FOG-Aleut-8F Rec'd 3/1/2005

Seabird distribution, abundance and diets in the eastern and central Aleutian Islands.

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Running title: Aleutian seabird distribution, abundance and diets

ABSTRACT

We examined the hypothesis that seabird distribution, abundance and diets differ among the eastern and central Aleutian Islands in response to distinct marine environments and energy pathways in each region. Research cruises were conducted in June 2001 and May – June 2002. We determined the distribution, abundance, diet and prey consumption of seabirds, and related these to zooplankton abundance and water masses that possess different physical properties. We found that distribution, abundance and diets of seabirds could be partitioned into two regions that correspond to marine environments determined by the extent of the Alaska Coastal Current along the eastern and central Aleutian Islands. Short-tailed shearwaters (*Puffinus tenuirostris*) were the most abundant seabird in the coastal waters of the eastern Aleutian Islands, and northern fulmars (*Fulmarus glacialis*) were the most abundant seabird in the oceanic waters of the central Aleutian Islands. Seabird communities in the central and eastern Aleutian Islands were likely associated with different food webs. In the central Aleutian Islands, Short-tailed shearwaters and northern fulmars consumed shelf break species of euphausiids (*Thyssanoesa longipes*) and oceanic copepods (*N. cristatus*), respectively; in the eastern Aleutian Islands, both short-tailed shearwaters and northern fulmars consumed shelf species of euphausiids (*T. inermis*). Carbon transport to seabirds was highest in Unimak and Akutan passes where shearwaters removed large quantities of shelf euphausiids, followed by Samalga and Seguam passes where northern fulmars removed large amounts of oceanic copepods.

Key words:

Aleutian Islands, Aleutian passes, biogeographic boundaries, northern fulmar, seabird distribution, short-tailed shearwater.

INTRODUCTION

The Aleutian Islands are formed by the highest peaks of the submerged Aleutian ridge, between which waters flow from the North Pacific Ocean and the Bering Sea (Favorite, 1974). Passes between islands have different physiographic characteristics; the western and central Aleutian passes are relatively deep compared to those in the eastern Aleutian Islands (Favorite, 1974). The shelf along the Aleutian Islands is narrow and the continental slope is steep. The upper ocean circulation on the North Pacific side of the Aleutian Islands is characterized by the westward flow of the Alaskan Stream and the Alaska Coastal Current, and on the Bering Sea side by the eastward flow of the Aleutian North Slope Current (Favorite, 1974; Reed and Stabeno, 1999; Ladd *et al.*, 2004a; Stabeno *et al.*, 2004). Within the passes, both northward and southward tidal flow occurs (Reed, 1971; Favorite, 1974; Ladd *et al.*, 2004a), but the overall net flow of water through the passes is northward (Reed, 1990; Stabeno *et al.*, 2004).

The Aleutian Islands as a whole have been regarded as a relatively uniform marine environment (Springer, 1991). However, recent studies suggest there may be habitat differences at spatial scales smaller than the extent of the Aleutian archipelago. Populations of Steller sea lions (*Eumetopias jubatus*) inhabiting rookeries along the Aleutians Islands show different trends in recent decades (York *et al.*, 1996). Populations are declining in the central and western Aleutian Islands and remain stable in the eastern Aleutian Islands (York *et al.*, 1996). Prey use by the Steller sea lion along its range in the Aleutian Islands and the Alaska Peninsula shows differences at geographical scales that resemble the extent of the declining population (Sinclair and Zeppelin, 2002). In the central Aleutian Islands,

west of Samalga Pass, Steller sea lions feed primarily on Atka mackerel (*Pleurogrammus monopterygius*), whereas in the eastern Aleutian Islands and rookeries in the vicinity of the Alaska Peninsula, walleye pollock (*Theragra chalcogramma*) and salmonids (*Oncorhynchus* spp.) are the main prey consumed (Sinclair and Zeppelin, 2002). These diet differences suggest that it would be profitable to examine spatial variation in the components of the marine ecosystem of the Aleutian Archipelago to determine whether there are distinctively different marine environments in the eastern and central Aleutian Islands.

Different marine environments result in distinct food webs and seabird assemblages (Ainley, 1977; Hunt *et al*., 1981a; Springer *et al.*, 1987; Wahl *et al*., 1989; Elphick and Hunt, 1993; Spear and Ainley, 1998; Hyrenbach and Veit, 2003). For example, high-productivity regions (i.e., boundary currents and subpolar oceans) are used by diving seabirds that require dense prey to meet high energy requirements (Ainley, 1977; Piatt, 1990), while low-productivity regions (i.e., subtropical gyres and tropical water masses) are inhabited by surface-foragers with reduced flight costs that consume widely distributed prey (Ainley, 1977; Ballance *et al.*, 1997).

The at-sea distribution of birds (Hunt *et al.*, 1981b; Haney, 1986; Elphick and Hunt, 1993, Karnovsky *et al.* 2003) and the location of breeding colonies (Hunt *et al.*, 1981c; Springer and Roseneau, 1985) reflect the distribution of water masses containing suitable prey (Hunt *et al.*, 1999). In the northern Bering Sea within the coastal zone, an oceanic seabird assemblage subsists associated with the Anadyr Current that transports oceanic water and large-bodied zooplankton over the continental shelf northwest of St. Lawrence Island (Springer *et al.*, 1987; Elphick and Hunt, 1993); away from this current a coastal

food web and seabird community dominates the shelf region (Springer *et al.*, 1987, 1989; Elphick and Hunt, 1993). In the western Aleutian Islands within the oceanic domain, a coastal seabird community subsists associated with the availability of shallow habitat supporting coastal food webs around the Near Islands (Springer *et al.*, 1996); around Buldir Island, where shallows are nearly absent, an oceanic community dominates (Springer *et al.*, 1996).

Distinct water masses and the availability of shelf habitat are likely to determine different food webs and seabird communities along the Aleutian archipelago (Springer *et al.* 1996; York *et al.*, 1996, Sinclair and Zeppelin, 2002). In this paper we test the hypothesis that seabird distribution, abundance and diets differ among the eastern and central Aleutian Islands and respond to distinct marine environments and energy pathways in each region. We predicted that marine environments resulting from differences in water mass properties and availability of shelf habitat would determine distinct food webs and seabird assemblages in the eastern and central Aleutian Islands. This work was part of a multidisciplinary research program to define mechanisms important for spatial heterogeneity along the Aleutian archipelago which may have influenced the varying population trends of Steller sea lions in these areas.

MATERIALS AND METHODS

Study area

We conducted research cruises along the eastern and central Aleutian Islands on 4–25 June 2001 and 16 May – 20 June 2002. Sample design consisted of transects through passes

connecting the North Pacific Ocean and the Bering Sea (Fig. 1). We surveyed Seguam, Amukta, Akutan and Unimak passes in 2001. We added Tanaga, Samalga and Umnak passes to our survey in 2002. These passes differed greatly in physiographic characteristics such as width, depth and cross-sectional area (Table 1). Strong currents, tide rips and swirls associated with changes in bathymetry are common in these passes, with the apparent exception of Amukta Pass (NOAA, 2002), the pass with the largest cross-sectional area (Table 1). We determined the distribution, relative abundance, diet composition and estimated overall prey consumption of seabirds, the distribution and abundance of zooplankton and the physical properties of the water in these passes (see also Ladd *et al.*, 2004a; Coyle, 2004).

Distribution and abundance of foraging seabirds

We determined the distribution and abundance of seabirds by counting seabirds from the bridge of the RV Alpha Helix (eye height = 7.7 m above the sea surface) while the ship was underway. Vessel speed varied from 11 km h^{-1} to 19 km h^{-1} depending on whether we conducted acoustic or CTD surveys. We counted birds continuously during daylight hours in a 300 m arc from directly ahead of the vessel to 90° off the side with best visibility (i.e., lowest glare) and logged data into a portable computer. Observers switched to a snapshot method of counting when large aggregations of birds (>1,000 individuals) were encountered crossing the vessel's bow (Tasker *et al.*, 1984). Seabird behaviors were recorded as flying, sitting on the water, and feeding. Seabirds sitting on the water were assumed to be about-to-forage, or resting from a previous foraging bout. For the analyses in this paper, we used only data for birds feeding or sitting on the water.

Both short-tailed (*Puffinus tenuirostris*) and sooty shearwaters (*P. griseus*) occur in the southern Bering Sea. These species are almost indistinguishable in the field (Hunt *et al.*, 1981b), and estimates of sooty shearwaters in the Bering Sea based solely on wing coloration tend to be exaggerated as suggested by collected individuals identified by bill length (Schneider and Shuntov, 1993). We were careful to look for sooty shearwaters. Only in one instance did we find about 5% sooty shearwaters mixed in a large flock of short-tailed shearwaters. The vast majority of birds were short-tailed shearwaters, judging from birds collected in the passes and identified by bill length. Collections in 1999 (n = 12), 2001 (n = 15) and 2002 (n = 4) yielded short-tailed shearwaters. Thus, for purposes of our analysis, we assumed that all shearwaters were short-tailed shearwaters.

Distribution and abundance of zooplankton

We determined the distribution and abundance of zooplankton using a multiple opening-closing net system (MOCNESS, 1-m^2 opening, 500-µm mesh-net) as outlined in Coyle (2004). All organisms were identified to the lowest taxonomic level possible (Coyle, 2004) and the integrated zooplankton biomass (g m^{-2}) for the upper 40 m was computed for each sampling station. We considered a 40-m water column representative of the organisms that may be available to foraging seabirds in the vicinity of the passes.

Diet composition of foraging seabirds

We determined the prey of the dominant foraging seabirds by shooting birds that were feeding or sitting on the water. We limited our collections to areas where birds were foraging to ensure that they had obtained their prey near the collection site (Table 2). We

included data from shearwaters and one fulmar collected in Akutan Pass in 1999. The contents of the proventriculus (area of chemical digestion) were removed, weighed and preserved in 80% ethanol for later identification. Prey items were identified to the lowest taxonomic level possible using a binocular microscope. The proportion of prey items by volume and the proportion of zooplankton organisms by number for each bird were averaged across birds by year and pass. This approach avoided the possibility that a few birds with particularly large amounts of prey would have a disproportionate influence on our assessment of seabird diet composition.

Energy requirements and prey consumption of seabirds

We used separate allometric equations for Procellariiformes ($FMR = 11.49\ m^{0.718}$, n = 12, $r^2 = 0.814$) and Charadriiformes ($FMR = 22.06\ m^{0.594}$, n = 14, $r^2 = 0.921$) to predict daily energy requirements of seabirds (*FMR*, in kJ d^{-1}) based on body mass values (*m*, in g) (Table 3, Ellis and Gabrielsen, 2001). The mean body mass of each seabird species was obtained from published values (Dunning, 1993). Caloric contents of prey used by seabirds were taken from Davis *et al.* (1998) and converted to standard international units (Table 4). An assimilation efficiency of 75% was used to convert daily energy requirements to prey consumed, as assumed by Hunt *et al.* (2000). Daily prey consumption (kg km^{-2}) was computed by apportioning energy requirements to prey. We used diet data from this study to estimate prey consumption for short-tailed shearwaters and northern fulmars (*Fulmarus glacialis*), as well as for least auklets (*Aethia pusilla*). Diet data for all other species came from the literature (Hunt *et al.*, 1981a, 1998; Hunter *et al.*, 2002; Piatt and Kitaysky, 2002a,

2002b; Sanger, 1987). When available, we used separate diet estimates for the central and eastern Aleutian Islands.

Data analysis

We modeled the presence of seabird aggregations along the Aleutian Islands using logistic regression (SYSTAT, Systat Software Inc., Richmond, California, USA, v. 9.01). Seabird densities (birds km^{-2}) in 5-km bins were re-coded as a binary variable in which 1 indicates the presence of bird aggregations larger than $\overline{X} \pm 2SD$ and 0 indicates the absence of such aggregations.

We tested for autocorrelation at lags 1, 2 and 3 (Table 5) on all transects included in this study (n = 38). By chance, we would expect at least 2 autocorrelations to be significant (5%) per species; we found less autocorrelation than expected by chance for shearwaters at any lag, and more autocorrelation than expected by chance for northern fulmars, small alcids and large alcids (Table 5). Autocorrelation in northern fulmars and large alcids decreased from lag 1 to 3, autocorrelation in small alcids increased at lag 2 and decreased again at lag 3. Inspection of the data showed that this autocorrelation most likely reflected regional distribution patterns and not the existence of flocks larger than the 5-km. Thus, we concluded it appropriate to use 5-km bins size for the analyses.

Variables in the logistic regression model included year (2001 and 2002), month (May and June), longitude (central and eastern) and latitude (north, pass, and south). Year, month and longitude were re-coded using the highest value (i.e., 2002, June, and central) as the reference group. Latitude was re-coded as two dummy variables using pass as the

reference group. We included Samalga Pass [considered by Ladd *et al.* (2004a) as a transition zone] in the central region because most of the water in the pass was similar to that in the central Aleutians and our transects were carried out in the "oceanic" water (Ladd *et al.*, 2004a). We considered all transit surveys conducted along the Bering Sea and North Pacific sides of the Aleutian Islands as north and south, respectively. We did not separate bins corresponding to transects through passes by water mass types corresponding to the Bering Sea and North Pacific which has been done in a separate paper (see Ladd *et al.*, 2004b). We conducted a multivariate logistic regression analysis of seabird aggregations as a function of all the variables mentioned above to determine the preliminary models (Table 6). The significance ($p < 0.05$) of the t-ratio (t-ratio squared = Wald Statistic) was used to select variables for inclusion in the final models (Table 7) (Hosmer and Lemeshow, 1989). All two-way interactions between variables were investigated and found to be not significant (t-ratios, $p > 0.05$).

We used Pearson's correlation to examine relationships between mean density of seabirds in the passes for each year surveyed and the physiographic characteristics of the passes (i.e., cross-section area). We used Mann-Whitney *U* tests and Kruskal-Wallis one-way analyses of variance to compare the diets of seabirds among passes and years. Due to the small sample sizes, we considered each bird as a sample unit even though seabirds foraging in a given flock often contained similar foods and may not have been truly independent samples. The Mann-Whitney *U* test was used to compare the abundance of zooplankton (g m^{-2}) in the upper 40 m between regions along the Aleutian Islands.

RESULTS

In 2001, we surveyed 353 km and counted 27,236 seabirds feeding or sitting on the water between Seguam Pass (western limit) and Unimak Pass (eastern limit). In 2002, our surveyed area extended farther west, and we surveyed 831 km and counted 123,079 seabirds feeding or sitting on the water between Tanaga Pass (western limit) and Unimak Pass (eastern limit). The most abundant foraging seabird species were the short-tailed shearwater (62.8% of birds observed feeding or on the water in 2001 and 71.2% in 2002), northern fulmar (19.8% in 2001 and 12.8% in 2002) and small alcids (13.7% in 2001 and 12.9% in 2002) (Table 3). Whiskered auklets (*Aethia pygmaea*), crested auklets (*A. cristatella*) and ancient murrelets (*Synthliboramphus antiquum*) were the most abundant small alcids in 2001. Least auklets and ancient murrelets were the most abundant small alcids in 2002. Tufted puffins (*Fratercula cirrhata*) were the most abundant large alcids in 2001 and 2002 comprising 2.6% and 2.3% of birds observed feeding or on the water.

Distribution and abundance of foraging seabirds

Short-tailed shearwaters

Shearwaters, in particular short-tailed shearwaters, were most abundant in the eastern Aleutian Islands (Table 8) and represented 86.2% of 19,759 and 95.1% of 91,511 foraging seabirds counted in this region in 2001 and 2002, respectively. High densities of shearwaters were observed in Akutan Pass in 2001 and in Unimak Pass in 2001 and 2002 (Figs 2a, b). Large aggregations of shearwaters along the Aleutian Islands were influenced by year, longitude and latitude (t-ratio, $p < 0.05$; Table 6), but not by month (t-ratio, $p >$

0.05). Both preliminary and final models were highly significant (X^2 test, $p < 0.001$) and correctly predicted the presence of large aggregations of shearwaters in 83% of the cases (Tables 6 and 7). The final model showed that large aggregations of short-tailed shearwaters were negatively correlated with year, longitude and latitude (Table 7). The odds ratio indicated that large aggregations of shearwaters were 2.7 times (95% Confidence Interval, CI = 1.7 – 4.5) more common in 2001 than in 2002. Large aggregations of shearwaters occurred 3.2 times (95% CI = 1.8 – 5.5) more often in the eastern than in the central Aleutians Islands. Large aggregations of shearwaters occurred one fourth (95% CI = 0.1 – 0.6) as frequently in the North Pacific side of the Aleutians as compared to the passes and Bering Sea side pooled together.

Northern fulmars

High densities of northern fulmars were observed in the central Aleutian Islands (Table 8). Northern fulmars comprised 70.1% of 7,477 and 49% of 31,568 foraging seabirds counted in this region in 2001 and 2002, respectively. Large aggregations of fulmars were recorded between Seguam and Samalga passes in 2001 and 2002 (Figs 2c, d). Large aggregations of northern fulmars along the Aleutian Islands were influenced by month and longitude (t-ratio, $p < 0.05$; Table 6), but not by year and latitude (t-ratio, $p > 0.05$). Both preliminary and final models were highly significant (X^2 test, $p < 0.001$) and correctly predicted the presence of large aggregations of fulmars in 66% of the cases (Tables 6 and 7). The final model showed that large aggregations of northern fulmars were positively correlated with month and longitude (Table 7). Large aggregations of fulmars occurred 4.4 times (95% CI = 3.0 – 6.2) more often in the central than in the eastern Aleutians Islands. The odds ratio

indicated that large aggregations of fulmars were 2.2 times (95% CI = 1.5 – 3.3) more common in June than in May. This trend may be an artifact of our sampling owing to differences in timing of the cruises and when we moved from an area with low densities of fulmars to an area with high densities.

Small alcids

Small alcids were more abundant in the central Aleutian Islands in 2002, but not in 2001 (Table 8). Small alcids comprised 25% of 7,477 and 46.7% of 31,568 foraging seabirds counted in this region in 2001 and 2002, respectively. High densities of whiskered auklets were found in Akutan Pass in 2001 (Fig. 3a) and high densities of least auklets were observed between Tanaga and Atka passes in 2002 (Fig. 3b). Large aggregations of small alcids along the Aleutian Islands were influenced by month (t-ratio, $p < 0.05$; Table 6), but not by year, longitude and latitude (t-ratio, $p > 0.05$). Both preliminary and final models were significant (X^2 test, $p < 0.05$) and correctly predicted the presence of large aggregations of small alcids in 62% of the cases (Tables 6 and 7). The final model showed that large aggregations of small alcids were negatively correlated with month (Table 7). The odds ratio indicated that large aggregations of small alcids were 1.6 times (95% CI = 1.2 – 2.2) more abundant in May than in June: this trend is likely an artifact of our sampling.

Large alcids

The densities of large alcids were highest in the eastern Aleutian Islands (Table 8), where they comprised 3.4% of 19,759 and 3.1% of 91,511 foraging seabirds counted in this region

in 2001 and 2002, respectively. Large aggregations of large alcids were common between Umnak and Unimak passes in 2001 and 2002 (Figs 3c, 3d). Large aggregations of large alcids (mostly tufted puffins) along the Aleutian Islands were influenced by month and longitude (t-ratio, $p < 0.05$; Table 6), but not by year and latitude (t-ratio, $p > 0.05$). Both preliminary and final models were highly significant (X^2 test, $p < 0.001$) and correctly predicted the presence of large aggregations of large alcids in 56% of the cases (Tables 6 and 7). The final model showed that large aggregations of large alcids were negatively correlated with longitude and positively correlated with month (Table 7). Large aggregations of large alcids occurred 2.3 times (95% CI = 3.0 – 6.2) more often in the eastern than in the central Aleutians Islands. The odds ratio indicated that large aggregations of large alcids were 1.5 times (95% CI = 1.1 – 2.1) more common in June than in May, this trend is likely an artifact of our sampling.

Distribution and abundance of foraging seabirds in relation to the passes

The species composition of foraging seabirds varied among passes in 2001 and 2002 (Tables 9 and 10). Short-tailed shearwater was the most abundant species in Unimak (2001: 91.5%, n = 1,690; 2002: 73.9%, n = 4,319) and Akutan passes (2001: 88.8%, n = 17,247). The densities of shearwaters in Unimak and Akutan passes were two and three orders of magnitude higher than in other passes. The northern fulmar was the most abundant species in Seguam Pass (2001: 86.5%, n = 1,913; 2002: 87.4%, n = 3,878) and in Samalga Pass (2002: 97.2%, n = 2,389). The densities of fulmars in these passes were two-orders of magnitude higher than in other passes, regardless of year surveyed. In 2001, small alcids (whiskered auklets) were most abundant in Akutan Pass; and in 2002, in Umnak (Anicent

murrelets) and Tanaga (least auklets) passes. Large alcids were abundant in Unimak Pass in 2001, and in Akutan and Umnak passes in 2002.

The species composition of foraging seabirds may have been related to the physiographical characteristics of the passes (Fig. 4). There was a strong negative relationship between the log-transformed density of shearwaters ($r = -0.937$, $n = 6$, $p > 0.01$) and tufted puffins ($r = -0.830$, $n = 11$, $p < 0.01$) relative to the log-transformed cross-sectional area of the passes (Figs 4a, c). Northern fulmars ($r = 0.121$, $n = 10$, $p > 0.05$) and small alcids ($r = -0.320$, $n = 11$, $p > 0.05$) seemed insensitive to the cross-section area of the passes (Figs 4b, d).

Diet composition of seabirds

Short-tailed shearwaters

Zooplankton were the main prey consumed by short-tailed shearwaters foraging along the Aleutian Islands (Fig. 5a). Euphausiids represented more than 80% by number of the items consumed. There were differences in the species of euphausiids consumed between the central and eastern Aleutian Islands in 2002. Shearwaters foraging in Seguam Pass (central region) consumed primarily the euphausiid *Thyssanoesa longipes* (26.5% by number), together with small amounts of *T. spinifera* (8.4% by number), *T. inermis* (6.7% by number), and *Euphausia pacifica* (5.6% by number). Shearwaters foraging in Akutan Pass (eastern region) consumed mainly *T. inermis* (57.4% by number) and smaller amounts of *T. spinifera* (13.6% by number) and *T. longipes* (0.9% by number). The proportion of *T. inermis* consumed in Akutan Pass was significantly higher than in Seguam Pass (Mann-Whitney U test, df = 1, $n = 9$, $p = 0.014$). The proportion of *T. longipes* was not

significantly different between Akutan and Seguam passes (Mann-Whitney U test, df = 1, n = 9, p = 0.081).

The euphausiids consumed by shearwaters in Akutan Pass did not differ significantly between years (Kruskall-Wallis test, df = 2, n = 31, p > 0.05, Fig. 6). The euphausiid *T. inermis* was the main prey in 1999 (19.2% by number), 2001 (26.9% by number), and 2002 (57.4% by number). The second most important prey was *T. spinifera* in 1999 (13.0% by number) and 2002 (13.6% by number). In 2001, *T. spinifera* and *T. raschi* were both consumed in small amounts (1.5% and 1.8% by number respectively). A large proportion of unidentified euphausiids (58.4% and 69.7% by number, respectively) was consumed both in 1999 and 2001. Many of the euphausiids (at least 25.8% by number) consumed in 1999 were furcillids and it was not possible to identify them to species.

Northern fulmars

The main prey consumed by northern fulmars along the Aleutian Islands were zooplankton (Fig. 5b), which represented more than 95% by number of the items consumed. Fulmars consumed different types of zooplankton in the central and eastern Aleutian passes in 2002; copepods were primarily consumed in the central region (Mann-Whitney U test, df = 1, n = 19, p = 0.021), while euphausiids were the main prey consumed in the eastern Aleutian passes (Mann-Whitney U test, df = 1, n = 19, p = 0.009). Northern fulmars foraging in Seguam Pass consumed primarily the copepods *Neocalanus cristatus* (39.4% by number) and *N. plumchrus-flemingeri* (30.3% by number). Fulmars collected in Samalga Pass were feeding mainly on *N. plumchrus-flemingeri* (30.3% by number) and *N. cristatus* (24.8% by number). In Akutan Pass, northern fulmars consumed mainly *T. spinifera* (43.8% by

number) and *T. inermis* (32.1% by number). Few euphausiids were found in fulmars collected in the central region, and no copepods were found in the two fulmars collected in the eastern region.

Least auklets

The main prey consumed by least auklets in Tanaga Pass was zooplankton, primarily the copepod *N. plumchrus-flemingeri* (63.1% by number).

Distribution and abundance of zooplankton

The species composition of copepods sampled by net tows differed between the central and eastern Aleutian Islands (Table 11). In both 2001 and 2002, *N. cristatus* was more abundant in the central Aleutian Islands, and *Calanus marshallae* was more abundant in the eastern Aleutian Islands (Mann-Whitney U test, df = 1, $p < 0.05$). There were no statistically significant differences in the abundance of *N. plumchrus-flemingeri*, *Metridia* spp. and *Eucalanus bungii* between regions in 2001 and 2002 (Mann-Whitney U test, df = 1, $p > 0.05$).

The species composition of euphausiids also differed between the central and eastern Aleutian Islands (Table 11). In both 2001 and 2002, *Euphausia pacifica* was more abundant in the central Aleutian Islands, and *Thyssanoesa inermis* was more abundant in the eastern Aleutian Islands (Mann-Whitney U test, df = 1, $p < 0.05$). The euphausiid *T. inspinata* was more abundant in the central Aleutian Islands in 2001 and in the eastern Aleutian Islands in 2002 (Mann-Whitney U test, df = 1, $p < 0.05$). We found no significant differences in the abundance of *T. spinifera* in 2001 (Mann-Whitney U test, df = 1, p >

0.05), although *T. spinifera* was more abundant in the eastern Aleutian Islands in 2002 (Mann-Whitney U test, df = 1, $p < 0.01$). There were no statistically significant differences in the abundance of *T. longipes* between regions in either 2001 or 2002 (Mann-Whitney U test, df = 1, $p > 0.05$).

The species composition of zooplankton varied among passes in 2001 and 2002 (Table 12). In 2001, the copepod *E. bungii* was the most abundant species in Seguam, Akutan and Unimak passes; and in 2002, in Samalga Pass. In 2002, the copepod *N. plumchrus-flemingeri* was the most abundant species in Tanaga, Seguam, Akutan and Unimak passes. The euphausiid *T. inermis* was the most abundant species in Akutan Pass in 2001, and *T. longipes* was the most abundant in Tanaga, Seguam, Akutan and Unimak passes in 2002.

Prey consumption by seabirds

The energy required and prey consumed by seabirds feeding or sitting on the water showed marked differences between the central and eastern Aleutian Islands. Prey consumption by seabirds was 2.4 to 3.1 times higher in the eastern than in the central Aleutian Islands in 2001 and 2002 (Fig. 7; note differences in scale of the *Y* axes). In the eastern Aleutian Islands in 2001 and 2002, short-tailed shearwaters accounted for 91% and 96% of the energy required by seabirds, representing about 38 and 78 kg km^{-2} d^{-1} of prey consumed, respectively. In the central Aleutian Islands in 2001 and 2002, northern fulmars accounted for 83% and 75% of the energy required by seabirds, representing 14 and 20 kg km^{-2} d^{-1} of prey consumed, respectively. In the eastern passes, euphausiids (*Thyssanoesa* spp.) were the main prey consumed by seabirds and accounted for 93% and 96% of the prey biomass

consumed in 2001 and 2002, respectively. In the central passes, copepods (*Neocalanus* spp.) accounted for 86% and 90% of the prey biomass consumed in 2001 and 2002, respectively.

In 2001, the estimated prey consumption in the passes was highest in Akutan Pass (Fig. 8a) where short-tailed shearwaters consumed a minimum of 152 kg km^{-2} d^{-1} of euphausiids. In contrast, in 2002, prey consumption was lowest in Akutan Pass, and most prey was consumed by tufted puffins. In 2001, the amount of prey consumed in Seguam and Unimak passes were similar, but the types of prey differed; in Seguam Pass northern fulmars consumed 15 kg km^{-2} d^{-1} of copepods, and in Unimak Pass short-tailed shearwaters consumed over 14 kg km^{-2} d^{-1} of euphausiids. In 2002, prey consumption in the passes was highest in the central passes such as Seguam (Fig 8b) and Samalga (Fig 8b) where northern fulmars consumed over 33 kg km^{-2} d^{-1} and 35 kg km^{-2} d^{-1} of copepods, respectively. Prey consumption was also high in Tanaga Pass were small alcids, particularly least auklets, consumed 27 kg km^{-2} d^{-1} of copepods. Among the eastern passes, prey consumption was highest in Umnak and Unimak passes where tufted puffins and short-tailed shearwaters were the most abundant seabirds, respectively, and consumed 7.4 kg km^{-2} d^{-1} and 7.3 kg km^{-2} d^{-1} of prey, respectively. During both 2001 and 2002, prey consumption was lowest in Amukta Pass.

DISCUSSION

Marked changes in physical properties of the water observed around Samalga Pass in 2001 and 2002 (Ladd *et al.*, 2004a) showed that the Aleutian Archipelago could be divided into

two distinct marine environments that extend over a much larger geographical scale than that determined solely by the local availability of shelf habitat (Springer *et al.*, 1996). The central Aleutian Islands (from Samalga to Amchitka Pass), influenced by the Alaskan Stream and the deep Bering Sea, were identified as an oceanic marine environment, whereas, the eastern Aleutian Islands (from Unimak to Samalga Pass), influenced by the Alaska Coastal Current, were identified as a coastal marine environment (Ladd *et al.* 2004a).

The distributions and abundances of the two dominant seabird species could be partitioned into two regions that corresponded to the marine environments determined by the extent of the Alaska Coastal Current. Aggregations of shearwaters were most common in coastal waters of the eastern Aleutians, while aggregations of fulmars were most common in oceanic waters of the central Aleutian Islands. Short-tailed shearwaters are abundant in the Bering Sea during summer, where birds forage for euphausiids in shelf waters (Hunt *et al*., 1981a, 1981b, 1996; Schneider and Shuntov, 1993). Fulmars are abundant throughout the year over all free-ice waters in the Bering Sea (Hunt *et al*., 1981b). Overall, the distribution patterns of shearwaters and fulmars around the Aleutian Islands matches well the eastern Bering Sea and the Gulf of Alaska, where short-tailed shearwaters are associated with coastal waters over the shelf areas (Hunt *et al*., 1981b, 1996; Harrison, 1982; Schneider and Shuntov, 1993) and northern fulmars are associated with oceanic waters near the shelf break (Hunt *et al.*, 1981b).

We found similar patterns in the distribution and abundance of some less dominant alcids species. Tufted puffin aggregations were most common in coastal waters of the eastern Aleutians. Tufted puffin foraging habitats include offshore, shelf and slope waters

throughout Alaska, becoming more common near island colonies than away from land during the summer (Hunt *et al*., 1981b). Large feeding flocks of tufted puffins commonly occur near the Aleutian passes, where rip currents concentrate prey (Piatt and Kitaysky 2002a). Among small alcids, whiskered auklets were particularly abundant in Akutan Pass, high numbers of crested auklets were observed in the central Aleutians, and least auklets were in great abundance in the westernmost portion of our study area. Small alcids in the Bering Sea are known to inhabit predator free, offshore islands with ready access to oceanic zooplankton (Springer *et al*., 1987); the central Aleutian Islands appear to be such a place. Crested and least auklets in the Pribilof and central Aleutian Islands appear to specialize on euphausiids and calanoid copepods, respectively (Hunt *et al*., 1981a, 1998).

Because seabirds are central place foragers during the breeding season, the location of seabird colonies reflects both the availability of safe nesting sites and the availability of food (Hunt *et al.*, 1999). The three largest northern fulmar colonies in Alaska are located on St. Matthew (northern Bering Sea), Chagulak (central Aleutians, Fig. 1) and Semidi Islands (Gulf of Alaska) (U.S Fish and Wildlife, 2000). The colony on Chagulak Island is about 500,000 birds (U.S Fish and Wildlife, 2000). In the Shetland Islands, banded breeding northern fulmars have been found foraging about 35 km from their nests, and indirect evidence based on time spent at sea suggests a potential range of 120 km from the colony (Furness and Todd, 1984). We found that most fulmars were flying greater distances from the colony and foraging in high densities 200-250 km away from Chagulak Island. Few northern fulmars were feeding in Amukta Pass, the nearest pass to the colony, compared to Seguam and Samalga passes (see Tables 6 and 7). The at-sea distribution patterns for small alcids and tufted puffins also correspond to the location of their colonies. More than

400,000 least auklets and 200,000 crested auklets nest on the central Aleutian Islands, however, none are reported on the eastern Aleutians (U.S. Fish and Wildlife, 2000). More than 1,000,000 tufted puffins nest on the eastern Aleutian Islands, compared to 150,000 on the central Aleutian Islands (U.S. Fish and Wildlife, 2000). As reviewed by Hunt *et al.* (1999), both the at-sea distribution of birds and the location of breeding colonies may reflect the distribution of water masses containing suitable prey.

Short-tailed shearwaters and northern fulmars used different prey in the eastern and central Aleutian Islands. In the eastern Aleutians, shearwaters and fulmars consumed shelf species of euphausiids, whereas in the central Aleutian Islands, they consumed shelf-break species of euphausiids and oceanic copepods, respectively. Short-tailed shearwaters in the North Pacific and the Bering Sea are known to forage on zooplankton, apparently changing from euphausiids in summer to hyperiid amphipods in fall (Hunt *et al*., 1981a). Cephalopods and fish can be part of the diet in any season, and vary in importance among areas (Ogi *et al*., 1980; Hunt *et al*., 1981a, 2002). Northern fulmars in the North Pacific and the Bering Sea have been considered as primarily scavengers that consume large amounts of fish (70% by volume). They also have been recorded consuming cephalopods (20% by volume), but very little krill and zooplankton (< 6% by volume) (Hunt *et al*., 1981a; Hatch, 1993). Our results suggest that zooplankton may be a more important prey than previously realized.

Zooplankton distribution and biomass in the top 40 meters of the water column showed similar patterns to those found in the diet of the dominant seabirds. A coastal community with high densities of *C. marshallae* and *T. inermis* flourished in the eastern Aleutians; whereas, an oceanic community with high densities of *N. cristatus* and *E.*

pacifica inhabited in the central Aleutian Islands (this study; Coyle, 2004). The oceanic zooplankton community in the North Pacific is generally dominated by *N. cristatus*, *N. plumchrus-flemingeri* and *Eucalanus bungii*; which are replaced in coastal waters by *C. marshallae* (Coyle, 2004). Similarly, *T. longipes* is abundant in oceanic waters and is replaced by *T. raschii* and *T. inermis* over the shelf (Motoda and Minoda, 1974).

Seabird diets also reflected selectivity in prey species consumed. For example, northern fulmars and small alcids foraged preferentially on oil-rich copepods such us *N. cristatus* and *N. plumchrus-flemingeri*, but consumed only traces (< 1% by number) of *E. bungii* a large-bodied clear-colored copepod, even though it contributed significantly to the total copepod biomass in 2001 and 2002 (Coyle, 2004). Northern fulmars north of Unimak and Akutan passes did not consume *C. marshallae*, the most abundant copepod, feeding instead on coastal species of euphausiids which were largely available in the area.

Our analysis suggested that large aggregations of shearwaters were four times more common over the 'Pass-Bering Sea' portion of transects than on the North Pacific side. However, we found no differences in the abundance of northern fulmars, small alcids and tufted puffins between the North Pacific, the passes, and the Bering Sea side. Previous studies suggested there was higher zooplankton biomass on the Bering Sea side of the western Aleutian Islands, due to distinct water masses north and south of the archipelago (Motoda and Minoda, 1974; Coyle *et al.*, 1998). However, Coyle (2004) found no significant differences in zooplankton biomass in the top 100 m of the water column between north and south of the central and eastern Aleutian Islands.

Tidal flows in the Aleutian passes are high (Stabeno *et al*., 2004) and interactions between tides and physiography are likely to produce distinct aggregations of prey and

result in particular assemblages of seabirds in some passes. Short-tailed shearwaters and tufted puffins occurred in high numbers in the shallow-narrow passes, while northern fulmars and small alcids were in areas of tide rips. Short-tailed shearwaters in Unimak and Akutan Passes foraged over the North Pacific-Mixed Water front over several surveys of these passes (Ladd *et al.*, 2004b). Tidal fronts are places where vertical mixing enhances primary production (Pingree *et al.*, 1974, Fogg *et al.*, 1985); fronts are also places where strong convergent flow may physically aggregate buoyant zooplankton (Pingree *et al.* 1974; Franks, 1992), making even small zooplankton profitable prey for seabird predators (Vlietstra *et al.*, 2004). In 2002, north of Unimak and Akutan passes, we found immense flocks of shearwaters foraging over an area colored with euphausiids at the surface and with large concentrations of euphausiids near the bottom (Jahncke *et al*. unpublished data). Vertically migrating zooplankton may become concentrated at the surface when swimming against the current (Simard *et al*., 1986; Coyle *et al*., 1992) or may be advected into shallow regions and become trapped near the bottom in their attempt to complete their downward migration (Genin *et al*., 1988; Hunt *et al.*, 1996).

Tufted puffins, small alcids and northern fulmars foraged over the well-mixed water region of the passes. In most passes, tufted puffins and small alcids were associated with tide rips and convergence areas occurring over the middle of the pass (Ladd *et al.*, 2004b). In Samalga and Seguam passes, we found northern fulmars foraging on *N. cristatus* in tight groups over slicks or loosely spread over fronts that formed over the well mixed water region of the pass (Ladd *et al.*, 2004b). Foraging stages of *N. cristatus* normally occur below the thermocline (Mackas *et al.*, 1993). Tidal flow over the passes may advect *N. cristatus* from deep water to the surface (Coyle, 1998). For the pycnocline to be pushed up

by tides, the pass needs to be deep enough so that waters from the vicinity of the pycnocline will be advected into the pass (Unimak, Akutan and Umnak passes) but not so deep (Amukta Pass) that the pass remains stratified. Amukta Pass, the widest and deepest pass surveyed, had the lowest density of seabirds compared to all other passes. Amukta was strongly stratified, even over the shallowest part of the pass (Ladd *et al.*, 2004a), and lacked features that are apparently important for foraging seabirds in this area.

Carbon transport to seabirds was highest in Unimak and Akutan passes where shearwaters remove large quantities of shelf euphausiids, followed by Samalga and Seguam passes where northern fulmars removed large amounts of oceanic copepods. Short-tailed shearwaters, migrant visitors in this region, accounted for about 90% of the prey consumed in the eastern Aleutian Islands, representing more than 40 kg km^{-2} d^{-1} of prey. Among resident birds, the northern fulmar accounted for about 80% of the prey consumed in the central Aleutian Islands, representing about 20 kg km^{-2} d^{-1} of prey. The interannual difference between prey consumption in the eastern passes is highly dependent upon encountering foraging shearwaters. Large aggregations of shearwaters were about 3 times more common in 2001 than in 2002. In 2001, large flocks of foraging shearwaters were present on all transects through Akutan Pass. In 2002, we encountered no foraging shearwaters in Akutan Pass and only low numbers on our transect through the center of Unimak Pass. However, while on transit, we encountered immense numbers of shearwaters north and west of our Unimak transect (Jahncke *et al*. unpublished data). Had they occurred on our transect, estimates of prey consumption by shearwaters in Akutan Pass would have been considerably greater in 2002 than 2001.

Our results show that the distribution and abundance of seabirds and zooplankton species were likely associated with differences in the marine environment that determine distinct energy pathways (i.e., food webs) in the eastern and central Aleutian Islands. However, the effect of local availability of shelf habitat as suggested by Springer (1991) cannot be ruled out. A clear separation of the relative importance of water masses and shelf habitat is difficult to make because the coastal waters of the Alaska Coastal Current occur along the eastern region of the Aleutians, which has a larger area of shallow shelf than do the central Aleutian Islands (Favorite, 1974). Nevertheless, given the striking differences in temperature, salinity and nutrients (Ladd *et al.*, 2004a), and significant differences in zooplankton (Coyle, 2004) and fish communities (Logerwell *et al*., 2004), we conclude that differences between the avifaunas of the eastern and central Aleutian Islands reflect a significant biogeographic boundary at Samalga Pass. It is likely that at large scales different water masses offer a different suite of zooplankton species (i.e., potential prey); while at small scales local availability of shelf habitat (physiography) and tides produce hydrographic features that make this prey available to seabirds.

ACKNOWLEDGEMENTS

We thank the captain and crew of the R/V Alpha Helix for their support during this project. We thank Robert L. Pitman, Leandra de Souza, Lucy S. Vlietstra and Sophie W. Webb for assistance in the field. Leandra de Souza kindly volunteered her time to help process shot birds. T. Chris Stark helped with the copepods identification. We are grateful to Alistair J. Cullum for writing WinFlock. Chris Rintoul provided a base map of the Aleutian area.

David C. Duffy, F. Lynn Carpenter, David M. Checkley, Jr., Bradford A. Hawkins, Nina Karnovsky, William J. Sydeman and one anonymous reviewer provided useful comments that improved the quality of this manuscript. J. Jahncke was supported by a Fellowship from the Graduate Assistance in Areas of National Need (GAANN) while working on this paper. This study was supported by the National Oceanic and Atmospheric Administration's (NOAA) Coastal Ocean Program.

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Table 1. Width, depth and cross-sectional area of the passes surveyed in 2001 and 2002. Widths and depths and cross-sectional area were taken from Ladd *et al*. (2004a).

Region	Passes	Width (km)	Depth (m)	Cross-section area (km^2)
Eastern	Unimak	19	52	0.78
	Akutan	7	30	0.16
	Umnak	7	60	0.33
Central	Samalga	29	200	4.56
	Amukta	68	430	22.97
	Seguam	30	165	3.89
	Tanaga	32	235	5.91

Table 2. Dates and locations of bird collection sites, and mean net body mass (± 1 SD) and proventriculus mass (± 1 SD) of birds collected in these areas.

Pass	Date	Time	Latitude	Longitude	Species collected	Sample size	Net body mass (g)	Proventriculus mass (g)
Tanaga	31 May 2002	23:30	51° 42.00’	178° 20.25’	Least auklet	5	99 ± 4	4 ± 1
Seguam	04 June 2002	17:30	52° 10.82’	172° 44.95’	Fulmar	9	671 ± 50	57 ± 23
					Shearwater	5	600 ± 36	36 ± 17
Samalga	08 June 2002	15:30	52° 49.36’	169° 28.08’	Fulmar	8	733 ± 89	76 ± 30
Akutan	25 July 1999	18:20	54° 04.66’	166° 22.00’	Fulmar	1	752	8
					Shearwater	7	540 ± 93	21 ± 15
	19 August 1999	09:00	54° 06.59’	166° 22.69’	Shearwater	5	546 ± 88	6 ± 4
	14 June 2001	18:30	53° 56.34’	165° 50.04’	Shearwater	8	570 ± 46	55 ± 9
	16 June 2001	17:00	54° 02.10’	166° 06.62’	Shearwater	7	560 ± 45	46 ± 18
	16 June 2002	20:00	54° 23.32’	165° 44.22’	Fulmar	1	560	100
					Shearwater	4	705 ± 32	26 ± 12

Table 3. Seabird mean body mass (Dunning, 1993), estimated overall daily energy requirement, and total number of seabirds counted feeding and sitting on the water in the eastern and central Aleutian Islands during surveys conducted in 2001 and 2002. Values between parentheses represent the total area surveyed in each region and year.

		Mean body mass (kg)	Energy requirement (kJ d^{-1})	2001		2002	
				Central (172 km^{-2})	Eastern (181 km^{-2})	Central (391 km^{-2})	Eastern (440 km^{-2})
Northern fulmar	*Fulmarus glacialis*	0.544	952.9	5,238	163	15,471	315
Short-tailed shearwaters	*Puffinus tenuirostris*	0.543	951.9	63	17,033	649	87,030
Black-legged kittiwake	*Rissa tridactyla*	0.407	859.0	-	-	2	28
Common murre	*Uria aalge*	0.993	1,629.8	8	37	4	82
Thick-billed murre	*Uria lomvia*	0.964	1,595.5	9	26	9	83
Unidentified murre		0.979	1,612.7	8	15	7	57
Ancient murrelet	*Synthliboramphus antiquus*	0.206	526.8	96	325	735	718
Cassin's auklet	*Ptychoramphus aleuticus*	0.188	493.4	9	4	16	143
Parakeet auklet	*Cyclorrhynchus psittacula*	0.258	619.2	1	2	80	21
Least auklet	*Aethia pusilla*	0.084	276.7	28	3	13,259	23
Whiskered auklet	*Aethia pygmaea*	0.121	359.6	498	1,331	71	14
Crested auklet	*Aethia cristatella*	0.264	629.6	792	3	374	19
Unidentified small alcid		0.150	419.0	445	199	211	178
Tufted puffin	*Fratercula cirrhata*	0.779	1,369.1	128	576	253	2,621
Horned puffin	*Fratercula corniculata*	0.619	1,160.8	1	16	3	23

Table 4. Energy density of prey consumed by seabirds during this study. Modified from Davis *et al.* (1998, Table 3).

Prey type	Organism or group	Energy density ($kJ\ g^{-1}$ wet wt)
Gelatinous zooplankton	Small medusae	0.569
Euphausiids	*Thyssanoessa* spp.	3.111
Copepods	*Neocalanus cristatus*	2.625
Amphipods	Hyperiid amphipods	2.466
Other Invertebrates	*Limacina* spp.	2.613
Squid (mean value)	Cephalopoda	5.504
Fish (mean value)	Teleostei (non-salmonids)	5.677

Table 5. Number of transects that showed spatial autocorrelation in seabird densities using 5-km bins (re-coded as a binary variable) at lags 1, 2 and 3 for a total of 38 transect lines included in the study.

	Lag 1	Lag 2	Lag 3
Short-tailed shearwaters	1	1	1
Northern fulmars	3	3	1
Small alcids	2	5	3
Large alcids	12	7	4

Table 6. Results of the preliminary logistic regression model on presence of seabird aggregations using all variables.

	Short-tailed shearwaters		Northern fulmars		Small auklets		Tufted puffins	
Variable	Coefficient	t-ratio	Coefficient	t-ratio	Coefficient	t-ratio	Coefficient	t-ratio
Constant	-2.483**	-5.098	-0.846*	-2.405	-0.160	-0.515	-1.656**	-5.414
Year	-0.914**	-3.220	-0.270	-1.221	-0.249	-1.144	0.281	1.420
Month	0.282	0.746	0.767**	2.855	-0.685**	-3.049	0.648**	3.030
Longitude	-1.164**	4.070	1.467**	-7.814	0.249	-1.487	-0.824**	5.233
Latitude (north)	0.297	1.027	-0.200	-0.853	-0.143	-0.626	-0.331	-1.612
Latitude (south)	-1.336**	-2.897	0.106	0.445	-0.424	-1.938	0.075	0.359
Model Chi-Square [df]	50.84 [5]**		88.44 [5]**		13.49 [5]*		39.38 [5]**	
% Correct predictions	83.7		66.8		62.2		56.6	
McFadden's Rho^2	0.102		0.101		0.015		0.039	

* Indicates significance at the 0.05 level, ** Indicates significance at the 0.01 level

Table 7. Logistic regression results of the final model on the presence of seabird aggregations as a function of selected variables.

	Short-tailed shearwaters		Northern fulmars		Small auklets		Tufted puffins	
Variable	Coefficient	t-ratio	Coefficient	t-ratio	Coefficient	t-ratio	Coefficient	t-ratio
Constant	-2.198**	-7.291	-1.058**	-5.771	-0.730**	-5.393	-1.348**	-7.963
Year	-1.011**	-3.953						
Month			0.795**	3.900	-0.477**	-2.807	0.422*	2.500
Longitude	-1.151**	4.028	1.472**	-7.924			-0.816**	5.267
Latitude (north)	0.345	1.216						
Latitude (south)	-1.387**	-3.056						
Model Chi-Square [df]	50.27 [4]**		84.45 [2]**		7.76 [1]**		35.10 [2]**	
% Correct predictions	83.7		66.6		61.9		56.4	
McFadden's Rho^2	0.101		0.096		0.009		0.035	

* Indicates significance at the 0.05 level, ** Indicates significance at the 0.01 level

Table 8. Density of seabirds feeding and sitting on the water ($\overline{X} \pm SD$ birds km^{-2}) in the central and eastern Aleutian Islands during 2001 and 2002. Values between parentheses represent the total number of 5-km bins sampled in the region. Survey effort and areas surveyed varied between years, see text for details.

	2001		2002	
	Central (n = 118)	Eastern (n = 124)	Central (n = 267)	Eastern (n = 306)
Short-tailed shearwaters	0.4 ± 0.2	93.2 ± 55.6	1.6 ± 1.3	190.3 ± 85.4
Northern fulmars	29.6 ± 9.7	0.9 ± 0.3	41.5 ± 15.8	0.7 ± 0.2
Small alcids	10.7 ± 5.5	10.1 ± 6.5	36.9 ± 14.4	2.6 ± 0.4
Large alcids	0.9 ± 0.2	3.7 ± 0.5	0.7 ± 0.1	6.5 ± 1.1

Table 9. Density of seabirds feeding and sitting on the water ($\overline{X} \pm SD$ birds km^{-2}) in the Aleutian passes during 2001. Values between parentheses represent the total number of 5-km bins sampled in the region. Survey effort and areas surveyed varied between years; see text for details.

	Central		Eastern	
	Seguam (n = 34)	Amukta (n = 20)	Akutan (n = 28)	Unimak (n = 30)
Short-tailed shearwaters	0.1 ± 0.1	0.0 ± 0.0	371.7 ± 239.8	34.4 ± 31.2
Northern fulmars	32.5 ± 8.5	0.5 ± 0.2	0.5 ± 0.2	0.2 ± 0.1
Small alcids	2.6 ± 1.5	0.5 ± 0.2	39.5 ± 28.2	0.3 ± 0.2
Large alcids	0.5 ± 0.2	0.8 ± 0.3	6.0 ± 1.8	2.9 ± 0.7

Table 10. Density of seabirds feeding and sitting on the water ($\overline{X} \pm SD$ birds km^{-2}) in the Aleutian passes during 2002. Values between parentheses represent the total number of 5-km bins sampled in the region.

	Central				Eastern		
	Tanaga (n = 40)	Seguam (n = 31)	Amukta (n = 16)	Samalga (n = 30)	Umnak (n = 25)	Akutan (n = 68)	Unimak (n = 119)
Short-tailed shearwaters	0.0 ± 0.0	3.1 ± 1.9	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	17.9 ± 11.4
Northern fulmars	0.2 ± 0.1	72.9 ± 33.4	0.5 ± 0.2	76.8 ± 51.0	0.0 ± 0.0	0.4 ± 0.3	0.6 ± 0.2
Small alcids	203.1 ± 92.5	3.4 ± 1.8	0.3 ± 0.1	0.2 ± 0.1	14.9 ± 4.1	2.1 ± 0.6	1.6 ± 0.5
Large alcids	0.3 ± 0.1	1.7 ± 0.4	0.3 ± 0.1	0.7 ± 0.2	22.1 ± 8.0	4.8 ± 1.3	3.6 ± 0.5

Table 11. Biomass of zooplankton ($\overline{X} \pm SD$ g m^{-2}) integrated over the upper 40 m of the water column for the central and eastern Aleutian Islands during 2001 and 2002. Values between parentheses represent the total number of MOCNESS tows in the region.

	2001		2002	
	Central (n = 8)	Eastern (n = 17)	Central (n = 22)	Eastern (n = 27)
Copepods				
Neocalanus cristatus	2.82 ± 1.03	1.02 ± 0.35	6.49 ± 1.59	1.55 ± 0.28
N. plumchrus-flemingeri	7.06 ± 2.87	3.54 ± 0.47	11.63 ± 1.91	10.08 ± 1.85
Metridia spp.	1.67 ± 0.73	0.97 ± 0.33	1.65 ± 0.33	1.92 ± 0.67
Eucalanus bungii	18.80 ± 10.19	8.46 ± 2.16	7.96 ± 1.33	5.08 ± 0.62
Calanus marshallae	0.31 ± 0.15	1.53 ± 0.19	0.17 ± 0.03	1.65 ± 0.37
Euphausiids				
Euphausia pacifica	0.31 ± 0.17	0.06 ± 0.03	0.27 ± 0.09	0.12 ± 0.09
Thyssanoesa inspinata	0.26 ± 0.14	0.02 ± 0.01	0.06 ± 0.02	0.36 ± 0.36
T. longipes	0.08 ± 0.04	0.62 ± 0.35	1.32 ± 0.46	3.06 ± 1.87
T. spinifera	0.17 ± 0.13	0.68 ± 0.30	0.04 ± 0.02	0.36 ± 0.13
T. inermis	0.00 ± 0.00	3.75 ± 2.07	0.00 ± 0.00	1.63 ± 0.60

Table 12. Biomass of zooplankton ($\overline{X}$ g m^{-2}) integrated over the upper 40 m of the water column in the Aleutian passes during 2002. Values between parentheses represent the relative contribution of each species to the total copepod or euphausiid biomass in each pass. N represents the total number of MOCNESS towed in the pass.

	2001			2002				
	Seguam n = 8	Akutan n = 12	Unimak n = 5	Tanaga n = 9	Seguam n = 9	Samalga n = 9	Akutan n = 14	Unimak n = 13
Copepods								
Neocalanus cristatus	2.82 (9%)	1.02 (8%)	1.01 (5%)	8.05 (25%)	6.76 (26%)	2.4 (11%)	1.89 (10%)	1.18 (5%)
N. plumchrus-flemingeri	7.06 (23%)	3.22 (25%)	4.3 (19%)	16.91 (52%)	9.52 (36%)	4.49 (20%)	8.49 (45%)	11.78 (54%)
Metridia spp.	1.67 (5%)	0.77 (6%)	1.45 (6%)	1.67 (5%)	2.26 (9%)	0.23 (1%)	1.47 (8%)	2.4 (11%)
Eucalanus bungii	18.8 (61%)	6.2 (49%)	13.88 (62%)	5.42 (17%)	7.55 (29%)	14.58 (66%)	5.26 (28%)	4.89 (22%)
Calanus marshallae	0.31 (1%)	1.46 (12%)	1.7 (8%)	0.18 (1%)	0.08 (0%)	0.32 (1%)	1.6 (9%)	1.71 (8%)
Euphausiids								
Euphausia pacifica	0.31 (38%)	0.03 (1%)	0.12 (3%)	0.3 (16%)	0.35 (16%)	0.01 (5%)	0.05 (1%)	0.2 (3%)
Thyssanoesa inspinata	0.26 (32%)	0.01 (0%)	0.03 (1%)	0.04 (2%)	0.1 (4%)	0.01 (7%)	0 (0%)	0.75 (11%)
T. longipes	0.08 (10%)	0.25 (5%)	1.52 (33%)	1.44 (79%)	1.78 (79%)	0.03 (25%)	1.97 (49%)	4.23 (60%)
T. spinifera	0.17 (20%)	0.34 (6%)	1.49 (32%)	0.06 (3%)	0.03 (1%)	0.06 (45%)	0.4 (10%)	0.32 (4%)
T. inermis	0 (0%)	4.7 (88%)	1.47 (32%)	0 (0%)	0 (0%)	0.02 (17%)	1.64 (40%)	1.61 (23%)

FIGURE LEGENDS

Figure 1. Map of the Aleutian Islands showing passes surveyed in 2001 and 2002. Amchitka and Atka passes are shown for geographical reference. Chagulak Island, the highest largest northern fulmar colony in the area, is indicated surrounded by a circle of 300 km in diameter.

Figure 2. Distribution and abundance of short-tailed shearwaters (a and b, birds km^{-2}) and northern fulmars (c and d) along the Aleutian Islands in 2001 and 2002, repectively.

Figure 3. Distribution and abundance of small (a and b, ancient murrelets, least and whiskered auklets; birds km^{-2}) and large alcids (c and d, mostly tufted puffins) along the Aleutian Islands in 2001 and 2002, respectively.

Figure 4. Relationship between seabird abundance and the sill cross-sectional area of the passes for a) short-tailed shearwaters, b) northern fulmars, c) tufted puffins, and d) small alcids. The solid line represents the trend using all data.

Figure 5. Diet composition by number of a) short-tailed shearwaters and b) northern fulmars at three passes along the Aleutian Islands in 2002. Samples of northern fulmars in Akutan Pass were collected in 1999 and 2002. Sample size is denoted on top of each bar.

Figure 6. Interannual variation in diet composition by number of short-tailed shearwaters in Akutan Pass during 1999, 2001 and 2002. Sample size is denoted on top of each bar.

Figure 7. Prey consumption by seabirds in the central and eastern Aleutian Islands in 2001 (a and b) and 2002 (c and d). NOFU = northern fulmar, STSH = short-tailed shearwaters, SMAL = small alcids, TUPU = tufted puffins. Note difference in the scale of the *Y* axis.

Figure 8. Prey consumption by seabirds in the Aleutian passes in a) 2001 and b) 2002.

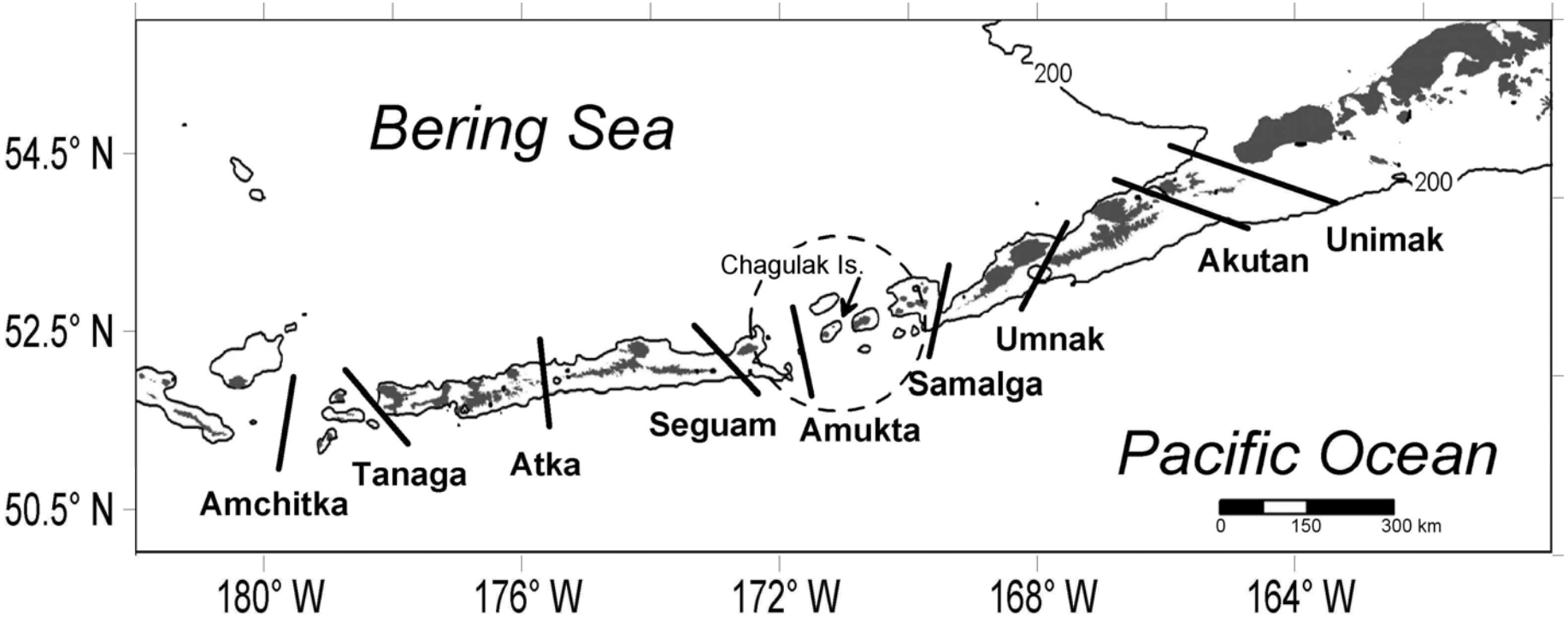
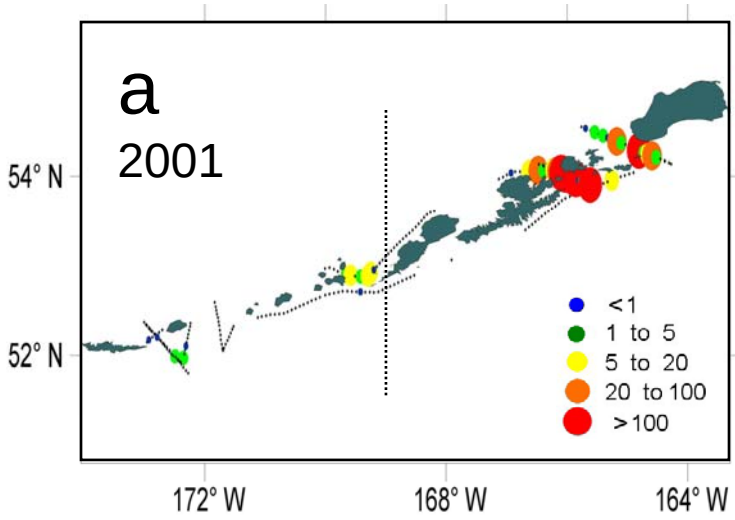
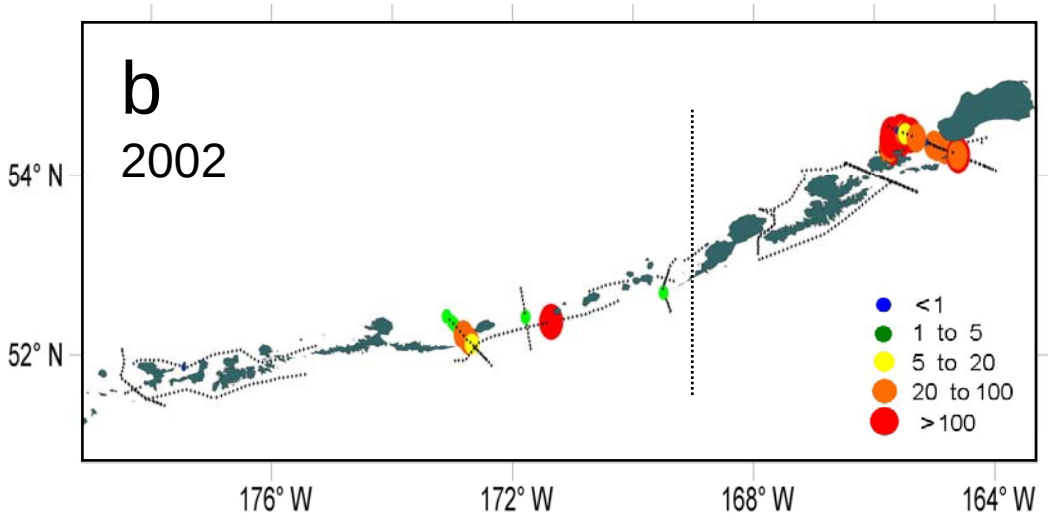

Bering Sea
Pacific Ocean
200
200
Chagulak Is.
Amchitka
Tanaga
Atka
Seguam
Amukta
Samalga
Umnak
Akutan
Unimak
0
150
300 km
54.5° N
52.5° N
50.5° N
180° W
176° W
172° W
168° W
164° W

Fig. 1

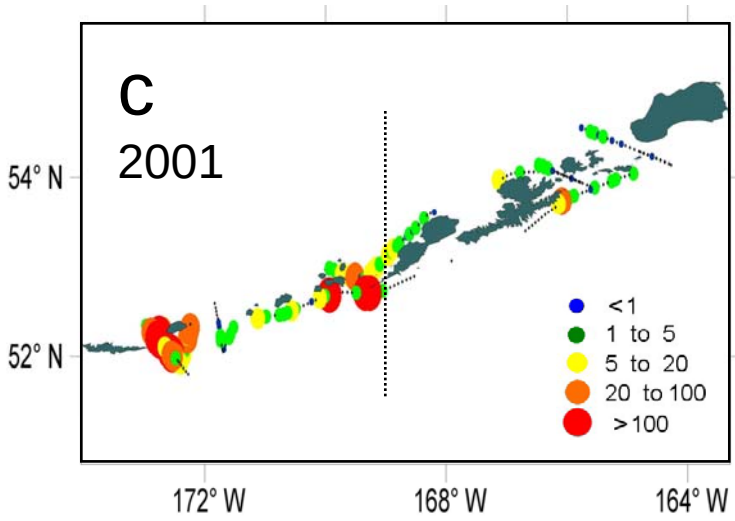
Fig. 2

Short-tailed shearwaters





Northern fulmars



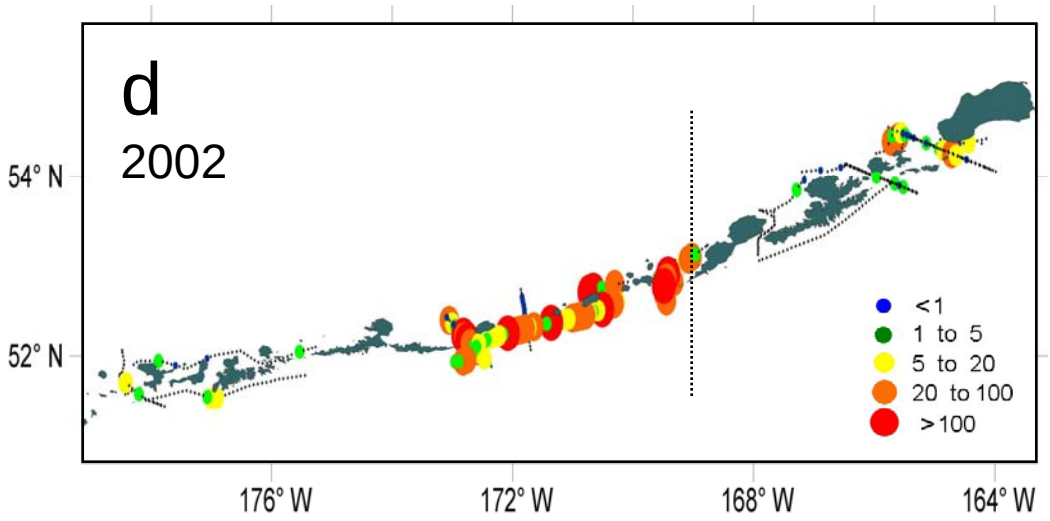
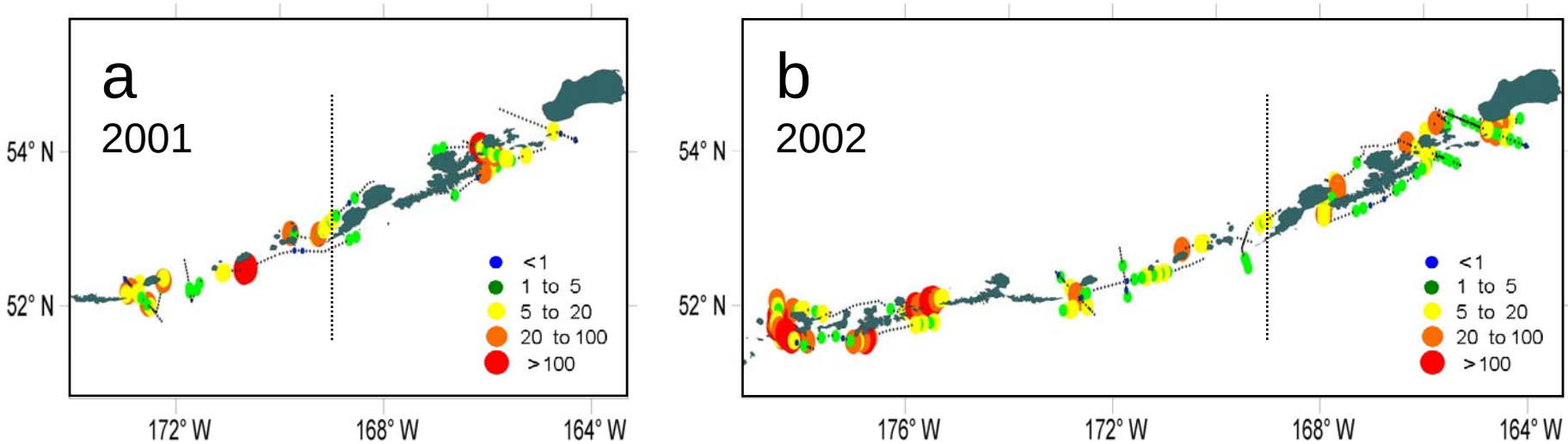
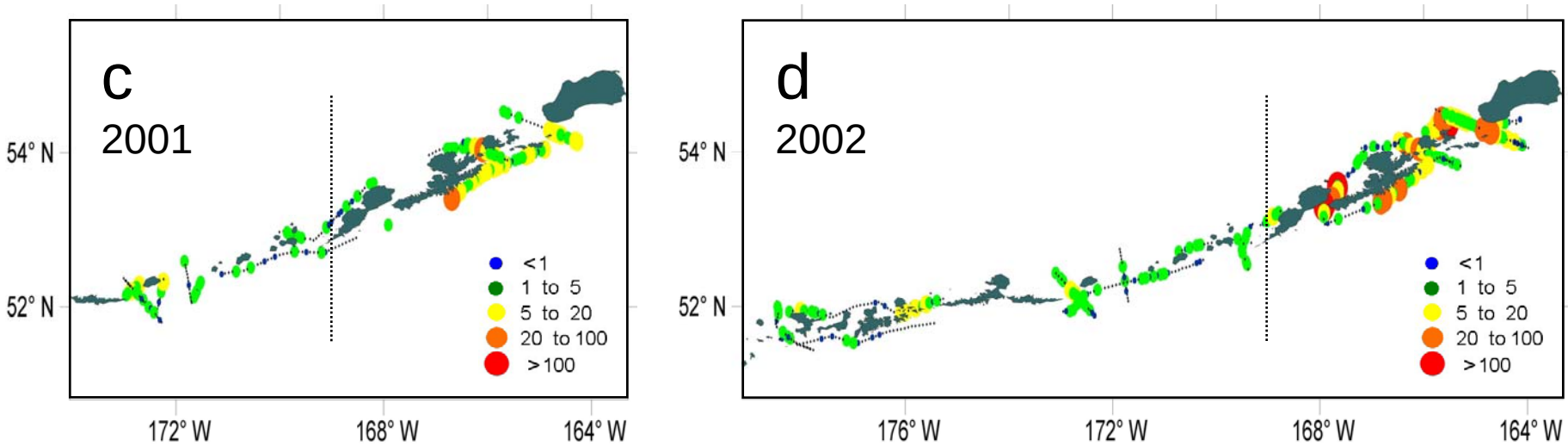


Fig. 3

Small alcids



Large alcids



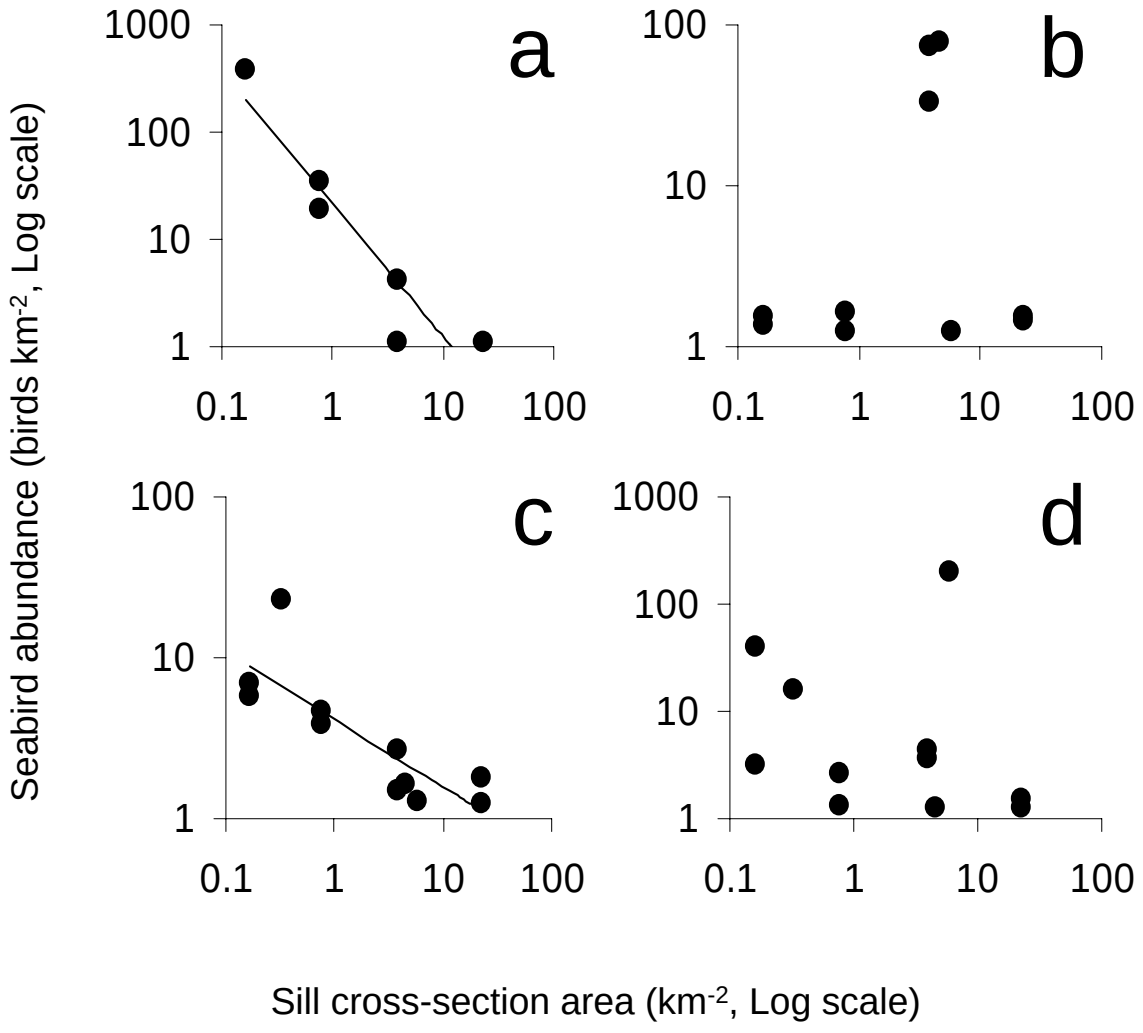

a
b
c
d
1000
100
10
1
0.1
1
10
100
Seabird abundance (birds km-2, Log scale)
Sill cross-section area (km-2, Log scale)

Fig. 4

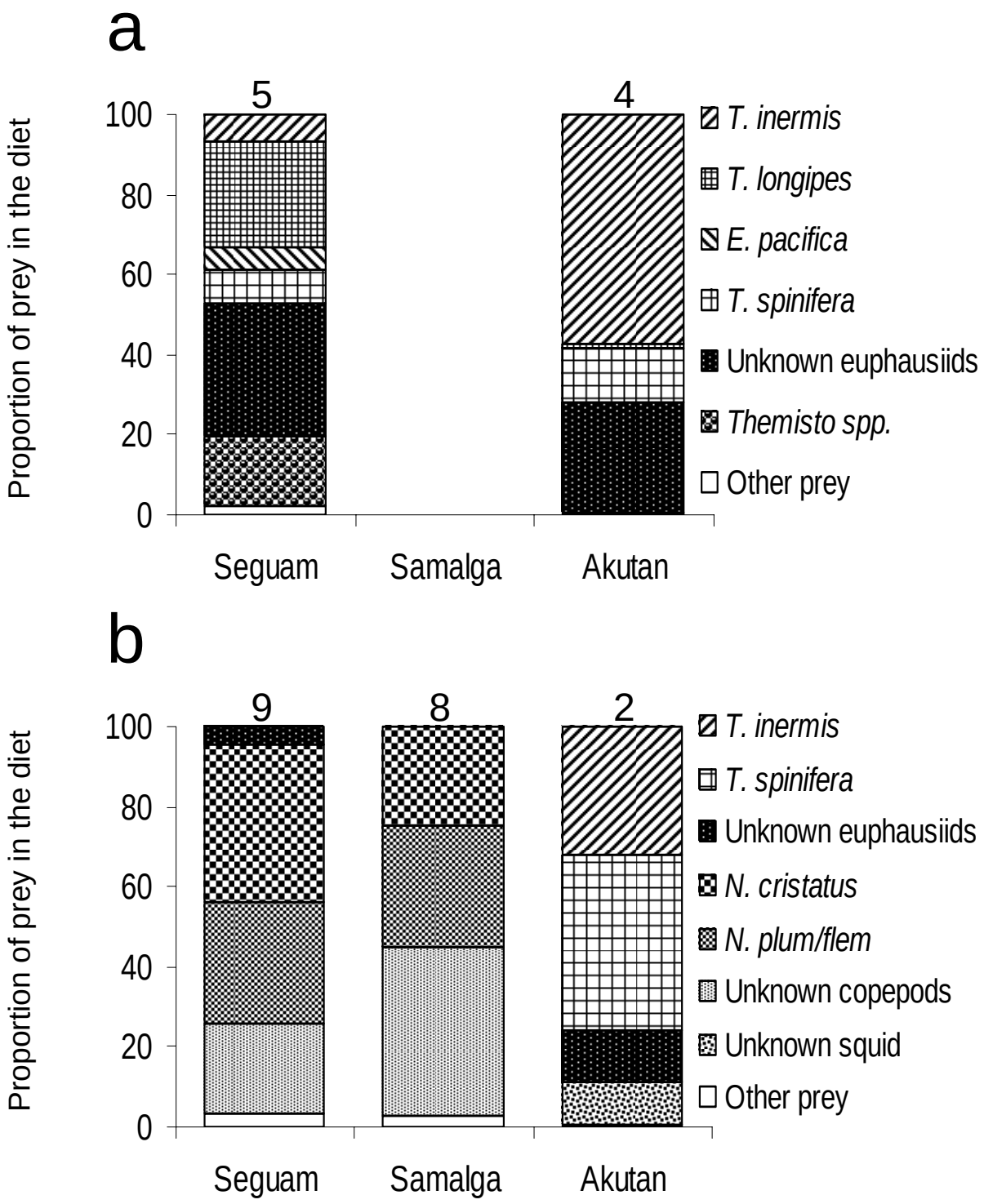

a
5
4
100
80
60
40
20
0
Proportion of prey in the diet
T. inermis
T. longipes
E. pacifica
T. spinifera
Unknown euphausiids
Themisto spp.
Other prey
Seguam
Samalga
Akutan
b
9
8
2
100
80
60
40
20
0
Proportion of prey in the diet
T. inermis
T. spinifera
Unknown euphausiids
N. cristatus
N. plum/flem
Unknown copepods
Unknown squid
Other prey
Seguam
Samalga
Akutan

Fig. 5

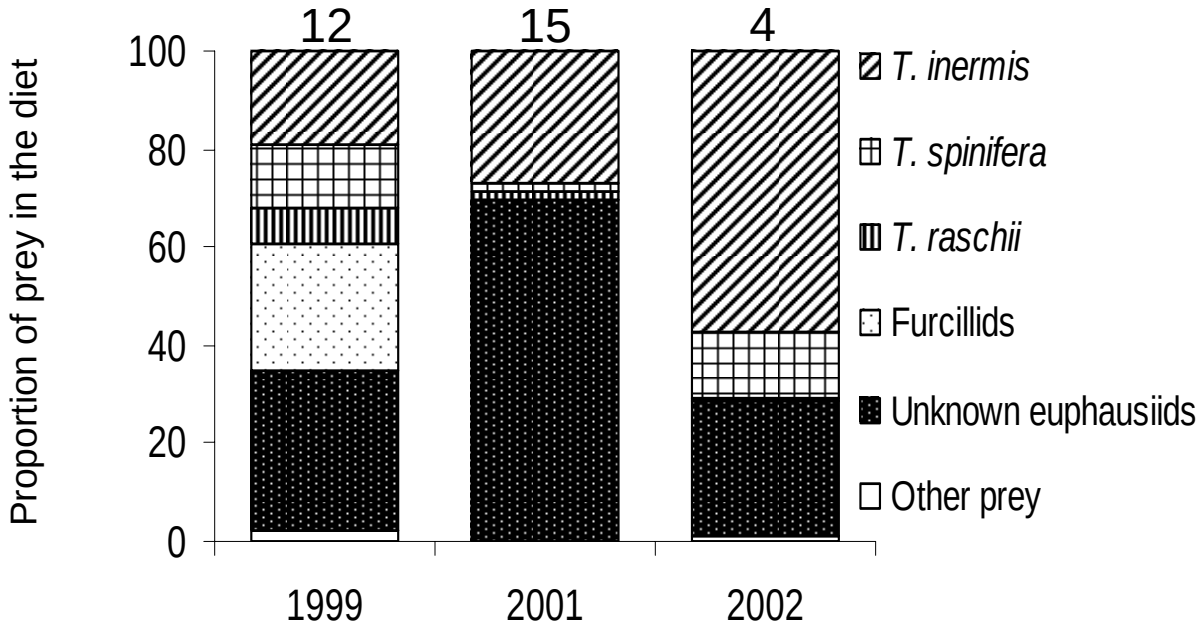

12
15
4
100
80
60
40
20
0
Proportion of prey in the diet
1999
2001
2002
T. inermis
T. spinifera
T. raschii
Furcillids
Unknown euphausiids
Other prey

Fig. 6

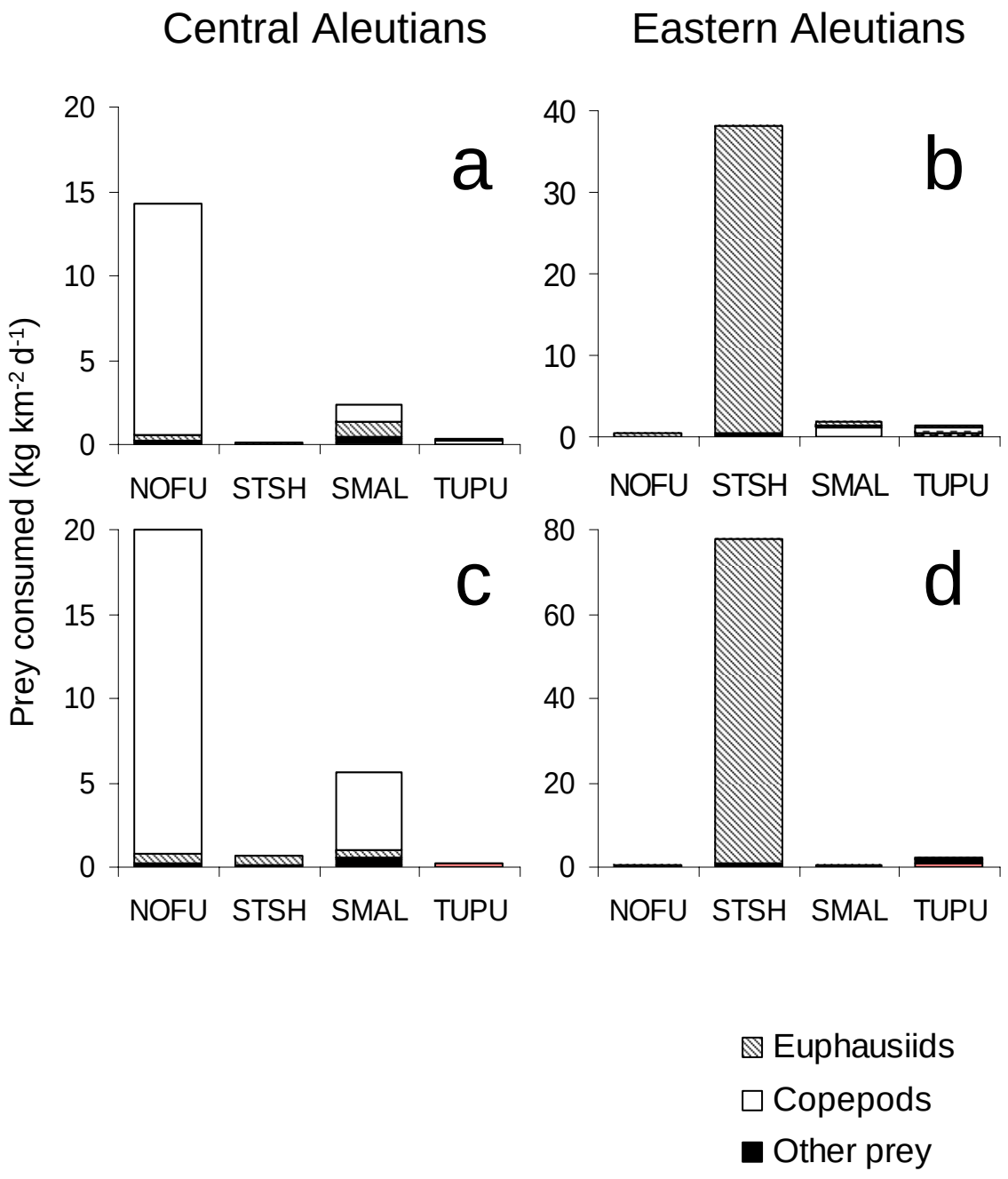

Central Aleutians
Eastern Aleutians
Prey consumed (kg km-2 d-1)
a
b
c
d
NOFU
STSH
SMAL
TUPU
Euphausiids
Copepods
Other prey

Fig. 7

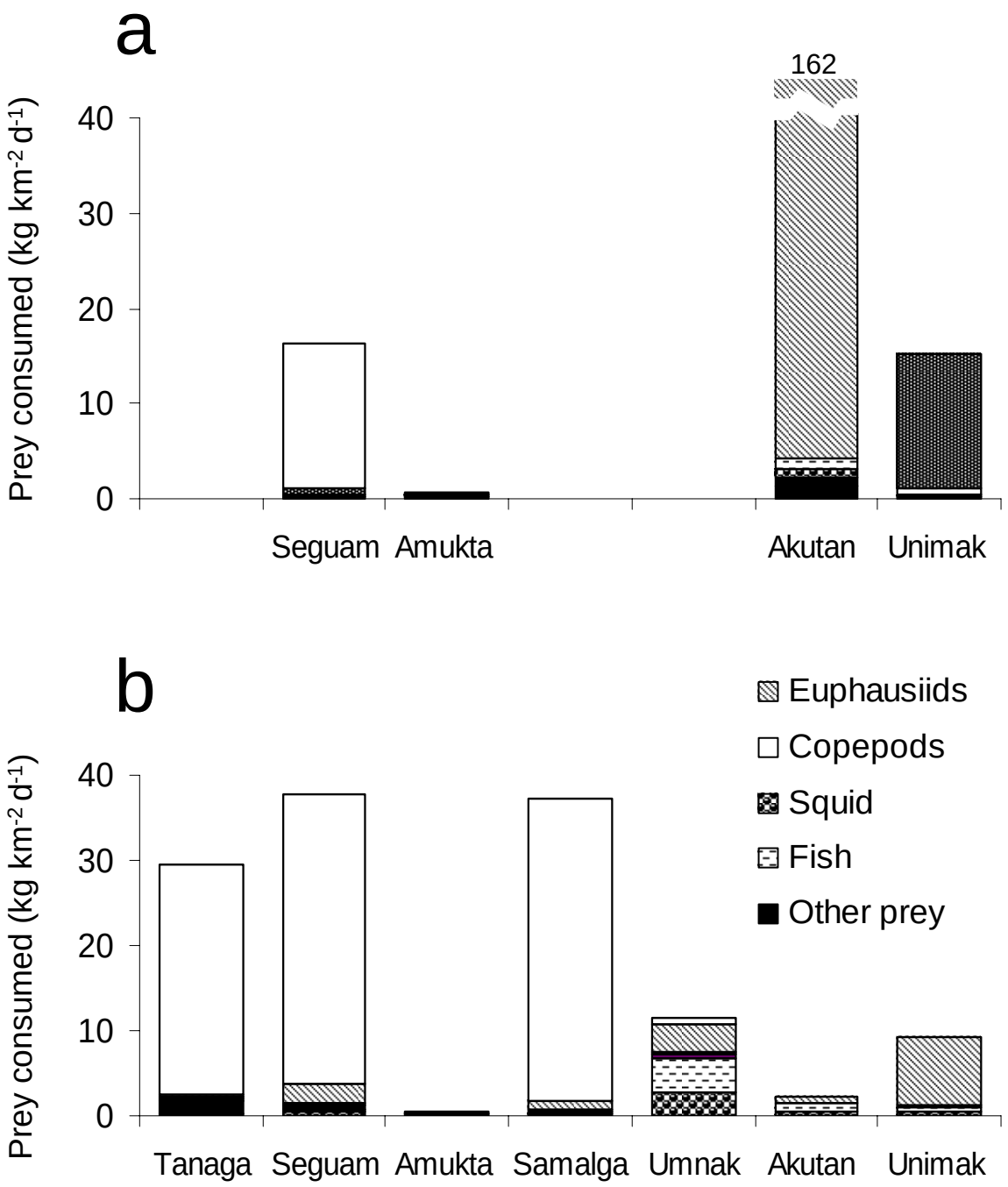

a
162
Prey consumed (kg km-2 d-1)
40
30
20
10
0
Seguam
Amukta
Akutan
Unimak
b
Euphausiids
Copepods
Squid
Fish
Other prey
Prey consumed (kg km-2 d-1)
40
30
20
10
0
Tanaga
Seguam
Amukta
Samalga
Umnak
Akutan
Unimak

Fig. 8