

**Regional patterns of marine mammal distribution, abundance and diet from
the Alaska Peninsula to the central Aleutian Islands: an exploratory analysis**

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ABSTRACT

Regional patterns in diet and population trends among adult females of the western stock of Steller sea lions (*Eumetopias jubatus*) indicate metapopulation structure extending west from the Alaska Peninsula across the Aleutian Island chain. Linkages between diet and decline of these endangered pinnipeds have been inferred, but causal mechanisms have not been identified. The 2001-2002 Aleutian Passes Cruises provided an opportunity to examine bio-physical indices in relation to Steller sea lion (SSL) metapopulation patterns, as well as distribution patterns observed among cetaceans during the cruise. Patterns in distribution of four cetacean species: fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), minke (*Balaenoptera acutorostrata*), and sperm whales (*Physeter macrocephalus*) were strongly aligned with regional breaks in Steller sea lion diet and population trend. Killer whales (*Orcinus orca*) were frequently seen near all passes sampled, and were particularly common along the north Aleutian Island coastlines between Unimak Pass and Samalga Pass. However, most encounters proved to be with the piscivorous (resident) killer whale ecotype; no mammal-eating (transient) killer whales were seen during the 2001 cruise and only 8% (39 of 500) of the killer whales seen in 2002 were the transient ecotype. Generalized additive models (GAMs) were used to explore how oceanographic characteristics (salinity, temperature, fluorescence, and depth) and proximity to six Aleutian passes relate to SSL metapopulation patterns and cetacean distribution. The GAMs indicated the depth of the nearest pass was significant for Steller sea lion population trend and diet diversity and that the frequency of herring and salmon in diets was significant for population trend. For the distribution of Dall's porpoise (*Phocoenoides dalli*), humpback, minke, sperm, and killer whales, proximity to the nearest measured pass was significant. Fluorescence in the top 50 meters was significantly related to the occurrence of humpback, minke, and killer whales,

while surface temperature was significant for humpback, killer, and sperm whales. Results of the GAM analyses support field observations and suggest foci for future investigation of the relationships between physical variables and interspecific patterns of marine mammal distribution and population trends.

Key words: bio-physical, cetaceans, diet, generalized additive models, GAMs, killer whales, metapopulation, orca, population trend, Steller sea lion

INTRODUCTION

Concurring interspecific population declines of marine predators in the northern North Pacific and Bering Sea began in the late 1970s (Anonymous, 1993; Hunt and Byrd, 1999; Hunt *et al.*, 2003; National Research Council, 1996; Piatt and Anderson, 1996; Sinclair, 1988, Springer, 1998; Springer *et al.*, 2003; York and Hartley, 1981). For some species, periods of decline were interspersed with apparent stability and growth, while others continued a steady plummet at rates of 5-8% per year (Byrd *et al.*, this volume; Hunt *et al.*, 2003; Loughlin and York, 2002; Sease and Gudmundson, 2002; Springer, 1998; York and Kozloff, 1987). In some cases, there are strong parallels between population declines and diet (Anonymous, 1993; Hunt *et al.*, 2003; Sinclair, 1988; Sinclair *et al.* 1994; Sinclair and Zeppelin, 2002; Springer, 1998). However, despite over twenty years of directed inquiry, forcing mechanisms unequivocally linking diet to declines are lacking, perhaps because few studies have explored the influences of physical oceanography on prey availability (bottom-up structuring) at a regional scale (Hunt *et al.*, 2002).

The precipitous decline of the Western Stock of Steller sea lions (SSL) provides a case study for exploration of linkages between ecosystem variability and fluctuations of apex predator populations. The range of this endangered population extends from central Gulf of Alaska westward along the Aleutian Islands, with inference of metapopulation structure provided by longitudinal patterns in population trend and diet (Call and Loughlin, this volume; Sinclair and Zeppelin, 2000; Sinclair and Zeppelin, 2002; York *et al.*, 1996), branding studies (Raum-Suryan, 2002), and more recently genetic analysis (O’Corry-Crowe, pers. comm.). Specifically, collated patterns of diet and decline among the Western Stock of Steller sea lions provide evidence of at least four (Sinclair and Zeppelin, 2002; York *et al.*, 1996) and as many as six (Call and Loughlin, this volume) sub-populations along the Aleutian Islands. Analysis of over 2,300 scats collected

at 34 rookeries across the range of the Western Stock during the 1990s indicated regional specificity in diet (Sinclair and Zeppelin, 2002). Prey composition varied significantly by geographic area, with the most distinct regional boundary occurring at Samalga Pass (Fig. 1a). Similarly, population counts conducted during 1976-1994 demonstrated regional trends (York *et al.*, 1996), with boundaries that align themselves with those of diet, again with the most dramatic change point occurring at Samalga Pass (Sinclair and Zeppelin, 2002) (Fig. 1b). Sinclair and Zeppelin (2002) argued that the correspondence between patterns of diet and population trend indicated that diet is linked to the SSL decline, if not directly then by some associated trophic-cascade mechanism.

Three potential factors most commonly cited as reasons for the decline of the Western Stock of SSL include: 1) direct or indirect competition with commercial fisheries; 2) changes in ocean climate that affect productivity and prey availability in sea lion habitat; and 3) predation by killer whales (NMFS, 2001; NRC, 2004). Other factors potentially related to the SSL decline include disease, parasitism, and a suite of explanations regarding behavioral ecology which include diet and foraging behavior (DeMaster and Atkinson, 2002; NMFS, 2001). Management actions to mitigate the first factor have restricted the location of the commercial groundfish fishery within the range of the Western Stock in offshore Alaskan waters. The Aleutian Passes study was initiated in part to investigate aspects of the latter two factors to improve the basis for future management decisions.

The 2001-2002 Aleutian Passes Cruises (APC) provided the opportunity to examine the influence of bio-physical parameters within proposed metapopulation regions of SSL habitat, as well as document distribution patterns of cetaceans in the central and eastern Aleutian Islands. This study, and others in this volume (Byrd *et al.*, this volume; Call and Loughlin, this volume;

Fadely *et al.*, this volume), represent initial efforts to examine the influence of bottom-up structuring on patterns of apex predator distribution, population trends, and diet along the Aleutian Islands. Conversely top-down forcing, that is predation of SSL by killer whales (*Orcinus orca*), has received widespread attention (e.g., Lord, 2001; Springer, *et al.*, 2003), but very little focused research. This is the first presentation of killer whale distribution and ecotype with reference to diet and population trends at SSL rookeries and oceanographic parameters. Abundance estimates and predation rates, which incorporate APC data, will be presented in subsequent manuscripts (Wade *et al.*, 2003).

The central hypothesis investigated here is that the physical properties of the passes broadly influence the distribution patterns of both transitory (cetaceans) and stationary (SSL rookery population trends) predators along the central and eastern Aleutian Islands. In order to explore the relative influences of a broad array of measured environmental parameters with disparate data on multiple marine mammal species, we constructed generalized additive models (GAMs). GAMs were constructed to explore potential correlations between diet, decline and/or distribution patterns of six apex predators with the physical characteristics of the eastern (Unimak, Akutan and Umnak), transition (Samalga), and central Aleutian passes (Amukta, Seguam, and Tanaga) (see: Ladd *et al.*, this volume). We suggest that the observed patterns, explored through application of GAMs, provide strong inference for the relevance of bottom-up influences in the diet and distribution marine mammals.

METHODS

Steller sea lion diet and population

Regional relationships between diet and population trend among the Western Stock of Steller sea lions were updated and reevaluated to include newly available data through 2001, following methods described in Sinclair and Zeppelin (2002). For modeling purposes, diet and population data were then reduced to that occurring only on the 16 rookeries within the APC study area and diversity and cluster analyses were reconstructed.

Steller sea lion scats (n = 2,564) were collected May through September, 1990-2001 across the range of the Western Stock. Only data collected within the APC study area were used for modeling, and these included 1,262 scats collected May through September from 14 of the 16 sites analyzed for population trend during 1990-2001 (Table 1). The relative importance of prey species was determined by their frequency of occurrence in scat samples, which at this time of year, represent primarily the diet of adult females. Similarities in prey composition between rookeries were determined by principal components analysis (PCA) and an agglomerative hierarchical cluster analysis (Ludwig and Reynolds, 1988). Principal components analysis was calculated on a correlation matrix using prey species as variables and 14 rookery sites as observations, thereby reducing data to those species accounting for most of the variance. To minimize zeros in the analysis, only prey that occurred in $\geq 5\%$ of the scats across all sites were included as variables in the PCA. Cluster analysis was then conducted on the PCA factors using squared Euclidian distance (Ludwig and Reynolds, 1988) as a measure of similarity between sites, and Ward's (1963) method to compare cluster distances. Diet diversity at the 14 rookeries within the APC study area which had diet information was calculated using Shannon's index of

diversity, H , where p_i is the proportion of the i th species in the scat sample (Ludwig and Reynolds, 1988):

$$H = \sum_{i=1}^n p_i \ln p_i \quad [1]$$

Steller sea lion population trend values were calculated by regressing the natural logarithm of the 1976-2001 non-pup counts over time (Sease and Gudmundson, 2002; York *et al.*, 1996) on the 16 rookeries within the APC study area. Counts were averaged in years where multiple counts were made.

Cetacean distribution

Visual surveys for cetaceans were conducted for 12 to 16 hours each day during the APC, from 4-23 June 2001, and 19 May–18 June 2002. In 2001, the area surveyed extended west from Seward, Alaska to Seguam Pass (including the Gulf of Alaska south of the Kenai Peninsula, Shelikof Strait and along the Alaska Peninsula). In 2002, the cetacean survey focused solely on the area from Unimak Pass to Tanaga Pass (see Fig. X, intro chap., this volume). Visual surveys were conducted from port and starboard stations on the bridge whenever the ship was in transit. Observers searched for cetaceans from the bow to 90° abeam with naked eye and handheld binoculars. Data were recorded by the starboard observer using WinCruz software on a laptop computer interfaced to the ship's global positioning system (GPS). When marine mammals were seen, bearing (in 2001 only), distance (reticular), species, group size, course, and speed were recorded. When possible, during encounters with killer whales, the ship was diverted or a small zodiac deployed, to allow close approach for photographic and biopsy sampling. These efforts provided data needed for the subsequent identification of individual whales (see Ford *et al.*, 1994) and their assignment to either mammal-eating or fish-eating (resident) ecotypes (see Barrett-Lennard *et al.*, 1996).

The effort and cetacean sightings along the visual survey trackline were plotted in ArcMap 8.2 (ESRI, 2002). Cetacean sightings were plotted from Seward to Tanaga Pass to provide an interspecies comparison of distribution patterns. However, for modeling purposes, in order to correspond cetacean sightings with the area of intensive bio-physical sampling in both years, sightings data were restricted to the Aleutian passes study area extending from Unimak to Tanaga Pass (see Fig. X, intro chap, this volume).

To facilitate modeling cetacean distribution, the study area was post-stratified by constructing a grid in ArcMap that consisted of 108, 10 km wide blocks (Fig. 2). These blocks were then split into north and south sections at the mid-point of the nearest island. The distance of each block to the center of the nearest sampled pass was measured from the center point of each block. The presence of on-effort trackline and each cetacean species was determined for each block. In total, there were 153 blocks with survey effort. Since the cruise was not designed as a population survey, no tally was made of the number of sightings by species within each survey block, however this information is provided in Table 2. Instead, cetaceans were scored only as present or absent in each block. There were sufficient sightings of five cetacean species to model their occurrence in blocks with effort: Dall's porpoise, killer, sperm, minke, and humpback whales.

Oceanographic characteristics for each pass were determined by integrating the field sampling values over the top 50 meters (see Ladd *et al.*, this volume, for description of oceanographic collections). For each SSL rookery and each block with cetaceans, the nearest measured pass was determined and the oceanographic characteristics of that pass were linked to the block or rookery. When a pass was sampled more than once, average temperature, salinity, and fluorescence, and maximum depth values were used. Average values were used in 2001 for

Akutan Pass which was sampled on June 14th and 15th. In 2002, research was initiated earlier than in 2001, with the result that fluorescence values in the passes were higher at the beginning of the survey; presumably due to the end of the spring phytoplankton bloom. To avoid confounding model results, the first eight days of the 2002 cruise were removed from the data set with May 27th being the first day used and fluorescence values falling below 2.5 volts. This resulted in the loss of the May transects of Akutan and Unimak Passes in 2002, however both passes were sampled in June of that year and those values were used in analyses.

Modeling¹

Generalized additive models (GAMs) were constructed for SSL diet diversity and rookery population trend (with and without prey frequency of occurrence values), and for the five predominant cetacean species in relation to the oceanographic and geographic aspects of the passes. As a nonparametric extension of generalized linear models (GLMs), GAMs share the same statistical properties but, the functional relationship between the response variable and each predictor variable is estimated rather than restricted to a particular functional form (Hastie and Tibshirani, 1999). The complete model is the sum of all predictor functions, $f(x)$, plus a constant, c :

$$y = c + \sum_{i=1}^n f(x) \quad [2]$$

Estimates of diet diversity and population trend for 1990-2001 were modeled as Gaussian response variables with identity link functions. For cetacean distribution, the presence/absence

¹ Population trend values were calculated for 16 different rookeries in the APC study area. No diet information was available for the rookery at Agligadak. Non-pup counts were conducted separately for Cape Yakak and Lake Point on Adak, but scats were combined. To model diet diversity, Cape Yakak and Lake Point were combined as a single rookery. To model population trend with and without diet as explanatory variables, Cape Yakak and Lake Point were modeled separately. Thus models of diet diversity used 14 rookeries; excluding Agligadak and combining Cape Yakak and Lake Point. Models of population trend with diet as explanatory variables used 15 rookeries; excluding Agligadak and modeling Cape Yakak and Lake Point separately. Finally models of population trend without diet as explanatory variables used all 16 rookeries.

of each species was modeled as a generalized additive logistic model; a binomial response variable with a logit link function. Continuous explanatory variables were modeled as linear functions, smoothing splines with 3 equivalent degrees of freedom, or removed from the model. Three equivalent degrees of freedom for smoothing splines were selected to allow nonlinear effects, but to limit unrealistic tracking of the data. Categorical explanatory variables were modeled as linear functions or removed from the model.

Oceanographic and geographic variables were chosen as explanatory variables based on their availability from the cruise and their likelihood of serving as a characteristic signature of the measured pass as well as a potential influence on productivity and predator distribution. Because of correlations between explanatory variables, six sets of explanatory variables were fit for each response variable. Each of the sets constructed used four explanatory variables: 1) mean fluorescence in the nearest measured pass, 2) maximum depth, mean temperature or mean salinity in the nearest measured pass, 3) distance to the nearest pass with or without blocks/rookeries west being negative values, and 4) the direction to the block/rookery from Samalga Pass. Nitrate was also measured during field studies but was excluded in the GAMs because it was correlated with salinity and temperature and unavailable for Umnak Pass. For Steller sea lion population trend, an additional 18 sets were constructed by adding one of the three diet variables (diet cluster, diet diversity, or frequency of occurrence of seven prey species) as explanatory variables to the four oceanographic and geographic variables.

For each set of explanatory variables, initial models with all variables were fit using the gam function in S-PLUS 2000 (MathSoft, 2000). Stepwise model selection, using the step.gam function, was then used to determine which variables in each set were significant using Akaike's information criterion (AIC). The resulting 6 (or 24) models were compared using the Cp statistic

in the S-PLUS anova function to determine the overall best fit models described here. The Cp statistic, which is the Pearson chi-squared version of AIC, was chosen since the models were not necessarily nested.

RESULTS

Western Stock SSL diet and population trend

Analyses of the additional three years of SSL diet and population data did not alter the boundaries of the proposed metapopulation regions, reinforcing the inference that diet and population decline patterns among the Western Stock are linked. From Kodiak Island westward, prey species that comprised each of three clusters, and clustering by population trends within diet regions, remained closely aligned as in Sinclair and Zeppelin (2002) (Fig. 1a, b). Again the strongest boundary between clusters was at Samalga Pass. Rookeries in the vicinity of Unimak Pass, the area of greatest long-term population stability (York *et al.*, 1996), remained the area of highest diet diversity when data was extended through 2001 across the range of the Western Stock.

Diet data (1990-2001) was available for 14 of the 16 rookeries falling within the APC study area (Figure 2). Seven prey species occurred at frequencies $\geq 5\%$ falling into two clusters, one on either side of Samalga Pass. Cluster 2 (east of Samalga Pass) contained both the highest and lowest values for prey diversity but, averaged higher overall relative to Cluster 1 (west of Samalga Pass) (Table 1). Population trend data (1976-2001) was available for all of the 16 rookeries falling within the APC study area. The area of greatest stability in population trend counts fell within Cluster 2 (Table 1).

Cetacean distribution

Nine species of cetaceans were seen during the APC (Table 2, Fig. 3). Seven species were observed on both cruises, with the distribution pattern of four (fin, humpback, minke and sperm whales) aligning with regional patterns of SSL diet and population trends across the range of the Western Stock. For example, fin whale distribution (Fig. 3a) extended from Shelikof Strait west

to the Shumagin Islands, corresponding to SSL diet cluster 3 (Fig. 1a). Humpback whale distribution was coincident with SSL diet cluster 2 with many sightings at the Shumagin Islands and at Unimak and Akutan Passes, but only single sightings at Umnak, Samalga, and Amukta Passes. Conversely, with the exception of a single sighting, killer and minke whales were only seen west of Unimak Pass in SSL diet cluster areas 2 and 1, and sperm whales only west of Samalga Pass in the region of SSL diet cluster 1 (Fig. 3a, b). The consistency in pattern between SSL population trend/diet demarcations (Fig. 1a, b) and large whale distribution (Fig. 3a, b), species with widely divergent diets and habits, suggests reliance on bio-physical (bottom-up) structuring of the nearshore ecosystem. Of note, the distribution of Dall's porpoise did not reflect the longitudinal pattern of the large whales, but were seen across the entire area surveyed. Sightings of the remaining three species (harbor porpoise, Pacific white-sided dolphin and Baird's beaked whale) were too rare to infer distribution pattern (Fig. 3b).

Killer whales were frequently seen near all passes sampled, and were particularly common along the north Aleutian Island coastlines between Unimak Pass and Samalga Pass (Figs. 3b and 4). Killer whale ecotype was determined for 29 of 42 encounters by genetic analyses of biopsied tissue, and by photographic identification of individual whales. Where ecotype was determined, most encounters proved to be with the piscivorous ('resident') killer whale ecotype (Fig. 4). No mammal-eating ('transient') killer whales were identified during the 2001 cruise and only 8% (39 of 500) of the killer whales identified in 2002 were the 'transient' ecotype. The four encounters with transient killer whales occurred in Unimak and north of Akutan Pass. In addition, there was one sighting of the ecotype called 'offshore', animals which also appear to focus their diet on fish (Herman *et al.*, 2004).

Modeling data within the APC study area

The results of the GAMs for Steller sea lion diet diversity and population trend reflected the importance of rookery location with regard to maximum depth of the nearest measured pass on these rookeries (Table 3). When modeled as a function of pass oceanography and geography, diet diversity (14 rookeries) was a function of pass depth alone with diversity increasing as depth decreases (Fig. 5a). Population trend was significantly related to maximum depth and relationship (east vs. west) to Samalga Pass when modeled as a function of pass oceanography and geography alone (16 rookeries) (Fig. 5b, c). In this model, rookeries near deeper passes and east of Samalga Pass had higher growth rates. Population trend was also modeled with diet information as a function of pass oceanography and geography for the 15 rookeries¹ containing diet cluster, diet diversity, or frequency of occurrence values, and as a model control on the same 15 rookeries excluding the diet information. The best fit model was that which included the frequency of occurrence of herring (*Clupea pallasii*) and salmon (*Salmonidae*) as well as maximum depth. In this model, population trend was positive with increasing depth in the nearest measured pass as well as increased frequencies of occurrence of herring and salmon (Fig. 6).

The best fit models for cetacean distribution varied among the five species (Table 3), but all showed significant relationships with distance to the nearest measured pass and all except Dalls porpoise showed significant relationships with fluorescence, temperature, or both. The probability of sighting increased closer to the passes for all five cetacean species (Fig. 7a-e). Whether the block was east or west of the nearest pass was a factor for humpback whales and Dall's porpoise (Fig. 7a, b) since the best fit models for both species used a combined distance-direction variable rather than simple distance. Both humpback and Dall's had unimodal

relationships with distance which peaked at small distances and remained higher west of the passes. Humpback whales were most often observed within passes.

Fluorescence in the top 50 meters of the pass was significantly related to the distribution of humpback, minke and killer whales (Table 3; Fig. 8a-c). The relationship between humpback presence and fluorescence was a unimodal smooth function which peaked at around 0.18 volts which corresponds to Unimak Pass (Fig. 8a). Minke and killer whales were linearly related to fluorescence. The probability of sighting minke whales increased near passes with higher fluorescence values, such as Tanaga and Samalga (Fig. 8b), but killer whales were more likely to be sighted near low fluorescence, such as Umnak and Amukta (Fig. 8c).

Mean temperature in the top 50m was significantly correlated to the distribution of humpback, sperm and killer whales (Fig. 9a-c). Humpbacks were linearly related to mean temperature in the nearest pass, with higher probability of sighting near warmer (eastern) passes (Fig. 9a). The relationship between sperm whale presence and mean pass temperature was a smooth function which generally increased with decreasing temperature except for a slight decline between 4.37°C (Tanaga Pass) and 4.24°C (Seguam Pass) (Fig. 9b).

The partial relationship between the probability of killer whale sightings and temperature was a linear relationship, with increased sightings associated with lower temperatures (Fig. 9c). However, when killer whale presence was modeled as a function of temperature alone, this relationship reversed. Exploring bivariate models by pairing temperature with each of the other significant variables in turn revealed that the relationship between killer whales and temperature reversed when direction to Samalga was included, thus illustrating an interaction between these two variables.

Dall's porpoise occurrence was significantly related to the maximum depth in the nearest pass (Fig. 10). This relationship was a smooth function with Dall's presence generally increasing with increasing depth except for a slight decline between 125m (Akutan Pass), 166m (Umnak Pass) and 168m (Unimak Pass). That the model highlights a significant relationship between the presence of Dall's porpoise and maximum depth in the pass, like Steller sea lions, is interesting since they were observed throughout the extent of the cruise. For the cetacean models, 58% of the 153 blocks had Dall's porpoise sightings, but only 10 to 23% of the blocks had sightings of the whale species limiting the power of the GAMs.

Among cetaceans, the direction east or west of Samalga Pass specifically, was only significant for killer whales. Killer whales had a higher probability of occurrence east of Samalga Pass (Table 3, Fig. 11). Mean salinity in the nearest measured pass was not significant for any of the predators.

DISCUSSION

We are accustomed to latitudinal boundaries in ocean climate such as Point Conception in California, or Cape Hatteras in North Carolina, where changes in species composition and water mass properties are both abrupt and predictable (Emery, 1960; McGowan, 1974; Reid, *et al.* 1958; Sverdrup, *et al.* 1942). But, persistent, broad longitudinal zones have not been described prior to the research along the Aleutian Island chain, as presented in this volume. The parallel geographic breaks in long-term Steller sea lion diet and rookery trends, together with short-term observations of distributional patterns among both baleen and odontocete cetaceans suggests a constancy to the marine environment that is remarkable considering the diversity in behavior and foraging requirements represented by such a diverse assemblage of predators.

Results presented here and in other studies in this volume (Byrd *et al.*; Call and Loughlin; Coyle; Fadely *et al.*; Ladd *et al.*; Logerwell *et al.*) suggest that regional physical characteristics of hydrography and current flow generated by the passes along the eastern and central Aleutian Islands are not only predictable, but comprise a series of eco-boundaries, with the most pronounced break at Samalga Pass. Although the cetacean distributions from the APC surveys can convey only a brief snapshot, we suggest that the patterns presented are representative for each species, at least during this time of year. This suggestion is bolstered by results from a cetacean survey conducted in July and August of 2001 and 2002 (Zerbini *et al.*, 2004), where patterns of cetacean distribution essentially mirrored those presented here. Zerbini *et al.* (2004) concluded that these animals are residing in traditional, pre-whaling summering grounds, lending support to the idea that the distributional boundaries may be long standing.

Construction of GAMs served as a useful tool to investigate which features associated with the passes might contribute to boundary delineation. These models do not assume linearity,

yet captured linear relationships between physical components of pass signatures and mammal distributions. The consistency between the GAMs results and our observation of SSL rookery population trend, diet, and cetacean distributions suggest that the observed patterns have biological foundation and that future research on these populations should be conducted with consideration of these patterns. This is especially true in the case of the metapopulation structure proposed for the Western Stock of SSL. Current research emphasis contrasts diet, health, and growth patterns between the thriving Eastern Stock and the endangered Western Stock as a means of elucidating the extenuating causes of decline. Yet, this and other studies suggest a finer scale of research is needed where the focus is on comparisons between sub-populations of the Western Stock.

The best fit GAMs of predators and descriptive variables all identified geographic proximity (distance for cetaceans, depth for SSLs) to the nearest measured pass as a significant explanatory variable. However, the physical parameters measured within the passes varied in the significance of their influence on the distribution of predator species, with identified pattern generally attributable to diet. The variables that lack significance to particular species can teach us as much as those that are significant. For example, distributions of humpback and sperm whales were clearly attributable to boundaries between neritic and oceanic water signatures (Ladd *et al.*, this volume) and zooplankton prey fields (Coyle, this volume) at Samalga Pass as determined by temperature. Humpback distribution was particularly aggregated near Unimak and Akutan passes, where abundance indices of neritic *Calanus marshallae* and *Pseudocalanus* spp. were high. It is unclear whether the whales were consuming the zooplankton directly, or feeding upon forage fish consumers of the plankton. Conversely, sperm whales generally feed on large, deep living, squid and fish in oceanic waters (Rice, 1989) and were observed in this

study in the portion of the APC most strongly influenced by a limited continental shelf and oceanic signature as indicated by cold temperatures. Of note, minke whale distribution crossed the neritic/oceanic boundary observed at Samalga Pass (Coyle, this volume; Ladd *et al.*, this volume), and a significant increase in the probability of sighting minke whales was associated with high fluorescence.

Our results are similar to the findings of Byrd *et al.* (this volume) who used a simple linear model to determine that population trends of birds that are nearshore piscivores are positively related to increased distance from the nearest pass. This same pattern was detected for Steller sea lions (adult females are also nearshore piscivores), prior to reducing our models to the 16 rookeries falling within the APC study area. Byrd *et al.* (this volume) also determined that like the large baleen whales in this study, planktivorous and offshore feeding birds were more abundant near the passes.

The results of our exploration with GAMs provide strong inference for the relevance of bottom-up structuring in the diet and distribution of marine mammals. By identifying either fluorescence (our best measure of primary productivity) and temperature (the variable most representative of boundary zone delineations) as significant explanatory variables among all large cetaceans, the models suggest that the link between hydrography and prey resources is relevant to both apex predators such as sperm and killer whales, as well as secondary level predators such as minke and humpback whales. Dall's porpoise, consumers of both oceanic (myctophid fishes) and nearshore (juvenile Pollock, herring) prey (Beamish *et al.*, 1999; Crawford 1981), bridge the trophic level between the two groups, as reflected in their presence throughout the study area and the lack of significance of hydrographic variables to their distribution in the models. The similarity in relationship between the presence of Dall's porpoise

and SSL population trend to maximum depth in the pass may be related to diet as well. There is diet overlap between Dall's porpoise (Beamish *et al.*, 1999; Crawford, 1981) and Steller sea lions in both the species and size of prey consumed, particularly in the consumption of herring and salmon, the two prey species significantly related to population strength in Steller sea lion models.

The studies in this volume indicate that the dynamic regional signatures associated with at least some of the Aleutian passes may have far reaching ecological effects. Long-term diet (12 yr) and population trend (25 yr) data for Steller sea lions provides the best example of the potential extent of these signatures in effecting the associations between predator and prey. For examples, prey consumed in summer by post-parturient SSLs of the Western Stock are largely those that show strong, predictable, nearshore migratory movements along the Aleutian Island chain (Fadely *et al.*, this volume; Loggerwell *et al.*, this volume; McDermott *et al.*, this volume; Sinclair and Zeppelin, 2002). Among otariid pinnipeds, population gain and decline is most heavily influenced by the reproductive success of these adult females and survival of juveniles (York, 1994). Similar to other otariids (Baker *et al.*, 1995; Kenyon and Wilke, 1953), female Steller sea lions are thought to return to the rookery of their birth (natal rookery) to mate and raise their young (Sinclair and Zeppelin, 2000; Sinclair and Zeppelin, 2002; Raum-Suryan *et al.*, 2002) and pups may remain with their mothers for up to two years (Loughlin *et al.*, 2003) learning to forage specifically in waters within the region of their natal rookery (Sinclair and Zeppelin, 2002). In this way, consistency in the quality of diet composition and predictability of oceanographic conditions in the region of the natal rookery, may influence future reproductive success and therefore the population trend of Steller sea lions (Sinclair and Zeppelin, 2002).

In addition to the relevance of prey availability and quality, prey diversity appears to have some influence on population success among otariid pinnipeds (Call and Loughlin, this volume; Merrick *et al.*, 1997; Sinclair, 1988; Sinclair *et al.*, 1994; Sinclair and Zeppelin, 2002). Foraging behavior of juvenile Steller sea lions is measurably more robust in areas of complex habitat and higher diet diversity (Fadely *et al.*, this volume) and measures of diversity were highest in the region of greatest population stability in this study. It is well known that habitat complexity leads to a diversity of prey resources (Feder *et al.*, 1974). Current flow, and its changing east to west pattern from the Alaska Peninsula to the central Aleutian Islands is key to nutrient distribution and the creation of fronts and boundaries as noted by Ladd *et al.* (this volume) and cited as relevant (Byrd *et al.*, this volume; Call and Loughlin, this volume; Coyle; Fadely *et al.*, this volume; Ladd *et al.*, this volume; Logerwell *et al.*, this volume) across the trophic scale. We suggest that flow, as generated by signature passes, provides a complex habitat of boundary regions that concentrate nutrients, primary producers, and secondary prey resources which both directly and indirectly increase the likelihood of successful foraging for predators, in large part due to predictability and diversity of prey. The GAMs serve as a first step in the process of identifying the specific structural influences within current flow that influence species specific distributions.

There were too few encounters with killer whales on the APC surveys to draw any conclusions regarding their role as ‘top down’ structuring elements of the Aleutian Passes ecosystem. The mammal eating (transient) killer whale ecotype was seen only four times in 2002, always near Unimak and Akutan passes where aggregations of the piscivorous (resident) killer whale ecotype are also common. Both ecotypes are capable of ranging over thousands of kilometers so the distribution presented here, as with the other cetaceans, should be considered

only a ‘regional snapshot’ of killer whale occurrence. Though not specifically informative to this study, the killer whale photo-ID and biopsy data from the APC surveys was a significant contribution to the broader assessment of killer whales in the Gulf of Alaska and Aleutian Islands conducted from 2001-03 (Wade *et al.*, 2003). Specifically, photographs taken from the ALPHA HELIX constituted ‘marks’, which will be used in the calculation of mark-recapture estimates of killer whale population size by ecotype. These estimates, coupled with additional investigation of killer whale distribution and dietary preference (e.g., Herman *et al.*, 2004) will provide the foundation required for interpretation of hypotheses regarding the role of killer whales in the Alaskan marine ecosystem (Springer *et al.*, 2003).

Future consideration

The observation of coherent longitudinal pattern across a complex suite of marine mammal data supports the contention that physical (bottom-up) forcing is a key organizational feature of the eastern and central Aleutian Island ecosystem. Results from the GAM exercise highlight the complexities of this ecosystem and provide a basis for future exploration of oceanographic parameters characteristic of regional boundaries. Continued development of such models may eventuate in the advancement of predictive ecosystem-based management, whereby oceanographic pattern and associated multi-species groups are the focus, as opposed to the current standard of single-species management.

This study suffered from a high degree of unevenness in sampling scale, a problem common in ecological studies. In fact, interfacing of phenomena that occur on very different scales of space, time and ecological organization has been identified as *the* central problem in ecology (Levin, 1992). Here we attempted to relate a 12-25 year diet and population trend for SSL with cetacean observations and oceanographic sampling conducted over 2 years. In doing

so, we are not only assuming that the relative patterns in the oceanographic characteristics of the Aleutian Passes in 2001 and 2002 are representative of 12-25 year span of biological response, but that 25 years is sufficiently representative of a highly variable population trend over a reduced portion of the range. The cetacean models were better aligned with oceanographic measures on a temporal scale, but suffer from narrow focus of geographic scale for animals that can cover great distances in short periods. Further exploration of extant oceanographic and geological data from the APC and other surveys should be the next step in the pursuit of a framework for ecosystem-based modeling. Such an effort will likely rely on alternative model structures, in what has been termed a "rhomboidal" modeling approach (deYoung *et al.*, 2004). This approach requires simplifying food web structure to make simulation of marine organism population structure tractable. Such exploration is sorely needed as preparation for planned ecosystem-focused multi-disciplinary studies (e.g. BEST), whereby the response of marine ecosystems to climate variability is to be explored.

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Over thirty years of applied field and laboratory studies by researchers at the National Marine Mammal Laboratory (NMML) have laid the foundation for many of the studies conducted today. We thank them for their pioneering efforts. We also thank the captains and crew of the R/V *Alpha Helix* for the success of both Aleutian Passes cruises, the marine mammal observers (Nancy Black, Bob Pitman and Jack Swenson) and 2001 Team Leader Lori Mazzuca (NMML/Kodiak) for their dedication to survey effort and killer whale photo and biopsy sampling. Thanks are also extended to Marilyn Dahlheim (NMML) and Dave Ellifrit for the long hours of effort required to provide positive identifications of individual transient killer whales.

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Table 1. Population trends, frequencies of prey occurring at $\geq 5\%$, diet diversity, and cluster values for Steller sea lion rookeries falling within the Aleutian Passes Cruise study area in 2001 and 2002.

Rookery site	Latitude °N	Longitude °W	Steller sea lion population trend 1976-2001	Scat sample size	Prey percent frequency of occurrence values						Diet diver- sity	Clus- ter	
					Atka mack- erel	Ceph- alo- pods	Sal- mon	Walleye pollock	Pacific herring	Pacific sand lance	Pacific Cod		
UGAMAK	54.21042	164.78417	-0.0818	104	7.9	1.4	40.7	37.1	20.7	5.7	4.3	1.77	2
AKUN/BILLINGS HEAD	54.29322	165.53142	-0.0702	71	28.2	1.4	7	29.6	54.9	4.2	15.5	1.82	2
AKUTAN/CAPE MORGAN	54.05906	166.02777	-0.0655	78	17.9	0	65.4	21.8	43.6	1.3	3.8	1.59	2
BOGOSLOF/FIRE ISLAND	53.92822	168.03417	-0.0963	123	26	20.3	26	69.1	14.6	3.3	2.4	2.01	2
OGCHUL	52.99517	168.40402	-0.0945	11	18.2	0	63.6	36.4	0	0	0	0.98	2
ADUGAK	52.91167	169.17500	-0.0854	79	77.2	6.3	16.5	15.2	6.3	0	10.1	1.66	1
YUNASKA	52.69000	170.60583	-0.1063	105	92.4	21.9	8.6	22.9	0	0	4.8	1.54	1
SEGUAM/SADDLE RIDGE	52.35058	172.56667	-0.096	160	86.3	9.4	8.1	3.8	0	2.5	4.4	1.27	1
AGLIGADAK	52.10150	172.90383	-0.1768										
AMLIA/SVIECH. HARBOR	52.03000	173.39833	-0.0943	40	95	5	12.5	25	0	3.8	25	1.8	1
KASATOCHI/NORTH POINT	52.18517	175.51667	-0.0936	156	74.4	25	47.4	37.2	0	1.9	9	1.85	1
ADAK/LAKE POINT	51.62333	176.99333	-0.0111	37	81.1	16.2	64.9	24.3	0	2.7	2.7	1.64	1
ADAK/CAPEYAKAK	51.59167	176.95167	-0.0486										
GRAMP ROCK	51.48117	178.34300	-0.063	60	96.7	31.7	23.3	8.3	0	0	3.3	1.28	1
TAG	51.55833	178.57500	-0.0842	101	97	18.8	3	1	1	0	5	1.05	1
ULAK/HASGOX POINT	51.31333	178.98750	-0.0687	137	96.4	33.6	17.5	8	0	0	1.5	1.23	1

Table 2. Cetacean sighting summary during the 2001 and 2002 Aleutian Passes study.

	2001		2002	
	Number of sightings	Number of individuals	Number of sightings	Number of individuals
Harbor porpoise	5	11	1	1
Dall's porpoise	143	769	261	1410
Pacific white-sided dolphin	0	0	1	2
Killer whale	15	113	27	500
Baird's beaked whale	0	0	1	3
Sperm whale	11	18	35	38
Humpback whale	31	57	34	202
Minke whale	16	16	19	19
Fin whale	46	117	1	1

Table 3. Sample size and explanatory variables for each generalized additive model of Steller sea lion diet diversity, SSL population trend, and humpback, minke, sperm and killer whale and Dall's porpoise occurrence. Shaded boxes indicate variables which were not used in that model. Significant variables are indicated by the type of relationship which was modeled (factor, linear function, and smooth function). For cetacean occurrence, the sample size numerator indicates the number of blocks with sightings and the denominator is the number of blocks with effort.

	SSL diet diversity	SSL pop. trend	w/out diet	w/ diet cluster	w/ diet diver-sity	with FO	Hump-back whales	Minke whales	Sperm whales	Killer whales	Dall's whales
Sample size	14	16	15	15	15	15	18/153	23/153	16/153	35/153	88/153
Mean pass fluorescence				linear			smooth	linear		linear	
Mean pass temperature							linear		smooth	linear	
Mean pass salinity											
Maximum pass depth	linear	linear				linear					smooth
Distance to nearest pass								smooth	linear	linear	
Distance to nearest pass (west is negative)			smooth	smooth	smooth						smooth
East/west of Samalga Pass		factor								factor	
Atka mackerel fo											
Cephalopod fo											
Herring fo						linear					
Pacific cod fo											
Pollock fo											
Salmon fo											
Sand lance fo											
Diet cluster				factor							
Diet diversity											

FIGURES

Figure 1. Cluster patterns of Steller sea lion diet 1990-1998 (a) and population trend 1976-1994 (b) redrawn from Sinclair and Zeppelin (2002).

Figure 2. A grid overlay of the Aleutian Passes Cruise study area consisting of 108, 10 km wide blocks. The center point of each block was the point from which distance to the center of the nearest measured pass was made for on-effort cetacean sightings falling within that block.

Figure 3. Distribution of large (a) and small (b) cetaceans observed in the Aleutian Passes Cruise study area, during the summer of 2001 and 2002..

Figure 4. Distribution of resident vs. transient type killer whales based on biopsy samples collected from animals observed in the Aleutian Passes Cruise study area, during the summer of 2001 and 2002.

Figure 5. Generalized additive model function and residual values for Steller sea lion diet diversity (diet diversity with oceanographics - see Table 3, column 1) in relation to maximum depth in the nearest pass (A) and the model and residual values for Steller sea lion population trend (population trend on 16 rookeries with oceanographics - see Table 3, column 2) in relation to maximum depth in the nearest pass (B) and direction to Samalga Pass (C). Dashed lines represent upper and lower pointwise twice-standard-error curves. Direction to Samalga was a categorical variable and the width of each function bar represents the sample size.

Figure 6. Generalized additive model functions and residual values for Steller sea lion population trend (population trend with oceanographics on 15 rookeries, see Table 3, column 3) in relation to maximum depth in the nearest pass (A), and (see Table 3, column 6) the frequency of occurrence of herring (B) and salmon (C). Dashed lines represent upper and lower pointwise twice-standard-error curves.

Figure 7. Generalized additive model partial functions and residual values for humpback whale (A), Dall's porpoise (B), minke whale (C), sperm whale (D), and killer whale (E) occurrence in relation to distance to the nearest pass. For humpback whale and Dall's porpoise, the significant variable combined distance and direction to the nearest pass such that the sign indicated the direction and the absolute value indicated the distance. Dashed lines represent upper and lower pointwise twice-standard-error curves.

Figure 8. Generalized additive model partial functions and residual values for humpback (A), minke (B), and killer whale (C) occurrence in relation to fluorescence in the top 50 meters of the nearest pass. Dashed lines represent upper and lower pointwise twice-standard-error curves.

Figure 9. Generalized additive model partial functions and residual values for humpback (A), sperm (B), and killer whale (C) occurrence in relation to temperature in the top 50 meters of the nearest pass. Dashed lines represent upper and lower pointwise twice-standard-error curves.

Figure 10. Generalized additive model partial function and residual values for Dall's porpoise occurrence in relation to maximum depth in the nearest pass. Dashed lines represent upper and lower pointwise twice-standard-error curves.

Figure 11. Generalized additive model partial function and residual values for killer whale occurrence in relation to direction to Samalga Pass. Direction to Samalga was a categorical variable and the width of each function bar represents the sample size.

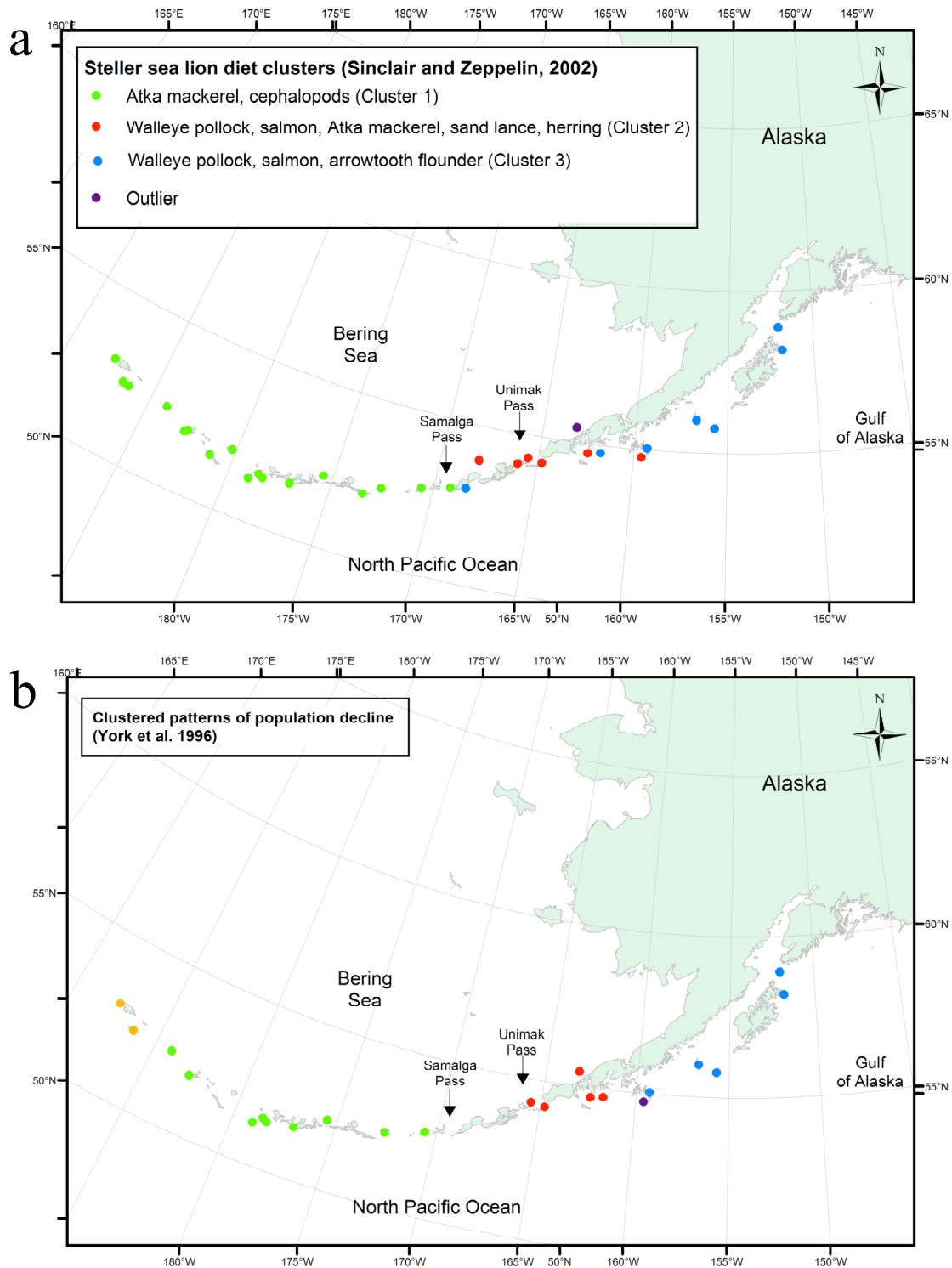
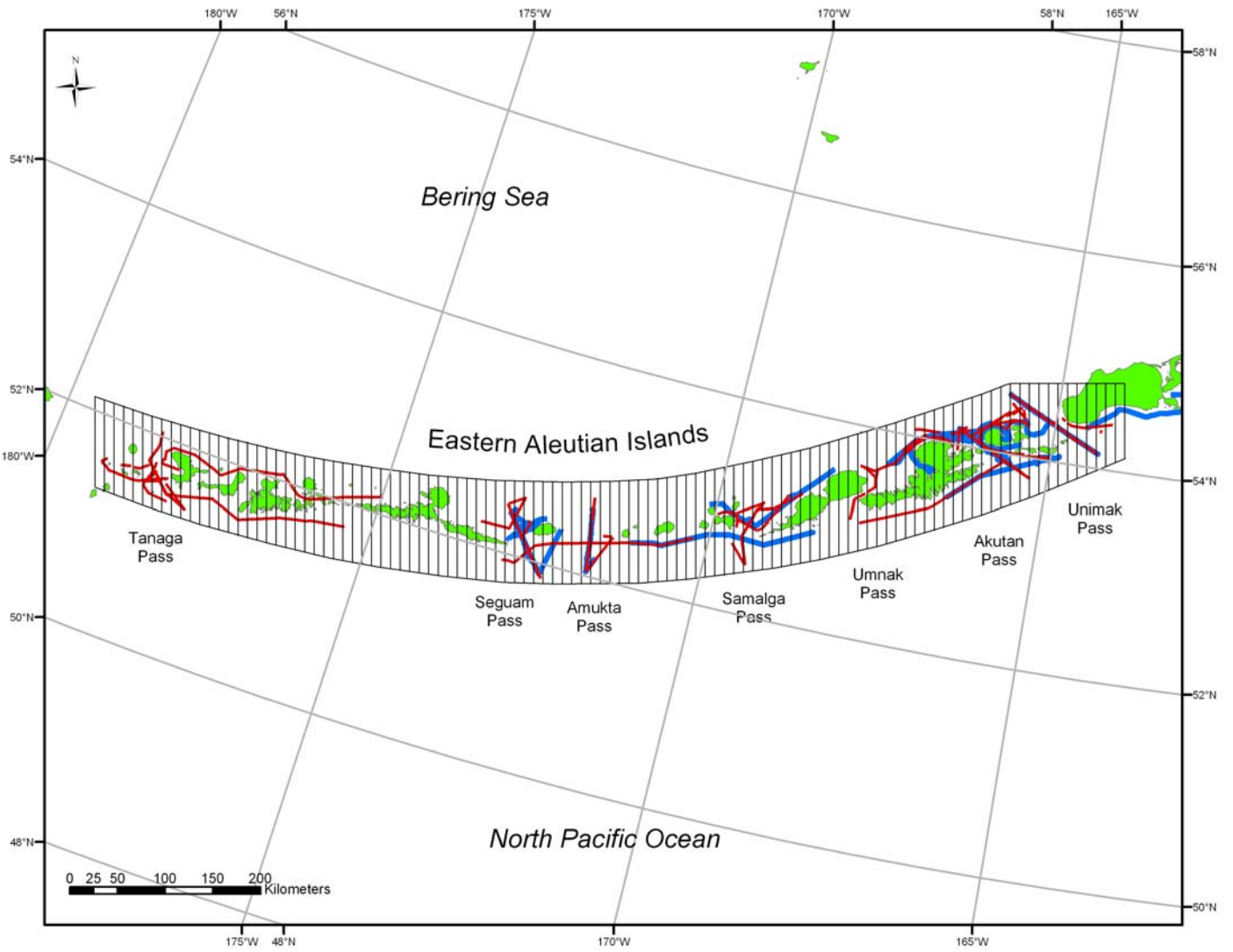
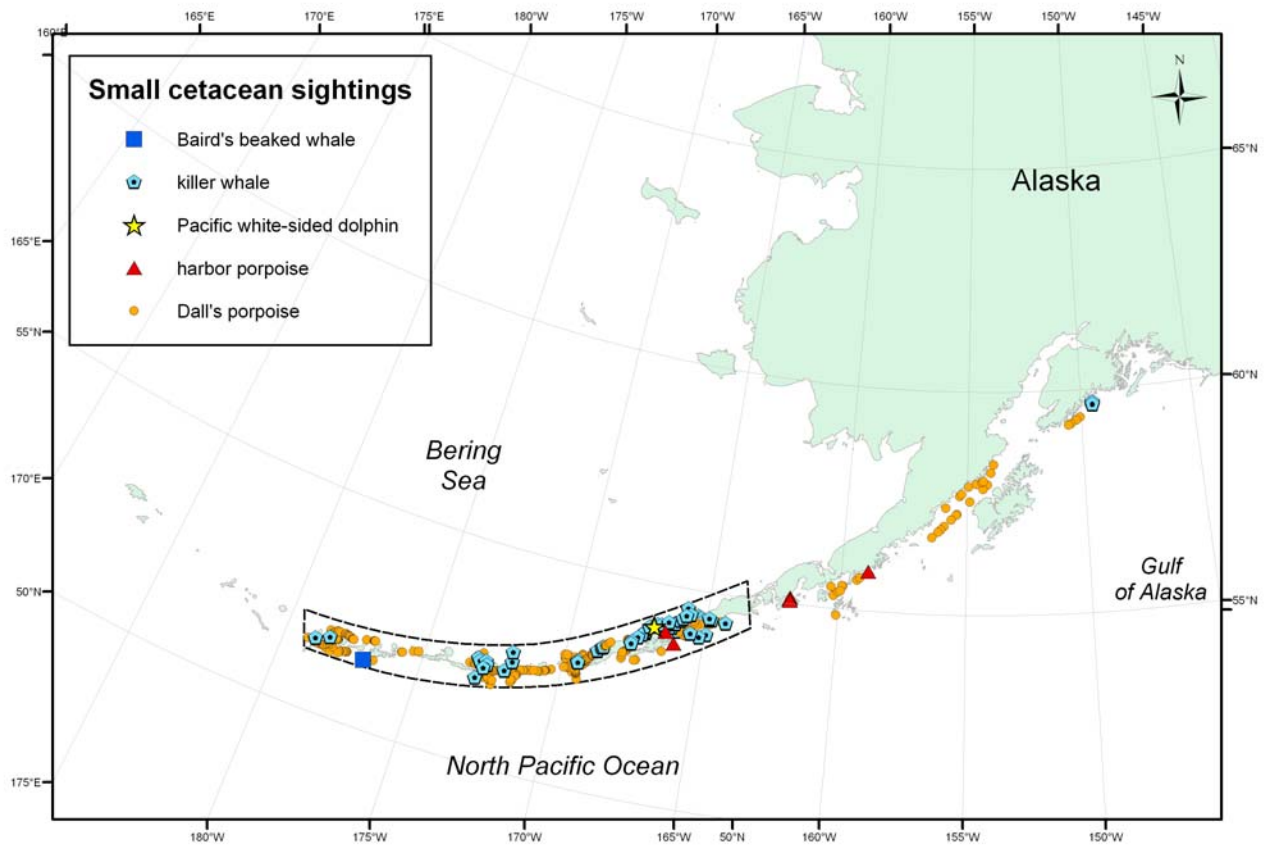
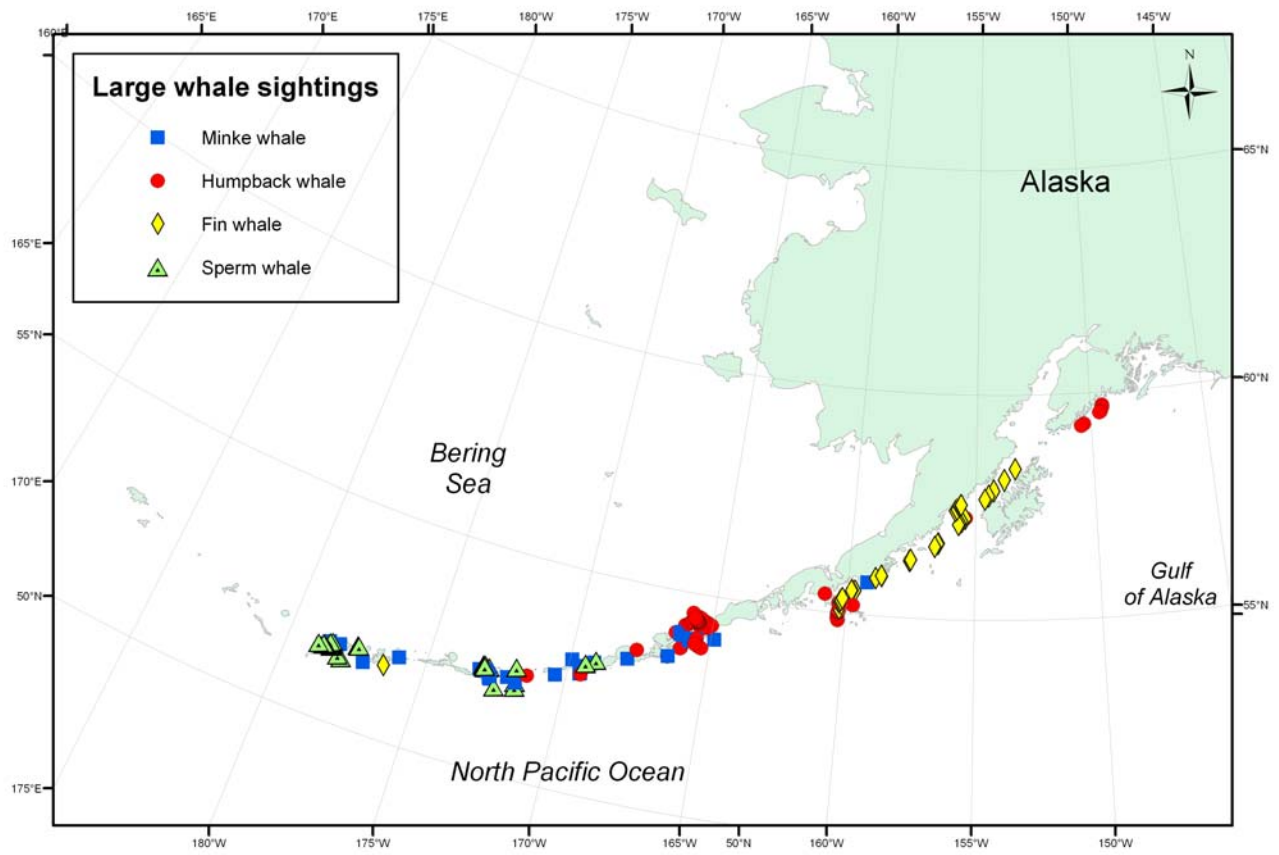
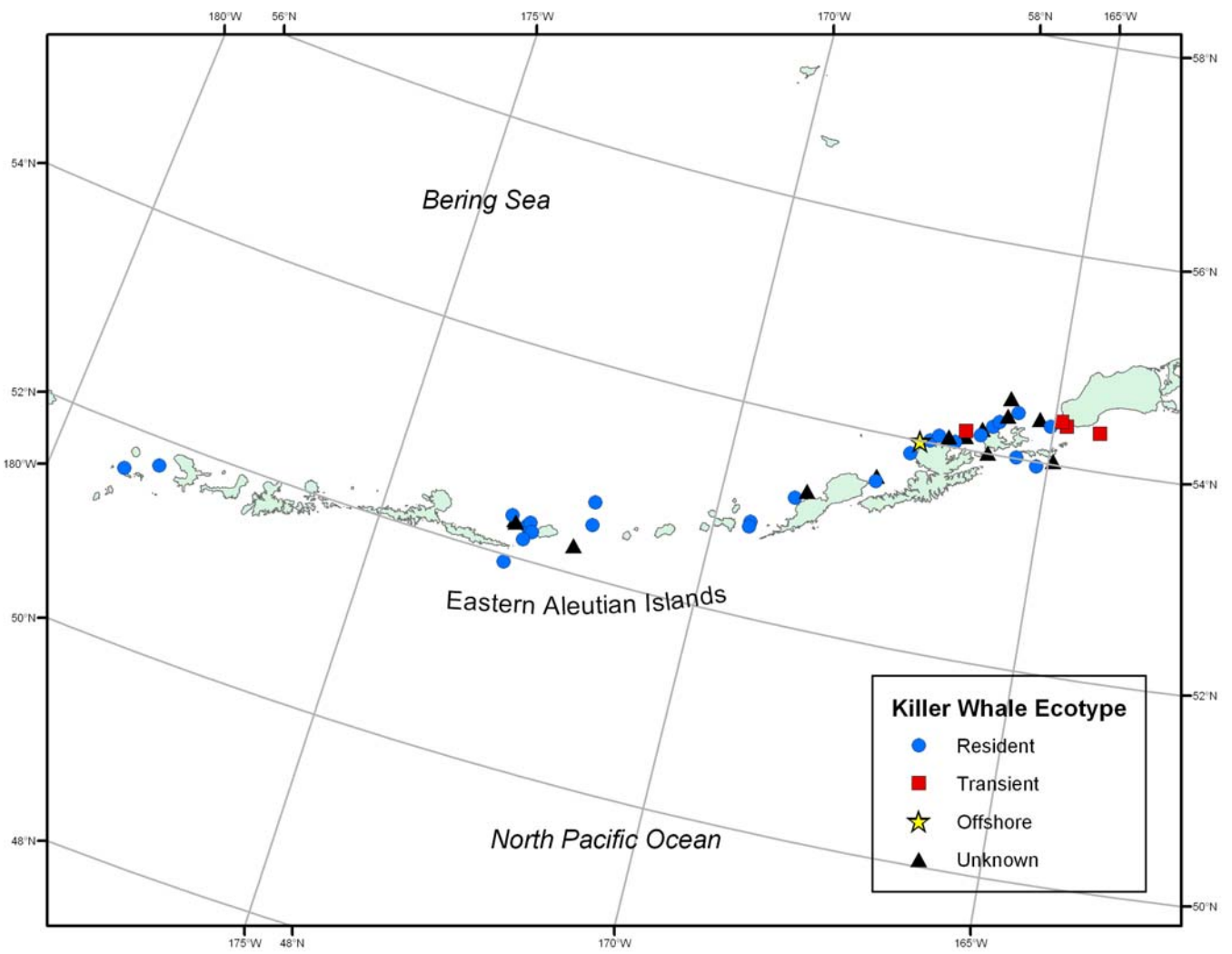


Figure 1. Cluster patterns of Steller sea lion diet 1990-1998 (a) and population trend 1976-1994 (b) redrawn from Sinclair and Zeppelin (2002).







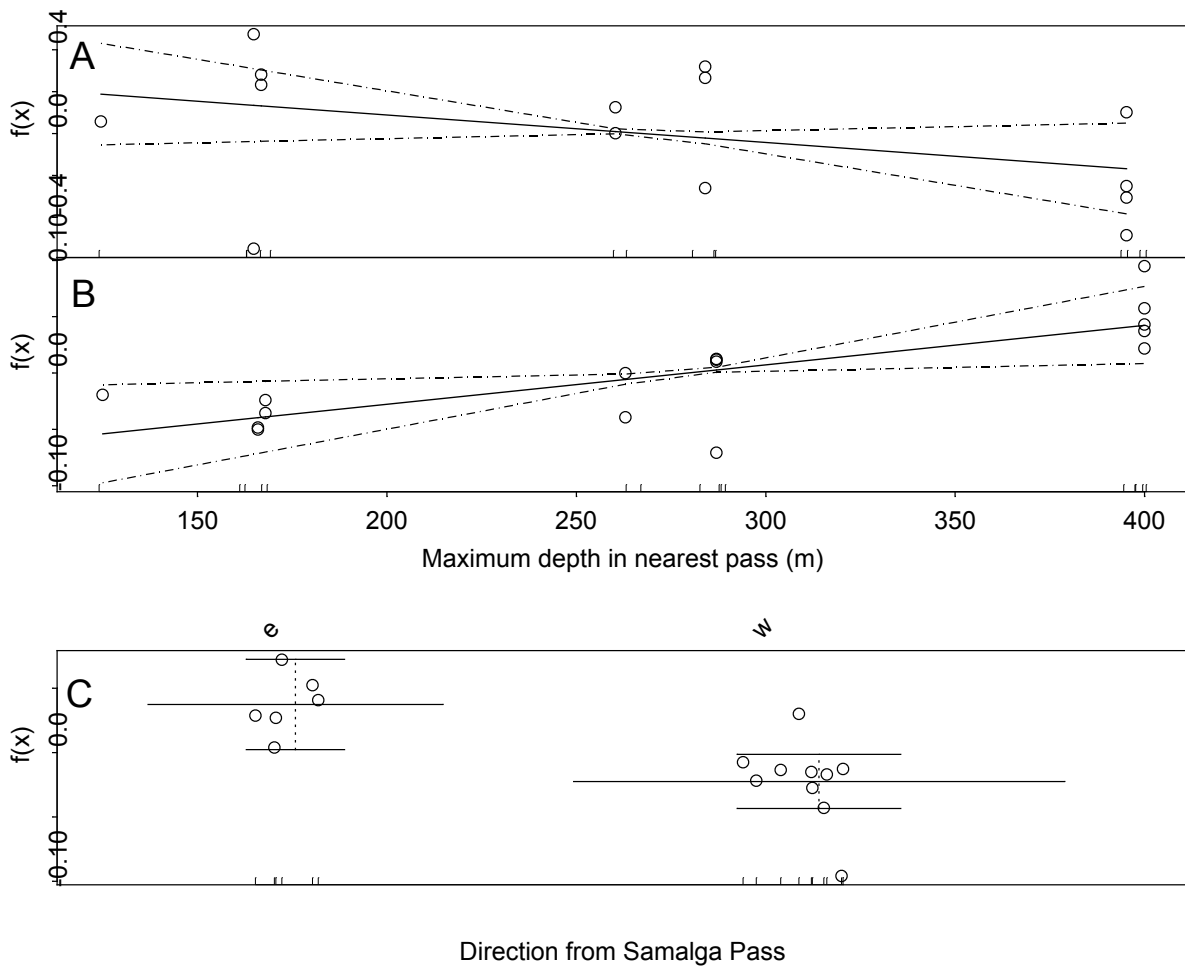


Figure 5. Generalized additive model function and residual values for Steller sea lion diet diversity (diet diversity with oceanographics - see Table 3, column 1) in relation to maximum depth in the nearest pass (A) and the model and residual values for Steller sea lion population trend (population trend on 16 rookeries with oceanographics - see Table 3, column 2) in relation to maximum depth in the nearest pass (B) and direction to Samalga Pass (C). Dashed lines represent upper and lower pointwise twice-standard-error curves. Direction to Samalga was a categorical variable and the width of each function bar represents the sample size.

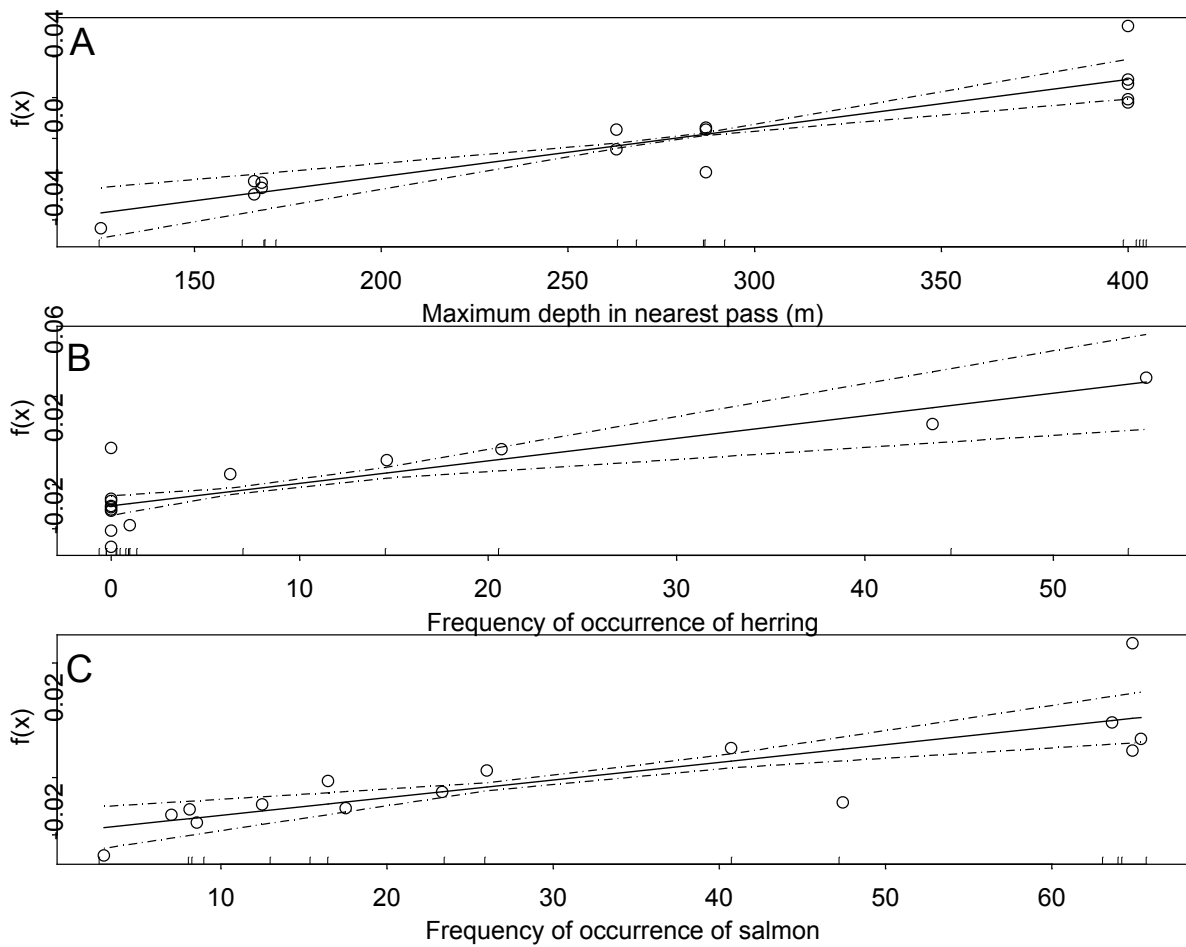


Figure 6. Generalized additive model functions and residual values for Steller sea lion population trend (population trend with oceanographics on 15 rookeries, see Table 3, column 3) in relation to maximum depth in the nearest pass (A), and (see Table 3, column 6) the frequency of occurrence of herring (B) and salmon (C). Dashed lines represent upper and lower pointwise twice-standard-error curves.

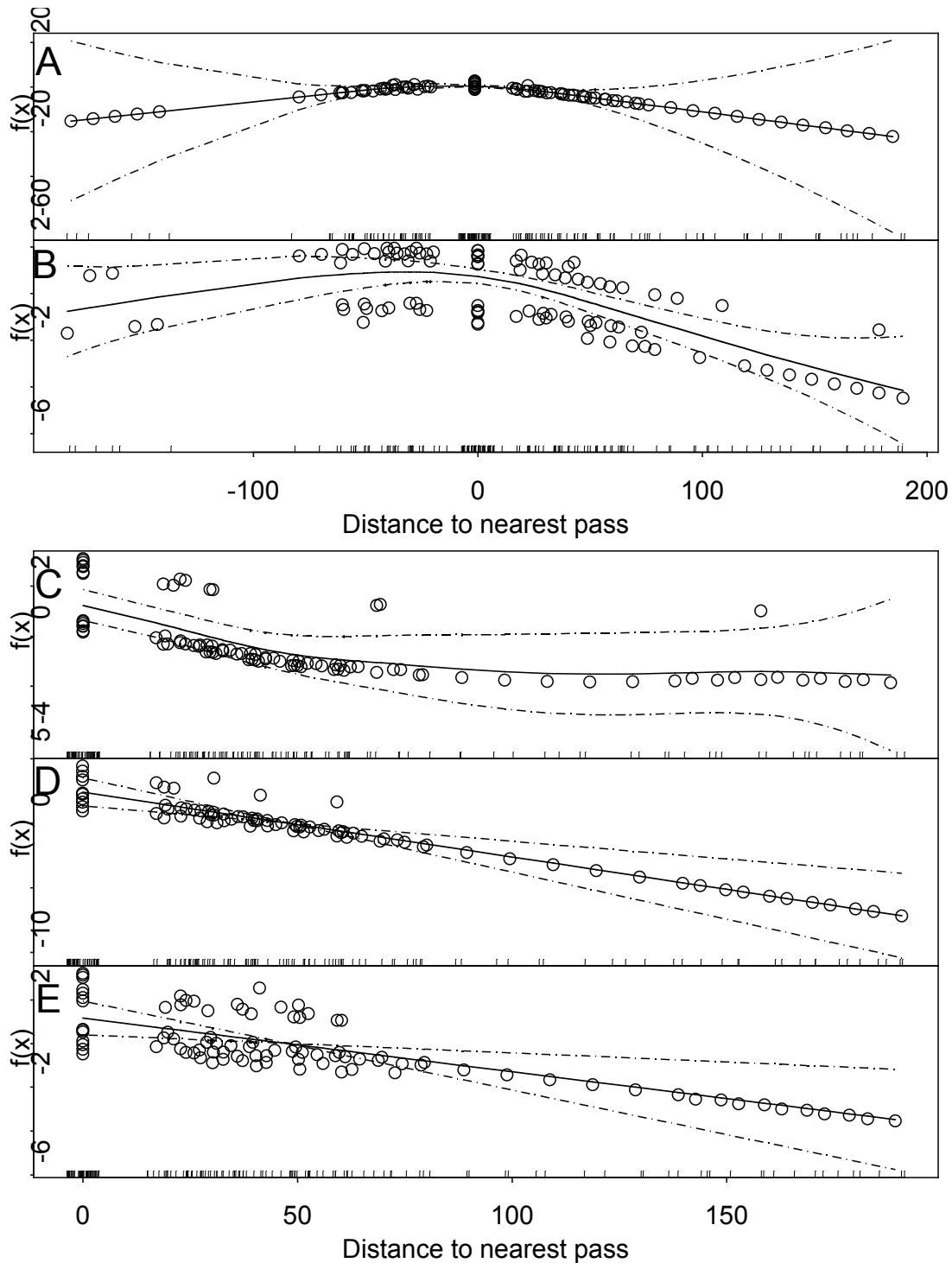


Figure 7. Generalized additive model partial functions and residual values for humpback whale (A), Dall's porpoise (B), minke whale (C), sperm whale (D), and killer whale (E) occurrence in relation to distance to the nearest pass. For humpback whale and Dall's porpoise, the significant variable combined distance and direction to the nearest pass such that the sign indicated the direction and the absolute value indicated the distance. Dashed lines represent upper and lower pointwise twice-standard-error curves.

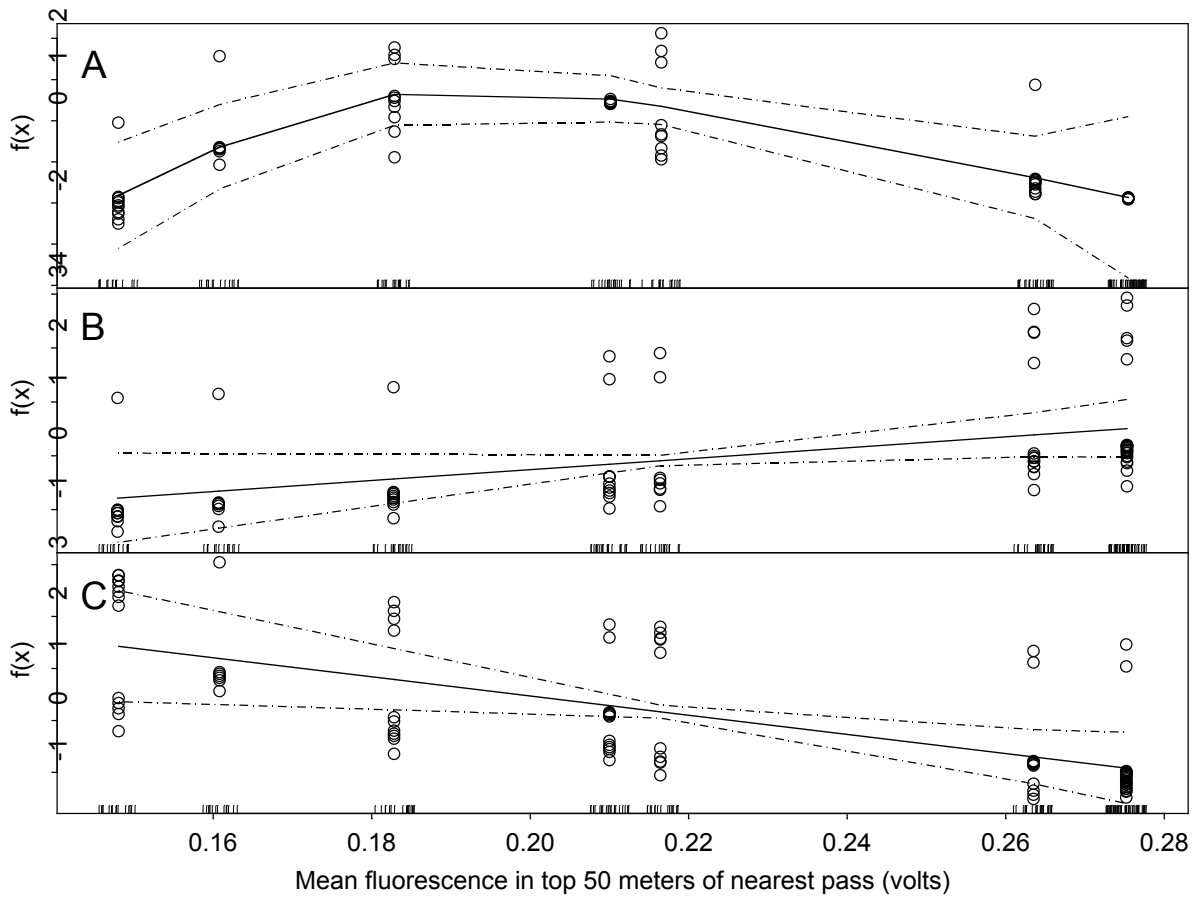


Figure 8. Generalized additive model partial functions and residual values for humpback (A), minke (B), and killer whale (C) occurrence in relation to fluorescence in the top 50 meters of the nearest pass. Dashed lines represent upper and lower pointwise twice-standard-error curves.

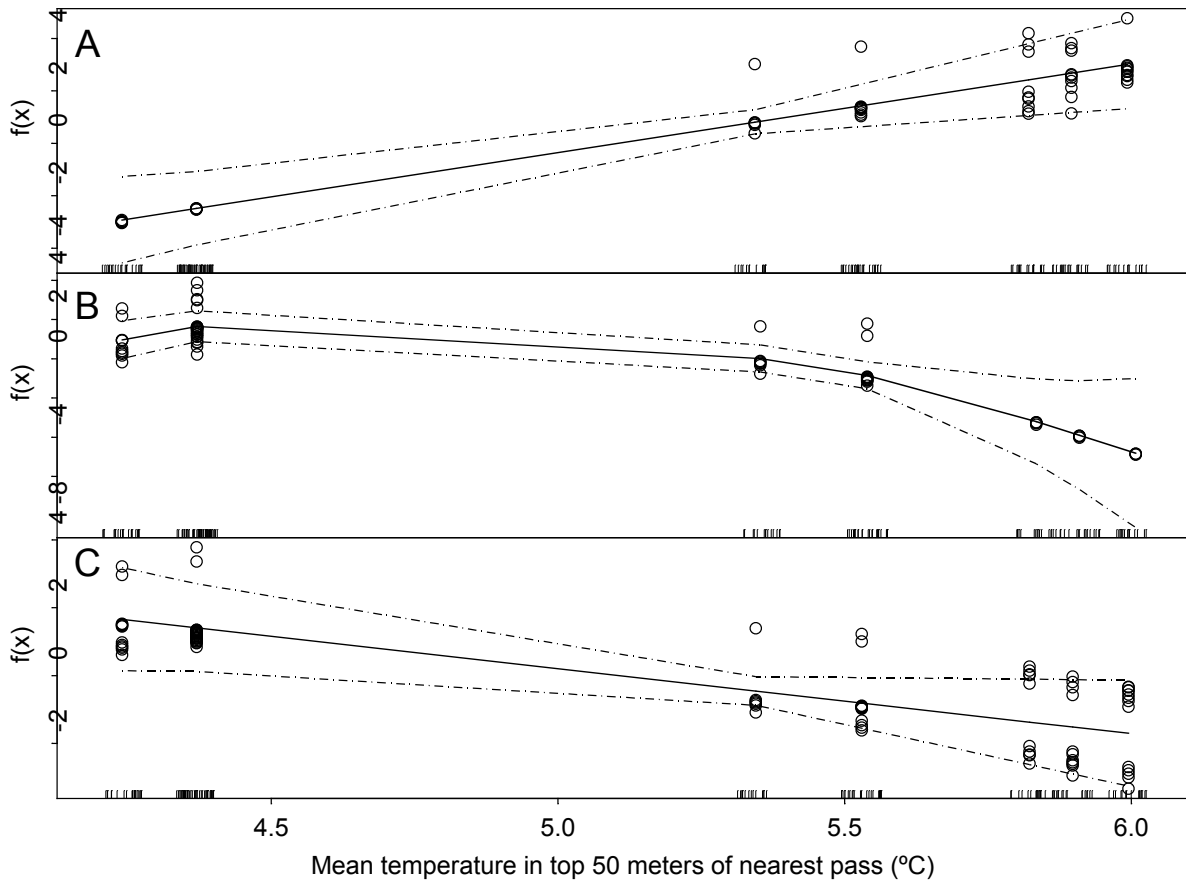


Figure 9. Generalized additive model partial functions and residual values for humpback (A), sperm (B), and killer whale (C) occurrence in relation to temperature in the top 50 meters of the nearest pass. Dashed lines represent upper and lower pointwise twice-standard-error curves.

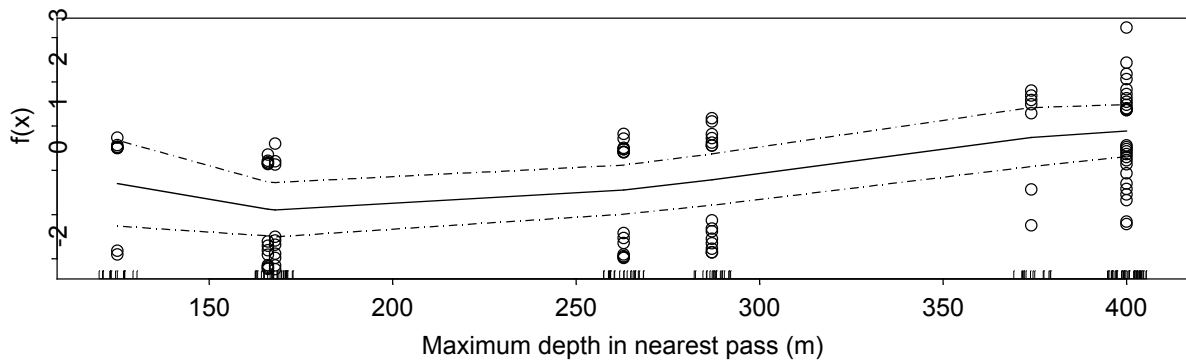


Figure 10. Generalized additive model partial function and residual values for Dall’s porpoise occurrence in relation to maximum depth in the nearest pass. Dashed lines represent upper and lower pointwise twice-standard-error curves.

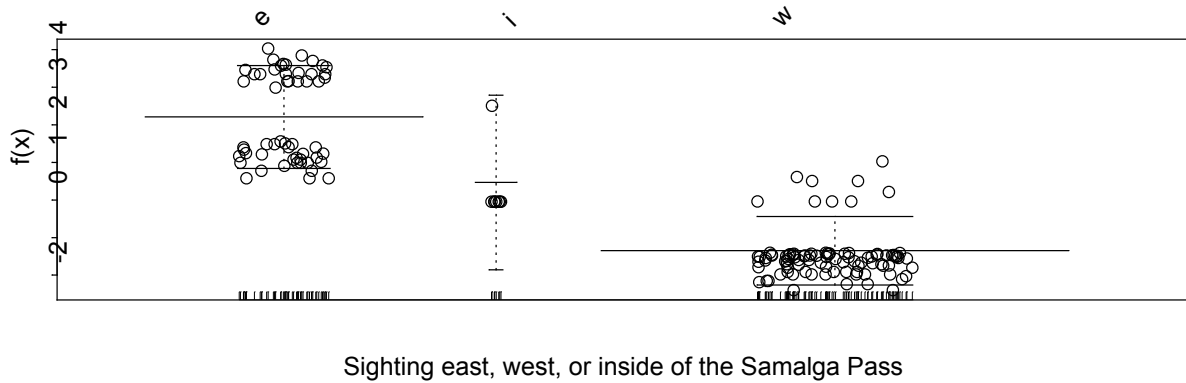


Figure 11. Generalized additive model partial function and residual values for killer whale occurrence in relation to direction to Samalga Pass. Direction to Samalga was a categorical variable and the width of each function bar represents the sample size.