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Top predator distribution and abundance across the eastern Gulf of Alaska: Temporal variability and ocean habitat associations

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Abstract

We studied interannual variation in marine bird and mammal distribution and abundance in the eastern Gulf of Alaska (GOA) over 8 years, 1996–2003. We identified and enumerated seabirds, pinnipeds and cetaceans along a replicated 1500 km survey path, representing 450 km² of coastal and 2000 km² of oceanic habitat. Near-surface temperature (5 m depth) fluctuated considerably from year to year, in part due to the timing of the survey, with an early survey in 1996 and a late survey in 2002. Many species were observed across the entire gradient, particularly procellariiform (tubenose) seabirds and Dall's porpoise (*Phocoenoides dalli*). We observed peaks in abundance in the oceanic zone in 1998, 2001, and 2002, owing primarily to influxes of dark shearwaters (*Puffinus* spp.) and Leach's storm-petrels (*Oceanodroma leucora*). Rank correlations indicated similar year-to-year changes in density between species, and species-specific responses to temperature and ocean productivity as indexed by nitrate and chlorophyll *a* concentrations. We developed topographic/bathymetric models of habitat selection for the coastal zone. Although we found some distinct habitat preferences in this zone, overall we observed a continuum in the marine bird and mammal community across the entire eastern GOA. The strength of the coupling between coastal and oceanic environments as provided by variation in top predator dispersion appears related to large-scale variations in oceanography, though we have yet to fully investigate causal mechanisms.

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1. Introduction

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Continental shelves and upwelling systems contribute almost half of the global ocean's primary productivity and fisheries catches (Glantz and Thompson, 1981; Pauly and Christensen, 1995).

In particular, eastern boundary currents, like the California Current System (CCS), are characterized by elevated primary productivity and species diversity, which in turn supports substantial fishery and top predator resources (Briggs et al., 1987; Chavez et al., 2003; Dotson and Charter, 2003; McGowan et al., 1996; Whitney et al., this issue). These productive systems are also highly variable, characterized by large-scale and long-term changes in the structure and functioning of biological communities.

Ocean climate–ecosystem fluctuations are of increasing interest to marine ecologists and fisheries oceanographers (Botsford et al., 1997; Chavez et al., 2003; Dayton et al., 1999; Logerwell et al., 2003; McGowan et al., 2003). Such studies require time-series of physical–biological measurements at appropriately large spatial scales, since the profound effects of ocean climate on coastal and open-ocean ecological communities are often characterized by temporal lags and non-linear responses (Chavez et al., 1999; Hyrenbach and Veit, 2003; McGowan et al., 2003). In addition to bottom-up changes in ecosystem structure associated with climate, variation in the extent and location of water masses strongly influences the distributions of marine species, from plankton to highly mobile nekton-like-tunas and seabirds (Haury et al., 1993; Lehodey et al., 1997; Wahl et al., 1989). While marine scientists recognize the ecological significance of changing water mass distributions, little is known about the extent to which water-mass boundaries shift from year-to-year. In particular, delineation of coastal and oceanic ecosystems is difficult due to the dynamic nature of the frontal systems that often separate shelf-slope and offshore waters. The influence of meso-scale eddies known to transport nutrients and organisms across this porous coastal–oceanic interface may also influence the seasonal onshore–offshore movements of many mobile marine species (Briggs et al., 1987; Chen et al., 2003; Dower and Perry, 2001; Forney and Barlow, 1998; Whitney and Robert, 2002).

Studies of marine bird and mammal communities have shed considerable light on how changes in ocean climate affect coastal and oceanic ecosystems and the linkage between these systems.

For example, in the southern CCS, Hyrenbach and Veit (2003) documented onshore–offshore gradients in avifauna, and related changes in community structure to long- and short-term variations in ocean temperature and productivity. Benson et al. (2002) provided a similar example for cetaceans in productive coastal upwelling areas during a sequence of El Niño and La Niña years (1997–99). Though productivity was depressed during El Niño, prey availability within Monterey Bay was high in comparison to conditions in oceanic waters beyond 50 km from shore, resulting in higher density of whales than expected in this environment. To our knowledge, no study has yet examined year-to-year changes in upper-trophic predator communities within a large domain encompassing both coastal and pelagic waters of the subarctic North Pacific Ocean.

Herein, we examine temporal variation in top predator communities across the boundary between coastal (CCS) and oceanic (Gulf of Alaska: GOA) waters of the eastern North Pacific Ocean. This study is based on 8 years of spring/summer surveys conducted in conjunction with the Canadian Department of Fisheries and Oceans' (DFO) Line P program (Whitney and Freeland, 1999). Our objectives are three-fold: (1) to investigate interannual variability in the distribution and abundance of marine birds and mammals in coastal and oceanic regions; (2) to evaluate linkages between coastal and open-ocean systems based on analyses of species-specific responses to oceanographic variability in this environment; and (3) to characterize predator habitats in the coastal region, based on water depth, distance from the coastline, and a variety of bathymetric indices. Because continental shelves have been found to be more productive than oceanic waters, and are thus capable of supporting higher abundances of top predators (Briggs et al., 1987; Hyrenbach and Veit, 2003; Vermeer et al., 1989; Whitney et al., this issue), we anticipate greater marine bird and mammal abundance in coastal waters. However, we hypothesize that changes in oceanographic conditions that influence productivity will influence the dispersion of top predators in our study area (Bertram et al., 2001; Hay, 1992; Wahl et al., 1989). Therefore, we anticipate positive

relationships between marine bird and mammal distribution and abundance in response to changes in nitrates, and chlorophyll *a* concentration, as proxies for primary productivity in the region.

2. Materials and methods

2.1. Study area

In 1949, oceanographic sampling began on ships used for enhanced weather forecasting off British Columbia, Canada. Since then, vessels from the DFO have followed the same 1500 km cruise track from Vancouver Island (48.5°N, 124.8°W) to Ocean Station P (OSP: 50.0°N, 145.0°W) 2–3 times each year. We refer to this standardized transect as ‘Line P.’ The bathymetry along Line P is complex, dropping below 1000 m water depth approximately 60 km from the coast. The productivity of the coastal region is enhanced by a constant nutrient supply from Juan de Fuca Strait and coastal upwelling (Allen et al., 2001; Denman et al., 1981; Hay et al., 1992; Mackas et al., 1997; Whitney et al., this issue). In comparison, the oceanic domain (herein defined as >2750 m depth) is characterized by gradual deepening and punctuated with scattered deep seamounts and ridges (Fig. 1). Therefore, Line P provides substantial spatial coverage for examining coastal–oceanic coupling in the eastern GOA.

Beginning in 1996, the Canadian Wildlife Service (CWS), in collaboration with DFO, began regular surveys of marine birds and mammals along the Line P transect. PRBO Conservation Science (formerly Point Reyes Bird Observatory) joined the project in 2000. Generally, surveys are conducted three times per year (K.H. Morgan and W.J. Sydeman, unpublished data), although herein we report results from spring/summer (May–July) observations only. Surveys were conducted at approximately the same time each year (1996: 8–29 May; 1997: 4–25 June; 1998: 3–24 June; 1999: 2–23 June; 2000: 31 May–14 June; 2001: 31 May–26 June; 2002: 30 June–26 July; 2003: 27 May–16 June). Clearly, the 1996 survey was early and the 2002 survey was late relative to the other years.

Observations of marine birds and mammals were conducted aboard the *CCGS J.P. Tully* using standardized techniques (Buckland et al., 1993; Tasker et al., 1984). Observations were made from a platform above the bridge, approximately 16.5 m above the water or from the bridge during inclement weather. Surveys were conducted during daylight while the ship was underway at speeds between 5 and 12 knots (9.25–22.2 km h⁻¹). Observations were halted during periods of heavy rain, fog, or rough seas, and when impaired visibility of the survey strip made identification or enumeration of marine birds and mammals impossible. Identifications were confirmed using either 8× or 10× binoculars. Individual transects were a running series of 5-min counts, carried out as the ship remained at a constant speed. Position was noted at least once per hour or when ship direction changed using the ship’s or a handheld (Garmin 12 XL) GPS unit. Within each 5-min count period, all birds seen within the survey strip out to 250 m on one side of the ship were identified and tallied. Birds seen on the water were noted separately from those in flight, but both behaviours were included in our analyses. Unidentified birds were noted to the lowest taxonomic level possible. Frequently, additional oceanographic projects were under simultaneous investigation during Line P cruises, and consequently the vessel often deviated from the track line. Only those surveys that fell within 25 km (on either side) of the track line are included here (Fig. 1).

2.2. Data synthesis

We considered two regions: the oceanic domain included waters >2750 m between 127.01°W and 144.30°W, and the coastal domain included waters < 2750 m between 125.00°W and 127.00°W (Fig. 1). The continental shelf drops rapidly at ~127°W and then gradually slopes down to the abyssal plain (Fig. 1).

Seven focal seabird species and three mammal species were selected based on their high relative abundance and consistent occurrence throughout the study period across both coastal and oceanic regions. Focal seabirds include black-footed albatross (*Pheobastria nigripes*), rhinoceros auklet

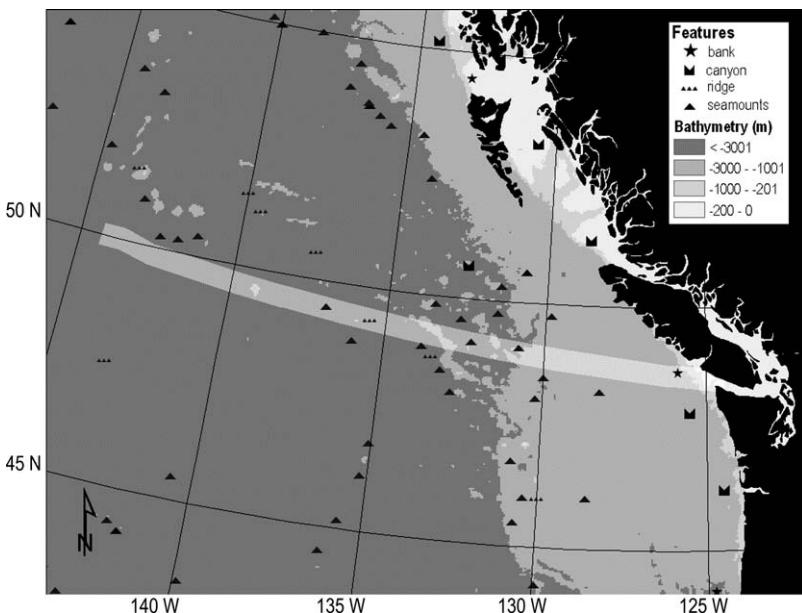


Fig. 1. Line P survey transect lies in the Northeast Pacific transition zone, at the northern boundary of the California Current upwelling system and southern boundary of the Gulf of Alaska downwelling system. In the coastal zone, the trackline crosses a major underwater bank (La Perouse).

(*Cerorhinca monocerata*), Cassin's auklet (*Ptychoramphus aleuticus*), tufted puffin (*Fratercula cirrhata*), fork-tailed storm-petrel (*Oceanodroma furcata*), Leach's storm-petrel (*O. leucomelas*), northern fulmar (*Fulmarus glacialis*), dark shearwater species (comprised of sooty shearwaters [*Puffinus griseus*], and short-tailed shearwaters [*P. tenuirostris*]). Northern fur seal (*Callorhinus ursinus*), Dall's porpoise (*Phocoenoides dalli*), and Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) comprised the mammal focal species.

Fine-scale bathymetric data were acquired for the study area from the Nautical Data International (NDI) digital ocean chart for Vancouver Island and the ETOPO-2 seafloor and elevation grid (Smith and Sandwell, 1997). The NDI data comprise 400 m grids covering 85 km of the coastal region (Fig. 1). The ETOPO-2 database represents topography for 2' latitude/longitude crossings on a global grid (NDI: <http://www.ndi.ca/>; ETOPO-2: <http://www.ngdc.noaa.gov/mgg/fliers/01mgg04.html>). The NDI fine-scale dataset describes well the highly complex coastal bathy-

metric environment, while the coarser oceanic environment is sufficiently represented by the ETOPO-2 database. We used the spatial scales of these databases to establish the dimensions of the survey bins for analysis of factors affecting marine bird and mammal distributions.

Hydrographic data were collected by a variety of means including reversing thermometers, conductivity-temperature-depth (CTD) casts, and underway sensors that record water properties continuously from a depth of 5 m. All physical data are available from the Line P website (http://www-sci.pac.dfo-mpo.gc.ca/osap/data/linep/linepselectdata_e.htm). Nitrate concentrations were analyzed using a Technicon AAII Autoanalyzer and modified Technicon procedures (Barwell-Clarke and Whitney, 1996). Chlorophyll *a* measurements were obtained following the fluorometric procedure of Strickland and Parsons (1972).

For the coastal domain, marine bird densities (number km^{-2}) and mammal 'encounter rates' (individuals km^{-1}) were calculated using 6-km

transect lengths, resulting in 150 survey bins over the eight years. For the oceanic realm, we selected 50-km transect lengths resulting in 95 bins. For each bin, a 1-km wide polygon was overlaid on top of the midpoint to calculate bathymetric habitat indices (see below). Transects in the vicinity of Station P were not included in our analysis due to slow cruising speeds and station-related sampling activities.

2.3. Data analysis

Initially, we evaluated interannual variability in distribution and abundance by conducting a two-way ANOVA on log-transformed densities and encounter rates. We included the terms 'year,' 'region' (either coastal or oceanic), and an interaction term between year and region for each species. We were specifically interested in the interaction term, which tested whether year-to-year fluctuations in abundance varied by region (Table 1 a and b).

Next, we explored associations of year-to-year variation in species relative abundance in relation to each other (Table 2) and with respect to ocean temperature, nitrate concentration, and chlorophyll *a* concentration (Table 3) using Spearman rank correlations. This analysis was stratified by coastal and oceanic regions.

We explored bathymetric habitat associations using the ArcMap v. 8.3 (ESRI, 2000) Geographic Information System (GIS). Due to the homogeneity in bathymetry within the oceanic region, we restricted this analysis to the coastal realm. We considered three bathymetric indices and five distance metrics to specific habitat features: median depth, depth coefficient of variation (CV: (STD/mean) 100%), where STD is the standard deviation, and contour index (CI: ([max. depth–min. depth]/max. depth) 100%) within each bin (see also Yen et al., 2004). Using the midpoint of each survey bin, we measured the shortest distance to the mainland, the continental shelf break (200 m isobath), the continental slope (1000 m isobath), and pelagic waters (3000 m isobath). Next, we considered the effects of distance from the centroid of La Perouse Bank, a shallow (37 m depth,

48.67°N 125.83°W) bank on the continental slope off British Columbia (Fig. 1, Table 4).

Because the abundance estimates (for both density and encounter rates) were not normally distributed and could not be adequately transformed for parametric analyses, we used a non-parametric approach to investigate bathymetric habitat associations (Sokal and Rohlf, 1981; Yen et al., 2004). First, we categorized density or encounter rate in each bin into four classes, '0' when a species is absent, '1' at low densities (1–33 percentile), '2' at average densities (34–66 percentile), '3' at high densities (>66 percentile). To assess relationships between abundance and bathymetric characteristics, we evaluated several transformations for each predictor variable. Instead of arbitrarily applying one transformation to the entire dataset, we allowed the data to determine which transformations were most appropriate for each variable. This was done by fitting an ordered logistic regression (using the ranked abundance codes as above) against each of the predictor variables transformed as follows: (1) untransformed, (2) logarithmic, (3) squared, and (4) square root. A 'year' term was also included. The likelihood ratio statistic (LRS) and 'quasi-coefficient of determination' (Hosmer and Lemeshow, 2000) were used to evaluate which transformation was most appropriate. The transformation with the best fit, expressed as the largest (and most significant) LRS and pseudo R^2 value, was selected and used in a multi-variable ordered logistic regression analysis.

Next, we used a backwards stepwise procedure to identify the most important bathymetric predictor variables. Backward stepwise logistic regression is ideal for exploratory analyses (Hosmer and Lemeshow, 2000). Variables were removed from the model when $p > 0.05$, yielding a reduced model containing only significant predictor variables.

Finally, once we had constructed a 'habitat' model for each species, we tested for year-to-year persistence of relationships by examining interannual variability in habitat associations (Table 5). To examine persistence, we fit models including 'year' as a covariate, as well as the interactions between year and each bathymetric variable. We evaluated these models with and without

Table 1

(a) Average species abundance for each region (seabirds: birds/km²; marine mammals: #/km). (b) ANOVA of density by year (1996–2003) and region (coastal/oceanic)

	Black-footed albatross	Rhinoceros auklet	Cassin's auklet	Tufted puffin	Fork-tailed storm-petrel	Leach's storm-petrel	Northern fulmar	Dark shearwaters	Northern fur seal	Dall's porpoise	P. white-sided dolphin	
a	Coastal abundance/ std	0.478 1.10	0.140 0.37	0.134 0.69	0.022 0.15	0.919 5.81	0.167 0.79	0.995 3.89	20.563 119.13	0.031 0.10	0.039 0.21	0.277 1.39
	Oceanic abundance/ std	0.048 0.09	0.004 0.02	0.013 0.08	0.027 0.11	0.174 0.23	1.069 1.58	0.005 0.02	0.853 1.68	0.017 0.06	0.054 0.10	0.009 0.09
b	Region d.f. = 1	18.73 <0.001	9.40 0.002	2.00 0.16	0.22 0.64	1.64 0.20	42.36 <0.001	4.42 0.04	1.97 0.16	0.95 0.33	0.00 0.97	2.83 0.09
	Year d.f. = 7	2.56 0.01	2.61 0.01	1.99 0.06	1.24 0.28	0.94 0.48	4.28 <0.001	2.68 0.01	1.20 0.31	2.82 0.01	1.8 0.09	2.30 0.03
	Year Region d.f. = 7	2.71 0.01	2.23 0.03	— —	— —	— —	4.13 <0.001	2.68 0.01	— —	2.14 0.04	— —	— —

The top number shown is the *F*-value, the bottom is the *p*-value for the analysis. Cassin's auklet, tufted puffin, fork-tailed storm-petrel, dark shearwater, northern fur seal and Pacific white-sided dolphins did not demonstrate significant year *region interactions, hence the *F*- and *p*-values reflect a reduced model including just main effects for these species.

Table 2
Spearman rank correlation matrix on density (encounter rates for mammals) stratified by region

Oceanic	Coastal										
	Black-footed albatross	Rhinoceros auklet	Cassin's auklet	Tufted puffin	Fork-tailed storm-petrel	Leach's storm-petrel	Northern fulmar	Dark shearwaters	Northern fur seal	Dall's porpoise	P. white-sided dolphin
Black-footed albatross		0.491	0.870	0.026	0.749	0.230	-0.029	0.694	-0.297	0.268	0.142
Rhinoceros auklet	0.559		0.746	-0.266	0.516	0.198	0.136	0.530	0.261	-0.209	0.188
Cassin's auklet	0.423	0.901		-0.238	0.856	0.381	-0.002	0.850	-0.138	0.052	0.317
Tufted puffin	0.308	0.435	0.135		-0.429	-0.453	0.614	-0.340	0.421	0.557	-0.346
Fork-tailed storm-petrel	0.151	0.654	0.467	0.563		0.777	-0.190	0.697	-0.363	-0.110	0.164
Leach's storm-petrel	-0.102	0.267	0.070	0.645	0.821		-0.166	0.223	-0.258	-0.342	-0.112
Northern fulmar	-0.311	-0.068	0.341	-0.565	-0.096	-0.133		-0.058	0.893	-0.191	-0.028
Dark shearwater	-0.154	0.377	0.464	-0.210	0.389	0.357	0.369		-0.223	0.070	0.757
Northern fur seal	0.565	0.834	0.861	0.119	0.436	-0.100	0.101	0.174		-0.366	-0.094
Dall's porpoise	0.337	-0.084	-0.169	-0.186	-0.144	0.025	-0.214	0.419	-0.220		-0.031
P. white-sided dolphin	-0.211	0.110	-0.123	0.660	0.712	0.926	-0.220	0.091	-0.269	-0.168	

Cells in grey refer to correlations for the coastal region, whereas clear cells represent the oceanic region. Negative values suggest that the pairs do not correspond in time, whereas positive values suggest temporal concordance. Bold numbers indicate Bonferroni corrected significant correlations.

Table 3

Spearman rank correlations of species abundance (seabird densities and mammal encounter rates) with values of coastal and oceanic surface temperature, nitrate concentration (μM), and chlorophyll *a* concentration ($\mu\text{g/L}$)

Species	Surface temp		Nitrate		Chlorophyll <i>a</i>	
	Coastal	Oceanic	Coastal	Oceanic	Coastal	Oceanic
Black-footed albatross	0.381	−0.524	0.405	−0.071	0.167	0.238
Northern fulmar	0.405	—	0.214	—	0.286	—
Dark shearwaters	0.667	0.238	0.405	−0.167	0.095	0.000
Leach's storm-petrel	−0.390	0.214	0.390	0.095	0.537	0.500
Fork-tailed storm-petrel	−0.264	0.191	0.395	−0.048	0.755	0.214
Cassin's auklet	−0.165	—	0.228	—	0.774	—
Rhinoceros auklet	0.096	—	0.168	—	0.479	—
Tufted puffin	0.136	−0.634	0.355	0.781	−0.409	0.000
Northern fur seal	−0.330	0.048	−0.114	−0.262	0.165	−0.119
Dall's porpoise	0.659	−0.071	0.122	−0.119	−0.244	0.571
P. white-sided dolphin	0.791	—	0.218	—	0.000	—

Regions where certain species were not observed in substantial numbers were excluded from the analysis. Bold correlation coefficients are significant at $p < 0.05$, bold and italic values indicate $p < 0.10$.

Table 4

Variables describing the bathymetric environment considered in this study

Variable	Description	Coastal (km)		Oceanic (km)		Mean \pm std (km)	
		Min	Max	Min	Max	Coastal	Oceanic
Land	Distance from bin midpoint to closest land	10.5	85.2	91.4	859.5	52.8 ± 18.8	426.1 ± 222.2
Median	Median depth value within bin	0.05	2.0	2.2	4.2	0.6 ± 0.6	3.4 ± 0.6
200 m	Distance from bin midpoint to 200 m isobath	0.04	43.2	51.8	846.0	13.6 ± 10.6	408.9 ± 228.8
1000 m	Distance from bin midpoint to 1000 m isobath	0.6	94.7	4.5	184.3	31.4 ± 24.1	69.2 ± 43.8
3000 m	Distance from bin midpoint to 3000 m isobath	231.3	384.9	0.3	217.6	296.1 ± 38.5	45.4 ± 54.8
CV depth	Depth coeff. of variation within bin	0.9%	68.5%	0.8%	22.4%	$11.3\% \pm 11.3$	$6.4\% \pm 4.9$
CI depth	Contour index within bin	3.3%	90.5%	3.7%	54.7%	$29.6\% \pm 18.8$	$23.3\% \pm 14.2$
Seamount	Distance from bin midpoint to closest seamount	101.6	259.0	7.6	163.9	167.6 ± 39.6	58.9 ± 32.3
Bank	Distance from bin midpoint to closest bank	7.4	89.0	105.5	903.0	40.2 ± 23.0	576.1 ± 243.9
Canyon	Distance from bin midpoint to closest canyon	24.5	148.2	162.6	824.5	96.6 ± 27.7	356.7 ± 198

For CV and CI, values are expressed as a percentage.

interactions by comparing LRS values. The LRS test was performed for the full unrestricted model (including all year-interaction terms) and the restricted model (no interaction terms included). We interpreted significant interaction terms as evidence of annual variation in bathymetric habitat associations. For species with significant year-to-year interactions, we report regression coefficients for interaction terms (Table 6). Yen et al. (2004) also followed this procedure for determining the persistence of bathymetric habitat associations.

3. Results

3.1. Near-surface ocean temperature

Near-surface temperature showed warming from west to east along the Line P transect, with a drop in temperature near shore, reflecting coastal upwelling (Fig. 2). There was considerable inter-annual temperature variation, with 2002 being warmest and 1996 coolest; this variation was due, in part, to the survey dates occurring later in 2002

Table 5

Final bathymetric associations for each species after controlling for year, showing the nature of the habitat relationships in the coastal region

	Black-footed albatross	Cassin's auklet	Fork-tailed storm-petrel	Leach's storm-petrel	Northern fulmar	Dark shearwaters	Northern fur seal	P. white-sided dolphin
Land	5.58	−5.32e-9	−23.12					2.48
Median	−0.74				−1.56e-6	−1.16e-6		
200 m			15.18	7.0e-5			0.02	
1000 m								
3000 m		−72.66						
CV depth								
CI depth	1.32		0.0005		−0.04			
bank		5.77						
Model χ^2	77.20	21.59	40.92	37.60	62.37	51.41	23.69	11.74
d.f.	10	6	8	5	8	8	4	3
Model P	<0.0001	0.001	<0.0001	<0.0001	<0.0001	<0.0001	0.0001	0.008
Model R^2	0.218	0.199	0.164	0.255	0.208	0.124	0.174	0.131

Positive relationships indicate higher densities farther away from a feature (distance), at greater depths (median depth), or with increasingly heterogeneous bathymetry (CV, CI; these are expressed as a percentage). Negative relationships signify higher densities closer to a feature, at shallower depths, or with increasingly homogeneous bathymetry.

Table 6
Results of the analyses stratified by year

Species	Transformed variables	Year (coefficient)							
		1996	1997	1998	1999	2000	2001	2002	2003
Cassin's auklet	Sqr	Land	−1.49e−08	—	—	1.80e−08	—	−8.42e−09	−1.12e−08
	LN	Bank	−16.11	—	—	−8.24	—	14.88	10.72
Fork-tailed storm-petrel	LN	200 m	16.71	—	—	26.60	13.04	—	29.98
	LN	Land	−25.76	—	—	−41.97	−16.93	—	−50.67
Dark shearwaters	Sqr	Median	−9.38e−07	−2.55e−06	−3.24e−07	−4.72e−06	−3.31e−06	−1.91e−06	−8.52e−07
Northern fulmar	LN	CI	−0.47	1.09	0.77	−0.072	−0.51	2.28	1.52

For those variables that showed significant interannual interactions, habitat models were analyzed separately by year. Coefficients from the final habitat model are shown (ln = logarithmic, sqr = square). Blank cells indicate insufficient data to calculate a coefficient value.

(July) and earlier in 1996 (May). In addition, there was a complete overlap of monthly temperatures east of $\sim 130^{\circ}\text{W}$ (the coastal zone), indicating that the timing of the surveys affected results in the oceanic zone more so than the coastal zone. The 1996 and 2002 temperatures did, however, fall within the normal long-term (1956–2002) average ranges for May and July surface temperatures, respectively. Nonetheless, we feel interpretation of results concerning 1996 and 2002 should be done with caution.

In most years, the oceanic–coastal temperature patterns were similar—in other words, when it was cold in the oceanic region it was also relatively cold coastally. However, this was not true in 2001 when warm coastal temperatures declined rapidly towards the oceanic region. The 2001 survey ranked both as the second warmest year based on coastal measurements, and the second coldest year based on oceanic measurements. The 1997–1998 El Niño period resulted in generally warmer surface waters in both regions (Fig. 2).

3.2. Marine bird and mammal distribution and abundance by region

Rhinoceros auklet, Cassin's auklet, Pacific white-sided dolphin, northern fulmar, and to a lesser extent, northern fur seal were mostly restricted to the coastal region. Dark shearwaters, tufted puffin, storm-petrels (fork-tailed and Leach's), black-footed albatross, and Dall's porpoise occurred throughout Line P (Fig. 3). Variation existed in seabird density/mammal encounter rates by region for black-footed albatross, rhinoceros auklet, Leach's storm-petrel, northern fulmar, northern fur seal, and Pacific white-sided dolphin (Table 1). Densities of black-footed albatross, Rhinoceros auklet, and northern fulmar were significantly higher in the coastal region, whereas density of Leach's storm-petrel was significantly higher in the oceanic region. Notably, there was no significant variation in density of dark shearwaters between regions.

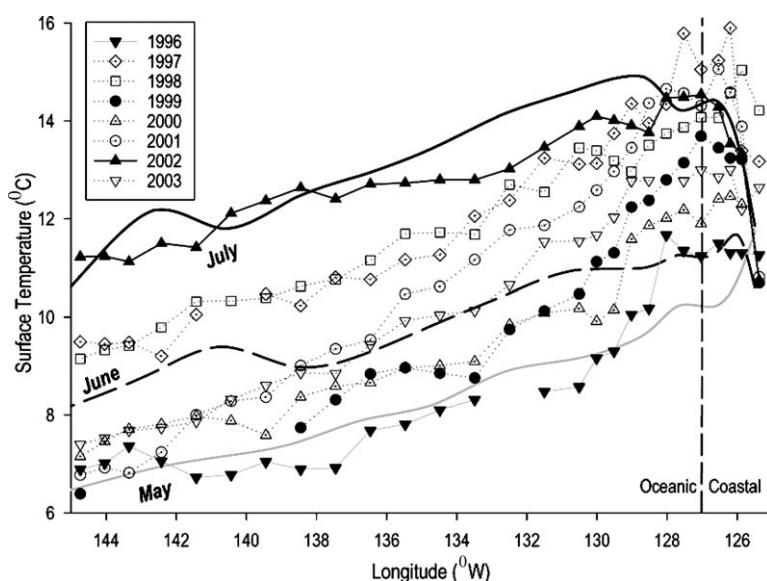


Fig. 2. Near-surface temperature variation at sampling stations from 1996 to 2003, as well as the 1956–2002 long-term mean temperatures for May (solid grey), June (short-dashed black), and July (solid black). Surface temperature for cruises that took place in May is expressed in solid grey, in June is dotted, and in July is solid black (1996: 8–29 May; 1997: 4–25 June; 1998: 3–24 June; 1999: 2–23 June; 2000: 31 May–14 June; 2001: 31 May–26 June; 2002: 30 June–26 July; 2003: 27 May–16 June). The values taken from 1996 and 2002 did not deviate strongly from the normal May and July temperatures, respectively.

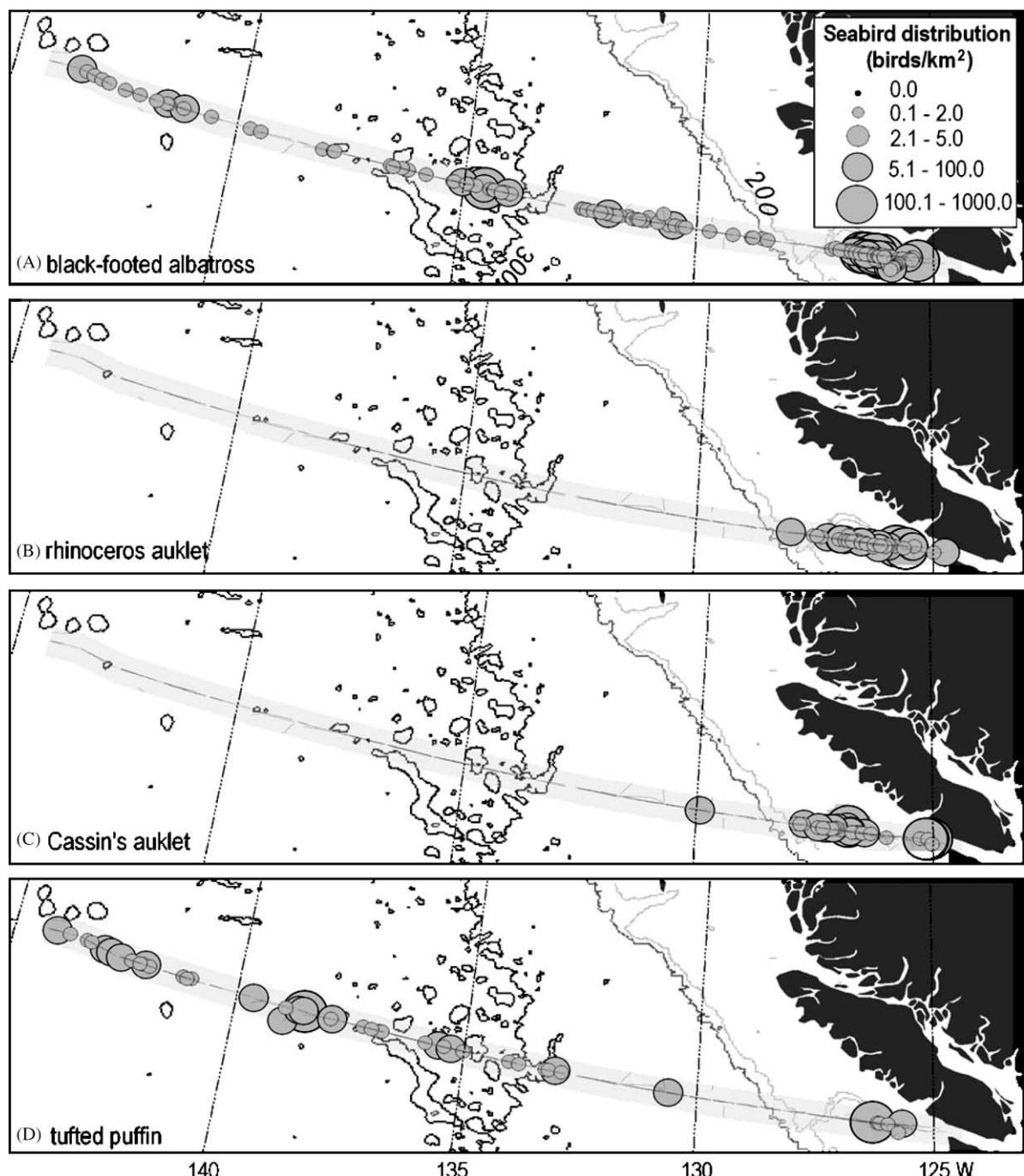


Fig. 3. Distributions of the marine birds (A–H) and mammals (I–K) examined here (1996–2003). The continental shelf extends to the 200 m isobath, the shelf-break extends between 200 and 1000 m and the slope is the area between 1000 and 3000 m depth. The 127°W delineates the western extent of the coastal domain. Dotted lines indicate surveys in an area, but where no individuals were sighted.

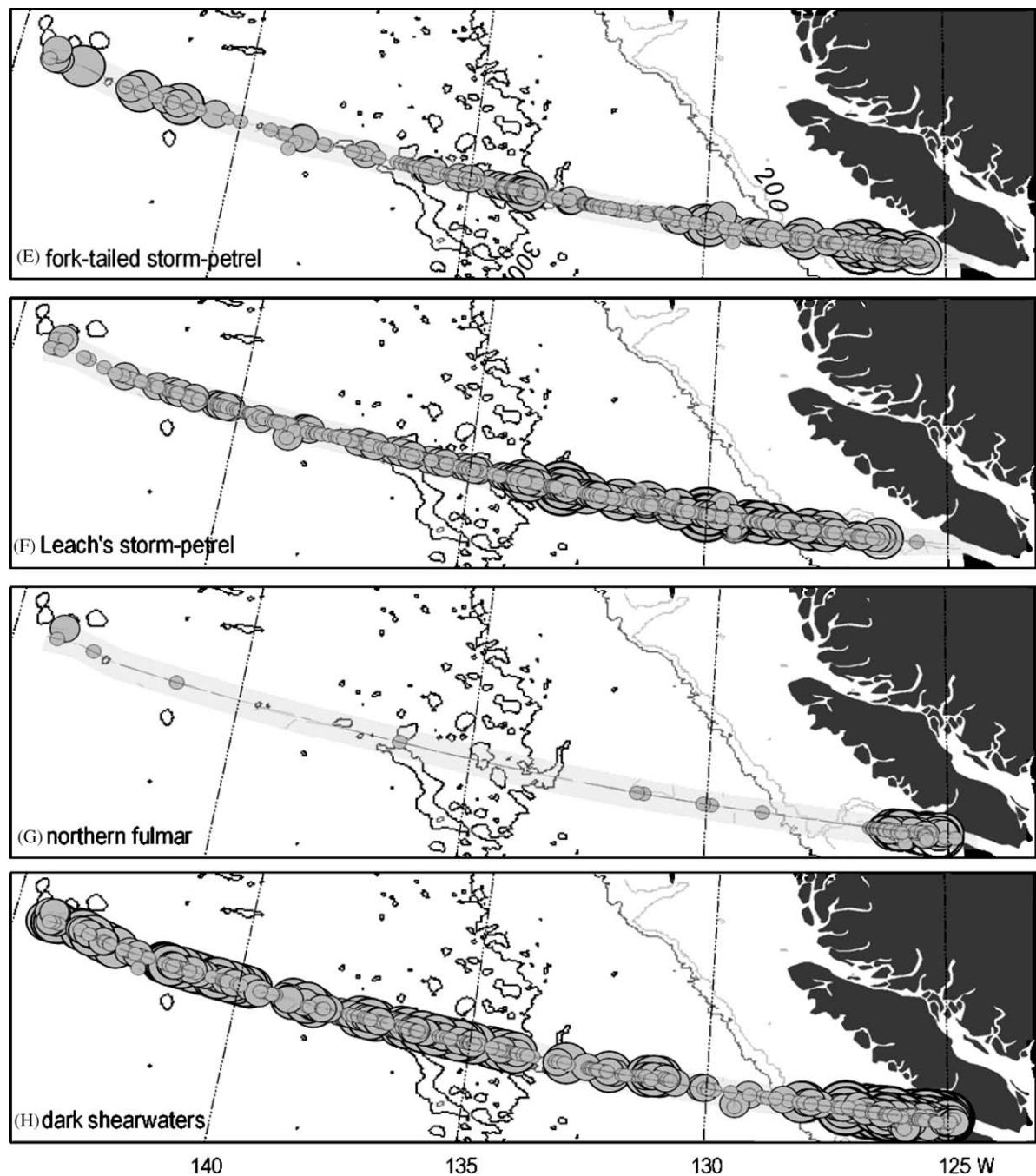


Fig. 3. (Continued)

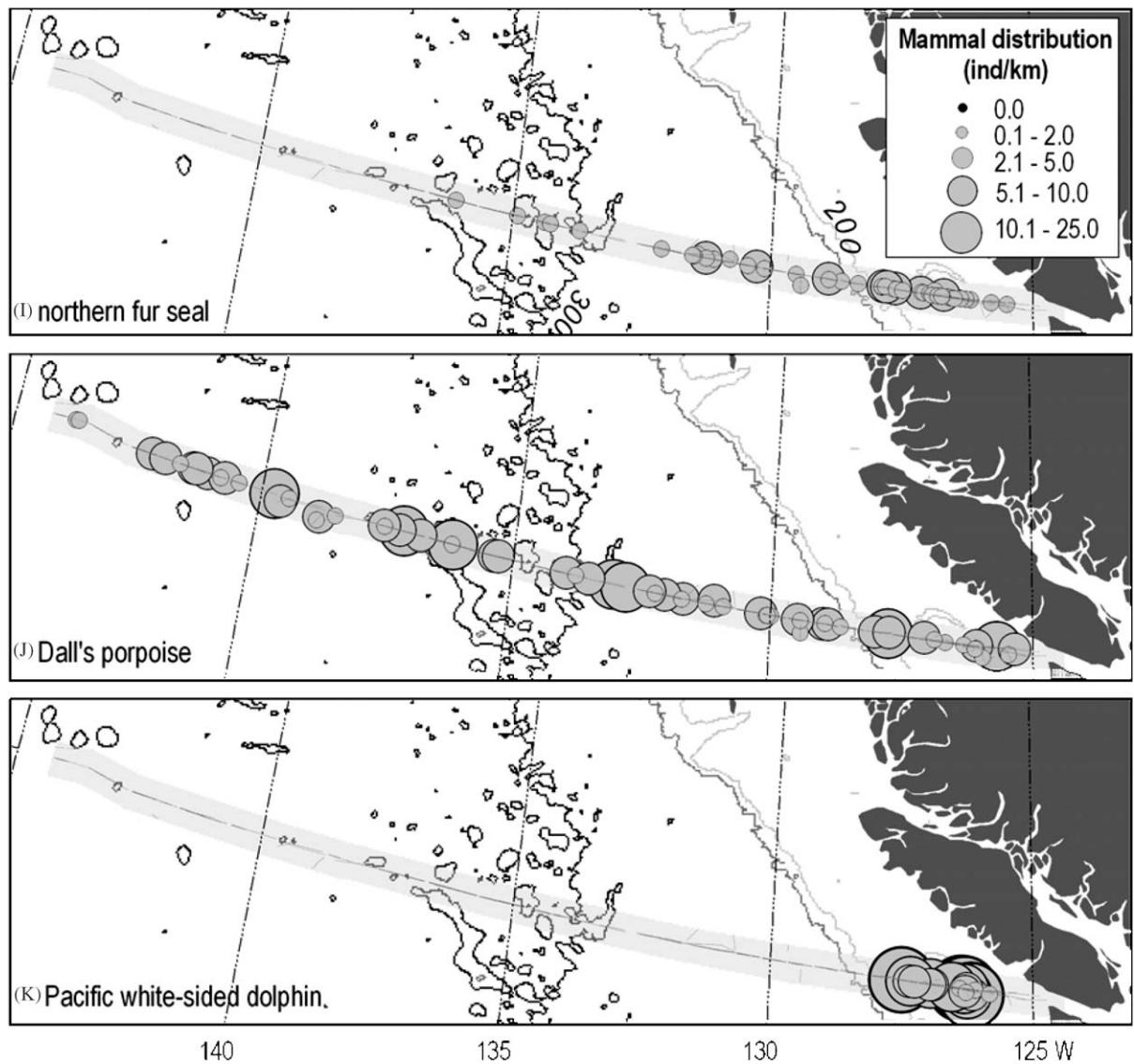


Fig. 3. (Continued)

3.3. Interannual variation in marine bird density

There was significant interannual variation in densities of black-footed albatross, rhinoceros auklet, Leach's storm-petrel, and northern fulmar, with year-region interactions also existing for these birds, as well as Dall's porpoise (Table 1). There was concordance between some species in annual density estimates and, where significant,

correlations were positive (Table 2). For example, in the coastal region, the density of black-footed albatross was positively correlated with the densities of Cassin's auklet, dark shearwaters, and fork-tailed storm-petrels. Leach's and fork-tailed storm-petrel densities were positively correlated with each other in both regions. In the oceanic zone, northern fur seal density was positively correlated with both auklets, and the Pacific

white-sided dolphin was correlated with both storm-petrels.

Dark shearwaters peaked in density in the coastal zone in 1998 and 2001 and to a lesser extent 2002 (Fig. 4A). Fork-tailed storm-petrel and black-footed albatross also peaked in 2001, whereas northern fulmar peaked in 2002. In the oceanic region, dark shearwater densities were highest in 2002 (Fig. 4B). Leach's storm-petrel density peaked in 2001. Ocean productivity varied differently for the different regions. High coastal chlorophyll *a* concentrations occurred in 1999 and 2001, with a peak in nitrate concentration in 2002. Warm surface layers in these years were likely a response to stronger stratification and a shallower mixed layer. The strong stratification in 2002 included a cool water mass underlying the mixed layer along Line P (Freeland et al., 2003).

Spearman rank correlations of species-specific relative abundance and yearly averages of surface temperature, nitrate concentration, and chlorophyll *a* concentration revealed strong coastal chlorophyll associations with fork-tailed storm-petrel and Cassin's auklet (Table 3). Leach's storm-petrel density was positively associated with chlorophyll in both coastal and oceanic zones. A positive association between Dall's porpoise and chlorophyll existed in the oceanic zone. In the coastal realm, dark shearwaters, Dall's porpoise, and Pacific white-sided dolphin were observed in greater abundance at higher temperatures, while in the oceanic realm, black-footed albatross and tufted puffins displayed a negative association to surface temperature. Tufted puffin displayed a positive correlation with nitrates in the oceanic region.

3.4. Distributions in relation to *El Niño/La Niña* events

To illustrate interannual changes in species' distributions, we plotted density against longitude for four species (fork-tailed storm-petrel, Leach's storm-petrel, dark shearwaters, and Dall's porpoise) in 1997, 1998, and 1999 (Fig. 5). The years 1997 and 1998 were characterized by *El Niño* conditions in coastal British Columbia. In contrast, 1999 was a *La Niña* year with high nutrient

levels related to strong upwelling (Whitney and Welch, 2002). Both storm-petrel species displayed a shift towards coastal waters during 1999. In particular, fork-tailed storm-petrel was found very near-shore in 1999. Leach's storm-petrel appears to be primarily a bird of oceanic regions, but appeared in limited numbers in the coastal region in 1999. Dall's porpoise also exhibited a coastal shift during 1998 compared to 1997 and 1999. Dark shearwaters occupied similar ranges each year, with greater abundance coastally during 1997–98. In 1999, they declined in both regions. Notably, there was a distinct gap in the dark shearwater distribution in all of these years between 127° and 134°W, a pattern generally supported over the entire time series, 1996–2003 (Figs. 3 and 5).

3.5. Coastal bathymetric habitat associations

A synopsis of marine bird habitat associations in the coastal region (Table 5) is as follows: black-footed albatross was observed at higher densities away from land but with an apparent preference for relatively shallow habitats (Table 5, Fig. 3); Cassin's auklet was found in greater densities close to land, and also closer to oceanic waters; both storm-petrels showed a tendency to occur away from the 200 m isobath, with fork-tailed storm-petrels displaying greater densities in proximity to land and steep topography; northern fulmar and dark shearwaters were found at higher abundances in shallower water; northern fur seals tended to occur in higher densities away from the shelf break (200 m isobath); and Pacific white-sided dolphin was at highest densities away from land. We found no relationships with bathymetric characteristics in the coastal region for tufted puffin and Dall's porpoise.

3.6. Persistence of habitat associations

Cassin's auklet, fork-tailed storm-petrel, dark shearwaters, and northern fulmar showed interannual variation in bathymetric habitat associations (Table 6). Relationships with bathymetry appeared to reflect variability in the oceanographic environment. For example, Cassin's auklet density

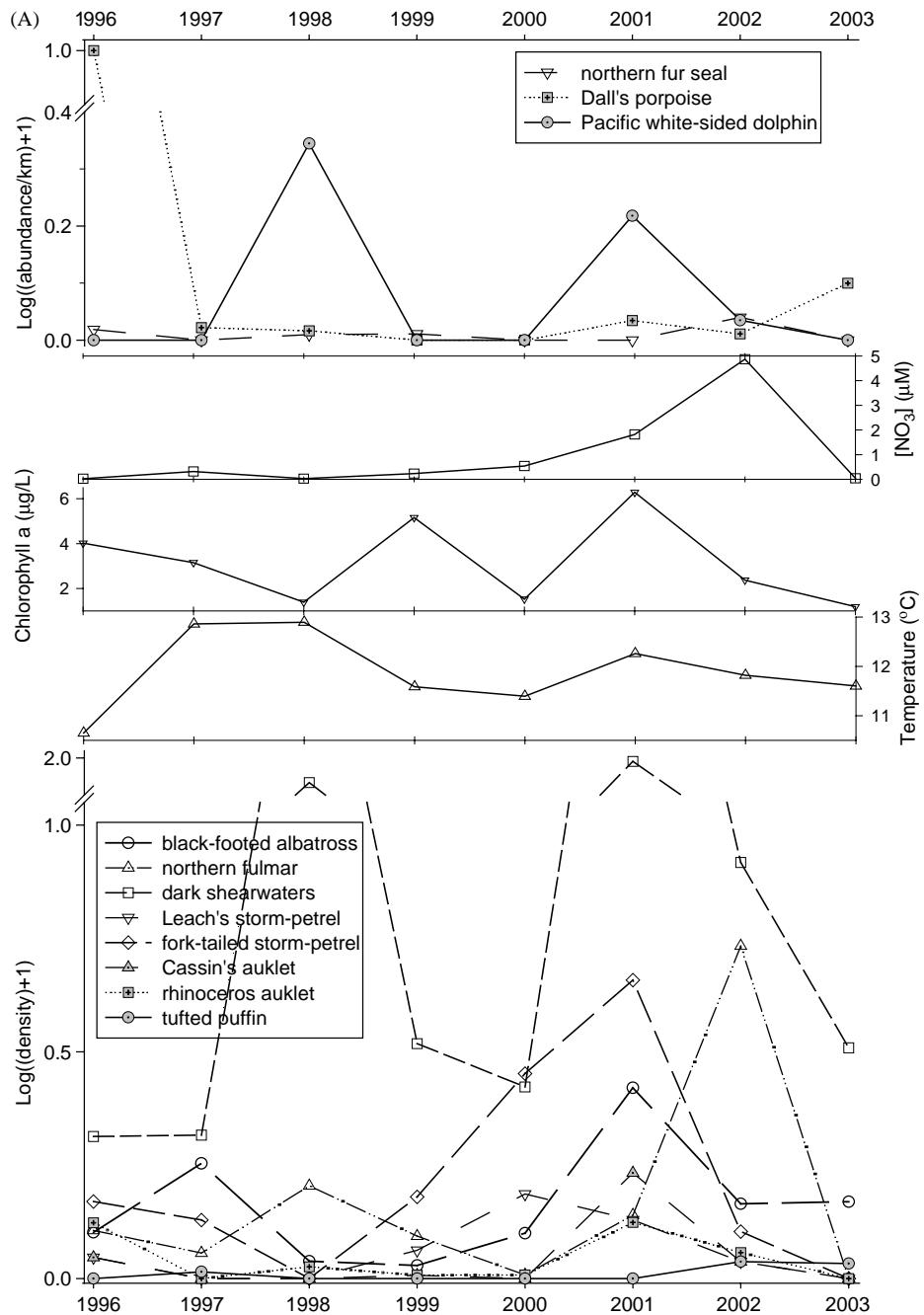


Fig. 4. Annual variation in seabird density in (A) coastal and (B) oceanic regions in relation to nitrate and chlorophyll *a* concentrations, and surface temperature. High abundances corresponded to elevated temperature and chlorophyll *a* levels.

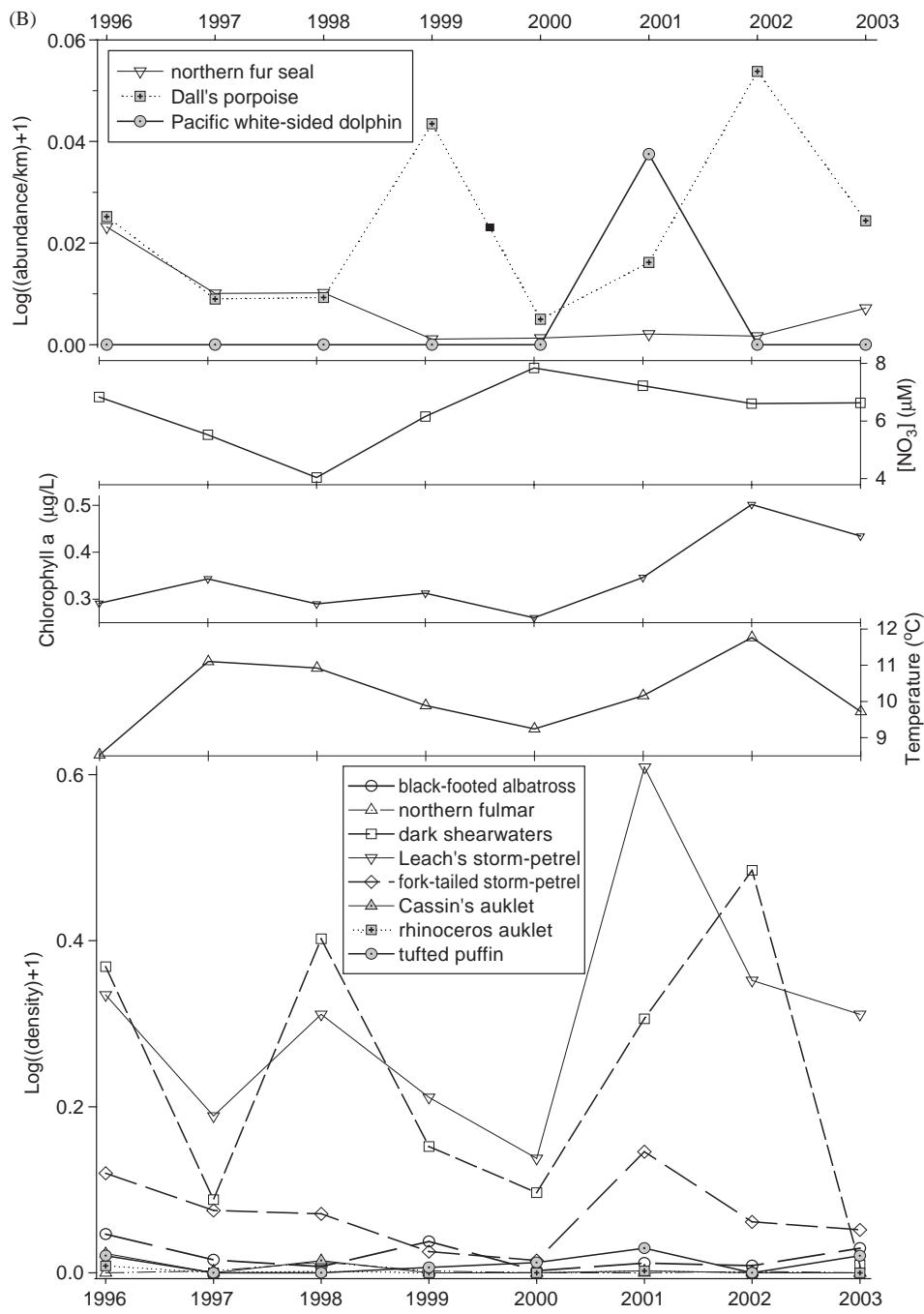


Fig. 4. (Continued)

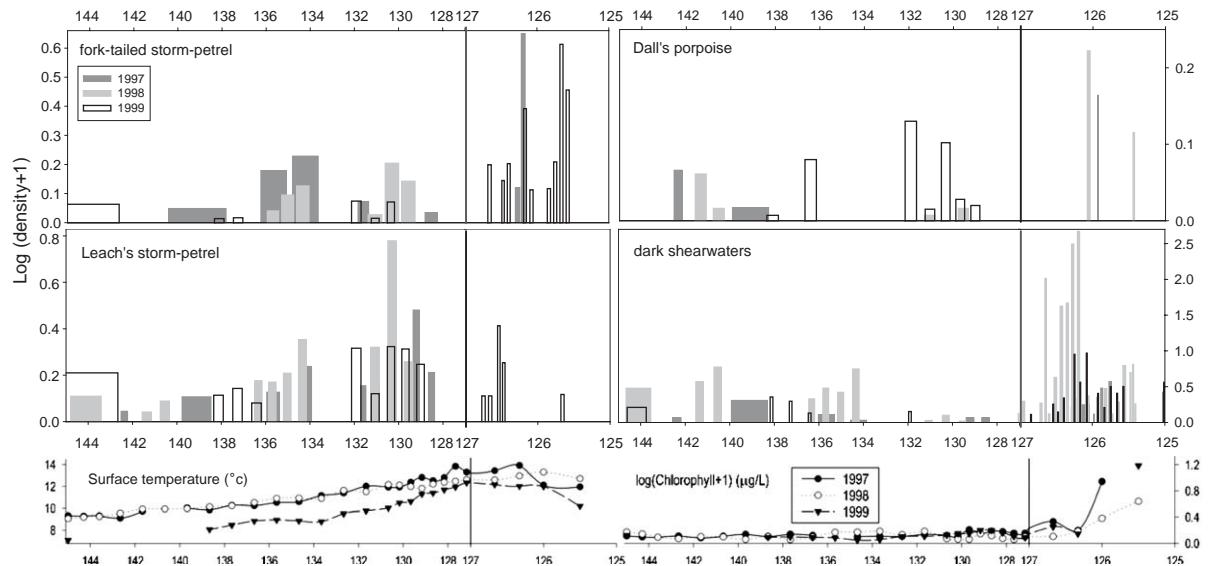


Fig. 5. Interannual variation in distribution of four species of interest, fork-tailed and Leach's storm-petrels, Dall's porpoise, and dark shearwaters. Three sequential years, 1997, 1998, and 1999, were chosen. The distribution of storm-petrels shifted coastally during 1999 when high levels of chlorophyll *a* were documented. Dark shearwaters did as well but less dramatically. Dall's porpoise concentrated on the region near La Perouse Bank.

decreased very close to land in 1999 and also was found in proximity to La Perouse Bank 1996 and 1999, but away from the bank in 2001 and 2002. Dark shearwaters displayed varying affinities for median water depths. Northern fulmars showed positive associations with the contour index occurring during warm coastal years (Fig. 4A: 1997, 1998, 2001, and 2002), and negative associations during cooler years (1996, 1999, and 2000). Fork-tailed storm-petrels exhibited higher affinity for land and away from the shelf-break in 4 years, 1996, 1999–2000, and 2002.

4. Discussion

We examined spatio-temporal variation in the distribution and abundance of select marine birds and mammals in the eastern GOA. The study area includes the continental shelf west of Vancouver Island, an abrupt shallow-water feature (La Perouse Bank), and a vast expanse of oceanic habitat associated with the eastern North Pacific

subarctic gyre. By working on this large geographic scale (approximately 1500 linear km), change in distribution and abundance of marine birds and mammals in one region may be associated with change in other regions, and related to oceanographic factors that promote changes in distribution. We also studied this top predator community over many years, including a major El Niño/La Niña cycle (1997–1998–1999) that dramatically affected both coastal and oceanic ecosystems of this region (Whitney and Welch, 2002). The relatively long-term perspective provided by our 8-year study (1996–2003) provides insight into how coastal and oceanic regions change over time, and how marine birds and mammals respond to this variation. Our study demonstrates species-specific differences in abundance between coastal and oceanic ecosystems, habitat preferences for seabirds in the coastal region based on water depth and other bathymetrically defined habitat characteristics, and apparent redistributions of marine bird and mammals between coastal and oceanic regions in

response to environmental variation. Below, we interpret these fluctuations relative to interannual changes in ocean temperature, nutrients (nitrate), and primary productivity (chlorophyll *a*) as proxies for ocean productivity.

4.1. Temporal and spatial variation in distribution and abundance

Upper trophic-level marine predators are not randomly distributed across the eastern GOA seascape. Instead, they have distinct broad- and fine-scale ocean habitat preferences. Others have found similar differences in community structure, with greater relative abundance and biomass in coastal realms (Briggs et al., 1987; Hunt et al., 2000; Hyrenbach and Veit, 2003). This pattern is explained by the energy budget of seabirds in coastal versus oceanic regions, assuming that coastal species require more energy and occupy this region to take advantage of higher levels of ocean productivity there (Ballance et al., 1997). Another explanation is that as central place foragers, seabird density is higher in proximity to the breeding colonies that occur in coastal regions (Odekoen et al., 2001). The densities of black-footed albatross, rhinoceros auklet, and northern fulmar were clearly greater in the coastal region, whereas that of Leach's storm-petrel was greater in the oceanic region. Rhinoceros auklet, Cassin's auklet, and fork-tailed storm-petrel breed in coastal British Columbia, with some colonies in proximity to the Line P transect. However, unlike Cassin's auklet and fork-tailed storm-petrel, we did not find any relationships between rhinoceros auklet density and distance from land within the observed range of distribution (Table 5), associations that would be indicative of density–distance functions with local breeding colonies. Rhinoceros auklet is a relatively deep diving species that acquires prey by visual pursuit (Gaston and Dechesne, 1996), whereas the black-footed albatross, northern fulmar, and storm-petrel glean prey from the surface or neuston layer (Warham, 1990). Generally, pursuit divers show greater energetic requirements than surface foragers (Ellis and Gabrielsen, 2002), which may account for greater rhinoceros auklet density in the coastal

region, but it does not explain why black-footed albatross and northern fulmar preferentially use this habitat. Dark shearwaters, the dominant group in terms of density (Table 1), were found in greater densities with shallower median water depths in the coastal realm (Table 5). The black-footed albatross, dark shearwaters, and northern fulmar are migrant species that visit coastal British Columbia from Hawaii, the southern hemisphere, and Alaska, respectively. These species feed on a variety of prey types, including squid, euphausiid crustaceans, forage fishes, and neuston in the upper water column. Unlike shearwaters (Burger, 2001), black-footed albatross, and northern fulmar do not dive deeply (no greater than 10 m; Prince et al., 1994; Weimerskirch and Sagar, 1996). Given that these species do not show similar biogeographical affinities, and that their foraging behavior is variable, we believe that the best explanation for their greater densities in the coastal region is simply higher productivity of prey species found there under certain oceanographic conditions.

In comparing bird densities in coastal versus oceanic regions, we noted no difference in density of tufted puffin between coastal and oceanic realms. Tufted puffin breeds locally in British Columbia, yet showed no associations with bathymetry, water depth or distance from land. During the breeding season, tufted puffins rely on sandlance (*Ammodytes* spp.) for successful reproduction (Gjerdrum et al., 2003), and sandlance generally occur in shallow, sandy, near-shore habitat. Thus, it is perplexing why tufted puffins did not demonstrate differences in density between coastal and oceanic regions. The other species with a similar pattern was Dall's porpoise. In fact, the overall pattern of distribution between Dall's porpoise and tufted puffin is quite similar (Fig. 3D and J). The diet of tufted puffins in oceanic habitat is poorly known, but may consist of myctophids (lanternfish) and squids (Piatt and Kitaysky, 2002). The diet of Dall's porpoise in the North Pacific is also not well known, but in the GOA apparently consists primarily of myctophids. Thus, it seems possible that both of these species, while occurring in both regions, are primarily organisms of the open-ocean, with reliance on myctophids. It is also likely that most of the

puffins in the oceanic region were subadult, non-breeding birds, able to forage in the open ocean because they were not restricted to foraging in proximity to colonies to care for dependent young.

The last species to consider is the Leach's storm-petrel. Leach's storm-petrel was the only species with significantly greater densities in the oceanic region (Table 1). They also showed a disassociation with the 200 m isobath (Table 5), indicative of an offshore distribution even in the coastal realm (Fig. 3F). Densities of this storm-petrel were almost an order of magnitude greater in the oceanic realm. Leach's storm-petrel feed by gleaning prey from the surface, and have relatively low energetic requirements (Ellis and Gabrielsen, 2002). Hyrenbach and Veit (2003) demonstrated very similar patterns of abundance for this species off southern California. Ballance et al. (1997) suggested that this species can occupy low-productivity oceanic habitats in light of their low 'wing-loading' (high wing area relative to small body mass), relatively slow metabolism, and ability to concentrate and store prey as high-energy oil (lipids).

This study showed that marine bird and mammal distributions in coastal and oceanic regions changed similarly through time (Table 2). Indeed, in both coastal and oceanic regions, all significant correlations between species' densities (and encounter rates for mammals) were positive. This suggests that some species may respond in a similar manner to broad-scale environmental factors, such as changes in ocean productivity. Unfortunately, we lack information on the abundance and availability of the specific prey used by these predators.

We considered surface temperature, nitrate and chlorophyll *a* concentrations as proxies for ocean conditions and yearly fluctuations in the ocean environment off British Columbia (Harris, 2001; Whitney et al., 1998; Whitney and Freeland, 1999). These variables may serve as proxies for prey availability. Primarily, the procellariiform seabirds (shearwaters and storm-petrels) fluctuated in abundance relative to patterns of ocean productivity, but we also found some interesting correlations for alcids (Table 3). Some species were more abundant in the coastal zone when productivity

(chlorophyll *a*) was higher (e.g., storm-petrels), but it is unclear whether this was due to a decrease in productivity in the oceanic realm, or preferential foraging in the coastal zone to take advantage of higher productivity there. Peaks in abundance of dark shearwaters, storm-petrels, northern fulmar, and black-footed albatross in the coastal zone were observed in 2001–2002, possibly a reflection of a new oceanographic regime of the late 1990s and early 2000s (Peterson and Schwing, 2003). A peak in dark shearwater density also was observed in 1998, at the end of a strong El Niño event when productivity was generally reduced.

Dark shearwater aggregations occurred near the coast, where nutrients were continuously supplied to the continental shelf by tidal mixing and estuarine circulation associated with the Fraser River, Haro Strait, and Juan de Fuca Strait. However, while we found some correlations with nitrate and chlorophyll *a* concentrations, and interpret these findings in relation to temporal patterns of ocean productivity, none of the organisms considered in this study consumes phytoplankton. Indeed, these focal species are secondary and tertiary consumers, feeding primarily on macrozooplankton (e.g., amphipods and euphausiid crustaceans), squids, and forage fishes. Obtaining data on the prey of these species, and how prey availability fluctuates in coastal and oceanic regions, will be necessary to understand variation in predator distribution and abundance (e.g., Burger et al., 2004). Consequently, while we have demonstrated how variation in predator dispersion may be related to temporal variability in coastal and oceanic ecosystems, we do not yet have a mechanistic understanding of why such changes in distribution and abundance occur.

4.2. Distribution in relation to oceanography

All species were found in both coastal and oceanic systems but, as discussed above, there were some large differences in abundance between regions. A variety of studies of seabirds at sea have found fluctuations in abundance relative to ocean temperature (cf. Hyrenbach and Veit, 2003). Since chlorophyll *a* is a more direct indicator of ocean productivity than temperature, it may

provide the clearest picture of the species whose distribution can best be predicted from changes in ocean productivity. Cooler waters and high nitrate generally indicate stronger winter mixing, which results in deep nutrients being supplied to the upper ocean and a deeper spring mixed layer. Subarctic species of plankton and fish would then be predominant. In this study, fork-tailed storm-petrel and Cassin's auklet exhibited positive associations with chlorophyll *a* concentration in the coastal region (Table 3). Tufted puffin density in the oceanic region was negatively correlated with temperature and positively correlated with nitrate concentrations. These relationships indicate that these species become more abundant, especially in the coastal region with increasing ocean productivity. Unexpectedly, we found positive correlations between the density of dark shearwaters and encounter rates of Dall's porpoise and Pacific white-sided dolphin in the coastal region with surface temperature. As temperature and productivity are generally negatively correlated in coastal British Columbia, these correlations suggest, in contrast to the rhinoceros auklet, tufted puffin, and storm-petrels, that these species become more abundant with decreasing ocean productivity. Black-footed albatross and northern fulmar also showed positive associations with temperature in the coastal realm, though these correlations were not significant. Nonetheless, these species add to the list of species exhibiting a counter-intuitive response to temperature and ocean productivity. Our explanation for this pattern is that these species shifted to the very near-shore environment during these warm-water years where near-shore shelf habitat may have been one of the few sites of elevated productivity and prey aggregation. Biological productivity in the near-shore environment is maintained by tidal mixing, estuarine circulation, and upwelling; physical processes that are more intense near-shore, even in years of elevated sea-surface temperature (Benson et al., 2002). Moreover, warm coastal waters also suggest enhanced poleward flow that could result in southern plankton and fish species invading the BC coast (e.g., Mackas and Galbraith, 2002). However, as with other aspects of this correlative study of predator–ocean habitat

relationships, it remains unclear what mechanisms drive these relationships.

4.3. Bathymetry affecting distribution

Bathymetric characteristics can be useful indicators of marine wildlife-habitat associations because they are fixed in space, and yet produce predictable hydrographic variations such as upwellings and eddies (Yen et al., 2004). Seamounts and banks in coastal and oceanic systems are known for their productivity (reviewed by Genin, 2004), and concentrations of marine birds (Haney et al., 1995; Yen et al., 2004; K.H. Morgan, unpublished data). Likewise, the shelf break and slope region (200–1000 m isobath) may be considered a 'hotspot' where birds and mammals aggregate if there is a corresponding frontal system that concentrates prey (Franks, 1992; Keiper et al., 2005). Along Line P, the bathymetry of the coastal area is highly complex, but farther offshore there is relatively low structural complexity. This difference in structural complexity is paralleled in the relationship between bathymetry and seabird distribution. The index of bathymetric complexity (CI, Table 4) was one of the most important determinants of seabird dispersion in the coastal ecosystem. Associations with various bathymetric variables can help to systematically group different species. Cassin's auklet, a local breeder constrained to forage close to land, was found between land and the 3000-m isobath, while black-footed albatross, northern fulmar, and shearwaters were more closely correlated with shallow waters. Northern fulmar were found over steep bathymetry, likely the shelf-break, whereas black-footed albatross appeared to prefer gentler sloping bathymetry, such as the continental shelf.

Marine bird–bathymetric associations were not static but varied between years. Cassin's auklet were strongly associated with La Perouse Bank only during 1996 and 1999, both cool years with relatively high chlorophyll *a* concentration. Northern fulmar were at higher densities over gentler sloping bathymetry during cool years and steep bathymetry during warm years. Interannual fluctuations in species-specific bathymetric habitat affinities underscore the importance of

investigating how environmental variability affects top predator ocean habitat selection on multiple spatial scales.

4.4. Conclusion—coastal-oceanic ecosystems and environmental variation

Marine birds and mammals are highly mobile organisms that rapidly respond to physical and biological fluctuations in the ocean. While we found differences in the marine bird and mammal abundance between coastal and oceanic ecosystems, we describe a continuum in community structure dependent, in part, on variability in ocean productivity. While all species were found, to some extent, in both regions, peak distributions shifted depending upon ocean climate. Distributions tracked ecosystem changes with some species increasing and some decreasing, especially in the coastal region, with changes in oceanographic conditions. Though much remains to be determined, including spatial associations between predators and prey, we conclude that the conceptual boundary between coastal and oceanic ecosystems in the eastern GOA is porous. Ultimately, determining how trophic relationships and prey consumption by marine birds and mammals varies temporally (by season and from year to year) will be necessary to fully understand linkages of coastal and oceanic ecosystems in the North Pacific Ocean.

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