydroacoustic transects within a 10 km radius of the center of each murrelet study site. Although we can not be certain that most adult murrelets on the water at our study sites nested in the vicinity,we used the 10 km radius to objectively identify which hydroacoustic transects to include. The 10 km radius was the average straight-line distance traveled between consecutive days for radio tagged murrelets in 1993 and 1994 (Kuletz et al. 1995). For 1995 we used fish biomass values presented in Haldorson et al. (1996). Ken Coyle (Univ. Of Alaska, Fairbanks) provided the 1996 and 1997 data. Once acoustic target-strength studies are completed, we will use that data and re-analyze the earlier relation between juvenile density and fish biomass.

Fish biomass was determined for each transect by K. Coyle as average prey biomass per m^2. Each nearshore hydroacoustic survey block (~ 10 km in length) consisted of a zig-zag series of approximately 1.2 km-long transects. We calculated biomass for each study site using the mean biomass of all transects in the selected nearshore blocks. In 1995, APEX conducted two surveys, of which we used the earlier July survey that best matched the timing of murrelet chick rearing.

A second index of fish abundance was obtained from aerial surveys of PWS conducted by E. Brown (Project 98163T). The aerial surveys provided numbers of schools, and in most cases, school size (surface area), and species identification. In 1997 and 1998 the murrelet crew participated in ground-truthing species identification by filming and sampling fish located by E. Brown. The full use of these data, particularly for fine and micro scale analyses with murrelet data, will not be presented here pending finalization of the data by E. Brown and G. Ford.

Murrelet diet

In 1997 and 1998 we determined chick diet by observing murrelets on the water that were holding fish near dusk. At these times, adults are most likely to capture prey for their chicks and they often hold the single fish on the water for extended periods (Carter and Sealy 1987). Between 6 July and 18 August we conducted 38 'diet cruises', between 1800 - 2200 h, from a 5 m or 7.5 m vessel by slowly traveling through nearshore waters of our study sites. We identified all fish held by murrelets to the nearest taxon possible using binoculars and estimated fish length by the bill length of the bird. We also recorded all murrelets encountered during a diet cruise to obtain a percentage of birds feeding chicks.

Opportunistic diet observations. -- We opportunistically observed adult murrelets feeding themselves during our surveys and while in transit between sites. Additionally, the behavior of birds and their association with forage flocks was recorded during the productivity surveys. We attempted to capture prey below feeding murrelets using a dip net. Prey samples were labeled with date, location and associated feeding activity, frozen within 6 h and transported to Kathy Turco (University of Alaska, Fairbanks) for identification and measurement.

Foraging behavior

The foraging patterns of birds was observed during land-based foraging watches (N = 46 watches, 2-3 h each), with sampling blocks as self and chick feeding periods at Jackpot and Naked. Chick-feeding periods were considered to be before 0900 and after 1700 h. Mid-day was considered to be primarily a self-feeding period. I will test for differences between groups in proportion of diving birds, group size, and diving times of birds.

Capture and marking of juveniles

As a pilot study, we attempted to capture murrelets using a dipnet and spotlights from a boat. This was primarily to gauge the effectiveness of the capture method for juveniles and to attach radio-tags. The goal was to determine the turnover rate of juveniles in the study sites, foraging patterns, and to obtain body measurements of juveniles. Radio tags were donated by the U.S. Forest Service (Juneau). Captured birds were measured, weighed to the nearest gram with pesola hand-held scales, and fitted with USFWS aluminum bands. We glued a 2 g radio tag (Holohill) to the back of the juvenile murrelets. Tracking was done opportunistically by boat on 16 days.

In 1997 we found that, although juveniles remain near shore until about 2300 h, they would swim offshore as darkness approached. At Naked Island, scattered adults and juveniles can be found about 3 km off shore of the west side of the island and north towards Storey Island. A crew of 4 (boat operator, 2 spotlighters, 1 dipnetter) cruised this area at approximately 2400-0330 on 7 nights between 29 July and 12 August.

Data analysis

The primary hypothesis we will test is that murrelet productivity will be higher in areas and in years when forage fish availability is relatively higher. Preliminary analysis from 1995-97 supported this hypothesis (Kuletz and Kendall 1998b)

We conducted preliminary analyses using juvenile murrelet densities. The juvenile:adult ratios will be examined in detail in the final report and manuscripts. For 1995 and 1997, we regressed the average fish biomass at a site in July (main chick rearing period) with the juvenile density at the site during the core fledging period (average of 5 core surveys, primarily early to mid-August). We also examined among-year trends in productivity and fish biomass at Naked Island with 3 years data. At this stage, we provide only descriptive comparisons of juvenile murrelet density vs. number of fish schools counted during aerial surveys, and murrelet diet among areas.

We regressed average juvenile density at a site during 5 core surveys to both average June adult density at a site (sequential surveys) and the average adult density in July-August (concurrent surveys). This was a continuation of a test of the hypothesis that, due to post-breeding dispersal of adults, June (incubation period) counts of adults should correlate better to July-August counts of juveniles than would concurrent counts of adults (see Kuletz and Kendall 1998a). If the relationship remains consistent, we will eventually compare slopes of the regression of the ratio index among sites and years.

RESULTS

During our surveys in 1998 we counted 158 juveniles at the 3 sites. We found most juveniles (89%) as solitary individuals, with no evidence of clumping, although we consistently found juveniles on certain transects. We observed juveniles an average of 61 m from shore in average water depth of 55 m. Most juveniles were in waters adjacent to cobble beaches (51%) or rocky shoreline (28%) or sandy beaches (11%), and in sheltered waters (67%) as opposed to exposed. Only 4% of juveniles were associated with kelp beds. These descriptive results agree with the detailed analyses of habitat associations for both adults and juveniles presented in the attached manuscript (Kuletz and Kendall ms). The final report will test the individual locations of juveniles in 1997-98 against the model derived from 1995 transect data. Analyses presented below are considered preliminary and final results will be subject to additional statistical analyses.

Murrelet productivity and fish abundance

Juvenile murrelet density at sites corresponded to the number of fish schools counted from the air in 1998, as it did in 1997 (Table 1). However, in 1998 the total surface area (m^2) of fish schools was highest per survey day at Jackpot, due to some dense schools of herring there in July. It was not clear if these herring were in the size range appropriate for murrelets. Aerial surveys indicated that Naked had more fish available in August, particularly sand lance. Pacific herring was the most common prey observed within 10 km of Galena and Jackpot, and Pacific sand lance was the primary species around Naked.

Murrelet abundance and chronology

Adult murrelet densities in 1998 were similar to those in 1994-96, leaving the very high numbers observed in 1997 an outlier (Table 2). Compared to previous years, juvenile densities remained high at Naked Island, (1.53/km^2). Jackpot (0.49/km^2) and Galena (0.21/km^2) were both lower than in 1997. Among sites, the relative abundance of juveniles (Naked >> Jackpot > Galena) was similar to that of previous years. For the third time (1995, 1997, 1998), we found a positive relation between June adult densities and juvenile densities among sites in July-August ($R = 0.98$, $P = 0.09$).

The pooled and standardized adult densities (Fig. 2) showed greater temporal variability than in previous years, with peak densities at Naked and Galena occurring in June rather than

July. However, adult murrelet densities again generally declined through August, with the exception of 2 spikes in attendance at Galena. The extreme fluctuations in the daily percentage of juveniles (Fig. 2) occurred despite standardization (to the highest density per site), due to the extreme differences in chronology between Naked and Jackpot. As in previous years, in 1998 juveniles appeared first and peaked earliest at Naked.

Murrelet nest initiation and fledging appeared to be about 1-2 weeks late relative to previous years. During June surveys, 3% of the 1,976 adults (where plumage was recorded). An additional 47% of the birds were in transitional plumages. The plumages indicated differences in chronology among sites. In June, the proportion of birds in basic plumage were 1% at Naked, 2% at Jackpot and 8% at Galena. The proportion of birds in transitional plumage were 40% at Naked, 49% at Jackpot and 61% at Galena. These numbers compare with previous June records of 0.03% in basic and 20-40% transitional.

Murrelet diet

As in 1997, the primary prey fed to chicks was Pacific herring and Pacific sand lance. However, whereas their total proportions were roughly equivalent in 1997, in 1998 total chick-feeding observations were 80% herring, 12% sand lance, 2% capelin and 6% other species. The high percentage of herring occurred because most of the observations of birds during diet cruises were at Jackpot (N = 296; 215 identified), where 88% of the fish were herring. Only 51 birds with fish were observed at Naked (24 identified) where 88% were sand lance.

Incidental observations of birds with fish (N = 61 identified) at all 3 sites showed 41% herring, 52% sand lance, 5% capelin and 2% gadids. Of these, most of the herring were observed at Jackpot (84%) and most of the sand lance (94%) were at Naked.

The 16 dipnetted fish samples we obtained opportunistically show both sand lance and herring at Naked and herring at Jackpot (Table 3). However, at Naked, most of the herring samples were 40-60 mm, while most sand lance were 60-90 mm, with the exception of 1 sample in the 40-50 mm range. Two of the sand lance samples at Naked were taken in the same dipnet sample that contained primarily herring. Only 1 sample, comprised of herring, was obtained at Jackpot and these fish were considerably larger (120-130 mm) than the herring at Naked. This sample was taken below birds feeding in central Jackpot Bay, where murrelets were frequently observed holding fish at night. Based on fish lengths estimated from murrelet bill-length, the fish in this sample were in the same range as the herring held for chicks.

In 1998 the mean number of murrelets holding fish in the evening at Naked was 2.71 (SE = 1.44, N = 25 cruises) per cruise, but was much higher at Jackpot (x = 14.6, SE = 12.91, N = 23). The proportion of birds holding fish jumped dramatically at Jackpot in late July, and continued to be high at our last diet cruise on 26 August. The peak number of birds holding fish (44) occurred on 30 July, and the continued fish-holding through August suggests that peak fledging could have occurred in early September.

Foraging observations

The results of the forage watches will be presented in a later paper. To determine if murrelets alter their foraging and other activities when feeding chicks, I will test for differences in proportion of diving birds, group size, and diving times of birds.

The behavior of individual birds observed during the boat-based productivity surveys will also be used to test for differences in foraging patterns between sites of low and high fish density. Preliminary examination indicates that birds foraging at Naked were more likely to be associated with feeding flocks (46% of 115 observations) than murrelets at Jackpot (22% of 88 observations). Because we surveyed each site repeatedly, often in conjunction with aerial fish surveys, it will also be possible to test the relation between murrelet distribution and the predictability as well as immediate distribution of forage fish. These relationships will be examined at various spatial scales.

Juvenile murrelet catch and tracking effort

At Naked Island we caught 5 adults and 4 juvenile murrelets over 7 nights, averaging 1.28 birds/ night and catching 0-4 birds on a given night. The juveniles were caught on the 5 and 11 of August and averaged 136 g (SD = 17). Average weight for adults was 231 g (SD = 16). Radio-tags were glued to the juveniles and the birds were tracked by boat as time and weather allowed. The 2 juveniles caught on 5 August were last detected on 12 August (8 days). One bird tagged on 11 August was not detected after the night of release and the other was last detected on 14 August (4 days). Because a series of storms and our survey responsibilities interfered with tracking efforts, these should not be considered accurate estimates of turnover rates. We did make visual contact with 2 birds and obtained limited habitat use data.

DISCUSSION

In both 1997 and 1998, measures of murrelet productivity have generally been consistent with the relative counts of fish schools among these sites, although the large schools of herring at Jackpot in July 1998 is inconsistent with this pattern. Aerial surveys also support the pattern of sand lance availability at Naked, and the availability of both herring and sand lance later in summer at this site, compared to Jackpot and Galena. Late summer availability of forage fish may enhance murrelet productivity and/or juvenile survival at Naked.

It is unclear why large numbers of birds were observed holding fish for chicks in central Jackpot Bay, and yet few juveniles were observed in that entire study area. Additionally, the aerial surveys did not detect schools of herring at Jackpot in August. Because the murrelets were taking these fish in the late evening, perhaps vertical migration of the fish made them difficult to detect from the air. Carter (1984) suggested the murrelets in British Columbia switched, when chick-feeding, to smaller patches of large fish that rose to the surface at twilight. Rhinoceros auklets (*Cerorhinca monocerata*) display a similar shift in foraging technique when provisioning chicks (Davoren and Burger, in review) .

At Naked, the exclusive use of sand lance to feed chicks could be related to size differences in the fish and not solely a species preference. The herring at Naked were below the size range used for murrelet chicks, whereas the sand lance were consistent with observations in other regions (review in Burkett 1995). Adults were clearly taking both herring and sand lance when self-feeding, but were feeding their chicks the larger sand lance. The late chick-rearing period at Jackpot may thus be a response not just to fish availability (since herring were observed there in July), but the length of time necessary for juvenile herring to reach adequate size for chicks. However, the herring held for chicks at Jackpot appeared to be near the size limit used by murrelets, and might have been too large for the smaller chicks. Large fish, including herring, have been known to choke the chicks of other birds in PWS (Golet, unpubl. data).

Whether murrelets foraging in the evening at Jackpot were from other areas or nesting locally, our results suggest that murrelets in the region would have been fledging chicks late in the summer, and possibly into mid-September. Our surveys could thus have underestimated productivity at Jackpot, since we could not survey beyond late August. If these chicks fledged successfully, they might have met with less than optimum conditions due to poor weather and possibly low fish availability nearshore. Both the timing and sizes of fish available are important, and any model of murrelet recruitment should incorporate the dual needs of adults foraging for themselves and those foraging for chicks (review in Ydenberg 1994).

Juvenile capture and measurements

The limited data we obtained in this pilot study, when combined with other data available on juvenile murrelets, suggest that juveniles are near the edge of survival when they fledge. Juveniles fledge at 57-70% of adult weight (Hamer and Nelson 1995; Kuletz unpubl. data). Three juveniles found dead in the water in August (1995-98) weighed 90-115 g. , not much less than the 117 g chick weighed in the nest the day before fledging (Kuletz and Marks 1997). Two juveniles found in forests on Kodiak Island averaged 120 g (SD = 4; unpubl. data). In contrast, the 4 juveniles we caught at sea were 136 g (SD = 17) with the heaviest at 153 g. Although these data are anecdotal, they suggest that weight gain immediately after fledging is critical for early survival of juvenile murrelets. Juveniles have shorter dive times (Kuletz and Marks 1997, Kuletz et al. 1995) and prefer shallow, protected water close to shore (Kuletz and Kendall, ms) or within kelp beds (Kuletz and Piatt, in press). Their lower diving capabilities may require that fish of adequate size be available in these habitats during the first critical weeks of fledging.

Summary

Diet was again associated with murrelet nesting chronology. Both fish-holding and the appearance of juveniles indicated that murrelets at Naked initiated nests and fledged chicks 1-2 weeks earlier than murrelets at Jackpot or Galena. Fledging began and peaked earliest at Naked, where sand lance appeared to be available throughout the breeding season. At Naked, the single peak occurred late (10 August) compared to 1995-97. At Jackpot, where herring use predominated, most of the juveniles did not appear until mid to late August. The timing of fish availability may have been more important than differences in prey quality.

Although there were significant and consistent differences among sites in juvenile density, the variance within sites has been relatively low, or at least lacking in 'boom and bust' years characteristic of many seabirds. However, based on preliminary analyses using backscatter estimates of total fish biomass, the fluctuations in murrelet productivity that we observed have been sensitive to fluctuations in prey abundance within a fairly narrow range. At these sites, average fish biomass has ranged from 0.2 to 1.7 g/m^2, with the steepest change in juvenile density occurring between 0.4 and 1.7 g/m^2. This suggests that, although murrelets can be successful in a region with an average low fish biomass (compared to an area like Lower Cook Inlet), the PWS population might be negatively affected by even slight decreases in biomass beyond what has been recorded during APEX studies.

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LITERATURE CITED

Agler, B. A., S. J. Kendall, and D. B. Irons. (In Press, 1998). Abundance and distribution of marbled and Kittlitz's murrelets in southcentral and southeast Alaska. Condor.

Burkett, E.E. 1995. Marbled murrelet food habits and prey ecology. Pages 223-246 In: C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report, PSW-GTR-152.

Carter, H. R. 1984. At-sea biology of the marbled murrelet (*Brachyramphus marmoratus*) in Barkley Sound, British Columbia. Thesis, University of Manitoba, Winnipeg, Manitoba, Canada.

Carter, H. R., and S. G. Sealy. 1987. Fish-holding behavior of marbled murrelets. Wilson Bulletin 99:289-291.

Davoren, G.K. and A.E. Burger. In review. Differences in prey selection and behavior during self-feeding and chick provisioning in rhinoceros auklets. Submitted to Animal Behavior.

Furness, R. W., and P. Monaghan. 1987. Seabird ecology. Chapman & Hall, New York, New York, USA.

Furness, R. W. and D. N. Nettleship. 1991. Seabirds as monitors of changing marine environments. symposium 41, ACTA XX Congressus Internationalis Ornith. New Zealand Ornithological Congress.

Haldorson, L., T. Shirley, and K. Coyle. 1996. Biomass and distribution of forage species in Prince William Sound. APEX Project 95163A annual report. University of Alaska, Fairbanks, Juneau .

Hamer, T. E., and S. K. Nelson. 1995. Nesting chronology of the marbled murrelet. Pages 49-56 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report, PSW-GTR-152.

Kuletz, K.J. and S.J. Kendall. 1998a. Marbled Murrelet productivity relative to forage fish abundance and chick diet. *Exxon Valdez* oil spill restoration project annual report, Project 97231. U. S. Fish and Wildlife Service. Anchorage, Alaska, USA.

Kuletz, K.J. and S.J. Kendall. 1998b. A productivity index for marbled murrelets in Alaska based on surveys at sea. Journal of Wildlife Management 62(2):446-460.

Kuletz, K.J., D. Irons, J.F. Piatt, B. Agler, and D.C. Duffy. 1997. Long-term changes in diets and populations of piscivorous birds and mammals in Prince William Sound, Alaska. Pages 703-706 In: Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the role of forage fishes in marine ecosystems. Alaska Sea Grant College Program Report No. 97-01. University of Alaska Fairbanks, 1997.

Kuletz, K. J. and J.F. Piatt. In press. Juvenile marbled murrelet nurseries and the productivity index. Wilson Bulletin.

Kuletz, K. J. 1996. Marbled murrelet abundance and breeding activity at Naked Island, Prince William Sound, and Kachemak Bay, Alaska, before and after the *Exxon Valdez* oil spill. Pages 770-784 *in* S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright, editors. Proceedings of the *Exxon Valdez* oil spill symposium. American Fisheries Society Symposium 18.

_____, and D. K. Marks. 1997. Post-fledging behavior of a radio-tagged juvenile marbled murrelet. Journal of Field Ornithology 68:421-425.

_____, _____, R. A. Burns, L. M. Prestash, and D. A. Flint. 1995a. Marbled murrelet foraging patterns and a pilot productivity index for murrelets in Prince William Sound, Alaska. *Exxon Valdez* oil spill restoration project final report, Project 94102. U. S. Fish and Wildlife Service. Anchorage, Alaska, USA.

Ostrand, W.D., K.O. Coyle, G.S. Drew, J.M. Maniscalco, and D.B. Irons. 1998. Selection of forage fish schools by murrelets and tufted puffins in Prince William Sound, Alaska. Condor 100:286-297.

Piatt, J. F., C. J. Lensink, W. Butler, M. Kendziorek, and D. K. Nysewander. 1990. Immediate impact of the *Exxon Valdez* oil spill on marine birds. Auk 107:387-397

_____, and P. Anderson. 1996. Response of Common Murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem. In: S.D. Rice, R.B. Spies, D.A. Wolfe, and B.A. Wright (eds). *Exxon Valdez* Oil Spill Symposium Proceedings. Am. Fish. Soc. Symp. No. 18.

Wittenberger, J.F. and G.L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. Pages 1-77 In: Famer, D.S., J.R. King, and K.C. Parkes (eds). Avian Biology Vol. 8.

Ydenberg, R.C. 1994. The behavioral ecology of provisioning in birds. Ecoscience 1(1):1-14.

FIGURES

Figure 1. Marbled murrelet study sites in Prince William Sound, Alaska, in 1995 (6 sites) and 1997 - 1998 (Galena, Naked, Jackpot). Shoreline areas surveyed, and pelagic transects at Naked Island and Port Nellie Juan, are shown in black. The circles are the 10 km radius used to determine fish abundance.

Figure 2. Standardized adult murrelet densities (bars) and the daily percentage of juveniles (line) for three study sites in PWS, Alaska, in 1998.

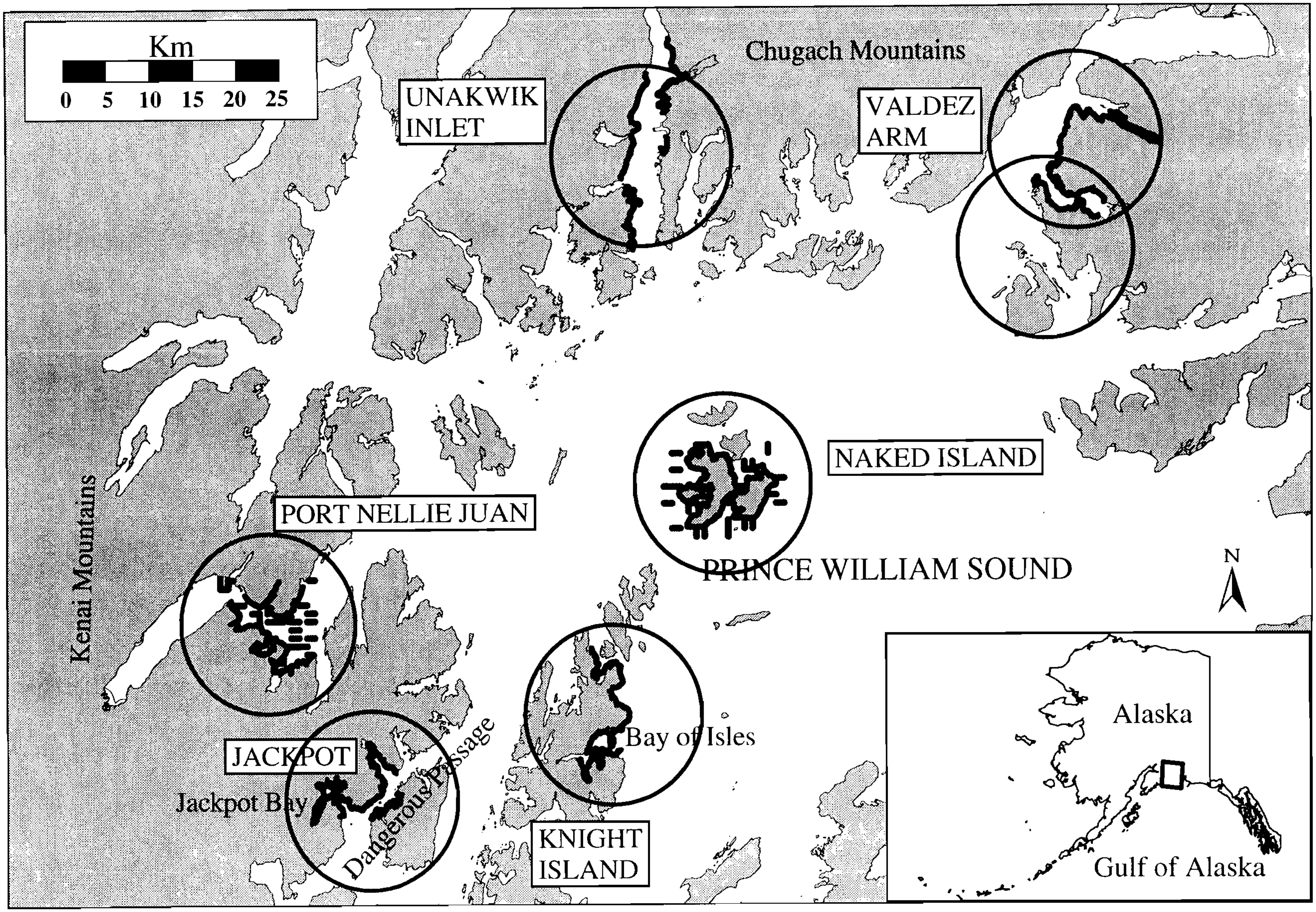
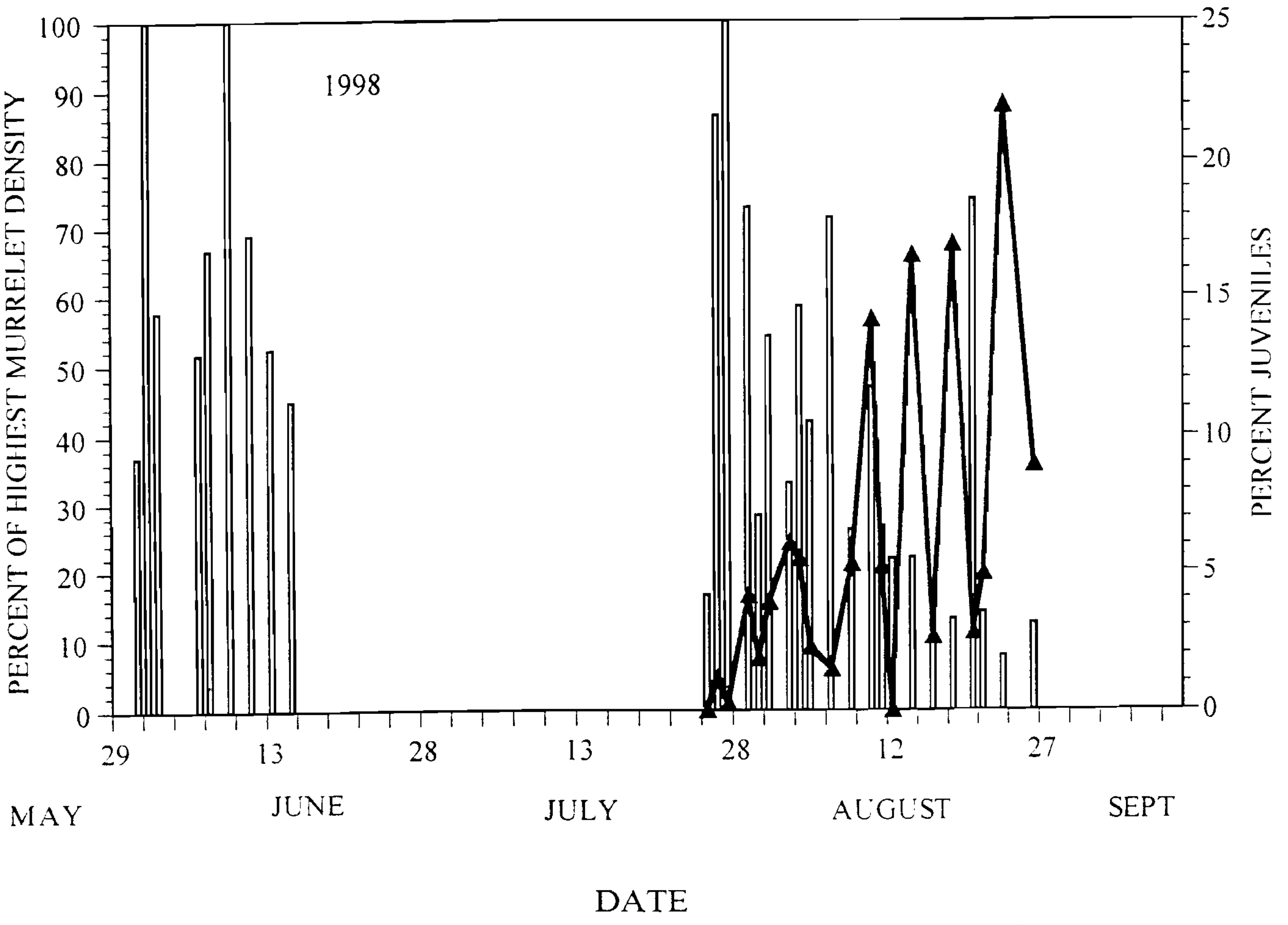

Km
0 5 10 15 20 25
UNAKWIK INLET
Chugach Mountains
VALDEZ ARM
NAKED ISLAND
Kenai Mountains
PORT NELLIE JUAN
PRINCE WILLIAM SOUND
N
Bay of Isles
JACKPOT
Jackpot Bay
Dangerous Passage
KNIGHT ISLAND
Alaska
Gulf of Alaska

Figure 1



1998
PERCENT OF HIGHEST MURRELET DENSITY
100
90
80
70
60
50
40
30
20
10
0
PERCENT JUVENILES
25
20
15
10
5
0
29
13
28
13
28
12
27
MAY
JUNE
JULY
AUGUST
SEPT
DATE

Table 4. Total numbers of key species sighted from the air by day, 1998.

Month	Day	Alcids	GW*	Kittiwakes	DP*	HS*	HW*	Orcas	Sea Lions	Sea Otters	Capelin	Eulachon	Herring	Sand Lance	Jellyfish
July	6	3	2	1062		1			7	2			43	2	67
	7	12	11	2119	4	4			161	26			96	26	88
	8			1617					13	35			65	35	40
	10	308		4013	2	51	10		39	34	10	5	41	34	7
	11	3		1698			5		5	36	18		16	36	14
	12	1723		4906		81	2		39	104	18		74	104	47
	13	100		5764	7		1	8	15	107	7	17	124	107	5
	14	17		522					4	5			11	5	11
	15			1552	2				9	17			104	17	52
	16	23		1401					218	16			56	16	45
	17	2		887			1		2	8			49	8	36
	18	224		2384		8	8		60	165		1	25	165	16
	19	164		2492			10		47	185			34	185	133
	20	16		393			1		1	11			2	11	3
	23	22	45	1364				3	18	11			41	11	8
	24	151	37	1550	4	3			224	12			21	12	11
	26	107		4759			7		208	151			9	151	3
	28	110		1267		1	2			157			39	157	42
	30	292	21	3385		2	7	2	135	125			156	125	25
	31	281	7	1552					30	8			11	8	22
July Total		3558	123	44687	19	151	54	13	1235	1215	53	23	1017	1215	675
August	1	209	38	930					7	2			2	2	5
	3	122	1	1885			7		6	71			116	71	15
	4	257		2934		90	3	1	70	61			130	61	39
	5	202	4	2599		96	5		52	50			84	50	14
	7	136	2	1462					20	1			15	1	4
	8	175	4	1467					104				41		1
	9	105	5	1632					84	12			23	12	4
	10	401		612					19	4			17	4	
	11	58		156											13
August Total		1665	54	13677		186	15	1	362	201			428	201	95
Grand Total		**5223**	**177**	**58364**	**19**	**337**	**69**	**14**	**1597**	**1416**	**53**	**23**	**1445**	**1416**	**770**

- GW = Glacous-Winged Gulls, DP = Dahl Porpoise, HW = Humpback Whales, HS = Harbor Seals

Environmental Factors and Marine Habitat Associations of Adult and Juvenile Marbled Murrelets in Prince William Sound, Alaska : Implications to Monitoring Murrelet Productivity

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ABSTRACT

Monitoring the reproductive success of a non-colonial seabird poses special problems. For the marbled murrelet (*Brachyramphus marmoratus*), a threatened species along the eastern Pacific coast, productivity is measured by surveying juveniles at sea during the fledging period. Power to detect trends in juvenile murrelet densities are usually low, due to their low numbers and dispersal at sea. One way to reduce variance in counts would be to determine if juveniles exhibit habitat preferences, and if so, stratify survey effort by habitat. I examined the influence of habitat and survey conditions on juvenile murrelet densities at six study areas in Prince William Sound (PWS), Alaska. The areas, comprised of shoreline transect sections, were surveyed 7-10 times each in July and August 1995. I used stepwise multiple regression to model both adult and juvenile densities at the transect level. Based on the most parsimonious model, I used analysis of deviance tests on logistic regression models to select the best predictor of presence or absence of juveniles. In preliminary models, Area effect was an overwhelming factor, necessitating nested analyses. Weather-related, surface marine conditions, and tidal state did not significantly add to the models. The best model for juvenile density included shoreline type, exposure, and water depth. In PWS, juveniles are most likely to occur along rocky shoreline with moderate exposure and relatively shallow waters. Water depth was the only significant predictor variable for adults, once Area and date effects were controlled. The best habitat models explained 36% of the variance in juvenile numbers and 23% of adult numbers. Variability in counts of juveniles can probably be reduced by stratifying habitats for surveys, however, a large amount of variability was unexplained. Area effect was clearly important, suggesting that monitoring efforts should be built around a core of consistently productive sites. Further, Area could be incorporated as a stratifying factor in a monitoring scheme. Factors not included in these analyses, such as local inland nesting habitat and forage fish availability, likely are important to juvenile murrelet distribution.

INTRODUCTION

The conservation of threatened and endangered species requires adequate monitoring of population trends. For most seabird species, it is possible to study reproductive success because they nest in dense colonies (Wittenberger and Hunt 1985) . Non-colonial species, such as the marbled murrelet (*Brachyramphus marmoratus*; Alcidae), however, pose a special problem.

This small diving seabird nests inland, typically in the branches of old-growth trees. Murrelets are noncolonial, widely dispersed, and they conduct much of their nesting activity in darkness or twilight. Once fledged, the chick is on its own, with no obvious parental association. These behaviors have hindered study of marbled murrelet reproduction (Nelson 1996, Ralph et al. 1995).

Currently, the most practical option for studying the reproductive performance of marbled murrelets is to count juveniles at sea during the fledging and early juvenile period (Kuletz and Kendall 1998, Ralph and Long 1995, Strong et al. 1995). Power to detect changes in juvenile murrelet abundance is generally low, unless multiple sites are surveyed within a region, or where adult murrelet abundance is high (approximately >10 birds/km^2; Kuletz and Kendall 1998). Power to detect changes in juvenile densities would be most improved by reducing variance in juvenile counts during a 3 to 5-week core survey period (Kuletz and Kendall 1998).

Reduced variability in survey data can be achieved by standardizing protocol and by stratifying sampling effort. Counts of murrelets and other seabirds are potentially influenced by factors that affect observability, such as seas, rain, sun glare, and observer expertise. Seabird abundance is influenced by fluctuating or cyclic environmental conditions such as weather, daylight, tides, season, water temperature, salinity and clarity, and prey abundance (Carter and Sealy 1990, Hunt et al. 1993, Schneider and Piatt 1986). Seabirds may also be associated with stable habitat features, such as shoreline type, exposure, and water depth (Tyler et al. 1993, Vermeer et al. 1992). Adults and juveniles may exhibit different distribution patterns at sea (Gaston and Nettleship 1981), and juvenile murrelets in some areas appear to remain closer to shore than adults (Anderson and Beissinger 1995, Sealy 1975, Strachen et al. 1995), suggesting different habitat selection among age classes.

Many habitat and environmental factors may be correlated. For example, rough seas, which can affect seabird foraging (Furness and Monaghan 1987), are more typical along exposed coasts, and forage fish species may be associated with certain shoreline substrates (Robards et al., submitted). Identifying key habitat features associated with murrelets or their prey would allow stratification of sampling. Furthermore, knowledge of important effects on observability can lead to a more effective survey protocol. By reducing variance in murrelet counts we can reduce survey effort and improve our ability to make statistical comparisons. For murrelets, the ratio of juveniles to adults counted on the same surveys is often used as an index of productivity (Anderson and Beissinger 1995, Ralph and Long 1995, Strong et al. 1995). Because ratios would be sensitive to age-specific differences in habitat use, it is important to determine if adult and juvenile habitat use is similar during the survey period.

In this paper I examine at-sea counts of murrelets, particularly juveniles, to determine if environmental factors can be identified that might guide survey protocol or the stratification of habitats to reduce variance in counts. To do this I examined data I collected in 1995 in Prince William Sound, Alaska.

METHODS

Study Area. --The study was conducted in Prince William Sound (PWS), Alaska, a large embayment with approximately 3,000 km of shoreline, in the northern Gulf of Alaska. The area is characterized by deep, relatively protected waters, numerous islands, bays, and fjords, and glacial influence. Tree line is at 30-600 m elevation, and forests include Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*T. mertensiana*). Unforested areas include bog meadows, willow and alder thickets, or barren rock. Study sites (Fig. 1) included stretches of shoreline at Unakwik Inlet (Unakwik), Valdez Arm (Valdez), Naked Island (Naked), Port Nellie Juan (PNJ), Knight Island (Knight), and Dangerous Passage-Jackpot Bay (Jackpot).

Each study site had between 45 and 60 km of shoreline, and included a variety of habitats. Unakwik, a mainland fjord, has a tidewater glacier at its terminus, and water depths to 350 m, but it is divided midway up its length by a 10 m deep sill. Valdez, a fjord on the northeastern mainland, includes 2 large bays off the main channel, which is 400 m deep. Naked and Knight are large islands in western PWS. Naked has 4 large bays and is surrounded by waters <100 m deep within 1 km of shore. The portion of Knight we surveyed has exposed shoreline with water 200 m deep within 1 km of shore but includes a narrow passage and the highly convoluted Bay of Isles with shallow, protected water. Port Nellie Juan, a fjord on the western mainland, is up to 700 m deep, bordered by steep mountains to 1,700-m elevation, with 1 tidewater and 7 hanging glaciers. Jackpot, in southwest PWS, includes 2 sheltered bays and shoreline along Dangerous Passage, which is 170 m deep.

Mean air temperature during our surveys ranged from 12.4 to 14.1°C, surface water temperature ranged from 8.9 to 13.0°C and surface salinity ranged from 9.5 to 25.2 o/oo. Tidal range was approx 5 m at all sites, but the intensity of tidal flow varied greatly, depending on local topography and bathymetry (Burrell 1987).

We distributed study sites to sample from a variety of habitats and to minimize foraging overlap by marbled murrelets raising chicks. Site boundaries were $\geq$16 km apart (straight-line distance), the mean foraging range for radiotagged marbled murrelets in PWS (Kuletz et al. 1995), and greater than the distance a radiotagged juvenile moved over 2 weeks after fledging from its nest (Kuletz and Marks 1997).

Data Collection - Murrelet Densities

We surveyed each site 7-10 times between 18 July and 28 August. Each survey took a full day (0700 - 1600 h). Two crews, operating independently, surveyed from 7.5 m vessels traveling 100 m from shoreline. A boat operator and 2 observers recorded all birds 100 m either side of and ahead of the boat. We usually surveyed each site about every 3-4 days, with crews rotating among sites to minimize observer bias. Due to weather and logistic problems, we occasionally missed sites on a survey rotation, resulting in uneven sample sizes.

Juvenile marbled murrelets look similar to adults in winter plumage. When we encountered potential juvenile murrelets (in black-and-white plumage) we paused to identify the age class. I refer to hatching-year birds as 'juveniles', and after-hatch-year birds as 'adults', although the latter category includes non-breeding and sub-adult birds that can not be distinguished visually (Sealy 1975).

I standardized marbled murrelet counts as densities (birds/km^2) to compensate for differences in transect lengths or the occasional inability to complete sections of shoreline due to poor surveying conditions.

Data Sources for Environmental Conditions and Habitat Features

I examined the associations between murrelets and environmental or habitat features using data available for shoreline sections. Each Area (45-60 km of shoreline each) was divided into 9-18 transects (x = 4.7 km in length; range 1-9 km). These shoreline transects had been digitized to a geographic information system (GIS). Transect boundaries generally followed land forms, so boundaries were typically defined by prominent points, bays and shorelines with different exposures.

Prior to each transect we recorded time, sea state, swell height, wind speed and direction, precipitation, percentage cloud cover, sunglare, observer conditions, and sea surface temperature (SST). On each survey day we used a minimum of 4 stations to collect data on water clarity using a secchi disk (SECCHI) and sea surface salinity (SSS) with a digital conductivity meter. To derive time relative to sunrise or tidal state, I used the start time and date of each transect in Paradox scripts (Borland International 1992). The Paradox script calculated tide as hours from low tide. For analysis I used the 12-hour tide divisions to create 3 additional tide variables in 6-hour blocks (ebb vs flood), 3-hour blocks, and 2-hour blocks. Tide Range for the day was included as a separate variable, using a tide table for Cordova, PWS.

Because we did not take environmental measurements on every transect, for some analyses I used the day's average measure of salinity (xSSS) and water clarity (xSECCHI). Preliminary analyses indicated that these measurements did not vary significantly within an Area on the same day, with the exception of transects near tidewater glaciers in Unakwik and PNJ. For analyses that examined specifically the influence of SSS, SST and SECCHI on murrelet abundance at the transect level, I used only those transects with all measurements.

Static habitat features included water depth, shoreline type, and exposure. Water depth was obtained from GIS coverage of PWS given in 20 m increments from 0-120m depth, and increasingly larger increments from 120 to 450 m. Using GIS, S. Kendall (USFWS, unpubl. data) determined the area covered by each depth category from 0-200 m offshore of the transect, to provide a weighted depth (DEPTH) for each transect. I also used the maximum depth (MaxDepth) of the transect as a separate variable.

Shoreline type (SHORE) was obtained from GIS coverage resulting from surveys conducted by the Alaska Department of Natural Resources. The three categories of SHORE included 1) fine grain/sand beaches, 2) coarse grain/cobble beaches, and 3) rocky shore. Exposure (EXPOSURE) of transects (defined by D. Irons, USFWS, unpubl. data), was the perpendicular distance from transect midpoint to the nearest point of land beyond the transect shoreline, based on nautical charts. The three EXPOSURE categories were <1 km, 1-5 km, and >5 km from transect midpoint to nearest land.

Data Analyses

For statistical tests I used S-Plus (MathSoft 1997). I used the Spearman's correlation coefficient (*r*) to test for significant correlations between variables. Murrelet densities by transect were generally very low and highly skewed, particularly for juveniles (Fig. 2), therefore, I transformed murrelet densities (ln X+.01) for multivariate analyses. Because the independent variables included categorical and continuous variables I used the general linear model (GLM). First, I used stepwise linear regression (SLR) to develop the best model from among all variables. Second, I tested the best predictors with logistic regression models, using GLM for a binomial distribution and analysis of deviance goodness of fit tests for significance. For all tests, alpha = 0.05.

Selection of datasets for different models. -- Juvenile occurrence was rare during early surveys, and at some sites, juveniles did not appear until the second week, presumably due to differences in local chronology (see Kuletz and Kendall 1998). To minimize the effect of high numbers of zero values, I selected surveys (from 833 total) that occurred after at least one juvenile had been observed at all sites, so that n = 474 transects (dataset T474). Zero values for juveniles, however, remained high. I then eliminated all transect surveys where no juvenile was observed, resulting in a sample size of 242 (dataset NOZEROS). In the final SLR models, it was necessary to drop Knight transects if SHORE was included in nested analyses, because all Knight transects where juveniles occurred had the same SHORE type, resulting in inestimable effects; for this reduced set, n = 221 (dataset NOKNIGHT). I returned to the T474 dataset for logistic regression (predicting presence/absence of juveniles), because it contained transects with no juveniles.

RESULTS

Correlations between variables. -- Variables that could potentially affect observability during surveys, such as sea conditions, precipitation (included in observer conditions), and glare, showed little correlation with adult or juvenile densities (Table 1). Juvenile densities were not correlated with marine features such as tidal state, SST and SECCHI, although juveniles were weakly correlated with SSS. Adults were negatively correlated with SST and SECCHI. Sea surface variables were also correlated with date.

Among stable habitat features (Table 1), EXPOSURE tended to be associated with higher Seas, Swell height, and poor observer conditions (although this did not appear to result in significant affects on murrelet densities). Deeper waters tended to be found off rocky shores, with shallow waters in the inner bays with fine grained beaches. The lower SSS and SECCHI relationship to deeper waters is likely due to the glacial runoff in some deep fjords. Juvenile densities were significantly, but not strongly, correlated to adult densities at the transect level ($r=0.33$, $P < 0.001$).

Stepwise Linear Regression

Preliminary models. -- In preliminary models, Area explained most of the variance for both juvenile and adult densities, and the contribution of other variables could not be estimated. For juveniles, one regression that loaded 13 unnested predictor variables appeared to make a good fit ($R^2 = 0.34$, $F_{7,60} = 4.45$, $P = 0.0004$), but the only significant predictors in the final model were Area ($F = 4.36$, $P = 0.002$) and MaxDepth ($F = 7.13$, $P = 0.01$), which was correlated with Area. Similarly for adults, a preliminary regression with all variables, and not including Area, was significant ($R^2 = 0.39$, $F_{3,64} = 14.4$, $P < 0.0001$), but the primary predictor was Date ($F = 31.5$, $P < 0.0001$). Adults leave PWS at a steady rate in late summer (Kuletz and Kendall 1998), so this exodus would overshadow habitat associations. A regression that omitted Date only explained 17% of the variance, and the best predictor was SST, which was significantly correlated with date. I could not account for nesting habitat, large scale oceanographic features, or prey availability at the study sites. Because my goal was to identify physical features associated with juveniles at a finer scale, while controlling for inherent productivity of an area, regressions were subsequently nested by Area, and Date was not included.

Best-fit models. -- Even when sea surface variables (SST, SSS, SECCHI) and tide were nested by Area, the model was a poor predictor of juvenile abundance ($R^2 = 0.16$, $F = 2.7$, $P = 0.03$), and only Area was significant in the final model. Similarly, variables that might affect observability (Glare, Seas, SunRise, Weather) and tide, when nested by Area, only explained 14% of the variance, and only Area was significant in the best fit ($F = 8.83$, $P < 0.0001$). Physical features nested by Area made a stronger model ($R^2 = 0.36$, $F = 5.75$, $P < 0.0001$), and the best fit included SHORE, EXPOSURE, and DEPTH nested in Area, all of which were significant contributors (Fig. 3). Results for adult densities were similar, but with lower predictive power; using the same dataset, and nesting SHORE, EXPOSURE and DEPTH in Area, $R^2 = 0.23$, $F = 3.02$, $P < 0.0001$. For adults, however, only DEPTH ($P = 0.006$) and Area ($P < 0.0001$) were significant contributors in the final model.

Logistic Regression

The Stepwise regression identified the best predictor variables as SHORE, EXPOSURE, and DEPTH, all nested in Area. For the nested analyses, it was necessary to remove all zero values for juveniles, and where SHORE was included, the Knight observations had to be removed because all juveniles there occurred on the same SHORE type. For a more robust test of these variables as predictors of juvenile presence or absence, I used the T474 dataset (which omitted very early surveys, but retained transects with no juveniles) for a series of logistic regressions. The results for juveniles (Table 2) indicate that SHORE contributed the most deviance, and thus higher Akaike's Information Criterion (AIC) scores when added to the models. DEPTH and EXPOSURE were fairly equal in contribution to the model with lower AIC. For adults (Table 3), DEPTH contributed lower deviance than the other variables, and SHORE and EXPOSURE were more equally weighted among models.

Predictor variables relative to juveniles. -- The relationship between juveniles and DEPTH was clear from scatterplots and previous analyses, with juvenile abundance decreasing with DEPTH. Scatterplots indicated that most juveniles were in waters < 25 m deep. For SHORE and EXPOSURE, it was not intuitive what the relationship was relative to juvenile abundance, and neither variable correlated with juveniles in paired comparisons. I used a boxplot to examine average juvenile density by transect for SHORE and EXPOSURE (Fig. 4). Both variables show outliers that could have influenced regressions, although Area effect is not accounted for in these graphs. For SHORE, juvenile density is similar for coarse/cobble beach and rocky coast, and both categories have outliers that are strongly weighted against the low variance within the fine grain beach category. For EXPOSURE, the moderately exposed coast (1-5 Km) is only slightly higher in mean juvenile density than the more exposed coasts (>5 Km), and both have several outliers.

DISCUSSION

These results indicate that it is possible to identify key habitat associations for juvenile murrelets. The positive relation between juvenile occurrence and shallow, semi-protected waters off of rocky coasts, while not previously demonstrated in a rigorous analysis, was not unexpected. Murrelet adults typically forage in relatively shallow waters (Kuletz et al. 1995, Ostrand et al. 1998). Juvenile murrelets, in particular, may require shallow, protected waters, because of their relatively small size. Juvenile murrelets fledge at 58-70% of adult mass (Nelson and Hamer 1995, Kuletz and Marks 1997), and small body size is associated with weaker diving capacity (Watanuki et al. 1995). Diving times of juvenile murrelets are shorter, and more frequent, than those of adults (Strachen et al. 1995, Kuletz et al. 1995), suggesting their dives are not as deep as those of adults.

The significant loading factors for SHORE and EXPOSURE are possibly more equivocal, since no clear pattern emerged when these variables were examined independently against the average juvenile density for each transect. Results do indicate that extremely protected waters off of fine grained beaches, such as often occurs at the heads of long fjords with tidal flats, will be least likely to attract juvenile murrelets.

None of the sea surface features (SST, SSS, SECCHI) were incorporated into final models predicting murrelet occurrence. Large-scale effects from sea surface variables have been noted for seabirds (Hunt et al. 1993, in press; Tyler et al. 1992), including murrelets (Ainley et al. 1995), but they are usually secondary to the fronts and upwelling with which changes in these variables are often associated. Fine-scale interactions, if they do occur, are more difficult to detect (Hunt et al. in press, Schneider and Piatt 1986).

Juvenile and adult murrelets did not demonstrate strong differences in habitat selection, and the weak, but significant, correlation between their numbers suggests a generally congruous preference for habitats. Adults, being more ubiquitous in the region, did not have as strong an association as juveniles to specific Shore or Exposure types. Adults, however, decline steadily in late summer, which could both mask habitat associations and reduce the correlation with juveniles at the transect scale.

Factors that could affect counts by lowering observability of the birds did not appear to be significant in this study. These factors were already partly controlled for by a survey protocol that limits surveys to reasonable conditions (Kuletz 1996). Factors that could potentially be important locally, such as weather-related effects or tidal phase (Speckman 1996) were likely minimized by covering a large total area in a variety of habitats over the course of 5 weeks.

Management Implications. -- These results suggest that in PWS, monitoring efforts could be improved for juveniles by focusing on, or creating a sampling strata for moderately protected, rocky coasts, particularly where water averages roughly < 25 m in depth < 200 m from shore. Even in regions where large kelp beds attract juvenile marbled murrelets (Kuletz and Piatt, in press), shallow water appears to be critical for juvenile murrelets. Recent improvements in bathymetric GIS coverages could be used to *a priori* identify water depth and exposure within study areas.

Clearly, however, a key finding of this study is that undefined variables, at the scale of approximately 50 km, make Area effects strong. Murrelet densities varied significantly among these study Areas (see Kuletz and Kendall 1998). Until we can identify and measure the additional biological and physical features that influence juvenile murrelet distribution, a monitoring program should locate specific areas that are consistent 'hot spots'. Similar suggestions have been made for monitoring juveniles in Kachemak Bay, Alaska (Kuletz and Piatt, in review) and adult murrelets in British Columbia (Rodway et al. 1995) and southeast Alaska (Speckman 1996). In Kachemak Bay, juvenile murrelets were more highly clumped and in more exposed habitat than found in this study, but were associated with large kelp beds. Results reported here indicate that stratification by habitat can also be applied in areas that lack large kelp beds.

In PWS, statistical power to detect trends in juvenile murrelet abundance were highest at sites with consistently high murrelet densities (Kuletz and Kendall 1998), as it was for adult murrelets at two sites in southeast Alaska (Speckman 1996). While statistical power is desirable in monitoring population trends, trends at sites with intermediate or low numbers of murrelets should not be ignored, as they may be the first to indicate declines in a regional population (Perrins et al. 1991). Thus, the optimum approach may be to maintain coverage of both high and low density sites within a region, but monitor and analyze them as separate strata.

In PWS, Naked Island is an example of a site with consistent and high juvenile murrelet abundance. Compared to other sites in 1994 (2 sites), 1995 (6 sites), and 1997-1998 (3 sites), Naked had the highest juvenile density. Additionally, productivity has been relatively consistent from 1994-1998, ranging from 1.46-1.52 juveniles/Km^2, which increases power to detect significant changes. Although a selection of habitats should be included in any monitoring plan, sites similar to Naked, once identified, could form a core study population.

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LITERATURE CITED

Ainley, D.G., S.G. Allen, and L.B. Spear. 1995. Offshore occurrence patterns of marbled murrelets in central California. Pages 361-370 *In*: C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report, PSW-GTR-152.

Andersen, H. L., and S. R. Beissinger. 1995. Preliminary observations of juvenile: adult ratios of marbled murrelets in Auke Bay, southeast Alaska. Northwestern Naturalist 76:79-81.

Borland, Intl., Inc. 1992. Paradox User's Guide for 5.0.

Burrell, D.C. 1987. Interaction between silled fjords and coastal regions. Pages 187-216 *In*: D.W. Hood and S.T. Zimmerman (eds). The Gulf of Alaska: Physical environment and biological resources. U.S. Dept. Commerce and U.S. Dept. Interior, Mineral Management Services, OCS study, MMS 86-0095.

Carter, H. R. and S. G. Sealy, 1990. Daily foraging behavior of marbled murrelets. Studies in Avian Biology 14:93-102.

Furness, R. W., and P. Monaghan. 1987. Seabird ecology. Chapman & Hall, New York, New York, USA.

Gaston, A. J., and D. N. Nettleship. 1981. The thick-billed murres of Prince Leopold Island. Can.Wildl. Serv. Monog. Ser. 6.

Hunt, G.L., Jr., N.M. Harrison, and J.F. Piatt. 1993. Foraging ecology as related to the distribution of planktivorous auklets in the Bering Sea. Pages 18-26 *In*: K. Vermeer, K.T. Briggs, K.H. Morgan, D. Siegel-Causey (eds). The status, ecology, and conservation of marine birds of the North Pacific. Can. Wildl. Serv. Spec. Publ., Ottawa.

Hunt, G.L., Jr., F. Mehlum, R. W. Russell, D. Irons, M.B. Decker, and P.H. Becker. In press. Physical processes, prey abundance, and the foraging of seabirds. *In*. Adams, N.J. and Slotow (eds), Proc 22nd Int. Ornith. Congress, Durban.

Kuletz, K. J. 1996. Marbled murrelet abundance and breeding activity at Naked Island, Prince William Sound, and Kachemak Bay, Alaska, before and after the *Exxon Valdez* oil spill. Pages 770-784 *in* S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright, editors. Proceedings of the *Exxon Valdez* oil spill symposium. American Fisheries Society Symposium 18.

Kuletz, K.J. and S.J. Kendall. 1998. A productivity index for marbled murrelets in Alaska based on surveys at sea. Journal of Wildlife Management 62(2):446-460.

_____, and D. K. Marks. 1997. Post-fledging behavior of a radio-tagged juvenile marbled murrelet. Journal of Field Ornithology 68:421-425.

_____, _____, R. A. Burns, L. M. Prestash, and D. A. Flint. 1995. Marbled murrelet foraging patterns and a pilot productivity index for murrelets in Prince William Sound, Alaska. *Exxon Valdez* oil spill restoration project final report, Project 94102. U. S. Fish and Wildlife Service. Anchorage, Alaska, USA.

Kuletz, K.J. and J.F. Piatt. In Press. Juvenile marbled murrelet nurseries and the productivity index. Wilson Bulletin.

MathSoft. 1997. S-Plus Guide to Statistics, Data Analysis Products Division, MathSoft, Inc., Seattle.

Nelson, S.K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). *In* The Birds of North America, No.276 (A. Poole and F. Gill (eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.

Nelson, S. K., and T. E. Hamer. Nesting biology and behavior of the marbled murrelet. Pages 57-68 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report, PSW-GTR-152.

Ostrand, W.D., K.O. Coyle, G.S. Drew, J.M. Maniscalco, and D.B. Irons. 1998. Selection of forage fish schools by marbled murrelets and tufted puffins in Prince William Sound, Alaska. Condor 100:286-297.

Perrins, C.M., J-D. Lebreton, and G.J.M. Hirons (eds). 1991. Bird population studies: Relevance to conservation management. Oxford Ornithology Series, Oxford University Press, New York..

Ralph, C. J., G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. 1995. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report, PSW-GTR-152.

_____, and L. L. Long. 1995. Productivity of marbled murrelets in California from observations of young at sea. Pages 371-380 *In:* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report, PSW-GTR-152.

Robards, M.D., J.F. Piatt, and G.A. Rose. Submitted. Maturation, fecundity, and intertidal spawning of Pacific Sand lance (*Ammodytes hexapterus*) in the Northern Gulf of Alaska. Marine Biology.

Rodway, M.S., J-P.L. Savard, D.C. Garnier, and M.J. F. Lemon. 1995. At-sea activity patterns of marbled murrelets adjacent to probable inland nesting areas in the Queen charlotte Islands, British Columbia. Northwest. Nat. 76:82-89.

Sealy, S. G. 1975. Aspects of the breeding biology of the marbled murrelet in British Columbia. Bird-Banding 46:141-154.

Schneider, D.C. and J.F. Piatt. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Maine Ecology Progress Series 32: 237-246.

Speckman, S.G. 1996. Marbled murrelet distribution and abundance in relation to the marine environment. Master's Thesis, University of Alaska, Fairbanks.

Strachen, G.M., M. McAllister, and C.J. Ralph. 1995. Marbled murrelet at-sea and foraging behavior. Pages 247-253 *In*: C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report, PSW-GTR-152.

Strong, C.S., B. S. Keitt, W. R. McIver, C. J. Palmer, and I. Gaffney. 1995. Distribution and population estimates of marbled murrelets at sea in Oregon During the summers of 1992 and

1993. Pages 339-352 *In*: C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report, PSW-GTR-152.

Tyler, W.B., K.T. Briggs, D.B. Lewis, and R.G. Ford. 1993. Seabird distribution and abundance in relation to oceanographic processes in the California Current System. Pages 48-60 *In*: K. Vermeer, K.T. Briggs, K.H. Morgan, D. Siegel-Causey (eds). The status, ecology, and conservation of marine birds of the North Pacific. Can. Wildl. Serv. Spec. Publ., Ottawa.

Vermeer, K., K.H. Morgan, and G.E. John Smith. 1992. Habitat analysis and co-occurrence of seabirds on the west coast of Vancouver Island. Pages 78-85 *In*: K. Vermeer, R.W. Butler, and K.H. Morgan (eds). The ecology, status, and conservation of marine and shoreline birds on the west coast of Vancouver Island. Can. Wildl. Serv. Occasional Paper No. 75, Ottawa.

Watanuki, Y., A. Kato, and Y. Naito. 1995. Diving performance of male and female Japanese cormorants. Pacific Seabird Bull. 21(1).

Wittenberger, J.F. and G.L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. Pages 1-77 In: Famer, D.S., J.R. King, and K.C. Parkes (eds). Avian Biology Vol. 8.

Figures

Figure 1. The six study Areas (outlined in black) in Prince William Sound, Alaska, surveyed in July and August 1995.

Figure 2. Frequency distribution of juvenile murrelet densities (in 1/Km^2 intervals) for transects that had at least one juvenile present during surveys conducted in Prince William Sound, Alaska, in July and August 1995 ($n = 242$ transects).

Figure 3. Plots for the residual-fit spread (top) and fitted model (bottom) for juvenile murrelet density, with Area and Area-nested variables SHORE, EXPOSURE, and DEPTH. Data included only transects with at least one juvenile. The residuals show a good spread, suggesting they explain some variation in the data, however, the variability increases with increasing fitted values. In the final fitted model ($R^2 = 0.36$, $P < 0.0001$), all variables were significant (all Ps < .002).

Figure 4. Boxplots showing the median, variance and outliers for average juvenile density on transects relative to (top) SHORE and (bottom) EXPOSURE. The average juvenile density was calculated for each transect ($n = 40$) surveyed (7-10 times each) in July and August 1995, in Prince William Sound, Alaska. Both variables show outliers that could have influenced regressions, although Area effect is not accounted for in these graphs.

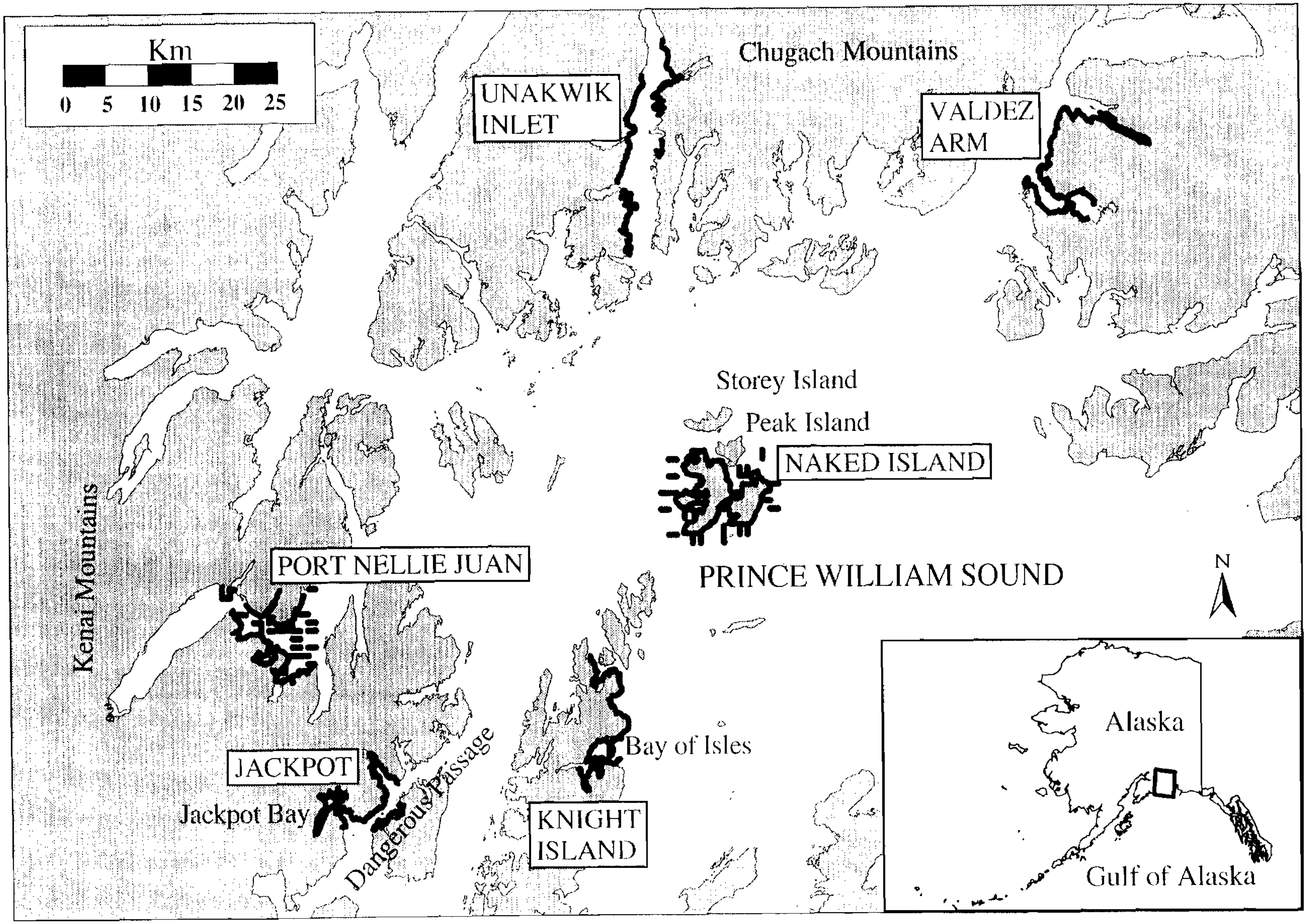
Km
0 5 10 15 20 25
Chugach Mountains
UNAKWIK INLET
VALDEZ ARM
Storey Island
Peak Island
NAKED ISLAND
Kenai Mountains
PORT NELLIE JUAN
PRINCE WILLIAM SOUND
N
Bay of Isles
Dangerous Passage
JACKPOT
Jackpot Bay
KNIGHT ISLAND
Alaska
Gulf of Alaska

Fig 2

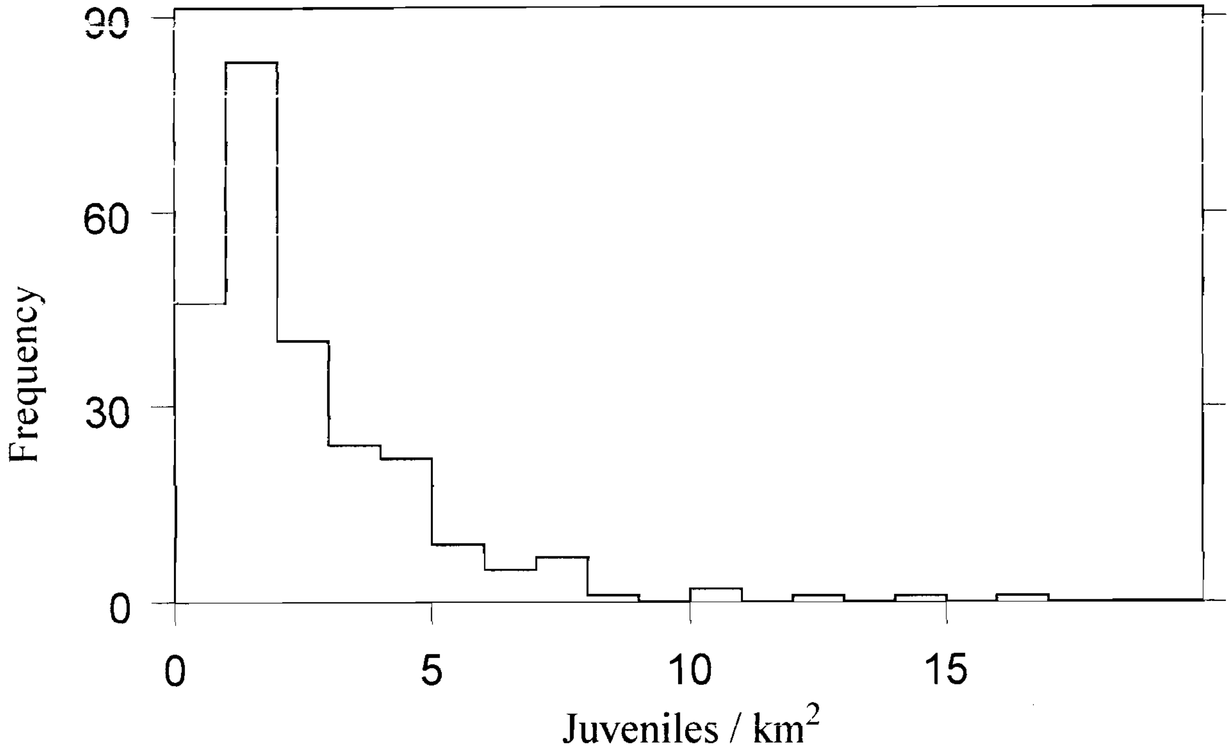

Fig 2

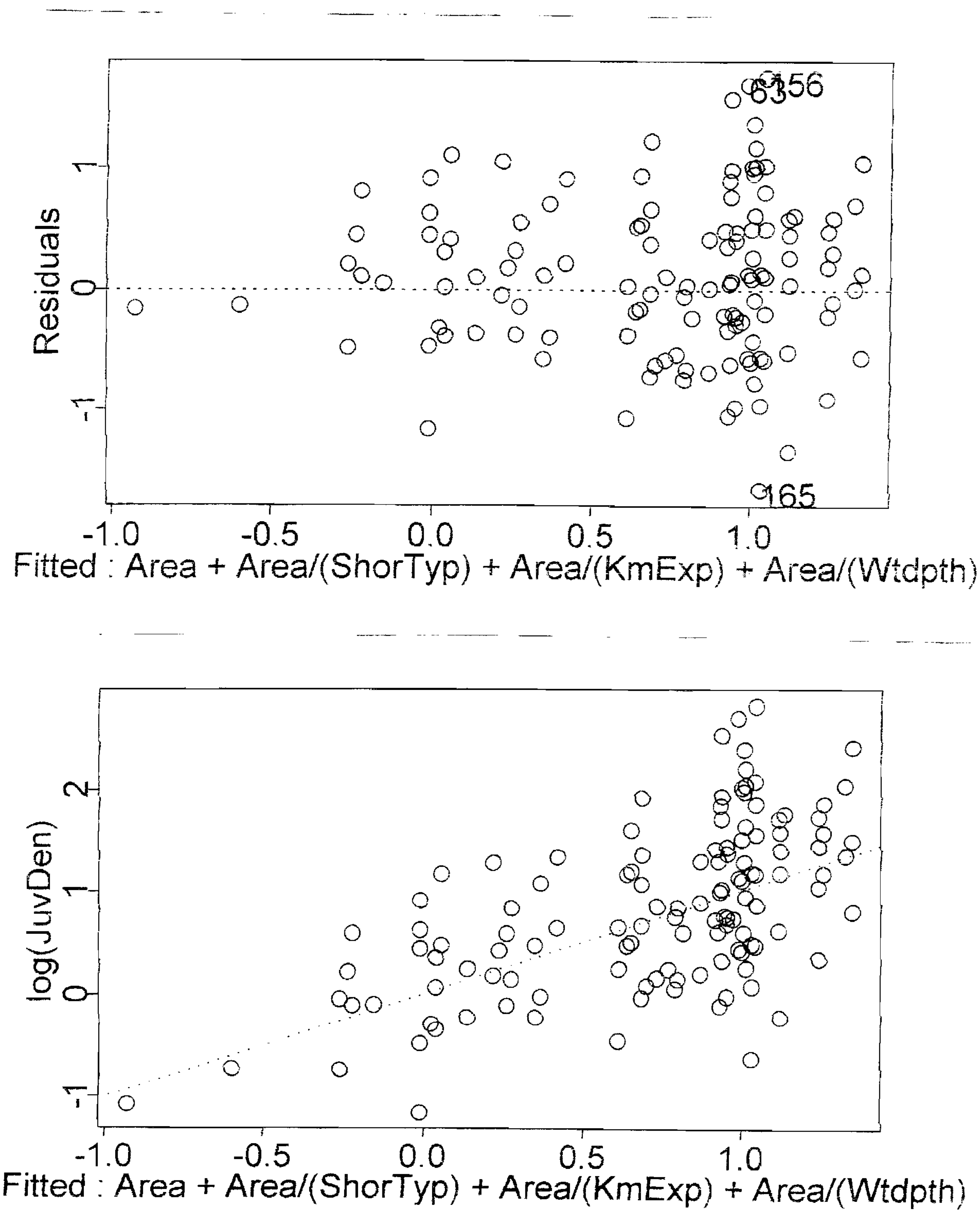

Figure 3. Plots for the residual-fit spread (top) and fitted model (bottom) for juvenile murrelet density, with Area and Area-nested variables Shore, Exposure, and Depth. Data included only transects with at least one juvenile. The residuals show a good spread, suggesting they explain some variation in the data, however, the variability increases with increasing fitted values. In the final fitted model ($R^2 = 0.36$, $P < 0.0001$), all variables were significant (all Ps < .002).

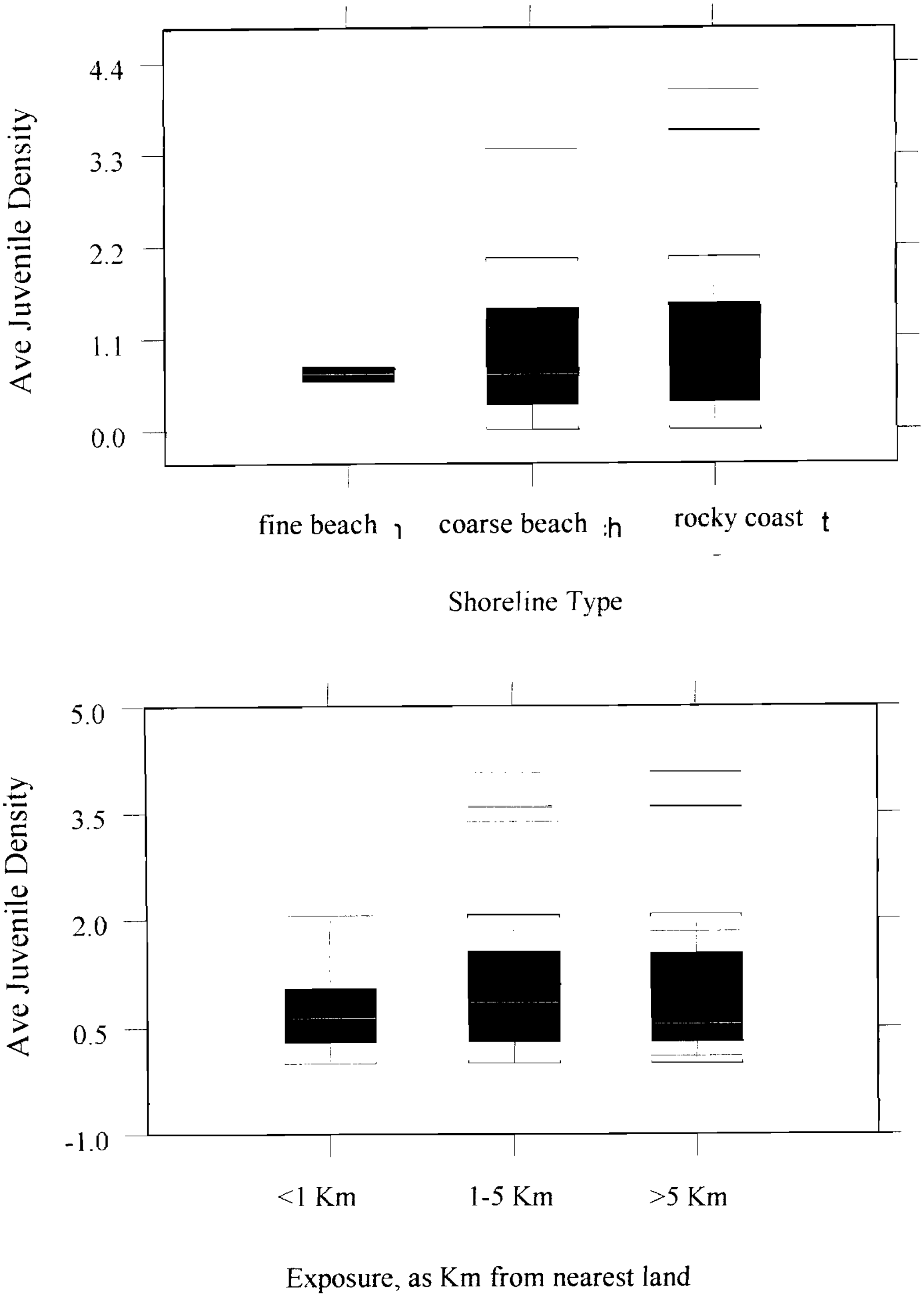
Ave Juvenile Density
4.4
3.3
2.2
1.1
0.0
fine beach
coarse beach
rocky coast
Shoreline Type
Ave Juvenile Density
5.0
3.5
2.0
0.5
-1.0
<1 Km
1-5 Km
>5 Km
Exposure, as Km from nearest land

Fig. 4

Table 1. Spearman correlation coefficients for variables of 474 transect samples surveyed in Prince William Sound, Alaska, in July and August, 1995. Correlation coefficients >0.20 are highlighted. Adults = adult murrelet density, Juv = juvenile density, SST= sea surface salinity, Seas= wave conditions, Swell= swell height, xSecc=mean Secchi reading for the day, xSSS= mean sea surface salinity for the day, Cond=observer conditions, TideR= tidal range for the day, Shore= shoreline type, Expos= Exposure of coast, Depth= weighted water depth for the transect, MaxD= maximum depth for the transect. Not included in the table are variables Glare, three types of tidal phase, and hours from sunrise, since they had no significant correlations. Also not included were specific measurements of transect salinity and secchi, because they had many missing values and were highly correlated with daily averages.

	Adults	Juv	SST	Seas	Swell	xSecc	xSSS	Cond	TideR	Shore	Expos	Depth
Adults	*											
Juv	**.33**	*										
SST	**-.40**	-.14	*									
Seas	-.02	-.04	.04	*								
Swell	-.05	-.04	.02	**.54**	*							
xSecc	**-.40**	-.19	**.63**	-.04	.00	*						
xSSS	-.11	**.24**	.14	**.22**	**.33**	**.40**	*					
Cond	-.04	-.06	-.00	**.55**	**.52**	-.05	**.28**	*				
TideR	.13	.01	**.23**	.12	.12	**-.39**	-.12	.12	*			
Shore	-.01	-.01	.09	-.04	-.15	-.00	**-.28**	-.16	-.00	*		
Expos	-.01	.01	-.01	**.23**	**.32**	.00	.15	**.24**	-.00	-.09	*	
Depth	.08	.12	-.15	-.07	-.19	**-.23**	**-.37**	-.14	.04	**.21**	-.02	*
MaxD	-.03	.05	-.01	-.09	**-.21**	**-.24**	**-.55**	-.19	.04	**.42**	-.14	**.64**

Table 2. Results of logistic regressions for predicting the presence or absence of juvenile marbled murrelets on transects surveyed in July and August, 1995, in Prince William Sound, Alaska. A general linear model was used, specifying a binomial distribution. Variables were added sequentially and start order rotated to test for analysis of deviance between models.

Fit	Terms	Resid. Df	Resid. Dev	Test	Df	Deviance	AIC	dif f in AIC
1	Area/(ShorTyp)	446	564.5801					
2	Area/(ShorTyp + KmExp)	440	550.1831	+KmExp %in% Area	6	14.39704	26.39	
3	Area/(ShorTyp + KmExp + Wtdpth)	434	543.1976	+Wtdpth %in% Area	6	6.98548	18.99	07.4
1	Area/(KmExp)	462	581.9756					
2	Area/(KmExp + ShorTyp)	440	550.1831	+ShorTyp %in% Area	22	31.79254	75.79	
3	Area/(KmExp + ShorTyp + Wtdpth)	434	543.1976	+Wtdpth %in% Area	6	6.98548	18.99	56.8
1	Area/(Wtdpth)	462	588.7912					
2	Area/(Wtdpth + ShorTyp)	440	558.6612	+ShorTyp %in% Area	22	30.13005	74.13	
3	Area/(Wtdpth + ShorTyp + KmExp)	434	543.1976	+KmExp %in% Area	6	15.46363	27.46	46.67
1	Area/(KmExp)	462	581.9756					
2	Area/(KmExp + Wtdpth)	456	575.0406	+Wtdpth %in% Area	6	6.93498	18.93	
3	Area/(KmExp + Wtdpth + ShorTyp)	434	543.1976	+ShorTyp %in% Area	22	31.84304	75.81	56.91

Table 3. Results of logistic regressions for predicting the presence or absence of adult marbled murrelets on transects surveyed in July and August, 1995, in Prince William Sound, Alaska. A general linear model was used, specifying a binomial distribution. Variables were added sequentially and start order rotated to test for analysis of deviance between models.

Fit	Terms	Resid. Df	Resid. Dev	Test	Df	Deviance	AIC	dif f in AIC	P
1	Area/(ShorTyp)	446	263.1860						
2	Area/(ShorTyp + KmExp)	440	253.4314	+KmExp %in% Area	6	9.75460	21.75		
3	Area/(ShorTyp + KmExp + Wtdpth)	434	242.9685	+Wtdpth %in% Area	6	10.46288	22.46	0.71	
1	Area/(KmExp)	462	270.4671						
2	Area/(KmExp + ShorTyp)	440	253.4314	+ShorTyp %in% Area	22	17.03575	61.04		
3	Area/(KmExp + ShorTyp + Wtdpth)	434	242.9685	+Wtdpth %in% Area	6	10.46288	22.46	38.58	
1	Area/(Wtdpth)	462	273.8960						
2	Area/(Wtdpth + ShorTyp)	440	257.4342	+ShorTyp %in% Area	22	16.46185	60.46		
3	Area/(Wtdpth + ShorTyp + KmExp)	434	242.9685	+KmExp %in% Area	6	14.46567	26.47	33.99	
1	Area/(KmExp)	462	270.4671						
2	Area/(KmExp + Wtdpth)	456	268.5295	+Wtdpth %in% Area	6	1.93767	13.94		
3	Area/(KmExp + Wtdpth + ShorTyp)	434	242.9685	+ShorTyp %in% Area	22	25.56096	69.56	55.62	

S Jellyfish

Exxon Valdez Oil Spill
Restoration Project Annual Report

JELLYFISH AS COMPETITORS AND PREDATORS OF FISHES

Restoration Project (APEX) 98163S

Annual Report

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May 1999

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ABSTRACT

At high densities, jellyfish can seriously effect populations of zooplankton and ichthyoplankton, and may be detrimental to fisheries through competition for food with fishes and by direct predation on the eggs and larvae of fish. In this project report, I examine the roles of jellyfish as competitors and predators of fishes. This was accomplished by participating in ongoing APEX research cruises in Prince William Sound, in which zooplankton, and medusa and ctenophore distributions and densities were determined. Additionally, medusae and ctenophores were collected for gut content analysis and gut passage time experiments in order to calculate feeding rates on zooplankton. This project has coordinated with other APEX investigators, who provided logistic support in the field, and sampling for zooplankton. I have compared jellyfish diets with forage fish diets from previous APEX research, in order to determine dietary overlap and the potential for competition. In collaboration with APEX and SEA scientists, I have compiled historical, and existing data in order to better understand the importance of jellyfish in the food web of Prince William Sound. In this year, one submitted publication has resulted from such collaboration.

Study History. In July, 1996, I was invited to participate in the SEA sampling in Prince William Sound by Dr. Gary Thomas. During the field work, I observed the abundance of jellyfish in northern Prince William Sound from aerial surveys and from trawls and acoustic surveys. Massive aggregations of *Aurelia* 1/4 to 2 km long were seen commonly from the air and by acoustics. *Cyanea* and *Aequorea* were distributed throughout Prince William Sound, but had higher densities in some areas (e.g. Irish Cove). The plane and acoustics boat would notify the seiner where to set his net on a fish school, but often more jellyfish than fish were in the net. I also compiled existing data from the Alaska Dept. Of Fish and Game collected during SEA cruises that showed in drift seines, which were not set specifically on fish schools, jellyfish biomass often exceeded fish biomass in Prince William Sound. Researchers from SEA and APEX observed the great abundance of jellyfish in Prince William Sound and recognized the need to understand their effects on the zooplankton and fish populations there.

In anticipation of EVOS funding starting in October, 1997, APEX investigators invited me to participate in the July-August cruise. The jellyfish populations were considerably different from 1996, being generally less abundant and with *Aequorea* in low numbers. Specimens of five species (*Cyanea, Aurelia, Aequorea, Clytia, Pleurobrachia*) were collected for gut content analysis.

INTRODUCTION

Not only do jellyfish and ctenophores feed on the same zooplankton foods as fish larvae and zooplanktivorous fishes, but they eat the eggs and larvae as well (Purcell, 1985; 1990, Purcell and Grover, 1990; Baier and Purcell, 1997). The dual role of soft-bodied plankton as predators and competitors of fishes has been suggested many times (e.g. Purcell, 1985; Arai, 1988), but seldom has been evaluated directly (existing studies are Purcell and Grover, 1990; Baier and Purcell, 1997). Jellyfish predation on zooplankton could affect the larvae of numerous fish species, many of which are commercially important (e.g. herring, rockfish, cod, flatfish; Fancett, 1988; Purcell, 1989, 1990) as well as the juveniles and adults of zooplanktivorous fish species (e.g. herring, walleye pollock, sandlance, pink salmon) that are important as forage fish of marine vertebrates, specifically piscivorous fish, sea birds, and harbor seals. The following background provides details of research on gelatinous species to determine their effects on zooplankton and ichthyoplankton populations.

Dietary analyses. Copepods are the main prey items of most gelatinous predators. Several estimates of predation effects of gelatinous species on copepod populations suggest that the effects are too small to cause prey population declines (e.g. $\leq 10\%\ d^{-1}$; Kremer, 1979; Larson, 1987a,b; Purcell et al., 1994b). However, some studies indicate much higher predation and possible reduction of zooplankton standing stocks (e.g. Deason, 1982; Matsakis and Conover, 1991; Purcell, 1992). Copepod capture by *Chrysaora quinquecirrha* was significantly related to prey density, medusa size, and temperature. During July and August 1987 and 1988 in two tributaries of Chesapeake Bay, medusae consumed from 13 to 94% d^{-1} of the copepod standing stocks, and may have caused the observed copepod population decline. The predation effect is directly dependent on the jellyfish population size (Purcell, 1997)

The possibility of competition for food among jellyfish and fish has been directly examined in only a few studies. Potential competition between medusae and first-feeding herring during one spring in British Columbia was found unlikely to be important due to the great abundance of copepod nauplii consumed by the larvae (Purcell and Grover, 1990). However, when the prey were copepodites, chaetognaths consumed significant percentages of the same prey as fish larvae off the southeast U.S. coast (Baier and Purcell, 1997).

The diets of some species include high proportions of fish eggs and larvae when available. Such predators include hydromedusae, in particular *Aequorea victoria*, whose diet consisted of almost exclusively Pacific herring (*Clupea pallasi*) larvae in April when the larvae hatched (Purcell and Grover, 1990) and a variety of eggs and larvae of other species of fish later in the spring in addition to gelatinous and crustacean prey (Purcell, 1989). Semaeostome scyphomedusae also may contain large numbers of ichthyoplankton prey when available in addition to gelatinous and crustacean prey (e.g. *Cyanea capillata, Chrysaora quinquecirrha* in Fancett, 1988 and Purcell et al., 1994a). Predation effects by pelagic cnidarians on fish eggs and larvae often are substantial ($\geq 30\%\ d^{-1}$ of the populations) in environments where predators are numerous, as for *C. quinquecirrha* and *A. victoria* (Purcell, 1989; Purcell and Grover, 1990; Purcell et al., 1994a). Other estimates, based on laboratory experiments, of predation effects by pelagic cnidarians on fish eggs were low (0.1 to 3.8% d^{-1}; Fancett and Jenkins, 1988).

At high jellyfish densities, as can occur especially in semi-enclosed bodies of water (Purcell, 1990), such as Prince William Sound (Prince William Sound), predation on copepods may limit copepod populations and cause competition for food with zooplanktivorous fish species and fish larvae . Predation by jellyfish on fish eggs and larvae can be very severe. Medusae have potentially great effects on fish populations because of their often great abundances and feeding that increases directly with prey density without saturation.

OBJECTIVES

1. Determine annual variation in species composition, size distributions, and abundances of jellyfish and ctenophores in Prince William Sound.

2. Collect gut content data for key gelatinous predators (*Aurelia, Cyanea, Chrysaora, Aequorea* and other hydromedusae, *Pleurobrachia* ctenophores) in order to evaluate the diet of the several key species and to evaluate interannual variation..

3. Determine the gut passage (digestion) times for key predator species fed key prey taxa (i.e. copepods, larvaceans).

4. Calculate size-specific feeding rates for each key predator species based on gut contents and gut passage times, and correlate feeding rates with medusa size and prey densities in order to be able to estimate feeding impacts in other years from jellyfish size distributions and jellyfish and zooplankton densities.

5. Calculate dietary overlap indices for medusae and forage fish species.

6. Calculate predation impacts on key prey taxa based on feeding rates and densities of predator and prey species.

7. Contribute these results to the APEX, SEA and overall EVOS modeling efforts.

8. Compile historical data (Gulf of Alaska) and all available EVOS data (Prince William Sound) on jellyfish distributions and abundances.

METHODS

Distribution and abundance of zooplankton and jellyfish

In July, 1997 and 1998, zooplankton samples were collected at 8 previously determined stations at each of three areas, northeastern, central, and southwestern Prince William Sound at night in 60 m vertical hauls by APEX investigator Dr. Tom Shirley using a 20 cm diameter bongo plankton net (see Table 2, 97163A Annual Report). Zooplankton were identified and counted from subsamples by my technician. Small gelatinous species (ctenophores and hydromedusae) were counted from whole samples. In addition, Tucker trawl samples were taken by Dr. Shirley at night, and the hydromedusae were removed for later identification by my technician. CTD data were collected (see Table 1, 97163A Annual Report), and will be made available to me for all appropriate cruises.

In order to determine the abundance of large jellyfish (*Cyanea, Aurelia, Aequorea*) samples were taken with a 20 m herring seine. In 1998, the seine was set at the same 24 stations as above (see Table 3, 97163A Annual Report). The samples were processed on board ship; the medusae were identified, counted, the swimming bell diameter measured, and biovolumes of each species measured. Abundances of the large jellyfish were estimated by calculating the volume of water filtered by the seine (57,642 m^3).

Analysis of predation rates on zooplankton

In order to determine the gut contents of jellyfish, in both 1997 and 1998, small hydromedusae (*Clytia*), ctenophores (*Pleurobrachia*), and large medusae (*Cyanea, Aurelia, Aequorea*) were dipped from the surface at the above sampling locations, and were immediately preserved in 5% Formalin. Prey in the guts were identified, counted, and measured using a dissecting microscope.

In order to measure the gut passage times for zooplankton prey, in 1998, individual medusae were collected in dip nets and maintained at ambient water temperatures in 94 liter coolers filled with filtered (32 μm) seawater with some *Artemia* nauplii. One or more medusae were preserved immediately, and then one or more medusae were preserved at 1 or 2 h intervals. The gut contents of the medusae were analyzed later in the laboratory for partly digested prey. The length of time when the different prey types are no longer recognized in the gut contents are used in calculations of feeding rates.

In order to calculate jellyfish feeding rates and effects on zooplankton populations, data on the numbers of prey in the guts are divided by gut passage times to calculate feeding rate (No. of prey eaten h^{-1} $medusa^{-1}$). The individual feeding rates are multiplied by medusa densities and divided by prey densities to determine the impacts of the medusae on the prey populations.

Underwater video. In order to determine the frequency of associations of juvenile pollock and aggregations of *Aurelia* medusae, and to determine swimming behavior in the aggregations, four aggregations were videotaped using a Hi-8 VCR and monitor attached to a closed-circuit underwater camera system (Fisheye, Inc). The videotapes were analyzed with an editing Hi-8 VCR. Those results are presented in the attached manuscript.

Data compilation from SEA and APEX investigators. In addition to the field work on jellyfish, data were sent from several collaborators and analyzed by my technician. Dr. Paul Anderson sent historical data on large jellyfish from shrimp trawls in the Gulf of Alaska from 1973-1995. Dr. Ken Coyle sent SEA data on hydromedusae from Prince William Sound in 1994

- 1997. Dr. Kevin Stokesbury sent SEA seine data from 1996. Evelyn Brown sent data on *Aurelia* aggregations from aerial surveys in 1995, 1996, and 1997. Dr. Molly Sturdevant sent zooplankton, hydromedusa, and forage fish dietary data from the summers of 1995 and 1996.

RESULTS The following results and analyses are preliminary.

Distribution and abundance of zooplankton and jellyfish

Zooplankton. Sample analyses (1997, 1998) were completed. The densities of zooplankton appeared to be greater in 1996 than in either 1995 or 1997 (Fig. 1). The Percent Similarity Indices (PSI. Schoener 1974), were calculated to compare the proportions of zooplankton taxa among regions and years (1995, 1996, 1997, 1998). The similarity was $\geq 86\%$ for all comparisons, indicating that the different regions and years were very similar in percentage composition, which allowed further analysis comparing jellyfish and forage fish diets.

	PSI (%)
1995 versus 1996	93.9
1995 versus 1997	86.6
1995 versus 1998	86.0
1996 versus 1997	92.3
1996 versus 1998	88.9
1997 versus 1998	92.3

Jellyfish densities. Hydromedusa abundances were compared among 1995, 1996, and 1997, and found to be greater in 1996 (Fig. 2). Densities of *Aurelia* medusae also were greater in 1996 than in 1995 or 1997 (see Appendix 1). Jellyfish biovolumes measured from purse seine hauls in 1998 were similar among regions (North 0.34 ml m^3, Central 0.56 ml m^3, South 0.45 ml m^3), and the three large species had similar biovolumes overall (*Cyanea* 0.14 ml m^3, *Aurelia* 0.21 ml m^3, *Aequorea* 0.38 ml m^3). Those seine hauls did not include any aggregations, and the biovolume of *Aurelia* would be greater if those were included.

Analysis of predation by jellyfish on zooplankton

Gut content analysis (Fig. 3) showed that *Aurelia* and *Pleurobrachia* ate mainly crustaceans (copepods < 1.5 mm, and cladocerans). By contrast, *Cyanea* and *Aequorea* ate mainly larvaceans plus some crustaceans. Very few fish eggs or larvae have been found in the gut contents, therefore it appears that in July, when small ichthyoplankton were not numerous, the jellyfish are not consuming large numbers. Data for jellies collected in 1997 are complete. *Aequorea* and *Aurelia*, but not *Cyanea*, have been analyzed for 1998. Similar patterns were seen for forage fish, with juvenile walleye pollock, sandlance and herring consuming mostly small copepods, and pink salmon eating mostly larvaceans (Fig. 3). Prey selection indices (Pearre 1982) showed statistically significant ($p < 0.05$) positive selection for cladocerans by *Aurelia,* *Pleurobrachia,* and *Cyanea*, for small copepods by *Aurelia*, and for larvaceans by *Cyanea* and *Aequorea* (Fig. 4A). Significant negative selection against copepods was shown for *Pleurobrachia, Cyanea*, and *Aequorea*, and against larvaceans by *Aurelia.* Among forage fish species, juvenile walleye pollock showed significant positive selection for large copepods and negative selection against small copepods (Fig. 4B). Pink salmon showed significant negative selection against copepods, and positive selection for larvaceans. Sandlance and herring showed weak and mixed selection for the various prey categories.

Comparisons of diet similarity among jellyfish intermediate PSI values for most species, with *Aurelia* and *Pleurobrachia*, the main crustacean eaters having the most similar diets. Among forage fish, juvenile walleye pollock, sandlance and herring had high PSI values, and pink salmon had low PSI values when compared with other species.

1997 Jellyfish	PSI (%)
Aurelia versus *Pleurobrachia*	84.2
Aurelia vs *Aequorea*	65.1
Aequorea versus *Pleurobrachia*	50.1
Cyanea versus *Aequorea*	48.7
Cyanea versus *Aurelia*	38.9
Cyanea versus *Pleurobrachia*	28.4
1995 Forage Fish	
pollock versus sandlance	77.7
pollock versus herring	71.0
Sandlance versus herring	51.1
1996 Forage Fish	
sandlance versus herring	81.5
herring versus pink salmon	34.2
sandlance vs pink salmon	16.9

Percent diet similarities comparing jellyfish and forage fish showed the highest PSI values among mainly crustacean-eating species (highlighted top left) and among mainly larvacean-eating species (highlighted bottom right).

	Percent Diet Similarity (%)			
	Pollock	Sandlance	Herring	Salmon
Aurelia	67.2	61.6	67.4	18.7
Pleurobrachia	41.1	47.8	45.2	5.3
Cyanea	34.8	29.6	42.5	78.1
Aequorea	55.2	43.4	56.0	59.0

Digestion experiments of 6 - 8 hr duration were conducted for *Cyanea* (11 exper.), *Aurelia* (4 exper.), and *Aequorea* (2 exper.). Gut contents of specimens from only one experiment for each species have been analyzed so far. These preliminary results agree with the sparse published data (Martinussen and Båmstedt 1999) that *Cyanea* digests copepods in about 1.5 h, but *Aurelia* digests them in about 4 h. No previous data exist for digestion of larvaceans.

Because gut content (1998) and digestion rate sample analyses are incomplete, and because no abundance data exist for large jellyfish in 1997, I have not attempted to calculate feeding rates (Objective 4) and predation impacts (Objective 6) at this time. Those objectives will be met in 1999-2000.

Data compilation from SEA and APEX investigators. Hydromedusa data were received from Drs. Coyle and Sturdevant and compiled. Further analysis of hydromedusae is pending receipt of data from Robert Foy after the completion of his dissertation. Results from my analysis of hydromedusa, zooplankton, forage fish dietary data sent by Dr. Molly Sturdevant appear in previous sections of this report. Historical data on jellyfish by-catches from trawls in the Gulf of Alaska, sent by Dr. Anderson, showed a large biomass peak in 1980, when a faunal shift from shrimp and forage fish to ground fish was occurring (Fig. 5). Further analysis of these data are pending comparisons with climatological data. Analyses of data on aggregations of *Aurelia* appear in the following manuscript, which has been submitted to *Marine Ecology Progress Series*. Data on jellyfish diets and abundance were given to Thomas Okey for inclusion in the Ecopath model for Prince William Sound.

CONCLUSIONS

Among the years examined to date (1995, 1996, 1997), 1996 had markedly higher zooplankton, hydromedusa, and *Aurelia* abundances than the other years. This may have been due to apparently lower stratification in 1996 than in the other years.

The various jellyfish species ate a variety of zooplankton, and their diets overlapped substantially with those of forage fish species. Two main groups emerged -- species that ate mainly crustaceans (copepods and cladocerans); *Aurelia, Pleurobrachia*, juvenile walleye pollock, herring and sandlance, and species that ate mainly larvaceans; *Cyanea, Aequorea*, and pink salmon. These groups also were reflected by prey selection indices.

These data provide the basis for comparing the biomasses and predation pressure on zooplankton among jellyfish and forage fish in Prince William Sound.

ACKNOWLEDGMENTS

I thank my numerous collaborators in APEX and SEA for making their jellyfish data available to me. I thank Captain John Hershlieb and Karen Hershlieb of the F/V *Pagan*, for making the field work so successful. I am very grateful for funding for this research by the *Exxon Valdez* Oil Spill Trustee Council.

LITERATURE CITED

ARAI M.N., 1988. Interactions of fish and pelagic coelenterates. Can. J. Zool. 66:1913-1927.

BAIER C.T., PURCELL J.E., 1997. Chaetognaths as predators and competitors of larval fish in the South Atlantic Bight. Mar. Ecol. Prog. Ser., 146:43-53.

DEASON E.E., 1982. *Mnemiopsis leidyi* (Ctenophora) in Narragansett Bay, 1975-70: Abundance, size composition and estimation of grazing, Estuar. Coast. Shelf Sci., 15:121-134.

FANCETT M.S., 1988. Diet and prey selectivity of scyphomedusae from Port Phillip Bay, Australia. Mar. Biol., 98:503-509.

FANCETT M.S., JENKINS G.P., 1988. Predatory impact of scyphomedusae on ichthyoplankton and other zooplankton in Port Phillip Bay. J. exp. mar. Biol. Ecol., 116:63-77.

KREMER P., 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Estuaries, 2:97-105.

LARSON R.J., 1987a. Daily ration and predation by medusae and ctenophores in Saanich Inlet, B.C., Canada. Neth. J. Sea Res., 21:35-44.

LARSON R.J. 1987b. Trophic ecology of planktonic gelatinous predators in Saanich Inlet, British Columbia: Diets and prey selection. J. Plankton Res., 9:811-820.

MARTINUSSEN, M.B., BAMSTEDT, U., 1999. Nutritional ecology of gelatinous planktonic predators. Digestion rate in relation to type and amount of prey. J. Exp. Mar. Biol. Ecol. 232:61-84.

MATSAKIS S., CONOVER, R.J., 1991. Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can. J. Fish. Aquat. Sci., 48:1419-1430.

PEARRE, S., JR., 1982. Estimating prey preference by predators: uses of various indices, and a proposal of another based on χ^2. Can. J. Fish. Aquat. Sci. 39:914-923.

PURCELL J.E., 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull. Mar. Sci., 37:739-755.

PURCELL J.E., 1989. Predation by the hydromedusa *Aequorea victoria* on fish larvae and eggs at a herring spawning ground in British Columbia. Can. J. Fish. Aquat.Sci. 46:1415-1427

PURCELL J.E., 1990. Soft-bodied zooplankton predators and competitors of larval herring (*Clupea harengus pallasi*) at herring spawning grounds in British Columbia. Can. J. Fish. Aquat. Sci., 47:505-515.

PURCELL J.E., 1992. Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay. Mar. Ecol. Prog. Ser., 87:65-76.

PURCELL J.E., 1997. Pelagic cnidarians and ctenophores as predators: Selective predation, feeding rates, and effects on prey populations. Ann. Inst. Oceanogr. Paris, 73:125-137.

PURCELL J.E., GROVER J.J., 1990. Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. Mar. Ecol. Prog. Ser., 59:55-67.

PURCELL J.E., NEMAZIE D.A., DORSEY S.E., HOUDE E.D., GAMBLE J.C., 1994b. Predation mortality of bay anchovy (*Anchoa mitchilli*) eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Mar. Ecol. Prog. Ser., 114:47-58.

PURCELL J.E., WHITE J.R., ROMAN M.R., 1994b. Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay. Limnol. Oceanogr., 39:263-278.

SCHOENER, T.W., 1974. Resource partitioning in ecological communities. Science 185:27-39.

FIGURE CAPTIONS

Fig. 1. Zooplankton (numbers per m^3) in North (N), Central (C), and South (S) regions of Prince William Sound. Cope = copepods. Data of Sturdevant (1995, 1996) and Purcell/Shirley (1997). Samples collected with 243 or 250 μm mesh plankton net.

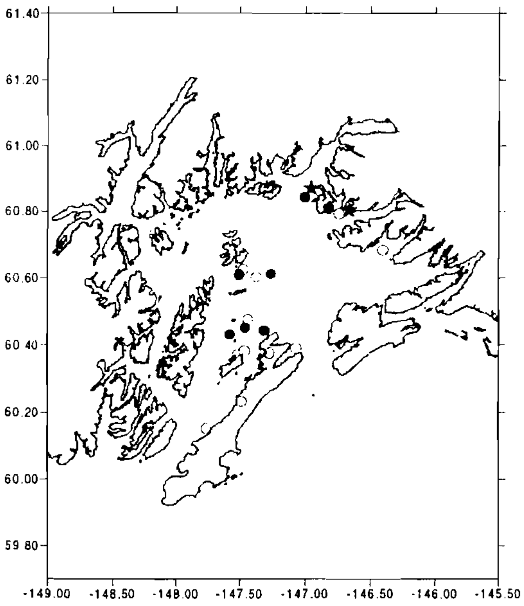
Fig. 2. Densities of small jellyfish (hydromedusae) in Prince William Sound were greater in 1996 (mean 11.2 medusae m^{-3}) than in 1995 (2.2 m^{-3}) or in 1997 (2.5 m^{-3}). Data of Sturdevant (1995, 1996) and Purcell/Shirley (1997).

Fig. 3. Gut contents of jellyfish and forage fish from Prince William Sound. Cope = copepods. Data of Purcell (jellyfish) and Sturdevant (fish).

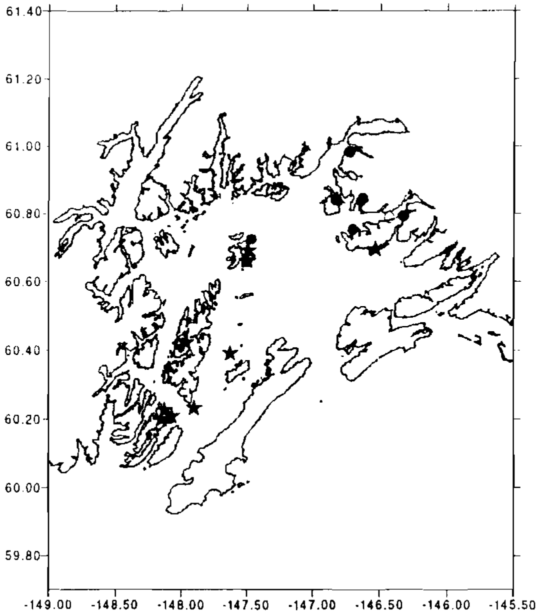
Fig. 4. Prey selection by (A) jellyfish and (B) fish from Prince William Sound. The percentages of samples showing statistically significant ($p < 0.05$) differences from percentages of zooplankton available in the environment. Data of Purcell (jellyfish) and Sturdevant (fish).

Fig. 5. Extremely large biomass of jellyfish occurred in the Gulf of Alaska in 1980. This was during the dramatic faunal shift from shrimps to ground fish (Anderson et al. 1997).

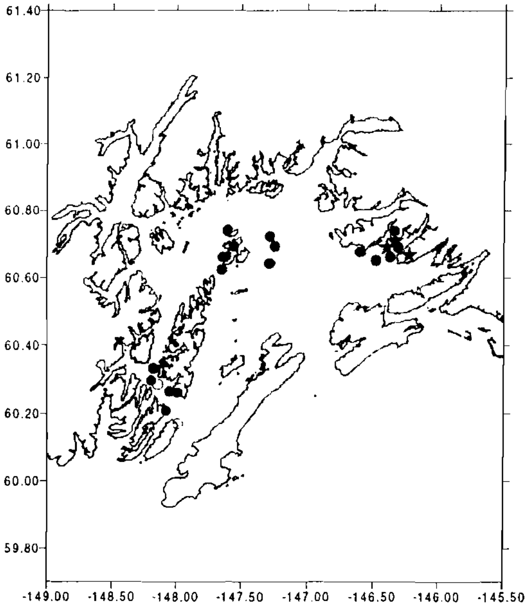
1995 PWS Hydromedusae Abundance



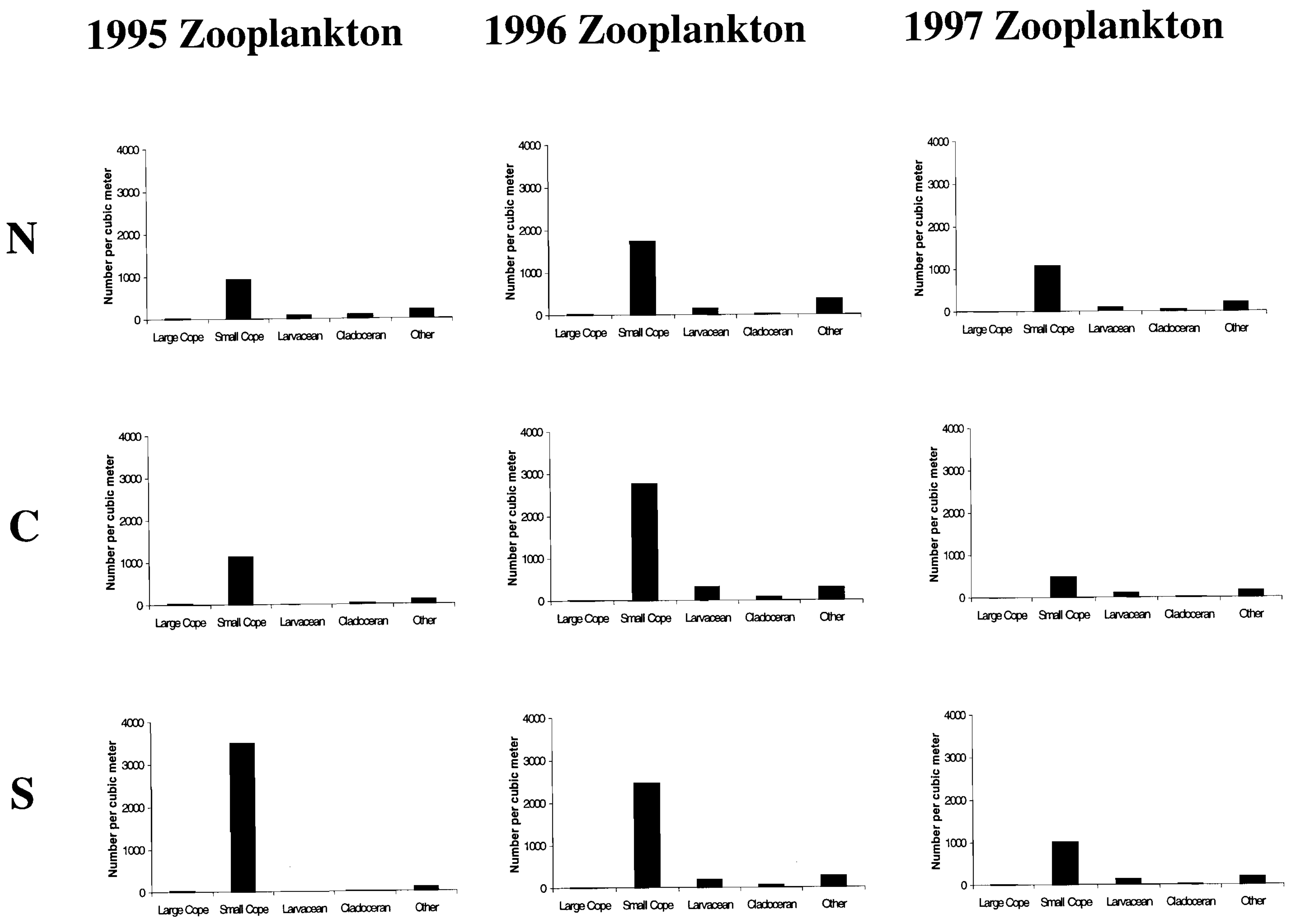
1996 PWS Hydromedusae Abundance

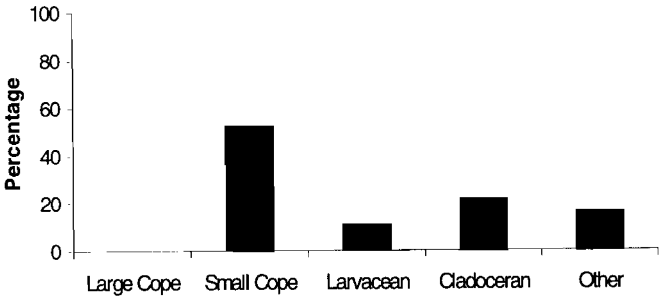


1997 PWS Hydromedusae Abundance

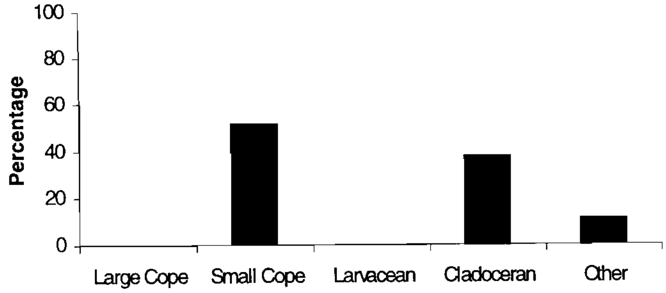


★ > 5/m^3 ● >1/m^3 ○ <1/m^3

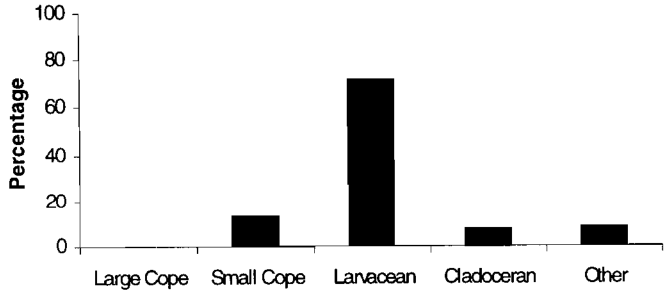

1995 Zooplankton
1996 Zooplankton
1997 Zooplankton
N
C
S
Number per cubic meter
4000
3000
2000
1000
0
Large Cope
Small Cope
Larvacean
Cladoceran
Other



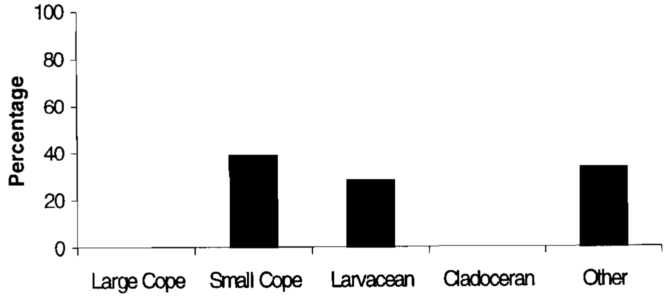
1997 PWS Aurelia Gut Contents



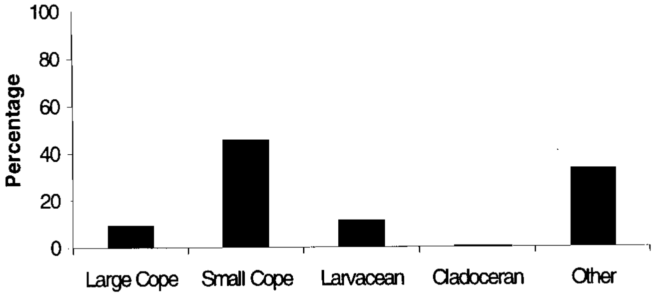
1997 PWS Pleurobrachia Gut Contents



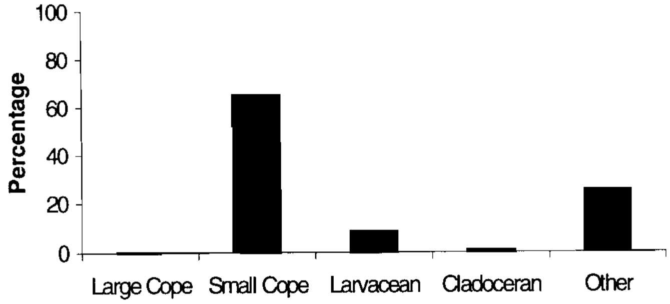
1997 PWS Cyanea Gut Contents



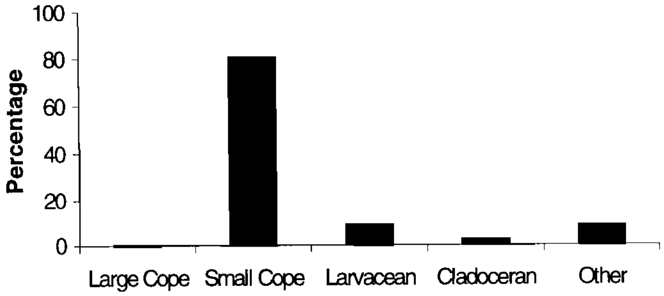
1997 PWS Aequorea Gut Contents



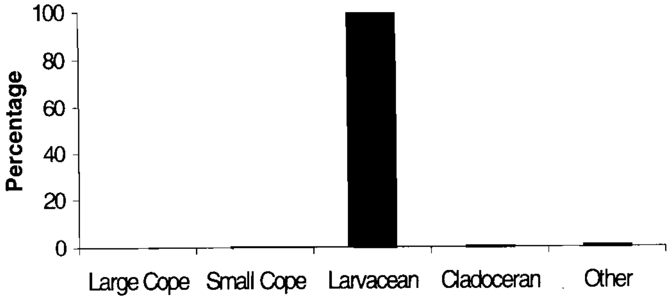
1995 PWS Pollock Gut Contents - Central



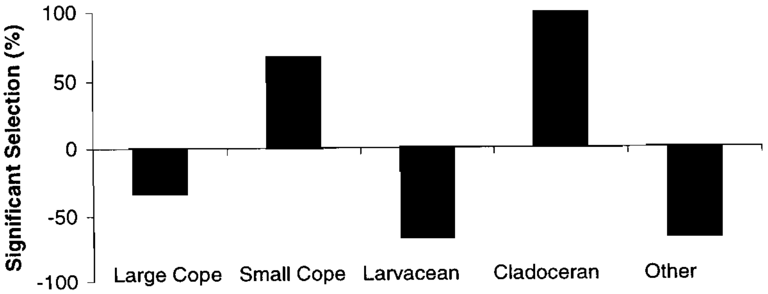
1996 PWS Sandlance Gut Contents- North



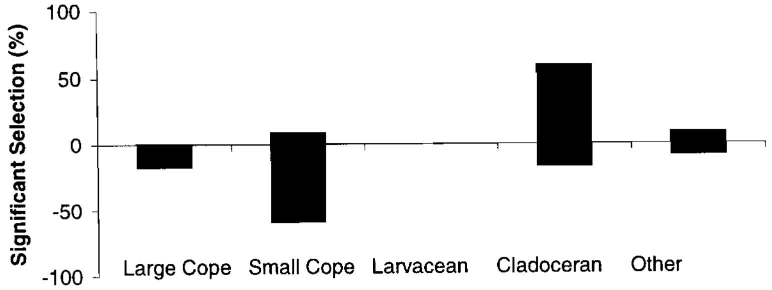
1996 PWS Herring Gut Contents - North



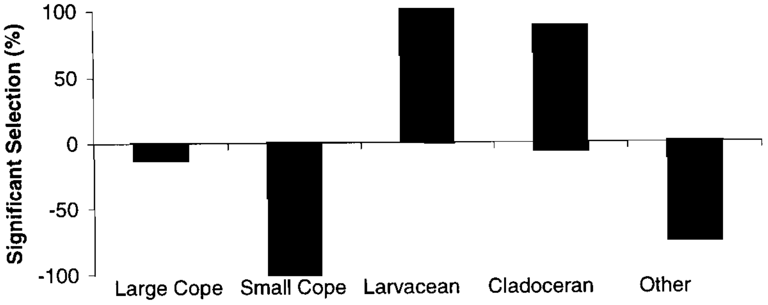
1996 PWS Salmon Gut Contents -North



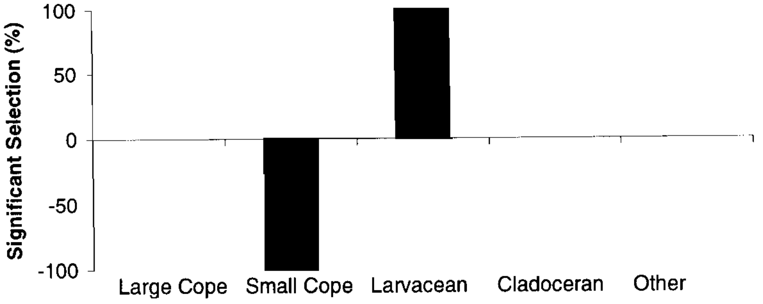
1997 PWS Jellyfish Selection Aurelia (3)



1997 PWS Jellyfish Selection Pleurobrachia (12)

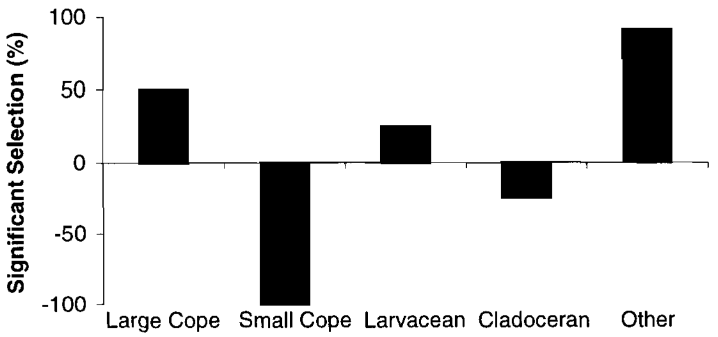


1997 PWS Jellyfish Selection Cyanea (16)

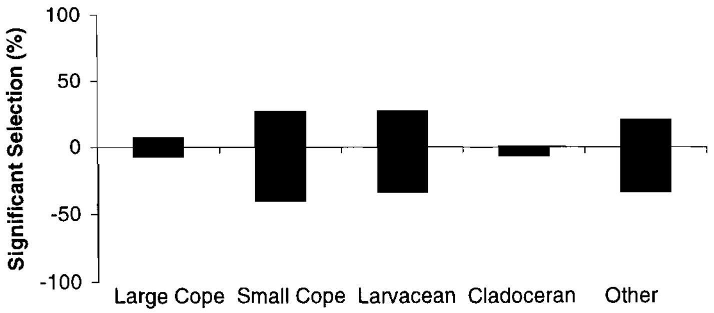


1997 PWS Jellyfish Selection Aequorea (1)

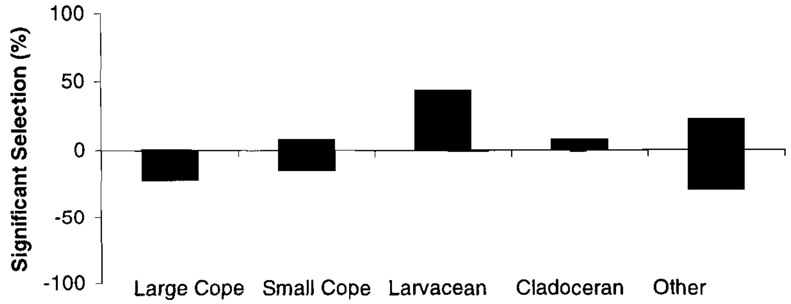
1995,1996 PWS Fish Selection Pollock(12)



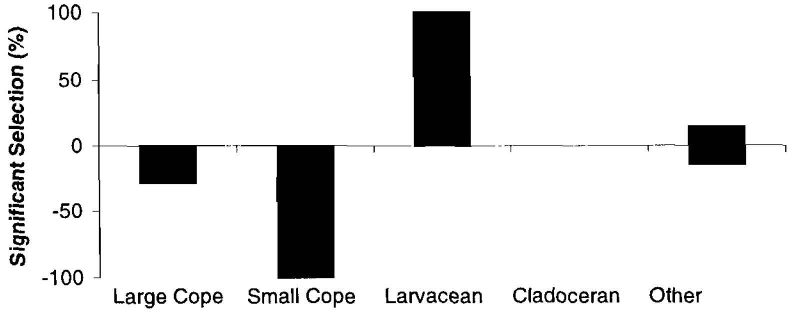
1995,1996 PWS Fish Selection Sandlance (15)

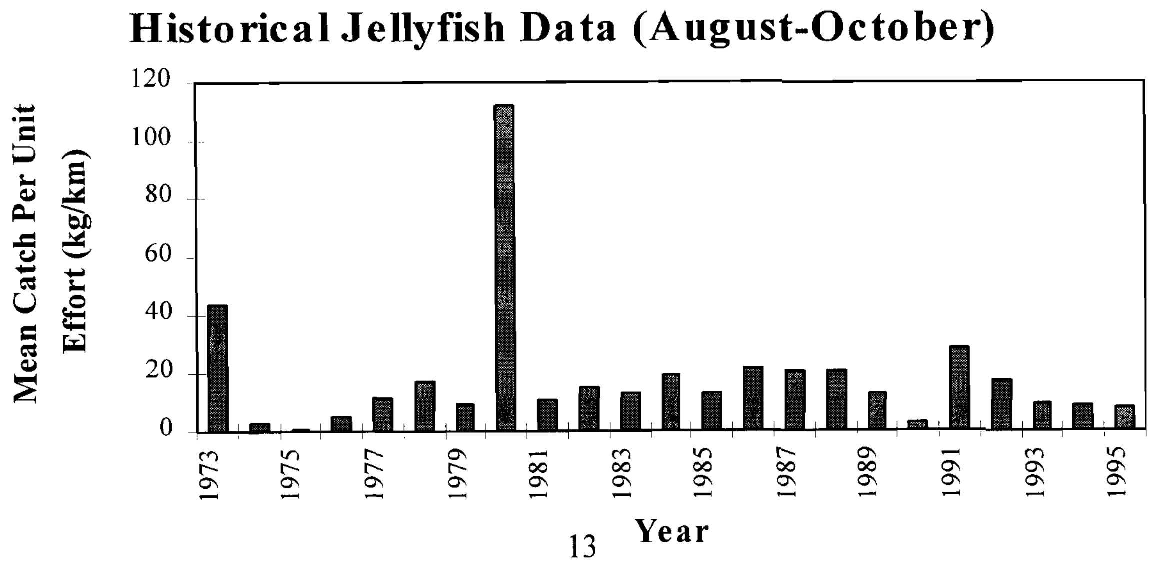


1995,1996 PWS Fish Selection Herring (14)



1995,1996 PWS Fish Selection Salmon (7)




Historical Jellyfish Data (August-October)
Mean Catch Per Unit Effort (kg/km)
120
100
80
60
40
20
0
1973
1975
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
Year

Aggregations of the jellyfish *Aurelia aurita*: Abundance, distribution, association with age-0 walleye pollock, and behaviors promoting aggregation in Prince William Sound, Alaska, USA

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KEY WORDS: jellyfish, Scyphozoa, medusae, *Aurelia aurita*, aerial surveys, acoustics, underwater video, behavior, swimming, aggregation, pollock, *Theragra chalcogramma*

Abstract

Aurelia aurita medusae occurred in aggregations with hundreds to millions of jellyfish. The aggregations wre widely distributed in inlets of Prince William Sound (PWS), Alaska. Aerial surveys of PWS in June to August in 1995, 1996, and 1997 showed marked interannual variation in the numbers of aggregations observed, from a minimum of 38 in 1997 to a maximum of 557 in 1996. Acoustic surveys showed that the aggregations extended from 0- 5 to 15 m depth. Age-0 walleye pollock (*Theragra chalcogramma*) were associated with *A. aurita*, both within and below the aggregations. All seine catches that contained pollock also contained jellyfish. Underwater video analysis showed that all medusae swam in the same direction, either up or down, in dense parts of the aggregations, suggesting that they were orienting in response to water column flow or shear, possibly generated from tidal exchange in the deep, narrow bays.

Introduction

Aurelia aurita, commonly called the "moon jelly", is a cosmopolitan scyphomedusan occurring between 70° N to 40° S (reviewed in Möller 1980). It is undoubtedly the most studied jellyfish in the world, and several recent ecological studies exist from many countries (e.g. Grøndahl 1988, Båmstedt 1990, Behrends and Schneider 1994, Lucas and Williams 1994, Olesen et al. 1994, Sullivan et al. 1994, Nielsen et al. 1997, Toyokawa et al. 1997). Great numbers of *A. aurita* medusae often occur in semi-enclosed bays and inlets, where they have been shown to reduce zooplankton and ichthyoplankton densities and change zooplankton species compositions (Möller 1980, Behrends and Schneider 1994, Olesen et al. 1994, Schneider and Behrends 1998).

Aurelia aurita medusae have been reported in discrete, high-density aggregations in many locations (Yasuda 1969, Möller 1980, Hernroth and Grøndahl 1985, Papathanassiou et al. 1987, Hamner et al. 1994, Toyokawa et al. 1997). The factors that lead to formation of aggregations are unknown, but jellyfish probably react behaviorally to physical conditions in the water column. *A. aurita* sometimes are found at the surface in convergences between Langmuir circulation cells (Hamner and Schneider 1986, Purcell unpublished data). In Saanich Inlet, British Columbia, Canada, medusae swam towards the southeast in sunlight, regardless of the sun's position, and aggregated along the eastern shore of the inlet (Hamner et al. 1994). Most jellyfish in the aggregations occurred in the surface 2 m, and reached densities of nearly 75 medusae m^{-3}. Acoustical records at 50 and 200 kHz were used to describe the circular to eliptical aggregations in Tokyo Bay, Japan, which began 6 to 8 m below the surface and reached depths of 16 to 20 m (Toyokawa et al. 1998).

Aggregations of some other scyphomedusan species have been described: *Stomolophus meleagris* (in Shanks and Graham 1987), *Pelagia noctiluca* (in Malej 1989), *Phyllorhiza punctata* (in Garcia 1990), *Linuche unguiculata* (in Larson 1992), *Cotylorhiza tuberculata* (in Kikinger 1992), and *Chrysaora fuscescens* (in Graham 1994). It should be noted that other large medusae (*Cyanea capillata, Aequorea forskalea*) did not aggregate in PWS.

The relationships of jellyfish and fish have been of particular interest because of the potential effects on commercially important fisheries. These interactions include predation on ichthyoplankton by jellyfish (reviewed in Purcell 1985, 1997, Arai 1988), potential competition between jellyfish and zooplanktivorous fish and fish larvae for prey (reviewed in Arai 1988, Purcell 1997), predation by fishes on medusae (reviewed by Arai 1988, Ates 1988, Harbison 1993), and commensal associations between fish and medusae (reviewed in Mansuetti 1963). The effects of medusae on fish may be negative (predation, competition) or positive (food, protection).

Juveniles of several fish species are known to associate with individual scyphomedusae (reviewed by Mansuetti 1963). Age-0 walleye pollock (*Theragra chalcogramma*) in Alaskan waters swim among the tentacles of *Cyanea capillata* and *Chrysaora melanaster* (van Hyning and Cooney 1974, Brodeur 1998). Brodeur (1998) used an ROV and observed up to 5 walleye pollock with *C. capillata* and up to 30 with *C. melanaster* at depths of 30 to 40 m during the day. Juveniles of several fish species have been seen under the swimming bell of *Aurelia aurita* medusae: cods (*Gadus* spp.), haddock (*Melanogrammus aeglefinus*), scads (*Trachurus* spp.), bluntnose jacks (*Hemicarnax amblyrhynchus*), and bumpers (*Chloroscombrus chrysurus*)(reviewed by Mansueti 1963).

Walleye pollock are an important commercial species in Alaskan waters and are primary forage fish for sea birds, marine mammals and fish including mature pollock which are cannibalistic (Clausen 1983, Hatch & Sanger 1992, Livingston 1993). Walleye pollock congregate and spawn in deep water in late March and April and the larvae occupy the upper 50 m of the water column in late May (Hinckley et al. 1991, Kendall et al. 1996). Walleye pollock metamorphose into juveniles in August and September (Hinckley et al. 1991, Kendall et al. 1996). In Prince William Sound, Alaska, juvenile walleye pollock are second only to juvenile Pacific herring (*Clupea pallasi*) in abundance nearshore (Stokesbury unpublished data).

Prince William Sound (PWS) has been the location of intensive ecological research following the *Exxon Valdez* oil spill in 1989. It is a complex fjord-type estuary (Schmidt 1977) located on the northern margin of the Gulf of Alaska at 60° N 146° W covering about 8800 m^2 and having 3200 km of shoreline (Grant and Higgens 1910) (Fig. 1). Many of the marine birds and mammals whose populations were injured by the oil spill feed on forage fish (herring *Clupea pallasi*, sandlance *Ammodytes hexapterus*, capelin *Mallotus villosus*, and walleye pollock). The research presented here is part of two multi-investigator projects -- SEA (Sound Ecosystem Assessment) and APEX (Alaska Predator Ecosystem eXperiment) that assess forage fish distribution and abundance using aerial surveys and acoustics, with seining and underwater video for target verification. Aggregations of *Aurelia aurita* were clearly visible during the aerial and acoustic surveys. Schools of age-0 walleye pollock sometimes were observed within and beneath those aggregations. Here, we report the distribution and abundance of *A. aurita* aggregations, their association with age-0 pollock, and the behavior of the jellyfish in the aggregations, in order to better understand their formation and maintenance.

Materials and Methods

Distribution and abundance of *Aurelia aurita* aggregations

Monthly broadscale aerial surveys were conducted from March through August in 1995, May through August in 1996 and June and July in 1997 (see Brown and Norcross, 1997)(Fig. 1). A total of 14,232 km^2 ground surface area was covered during broadscale surveys and the surface area flown per month was variable ranging from 244 km^2 in August of 1996 to a high of 2009 km^2 in July of 1996 (Fig. 2). The survey design was a modified line transect associated with the nearshore, although we sampled offshore areas when crossing bays and bodies of water to reach other shorelines. An altitude-dependent visual swath was established based on ability to observe fish schools and jellyfish aggregations between 20 and 40 degrees measured from the wing.

However, survey altitude was generally established at 274-366 m). Both flight path (transect) and targets were recorded during the survey. A hand held GPS connected to a lap top computer with a flight log program recorded latitude, longitude, and time of day in a 2-second interval and logging was interrupted in order to record targets. Therefore the target location was associated with the coordinates prior to the brief interruption of logging.

Jellyfish, especially *Aurelia aurita*, were easily enumerated by aerial survey because they formed large, white irregularly shaped aggregations that were clearly visible from the aircraft (Fig. 3). The shapes of the aggregations, aggregation counts and surface area estimates (by size category) were recorded during each survey. Size categories were established using a sighting tube to calibrate the ranges. The sighting tube was constructed of PVC pipe with a grid drawn on mylar on the end. The tube was calibrated for ground distance covered by reference line (X) for any survey altitude, when length of the grid reference line (L), focal length of the tube (F), and survey altitude (A) are known, by using the equation $X = A\left({}^{L}/{}_{F}\right)$ (Lebida and Whitmore 1985; Brady 1987). The average size categories of the aggregations are given in Table 1.

For comparisons of seasonal and interannual abundance, the total numbers and surface areas of aggregations were summed over each month and then divided by the total surface area flown during that month to obtain densities. Densities were expressed as numbers of aggregations or surface area (m^2) over the survey region (km^2).

Association of *Aurelia aurita* aggregations with age-0 walleye pollock

The PWS coastline was acoustically surveyed in July 1996. Four vessels were used during each 10 day survey (12 hours per day); an acoustic vessel, a seiner, an oceanographic vessel, and a catch processing vessel. Surveys were conducted in daylight between 0800 and 2000 h.

The acoustic vessel followed a zig-zag pattern along the shore to a distances of ≈1 km at a speed of 14 to 17 km h^{-1}. A Wesmar model 600E search light sonar was used to locate schools along the transect. When a school of fish was encountered, the acoustic vessel slowed to 9 to 11 km h^{-1} and completed a series of parallel transects perpendicular to shore using a 120 kHz BioSonics 101 echosounder with a preamplifier dual-beam transducer mounted ≈1 m under the water surface (Stokesbury et al. submitted). The standard equation $TS = 20 \log x - 66.0$ bB was used to convert reflected acoustic energy into biomass (Foote & Traynor 1988, MacLennan & Simmonds 1991).

Echo integration measurements were made in roughly 20 m (16 pings/cell at 0.5 ping s^{-1} and 2.5 to 3.0 m s^{-1} speed) horizontal by 1 m depth data cells during the July 1996 survey. Latitude and longitude was recorded simultaneously with each data cell from the GPS and provide an accurate measure of horizontal distance. Nonbiological noise was removed from these data. Species proportions and size modes per species were determined from the fish collections (described below). The species proportions, based on the number individuals per fish species in the random subsample, were converted to biomass using length/weight regressions. The echo integration measurements (kg m^{-3}) were converted into numbers of individual fish per species by use of the species proportions obtained in each seine catch. Based on frequency distributions of the data, we assumed that cells containing <0.5 fish m^{-3} were not aggregations of fish but probably zooplankton, therefore they were removed from the data set (MacLennan & Simmonds 1991, Gunderson 1993). Fish located near the bottom were difficult to distinguish acoustically; if the signal appeared corrupted, the bottom 5 m were removed. Visual examination of the echograms and fish collections agreed with these assumptions.

Once the acoustic vessel surveyed a fish school, it was sampled to determine species composition and size structure. Fish were sampled using an anchovy seine 250.0 m long by 34.0 m deep with 25.0 mm stretch mesh. Each collection was speciated and 1000 fish were randomly subsampled and measured for fork length (mm). Jellyfish also were identified in the seine catches, and relative abundances of the different species estimated.

Vertical water profiles measuring temperature and salinity at 1 m intervals, using a SeaBird instrument (SEACAT SBE19), were collected within each bay that was acoustically sampled.

Behavior of jellyfish in the aggregations

In order to determine *Aurelia aurita* swimming behavior in the aggregations, the aggregations were videotaped using a Hi-8 VCR and monitor attached to a closed-circuit underwater camera system (Fisheye, Inc. Everett, WA). Ten aggregations were filmed in July 1996, 1997, and 1998 for a total of 80 minutes of video footage. All of the video footage was examined, and two aggregations were analysed in detail with an editing Hi-8 VCR (Sony EV-S2000NTSC) and a Panasonic high resolution monitor.

Five types of information were evaluated for medusae in the aggregations. (1)Angular swimming direction measurements were taken by marking the orientation of the oral-aboral axis relative to vertical on the video monitor and using a circular protractor to measure the swimming direction. 0° was towards the water surface, and 90° was towards the right. Video analysis was limited to two-dimensions, therefore some inaccurracy is inherent in all of our measurements. (2) Turning behavior was examined by following the paths of jellyfish for as long as each remained in view without contacting another jellyfish in low densitiy areas, and after contact with other jellyfish in high density areas of an aggregation. No quantitative analysis of the swimming paths were attempted because of the lack of three dimensional resolution and short duration that individual medusae could be tracked. (3) Frequency of the swimming beat, which was used as an index of activity, was determined by counting the number of swimming bell contractions for as long as the medusae could be followed (< 30 s). (4) The vertical distance moved relative to the body depth was used instead of actual displacement, which could not be determined. This index should not be affected much by medusa sizes, which were very similar for medusae within an aggregation. Relative distances (vertical distance ÷ body depth) were measured from the video monitor for one full swimming beat cycle (< 3 s), and standardized to 1 s. (5) Relative densities of medusae were determined by counting the superposition of medusae on 42 points marked on the video monitor at 30 arbitrary times (10 s intervals) during the videotapes. Actual densities of medusae could not be measured.

Results

Distribution and abundance of *Aurelia aurita* aggregations

Aggregations of *Aurelia aurita* medusae were clearly visible during aerial surveys (Fig. 3). A total of 995 aggregations were observed during the 10 monthly surveys in Prince William Sound from 1995 to 1997. The majority (81.2%) of the aggregations were categorized as small (approximately 40 m^2 in surface area). The medium size category (approximately 100 m^2 in surface area) made up most of the remaining total (14.7%) (Fig. 4).

The abundance of aggregations followed a seasonal pattern (Fig. 5). Aggregations were not observed during aerial surveys of PWS in March, April and May. Aggregations were first visible in June of 1996. Both numbers of aggregations and total surface areas per km^2 of survey area peaked in August of 1995 and July of 1996, however, this trend was not observed in 1997. Between the months of July and August in 1995 and 1996, the abundance curve based on densities of surface areas departed from the abundance trends based on densities of numbers of aggregations. This was probably due to growth of individuals, which would increase the overall sizes of the aggregations. No aerial surveys were conducted in September, and no aggregations were observed during surveys in October.

Dramatic interannual variation in the numbers and densities of *Aurelia aurita* aggregations was observed. Moderate densities of aggregations occured in 1995, with two-fold greater densities in 1996 than 1995, and generally low densites for both summer months surveyed in 1997 (Fig. 5). Significantly more aggregations and greater surface areas were found in 15 inlets of PWS (Table 2) in 1996 than in 1995 (ANOVAs, $p < 0.05$) or in 1997 (ANOVAs, $p< 0.01$).

Most aggregations were observed in bays off the main sound (Fig. 6), possibly due to the concentration of survey effort there (Fig. 1). Aggregations were observed consistently in 15 bays during one or more survey in every year. The aggregations were most widely distributed in 2 - 21 July 1996 (15 of 15 bays plus other sites not occupied in other years), as compared with 9 of 15 bays plus other sites in 5 - 22 August 1995 and 5 of 15 bays in 12 - 21 June 1997 (Table 2). Bays in southwestern PWS (Whale, Drier, Jackpot) and in northeastern PWS (Port Fidalgo, Port Gravina, Simpson Bay) had the highest numbers and surface areas of aggregations in 1995 and 1996. Ewan Bay and Port Fidalgo were the only locations that had aggregations every year. Also striking was the lack of aggregations in the large inlets of northern PWS that were surveyed by air (Unakwik Inlet, and Port Valdez and Valdez Arm)(Fig. 6).

Association of *Aurelia aurita* aggregations with age-0 walleye pollock

Schools of young-of-the-year walleye pollock were observed in videotapes and acoustically under and within aggregations of *Aurelia aurita* medusae. The juvenile fish were observed associated with 2 (in Paddy Bay and Port Gravina in July 1996) of the 10 videotaped aggregations. In Simpson and Drier Bays, where acoustic transects were completed through jellyfish aggregations, *A. aurita* appeared to extend from the water's surface to the beginning of the thermocline (Fig. 7). Mean densities of young-of-the-year walleye pollock schools observed in Simpson and Drier Bays were 13.9 m^{-3} and 35.0 m^{-3}, respectively (Table 3).

Seine catches along the transects in Simpson and Drier Bays confirmed that the acoustic targets were predominately age-0 walleye pollock. The largest catches of juvenile walleye pollock from 52 seine sets in July, 1996 in PWS were from Simpson Bay (394 fish) and Drier Bay (7,000 fish). Age-0 walleye pollock averaged 11.2 ± 28.6 m^{-3} in the other seine catches. Sizes of the fish (mean fork length < 61 mm) showed them to be young of the year.

Aurelia aurita was the only large medusa collected in the seine catch in Simpson Bay. Some *Aequorea forskalea* and *Cyanea capillata* medusae also occurred in the seine catch from Drier Bay. The jellyfish catches in Drier and Simpson Bays were much greater than in all but one of the other 50 seine sets in other locations.

In all seine sets in which they were collected (27%), age-0 walleye pollock were collected with jellyfish; they did not occur alone or with herring only (Table 4). By constrast, herring often occurred alone (27%) in the seine catches. Jellyfish, juvenile walleye pollock, and herring occurred together in 4 of 52 seine samples. Although juvenile walleye pollock were only collected with jellyfish, herring were as likely to be collected alone as with jellyfish. The difference between the two fish species occurring with and without jellyfish was significant (Chi-square = 7.9, $p = 0.005$). Jellyfish occurred alone in 25% of the seine samples.

Behavior of jellyfish in the aggregations

Aurelia aurita medusae were observed on videotapes of 10 aggregations. Two aggregations were studied in detail where camera motion was minimized. A video transect through Aggregation 1 was taken at 4.3 m depth on 18 July 1998 at 17:00 hr along the southwestern part of Chenega Island (60° 19.55' N, 148° 9.20' W), where bottom depth was 21.5 m. Aggregation 2, which extended from the surface to 12.3 m, was videotaped at 4.6 m at 08:00 hr on 29 July 1998 in Jackpot Bay (60° 20.22' N 148° 16.17' W). The following results for Aggregations 1 and 2 were representative of those for other aggregations.

We tested three hypotheses to explain the occurrence of *Aurelia aurita* aggregations. The first was that increased turning by medusae in response to some unknown stimulus, or after contact with one another, would lead to increased densities, such as shown for the scyphomedusa *Linuche unguiculata* (Larson 1992), and for other plankton (e.g. Buskey et al. 1996). All medusae were swimming, and most were oriented vertically (Table 5, Figs. 8, 9). Of the several thousands of medusae on the videotapes, only 29 medusae were observed turning without contact with other medusae (24 turned from horizontal to downward swimming, and 5 from horizontal to upward swimming). If turning were the mechanism for aggregation, we would expect to see a higher proportion of non-vertical medusae in the densest parts of the aggregations. In Aggregation 1, the opposite was observed; medsae in low density locations showed greater deviations from vertical (Fig. 9).

In Aggregation 2, a dense central column of upward-swimming medusae spread horizontally near the surface (96% relative density), where several layers of medusae in this sub-surface canopy swam upwards while repeatedly contacting one another. On the lower and outer edges of the horizontal canopy of the aggregation (91% relative density), some medusae were observed turning from upward to downward orientation, moving into areas of lower (25%) relative density and generally downward swimming orientations. The up-to-downward turning observed in Aggregation 2 took medusae away from the densest part of the aggregation. In both aggregations, the relative densities of the medusae were significantly different between the dense areas of medusae swimming in one direction (either upward or downward) and the areas of medusae in mixed orientations (Tables 5, 6). Eight other aggregations had a similar structure, with a dense central core oriented either vertically or in a horizontal or tilted layer, with medusae generally swimming upwards on both sides of the dense layer. We reject the first hypothesis; increased turning did not lead to increased densities of medusae.

Our second hypothesis was that swimming was reduced where medusae occurred in high densities as compared with low densities. This could result in them concentrating, as seen for *Daphnia* (Larsson and Kleiven 1996). This hypothesis was tested by using two indicators of swimming -- swimming beat frequency and vertical distance moved. Medusae in most aggregations, where individual medusae could be followed for only 2 to 3 seconds (1 full beat), did not show differences in swimming beat frequencies depending on density or orientation (Tables 5, 6). Medusae in Aggregation 1 showed very similar rates for upward- and downward-swimming medusae at high and low relative densities (ANOVA, $p = 0.36$). The beat frequencies of upward- (mean 0.43 beats s^{-1}, $n = 20$) and downward- (mean 0.41 beats s^{-1}, $n = 15$) swimming medusae were compared from the low density areas of three additional aggregations and found not to be significantly different (ANOVA, $p = 0.48$). Medusae in the high density areas of those aggregations could not be tracked long enough to determine the beat frequencies. Generally, medusae in high densities had equivalent swimming beat frequencies to those in low densities

By contrast, swimming beat frequencies differed in different areas of Aggregation 2, where individual medusae could be followed for up to 25 s (Tables 5, 6). In areas of high relative densities in Aggregation 2, uniformly upward-swimming medusae had higher beat frequencies (0.57 beats s^{-1}) than downward-swimming medusae (0.36 beats s^{-1}), which had just reversed swimming direction at the bottom of the dense canopy of the aggregation (ANOVA, $p = 4 \times 10^{-8}$). The reduced swimming beat frequency of the downward-turning medusae could slow their movement away from the densest part of the aggregation. In areas of low density where medusae were oriented in mixed directions, the beat frequencies of upward- and downward-swimming medusae were not significantly different (ANOVA, $p = 0.16$). Upward-swimming medusae also had similar beat frequencies in both high and low density areas (ANOVA, $p = 0.58$).

We examined Aggregation 2 to test whether the vertical distance moved relative to body depth differed between dense and less dense areas of the aggregation. There was a significant difference in relative distance s^{-1} among the different areas of the aggregation (ANOVA, $F = 8.02$, $p = 2.44 \times 10^{-4}$). Medusae swimming up in low density areas moved further ((1.04 s^{-1}) than medusae swimming up in high densities or down in both low and high densities (0.30 - 0.41 s^{-1}; Table 5)(ANOVAs, $F = 10.07 - 11.12$, $p < 0.01$ for all pairs compared). Comparisons among all other pairs (downward-swimming medusae in high densities, in low densities, and upward-swimming medusae in high densities) were not significant ($F = 0.21 - 1.03$); the small vertical distance traveled by those medusae would help to concentrate them. Medusae oriented upward in high densities were impeded in vertical motion by collisions with other medusae. We could not reject the second hypothesis; reduced swimming, resulting from contacts among medusae, could have lead to increased densities of medusae.

Our third hypothesis was that medusae swam directionally in response to flow fields in the water column, and that differences in speed between medusa swimming and water flow resulted in aggregation. Medusae have been observed orienting and aggregating in convergent zones of Langmuir circulations and fronts (Hamner and Schneider 1986, Shanks and Graham 1987, Graham 1994). Convincing evidence supporting this hypothesis was found in Aggregation 1 (Fig. 9, Table 5). A 3-min horizontal transect through this aggregation showed three areas; one side where medusae were swimming downwards in high (46%) relative density, a central area where medusae were in mixed orientations and low (7%) relative density, and the opposite side where medusae were swimming upwards in high (22%) relative density. The relative densities were significantly different among the three areas (Table 6). Unfortunately, no data on water flow were available, and we must deduce that the highly directed swimming by medusae was most likely in response to flow or shear in the water column.

In summary, we observed three factors that could act to concentrate *Aurelia aurita* medusae. One was that their swimming was highly directional in some areas, apparently oriented against flow or shear fields in the water column. Second, upwards-swimming medusae that were already densely aggregated were unable to move as far as medusae in low density areas. And third, although some upwards-swimming medusae underneath dense aggregations reversed swimming direction taking them out of the densest areas, their swimming beat frequency and relative vertical distance moved were lower than for other medusae.

Discussion

Distribution and abundance of *Aurelia aurita* aggregations

Marked interannual differences were seen in the numbers of *Aurelia aurita* aggregations in Prince William Sound (PWS), with 1996 having by far the greatest number. 1996 also showed high densities of hydromedusae in PWS (Coyle, Cooney, and Sturdevant unpublished data). That year was characterized by deep mixing (Vaughan submitted), and high zooplankton densities (Sturdevant et al. 1997). 1997 was an unusually warm year (Haldorson and Shirley 1998), reflecting atmospheric effects of the extremely strong El Niño that developed in the southern hemisphere. 1997 also showed low densities of hydromedusae and zooplankton (Purcell and Shirley unpublished data).

Aurelia aurita aggregations were observed in nearly every small bay and inlet of PWS, however, they were noticeably absent in large inlets in the north (Unakwik Inlet, Valdez Arm and Port Valdez). These large inlets are very steep and deep, and perhaps the steep topography does not promote vertical water fluxes (Simpson and Hunter 1974) or aggregation formation. We believe that the combination of tidally-driven water circulation patterns in bays and the behavior of *A. aurita*, which appears to utilize flow or shear in the water column, promotes aggregation of the medusae in the small bays and inlets.

Toyokawa et al. (1997) reported that *Aurelia aurita* aggregations drifted with the tidal currents, however Hamner et al. (1994) states that the aggregations maintained their position along the eastern shoreline of Saanich Inlet and did not move with the tides. Our sampling did not allow us to observe whether or not the aggregations drifted with the tides.

Association of *Aurelia aurita* aggregations with age-0 walleye pollock

Associations between juvenile walleye pollock and individual *Cyanea capillata* and *Chrysaora melanaster* have been described previously (summarized in Brodeur 1998). Acoustic records and seine catches in Simpson and Drier Bays in July 1996 suggest that the pollock were associated primarily with *Aurelia aurita* aggregations and not other jellyfish species. Throughout an intense 10 day broadscale survey of the nearshore ichthyofauna, young-of-the-year walleye pollock were only collected in association with *A. aurita*. Yet, young-of-the-year walleye pollock were the second most abundant fish collected during this survey (Stokesbury unpublished data). Furthermore, two schools of age-0 walleye pollock was documented by underwater video in association with aggregations of *A. aurita*. To our knowledge, the association of fish schools with jellyfish aggregations has not been reported previously.

Commensal relationships among fish and jellyfish are believed to protect the juvenile fish from their many vertebrate predators (e.g. Brodeur 1998) and possibly provide food, either as prey stolen from the jellyfish or the jellyfish themselves. Juvenile butterfish (*Peprilus* *triacanthus*) were eaten by birds when displaced from their jellyfish host, *Cyanea capillata* (Duffy 1988), and are known to eat parts of the jellyfish (Mansueti 1963). Juvenile walleye pollock are eaten by a variety of fish, sea birds, and pinnepeds (Table 7). For example, young-of-the-year walleye pollock make up 19% of the diet of tufted puffins (*Fratercula cirrhata*), and those birds consumed an estimated 11 billion individuals along the Gulf of Alaska in 1986 (Hatch and Sanger 1992). Interestingly, in PWS, age-0 walleye pollock were eaten by only one bird species, but older juveniles were eaten by several species (Table 7). Perhaps the association of age-0 walleye pollock with aggregations of *Aurelia aurita* medusae reduces capture of that age class by diving birds in PWS.

Behavior of jellyfish in the aggregations

Hamner et al. (1994) described the formation of *Aurelia aurita* aggregations in Saanich Inlet, a fjord on Vancouver Island, where the jellyfish swam horizontally towards the southeast in sunlight. They did not show horizontal swimming before sunrise, when the sky was overcast, or at night. Aggregations in PWS existed during both clear and overcast days. Jellyfish in PWS (~60.5° N) would have experienced approximately 19 h of daylight in mid-June, 18.5 h in mid-July, and 15.5 h in mid-August, which is more than in Saanich Inlet (49° N). All of our sampling was in daylight, and we do not know if the aggregations dispersed during the short night in PWS, or how long each aggregation persists.

Our observations on the swimming behavior of *Aurelia aurita* medusae in aggregations concur with data on isolated medusae from Costello et al. (1998), specifically, that most individuals swim all the time (98 ± 2%) and that most swim in vertical paths. Hamner et al. (1994) reported that once *A. aurita* medusae reached an aggregation, their directed horizontal swimming changed to vertical. We did not oberve horizontal directional swimming by medusae in PWS.

In PWS, jellyfish in one part of Aggregation 1 all swam upwards and all individuals in another part swam down, suggesting that the medusae in this aggregation were swimming in a convection cell on a scale of about 10 m in diameter. This is supported by Toyokawa et al. (1997), who described "ring-like" structure of some *Aurelia aurita* aggregations. In other locations, jellyfish, including *A. aurita*, have been seen in parallel rows at the water surface. Presumably, these medusae were concentrated in Langmuir cells, which are wind-driven, surface convection cells that are perpendicular to the wind direction (Hamner and Schneider 1986, Larson 1992). In PWS, aggregations of *A. aurita* were generally elongated (Table 1) and began either near the surface or at about 4 m below the water surface. We believe that the convection currents experienced by *A. aurita* in PWS probably were from multiple origins, including wind-driven Langmuir cells that form in the inlets (S.M. Gay, pers. comm.). Also, the kinetic energy of high-speed currents is converted to strong vertical water flows by friction over shallow bottom topography (Mackas et al. 1985). The large tides (about 8 m amplitude) in the narrow fjords of PWS may frequently create regions of strong shear in the water column. In summary, we believe that the directional swimming observed in aggregations of *A aurita* suggests that the medusae orient to differences in flow or shear in the water column, and that this determines whether or not an aggregation forms.

A few species of jellyfish, including *Aurelia aurita, Chrysaora fuscesens,* and *Stomolophus meleagris*, have been observed swimming against the prevailing water flow, which concentrates them in downwelling convergences between Langmuir cells (Hamner and Schneider 1986), and also occurs in aquaria with circular flow (Purcell, Graham pers. obs.). The swimming currents generated ("bioconvection") by the medusae in the aggregations may promote formation and persistence of the aggregations, as for microorganisms (Kils 1993). The mechanism by which medusae orient to flow is not known. *Aurelia aurita* has oscelli for sensing light, and statocyts for sensing gravity at eight evenly-spaced locations around the swimming bell margin (Hyman 1940). Thus, the sensory capabilities exist to control their orientation.

Behavioral mechanisms probably are responsible for maintaining aggregations of *Aurelia aurita* in PWS. They swam in straight paths and therefore did not maintain the aggregations by swimming in circles, as seen for *Linuche unguiculata* (Larson 1992), or increased rates of turning (klinokinesis) as used for swarm formation in copepods (Buskey et al. 1996). Our results are in contrast to those of Hamner et al. (1994), who reported "constant collision and turning" by *A. aurita* in high density aggregations. Reduced swimming, which acted to concentrate *Daphnia* in high food concentrations (Larsson and Kleiven 1996), may act to concentrate *A. aurita* in dense aggregations where contacts between medusae occur.

We do not know if chemical cues attracted medusae to aggregate. Chemoreception that could facilitate intraspecific interactions has not been investigated for any gelatinous zooplankton, to our knowledge. Observations of the mating behavior of male cubomedusae, *Tripedalia cystophora*, did not demonstrate chemoreception, but it was not tested directly (Stewart 1996). The only example of distance chemoreception between different species of medusae of which we are aware is for hydromedusae; *Stomotoca atra* ceased swimming in the presence of *Aequorea victoria*, a potential predator (Lenhoff 1964). Other examples suggest that chemoreception is used to locate food. *Aurelia aurita* medusae aggregated near high food (*Artemia* nauplii) concentrations and water conditioned by the prey in laboratory experiments (Arai 1992). *Beroe* spp. ctenophores may use chemoreception to locate their ctenophore prey (Falkenhaug et al. 1995). These tantalizing examples suggest that gelatinous species may use distance chemoreception in a variety of ways.

Aurelia aurita medusae may gain several advantages from aggregation. First, Hamner et al. (1994) found that about 5% of male *Aurelia aurita* were releasing sperm in aggregations, and concluded that the aggregations function to increase fertilization success. Second, vertical swimming is displayed by a variety of estuarine organisms, which serves to retain them in the estuaries (e.g. Wooldridge and Erasmus 1980, Tankersly et al. 1995). Retention near shore is advantageous because *A. aurita* medusae release planulae that settle on hard substrata (Hernroth and Grondahl 1985). Third, there may be advantages for feeding. Plankton densities are greater near shore than off shore in PWS (Cooney, Coyle, Sturdevant, Purcell, and Shirley unpublished data). Also, plankton organisms are concentrated in convergences and fronts (e.g. Graham 1984), so the medusae would aggregate where food densities are greatest. Thus, the potential advantages of aggregation are numerous.

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References

Arai MN (1988) Interactions of fish and pelagic coelenterates. Can J Zool 66:1913-1927

Arai MN (1992) Attraction of *Aurelia* and *Aequorea* to prey. Hydrobiologia 216/217:363-366

Ates RML (1988) Medusivorous fishes, a review. Zool Mededelingen 62:29-42

Båmstedt U (1990) Trophodynamics of scyphomedusae *Aurelia aurita.* Predation rate in relation to abundance, size and type of prey organism. J Plankton Res 12:215-229

Behrends G, Schneider G (1995) Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). Mar Ecol Prog Ser 127:39-45

Brady JA (1987) Distribution, timing, relative biomass indices for Pacific herring as determined by aerial surveys in Prince William Sound 1978-1987. Prince William Sound Data Report No. 87-14. Alaska Department of Fish and Game, Division of Commercial Fisheries, Juneau, AK, 11 pp.

Brodeur RD (1998) *In situ* observations of the association between juvenile fishes and scyphomedusae in the Bering Sea. Mar Ecol Prog Ser 163:11-20

Brown ED, Norcross BL (1997) Assessment of forage fish distribution and abundance using aerial surveys: survey design and methodology. Pp 25-53 in Cooney RT (ed) Sound Ecosystem Assessment (SEA) -- an integrated science plan for the restoration of injured species in Prince William Sound. FY96 Annual Report for the Exxon Valdez Trustee Council, Anchorage, Alaska

Buskey EJ, Peterson JO, Ambler JW (1996) The role of photoreception in the swarming behavior of the copepod *Dioithona oculata*. Pp 301-313 in Zooplankton: sensory ecology and physiology. Lenz PH, Hartline DK, Purcell JE, Macmillan J (eds). Gordon and Breach Publ

Clausen DM (1983) Food of walleye pollock, *Theragra chalcogramma*, in an embayment of southeastern Alaska. Fish Bull 81:637-642

Costello JH, Colin SP (1994) Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. Mar Biol 121:327-334

Costello JH, Klos E, Ford MD (1998) *In situ* time budgets of the scyphomedusae *Aurelia aurita, Cyanea* sp., and *Chrysaora quinquecirrha*. J Plankton Res 20:383-391

Duffy DC (1988) Predator-prey interactions between common terns and butterfish. Ornis Scand 19:160-163

Faulkenhaug T and Stabell OB (1995) Chemical ecology of predator-prey interactions in ctenophores. Mar Fresh Behav Physiol 27:249-260

Foote KG, Traynor JJ (1988) Comparison of walleye pollock target strength estimates determined from *in situ* measurements and calculations based in swimbladder form. J acoust Soc Am 83:9-17

Garcia JR (1990) Population dynamics and production of *Phyllorhiza punctata* (Cnidaria: Scyphozoa) in Laguna Joyuda, Puerto Rico. Mar Ecol. Prog Ser 64:243-251

Graham WM (1994) The physical oceanography and ecology of upwelling shadows. PhD Dissertation, University of California, Santa Cruz, 204 pp.

Grant, U.S., and Higgens, D.F. 1910. Reconnaissance of the geology and mineral resources of Prince William Sound, Alaska, U.S. Geological Survey Bulletin No. 443. 89 p.

Grøndahl F (1988) A comparative ecologial study on the scyphozoans *Aurelia aurita, Cyanea capillata* and *C. larmarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. Mar Biol 97:541-550

Gunderson RD (1993) Surveys of Fisheries Resources. John Wilet & Sons, Inc., New York

Hamner WM (1995) Sensory ecology of scyphomedusae. Mar freshwater Behav Physiol 26:101-118

Hamner WM, Schneider D (1986) Regularly spaced rows of medusae in the Bering Sea: Role of Langmuir circulation. Limnol Oceanogr 31:171-177

Hamner WM, Hamner PP, Strand SW (1994) Sun-compass migration by *Aurelia aurita* (Scyphozoa): population retention and reproduction in Saanich Inlet, British Columbia. Mar Biol. 119:347-356

Harbison GR (1993) The potential of fishes for the control of gelatinous zooplankton. ICES CM 1993/L:74

Hatch SA, Sanger GA (1992) Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Mar Ecol Prog Ser 80:1-14

Hay SJ, Hislop JRG, Shanks AM (1990) North Sea scyphomedusae: summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Neth J Sea Res 25:113-130

Hernroth L, Grøndahl F (1985) On the biology of *Aurelia aurita* (L.). 2. Major factors regulating the occurrence of ephyrae and young medusae in the Gullmar Fjord, western Sweden. Bull mar Sci 37:567-576

Hinckley S, Bailey KM, Picquelle SJ, Schumacher JD, Stabeno PJ (1991) Transport, distribution, and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can J Fish Aquat Sci 48:91-98

Hyman LH (1940) The invertebrates: Protozoa through Ctenophora. McGraw-Hill, NY

Kendall AWJ, Schumacher JD, Kim S (1996) Walleye pollock recruitment in Shelikof Strait: applied fisheries oceanography. Fish Oceanogr 5 (Suppl. 1):4-18

Kikinger R (1992) *Cotylorhiza tuberculata* (Cnidaria: Scyphozoa) -- life history of a stationary population. Pubbl. Staz. Zool. Napoli (I: Mar Ecol) 13:333-362

Kils U (1993) Formation of micropatches by zooplankton-driven microturbulences. Bull Mar Sci 53:160-169

Larson RJ (1992) Riding Langmuir circulations and swimming in circles: a novel form of clustering behavior by the scyphomedusa *Linuche unguiculata*. Mar Biol 112:229-235

Larsson P, Kleiven OT (1996) Food search and swimming speed in *Daphnia*. Pp 375-387 in Zooplankton: sensory ecology and physiology. Lenz PH, Hartline DK, Purcell JE, Macmillan J (eds). Gordon and Breach Publ

Lebida RC, Whitmore DC (1985) Bering Sea herring aerial survey manual. Bristol Bay Data Report No. 85-2. Alaska Department of Fish and Game, Division of Commercial Fisheries, Anchorage AK

Lenhoff HM (1964) Reversible inhibition of swimming in *Stomotoca atra* by mesogleal extracts of some other medusae. Biol Bull 126:115-120

Livingston PA (1993) Importance of predation by groundfish, marine mammals and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasi* in the eastern Bering Sea. Mar Ecol Prog Ser 102:205-215

Lucas CH, Williams JA (1994) Population dynamics of scyphomedusa *Aurelia aurita* in Southampton water. J Plankton Res 16:879-895

Mackas DL, Denman KL, Abbott MR (1985) Plankton patchiness: biology in the physical vernacular. Bull Mar Sci 37:652-674

MacLennan DN, Simmonds EJ (1991) Fisheries Acoustics. Chapman & Hall, London

Malej A (1989) Behaviour and trophic ecology of the jellyfish *Pelagia noctiluca* (Forsskal, 1775). J Exp Mar Biol Ecol 126:259-270

Mansueti R (1963) Symbiotic behaviour between small fishes and jellyfishes, with new data on that between the stromateid, *Peprilus alepidotus*, and the scyphomedusae, *Chrysaora quinquecirrha*. Copeia 1963:40-80

Möller H (1980) Scyphomedusa as predators and food competitors of larval fish. Merresforschung 28:90-100

Nielsen AS, Pedersen AW, Riisgård HU (1997) Implications of density driven currents for interaction between jellyfish (*Aurelia aurita*) and zooplankton in a Danish fjord. Sarsia 82:297-305

Okey TA, Pauly D (1998) Trophic mass-balance model of Alaska's Prince William Sound Ecosystem, for the post-spill period 1994-1996. University of British Columbia Fisheries Centre Research Reports 6, 1-144

Olesen NJ, Frandsen K, Riisgård HU (1994) Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. Mar Ecol Prog Ser 105:9-18

Papathanassiou E, Panayotidis P, Anagnostaki K (1987) Notes on the biology and ecology of the jellyfish *Aurelia aurita* Lam. In Elefsis Bay (Saronikos Gulf, Greece). Mar Ecol 8:49-58

Purcell JE (1985) Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull Mar Sci 37:739-755

Purcell JE (1997) Pelagic cnidarians and ctenophores as predators: Selective predation, feeding rates and effects on prey populations. Ann Inst Oceanogr Paris 73:125-137

Purcell JE, Nemazie DA, Dorsey SE, Houde ED, Gamble JC. (1994) Predation mortality of bay anchovy (*Anchoa mitchilli*) eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Mar Ecol Prog Ser 114:47-58

Schmidt, G.M. 1977. The exchange of water between Prince William Sound and the Gulf of Alaska. Masters Thesis, University of Alaska, Fairbanks AK. 116 p.

Schneider G, Behrends G (1998) Top-down conrol in a neritic plankton system by *Aurelia aurita* medusae -- a summary. Ophelia 48:71-82

Shanks AL, Graham WM (1987) Orientated swimming in the jellyfish *Stomolophus meleagris* L. Agassiz (Scyphozoan: Rhizostomida). J Exp Mar Biol. Ecol 108:159-169

Simpson JH (1994) Fronts in the Irish Sea. Nature 250:404-406

Springer AM (1992) A review: walleye pollock in the North Pacific -- How much difference do they really make? Fish Oceanogr 1:80-96

Stewart SE (1996) Field behavior of *Tripedalia cystophora* (Class Cubozoa). Pp 511-524 in Zooplankton: sensory ecology and physiology. Lenz PH, Hartline DK, Purcell JE, Macmillan J (eds). Gordon and Breach Publ

Stokesbury KDE, Kirsch J, Brown ED, Thomas GL, Norcross BL (submitted) Seasonal variability in Pacific herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) spatial distributions in Prince William Sound, Alaska. Fish Bull US

Sturdevant M (1997) Diet overlap, prey selection and potential food competition among forage fish species (Restoration Project 96163C) In Duffy DC (ed) APEX Project: Alaska Predator Ecolsystem Experiment in Prince William Sound and the Gulf of Alaska. Exxon Valdez Oil Spill Restoration Project Annual Report, Anchorage, AK

Sullivan BK, Garcia RJ, McPhee-Klein G (1994) Prey selection by the scyphomedusan predator *Aurelia aurita*. Mar Biol 121:335-341

Toyokawa M, Inagaki T, Terazaki M (1997) Distribution of *Aurelia aurita* (Linnaeus, 1758) in Tokyo Bay; observations with echosounder and plannkton net. Proc 6th International Conference on Coelenterate Biology, 1995:483-490

Tankersely RA, McKelvery LM, Forward RB Jr (1995) Responses of estuarine crab megalopae to pressure, salinity and light: Implications for flood tide transport. Mar Biol 122:391-400 van Hyning JM, Cooney RT (1974) Association of walleye pollock, *Theragra chalcogramma*, with the jellyfish, *Cyanea*. Copeia 1974:791

Vaughan SL, Tuttle LM, Osgood KE, Gay SM (draft) Upper layer circulation and water mass variability in Prince William Sound, Alaska

Wooldridge T, Erasmus T (1980) Utilization of tidal currents by estuarine zooplankton. Est Coast Mar Sci 11:107-114

Yasuda T (1969) Ecological studies on the jelly-fish, *Aurelia aurita*, in Urazoko Bay, Fukui Prefecture. I. Occurrence pattern of the medusa. Bull Jap Soc Scient Fish 35:1-6

Zavodnik D (1987) Spatial aggegations of the swarming jellyfish *Pelagia noctiulca* (Scyphozoa). Mar Biol 94:265-269

Table 1. Average size categories for jellyfish aggregations according to length (L) and width (W) using sighting tube during aerial surveys of Prince William Sound.

Category	L X W (Tube units)	L X W (m at 308 m altitude)	Surface Area (m^2 at 308 m)
dab	0.25 X 0.10	4.9 X 2.0	10
small	0.50 X 0.20	9.7 X 3.9	38
medium	1.00 X 0.25	19.5 X 4.9	96
large	2.00 X 0.50	39.0 X 9.7	378

Table 2. *Aurelia aurita.* Numbers of aggregations and their combined surface areas in Prince William Sound in bays where they most frequently occurred. Data are presented for the survey in each year having the greatest number of aggregations. The bays are listed from southwest PWS clockwise around the coastline.

Location	5-22 August 1995		2-21 July 1996		12-21 June 1997	
	No.	Area (m^2)	No.	Area (m^2)	No.	Area (m^2)
Whale Bay	7	498	17	646	0	0
Drier Bay	8	478	145	8544	0	0
Jackpot Bay	18	916	68	3222	0	0
Ewan Bay	3	172	7	324	2	20
Paddy Bay	0	0	7	266	5	200
Naked Island	0	0	7	266	0	0
Eaglek Bay	0	0	81	3460	18	602
Wells Bay	0	0	54	2052	0	0
Jack Bay	0	0	4	152	0	0
Galena Bay	0	0	45	2206	2	48
Port Fidalgo	28	2034	17	2122	1	38
Port Gravina	16	898	22	1864	0	0
Orca Bay	3	173	4	550	0	0
Sheep Bay	1	378	3	144	0	0
Simpson Bay	10	380	12	688	0	0

Table 3. *Aurelia aurita* and *Theragra chalcogramma.* Characteristics of acoustic transects in Simpson and Drier Bay in Prince William Sound. Depths of jellyfish aggregations and densities and depths of walleye pollock were determined by acoustics. Percentages of the catch and size (fork length) of walleye pollock were determined from seine catches. Numbers represent means ± 1 standard deviation.

	Simpson Bay	**Drier Bay**
Date	2 Jul 1996	8 Jul 1996
Latitude and longitude	60.676° N 145.858° W	60.320° N 147.775° W
Bottom depth (m)	26.8 ± 13.6	39.5 ± 3.2
***A. aurita* (% of seine catch)**	99%	97%
Depth (m)	0 - 10	0 - 20
***T. chalcogramma* (No. m^{-3})**	13.9 ± 28.3	35.9 ± 76.8, 34.4 ± 59.7
% of seine catch	1%	3%
Mean depth (m)	12.8 ± 7.6	16.1 ± 11.6
Size (mm)	49.9 ± 6.3	60.8 ± 4.6

Table 4. *Aurelia aurita*, *Theragra chalcogramma,* and *Clupea pallasi.* Matrix of occurrence in 52 seine catches in Prince William Sound in 2 - 11 July, 1996. Seine sets were made on fish schools located acoustically. Catches having just jellyfish are at the intersection of the jellyfish row and column. Only 4 catches contained jellyfish, walleye pollock, and herring, and these are not included in any column.

	Jellyfish	**Pollock**	**Herring**
Jellyfish	13	10	11
Pollock	--	0	0
Herring	--	--	14

Table 5. *Aurelia aurita.* Medusa swimming beat frequencies, relative vertical distance moved per second, and relative densities for areas in aggregations where medusae swimming unidirectionally up, unidirectionally down, or where medusae were in mixed orientations, as analysed from video tapes. Numbers are means ± 1 standard deviation. The numbers of measurements are in parentheses. Relative distance (distance ÷ body depth) is a measure of the vertical displacement during one swimming beat (standarded to 1 s), because actual distances could not be determined. Relative density is a measure of the percentage of the video image covered by jellyfish, and is used to compare the abundances of jellyfish because absolute density could not be determined.

	Location in aggregation			
Variable	**Up**	**Down**	**Mixed up**	**Mixed down**
Swim beat (no. s^{-1})				
Aggregation 1	0.51 ± 0.30 (7)	0.51 ± 0.09 (12)	0.51 ± 0.05 (5)	0.57 ± 0.09 (9)
Aggregation 2	0.57 ± 0.11 (18)	0.36 ± 0.06 (16)	0.59 ± 0.10 (11)	0.67 ± 0.13 (9)
Relative distance (s^{-1})				
Aggregation 2	0.36 ± 0.32 (13)	0.41 ± 0.20 (12)	1.04 ± 0.65 (11)	0.30 ± 0.34 (10)
Relative density (%)				
Aggregation 1	22 ± 5 (10)	46 ± 11 (10)	7 ± 15 (10)	
Aggregation 2	96 ± 5 (5)	91 ± 13 (9)	25 ± 11 (5)	

Table 6. *Aurelia aurita.* F values and statistical significance from analyses (one-way ANOVAS) of the swim beat frequency (number s^{-1} in lower left half of table) and the relative densities (% in upper right half of table) for areas where medusae swimming unidirectionally up, unidirectionally down, or where medusae were in mixed orientations. Swim beat freqencies were not significantly different overall for Aggregation 1, and for Aggregation 2, the overall significance for swim beats was $F = 29.59$, $p = 3.58 \times 10^{-10}$. The relative densities were significantly different overall among areas in both aggregations, with the overall significance being $F = 160.67$ and $p < 1 \times 10^{-14}$ for Aggregation 1, and $F = 87.67$ and $p = 1.27 \times 10^{-10}$ for Aggregation 2. For the tests below, F values are presented for Aggregate 1, Aggregate 2. NS = not significant, * = $p < 0.05$, ** = $p < 1 \times 10^{-7}$.

Orientation	**Up**	**Down**	**Mixed**
Up	-----	38.82**, 1.14 NS	65.88**, 266.43**
Down	NS, 51.30**	----	100.77**, 89.19**
Mixed -- down	NS, 4.40*	NS, 65.93**	----
Mixed -- up	NS, 0.32 NS	NS, 59.05**	NS, 2.16 NS

Table 7. Predators of juvenile walleye pollock, *Theragra chaleogramma* in Prince William Sound. NG = not given. From Okey and Pauly (1998).

Predators	Importance in diet (% by weight)	Age class of prey
Age 1-2 pollock	1.7	0
Pacific cod	7.4	0
Sablefish	10.5	0
Arrowtooth flounder	3.7	0
Halibut	57.4	0-2
Fork-tailed storm pretel	5.0	0
Common murre	25.0	1-3
Pigeon guillemot	11.8	1-3
Ancient Murrelet	13.0	1.3
Tufted puffin	13.0	1-3
Horned puffin	1.0	1-3
Harbor seal	47.0	NG

Figure Captions

Figure 1. Maps of Prince William Sound with flight paths of aerial surveys in 1995, 1996, and 1997

Figure 2. Variation in surface area covered in aerial surveys of Prince William Sound during 1995, 1996, and 1997

Figure 3. *Aurelia aurita.* Aerial photo of jellyfish aggregation in Prince William Sound in July, 1996

Figure 4. *Aurelia aurita.* Size frequency distrubution of aggregations in Prince William Sound in 1995, 1996, and 1997. d = dab, s = small, m = medium, l = large. Approximate sizes of each category are given in Table 1. The percentages of 995 aggregations in each category are given above each bar

Figure 5. *Aurelia aurita.* Seasonal and interannual variation in densities of jellyfish aggregations in Prince William Sound as estimated from aerial surveys in 1995, 1996, and 1997. Data presented as the numbers of aggregations km^{-2} and as surface areas of aggregations km^{-2}

Figure 6. *Aurelia aurita.* Distributions of aggregations of medusae in Prince William Sound during aerial surveys in June, July, and August, 1995, 1996, and 1997.

Figure 7. Depth profiles of temperature and salinity in Simpson and Drier Bays of Prince William Sound, where acoustic transects are reported (Table 2)

Figure 8. *Aurelia aurita.* Underwater videotape image from a jellyfish aggregation

Figure 9. *Aurelia aurita.* Vector diagram of mean medusa swimming direction (angle of the sticks), and abundance (length of the sticks) during a 3-min videotape transect through a jellyfish aggregation. Sticks above the horizontal axis represent swimming upwards, with straight up (0°) being vertical swimming up. Sticks below the axis represent swimming downwards, with straight down (180°) being vertical swimming down. The lengths of the sticks represent the numbers of medusae for which swimming direction was measured at each time interval. The videotape frames were "frozen" at 10 s intervals, and swimming direction determined for all medusae in that image.

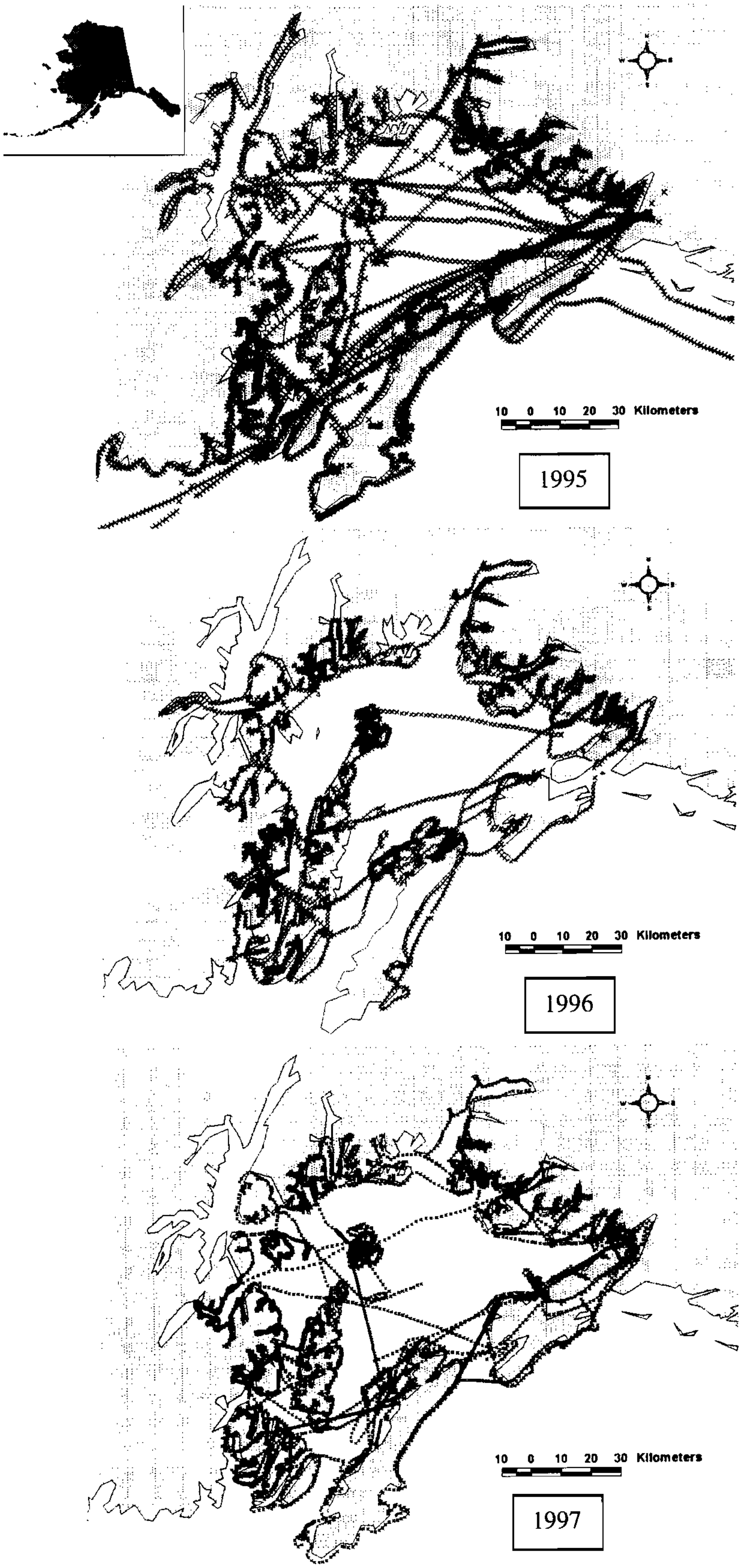
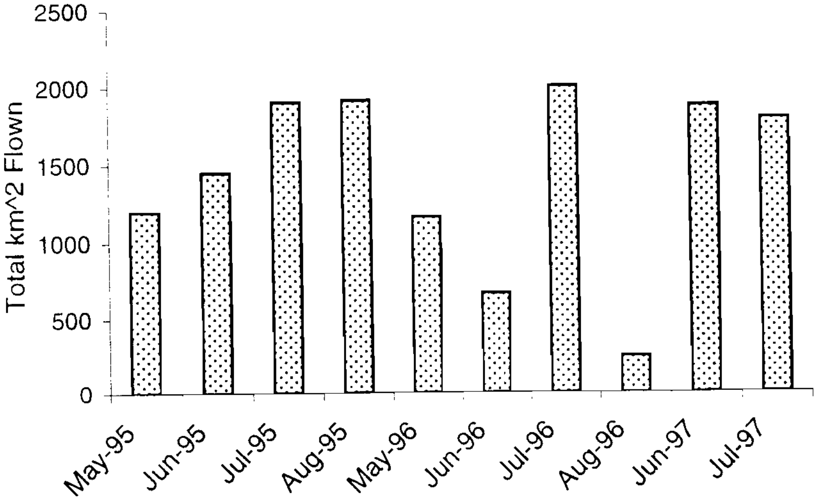
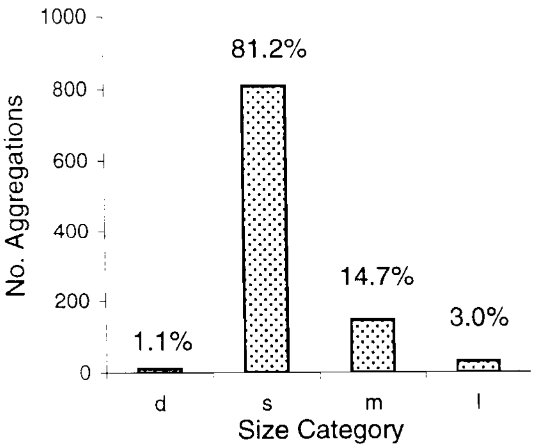

10 0 10 20 30 Kilometers
1995
10 0 10 20 30 Kilometers
1996
10 0 10 20 30 Kilometers
1997

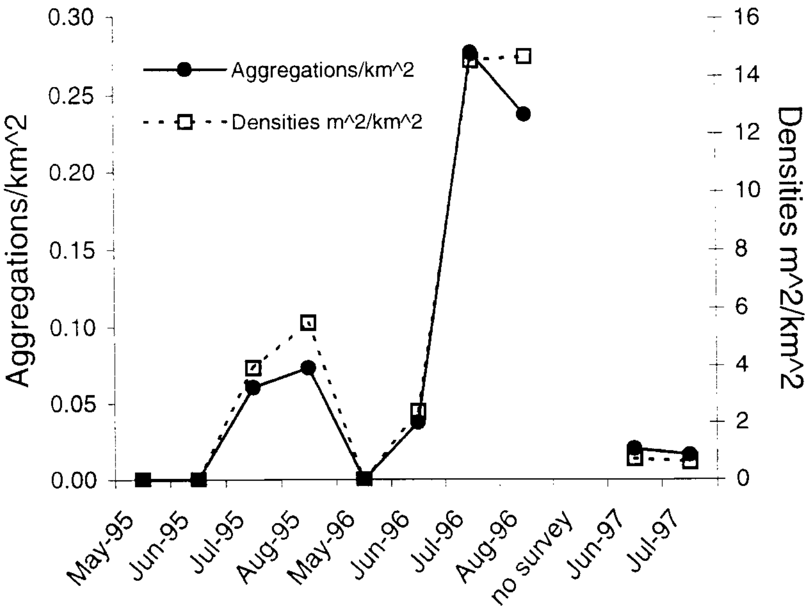
Fig. 1

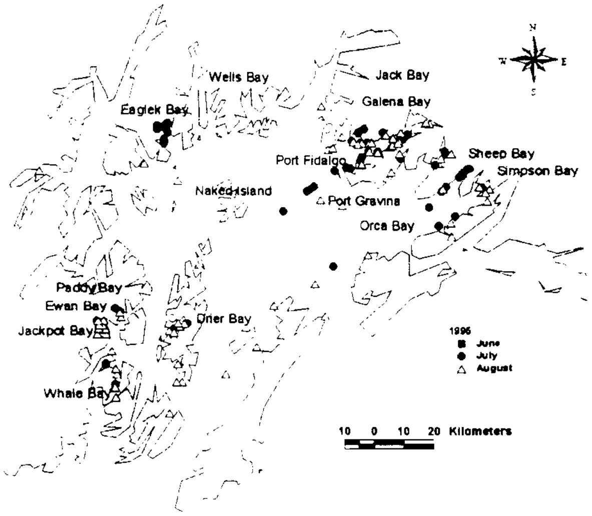


2500
2000
1500
1000
500
0
Total km^2 Flown
May-95
Jun-95
Jul-95
Aug-95
May-96
Jun-96
Jul-96
Aug-96
Jun-97
Jul-97



1000
800
600
400
200
0
No. Aggregations
81.2%
14.7%
3.0%
1.1%
d
s
m
l
Size Category


Aggregations/km^2
Densities m^2/km^2
0.30
0.25
0.20
0.15
0.10
0.05
0.00
16
14
12
10
8
6
4
2
0
May-95
Jun-95
Jul-95
Aug-95
May-96
Jun-96
Jul-96
Aug-96
no survey
Jun-97
Jul-97


N
W
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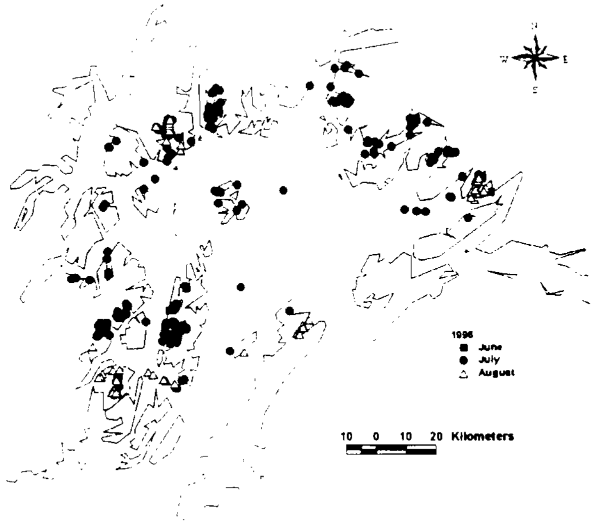
S
Wells Bay
Jack Bay
Galena Bay
Eaglek Bay
Sheep Bay
Port Fidalgo
Simpson Bay
Naked Island
Port Gravina
Orca Bay
Paddy Bay
Ewan Bay
Jackpot Bay
Otter Bay
Whale Bay
1996
■ June
● July
△ August
10 0 10 20 Kilometers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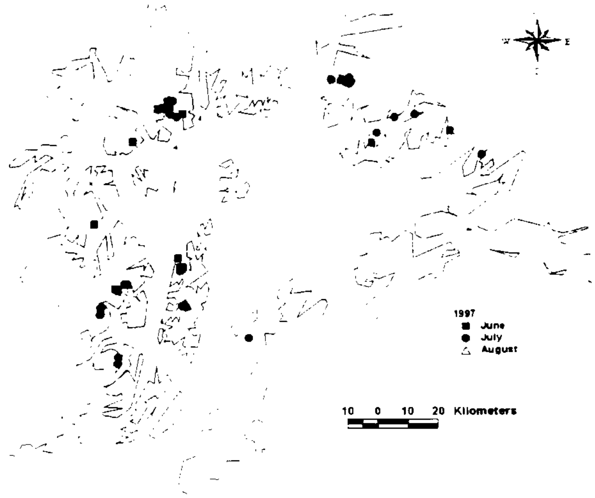
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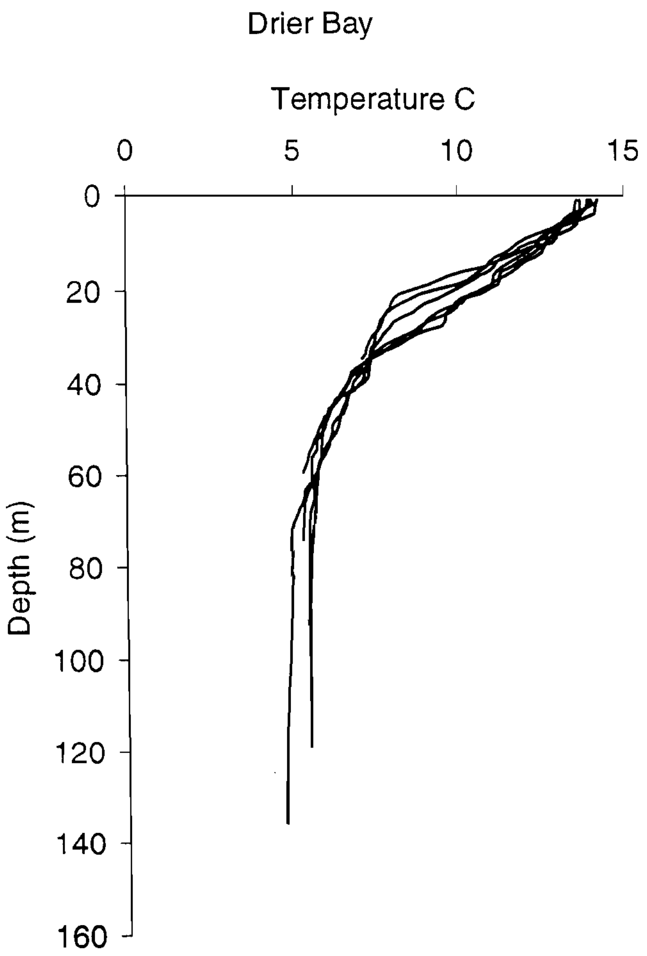
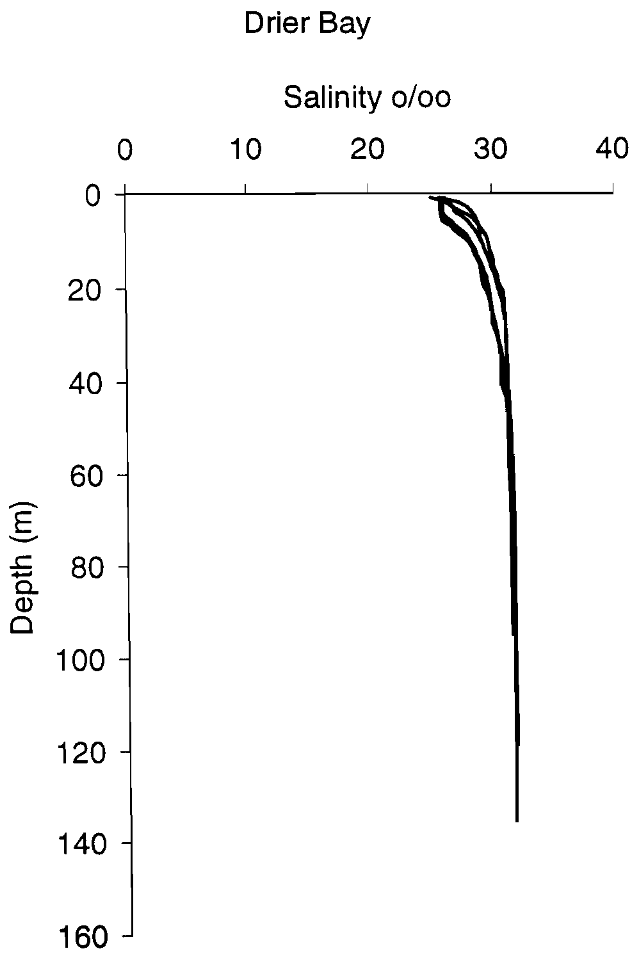
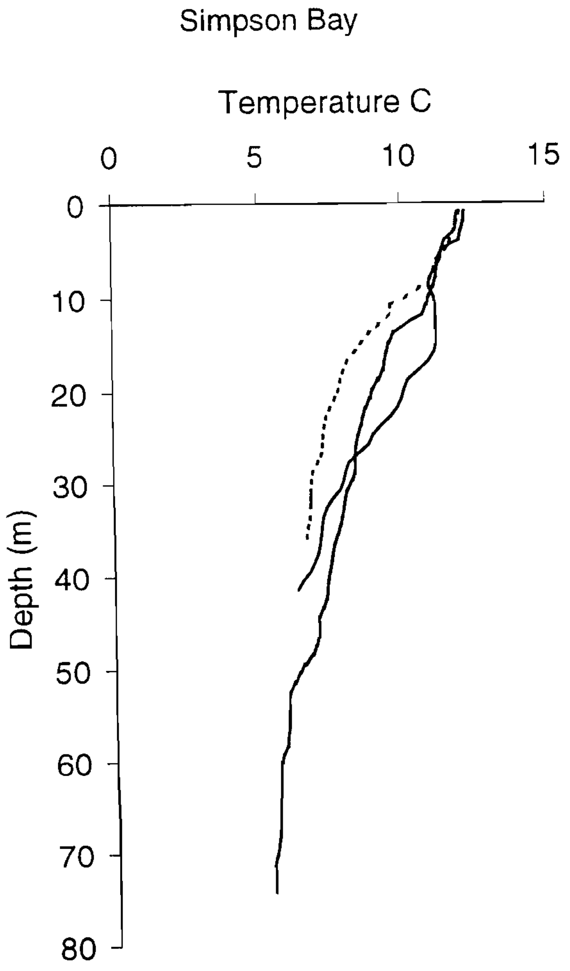
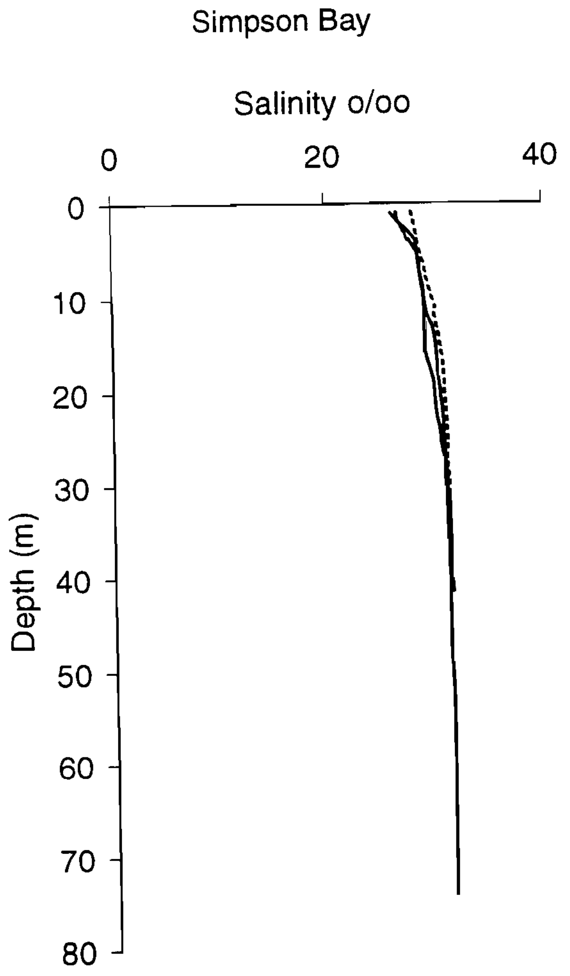
Fig 4


Drier Bay
Temperature C
0
5
10
15
0
20
40
60
80
100
120
140
160
Depth (m)


Drier Bay
Salinity o/oo
0
10
20
30
40
0
20
40
60
80
100
120
140
160
Depth (m)


Simpson Bay
Temperature C
0
5
10
15
0
10
20
30
40
50
60
70
80
Depth (m)


Simpson Bay
Salinity o/oo
0
20
40
0
10
20
30
40
50
60
70
80
Depth (m)

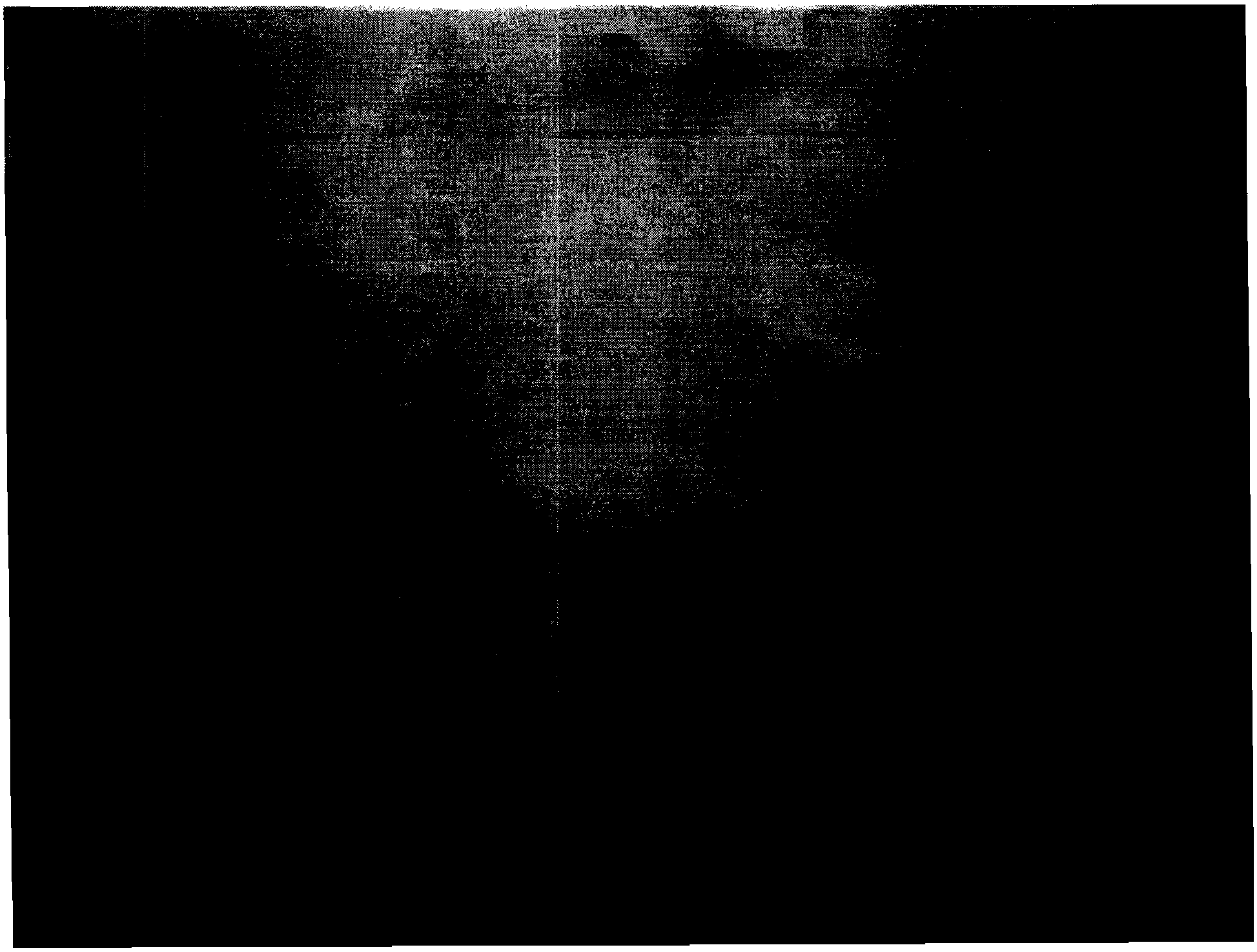


Fig 8

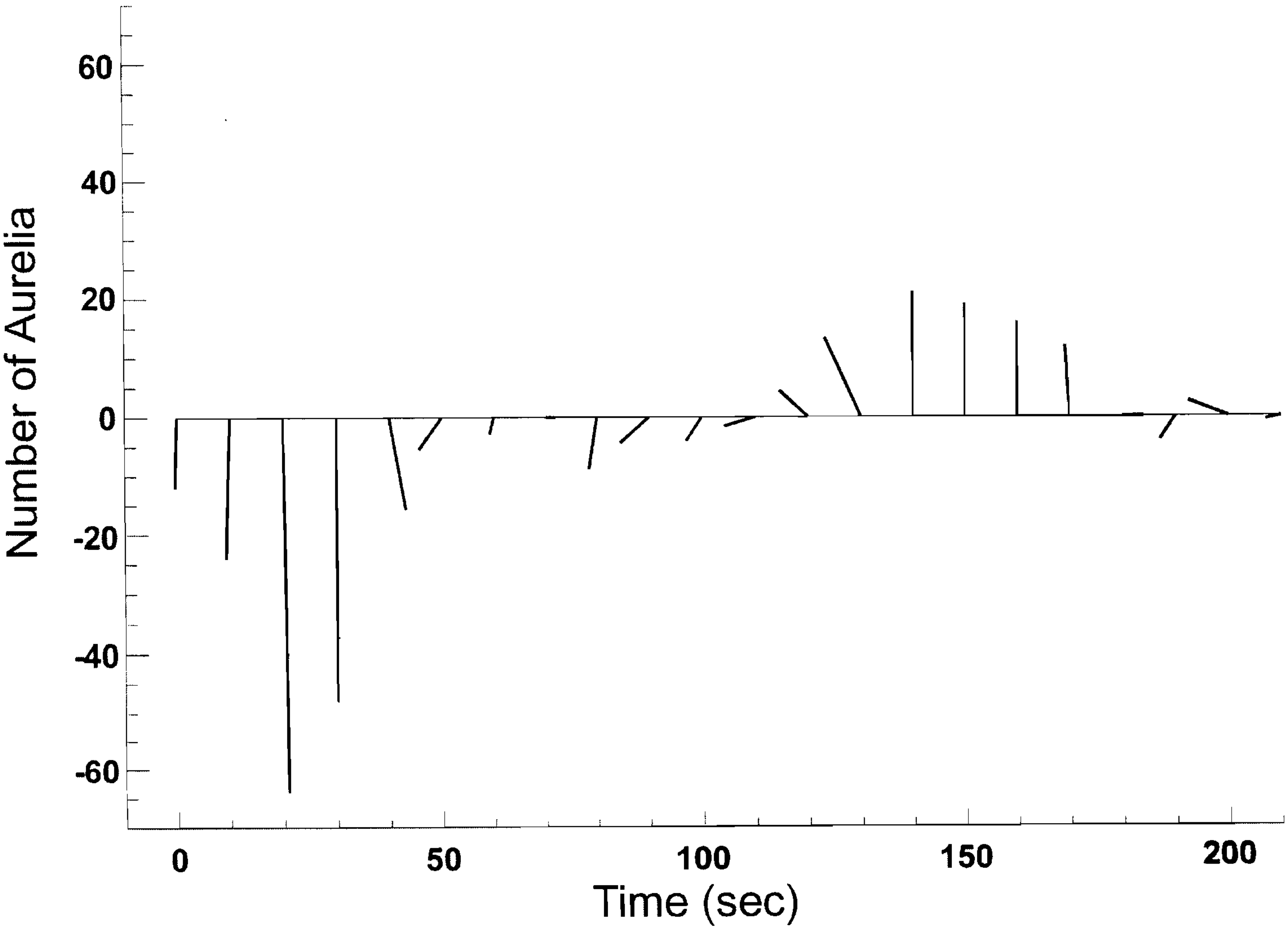


Fig 9

T Aerial Surveys

Exxon Valdez Oil Spill
Restoration Project Annual Report

Aerial Survey Support for the APEX Project

Restoration Project 99163T
Annual Report

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Aerial Survey Support for the APEX Project
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Annual Report

Study history: Restoration Project 99163-T was initiated after a round of data sharing between the Sound Ecosystem Assessment (SEA) project, Restoration Project 99320, and the Alaska Predator Ecosystem Experiment (APEX) project, Restoration Project 99163. In the 1998 annual meeting and review for *Exxon Valdez* Oil Spill (EVOS) science the principal investigator of this project present data on broadscale distributions of surface schooling forage fishes in Prince William Sound from 1995-1997. In addition, modelers working with the APEX project found a significant correlation between foraging activity of sea birds and the fish distributions from the aerial surveys. It was decided at that meeting that an aerial component should be added to the APEX program to provide additional information on fish distribution for modelers and other researchers with the APEX umbrella. Therefore, this project was conceived to as a service and data delivery project for that program. The first field season was 1998 and a second (final) field season is anticipated for 1999. This is a continuing project.

Abstract: The objective of this project was to provide information on pelagic schooling fishes in the surface waters of Prince William Sound in order to better understand reproductive and foraging dynamics of various sea bird species. The scope of the project focuses on the study areas of the APEX project within Prince William Sound, Alaska. The individual objectives for this project were completed between the dates of July 1 and August 9, 1998. Preliminary data was delivered to the APEX program via Glen Ford, APEX modeler. Net catches from our survey and other APEX projects were compiled to provide corrections for species identification. Final edited data was delivered on December 14, 1998. We were not able to over fly the acoustics program within APEX due to a non-overlap in over flights and cruises. However, we were able to conduct a single broadscale survey within Prince William Sound during the course of July, 1998. In meeting our objectives, we flew 15 repeat surveys over the northern and central study regions and 5 repeat surveys (coordinating with kittiwake researchers) over the Jackpot study region (coordinating with marbled murrelet researchers).

Key Words: Aerial Surveys, line transects, forage fish, sea birds, kittiwakes, *Clupea pallasi*, Pacific herring, juvenile, *Ammodytes hexapterus*, sand lance, capelin, *Mallotus villosus*, eulachon, *Thaleichthys pacificus*, Prince William Sound, distribution

Project Data: Distribution, abundance, and species composition of forage fish; distribution, abundance and behavior of "white" sea birds; limited alcid (diving bird) and marine mammal distributions; fish lengths; jellyfish distribution and abundance.

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Executive Summary

The objective of this project was to provide data to other Alaska Predator Ecosystem Experiment (APEX) projects on distribution, abundance and species composition of forage fish in Prince William Sound (PWS), Alaska. The data from this project was and is being used to address APEX hypotheses concerning food limitation to seabirds and affects of variability in prey availability on seabird foraging patterns. From research conducted in PWS from 1995-1997, we knew that four forage fish species including Pacific herring (*Clupea pallasi*), sand lance (*Ammodytes hexapterus)*, capelin (*Mallotus villosus)*, and eulachon (*Thaleichthys pacificus*) form distinct schools in surface waters during the summer (June and July) which are easily spotted from aircraft. Data on surface school distribution from those years was significantly correlated to seabird foraging activities during the same years. Using methodology developed in 1995-97, we conducted repeat surveys over known seabird foraging regions within PWS from early July to early August. A total of 160 hours were flown during 28 survey days. A total of 13 repeat surveys were conducted in the North study area and 14 in the Central area. The Jackpot area was surveyed five times (Figure 1, Table 1) during the period beginning July 6 and ending August 11, 1998. An area totaling 9,923.8 km^2 with a lineal distance of 22,103.2 km was surveyed during the study period (Table 2). The average transect width was 449.2 m and transect lengths ranged from 81.3 to 3,653,4 km. Information or "sightings" such as numbers of fish schools or jellyfish aggregations, species of fish, surface area of schools or jellyfish aggregations, numbers of birds or mammals, and behavior of birds were recorded on the computer log program. A detection model for aerial surveys was developed the probability detection function consisting of the perpendicular distances from the center of the transect to the sightings. The key parameters needed to calculate densities was the probability of detection estimated at 0.83 from previous studies and *f*(d) estimated at 0.18 for kittiwakes, 0.31 for herring and 0.28 for sand lance. Validations from net catches, diver observations and underwater video segments were collated to correct aerial species identification. Peak counts of key species within the study regions and broadscale survey path were plotted for each survey period or weekly. Total numbers of individual schools or animals sighted were estimated for each survey day. During the survey period, a total of 5,223 alcids , 53,364 kittiwakes, 337 harbor seals, 69 humpback whales, 1,597 sea lions, 1,416 sea otters, 53 capelin schools, 23 eulachon schools, 1,445 herring schools, 1,416 sand lance schools and 770 jellyfish aggregations were sighted. Total surface area of schools and jellyfish were also calculated by day. Total surface area (m^2) of all species over the study period were 1,285.7 for capelin, 4,231.5 for eulachon, 52,117.9 for herring, 109,545.6 for sand lance and 65,465.53 for jellyfish. The data resulting was delivered to APEX modelers and other researchers for use in their respective analyses.

Introduction

The objective of this project is to provide data to other Alaska Predator Ecosystem Experiment (APEX) projects on distribution, abundance and species composition of forage fish in Prince William Sound (PWS), Alaska. This project is a single component of the APEX study complex and addresses food availability as a limitation for recovery of a suite of sea bird species injured for the oil spill.

Little was known about the distribution and relative abundance of juvenile Pacific herring, *Clupea pallasi*, and other forage fish in Prince William Sound (PWS), Alaska prior to the *Exxon Valdez* oil spill in 1989. Herring, sardines, anchovy, capelin, and sand lance are known to school in tight aggregations with distinctive shapes and are often found in oceanic surface waters (Mais 1974; Squire 1978; Blaxter and Hunter 1982; Hara 1985; Misund 1993; Carscadden et al. 1994). Many pelagic fish are arranged in shoal or school groups (Cram and Hampton 1976; Fiedler 1978). Distribution of herring and capelin is thought to be contiguous. Known areas of seasonal aggregations are unique to a particular population (Templeman 1948; Campbell and Winter 1973; Sinclair 1988; Stocker 1993). Given that these forage species form distinct, easily identifiable schools, the visual aerial technique described in this report is able to provide data on surface schools available for forage food by sea birds. Since 1995, aerial surveys have added considerably to the base of knowledge on forage fish in PWS and the immediate vicinity.

The main foraging species within Prince William Sound (PWS) include Pacific herring, sand lance *(Ammodytes hexapterus)*, capelin *(Mallotus villosus)*, eulachon (*Thaleichthys pacificus*), juvenile pollock (*Theragra chalcogramma*), and juvenile salmon (*Onchorynchus sp.*). The first four species listed form distinct schools in surface waters during the summer (June and July) which are easily spotted from aircraft. However, capelin and eulachon are visible for a narrow window of time (June) after which they disperse and move to deeper waters, becoming invisible to aerial spotters (E.Brown, unpublished data; reflected in APEX catches, Haldorson et al. 1996). Distinct foraging patterns of birds, seen from aircraft, form over post-spawn adult capelin; if those observations are coupled with net catches, information about capelin may be refined (E. Brown, unpublished data). The main target species for this project, therefore, are juvenile herring, sand lance, and post-spawn or juvenile capelin since aerial surveys will be conducted mainly in July.

Methodology for this project was developed in 1995-1996, but the database extends to 1997 (Brown and Norcross 1997; Brown and Borstad 1998; Brown 1998; Brown et al., in prep) and now 1998. Broadscale measurements of forage fish distribution and abundance were completed for June and July, all three years. However, in 1995-1996, other months were also sampled. In addition, fine scale and repeat measurements were taken for a subset of herring nursery bays in eastern, northern , southwestern and central PWS. All of this data has been made available to the APEX project for analyses of earlier data.

For this project, a single broadscale survey was conducted in July, 1999, which will include all of APEX study areas. In addition, we conducted daily, repeat surveys (15) over two APEX study regions in PWS which represented the foraging range of two colonies

(Black-legged kittiwakes). We also directed net catches on schools observed from the air through all regions surveyed for validation. Data collected was made available to all bird researchers within APEX and we coordinated with them to insure that their needs were met. There was no working hypothesis for this project.

Objectives

For FY99, we had the following objective:

Provide aerial support for the APEX project, deliver the resulting data, and assist APEX researchers in its use and interpretation. We addressed that objective with the following tasks:

1) Coordinate with sea bird and other researchers from the APEX project to develop field survey plans addressing the overall objectives of APEX.

2) Conduct daily repeat surveys over the APEX study area which represents the foraging range of birds from a single; set small catcher and sea bird "chase" skiffs on schools with foraging flocks in order to obtain more detailed observations.

3) Over fly the entire APEX study region during times when acoustic vessels are performing surveys to obtain a broadscale data set, which will include nearshore schools invisible to acoustics.

4) During broadscale flights, coordinate with other sea bird researchers to enable synoptic measurements of bird distributions from ground surveys and fish/bird distributions from the air.

5) Process the data during and after the field season; build into the three-year database of aerial data already in place; obtain a data set of field net-catches.

6) Work with modelers and other researchers to deliver the data appropriately, accurately and in a timely manner.

7) Work with APEX projects to finalize annual reports, prepare presentations and complete publications.

The objective and tasks were completed as given except task number 3. We were not able to over fly the APEX acoustic survey due to a lack of overlap in the survey/cruise dates.

Methods

Prior to each survey, we established the flight and weather. In order to minimize the effect of survey condition bias on accuracy of the results, criteria were established for determining whether or not to proceed with a survey. We flew if the winds were under 25 knots (creating a sea state of less than 1 Beauport scale and no white capping), if the average ceiling (cloud cover) was at least 250m, and precipitation was either absent or very patchy. Conditions outside the criteria can significantly affect the quality and accuracy of the survey data.

At the start of the field season, flight paths were established in the northern, central, and Jackpot APEX study regions (Figure 1). During the survey, the pilot stayed on the established flight path as closely as possible. Both flight path (transect) and features along path were recorded using the DLog program provided by Glen Ford. A GPS mounted to the dash of the aircraft was connected to a lap top computer and dumped latitude, longitude, and date in 2-second intervals. Time was recorded from the computers internal clock. At the beginning of each flight, header information including weather, water visibility, wind, wind direction, tide stage, wave height and other notes concerning the survey were recorded in the log program. Information or "sightings" such as numbers of fish schools or jellyfish aggregations, species of fish, surface area of schools or jellyfish aggregations, numbers of birds or mammals, and behavior of birds were recorded on the computer log program.

Validations were conducted with net catches and aircraft video. A small number of net captures by small mesh purse seine and anchovy purse seine were guided from the aircraft to be used to validate and correct species assignments. However, a number of validations were obtained from other projects sampling fish during the time period of the aerial surveys. In that case, matching validations was a post-processing procedure using GIS and matching date codes. Digital video images of many schools and foraging flock configurations were collected and used in identifying validations and evaluating schools shape. Although there is more we can accomplish with the images in terms of sea bird/forage fish school dynamics, that analysis was not covered within the scope of this study.

Single or double letter codes were developed for fish, bird and mammal species (such as h for herring, sd for sand lance, kw for kittiwakes, hs for harbor seals etc). Bird behavior was recorded as foraging or plunging (pl), resting on water (rw), resting on shore (rs), aggregated tightly on water over school (tw), traveling (tr) or flying in a "broad area search" (bs). We used gridded maps to facilitate communication between aerial and ground crews concerning the location of birds and fish.

Fish schools were counted and surface area estimated using a sighting tube. The sighting tube is constructed of PVC pipe with a grid drawn on mylar on the end. The focal length of the tube is 216 mm and can be calibrated for ground distance covered by reference line (X) for any survey altitude, when length of the grid reference line (L), focal length of the tube (F), and survey altitude (A) are known, by using the equation:

$X = A\ ({}^{L}/_{F})$ (Lebida and Whitmore 1985; Brady 1987). (1)

The use of the grid is particularly important for large schools. For elliptical shaped schools, maximum length and maximum width provided a rough estimate of surface area; for irregularly shaped schools (U-shaped, long wavy bands, etc.) length and width of separate sections were measured and combined to give a total estimate. The sighting angle established from fish survey protocols and a detection curve analysis was established at between 20 and 40 degrees from the wing tip with optimal sighting occurring at 30 degrees. The sighting angle for sea birds can be decreased. The swath or effective transect width is calculated using standard geometry from the wing angles and altitude.

For estimating total school or sea bird density and forage fish abundance available at the surface (not including subsurface fish), the appropriate model is outlined by Quang and Lanctot (1991:

$$\hat{D} = \frac{n\hat{f}(d)}{L}, \ \hat{N} = 2A\hat{D} \text{ or } \hat{N} = \frac{n}{\hat{p}}, \ C = \frac{1}{\hat{p}}$$

where D is density, n is the observed schools or birds, *f*(d) is the maximum height of the probability density function (*f*(x)) of distances (x) at distance d from the center of the transect, L is the length of the transect, N is the total number of animals estimated in the area, A is the area sampled, p is the probability of detection and C is the visibility coefficient. Estimates of variance should include estimates of variance for p and surveyor bias (calculated via double counting, Brown and Norcross 1997; Brown et al., in prep). For this study, only one parameter needed to be estimated (*f*(d)). The estimate of p (0.83) was obtained in an earlier study using independent sampling techniques and is described in a publication in preparation that will appear in the EVOS final report for SEA project 99320T (Brown et al., in prep; also in Brown and Borstad 1998). In order to estimate *f*(d), we collected angles on a subset of sightings. This was accomplished by marking the strut of the aircraft with a series of graduated marks indicating angle off the wing and collecting the angles by flattening the aircraft (using the gyroscope) and taking a measurement. The angles were converted to distance from transect centerline using simple geometry and the frequency distribution of the distances (x) were plotted (i.e. the *f*(x)). In this model, a beta curve best represents the probability density function of x and *f*(d) is obtained from the plot of x.). In order to expand the estimate to include subsurface distributions, acoustics must be incorporated. That was outside the scope of this study.

Results and Discussion

A total of 13 repeat surveys were conducted in the North study area and 14 in the Central area. The Jackpot area was surveyed five times (Figure 1, Table 1) during the period beginning July 6 and ending August 11, 1998. A area totaling 9,923.8 km^2 with a lineal distance of 22,103.2 km was surveyed during the study period (Table 2). The average transect width was 449.2 m and transect lengths ranged from 81.3 to 3,653,4 km.

We coordinated with sea bird researchers working with radio tagged kittiwakes in the north and central regions, Pigeon guillemot and marbled murrelet researchers in the central region, and marble murrelet researchers in the Jackpot region during each survey day in the appropriate regions. We also reported several sightings of killer whales for the EVOS killer whale researcher (C. Matkin, Project 99012A) in order to facilitate his research. Finally, we conducted double counts on 5 of the survey days to calibrate our estimate of surveyor bias.

The probability detection functions were plotted for kittiwakes, herring and sand lance (Figure 2). The estimates for *f*(d) are approximately 0.18 at d = 700 m for kittiwakes (n = 1019), 0.31 at d = 600 m for herring (n = 345) and 0.28 at d = 600m for sand lance (n=274). Any expressions of density or numbers of birds or schools should reflect these values in the estimates.

For validations, we were able to use 4 diver observations (Steve Jewett, UAF, unpublished data), 2 underwater video observations and 21 net catches (APEX project) occurring during our survey period to validate 116 sightings (Table 3). We were able to use some catches for multiple sighting validations because schools occurred in school groups or shoals and a single catch may be used to characterize that particular shoal. Ages of fish were only determined when average lengths were supplied. These validations were used to correct some misidentified species. As a result, 36 records were corrected for species, both occurring in the area (Green Island) with major overlap between age-0 herring and sand lance schools (also reflected in the catches; see Haldorson et al., this annual reporting series from APEX).

Peak counts of key species within the study regions and broadscale survey path were plotted for each survey period or weekly (Figures 3-7). Total numbers of individual schools or animals sighted were estimated for each survey day (Table 4). During the survey period, a total of 5,223 alcids , 53,364 kittiwakes, 337 harbor seals, 69 humpback whales, 1,597 sea lions, 1,416 sea otters, 53 capelin schools, 23 eulachon schools, 1,445 herring schools, 1,416 sand lance schools and 770 jellyfish aggregations were sighted. Total surface area of schools and jellyfish were also calculated by day (Table 5). Total surface area (m^2) of all species over the study period were 1,285.7 for capelin, 4,231.5 for eulachon, 52,117.9 for herring, 109,545.6 for sand lance and 65,465.53 for jellyfish.

Finally, the principal investigator participated as co-author in two publications that include the aerial data. A paper on jellyfish (Purcell et al., in prep) is due out this year as well as a paper on a foraging model for kittiwakes by David Ainley and other unknown co-authors (title unknown at this point). This investigator also provided numerous verbal and written comments for the various researchers in APEX to aid in their interpretation, analysis and reporting of their respective studies.

Next year, we are proposing a publication analyzing the three-year distribution of forage fish in PWS in relation to environmental factors such as zooplankton and ocean state (from the SEA data set).

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Literature Cited

Brown, E.D. and B.L. Norcross. 1997. Assessment of forage fish distribution and abundance using aerial surveys: survey design and methodology, Appendix I, Chapter 11 in 11 *in* Cooney, R.T. 1997. Sound Ecosystem Assessment (SEA) – an integrated science plan for the restoration of injured species in Prince William

Brown, E.D. and G.A. Borstad. 1998. Progress Report on Aerial Survey Development Appendix III, Chapter 10 in Cooney, R.T. 1997. Sound Ecosystem Assessment (SEA) – an integrated science plan for the restoration of injured species in Prince William Sound. FY96 Annual Report for the Exxon Valdez Trustee Council, Anchorage, Alaska. Pages 80-97.

Brown, E.D. 1998. Preliminary documentation of temporal and spatial variability of Pacific herring, other forage fish, and seabirds in Prince William Sound, Alaska, Appendix II, Chapter 10 in Cooney, R.T. 1997. Sound Ecosystem Assessment (SEA) – an integrated science plan for the restoration of injured species in Prince William Sound. FY96 Annual Report for the Exxon Valdez Trustee Council, Anchorage, Alaska. Pages 44-79.

Brown, E.D., G.A. Borstad, S.M. Moreland, and B.L Norcross. In prep. Assessment of forage fish distribution and abundance using aerial surveys: survey design, methodology, and error. To be submitted to Ecological Applications.

Blaxter, J.H.S., and J.R. Hunter. 1982. The biology of clupeoid fishes. Adv. Mar. Biol. 20: 1-223.

Brady, J. A. 1987. Distribution, timing, relative biomass indices for Pacific herring as determined by aerial surveys in Prince William Sound 1978-1987. Prince William Sound Data Report No. 87-14. Alaska Department of Fish and Game, Div. of Commercial Fisheries, Juneau, AK. 11 pp.

Carscadden, J., B. Nakashima, and D.S. Miller. 1994. An evaluation of trends in abundance of capelin (Mallotus villosus) from acoustics, aerial surveys and catch rates in NAFO Division 3L, 1982-89. J. Northw. Atl. Fish. Sci. 17: 45-57.

Campbell, J.S., and G.H. Winter. 1973. Some biological characteristics of capelin, *Mallotus villosus*, in the Newfoundland area. ICNAF Redb. 1973 (III): 137-144 (also ICNAF Res. Doc. 73/90, Ser. No. 3048).

Cram, D.L., and I. Hampton. 1976. A proposed aerial/acoustic strategy for pelagic fish stock assessment. J. Const. Int. Explor. Mer. 37(1): 91-97.

Fiedler, P.C. 1978. The precision of simulated transect surveys of northern anchovy, *Engraulis mordax*, school groups. Fish. Bull., U.S. 76(3): 679-685.

Hara, I. 1985. Shape and size of Japanese sardine school in the waters off the southeastern Hokkaido on the basis of acoustic and aerial surveys. Bull. Jap. Soc. Sci. Fish. 51(1): 41-46.

Haldorson, L., T. Shirley, K. Coyle and R. Thorne. 1996. APEX: Forage species studies in Prince William Sound, Project 163A-1996 Annual Report. Report to the EVOS TC, April 1996, Anchorage, Alaska. 93 pp.

Lebida, R.C. and D.C. Whitmore. 1985. Bering Sea herring aerial survey manual. Bristol Bay Data Report No. 85-2. Alaska Department of Fish and Game, Div. Commercial Fisheries, Anchorage AK.

Mais, K.F. 1974. Pelagic fish surveys in the California Current. Calif. Dept. Fish Game, Fish. Bull. 162:1-79.

Misund, O.A. 1993. Abundance estimation of fish schools based on a relationship between shcool area and school biomass. Aquat. Living Resour. 6:235-241.

Quang, P.X. and R.B. Lanctot. 1991. A line transect model for aerial surveys. Biometrics 47: 1089-1102.

Sinclair, M. 1988. Marine Populations. An Essay on Population Regulation and Speciation. Washington Sea Grant, Seattle WA. 252 pp.

Squire, J.L., Jr. 1978. Northern anchovy school shapes as related to problems in school size estimation. Fish. Bull., U.S. 76(2): 443-448.

Stocker, M. 1993. Recent management of the British Columbia herring fishery, p. 267-293. In L.S. Parsons and W.H. Lear [eds.] Perspectives on Canadian marine fisheries management. Can.Bull.Fish.Aquat.Sci. 226.

Templeman, W. 1948. The life history of the capelin (*Mallotus villosus*) in Newfoundland waters. Res. Bull. Newfoundland Govt. Lab. No. 17, p. 1-151.

Table 1. Flight Log for 1998 Aerial Surveys in Prince William Sound, Alaska (next two pages)

Flightpaths	Air-craft	Pilot	V	Notes	GMT date	AST Time
980706a.raw	185	tim	n	North region survey to Tatitlek;test DLOG program; flt path not established	7/6/98	14:00:00
980706b.raw	185	tim	n	North region survey Val. Arm North Shore; test DLOG program; flt path not established	7/6/98	17:00:00
980707a.raw	185	tim	n	North region survey; set flight path today; files a-d	7/7/98	10:00:00
980708a.raw	185	tim	n	North region survey; adjusted flt path; files a-d	7/8/98	12:00:00
-0-	185	tim	n	aborted Central region survey due to weather and vis.	7/9/98	11:00:00
980710a.raw	185	tim	n	First Central region survey; set flt path; project meeting at Eleanor; single file	7/10/98	12:45:00
980711a.raw	185	tim	n	Central region; good complete survey; files a-d	7/11/98	12:00:00
980712a.raw	185	tim	n	Central region; good complete survey; files a-f	7/12/98	10:30:00
980712b.raw	185	tim	n	Central region; good complete survey; files a-f	7/12/98	11:30:00
980712c.raw	185	tim	n	Central region; good complete survey; files a-f	7/12/98	13:43:00
980712c.bs	185	tim	n	Broadscale Survey in Jackpot region and SW	7/12/98	15:16:00
980712e.raw	185	tim	n	Central region; good complete survey; files a-f; file d logon error no data loss	7/12/98	16:02:00
980712f.raw	185	tim	n	Central region; good complete survey; files a-f	7/12/98	17:56:00
980713a.bs	185	tim	n	Broadscale Survey at outer Montague and Latouche	7/13/98	11:21:00
980713b.bs	185	tim	n	Broadscale Survey at SW passes	7/13/98	13:42:00
980714a.raw	185	tim	n	North Area region; survey to Bligh Island only; weathered out rest	7/14/98	14:10:00
980714b.bs	185	tim	n	Attempted Broadscale in the North; aborted due to weather so garbage file	7/14/98	16:19:00
980715a.raw	185	tim	n	North Area region; complete survey files a-c	7/15/98	11:18:00
980715b.raw	185	tim	n	North Area region; complete survey files a-c	7/15/98	13:47:00
980715c.raw	185	tim	n	North Area region; complete survey files a-c	7/15/98	16:07:00
980716a.raw	185	tim	n	North Area region; complete survey files a-c	7/16/98	12:05:00
980716b.raw	185	tim	n	North Area region; complete survey files a-c	7/16/98	14:17:00
980716c.raw	185	tim	n	North Area region; complete survey files a-c	7/16/98	17:07:00
980717a.bs	185	tim	n	North shore and NW PWS broadscale survey files a and b	7/17/98	12:15:00
980717b.bs	185	tim	n	North shore and NW PWS broadscale survey files a and b	7/17/98	14:22:00
980718a.raw	185	tim	n	Central region survey; complete files a-d	7/18/98	11:02:00
980718b.raw	185	tim	n	Central region survey; complete files a-d	7/18/98	12:02:00
980718c.raw	185	tim	n	Central region survey; complete files a-d	7/18/98	13:07:00
980718d.raw	185	tim	n	Central region survey; complete files a-d	7/18/98	15:05:00
980719a.raw	185	tim	n	Central region survey; complete files a-f	7/19/98	11:30:00
980719b.raw	185	tim	n	Central region survey; complete files a-f	7/19/98	12:26:00
980719c.bs	185	tim	n	Broadscale Survey in Jackpot region and SW	7/19/98	12:58:00
980719d.raw	185	tim	n	Central region survey; complete files a-f	7/19/98	14:01:00
980719e.raw	185	tim	n	Central region survey; complete files a-f	7/19/98	14:34:00
980719f.raw	185	tim	n	Central region survey; complete files a-f	7/19/98	15:06:00
980720a.raw	185	tim	n	Central region survey; incomplete survey Naked and Knight files a and b	7/20/98	11:37:00
980720b.raw	185	tim	n	Central region survey; incomplete survey Naked and Knight files a and b	7/20/98	12:35:00
980723a.raw	185	tim	n	North Area survey; complete survey files a-c poor survey conditions	7/23/98	13:41:00
980723b.raw	185	tim	n	North Area survey; complete survey files a-c poor survey conditions	7/23/98	15:43:00
980723c.raw	185	tim	n	North Area survey; complete survey files a-c poor survey conditions	7/23/98	17:33:00
980724a.raw	185	tim	n	North Area survey; complete survey files a-c poor survey conditions	7/24/98	13:58:00
980724b.raw	185	tim	n	North Area survey; complete survey files a-c poor survey conditions	7/24/98	16:09:00
980724c.raw	185	tim	n	North Area survey; complete survey files a-c poor survey conditions	7/24/98	17:58:00
980726a.sm	185	tim	n	Central Area partial survey; Stephanie practice excluded Naked and Knight	7/26/98	14:21:00

980726b.sm	185 tim	n	Central Area partial survey; Stephanie practice excluded Naked and Knight	7/26/98	15:27:00
980726c.sm	185 tim	n	Central Area partial survey; Stephanie practice excluded Naked and Knight	7/26/98	17:53:00
980728a.raw	185 davee	n	Central Area survey; complete survey a-f; flight paths flown but GPS off; new aircraft	7/28/98	13:35:00
980728b.raw	185 davee	n	Central Area survey; complete survey a-f; flight paths flown but GPS off; new aircraft	7/28/98	14:33:00
980728c.raw	185 davee	n	Central Area survey; complete survey a-f; flight paths flown but GPS off; new aircraft	7/28/98	15:01:00
980728d.raw	185 davee	n	Central Area survey; complete survey a-f; flight paths flown but GPS off; new aircraft	7/28/98	15:11:00
980728e.raw	185 davee	n	Central Area survey; complete survey a-f; flight paths flown but GPS off; new aircraft	7/28/98	15:32:00
980728f.raw	185 davee	n	Central Area survey; complete survey a-f; flight paths flown but GPS off; new aircraft	7/28/98	16:36:00
980730a.raw	185 tim	y	Central Area survey; complete survey a-f with camera	7/30/98	9:22:00
980730b.raw	185 tim	y	Central Area survey; complete survey a-f with camera	7/30/98	12:01:00
980730c.raw	185 tim	y	Central Area survey; complete survey a-f with camera	7/30/98	13:41:00
980730d.raw	185 tim	y	Central Area survey; complete survey a-f with camera	7/30/98	16:40:00
980730e.raw	185 tim	y	Central Area survey; complete survey a-f with camera	7/30/98	17:28:00
980730f.raw	185 tim	y	Central Area survey; complete survey a-f with camera	7/30/98	18:35:00
980730a.sm	185 tim	y	Dual count second surveyor	7/30/98	9:22:00
980730b.sm	185 tim	y	Dual count second surveyor	7/30/98	12:01:00
980730c.sm	185 tim	y	Dual count second surveyor	7/30/98	13:56:00
980730d.sm	185 tim	y	Dual count second surveyor	7/30/98	16:37:00
980730e.sm	185 tim	y	Dual count second surveyor	7/30/98	17:28:00
980730f.sm	185 tim	y	Dual count second surveyor	7/30/98	17:32:00
980730g.sm	185 tim	y	Dual count second surveyor; corresponds with 980730f.raw	7/30/98	18:35:00
980731a.sm	185 tim	y	North area complete survey; Stephanie primary files a-d	7/31/98	11:35:00
980731b.sm	185 tim	y	North area complete survey; Stephanie primary files a-d	7/31/98	13:29:00
980731c.sm	185 tim	y	North area complete survey; Stephanie primary files a-d	7/31/98	15:26:00
980731d.sm	185 tim	y	North area complete survey; Stephanie primary files a-d	7/31/98	17:10:00
980801a.sm	185 tim	y	North area complete survey; Stephanie primary files a-c	8/1/98	9:34:00
980801b.sm	185 tim	y	North area complete survey; Stephanie primary files a-c	8/1/98	12:00:00
980801c.sm	185 tim	y	North area complete survey; Stephanie primary files a-c	8/1/98	13:13:00
980803a.raw	185 tim	y	Central region survey double counts; Evelyn primary files a-c	8/3/98	11:28:00
980803b.raw	185 tim	y	Central region survey double counts; Evelyn primary files a-c	8/3/98	12:19:00
980803b.raw	185 tim	y	Central region survey double counts; Evelyn primary files a-c	8/3/98	13:16:00
980803a.sm	185 tim	y	Dual count second surveyor	8/3/98	11:28:00
980803b.sm	185 tim	y	Dual count second surveyor	8/3/98	12:20:00
980803c.sm	185 tim	y	Dual count second surveyor	8/3/98	13:17:00
980804a.sm	185 tim	y	Dual count second surveyor	8/4/98	10:46:00
980804b.sm	185 tim	y	Dual count second surveyor	8/4/98	11:36:00
980804c.sm	185 tim	y	Dual count second surveyor	8/4/98	12:10:00
980804d.sm	185 tim	y	Dual count second surveyor	8/4/98	12:39:00
980804e.sm	185 tim	y	Dual count second surveyor	8/4/98	14:29:00
980804a.raw	185 tim	y	Central region complete survey; double counted primary Evelyn files a-e	8/4/98	10:46:00
980804b.raw	185 tim	y	Central region complete survey; double counted primary Evelyn	8/4/98	11:36:00
980804c.raw	185 tim	y	Jackpot region survey	8/4/98	12:07:00
980804d.raw	185 tim	y	Central region complete survey; double counted primary Evelyn	8/4/98	12:38:00
980804e.raw	185 tim	y	Central region complete survey; double counted primary Evelyn	8/4/98	14:27:00
980805a.raw	185 tim	y	Central region complete survey; last double count survey files a-d	8/5/98	10:03:00
980805b.raw	185 tim	y	Central region complete survey; last double count survey files a-d	8/5/98	10:57:00
980805c.raw	185 tim	y	Central region complete survey; last double count survey files a-d	8/5/98	12:04:00

980805d.raw	185 tim	y	Central region complete survey; last double count survey files a-d	8/5/98	13:26:00
980805a.sm	185 tim	y	Dual count second surveyor	8/5/98	10:01:00
980805b.sm	185 tim	y	Dual count second surveyor	8/5/98	10:57:00
980805c.sm	185 tim	y	Dual count second surveyor	8/5/98	12:05:00
980805d.sm	185 tim	y	Dual count second surveyor	8/5/98	13:26:00
980807a.sm	185 tim	y	North area survey; Stephanie is primary	8/7/98	9:31:00
980807b.sm	185 tim	y	North area survey; Stephanie is primary	8/7/98	13:22:00
980807c.sm	185 tim	y	North area survey; Stephanie is primary	8/7/98	15:15:00
980808a.sm	185 tim	y	North area survey; Stephanie is primary	8/8/98	9:18:00
980808b.sm	185 tim	y	North area survey; Stephanie is primary	8/8/98	11:54:00
980808c.sm	185 tim	y	North area survey; Stephanie is primary	8/8/98	13:52:00
980809a.sm	185 tim	y	North area survey; Stephanie is primary	8/9/98	9:18:00
980809b.sm	185 tim	y	North area survey; Stephanie is primary	8/9/98	12:13:00
980809c.sm	185 tim	y	North area survey; Stephanie is primary	8/9/98	14:14:00
980810a.sm	185 tim	y	Last Central region survey; Stephanie is primary	8/10/98	11:32:00
980810b.sm	185 tim	y	Last Central region survey; Stephanie is primary	8/10/98	12:22:00
980811a.sm	185 tim	y	Last Central region survey; Stephanie is primary	8/11/98	10:34:00

V = Video taken

Table 2. Summary of flight path (transect) statistics by day.

Date	Total Area Surveyed (km^2)	Average Transect Width (m)	Length of Transect (km)
7/6/98	221.46	486.85	457.90
7/7/98	354.20	455.33	777.90
7/8/98	308.44	445.36	692.78
7/10/98	1,633.60	446.83	3653.36
7/11/98	274.64	451.19	607.82
7/12/98	434.34	454.88	954.78
7/13/98	314.68	456.48	689.26
7/14/98	147.54	435.42	338.58
7/15/98	371.62	454.52	817.62
7/16/98	332.12	454.45	730.85
7/17/98	252.47	452.01	558.44
7/18/98	313.34	455.33	688.16
7/19/98	431.00	455.33	946.57
7/20/98	97.57	444.16	219.80
7/23/98	323.11	455.33	709.62
7/24/98	338.92	455.33	744.34
7/26/98	249.63	444.50	562.18
7/28/98	209.55	455.33	460.22
7/30/98	687.38	455.33	1509.63
7/31/98	371.71	455.33	816.35
8/1/98	245.28	425.13	573.67
8/3/98	305.13	439.44	693.38
8/4/98	343.89	455.33	755.25
8/5/98	248.43	354.30	698.72
8/7/98	325.68	455.33	715.25
8/8/98	326.83	455.33	717.79
8/9/98	324.75	455.33	713.22
8/10/98	99.46	455.33	218.44
8/11/98	37.03	455.33	81.32
Total	9,923.83		22,103.16
Average Width		449.24	

Table 3. Validations collected from net catches, diver observations and underwater video in 1998 (next two pages)

Aerial I.D.	School shape	Validation type	Validation species	Age	Latitude	Longitude	Set No.	Coorproj	Set time	Set date
Sand lance	Round	Diver	Sand lance		60.416	-147.631		NVP		7/10/98
Capelin	Round	Net Catch	Capelin		60.281	-147.263	98020003	APEX	1824	7/11/98
Capelin	Round	Net Catch	Capelin		60.281	-147.263	98020003	APEX	1824	7/11/98
Capelin	Round	Net Catch	Capelin		60.281	-147.263	98020003	APEX	1824	7/11/98
Herring	Round	Diver	Herring	2+	60.449	-147.764		NVP		7/11/98
Sand lance	Oval	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Sand lance	Oval	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Sand lance	Oval	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Sand lance	Oval	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Herring	Round	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Herring	Round	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Herring	Round	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Herring	Round	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Herring	Round	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Sand lance	Round	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Sand lance	Streak	Net Catch	Sand lance	0	60.244	-147.491	98020004	APEX	1115	7/12/98
Herring	Oval	Diver	Sand lance		60.070	-147.846		NVP		7/12/98
Sand lance	Oval	Diver	Sand lance		60.070	-147.846		NVP		7/12/98
Sand lance	Oval	Diver	Sand lance		60.070	-147.846		NVP		7/12/98
Sand lance	Round	Diver	Sand lance		60.070	-147.846		NVP		7/12/98
Sand lance	Round	Diver	Sand lance		60.070	-147.846		NVP		7/12/98
Sand lance	Oval	Net Catch	Sand lance	0-1	60.658	-147.436	98020006	APEX	1149	7/13/98
Sand lance	Oval	Net Catch	Sand lance	0-1	60.658	-147.436	98020006	APEX	1149	7/13/98
Sand lance	Oval	Net Catch	Sand lance	0-1	60.658	-147.436	98020006	APEX	1149	7/13/98
Sand lance	Oval	Net Catch	Sand lance	0-1	60.658	-147.436	98020006	APEX	1149	7/13/98
Sand lance	Oval	Net Catch	Sand lance	0-1	60.658	-147.436	98020006	APEX	1149	7/13/98
Sand lance	Oval	Net Catch	Sand lance	0-1	60.658	-147.436	98020006	APEX	1149	7/13/98
Sand lance	Oval	Net Catch	Sand lance	0-1	60.658	-147.436	98020006	APEX	1149	7/13/98
Herring	Round	Net Catch	Sand lance	0-1	60.658	-147.436	98020006	APEX	1149	7/13/98
Sand lance	Streak	Net Catch	Sand lance	0-1	60.658	-147.436	98020006	APEX	1149	7/13/98
Sand lance	Oval	Diver	Sand lance		60.293	-147.231		NVP		7/13/98
Sand lance	Round	Diver	Sand lance		60.293	-147.231		NVP		7/13/98
Herring	Round	Net Catch	Herring	0-adult	60.608	-145.859	98020007	APEX	1748	7/14/98
Herring	Round	Net Catch	Herring	0-adult	60.608	-145.859	98020007	APEX	1748	7/14/98
Herring	Round	Net Catch	Herring	0-adult	60.608	-145.859	98020007	APEX	1748	7/14/98
Herring	Oval	Net Catch	Herring	0-1	60.628	-145.891	98020008	APEX	1010	7/15/98
Herring	Round	Net Catch	Herring	0-1	60.628	-145.891	98020008	APEX	1010	7/15/98
Herring	Round	Net Catch	Herring	0-1	60.628	-145.891	98020008	APEX	1010	7/15/98
Herring	Round	Net Catch	Herring	0-1	60.628	-145.891	98020008	APEX	1010	7/15/98
Sand lance	Streak	Net Catch	Sand lance	0	60.653	-147.319		APEX	1545	7/16/98
Sand lance	Oval	Net Catch	Sand lance	0	60.683	-147.550		APEX	1245	7/17/98
Sand lance	Oval	Net Catch	Sand lance	0	60.683	-147.550		APEX	1245	7/17/98
Sand lance	Oval	Net Catch	Sand lance	0	60.683	-147.550		APEX	1245	7/17/98
Sand lance	Oval	Net Catch	Sand lance	0	60.683	-147.550		APEX	1245	7/17/98

Sand lance	Round	Net Catch	Sand lance	0	60.683	-147.550		APEX	1245	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.999	-147.222	98020009	APEX	2130	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.973	-147.271	98020010	APEX	2242	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.973	-147.271	98020010	APEX	2242	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.973	-147.271	98020010	APEX	2242	7/17/98
Herring	Round	Net Catch	Herring	1-adult	60.973	-147.271	98020010	APEX	2242	7/17/98
Sand lance	Round	Net Catch	Herring	1-adult	60.973	-147.271	98020010	APEX	2242	7/17/98
Sand lance	Round	Net Catch	Herring	1-adult	60.973	-147.271	98020010	APEX	2242	7/17/98
Sand lance	Round	Net Catch	Herring	1-adult	60.973	-147.271	98020010	APEX	2242	7/17/98
Sand lance	Round	Net Catch	Herring	1-adult	60.973	-147.271	98020010	APEX	2242	7/17/98
Sand lance	Round	Net Catch	Herring	1-adult	60.973	-147.271	98020010	APEX	2242	7/17/98
Sand lance	Oval	Net Catch	Herring	2-adult	60.905	-147.318	98020011	APEX	1100	7/18/98
Herring	Round	Net Catch	Herring	2-adult	60.905	-147.318	98020011	APEX	1100	7/18/98
Herring	Round	Net Catch	Herring	2-adult	60.905	-147.318	98020011	APEX	1100	7/18/98
Sand lance	Round	Net Catch	Herring	2-adult	60.905	-147.318	98020011	APEX	1100	7/18/98
Sand lance	Round	Net Catch	Herring	2-adult	60.905	-147.318	98020011	APEX	1100	7/18/98
Sand lance	Round	Net Catch	Herring	2-adult	60.905	-147.318	98020011	APEX	1100	7/18/98
Sand lance	Round	Net Catch	Herring	2-adult	60.871	-147.400	98020012	APEX	1200	7/18/98
Sand lance	Round	Net Catch	Herring	2-adult	60.871	-147.400	98020012	APEX	1200	7/18/98
Herring	Round	Net Catch	Herring	2	60.344	-148.250	98020015	APEX	1630	7/19/98
Sand lance	Round	Net Catch	Herring	2	60.344	-148.250	98020015	APEX	1630	7/19/98
Sand lance	Round	Net Catch	Herring	2	60.344	-148.250	98020015	APEX	1630	7/19/98
Sand lance	Round	Net Catch	Herring	2	60.344	-148.250	98020015	APEX	1630	7/19/98
Herring	Oval	UW Video	Herring	1	60.820	-146.652		APEX	1350	7/21/98
Sand lance	Oval	Net Catch	Mixed sd,h)	0	60.856	-146.811		APEX	1730	7/21/98
Sand lance	Oval	Net Catch	Mixed sd,h)	0	60.856	-146.811		APEX	1730	7/21/98
Sand lance	Round	Net Catch	Mixed sd,h)	0	60.856	-146.811		APEX	1730	7/21/98
Herring	Oval	Net Catch	Herring		60.569	-147.619		APEX	920	7/24/98
Sand lance	Oval	Net Catch	Sand lance	0	60.525	-147.620		APEX	1400	7/24/98
Sand lance	Oval	Net Catch	Sand lance	0	60.525	-147.620		APEX	1400	7/24/98
Sand lance	Oval	Net Catch	Sand lance	0	60.418	-147.627		APEX	1745	7/24/98

Sand lance	Oval	Net Catch	Sand lance	0	60.418	-147.627	APEX	1745	7/24/98
Sand lance	Oval	Net Catch	Sand lance	0	60.418	-147.627	APEX	1745	7/24/98
Sand lance	Oval	Net Catch	Mixed h,sd)	0	60.304	-147.355	APEX	1100	7/25/98
Sand lance	Oval	Net Catch	Mixed(h,sd)	0	60.304	-147.355	APEX	1100	7/25/98
Sand lance	Oval	Net Catch	Mixed(h,sd)	0	60.304	-147.355	APEX	1100	7/25/98
Sand lance	Round	Net Catch	Mixed(h,sd)	0	60.304	-147.355	APEX	1100	7/25/98
Sand lance	Round	Net Catch	Mixed(h,sd)	0	60.304	-147.355	APEX	1100	7/25/98
Sand lance	Oval	Net Catch	Herring	0	60.254	-147.408	APEX	1300	7/25/98
Sand lance	Round	Net Catch	Herring	0	60.254	-147.408	APEX	1300	7/25/98
Sand lance	Oval	Net Catch	Herring	0	60.254	-147.408	APEX	1300	7/25/98
Sand lance	Oval	Net Catch	Sand lance	0	60.254	-147.408	APEX	1300	7/25/98
Herring	Oval	Net Catch	Sand lance	0	60.246	-147.434	APEX	1400	7/25/98
Sand lance	Oval	Net Catch	Sand lance	0	60.246	-147.434	APEX	1400	7/25/98
Sand lance	Oval	Net Catch	Sand lance	0	60.246	-147.434	APEX	1400	7/25/98
Sand lance	Round	Net Catch	Sand lance	0	60.246	-147.434	APEX	1400	7/25/98
Sand lance	Round	Net Catch	Sand lance	0	60.246	-147.434	APEX	1400	7/25/98
Sand lance	Oval	UW Video	Herring	0	60.275	-147.334	APEX	1030	7/30/98
Herring	Round	UW Video	Herring	0	60.275	-147.334	APEX	1030	7/30/98
Herring	Round	UW Video	Herring	0	60.275	-147.334	APEX	1030	7/30/98
Herring	Oval	Net Catch	Herring	0	60.298	-147.319	APEX	1045	7/30/98
Herring	Round	Net Catch	Herring	0	60.298	-147.319	APEX	1045	7/30/98
Herring	Round	Net Catch	Herring	0	60.298	-147.319	APEX	1045	7/30/98

Table 4. Total numbers of key species sighted from the air by day, 1998.

Month	Day	Alcids	GW*	Kittiwakes	DP*	HS*	HW*	Orcas	Sea Lions	Sea Otters	Capelin	Eulachon	Herring	Sand Lance	Jellyfish
July	6	3	2	1062		1			7	2			43	2	67
	7	12	11	2119	4	4			161	26			96	26	88
	8			1617					13	35			65	35	40
	10	308		4013	2	51	10		39	34	10	5	41	34	7
	11	3		1698			5		5	36	18		16	36	14
	12	1723		4906		81	2		39	104	18		74	104	47
	13	100		5764	7		1	8	15	107	7	17	124	107	5
	14	17		522					4	5			11	5	11
	15			1552	2				9	17			104	17	52
	16	23		1401					218	16			56	16	45
	17	2		887			1		2	8			49	8	36
	18	224		2384		8	8		60	165		1	25	165	16
	19	164		2492			10		47	185			34	185	133
	20	16		393			1		1	11			2	11	3
	23	22	45	1364				3	18	11			41	11	8
	24	151	37	1550	4	3			224	12			21	12	11
	26	107		4759			7		208	151			9	151	3
	28	110		1267		1	2			157			39	157	42
	30	292	21	3385		2	7	2	135	125			156	125	25
	31	281	7	1552					30	8			11	8	22
July Total		3558	123	44687	19	151	54	13	1235	1215	53	23	1017	1215	675
August	1	209	38	930					7	2			2	2	5
	3	122	1	1885			7		6	71			116	71	15
	4	257		2934		90	3	1	70	61			130	61	39
	5	202	4	2599		96	5		52	50			84	50	14
	7	136	2	1462					20	1			15	1	4
	8	175	4	1467					104				41		1
	9	105	5	1632					84	12			23	12	4
	10	401		612					19	4			17	4	
	11	58		156											13
August Total		1665	54	13677		186	15	1	362	201			428	201	95
Grand Total		**5223**	**177**	**58364**	**19**	**337**	**69**	**14**	**1597**	**1416**	**53**	**23**	**1445**	**1416**	**770**

- GW = Glacous-Winged Gulls, DP = Dahl Porpoise, HW = Humpback Whales, HS = Harbor Seals

Table 5. Total surface area (m^2) of fish schools and jellyfish aggregations sighted along the transects by date, 1998.

Month	Day	Capelin	Eualchon	Herring	Jellyfish	Sand Lance
July	6			1407.63	3767.50	65.53
	7			2948.30	8128.29	431.75
	8			1279.05	4087.43	1315.11
	10	97.54	767.92	1958.24	442.79	2504.71
	11	344.00		455.94	6611.84	3076.81
	12	456.39		4719.25	4453.94	6984.22
	13	387.78	3179.21	5643.89	406.71	15344.92
	14			203.70	905.10	117.56
	15			3334.39	5621.51	445.92
	16			2013.10	4522.62	729.12
	17			3428.27	1263.00	639.93
	18		284.41	473.85	1707.44	13222.81
	19			1592.92	8695.90	10353.65
	20			25.32	212.36	592.06
	23			1235.87	1888.52	456.55
	24			565.79	1220.14	436.98
	26			108.12	0.00	22783.58
	28			849.40	2638.42	9193.62
	30			5531.75	1651.50	8264.11
	31			332.38	1477.06	489.84
July Total		1285.71	4231.54	38107.15	59702.08	97448.78
	1			30.53	86.58	38.72
	3			5948.07	2276.04	4805.00
	4			5087.05	1815.77	4172.37
	5			1300.72	919.52	2252.03
	7			218.17	474.02	2.98
	8			811.89	9.48	
	9			349.96	182.03	778.82
	10			264.33		46.86
	11				0.00	
August Total				14010.71	5763.45	12096.77
Grand Total		**1285.71**	**4231.54**	**52117.86**	**65465.53**	**109545.56**

Figure 1. APEX study regions and established flight paths.

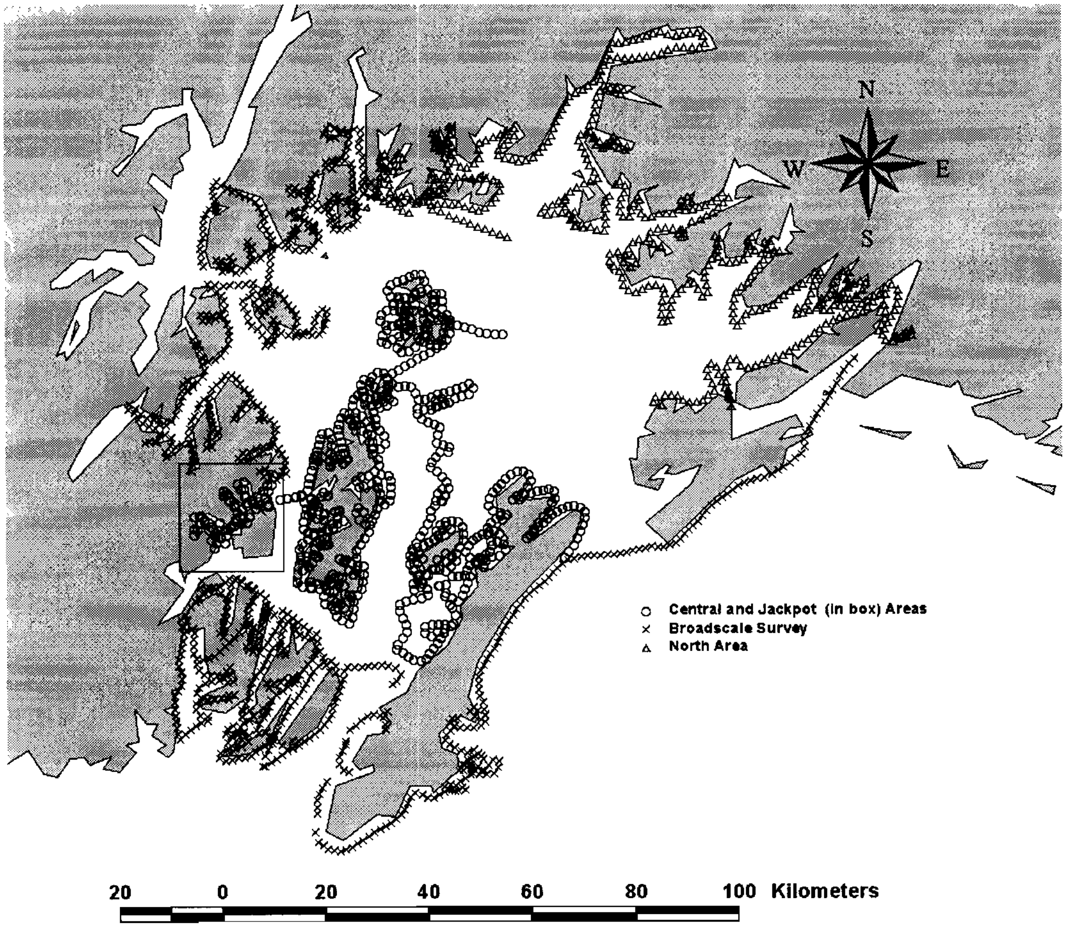
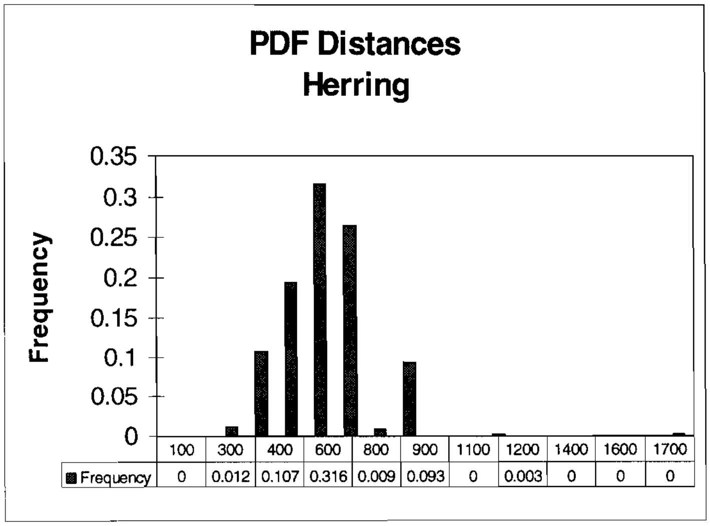
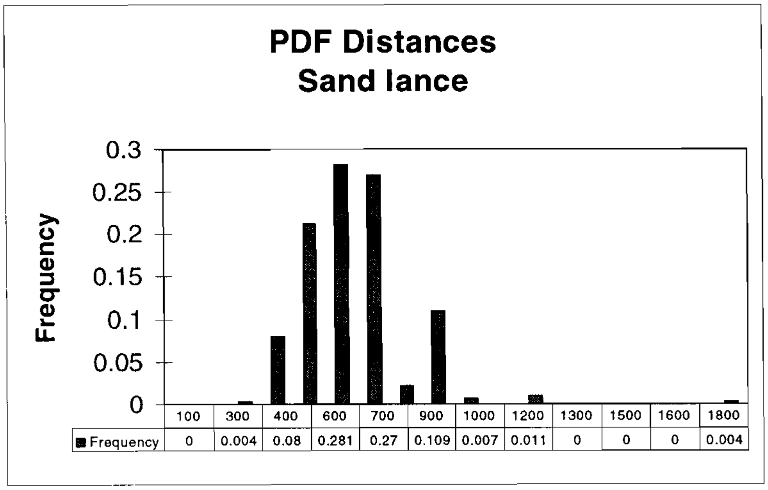


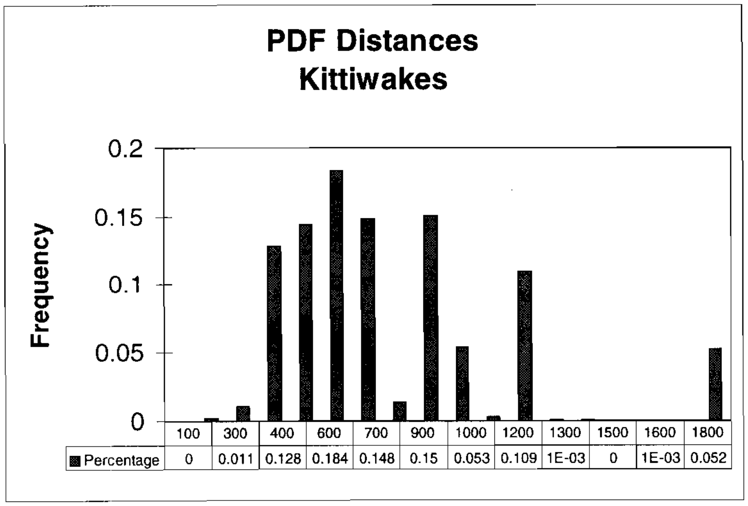
Figure 2. Probability density functions for kittiwakes, herring and sand lance



	100	300	400	600	800	900	1100	1200	1400	1600	1700
■ Frequency	0	0.012	0.107	0.316	0.009	0.093	0	0.003	0	0	0



	100	300	400	600	700	900	1000	1200	1300	1500	1600	1800
■ Frequency	0	0.004	0.08	0.281	0.27	0.109	0.007	0.011	0	0	0	0.004



	100	300	400	600	700	900	1000	1200	1300	1500	1600	1800
■ Percentage	0	0.011	0.128	0.184	0.148	0.15	0.053	0.109	1E-03	0	1E-03	0.052

Figure 3. Peak counts of key species sighted in APEX study regions during period 1, 7/6 – 7/13, 1998.

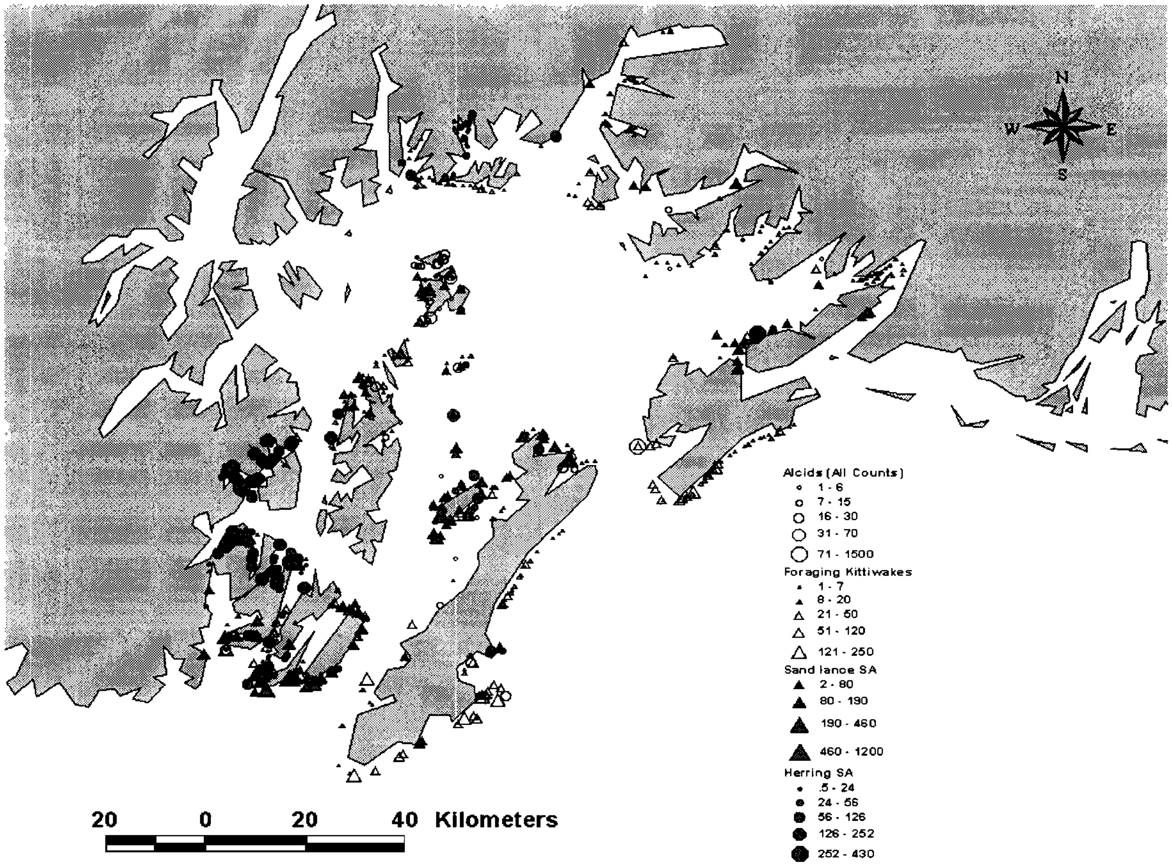


Figure 4. Peak counts of key species sighted in APEX study regions during period 2, 7/14 – 7/20, 1998.

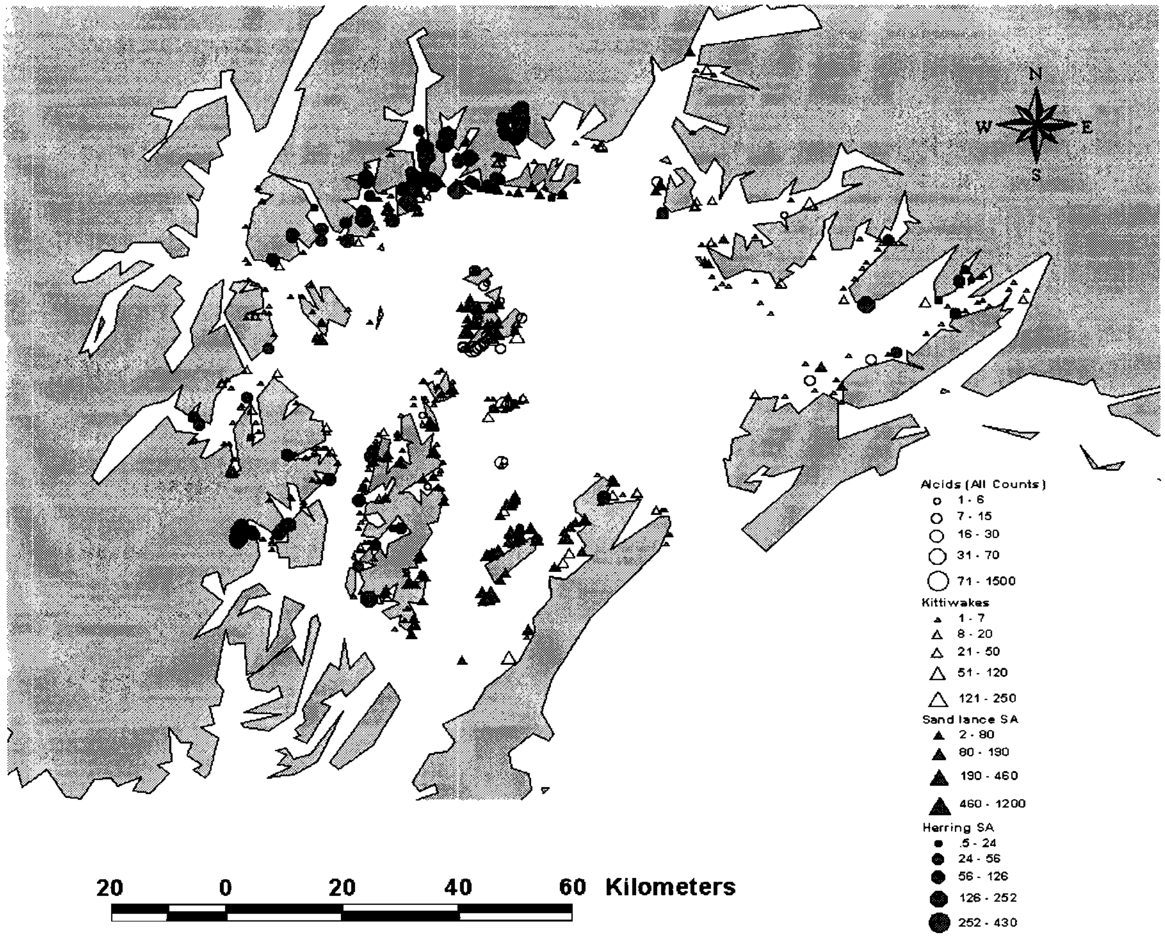


Figure 5. Peak counts of key species sighted in APEX study regions during period 3, 7/23 – 7/30, 1998.

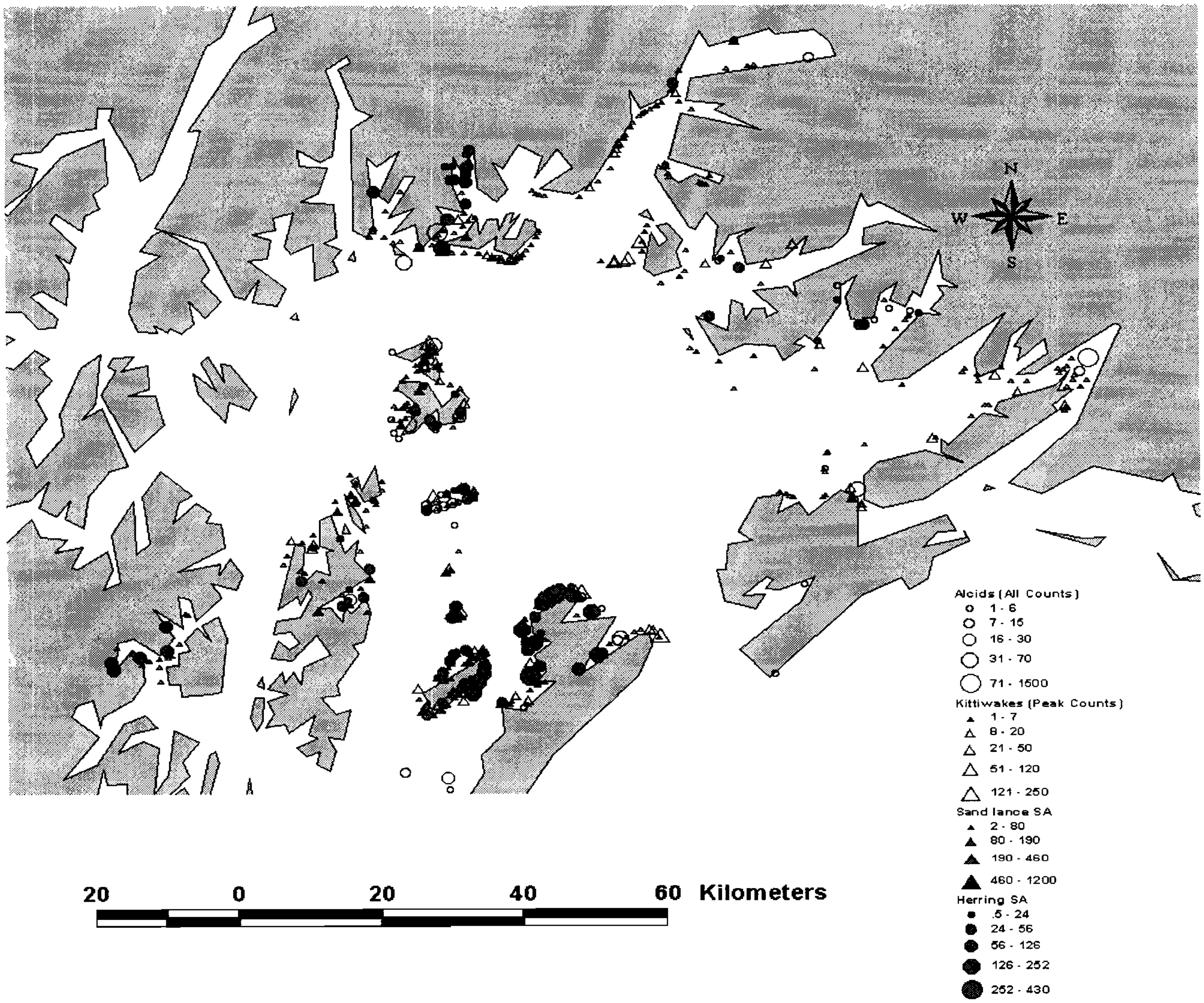


Figure 6. Peak counts of key species sighted in APEX study regions during period 4, 7/31 – 8/5, 1998.

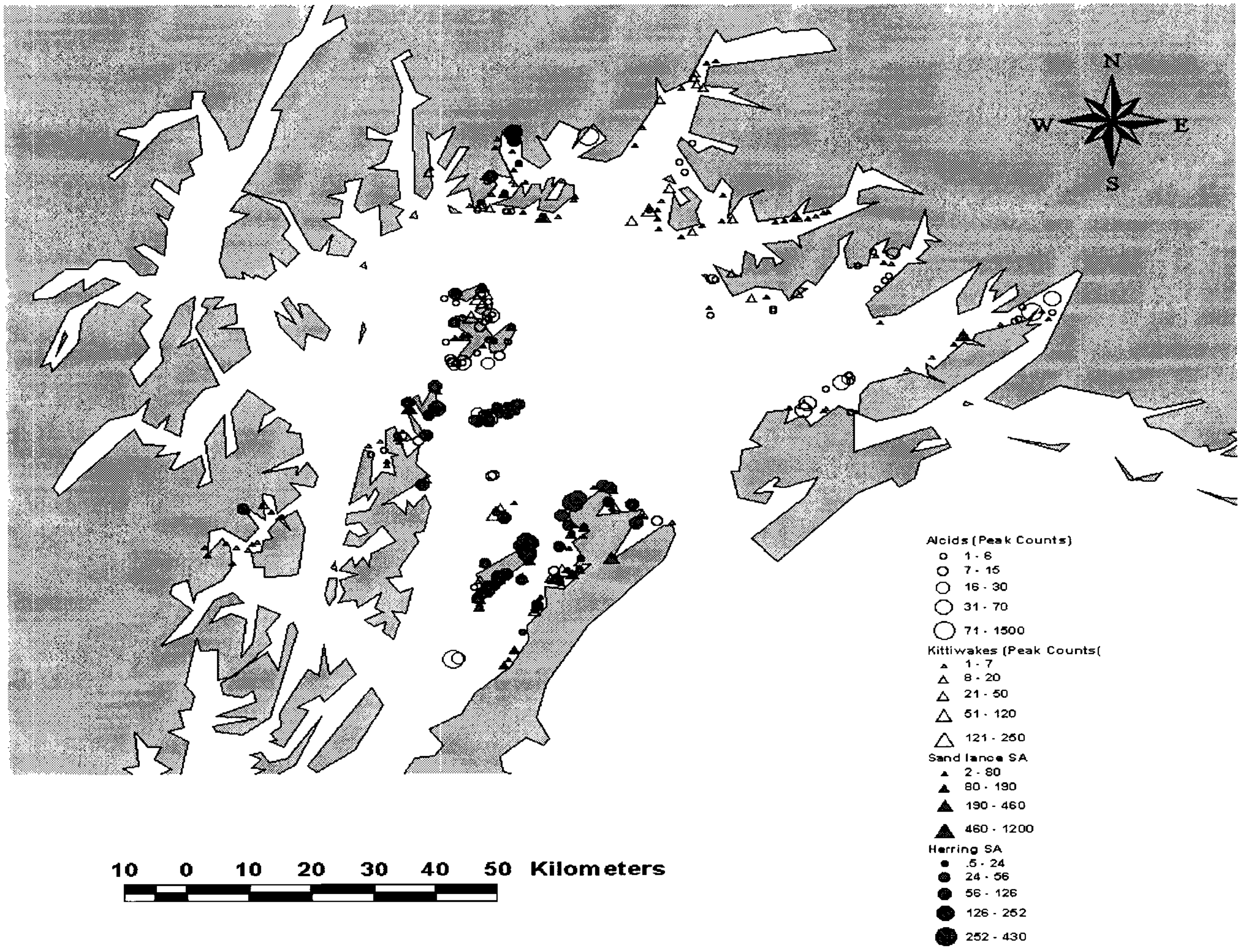


Figure 7. Peak counts of key species sighted in APEX study regions during period 5, 8/7 – 8/11, 1998.