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Restoration Project Annual Report

The Factors that Limit Seabird Recovery in the EVOS Study Area: A Modeling Approach

Restoration Project 98163Q
Annual Report

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

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Study History: The project effort was initiated in February 1997 as a new project. Field work has not been a direct component of this project, which relies on the data gathered by all other APEX projects as well as data in the literature. In a sense, many APEX principle investigators are part of Restoration Project 98163Q. By the nature of our work --- inter-relating the data gathered by other investigators in APEX --- we, generally, are at least one year behind the other APEX projects.

Abstract: We use mathematical models to assess the degree to which food supply could be affecting recovery of seabirds in the EVOS study area, indicate the mechanisms by which this could come about, and identify the scale at which interactions are occurring between food availability and the species and colonies being studied by APEX. In the first two years of effort we concentrated on acquiring and formatting data, and developing initial models to tie food supply to seabird demography; a significant relationship was detected for Black-legged Kittiwakes. We explored the feasibility of working with Pigeon Guillemots, as well, but the available data proved to be inadequate, although in the future this is likely to change. The models that we were successful in developing compared kittiwake foraging effort, using data gathered by APEX component B, G and E, and prey availability, from APEX component A and a SEA component. Best correspondence existed between kittiwake foraging and aerial spotting of fish schools. Logistic regression models indicated the temporal, physical and biological habitat features that brought closest correspondence between kittiwake foraging and fish availability. A foraging model linked kittiwake foraging behavior and effort to the density and distribution of prey schools.

Key Words: Black-legged Kittiwake, capelin, eulachon, *Exxon Valdez*, foraging behavior, foraging model, herring, prey availability, prey selection, sandlance, mathematical modeling.

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

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EXECUTIVE SUMMARY

We used mathematical models to assess ways in which food supply could be affecting recovery of seabirds in the EVOS study area. Thus, we addressed the main APEX (Alaska Predator Experiment) hypothesis that food supply is limiting recovery of certain avian populations from the *Exxon Valdez* oil spill. Data inputs comprised information from the field components of APEX supplemented with data published elsewhere. We confined our effort in 1998 to the Black-legged Kittiwake *Rissa tridactyla*, the species in Prince William Sound for which data were sufficient for analysis. We found that foraging activity was affected by food availability, as determined from fish school assessments (aerial spotting 1996, 1997, 1998). Herring *Clupea pallasi* and sandlance *Ammodytes hexapterus* schools were the most common prey over which kittiwakes foraged; capelin *Mallotus villosus* and eulachon *Thaleichthys pacificus* schools were much less common but appeared to be favored. The link between foraging and prey was affected by such factors as prey species, school density, year, time of day, tide state and distance from the colony, as well as other factors. A foraging model successfully linked kittiwake searching behavior to localities where the presence of prey schools was most predictable.

INTRODUCTION

The general hypothesis of the APEX project is that a change in the relative abundance of forage fish species has prevented recovery of injured avian populations in Prince William Sound; within this general hypothesis a series of 10 working hypotheses are being investigated by the various APEX components (see Duffy 1996, p. 6-7). The data being collected to test these hypotheses differ in temporal and spatial scale. Some additional data at the time scale of decades exist. However, most of the data are at much smaller scales than the general hypothesis, which is at the scale of decades (time for recovery in long-lived species) and at the spatial scale of the entire sound. Statistical inference can be used to bridge some but not the entire gap. We discussed how this task would be undertaken, in a conceptual way, in a previous Annual Report (Ainley et al. 1997). Our approach integrates the available information, bridges the gap from data to the hypothesis, and identifies variables that need to be linked. The model output allows avian recovery rates to be evaluated in relation to prey availability, using data and knowledge gathered for this ecosystem (Ford et al. 1998).

After exploring the data available to us, i.e. those from the 1996, 1997 and 1998 field seasons, it became clear that the formulation of our models would be most successful for the Black-legged Kittiwake *Rissa tridactyla* in Prince William Sound (PWS). We sought to relate the kittiwake data — reproductive success as well as foraging effort — to the availability of forage fish. We discussed preliminary findings in regard to prey availability, foraging behavior and breeding success previously (Ford et al. 1998). Here we report results from more intensive investigation between foraging behavior and prey availability.

OBJECTIVES

Hypotheses to be evaluated by mathematical modeling using existing data, under the null hypothesis:

1. Kittiwake foraging behavior and occurrence patterns in Prince William Sound can not be explained by the abundance and distribution of prey schools.

2. No differences in 1 will be evident in pre- and post-spill comparisons, where possible.

METHODS

Kittiwake Foraging Effort

We began with the foraging effort data compiled by APEX Project 163E (David Irons, Robert Suryan and Jeb Benson). Data were available for 1995-1998, for 3 kittiwake colonies: Icy Bay, Eleanor Is and Shoup Bay, but not for all years and all colonies. As fish availability data were not obtained in 1995 (see below), we did not consider the kittiwake data acquired for that year. Useable data were available for Eleanor and Icy in 1996, and all three in 1997 and 1998. The data were collected by following radio-tagged individuals in a boat; positions and behavior, as well as other data, were then recorded regularly. More details on data collection are contained in Irons (1992) and Irons et al. (1997). In the present report, we consider 1996 -1998 data. Data acquisition occurred from about 3 July through 10 August each year.

The data were provided to us in ASCII format. These were processed and loaded into CAMRIS by computing the rate of movement (km/hr) between each pair of sequential observations of kittiwakes and assigning that rate to the latitude/longitude midpoint of the pair. Points representing intervals of slow movement were overlaid on a map of Prince William Sound. Slow movement was considered to be foraging. We placed a 1 km grid over the sound and counted the number of slow-movement points occurring in each grid cell. A binary search procedure was then used to find the density isopleths that would contain 85%, 90% and 95% of these points. In other words, for example, the 90% isopleth contained the minimum area of 90% of the foraging activity. These regions were termed "foraging grounds" and were assumed to be equivalent to "patches" in the traditional sense of optimal foraging theory. Note that we could have used the actual foraging observations to define the foraging grounds and would have gotten similar results. Using the movement rates instead of the observations helped to compensate for areas where the kittiwakes search for food but actually find nothing on which to feed, and also allows us to compute the feeding rate, i.e. the number of feeding behaviors per unit time while in the patch. Using speed to define the patch and then using behavioral observations to define feeding rates avoids circularity.

Fish Abundance

We had found previously that fish schools spotted from the air correlated much more closely with kittiwakes than schools identified by hydroacoustics (Ford et al. 1998).

Therefore, we confined our subsequent effort to aerial spotting data, obtained by Evelyn Brown, working in the SEA program (until joining APEX in 1998). Flights were conducted at low level (200 m elevation) from 10 June to 11 August 1996-1998. Length of survey tracks in 1996, 1997, and 1998 were 6,729; 7,358; and 21,256 km, respectively, for a total on 35,343 km (Figure 1). All shorelines in the Sound were over-flown, as we had determined earlier that kittiwakes rarely forage in deep waters (see also Ostrand and Flint 1995, Ostrand and Maniscalco 1996). This was at least one of the reasons we found little correspondence between kittiwakes and hydroacoustic data (collected in deeper water owing to logistical constraints).

Fish schools were spotted and identified from the air, and each school was measured to determine major and minor axis lengths using a calibrated cylinder. The product of the axis lengths provided an index of school size. However, a preliminary analysis found no relationship of kittiwake occurrence to the size of schools. Forage fish were identified as herring *Clupea harengus*, capelin *Mallotus vilosus*, sandlance *Ammodytes hexapterus*, eulachon *Thaleichthys pacificus*, salmon *Onchorhyncus* spp., walleye pollock *Theragra chalcogramma*, or unidentified forage fish. Some ground truthing of schools was conducted, but results (positive) are not reported on herein. Besides fish schools also recorded were number of Black-legged Kittiwakes, Humpback Whales *Megaptera novaeangliae*, Glaucous-winged Gulls *Larus glaucescens* and unidentified gulls. For each sighting of a bird, the following behaviors were recorded: 1) resting on shore, 2) flying in a steady direction (traveling), 3) resting on the water, 4) milling, or 5) actively feeding (plunging, dipping).

Data collected during aerial transects were logged directly into a laptop computer using dLOG software (Ford, 1997). A GPS unit was linked to the computer so that geographic position was recorded at 5 second intervals or whenever the observer entered an observation. The resultant ASCII files were checked for accuracy and transmitted to us for post processing.

Kittiwake Foraging Grounds Versus Fish Abundance.

We determined the minimum spatial scale in which we could see relationships between kittiwake foraging behaviors and fish school density. In a preliminary analysis, we found that foraging bird occurrence patterns were related only to herring, sandlance, eulachon and capelin. Therefore, in all further analyses we confine our efforts only to these forage fish species. We found that strong statistical relationships resulted when data were binned into blocks 1.5 nm (2.8 km) on a side (= 7.7 km^2). These we called survey blocks.

Regression Analyses

We used forward and backward step-wise multiple regression analyses (CRC 1995) to model density of feeding kittiwakes (the dependent variable) in relation to physical, temporal (year and date), and biological variables (Table 1). The sample unit for these analyses was one survey block sampled on a particular day. All independent variables were analyzed as continuous except tide phase and year, analyzed as categorical.

Variables — For each block for each day we assigned values for ocean depth, distance to shore, and an index of distance to kittiwake colonies weighted by colony size.

Initially, we grouped all the colonies in Prince William Sound into 7 colony clusters (Figure 2). The clusters were defined by spatial proximity, overlap in foraging area (Suryan et al. Ms), and observations that in some years certain colonies changed in size but in a direction that was reciprocal to that of colonies in the immediate area (R. Suryan pers. comm.). Therefore, some sort of "meta-colony" is included in each cluster. We then determined the coordinates for the mid-point for these clusters (Figure 2). For a given block, colony index was the sum of values ($n = 7$) for the distance between clusters divided by the number of kittiwakes composing that cluster.

The counts of kittiwakes and schools of herring, sandlance, eulachon, and capelin were summed for each survey block. We calculated "densities" per block for each species as the number of birds or schools divided by the *length* of survey transects per block per day. In this way, we corrected for survey effort block by block. Transect lengths per survey block/day averaged 3.47 km, SD = 2.71 (range = 0.01 - 35.98 km; n = 10,181 blocks/day). Tide stage at the time of survey for each block was grouped into three phases: ebb, slack, and flood, as 1, 2, and 3, respectively.

We grouped the kittiwake behaviors including resting on the water, milling, and actively feeding as representing "feeding" birds (birds that were sitting on shore or flying in a steady direction were excluded). We included birds resting on the water under the feeding category because satiated birds often rest on the water just after feeding, and therefore usually represent feeding activity in the area.

Analyses — We log-transformed density to satisfy assumptions of normality (Skewness/Kurtosis Test for Normality of residuals, $P > 0.05$). Because densities included values of zero, transformations were calculated as the log (density $\pm$ 0.05; 0.056 was the lowest density > 0). All regressions were of the log-transformed counts, and to facility presentation of data in graphs we used the log of bird density per 100 km (i.e., density was multiplied by 100 prior to log-transformation). Normality was not achieved, but least-squares regression analyses are considered to be very robust with respect to non-normality (Seber 1977, Kleinbaum et al. 1988). Although regression analyses yield the Best Linear Unbiased Estimator relating density to independent variables, even in the absence of normally distributed residuals, P-values at the lower levels of significance must be regarded with caution (Seber 1977). Therefore, to reduce the chances of Type I error we assumed significance at $P \leq 0.02$.

Second- and third-order polynomials as well as all possible interactions were tested for and between independent variables. We also used one-way ANOVAs, followed by Sidak multiple comparison tests (an improved Bonferroni test [SAS Institute, Inc. 1985]), to statistically compare each habitat variable among years and tide phases. Unless noted otherwise, variance is reported as the standard error.

All variables except 'tide phase' and 'year' (analyzed as categorical [= cat.] in the model reported) were analyzed as continuous. Main effects were calculated before interaction terms were introduced into the model. The terms 'tide phase' and 'Julian date' were included in the model as main effects when testing interaction relationships.

FORAGING BY BLACK-LEGGED KITTIWAKES IN PRINCE WILLIAM SOUND, ALASKA: I, PHYSICAL, TEMPORAL AND BIOLOGICAL FACTORS AFFECTING TEMPORAL AND SPATIAL VARIATION IN FORAGING DENSITY

RESULTS

The regression analyses are based on counts of 59,101 Black-legged Kittiwakes, 176 Glaucous-winged Gulls, and 75 Humpback Whales; 3,379, 2,481, 54, and 48 schools of herring, sandlance, eulachon, and capelin, respectively. We found no negative or positive relationships of kittiwakes to either whales or to gulls. The latter will not be considered further.

Abundance of Prey Species

Overall, herring schools were significantly more abundant than those of sandlance (0.096 ± 0.0033 and 0.070 ± 0.0037 schools km^{-1}, respectively, $n = 10{,}181$ survey segments), a difference that was highly significant (Sidak tests, $P < 0.0001$; Figure 3). Abundance of eulachon and capelin schools was significantly lower than that of herring and sandlance ($0.0015 \pm .0006$ and 0.0014 ± 0.0005 schools km^{-1}, respectively, $P < 0.0001$), being about 65 and 45 times lower than that of the former two species, respectively. Abundance of eulachon and capelin did not differ significantly ($P = 0.9$).

Sandlance abundance was higher, and herring abundance lower, in 1996 compared to 1997 and 1998 (Figure 3; Sidak tests, both $P < 0.0001$). Abundance of both species differed insignificantly between 1997 and 1998 (both $P > 0.3$). Abundance of eulachon and capelin differed insignificantly between the three years (all $P > 0.1$).

Within a year, the abundance of herring, eulachon and capelin decreased with Julian date (Table 2, Figure 4). In the case of herring, the relationship was quadratic because the decrease leveled off after 10 July. Sandlance, on the other hand, increased over time, peaking 20-30 July, and decreasing slightly thereafter.

Temporal, Spatial and Biological Variables: Main Effects

The regression model, including all significant main effects and interactions, explained 18.8% of the variance in log-transformed abundance of feeding kittiwakes during the three years (Table 1; $F[50,10130] = 48.77$). Each of the terms, including ocean depth, distance from shore, colony distance index; and counts of herring, sandlance, eulachon, and capelin schools, had significant linear relationships with kittiwake density (Figures 4, 5). Although Julian date and tidal phase were not significant as main effects, they were retained in the model because they had significant interactions with other independent terms (see below). Thus, few of the covariates were rejected from the final model.

Kittiwake density increased with year (see Table 1: continuous effect; Figure 5) and with number of schools of herring, sandlance, eulachon, and capelin (Figure 6). Kittiwake density decreased with ocean depth, distance from shore, and colony distance index (Figure 5). Kittiwake density also was related to number of herring, sandlance, and capelin schools in a curvilinear (quadratic) fashion (Table 1). These latter effects were due to a steep increase in kittiwake density from blocks having zero fish schools to those having one fish school, followed by leveling or slight decline in blocks having more than one school (Figure 6).

Temporal and Spatial Variables: Interactions

Five interactions existed between temporal and/or spatial variables and their relationship with kittiwake density (Table 1, Figure 7). These interactions included those of year with Julian date, distance from shore, colony distance index, and tide phase; and an interaction between Julian date and tide phase. There were no interactions between ocean depth and other covariates.

First, densities of feeding kittiwakes were highest early in the study period during 1996 and 1998, and highest late in the period during 1997. Statistically, an interaction between year and Julian date affected kittiwake density positively in 1997, compared to significant negative relationships in 1996 and 1998 (all $P < 0.0001$).

Second, the tendency for kittiwakes to feed closer to shore increased with year. That is, the interaction between year and distance from shore became increasingly negative from 1996 to 1998 ($P < 0.0001$).

Third, assuming that colony sizes did not vary much (which was true), density of feeding kittiwakes increased with increase in distance from the colony, but varied by year. The interaction between kittiwake density and the distance index were significantly negative in both 1997 and 1998, compared to a significant positive relationship in 1996.

Fourth, the relationship of feeding densities relative to tide phase changed by year. There was a significant association between feeding kittiwakes and flood tides (i.e., a positive relationship; see Methods for numerical coding of tide phase) during 1996, a significant association with ebb tides in 1997, and lack of an association with any tide phase in 1998.

Finally, there was a curvilinear interaction between Julian date and tidal phase. Feeding kittiwakes were associated with ebb tides during late-June and July (i.e., a negative relationship), followed by a significant relationship with flood tides during early August. The relationship was quadratic.

Biological Variables: Interactions

No interactions between pairs of fish species affected the density of foraging kittiwakes (Table 1). That is, the relationship between kittiwake density and a given species of fish was not dependent on the presence or absence of another fish species. On the other hand, spatial or temporal variables affected the density of kittiwakes foraging over herring (3 interactions), sandlance (4), and eulachon (3). These interactions are as follows, by fish species:

Pacific herring — Year, distance from shore, and tide phase interacted with the density of herring schools to affect kittiwake density (Table 1). First, in regard to year, a more positive association existed between feeding kittiwakes and herring abundance in 1997 compared to 1996 and 1998 (all three relationships significant, $P < 0.01$, Figure 8. Thus, the strength of the relationship between feeding kittiwakes and herring abundance did not track the annual abundance of herring, the schools of which were far more prevalent in 1996 than in the next two years (cf. Figure 2).

Second, the density of foraging kittiwakes and of herring schools increased with distance from shore (Figure 8). Only the relationship at 250 m from shore (the nearest category) was insignificant. Recall, however, that density of foraging kittiwakes and forage-fish schools showed no relationships farther from shore (at least as determined from hydroacoustic data). Thus, the category '>2000 m' (see Figure 8) does not extend indefinitely to greater and greater distances. Rather, it is near to the limit of kittiwake and fish school associations.

Third, a positive relationship existed between kittiwake density and herring abundance at each tide phase ($P < 0.0001$). The most positive association occurred between kittiwakes and herring schools during flood tides, and the least positive relationship occurred during slack tide (Figure 8).

Sandlance — The same variables as for herring, with the addition of date, interacted with the density of sandlance schools to affect density of foraging kittiwakes (Table 1). First, in regard to year, sandlance abundance and density of feeding kittiwakes were positively associated in both 1997 and 1998, but not so in 1998 (Figure 9). Thus, the strength of the relationship between feeding kittiwakes and sandlance abundance tracked the annual abundance of this species in the study area (cf. Figure 2).

Second, within a year, the association between densities of feeding kittiwakes and sandlance schools declined with date (Figure 9). Regardless, the association with date was significant for each of the five date categories (all $P < 0.01$).

Third, the interaction between density of foraging kittiwakes and sandlance schools as a function of distance from shore was similar to that shown for herring: higher densities of both with greater distance (Figure 9). The positive relationship between densities of feeding kittiwakes and sandlance school abundance was significant at each of the five distance categories except 750 m.

Finally, as with herring, kittiwake and sandlance density exhibited a strong association at flood tides compared to ebb tides, but also such an association at slack tide (Figure 9). Unlike herring, a strong association existed at slack tides, too. Overall, there was a significant positive relationship between density of feeding kittiwakes during each of the three tide phases (all $P < 0.02$).

Eulachon — Three environmental variables had significant interactions with kittiwake and eulachon associations. First, as with herring and sandlance, distance from shore and tide phase were important, but also important was distance from colony (Table 1). In regard to distance from shore, the relationship was the same as for the other two prey species (Figure 10). The relationship was significant only at distances of 1,250 and, especially, at distances > 2,000 m from shore.

Second, the interaction between eulachon and kittiwake density with tide phase was similar to that shown by sandlance. The interaction reflected a highly significant relationship at flood tides ($P < 0.0001$), a slightly less significant association during slack tides ($P < 0.01$), and no relationship during ebb tides ($P = 0.8$; Figure 10).

Finally, the strength of the association between densities of foraging kittiwakes and eulachon abundance increased with distance from the colony (Figure 10). The relationship was quadratic because the relationship between kittiwakes and eulachon was insignificant at indices of 225 to 325 (no eulachon schools were seen at the colony index of 375), compared to the highly significant relationship recorded at indices > 400.

Prey Species Preference by Kittiwakes

Densities of feeding kittiwakes, to a highly significant degree, were greater when associated with eulachon and capelin than when associated with herring and sandlance (Sidak tests, both $P < 0.0001$, Figure 11). Densities of feeding kittiwakes associated with herring schools did not differ significantly from those associated with sandlance ($P > 0.1$): and densities of kittiwakes feeding on eulachon did not differ from those feeding on capelin ($P > 0.5$).

Densities of feeding kittiwakes increased significantly, in increasing order, when schools of herring, sandlance, capelin, and eulachon were present (see above, Main effects). Thus, although kittiwakes were seen in association with herring and sandlance schools greater than 40 and 20 times more often, respectively, than with schools of eulachon and capelin, densities of feeding kittiwakes were much greater when associated with eulachon and capelin. Therefore, although herring and sandlance contributed more to the diet, kittiwakes may prefer eulachon and capelin when available.

DISCUSSION

A large number of factors contributed to the explanation of where and when kittiwakes foraged in Prince William Sound during the summers of 1996-1998. The regression model explained 18.8% of the variance, which is not a remarkable value, but a substantial one considering that in single-year models (1996, 1997 or 1998, alone) the variance explained increased to as high as 40%. In other words, when year was added as a variable it became a surrogate for many other mostly unknown factors that affect kittiwake foraging and, of course, were not measured in our study.

In the case of most, but not all, significant variables, the relationship between kittiwake occurrence and that of fish schools is understandable in the context of current knowledge. Here we will review these relationships.

Differences in composition of the diet fed to kittiwake chicks at Shoup Bay and Eleanor Island colonies in 1996 and 1997 (Suryan et al. Ms; 1998 data not yet available), both sites being within our study area, were consistent with variation in prevalence of fish schools. The latter was assessed (and reported herein) also during the chick-feeding period. For instance, our results showed herring schools to be more prevalent in the study area in 1996 than in 1997, and sandlance schools to be more prevalent in 1997 than 1996. Accordingly, herring were more prevalent in the kittiwake diet in 1996 than 1997, and vice versa for sandlance. Similarly, eulachon schools were much more prevalent in the Sound in 1997 compared to 1996, and eulachon were evident in the diet at Eleanor Island in 1997, but not 1996. Thus, variation in diet reflected variation in prey availability to a substantial degree.

What was not supported by our study was a reflection of diet composition relative to the abundance of one fish species relative to others. In other words, our results showed herring schools to be about twice as abundant as sandlance schools, which was borne out in the diet only at Shoup Bay in 1996. In that year, herring contributed 60% and sandlance 30% to overall diet (Suryan et al. Ms). On the other hand, at Shoup Bay in 1997 and at Eleanor Island in both years, sandlance was more prevalent in the diet by 20-50% compared to herring. The elevated importance of herring to Shoup Bay parents in 1996 may have been related to the greater availability that year of age class 1+ herring; or, at least, those were the fish that dominated diets in 1996 (but not 1997). Older herring are much more energy-rich compared to the age 0 herring taken in 1997 (Anthony et al. 1998). This pattern was not perfect, however, because at Eleanor the age composition of herring fed to chicks showed the same pattern, but sandlance nevertheless were the more commonly taken prey (Suryan et al. Ms). That is, sandlance were taken over age 1+ herring.

Our data did show an actual preference of kittiwakes for capelin and, especially, eulachon, if the density of kittiwakes foraging over schools of these species, versus those of other prey species, is an indication. Not surprising, the energy density of eulachon is double that of the other forage fish (Anthony et al. 1998). Eulachon, therefore, appear to be a much-sought prey. Why kittiwakes would select capelin over herring and sandlance is not readily clear on the basis of our data. Capelin, sandlance and, to a lesser extent, herring were much more available during the early summer. Capelin, too, captured early in the summer would be much more valuable energetically than herring or sandlance (Anthony et al. 1998). Sandlance also decrease in energy density over the course of the summer. These relationships may explain, therefore, the decreasing interaction of date with kittiwake and sandlance school density; kittiwakes are much more abundant over sandlance schools early than later in the summer.

In regard to the density of kittiwakes as a function of the density of prey schools, the response of kittiwakes was similar regardless of prey species. That is, few, if any, kittiwakes occurred in areas where no prey schools were evident, but appreciable numbers were present in the company of at least one prey school. The fact that kittiwake density did not increase as a function of the number of schools, once at least one prey school was present, could be an argument supporting a relationship to an avoidance of (or, the result of) interference competition. When kittiwakes descend upon a school, the school responds immediately to become less available to surface-foraging predators. Thus, if foraging kittiwakes move from one school to a more-susceptible nearby school, which they do if given the chance, having more schools in a local area would not necessarily encourage more kittiwakes to accumulate (and have an equal chance of foraging success). In fact, Irons (1992) noted that kittiwakes on their flights out to secure food for chicks commonly over-flew foraging conspecifics (see below).

The fact that kittiwakes tended to feed as close as possible to the colony, at least most of the time (see below), is not surprising, nor hard to explain in terms of reducing foraging and reproductive effort. Foraging over shallow water, close to shore must have to do with foraging effort, too, by way of exploiting increased prey availability or susceptibility of prey to capture. That fact that the shallow water is offshore, i.e. not immediately adjacent to the beach, but over shoals and reefs (i.e., tendency to feed in shallow water) has to be a factor related to prey behavior and availability/susceptibility. Foraging by kittiwakes over shoals and reefs in Prince William Sound has been noted previously (Irons 1992). The various relationships to tide stage are support for taking advantage of an increased susceptibility of prey as a foraging strategy (see, too, Irons 1992). Sandlance burrow in the sand at low tides and, thus, would be available to a surface-foraging predator only at flood and high slack tides. The behavior of eulachon, too, explains their availability at flood and high slack tides compared to ebb tides. The species is anadromous and moves into spawning rivers on flood tides. Herring, on the other hand, are taken at any moving tide, either ebb or flood (but not slack). Predatory fish feed at that time, too, if the success rate of human fishermen is a good indication (we're saying, yes, it is).

Therefore, forage fish must be more susceptible to capture at that time. Tidal currents flowing around and over reefs, and the turbulence generated in the process, might increase susceptibility of forage fish to surface predators as well.

That kittiwake density over eulachon schools increases with greater distance from the colony is a complex issue to explain. Eulachon are more prevalent in the southern portion of the Sound (see below, Part II), and the total of kittiwake pairs at colony clusters in the northern part of the Sound (12,500 pairs) are twice as great as the total nesting in the south. Thus, the northern colonies would dominate the index (see Methods, for the way the index was calculated). The result would show foraging for eulachon at greater distances from colonies; certainly true for northern colonies but not for the smaller southern colonies. Similar arguments might help to explain why kittiwakes tended to feed farther from colonies in 1997, the year when sandlance were so prevalent. Sandlance, too, are found much more in the southern part of Prince William Sound than they are in the north.

Here we have attempted to explain some of the relationships between kittiwake foraging and various temporal, spatial and biological variables. The fact that adding years to our study (3 instead of any 1) reduced our power to explain relationships, at the least, would support an argument for additional years of investigation if the objective was to understand even better the foraging ecology of kittiwakes in Prince William Sound. As it is, a significant portion of unexplained variance could be related to the way that individual kittiwakes respond to various factors as a result of their short-term and long-term experience. For instance, Irons (1992) discovered that individual kittiwakes have habitual foraging areas that they visit repeatedly regardless of near-future foraging success. We will explore some of these experiential factors in the development of a foraging model based on kittiwake search behavior (see below).

FORAGING BY BLACK-LEGGED KITTIWAKES IN PRINCE WILLIAM SOUND, ALASKA: II, PROVISIONAL MODEL TO DESCRIBE PREY-SEARCHING STRATEGIES

RESULTS

Relationship between Kittiwake Behavior and Fish Distribution

We explored the statistical relationships between types of kittiwake behavior and forage-fish school abundance. Our goal was to predict kittiwake foraging behavior from the distribution of forage-fish schools (Figure 12). Our first effort was to determine whether the frequency of various behaviors was related to the presence of forage-fish schools. We calculated the frequency of the most common behaviors in areas where schools were and were not observed (see Results of Part I, above). For this analysis, we partitioned the data set into the first (6 June to 20 June) and second (21 June to 11 August) halves of the breeding season.

Results showed that behavior frequency was significantly different in areas where forage-fish schools were observed than would be expected if behavior was random (Chi-square, $P<0.01$, Figure 13). In areas where aerial transects indicated the presence of forage-fish schools, kittiwakes were less likely to engage in straight flight and more likely to engage in back-and-forth flight, resting on water, and plunge diving.

The plunge-dive rate was chosen as the best indicator of successful foraging, since a high percentage of plunge dives result in the capture of prey items (pers. obs.). The regression of the plunge-dive rate on the density of forage-fish schools showed a strong non-linear relationship between the two variables (Figure 14), indicating that the density of forage-fish schools is a good predictor of foraging behavior. The non-linearity of the relationship suggests that the behavioral response to the density of schools is asymptotic (see above, Part I), and that a doubling of school density results in a constant increment in the rate of plunge diving.

Previous analysis of behavioral data (Ford et al. 1998) showed that plunge diving and other feeding-related behaviors are associated with relatively slow rates of linear movement. In general, when the movement rate of a kittiwake drops below 25 km/hr, it is usually either searching for food, diving, or waiting for a fish school to come near enough to the surface to be accessible. Areas where a high density of foraging behaviors occur, called foraging grounds, can be easily delineated using behavioral data by plotting the locations of all observations where the rate of movement is 25 km/hr or less and then generating isopleths of the density of these slow movements.

Foraging grounds for the Shoup Bay and Eleanor Island colonies in 1996, 1997, and 1998 are shown in Figure 15. Different years are associated with distinct differences in the location of foraging areas. For the Eleanor Island colony, Smith Island was a very active feeding area in 1998, but not in 1996 or 1997. By comparison, the Green Island vicinity and the northwest side of Montague Island were much more active in 1997 than in 1996 and 1998. Birds from the Shoup Bay colony were not tracked in 1996, but their foraging areas also shifted somewhat between 1997 and 1998. In 1997, the principle focus of activity was the southern side of Glacier Island. In 1998, the focus shifted to the northern side of Glacier Island and to Columbia Bay and to Long Bay. It is likely that these shifts in foraging grounds reflect a shift in the distribution of forage-fish schools, but data describing forage fish distribution prior to 1998 cannot be used to resolve these fine scale differences. Comparison of Figure 15 (foraging grounds) with Figure 12 (distribution of forage-fish schools) shows that, as would be expected, there is a strong correspondence between foraging grounds and areas with high densities of forage-fish schools (see Discussion).

Modeling Kittiwake Foraging Behavior

Kittiwakes foraging bouts consist of intervals of straight flight interspersed with sporadic searching behaviors alternating with intervals of intense searching and plunging behavior. These sequences for Eleanor Island and Shoup Bay in 1998 are illustrated in Figure 16. Kittiwakes appear to engage in a low level of search activity even during intervals of straight flight, so that even commutes are punctuated by occasional searching behaviors and plunge dives.

Our basic model of kittiwake foraging behavior makes the classical optimal foraging assumption that individuals are attempting to maximize their food uptake rate (see for example Orians and Pearson 1979). Assuming that completed plunge dives are a good index of foraging success, and knowing that the plunge-dive rate can be predicted by the density of forage fish, birds should select travel itineraries that maximize their expected foraging rate. The quality of such an itinerary is dependent not just on the endpoint of the journey, but on the quality of the intervening habitat. Our model finds the optimal foraging path using the following algorithm based in part on the model presented in Ford (1983):

1. Divide the study area into a grid and calculate the density of forage-fish schools in each cell;
2. Create a candidate itinerary consisting of a series of adjacent grid cells ("rook's move" only);
3. Compute the mean expected foraging rate over the entire candidate itinerary;
4. Repeat steps 2 and 3 until all possible itineraries have been examined; and
5. Output the itinerary with the greatest expected foraging rate.

This model predicts that an optimally foraging kittiwake starting from Shoup Bay should move down the western side of Valdez Arm, turn west at Point Freemantle into the channel between Glacier Island and the mainland, and pass first into Columbia Bay and then into Long Bay. Based on radio-tracked kittiwakes from the Shoup Bay colony, this is the most common itinerary.

In this form, the foraging model predicts only a single optimal path, yet kittiwakes select a variety of different paths. It is likely that this results from unpredictability in the abundance of fish schools. In Part I, above, we found that certain factors did help to predict the occurrence of forage-fish schools, and certainly these factors are likely used by kittiwakes. However, a high degree of unpredictability still remained. We examined predictability by calculating the degree to which a kittiwake could use the density of forage fish cell in one area (1.5-nm cell) related to the density of forage fish nearby (other 1.5-nm cells) for various times and distances between cells. Figure 17 shows the resultant correlation coefficient as a function of time and distance. Using this measure of variability, the knowledge of the density of forage-fish schools at one point in space and time is of almost no use in predicting the density of schools more than about 20 miles away or 5 days in the future.

DISCUSSION

Based on these results, we assume that the variation in the kittiwakes' solution to the optimal-foraging problem results from uncertainty on the part of a kittiwake's as to the distribution of forage-fish schools and their availability. For one thing, as noted above, the location of foraging areas differed among years; for another, as noted in Part I, while a number of factors can be used to predict fish availability to kittiwakes, additional and (at least to us) unknown factors remain. The extent to which a kittiwake is aware of these other factors remains to be determined. Following the 1999 field season, we will be able to determine whether annual changes in foraging-ground locations track annual changes in the distribution of forage-fish schools.

To simulate the effect of uncertainty in predicting the availability of forage fish, we ran the foraging model many times, each time perturbing the value of the density of forage-fish schools in each of the grid cells around the mean value using a normally-distributed random deviate. This resulted in the distribution of simulated foraging paths for the Shoup Bay colony shown in Figure 18. As would be expected, the itinerary that passes down the west side of Valdez Arm and into Columbia Bay remains the most popular. The stochastic version of the foraging model, however, results in a family of foraging-trip itineraries that mimic most of the itineraries followed by radio-tagged kittiwakes leaving the Shoup Bay colony. At this point, we consider the correspondence between the observed and the predicted behaviors to be highly promising, and will continue to develop it as a means for predicting foraging success and colony productivity.

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Table 1. Results of multiple regression analyses indicating relationships between kittiwake density (log-birds per 100 km) and temporal, spatial, and biological variables in Prince William Sound, Alaska, 1996-1998. The analysis was weighted by the kilometers surveyed per transect block surveyed per day.

	Regression coefficient sign	*F*-value	*P*-value	df
Main effects:				
Year (continuous)	+	486.13	<0.0001	1
Year (categorical)	(cat.)	190.23	<0.0001	2
Depth	-	18.97	<0.0001	1
Distance from shore	-	85.77	<0.0001	1
Colony index	-	29.16	0.001	1
Herring	+	204.09	<0.0001	1
Herring^2	-	60.88	<0.0001	1
Sandlance	+	63.95	<0.0001	1
Sandlance^2	-	14.16	0.0001	1
Sandlance3	+	11.90	0.001	1
Eulachon	+	8.09	0.01	1
Capelin	+	18.34	<0.0001	1
Capelin^2	-	31.72	<0.0001	1
Rejected terms:				
Julian date	ns	5.21	0.023	1
Latitude	ns	4.47	0.035	1
Tide phase	(cat.)	3.01	0.044	2

Table 1 continued

	Regression coefficient sign	*F*-value	*P*-value	df
Interactions:				
Year x Julian date	(cat.)	7.39	0.001	2
Year x Distance from shore	(cat.)	6.31	0.01	2
Year x Colony index	(cat.)	6.78	0.001	2
Year x Tide phase	(cat.)	9.45	<0.0001	4
Tide phase x Julian date	(cat.)	6.83	0.001	2
Tide phase x Julian date^2	(cat.)	4.67	0.01	3
Tide phase x Julian date^3	(cat.)	5.59	0.001	3
Herring x Year	(cat.)	31.22	<0.0001	2
Herring x Distance from shore	+	7.32	0.01	1
Herring x Tide phase	(cat.)	8.66	0.01	2
Sandlance x Year	(cat.)	5.84	0.01	2
Sandlance x Julian date	-	16.74	<0.0001	1
Sandlance x Distance from shore	+	5.64	0.02	1
Sandlance x Tide phase	(cat.)	14.72	0.0001	2
Eulachon x Distance from shore	+	16.31	<0.0001	1
Eulachon x Colony index	+	22.29	<0.0001	1
Eulachon x Colony index^2	+	6.44	0.01	1
Eulachon x Tide phase	(cat.)	26.13	<0.0001	2

Table 2. Regression models for the relationship between school abundance and date for four species of kittiwake forage fishes in Prince William Sound, Alaska. Data grouped across years 1996, 1997, and 1998.

	Regression coefficient ± SE	P-value
Herring		
Date	-0.00087 ± 0.00021	<0.0001
Date^2	-0.000026 ± 0.000012	0.02
Date^3	$6.58e^{-06} \pm 2.25e^{-06}$	0.01
Sandlance		
Date	0.00052 ± 0.00020	0.01
Date^2	0.000058 ± 0.000011	<0.0001
Date^3	$-5.04e^{-06} \pm 1.56e^{-06}$	0.001
Eulachon		
Date	-0.00010 ± 0.000040	0.01
Capelin		
Date	-0.000065 ± 0.000029	0.01

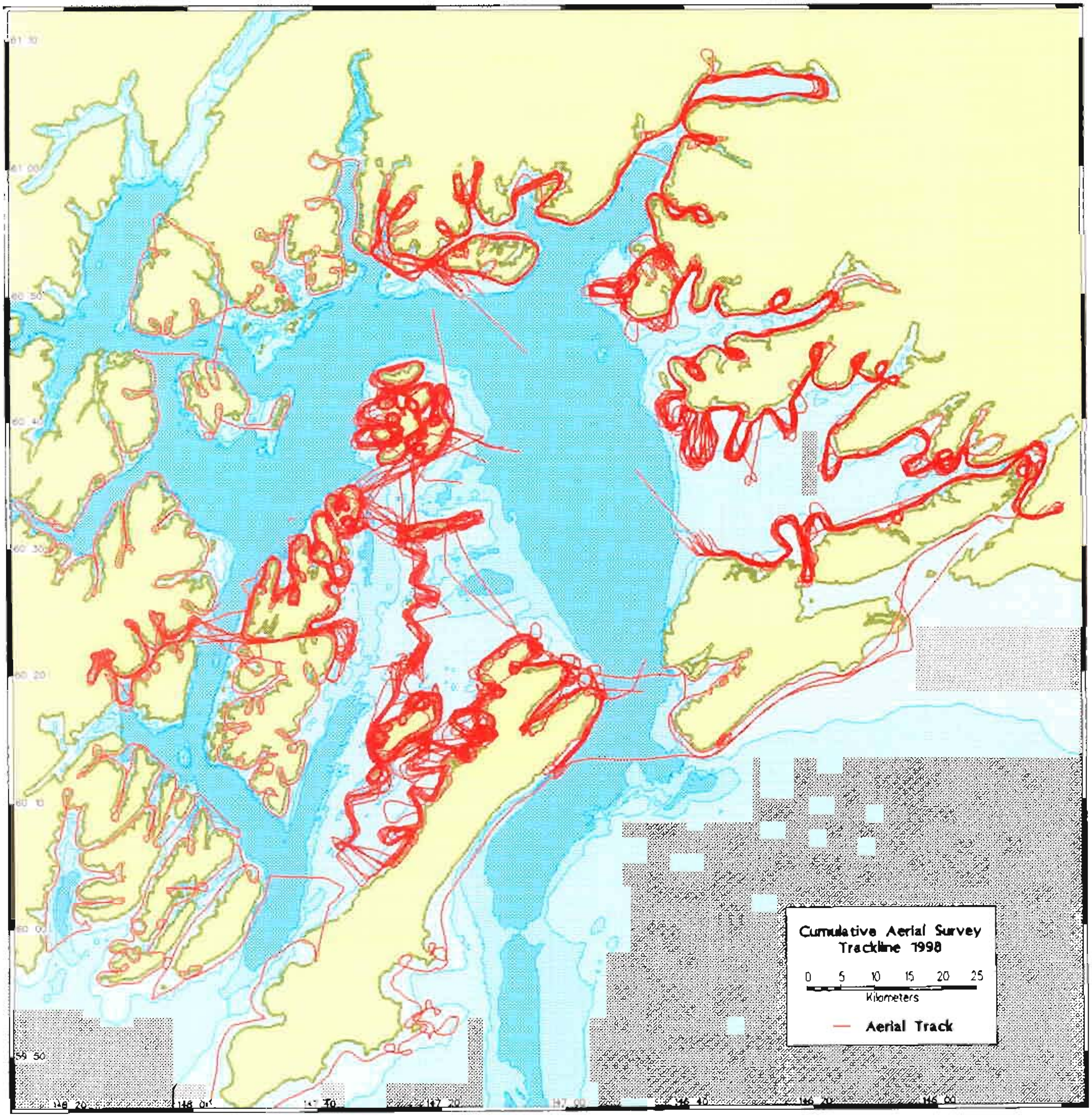

Figure 1. Prince William Sound showing aerial survey tracks for 1998; tracks for 1996 and 1997 were similar to these. Tracks are based on automated logging of aircraft position at 5 sec intervals using a GPS unit.

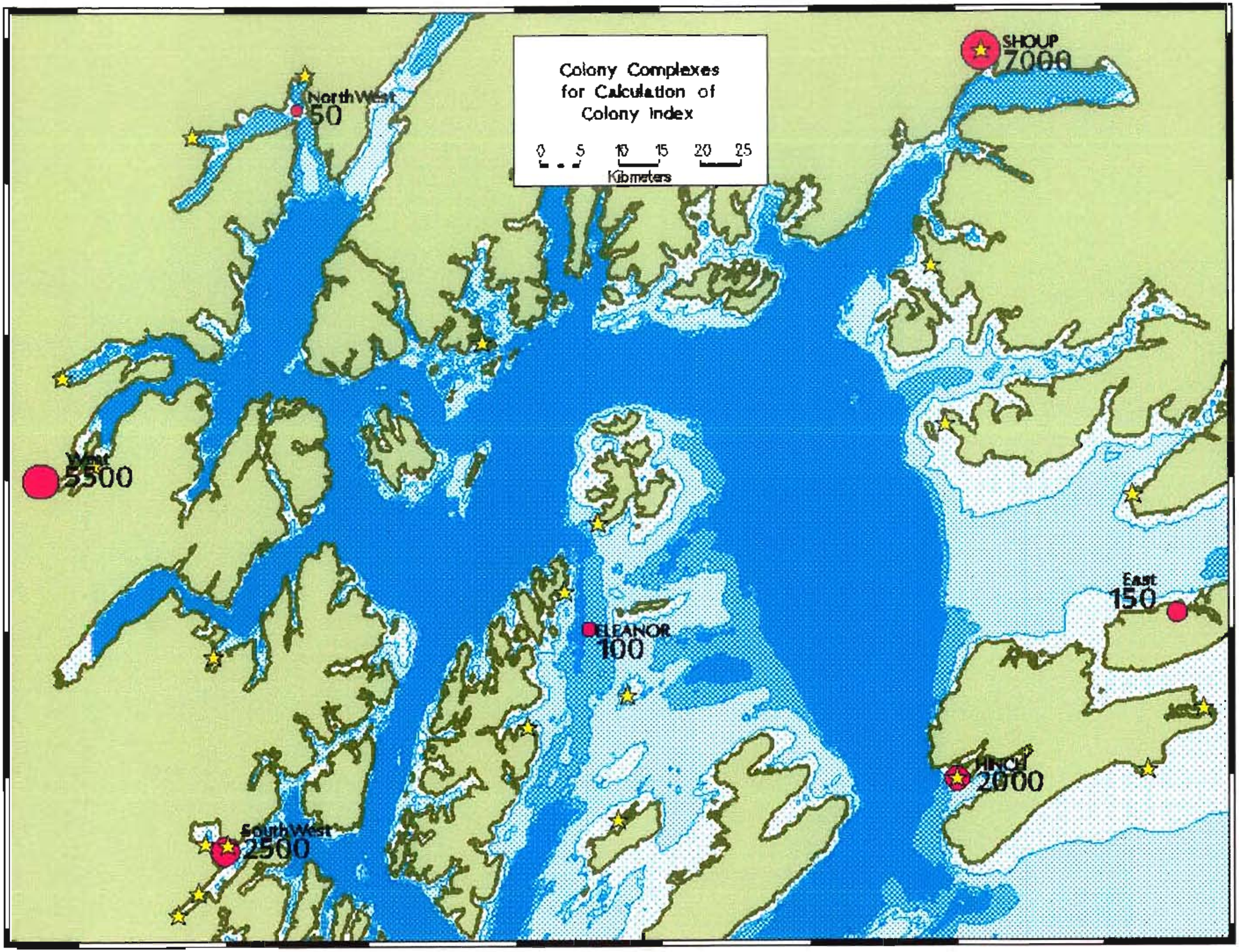

Figure 2 Prince William Sound and the locations of Black-legged Kittiwake colonies (stars). Red dots indicate the location of the position used to calculate distance to the 7 colony clusters Colony sizes from Sowls et al. (1978), with updates from Irons, Suryan et al (pers.comm.)

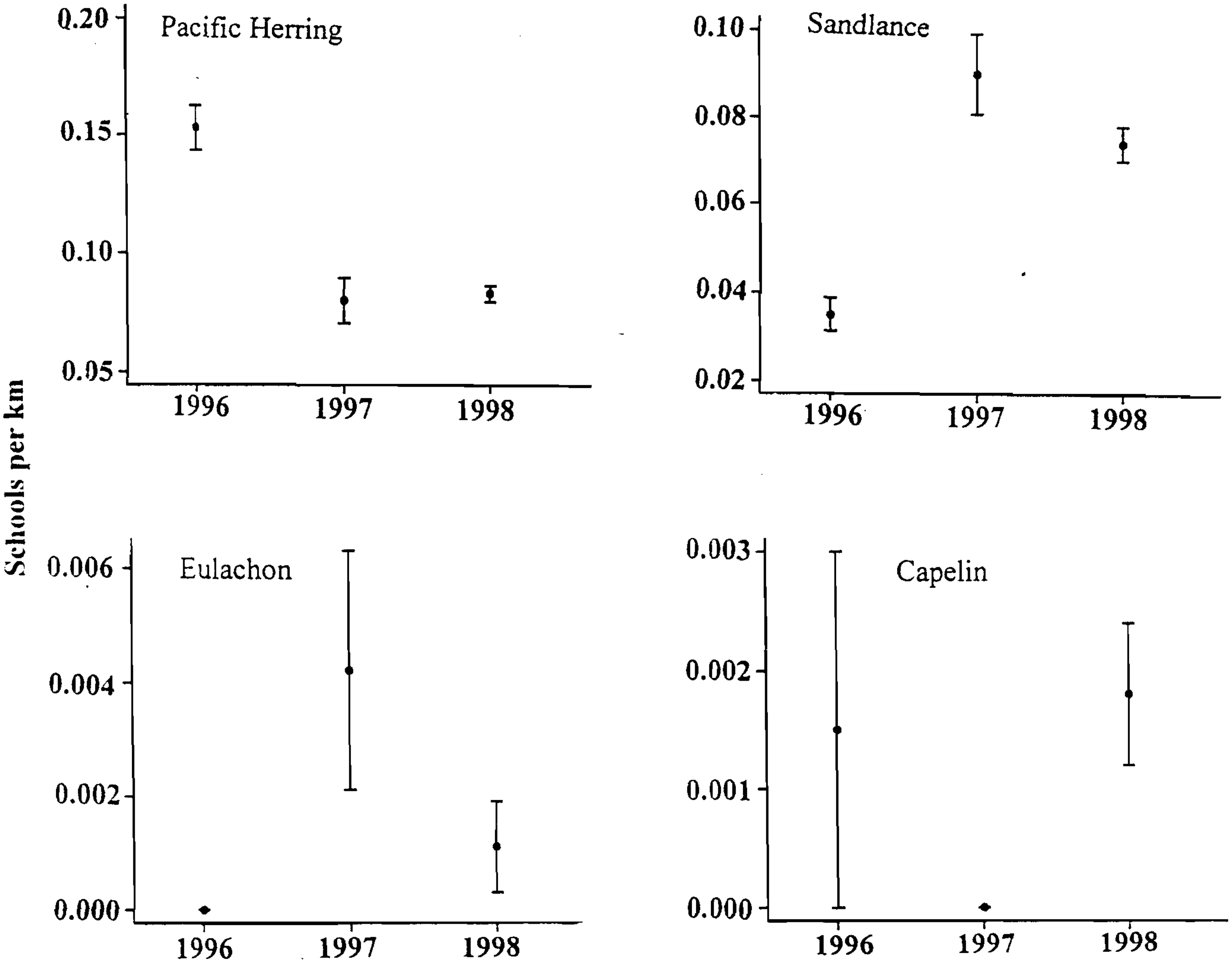

Figure 3. Densities of schools by year of four species of fish preyed upon by Black-legged Kittiwakes in Prince William Sound, Alaska. Densities are number of schools per km for each survey block sample (n = 10,181). Calculations were weighted by the kilometers of track line surveyed per sample.

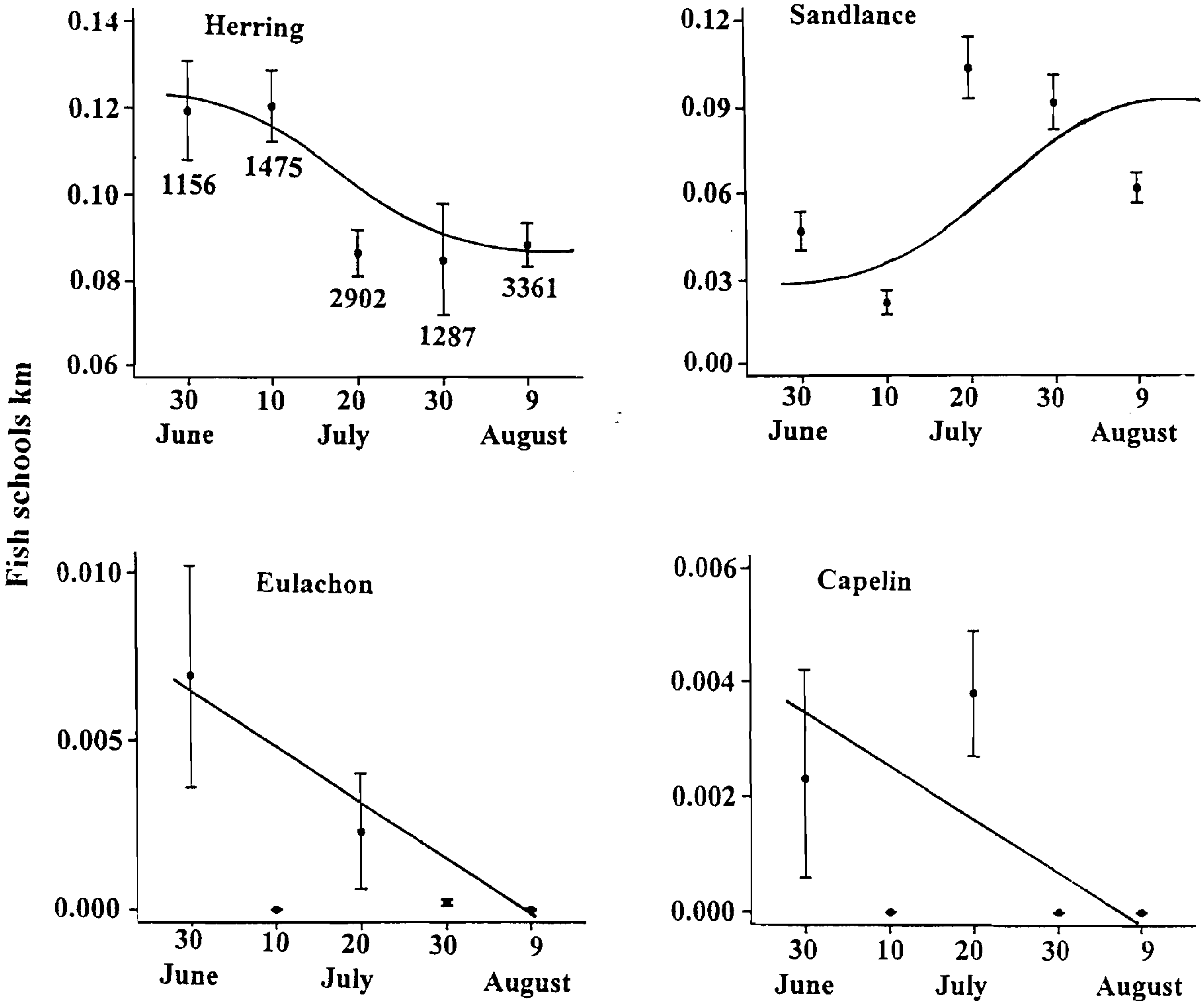

Figure 4. Density by date within year of schools of fish preyed upon by Black-legged Kittiwakes in Prince William Sound, Alaska. Densities are number of schools per kilometer for each survey block sample (n = 10,181). Calculations were weighted by the kilometer of track line surveyed per sample.

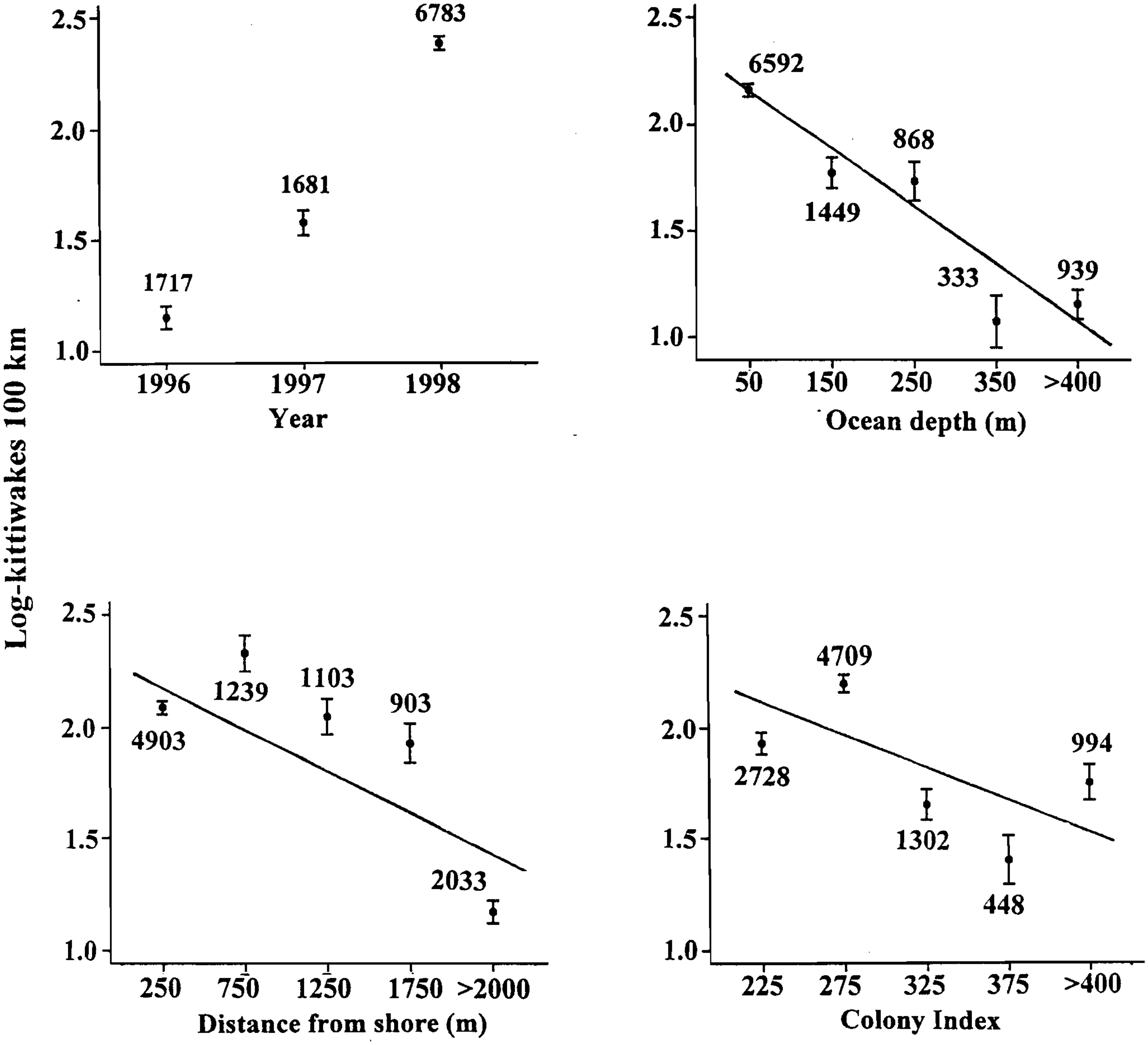

Figure 5. Densities (log-transformed) of feeding Black-legged Kittiwakes with respect to four environmental variables. Shown are the means, SE, and the sample sizes (numbers adjacent to means = the number of blocks sampled). Lines of best fit are shown for the variables that were analyzed as continuous.

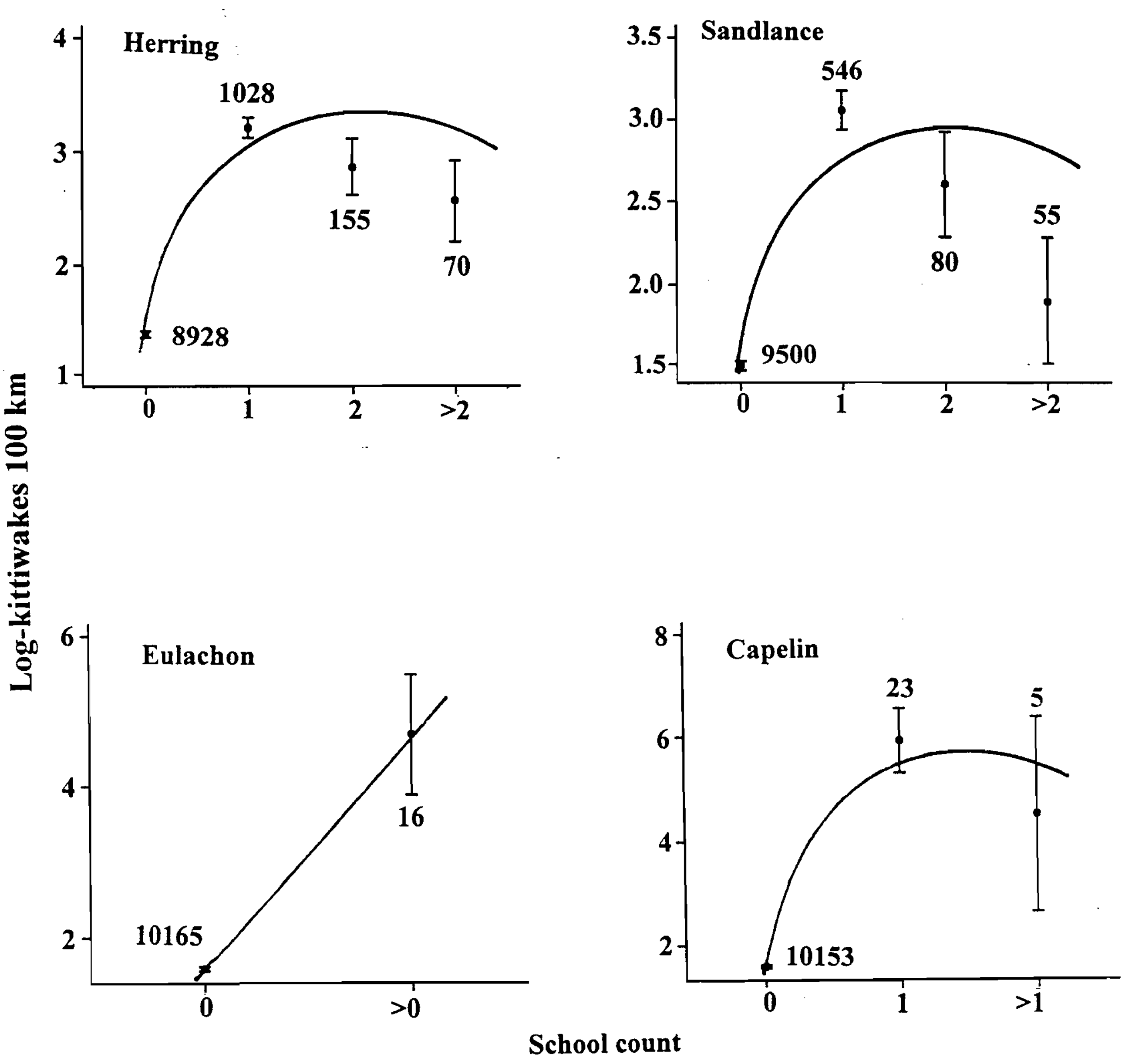

Figure 6. Densities (log-transformed) of feeding Black-legged Kittiwakes with respect to abundance of four species of forage fishes. Shown are the means, SE, sample sizes (numbers adjacent to means = the number of blocks sampled), and lines of best fit.

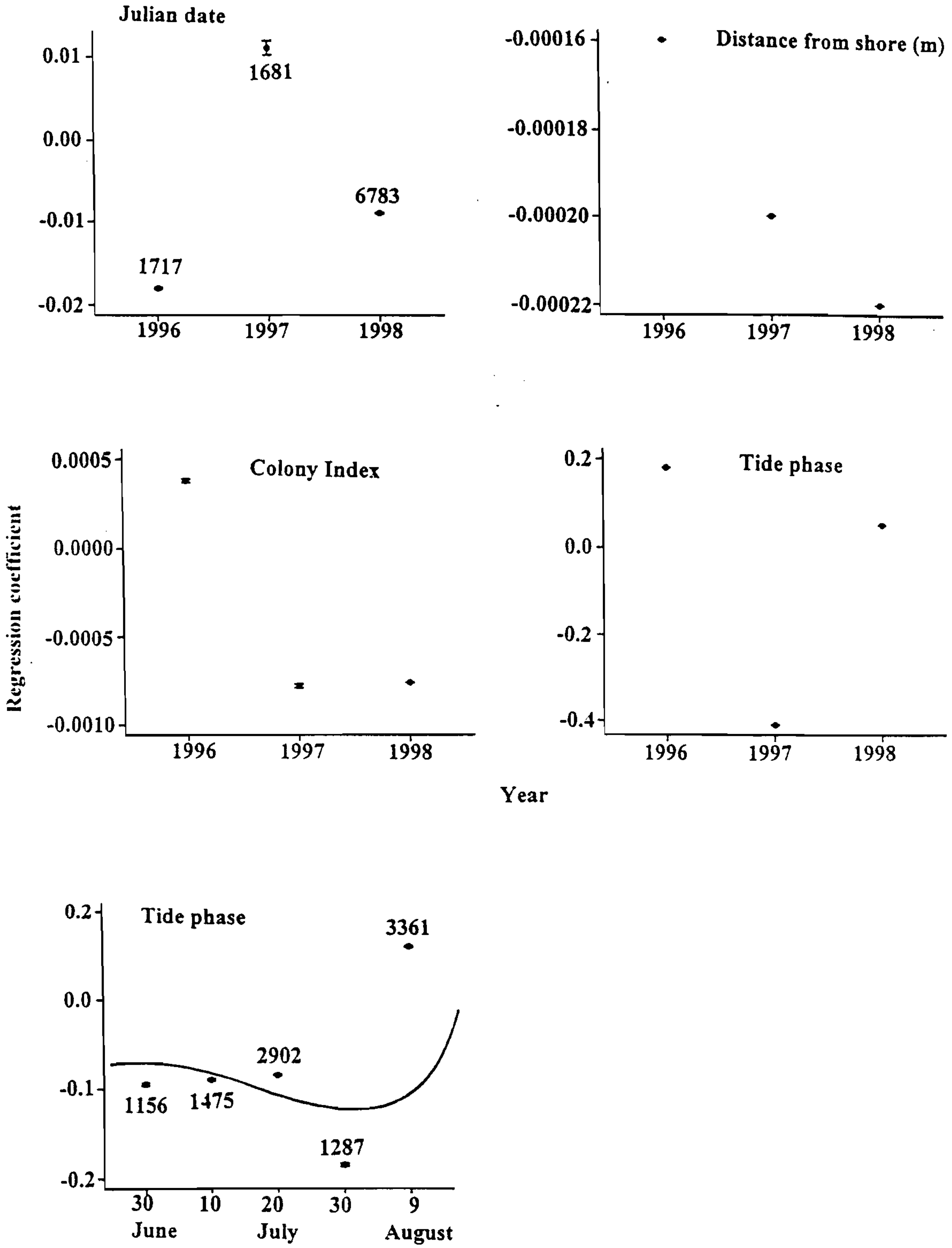

Figure 7. Regression coefficients for the relationship between log-transformed densities of feeding Black-legged Kittiwakes and environmental variables (given at the top of each graph) with respect to temporal period (year and date; x-axis). Shown are the coefficient means and SE. Sample sizes (numbers adjacent to means = the number of blocks sampled) are shown adjacent to means for date. Sample sizes for year -- 1996, 1997, and 1998 -- were 1717, 1681, and 6783, respectively. Line of best fit is shown for date, analyzed as a continuous term.

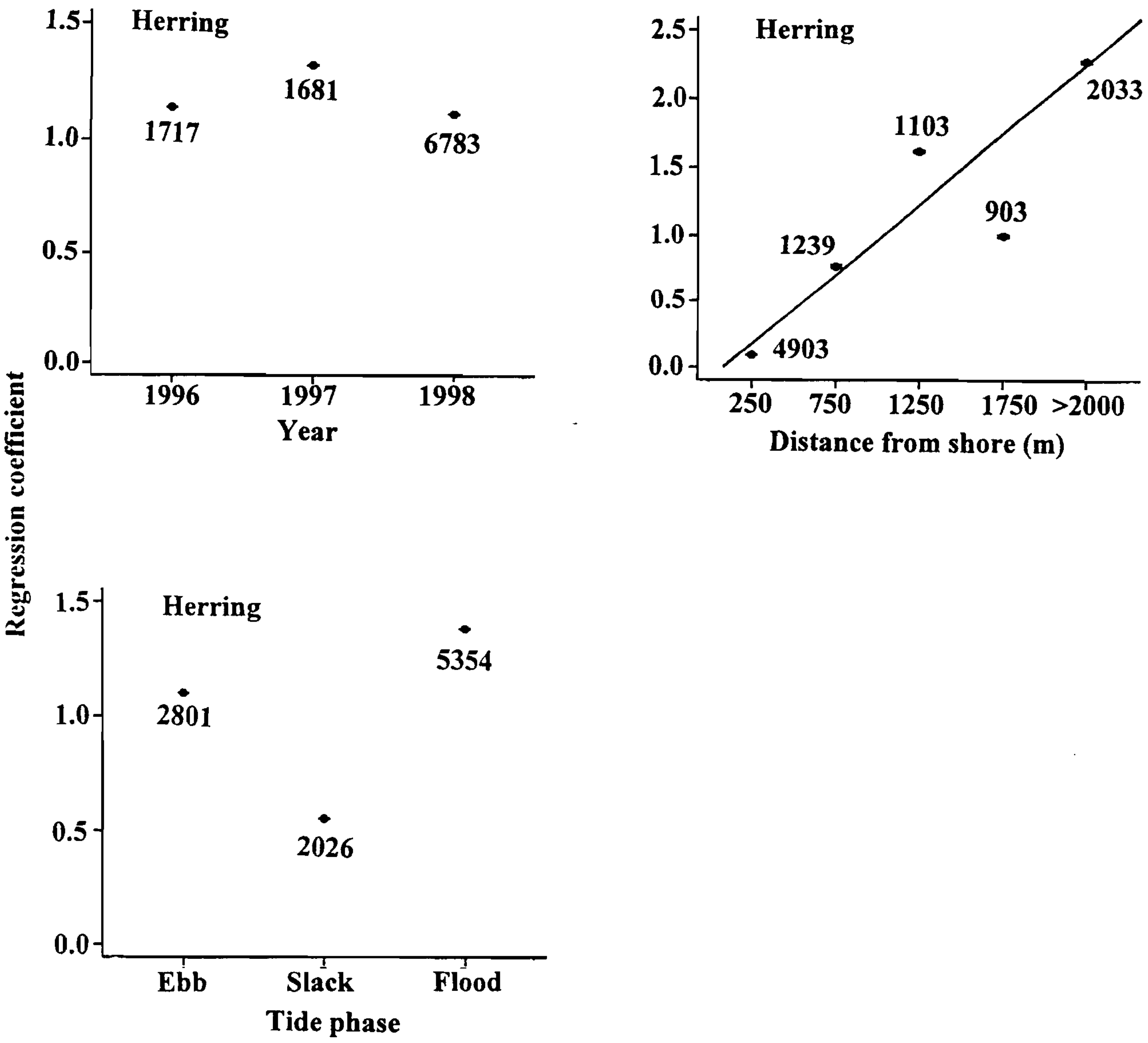

Figure 8. Regression coefficients for the relationship between log-transformed densities of feeding Black-legged Kittiwakes and abundance of herring schools, shown with respect to year, increments of distance from shore, and tide phase (x-axis). Shown are the coefficient means, SE, and sample sizes (numbers adjacent to means = the number of blocks sampled). Line of best fit is shown for distance from shore, analyzed as a continuous term.

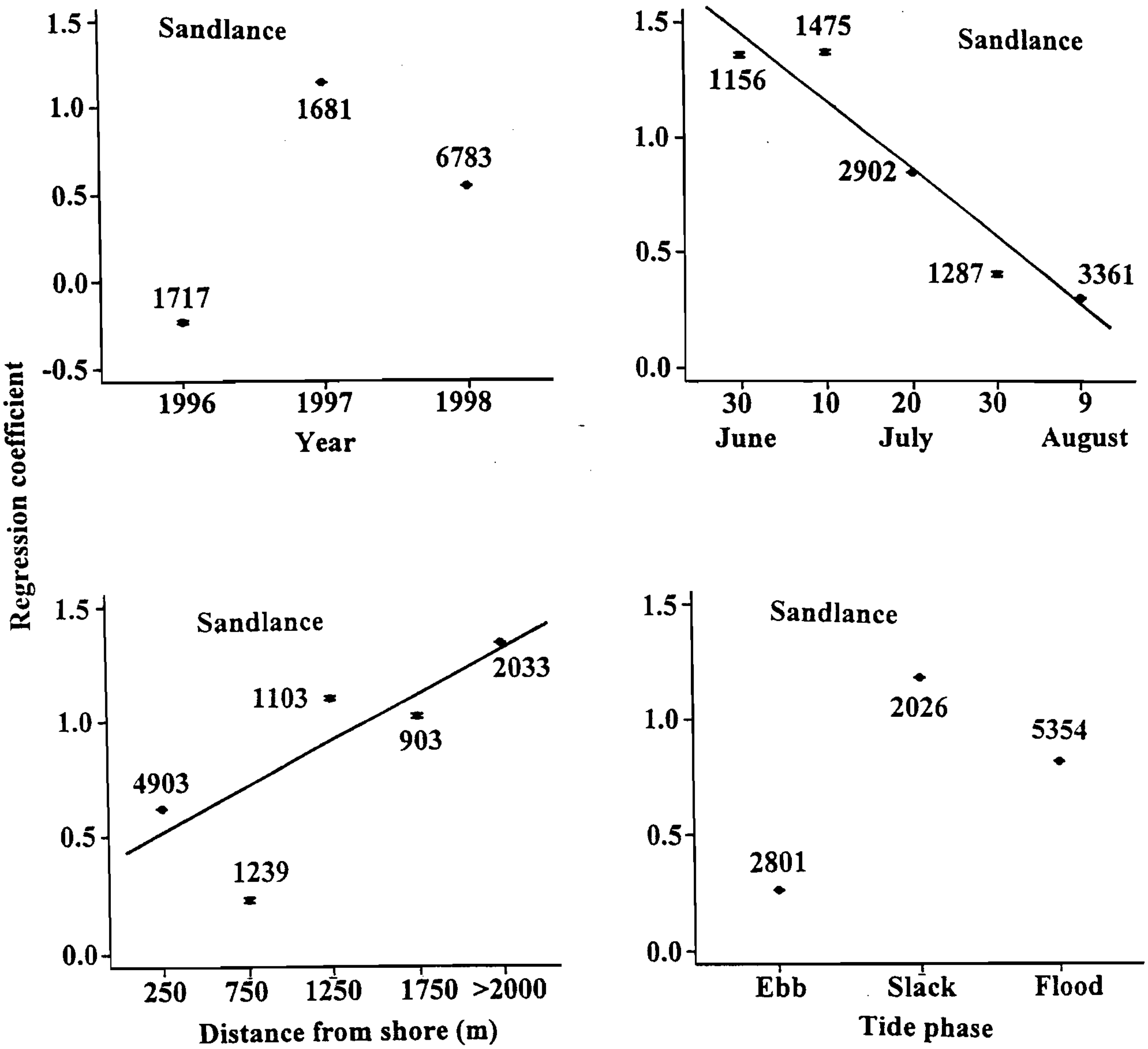

Figure 9. Regression coefficients for the relationship between log-transformed densities of feeding Black-legged Kittiwakes and abundance of sandlance schools, shown with respect to year and increments of date, distance from shore, and tide phase (x-axis). Shown are the coefficient means, SE, and sample sizes (numbers adjacent to means = the number of blocks sampled). Lines of best fit are shown for date and distance from shore, analyzed as a continuous terms.

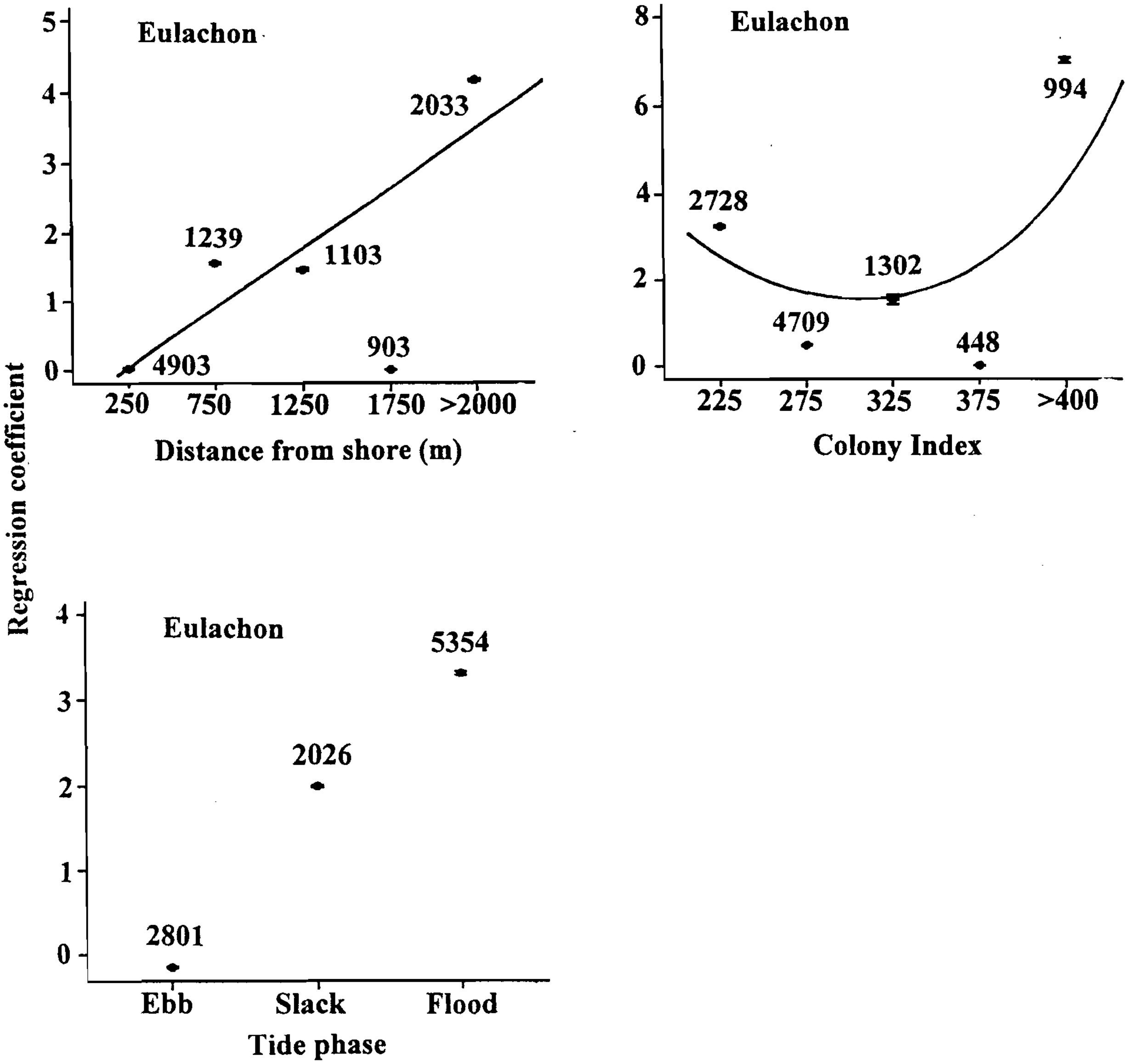

Figure 10. Regression coefficients for the relationship between log-transformed densities of feeding Black-legged Kittiwakes and abundance of eulachon schools, shown with respect to distance from shore, colony index and tide phase (x-axis). Shown are the coefficient means, SE, and sample sizes (numbers adjacent to means = the number of blocks sampled). Lines of best fit are shown for distance from shore and colony index, analyzed as a continuous terms.

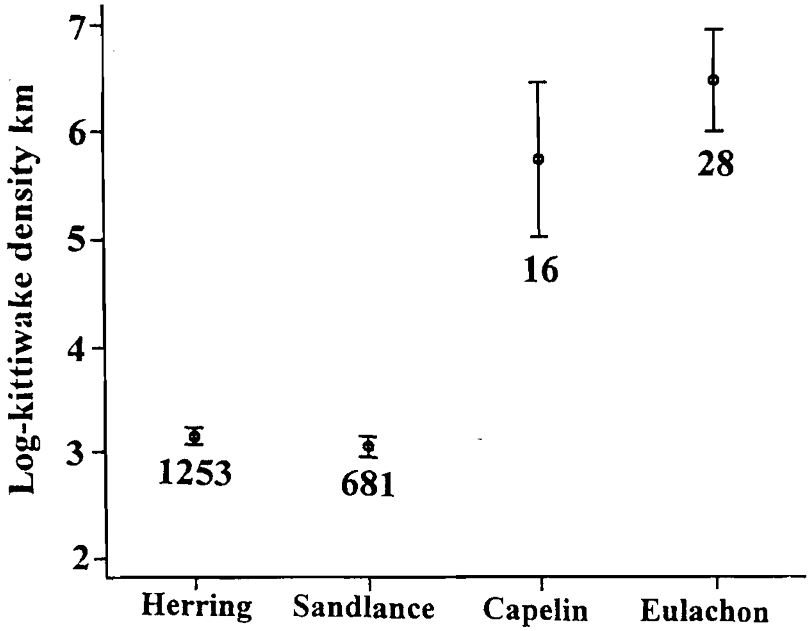

Figure 11. Density (log-transformed) of feeding Black-legged Kittiwakes observed within survey blocks in which at least one school of a given species of fish was observed. Shown are the means, SE, and sample sizes (numbers adjacent to means = the number of blocks sampled in which a school was seen).

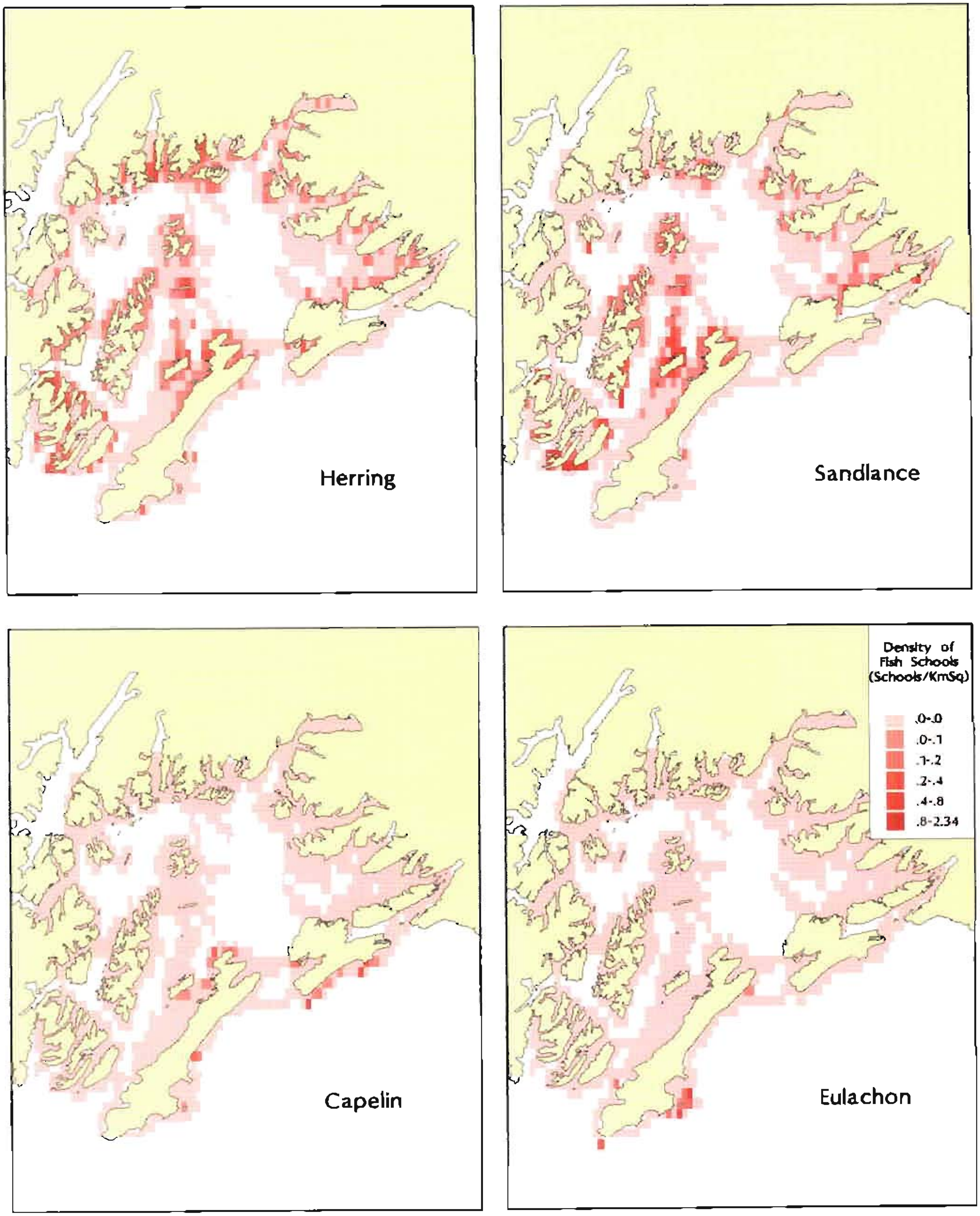

Figure 12. The density of schools of forage fish in 1998 based on aerial survey data. Density of fish schools was estimated as the number of schools in a 1.5-nm2 block divided by the product of the length of trackline within that block and the effective transect width for fish school spotting. Effective transect width was estimated as 1/f0 using program DISTANCE.

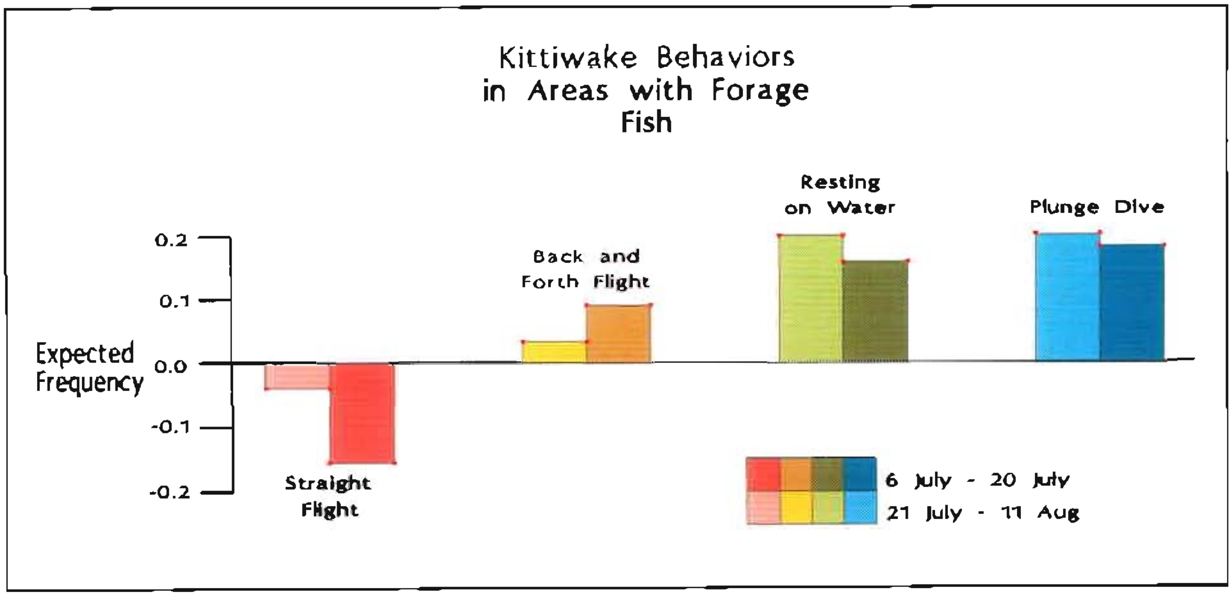

Figure 13. The frequency of various behaviors in 1.5-nm blocks where fish schools were observed. Bars above the line and below the line, respectively, indicate behaviors that occur more or occur less frequently than expected if behaviors were independent of fish density.

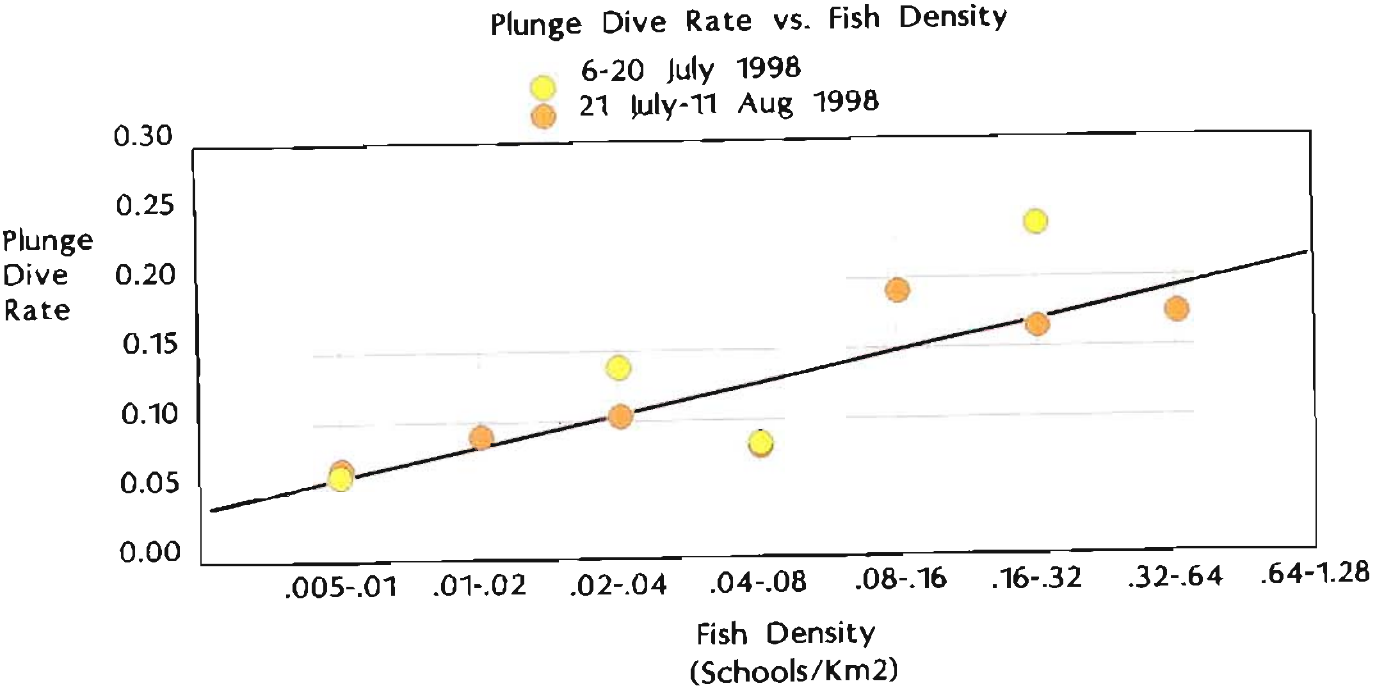

Figure 14. The regression of plunge-dive rate on the density of forage-fish schools in 1998. All observed behaviors initially were binned into seven spatial categories based on the density of forage-fish schools in the 1.5-nm block where kittiwakes occurred. Plunge-dive rate is the proportion of all behaviors that were plunge dives.

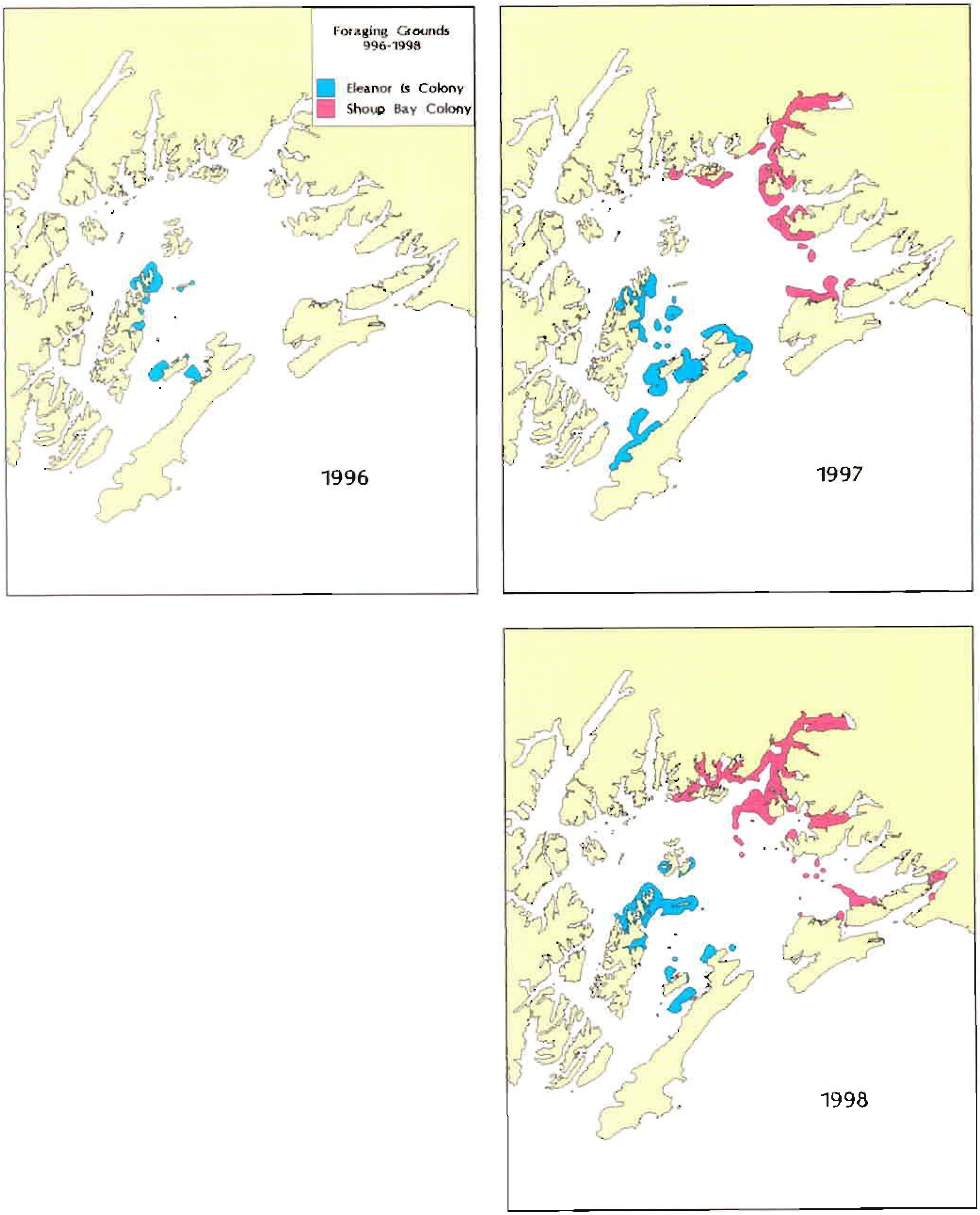

Figure 15. Foraging grounds for the Eleanor Island and Shoup Bay colonies in 1996, 1997, and 1998. Foraging grounds are defined as the minimum areas containing 95% of all observations where the movement rate was less than 25 nm/hr.

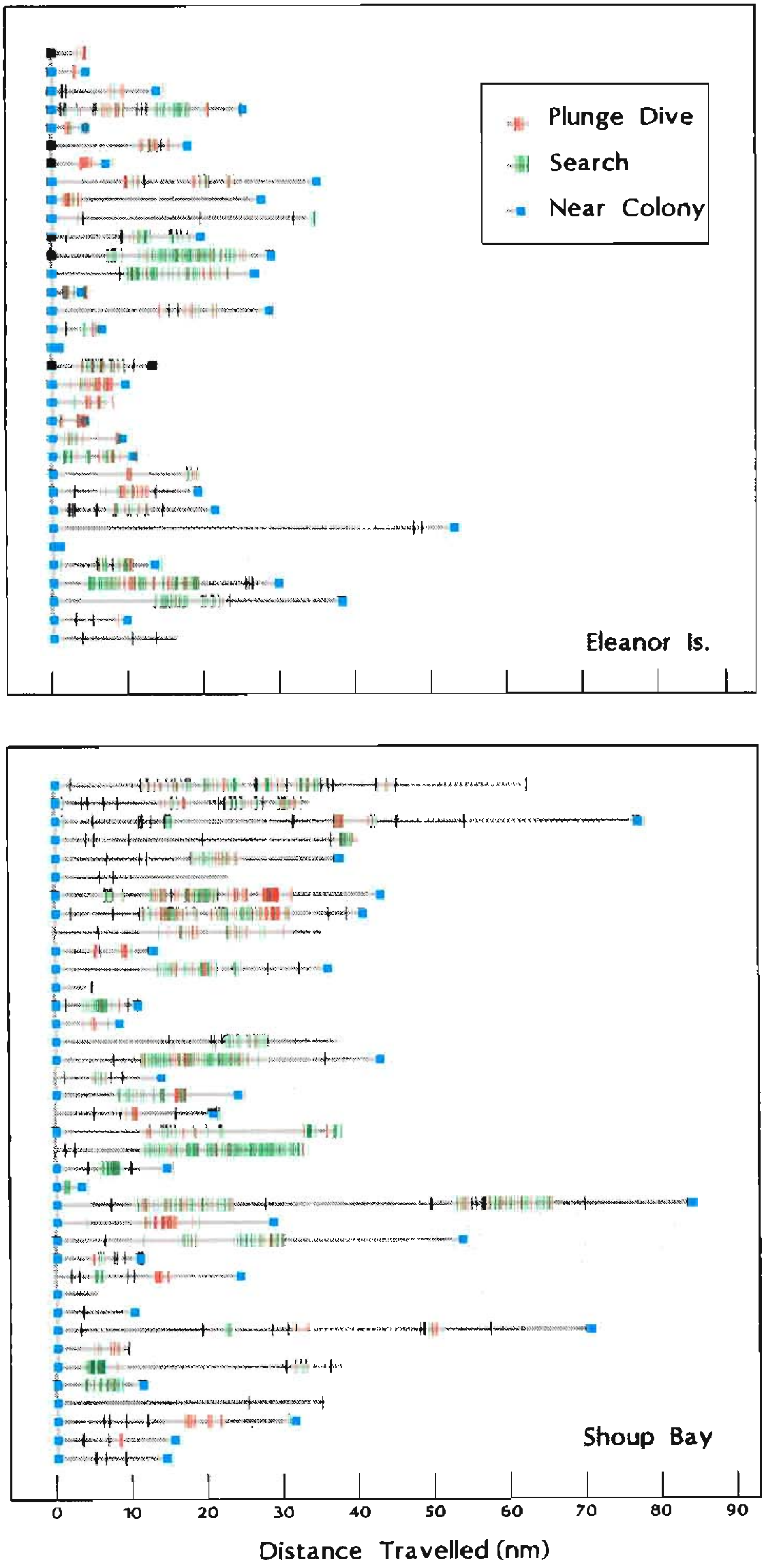

Figure 16. Searching and plunging behaviors displayed as a function of total distance moved on a foraging trip. Data for individual birds from Eleanor Island and Shoup Bay are displayed in the upper and lower panels, respectively. Distance is calculated as the sum of the straight-line distance between one observation and the next.

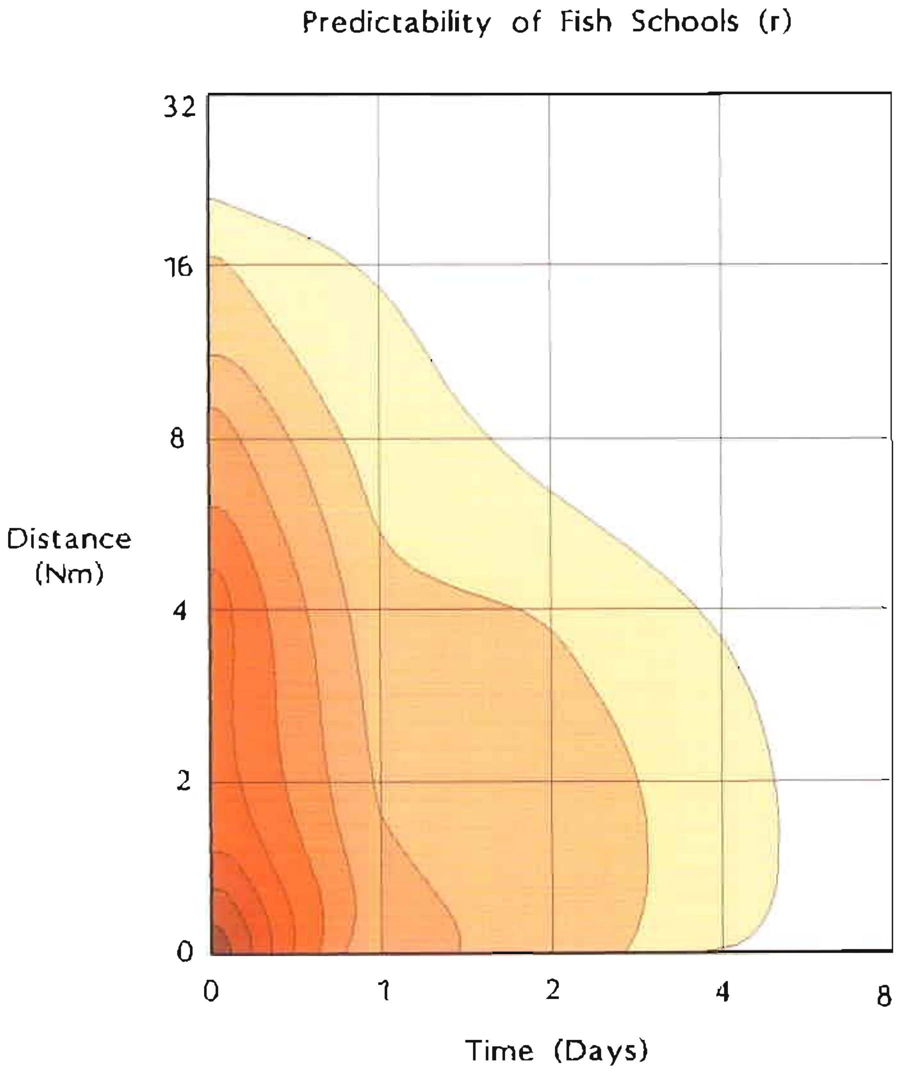

Figure 17. The spatial and temporal; predictability of forage-fish schools. The height of the surface represents the correlation coefficient for the density of forage-fish schools for all pairs of cells separated by a given distance and time.

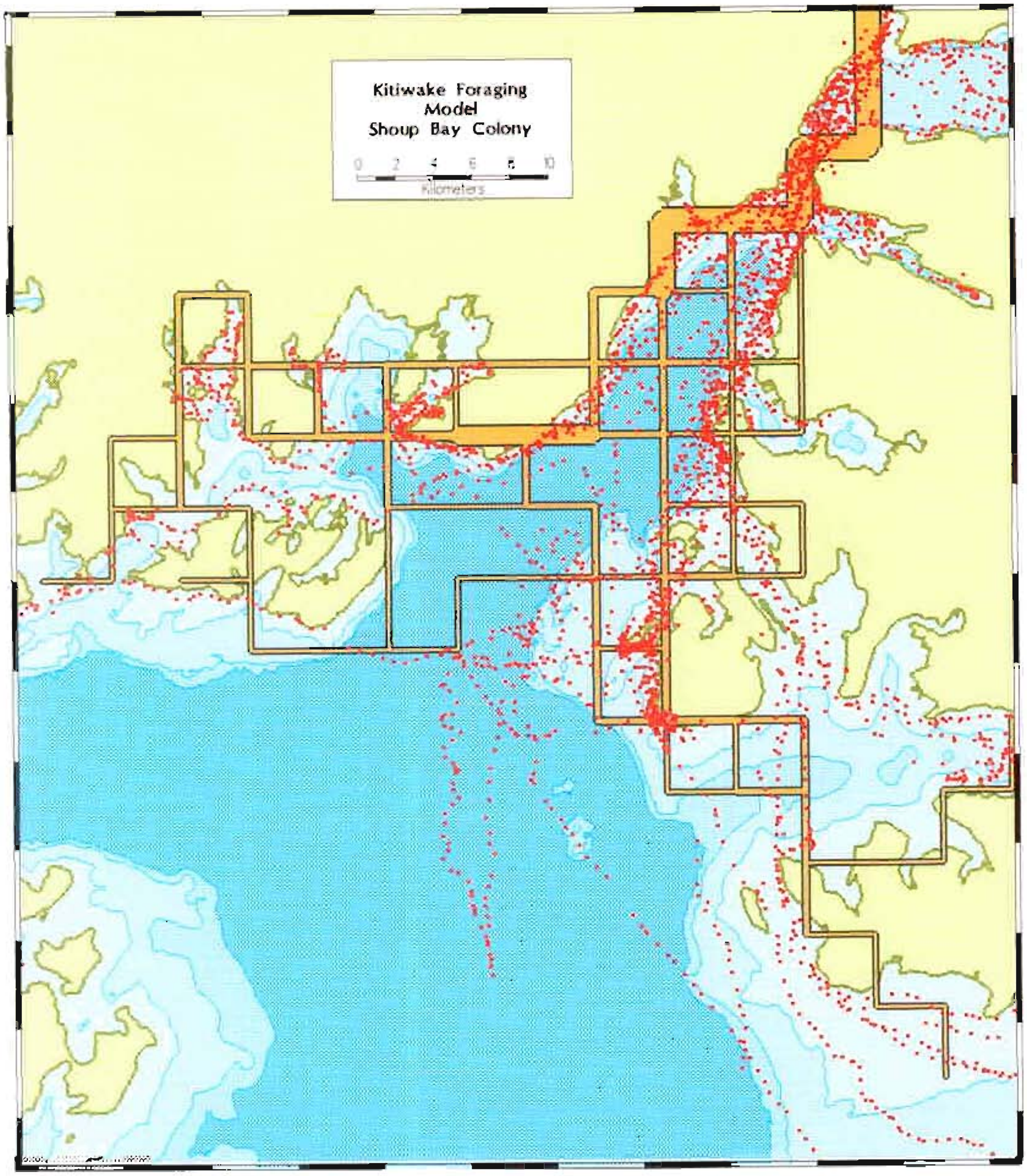

Figure 18. Observed and predicted foraging-trip itineraries for kittiwakes from the Shoup Bay colony. Data points represent sightings of individual birds; lines represent predicted itineraries. The thickness of a line segment is proportional to the predicted frequency of that line segment in the predicted family of itineraries. Predicted itineraries were generated by using "rook's moves" on a square grid.