

APPENDIX B

APEX: 96163B

Exxon Valdez Oil Spill
Restoration Project Annual Report

Seabird/Forage Fish Interactions Component
APEX

Restoration Project Component 96163B
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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Seabird/Forage Fish Interactions Component
APEX

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Annual Report

Study History: This is an ongoing study which began with a pilot effort in 1994 to test field methods. In 1995, the study was expanded to look at seabird foraging in several habitats in 3 study sites within Prince William Sound. Data collected in 1994 and 1995 indicated that seabird activity was concentrated in shallow water nearshore. In response to these findings the 1996 study expanded data collection by adding an extensive survey of nearshore habitats.

Abstract: We sought to determine if forage fish characteristics and/or interactions among seabirds limit food availability. We also examined the relationship between seabird foraging groups size and the characteristics of associated forage fish. Additionally, we compared strip transect and telemetry methods of determining the foraging range of black-legged kittiwakes (*Rissa tridactyla*). Seabird/forage fish interactions were monitored by conducting systematically arranged transects, 21 July-11 August 1995 and 14-28 July 1996 in three study areas in Prince William Sound Alaska, Alaska. The study sites were located in Valdez Arm, Naked and Knight Islands, and Jackpot and Icy bays. In 1996 nearshore survey blocks were added in these three areas. Hydroacoustic and bird-observation data were collected simultaneously during these surveys. We collected additional data on seabird/forage fish interactions at 22 mixed species feeding flocks in both 1995 and 1996. We determined that *Brachyrampus* murrelets selected forage fish schools in shallow water habitats, that are generally associated with high energy forage fish that have declined in abundance. Whereas, tufted puffins (*Fratercula cirrhata*) were generalist foragers. We speculated that differences in forage selection and life history differences of these species may be linked to the differential response of these species to the Exxon Valdez oil spill. We determined that there may be a commensal relationship between black-legged kittiwakes and marbled murrelets (*Brachyrampus marmoratus*) with kittiwakes the beneficiary and a competitive interaction between kittiwakes and glaucous-winged gulls at mixed species feeding flocks. The total number of birds in mixed species feeding flocks was positively related to the chord length of associated fish schools and negatively related to density and depth of water to schools. Our comparison of strip transect and telemetry sampling indicated that a survey design of insufficient size and the declining probability of encountering birds as distance from the colony increase, were major sources of bias associated with the strip transect method.

Key Words: *Brachyrampus marmoratus*, Exxon Valdez oil spill, forage fish, foraging, *Fratercula cirrhata*, glaucous-winged gulls, kleptoparasitism, *Larus glaucescens*, marbled murrelets, radio telemetry, randomization, resource selection, seabirds, tufted puffins.

Project Data: *Description of data* - Major data sets of all birds observed during the 1994, 1995 and 1996 on pelagic APEX cruises. Several subsets of the 1995 data give locations of individual species and locations within each study areas. There is an additional data set of bird locations for the 1996 APEX nearshore survey. There are also data sets of behavior data collected on mixed species feeding flocks for 1995 and 1996. We maintain a file of video tapes of mixed species feeding flocks recorded in 1995 and 1996. We developed a data set of the characteristics of fish schools encountered during the 1995 APEX cruise. There are subsets of the fish school set that give characteristics of schools associated with *Brachyrampus* murrelets, tufted puffins (*Fratercula cirrhata*), black-legged kittiwakes (*Rissa tridactyla*), and feeding flocks. We have an unprocessed data set for 1996 on the formation of feeding flocks, that gives location, time and date of occurrence, and initiating species on each flock observed. Format - These data sets are in ASCII text format except the initiators of flocks set which is on field data sheets and the video tape file. *Custodian* - Contact William Ostrand through the Office of Migratory Bird Management, U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503 (phone: 907-786-3849, fax: 907-786-3641, or email: William_Ostrand@mail.fws.gov). *Availability* - Copies of all data that are recorded as computer files are available on floppy disc.

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Executive Summary: The Seabird/Forage Fish Interactions component of APEX has examined several aspects of seabird activity at sea. In the 1996 annual report we have presented our findings on the following topics: 1) A comparison the characteristics of forage fish schools selected by murrelets and tufted puffins with implications on their differential response following the *Exxon Valdez* oil spill. 2) The characteristics of fish schools associated with mixed species feeding flocks. 3) A comparison of radio telemetry and strip transect methods of determining foraging ranges of black-legged kittiwakes. 4) The composition and behaviors at mixed species feeding flocks. 5) A summary of bird data collected during the 1996 nearshore APEX survey.

To compare the characteristics of forage fish schools selected by murrelets and tufted puffins we collected hydroacoustic and bird-observation data simultaneously along transects in three areas in Prince William Sound from 21 July - 11 August 1995. We derived depth to each fish school, area, and density of forage-fish schools and total depth of water, distance to shore, and distance to the nearest seabird colony for each forage-fish school. Subsequently we determined which schools were associated with Tufted Puffins, a species that has been increasing in abundance following the spill, and Brachyramphus murrelets, 2 species with stable populations following the spill. The probability of the association of fish schools with birds was determined through the use of a resource selection function based on logistic regression. Our analysis indicated that Tufted Puffins were generalist foragers which selected fish schools near their colony.

Brachyramphus murrelets selected larger, denser fish schools in shallower water when compared to available fish schools. Fish species that were high in energy content were associated with shallow water habitats. There are indications that these fish species have experienced local population declines. Walleye Pollock (Theragra chalcogramma), a low energy content forage species, was abundant in deep water habitats and their biomass has been increasing in the northern Gulf of Alaska. Our study indicated that Brachyramphus murrelets foraged in habitats associated with high energy content forage species. If Walleye Pollock provided sufficient energy for reproduction, we might have expected Brachyramphus murrelets to use a foraging strategy that would have allowed them to maximize their consumption of this abundant species. We suggest that the generalist foraging and the nesting strategies of Tufted Puffins has allowed this species to adjust to ecological change and increase its population. Whereas, Brachyramphus murrelets need for high energy foods and a foraging strategy that selects habitats associated with high energy forage species, that have declined in abundance, may be a major reason for this species failure to recover following the oil spill.

We made comparisons between schools associated with flocking birds and those not associated with flocking birds encounter during the 1995 APEX survey using Wilcoxon rank sum tests and logistic regression analysis. Feeding flocks chose fish schools which were close to shore and in shallow bottom depths, as well as those which had a narrow chord length. However, fish schools found nearshore were significantly more narrow than offshore fish schools suggesting that flocking birds chose feeding habitat rather than school size. At the feeding flocks, bird numbers were positively correlated with fish school chord length and negatively correlated with density and depth to the schools.

We compared strip transect and telemetry methods of determining foraging range by using randomization tests. We evaluated factors that could bias either method and indicate how they may have affected the respective data sets. We also used bootstrap resampling to: determine the effect of reducing our sampling effort for both methods, speculate on the benefits of increased sampling, and compare the time required to obtain similar variability by both methods. The mean distance birds were observed from their colony determined by telemetry were significantly greater than the mean value calculated from strip transects. We determined that this difference was due to 2 sources of bias: 1) a decreasing probability of sighting birds at increasing distance from their colony on strip transect surveys. 2) The maximum distance birds were observed from the colony through telemetry exceeded the extent of the strip transect survey. We compared the observed number of birds seen on the strip transect survey to the predictions of a model of the declining probability of sighting birds at increasing distance from the colony (DPSB). Field data were significantly different from modeled data; however, the field data were consistently equal to or below the model predictions indicating a general conformity to prediction of a DPSB. We concluded that telemetry data provided a more accurate measure of foraging distance than strip transect data for colonial birds. Furthermore, studies that have used strip transect sampling that have not accounted for DPSB may have underestimated foraging range. Variability was less for strip transect sampling and less time was required to collect the data. We concluded that strip transect sampling yielded more precise data whereas telemetry data was more accurate.

We examined the behaviors of seabirds at feeding flocks in Prince William Sound, Alaska during July/August 1995 to determine the factors which may enhance or limit the availability of forage to surface feeding birds. The presence of lairds and alcids at feeding flocks was positively correlated, suggesting complimentary feeding habits. On the other hand, the frequency of kittiwake plunge dives was negatively correlated with the relative presence of larger gulls in the flock. Kittiwakes preferred to plunge-dive for fish while Glaucous-winged Gulls hop-plunged from the water surface to maintain their position at the center of the feeding flock. Kittiwakes had a feeding success of 80.6% and lost 4.8% of their captures to intraspecific piracy and 6.7% to interspecific piracy. Kleptoparasitism was most intense against kittiwakes in tightly aggregated feeding flocks and against alcids in loosely aggregated flocks. Jaegers preferred to kleptoparasitize kittiwakes in the largest flocks.

During July of 1996 we conducted a nearshore survey to assess seabird distributions and examine their behavior at feeding flocks. We systematically selected 12-km blocks of shoreline within which we ran 20 1-km long transects to and from shore at oblique angles. The average number of birds per transect and transect block were 6.62 and 131.57, respectively and were not significantly different among the three study areas ($P > 0.10$ in both cases). However, species composition of the blocks differed significantly among the study areas ($P < 0.001$). Bird flocks were feeding primarily on juvenile herring and sand lance. Flocks in the northeastern area were significantly larger than flocks in the other two areas ($P = 0.01$) and were feeding on herring more often. The feeding rate of black-legged kittiwakes did not increase significantly with the presence of marbled murrelets ($P = 0.3801$), but did decrease significantly with the presence of glaucous-winged gulls ($P = 0.0225$). Changes in flocks from 1995 included; reduced presence of

kittiwakes and tufted puffins, increased presence of marbled murrelets and glaucous-winged gulls, more tightly aggregated feeding flocks, reduced feeding success of kittiwakes and greater feeding success of gulls, reduced kleptoparasitism of kittiwakes and increased kleptoparasitism of gulls. The implications of these changes are discussed briefly.

Introduction: This annual report is comprised of 4 manuscripts, chapters I - IV, that have been prepared for publication in scientific publications. In addition, chapter V presents general findings of the nearshore survey conducted in 1996.

Objectives: The Seabird/Forage Fish Interactions component of APEX had 3 major objectives for 1996:

- 1) Forage fish characteristics limit availability of seabird prey. This objective is the focus of chapter I and a portion of chapter II.
 - 2) Interactions among seabirds limit availability of seabird prey. This objective is the subject of chapter IV and portions of chapter V.
 - 3) Seabird foraging group size and species composition reflect prey patch size. Findings on this objective are discussed in chapter II.
- In addition to these objectives, a comparison between radio telemetry and strip transect methods of determining the foraging range of black-legged kittiwakes is discussed in chapter III.

CHAPTER I: SELECTION OF FORAGE-FISH SCHOOLS BY MURRELETS AND TUFTED PUFFINS IN PRINCE WILLIAM SOUND, ALASKA AS FACTORS IN RECOVERY FOLLOWING THE EXXON VALDEZ OIL SPILL

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Abstract: As of 1996, local populations of 7 piscivorous pursuit diving bird and mammal species had not recovered from the perturbations caused by the 1989 Exxon Valdez oil spill in Prince William Sound, Alaska (PWS). We hypothesized that these species shared a common food limitation and to gain insight into the possible limitation we compared the foraging strategies of injured and non-injured species of birds from the same sub-order. We collected hydroacoustic and bird-observation data simultaneously along transects in three areas in PWS from 21 July - 11 August 1995. We derived depth to each fish school, area, and density of forage-fish schools and total depth of water, distance to shore, and distance to the nearest seabird colony for each forage-fish school. Subsequently we determined which schools were associated with Tufted Puffins (Fratercula cirrhata), a non-injured species that has been increasing in abundance following the spill, and Brachyramphus murrelets (Brachyramphus spp.), 2 injured species with stable population following the spill. The probability of the association of fish schools with birds was determined through the use of a resource selection function based on logistic regression. Our analysis indicated that Tufted Puffins were generalist foragers that selected fish schools that were near their colony. Brachyramphus murrelets selected larger, denser fish schools in shallower water when compared to available fish schools. Fish species that were high in energy content were associated with shallow water habitats. There are indications that these fish species have experienced local population declines. Walleye Pollock (Theragra chalcogramma), a low energy content forage species, was abundant in deep water habitats and their biomass has been increasing in the northern Gulf of Alaska. Our study indicated that Brachyramphus murrelets foraged in habitats associated with high energy content forage species. If Walleye Pollock provided sufficient energy for reproduction, we might have expected Brachyramphus murrelets to use a foraging strategy that would have allowed them to maximize their consumption of this abundant species. We suggest that the generalist foraging and the nesting strategies of Tufted Puffins has allowed this species to adjust to ecological change and increase its population. Whereas, Brachyramphus murrelet's need for high energy foods and a foraging strategy that selects habitats associated with high energy forage species, that have declined in abundance, may be a major reason for of this species failure to recover following the oil spill.

Key words: Brachyramphus brevirostris, Brachyramphus marmoratus, Brachyramphus murrelets, foraging, Fratercula cirrhata, Kittlitz's Murrelets, Marbled Murrelets, Prince William Sound, resource selection, Tufted Puffins.

On 24 March 1989 the oil tanker M/V Exxon Valdez grounded on Bligh Reef in Prince William Sound, Alaska (PWS), resulting in the spill of more than 42,000,000 liters of crude oil (Spies et al. 1996). Seabirds were severely impacted by the spill: 3,400 bird carcasses were recovered from PWS and 30,000 from the total spill affected area. Piatt et al. (1990) estimated total seabird mortality at 100,000 - 300,000. As of 1996, 9 bird and mammal species had not recovered from the population perturbation (Exxon Valdez Oil Spill Trustee Council 1996). Seven of these, Pelagic Cormorants (Phalacrocorax pelagicus), Red-faced Cormorants (Phalacrocorax urile), Doubled-crested Cormorants (Phalacrocorax auritus), Common Murres (Uria aalge), Marbled Murrelets (Brachyramphus marmoratus), Pigeon Guillemots (Cepphus columba), and Harbor Seals (Phoca vitulina), are piscivorous pursuit diving species. In addition Kittlitz's Murrelet (Brachyramphus brevirostris) were injured by the spill and the status of their recovery is unknown (Exxon Valdez Oil Spill Trustee Council 1996). All of these species forage

on small schooling fishes which suggests that population recovery may be impeded by a common food or energy limitation. Long term effects of the oil spill (Spies et al. 1996) and/or a broader ecological shift in the Alaska Coastal Current (Piatt and Anderson 1996) could have altered the food web, resulting in a food limitation.

Marbled Murrelets were among the most common seabirds within PWS (Agler et al. 1997) and as a study species, provided the greatest potential for obtaining an adequate sample size for a comparative foraging study. A disproportionately high number of dead murrelets, 390, compared to their proportion of the total marine bird population were recovered in PWS after the oil spill (Piatt 1990). Subsequent to the spill, the murrelet population has remained stable and has not recovered (Agler et al. 1997). Tufted Puffins (*Fratercula cirrhata*), were also common within PWS (Agler et al. 1997) and were not severely impacted by the Exxon Valdez oil spill (Piatt et al. 1990, Exxon Valdez Oil Spill Trustee Council 1996). Following the spill, there has been an upward trend in their population (Agler 1997). The coexistence of these species provided an opportunity to contrast the foraging strategies of 2 alcids, which were affected differently by the oil spill. Differences in the selection of forage resources among these species, would support the food limitation hypothesis and provide insight the mechanisms causing a limitation.

Hydroacoustic sampling of forage resources while simultaneously conducting bird surveys has provided much of our current information on the relationship between seabirds and their prey (Hunt 1988). Several studies using these techniques have correlated seabird and forage abundances. However, the strength of these relationships generally weakened as the scale became finer (Obst 1986, Heinemann et al. 1989, Schneider and Piatt 1986, Erikstad et al. 1990, Hunt et al. 1990, Piatt 1990). Mehlum et al. (1996) correlated Brünnich's Guillemots (*Uria lomvia*) abundance to forage density at a fine scale by including a prey density threshold that excluded non-preferred food items from their correlation analysis. In examining fine scale relationships between Common Terns (*Sterna hirundo*) and forage-fish, Safina and Burger (1985) did not find a relationship between predator and prey abundance but did find a significant relationship between birds, depth to prey, and the presence of predatory fish. These studies suggest that marine birds may select patches based upon more factors than prey abundance at fine scales. Furthermore, studies of feeding flocks in the tropics (Duffy 1983) and Alaskan waters (Hoffman 1981) have demonstrated that the species composition of feeding flocks was related to characteristics of associated fish schools. Therefore, we anticipated that differences in the foraging strategies of murrelets and Tufted Puffins would be most apparent if we examined the selection of fish schools by birds through multivariate methods to evaluate several possible factors.

STUDY AREA AND METHODS

We conducted this study in PWS, an inland waterway of 10,000 km², located on the southern coast of Alaska. The climate is maritime with record annual precipitation > 8 m and moderate temperatures for the subarctic. The coastline of PWS is rugged, with mountains up to 4-km elevation, and numerous fjords and tidewater glaciers. Three study sites were selected for sampling (Fig. 1): 1) the northern study area which included Valdez Arm and Port Valdez, 2) the central study area which included waters near Naked and Knight Islands, and 3) the southern study area which included Icy and Jackpot Bays.

We collected hydroacoustic and bird location data simultaneously while traveling systematically arranged transects (Anderson et al. 1979, Litvaitis et al. 1994). To locate transects, we randomly selected the starting point from 20 equally spaced points within the first 2' latitude of the southern boundary of each study area. We arranged east-west transects at 2' latitude intervals north of the initial starting latitude and added zigzag transects to increase data collection of nearshore habitats (Fig. 1). Zigzag transects were inserted at points where east-west transects terminated at land. We drew zigzag transects from the end of the previous east-west transect, to a point half the perpendicular distance to the next east-west transect at which the water depth was 100 m. From the 100-m depth point we drew a transect to the beginning of the next east-west transect. Potential transect segments that were < 1 nautical mile were not included, other potential segments were deleted for safety considerations. After deletions, 41 east-west and 25 zigzag transects remained in the survey design. By study area there were 15, 18, and 8 east-west and 8, 9, and 8 zigzag transects in the north, central, and south study areas, respectively. We determined the total length and mean \pm standard deviation (SD) of both east-west and zigzag transects (Table 1). We chartered a 24-m vessel, the M/V Pacific Star, to replicate the hydroacoustic/bird transect survey twice during 21 July- 11 August 1995.

Hydroacoustic data were collected with a 420 kHz BioSonics Model 120-121 echo-integration system. The data were integrated for 30-second intervals and over 1-m depth intervals, corrected for calibration, and stored to disk. Transects were run at 6 knots with the transducers towed beside the vessel. The effective range of the equipment was 65 m from the transducers. Global Positioning System (GPS) data were written to each record. Length and species composition information from net samples of the target species (Haldorson et al. 1996) was used with length-target strength relationships (R. Thorne, BioSonics Inc., Seattle, Wash., unpubl. data) to scale the acoustic data. We obtained net-sample data from a separate vessel which was directed by the hydroacoustic vessel to trawl through schools with a Canadian midwater herring trawl (100-m² opening). We selected schools for trawling which had the greatest species and/or age class composition uncertainty. These trawls were only effective on the larger schools; therefore, the samples may not have been representative of all schools.

Bird observations were made from the second deck of the M/V Pacific Star, 8-m above the water. Continuous counts were made of all seabirds observed within 100 m of the starboard side of the vessel, the same side from which acoustic data were taken. We assigned the following behavioral codes to each observation: 1) flying, 2) on the water, 3) on a floating object, 4) foraging, and 5) potentially foraging. Foraging was defined as the actual observation of foraging behavior such as diving for food or holding food in the bill. Potential foraging was defined as ≥ 2 associated birds on the water or circling above. Bird observations were made by scanning ahead of the ship using binoculars. Recorded observations were made prior to the ships presence influencing bird activities. Data were recorded when the ship was closest to the point at which the birds were first observed. We directly recorded data into a computer file using custom software that also recorded the ships position and time for each data entry. GPS data were obtained from the same device accessed by the acoustic system.

Some previous acoustic/seabird studies have not included flying birds in their analysis because of the greater probability that birds on the wing are not associated with acoustic targets (Piatt 1990, Decker 1995). We have adapted this convention for our analysis by including birds

foraging, potentially foraging, and on the water. During surveys we were confident that nearly all of observed murrelets were Marbled Murrelets; however, there is a possibility that we have incorrectly identified some kittlitz's as marbled. Therefore, we have chosen to refer to these species collectively as Brachyramphus murrelets.

We displayed acoustic data with contouring and 3 dimensional surface-mapping software (Keckler 1995). These images were then used to determine school density, depth to top of schools, depth to bottom of schools, height of school, chord length of schools, and bottom depth for values < 60 m for each fish school observed. The chord lengths of fish schools were determined by averaging widths measured at 2-m depth intervals. Height of school was multiplied by chord length to approximate a 2 dimensional area. We ascribed categorical density values of low, medium and high for average densities of 0.01-0.20, 0.21-0.35, and > 0.35 g/m³, respectively. As a result of integrating acoustic data at 30-second intervals, schools with a chord length of < 40 m were either not displayed or were extrapolated to a chord length of 40 m. Therefore, the smallest fish schools were not well represented.

A geographic information system (GIS) was used to examine the spatial relationship between forage-fish schools, depth, distance to shore, and locations of bird colonies. GPS data for fish schools and colony locations were converted into GIS layers. Forage-fish school data were intersected with National Oceanographic and Atmospheric Administration (NOAA) bathymetry data to return depths for each school. Acoustic data had previously recorded depths to 60 m; therefore, GIS data for depth > 60 m were merged with acoustic bathymetric data. Digital NOAA coastline data were used to calculate distance to shore for each forage-fish school. Finally, we used GIS to calculate the distance to the nearest Tufted Puffin colony (U. S. Fish and Wildl. Serv., Anchorage, Alas., unpublished data) for each school. These data sets were then combined with acoustic data on fish school characteristics for analysis.

We used custom software to determined which of the forage-fish schools had Brachyramphus murrelet or Tufted Puffin locations within 100 m of the edge of the school. We selected 100 m as the distance of association to be consistent with other sources of variation: 1) The transect width allows birds up to 100-m distant to be associated with schools beneath the ship. 2) GPS data have an accuracy of about ± 100 m (Leick 1992).

We used resource selection functions based upon logistic regression to model the selection of fish schools by birds (Manly et al. 1993). We checked variables for independence through correlation analysis. Paired variables with a correlation coefficient (r) > 0.50 were not used in the analysis. We incorporated the variables: area, depth to the top of the school, bottom depth, distance to shore, biomass density of the school, area of the school, and distance to the nearest Tufted Puffin colony. The 3-level categorical variable, density, was converted to 3 separate binomial variables, low, medium, or high density, for these analyzes. Only medium and high density levels were used in the models since knowledge of these 2 levels determines the value of low density. Positive coefficients of either medium or high density indicated that selection was in favor of these categories when compared to low density schools. If a coefficient for either medium or high density was significant then both levels remained in the model. For the Brachyramphus murrelets regression, distance to colony was not applicable and not used. We ascribed variables moderately significant and highly significant for $P = 0.15$ to $P = 0.05$ and $P < 0.05$, respectively. We began analysis with all variables in the models and systematically deleted

non-significant variables from the regressions singly and ordinally, beginning with highest P values, until all terms in the model were moderately or highly significant. The models selected by this method were checked to determine if they had the lowest Akaike's information criterion (AIC) value (Akaike 1973) of all possible configurations. The AIC statistic describes fit of the model while penalizing for including variables that explain minimal error (Akaike 1973). We considered models to be significant if, based on the likelihood ratio test, the covariates explained 95% of the variation ($P \leq 0.05$).

RESULTS

Of 326 Brachyramphus murrelets and 122 Tufted Puffin sightings, 70 and 9 were associated with forage-fish schools, respectively. The mean number of Brachyramphus murrelets and Tufted Puffins per sighting was 1.7 ± 1.1 SD and 1.2 ± 0.7 , respectively. Our forage fish net sampling indicated that the principle species were Walleye Pollock (Theragra chalcogramma), Capelin (Mallotus villosus), Sand Lance (Ammodytes hexapterus), and juvenile Herring (Clupea harengus). For the hydroacoustically sampled forage-fish schools ($n = 614$) mean values for depth to the top of the school, total depth at the school location, distance to shore, and area (chord length x height of school) were 14.5 ± 17.6 m, 109.2 ± 43.2 m, 2299.2 ± 2051.2 m, and 1842.3 ± 4936.6 m², respectively. Correlation analysis indicated that all of the variables included in our modeling were independent ($r \leq 0.5$). The resource selection models were significant (Table 2) and had AIC and concordance values 423.8 and 66.3 % for the Brachyramphus murrelets and 75.2 and 89.9 % for the tufted puffin models.

DISCUSSION

The variables we examined fall into 2 general types: those that describe the location of the school in relation to physical features (distance from the nearest colony, distance from shore, total depth of water), and those that describe characteristics of fish schools (density, area, and depth to the top of schools). Inclusion of only location variables in the resource selection model would indicate that, based on the available data, birds were selecting habitat types and were not discriminating among fish schools. Similarly, a model that contained only characteristics of schools would indicate that birds were foraging broadly for schools that satisfied their search image. Our resource selection model for Brachyramphus murrelets contained both location (depth of water) and school characteristic variables (density and area). Interpretation of this model must be done cognizant of our inability to hydroacoustically sample small schools frequently observed in shallow water, that may have been foraged on extensively by Brachyramphus murrelets (Strachan et al. 1995). When the smallest schools were not considered, Brachyramphus murrelets foraged in shallow water habitats and within those habitats selected larger and denser schools.

The resource selection model for Tufted Puffins contains only a location variable (distance from the nearest Tufted Puffin Colony), suggesting that this species does not discriminate among fish schools and makes selections based only on flight distances. Our level of concordance and AIC value for the Tufted Puffin model indicate that this species was efficient at locating fish schools near their colony. Tufted Puffins prey upon several different fish species (Baird 1990). Hatch and Sangar (1992) have shown that they take Walleye Pollock in proportion to their availability by age class. Although we were not able to identify the species composition

of all schools associated with Tufted Puffins, our model is consistent with Hatch and Sangar's (1992) findings of generalized foraging.

Both Tufted Puffins and Brachyramphus murrelets forage extensively as individuals or in small groups. Aside from this common foraging trait, our results suggest that these species used different foraging strategies to find different types of forage-fish schools. During the 1995 survey, large Walleye Pollock schools, identified through trawling, were located in deep water of the central study area (Haldorson et al. 1996). We observed Tufted Puffins associated with these schools but not Brachyramphus Murrelets. Herring, which were the most abundant forage species in shallow water habitats during the 1995 survey of PWS (Haldorson et al. 1996) declined following the spill (Brown et al. 1996) and had not recovered as of 1996 (Exxon Valdez Oil Spill Trustee Council 1996). Sand Lance, also associated with shallow water habitat (Dick 1982) have declined in frequency of occurrence in the diet of Marbled Murrelets and Pigeon Guillemots (Cephus columba) while Walleye Pollock has increased (Kuletz et al. in press). On a more coarse scale, the ecosystem shift in the Northern Gulf of Alaska (Piatt and Anderson 1966) resulted in an increase in pollock biomass and a decline Capelin (Piatt and Anderson 1966). Capelin were also associated with shallow water habitats during the 1995 survey of PWS (Haldorson 1996). These findings collectively suggest an increase in Pollock and a decline in other major schooling forage fishes.

Our model indicates that although Brachyramphus murrelets adapted to the shift in available forage fishes by incorporating Pollock into their diet; however, their foraging strategy did not maximize consumption of this species. We speculated that this may be the result of less efficient foraging in deep water because of possible downward escape by prey, or because prey are more predictably available due to advection in shallow water (Hunt 1988). These factors did not constrain Tufted Puffins and we were not able to identify biological reasons why they would differentially affect Brachyramphus murrelets. We proposed an alternative explanation based upon energetics.

Roby et al. (1996) determined that in PWS the lipid content and energy density of Herring, Sand Lance, and Capelin were variable but high when compared to Walleye Pollock, which was among the lowest of the sampled fishes. Brachyramphus murrelets, in response to a relatively short nestling period (De Santo and Nelson 1995), rapid chick growth when compared to most alcids, and chick provisioning limited to crepuscular periods (Nelson and Hamer 1995), may require higher energy food to maintain productivity. Murrelets adjusted to the shift in the food web by incorporating Walleye Pollock into their diet, but forage in habitats with the highest quality food items. If Walleye Pollock provided sufficient energy for reproduction, we might have expected Brachyramphus murrelets to use a foraging strategy that would have allowed them to maximize their consumption of this abundant species. In contrast, Tufted Puffins have the longest nestling period of the alcids (De Santo and Nelson 1995), the daily provisioning of nestlings period may extend to 17 hour (Amaral 1977) and their co-genera, the Atlantic Puffin (Fratercula corniculata), is capable of extending the nestling period in times of food stress (Harris 1984). A possible variable length nesting cycle, a nearly unlimited provisioning period, and a generalist foraging strategy should buffer Tufted Puffins from productivity declines due a change in available forage to a greater extent than species with more constrained foraging and nestings strategies. We suggest that the foraging and nesting strategies of Tufted Puffins has allowed this

species to adjust to ecological change. Whereas, Brachyramphus murrelet's need for high energy foods and a foraging strategy that selects habitats with high energy forage species, that have declined in abundance, may be a major reason for of this species failure to recover following the oil spill.

ACKNOWLEDGMENTS

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Table I-1. Transect lengths (km) for 3 study areas in Prince William Sound, Alaska. Zigzag transects surveyed nearshore and east-west transects surveyed open water.

Study Area	Northern area	Central area	Southern area	All areas
Total east-west	99.3	152.8	23.3	275.4
$\bar{x} \pm SD$ east-west	6.6 ± 4.9	8.5 ± 4.1	2.9 ± 1.9	6.7 ± 4.6
Total zigzag	12.1	15.1	14.4	41.6
$\bar{x} \pm SD$ zigzag	1.5 ± 0.7	1.7 ± 0.8	1.8 ± 0.4	1.7 ± 0.7
East-west + zigzag	111.4	168.9	37.7	317.0

Table I-2. Models of the likelihood that fish schools will be associated with diving birds using characteristics of the schools as independent variables.

No. schools not associated with birds	No. schools associated with birds	Model	Model \underline{P}
545	70	BMurrelets ^a = -0.01TDepth ^b (0.0004) ^c + 0.00004Area ^d (0.03) + 0.62MDensity ^e (0.05) + 0.53HDensity ^f (0.12)	0.0002
606	9	TPuffins ^g = -0.00026DColony ^h (0.02)	0.0001

^aThe probability of selection by Marbled or Kittlitz's Murrelets.

^bTotal water depth.

^c \underline{P} value of the associated independent variable.

^dThe chord length * the mean height of the school.

^eSelection for medium density fish schools over low density schools. If either medium or high density variables were significant then both were retained in the model.

^fSelection for high density fish schools over low density schools.

^gThe probability of selection by Tufted Puffins.

^hDistance to the nearest Tufted Puffin colony.

Fig. I-1. The transects used to conduct acoustic and seabird surveys in Prince William Sound, Alaska.

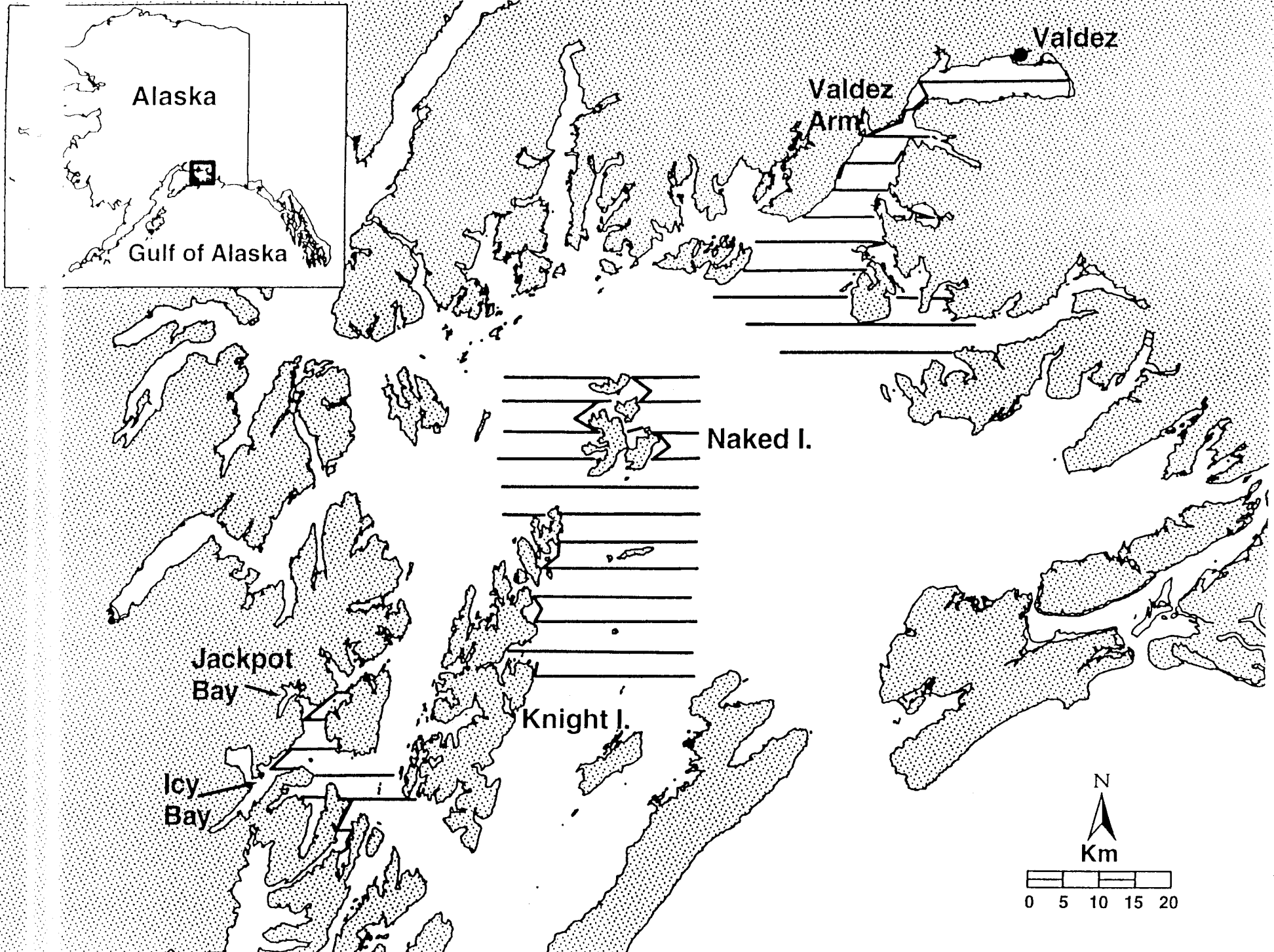


Fig. I-2. A 3 dimensional plot of hydroacoustic data collected during a survey of Prince William Sound, Alaska. Black spires represent the bottom. Grey polygons represent fish schools. Darker shades of grey in polygons indicate a greater biomass density.

Distance (km)

0.0

5.0

10.0

15.0

20.0

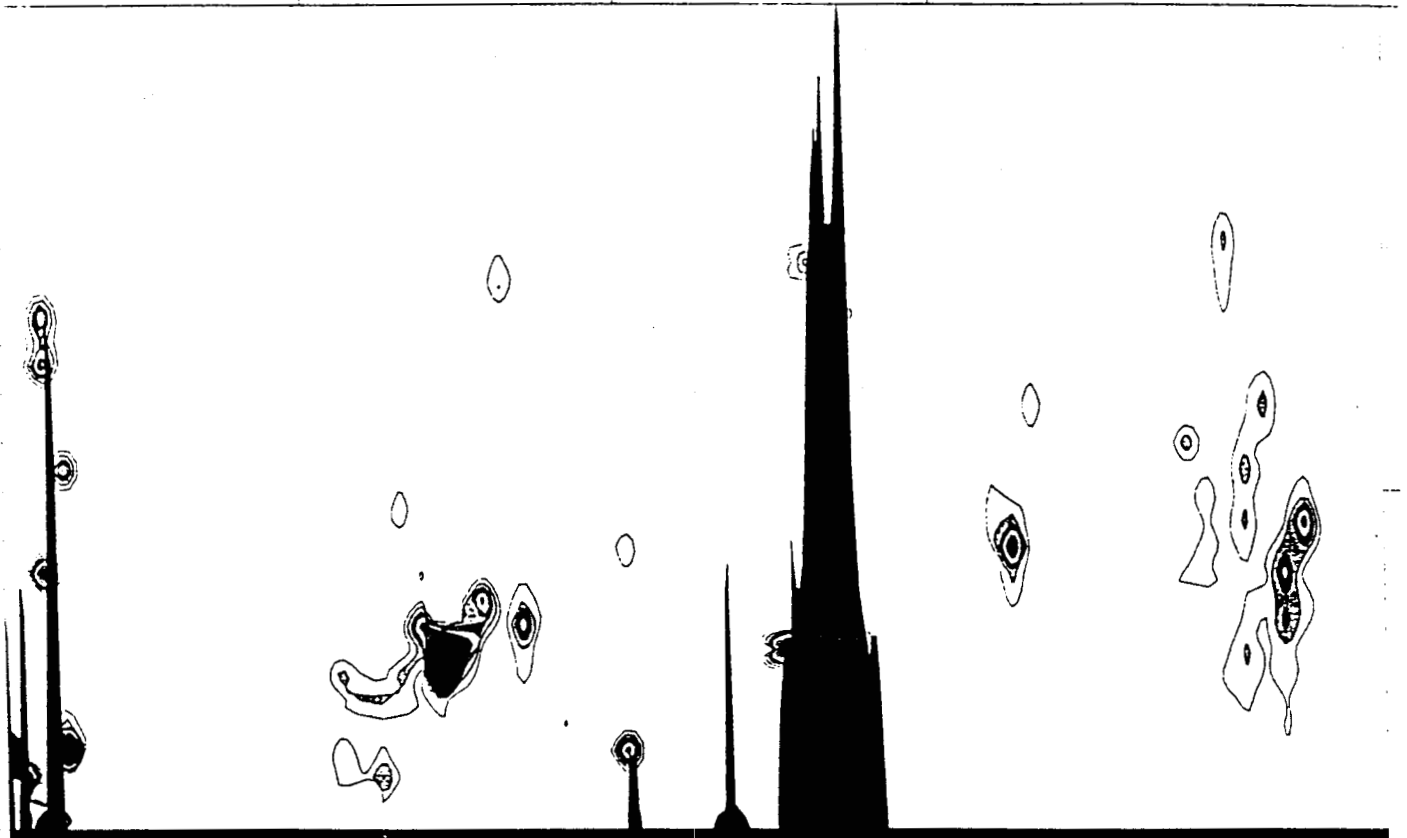
0

-20

-40

-60

Depth (m)



**CHAPTER II: SELECTION OF FISH SCHOOLS BY FLOCKING SEABIRDS IN
PRINCE WILLIAM SOUND, ALASKA**

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Abstract: We examined the size and location characteristics of fish schools encountered along line transects in Prince William Sound, Alaska during July/August 1995. We made comparisons between schools associated with flocking birds and those not associated with flocking birds using Wilcoxon rank sum tests and logistic regression analysis. Feeding flocks chose fish schools which were close to shore and in shallow bottom depths, as well as those which had a narrow chord length. However, fish schools found nearshore were significantly more narrow than offshore fish schools suggesting that flocking birds chose feeding habitat rather than school size. At the feeding flocks, bird numbers were positively correlated with fish school chord length and negatively correlated with density and depth to the schools.

INTRODUCTION

The marine environment is vast and its biological content is largely hidden from the sight of surface and aerial predators. However, it is here that seabirds must search for prey to sustain themselves and their offspring. Environmental and biological parameters which seabirds may cue on to search for and obtain food have been the topic of much recent research (e.g. Woodby 1984, Heinemann et al. 1989, Erikstad et al. 1990, Piatt et al. 1991). Fish schools that are not utilized by seabirds, may be unavailable (i.e. too deep or too far from nesting colony), of low quality, quantity or density, or they simply have not been discovered by the birds. Describing the characteristics of the available forage may explain otherwise paradoxical distributions of seabirds (Springer et al. 1987). Studies of seabirds, coupled with fisheries hydroacoustics, offer valuable insights to some of the complex relationships that puzzle marine ecologists. Transect surveys at sea have helped to explain the distribution of seabirds with respect to their prey and environmental factors such as depth of water (Vermeer et al. 1989, Stone et al. 1995), distance from land (Vermeer et al. 1989), depth to food source (Hunt et al. 1990), density of the prey (Piatt 1990), water temperature and salinity (Haney 1991, Vermeer et al. 1991), tides and currents (Braune and Gaskin 1982, Coyle et al. 1992), bottom topography (Cairns and Schneider 1990), and the presence of other oceanographic features such as fronts and upwellings (Schneider 1982, Kinder et al. 1983, Brown and Gaskin 1988).

In the aforementioned studies, observations of birds were typically recorded while fisheries hydroacoustics measured prey densities along strip transects. Birds in the air were included in some of these studies, while birds sitting on the water were included in all of them. However, flying birds are not necessarily using the area surveyed for feeding and birds on the water may be inactive or resting after feeding on prey which has moved away (Hoffman et al. 1981). Therefore, these observations may confound correlations between birds and their prey.

In this study, we compared fish schools at which birds were feeding in flocks of three or more with fish schools where birds were not obviously feeding in flocks. Variables of fish schools which were compared included chord length (the horizontal distance traveled over the school), depth to the school, bottom depth, relative density, distance from shore, and distance from the nearest Black-legged Kittiwake (*Rissa tridactyla*) colony. We also wished to determine if some of these variables would be useful in helping to predict the number of seabirds at feeding flocks.

STUDY AREA

Prince William Sound (PWS), Alaska is a large estuarine embayment of the northern Gulf of Alaska which provides important foraging and breeding habitat for many seabirds (Isleib and Kessel 1973, Irons et al. 1988). Water depths exceed 870 m and the numerous bays and fjords along with more than 150 islands form at least 5000 km of shoreline. High precipitation rates keep the sea-surface salinity low and catabatic winds flowing down the fjords transport this low-salinity (about 25 ppt during this study; Haldorson et al. 1995) water out of PWS, generally through Montague Strait and the

smaller straits and passages of the southwestern region. The Alaska coastal current provides the major inflow of marine water through Hinchinbrook Entrance (Royer et al. 1990). Diurnal tidal changes in PWS can also create currents exceeding 5 km/hr through narrow passages.

Seabirds which commonly forage in flocks in PWS during summer include Black-legged Kittiwakes, Glaucous-winged Gulls (Larus glaucescens), Mew Gulls (Larus canus), Marbled Murrelets (Brachyramphus marmoratus), Tufted Puffins (Fratercula cirrhata) and Horned Puffins (F. corniculata). These birds feed on a variety of forage fish including: Pacific herring (Clupea pallasii), capelin (Mallotus villosus), Pacific sand lance (Ammodytes hexapterus), walleye pollock (Theragra chalcogramma), and eulachon (Thaleichthys pacificus) (Sanger 1987, Haldorson et al. 1995). Three focal areas in PWS (Northeastern, Central, Southwestern) were chosen for study because their habitat is critical to these seabird species of interest.

METHODS

Field Procedures

From a random starting point, strip transects were selected along lines of latitude 2 nm apart in the three areas of primary interest. Since many seabirds are often found nearshore or in relatively shallow waters (Vermeer et al. 1989, Stone et al. 1995), we also ran zig-zag transects on a straight line from shore to the halfway point between adjacent transects where water depth was 100 m. From this point, sampling continued to the beginning of the next transect. All transects were replicated once.

The study period (July 20 - Aug. 12) was chosen to include the peak time of chick provisioning for many seabirds in PWS. Seabird observations were made using 8 x 40 binoculars, 6 m above the water line from a 26 m vessel while conducting hydroacoustic surveys to estimate forage fish distributions and abundances. Data on bird observations were entered directly into a computer which was linked to a Global Positioning System (GPS) to record the location of each observation. We departed from our transect lines to more closely examine feeding flocks within 300 m of either side of our vessel.

Hydroacoustic and trawl data were used to determine species composition of fish schools, water depth to the schools, chord lengths (lengths of the horizontal cross sections) and densities of the schools. These data were collected along the main transects and along short transects conducted at feeding flocks. Hydroacoustic measurements were made from the same vessel from which bird surveys were conducted. We used a BioSonics system with 120 and 420 kHz down-looking and 420kHz side-looking transducers to measure deep and near-surface targets, respectively. Both transducers used a single beam with a 6° viewing angle and data were integrated over 1 m depth intervals to a depth of 65 m. The acoustic data were also linked with the GPS to record locations of fish schools along each transect.

Trawl samples were collected from a separate vessel which was directed by the hydroacoustic vessel to schools of forage species. A modified Canadian midwater herring trawl (100 m² opening), an improvised pair trawl, and a dip net were used to

verify fish school compositions. These trawls were only used on the larger fish schools and hence the fish collected from them were not representative of all schools.

Laboratory Procedures

A BASIC program was written to integrate the acoustic data using calibrated target strengths of fishes and length-weight relationships of captured fish. Acoustic target strengths, which were collected using the default target strength of -42.2 dB, were then scaled using fish species and size estimates from trawl data using the equations:

$$\text{pollock} \quad TS = 20 (\log L) - 66 \quad (\text{MacLennan and Simmonds 1992})$$

$$\text{herring} \quad TS = 20 (\log L) - 68 \quad (\text{Thorne et al. 1983})$$

$$\text{capelin} \quad TS = 20 (\log L) - 68 \quad (\text{R. Thorne, pers. comm.})$$

where TS is the calculated target strength and L is the length of the fish in centimeters (equations provided by BioSonics, Inc.). The estimates of fish numbers were used to compute a biomass estimate per cubic meter using the following length-weight relationships for the dominant species where W = weight in grams and L = length in mm:

$$\text{pollock} \quad W = (1.89 \times 10^{-6}) L^{3.272} \quad (\text{Haldorson et al. 1995})$$

$$\text{herring} \quad W = (5.007 \times 10^{-6}) L^{3.196} \quad (\text{L. Haldorson, pers. comm.})$$

$$\text{capelin} \quad W = (2.5 \times 10^{-6}) L^{3.213} \quad (\text{Pahlke 1985})$$

Hydroacoustic profiles for each transect were printed using Surfer software (Keckler 1995, Figure 1). From those profiles we examined every fish school to determine chord length, depth to the top of the schools, bottom depth (when less than 65 m), and average density. The chord lengths of fish schools were determined to be the average of widths measured at 2 m depth intervals and the density of the fish schools were graded as low, medium and high, based on average densities of 0.01-0.20, 0.21-0.35, and $> 0.35 \text{ g/m}^3$, respectively. Distance from shore, depth of water 65 - 150 m, and distance from the nearest bird colonies were obtained from Geographic Information System (GIS) computer analysis. Water depths of greater than 150 m were not available in the latest GIS depth coverage for PWS. Therefore, these data were estimated from National Oceanic and Atmospheric Administration charts (numbers 16701, 16705, and 16708).

Side-looking hydroacoustic data were available for the transects at feeding flocks. These data were analyzed by examination of echograms to determine number of fish schools and their chord lengths. The upper depths of these fish schools were assumed to be at 1 m.

Data Analyses

All data analyses were conducted with S-Plus for Windows 3.1 (Statistical Sciences, Inc. 1993). We determined with stem and leaf and boxplots of the acoustic data that transformations were necessary to reduce outliers and make the data more symmetrical about the medians. Transformations which improved plots of the variables were square root of the upper depth of the fish schools, the cube root of their chord length and depth to bottom, and the fourth root of the distance to shore. We did not transform the categorical variable density. We used Wilcoxon rank sum tests to determine if the above mentioned characteristics of fish schools were significantly different between

nearshore schools and offshore schools. Wilcoxon rank sum tests were also used to determine significant differences in characteristics between those schools being fed upon by seabirds in flocks and those not being fed upon. The characteristics which were significantly different or which may have been biologically meaningful were then used in a logistic regression (Hosmer and Lemeshow 1989) to determine the log likelihood of any particular school being fed upon. We also more closely examined the fish schools associated with feeding flocks using multiple linear regression (Kleinbaum et al. 1988). Chord length, depth to school, and relative density were used as independent variables to produce a linear fit which may determine how many birds will flock at a particular fish school. Side-looking hydroacoustic data were available from the transects conducted at feeding flocks. Therefore, we pooled the down- and side-looking data to more closely examine the variables which could help to explain the number of birds at a feeding flock. Distance to shore and bottom depth were not available for the side-scanning hydroacoustic data. Hence, we could not use these variables for further analysis.

The fish school variables were transformed as mentioned above. Whereas, the number of larids and total birds in the flocks were log transformed. Two flocks had no larids participating in them. Therefore, in order to avoid negatively infinite values, we added 0.8 to the entire data set before applying the regression analysis which had total larids as the dependent variable.

RESULTS

Initial comparisons of fish schools

During 18 days and 120 transects totaling 587.7 km, only 22 feeding flocks were encountered which ranged in size from 3 to 1065 birds. From the down-looking hydroacoustic data, we analyzed data on 614 fish schools which were not associated with feeding flocks and 26 fish schools which were associated with feeding flocks (Table 1). One hundred and thirty-two of the 614 schools not associated with flocks were found on the nearshore transects. Fish schools which had a chord length of less than 30 m did not show up on many of the plots which had longer than average transect lengths. Therefore, our estimates for chord length were positively biased. However, this bias was equally applied to fish schools associated with flocks and fish schools which were not associated with flocks.

Nearshore fish schools were associated with significantly shallower bottom depths and were significantly closer to the surface than offshore fish schools (Wilcoxon rank sum test; $P < 0.001$, Table 1). Chord length of the fish schools was also significantly narrower nearshore (Wilcoxon rank sum test; $P < 0.001$, Table 1). Characteristics which were significantly different when comparing fish schools from combined nearshore and offshore transects with the fish schools associated with feeding flocks included chord length, bottom depth, and distance to shore (Figure 2). When just the fish schools from the nearshore transects were compared with the feeding flock fish schools, only bottom depth was significantly different (Figure 3).

Logistic regression analyses of fish schools

Distance to nearest kittiwake colony was eliminated from the logistic regression analysis because of the small difference in this variable and because kittiwakes often fly long distances (> 45 km, Irons 1992) while searching for prey in PWS. Although there was also little difference in the density of the fish schools and depth to them, we felt that these could be important biological variables. Therefore, the initial logistic regression comparing all the fish schools with the fish schools which feeding flocks of birds were associated with included these variables along with chord length, upper depth, bottom depth and distance to shore of each fish school. Of these variables, bottom depth and distance to shore as well as chord length and distance to shore had high degrees of correlation (Table 2). Comparisons of the fish schools from only the nearshore transects with the those at feeding flocks had smaller correlations (Table 3).

Chord length and density of the fish schools did not offer a significant contribution to the initial logistic regression fit. However, examination of the residuals (Table 4) revealed at least five outliers. Four of these were associated with three bird flocks which may not have had an accurate hydroacoustic picture of what they were feeding on because of a great distance between the vessel and the flock. The fifth was a school which did not show up on the software plot when graded with the proper maximum biomass. Those five schools were removed from further analysis. Diagnostic analyses on the reduced data set revealed one more outlier, the only other fish school suspected as being too far from a flock. With the removal of the foregoing six fish schools, density was still an insignificant contributor to the fit. Therefore, we decided to remove this variable from further analysis. An ANOVA of additive models was used to determine that the variables upper depth of fish school and chord length did not add significantly to the fit of the logistic regression. The linear fit for the remaining variables produced the results expressed in Table 5.

We also applied a logistic regression to compare only the fish schools on the nearshore transects with the schools associated with feeding flocks. Through diagnostic analyses, we discovered and removed the same outliers which were associated with the feeding flocks as before. The linear fit was not dissimilar from the fit obtained by the analysis using all the fish schools except that the addition of depth to the fish school was slightly significant (Table 6).

Bird numbers at feeding flocks and associated fish schools

Using linear regression analysis of the fish schools at only the feeding flocks, we were able to learn what might be important variables for determining the size of a feeding flock. Chord length was positively correlated, while density and upper depth of fish schools were negatively correlated with flock size in the best fit regression equation (see below). The upper depth of the fish school was, however, more correlated with flock size than density. Removing density from the analysis resulted in a much higher p-value for upper depth of the school but added little to the overall significance of the regression. We also determined from Cp plots (Mallows 1973) that the best regression equation for these data would include all three of these variables.

The best fit regression equation using characteristics of the fish schools as independent variables and total number of birds as the dependent variable was

$$\ln(\text{total birds}) = 1.484(\text{CL})^{1/3} - 0.348(\text{UD})^{1/2} - 0.574(\text{DE}) + 1.158$$

where CL is the chord length of the school, UD is the upper depth of the school, and DE is the relative density of the school ($R^2 = 0.8358$, $N = 17$, F-stat. = 22.0622 on 3 and 13 df, p-value < 0.001).

Results of a regression analysis using larids as the dependent variable were similar to the results using all birds producing the fit

$$\ln(\text{total larids}) = 1.759(\text{CL}) - 0.485(\text{UD}) - 0.783(\text{DE}) + 0.613$$

($R^2 = 0.8474$; $N = 17$, F-stat. = 24.9875 on 3 and 13 df, p-value < 0.001).

Three-dimensional perspective plots allowed a visual interpretation of the data (Figure 4). Depth to school and chord length may be important variables considered together (Figure 4a). Density appears to increase with increasing bird numbers when chord length is narrow. Yet, at mid to wider chord lengths total birds decrease at mid densities and increase at low or high densities (Figure 4b). At shallow school depths a similar relationship also appears with density and total bird numbers (Figure 4c).

DISCUSSION

Traditionally, transects are used as the sampling unit to determine correlations between seabirds and their prey. Transects can be easily added together or subdivided to determine the scales on which seabirds select feeding areas (Schneider and Piatt 1986, Hunt and Schneider 1987, Schneider 1993). By using the fish schools as the sampling unit, we hoped to learn the characteristics of those schools that are exploited regardless of the scale. We also examined only fish schools associated with seabird flocks that were obviously feeding and compared those schools with schools not associated with feeding flocks. The anticipated advantage of this method was to determine a better correlation with actively feeding birds and their prey.

Comparisons of fish schools

Feeding seabirds may affect the behavior of fish by changing their distribution in the water column (Logerwell and Hargreaves *in press*), and probably school size and density (Maniscalco and Ostrand, Unpubl. Data). Therefore, it cannot be known if those characteristics of fish schools associated with feeding flocks were the result of the seabirds' preference for those schools or their effect upon the schools. However, the general location of fish schools, which includes distance from shore and bottom depth, are probably not greatly affected by the relatively small and ephemeral feeding flocks of PWS.

Bottom depth, distance to shore, and chord length were significant variables by themselves for the formation of feeding flocks in PWS as determined from our initial comparisons of the fish school characteristics. The significance of the former two variables suggests that the seabirds in PWS are selecting habitat rather than fish schools. Proximity to shore and shallow depths have also been associated with higher densities of alcids and larids in other areas (Vermeer et al. 1989, Gaston and Brown 1990, Stone et al. 1995).

The positive correlation between bottom depth and distance to shore makes it difficult to determine which of these might have been more important. This relationship was the main impetus for reanalyzing the data with only the nearshore transects where the correlation between bottom depth and distance to shore was much smaller (Table 3). In that reanalysis, only bottom depth was significant. Areas of upwelling created by shallow bottom depths and irregular bottom topography in conjunction with tidal currents appear to attract alcids and larids regardless of distance to shore (Braune and Gaskin 1982, Cairns and Schneider 1990, Coyle et al. 1992). Several replicate surveys at different tidal stages would be necessary to determine if currents and bottom topography had an effect on the feeding behavior of seabirds in PWS.

The notion that seabirds chose fish schools with narrower chord lengths than normal could be a bit perplexing. However, fish schools nearshore had significantly smaller chord lengths than those farther from shore. Also, chord lengths of nearshore fish schools were not significantly different from chord lengths of the feeding flock fish schools and this variable was not a significant contributor to either logistic regression analysis. Therefore, we believe that seabirds in PWS may not select fish schools for their size nor density, but chose fish in areas where forage is easily accessible. This may be realized by the fact that nearshore fish schools were significantly shallower in the water column. Though, feeding seabirds may have driven the fish deeper into the water (Logerwell and Hargreaves *in press*), giving us a positive correlation with fish depth and flock presence in the logistic regression with only the nearshore fish schools.

Forage fishes in PWS can be found at much deeper depths than are accessible by the local seabirds. Larids typically penetrate the water to only shallow depths (Ashmole 1971). The diving depths of marbled murrelets, Tufted and Horned Puffins are not specifically known. However, the maximum diving depth of the Atlantic puffin, a congener to puffins in PWS, is about 68 m (Burger and Simpson 1986). Marbled Murrelets forage most often in water depths between 20 and 80 m (Strachan et al. 1995) and, based on their size (Burger 1991), probably do not normally dive deeper than 40 m. The average bottom depth at the feeding flocks examined in PWS was 50 m and the average depth to the fish schools was only 16 m (Table 1). Shallow areas which help restrict prey to accessible depths in the water column during predictable times provide a reliable source of food for many coastal seabirds in the northern hemisphere (Springer and Roseneau 1985, Vermeer et al. 1987, Brown and Gaskin 1988, Coyle et al. 1992). Based on these studies and others (e.g. Braune and Gaskin 1982, Cairns and Schneider 1990), shallow bottom depths, especially those which induce upwellings, maybe more important than distances to shore for many birds.

Bird numbers at feeding flocks and associated fish schools

The number of feeding seabirds at fish schools appeared to increase with increasing size and decreasing depths of the fish schools as judged from the perspective plots. This is in accord with a typical numerical response (Hassell and May 1974) where predators will aggregate with an increase of prey availability. Flock size increasing with decreasing depth to the fish schools was also expected. Pursuit diving birds often drive forage to near the surface (Grover and Olla 1983, Mahon et al. 1992) and this frequently attracts plunge-diving birds such as larids (Hoffman et al. 1981, Mahon et al. 1992).

The role that density plays in helping to determine bird numbers at feeding flocks appeared to be somewhat ambiguous. Dense fish schools may have smaller chord lengths and hence would be discovered less frequently by predators than fish schools which are spread out more evenly (Brock and Riffenburgh 1960). Whereas, schools with longer chord lengths might attract more birds because there would be a greater area of attack. Small, tightly aggregated feeding flocks of alcids may also affect the density of fish by breaking off a portion of a fish school and driving it to the sea surface into a tight writhing mass (Grover and Olla 1983).

In conclusion, proximity to shore and shallow bottom depths are likely key features for determining where seabirds will feed in flocks in PWS. Areas such as these which consistently harbor large fish schools, high in the water column can attract many feeding seabirds and should be of special interest to managers who make decisions concerning critical habitat. This research was part of ongoing studies in PWS determining long term changes following the Exxon Valdez oil spill of 1989 and to aid in our understanding of coastal ecosystems. The results presented here should be useful to future researchers in understanding ecosystem relationships between apex predators and their prey.

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Table II-1 - Average characteristics of fish schools from nearshore, offshore, and flock transects.

	Nearshore	Offshore	Flocks
	(n = 132)	(n = 482)	(n = 26)
chord length (m)	188.5	350.2	194.8
depth to school (m)	8.9	15.9	15.6
bottom depth (m)	75.8	118.7	50.3
density (scaled 1 - 3)	1.48	1.56	1.69
distance to shore (km)	0.55	2.78	0.48
distance to nearest kittiwake colony (km)	12.4	16.9	13.6

Table II-2 - Correlation matrix of the variables from all of the fish schools (Spearman rho; p-values in parentheses).

	chord length	depth to fish	bottom depth	density	dist. to shore
chord length	1.0000				
depth to fish	-0.032 (0.429)	1.0000			
bottom depth	0.256 (0.000)	0.016 (0.682)	1.0000		
density	0.380 (0.000)	0.118 (0.003)	0.112 (0.005)	1.0000	
dist. to shore	0.491 (0.000)	0.213 (0.000)	0.584 (0.000)	0.180 (0.000)	1.0000

Table II-3 - Correlation matrix of the variables from the nearshore fish schools (Spearman rho; p-values in parentheses).

	chord length	depth to fish	bottom depth	density	dist. to shore
chord length	1.0000				
depth to fish	-0.221 (0.007)	1.0000			
bottom depth	-0.193 (0.018)	0.140 (0.085)	1.0000		
density	0.472 (0.000)	0.144 (0.077)	0.082 (0.316)	1.0000	
dist. to shore	0.008 (0.918)	0.129 (0.113)	0.152 (0.061)	0.092 (0.256)	1.0000

Table II-4 - List of diagnostic plots analyzed for the logistic regression and their results. All identified outliers were removed from further analyses.

Diagnostic Plot	Results
predicted values vs. standard residuals	no outliers detected
predicted values vs. absolute residuals	no outliers detected
index plot of standard deviance residuals	fish school numbers 625, 626, and 635 identified as outliers
quantiles of standard normal distribution with 95% confidence envelope	few points outside the envelope
partial residuals	school number 615 identified as an outlier
index plot of Cook's distances	fish school numbers 106, 616, 625, 626, and 635 identified as outliers
predicted values vs. Cook's distances	fish school numbers 625, 626, and 635 identified as outliers
leverage values (h) vs. predicted values	fish school numbers 616, 625, 626, and 635 identified as outliers
leverage values (h) vs. Pearson chi-square statistic	fish school numbers 625, 626, and 635 identified as outliers
leverage values (h) vs. Cook's distances	fish school numbers 616, 625, 626, and 635 identified as outliers

Table II-5 - Results from the logistic regression analysis using fish schools encountered on all of the transects (Residual Deviance = 96.306 on 630 df).

	Parameter Value	Std. Error	t-value
intercept	11.6099	2.3381	4.9654
distance to shore	-1.6025	0.3339	-4.7999
bottom depth	-1.9358	0.4317	-4.4838

Table II-6 - Results from the logistic regression analysis using fish schools encountered on just the nearshore and feeding flock transects (Residual Deviance = 75.203 on 148 df).

	Parameter Value	Std. Error	t-value
intercept	11.6768	2.7520	4.2430
depth to school	0.48717	0.1820	2.6762
distance to shore	-1.2412	0.3572	-3.4746
bottom depth	-2.6236	0.6125	-4.2834

Figure II-1 - An example of a hydroacoustic profile recorded at a feeding flock on the east side of Peak Island showing a large fish school near the surface and a shallow bottom.

Flock # 4 - East Peak Is.

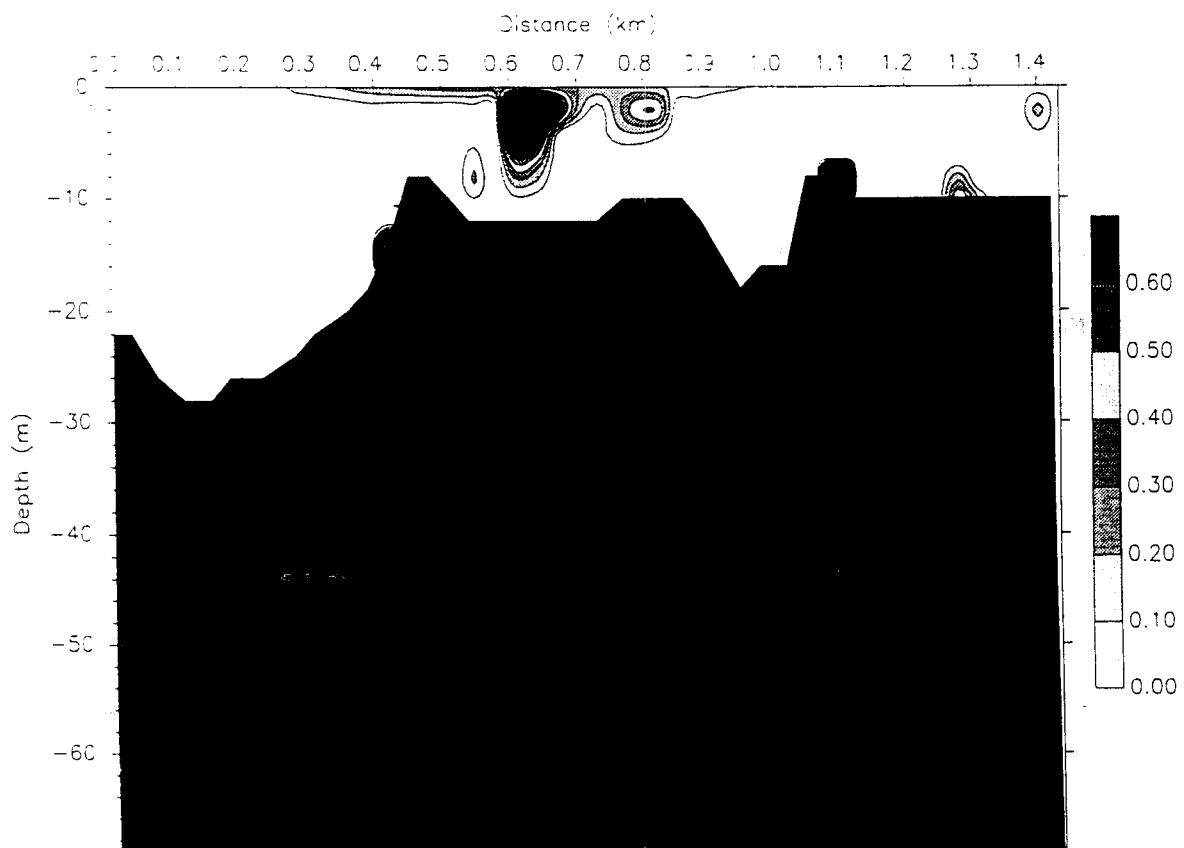


Figure II-2 - Comparisons of fish schools from both nearshore and offshore transects with fish schools at feeding flocks showing standard error bars. See text for transformations.

+ The variable density was relatively scaled (1 to 3) and not transformed.

* $p < 0.05$, ** $p < 0.001$ (Wilcoxon rank sum tests)

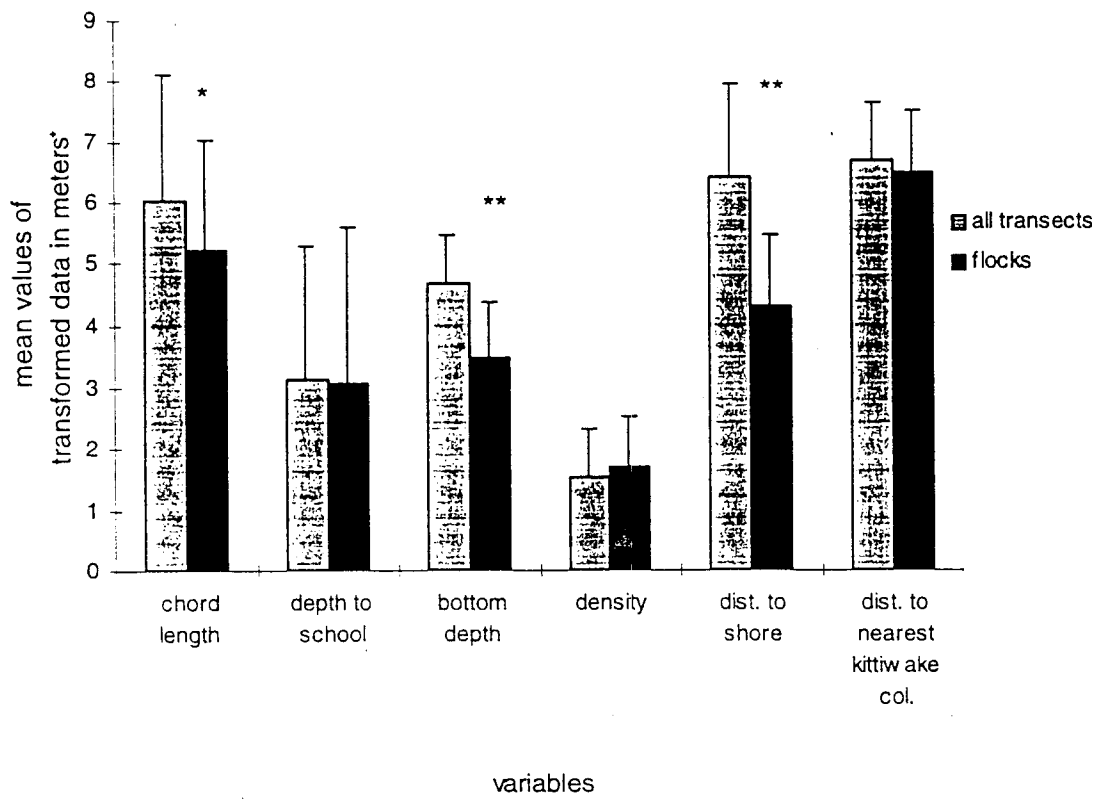


Figure II-3 - Comparisons of nearshore fish schools with fish schools at feeding flocks showing standard error bars. See text for transformations.

+ The variable density was relatively scaled (1 to 3) and not transformed.

** $p < 0.001$ (Wilcoxon rank sum tests)

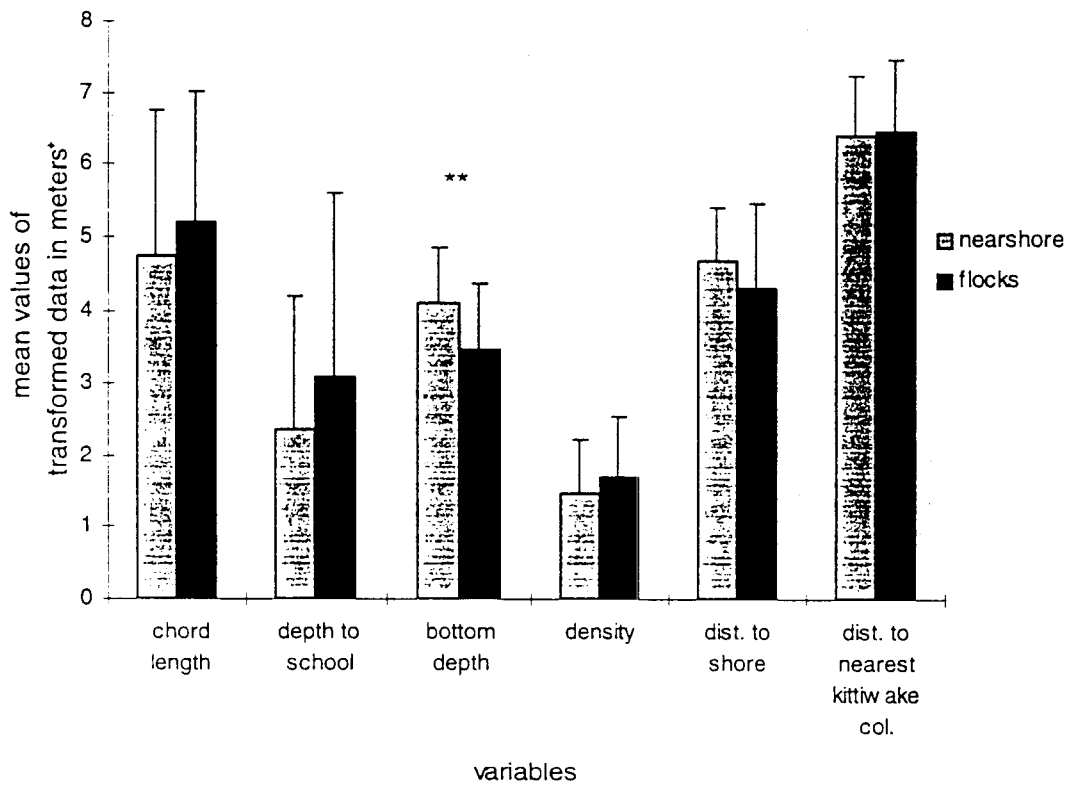
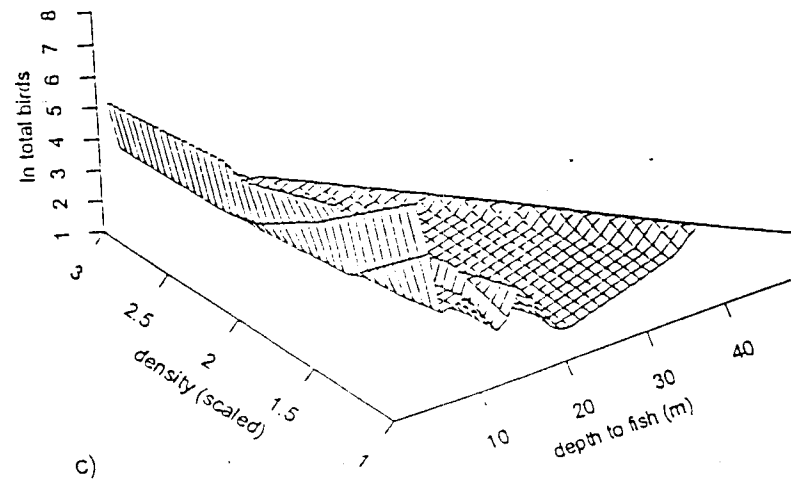
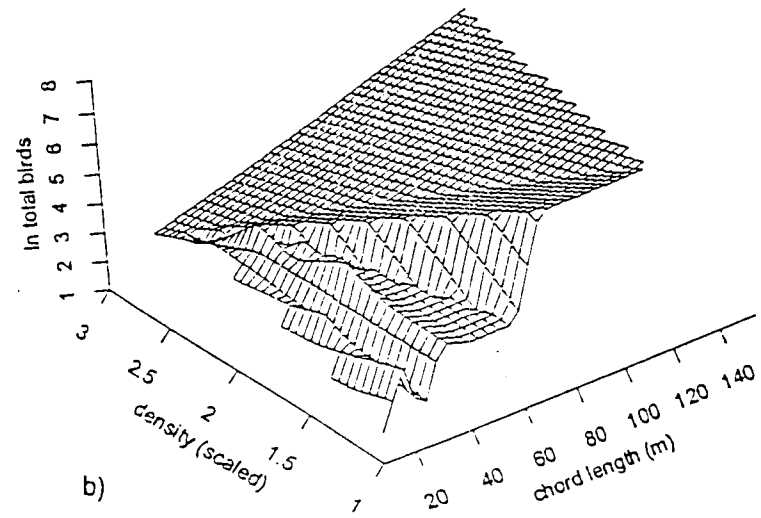
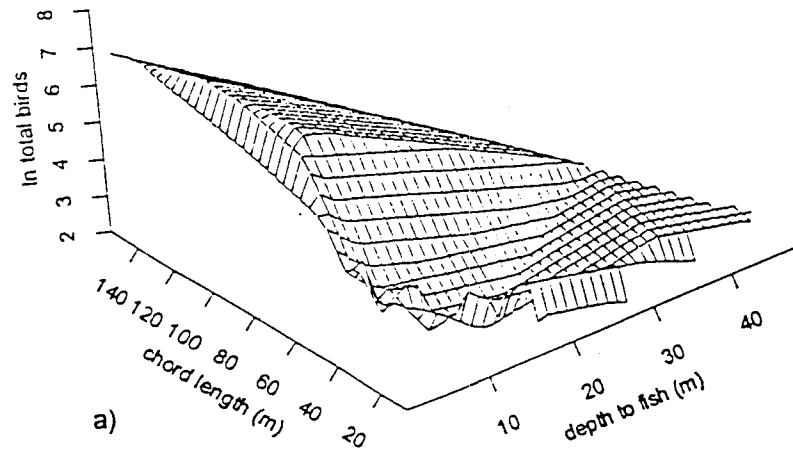


Figure II-4 - Three-dimensional perspective plots showing the relationship of chord length, depth to fish school, and density on the dependent variable of total number of birds at the feeding flocks.



**CHAPTER III: RANDOMIZATION EVALUATIONS OF RADIO TELEMETRY
AND STRIP TRANSECT METHODS OF DETERMINING FORAGING RANGES
OF BLACK-LEGGED KITTIWAKES**

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Abstract: We compared strip transect and telemetry methods of determining foraging range by using randomization tests. We evaluated factors that could bias either method and speculated on how they may have affected the respective data sets. We also used bootstrap resampling to: determine the effect of reducing our sampling effort for both methods, speculate on the benefits of increased sampling, and compare the time required to obtain similar variability by both methods. The mean distance birds were observed from their colony determined by telemetry were significantly greater than the mean value calculated from strip transects. We determined that this difference was due 2 sources of bias: 1) a decreasing probability of sighting birds at increasing distance from their colony on strip transect surveys. 2) The maximum distance birds were observed from the colony through telemetry exceeded the extent of the strip transect survey. We compared the observed number of birds seen on the strip transect survey to the predictions of a model of the declining probability of sighting birds at increasing distance from the colony (DPSB). Field data were significantly different from modeled data; however, the field data were consistently equal to or below the model predictions indicating a general conformity to prediction of a DPSB. We concluded that telemetry data provided a more accurate measure of foraging distance than strip transect data for colonial birds. Furthermore, studies that have used strip transect sampling that have not accounted for DPSB may have underestimated foraging range. The simulated reduction of sampling effort for both methods indicated that as sample size was reduced the rate of change in variability was lower for strip transect sampling than telemetry indicating that changes in telemetry sampling efforts would have a greater affect on standard error values. Variability was less for strip transect sampling and less time was required to collect the data. We concluded that strip transect sampling yielded more precise data whereas telemetry data was more accurate.

Key words: Alaska, Black-legged Kittiwakes, bootstrapping, habitat use, Prince William Sound, radio telemetry, randomization tests, *Rissa tridactyla*, seabirds.

Radio telemetry and strip transects are both commonly used to evaluate resource selection by animals (Litvaitis et al. 1994). However, we found few habitat selection studies for seabirds that utilized telemetry (e.g. Harrison et al. 1981, Trivelpiece et al. 1986, Anderson and Ricklefs 1987) with strip transects the more commonly used method (e.g. Heinemann et al. 1989, Piatt et al. 1989, Erikstad et al. 1990). Consequently comparisons of the techniques have not been made with colonial seabirds as the study subject.

Comparison of these techniques with traditional statistical methods is problematic because of differences in the nature of the data sets. Telemetry consists of locations of individual birds from a known colony which differs greatly from the set of chance encounters of birds obtained by strip transect methods. Computer intensive methods can frequently be applied to problems which cannot be easily addressed by conventional methods (Noreen 1989). We compared telemetry and strip transect data collected on Black-legged Kittiwakes (*Rissa tridactyla*) in Prince William Sound (PWS), Alaska using randomization tests. We also used bootstrapping methods to simulate the effect of reducing strip transect and telemetry sampling.

We assumed that there would not be significant differences in measures of habitat use determined by both telemetry and strip transect sampling methods, when data were collected on the same population during the same time period. If differences were observed they were probably the result of bias associated with sampling methods and we could speculate on their origin. We also hypothesized that because descriptors of data distribution (variance, standard deviation, and standard error) are exponential functions (Zar 1984), variability of the data would increase exponentially as the sampling effort decreased (Green 1979). By examining how data variability changed with decreasing sampling effort we determined the adequacy of our sampling and the effect of changing sample sizes.

We compared the mean distance birds were observed from their colony as determined by both field methods. We speculated that as the distance from the colony is increased the area in which birds could be observed also increases thereby reducing the probability of sighting birds. We suggest that sighting probability is a function of the area of the marine habitat available to birds for foraging. Island colonies, because they are surrounded by water and thus have the greatest available foraging area, should have the greatest bias associated with strip transect sampling. To describe this bias, we adapted a model from Kinder et al. (1983) and Decker (1995). We considered the available foraging habitat of an island colony as a series of concentric rings. The number of birds expected to be observed (n_i) in any ring (I) is inversely related to the area of a ring and can be calculated by

$$n_i = N_i a_i / \pi (r_{o_i}^2 - r_{i_i}^2) \quad \text{formula 1}$$

where N_i is the total number of birds within ring I, r_{i_i} is the inner radius and r_{o_i} is the outer radius of ring I, and a_i is the area surveyed within ring I. Foraging theory suggests that if foraging patches are equal in quality that birds should select patches near the colony (Stephen and Krebs 1986), hence as r_{i_i} and r_{o_i} increases N_i should decrease. If we make a conservative assumption that the number of birds (N_i) remains constant as the distance from the colony increases, then the predicted number of birds observed decreases (n_i). We assume that the probability of sighting birds within rings remains constant, i.e. the birds are randomly distributed within rings. For fjords and bays, as in this study, the above formula can be modified by introducing a variable (j), the proportion of ring I that is marine habitat:

$$n_i = N_i a_i / j_i \pi (r_{o_i}^2 - r_{i_i}^2) \quad \text{formula 2}$$

This equation may be solved to approximate the number of birds within a ring:

$$N_i = n_i j_i \pi (r_{o_i}^2 - r_{i_i}^2) / a_i \quad \text{formula 3}$$

We approximated formula 2 and compared the predicted n_i values to those obtained from strip transect sampling to test our predictions of the diminishing probability of sighting birds as distance from their colony increases (DPSB).

We anticipated 3 additional sources of bias that could have influenced the comparison of flight distances from the colony: 1) Transmitters were only attached to birds with chicks. Birds without chicks, free of provisioning and nest attendance requirements, may be more likely to range further during foraging flights (e.g. Wilson et al. 1988). Observations of non-nesting kittiwakes would tend to increase the mean

distance from the colony for the strip transect data set. 2) Gessamen and Nagy (1988) and Gessamen et al. (1991) have demonstrated that the attachment of radio transmitters can increase the energy demands of flight. If the kittiwakes in this study were affected similarly then bird with attached transmitters may have made shorter foraging flights. This source of bias would reduce the mean distance from the colony for the telemetry data set. 3) The potential maximum distance from colony obtained from telemetry was unlimited whereas the furthest point from strip transect data was constrained by the survey design. If the survey did not cover the full extent of the foraging range of kittiwakes from the study colony then a smaller mean distance would be obtained from the strip transect data. If the mean distance from colony, determined by strip transects was greater then bias sources 1 and/or 2 had a greater effect than other factors. If the telemetry data yielded a greater mean distance from colony we planned to reduce the affect of factor 3 by deleting flight distances within the telemetry data set that exceeded the distance to the furthest point on the strip transect survey and repeat the analysis.

METHODS

We conducted this study in PWS, an inland waterway, 10,000 km², located on the southern coast of Alaska. The climate is maritime with record annual precipitation > 8 m and moderate temperatures for the subarctic (Royer 1979). The coastline is rugged, with mountains up to 4-km elevation, and numerous fjords and tidewater glaciers. We selected the Black-legged Kittiwake colony located at Shoup Bay (61° 09' N, 146° 35' W), the largest in PWS with 5628 breeding pairs in 1995 (D. B. Irons, US Fish & Wildl. Serv., Anchorage, Alaska, unpubl. data) for the focus of this study. Shoup Bay adjoins Port Valdez and Valdez Arm in northern PWS.

For the telemetry study, birds on accessible nests with eggs or chicks were captured with a noose-pole. Advanced Telemetry Systems, Inc. radio transmitters, 166 to 167 MHZ, were attached to 24 adult birds. The radio packages weighed approximately 9 gm, which is less than 2.5% of a kittiwake's body weight, and were attached under the base of the tail (Anderson and Ricklefs 1987, Irons 1992). Flight tracks were determined by following radio tagged birds in a 8-m boat 14 July - 5 August 1995. Birds were tracked both visually and with telemetry equipment. A following distance of 50 - 100 m was maintained to limit the effect of tracking upon behavior. Bird locations were determined, using a global positioning system instrument (GPS), at foraging sites and where birds changed direction of their flight. Only followings that were successful in determining the furthest point from the colony of the flight were used in analysis (n = 7). Return flight locations were not included the analysis (Fig. 1).

We chose the boundaries for the strip transect study area based upon the expected foraging range of Black-legged Kittiwakes at the Shoup Bay colony. Predictions of foraging ranges were determined using previous radio telemetry studies of Black-legged Kittiwakes from the same colony (Irons 1992). We randomly selected the starting point for transects (n = 24) from 20 points equally spaced within the first 2' of the southern boundary of the study area. We arranged 11 east/west transects at 2' latitude intervals north of the initial starting latitude and 13 zigzag transects to increase data collection of nearshore habitats (Fig. 2). Zigzag transects were inserted where east/west transects

terminated at land. From the location at which the previous east-west transect terminated, the zigzag transect extended to the point half the distance to the next east-west transect at which the water depth was 100 m. An additional transect extended to the beginning of the next east-west transect. Potential transect segments that were < 1.0 nautical mile were not included and additional potential segments were deleted for safety considerations.

We replicated the strip transects of the study area twice, 26-28 July and 5-7 August 1995. Observations were made from the second deck, 8-m above the water, on the 24-m vessel, the M/V Pacific Star. Continuous counts were made of all kittiwakes observed within 100 m of the starboard side of the vessel. We used only locations of flying birds for this study ($n = 255$). Bird observations were made by scanning ahead of the ship using binoculars. Recorded observations were made prior to the ship's presence influencing bird activities. Data were recorded when the ship was closest to the point at which the birds were first observed. We recorded data directly into a computer file using custom software that also recorded the ship's position and time for each entry. Positions were determined with a GPS.

We developed a set of random locations from the telemetry field data to mimic the chance sightings that were obtained from the strip transects. We assume that the birds flew in a straight line between the GPS locations that had been recorded during flight following. A geographic information system (GIS) was used to convert the GPS locations into contiguous tracts. Then we converted these routes to points with a resolution of approximately 100 m. For each point along tracts we calculated the distance to the study colony. This data set was then used as the pool of potential Black-legged Kittiwake locations from the telemetry method. We also used the GIS to calculate the distance to shore and the distance to the nearest colony from bird observations made along the strip transects.

To compare telemetry and strip transect data we modified a randomization program from Noreen (1989). A random subset ($n = 255$) was extracted from the telemetry flight data ($n = 1504$) to yield a data set of equal size to strip transects. Mean distances from the study colony were calculated for the strip transect and telemetry data and the difference for these variables was then determined. We then conducted a randomization test, 1000 shuffles, and used the difference in mean values as the actual test statistic to determine the significance level (Noreen 1989). The number of randomly sampled test statistics greater than or equal to the actual test statistic divided by the number of shuffles provided an approximate probability. We determined the maximum distance from the study colony on the strip transect survey and the greatest distance that radio tagged birds were observed from the colony. To reduce the effect of unequal maximum distances from colony among data sets, all values greater than the smaller maximum value were deleted. We used a randomization test, 1000 shuffles (Noreen 1989) to determine if the deletions resulted in a significant change in the data set. We then reran comparison of the strip transect and telemetry data using the reduced data set.

To test the model of DPSB, we calculated expected values of n_i using formula 2 and compared them to the mean n_i values observed during the 2 replicates of the strip transect survey. We measured the area of available foraging habitat within 12 concentric

rings, with widths of 2 nautical miles (Fig. 3), using GIS. The outer most ring contained the furthest distance from the study colony on the strip transect survey. We determined the mean number of kittiwakes observed in each ring during the 2 strip transect surveys. We multiplied the transect length within in each ring by the transect width, 100 m, to determine the area surveyed within each ring. For the inner most ring we used values for area available, area surveyed, and number of birds observed, in formula 3 to determine a value for N_1 . To be consistent with our assumption that each ring contained the same number of birds we used the calculated value of N_1 for N_i and the respective values for area surveyed and available area in formula 2 to determine values for n_i for all rings. We compared the expected n_i values calculated using the model with the mean observed values graphically (Fig. 6) and with a chi-square test. Using N_1 for all N_i values ensured that the observed and predicted values of n_i would be equal thereby facilitating the graphical and statistical comparisons.

To evaluate the effect of reducing the sampling effort we wrote a bootstrapping program that simulated decreased sampling. We randomly selected 48 transects, with replacement, from the strip transect data set and used the kittiwake locations from those transects to create a pseudo survey. Mean distance from the Shoup Bay colony was then calculated for pseudo survey. We then repeated the process for 1000 iterations and calculated the mean of mean distances and standard error. We repeated the randomization with successively fewer number of transects ($\underline{n} = 48..1$). We applied the same bootstrapping program to the telemetry data set, simulating the affect of reducing the number of kittiwake flights ($\underline{n} = 7..1$).

RESULTS

The mean distances from the Shoup Bay colony calculated from telemetry and strip transects were 35.5 km and 22.2 km, respectively ($\underline{P} = 0.001$, $\underline{n} = 255$, $\underline{NS} = 1000$). The maximum distance from colony for the telemetry data set and the furthest point from colony on the strip transect survey was 62.3 km and 47.3 km, respectively. We deleted 314 locations from the telemetry data set with values greater than 47.3 km. The mean distance to colony for the telemetry data was reduced significantly to 29.4 km ($\underline{P} = 0.001$, $\underline{n}_1 = 1504$, $\underline{n}_2 = 1190$, $\underline{NS} = 1000$). We again randomly selected 255 locations from the reduced data set, reran randomization comparison of sampling methods, and determined the telemetry and strip transect data remained significantly different ($\underline{P} = 0.001$, $\underline{n} = 255$, $\underline{NS} = 1000$).

Our expected number of kittiwakes obtained using formula 2 was significantly different from the number observed in rings ($\underline{X}^2 = 37.9$, $df = 11$, $\underline{P} = 0.001$). The observed values were consistently equal to or below the expected values (Fig. 4).

Simulating a reduced sampling effort for both strip transect and telemetry studies resulted in exponentially increasing variability (Fig. 5). SE values for the telemetry data set were greater than those obtained by the strip transect method (2976 and 2628 SE distance to colony, for telemetry and strip transects respectively). SE values most similar to those obtained by the telemetry method were achieved with a reduced sampling effort of 34 transects (2976 and 2891 SE for telemetry and strip transects, respectively) out of 48 transects surveyed.

DISCUSSION

If either the energy cost of carrying radio transmitters and/or the bias associated with using only birds with chicks in the telemetry study had a greater effect than other sources of bias, then we expected strip transect data to yield a greater mean distance from the study colony. However, this was not the case. The greater mean distance from colony calculated from the telemetry data suggests that the differences in maximum distance from colony for each data set and/or DPSB had greater influence. Our adjustment to the telemetry data set and subsequent comparison of the reduced data set to the original isolated a significant bias associated with differences in maximum distances. This problem is the result of underestimating the foraging range of kittiwakes when designing the strip transect survey. However, this source of bias does not account for all of the error. By eliminating distances that were larger than those that could be obtained from strip transects we identified a significant bias associated with DPSB. Both sources of error had an influence on our results.

The model of DPSB did produced significantly different results from field observations. Differences may have resulted from assuming an equal number of birds in all rings and a consistent probability of sighting birds within rings. Kittiwakes within PWS (Irons 1992) and other seabird species elsewhere (e.g. Hunt et al. 1990 and Coyle et al. 1992) have been shown to be associated with areas where forage is consistently available. Our telemetry data also indicated that kittiwake activity was relatively high in a few areas and absent in other areas (Fig. 1). However, in all cases the observed number of birds within each ring was equal to or less than predicted by the model indicating that although the distribution of kittiwakes is patchy, their density does decline to or below predictable levels as distance from their colony increases. These findings indicating a general conformity to the prediction of a DPSB. The results of our randomization comparison and modeling efforts were consistent, confirming our speculation on the bias of strip transect data due to DPSB. We conclude that telemetry data gave a more representative indication of foraging distances than did strip transect sampling. Studies that have used strip transect data to describe the distribution of birds relative to colony location and have not accounted for DPSB (e.g. Wilson et al. 1988, Leopold et al. 1995) were likely to underestimate foraging ranges. This bias could be reduced using weighted averages on the strip transect data as opposed to simple means as we have done. We have used mean distances from colony to make comparisons among our data sets; however, wildlife biologist more frequently use these types of data to determine foraging ranges or foraging distance (e.g. Wilson et al. 1988, Leopold et al. 1995). Weighted means are not applicable to these more common methods of interpretation, yet the DPSB remains a source of bias. In these applications, bias can be reduced by sampling the same proportion of the total area within each ring.

Our simulation of reducing sampling effort resulted in a exponential increases in variability as sample size was decreased for both methods; however, the rate of change in variability was greater for the telemetry data (Fig. 4). These results indicate that we could greatly reduce our strip transect sampling before the standard error increases dramatically. Similarly we can project that a considerable increase in sampling effort

would be required to make a relevant reduction in standard error of strip transect data. Variability of the telemetry data is noticeably declining with 7 flight followings. We expect that an increase in our sampling effort would continue to result in a reduction in variability. Similar levels of variability to those obtained by telemetry could have been achieved by a reduced strip transect survey. Strip transect data was collected in 6 days and our simulation indicates that similar variability to telemetry data could be obtained with less time; whereas, the telemetry data was collected in 7 days of following kittiwakes with additional time spent on capturing birds and unsuccessful chases. This comparison indicates that our strip transect sampling yielded similar variability for less time spent sampling.

We have shown that telemetry yields less bias predictions of foraging range. However, we have also demonstrated that telemetry will require greater field time to achieve similar levels of variability to those obtained by the strip transect method. In essence then, the statistical trade off between methods is one of accuracy versus precision.

ACKNOWLEDGMENTS

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Fig. III-1. The flight tracts of 7 Black-legged Kittiwakes followed by boat during telemetry studies conducted in Valdez Arm, Prince William Sound, Alaska.

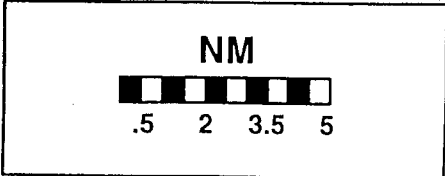


Fig. III-2. Transects conducted to obtain location data on Black-legged Kittiwakes in Valdez Arm, Prince William Sound, Alaska.

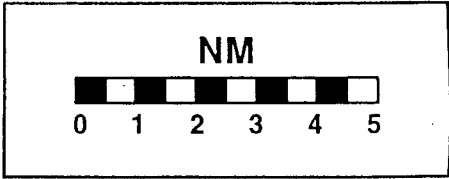
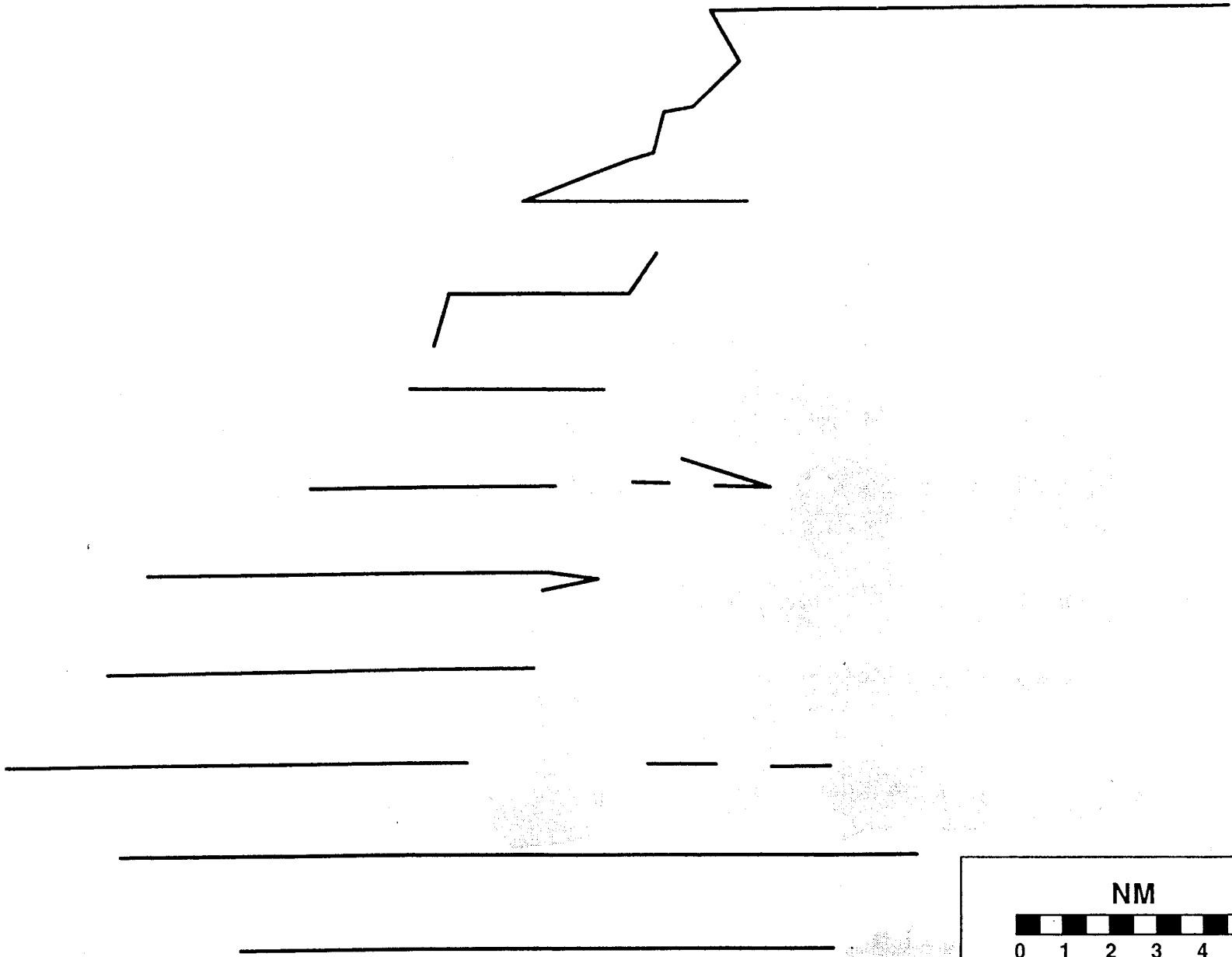


Fig. III-3. Concentric rings extending out at 2 nautical mile intervals from the Shoup Bay colony located in Valdez Arm, Prince William Sound, Alaska.

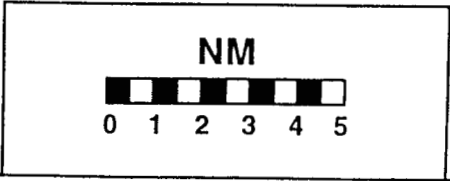
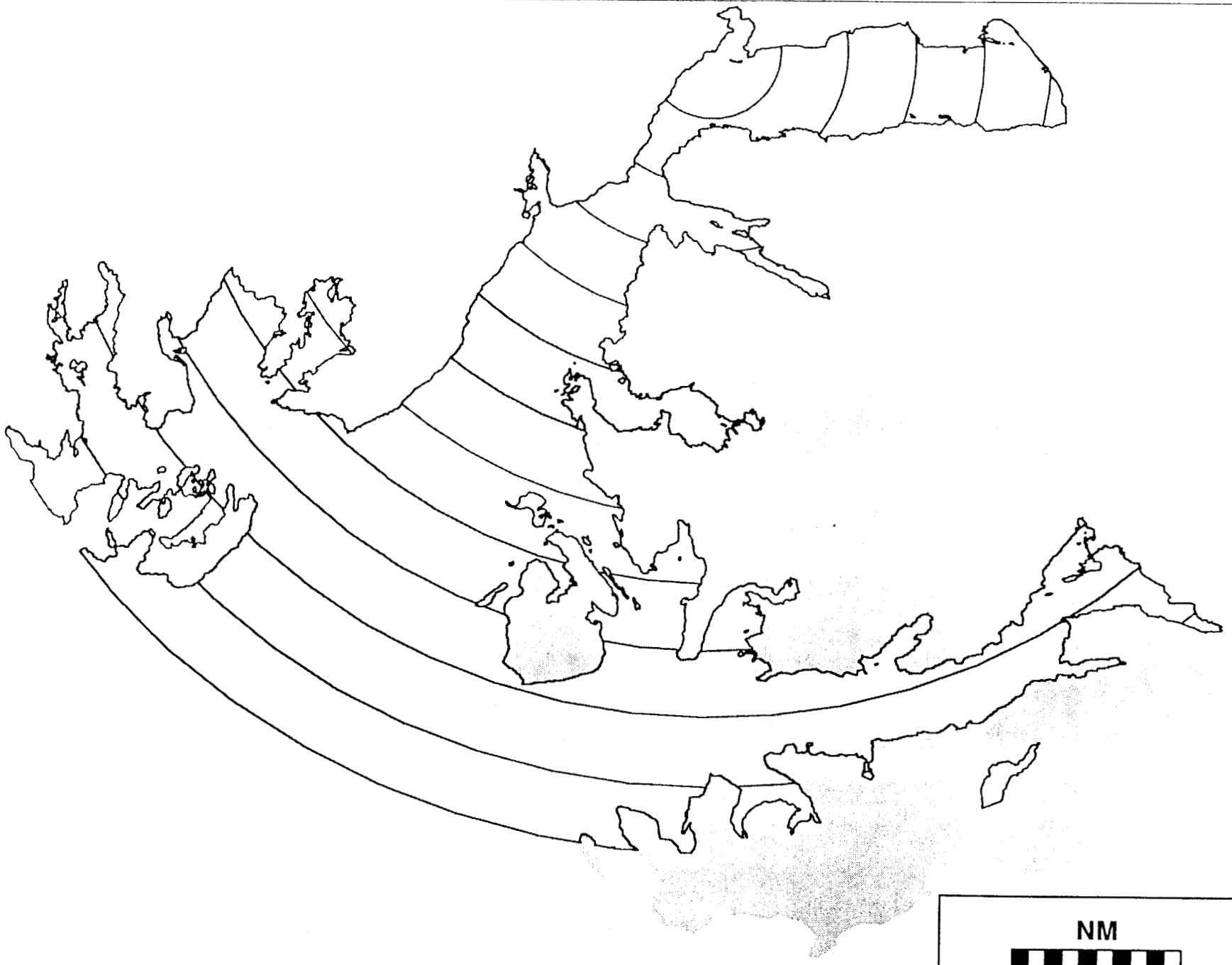


Fig. III-4. Comparison of the number of Black-legged Kittiwakes observed within concentric rings (Fig. 3), extending from the Shoup Bay Colony, Prince William Sound, Alaska, to numbers predicted by a model of diminishing probability of encountering birds at increasing distance from a colony. Observed data was obtained on 2 surveys of systematically arranged transects (Fig. 2).

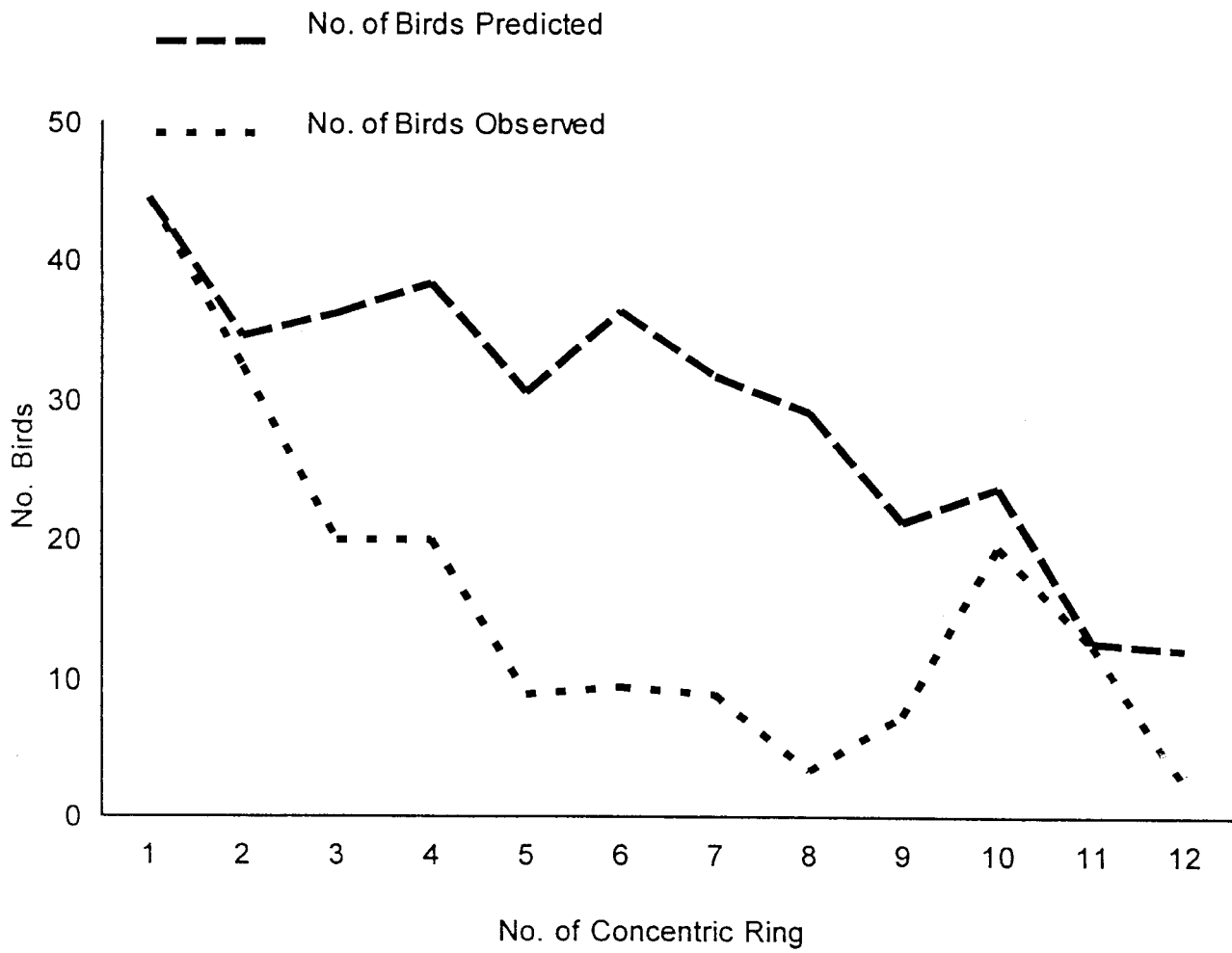
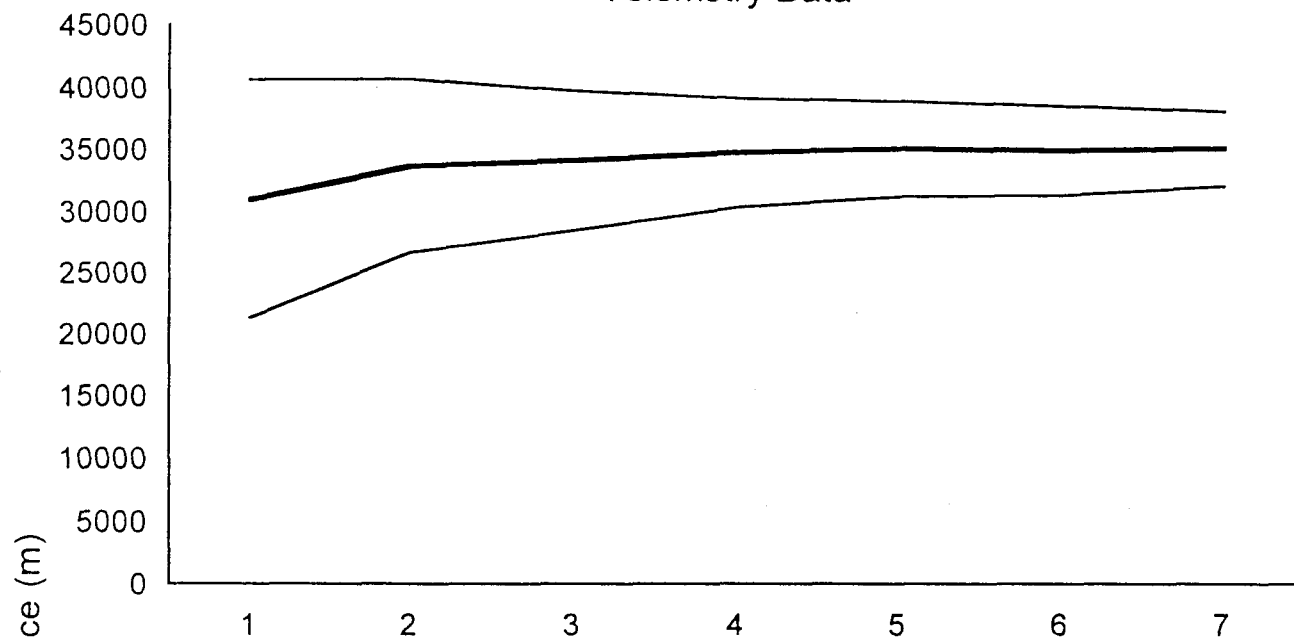
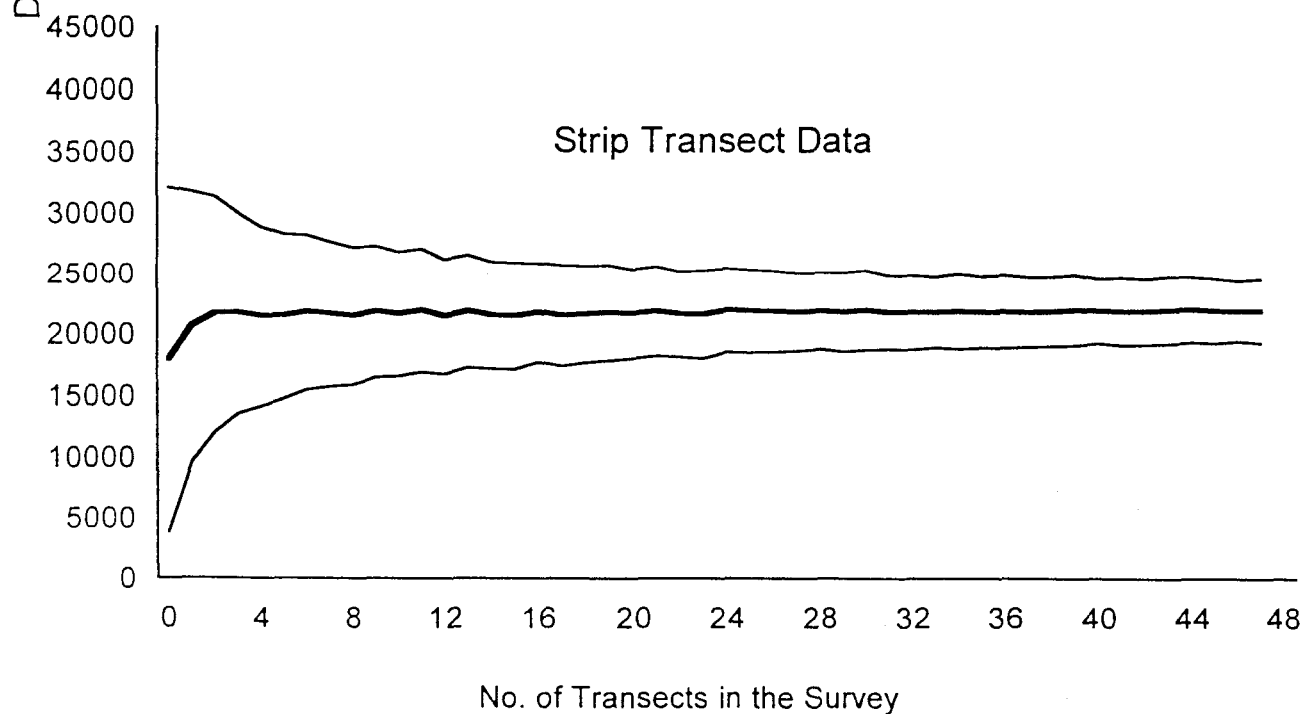


Fig. III-5. The results of a bootstrapped simulated reduction of the sampling efforts of telemetry and strip transect studies of Black-legged Kittiwake in Valdez Arm, Prince William Sound, Alaska. The simulation examined how the mean (bold lines) and standard errors (fine lines) values for distance birds were observed from their colony changed as sampling effort was reduced.

Telemetry Data



No. Birds with Transmitters Followed



Strip Transect Data

No. of Transects in the Survey

**CHAPTER IV: FLOCK COMPOSITION AND SEABIRD BEHAVIORS AT
FEEDING ASSEMBLAGES IN PRINCE WILLIAM SOUND, ALASKA**

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Abstract: We examined the behaviors of seabirds at feeding flocks in Prince William Sound, Alaska during July/August 1995 to determine the factors which may enhance or limit the availability of forage to surface feeding birds. The presence of larids and alcids at feeding flocks was positively correlated, suggesting complimentary feeding habits. On the other hand, the frequency of kittiwake plunge dives was negatively correlated with the relative presence of larger gulls in the flock. Kittiwakes preferred to plunge-dive for fish while Glaucous-winged Gulls hop-plunged from the water surface to maintain their position at the center of the feeding flock. Kittiwakes had a feeding success of 80.6% and lost 4.8% of their captures to intraspecific piracy and 6.7% to interspecific piracy. Kleptoparasitism was most intense against kittiwakes in tightly aggregated feeding flocks and against alcids in loosely aggregated flocks. Jaegers preferred to kleptoparasitize kittiwakes in the largest flocks.

Key words: seabirds, feeding behaviors, feeding success, kleptoparasitism, Prince William Sound

INTRODUCTION

Seabirds often gather in flocks to exploit patchily distributed prey (Brown 1980, Obst 1985, Heinemann et al 1989). Behavioral studies of seabirds at mixed-species feeding flocks have added substantially to our view of how food is obtained by this group of animals searching in an environment which is generally hidden from sight (e.g. Sealy 1973, Hoffman et al. 1981, Chilton and Sealy 1987, Mahon et al. 1992). Species composition of seabird flocks may vary widely depending on the feeding situation (Duffy 1983). Many seabirds play specific roles in the formation, continuation, or breakup of the flocks (Hoffman et al. 1981, Duffy 1983, Chilton and Sealy 1987, Mahon et al. 1992). The presence or absence of certain key seabirds can affect the availability of forage to a number of other species. For instance, cormorants which dive in the middle of fish schools may have the effect of breaking up the schools and making them unavailable to other seabirds (Hoffman et al. 1981). Duffy (1986) found that roseate terns (*Sterna dougalli*) were more successful when foraging alone in dispersed flocks than in tightly spaced flocks with common terns (*S. hirundo*). Yet, individual foraging success of certain species can increase with the number of birds involved (Gotmark et al. 1986).

Methods by which seabirds feed vary from dipping in petrels to pursuit diving in auks and penguins (Ashmole 1971). Depending upon their feeding circumstances at sea, gulls and kittiwakes may choose to surface seize, plunge-dive, hop-plunge, dip or kleptoparasitize (steal food which had been captured by another animal). These behaviors may depend upon the density of birds in the aggregation or upon how the forage is made available. Both of these factors were used to delineate different types of feeding flocks (Hoffman et al. 1981). The feeding method of a particular seabird species may make forage unavailable to other species through interference competition (Shealer and Burger 1993) or through dispersion of the prey (Hoffman et al. 1981).

Kleptoparasitism is one feeding strategy which is common in many gulls and is a way of life for jaegers (Brockman and Barnard 1979). The success of a kleptoparasite

could be dependent on factors such as weather condition, size of prey carried by host, or stage of the breeding season (Furness 1987). Instances of kleptoparasitism in many birds may increase with decreasing access to food (Brockman and Barnard 1979, Duffy 1980, Temeles and Wellicome 1992, Oro and Martinez-Vilalta 1994, Oro 1996). High rates of this feeding strategy in seabirds could adversely affect populations of the host (Furness 1987) and failure of one host species to breed could cause increased pressures on an alternate host (Arnason and Grant 1978).

In this chapter we describe the species composition seabirds at different flock types in Prince William Sound, Alaska. Prey capture techniques by gulls and kittiwakes are compared between the flock types. We further attempt to determine how the behaviors of different seabirds affect the availability, accessibility, and retention of their forage by examining cooperation between alcids and larids, interference competition between gulls and kittiwakes, and kleptoparasitism by jaegers and other larids.

STUDY AREA

Prince William Sound (PWS), Alaska is a large estuarine embayment of the northern Gulf of Alaska which provides important foraging and breeding habitat for many seabirds (Isleib and Kessel 1973, Irons et al. 1988). Water depths exceed 870 m and the numerous bays and fjords along with more than 150 islands form at least 5000 km of shoreline. High precipitation rates keep the sea-surface salinity low and catabatic winds flowing down the fjords transport this low-salinity water out of PWS, generally through Montague Strait and the smaller straits and passages of the southwestern region. The Alaska coastal current provides the major inflow of marine water through Hinchinbrook Entrance (Royer et al. 1990). Diurnal tidal changes in PWS can also create currents exceeding 5 km/hr through narrow passages.

Seabirds which commonly forage in flocks in PWS include black-legged kittiwakes (*Rissa tridactyla*), glaucous-winged gulls (*Larus glaucescens*), mew gulls (*Larus canus*), marbled murrelets (*Brachyramphus marmoratus*), tufted puffins (*Fratercula cirrhata*) and horned puffins (*F. corniculata*). The former three species are members of the family Laridae and the latter three are members of the alcidae. We occasionally refer to these birds as larids and alcids, respectively. Jaegers (*Stercorarius* spp., family: Laridae) kleptoparasitize at these flocks to an unknown extent. Three focal areas in PWS (Figure 1) were chosen for study because of their habitat which is critical to these seabird species of interest.

Some of the forage fish available to nesting seabirds in PWS include, Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), walleye pollock (*Theragra chalcogramma*), and eulachon (*Thaleichthys pacificus*) (Sanger 1987, Haldorson et al. 1995). Herring in PWS did not appear to be seriously affected immediately following the spill. However, in 1993, greatly reduced numbers of herring returned to spawn and many of them had ulcers and hemorrhages of the skin and fins (Meyers et al. 1994, Brown et al. 1996). Declines in sand lance delivered to nestling pigeon guillemots (*Cephus columba*) following the spill may also

reflect a decrease in the abundance of this prey species (Hayes 1995, Oakley and Kuletz 1996).

METHODS

Field Procedures

From a random starting point, we selected transects in the three areas of primary interest along lines of latitude 2 nm apart. Since many seabirds are often found nearshore or in shallow depth gradients (Vermeer et al. 1989, Stone et al. 1995), zig-zag transects were conducted nearshore by sampling on a straight line from shore to the halfway point between adjacent transects where water depth was 100 m. From this point, the ship continued sampling to the beginning of the next transect. The study period (July 20 - Aug. 12) was chosen to include the peak time of chick provisioning for many seabirds in PWS. Observations were made with 8 x 40 binoculars, 6 m above the water line from a 26 m vessel traveling at approximately 5 knots while conducting hydroacoustic surveys to estimate forage fish and seabird distributions and abundances. Transect lines were left to more closely examine feeding flocks within 300 m of either side of our vessel.

Trawl data were collected from a separate vessel which was directed by the hydroacoustic vessel to sample schools of forage species in which there was the most uncertainty as to prey species and/or age class composition. A modified Canadian midwater herring trawl (100 m² opening), an improvised pair trawl, and a dip net were used to verify fish school compositions as estimated from the acoustic data. These trawls were only used on the larger fish schools and hence the fish collected from them were not representative of all schools.

We collected behavioral data on feeding flocks upon leaving the transect and continued to do so until the flock broke up naturally or became disturbed by our presence. A feeding flock was defined as an aggregation of three or more seabirds actively feeding as observed by diving alcids with fish in their bill or larids plunge-diving, dipping, or hop-plunging. While at a feeding flock, one observer videotaped the flock for later analysis while another recorded detailed information on the flock, including: location (lat. and long.), date, time, weather conditions, wind speed and direction, sea state, water and air temperatures, area covered by flock in m², any noticeable physical features (e.g. upwellings, fronts), flock composition with numbers and locations of each species within the flock, kleptoparasitic and aggressive interactions with as much detail as possible, other feeding methods used and their success, and the duration and fate of the flock if known. We categorized feeding methods as surface-seizing, dipping, surface-diving, plunging, pursuit-plunging, piracy (Ashmole 1971), and hop-plunging (Hoffman et al. 1981). Flock types were loosely classified following Hoffman et al. (1981): I) small, short duration flocks over tightly clumped prey; II) large, persistent flocks over more broadly dispersed prey; III) flocks associated with sites where forage was concentrated by downwelling or other hydrophysical influence, determined by a subjective evaluation of oceanographic features.

After approximately 15 minutes of examining seabird behaviors at the flocks or as soon as the flocks stopped feeding, our vessel was maneuvered through the area of

activity to produce an acoustic profile of the forage. This was normally done more than once with the location of greatest feeding activity to the right of the vessel where the side-looking transducer was viewing. However, on a few occasions the forage was in too close to shore for the vessel to maneuver safely.

Data Analyses

Analysis of the videotapes included categorizing the feeding methods used, frequency of these methods, and frequency of kleptoparasitic and aggressive interactions. We computed the independence of the different flock types by species composition using a Chi-square contingency table. The association between kittiwakes and murrelets, murrelets and puffins, and the relationship of kittiwake dive frequencies and gull presence in the flocks was analyzed using Spearman's rank correlation. These data were analyzed in S-Plus (Statistical Sciences, Inc. 1993). Chi-square and Fisher's Exact Test were also used to compare and contrast the behaviors of different seabirds at the different flock types.

RESULTS

Flock types and species composition

In PWS flocks are generally smaller than those encountered in more oceanic regions (e.g. Hoffman et al. 1981, Duffy 1983). During 18 days of hydroacoustic sampling 120 transects totaling 587.7 km, only 22 feeding flocks were encountered and ranged in size from 3 to 1065 birds (mean = 135.8). Fifteen bird species participated in feeding flocks with a maximum of 11 species at a Type II flock (Appendix 4). Species participation in the three flock types was significantly different overall ($\chi^2 = 214.65$, $df = 8$, $P < 0.001$; Table 4.1). However, species compositions of Type I and II flocks were not significantly different ($\chi^2 = 7.025$, $df = 4$, $P = 0.135$).

Black-legged kittiwakes and marbled murrelets were the most numerous species in all three flock types (Appendix 4). A scatter plot of their presence in the flocks suggested rank ordering them before analysis. Kittiwake presence in flocks was positively correlated with murrelet presence (Spearman's $\rho = 0.613$, $P = 0.005$, Figure 4.1). Tufted puffins and glaucous-winged gulls were also a predominant species in Type I and II flocks, and the correlation results for all larids and alcids at the flocks were the same as those for kittiwakes and murrelets.

Marbled murrelets and tufted puffins were present together in great numbers in Type II flocks. However, in the only two Type I flocks in which tufted puffins participated, murrelets had a presence of zero and one. A significant negative correlation was not detected, perhaps because of the small sample size.

Type I flocks were composed of 7 to 174 birds ($N = 14$; Table 4.1; Appendix 4) with the mean number of species being 3.3 ($SD = 1.49$). At these flocks, we often saw the fish held in tight balls by pursuit-diving birds which dived and resurfaced near the periphery of the flock, as also observed by Hoffman et al. (1981) and Mahon et al. (1992). In some cases, this ball of fish appeared to be only a small portion which was separated from a much larger fish school residing near the bottom of the water column as seen in

hydroacoustic plots of the area (Chapter 1). Herring and capelin were found to be common prey at PWS Type I flocks as determined by trawling.

We encountered two Type II flocks of 984 and 1065 birds with 11 and 8 species participating in them, respectively. These were much smaller in size than the Type II flocks described by Hoffman et al. (1981), who described such flocks as ranging in size from 5,000 to 50,000 individuals. However, we still considered them to be Type II flocks because: (1) they were significantly larger than flock Types I and III ($\chi^2 = 1696.1$, d.f. = 2, $P < 0.001$), (2) both of them lasted for at least two days, and (3) they were loosely aggregated assemblages feeding on post-spawning male capelin in one case and either capelin or herring in the second case. Type III flocks were composed of 11 to 168 birds ($N = 6$; Table 4.1) with the mean number of species being 4.2 ($SD = 2.40$). Five of these flocks were concentrated around points of land and one at the mouth of a shallow passage. Herring of various age groups were found in a trawl at one of these flocks.

Larid behaviors at flocks

Alcids pursuit-dived from the outskirts of Type I flocks and from throughout Type II and III flocks. We did not concentrate any part of our observations on these birds because of the difficulty of following these birds from where they dived to where they resurfaced.

Glaucous-winged gulls hop-plunged more frequently than any other foraging method at all flock types (Figure 4.2a). At Type I flocks, glaucous-winged gulls normally sat on the water directly over the fish school, while kittiwakes sat on the water around the periphery of the school or circled above it. To maintain their position in this flock type, gulls hop-plunged as opposed to plunge-dived. The latter foraging method was used more often in Type II and Type III flocks (Fisher's exact test; $P < 0.001$). Kittiwakes also hop-plunged more often in Type I flocks than in Type II and III flocks combined ($\chi^2 = 14.356$; $P < 0.001$). Yet, in all flock types, plunge-diving was their preferred method of feeding (Figure 4.2b). We were able to detect a weak but insignificant negative correlation between the frequency of kittiwake plunges and the relative presence of larger gulls in the flock (Spearman rho = -0.5664, $P = 0.0587$).

Kleptoparasitism

Kittiwakes had an overall feeding success of 80.6% ($N = 129$) and lost 4.8% of their captures to intraspecific piracy and 6.7% to interspecific piracy. Glaucous-winged gulls had a feeding success of 55.3% ($N = 38$) and lost no prey to kleptoparasitism.

Kleptoparasitism against kittiwakes occurred more frequently in the tightly aggregated Type I flocks compared to Type II and III flocks combined ($\chi^2 = 83.55$; $P < 0.001$; Table 4.2, Figure 4.3). Intraspecific kleptoparasitic attempts by kittiwakes were observed most often in Type I flocks, while attempts directed against alcids were more commonly seen in Type II flocks (Table 4.2, Figure 4.3). Glaucous-winged gulls attempted to rob alcids only in Type I flocks (Table 4.2, Figure 4.3). Gulls and kittiwakes kleptoparasitized alcids less than expected in Type I flocks ($\chi^2 = 15.32$, d.f. = 1, $P < 0.001$), but not in Type III flocks ($\chi^2 = 1.780$, d.f. = 1, $P = 0.182$).

Jaegers preferred to kleptoparasitize at the large Type II flocks (78% of observed attempts; Figure 4.3). Thirty-one out of 32 observed jaeger robbing attempts were

directed toward kittiwakes, and the other toward a juvenile glaucous-winged gull. One large capelin feeding flock had a group of 15 Pomarine and 2 Parasitic Jaegers sitting on the water about 1 km away. They appeared to be making occasional sorties (usually alone) into the feeding flock. Their method of attack in Type II flocks was to concentrate efforts on kittiwakes which had recently caught a fish and those with fish visible in their bill.

DISCUSSION

Flock types and species composition

In PWS flocks are generally smaller than those encountered in more oceanic regions (e.g. Hoffman et al. 1981, Duffy 1983). Feeding flocks of murrelets, kittiwakes, gulls, puffins, and guillemots fed on schools of herring, capelin, and sand lance that were nearshore (Ostrand and Maniscalco, unpubl. data). Conspecifics and congeners of these birds have also been found to be distributed nearshore in other boreal environments (Vermeer et al. 1989, Stone et al. 1995) to obtain easy access to their prey. Our observations on only 22 feeding flocks during 18 days were likely the result of spending a much greater proportion of time on offshore portions of transects.

Seabird prey can be concentrated by upwelling or downwelling in both oceanic and coastal regimes (e.g. Wahl et al. 1989, Schneider et al. 1990, Coyle et al. 1992). Such flow gradients are often found around islands and points of land (Hamner and Hauri 1981, Kinder et al. 1983). These processes may work in PWS during the summer to make herring more vulnerable to seabird predation and forming Type III flocks. Sand lance are also common in shallow waters and nearshores which have sandy substrates and relatively high bottom current velocities (Auster and Stewart 1986). These conditions occur around many of the land masses in PWS. The capelin concentrations discovered nearshore appeared to be post-spawning aggregations which are known to attract alcids (Piatt 1990) and many other seabirds (Hoffman et al. 1981). The hydroacoustic profiles suggest that the predominant concentration of capelin in these schools reside near the bottom of the water column. Alcids appear to be the driving force in Type I flocks where capelin are concentrated in tight balls near the surface and hence become accessible for gulls and kittiwakes (Grover and Olla 1983). In the large Type II flocks, individual capelin appear to separate from the main school for unknown reasons and swim to near the surface where they are vulnerable to plunge-diving birds.

In British Columbia Marbled Murrelets may have been the catalyst in the formation of feeding flocks by forcing fish schools into tight balls and driving them to the surface (Mahon et al. 1992). This is a likely cause for the association between murrelets and kittiwakes at the flocks. Not only do alcids make prey easily available to larids (Grover and Olla 1983), but larids may make the fishes more vulnerable to capture by alcids by plunge-diving into the middle of a school and forcing individual fish outward for easier capture (Major 1978).

Our observations of murrelet participation in flocks were consistent with observations made within intercoastal waters of British Columbia (Mahon et al. 1992) and inconsistent with the low murrelet participation in flocks of outside waters (Porter and Sealy

1981, Chilton and Sealy 1987). Hunt (1995) reviewed these and other studies and was unable to conclude why there was this difference in murrelet flock participation. The relative absence of murrelets in tightly aggregated flocks with many puffins in PWS does suggest, however, that murrelet feeding activity may be inhibited by larger alcids in this type of situation (see also Chilton and Sealy 1987, Piatt 1990).

Larid behaviors at flocks

Glaucous-winged gulls may deter smaller gulls and kittiwakes from feeding at densely aggregated flocks. Porter and Sealy (1982) observed that smaller California gulls usually hovered over flocks and plunge-dived, while glaucous-winged gulls flew directly into the center and hop-plunged or dipped for prey. These behaviors are similar to what we have observed with kittiwakes and gulls in PWS feeding flocks. One feeding flock was encountered which had 12 glaucous-winged gulls sitting on the water over a tight ball of capelin and occasionally plunge-diving. Kittiwakes were entirely absent from this flock, though many were seen within a few kilometers. Interference competition such as this has also been noted in brown noddies (*Anous stolidus*) which deterred the feeding attempts made by roseate terns near Puerto Rico and may have been stronger during periods of food shortage (Shealer and Burger 1993). We observed that kittiwakes partially compensated for the presence of glaucous-winged gulls at densely aggregated Type I feeding flocks by remaining on the water and hop-plunging more often in these flocks but always outside the central core of gulls. The negative correlation we found between kittiwake dive rates and gull presence in the flocks is further suggestive that interference competition does take place amongst larids in PWS. Unfortunately, keeping track of individual birds is difficult in Type I flocks, therefore correlations between feeding success of kittiwakes and gull presence were not possible to determine. Glaucous-winged gulls are unable to dominate the more loosely aggregated fish at Type II and III flocks and hence plunge-dived more often in those situations.

Kleptoparasitism

Densely aggregated Type I flocks promoted kleptoparasitism within the gulls and kittiwakes but did not facilitate piracy by jaegers, perhaps because of their low success rate in this type of flock (Hoffman et al. 1981). Alcids were attacked less frequently in Type I flocks because of their ability to dive and resurface around the outer edge of these flocks and avoid the attacking kittiwakes (Hoffman et al. 1981, Chilton and Sealy 1987). The inability to keep fish tightly balled as in Type II and III flocks causes diving birds to resurface randomly. Without the focal point of a tight fish school, kittiwakes may cue on the resurfacing alcids for feeding opportunities. Our observations of greater numbers of alcid attacks at those flock types supports this hypothesis.

Parasitic and pomarine jaegers were most commonly observed in the largest (Type II) feeding flocks. Kittiwakes were preferentially chased, rather than the larger gulls, probably because kittiwakes were smaller hosts or they delayed the swallowing of their prey or both. On the St. Lawrence River, smaller common terns were chased more often by parasitic jaegers than were black-legged kittiwakes and almost half of the chased terns had fish dangling from the bill, whereas none of the chased kittiwakes carried visible fish

(Belisle and Giroux 1995). A review by Furness (1987), however, suggests that the parameters regarding a bird's susceptibility to chase remain equivocal.

Although most studies of jaeger piracy have been conducted near colonies (e.g. Andersson 1976, Birt and Cairns 1987), these birds are not common raiders at colonies in PWS (David Irons, pers. comm.). The relatively small colony sizes of PWS seabirds (Sowls et al. 1978) may limit kleptoparasitic opportunities at these locations. Foraging at large feeding flocks where bird densities are higher could be more beneficial (Furness 1987), especially when a host has been observed catching a fish (Hoffman et al. 1981).

Evolutionary stable kleptoparasitic interactions may deprive hosts of about 1% of their food (Furness 1987). The estimated loss of secured prey by kittiwakes to interspecific kleptoparasitism in PWS was close to 7%. Increased rates of kleptoparasitism could be indicative of periods of food shortage (Furness 1987). This hypothesis was tested by Oro and Martinez-Vilalta (1994) and Oro (1996) who showed a correlation between a greater number of attempted food robberies by gulls and a trawling moratorium which reduced the accessibility of their food near Spain. On the other hand, changes in food abundance from year to year may be positively, not negatively, correlated with robbing attempts by opportunistic kleptoparasites such as gulls (Rice 1985, 1987). Furness (1987) also argues that high success rates of robbing attempts could indicate that some birds may have been more willing to relinquish their catches when prey was abundant. Therefore, higher food losses to kleptoparasitism such as reported by Hulsman (1976) and this study may not imply much without comparing trends in forage fish abundance.

Intraspecific kleptoparasitism as seen in Kelp Gulls (*Larus dominicanus*) at a rate of 15% may benefit this species (Steele and Hockey 1995). Although our data concerning kittiwakes is not directly comparable, kleptoparasitism among kittiwakes in PWS be not be adversely affecting their populations. A significant change in rates of kleptoparasitism in PWS in the coming years may be indicative of changes in the abundance of seabirds and/or their prey.

Physical and biological processes which make forage easily available or difficult to obtain for seabirds in PWS are not necessarily the same as in other ecosystems, although there are some apparent similarities. Seabird behavior is more complex than presented here and all of the aspects analyzed in this paper should be studied further to better understand seabird ecology in PWS and elsewhere.

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Table IV-1 - Total numbers of the most common seabirds and total birds at the different flock types with percent contribution of these species at each flock type (n = number of flocks).

	Type I (n = 14)	Type II (n = 2)	Type III (n = 6)
black-legged kittiwake	277 (43%)	860 (42%)	105 (35%)
glaucous-winged gull	55 (9%)	250 (12%)	13 (4%)
marbled murrelet	141 (22%)	420 (20%)	112 (38%)
tufted puffin	143 (22%)	450 (22%)	12 (4%)
other birds	26 (4%)	69 (3%)	54 (18%)
all birds	642 (100%)	2049 (100%)	296 (100%)

Table IV-2 - Kleptoparasitism of alcids and kittiwakes by all larids combined in Type I and III flocks.

Flock Type	Host	Host total abundance	Host relative abundance	Expected # of chases	Observed # of chases
I	alcid	180	0.4286	12.43	2
I	kittiwake	240	0.5714	16.57	27
III	alcid	143	0.6272	10.66	8
III	kittiwake	85	0.3728	6.34	9

Figure IV-1 - Scatter plot of Marbled Murrelets and Black-legged Kittiwakes at feeding flocks.

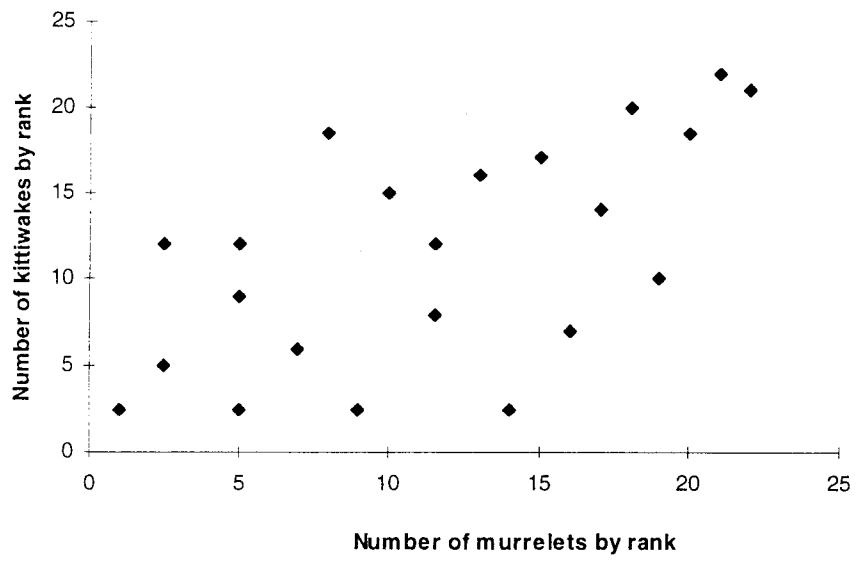
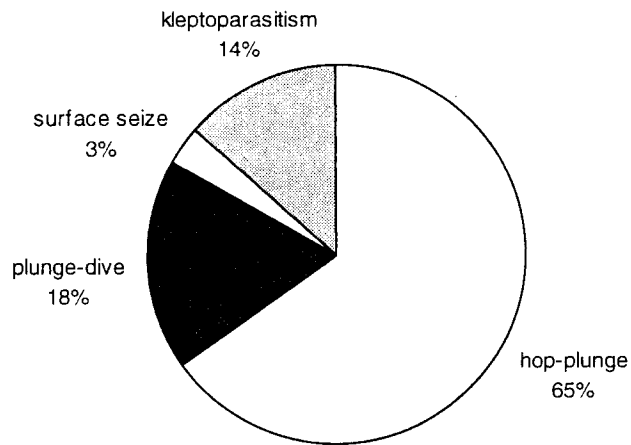


Figure IV-2 - Frequency of feeding techniques used by a) glaucous-winged gulls and b) black-legged kittiwakes at all flock types combined.

a) Glaucous-winged Gulls



b) Black-legged Kittiwakes

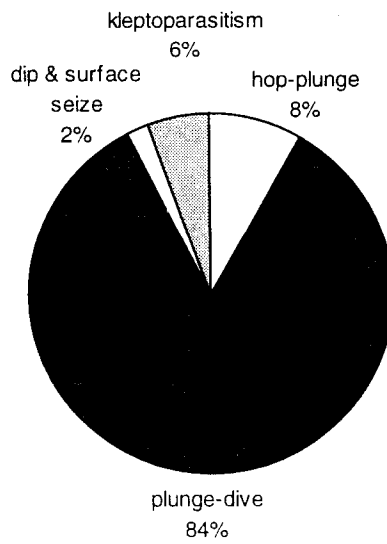
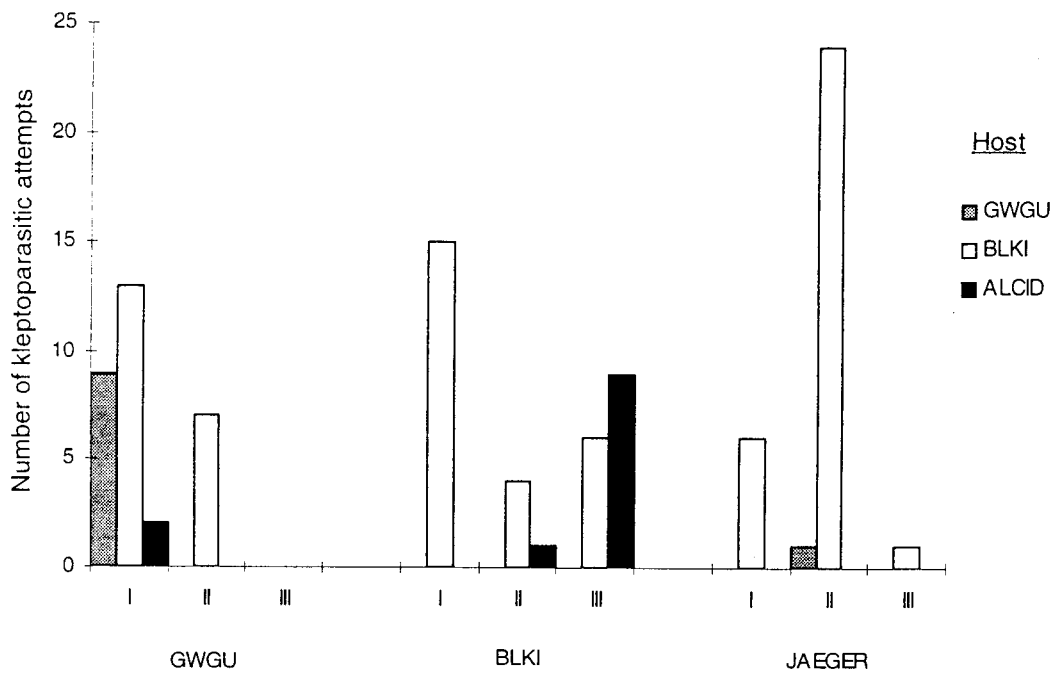


Figure IV-3 - Number of observed kleptoparasitic attempts segregated by flock type and species involved.



Kleptoparasite and flock type

**Chapter V: July 1996 Species Composition and Behavioral Results from
Nearshore Transects and Flocks Observed on Nearshore Transects**

John M. Maniscalco
William D. Ostrand

Abstract

We conducted seabird/ hydroacoustic surveys in three different areas (northeast, central, southwest) of Prince William Sound, Alaska during July of 1996 to assess seabird distributions and examine their behavior at feeding flocks. We systematically selected 12-km blocks of shoreline within which we ran 20 1-km long transects to and from shore at oblique angles. The average number of birds per transect and transect block were 6.62 and 131.57, respectively and were not significantly different among the three areas ($P > 0.10$ in both cases). However, species composition of the blocks differed significantly among the study areas ($P < 0.001$). Bird flocks found within 300 meters of these transects were feeding primarily on juvenile herring and sand lance. Flocks in the northeastern area were significantly larger than flocks in the other two areas ($P = 0.01$) and were feeding on herring more often. The feeding rate of black-legged kittiwakes did not increase significantly with the presence of marbled murrelets ($P = 0.3801$), but did decrease significantly with the presence of glaucous-winged gulls ($P = 0.0225$). Changes in flocks from 1995 included; reduced presence of kittiwakes and tufted puffins, increased presence of marbled murrelets and glaucous-winged gulls, more tightly aggregated feeding flocks, reduced feeding success of kittiwakes and greater feeding success of gulls, reduced kleptoparasitism of kittiwakes and increased kleptoparasitism of gulls. The implications of these changes are discussed briefly.

Many seabirds in certain regions of the world are commonly distributed near shore and in shallow waters (Vermeer et al. 1989, Stone et al. 1995). Prince William Sound (PWS) is no exception (Chapter II). For this reason and judging from the results of our 1994 and 1995 surveys, we decided to conduct additional surveys nearshore in 1996. We may be able to better determine what factors are important for seabird prey selection by concentrating our efforts in their preferred habitat.

In this chapter we provide preliminary results on the species composition of the nearshore transects and transect blocks from July 1996. We also describe the feeding flock composition and seabird behaviors observed at the flocks during the same period and draw some contrasts with our observations of 1995 feeding flocks.

Methods

Field Procedures

Twelve kilometer sections of shoreline were systematically selected in each of the three study areas in PWS (seven in the southwest, seven and one half in the central, and nine in the northeast). Within each of these shoreline sections 20 one-kilometer transects were surveyed at an oblique angle to and from shore (See annual report by Haldorson et al. for further details). We counted seabirds and recorded their behaviors while surveying these transects with down and side looking hydroacoustics. Fish species and size distributions in the the 12-km sections were determined through purse seining, beach seining, cast netting, dip netting, and visually with an underwater video camera.

The study period (15 - 27 July 1996) was chosen to include the peak time of chick provisioning for many seabirds in PWS. Observations were made with 8 x 40 binoculars, 6 m above the water line from a 26 m vessel traveling at approximately 5 knots while conducting hydroacoustic surveys to estimate forage fish and seabird distributions and abundances. Transect lines were left to more closely examine feeding flocks within 300 m of either side of our vessel.

We collected behavioral data on feeding flocks upon leaving the transect and continued to do so until the flock broke up naturally or became disturbed by our presence. A feeding flock was defined as an aggregation of three or more seabirds actively feeding as observed by diving alcids with fish in their bill or larids plunge-diving, dipping, or hop-plunging. While at a feeding flock, one observer videotaped the flock for later analysis or recorded detailed information on dive types and success into a microcassette recorder. A second observer recorded other information on the flock, including: location (lat. and long.), date, time, weather conditions, wind speed and direction, sea state, water and air temperatures, area covered by flock in m², any noticeable physical features (e.g. upwellings, fronts), flock composition with numbers and locations of each species within the flock, kleptoparasitic and aggressive interactions with as much detail as possible, other feeding methods used and their success, and the duration and fate of the flock if known. We categorized feeding methods as surface-seizing, dipping, surface-diving, plunging, pursuit-plunging, piracy (Ashmole 1971), and hop-plunging (Hoffman et al. 1981). Flock types were loosely classified following Hoffman et al. (1981): I) small, short duration flocks over tightly clumped prey; II) large, persistent flocks over more broadly dispersed prey; III) flocks associated with sites where forage was concentrated by downwelling or other hydrophysical influence, determined by a subjective evaluation of oceanographic features.

After approximately 15 minutes of examining seabird behaviors at the flocks or as soon as the flocks stopped feeding, our vessel was maneuvered through the area of activity to produce an acoustic profile of the forage. This was normally done more than once with the location of greatest feeding activity to the right of the vessel where the side-looking transducer was viewing. However, on a few occasions the forage was in too close to shore for the vessel to maneuver safely.

Data Analyses

In the analysis of species composition of transects and transect blocks we included all observed gulls and kittiwakes and alcids and other diving birds such as loons and cormorants if they were recorded as on the water, foraging, or potentially foraging. We deleted the half block from the central area for the analysis of species composition by blocks. We used ANOVA to determine if there were any differences among the three study areas in species numbers observed on transects. Kruskal-Wallis and Chi-square statistics were used to analyze differences among the study areas in species numbers observed in total blocks of transects.

Descriptive statistics were used to summarize feeding flock composition and the behaviors of gulls and kittiwakes at the flocks. We analyzed differences in behaviors between 1995 and 1996 with Chi-square statistics. Linear regression was used to

determine the rate of decrease in kittiwake feeding attempts with increased presence of glaucous-winged gulls.

RESULTS

Species composition of the nearshore transects and blocks

The overall average number of birds per transect was 6.62 (± 14.92 SD) with 8.32, 6.16, and 5.34 birds per transect in the central, northeastern, and southwestern areas, respectively (Figure 1). Those differences were not significant (ANOVA, $P = 0.2056$). However, the distribution of bird numbers on transects was not normal (Figure 2). Black-legged kittiwakes and marbled murrelets were the most abundant birds in all three areas (Figure 3). There were no significant differences in the average number of murrelets (ANOVA, $P = 0.9776$) nor kittiwakes (ANOVA, $P = 0.3307$) per transect in the three study areas (Figure 1).

Seven and one half of the 23.5 blocks surveyed were in the central study area and seven and nine were in the southeastern and northeastern study areas, respectively. The average numbers of all bird species per block was 131.57 and was not significantly different among the three study areas (Kruskal-Wallis t -value = 2.0966, $P > 0.10$; Figure 4). Numbers of kittiwakes, glaucous-winged gulls, and marbled murrelets also did not differ significantly between the three study areas (all Kruskal-Wallis P -values > 0.10 ; Figure 5). However, the overall species composition of the blocks in the study areas did differ significantly ($\chi^2 = 469.4$, d.f. = 10, $P < 0.001$; Figure 6). This difference was due primarily to an abundance of tufted puffins in the central area which were absent from the northeastern and southwestern regions.

Species composition of flocks

In July of 1996 we observed 22 feeding flocks on the nearshore transect series. Twenty of these were Type I flocks and the other two were Type III flocks. We did not observe any large Type II feeding flocks. The flocks ranged in size from 8 to 194 birds (mean = 67.4 ± 11.0 SE; Table 1). Many of these flocks consisted of less than fifty birds (Figure 7). We encountered five flocks in the southern area, six flocks in the central area, and 11 flocks in the northern area. The average number of birds participating in the flocks was significantly greater in the northern area (ANOVA, $P = 0.01$; Figure 8).

Based on visual identification, purse seining, beach seining and other fish catching methods we were able to determine with a good degree of certainty what 16 out of the 22 observed flocks were feeding upon. Nine of the flocks were feeding on herring (usually young of the year) and seven of the flocks were feeding on sandlance. Herring was observed as the prey species in seven of the eleven northeastern area flocks; whereas sand lance was more important in the central area, appearing as prey in four out of six flocks (Figure 9). One or more flocks in the southwestern and central areas may have been feeding on juvenile salmon.

The species composition of these flocks was significantly different from the composition of the flocks observed in 1995 ($\chi^2 = 690.88$; Figure 10) as well as just the Type I flocks from 1995 ($\chi^2 = 478.17$; Figure 11). The biggest changes were decreases in the relative presence of kittiwakes and tufted puffins and increases in the relative

presence of marbled murrelets and glaucous-winged gulls. The ratio of kittiwakes to glaucous-winged gulls at all of the flocks increased significantly from 0.256 in 1995 to 0.441 in 1996 ($\chi^2 = 25.167$).

Feeding methods, success, and kleptoparasitism

The feeding methods of black-legged kittiwakes were significantly different in 1996 compared to 1995 ($\chi^2 = 34.74$) as were those of glaucous-winged gulls ($\chi^2 = 148.16$). Kittiwakes and gulls plunge-dived less and hop-plunged more in 1996 compared to 1995 (Figure 12).

On average, each kittiwake made 0.0404 feeding attempts per minute or made a feeding attempt once every 24.74 minutes and was successful once every 41.49 minutes at the flocks. Their feeding success was much lower than in 1995 but they lost nothing to interspecific kleptoparasitism in 1996 (Figure 13). On average, each glaucous-winged gull made 0.0581 feeding attempts per minute or made a feeding attempt once every 17.2 minutes and was successful once every 19.66 minutes. Their success rate was much higher than observed in 1995 (Figure 14).

The feeding rate of black-legged kittiwakes did not increase significantly with the presence of marbled murrelets ($R^2 = 0.2135$, $P = 0.3801$, $n = 19$) but did decrease significantly with increasing numbers of glaucous-winged gulls present in the flocks ($R^2 = 0.5201$, $P = 0.0225$, $n = 19$; Figure 15). However, combining the data from 1995 and 1996 did not improve the regression ($R^2 = 0.3491$; $P = 0.0586$; $n = 30$).

Kleptoparasitic attempts directed toward kittiwakes decreased from 1995 to 1996 whereas, those directed toward glaucous-winged gulls increased over the same period (Figure 16). Kittiwakes were never observed attempting to rob from glaucous-winged gulls in 1995, but in 1996 kittiwakes would occasionally try to steal from gulls which acquired a mouthful of small sand lance or herring and some of the fish were flopping out. There were no kleptoparasitic attempts directed toward alcids in 1996 as observed in 1995. Kleptoparasitism by jaegers was minimal in 1996 (only two unsuccessful attempts observed at one flock).

Table 2 summarizes the changes in seabird behaviors from 1995 to 1996.

DISCUSSION

Species composition of the nearshore transects and blocks

The lack of difference in numbers of the major bird species among the three study areas may indicate that PWS has a relatively uniform avian ecosystem structure. However, tufted puffins were found only in the central area and this probably led to our determination of differences in species composition among study areas as analyzed by transect blocks. Further analyses may be necessary to determine that no other statistical differences exist.

Species composition of flocks

We observed the same number of feeding flocks on one survey of the nearshore transects in 1996 as we had on two surveys of the predominantly offshore transects of 1995 (Chapter II this report). Type II flocks were not observed in 1996 probably because the large capelin feeding flocks that we had seen in August of 1995 were not present

within the study area during the 1996 cruise. The greater number and average size of the feeding flocks observed in the northeastern study area may have resulted from differences in forage fish abundance, quality, or accessibility. The present results show that herring may be fed upon more in the northeastern study area and sand lance in the central area. Both of these have the highest lipid and energy content of the widely available forage fishes in PWS (D. Roby and J. Anthony, unpubl. data). Differences in seabirds' diet among the different areas probably reflect variable abundances of these fishes. We anxiously await the results of the hydroacoustic data to make comparisons.

The reasons for changes in the species composition of flocks are unknown. A decrease in the amount of offal produced by fisheries vessels in PWS may increase the presence of glaucous-winged gulls at the feeding flocks as they look for other feeding opportunities. Decreases in the number of tufted puffins and increases in the number of marbled murrelets at the flocks may have resulted from changes in the distribution or abundance of one or more forage fishes. Other possibilities for these changes include variation because of small sample sizes, and different locations of transects in 1995 and 1996.

Feeding methods, success, and kleptoparasitism

The increase in hop-plunging is partially due to an increase in the number of tightly aggregated Type I flocks which promote this behavior (Chapter IV this report). Marbled murrelets also foster the formation of tightly balled fish (Mahon et al. 1992) which in turn cause the tight formation of feeding flocks. Greater proportionate numbers of murrelets in the feeding flocks of 1996 probably facilitated the formation of tightly balled fish and hence tightly aggregated flocks with a lot of hop-plunging. Larger and more aggressive seabird species can dominate feeding opportunities where food is densely aggregated (Hudson and Furness 1989).

This decrease in the feeding rate of kittiwakes with increases in gull numbers probably explains the decrease in the feeding frequency of kittiwakes from 1995 to 1996 since the relative presence of glaucous-winged gulls at the flocks was much higher in 1996 than in 1995. Larger seabirds can interfere with the ability of smaller seabirds to obtain food (Shealer and Burger 1993).

Glaucous-winged gulls were probably kleptoparasitized more in 1996 than kittiwakes because their capture success was higher than kittiwakes. Birds that are obviously getting food are more likely to be kleptoparasitized than those which are likely to have none (Furness 1978, 1987). The paucity of jaeger kleptoparasitism can be explained by the smaller flocks observed in 1996. Jaegers appeared to favor thievery at the large Type II flocks as observed in 1995 (Chapter IV this report).

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- Vermeer, K., K.H. Morgan, G.E.J. Smith, and R. Hay. 1989. Fall distribution of pelagic birds over the shelf off SW Vancouver Island. *Col. Waterbirds* 12:207-214.

Table V-1. Species composition of flocks observed on nearshore transects during July 1996 cruise.

Species	#	796-1	796-2	796-3	796-4	796-5	796-6	796-7	796-8	796-9	796-10	796-11	796-12	796-13	796-14	796-15	796-16	796-17	796-18	796-19	796-20	796-21	796-22	Totals	Means	
Species	type	3	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1			
LO	LO												16		3		6	1							26	1.18
CO	CO									1							1								2	0.09
JA	JA						1									2									3	0.14
PA	PA																								0	0.00
MG	MG																							1	1	0.05
HG	HG																								0	0.00
WGU	WGU	1	1	3		4		9	1		3	16	1	15		27	28	6	12	20	14	21		182	8.27	
BLK	BLK	12	3	17	5	3	15	12	45	5	20	22	33	43	16	14	50	26	3	21	45		3	413	18.77	
ARTE	ARTE																								0	0.00
CMU	CMU																		1						1	0.05
PIG	PIG		6					1		5	2				1										15	0.68
WGU	WGU	3	183	2	5	5	13	2	8	6	44	56	32	65	110	22	19	66	3	47	15	17	91	814	37.00	
PGU	PGU		1		1			1	5	2	10	4													24	1.09
HMU	HMU																								0	0.00
HPU	HPU										2														2	0.09
TOTAL	TOTAL	16	194	22	11	8	33	15	68	15	81	87	97	109	145	38	103	122	12	80	80	31	116			

Species Codes

- LO = Pacific loon
- CO = pelagic cormorant
- JA = parasitic jaeger
- PA = pomarine jaeger
- MG = mew gull
- HG = herring gull
- WGU = glaucous-winged gull
- BLK = black-legged kittiwake
- ARTE = Arctic tern
- CMU = common murre
- PIG = pigeon guillemot
- HMU = marbled murrelet
- HPU = horned puffin
- TU = tufted puffin
- PAU = parakeet auklet

Table V-2. Summary of feeding flock changes between 1995 and 1996 (except for first line).

Ratio of GWGU to BLKI '93 to '96 in PWS (Agler et al.)	↑
Ratio of GWGU to BLKI at feeding flocks	↑
Proportion of small, tightly aggregated feeding flocks	↑
Proportion of MAMU at feeding flocks	↑
Proportion of hop-plunging by BLKI and GWGU	↑
Feeding success of BLKI	↓
Feeding success of GWGU	↑
Kleptoparasitism of BLKI	↓
Kleptoparasitism of GWGU	↑

Figure V-1. Average number of species per nearshore transect in the three study areas during July 1996.

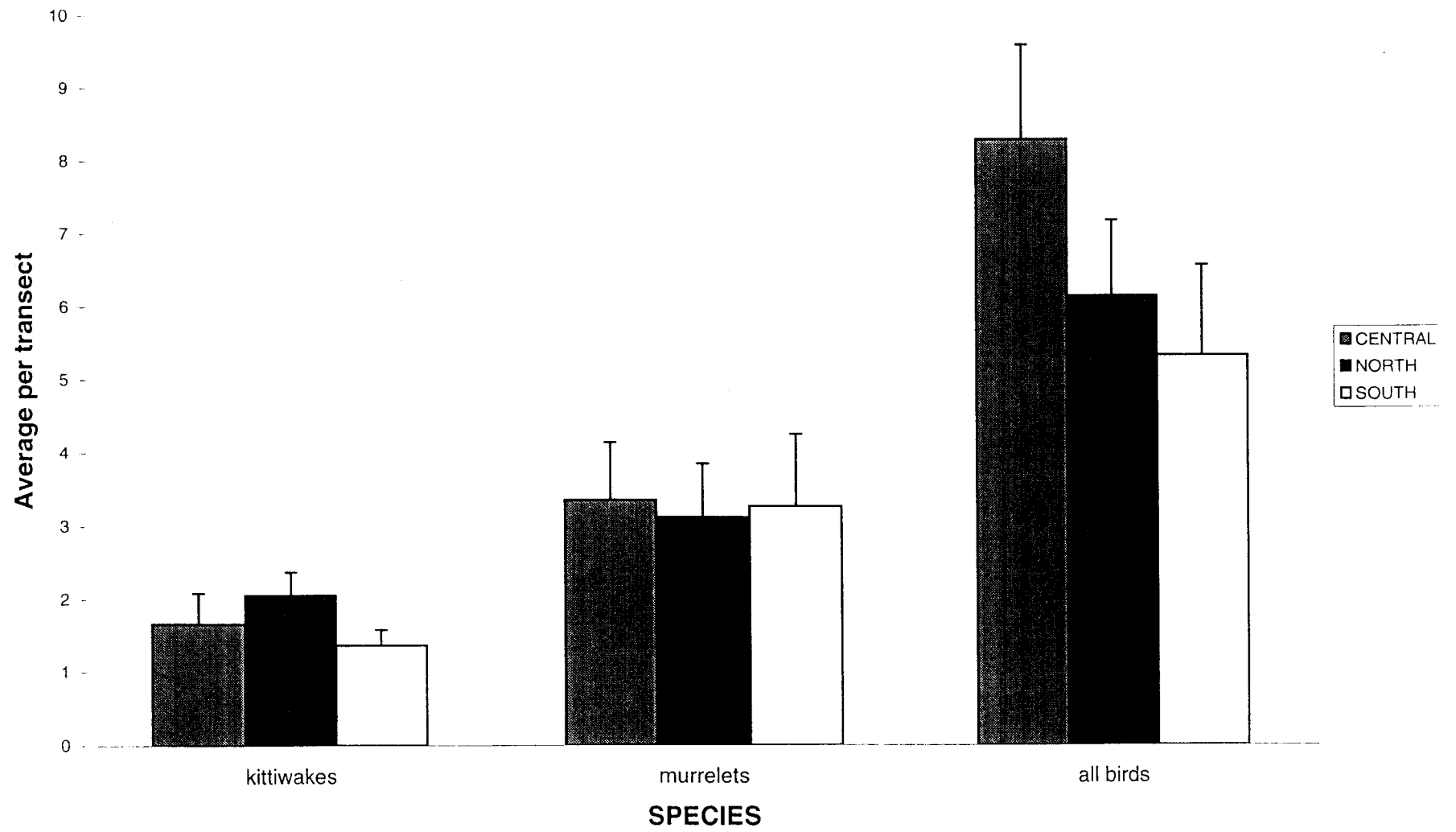


Figure V-2. Histogram of nearshore transects with “x” number birds on them from July 1996.

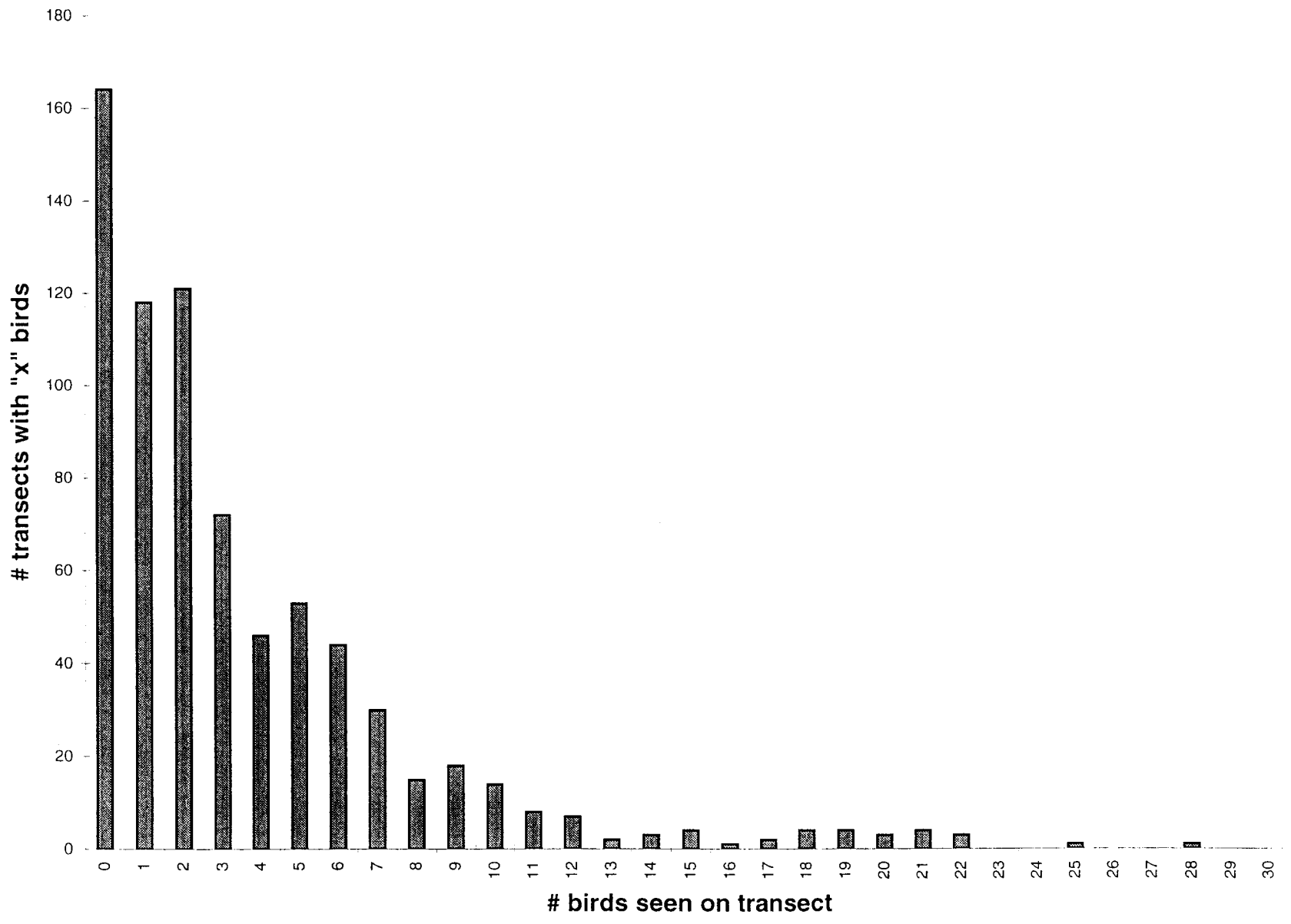


Figure V-3. Cumulative numbers of birds per nearshore transect in the three study areas from July 1996.

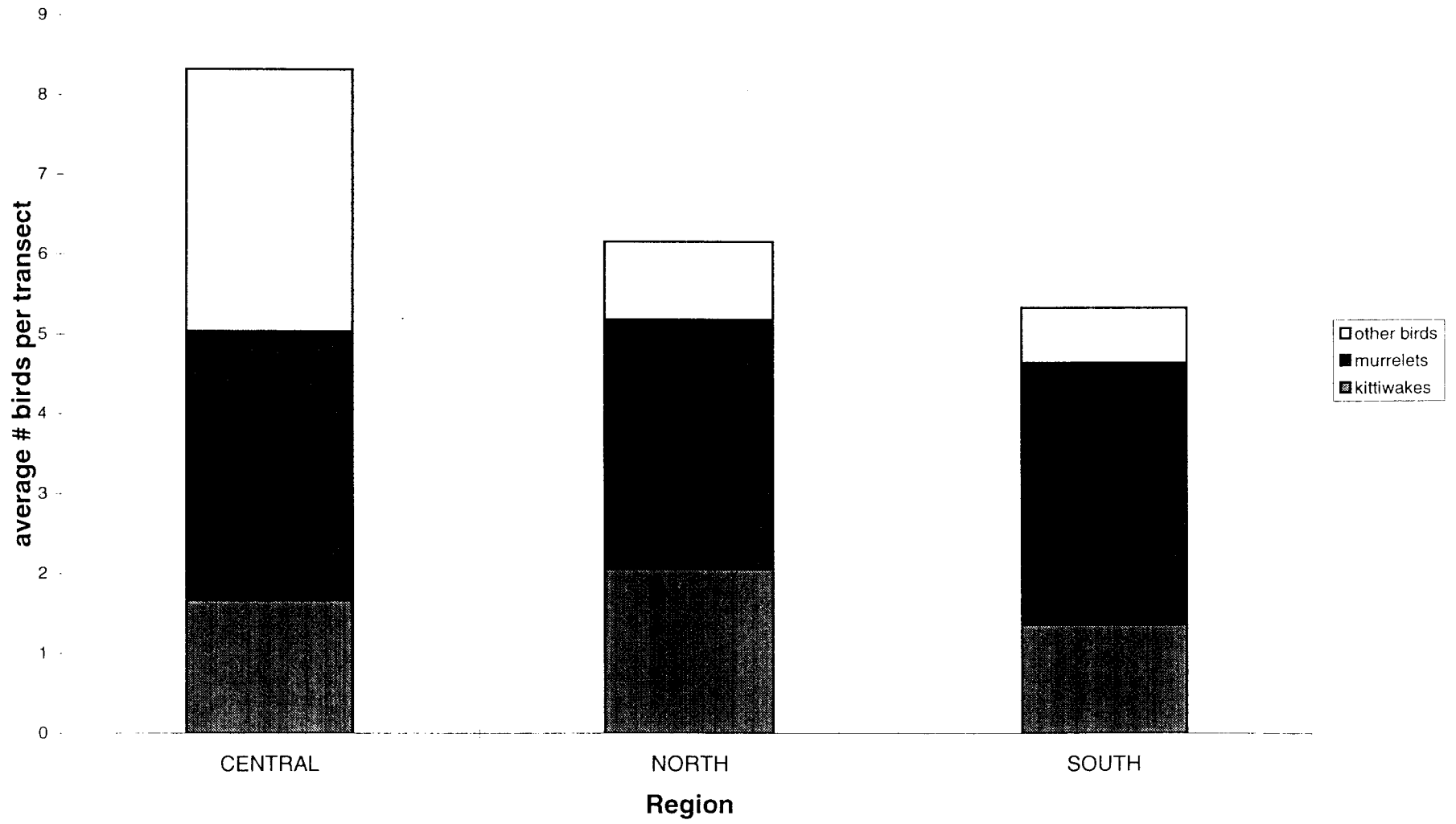


Figure V-4. Average numbers of all birds per 12-km nearshore block in the three study areas from July 1996.



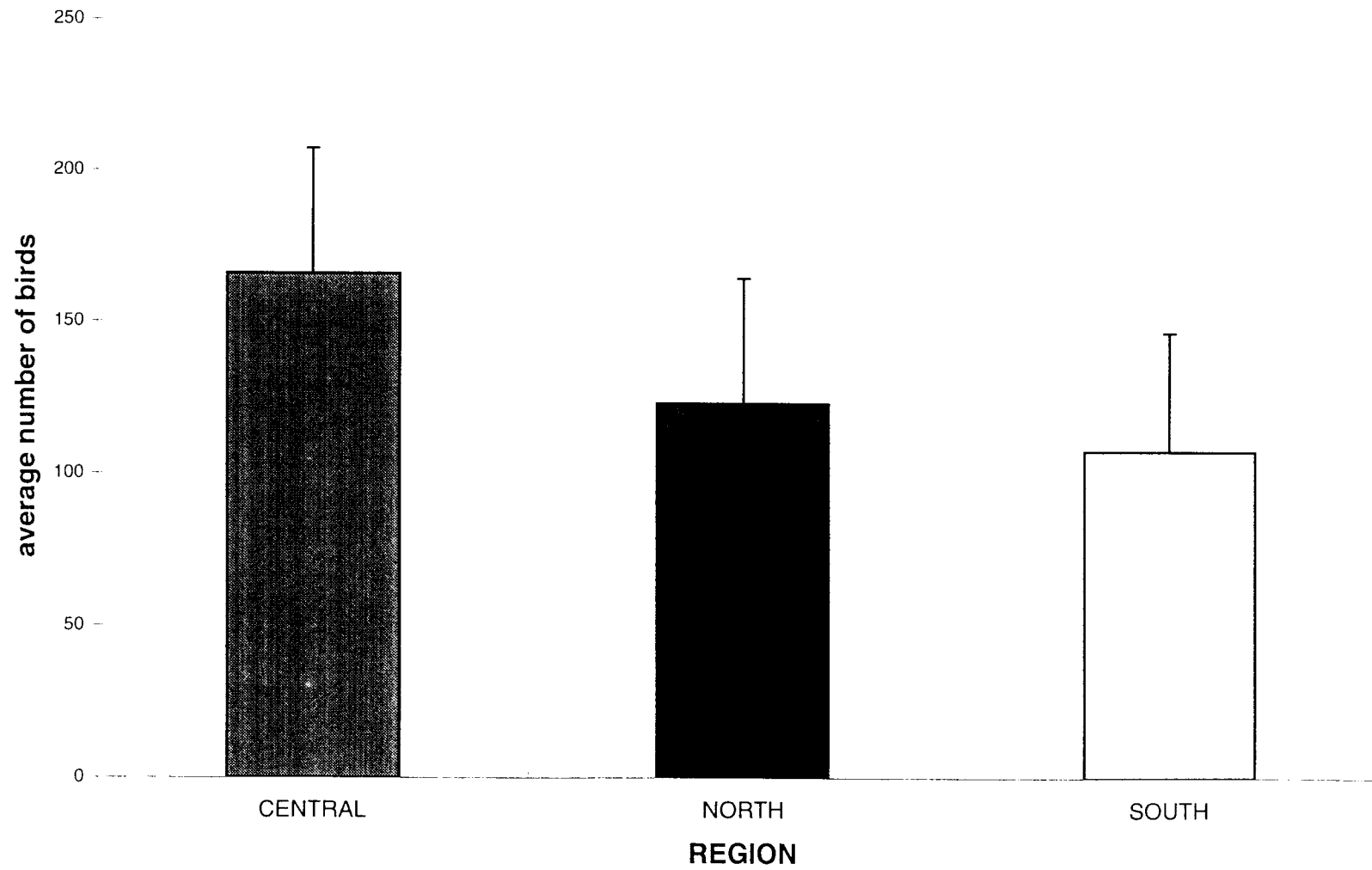


Figure V-5. Average numbers of black-legged kittiwakes, glaucous-winged gulls, and marbled murrelets per nearshore 12-km block in the three different study areas from July 1996.

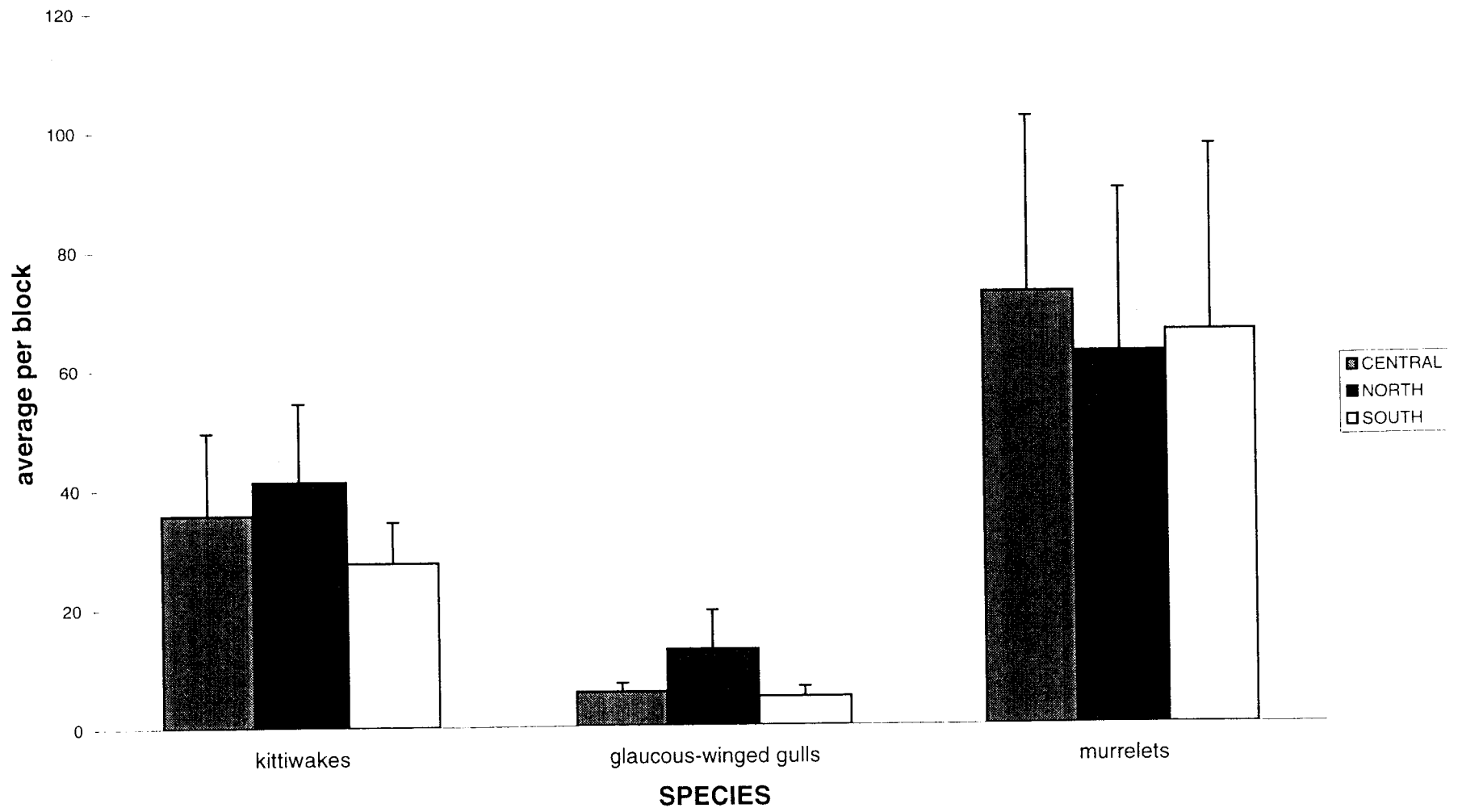


Figure V-6. Percent species composition of the nearshore study blocks in the three different areas from July 1996. See Table 1 for species codes.

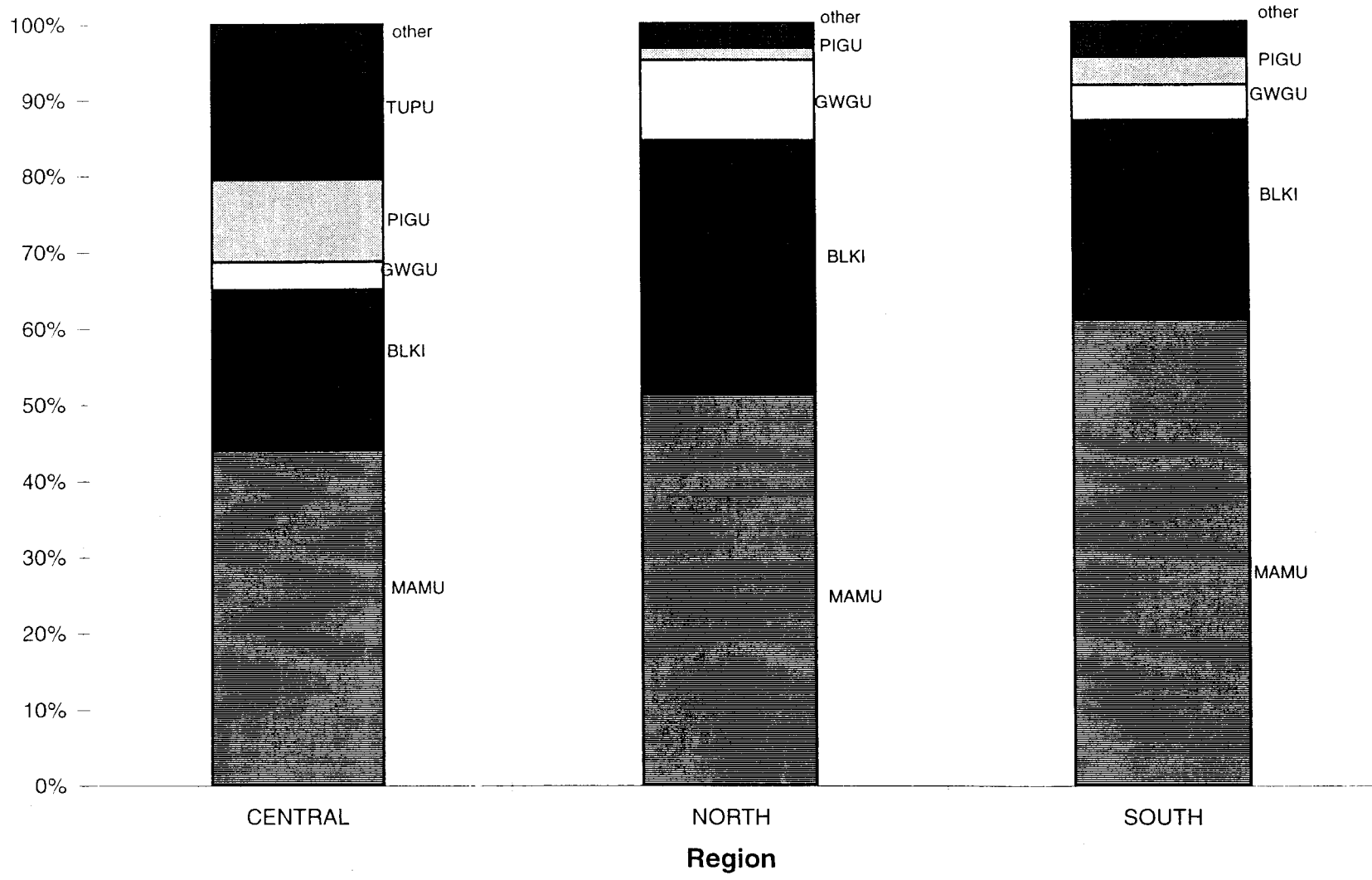


Figure V-7. Size distribution of flocks observed on nearshore transects during July 1996 forage fish cruise.

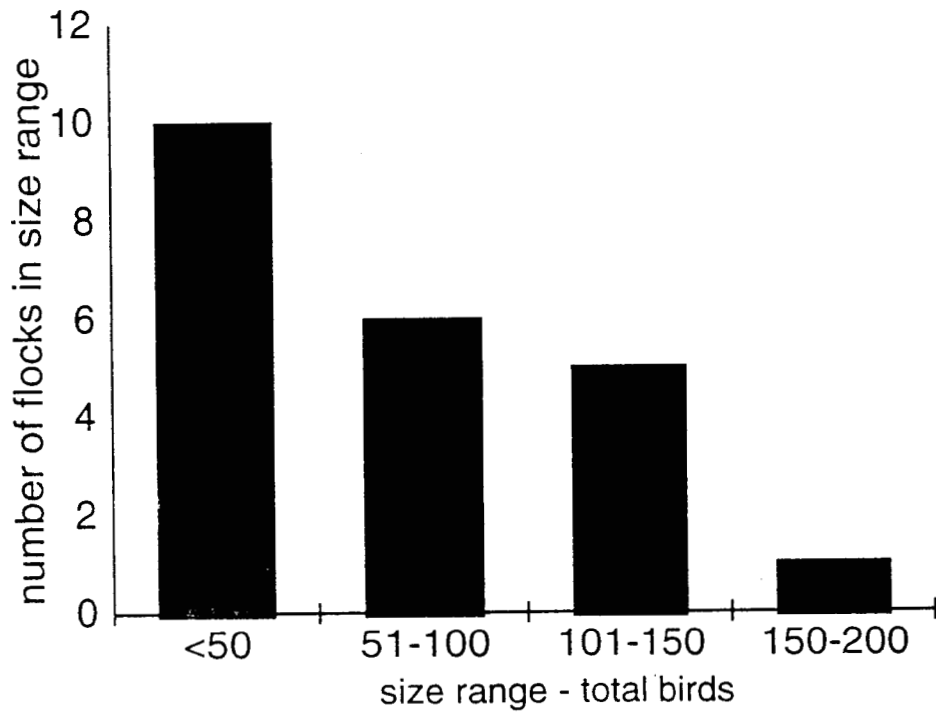


Figure V-8. Average number of birds (flock size) participating in feeding flocks in the three different study areas during July of 1996.

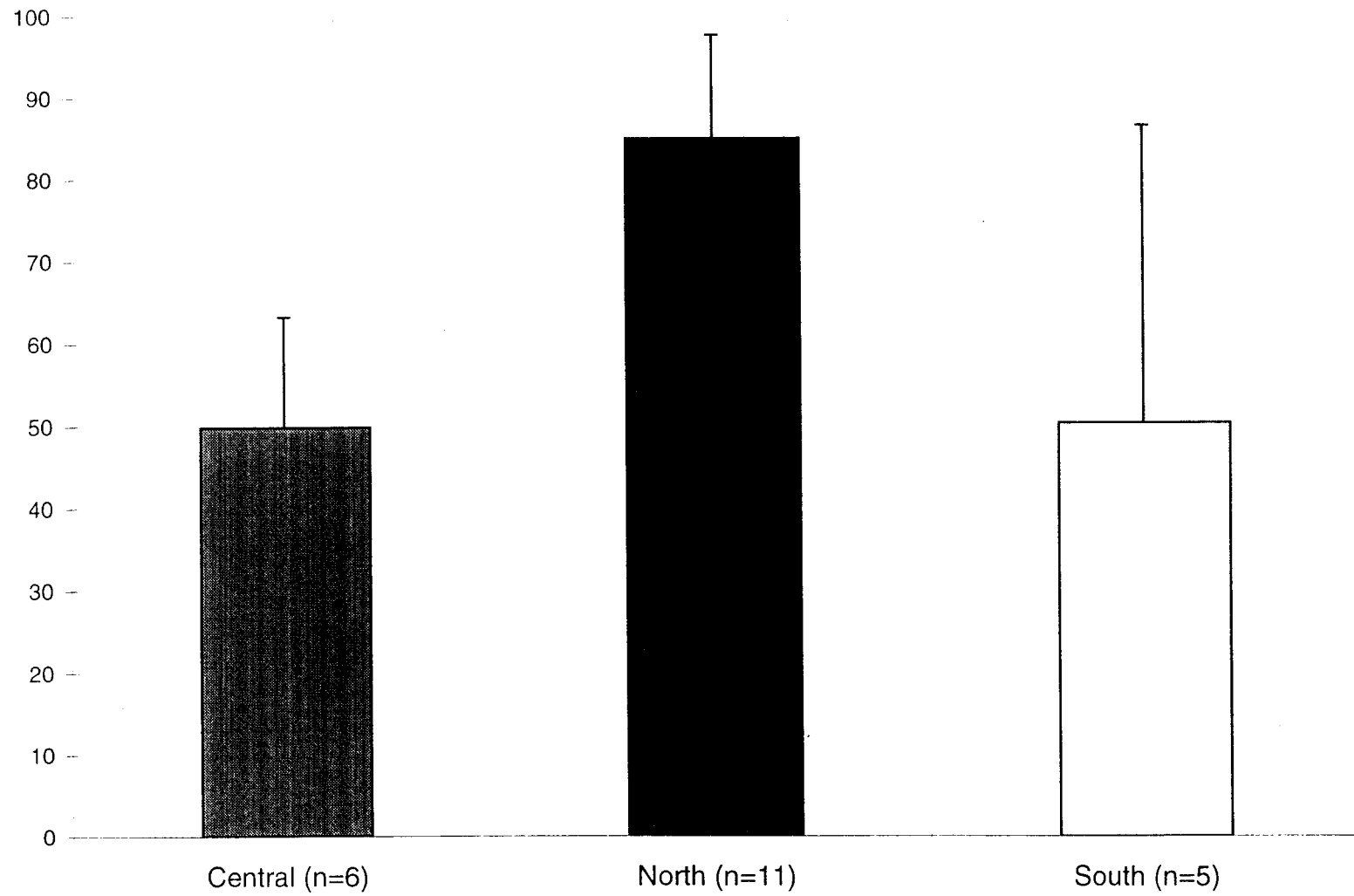


Figure V-9. Fish species being fed upon by flocking seabirds in the three different study areas during July of 1996.

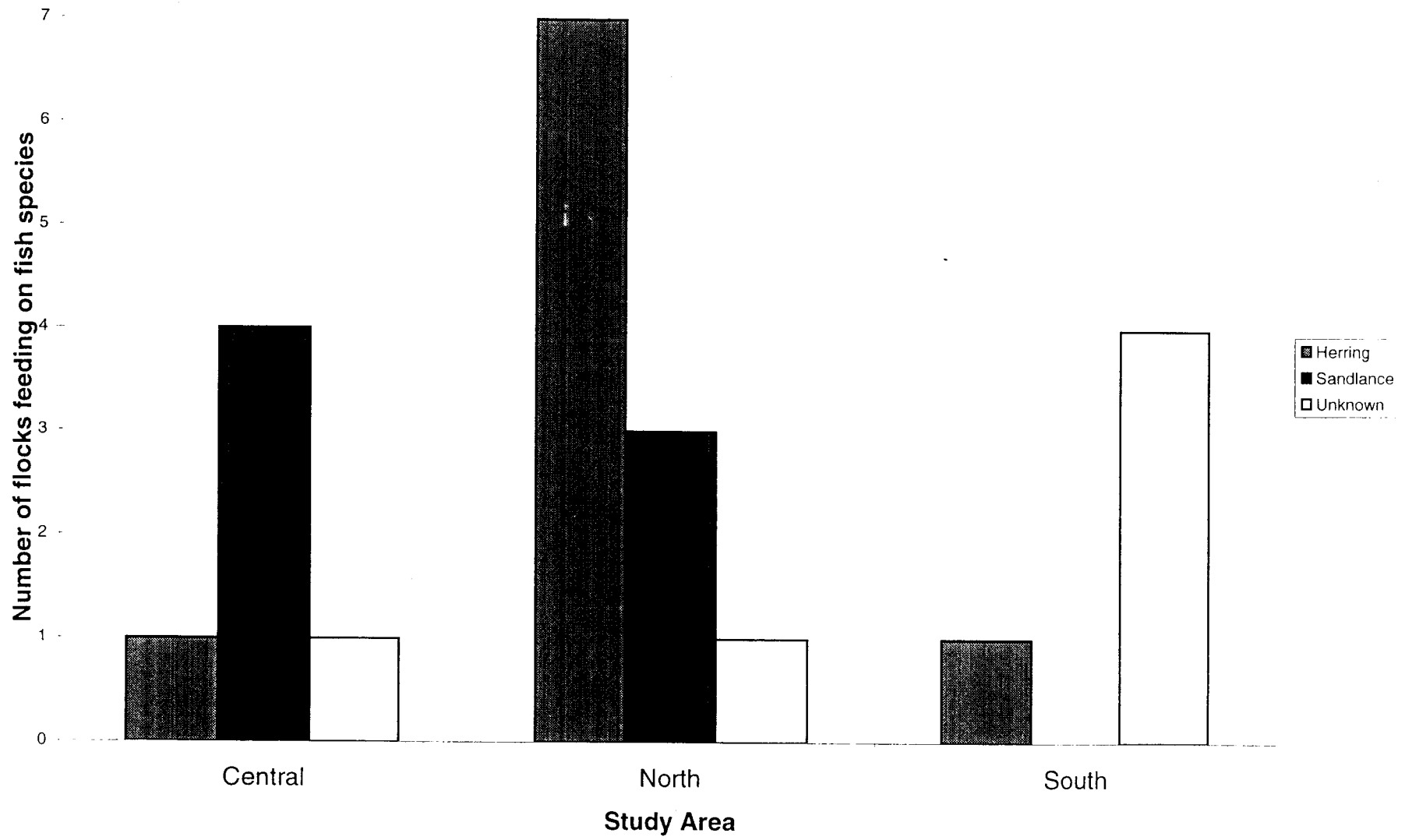


Figure V-10. Percent species composition of feeding flocks observed during 1995 and 1996. See Table 1 for species codes.

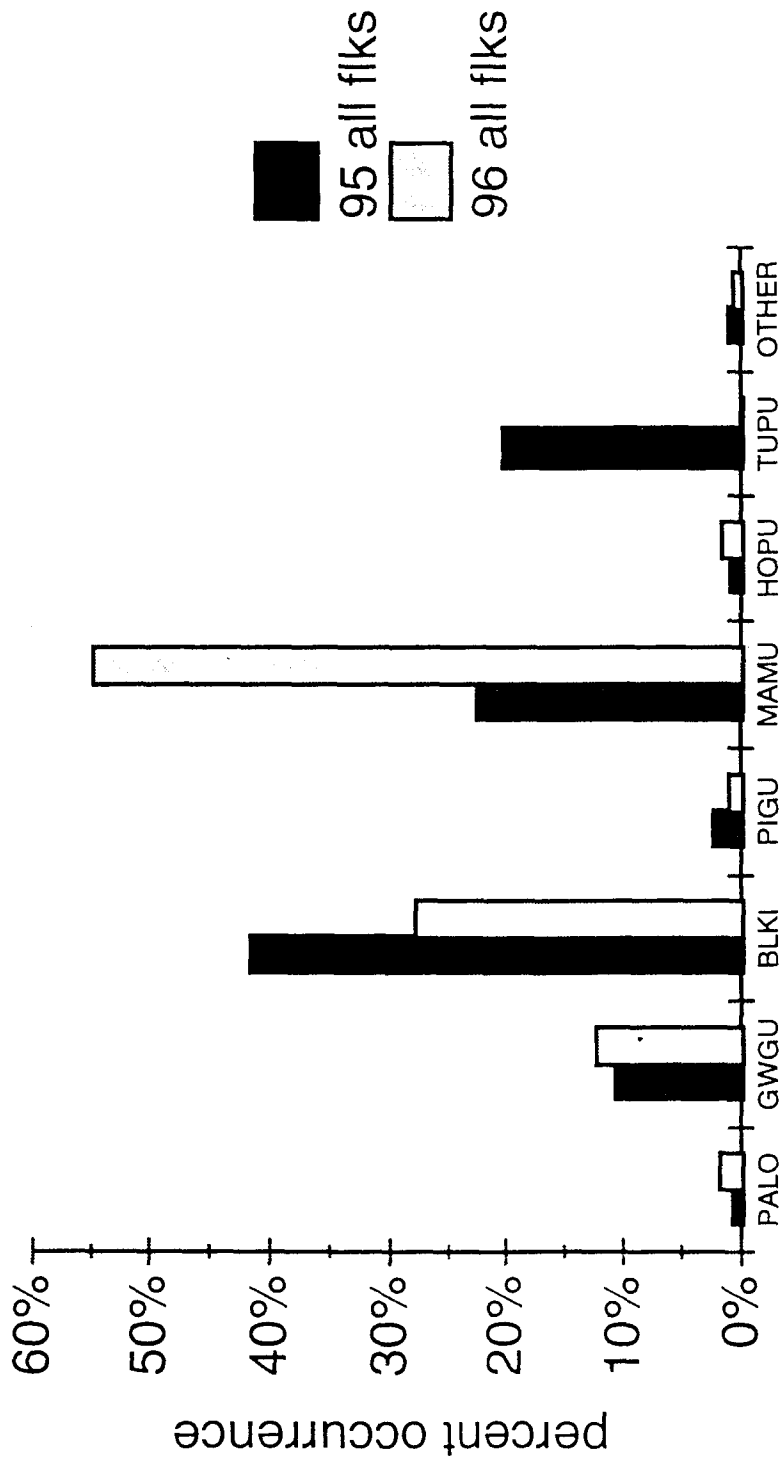


Figure V-11. Percent species composition of Type I flocks observed during 1995 and 1996. See Table 1 for species codes.

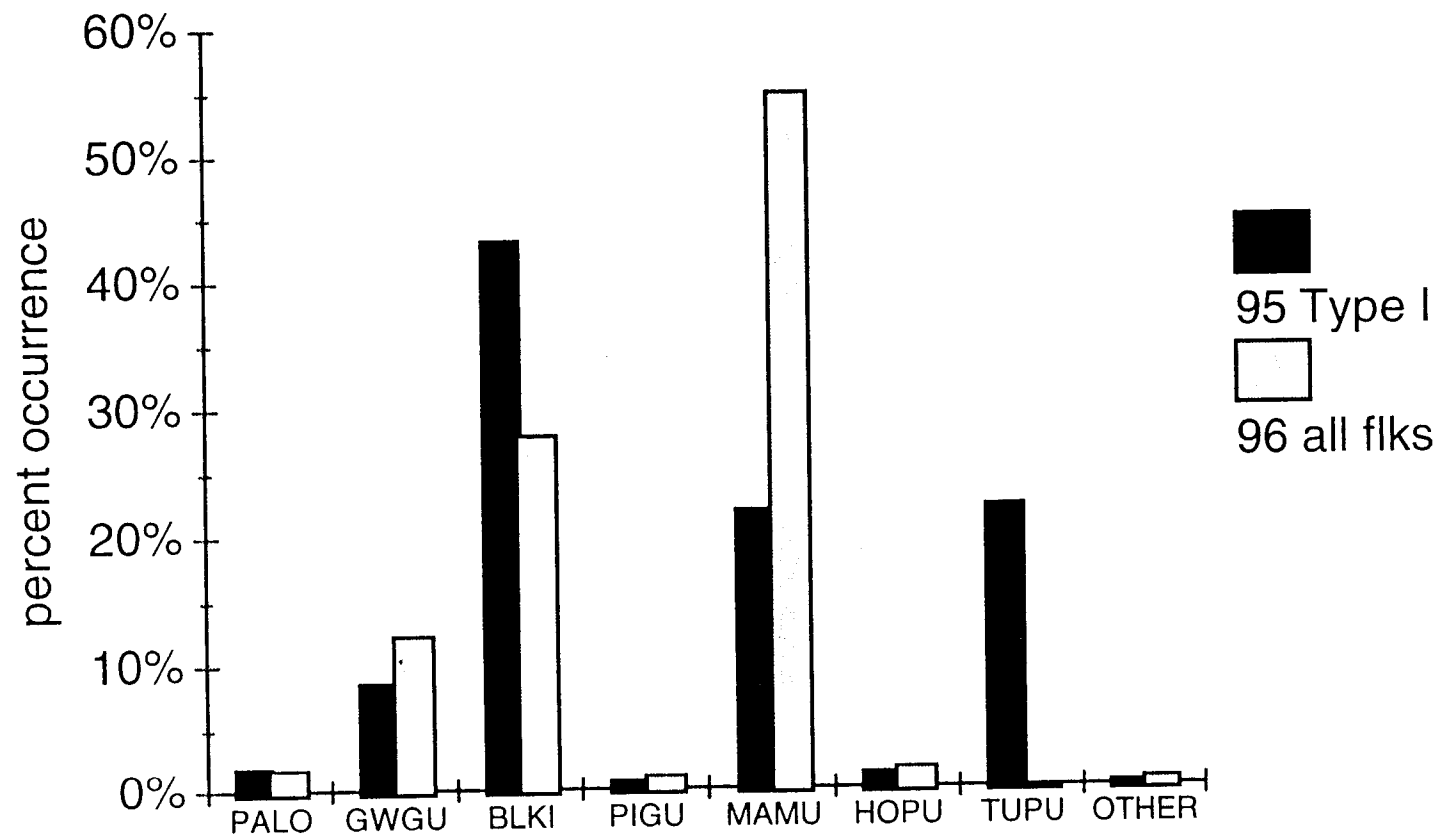


Figure V-12. Percentage of feeding methods observed by black-legged kittiwakes (BLKI) and glaucous-winged gulls (GWGU) during 1995 and 1996.

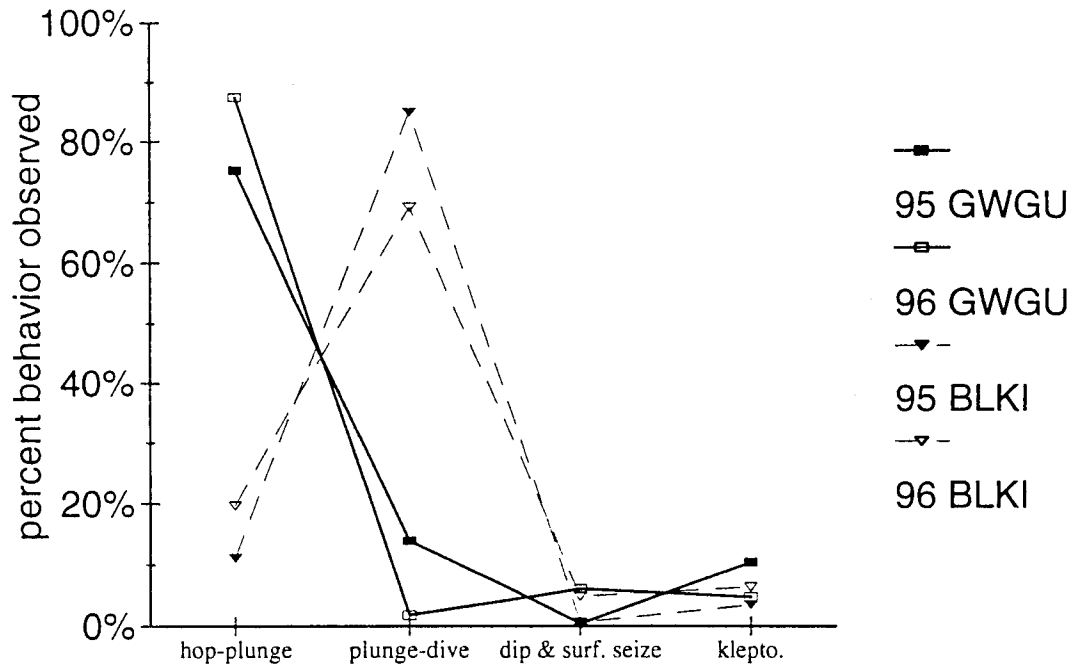


Figure V-13. Feeding success and losses for black-legged kittiwakes in 1995 and 1996.

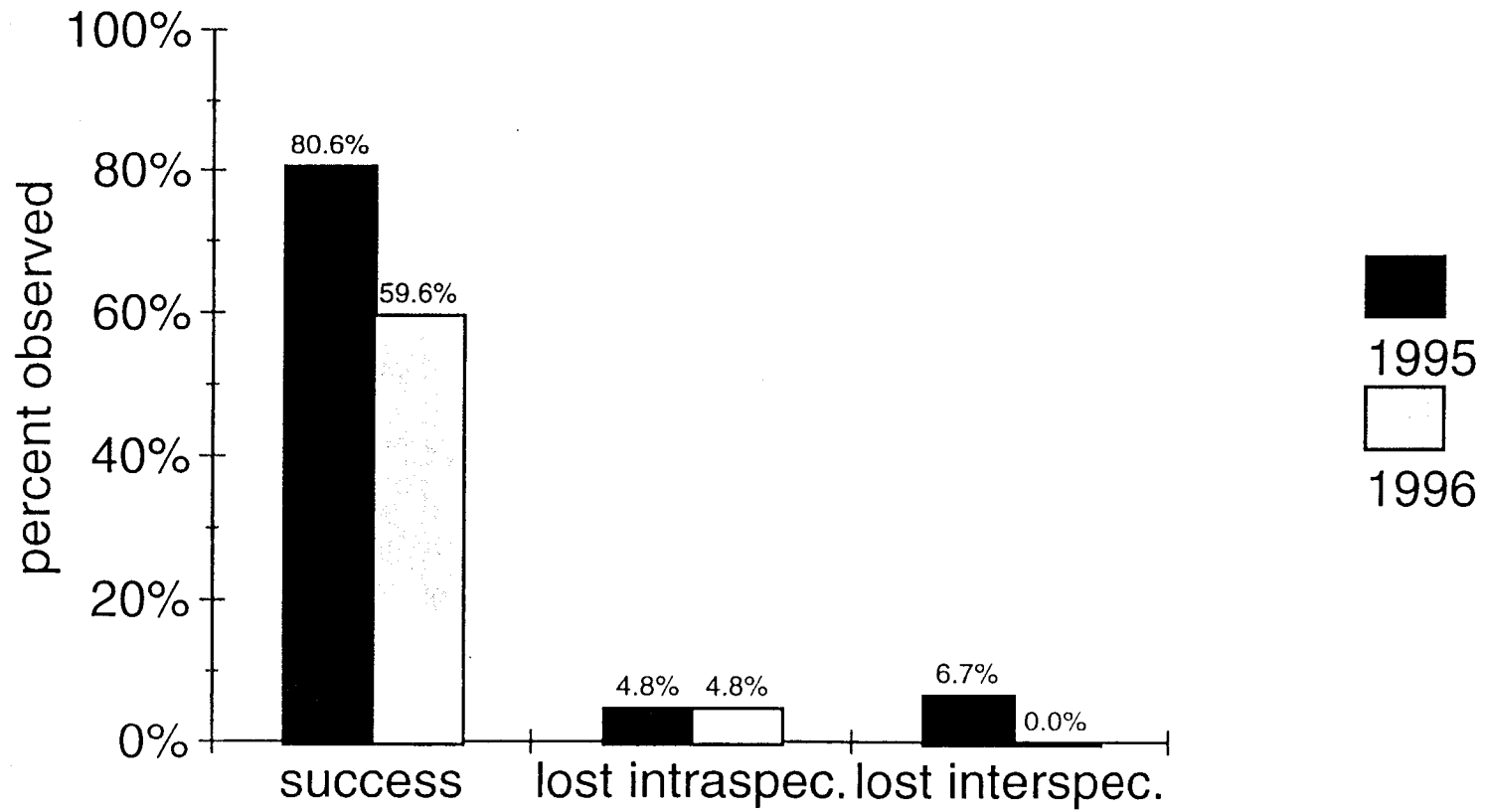


Figure V-14. Feeding success and losses for glaucous-winged gulls in 1995 and 1996.

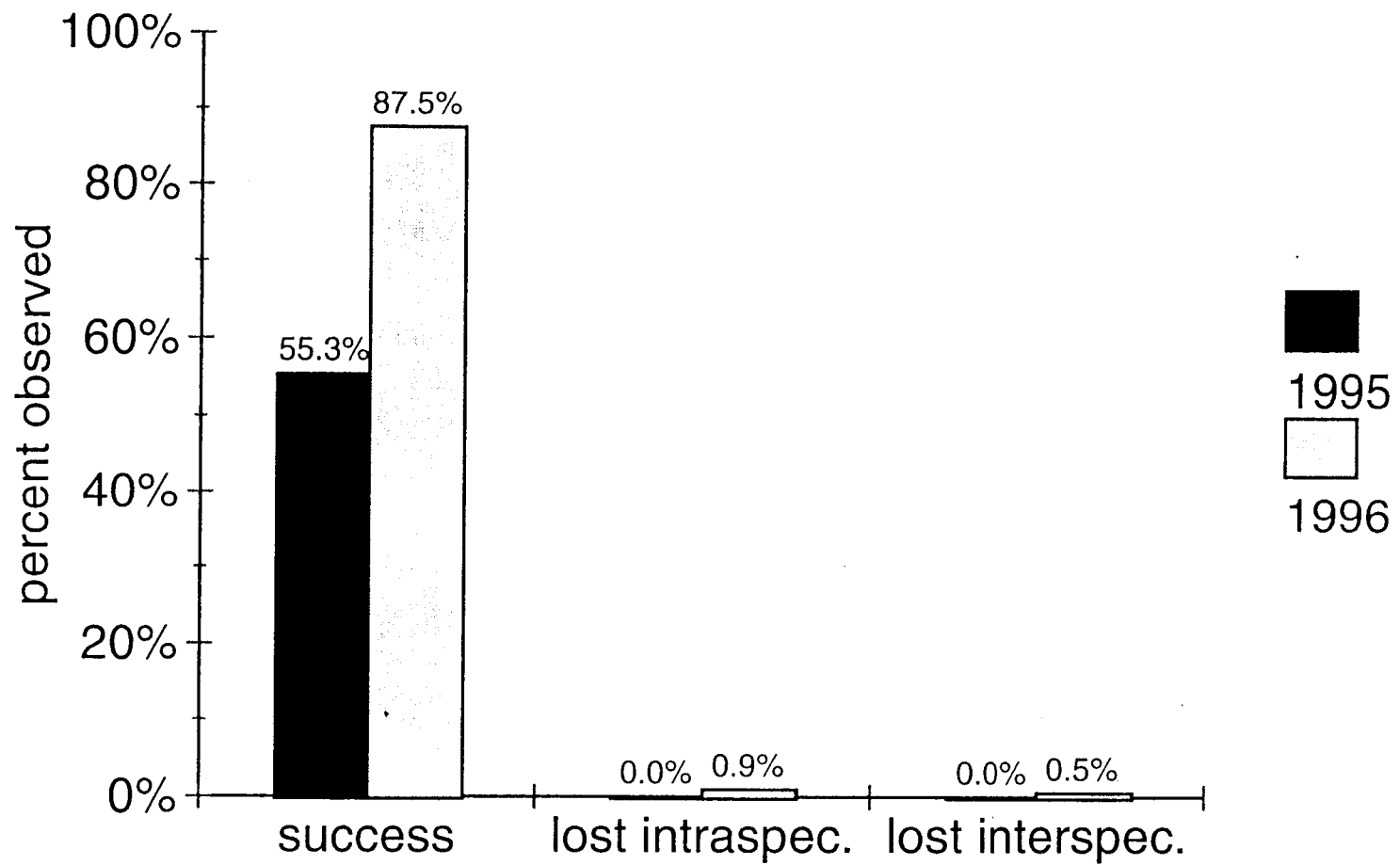


Figure V-15. Regression of the feeding rate of black-legged kittiwakes (BLKI) on glaucous-winged gull (GWGU) numbers at the flocks from July 1996.

$R^2 = 0.520$; $P = 0.022$

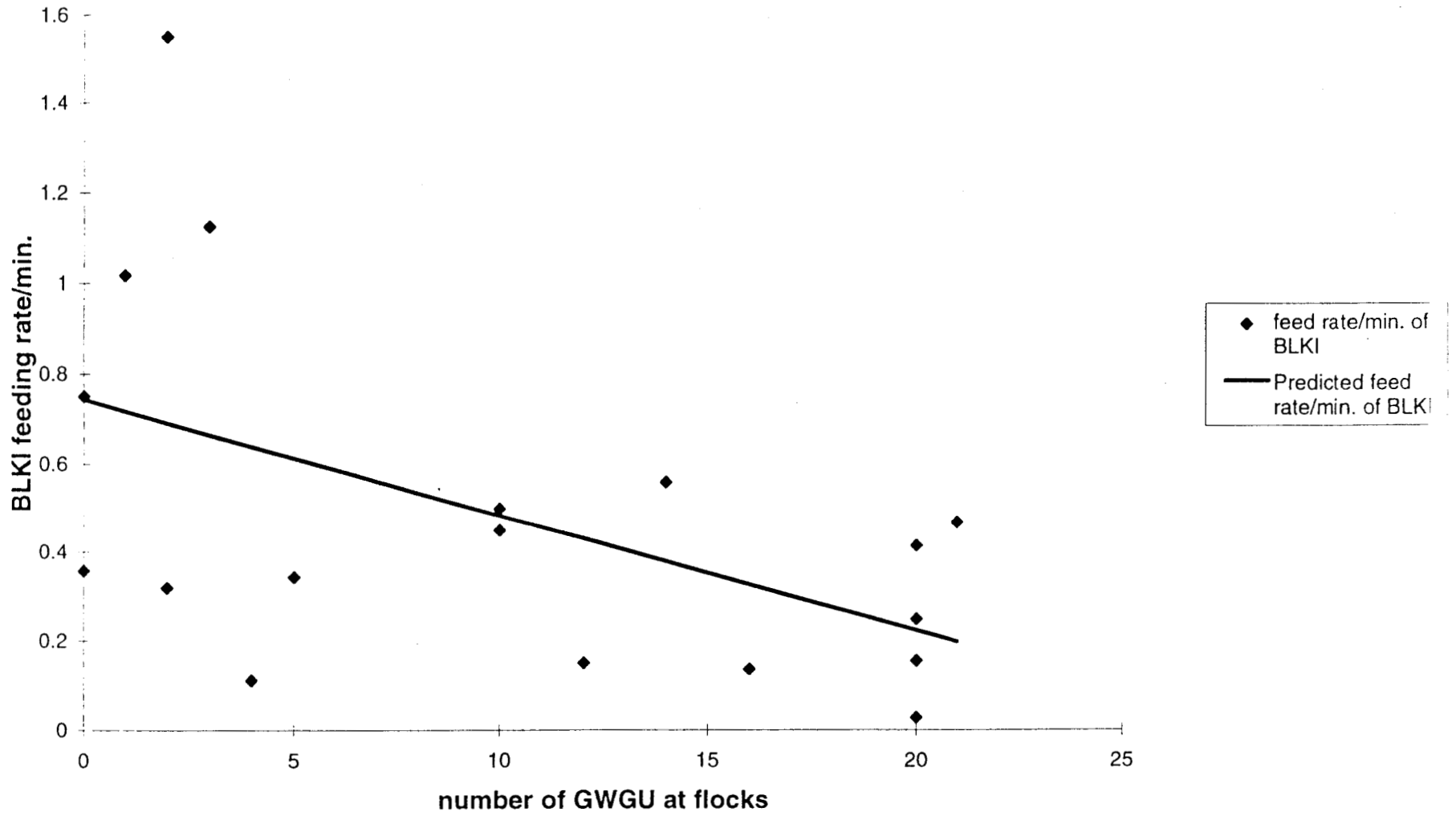
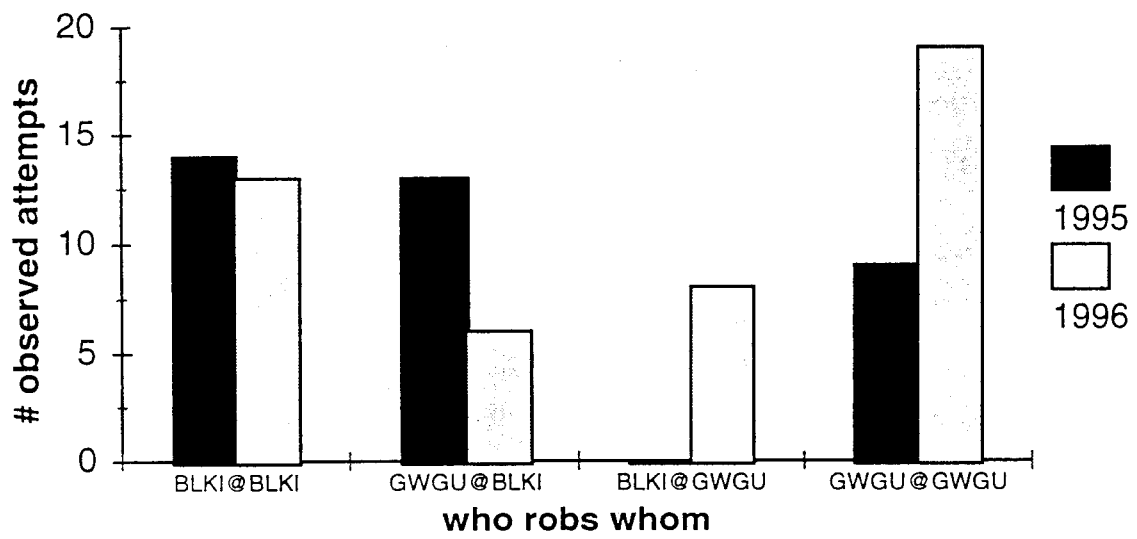


Figure V-16. Kleptoparasitism of kittiwakes (BLKI) and glaucous-winged gulls (GWGU) in 1995 and 1996.



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