E
Kittiwake Studies

Exxon Valdez Oil Spill
Restoration Project Annual Report

KITTIWAKES AS INDICATORS OF FORAGE FISH AVAILABILITY

Restoration Project 97163E
Annual Report

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

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KITTIWAKES AS INDICATORS OF FORAGE FISH AVAILABILITY

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Study History: Field work for project 95163E began during the summer of 1995 and consisted of detailed studies of the reproductive biology and foraging ecology of Black-Legged Kittiwakes in Prince William Sound (PWS), Alaska. In 1995, studies were conducted at one colony in northeastern (Shoup Bay) and two colonies (Eleanor Island and Seal Island) in central PWS. Research at Shoup Bay was conducted in conjunction with ongoing studies funded by the U.S. Fish and Wildlife Service (USFWS). In 1996, we expanded the study to include North Icy Bay rather than Seal Island, thereby having sites representing northeastern (Shoup Bay), central (Eleanor Island), and southwestern (North Icy Bay) PWS. Additionally, we can make comparisons with long-term demographic (Shoup Bay) and population studies (all of PWS) conducted by the USFWS. This allows us to more accurately address relationships of variation in prey and decadal trends in populations. In 1997, we conducted work at the same three sites as in 1996.

Abstract: The distribution of Black-legged Kittiwakes *(Rissa tridactyla)* nesting in Prince William Sound (PWS), Alaska has changed dramatically since the early 1970's. Sixty-three percent of the population now nests in northern PWS compared to 30% in 1972. Population analyses indicated that between 1984 and 1997, fecundity at northern colonies was sufficient to maintain a stable or net population increase ($P = 0.036$) in contrast to southern colonies where fecundity was insufficient to maintain the population ($P = 0.045$). These changes and trends corresponded with a decrease in the availability of high quality forage fishes in the Gulf of Alaska (GOA) and a decline in breeding success of piscivorous seabirds. We hypothesize that these changes in the GOA primarily affected kittiwakes in southern PWS where oceanographic conditions and prey associated with the Alaska Coastal Current are more similar to those found at colonies in the GOA. This resulted in a shift of the nesting population to the north where local forage fish production (primarily Pacific herring, *Clupea pallasi*, and Pacific sand lance, *Ammodytes hexapterus*) allowed high kittiwake productivity in portions of PWS compared to the GOA. As part of the APEX project we are conducting detailed studies of three kittiwake colonies located in northeastern (Shoup Bay), central (Eleanor Island), and southwestern (North Icy Bay) PWS. Based on the above hypothesis, we would expect the northern colonies to be most successful when forage fish production (primarily herring) within PWS is high. Whereas breeding success of central and southern colonies is more influenced by forage fish production in GOA waters. Our results for 1996 and 1997 partially support this hypothesis and, in cooperation with other APEX components, will allow us to further examine the relationship between PWS and GOA ecosystems. Additionally, results of these studies will help determine factors limiting the productivity of kittiwakes in portions of PWS.

Data collected during this study and Irons (1992) will allow us to model relationships of reproductive success, chick diets, chick growth rates, and foraging effort, as indicators of relative prey quality and availability. By working with other APEX components and the SEA project (EVOS project #320), the above parameters can be used to predict the effects of changes in oceanographic conditions and forage fish availability on population dynamics of kittiwakes in PWS.

Key Words: Black-legged Kittiwake, Rissa tridactyla, foraging behavior, fecundity, survival, foraging trip, diets, Pacific herring, Pacific sand lance, capelin, prey abundance, population change, reproductive success, immigration, emigration, Prince William Sound, Alaska.

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

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This report is comprised of two manuscripts that address four of the eleven APEX project hypotheses.

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

Hypotheses addressed:
7) Seabird diet composition reflect changes in relative abundance and distribution of forage fishes at relevant scales around colonies.
8) Changes in seabird productivity reflect differences in forage fish abundance, as measured in adult foraging trips.
10) Seabird species within a community react predictably to different prey bases.

Suryan, R. M. and D. B. Irons. Population dynamics of kittiwakes in Prince William Sound Alaska: productivity of individual colonies and population trends.

Hypotheses addressed:
1) The trophic structure of PWS and GOA has changed at the decadal scale.
8) Changes in seabird productivity reflect differences in forage fish abundance.

INTERANNUAL VARIATION IN DIET AND FORAGING EFFORT OF KITTIWAKES IN RELATION TO PREY ABUNDANCE

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Running Head: foraging activities and prey abundance

Key Words: kittiwake, *Rissa tridactyla*, foraging effort, prey abundance, nestling diets, time budgets, radio-telemetry

Abstract: We studied nestling diets and foraging activities of breeding black-legged kittiwakes (*Rissa tridactyla*) during five years (1989-90 and 1995-97) of low to high prey abundance at two colonies, Shoup Bay and Eleanor Island, in Prince William Sound, Alaska. Fifteen to 40 adult kittiwakes were radio-tagged annually and foraging activities and flight paths were recorded while following individuals using a high speed (65 km/hr) boat. Years of moderate to poor food availability were associated with significant ($P < 0.05$) changes in diet (prey switching) and increased foraging effort (duration, distance, and travel time). Foraging effort was consistently greater at Shoup Bay ($P < 0.05$) with a mean trip duration of 4 hr and distance of 40 km in good food years, increasing to a maximum average of 6 hr and 60 km during a poor food year. Foraging trips of kittiwakes at Eleanor Island averaged 2 hr and 5 km during good food years and increased to a maximum of 5.6 hr and 35 km during the worst year. Poor food years were associated with a decline of herring in diet and those herring consumed were primarily age 0 compared to age 1 in other years. Greater occurrence of Pacific herring (*Clupea pallasi*) in nestling diets were significantly correlated with shorter foraging trips of adults at Shoup Bay. An opposite relationship existed for sand lance (*Ammodytes hexapterus*). These correlations were not significant ($P > 0.20$) at Eleanor Island. Consequences of reduced herring were greatest at Shoup Bay where alternative prey close to the colony did not exist. Whereas kittiwakes from Eleanor Island were able to compensate for reduced availability of herring near the colony by obtaining sand lance and capelin. Amount of time spent traveling increased with greater trip duration, but time searching and capturing prey showed no distinct trends and may reflect foraging strategies that vary with different prey consumed or flock versus individual foraging.

INTRODUCTION

Seabirds have been proposed as useful indicators of marine resources by many authors (Ashmole 1971; Boersma 1978; Ricklefs et al. 1984; Cairns 1987; Croxall et al. 1988; Harris and Wanless 1990; Furness and Barrett 1991; and others). In the Bering Sea, for example, researchers assessed changes in marine trophic level dynamics by comparing diets and reproductive success of seabirds among different regions, depth strata (divers vs. surface feeders), and trophic levels (planktivores vs. piscivores; Springer 1993). In addition various demographic and reproductive measures can indicate environmental change of different magnitudes and time-scales. The most immediate changes in forage fish distribution and abundance would presumably be detected in nestling diets and foraging time budgets of breeding adult seabirds (Cairns 1987).

Interestingly, relatively few forage species have been implicated with the reproductive success of piscivorous seabirds in northern, polar and subpolar regions. The most common of these species or groups being sand lance (*Ammodytes* spp.; Springer et al. 1987; Hamer et al. 1993; Monaghan et al.1994; Harris and Wanless 1991), capelin (*Mallotus villosus*; Brown and Nettleship 1984; Furness and Barrett 1985; Springer et al. 1987), and cods (gadidae; Springer et al 1986, 1987). In many instances one prey species dominated seabird diets and declines in this prey item caused reduced reproductive performance. For example, Baird (1990) reported a decline in reproductive success in black-legged kittiwakes associated with a dietary change from capelin to sand lance, invertebrates, and other fishes. Hamer et al. (1993) reported no change in the predominately sand lance diet of kittiwakes during a poor food year that lead to declines in breeding success. Sand lance is considered a energetically valuable prey item (Van Pelt et al. 1997). In addition to the energetic value of prey consumed, the effort of obtaining sufficient quantities is equally important. Availability of prey to seabirds is often affected by oceanographic conditions and habitat (Springer et al. 1984; Hunt1990; Ostrand et al. in press). Availability can also be affected by inter- and intra-specific competition (Birkhead and Furness 1985; Hunt et al. 1986; Maniscalco and Ostrand et al. 1996). Determining foraging strategies of seabirds confronted with varying environmental constraints is an essential link in solving ecological relationships between diet and reproductive success (and potential survival costs leading to demographic consequences; Golet et al. in press).

In this paper we contrast the diets and foraging activities of kittiwakes in Prince William Sound (PWS) during years ranging from low to high food abundance. Foraging activities were determined by following radio-tagged birds at sea. We also contrast how kittiwakes from two colonies within PWS respond to changes in availability of primary forage species.

METHODS

Prince William Sound is an inland marine/estuarine waterway located along the north coast of the Gulf of Alaska (GOA; Fig. 1). The abundant fjords, bays, and islands in PWS provide shoreline habitat in excess of 4000 km. This area is also characterized by heterogeneous bathymetry and large tidal fluctuation (5.5 m between high and low tide), although the water column is typically stratified throughout the summer (Niebauer et al. 1994, Halderson et al. 1997).

Two kittiwake colonies were selected for study. The Shoup Bay colony is the largest (7000 pairs) in PWS and is located in a fjord in the northeastern region (Fig. 1). The Eleanor Island colony is much smaller (270 pairs) and located among the islands of central PWS (Fig. 1).

Relative prey abundance was determined using two different measures. During 1995 to 1997 Haldorson et al. (1996, 1997 and 1998) conducted hydroacoustic and trawl sampling of forage fishes within regions encompassing the two study colonies (Fig. 1). Results of this sampling (see Haldorson et al. 1997 for methods) indicated that prey abundance for the Shoup Bay Colony was greatest in 1996 and dramatically declined in 1997. Around Eleanor Island, prey abundance was low in 1996 and 1997.

Hydroacoustic sampling was not conducted during the initial two years of this study (1989 and 1990). Therefore, prey abundance (herring) was inferred from independent fisheries data collected during this time. These data indicated high juvenile (age 1) abundance in 1989 (record spawn the previous year; Alaska Department of Fish and Game) and low juvenile abundance in 1990 (reduced larvae survival in 1989; Brown et al. 1996; Norcross et al 1996). Also, based on several kittiwake breeding and foraging parameters, Irons (1992) concluded that kittiwake prey in PWS was abundant in 1989 and scarce in 1990. Overall, prey abundance was relatively high at Shoup Bay in 1989, 1995, and 1996 and low in 1990 and 1997. Prey abundance at Eleanor Island was high in 1989 and 1995, then declined in 1996 and 1997 (data were not collected at Eleanor Island in 1990).

Diet samples (regurgitations) were collected opportunistically from nestlings throughout the colony. Samples were collected while handling chicks and stored in isopropyl alcohol or frozen. Typically, no more than one sample was collected per nestling. Prey were identified using otoliths or morphological characteristics (all species) and scales (Pacific herring). Otoliths were measured to the nearest 0.01 mm using an ocular micrometer. Diet data are presented solely as percent occurrence for two reasons; 1) to allow comparison among all years (1989 and 1990 data were limited to calculation of percent occurrence only) and 2) in relating foraging effort to diets we were concerned with how many foraging trips involved catching a particular prey item (important when addressing spatial distribution of different prey). Age classes of herring based on otolith length were inferred from length frequency distributions and confirmed by personnel from the Alaska Department of Fish and Game.

Adult Black-legged Kittiwakes were captured at their nests using a noose pole or leg noose (Suryan and Benson in prep) and radio transmitters (Advanced Telemetry Systems, Inc (ATS), 164 - 167 MHZ, 9 - 11 g) were attached to 15 - 40 birds at each colony. Transmitters were attached to the ventral surface at the base of tail feathers (Anderson and Ricklefs 1987; Irons 1992) with two plastic cable ties and Loctite 494 instant adhesive. Head, breast, tail and underwings of radio-tagged kittiwakes were dyed (Nyanzol D and Rhodomine B) one of three unique color combinations. The dye permitted easy identification of kittiwakes during at-sea tracking.

Foraging trip duration, distance, location, and behavior were determined while tracking radio-tagged kittiwakes from a 7.3 m Boston Whaler (capable of traveling 65 km/hr) with an ATS receiver and a four element yagi antenna. Kittiwakes rearing chicks were selected for tracking. Observers waited near the colony until a radio-tagged bird left, then attempted to keep the kittiwake in view until it returned to the colony. Behaviors recorded included traveling (straight flight), searching for prey (back and forth flight), foraging (surface plunge or surface seize; Ashmole 1971), resting, and lost (bird out of view). Since duration of pursuit and handling of prey for kittiwakes is negligible compared to search time (Irons 1992), foraging was combined with searching in final analyses. Observers also recorded locations of foraging flocks and whether the radio-tagged kittiwake joined or passed them. Foraging flocks consisted of at least two birds (of any species) foraging less than 10 m apart. Dispersed foraging flocks were also recorded and defined as at least two birds foraging in a area greater than 10 m and less than 500 m. Locations of foraging kittiwakes, foraging flocks, and flight paths of radio-tagged kittiwakes were determined using a Lowrance LMS-350A geographic positioning system. Atlas GIS software was used to plot foraging trips and measure distance to shore for foraging locations and maximum foraging distance from colony. Foraging trip distance is reported as the linear, one-way distance between the colony and the furthest foraging location of the trip.

Percent occurrence of individual prey items were compared among years and between colonies using a contingency table (presence vs. absence) and chi-square analysis (Zar 1984). A Tukey-type multiple comparison test for proportions was used when significant differences were detected in chi-square analyses (Zar 1984). Means were compared using nonparametric statistics (Mann-Whitney and Kruskal-Wallis tests). To estimate power ($1 - \beta$) in failing to reject the null hypthesis, we used parametric statistics since power analyses are limited to such methods. Relationships between foraging effort and diets were determined using correlation analysis (Zar 1984).

RESULTS

Diets and foraging

The two years of poor food availability (1990 and 1997) for kittiwakes at Shoup Bay resulted in changes in diet and foraging effort compared to years when food was abundant (1989, 1995, and 1996). During good food years, diets were dominated by primarily herring and secondarily sand lance (Fig. 2a). In the poor food years, sand lance dominated the diets; with significant declines in the occurrence of herring ($X^2 = 36.9$, $P < 0.01$ for 1990 and 1997) and increases in occurrence of sand lance ($X^2 = 20.8$, $P < 0.01$ for 1990 and 1997; although 1995 and 1997 were not significantly different, $P > 0.05$; Fig. 2a). Other prey items were consumed, but never in sufficient quantity to compensate for lack of herring or sand lance (Fig. 2a). Additionally, herring consumed during the two years of poor food abundance were primarily age 0, compared to predominately greater percentages of age 1 in other years ($X^2 = 76.78$, $P < 0.01$; Fig. 2b).

In all years foraging effort was relatively high for kittiwakes at Shoup Bay with average trip durations from 3.7 to 6.0 hrs and distances 42 to 60 km. Corresponding to changes in diet, foraging effort increased during years of poor food availability (Fig 2c); however, because of within year variation of data, these increases were not statistically significant ($P > 0.20$). Our power to detect a difference was low (less than 0.30) therefore, it is possible that differences did exist, but large variation within years prevented detection of statistical significance. Foraging effort was most dramatic in 1990 with birds ranging 60 km from Shoup Bay on average and trip durations averaging 6 hrs (Fig. 2c). A similar, albeit not as extreme, result occurred in 1997 in response to reduced prey abundance. The maximum distance traveled to the furthest foraging location was 120 km.

Although Shoup Bay and Eleanor Island colonies are in relatively close proximity, their respective food supplies were to some extent independent. As at Shoup Bay, herring and sand lance were important prey items at Eleanor Island, with dominance varying among years. Capelin, however, was an important prey item at Eleanor Island and had minimal significance at Shoup Bay; occurring in significantly greater proportions at Eleanor Island in 1996 ($X^2 = 60.6$, $P < 0.01$) and 1997 ($X^2 = 15.1$, $P < 0.01$) compared to Shoup Bay (Fig. 3a).

For kittiwakes at Eleanor Island, 1989 and 1995 were years of good food availability near the colony, in contrast to 1996 and 1997 when prey biomass was reduced. This resulted in dietary changes and considerable variation in foraging effort among years. During poor food years there was a significant reduction in the occurrence of herring ($X^2 = 39.3$; $P < 0.01$) and a increase in sand lance ($X^2 = 7.8$; $P < 0.01$) and capelin ($X^2 = 11.6$; $P < 0.05$; Fig. 3a). In 1997, there was a significant reduction ($X^2 = 18.47$; $P = 0.001$) in the percent of age 1 herring in the diet (Fig. 3b), as also observed at Shoup Bay (Fig. 2b). These changes corresponded with significantly increased foraging trip duration ($H = 14.98$, $P = 0.001$) and distance ($H = 18.13$, $P < 0.001$; Fig. 3c). Maximum distance to the furthest foraging location was 67 km. In all years, except 1997, foraging trip duration and distance was significantly less ($P = 0.007$) for kittiwakes at Eleanor Island compared to Shoup Bay.

Relationship between foraging effort and diet.

Increased foraging effort at Shoup Bay was negatively correlated with the occurrence of herring in the diet (Fig 4). The opposite was true when considering sand lance; there was a significant positive correlation (Fig 4). This may indicate that sand lance were more time consuming to obtain for kittiwakes at Shoup Bay; potentially related to differences in schooling behavior of sand lance causing them to be difficult to obtain. Alternatively, sand lance may have simply occurred farther from the colony. Based on the greater distance of foraging trips associated with a sand lance diet, our data indicated that in most situations, kittiwakes must have traveled farther to obtain sand lance.

These relationships indicated similar trends for kittiwakes at Eleanor Island, although the correlations were not significant ($P > 0.20$; Fig 4). The greater occurrence of sand lance in diets was not associated with such long foraging trips as with Shoup Bay. This indicated that kittiwakes from Eleanor Island were able to obtain sufficient quantities of sand lance in closer proximity to the colony.

Identification of forage fish schools throughout PWS in 1997 supports the foraging and diet data obtained from kittiwakes. Net samples indicated schools of herring were more common in the northern PWS (closer to Shoup Bay), while schools of sand lance and capelin were more associated with central and southern waters (within the foraging range of kittiwakes from Eleanor Island; Fig. 5)

Time budgets

The amount of time spent traveling, searching, and at rest during foraging trips varied markedly among years at both colonies (Fig. 6). As trip duration increased, the amount of travel time generally increased; indicating that birds were extending foraging ranges to find food. This supports the observation previously stated that greater foraging trip durations were associated with birds traveling farther from the colony. The amount of time spent searching for and obtaining prey, however, did not increase consistently with greater trip duration (Fig. 6). Search time may vary in relation to abundance of prey, schooling characteristics of prey species, or with competition among predators. Prey switching among years (Figs. 2a and 3a) likely caused some of this variation, however, other factors are undoubtedly involved. For example, kittiwakes at Eleanor Island significantly increased ($H = 19.71$, $P < 0.001$) search time (Fig. 6). Increased search effort was also observed at Shoup Bay in 1997, but the differences were not statistically significant ($H = 3.22$, $P = 0.36$; Fig 6). The one common factor between sites in 1997 that was not present in other years was the increased use of foraging flocks (see below). This potentially caused increased inter- and intra-specific competition resulting in greater time required to obtain prey.

Use of foraging flocks and distance to shore.

There was significant variation among years in the use of foraging flocks and the proximity to shore of foraging activities. During 1995 and 1996 adults often fed alone, only joining flocks 30 to 50% of the time (Fig. 7) . In 1997 kittiwakes from Shoup Bay ($U = -2.73$; $P = 0.006$) and Eleanor Island ($H = 7.04$; $P = 0.03$) fed significantly more often in flocks (Fig. 7); reflecting potentially different schooling behavior of the prey species or age classes consumed in this year. Alternatively, this may reflect less abundant prey causing increased concentration of birds on the limited fish schools available.

Kittiwakes from Eleanor Island fed progressively farther from shore during the latter two years with 1997 being significantly greater ($H = 12.01$, $P = 0.003$; Fig. 7). This coincided with a change in diet (Fig. 2) and longer foraging trips to waters near the GOA. Kittiwakes from Shoup Bay showed no significant change in the distance they foraged from shore (Fig. 7). Still, relative to the amount of open water in PWS, kittiwakes primarily used shoreline habitat for foraging which was likely because their primary prey, herring and sand lance, were typically associated with near-shore habitats (Fig. 6).

DISCUSSION

Reduced prey availability resulted in dietary changes and increased foraging effort for kittiwakes at Shoup Bay and Eleanor Island. Diets and foraging effort were linked to a few key prey species. In particular, reduced herring (primarily age1) during poor food years was directly correlated with increased foraging effort. Foraging effort was much greater at Shoup Bay, since kittiwakes from Eleanor Island were able to obtain sand lance and capelin in closer proximity to the colony.

These two colonies provide insight into seabird, forage fish and oceanographic relationships in several ways. First, they provide contrast in foraging effort and diet while being in such close proximity. Second, prey consumption is relatively diverse, in contrast to kittiwake colonies in the United Kingdom where diets consist of primarily sandeels (*Ammodytes marinus*) in good and bad years (Hamer et al. 1993). Third, the common occurrence of herring in the diet is in contrast to most reported colonies in the GOA (Baird 1990; Hatch et al. 1992), Bering Sea (Springer et al. 1987) and Chukchi Sea (Springer et al. 1984). Fourth, breeding success has been consistently better compared to colonies throughout the GOA; likely due to the availability of herring (Suryan and Irons in prep.).

Diets

Being limited to the availability of surface schooling prey, kittiwakes tend to have a fairly specialized summer diet (Hatch 1987). Although kittiwakes in PWS regularly consumed over eight different species or prey types, there was only a few dominant species whose relative abundance significantly affected foraging effort. In particular, herring has proven to be an important prey item in PWS. Years of reduced prey abundance and increased foraging effort at both colonies were associated with decreased occurrence of herring in diets. This was particularly evident at Shoup Bay where kittiwakes appeared restricted to sand lance when attempting to compensate for lack of herring. Sand lance can be as energetically valuable as herring (Martensson et al. 1996), the only limitation was that sand lance seemed to be more difficult to obtain particularly in proximity to the Shoup Bay colony. This may reflect habitat preferences of the two forage species. The Shoup Bay colony is located 25 km within a fjord in northeastern PWS. Herring tend to be more abundant than sand lance in the fjords and bays along the perimeter of PWS (Stokesbury et al. in prep).

In contrast, kittiwakes from Eleanor Island were not as limited in diet alternatives to herring. As herring declined in their diets these birds increased their foraging range to include sand lance and capelin. Capelin, in particular, are more associated with GOA waters; which have a greater influence on the central and southwestern waters of PWS compared to northern regions (Niebauer et al. 1994) . The closer proximity of sand lance and capelin schools (along with other species potentially associated with the GOA; e.g. eulachon (*Thaleichthys pacificus* in 1997) allowed kittiwakes from Eleanor Island to compensate for lack of herring without increasing foraging effort to such extremes as birds from Shoup Bay.

Foraging trip duration and distance

While foraging trip or colony absence durations are commonly reported for studies of colonial seabirds, trip distance is typically unknown. In years of good food availability in Atlantic colonies, foraging trips of kittiwakes were reported to be 2 to 3 h duration (Hamer et al. 1993) and distances (also linear over water to furthest foraging location) were less than 10 km (Gabrielsen and Mehlum 1988; Hamer et al. 1993). This is similar to what we typically observed at Eleanor Island. It is, however, markedly less than Shoup Bay where foraging trip distances averaged 40 km in good years. In a poor food year Hamer et al. (1993) reported that average foraging trip distances of kittiwakes in Shetland were greater than 40 km (the maximum signal reception range from shore-based telemetry stations). Measured foraging distances of kittiwakes at Shoup Bay during poor food years was also greater than 40 km, reaching a maximum of 60 km. With the 4 yrs of study at Eleanor Island foraging trip duration and distance increased as prey availability near the colony decreased, but the adults never exceeded a 40 km average, however it was close in 1997. Although we observed kittiwakes traveling over 80 km from the colony during a foraging trip, it appears that an average distance of over 45 km and duration > 5 hrs is approaching the limit that adults can maintain while successfully provisioning young.

Time budgets

Remote monitoring of general time budgeting (duration of flight, swimming, diving, etc) has been successful for diving seabirds (Gabrielsen and Mehlum 1988; Monaghan et al. 1994), but has not been possible for small surface-feeding species. In addition, these methods are often lack insights to exact locations associated with different behaviors, distances traveled, and other details difficult to obtain from remote monitoring. Using boats to follow animals at sea provides a unique opportunity to link detailed behavioral observations with exact locations and accurately determine foraging areas (Suryan and Harvey in press).

As food supply near a colony declines, seabirds may respond in two different ways; 1) extend their foraging range by increasing travel time away from the colony or 2) spend more time searching for food in a particular foraging range. It is possible that a species would invoke either of these strategies depending on current conditions and knowledge of available prey from the recent past (Irons 1992). Kittiwakes in our study typically increased travel duration and distance from the colony in years of low food abundance, but amount of time spent obtaining prey was not as consistent. This implied that kittiwakes used both strategies mentioned above. Some birds traveled farther to locate prey that was more abundant or otherwise easier to obtain (spending similar amounts of time obtaining food as in good food years) and other instances birds spent more time searching, implying that even by increasing their foraging area, they were unable to locate prey in greater abundance and therefore easier to obtain.

Kittiwakes at Eleanor Island showed greater variation such as increased travel while decreasing search time among years. We believe this likely reflects the prey switching observed at Eleanor Island. For example, capelin (post-spawning males) occurred during mid to late July in predictable areas (over a period of weeks) near Montague and Green Islands (Fig. 6). Kittiwakes were sometimes observed flying directly to these areas then easily taking the lethargic fish that floated to the surface, a foraging option not readily available to kittiwakes from Shoup Bay.

In terms of time budgeting and foraging trip distance, kittiwakes showed marked contrast to that reported for common murres in response to reduced food supplies. Monaghan et al. (1994) observed murres remaining relatively close to the colony (< 10 km) during good and poor food years. The birds, however spent a much greater amount of time diving (i.e. searching) rather than traveling with significantly longer trip durations in a poor food year; This may be a more typical response of a diving bird that is able to forage in a three dimensional environment. Conversely, kittiwakes traveled much farther from the colony when food was scarce as seen in this study and also reported by Hamer et al. (1993). Furness and Barrett (1996) reported during a year of good food supply that kittiwakes traveled an estimated 27 km while common murres and shags (*Phalacrocorax aristotelis*) remained within 12 km of their colonies. These observed differences are potentially related to flight energetics with wing loading being much less for kittiwakes compared to murres and shags, therefore, permitting greater foraging range in search of available surface schooling prey.

Use of foraging flocks and near-shore foraging

Flock foraging and information transfer has been suggested as important mechanisms for seabirds to locate prey. Irons (1998) challenged this paradigm by demonstrating that in 1989 kittiwakes at Shoup Bay often passed by foraging flocks and consistently used particular foraging areas. Ostrand et al. (in press) also observed tufted puffins and marbled murrelets foraging extensively as individuals or in small groups in PWS. We also found breeding birds often foraged alone rather than joining flocks, particularly during good food years. This, however, was not the case in 1997 when kittiwakes usually fed in flocks rather than alone. Given sufficiently available prey, kittiwakes may opt to feed alone; resorting to flock foraging when abundance is low. Hudson and Furness (1989) described the competitive feeding associated with flocks of seabirds near whitefish trawlers and mentioned that kittiwakes were rarely able to obtain offal, remaining at the periphery and rarely joining the flock. Maniscalco and Ostrand (1997) reported a high rate of inter- and intra-specific kleptoparasitism of kittiwakes in foraging flocks, further implicating increased competition and energy costs in flock foraging (Ostrand et al. in press). If kittwakes are not sufficiently aggressive to benefit by flock foraging, they may opt to feed alone, unless flocks are the only way to obtain the desired prey. An increase in the use of foraging flocks corresponded with increased search and prey capture time. In some cases flock foraging may be beneficial depending on the prey species or if a surface feeder is benefitting from activities of diving birds causing fish to school near the surface (competition being more among surface feeders and not with diving birds).

We typically observed kittiwakes foraging near-shore, with the exception of the latter two years at Eleanor Island. Ostrand et al. (in press) also noted the use of near-shore habitats for foraging by marbled murrelets in PWS. This was attributed to dispersed, low density prey associated with a stratified water column in the nearshore during summer (Ostrand et al. in press). Stokesbury et al. (in prep.) noted that in July herring were primarily distributed in surface waters of bays in PWS, forming single cohort schools. Sand lance are also typically located nearshore during this time of the year (Harris and Hartt 1977; Springer et al. 1984). Since kittiwakes at Shoup Bay consumed predominately herring and sand lance in bays of the northern and eastern region of PWS, it is not surprising that they consistently used the nearshore habitat. In contrast, kittiwakes from Eleanor Island tended to feed farther offshore as they spent more time foraging on capelin, sand lance, and eulachon in GOA influenced waters around southern PWS. In certain years, the influence of the Alaska coastal current in this region of PWS may present more advection creating a different foraging environment than what Ostrand et al. (in press) described for the majority of PWS (and as we observed for the Shoup Bay colony).

In conclusion, we demonstrated that kittiwakes in PWS exhibited prey switching and a considerable increase in foraging effort in response to reduced food supplies. This increased effort included more time spent traveling farther from the colony. Time spent spent searching and capturing prey, however, showed no consistent trend; with the exception of increased search time associated with increased use of foraging flocks. Search and capture time is likely confounded by prey switching and the different foraging strategies required to obtain particular species. Poor food years at Shoup Bay were directly related to reduced herring in diets with little alternative prey in close proximity to the colony. In contrast, kittiwakes at Eleanor Island were able to locate sand lance and capelin in relatively close proximity when food supplies near the colony were reduced. These data support the premise that kittiwakes are able to dramatically vary their foraging effort in response to regional changes in prey availability.

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LITERATURE CITED

Ashmole, N. P. 1971. Seabird ecology and the marine environment. In Avian biology, Volume 1 (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York, USA. pp 224-286.

Baird, P. H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scandinavica 21:224-235.

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

Boersma, P. D. 1978. Breeding patterns of Galapagos Penguins as an indicator of oceanographic conditions. Science 200:1481-1483.

Brown, E. D., T. T. Baker, J. E. Hose, R. M. Kocan, G. D. Mary, M. D. McGurk, B. L. Norcross, and J. Short. 1996. Injury to the early life history stages of Pacific herring in Prince William Sound after the *Exxon Valdez* oil spill. Am. Fish. Soc. Symp. 18:448-462.

Brown, R. G. B. and D. N. Nettleship. 1984. Capelin and seabirds in the Northwest Atlantic. *In* Marine birds: their feeding ecology and commercial fisheries relationships. *Edited* by D. N. Nettleship, G. A. Sanger, and P. F. Springer. Can. Wildl. Serv. Spec. Publ. pp 184-194.

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

Croxall, J. P., T. S. McCann, P. A. Prince and P. Rothery. 1988. Reproductive performance of seabirds and seals at South Georgia and Sigany Island, South Orkney Islands, 1976-1987: Implications for Southern Ocean Monitoring Studies. Pages 261-285 *in* D. Sahrhage, editor. Antarctic Ocean and Resources Variability. Springer-Verlag, Berlin Heidelberg, Germany.

Furness, R. W. and Barrett. 1985. The food requirements and ecological relationships of a seabird community in North Norway. Ornis Scandinavica 16:305-313.

Furness, R. W., and R. T. Barrett. 1991. Seabirds and Fish Declines. National Geographic Research and Exploration 7:82-95.

Gabrielsen, G. W. and F. Mehlum. 1988. Kittiwake activity monitored by telemetry. Biotelemetry X 31 July to 5 August. Fayetteville, AR, USA.

Haldorson, L., T. Shirley, K. Coyle, and R. Thorne. 1996, 1997, 1998. Forage species studies in Prince William Sound. *In* D. C. Duffy [ed.], APEX: Alaska predator ecosystem experiment, *Exxon Valdez* oil spill restoration project annual report, *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK.

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

Harris, C. K. and A. C. Hartt. 1977. Assessment of pelagic and nearshore fish in three bays on the east and south coasts of Kodiak Island, Alaska. Fisheries Research Inst. Univ. Wash., Seattle, WA. Publ.

Harris, M. P., and S. Wanless. 1990. Breeding success of British kittiwakes *Rissa tridactyla* in 1986-88: evidence for changing conditions in the northern North Sea. Journal of Applied Ecology 27:172-187.

Harris, M. P. and S. Wanless. 1991. The importance of the lesser sandeel *Ammodytes marinus* in the diet of the shag *Phalacrocorax aristotelis*. Ornis Scandinavica 22:375-382.

Hatch, S. A. 1987. Did the 1982-1983 El Nino-Southern Oscillation affect seabirds in Alaska? Wilson Bull. 99(3):468-474.

Hatch, S.A., G.V. Byrd, D.B. Irons, and G.L. Hunt Jr. 1992. Status and Ecology of kittiwakes in the North Pacific. *In* Status, ecology, and conservation of marine birds of the North Pacific (Vermeer, K., K.T. Briggs, K.H. Morgan, and D. Siegel-Causey, eds). Canadian Wildlife Service, Ottawa, pp 140-153.

Hudson, A. V. and R. W. Furness. 1988. The behaviour of seabirds foraging at fishing boats around Shetland. Ibis 131:225-237.

Hunt, G. L., N. M. Harrison, and R. T. Cooney. 1990. The influence of hydrographic structure and prey abundance on foraging of Least Auklets. Stud. Avian Biol. 14:7-22.

Hunt, G. L. Jr., Z. A. Eppley, and D. C. Schneider. 1986. Reproductive performance of seabirds: the importance of population and colony size. Auk 103:306-317.

Maniscalco, J. M. and W. D. Ostrand. 1996. Seabird behaviors at forage fish schools in Prince William Sound, Alaska. *In* Proc. of the international symposium on the role of forage fishes in marine ecosystems. Alaska Sea Grant College Program, Univ. Alaska Fairbanks, AK.

Martensson, P. E., A. R. Lager Gotaas, E. S. Nordoy and A. S. Blix. 1996. Seasonal changes in energy density of prey of Northeast Atlantic seals and whales. Mar. Mamm. Sci. 12(4): 635-640.

Monaghan, P., P. Walton, S. Wanless, J. D. Uttley, and M. D. Burns. 1994. Effects of prey abundance on the foraging, diving, efficiency and time allocation of breeding guillemots *Uria aalge*. Ibis 136: 214-222.

Niebauer, H. J., T. C. Royer, and T. J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. J. Geophys. Res. 99(C7): 14.133-14.126.

Norcross, B. L. and M. Frandsen. 1996. Distribution and abundance of larval fishes in Prince William Sound, Alaska, during 1989 and after the *Exxon Valdez* oil spill. Am. Fish. Soc. Symp. 18:463-486

Ostrand, W. D., K. E. Coyle, G. S. Drew, J. M. Maniscalco, and D. B. Irons. In press. Selection of forage-fish schools by murrelets and tufted puffins in Prince William Sound, Alaska. Condor.

Ricklefs, R. E., D. C. Duffy, and M. Coulter. 1984. Weight gain of Blue-footed Booby chicks: an indicator of marine resources. Ornis Scandinavica 15:162-166.

Springer, A. M., compiler. 1993. Report of the seabird working group. *in*: Is it food? Addressing marine mammal and seabird declines. Alaska Sea Grant rep. Univ. of Alaska, Fairbanks. AK-SG-93-01.

Springer, A. M., E. C. Murphy, D. G. Roseneau, C. P. McRoy, and B. C. Cooper. 1987. The paradox of pelagic food webs in the northern Bering Sea- I. Seabird food habits. Cont. Shelf Res. 7(8):895-911.

Springer, A. M., D. G. Roseneau, D. S. Lloyd, C. P. McRoy, and E. C. Murphy. 1986. Mar. Ecol. Progr. Ser. 32:1-12.

Springer, A. M., D. G. Roseneau, E. C. Murphy, and M. I. Springer. 1984. Environmental controls of marine food webs: food habits of seabirds n the eastern Chukchi Sea. Can. J. Fish. Aquat. Sci. 41:1202-1215.

Stokesbury, K. D., J. Kirsch., E. D. Brown, G. L. Thomas, and B. L. Norcross. In prep. Seasonal variability in Pacific Herring (*Clupea herrengus*) and walleye pollock (*Theragra chalcogramma*) spacial distributions in Prince William Sound, Alaska.

Suryan, R. M. and J. T. Harvey. In press. Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behavior, foraging activity, and haul-out site use off the northern San Juan Islands, Washington. Mar. Mamm. Sci.

Suryan, R. M. and J. E. Benson. In prep. A leg noose for capturing adult nesting birds.

Suryan, R. M. and D. B. Irons. In prep. Population dynamics of kittiwakes in Prince William Sound, Alaska: Productivity of individual colonies and population trends.

Van Pelt, T. I., J. F. Piatt, B. K. Lance, and D. D. Roby. 1997. Proximate composition and energy density of some North Pacific forage fishes. Comp. Biochem. Physiol. 118A(4)1393-1398

Figure 1. Location of the two study colonies, Shoup Bay and Eleanor Island, in Prince William Sound, Alaska. Oval boundaries encompassing colonies depict foraging range of adult kittiwakes from respective colonies. Dashed lines indicate sampling areas for hydroacoustic and trawl surveys conducted by Haldorson et al. (1997, 1998).

Figure 2. Annual percent occurrence of prey in nestling diets (a), age class of herring consumed (b), and foraging trip duration and distance (c) for adult kittiwakes nesting at Shoup Bay in Prince William Sound.

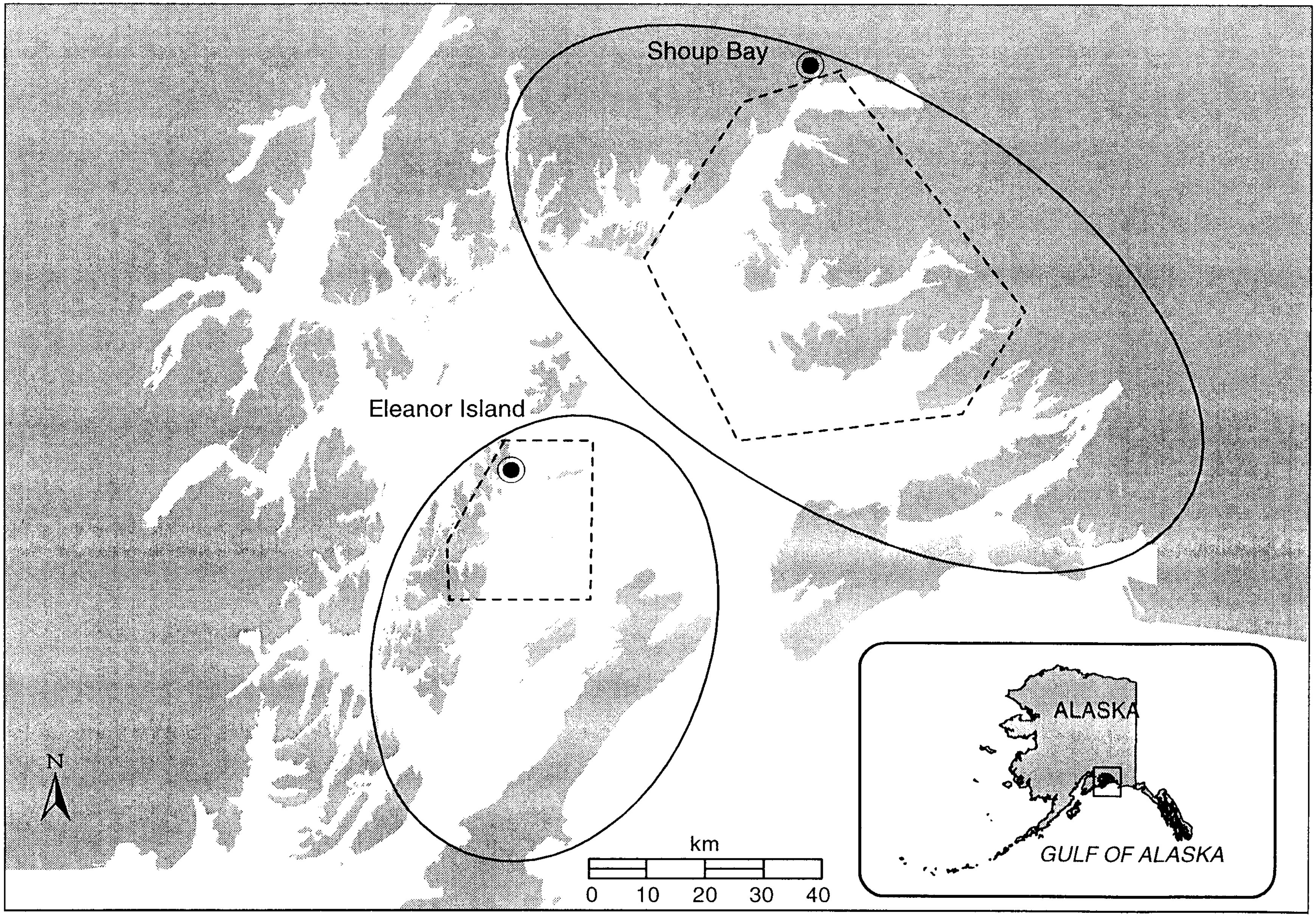
Figure 3. Annual percent occurrence of prey in nestling diets (a), age class of herring consumed (b), and foraging trip duration and distance (c) for adult kittiwakes nesting at Eleanor Island in Prince William Sound.

Figure 4. Relationship between foraging trip duration and percent occurrence of herring, sand lance, and capelin in nestling diets of kittiwakes at Shoup Bay and Eleanor Island.

Figure 5. Identification of forage fish schools sampled throughout Prince William Sound in 1997.

Figure 6. At sea time budgets of foraging kittiwakes from Shoup Bay and Eleanor Island.

Figure 7. Use of foraging flocks and foraging distance from shore for kittiwakes nesting at Shoup Bay and Eleanor Island, Prince William Sound.



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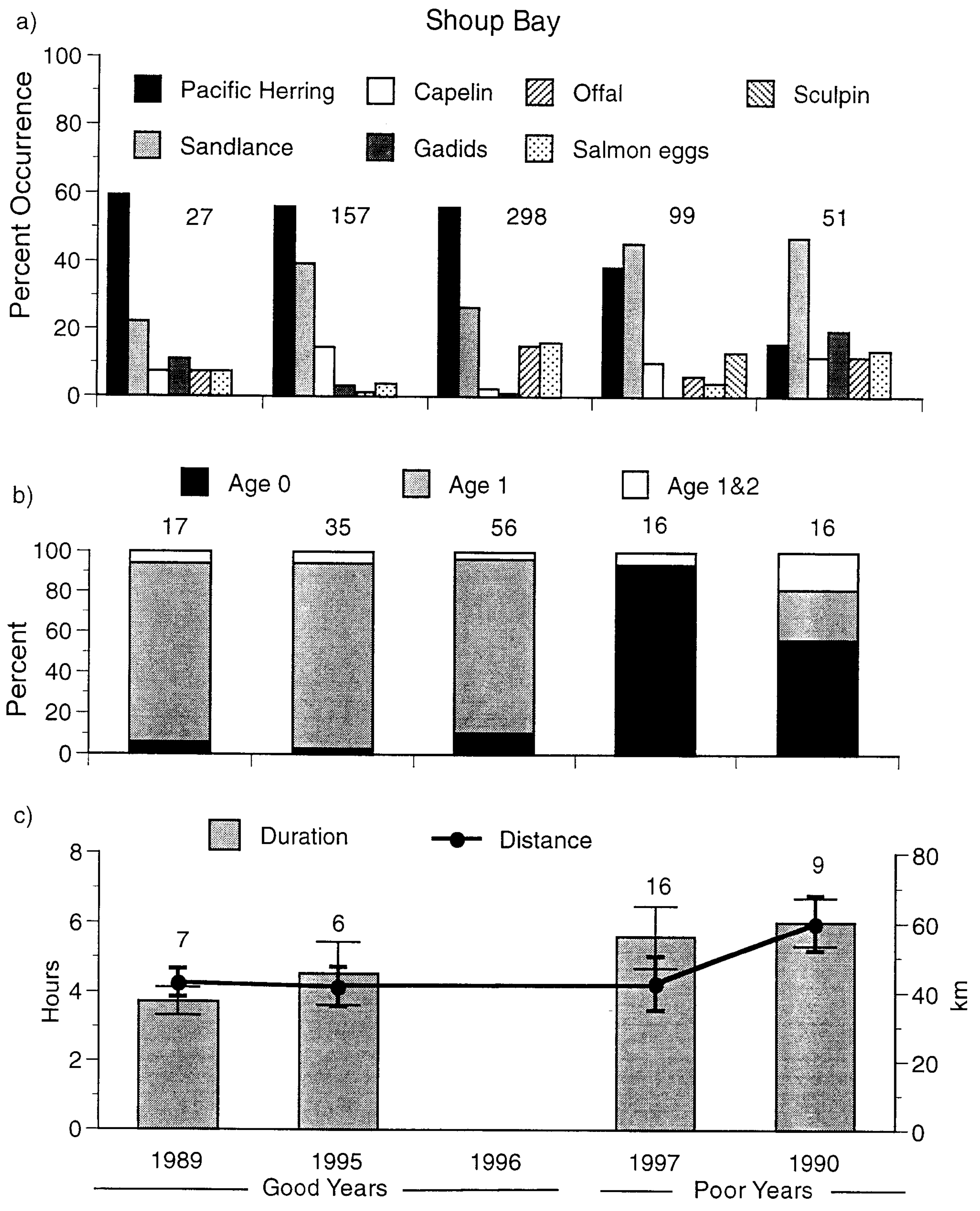

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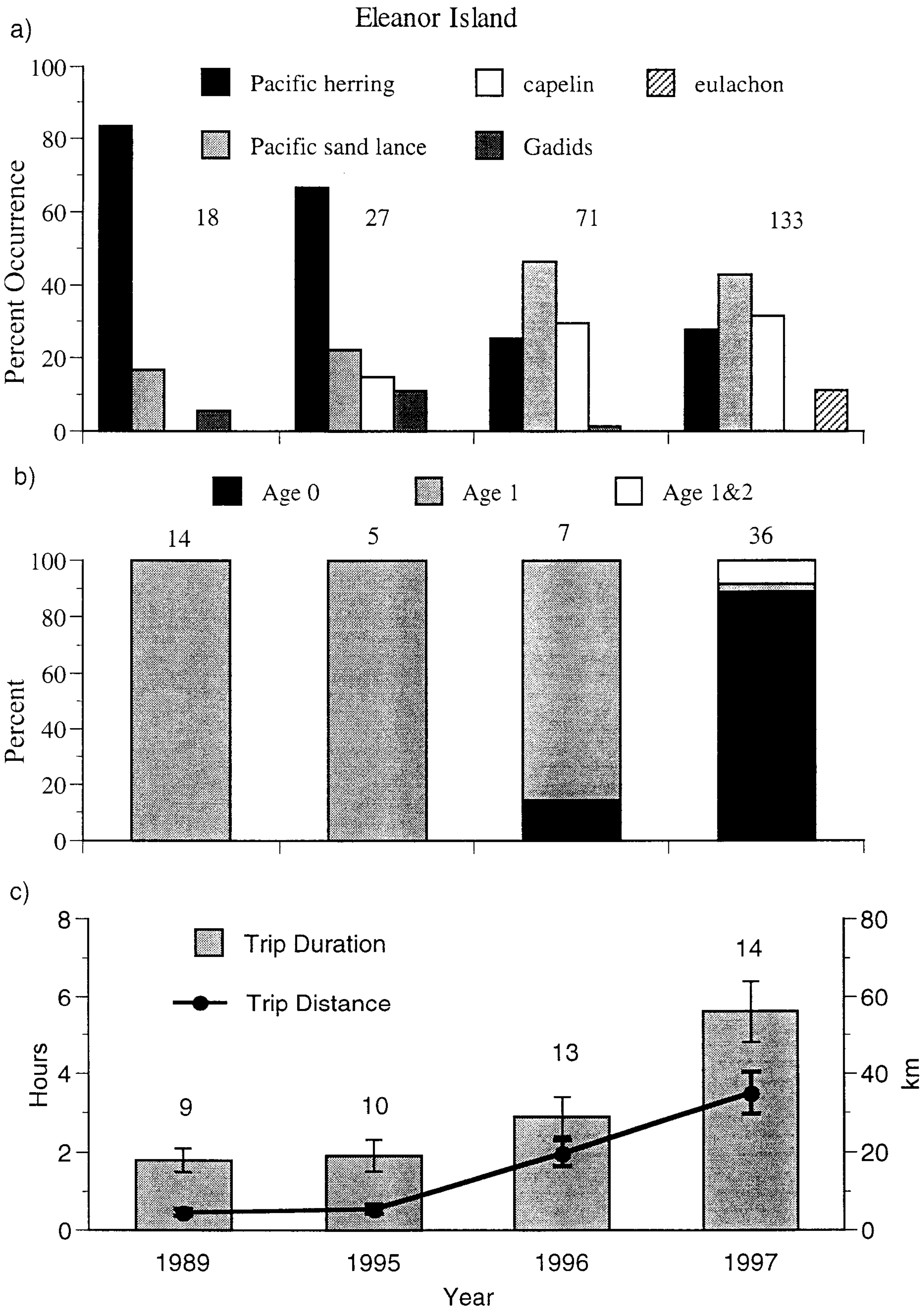

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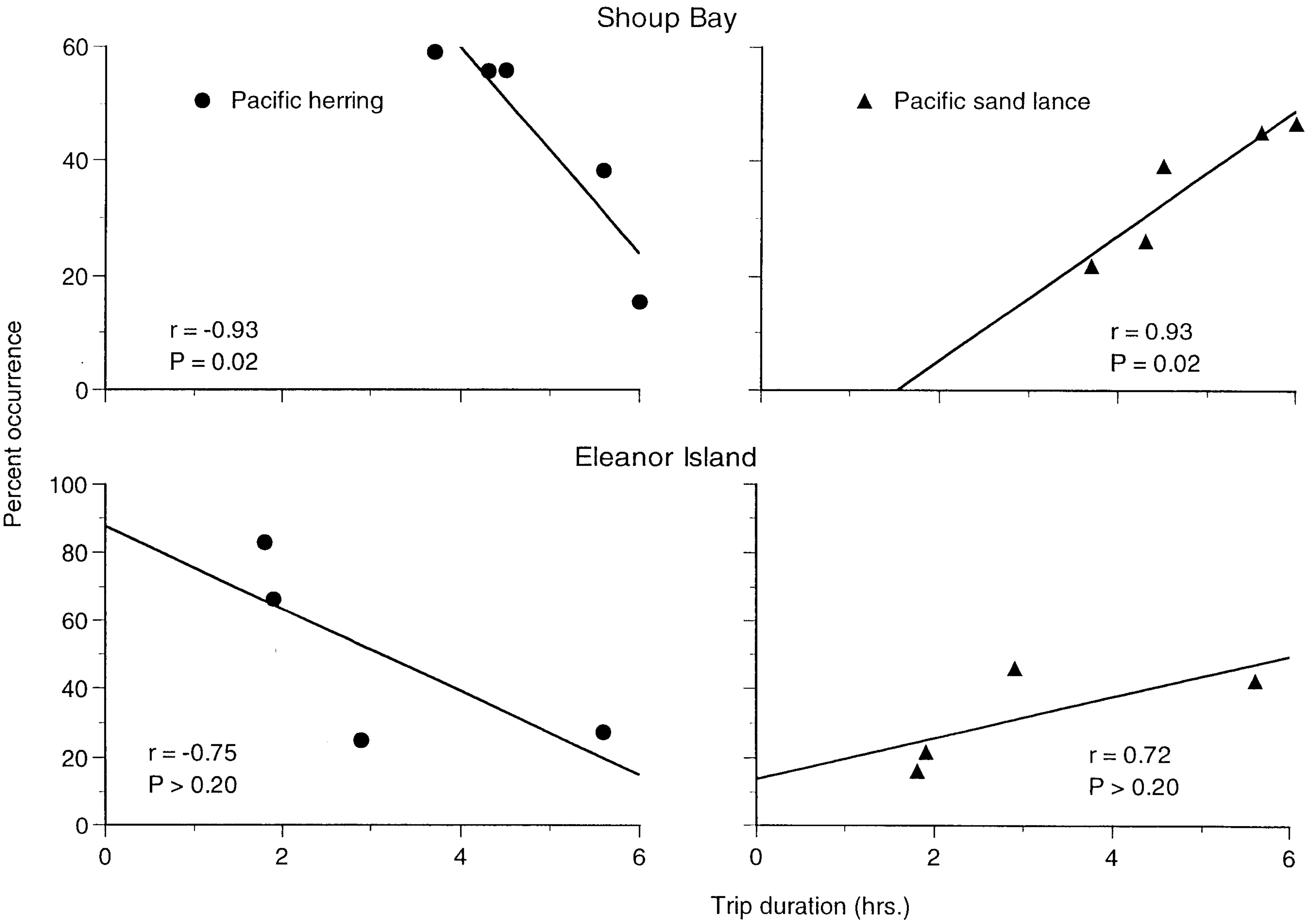

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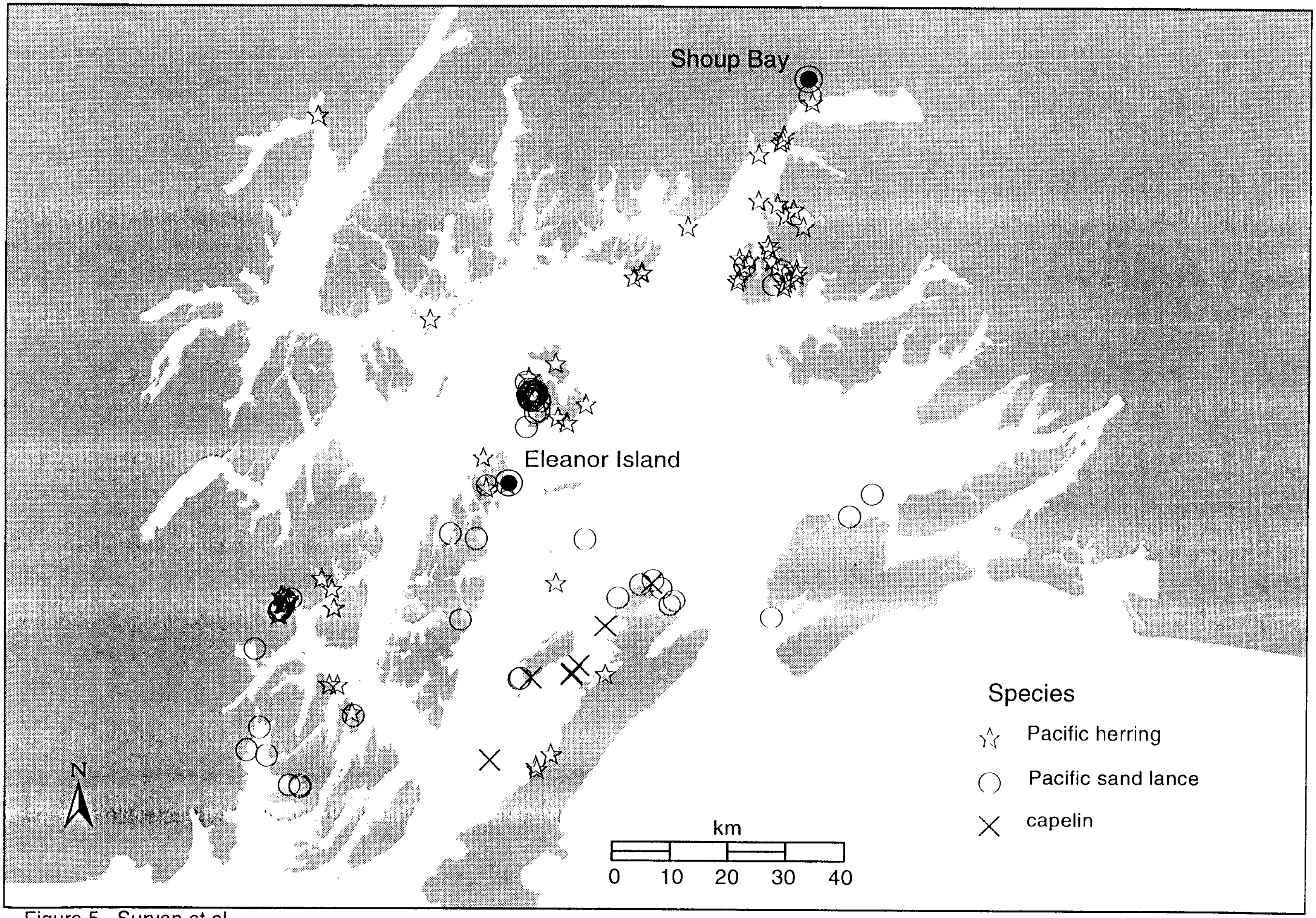
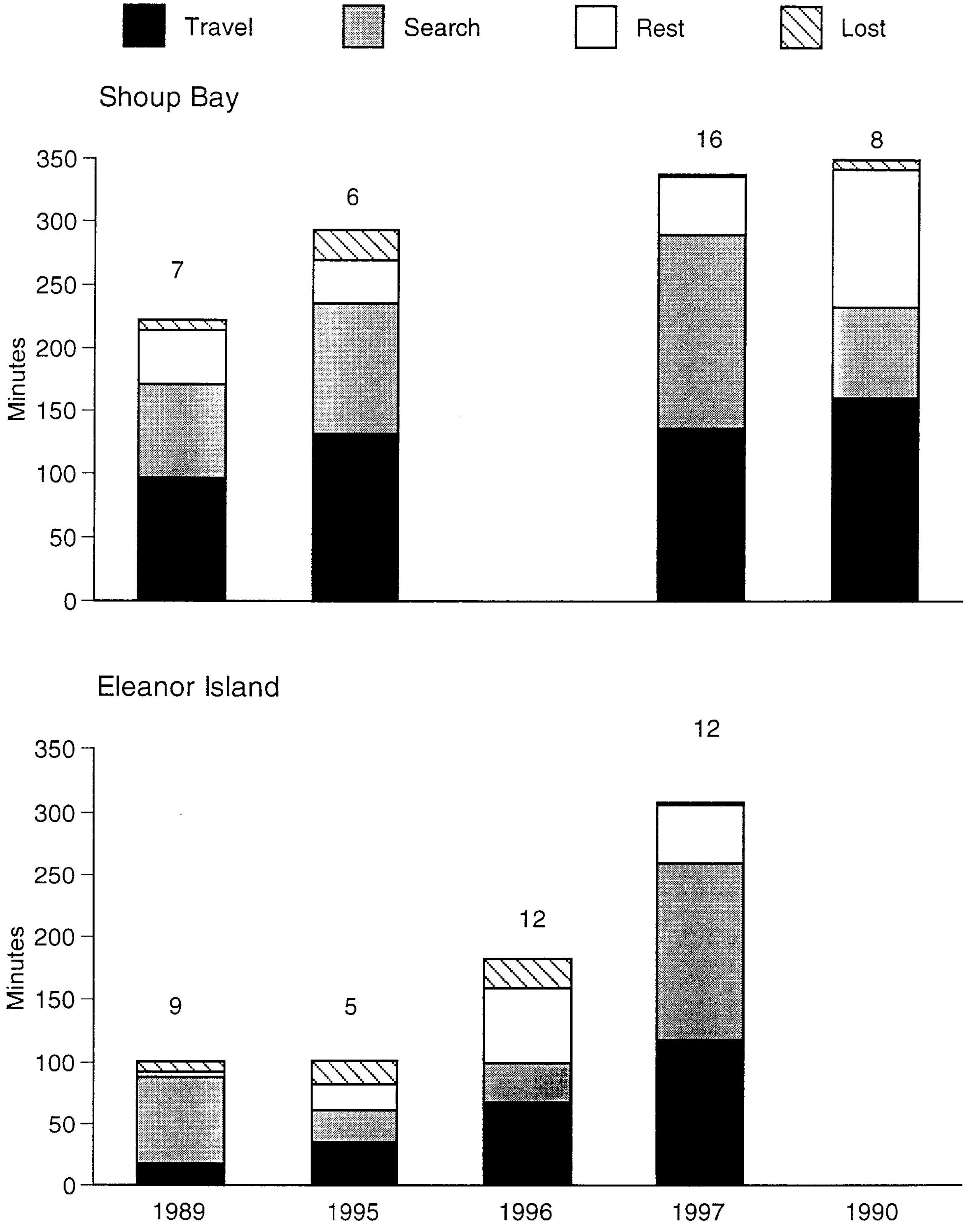


Figure 5. Suryan et al.



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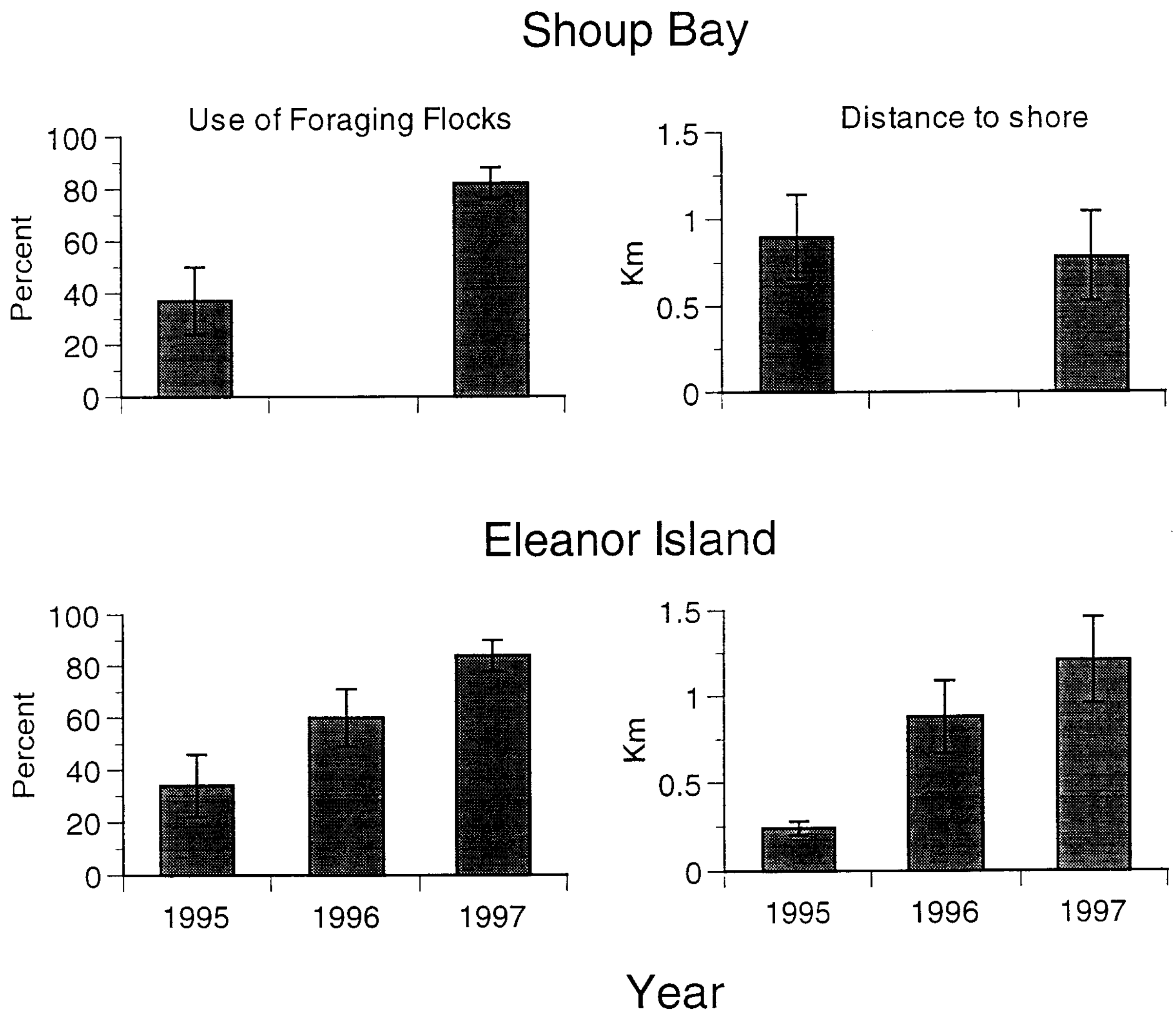

Figure 7. Suryan et al.

POPULATION DYNAMICS OF KITTIWAKES IN PRINCE WILLIAM SOUND, ALASKA: PRODUCTIVITY OF INDIVIDUAL COLONIES AND POPULATION TRENDS

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***Abstract*.** While the nesting population of Black-legged Kittiwakes (*Rissa tridactyla)* in Prince William Sound (PWS), Alaska has only a weak increasing trend since the early 1970's, the numbers of pairs within regions and at colonies has changed dramatically. Sixty-nine percent of the population in 1997 nests in northern PWS compared to 55% in 1985 and 30% in 1972. A population model using monte carlo simulations (5000 repetitions) was developed to help explain these observed changes and provide insight into the regulation of colony sizes. These analyses indicated that between 1984 and 1997 favorable conditions (e.g. availability of herring) in northern PWS allowed sufficient fecundity at northern colonies to maintain a net population increase ($p = 0.036$) in contrast to southern PWS where fecundity was insufficient to maintain the population ($p = 0.045$). These trends corresponded with the influence of the Alaska Coastal Current in southern PWS and the reported decrease in the availability of high quality forage fishes in the Gulf of Alaska, resulting in a decline in breeding success of piscivorous seabirds. In northern PWS where food was sufficient to support high breeding success, a positive relationship existed ($r^2 = 0.83$, $P < 0.001$) between colony size and fecundity. We would, therefore expect an opposite relationship in southern PWS where food appeared limited, although there was no relationship ($P = 0.54$). The limited success of small colonies (< 500 pairs) was likely influenced by predation. Projected population sizes compared to observed indicated evidence of immigration at large and small colonies while emigration was evident at only small, failing colonies. A positive relationship existed ($P < 0.001$) between the rate of colony growth and breeding success, indicating most kittiwakes immigrated or recruited to successful colonies, with a few exceptions. Immigration may be important in maintaining a few small-medium sized failing colonies. Source and sink metapopulation models are applicable to the PWS kittiwake population with the caveat that some source colonies have not yet reached carrying capacity and are still net importers of individuals.

INTRODUCTION

Food limitation during the breeding season has been proposed by several authors as an important factor limiting seabird populations (see Birkhead and Furness 1985 and Furness and Monaghan 1987 for reviews). Gaston et al. (1983) and Hunt et al (1986) provided evidence that intraspecific competition for food was greater at large colonies resulting in reduced reproductive parameters compared to small ones. Along with colony size, changes in prey availability, which may be caused by changes in oceanographic conditions(Hunt et al. 1990; Hunt 1991), also can limit reproduction in seabird populations (Piatt and Anderson 1996). In the Gulf of Alaska (GOA), environmental change on the decadal scale has been described (Royer 1989). Piatt and Anderson (1996) correlated these changes with the decline in the abundance of primary forage fishes, which lead to reduced breeding success and population declines of piscivorous seabirds and marine mammals.

Although food is thought to be a major factor in limiting seabird populations, there is evidence that other factors such as predation (Heubeck and Mellor 1990, Danchin and Monnat 1992) and parasites (Danchin and Monnat 1992) can affect reproductive success and size of individual colonies. Baird (1990) noted a decrease in breeding success of a kittiwakes associated with increased predation by Glaucous-winged Gulls (*Larus glaucescens*), American Crows (*Corvus brachyrhynchos*), and Common Ravens (*Corvus corax*). Although, Baird (1990) also described declines in prey availability the same year and noted the uncertainty of the association between increased predation and limited food availability in causing poor breeding success.

In this paper we evaluate the kittiwake population in PWS by regions related to oceanographic conditions which would be expected to primarily influence prey availability and, in turn, population size and breeding success. In addition, we propose factors that regulate colony growth, and productivity.

METHODS

Prince William Sound is located along the north coast of the GOA. Two oceanographic regimes primarily characterize PWS; glaciated fjords and an inland sea of sufficient size to allow horizontal cyclonic circulation (Niebauer et al. 1994). The Alaska Coastal Current (ACC) flows westward entering PWS through Hitchinbrook Entrance and exiting through Montague Strait (Niebauer et al. 1994; Fig 1). The influence of the ACC and its penetration into PWS varies seasonally and annually (Niebauer et al. 1994; Cooney 1997). Twenty-five kittiwake colonies are presently active and distributed on cliffs of islands and glacial fjords throughout PWS (Fig. 1). Sizes of colonies ranged from less than 20 to over 7000 pairs. To help describe trends in population dynamics of kittiwakes, we have divided PWS in "northern" and "southern" regions as depicted in Fig. 1. The colonies in southern PWS are those nearest the influence of the ACC.

Counts of the nesting population of Black-legged Kittiwakes in PWS were first conducted in 1972 by Isleib and Kessel (1973). There was a 12 yr hiatus until 1984 when Irons (1996) began collecting annual breeding population and productivity data. Breeding population size was determined by counting nests (i.e. breeding pairs) in June or early July at all colonies in PWS.

Productivity was estimated by counting nestlings in early August, just prior to fledging. Each colony was divided into plots. Counts of individual plots were not replicated, however, they did consist of a complete census of each colony. The same methods were used in all years of the study (Irons 1996) and were conducted primarily by the same two observers. Observers used binoculars (7X to 10X) and conducted counts from a boat (7.6 m).

Annual fecundity was defined as number of fledglings per pair. Fecundity estimates calculated from these methods could be biased in two, opposite ways. Fecundity could be underestimated because some nestlings were obscured by adults or topographic features during counts. Conversely, the true number of fledglings could be overestimated due to mortality of nestlings after counting but prior to fledging (although surveys were conducted late in the nesting season to minimize this). Correction factors (that accounted for both possibilities) were therefore determined by comparing fecundity estimates from boat-based counts with study plots being monitored for concurrent studies. Plots were located at four colonies from 1993 to 1997 (actual number of years varied with colony). Two sites represented small island colonies with less than 500 nests and plots encompassed the entire nesting population (i.e. censuses). The other two sites were medium to large (1800 - 7000 nests), fjord colonies. Eleven to 18 plots containing 162 to 430 nests were used to represent these colonies. Plots were checked every three days until nestlings were at least 34 days old and ready to fledge. Plots were considered the most accurate estimate of fecundity. Therefore, a correction factor was simply the average (± SD) fecundity determined from plots divided by fecundity from boat counts. Two correction factors were developed; one for small colonies (50 - 1000 nests) and one for medium to large colonies (> 1000 nests; Table 1). A correction was not applied at extremely small colonies (< 50 nests) where all nests were easily viewed. Selection of a correction factor was based on both size and location of a colony (e.g. if a small colony was located high on a cliff and difficult to observed, we used the large colony correction factor; correcting for a higher proportion of missed fledglings).

In 1991, about 850 adult kittiwakes and 510 nestlings were captured at the Shoup Bay colony and color-banded for individual identification. Annual resighting efforts were conducted prior to egg laying (1992 to 1997) at this colony to estimate adult survival, mean age at first breeding, and survival to breeding age. Adult survival estimates were obtained from Golet et al. (*in press*) for kittiwakes at the Shoup Bay colony and averaged over four years (1991 to 1995). Methods for resighting and calculation of adult survival rates are described in Golet et al. (*in press*) .

Mean age at first breeding was calculated for all fledglings color-banded in 1991 that returned to Shoup Bay to nest in subsequent years (Table 1). This estimate may be slightly low since a few 1991 cohort birds may be observed nesting for the first time at 7 or more years.

Survival to breeding age (combined juvenile and subadult survival) was based on the number of banded fledglings and the proportion of those birds resighted that survived to the mean age at first breeding (Table 1). Survival to breeding age is a minimum estimate since we do not know, at this time, the number of individuals that are alive but nesting at other colonies in Prince William Sound and the number that may be first observed in future years (i.e. unknown dispersal or resighting probabilities). During colony counts few birds banded as chicks at Shoup Bay were sighted, indicating high natal philopatry at Shoup Bay (a successful, rapidly growing colony).

Therefore, the estimate of survival to breeding age is probably only slightly low.

We determined whether productivity compensated mortality using the formula provided by Ricklefs (1973):

$$F_{equil} = (1 - S_{adult}) \cdot S_{breed}^{-1}$$

Where F_{equil} is the number of female offspring per female (or pair) per year for a population at equilibrium, S_{adult} is the finite survival rate of adults and S_{breed} is the finite survival rate from fledging to breeding age. The effect of S_{breed} on F_{equil} is a combination of mean age at first breeding and survival to first breeding. Our potential low estimates of these parameters would produce a fecundity value that was biased high. This bias, however, has minimal affect on the results and conclusions of this paper, since most comparisons are relative among colonies within PWS. Monte Carlo simulations with 5000 repetitions (assuming a normal distribution) were used to develop a value for mean F_{equil} (± 95% confidence intervals, C.I.) based on S_{adult} and S_{breed} (means ± 2 SD, approximately 95% C.I., were used in simulations).

A colony was classified as whether fecundity was greater than, equal to, or less than mortality. Fecundity for each colony was determined by dividing the total number of nests summed over 14 years (1984 - 1997) by the total number of nestlings then multiplied by the appropriate correction factor. Observed fecundity was compared to F_{equil} by calculating Z, the normal deviate (Zar 1984). Values were considered significantly different if the proportion of the normal curve (for values of F_{equil}) lying beyond Z was ≤ 0.05.

Additionally, we addressed the working hypothesis that demographic parameters could be used to explain observed changes in populations at individual colonies and PWS as a whole. We evaluated the potential for immigration or emigration by treating individual colonies, regions, and PWS as closed populations (assuming no immigration or emigration) and comparing projected colony sizes based on above demographic parameters and observed fecundity to actual counts (primarily between 1989 and 1997). If projected population size (assuming 100% natal philopatry) was significantly less than observed , there was a potential for immigration. Conversely, emigration was implied if the projected population size (assuming 0% natal philopatry) was greater than observed. A large annual change in survival or adults that skip nesting could produce results that would be considered immigration or emigration using this method. The model, however, incorporated a large amount of variability in these parameters and through simulations this variability is reflected in the confidence intervals for each prediction. We, therefore, were able to detect only gross cases of net immigration or emigration compared to relying on resighting of individually color-banded birds.

Annual projected colony sizes were determined using the formula:

$$N_{T+1} = [(1 + A) \cdot N_T \cdot S_{adult}] \cdot (1 - A) + [(F_{T-5} \cdot C) \cdot 2^{-1} \cdot S_{breed}]$$

Where N is number of females (or pairs) in the population at time T, A is the proportion of adults that skip nesting, S_{adult} and S_{breed} are the same as in previous formula, F_{t-5} is the number of fledglings at T-5 years (divided by two to represent females), and C is the correction factor for boat-based productivity estimates. Since counts of fledglings were first conducted in 1984, most projections began in 1989; at which time the number of new recruits (F_{T-5}) to the population was known. Random values (± 2 SD) of demographic variables (S_{adult}, S_{breed}, A, C) were selected from a normal distribution for input into the model. Projected annual population sizes and 95% C.I. were determined using Monte Carlo simulations with 5000 repetitions, similar to methods described above.

Projected population size was compared with that observed by calculating Z as described above. Observed trends in colony growth or decline were evaluated using linear regression ($\alpha = 0.05$). Linear regression was also used to evaluate relationships between fecundity, colony size, and rate of change in colony size.

RESULTS

As a whole, the kittiwake population in PWS has exhibited a weak increasing trend ($r^2 = 0.28$; $P = 0.06$) since 1972. Fecundity (0.31 fledglings/pair) during the past 14 yrs has been slightly above F_{equil} (0.27 fledglings/pair, SD = 0.09), but not significantly ($Z = 0.39$, $P = 0.348$), supporting a stable to slightly increasing population. The projected population generally modeled observed trends except for two years (1990 and 1991) where population increases indicated immigration (Fig. 2).

When evaluated on a regional scale there are striking differences between population trends and fecundity within PWS. A general pattern has been for colonies in the North to increase while southern colonies typically decreased (Fig. 3). Sixty-nine percent of the population now nests in northern PWS compared to 55% in 1985 and 30% in 1972. In addition, fecundity at northern colonies (0.44 fledglings/pair) remained significantly ($Z = 1.80$, $P = 0.036$) above F_{equil} in contrast to southern colonies where fecundity (0.12 fledglings/pair) was significantly ($Z = -1.70$, $P = 0.045$) below F_{equil} during the same time period (1984 to 1997). The increasing population trend ($r^2 = 0.70$; $P < 0.001$) in the North fit a model which assumed a closed population, except for 1991 (Fig. 2). In southern PWS, a pulse immigration in 1990 caused the observed population size to be greater than predicted. After 1990 the predicted trend generally agreed with the observed (Fig. 2).

It appears that factors affecting breeding success differed between north and south PWS. A comparison with data from the GOA indicates that productivity in southern PWS was more similar to colonies in the GOA and productivity in northern PWS was consistently higher than these (Fig. 4). This supports the hypothesis that southern colonies are more influenced oceanographic conditions and prey associated with the GOA and the influence of the ACC in southern PWS (Fig. 1).

Given these regional differences, we then evaluated population trends and fecundity of individual colonies. At this fine scale there were dramatic differences in how colony size changed in northern and southern PWS (Fig. 3). In the north, change in colony size ranged from a net increase of 6342 breeding pairs at Shoup Bay to a net decrease of 465 pairs at the Yale Glacier colony (Fig. 3). In the south, the greatest increase was 1327 breeding pairs at North Icy Bay and the greatest decrease was 4036 pairs at the Boswell Rocks colony (Fig. 3). Fecundity varied more dramatically in northern PWS than southern PWS. In the north, fecundity ranged from 0.33 nestlings/pair above F_{equil} to 0.27 below (Fig 5). In southern PWS, fecundity ranged from equilibrium to 0.27 nestlings/pair below F_{equil} (Fig. 5).

Given this great variation in colony growth and fecundity, we next assessed their potential relationship. Fecundity explained 70% of the change in colony size (Fig. 6), indicating colonies that were reproductively successful, grew and colonies that failed reproductively, declined. Regardless of the strong relationship between fecundity and colony growth, there were several notable exceptions. Two colonies in northern PWS (SHBA and BLGL) and four colonies in southern PWS (NIBA, NAIS, SEIS, PIRO) grew much more than expected based on fecundity; indicating immigration of birds from other colonies were responsible for the positive growth of these colonies (Fig. 7). Four small colonies in southern PWS (SHPO, BAIS, GRRO, TIGL) declined more than expected based on fecundity alone, indicating birds emigrated (Fig. 7).

To investigate why some colonies were successful and some failed we compared fecundity to colony size for northern and southern PWS. In the north, breeding success was positively correlated with colony size ($P < 0.001$) indicating sufficient food to maintain large colonies and some other limiting factor, potentially predation, for small colonies (Fig. 8). In the south, there was no relationship ($P = 0.54$) between success and colony size, indicating limitation by potentially food and predation (Fig 8).

DISCUSSION

Evaluated as a whole, there was relatively minor change in the kittiwake population in PWS with fecundity sufficient to compensate mortality. A closer evaluation, however, reveals striking regional and intercolony variation in population trends and fecundity. The majority of the population now nests in northern PWS where conditions have been substantially more favorable for chick rearing. Population regulation at individual colonies appears to be controlled by prey availability and predation. Most kittiwakes appear to be recruiting and/or immigrating to successful colonies with a few exceptions. These exceptions may be important to the initiation, growth and maintenance of small to medium-sized colonies.

Dramatic fluctuations in colony size at annual and decadal scales are relatively common for black-legged kittiwakes (Barret and Shei 1977, Coulson 1983, Godo 1985, Hatch 1987, Harris and Wanless 1990, Murphy et al. 1991, Danchin and Monnat 1992, Hatch et al. 1992, Heubeck and Mellor 1994). Annual variation in kittiwake breeding success can often be correlated with broad-scale fluctuations of oceanographic conditions and changes in prey availability (Barbera and Chavez 1983, Springer et al. 1986, Murphy et al. 1991). A notable long-term trend is the 70 yr increase of breeding kittiwakes throughout the United Kingdom followed by a marked, regional decline between 1969 and 1979 (Coulson 1983). The decline primarily occurred along the western seaboard, with favorable conditions persisting in the East (Coulson 1983); similar to the north-south trends we observed in PWS . Coulson (1983) attributed the increase to recovery from human exploitation in the 19th century and increased prey availability.

In PWS, we attribute the northerly shift in distribution of breeding birds and greater regional fecundity to the availability of forage fishes. These occurrences coincided with oceanographic changes in the GOA (Royer 1989) and associated decline in breeding success of piscivorous seabirds at GOA colonies (Piatt and Anderson 1996); similar to that of kittiwakes in southern PWS. We suggest that the regime shift in the GOA primarily affected kittiwakes in southern PWS where oceanographic conditions and prey associated with the ACC are more similar to those found at most colonies in the GOA. Diets of kittiwakes in PWS also reflect these regional differences. Nestling diets at a northern colony, Shoup Bay, are consistently dominated by primarily Pacific herring (*Clupea herrengus*) and secondarily Pacific sand lance (*Ammodytes hexapterus*; Suryan et al. in prep.). In contrast, nestling diets at colonies in central and southern PWS are often dominated by sand lance and capelin (*Mallotus villosus*) (Suryan et al. in prep., Suryan and Irons unpubl. data). Herring is nonexistent or rare in nestling diets throughout colonies in the GOA (Hatch et al. 1992) where capelin and sand lance are primary prey; portraying the similarity with southern PWS colonies. The decline in abundance of capelin and sand lance in the GOA since the late 1970's strongly correlates with declines in population sizes and breeding success of piscivorous seabirds (Piatt and Anderson 1996). This correlation is observable in southern PWS with northern PWS appearing independent of these changes. The availability of herring (and sand lance to a lesser extent), particularly in the northern regions, appears to have supported growing kittiwake populations in contrast to southern PWS and the GOA.

In addition to regional differences, intercolony variation in population trends and breeding success were also striking. A variety of hypotheses regarding regulation of seabird colonies can be invoked in trying to explain observed inter-colony variation in PWS. Authors have suggested competition for food around seabird colonies and its potential for limiting reproductive success (Ashmole 1963, Birkhead and Furness 1984). Hunt et al. (1986) tested this relationship by demonstrating increased competition at larger colonies was reflected in depressed reproductive output (e.g. breeding success, nestling growth rates) compared to smaller colonies. By suggesting competition, these authors are implying a limited food source and a density dependent negative relationship with seabirds. In this context, we would expect large colonies in PWS to be the least successful. This does not appear to be the case. In northern PWS there is a positive relationship between colony size and breeding success, indicating in most years sufficient prey is available so as not to induce density dependent competition. The fact that small colonies were less successful under these conditions indicated regulatory factors other than food limitation.

Two to three thousand Bald Eagles occur throughout PWS (Agler et al. 1997). Bald Eagles and other predators (Common Raven, Peregrine Falcon, *Falco peregrinus*) often cause total reproductive failure at small kittiwake colonies in PWS (Irons unpubl. data). We suggest that the relative effect of predation at small colonies likely limits breeding success. In southern PWS where food appeared limited, we would expect the proposed negative relationship between population size and breeding success to exist. This, however is not the case, indicating a combination of limited food and predation in regulating colony success. When predation and food are both regulatory factors, an optimal colony size should exist, below which breeding success is regulated by predation and above which breeding success is controlled by limited prey.

Predation and parasitism have been implicated in the failure and abandonment of kittiwake colonies (Heubeck and Mellor 1990, Danchin and Monnat 1992). These are confounding factors when determining if prey availability is responsible for declines in population size and fecundity. The degree of relationship between forage fish availability and depredation of seabirds is unclear, but in some situations likely to be substantial. One example is in the Shetland Islands where Heubeck and Mellor (1994) correlated a decrease in sandeel abundance with increased proportions of bird meat in diets of nonbreeding Great Skuas (*Catharacta skua*). This continued, resulting in an increase of bird meat in chick meals in addition to adult skua meals.

Fecundity was positively related to rate of colony growth. This relationship could be based on higher fecundity directly reflecting growth through natal recruitment and/or successful colonies being attractive to recruits from other colonies. If each colony was a closed population then growth would be directly related to fecundity. Since we demonstrated that colonies are not closed populations (as with Atlantic colonies, e.g. Porter and Coulson 1987, Danchin and Monnat 1992, Heubeck and Mellor 1994), growth is also likely related to recruitment from other colonies. In particular, Boulinier et al. (1996) and Boulinier and Danchin (in press) described the value of conspecific reproductive success in nesting habitat selection of new recruits. Prospecting and eventual breeding at a successful colony would lead to increased probability of reproductive success. The combination of these factors help to explain the observed relationship between fecundity and rate of colony growth.

Source and sink metapopulation theory has been used to describe relationships between a productive metapopulation (source) that supports an unproductive metapopulation (sink) through dispersal (Pulliam 1988). Typically the source population is defined as no net change in population size over several generations (a net exporter of individuals), in contrast to a sink which is a net importer of individuals (Pulliam 1988). This definition implies a source population is at or near carrying capacity. This does not seem to be the case for kittiwake colonies in PWS where two "source" colonies must have been net importers of individuals to sustain the rate of observed growth. We did, however, detect movement to stable or failing (sink) colonies. Although the majority of kittiwakes appeared to be recruiting and/or immigrating to successful colonies, there were exceptions which may be important for initiation and maintenance of these less successful colonies. In order to fully apply source and sink metapopulation theory we would have to determine movements of marked individuals among colonies and modify models to fit inconsistencies with definitions as described above.

Classification of source and sink populations can be valuable in influencing management decisions. Wooton and Bell (1992) described Peregrine Falcons in northern California as a source population and Southern California as a sink population. Given this, they argued that management efforts should be directed to Northern California. The dramatic annual variation in ocean conditions that affect prey and, in turn, seabird breeding success, however, poses complications in applying definitions of source and sink metapopulations, particularly for management purposes. For example, in 1972, Boswell Rocks was potentially a "source" colony and would deserve more consideration in management decisions than Shoup Bay. In 1997, however, the opposite decision would have been made. As one would expect, a source may not always be a source and a sink not always a sink. This exemplifies the importance of long-term data sets for long-lived species in identifying "source" or "sink" populations. Morris (1991) suggested that emigration to sink habitats is likely to be an evolutionarily stable strategy only if there is reverse migration back to the source. Given fluctuations in ocean conditions and the strong correlation with regional population changes in PWS, this reversing may be occurring on a multi-decadal scale.

Effect of Demographic Parameters on Results

Mean age at first breeding reported here was slightly higher than 3.9 yrs reported by Danchin and Monnat (1992) and 4.5 yrs reported by Coulson (1977) and Porter and Coulson (1987),. Porter and Coulson (1987) observed a decline in age at first breeding from 5 to 4 yrs in response to high adult mortality, therefore, some variation is likely given regional conditions. Our minimum estimate of survival to breeding age was also greater than that reported by Coulson and White (1959) and Coulson (1988). Using adult survival values for survival from 1 yr to breeding age, Coulson and White (1959) estimated a first year survival of 0.79 and Coulson (1988) estimated 0.70. Employing the same method, our estimate of first year survival would be 0.78, near the high reported for the Atlantic. Given that adult survival rates are significantly higher for the Pacific compared to Atlantic kittiwake populations (Golet et al. in press), we would expect first year survival in the Pacific to be at least equal to and possibly greater than in the Atlantic. Our minimum estimate is consistent with expectations.

Philopatry to a natal colony has been reported at 11% (Porter and Coulson 1987) and 36% (Coulson and Nevede Mevergnies 1992) in the Atlantic. Our estimate of survival to breeding age required the assumption that natal philopatry was 100% and survival was still greater than that reported in the Atlantic. This implies that our estimate of S_{breed} is considerably low or natal philopatry is extremely high. Shoup Bay is the largest, fastest growing, and most productive colony in PWS and therefore likely attractive to recruits. In addition, few fledglings banded at Shoup have been located at other colonies (Irons unpubl. data). We believe that philopatry to the Shoup Bay colony is extremely high and that S_{breed} is only slightly biased low. This would likely not be true for other colonies in PWS.

Our calculated value of F_{equil} would essentially represent a λ (the multiplication rate of the population) equal to one. Danchin (1992) warned against discrepancies in calculating β (an estimate of λ) based on all females entering the breeding population at a mean age with constant fecundity, probability of breeding, and survivorship in subsequent years. Our model violates two of these four considerations in using 5 yrs as a mean age at first breeding and survival constant with age (0-5 and 5+ yrs). We emphasize, however, the primary conclusions of these analyses are inter-regional and intercolony comparisons. Therefore, eliminating the effect a potential bias in calculation of F_{equil} would have on our results.

Differences in survival among successful and unsuccessful colonies could affect the model presented in this paper. Given the similarity in adult survival among colonies in the GOA (Golet et al. in press) and particularly with Middleton Island (a colony with low breeding success; Hatch et al. 1993), we wouldn't expect much variation in survival estimates. Danchin and Monnat (1992) reported that age at first breeding and adult survival was not significantly different between an increasing and decreasing colony. They did, however, report that proportion of adults that skipped breeding were greatest at the declining colony. We used estimates for skipped breeding from a successful colony, therefore projections from our model may be biased high when applied to colonies with low breeding success.

Conclusions

In conclusion, the redistribution of breeding kittiwakes from southern to northern PWS over the past two decades directly correlates with reported decrease in available forage fishes in the GOA and the associated decline in seabird and marine mammal productivity. Conditions in northern PWS during this period (likely the availability of herring) were favorable in producing high breeding success compared to southern PWS and the GOA. If conditions affecting the availability of surface schooling forage fishes in the GOA improve, we expect these changes to be reflected in greater breeding success at southern colonies. Population regulation at individual colonies appeared to be controlled primarily by prey availability and secondarily predation. In northern PWS large colonies were the most successful indicating food was not limited. Breeding success at most small colonies in the north was likely limited by predation. In southern PWS where food was limited, we would have expected an inverse relationship between colony size and breeding success. The relative effect of predation at smaller colonies however appeared to confound this relationship and limit breeding success at small colonies. Individual colonies in PWS are not closed populations with most kittiwakes recruiting and/or immigrating to successful colonies with a few exceptions. These exceptions may be important in the initiation, growth and maintenance of some small to medium-sized colonies. The application of source and sink metapopulation theory is appropriate to kittiwakes in PWS with some restrictions. Source colonies were not limited by nesting habitat or food and therefore continued to attract individuals. Once these colonies reach carrying capacity they will likely become net exporters and more closely fit traditional source/sink definitions. The population model developed for PWS was accurate in describing most observed changes in kittiwake populations at individual colonies and PWS as a whole.

LITERATURE CITED

(Please note that the Literature Cited section is incomplete)

Agler, B. A. And S. J. Kendall. 1997. Marine bird and sea otter population abundance of Prince William Sound, Alaska: trends following the *T/V Exxon Valdez* oil spill, 1989-96. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 96159), U. S. Fish and Wildl. Serv., Anchorage, Alaska 152 pp. + appendices.

Baird, P. H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scandinavica 21:224-235.

Birkhead, T. R. and R. W. Furness. 1985. Regulation of seabird populations. Pp. 145-167 *in* Behavioural ecology: ecological consequences of adaptive behaviour (R. M. Sibley and R. H. Smith, Eds.). The 25th Symp. of the British Ecol. Soc., Reading 1984. London, Blackwell.

Danchin, E. 1992. Modeling seabird populations and implications for management. The importance of models to study the demography of wild bird populations. Ardea 80 (1): 157-160.

Cooney, R. T. 1997. Sound Ecosystem Assessment (SEA): A science plan for the restoration of injured species in Prince William Sound, Alaska. *Exxon Valdez* oil spill restoration project annual report (restoration project 96320), Institute of Marine Science, Univ. of Alaska Fairbanks, Fairbanks, Alaska. 99775-7220.

Danchin, E. and J-Y Monnat. 1992. Population dynamics modeling of two neighboring kittiwake *Rissa tridactyla* colonies. Ardea 80:171-180

Furness, R. W. and P. Monaghan. 1987. Seabird ecology. Chapman and Hall, New York, NY. 164 pp.

Gaston, A. J., L. N. de Forest, G. Donaldson, and D. G. Noble. 1994. Population parameters of thick-billed murres at Coats Island, Northwest Territories, Canada. Condor 96:935-948.

Golet, G. H., D. B. Irons, and J. A. Estes. In press. Survival costs of chick rearing in Black-legged Kittiwakes. J. Anim. Ecol.

Hatch, S. A. 1987. Did the 1982-1983 El Nino-Southern Oscillation affect seabirds in Alaska? Wilson Bull. 99(3):468-474.

Hatch, S. A., G. V. Byrd, D. B. Irons, and G. L. Hunt Jr. 1992. Status and Ecology of kittiwakes in the North Pacific. *In* Status, ecology, and conservation of marine birds of the North Pacific (Vermeer, K., K.T. Briggs, K.H. Morgan, and D. Siegel-Causey, eds). Canadian Wildlife Service, Ottawa, pp 140-153.

Heubeck, M. and R. M. Mellor. 1994. Changes in breeding numbers of kittiwakes in Shetland, 1981-1994. Scottish Birds 17:192-204.

Hunt, G. L. Jr. 1991. The distribution of seabirds at sea: physical and biological aspects of their marine environment. Proc. Int. 100 DO-G Meeting, Current Topics in Avian Biology, Bonn 1988.

Hunt, G. L. Jr., Z. A. Eppley, and D. C. Schneider. 1986. Reproductive performance of seabirds: the importance of population and colony size. Auk 103:306-317.

Hunt, G. L., N. M. Harrison, and R. T. Cooney. 1990. The influence of hydrographic structure and prey abundance on foraging of Least Auklets. Stud. Avian Biol. 14:7-22.

Irons, D. B. 1996. Size and productivity of black-legged kittiwake colonies in Prince William Sound before and after the *Exxon Valdez* oil spill. *In* Rice, S. D., Spies, R. B., Wolfe, D. A., and B. A. Wright (eds.). Exxon Valdez Oil Spill Symposium Proceedings. Am. Fish. Soc. Symp. no. 18.

Isleib, P. and B. Kessel. 1973. Birds of the north gulf coast - Prince William Sound Region, Alaska. Biol. Paper Univ. of Alaska 14. 149 pp.

Niebauer, H. J., T. C. Royer, and T. J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. J. Geophys. Res. 99(C7): 14.133-14.126.

Piatt, J. F., and P. J. Anderson. 1996. Response of Common Murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem. *In* Rice, S. D., Spies, R. B., Wolfe, D. A., and B. A. Wright (eds.). Exxon Valdez Oil Spill Symposium Proceedings. Am. Fish. Soc. Symp. no. 18.

Royer, T. C. 1989. Upper ocean temperature variability in the northeast Pacific Ocean: is it an indicator of global warming? J. Geoph. Res. 94(C12): 18.175-18.183.

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

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 718 pp.

To Be Continued......

Table 1. Demographic and model parameters for Black-legged Kittiwakes nesting in Prince William Sound, Alaska.

	n	mean	SD
Adult survival (5+ yrs of age)[a]	4 yrs 474-616 birds	0.922	0.013
Survival from fledging to breeding age[b]	203 of 357 fledglings	0.567	0.026
Age at first breeding[b]	116 birds	4.97	0.88
Probability of breeding[a]	4 yrs 399-622 birds	0.936	0.445
Fledgling Sex Ratio[c]		50:50	
Correction Factor			
small (50 - 1000 nests)	4	1.230	0.172
medium to large (> 1000 nests)	7	1.311	0.253

[a] Golet et al. In Press. Probability of breeding is a combination of "skipped attending" and "skipped nesting" reported by Golet et al. in press

[b] Estimate from this study

[c] Assumed

LIST OF FIGURES

Figure 1. Location and size (number of pairs in 1997) of Black-legged Kittiwake colonies in Prince William Sound, Alaska. Line divides northern and southern PWS. Northern PWS comprises those colonies with foraging ranges more likely associated with oceanographic conditions specific to PWS waters vs. GOA influences in southern PWS. Approximate summer influence of the Alaska Coastal Current in Prince William Sound is depicted by diagonal lines (//). Colonies are identified by a four letter code throughout text (Bay of Isles, BAIS, Blackstone Glacier, BLGL, Boswell Rocks, BORO, Chenega Glacier, CHGL, Coxe Glacer, COGL, Eaglek Bay, EABA, Eleanor Island, ELIS, Ellamar, ELLA, Gravina Rocks, GRRO, Gull Island, GUIS, Icy Bay, ICBA, Middle Green Island, MGIS, Naked Island, NAIS, Nellie Juan Glacier, NJGL, North Icy Bay, NIBA, Passage Canal, PACA, Pinnacle Rocks, PIRO, Porpoise Rocks, PORO, Seal Island, SEIS, Sheep Point, SHPO, Shoup Bay, SHBA, Suprise Glacier North, SGNO, The Needle, THNE, Tiger Glacier, TIGL, Yale Glacier, YAGL)

Figure 2. Observed (--●--) versus projected (—■—; ± 95% confidence limits) population size for Prince William Sound (PWS) overall, northern and southern PWS.

Figure 3. Net changes in colony size of Black-legged Kittiwakes in northern and southern Prince William Sound, Alaska, between 1972 and 1997.

Figure 4. Fecundity (fledglings/pair) of Black-legged Kittiwakes nesting at colonies in northern vs. southern Prince William Sound (PWS; see Fig. 1 for demarcation), and the Gulf of Alaska (GOA; Hatch et al. 1992) from 1984 to 1997.

Figure 5. a) The difference between fecundity (F) and fecundity at population equilibrium (F_{equil}; bars) for colonies in north and south Prince William Sound, Alaska. Asterisks denote a significant difference between F and F_{equil} at $\alpha = 0.05$ (**) and $\alpha = 0.10$ (*).

Figure 6. Linear regression relationship between annual population change (pairs/year) and difference between fecundity (F) and fecundity at population equilibrium (F_{equil}) for colonies in Prince William Sound, Alaska. Data include only those colonies where a significant trend in population growth or decline was detected (using linear regression).

Figure 7. Percent change in population size for 26 kittiwake colonies in northern and southern Prince William Sound, Alaska. Circles (●) denote observed population change between 1988 (for most colonies) and 1997. Triangles denote predicted population change assuming 100% (▼) and 0% (▲) natal philopatry. Error bars on predicted change represent 95% confidence intervals. Colonies are arranged by size beginning with the largest for each region.

Figure 8. Linear regression relationship between mean population size (1985 - 1997) and difference between fecundity (F) and fecundity at population equilibrium (F_{equil}) for colonies in northern and southern Prince William Sound, Alaska.

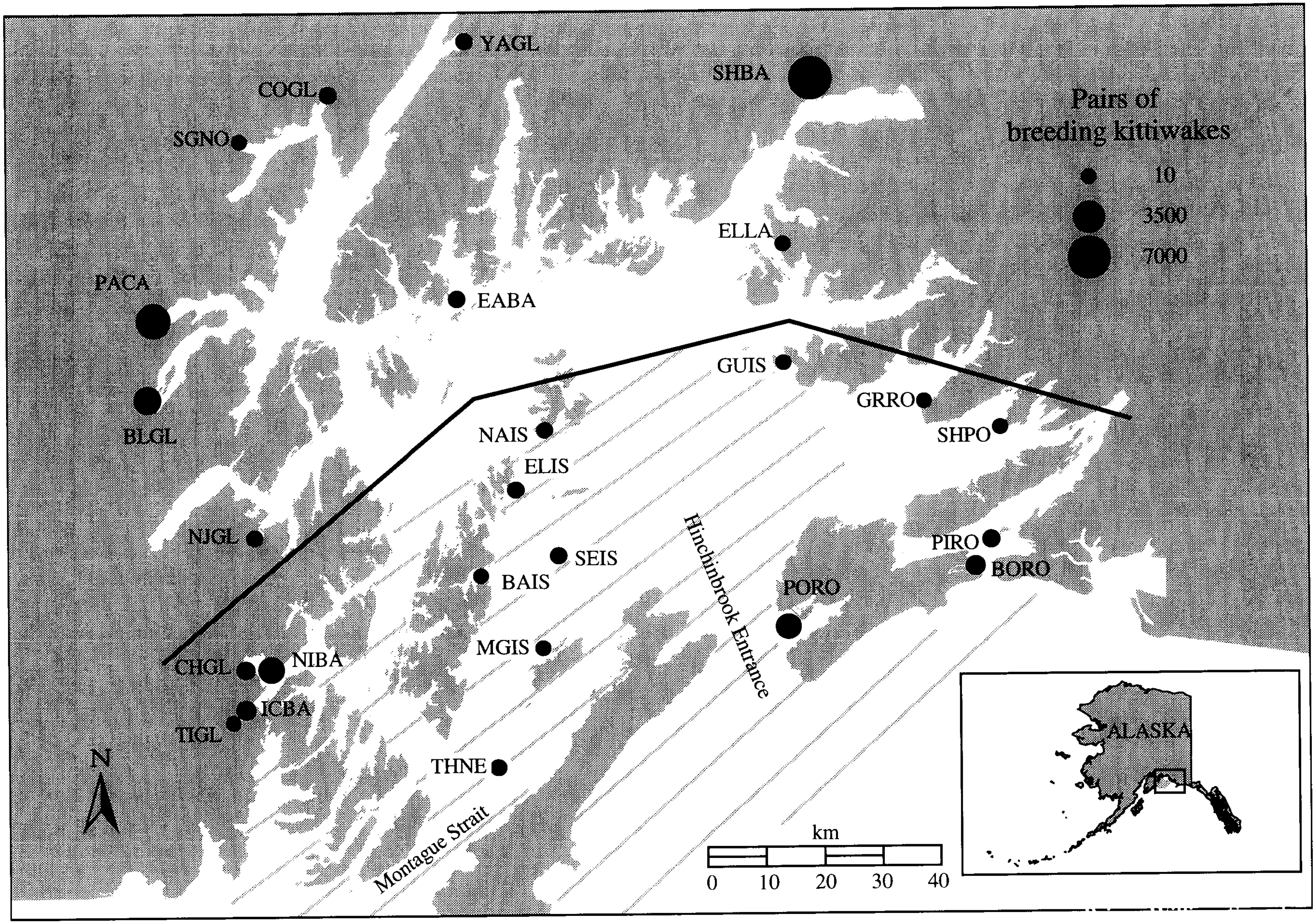
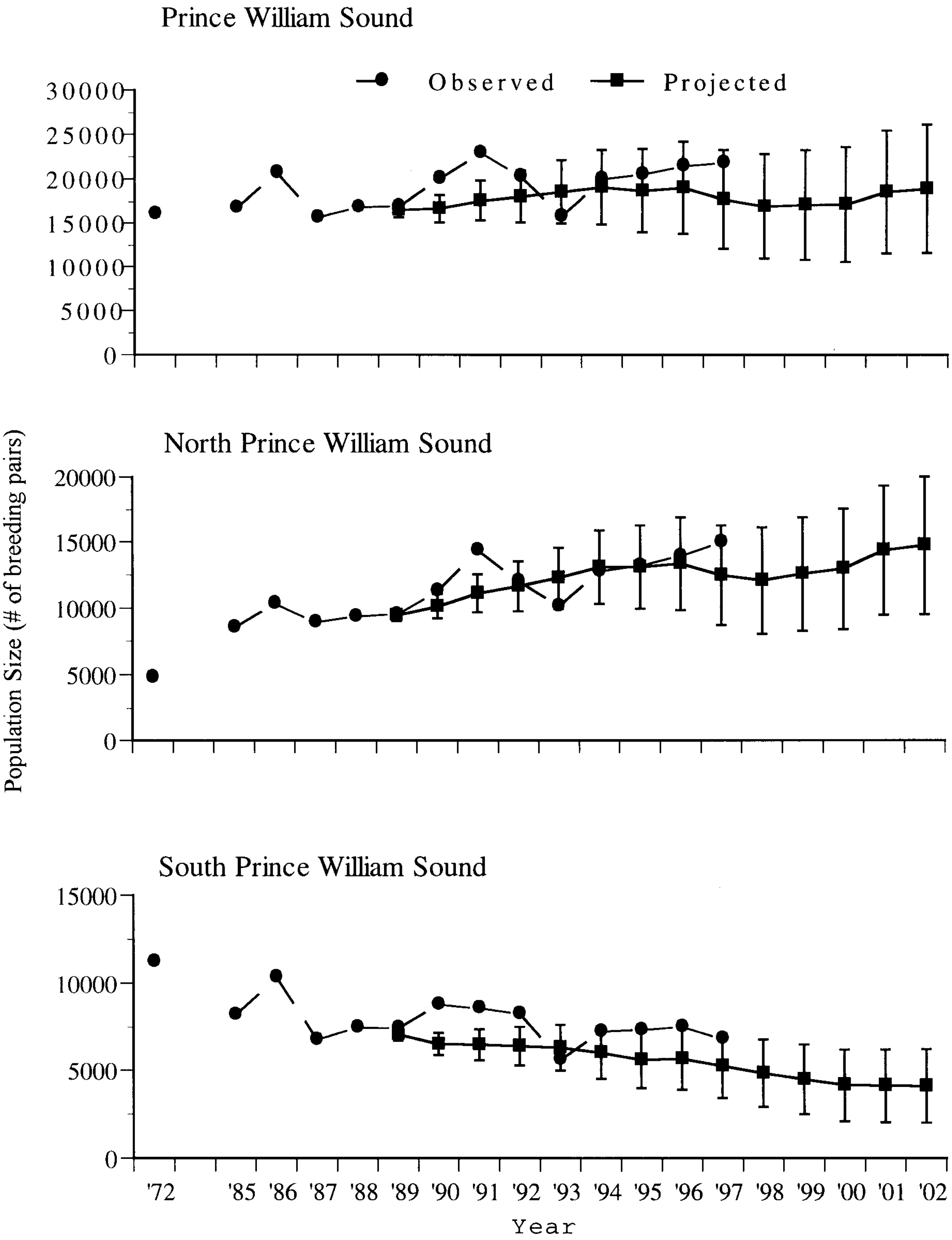


Figure 1. Suryan and Irons



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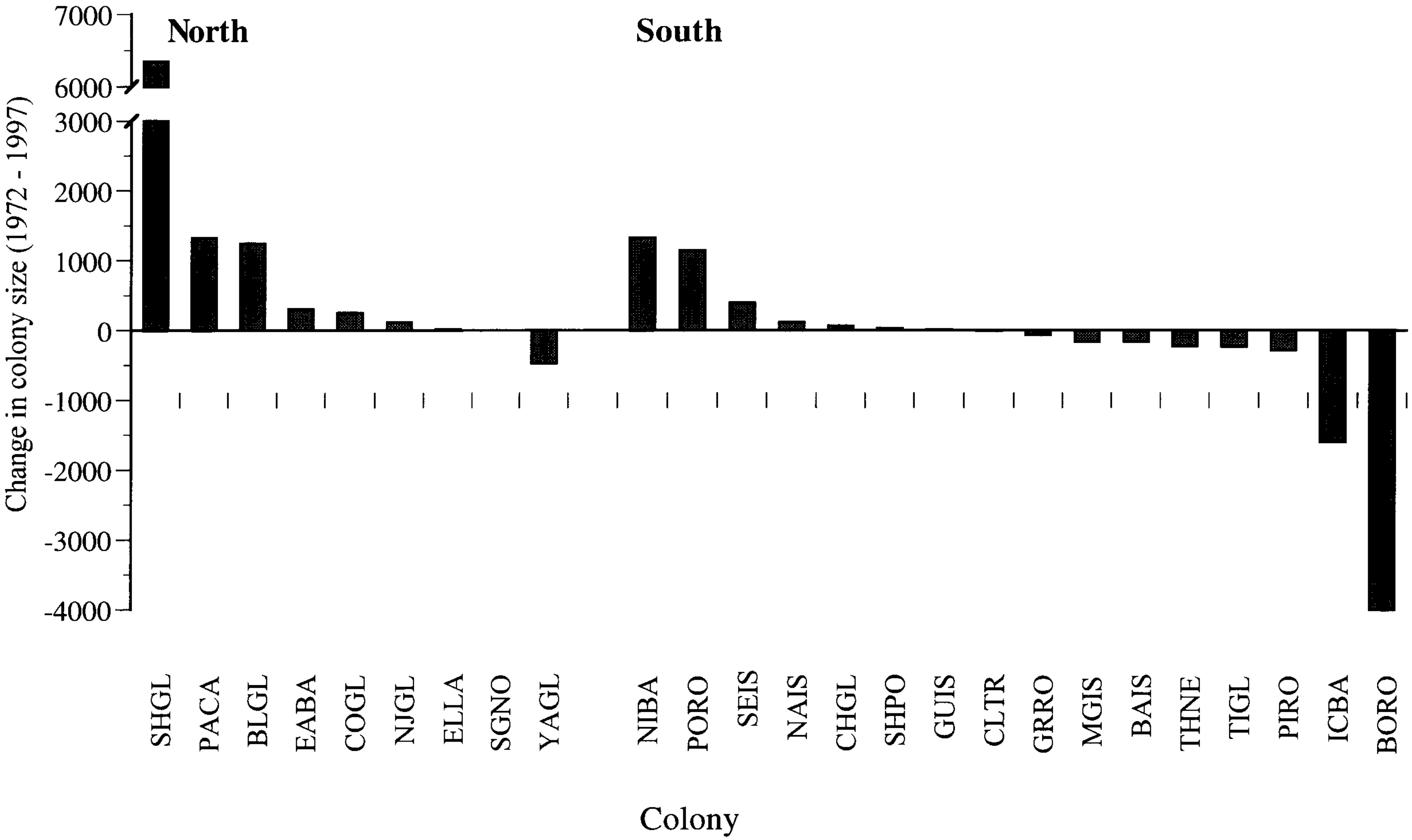

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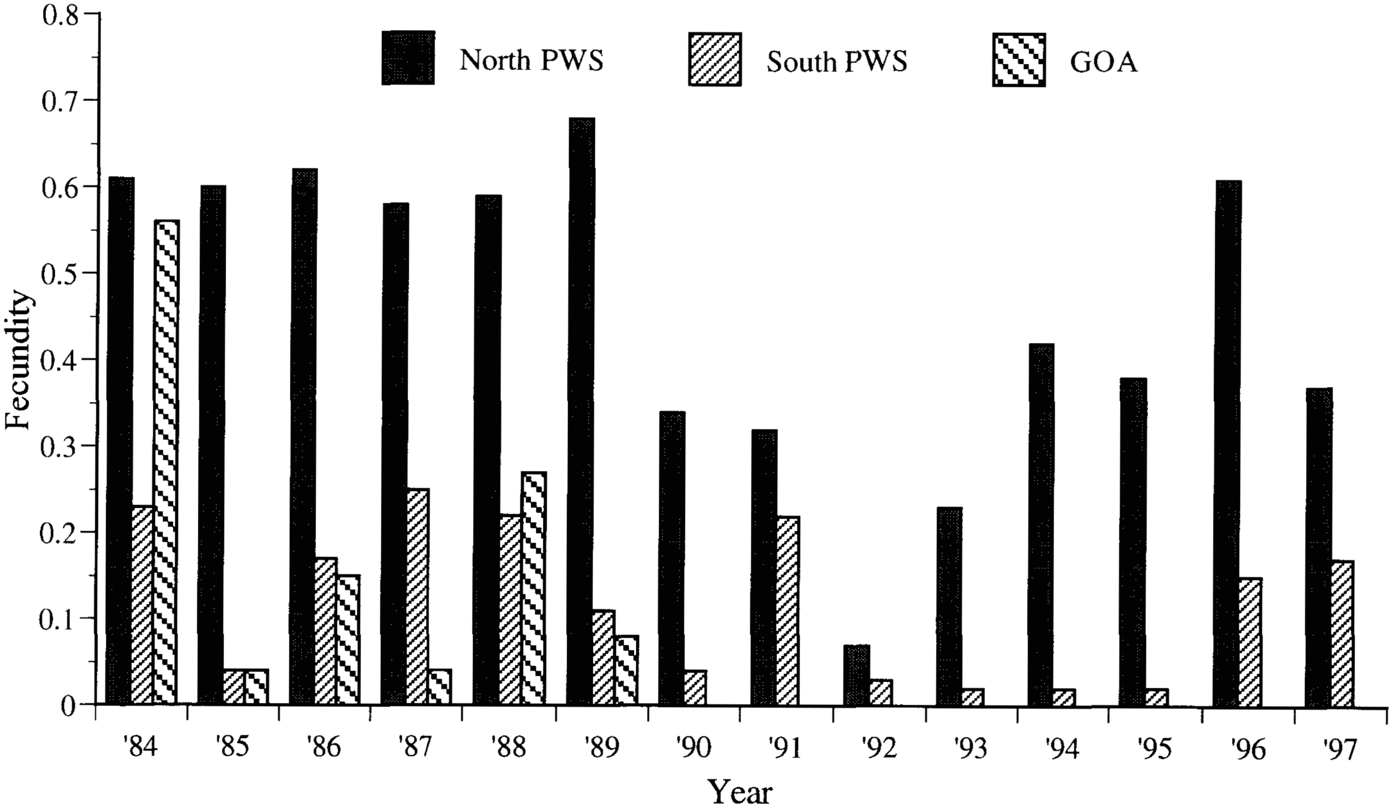

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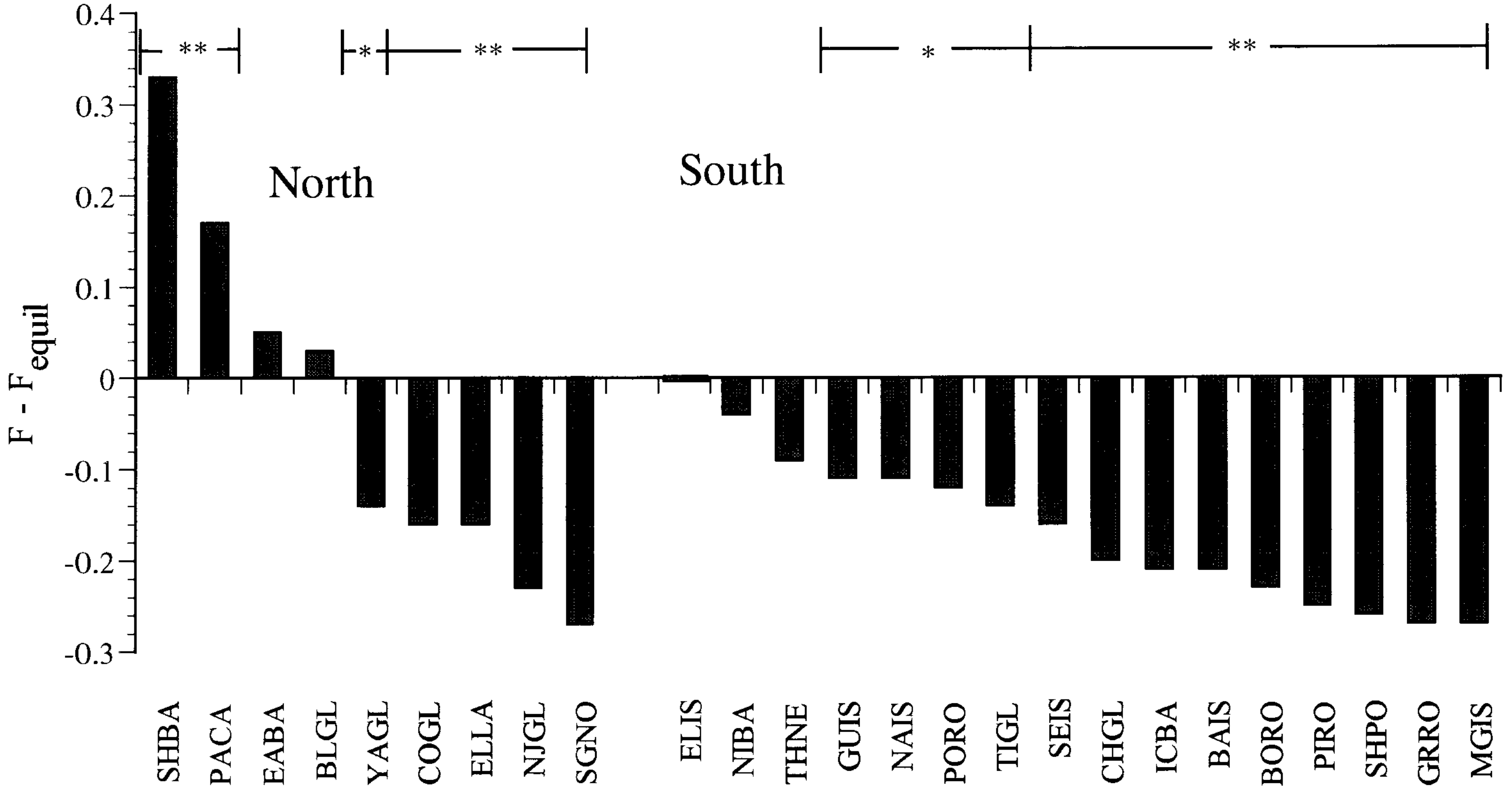

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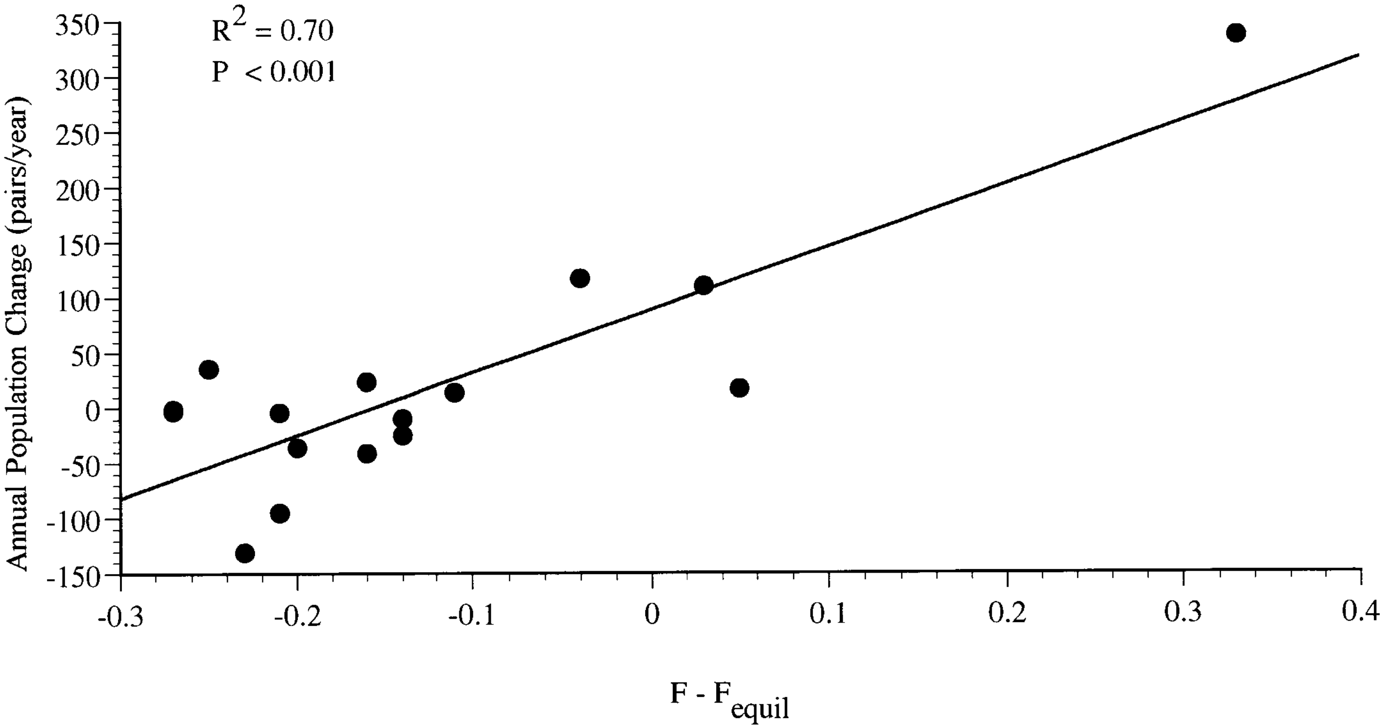

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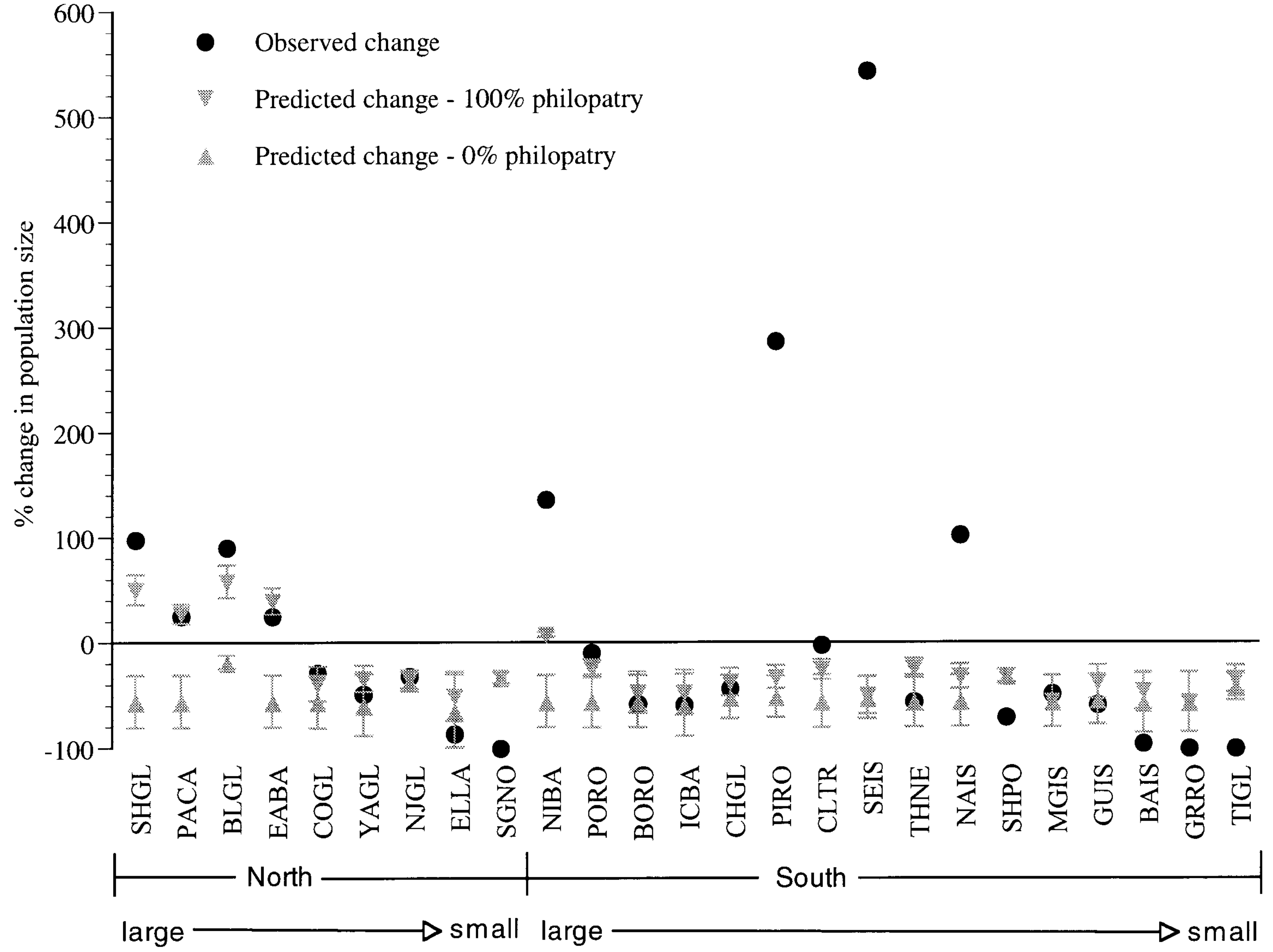

Figure 7. Suryan and Irons

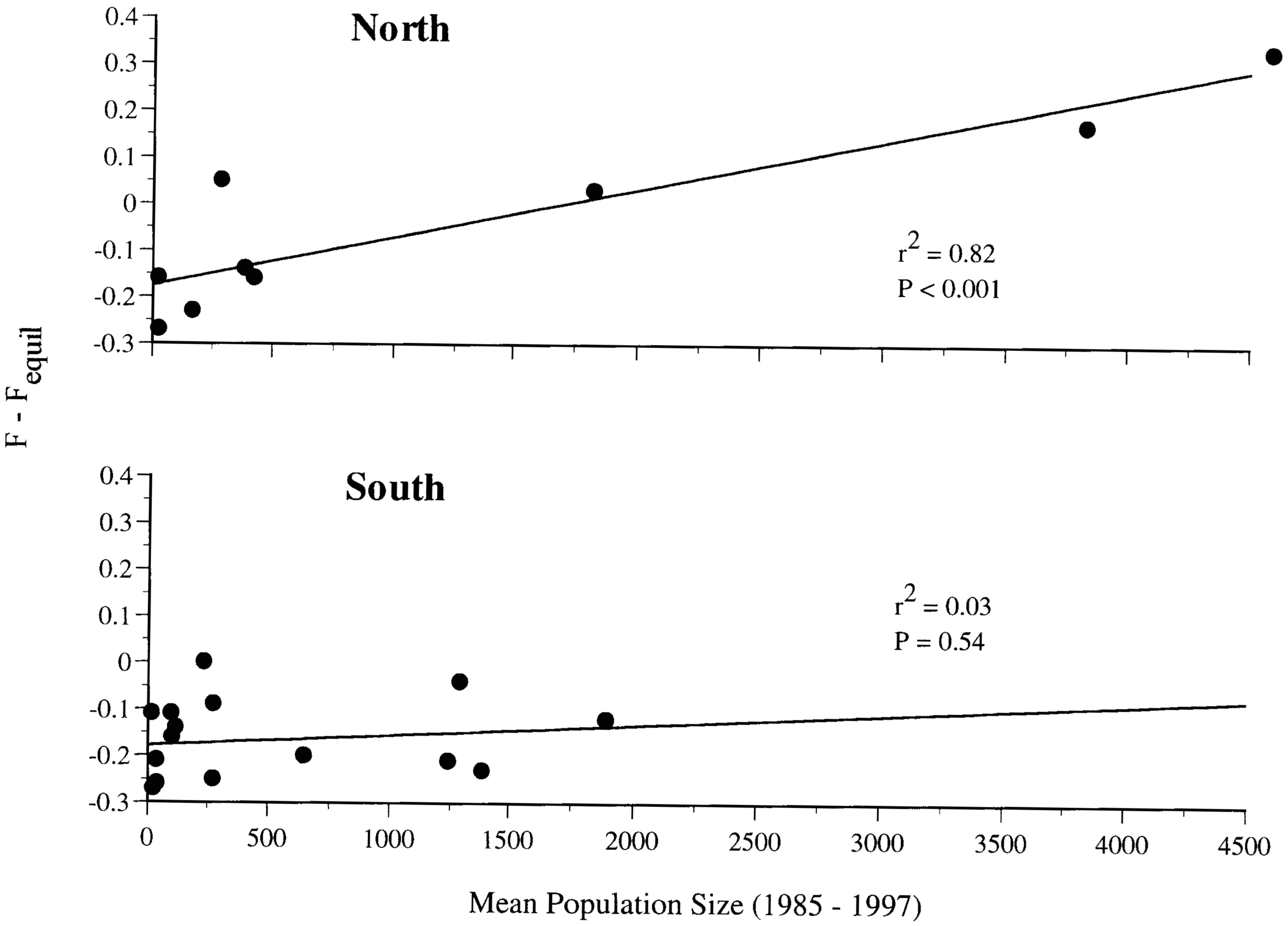

Figure 8. Sury an and Irons