Exxon Valdez Oil Spill
Restoration Project Draft Final Report

Sound Ecosystem Assessment (SEA): An Integrated Science Plan for the Restoration of Injured Species in Prince William Sound, Alaska

Restoration Project 98320
Final Report

Robert T. Cooney

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for:

Alaska Department of Fish and Game
Habitat and Restoration Division
333 Raspberry Road
Anchorage, Alaska 99518

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Chapter 1:

Summary

Sound Ecosystem Assessment (SEA): An Integrated Science Plan for the Restoration of Injured Species in Prince William Sound, Alaska

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Study History: The SEA program was initiated in April, 1994, as an integrated, interdisciplinary, multi-project study of processes influencing the recovery of damaged pink salmon and herring populations in Prince William Sound, Alaska. Annual reports of progress toward stated SEA goals have been submitted as a SEA annual report series (1994-97). The latest report in this series was submitted in April, 1998, under the title SEA97, Sound Ecosystem Assessment (SEA): An Integrated Science Plan for the Restoration of Injured Species in Prince William Sound. That report contained 12 chapters contributed by the principal investigators and the SEA lead scientist. The FY 98 draft Final Report, submitted as this document, details progress by SEA investigators during all years of the planned 5-year study. Results from the last funded field year of SEA work (FY 98) are also reported.

Abstract: The Sound Ecosystem Assessment (SEA) program concluded its field and laboratory work in fall 1998. Progress after that addressed the formal reporting requirements for the study to include a series of oral presentations for the 1999 Oil Spill Symposium, a single, integrated and peer-reviewed final report to the Trustee Council, and a selection of technical manuscripts written for a special volume of the journal, Fisheries Oceanography. The results of SEA research provide an ecosystem-level context within which the principal mechanisms influencing the survival of juvenile pink salmon and herring have been described – notably, relationships between the biophysical environment and annual losses to predation and starvation. These mechanisms have been captured in a series of numerical models including 3-dimensional ocean state simulation, plankton model linking upper-layer springtime mixing events to levels of primary and secondary production, pink salmon survival model driven by the bioenergetics of fry and their predators interacting with common plankton forage fields, and juvenile herring overwintering simulation based on the physiology of starvation. These models, singly and in combination, provide a means for experimentally investigating seasonal, interannual and decadal-scale shifts in factors influencing production of pink salmon and herring in Prince William Sound over the long term.

Key Words: Biophysical models, circulation, ecosystem modeling, marine acoustics, marine food webs, numerical models, nutrients, oceanography, Pacific herring, phytoplankton, pink salmon, Prince William Sound, somatic energy, stable isotopes, zooplankton.

Citation:
Cooney, Robert T. 1999. Sound Ecosystem Assessment (SEA): An integrated science plan for the restoration of injured species in Prince William Sound, Alaska, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320), Alaska Department of Fish and Game, Habitat and Restoration Division, Anchorage, Alaska.

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1	SEA 1998 Synthesis	98320A	Cooney, R.T. 1999. Sound Ecosystem Assessment (SEA): An Integrated Science Plan for the Restoration of Injured Species in Prince William Sound: Preface, Alaska *Exxon* Valdez Oil Spill Restoration Project Final Report (Restoration Project 98320A), Alaska Department of Fish and Game, Habitat and Restoration Division.	1-1 to 1-3
			Cooney, R.T., J.R. Allen, M.A. Bishop, D.L. Eslinger, T. Kline, B.L. Norcross, C.P. McRoy, J. Milton, J. Olsen, V. Patrick, A. J. Paul, D. Salmon, D. Scheel, G.L. Thomas, S.L. Vaughan, and T.M. Willette. 2001. Ecosystem controls of juvenile pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring (*Clupea pallasi*) populations in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):1-13.	1-4
2	Juvenile salmon predation	98320E	Willette, T.M., G. Carpenter, K. Hyer, M. Clapsadl, P. Saddler, and M. Powell. 1999. Sound Ecosystem Assessment: Juvenile Salmon Predation, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320E), Alaska Department of Fish and Game, Division of Commercial Fisheries, Cordova, Alaska.	2-1 to 2-8
			Carpenter, G., and T.M. Willette. Diurnal changes in juvenile salmon foraging behavior and predation risk. *Journal of Fish Biology*, in revision.	2-A-1 to 2-A-27
			Paul, A.J., and T.M. Willette. 1997. Geographical variation in somatic energy content of migrating pink salmon fry from Prince William Sound: A tool to measure nutritional status. Pages 707-720 in: Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, Anchorage, Alaska, November 13-16, 1996. Lowell Wakefield Fisheries Symposium 14, Alaska Sea Grant College Program Report no. 97-01. University of Alaska Fairbanks, Fairbanks, Alaska.	2-4
			Scheel, D, and K.R. Hough. 1997. Salmon fry predation by seabirds near an Alaskan hatchery. *Marine Ecology Progress Series* 150:35-48.	2-4
			Willette, T.M. 2001. Foraging behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha*) and size-dependent predation risk. *Fisheries Oceanography* 10 (Suppl. 1):14-41.	2-4
			Willette, T.M. Limitation of feeding and growth rates of juvenile pink salmon (*Oncorhynchus gorbuscha*) in relation to foraging behavior and subsequent effects on mortality of wild and hatchery-origin salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, in revision.	2-B-1 2-B-41
			Willette, T.M., R.T. Cooney, and K. Hyer. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Canadian Journal of Fisheries and Aquatic Sciences* 56:364-376.	2-4
			Willette, T.M., R.T. Cooney, V. Patrick, D.M. Mason, G.L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):14-41.	2-4

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3	Phytoplankton and Nutrients	98320G	McRoy, C.P., E.P. Simpson, K. Tamburello, A. Ward, and J. Cameron. 1999. Sound Ecosystem Analysis: Phytoplankton and Nutrients, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320G), Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska.	3-1 to 3-48
			Eslinger, D.L., R.T. Cooney, C.P. McRoy, A. Ward, T.C. Kline, Jr., E.P. Simpson, J. Wang, and J.R. Allen. 2001. Plankton dynamics: observed and modelled responses to physical conditions in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):81-96.	3-4
			Jin, M., J. Wang, P. Simpson, P. McRoy, and G. Thomas. A 3-D coupled physical-biological model and its application to the spring plankton bloom of 1996 in Prince William Sound, Alaska. *Journal of Geophysical Research*, submitted.	3-A-1 to 3-A-35
4	Role of Zooplankton	98320H	Cooney, R.T. 1998. The Role of Zooplankton in the Prince William Sound Ecosystem. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320H), Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska.	4-1 to 4-16
			Cooney R.T., K.O. Coyle, E. Stockmar, and C. Stark. 2001. Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):97-109.	4-3
			Eslinger, D.L., R.T. Cooney, C.P. McRoy, A. Ward, T.C. Kline, Jr., E.P. Simpson, J. Wang and J.R. Allen. 2001. Plankton dynamics: observed and modelled responses to physical conditions in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):81-96.	4-3
			Foy, R.J., and A.J. Paul. 1999. Winter feeding and changes in somatic energy content for age-0 Pacific herring in Prince William Sound, Alaska. *Transactions of the American Fisheries Society* 128(6):1193-1200.	4-3
			Kirsch, J., G.L. Thomas, and R.T. Cooney. 2000. Acoustic estimates of zooplankton distributions in Prince William Sound, spring 1996. *Fisheries Research* 47:245-260.	4-3
			Kirsch, J., L.B. Tuttle, R.T. Cooney, and G.L. Thomas. [1999?]. Vertical and horizontal structure in upper-layer Neocalanus populations during the spring in Prince William Sound, Alaska. Unpublished manuscript.	4-A-1 to 4-A-31
			Willette, T.M., R.T. Cooney, and K. Hyer. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Canadian Journal of Fisheries and Aquatic Sciences* 56:364-376.	4-3
			Willette, T.M., R.T. Cooney, V. Patrick, D.M. Mason, G.L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):14-41.	4-3
5	Biophysical Modeling and Remote Sensing	98320R	Eslinger, D.L. 1999. Biophysical Modeling and Validation Through Remote Sensing, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 99320R), Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska.	5-1 to 5-33

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			Norcross, B.L., and E.D. Brown. 2001. Estimation of first-year survival of Pacific herring from a review of recent stage-specific studies. Pages 535-558 in: Funk, F., J. Blackburn, D. Hay, A.J. Paul, R. Stephenson, R. Toresen, and D. Witherell, eds. Herring: Expectations for a New Millennium. International Herring Symposium, Anchorage, Alaska, February 23-26, 2000. Lowell Wakefield Fisheries Symposium 18, Alaska Sea Grant College Program Report no. 01-04. University of Alaska Fairbanks, Fairbanks, Alaska.	10-4
			Norcross, B.L., E.D. Brown, R.J. Foy, M. Frandsen, S.M. Gay, T.C. Kline, Jr., D. M. Mason, E.V. Patrick, A. J. Paul, and K.D.E. Stokesbury. 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):42-57.	10-4
			Stokesbury, K.D.E., R.J. Foy, and B.L. Norcross, B.L. 1999. Spatial and temporal variability in juvenile Pacific herring, *Clupea pallasi*, growth in Prince William Sound, Alaska. *Environmental Biology of Fishes* 56(4):409-418.	10-5
			Stokesbury, K.D.E., J. Kirsch, E.D. Brown, G.L. Thomas, and B.L. Norcross. 2000. Spatial distributions of Pacific herring, *Clupea pallasi*, and walleye pollock, *Theragra chalcogramma*, in Prince William Sound, Alaska. Fishery Bulletin 98(2):400-409.	10-5
			Stokesbury, K.D.E., J. Kirsch, E.V. Patrick, and B.L. Norcross. 2002. Natural mortality estimates of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 59(3):416-423.	10-5
11	Fish energetics	98320U	Paul, A.J. 1999. Sound Ecosystem Assessment: Fish Energetics, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320U), University of Alaska, Institute of Marine Science, Seward Marine Center Laboratory, Seward, Alaska.	11-1 to 11-8
			Foy, R.J., and A.J. Paul. 1999. Winter feeding and changes in somatic energy content for age-0 Pacific herring in Prince William Sound, Alaska. *Transactions of the American Fisheries Society* 128(6):1193-1200.	11-7
			Norcross, B.L., E.D. Brown, R.J. Foy, M. Frandsen, S.M. Gay, T.C. Kline, Jr., D. M. Mason, E.V. Patrick, A. J. Paul, and K.D.E. Stokesbury. 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):42-57.	11-7
			Paul, A.J. 1997. Use of bioenergetic measurements to estimate prey consumption, nutritional status and thermal habitat requirements for marine organisms reared in the sea. *Bulletin of the National Research Institute of Aquaculture* (Japan), Suppl. 3:59-68.	11-7

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			Paul, A.J., and J.M. Paul. 1998. Spring and summer whole-body energy content of Alaskan juvenile Pacific herring. *Alaska Fishery Research Bulletin* 5(2):131-136.	11-7
			Paul, A.J., and J.M. Paul. 1999. Energy contents of whole body, ovaries and ova from pre-spawning Pacific herring. *Alaska Fishery Research Bulletin* 6(1):29-34.	11-7
			Paul, A.J., and J.M. Paul. 1999. First-year energy storage patterns of Pacific herring and walleye pollock: Insight into competitor strategies. Pages 117-127 in: Ecosystem Approaches for Fisheries Management: Proceedings of the Symposium on Ecosystem Considerations in Fisheries Management, September 30-October 3, 1998, Anchorage, Alaska. Lowell Wakefield Fisheries Symposium 16, Alaska Sea Grant College Program Report no. 99-01. University of Alaska Fairbanks, Fairbanks, Alaska.	11-7
			Paul, A.J., and J.M. Paul. 1999. Interannual and regional variations in body length, weight and energy content of age-0 Pacific herring from Prince William Sound, Alaska. *Journal of Fish Biology* 54:996-1001.	11-7
			Paul, A.J., J.M. Paul, and E.D. Brown. 1996. Ovarian energy content of Pacific herring from Prince William Sound, Alaska. *Alaska Fishery Research Bulletin* 3(2):103-111.	11-7
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			Paul, A.J., and T.M. Willette. 1997. Geographical variation in somatic energy content of migrating pink salmon fry from Prince William Sound: A tool to measure nutritional status. Pages 707-720 in: Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, Anchorage, Alaska, November 13-16, 1996. Lowell Wakefield Fisheries Symposium 14, Alaska Sea Grant College Program Report no. 97-01. University of Alaska Fairbanks, Fairbanks, Alaska.	11-8
12	Synthesis and Integration	98320Z	Cooney, R.T. 1999. Sound Ecosystem Assessment (SEA): Synthesis and Integration, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320Z), Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska.	12-1 to 12-6

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			Cooney, R.T., J.R. Allen, M.A. Bishop, D.L. Eslinger, T. Kline, B.L. Norcross, C.P. McRoy, J. Milton, J. Olsen, V. Patrick, A. J. Paul, D. Salmon, D. Scheel, G.L. Thomas, S.L. Vaughan, and T.M. Willette. 2001. Ecosystem controls of juvenile pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring (*Clupea pallasi*) populations in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):1-13.	12-3

Preface

Each of the individual SEA draft final reports compiled here as separate chapters has been written as a stand-alone document. Bundling the reports under a single cover with an added summary chapter is done at the request of the EVOS Chief Scientist to provide the Trustee Council and its member agencies easy access to all results from work performed from 1994-98.

SEA was designed in the fall of 1993 to test a series of ideas about mechanisms restraining the recovery of pink salmon and herring populations damaged by the oil spill of 1989. Refinements to these conjectures continue to focus the research:

a. The survival of juvenile pink salmon and post-larval Pacific herring rearing in Prince William Sound is determined primarily by predation losses to marine birds, mammals and other fishes.

b. Predation losses are related in part to the energetic condition and size of juvenile Pacific herring and pink salmon. Condition and size are determined by growth rates which vary between regions of the Sound, and from year to year as a function of food and water temperature.

c. For juvenile Pacific herring, the somatic energy content of individuals at the beginning of the winter fast is a critical overwintering survival determinant. Young-of-the-year herring particularly, and older juveniles in general with low levels of somatic energy prior to winter, are at risk to starvation.

d. Predation losses are modified by the species composition of predator communities and their numbers and distributions in juvenile rearing areas. Predation losses are also governed by the amounts, kinds and time/space distributions of alternative prey for predators that also feed on juvenile pink salmon and Pacific herring. Macrozooplankton serves as ecologically important alternative prey during some seasons and years.

e. Macrozooplankton populations are established by local reproduction driven by phytoplankton productivity and modified by circulation processes that both flush the region and seed the Sound from adjacent shelf and open ocean populations.

These ideas were instrumental in structuring multi-disciplinary observational and modeling programs in SEA, and served as loci for data analysis and interpretation. An Ocean State and Plankton Dynamics sub-group focused on describing and modeling seasonal changes in circulation, temperature, salinity and plankton production. A Juvenile Salmon Recruitment Dynamics program described the effects of predation during early marine residence and provided a modeling environment to link the bioenergetics of survival to oceanographic and meteorological conditions. A Juvenile Herring Recruitment Dynamics sub-group described the seasonally varying characteristics of near-shore rearing environments and juvenile trophic dependencies, and completed a numerical model capturing the essence of the starvation process during the winter plankton hiatus.

Chapter 1: 98320A
Citations to published articles

Cooney, R.T., J.R. Allen, M.A. Bishop, D.L. Eslinger, T. Kline, B.L. Norcross, C.P. McRoy, J. Milton, J. Olsen, V. Patrick, A. J. Paul, D. Salmon, D. Scheel, G.L. Thomas, S.L. Vaughan, and T.M. Willette. 2001. Ecosystem controls of juvenile pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring (*Clupea pallasi*) populations in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):1-13.

Chapter 2

Juvenile Salmon Predation

Exxon Valdez Oil Spill
Restoration Project Final Report

Sound Ecosystem Assessment: Juvenile Salmon Predation

Restoration Project 98320E
Final Report

T. Mark Willette
Greg Carpenter
Karen Hyer
Mark Clapsadl
Penny Saddler
Margaret Powell

Alaska Department of Fish and Game
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Cordova, Alaska 99574

May 1999

Study History: This project was initiated under Restoration project 94320E and was continued under Restoration Projects 95320E, 96320E, 97320E. Annual reports were issued by Willette et al. under the title Sound Ecosystem Assessment: Juvenile Salmon Predation each year from 1994 through 1997. This is the final report for the project.

Abstract: This project is a component of the Sound Ecosystem Assessment (SEA) program which was designed to acquire an ecosystem-level understanding of the processes that constrain pink salmon and herring production in Prince William Sound (PWS). This project collected data needed to test several hypotheses related to predator-prey interactions affecting the mortality of pink salmon (*Oncorhynchus gorbuscha*) in PWS. Approximately 726 million juvenile pink salmon entered Prince William Sound, Alaska from bordering streams and hatcheries each year. Predation during the spring plankton bloom (May to mid-June) accounted for the mortality of 413 million juveniles (57%) and therefore appeared to be the primary mechanism causing mortality during this life stage. Two planktivorous fish, herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) probably consumed the greatest numbers of juvenile salmon. Several piscivorous fish (*Gadus macrocephalus, Microgadus proximus*, and *Salvelinus malma*) probably consumed the second greatest numbers and an assemblage of nearshore demersal fishes (Cottidae, Hexagrammidae, and *Sebastes spp.)* and seabirds (*Rissa tridactyla, Larus spp.*) probably consumed the smallest numbers of salmon. Relative attack|capture probabilities for planktivores feeding on juvenile salmon decreased over salmon lengths from 3-5 cm, but increased over this same length range for piscivores and demersal fishes feeding on salmon. Generally, juvenile pink salmon mortality probably increased from early May, (–0.0034) to early June (–0.0359) due to increasing depredation by herring and pollock and declining numbers of salmon. Mortality of pink salmon (release to adult return) from Wally H. Noerenberg Hatchery, adjacent to our study area, was greatest in 1994 (-0.0091), decreasing in 1995 (-0.0074), 1996 (-0.0070), and 1997 (-0.0056). This decline in mortality corresponded to a decline in adult pollock densities in our study area. Our results indicate that the copepod *Neocalanus* plays a unique role in modifying predation losses of juvenile pink salmon. Reduced large copepod densities probably caused (1) reduced growth when juvenile salmon densities were high, (2) greater predation losses to planktivores as these predators switched to alternative prey including salmon, and (3) dispersion of foraging juvenile salmon offshore leading to greater predation losses to piscivores and demersal fishes. Numerical model simulations indicated that predator size was an important factor modifying the predation process. Episodic periods of high juvenile mortality resulted when adult pollock switched to feeding on high-density groups of salmon as pteropod densities declined in June. Similar high depredation by immature pollock did not occur. Our results indicate that bottom-up processes affecting the spring *Neocalanus* bloom influence juvenile salmon growth rates and foraging behavior, but also modify top-down processes, through size-selective depredation of juvenile salmon and by altering the timing of a shift from planktivory toward piscivory among major predators on juvenile salmon. High mortality occurring after the *Neocalanus* bloom is reduced for juveniles that reach lengths exceeding 6-7 cm.

Key Words: *Exxon Valdez*, pink salmon, *Oncorhynchus gorbuscha*, Pacific herring, *Clupea pallasi*, walleye pollock, *Theragra chalcogramma*, Pacific tomcod, *Microgadus proximus*, mortality, predation, food habits.

Project Data: *Description of data* – Seven sets of digital data were developed during this project: (1) catches of various fish species in several types of nets, (2) lengths and weights of fish, (3) stomach contents of fish, (4) recoveries of tagged juvenile salmon, (5) zooplankton density and species composition estimated from nets, (6) ocean temperature and salinity measurements, and (7) light intensity measurements. Each data set is accompanied by documentation giving more information about their contents, including definitions of codes and terms, and other details that will facilitate access to and use of these data. All data are in R:Base format except ocean temperature\salinity and light intensity data which are in text files. *Custodian* – Contact Mark Willette, Alaska Department of Fish and Game, Commercial Fisheries Division, P.O. Box 669, Cordova, Alaska 99574 (work phone (907) 424-3214, fax (907) 424-3235, e-mail markw@fishgame.state.ak.us. *Availability* - copies of all data are available on diskette for the cost of duplication.

Citation: Willette, T. M., Carpenter, G., Hyer, K., Clapsadl, M., Saddler, P., and Powell, M. 1999. Sound Ecosystem Assessment: Juvenile Salmon Predation. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320E), Alaska Department of Fish and Game, Cordova, Alaska.

Chapter 2: 98320E
Citations to published articles

Paul, A.J., and T.M. Willette. 1997. Geographical variation in somatic energy content of migrating pink salmon fry from Prince William Sound: A tool to measure nutritional status. Pages 707-720 in: Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, Anchorage, Alaska, November 13-16, 1996. Lowell Wakefield Fisheries Symposium 14, Alaska Sea Grant College Program Report no. 97-01. University of Alaska Fairbanks, Fairbanks, Alaska.

Scheel, D, and K.R. Hough. 1997. Salmon fry predation by seabirds near an Alaskan hatchery. *Marine Ecology Progress Series* 150:35-48.

Willette, T.M. 2001. Foraging behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha*) and size-dependent predation risk. *Fisheries Oceanography* 10 (Suppl. 1):14-41.

Willette, T.M., R.T. Cooney, and K. Hyer. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Canadian Journal of Fisheries and Aquatic Sciences*, 56:364-376.

Willette, T.M., R.T. Cooney, V. Patrick, D.M. Mason, G.L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):14-41.

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Objectives

1. *Estimate the juvenile salmon consumption rate for fish predators in Prince William Sound.*

This objective was addressed in the following journal articles:

Willette, T.M., Cooney, R.T., Patrick, V., Thomas, G.L., and Scheel, D. 1999. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fish. Oceanogr. (in review).

Willette, T.M. 1999. Effects of juvenile salmon size and foraging behavior on predation risk. Fish. Oceanogr. (in review).

2. *Estimate the species and size composition of fish predators in Prince William Sound.*

This objective was addressed in the following journal articles:

Willette, T.M., Cooney, R.T., Patrick, V., Thomas, G.L., and Scheel, D. 1999. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fish. Oceanogr. (in review).

Willette, T.M. 1999. Effects of juvenile salmon size and foraging behavior on predation risk. Fish. Oceanogr. (in review).

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. Can. J. Fish. Aquat. Sci. **56**: 364-376.

3. *Conduct preliminary tests of prey/predator (prey switching) hypotheses.*

This objective was addressed in the following journal articles:

Willette, T.M., Cooney, R.T., Patrick, V., Thomas, G.L., and Scheel, D. 1999. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fish. Oceanogr. (in review).

Willette, T.M. 1999. Effects of juvenile salmon size and foraging behavior on predation risk. Fish. Oceanogr. (in review).

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. Can. J. Fish. Aquat. Sci. **56**: 364-376.

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Some processes affecting mortality of juvenile fish during the spring bloom in Prince William Sound, Alaska. In: Proceedings of an international symposium on ecosystem considerations in fisheries management. Alaska Sea Grant College Program Report, University of Alaska Fairbanks, Fairbanks, Alaska.

Willette, T.M. 1999. Limitation of feeding and growth rates of juvenile pink salmon (*Oncorhynchus gorbuscha*) in relation to foraging behavior and subsequent effects on mortality of wild- and hatchery-origin salmon. Can. J. Fish. Aquat. Sci. (in review).

Carpenter, G., and Willette, T.M. 1999. Diurnal changes in juvenile salmon foraging behavior and predation risk. J. Fish Biol. (in review).

Appendix 1: Journal articles produced during this project.

Willette, T.M., Cooney, R.T., Patrick, V., Thomas, G.L., and Scheel, D. 1999. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fish. Oceanogr. (in review).

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. Can. J. Fish. Aquat. Sci. **56**: 364-376.

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Some processes affecting mortality of juvenile fish during the spring bloom in Prince William Sound, Alaska. In: Proceedings of an international symposium on ecosystem considerations in fisheries management. Alaska Sea Grant College Program Report, University of Alaska Fairbanks, Fairbanks, Alaska.

Willette, T.M. 1999. Effects of juvenile salmon size and foraging behavior on predation risk. Fish. Oceanogr. (in review).

Willette, T.M. 1999. Limitation of feeding and growth rates of juvenile pink salmon (*Oncorhynchus gorbuscha*) in relation to foraging behavior and subsequent effects on mortality of wild- and hatchery-origin salmon. Can. J. Fish. Aquat. Sci. (in review).

Carpenter, G., and Willette, T.M. 1999. Diurnal changes in juvenile salmon foraging behavior and predation risk. J. Fish Biol. (in review).

Diurnal changes in juvenile salmon foraging behavior and predation risk

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FOR SUBMISSION TO THE JOURNAL FISH BIOLOGY

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Abstract

Analyses of field data were used to examine diurnal changes in foraging behavior and the risk of predation for juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Juvenile pink salmon fed continuously throughout the day, but feeding rate was greatest at dawn and stomach fullness peaked at dusk. Juvenile pink salmon formed very dense aggregations in shallow water at night to avoid predators in deeper water. Total food consumption of potential predators on salmon increased during twilight and at night due to higher abundances and feeding rates for several taxonomic groups. Predation on juvenile salmon in nearshore habitats was probably greatest during near dawn and dusk when light intensities were between 0.1 and 100 lux. As light intensities declined below 1000 lux, the profitability of feeding for juvenile salmon declined relative to the risk of predation. Juvenile salmon in PWS may have been vulnerable to predation for a shorter period of time each day in early May than later in the season, because surface light intensities were within the range of greatest vulnerability for a shorter time each day.

Introduction

Juvenile salmon and their predators exhibit diurnal patterns of distribution and feeding that affect their interaction. Juvenile pink salmon (*Oncorhynchus gorbuscha*) feed continuously throughout the day (Godin 1981), exhibit peaks in activity at various times during the day (Godin 1979), and migrate vertically into shallower waters at night (Godin 1984). Several potential predators on juvenile salmon migrate from deep water into the surface layer at night (Clark and Green 1990; Sogard and Olla 1993; Grant and Brown 1997). These behavioral patterns result in an overlap in the distributions of predator and prey that affect juvenile salmon mortality. Diurnal behavior patterns result from the need to concentrate vital activities to the time of day when the balance between food availability and predation risk is optimal for survival (Helfman 1993). This balance is often a function of the variable responses of predator and prey to light intensity.

In some cases, fluctuations in light intensity may be more important than prey density in controlling predation and thus prey mortality (Aksnes and Giske 1993). The variability in light intensity in aquatic environments can be extreme often changing more than seven orders of magnitude between bright daylight and night (Whitney 1969). Reactive distances decline with light intensity at different rates for various fishes affecting their interaction (Gerking 1994). At twilight, fish activity generally increases, and piscivores tend to be more successful at capturing prey (Helfman 1993). Juvenile salmon may be especially vulnerable to predators during brief periods at dawn and dusk. At these times, surface-oriented preys are silhouetted against the sky, but prey cannot distinguish bottom dwelling predators from the dark background (Pitcher and Turner 1986).

The presence of a predator may modify the foraging behavior of small fish by restricting feeding time and location, and reducing feeding rate. In the presence of predators, juvenile pink salmon occupied vegetation with less prey, but predator avoidance behaviors were relaxed when hungry

(Magnhagen 1988). Feeding rates (Metcalfe et al. 1987a), the efficiency of prey selection (Metcalfe et al. 1987b), and growth (English 1983) are generally reduced in the presence of predators, because more time is spent scanning for them. These effects on foraging behavior may significantly effect population size and structure (Jakobsen et al. 1988).

In the present study, we will test the following hypotheses related to these processes: (1) juvenile salmon diet composition is correlated with time of day and feeding rate is greater at dawn and dusk, (2) juvenile salmon aggregate nearshore at night and disperse offshore at dawn, (3) predator relative abundance and feeding rate is greater at dawn and dusk, (4) predation on juvenile salmon is greater at dawn and dusk and correlated with light intensity.

Methods

Field sampling and laboratory analysis

Nearshore fishes and their prey were sampled at several sites in western PWS from early May to mid June 1995 (Figure 1). Diel sampling was conducted approximately every 3 hours over a 24-hour period from 1 to 4 times per month at each site. Samples aggregated by site and date formed "sample units". A mid-water wing trawl (40 m x 28 m) equipped with a net sounder was used to sample pelagic fish in the passages of PWS. The net was towed at about 1.5 $m \cdot sec^{-1}$ for approximately 30 min in the 0-60 m layer of the water column. Nearshore fishes were sampled with 'anchovy' purse seines (250 m x 20 m, 1.5 cm stretch mesh) set in an approximate semi circle with the net open in the direction of the prevailing current for 20 min. Anchovy seine sampling was conducted within 1 km of the shore and up to the 20-m isobath. Nearshore fishes were also sampled with variable-mesh gill nets set out from shore at two stations within each site. Juvenile salmon were sampled inshore of the 20-m isobath with a small-mesh purse seine (60 m x 10 m, 0.5 cm stretch mesh) deployed from a skiff, and the relative abundance of juvenile salmon (low, moderate, or high) nearshore was estimated from visual shoreline surveys. In each study area, temperature and salinity were measured with a conductivity-temperature-depth profiler (CTD) to a depth of 100-m. A pyrometer equipped with a quantum sensor (Li-Cor Model LI-1000) was used to measure light intensity at 30-min intervals throughout each diel study.

The diet composition of nearshore fishes was estimated from specimens collected in 1995 (n=10,155). At least 30 specimens from each fish species were randomly selected from each net set for stomach contents analysis. Fork length and wet weight were measured, and stomachs excised and preserved in formalin for later analysis. In the laboratory, total stomach contents wet weight and the weight of juvenile salmon in the stomachs was measured. The number of juvenile salmon in each stomach was estimated by dividing the weight of juvenile salmon in the stomach by the mean wet weight of whole individual juvenile salmon found in the stomach. At least 20 specimens of juvenile pink salmon were randomly selected from each net set for stomach contents analysis and preserved in formalin or frozen. In the laboratory, fork length (FL), wet weight, and total stomach content weight were measured. The proportion of the diet composed on large copepods (>2.5 mm), small copepods (<2.5 mm), amphipods, euphausiids and cladocerans, pteropods, and 'other' zooplankters was visually estimated.

Nearshore fishes were placed into 9 taxonomic groups: immature (<30 cm) and adult (>30 cm) walleye pollock (*Theragra chalcogramma*), herring (*Clupea pallasi*), gadids (*Gadus macrocephalus, Microgadus proximus*), adult salmon (*Oncorhynchus spp.*), trout (*Salvelinus malma, Salmo mykiss*), benthic fishes (Cottidae, Hexagrammidae, Stichaeidae, Cyclopteridae, Zoarcidae, Bathymasteridae), pelagic rockfish (*Sebastes melanops, S. flavidus, S. ciliatus*), and demersal rockfish (*Sebastes nebulosus, S. caurinus. S. maliger, S. rubberimus,* and others). Several other taxonomic groups of fishes (Osmeridae, Ammodytidae, Gasterosteidae, Zaproridae, Pleuronectidae, Anarhichadidae, Anoplopomatidae, and Lamnidae) were not included in the analysis because they were relatively rare and did not consume significant numbers of juvenile salmon.

Diurnal changes in juvenile salmon foraging and distribution

We conducted several analyses of variance (ANOVA) to test the hypothesis that juvenile salmon diet composition is correlated with time of day and feeding rate is greater at dawn and dusk. The dependent variables in the analyses were the proportion of the diet (arcsine square root transformed) composed of various prey and an index of stomach fullness. The independent variables in the analyses were sample site-date and time of day (0000-0300 hrs, 0300-0600 hrs, 0600-0900 hrs, 0900-1200 hrs, 1200-1500 hrs, 1500-1800 hrs, 1800-2100 hrs, and 2100-2400 hrs). Preys were aggregated into 5 taxonomic groups: (1) large copepods, (2) small copepods, (3) amphipods, euphausiids and cladocerans, (4) pteropods, and (5) 'other zooplankton'. The residuals from a linear regression of mean stomach content weight (natural logarithm transformed) on juvenile salmon FL was used as an index of stomach fullness (Perry et al. 1996). Only stomach data from habitats inshore of the 20-m isobath were used in these analyses. All two-way interaction terms were initially included in each analysis, and a stepwise procedure was used to develop the most parsimonious model.

We used data from underwater video cameras to test the hypothesis that juvenile salmon aggregate nearshore at night and disperse offshore at dawn. Fixed up-looking video cameras were used to estimate the relative abundance of juvenile salmon in nearshore habitats. Cameras were installed at 2 locations where juvenile salmon were relatively abundant and were operated continuously for several days. A cable running to a pulley on the bottom and back to shore held each camera. The cable was adjusted periodically to maintain the camera 2.5-m below the surface as the water level changed with the tide. After the field season, videotapes were reviewed manually, and the relative abundance (low, moderate, or high) and length of time juvenile salmon were present in the field of view was recorded. An index of the relative abundance of juvenile salmon during each 3-hr time period was calculated from the product of salmon relative abundance during each salmon observation event and the length of time of the event. This index was then divided by the total time of video observation during each 3-hr time period, because total observation time during each period was not constant. We also conducted an ANOVA to test for a difference in catch per net set of juvenile salmon by time of day in anchovy seines offshore of the 20-m isobath. The dependent variable in the analysis was the catch per net set (natural logarithm transformed), and the independent variables were sample site-date and time of day.

Diurnal changes in relative abundance and feeding rates of nearshore fishes

We conducted two ANOVAs to test the hypothesis that predator relative abundance and feeding rate is greater at dawn and dusk. The independent variables in the analyses were sampling site-day and time of day. In the first analysis, the dependent variable was catch per net set (natural logarithm transformed) of predators in various gear types. Catch data from mid-water trawls was used for adult pollock, small mesh purse seines for herring and salmon, and variable-mesh gillnets for all other predator groups. In the second analysis, the dependent variable was the ratio (arcsine square root transformed) of total stomach content weight to fish body weight. A stepwise procedure was applied when appropriate.

Diurnal changes in predation on juvenile salmon

We conducted two ANOVAs to test the hypothesis that predation on juvenile salmon is greater at dawn and dusk and correlated with light intensity. The dependent variable in both analyses was the number of juvenile salmon in predator stomachs (natural logarithm transformed). We estimated the mean time of day at which the salmons found in each predator stomach were captured, because light intensity at the time the predator was sampled may have been different from when the salmon was captured by the predator. The mean time of day that the salmon were captured was calculated by subtracting the time since prey capture (t) from the time of day when the predator was sampled. The time since prey capture was estimated from mean prey weight at capture (w_t), mean initial prey weight (w_o, back calculated from length), and temperature-specific gastric evacuation rate, i.e. $t = \frac{\log(w_t) - \log(w_o)}{\alpha}$. The independent variables in the first analysis were time of day and predator taxonomic group. The independent variables in the second analysis were light intensity defined as a class variable (0.01-0.1, 0.1-1.0, 1.0-10, 10-100, 100-1,000, 1,000-10,000, and 10,000-100,000 lux) and predator taxonomic group. Data collected during 1996 and 1997 (Willette 1999) were included in these analyses to increase sample size.

Results

Diurnal changes in juvenile salmon foraging and distribution

Feeding rates of juvenile salmon peaked at dawn and dusk, and diet composition was correlated with time of day. Stomach fullness indices were correlated with time of day with maximum values near noon and midnight (Fig. 2). Juvenile salmon also consumed more pteropods in the evening and 'other zooplankton' at night (Fig. 2). The sample site\date by time-of-day interaction term in the model was significant for large copepods (R^2=0.932, df=203, p=0.005), small copepods (R^2=0.819, df=203, p=0.042), and amphipods, euphausiids, and cladocerans (R^2=0.771, df=203, p=0.052). Large copepods dominated juvenile salmon diets during early May, but small copepods generally dominated the diet later in the season (Fig. 3). The percent of the diet composed of large copepods was significantly different by time of day at site 525 on May 8 (*p* = 0.001) and at site 509 on June 13 (*p*=0.026). The percent of the diet composed of small copepods was significantly different by time of day at site 525 on May 8 (*p*=0.013) and at site 504 on June 9 (*p* =0.001). The percent of the diet composed of amphipods, euphausiids and cladocerans was significantly different by time of day at site 525 on May 13 ($p < 0.001$), site 506 on June 1 (p=0.013) and at site 525 on June 3 (p=0.014). The percent of the diet composed of other zooplankton was significantly different by time of day at site 525 on May 13 (p=0.033).

Underwater video observations indicated that juvenile salmon aggregated nearshore at night and dispersed offshore at dawn. The relative abundance of juvenile salmon estimated from these observations increased by a factor of 4 from mid day to evening (Fig. 4). Video cameras were operated in nearshore habitats for approximately 90 hours, but observations were hindered by extremes in light intensity during the darkest part of the night and at mid day. Visual observations during shoreline surveys conducted every 3 hours were consistent with this pattern of change in abundance, but catch per net set of juvenile salmon in the anchovy seines offshore of the 20-m isobath were not significantly different by time of day.

Diurnal changes in relative abundance and feeding rates of nearshore fishes

Predator relative abundance was greater at dawn and dusk for 5 taxonomic groups of fishes. From mid day to dusk, geometric mean catch per net set increased by a factor of 2 for adult pollock, 8 for immature pollock, 4 for gadids, 6 for demersal rockfish, and 3 for benthic fish (Fig. 5). The sample site by time of day interaction term in the model was only significant for benthic fish. Mean catch per net set for benthic fish reached a minimum between 0900 to 1500 hrs at 10 of 16 sites sampled.

Diel patterns of feeding differed among the 9 taxonomic groups of fishes, but many groups were feeding actively at dawn. Stomach fullness was significantly different among 3-hr sampling periods and the interaction term in the model was not significant for 6 of the groups (Fig. 6). Stomach fullness of immature pollock, gadids, trout, salmon, and pelagic rockfish increased in the morning. Immature pollock, gadids, and trout exhibited a second peak in stomach fullness in the evening. The sample site by time of day interaction term in the model was significant for herring (R^2=0.307, df=4956, $p<0.001$) and adult pollock (R^2=0.254, df=4177, $p<0.001$). Stomach fullness of herring was high during early May and varied considerably by time of day with peaks during the evening hours in some cases. Later in the season, stomach fullness of herring declined and was less variable. Conversely, stomach fullness of adult pollock was low in early May and varied little by time of day. In June, pollock stomach fullness was generally higher and more variable than in May.

Diurnal changes in predation on juvenile salmon

The numbers of juvenile salmon found in stomachs of 5 taxonomic groups of fishes were significantly correlated with light intensity or time of day, but light intensity always accounted for a greater amount of variance (Fig. 7). The relationships between number of salmon consumed and light intensity and time of day were significantly different ($p<0.001$) among predator groups. The greatest numbers of salmon were consumed by pollock and trout at light intensities from 0.1-10 lux and by gadids and pelagic rockfish from 10-100 lux. The number of salmon consumed was significantly correlated with time of day for immature pollock and gadids, and both predators consumed the greatest number of salmon during the darkest part of the night.

Discussion

Juvenile pink salmon fed continuously throughout the day, but feeding rate was greatest at dawn and stomach fullness peaked at dusk. Similar diel patterns of stomach fullness have been observed for pink salmon in other areas (Simenstad et al. 1980; Godin 1981). The minimum light intensity for juvenile pink salmon feeding on live prey is between 1.0 and 0.1 lux, but feeding rate declines with light intensity below 1000 lux (Bailey et al. 1975). High feeding rates at dawn probably resulted from hunger, because feeding at night was negligible. A second peak in feeding rate at dusk may be a genetic adaptation to maximize growth by maximizing stomach fullness before the nighttime fast. It is unlikely that high feeding rates at dusk result from greater prey vulnerability, because reactive distance declines with light intensity (Gerking 1994). Also, the diel pattern of feeding we observed was not associated with consumption of specific prey types that may at times become more vulnerable due to their behavior. An increase in consumption of pteropods during mid day suggested that the reactive distance for salmon feeding on pteropods declined below peak light intensities at mid day.

Juvenile pink salmon formed very dense aggregations in shallow water at night to avoid predators in deeper water. We could not observe juvenile salmon with underwater video cameras during the darkest part of the night (Figs. 4 & 8), but observations made during shoreline surveys using spotlights indicated that salmon aggregations were maintained at night. Our visual observations also indicated that this behavior was clearly related to light intensity, because the aggregations became larger and denser as light intensity declined and vice versa. Juvenile salmon and other fishes cannot generally maintain school formations at light intensities below 10^{-3} lux (Blaxter 1970). But, the aggregations we observed were not schools, because polarization among individuals was not maintained. Mechanical stimuli through the lateral line system resulting from the very close proximity of individuals may have been involved in maintaining these aggregations at very low light intensities. Juveniles probably formed these aggregations to avoid predators that increased in abundance at night (Fig. 5). Seine catches of juvenile salmon offshore were not correlated with time of day suggesting that aggregations observed nearshore were largely composed of individuals that had been inshore of the 20-m isobath as dusk approached. Mimic shiners (*Notropis volucellus*) also migrate inshore at night to avoid predators, but their behavior is highly variable depending on predator abundance (Hanych et al. 1983).

Total food consumption of fishes in nearshore habitats increased during twilight and at night due to higher abundances and feeding rates for several taxonomic groups. Higher catches during this time of day were probably due in part to vertical migrations into surface waters (Clark and Green, 1990; Sogard and Olla 1993). However, the magnitude of the changes in mean catch per net set we observed may not accurately reflect changes in abundance due to gear avoidance during the day or greater activity at night causing higher gill-net catches. Low stomach fullness during the darkest part of the night indicated that feeding rate was reduced at low light intensities (Blaxter 1970). Total food consumption by several groups may have been greatest at dawn, because relative abundances remained high and feeding rates were at their daily maximum (Figs. 5 & 6).

Predation on juvenile salmon in nearshore habitats was probably greatest during twilight and at night. Consumption of salmon by immature pollock and gadids was relatively high during this time of day. Although, predation on salmon by demersal rockfish and benthic fish was not correlated with time of day, higher relative abundances or activity levels during twilight and at night probably increased encounter rates with juvenile salmon. Our analysis indicated that predation on salmon was greatest when light intensities were between 0.1 and 100 lux (Fig. 7). In laboratory studies, predation on juvenile salmon by northern squawfish and rainbow trout increased as light intensities declined from 2.0-3.0 lux to 0.1 lux (Ginetz and Larkin 1976; Peterson and Gadomski 1994). Our method of estimating the actual time of day and thus light intensity when juvenile salmon were captured was not as accurate as was possible in the laboratory, but any error was probably random and thus did not bias our results. Our results suggest that predation on juvenile salmon was greatest at higher light intensities than observed in the laboratory, but we do not know the actual water depth where the salmon were captured. It is likely that the predation occurred anywhere within the upper 20-m of the water column. Light intensities were an order of magnitude lower within the deeper portions of this layer compared to the surface.

As light intensities declined below 1000 lux, the profitability of feeding for juvenile salmon declined relative to the risk of predation. Feeding often involves a tradeoff between predation risk and the growth needed to reach a viable size for later survival (Walters and Juanes 1993). As light intensities decline, reactive distances for juvenile salmon feeding on zooplankton decline (Bailey et al. 1975; Gerking 1994). Our data indicated that juvenile salmon stopped feeding when light intensities fell below about 10 lux (Fig. 2 & 8), and juveniles in nearshore habitats sought refuge from predation by forming large aggregations in shallow water. This behavior probably resulted from a declining profitability associated with feeding in risky habitats.

Juvenile salmon in PWS may have been vulnerable to predation for a shorter period of time each day in early May than in late May and June, because surface light intensities were within the range of greatest vulnerability for a shorter period of time each day in early May. Surface light intensities were between 0.1 and 100 lux for about 3-5 hrs each day in early May, but during late May and early June surface light intensities were within this range for 6-7 hours each day (Fig. 8). Juvenile salmon may reduce their vulnerability during this twilight period by migrating to depths where light intensities are below the minimum visual threshold for most predators. But, our data indicated that this did not occur, because catches of juvenile salmon in anchovy seines did not decline at night. Although juvenile salmon size and availability of alternative prey are important factors affecting predation losses of salmon (Willette et al. 1999), seasonal patterns of light intensity may in part explain increasing individual predation rates on juvenile salmon from early May to June (Willette 1999).

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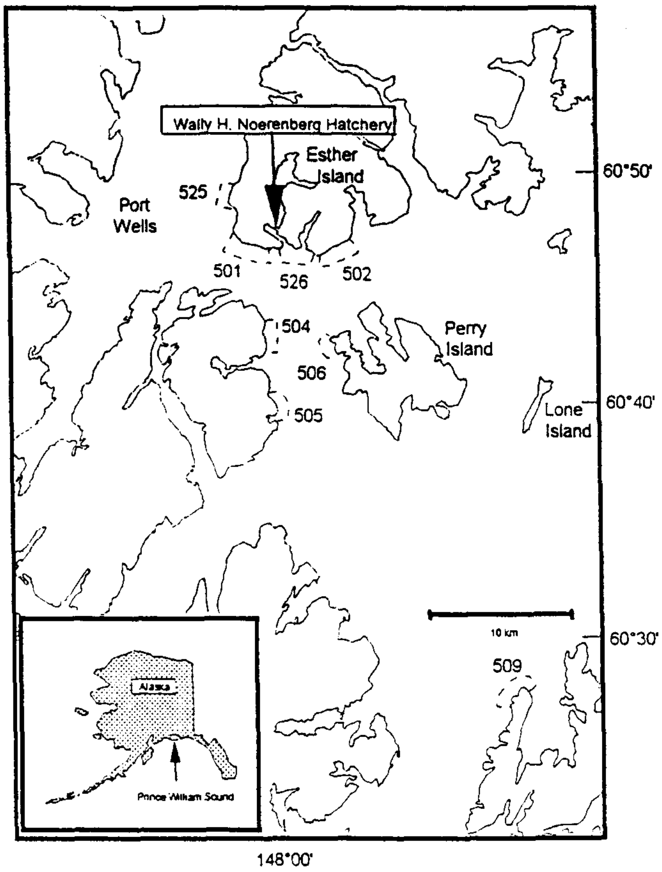
List of Figures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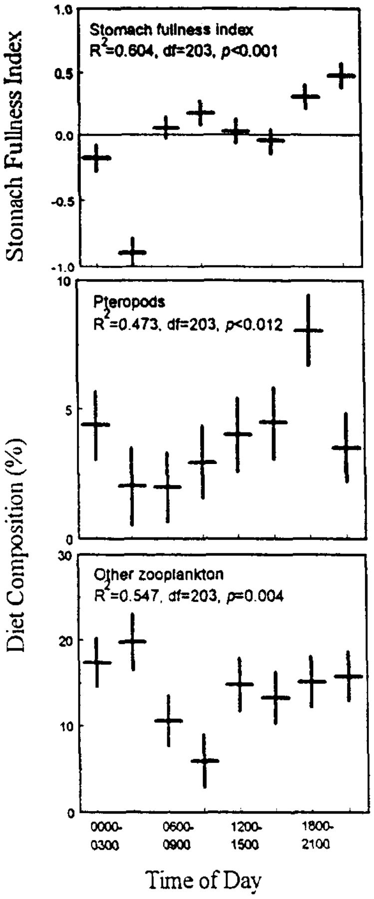
Alaska
Prince William Sound
148°00'

Figure 1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R^2=0.604, df=203, p<0.001
Pteropods
R^2=0.473, df=203, p<0.012
Other zooplankton
R^2=0.547, df=203, p=0.004
Stomach Fullness Index
Diet Composition (%)
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0.5
0.0
-0.5
-1.0
10
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10
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0000-
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1200-
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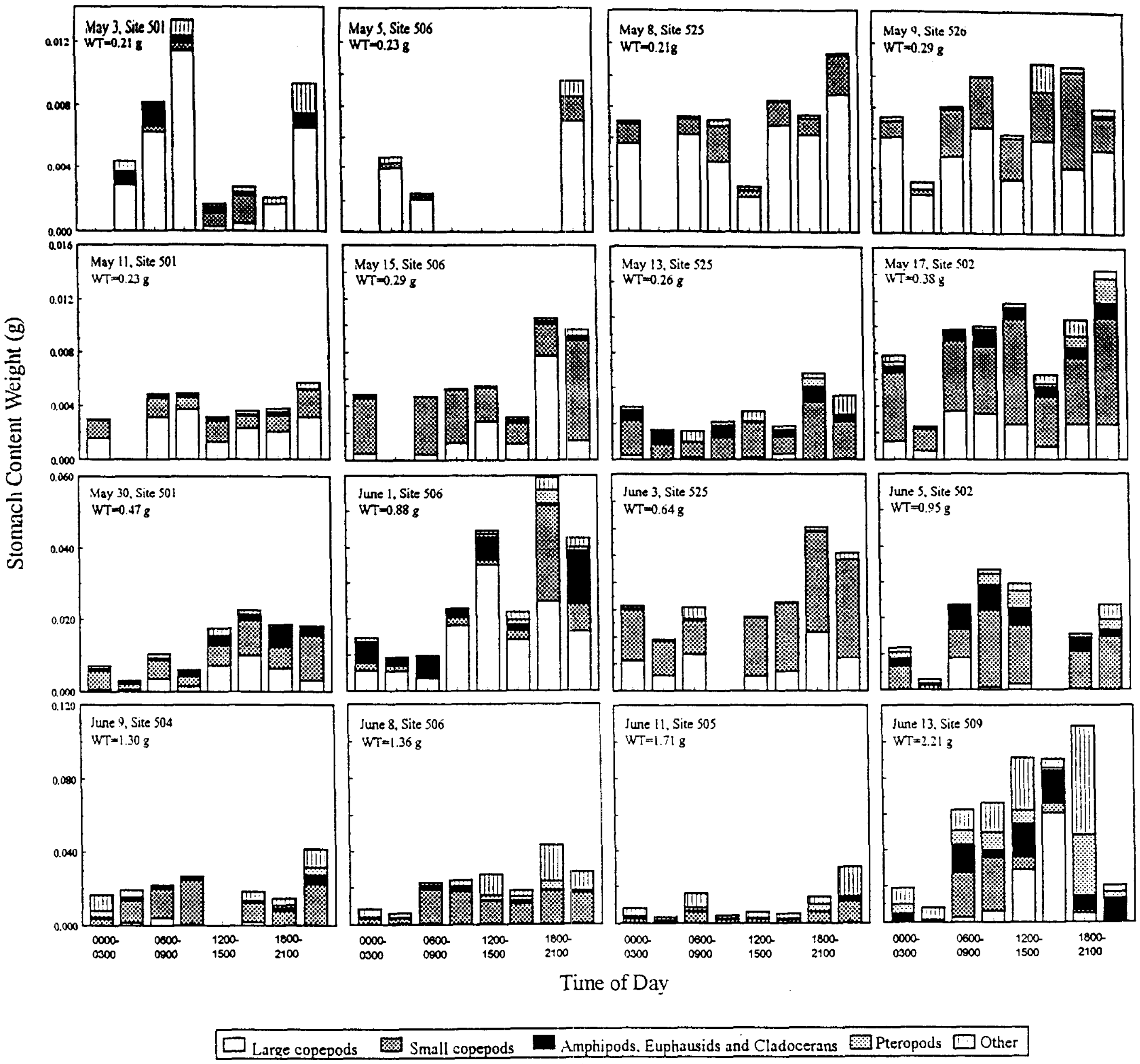
Time of Day

Figure 2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June 11, Site 505
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June 13, Site 509
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0.008
0.004
0.000
0.016
0.012
0.008
0.004
0.000
0.060
0.040
0.020
0.000
0.120
0.080
0.040
0.000
Stomach Content Weight (g)
0000-0300
0600-0900
1200-1500
1800-2100
Time of Day
Large copepods
Small copepods
Amphipods, Euphausids and Cladocerans
Pteropods
Other

Figure 3

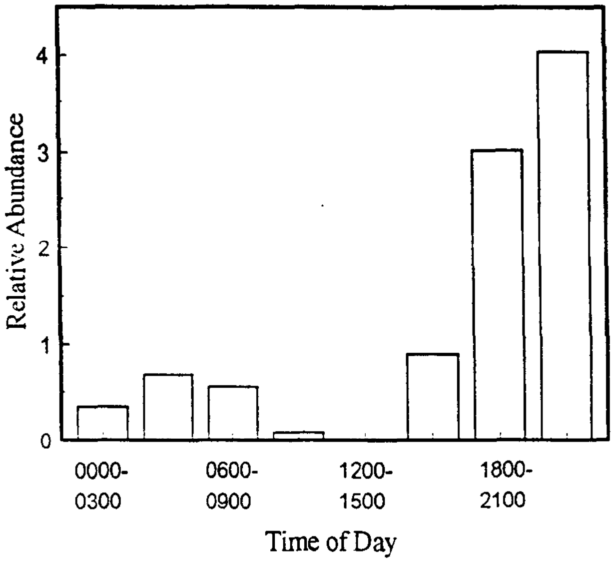
4
3
2
1
0
Relative Abundance
0000-
0300
0600-
0900
1200-
1500
1800-
2100
Time of Day

Figure 4

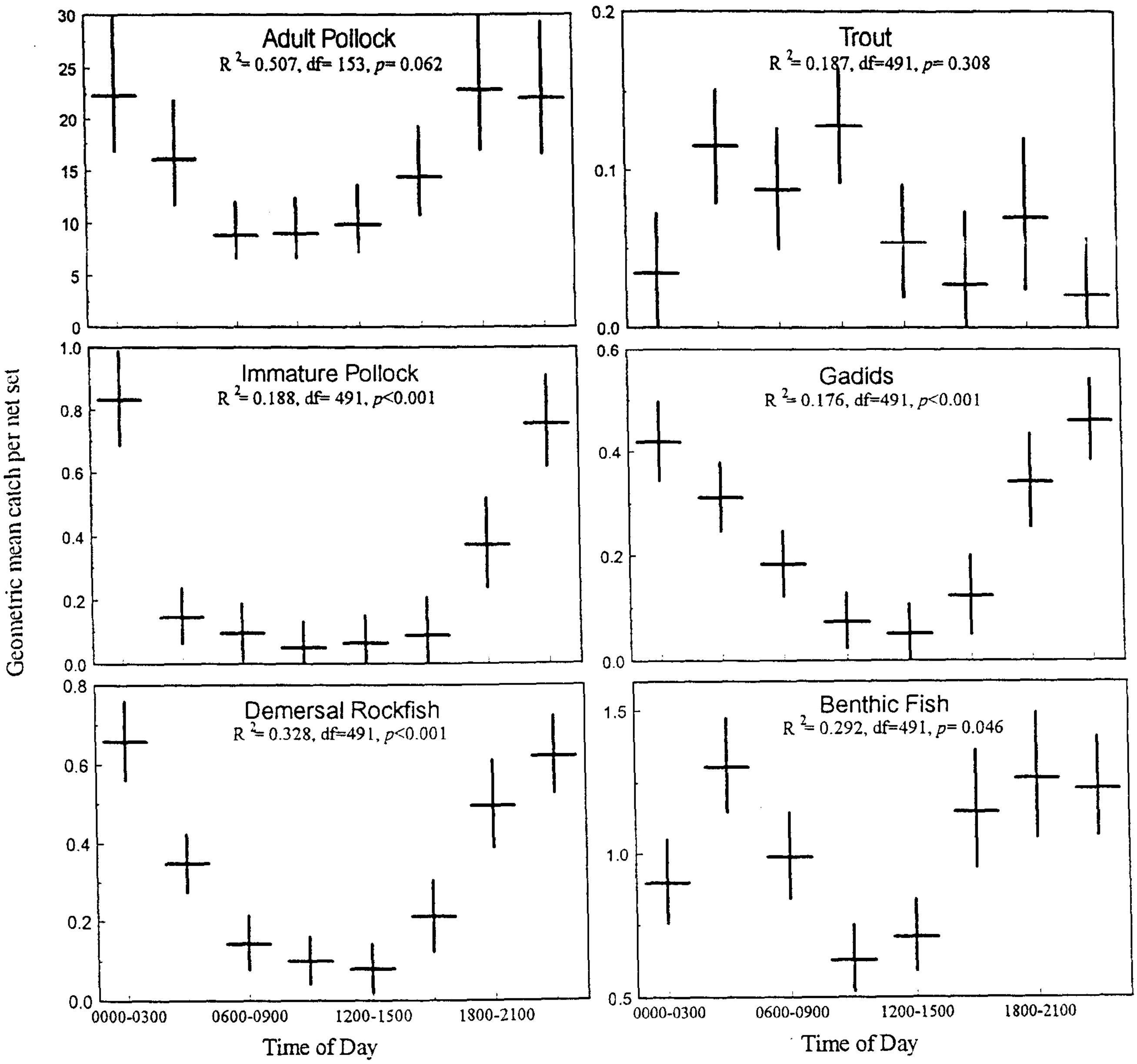
Adult Pollock
R² = 0.507, df= 153, p= 0.062
Trout
R² = 0.187, df=491, p= 0.308
Immature Pollock
R² = 0.188, df= 491, p<0.001
Gadids
R² = 0.176, df=491, p<0.001
Demersal Rockfish
R² = 0.328, df=491, p<0.001
Benthic Fish
R² = 0.292, df=491, p= 0.046
Geometric mean catch per net set
0000-0300
0600-0900
1200-1500
1800-2100
Time of Day
30
25
20
15
10
5
0
0.2
0.1
0.0
1.0
0.8
0.6
0.4
0.2
0.0
0.6
0.4
0.2
0.0
0.8
0.6
0.4
0.2
0.0
1.5
1.0
0.5

Figure 5

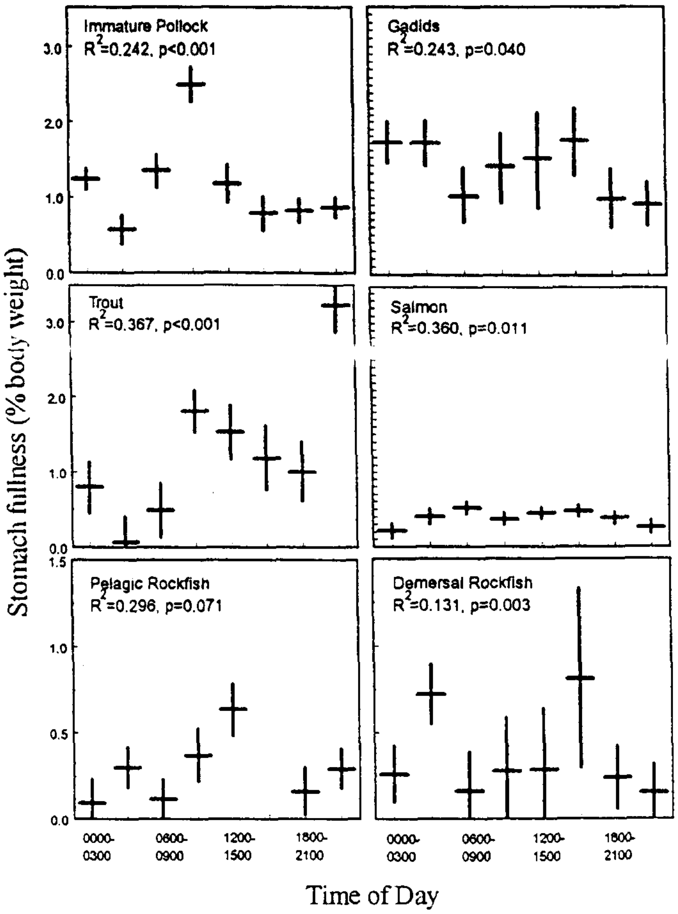
Immature Pollock
R^2=0.242, p<0.001
Gadids
R^2=0.243, p=0.040
Trout
R^2=0.367, p<0.001
Salmon
R^2=0.360, p=0.011
Pelagic Rockfish
R^2=0.296, p=0.071
Demersal Rockfish
R^2=0.131, p=0.003
0.0
1.0
2.0
3.0
0.5
1.5
0000-0300
0600-0900
1200-1500
1800-2100
Stomach fullness (% body weight)
Time of Day

Figure 6

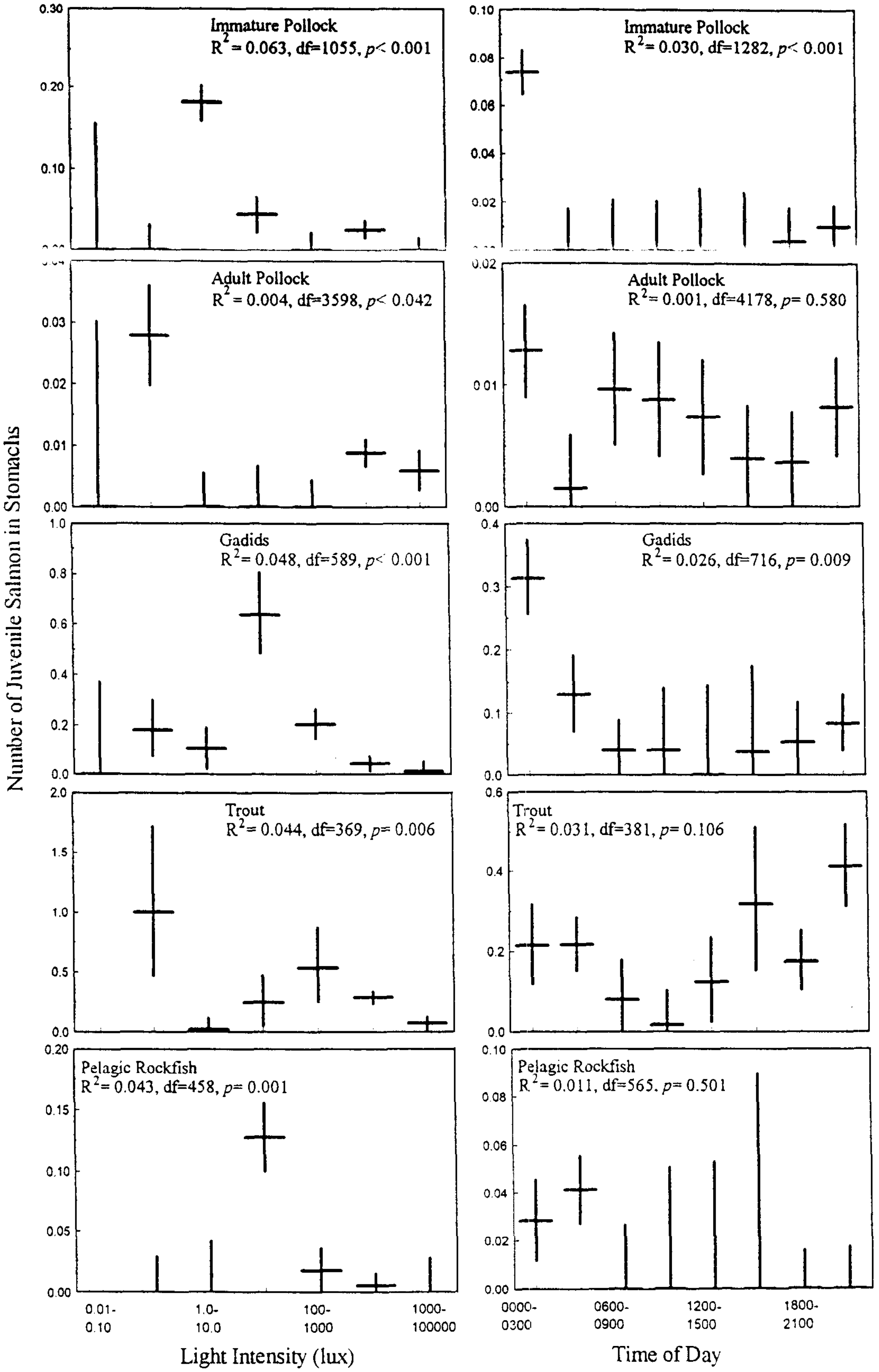
Number of Juvenile Salmon in Stomachs
Immature Pollock
$R^2 = 0.063$, df=1055, $p < 0.001$
Immature Pollock
$R^2 = 0.030$, df=1282, $p < 0.001$
Adult Pollock
$R^2 = 0.004$, df=3598, $p < 0.042$
Adult Pollock
$R^2 = 0.001$, df=4178, $p = 0.580$
Gadids
$R^2 = 0.048$, df=589, $p < 0.001$
Gadids
$R^2 = 0.026$, df=716, $p = 0.009$
Trout
$R^2 = 0.044$, df=369, $p = 0.006$
Trout
$R^2 = 0.031$, df=381, $p = 0.106$
Pelagic Rockfish
$R^2 = 0.043$, df=458, $p = 0.001$
Pelagic Rockfish
$R^2 = 0.011$, df=565, $p = 0.501$
0.30
0.20
0.10
0.10
0.08
0.06
0.04
0.02
0.02
0.03
0.02
0.01
0.00
0.01
0.00
1.0
0.8
0.6
0.4
0.2
0.0
0.4
0.3
0.2
0.1
0.0
2.0
1.5
1.0
0.5
0.0
0.6
0.4
0.2
0.0
0.20
0.15
0.10
0.05
0.00
0.10
0.08
0.06
0.04
0.02
0.00
0.01-
0.10
1.0-
10.0
100-
1000
1000-
100000
0000-
0300
0600-
0900
1200-
1500
1800-
2100
Light Intensity (lux)
Time of Day

Figure 7

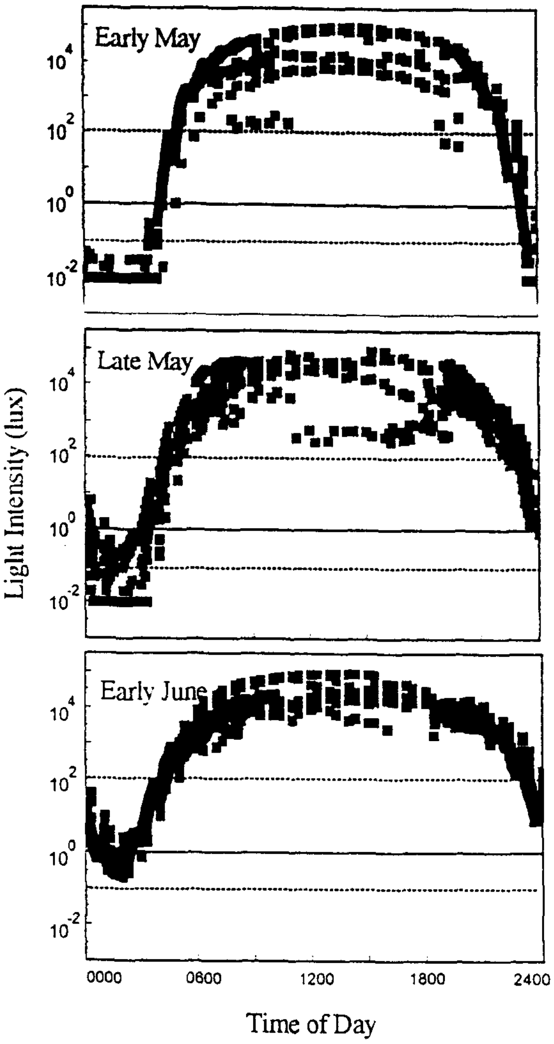
Early May
Late May
Early June
Light Intensity (lux)
10^4
10^2
10^0
10^{-2}
0000
0600
1200
1800
2400
Time of Day

Figure 8

Limitation of feeding and growth rates of juvenile pink salmon (*Oncorhynchus gorbuscha*) in relation to foraging behavior and subsequent effects on mortality of wild and hatchery-origin salmon

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Abstract: Several hypotheses were tested regarding processes affecting foraging behavior, growth and size-dependent mortality of wild- and hatchery-origin juvenile pink salmon (*Oncorhynchus gorbuscha*) rearing in Prince William Sound, Alaska. Daily rations of juvenile pink salmon averaged over large spatial scales were often near maximum ration, and feeding and growth rates of juveniles were only weakly density dependent. Juvenile pink salmon that consumed large copepods (primarily *Neocalanus* and *Calanus*) probably achieved high growth rates, and juveniles dispersed from nearshore predation refugia when copepod densities declined. The higher feeding and growth rates achieved by juveniles consuming *Neocalanus* reduced their mortality by minimizing their foraging times in risky habitats, and their vulnerability to size-selective predation. Interactions among wild- and hatchery-origin juveniles resulted more from differential size-dependent predation losses among groups than from limitation of feeding and growth. Differential predation losses among groups are probably amplified when *Neocalanus* densities or ocean temperatures are low. Decadal oscillations in production of coastal and oceanic ecosystems in the Gulf of Alaska may cause changes in the carrying capacity of nearshore predation refugia amplifying mortality differences between wild- and hatchery-origin salmon.

Introduction

Limitation of feeding and growth rates of juvenile Pacific salmon (*Oncorhynchus*) during early sea life has been difficult to evaluate, yet variations in growth likely influence recruitment due to size-selective predation (Parker 1971; Healey 1982a). Model simulations (Walters et al. 1978), comparisons of prey production and juvenile forage demand (Bailey et al. 1975; Healey 1979; Brodeur et al. 1992; Cooney 1993; Simenstad and Salo 1980), comparisons of actual ration with maximum ration, and juvenile condition (Healey 1991; Perry et al. 1996) have all been used to examine this question. Most investigators concluded that juvenile salmon growth was not food limited during their first month of marine residence in nearshore habitats (Walters et al. 1978; Simenstad and Salo 1980; Cooney 1993), but food supply may have limited salmon production in some cases (Bailey et al. 1975; Healey 1979). Conversely, most investigators concluded that growth was at times limited by food abundance after juveniles migrated into the coastal zone (Healey 1991; Brodeur et al. 1992; Perry et al. 1996).

Walters et al. (1978) identified several questions that needed further investigation to improve our understanding of these processes: (1) how efficient are juvenile fish at finding food when it becomes scarce, (2) how much would food abundance have to be reduced to cause growth effects, and (3) are juvenile salmon strongly restricted to nearshore habitats or would they simply and safely move offshore in the face of competition ? Subsequently, Healey (1982) concluded that migration of juvenile salmonids from nearshore habitats was not related to foraging success, while Simenstad and Salo (1980) found that migration of chum salmon from nearshore habitats coincided with a decline in abundance of their preferred prey (harpacticoid copepods). Healey (1991) concluded that juvenile salmon aggregated on prey patches and migrated from the coastal zone when foraging success declined (Healey 1982b). More recently, reduced growth was observed among juvenile pink salmon (*O. gorbuscha*) in Prince William Sound (PWS), Alaska when zooplankton biomass was less than about 0.3 g m^{-3} and the number of juveniles in hatchery release groups exceeded 20 million (Willette et al. 1999). Dispersion of juveniles from nearshore predation refugia and higher predation losses were also observed when densities of large calanoid copepods (primarily N*eocalanus* and *Calanus*) in nearshore habitats declined (Willette 1999). Dispersion of juveniles offshore probably was not motivated by hunger, because it was not correlated with stomach fullness.

Walters and Juanes (1993) predicted that juvenile foraging time in risky habitats adjacent to refugia would be a function of the minimum needed for growth to a viable size for later survival plus an additional time inversely proportional to the predation risk per time. Foraging times should further be an inverse function of juvenile density and prey density assuming juveniles exhibit a heritable variation in behavioral traits that cause foraging times to vary with changes in prey density. Walters and Juanes (1993) did not explicitly consider effects of prey type on feeding and growth rates of juveniles, but Willette's (1999) results suggest that prey type has an important effect on the foraging behavior of juvenile salmon. Feeding rates of juvenile pink and chum salmon (*O. keta*) were 3-4 times higher when *Calanus* rather than *Pseudocalanus* were consumed, and each species selected for *Calanus* and against *Pseudocalanus* both in tanks studies (LeBrasseur 1969; Parsons and LeBrasseur 1973) and in situ (Simenstad and Salo 1980).

In the present study, I will test 4 hypotheses related to these processes: (1) juvenile pink salmon growth is not food limited, (2) feeding and growth rates of juvenile pink salmon are not related to prey type, (3) zooplankton species composition and juvenile salmon diet composition are not different between nearshore and offshore habitats, and (4) feeding and growth rates of juvenile pink salmon are not related to juvenile density. Finally, I will examine the overlap in distributions of wild- and hatchery-origin juvenile pink salmon and the relative size-dependent predation losses from each group in PWS.

Methods

Field sampling and laboratory analyses

This study was conducted in Prince William Sound (PWS), Alaska which is an approximately 8,800 km^2 semi-enclosed basin reaching depths to 750 m. Juvenile salmon and their prey were sampled in PWS from early May to September, 1994 (Willette et al. 1999) and from early May to mid June, 1995-1997 (Fig. 1). Each year in late April or early May, four hatcheries released approximately 500 million juvenile pink salmon into western and northern PWS, and these fish mixed with about 250-500 million wild pink salmon emigrating from nearly 1,000 local streams. As a result, juvenile salmon densities in nearshore refugia varied greatly from western to eastern PWS. This feature was used to examine effects of juvenile density on feeding and growth. In 1994, samples were collected at several sites each day. These samples were only used to evaluate whether juvenile pink salmon growth was food limited. In 1995, sampling was conducted approximately every 3 hrs throughout a 24-hr period at a single site each day. In 1996-1997, samples were collected every 3 hrs from about 21:00 to 09:00 hrs at each site. Each year, juvenile salmon were sampled with purse seines (250 m x 20 m, 1.5 cm stretch mesh) set in an approximate semi circle with the net open in the direction of the prevailing current for 20 min. Seine sampling was conducted within 1-km of the shore and up to the 20-m isobath. Inshore of the 20-m isobath, juvenile salmon were sampled with a small-mesh purse seine (40 m x 10 m, 0.5 cm stretch mesh) deployed from a skiff. In 1995-1997, visual shoreline surveys were conducted to estimate the relative density of juvenile salmon inshore of the 20-m isobath. At least 2 zooplankton samples were collected every 3 hours at each site at stations located near the 20-m isobath to estimate the density of large calanoid copepods and other macrozooplankton available to juvenile salmon. These samples were collected with a 0.5-m ring net (243 μm mesh) towed vertically from a depth of 20-m to the surface. In each study area, temperature and salinity were measured with a conductivity-temperature-depth profiler (CTD) to a depth of 100-m. One thousand and sixty-nine purse seine sets, 610 small-mesh purse seines sets, and 596 zooplankton casts were taken during the 4 years of the study.

The diet composition of juvenile pink salmon was estimated from at least 10 specimens randomly selected from each net set and preserved in formalin for later stomach contents analysis. In the laboratory, fork length (FL), wet weight, and total stomach contents wet weight was measured to 0.01 g. For samples collected in 1994, prey items in the gut were identified to the lowest possible taxonomic level and enumerated (Willette et al. 1997). For samples collected in 1995 and 1996, the proportion of total stomach contents weight in 8 taxonomic groups (large calanoid copepods, >2.5 mm; small calanoid copepods, <2.5 mm; cladocerans; ostracods; amphipods; euphausiids; pteropods and 'other zooplankton') was visually estimated. In 1997, cladocerans, ostracods, amphipods, euphausiids, and pteropods were further aggregated with the 'other zooplankton' group. In 1996 and 1997, at least 20 specimens were also randomly selected from each net set and frozen for later measurement of dry-weight condition and moisture content. The wet weight and dry weight of these fish was measured to 0.01 mg with the head and stomach removed. For juvenile pink salmon less than 8 cm FL, energy content was estimated from moisture content (R^2=0.952, df=53, p<0.001) using data provided by Parker and Vanstone (1966). Zooplankton samples were analyzed using standard subsampling techniques (Coyle et al. 1990) after measurement of total wet weight. Zooplankters were enumerated into three taxonomic groups as previously described, and biomass was calculated as the product of abundance and the mean individual wet weight for each taxonomic group (Coyle et al. 1990).

Juvenile growth and food limitation

I tested the hypothesis that the growth of juvenile pink salmon was not food limited by testing for a difference between the daily ration of juvenile pink salmon in PWS during 2-week periods and maximum daily ration (Table 1). Daily ration (I) of juvenile salmon in PWS was estimated from $I = 24\overline{S}\alpha$ (Eggers 1977), where $\overline{S}$ was the daily mean stomach content wet weight and α was the temperature-specific gastric evacuation rate. The sampling design was not adequate to estimate ration for each day, so the data were aggregated over 2-week sampling periods to insure that samples from throughout the day were available. Data from Brett and Higgs (1970) were used to estimate temperature-specific gastric evacuation rate. Brett and Higgs (1970) starved the fish in their study before and after measurement of evacuation rate, but gastric evacuation rate of juvenile Atlantic salmon (*Salmo salar*) doubled when the fish were fed continuously rather than starved before and after measuring evacuation rate (Talbot et al. 1984). Therefore, I increased gastric evacuation rates estimated from Brett and Higgs (1970) by a factor of 2 to account for the effect of continuous feeding which is common in juvenile pink salmon under natural conditions (Godin 1981). I did not correct evacuation rates for fish size, because juvenile Atlantic salmon within the size range of those in PWS did not exhibit a difference in evacuation rate related to fish size (Talbot et al. 1984). The energy content of the daily ration (kJ g^{-1} wet weight) was estimated from the product of wet weight and energy density of prey. Energy densities and percent dry weight of zooplankton were estimated from data provided by Norrbin and Bamstedt (1984), Harris (1985), and Higgs et al. (1995): large calanoid copepods (27.6 kJ g dry wt^{-1}, 23.1% dry wt), small copepods (24.7 kJ g dry wt^{-1} , 17.7% dry wt), cladocerans and ostracods (25.8 kJ g dry wt^{-1}, 25.5% dry weight), amphipods and euphausiids (22.7 kJ g dry wt^{-1}, 22.7% dry wt), pteropods (14.0 kJ g dry wt^{-1}, 12.8% dry wt), and other zooplankters (19.3 kJ g dry wt^{-1}, 25.5% dry wt). Maximum daily ration was estimated from temperature- and size-specific growth at maximum ration for juvenile sockeye salmon fed a commercial food (Brett 1974). I increased Brett's estimates of sockeye growth by 1.45, because his data indicated that juvenile pink salmon grew faster than sockeye on the same ration. I assumed a gross growth conversion efficiency of 30%, which is near the upper range for juvenile salmonids considering interacting effects of temperature, ration size and type, and body size (Brett et al. 1969; Biette and Geen 1980; Brett et al. 1982). Overlap between the 95% confidence interval on the estimated daily ration of juvenile pink salmon in PWS and maximum daily ration was used to determine whether the rations were different. The 95% confidence intervals on the daily ration were calculated from confidence intervals on mean stomach content weight.

Growth rates of juvenile pink salmon in PWS were estimated from recoveries of coded-wire tagged (CWT) juveniles (0.25-0.35 g) released from the Wally H. Noerenberg Hatchery in late April and early May, 1994-1995 (Willette 1996). Growth rates of these 'early-release' groups were adjusted for size-selective predation using relative attack-capture probabilities for pollock and herring preying on juvenile salmon (Willette 1999) and mortalities estimated from recoveries of CWT adults (Geiger 1990). During both years, 2 CWT groups of pink salmon (1.0-1.5 g) were also released from the Wally H. Noerenberg Hatchery (WHN) in mid-June. Mortality of the early-release groups during the initial 45-days of marine residence was estimated from mortalities of the late-release groups assuming that the mortality of both groups was the same after mid-June. Seine sampling indicated that both groups occurred together and were similar in size after mid-June. Growth rates (kJ day^{-1}) were estimated assuming an energy density of 3.34 kJ g wet weight^{-1} for juvenile pink salmon (Paul and Willette 1997). Gross growth conversion efficiencies under natural foraging conditions were then calculated from growth and daily ration estimates. Mean energy content of juvenile pink salmon during each sampling period was estimated during 1996 and 1997 for comparison with daily rations.

Effect of prey type on feeding and growth rates

I conducted an analysis of covariance (ANCOVA) to test hypothesis that juvenile salmon feeding rate was not different when large versus small calanoid copepods were consumed. I estimated feeding rate (kJ hr^{-1}) from the increase in mass of large and small copepods in the stomachs of juvenile salmon between samples collected during the night and those collected about 3-hours later shortly after dawn. Because feeding typically ceases at night (Godin 1981), juveniles were probably actively feeding at dawn. Estimated losses to gastric evacuation were added to the change in mass, and feeding rates were standardized to the mean FL of juveniles used in the analysis. The dependent variable in the ANCOVA was the feeding rate, and the independent variables were the biomass of large or small copepods and prey taxonomic group. No intercept term was included in the model. Only data from 1995 and 1996 were available for this analysis.

I also conducted an analysis of variance (ANOVA) to test the hypothesis that juvenile salmon stomach fullness indices were not related to diet composition. Data from all 4 years of the study were available for this analysis, because samples collected during and immediately after night were not required. The stomach fullness index was estimated from the residuals from a linear regression of mean stomach contents weight (natural logarithm transformed) on juvenile salmon FL (Perry et al. 1996). Separate analyses were conducted for large copepods, small copepods, and 'other zooplankton', because diet proportions were not independent among prey groups. The independent variable in the analysis was the proportion of the diet composed of each prey group. A class variable was established for diet composition (0-25%, 25-50%, 50-75%, and 75-100%), because graphical analysis indicated a non-linear relationship between stomach fullness index and diet composition.

Three additional ANCOVAs were conducted to test the hypothesis that juvenile salmon condition was not related to diet composition. The dependent variable in the analysis was the mean energy content of juveniles, and the independent variables were mean juvenile salmon FL, mean stomach fullness, and mean proportion (arcsine-square root transformed) of the diet composed of large copepods, small copepods, and 'other zooplankton'. Separate ANCOVAs were conducted for each of the 3 prey taxonomic groups, because diet proportions were not independent among prey groups. Juvenile salmon FL was included as an independent variable in the model, because moisture content of juvenile salmon declines steadily with size on a constant ration (Brett 1974). A class variable was established for the stomach fullness index as previously described based upon whether regression residuals were less than or greater than zero. All two-way interaction terms were initially included in the analysis. A stepwise procedure was used to develop the most parsimonious model. The variance inflation factor was calculated to assess whether multicollinearity may have affected estimation of regression coefficients and their statistical significance (Neter et al. 1989). Net set was used as the sample unit.

Foraging habitat and diet composition

I conducted several ANOVAs to test the hypothesis that zooplankton densities and juvenile salmon feeding rate and diet composition were not different between nearshore and offshore habitats. In the first set of analyses, the dependent variables were total zooplankton biomass, and the densities of large copepods, small copepods, and 'other zooplankton'. In the second set of analyses, the dependent variables were mean stomach fullness index, and mean proportion of the diet (arcsine square root transformed) composed of large copepods, small copepods, and 'other zooplankton'. In all analyses, net set was used as the sample unit, and the independent variables were sampling period and habitat (nearshore versus offshore). Only data from 1995 were used to test for a difference in zooplankton biomass and densities between habitats, because this was the only year that zooplankton sampling was stratified by habitat. In 1995, zooplankton samples were collected at two stations nearshore and two stations offshore every three hours during daylight at each study site. Nearshore zooplankton stations were located near the 20-m isobath, and offshore stations were approximately 2-km from shore in water generally exceeding 200-m depth. Samples of juvenile salmon collected inshore of the 20-m isobath were classified as nearshore.

Effect of juvenile density on feeding and growth rates

Four analyses were conducted to test the hypothesis that juvenile salmon feeding rate and condition were not related to juvenile density. Samples aggregated by site and date formed sample units for these analyses, because juvenile density was estimated over these units. In the first analysis, I tested for a difference in stomach fullness indices among sites with different juvenile salmon densities. The independent variables were mean total zooplankton biomass and juvenile density at each site. In the second analysis, I tested for a difference in the proportion of the diet (arcsine-square root transformed) composed of large calanoid copepods among sites with different juvenile densities. The independent variables were the mean density of large calanoid copepods and juvenile density at each site. In the third analysis, I tested for a difference in the energy content of juvenile salmon among sites with different juvenile densities. The independent variables were mean juvenile salmon FL and juvenile density at each site. Separate analyses were conducted using data from 1996 and 1997, because no sites with high juvenile densities were sampled in 1997. Finally, I also tested for a difference in total zooplankton biomass and density of large calanoid copepods among sites with different juvenile densities.

Interactions between wild- and hatchery-origin juvenile salmon

Two analyses were conducted to examine interactions between wild and hatchery-origin juveniles. In the first analysis, I evaluated the extent of overlap in the spatial distributions of wild- and hatchery-origin juveniles by sampling period and area. Origins of juvenile salmon were determined from recovery of CWT juveniles in 1994-1995 (Willette 1996) and otolith thermal marked juveniles in 1996-1997. In 1994-1995, ratios of tagged to untagged juveniles in each tag-code group were used to estimate the total number of juveniles from each hatchery in each net set. The number of wild juveniles in each net set was estimated by subtracting the number of hatchery juveniles from the total catch. The estimated total numbers of wild- and hatchery-origin juveniles captured were then summed by sampling period and area. In 1996 and 1997, stock composition was estimated by enumerating wild- and hatchery-origin juveniles in random samples taken from each net set and then summing by sampling period and area.

In the second analysis, I examined apparent size-dependent predation losses for wild- and hatchery-origin juveniles. I estimated the growth in length of wild- and hatchery-origin juveniles combined and predicted the length of each fish in the next sampling period assuming constant growth among all groups. I then used Chi-square analysis to test for differences between actual and predicted length-frequency distributions for each group separately. The magnitude of size-dependent predation on each group was then evaluated by comparing differences between actual and predicted length distributions with length distributions of juvenile salmon from predator stomachs collected at the same time. Willette (1999) described the methods used to sample predators and analyze stomach contents. Length distributions of juvenile salmon in stomachs of planktivores (*Theragra chalcogramma* and *Clupea pallasi*) and piscivores\demersal fish (Gadidae, Cottidae, Hexagrammidae, Stichaeidae, Cyclopteridae, Zoarcidae, Bathymasteridae, *Salvelinus spp*, and *Sebastes spp.*) were calculated separately, because Willette (1999) found that these two predator groups tended to select for different sizes of juvenile salmon.

This analysis was only conducted for groups of juvenile salmon that had fully recruited to nearshore habitats at the time samples were collected. In 1996, actual length distributions measured in early July were compared with distributions predicted from lengths measured in early June. In 1997, a unique otolith thermal mark was applied to about 76 million juveniles released from WHN Hatchery, so it was possible to compare actual and predicted length distributions over 4 sampling periods from early May to late June. Otherwise, the analysis for 1997 was limited to comparisons between early and late June.

Results

Juvenile growth and food limitation

Daily rations of juvenile pink salmon in PWS were less than maximum daily ration in late June 1994, late May 1996, and early May 1997 (Tables 1&2). Maximum rations estimated by Brett (1974) were less than daily rations of juveniles in PWS during early Sept. 1994, and early June 1995 and 1997. Growth rates of juveniles in PWS, adjusted for size-selective predation, ranged from 3.5-5.0% body wt day^{-1}. Mortality and apparent growth from size-selective predation during the initial 45-days of marine residence were about 4 times higher in 1994 ($z=-0.085$, $g=0.24$ mm FL day^{-1}) than in 1995 ($z=-0.020$, $g=0.07$ mm FL day^{-1}). Estimated gross growth conversion efficiencies for juveniles in PWS increased from about 30-75% from late May to June, 1994. This trend coincided with a decline in stomach fullness (Table 1), a decline in the proportion of large copepods in the diet (early May 64%; late May 59%; early June 9%; late June 9%; early July 22%; early Sept 43%), and an increase in the proportion of pteropods (early May 0%; late May 0%; early June 7%; late June 14%; early July 10%; early Sept 0%) and 'other' zooplankton (early May 13%; late May 20%; early June 33%; late June 51%; early July 51%; early Sept 35%) in the diet.

Effect of prey type on feeding and growth rates

Feeding rates of juvenile salmon consuming large versus small copepods were significantly different ($R^2=0.698$, df=28, $p<0.001$). The slope of the regression between feeding rate and zooplankton biomass was about 2 times higher for juveniles feeding on large versus small copepods (Fig. 2a). Mean stomach fullness indices were also significantly correlated with the proportion of the diet composed of large copepods ($R^2=0.019$, df=523, $p=0.018$), small copepods ($R^2=0.017$, df=523, $p=0.027$), and 'other zooplankton' ($R^2=0.029$, df=523, $p=0.001$).

Mean stomach fullness index was significantly higher ($p<0.050$) when the proportion of the diet composed of large copepods was greater than 50% compared to <25% (Fig. 2b). Mean stomach fullness index was also significantly higher (*p*<0.050) when the proportion of the diet composed of small copepods and 'other zooplankton' was <25% compared to 25-75%. The energy content of juvenile salmon was positively correlated with the proportion of large calanoid copepods in the diet and negatively correlated with the proportion of small copepods in the diet (Fig. 3). Juvenile salmon FL was also significantly correlated with energy content.

Foraging habitat and diet composition

The mean density of large copepods and the proportion of juvenile salmon diets composed of large copepods were about 50% greater offshore than nearshore during May 1995 (Table 3). In contrast, the proportion of the diet composed of small copepods was significantly higher nearshore than offshore in both May and June 1995, but densities of small copepods were not. During June 1995, total zooplankton biomass was higher offshore than nearshore, mean stomach fullness index was about 2 times higher offshore than nearshore, and the juvenile diets offshore were composed primarily of 'other zooplankton'. In 1996, the proportion of juvenile salmon diets composed of large copepods was again higher offshore than nearshore, and small copepods composed a greater proportion of the diet nearshore (Table 4). In 1997, there were no differences in diet composition of juvenile salmon between nearshore and offshore habitats during any sampling periods, but densities of large copepods in early May were very low and 'other zooplankton' were more abundant than in the previous 2 years (Table 4).

Effect of juvenile density on feeding and growth rates

The mean stomach fullness index of juvenile salmon was not significantly different among sites with different juvenile densities, and the proportion of large copepods in juvenile diets was positively correlated with copepod density (Fig. 4a). The regression slope for high-density sites was significantly lower (*p*=0.002) than for low- or moderate-density sites. Regression intercepts and least-squares mean diet proportions were not different among sites with different juvenile densities. In 1996 and 1997, least-squares mean energy content of juveniles was lower at sites with moderate compared to low juvenile densities, but the difference was only significant (p=0.023) in 1996 (Fig. 4b). Juvenile salmon FL was also significantly correlated with energy content. Total zooplankton biomass was significantly correlated (R^2=0.335, df=19, p=0.031) with juvenile density in 1996 (low: mean=0.28; moderate: mean=0.36; high: mean=0.56) but not in 1997. Large copepod densities were significantly correlated with juvenile density in 1996 (R^2=0.538, df=19, p=0.001; low: mean=3.6; moderate: mean=24.3; high: mean=104.1) and 1997 (R^2=0.251, df=23, p=0.013; low: mean=16.7; moderate: mean=36.4).

Interactions between wild- and hatchery-origin juvenile salmon

Juveniles originating from the WHN hatchery composed greater than 80% of the juvenile stock in the Wells\Perry passage area in early May, 1994-1997 (Table 5). In early June 1994, the proportion of WHN juveniles declined rapidly to <30%, and the proportion of wild juveniles increased to >50% of the stock. In 1995-1997, a temporal decline in the WHN stock was not observed, and wild juveniles composed <30% of the stock in this area. Wild juveniles and fish originating from the Cannery Creek Hatchery (CCH) generally composed about 15% and 50% of the stock in the Unakwik area. In eastern PWS, wild juveniles composed 99% of the stock during early May, but by late May fish originating from the Solomon Gulch Hatchery (SGH) composed >40% of the stock.

Comparison of predicted and actual length distributions of wild- and hatchery-origin juveniles indicated that predation losses were probably greater among the smaller individuals present during each sampling period. In early June 1996, CCH and WHN hatchery juveniles exhibited length modes near 4-5 cm FL and wild juveniles near 5-6 cm FL (Fig. 5). In early July 1996, predicted length distributions for CCH and WHN hatchery juveniles were skewed toward smaller sizes compared to actual distributions, whereas predicted length distributions for wild juveniles were skewed toward larger sizes. During this same period, the length modes for juvenile salmon found in the stomachs of planktivores and piscivore\demersal fish were around 4-5 cm FL (Fig. 6). During May 1997, length modes for WHN hatchery juveniles were <6 cm FL, and predicted length distributions were skewed toward smaller sizes compared to actual distributions (Fig. 5). During this same period, length modes for juvenile salmon found in planktivore stomachs were about 4 cm FL, and the length mode for salmon in piscivore\demersal fish stomachs was 5-6 cm FL (Fig. 6). From early to late June 1997, length modes were near 5 cm FL for CCH juveniles, 6 cm FL for wild juveniles, and 8 cm FL for WHN juveniles. In late June, predicted length distributions were skewed toward smaller sizes for CCH juveniles and toward larger sizes for WHN juveniles compared to actual distributions. During this same period, the length mode for juvenile salmon found in piscivore\demersal fish stomachs was around 5 cm FL (Fig. 6). Chi-square tests indicated that all predicted and actual length distributions were significantly different ($p<0.004$) from each other.

Discussion

Daily rations of juvenile pink salmon in PWS were often near maximum. This conclusion was based on comparison of rations estimated from stomach content analysis and growth rates of juvenile salmon fed to excess in the laboratory. Rations estimated from stomach content analysis were strongly dependent on assumed temperature-specific gastric evacuation rates. I examined the accuracy of my ration estimates by comparing gross growth conversion efficiencies with measured growth rates of tagged fish. Conversion efficiencies were within the expected range except in late June 1994 (Table 2). Actual conversion efficiencies probably vary with ration (Paloheimo and Dickie 1966) and temperature (Brett et al. 1969), but it is unlikely that conversion efficiencies often approach 75% (Biette and Geen 1980). It seems more likely that growth was overestimated in late June 1994. I corrected my growth estimates for size-selective predation by assuming constant predation losses throughout the juvenile period. In early June, juvenile pink salmon were beginning to migrate into neritic habitats and probably suffered strong size-selective predation (Healey 1982a; Willette et al. 1999) that biased growth estimates.

Juvenile pink salmon that consumed large copepods (primarily *Neocalanus*) probably achieved high growth rates, because their high feeding rates sustained high stomach fullness with lower feeding metabolic costs. When feeding rates exceeded gastric evacuation rates, juveniles were able to maintain full stomachs and thus consume higher daily rations. Ration is a function of mean stomach content weight (Eggers 1977), and gastric evacuation rate increases with meal size (Smith et al. 1989). Juveniles that consumed largely *Neocalanus* also exhibited higher estimated energy content (Fig. 3). Energy content estimated from moisture content probably reflected recent feeding rate, because diel changes in moisture content were correlated with stomach fullness and with daily ration when juveniles in the laboratory were fed between maintenance and maximum ration (Parker and Vanstone 1965; Brett et al. 1969). Juveniles consuming *Neocalanus* probably incurred lower feeding metabolic costs, because less active foraging time was required to obtain maximum ration. Metabolic rates of juvenile sockeye doubled from routine rates while feeding and declined by about 13% per hour after cessation of feeding (Brett and Zala 1975). Several investigators have concluded that the relation between food and growth is strongly dependent on the amount of energy required to search for and capture prey (Mann 1966; Paloheimo and Dickie 1966; Warren and Davis 1966; Kerr and Martin 1970).

Neocalanus and other similar size prey were probably more important for sustaining high growth when prey density was below that needed to obtain maximum ration. LeBrasseur (1969) observed no relation between prey size and growth of juvenile chum salmon fed *Calanus*, *Pseudocalanus*, and euphausiids at high ration levels. Similarly, Mills et al. (1989) found no relation between prey size and growth of yellow perch when the fish were fed 40% of their dry weight per day. However, when rations were reduced to 25% of dry weight per day, growth was a function of prey size with peak rates similar to those achieved at the higher ration. In situ growth of juvenile chinook salmon was correlated with densities of zooplankton 1.5-4.5 mm in length but not smaller prey (English 1983). Maximum daily rations were achieved when densities of this size range of prey exceeded about 0.5 g m^{-3}. Maximum rations for juvenile pink salmon in PWS were about 0.5 kJ day^{-1} (Table 2). If 20 hours of daylight were available for feeding each day, feeding rates near 0.025 kJ $hour^{-1}$ were required to achieve maximum ration. Juvenile pink salmon could have acquired this ration feeding on *Neocalanus* if prey densities exceeded 0.5 g m^{-3} or feeding on *Pseudocalanus* if prey densities exceeded 2.5 g m^{-3} (Fig. 2). During the 4 years of this study, peak *Neocalanus* densities measured from vertical net tows were about 0.6 g m^{-3}, but peak *Pseudocalanus* densities were only about 1.5 g m^{-3}. Thus during the *Neocalanus* bloom, juveniles could have probably acquired maximum ration by selecting for *Neocalanus* but without having to search for high-density prey patches. Juveniles feeding on *Pseudocalanus* probably could not have acquired maximum ration without finding very high-density prey patches.

Juvenile pink salmon searched for high-density patches of *Neocalanus* and other similar size prey after the copepod bloom. The proportion of salmon diets composed of large copepods and large copepod densities were typically higher offshore than nearshore (Tables 3 & 4). Juveniles dispersed offshore when *Neocalanus* densities nearshore declined, but dispersion offshore was not correlated with total zooplankton density or stomach fullness (Willette 1999). These observations support Walters et al. (1978) assumption that juveniles must exploit high-density prey patches to achieve the relatively high growth rates observed among juvenile salmon in situ. But, selection for prey sizes that sustain high growth rates is probably equally important when prey densities are within the range typically measured in situ using vertical net tows.

The higher feeding and growth rates achieved by juveniles consuming *Neocalanus* reduced their mortality by minimizing their foraging times in risky habitats, as well as the duration of their vulnerability to size-selective predation. Walters and Juanes (1993) predicted that juvenile foraging times in risky habitats adjacent to refugia are a function of the minimum time needed for growth to a viable size for survival upon emergence from the refuge plus an additional time inversely proportional to predation risk. Within this context, higher feeding rates achieved by juveniles consuming *Neocalanus* resulted in immediate benefits by reducing foraging time and thus predation risk. Additionally, the higher growth rates achieved by these individuals also increased their survival upon emergence from the refuge because of their larger size.

Observed feeding and growth rates of juveniles were only weakly density dependent. Dispersion or aggregation of juveniles in response to varying prey densities eliminated any expected inverse correlation between juvenile density and stomach fullness or diet composition resulting from food limitation (Fig. 4a). Although estimated daily rations were near maximum ration when data were pooled over large spatial scales (Table 2), juvenile energy content was reduced when juvenile densities were high (Fig. 4b). Behavioral responses of juveniles to varying prey availability probably resulted in strong size-dependent mortality rather than reduced growth, because low densities of preferred prey caused foraging juveniles to disperse from nearshore refugia and suffer higher predation losses (Walters and Juanes 1993; Willette 1999).

My analysis of differential size-dependent predation losses among various marked groups of juveniles indicated that smaller fish probably suffered higher mortality than larger fish. Predicted length distributions were always skewed toward smaller sizes compared to actual distributions for groups composed of relatively small fish during the previous sampling period (Fig. 5), and the small sizes of salmon in these groups was similar to the sizes of salmon in predator stomachs (Fig. 6). Actual length distributions resulted from both growth and size-dependent predation losses. I estimated growth from regression of ln(FL) on date for all groups combined, because behavioral responses of juveniles to varying prey densities probably led to minimal growth differences among groups rearing in the same area (Table 5). However, if mortality were higher among smaller individuals (Willette et al. 1999), growth was overestimated by this method. Predicted length distributions were skewed toward larger sizes compared to actual distributions for wild juveniles in 1996 and WHN juveniles in 1997. In both cases, these fish were the largest of the 3 groups during the prior sampling period, and they were generally larger than salmon found in predator stomachs. These differences between actual and predicted distributions probably resulted from overestimation of growth.

Interactions among wild- and hatchery-origin juveniles resulted more from differential size-dependent predation losses among groups than from limitation of feeding and growth rates. The interaction was a function of the relative sizes of individuals among groups after they mixed together. The larger fish within a school were probably sheltered from predation by the presence of smaller fish (Parker 1971). Wild juveniles were generally larger than juveniles released from CCH hatchery, but they were only slightly larger than WHN juveniles during May (Fig. 5). By late June and July, WHN juveniles were typically larger than wild juveniles. This may have resulted from continuing emigration of wild fry from streams bordering PWS (Cooney et al. 1995). During the 2 years of this study, interactions with hatchery-origin salmon probably did not cause higher predation losses among wild salmon. However, the nature of the interaction among groups of juvenile salmon is complex and probably changes from year to year.

Differential size-dependent predation losses are probably amplified when *Neocalanus* densities or ocean temperatures are low. Coherent decadal variations in ocean temperatures and zooplankton biomass affect both the coastal and oceanic ecosystems in the Gulf of Alaska (Emery and Hamilton 1985; Brodeur and Ware 1992; Sugimoto and Tadokoro 1997). The salmon enhancement program in Alaska was initiated after a period of low wild salmon returns and cold winters during the early 1970's. After a regime shift in 1977, ocean temperatures, zooplankton biomass, and salmon production in the region were relatively high (Brodeur and Ware 1992; Hare and Francis 1994). A return to lower salmon production and lower zooplankton stocks may have begun in the early 1990's (Beamish et al. 1998). Cooler winter temperatures will probably delay stream emigrations of wild salmon fry (Cooney et al. 1995) reducing their size relative to hatchery-reared salmon. Concurrent declines in *Neocalanus* density will reduce the carrying capacity of nearshore predation refugia causing juveniles to disperse offshore in search of prey (Willette 1999). Differences in sizes of wild and hatchery-origin juveniles may then lead to greater differential size-dependent predation losses among groups and more variable intra-annual adult returns to the 4 hatcheries and the various streams bordering PWS. Numerical models may enable us to further examine the nature of these processes and determine the efficacy of various hatchery release practices that may minimize differential mortality among groups of juvenile salmon.

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Table 1. Mean whole body wet weight (g) and stomach fullness (% body weight) of juvenile pink salmon, mean 2-m ocean temperature (°C), number of sites sampled, and number of specimens analyzed stomach contents and growth or condition during May-Sept., 1994-1997.

Year	Sampling Period	Mean Weight	Stomach Fullness	Ocean Temp.	No. Sites	Sample sizes Diet	Sample sizes Growth
1994	Early May	0.29	2.35	5.3	3	30	119
	Late May	0.57	2.31	7.6	9	74	25
	Early June	1.49	1.40	9.1	29	265	15
	Late June	3.53	0.99	9.9	8	89	14
	Early July	3.84	1.65	12.9	15	154	2
	Early Sept.	22.39	1.52	11.5[1]	8	71	0
1995	Early May	0.26	2.63	6.7	8	1,335	0
	Early June	1.11	2.54	8.8	8	2,112	109
1996	Early May	0.28	2.99	7.3	5	804	734
	Late May	0.56	2.03	10.5	7	968	487
	Early June	0.96	1.92	12.0	8	1,278	877
1997	Early May	0.44	1.56	7.9	1	127	127
	Late May	0.69	3.09	11.3	9	1,067	1,066
	Early June	1.66	2.93	12.7	9	988	982

[1] Mean 0-20 m temperature used due to deeper distribution of larger juveniles.

Table 2. Comparison of growth (kJ day^{-1}) and ration (kJ day^{-1}) of juvenile pink salmon in Prince William Sound with maximum growth (kJ day^{-1}) and ration (kJ day^{-1}) from Brett (1974). Significant differences between maximum and actual rations are indicated in bold. Energy content (kJ g wet $weight^{-1}$) and gross growth conversion efficiencies (CE) estimated from field data are also indicated.

	Sampling	Field Estimated				Max. (Brett 1974)		
Year	Period	Growth	Energy	Ration	CE (%)	Growth	Ration	Diff
1994	Early May	-	-	0.382 (±0.024)	-	0.108	0.358	0.024
	Late May	0.169	-	0.554 (±0.286)	30.5	0.140	0.467	0.087
	Early June	0.152	-	0.311 (±0.135)	48.7	0.129	0.431	-0.120
	Late June	0.163	-	0.219 (±0.069)	74.6	0.105	0.350	**-0.131**
	Early July	0.119	-	0.515 (±0.159)	23.2	0.138	0.460	0.055
	Early Sept.	-	-	0.550 (±0.155)	-	0.065	0.216	**0.334**
1995	Early May	-	-	0.537 (±0.065)	-	0.166	0.552	-0.015
	Early June	0.165	-	0.618 (±0.136)	26.7	0.133	0.442	**0.176**
1996	Early May	-	4.86	0.708 (±0.159)	-	0.186	0.620	0.088
	Late May	-	4.79	0.605 (±0.128)	-	0.221	0.736	**-0.131**
	Early June	-	4.69	0.656 (±0.155)	-	0.202	0.675	-0.019
1997	Early May	-	4.58	0.291 (±0.024)	-	0.169	0.562	**-0.271**
	Late May	-	4.87	0.853 (±0.367)	-	0.210	0.699	0.154
	Early June	-	4.82	0.903 (±0.232)	-	0.193	0.644	**0.259**

Table 3. Mean total zooplankton biomass (g m^{-3}) and density (no. m^{-3}) of large copepods, small copepods, and other zooplankters at nearshore and offshore stations during May and June, 1995. Also, mean stomach fullness index and proportion of the diet composed of large copepods, small copepods, and other zooplankters for juvenile pink salmon captured nearshore and offshore are indicated. Statistical tests are for a difference between means for nearshore and offshore stations.

Month	Variable	Mean Nearshore	Mean Offshore	*p*-value
Zooplankton density				
Early May	Lg. copepods	89 (14)	137 (9)	0.063
	Sm. copepods	2445 (298)	2578 (199)	0.712
	Other zooplankton	269 (39)	261 (26)	0.860
	Total biomass	0.50 (0.05)	0.58 (0.03)	0.188
Early June	Lg. copepods	15 (14)	54 (13)	0.045
	Sm. copepods	2666 (298)	3489 (267)	0.041
	Other zooplankton	425 (39)	545 (35)	0.025
	Total biomass	0.43 (0.05)	0.63 (0.04)	0.003
Diet composition				
Early May	Lg. copepods	0.44 (0.02)	0.66 (0.07)	0.002
	Sm. copepods	0.41 (0.02)	0.17 (0.07)	0.004
	Other zooplankton	0.14 (0.02)	0.16 (0.07)	0.747
	Stomach fullness index	0.005 (0.002)	0.008 (0.008)	0.726
Early June	Lg. copepods	0.12 (0.02)	0.05 (0.03)	0.042
	Sm. copepods	0.43 (0.02)	0.12 (0.03)	<0.001
	Other zooplankton	0.44 (0.02)	0.83 (0.03)	<0.001
	Stomach fullness index	-0.006 (0.002)	0.006 (0.003)	0.002

Table 4. Mean proportion of the diet composed of large copepods, small copepods, and other zooplankters for juvenile pink salmon captured nearshore and offshore, 1996-1997. Also, mean density (no. m^{-3}) of large copepods, small copepods, and other zooplankters at stations near the 20-m isobath are indicated. Totals refer to mean zooplankton biomass or stomach fullness indices for juvenile salmon. Statistical tests are for a difference between means for nearshore and offshore stations.

Month	Variable	Zoop.	Diet Composition		
		Density	Nearshore	Offshore	*p*-value
1996					
Early May	Lg. copepods	84 (7)	0.50 (0.02)	0.66 (0.06)	0.053
	Sm. copepods	3737 (426)	0.27 (0.03)	0.12 (0.08)	0.117
	Other zooplankton	290 (81)	0.23 (0.03)	0.22 (0.08)	0.870
	Total	0.46 (0.03)	0.004 (0.002)	0.002 (0.004)	0.613
Late May	Lg. copepods	19 (7)	0.06 (0.02)	0.15 (0.04)	0.025
	Sm. copepods	3824 (417)	0.48 (0.03)	0.18 (0.05)	<0.001
	Other zooplankton	680 (78)	0.44 (0.03)	0.66 (0.06)	0.001
	Total	0.35 (0.03)	-0.006 (0.001)	-0.008 (0.003)	0.444
Early June	Lg. copepods	5 (7)	0.01 (0.02)	0.05 (0.03)	0.005
	Sm. copepods	4740 (417)	0.33 (0.03)	0.16 (0.04)	<0.001
	Other zooplankton	1689 (78)	0.66 (0.03)	0.79 (0.04)	0.008
	Total	0.37 (0.03)	-0.013 (0.001)	-0.006 (0.002)	0.004
1997					
Early May	Lg. copepods	11 (8)	0.00 (0.04)	-	-
	Sm. copepods	3083 (1080)	0.22 (0.11)	-	-
	Other zooplankton	1602 (628)	0.77 (0.12)	-	-
	Total	0.26 (0.10)	-0.006 (0.01)	-	-
Late May	Lg. copepods	22 (4)	0.01 (0.01)	0.00 (0.02)	0.219
	Sm. copepods	3240 (571)	0.28 (0.03)	0.29 (0.05)	0.557
	Other zooplankton	1439 (317)	0.70 (0.03)	0.71 (0.06)	0.996
	Total	0.35 0.03)	-0.004 (0.004)	0.001 (0.006)	0.586
Early June	Lg. copepods	37 (4)	0.03 (0.01)	0.00 (0.01)	0.654
	Sm. copepods	4815 (558)	0.14 (0.04)	0.18 (0.03)	0.554
	Other zooplankton	2660 (310)	0.83 (0.04)	0.82 (0.03)	0.861
	Total	0.37 (0.03)	0.001 (0.005)	0.001 (0.004)	0.999

Table 5. Stock composition of juvenile pink salmon by sampling period and area in Prince William Sound, 1994-1997. Estimates based upon recoveries of coded-wire tags in 1994 and 1995 and otolith thermal marks in 1996 and 1997. Acronyms for hatcheries: Armin F. Koernig (AFK), Wally H. Noerenberg (WHN), Cannery Creek (CCH), and Solomon Gulch (SGH).

			Stock Composition (%)					No.	No.
Year	Period	Area	AFK	WHN	CCH	SGH	Wild	tags	Scan
1994	Early May	3	0	83	0	0	17	198	143.4
	Late May	2	0	46	1	2	51	49	59.9
	Early June	3	0	14	13	8	65	27	47.9
		2	0	25	1	3	71	109	226.7
	Late June	3	0	19	24	5	52	30	25.3
		2	0	15	19	4	62	154	226.4
		1	28	3	1	1	67	50	90.9
	Early July	2	0	3	33	0	64	20	31.4
		1	59	3	8	4	25	497	397.6
1995	Early June	3	0	89	1	0	10	271	180.7
1996	Early May	3	0	99	0	0	1	1643	-
	Mid. May	3	0	98	0	0	2	639	-
		4	72	0	17	461	-		
	Early June	3	0	82	0	0	18	832	-
		4	0	15	60	6	19	927	-
	Early July	1-3	18	11	29	10	32	916	-
1997	Early May	3	0	93	0	0	7	374	-
		4	0	2	58	4	36	399	-
		5	0	0	0	1	99	181	-
	Mid May	3	0	69	0	1	30	347	-
		4	0	5	66	16	13	700	-
		5	0	0	0	43	57	467	-
	Early June	3	0	65	11	4	20	567	-
		4	0	0	92	2	6	378	-
		5	0	0	0	25	75	473	-
	Late June	1	36	17	10	7	30	1216	-

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Fig. 1. (a) Location of study areas in Prince William Sound, 1994-1997, and (b) total adult returns of wild- and hatchery-origin pink salmon to Prince William Sound, 1962-1998. Approximate numbers of juvenile pink salmon released from each hatchery in recent years is also indicated.

Fig. 2. (a) Feeding rates of juvenile pink salmon consuming large copepods (solid squares and heavy- solid regression line) and small copepods (open circles and light-solid line) in relation to zooplankton biomass. (b) Mean stomach fullness index (and SE) for juvenile pink salmon in relation to the proportion of the diet composed of large copepods (solid circles), small copepods (solid squares), and other zooplankton (open circles).

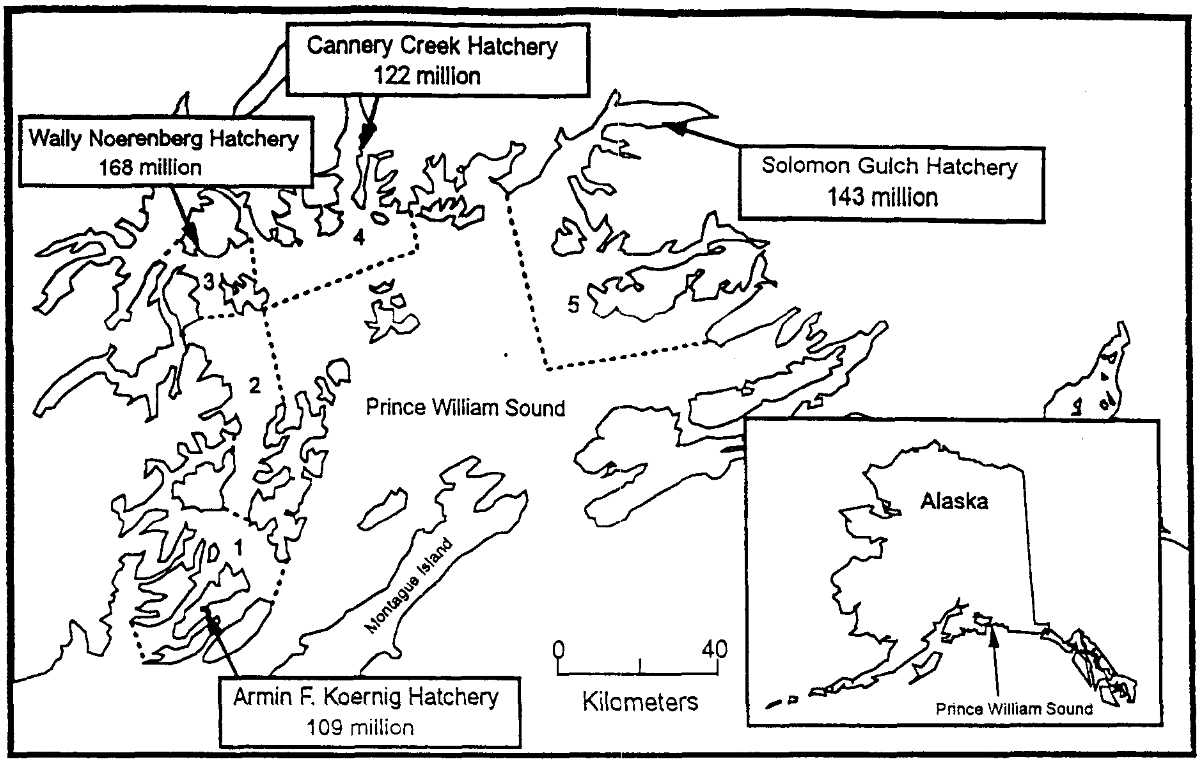
Fig. 3. Relationships between estimated energy content of juvenile pink salmon and the proportion of their diet composed of large copepods and small copepods.

Fig. 4. (a) Relationship between juvenile diet composition and juvenile density (low densities: solid circles; moderate densities: open circles; high densities: solid squares). (b) Mean energy content (and SE) of juvenile pink salmon in relation to juvenile density in 1996 (solid circles) and 1997 (solid squares).

Fig. 5. Length frequency distributions (solid lines) for wild- and hatchery-origin juvenile salmon during 2-week sampling periods, May-July 1996-1997. Dashed lines indicate the length-frequency distribution for each group predicted from the length distribution during the previous period assuming equal growth among groups.

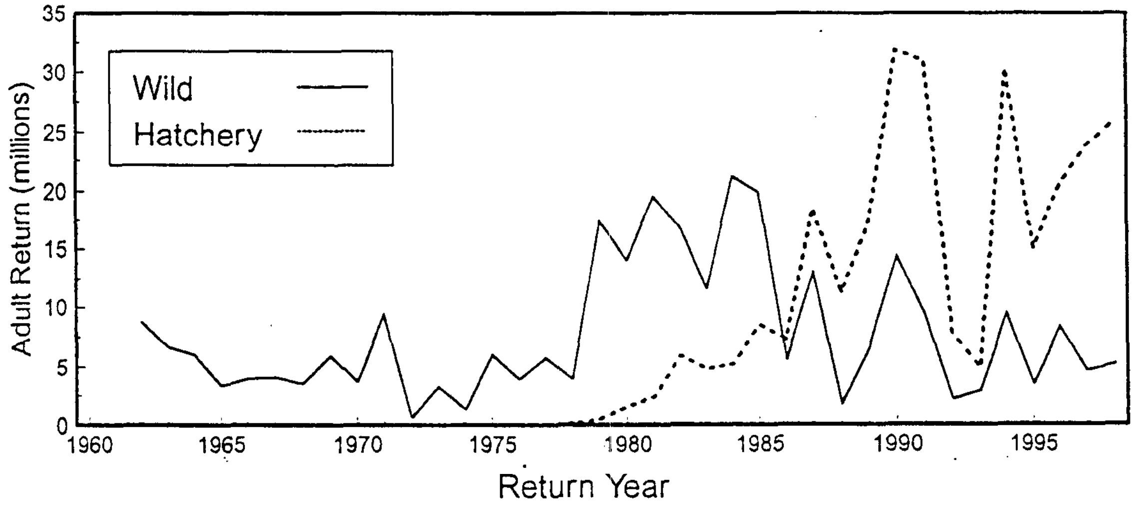
Fig. 6. Length frequency distributions for juvenile salmon found in the stomachs of planktivores (solid line) and piscivores\demersal fish (dashed line) during 2-week sampling periods, May-June 1996-1997.

a.



Cannery Creek Hatchery
122 million
Wally Noerenberg Hatchery
168 million
Solomon Gulch Hatchery
143 million
4
3
5
2
Prince William Sound
1
Montague Island
Armin F. Koernig Hatchery
109 million
0
40
Kilometers
Alaska
Prince William Sound

b.



35
30
25
20
15
10
5
0
Adult Return (millions)
Wild
Hatchery
1960
1965
1970
1975
1980
1985
1990
1995
Return Year

Figure 1

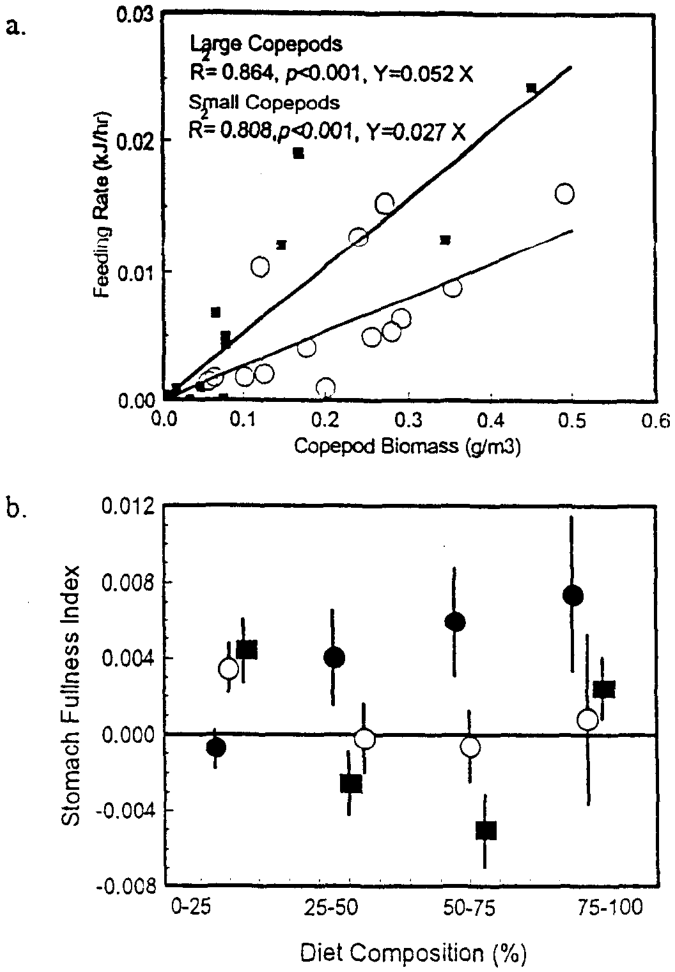

a.
Large Copepods
R2= 0.864, p<0.001, Y=0.052 X
Small Copepods
R2= 0.808, p<0.001, Y=0.027 X
Feeding Rate (kJ/hr)
0.03
0.02
0.01
0.00
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Copepod Biomass (g/m3)
b.
Stomach Fullness Index
0.012
0.008
0.004
0.000
-0.004
-0.008
0-25
25-50
50-75
75-100
Diet Composition (%)

Figure 2

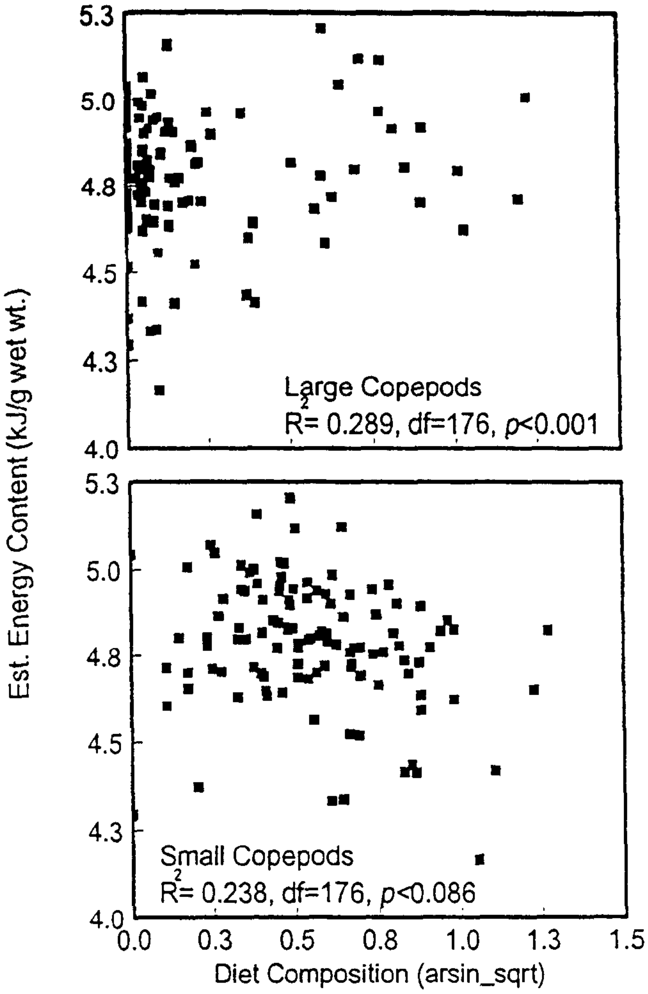

5.3
5.0
4.8
4.5
4.3
4.0
Large Copepods
R^2= 0.289, df=176, p<0.001
5.3
5.0
4.8
4.5
4.3
4.0
Small Copepods
R^2= 0.238, df=176, p<0.086
0.0
0.3
0.5
0.8
1.0
1.3
1.5
Diet Composition (arsin_sqrt)
Est. Energy Content (kJ/g wet wt.)

Figure 3

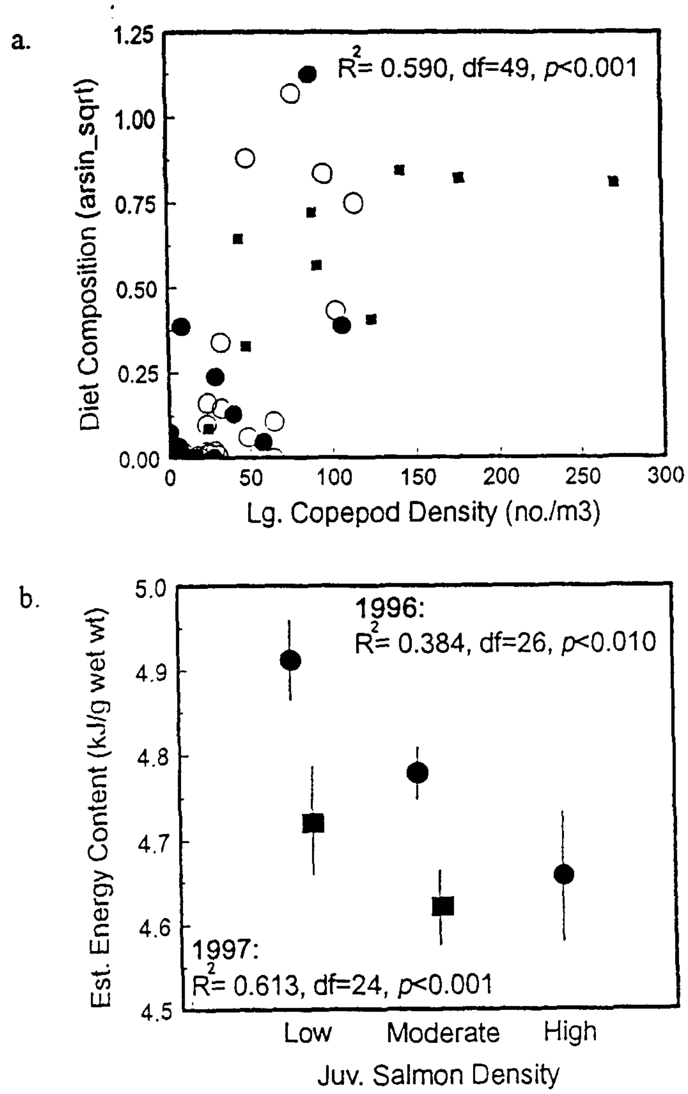

a.
R^2= 0.590, df=49, p<0.001
Diet Composition (arsin_sqrt)
1.25
1.00
0.75
0.50
0.25
0.00
0
50
100
150
200
250
300
Lg. Copepod Density (no./m3)
b.
1996:
R^2= 0.384, df=26, p<0.010
1997:
R^2= 0.613, df=24, p<0.001
Est. Energy Content (kJ/g wet wt)
5.0
4.9
4.8
4.7
4.6
4.5
Low
Moderate
High
Juv. Salmon Density

Figure 4

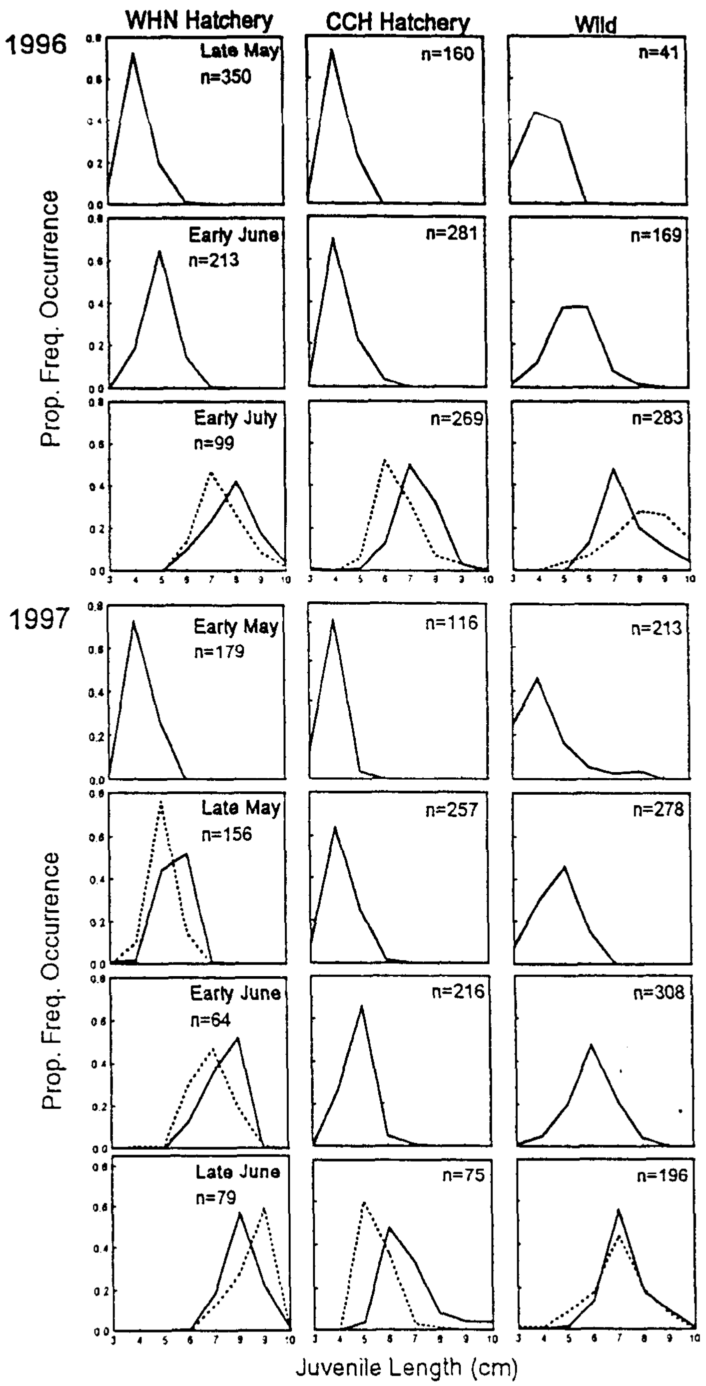
WHN Hatchery
CCH Hatchery
Wild
1996
1997
Late May
n=350
n=160
n=41
Early June
n=213
n=281
n=169
Early July
n=99
n=269
n=283
Early May
n=179
n=116
n=213
Late May
n=156
n=257
n=278
Early June
n=64
n=216
n=308
Late June
n=79
n=75
n=196
Prop. Freq. Occurrence
0.0
0.2
0.4
0.6
0.8
3
4
5
6
7
8
9
10
Juvenile Length (cm)

Figure 5

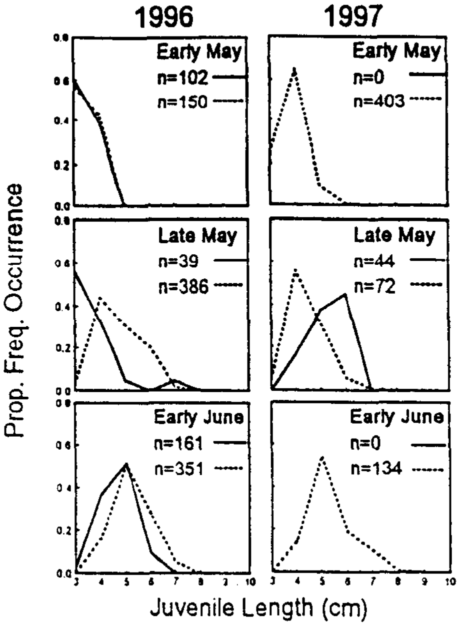

1996
1997
Early May
n=102
n=150
Early May
n=0
n=403
Late May
n=39
n=386
Late May
n=44
n=72
Early June
n=161
n=351
Early June
n=0
n=134
0.8
0.6
0.4
0.2
0.0
3
4
5
6
7
8
9
10
Prop. Freq. Occurrence
Juvenile Length (cm)

Figure 6

Chapter 3:

Phytoplankton and Nutrients

Exxon Valdez Oil Spill
Restoration Project Final Report

Sound Ecosystem Analysis: Phytoplankton and Nutrients
Restoration Project Final 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.

Restoration Project 98320G
Final Report

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E. Paul Simpson
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Institute of Marine Science
University of Alaska Fairbanks
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June 1999

Sound Ecosystem Analysis: Phytoplankton and Nutrients

Restoration Project 98320G
Final Report

Study History: The project was initiated as Restoration Project 94320G. A "Draft Final Report" was produced as an annual report in 1995, 1996, 1997 and 1998 under the title "SOUND ECOSYSTEM ANALYSIS: Phytoplankton and Nutrients" and continues under the present grant number. The project began in May 1994 with D. Eslinger as a co-principal investigator to include the biological modeling; in 1996 the modeling work was designated a separate SEA component (see elsewhere). The tactic for field studies was to combine sound-wide observations collected in spring and summer from ships with an intensive time series of observations collected daily from a single location in April, May and June. The field work did not get started early enough in 1994 to include the spring phytoplankton bloom but good coverage of this singular event was obtained for 1995, 1996 and 1997. As this is a time series project, publications and theses resulting from the data are in preparation. Numerous abstracts have been published as parts of conference proceedings and one thesis was completed in 1997 (see appendix).

Abstract:

This project was a part of Sound Ecosystem Assessment, a program that sought to understand the reasons for the recovery of pink salmon and herring stocks following the *Exxon Valdez* Oil Spill. This component of the project examined the quantity, nature and variability of the phytoplankton community that develops each spring in Prince William Sound. Data were collected to describe events in the upper 100 m of the water column by measuring inorganic nutrient and chlorophyll *a* concentrations with ancillary temperature and salinity values, phytoplankton enumerations and identification, and carbon and nitrogen content and stable isotope ratios of particulates. Field work combined regional sampling from ships with an intensive time series of samples from a single location in Elrington Passage. Results, from 4 years of field work, indicate that the phytoplankton bloom in Prince William Sound varies in duration, distribution and composition depending on climate and ocean conditions. The spring bloom is always dominated by diatoms. Fueled by nitrate from winter mixing, the bloom begins in early April, and lasts until early May when grazing and nutrient depletion take control to limit production. The post-bloom period is dominated by small flagellates. Production averaged 2.33, 2.75 and 1.49 gC m^{-2} d^{-1} for 1995, 1996 and 1997 respectively. Regional variations in primary production were calculated from nutrient depletion using silicate and nitrate+nitrite inventories. The data support the hypothesis that interannual variation in the production cycle directly affects upper trophic level production. Returns of wild pink salmon correlate well with interannual variability in ocean/climate processes and productivity. The phytoplankton production system in the sound is robust and healthy; we found no lingering evidence of an impact from the oil spill.

Key Words: *Exxon Valdez*, phytoplankton, nutrients, primary productivity, chlorophyll, carbon, isotopes

Project Data: *Description of Data* - Data collected by this project included measurements of temperature, salinity, primary nutrients, chlorophyll a, particulate carbon and nitrogen as well as their stable isotope ratios, and identification and enumeration of phytoplankton species. *Format-*

The data are stored on an electronic database that can be accessed from the Internet. *Custodian & Availability* - All data collected by this project is available electronically via the SEA web site database maintained by the Prince William Sound Science Center, Cordova AK. Other inquiries can be directed to the principal investigator.

Citation: McRoy, C.P., E.P. Simpson, K. Tamburello, A. Ward, and J. Cameron. 1999. Sound Ecosystem Analysis: Phytoplankton and Nutrients, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320G), Institute of Marine Science, University of Alaska, Fairbanks, Alaska

Chapter 3: 98320G
Citations to published articles

Eslinger, D.L., R.T. Cooney, C.P. McRoy, A. Ward, T.C. Kline, Jr., E.P. Simpson,J. Wang, and J.R. Allen. 2001. Plankton dynamics: observed and modelled responses to physical conditions in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):81-96.

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Executive Summary

As one of the several investigations constituting the Sound Ecosystem Assessment (SEA) program, this study was designed to examine the dynamics of the spring bloom of phytoplankton, as influenced by ocean mixing and nutrient supply, on the year-class success of pink salmon and herring in the ecosystem of Prince William Sound. The decline of these fishery species in the years immediately following the *Exxon Valdez* Oil Spill led to formulation of SEA to examine the processes that could be involved in the restoration of the populations to their former abundance.

Many factors and processes contribute to the year-class strength of a species in the sea. In this project we attempted to examine the role of the annual production of phytoplankton as a key element in the process. Can it be that the year to year differences in the quantity of plant life set the magnitude for all subsequent levels in the food web? If so. what oceanographic and climate processes control this quantity? Could the mix of algal species available each spring be a deciding factor for how much food is transferred to the next trophic step? Experience from terrestrial ecosystems certainly would indicate this. Finally, does the physiological quality of the phytoplankton assemblage play a crucial role? These are some of the questions central to this investigation.

The project concludes that, with respect to the dynamics of the phytoplankton community, there is no lingering effect of the oil. We could detect no such effects in the period of the field studies of this project (1994-97). This indicates that variability of natural processes was crucial in determining the observed changes. Recent reviews on the climate and oceanography of the North Pacific Ocean show direct links between physical changes and the returns of salmon. Such relationships are a priori evidence for ecosystem forcing from a bottom up (phytoplankton dynamics) rather than top down (predator dynamics) point of view. From data gathered here, we can but agree. Our second major conclusion is that the quantity and quality of the phytoplankton community in a given year has direct bearing on the strength of upper trophic level populations, particularly pink salmon. The following is a brief summary of what we did and how we did it.

Our basic data set includes measurements of dissolved inorganic nutrients (nitrate, nitrite, silicate and phosphate), phytoplankton chlorophyll *a*, identification and enumeration of phytoplankton species, carbon and nitrogen content of small particulates from the water, and stable isotope ratios of carbon and nitrogen in these particles. These several parameters provide an adequate description of the phytoplankton and the nutrients that limit their growth. We used two types of platforms to collect samples for these measurements. First we used ships that were deployed by other component projects of SEA to examine regional differences in the sound. These cruises were somewhat irregular and not entirely suited to fully examining the phytoplankton cycle because they were determined by the objectives of other projects. To supplement our regional coverage of the sound we set up a laboratory base first at the WN hatchery on Esther Is. (1994) then at AFK on Evans Is. (1995-1997) and sampled a nearby location (Lake Bay or Elrington Passage) every day during spring and early summer. Sampling consisted of collecting water from 6 depths dispersed throughout the upper 100 m of the water column.

Over the course of the project, six graduate students and one undergraduate were supported. Two theses and a dissertation will be produced from the results. In addition, six others worked on the project as field or laboratory technicians. This team participated in 15 cruises and 4 seasons at hatcheries to collect water from 803 oceanographic stations and analyze 4732 samples for nutrients and 3643 for chlorophyll *a*. Because of time and/or costs other measurements could only be made on a subset of the samples. The results are presented as regional analyses from the ship-board data and as time series analyses from the hatchery-based data. This report adds to results presented in earlier reports.

In Prince William Sound the phytoplankton bloom is the major annual event that supplies the food web with the carbon needed for upper trophic levels. The bloom begins in early April and finishes in early May. The bulk of the bloom biomass consists of diatoms; we identified 23 species from all years but a different community mix of relative abundance occurred in each year. The major difference occurred in 1996 when the smaller (<20 µm) cells of *Skeletonema* sp. dominated the community. In other years the bloom consisted of species of *Thalassiosira* sp. and *Chaetoceros* sp. with larger cell sizes (>50 µm). Cell size of the diatom community is a major variable in the food web since this can affect the amount of carbon available to herbivores. Diatoms are very scarce in the post-bloom water column. Flagellates are always present in bloom and post-bloom waters. While these cells are always numerically abundant, due to their small size, they constitute only a small biomass. Flagellates dominate the post-bloom waters.

Due to winter mixing of the surface layer, the phytoplankton bloom begins in conditions of abundant nutrients that lead to high growth. The average primary production rates during the spring bloom are 2.33, 2.75 and 1.49 $gCm^{-2}\,d^{-1}$ for 1995, 1996 and 1997 respectively, a nearly two-fold difference between the highest and lowest value. The bloom terminates by depletion of nutrients in combination with consumption by herbivorous zooplankton. The combination of zooplankton grazing and nutrient depletion in the surface layer lead to a post-bloom phytoplankton community that differs in character and quantity from the bloom community. The carbon isotope ratios show marked enrichment of ^{13}C during the bloom followed by depletion in the post-bloom period.

Regional primary production, estimated from uptake ratios of silicate and nitrate+nitrite, is lower in the central sound than in waters to the north or south of this area. The latter regions appear to be limited by nitrate or silicate, depending on conditions in a given year, but the central sound apparently becomes silicate limited. Throughout the sound the post-bloom period presents an enigma since upwelling and other mixing processes renew both silicate and nitrate concentrations to as high as 10 µM but no increase in diatoms occurs. Since diatoms do not increase again and only nitrogen-based producers dominate the post-bloom period, we conclude that selective grazing by zooplankton keeps the diatom populations at low levels. We have no evidence for seeding of plankton or nutrients from the Gulf of Alaska.

We found that the North Pacific Index, a proxy for climatic conditions influencing the surface ocean, calculated for March explained at least 81% of the variance in the observed spring bloom production rates for our data and for other historical studies in Prince William Sound and Auke Bay. In the years of this project the variability of phytoplankton accounted for 97% of the zooplankton biomass variability. A summary of trends in the data collected here in relation to returns of wild pink salmon show a relationship consistent with what would be expected if bottom-up processes exert a major control on upper level ecosystem production. The relationship to hatchery-reared fish is ambiguous, as is that for herring.

INTRODUCTION:

The project seeks to determine the effects of a primary driving force, the dynamics of phytoplankton productivity, on ecosystem variability. In this component our hypothesis is that the timing, quantity and species composition of the plant community, that is, the phytoplankton, are a major determinant of variability in upper trophic levels; this is a bottom-up scenario of ecosystem forcing.

The Sound Ecosystem Assessment program (SEA) aims to understand and predict restoration of populations of pink salmon and herring in Prince William Sound. Fundamental to this goal is the understanding of controls of ecosystem processes that nourish the food web at its primary level. Restoration of marine populations that have been damaged by human activity is usually limited to a few options that focus on controlling loss rate processes, i.e. harvest level, predator control, etc., or minor habitat modification. Pink salmon and herring offer a spectrum of control strategies since a large portion of salmon are protected in hatcheries in their early life and herring are completely wild, subject to the variance of nature. The dual populations of pink salmon are particularly useful since the wild fish are a result of the vagaries of natural processes whereas the hatchery fish, in their early life history, are protected. For young fish in hatcheries there is always enough food and there are no predators. What then is the role of the annual cycle of primary production in the success of these upper trophic level species? Does the magnitude of the phytoplankton production determine the strength of a year class? Is the phytoplankton species composition an important determinant of the grazing zooplankton community? Does any of this matter or is there always enough food at the right time of the year so that upper trophic level populations are determined by the top consumer on the food web? One central SEA hypothesis concerns the impact of circulation and physical conditions on the restoration of fish stocks (the "Lake-River Hypothesis"). This proposes that the circulation of Prince William Sound alternates irregularly between years of strong through-flow, river-like conditions, and relatively stagnant, lake-like conditions (Cooney 1998). The consequence is a high biomass of large zooplankton (copepods) in 'lake' years that are the major food for target fish (salmon, herring) and their predators (termed 'middle-out' food web control by Cooney and associates). In alternate 'river' years, the large zooplankton are sparse and predation on the target fish species predominates (top-down control).

While middle-out or top-down are principal hypotheses being tested by SEA research, the possibility of bottom-up control, where the production of upper trophic level species is modulated by variations in light- and nutrient-driven phytoplankton production, is the question central to our investigation. In this hypothesis, the production and/or composition of the zooplankton community is determined by variations in phytoplankton primary production and by the species composition of the phytoplankton community. For example, a phytoplankton community dominated by large diatoms can support a high biomass of large oceanic copepods, whereas a phytoplankton population dominated by smaller flagellates results in a reduced number of larger copepods, or in a shift to a zooplankton community dominated by smaller neritic copepod species. Variations in the timing of phytoplankton populations have been previously suggested to be a control of ecosystem events in Prince William Sound (McRoy 1988). A further complication in the interrelationship is that the large zooplankton are one year old when they become major prey for fishes (Cooney, personal communication) so their abundance must be determined by the events of the previous year and their specific biomass by the production cycle of the present year.

In this component, we provide the nutrient and phytoplankton data that are essential to evaluate the influence of phytoplankton dynamics on the food web and to test the bottom-up hypothesis. We characterize the interannual spatial and temporal variation in nutrient and phytoplankton fields and evaluate the role of phytoplankton production in zooplankton recruitment and growth (especially for *Neocalanus* and *Pseudocalanus*). In a general sense we will provide an answer to the question, "Is it food?"

A central tenet of the Lake/River Hypothesis is the variable advection of Gulf of Alaska waters into Prince William Sound (Eslinger et al. in prep.). This advection affects not only zooplankton populations, but also the Prince William Sound phytoplankton populations and production.

OBJECTIVES:

This study was designed to investigate the role of phytoplankton and nutrient cycling in the recovery process of pelagic species deemed to have been injured by the EVOS. Our hypothesis is that variations in ocean processes controlling nutrient supply and phytoplankton growth lead to interannual variations in phytoplankton species and production that ultimately have a significant influence on variations of upper trophic level populations, particularly pink salmon and herring. The original set of objectives follows:

1) To measure the timing and biomass of phytoplankton cycles;
2) To measure the primary production of phytoplankton;
3) To determine the spatial and temporal patterns in phytoplankton distribution using satellite imagery;
4) To determine the species structure of phytoplankton communities;
5) To measure the distribution and quantity of major inorganic nutrients including nitrate+nitrite, ammonium, phosphate, silicate;
8). To determine the possible linking between phytoplankton and upper trophic levels.

METHODS:

Field work was done from two types of platforms. Ships were used for sample collection in conjunction with other SEA components. As these schedules and cruise tracks were determined by other projects, coverage of the time and space scales has many data gaps. The other platform was a skiff used from a shore facility (AFK Hatchery) to sample a single location in Elrington Passage (60°01'N, 148°00'W). Stations visited over the course of this study are indicated in Figure 1.

Shipboard Sample Collection

Fifteen oceanographic cruises were conducted between May 1994 and May 1997. Water samples after 1994 were collected from 0, 5, 10, 25, 50 and 100 m using a Niskin bottle rosette. When possible, stations over 500 m were also sampled at 100 m intervals. During the September 1994 cruise, water was collected from 0, 10, 20, 30, 50 and 100 m. Water was collected from 20 m only during the first 4 cruises of 1994.

Shore-based Sample Collection

Using a small skiff fitted with a hydrographic winch, we sampled a single station in Elrington Passage during the spring bloom (April to mid-June) in 1995, 1996 and 1997. CTD profiles, Secchi depth observations and water samples were collected daily from 0, 10, 20, 30, 50 and 75 m. A single zooplankton net tow was collected weekly for the zooplankton component of SEA. These data provide temporal continuity to the shipboard sampling.

Dissolved Inorganic Nutrients

Phytoplankton require the major inorganic nutrients (nitrogen, phosphorus and silica) for growth supplied by oceanographic circulation and land run-off. Since phytoplankton also require light, the problem is understanding how the nutrients are supplied to the illuminated zone of the sea. We routinely collected water samples for quantitative nutrient analysis. In the field and on shipboard, water samples were collected with Niskin bottles at standard depths over the upper 100 m. A small aliquot (250 ml) was filtered using acid-washed (10% HCl) 0.45 µm nominal pore size, glass fiber filters and stored frozen in acid-washed polypropylene bottles until analyzed on shore. Chemical determination of the quantity of dissolved nitrogen (as nitrate, nitrite and ammonium), phosphate and silicate were measured using prescribed Continuous Flow Analysis protocols (Alpkem Corp. 1986) with an Alpkem 305 Auto-Analyzer in our laboratory in Fairbanks.
The autoanalyzer was calibrated each day using standard curves measured before, after and, in some cases, during the sample stream and by incorporating 1-3 standard solutions within each batch of 10 samples. Carryover effects were detected using 10 repeated standard solutions at the beginning of the sample sequence.

Phytoplankton Community Composition

The composition of the phytoplankton community can be as important as the total primary production in determining zooplankton species and abundance. We collected 50-ml aliquots from water samples and preserved them in Lugol's solution for species identification. Identifications and cell counts were done using an inverted microscopy method (Sournia 1978). On low (20x) magnification, all visible cells in two transects are counted. On high (40x) magnification, fields are counted until a total of 300 cells are reached. For cell volume calculations and calculation of carbon content, cells identified to genus were grouped according to the maximum cell dimension. At least 20 cells of each species were measured for size class. The procedure is labor intensive and only a portion of the samples collected can be counted.

Phytoplankton Biomass

Phytoplankton biomass in each water sample was determined using standard chlorophyll techniques (Parsons et al., 1984). Data were collected at locations that allowed mapping the areal patterns and description of water column profiles. At each location (station) water samples were collected with a Niskin bottle. Chlorophyll and phaeopigments were measured by filtering 250-1000 ml water, depending on the phytoplankton abundance, through 0.45 µm nominal pore size, glass fiber filters. The filters were ground with a tissue grinder and the chlorophyll was extracted in 10 ml 90% acetone. The remains of the filters were removed by centrifugation. Fluorescence of extracts was measured using a Turner Designs model 10-AU fluorometer. The fluorometer was calibrated with spinach chlorophyll using a Hitachi model 100-40 spectrophotometer (Parsons et al. 1984). Blank filters were accounted for when calculating phaeopigment concentrations.

Particulate Carbon, Nitrogen and Stable Isotopes

For determination of nitrogen and carbon content and stable isotope ratio of small particulates, a one-liter sample was filtered onto a glass fiber filter using baked 0.45 µm pore size glass fiber filters and stored frozen in glass vials. In 1994 all such samples were sent to a laboratory at the University of California Santa Cruz for analysis of PC and PN only. After 1994 all particulate samples were analyzed at the University of Alaska Stable Isotope Facility on a Europa Scientific Model 20/20 mass spectrometer. Results of these measurements are $\delta^{13}C/^{12}C$, $\delta^{15}N/^{14}N$, %C and %N for each sample. The isotope ratio values, expressed in delta notation, are given relative to Vienna Peedee Belemnite for carbon and air for nitrogen.

Nutrient Uptake Ratios

The ratio of N+N to PO4 taken up by the phytoplankton was estimated by comparing the change in depth averaged N+N (ΔN) with the change in depth averaged phosphate (ΔP) at stations visited repeated throughout the sound. The N:P ratio is the slope of the regression of ΔN against ΔP excluding very low ΔP values from stations with a very long time between visits. Similar comparisons of ΔSi with ΔP and ΔSi with ΔN were made to estimate Si:P and Si:N uptake ratios. This method is analogous to the technique used by Stefánsson and Richards (1963) to estimate nutrient uptake ratios, although they used a spatial measure of nutrient differences (ΔSi, ΔN and ΔP). Data were plotted onto maps of Prince William Sound using Generic Mapping Tools (GMT)(Wessel and Smith 1991) on a NeXT computer to observe spatial patterns. Data manipulations and other figures were produced using Mathematica (Wolfram Research 1993).

Phytoplankton Primary Production

We estimated production using nutrient depletion data. Productivity data are also available in our historical database (McRoy, unpublished data; Goering et al. 1973b). Historical methods used uptake of ^{14}C by phytoplankton in containers under neutral density filters (Strickland and Parsons 1972; Parsons et al., 1984).

Daily and total new primary production (Dugdale and Goering 1967) rates were estimated from the changes in N+N and silicate in 4 regions: the central sound, Hinchinbrook Entrance, and the north and south regions of Montague Strait. Total new phytoplankton production (mgC m^{-3} y^{-1}) and average daily production (mgC m^{-3} d^{-1}) were estimated by multiplying the change in depth averaged N+N (ΔN) by the estimated molar C:N ratio of 6.84 times the mass of carbon. Diatom production was estimated using silicate depletion by multiplying the change in depth averaged silicate (ΔSi) by the estimated molar C:Si ratio of 4.33 times the mass of carbon. The C:N and C:Si ratios were estimated based on the N:P and Si:P ratios measured above and an assumed C:P ratio of 106:1.

Personnel

The following people, in addition to SEA colleagues, have contributed to sample and data collection and analysis over the life of the project:

P. Simpson	Graduate Student
A. Ward	Graduate Student
K. Tamburello	Graduate Student
M. Donovan	Graduate Student
G. Holmes	Graduate Student
E. Brown	Graduate Student
E. Suring	Undergraduate Student
J. Cameron	Senior Technician
B. Bergeron	Technician
D. Clayton	Technician
S. McCullough	Field Technician
P. Cassidy	Field Technician
C. Morrow	Field Technician

RESULTS:

Samples were collected to document the time series of events in the annual plankton production cycle as well as to examine spatial variations in Prince William Sound. These data were collected in conjunction with other SEA projects and reside in the SEA data base after appropriate verification. Over the course of the study, we collected data from 803 oceanographic stations and analyzed 4732 water samples for dissolved nutrients and 3634 samples for chlorophyll *a* content (Tables 1 and 2). In addition 285 water samples were examined for identification and enumeration of phytoplankton species, and for another 741 samples the stable isotope ratios of the particulates were measured. This final report builds on, rather than repeats, the results presented in annual reports submitted in for each year.

Phytoplankton Communities

In 1995, 1996 and 1997 the phytoplankton community was composed of 23 diatom species and 8-10 flagellates (Table 3). In 1995 *Skeletonema costatum, Thalassiosira* sp. and *Chaetoceros* sp. were the most common species. *Leptocylindrus* sp. appeared inconsistently, composing only a small portion of the bloom.

In 1996, the same taxa reappeared but the smaller diatoms tripled in abundance while the larger species declined (Ward 1997). *Skeletonema costatum* and *Chaetoceros* sp. were the most abundant taxa. *Thalassiosira* sp. and *Leptocylindrus* sp. constituted less of the community in 1996 than in 1995. For both 1995 and 1996, other diatoms, in order of abundance, were *Fragilariopsis* sp., *Asterionella glacialis, Navicula* sp., *Eucampia* sp., *Stephanopyxis nipponica* and *Rhizosolenia stolterforthii* (Ward 1997). In 1995 and 1996 *Pseudo-Nitzschia* spp were identified as part of the community. In 1997 we revised the list to include a similar taxa identified as *Nitzschia* sp. For this report *Nitzschia* sp. is used to include *Pseudo-Nitzschia* and *Nitzschia* sp.

The most abundant centric diatoms were *Skeletonema costatum, Thalassiosira* sp., *Chaetoceros* sp., *Leptocylindrus* sp., *Stephanopyxis nipponica* and *Fragilariopsis* sp. *Skeletonema costatum* is a small diatom that generally forms chains. The diameter of these cells ranges from 7.5 - 17.5 µm. Like *Skeletonema costatum, Thalassiosira* sp. can be chain forming or unattached cells. These diatoms range from 10 - 55µm. *Chaetoceros* sp. are chain-forming diatoms with long setae that vary in length from 2.5 to 40 µm. *Leptocylindrus minimus* and *Leptocylindrus danicus* are diatoms that form chains by abutting valve faces (Tomas 1996). *L. danicus* is larger, averaging 11.5 µm in width, often appearing singly or in chains of two or three cells. *L. minimus* is smaller, having an average width of 2.5µm and more cells per chain (Ward 1997). *Rhizosolenia fragilissima,* also known as *Dactyliosolen fragilissimus* (Tomas 1996), averages 22 x 5 µm (l x w). These cells form chains by uniting the valve surfaces of two cells. They often appear in chains of only a few cells. *Fragilariopsis* sp., which appear rectangular in girdle view, are in ribbons united by the entire or the greater part of the valve surface (Tomas 1996). *Stephanopyxis nipponica* are distinguished from other similar looking taxa by their long external siliceous extensions of labiate processes, uniting cells in chains (Tomas 1996). Cell diameters range from 24-36µm. The only abundant pennate diatom, for any year, was the *Nitzschia* sp. group. These are narrow, elongate, pennate diatoms that are either multi-celled or solitary. Their length is as great as their width, 2µm, and they have the smallest cell volume of any phytoplankton, except the flagellates, in this study (Ward 1997).

Phytoplankton Abundance

The only taxa that constituted >1% of the bloom in all three years were *Nitzschia* sp., *Thalassiosira* sp. and the flagellates (Figure 2). During the bloom in 1995 flagellates constituted 66% of bloom cells. The diatom *Thalassiosira* sp. accounted for 17% and *Skeletonema costatum,* 9%. In 1996, the flagellate population was lower (17%) and the diatom, *S. costatum,* made up most of the phytoplankton community with 63%. In 1997, *S. costatum* all but disappeared, constituting only 1% of the total phytoplankton community. In this year *Thalassiosira* sp. had the highest abundance (47%) and the flagellate community increased slightly in abundance from 1996, constituting 20%.

Since small flagellates enter the microbial loop and are not considered a primary source of food for larger zooplankton (Mann 1993) we focused on the diatom community (Figure 3). During the bloom of 1995, *Thalassiosira* sp. had the highest abundance, 52% of the total diatom community, and *S. costatum* constituted 24% and *Rhizosolenia spp.* 13%. The composition of the major components changed in the in 1996. *S. costatum* accounted for 76% of the diatom community, where as in 1995 it accounted for only 24%. *Chaetoceros* sp. had the second highest abundance, with 15%, and *Nitzschia* sp. composed 5%. *Thalassiosira spp.* abundance, which only constituted 4% of the total diatom community, decreased from the previous year.

In 1997, the *Thalassiosira* sp. population rebounded to 59%, the highest abundance in the diatom community. In this year, *Fragilariopsis* sp. and *Stephanopyxis nipponica* constituted 3% and 5% respectively. During the post-bloom period only *Nitzschia* sp. and flagellates constituted >1% of the total phytoplankton community in every year (Table 4). Analyzing all the taxa from the post-bloom period of 1995, flagellates were 98% of the community (Figure 4). *Chaetoceros* sp. and *Nitzschia* sp. each accounted for 1%. In 1996, flagellates again dominated the post-bloom community with 90%. *Chaetoceros* sp. was the second most abundant with 5% and *Leptocylindrus* sp., *Nitzschia* sp. and *Rhizosolenia* sp. constituted the remaining 5%.

During the post-bloom period in 1997, the flagellate population decreased to 42% and *Chaetoceros* sp. had the second highest abundance with 22%. *Thalassiosira* sp., *Nitzschia* sp., and *Leptocylindrus* spp. accounted for 13, 12 and 11% respectively.

Removing the flagellates from the post-bloom period, the taxon composition reveals a more detailed description of the diatom community (Figure 5). In 1995, *Nitzschia* sp. was the most numerous diatom, constituting 49%. *Chaetoceros* sp. accounted for 37%, *Leptocylindrus* sp., 12% and *Thalassiosira* sp. and *Rhizosolenia* sp. each constituted 1%. In 1996, the most abundant diatom during the post-bloom period was *Chaetoceros* sp. and the remaining 51% of the diatom community was composed of *Nitzschia* sp., *Leptocylindrus* sp., *Rhizosolenia* sp., *Skeletonema costatum* and *Thalassiosira* sp. (in order of significance).

The 1997 post-bloom period consisted of taxa similar to those occurring in 1995 and 1996. *Chaetoceros* spp. was again the most abundant, accounting for 38% of the diatom community, *Thalassiosira* sp. constituted 22%, and *Nitzschia* sp. and *Leptocylindrus* sp. represented 20 and 18% respectively.

Nitzschia sp. was present in the post-bloom period of each year in the study (Figure 4). In 1996 and 1997 *Chaetoceros* sp. and *Leptocylindrus* sp. were present in the post-bloom period suggesting that they may not be a preferred food source for zooplankton. This scenario is very possible since all of these cells are fairly long, skinny, often chain-forming diatoms, which may make them hard for zooplankton to handle and consume.

Phytoplankton Carbon and Chlorophyll

The carbon content of phytoplankton cells was determined by converting cell counts and dimensions for each taxa from literature equations that estimate the plasma layer of a cell and it concomitant carbon. These data can then be compared to the chlorophyll a estimate of biomass and the direct biomass values of carbon for particulates as measured by mass spectrometry.

The 1996 phytoplankton community mean cell volume, 873 μm^3, was significantly lower than the mean cell volume for 1995 and 1997 (Table 5, Figure 6). This small value in 1996 is credible because the major diatom taxa during the bloom in this year was *S. costatum*, a small chain forming diatom with a mean cell volume (for the species) of 541 μm^3, also flagellate cells contributing to the average were only 99.5 to 1270 μm^3. In 1995 and 1997 when the mean cell volumes were 2876 and 3290 μm^3 respectively, the large diatom *Thalassiosira* sp. (cell volume = 7056 μm^3) was the most abundant diatom taxon of the diatom community. A cell volume such as *S. costatum* has an expected doubling time of about 1 day whereas the larger cells, e.g., *Thalassiosira* sp., the doubling time would be about 2 to 3 days (Harris 1986).

The abundance mean value (cells ml^{-1}) for each year of the study shows the opposite pattern than the cell size data (Figure 6). The mean abundance for 1996 (5043 cells ml^{-1}) was more than twice that for the 1995 and 1997 (Table 5). The overall mean abundance for all samples (n=200) for all years was 2847 ±2961 s.d. cells ml^{-1}. For all three study years the mean abundance, as measured by cell counts, is highly correlated to mean chlorophyll *a* concentration with an r^2 of 0.996 (Figure 6).

The mean carbon value in 1996, 209 mg/m^3, was significantly larger than 1995 and 1997 (Table 5) and the mean chlorophyll *a* for 1996 (6.2 mg m^{-3}) was also significantly larger than for 1995 and 1997. The overall ratio of carbon to chlorophyll *a* for the three years ranged from 24, in 1995, to 34 in 1996 and 1997 (Figure 7). The overall low values indicate nutrient stress of the phytoplankton communities in each year, especially in 1995 (Eppley et al. 1970).

The Spring Bloom

In Prince William Sound the spring bloom is the major annual event that supplies the food web with the carbon needed for all trophic levels. The increase in phytoplankton begins in early April (Figure 8) but the exact timing and character of the bloom depend on the oceanographic conditions of a given year (Eslinger et al. in prep). At the onset of the bloom abundant nutrients are available for growth and these are rapidly depleted by the phytoplankton (Figure 10). Concomitantly, zooplankton begin their migration from depth to the surface layer in late April and early May and reach a peak biomass in late May or early June (Figure 9). The combination of zooplankton grazing and nutrient depletion in the surface layer lead to a post-bloom phytoplankton community that differs in character and quantity from the bloom community. Zooplankton grazing must be the ultimate control of the phytoplankton in early summer since the pulses of nutrients, due to tidal pumping, that occur in the surface layer do not result in an increase in biomass, though they may increase productivity.

The results of overall primary production rates during the spring bloom are 2.33, 2.75 and 1.49 $gCm^{-2}\ d^{-1}$ for 1995, 1996 and 1997 respectively, a nearly two-fold difference between the highest and lowest value. These rates fall well within the values for the spring bloom measured by Goering et al. (1973a and 1973b) in Port Valdez and Valdez Arm using direct ^{14}C uptake. The total production can be twice these values if the f ratio is less than 0.5 as would be expected for the region (Sambrotto and Lorenzen 1987).

The time course of carbon isotope ratios over the spring shows the expected enrichment of ^{13}C during the bloom followed by depletion in the post-bloom period (Figure 11). The nitrogen isotope data reflect excursions around the median value for phytoplankton. The greater variability in the post-bloom period reflects an increase in small animal plankton in the surface waters.

Regional Primary Productivity

The calculated regression lines relating ΔSi, ΔN and ΔP (Figure 12) are:

$\Delta Si = 24.49\ \Delta P - 0.1$ (μM),

$\Delta N = 15.46\ \Delta P + 0.84$ (μM),

$\Delta Si = 1.59\ \Delta N - 1.99$ (μM).

The Si:N:P uptake ratios were set to 24.5:15.5:1. This produced a C:N ratio for estimating diatom production of 6.84 and a C:Si ratio for estimating diatom production of 4.33. The highest production rates in the central sound occurred between the March and April cruises and in Hinchinbrook Entrance occurred between April and May (Table 6). Annual diatom production in the central sound is a smaller proportion of total production in the south (70%) than in the north (98%), and nitrate-based production continues at least a month longer than silicate-based (diatom) production. Production in the central sound and Hinchinbrook Entrance was generally higher in 1996 than during the same period in 1995. Maximum diatom production in Montague Strait usually occurs between the April and May cruises (Table 6). North of Knight Island passage in 1995 the nitrate based total production estimate is greatest between the May and June cruises. Estimated production rates vary more in Montague Strait than in the central sound.

Dissolved Nutrient Ratios

In 1995 the dissolved Si:N ratio in the surface waters increased over the summer. In 1996 high SiO_4 concentrations were observed in the upper 10 m in the northwest region of the sound (Figure 13), after which deep water Si:N ratios throughout the sound increased to greater than 2.

Sound-wide dissolved Si vs. N regression slopes prior to June 1996 ranged from 0.852 to 1.52 and except in May 1995 have a positive intercept on the silicate axis (Figure 14). The slope increases to 2.0 in June 1996 and further to 2.77 in May 1997. Regression intercepts tend to become more positive and slopes tend to decline over the summer. Most regions of the sound mirror the overall patterns. The central sound, however, has a steeper Si vs. N regression slope in April and May with a positive intercept on the N+N axis (Figure 15).

DISCUSSION:

The phytoplankton production rates estimated from nutrient depletion must be considered conservative because they do not account for nutrient inputs due to deep mixing, upwelling or advection. Production estimates may be revised later using the Prince William Sound circulation model. The increasing surface silicate concentrations after the bloom are a strong indicator that such nutrient replenishment occurs throughout the sound. Increased shear in Hinchinbrook Entrance probably mixes substantial deep nutrients into the surface waters which will tend to reduce all production calculations for there. A cyclonic gyre develops around the central sound in the summer (Vaughn et al. 1998) which upwells deep nutrients at 60° 30"N and supports the moderate phytoplankton biomass observed there later in the summer. This is certainly new production, but it is not reflected in the production estimates based on nutrient depletion.

Spring Bloom Production

The spring phytoplankton bloom in Prince William Sound consists primarily of diatoms (Ward 1997) which rapidly deplete dissolved nutrient concentrations. The phytoplankton bloom in the central sound clearly appears to end when silicate is depleted (Figure 15). In other regions of the sound, however, it is difficult to determine whether the bloom ceases because the diatoms run out of silicate or nitrate.

Except for May 1996 and May 1997, the ratio of dissolved silicate to nitrate (Figure 14) is less than the estimated ratio of silicate to nitrate uptake of 1.6 (Figure 12). which implies that silicate may limit bloom diatom production in Prince William Sound prior to 1997. The 1.6 ratio of silicate to nitrate uptake estimated here is less than the 50:16 ratio reported by Broecker and Peng (1982) but greater than the 22:16 ratio observed by Stefánsson and Richards (1963). Paasche and Østergren (1980) measured particulate C:Si ratios ranging from 5.7 to 230 depending on the time of year. Assuming a C:N ratio of 106:16, this corresponds to a maximum particulate Si:N ratio of 1.16 during the bloom. Harrison et al. (1977) measured Si:N ratios in diatom culture between 0.43 and 2.0 depending on the nutrient conditions. Brzezinski (1985) measured diatom Si:N ratios, also in culture, ranging from 0.41 to 1.95. Although reported natural particulate Si:N ratios as high as 1.6 were not reported, diatom species exist with a higher ratio, so a ratio of 1.6 in Prince William Sound is possible. It is also possible that a silicate pump mechanism may be acting to increase the apparent ratio of silicate to nitrate uptake in Prince William Sound, in which case silicate limitation would be likely (Dugdale et al 1995).

The surface water appears to run out of N+N before it runs out of silicate (Figure 14). which suggests nitrate may be limiting diatom bloom production. Calculated regression intercepts in April, when the central sound bloom occurs, and May when the bloom occurs in the passageways between the central sound and the Gulf of Alaska, are between –0.84 and 3 µM SiO_4. Egge and Aksnes (1992) found that diatom dominance of the phytoplankton community ceases when silicate concentrations drop below 2 µM, however, so a slight positive residual silicate concentration may not necessarily indicate sufficient silicate for continued diatom production. Ward (1997) observed weak silicification and the production of diatom resting spores, from which she concluded that silicate limits the diatom bloom in southwest Prince William Sound.

Post-bloom Production

Upwelling and deep mixing events bring substantial additional silicate and nitrate to the surface after the diatom bloom ends. This has been described previously (McRoy 1998) and it is confirmed by the redistribution of silicate from the deep water to the surface and the continued depletion of N+N throughout the water column as the summer progresses.

Both nitrate and silicate are introduced into the surface waters, but the non-siliceous post-bloom phytoplankton only use the nitrate throughout the rest of the summer. This is consistent with the observations of Paasche and Østergren (1980), who measured particulate C:Si ratios ranging from 5.7 to 230 depending on the time of year and explained the differences based on changing species composition. This corresponds to Si:N ratios that vary from 1.16 during the bloom to 0.03 post-bloom. In Prince William Sound, however, the eventual result of the species composition change is a buildup of silicate and increasing Si:N ratios in the surface water.

The reason for the lack of post-bloom diatom production is not lack of nutrients, since surface silicate concentrations around 10 µM exists in conjunction with nitrate concentrations ranging between 0 and 10 µM, and ammonium is also available after the bloom. Zooplankton grazing probably prevents diatoms from utilizing these available nutrients. Zooplankton biomass increases dramatically in Prince William Sound after the bloom due to the vertical immigration and growth of the large copepods *Neocalanus plumcrus* and *N. cristatus*. These large copepods are probably able to control the post-bloom diatom abundance at very low levels until they emigrate back to deeper water later in the summer.

The large copepods almost certainly eat the non-siliceous successors to the bloom diatoms (Urban et al. 1993), but these are probably small flagellates (Ward 1997) which the large zooplankton can not eat fast enough to control. The continued decline in nitrate through the summer implies that the post-bloom phytoplankton are not entirely controlled by zooplankton. The copepods may be feeding on the microzooplankton as well as the flagellates that may ease grazing pressure on the flagellates. Simpson et al. (in prep.) found evidence that microzooplankton control of nanoplankton in the Bering Sea degrades at high total phytoplankton, and presumably high macrozooplankton abundance.

The higher silicate to nitrate ratios at the end of 1996 are likely a result of increased post-bloom production that year compared to 1995 and increased fluvial silicate inputs. Estimated production based on nitrate depletion was higher in the central sound between April and June 1996 than during the same period of 1995. There was less wind during the diatom bloom in

1996 than in 1995 (Ward 1997, Eslinger et al. in prep.) which mixed less deep nutrients up. The result was a shorter diatom bloom in 1996 which used up less of the deep silicate earlier (between March and April) leaving more deep nutrients available for production later (between April and June). The post-bloom flagellates used more nitrate in 1996 and left a larger pool of silicate behind. The increased silicate in the upper 10 m of the northwest region of the sound in May 1996 from the numerous glaciers feeding into that area (Figure 13) further increased silicate concentrations.

The increased Si:N ratios of June 1996 are also apparent in May 1997. That year was another with low winds, similar to 1996, so high Si:N ratios might be expected, except that the high ratios were observed much earlier in 1997 than in 1996. These were the last 2 cruises of this study, so whether these high ratios were continuous between these times or recurred after a March similar to 1995 or a September similar to 1994 or 1995 is unknown. We do know, however, that biological and nutrient conditions in May 1997 were very different than those observed in May 1995 and 1996. Such changes could be a result of nearly triple deep water Si:N ratios.

Bottom Up Control of the Food Web

This project examined the relationship of phytoplankton community structure and primary productivity to production in upper trophic levels with an emphasis on pink salmon and herring. We find that our own data support the hypothesis that variations in ocean processes controlling nutrient supply and phytoplankton production and species determine upper trophic level variations. On a very general level nearly everyone will agree with this tenet since it is fundamental to ecology and, in the world ocean, more primary production in a region results in higher fisheries yields (Mann 1993). Yet the question remains about the role of interannual variability in primary production and community species composition in explaining upper trophic level variance. Furthermore, is this merely a question of phenology, i.e. the variance in the relative scheduling of primary and secondary production processes?

This is hardly a new quest. In the subarctic North Pacific Ocean, Taniguchi (1973) reported that phytoplankton production controlled the biomass and food requirements of herbivorous zooplankton. Another study, by Brodeur and Ware (1992), found that the long-term variation in biomass of macrozooplankton was a result of bottom-up controls by the physical environment. However, Shiomoto and colleagues proposed an opposite view (Shiomoto et al. 1993). They reasoned that interannual variations in pink salmon could not be accounted for by concomitant changes in productivity and nutrients since these did not correspond to the odd year phenomenon, where even year classes are larger than odd, in pink salmon. Rather these investigators concluded that feeding effects of pink salmon controlled macrozooplankton and phytoplankton biomass.

In the three years of this study for which we have adequate data to describe the spring bloom we found high phytoplankton productivity and biomass in 1996 and lower values in 1995 and 1997 (Table 7). This pattern is consistent with the results of Shiomoto et al. (1997) who reported high phytoplankton productivity in even numbered years in the North Pacific. We also found a lower nitrogen nutrient inventory in 1997 and a high silicate: N+N ratio in this year indicating variations in upper layer ocean processes. We attribute the circulation differences to the impact of the El Niño event that occurred in the Pacific in 1997. During the study there were also differences in the species composition of the bloom that resulted in variations in the carbon to chlorophyll ratio. Primary production along the coast of the Gulf of Alaska is apparently driven by the oceanography of the

North Pacific (Figure 16). The North Pacific Index (NPI; Trenberth and Hurrell 1994) for March explains 81% of the variation in primary production for all available measurements, regardless of year, of Prince William Sound and for Auke Bay in Southeast Alaska. Although the exact mechanism is not known, this relationship suggests that the upper ocean conditions prior to the bloom set the magnitude of bloom production for any given year. The ecological paradigm to explain the relationship involves nutrient supply and the degree of vertical mixing of surface waters (Lalli and Parsons 1993).

Phytoplankton biomass and production apparently directly influence the quantity of zooplankton (Table 7). In the 3 study years the estimated phytoplankton productivity accounts for 97% of the variation in the maximum zooplankton biomass. This is a strong relationship but it is limited by only 3 years of data. Similarly the returns of wild pink salmon and the growth of herring follow the trend set by primary production. The returns of hatchery pink salmon, however, do not follow this trend, suggesting that events in the early life history of the fish are crucial to the survival of adults. The hatchery fish are not directly coupled to interannual variations in ocean processes and productivity since natural processes do not feed them until they are released from the pens. Additional evidence for the direct influence of ocean processes (and climate) on the variation in the strength of the pink salmon population of any year is from an unlikely source. The mass balance of the Wolverine Glacier (in Prince William Sound) since 1965 and the returns of wild pink salmon follow a remarkable similar trend (Figure 17). Climate conditions as primary physical forcing controls on both glacial and ocean processes must lead to this concordance of long-term trends between the fish and the glaciers. The data on the hatchery-raised pink salmon do not show this trend but do show a response to regime shift events (Figure 18).

Finally, the impetus for this research and its associated projects was to study the damage caused by the *Exxon Valdez* oil spill. We did not begin the project until 1994, but from the perspective of phytoplankton production ecology there were no apparent lingering effects of the oil spill. In the study years the timing of the peak of the spring bloom was close to the mean date (day 118) for all previous years of study of the sound (McRoy 1998), indicating a sequence of natural events. In addition the phytoplankton communities are constituted by species that are normal to the waters of the North Pacific Ocean (Horner et al. 1973, Booth et al. 1993). We conclude that climate, through its influence on ocean processes and their control of phytoplankton and nutrients, is the significant source of variability of the food web.

CONCLUSIONS:

1. Physical processes, through climatic conditions and oceanography, drive interannual variability in primary level ecosystem processes.
2. Diatom abundance is controlled by nutrients during the bloom and by zooplankton grazers after the bloom.
3. Phytoplankton Si:N:P uptake ratios observed sound wide were 24.5:15.5:1.
4. Phytoplankton community composition and productivity are keys to carbon transfer to upper trophic levels.
5. Interannual variability in timing of producer-consumer interaction is not a critical factor in the variability of upper trophic level production.
6. Herbivore populations appear to be determined by primary production and phytoplankton community structure rather than "seeding" from the Gulf of Alaska.

7. Pink salmon year class success in directly linked to primary level ecosystem processes. Data are insufficient to determine the relationship between primary production and herring populations.
8. No lingering effects of the oil spill could be found. The sound is robust and healthy from the perspective of phytoplankton community structure and productivity.

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Appendix: List of Papers Presented and Theses

1. Papers Presented (with published abstracts) and in preparation:

Eslinger, D.L., R.T. Cooney and C.P. McRoy. 1997. Physical forcing of interannual variability in plankton populations in Prince William Sound, Alaska: results of a biophysical model. AGU/ASLO Ocean Sciences meeting, San Diego CA, February 1997.

Eslinger, D.L., R.T. Cooney, C.P. McRoy, A. Ward, T. Kline, E.P. Simpson, J. Wang and J.R. Allen. In prep. Plankton dynamics: observed and modeled responses to physical forcing in Prince William Sound, Alaska. SEA Synthesis Volume, Fisheries Oceanography.

McRoy, C.P., D.L. Eslinger, B. Bergeron, D. Clayton and A. Ward. 1995. Seasonal patterns of phytoplankton and nutrients in Prince William Sound, Alaska. AAAS, Arctic Division Science Conference, Fairbanks, AK, September 1995.

McRoy, C.P. R.T. Cooney, A. Ward, E.P. Simpson, D.L. Eslinger, T.C. Kline, S.L. Vaughan and J. Wang. 1997. The architecture of the Prince William Sound ecosystem: nutrients, phytoplankton and zooplankton interactions. American Society of Limnology & Oceanography, Annual Meeting, Santa Fe NM, February 1997.

McRoy, C.P., E.P. Simpson, A. Ward and K. Tamburello. 1999. Interannual variance in seasonal cycles of primary production and nutrients in Prince William Sound. American Society of Limnology & Oceanography, Annual Meeting, Santa Fe NM, February 1999.

Simpson, E.P. and C.P. McRoy. 1997. The architecture of the Prince William Sound ecosystem: I. Variability of chlorophyll and nutrient fields. Arctic Division, AAAS Meeting, Valdez AK, September 1997.

Simpson, E.P. and C.P. McRoy. In prep. The oceanography of Prince William Sound, Alaska: physical and chemical bases of regional phytoplankton variability.

Vaughan, S.L. and C. P. McRoy. 1997. Relating phytoplankton abundance to upper layer water mass variability in Prince William Sound, Alaska. The Oceanography Society meeting, Seattle WA, April 1997.

Ward, A. and C. P. McRoy. 1997. The spring phytoplankton bloom in Prince William Sound, Alaska. The Oceanography Society meeting, Seattle WA, April 1997.

2. Theses:

Ward, A. 1997. A temporal study of the phytoplankton spring bloom in Prince William Sound, Alaska. MS Thesis, University of Alaska Fairbanks. 85 pp.

Simpson, E.P. In prep. In search of the iron curtain. Ph.D. Dissertation, University of Alaska Fairbanks.

Tamburello, K. In prep. Carbon/chlorophyll ratios in phytoplankton: a critical link in the fisheries question. University of Alaska Fairbanks.

Table 1. Summary of data collection, including number of samples and sampling days for 1994 in Lake Bay and 1995, 1996 and 1997 in Elrington Passage, Prince William Sound.

Data Collection	1994	1995	1996	1997	Totals all years
Sampling Dates (Julian)	143-204	107 - 170	97 - 169	91-166	91-204
Sampling Depths	0, 5, 10, 25, 50, 75	0, 5, 10, 25, 50, 75	0, 5, 10, 25, 50, 75	0, 5, 10, 25, 50, 75	0, 5, 10, 25, 50, 75
No. Sampling Days	61	64	73	73	271
CTD Casts	71	63	73	73	281
Secchi Depth Measurements	71	63	73	73	281
Chlorophyll *a* Measurements	355	372	437	435	1870
Size Fractionation Measuremen	0	0	68	219	287
Nitrate + Nitrite Measurements	355	372	438	435	1600
Silicate Measurements	355	369	438	435	1597
Phosphate Measurements	355	372	438	435	1600
Species Composition and Abundance	22	73	80	110	285
Carbon Biomass Measurements	355	68	80	110	613
Stable Isotope Measurements			383	152	535

Table 2. Summary of sample collection for 1994, 1995, 1996 and 1997 from oceanographic cruises in Prince William Sound.

Data Collection	1994	1995	1996	1997	Totals all years
No. Cruises	6	5	3	1	15
No. Stations	238	153	112	29	532
Chlorophyll *a* Measurements	0	918	672	174	1979
Size Fractionation Measurements	0	329	0	0	329
Nitrate + Nitrite Measurements	470	918	672	174	2234
Silicate Measurements	470	918	672	174	2234
Phosphate Measurements	470	918	672	174	2234
Species Composition and Abundance	215	760	672	174	1821
Stable Isotope Measurements			206		206

Table 3. List of all phytoplankton taxa, in the upper 50m, from the spring of 1995 and 1996 (Ward 1997) and 1997 (this study) in Elrington Passage, Prince William Sound.

1995 & 1996	**1997**
Diatoms	
Asterionella glacialis	*Asterionella glacialis*
Biddulphia sp.	*Chaetoceros* spp
Chaetoceros spp.	*Chaetoceros convolutus.*
Chaetoceros deciprens	*Chaetoceros decipiens*
Cocconeis sp.	*Coscinodiscus* spp
Eucampia spp.	*Eucampia* spp
Fragilariopsis sp.	*Fragilariopsis* spp.
Grammatophora sp.	*Grammatophora* spp.
Leptocylindrus danicus	*Gymnodinium* spp.
Leptocylindrus minimus	*Leptocylindrus danicus.*
Leptocylindrus spp.	*Leptocylindrus minimus.*
Licmorphora glacialis	*Licmophora glacialis*
Navicula spp.	*Navicula* spp
Pseudo-Nitzschia spp.	*Nitzschia* spp
Rhizosolenia fragilissima	*Nitzschia closterium.*
Rhizosolenia stolterforthii	*Rhizosolenia* spp.
Rhizosolenia spp.	*Skeletonema costatum*
Skeletonema costatum	*Stephanopyxis nipponica*
Stehpanopyxis nipponica	*Thalassiosira nitzschioides*
Thalassiosira nitzschioides	Unidentified centric diatom
Unidentified centric diatom	Unidentified pennate diatom
Unidentified pennate diatom	Unidentified diatom
Unidentified diatom	
Flagellates	
Ceratium furca	*Ceratium furca*
Ceratium spp.	*Ceratium* spp
Dinophysis spp.	*Dinophysis* spp.
Distenphanus speculum	*Ebria tripartita*
Ebria tripartita	*Oxytoxum* spp.
Oxytoxum spp.	*Protoperidinium* spp.
Peridinium spp.	Unidentified flagellate
Unidentified flagellate	Unidentified dinoflagellate
Unidentified silicoflagellate	
Unidentified dinoflagellate	

Table 4. Occurrence of dominant phytoplankton taxa in Elrington Passage during the bloom and post-bloom season (April to mid-June) for all study years.

Taxa	1995 Bloom	1995 Post-Bloom	1996 Bloom	1996 Post-Bloom	1997 Bloom	1997 Post-Bloom
Chaetoceros spp.	+	+	+	+	+	+
Fragilariopsis sp.	o	o	o	o	+	o
Leptocylindrus spp.	+	o	o	+	o	+
Pseudo-Nitzschia spp. (*Nitzschia* spp.)	+	+	+	+	+	+
Rhizolsolenia spp.	+	o	o	+	o	o
Skeletonema costatum	+	o	+	o	+	o
Stephanopyxis nipponica		o	o	o	+	o
Thalassiosira spp.	+	o	+	o	+	+
Unidentified flagellate	+	+	+	+	+	+

Table 5. Summary of quantitative data characterizing the phytoplankton community in Elrington Passage during the spring bloom and early post-bloom season (April to mid-June) for all study years.

Year	1995	1996	1997	Overall
Chlorophyll a (mg m^{-3})				
Mean	4.60	6.19	3.53	4.69
Range	0.3-18.85	0.3-19.84	0.1-13.58	
SD	4.62	5.15	2.45	4.26
n	310	364	450	1124
Carbon Biomass (mg m^{-3})				
Mean	108	209	120	152
Range	6.5-306	7.0-647	3.7-333	
SD	72.0	159	73.0	125
n	68	80	52	200
Abundance (cells ml^{-1})				
Mean	1811	5043	823	2847
Range	292-4738	325-15301	216-1736	
SD	1050	3546	339	2961
n	68	80	52	200

Table 6. Regional new production (upper 50 m averaged) estimated by nutrient depletion.

	Year Loc.	Daily (mg C m^{-} d^{-1})				Annual (C m^{-3} y^{-1})
Months		3-4	4-5	5-6	6-9	
Total	1995 CS	34.37	8.61	3.27	0	1234
Diatom	1995 CS	33.82	15.14	0	0	1216
Total	1995 HE	5.56	24.69	9.92	0	1158
Diatom	1995 HE	6.57	25.16	0	0	818
Total	1995 KN	6.43	11.79	13.32	0.77	1020
Diatom	1995 KN	2.02	21.10	1.50	0.47	660
Total	1995 KS	0	32.12	5.41	1.08	977
Diatom	1995 KS	1.09	36.03	0	1.13	857
Total	1996 CS		17.74	14.64		967
Diatom	1996 CS		21.31	4.87		614
Total	1996 HE		41.88	11.59		1287
Diatom	1996 HE		54.22	0.96		1020
Total	1996 KN		18.18	7.27		640
Diatom	1996 KN		38.81	0		699
Total	1996 KS		21.56	10.80		874
Diatom	1996 KS		42.92	1.04		860

Locations:
CS includes central sound stations north of 60°30"N
HE includes Hinchinbrook Entrance stations south of 60°30"N
KN includes Montague Strait stations north of Knight Island Passage.
KS includes Montague Strait stations south of Knight Island Passage.

Table 7. Comparison of interannual differences in features related to the bottom-up hypothesis of ecosystem control in Prince William Sound.

FEATURE	1995	1996	1997
Initial N+N Content of Water Column (mmole m-2)	604	597	368
Silicate / N+N Ratio	1.55	1.55	3.00
Maximum Phytoplankton Biomass (mg Chl *a* m^{-2})	723	863	423
Year Day of Maximum Biomass	113	116	106
Dominant Diatom Species	*Thalassiosira sp.* *Skeletonema sp.* *Chaetoceros sp.*	*Skeletonema sp.*	*Thalassiosira* sp.
Carbon / Chlorophyll Ratio	23.4	33.8	34.0
Calculated Primary Production During Bloom (g C m^{-2} d^{-1})	2.33	2.75	1.49
Zooplankton, maximum settled volume (ml) from R.T. Cooney	5.61	6.21	4.97
Wild Pink Returns (x 10^6) (M. Willette data)	7.77	7.92	4.49
Herring Growth, fork length of 0 class (mm) in Oct., Zaikof Bay (K. Stokesbury data)	78.19 ±14.77	93.49 ±8.49	75.94 ±7.54

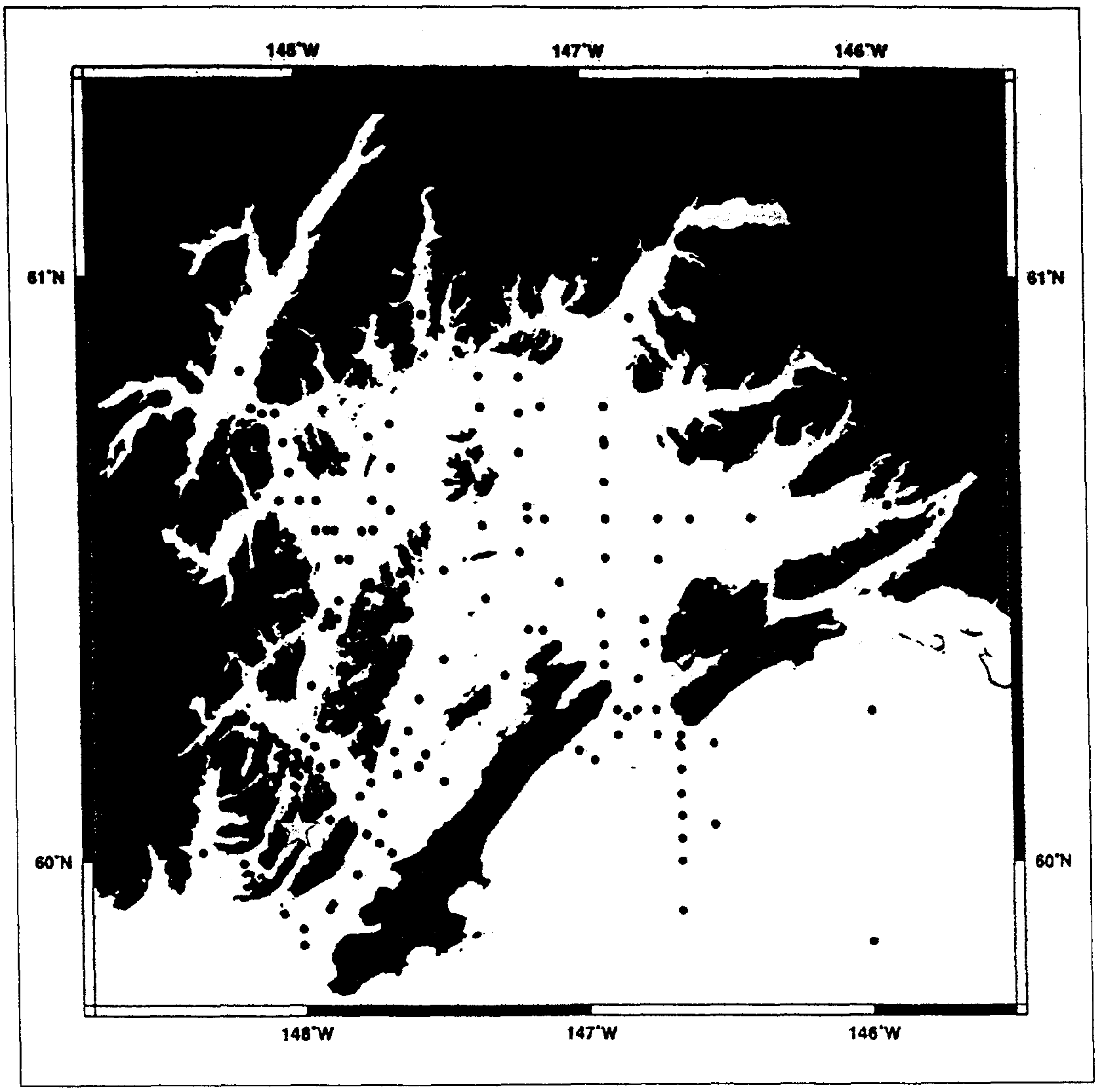

Figure 1. Locations of all stations in Prince William Sound sampled for phytoplankton and nutrients during the SEA project.

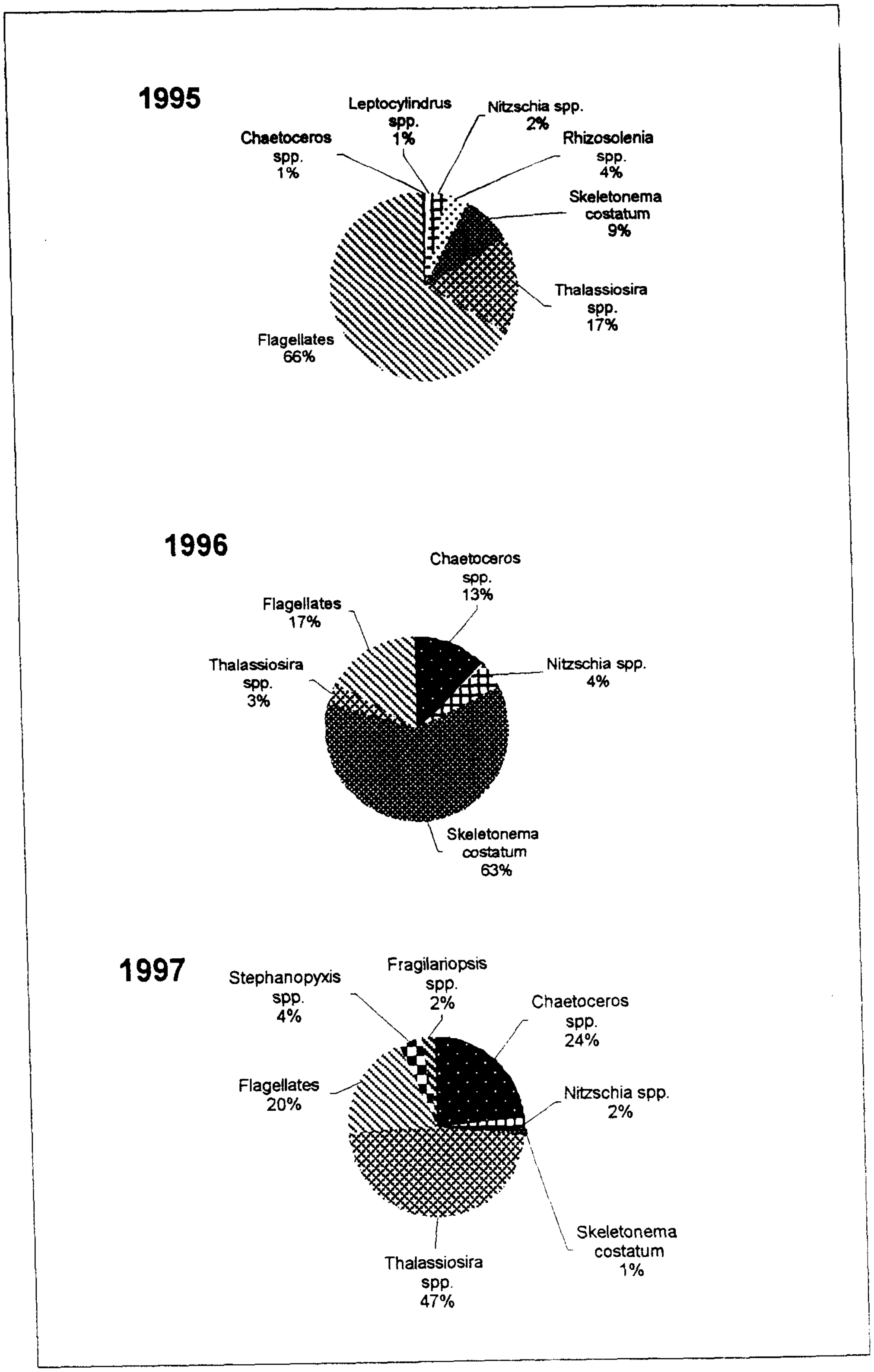

Figure 2. Abundance (%) of major phytoplankton taxa during the bloom period, for all depths, from Elrington Passage, Prince William Sound, for all years of study.

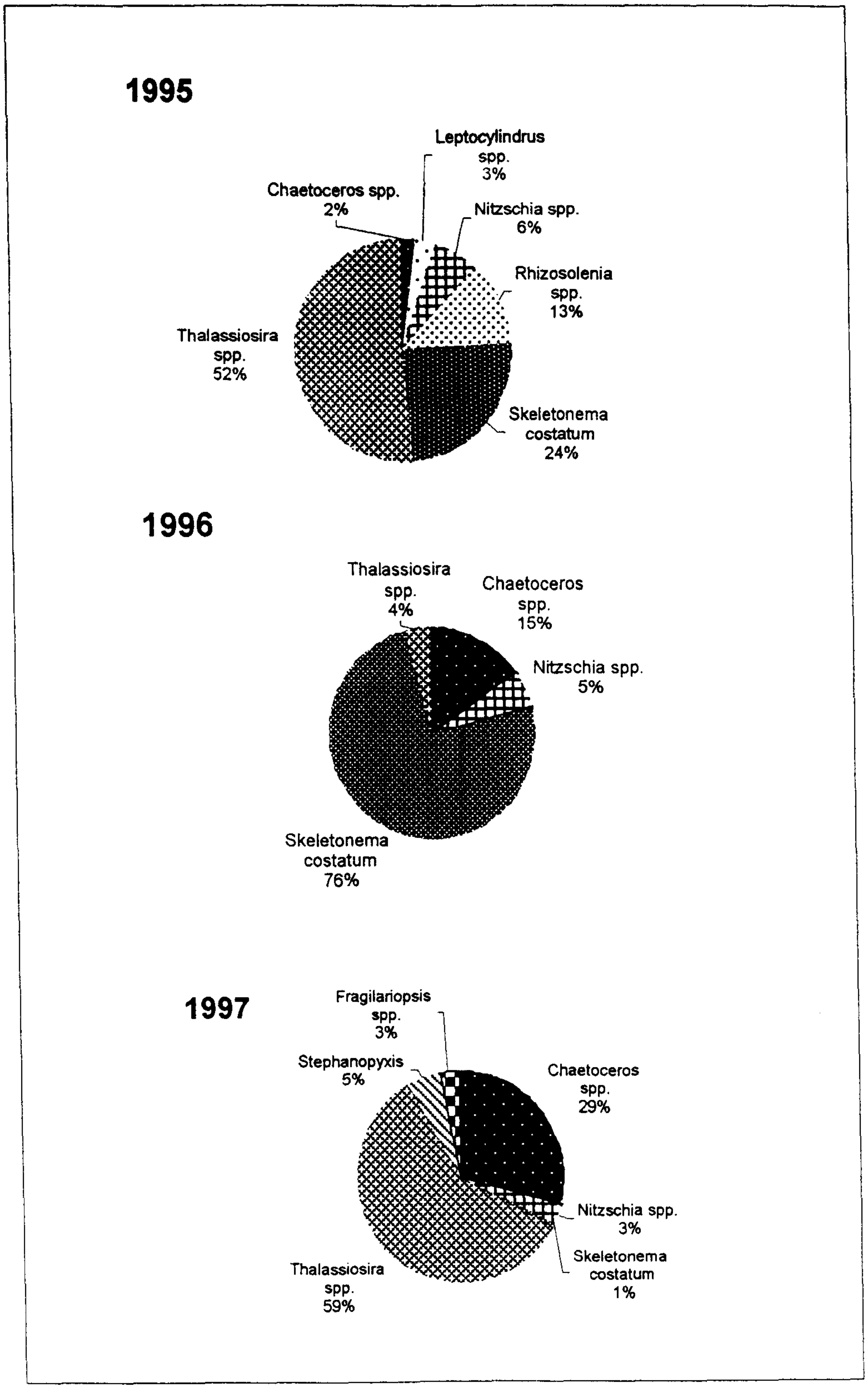

Figure 3. Abundance (%) of major diatom taxa during the bloom period, for all depths, from Elrington Passage, Prince William Sound, for all years of the study.

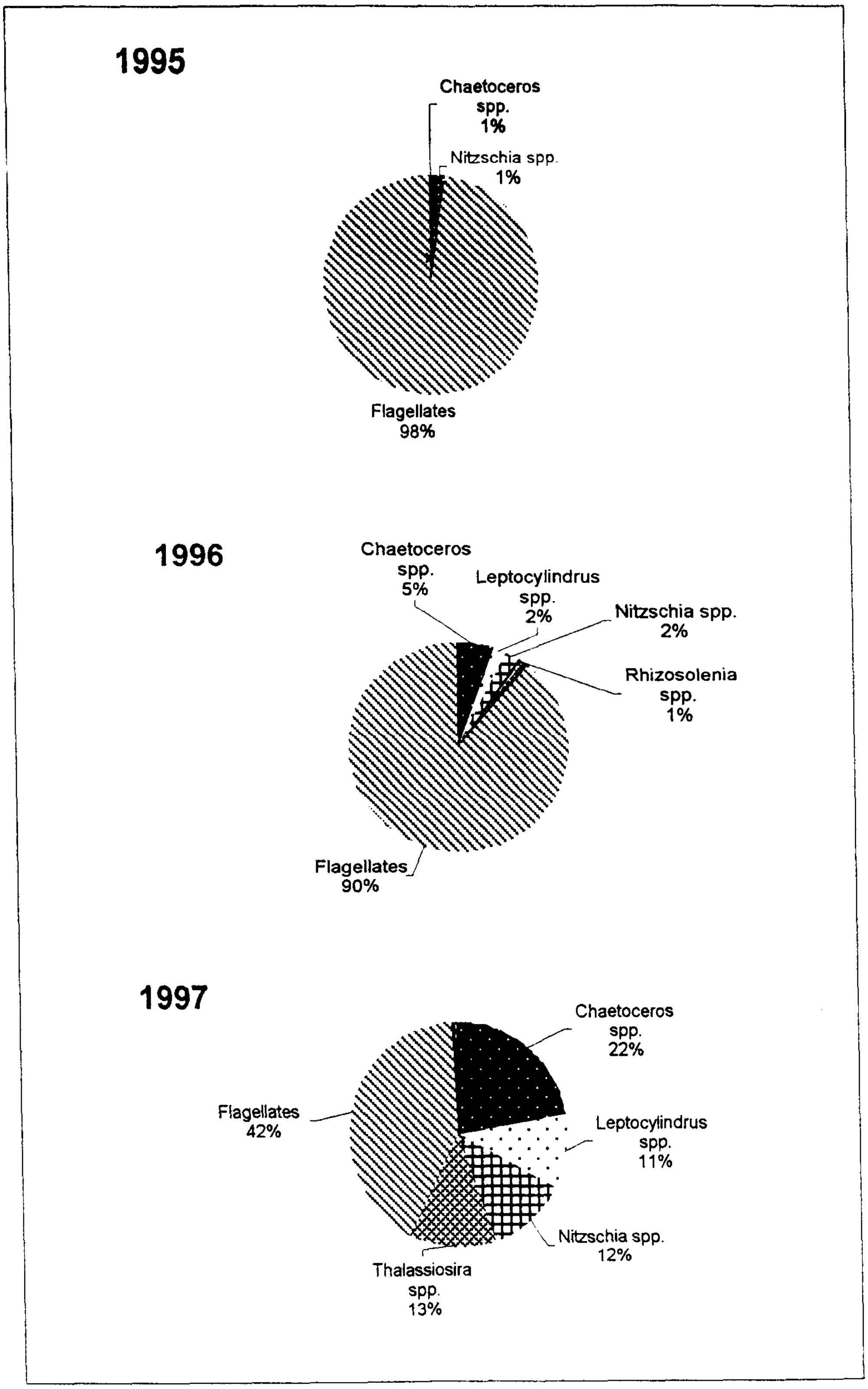

Figure 4. Abundance (%) of major phytoplankton taxa during the post-bloom period, for all depths, from Elrington Passsage, Prince William Sound, for all years of study.

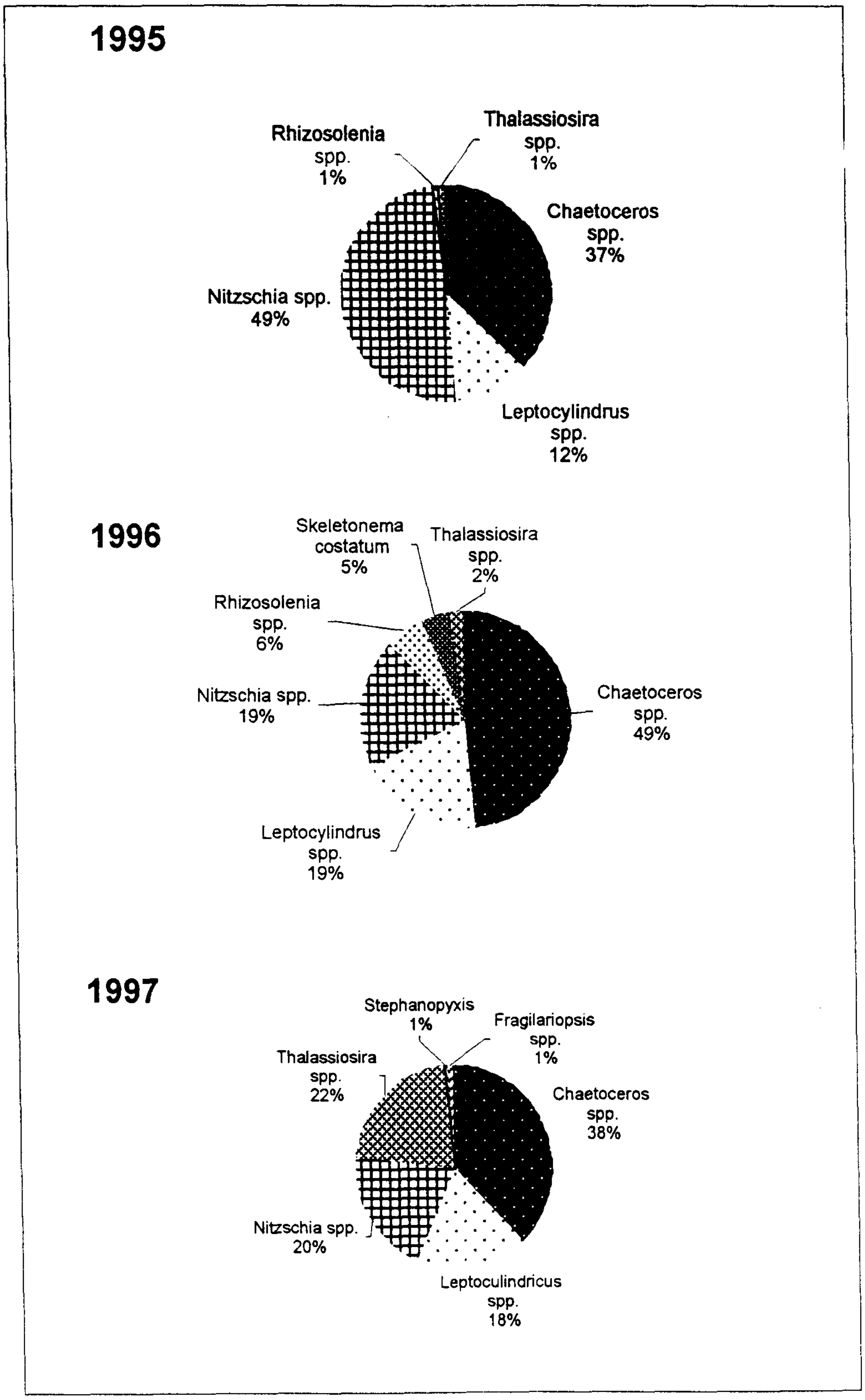

Figure 5. Abundance (%) of major diatom taxa during the post-bloom period, for all depths, from Elrington Passage, Prince William Sound, for all years of study.

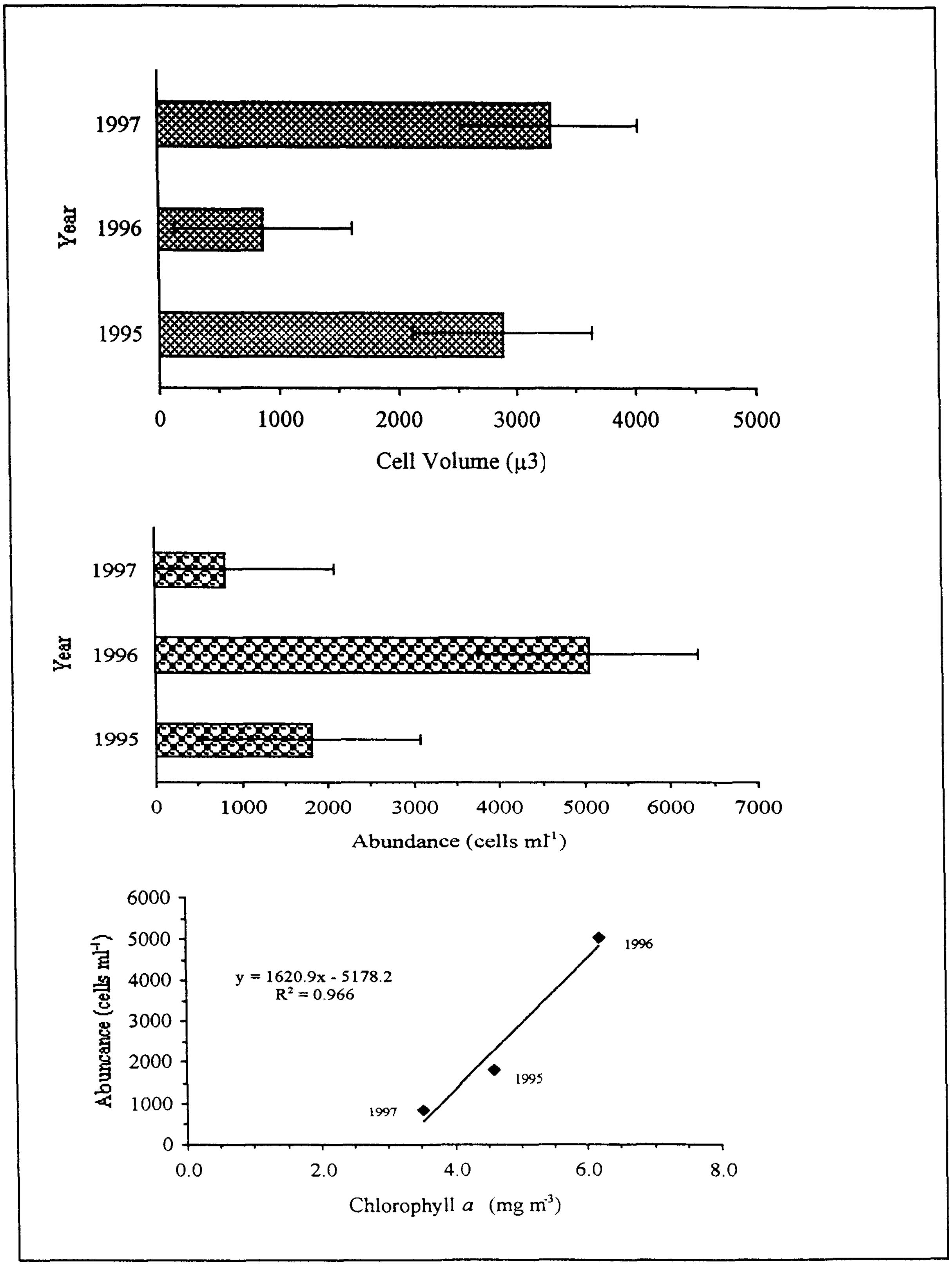

Figure 6. Average cell volume (upper) and abundance (middle) and abundance in relation to chlorophyll *a* (lower) for all sampling depths and times in 1995, 1996 and 1997 from Elrington Passage, Prince William Sound.

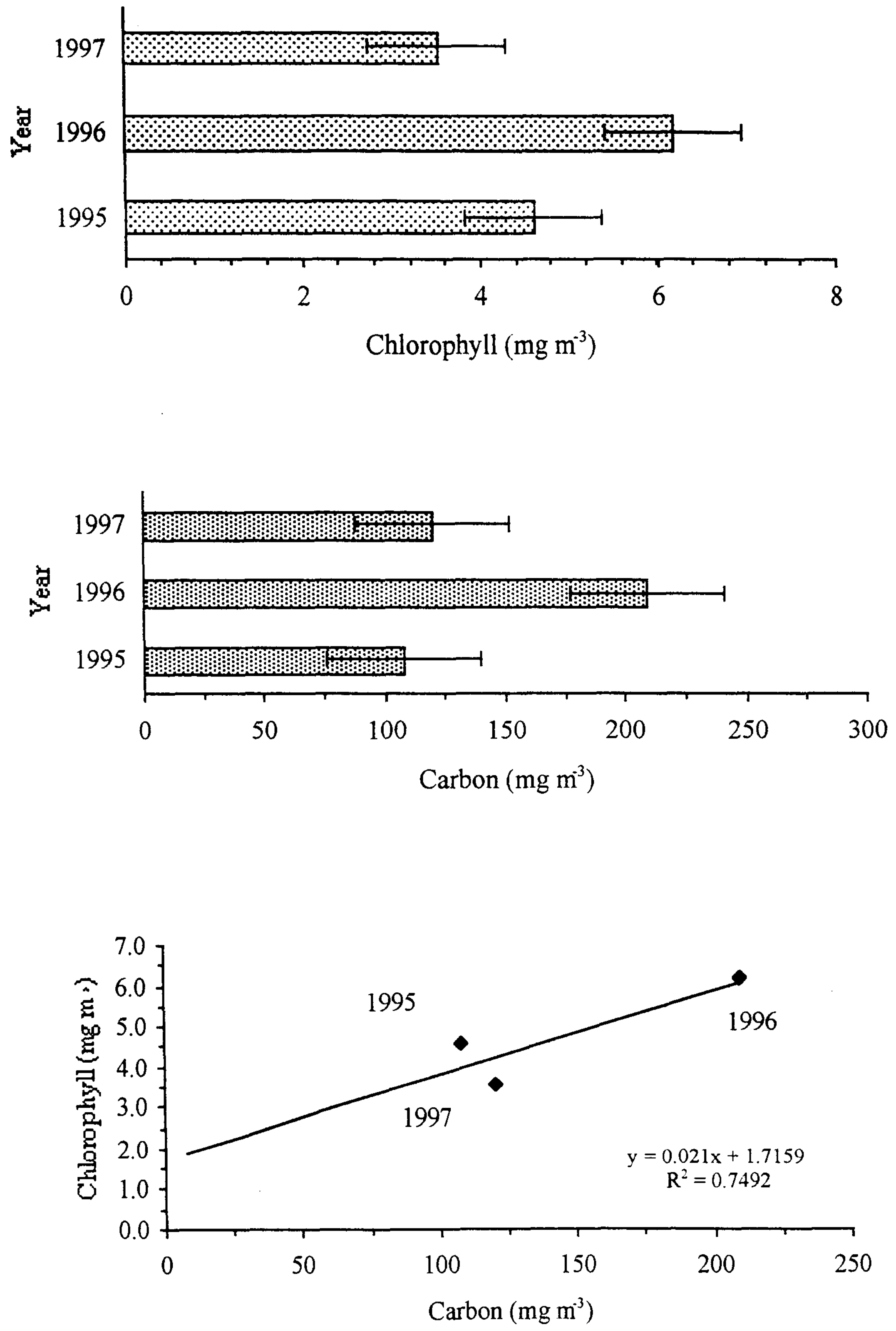

Figure 7. Average chlorophyll *a* (upper), and cell carbon (middle) and their ratio (lower) for all sampling depths and times in 1995, 1996 and 1997 from Elrington Passage, Prince William Sound.

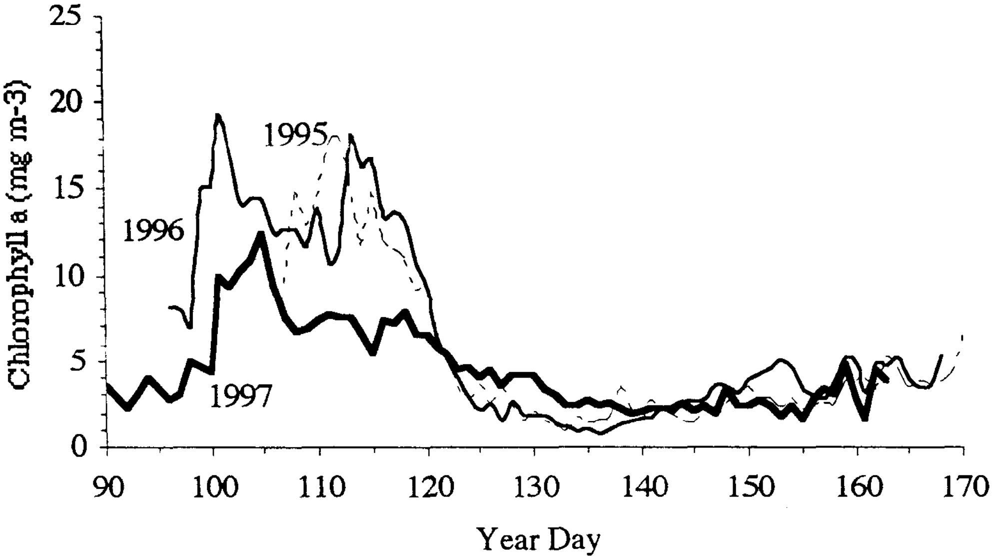

Figure 8. Daily time course of phytoplankton biomass (depth-averaged for upper 10 m) in Elrington Passage, Prince William Sound, for 1995, 1996 and 1997.

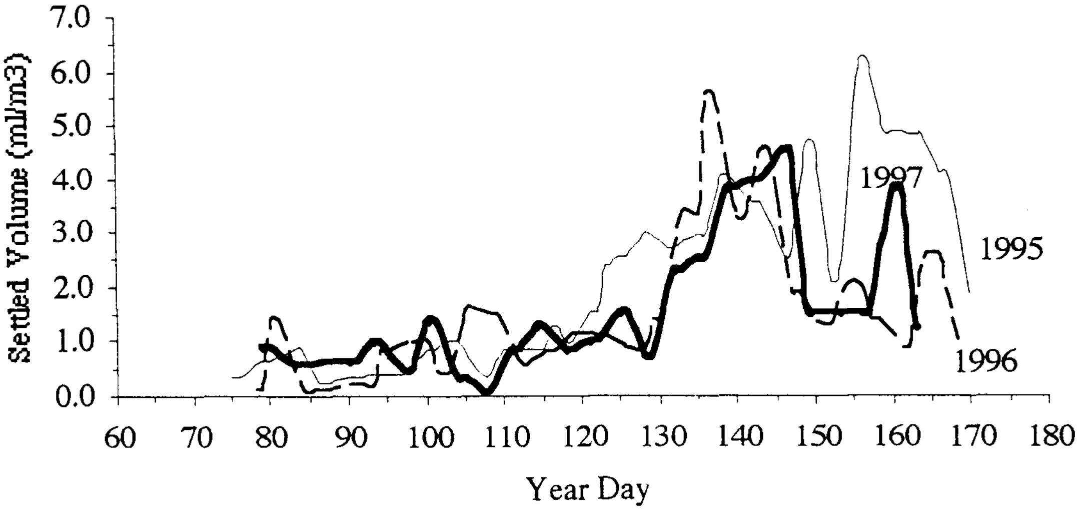

Figure 9. Weekly time course of zooplankton biomass in Elrington Passage, Prince William Sound for 1995, 1996 and 1997 (data from R.T. Cooney).

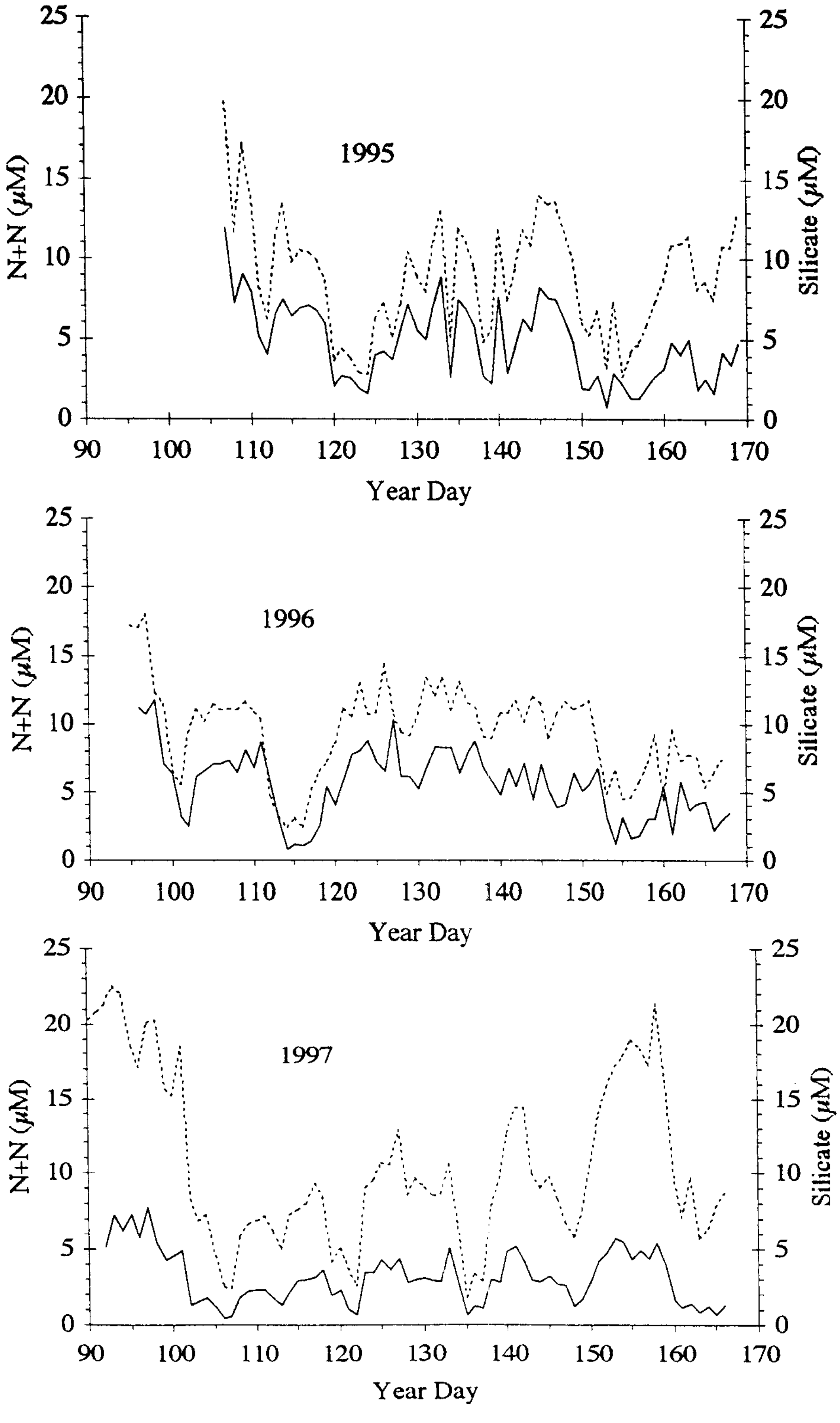

Figure 10. Depth average (upper 10 m) time series of nitrate+nitrite (solid line) and silicate (dash line) in Elrington Passage during the spring bloom and post bloom season for the 3 study years.

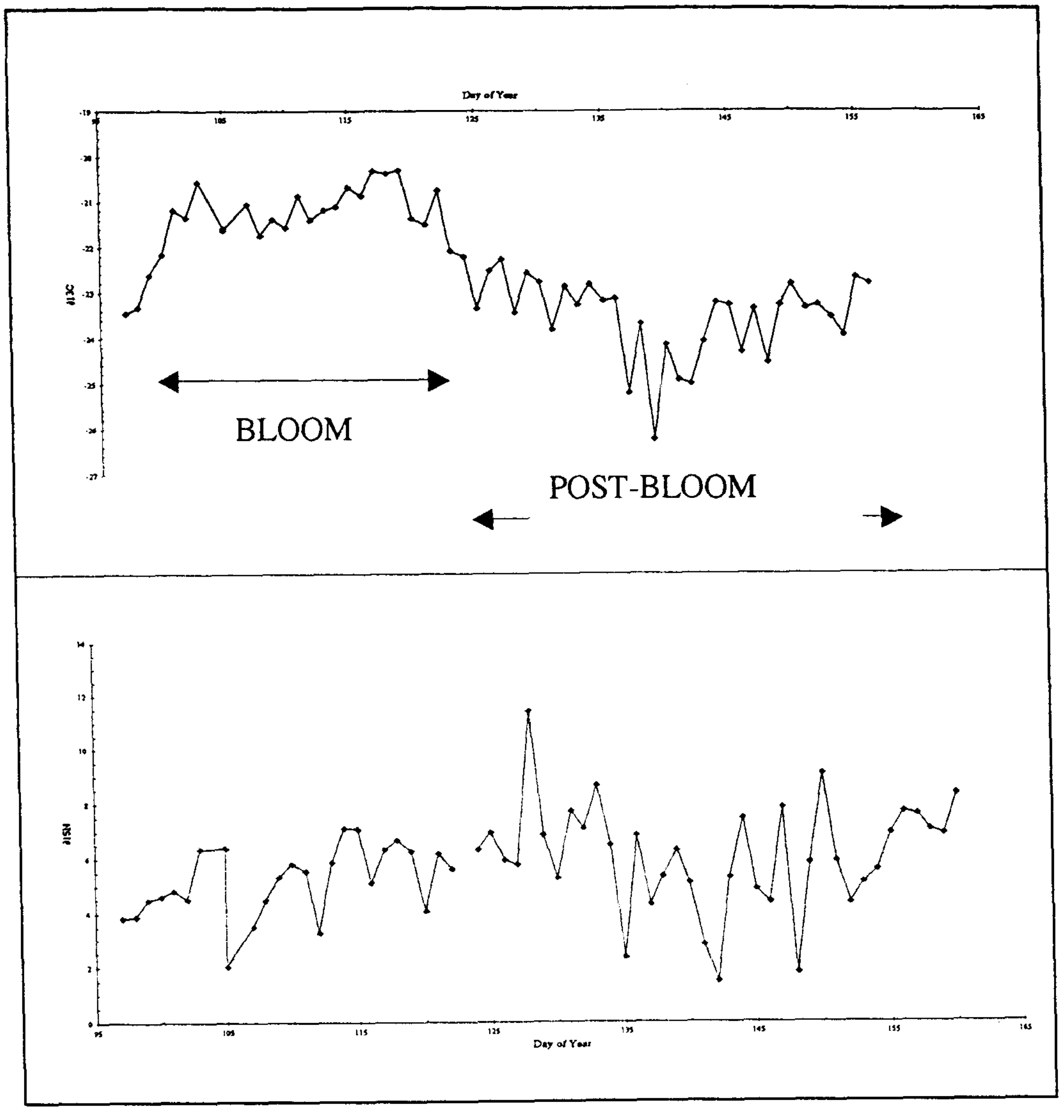

Figure 11. Time series of carbon (upper) and nitrogen (lower) isotope ratios for particulates in surface waters in Elrington Passage, Prince William Sound, 1996.

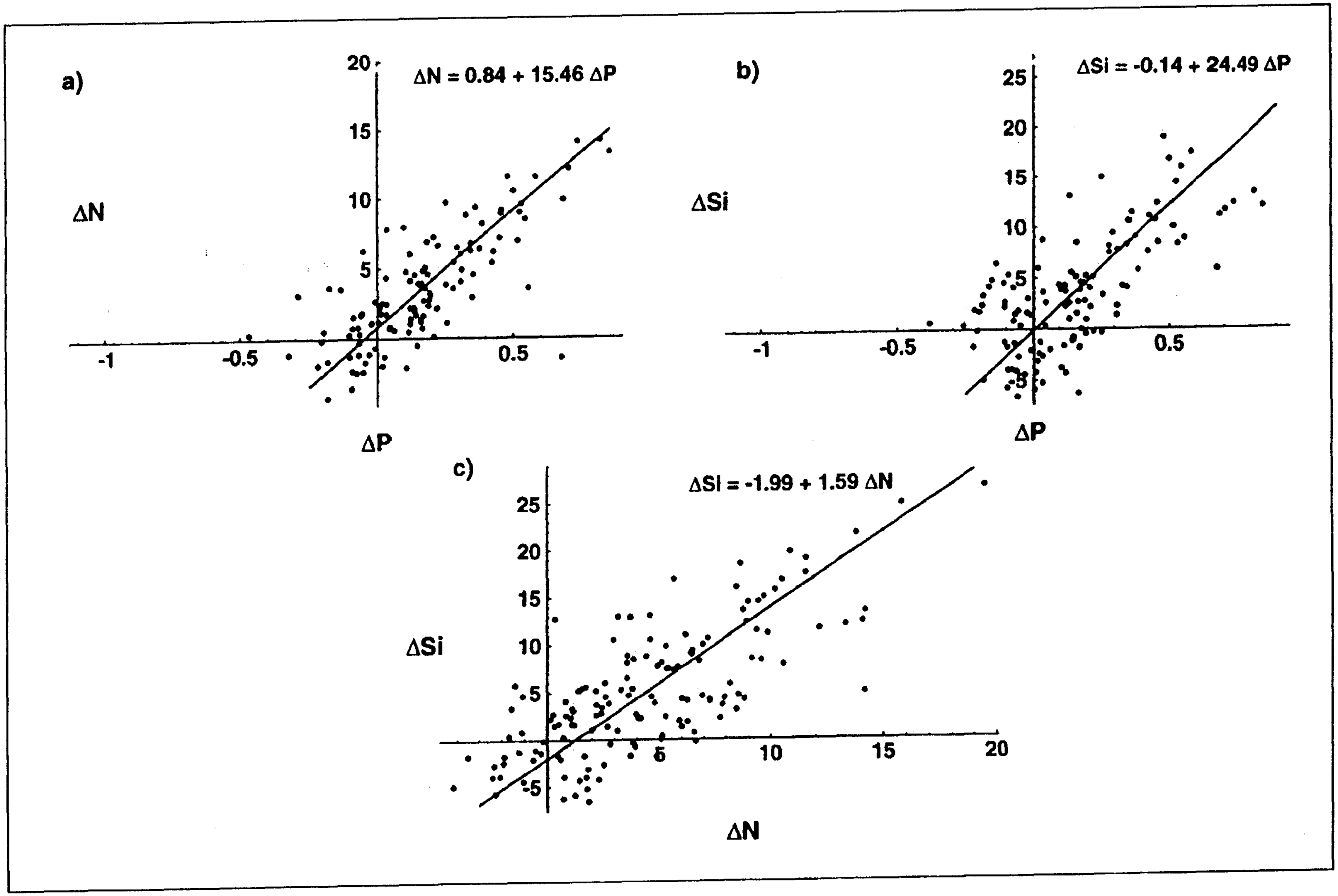

Figure 12. Stoichiometric nutrient uptake relationships for all stations visited twice or more in any year. Anomalous low ΔP (gray values) were excluded from calculations. Si:N:P ratios are 24.5:15.5:1.

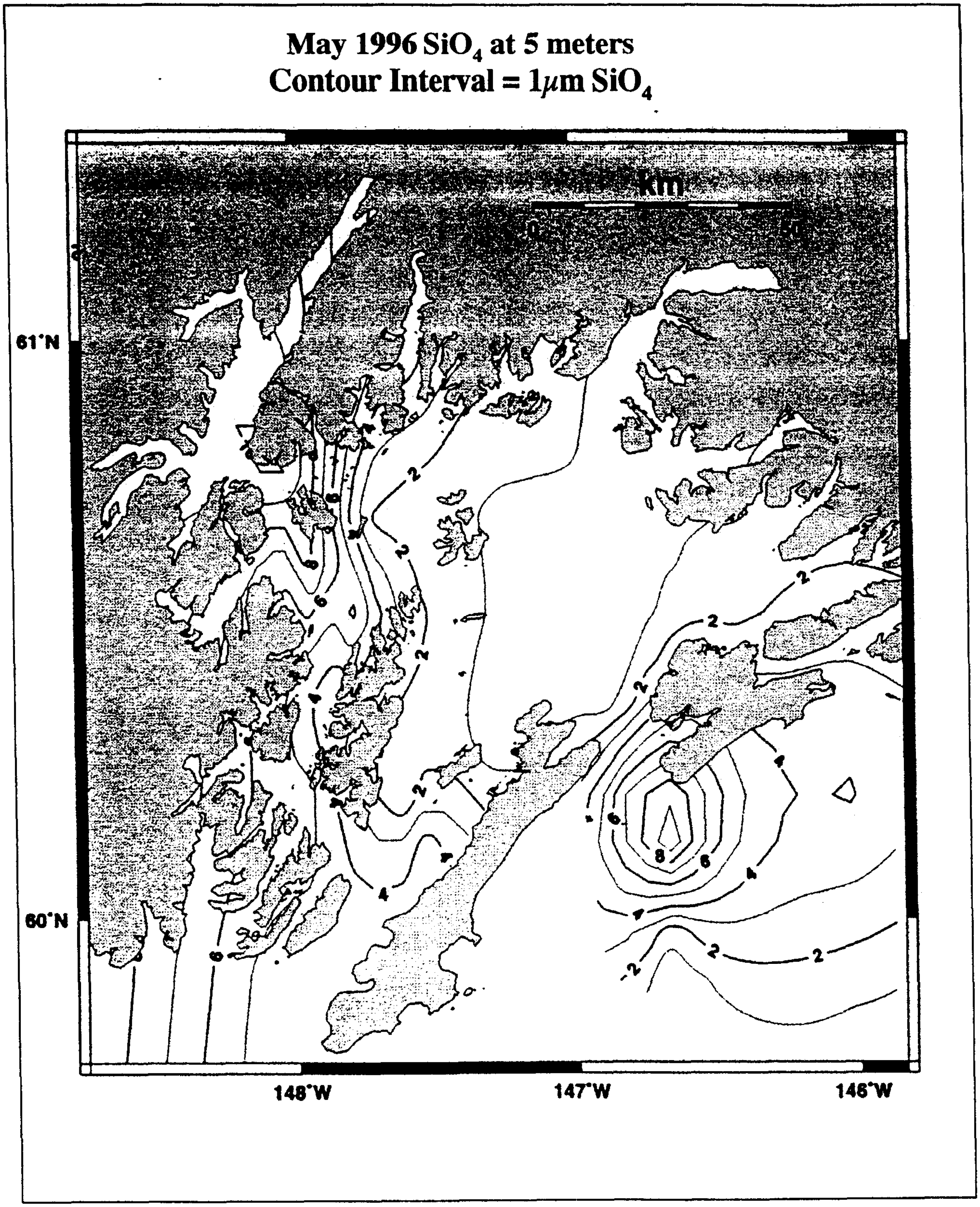
May 1996 SiO_4 at 5 meters
Contour Interval = 1μm SiO_4

Figure 13. Silicate (contour interval = 1 μM) in the 5 m layer for May 1996 In Prince William Sound.

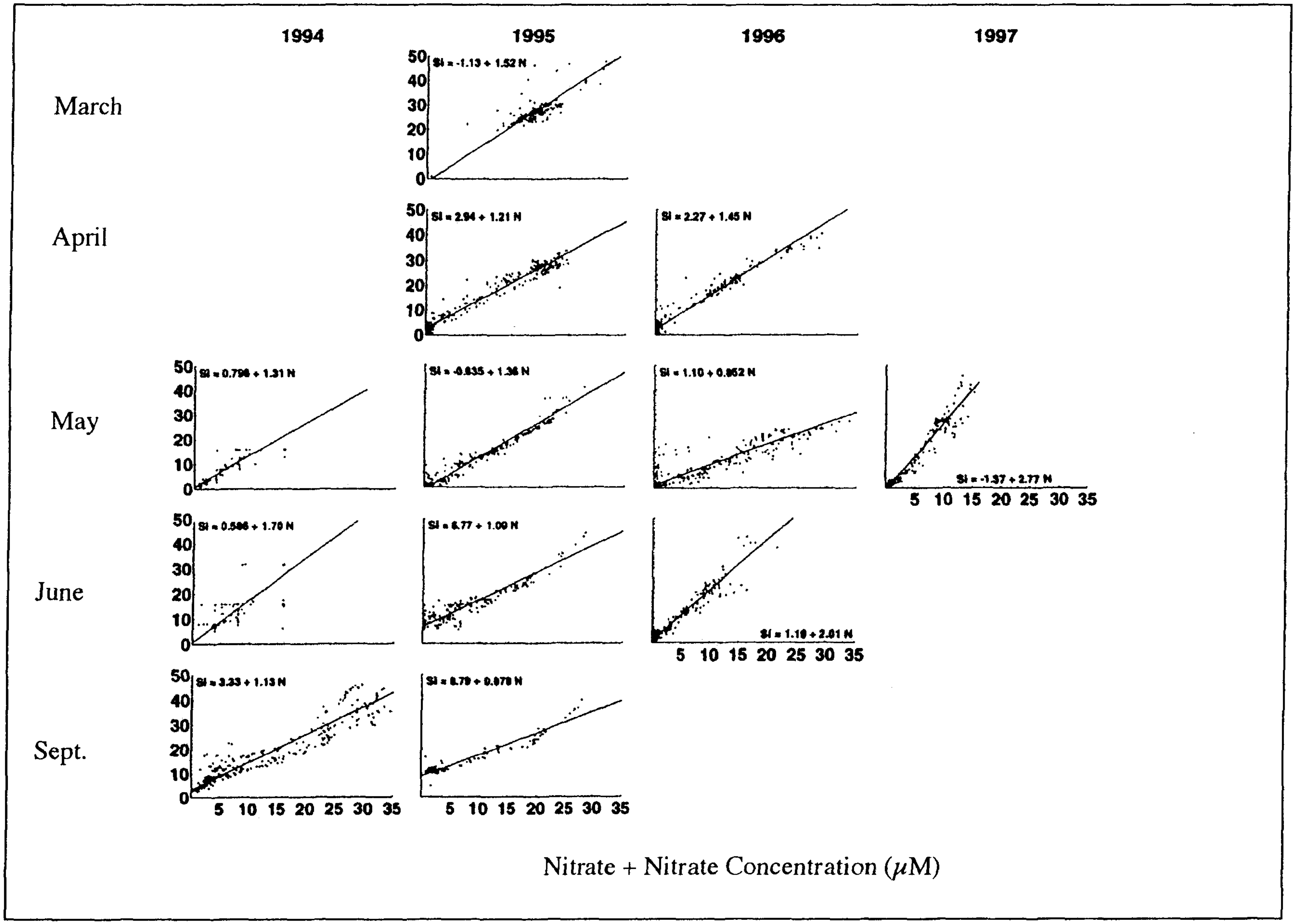

Figure 14. Nutrient-nutrient (Silicate vs. N+N) plot of all data points for each cruise during the SEA project.

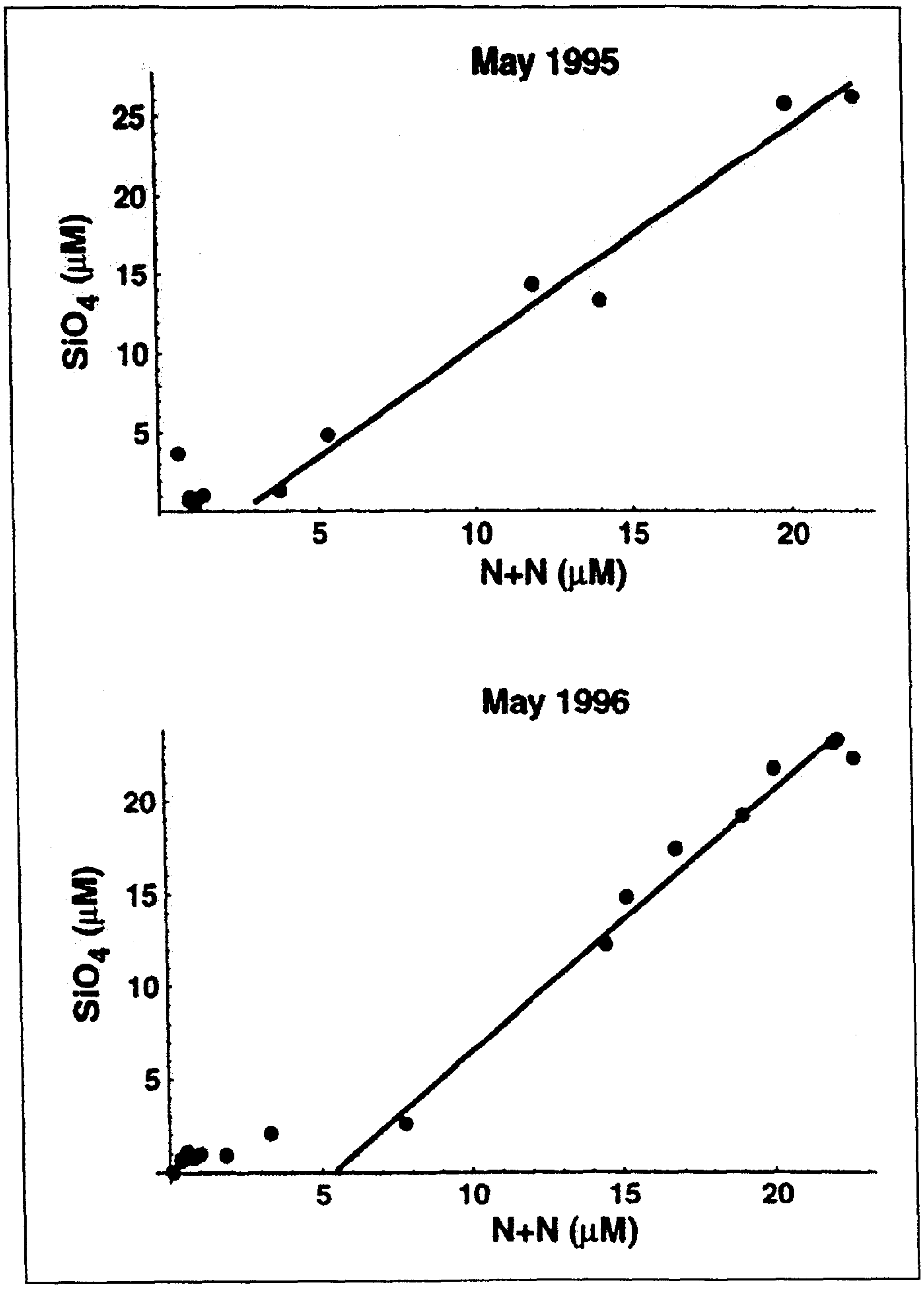

Figure 15. Dissolved silicate vs. N+N in the central basin of Prince William Sound in May.

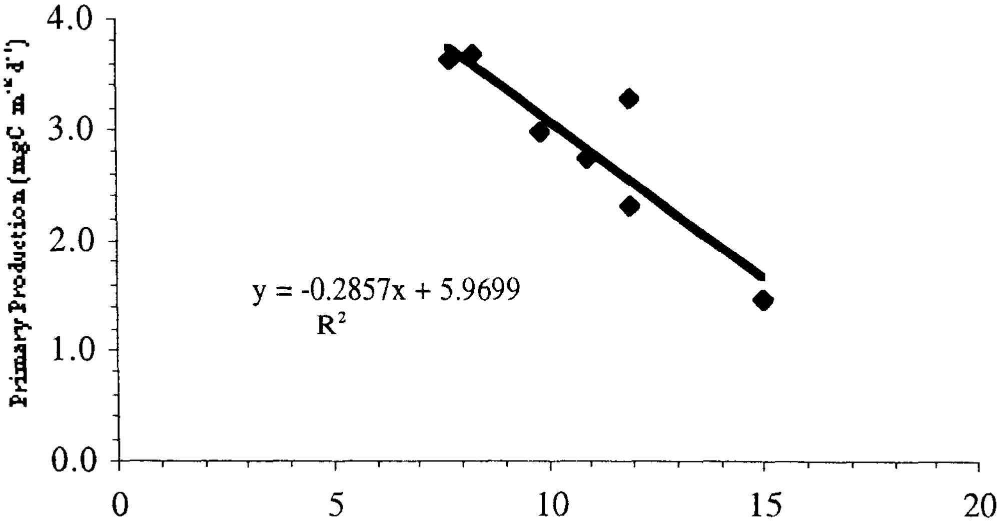

Figure 16. Relationship of the North Pacific Index for March to primary production measurements from Valdez Arm (1971 & 1972), Auke Bay (1986-1989) and Elrington Passage (1994-1997).

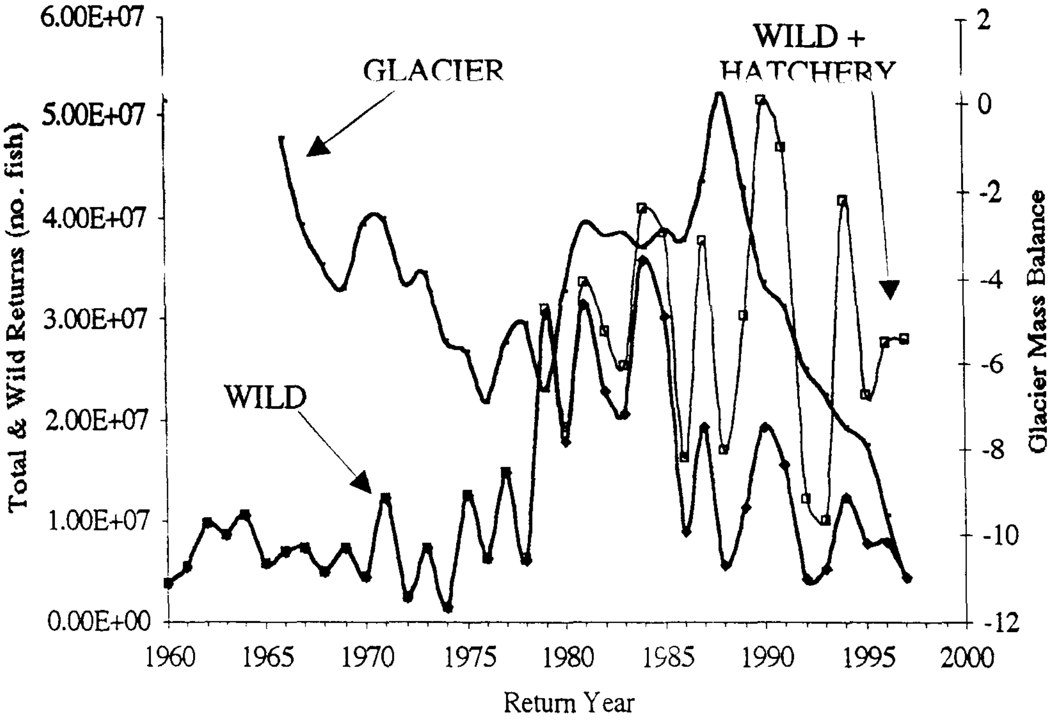

Figure 17. Returns of wild and hatchery pink salmon (ADF&G data) in Prince William Sound and mass balance of Wolverine Glacier (USGS data).

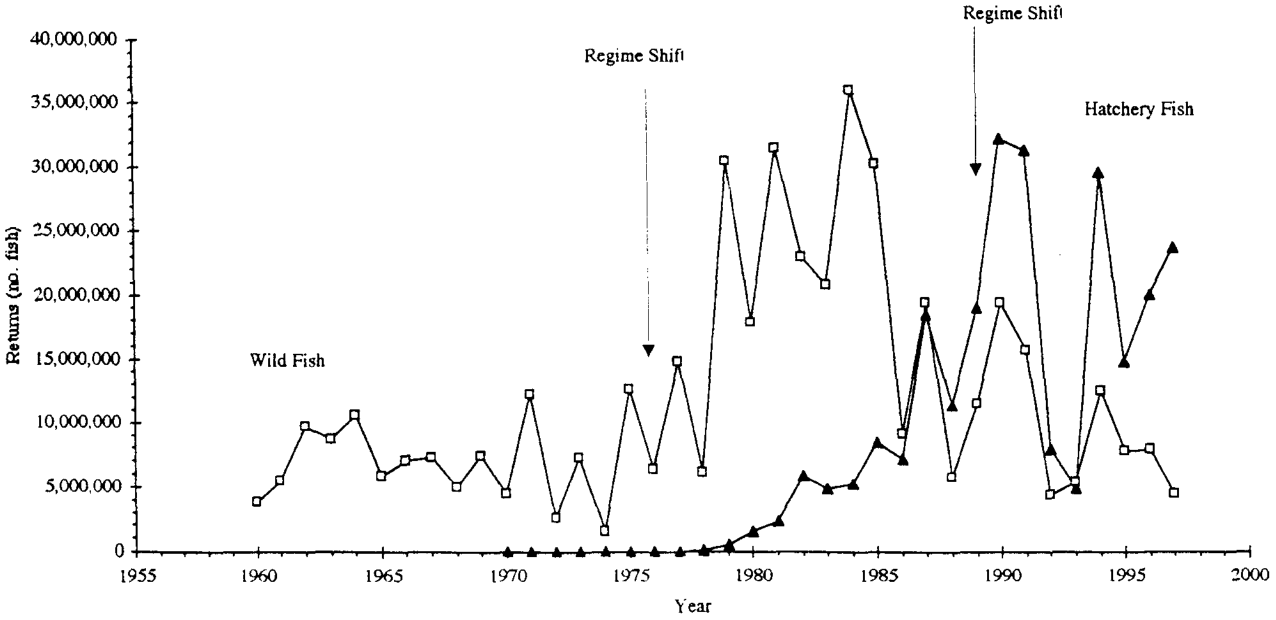

Figure 18. Returns of wild and hatchery pink salmon in relation to regime shift events in the North Pacific Ocean.

A 3-D Coupled Physical-Biological Model and Its Application to the Spring Plankton Bloom of 1996 in Prince William Sound, Alaska

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Abstract

A 3-D coupled biological-physical model of Prince William Sound (PWS) was developed to simulate the spring plankton bloom. The physical model is based on an existing 3-D circulation model developed from the SEA (Sound Ecosystem Assessment) project under forcing of monthly heat flux, freshwater discharge of a line source, daily wind, Alaska Coastal Current (ACC) inflow/outflow and tide. The biological model consists of four compartments: 1) (dissolved organic nitrogen +nitrite) DIN, 2) (phytoplankton) P, 3) (zooplankton) Z, and 4) (detritus) D. A mixed layer model is introduced to calculate vertical mixing caused by wind stirring and surface cooling.

The spring plankton bloom in 1996 was simulated using this coupled model. The model exhibited a spring plankton bloom, which is a feature of a steadily repeating annual cycle of phytoplankton population. The spring phytoplankton bloom starting and ending time and its magnitude compared well with field observations at several layers from 0 m to 50 m at a Station AFK in the sound. In the western sound, the bloom occurred earlier, but was less intensive, and the bloom depth was shallower than in the east. In the central, and eastern sound and Montague Strait, the plankton blooms occurred following the bloom in the western sound, but stronger and deeper. Thus, the phytoplankton bloom lasted longer. There was a shallower but higher phytoplankton concentration core related to an anticyclonic gyre in the eastern sound at the beginning of the bloom, and disappeared later as circulation changed.

1. Introduction

Prince William Sound (PWS or the sound), located along the southern coast of the Gulf of Alaska, is a combination of fjords and estuaries formed by preglacial erosion, glacial excavation and tectonism. Because of its rich resources including seabirds, mammals, salmon, herring, and many other animals, a systematic study of the ecosystem of the sound is essential and timely in order to provide scientific knowledge as a basis for management decisions.

Some observational studies were made before 1989 (Schmidt, 1977; Royer et al., 1979; Niebauer et al., 1994). However, because North America's largest oil spill, caused by the *Exxon Valdez* on March 24, 1989, seriously damaged the ecosystem in the sound and the adjacent coastal waters (such as Cook Inlet and Kachemak Bay), extensive observational programs have since been carried out in the sound. The SEA (Sound Ecosystem Assessment) project was one of the major herring studies following the spill. This interdisciplinary project started in 1994 and focused on salmon, herring habitat, ecology, and physical oceanography. The physical component in SEA project emphasized field program and numerical modeling of the sound.

Among the SEA projects, a major biological research question was the timing and magnitude of the spring bloom of phytoplankton repeating every year. The bloom usually begins from early April and lasts about 30 days, depending on the biological and physical environment. Bakun (1973) found that settled zooplankton volumes, averaged for April/May at a location in Elrington Passage (Station AFK in Figure 2a) pink salmon hatchery, were statistically associated with the April/May Bakun upwelling index computed from a location just outside the sound (60N, 146W). Over the period 1981-

1993, approximately 74% of the interannual variability in an April/May zooplankton time-series was explained by this index (Cooney et al., 1995). The negative/positive upwelling index hypothesized to be related to strong/weak Alaska Coastal Current (ACC) throughflow into the sound. Another equally plausible hypothesis explaining the variance in the multi-year zooplankton time-series was nutrient-limited, bottom-up regulation of zooplankton by food supply (Eslinger et al., 2001). These hypotheses suggest that advection, convection, and vertical mixing are significant modulators of plankton production. Thus, it is important to couple a biological model with the 3-D circulation field. Presently, a 3-D PWS circulation model (Wang et al., 2001) and a one-dimensional biological model (Eslinger et al., 2001) have been developed as parts of the SEA projects.

The 3-D PWS circulation model includes forcing of ocean tide, freshwater runoff, surface heat flux, ACC inflow, and wind stress. The 3-D structure and seasonal cycles of circulation patterns, along with temperature and salinity fields, and the mixed layer depth are calculated in the model. We found that two circulation regimes, cyclonic and anticyclonic, characterize the complex flow patterns that depend on the intensities of the ACC thoughflow, freshwater discharge, and wind stress. A lake-like sound occurs in the April anticyclonic circulation due to the minimum ACC throughflow. A river-like sound occurs in the September-to-winter season cyclonic circulation due to the maximum ACC throughflow (Wang et al., 2001).

Using a critical depth model for the Bering Sea spring phytoplankton bloom (Eslinger, 1990), the one-dimensional biological model was modified and expanded to examine the annual phytoplankton and zooplankton dynamics in the sound (Eslinger et al., 2001). The model domain is the upper 100 meters of a significantly deeper water column (maximum 700 m), with bottom boundary layer, advection, and tidal effects. Solar radiation data are from a radiation model (Frouin et al., 1989). Local meteorological forcing (surface winds, water column temperature and surface heat flux) and biological fluorescence from the C-LAB mooring (location shown in Fig. 2) data set were used to drive and validate the simulations for 1993-1997. All simulations began with identical initial temperature fields and concentrations of nutrients, phytoplankton, and zooplankton. The model described the general features of the seasonal phytoplankton cycle. The modeled interannual variability in the timing of phytoplankton bloom onset, rate of increase, duration, and maximum chlorophyll concentration are compared with the time series of field measurements from the Station AFK in Elrington Passage and C-LAB mooring (location shown in Figure 2a). Some unexplainable questions existed because of lack of 3-dimensional interactions of the physical (advection, tidal mixing, spatial distribution of flow) and biological environments and accurate initial data for phytoplankton, zooplankton, and nutrients.

A coupled 3-D physical-biological model has not been established in the sound. Previously, a passive tracer simulation was performed using a 3-D PWS circulation model (Wang et al. 2001). An application of this model to the passive drifters of zooplankton that overwintered in 1996 qualitatively simulated the distribution of *Neocalanus* as observed by nets and high-frequency acoustics in May 1996 in the north and west regions (Kirsch et al., 2000). Nevertheless, these passive tracer studies of the zooplankton could not fully explain the interactions between physical and biological components. Therefore, in 1999, the Oil Spill Recovery Institute, Alaska (OSRI) supported the development of a physical-biological model.

This study reports the development of a coupled 3-D physical-biological model and investigation of how 3-D circulation modifies the spring phytoplankton bloom, and how the 3-D thermohaline structure of the sound affects the timing and magnitude of the spring bloom. The physical model is based on the existing 3-D PWS model (Wang et al., 2001). The biological NPZD model has one component of phytoplankton, zooplankton, nitrate +nitrite, detritus, respectively, rather than two pieces of phytoplankton and zooplankton, and additional nutrients besides the nitrate +nitrite in Eslinger's model (Eslinger et al., 2001), because this NPZD model is sufficient to describe the spring phytoplankton bloom in the sound. The purpose of this study is not to develop a more accurate biological model than that of Eslinger et al.'s model, rather to extend the 1-D biological model to a 3-D model and examine the interactions between physical environment and biological populations using this 3-D coupled model. Thus, a simple but efficient biological model in this study may be sufficient to simulate the spring bloom processes in the sound. Nitrate +nitrite is the primary nutrient limitation factor of the spring plankton bloom in the sound, although models with additional nutrients can better describe the bloom, especially the post-bloom processes.

In section 2, we introduce the 3-D coupled physical-biological model. In section 3, we describe the model domain and initial and boundary conditions. In section 4, we discusse the model results with comparisons to observations. In section 5, we summarize our investigations and outline some suggestions for further studies.

2. A three-dimensional coupled biological-physical model

2.1. The 3-D circulation model

A modified version of the Blumberg's (1991) ECOMSI (Estuarine and Coastal Ocean Model with Semi-Implicit scheme) is used, with a newly-implemented predictor-correct scheme for time integration (Wang and ikeda, 1997). The model has the following similar features as the Prince Ocean Model (POM; Mellor, 1991): (1) horizontal curvilinear coordinates (not used here); (2) an Arakawa grid; (3) sigma (terrain-following) coordinates in the vertical with realistic bottom topography; (4) a free surface; (5) a level 2.5 turbulence closure model for the vertical viscosity and diffusivity (Mellor and Yamada, 1982); and (6) a mean flow shear parameterization for horizontal viscosity and diffusivity (Smagorinsky, 1963). Differing from POM, ECOMSI uses: (7) a semi-implicit scheme for the shallow water equations (Blumberg 1991); and (8) a predictor-correct scheme for the time integration to avoid inertial instability (Wang and Ikeda, 1996, 1997; Wang et al., 2001). The model equations, time integration method and boundary conditions were described by Wang et al. (2001).

The model domain includes the entire sound with two open boundaries, one at Hinchinbrook Entrance and the other at Montague Strait (Fig. 2a), allowing water exchange with the Gulf of Alaska coastal waters (Schmidt, 1977; Mooers and Wang, 1998). The model grid spacing is 1.2 km (Fig. 2a) which is eddy-resolving because the internal Rossby radius of deformation is about 5km in winter (50km in summer; Niebauer et al. 1994). There are 15 vertical sigma levels, with a relatively high resolution in the upper 50m to resolve the upper mixed layer.

Initial temperature and salinity fields used are based on a typical spring profile observed in the central sound in March 1995 (T/S ranges from 4°C/31.2 PSU at surface to about 6°C/32.3 PSU at 400m; Wang et al., 2001). These were specified to be horizontally uniform. The model was spun-up for one year from these initial conditions under seasonal forcing. The restart file was saved for use as initial conditions for the prognostic runs. Vertical viscosity diffusivity was determined at each time step and each grid point from the Mellor-Yamada 2.5 turbulence closure model. The model forcing includes freshwater runoff of a line source, heat flux, ACC throughflow, wind, and M_2 tide.

2.2. The NPZD biological model

Previous studies examined the following features of the spring plankton bloom in the sound:

(1) The spring plankton bloom of the sound can be explained by the Sverdrup (1953) theory during spring in high latitudes, as solar heating increases and mixing decreases. The mixed layer depth rises above the critical depth and net photosynthesis exceeds net respiration throughout the water column, enabling the phytoplankton to bloom. Thus, a well responding mixed layer model is necessary to examine the bloom.

(2) A strong seasonal cycle and interannual variations of the plankton community of the sound are affected mainly by physical conditions (wind, surface cooling and mixed layer depth, etc.) during a relatively short critical period, e.g. from day 90 to 130 in 1996 (Eslinger et al., 2001).

(3) High vertical resolution is essential to a biological model (Eslinger et al., 2001).

(4) The spring bloom of the sound is nutrient limited.

(5) Advection by circulation and thermohaline change by freshwater runoff can also affect the bloom.

Based on this knowledge, the NPZD biological model described here consists of four compartments (nutrient, phytoplankton, zooplankton, and detritus) with relationships shown in Fig. 1. The equations controlling these compartments are described in the following:

Dissolved inorganic nitration + nitrite concentration, N (mg N m^{-3}):

$$\frac{\partial N}{\partial t} = (-\mathrm{Gr} + \mathrm{Resp} + \mathrm{R_p} + E_c + \mathrm{R_d}) / C_{toN} + \mathrm{Mix} - \mathrm{Adv} - \mathrm{Diff} \tag{1}$$

Phytoplankton biomass concentration, P (mg C m^{-3}):

$$\frac{\partial P}{\partial t} = \mathrm{Gr} - \mathrm{Resp} - \mathrm{R_p} - I_g + \mathrm{Mix} - \mathrm{Adv} - \mathrm{Diff} \tag{2}$$

Zooplankton biomass concentration, Z (mg C m^{-3}):

$$\frac{\partial Z}{\partial t} = I_g - E_c - E_g - \mathrm{M_z} + \mathrm{Mix} - \mathrm{Adv} - \mathrm{Diff} \tag{3}$$

Detritus (fecal pellets) biomass concentration, D (mg C m^{-3}):

$$\frac{\partial D}{\partial t} = E_g - \mathrm{R_d} + \mathrm{Mix} - \mathrm{Adv} - \mathrm{Diff} \tag{4}$$

where Gr is phytoplankton growth rate, the limitation factors of which include light and nutrient: $\mathrm{limit_L}$ and $\mathrm{limit_N}$:

$$\mathrm{Gr} = \mathrm{P} * \mu_0 * \exp(k_g * T) * \min\{\mathrm{limit_L}, \mathrm{limit_N}\} \tag{5}$$

$$\mathrm{limit_L} = (1 - \exp(-\mathrm{k_a} * \mathrm{PAR} / I_0)) * \exp(-\mathrm{k_i} * \mathrm{PAR} / I_0) \tag{6}$$

$$\mathrm{limit_N} = (\mathrm{N} - s_0) / (\mathrm{k_S} + \mathrm{N} - s_0) \tag{7}$$

T is water temperature; μ_0 is the maximum possible growth rate at 0°C; $\mathrm{k_a}$ describes the ability of the phytoplankton to absorb light; I_0 is the minimum light level at which photosynthesis begins; PAR (W/m) is photosynthetically available radiation within the waveband of 400-700nm and is attenuated with depth, i.e. $PAR(z) = PAR(0)e^{-k_{PAR}z}$, where z is depth, and z=0 denotes sea surface,

$$k_{PAR} = k_{Nchl} + k_{chl} \tag{8}$$

$$k_{ch\,l} = k_p * P / C_{toChl} \tag{9}$$

$$k_{Nchl} = k_0 + k_{part} * k_{chl} \tag{10}$$

Resp is the phytoplankton respiration rate:

$$Resp = P * r_0 * \exp(k_r * T) \tag{11}$$

where r_0 is the respiration rate at 0°C.

R_p is phytoplankton reminerization rate, and M_p is mortality rate of phytoplankton, which is not used when Ingest is used:

$$R_p = P * r_{m0} * \exp(k_{rm} * T) \tag{12}$$

$$M_p = m_{p0} * \exp(k_m * T) * P^2 \tag{13}$$

I_g is ingestion rate of phytoplankton by zooplankton, E_c is the excretion rate of zooplankton, and E_g is egestion rate of zooplankton:

$$I_g = Z * g_{r0} * \exp(k_{gr}*T) * (1-\exp(C_{iv}*(P_0 - P))) \tag{14}$$

$$E_c = (A_{Ef} - G_{Ef}) * I_g \tag{15}$$

$$E_g = (1 - A_{Ef}) * I_g \tag{16}$$

R_d is the reminerization rate of detritus, and M_z is mortality rate of zooplankton:

$$R_d = D * r_{fp} * e^{(k_{fp}*T)} \tag{17}$$

$$M_z = m_{z0} * \exp(k_m * T) * Z^2 \tag{18}$$

"Mix" is vertical mixing of P, N, Z and D within the upper mixed layer. The mixed layer depth is calculated for each time step using the Froude number based on the mixed layer model of Thompson (1976). The Froude number of a slab is defined as:

$$F = \frac{u^2 + v^2}{g \frac{\Delta\rho}{\rho_0} h} \tag{19}$$

which shall not be allowed to exceed 1, where $\Delta\rho$ is the density change across the bottom of the slab. The density, ρ, is calculated as a function of water temperature and salinity (Mellor, 1991).

Hourly buoy data at NOAA Station 46060 (location shown in Fig. 2a), including wind and air temperature, were used to calculate the total sea surface heat flux:

$$Q_{ht} = Q_{solar} + Q_{sh} + Q_{lh} + Q_{alw} - Q_{wlw} \tag{20}$$

where Q_{solar} is the solar radiation with wavelength from 250 nm to 4000 nm [PAR(z=0) is included with wavelength from 400 nm to 700 nm]; Q_{sh} is sensible heat flux, Q_{lh} is latent heat flux; and Q_{alw}, Q_{wlw} are air and water long-wave emission, respectively. The algorithm is based on Parkinson and Washington (1979).

Adv and Diff are the large-scale advection and diffusion:

$$Adv = (u\frac{\partial}{\partial x} + v\frac{\partial}{\partial y} + (w - w_\phi)\frac{\partial}{\partial z})\phi \tag{21}$$

$$Diff = (A_x\frac{\partial^2}{\partial x^2} + A_y\frac{\partial^2}{\partial y^2} + A_z\frac{\partial^2}{\partial z^2})\phi \tag{22}$$

where u, v, and w are 3-D sea water velocity from the 3-D circulation model; A_x, A_y are horizontal diffusion coefficients; A_z is vertical diffusion coefficient; ϕ denotes any variable of P, N, Z or D; nutrient and zooplankton sinking rate w_N, w_Z are set to 0; detritus sinking rate w_D is set to a constant of 0.35 (m/h); phytoplankton sinking rate w_P is

$$w_P = w_{\max} \times [1 - tanh(N * 0.549306 / k_S)] \quad (23)$$

The constants used in these equations are listed in Table 1.

Table 1. Values of constants used in the model equations

Parameter	Value	Parameter	Value
A_{Ef}	0.7	C_{iv}	0.246 (l mg C^{-1})
C_{toChl}	40	C_{toN}	5.69
G_{Ef}	0.3	g_{r0}	0.0125 (h^{-1})
K_a	0.057	k_{fp}	0.03 (°C^{-1})
K_g	0.0633 (°C^{-1})	k_{gr}	0.0693 (°C^{-1})
k_i	0.001316	k_m	0.069 (°C^{-1})
k_p	0.0148 (m^{-1} (mg chl $m^{-3})^{-1}$)	k_0	0.159 (m^{-1})
K_{part}	2.35428	k_r	0.069 (°C^{-1})
k_{rm}	0.03 (°C^{-1})	k_S	1.5 (mg N m^{-3})
m_{p0}	0.0049385 (h^{-1})	m_{z0}	.0004283 (h^{-1})
P_0	0.2447 (mg C l^{-1})	r_0	0.003 (h^{-1})
r_{fp}	0.0000923 (h^{-1})	r_{m0}	0.000923 (h^{-1})
s_0	0.0 (mg N m^{-3})	$w_{\max}$	0.18 (m h^{-1})

3. The Numerical Scheme

The horizontal model grid is 1.2 km (Fig. 2a) for both the physical and biological models. There are 15 vertical sigma layers for the 3-D circulation model and 33 vertical layers for the biological model. There is a 3 m resolution in the upper 99 m, with one layer below 99 m. Because the NPZD model has higher vertical resolution (3 m) than the physical model, the output of the physical model (velocity, temperature, and salinity) was interpolated to the vertical grid points of the biological model. Similar to the Eslinger at al.'s model, the coupled model uses a mixed layer model to deal with the rapid changes of the mixed layer depth in response to surface warming or cooling and wind mixing. Thus the important vertical process in spring plankton bloom mechanics at high latitudes can be included in the coupled model. In addition, the mixed layer model uses a different mechanism of vertical mixing (due to vertical instability defined by the Froude number) rather than the turbulent closure model in the 3-D physical model. The time step is 1 hour for the biological model and 100 s for the physical model.

A one-year simulation was conducted using this coupled model. Due to lack of data, the initial condition for the biological model was set to be homogeneous at each grid and each layer, similar to the Eslinger et al.'s (2001) model:

$$P = 20 \text{ mg C } m^{-3} = 0.5 \text{ mg Chl. } m^{-3} \tag{24}$$

$$Z = 0.2 \text{ mg C } m^{-3} \tag{25}$$

$$N = 160 \text{ mg N } m^{-3} = 11.4\,\mu M \tag{26}$$

$$D = 0 \text{ mg C } m^{-3} \tag{27}$$

The open boundary condition for the 3-D circulation conserves the volume transport, and the outflow at Montague Strait was specified to be equal to the inflow from Hinchinbrook Entrance, which was based on moored buoy data at Hinchinbrook Entrance during the SEA project. The M_2 tide harmonic constants for amplitude and phase

(Schwiderski 1980) were prescribed for the surface elevation at both Hinchinbrook Entrance and Montague Strait (Wang et al., 2001).

Because of lack of time series of observations for biological components at Hinchinbrook Entrance and Montague Strait, the open boundary conditions for the biological model were specified to be a zero gradient (no flux) for all biological components (nutrient, phytoplankton, zooplankton, and detritus) at each layer. This means that no matter what throughflow (inflow or outflow) it is at the open boundaries (Hinchinbrook Entrance and Montague Strait), the same concentrations of the inner boundary grid points were used to the outer boundary grid points. Using these conditions, we can know how the ACC throughflow influences the advection of biological components inside the sound, but we do not know those if the biological components from the ACC throughflow differ from those inside the sound. Thus, observations of biological components at Hinchinbrook Entrance and Montague are necessary for future studies.

4. Model Results and Comparison to Field Data

4.1. Patterns of circulation, temperature, salinity, and sea surface heat flux

The modeled surface current (averaged over a M_2 tide cycle), temperature, and salinity of the sound on April 16 are shown in Figs. 2b-d. There is a large anticyclonic circulation in the central sound and three small cyclonic circulations in the central and northeastern sound (Fig. 2b). In the western sound, water flows from north to south, and exits through Montague Strait. In mid-April, water temperature in the northwestern sound is warmer than water in the southeastern sound. The water is fresher in the northwest because of the addition of freshwater runoff from snow and glacier melting along the western coast. Thus, the surface water stratification occurs earlier in the west than in the east. Correspondingly, the phytoplankton bloom starts earlier in the western sound.

Figures 3a-d show the measured hourly air temperature, wind speed, water temperature, and calculated daily mean net sea surface heat flux (including short/long wave radiation and latent/sensible heat flux), respectively, at Station 46060. In addition to a diurnal cycle, the air temperature starts to rise steadily after day 94. At this time, the daily mean net sea surface heat flux also becomes positive and increases with time. This provides a physical environment for the beginning of the phytoplankton spring bloom. The wind was strong during days 95 to 100, after which the wind was calm. Sea surface temperature increased slowly with time and there were fluctuations between days 102 to 106 that might be caused by advection because there was no significant fluctuation of wind, air temperature or surface heat flux during the same period.

4.2. The 1996 phytoplankton spring bloom

Figures 4a-d show a comparison of the observed and modeled time series of phytoplankton biomass as estimated by chlorophyll *a* at 0 m, 5 m, 10 m and 25-50 m average at Station AFK in Elrington Passage (location shown in Fig. 2a). Chlorophyll *a* concentrations of the surface layer (0m, 5m and 10m) show a similar pattern, except for some small differences at the peak. This indicates that the upper 10 m was well mixed during the bloom period. The simulated results show good agreement with field observations on the bloom start, end timing, and peak of the bloom as measured chlorophyll *a*. The bloom started on day 97, reached the peak of 22 mg/m^3, remained at a high from day 99-121, and ended on day 122 for a total bloom period of 25 days. The bloom averaged over 25-50 m denotes an average across the thermocline. The bloom in this layer had a slight delay, when compared with the surface layer. The peak was lower. The simulated start timing and the peak value of the bloom at 25-50 m compares well to the field observations. However, the observed data show a faster decline than the modeled results. This faster decline of biomass in the 25-50 m layer might be caused by advection of more zooplankton into this region, which grazes more phytoplankton. The observation data also show a second peak at day 114 to 116, especially at depth 25-50m. This peak was not captured by the model. Because there was no meteorological data at Station AFK, we had to use the meteorological data of NOAA Station 46060, which is located in the central sound. Since Station 46060 is in the open sea and Station AFK is in a narrow strait channeled by mountains, the differences of meteorological conditions between the two stations can cause the discrepancy in the modeled vertical mixing that brings up nutrients from below the thermocline by local wind or surface cooling to support a second bloom peak.

The modeled and observed N + N in the 0-25 m layer (Fig. 5a) at Station AFK started to decrease earlier and sharper than that in 25-50 m layer (Fig. 5b). This means that the phytoplankton bloom occurred mainly in the upper 25 m. After bloom, the modeled N + N was staying low, but the observed N + N rose up. Those nutrients should be flown from the Alaska coastal water outside the sound. The modeled N + N at 25-50 m is close to the observed, but did not go up after the bloom.

The zooplankton was collected at Station AFK by recording the settled volume of zooplankton to the nearest ml (mini-liter) and by rebottling individual samples for processing. The settled volumes were converted to biomass using a factor of 0.7 g wet weight ml^{-1} (Wiebe et al., 1975). Because the modeled zooplankton has a different unit from the observed data, we drawn two y-axes with different units to combine the modeled and observed zooplankton into one plot (Fig. 6). The comparison of the modeled and observed zooplankton averaged in the upper 50m at Station AFK displays a similar trend that zooplankton kept rising up from the beginning of phytoplankton bloom.

Figures 7a and 7b show the modeled time series over 0 to 60 m of N + N and chlorophyll *a* at Station AFK. Strong surface mixing on days 95 to 97 corresponded to strong wind forcing. As a result, vertical mixing on days 103 to 105 was caused by surface cooling. Those mixing processes uploaded the deep nutrients to the photosynthesis area. After the nutrients were depleted in the euphotic layer, the phytoplankton started to decline and sink.

Figures 8a-d show the time series of the modeled upper 25m averaged N + N, chlorophyll *a*, zooplankton, and detritus over the entire sound. Chlorophyll concentration increased from day 94 to a maximum of $22\text{mg}/m^3$ around day 102, and started to decline after day 107. The bloom ended after day 120 (Fig. 8b). Nitrate + nitrite concentration (Fig. 8a) were high before the bloom and were rapidly depleted. Zooplankton biomass (Fig. 8c) increased steadily throughout the bloom. Detritus also showed a continuous increase and reached a maximum around day 125, and then sharply declined because of the sinking of phytoplankton and detritus.

4.3. Plan and section view of the phytoplankton spring bloom

Figures 9a-d show the plan view of N + N and phytoplankton biomass averaged over the upper 25m on April 7 (day 97) and April 10 (day 100). April 7 was the beginning of the bloom. The bloom in the western sound occurred earlier than the bloom in the eastern sound. Thus, N + N was depleted more in the west. This was related to stronger stratification because of warmer and fresher surface water in the western sound (Fig. 2c and 2d). On April 7, there was an area of low phytoplankton biomass in the central sound that was consistent with the anticyclonic gyre (Fig. 2b). April 10 was the peak of the spring bloom. Phytoplankton biomass in the eastern sound was higher than that in the west because the eastern sound had a deeper mixed layer and more vertical mixing to bring up deeper nutrients.

The plan view of the upper 25m-averaged N + N, phytoplankton, zooplankton, and detritus on April 28 (day 118) are shown in Figs 10a-d. When phytoplankton bloom in the western sound ended, and the bloom in the eastern sound also started to decline. Nutrients were low in the entire sound, while concentrations of phytoplankton, zooplankton, and detritus in Montague Strait, the central and eastern sound were high. The high phytoplankton biomass layer reached a deeper layer (shown in Fig. 11b) in the east than in the west. The more intensive blooms in those areas produced more phytoplankton, and thus, provided a more attractive living environment for the larva and herring

Figures 11a-d show the cross-section (the thick red line in Fig. 2a) view of N + N, phytoplankton on April 7 (day 97) and April 10 (day 110). The phytoplankton bloom in the west began earlier than in the east (Fig. 11b), particularly in the water with a shallower mixed layer. However, the bloom was shallower in the west due to strong vertical stratification that prevents vertical mixing. In the central sound there was a core of high phytoplankton biomass located in the anticyclonic gyre, where mixed layer was relatively shallower and phytoplankton biomass was higher on day 97. This core disappeared on day 110 (Figs. 11c and 11d). The spring bloom in both western and eastern sound reached its peak values on April 10 (day 110), but the depth in the western sound was shallower than in the east (Figs. 11c and 11d). As expected, nutrient concentration was lower where phytoplankton biomass was higher due to nutrients uptake by phytoplankton in the surface mixed layer.

Section views of N + N and phytoplankton on April 13 (day 103) and May 4 (day 124) are shown in Figs. 12a-d. Strong vertical mixing was apparent on April 13 (Fig. 12a, b) compared to May 4 (Fig. 12c, d). Vertical mixing was caused by large fluctuations of surface water temperature (Fig. 3c). In the central and eastern sound, the maximum mixed layer depth reached 55 m, but the mixed layer in the anticyclonic gyre was relatively shallower (48 m). In the western sound, the mixed layer depth increased from west to east. Vertical mixing played a very important role on bringing more nutrients from beneath the mixed layer to the euphotic zone and extending the bloom period. After the mixed layer returned to normal, all the nutrients brought up from the lower depth supported the bloom to last longer. On day 124, the nutrients in the mixed layer were almost consumed, and the bloom went down with low nutrient in the surface layer. Thus, phytoplankton sank down (Figs. 12c and 12d).

5. Conclusions

This study is the first attempt to develop a coupled 3-D physical and biological model in Prince William Sound, Alaska. The model successfully simulated the spring phytoplankton bloom for 1996. This represents a steadily repeating annual cycle of phytoplankton population in the sound. The modeled timing (starting and ending) and the magnitude of the spring bloom compare reasonably well with observed data at several depths over a 50 m water column at Station AFK in Elrington Passage. The spring phytoplankton bloom began in early April, when the surface water absorbed solar heating and the mixed layer became shallow. Another favorable factor promoting the spring bloom was that ACC throughflow in April was at its minimum in 1996 (Wang et al., 2001). This prevented the phytoplankton from massively flowing out of the sound. Thus, the phytoplankton produced in the spring bloom could be retained in the central, eastern sound, and Montague Strait to support overwintering zooplankton.

The phytoplankton bloom occurred earlier, but less intensive in the western sound than in the east. The bloom depth tended to be deeper from the west to the east in the western sound. In the central, and eastern sound, and Montague Strait, phytoplankton blooms occurred later, but also stronger and deeper, which produced more phytoplankton in the bloom.

Because the spring phytoplankton bloom lasted more than 20 days, and phytoplankton flow with water passively, the circulation pattern in the sound was important to redistribute the phytoplankton biomass. There was a shallower but higher phytoplankton concentration core related to the anticyclonic gyre in the eastern sound at the beginning of the bloom, which converged high phytoplankton biomass into the gyre center. This high phytoplankton core disappeared later as circulation pattern changed.

Vertical mixing played an important role in bringing more nutrients from below the mixed layer, which extended the duration of the bloom. In this model study, a surface cooling process deepened the mixed layer in the central sound to more than 50 m from a normal 25 m. Thus, any factors that may cause vertical mixing, such as strong winds or surface cooling during the period of the spring bloom, could significantly change the duration and total phytoplankton production.

Acknowledgements. We appreciate financial support from the Oil Spill Recovery Institute (OSRI) awarded to Jia Wang. We also thank the International Arctic Research Center-Frontier Research System for Global Change for providing computer resources during the course of this study.

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Figure captions

Fig. 1. Biological cycle among the components in the biological model.

Fig. 2. Model grid (a), surface current (b), temperature (c) and salinity (d) on April 16. In Fig 2a, the thick red line is the section as discussed in Figs 10a-d and 11a-d; "■" denotes Station AFK; "o" denotes Station C-LAB; "×" denotes Station 46060.

Fig. 3. Hourly air temperature (a), wind speed (b), water temperature (c), and daily net sea surface heat flux (c) at Station 46060.

Fig. 4. Comparison of observed (dashed) and calculated (solid) chlorophyll *a* concentration at depth of (a) 0m, (b) 5m, (c) 10m, and (d) the mean of 25-50m at Station AFK, in spring of 1996.

Fig. 5. Comparison of observed (dashed) and calculated (solid) N + N concentration at depth of (a) 0–25 m, and (b) 25-50 m at Station AFK, 1996.

Fig. 6. Modeled (dashed, left y-axis) and observed (red solid, right y-axis) zooplankton averaged from 0 to 50 m at Station AFK, 1996.

Fig. 7. Calculated N + N (μM) time series (a) and chlorophyll (mg/m^3) time series (b) at Station AFK, 1996.

Fig. 8. Simulated time series of surface 25m averaged N + N (a), chlorophyll *a* (b), zooplankton (c), and detritus (d).

Fig. 9. Plan view of upper 25m-averaged N +N (a, c), phytoplankton (b, d) on April 7 and April 10, 1996.

Fig. 10. Plan view of upper 25m-averaged N + N (a), phytoplankton (b), zooplankton (c), and detritus (d) on April 28, 1996.

Fig. 11. Section view of N +N (a, c), phytoplankton (b, d) on April 7 and April 10, 1996.

Fig. 12. Section view of N + N (a, c), phytoplankton (b, d) on April 13 and May 4, 1996.

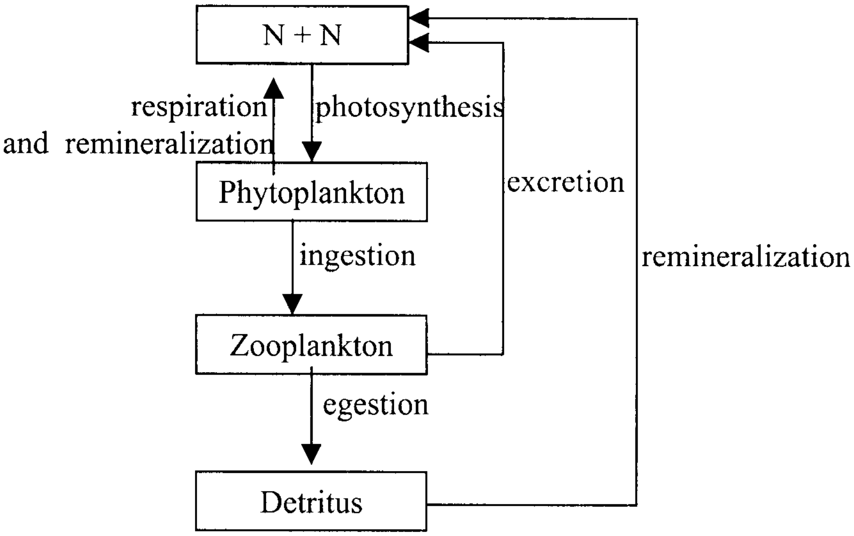

N + N
respiration
and remineralization
photosynthesis
Phytoplankton
excretion
ingestion
remineralization
Zooplankton
egestion
Detritus

Fig. 1.

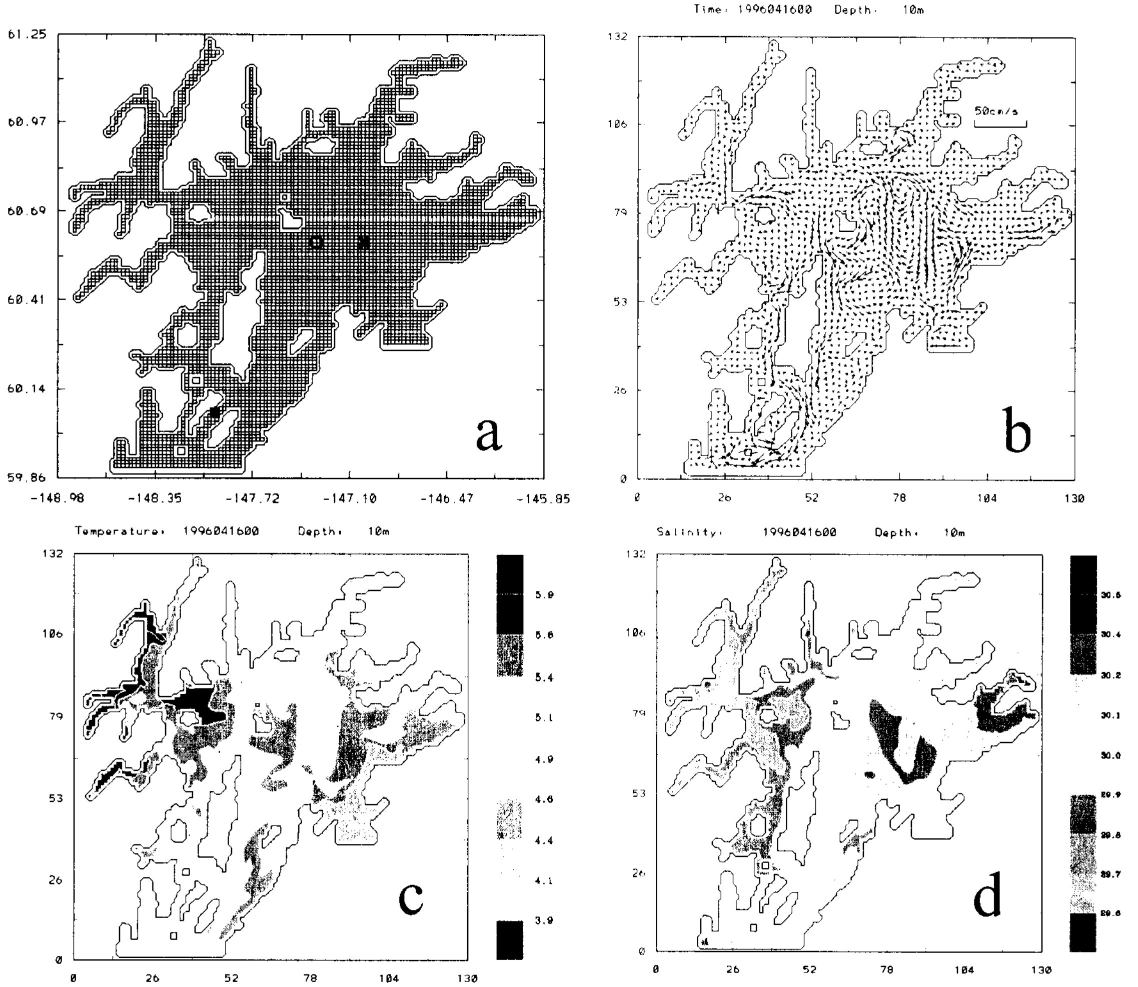

61.25
60.97
60.69
60.41
60.14
59.86
-148.98
-148.35
-147.72
-147.10
-146.47
-145.85
a
Time: 1996041600 Depth: 10m
132
106
79
53
26
0
0
26
52
78
104
130
50cm/s
b
Temperature: 1996041600 Depth: 10m
5.9
5.6
5.4
5.1
4.9
4.6
4.4
4.1
3.9
c
Salinity: 1996041600 Depth: 10m
30.5
30.4
30.2
30.1
30.0
29.9
29.8
29.7
29.6
d

Fig. 2

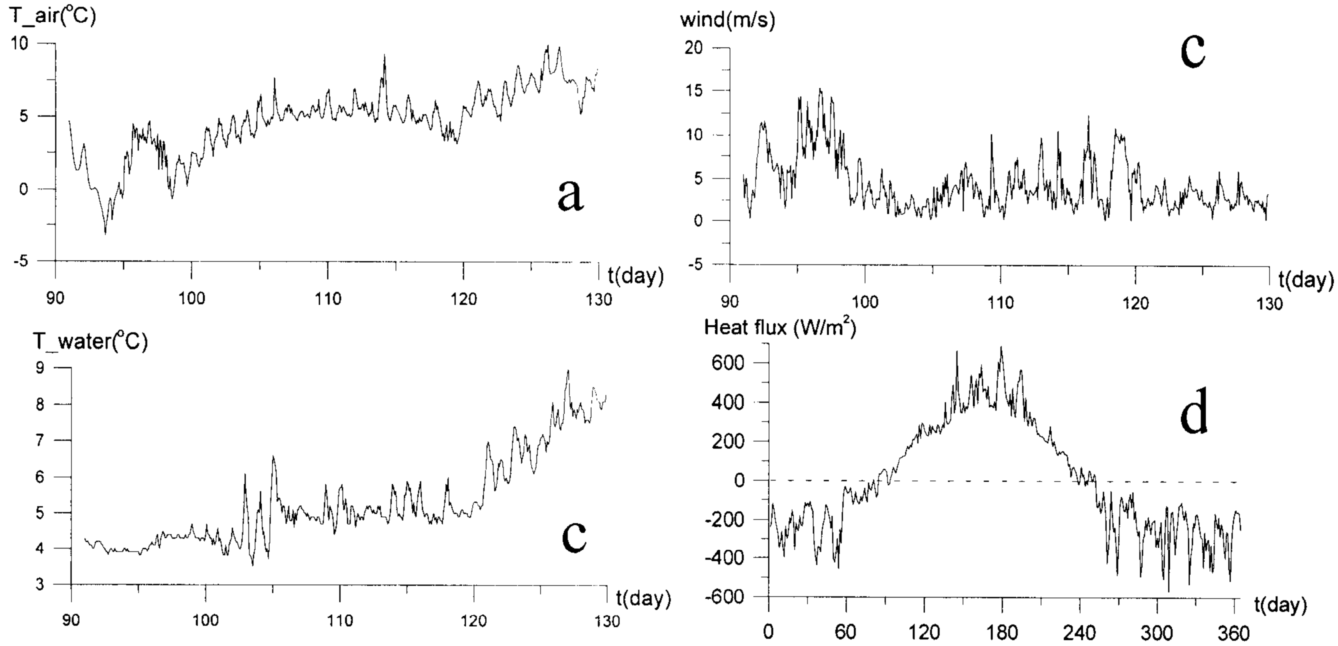
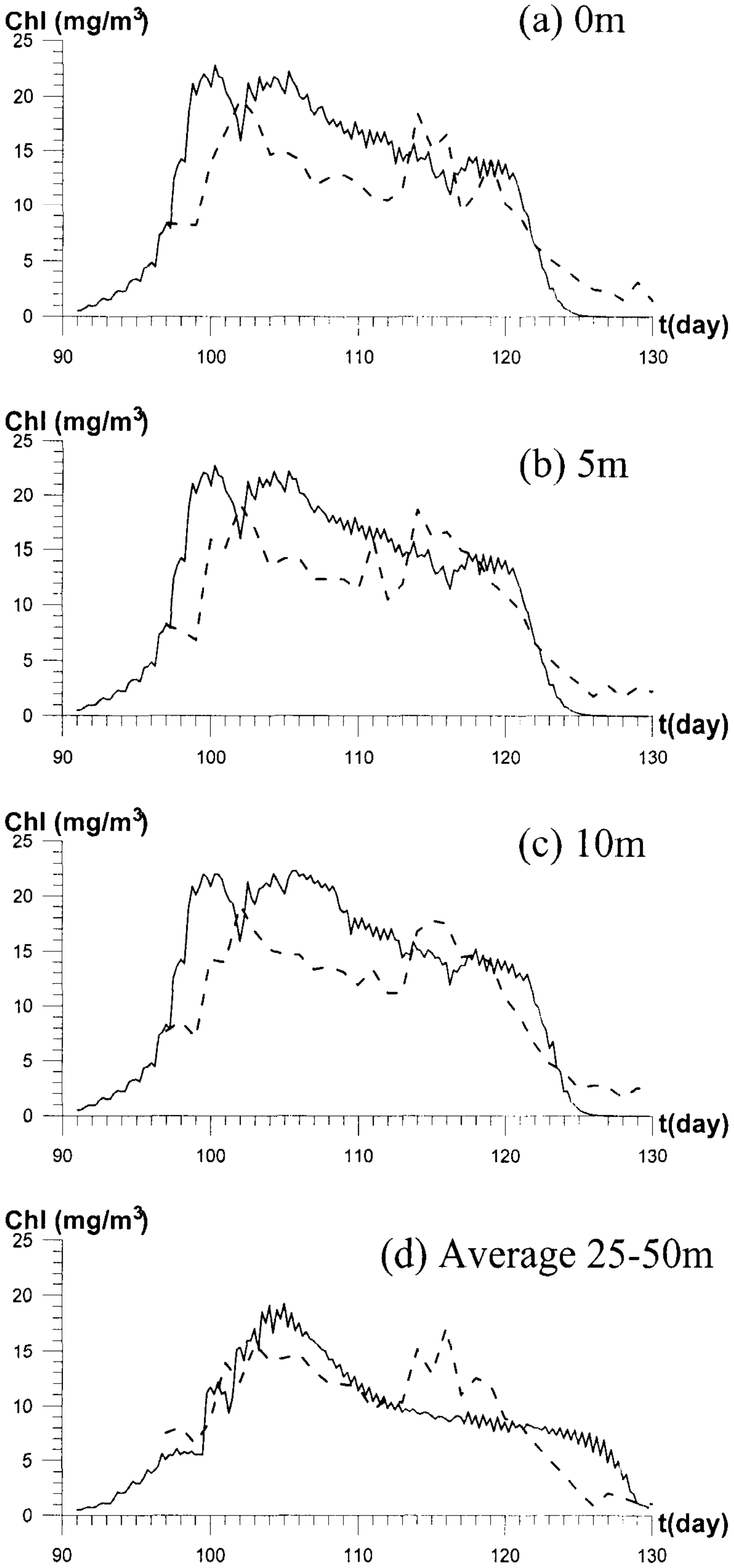

T_air(°C)
10
5
0
-5
90
100
110
120
130
t(day)
a
wind(m/s)
20
15
10
5
0
-5
90
100
110
120
130
t(day)
c
T_water(°C)
9
8
7
6
5
4
3
90
100
110
120
130
t(day)
c
Heat flux (W/m²)
600
400
200
0
-200
-400
-600
0
60
120
180
240
300
360
t(day)
d

Fig. 3.



Chl (mg/m3)
(a) 0m
25
20
15
10
5
0
t(day)
90
100
110
120
130
Chl (mg/m3)
(b) 5m
25
20
15
10
5
0
t(day)
90
100
110
120
130
Chl (mg/m3)
(c) 10m
25
20
15
10
5
0
t(day)
90
100
110
120
130
Chl (mg/m3)
(d) Average 25-50m
25
20
15
10
5
0
t(day)
90
100
110
120
130

Fig. 4

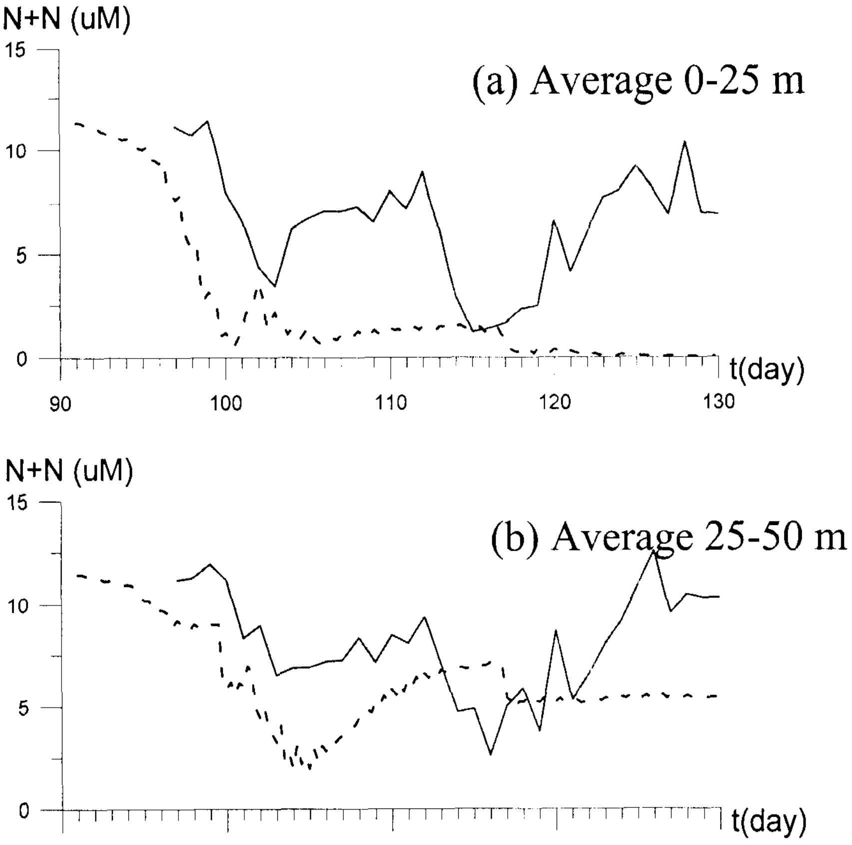

N+N (uM)
15
10
5
0
(a) Average 0-25 m
t(day)
90
100
110
120
130
N+N (uM)
15
10
5
0
(b) Average 25-50 m
t(day)
90
100
110
120
130

Fig. 5

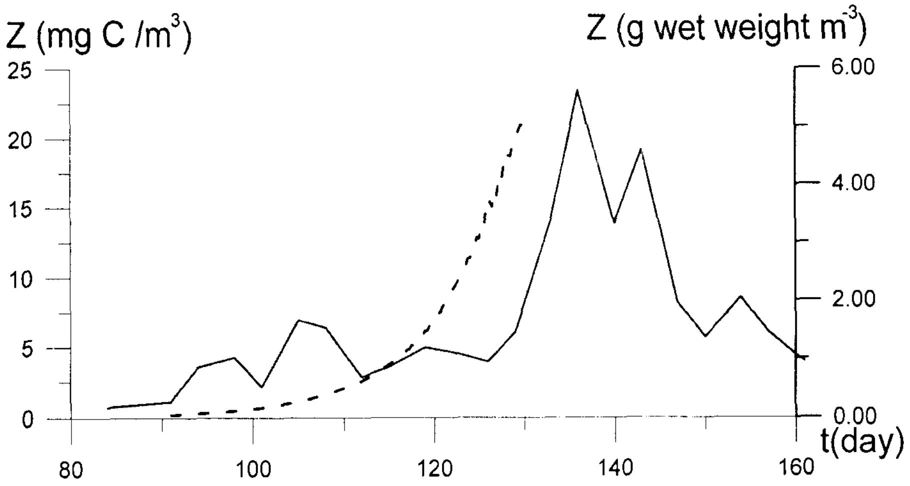

Z (mg C /m^3)
Z (g wet weight m^{-3})
25
20
15
10
5
0
6.00
4.00
2.00
0.00
t(day)
80
100
120
140
160

Fig 6

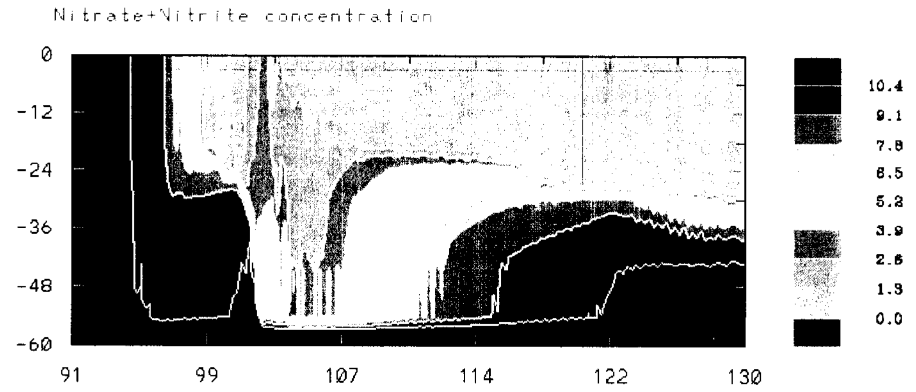


Fig 7a

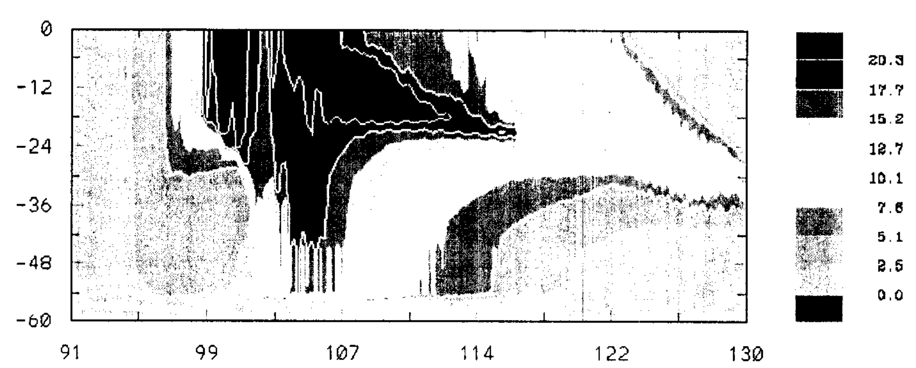


Fig. 7b.

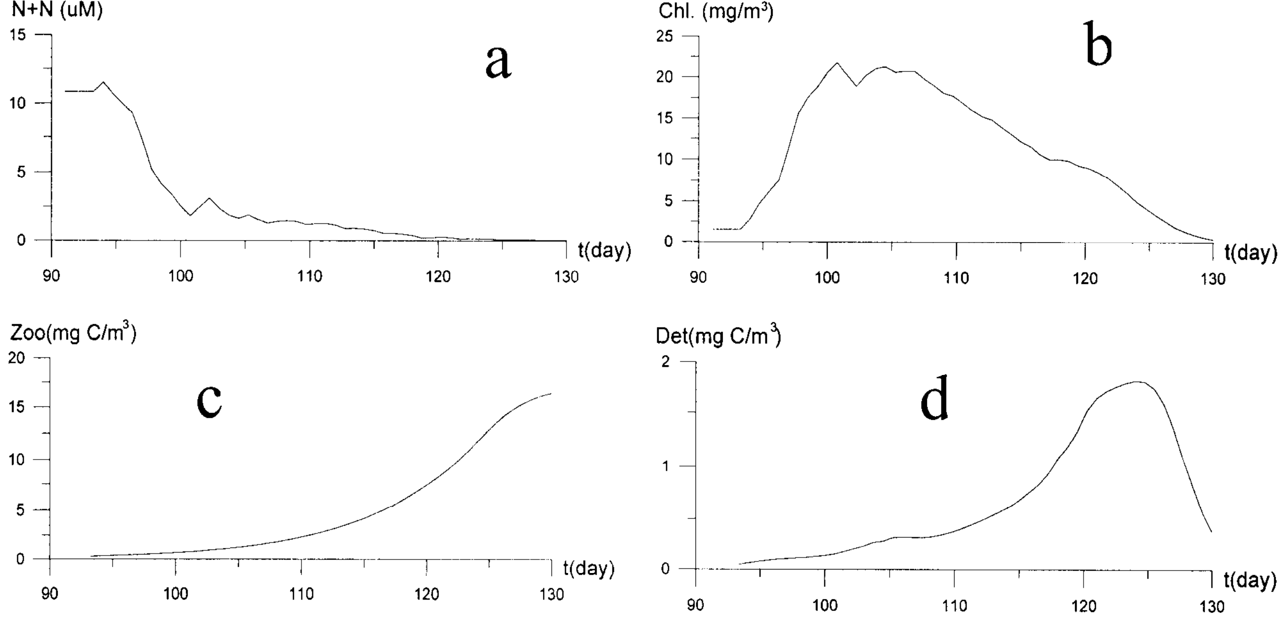


Fig. 8.

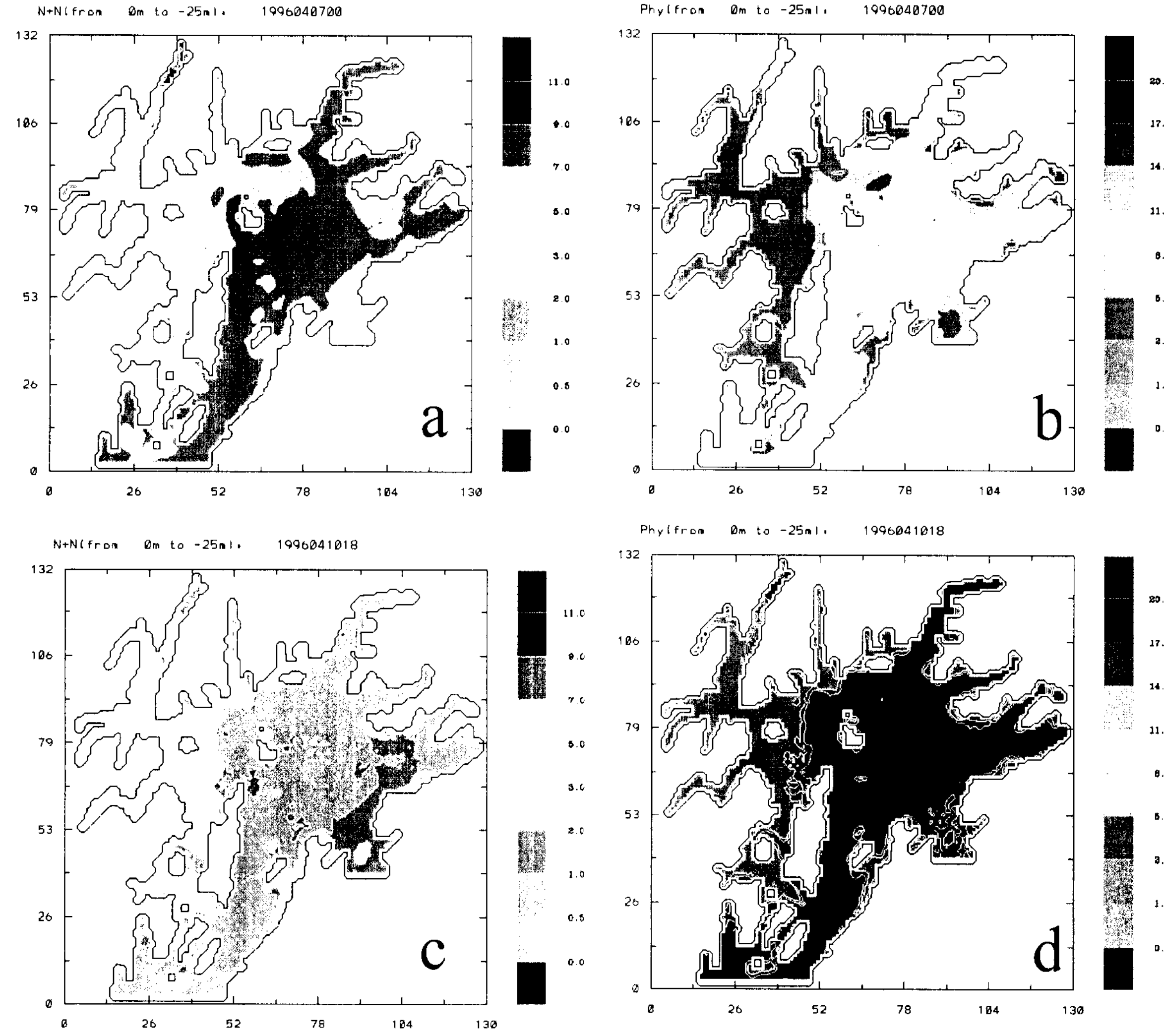
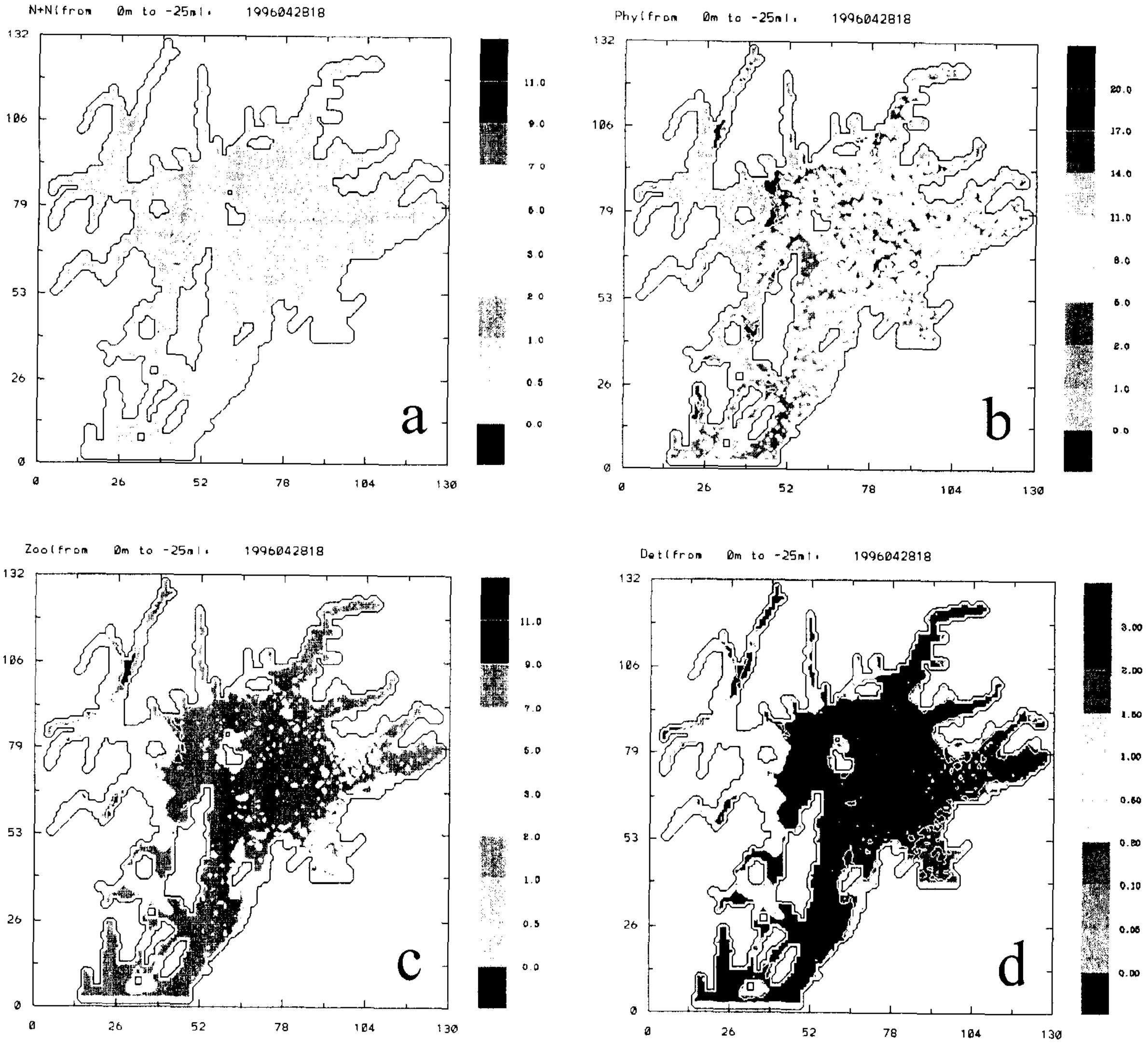

N+N(from 0m to -25m), 1996040700
Phyl(from 0m to -25m), 1996040700
N+N(from 0m to -25m), 1996041018
Phyl(from 0m to -25m), 1996041018
0
26
52
78
104
130
132
106
79
53
26
0
11.0
9.0
7.0
5.0
3.0
2.0
1.0
0.5
0.0
20.0
17.0
14.0
11.0
8.0
5.0
2.0
1.0
0.0
a
b
c
d

Fig. 9.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Phy(from 0m to -25m), 1996042818
Zoo(from 0m to -25m), 1996042818
Det(from 0m to -25m), 1996042818
0
26
53
79
106
132
0
26
52
78
104
130
11.0
9.0
7.0
5.0
3.0
2.0
1.0
0.5
0.0
20.0
17.0
14.0
11.0
8.0
5.0
2.0
1.0
0.0
3.00
2.00
1.50
1.00
0.60
0.20
0.10
0.05
0.00
a
b
c
d

Fig. 10.

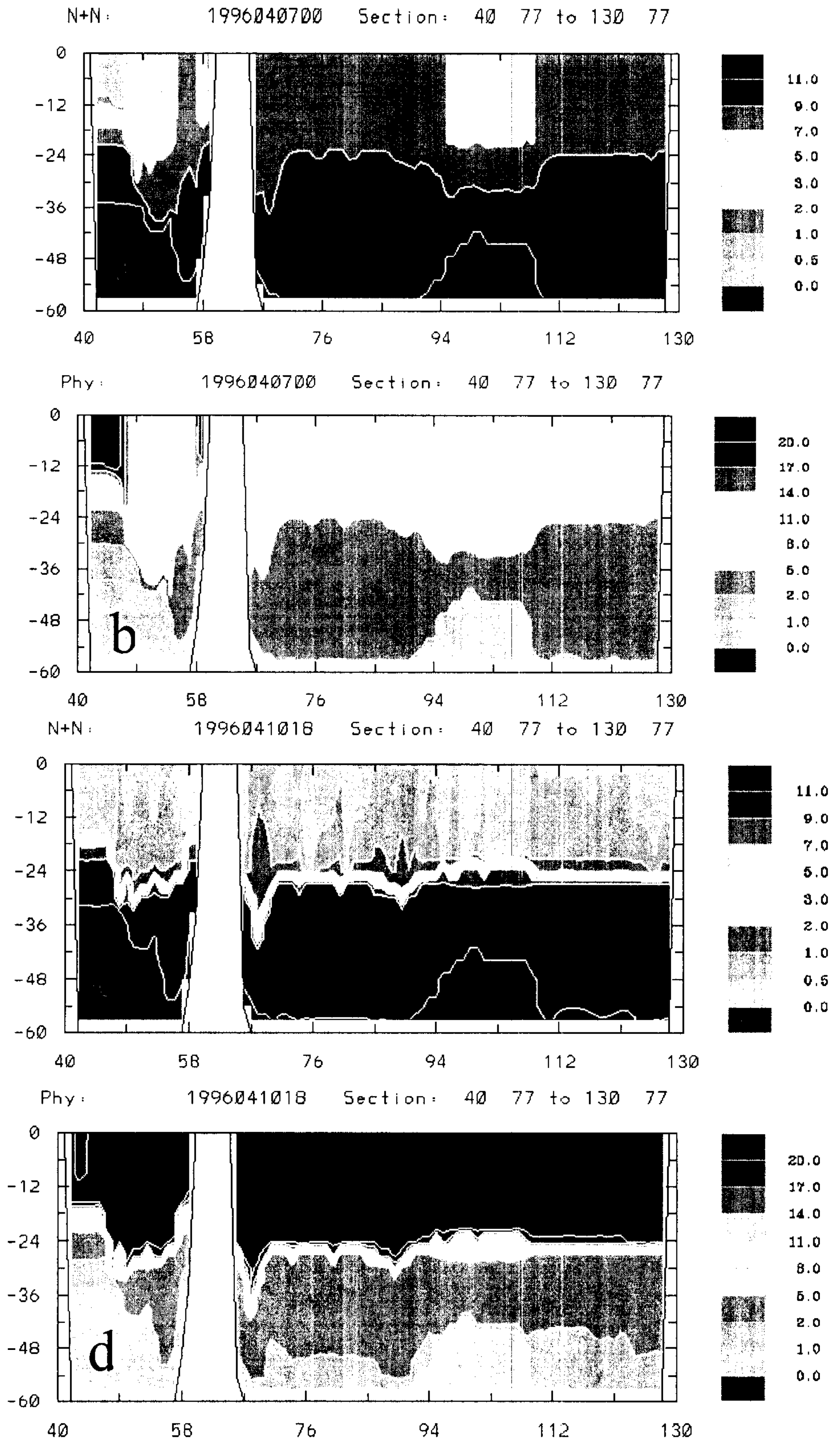
N+N: 1996040700 Section: 40 77 to 130 77
Phy: 1996040700 Section: 40 77 to 130 77
N+N: 1996041018 Section: 40 77 to 130 77
Phy: 1996041018 Section: 40 77 to 130 77
b
d
0
-12
-24
-36
-48
-60
40
58
76
94
112
130
11.0
9.0
7.0
5.0
3.0
2.0
1.0
0.5
0.0
20.0
17.0
14.0
11.0
8.0
5.0
2.0
1.0
0.0

Fig. 11.

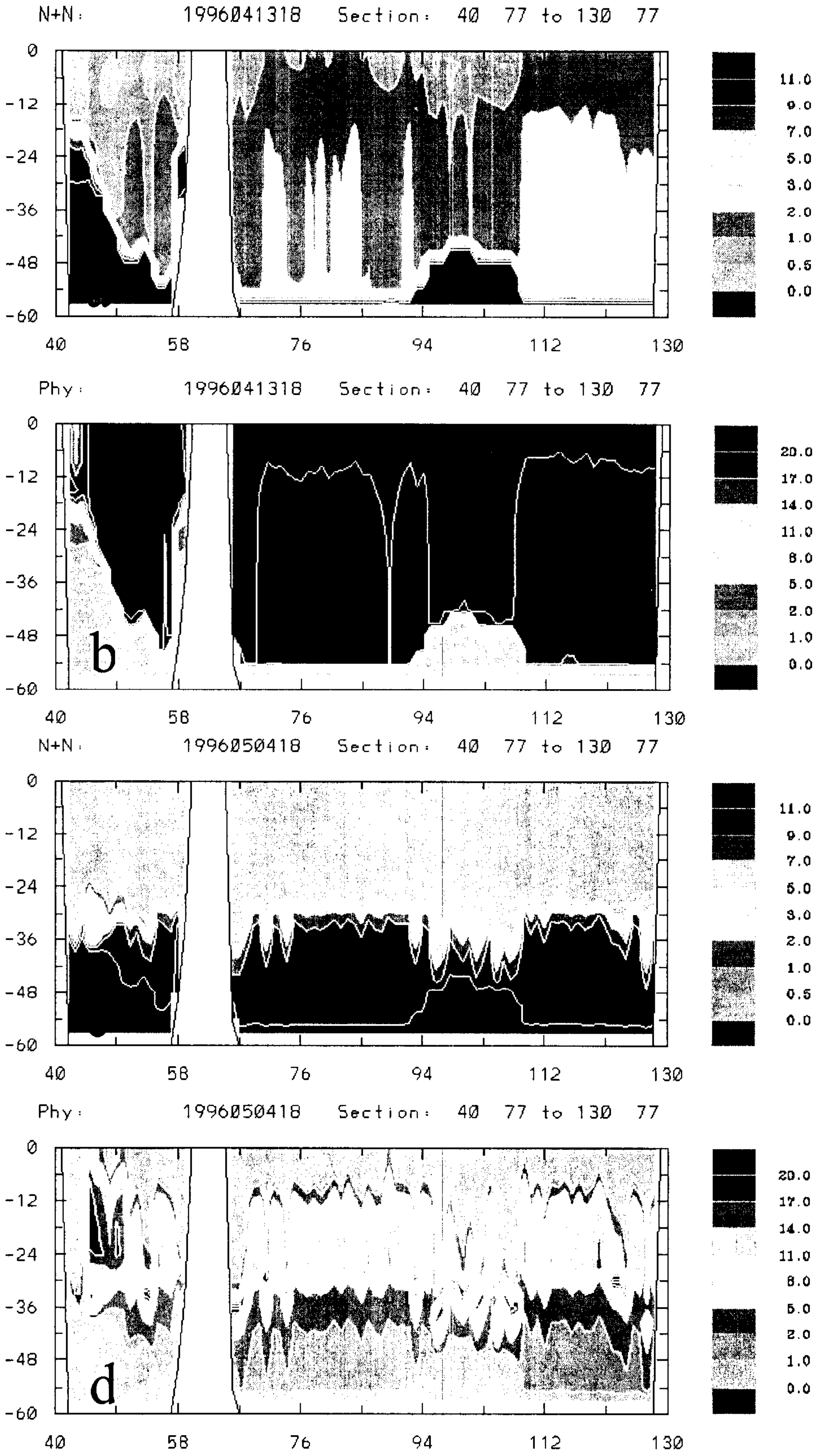
N+N: 1996041318 Section: 40 77 to 130 77
0
-12
-24
-36
-48
-60
40
58
76
94
112
130
11.0
9.0
7.0
5.0
3.0
2.0
1.0
0.5
0.0
Phy: 1996041318 Section: 40 77 to 130 77
b
20.0
17.0
14.0
11.0
8.0
5.0
2.0
1.0
0.0
N+N: 1996050418 Section: 40 77 to 130 77
Phy: 1996050418 Section: 40 77 to 130 77
d

Fig. 12.

Chapter 4

The Role of Zooplankton

Exxon Valdez Oil Spill
Restoration Project Final Report

The Role of Zooplankton in the Prince William Sound Ecosystem

Restoration Project 98320-H
Draft Final Report

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September, 1998

The Role of Zooplankton in the Prince William Sound Ecosystem

Restoration Project 98320-H
Draft Final Report

Study History: Project 320-H received funding in 5 consecutive fiscal years beginning in FY 94 and concluding in FY 98 to investigate the role of zooplankton in processes influencing the survival of juvenile pink salmon and herring; FY 99 was designated a close-out year. Project H was a core component of the larger Sound Ecosystem Assessment (SEA) program. Zooplankton serves as food for may fish, bird and marine mammal stocks. SEA investigated its role as forage for juvenile fishes including pink salmon and herring, and also as alternative prey for predators that also consume juvenile pink salmon and herring in seasonally varying complex food webs. Previous annual reports of project 320-H appear in the integrated SEA report series for FY 94, FY 95, FY 96 and FY 97. This final report includes work completed in FY 98.

Abstract: Zooplankton retained by 0.335-mm netting in Prince William Sound responds predictably to seasonal variability in the local marine production cycle. Animal plankton populations in the upper 50 m fall to seasonal lows in February (10 mg m^{-3}) before rebounding in mid summer (600 mg m^{-3}) in response to spring and summer plant production. The zooplankton community is dominated in all seasons by calanoid copepods. Small species such as *Pseudocalanus* spp. account for most of the numbers and much of the total biomass. However, the seasonally predictable occurrence of much larger forms, *Neocalanus* spp., in late April and early May contributes substantial biomass; some becomes food for juvenile salmon and some affords a predation refuge for fry being consumed by adult and juvenile pollock and adult herring at this same time. A relationship termed River/Lake, predicting upper-layer zooplankton stocks on the basis of easterly wind forcing in April and May, was present from 1981-1991 but absent after that. Since 1992, springtime zooplankton stocks have averaged about 50% of those in the previous decade.

Key Words: Oil spill, Zooplankton, *Pseudocalanus*, *Neocalanus*, Prince William Sound, SEA.

Project Data: *Description of the data* - Counts and biomass by species, composites of species, and for higher taxonomic categories are available by time, date and location from 1994-1997 as part of the formal SEA data base. *Format of the data* - data resides in flat files accessible through the Advanced Visualization Laboratory (AVL), University of Maryland, from the Prince William Sound Science Center, Cordova, Alaska, and from the INGRESS data base at the Institute of Marine Science, University of Alaska Fairbanks. *Custodian* - Dr. Charles Falkenberg, AVL, University of Maryland (SEA data base); Dr. Ken Coyle, Institute of Marine Science, University of Alaska Fairbanks (INGRESS data base).

Citation: Cooney, R. T. 1999. The role of zooplankton in the Prince William Sound ecosystem. Restoration Project Final Report (Restoration Project 98230-H), Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska, 99775-7220.

Chapter 4: 98320H
Citations to published articles

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Eslinger, D.L., R.T. Cooney, C.P. McRoy, A. Ward, T.C. Kline, Jr., E.P. Simpson, J. Wang and J.R. Allen. 2001. Plankton dynamics: observed and modelled responses to physical conditions in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):81-96.

Foy, R.J., and A.J. Paul. 1999. Winter feeding and changes in somatic energy content for age-0 Pacific herring in Prince William Sound, Alaska. *Transactions of the American Fisheries Society* 128(6):1193-1200.

Kirsch, J., G.L. Thomas, and R.T. Cooney. 2000. Acoustic estimates of zooplankton distributions in Prince William Sound, spring 1996. *Fisheries Research* 47:245-260.

Willette, T.M., R.T. Cooney, and K. Hyer. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Canadian Journal of Fisheries and Aquatic Sciences* 56:364-376.

Willette, T.M., R.T. Cooney, V. Patrick, D.M. Mason, G.L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (Oncorhynchus gorbuscha) in Prince William Sound, Alaska. *Fisheries Oceanograph*y 10 (Suppl. 1):14-41.

Table of Contents

Appendix I. - Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. R. T. Cooney, K. O. Coyle, E. Stockmar and C. Stark. (Prepared for the SEA special volume of Fisheries Oceanography).

Appendix II - Vertical and horizontal structure in upper-layer *Neocalanus* populations during the spring in Prince William Sound, Alaska. J. Kirsch, L.B. Tuttle, R. T. Cooney, and G. L. Thomas. (Prepared for the SEA special volume of Fisheries Oceanography).

Appendix III - Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring. T. M. Willette, R. T. Cooney and K. Hyer. (Published - Canadian Journal of Fisheries and Aquatic Sciences, 56:364-376).

Appendix IV - Ecological processes influencing mortality of juvenile pink salmon (Oncorhynchus gorbuscha) in Prince William Sound, Alaska. T. M. Willette, R. T. Cooney, V. Patrick, G. L. Thomas, and D. Scheel. (Prepared for the SEA special volume of Fisheries Oceanography).

Appendix V - Acoustic estimates of zooplankton distributions in Prince William Sound, spring 1996. J. Kirsch, G. L. Thomas and R. T. Cooney. (In review by Fisheries Research).

Appendix VI - Plankton dynamics: observed and modeled responses to physical forcing in Prince William Sound, Alaska. D. L. Eslinger, R. T. Cooney, C. P. McRoy, A. Ward, T. Kline, E. P. Simpson, J. Wang and J. R. Allen. (Prepared for the SEA special volume of Fisheries Oceanography).

Executive Summary

Studies of zooplankton populations in Prince William Sound under project 320-H focused on three aspects of near-surface assemblages: 1) Seasonality in numbers and biomass for dominant species; 2) patterns of vertical and horizontal distribution; and 3) relationships to seasonal and yearly shifts in ocean climate. In addition, measurements of sizes of selected species were undertaken to support the estimation of acoustic target-strengths and to assist with calibrating an optical plankton counter. The overall results of the work were applied to tests of the major hypotheses structuring the SEA study (See the summary chapter for this report).

Copopoda dominate the numbers and biomass of zooplankters retained by 0.335-mm mesh netting in Prince William Sound. The small constituents (*Pseudocalanus*, *Acartia* and *Oithona*) comprise most of the numbers and much of the biomass in the upper 50 m in all seasons. However, in the early spring, a group of larger copepods (*Neocalanus*, *Calanus*, and *Metridia okhotensis*) becomes prominent. These zooplankters complete much of their seasonal growth in layered populations near the surface which are continuous over horizontal distances of tens of kilometers. In addition to the Copepoda, larvaceans (*Oikopleura*, *Fritillaria*), euphausiids (*Thysanoessa* and *Euphausia*), and pteropods (*Limicina*) contribute substantially to upper-layer numbers and biomass at different times in Prince William Sound. SEA observations are consistent with the results of other studies conducted in the oceanic and coastal areas of the Gulf of Alaska (Coyle, et al., 1990; Mackas, et al., 1993; Damkaer, 1977; Miller, 1993; Cooney, 1987; Cooney, 1986; Napp et al., 1996; Incze, et al., 1997).

A predictable seasonal succession begins in late winter with the arrival of copepodite stages I and II of *Neocalanus flemingeri* and *N. plumchrus* at the surface arising from local deepwater spawning populations. These tiny life stages mingle with the seasonally depleted survivors of other overwintering mixed-layer zooplankton stocks in February and early March, weeks before the initiation of the spring diatom bloom signals the beginning of the annual marine production cycle.

Upper layer zooplankton stocks respond to a burst of phytoplankton production that can begin as early as late March and that reaches a seasonal high in mid to late April. The appearance of large numbers of euphausiid eggs in April marks a period of reproduction for *Thysanoessa* when food becomes available. *Calanus* and *Pseudocalanus* must also feed before beginning to reproduce, so there is a lag of weeks or even months between the peak of the spring plant production and seasonal highs in populations of these copepods. However, because *Neocalanus* reproduces independently of the energy of the diatom bloom in any year, its early copepodite stages couple immediately to the plant mass and rapid growth produces the first copepodite V stages by late

April. These large plankters, 3-5 mm in length and approximately 2 to 3 mg live weight, dominate the zooplankton for 2-3 weeks each spring. After the stage V copepodites have completed their surface development, *Neocalanus* spp. migrate away from the upper layers for deep water refuges below 400 m in the Sound. Most have left the upper 50 m by mid June.

The month of May represents a transition from winter/spring cold, saline conditions to the summer season of upper-layer warming and freshening. This transition is accompanied by a further succession in the zooplankton community that features the continuing development of *Pseudocalanus* and another small copepod, *Acartia*, and increasing numbers of *Limicina* and *Oikopleura.* These latter taxa are believed to be better adapted to neritic conditions and also to shifts in plant stocks from large diatoms in April and early May to small flagellates and diatoms in the summer and fall. Small copepods (*Pseudocalanus*, *Acartia* and *Oithona*) reach seasonal highs in June and July.

Following a peak in upper-layer biomass in June, all stocks begin a slow decline that falls to a annual low in February. During this decline, *Pseudocalanus* retains its general dominance although other taxa, including *Metridia*, *Cyphocaris*, *Mesocalanus* , *Parathemisto* and *Thysanoesssa* become important as the overall assemblage shrinks in abundance and biomass.

Relationships between the composition of the zooplankton community, and the abundance and biomass of selected species was examined in light of hypotheses linking juvenile pink salmon survival to ocean state and plankton dynamics. Both wild and hatchery-released juveniles enter the edge-zone of the Sound between late March and early June each year. The strong co-occurrence between fry and late-stage *Neocalanus* suggests benefits for salmon, particularly since fry readily consume these lipid-rich large calanoids.

A collaborative study in May, 1996, in which nets, high-frequency acoustics, and optical plankton counting were utilized simultaneously, demonstrated that *Neocalanus flemingeri* and *N. plumchrus* copepodite stage V could occur in dense, near-surface layers with numbers exceeding 500 m^{-3} at many locations. On the basis of functional response feeding models for adult pollock and herring consuming large copepods, it was determined (Willette et al, 1999; Appendix III this report) these planktivores would switch to alternative prey when the biomass of large copepods fell below about 1.0 g m^{-3}. The copepodite stage V of *N. flemingeri* and *N. plumchrus* averages about 2.0 mg live weight, establishing a nominal threshold of approximately 500 m^{-3} in layered populations needed to maintain the critical trophic linkage with zooplankton that creates a predation shelter for fry and other small fishes.

A computer simulation of Sound-wide circulation for winter and spring conditions in1996, combined with the release of modeled *Neocalanus* from regions deeper than 400 m in the Sound, confirmed that progeny from local populations could be retained locally in sufficient numbers to account for much of the stage V bloom in May, and further that these progeny tended to occur most abundantly as late stages in the western and northwestern locations of the region - the fry out-migration corridor. Results from this simulation were verified by nets and acoustic surveys.

Finally, resolution of the Lake/River conjecture was hindered when it was discovered that the strong relationship between the magnitude of springtime easterly winds in the northern Gulf of Alaska and subsequent zooplankton stocks in April and May disappeared abruptly after 1991. Additional analyses demonstrated that the conditions of fall and spring winds that characterized the "Lake/River" pattern in the decade of the 80s were not present before or after that time. Apparently a rare meteorological condition, perhaps part of the ocean regime shift of 1978, established the pattern of climate forcing that led to enhanced upper-layer zooplankton during springs of weak easterly winds and diminished zooplankton when the winds were strong. The continuing hatchery plankton watch in Prince William Sound also demonstrates that springtime zooplankton settled volumes have fallen by approximately 50% after 1991, and that much of this biomass is accounted for by declines in the month of April. I am unable to determine if this diminishment is part of a more recent regime shift (1990-91) in the northeast Pacific that has reportedly also been accompanied by lower surface zooplankton stocks in the Gulf of Alaska and Bering Sea. It seems likely that it is.

Introduction

During the planning phases of SEA in the fall of 1993, a simplistic carbon budget was developed for Prince William Sound. The budget distributed carbon from an estimated annual primary productivity of 200 gCm^{-2} through zooplankton to 0-age and 1+ age juvenile fishes, and then to apex consumers. In that exercise, the amount of carbon consumed by 0-age fish was calculated on the basis of the numbers of wild and hatchery fry rearing for 120 days in the region, their measured growth rates from wire-tagged recovered juveniles, and literature values of juvenile salmon gross-growth efficiency (Cooney, 1993; Cooney and Brodeur, 1998). The resulting salmon forage demand was then increased by an order of magnitude to roughly estimate zooplankton consumed by all 0-age fishes in the region, including herring, pollock and other prominent species. Since less than half of the zooplankton production could be accounted for by the estimated demand of age-0 fishes, the remainder was distributed to older juveniles and apex consumers. All trophic levels were judged capable of utilizing some zooplankton.

The resulting hypothetical budget (Figure 1) suggested a strong dependence by consumers at all levels on zooplankton, and a potential for variability in zooplankton mass to modulate the eating of small fishes by larger consumers under some conditions. We reasoned that when zooplankton stocks were high (seasonally or interannually), the region would reflect elevated planktivory and the consumption of the smallest fishes would decline. Conversely, when zooplankton stocks were weak, it seemed likely that large fishes would supplement their forage demand by eating more small fish - a general shift to piscivory. In this way, bottom-up processes, limited annually by nutrient concentrations and modified by surface flushing, could influence top-down predation in a manner not previously described. The exploration of these ideas in the field and from computer models created the need for a program to describe the role of zooplankton in the Prince William Sound ecosystem. The results of that program, and specifically the contributions made by project H, are reported here.

Objectives

The following represent collaborative and project-specific goals developed for studies of zooplankton in relation to the survival of juvenile pink salmon and herring:

1. Describe seasonality in upper-layer zooplankton stocks and shifts in species composition.

2. Describe the deep-water (upper 500 m) distributions of selected zooplankters during the spring and summer.

3. Describe the vertical and horizontal distributions of selected upper-layer zooplankters prior to, during and following the spring diatom bloom.

4. Describe the role of zooplankton in processes affecting the survival of juvenile pink salmon and herring in Prince William Sound.

5. Provide size information (length, width) for selected zooplankters to assist with the estimation of acoustic target strengths.

6. Supply zooplankton distribution, abundance and species composition information for selected field samples to assist with the calibration of the optical plankton counter.

In addition to these project-specific objectives, collaborations were established with investigators studying the observed and modeled physical oceanography and phytoplankton dynamics in the Sound to provide insight into the nature of the River/Lake phenomenon.

Methods

Specific field and laboratory methods are described in each of the manuscripts appended to this report. Most sampling was conducted using 0.5-m diameter ring nets (0.335-mm Nitex), towed vertically in the upper 50 m. The net was lowered backwards into the water column, then immediately retrieved at about 1.0 m sec^{-1}. Following each vertical tow, the net was carefully rinsed at the surface, and catches of plankton transferred to 250 ml bottles and preserved in 10% seawater formalin.

In May, 1996, a 1-m multiple opening-closing net environmental sensing system (MOCNESS) was deployed to study layering by large calanoids. The MOCNESS fished 10 nets (0.505-mm Nitex). The first net served as a drogue as the apparatus was lowered to depth. While the frame was slowly retrieved with the vessel underway at approximately 1.5 m sec-1, nets were sequentially opened and closed in 10 and 5 meter intervals using cable telemetry. Depths of opening and closing and the duration and speed of each tow were monitored and recorded. This information provided a means for computing the volume filtered by each net and confirmed the depth of sampling. At the surface, samples were carefully rinsed from each net and preserved in one or more 32 oz. bottles for processing.

In the laboratory, plankton samples were scanned in total for large, rare animals (identified and counted directly) and then quantitatively subsampled. Organisms in a subsample of 100-150 specimens were identified to species or the lowest possible taxonomic category and counted. In some cases (the dominant Calanoida) individual copepodite stages were enumerated separately. Blotted wet weights, plus an inventory of wet weights for species from Prince William Sound were use to convert numbers per species to biomass per species in each sample (Coyle, et al., 1990).

The total length of specimens and maximum width of the carapace were provided for samples of juvenile euphausiids to estimate acoustic target strengths. Prosome length and width were measured for selected copepods, and the diameter of the shell of pterpods were provided for similar estimation. These measurements were also used to assist in the calibration of the optical plankton counter.

Results

The following appended manuscripts for which the principal investigator served as lead author or co-author report the application of data and insight to the previously listed Project H objectives. Because SEA was a collaborative effort, much of the work is being published as the result of interdisciplinary teamwork.

1. Results applied to Objective 1 - Seasonality of the zooplankton. See Appendix I. - Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. R. T. Cooney, K. O. Coyle, E. Stockmar and C. Stark. (Prepared for the SEA special volume of Fisheries Oceanography).

2. Results applied to Objective 2 - Deepwater vertical distributions. See Appendix I. - Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. R. T. Cooney, K. O. Coyle, E. Stockmar and C. Stark. (Prepared for the SEA special volume of Fisheries Oceanography).

3. Results applied to Objective 3 - Upper-layer vertical and horizontal distributions. See Appendix II - Vertical and horizontal structure in upper-layer *Neocalanus* populations during the spring in Prince William Sound, Alaska. J. Kirsch, L.B. Tuttle, R. T. Cooney, and G. L. Thomas. (Prepared for the SEA special volume of Fisheries Oceanography).

4. Results applied to Objective 4 - Role of zooplankton in processes affecting pink salmon survival. See Appendix III - Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring. T. M. Willette, R. T. Cooney and K. Hyer. (Published - Canadian Journal of Fisheries and Aquatic Sciences, 56:364-376) and Appendix IV - Ecological processes influencing mortality of juvenile pink salmon (Oncorhynchus gorbuscha) in Prince

William Sound, Alaska. T. M. Willette, R. T. Cooney, V. Patrick, G. L. Thomas, and D. Scheel. (Prepared for the SEA special volume of Fisheries Oceanography).

5. Results applied to Objective 5 - Estimating zooplankton acoustic target strength. See Appendix V - Acoustic estimates of zooplankton distributions in Prince William Sound, spring 1996. J. Kirsch, G. L. Thomas and R. T. Cooney. (In review by Fisheries Research).

6. Results applied to Objective 6 - Providing size information to calibrate the optical plankton counter. See Appendix II - Vertical and horizontal structure in upper-layer *Neocalanus* populations during the spring in Prince William Sound, Alaska. J. Kirsch, L.B. Tuttle, R. T. Cooney, and G. L. Thomas. (Prepared for the SEA special volume of Fisheries Oceanography).

A discussion of the River/Lake hypothesis is found in Appendix VI - Plankton dynamics: observed and modeled responses to physical forcing in Prince William Sound, Alaska. D. L. Eslinger, R. T. Cooney, C. P. McRoy, A. Ward, T. Kline, E. P. Simpson, J. Wang and J. R. Allen. (Prepared for the SEA special volume of Fisheries Oceanography) under the section titled "Interdecadal Variability".

Discussion

The results of work conducted by project H described in appended published manuscripts or manuscripts designed for publication, clearly demonstrate the importance of the net zooplankton community in Prince William Sound as a modifier of processes influencing the mortality of juvenile fishes. The emergence of wild pink salmon fry into nearshore nursery areas from late March through early June, in co-occurrence with the large calanoid bloom each spring can no longer be termed coincidental. In addition to a strong trophic coupling between *Neocalanus* and fry (described previously from fry feeding studies in the region; Parker, 1997; Barnard, 1981; Urquhart, 1979; Sturdevant et al., 1996), it is now apparent that the layering behavior of maturing *Neocalanus* provides seasonally available lipid-rich forage for other planktivores including adult and juvenile walleye pollock and adult herring. Because pollock and adult herring also eat juvenile salmon, fry enjoy a temporary predation refuge whenever populations of large copepods exceed about 500 m^{-3} in stratified waters adjacent to shallower nurseries. At or above this plankton concentration, pollock and herring feed almost exclusively on zooplankton. However, at abundances below this critical limit, pollock and herring require alternative prey to compensate their diets, and fry also begin searching for food outside their protected nearshore nurseries. Observed and modeled shifts in foraging behavior at low copepod abundance by predator and prey place the fry at much greater risk to predation at low large copepod abundance (see Project E - Final Report). These findings generally confirm the prey/switching hypothesis that guided the juvenile salmon research, and provide a mechanism for numerical modeling purposes (see Project J - Final Report). In this way, meteorological processes affecting the Prince William Sound pelagic ecosystem in the spring couple with the physical oceanography to influence the development and stock abundance of zooplankton, which in turn modulate top down losses of small fish to larger predators.

Our studies of the seasonal patterns in zooplankton distribution and abundance reveal that Prince William Sound is unique in the northern Gulf of Alaska. A sizeable region deeper than 400 m provides a nearshore overwintering habitat for several interzonal copepods that does not occur at other coastal locations north of the inside waters of southeast Alaska. Studies of the stable isotope (carbon and nitrogen) composition of selected interzonal copepods (*Neocalanus* spp.) clearly demonstrate that diapausing populations in the Sound reflect local and offshore origins (See Project I Final Report; Kline, in press). Often 50% or more of *Neocalanus cristatus* taken from deepwater overwintering populations exhibit affinities with the Gulf of Alaska. This intrusion of zooplankton from off-shore shelf and ocean stocks suggests deep and shallow transport mechanisms that remain to be completely described. Cooney (1988) calculated that nearly 10^6 metric tons of zooplankton invade the northern shelf region Of the Gulf each year in association with the wind-forced on-shore transport. It is not surprising that some of this biomass "feeds" Prince William Sound.

From 1981-1991, springtime settled zooplankton volumes measured at a salmon hatchery located in southwestern Prince William Sound were strongly correlated with the strength of easterly winds computed for a location on the shelf south and east of Hinchinbrook Entrance. During springs when the easterlies were strong, zooplankton stocks at the AFK hatchery were diminished relative to stocks occurring under weak easterly winds in the spring. SEA hypothesized that this relationship reflected a gradient in upper-layer flushing. Under strong onshore transport in the upper 50-90 m forced by easterly winds, we reasoned that flow of the Alaska Coastal Current into Hinchinbrook Entrance and out at Montague Strait (Neibauer, et al., 1994) would be enhanced resulting in local copepods being flushed from the region. This could occur because springtime *Neocalanus* populations in the Sound would always be higher than those in the intruding water because of deepwater trapping and elevated adult overwintering populations (Cooney, 1987). When the flow-through was diminished under weak easterly wind-forcing, the progeny of these adults would be retained in higher abundance. Unfortunately, the River/Lake phenomenon was apparently only a temporary condition. After 1991, and despite a similar range in the magnitude of springtime easterly winds, the statistical correlation between these winds and springtime zooplankton completely disappeared.

The simplest explanation for this dramatic shift is that there has been a diminishment of offshore *Neocalanus* stocks since 1992 resulting in reduced summer "seeding", lower overwintering populations and fewer local progeny in the spring. If wind-forced currents in April and May continue to influence upper-layer flushing as they did in the past but there is no reflection of the flushing process on local zooplankton, then water entering the region from outside must contain about the same numbers of *Neocalanus* as those now recruited locally. Under this new condition, local stock abundance would be independent of springtime upper-layer flushing rates (the present case) and the River/Lake relationship (whatever it was) would cease to exist. Brodeur and Ware (1992) report very high oceanic zooplankton stocks during the 1980s, and Sugimoto and Tadokoro (1997) do point to a reduction that occurred in the early 1990s. We also record about a 50% diminishment in springtime zooplankton biomass since 1991 so some attenuation of Prince William Sound zooplankton has occurred in the present decade. Whether this reduction is related to the demise of the River/Lake condition cannot be ascertained, but it seems likely.

Conclusions

1. The net zooplankton community in Prince William Sound is typically Subarctic; copepods dominate by number and biomass in all seasons; pteropods, larvaceans and euphausiids are also occasionally important.

2. Seasonal patterns in number and biomass reflect the strong cyclic nature of the marine production cycle. Zooplankton peaks in June and July in response to growth and reproduction fueled by primary production. Stocks fall to seasonal lows in February. A predictable seasonal succession characterizes the development and dominance of species each year.

3. Under certain apparently rare conditions of ocean climate and levels of source populations over the shelf and in the bordering Gulf of Alaska, springtime zooplankton biomass in the Sound can be predicted by the strength of easterly winds in April and May. This condition was present from 1981 to 1991. It no longer is manifesting in the region.

4. *Neocalanus* spp. form dense near-surface layers in April and May that afford energetically efficient foraging loci for juvenile and adult pollock and adult herring.

5. The dominance of *Neocalanus* spp. in April and May has profound implications for the survival of juvenile pink salmon. These large calanoids not only serve as food for fry during early marine residence, but they also serve as alternative prey for fry predators like pollock and adult herring. At levels of abundance of 500 m^{-3} or greater, pollock and herring can feed efficiently on *Neocalanus*. However, below this threshold, these two fry predators must switch to other prey.

6. A three-dimensional computer simulation of the general *Neocalanus* life history in relation to modeled ocean currents in Prince William Sound (1996 conditions), demonstrates a unique recirculation mechanism that tends to disperse locally produced early life stages in ways that enhances their chance of retention in the western fry out-migration corridor 90 days after copepod spawning occurs in the deep water.

7. The ability of Prince William Sound to support planktivores is enhanced by its size, depth and physical communication with zooplankton in the Gulf of Alaska.

Acknowledgments

I thank my long-time colleague Ken Coyle for his assistance with this project. I also thank Elizabeth Stockmar and Chris Stark for their careful work in the plankton laboratory. Jennifer Allen, Meibing Jin and Jia Wang were responsible for preparing and running computer simulations of the *Neocalanus* life cycle during spring in Prince William Sound. Jay Kirsch, Loren Tuttle, Michael Donovon, and Shari Vaughan helped with sample collection in the field, and hatchery managers at the Prince William Sound Aquaculture Corporation facilities at Port San Juan and Esther Bay saved plankton for this study. I thank Charles Falkenberg and Jennifer Allen for timely assistance with electronic data transfers to and from the SEA data base.

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List of Figures

Figure 1. SEA carbon budget of the pelagic ecosystem of Prince William Sound created in 1993 to assist with planning the study.

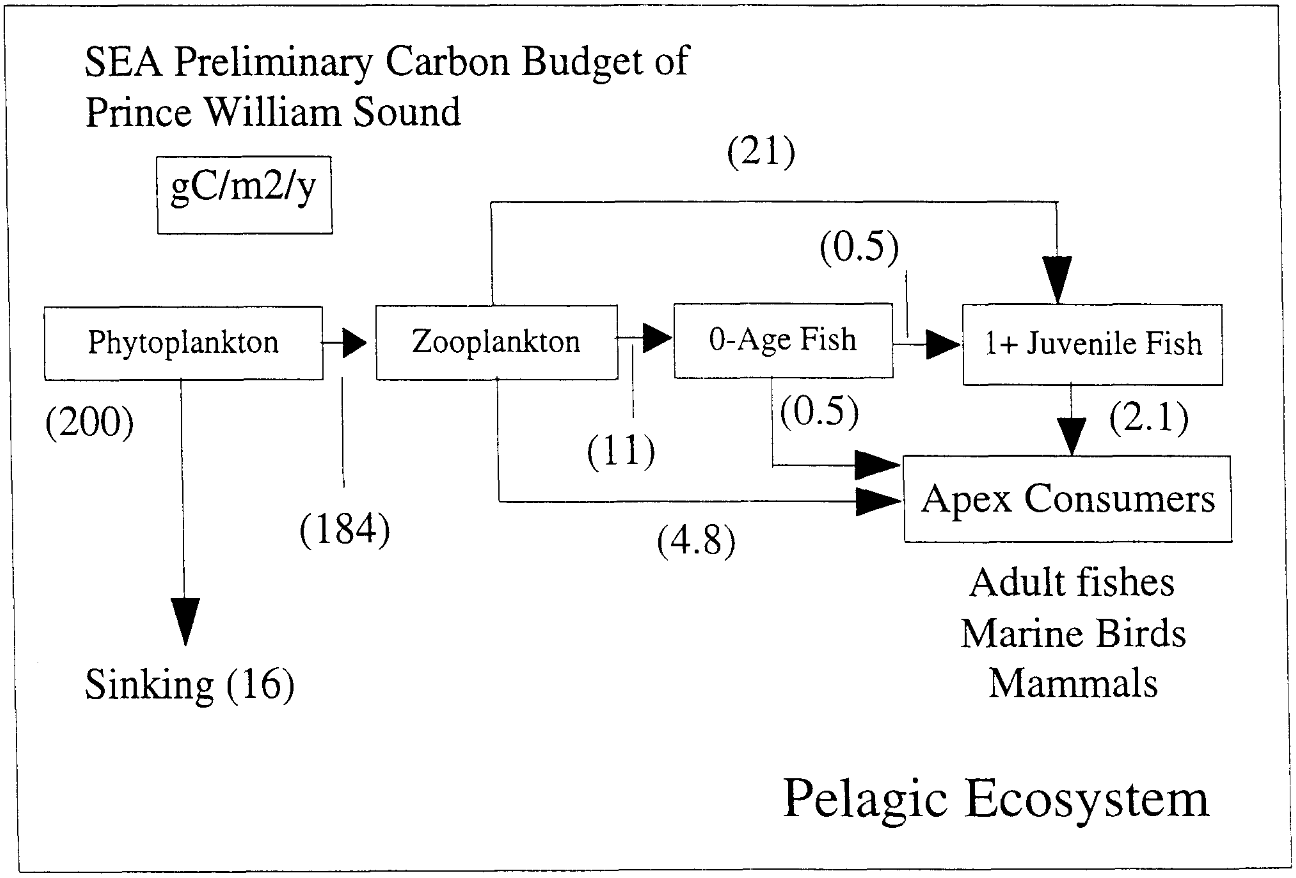

Figure 1. SEA carbon budget of the pelagic ecosystem of Prince William Sound created in 1993 to assist with planning the study.

Appendix II

Vertical and horizontal structure in upper-layer Neocalanus populations during the spring in Prince William Sound, Alaska.

(Prepared for the SEA special volume of Fisheries Oceanography)

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Vertical and horizontal structure in upper-layer Neocalanus populations during spring in Prince William Sound, Alaska

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ABSTRACT

An understanding of how zooplankton production varies over space and time is important in achieving an ecosystem-level model of Prince William Sound (PWS), since zooplankton is an important link between primary production and the upper trophic levels. Acoustical, optical and net surveys of a composite of *Neocalanus flemingeri* and *N. plumchrus* stage 5 copepodites revealed near-surface *in situ* layers exceeding 500-1000 individuals m^{-3} in the upper 50 m at many locations inside and outside Prince William Sound. Vertical structuring was best defined in the deeper, seasonally stratified regions, as seen by the populations that were sometimes found in chlorophyll maxima. Where the water column is mixed, there is a reduced tendency for copepod populations to layer. Frequency distributions of patch size in the horizontal dimension demonstrate coherence over distances of many kilometers. Our findings document the presence of dense, upper-ocean populations of late-stage *Neocalanus* spp. throughout the region prior to their ontogenetic migration to deeper water in late May and June.

INTRODUCTION

Investigations of factors influencing the production of pink salmon *(Onchorynchus gorbuscha*) and Pacific herring *(Clupea pallasi*) populations in Prince William Sound have implicated macrozooplankton, principally the largest calanoid copepods, pteropods and euphausiids as alternative prey for fishes and birds that also consume small forage fishes like juvenile salmon and herring (Willette et al., 1999a). During years or seasons when large calanoids are present in high abundance, adult and juvenile walleye pollock *(Theragara chalcogramma)* and adult herring apparently reduce their trophic dependency on small fish by eating more copepods. This may only be energetically feasible when *in situ* concentrations of calanoids are sufficiently high to permit filter or gulp feeding. Functional feeding-response models for herring and adult pollock targeting large calanoid copepods indicate these predators switch to alternative prey (fish) when calanoid densities drop below 0.2 and 1.0 g m^{-3} respectively (Willette, 1999a). For adult pollock, this means concentrations of primarily C5 stage *Neocalanus* approaching 500 individuals m^3 in the water column. These concentrations are rarely reported in vertically towed nets integrating the upper layers in Prince William Sound (see Cooney, et al., this volume).

Studies of upper-layer zooplankton densities over and adjacent to Georges Bank employed quantitative, high-frequency acoustic methods to discern scales of horizontal and vertical patchiness (Wiebe, et al., 1997). Distributions of large calanoid copepods were frequently described as continuous features (layers/swarms) of the near-surface volume backscattering. Similar findings have been reported by Coyle et al. (1998) for locations in the northern North Pacific Ocean. More recently, Cowles et al. (1998) and Holliday et al. (1998)

describe vertical structuring in plankton populations and important trophic consequences. PWS is shallower and closer to shore, so a comparison is needed.

Pollock rise to the surface to feed on plankton after spawning in March and April. *Neocalanus* populations represent a rich source of near-surface lipids elaborated prior to the descent of the maturing copepods to deep overwintering depths in early June (Miller, 1993). Apparently, the gill-rakers of adult pollock are ideally-sized for removing the largest *Neocalanus* from layers and swarms in the water column. This feeding behavior has been documented by Yoshida (1994) for pollock in the Bering Sea but not reported elsewhere.

In early May 1996, high-frequency acoustic techniques, optical plankton sampling and quantitative nets (MOCNESS) were employed simultaneously to survey stocks of late-stage *Neocalanus* and other macrozooplankters in the upper 50 m of Prince William Sound and adjacent shelf waters. Our work sought evidence of copepod layers near the surface where adult pollock are frequently sampled in April and May with large percentages of *Neocalanus* stage C4 and C5 in their stomachs (Cooney and Willette, 1997).

Our inquiry sought evidence for *Neocalanus* layering behavior and elevated abundance in the upper 50-m over distances of 10s of kilometers in Prince William Sound and adjacent shelf waters. The purpose of this paper is to compare results from three instruments (acoustics, nets, and optics), and to report spatial variation of density distribution of neocalanus stage V copepods for discrete locations and transects occupied in early May 1996. Because of the semi-continuous nature of our survey, and the increased resolution of acoustical and optical observations in the horizontal and vertical dimensions, we are able to discern features of the numerical distributions of *Necalanus* spp. stage C5 that are otherwise missed and/or undersampled by nets alone.

METHODS

Field measurements

A broadscale acoustic, optical and net survey of Prince William Sound and adjacent Gulf of Alaska was conducted May 2-10, 1996 (Figure 1) aboard the University of Alaska's R/V *Alpha Helix.* The survey came after the spring phytoplankton bloom, when large late-stage copepodites of *Neocalanus* spp. occur closest to the ocean surface (Cooney 1986, 1993). Measurements were performed during the day to avoid vertically migrating nekton such as fishes, squids, euphausiids, and other organisms that move into the upper 50 m at night.

A Multiple Opening/Closing Net and Environmental Sampling System (MOCNESS, Wiebe et al 1985) with nine 1 m^2-opening, 0.505 mm-mesh nets and on-board CTD collected *Neocalanus* at 24 locations (Figure 1). At each location, the MOCNESS sampled 5 and 10 m increments in slow oblique tows from 50 m to the surface; each net filtering about 100 m^3. Later, numbers and biomass were determined from standard subsampling and counting procedures in the laboratory. *Neocalanus* stage C5 was measured for length and width; length included the prosome and abdomen. These measurements were used to interpret the acoustical and optical records.

Our acoustic system consisted of a 420 kHz BioSonics Digital Transducer scientific echosounder with a dual-beam transducer (although only the narrow beam was used for this analysis, as we did not attempt to resolve individual targets) mounted on a 3 m long fin towed at approximately 5 knots (2.5 m/s). Parameters of the acoustic system during the survey were: source level (SL) =+224.0 dB re 1μPa, receiver gain (RG) =-42.9 dB re 1C/μPa, transducer directivity (b2) =.000274 (unitless), and pulse duration=400μs. These parameters result in an echo integration constant of 6.61e+14 count-meters. The trigger interval was set to 0.4 seconds (2.5 pings per second), but was somewhat variable due to the computer's limited ability to acquire and store digitized signals in real-time. Signals were gated between 3 m and 50 m.

In-house data processing included an echo-square integrator (32 pings per cell, yielding cells 30 m x 1 m) with a notch-gate to remove fish (Kirsch et al 1999), a map generator for both survey plotting and visualization of geographical distributions of zooplankton, a database to match acoustic files with MOCNESS files, and programs to implement scattering models and matrix equations. The echo-integrator applied an absorption constant (MacLennan and Simmonds 1992) of $\alpha = 0.098$ dB/m based on temperatures and salinities measured with a CTD during the cruise. Output files included a database of volume backscattering strength (S_V), and color echograms and maps.

The MOCNESS catches plankton by opening and closing nets at specific depths as it is raised or lowered in the water column. It has specific selectivities and efficiencies depending on a plankter's size, swimming speed, and ability to detect and avoid the net. Hence, a net catches only those plankters that are retained by its mesh size and are not able to escape its path. We assume that it is an ideal sampler for the target species of this study: C5 stage *Neocalanus* spp. To avoid encountering other targets in the water column not as readily sampled/caught by the MOCNESS (e.g. fish) , we sampled during the day, and edited the data to remove suspect features (large fish returns).

Multifrequency methods (Peiper et al 1990, Holliday et al 1980) are preferred for the separation of nekton and plankton, but since only one frequency was used during most of this survey, another method was developed. The BioSonics Digital Transceiver samples at a rate of 41667 samples s^{-1}, which, at a speed of sound of 1470 m s^{-1}, yields a vertical resolution of 17.6 mm. At this level of resolution, even high zooplankton densities yield signals smaller in amplitude than a single fish. To remove signals from fish, we used the inverse of thresholding - notch-gating - retaining samples below a selected threshold but omitting those above this level, as described by Kirsch et al (1999).

Absolute Density Estimation

To calculate the absolute density (D_{ij}) for a species of interest, it is necessary to know the average backscattering cross-section (σ_{ij}) for that species in each survey area, the measurement of which is typically not feasible due to high densities of small zooplankton, which cause target discriminators to fail in detection of individual echo peaks.

The variable σ is often represented by its logarithmic equivalent, known as target strength (TS). When in-situ TS measurement is impossible, models are used to predict a distribution of TS. The TS of an animal is dependent on animal size, shape, material composition, orientation, and the frequency of the sonar, so TS models use these values as input parameters. We used a bent cylinder model for copepods and euphausiids, and an elastic sphere model for pteropods (Stanton et al., 1994). Variability in animal sizes can be compensated for by applying size measurements from MOCNESS samples to these scattering models.

Of the five input parameters of the model, the least is known about the reflection coefficient R_j of the animal's material. The method for determination of this parameter is described in Kirsch et al (1999). An alignment algorithm was used to partition the acoustic information into blocks that spatially overlap the same space sampled by the MOCNESS. Since the acoustic volume backscattering coefficient (sv) is the sum of the multiple of average density (D_{ij}) and average backscattering cross-section (σ_{ij}) for each species, sv_i can be predicted for acoustic data where there are corresponding net samples, and compared to the measured sv values. The predicted sv was adjusted to agree with the measured sv in a least-squares sense, using a Single Value Decomposition matrix equation (Press et al 1993). The solution to this equation yielded R = 0.0178, 0.1532, and 0.0341 for copepods, pteropods, and euphausiids, respectively (Kirsch et al 1999).

The absolute density D of taxa j in area i was estimated by multiplying each species' σ_{ij} (determined by the models) by its catch proportion r_{ij} (from MOCNESS). The sum (over taxa j) of these values was then divided into the echo integration cells sv_i (from 420 kHz), and multiplied by the species proportion r_{ij}, as in the following equation:

$$D_{ij} = \frac{sv_i}{\Sigma_j \; r_{ij}\sigma_{ij}} \, r_{ij} \qquad (1)$$

Patchiness

Estimates of spatial scales and variances were obtained from spectral analysis of the absolute density data sets. Data analysis was similar to the method used by Greenblatt (1982) and Greenlaw and Pearcy (1985). For each day, the areal density observations were first-difference filtered to yield sequences of changes in the absolute densities. Taking the difference between each sample and its neighbor removed the mean values of (or "detrended") the data (Jenkins and Watts, 1968). The data was then Fourier transformed to the frequency domain, then squared to determine Power Spectral Density, and low-pass filtered to compensate for the high-pass filter effects of the first-difference process. These power spectral levels are in units of variance, are labeled "variance spectra", and represent estimates of the distribution of variance in absolute density over a range of spatial scales encountered along acoustic transects.

Canonical correlation

Canonical correlation was run on the MOCNESS data from cruise HX192 to look for correlations between the physical variables measured by the MOCNESS and abundance of the major taxa in the samples. The physical variables included average depth(1), temperature(2), salinity(3) and fluorescence(4) recorded for each net. The five biologlical variables included abundance of Calanus marshallae copepodids(1), Neocalanus copepodids(2), Metridia copepodids(3), Chaetognaths(4) and Pteropods(5). A total of 189 samples were included in the analysis. The data were sorted using an INGRES data base. Statistics were run using FORTRAN calls to IMSL statistical routines.

Aquashuttle measurements

A Chelsea Instruments Aquashuttle was also deployed along selected acoustic transects. The Aquashuttle includes a Chelsea Instruments CTD which colletcts temperature (C) and salinity data, a fluorometer to measure chlorophyll ($\mu g\ l^{-1}$), and a Focal Technologies Optical Plankton Counter (OPC) which counts and measures zooplankton-sized particles in the water. The Aquashuttle was undulated from 50 m to the surface along each transect. The data were later interpolated using Inverse Distance Weighting. This procedure allows a comparison of physical properties with the vertical distributions of primary production and zooplankton along a transect.

The OPC measures the cross-sectional area of particles passing through a light beam. Laboratory measurements conducted by Eddy Jin (unpublished data) agreed with data presented at a GLOBEC workshop (GLOBEC 1991) which showed that *Neocalanus* spp stage 5 has a spherical diameter of about 2 ± 1 mm. This diameter was used to bin the OPC data into particles smaller than *Neocalanus* spp, *Neocalanus*-sized particles, and particles larger than *Neocalanus*.

RESULTS

Thermal structure in early May

Sampling in Prince William Sound and adjacent shelf waters was conducted under unusually quiescent surface conditions in early May, 1996; there were no storms, and little wind during the nine-day cruise. Surface temperatures were in the range 6.0-8.0 C, while temperatures averaged over the water column to 50 m ranged between 4.5 and 6.0 C (Figure 2). Integrated temperatures were warmest over the continental shelf, in Montague Strait and in the central and eastern portions of Prince William Sound, but coolest in the northern and western regions.

Abundance and scales of horizontal patchiness

Acoustic transects ranging in length from 25 to 60 km were occupied on each of nine days in Prince William Sound and for Gulf of Alaska waters over the continental shelf directly south of Hinchinbrook Entrance (Figure 1). Acoustic densities for the composite of *Neocalanus flemingeri* and *N. plumchrus* stage C5, averaged over the upper 50 m, ranged from less than 50 to over 600 m^{-3}, while similar estimates for the MOCNESS ranged from less than 50 to over 250 m^{-3} (Figure 2). Our net samples indicated three regions of generally high abundance: 1) Knight Island Passage and the northwestern part of the Sound; 2) a region north of Hinchinbrook entrance; and 3) the continental shelf edge. Patterns derived from the semi-continuous acoustic and optical surveys demonstrated similarities with the nets in some regions but not for others. The dominant catch in the MOCNESS was neocalanus, followed by euphausiids (Figure 3). Fish or squid were not caught in the nets.

Table I. Neocalanus densities by area

Day in May	Location	Average #/m^2	Maximum #/m^2
2	Knight Is Pass	6948	39321
3	Wells to Unakwik	6976	34805
4	Knight Is Pass (#2)	6935	29433
5	North Gulf of AK	3545	16542
6	Montague Strait	902	13187
7	Hinchinbrook	11615	60665
8	Deep hole / Perry/Wells	6773	48847
9	Wells Pass	4306	16743
10	Central to Orca	6651	32024

Calculation of variance spectra provided power spectral density (PSD) estimates for transects occupied each day. These spectra demonstrate that horizontal patch structure was generally similar for all areas, and that coherence was strongest over horizontal distances approaching or exceeding 10 km (Figure 4). The declining slope of the line defining the relationship between spectra and spatial frequency (cycles/km) for Neocalanus stage C5 ranged between -3.97/3 and -5.42/3, which is near a slope -5/3 which is the expected slope of a spectrum in which turbulent mixing is a controlling force (Munk 1981, Wiebe et al

1996). In a turbulent flow regime, the turbulent energy spectral density function is proportional to $\kappa^{-5/3}$ (where κ is the spatial wavenumber $2\pi/\lambda$) in a range of wavenumbers between the scales of turbulent generation and dissipation.

Abundance and scales of vertical patchiness

The highest abundance (> 1000 m^{-3}) of *Neocalanus* C5 sampled by the MOCNESS was observed in the surface water at station 9 at the shelf break near Middleton Island south of Hinchinbrook Entrance, while at 10 of 23 other stations, *Neocalanus* C5 exceeded 500 m^{-3} (Figure 2). Most locations of high density were located in the western and northwestern region of the Sound. When the abundance was high, *Neocalanus* was generally restricted to layers 10-20 m in vertical thickness.

In contrast, except for one shelf break collection near Middleton Island, net-measured abundance over the continental shelf, and in southern and central Prince William Sound, was consistently below 500 m^{-3}. Densities of *Neocalanus* in Orca Inlet and Montague Strait were also very low (Figure 2) with little evidence of layering in the Strait.

Abundance patterns were generally similar in the vertical acoustic records taken while the MOCNESS was in the water (Figure 5). However, the acoustic estimates were almost always higher; a few locations approaching or exceeding 1500 m^{-3}. Also, there are some obvious discrepancies between the nets and the acoustics. For example, the last net sample (station 25) taken in Orca Bay records densities less than 100 m^{-3}, whereas the acoustics estimate the C5 stage in excess of 1500 m^{-3} near the surface. A somewhat similar difference was noted for a location north of Hinchinbrook Entrance (station 15). Here the nets recorded peak densities < 400 m^{-3}, whereas the acoustics estimated stocks exceeding 1500 m^{-3}.

Vertical distributions relative to hydrography and fluorescence

We selected three locations in Prince William Sound to examine relationships between upper layer vertical distributions of *Neocalanus*-sized particles determined using OPC counts, volume scattering (Sv) measurements, and temperature and chlorophyll (fluoresence) measurements. Along a transect in northern Knight Island Passage, there was evidence for surface thermal stratification, and generally overlapping distributions of *Neocalanus*-sized particles, chlorophyll and total acoustic volume scattering (Figure 6). In contrast, a transect from lower Montague Strait exhibited mixed conditions with temperature and chlorophyll generally homogeneous with depth. *Neocalanus*-sized particles were dominated by the pteropod *Limacina helicina* at this location, and overall, plankton densities were very low (Figure 7). A transect in central Prince William Sound exhibited intermediate patterns; a sharp thermal signal at the surface (5 m), a well-defined layer of chlorophyll between 25 and 40 m, corresponding with a concentration of *Neocalanus*-sized particles most abundant at distances about 30-34 km from the start of the transect. Volume scattering was intense and distributed between the surface and about 40 m along the entire transect, but did not correspond with onset of chlorophyl and OPC count concentrations (Figure 8). Variance spectra computed for daily acoustic transects demonstrated vertical patchiness on the order of 20-30 m (Figure 9).

Canonical Correlation

Highly significant but relatively weak correlations were observed for the first two canonical correlation coefficients (see tables below).

Table II. Canonical Correlations Statistics

	Canonical correlations	Wilks Lambda	Raos F	Num. df	Denom. df	Prob of Larger F
1	0.8430	0.1840	19.906	20	597.9	0.0000
2	0.5903	0.6361	7.445	12	479.2	0.0000
3	0.1392	0.9764	0.730	6	364.0	0.6261
4	0.0658	0.9957	0.398	2	366.0	0.6722

Table III. Correlations Between the Physical Variables and the Group One Canonical Scores

	1	2	3	4
1	-0.1229	0.9568	0.2417	0.1053
2	0.5547	-0.4923	-0.5620	-0.3662
3	0.6093	0.5133	0.3889	0.4627
4	0.1621	-0.1791	0.8521	-0.4644

Table IV. Correlations between the biological variables and the Group Two canonical scores

	1	2	3	4
1	-0.2194	0.7602	0.1371	-0.5469
2	-0.0757	0.7937	0.2373	0.4474
3	0.5047	0.3213	0.5935	0.3574
4	0.8661	0.3064	-0.0023	-0.3843

Both the first and second correlation coefficients were negative. The correlations between the first canonical scores and variables suggest that as the temperature and salinity increase, the densities of Chaetognaths and Pteropods tend to decrease, but there are no correlations with depth. In contrast, the densities of Calanus and Neocalanus copepodids have a substantial negative correlation with depth, a positive correlation with temperature and a somewhat negative correlation with salinity. They therefore tend to be more abundant near the surface where salinity is somewhat reduced and temperatures elevated. The redundance coefficients for the first and second canonical correlations were 0.26, suggesting that about one quarter of the distributional variation of these taxa might be due to the physical variables examined. In general, higher densities of calanoids were observed in the northwestern part of the sound (Knight Island Passage region), where surface salinities tended to be lower and temperatures higher. The above correlations are therefore consistent with the observed geographic distributions. There was no correlation with fluorescence.

DISCUSSION

A large-scale regional census of C5 stage *Neocalanus flemingeri* and *N. plumchrus* measured with nets, optics, and high-frequency acoustics found evidence for extensive layering of these large, late stage copepodite in the upper 50 m of Prince William Sound and nearby shelf waters. A population was considered layered when most of the abundance occurred in half or less of the sampled domain, 0-50 m. At most locations, our acoustic estimates exceeded the net catches by about a factor of 2-3. This result is not wholly unexpected since the nets routinely integrated populations over vertical distances of 5 or 10 m, while the vertical resolution of the acoustics was on the order of 1 m. It seems likely that sub-structure in near-surface distribution of *Neocalanus* could account for these differences; the nets would report negatively-biased estimates when layers were on the order of 1 or 2 meters in thickness. However, at the time of the survey, we were more interested in gross features of swarms and layers in both the horizontal and vertical dimension, not fine-scale detail, so did not sample adaquately for thin layers. More significant differences between net catches and acoustic estimates (stations 15 and 25) (Figure 5) suggest other sources of error, perhaps signal augmentation by targets that were not quantitatively captured by the nets (small fish or squid) that were not excluded by our "notch-gating". We note that both of these cases occurred closely together in the southeastern portion of the Sound suggesting a local problem.

Our acoustic survey documented wide-spread upper-layer populations of *Neocalanus flemingeri* and *N. plumchrus* throughout the study domain. Scales of patchiness agree well with the observations of Greenblatt (1982), Greenlaw and Pearcy (1985), and Wiebe at al (1997). In the horizontal dimension, layers and swarms on scales of 10 km were dominant. Similarly, in the vertical dimension, we saw layering routinely spanning 20-30 m in the upper 50 m.

Inside Prince William Sound, the MOCNESS found Neocalanus C5 was most abundant in Knight Island Passage, and the northwestern part of the Sound near Esther Island and Lone Island (Figure 5). This stage was also very abundant at the surface near the continental shelf break east of Middleton Island. Much lower abundance and a tendency to be dispersed, or be deeper in the water column, occured in Unakwik Inlet, at locations over the continental shelf, in central and southern Montage Strait, and in Valdez Arm. Differences between this pattern and that determined by the semi-continuous acoustics are probably associated with aliasing by the relatively small number of net samples compared with the numbers of observations acquired during the acoustic survey. However, general agreement between the two methods demonstrating northwest and southwest regions of elevated abundance points to reasonable concordance in areas where densities were very high.

Patterns emerging from the optical plankton counter are more difficult to interpret since 1-4 mm particles include a wide range of taxa in PWS. For our study, we judge these observations to be most important for linking general vertical distributions with temperature structure and phytoplankton stocks. In the northwestern part of the Sound, the OPC demonstrated close correspondence between *Neocalanus*-sized particles and chlorophyll at the base of the shallow thermocline. Elevated OPC counts in Montague Strait are probably associated with large numbers of pterpods in that water.

The tendency for *Neocalanus* C5 to occur in elevated, layered populations in Prince William Sound and adjacent water provides predictable and concentrated forage in the upper layers for planktivores like adult pollock and herring (Steinhart, et al, 1999; Thomas et al, 1999). The western part of Prince William Sound is a major outmigration corridor for juvenile salmon released from salmon hatcheries at Esther Island and Cannery Creek each year. In years when *Neocalanus* populations are weaker than average, the presence of fry predators in the corridor could exert higher losses on alternative prey like small fish, of which juvenile salmon are representatives (Willette et al., 1999b). However, our combined results demonstrate that Neocalanus occurs in relatively high abundance throughout the region so pollock and herring are not necessarily drawn to the fry corridor. During pink salmon outmigration in 1996, C5 abundance in excess of 500 m^{-3} was relatively common. Obvious exceptions were regions of mixing and instability, including locations over the continental shelf and in lower Montague Strait.

We conclude that populations of late-stage *Neocalanus flemingeri* and *N. plumchrus* swarm near the surface throughout Prince William Sound in spring as they store lipid reserves prior to their migration to overwintering depths in late May and early June. During this period, densities exceeding 500-1000 copepodites m^{-3} may occur in subsurface layers. At seasonally stratified locations, these populations are sometimes found in chlorophyll maxima. Where the water column is mixed, there is a reduced tendency for copepod populations to layer.

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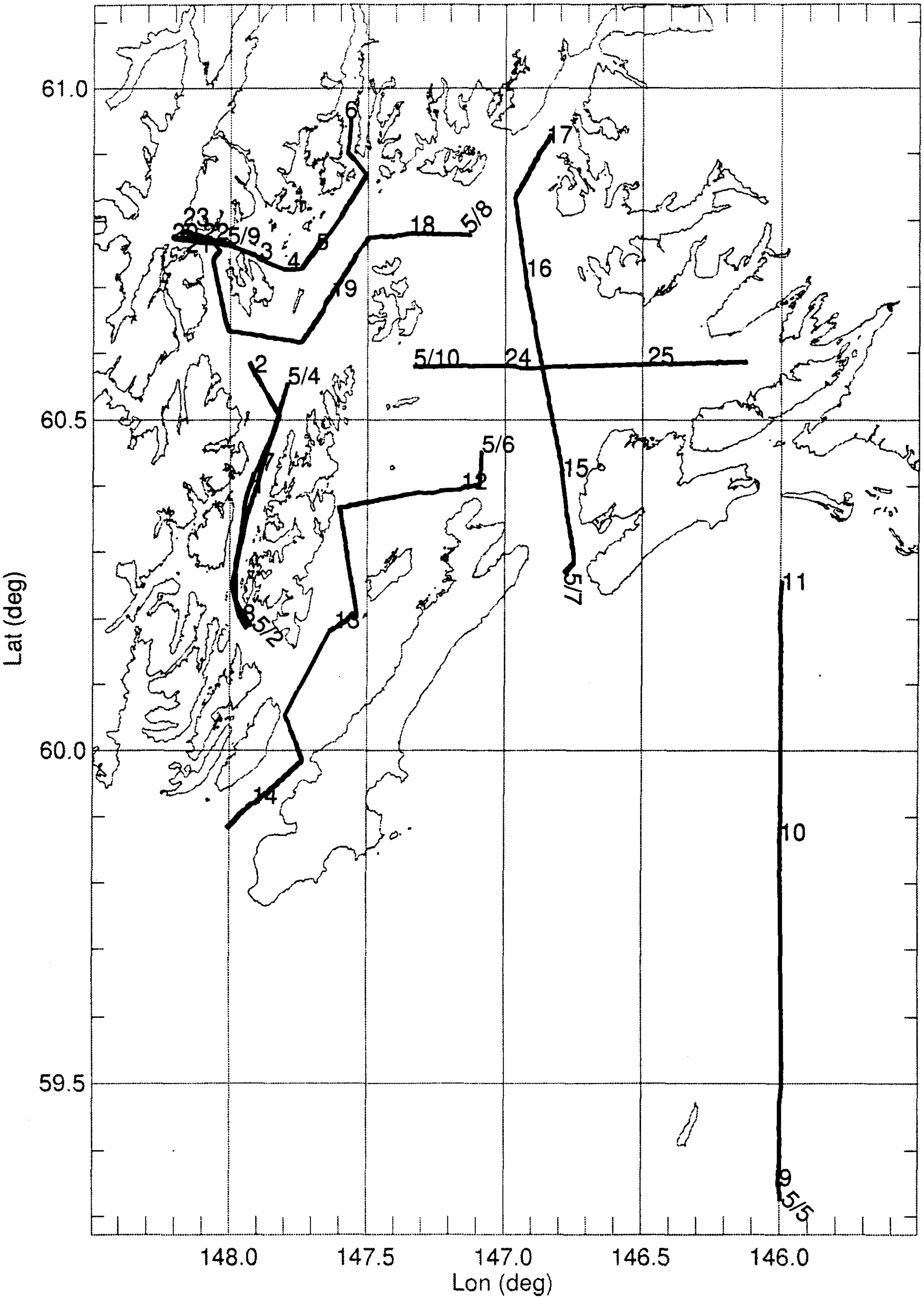
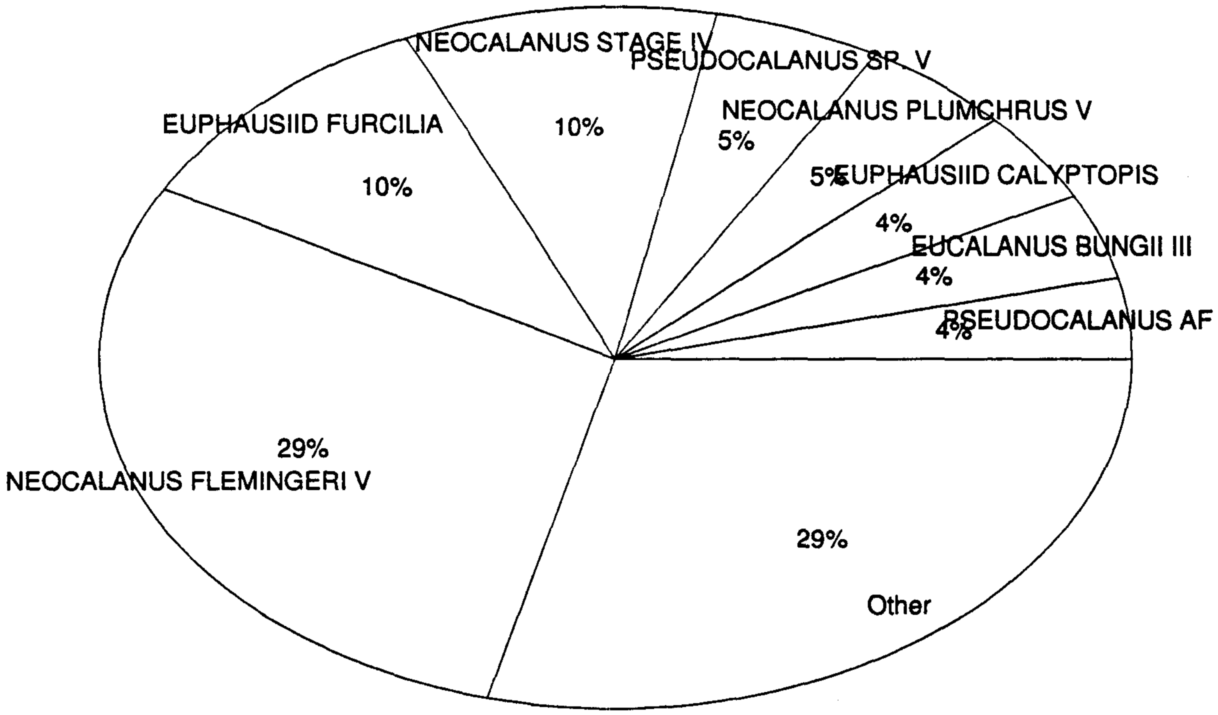


Figure 1.

Figure 1. Acoustic/MOCNESS survey.

By count



By biomass

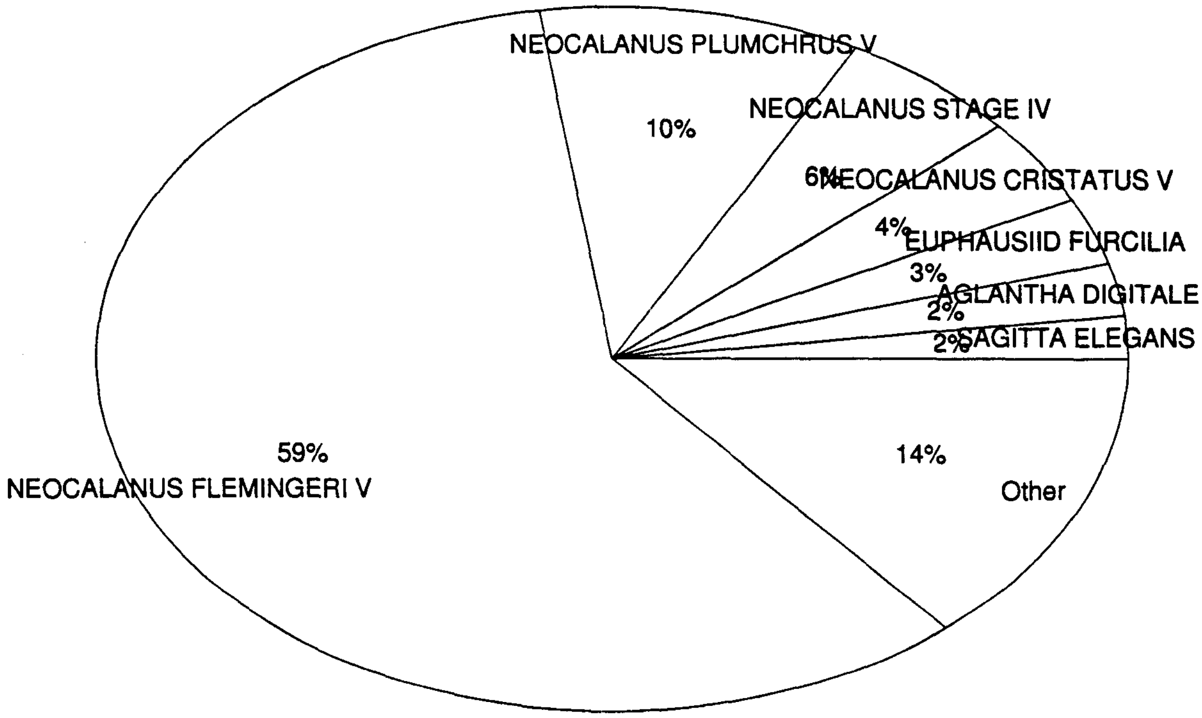
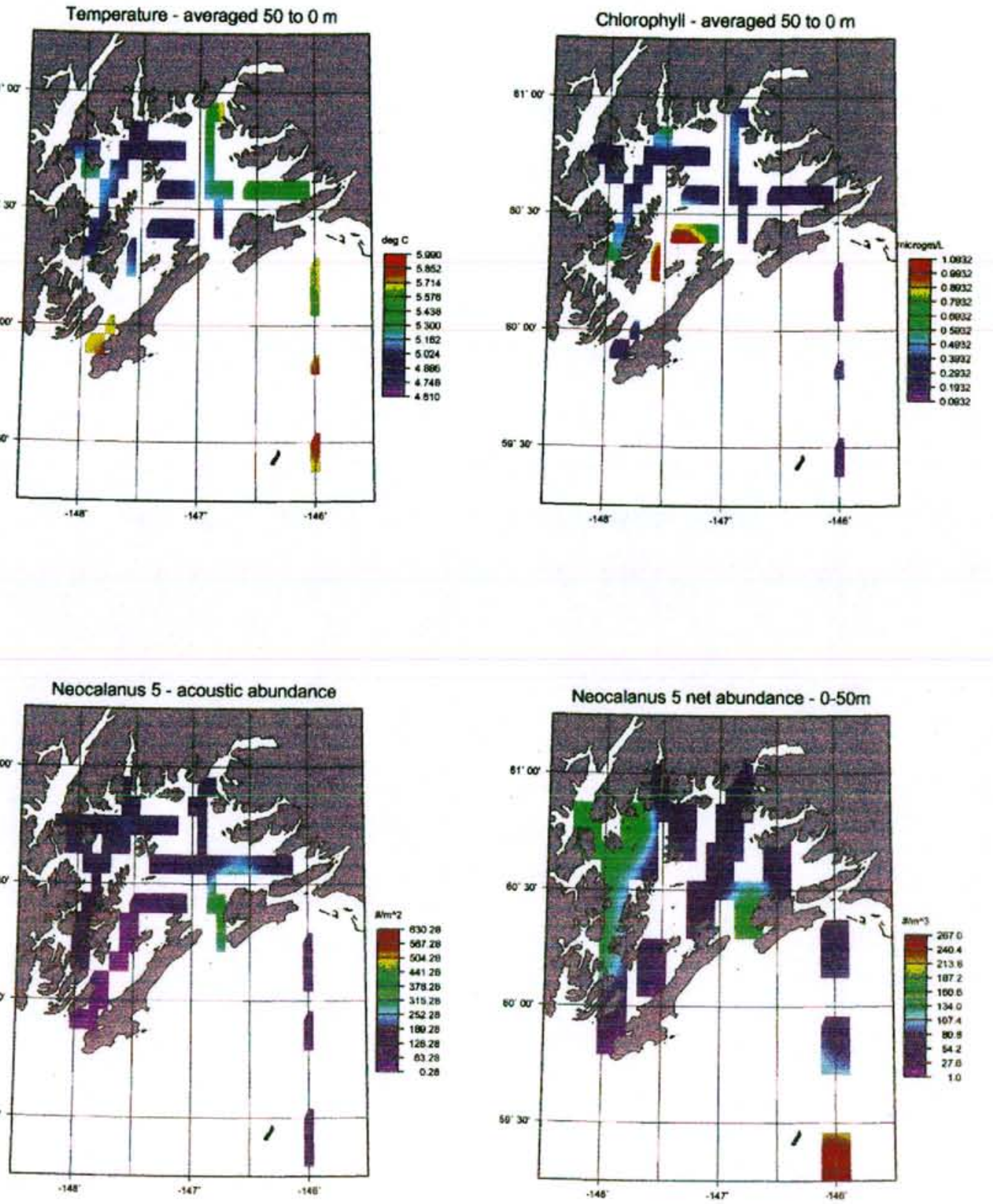


Figure 2.

Figure 3. MOCNESS catch composition


Temperature - averaged 50 to 0 m

Chlorophyll - averaged 50 to 0 m

Neocalanus 5 - acoustic abundance

Neocalanus 5 net abundance - 0-50m

Figure 3.

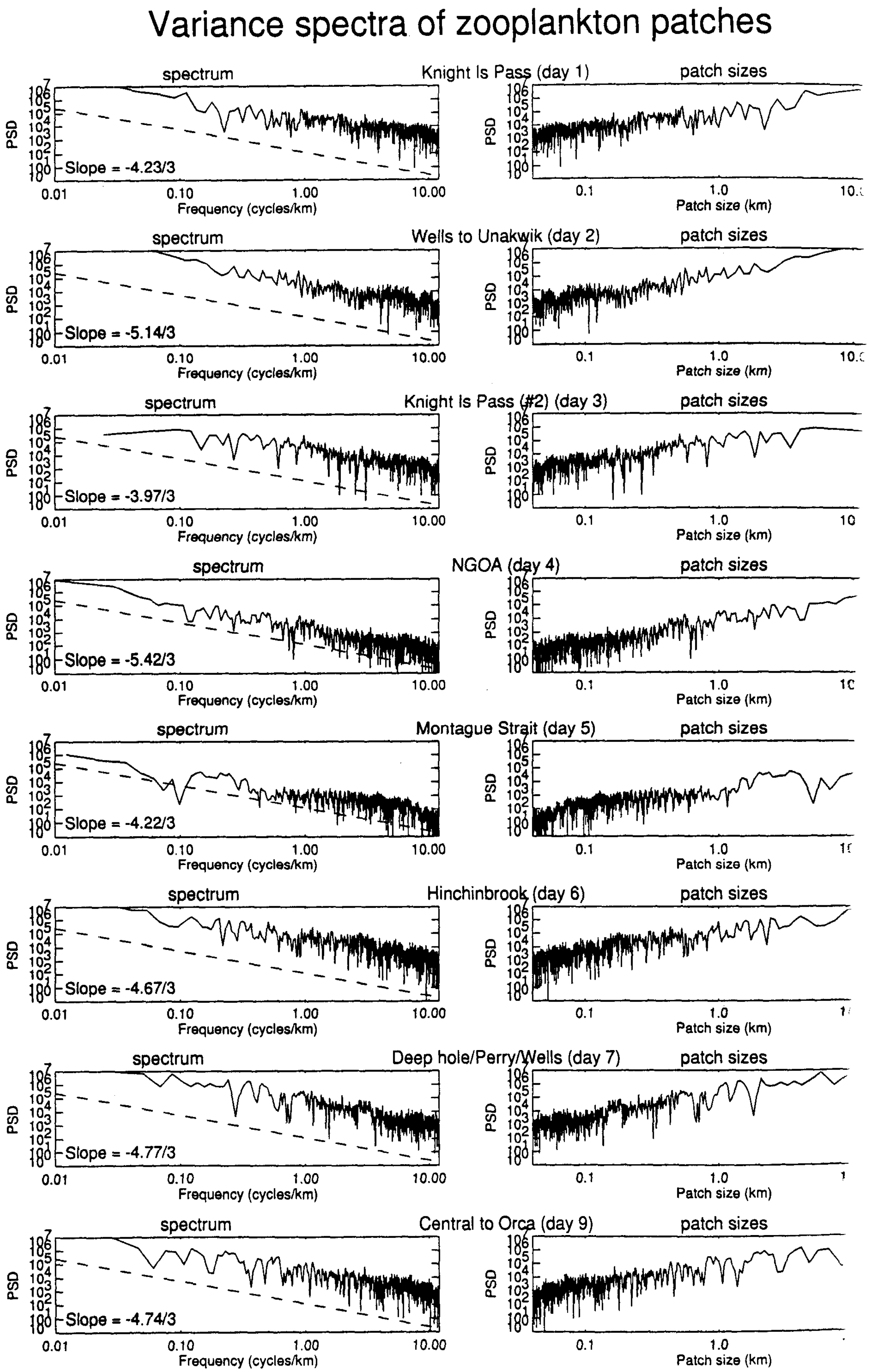
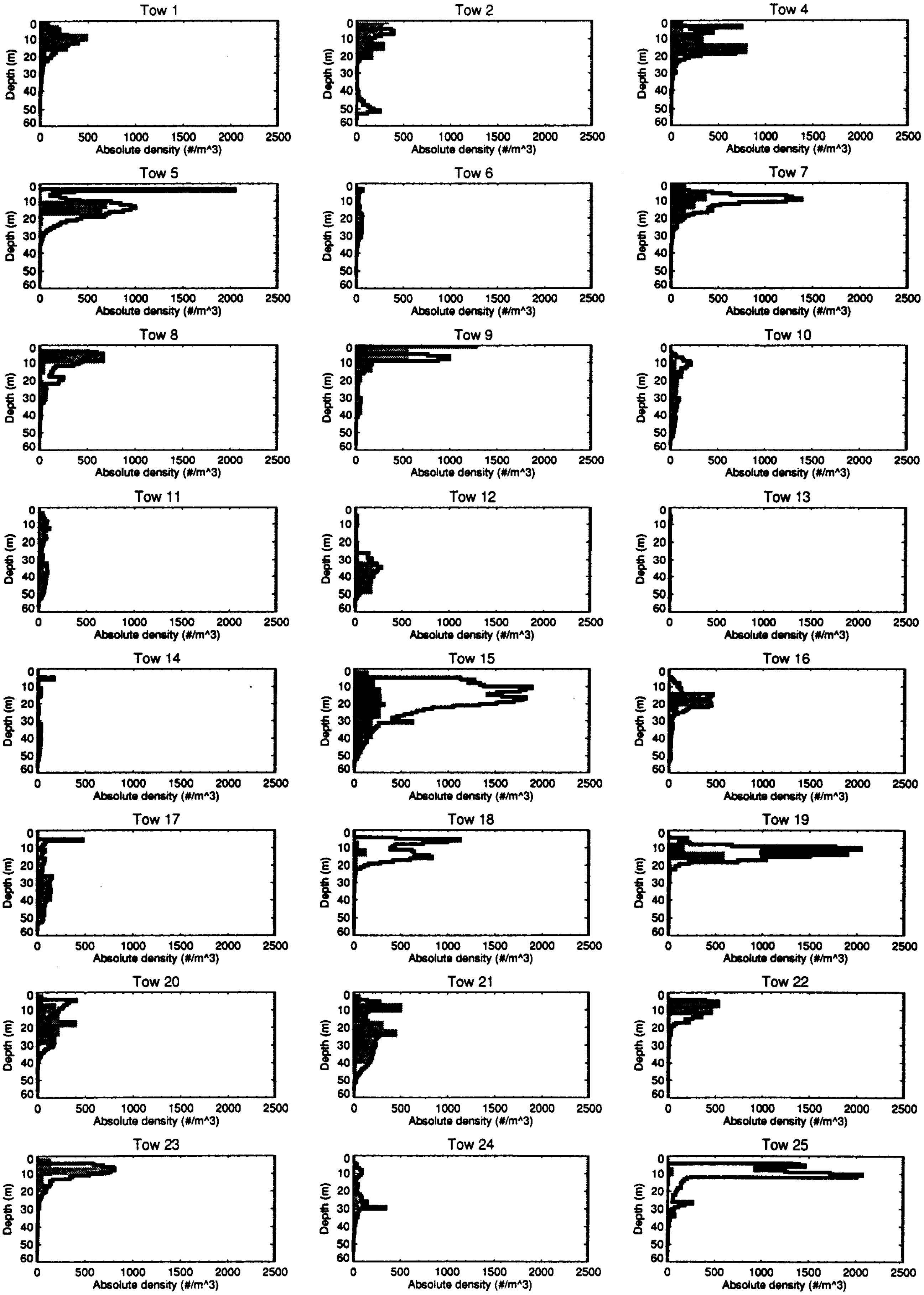
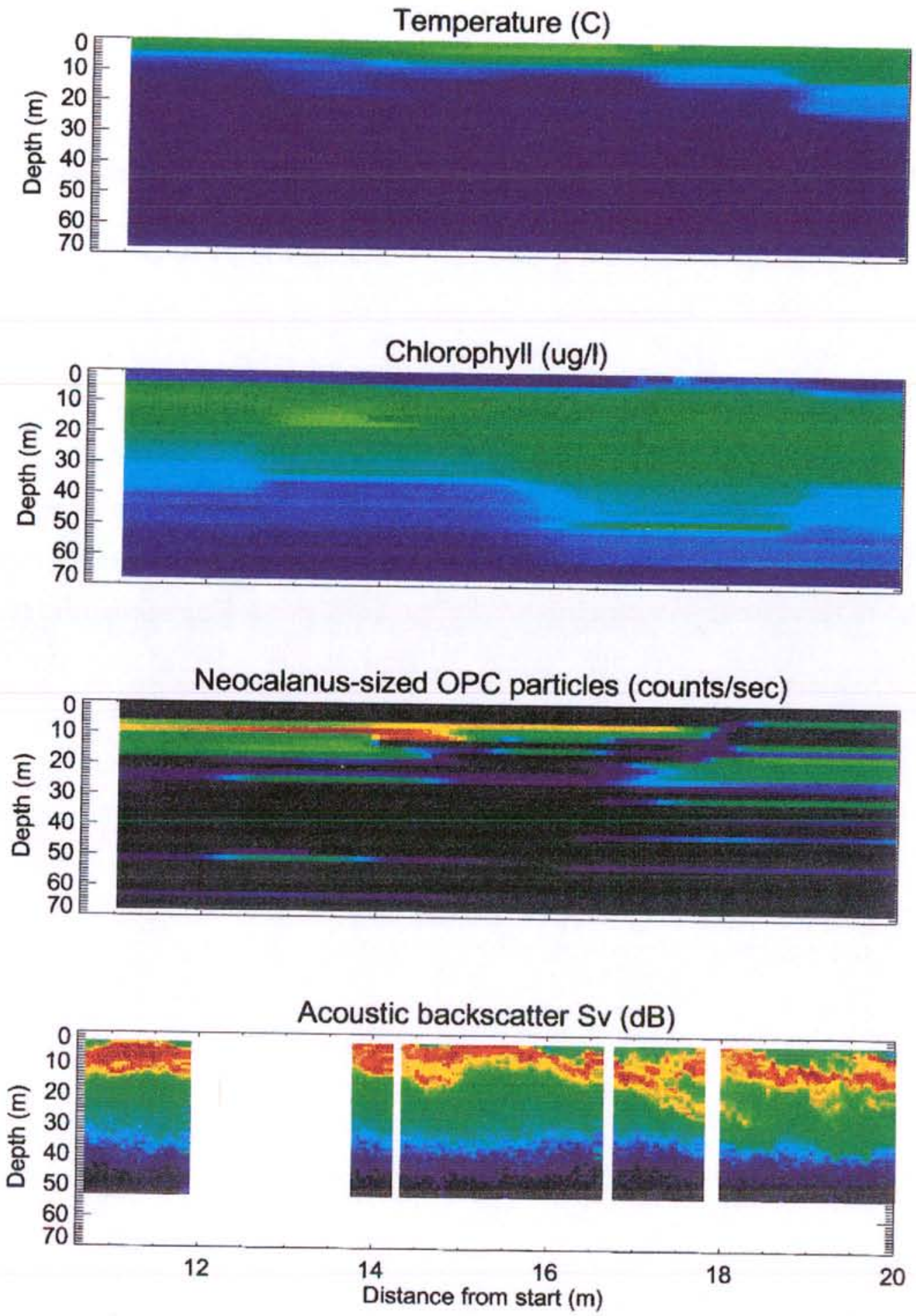

Variance spectra of zooplankton patches
spectrum
Knight Is Pass (day 1)
patch sizes
Slope = -4.23/3
spectrum
Wells to Unakwik (day 2)
patch sizes
Slope = -5.14/3
spectrum
Knight Is Pass (#2) (day 3)
patch sizes
Slope = -3.97/3
spectrum
NGOA (day 4)
patch sizes
Slope = -5.42/3
spectrum
Montague Strait (day 5)
patch sizes
Slope = -4.22/3
spectrum
Hinchinbrook (day 6)
patch sizes
Slope = -4.67/3
spectrum
Deep hole/Perry/Wells (day 7)
patch sizes
Slope = -4.77/3
spectrum
Central to Orca (day 9)
patch sizes
Slope = -4.74/3
PSD
10⁰ 10¹ 10² 10³ 10⁴ 10⁵ 10⁶ 10⁷
0.01
0.10
1.00
10.00
Frequency (cycles/km)
0.1
1.0
Patch size (km)

Figure 4.



Neocalanus V depth distributions: 420kHz acoustic (black) and MOCNESS (grey) compared

Figure 5.


Temperature (C)

Chlorophyll (ug/l)

Neocalanus-sized OPC particles (counts/sec)

Acoustic backscatter Sv (dB)

Figure 6.

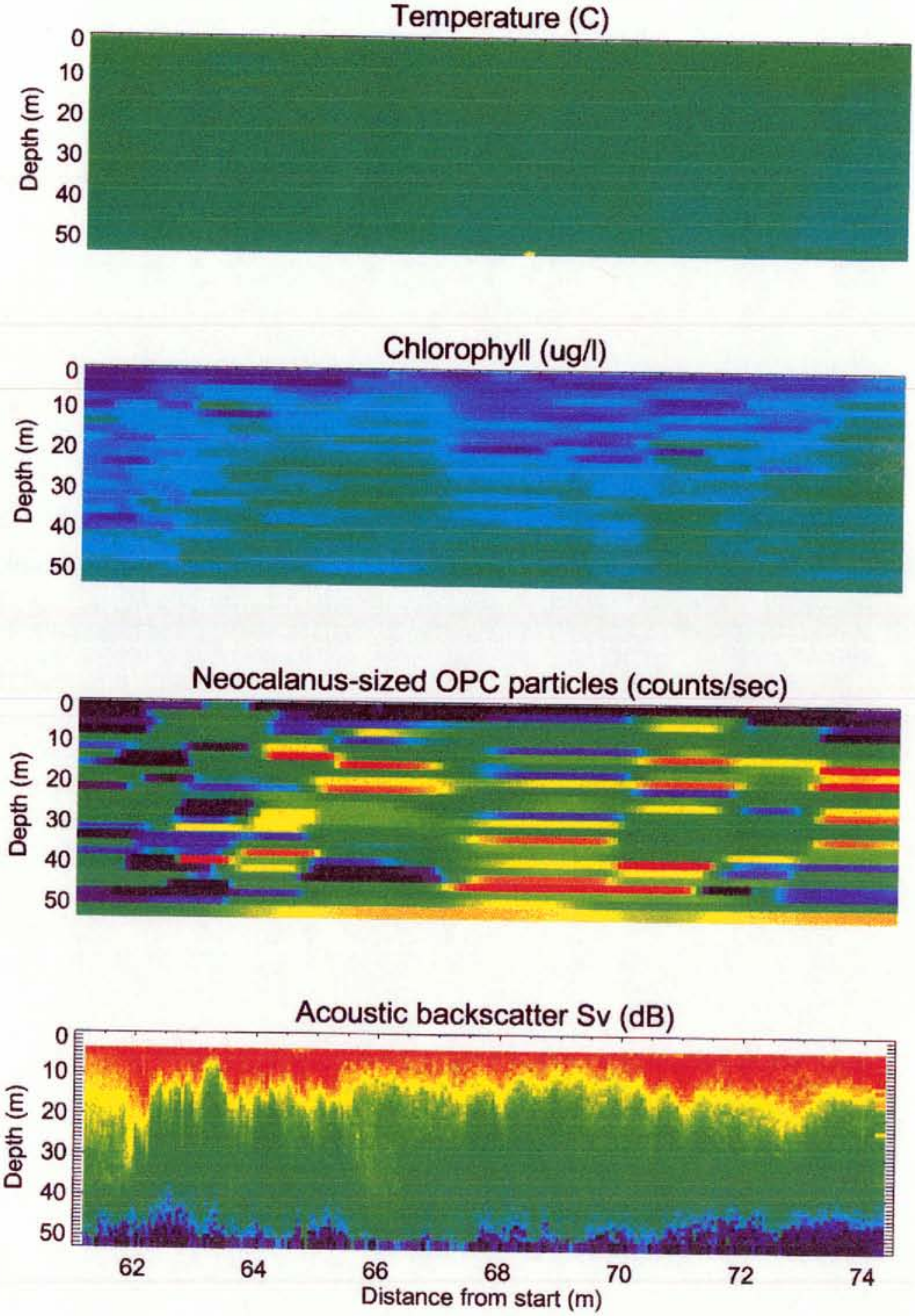
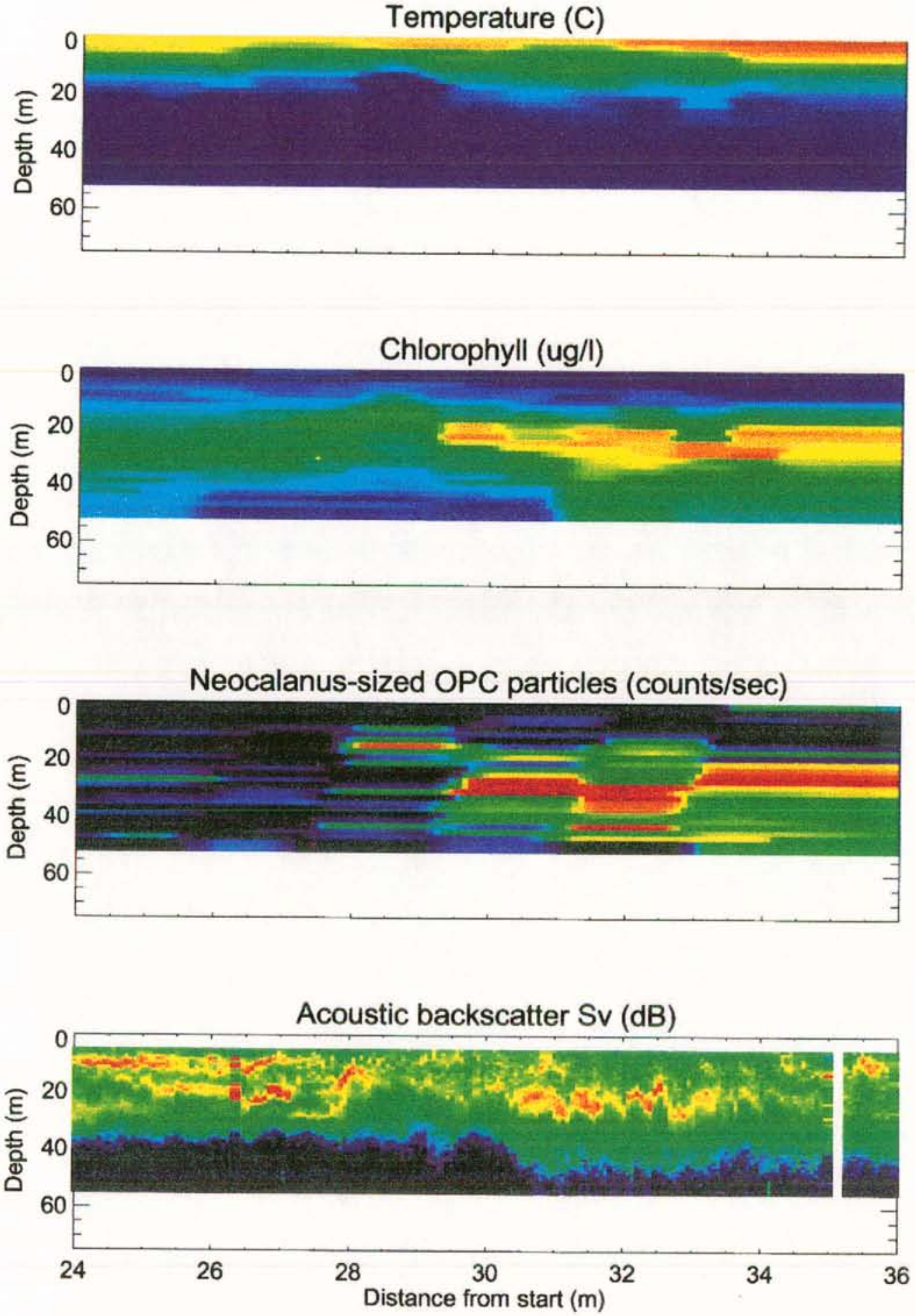

Temperature (C)
Chlorophyll (ug/l)
Neocalanus-sized OPC particles (counts/sec)
Acoustic backscatter Sv (dB)
Depth (m)
0
10
20
30
40
50
62
64
66
68
70
72
74
Distance from start (m)

Figure 7.


Temperature (C)

Chlorophyll (ug/l)

Neocalanus-sized OPC particles (counts/sec)

Acoustic backscatter Sv (dB)

Figure 8.

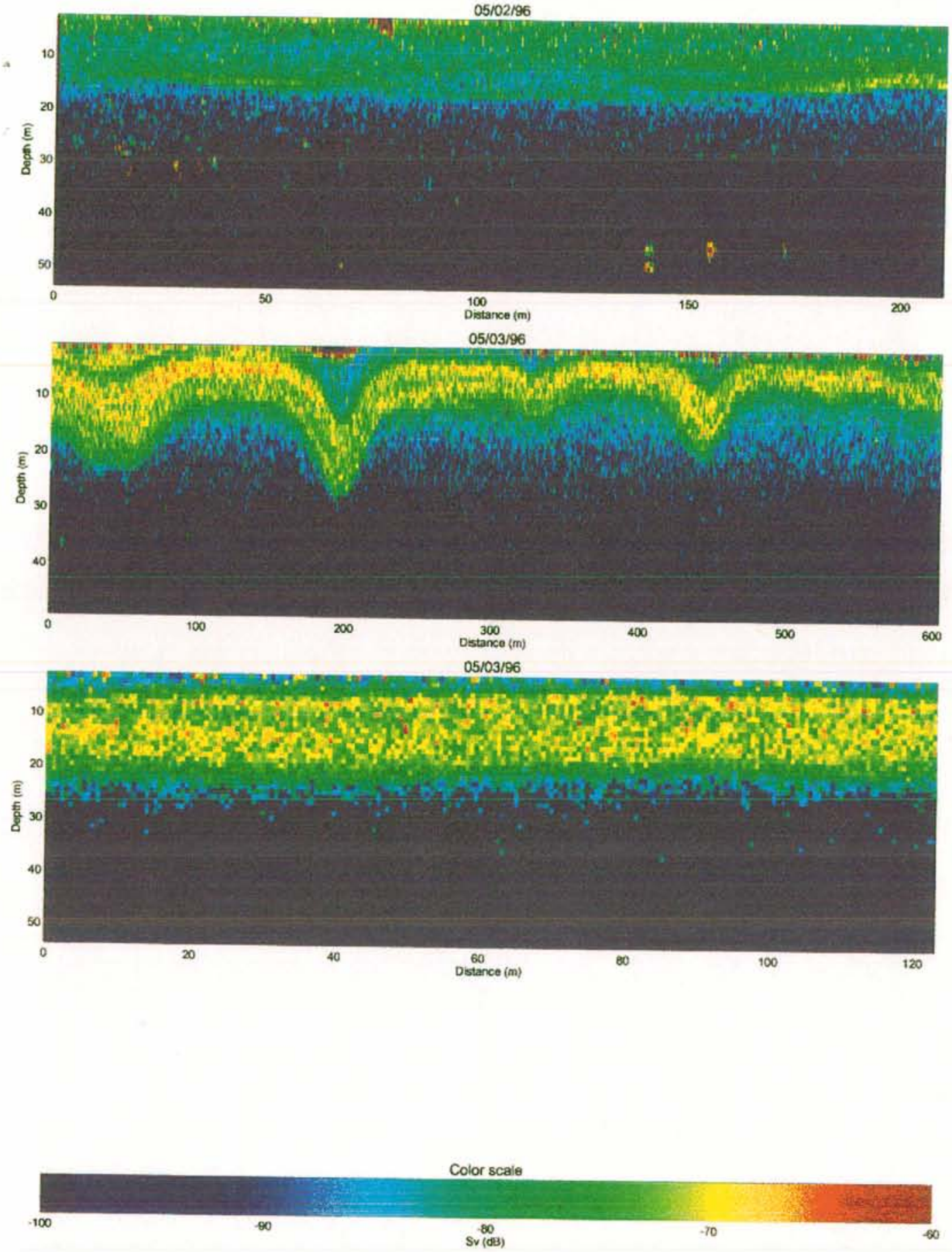


Figure 7. Typical scattering layers of zooplankton at 420 kHz

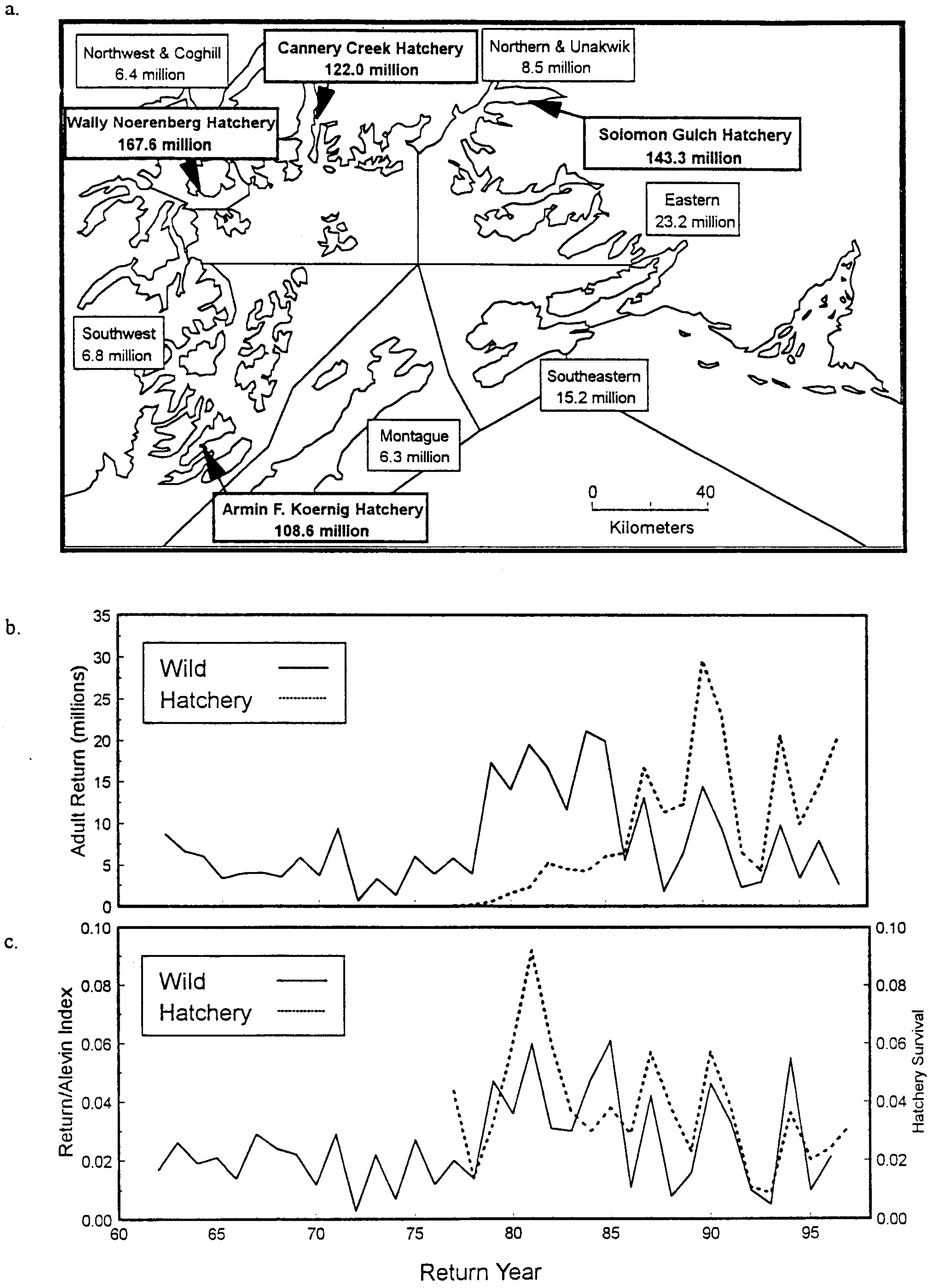

a.
Northwest & Coghill
6.4 million
Cannery Creek Hatchery
122.0 million
Northern & Unakwik
8.5 million
Wally Noerenberg Hatchery
167.6 million
Solomon Gulch Hatchery
143.3 million
Eastern
23.2 million
Southwest
6.8 million
Southeastern
15.2 million
Montague
6.3 million
Armin F. Koernig Hatchery
108.6 million
0
40
Kilometers
b.
Adult Return (millions)
35
30
25
20
15
10
5
0
Wild
Hatchery
c.
Return/Alevin Index
0.10
0.08
0.06
0.04
0.02
0.00
Hatchery Survival
60
65
70
75
80
85
90
95
Return Year

Figure 1

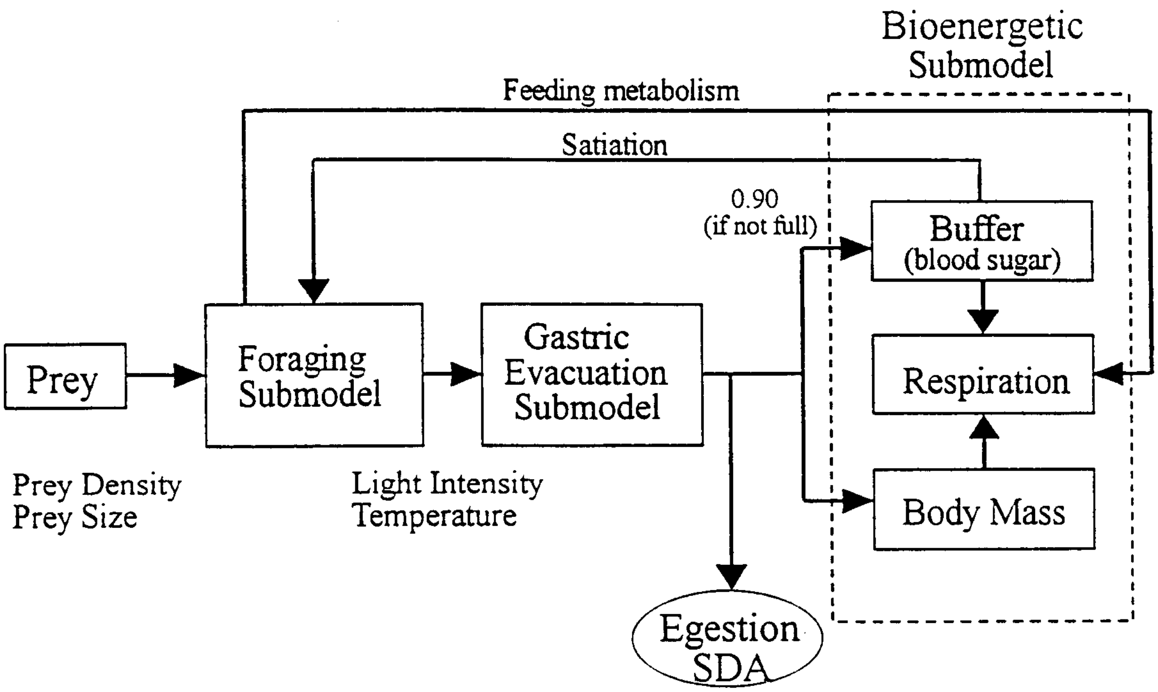
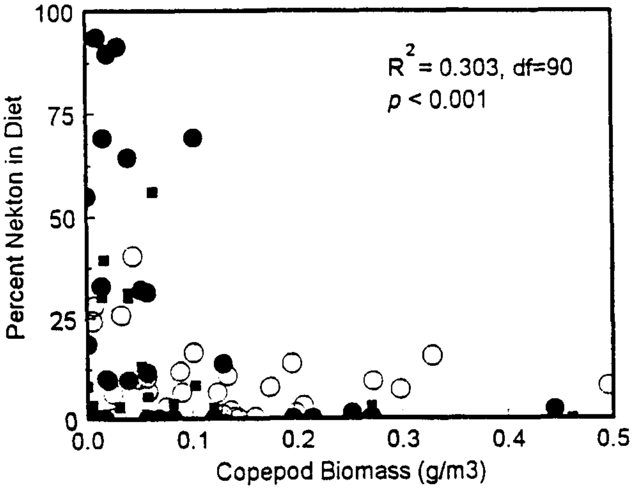

Bioenergetic Submodel
Feeding metabolism
Satiation
0.90 (if not full)
Buffer (blood sugar)
Prey
Foraging Submodel
Gastric Evacuation Submodel
Respiration
Body Mass
Prey Density
Prey Size
Light Intensity
Temperature
Egestion SDA

Figure 2



100
75
50
25
0
0.0
0.1
0.2
0.3
0.4
0.5
Percent Nekton in Diet
Copepod Biomass (g/m3)
$R^2 = 0.303$, df=90
$p < 0.001$

Figure 3

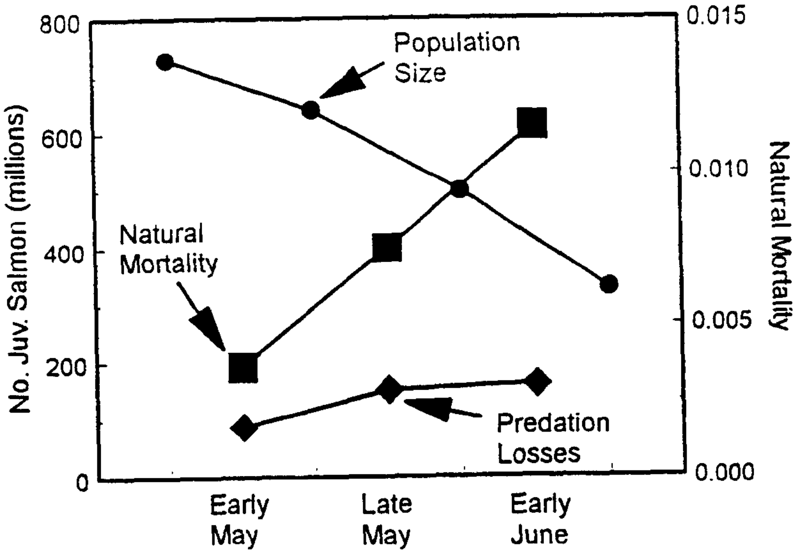

800
600
400
200
0
No. Juv. Salmon (millions)
0.015
0.010
0.005
0.000
Natural Mortality
Population Size
Natural Mortality
Predation Losses
Early May
Late May
Early June

Figure 4

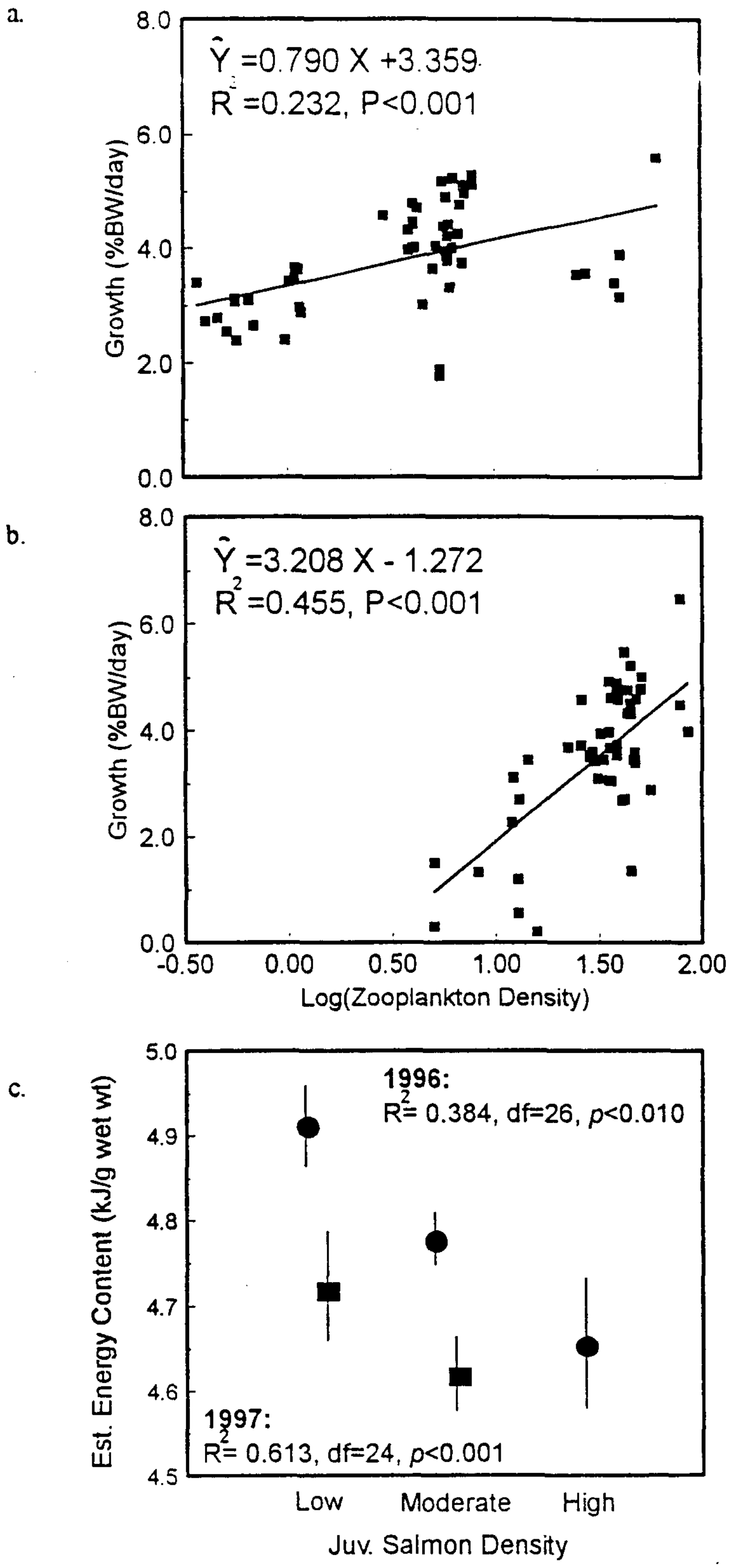
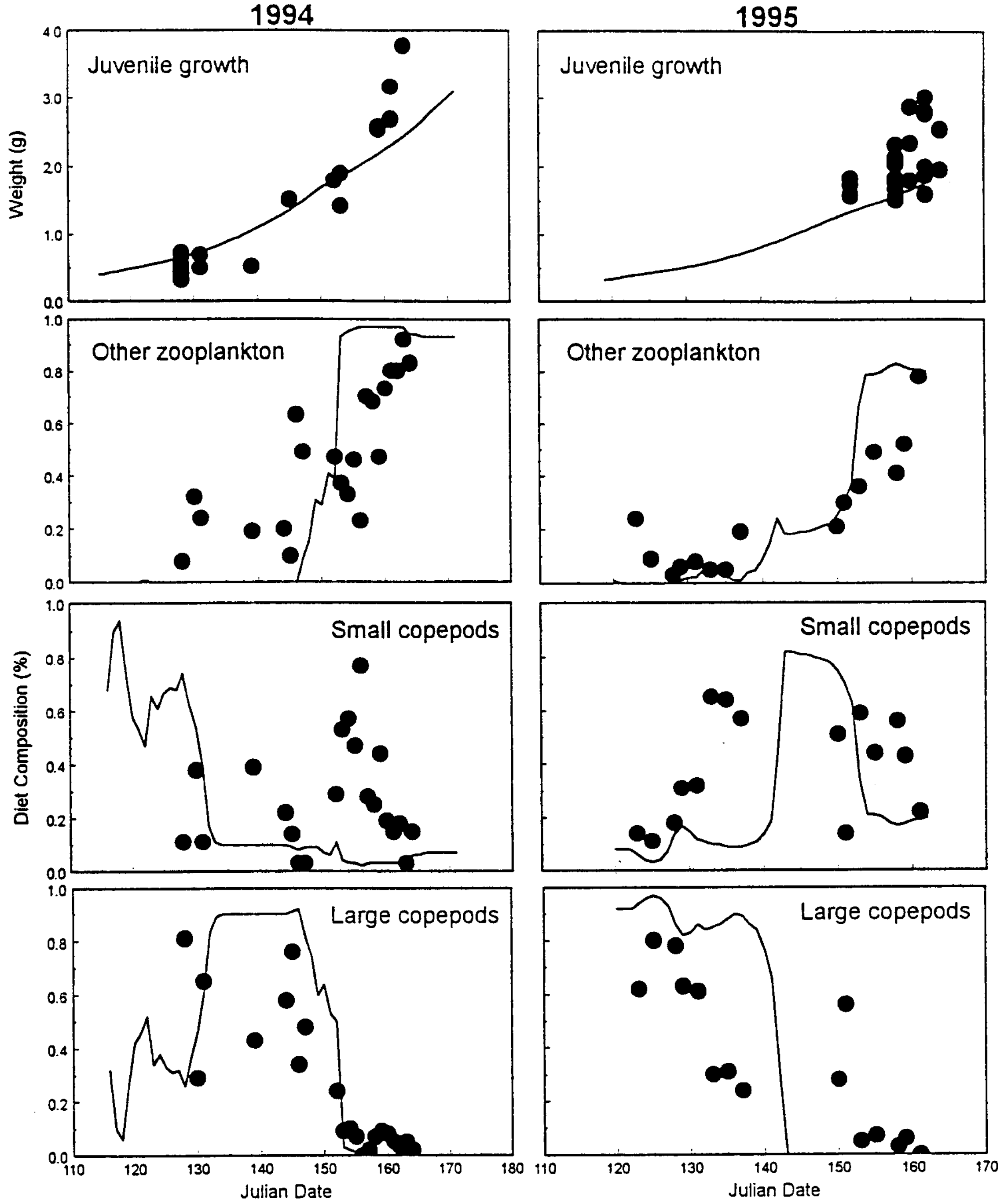
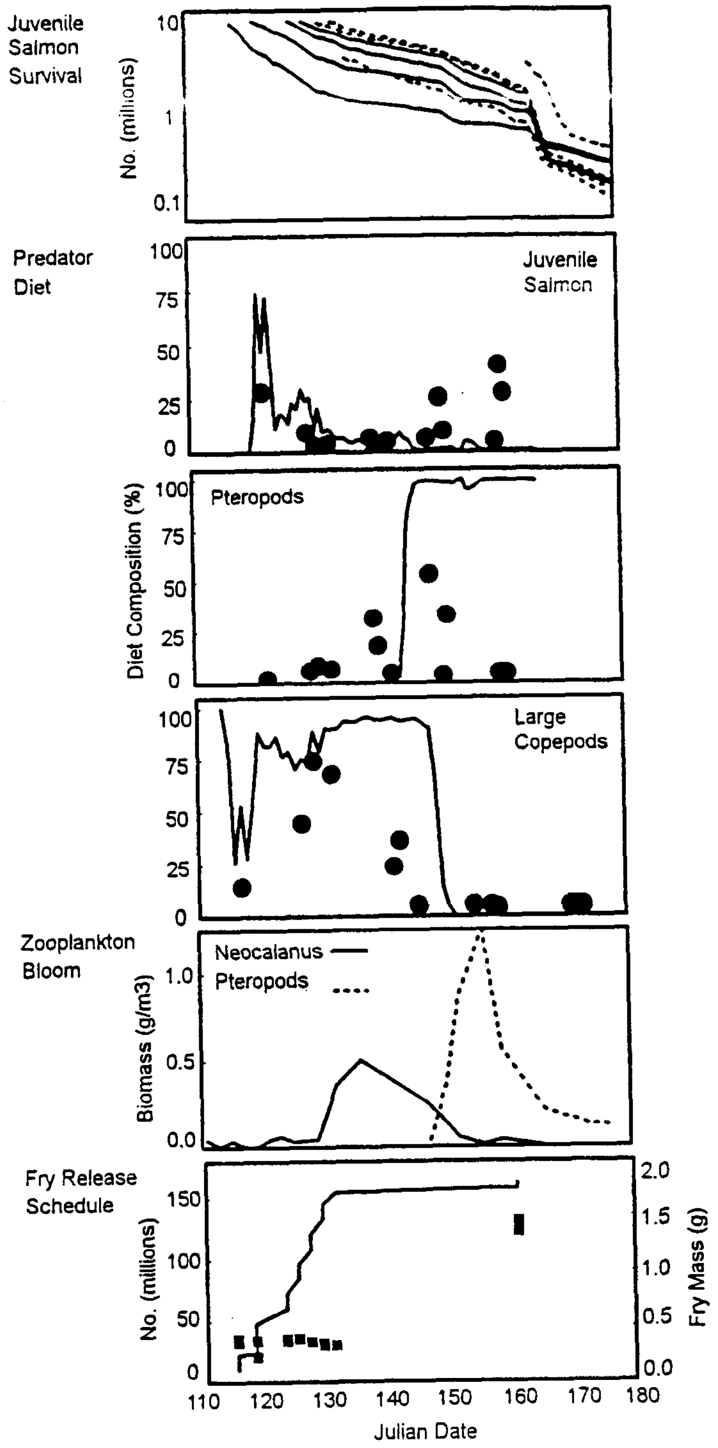

a.
8.0
6.0
4.0
2.0
0.0
Growth (%BW/day)
$\hat{Y}$ =0.790 X +3.359
R^2 =0.232, P<0.001
b.
8.0
6.0
4.0
2.0
0.0
Growth (%BW/day)
$\hat{Y}$ =3.208 X - 1.272
R^2 =0.455, P<0.001
-0.50
0.00
0.50
1.00
1.50
2.00
Log(Zooplankton Density)
c.
5.0
4.9
4.8
4.7
4.6
4.5
Est. Energy Content (kJ/g wet wt)
1996:
R^2= 0.384, df=26, p<0.010
1997:
R^2= 0.613, df=24, p<0.001
Low
Moderate
High
Juv. Salmon Density

Figure 5



1994
1995
Juvenile growth
Juvenile growth
Weight (g)
0.0
1.0
2.0
3.0
4.0
Other zooplankton
Other zooplankton
Small copepods
Small copepods
Large copepods
Large copepods
Diet Composition (%)
0.0
0.2
0.4
0.6
0.8
1.0
110
120
130
140
150
160
170
180
Julian Date
110
120
130
140
150
160
170
Julian Date

Figure 6



Juvenile Salmon Survival
No. (millions)
10
1
0.1
Predator Diet
Juvenile Salmon
100
75
50
25
0
Diet Composition (%)
Pteropods
Large Copepods
Zooplankton Bloom
Biomass (g/m3)
Neocalanus
Pteropods
1.0
0.5
0.0
Fry Release Schedule
No. (millions)
150
100
50
0
Fry Mass (g)
2.0
1.5
1.0
0.5
0.0
110
120
130
140
150
160
170
180
Julian Date

Figure 7

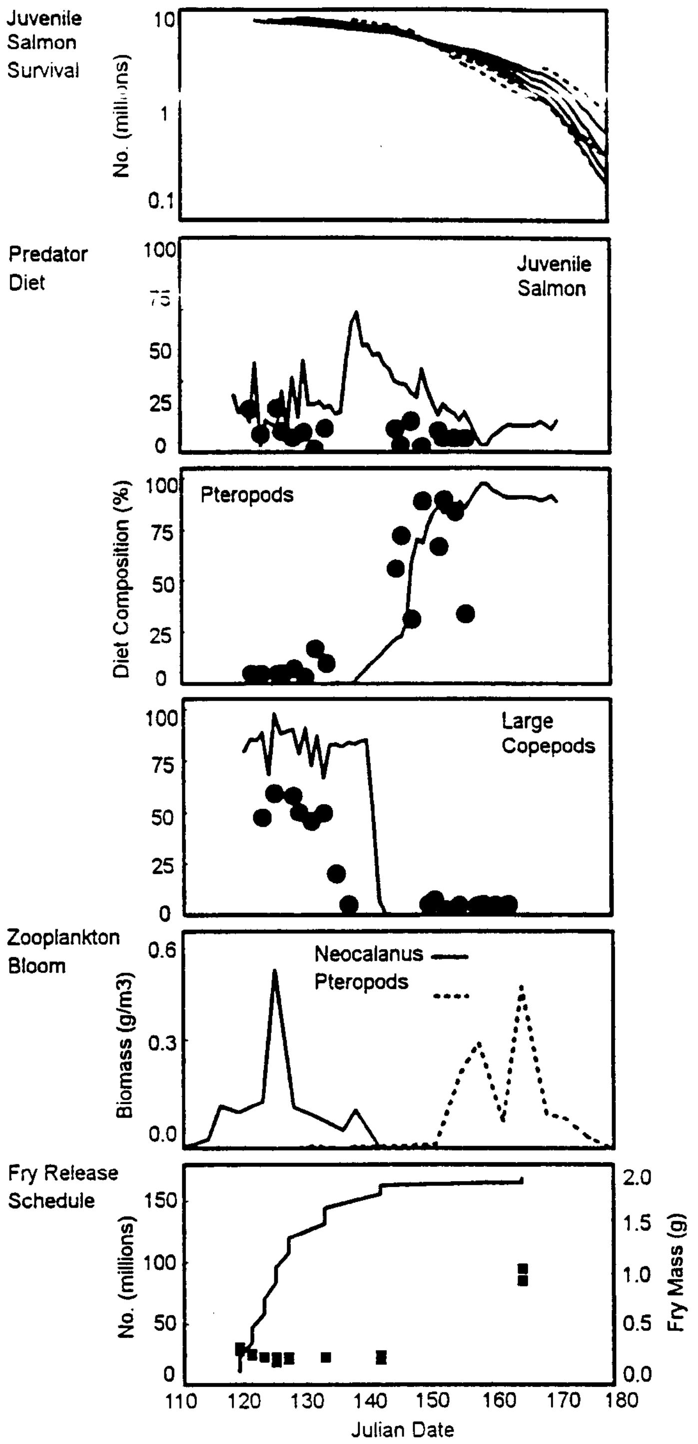

Juvenile Salmon Survival
No. (millions)
10
1
0.1
Predator Diet
Juvenile Salmon
100
75
50
25
0
Diet Composition (%)
Pteropods
100
75
50
25
0
Large Copepods
100
75
50
25
0
Zooplankton Bloom
Neocalanus
Pteropods
Biomass (g/m3)
0.6
0.3
0.0
Fry Release Schedule
No. (millions)
150
100
50
0
Fry Mass (g)
2.0
1.5
1.0
0.5
0.0
110
120
130
140
150
160
170
180
Julian Date

Figure 8

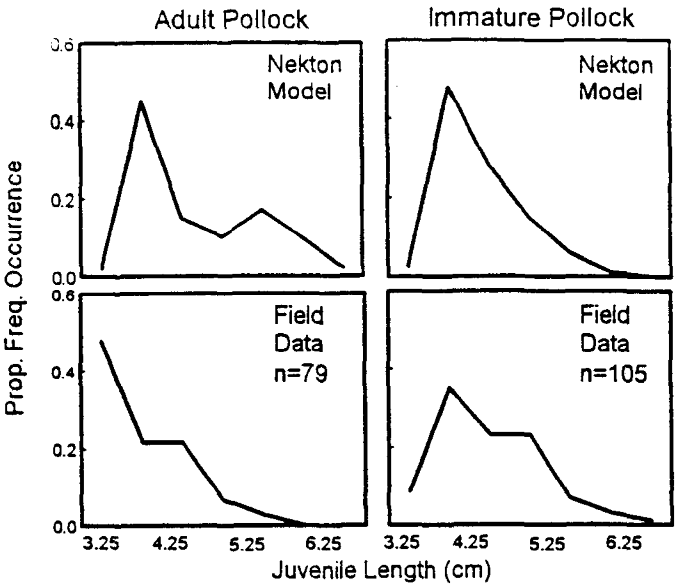

Adult Pollock
Immature Pollock
Nekton Model
Nekton Model
Field Data n=79
Field Data n=105
Prop. Freq. Occurrence
0.6
0.4
0.2
0.0
0.6
0.4
0.2
0.0
3.25
4.25
5.25
6.25
3.25
4.25
5.25
6.25
Juvenile Length (cm)

Figure 9

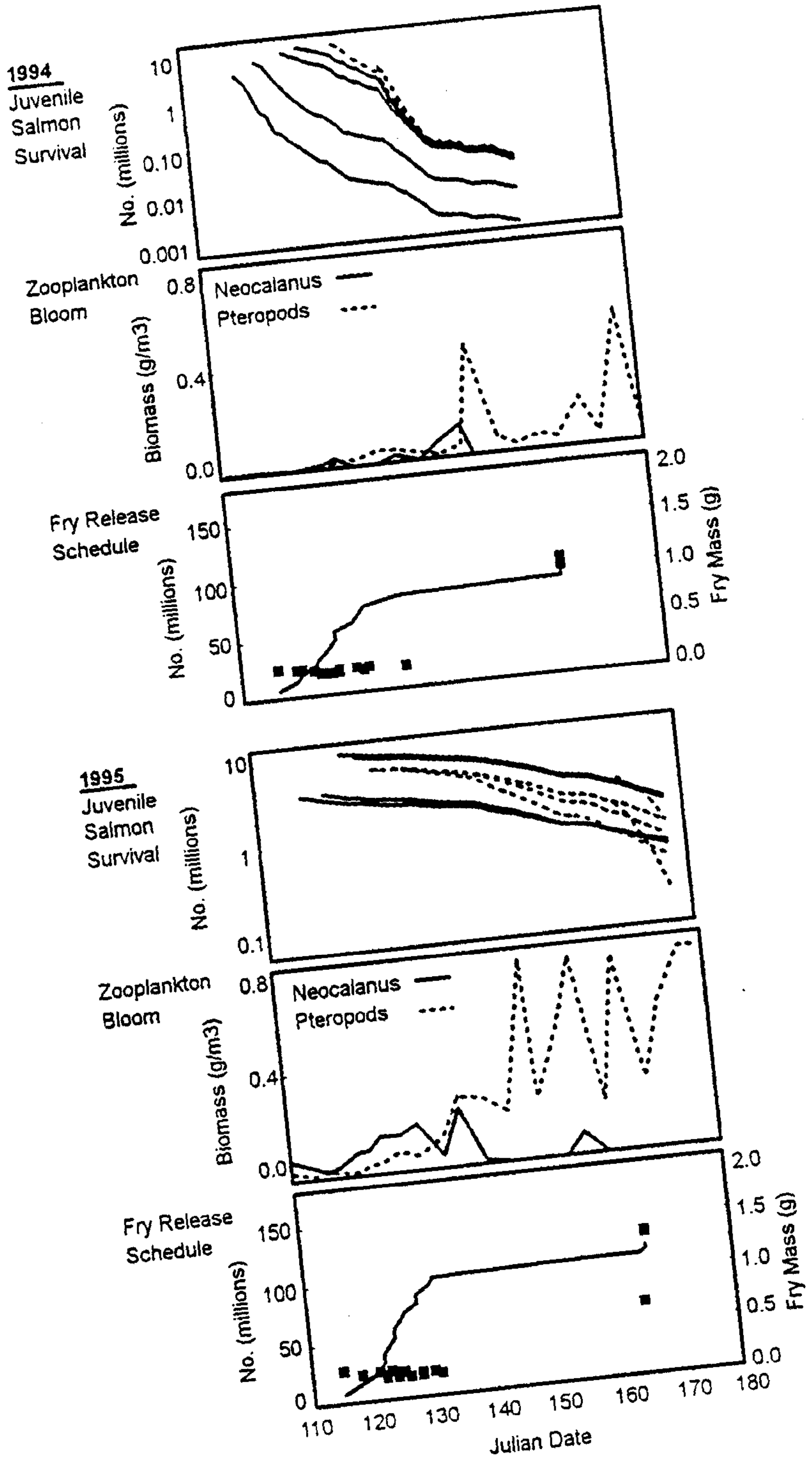

1994
Juvenile Salmon Survival
No. (millions)
10
1
0.10
0.01
0.001
Zooplankton Bloom
Biomass (g/m3)
0.8
0.4
0.0
Neocalanus
Pteropods
Fry Release Schedule
No. (millions)
150
100
50
0
Fry Mass (g)
2.0
1.5
1.0
0.5
0.0
1995
Juvenile Salmon Survival
No. (millions)
10
1
0.1
Zooplankton Bloom
Biomass (g/m3)
0.8
0.4
0.0
Neocalanus
Pteropods
Fry Release Schedule
No. (millions)
150
100
50
0
Fry Mass (g)
2.0
1.5
1.0
0.5
0.0
110
120
130
140
150
160
170
180
Julian Date

Figure 10

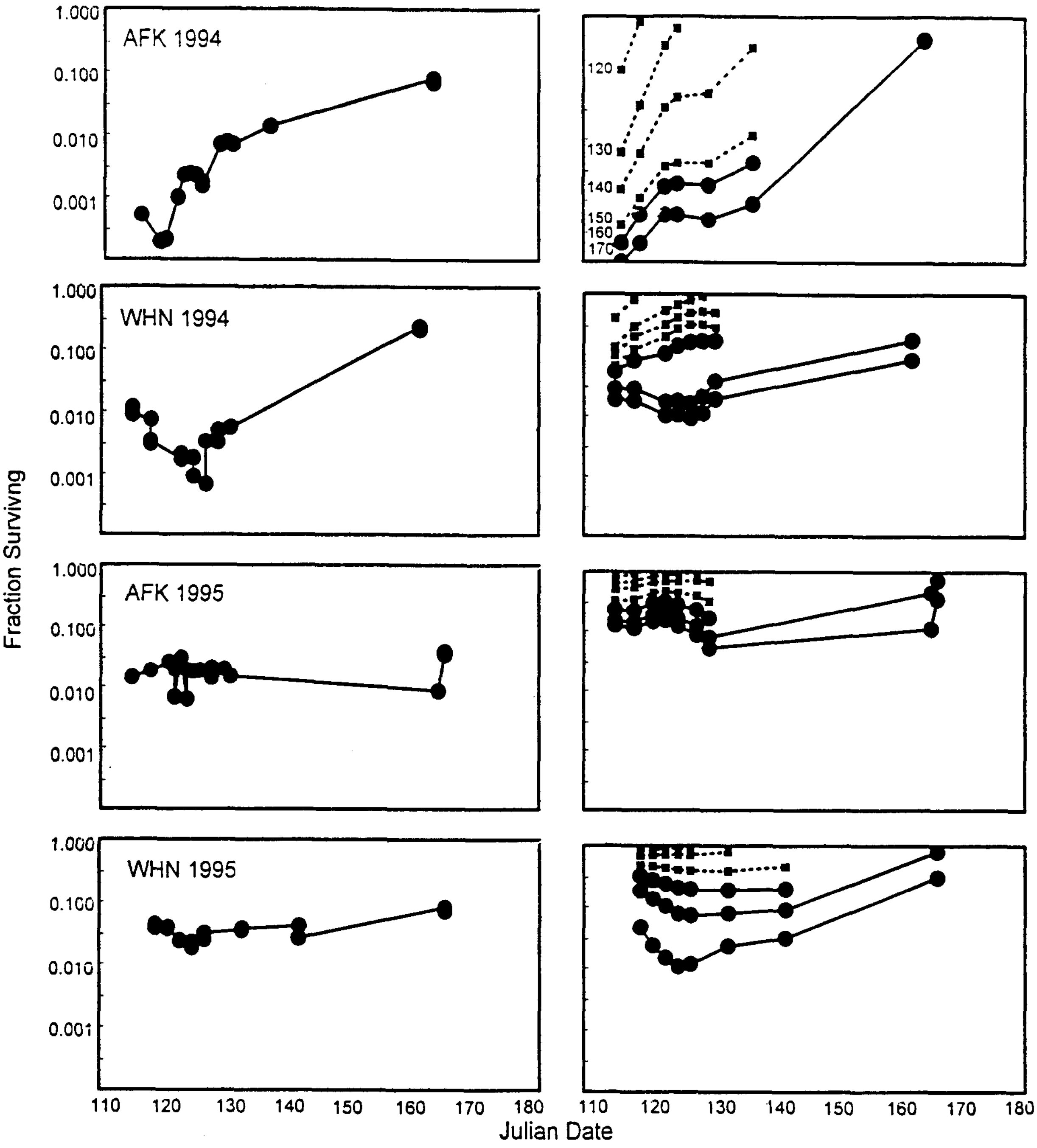

Fraction Survivng
1.000
0.100
0.010
0.001
AFK 1994
WHN 1994
AFK 1995
WHN 1995
120
130
140
150
160
170
110
120
130
140
150
160
170
180
Julian Date

Figure 11

Chapter 5

Biophysical Modeling and Remote Sensing

Exxon Valdez Oil Spill
Final Report

Biophysical Modeling and Validation Through Remote Sensing

Restoration Project 99320-R
Final Report

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June 1999

Biophysical Modeling and Validation Through Remote Sensing

Restoration Project 99320-R
Final Report

Study History: This project is the result of an internal reorganization within the Sound Ecosystem Assessment (SEA) program. Some of the work performed under SEA core projects 95320-G and 95320-J in FY94 and FY95 has been done under this project since. This project has constructed accurate one- and three-dimensional models of coupled upper layer (100 meters) physical, phytoplankton, and zooplankton dynamics in Prince William Sound. From these models, we can understand the sources and mechanisms of variability in food for young Pacific herring and pink salmon.

Abstract: The one-dimensional coupled physical and biological modeling of phytoplankton and zooplankton dynamics in Prince William Sound and the Gulf of Alaska have shown there to be two general types of response to different springtime physical dynamics. Warm, quiescent springs lead to brief intense phytoplankton blooms and relatively low zooplankton biomass, whereas, colder, stormy springs lead to longer phytoplankton blooms and higher zooplankton biomass. The three-dimensional model showed that these different types of responses also occur within the same year in different portions of Prince William Sound due to different local wind forcing. This bio-physical modeling work has enabled us to understand some of the causes of variability in food for larval Pacific herring and juvenile Pacific herring and pink salmon. The knowledge gained from this study should play an integral role in understanding the variability in these stocks and how we can best manage them to ensure their recovery.

Key Words: biophysical modeling, biological oceanography, physical oceanography, phytoplankton, Prince William Sound, spring bloom, zooplankton

Citation: Eslinger, David L. 1999. Biophysical Modeling and Validation Through Remote Sensing, *Exxon Valdez* Oil Spill Final Report (Restoration Project 99320-R), Alaska Department of Fish and Game, Anchorage, Alaska.

Chapter 5: 98320R

Citations to published articles

Eslinger, D.L., R.T. Cooney, C.P. McRoy, A. Ward, T.C. Kline, Jr., E.P. Simpson, J. Wang and J.R. Allen. 2001. Plankton dynamics: observed and modelled responses to physical conditions in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):81-96.

Wang, J., M. Jin, E.V. Patrick, J.R. Allen, D.L. Eslinger, C.N.K. Mooers, and R.T. Cooney. 2001. Numerical simulations of the seasonal circulation patterns and thermohaline structures of Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):132-148.

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Executive Summary:

Biophysical modeling of phytoplankton and zooplankton, in combination with field data collected as part of 320-G and 320-H, shows that phytoplankton and zooplankton populations in Prince William Sound and the northern Gulf of Alaska are determined by the winds and the differences between air and water temperatures which occur over a relatively short, critical time period in early spring. Although this critical time period may be as short as two weeks, the meteorological conditions occurring during that time will play a dominant role in the dynamics of the phytoplankton and zooplankton populations for the rest of the summer. Changes in the amount of convective mixing, caused by cold air, and of wind mixing, caused by high winds, during the early part of the phytoplankton bloom change the timing and duration of the bloom, the total primary production occurring during the bloom, and the partitioning of that primary production between the upper water column food chain, and the benthic food chain.

Both one-dimensional and three-dimensional models of the coupling between physical forcing and the nutrient, phytoplankton and zooplankton dynamics have been constructed. We devised a method of using winds, measured at various stations within the PWS region, in conjunction with local knowledge of the effects of topographic steering to develop a tool with which we produced spatially varying wind fields. We used these spatially varying winds and the same model bathymetry as the physical modeling effort is using, to construct a three-dimensional model of plankton dynamics. We examined the effects of bathymetry and varying winds on the plankton populations. The physical model results are based on a drastically different modeling grid in the vertical direction and could not be used directly to advect plankton in this model. Therefore, the 3-D plankton model does not include horizontal advection. The effects shown are due to local processes only. We found that local effects are significant and that this model does a good job in simulating the results of field programs.

We found the springtime physical and plankton dynamics in Prince William Sound to be similar to those for other high latitude systems, *i.e.*, spring phytoplankton and zooplankton blooms occur in response to vernally increasing air temperatures and decreasing wind speeds, stratification-induced nutrient limitation during the summer and a fall boom in response to mixing caused by cooling temperature and increasing wind speeds. However, we have shown from both the one-dimensional and three-dimensional modeling efforts that subtle variations in the timing, strength, and variability of the meteorological forcing during the early spring lead to substantial variations in the total new primary production by phytoplankton, the transfer of that production to the zooplankton, and the partitioning of the production between the upper water column and the mid-level or benthic components of the food web. The system we have described is an accurate simulation of the field observations during the years of the SEA study. Although this system is complex and highly nonlinear in its response to slight variations, it can now be understood and, to some extent, predicted. This bio-physical modeling work has enabled us to understand some of the causes of variability in food for larval Pacific herring and juvenile Pacific herring and pink salmon. The knowledge gained from this study should play an integral role in understanding the variability in these stocks and how we can best manage them to ensure their recovery.

Introduction:

Pacific herring and pink salmon have been identified as non-recovering resources injured by the *Exxon Valdez* oil spill. An ecosystem approach has been recognized by the EVOS Trustee Council as being necessary to reaching an understanding of the underlying processes and variables which may be constraining recovery of these injured resources. The currently proposed work is critical to the ecosystem study being undertaken by the SEA program. The role of the physical environment in controlling plankton populations, and the role of these populations in the life history of Pacific herring and pink salmon, must be understood for the intelligent, informed planning of successful restoration efforts.

This project directly addresses the SEA pink salmon and Pacific herring restoration objectives. The phytoplankton and zooplankton serve directly as food for both herring and pink salmon at various life stages. Two large calanoid copepod species, *Neocalanus cristatus* and *N. plumchrus*, in particular, are thought to be potentially important as both a dietary item and a refuge from predation for pink salmon. Larval and juvenile herring feed on different stages of calanoid copepods, which reproduce throughout the spring and summer. The reproductive effort of these copepods is dependent on the timing, magnitude, and duration of the phytoplankton primary production in the spring bloom period and throughout the summer. The interactions between the various types of phytoplankton (*e.g.,* diatoms, flagellates) and zooplankton (*e.g.,* oceanic copepods, neritic copepods) varies both between and within years. The timing of the major increase in biomass of phytoplankton or zooplankton, sometimes called the spring phytoplankton or zooplankton bloom, respectively, may be important to the first feeding and subsequent survival of the larval herring and juvenile herring and salmon, *e.g.* Cushing's match-mismatch hypothesis. This project examines these issues through the use of numerical models, remote sensing, and field observations.

Our results indicate that physical forcing dominates the dynamics at the lower trophic levels. The physical signal propagates up through the food chain and has relevant consequences months after the biological and physical interactions actually occurred. These effects are highly nonlinear, but can be accurately simulated using the present model.

Objectives:

There have been seven major objectives over the life of this project:

1. To determine the spatial and temporal variability of the physical environment using a combination of remote sensing techniques and field observations.
2. To supply satellite-derived sea surface temperature imagery to other SEA investigators.
3. To deploy and maintain the C-LAB buoy, which will provide high temporal resolution time series of wind velocity, air temperature, surface water temperature, and subsurface temperatures at 10 depths.
4. To construct a one-dimensional model of the physical/biological processes affecting

plankton dynamics in Prince William Sound.

5. To examine interannual variability in plankton stocks using the 1-D model and field data.
6. To construct a three-dimensional model of the physical/biological processes affecting plankton dynamics in Prince William Sound.
7. To examine spatial variability in plankton stocks using the 3-D model and field data.

Our success in meeting these objectives will be addressed as follows: objectives 1 through 3 are directly addressed in the report; objectives 4 and 5 are addressed in the attached draft manuscript, which is under preparation for publication in a special SEA issue of *Fisheries Oceanography*; and objectives 6 and 7 are addressed in this document. Initially, objectives 6 and 7 were also to be covered under that manuscript, however, page and space constraints have prevented that. Therefore, they are addressed separately in this report..

Methods:

Objectives 1, 2 and 3

These three objectives are more operational objectives designed to support the other four modeling objectives, and to support the needs of other SEA researchers. The first objective, to determine the spatial and temporal variability of the physical environment using a combination of remote sensing techniques and field observations, is addressed in some detail in Appendix A, as background material. In addition, we will illustrate the measured biological and physical variability found in Prince William Sound as we address objectives 2 and 3: to supply satellite-derived sea surface temperature imagery to other SEA investigators, and to deploy and maintain the C-LAB buoy, which will provide high temporal resolution time series of wind velocity, air temperature, surface water temperature, and subsurface temperatures at 10 depths, respectively.

We operated a satellite ground station to receive and process High Resolution Picture Transmission (HRPT) imagery from NOAA satellites carrying Advanced Very High Resolution Radiometer (AVHRR) sensors. From this data, we are able to derive sea surface temperature. Figure 1 shows the SEA Gulf of Alaska (GOA) remote sensing region. We used the standard Alaskan State Plane projection (the federal version, not the state version) which uses an Alber's conic projection with center at 60° North Latitude, 154° West Longitude and standard parallels at 55° and 65° North Latitude. Images were projected with a resolution of 1.113 kilometers per pixel, the maximum available from the satellite, for this region. Because Prince William Sound is fairly small within this imagery, a smaller section was extracted and mapped at 555 meters per pixel resolution. This did not increase the resolution of the actual satellite data, but allowed users to extract data from the imagery with a higher registered resolution.

Excessive cloud cover was a frequent problem. To get around the cloudiness issue, in 1995, we began calculating weekly composite images. The most cloud free images from each day were selected and the mathematical mean of all co-registered points was calculated. Every attempt was made to use imagery from the same satellite and time of day, when weather permitted.

However, at times, we averaged between satellites and images for different times of day. Although the raw data from all satellites is theoretically converted to be comparable, there are still some problems with inter-satellite differences. There may be large diurnal differences as well. However, even given these caveats, it was felt that there was merit in producing composite images. These images sacrifice some absolute accuracy for spatial coverage. They were not used in any of the analyses down with the imagery (as a data source for the salmon model, for instance), however, they allowed investigators to put field observations from within the Sound into a regional context. Unfortunately, these images were time-intensive to produce, and were discontinued in 1996 as budget constraints limited the amount of manpower available.

We processed and archived AVHRR SST since 1994, and made an archive of over 10,000 SST images available to the SEA project. These images are stored on 8 mm tape(the majority), CD-ROM (three years worth), and hard disk (working imagery). In early FY97, we delivered a subset of these images to the Prince William Sound Science Center (PWSSC) in CD-ROM format, for use by the PWSSC SEA investigators. Data were delivered as both imagery and as binary data files. Since that time, we have been delivering the imagery over the world wide web as requested. To aid in our distribution of these data, we maintained a web site as part of the Alaskan Environmental Satellite Oceanography Project (AESOP). This site can be found at http://aesop.ims.uaf.edu:8000/index.html. From this site, on can view small, thumbnail images, for both the GOA and PWS regions, of all passes collected on a particular day. Because of the tremendous number of images acquired daily, some of the older images are no longer on line.

At the initiation of the SEA program, we expected to have ocean color data available from both the Ocean Color and Temperature Scanner (OCTS) on the Japanese ADEOS satellite and the Sea-viewing Wide Field-of-view (SeaWiFS) sensor on the NASA/Orbital Sciences SeaStar satellite. Unfortunately, launches of both were pushed back by several years and no data were available during the SEA field season. However, some SeaWiFS data was collected in spring on 1998 and was used to examine the character of the spring phytoplankton bloom. The raw data were collected in Fairbanks and sent to NASA for archival. The data were processed using the NASA SeaDAS processing package and the standard NASA SeaWiFS Project global ocean color algorithms. Although we recognize that these algorithms may not produce chlorophyll concentrations that are accurate for high latitude waters, they are the best currently available, they are consistent from image to image, and, therefore, they allow us to examine the timing and progression of the spring phytoplankton bloom using the SeaWiFS data.

The third objective, to deploy the Continuous-Linked Automated Buoy (C-LAB), was performed in all years. The buoy was deployed southeast of Naked Island, in Prince William Sound (Figure 2), and was one of our standard field sampling locations. The buoy measured wind speed and direction, air temperature, surface (bulk 1 meter) water temperature and fluorescence at 10 meters. In addition, the buoy had a thermistor string which measured temperature at depths of 1, 5, 10, 15, 20 , 25, 30, 50, 75, and 100 meters. Measurements were made hourly and were reported back approximately 12 to 18 times per day via the ARGOS telemetry service on the NOAA NIMBUS satellites. Data were automatically sent to IMS and were processed and displayed on the web in near real time. The C-LAB web site can be reached from the AESOP site given above or directly at http://murre.ims.alaska.edu:8000/~eslinger/CLAB/clab.html.

Weather made the timing of the initial buoy deployment variable. During the course of the SEA project, we replaced the two original thermistor strings with two of a newer model. These worked somewhat better, but, unfortunately, the entire mooring appeared to fail in early 1998. As we had no field program at the time, we were unable to recover the mooring until the fall, when we recovered it using the R/V/ *Alpha Helix.* Although the C-LAB did not work throughout the entire SEA project, the data it provided us has been critical in producing our understanding of the timing and duration of vernal warming, stratification, and phytoplankton response.

Objectives 4 and 5

These two objectives: to construct a one-dimensional model of the physical/biological processes affecting plankton dynamics in Prince William Sound, and to examine interannual variability in plankton stocks using the 1-D model and field data are addressed in the draft manuscript attached as Appendix A. This manuscript, *Plankton Dynamics: Observed and Modeled Responses to Physical Forcing in Prince William Sound, Alaska*, directly addresses these two objectives in addition to other issues. The methods section of interest is the **Trophodynamic Modeling** section. This manuscript is in the stage of undergoing its second round of internal (authors and other SEA team members) review, prior to submission to *Fisheries Oceanography.*

Objectives 6 and 7

Because of the availability of a wide array of data sets during 1996, the SEA team decided to focus on that year for the physical and biophysical 3-D modeling efforts. The results of our previous 1-D work showed that local winds dominate the phytoplankton and zooplankton dynamics during early spring and cause effects that continue for months thereafter. As part of the SEA project, we collected winds from 9 locations within Prince William Sound from a variety of sources, the C-LAB buoy, National Data Buoy Center (NDBC) weather buoy's and stations and airport weather stations operated by the National Weather Service (NWS). Station names, types, locations are shown in Table 1. These winds were measured at discrete points and a method was necessary to apply them over the entire model domain. Because of the high degree of steering of the winds by the local topography, it was felt that measured local winds could be applied to larger regions of the Sound using an expert system type of approach. We created a methodology to use local knowledge from pilots and fishermen to define regions within the Sound where the measured winds would apply. These regions vary in there size, shape, and extent depending on wind direction and speed. Winds for 1996 from the nine regions were run through the wind interpolation system to create a set of forcing winds that was used to examine the spatial and temporal variability of the phytoplankton and zooplankton populations of the Sound.

Results:

Objective 1, 2 and 3

Figure 3 shows a representative scene from a single pass of the NOAA-12 satellite. Sea surface temperatures (SST) are shown in color; land and clouds are shown in shades of gray. This image is as good an image as one can expect for the region, given the frequent cloud cover. Figure 4 shows a detail of Prince William Sound SST. Figure 5 shows the results of our composting efforts. These composite images were pretty, but took a great deal of extra work. We decided they were not effective us of our resources and discontinued them after 1995.

In Figure 6, the daily thumbnail collages are shown for both the GOA region and the PWS subsection. SEA investigators could access these images over the web and then request cloud free images. Additional images can be found from the Northern Gulf of Alaska link: http://murre.ims.uaf.edu:8000/AVHRR/GoA/index.html and the Prince William Sound link: http://murre.ims.uaf.edu:8000/AVHRR/PWS/index.html on the AESOP web pages. As noted on these pages, these are working image archive sites and from time to time older collage images may be removed to make room for newer images.

Figures 7 through 11 show the C-LAB results for 1994 through 1997 respectively. Recall that the instrument failed in early 1998. Those data are not shown. In all cases, one can see vernal warming, a thermal stratification and a spring phytoplankton bloom. The bloom was sort-lived, however, due to nutrient depletion in the surface stratified layers. The strong stratification began to break down in the fall when winds increased and air temperatures began to decrease. In response to the mixing of surface and sub-surface waters, a fall bloom generally occurred (*cf.*, Figures 8–10). The autumnal mixing decreased surface temperatures, while increasing deeper (relative) temperatures. A comparison of the temperature contour panels in Figures 9 and 10 give a good understanding of the process of cooling the entire water column. Note that because of the mixing of the surface heat into the upper water column, minimum upper-layer (the top 100 meters as sampled by the C-LAB) water temperature occurred in March and not in December as one might expect (*cf.* Figures 7 and 10).

Objective 4 and 5

Results are given in Appendix A, **RESULTS** section. The model results are interspersed with those of the SEA phytoplankton and zooplankton field programs.

Objectives 6 and 7

The model grid is shown in Figure 11. The grid is 130 (east–west) by 132 (north–south) with square grid cells of 1.2 kilometers per side. Samples of the regions defined by the wind interpolation system are shown in Figure 12. Notice that as wind speed increases from low to moderate easterly winds, the region using C-LAB winds (the dark purple region) expands to the west. The model initial conditions (model day 70) are shown in Figure 13 for phytoplankton and zooplankton. Model phytoplankton and zooplankton were initially homogeneous throughout the Sound, both vertically and horizontally and had concentrations of 2.0 mg Chl m^{-3} and 0.0 g wet weight m^{-2} respectively. Nutrient concentrations and water temperatures were also homogeneous, and were the same as those used in the 1-D modeling: 20 mM nitrate, 0.0 mM ammonium, 40 mM silica, and 4° C.

The time course of the model near-surface phytoplankton bloom is shown in Figure 14. These series of figures show the spatial distribution of total phytoplankton chlorophyll (both diatom and flagellate) averaged over the upper ten meters of the water column. A time series of the same vales for approximate C-LAB location, marked by the small black cross) is shown under each figure. The bold green line shows phytoplankton concentrations up to that point in time. From the model initiation on day 70, phytoplankton quickly began to increase in shallow areas near the coast and over submerged pinnacles. This was due to the effective reduction in the mixed layer depth due to the shallow water depth. By day 90 (Figure 14a), there had also been a reduction in wind speed in the western and central portions of the Sound so that the spring bloom was well underway (the yellow and orange colors). In the more eastern portions of the Sound, the winds were still high, although a slow increase in phytoplankton had occurred (the green regions). Winds in the western sound increased on day 91 and the surface phytoplankton bloom was mixed deeper into the water column, seen as a spike in the chlorophyll time series plot. By day 100, wind speeds had slightly decreased over most of the Sound, although they remained variably strong in the eastern Sound. These patterns in winds produced a wide spread, gradual increase, with lower chlorophyll concentrations occurring in the north and eastern Sound.

With the stage now set, a Sound-wide bloom quickly occurred over the next week. Near-surface chlorophyll concentrations shot up from approximately 4–6 mg Chl m^{-3} on day 100 to $\geq$20 mg Chl m^{-3} on day 104 (Figure 14c). By day 108, near-surface concentrations were declining to $\leq$16 mg Chl m^{-3} (Figure 14d), and rapidly declined to around 4 mg Chl m^{-3} by day 112 (Figure 14e). The bloom gradually declined as nutrient became limiting in areas with strong, shallow stratification. By day 130, chlorophyll concentrations in the western sound were in the 1–2 mg Chl m^{-3} range and in the 2–4 mg Chl m^{-3} range in the eastern sound (Figure 14f). Low values persisted across the sound throughout the summer (Figure 14g, h) until a small fall bloom began around day 270 and continued for about 30 days (*cf.* day 290, Figure 14i).

The model bloom progression pattern: a slow gradual sound-wide increase, then a very rapid (2 day) bloom to very high chlorophyll values, followed by a rapid, but slowing decline; is similar to that seen in the spring 1998 SeaWiFS chlorophyll data (Figure 15). The SeaWiFS imagery phytoplankton dynamics were similar to those in the 3-D model. In the SeaWiFS field data, there was a slow increase of chlorophyll over much of the sound from day 65 (not shown) through day 111 (*i.e.*, Figure 15a-c). Then over the next two days chlorophyll concentrations increased from around 2–4 mg Chl m^{-3} to $\geq$16 mg Chl m^{-3} (Figure 15d). Unfortunately, an extended cloudy period followed the bloom, and the next available image, day 133, shows near-surface concentrations had decreased to values similar to pre-bloom levels (Figure 15e). These low values seem to have continued throughout the summer, but there was some spatial variability, with slightly higher chlorophyll concentrations occurring in the eastern Sound on day 143 (Figure 15f), similar to what was observed in the model (*cf.*, Figure 14g).

Model zooplankton biomass integrated over the upper 100 meters is shown in Figure 16, where the spatial distribution is color coded and a time series from one location is shown by the red line below each image. By day 90, zooplankton concentrations were still quite low except in nearshore areas (Figure 16a). As near-surface chlorophyll concentrations increased, zooplankton increased as well, so that by day 100 (Figure 14b) zooplankton biomass was 2–4 g m^{-1} in the eastern sound, which was the area of the initial phytoplankton increase (*cf.*, Figure 14b). Zooplankton concentrations continued to increase throughout the course of the phytoplankton bloom (*cf.*, Figures 16c–e, 14c–e), although the rate of increase in zooplankton biomass was much slower than that for phytoplankton. This can be seen by examining the slopes of the red and green lines respectively during the bloom period.. Zooplankton continued to increase in the eastern Sound (Figure 16f), after the main phytoplankton bloom ceased in the western and central Sound. Zooplankton remained relatively higher than did phytoplankton after the bloom period, although it too gradually decreased through the summer (Figure 16g, h). When the fall phytoplankton bloom began, there was a zooplankton response, particularly in the area near the north end of Montague Island (Figure 16i).

Discussion:

Objectives 1, 2 and 3

Phytoplankton dynamics seem to follow the classic Sverdrup (1953) critical depth theory, with the added twist of density-driven mixing due to convective cooling, being very important. In 1994, there was a initial increase in chlorophyll near day 100, which was followed by a brief mixing event, caused by increased winds and more importantly, by a marked decrease in air temperature, which destroyed the stratification and decreased surface chlorophyll. Following this “last gasp' of winter, the main spring bloom occurred as the water column began to thermally stratify. In is important to note that the C-LAB buoy did not make salinity measurements. Results from the SEA Physical Oceanography program indicate there also may be a salinity component to this stratification (Vaughan, *et al.*, this report). Following the spring bloom decline, there was a small increase in chlorophyll concentrations after day 150. These may have been in response to deepening of the mixed layer and a subsequent increase in surface nutrients as indicated by the reduction in surface stratification near day 145, similar to the summer bloom observed in Auke Bay, AK by Iverson *et al.* (1973). An alternative explanation is that phytoplankton increased in abundance in response to a reduction in zooplankton grazing pressure at around this time as large *Calanus* and *Neocalanus* copepods left the surface layer (Ward, 1997). A similar time course of the spring bloom occurred in all years for which we had spring C-LAB data. The exact timing of the reduction in winds and the cessation of cold front passage varied a bit, as did the timing and character of the resultant phytoplankton bloom. These are discussed more fully in the **DISCUSSION** section of Appendix A.

There was a fall phytoplankton bloom in several years. A fall bloom would be expected at these latitudes as the summer stratification breaks down and light has not yet become limiting (*e.g.*, Platt, 1971). The fall bloom began around day 270 and continued until around day 330–345. This bloom is expected to have provided local zooplankters with a much needed pulse of energy just prior to winter. This pulse would likely also be transferred up the trophic ladder to overwintering herring. If one assumes the area under the fluorescence curve is some indication of total phytoplankton biomass (this isn't a particularly rigorous assumption, but is useful for discussion purposes), then these fall blooms may be contributing as much biomass to the surface layer as are the spring phytoplankton blooms.

In 1996, there was a large phytoplankton bloom in late summer. At the time, it was thought to be an artifact of fouling, but later examination of the mooring proved that was not the case. Unfortunately, there were no other observations of phytoplankton biomass at that time and we, SEA, lacked the resources to mount a field campaign to verify this apparent late-summer bloom. Its occurrence is as yet unexplained. There are some tantalizing hints that the bloom may be a response to upward movement of the water column — the isothermals tilt upward prior to the bloom. This could be an indication of some deep water dynamics that raised the surface waters and provided a pulse of nutrient rich water from the aphotic zone to reach the euphotic zone. This matter warrants further investigation.

Objective 4 and 5

Specific discussion is in the **DISCUSSION** section of Appendix A. The important points are that the 1-D model has allowed us to show that the timing and character of the springtime phytoplankton bloom are determined by the meteorological forcing that occurs over a few weeks time in early spring, near day 90–120. The variability in the meteorology leads to significant differences in the phytoplankton response, which in turn lead to differences in zooplankton biomass that may persist for months. The simple mixed layer model developed as part of the SEA program works well for years 1992 and later, but did not work at all well for the previous decade. That may indicate that prior to 1992, other significant forcing mechanisms (advection?) dominated the local wind effects simulated by the 1-D model.

Objective 6 and 7

From the model initiation on day 70, phytoplankton quickly began to increase in shallow areas near the coast and over submerged pinnacles. This was due to the effective reduction in the mixed layer depth due to the shallow water depth. This phenomenon is well understood and was reported as early as 1946 for Georges Bank (Riley, 1946). This phytoplankton production was rapidly converted in zooplankton biomass, leading the high zooplankton biomass found in the coastal areas. Because of the shallowness of the water column and the regeneration of nutrients from biomass and fecal pellets which sink to the bottom, these coastal areas remain high in zooplankton biomass much of the year. Phytoplankton production is also occurring, of course, but the phytoplankton and zooplankton are tightly coupled and the primary production that occurs leads quickly to zooplankton biomass increases, not phytoplankton biomass increases. The spatial and temporal variability seen in the model is very similar to that seen in the SeaWiFS data. The model did not include advection, however, so the obvious advective features in the SeaWiFS imagery do not appear. But the slow phytoplankton increase followed by a rapid intense bloom when conditions are right, *i.e.* when winds relax and there is no convective mixing, are seen in both model results and satellite imagery. Variability in the local wind field causes spatial variability in the phytoplankton and zooplankton fields. Cross-sound gradients occur due to differences in the strength and duration of wind mixing. The eastern Sound had higher phytoplankton concentrations longer than the western sound in the model simulation. This occurred in response to more windy conditions and lead to a slower phytoplankton bloom. This slow bloom also allowed for tighter coupling with the zooplankton and produced higher zooplankton biomass in the eastern Sound (*cf.*, Figures 14 f, g and 16f, g). The spatial variability seen in the model is very similar to that measured in the phytoplankton and zooplankton SEA field programs (McRoy, this report and Cooney, this report).

Conclusions:

We found the springtime physical and plankton dynamics in Prince William Sound to be similar to those for other high latitude systems, *i.e.*, spring phytoplankton and zooplankton blooms occur in response to vernally increasing air temperatures and decreasing wind speeds, stratification-induced nutrient limitation during the summer and a fall boom in response to mixing caused by cooling temperature and increasing wind speeds. However, we have shown from both the one-dimensional and three-dimensional modeling efforts that subtle variations in the timing, strength, and variability of the meteorological forcing during the early spring lead to substantial variations in the total new primary production by phytoplankton, the transfer of that production to the zooplankton, and the partitioning of the production between the upper water column and the mid-level or benthic components of the food web. The system we have described is an accurate simulation of the field observations during the years of the SEA study. Although this system is complex and highly nonlinear in its response to slight variations, it can now be understood and, to some extent, predicted. This bio-physical modeling work has enabled us to understand some of the causes of variability in food for larval Pacific herring and juvenile Pacific herring and pink salmon. The knowledge gained from this study should play an integral role in understanding the variability in these stocks and how we can best manage them to ensure their recovery.

Acknowledgments:

I hesitate to supply a list of names, for fear of omission. I would like to state that this work could not have been made possible without the work of the entire SEA field, modeling, financial and analysis teams. I would like to thank and acknowledge everyone who pulled a net, picked a sample, wrote a line of code or analyzed an image. I n addition, without the help of all the support staff who made the money flow when we needed it, this work would never have happened. I must specifically thank Lawrence J. Miller for carrying the lions share of the image analysis task. Sarah J. Thornton, Natalia Pintchouk are thanked for their work and patience during modeling effort. Lastly, I wish to thank Dr. R. Ted Cooney for being the SEA Principal Investigator and, more importantly, for mentoring me through this process. Without his vision, knowledge, patience and guidance, the SEA project would never have happened. Thank you ted and the best of luck in Montana!

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Iverson, R.L., H.C. Curl,Jr., H.B. O'Connors,Jr., D. Kirk,and K. Zakar 1974. Summer phytoplankton blooms in Auke Bay, Alaska, driven by wind mixing of the water column. *Limnology and Oceanography*, 19, 271–278.

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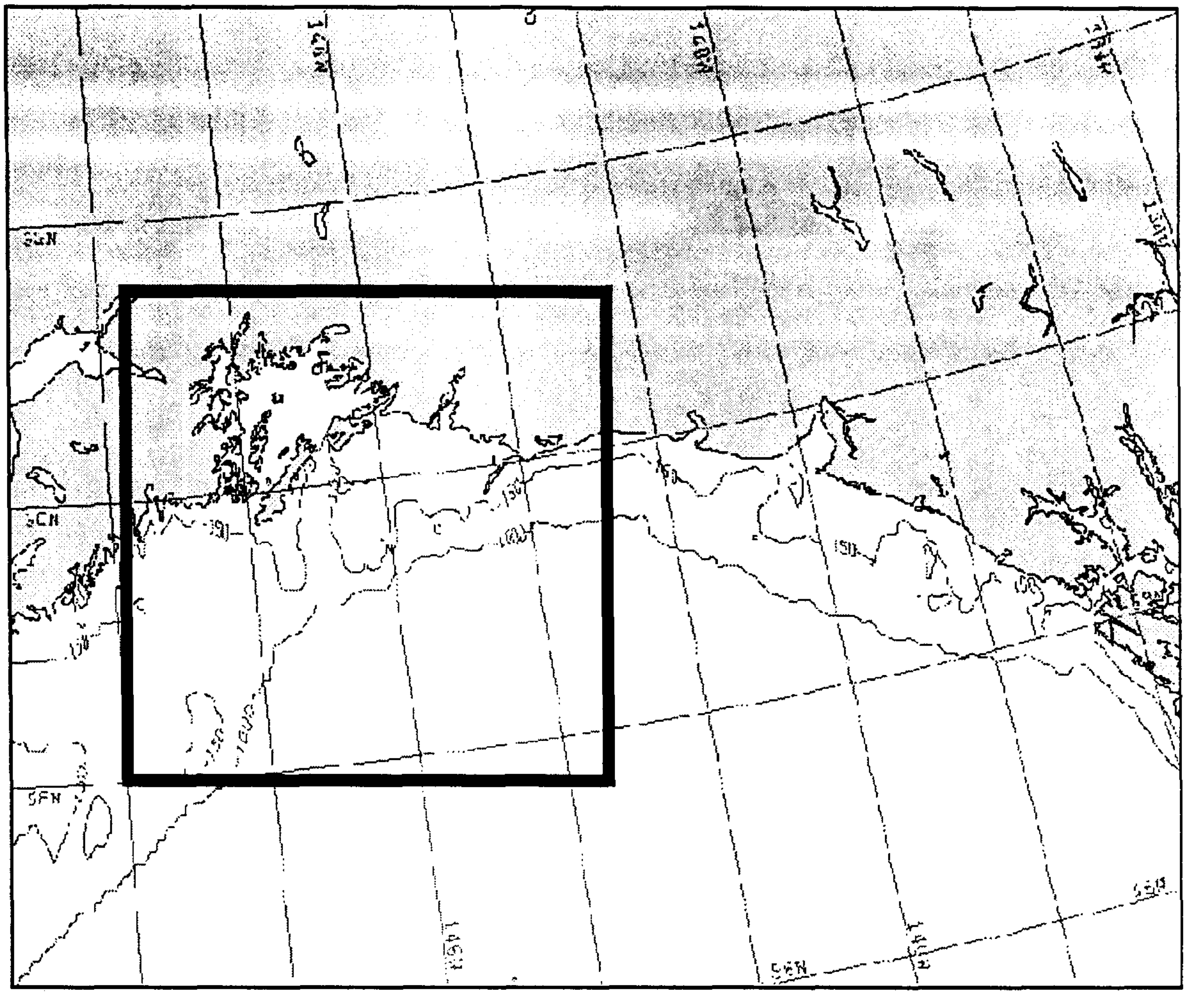
Ward, Alison. 1997. *A temporal study of the phytoplankton spring bloom in Prince William Sound, Alaska.* M. S. Thesis. University of Alaska Fairbanks, Fairbanks, Alaska. 85 p.

Tables:

Table 1. Primary production and particle flux from surface waters. Shown in both biomass (g C m^{-2}) and as percent of new production.

C-LAB	Buoy	SEA
Applegate Rocks	Met Station	SEA
Bligh Reef	C-MAN	NDBC
Potato Point	C-MAN	NDBC
Mid-Sound	Buoy	NDBC
Seal Rocks	Buoy	NDBC
Cordova	Met Station	NWS
Valdez	Met Station	NWS
Whittier	Met Station	NWS



SEADATA Remote Sensing Region
Albers conic projection: Center: 60 N, 154 W; Std. Parallels: 55 N, 65 N
Center of Region of Interest: 59.654 N, 143.050 W
Upper Left: 63.572 N, 151.133 W   Upper Right: 62.027 N, 132.882 W
Lower Left: 56.590 N, 151.681 W   Lower Right: 55.327 N, 136.719 W
850 x 700 pixels, Pixel Size = 1.113 km
*Smaller square shows the higher resolution (555m)
Prince William Sound detail region.

Figure 1. The standard projection used for SEA satellite products and the numerical modeling work. This is the Federal state plane projection for Alaska.

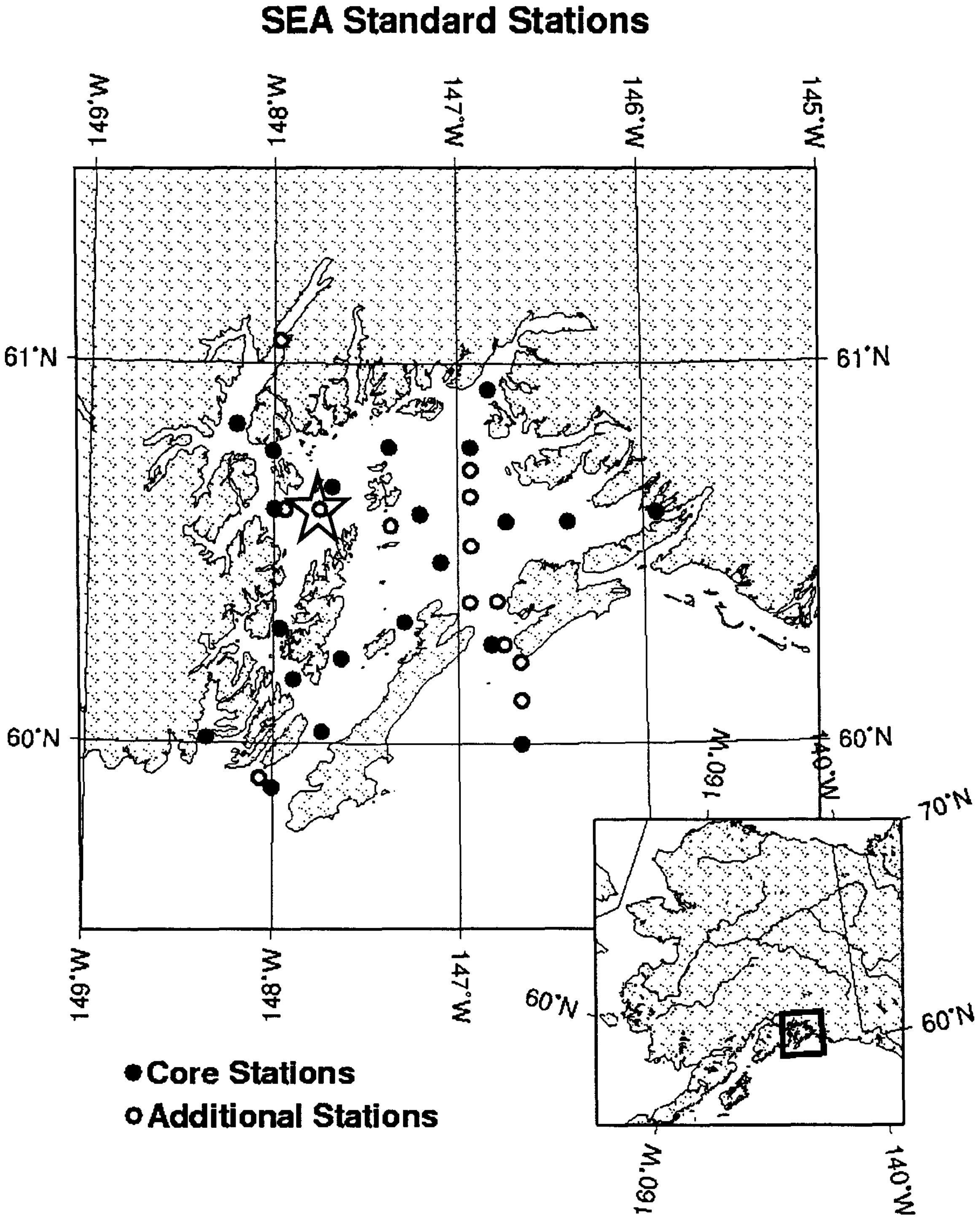


Figure 2. SEA field stations. The C-LAB buoy location is indicated by the hollow circle at the center of the star.

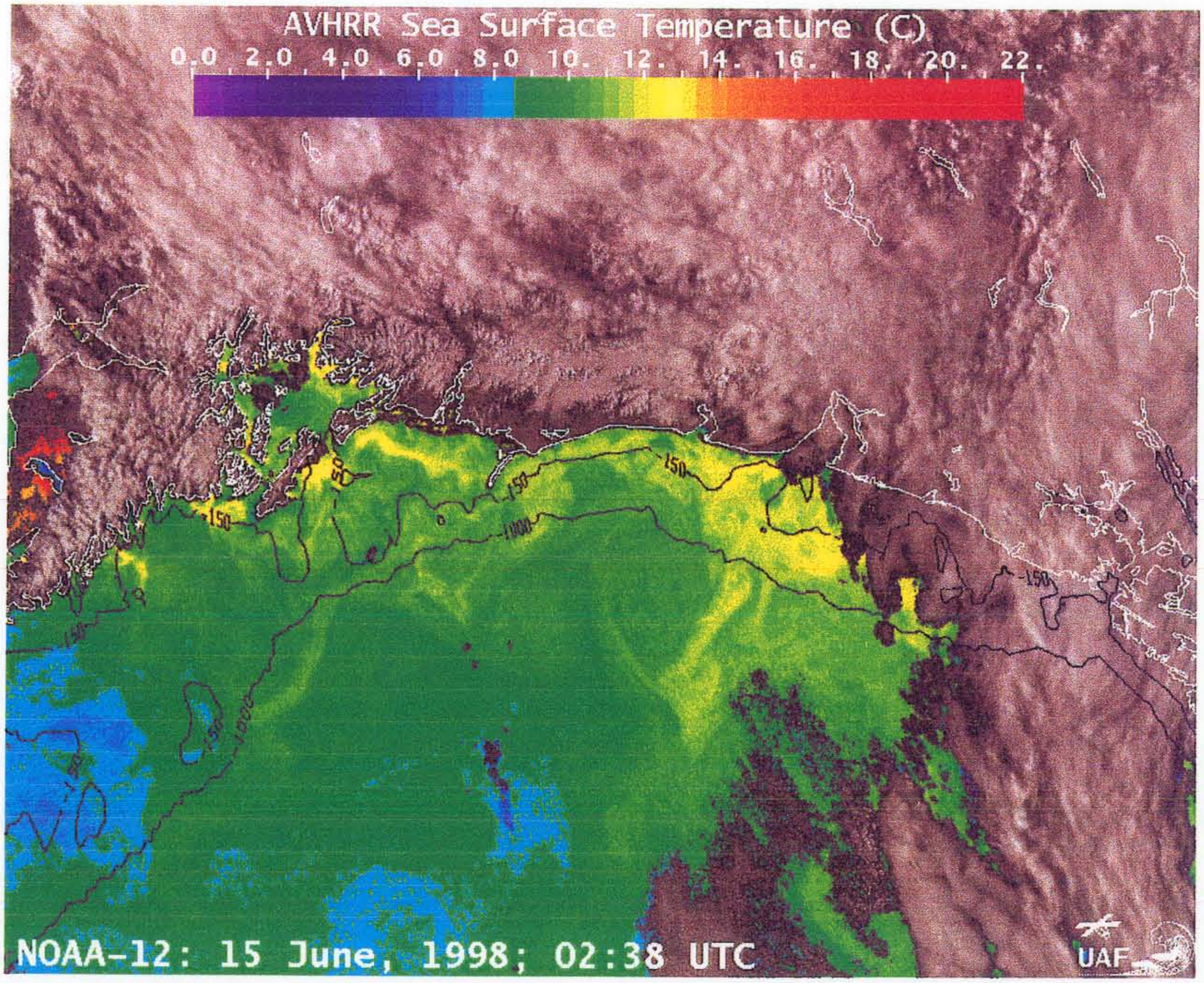


Figure 3. Sea surface temperature from NOAA-12 satellite. This is a standard SEA satellite product.

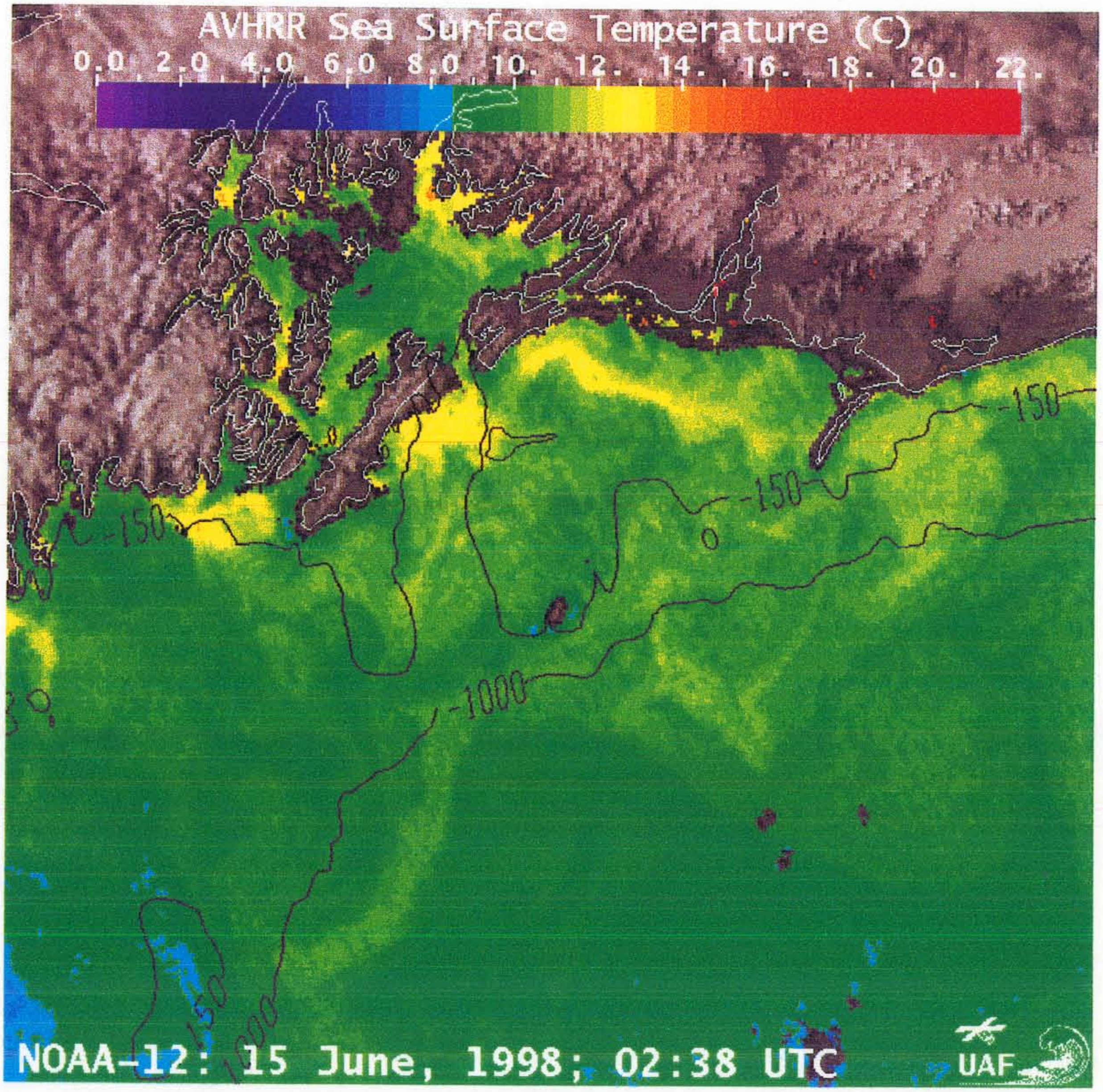


Figure 4. Detail of sea surface temperature for Prince William Sound. Same data as in Figure 3.

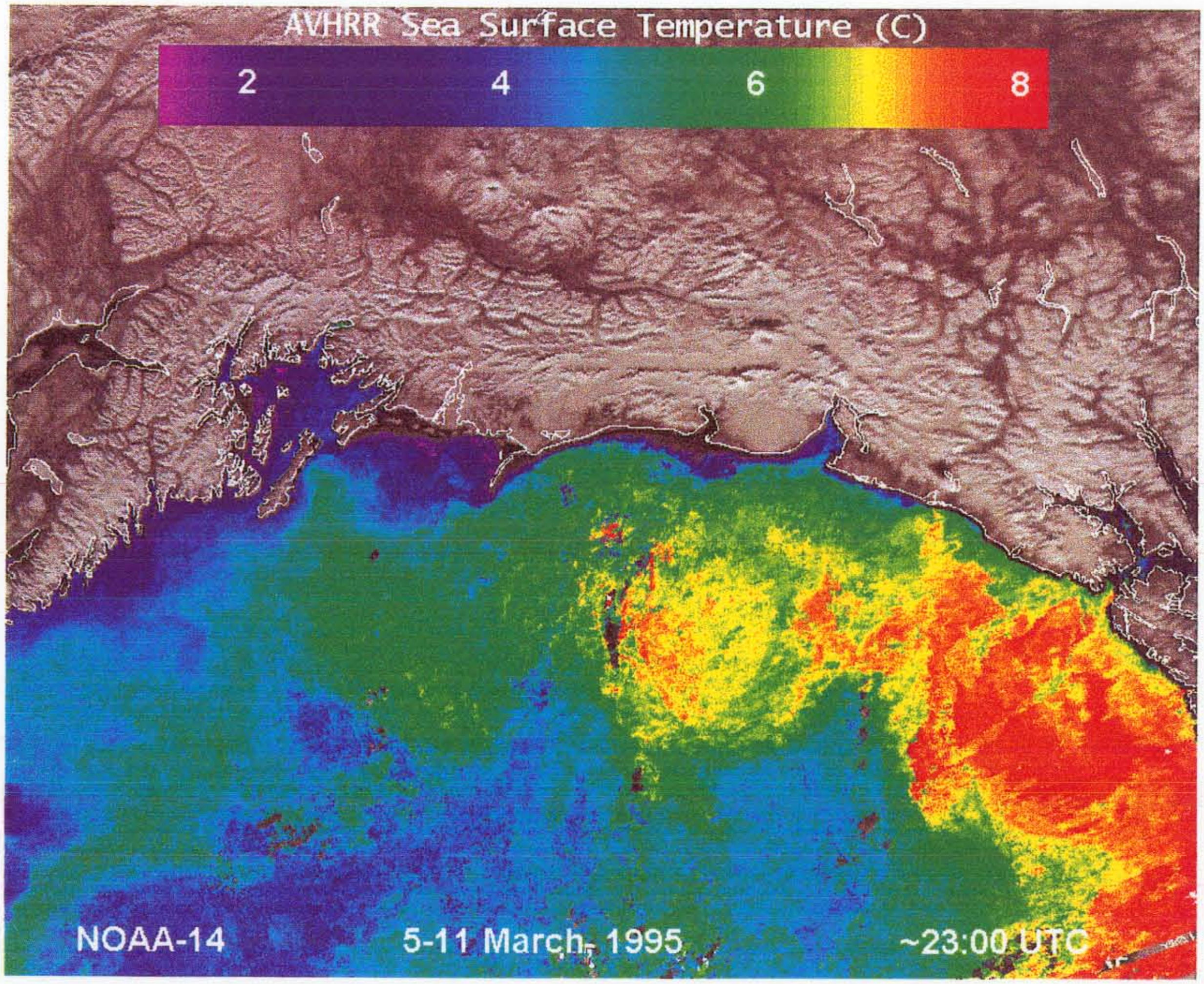


Figure 5. Sea surface temperature from NOAA satellites. This weekly composite image eliminates most of the cloud coverage. Note: this color bar is not the standard color bar.

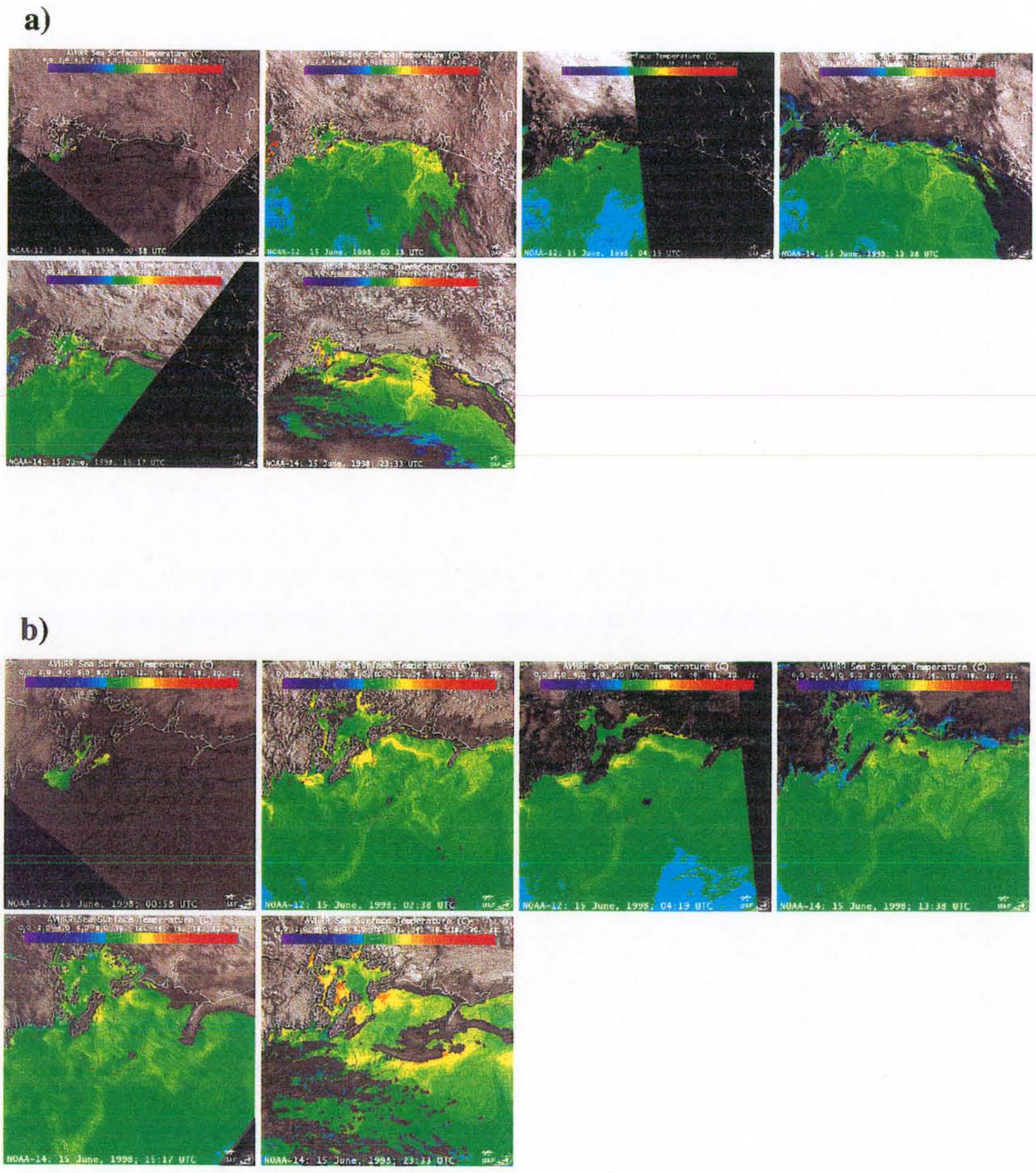


Figure 6. Example daily indices of all available AVHRR sea surface imagery for a) Gulf of Alaska scenes and b) Prince William Sound enlargements.

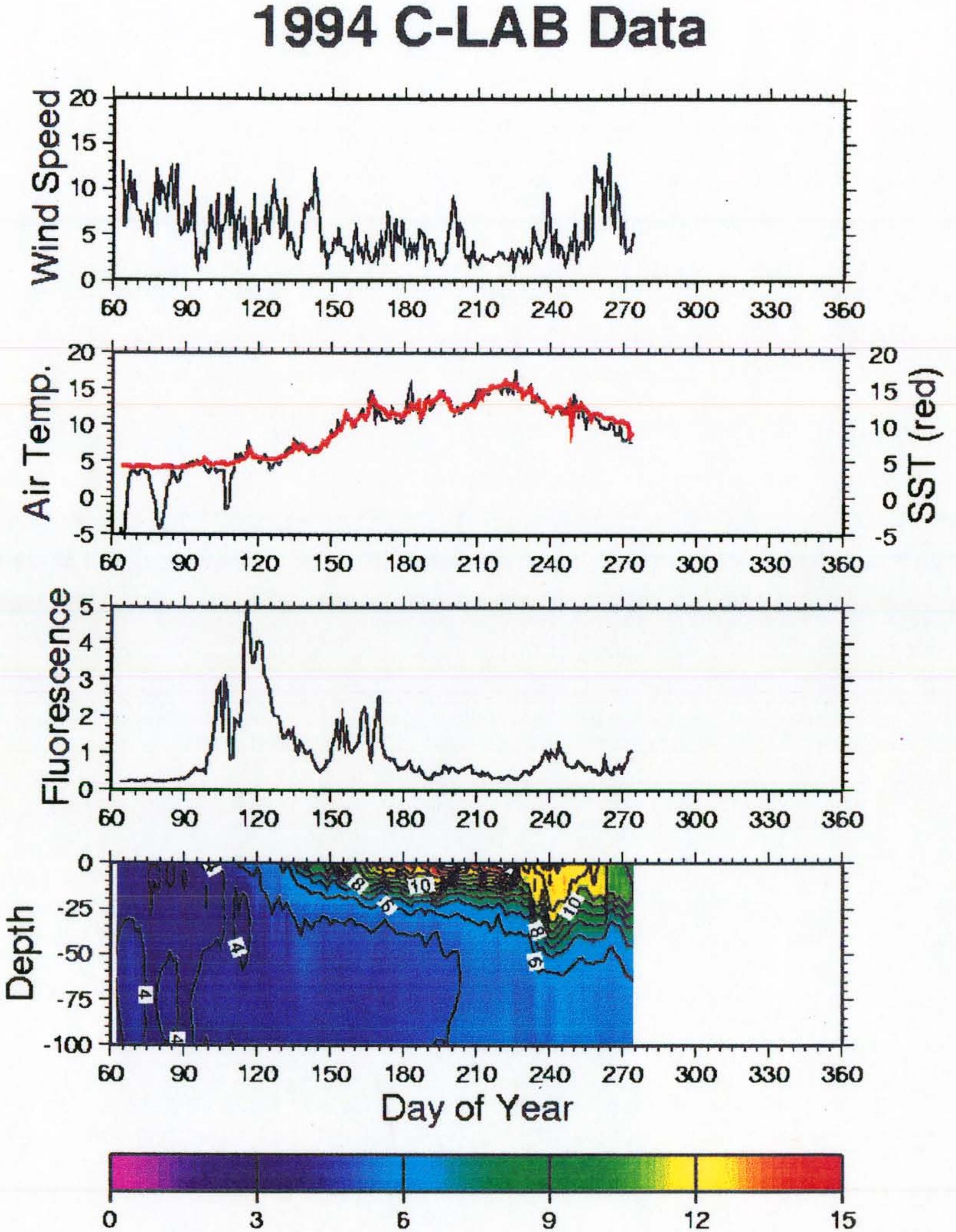
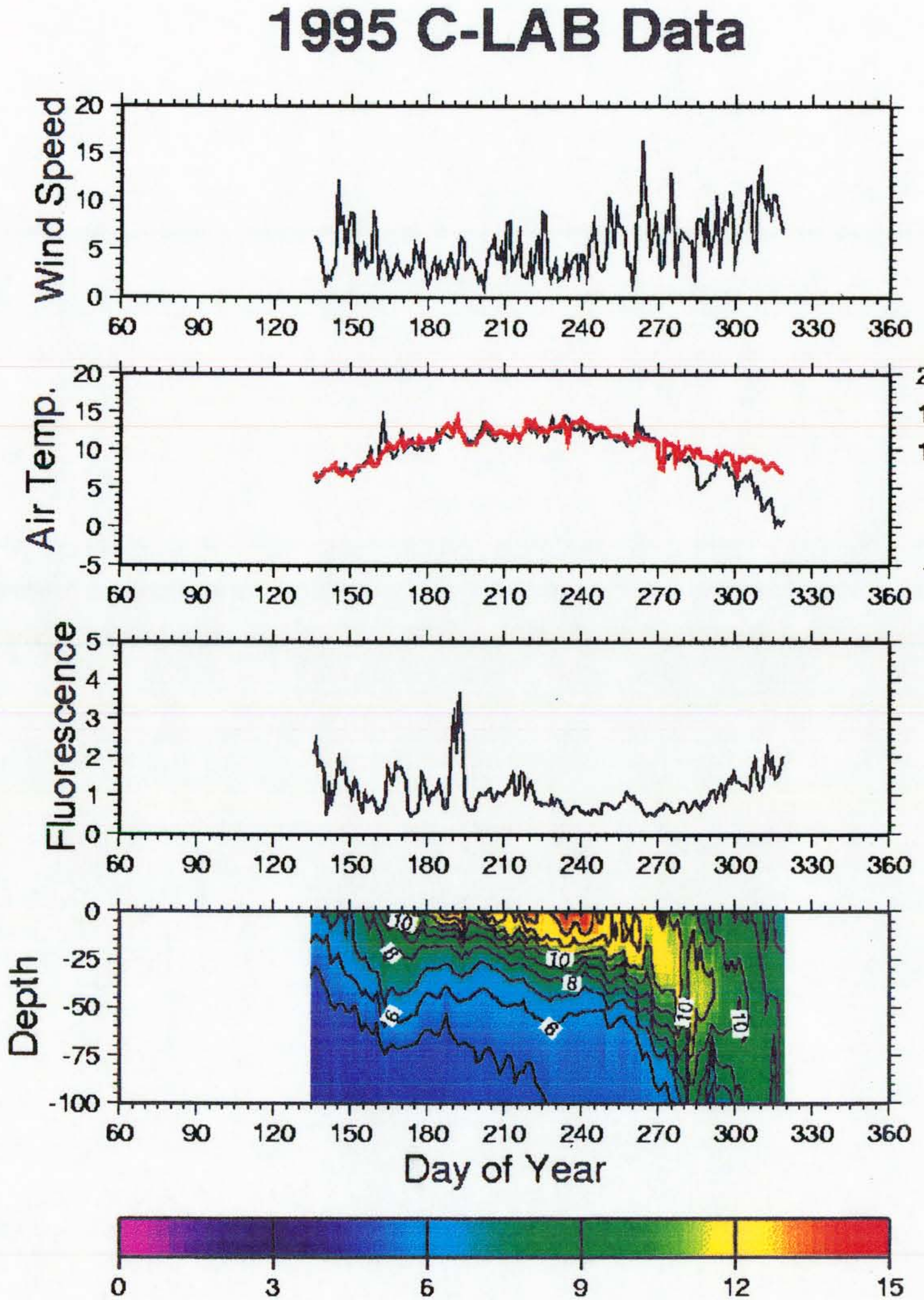


Figure 7. C-LAB data for 1994.



1995 C-LAB Data

Figure 8. C-LAB data for 1995.

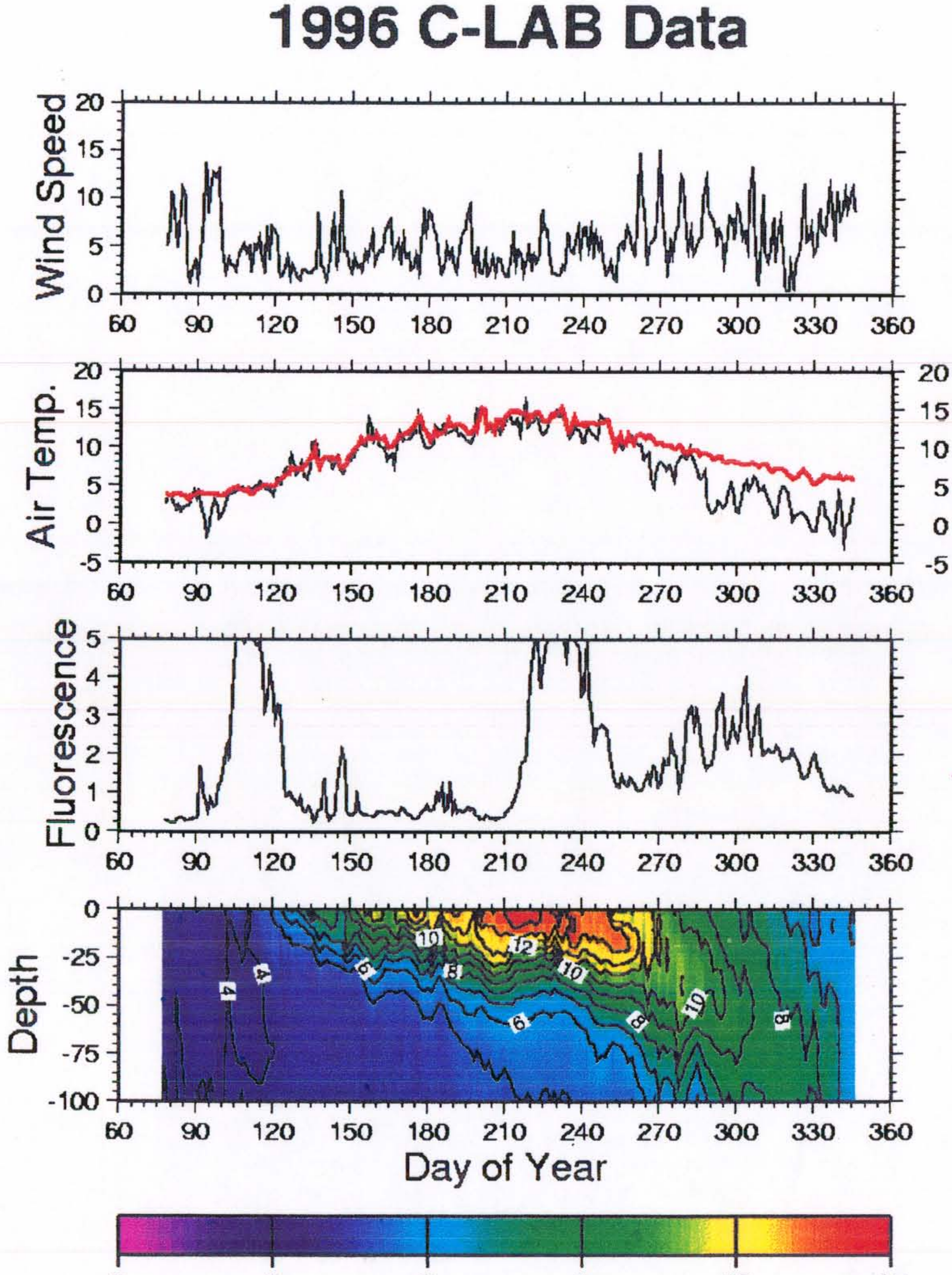


Figure 9. C-LAB data for 1996.

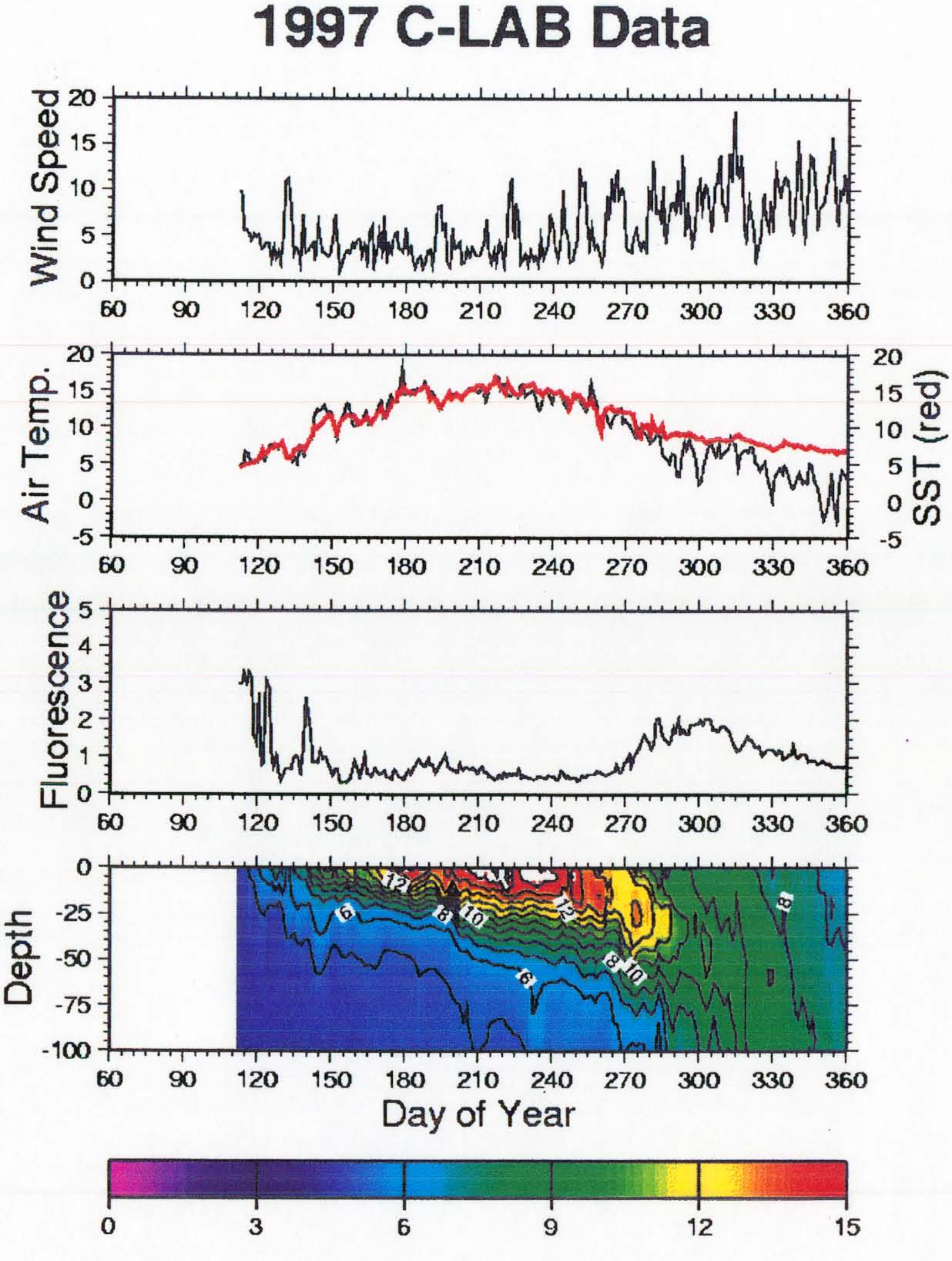


Figure 10. C-LAB data for 1997.

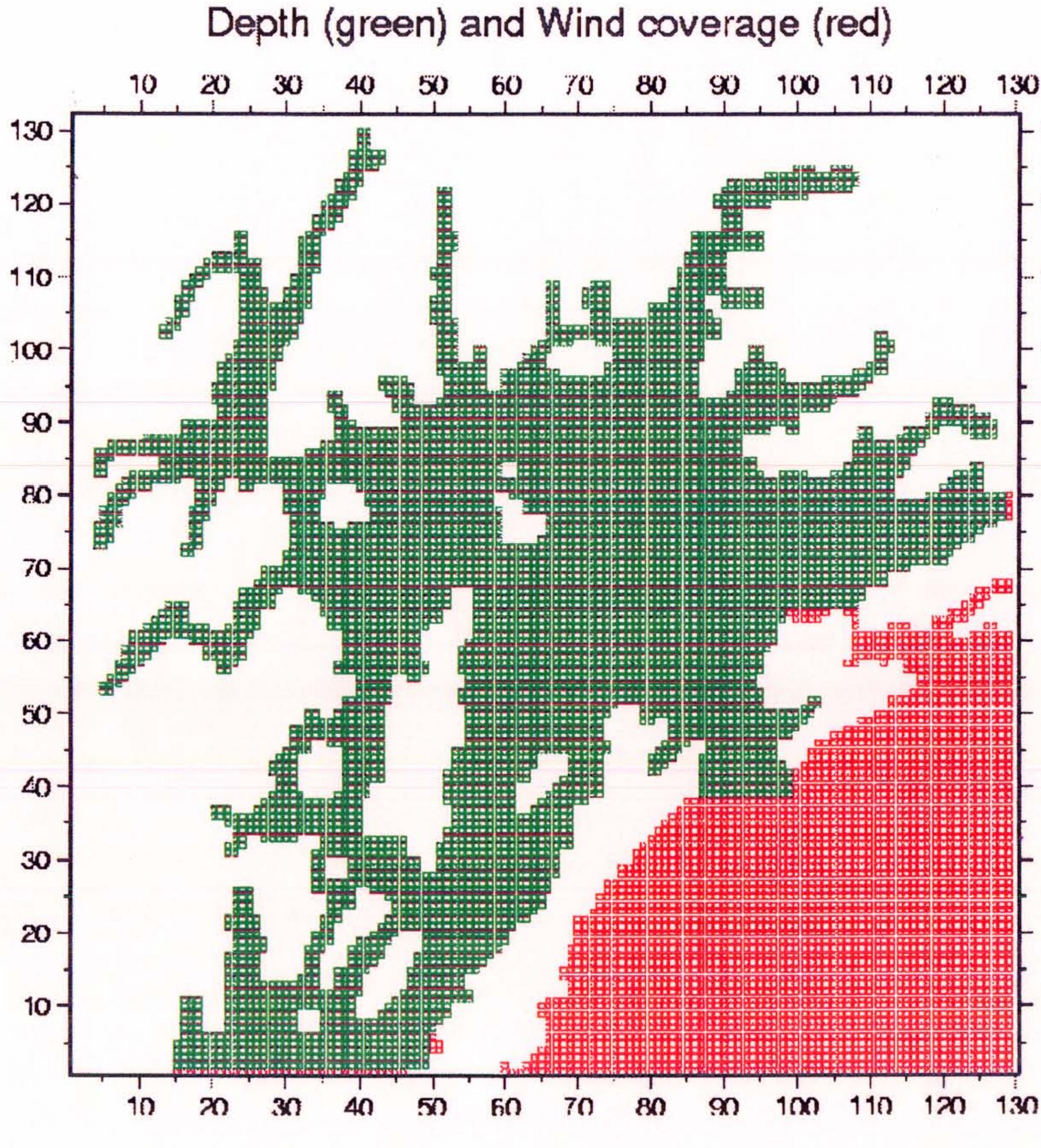
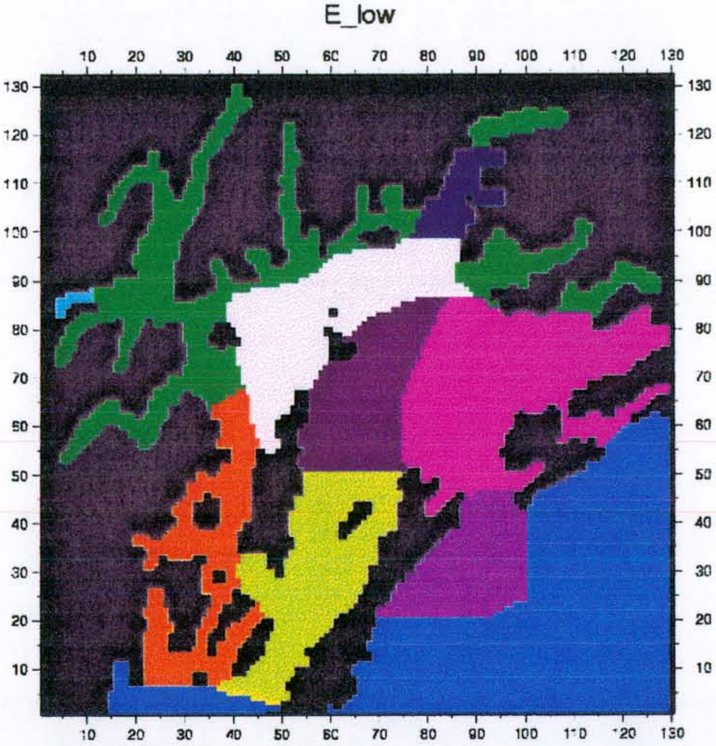


Figure 11. SEA model domain grid. Winds were available in red region, although depth was available only in the green subsection. Therefore, the model was run only for the green region.

a)



b)

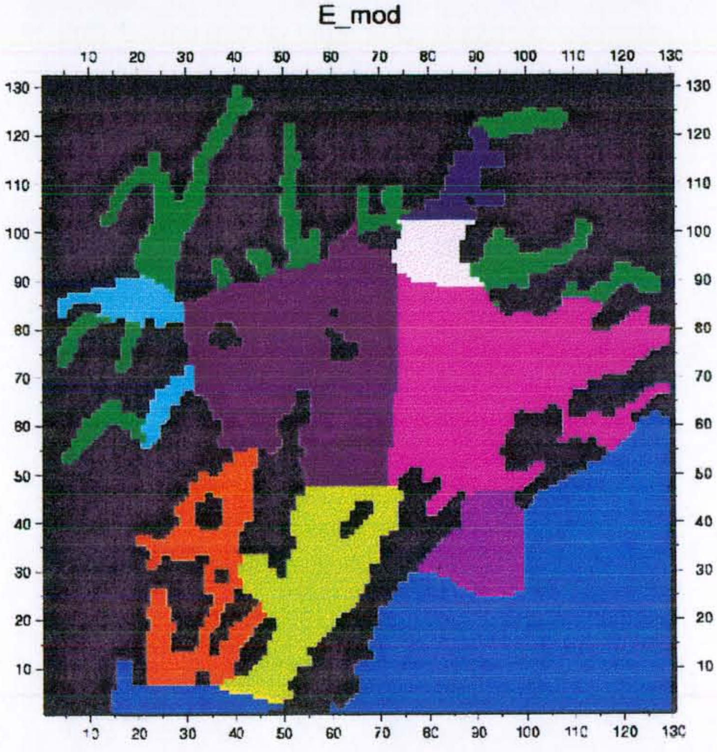


Figure 12. SEA wind interpolator results showing the different regions that are expected to have similar winds, and how those regions change under conditions of a) low easterly winds and b) moderated easterly winds.

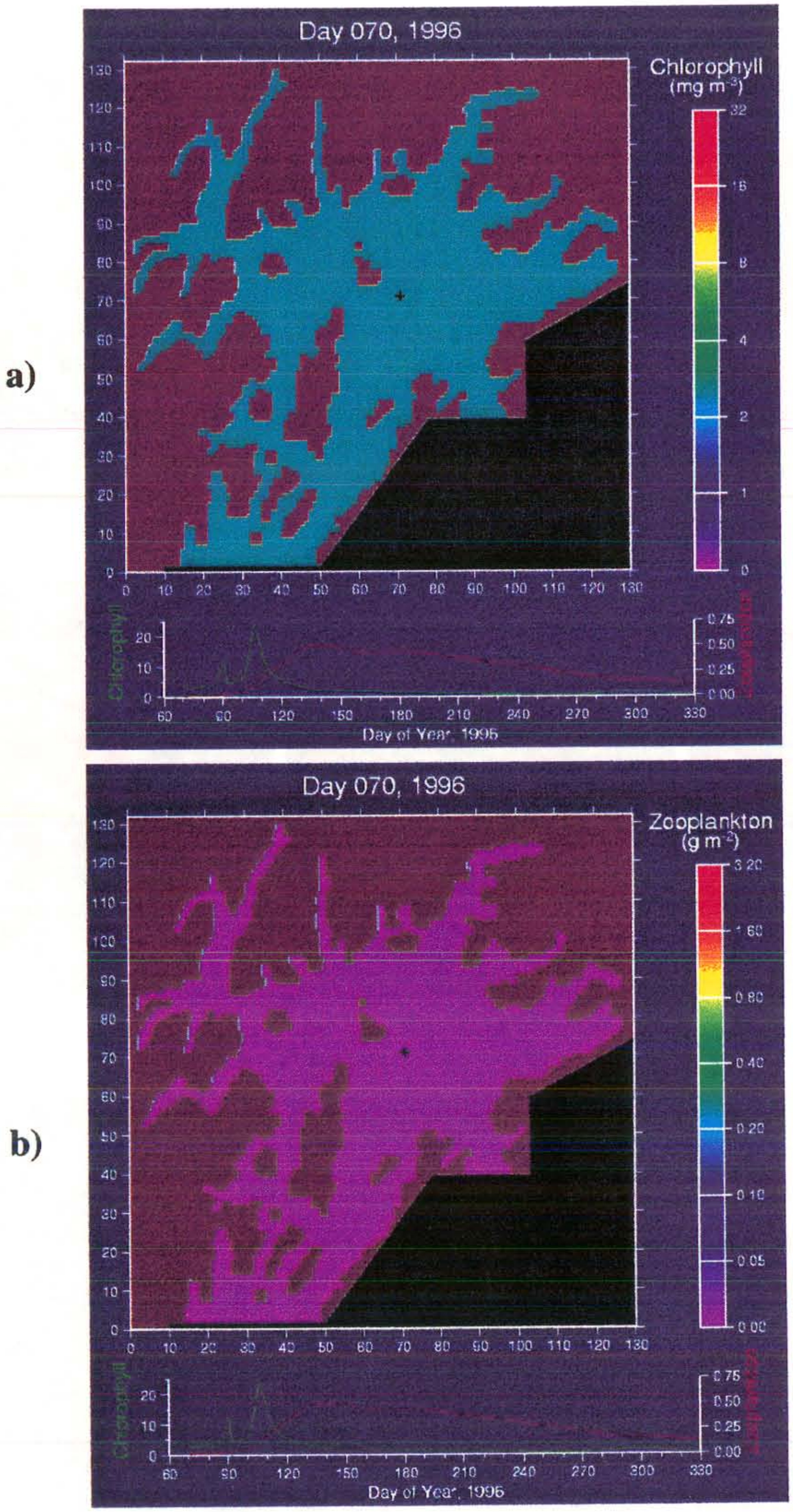


Figure 13. 3-D model results integrated over upper 10 meters. Initial conditions (day 70) for a) phytoplankton and b) zooplankton.

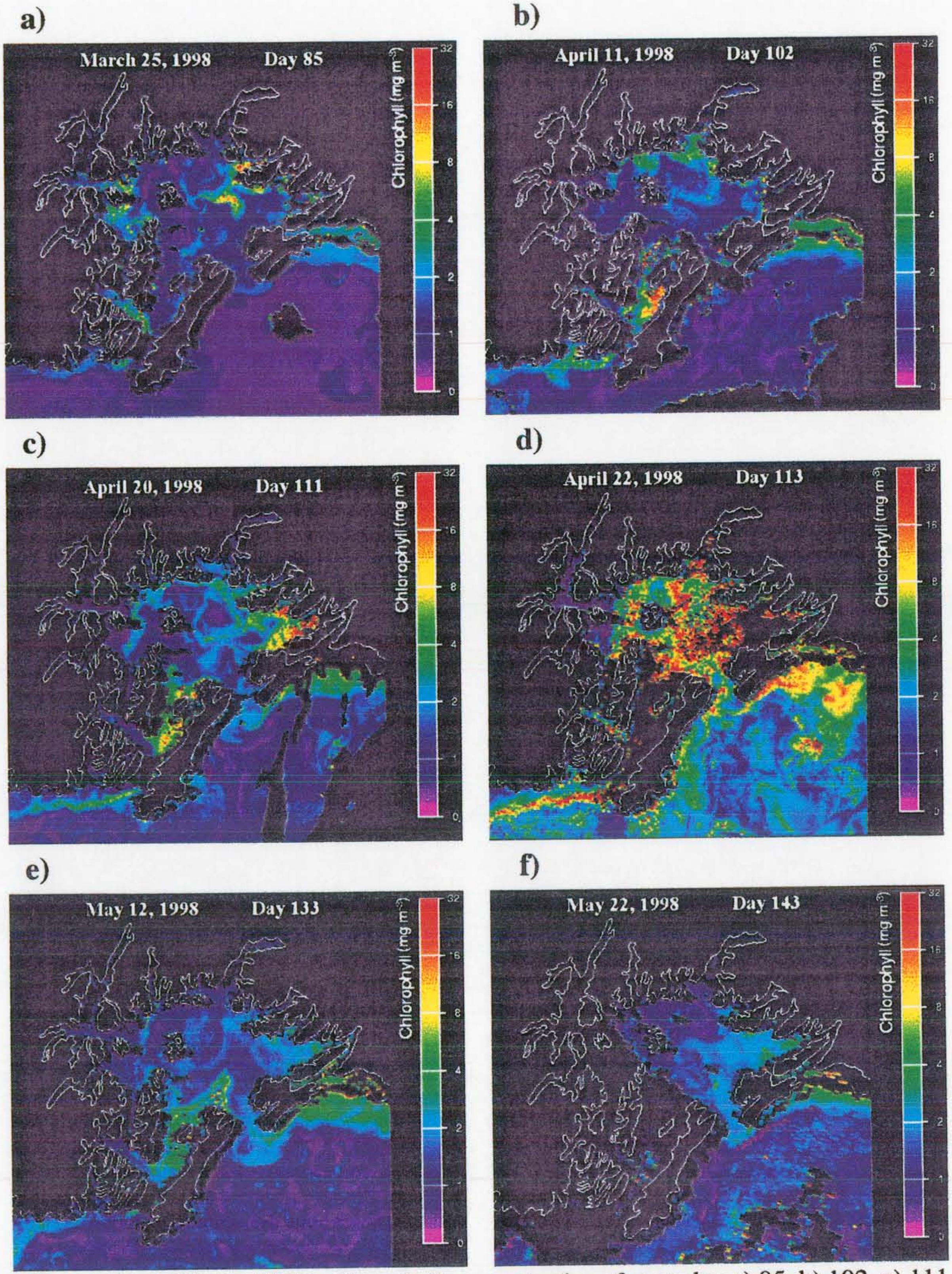


Figure 15. 1998 SeaWiFS chlorophyll concentrations for on day a) 85, b) 102, c) 111, d) 113, e) 133, and f) 143. Clouds and land are black.

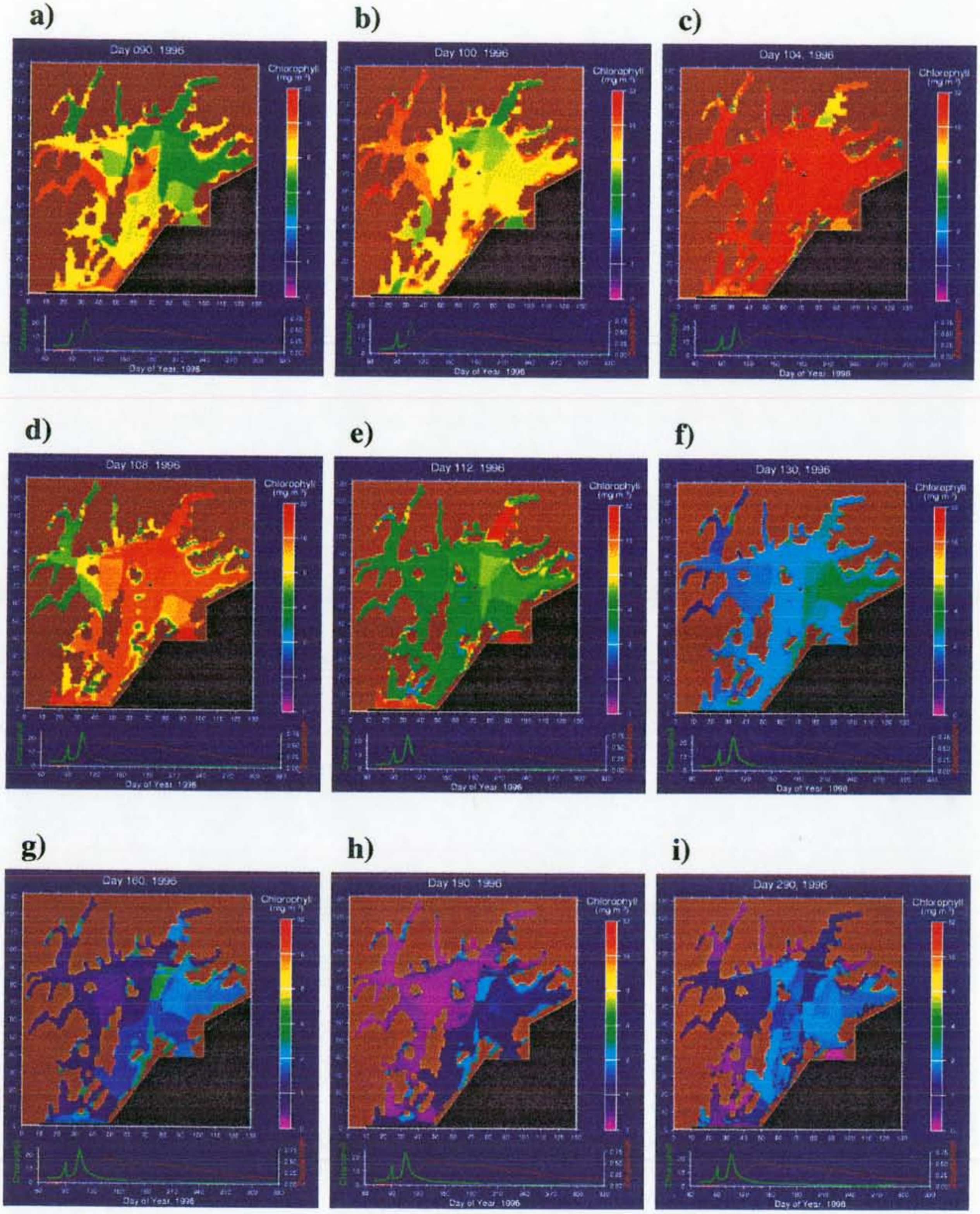


Figure 14. 3-D model phytoplankton chlorophyll concentrations integrated over upper 10 meters on day a) 90, b) 100, c) 104, d) 108, e) 112, f) 130, g) 160, h) 190, and i) 290.

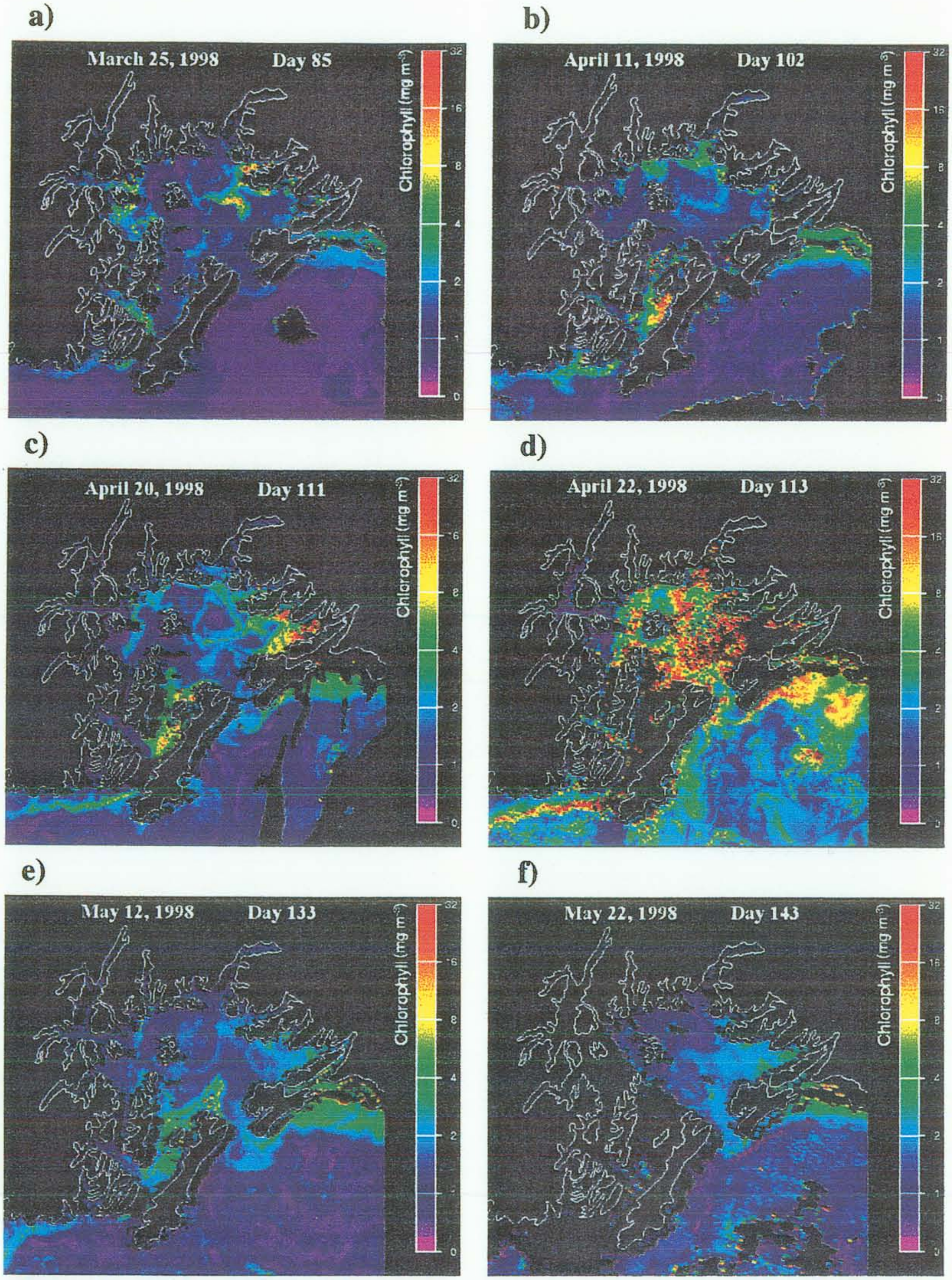


Figure 15. 1998 SeaWiFS chlorophyll concentrations for on day a) 85, b) 102, c) 111, d) 113, e) 133, and f) 143. Clouds and land are black.

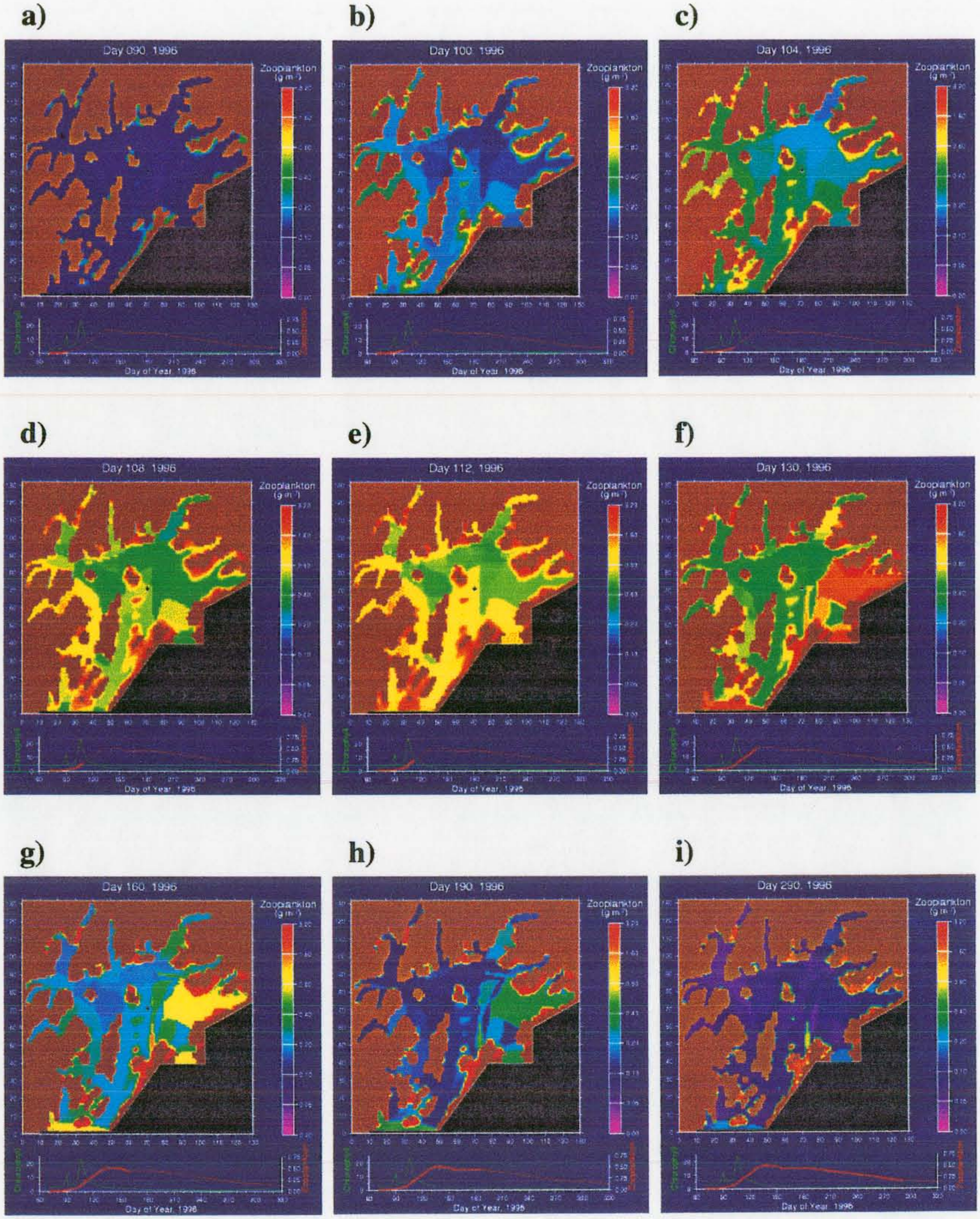


Figure 16. 3-D model zooplankton chlorophyll concentrations integrated over upper 10 meters on day a) 90, b) 100, c) 104, d) 108, e) 112, f) 130, g) 160, h) 190, and i) 290.

Chapter 6

Stable Isotopes as Food-Web Tracers

Exxon Valdez Oil Spill
Restoration Project Final Report

Sound Ecosystem Assessment: Confirming Fish Food Web Dependencies in the Prince William Sound Ecosystem Using Natural Stable Isotope Tracers (SEA-FOOD)

Restoration Project 94-98320I
Draft Final Report

Modified & Updated: 19 May 1999

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April 1999

Sound Ecosystem Assessment: Confirming Fish Food Web Dependencies in the Prince William Sound Ecosystem Using Natural Stable Isotope Tracers (SEA-FOOD)

Restoration Project 94-98320I
Draft Final Report

Study History: Project 320I was part of the five-year (1994-1999) Sound Ecosystem Assessment (SEA) project which was funded to address questions relating the role of oceanographic processes to the failure or poor recovery of salmon and herring populations that crashed in Prince William Sound subsequent to the *Exxon Valdez* oil spill using natural biogeochemical markers in the form of carbon and nitrogen stable isotopes. DPD and annual report titles were the same as this final report.

Abstract: The Objectives of project 320I were (1) to determine the $^{15}N/^{14}N$ and $^{13}C/^{12}C$ natural abundance of species collected from the Prince William Sound ecosystem with a focus on those components important to man or important in the food webs supporting these species, (2) to determine isotope ratios on prey species (fishes) favored by marine mammals in different regions of Prince William Sound, (3) to synthesize the data obtained in context with conceptual food webs to validate feeding models and expand the natural history information, and (4) contribute stable isotope results to formal tests of the Lake/River-driven prey switching hypothesis developed by SEA to explain pink salmon and herring production trends. These objectives were met by producing the enclosed manuscripts, by providing data to Amy Hirons (Ph. D. student of Don Schell, UAF who is using $^{15}N/^{14}N$ and $^{13}C/^{12}C$ natural abundance in a study on pinnipeds in PWS), and by making presentations at scientific forums (American Geophysical Union, Lowell Wakefield, and EVOS symposia).

The Next Step: It is important to end a scientific project by assessing where one should go next. It is clear from the enclosed manuscripts that the advective regime connecting the northern Gulf of Alaska (GOA) with Prince William Sound (PWS) may be important for recruitment and nutritional processes in the Prince William Sound ecosystem. This research program has shown that juvenile fishes can have significant dependence on GOA carbon. Accordingly, they are subject to changes in carbon flow occurring between GOA and PWS. Is there a relationship between the strength of this process and changes in marine populations in PWS and elsewhere in the North Pacific that have been referred to as regime shifts? Manuscript 5 suggests that natural stable isotope abundance may be a tool useful for addressing this question -- for unraveling regime shift processes.

Chapter 6: 98320I

Citations to published articles

Eslinger, D.L., R.T. Cooney, C.P. McRoy, A. Ward, T.C. Kline, Jr., E.P. Simpson, J. Wang and J.R. Allen. 2001. Plankton dynamics: observed and modelled responses to physical conditions in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):81-96.

Kline, T.C., Jr. 1997. Confirming forage fish food web dependencies in Prince William Sound using natural stable isotope tracers. Pages 257-269 in: Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, Anchorage, Alaska, November 13-16, 1996. Lowell Wakefield Fisheries Symposium 14, Alaska Sea Grant College Program Report no. 97-01. University of Alaska Fairbanks, Fairbanks, Alaska.

Kline, T.C., Jr. 1999. Temporal and spatial variability of 13C/12C and 15N/14N in pelagic biota of Prince William Sound, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 56(Suppl. 1):94-117.

Kline, T.C., Jr. and Pauly, D. 1998. Cross validation of trophic level estimates from a mass-balance model of Prince William Sound using 15N/14N data. Pages 693-702 in: Funk F., ed. Fishery stock assessment models: Proceedings of the International Symposium on Fishery Stock Assessment Models for the 21st Century, Anchorage, Alaska, October 8-11, 1997. Lowell Wakefield Fisheries Symposium 15, Alaska Sea Grant College Program Report no. 98-01. University of Alaska Fairbanks, Fairbanks, Alaska.

Products:

Project 320I products were whole manuscripts or contributions to manuscripts:

1. Kline, T. C. Jr. 1997. Confirming forage fish food web dependencies in the Prince William Sound ecosystem using natural stable isotope tracers. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 9701. University of Alaska Fairbanks. P. 257 - 269. (reprint enclosed)

2. Kline, T. C. Jr. 1998. Salmon Fry. In: T. A. Okey and D. Pauly (eds), A Trophic Mass-Balance Model of Alaska's Prince William Sound Ecosystem, for the Post-Spill Period 1994-1996. Fisheries Centre Research Reports 1998 Volume 6 Number 4. Fisheries Centre, University of British Columbia, Vancouver, Canada. p. 26-31. (included in the ECOPATH project (Pauly and Pimm, P.I.s) final report and not here)

3. Kline, T. C. Jr. and D. Pauly. 1998. Cross-validation of trophic level estimates from a mass-balance model of, and $^{15}N/^{14}N$ data from, Prince William Sound. Proceedings of the International Symposium on Fishery Stock Assessment Models for the 21st Century -- Combining Multiple Data Sources. Alaska Sea Grant College Program Report. University of Alaska Fairbanks. IN PRESS (corrected galley proof enclosed)

4. Kline, T. C. Jr. 1999. Temporal and Spatial Variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in Pelagic Biota of Prince William Sound, Alaska. Canadian Journal of Fisheries and Aquatic Sciences. 56 (Suppl. 1): IN PRESS (final version of manuscript enclosed)

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Project 320I contributed data that were merged with those from project 311 for manuscripts 5, 7, and 8.

Manuscripts 1, 3, and 4 are included in this final report.

Key Words: Stable isotopes, SEA project, Prince William Sound, Oceanography

Project Data: *Description of data* - Data consist of natural carbon and nitrogen stable isotope abundance measurements expressed in intentionally recognized delta units. *Format* - Data are published in various scientific manuscripts in the form of tables, figures, and an appendix. *Custodian* - Contact Dr. Thomas C. Kline, Jr., Prince William Sound Science Center, P. O. Box 705, Cordova, AK 99754. e-mail: tkline@grizzly.pwssc.gen.ak.us. *Availability* - See literature citations or contact Dr. Kline for specific data which can be e-mailed.

Citation: Kline, T. C., Jr. 1999. Sound Ecosystem Assessment: Confirming Fish Food Web Dependencies in the Prince William Sound Ecosystem Using Natural Stable Isotope Tracers (SEA-FOOD). *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 94-98320I), Prince William Sound Science Center

Chapter 7

Information Systems and Model Development
(Pacific Herring)

Exxon Valdez Oil Spill
Restoration Project Final Report

Information Systems and Model Development (Pacific Herring)

Restoration Project 98320J
Final Report

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January 2000

Information Systems and Model Development
(Pacific Herring)

Restoration Project 98320J
Final Report

Study History: The project addressed two aspects of the Sound Ecosystem Assessment (SEA) program: (1) the development of the numerical models and (2) the design, implementation, and operations of major portions of the program information systems. The project period was July 1993 through January 2000 and was sponsored by EVOSTC during the period April 1994 through January 1999. This document is to serve as the Final Report for all of the aspects of the project that addressed the question of the population development of Pacific herring through the development of numerical models for the drift and fate of larvae and for the physiological response of juveniles to winter fasting. The report format differs from the standard format. The format of the report is the result of a special effort conducted during the winter of 1999-2000 in collaboration with W. Hauser (Alaska Dept. of Fish & Game) and P. Mundy (EVOSTC).

Abstract: A set of numerical models were developed which, together with forcing information and model simulations from other SEA projects, provide a complete suite of tools whereby the population development of Pacific herring in Prince William Sound can be numerically represented and quantitatively and adaptively tracked. Three basic aspects of the project results are reported in depth. (1) A comprehensive User's Reference targeting end-user groups and resource managers. (2) A complete Validation Reference for the fasting physiology model. (3) A complete Calibration Reference for the fasting physiology model. The report format itself is a project result and is presented for consideration as a prototype for an alternative for projects involving numerical models, extensive collaborations, and significant requirements for demonstrated and documented applicability that includes cost-benefit analysis. The results are the product of the combined contributions from multiple SEA projects and the report (other than its preparation) cannot be attributed to any single project or and one individual.

Key Words: Advective transport, age structure analysis, fasting, juvenile, larval drift, overwinter, Pacific herring, physiology, Prince William Sound, proximate analysis, starvation.

Citation:
Patrick, V. 2000. Information systems and model development (Pacific herring), *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320J), Alaska Department of Fish and Game, Habitat and Restoration Division, Anchorage, Alaska.

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Willette, T.M., R.T. Cooney, V. Patrick, D.M. Mason, G.L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (Oncorhynchus gorbuscha) in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):14-41.

Chapter 8

Observational Physical Oceanography

Exxon Valdez Oil Spill
Restoration Project Finan Report

Oceanography in Prince William Sound: 1994-1998

Restoration Project 98320-M
Final Report

This final 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 final report.

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June 1999

Oceanography in Prince William Sound: 1994-1998

Restoration Project 98320-M
Annual Report

Study History: Unexpectedly small Prince William Sound pink salmon runs in 1992 and 1993, and the almost complete collapse of the herring fishery in 1993, prompted the EVOS Trustee Council to initiate ecosystem-level studies of the region to investigate possible environmental reasons for these disasters. A collaborative effort involving the University of Alaska Fairbanks, the Prince William Sound Science Center, the Prince William Sound Aquaculture Corporation, and Alaska Department of Fish and Game resulted in the development of a coordinated plan in the fall of 1993. After substantial review, Sound Ecosystem Assessment (SEA) was approved for funding April 11, 1994. A scope of work for SEA was projected over 5-8 years at that time. Annual reports were issued in 1995 by D. K. Salmon entitiled Descriptive Physical Oceanography (project number 94320-M), in 1996 by S. L. Vaughan entitiled Observational Physical Oceanography in Prince William Sound and the Gulf of Alaska (project number 95320-M), in 1997 by S. L. Vaughan entitled Water Mass Variability and Circulation of PWS (project number 96320-M), and in 1998 by S. L. Vaughan entitled SEA: Observational Oceanography in Prince William Sound, all as chapter contributions to the single compiled report of all SEA FY94, FY95, FY96 and FY97 projects. Project results were presented in 1996-1998 at several professional meetings. Several journal articles have been prepared for submission.

Abstract: Hydrographic surveys and current velocity measurements in 1994 through 1998 show significant seasonal and interannual variability in water mass properties and circulation patterns in central Prince William Sound (PWS), and in the PWS nearshore areas. Stratification occurs first in the nearshore fjords. In the central Sound, stratification first appears in early spring in the north, due primarily to freshwater runoff. An associated surface horizontal density front forms in the central Sound, which may last through June. The spring and summer circulation in the central Sound can be cyclonic or anticyclonic. Easterly offshore winds can cause Ekman layer inflow at both Hinchinbrook Entrance and Montague Strait. Deeper outflow accompanied the inflow at both locations, and it is not known how far the inflow penetrated northward. In the absence of the easterly wind forcing, the upper layer summer and early fall pattern seems to be outflow at Hinchinbrook Entrance and inflow at Montague Strait. A robust feature of the central Sound circulation is the closed cyclonic gyre in September, which was accompanied by isopycnal doming. Stratification formation, basin scale circulation, and exchange between PWS and the Gulf of Alaska (GOA) can potentially impact primary and secondary production and ultimately juvenile pink salmon and Pacific herring survival.

Key Words: physical oceanography, temperature, salinity, circulation, Prince William Sound.

Citation: Vaughan, S.L., S.M. Gay, and L.B. Tuttle, 1999: Oceanography in Prince William Sound: 1994-1998. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 98320-M), Prince William Sound Science Center, Cordova, Alaska, 99574.

Chapter 8: 98320M

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Table of Contents

Executive Summary

Sixteen oceanographic cruises were conducted in PWS from April 1994 to May 1997 as part of the SEA program. Measurements of temperature (T), salinity (S), dissolved oxygen, current velocities, fluourescence, nutrient content, phytoplankton abundance, and zooplankton abundance were collected on nearly all cruises. Satellite-tracked drifting buoys circulated in the region in 1996, 1997 and 1998. An upward-looking ADCP mooring was deployed in Hinchinbrook Entrance from June 1995 to October 1995, and from September 1996 to May 1997. In addition, nearshore surveys of two bays (Ziakof Bay and Simpson Bay) and two fjords (Whale Bay and Eaglek Bay) were conducted in March and October, and in some summer months from October 1995 to March 1998. Measurements of temperature, salinity, current velocity, fluorescence, and zooplankton concentrations were made simultaneously.

Initial surface stratification does not occur simultaneously throughout PWS. Stratification occurs first in the nearshore fjords. If earlier stratification results in earlier phytoplankton and zooplankton blooms, the nearshore regions might be preferable overwintering habitats for juvenile fish.

In the central Sound, stratification first appears in early spring in the north, due primarily to freshwater runoff. An associated surface horizontal density front forms in the central Sound, which may last through June. April and May phytoplankton blooms have maximum values in the northern Sound (McRoy et al, 1998). A stratified surface layer next to a well mixed region, may result in a prolonged phytoplankton bloom. Physical process that enhance or impede initial stratification formation, and sustain a horizontal density front might be responsible for the temporal variability and biomass differences observed interannually in phytoplankton and zooplankton blooms in central PWS (Eslinger et al, 1998). Interannual differences in the strength and duration of the spring blooms have been observed in the nearshore regions as well (McRoy et al, 1998), so other factors must also contribute.

The spring and summer circulation in the central Sound can be cyclonic or anticyclonic. The mechanisms responsible for this variability have not yet been identified. Closed circulations might act to retain biological organisms in the central Sound. A robust feature of the central Sound circulation was the closed cyclonic gyre in September, which was accompanied by isopycnal doming. The weakened stratification in the center of the gyre might promote a secondary fall phytoplankton bloom.

Organisms entering the central Sound from one bay or fjord might use the basin scale circulation as a conveyor belt for transport to a different bay or fjord. Whether a cyclonic circulation promotes transport to the nearshore regions more than an anticyclonic circulation is unclear. It is not uncommon for drifters to travel from the central Sound to a nearshore region, or from one nearshore region to another.

Easterly offshore winds can cause Ekman layer inflow at both Hinchinbrook Entrance and Montague Strait. Deeper outflow accompanied the inflow at both locations, and it is not known how far the inflow penetrated northward. The density front in the central Sound may isolate the northern Sound from GOA influence in the upper layer. In the absence of the easterly wind forcing, the upper layer summer and early fall pattern seems to be outflow at Hinchinbrook Entrance and inflow at Montague Strait. Whether these exchanges seed PWS with GOA zooplankton, or flush PWS zooplankton out into the GOA is unknown.

Introduction

The Sound Ecosystem Assessment (SEA) was aimed at identifying the primary factors that control the production of pink salmon and Pacific herring in Prince William Sound (PWS). A main hypothesis of SEA was that physical conditions, such as ocean temperature and salinity, current velocities, and atmospheric forcing, primarily determine the survival of embryos and juvenile fish. Processes that control the physical environment include tidal motions, wind stress, seasonal heating and cooling, precipitation and evaporation, river/glacial runoff, exchange with the northern Gulf of Alaska (GOA) water, and longer term events like El Nino and the Southern Oscillation (ENSO). Physical features, such as fronts, mixed layers, and circulation patterns, most directly affect the distribution of phytoplankton and zooplankton, the major food source for juveniles of both species. Currents and changing water mass properties can also impact the juveniles directly.

PWS is a small, subarctic, semi-enclosed sea, surrounded by mountains, glaciers, coastal rivers, and numerous bays and fjords (e.g., Muench and Schmidt, 1975). The central basin depths range from about 400 to 450m. A deep basin in the northwest Sound reaches depths of approximately 800m. The main connections between the Sound and the northern GOA are Hinchinbrook Entrance and Montague Strait. The coldest, saltiest, and most homogeneous water occurs in March. The warmest, freshest, and most stratified water occurs in September (e.g., Muench and Schmidt, 1975). Density is primarily determined by salinity. Instanteous currents are dominated by tidal flows, particularly in channels and nearshore regions.

Pink salmon and Pacific herring are both commercially valuable species for PWS, but they have very different life cycles. Pacific herring spend their juvenile years in the nearshore bays and fjords along the periphery of PWS. Pink salmon juveniles emerge from the inland streams in spring and exit the Sound by fall. They mature in the GOA. Because of these different life cycles, the field component of SEA oceangraphy used two separate survey designs. Sound-wide surveys were conducted four or five times per year to capture the larger scale processes and to provide data for the boundary conditions and verification of the PWS numerical circulation model (SEA project 320-J). Smaller scale surveys that focused on four nearshore regions (two bays and two fjords) were conducted at least twice per year in conjunction with the SEA herring project (320-T).

The majority of the findings from both observational components are presented in the two manuscripts attached as appendices. Program objectives that have not yet been incorporated into manuscripts are noted below and presented in the main body of this report. Results and conclusions from previous EVOS reports are either referenced or summarized.

Objectives

The overall objective of the physical oceanographic component of SEA was to identify the dominant physical processes that influence the distribution and abundance of juvenile pink salmon and Pacific herring in PWS. Specific objectives taken from proposals submitted from FY94 to FY98 are listed below. The objectives that are address in the attached manuscripts are designated by (M); those addressed in the body of this report are designated by (R).

1. Determine the seasonal and interannual variability of the large scale (O(50 km))

water mass properties (temperature, salinity, and potential density) of PWS. (M)

2. Document the current velocities and transport through Hinchinbrook Entrance as a function of time and depth. (M)

3. Document the current velocities and transport through Montague Straight as a function of distance and depth. (M)

4. Determine the monthly, seasonal, and interannual means and variability of the large scale meteorological variables. (M)

5. Survey Sound-wide distributions of macrozooplankton during the spring-time pink salmon fry outmigration window using the OPC. (M)

6. Document mesoscale structures (O(¡10km)), such as eddies and density fronts, and correlate with zooplankton and nekton distributions in PWS. (M)

7. Document small scale structures (O(1km)) in the nearshore regions and correlate with juvenile fish distributions. (M)

8. Characterize the herring overwintering environment in PWS bays and fjords. (M)

9. Use large scale physical oceanographic measurements (hydrographic and current velocity) and meteorological data to characterize 'river' and 'lake' conditions. (R)

10. Provide the large scale physical oceanographic data to validate the numerical circulation model, and for assimilation into the model. (R)

11. Use the model results to identify critical regions and time periods for data collection. (R)

12. Design a cost-effective monitoring scheme for oceanographic and meteorological variables for these regions and times. (R)

Details of the Methods section may be found in previous annual reports (Vaughan et al, 1997; Vaughan et al, 1998a). Results related to the objectives addressed in manuscript form will be summarized and referenced. Results and discussion of the remaining objectives are presented below.

Methods

Sixteen oceanographic cruises were conducted from April 1994 to May 1997 as part of the SEA program (Vaughan et al, 1997; Vaughan et al, 1998a; Appendix A). Hydrographic stations were occupied throughout PWS, and just south of Hinchinbrook Entrance in the northern GOA. Temperature and salinity data were acquired using a CTD lowered from the ship and from a towed instrument. Current measurements were acquired using a towed, downward-looking acoustic Doppler current profiler (ADCP). Satellite-tracked drifting buoys circulated in the region in 1996, 1997 and 1998. An upward-looking ADCP mooring was deployed in Hinchinbrook Entrance from June 1995 to October 1995, and from September 1996 to May 1997.

In addition, nearshore cruises were conducted in March and October, and in some summer months from October 1995 to March 1998 (Appendix B). The nearshore areas surveyed included two bays, Ziakof Bay and Simpson Bay, and two fjords, Whale Bay and Eaglek Bay. Measurements of temperature, salinity, current velocity, fluorescence, and zooplankton concentrations were made simultaneously.

Results

1. The seasonal and interannual variability of temperature and salinity in the central Sound is largely confined to the upper 100m, which contains the euphotic zone (Appendix A). The water column is vertically uniform in winter. Minimum temperatures and maximum salinities occur in March. Surface warming and freshening begins and continues through the summer. Maximum temperatures, minimum salinities and maximum stratification occur in September.

In the central Sound, little variability in the seasonal cycle of heating and freshening occurred from 1994 to 1997, but interannual differences were present elsewhere (Appendix A). In the northern portions of PWS and in Knight Island Passage, conditions were fresher at the surface in 1995. At Hinchinbrook Entrance and Montague Strait, the surface layer was freshest in 1994. At least two sources of freshwater input, runoff from watersheds in northwest PWS and inflow from the GOA, can increase surface buoyancy and stratification in PWS, and may vary interannually.

2. The current velocities and transport through Hinchinbrook Entrance vary seasonally. Interannual variability was not documented thoroughly. In 1996, the largest horizontal gradients occured in April (Vaughan et al, 1997). The summer and early fall months of 1995 were characterized by outflow above 150m and inflow below (Appendix A). Strong easterly wind events caused upper layer inflow velocity bursts down to the Ekman depth. Periods of outflow at deeper depths were associated with the surface Ekman layer inflow. Upper layer outflow in the summer and early fall at Hinchinbrook Entrance was confirmed by drifting buoy trajectories in 1996, 1997 and 1998 (Vaughan et al, 1998b). In contrast, the fall of 1997 and early winter months of 1998 were characterized by inflow above 150m and weak outflow below (Vaughan et al, 1998a). Late winter and spring months of 1997 were characterized by more barotropic inflows and outflows (Vaughan et al, 1998a).

Comparing transports at Hinchinbrook Entrance above and below 150m between 1978-1979 (Niebauer et al, 1994) and 1995-1997 (Appendix A), trends in the two data sets are similar above 150m. The 1978 transports were greater by about 0.1 Sv or more. In October through December, the Sound may have been been flushed more thoroughly in 1978 than in 1996.

3. At Montague Strait, drifting buoy trajectories revealed upper layer inflow during the summer and early fall months of 1997 and 1998 (Appendix A). In April 1996, areas of both surface inflow and outflow were observed (Vaughan et al, 1998a). At Montague Strait also, strong easterly wind events caused upper layer inflow velocity bursts down to the Ekman depth (Appendix A).

4. Monthly means of air temperature and precipitation exhibited a strong seasonal cycle and some interannual differences (Appendix B). More variability existed in the winter air temperatures than in summer. The highest mean precipitation occured in fall 1995. The warmest winter air temperatures occured in 1996/97 (Appendix B). Individual wind events, rather than monthly means, were responsible for the upper layer Ekman inflows into PWS (Vaughan et al, 1998a).

5. Sound-wide distributions of macrozooplankton were measured using both the OPC and relative backscatter calculated from the towed ADCP. The following is taken from the 320-M FY98 Annual Report (Vaughan et al, 1998a). Simultaneous observations using the OPC, net samples and acoustic absolute backscatter documented the vertical structure of

spring macrozooplankton populations (Kirsch et al, 1999).

In May 1996, there were greater numbers of zooplankton and less fluorescence than in May 1997. Stratification was greater in May 1996 than in May of either 1995 or 1997. In May 1996, the low numbers of phytoplankton in the stratified layer may have resulted from nutrients being depleted and not renewed. The deep mixed layer in May 1997 may have allowed phytoplankton growth and zooplankton dispersal.

The relative backscatter calculations also suggested that zooplankton abundance was reduced in May 1997, and that April 1996 values were increased. Backscatter was lower in the central Sound in May 1997 than in May 1995, and higher in April 1996 than in April 1995. Backscatter was also higher in May 1995 than in April 1995. Backscatter was high over the 'black hole' in the northwest Sound in June 1995. This maximum was not present in June 1996.

The spatial distribution of the zooplankton, as inferred from relative backscatter, changed seasonally. In April and especially May of both 1995 and 1997, more zooplankton were in the northern Sound, in regions of increased surface stratification. By June, more zooplankton were found in the southern Sound, in regions of reduced stratification. The movement of zooplankton from regions of high stratification to low stratification as the seasons progress is in agreement with theoretical primary productivity curve dynamics.

Spring of 1996 was the most productive year for zooplankton. May 1996 was unusually calm and warm. A strongly stratified surface layer formed. It is unclear whether the large number of zooplankton observed resulted from this mixed layer formation, or from favorable conditions in a prior season, like increased zooplankton abundance over the 'black hole' diapausing region in the previous June (1995).

6. Stratification occurs first in the nearshore fjords (Appendix B). Stratification enhances primary production during periods of low light levels, which occur in spring and fall in the subarctic. If earlier stratification results in earlier phytoplankton and zooplankton blooms, the nearshore regions might be preferable overwintering habitats for juvenile fish.

In the central Sound, stratification first appears in early spring in the north, due primarily to freshwater runoff (Appendix A). An associated surface horizontal density front forms in the central Sound, which may last through June. Horizontal density fronts allow exchange between deeper nutrient-rich waters and the surface mixed layer. April and May phytoplankton blooms have maximum values in the northern Sound (McRoy et al, 1998). A stratified surface layer next to a well mixed region, may result in a prolonged phytoplankton bloom. Physical processes that enhance or impede initial stratification formation, and sustain a horizontal density front might be responsible for the temporal variability and biomass differences observed interannually in phytoplankton and zooplankton blooms in central PWS (Eslinger et al, 1998).

7. Tidal fronts observed within the four nearshore study regions were ephemeral in nature, and shifted in location during the course of a tidal cycle (Appendix B). Frontal formation due to tides may assist in retaining locally spawned fish within certain bays and fjords, such as Whale Bay and Zaikof Bay. Features such as strong surface flows in August may promote transport of larvae into fjord and bay basins during summer. Retention could potentially occur in basins that exhibit flow reversals over depth (Appendix B).

8. During the winter, the juvenile herring within the fjords do not typically frequent the deep main basins, which remain stratified throughout the year, but rather occupy the shallow inner basins that undergo more thorough vertical mixing during the winter similar

to that of the bays (Appendix B). In late winter, the deep water temperatures within the fjords were slightly warmer than in the bays. The colder temperatures in the bays may be advantageous to juvenile herring by reducing metabolic rates at a time when they are thought to be fasting.

9. The 'river/lake' hypothesis was based on the correlation of zooplankton abundance at AFK hatchery to the Bakun upwelling index (Bakun, 1973) in spring since about 1981. The idea was that negative values of the upwelling index ('downwelling') produced onshore GOA flow, which entered PWS at Hinchinbrook Entrance, circulated through the Sound, and exited at Montague Strait, flushing the Sound of zooplankton. During the SEA study years (1994-1998), this correlation seems to have disappeared (T. Cooney, pers. comm.). Also, inflow at both Montague Strait and Hinchinbrook Entrance was observed during strong easterly wind events (Appendix A). Zooplankton from the AFK region could have been flushed out by inflow at Montague Strait. The central Sound need not be affected at all. Until the 'river/lake' hypothesis receives a new definition, further discussion is not warranted.

10. Physical oceanographic data products to validate the numerical circulation model have been prepared and distributed, but validation is still not complete. A detailed outline of the model validation manuscript is attached as Appendix C. Observational products used for initialization of the current version of the model include T/S at Hinchinbrook Entrance, transports at Hinchinbrook Entrance, and surface restoring T/S from 1996.

11. Since the model has not yet been validated, it has not been used to identify critical regions and time periods for data collection. The observations have indicated that April and May are critical times because of stratification formation. North to south sections of T and S are also critical during this time to capture the strength and position of the central Sound density front. September may also be critical to document the existance of the closed cyclonic gyre in the central Sound and the associated isopycnal doming.

12. A cost effective monitoring scheme has been designed and proposed to a few agencies with partial success. Monitoring implies longer (interannual) time scales and time series measurements. This monitoring plan has three main components:

1. Create a time series of temperature, salinity, and current velocity measurements at selected stations and transects.
2. Obtain time series measurements of current velocity at Hinchinbrook Entrance.
3. Document mesoscale circulation patterns in PWS and the coastal GOA using satellite tracked drifting buoys.

Oceanographic surveys should be conducted at least twice per year in May and September. Temperature and salinity as a function of depth should be collected using a CTD lowered from the ship at the following locations in PWS: a north/south section (5 stations) in central PWS; an east/west section (5 stations) in central PWS; over the 'black hole'; the upper, middle and lower part of Knight Island Passage; the upper, middle and lower part of Montague Strait; Hinchinbrook Entrance; and south of Hinchinbrook Entrance in the GOA. Mean current velocities using a downward looking ADCP towed from the ship should be calculated from repeat transects at Hinchinbrook Entrance and Montague Strait.

An upward looking ADCP mooring (150 kHz) should be deployed in Hinchinbrook Entrance in September of each year and retreived in May. The dates correspond to the hydrographic survey dates, and cover the fall and early winter periods of maximum transport.

Ideally, two mooring should be used to provide continual coverage. The time series would also provide a boundary condition for the numerical circulation model.

Finally, at least five ARGOS satellite tracked drifting buoys, drogued at a mean depth of approximately 15 meters, should be deployed in central PWS in May of each year. The drifters will document the central Sound circulation in spring and early summer, which can be cyclonic or anticyclonic. Simultaneous hydrographic measurements in May and meteorological measurements should help identify the mechanism responsible for the varying circulation pattern. Also, summer and early fall of previous years were times of upper layer outflow at Hinchinbrook Entrance and inflow at Montague Strait. Drifters released in May over several years will reveal is this pattern is typical or anomalous.

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Chapter 9

Plankton and Nekton Acoustics

Exxon Valdez Oil Spill
Restoration Project Final Report

Nekton-Plankton Acoustics

Restoration Project 98320N
Final Report

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Nekton-Plankton Acoustics

Restoration Project 98320N
Final Report

Study History: The small runs of Prince William Sound pink salmon in 1992 and 1993, and the collapse of the herring population in 1993, prompted the *Exxon Valdez* Oil Spill Trustee Council to initiate the ecosystem-level studies to improve existing predictive tools. In 1993, the Sound Ecosystem Assessment (SEA) science plan was developed using the GLOBEC program as a guide. Funding of research began in the spring of 1994. The Nekton-Plankton Acoustics project (98320N) (SEAFISH) evaluated applications of acoustic measurement technology to collect information on fish and macrozooplankton distribution and abundance. Beginning in 1994, four annual reports were produced as part of the consolidated SEA report. Appended to this report are citations to three journal articles resulting from this project that have been published in the peer-reviewed literature.

Abstract: The major contribution of the Nekton-Plankton Acoustics project was to develop accurate estimation procedures for animal abundance and distribution information. These data were used for testing of the river-lake and prey-switching hypotheses and the development of predictive numerical models. The results include estimates of nekton predators and macrozooplankton prey along the outmigration corridor for the pink salmon in the spring and fall and winter density and distribution of the juvenile and adult herring and pollock populations. Other products include: stock assessments of adult pollock biomass in Feb-Mar 1995 and 1997 (37 and 36 thousand mt) and adult herring biomass in Sep 1993, Oct-Nov 1994, April 1995, Oct-Nov 1995, Mar-April 1996, and April 1997 (20, 13, 13, 24, 23, 40 thousand mt, respectively).

Key Words: *Clupea harengus, Exxon Valdez* oil spill, hydroacoustics, macrozooplankton assessment, *Oncorhynchus gorbuscha*, Pacific herring, pink salmon, population trends, salmon fry predators, stock assessment, *Theraga chalcogramma*, walleye pollock.

Citation:

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Chapter 9: 98320N

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1999 Final Report

Sound Ecosystem Assessment (SEA), Nekton-Plankton Acoustics - Project 94-99320N

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Summary

Background

The small runs of Prince William Sound (PWS) pink salmon in 1992 and 1993, and the collapse of the herring population in 1993, prompted the people in the region to ask the EVOS Trustee Council to support more fundamental fisheries research. About the same time, a National Science Foundation group of scientists working on the Ocean Ecosystem Dynamics Program (GLOBEC) concluded that our inability to predict changes in marine fish populations prevented us from separating natural and anthropogenic impacts (Cullen 1991). Acknowledging this situation, the EVOS Trustee Council funded the PWS Science Center (Science Center) in Cordova, Alaska to host development of the Sound Ecosystem Assessment (SEA) science plan. The SEA planning group included researchers and managers from several universities and agencies, local fishermen, Alaska Natives and concerned citizens. Scientists at the Science Center introduced the GLOBEC program as a guide in the SEA plan development. After strong endorsement by peer review, the EVOS Trustee Council announced a their intention to fund a 25 million dollar, five-year ecosystem program based upon the plan. Funding of SEA research began in the spring of 1994.

This report is part of the SEA program final report. The general goals of the SEA program were to improve the prediction of changes in the abundance of pink salmon and Pacific herring in Prince William Sound. The pink salmon survival study focused, but not exclusively, on hatchery fish since they represent over 90% of the juvenile salmon in the Sound during the spring. The herring survival studies focused on the first winter period for age 0 juveniles since the over-summer survival was not deemed tractable. Both fish stocks are assumed to be distinct to PWS and both were damaged by the 1989 oil spill and a part of the EVOS Trustee Council restoration program.

The SEA program was tasked to develop two predictive products. First, was an ecosystem-based, numerical model that predicts returning number of adult pink salmon spawners by indirectly estimating marine mortality of juvenile pink salmon in the spring. Second, was a population-energetics based, numerical model that predicts survival of juvenile herring over the winter. The development and operation of these numerical models requires accurate measurement technologies to assess the distribution, density and size of specific animal populations. The nekton-plankton acoustics project (94-99320-N) developed applications of acoustic measurement technology for this purpose.

Nekton-plankton acoustics project

We developed hydroacoustic applications to measure the distribution and abundance of pink salmon fry prey and predators (Steinhart et al 1999, Chapter 1; Kirsch et al. 1999, Chapter 2), and herring populations (Thomas et al. 1997, Chapter 3) in Prince William Sound. This information is a prerequisite for the development, verification and application of better tools to predict changes in the pink salmon and herring populations in the Sound. Improving the prediction of changes in pink salmon and herring populations was a primary goal of the Sound Ecosystem Assessment (SEA) program. Since these papers are undergoing peer review for publication in peer reviewed journals their citation requires prior contact and permission by the authors.

Unforeseen at the start of the SEA program was that walleye pollock dominated the pelagic fish assemblage of the Sound. Despite this, walleye pollock are not found as one of the ecosystem components of the EVOS restoration program (EVOS Trustee Council 1998). This is an oversight since they are the most dominant pelagic fish species in the Sound and elsewhere in the North Pacific they are being protected as a forage species to stimulate the recovery of depleted marine mammal and bird populations. This unexpected finding of the SEA program could have major implications on other aspects of the EVOS Restoration Program goals (Thomas et al. 1999, Chapter 4).

Pink salmon fry survival: Prey and predator assessment

After pink salmon fry are released from the hatcheries and the wild fry leave the streams, there is no way to directly measure their abundance until they return as adults the next year. In 1994, SEA investigators concluded that the development of anover-spring survival model for pink salmon fry was the first step in improving the prediction of adult salmon returns. The mechanisms of over-spring mortality was introduced in the two primary SEA hypotheses: river-lake and prey switching. The SEA modeling efforts have shown that numbers of the primary pelagic predator (adult walleye pollock) and primary macrozooplankton prey (*Neocalanus* spps.) along the spring outmigration route best explain the survival of fry released at the hatcheries. The temporal dynamics and contiguousness of the adult walleye pollock and *Neocalanus* copepod populations make hydroacoustics the appropriate choice of methods to use for assessing their densities.

Predator abundance

Two approaches were used to estimate the number of adult walleye pollock predators in the Sound ecosystem. First, we measured the adult walleye pollock along the fry outmigration path during the spring (Steinhart et al 1999). We used echocounting to estimate the relative abundance of adult walleye pollock because they were found as individual fish in the water column at this time of year. However, the near-surface distribution of the adult walleye pollock and their overlap with dense layers of zooplankton resulted in underestimating their densities using standard echo counting techniques. Do to this underestimation, all estimates of adult pollock in the spring are considered to be relative abundance. Second, to get a better understanding of the absolute abundance of adult pollock in the Sound we measured their biomass in the winter when the fish aggregated in relatively small areas prior to spawning (Thomas et al 1999). This was a less direct measure of fry predators since the portion of spawning adults that feed along the fry outmigration path is unknown. However, the midwater distribution of the fish at this time of year allowed for high precision estimates of biomass yielding the best assessment of absolute abundance, which is needed to understand the potential magnitude of predation.

We believe these two acoustic assessment approaches have different strengths that when combined offer the best overall description of the adult walleye pollock population that the pink salmon fry must face each year on their outmigration. Thus, hydroacoustic surveys of adult walleye pollock in the spring and winter provide the predator density information needed to use the over-spring fry survival model to estimate adult pink salmon returns the following year. If the future EVOS monitoring program is to use the SEA fry survival model to predict adult pink salmon returns, acoustic surveys of predator abundance will need to be incorporated into the monitoring program.

Prey assessment

The patchiness of macrozooplankton prey makes representative sampling of density with plankton nets improbable. Yet knowledge of prey abundance is a critical component of the fry survival mechanisms of river-lake and prey switching. To overcome this limitation, we used synoptic MOCNESS and hydroacoustic measurements to scale a Sound wide acoustics survey of macrozooplankton backscatter (Kirsch et al. 1999). Benfield et al. (1998) has had some success with replacing the costly MOCNESS sampling with a plankton video recorder to identify species and measure sizes of dominant macrozooplankton. If the future EVOS monitoring program is to use the SEA fry survival model to predict adult pink salmon returns, the spring survey of macrozooplankton densities will need to be incorporated into the monitoring program. Some efficiency can be accomplished by using a multi-frequency approach on the spring survey to synoptically assess both the predator and prey densities. In addition, these acoustic surveys of macrozooplankton may be desirable for the study of other planktivores in the Sound.

Pacific Herring: Assessment of over-winter and over-summer survival

The development of an overwinter survival model for juvenile herring survival was considered a tractable problem by SEA investigators in 1994 (as opposed to the estimation of over-summer survival). Two approaches were used to estimate the abundance of herring year-classes in the Sound. First, hydroacoustic surveys of the adult herring overwintering in the Sound were conducted in conjunction with Alaska Department of Fish and Game to estimate the recruitment of juveniles into the adult population. The acoustic biomass estimates were shown to be highly precise (Thomas et al. 1997). Second, hydroacoustic survey procedures were developed to directly estimate the age 0 and 1 herring abundance in the fall and spring. By conducting juvenile surveys, the time interval to verify model predictions was reduced from three years to every six months (by the number of age 0 fish surviving the first summer and subsequently the first winter). Shortening the interval of measurement to six months makes the development of an over-summer survival model for age 0 herring feasible.

Our acoustic surveys show that the adult herring population in Prince William Sound has undergone a second collapse (1992-93 and 1997-98) in biomass since the spill in 1989. These collapses are unique to the PWS herring population so in light of the possible immune system and genetic damage shown for other species the linkage to the 1989 oil spill cannot be dismissed. Also, with the herring's importance as a forage fish, knowledge of their abundance and distribution is critical to understanding the recovery of many piscivorus species of marine birds and mammals. Thus, herring monitoring is a likely candidate for the future EVOS monitoring program. Since the fall and spring acoustic survey methods we developed yield precise estimates of the distribution and abundance of the adult and juvenile herring, they are important candidates for inclusion with the EVOS monitoring program. Once verified, the application of the SEA over-winter survival model may replace the need for spring surveys of the juveniles but the fall-juvenile and spring-adult surveys will remain critical to understanding the annual changes in the herring population that can have pronounced impacts on the productivity of birds and mammals in the Sound.

Walleye pollock: The Sound's "waist-taxon"

Pollock were shown to be the super-dominant, waist-taxon in the Bering Sea trophic structure (Livingston et al. 1997). Thomas et al. (1999) describes pollock as the super-dominant, waist-taxon of the Sound's trophic structure. We hypothesize that herring may compete with pollock for the waist-taxon position in the trophic structure during more stormy weather regimes. In any event, knowledge waist-taxon abundance, where they occur, is a prerequisite to understanding the fate of lower trophic level production and the productivity and diversity of higher trophic levels (birds and mammals). Thus, incorporation of acoustic surveys of pollock and herring are a prerequisite for the EVOS monitoring program if one goal is to track changes in damaged fish, bird and mammal populations so that recovery can be assumed.

Chapter 1 – Steinhart et al. 1999

Note: Do not cite without prior contact and permission from authors. This paper is undergoing peer review for publication in a scientific journal

Co-occurring patches of walleye pollock (*Theragra chalcogramma*) and zooplankton in Prince William Sound, Alaska, USA.

by

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ABSTRACT

We conducted two acoustic surveys of Prince William Sound (PWS) in the spring of 1995. The primary goal of these surveys was to observe the spring zooplankton bloom and the distribution of post-spawning walleye pollock (*Theragra chalcogramma*), one of the dominant fish species in the Sound. In this paper, we examine the spatial distributions of pollock and zooplankton in April and May, 1995. Zooplankton biomass varied from 0.1-1.7 g/m3 from the net tows, while acoustic estimates of zooplankton biomass varied by three orders of magnitude (1000 x). We observed near surface (0-50 m) patches of zooplankton from 100 m to 5000 m long. In April, these patches were composed of 85% calanoid (72% *Neocalanus spp.*) copepods by weight. By May, calanoid copepods accounted for only 55% (24% *Neocalanus spp.*) of the biomass, but pteropod denisty doubled (from 0.7 to 2.2 g/m^3). Acoustic data showed post-spawning walleye pollock abundance was highest near the surface (0-50 m), and was positively correlated with zooplankton biomass ($r^2=0.42$ in April, and $r^2=0.31$ in May). Post-spawning walleye pollock were feeding heavily on the plankton found in the patches: copepods in April and pteropods in May. Early-spring feeding on zooplankton by adult walleye pollock is not fully understood, but collaborates with other pollock studies in the Bering Sea, and could be an important factor affecting the production of pollock in PWS.

INTRODUCTION

Walleye pollock (*Theragra chalcogramma*) are one of the most abundant fish in Prince William Sound (Thomas et al. 1997). Acoustic surveys in Prince William Sound (PWS) have estimated the pre-spawning biomass of pollock at over 100,000 tonnes (Alaska Department of Fish and Game [ADF&G], Cordova, Alaska, unpublished data). Pollock are important to the marine ecosystems of Alaska, both as predators (Dwyer et al. 1987; Bailey 1989) and while juveniles, as prey (Smith 1981; Hatch and Sanger 1992; Springer 1992). Although earlier studies have looked at behavior, distribution and abundance of adult pollock in the Gulf of Alaska (GOA) and the Bering Sea from summer through winter (Traynor 1986; Brodeur and Wilson 1996), little is known about the spring distribution and behavior of post-spawning pollock in PWS. With such a large adult pollock population in PWS, their dual role as both a predator and a competitor could be important to the recruitment of other economically important fishes in Prince William Sound (Walters et al. 1986; Cooney 1993); such as, Pacific herring (*Clupea pallasi*) and pink salmon (*Oncorhynchus gorbuscha*).

The match-mismatch hypothesis (Cushing 1972; Cushing 1982) has suggested that much of the variability in recruitment success of marine fish is due to the time of fish hatching and how it coincides with the plankton production cycle: a bottom-up hypothesis. In contrast, predation by a dominant fish can also explain survival of other fish and lower trophic levels: a top-down hypothesis (Carpenter et al. 1995). These two hypotheses are not entirely separate: direct and indirect effects of each process can lead to the same results. For example, during a year where the fish hatch is not timed with the zooplankton bloom, or during a poor production year, there will be less food for growth and survival of young fish (a direct bottom-up effect of low zooplankton abundance). Optimal foraging theory suggests that with reduced zooplankton abundance, predators of zooplankton may switch their diet (Werner and Mittelbach 1981), and may include more juvenile fish (Willette et al., MS submitted). During a year of low production or mismatched larval fish hatch, not only is their less food for young fish, but they may experience high rates of mortality from predators (an indirect bottom-up effect, or a direct top-down effect).

After the 1989 *Exxon Valdez* oil spill, stocks of Pacific herring and pink salmon in PWS have had variable recruitment success. The low returns of hatchery-released pink salmon in 1992 and 1993 are hypothesized to be the result of poor survival during their outmigration from PWS (Willette 1996). Both bottom-up and top-down mechanisms are suspected, and adult pollock, being one of the most abundant pelagic fish in PWS, is one of the most likely candidates for causing the decline. Walleye pollock have been shown to be both a predator of pink salmon fry, and a competitor for zooplankton in PWS (Willette et al., MS submitted). The outmigration of pink salmon fry starts in mid-April with a large hatchery releases which continue through the month of May. The smolts migrate through PWS for approximately 2 months (ADF&G, unpublished data). During this outmigration, competition with pollock for zooplankton may result in lower salmon survival. Furthermore, low plankton biomass may cause the pollock to consume more salmon smolts, compounding salmon mortality (Willette et al., MS submitted). In the Bering Sea, pollock switched their diet to include more fish during periods of low zooplankton abundance (Dwyer et al. 1987; Bailey 1989).

Although the PWS hatcheries attempt to match the pink salmon releases with the spring zooplankton bloom, changes in climatic conditions can effect the success of this strategy. The formation of stable layers or patches of plankton can be important for the survival of young fishes (Lasker 1975, Leggett 1986). If the smolts are released at a time when plankton abundance is low, or when storms prevent the formation of zooplankton patches, the effects of competition and predation by pollock may be accentuated. Therefore, understanding the distribution of adult pollock and zooplankton patches is important to understanding the survival of pink salmon, and other fishes in PWS.

Our objective was to describe the spatial distribution of pollock and zooplankton in Prince William Sound during the spring of 1995. Specifically, we looked at the spatial and temporal overlap of post-spawning adult walleye pollock and the suite of calanoid copepod species that comprise much of the spring zooplankton bloom (*Calanus* spp., *Neocalanus* spp., and *Pseudocalanus* spp.). We hypothesized that walleye pollock and zooplankton would be found in co-occurring patches during the spring. Describing the extent of this co-occurence is a fist step in developing a better understanding of predator/prey interactions in PWS.

MATERIALS AND METHODS

Prince William Sound is located at the northern edge of the Gulf of Alaska (Fig. 1). This large fjord/estuary covers an area of approximately 8800 km^2, and has about 3200 km of shoreline (Grant and Higgins 1910). Coastal rainforests, high mountains, and glaciers border the shoreline of PWS. The area is exposed to seasonally intense storms moving in from the Gulf of Alaska, resulting in 5-7 m of annual rainfall.

In 1995, two broadscale surveys of PWS were conducted during 27 April to 1 May, and 23-27 May (Fig. 1). Fish and zooplankton were measured with hydroacoustics and the acoustic targets were verified with vertical plankton tows and mid-trawl hauls. All sampling was conducted during daylight hours.

Acoustic data were collected using a BioSonics 101-120 kHz 6°/15° dual-beam echosounder. The transducer was mounted on a tow-body which was towed alongside the boat at a depth of 2 m at an approximate speed of 2 m/s. The parameters of the acoustic system were: source level = 225.023 dB; receiver gain = -159.282 dB; transducer directivity = 0.0010718; pulse width = 0.4 ms. We set the noise threshold to 0.04 V, and the range to 250 m for these cruises. The acoustic system was calibrated before each cruise using a tungsten-carbide ball, of known target strength, suspended within the beam of the transducer (Foote and MacLennan 1982). The data were processed in real-time using BioSonics ESP software on a 486 computer and were geo-referenced and time-coded using data from a Magellan DLX-10 GPS receiver. Echo integration, dual-beam target strength (TS), and GPS data were stored on the computer hard disk, and backed up on a tape drive. Raw acoustic signals were stored on Digital Audio Tape and printed on paper echograms.

Once the cruise was completed, the acoustic files were transferred to UNIX workstations for data reduction and analyses. Initial processing of acoustic information was done with in-house software written to apply the acoustic calibrations and to correct euphausiids (-93.8 dB), and pteropods (-89.2 dB). The target strengths of these zooplankton were estimated from mean lengths and widths taken throughout PWS, and from estimates of the reflection coefficient, R (see Kirsch et al., MS submitted, for complete details). We did not include all plankton species in this analysis because many of the plankton caught in the zooplankton nets were either too small to be seen with our 120 kHz transducer, or had low densities, so they would have a Sv that was negligible compared to that of the primary species.

Zooplankton were sampled with vertical net tows using a 0.5 m ring net with 333 μm mesh (18 tows in April, 10 tows in May). The net was towed vertically through the top 50 m. Most hauls were done at the beginning or end of the acoustic transects, but some net hauls were pulled through distinct patches of plankton. The samples were preserved in a formalin solution. In the lab, the zooplankton were enumerated, measured, and identified to species. The mean length of each species was used to calculate the mean weight, and then multiplied by the number of individuals in the sample to yield biomass estimates.

Once the acoustic data arrays for pollock-sized targets and zooplankton were generated, we analyzed the data to look for spatial overlap between the two distributions. First, we generated maps of zooplankton patches and pollock densities. We visually identified zooplankton layers or patches using the electronic echograms and measured the length of the patch, which we call the chord length. Given our ping rate, boat speed, and echo-integration report size (32 pings), the smallest patch that could be identified was approximately 50 m in chord length. We assumed the patches were round, and that the chord length was a suitable estimate of the diameter. Since the assumption that zooplankton patches are round is flawed, we only used this data to generate images of zooplankton and pollock distributions. We then used the acoustic estimates of pollock and macro-zooplankton density to calculate regressions between pollock density in different depth ranges (0-50 m, 0-100 m, and 0-150 m) and macro-zooplankton density (top 50 m) at several different horizontal spatial scales (cell sizes: 50 m to 10,000 m long).

RESULTS

The spring zooplankton community in Prince William Sound was comprised of several species, but was dominated by calanoid copepods: 89% in April and 72% in May (by weight). Total zooplankton biomass in the top 50 m declined by approximately 50% from April to May, mostly due to a decline in the number of *Neocalanus spp.* (Fig. 2). Vertical plankton net hauls found a significant decline in mean zooplankton biomass from 0.54 g/m^3 in April to 0.28 g/m^3 in May (heteroscedastic t-test for unequal variances, df=22, t=2.45, p=0.011). During April, *Neocalanus spp.* made up 72% of the total zooplankton biomass, but by May, *Neocalanus spp.* accounted for only 24%. The acoustic data showed a significant decline in mean macro-zooplankton density (*Neocalanus spp.*, euphausiids, and pteropods) from 420 $plankton/m^3$ in April, to 260 $plankton/m^3$ in May (heteroscedastic t-test for unequal variances, df=27, t=9.73, $p<<0.05$).

Not only were zooplankton most abundant during the April cruise, they were also more patchy. Zooplankton biomass estimates from net hauls ranged from 0.15-1.7 g/m^3 ($s^2=0.18$, n=18) in April, and 0.14-0.54 g/m^3 ($s^2=0.02$, n=10) in May. The variance in zooplankton biomass from the nets was significantly higher for the April than the May cruise ($F_{(17,9)}$=11.61, p= 0.0004), suggesting more patchiness in the plankton distribution in April. The variance in acoustic estimates of macro-zooplankton in cells 50 m deep by 50 m long was twice as high during April (s^2=2.5 e^{12}) than during May (s^2=1.1 e^{12}). This was a statistically significant decrease, but the significance may be an artifact of the huge sample sizes of acoustic data sets (April n= 3963, May n=3890 cells).

Many patchy layers of zooplankton were seen with the hydroacoustic system (Fig. 3). In general, there were more zooplankton patches identified on the electronic echograms from the April cruise (n=37) than from the may cruise May (n=21). Zooplankton patches averaged 1,700 m chord length in April (range: 150-5,000 m), and 3,200 m in May (range: 300-7,000 m). Although we did not design these surveys to compare density between or within zooplankton patches, zooplankton biomass estimates from net tows varied up to an order of magnitude (0.15-1.7 g/m^3). The hydroacoustic data, which have a larger and more continuous coverage than the net hauls, found over three orders of magnitude (1-3,000 plankton/m^3) difference in acoustic backscatter attributed to zooplankton. From these data, we suggest that the observed zooplankton patches could vary by up to 1000 times the average zooplankton density outside of patches.

The mid-water trawl caught almost exclusively adult walleye pollock. In total, 596 pollock were caught and comprised 93% of the total catch. Additional fish captured included 31 lantern fish (Family Myctophidae), 9 sculpin (Family Cottidae), 2 capelin (*Mallotus villosus*), and 1 chinook salmon (*Oncorhynchus tshawytscha*). The lantern fish were caught in the haul at 125 m, the only trawl haul deeper than 60 m. The pollock averaged 508 mm fork length (range = 400-702 mm) and 870 g wet weight (range = 490-1410 g). The predicted TS was determined using TS=20Log (length) - 66 (Traynor and Williamson 1983). The predicted TS of these pollock coincided with the TS range we used to count pollock-sized targets (Fig. 4). Although there were a limited number of trawl hauls, pollock dominated the catch and the other fish captured in the trawl would have target strengths below our threshold so would not be counted by our echo-counting procedure, except for the one adult salmon captured. Therefore, we assumed that all pollock-sized targets observed during these cruise were adult pollock.

There appeared to be two layers of pollock during these cruises: a shallow layer (less than 50 m deep), and a sparse deep layer around 150 to 200 m (Fig. 5). Although there were few deep trawl hauls made during these acoustic surveys, the trawl data did show the highest catch per unit effort above 20 m (Fig. 6). Based on the shape, distribution, and target strengths of targets below 100 m, and on trawl data from other surveys from 1994-1997 (ADF&G, unpublished data), we believe that these deep targets were also adult pollock. The depth distribution of pollock changed slightly between the two surveys: pollock were more abundant near the surface during the April cruise than during the May cruise, although this difference does not appear significant. The acoustics also showed that there were slightly more pollock-sized targets in the deep layer during May.

Pollock stomachs were found to contain nearly 99% zooplankton (by weight) in April (n=196) and in May (n=34; Fig. 7). In April, calanoid copepods, primarily *Neocalanus spp*, comprised 65% of the stomach contents. In May, however, pteropods were the dominant prey item (43%), while less than 25% of the diet consisted of copepods. Pink salmon were identified on the stomach contents, but due to the break down of tissues during digestion, many fish remains were not readily identifiable and all ingested fish were lumped into a single category. Fish made up less than 1% of pollock diets during both cruises.

We saw pollock-sized targets with plankton patches during both April (Fig. 8) and May (Fig. 9). Although pollock were not always found coinciding with plankton, it appeared that they were more closely associated during the April survey. Indeed, we found positive correlations between pollock density and relative zooplankton density during both surveys in 1995. In general, the correlation between pollock and plankton was better during April than in May. The spatial scales used in the correlation analyses affected the correlation coefficients. In April, more pollock were found near the surface than in May, and the highest r^2 value (0.42) was found by regressing pollock density from 0-50 m in cells approximately 6,500 m long (Fig. 10). In May, we found that the highest r^2 was obtained by including deeper pollock: regressing pollock density from 0-100 m provided the highest r^2 value (0.31), using cells approximately 7,500 m long.

DISCUSSION

The results from our spring surveys in PWS found that post-spawning walleye pollock in Prince William Sound behaved differently than pollock in the Bering Sea and GOA during the summer-winter season. In those areas, adult pollock were found near the bottom during the daytime, with only juveniles commonly found near the surface (Traynor 1986; Bailey 1989). Pollock in the Bering Sea eat mainly euphausiids and larvaceans during the spring (Dwyer et al. 1987), but their spatial overlap with macro-zooplankton has only been assumed (Swartzman et al. 1995). In PWS, we found the highest densities of adult walleye pollock near the surface. Most previous studies have suggested that adult pollock remain deep in the water column (Bailey 1989; Brodeur and Wilson 1996), but this may be a result of sampling effort. When looking at acoustic data, it is essential to remember that sampling volume increases exponentially with range, so while only a few fish may be seen near the surface, they may equate to a high density. For this reason, or because some acoustic surveys are conducted with transducers towed deep in the water column, fish near the surface may have been missed in these previous studies. Our data suggest that the bulk of post-spawning pollock in PWS feed near the surface in early spring to exploit the large *Neocalanus spp.* population. Large copepods composed the bulk of pollock diets during the spring plankton bloom, and are an important food resource for post-spawning pollock in PWS. Paul et al. (1993) showed that for yellowfin sole (*Pleuronectes asper*), a demersal fish, that the spring plankton bloom provides up to 40% of the fishes total caloric intake for the year in the Bering Sea. *Neocalanus spp.* were the dominant zooplankton in April bloom, and could represent a significant portion of the annual caloric intake for adult walleye pollock.

The near-surface distribution of post-spawning pollock in the Sound appears to be to be in response to the availability of prey, as *Neocalanus spp.* undergo a seasonal vertical migration (Cooney 1987). In mid-spring, young copepods migrate up from great depths (400+ m) to respond to the spring phytoplankton bloom, where they remain for a short time. By early summer, the mature copepods have migrated down to 400+ m where they spend the winter. There is also evidence that oceanic copepods enter near-shore and coastal waters in the spring (Incze et al. 1997). We observed both a general decline in copeopod abundance near the surface between late April and late May, and changes in zooplankton patch size and species composition. During April, there were more dense patches of plankton, and more variability in plankton density, than in May. In April, the zooplankton patches were made up almost entirely of *Neocalanus spp*. During May, however, there were fewer high density zooplankton patches, and less variability in plankton distribution. In May, the layers of less patchy zooplankton may have been aggregations of species other than copepods. Pteropods, for example, were much more abundant in the high density areas, and may have been forming the few dense patches we observed during May.

Observations made during this study, as well as other research (Lasker 1975; Leggett 1986; Simard and Mackas 1989; Barange 1994), suggested that climate and currents can influence zooplankton distribution. Gusts of 20 m/s occurred on 23-24 of May 1995, and average daily wind speeds were higher during the May survey than during the April survey (NOAA, unpublished data). The reduced number and density of zooplankton patches and layers near the surface in May could have been the result of the increased winds at that time. In addition, small scale physical mixing from tide rips, Langmuir cells, and internal waves can affect plankton distribution by concentrating plankton in some areas (Haury et al. 1983; Wiebe et al. 1997). On several occasions, we saw a varying depth distribution of plankton layers on a small scale (Fig. 3). The effects of small-scale turbulence on zooplankton patchiness, and the effects of large-scale circulation patterns on zooplankton immigration to, and emigration from, the Sound are not entirely understood at this time, but may affect the number and density of macro-zooplankton available for post-spawning walleye pollock.

Seasonal shifts in adult pollock diets have been reported previously (Dwyer et al. 1987, Bailey 1989, Willette et al. MS submitted). In this study, pollock diets switched from primarily copepods to pteropods; however, another alternate prey, pink salmon fry, are typically found in the top 50 m during their spring out-migration, and are consumed by post-spawning walleye pollock (Willette 1996). The relatively low incidence of fish in diets of pollock we sampled may have been an artifact of the timing and location of the offshore surveys: in PWS salmon fry are usually more abundant in nearshore environments in April and May, before moving into pelagic areas in June (Willette et al., MS submitted). Although fish made up less than 1% of pollock diets during this study, it is important to remember that individual pollock don't need to eat many salmon fry to have a profound effect on salmon survival given the large number of pollock found in the Sound. Assuming there are approximately 25 million adult pollock (ADF&G, unpublished data), and 750 million salmon fry in PWS (Thomas and Mathisen 1993), then salmon survival will be zero if each pollock ate only 30 salmon fry per year. Therefore, it is not hard to imagine that predation by post-spawning pollock could have a profound impact on salmon survival.

Pollock density and macro-zooplankton were positively correlated during this study, and correlations between predators and prey are common in the literature (Schneider 1989; Rose and Leggett 1989; Rose and Leggett 1990; Veit et al. 1993; Deblois and Rose 1995). A positive correlation does not prove a causal relationship; however, since pollock diets were dominated by zooplankton during these surveys, it does support the hypothesis that adult pollock were attracted to and were feeding on macro-zooplankton patches. Even though zooplankton abundance explained less than 50% of the variation in pollock density that was observed, this type of spatial relationship can be difficult to quantify using simple correlation. Spatial associations between predators and their prey are notoriously weak, with correlation coefficients often less than 0.5 (Veit et al. 1993). Rose and Leggett (1990) suggest that positive correlations between predator and prey densities would occur at scales greater than the dimensions of the predator and prey aggregations. Predators, such as pollock, may be found close to their prey, but not right on top of them. For example, strong currents may concentrate zooplankton in some areas, but fish may avoid the strongest currents and feed on the edges of the aggregation. Indeed, we did find that the best correlation was when we pooled our acoustic data into bins larger than the mean patch sizes we observed. The relatively low correlation could also be due to other variables that we haven't examined yet; for example, behavior of fish and zooplankton due to tides, surface mixing, predator satiation, prey avoidance, and the abundance of alternate prey items, such as juvenile fish.

While the quasi-continuous nature of hydroacoustic data is extremely useful for studying spatial distributions, there are several potential sources of error with acoustic data. The small sample volume of the acoustic beam at short ranges, combined with the near-surface distribution and boat avoidance behavior of many fish may have underestimated densities. In addition, target strengths of fish are highly variable and depend on many factors (Traynor and Williamson 1983; Mukai and Iida 1996).

Partitioning acoustic data into different species is essential, but it only as reliable as the methods used to describe the species compostion of the fish assemblage. These potential errors all lead errors in estimates of fish abundance.

There are also problems with our use of acoustics to measure plankton abundance. A 120 kHz transducer was appropriate for measuring fish abundance, the primary objective of these surveys, but this frequency was too low to measure all zooplankton species due to scattering in the Rayleigh region. Errors in the estimation of plankton densities, lengths, and reflection coefficients will all effect the acoustic estimate of plankton biomass (Wiebe et al. 1997). Once again, the partitioning of acoustic data into different plankton species is only as accurate as the methods used to collect plankton. In addition, the coarse echo integration cell size (5 m deep and approximately 50 m long) were not conducive to finding, or describing the small scale patches of zooplankton.

Further research is needed to improve acoustic estimates of zooplankton and fish using different acoustic equipment and techniques. Digital transducers can provide a much finer spatial resolution than analog transducers. The high spatial resolution of digital acoustic data, which is already higher than analog equipment, is largely limited by current computer technology, and is improving a rapid rate. High spatial resolution of digital acoustic data allows for a finer scale analysis of zooplankton and fish patch sizes than with analog acoustic equipment. It also aids in removing unwanted targets before averaging to create the echo integration arrays, thus providing more accurate zooplankton and fish estimates. The use multiple acoustic frequencies further improves separation of fish targets from zooplankton targets. Using exclusively trawls and plankton nets to describe spatial distributions of fish and zooplankton in an area as large as Prince William Sound is futile due to limitations of time and money. By combining these tools with appropriately designed acoustic surveys, it is possible to obtain data with a higher spatial resolution, and covering a larger area, than with net sampling alone.

Understanding the mechanisms of juvenile fish mortality is critical in improving our ability to implement a multi-species management approach to protect the many important fisheries of PWS (Thomas et al. 1997). Understanding the spatial relationship between post-spawning walleye pollock and macro-zooplankton will lead to an increased knowledge of the roles of pollock in the trophic structure of PWS. It also demonstrates the importance of not relying solely on data from other locations (i.e. the Bering Sea) or during only a portion of the year (summer-winter) when attempting to describe the impact of a particular species in an ecosystem.

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Figure Legends

Fig. 1. Map of Prince William Sound showing sampling locations of acoustic transects from April (dashed lines) and May (solid lines) 1995. Also shown are zooplankton tows (circles) and trawls (triangles) from April (empty symbols) and May (filled symbols) 1995. Note that a some points may not be not visible due to overlapping with other points.

Fig. 2. Zooplankton biomass from vertical net hauls in the top 50 m of Prince William Sound for April and May 1995. The number of hauls (N) is given for each cruise.

Fig. 3. Paper echograms from two acoustic transects during April 1995 showing: A) Plankton layer with varying depth and density, possibly due to localized turbulence, waves or currents; B) Plankton patch with pollock-sized targets associated with areas of high density.

Fig. 4. Target strength (TS) frequencies from acoustic data files (black bars) and estimated TS from walleye pollock captured in the mid-water trawl in Prince William Sound during April and May 1995. Estimated TS were calculated using 20Log (length) - 66 (Traynor and Williamson 1983). The arrows mark the range of TS values that were used to produce estimates of pollock density.

Fig. 5. Depth distribution of pollock-sized targets (± 1 S. D.) from acoustic data collected in Prince William Sound during April and May 1995.

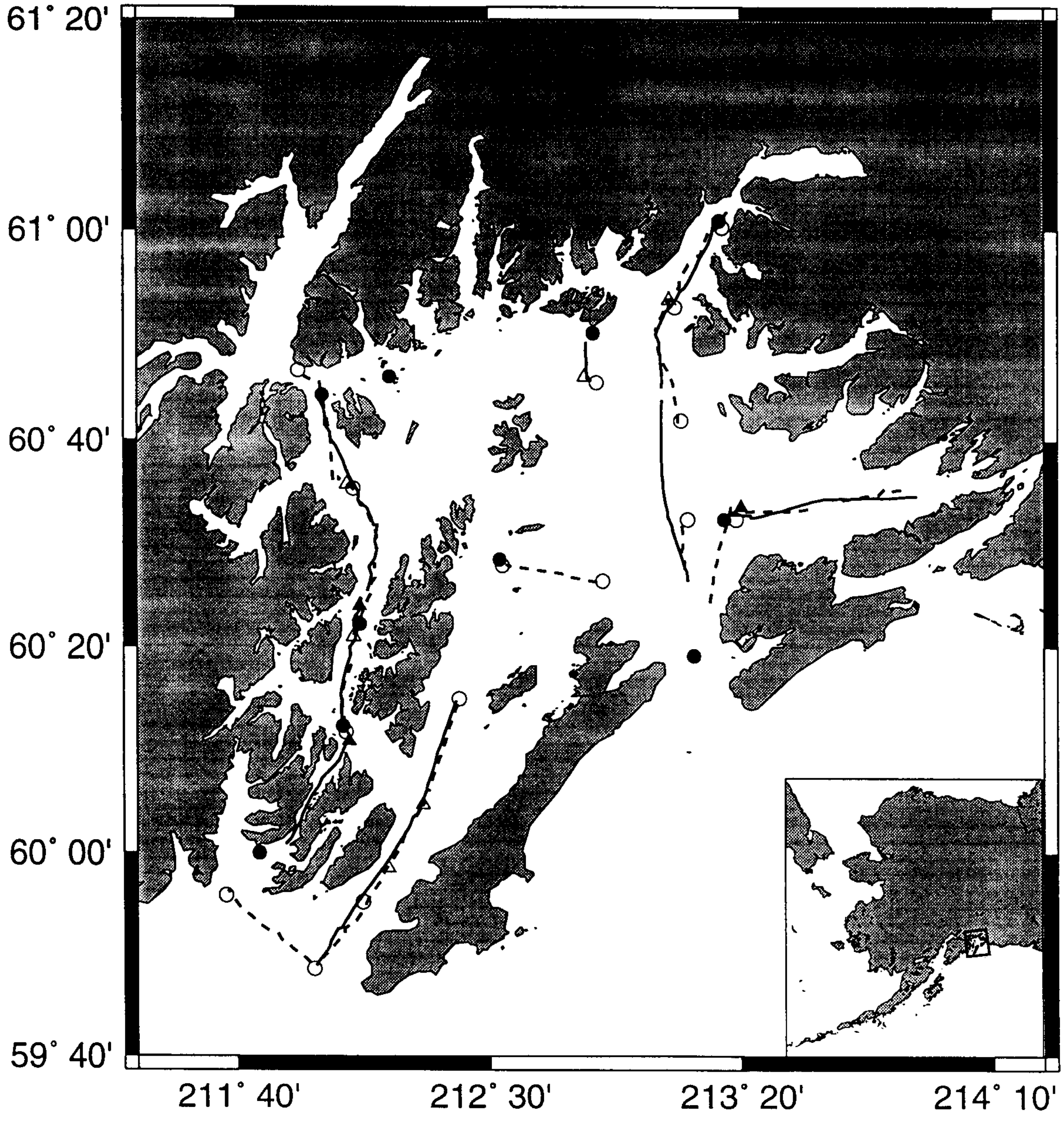
Fig. 6. Catch per unit effort of adult pollock from nine mid-water trawls performed in Prince William Sound in April and May 1995. There were no trawls between 73 and 122 m, or deeper than 138 m. Depth distribution of pollock-sized targets (± 1 S. D.) from acoustic data collected in Prince William Sound during April and May 1995.

Fig. 7. Adult pollock diet composition (percent by weight) in April and May 1995 in Prince William Sound. The sample size (N) is given for each cruise.

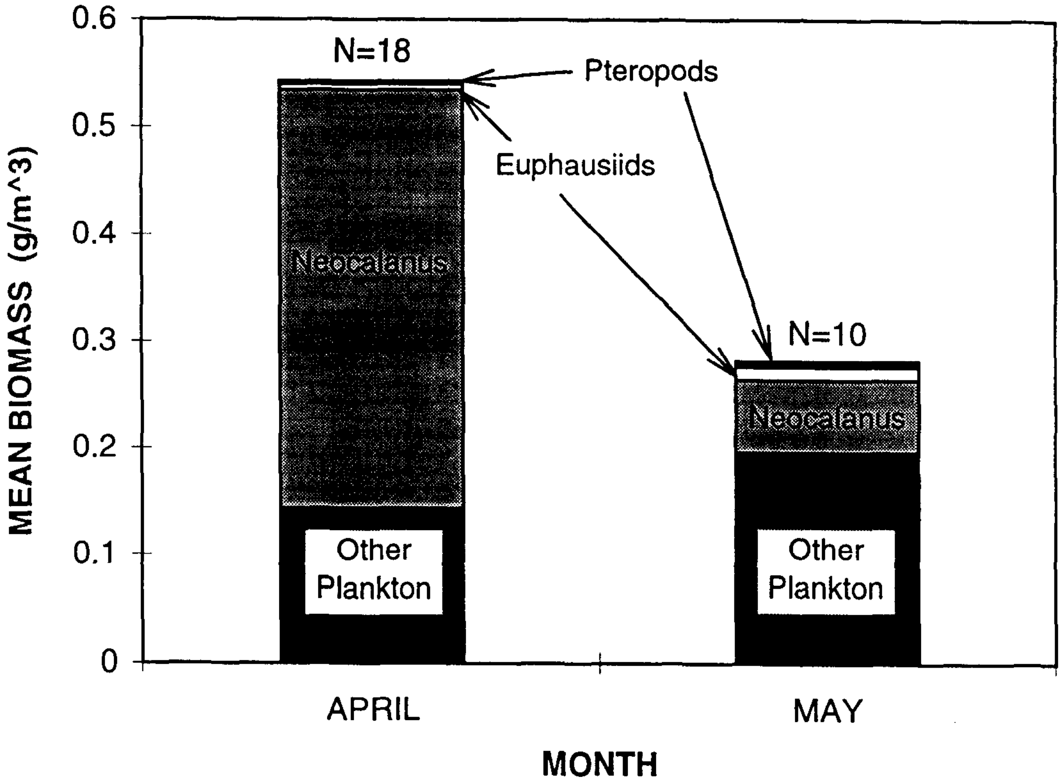
Fig. 8. Map of Prince William Sound showing acoustic estimates of pollock density ($\#/m^2$) from 0-50 m in April 1995. Solid circles represent the size and location of zooplankton patches identified from acoustic data. The squares represent the location of zooplankton patches that were too small (< 1,000 m) to be seen on the figure.

Fig. 9. Map of Prince William Sound showing acoustic estimates of pollock density ($\#/m^2$) from 0-50 m in May 1995. Solid circles represent the size and location of zooplankton patches identified from acoustic data. The squares represent the location of zooplankton patches that were too small (< 1,000 m) to be seen on the figure.

Fig. 10. Relationship between acoustic estimates of pollock density and macro-zooplankton abundance (0-50 m) in Prince William Sound. In April (circles and solid line), the best fit was found with pollock abundance from 0-50 m in cells approximately 6,500 m long (r^2=0.4, $y=5e^{-08} + 0.0004$). In May (squares and dashed line), the highest r^2 (r^2=0.31, $y=4e\text{-}08 - 7e^{-06}$) was with pollock density from 0-100 in cells approximately 7,500 m long



61° 20'
61° 00'
60° 40'
60° 20'
60° 00'
59° 40'
211° 40'
212° 30'
213° 20'
214° 10'


0.6
0.5
0.4
0.3
0.2
0.1
0
MEAN BIOMASS (g/m^3)
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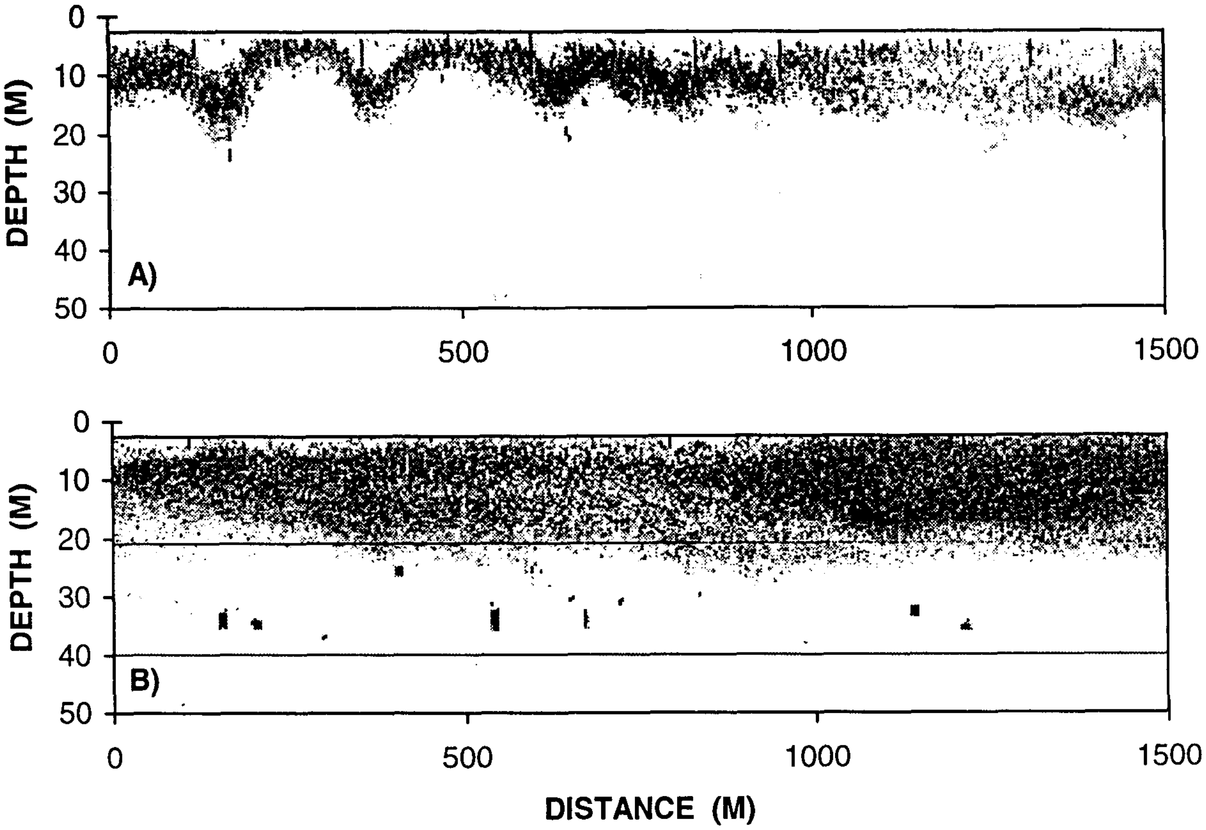
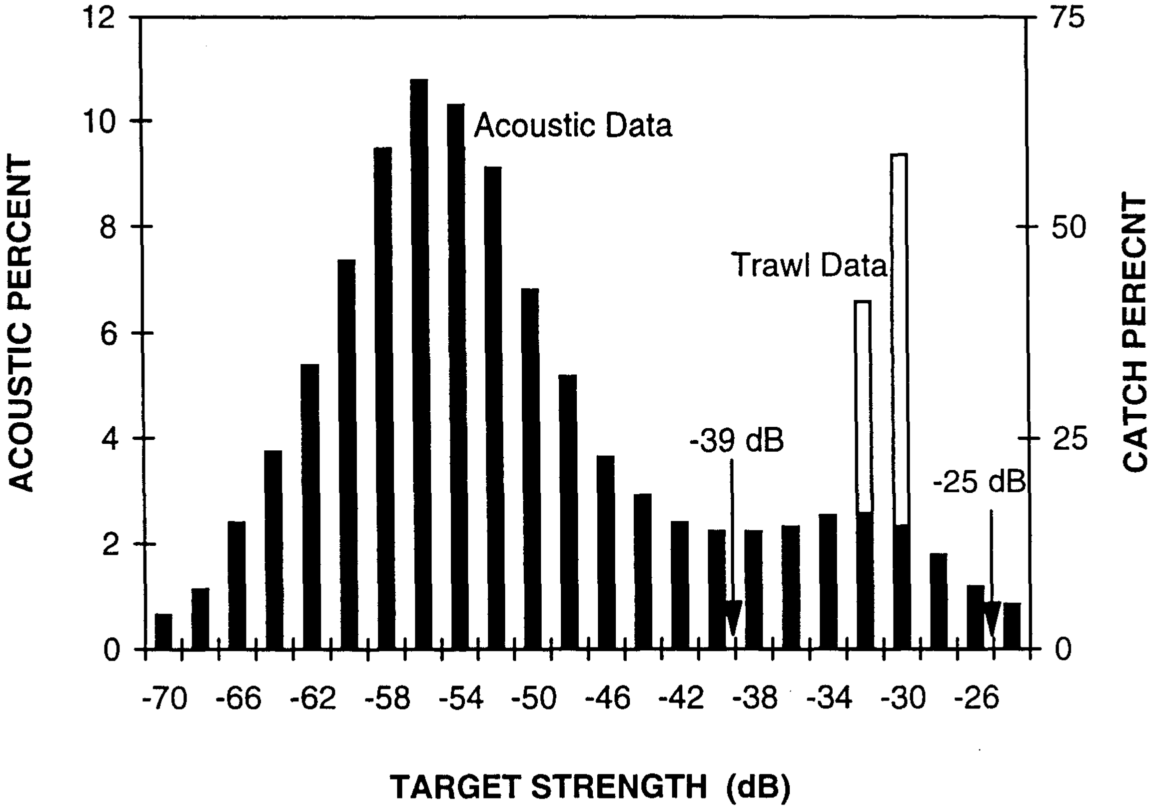
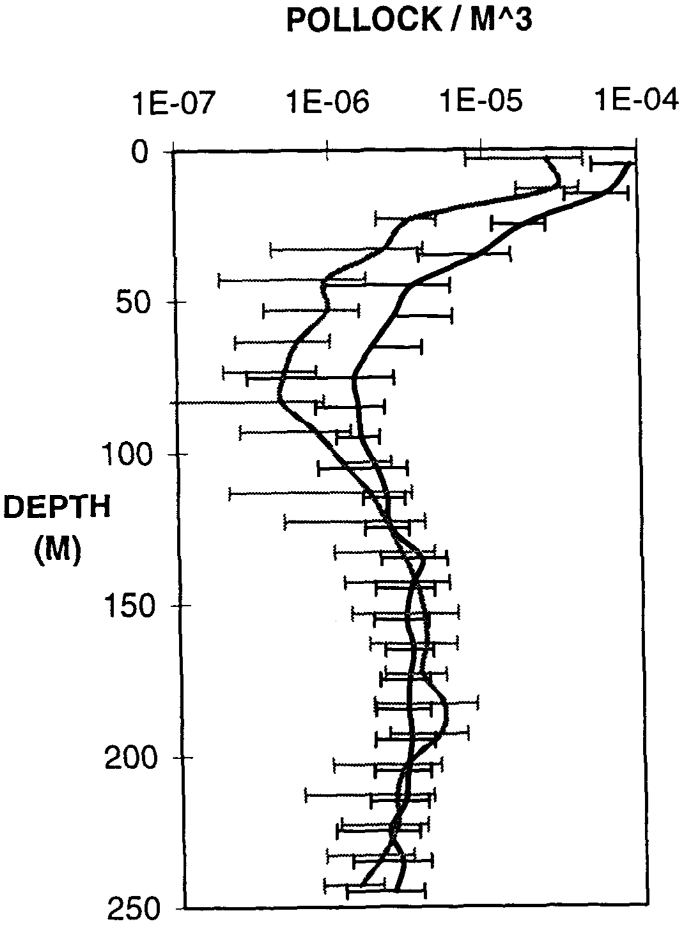
Pteropods
Euphausiids
Neocalanus
Other Plankton
N=10
Neocalanus
Other Plankton
APRIL
MAY
MONTH



A)
B)
DEPTH (M)
0
10
20
30
40
50
0
500
1000
1500
DISTANCE (M)


12
10
8
6
4
2
0
ACOUSTIC PERCENT
75
50
25
0
CATCH PERECNT
Acoustic Data
Trawl Data
-39 dB
-25 dB
-70
-66
-62
-58
-54
-50
-46
-42
-38
-34
-30
-26
TARGET STRENGTH (dB)


POLLOCK / M^3
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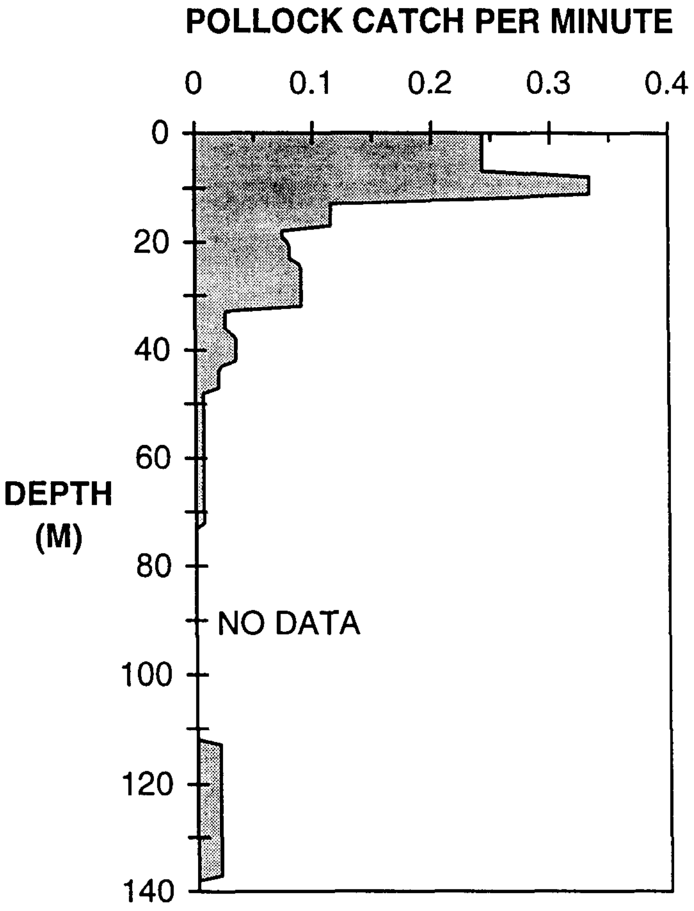
1E-06
1E-05
1E-04
0
50
100
150
200
250
DEPTH
(M)


POLLOCK CATCH PER MINUTE
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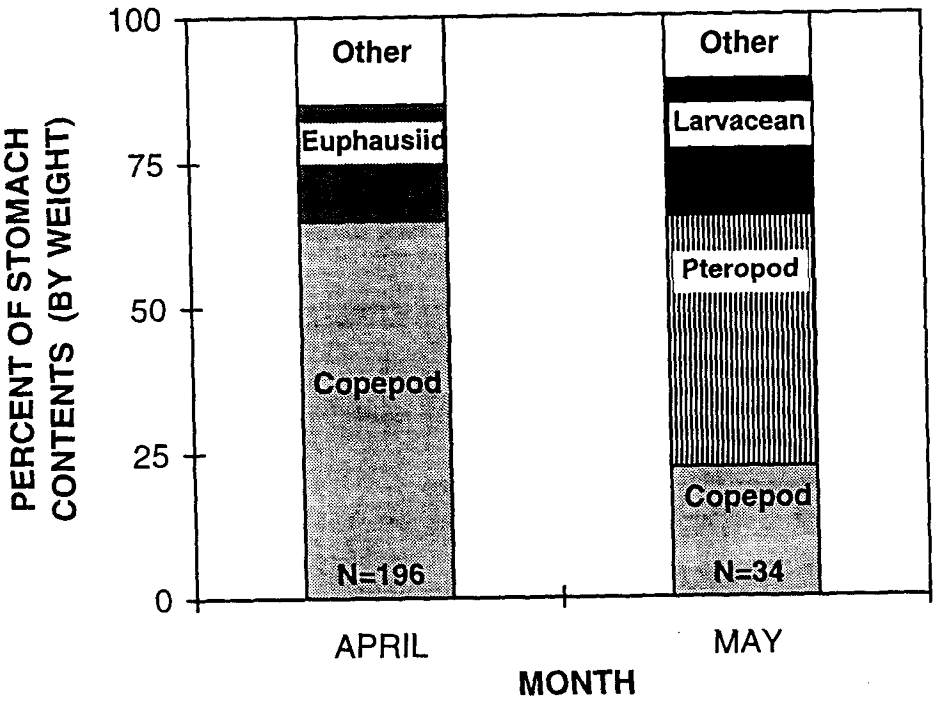
0.2
0.3
0.4
0
20
40
60
80
100
120
140
DEPTH
(M)
NO DATA


100
75
50
25
0
PERCENT OF STOMACH CONTENTS (BY WEIGHT)
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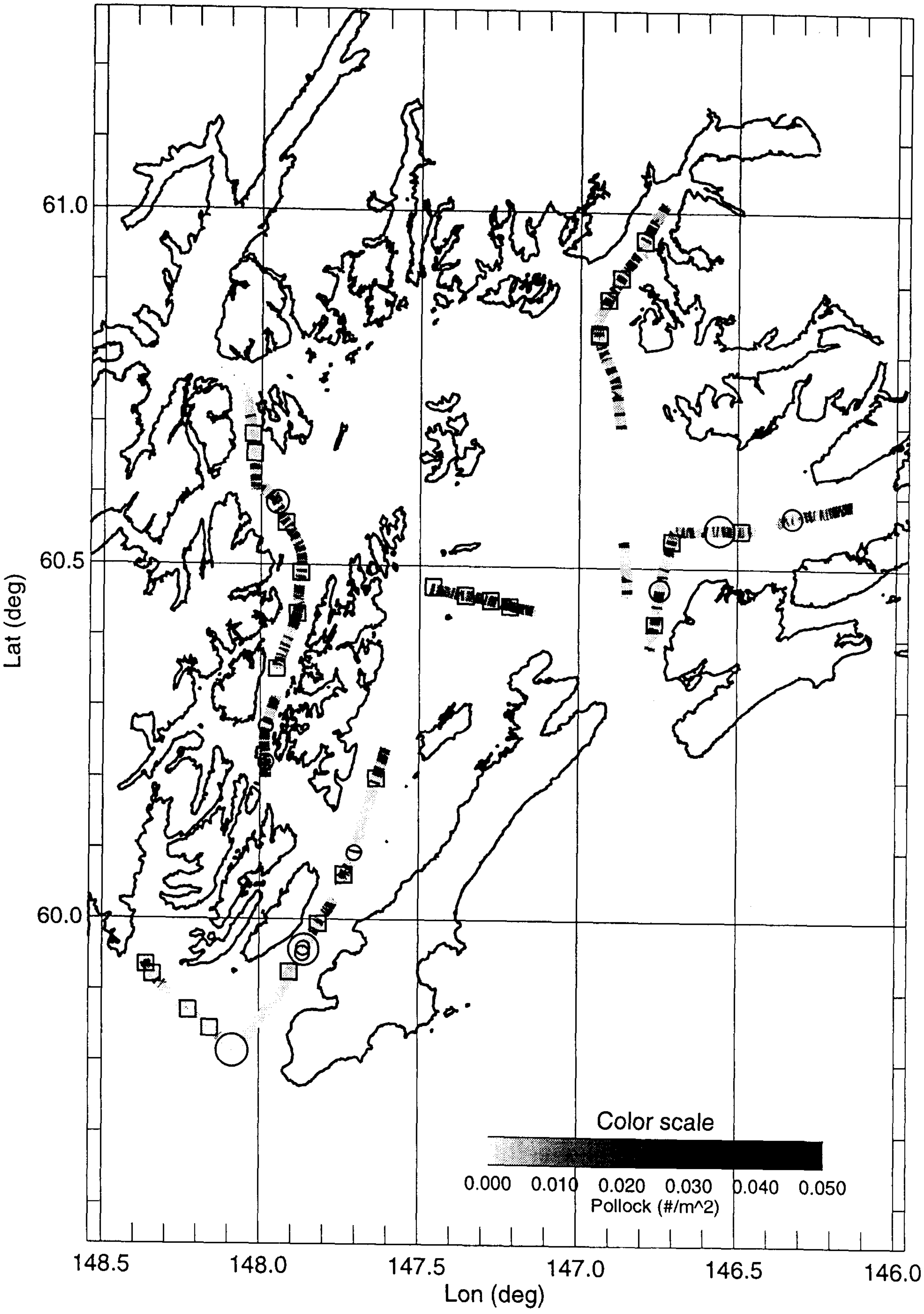
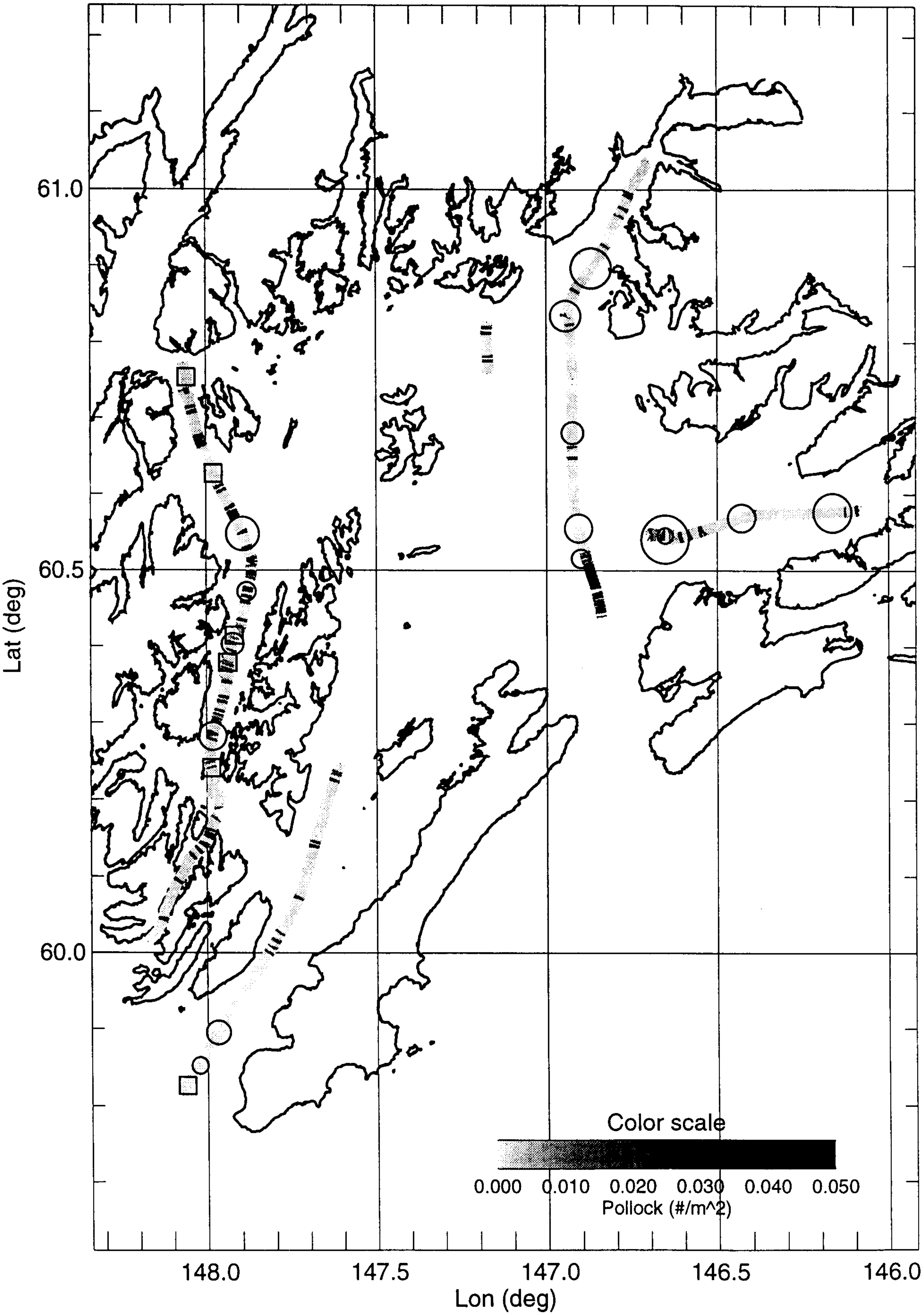
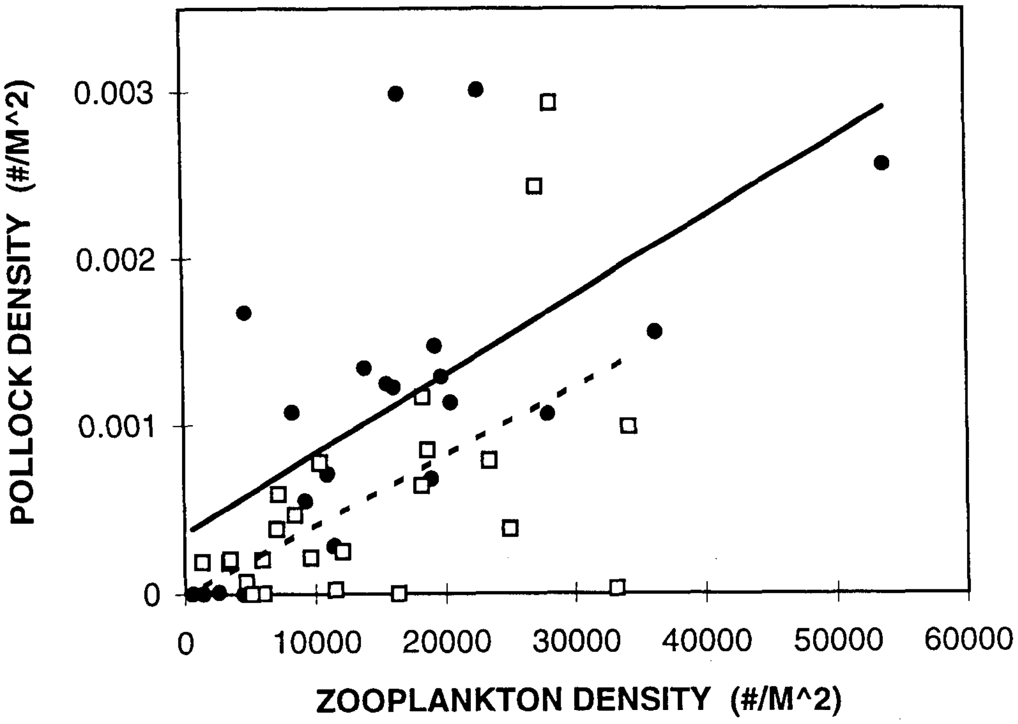
Copepod
N=196
Other
Larvacean
Pteropod
Copepod
N=34
APRIL
MAY
MONTH



61.0
60.5
60.0
Lat (deg)
148.5
148.0
147.5
147.0
146.5
146.0
Lon (deg)
Color scale
0.000
0.010
0.020
0.030
0.040
0.050
Pollock (#/m^2)


61.0
60.5
60.0
Lat (deg)
148.0
147.5
147.0
146.5
146.0
Lon (deg)
Color scale
0.000
0.010
0.020
0.030
0.040
0.050
Pollock (#/m^2)



POLLOCK DENSITY (#/M^2)
0.003
0.002
0.001
0
0
10000
20000
30000
40000
50000
60000
ZOOPLANKTON DENSITY (#/M^2)

Mortality estimates of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska.

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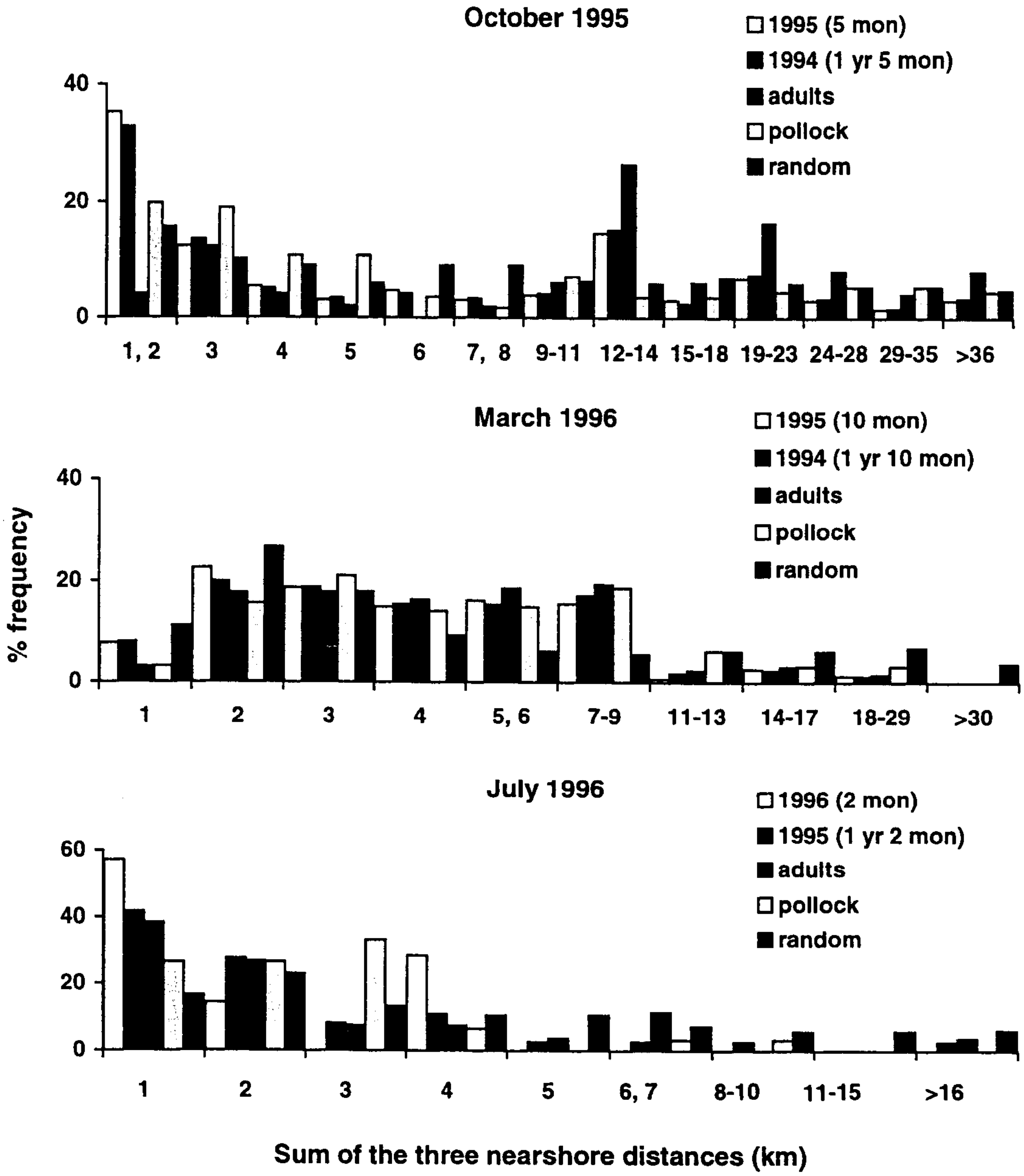

Fig. 6 Stokesbury et al.

Abstract

Pacific herring, *Clupea pallasi*, aggregations isolated within four bays in Prince William Sound, Alaska, were acoustically surveyed from June 1996 to March 1998. Life tables, estimating the amount of natural mortality occurring from metamorphosis until recruitment into the adult fishery, were compiled for the 1995, 1996 and 1997 Pacific herring cohorts within each bay. Severe mortality occurred between August and October in all four bays for young-of-the-year and 1-2 year old Pacific herring. Young-of-the-year Pacific herring were exposed to a second period of high morality between October and March. Intracohort-density-dependent mortality explained 51% of the variability in natural mortality. Intracohort-density-dependent mortality may result from food limitation during the winter, but probably not between August and October as food is abundant. Rather, intracohort-density-dependent mortality may result from shifts in foraging behavior as the risk of predation greatly increases the time juvenile herring forage outside, or on the extremity, of their schools. The slope of the linear equation comparing killing power to Pacific herring cohort density was 0.49 suggesting that although there is a reduction in individual output it is not enough to compensate for the increasing density, therefore the herring population of Prince William Sound is increasing.

Introduction

Pacific herring (*Clupea pallasi* Valenciennes, 1847) dominate the near-shore ichthyofauna of Prince William Sound, Alaska, providing primary forage for pisciovorous fishes, birds and marine mammals and supporting commercial bait, sac-roe, and roe on kelp fisheries (Meyers et al. 1994, Paine et al. 1996). In 1993, four years after the *Exxon Valdez* spilled 36,000 metric tons of North Slope crude oil into Prince William Sound, the Pacific herring population crashed and the fisheries were closed (Paine et al. 1996, Spies et al. 1996). The lack of local life history information combined with the highly variable characteristics of clupeoid populations confounded attempts to determine sources of mortality and the population's recovery time (Meyers et al. 1994, Paine et al. 1996).

Little is know of juvenile herring mortality and spatial distribution (Blaxter & Hunter 1982, McGurk 1993, Tanasichuk 1997). Clupeiod larval mortality rates have been estimated from laboratory and plankton samples (Robinson 1988, Wespestad & Moksness 1990, McGurk 1993, McGurk et al. 1993, McGurk & Brown 1996). Adult natural and fishery mortality rates have been estimated using fishery data and age structure analysis (Beverton 1963, Parmanne 1988, Tanasichuk et al. 1993). Generally, herring from several populations are believed to mix in nursery areas and segregate to different locations prior to spawning (Iles 1971, Hourston 1982, Iles & Sinclair 1982, Sinclair et al. 1985). However, in Prince William Sound each bay appears to be a unique nursery area where juvenile herring are isolated from other groups until their second summer of life (Stokesbury et al. 1999a, Stokesbury et al. 1999b).

We examined the changes in relative density and estimated natural mortality of Pacific herring within four bays in Prince William Sound, Alaska, from May 1996 to March 1998. We hypothesized that the densities and mortality rates of Pacific herring within each bay were unique. Further, we examined the effects of intraspecific density and temporal variability on instantaneous mortality rates to determine if density-dependent mortality occurs within these bays.

Methods

Prince William Sound, Alaska, contains a large body of water separated from the Gulf of Alaska by a series of mountainous islands (Fig. 1). The rocky coastline is irregular with numerous islands, passages, bays, and deep fjords. The Sound has a semi-diurnal tide with a maximum range of 4.4 m during this study.

Four bays, Simpson, Zaikof, Whale, and Eaglek were selected as study sites because they are spatially segregated and appeared to contain isolated aggregations of juvenile Pacific herring (Stokesbury et al. 1999a). These four bays were acoustically surveyed nine times between June 1996 and March 1998 (Fig. 1). During each seven-day cruise, each bay was surveyed three times over 24 hours beginning at 0000 h, 0800 h, and 1600 h.

The acoustic survey vessel (commercial fishing seiner, ≈17 m) followed a continuous parallel transect pattern; transect distances were Simpson Bay = 31200 m, Zaikof Bay = 35024 m, Whale Bay = 31164 m, and Eaglek Bay = 43750 m (Fig. 1). Care was taken to ensure that the same transect was sampled for each diel period during every survey. The acoustic vessel surveyed at 9 to 11 km h^{-1} with a 120 kHz BioSonics 101 echosounder using a preamplified dual-beam transducer towed ≈1 m below the water surface. The acoustic system was calibrated both with a hydrophone and a standard target. The acoustic signals were processed in real-time using the BioSonics ESP 221 echo square integration software and ESP 281 Dual beam software, and the raw signal was stored on digital audio tape (MacLennan & Simmonds 1992, Stokesbury et al. 1999b). Latitude and longitude were recorded simultaneously for each data cell from the GPS navigational system. Echo integration measurements were converted into data cells with 20 m lengths (16 pings per cell, 2 ping s^{-1}) and 1 m width and depth.

Once the acoustic vessel measured a fish school it was sampled to determine species composition and size structure. Fish were captured using a modified bottom trawl in deep water (1.52 x 2.13 m Nor'Eastern Astoria V trawl doors, head rope 21.3 m, foot rope 29.0 m, estimated 3 x 20.0 m mouth, 10.2 cm mesh wings, 8.9 cm middle and a 32.0 mm cod end liner deployed by the Alaska Department of Fish and Game R/V *Pandalus*, ≈20 m), one of two anchovy seines (250.0 x 34.0 m or 20.0 m, 25.0 mm stretch mesh deployed by a commercial fishing seiner, ≈17 m), or a small salmon fry seine in shallow water (50.0 x 8.0 m, 3.0 mm stretch mesh deployed from a 6 m skiff equipped with a 70 horsepower engine). The samples from each collection were speciated and 1000 herring, or the other dominant fish species, were randomly subsampled. Fork length (mm) was measured for all samples and wet weight (g) was recorded from 450 Pacific herring. Size modes of herring, representing young-of-the-year, 1 to 2 year old, or adult fish, were identified (Stokesbury et al. 1999a). Echo integration densities (kg m^{-3}) were converted into number of Pacific herring per size mode (fish m^{-3}). Based on frequency distributions, cells containing the equivalent of <0.5 fish m^{-3} were probably zooplankton and were removed from the data set (MacLennan & Simmonds 1992, Gunderson 1993). Piscivorous fish were dissected and their stomach contents were classified as herring, invertebrates and other fish, or empty.

A length dependent scaling constant was used to convert the reflected acoustic energy into a biomass estimate:

$$\text{TS re:w (dB re:kg)} = -6.0 \log x - 24.2 \text{ dB}$$

where x is the mean fork length (cm) of the fish collected in the area (Thorne 1977a, Thorne 1977b, Thorne 1983a, Thorne et al. 1983, Thorne & Thomas 1990). This equation differs from the more standard regression equation calculated by (Foote 1987) as it derives the target strength as a proportion of weight. Thorne's equation was developed for echo integration primarily using Pacific herring surveys from Alaska and Puget Sound (Thorne 1977b, Thorne et al. 1983). The inclusion of weight adjusts for the wide seasonal and spatial variation in weight-to-length relationship of Pacific herring observed in Prince William Sound (Stokesbury et al. 1999a). Acoustic estimates of Pacific herring densities depend upon the applied target strength equations. This is a limitation of acoustical data as many physical and biological variables affect target strength including depth, temperature, fish orientation, morphology of the fish, fat content, gonad development, and inter and intraschool behavior (Thorne 1983b, Foote 1987, Thorne & Thomas 1990, Misund 1993, Misund & Floen 1993, Misund et al. 1995, Huse & Ona 1996, McClatchie et al. 1996). Our estimates of density are relative and we assume their fluctuations reflect those of the absolute densities of Pacific herring within each bay.

Acoustic transect replicates were completed in two bays. Density estimates from these replicate tranects were compared using a chi-squared test at the 5% level of significance (Sokal & Rohlf 1981). Vertical positions of Pacific herring schools within each bay were examined by comparing their mean depth on a diel scale. When variances were heterogeneous data were transformed using log (x +1) before applying statistical tests. One-way ANOVA's were used to compare differences in means and correlations (Sokal & Rohlf 1981, Winer et al. 1991).

Life tables are a reliable method of determining age-specific mortality and are frequently used when it is possible to follow a group of individuals through time (Begon & Mortimer 1982, Krebs 1989). Prince William Sound Pacific herring spawn in early April. Juvenile age cohorts are easily identified by length frequencies as herring complete about 75% of their somatic growth before first maturity (Cushing 1967, Iles 1971, Winters & Wheeler 1994). Further, Pacific herring appear to remain isolated in bays during their juvenile phase (Stokesbury et al. 1999a, Stokesbury et al. 1999b). These characteristics allowed us to compile life tables.

Life tables estimating the amount of natural mortality occurring between metamorphosis and recruitment into the adult fishery were compiled for the 1995, 1996 and 1997 Pacific herring cohorts within the four bays from June 1996 to March 1998. The number of fish observed (a_x) during one transect survey were compared to the subsequent observation (a_{x+1}) along the same transect during the same diel time period from the next cruise, weeks to months later. If the number of fish within an age cohort observed along a transect was <30 the observation was deleted (Krebs 1989). The "killing -power" ($\log_{10}a_x - \log_{10}a_{x+1}$) ranges from 0 to 3 (0 = no mortality, 3 = high mortality) and reflects the rate of mortality between observations (Begon & Mortimer 1982).

Results

Pacific herring migrated to the surface during darkness (Table 1). The range of mean depths varied seasonally but the majority of herring were distributed in the top 20 m during the 0000 h transect for all surveys (Table 1). The 0000 h transects provided the clearest measures of Pacific herring density along all transects. The precision of our acoustical density estimates was moderate. Comparisons of observed herring densities along transects repeated one to four days apart, within the same survey, provided similar fish counts of the dominant age cohorts (Table 2).

Twenty-nine species of fish were collected in association with Pacific herring schools. Sixteen species were piscivorous and 11 preyed on Pacific herring. Walleye pollock (*Theragra chalcogramma*) was the primary predator and 94 of the 294 feeding pollock were preying upon Pacific herring. Thirty-one of the 38 and six of the 23, feeding Pacific cod (*Gadus macrocephalus*) and salmon, respectively, were preying on Pacific herring.

Juvenile Pacific herring endured two periods of high natural mortality. Severe mortality occurred between August and October in all four bays for young-of-the-year and 1-2 year old herring (Fig. 2). During this period densities were often reduced by several orders of magnitude. Juvenile Pacific herring were exposed to a second period of high mortality between October and March (Fig. 2).

Intracohort-density-dependent mortality explained 51% of the variability in natural mortality as the killing power of each Pacific herring size cohort was significantly correlated with the preceding density of that cohort (ANOVA, df = 18, F = 17.39, $r^2 = 0.51$, $p<0.001$; Fig. 3). The slope of the linear equation comparing killing power to Pacific herring cohort density was 0.49 indicating that natural mortality was less than recruitment and therefore density was increasing (Fig. 3). The killing power of each Pacific herring size cohort was not significantly correlated to the total density of herring within each bay (ANOVA, df = 18, F = 3.54, $r^2 = 0.17$ $p = 0.08$; Fig. 3).

Within bays a significant correlation between killing power and cohort density was only found for Simpson Bay (ANOVA, df = 7, F = 9.65, $r^2 = 0.62$, $p = 0.021$). The coefficient of determination (r^2) was high in Whale Bay but the correlation was not significant, possibly due to the low degrees of freedom (ANOVA, df = 4, F = 5.06, $r^2 = 0.63$, p=0.11). Eaglek and Zaikof Bays had no relationship between killing power and density although the degrees of freedom were also low.

The young-of-the-year cohort dominated Pacific herring assemblages within each bay. The killing power values of young-of-the-year herring were significantly correlated to the preceding young-of-the-year density measure (ANOVA, df = 13, F = 8.24, $r^2 = 0.41$, p=0.014; Fig. 4).

Discussion

High natural mortality occurred directly after the young-of-the-year metamorphosed from larvae in late July until the beginning of oceanic winter in late October. This is a period of high somatic growth and food limitation seems unlikely (Stokesbury et al. 1999a). Predation is probably the primary source of natural mortality. Both marine mammals and birds are actively feeding their young as well as increasing their own energy supplies in preparation for migrations (Livingston 1993). In early August the largest influx of predators is the returning wild and hatchery salmon numbering 8,374,327 wild, 20,410,280 hatchery and 4,596,623 wild, 23,702,628 hatchery for 1996 and 1997, respectively (Morstad et al. 1997). Although Pacific herring composed only a small proportion of the salmon stomach contents in May and June they may be more frequently preyed upon from August to October (M. Willette, pers. comm. ADF&G, Cordova, AK). For example, Pacific herring represented ≈26% of feeding salmon and gadids collected with herring schools. Newly recruited young-of-the-year Pacific herring are small, abundant, and aggregated in bays (Stokesbury et al. 1999b). The salmon spawning streams are also located primarily in bays. These Pacific herring would be the last prey the salmon encounter before entering the spawning streams. Interestingly at this time of year the primary tackle used by sport fishers to catch salmon is a silver spoon, which mimics young herring (W. Barber per. comm. University of Alaska – Fairbanks). Simpson and Whale have large wild salmon runs while Eaglek has both a strong wild salmon and hatchery salmon run (M. Willette, pers. Comm. ADF&G Cordova AK).

Pacific herring natural mortality was also high during their first winter from October to March. This natural mortality appeared to result from starvation and predation. Young-of-the-year Pacific herring must store a critical amount of energy during the summer or they will starve during the winter (Paul & Paul 1998, Paul et al. 1998, Foy & Paul in press). The smaller fish within the cohort have the least amount of surplus energy and their survival rate is probably low (Paul & Paul 1998, Paul et al. 1998). Growth data collected from each of these bays supported Paul's conclusions but mortality of larger Pacific herring resulting in negative incremental growth, also occurred (Stokesbury et al. 1999a). Pacific herring may be highly vulnerable to predators during the winter. Hunger suppresses the herring's antipredator behavior resulting in loosely packed schools of mixed size classes (Robinson & Pitcher 1989a, Robinson & Pitcher 1989b, Pitcher & Parrish 1993, Robinson 1995, Stokesbury et al. 1999b). Residential and returning migrational predators increase feeding at the end of oceanographic winter and may select the largest young-of-the-year Pacific herring as they have the highest energy content (Paul & Paul 1998, Paul et al. 1998). Predation varies weight-at-age in other herring stocks by as much as 20% (Sparholt & Jensen 1992).

Separating the Pacific herring population into its trimodal size distribution and examining each mode independently identified intracohort-density-dependent mortality. Shifts in relative

Pacific herring densities along transects could result from immigration and emigration or variations in spatial distribution with each bay. However, dominant size class densities were consistently measured over repeated transects and changes over time on an order of magnitude were readily identified.

Density dependent food limitation may affect growth in herring populations (Iles 1968, Iles 1971, Winters & Wheeler 1994, Tanasichuk 1997). However, studies demonstrating density dependent natural mortality are rare and researchers have concluded that clupeiod stocks tend not to have strong density dependent regulatory mechanisms (Cushing 1967, Blaxter & Hunter 1982).

Intracohort-density-dependent mortality may result from food limitation particularly during the winter, but probably not between August and October when food is abundant (Foy & Norcross in press). Rather, intracohort-density-dependent mortality may result from shifts in foraging time (Walters & Juanes 1993). Herring schools have a strong local effect on their environment as they occupy a small portion of the habitat intensely (Blaxter & Hunter 1982). The risk of predation greatly increases with the amount of time juvenile herring are required to forage outside or on the extremity of the schools, their spatial-behavioral refuge from predators. Therefore, mortality can be density dependent without exhibiting signs of competition such as changes in growth rate due to food limitation (Walters & Juanes 1993). This would explain the intra-cohort-specific natural mortality we observed between August and October as Pacific herring formed dense schools of a single cohort while growth rates appeared to be high in all bays.

The natural mortality sustained by juvenile herring in Prince William Sound was intracohort-density-dependent. The slope of the linear equation comparing killing power to Pacific herring cohort density was 0.49 suggesting that although there is a reduction in individual output it is not enough to compensate for the increasing density (Begon & Mortimer 1982), therefore the Pacific herring population of Prince William Sound is increasing.

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Table 1. *Clupea pallasi*. Mean depths and standard deviations (SD) and ANOVA comparisons of Pacific herring cohorts observed in the four bays acoustically surveyed in Prince William Sound Alaska.

Depth (m)	0000 h		0800 h		1600 h				
Simpson Bay	mean	SD	mean	SD	mean	SD	df=	F =	p=
YOY	13.2	2.01	22.7	2.0	21.4	1.93	2	10.40	<0.001
1-2 year old	14.5	2.04	23.7	2.0	21.6	2.17	2	7.28	<0.001
Adults	17.3	4.36	22.7	3.1	22.7	3.47	2	0.08	0.920
Zaikof Bay									
YOY	18.7	1.92	26.8	2.6	28.8	2.11	2	9.91	<0.001
1-2 year old	14.8	1.39	24.0	1.9	26.1	1.89	2	0.09	0.910
Adults	13.4	1.63	28.8	2.2	29.9	2.26	2	32.7	<0.001
Whale Bay									
YOY	24.4	2.34	24.1	3.1	27.6	2.85	2	0.32	0.730
1-2 year old	20.7	3.04	34.0	3.9	33.3	3.41	2	4.11	0.019
Adults	13.9	8.04	41.7	10.0	44.7	8.65	2	3.9	0.033
Eaglek Bay									
YOY	17.7	3.61	41.0	4.8	32.4	5.88	2	6.18	0.003
1-2 year old	30.2	3.59	48.8	4.3	43.1	5.19	2	6.29	0.002
Adults	30.0	4.45	51.8	5.1	46.2	7.09	2	6.14	0.003

Table 2. *Clupea pallasi*. Repeated measures of the number of Pacific herring observed within each year cohort along a continuous acoustic survey within two bays in Prince William Sound, Alaska; * p <0.01. Comparisons are between each observation for each age cohort, Yate's correction was applied due to the low number of degrees of freedom.

Zaikof Bay; 0800 h	5 Oct. 96		9 Oct. 96		
cohort	observed	%	observed	%	χ^2
1994	21	20	15	79	34.85*
1995	55	94	3	6	78.01*
1996	48	46	56	54	0.51
Simpson Bay; 0000 h	13 Aug. 97		14 Aug. 97		
1995	96	49	98	51	0.00
1996	114	28	297	72	18.96*
1997	9253	53	8286	47	0.20

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Figure 1. Location of the acoustic transects used to survey of the four bays in Prince William Sound, Alaska.

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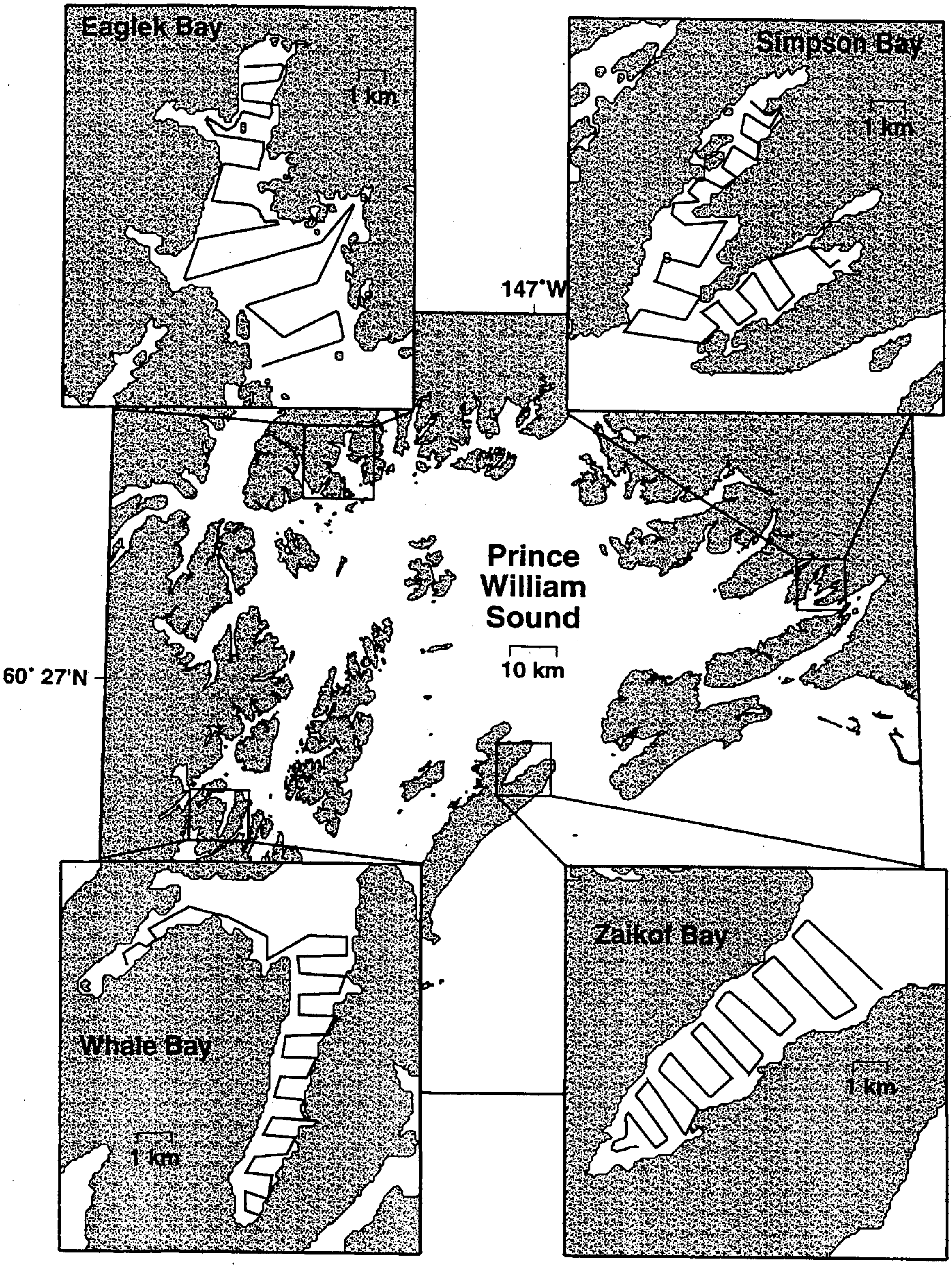

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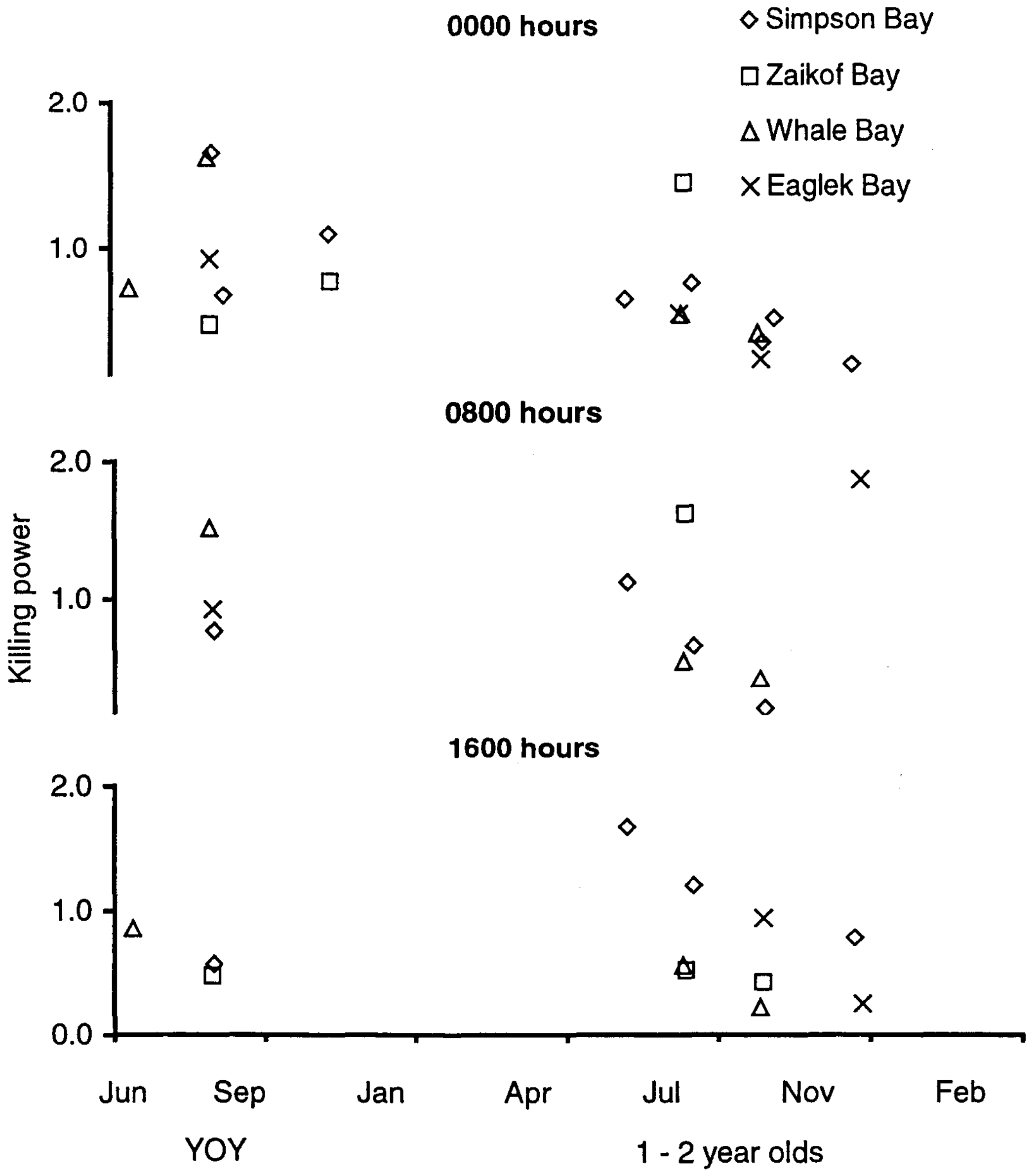
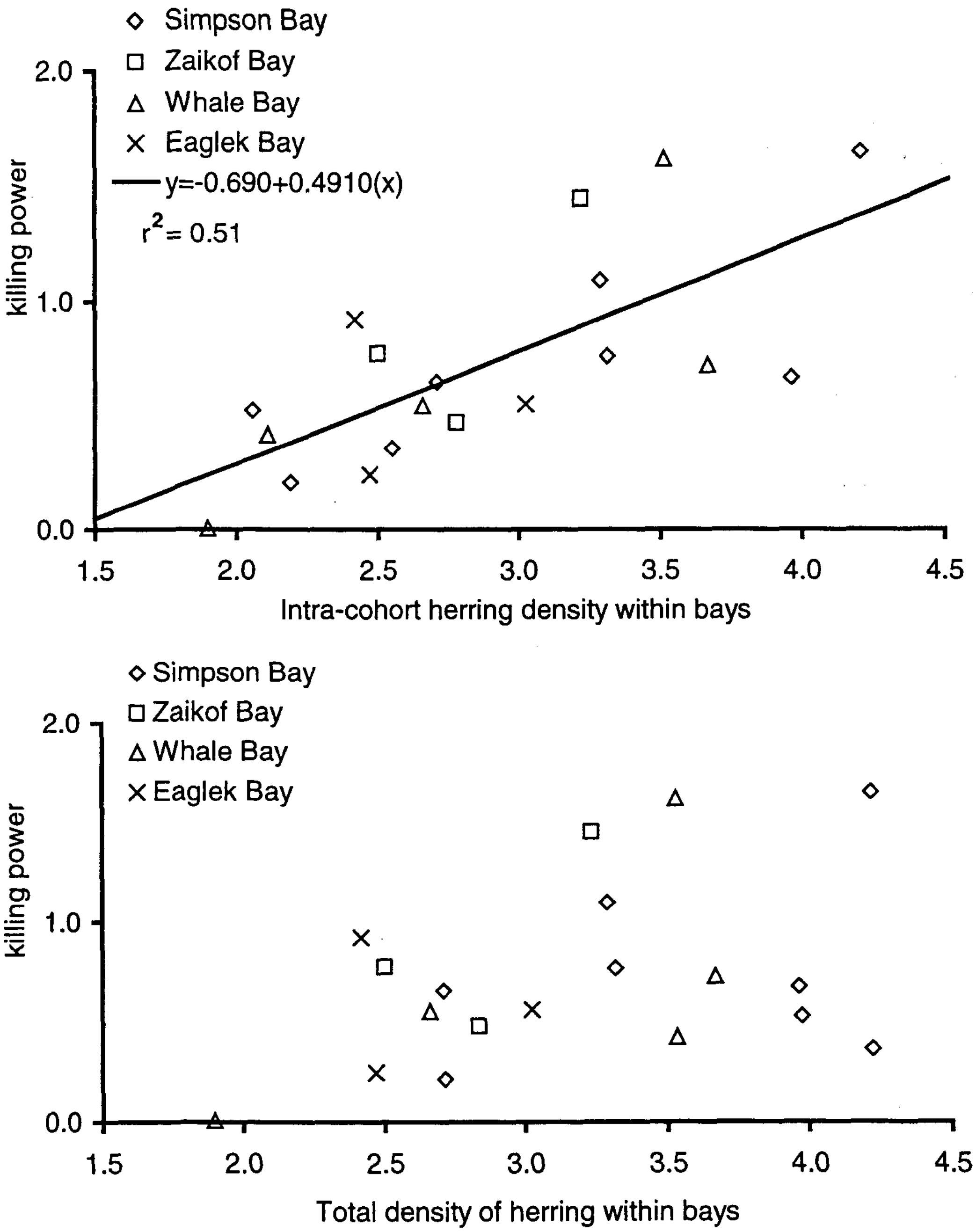


Figure 2. Stokesbury, et al



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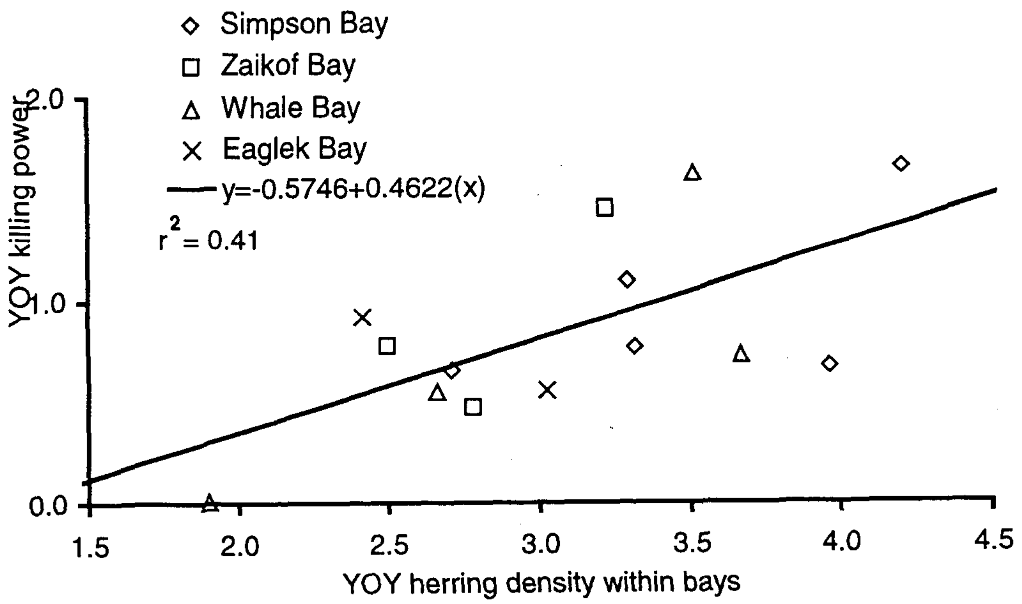

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The ecological role of walleye pollock *Theragra chalcogramma* in the trophic structure of Prince William Sound, 1993-1998.

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The ecological role of walleye pollock *Theragra chalcogramma* in the trophic structure of Prince William Sound, 1993-1998.

Abstract

A stock of walleye pollock *Theragra chalcogramma* has been observed to overwinter and feed in Prince William Sound. This stock was composed of three age-related length groups: large-mature fish, the adults (>400 mm, age 4+), small-immature fish, the juveniles (<120mm, age 0) and intermediate sized fish, subadults, (120-400 mm ages 1 to 3). In the winter, the adult walleye pollock were found in highly aggregated groups that were easily accessible to measurement. Echointegration-midwater trawl surveys estimated the abundance of adult walleye pollock to be about 37,000 mt in 1995, 38,000 mt in 1997 and 114,000 mt in 1998. The only other pelagic fish observed to overwinter in the Sound at a comparable abundance was the Pacific herring *Clupea harengus.* This finding indicates the marine food web of the Sound is similar to many other boreal and subboreal systems in that it has a "waist" and that the Sound's food web-waist is composed of two competing planktivores, walleye pollock and Pacific herring. In recent years, this food web-waist has been dominated by walleye pollock but our observations suggest that a few years of high herring recruitment could cause a shift the dominance of the food web-waist. Traditional knowledge and records suggest that herring have dominated the food web waist in the past.

We postulate a feeding mechanism to explain the shifting dominance of the food web-waist. Unlike the juvenile or subadults, after spawning the adult walleye pollock to move to the surface (0-50m) and into the Sound in spring to feed on macrozooplankton, primarily large calanoid copepods *(Neocalanus* spps). We hypothesize that the ability of the adult walleye pollock to feed on *Neocalanus* copepods depends upon high prey density in the form of patches or layers. When patches or layers of *Neocalanus* copepods are available in the spring, the walleye pollock can capture the bulk of the food or energy from lower trophic levels and dominate the food web-waist of the Sound. Furthermore, we suggest that in windy years when surface turbulence is high, the resulting decrease in prey patches reduce the walleye pollock's ability to feed successfully on *Neocalanus* copepods. Conversely, the herring's higher efficiency at raptorial feeding should favor it during windy climate regimes. Since walleye pollock and Pacific herring populations represent the food web-waist in the Sound, they store the bulk of the carbon or potential energy in the Sound's food web. Unless the dynamics of these two taxa are known and considered explicitly, models of the fate of lower level trophic production and the diversity and production of the piscivore assemblage will not represent dominant ecosystem processes.

Introduction

Walleye pollock *Theragra chalcogramma* is well known as a valuable commercial fish, an important forage fish and a dominant marine predator (Dwyer et al. 1987; Livingston 1993; Lloyd and Davis 1988; Springer 1992). The importance of the commercial fishery for walleye pollock is highlighted by the six million ton catch in 1985 worth over $1 billion in ex-vessel income, which made it the world's largest single-species fishery (Anonymous 1996). Surprisingly, this economic importance it is overshadowed by the pollock's ecological importance. Livingston et al. (1997) concluded the number of species in the Bering Sea offshore pelagic fish consumer guild was effectively one due to the super-dominance of walleye pollock.

Traditional understanding of marine food webs suggests they are complex and it is rare when one prey or predator dominates (Russel-Hunter 1970). This is clearly not the case in boreal seas where it is common for food webs to have "waists" where a single or a few taxon in a middle trophic position passes most of the food or energy from lower trophic levels to higher level predators (Rice 1992). Walleye pollock in the Bering Sea are a classic example of a single taxon dominating the food web-waist (Springer et al. 1984, 1987; Livingston 1997). Until recently, models of food webs have not considered cases where one or a few taxon capture the bulk of the lower trophic level production and dispense this energy to the levels above them (Rice 1995). Runge (1988) and Pimm (1991) have both shown that where this occurs that ecologists must first describe how the predators will respond in to changes in the species at the waist before investigating the peripheral structure. Inversely, one is also limited to describe how lower production affects changes in the species at the waist. The dynamics of food webs with waists are so dependent on the one or more species at the waist that the structure elsewhere will have little influence (Runge 1988; Pimm 1991; Rice 1995).

Eastern North Pacific Ocean

Walleye pollock populations throughout the Gulf of Alaska and Bering Sea have been studied since the 1950s (Traynor 1986; Dwyer et al. 1987; Bailey and Dunn 1979; Brodeur and Wilson 1996). Bottom trawl surveys that were initiated in the mid 1960s to assess red king crab *Paralithodes camschatica* were expanded in the 1970s to include demersal fish (Bakkala and Alton 1986). Since pollock was a major component of the trawl catch of demersal fish, these surveys became a major assessment tool. In 1979, the first acoustic-midwater trawl survey was conducted in conjunction with the bottom trawl assessment (Karp and Traynor 1988; Traynor et al. 1990). Subsequently, acoustic surveys were conducted in conjunction with the triennial bottom trawl assessments.

The majority of our knowledge about the walleye pollock's life history characteristics is pieced together from these stock assessment surveys, which were conducted in different areas and primarily in the summer months when surface conditions are most favorable (Karp and Traynor 1988; Radchenko and Sobolevskiy 1993). The pooling of this data has not been considered a major problem since few distinct stocks have been identified in Alaskan waters (Grant and Utter 1980). However in other areas such as British Columbia, many distinct stocks have been identified (Saunders et al. 1988), so there is a need for more information in Alaskan waters to reduce potential confounding due to the pooling of mixed stocks.

Prince William Sound

The 1991 triennial trawl survey assessed the pollock biomass in Prince William Sound at 9,000 mt (Anonymous 1997). This number was used with data from the Gulf to set a harvest quota of 1.5 mt in 1995 (Megrey 1988). However, studies initiated in Prince William Sound after the 1989 Exxon Valdez oil spill (EVOS) revealed a large pelagic population of walleye pollock (Thomas et al. 1997). These findings prompted further studies of walleye pollock with the objective of estimating their distribution and abundance and assess their role as dominant predators that could be influencing the recovery of pink salmon, Pacific herring and other injured species from oil spill damage (Wolfe et al. 1993).

This paper reviews observations of walleye pollock distribution and abundance made by acoustic-midwater trawl surveys conducted from 1994 to 1998 with respect to role walleye pollock play in the trophic structure of Prince William Sound.

Methods

Prince William Sound is a large fjord/estuary that covers an area of approximately 8800-km^2 and has about 3200 km of shoreline along the northern edge of the Gulf of Alaska (Grant and Higgins 1910). Coastal rainforests, high mountains and glaciers border the shoreline of PWS (Thomas et al. 1991). The Sound is exposed to seasonally intense storms moving in from the Gulf of Alaska, resulting in 5-7 m of annual rainfall.

Between 1993 and 1999, we conducted a series of acoustic-midwater trawl-purse seine surveys to determine the distribution and abundance of nekton predators and their influence on the survival of pink salmon fry. These surveys consisted of three spring-summer series (1994-1996) along the outmigration route of pink salmon fry and a series of fall-spring surveys to determine the overwinter abundance and distribution of prespawning walleye pollock (1995, 1997 and 1998) and Pacific herring (1993-1999).

Acoustic sampling

Acoustic data were collected using BioSonics 38 and 120 kHz echosounders with dual-beam transducers. The transducers were mounted on a towfins and towed alongside the boat at a depth of 2 m and at an approximate speed of 3 m/s. The acoustic systems were calibrated before each cruise using a tungsten-carbide ball of known target strength, suspended within the beam of the transducer (Foote and MacLennan 1982; 38 kHz: sl=215.76, pw=0.001, b^2=0.00219, rgn20=-156.474; 120 kHz: sl=225.075, pw=0.001, b^2=0.00107175, rgn20=-159.282). The data was processed in real-time on a laptop computer. Date were geo-referenced and time-coded with a GPS receiver. Echointegration, dual-beam target strength (TS) and GPS data were stored on the computer hard disk and backed up on a tape drive. Raw acoustic signals were stored on digital audiotape and printed on paper echograms.

Post-cruise processing consisted of transferring all PC data to UNIX workstations for data processing and analysis. Software written in IDL was used to apply acoustic calibrations and correct for absorption, remove untracked bottom, identify targets of interest, remove false targets, calculate biomass estimates and produce 2d images of fish distributions. AVS software was used to create 3d visualizations of fish distribution. Echointegration was used on all surveys due to the schooling behavior of the pollock. The target strength of walleye pollock was calculated as -20 Log L-66 (Traynor and Ehrenberg 1979) and then applied to the echointegration arrays to determine density.

Echo counting of pollock-sized targets was used to process spring surveys because the fish were found as single targets in the top 50 meters of the water column. We used a threshold to separate the walleye pollock targets from dense layers of plankton that were present near the surface. The echo-counting technique involved defining the range of possible target strengths that corresponded to an adult pollock. Targets between

–39 dB and –28 dB were counted as pollock using echo-counting software, which were then divided by the sample volume of the acoustic beam and averaged to yield densities in fish/cubic meter.

Multiple targets in the acoustic beam can affect the reliability of any echo-counting technique (Foote 1996). Multiple targets may either overlap just enough to cause the target discriminator to fail to recognize any of the multiple targets or they may sum their individual returns to yield artificially high single target strength. A comparison between the target discrimator and manual counts of pollock sized targets showed that auto counting underestimated the number of targets by 13-28%. We conducted a similar comparison between echo counting and echo-integration showed that echo counting resulted in an underestimate of pollock density by 18-33%. Given the near-surface distribution of the pollock, we also believe that boat avoidance added to underestimation of the absolute densities during the spring surveys. Thus, we consider the echo counts of walleye pollock at the surface in the spring as relative density and conduct only appropriate analyses with these data.

Net sampling

Mid-water trawls and purse seine sets were made during the hydroacoustic surveys to provide target verification and biological information. The trawl measured 40 m x 28 m and was equipped with a net sounder. The cod end of the trawl was lined with a 1.5 cm stretch mesh to retain small specimens. The depth and location of the trawling was directed to the depth of fish targets to verify acoustic targets. The length of trawl hauls was approximately 30 min at depth. Fish from the catch were identified, weighed, measured and had their stomachs removed and preserved in a 10% buffered formaldehyde solution for later diet analysis (Willette et al. 1999). A modified commercial anchovy purse seine was used to sample fish targets in the nearshore areas.

Vertical zooplankton tows were collected using a 0.5-m ring net with 333 um mesh. The net was towed vertically through the top 50 m at several locations on each survey (Cooney et al. 1999). The samples were preserved in a formalin solution. In the lab, the zooplankton were enumerated, measured and identified to species. The mean length of each species was used to calculate the mean weight and then multiplied by the number of individuals in the sample to yield biomass estimates.

Results and Discussion

In the winter of 1995, 1997 and 1998, echo integration-trawl surveys were conducted in PWS to determine the distribution and abundance of adult pollock after commercial fishery operations so there was prior knowledge of the areas where the adult pollock were concentrated. In the fall of 1995 to spring of 1996, reconnaissance surveys of PWS verified that there were no additional concentrations of pollock residing in the Sound and that the only other species of comparable biomass was the adult Pacific herring (Figure 1). The depth distribution of the prespawning pollock in PWS areas has ranged from 150-200 m over the study period (Figure 2). The length of the adult pollock caught on these surveys ranged from 23-69 cm (Figure 3 a,b,c). We estimated the biomass to be approximately 38,000 mt in 1995, 37,000 mt in 1997 and 114,000 mt in 1998.

In contrast to the adult pollock biomass, the adult herring biomass was low. The Pacific herring stock collapsed in 1993 after an outbreak of viral hemoragic septicemia (Kocan et al.1999; Marty and Meyers 1999). We estimated the biomass at 20,000 mt in the fall of 1993 and 13,000 mt in the fall of 1994. In 1995 and 1996, we observed recruitment and a resulting increase in the biomass of herring from 23,000 mt to 38,000 mt. After commercial fisheries in 1997 and 1998, the stock biomass was observed to decline to 17,000 and 18,000 mt, respectively. In the three years with comparable estimates the ratio of adult pollock to adult herring ranged from 1:1 to 6.33:1 (37/23 in 1995, 38/38 in 1997 and 114/18 in 1998). Between 1993-1999, walleye pollock and herring were the only two species that were observed to form overwintering schools of with biomass greater than 1000 mt.

These results show that the pelagic food web in Prince William Sound has a "waist" (Rice 1995) and that two species, walleye pollock and Pacific herring share the food web-waist. In contrast, the food web-waist of the Bering Sea is occupied by solely walleye pollock (Springer et al. 1984, 1987; Livingston 1997). However, it is important to note that if the summertime, offshore sampling design used in the Bering Sea (Traynor et al. 1990) were applied to Prince William Sound, like the Bering Sea, the walleye pollock would be the sole taxon in the food web-waist. In the 1950-1970s, there were major commercial and reduction fisheries (for food, oil and fishmeal) for Pacific herring in from Prince William Sound to the Bering Sea (ADF&G). This suggests that the Pacific herring and other fat-rich forage fishes (capelin and sandlance) may have been the dominant taxon of the food web-waist prior to the 1970s. Presumably after a climate shift, a groundfish-dominant trophic structure developed that persists to this day, which caused a massive reorganization of the higher predators (Anderson et al. 1999).

The recruitment of Pacific herring between 1994 and 1996, the recent (1980-1993) records of herring in Prince William Sound (Anonymous 1999) and the historical records (1900-1999) of the herring fisheries in the Eastern North Pacific suggest that the Pacific herring may compete with walleye pollock for the dominant taxon position of the food web-waist. If so, the mechanism for this competition and how climate forcing might influence it is of critical importance to explain shifts in trophic efficiency and higher trophic level predator production.

Postspawning, spring feeding migrations

In April after spawning, the distribution of adult walleye pollock in the Sound is highly dynamic (Figures 4 a,b,c,d). During this period the adult pollock were found at the surface as single fish and often mixed in with the zooplankton layer (Figures 5,6,7,8). Net sampling showed that the zooplankton layer was dominated by *Neocalanus* copepods in the early spring (Figure 9, 10), which was the primary prey of the adult walleye pollock (Figure 11). This feeding behavior was observed in the Bering Sea where the timing is lagged by about a month (Yoshida 1994). In the Sound, the vertical distribution of the walleye pollock changes rapidly in the spring suggesting the adult pollock track *Neocalanus* copepods through their spring ontogenetic migration (Figure 12).

In the spring, the adult pollock switched to pteropods and other macrozooplankton when the *Neocalanus* began leaving the surface on the reverse of their annual ontogenetic migration to the surface (Cooney 1987). Willette et al. (this issue) shows that when these macrozooplankton prey become less unavailable that the pollock switch juvenile fish. Walleye pollock are well known for cannibalism (Brodeur and Wilson 1996) and it is likely that the bulk of the juvenile fish consumed by the adult pollock are their young.

Paul et al. (1993) showed that over 30% of the total energy consumed in the year by yellowfin sole were derived from the spring zooplankton feeding. Given that a benthic predator, such as yellowfin sole, can derive such a large portion of its annual caloric intake from a near-surface pelagic prey resource indicates the relative ecological importance of spring feeding on macrozooplankton. The pelagic planktivores, such as walleye pollock and Pacific herring, may receive even more of their annual caloric intake from *Neocalanus* copepods in the spring. In the early spring, the adult pollock are emaciated after spawning so initial feeding success is important to growth and survival. The spring zooplankton bloom is probably the first large food supply available for this purpose. Corroborating the importance of this behavior is that the highest growth rate of the season is observed during the period when adult pollock are feeding on *Neocalanus* copepods (Figure 13). Since food web-waist taxon are classified by their ability to capture the bulk of the lower trophic level production (Rice 1995), and *Neocalanus* copepods represent a major pathway for capturing lower-trophic level production, we consider this spring feeding behavior the adult walleye pollock as a mechanism to explain competition between pollock and herring to dominate the food-web-waist.

Climate affects on filter feeding by adult pollock

Willette et al. (this issue) found the number of copepods in the adult walleye pollock stomachs range up to 1200. This number of prey of such small size suggests the pollock are filter feeding. Anatomical studies have shown that adult walleye pollock have a fine gillrakers that would be efficient for filter feeding (Matsubara 1943; Okada 1955; Wilimovsky et al. 1967). Wright et al. (1982) suggests the importance of fine gill rakers that allow a fish to filter feed increases a fish's competitive advantage and ultimately its fitness. Despite that direct observations of walleye pollock filter feeding have not been made, given the size of *Neocalanus*, the numbers consumed and the gill raker structure, filter feeding is a plausible feeding mechanism.

Whether filter feeding or not, there is a positive correlation between *Neocalanus* dominated patches of macrozooplankton and the density of adult walleye pollock (Figures 14, 15 and 16). The vertical distribution of the walleye pollock in the spring suggests that they track their primary prey, *Neocalanus* copepods (Figure 12). Due to the disparity in size between the adult pollock and their *Neocalanus* prey, we hypothesize that the formation of high density patches or layers of copepods is important to the adult walleye pollock's ability to exploit the spring zooplankton bloom. Leong (1970) demonstrated that a prey density threshold existed where northern anchovy *Engraulis mordax* switched from raptorial to filter feeding.

Davis et al. (1997) simulated the effects of physical turbulence on zooplankton patches showing patch dissipation and reduced growth in planktivores. Knowing the importance of *Neocalanus* feeding to pollock growth and the pollock must be sensitive to prey density for feeding success, we hypothesize that physical turbulence could be a major mechanism causing interannual and decadal variability in the feeding success of walleye pollock. With zooplankton patches dependent on low turbulence conditions and the adult walleye pollock dependent on the patches to successfully feed on zooplankton, we refer to this mechanism as the patch-dependence and response hypothesis.

Many investigators have referred to climate regime shifts based upon water temperature changes (Royer et al 1993; Muter et al.1995; Bailey et al. 1995). Thomas and Mathisen (1993) and Hollowed et al. (1998) and many others have shown positive correlations between temperature and fish production without proposing a direct mechanism. Bailey et al. 1995 concluded that warming conditions result in lower survival and production of Pacific herring and higher survival and production of walleye pollock. Bulatov (1988) shows that strong year classes of eastern Bering Sea pollock appear in warm, calm years. However, this only reflects the production of one year class of the pollock population and such trends are not supported in the western Bering Sea or Gulf of Alaska (Muter et al. 1995). The walleye pollock population is a complex assemblage of several age classes that are cannibalistic on each other at specific life history stages so inconsistency in the results from single cohort analysis is not surprising.

In contrast to temperature as the key physical condition driving this change in species, the patch-dependence and response hypothesis depends upon a turbulence-based mechanism. Turbulence is driven by the same Aleutian low, cyclonic storms that lower and raise the water temperatures in the Eastern North Pacific. Thus, we hypothesize that windy years create the turbulence that breaks up zooplankton prey patches, which results in failures of the adult pollock foraging. Likewise, relatively calm conditions allow walleye pollock to potentially double their annual intake of energy from the food web. If this patch-dependence and response hypothesis is supportable, it provides us with a plausible mechanism that links climate forcing with the walleye pollock dominance of the food-web-waist. Alternately, it also provides explanation for herring and possibly other fat-rich fishes, which are smaller and more efficient raptorial feeders (Stephens and Krebs 1986; Crowder 1985) to dominate the food web-waist.

In the Southern California blight, a dominance cycle exists between the two primary pelagic species, northern anchovy and sardine (Baumgartner et al. 1992). The northern anchovy is filter feeder as an adult, which is similar to the role that we hypothesize for the adult pollock. The California sardine has a similar feeding behavior to the Pacific herring being more of raptorial feeder than a filter feeder. Thus, in both regions we have competition between two dominant pelagic fishes where one is primarily a raptorial feeder and one that is specialized to filter feed. Unfortunately, without the deep anoxic basin in the North Pacific, that provided Baumgartner et al. (1992) the historical record of the Southern California sardine-anchovy cycle, we cannot test for a long-term dominance cycle between Pacific herring and walleye pollock.

Implications to the food web

Pinniped and seabird populations in the north Pacific are in decline (National Research Council 1996; Livingston et al. 1999). Species in decline are piscivorus (e.g. Steller sea lions, fur and harbor seals, murres and kittiwakes). Declines were first detected in western Alaska during the 1970s and were later detected elsewhere (Alaska Sea Grant College Program 1993).

Correlations between many independent observations strongly suggest food limitation as the reason for these declines but to date the underlying mechanisms have not been verified. Competition with commercial fisheries has been suggested as a mechanism, in part because the declines coincide with major growth in the fishing industry in the region (National Research Council 1996). Confounding this hypothesis is growing support for a "regime shift" hypothesis, which explains major changes in marine animal production on the basis of climate change (Livingston et al. 1999). Other possible causes, such as direct mortality related to fisheries, increased predation, disease, human take, disturbance at rookeries, or mortality from pollution are not similarly implicated.

Restrictions to fisheries, especially in the vicinity of Steller sea lion rookeries, have been suggested and in some case imposed (National Marine Fisheries Service 1999) on the assumption that fisheries depletion of pollock and other forage fish stocks has contributed to the declines. We refer to this idea as the "pollock-limited" hypothesis because of the inference that access to more pollock would reduce nutritional stress (this idea is also referred to as the depletion hypothesis). A competing hypothesis argues that marine regime shifts, possibly fueled by climate change, have resulted in an increase in pollock stocks at the expense of fat-rich fish (herring, sand lance, capelin). We refer to this as the "herring-limited" hypothesis. This idea incorporates another that is known as the "junk-food hypothesis" because it holds that the available diet of pollock is insufficiently energy-rich to support population growth in these species (Alaska Sea Grant College Program 1993, Roby et al. 1999). We have just added differential handling costs of pollock versus herring to the energy content idea.

The mechanism of food limitation differs between the herring-limited and pollock-limited hypotheses. Pollock may have been depleted or their distribution so disrupted by commercial fisheries that marine birds and mammals are starving for the lack availability of this food (pollock-limited hypothesis). Alternatively, piscivores are feeding on an abundance of pollock in the absence of adequate herring, but pollock is much more costly to catch when compared to herring and is nutritionally inadequate during at least one life stage critical for population growth (herring-limited hypothesis).

When escaping predators, small groups of herring, sand lance *Ammodytes hexapterus* and capelin *Mallotus villosus* have been observed to break away from larger, schools deep in the water column, flee to the surface and form high density, near-surface schools, commonly referred to by fishermen as bait-balls (Thorne and Thomas 1988). It is our hypothesis that pollock do not behave in this manner, but instead may flee downward and disperse when attacked by predators. We suggest that foraging costs on pollock and herring differ due to these species-specific schooling and predator-avoidance behaviors, as well as to the different fat content of the fish. Under the pollock-limited hypothesis, the effects of reduction and dispersal of pollock schools by commercial fishing may be cumulative and reduce pollock availability as food. Under the herring-limited hypothesis, declines in herring may force sea lions to forage on pollock, a prey that is inadequate by virtue of both its low energy concentration and the high energy expenditure required to feed on deep and dispersed schools.

When herring (and other fat-rich fish) aggregate at the surface, they fall prey not only to deep diving predators but also to other predators that cannot dive deep. Thus, just due to the escape behavior these energy-rich prey are available to support the production of a much wider diversity of marine animals. This surface-aggregating escape behavior of herring (and sand lance) may reduce the cost of capture for predators and increase the difference in net energy intake between a diet of pollock and a diet of herring. The predation event that disturbs deep schools of herring and causes the formation of near-surface bait-balls is currently unknown but could include a wide range of individual or combinations of predators, or even specific physical conditions as the catalyst (Thorne and Thomas 1988). Possible catalysts may include or deep-foraging predators such as humpback whales, sharks, or diving birds (Chilton & Sealy 1987) that disturb deep schools and chase fish toward the surface and the occurrence of such events appears correlated with tidal current velocities at specific locations (Thorne and Thomas 1990). Such a catalyst has been suggested as a mechanism for increased foraging efficiency in mixed-species flocks of seabirds (Hoffman et al. 1981, Chilton & Sealy 1987). Predators that modify prey behavior in a manner that makes the prey more accessible to other predators are referred to as "facilitating predators" (Hoffman et al. 1981, Kotler et al. 1992). Thus the energy gains available to predators on herring schools may depend on the presence of one or more co-occurring facilitating predators and these events may be tightly linked to physical conditions such as tide and bathymetry.

We hypothesize that a herring-rich system supports higher diversity and biomass of birds and mammals than are possible in a pollock-rich system, due to both differences in energy content and escape behavior of the fish. By linking this herring-limited hypothesis with the findings of this research that explain why pollock and sometimes herring dominate the pelagic fish guild to become the "waist taxon" of the pelagic food web (Rice 1995; Livingston et al. 1997; Thomas et al. 1999), we hope to develop better understand how climate change affects the makeup affects the diversity and productivity of higher trophic level predators, the seabirds and mammals, in the North Pacific. Thomas et al. (1999) refers to this as the middle-out hypothesis, where a couple of super-dominant, multi-year class, planktivores (pollock and herring) capture the bulk of the one and two-year carbon (*Neocalanus* is a two-year animal) being produced in Prince William Sound, while the ratio of planktivore abundance determines the energy available to different suites of higher trophic level predators, the seabirds and mammals.

Finally, as Runge (1988), Pimm (1991) and Rice (1995) contend, these results imply that studies of higher trophic level predators such as Steller sea lions, harbor seals, common murres and other declining, damaged or endangered species in Prince William Sound, the Gulf of Alaska and probably the eastern North Pacific Ocean must be based upon knowledge of the dynamics of walleye pollock and Pacific herring stock dynamics to determine changes due to climate and anthropogenic impacts such as commercial harvesting, oil spills, hatchery practices, etc.

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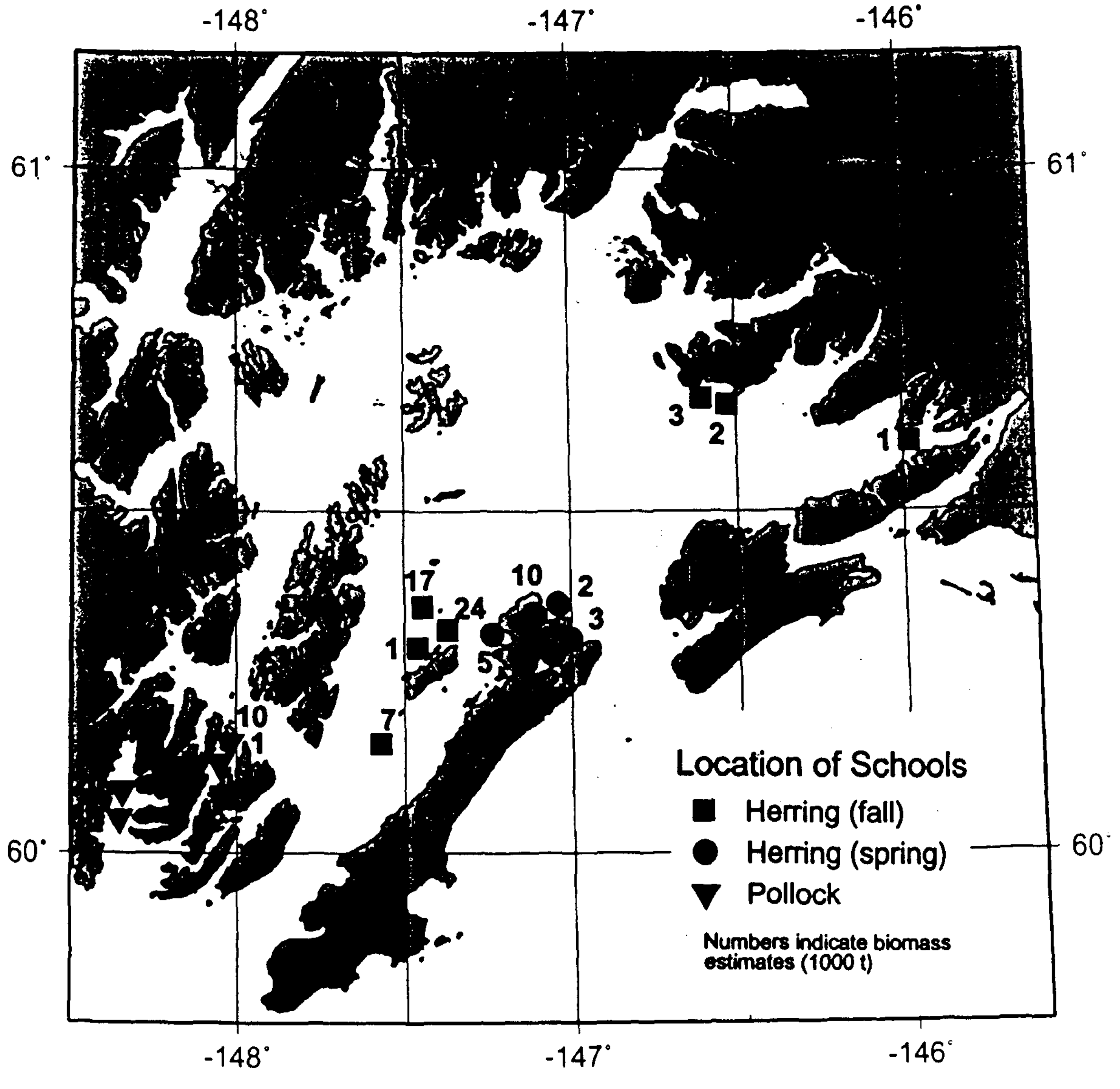
Prince William Sound, Alaska



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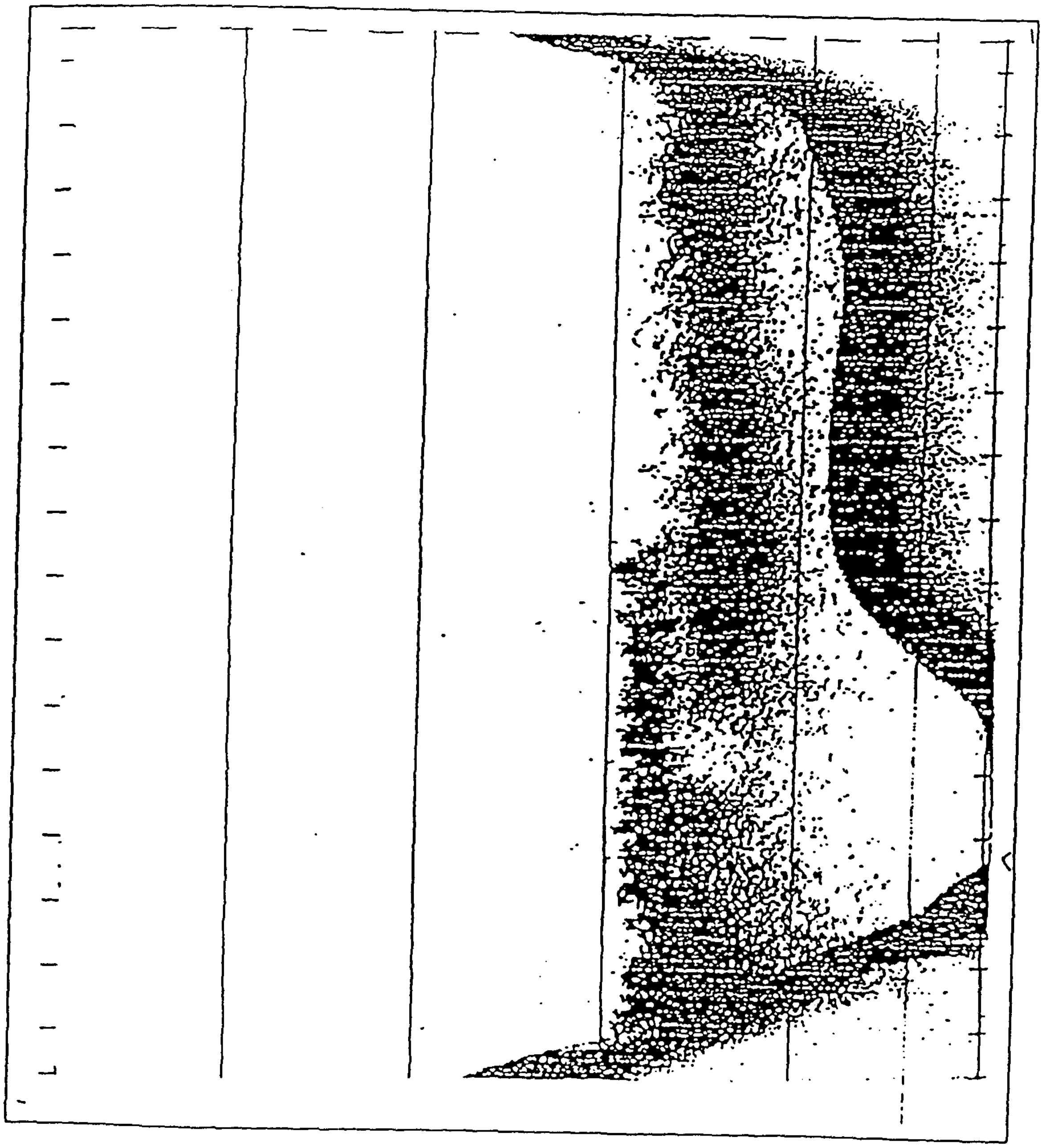

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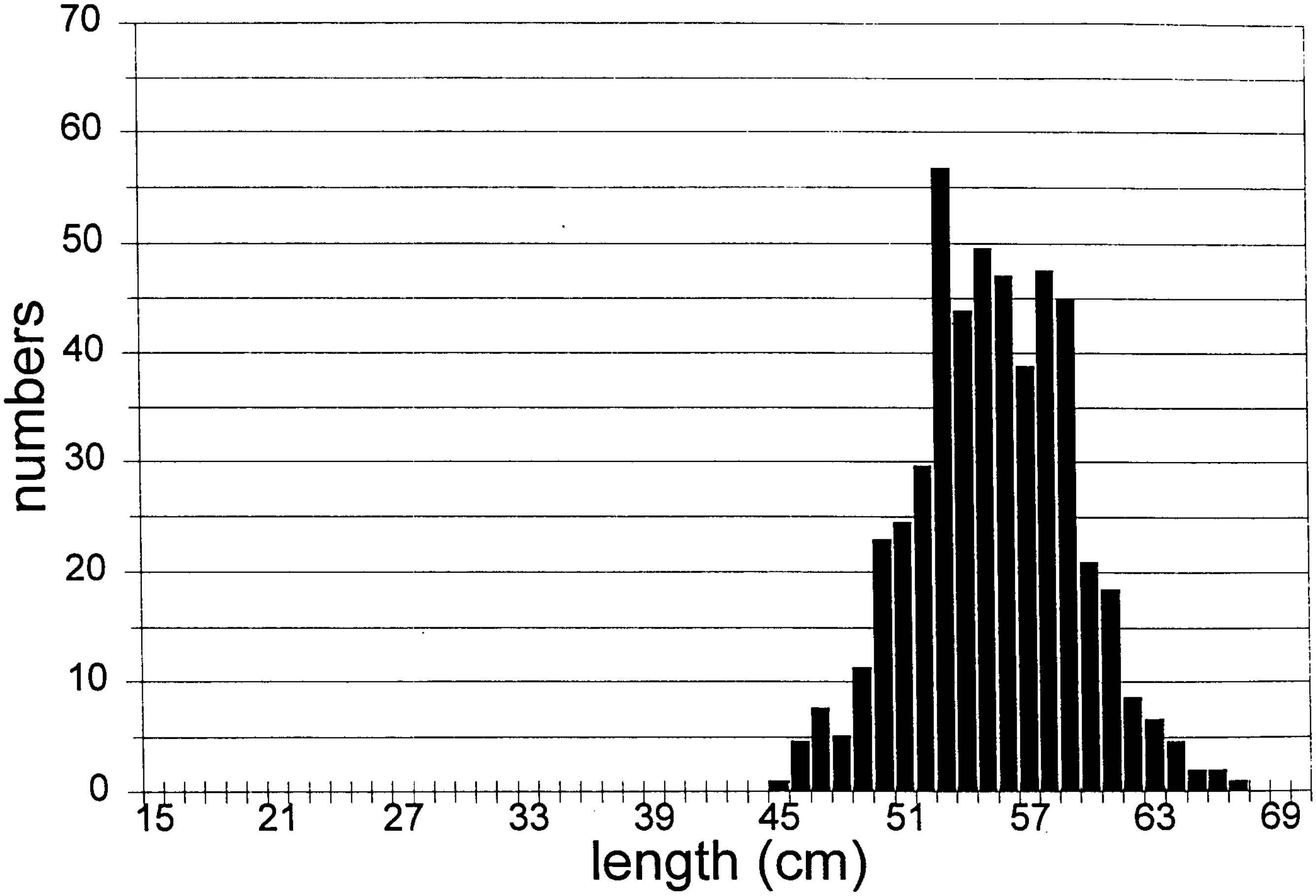
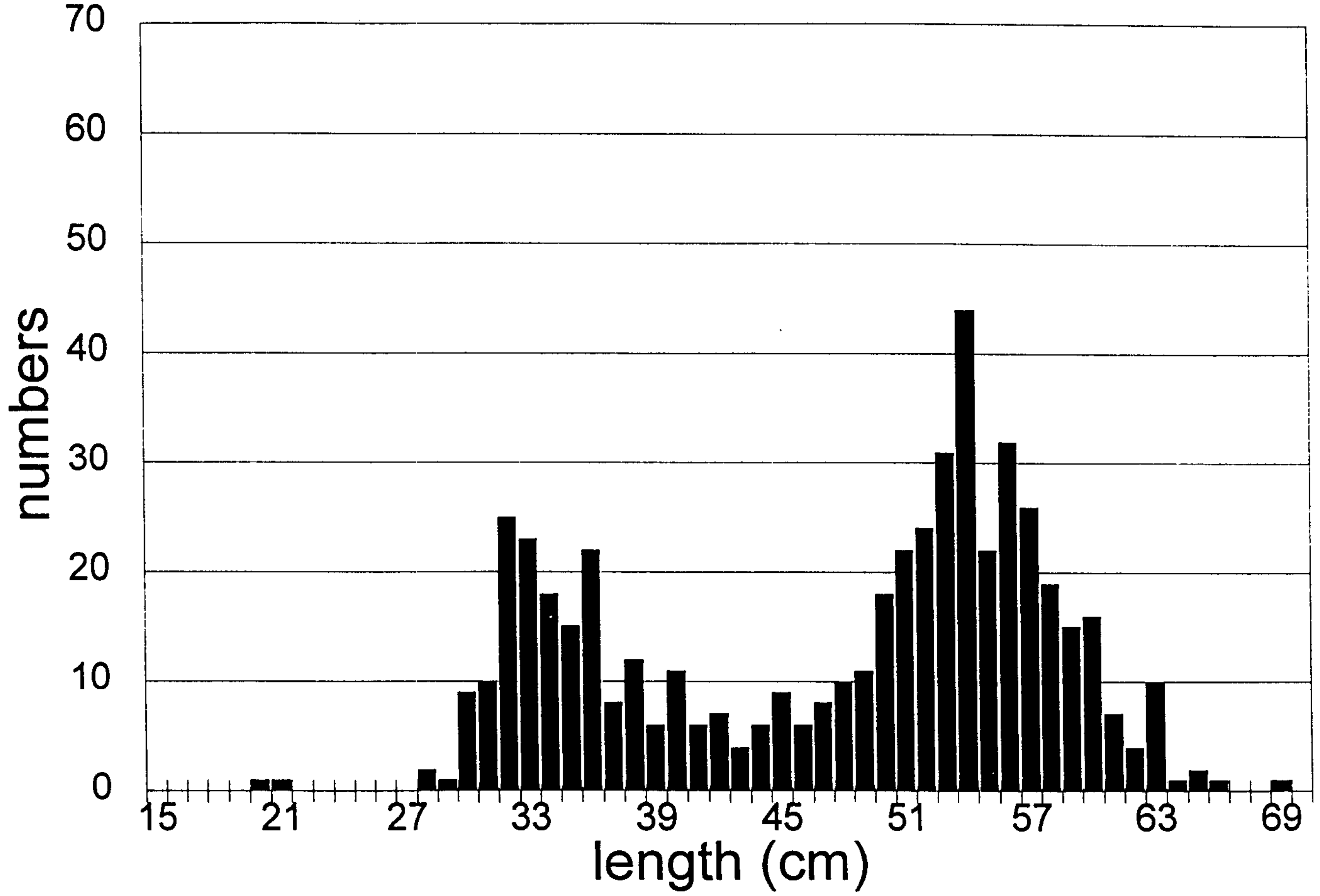


70
60
50
40
30
20
10
0
numbers
15
21
27
33
39
45
51
57
63
69
length (cm)

F 3A.



numbers
70
60
50
40
30
20
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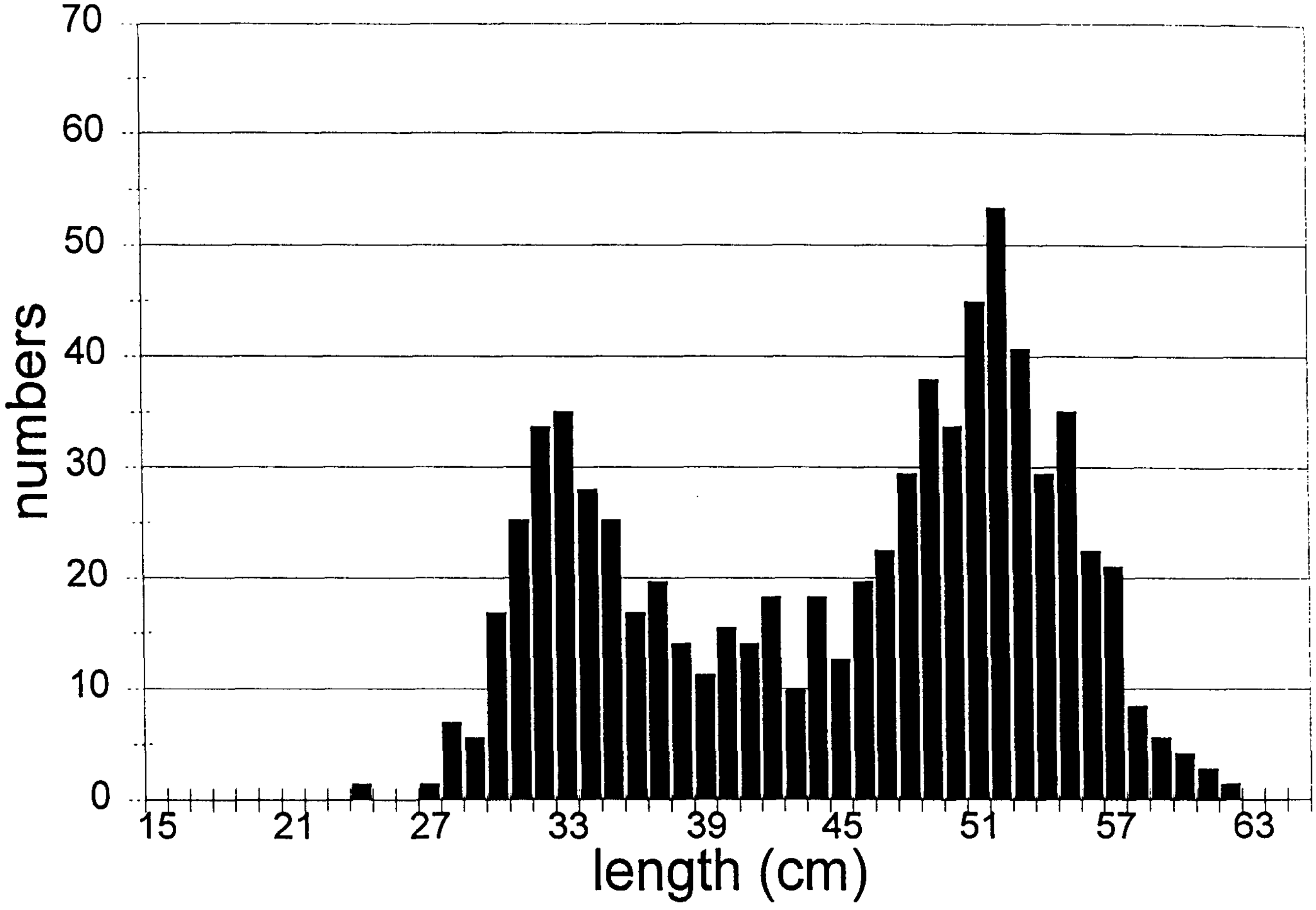
0
15
21
27
33
39
45
51
57
63
69
length (cm)

F3B



F3c

Pollock Distribution and Density : May - July, 1994

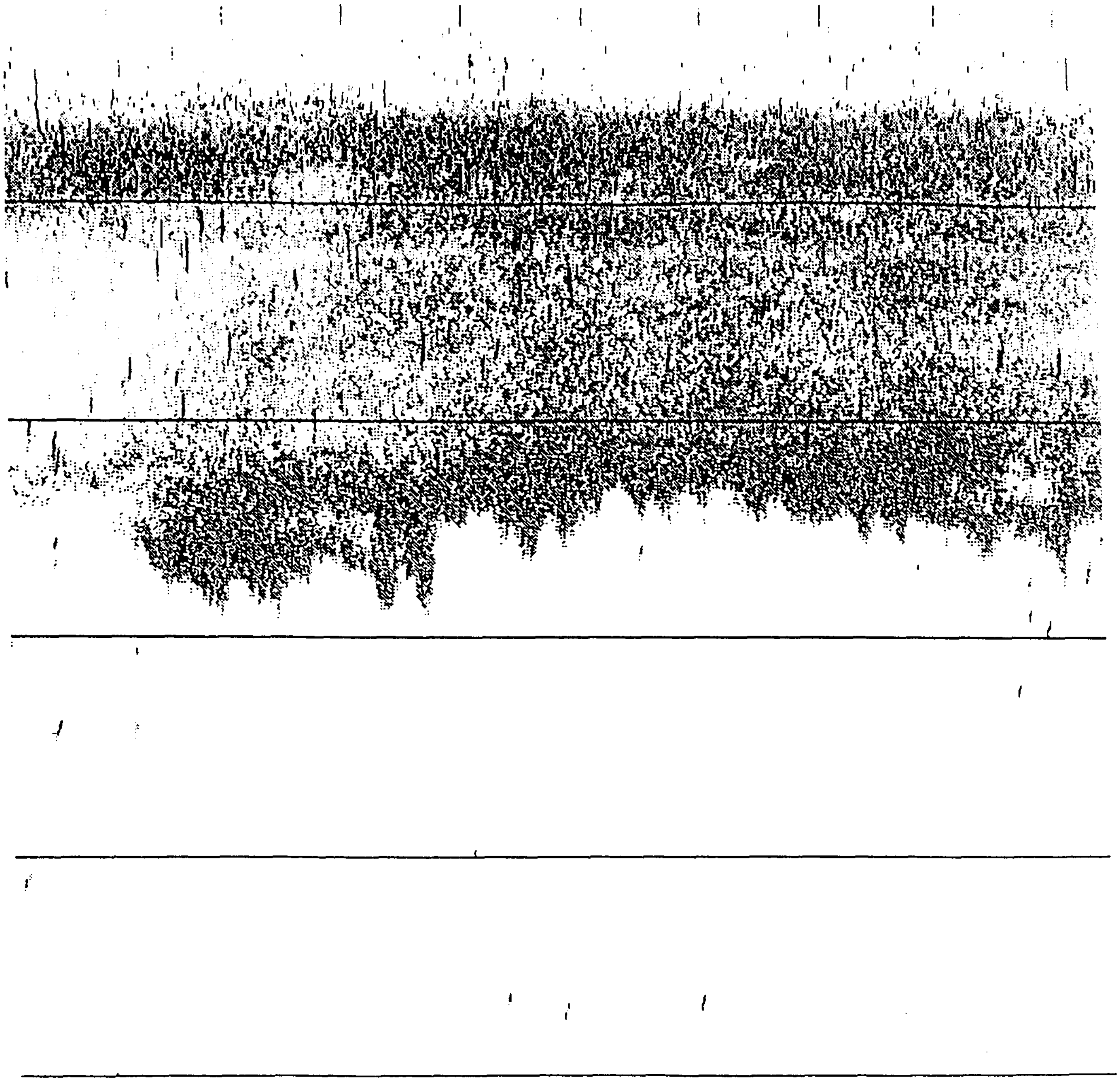
Pollock - Early May

Pollock - Late May

Pollock - Early June

Pollock - Mid July

F4 A, B, C, D



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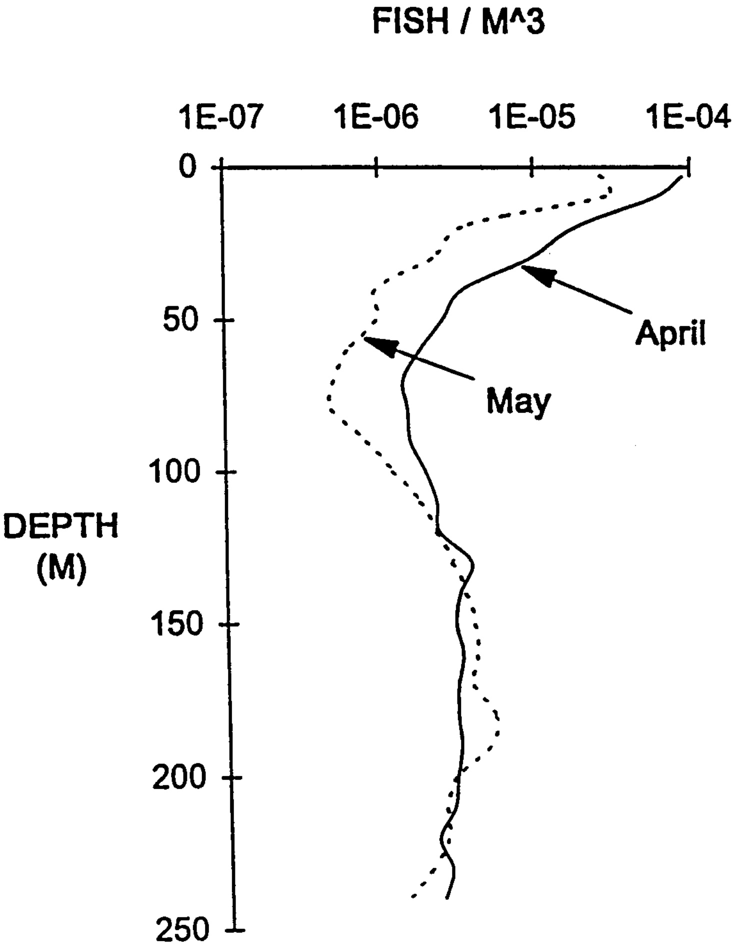
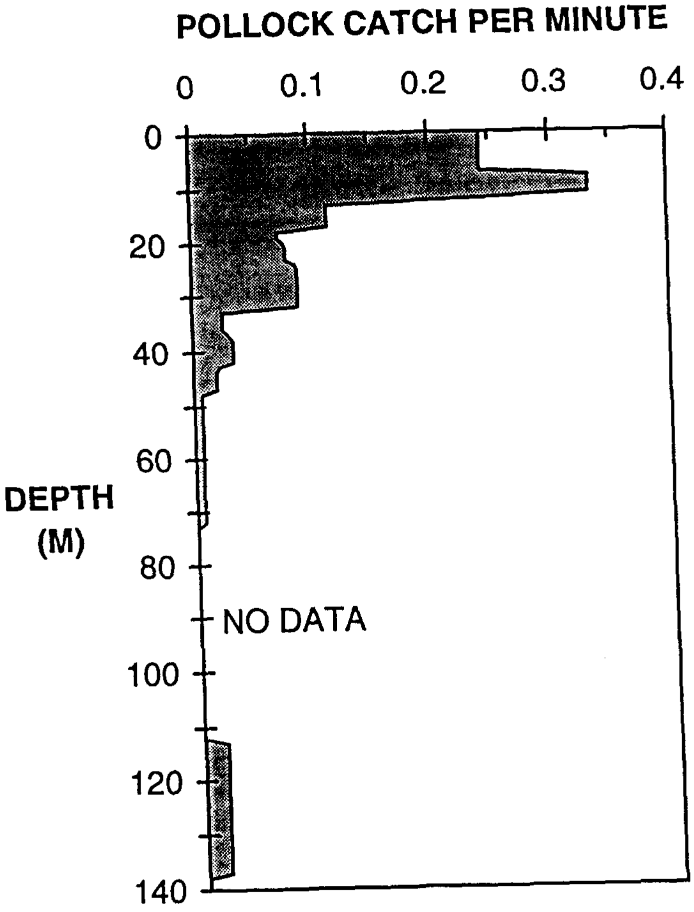
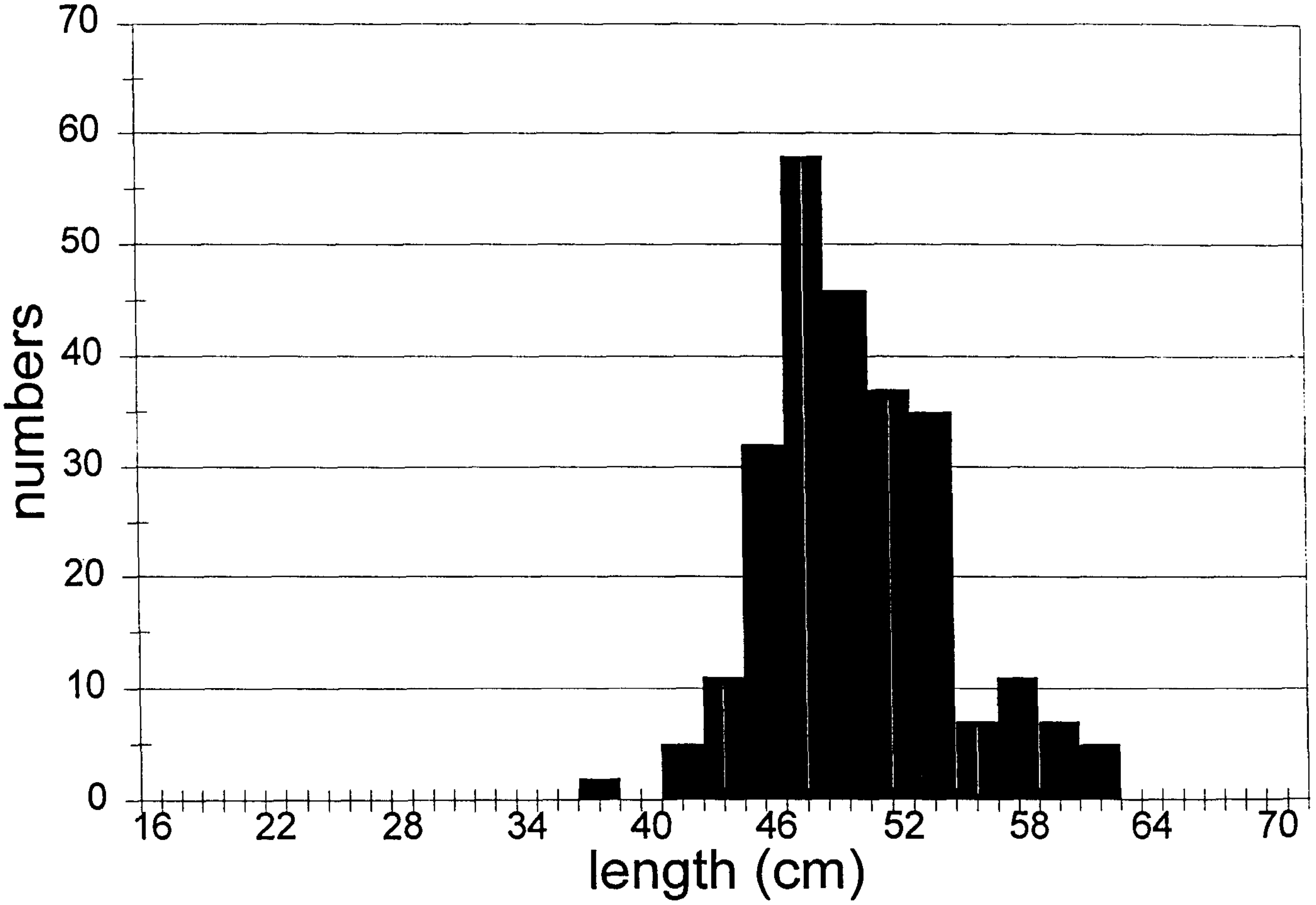

FISH / M^3
1E-07
1E-06
1E-05
1E-04
0
50
100
150
200
250
DEPTH
(M)
April
May

F 6

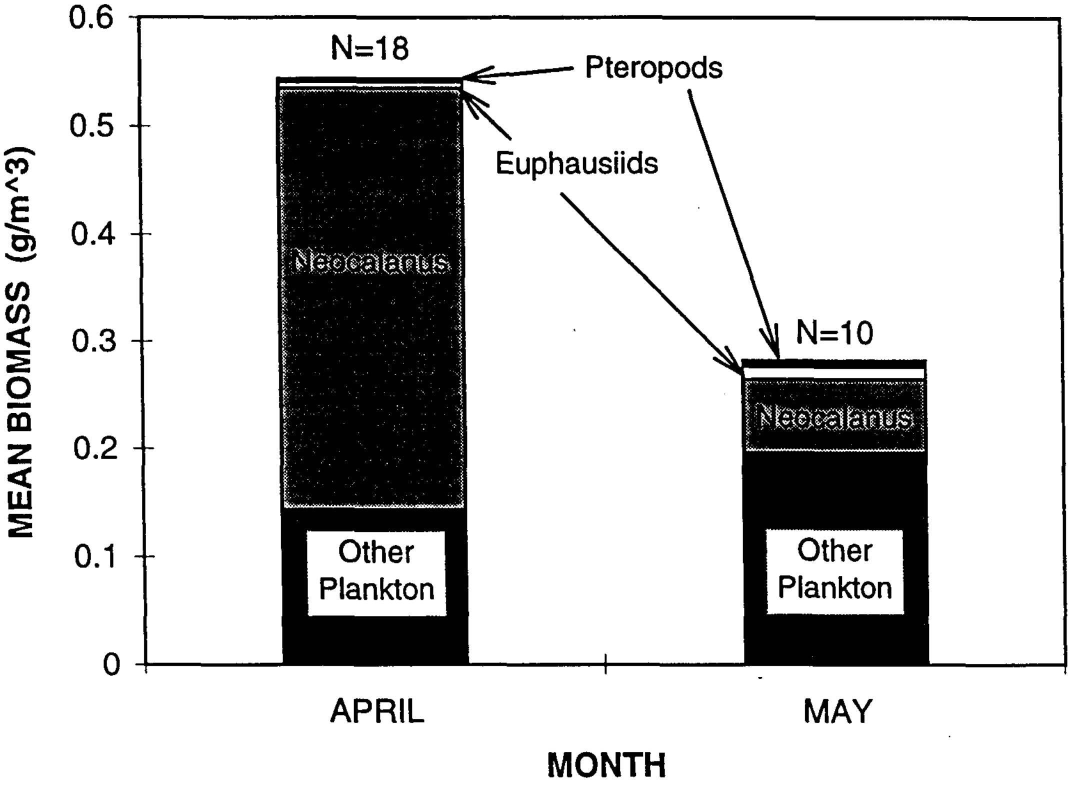

POLLOCK CATCH PER MINUTE
0
0.1
0.2
0.3
0.4
0
20
40
60
80
100
120
140
DEPTH
(M)
NO DATA

F7

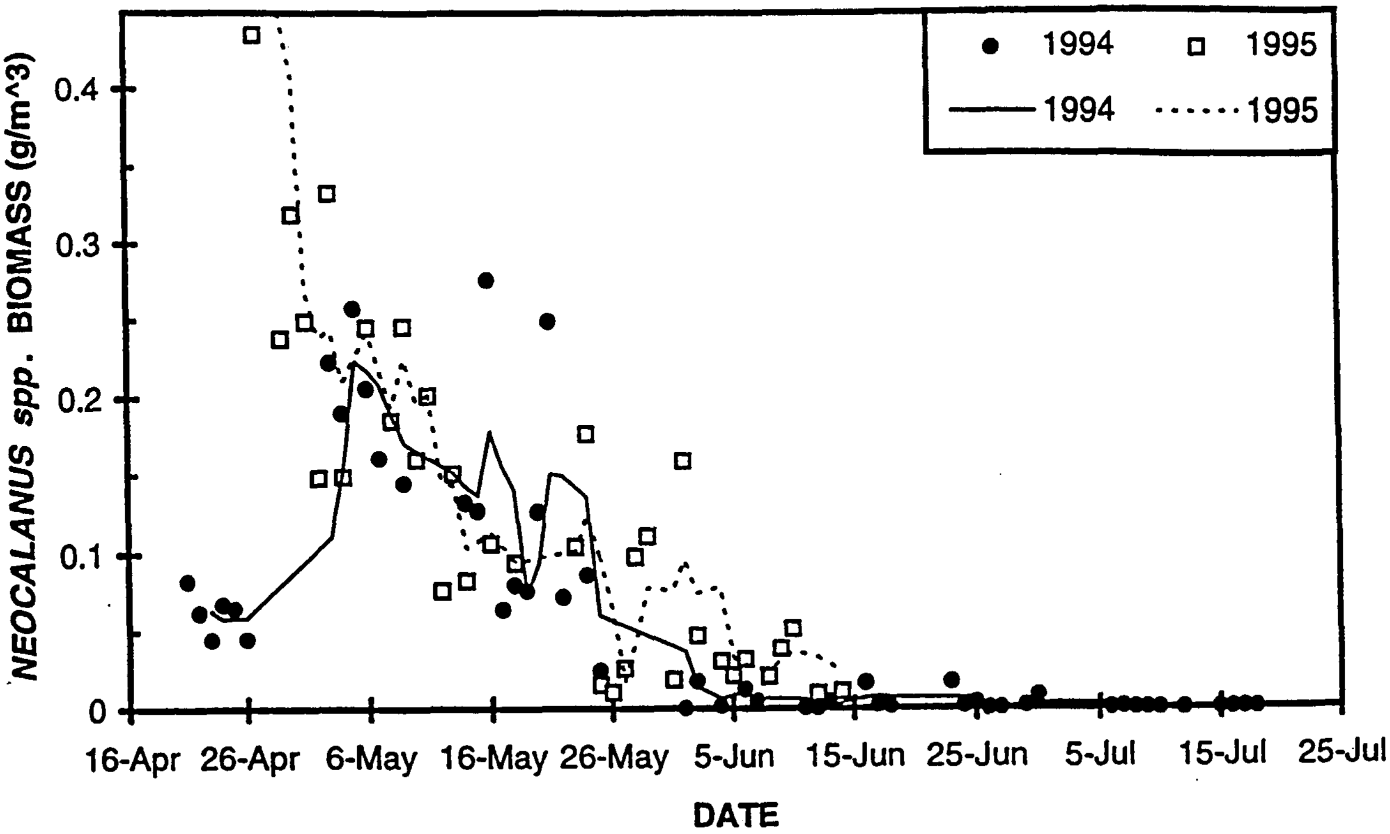


70
60
50
40
30
20
10
0
numbers
16
22
28
34
40
46
52
58
64
70
length (cm)

F8

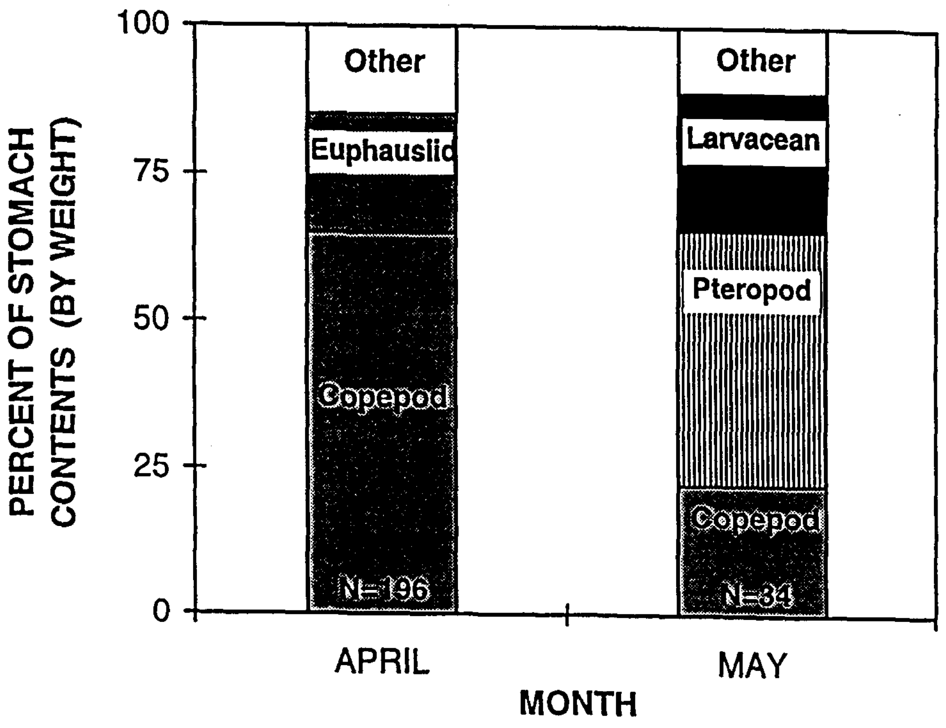

0.6
0.5
0.4
0.3
0.2
0.1
0
MEAN BIOMASS (g/m^3)
N=18
N=10
Pteropods
Euphausiids
Neocalanus
Neocalanus
Other Plankton
Other Plankton
APRIL
MAY
MONTH

F 9



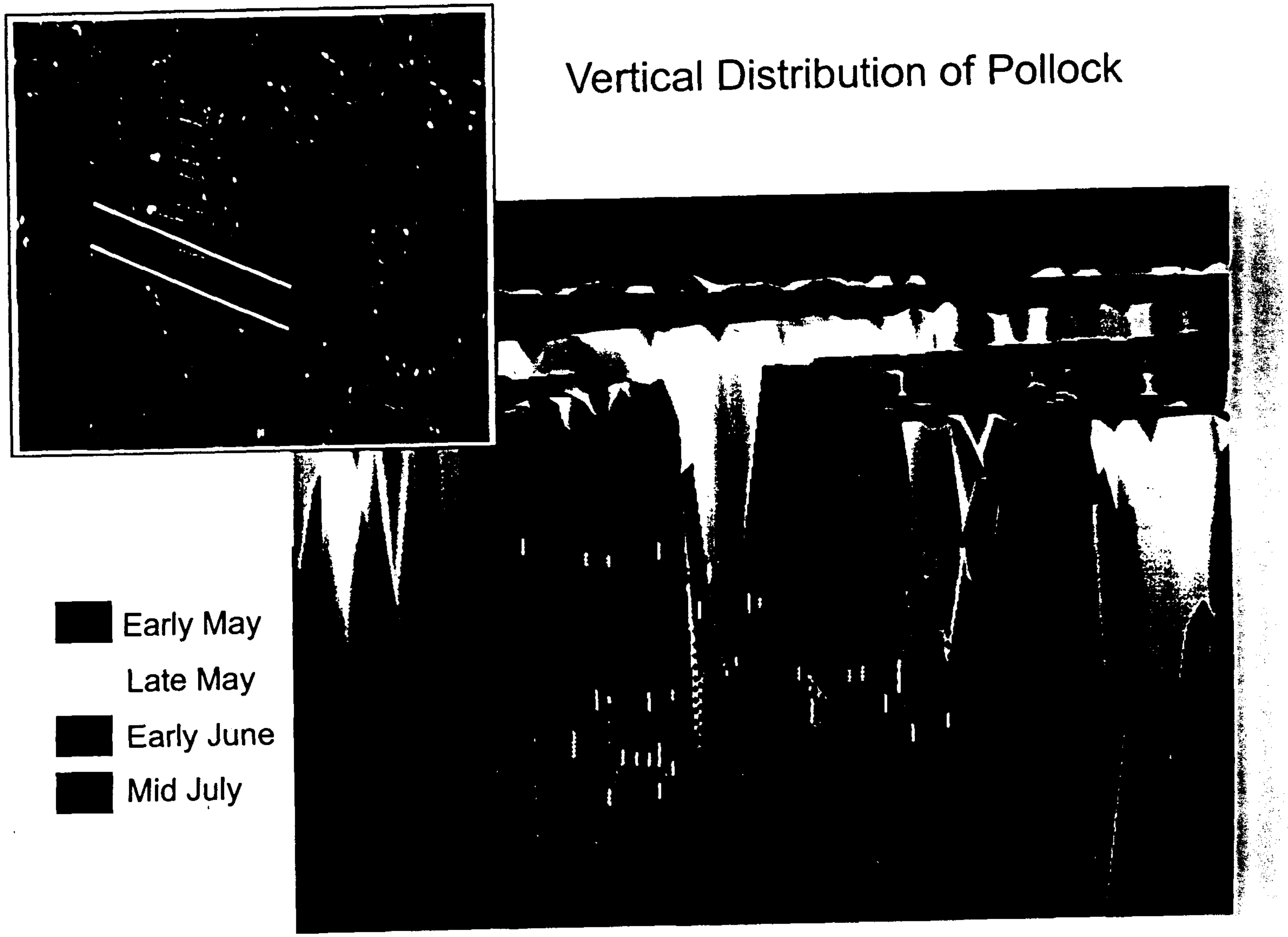
● 1994
□ 1995
1994
1995
NEOCALANUS spp. BIOMASS (g/m^3)
0.4
0.3
0.2
0.1
0
16-Apr
26-Apr
6-May
16-May
26-May
5-Jun
15-Jun
25-Jun
5-Jul
15-Jul
25-Jul
DATE

F-10


100
75
50
25
0
PERCENT OF STOMACH CONTENTS (BY WEIGHT)
Other
Euphauslid
Copepod
N=196
Other
Larvacean
Pteropod
Copepod
N=34
APRIL
MAY
MONTH

F-11

Vertical Distribution of Pollock



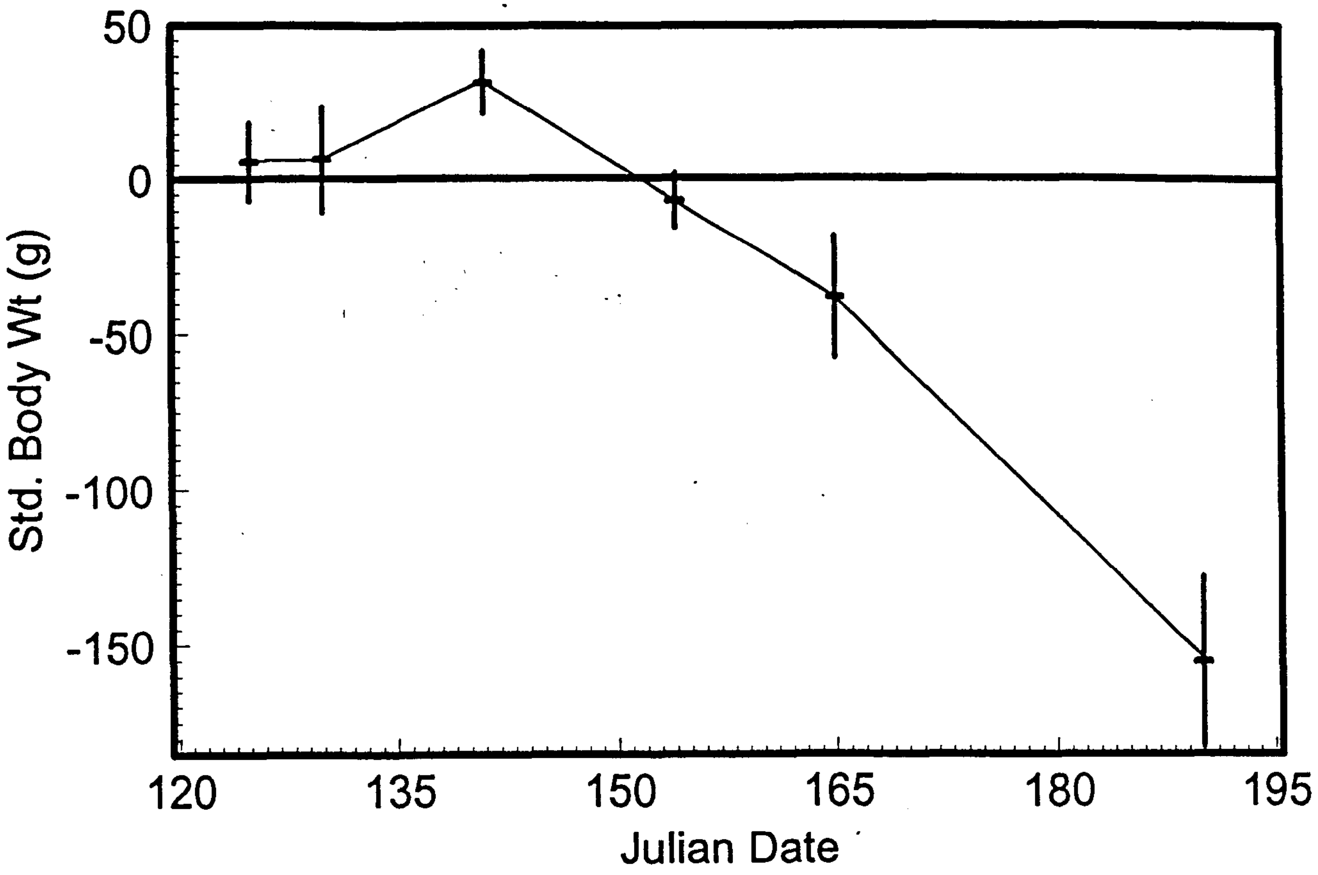
■ Early May

Late May

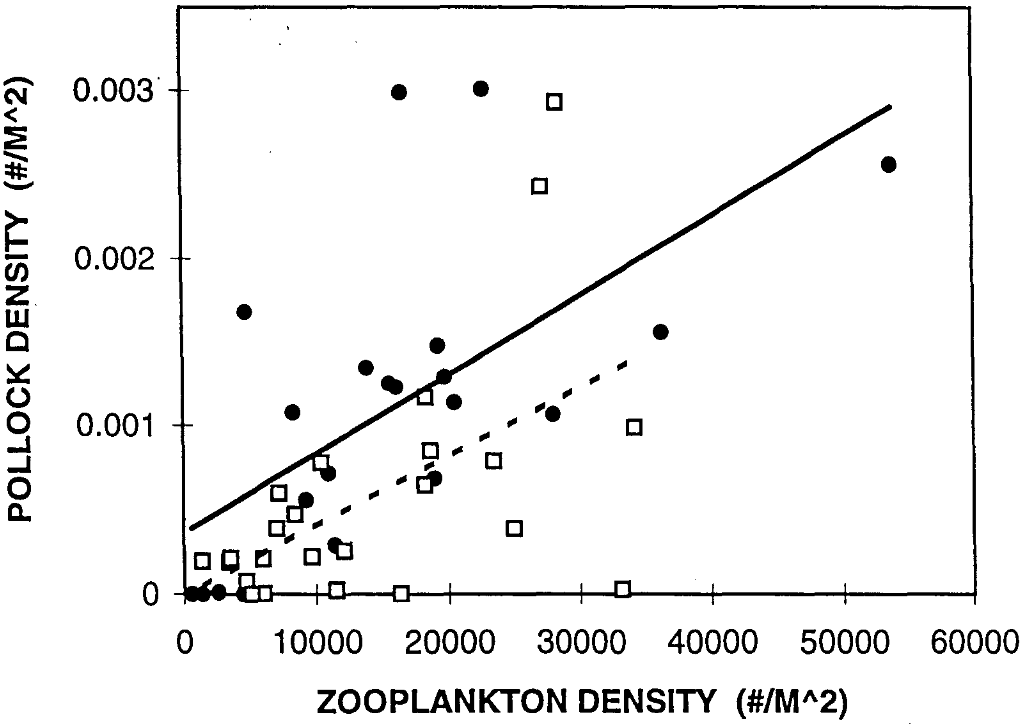
■ Early June

■ Mid July

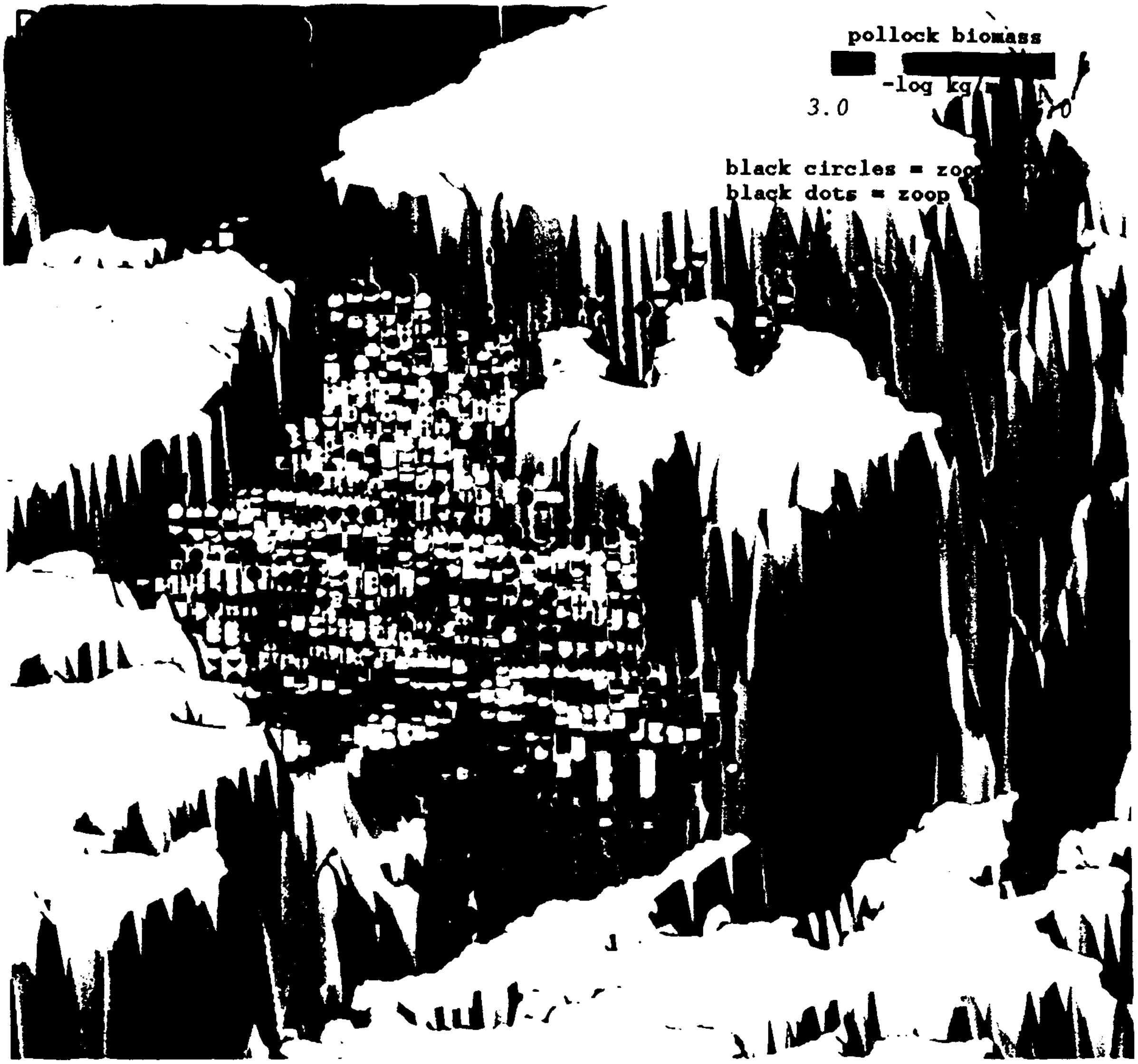
F12



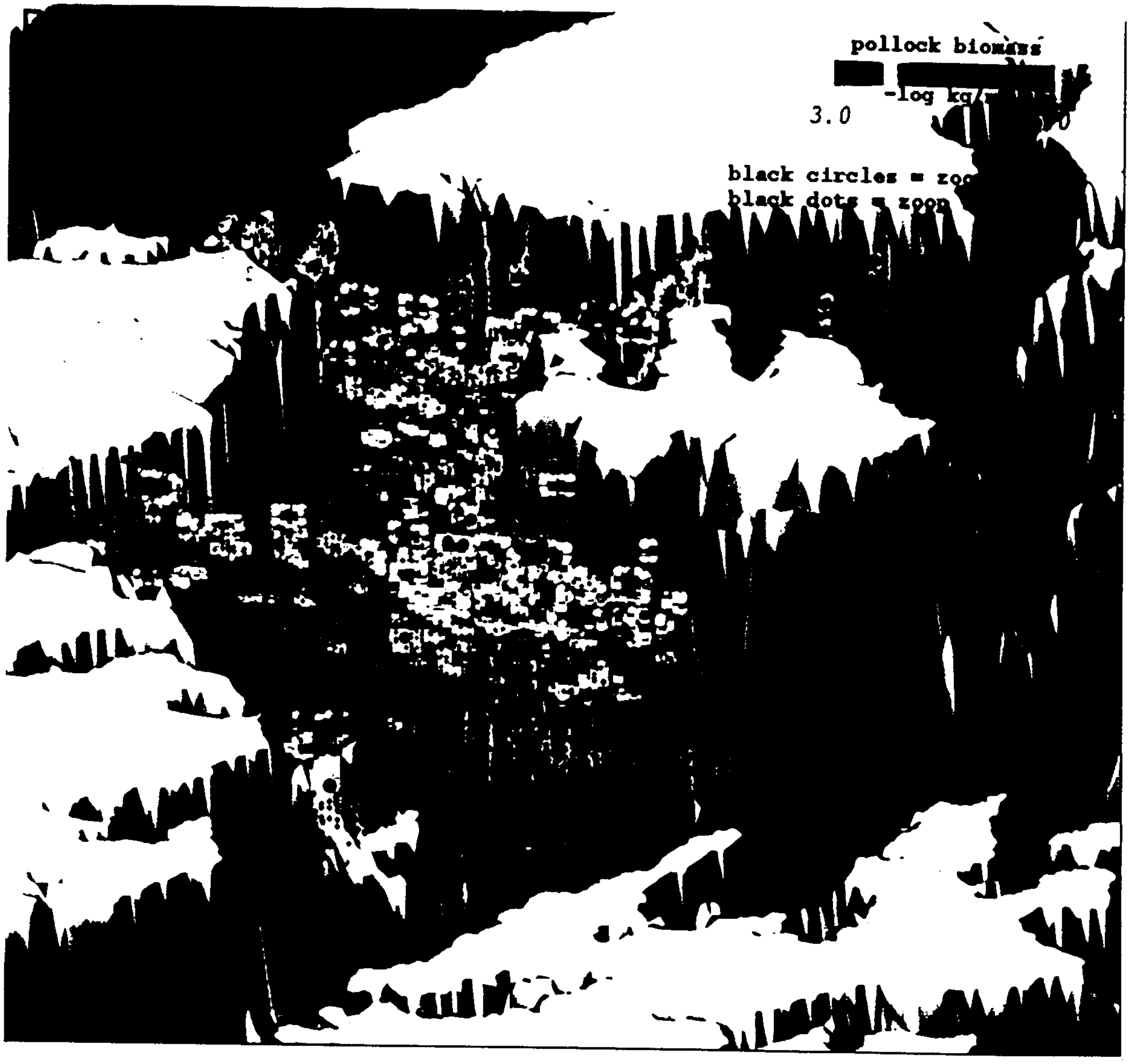
F 13


0.003
0.002
0.001
0
POLLOCK DENSITY (#/M^2)
0
10000
20000
30000
40000
50000
60000
ZOOPLANKTON DENSITY (#/M^2)

F 14



F 15



F -16

Chapter 3 – Thomas et al.
1997

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Development of an Ecosystem Model for Managing the Fisheries Resources of Prince William Sound

Second World Fisheries Congress
28 July-2 August 1996
Brisbane, Australia

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July 1996

INTRODUCTION

In 1988-90, a group of scientists working on the Ocean Ecosystem Dynamics Program (GLOBEC) of the National Science Foundation concluded that our inability to predict changes in marine fish populations has prevented us from separating natural and anthropogenic impacts (Cullen 1988). Using the GLOBEC program as a guide (GLOBEC 1991), in 1994, the Sound Ecosystem Assessment program

(SEA) was implemented to develop better predictive tools for fish production in the Prince William Sound, Alaska. SEA assumes that the physical (temperature, turbulence, currents, etc.) and biological (predators, prey and competitors) environment are major contributors to patterns of abundance and production of marine animals.

After failures in recruitment of Prince William Sound pink salmon *Onchorhynchus gorbuscha* and Pacific herring *Clupea harengus pallasi* in 1991-93 (Thomas and Mathisen 1993; ADF&G 1996), these stocks were classified as damaged by the EXXON VALDEZ oil spill Trustee Council (Wolfe et al. 1993). Efforts to restore these stocks are confounded by the poorly understood effects of climate, food and predators. These factors have been shown to account for up to 99.8% mortality in the early marine period for these fishes (Hjort 1914; Parker 1968; Ricker 1976; Hartt 1980; Bax 1983). During this period, slow growing individuals sustain a higher mortality because they are vulnerable to predators for a longer time (Parker 1971; Ricker 1976; Healey 1982; West and Larkin 1987). The long-term goal of the SEA program is to improve forecasting of fish recruitment in Prince William Sound.

The approach is to measure specific physical and biological conditions for input into numerical models. However, a more immediate need is to incorporate new knowledge of these species, where possible, into the ongoing management and restoration programs. Here we focus on the problem of measuring fish populations and the application of contemporary methods to improve accuracy and precision of biomass estimates.

More immediate concerns

The development of new measurement techniques to determine abundance and distribution of nekton and plankton is a prerequisite for testing the underlying hypotheses of the SEA models. Although model development is an eight to ten year goal, there is no reason why the new information on stock abundance, distribution and interactions cannot be used to create more effective restoration and management programs. Since pink salmon, Pacific herring and walleye pollock are all commercially exploited stocks, the establishment of exploitation rates have direct implications on restoration.

Presently, the stocks, pink salmon, herring and walleye pollock are all managed independently by establishing single-species harvest strategies. Single species harvest strategies are often based upon spawner-recruit relationships and stock assessment information. Missing are the effects of physics and other populations on the stock. With support that these species are influenced by climate-driven, predator-prey mechanisms and the acquisition of reasonably accurate, direct estimates of these stocks, an opportunity exists for testing the efficacy of multi-species management.

This paper addresses the findings after two years of the SEA program. Specifically, we review developments in the ability to measure the abundance and distribution of two dominant species (pollock and herring), and the implications of new information on current fisheries restoration and management.

METHODS

Prince William Sound is a complex fiord/estuary located at the northern margin of the Gulf of Alaska (Figure 1). High mountain peaks in excess of 4000 m border the Sound and receive the brunt of the seasonally intense cyclonic storms from the Gulf (Thomas et al. 1991). Depths exceeding 400 m occur in the western and central portions of the Sound which support overwintering populations of oceanic copepods.

Sampling design

The acoustic surveys were run from a variety of charter vessels according to standard echo integration practices (MacLennan and Simmonds 1992) using sphere-calibrated BioSonics 101,120 kHz and 102, 38 kHz dual beam and BioSonics ESP/EI and DB software programs. Each sonar system was equipped with a GPS receiver to geo-reference acoustic data. Echo integration, dual-beam target strength and GPS data were stored on hard drives and backed up on magnetic disks/tapes. Unprocessed data were stored on DAT recorders. The parameters of the two acoustic systems were: 120 kHz /SL = +225.075 dB, RG = -159.282dB, b2 = 0.0010718, PD = 0.4 ms;

38 kHz /SL = + 215.784, RG = -144.474, b2 = 0.00219, PD=1.0 ms.

Long day-lengths necessitated daylight surveys to monitor predator densities in the spring. Otherwise the acoustic surveys were conducted at night (Burczynski et al. 1986). Only red running lights were used on nighttime surveys to minimize boat avoidance and search-light sonars were used to monitor school behavior relative to the vessel track. The spring predator (walleye pollock) surveys took place mainly in the Wells and Perry Island Passages, in the northeastern corner of the Sound. This was to take advantage of the release of over 500 million salmon smolt by the hatcheries in this area. The fall-winter prespawning surveys of adult herring and pollock took place mainly in the north Montague Straits and Port Bainbridge areas. Since 1993, we conducted 11 spring predator surveys and eight fall-winter prespawner surveys.

On all surveys measurements were made on systematically stratified grids of parallel transects. On the prespawner surveys the grids were conducted only over fish school groups. This was the second of a two-stage survey design, with the first stage a search for school groups. Cochran (1977) describes the algorithms for estimating biomass and variance and discusses the biases associated with single and two-stage, stratified-systematic sampling designs. All acoustic sampling was supported by midwater trawl or purse seine catches to collect biological information.

Data Analysis

Batch processing to transform 2d arrays of acoustic targets from dB to kg and numbers, estimate and visualize biomass were conducted after transferring the data to a UNIX workstation. All data are stored in the appropriate format for post processing using Interactive Data Language (IDL), and Advanced Visualization systems (AVS) software.

Measured target strengths of individual fish were compared with length data of fish captured by the nets. To establish a fish size-target strength relationship, we used the relationships advanced by Thorne (1983 for target strength per kg versus length, Traynor and Ehrenberg (1979) for walleye pollock target strength versus length, and MacLennan and Simmonds (1992) for Pacific herring target strength versus length. Weighted mean densities and their variances were computed and extrapolated to biomass and 95% confidence limits using the delta method (Seber 1973).

Visualizations of biomass survey data were made using AVS. Geo-coded volume backscatter values were stored in a 1-d scatter arrays and displayed as scatter- dot clouds in 3-d space to view sampled locations. The 1-d scatter array was then converted to 3-d unstructured cell data (UCD) format. In UCD format each point is identified by its spatial relationship to neighboring points. Interpolation using Delauney triangulation

was used to generate the UCD structure. The 3-d UCD volume was converted to a geometry by applying a user-specified color map to the nodes and then displayed and manipulated in the AVS geometry viewer. Finally, serial slices throughout the UCD volume were taken using horizontal planes to show truncation of school group measurements. Isosurfaces of the school groups were examined at various thresholds, rotated in 3-d space and animated as time sequences to select views that best describe the truncation problem.

RESULTS AND DISCUSSION

Implications of new biomass information

Six surveys of prespawning herring and two of prespawning pollock were conducted between 1993-1996. Both species occur in highly aggregated school groups that are distinct enough in their vertical distribution and density that identification of their acoustic targets is not an issue. Only twelve school groups of herring in excess of 1000 mt were observed on the six surveys over three years (Figure 1). Only four school groups over 1000 mt of pollock were observed on two surveys in 1995 (Figure 1).

Four of the 12 herring concentrations were surveyed twice to determine repeatability of the measurements. In fall 1993, we estimated the same school group on Applegate Rocks to be 12,875 and 16,442 mt; in spring 1995, we estimated the same school group in Rocky Bay to be 10,480 and 8,050 mt; in winter 1996, we estimated the same group of fish in Zaikof Bay at 26,309 and 20,097 mt; in the spring of 1996, we estimated the same group of fish in Stockdale Harbor at 3,227 and 3,791 mt.

Upon close inspection, the largest source of error in estimates from the repeated transects over the herring or pollock aggregations is the lack of adequate coverage of the fish concentration. Figures 2-6 show the results of five consecutive surveys on a concentration of herring in Stockdale Harbor. The school isosurfaces show that the measurement of the herring school group was severely truncated on surveys #1 (Figure 2), #3 (Figure 4) and #5 (Figure 6), but not on surveys #2 (Figure 3) and #4 (Figure 5). The nearshore affinity of walleye pollock suggests that truncation of measurements is also a problem on their surveys. The biomass estimated on #2 and #4 were 3,227 and 3,791 mt, whereas the biomass of the other three surveys never exceeded 1,700 mt.

Another aspect of repeatability is the fall to winter-spring estimates. The fall 1994 and spring 1995 estimates of adult herring biomass were both about 13,000 mt. The fall 1995 and winter 1996 estimates of adult herring biomass were about 24,000 and 23,000 mt. The observed increases from spring to fall are due to recruitment and little overwinter mortality has been observed. Finally, in 1995 the biomass of prespawning pollock in Port Bainbridge was estimated to be 27,366+/- 7,227 mt from a survey of nine parallel transects.

The fact that there are so few school groups of prespawning herring and pollock in the Sound region, and that they do undergo localized movements which can allow good coverage if the surveys are continually repeated, suggests the use of a two stage survey design: (1) use aerial and sonar searches to locate the school groups, and (2) remain with the school group until repeatable measures are made.

These findings suggest that making "corrections" for fish too close to the shore (Hampton 1996) for Prince William Sound herring and pollock can result in unacceptable inaccuracy in the biomass estimation. Adoption of two stage procedure should result in repeated estimates of school group biomass within 10% of each other.

The single-species paradigm

Currently, the three dominant pelagic fish populations in the Sound, pink salmon, Pacific herring and walleye pollock are also three of the most important commercial fishes. As is the tradition in fisheries science (Hilborn and Walters 1992), each fishery is managed separately and with sparse data. With new information generated by the SEA program on abundance, distribution and interaction there is the possibility to take a multispecies approach and minimize the potential for contradictions between restoration and management activities.

The status of the pink salmon is somewhat independent of the system because 90% are produced by hatcheries (Thomas and Mathisen 1993), and they only spend 3 months in the Sound as juveniles before migrating to the ocean to feed (Willette 1993), and about two-three weeks in the Sound as adults while migrating to spawning areas. In contrast, Pacific herring and walleye pollock spend much of their life histories in the Sound.

The Sound's Pacific herring stock has been too low to support commercial harvests since 1993 (ADF&G 1996). Concurrently, the Sound's walleye pollock stock is considered to be part of a declining Gulf of Alaska stock (NMFS 1996). Thus, the Sound's walleye pollock are being harvested at a reduced exploitation rate (9% in 1995). Since the status of the Gulf of Alaska pollock stock is determined by a model prediction for the west-central stocks, where the predictions do not agree with survey data, this harvest rate is at least controversial. With recent findings that the walleye pollock and herring are the two dominant, competing pelagic species in the Sound, there is a concern that the current management strategy to build the pollock stock may contradict the restoration of the herring stock.

Walters et al. (1986) found herring survival to recruitment to be negatively related to cod abundance *Gadus macrocephalus*. Analysis of cod stomach contents supported the estimated mortality rates. We have found that walleye pollock are the primary predators of young pink salmon and herring. Thus, a negative correlation between walleye pollock abundance and the recruitment of herring is a good hypothesis for testing.

Sainsbury (1988) proposed that managers set up experimental fishing regimes for multispecies analysis. Present fishing regimes in the Sound are established independently for the walleye pollock, Pacific herring and pink salmon by the Alaska Department of Fish and Game and National Marine Fisheries Service, hence they are already subjects of an ongoing experiment. With both of these agencies represented by the EVOS Trustee Council there is unprecedented opportunity to merge information from both management and restoration programs and evaluate a multi-species management approach.

Hilborn and Walters (1992) identified the data requirements for multispecies biomass dynamics and age structured models as too demanding or expensive for practical utility. However, we anticipate that GLOBEC and SEA research and development programs will produce remote sampling methods that are accurate and cost effective enough to satisfy both the accuracy and cost constraints. To illustrate, one survey is less than $50KUS. Such are well within the amount that and costs can be borne by test fishing revenues (Thomas 1992). Such monitoring will also serve our long term goals by providing the information needed to initialize and verify the next generation numerical models for predicting fish population changes (GLOBEC 1991).

In-season management for escapement

We show that acoustic measurement techniques can make repeatable estimates of the size of herring and pollock school groups in the Prince William Sound region. Repeatable measurements of biomass have been made both within and between fall and spring surveys. The largest source of error in the biomass estimation procedure is truncation of the school groups by the survey volume. Visualization techniques have been developed to provide criteria for accepting repeated measurements as replicates. Use of new criteria for repeating biomass estimates in the field is expected to produce the accuracy needed for implementing in-season management practices. The implementation of in-season management practices can protect marine fish stocks and allow weak stocks to rebuild prior to having predictive models.

Current management of the walleye pollock fishery could be contradictory to the restoration of the collapsed herring stock and production strategies for hatchery salmon. With the ongoing SEA research program, we recommend that management agencies take advantage of this opportunity by experimenting with multi-species harvest strategies and implementing in-season management practices for herring and pollock.

Predictive Models

With short-term concerns over conservation of stocks satisfied by using accurate estimates of fish biomass to implement in-season management practices, research can focus on the development of predictive models. Accurate monitoring of the fish biomass is also essential for initializing and verifying model predictions. Thus, with the development, refinement and implementation of monitoring programs to accurately assess fish stock biomass, conservation practices and eventually, the prediction of animal population change is possible. Since the ability to predict animal population change is a prerequisite to the separation of natural and anthropogenic effects, we have a pathway to developing the ability to assess the effects of fishing, hatchery practices, oil spills and other man-induced impacts on natural populations.

SUMMARY

The Sound Ecosystem Assessment (SEA) program is developing and applying new survey designs to estimate the abundance and distribution of dominant fish stocks (Pacific herring and walleye pollock) in Prince William Sound. The long term goal is the development of numerical models to improve the prediction of fish population change. However, accurate estimates of biomass are not only needed to initialize and verify model predictions but are essential for implementing conservation practices that will sustain healthy fisheries. The current management of the walleye pollock fishery could be contradictory to the restoration of the collapsed herring stock and production strategies for hatchery salmon. We support the implementation of a biomass monitoring program for herring and pollock stocks in the Sound and the development of in-season management practices. Furthermore, we urge the adoption of experimental multi-species harvest strategies while the three dominant species (herring, pollock and salmon) are being monitored for changes in biomass. We see this to be an unprecedented opportunity for fisheries science to evaluate a new management paradigm.

ACKNOWLEDGMENTS

This research is funded by the EVOS Trustee Council. We thank the Council and its staff, the SEA program researchers, local area managers and Prince William Sound Science Center personnel and associates for support of this research. Special thanks goes to the fishermen in Prince William Sound who have contributed valuable insight on the fish distribution and behavior and are second to none as vessel skippers.

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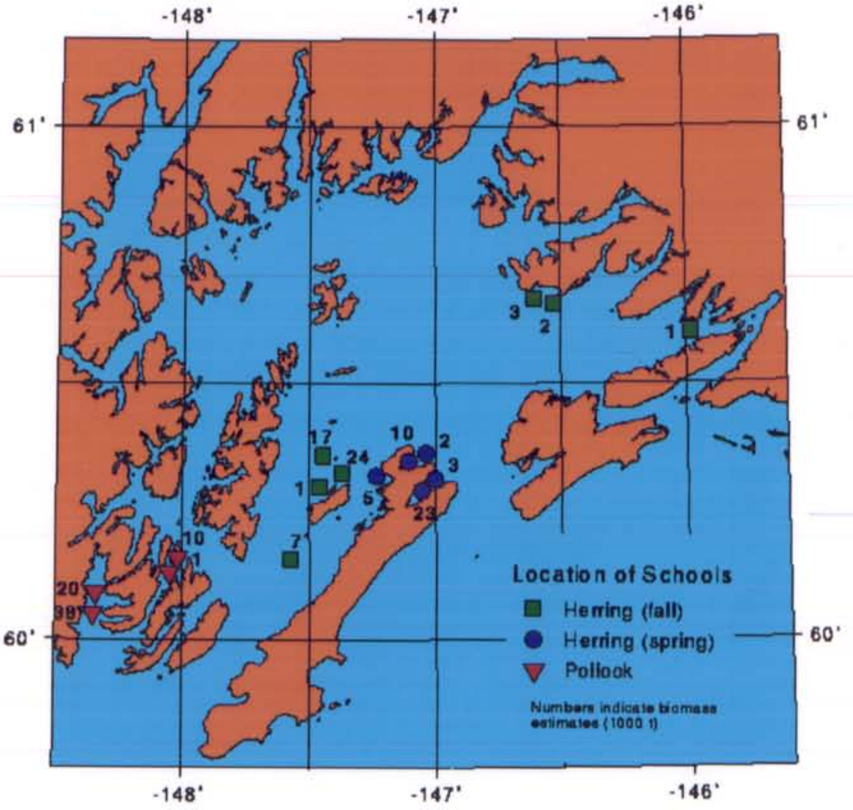
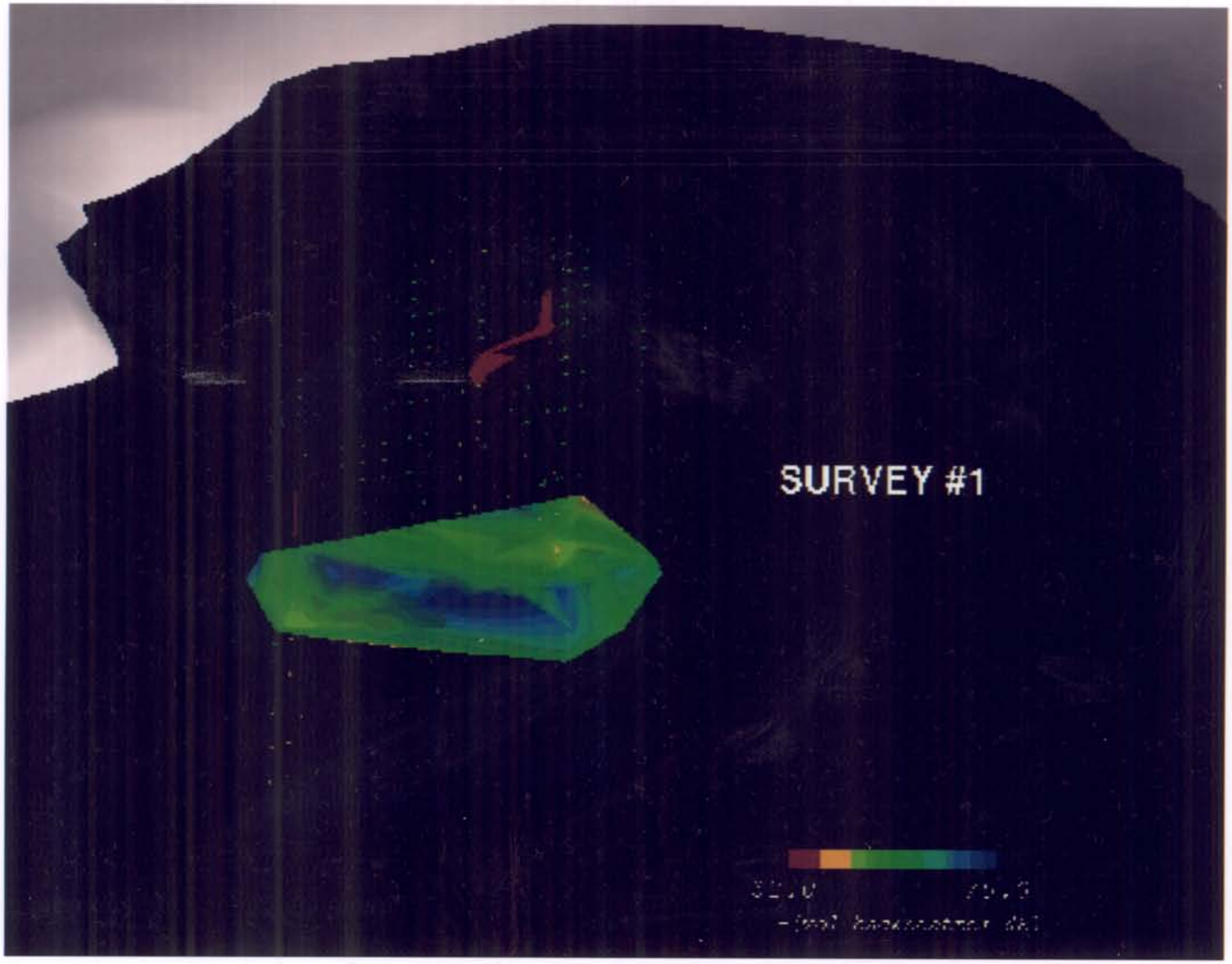
Wolfe, Douglas, Robert Spies, David Shaw and Pamela Bergman (editors). 1993. Proceedings of the EXXON VALDEZ Oil Spill Symposium. February 2-5, 1993. Anchorage Alaska. 355 pp.

LIST OF FIGURES

Prince William Sound, Alaska

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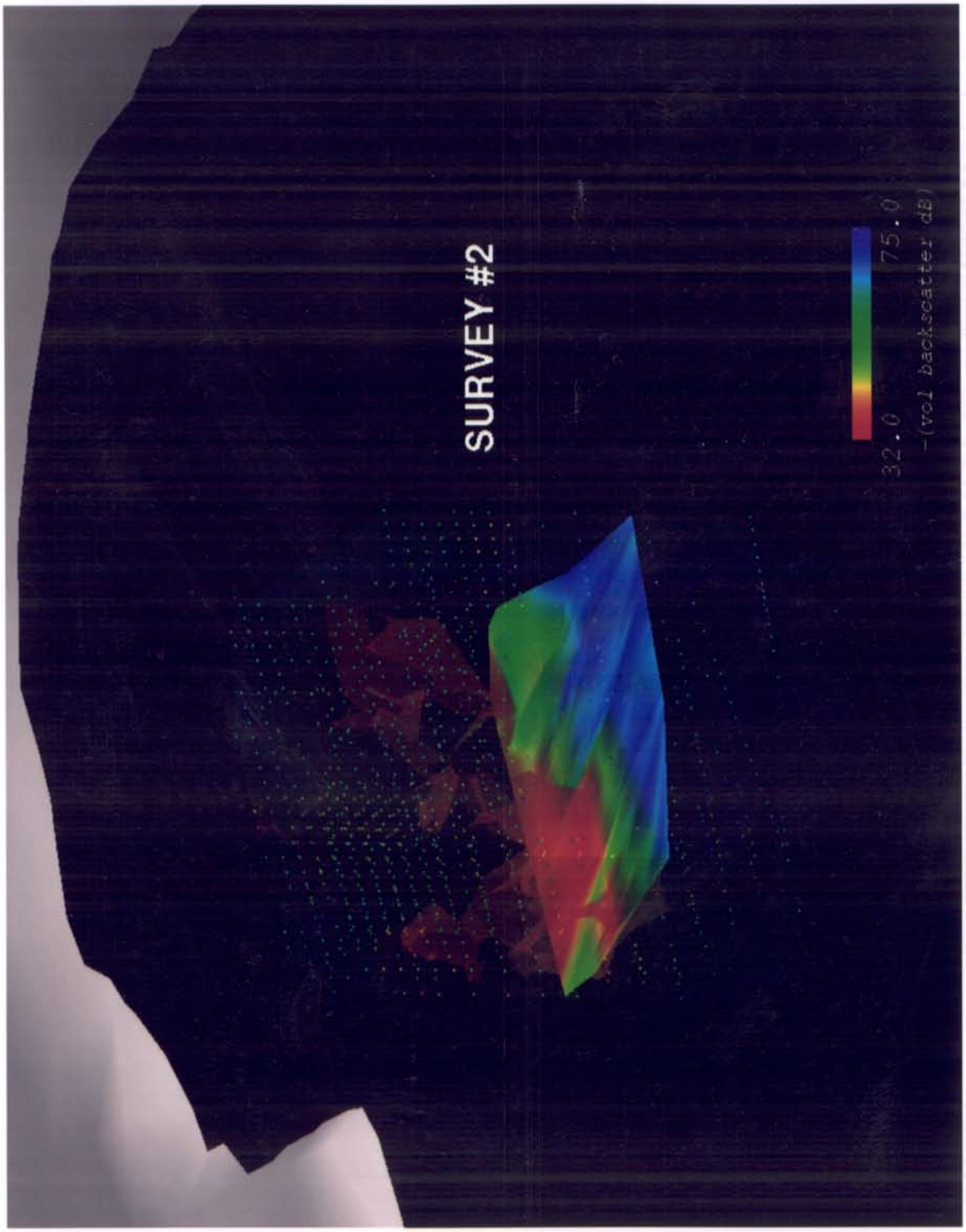
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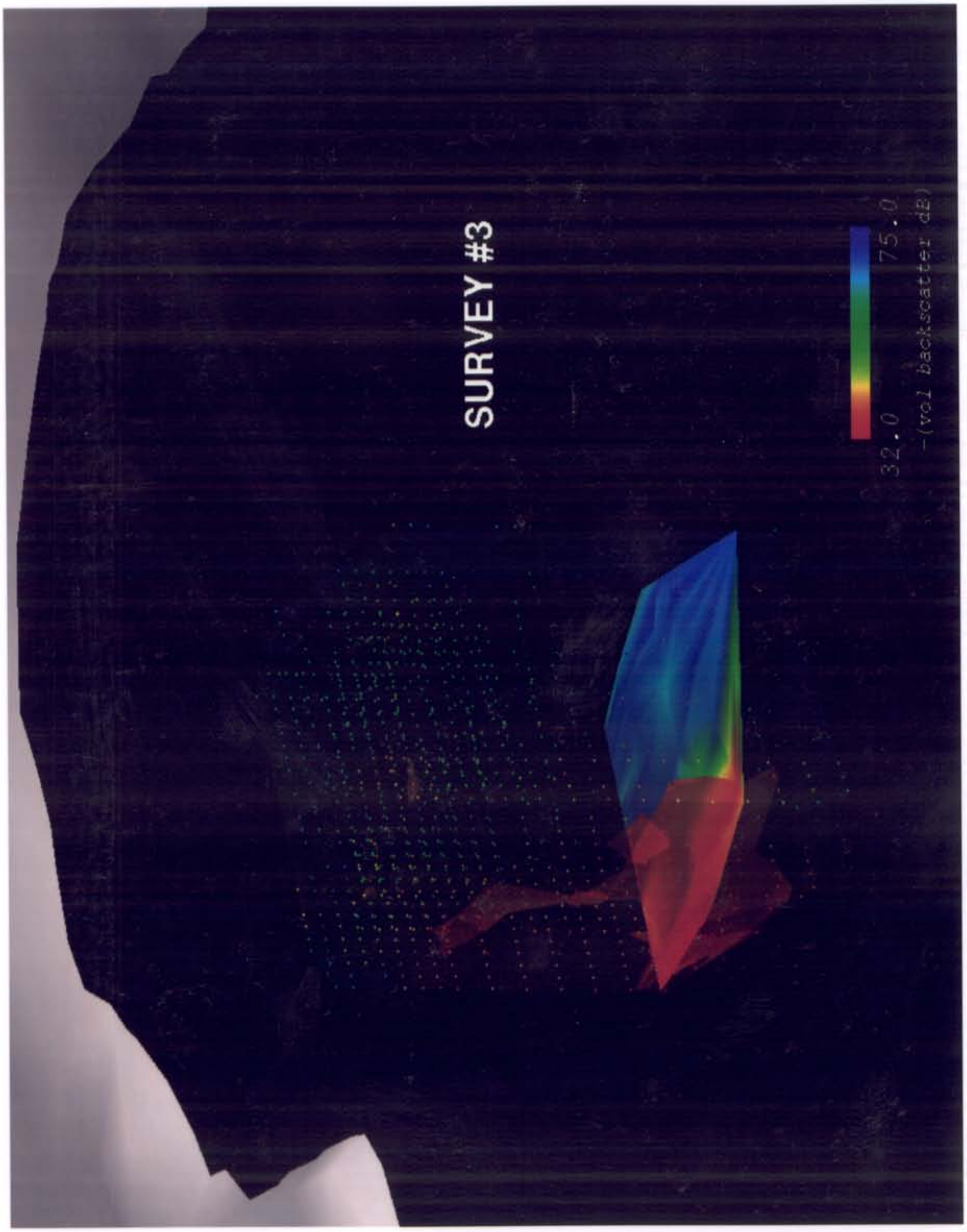
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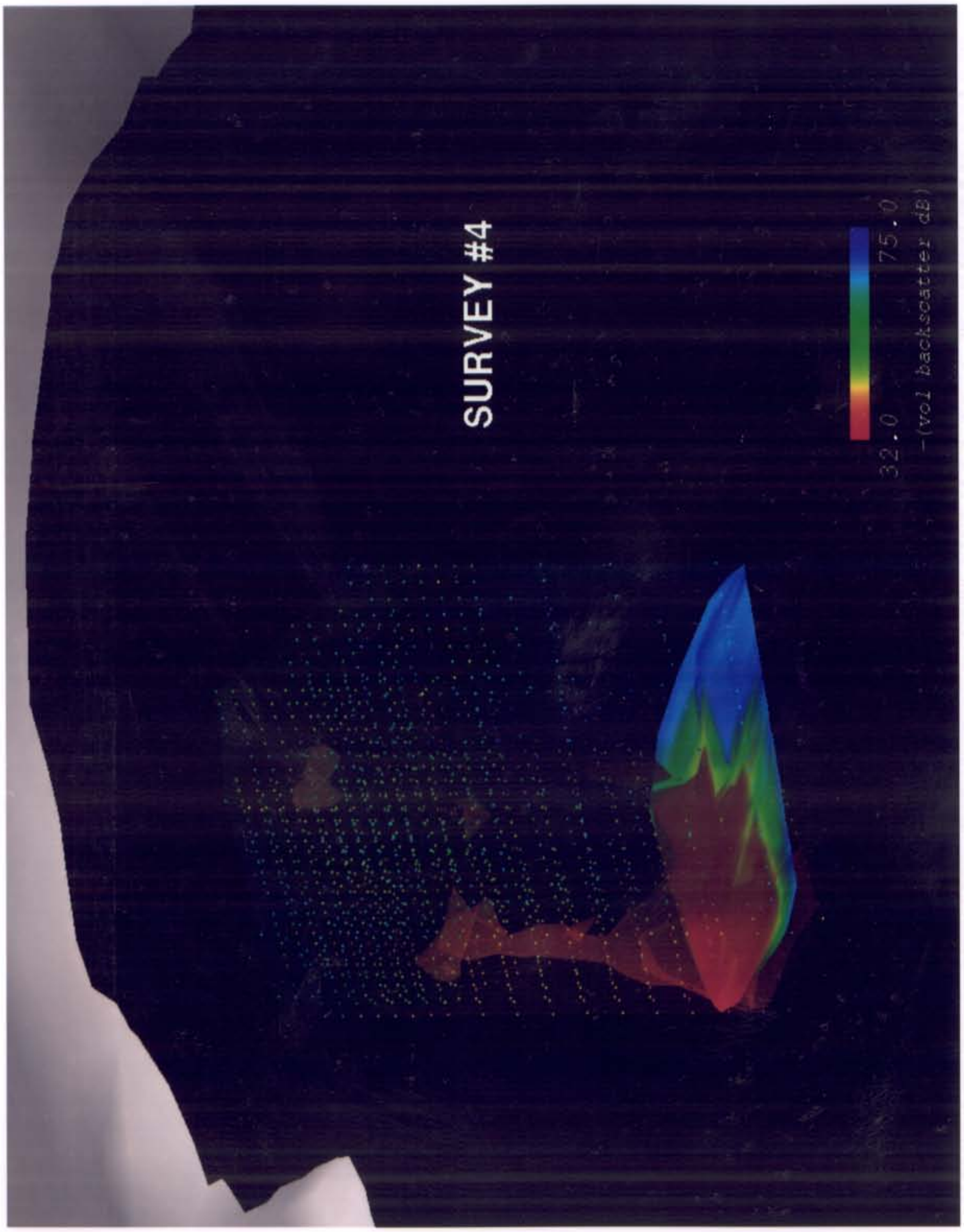
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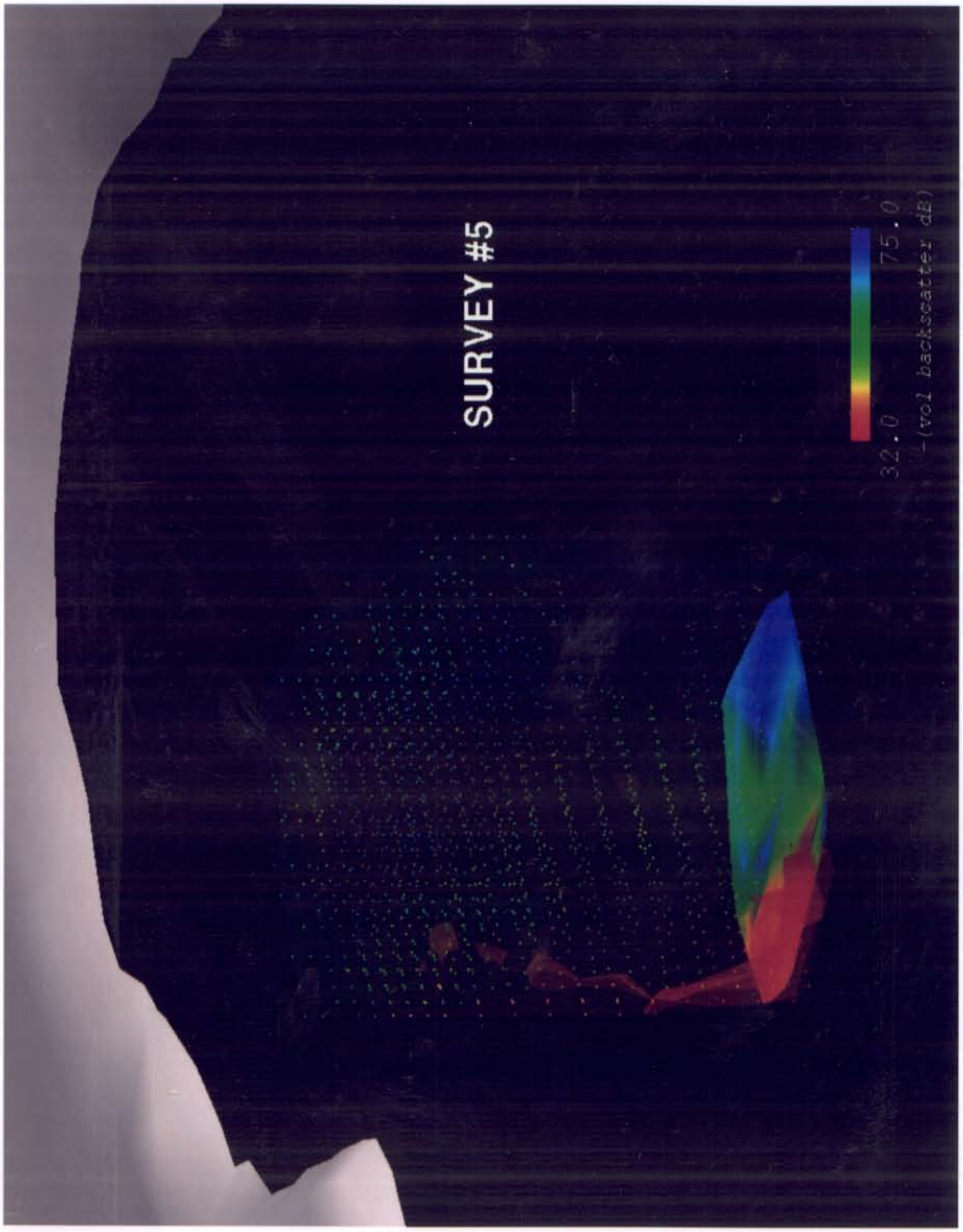
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Chapter 10

Juvenile Herring Growth and Habitats
and
Herring Traditional Ecological Knowledge (Project T Supplement)

Exxon Valdez Oil Spill
Restoration Project Final Report

Juvenile Herring Growth and Habitats

Restoration Project 99320T
Final Report

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Project Data: Spatial distribution (acoustic and aerial) of herring and other species of fishes captured, length frequencies of herring, herring stomach contents, zooplankton collections, CTD and larval fish data are part of the SEA database and are available from Dr. Brenda L. Norcross, Evelyn Brown or Michele Frandsen, Institute of Marine Science, University of Alaska-Fairbanks, Fairbanks, Alaska.

Local knowledge observations of herring in PWS and the Kenai Peninsula are in ARCVIEW 3.1, a GIS database. Information from each observation includes the range of years, location, method, verification and frequency. These data are also available from Dr. Brenda L. Norcross, Evelyn Brown or Michele Frandsen, Institute of Marine Science, University of Alaska-Fairbanks, Fairbanks, Alaska.

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Chapter 10: 98320T
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Table of Contents

Objectives

Three simply stated research objectives have guided the herring research in this project. Those objectives have been met and the results are presented in detail in the manuscripts that compose the appendices, as detailed below. Because this was a multi-investigator project, not all objectives were met solely within this section of SEA, but rather overlap with other aspects of SEA. In some cases, the manuscripts to which I refer are located in other SEA sections, as indicated here. In that case, at least one of the authors of the manuscript received support from 320T for his/her contribution to the project.

Objective 1. Develop an over-wintering survival model for juvenile herring.

Norcross, B.L., E.D. Brown, R.J. Foy, M. Frandsen, S.M. Gay, M. Jin, J. Kirsch, T.C. Kline, D.M. Mason, C.N.K. Mooers, E.V. Patrick, A.J. Paul, K.D.E. Stokesbury, S.J. Thornton, S.L. Vaughan, and J. Wang. (to be submitted) Life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. *Fisheries Oceanography*.
See Appendix I.

Patrick, E.V., D.M. Mason, R.J. Foy, B.L. Norcross, A.J. Paul, K.D.E. Stokesbury, and T.C. Kline. (to be submitted) Effects of physiological condition and water temperature on over-winter survival of age-0 Pacific herring: A modeling synthesis. *Fisheries Oceanography*.
See EVOS 320J.

Foy, R.J. and A.J. Paul. (2000) Winter feeding and changes in somatic energy content for age 0 Pacific herring in Prince William Sound, Alaska. *Transactions of the American Fisheries Society* (in press).
See EVOS 320U.

Objective 2. Develop a summer habitat model for juvenile herring.

Norcross, B.L., E.D. Brown, R.J. Foy, M. Frandsen, S.M. Gay, M. Jin, J. Kirsch, T.C. Kline, D.M. Mason, C.N.K. Mooers, E.V. Patrick, A.J. Paul, K.D.E. Stokesbury, S.J. Thornton, S.L. Vaughan, and J. Wang. (to be submitted) Life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. *Fisheries Oceanography*.
See Appendix I.

Foy, R. J. and B. L. Norcross. 1999. Spatial and temporal variability in the diet of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska. *Canadian Journal of Zoology* (in press).
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Stokesbury, K. D. E., R.J. Foy, and B.L. Norcross. 1999. Spatial and temporal variability in juvenile pacific herring, *Clupea pallasi*, growth in Prince William Sound, Alaska. *Environmental Biology of Fishes* (in press).
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Stokesbury, K. D. E., J. Kirsch, E. D. Brown, G. L. Thomas, and B. L. Norcross. 1999. Spatial distributions of Pacific herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) in Prince William Sound, Alaska. *Fisheries Bulletin (US)* (in press).
See Appendix IV.

Stokesbury, K. D. E., J. Kirsch, and B. L. Norcross. (submitted). Mortality estimates of juvenile Pacific herring , *Clupea pallasi*, in Prince William Sound, Alaska. *Marine Ecology Progress Series* (in review).

See Appendix V.

Objective 3. Develop a monitoring strategy for juvenile herring.

Norcross, B.L., E.D. Brown, R.J. Foy, M. Frandsen, S.M. Gay, M. Jin, J. Kirsch, T.C. Kline, D.M. Mason, C.N.K. Mooers, E.V. Patrick, A.J. Paul, K.D.E. Stokesbury, S.J. Thornton, S.L. Vaughan, and J. Wang. (to be submitted) Life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. *Fisheries Oceanography.*
See Appendix I.

Brown, E.D., S.M. Moreland, and B.L. Norcross. (to be submitted) Estimating forage fish and seabird distribution and abundance using aerial surveys: survey design and uncertainty. *Ecological Applications.*
See Appendix VI.

The objectives for the Supplement of /320T supported and complemented the main herring research objectives listed above. The primary goal of this project was to document historical knowledge about distribution of juvenile herring. This goal was met through a series of specific objectives, each of which was addressed in a single manuscript found in the appendix.

Objective 1. Compile historic information about the distribution and abundance of forage fish species from local and traditional knowledge.

Seitz, J., E.D. Brown, and B.L. Norcross. (to be submitted) Ecology of herring and other forage fish as recorded by resource users of Prince William Sound and Lower Cook Inlet. *Alaska Fishery Research Bulletin.*
See Appendix VII.

Objective 2. Disseminate the data and results of this project as broadly as possible including via a publication.

Seitz, J., E.D. Brown, and B.L. Norcross. (to be submitted) Ecology of herring and other forage fish as recorded by resource users of Prince William Sound and Lower Cook Inlet. *Alaska Fishery Research Bulletin.*
See Appendix VII.

Objective 3. Use the information to design ecological research and to assist resource managers in defining sensitive habitats.

Seitz, J., E.D. Brown, and B.L. Norcross. (to be submitted) Ecology of herring and other forage fish as recorded by resource users of Prince William Sound and Lower Cook Inlet. *Alaska Fishery Research Bulletin.*
See Appendix VII.

Alaska Predator Ecosystem Experiment (APEX) Project Support

Juvenile herring were determined to be an important forage fish in PWS (Haldorson et al. 1996). Thus, there is considerable overlap between research conducted by SEA and APEX. In 1997, SEA herring researchers were requested to cooperate and share data with researchers within APEX. As part of SEA320T overflights were coordinated with APEX acoustic surveys and ongoing sea bird research. The aerial database was shared with APEX to enhance modeling efforts linking fish distribution to bird foraging behavior and reproductive effort. In addition, SEA aerial and net catch data concerning jellyfish was shared with the APEX project for analysis and publication.

Ainley, D., E.D. Brown, G. Ford and other authors. (to be submitted) Analysis of aerial spotting data of fish schools, kittiwakes, and other phenomena. *Marine Ecology Progress Series.*
See APEX 163Q.

Purcell, J.E., E.D. Brown, K.D.E. Stokesbury, L.H. Haldorson, and T.C. Shirley (submitted) Aggregations of the jellyfish *Aurelia aurita*: Abundance, distribution, association with age-0 walleye pollock, and behaviors promoting aggregation in Prince William Sound, Alaska, USA. *Marine Ecology Progress Series.*
See APEX 163S

Provided aerial data and analysis for:

Irons, D.B. and R.M. Suryan. 1996. Kittiwakes as indicators of change in forage fish. Preliminary results of 1995 field season. APEX Component 95163E, US Fish and Wildlife Service, 1011 E. Tudor Rd. Anchorage, AK 99503.
See APEX 163E

EcoPath Modeling Project Support

As part of 320T biomass, production, and consumption estimates for carnivorous and omnivorous zooplankton and carnivorous jellies from the nearshore environement (<20 m depth) were calculated and supplied to the Ecopath Modeling Project for inclusion in a Prince William Sound Mass Balance Model. Diet composition (R. J. Foy) and biomass estimates (E. Brown) of juvenile herring from 1995 to 1997 were also included in the model.

Foy, R. J. 1998. Nearshore zooplankton. Edited by T. A. Okey and D. Pauly. Trophic mass-balance model of Alaska's Prince William Sound ecosystem, for the Post-Spill Period 1994-1996. The Fisheries Centre, University of British Columbia. 6(4):21-22.

Okey, T. A., R. J. Foy, and J. Purcell. 1998. Carnivorous jellies. Edited by T. A. Okey and D. Pauly. Trophic mass-balance model of Alaska's Prince William Sound ecosystem, for the Post-Spill Period 1994-1996. The Fisheries Centre, University of British Columbia. 6(4):22.

Okey, T. A., and R. J. Foy. 1998. Juvenile herring. Edited by T. A. Okey and D. Pauly. Trophic mass-balance model of Alaska's Prince William Sound ecosystem, for the Post-Spill Period 1994-1996. The Fisheries Centre, University of British Columbia. 6(4):33-34.

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Haldorson, L., T. Shirley, K. Coyle, and R. Thorne. 1996. Alaska Predator Ecosystem Experiment Forage Species Studies in Prince William Sound Project 163A, 1996 Annual Report prepared for *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska. 93 pp.

Estimating Forage Fish and Seabird Distribution and Abundance Using Aerial Surveys: Survey Design and Uncertainty

Submit to
Ecological Applications

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Abstract

We show that aerial visual surveys are a cost-effective method to assess distribution and abundance of forage fish and seabirds and produce repeatable results with an acceptable level of error. We fulfilled our main objectives concerning forage fish assessment: 1) develop an appropriate survey design incorporating detection error, surveyor bias, and survey constraints, 2) determine the accuracy of fish species and age class discrimination, 3) determine the repeatability of aerial measurements, and 4) determine the spatial resolution of aerial measurements needed for ecological analyses. We also fulfilled our secondary objective to develop abundance estimates for jellyfish aggregations and seabirds. We developed an adaptive modified line transect methodolgy and model incorporating a detection curve for Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes hexapterus*), and black-legged kittiwakes (*Rissa tridactyla*) and a detection correction factor for fish schools. We established survey condition constraints and an optimal survey altitude range of 274 - 366 m based on school size and sightability of sea birds. We developed logging software to obtain flight path and sighting coordinates and incorporated measurements of schools using a sighting tube. The altitude dependent flight swath or transect width for fish schools was estimated from the detection curve at 474 m at an altitude of 305 m. The detection correction factor was estimated at 0.727 resulting in an undercounting rate of approximately 37.5%. Using double counting, individual surveyor bias was estimated at 6.5% for school counts and 7.0% for school surface area estimates; these rates are lower than those reported for wildlife aerial surveys. Error in fish species identification was estimated from validation data at 3.9% for herring, and 20. 2% for sand lance; we were not able to discriminate age classes of herring and a model did not improve discrimination. We recommended methods to reduce the cost of obtaining validation samples for future surveys. We determined the precision of fish abundance estimates by performing repeat flyovers; our error rate was 14.6% for school counts and 18.3% for total school surface area estimates within a 36 hr period; surveyor bias is imbedded in this estimate. The variance of the density estimates will be mainly influenced by the variability of biological occurrence since the variance of the detection correction factor including surveyor bias was very low. The additional contribution of error from identification and repeatability of measurements is species specific. For herring the additional error for schools counts, 12 - 18.5%, and surface area estimates, 15.2 – 22.2%, should be applied depending on whether or the redundancy for surveyor bias is removed. For sand lance, the additional error is 27.7 – 34.2% for school counts and 30.9 – 37.9% for school surface area estimates. The spatial resolution of our data was established at approximately 500 m, but could be reduced with uninterrupted coordinate logging to 80 m. If a finer resolution or degree of precision is required, the technique can be combined with electronic imaging methods reviewed here.
Finally, we recommended a field survey design combining new and old technology to provide cost-effective, yet reasonably accurate and precise results.

Key Phrases: Species discrimination from aerial sightings; surveyor bias; repeatability of measurements; spatial resolution; optimal survey parameters; ecological applications of aerial data

Key Words: Aerial survey; line transect; forage fish; sea bird; distribution

Introduction

As in other regions of the world's oceans, pelagic forage fish play an important role in the ecosystem of the northern Gulf of Alaska, yet little is known about their distribution and abundance (U.S. GLOBEC, 1996 and 1997; *Exxon Valdez* Oil Spill Trustee Council, 1998). Currently, there is a need to develop cost-effective methods for studying forage fish, their predators, and prey. Prior information about distribution of fishes is needed in order to design effective surveys to assess populations. If the exact location of fish aggregations is not known and the distribution is highly contiguous, the number or size of sampling units or transects needed to assess distribution can be large (Cram and Hampton 1976; Fiedler 1978). Ship surveys used to resolve distribution questions can be costly because they are slow, have limited access to many nearshore areas where fish may aggregate, and sonar beams (used to assess schools acoustically) are narrow and cover a small swath of water. Conversely, surveys from aircraft are relatively cost-effective because they are fast, they are not limited by shallow water, and the sampling swath in measured in hundreds of meters. In addition, aerial surveys can cover a region over a shorter period of time enabling researchers to compare distributions from two separate regions in a single temporal period.

Fishermen have used aircraft to locate schools of sardine, anchovy, mackerel, menhaden, and tuna for many years (Lo et al. 1992; Squire 1993; Hunter and Churnside 1995). In northeastern Canada, aircraft have been used to determine abundance of mature spawning capelin (*Mallotus villosus)* since 1985 (Carscadden et al. 1994). Off the California coast, data from aerial spotter pilots have been incorporated in a stock assessment program of several pelagic fish species including anchovy (*Engraulis mordax*) and sardines (*Sardinops sagax*) (Squire 1993). The Alaskan herring (*Clupea pallasi*) fisheries have long depended on aircraft for stock assessment and to guide fishing vessels (Brady 1987; Funk et al. 1995).

Many pelagic fish are arranged in shoals defined as groups of tightly aggregated schools in a given location. Shoals contain species-specific school sizes, shapes, and fish density (Mais 1974; Fiedler 1978; Smith 1978; Squire 1978; Blaxter and Hunter 1982; Hara 1985a; Misund 1993; Carscadden et al. 1994). The formation of shoals facilitates population and ecological assessments using remote sensing techniques such as aerial surveys. Distributions of herring (*Clupea sp.*) and capelin (*Mallotus villosus*) are thought to be contiguous with known areas of seasonal school aggregations unique to a particular population (Templeman 1948; Campbell and Winter 1973; Sinclair 1988; Stocker 1993). Herring schools have been described as round (Misund 1993). Capelin schools are often described as gray with dynamic crescent or U-shaped shaped schools (Carscadden et al. 1994). Anchovy schools are crescent or irregularly shaped (Squire 1978; Hara 1985a) and become more elongated at night (Hara 1985b).

Aerial surveys typically lack precision and are not sufficiently accurate to provide a stand-alone estimate of stock biomass (Krebs 1989; Gunderson 1993; Hunter and Churnside, 1995). Variability due to sighting conditions, changes in vertical distribution of fish schools, and surveyor bias largely go unmeasured (Hunter and Churnside, 1995). It is therefore important to standardize as many survey parameters, such as aircraft speed, altitude, time of day, etc., that can affect aerial estimates (Caughley et al., 1976). Thus, the main purpose of this study was to develop methodology and improve the precision of visual aerial survey estimates of surface-schooling forage fish distribution and abundance. The specific objectives were to: 1) develop an appropriate survey design incorporating estimation of detection error and surveyor bias and defining optimal survey constraints, 2) determine the accuracy of fish species and age class discrimination from visual aerial observations, 3) determine the repeatability of aerial measurements, and 4) determine the spatial resolution of aerial measurements needed to use the results in ecological analyses. A secondary objective was to develop abundance estimates for jellyfish aggregations (*Aequorea sp.*) and foraging sea birds. This study demonstrates that aerial surveys are a useful tool for ecological research of forage fish, sea birds, and other marine species. In addition, surveyors can discriminate forage fish species and produce repeatable results with an acceptable level of error. . The methods described in this report outline an efficient, cost-effective way to obtain information on the distribution and abundance of forage fish and their predators. In addition, we have identified a model and the sources of error affecting the accuracy and precision of survey results.

Methods

Survey Design, Detection Functions, and Field Data Collections

During the initial planning phase of this study, we incorporated information from fishermen and aerial surveyors (Seitz 1998) about the distribution of surface schools of fish in Prince William Sound (PWS) and the Outer Kenai, Alaska (Figure 1). They reported that the surface schools occur most frequently during the summer months (May to August). Most of the fish shoals and seabird feeding activity was reported to occur in the nearshore region (less than 1 km from the beaches). The main forage fish species reported in the summer in PWS were juvenile Pacific herring (*Clupea pallasi*) and Pacific sand lance (*Ammodytes hexapterus*). The distribution of juvenile herring in the nearshore region was confirmed by recent studies in PWS (Stokesbury et al. 1999). Capelin (*Mallotus villosus*) and eulachon (*Thaleichthys pacificus*) were reported to occur only sporadically, for a limited period in June, and only on the fringe of the study area (outside PWS adjacent to the Gulf of Alaska; Figure 1).

Using the available information about forage fish distribution, we adopted an adaptive sampling method using a modified line transect (Thompson 1992; Krebs 1989) parallel to the shoreline. We based our initial design on earlier aerial surveys of Pacific herring in Alaska that used a similar line transect survey along shorelines (Lebida and Whitmore 1985; Brady 1987). The detection of fish schools was assumed to be perfect (p=1) along the sighting angle fixed at 30° from the wing of the aircraft when level. This was equivalent to the narrow-strip transect method (Thompson 1992) based on the assumption that there was perfect detection within a maximum width (w_0) from the transect centerline. All fish spotting was done from the right side of the plane only and therefore Thompson's equation for density was modified as follows:

$$\hat{D} = \frac{y}{w_0 L} \tag{1}$$

where y is the number of fish or total surface area of fish schools spotted along the transect length L, w_0 is the maximum distance from the center line to which detectability is uniform (w_0 is equivalent to transect or swath width), and $\hat{D}$ is the estimate of fish schools or school surface area along that transect section. Within a study region with an area A, the total number of fish schools or school surface area ($\hat{\tau}$) is estimated as:

$$\hat{\tau} = A\hat{D} = \frac{Ay}{2w_0 L} \tag{2}$$

There are two limitations to the narrow-strip method. The width of the transect is limited to the area falling within the visual range when sighting at 30°. Secondly, detectability may vary by species, school configuration and by distance from the centerline (directly underneath the aircraft) of the transect. In order to avoid those limitations, we adopted a line transect model designed for aerial surveys (Quang and Lanctot 1991) that allowed variable detection and thus removed the sighting angle limitation maximizing transect or swath width (Figure 2). Quang and Lanctot (1991) outlined the following model:

$$\hat{D} = \frac{y\hat{f}(d)}{L},\ \hat{\tau} = A\hat{D},\ \hat{p} = \frac{y}{\hat{\tau}},\ \hat{C} = \frac{1}{\hat{p}} \tag{3}$$

where p is the probability of detection, and C is the visibility coefficient (commonly applied in wildlife surveys; Quang and Lanctot 1991). The parameter $f(d)$ is the correction due to variable detection where $f(x)$ is the probability density function of sightings as a measure of perpendicular distance from the centerline and d occurs at the peak of this curve where perfect detection occurs. During aerial surveys, there is generally a "blind spot" that occurs directly under and some distance to the side of the aircraft (Figure 2). In this case, the appropriate probability density function for $f(x)$ takes the form of a truncated beta curve:

$$f(x) = K_f(\alpha,\beta)\left(\frac{x-a}{b-a}\right)^{\alpha-1}\left(\frac{b-x}{b-a}\right)^{\beta-1},\ c \le x \le h,\ a \le c < h \le b,\ \alpha < 2,\ \beta > 2 \tag{4}$$

where f integrates to 1 over $[c,h]$, x is the distance from the center of the transect to the sighting, a is the left-hand limit (not observed) to the beta curve and b is the right-hand limit (not observed). The truncation of the curve due to the blind spot under the aircraft occurs at c and the right hand truncation occurs at h. In this study, the distances x were plotted as probability density functions for each of the species of interest, the beta curve was estimated, and the quantities $f(d)$ for each species were estimated from the plots.

We were concerned that we may not be observing perfect detection at $f(d)$ due to variations in water visibility, reflection, surveyor bias, and other survey conditions. If this was the case, the density equation should be further modified to include a corrected probability of detection (p_{corr}) in the following manner:

$$\hat{D} = \frac{y\hat{f}(d)}{p_{corr}L},\ \hat{\tau} = A\hat{D},\ \hat{p} = p_{corr},\ \hat{C} = \frac{1}{\hat{p}} \tag{5}$$

The corrected probability of detection (p_{corr}) was estimated by two separate methods. For first method, we compared our visual estimates to an independent data set collected in the exact same space and time. The independent data we adopted were images of schools collected along the transect line using a Compact Airborne Spectrographic Imager (CASI). The imager has no bias, has visual accuracy up to twice that of the human eye (Borstad et al. 1992), and for the purposes of this study, assumed to have perfect detection of surface schools within the image swath. The estimate and uncertainty of p_{corr} is the slope and its variance derived from linear regressions of log-transformed data on school number and size where CASI data represent the independent variable and the visual estimates the dependent. The log transformation was required to normalize the skewed distribution of shoal size (number of schools at a given location) and total school surface area.

The second method used to derive the corrected probability of detection (p_{corr}) was similar to the double counting method developed by Rivest et al. (1995) for counting deer in harvest areas. For this method, two surveyors collect counts of schools and make estimates of school surface area simultaneously from a single aircraft without communicating with one another. This method eliminates the confounding effects of variable survey conditions. The equation is given as:

$$\hat{C} = 1 + \frac{y_{.1}y_{.2}}{y_{..}(y_{.3}+1)};\ \hat{p}_{corr} = \frac{1}{\hat{C}} \tag{6}$$

where C is the correction factor (equivalent to the visibility coefficient in equation (3)), $y_{.1}$ is the total number of schools seen and the associated surface area estimates made by surveyor 1, $y_{.2}$ is the total for surveyor 2, and $y_{.3}$ is the total number of schools seen and surface areas estimates made by both surveyors (overlap in observations). A variance estimator for c having small bias in small sample sizes is given by:

$$v(\hat{C}) = \frac{y_{.1}^2 y_{.2}^2}{y_{..}^2(y_{.3}+1)^2} - \frac{y_{.2}(y_{.2-1})y_{.1}(y_{.1}-1)}{y_{..}(y_{..}-1)(y_{.3}+1)(y_{.3}+2)} \tag{7}.$$

In wildlife applications, this correction factor is often estimated for individual stratum representing areas with varying visibility (e.g. woods versus field). In this study, we pooled all observations as a single stratum. However, for future applications, stratification can be accomplished if warranted by varying ocean conditions affecting sightability.

It may be important to single out bias caused by individual surveyors. Individual bias is a measure of calibration when training for new surveyors and used for comparison of individual surveyors if more than one are involved. The actual contribution of individual bias to overall error in aerial survey results is difficult to estimate and often goes unmeasured in aerial surveys. Surveyor bias is often a function of density as counting error generally increases with counting rate (Gunderson 1993) causing most surveyors tend to undercount (Krebs 1989). It is for these reasons that a measure of survey bias is critical.

In order to establish individual surveyor bias, we used double counts and the CASI data to produce independent estimates. Using the double count data, bias was measured as a direct comparison of results from two individual surveyors to one another, in order to estimate a level of error or bias. Since both surveyors experienced the same survey conditions during each count, simultaneous double counts eliminated the confounding bias from variable survey conditions generally encountered when estimating individual surveyor bias.

The bias was estimated as the proportion of error not explained by a linear regression (SSE/SSTO) between the counts of the two surveyors or between the CASI and visual surveyor. This can be estimated by subtracting the proportion of the total variance explained by the regression (SSR/SSTO or R^2) from one.

The main data output was a measure of relative rather than absolute density of fish and jellyfish since we did not measure the ratio of surface to subsurface (not observed) schools or aggregations. However, estimating absolute densities of seabirds, specifically black-legged kittiwakes was possible. Transects were not selected randomly due to the increased sampling effort and waste of aircraft charter time. We chose, instead to over fly the entire region of interest with no "dead" air time and therefore did not attempt to expand the density estimates to areas not surveyed. In our study, the length of a transect line (*L*) was determined to be all or part of a flight path on a given day and the density of features estimated from sightings along that segment only. We sampled offshore areas when crossing bays and bodies of water to reach other shorelines (see Figure 1 for an example of the flight path) in order to test the assumption of nearshore distribution.

In summary, density or abundance estimates derived from this study were a function of: 1) effective area surveyed estimated from altitude and distance flown along a flight path or transect length, 2) the estimate of *f(d)* and p_{corr}, and 3) the actual density of the sightings along the transect line. The variance for this estimate is estimated as:

$$v(\hat{D}) = v(\frac{y\hat{f}(d)}{p_{corr}L}) + \varepsilon_I + \varepsilon_R \qquad (9)$$

error from the model and data plus an error term due to identification error for fish species or age classes (ε_I) and another error term for repeatability of measurements (ε_R). Error from the model and data was estimated for the p_{corr} term, but must be bootstrapped for the remaining terms from the sample (Quang and Lanctot, 1991) when final densities are estimated. We estimated ε_I and ε_R in the context of this study for fish schools; methods for estimation are discussed in following sections.

Fish schools were counted and their surface area was estimated using a sighting tube constructed of PVC pipe with a grid drawn on mylar on the end (Figure 3). Dimensions of fish schools were measured to the nearest tick mark on the mylar grid. The length of the tube was 197 mm, the focal length 216 mm, and the inside width 50 mm. 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:

$X = A\ ({}^{L}/{}_{F})$ (Lebida and Whitmore 1985; Brady 1987). (8)

Length and width of fish schools were measured with the sighting tube. For circular schools, the diameter was measured and the surface area calculated for a circle (πr^2). For oblong, crescent or U-shaped, or irregular school shapes, length and width were multiplied to yield the surface area of a rectangle as an estimate of school size.

We estimated the school's distance (m) from the nearest shore. We calibrated ourselves for distance estimation by flying repeatedly over objects of known dimensions or by using the sighting tube to measure ground distances.

The visual swath or transect width, dependent on altitude, was initially established in 1995. We flew repeatedly over a reference site with known distances marked (an airport runway with numbers and letters) at a series of altitudes beginning at 137 m (450 ft). In this way, the swath width was established perpendicular to the airplane. The swath width included the area that could be measured at a fixed angle of 30°. Ground reference points of known or easily measurable distances and surface areas, such as a helipad, were used to train observers to the scale on the sighting tube grid for the specific altitude flown during a particular survey.

The swath width for data analysis was recalculated after the collection of perpendicular distances from the transect centerline. After the detection curve was estimated from the distances, the swath width was recalculated as the distance between *c* and *h* specific to altitude (equation (4); Figure 2). The distances were estimated from markings on the strut off the aircraft indicating the sighting angle (from the wings). In order to record a distance, the aircraft was leveled using the gyroscope on the instrument panel, the sighting was lined up with one of the marks on the strut, and the angle recorded. The angles were used to estimate ground distances by simple geometry (Figure 2).

Aerial survey transects were flown approximately parallel to shore within a broad-scale region covering PWS and the Outer Kenai from Hinchinbrook Entrance to Nuka Point (Figure 1).

A survey of the entire area required flying 6 days, 3-6 hrs each day, in a Cessna 185 float plane at approximately 203.7 km/hr (110 knots). Areas inaccessible due to insufficient space to perform a 360° turn or weather were not sampled. The shoreline was followed in a single line but flat 360° turns were allowed when recorded feature density was high to ensure complete counts within a given swath area.

Both flight path and features along path were recorded during the survey. A log program was specially designed for the project, and run from a lap top computer during the flight. The program downloaded latitude, longitude, date and time of day in 2-second intervals from a GPS connected to the computer. At the beginning of each flight, the pilot identity, weather, water visibility, wind, wind direction, tidal stage, wave height and other notes concerning the survey were recorded. During the flight, data recorded included: "sightings" such as numbers of fish or jellyfish schools, species of fish, surface area of schools, numbers of birds or mammals, behavior of birds, or oceanographic features (tidal fronts), estimates of distance(m) to shore, and changes in altitude (needed to estimate transect width; Figure 2). For each observation, the computer logging was interrupted, the sighting noted and the approximate location linked via the program to the last latitude and longitude recorded.

For the surveys in which the CASI was deployed, two aircraft were used simultaneously to produce synoptic results. We flew the visual surveys in the Cessna 185. The CASI equipment was mounted in a Dehavilland Beaver 216GB aircraft on floats with a hole cut in the bottom of the plane for the sensor array. The surveyors in the 185 performed a reconnaissance survey setting up straight line transect passes for the CASI. Then the two aircraft flew in formation at a distance apart where the visual swath and image swath overlapped. Because the swaths did not always overlap perfectly, school locations derived from visual and CASI surveys were compared within a defined geographic region rather than for each transect.

The CASI system acquired digital multispectral imagery of fish schools (Borstad et al. 1992). The resulting images were radiometrically calibrated (Borstad Associates, Sidney, B.C., Canada, Program CVTD3_3), corrected for aircraft roll, and scaled uniformly. Because the herring schools were small, the CASI instrument was configured to acquire data with the highest spatial resolution (small pixels) possible. The number of spectral channels and the aircraft speed determined the along-track pixel length. Only three channels were used allowing a 30 msec integration time: 1 at 405-455 wavelength (nm), 2 at 460-590, and 3 at 600-675. Wide spectral bands were defined, which gathered as much light as possible while still differentiating the schools from their surroundings. On some lines, the fore optics fstop were changed from 4 to 5.6 in order to further increase the signal levels.

The settings resulted in single pixel dimensions of 0.3 - 0.5 m wide and 1 - 2 m long. With these setting only a tiny school would be represented by a single pixel (as were seabirds). For the vast majority of schools measured, the settings provided in excess of 10 pixels per school. The altitude flown affected the image swath, but generally at 305 m the CASI image was 200 m wide. In order to prevent the images from becoming too large to handle on the computer, transects were restricted to less than 10 km and preferably between 4-6 km long. During post-processing, the 8 bit unsigned images were examined and the area for each school calculated. School dimensions and statistics were obtained using a custom program designed for the CASI on a Sun-Sparc5 Unix system. A full 512 X 1900 resolution window was used to process the images. Statistics were first recorded by transect line and checked for errors. Later, sections with concentrations of schools were extracted and geocoded so they could be linked in space with the visual sightings, since the two aircraft were not always lined up perfectly to record the same features at exactly the same time.

Accuracy of Species and Fish Age Class Discrimination

The accuracy of estimates of species and age-specific density are affected by discrimination error (ε_I). To establish discrimination error, we collected over 400 validation samples over the three-year time period of this study. School validation was often a post-processing procedure matching random net catch, underwater video, or diver observations to aerial sightings by aligning geographic positions and time codes after editing. Only sand lance and herring were sampled during validation collection.

Initially, we produced estimates of error from the raw validation data set by calculating the percentage of aerial species identifications that were correct. However, this estimate did not give us a way to discriminate age classes of herring. Therefore, we used discriminant function analysis (SAS Institute 1990; Johnson and Winchern 1992) to explore if a model could produce better separation between species and the age classes than estimates from the raw data. We developed four descriptive variables: 1) total school surface area (m^2) in a given location, 2) school shape (a ratio of school length over width), 3) distance from shore (m), and 4) depth of water at the location of the school (m). We originally developed a total of four class variables with the following coding: class 1 for age 0 herring, 2 for age1-2 herring, 3 for adult herring (age 2+), and 4 for sand lance.

In order to formulate the model, the analysis was conducted in a stepwise fashion. For parametric discriminant function analysis, the assumptions of normality and independence were addressed. Box and whisker and normal probability plots revealed that each variable was highly skewed. Natural log transformations of the variables resulted in normalizing three of the variables: surface area (SA), distance from shore (DS), and depth (DW) . The three transformed variables were not significantly different (α=0.05) from a normal distribution according to Kolmogorov-Smirnov goodness of fit tests. However, school shape (SS) remained skewed with relatively high values for skewness and kurtosis (Table 1). A Box Cox procedure (Statistica 1995) was performed on the variable for shape exploring other possible transformations but no improvements in distribution were observed. The variance of the school shape variable were small compared to the other three variables for all classes (Table 1). As a result, the influence of this variable on the analysis was small in comparison to the other three. The bivariate distributions of the transformed variables were roughly elliptical or circular for all three variables except shape. The discriminant function analysis is relatively robust to minor violations of the normality assumption (Manly 1994) and we therefore decided that a parametric analysis was appropriate in this case. In order to test for independence among the four discrimination variables we constructed a correlation matrix and determined that there were no significant correlations.

The next step was to test for a difference in means for all the variables by class (Figure 4a). If there were no differences in means, the discriminant function approach would be meaningless. We used a chi-squared test for equal covariance structure of the variables between classes and determined that we could not use a pooled estimate (χ^2 =231.26, 30 d.f., $p < 0.01$) . We used the Kruskal-Wallis single factor analysis of variance by ranks (Zar 1996) to test the hypothesis that school shape, size, and depth were identical among the four classes. The results were significant ($p < 0.0001$) over all four variables (Table 2) and we therefore concluded that the four classes have different distributions across the four variables. In order to determine where the differences occurred, we used a post hoc Tukey-Kramer procedure for unequal sample sizes. There were significant differences between each pair of classes for at least one of the discrimination variables except between herring age classes 1 and 3 and classes 2 and 3 (Table 2). This was an indication that discriminating among the herring age classes might be problematic. The differences in the clustering of variable means by class (Figure 4a) indicated that discriminant analysis was appropriate for this data set (Manly 1994).

The final steps included performing the discriminant function analysis (SAS Institute, 1990). Since validations were random, we assumed that the prior probabilities adopted from the proportions of each class in the validation sample were representative of the population of schools sightings over the time period sampled. We used a jackknife procedure (Lachenbruch's holdout, Johnson and Winchern 1992) within SAS to estimate the actual error rate.

Repeatability of Measurements

To assess precision of aerial estimates affected by variability in survey conditions and fish movement (ε_R), repeat surveys over defined areas were completed. A total of 21 repeat surveys were flown over eight different areas within the study region. The time delay between surveys varied from 1 to 36 hrs. We ran separate regressions on first and second counts of school numbers and on first and second estimates of total school surface area. We used multiple regression techniques (Johnson and Winchern, 1992; Statistica 1995) to incorporate time delay as a second independent variable with either school count or estimates of total school surface area:

$$Y_i = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \varepsilon_i \qquad (4)$$

where Y is the natural log-transformed second school count or surface area estimate over i repeat count observations, X_1 represents the natural log-transformed first aerial school count or surface area estimates, β_1 is the model parameter for the first aerial count, X_2 represents the time delay, β_2 is the model parameter for time delay, and ε represents the residual error of the model. The measure of repeatability is the amount of variability in the second count explained by the multiple regression model.

Resolution of Spatial Data

We determined the minimum resolution of features sighted along the transect lines. When sightings were being recorded, coordinate logging was interrupted and the resulting time gap between coordinates was even greater. This resulted in variability in the resolution or exact locations of features. To estimate the scale of resolution, we randomly sampled approximately 1500 pairs of coordinates from the flight path data set. We also sampled the coordinates before and after each sighting resulting in a total of 4800 pairs. We estimated the linear distance (m) between each pair. The distribution of the distances sampled were skewed, but natural log transformations resulted in near normal distributions. We calculated the 95% confidence intervals for the ln-transformed distances for coordinate pairs with and without sightings, then reported on the back-transformed intervals.

Results

The study was conducted in the field during the summer months from 1995 to 1997. The total linear distance flown was 32,006 km, the average swath or transect width was 440 m, and the total area covered was 14,295 km^2. During the three-year period, there were 6756 sightings including approximately 4400 fish schools or jellyfish aggregations. Surveys were flown monthly from April to August in 1995, May through August in 1996, and June and July in 1997.

Survey Constraints and Model Parameter Estimates

Criteria were established for determining whether a survey should be flown to minimize the bias created by variable survey conditions. We did not fly if winds were over 25 knots causing white-capping, if the average ceiling (cloud cover) was below 240 m (800 ft), or on rainy days.

Initially, we flew at an altitude of 457 m as recommended for other surveys of this type (Lebida and Whitmore, 1985; Carscadden et al. 1994). We determined the species-specific school size distribution in order to evaluate the appropriate altitude as were no literature values for juvenile herring or sand lance.

The preferred altitude range was established at 274 - 366 m (900-1200 ft) based on ability to discriminate foraging seabird flocks and fish school size. There were many small schools observed less than 10 m^2 total surface area. Juvenile herring schools (modal frequency 3-50 m^2; Figure 5) were much smaller than spawning aggregations (modal frequency 100 - 300 m^2 measured in Bristol Bay; Funk et al. 1995). Therefore the initial altitude of 457 m (1500 ft) was too high to distinguish the small schools and their associated predators. An altitude of 305 m (1000 ft) provided a swath width of 325 m, using a fixed angle of 30°, allowed distinction of an object as small as a single seabird or the smallest school observed. The swath width was increased through the recalculation of the detection curve.

To estimate the detection function parameter (*f(d)*), we collected over 1500 measurements of sighting angle. Sighting angle was collected only for the three major target species for the survey: herring schools (n=345), sand lance schools (n=274), and black-legged kittiwakes (n=1019). The angle measurements were used to derive the perpendicular distances (m) to the sightings (Figure 2). We then plotted the distances in three probability density functions (pdf; Figure 6) representing *f(x)* observed by species. The sighting angles for herring and sand lance ranged from 20 to 40° resulting in right and left hand detection curve trucations of 837 and 363 m respectively. The effective swath width was estimated at 474 m for fish (Figure 2). For herring, *f(d)* was estimated at 0.32 and 0.28 for sand lance, *f(d)* both where *d* is 600. For kittiwakes, the sighting angles ranged from 10 to 45° producing right and left hand truncations at 1,729 m (*h*) and 305 m (*c*). Therefore the effective swath width for kittiwakes is quite a bit larger than for fish at approximately 1424 m. From the curve (Figure 6), the kittiwake estimate for *f(d)* was approximately 0.18 where *d* was 700 m. Any expressions of density or numbers of herring, sand lance, or kittiwakes should reflect these values in the estimates.

The first estimate of the detection correction factor (p_{corr}) was derived from the slope of linear regressions of visual versus CASI data (example image in Figure 7). The regressions were forced through the origin in order to estimate realistic parameters; an intercept term would not be inappropriate for this analysis. This correction factor was estimated for fish schools only. We denoted six 16 km square regions where both visual and CASI sightings were made (Figure 8). We then gridded each region into successively small units at 8 km, 4 km and 2 km squares in order to increase the sample size yet avoid any problems of scale. With large grids, the sample size was small and thus parameter estimation error potentially large. If our grids were too small, shoals could be bisected adding an additional source of error to our estimate. The appropriate scale would occur where parameter estimation error was minimized. Within each gird square we queried the CASI and visual data sets for total numbers of fish schools sighted and total school surface area estimated. The totals for each square then became a data point for the regression analysis. Goodness of fit tests for all four log transformed variables (visual and CASI schools counts, visual and CASI surface area estimates) were not significantly different from a normal distribution. The regressions were plotted at each spatial scale for both total school counts and school surface area per grid. The residuals of all of the regressions were not correlated to the independent variables; error did not increase with larger counts or surface area estimates. Therefore the assumption of constant variability was met. For school counts, the parameter error was minimized (cv=0.066; Table 3) at the 2 km scale with a slope estimate of 0.928. For school surface areas, error was minimized (cv=0.025) at the 16 km scale with a slope estimate of 0.998. Therefore, for density estimates based on school counts, the appropriate p_{corr} is 0.928, which is equivalent to visual undercounting of 7.8% ($1-1/p_{corr}$). For fish school surface area density estimates, p_{corr} is negligible; visual undercounting was only 0.2%.

The second estimate of the corrected probability of detection was derived from the double count data. A total of 88 double counts were performed. The estimated correction factor C for school counts was 1.375 with a variance of 0.00032 and for school surface areas estimates of 1.376 with a variance of 0.0012. These resulted in estimates for p_{corr} of 0.727 for both school counts and surface area estimates equivalent to an undercounting rate of 37.5% for school counts and 37.6% for school surface area estimates. These rates varied considerably from those derived by using CASI.

Error from surveyor bias is incorporated in the density or abundance estimates via the inclusion of the p_{corr} term in the model. However, we wanted an estimate of individual surveyor bias for future calibration and training of new personnel. A regression analysis using double counts was completed for both estimates of school counts and school size or surface area. The correlation of surveyor with surveyor for school counts was found to be highly significant ($R^2 = 0.935$; $n = 88$; $p < 0.00001$). Surveyor bias for counting schools was estimated using $1-R^2$ at 6.5%. The residuals were shown to be independent of total school count ($r < 0.0001$; $p < 0.00001$); the variance did not increase with counts. The correlation for dual estimates of surface area was also highly significant ($R^2 = 0.930$; $n = 84$; $p < 0.00001$). Surveyor bias for estimating school surface area was therefore estimated at 7.0%. As with school counts, the residual plots were shown to be independent of the magnitude of surface area ($r < 0.0001$; $p < 0.00001$).

A second independent estimate of individual surveyor bias was derived from the analysis with the CASI data. The regression coefficients (R^2; Table 3) from the CASI versus visual plots represented the amount of variance explained by the regression function. The remaining variance was a measure of visual surveyor bias. For school counts, the coefficients had similar estimation error at all scales; the 16 km scale ($R^2 = 0.909$) resulted in the lowest bias estimate at 4.0% ($1-R^2$). For surface area estimates, the 16 km scale ($R^2 = 0.997$) has the lowest estimation error and resulted in a bias of 0.3%. These bias estimates are lower than those derived from double counts.

Accuracy of Species and Fish Age Class Discrimination

Prior to estimating the error using the discriminant function procedure, we calculated an identification error rate directly from the validation data set for comparison with the multivariate model results. We also examined the basic statistics of the parameters to be used in the analysis. We collected a total of 419 validation samples; 310 were herring schools (example shown in

Figure 9) and 109 were sand lance (example in Figure 10). For herring schools, 96.1% were properly identified from the air resulting in an identification error rate of 3.9%. All of the misidentifications involved age 0+ sandlance recorded as herring schools from the air. For sand lance schools, 80.4% were correctly identified and all the errors (19.6% error rate) involved age 0+ herring misidentified as sandlance. For the identification parameters in the model, we calculated that herring were found an average of 31.8 m from shore (+/- 2.26 m 95% CI), with an average school size or surface area of 24 m^2 (+/- 3.64 m^2). Sandlance were found an average of 10.2 m from shore (+/- 1.23 m) with an average school surface area of 55.8 m^2 (+/- 7.23 m^2). In terms of school shape, the majority (87.4%) of herring schools were round (shape = 1) while the majority (81.1%) of sandlance schools were oval or irregularly shaped (shape > 1).

In the initial run of the discriminant function model, we used all four variables (school surface area, shape, distance to shore and depth) across all four species-age classes for all months sampled (Table 4). The covariances of the individual classes were significantly different from one another; therefore, quadratic methods were adopted which use within class covariance (Johnson and Wichern 1992). The estimated actual error rate from cross validation was determined to be 66.7% for age-0 herring, 16.5% for age 1-2 herring, 100% for adult herring, and 18.4% for sand lance. Because of the high error rates among herring classes, herring schools were not distinguishable by age. Therefore, herring age classes were pooled into a single class for the second run. This is consistent with the prediction from the Tukey-Kramer results (Table 2).

In the secondary run (Table 5), the means for all four discrimination variables was plotted for each of the two classes (herring and sand lance; Figure 4b). The covariances of the individual classes were once again significantly different from one another ($\chi^2 = 156.08$; d.f.=10; $p < 0.0001$, $\alpha = 0.01$) and quadratic methods were once again used. The estimated actual error rate improved with herring (class 1) misclassified at a rate of 6.8% and sandlance (class 2) at a rate of 20.2%. The 2-class model is in general agreement with the estimates of 3.9% and 19.6% identification error (ε_I) in herring and sandlance school identification from the raw data.

Due to differences in temporal staging of herring schools by age and sand lance in the nearshore waters of PWS, we re-examined the validation data considering the month of collection. Out of all the aerial fish school sightings, sandlance comprise 13.3% of the fish schools spotted (from April through August). In the validation sample set (used in this analysis), sandlance comprise 26.2% of the schools; however, the validation set includes mainly sightings from May through July with only a few for August (Table 6). The age composition of herring shifts over the summer when the new year class metamorphose from the non-schooling larval stage to the schooling juvenile stage starting in July (Stokesbury et al. 1998; Table 6). In May and June, age 1-2 herring comprise the majority of surface schools sampled, adult herring are present and no age 0 were caught. Sand lance were not caught until June. The situation changed dramatically in July when aproximately half of the schools sampled were age 1-2 herring, age 0 herring were caught and a few adults. The occurrence of sand lance increased dramatically from June. In August, about 90% of the schools were split between age 0 herring and sand lance; a few age 1-2 herring schools remained to be sampled but no adults. This result is consistent with the observation that during August, age 1-2 herring migrate out of nursery bays adopting a more pelagic adult herring distribution; they are found in deeper, offshore areas at this time (Stokesbury et al. 1999).

The difference in species and age composition over the four months sampled is evident in the results of a Kruskal-Wallis test (Statistica 1995; Table 6) and plot of the means (Figure 11) where differences in the rankings of the four discrimination variables were compared by month. Log transformed school surface area, distance from shore, and depth were significantly different among months ($p < 0.0001$). However, there was not a significant difference in school shape among the months ($p = 0.84$). A post hoc Tukey-Kramer test was also performed illustrating that surface area of schools in May differs significantly from all other months ($p < 0.002$; Table 7). Distance from shore differs in July as compared to May ($p = 0.019$) and June ($p = 0.0008$), and depth in May differs from June and July ($p < 0.00001$). There was insufficient sample size by month for each of the herring age classes and sand lance validations over the four discrimination variables to run the discriminant function analysis by month. Therefore, the information about how distribution varies with month together with the monthly information about herring age composition and sand lance occurrence should be used to interpret the aerial survey results appropriately. This information comes directly from the validation data rather than a model.

Repeatability of Measurements

A multiple regression with time delay incorporated as a second independent variable explained the highest degree of error in repeat counts. Time delay was not significantly related to either the first count of numbers of schools or estimates of total school surface area. Therefore, multi-colinearity was not a problem in this model. Both regressions (school count and total surface area) were highly significant ($p<0.001$).

We estimated the parameters for the regression model with repeat counts of school numbers (equation (4)):

$$\text{repeat count} = 0.46 + 0.975 * \text{initial school count} - 0.0.29 * \text{time delay (hrs)} + \varepsilon_i .$$

Both regression coefficients were significant at the 5% level ($p < 0.001$ and $p = 0.02$ for the total count and time delay parameter respectively). The first school count explained the majority of the error in the second or repeat count. The adjusted R^2 was 0.854 and the error of repeat school counts were determined to be 14.6% ($1-R^2$; $\square_R$). In this case, adding time delay to a simple regression model of first and second counts resulted in explaining an additional 3.6% of the total variability (R^2 without time delay was 0.789).

The parameters for the regression model with repeat estimates of total school surface area were:

$$\text{repeat surface area} = 0.940 + 0.929 * \text{initial school surface area} - 0.047 * \text{time delay (hrs)} + \varepsilon_i .$$

As with counts, both regression coefficients were significant at the 5% level ($p < 0.0001$ and $p=0.036$) and the initial estimate explained the majority of error in the second. The adjusted R^2 was 0.817 and the error of repeat school surface area estimates was determined to be 18.3% ($1-R^2$). Adding time delay to a simple regression resulted in explaining an additional 3.0% of the total variability (R^2 without time delay was 0.787).

In both models, the residuals were not correlated with either independent variable.

Resolution of Spatial Data

It was important to understand the spatial resolution of our data in order to use it for spatial ecological analyses. We determined the minimum spatial scale by looking at the time delay between logged coordinates during sightings. The mean time delay between coordinates associated with sightings was 11.81 seconds and the 95% confidence interval fell between 11.63

and 11.99. This corresponded to a resolution along the transect line of 500 m with a 95% confidence interval between 492 and 508 m. In comparison, the mean time delay between coordinates along the flight path uninterrupted by sightings was 1.88 seconds (95% confidence interval between 1.84 and 1.92 seconds). The mean distance between logged flight path coordinates was 83 m with a 95% confidence interval between 81 and 85 m. Therefore, the minimum spatial scale appropriate for analysis using our aerial survey data is 500 m along the transect line.

Discussion

In the development of this methodology, we were able to overcome or account for many of the shortcomings that occur with aerial surveys. Our survey design most resembled the traditional aerial surveys designed for stock assessment of adult herring at spawning regions prior to the execution of a fishery (Lebida and Whitmore, 1985; Brady 1987) except that we incorporated a detection function and identified the sources of error. Using a mixture of traditional and more recently developed methods, we were able to cover a large region (was 14,295 km^2), collect a large amount of data (6756 sightings; 4400 fish schools or jellyfish aggregations), and account for error for a low relative cost.

Survey Constraints, Parameters, and Detection

There are variable survey conditions that can greatly affect survey results (Caughley et al., 1976). Many of the sources of bias resulting from variable weather and sighting conditions can be avoided simply by establishing the minimum guidelines. Other conditions, such as silt from river runoff and zooplankton blooms that impact water column visibility, cannot be avoided and remain a shortcoming of this methodology. Preferred altitude and visual swath are parameters that are specific to a survey depending on the survey goals and can be established satisfactorily.

In Alaska during the summer (June and July), the sun angle exceeded 20° for an entire 12 hr survey window per day so we did not feel it was an important factor. At a similar latitude, Carscadden et al. (1994) preferred sunny days with the sun angle between 20° and 45° in order to reduce glare and lands shadows for aerial photography of capelin schools. However, if our surveys were to be conducted during spring of fall months, light angle should be an important consideration and flights should be scheduled when the sun angle exceeds 20°.

The establishment of a preferred tide stage is a future task. There are many studies on vertical distribution of fish schools from day to night and how that might affect aerial survey results (Mais 1974; Squire 1978; Hampton et al. 1979). However, there are very few on the effects of tide on aerial detection. The forage fish we studied were most often found close to shore, the tidal range is PWS is large, and kittiwake foraging bouts (feeding on herring and sand lance) coincided with the tides (personal communication, Robert Suryan, U.S. Fish and Wildlife Service, Migratory Bird Division, Anchorage, Alaska). An increase in the number of repeat surveys over a given region is needed to test the affects of tide conclusively.

This is the first time that a detection curve has been estimated for forage fish schools. Probabilities of detection are most often found in aerial survey papers regarding wildlife (Quang and Lanctot 1991; Seber 1982). It was interesting to note, that as in aerial surveys of wildlife, the detection function for our two forage fish species is best described as a beta curve. We do recommend that during each field season, sighting angles are collected for a large number (over

200) of each of the key species involved in order to adjust the detection parameter (*f(d)*) if needed.

The estimates of the corrected probability of detection (p_{corr}) from the CASI results were very encouraging. The results of 7.8% undercounting of schools by visual observers versus 0.2% for estimations of surface area are relatively low. Rates ranging from 23-89% have been estimated for aerial wildlife surveys (Caughley 1974; Quang and Lanctot 1991). The disparity in the rate of undercounting for the two indices in our study is understandable. If many small schools are present that may not represent a large amount of school surface area, it is likely that the visual observer will miss a few. However, it is unlikely that the visual observer would miss any large schools that may represent the bulk of the school surface area or biomass in a given region.

The estimate of p_{corr} from the double count data were less encouraging. Our undercounting rates of 37.5% and 37.6% for school counts and surface area estimates respectively are more in line with what was found with surveys of wildlife. Our estimates of the correction factor c (1.375 and 1.376) are in the high end of the range of those estimated for aerial counts of deer sighted under different conditions (1.009 – 1.482; Rivest et al. 1995). One possible explanations for the increase in the undercounting rate is the inclusion of error and bias from two surveyors rather than one. Another explanation is that double counts were performed over the three-year period and during all months surveyed in comparison to the CASI surveys that were conducted in a compressed period of 10 days in a single month for one year only. A third explanation is that the double count data in this study include 5 individuals of varying experience where as the CASI surveys included only one individual's visual counts. Therefore, the double count data include a wider variety of survey conditions as well as error from multiple surveyors.

The estimates of individual surveyor bias from the double counts (6.5% for school counts and 7.0% for school surface area estimates) are generally smaller than those reported for wildlife aerial surveys that range from 10 to 30% (Krebs 1989; Caughley et al. 1974; Harris and Lloyd, 1977; Rivest et al. 1995). The estimates of bias from the CASI survey were even. Harris and Lloyd (1977) reported a bias of 10% using a similar method of comparing aerial visual counts to photographs of sea birds. The individual surveyor bias estimates from either method are comparably less than those estimated for surveys of wildlife and probably contribute a minor amount of uncertainty to the abundance estimates compared to other sources of variability. Either way, the inclusion of the p_{corr} term in our model accounts for error due to surveyor bias.

The decision to use CASI or double counts to estimate of p_{corr} and surveyor bias may lie in the consideration of cost. The parameters estimated using CASI result in more conservative estimates of abundance and are probably more accurate due to the lack of bias on the part of the imager. However, it is not possible to conduct a CASI survey for each individual. On the other hand, double counts are cost-effective since the only requirement is that a second surveyor join the survey. The lowered costs and improvements in resolution of digital video may enable us to replace CASI with color video, but the image post-processing costs are still high. In addition, if these surveys continue, the individual surveyors involved are likely to change and more double counts will be required for training. Our recommendation is to use the estimates from double counts because we feel that the advantages outweigh the disadvantages.

Variance estimators are available for density and total abundance accounting for variance in the corrected probability of detection (p_{corr}; Rivest et al. 1995) but are generally applicable for cases where sightability is constant. Since we include a detection function and sightability varies, it is probably more appropriate to obtain estimates for density and abundance via bootstrapping (Quang and Lanctot 1991). We did not make those estimates within the scope of this study but recommend that variance is estimated for biological interpretation of the field results.

Species Discrimination

Foraging and reproductive success of predators dependent on forage fish is often species and age-specific due to varying energy content of the prey (Hamer et al. 1993; Hunt et al. 1996; Van Pelt et al. 1997; Romano et al. 1998; Anthony et al. 1998). Therefore, species and age class discrimination is likely to be an important task for the use of aerial survey data in ecological analyses. Our estimates of identification error are relatively negligible for herring ($\varepsilon_I = 3.9\%$) but quite a bit larger for sand lance (19.6%). Because species and age composition vary on a monthly basis, but also on an annual basis reflecting variation in recruitment, it is recommended that validation samples be stratified temporally to aid in the interpretation of aerial survey results. Increased sampling effort will result in increased precision or a reduction of the estimated error rates whether they are calculated directly from the validation data set or modeled using discriminant function analysis. In July, when sand lance become more abundant and intersperse with age 0 herring, error in identification very likely increases. Validation effort should be directly in regions where the two species overlap. Increased sampling may also result in additional species added to the model. This is a desirable goal as capelin (*Mallotus villosus*) and eulachon (*Thaleichthys pacificus*) were observed from the air, there were indications that they were important seabird prey (Personal communication, Dr. Daniel D. Roby, Oregon State University, Corvallis) and there is currently very little known about the two forage species.

For herring, the situation of age class discrimination is problematic. It was disappointing that herring age classes could not be discriminated by the model, a situation that would probably not improve with increased sample sizes for age-0 and adult herring. However, if sufficient numbers of schools sighted from the air are sampled, the age composition of catches by region can be applied to the total monthly estimates of herring within those same regions. Also, since the majority of herring schools sampled were juveniles (age-1 or age-0), we feel that our results do address study objectives concerning trends in distribution and abundance of young herring.

Future analyses of the relationship between aerial sightings and the depth distribution of herring by age and size from acoustics will enable us to better understand the shift in age composition of surface schooling herring. We can also use herring and sand lance school density estimates from acoustics to expand aerial estimates of surface school abundance to regional biomass estimates.

In conclusion, it appears that herring and sandlance can readily be discriminated from the air. The inclusion of a discriminant function model did not improve estimates of species identification error rates due to the lack of ability to discriminate age classes or herring and to the species-specific temporal variability in occurrence. With appropriate catch sampling, results from aerial surveys can be used to gage annual shifts in distribution and abundance of the two species and used to examine ecological factors affecting those shifts on a broadscale.

Repeatability of Measurements

There is a paucity of discussion about repeatability of measurements in the aerial survey literature. The multiple regression analysis performed for this study was the first step toward accounting for the contribution of error from variation in replicate counts. The parameters associated with the initial count were close to one explaining a large proportion of the error. Probably both surveyor bias and natural variability, due to changes in vertical distribution of fish schools and randomness, contribute to this error. On the scale of 24-36 hrs, error from repeatability (ε_R) (14.6% for school counts and 18.3% for surface area estimates) could be reduced by our estimates of surveyor bias (6.5% and 4.0%) justifiably. Otherwise, the estimation of overall abundance indice error (equation (9)) will be overestimated due to the inclusion of suveyor bias error in p_{corr} as well.

Over longer temporal scale, we would expect that movement of schools would contribute a larger proportion of error to repeatability measurements. This could be investigated by comparing our results with synoptic acoustic surveys. We also suspect that our error rate not only varies with season, but by fish species and age as well since it is highly likely that vertical fish migration rates vary according to those three parameters. However, our sample size was too small to discern the effects of any of these factors. We therefore recommend that repeat counts continue to be conducted over a portion of any given study area, stratified over the temporal range of the study. The result would be species- and season-specific error rates, which could be, applied to total abundance estimates. With a larger sample size, the effect of tide on repeatability could be examined as well.

Resolution

It is very important that the scale of resolution be established prior to any use of aerial survey results in ecological analysis. In our case, our along transect resolution is on the order of 500 m but could be reduced to close to 80m along the transect if coordinate logging were not interrupted. For analyses of broadscale or meso-scale processes, such as regional changes in seabird foraging patterns in relation to fish distribution or abundance, our current resolution is adequate. For finer scale analyses, such as the analyses of school spacing to abundance or habitat characteristics, it would be necessary to incorporate some method of imaging along the flight path (video or CASI). In the future, we will adopt a logging program that is not interrupted during the recording of sightings to improve the resolution of scale.

Aerial versus Ground Survey Methodology and Recommendations

There are several advantages of aerial methodology over typical ground (acoustic or net) surveys of fish abundance. A large area can be covered in a shorter period of time and cost less than a survey conducted from vessels alone. Fish do not avoid aircraft but can be affected by vessels impacting acoustic survey results (Cram and Hampton, 1976). Logerwell and Hargreaves (1996) found a negative relation to forage fish, sampled with nets, and sea bird density due to fish avoidance of the nets. Forage fish are often in shallow or non-navigable waters where vessels, acoustics and nets cannot reach. Finally, our survey results are perfectly suited for a broad array of ecological analyses since they include not only information on forage fish species, but also associated jellyfish, seabird and marine mammal distributions.

The data from our survey method is of immediate use for ongoing research on forage fish abundance and distribution (Duffy 1998). However, there are many other uses for the data. Information about species distribution overlap of herring and sandlance can be extracted. We can overlay the broad- and meso-scale distributions with ocean conditions. We can detect seasonal and spatial changes in bird and mammal foraging on fish schools. This information may give sea bird and marine mammal researchers insight as to changes in diet, condition and reproductive success of their respective study animals. It can specifically provide insight as to when prey switching occurs for birds. An example is our observation of prey switching by kittiwakes from late May to early June in 1996. A reduction in kittiwakes associated with fish schools spotted from the air coincided with an increase in association with streams with out migration of salmon fry from streams in eastern PWS.

Aerial survey methodology has improved dramatically in the past 10 yrs. Access to military technology has lead to improvements in accuracy and identification of sources of error (Hunter and Churnside 1995). Unfortunately, this equipment is still relatively expensive to use and often requires highly trained staff to operate. The use of GPS, high resolution and night vision cameras, and remote sensing devices (Nakashima and Borstad 1993) such as LIDAR (LIght Detecting and ranging derived by Analogy from Radar; Oliver et al. 1994; Churnside et al. 1997; Lo et al. 1999) and CASI (Borstad et al. 1992) have allowed researchers more precision in mapping features, calculations of visual swath, and have resulted in unbiased survey estimates (Hunter and Churnside, 1995). New three-chip digital video cameras are also being used to image fish schools for aerial assessments (personal communication, Brian Nakashima, Canadian Department of Fisheries and Oceans, St. John, Nova Scotia). However, even with video images, post-processing costs can be high due to the sheer volume of images. The methods outlined for this survey are less expensive due to lower technology, but have associated problems of surveyor bias and detection error. We suspect that the most cost-effective yet sufficiently accurate monitoring tool available may be a combination of a broadscale survey using the techniques described in this report paired with a smaller scale acoustic survey and digital videography in areas with high fish and seabird density. This is a similar recommendation to Cram and Hampton (1976) concerning the combined use of aerial and acoustic techniques. The cost of collecting validation samples can be reduced through the use of underwater videos operated from vessels in lieu of net catches.

We conclude that reasonably accurate estimates of density and abundance of forage fish schools and sea birds can be obtained by our methods. The variance of the density estimates will be mainly influenced by the actual variability of occurrence since the variance of the corrected probability of detection p_{corr} is so low. The additional contribution of error from identification and repeatability of measurements is species and indice specific. For herring the additional error for schools counts, 12 - 18.5%, and surface area estimates, 15.2 – 22.2%, should be applied depending on whether or not surveyor bias is removed. For sand lance, the additional error is 27.7 – 34.2% for school counts and 30.9 – 37.9% for school surface area estimates.

Acknowledgments

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Table 1. Descriptive statistics for natural log transformed data including 4 class variables and 4 discrimination variables: school shape (SS), school surface area (SA), distance of school from shore in meters (DS), and depth of the water at the location of the school in meters (DW). The valid n for the sample is in parentheses.

Variable	Mean	Variance	Skewness	Kurtosis
CLASS 1: Age 0 Herring (36):				
SS	1.017	0.011	6.000	36.000
SA	3.827	0.236	-0.284	-0.284
DS	3.961	0.384	0 .051	1.774
DW	3.797	1.973	-0.339	-1.313
CLASS 2: Age 1-2 Herring (249)				
SS	1.166	0.192	2.644	5.970
SA	4.714	1.758	0.249	-0.181
DS	4.020	1.134	0.196	-0.714
DW	4.166	2.094	-0.934	0.007
CLASS 3: Adult Herring (25)				
SS	1.053	0.070	5.000	25.000
SA	3.953	1.421	0.181	-0.230
DS	3.867	1.051	0.164	-0.485
DW	3.691	1.575	-0.347	-1.184
CLASS 4: Pacific Sandlance (110)				
SS	1.415	0.538	2.096	5.420
SA	4.374	1.489	-0.453	0.113
DS	3.273	0.659	0.677	0.104
DW	3.576	0.550	0.212	-0.08

Table 2. Results of the Kruskal-Wallis and Tukey-Kramer tests for differences among the four fish classes (1=age 0 herring, 2=age 1-2 herring, 3=adult herring, 4=sand lance) over the four log transformed discrimination variables: school shape (SS), school surface area (SA), distance of school from shore in meters (DS), and depth of the water at the location of the school in meters (DW).

	K-W test statistic and p-value (3 d.f.; n = 420)	**p-value for significant T-K class comparisons by variable**
SA	24.69, p=0.0000	1&2; p=0.019, 2&4; p=0.006
SS	165.02, p =0.000	1&4, 2&4, 3&4; p<0.00001
DS	44.31, p =0.0000	1&4; p=0.019, 2&4; p<0.00001
DW	36.52, p =0.0000	2&4; p=0.0006

Table 3. Estimation of the model parameter p_{corr} from the slope (β_1) and of surveyor bias from the regression coefficient (1-R^2) of the linear relationship between log transformed CASI versus visual surveyor school counts and school surface area estimates at the four different gridded units. The standard error and coefficient of variations of the estimates are also given. The estimates with the lowest estimation error are in bold.

Unit Scale	β_1	se β_1	cv	R^2	se R^2	cv	Bias (%)
School Counts:							
16 km	0.980	0.090	0.092	**0.960**	**0.835**	**0.870**	**4.04**
8 km	0.953	0.081	0.085	0.909	0.789	0.868	9.14
4 km	0.940	0.069	0.073	0.883	0.822	0.931	11.73
2 km	**0.928**	**0.061**	**0.066**	0.861	0.752	0.873	13.95
School Surface Area:							
16 km	**0.998**	**0.025**	**0.025**	**0.997**	**0.408**	**0.409**	**0.30**
8 km	0.972	0.063	0.085	0.909	1.175	1.245	5.60
4 km	0.952	0.061	0.064	0.907	1.456	1.606	9.35
2 km	0.945	0.054	0.057	0.892	1.384	1.551	10.79

Table 4. Discriminant function analysis results (SAS Institute, 1990) using four fish classes over the four log transformed discrimination variables: school shape, school surface area, distance of school from shore in meters, and depth of the water at the location of the school in meters.

419 Observations	418 d.f total
4 Variables	415 d.f within classes
4 Classes	3 d.f. between classes

Class	n	Prior probability (from n)
1-Age 0 Herring	36	0.086
2-Age 1-2 Herring	249	0.594
3-Adult Herring	25	0.060
4-Sand lance	109	0.260

Cross-validation Results using Quadratic Discriminant Function:

Number of Observations / Percent Classified into class:

	1	2	3	4	Total
From class:					
1	12	23	0	1	36
	33.33	63.89	0.00	2.78	100.00
2	20	208	0	21	249
	8.03	83.53	0.00	8.43	100.00
3	5	17	0	3	25
	20.00	68.00	0.00	12.00	100.00
4	1	19	0	89	109
	0.92	17.43	0.00	81.65	100.00
Total	38	267	0	114	419
Percent	9.07	63.72	0.00	27.21	100.00

Error Rate Estimates by Class:

1	2	3	4	Overall Error Rate
0.667	0.165	1.000	0.184	0.263

Table 5. Discriminant function analysis results (SAS Institute, 1990) using two fish classes over the four log transformed discrimination variables: school shape, school surface area, distance of school from shore in meters, and depth of the water at the location of the school in meters.

```
                Discriminant Analysis

      419 Observations      418 DF Total
        4 Variables        417 d.f. within classes
        2 Classes            1 d.f. between classes

Class                n     Prior Probability (from n)

1-Herring          310            0.740
2-Sand lance       109            0.260

Cross-validation Results using Quadratic Discriminant Function:

  Number of Observations and Percent Classified into Class:
                     1           2          Total
From Class:
 1                 289          21          310
                 93.23        6.77       100.00

 2                  22          87          109
                 20.18       79.82       100.00

Total              311         108          419
Percent          74.22       25.78       100.00


              Error Rate Estimates by Class:

                  1           2     Overall Error Rate
     Rate       0.068       0.202        0.103
```

Table 6. Variations in percentages of herring age classes and fish species caught by month for validation. Results of the Kruskal-Wallis and Tukey-Kramer tests for difference among the four months sampled over log transformed discrimination variables: school shape (SS), school surface area (SA), distance of school from shore in meters (DS), and depth of the water at the location of the school in meters (DW) (Statistica, 1995).

Month:	**May (5)**	**June (6)**	**July (7)**	**August (8)**	**All Months**
Sample Size:	**62**	**133**	**194**	**31**	**424**
Fish Classes:					
All Herring	**100.0%**	**76.7%**	**66.5%**	**54.8%**	**73.8%**
Age 0	0	0	11.3%	45.2%	8.6%
Age 1-2	87.1%	68.4%	52.1%	9.7%	59.3%
Adult	12.9%	8.3%	3.1%	0	6.0%
Sand lance	**0**	**23.2%**	**33.5%**	**45.2%**	**26.2%**

Variable	**K-W statistic and p-value** (d.f. = 3; n=424)	**p-value for significant T-K monthly comparisons**
SA	28.84, p < 0.0001	5&6, p=0.001; 5&7, p = 0.0009; 5&8, p<0.0001
SS	0.84, p =0.84	n.s.
DS	27.49, p < 0.0001	5&7, p=0.19; 6&7, p=0.0008
DW	43.36, p < 0.0001	5&6 and 5&7, p<0.00001

Figures

Figure 1. The location of the study area on the south central coast of Alaska including Prince William Sound and the Outer Kenai; an example of the flight path (grey line) from a single broadscale survey (6 d) and the resulting fish school distribution (circles) for July of 1995 is shown.

Figure 2. A diagram of aircraft sighting angles, the geometric transformation to distance (m) along the ground, and an example of the transect or swath width as calculated as the distance between *c* and *h*.

Figure 3. Diagram of the sighting tube and the mylar grid with tick marks for measurements of schools.

Figure 4. Mean values of the four log transformed discrimination variables used in the discriminant function analysis for the four class model (a) and the two class model (b).

Figure 5. The probability density functions of the detection curves with the x-axis as perpendicular distances (m) to the sighting from the center of the transect line and the function value (*f(d)*) at *d* for herring (a), sand lance (b), and kittiwakes (c).

Figure 6. Modal frequency distribution of herring and sand lance schools sizes observed from the air and validated via net catches or other means.

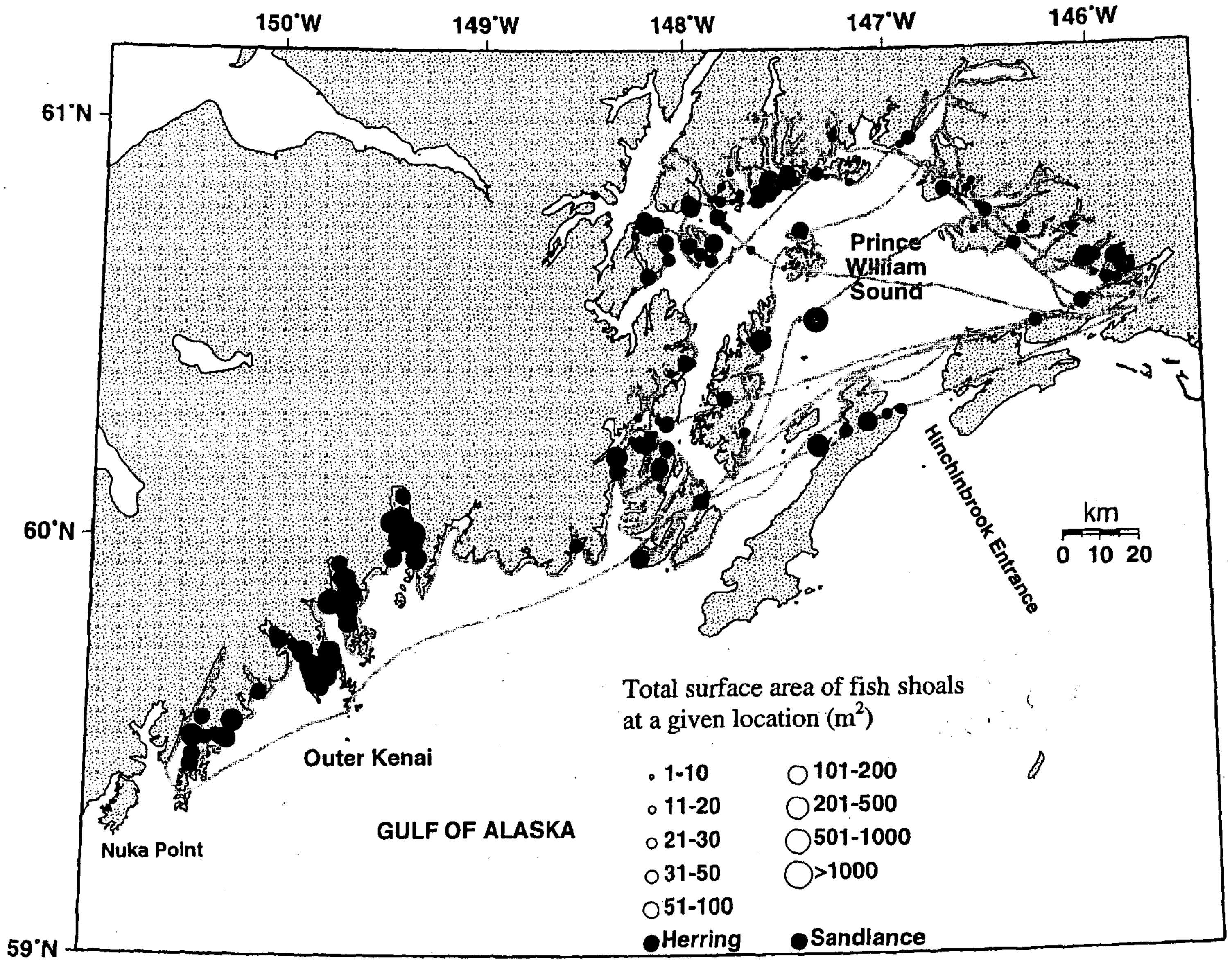
Figure 7. Images from the compact airborne spectrographic imager (CASI) system. The images have not been corrected for pixel distortion and appear compressed laterally as a result. The left image is herring schools and the right image is sandlance schools. The white spots in both images are individual kittiwakes.

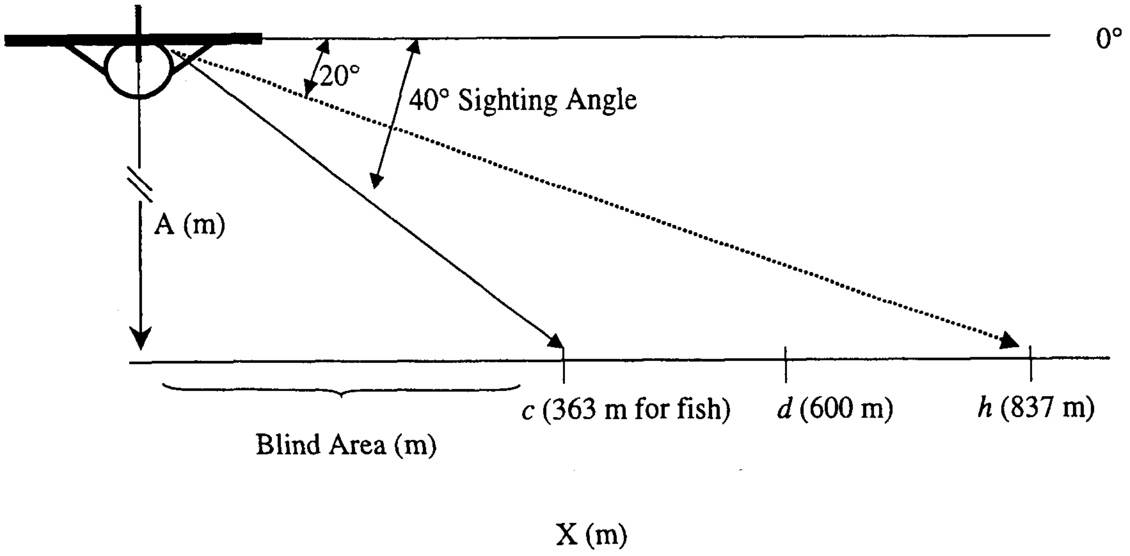
Figure 8. Six 16 km regions in Prince William Sound where both CASI and visual observations were made.

Figure 9. Two circular age-1 herring schools in a shallow embayment in southwestern Prince William Sound, Alaska. The white spots are kittiwakes resting on or near the schools.

Figure 10. A crescent shaped age-0 sand lance school in shallow water in northeastern Prince William Sound (validated with underwater video mounted on the *R/V Predator* shown in the photo).

Figure 11. Mean values of the four log-transformed discrimination variables by month.


150°W
149°W
148°W
147°W
146°W
61°N
60°N
59°N
Prince William Sound
Hinchinbrook Entrance
km
0 10 20
Outer Kenai
Nuka Point
GULF OF ALASKA
Total surface area of fish shoals at a given location (m^2)
1-10
11-20
21-30
31-50
51-100
101-200
201-500
501-1000
>1000
● Herring
● Sandlance



Transect Width (swath) = *h* - *c* = A[Tan(90-20°)-Tan(90-40°)]; at 305 m altitude, width = 474.2 m for fish schools

Figure 2

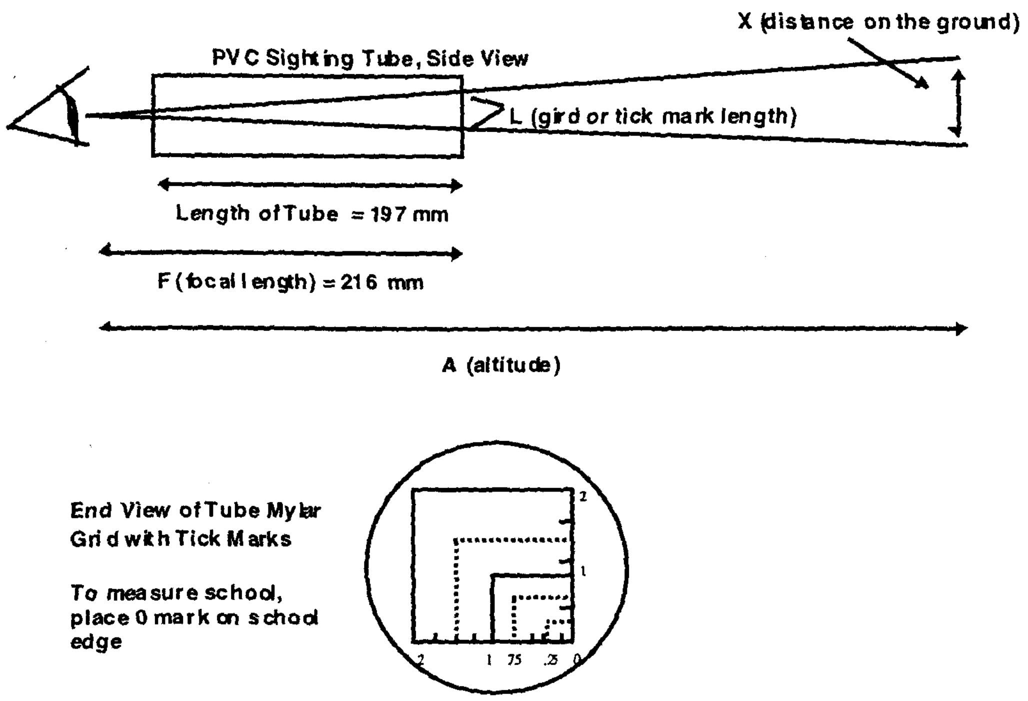

X (distance on the ground)
PVC Sighting Tube, Side View
L (gird or tick mark length)
Length of Tube = 197 mm
F (focal length) = 216 mm
A (altitude)
End View of Tube Mylar Grid with Tick Marks
To measure school, place 0 mark on school edge
2
1
2
1
75
.25
0

Figure 3

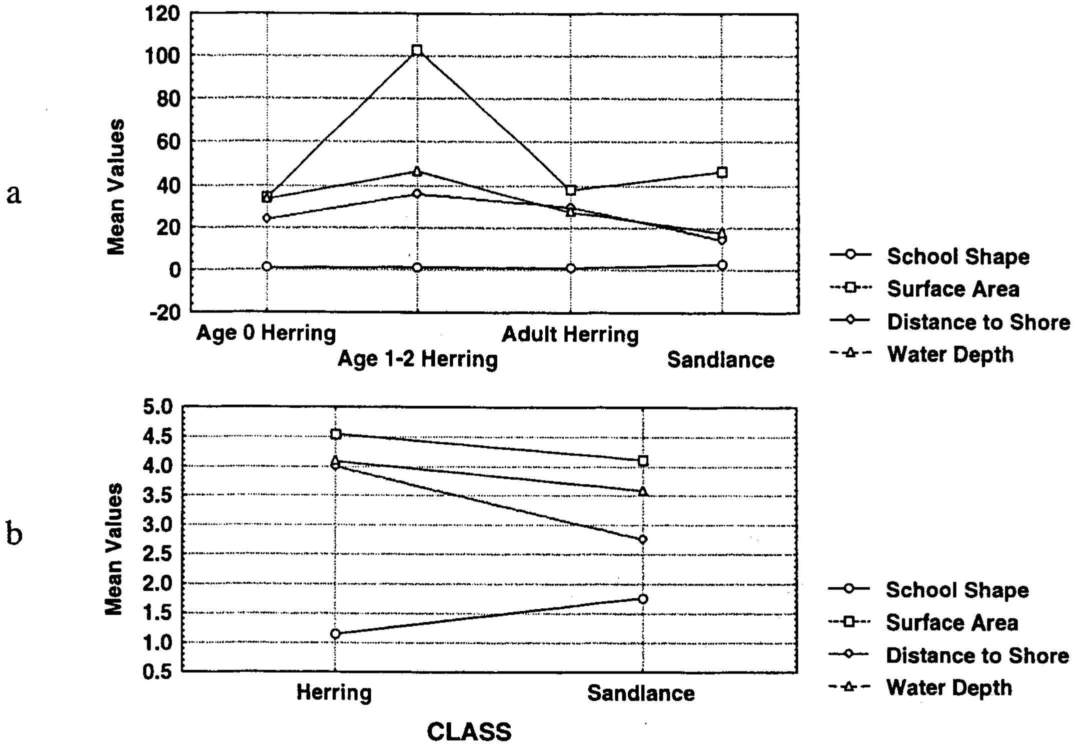

a
120
100
80
60
40
20
0
-20
Mean Values
Age 0 Herring
Age 1-2 Herring
Adult Herring
Sandlance
School Shape
Surface Area
Distance to Shore
Water Depth
b
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
Mean Values
Herring
Sandlance
CLASS
School Shape
Surface Area
Distance to Shore
Water Depth

Figure 4

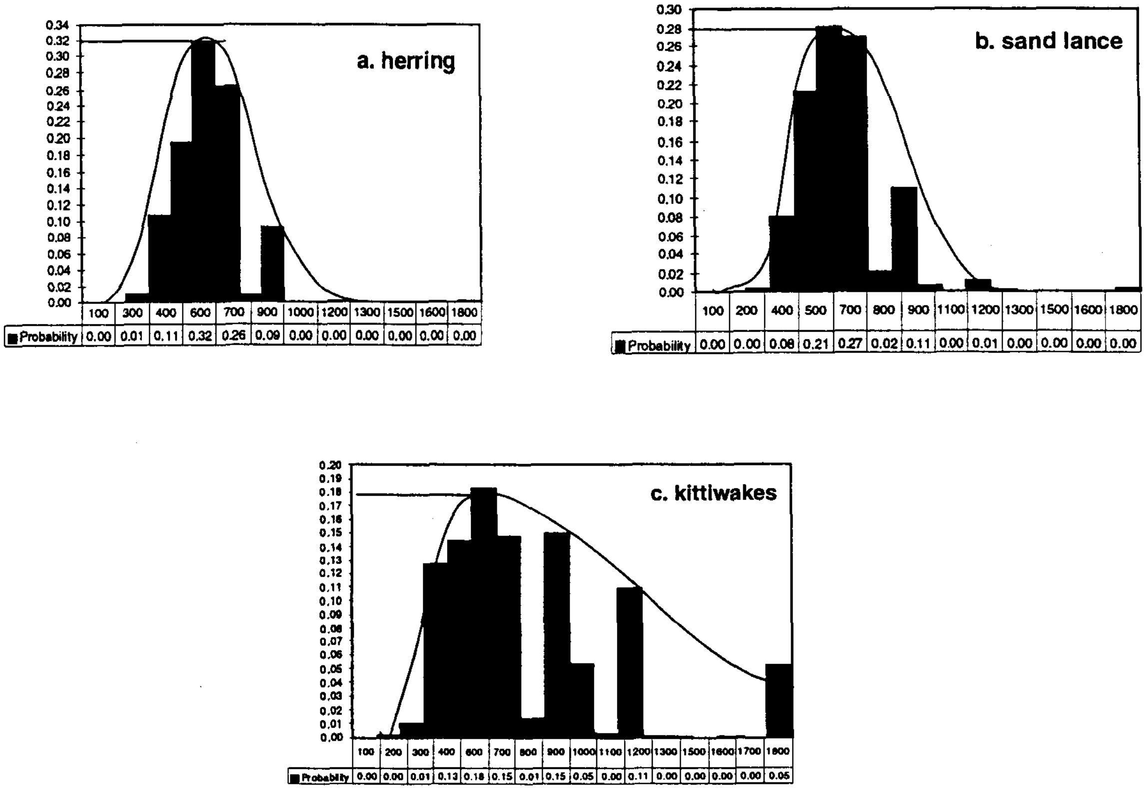

a. herring
0.34
0.32
0.30
0.28
0.26
0.24
0.22
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
100 300 400 600 700 900 1000 1200 1300 1500 1600 1800
Probability 0.00 0.01 0.11 0.32 0.26 0.09 0.00 0.00 0.00 0.00 0.00 0.00
b. sand lance
0.30
0.28
0.26
0.24
0.22
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
100 200 400 500 700 800 900 1100 1200 1300 1500 1600 1800
Probability 0.00 0.00 0.08 0.21 0.27 0.02 0.11 0.00 0.01 0.00 0.00 0.00 0.00
c. kittiwakes
0.20
0.19
0.18
0.17
0.16
0.15
0.14
0.13
0.12
0.11
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
100 200 300 400 600 700 800 900 1000 1100 1200 1300 1500 1600 1700 1800
Probability 0.00 0.00 0.01 0.13 0.18 0.15 0.01 0.15 0.05 0.00 0.11 0.00 0.00 0.00 0.00 0.05

Figure 5

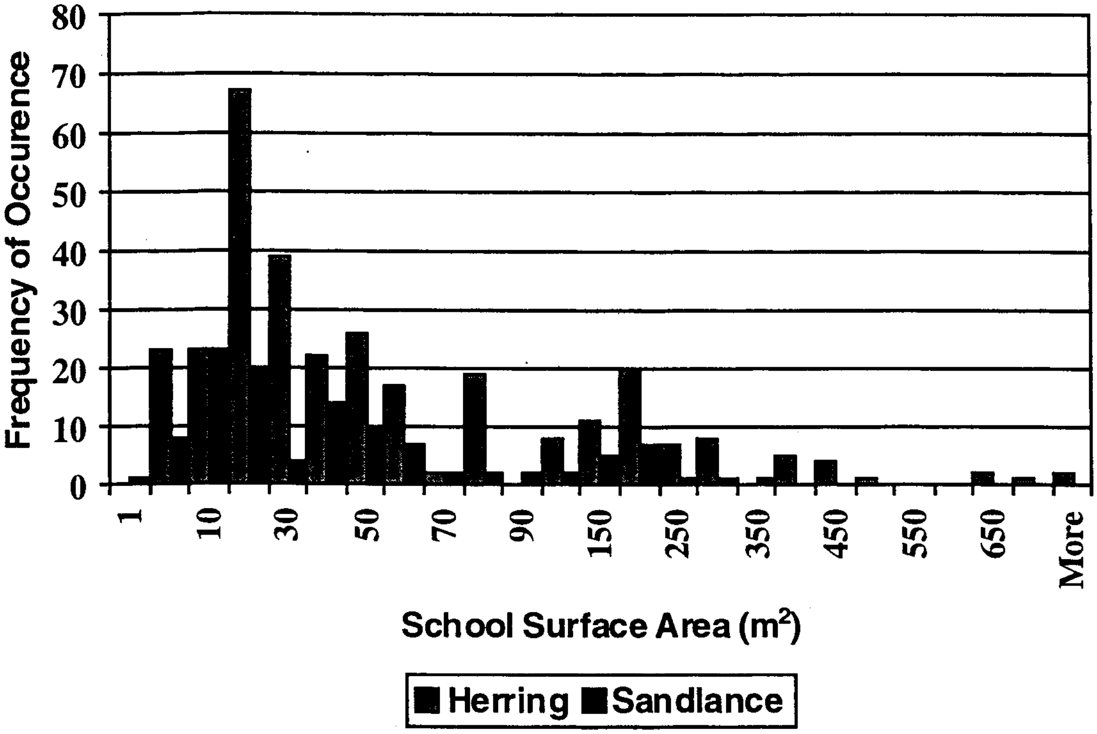
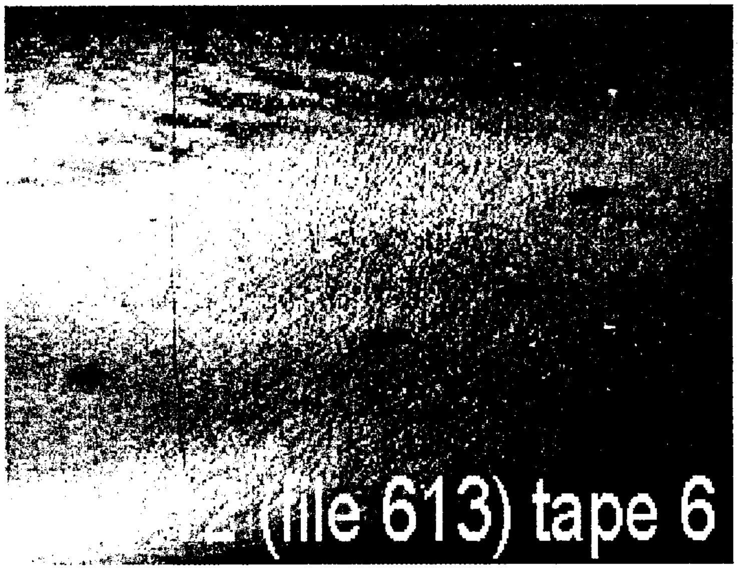
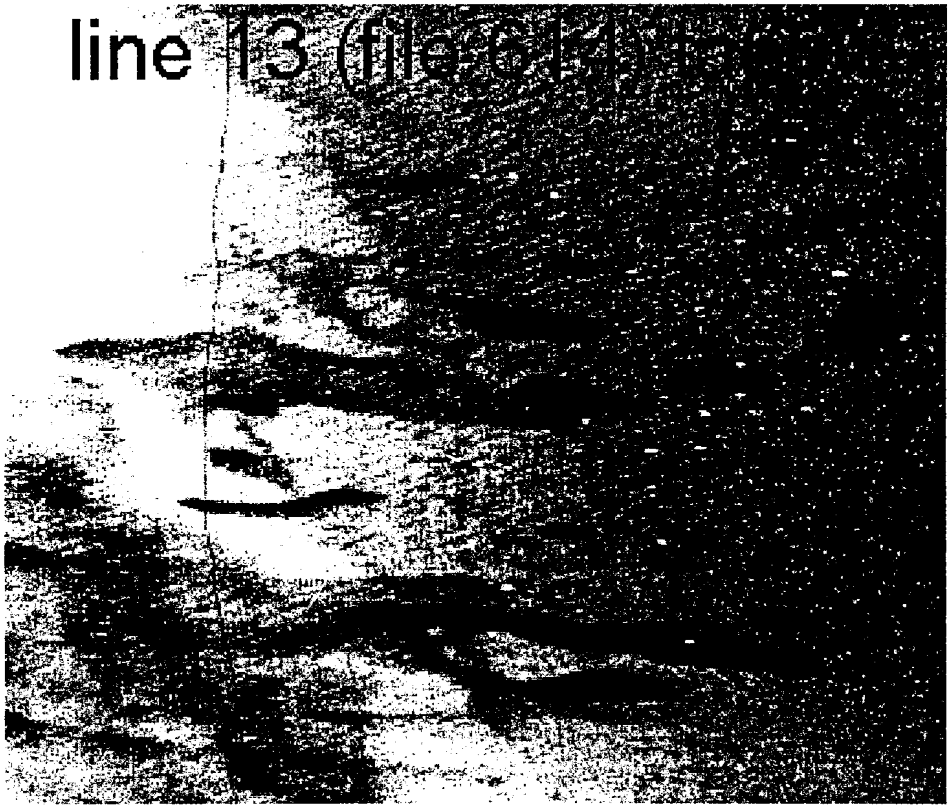

80
70
60
50
40
30
20
10
0
Frequency of Occurence
1
10
30
50
70
90
150
250
350
450
550
650
More
School Surface Area (m²)
Herring
Sandlance

Figure 6


(file 613) tape 6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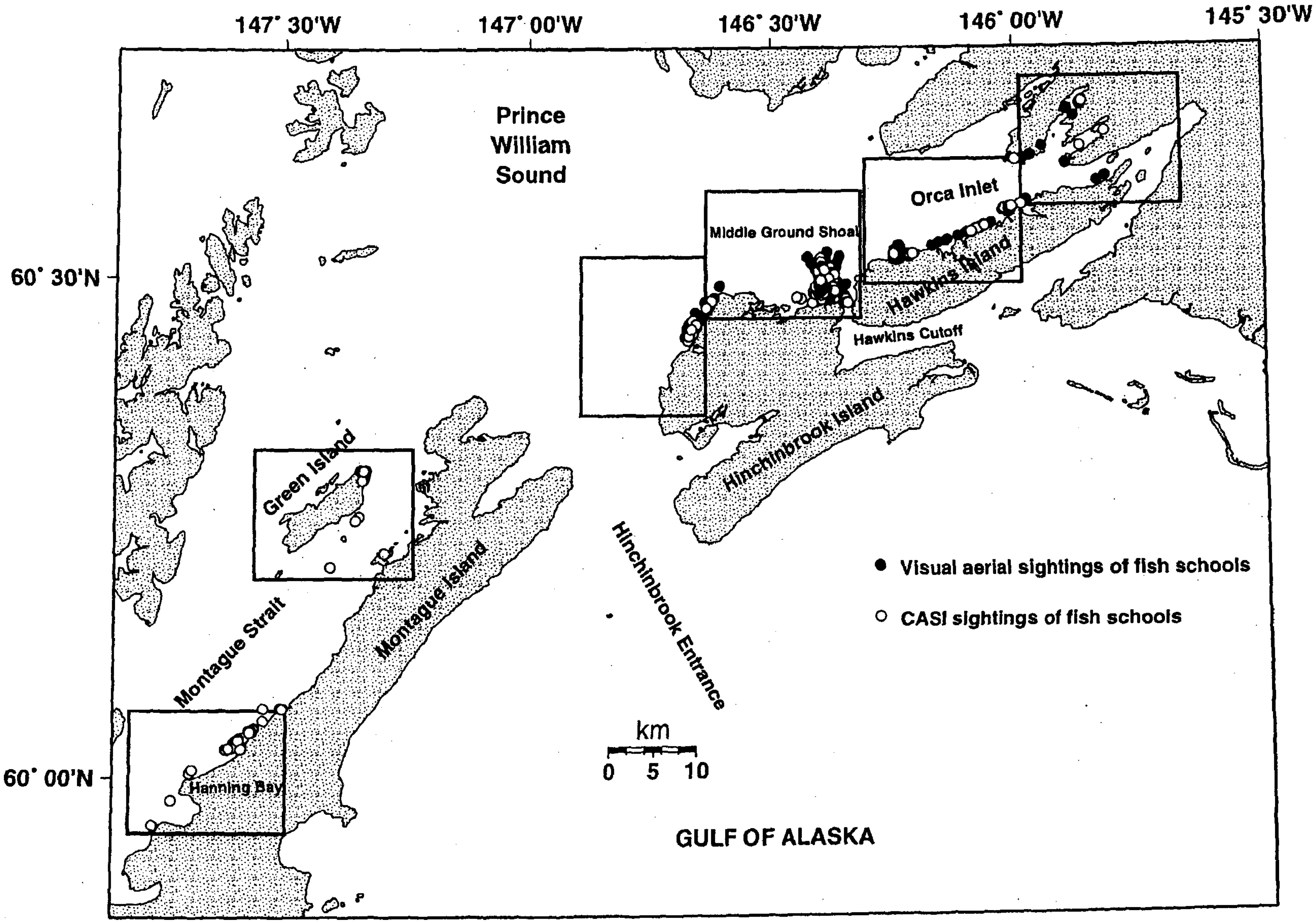
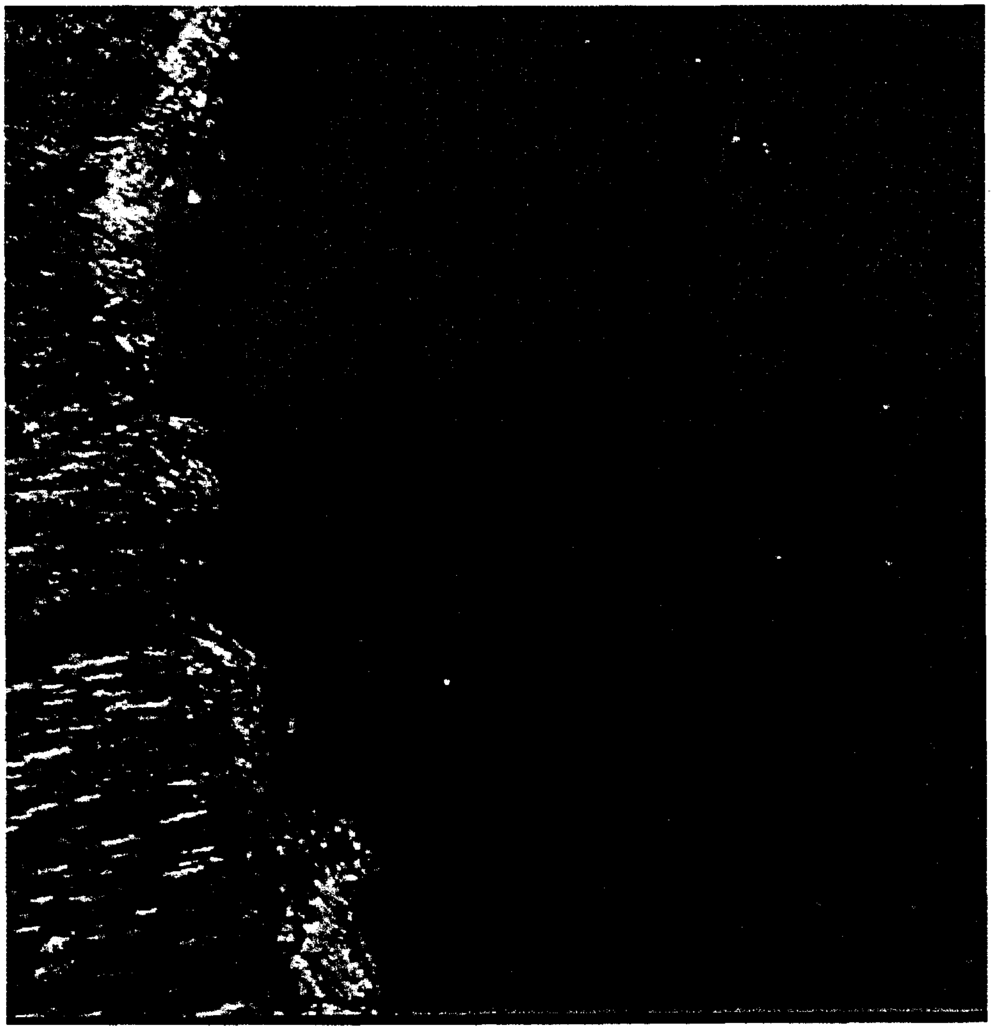
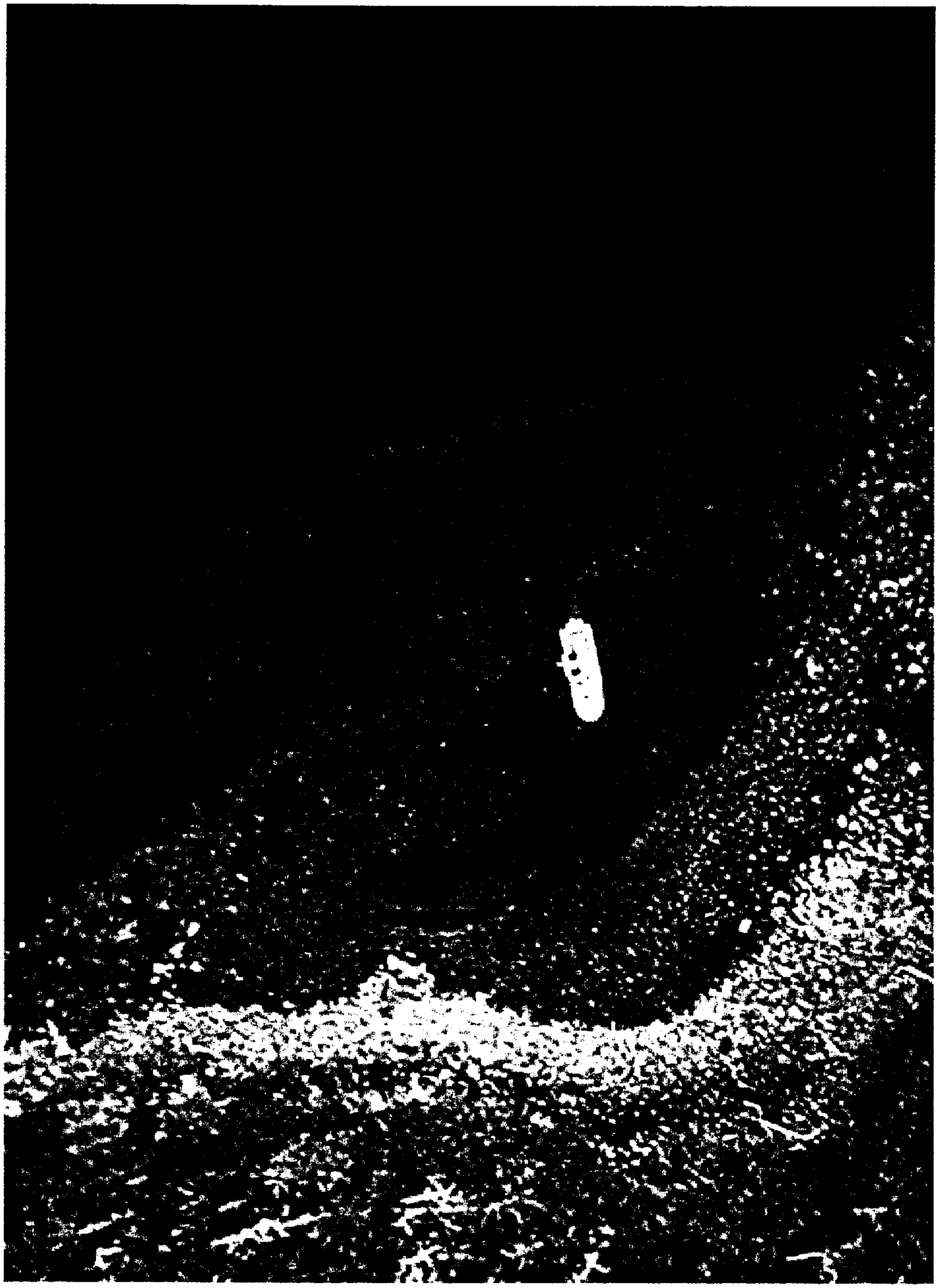

147° 30'W
147° 00'W
146° 30'W
146° 00'W
145° 30'W
60° 30'N
60° 00'N
Prince
William
Sound
Middle Ground Shoal
Orca Inlet
Hawkins Island
Hawkins Cutoff
Hinchinbrook Island
Hinchinbrook Entrance
Green Island
Montague Island
Montague Strait
Hanning Bay
km
0 5 10
GULF OF ALASKA
● Visual aerial sightings of fish schools
○ CASI sightings of fish schools





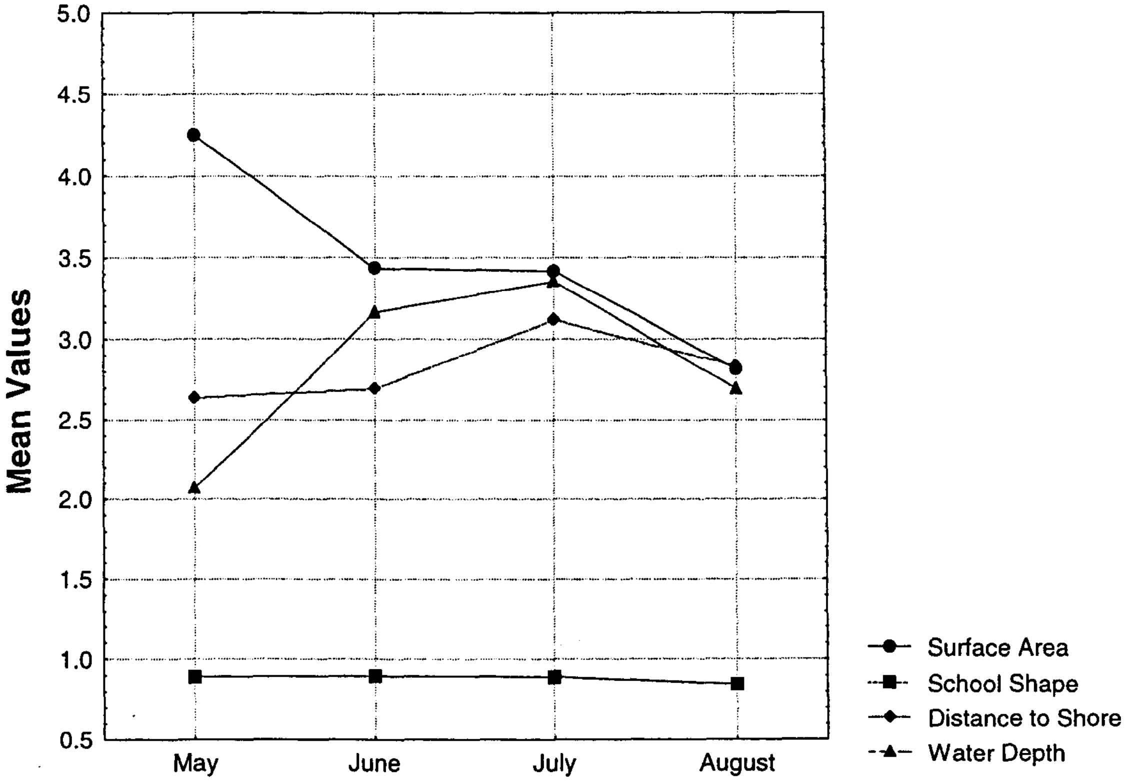

Mean Values
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
May
June
July
August
Surface Area
School Shape
Distance to Shore
Water Depth

Figure 11

Ecology of Herring and Other Forage Fish as Recorded by Resource Users of Prince William Sound and the Outer Kenai, Alaska

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Abstract

This project demonstrated that extensive qualitative ecological information about non-harvested age classes or species can be obtained from tek and local interviews. Our primary objective was to compile historic ecological knowledge about the distribution, abundance, and ecology of Pacific herring (*Clupea pallasi*) and other forage fish species in Prince William Sound (PWS) and the Outer Kenai (OK) in south central Alaska. This was accomplished by developing an oral interview questionnaire, selecting and interviewing key informants in 5 Alaskan communities, and by developing a geographic database. A secondary objective was to provide ecological information to aid in developing study or management plans concerning herring and other forage fish. Researchers taped recorded and mapped respondents observations. Survey questions fell into six categories: 1) life history stage and species of the fish observed, 2) fish behavior and school characteristics, 3) presence and behavior of co-occurring predators, 4) seasonal spatial distribution observed, 5) decadal shifts observed, 6) method of and activity during observation. A total of 48 interviews were conducted. The earliest observation was from 1934. Most of the respondents were commercial fishermen (34) and a large number of them were also pilots. Most of the observations were made from a plane. Other observations came from net catches, visual sightings, and sonar output. Most of the observations were made during the summer (June through August) due to the abundance of schools and an increase in activity during this season. Most observations concerned juvenile herring, but locations of herring spawning, overlap with adult herring, Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), capelin spawning, and eulachon (*Thaleichthys pacificus*) were also documented. Most respondents were able to distinguish herring from other species by their school shape, school color, behavior, and location within a bay. A couple pilots stated they needed sunshine to distinguish herring from sand lance because herring schools "flash silver" and sand lance remain brown in color. Schools of salmon fry were very hard to find and see. Juvenile herring were reported as broadly distributed mainly in bays in PWS and the OK and easily observed in the summer. Juvenile herring compressed at the heads of bays during the winter. The overlap with adult herring was reported to be limited to the winter and in a very limited number of sites. There were decadal shifts observed with an increase in juvenile herring from the 1970s to the 1980s and a large decline from the 1980s to the 1990s. Juvenile herring overlapped sand lance distribution to a large degree, capelin and eulachon to a small degree. Herring spawning locations prior to the 1970s were documented that had not been reported by the Alaska Department of Fish and Game. This ecological knowledge, that would have disappeared within the next decade with the death of many of our respondents, is now forever preserved via this report.

Key words: *Exxon Valdez* oil spill, nursery areas, Pacific herring, Pacific herring spawn, juvenile, forage fish, Pacific sand lance, capelin, eulachon, traditional ecological knowledge, local knowledge, distribution.

Introduction

The Prince William Sound (PWS) ecosystem, on the northern rim of the Gulf of Alaska, supports many ecologically important fish species. Two of these, salmon (*Oncorhynchus* sp.) and Pacific herring (*Clupea pallasi*), support subsistence activities and commercial fisheries. Juvenile and adult herring, juvenile salmon, and a host of other forage species including sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*) and eulachon (*Thaleichthys pacificus*), are prey for mammals and seabirds. Several of these predator species, particularly common murres, marbled murrelets, and pigeon guillemots, were severely impacted by the Exxon Valdez oil spill (EVOS) and had not recovered by 1994 (Agler et al. 1994). Little was known about forage fish prior to the 1989 Exxon Valdez oil spill (Duffy 1998). Historical data from official published sources regarding the distribution of forage fish and herring throughout Prince William Sound was limited. Neither was it possible to ascertain the historical distribution of these fishes through existing data. This study was initiated to tap into the extensive local knowledge from resource users in PWS and nearby areas about the distribution and ecology of forage fish, especially juvenile herring. This local traditional ecological knowledge (tek) provided basic information for the design and supplemented results from ecological research on forage fish species conducted during the last 5 years (Duffy 1998; Cooney 1998).

Our key target species, Pacific herring, usually spawn in their third year when they are about 185 millimeters long and weigh about 95 grams. Each female produces up to 40,000 eggs annually until they reach about 15 years (Hourston and Haegele, 1980). The eggs are deposited in mid-April in the nearshore low intertidal or subtidal zone on marine vegetation. After about two weeks, the eggs hatch into larval herring (Brown et al. 1996). About 10 weeks later, in July, they metamorphose into juvenile herring (Norcross et al., 1996) and utilize the bays of PWS as nursery areas (Stokesbury et al., in press). In spring, age-1 herring are still found in sheltered habitats such as bays, while most age-2 herring depart bays and join the adult population (Stokesbury et al., in press).

Over the last two hundred years in PWS, there have been numerous communities of indigenous people and communities that were based on biological resource extraction from the Russian fur trade to salmon fishing, herring fishing, and logging. Herring spawn on kelp has long been a favorite subsistence food. Residents of communities in the southwestern and northeastern areas of the sound, as well as cannery workers, remembered seeing spawn in the areas they lived and traveled. While the Alaska Department of Fish and Game has flown aerial surveys to document the miles of spawn laid down each day of the spawning season, their focus has been on gathering information to be used in managing the commercial herring fisheries. Herring is the best documented of all the forage species because of its use for commercial herring fisheries. The fisheries began in the PWS area about 1914 initially producing salt cured herring, oil, fertilizer, pickled herring and halibut bait. After World War I the fisheries expanded, herring reduction plants were built producing mostly oil for industrial uses and fertilizer after 1931 (Rounsefell and Dahlgren, 1932). Early reports mentioned the presence of small herring in PWS. George A. Rounsefell, Fisheries Biologist for the U.S. Department Commerce, Bureau of Fisheries, stated the oil and fertilizer industry required a constant, cheap supply of fat herring, too small for pickling. "Cheapness implies that they are too small to be used for pickling, necessitating that small herring be more abundant at times than large herring for the (oil and fertilizer) industry to be profitable (Rounsefell 1930:233)." The fish oil and fertilizer industry occurred primarily in PWS (Figure 1) and Chatham Strait in Southeast Alaska because of the large, fairly constant supply of small fat herring in these places in summer. In PWS, until 1931, the main product was salted herring, the oil and fertilizer was a secondary product. Processing plants were located at Port Fidalgo, Naked Island, McClure Bay in Port Nellie Juan, Main Bay, Whale Bay, Snug Harbor, Hanning Bay, McCleod harbor, Elrington and Prince of Wales Passages, and Puget Bay (Rounsefell and Dahlgren, 1932; Figure 1).

After the decline of the reduction fisheries in the late fifties, fishermen still harvested herring for bait for crab fishing. According to local processors the market was primarily in Cordova (Ken Roemhildt, North Pacific Processors, Cordova, personal communication). The harvests were unregulated and managers speculated they were probably small harvests (John Wilcock, Alaska Department of Fish and Game. Cordova, personal communication). In the early 70s, a couple of fishermen looking for schools of bait traveled throughout Prince William Sound. They found herring "every where they went, but not in sufficient quantities to harvest." They found the largest biomasses at Knowles Head and Montague Island. Herring fishing districts were established in 1977 and in the following years the bait fishery took place primarily in the fall, from September through December. Until the mid-80s, the areas where the bait fishery took place excluded the designated "sac roe" districts – the Eastern District (Port Gravina, Sheep and Simpson Bays), the Northern District (Columbia Bay, Glacier Island, and Valdez Narrows) and Montague districts.

With the development and availability of sonars, the fisheries changed. In the 1970s, a couple of fishermen (reported by respondent) had sonars, but in the 1970s most used fathometers to find herring. As technology improved fishermen purchased more sophisticated acoustic equipment. According to a Homer respondent , the way Alaskan fishermen learned how to catch fish in murky water under windy conditions was by observing a group of Seattle fishermen who had brought sonars up from the south. The herring fishermen learned how to use sonar from them. He stated that was in the early 80s, when herring was worth about $2000/ton. When the herring fishery developed in other regions, he purchased a sonar that winter (1985).

The commercial harvest of herring has been extremely variable over the years. Between 1929 and 1966 catches in Prince William Sound ranged from a high of 56,153 short tons (2000 lbs.) in 1938 to a low of 38 tons in 1959, with no catches recorded for 1960-1964 (Rounsefell 1930; Figure 2). The commercial herring fisheries reemerged in 1969 in PWS and the Outer Kenai (OK) on the Kenai Peninsula (Figure 1), with the discovery that there was a Japanese market for herring spawn on kelp and sac roe. The Whitney Fidalgo processing company owned a cannery in Port Graham. One respondent working for them at the time says they made it known that they would provide the seine gear for anyone willing to go catch herring for their roe. The first commercial harvests of sac roe occurred the same year, 1969, in Resurrection Bay on the OK and in PWS (Schroeder, 1989). In the OK, harvests ranged between 12 and 2100 tons, mainly from Resurrection Bay, from 1969 to 1974. The fishery was closed in the OK from 1975 until 1985. The fishery resumed from 1985 to 1987. The last harvest was in 1987 (Schroeder, 1989:13). There has been some effort to harvest since then, but the catches had high percentages of two to three year old fish (Wes Bucher, Alaska Department of Fish and Game, Homer, personal communication). During this same period in PWS, the harvest ranged from 387 tons in 1969 to 26,671 tons in 1992 (unpublished data, Alaska Department of Fish and Game, Cordova, Alaska). Prior to EVOS the population of herring in PWS was at a high level and increasing in size (Funk and Savikko, 1989), but the population collapsed in 1993 apparently from a disease (Meyers, et. al 1994) and only about 25% of the forecasted return of adults appeared (Funk 1995). The population has never fully recovered from the 1993 crash and the harvest has never returned to the levels seen in the late thirties (John Wilcock, Alaska Department of Fish and Game, Cordova, personal communication).

People are still alive that worked in the reduction fisheries, delivered mail by boat and who participated in harbor seal bounty hunting. The commercial fishermen who participated in this study had an average of 31 years experience fishing. Commercial salmon fishing still occurs in many regions of PWS. Most of the herring fishermen were involved in the early years of the modern sac roe fishery, while the salmon fishermen most often began their career working for an older relative; some were only six years old when they began fishing for salmon. Pilots delivered people, mail and materials several times a week to Chenega Bay, Tatitlek, fishing boats, canneries, and scientific field camps, in addition to flying aerial surveys for various state and federal resource management biologists. Spotter pilots, charter pilots and the fishermen who chartered planes during the seine season to look for salmon saw herring schools from the plane. In summary, there was a considerable pool of resource users who possessed valuable historic local knowledge about the ecology of the region.

The primary objective for this project was to compile historic information about the distribution, abundance, and ecology of Pacific herring and other forage fish species from local and traditional knowledge. This was accomplished by developing an interview protocol, selecting and interviewing key informants in several communities regarding PWS and OK (Figure 1), and by developing a geographic database. A secondary objective was to provide historic ecological information to cooperating researchers and resource managers for use in developing study or management plans concerning herring and other forage fish.

Methods

The research goal for this project involved collecting broad based ecological information on Pacific herring and other forage fish species but required surveys with a rather limited number of users groups, freight or mail carriers, and long-standing families. Our qualitative survey design and implementation is similar to methods used by Ives (1980) and Weiss (1994). The specific goals for cooperating researchers was the collection of all available historic ecological information including occurrence of disease for a variety of forage fish species from both PWS and the OK, large areas encompassing several different fisheries (Figure 1). The base of available respondents was small and we therefore used opportunistic rather than random sampling. In addition, the information desired was not considered sensitive requiring random sampling of a larger group to further protect identities. The pool of potential respondents was identified as anyone who currently or in the past regularly traveled through PWS and the OK. This included herring fishermen, salmon fishermen, spotter pilots, subsistence food gatherers, charter pilots, mail boat operators, charter captains, freight boat operators, long line fishermen, crab fishermen, hunters, and hatchery or cannery workers.

We proceeded in a stepwise fashion. We first designed and tested an initial broad-based and extensive survey questionnaire given orally to five individuals personally know to the authors through previous charter or field work and who would provide critical advice. We then were able to focus and revise the questions to most efficiently obtain the information sought (Appendix I). The next step was to obtain a list of potential respondents by conducting a series of phone and written solicitations for ecological information to various organizations and remote native communities. Our protocols for selecting respondents, contact with the public, and survey questioning were drawn from protocols established by the TEK advisory group (Alaska

Department of Fish and Game or ADFG, Division of Subsistence, 1997) as directed by our funding agency, the *Exxon Valdez* Oil Spill Trustee Council. The TEK protocols were established to provide guidance to researchers wanting to obtain and use local tek for EVOS Trustee Council (TC) funded ecological research. Project introduction and solicitations were sent to the Traditional Village of Eyak, and Cordova, District Fishermen United (CDFU), the Chenega Bay IRA Council, the Tatitlek IRA Council, the Valdez Native Association, Qutecak Native Tribe and individual respondents in Homer, Alaska. An initial phone list of potential respondents was drafted containing known and licensed users listed via permitting from ADFG and local contacts. Additional respondents were contacted through chain referral from the initial list. Permission to work in Chenega Bay and Tatitlek was obtained through their IRA Councils. All interested respondents and organizations were later contacted to schedule formal oral interviews. All oral interviews were taped. Prior to the interview, all respondents were asked to read and sign a statement regarding the anonymity of their information and protection of their identity. After the interview, the tapes were reviewed to double-check the data sheets and maps and additional notes were taken.

The questions asked of the respondents fell into six informational categories: 1) life history stage and species of the fish observed, 2) fish behavior and school characteristics, 3) presence and behavior of co-occurring predators, 4) seasonal spatial distribution observed, 5) decadal shifts observed, 6) method of and activity during observation (Appendix I). Respondents were asked about ecological information on adult and juvenile herring, herring spawning areas, capelin, cod, eulachon (locally called hooligan), pollock, sablefish (black cod), sand lance (often called needlefish), and smelt. Forage fish is the general term used to refer to any species of small fish that the respondent could not identify. Mixed herring referred to adults and juveniles found in the same area at the same time; and unknown herring referred to herring of undetermined life stage. Respondents also described herring migration patterns. They were asked about disease in the herring population, if they'd ever observed it before 1993 and if they had ever before seen a run failure such as occurred in 1993. We also sought information about the presence of predators such as sea birds and marine mammals associated with the fish schools. For designating specific locations, respondents were given a colored pen with which to draw on mylar covered navigational charts to designate specific locations. Respondents were asked to describe their method of observation, whether it was from a platform of some type, such as their boat – "visual," or whether they saw them from a plane, or whether they caught them. Respondents described the characteristics of schools of different species of schooling fish, how they appeared from the boat, the air and in sonar displays.

In order to determine seasonal and decadal trends, respondents were asked about the time frame of their observations. . Because we were particularly interested in juvenile herring, respondents were asked to judge how often they had observed juvenile herring in the places they had seen them, especially if their observations were over the course of a season, or a range of years. After the initial test survey, it became obvious that observations would fall into one of three easily identifiable (by respondents) seasons defined as 3-6 month periods: spring included March through May, summer included June through August, fall included September through November, and winter included December through February. However, due to the smaller number of observations, fall and winter were reported together. They were asked to judge if they had seen the herring or other fish species consistently, occasionally, or rarely. Consistently meant, "I'd see them almost every time I went there this time of year." Occasionally meant, "I'd see them once in a while this time of year." Rarely meant, "I remember them showing up there once or twice." The year ranges reflect the respondents' best estimate of the time frame in which the observations occurred. As this relies primarily on memory, the beginning or end of any range of years might not be exact. Each year range is therefore considered an approximation. Many respondents described the time of observations as in the "early," "middle" or "late" part of a decade. Decades were divided into three parts: years 0-3 were the "early" part of the decade; years 4-6 were the "middle" part of the decade; and years 7-9 were the "late" pat of the decade. We checked the estimated year ranges with respondents before assigning the beginning and ending years. Establishing a range of years allowed researchers to accommodate repeated observations by an individual in an area and then use a database to find which individual years overlapped with others' observations and to compare those observations over different periods.

A total of 48 interviews were conducted: eleven in Homer; twenty-one in Cordova; ten in Seward; three in Tatitlek; and three in Chenega Bay. The respondents fell into one of 8 categories of activity and variable years of experience in that activity within the survey region (Table 1). Thirty-four were commercial fishermen. Of the 34 fishermen, all fished salmon, 20 also fished herring, 8 were also herring spotter pilots, and 10 were salmon spotter pilots. Several of the respondents were Alaska natives from remote villages, but were not reported separately because of the low number and possible identification of the individual from the information. Nine individuals had other occupations as professional biologists, tender operators, sport fishing charter operators, mail carriers, or were engaged in other fisheries (excluding salmon and herring). Respondents' age ranged from 27 to 75 years; the average and median age was 53 years. The total number of years each respondent was active in PWS or OK was totaled then multiplied by the number of respondents in each type of activity (Table 1). Fishermen respondents (all fisheries) had a combined experience of 1122 years involvement in marine-related activities. The salmon fishermen had a combined total experience of 984 years commercial fishing. Commercial salmon fishing experience among respondents ranged from 2 to 68 years with an average of 31 years. Herring spotter pilot experience among respondents ranged from 1 to 36 years with an average of 14 years. Several of the respondents were pilots by occupation and had worked both in the fishing industry and as charter pilots. Individual professional pilots had up to 36 years of experience averaging 18 years. Average individual experience of persons in other occupations was 25 years.

The final step was to build a geographic database in order to summarize and visualize the data. We used ArcView version 3.1, the Geographic Information System (GIS) from the Environmental Systems Research Institute (ESRI), Inc. First a series of tables were constructed to enter all 6 data types. Then, maps drawn by the respondents were digitized to GIS by fish species, life history stage (adult, juvenile, or herring spawning area), season, and year range. In this way, the data could be summarized by a variety of parameters. The PWS area was segregated into 8 regions (Figure 3) while the OK area was considered as a single large region. In addition, since many of our respondents were commercial fishermen, we report observations by commercial salmon fishing districts as delineated by ADFG, Division of Commercial Fisheries Management and Development. Locations of salmon hatcheries were also identified as possible areas with a greater number of observations and therefore bias since increased use occurs nearby.

Results

Fish Species, Life History Stage, and School Characteristics

Many respondents commented on their ability to distinguish species and age of herring, as well as species and age-specific school characteristics. Respondents said that the visibility of juvenile herring schools was affected by water conditions, light, wind, the depth of the schools and the observational situation of the observer. Fishermen standing on their vessel decks or flying bridges saw herring when the schools were near the surface reporting behavior and school characteristics: "You see them flipping on the surface, occasionally you catch one in the net. When you're spotting salmon you see balls of juvenile herring everywhere", "From the boat juvenile herring are easy to see. From the air juvenile herring are usually in pretty small schools, little pods. They're not in big spawning schools. It's easy to tell juvenile herring from the boat", "Juvenile herring hang out close to the shoreline. They're dark in color, not brown. Brown is a sand lance or some other type of small fish. Herring are dark, kind of a blackish color." One of the respondents reported that juvenile herring like areas out of the current, near rock piles and eddies and that they behave differently than adults.

Pilots reported that herring looked different than salmon schools or other small schooling forage fishes. They described schools of juvenile herring as round schools with soft edges. Some pilots were able to distinguish juvenile herring from other forage fishes by their color, the shape of the schools, and their behavior: "From the airplane they look like their parents. There's a difference between needlefish and herring. They're darker. They're a different color than salmon", "It's difficult to tell capelin. From the air capelin are more brown-colored, while herring are usually black schools", "...from a plane the schools have a particular color and character. You can't mistake them.."

One pilot noted that the 0-2 year old herring are about 2-3 inches long, their schools are darker than other fishes, and he further speculated that they might need more protection, so they tend to stay tighter to the beach. The same pilot reported that "needlefish look like a cloud, he says. "They are brown, and have a non-defined border when you see them from the air, whereas juvenile herring have a well-defined border. Juvenile herring you'll see amongst rocks, along the shoreline." Another pilot reported "They are hard to tell from bait fish or needlefish in cloudy conditions with flat light. With enough light you can see the fish "flash." The herring flash is bright silver, but the baitfish looks brown and gold. The herring flash is much larger than the baitfish. The same pilot further noted that juvenile herring and other "bait fish" are out there eating and growing. They are aggregated in round schools, for protection. They stay off the beach, and can be found on top of a "cone of adults" (herring). They will be usually one to three fathoms from the surface and rarely against a beach. They like calm water with low currents, such as the backwaters of bays. If he were looking for juveniles while out flying he'd fly transects across the bays. However, he was mainly looking for salmon. He said that their fry (salmon) go into shallow water. He also stated that "The schools typically were 10 to 30 ton schools and if they were less than 10 tons, you'd have to be careful about calling them bait or herring. You'd have to have some light, because a lot of the baitfish were in little two to five ton schools. Eaglek's always been a good producer of juveniles. And if you flew around in there you'd see 15 schools, 20 schools at a peak, and at a lull you might see one."

Herring spotter pilots distinguished adult herring from juveniles by their behavior and the shape of their schools. Sac roe herring were described as "adults with a mission": "They are traveling and will be seen as a ball with a tail coming out ahead of it. Juvenile herring on the other hand, are off the beach, out in the middle of the bays, sunning themselves. They aren't moving around. They don't have a mission.", "You know, you look at a sac roe fish, you can tell if it's immature and you can tell when it's ripe by what it's doing. You know, these bait fish in the summertime, my sense is they're just eating and growing. And they're not moving around a lot. You never see the school shaped up. A traveling school would be shaped like a boomerang or a ribbon. And it'll be moving. At least it'll be strung out and have a knob on one end ."

Salmon fry were also noted to be abundant in summer. However, respondents said that there was no likelihood of mistaking salmon fry for herring schools. One pilot stated that "You can't see salmon fry from the air." He described seeing them from land, in amongst rocks, transparent, and hard to see even when close up. He said he had never seen migrating salmon fry from an airplane and never in 100- ton schools. "Fry migrate in schools of 100-150 fish. They travel along beaches in small schools – most are too hard to see."

During the 1980s, after sonar were in common use, many observations were noted relating to the "electronic pictures". Some respondents felt they could tell the difference between different species of fish, such as pollock or herring. Some felt they could tell the difference between adults and juveniles with their acoustic equipment. One fisherman noted that using his "downsounder", herring show up a "good red" while pollock look like "v," and are not as tightly schooled up as herring. He further noted that he could not tell juveniles from adults with the downsounder. In contrast, a different respondent felt he could tell the difference between juvenile and adult herring using his downsounder: "The fish react differently. The small fish are more skittish; move more radically than the adult fish. You won't catch them. Sets that are made in shallow water, up in the protected bay areas, and it seems like during daylight hours like at dawn, you'll get small fish. I use that rule to try and stay away from catching juvenile fish.." Fishermen were also able to estimate school size with their downsounders. One noted that you can tell the approximate size of schools with the sonar, if you can get all around them and look at them well. You can tell 30 tons from 50 tons, but probably not 30 tons from 40 tons.

Juvenile Herring

Observations of Pacific herring were by far the most commonly reported and contained the most auxiliary information. The PWS juvenile herring database consists of 2819 lines of observations by 34 observers for all the years and seasons respondents recalled seeing herring. The Kenai Peninsula juvenile herring database consists of 995 lines of observations by 13 observers. Observations of juvenile herring were documented from Port Dick on the Kenai Peninsula to Jeannie Cove and Patton Bay on the outside of Montague Island, and from Orca Inlet, around the Sound, including Port Nellie Juan and the bays along Knight island Passage (Figure 3).

Spatial Distribution in PWS

The PWS herring observations were reported by region (Table 2, Figure 3). The earliest observations of juvenile herring were from the summer of 1934 in Tatitlek Narrows, region 2, and 1938 in Port Wells, region 3. Native elders say in those days, people survived through hunting and fishing, trapping and part time cannery work at Nellie Juan, region 4, and Port Ashton, region 8. One elder recalled seeing little herring while salmon fishing in Port Wells as a young boy and the other recalled when she was a school girl in Tatitlek and herring were in the Narrows all year. As a child she saw adult herring and small fish she was told were herring. They reported that herring were so abundant the propellers of outboard motors would grind them up.

The bays in the eastern sound (region 1), especially Port Gravina (n=304), had the highest number of observations of any region in PWS (Table 2). Two or more respondents saw juvenile herring in Port Gravina from 1978 – 1996. From 1978 until 1994 four to six respondents each year saw juvenile herring in this area. Three respondents reported seeing juveniles there from 1982-1985. Schools of juvenile herring were mostly seen by plane (n=374).

Northeastern PWS, region 2, had the second highest number of observations of juvenile herring (n=484). In this region the most herring observations were reported in Port Fidalgo (n=215) and Valdez Arm (n=132). As in region 1, the schools were seen primarily from an airplane. The overlap in numbers of observers by year is high in region two. Between 1970 and 1992 at least four observers each year reported seeing juvenile herring in this region. The number of respondents who reported seeing juvenile herring in this region increased to six in 1972, and was at least that large until 1979. Between 1981-1987 there were at least seven to eight observers every year. One respondent's described the distribution of juvenile herring in region 2 and 3, "I know I see juveniles in Valdez Arm a lot, patchworks of fish all the way up inside as far up as you can go. I know. A lot of times you see the same thing in Eaglek Bay" (region 3).

Region 3, the north shore, also had a relatively high number of observations and a high degree of overlap in the numbers of respondents who saw juvenile herring in this area. Fourteen observers saw juvenile herring here from 1970 through 1998, 3 each year between 1981 and 1991. Most observations in this region were from airplanes and occurred in Eaglek Bay (n=103). At least three respondents saw juvenile herring schools in Eaglek Bay each year from 1982-1987. Fairmont and Wells Bay also had three observers almost every year of the 1980s. Columbia Bay was the first place in this region to have more than one observer, but no observations were recorded here after 1979.

Region 4, the northwestern corner of PWS including Port Wells, Eshamy, Herring Bay, Port Nellie Juan, Culross Passage, and Esther Island, had 343 observations . At least five respondents each year, from 1970 to 1986, saw juvenile herring in this area. The number of observers declined in 1987. Most observations were in Port Wells (n=120), followed by Port Nellie Juan (n=78). Juvenile herring were caught (n=119), seen from airplanes (n=107) and visually identified (n=103).

In region 5, including Naked Island and the associated islands northeast of Knight Island, Ingot and Eleanor, 7 respondents reported seeing juvenile herring around Naked Island. The most overlap occurred in the late 80s.

In region 6, including Montague Strait, the east side of Knight Island across the sound to the northwest shore of Hinchinbrook Island, there were 306 observations by 18 respondents. Montague (n=123) and Port Chalmers/Stockdale harbor (n=78) were the places in which respondents reported seeing the most herring schools.

Juvenile herring in region 7 (n=6) were seen in Jeanie Cove and Patton Bay by a fish survey pilot. He reported that catches during aerial surveys taught him how to identify schools. He was able to extend the record of herring observations to five previous years, back to 1989.

The third highest number of observations of juvenile herring (n=401) occurred in region 8 including Day Harbor and the southwestern passages. In this region juvenile herring were most often caught or seen close enough to identify. Within this region Day Harbor had the most observations (n=90). At least three respondents saw herring in this area between 1971 and 1989 and four each year between 1976 and 1986.

Seasonal distribution in PWS

Respondent observations indicated that herring are distributed differently throughout the year. However, comparisons of herring distribution and abundance by season were confounded by the fact that most of the resource related activity took place in spring and summer (Table 3). In spring respondents were focused on the commercial herring fisheries, which in Prince William Sound usually took place in April. Fishermen tried to avoid juvenile herring and pilots searched for adult schools of spawning herring in airplanes. In summer the commercial salmon fishery was the primary activity that engaged respondents. Pilots flying scientific surveys, charter flights, and fishermen who chartered flights to look for salmon also saw herring schools along their routes. In fall and winter juveniles were seen with sonar and, attracted to the deck lights, on the surface of the water in bays. Juvenile herring were also accidental caught in the winter by fishermen targeting shrimp, crab or herring schools for the bait fishery.

Many sightings of juvenile herring in the spring (Figure 4) occurred while fishermen or spotter pilots readied themselves for the herring fishery. One fisherman saw them while anchored up at Disk Island. A spotter pilot stopped in Port Nellie Juan on his way to Seward and jigged them from the floats of his plane to find out what they were. Several fishermen commented on the presence of juvenile herring in King's Bay. In the early 1970s, fishermen reported catching them in their seines in Columbia Bay while targeted adult herring. One fisherman commented about Glacier Island in the early 1970s, "there were juveniles all around that island." Another fisherman had a record of the same observation from his log dated in late 1970s: "April 22/23; fish caught in Chamberlain Bay, water temperature 37 degrees F; north side of Glacier Island 3-4 inch "feeders... 4/17/78 - in Columbia Bay almost all the herring are caught around Emerald Cove. I'm sure someone ran over and set on them, and found out they were juveniles...People were setting on krill and juvenile herring around Growler Bay. 4/10/78". A respondent recorded that more recently, in 1985, at Glacier Island someone made a set and caught herring three inches long. He reported, "they were very small and gilled in the net. It looked like a silver sheet." Pilots saw juvenile herring schools along the north shore when flying from Sheep Bay to Eaglek Bay. One pilot said he called them juveniles and he "wouldn't set a seine on them."

Another respondent does not remember ever having a problem with juveniles in the spring sac roe fisheries that took place along the north shore. He does remember smaller fish in the commercial harvest at Montague: "In the mid 80s all the roe fisheries were taking place.. in Eaglek Bay...those were all adult fish. As time went on we started trying to harvest fish down at Montague, and the fish always got smaller and mixed, they were always smaller there. We had somewhat of a quality problem. I wouldn't consider them juveniles, because they definitely were roe herring and they were sellable most of the time. In the spring when we went roe fishing...we never had a set with juvenile fish in it - in the northern area at all. We never had a problem with that. When we went in the northern part of the sound in the 80s and 90s we never had a problem with juveniles."

A resident of Tatitlek says it had been common to see juvenile herring in Tatitlek Narrows in spring when she was a young girl, in the 1930s. She stated: "...we always had little fish in the springtime...They told us they were baby herring...There should have been lots of herring around because the babies were here" meaning that herring spawning occurred nearby.

Respondents reported seeing juvenile herring in Stockdale Harbor and Port Chalmers during and after the spawn-on-kelp fishery sometime during the mid-70s to mid-80s. Port Fidalgo, Galena and Jack Bays were described as consistent places to see juvenile herring in spring. Several respondents reported that juveniles like deep bays with shallow estuaries at their heads." Two respondents also saw juvenile herring in Day Harbor over the mid-1970s through the 1980s. They saw herring there in both spring and summer, but more schools in summer.

In the summer, juvenile herring were observed in almost all of the bays and some open areas in PWS and the total number of observations peaked this season (Table 3, Figure 5). The commercial salmon fisheries occurred during this season along with many other activities relating to subsistence and recreation. Different areas of the sound were opened to fishing. While some fishermen targeted salmon near hatcheries, the heaviest use resulting in the largest number of observations occurring in the Eastern district for all years (ADFG; Figures 6-8). One pilot noted that he had seen juvenile herring in the summertime from Graveyard Point to Gilmour Point during his aerial surveys. All through the '80s he flew hundreds of hours looking for salmon. He would find schools of herring with some consistency in some areas such as Stockdale, Port Chalmers. They could be seen in sheltered waters (bays).

There were substantially fewer observations during winter and fall. We therefore combined the observations from fall and winter (Figure 9). It was a time with much less reported activity in PWS and the OK. Even though there may be and have been winter fisheries and air traffic, both were reduced in the fall and winter due to inclement weather and short days. In addition, waves and wind made schools of juvenile herring much harder to see unless the observer had sonar equipment.

In the winter, observations came from residents living remotely in PWS, from commercial shellfish fishermen, and herring bait fishermen. One native noted "they (sic herring) stay in the Tatitlek area all winter. Other mammals like seals, sea lions, whales, and winter kings all follow them. In the winter, if you find herring, the kings will be there. You can tell where herring are, by the birds feeding on them."

From 1960 – 1988, PWS was open for crab fishing September through May. These fishermen noted that sometimes crab will go "off the bite" and won't take the bait in crab pots because they are feeding on something else, such as herring moving through the area. From 1960 through 1991, there was also a trawl shrimp fishery in the sound most of the year, April through August and October through December. Fishermen trawling for shrimp also caught juvenile herring.

Region 1, the eastern bays of the sound, had the highest number of observations per respondent in the fall and winter (Figure 9). From 1977 to 1981, a few fishermen tried pair trawling for bait herring. They discovered juvenile herring in the bays and at the head of Port Gravina, and Sheep and Simpson Bays. A couple of times they mistakenly set on juvenile fish and thousands gilled in the trawl. After that they said they no longer tried catching herring in the heads of the bays: "We did go into a few bays and did have a juvenile experience. Juveniles - you always ran into them up in Beartrap. We'd go up and look for fish and sometimes we'd see them. We could tell the difference on the sonars and stuff. Every time we'd go into the heads of the bays they weren't good fish for us. But we did try and see what they were a couple of times and they were juveniles." Another fisherman reported about previous respondent "He caught juveniles in a shrimp trawl between 1985 and 1989. He used to shrimp trawl in Simpson Bay for subsistence. The juveniles would travel faster, in front of the trawl. If he sped up he could catch them. Once he caught some to give to ADFG biologists, who wanted some samples."

In region two, Port Fidalgo and Valdez Arm, there were few observations, but four different respondents who had seen them in Port Fidalgo and only one respondent who had mapped where he saw them in Valdez Arm. However, others remembered seeing them in Valdez

Arm even if they were unable to place them on a map. Fishermen reported that herring are in deep water during winter, observed while fishing for bait herring outside Knowles Head and Goose Island. One stated: "Adult herring winter in Valdez Narrows by Jack Bay. During the fifties, a Valdez fisherman would catch them there and can them, just like sardines. He used to fish Valdez Arm in the 50s. He set occasionally on small fish and they'd go right out of the [seine] net. In Alutiiq they call the small fish "natwusuk" - (little feed)...During the mid 60s they didn't see these schools of little fish any more. Perhaps it was just through not paying attention, but he says probably there weren't as many around. He also recalled seeing small fish in Port Fidalgo, Bidarka Point, and Fish Bay." In region 5, three respondents reported seeing juvenile herring in the Naked Island area ranging in time 1970 until 1996 in the winter. One of these respondents observed the herring from the air..

Region eight, the southwestern passages, had the next most observations (n=58). They were made during aerial surveys from 1994 – 1996.

Fishermen say there is a pattern of younger fish mixing with the adult fish around Montague Island during the early months of fall. As October nears and progresses, they say, the fish are more likely to be more segregated and they are more able to catch larger herring. Sometimes they caught and released catches, which had too many juveniles. They saw this in Stockdale Harbor and Port Chalmers. Others said juvenile herring spread out in the fall: "It's the only place I've ever fished where I caught substantial amounts of juvenile herring. The schools off Stockdale/Chalmers are more uniformly juvenile...We'd catch them out in front of this area (Stockdale/Chalmers). During the winter bait fishery they'd gill in the seines, in 1¼ to 1½ inch mesh. The fish were anywhere from 70-80 g to 40 g in size. We'd see mainly juvenile schools along the 30-fathom contour. In terms of seining, you can find juvenile herring along the bank, along the 30-fathom edge, a minimum. It drops off. We tend to stay away from that area." Another fisherman reported: "The guys who've fished bait herring will tell you that if you fish this in September (near Montague) you get very mixed fish and quite small. Then as October nears, each day you fish, the further you get into it, the larger the fish will become. There's apparently a migration of fish coming into this area. I don't know if they come out of the Montague Trench or what, but this is the area in which you do bait herring. The Cordova guys could describe it better than I could. That is an interesting pattern, the movement of smaller fish to larger fish." This same fisherman reported that juveniles were more spread out during fall and winter when fishermen were fishing for bait. He also reported that juveniles three years and younger mixed with adults.

Juvenile Herring in OK

Juvenile herring were observed by respondents to be widely distributed along the entire coast of the OK (Figure 10). In the Spring, herring were generally sighted in late May (Figure 11). The first fishermen to try catching herring for their roe noticed a migration of juveniles into the head of Resurrection Bay as their fishery was winding down. Here's the way one respondent saw it, along with his notes from that time: "One thing that happened consistently over there. We'd know the roe herring fishery was over when all of a sudden the fish we would catch would be juvenile herring. They would appear after the spawning biomass, which was in Seward most of May. Well you'd fish the harbor. We didn't have airplanes. Fish would come into Seward through most of May. We'd just drive around the harbor looking at our flashers, until you'd see bunch of indicators on the flasher that indicated there was something between me and the bottom. You'd turn around and round up that general area and catch whatever that was, it was always roe herring. Or else you'd go out at night and look for fluttering on the surface, or dimples, things like that. But then all of a sudden you'd start getting fish where you'd make the set and pull it in and there was no fish! You'd find out they were all juvenile herring. In late May and June the large size herring would disappear. They'd go back to the deep. These huge schools of herring would come into Resurrection Bay and they'd just be around out there. Then it was time to come back to Homer and start fishing here. So that was what happened there", (from the log, 5/9/71): "Tried again, snowed....couldn't bring net in through slush. Juveniles a constant presence – hard to see from water, but seen all over from the air", (from the log, 6/2/71): "The sea was black with fish from the ferry dock to Lowell Point. Set deep and had enough to sink the corks on the purse, and ended up with only 3 tons plus thousands gilled along the cork line. Most went out through the meshes. All were 2 ½ inch herring, no other size."

In summer, beginning in late May, fishermen fishing for salmon in Resurrection Bay, Aialik Bay, Nuka Bay, McCarty Fjord, Nuka Island, and in Port Dick observed juvenile herring (Figure 12). These fisheries are held along the coast within three miles of shore. In addition, there were several charter boat operators taking customers from Seward toward PWS, Aialik and Harris bays who observed juvenile herring. Seven respondents total saw juvenile herring in bays along the outer Kenai Peninsula during summer, from 1958 to 1998. Most observations were made in Aialik, Nuka, Resurrection, and Harris Bays as well as Port Dick. A pilot working with a fisherman checked the coast for herring during the 1970s. The fisherman caught small (juvenile) herring, which they estimated were the size of capelin (about 150 mm). They found juvenile herring every place they went. Most of the herring were two year-olds, which gilled in the net. The pilot reported that herring live from Harris Bay to Nuka Bay: "A lot live in Aialik Bay...We'd see them every time we went there from 1972-1975..To see the juveniles you have to get out in June. Juvenile herring like to go up in bays where it's decent (more protected)." Another respondent reported he'd found juvenile herring in the rocky areas of Crater Bay amid kelp.

During summer, three respondents saw juvenile herring in Aialik Bay each year from 1982 – 1989 and Port Dick 1980 – 1989. Two respondents saw juvenile herring every year in Aialik, Black/Thunder Bays, Nuka Bay and Harris Bay from 1980-1989. Crater Bay is within Harris Bay, which is just north of Two Arm Bay. One respondent noted of another fishermen: "He found herring in Crater and Two Arm Bays in March and April while cod fishing. They saw five-inch herring. This was during the 1990s, from 1991 until 1995. They saw them for three to four years. The birds come in the bays to feed. In the 90s there were die-offs of birds out there. You'd go out in the morning and see windrows of dead birds. You'd see the fish under the cod lights."

All the observations (n=107) by respondents (n=6) who saw herring in fall and winter were at the head of Resurrection Bay, many in the Seward boat harbor (Figure 13). One couple had observed herring over a 40 year period, from 1958-1998, September through November. During the winter months of December through February, five individuals saw herring at either the Seward boat harbor or the head of Resurrection Bay from 1969 – 1998. One respondent described them as three to four inch herring. Another mentioned he remembered seeing them in the Seward Harbor every year, but couldn't remember the first year he'd seen them.

The most interesting contrast between winter and summer observations of Kenai Peninsula juvenile herring is that so few respondents recorded seeing herring in the Seward boat harbor or in Resurrection Bay in summer. The respondents who did said they "did not catch the herring and did not see great amounts."

Decadal changes in distribution

In PWS, respondents reported more observations and noted that juvenile herring were more broadly distributed in the 1980s (n=1055) than the 1970s (n=795). However, this result is not obvious from the respondent maps (Figures 14 and 15). The number of observations decreased in the 1990s (n=838) and respondents reported that the herring were concentrated in fewer places during that decade (Figure16) as compared to the 1980s.

In the OK there were more observations in the 1980s (n=255) compared to the 1970s (n=180) and the 1990s (n=82) (Figures 17-19). Observations in all the bays except Resurrection increased in the 80s, especially Aialik, Nuka, Harris bays and Port Dick. Three observers saw juvenile herring in Port Dick for several years in the 70s and all the 80s. Respondents reported that juvenile herring distribution was greatly restricted in the 1990s as compared to the previous two decades.

The number of juvenile herring observations by commercial salmon fishing district was also compared by decade (Table 4; Figures 6-8). During all three decades, the eastern district had a large number of observations compared to other districts. In the 1970s and 1980s, the southwest district also had a large number. In the northern district, the number of observations was large in the 1970s, but lower than either the eastern or southwestern. In all districts, except the southwest district, observations peaked in the 1980s and were the lowest in the 1990s as did the number of observers. The observations of large numbers of juvenile herring in the 1980s is consistent with large years classes of adult herring reported by ADFG (Donaldson et al. 1992) in the 1980s. Herring cohorts from 1984, and 1988 were particularly large and in during the summer of 1985 biologists reported "an unusually large biomass of herring throughout the area, a significant portion of which were juvenile fish."

Herring Spawning and Eggs

The distribution of spawn documented by ADFG (unpublished data, Cordova Area Office) occurred primarily on the eastern, northern, and Montague districts of the sound (Figure 20). However, respondents in this project were able to add historic spawning sites in areas ADFG no longer monitors by aerial survey (Figures 21). In particular, herring spawning was reported by respondents along western coastlines in PWS, in Port Wells, and on the Copper River Delta. These locations were not included in the ADFG records. The traditional knowledge of elders holds that spawning patterns have changed since 1964. One native respondent reported of what an elder told him: " He says that people tell him years and years ago, Tatitlek was the first spawning area each spring, but it's not so now. There used to be a second season of spawning, in June, around Mummy Bay, in the early 50s. He says the uplift from the earthquake may have changed spawning patterns."

Other Forage Fish Species

In PWS and the OK, respondents reported locations of sand lance, eulachon, capelin, and capelin spawning areas (Figures 22 and 23). In PWS, sand lance were reported mainly on beaches and especially in bays in eastern, northern and southwestern areas. Within PWS, capelin were reported in outer bays and exposed beaches in the southwest, in the north, around northern Montague Island and on Hinchinbrook Island. Outside of PWS, capelin and smelt (species unknown) were reported in Day Harbor. Capelin spawning was reported on the southeastern exposed beaches of Montague and Elrington Islands and at the head of Day Harbor. Eulachon were reported only in southwestern passes of PWS. There were no other notes regarding the age of the fish observed. In the OK, sand lance were reported near many of the beaches along the coast from Resurrection Bay to Port Dick. Capelin were reported in or near Resurrection and Two Arm Bays. A pilot working with a fisherman reported that he found capelin only in Resurrection Bay and not along the entire OK coastline as were herring. In addition, smelt (unknown species) were reported outside of Two Arm Bay. Eulachon were reported outside of Aialik and Harris Bays.

Discussion

The major finding of this study is that juvenile herring are broadly distributed in both PWS and the OK and can be found during almost any season, but are easier to observe in the summer because of their shallow distribution. However, the biomass of herring varies considerably from place to place. Several respondents reported that PWS was one large nursery area and that bays were important for their development. However, they did not single out a particular bay or set of bays that were more important as nursery areas than any other bay. Others reported that the shallow estuaries at the heads of deep bays were places they had encountered juveniles and they felt these areas were nurseries. From examining the results from all respondents, there were several bays that were reported more often than any other bay. Port Gravina, Port Fidalgo, Port Wells, Port Chalmers, Stockdale Harbor, and Eaglek Bays were bays that stood out in PWS and Resurrection Bay, Port Dick, Day Harbor, and Aialik Bays along the OK.

We were also able to report on herring spawning and adult herring co-occurring with juvenile herring in regions and seasons outside of those studied by the management agency for commercial fisheries management. The observations of juvenile herring mixing with adults in northern Montague and occurring "on top" of the adult schools is not published in any other source to our knowledge. The addition of western PWS and the Copper River Delta as former spawning areas is also of historic ecological significance.

Another important documentation was a confirmation of what ADFG biologists from the Homer office have historically observed (Schroeder, 1989). They reported huge numbers of age-1 and age-2 herring along the OK coast in 1981 and 1989. Yet following these large biomasses there was not a productive fishery as would have been expected. Instead, there were a number of small fisheries for a handful of years in the 1980s limited to low value and consisting mainly of 3 and 4 year olds. Schroeder and respondents from our study believe that the reason a large fishery has not developed along the OK is that these herring are overflow from PWS spawning and larval drift, and that juveniles rearing on the OK eventually return to PWS to spawn. In other words, the OK can be considered one large nursery area for the PWS herring population and resulting commercial fishery. This has very significant ramifications on management and stock assessment for PWS since the OK is not considered part of the region and is excluded during surveys (Donaldson et al. 1992, 1993 and 1995).

Earlier this century fisheries biologists tried to grapple with the same issue of delineation of the herring populations. Rounsefell (1929) stated that "In determining the causes of the fluctuations in abundance one of the most important questions to be faced is that of the degree of migration, as upon that depends the relative interdependence of the populations of different regions. The existence of a single stock of herring, freely intermingling and migrating along the narrow coastal banks, would mean that any fluctuations or depletion would be widespread, and that any regulations, to be effective, would have to consider the whole coast as a unit. On the other hand, if local "races" were present, each locality would have to be treated as a separate unit, since it would then be possible to greatly reduce the supply in one area without affecting it elsewhere, (p.229)." Based on historic comments, we recommend that the delineation of the PWS herring population, the importance of nursery bays in PWS versus the OK, and effects on juvenile herring mortality in both regions are important future study subjects for fisheries biologists.

Our main disappointment was the low sample size due mainly to a restriction in funding available. We were able to conduct pre-interviews to set up the pool of respondents from which to sample. We were also not able to travel outside Alaska to seek available respondents living in Washington, California and other areas. If a sufficient number of respondents are available, a sampling design entailing random, stratified random, or post-stratification and re-sampling can be completed. The result would enable a true statistical analysis of the results. In our case, our sample sizes and selection methods were insufficient to allow a formal statistical analysis. The power with sample sizes of 3 and less is insufficient to responsibly deliver significant conclusions. We recommend a minimum of 100 respondents in order to result in at least 5 respondents in each biological (species), spatial (region), seasonal, or decadal strata. We also recommend conducting a pre-interview to identify, locate, and stratify the potential pool of respondents prior to respondent selection. Because of our low sample size, there were very likely juvenile herring or other forage fish in regions that were not reported simply because our respondents were not active in those areas.

This project demonstrated that extensive qualitative ecological information about non-harvested age classes or species can be obtained from tek and local interviews. These observations were shared with cooperating scientists who based their initial survey design on the results (Stokesbury et al., in press; Norcross et al. in prep). These observations were also shared with contractors from the National Oceanographic and Atmospheric Administration, Department of Commerce and assimilated with other ecological data to develop a geographic data base of sensitive marine areas in the EVOS impacted region (Jeffrey Dahlin, Research Planning, Inc., Columbia, South Carolina, personal communications). Knowledge that would have disappeared within the next decade with the death of many of our respondents is now forever preserved via this report.

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Table 1. Number of respondents involved in each activity category and average, median, and combined number of years of experience involved in that activity.

		Years of Experience		
Activity Category	**Number of Respondents**	**Average**	**Median**	**Total**
Fisherman	37	31	32	1122
Professional Pilot	17	18	18	331
Herring Spotter Pilot	13	14	12	195
Salmon Spotter Pilot	11	6	6	65.5
Biologist	5	16	18	65
Herring Fishermen	26	17	18	430
Salmon Fishermen	34	30	31	984
Other Occupations	9	21	18	206

Table 2. Numbers, locations, and method of observations of juvenile herring by region in Prince William Sound. The most frequently reported locations by regions included Port Gravina (PG), Port Fidalgo (PF), Eaglek Bay (EB), Port Wells (PW), Naked Island (NI), Port Chalmers (PC), Stockdale Harbor (SH), Jeanie Cove (JC), Patton Bay (PB), and Day Harbor (DH).

	Regions							
	1	2	3	4	5	6	7	8
Total Number of Observations	519	484	382	343	393	306	6	401
Number of Observers	15	16	14	13	7	18	1	12
Earliest Reported Observation	1970	1934	1970	1938	1970	1970	1994	1970
Most Frequently Reported Location	PG	PF	EB	PW	NI	PC, SH	JC, PB	DH
Number Reported There	304	215	103	120		78	6	90
Most Common Method of Observation	plane	plane	plane	caught	visual	plane	plane	caught
Second Most Common Method	caught	visual	caught	plane	plane	visual		visual
Third Most Common Method	sonar	caught			caught	caught		plane
Fourth Most Common Method	visual							sonar

Table 3. Numbers of juvenile herring observations by season in Prince William Sound (PWS) and the Outer Kenai (OK).

	Season			
Area	**Spring**	**Summer**	**Fall**	**Winter**
PWS	464	1776	374	204
OK	243	588	41	66

Table 4. Number of observations (n) and respondents (res) by decade and commercial salmon fishing district in Prince William Sound and the eastern portion of the Outer Kenai.

	1970s		1980s		1990s	
District	n	res	n	res	n	res
Southeast	27	2	80	2	1	1
Eastern	194	4	248	7	160	4
Northern	126	3	178	7	119	4
Southwest	196	5	161	6	31	5
Montague	10	1	77	4	70	4
Outer Kenai	18	2	27	2	0	0

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Appendix I: Interview Guide

ID BIRTHDATE
DATE COMMUNITY

1. What year did you begin working in the Sound?
2. Please describe what your work was like:

3. Which fisheries were involved in, in PWS?
   a) what time of year?
   b) Which years?
      I) salmon seine _____ to _____ summer
      ii) salmon gillnet _____ to _____ summer-fall
      iii) herring pound _____ to _____ spring
      iv) herring seine _____ to _____ spring
      v) herring gillnet _____ to _____ spring
      vi) dive _____ to _____ _______
      vii) handpick _____ to _____ _______
      viii) shrimp pot _____ to _____ _______
      ix) bottomfish _____ to _____ _______
      x) bait herring _____ to _____ _______

4. Were you ever a spotter for fisheries?
   a) Which fisheries?
   b) Which years?
      I) Salmon seine ____ to ____
      ii) Herring pound ____ to ____
      iii) Herring seine ____ to ____
      iv) Other __________

5. How did the amount of time you spent in the Sound change since you began working here?

6. What activities take you out in the Sound now?

7. What months are you usually out in the Sound?

8. During those months, how often do you go out?

9. SHOW ON THE CHART THE GENERAL AREA OF THE SOUND YOU USE.
10. During what years were you out in the Sound the most?
    a. DRAW CIRCLES AROUND THE PLACES YOU USE MOST INTENSIVELY.
    b. Describe your activities there/ frequency duration.

JUVENILE HERRING

11. Are there places you think are particularly important for juvenile herring?

a) Which places?

b) Why?

12. Where do you think juvenile herring (age 0-2, about 4 inches long) winter?

13. CIRCLE THE AREAS YOU'VE SEEN JUVENILE HERRING IN ORANGE.
    I) What years did you see them there?
    ii) What season/time of year did you see them?
    iii) Did you identify them? How?
    iv) Describe where you see them-nearshore/offshore, surface/deep
    v) Can you recall how much you observed?

14. How often did you see juveniles there: For each observation, mark frequency on the chart or table.

C-CONSISTENTLY-"I'd see them almost every time I went there this time of year."
O-OCCASIONALLY-"I'd see them every once in a while this time of year."
R-RARELY-"I remember them showing up there once or twice."

15. Do you remember seeing concentrations of animals feeding on the herring?

16. Tell me about the changes changes you've seen in abundance of herring in the Sound.

ADULT HERRING-RED

17. Where have you seen schools of adult herring in spring and fall aside from Northern Montague Island, Port Gravina, Port Fidalgo, Tatitlek Narrows, and Green Island?

18. How did you know they were herring?

19. How often have you seen them there?

20. At each place describe where you saw them-nearshore/offshore, surface/deep.

21. What other animals do/did you see with them?

22. Where do you find adult herring in winter?

23. Has the distribution of adult herring changed over the years you've been working in the Sound? Tell me about the changes you've noticed.

24. Did you fish for herring for home use or gather spawn on kelp this year?

25. Did you notice any signs of disease?

26. Had you ever seen disease in herring before 1993?

OTHER FORAGE FISHES-GREEN

27. Did you ever see or catch other forage fish such as sandlance or capelin while out in the Sound?
    a) Describe what you saw or caught.
    b) Could you identify them now? How?

    c) When-year, season?
    d) Where-place, surface, deep

28. Have you seen them there before?

29. How frequently?
30. Have you noticed a change in abundance of these fish?

31. What other animals do you remember commonly associated with these schools of fish?

POLLOCK

32. Describe any changes you've noticed in pollock abundance and distribution since you began fishing/working in the Sound.
33. Where, what time of year, which years?
34. How often have you seen them there?
35. How does weather or ocean state on pollock abundance.
36. Did fish ever disappear completely from an area that you fished/hunted/used?
    a) why do you think that they disappeared?

Figures

Figure 20. Composite of herring spawning locations documented by aerial surveys in Prince William Sound from 1973 to 1998 (unpublished data, Alaska Department of Fish and Game, Cordova).

Figure 21. Composite of herring spawning locations documented by respondents from this study in Prince William Sound from 1930 to 1998.

Figure 22. Composite of forage fish observations, excluding herring, in Prince William Sound.

Figure 23. Composite of forage fish observations, excluding herring, along the Outer Kenai.

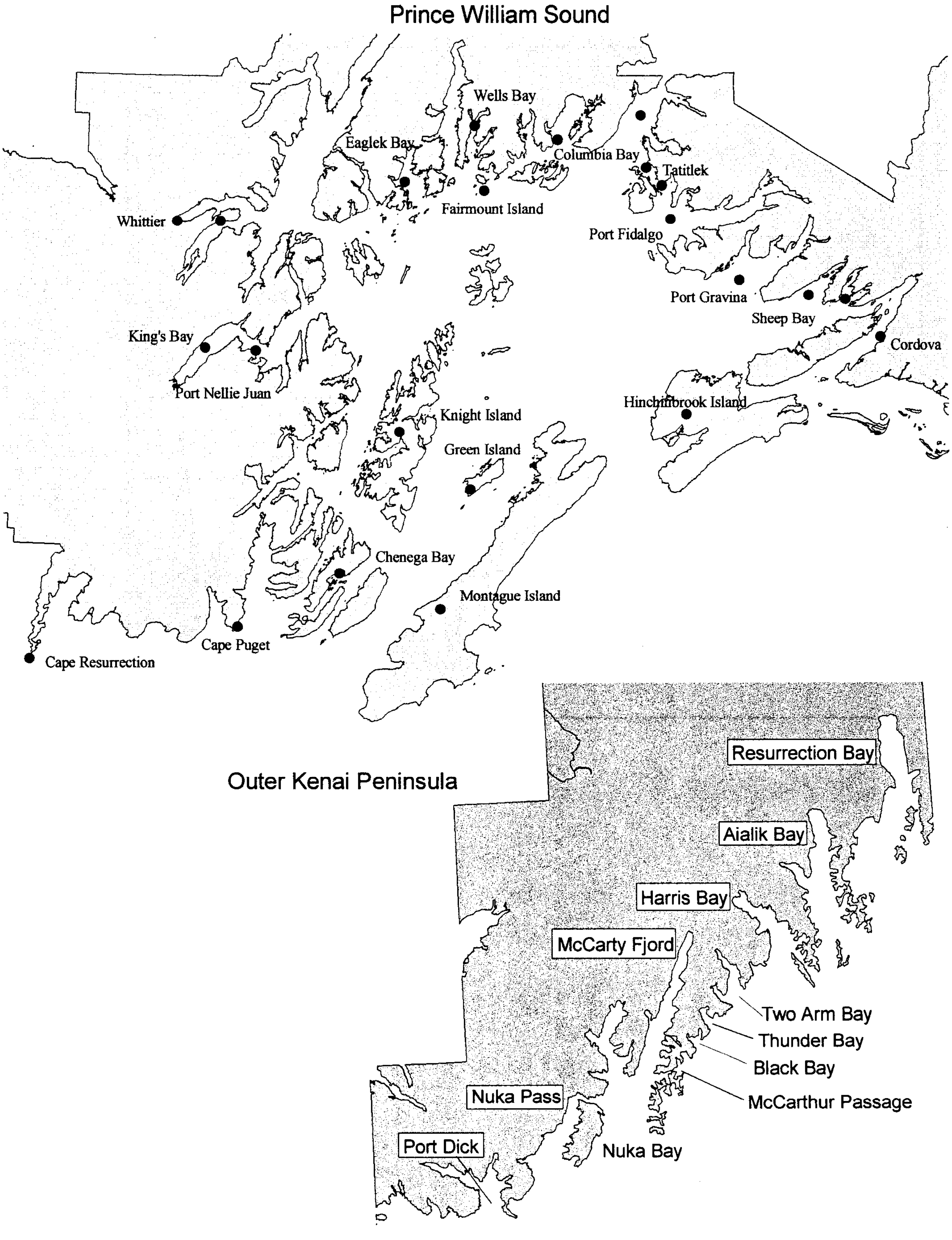

Prince William Sound
Wells Bay
Eaglek Bay
Columbia Bay
Tatitlek
Fairmount Island
Whittier
Port Fidalgo
Port Gravina
Sheep Bay
Cordova
King's Bay
Port Nellie Juan
Hinchinbrook Island
Knight Island
Green Island
Chenega Bay
Montague Island
Cape Puget
Cape Resurrection
Outer Kenai Peninsula
Resurrection Bay
Aialik Bay
Harris Bay
McCarty Fjord
Two Arm Bay
Thunder Bay
Black Bay
McCarthur Passage
Nuka Pass
Port Dick
Nuka Bay

Figure 1.

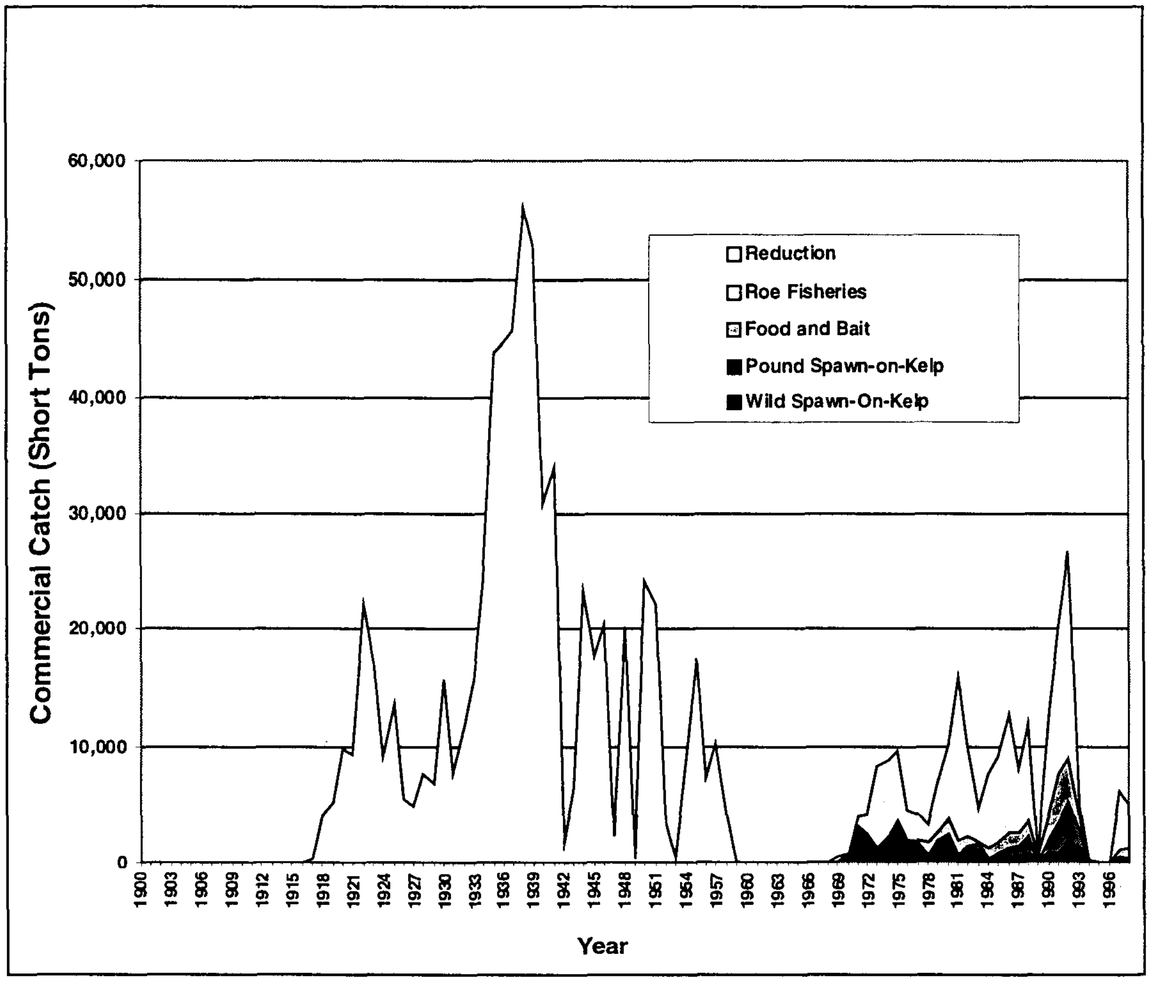

Commercial Catch (Short Tons)
60,000
50,000
40,000
30,000
20,000
10,000
0
1900
1903
1906
1909
1912
1915
1918
1921
1924
1927
1930
1933
1936
1939
1942
1945
1948
1951
1954
1957
1960
1963
1966
1969
1972
1975
1978
1981
1984
1987
1990
1993
1996
Year
□ Reduction
□ Roe Fisheries
▨ Food and Bait
■ Pound Spawn-on-Kelp
■ Wild Spawn-On-Kelp

Figure 2.

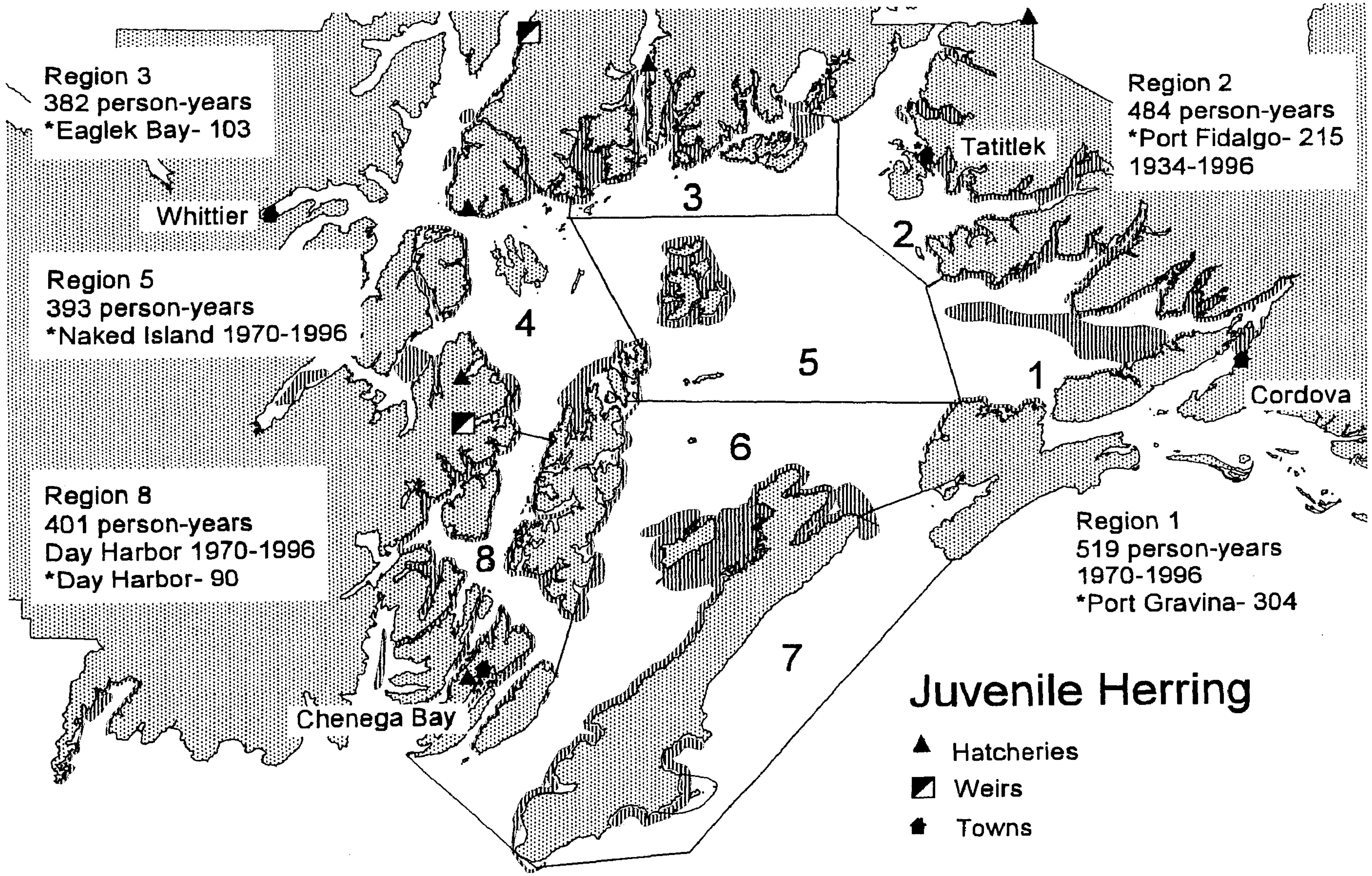

Region 3
382 person-years
*Eaglek Bay- 103
Region 2
484 person-years
*Port Fidalgo- 215
1934-1996
Tatitlek
Whittier
Region 5
393 person-years
*Naked Island 1970-1996
Region 8
401 person-years
Day Harbor 1970-1996
*Day Harbor- 90
Cordova
Region 1
519 person-years
1970-1996
*Port Gravina- 304
Chenega Bay
1
2
3
4
5
6
7
8
Juvenile Herring
Hatcheries
Weirs
Towns

Figure 3.

Figure 4.

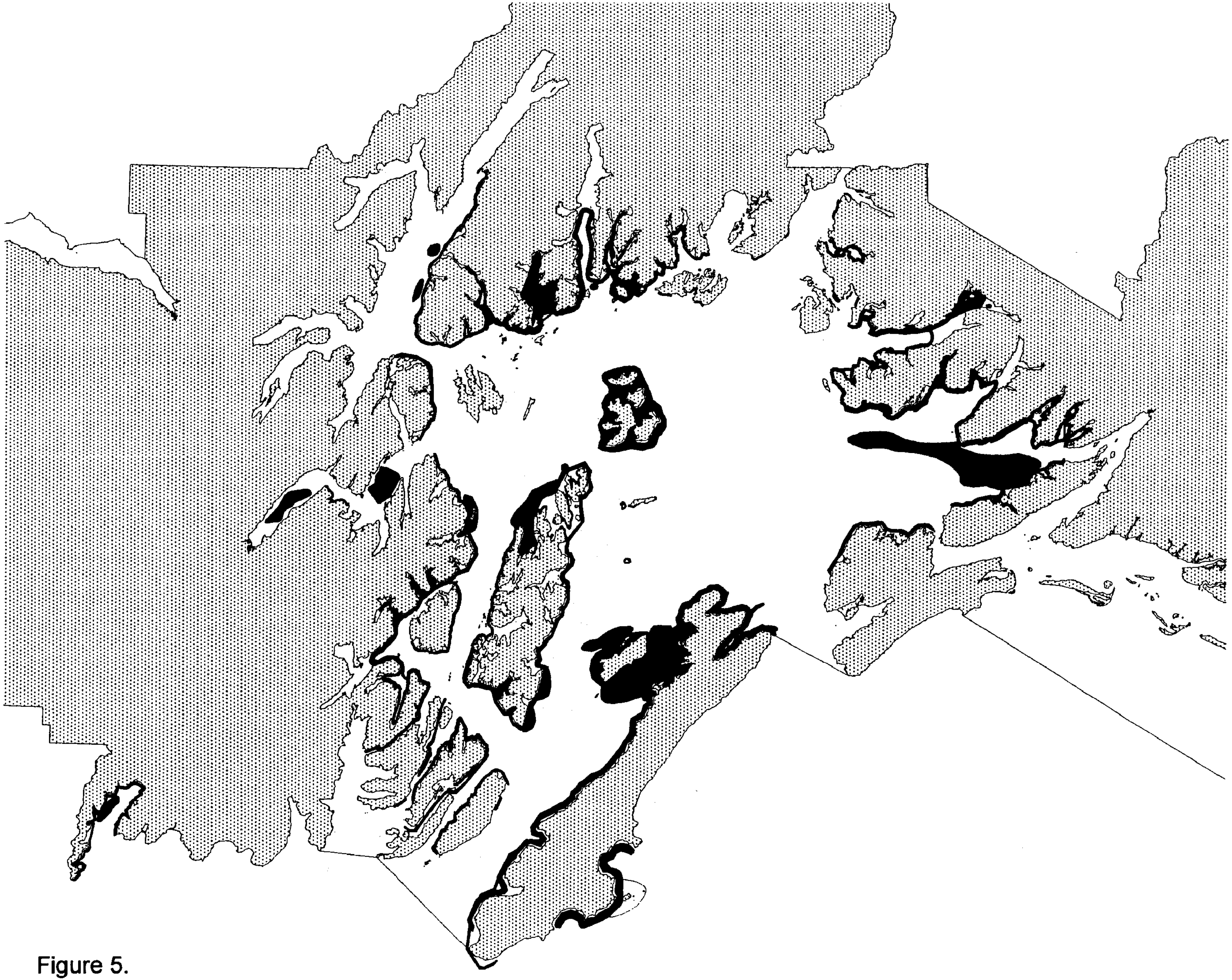


Figure 5.

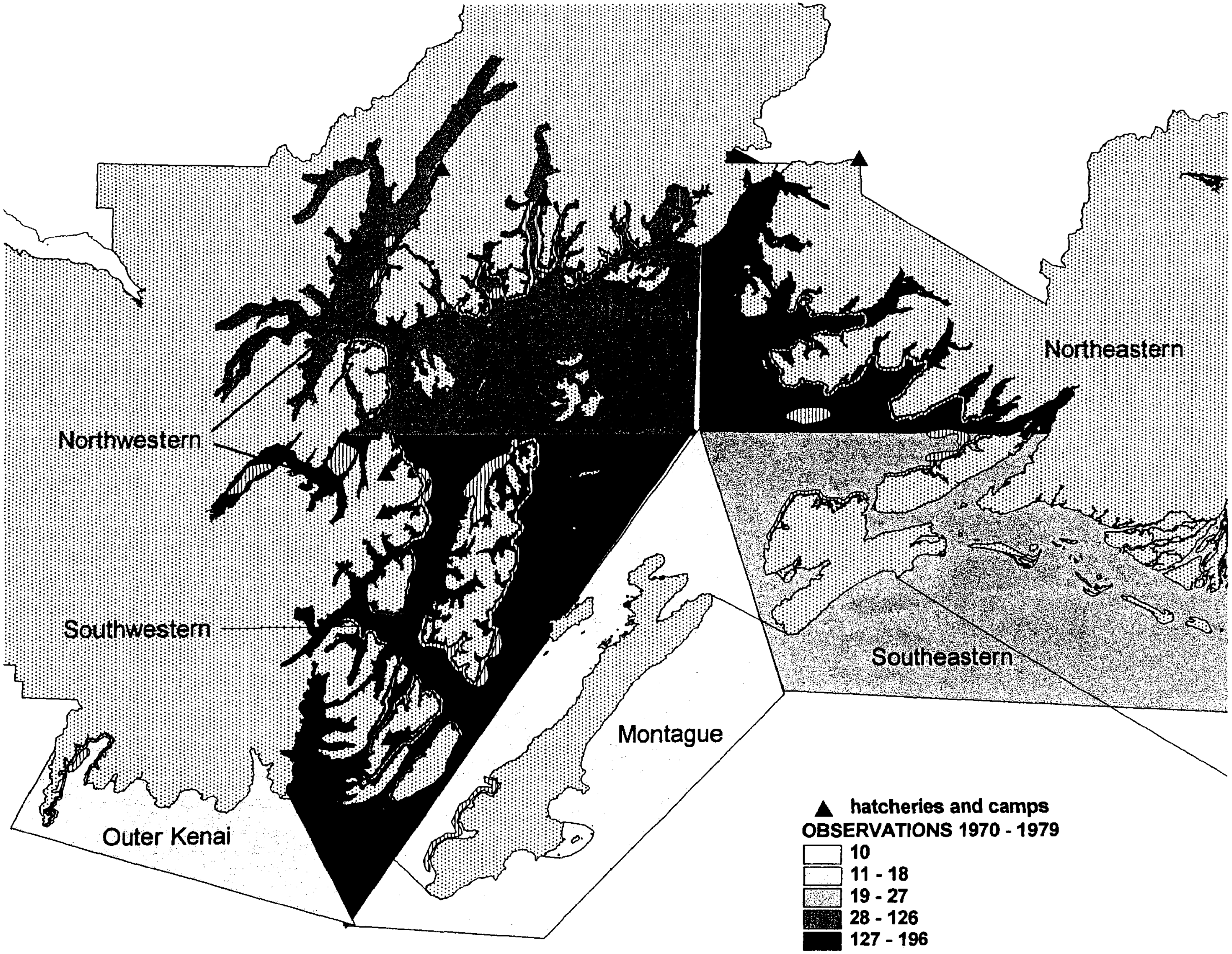

Northwestern
Northeastern
Southwestern
Southeastern
Montague
Outer Kenai
▲ hatcheries and camps
OBSERVATIONS 1970 - 1979
10
11 - 18
19 - 27
28 - 126
127 - 196

Figure 6.

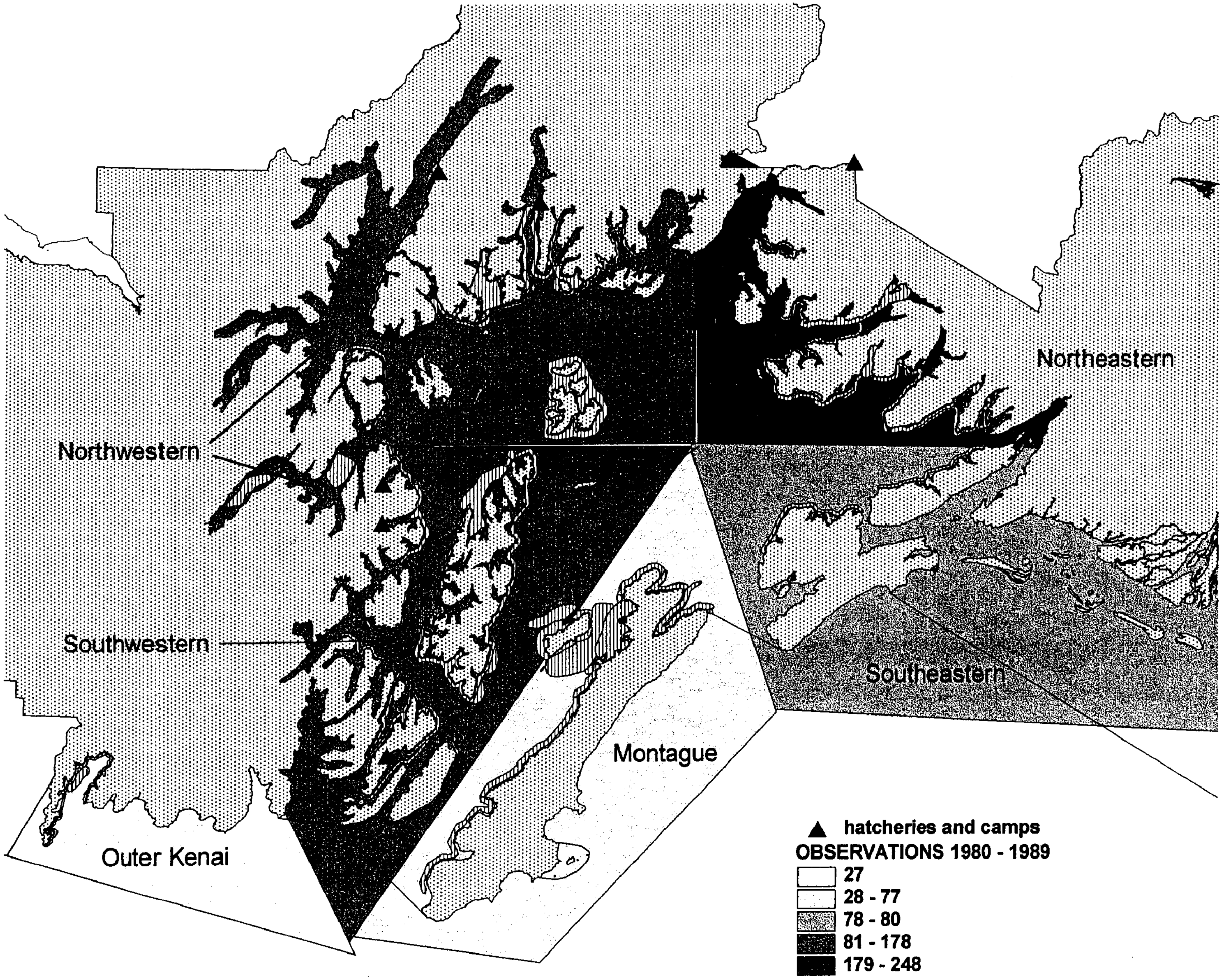

Northeastern
Northwestern
Southwestern
Southeastern
Montague
Outer Kenai
▲ hatcheries and camps
OBSERVATIONS 1980 - 1989
27
28 - 77
78 - 80
81 - 178
179 - 248

Figure 7.

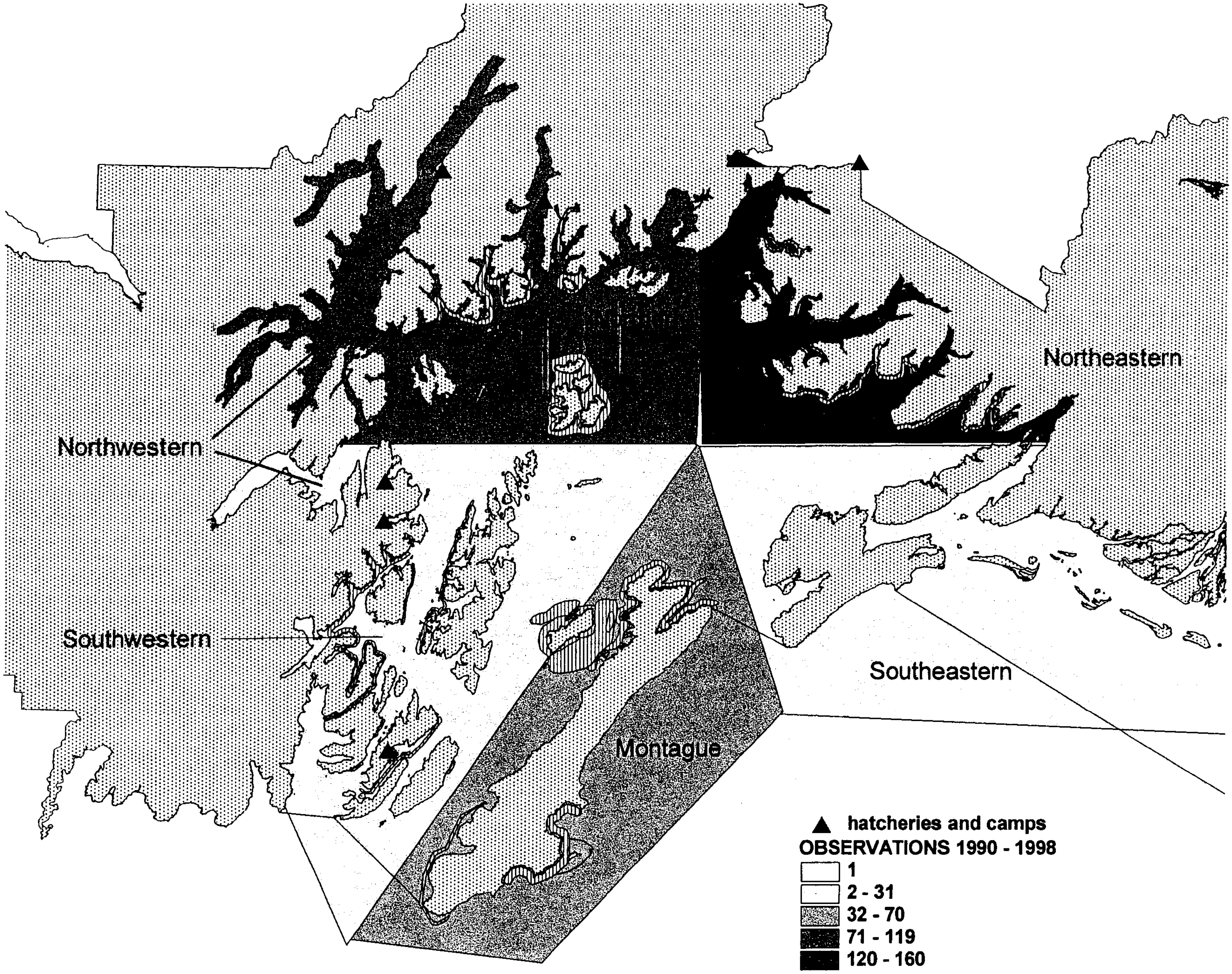
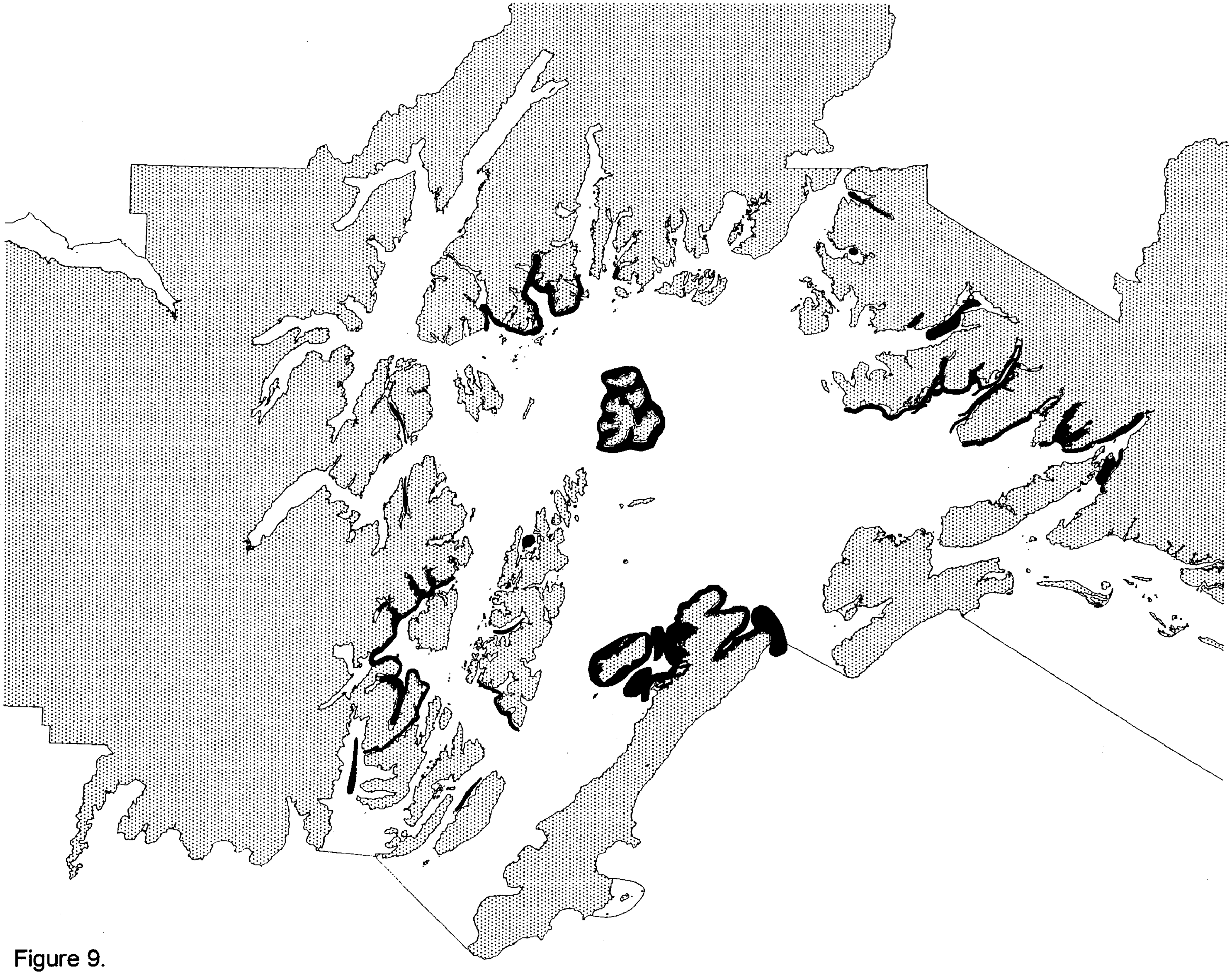

Northwestern
Northeastern
Southwestern
Southeastern
Montague
▲ hatcheries and camps
OBSERVATIONS 1990 - 1998
1
2 - 31
32 - 70
71 - 119
120 - 160

Figure 8.



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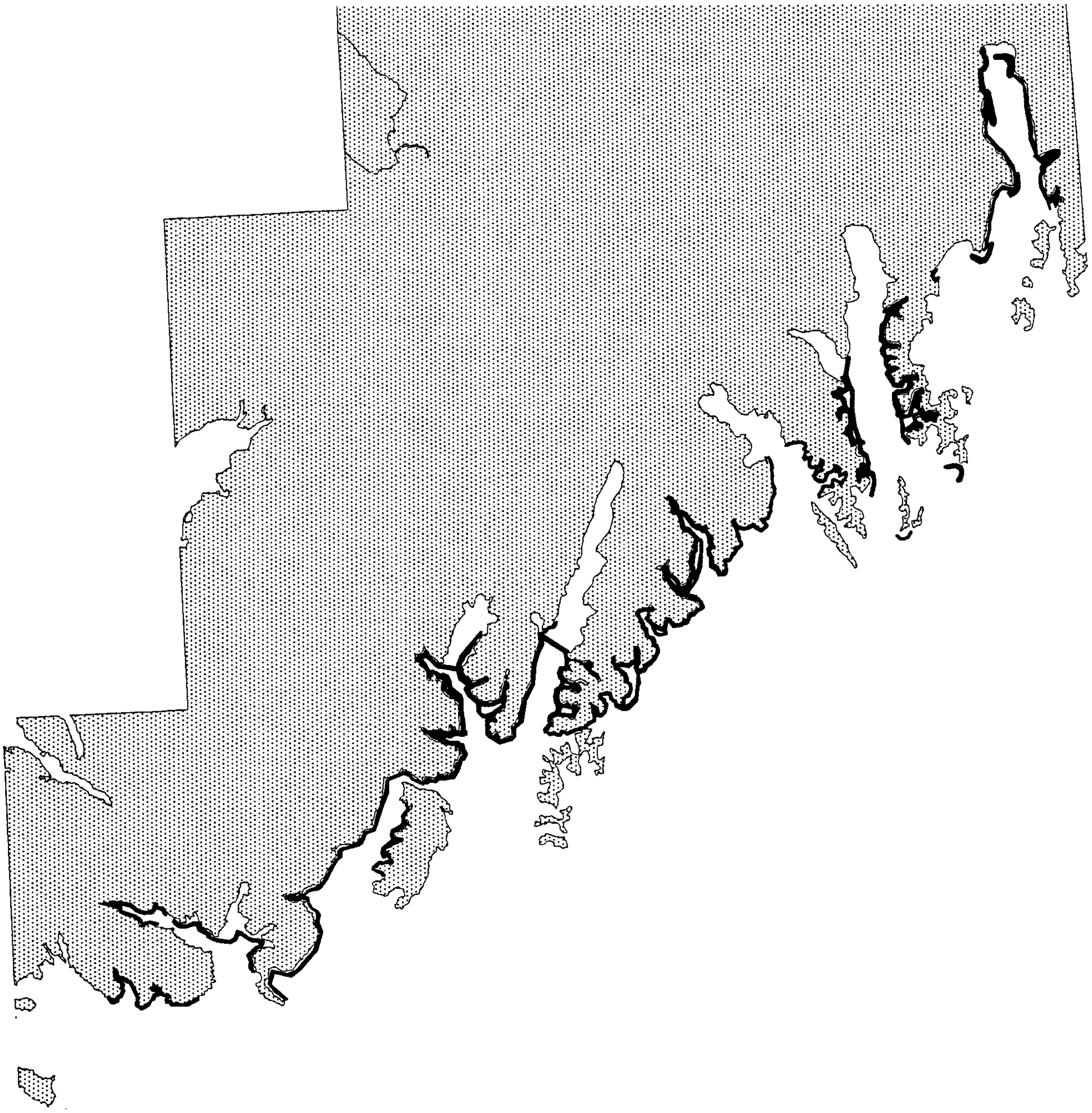

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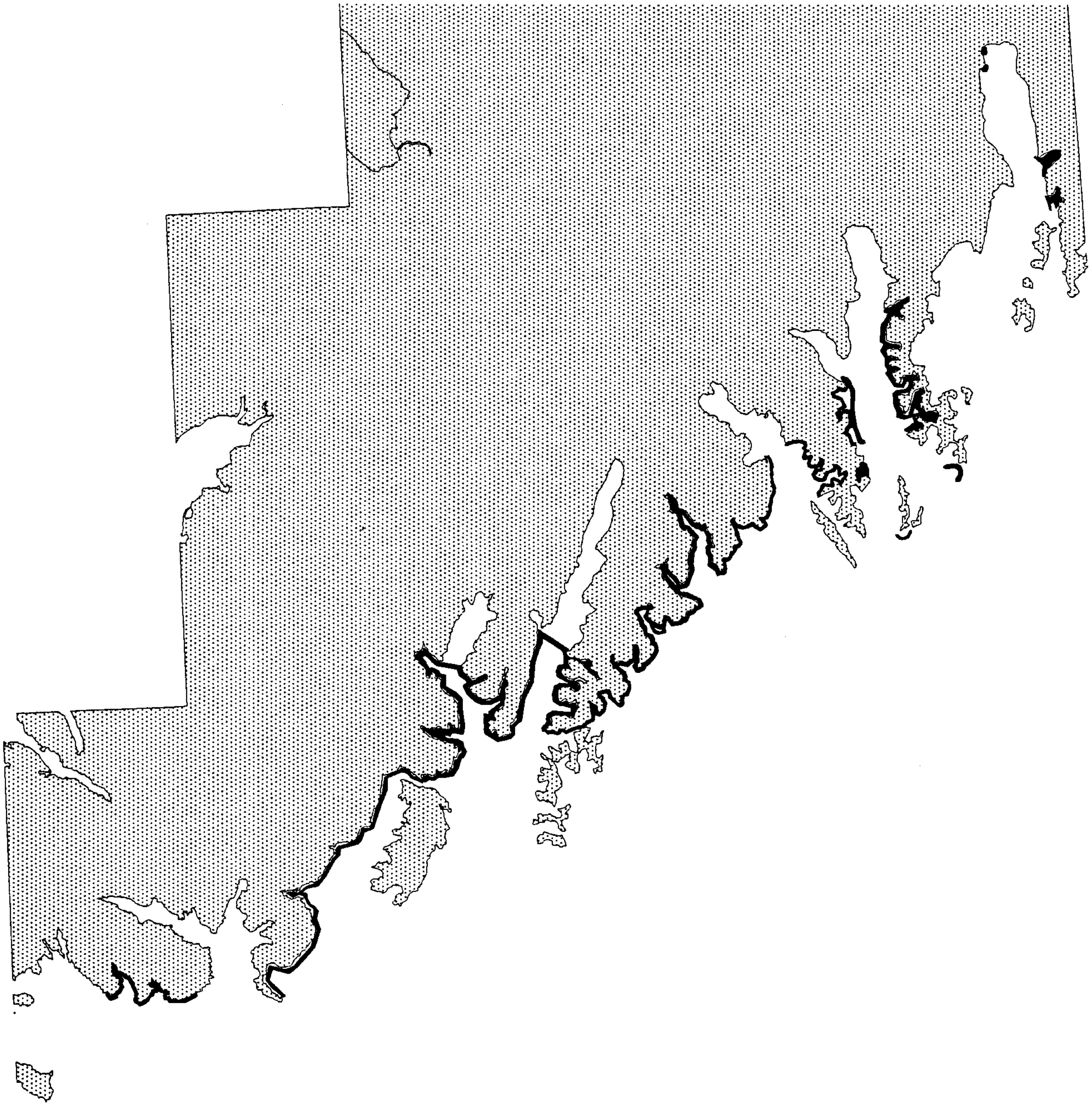

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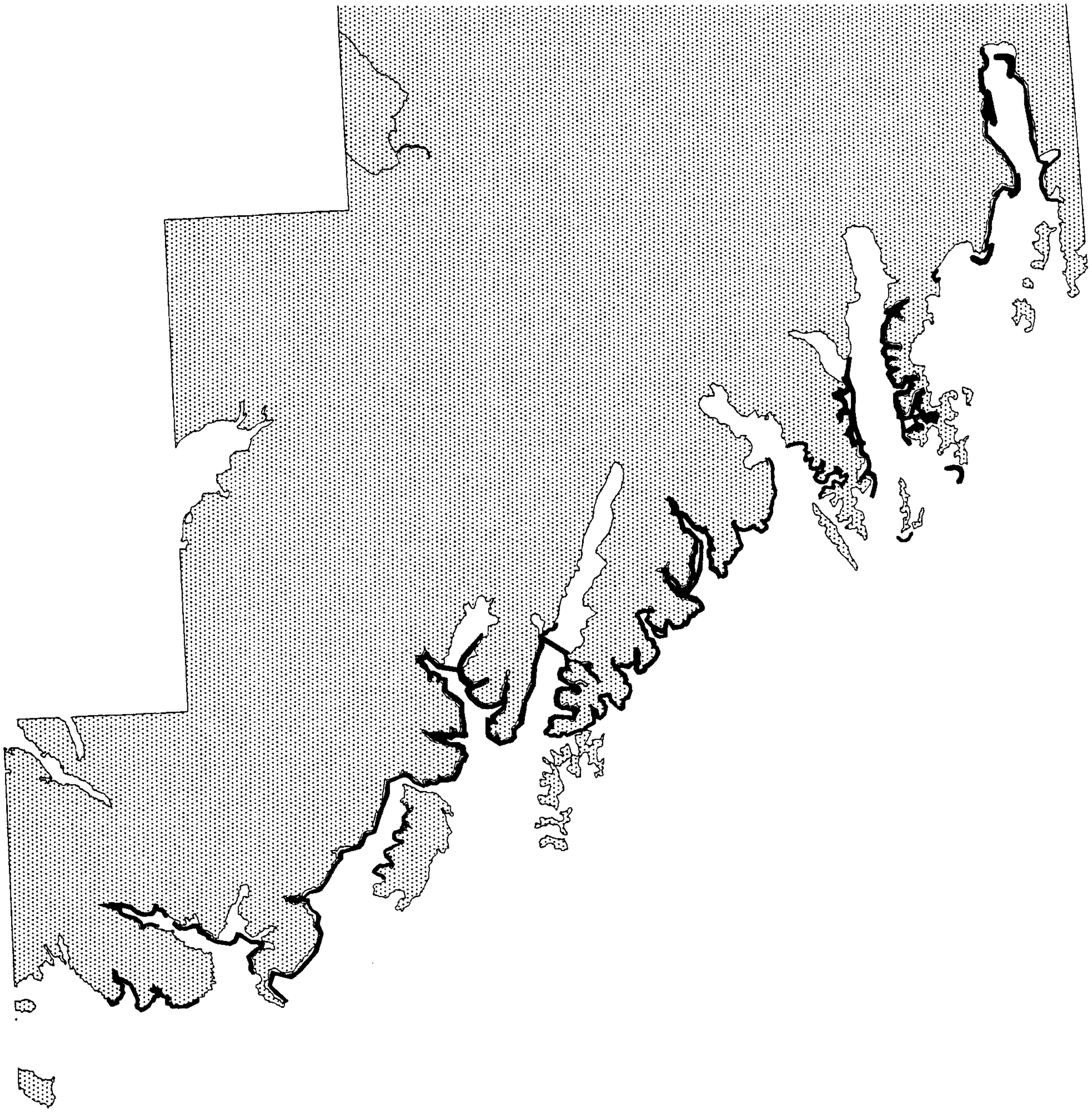

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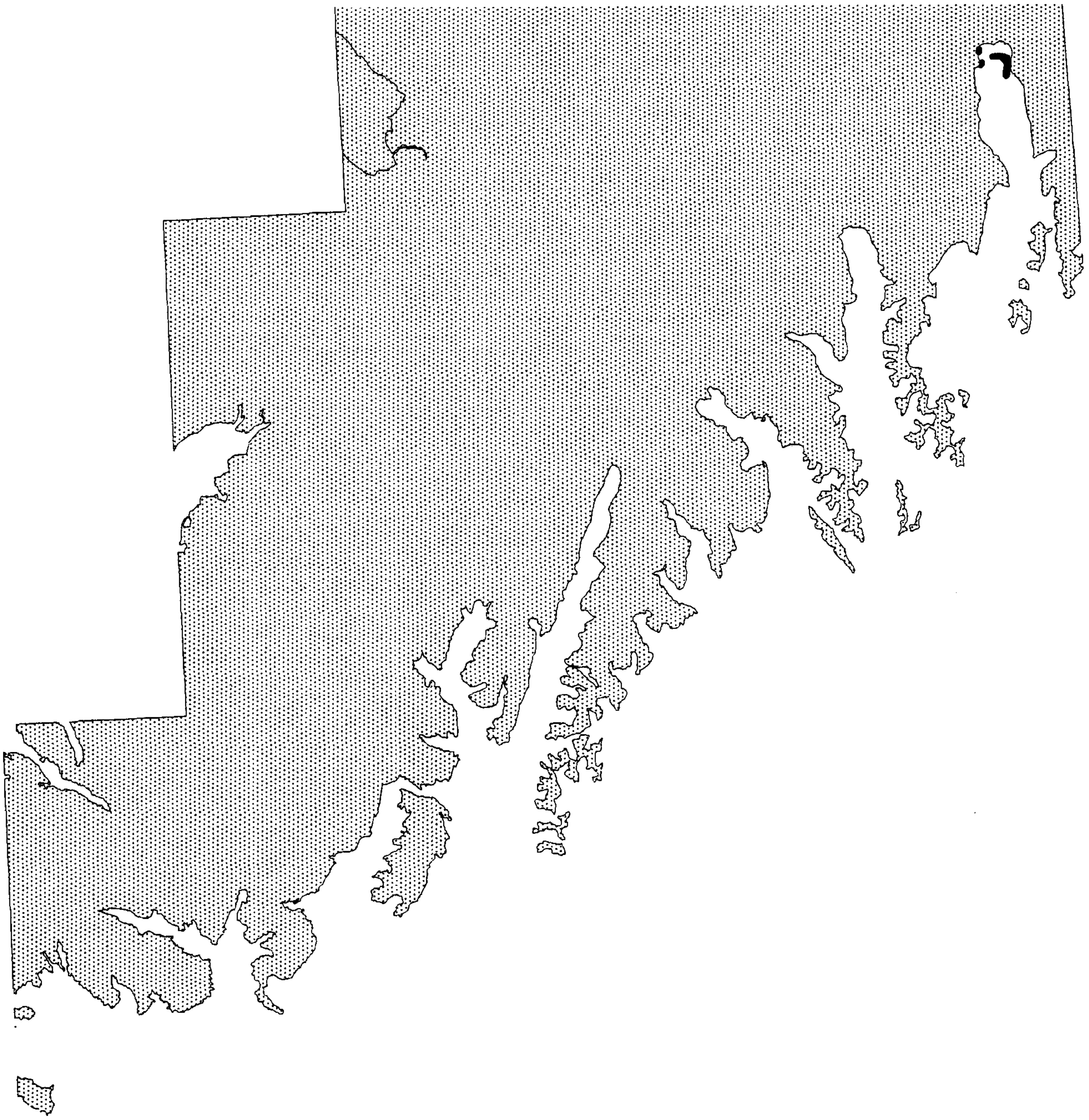

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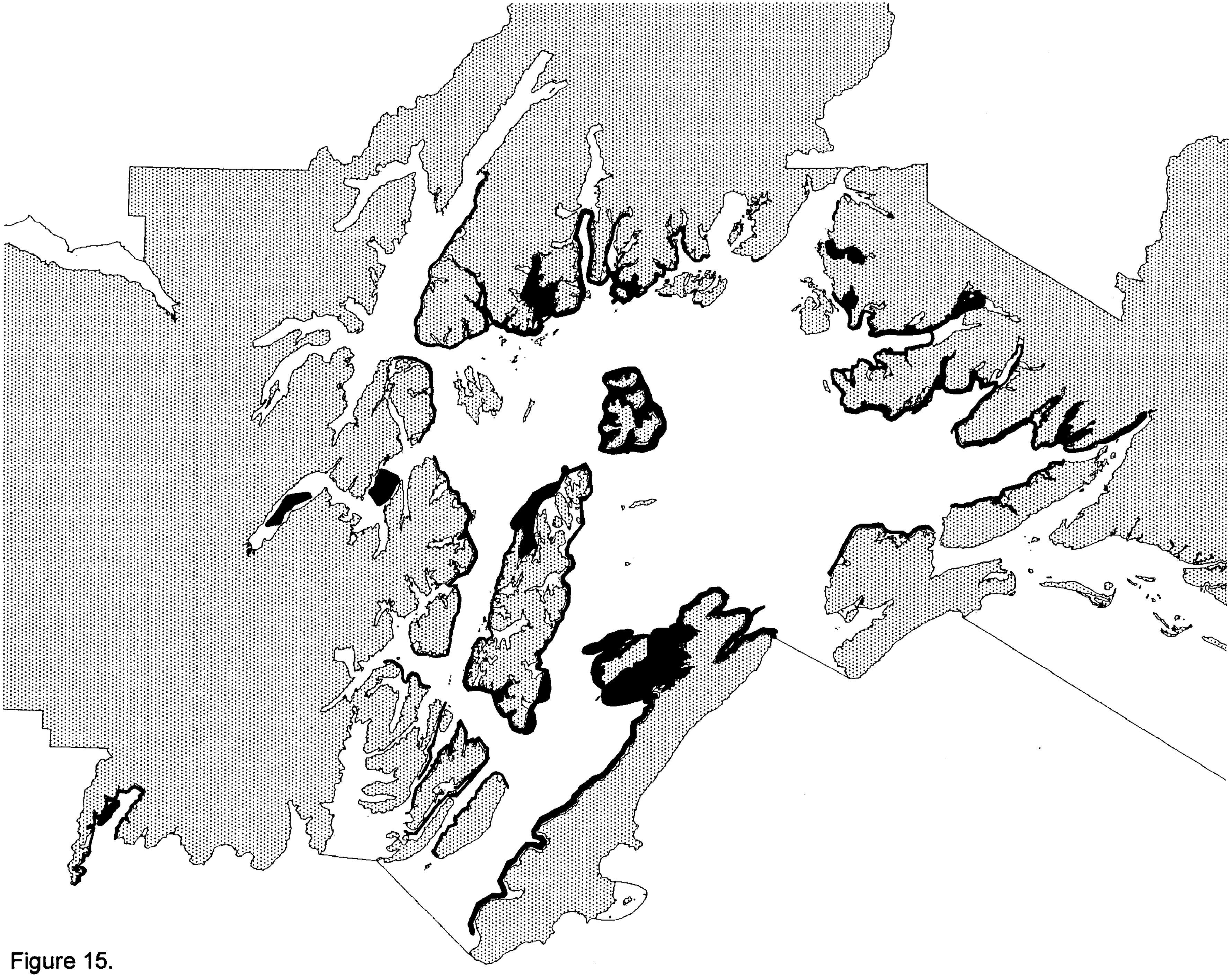

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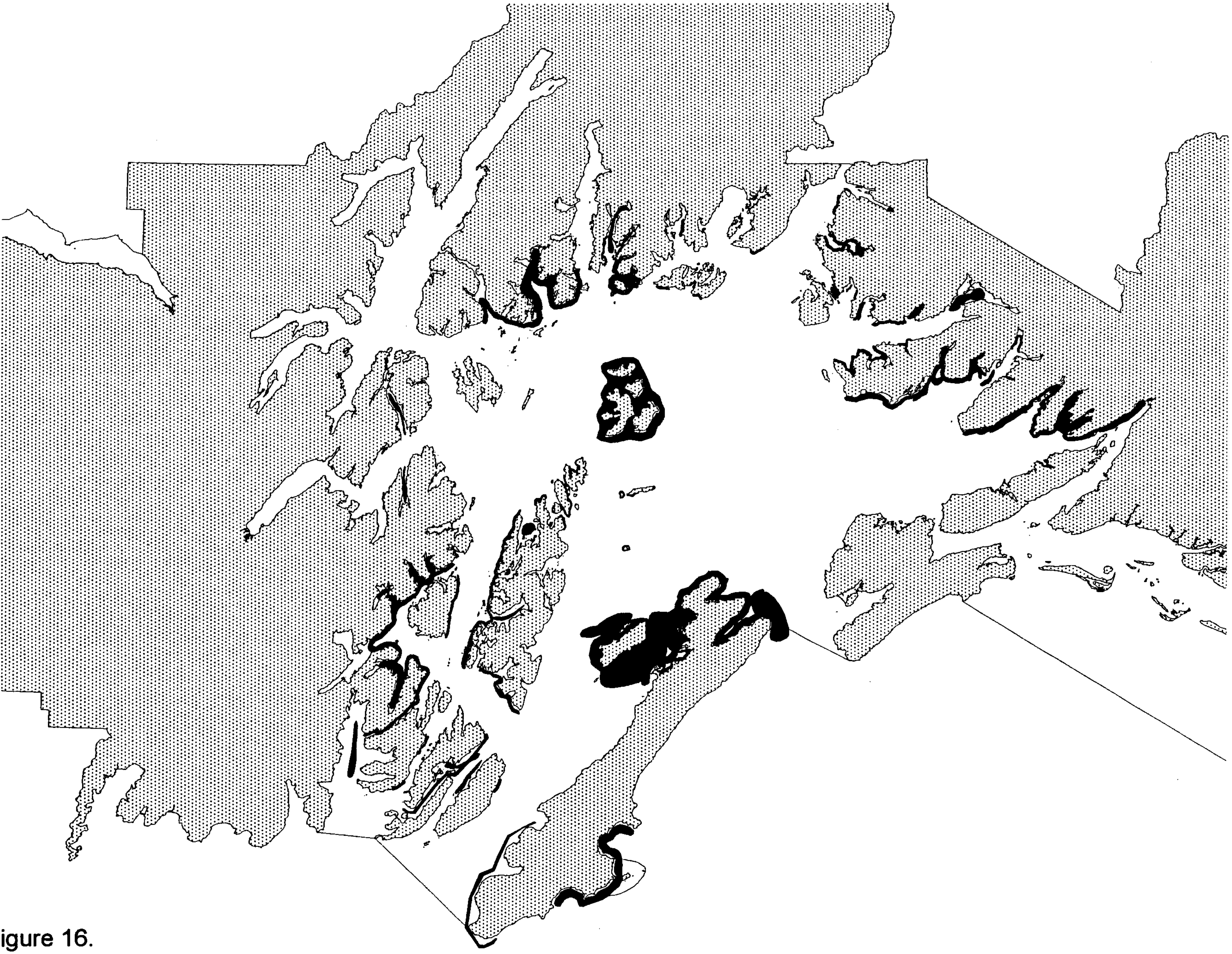

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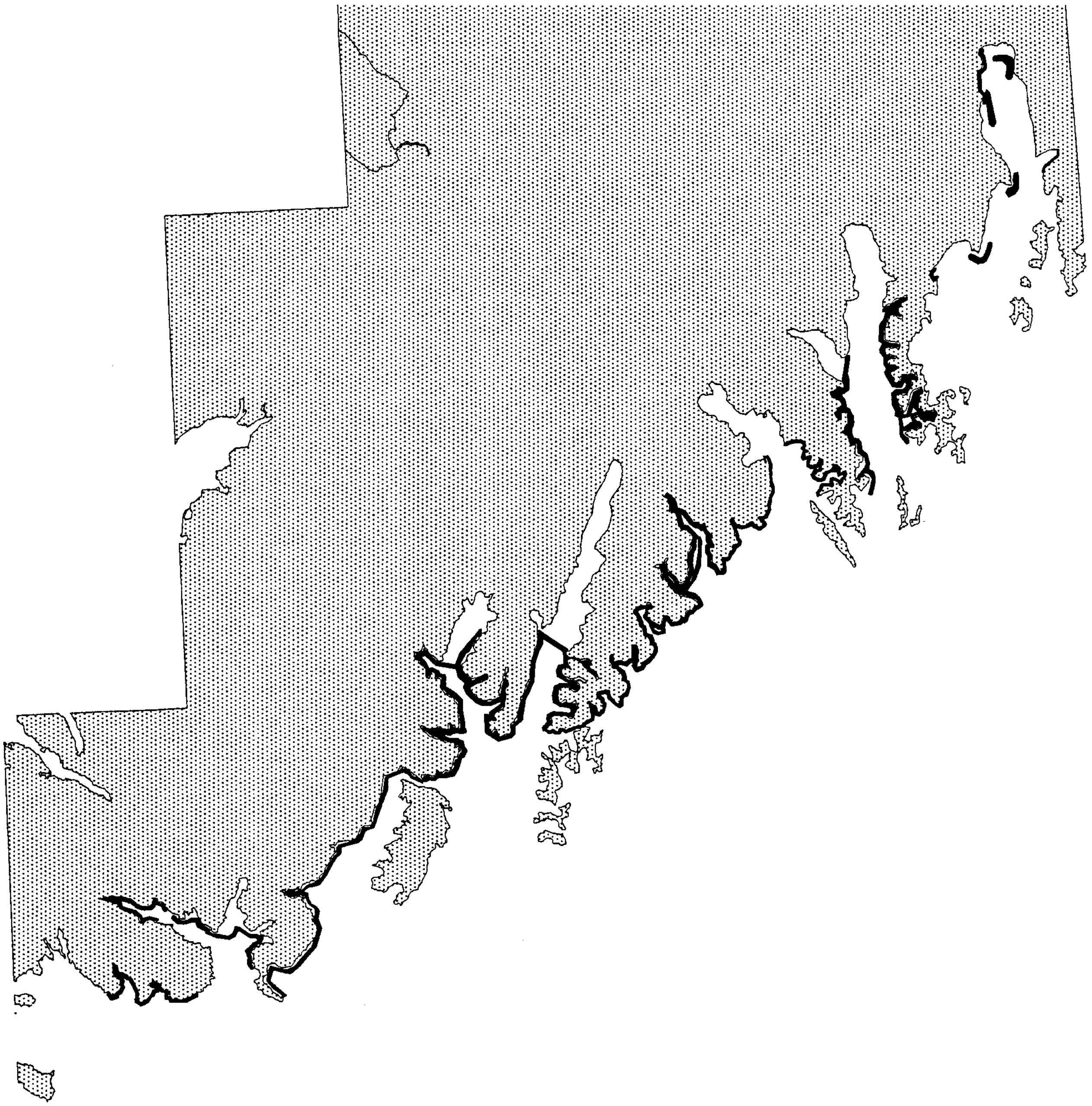

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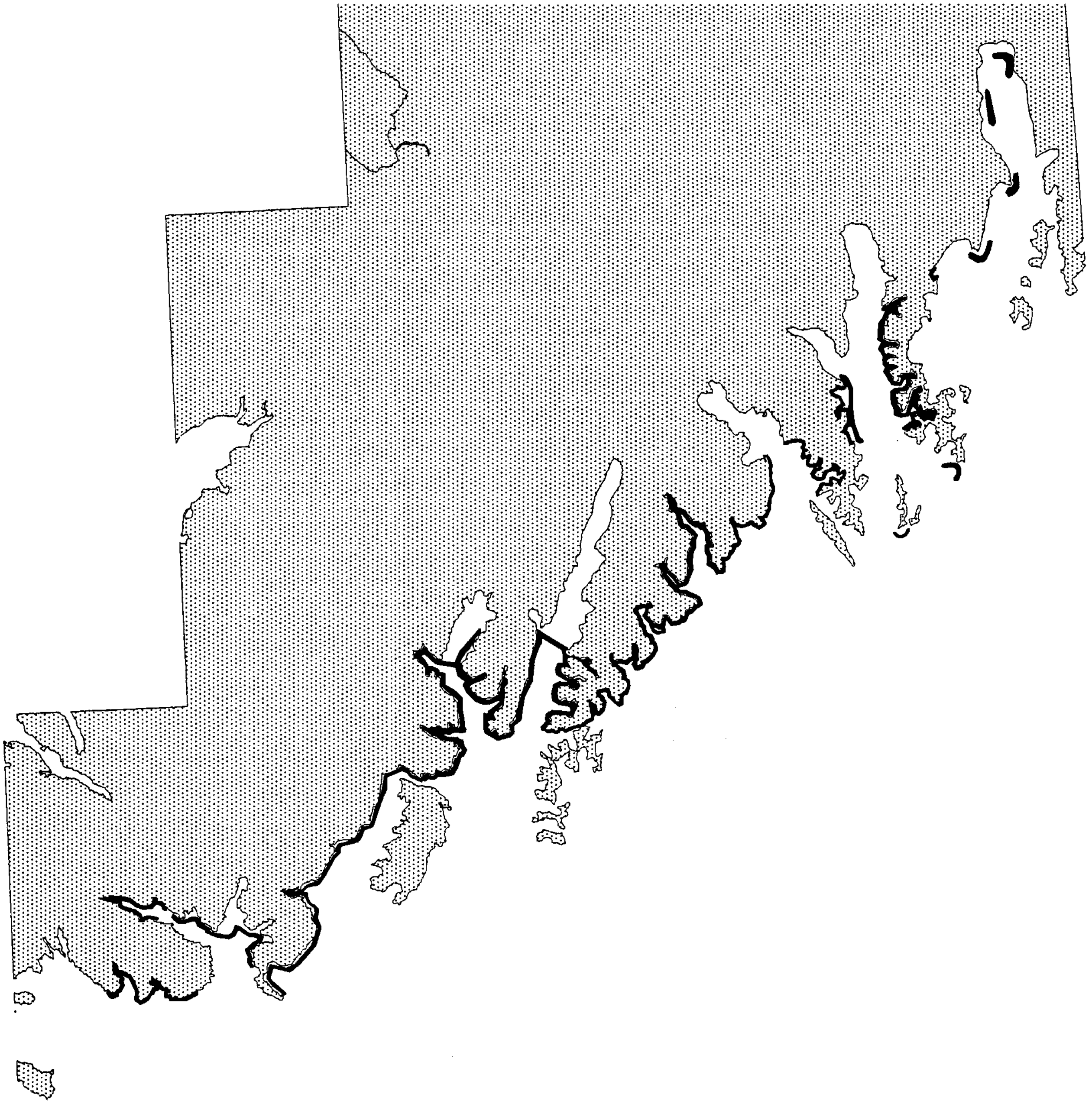

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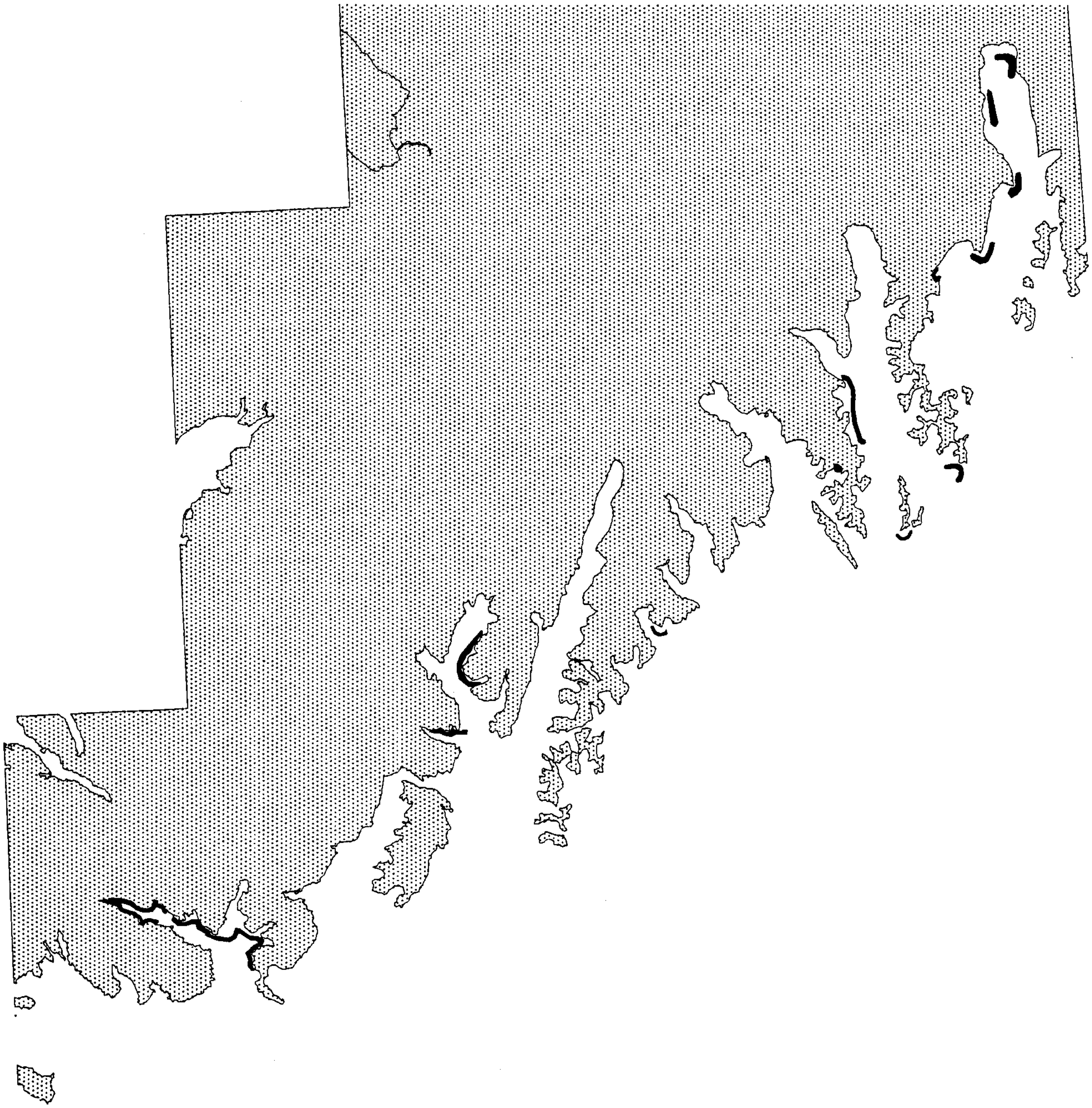
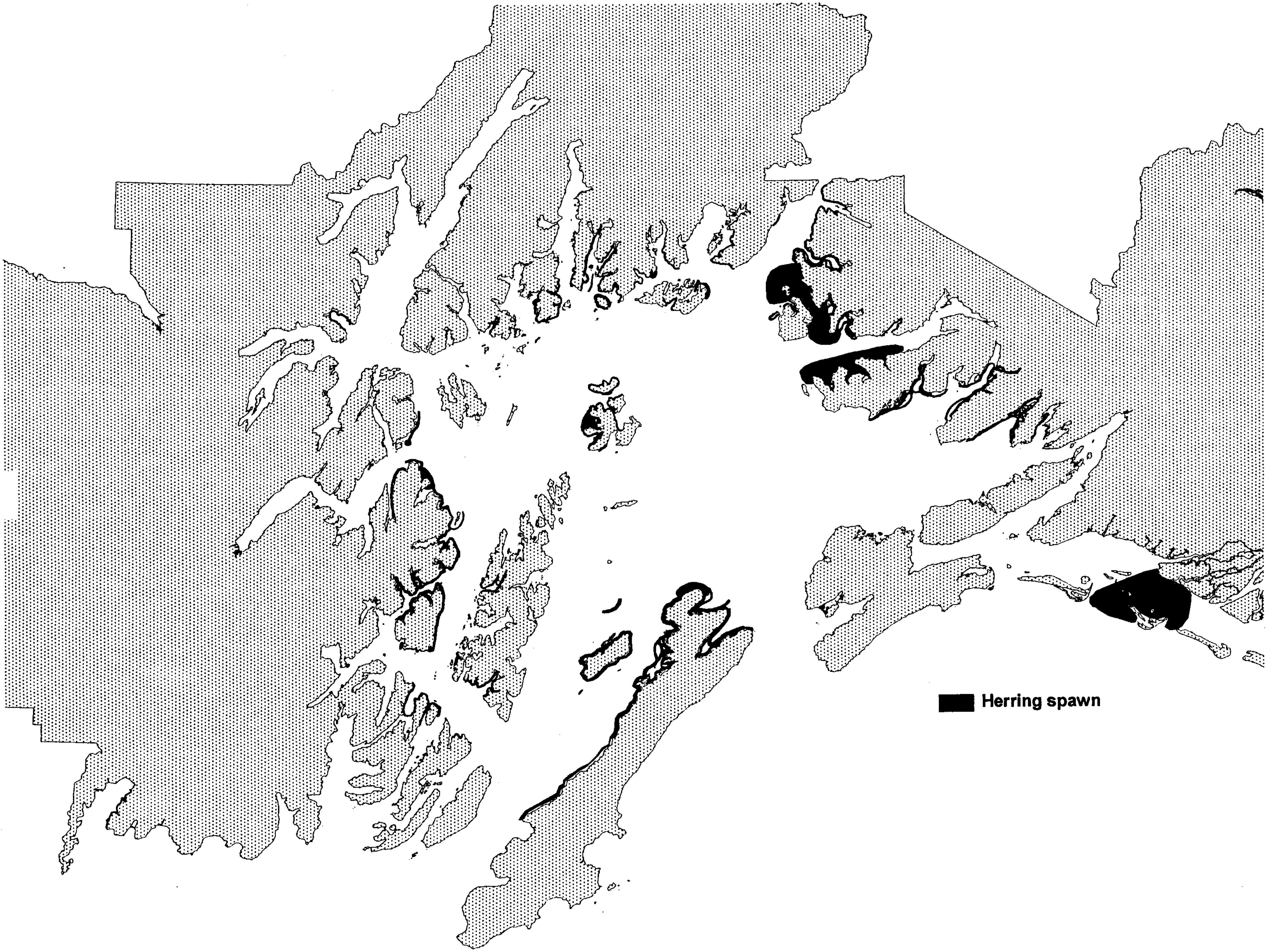


Figure 19.

Figure 20.



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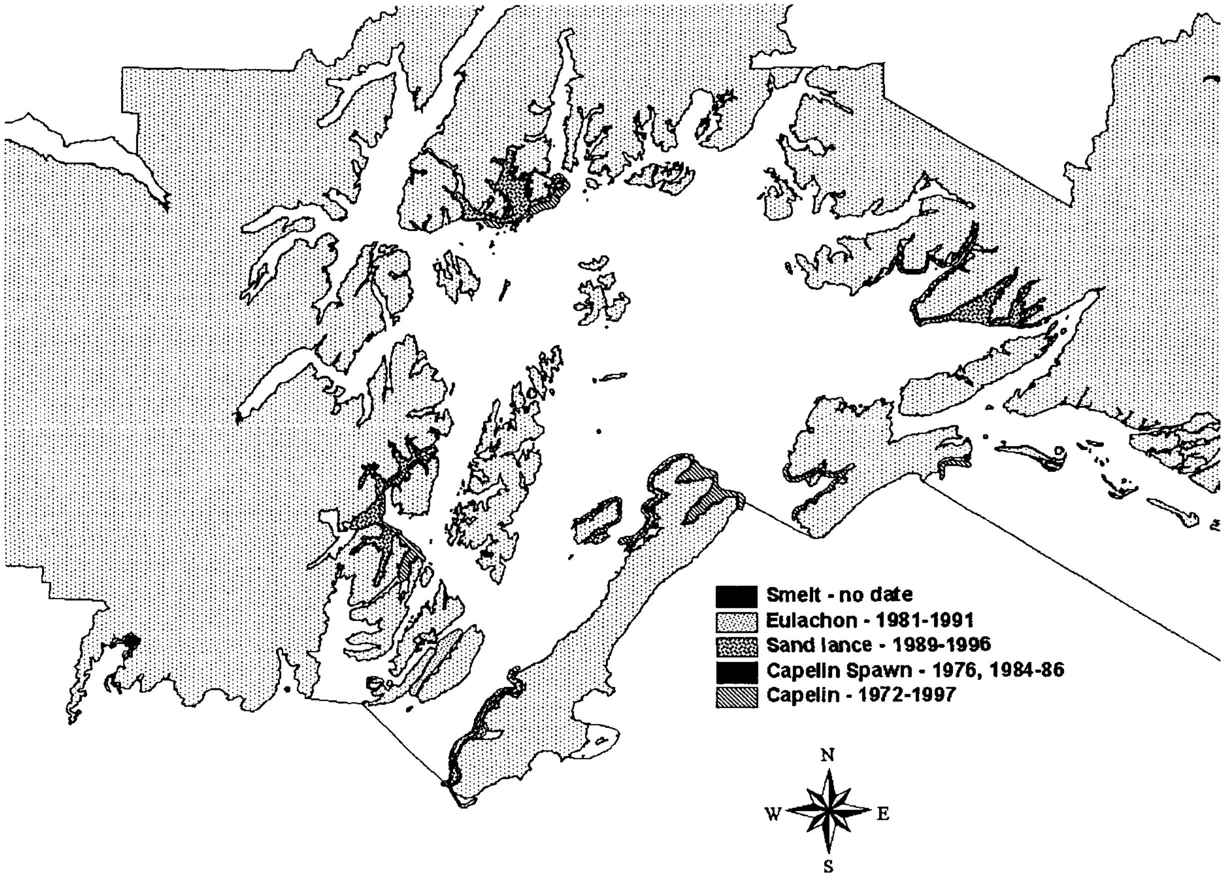
Smelt - no date
Eulachon - 1981-1991
Sand lance - 1989-1996
Capelin Spawn - 1976, 1984-86
Capelin - 1972-1997
N
W
E
S

Figure 22.

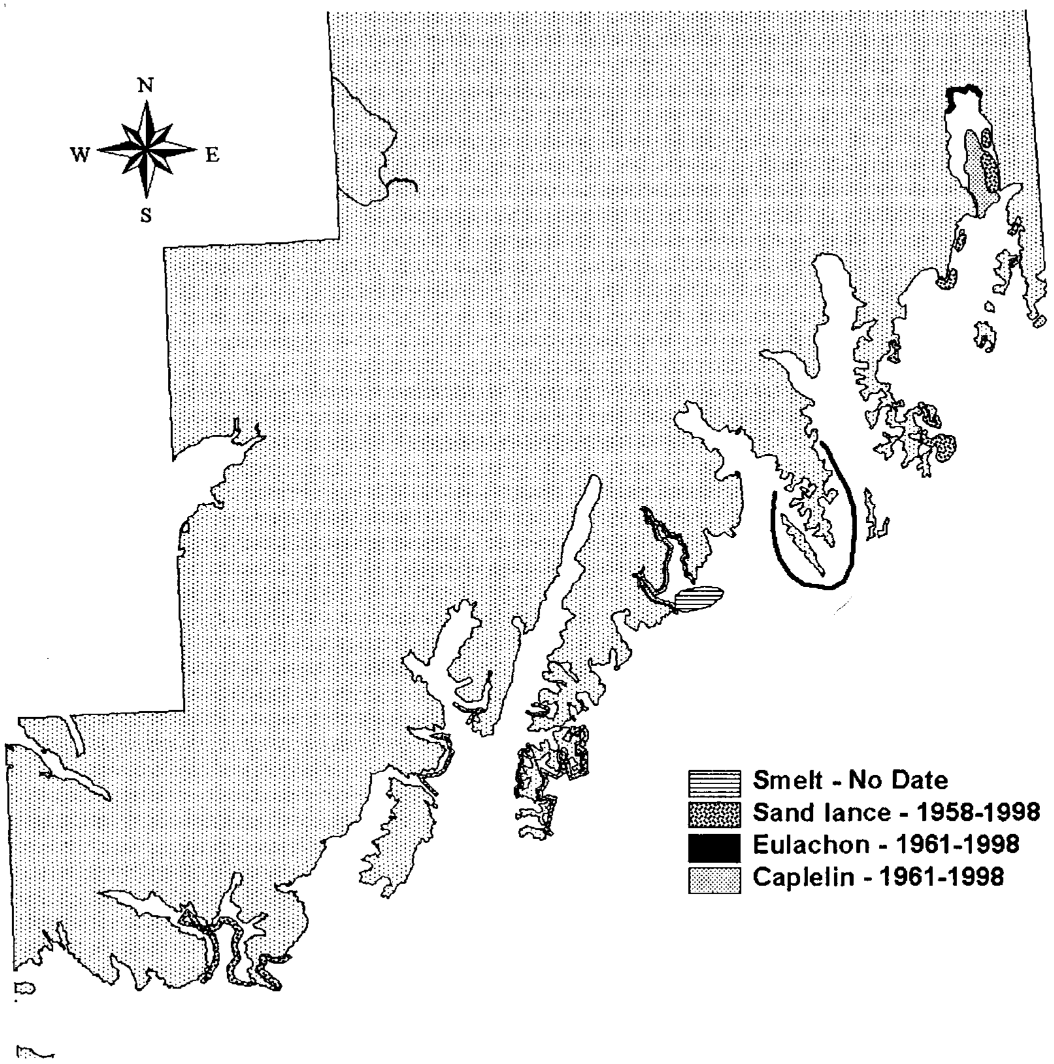
N
W
E
S
Smelt - No Date
Sand lance - 1958-1998
Eulachon - 1961-1998
Caplelin - 1961-1998

Figure 23.

Chapter 11

Fish Energetics

Exxon Valdez Oil Spill
Restoration Project Final Report

Sound Ecosystem Assessment: Fish Energetics

Restoration Project 320U
Final Report

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June 1999

Sound Ecosystem Assessment: Fish Energetics

Restoration Project 320U
Final Report

Study History: SEA was an integrated ecosystem study that explored how the pelagic community structure, and modifying physical oceanographic parameters, regulated the relative abundance of herring and pink salmon recruits. The focus of SEA 320U was to use somatic energy content of fish to identify the flow of energy into herring and a competitor, the pollock. The data from 320U supported inquiries into the SEA Over-Winter hypothesis, and the key question "is it food impeding recovery of herring." Sampling was carried out in Prince William Sound from 1995 to the spring of 1998.

Abstract: The project explored summer growth and overwinter energy costs for juvenile herring. A portion of the effort examined somatic energy content of age 0 pollock so the nutritional status of these competing forage species could be compared. Historically, herring and pollock have been among the most abundant pelagic forage fishes in central Alaska. After the Exxon Valdez oil spill the herring population exhibited reduced abundance and increased prevalence of disease. Comparison of the whole body energy content (WBEC) values for fall and spring collections of herring clearly demonstrated that stored energy is used extensively to get through the winter by all the age classes. For age 0 and age 1 herring, the acquisition of energy stores during summer was found to be critical in determining if they had enough energy to survive the winter's fast. During the years we sampled in October (1995-1997) age 0 herring, the recruits were generally food limited as evidenced by their inability to maximize energy storage for overwintering. Surviving the first winter was identified as an important recruitment bottleneck especially for age 0 herring.

Information about age 0 herring WBEC flowed from SEA 320U into the Over-Winter survival model (Patrick and Mason) which examined recruitment potential. That model can be used by ecosystem mangers interested in sea-birds and mammals that eat herring, and fishery managers concerned with human subsistence and commercial exploitation of herring to predict year class success.

Information on the tissue energy values from pink salmon fry, pollock and herring were provided to other researchers studying predators. We found that there was considerable seasonal, geographical and age-specific differences in WBEC in these key forage species.

The energy cost of spawning for herring was determined and the energy added to the ecosystem from spawning calculated. There was a marked decline in spawn output from 1989 to 1995.

Key Words: *Clupea*, Pacific herring, energetics, overwintering, walleye pollock, *Theragra*.

Project Data: The information gathered by SEA 320U was all synthesized into publications. All data produced during the effort appears in those publications (see objectives for a reference list). The WBEC measurement process destroys the tissues and no unanalyzed samples exist.

Table of Contents

Appendix 1. Paul, A. J., J. M. Paul and E. D. Brown. 1996. Ovarian energy content of Pacific herring from Prince William Sound, Alaska. Alaska Fishery Research Bulletin. 3(2):103-111.

Appendix 2. Paul, A. J., J. M. Paul, and E. D. Brown. 1998. Fall and spring somatic energy content for Alaskan Pacific herring (*Clupea pallasi*) relative to age, size and sex. J. Exp. Mar. Biol. Ecol. 223:133-142.

Appendix 3. Paul, A. J. and J. M. Paul. 1998. Comparisons of whole body energy content of captive fasting age zero Alaska Pacific herring (*Clupea pallasi Valenciennes*) and cohorts over-wintering in nature. J. Exp. Mar. Biol. Ecol. 226:75-86.

Appendix 4. Paul, A. J. and J. M. Paul. 1998. Spring and summer whole body energy content of Alaskan juvenile Pacific herring. Alaska Fishery Research Bulletin. 5(2):116-121.

Appendix 5. Paul, A. J. and J. M. Paul. 1999. Interannual and regional variations in body length, weight and energy content of age 0 Pacific herring from Prince William Sound, Alaska. J Fish Biol. 54:In press.

Appendix 6. Paul, A. J., J. M. Paul and R. L. Smith. 1998. Seasonal changes in whole-body energy content and estimated consumption rates of Age 0 walleye pollock from Prince William Sound Alaska. Esturine Coast. Shelf Sci. 47:251-259.

Appendix 7. Paul, A. J. 1997. The use of bioenergetic measurements to estimate prey consumption, nutritional status and thermal habitat requirements for marine organisms reared in the sea. Bull. Natl. Res. Inst. Aquacult. (Japan), Suppl. 3:59-68.

Appendix 8. Paul, A. J. and Mark Willette. Geographical variation in somatic energy of migrating pink salmon fry from Prince William Sound: a tool to measure nutritional status. *In*: Int. Symp. on the role of forage fishes in marine ecosystems. University of Alaska Sea Grant Report No. 97-01. pp. 707-720.

Appendix 9. Foy, R. J. and A. J. Paul. Winter feeding and changes in somatic energy content for age 0 Pacific herring in Prince William Sound, Alaska. Trans. Amer. Fish. Soc. In press.

Appendix 10. Paul, A. J. and J. M. Paul. 1999. First year energy storage patterns of Pacific herring and walleye pollock: insight in to competitor strategies. *In*: Int. Symp. on ecosystem considerations in fisheries management. University of Alaska Sea Grant Report AK-SG-99-01 pp. In press.

Objectives
Acknowledgments
Literature Cited

<u>Objectives</u>: The key objectives for SEA 320U, and the resultant publications where all the information and data relating to the objectives can be found, follow:

1. Describe the energy input of herring spawn to Prince William Sound. The results were published in the following peer reviewed journal paper.

Paul, A. J., J. M. Paul and E. D. Brown. 1996. Ovarian energy content of Pacific herring from Prince William Sound, Alaska. Alaska Fishery Research Bulletin. 3(2):103-111.

2. Describe the over-winter somatic energy cycle of juvenile and adult herring. The results were published in the following two peer reviewed journal papers.

Paul, A. J., J. M. Paul, and E. D. Brown. 1998. Fall and spring somatic energy content for Alaskan Pacific herring (*Clupea pallasi*) relative to age, size and sex. J. Exp. Mar. Biol. Ecol. 223:133-142.

Foy, R. J. and A. J. Paul. Winter feeding and changes in somatic energy content for age 0 Pacific herring in Prince William Sound, Alaska. Trans. Amer. Fish. Soc. In press.

3. Examine the energy cost of winter fasting for age-0 herring and critical somatic condition. The seasonal energy content of juvenile herring was measured and critical somatic energy condition determined in the laboratory so that estimates of *in situ* winter mortality could be made based on the occurrence of catabolic individuals. The results were published in the following peer reviewed journal paper. (Also see over-winter model in this SEA final report by V. Patrick)

Paul, A. J. and J. M. Paul. 1998. Comparisons of whole body energy content of captive fasting age zero Alaska Pacific herring (*Clupea pallasi Valenciennes*) and cohorts over-wintering in nature. J. Exp. Mar. Biol. Ecol. 226:75-86.

4. Measure seasonal somatic energy content of juvenile pollock and make comparisons of their nutritional status to that of juvenile herring. The results were published in the following peer reviewed journal paper and a technical report.

Paul, A. J., J. M. Paul and R. L. Smith. 1998. Seasonal changes in whole body energy content of recruiting walleye pollock and estimated consumption from Prince William Sound Alaska. Esturine Coast. Shelf. Sci. 47:251-259.

Paul. A. J. and J. M. Paul. 1999. First year energy storage patterns of Pacific herring and walleye pollock: insight in to competitor strategies. *In*: Int. Symp. on ecosystem considerations in fisheries management. University of Alaska Sea Grant Report AK-SG-99-01. pp. In press.

5. Measure the spring somatic energy content of wild and hatchery pink salmon fry, so a comparison of their nutritional status could be made. The results were published in the following peer reviewed journal paper and one technical report.

Paul, A. J. 1997. The use of bioenergetic measurements to estimate prey consumption, nutritional status and habitat requirements for marine organisms reared in the sea. Bull. Natl. Res. Inst. Aquacult.(Japan), Suppl. 3:59-68.

Paul, A. J. and Mark Willette. Geographical variation in somatic energy of migrating pink salmon fry from Prince William Sound: a tool to measure nutritional status. *In*: Int. Symp. on the role of forage fishes in marine ecosystems. University of Alaska Sea Grant Report 97-01. pp. 707-720.

6. Describe the interannual somatic energy profile of age zero herring relative to geographical location. The results were published in the following peer reviewed journal paper.

Paul, A. J. and J. M. Paul. 1999. Interannual and regional variations in body length, weight and energy content of age 0 Pacific herring from Prince William Sound, Alaska. J. Fish Biol. 54: In press.

7. Describe the interannual summer-fall somatic energy profile of post metamorphic age zero herring in Prince William Sound. The results were published in the following peer reviewed journal paper.

Paul, A. J. and J. M. Paul. 1998. Spring and summer whole body energy content of Alaskan juvenile Pacific herring (*Clupea pallasi*). Alaska Fishery Research Bulletin 5(2):116-121.

8. Aid in the production of the SEA overwinter bioenergetics model (V. Patrick & D. Mason, PIs). SEA 320 U provided the physiological measurements needed to construct the model and contributed to text creation. (See chapter in this SEA final report on Over-Wintering Model).

9. Relate the analysis of all the above objectives to SEA modeling efforts and help to produce one multi-authored synthesis report providing an overview of the early life history of Pacific herring. The results from this objective will appear in the SEA synthesis report on juvenile herring biology.

Acknowledgments: This study was sponsored by the *Exxon Valdez* Oil Spill Trustee Council

Sound Ecosystem Assessment project. Many SEA staff helped this study including: B. Norcross C. Adams, P. Shoemaker, R. Schmidt, M. McEwen, E. Brown, K. Stokesbury, R. Foy, L. Clayton, R. Smith, and J. McDonald. Facilities were provided by the Seward Marine Center Laboratory.

Literature Cited

Foy, R. J. and A. J. Paul. Winter feeding and changes in somatic energy content for age 0 Pacific herring in Prince William Sound, Alaska. Trans. Amer. Fish. Soc. In press.

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Paul, A. J. and J. M. Paul. 1999. Interannual and regional variations in body length, weight and energy content of age 0 Pacific herring from Prince William Sound, Alaska. J Fish Biol. 54:In press.

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Chapter 12

Synthesis and Integration

Exxon Valdez Oil Spill
Restoration Project Final Report

Sound Ecosystem Assessment (SEA): Synthesis and Integration

Restoration Project 98320-Z
Draft Final Report

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Sound Ecosystem Assessment (SEA): Synthesis and Integration

Restoration Project 98320-Z
Annual Report

Study History: Project 320-Z was established in FY 96 to assist the SEA lead scientist prepare and distribute single, integrated DPDs and Annual Reports. Funding was also provided to support the many aspects of synthesis and integration within the multi-project program. Conference calls, subgroup meetings and meetings and workshops of all investigators and selected staff and students are examples of synthesis activities supported by project 320-Z. The first annual report for this component of SEA was submitted by the SEA Lead Scientist as part of the SEA 1996 single, integrated annual report in April, 1997. Project 320-Z (re-titled 320-Z1 for FY 99) will close-out in 1999.

Abstract: Support for synthesis and integration activities in FY 98 and FY99 was used to receive, collate, copy, and submit the single, integrated FY 99 DPD and FY 97 Annual Report in May, 1998. Funding also supported participation of a SEA annual meeting, held in Fairbanks in late September, 1998. This meeting provided a forum for the first reading of draft manuscripts prepared for the SEA synthesis volume to be published in the journal Fisheries Oceanography in FY 00. SEA web services were used in December, 1998 and thereafter to circulate copies of synthesis manuscripts for internal review. A final oral collaborative report was presented to the Trustee Council at the March, 1999, public workshop as part of a dedicated SEA technical session. The SEA synthesis budget (Z1) in collaboration with work conducted by Dr. J.R. Allen (Z2), was used to plan and coordinate the dedicated technical session.

Key Words: Synthesis, Integration, SEA, EVOS.

Project Data: Synthesis and integration activities draw upon information generated by all the SEA components. Data sharing and transfer are aided by web and other network tools developed by project 320-J, Information Services and Modeling. SEA supports a web page at the following address: http://www.pwssc.gen.ak.us/sea/sea.html.

Citation: Cooney, R.. T. 1998. Sound Ecosystem Assessment (SEA): Synthesis and Integration, Exxon Valdez Oil Spill restoration project annual report (320-Z), Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska, 99775-7220.

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R.T. Cooney, J.R. Allen, M.A. Bishop, D.L. Eslinger, T. Kline, B.L. Norcross, C.P. McRoy, J. Milton, J. Olsen, V. Patrick, A. J. Paul, D. Salmon, D. Scheel, G.L. Thomas, S.L. Vaughan, and T.M. Willette. 2001. Ecosystem controls of juvenile pink salmon (Oncorhynchus gorbuscha) and Pacific herring (Clupea pallasi) populations in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):1-13.

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Executive Summary

Support for synthesis and integration activities in FY 98 and FY99 was used to receive, collate, reproduce, and submit the single, integrated FY 99 DPD and FY 97 Annual Report in April and May, 1998, respectively. Funding also supported participation in a SEA annual meeting held in Fairbanks in late September, 1998. This meeting provided a forum for the first reading of draft manuscripts prepared for the SEA synthesis volume to be published in the journal Fisheries Oceanography in FY 00. SEA web services were used in December, 1998 and thereafter to circulate copies of synthesis manuscripts for internal review. A final oral collaborative report of SEA overall findings was presented to the Trustee Council at the March, 1999 public workshop as part of a dedicated SEA technical session. The SEA synthesis budget (Z1) in collaboration with work conducted by Dr. J.R. Allen (Z2) was used to plan and coordinate the dedicated technical session.

Objectives

The following general objectives were approved in the FY 98 DPD:

1. Convene meetings of SEA principal investigators and staff as needed for program planning, and the debate and application of SEA results to overall program goals.

2. Use information from all SEA projects to provide the Trustee Council with a single, integrated Final Report for work completed in FY 98, and to prepare the submission of a series of technical manuscripts for a single, special volume of the journal Fisheries Oceanography.

Methods

The SEA Lead Scientist (Ted Cooney) works with an executive committee (David Eslinger, Vince Patrick, Kevin Stokesbury for Brenda Norcross, and Mark Willette) to establish agendas for meetings, to review issues arising in SEA, and to make recommendations about program direction and change. Subgroups and others requesting travel approach the Lead Scientist with requests which are then reviewed on the basis of need. Funds are expended until they are exhausted. Each year, the Lead Scientist serves as the focal point for the receipt of hard and electronic copies of budgets for the DPD and manuscripts for the single integrated annual report. The Lead Scientist also provides a synthesis chapter for the annual report - an expanded executive summary of progress requested by the EVOS Chief Scientist, Robert Spies. In FY99, the Lead Scientist work closely with Dr. J.R. Allen (320-Z2) to design and implement an internal review process for papers contending for the Fisheries Oceanography special volume.

Results

The SEA FY 99 single, integrated DPD was submitted for consideration by the Trustee Council on 15 April, 1998. The single, integrated SEA annual report of progress for 1997 was submitted

1 May, 1998. Project 320-Z assisted with travel for investigators to attend the SEA annual meeting in September 28 to review the status of papers proposed for the SEA synthesis volume in FY 00. Additional funds were allocated for various subgroup meetings in FY98 and FY to support the reporting and close-out of SEA.

Discussion

The SEA program was responsive to formal reviews of progress by EVOS peer reviewers, to proposal and reporting schedules, and to shifts in emphasis responding to streams of information generated by the field and laboratory studies. To accommodate these technical and management tasks, the EVOS TC allowed the development of a nominal synthesis and integration budget controlled by the Lead Scientist. These funds were very instrumental in providing the coordination and flexibility needed to address common management tasks.

As the study approached the termination of its funding and the need for an overall summing up of results both as required report and technical manuscripts, funds in 320-Z1 supported the communication between all investigators and their respective staffs and students. Without this support, it is doubtful that the process of science in a program as complex as SEA could have proceeded efficiently, or met its stated goals.

Conclusions

As SEA Lead Scientist, I acknowledge the valuable support available through funding for synthesis and integration activities. Science management has always been looked upon as necessary overhead to be tolerated at best. In this instance, and in the absence of a formal funding mechanism for internally managing the required tasks of SEA, the synthesis and integration budget went far beyond the mundane chores of producing single, integrated proposals and reports, to support the communication and debate of science in oral and written formats that have led to the successes that SEA discusses in its close-out documentation.

Acknowledgments

All SEA principal investigators and their staffs and students are gratefully acknowledged for their assistance with report and proposal preparation, and for their dedication to tasks set by SEA to resolve issues concerning ecosystem-dominated production limitations to pink salmon and herring production in Prince William Sound. I am particularly indebted to Rosemary Ruff, Kate Fenton and Margret Billington in Fairbanks, and to Nancy Bird and Penny Oswalt in Cordova for assistance with budgeting and proposal preparation. Jennifer Allen provided innovative network services that greatly assisted with communications in SEA. Lastly, I thank Bill Hauser for his skillful hand at program management. Without the continuous and untiring contributions from this entire team, SEA would have fallen short long ago of the expectations the stakeholders in the region have for the science.