EFFECTS OF THE JUAN DE FUCA EDDY AND UPWELLING ON DENSITIES AND DISTRIBUTIONS OF SEABIRDS OFF SOUTHWEST VANCOUVER ISLAND, BRITISH COLUMBIA

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SUMMARY

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I compared meso-scale averages of sea surface temperature (SST) and hydroacoustic indices of prey abundance with densities of seabirds measured year-round over the continental shelf off southwest Vancouver Island, British Columbia, Canada in 1993-1996. A fixed strip transect (total length 110 km; width 300 m) was divided into six legs (lengths 14-30 km) to sample different shelf habitats. Three foraging guilds were considered: divers (dominated by Common Murres *Uria aalge* and other alcids), surface-feeders (dominated by California Gulls *Larus californicus* in summer, and other gulls year-round), and shearwaters (mainly Sooty Shearwater *Puffinus griseus*). Mean SST, prey scores, and densities of most birds (all surface-feeders and most divers) were low and similar among the 6 transect legs during winter and spring (mid-December through mid-June), but these measures all increased and differed significantly among the legs during summer and autumn (mid-June through mid-December). In summer and autumn, cold SSTs, high prey scores, and high seabird densities were consistently associated with the effects of the seasonal eddy over the Juan de Fuca canyon, whose influence spilled over the adjacent shelf. SST alone, however, did not explain the observed patterns of prey and seabird dispersion. One leg characterized by cold, upwelled water supported low prey and bird abundance, while another leg adjacent to the outer canyon had high prey and bird abundance, but SST was not consistently low. These results suggest that SST alone (such as satellite imagery) cannot be used to predict seabird distribution in this area. The interactions of bathymetry, ocean currents, and physical conditions of seabirds and their prey need to be more clearly understood in this area before reliable predictions of seabird distributions based on satellite imagery are possible.

Keywords: continental shelf, Juan de Fuca Eddy, seabird densities, seasonal variations, upwelling, Vancouver Island

INTRODUCTION

Associations of seabirds with coarse- or meso-scale (1-100 km) physical processes in the ocean have been described from several parts of the world (Haney 1986, Hunt & Schneider 1987, Schneider 2002). Some meso-scale patterns have been described for seabird distributions in the northeast Pacific (Wahl *et al.* 1989, 1993), but the effects of oceanic processes over the continental shelf in this area are not well understood (Vermeer *et al.* 1987, 1989, Hay 1992, Logerwell & Hargreaves 1996). Understanding the distribution and abundance of seabirds relative to meso-scale ocean processes is important for several reasons. This spatial range covers the daily foraging range (ambit) of most seabirds. Moreover, several of the dynamic physical processes responsible for increased productivity and aggregations of prey are most evident at scales of 10s of km, but less evident at spatial scales smaller or larger than this range (Hunt & Schneider 1987, Schneider 2002). These physical processes include the effects of large ocean eddies, wind-induced upwelling plumes, broad oceanic fronts, island wakes, and tidal fronts.

Another reason for studying seabird distributions at meso-scales is that currents, eddies and upwelling plumes can be readily identified and tracked using satellite imagery at this spatial scale. Satellite imagery, predominantly of sea surface temperatures (SST), has been used to characterize ocean habitats of seabirds in a few studies (e.g., Briggs *et al.* 1987, Haney 1986, 1989a, b). Understanding the distribution of seabirds in relation to SST or other remotely-sensed parameter is needed before satellite imagery can be reliably used to predict the distribution of seabirds. Satellite images could be a valuable tool in predicting the distribution of seabirds in the event of a major oil spill. Knowing the likely distribution and relative densities of seabirds would help assess the likely risks from the spill, allow containment efforts to be directed to the most critical areas, and determine where aerial surveillance and other monitoring efforts should be concentrated.

The continental shelf off southwest Vancouver Island is a highly productive marine zone, which provides foraging opportunities for tens of thousands of seabirds (Vermeer *et al.* 1987, 1989, 1992, Hay 1992, Wahl *et al.* 1993, Logerwell & Hargreaves 1996). There is also a high risk of a major oil spill in the area, from many oil tankers and other large vessels transiting the Strait of Juan de Fuca to or from Seattle, Vancouver, and other large ports nearby (Cohen & Aylesworth 1990, Burger 1992). This paper, part of a series on the distribution, densities and species composition of seabirds off southwest Vancouver Island (Burger 2002a, Burger *et al.* in press), reports on the meso-scale distribution of seabirds recorded year-round along a 110 km transect route over the continental shelf (Fig. 1). Analysis focused on the likely effects of two powerful physical processes affecting sea temperatures, productivity and prey distribution: wind-induced upwelling along the inner continental shelf, and upwelling generated by the Juan de Fuca Eddy. In particular, this paper examines the distribution of the major groups of seabirds relative to sea surface temperatures. Besides improving our understanding of the biology of seabirds in this area, this is an important step towards using satellite imagery to monitor the likely distribution and abundance patterns of seabirds in this area.

STUDY AREA AND OCEAN PROCESSES

The continental shelf (delineated by depths less than 200 m) extends to approximately 50 km off the coast of southwest Vancouver Island (Thomson 1981, Freeland 1992). The shelf is cut by several deep canyons perpendicular to the shore, which create conditions favourable to upwelling of cold, nutrient-rich water (Denman *et al.* 1981, Allen *et al.* 2001). The largest of these is the Juan de Fuca Canyon, extending seaward from the Strait of Juan de Fuca (Fig. 1). During the summer a large anti-clockwise (cyclonic) eddy develops over this canyon at the mouth of the strait, which is responsible for massive upwelling of deep, nutrient-rich water (Thomson *et al.* 1989, Freeland & Denman 1982, Freeland 1992). This upwelled water spills over the southern edge of the continental shelf, creating a large pool of colder surface water over Swiftsure Bank and beyond. The effects of the eddy are clearly visible from satellite images of sea surface temperature (Fig. 2). Parts of the shelf area affected by the eddy are productive foraging grounds for birds, fish and whales, as well as commercially important fishing grounds (Healy *et al.* 1990, Vermeer *et al.* 1992).

Wind-induced upwelling over the shelf also affects the local hydrography and is evident at the sea surface. During summer, the prevailing northwest winds combined with the Coriolis force drag the surface water offshore, resulting in plumes of cold upwelled water moving seaward from the inner shelf (Thomson 1981, Freeland 1992). During winter, the prevailing southeast winds force surface water shoreward, inhibiting upwelling over the inner shelf. Chlorophyll and zooplankton densities over the shelf off southwest Vancouver Island are consequently highly seasonal, with winter densities about one tenth of summer values (Thomas & Emery 1986, Mackas 1992).

METHODS

Sea surface temperature (SST), hydroacoustic measures of prey abundance, and densities of birds were recorded from a moving vessel along a 110 km fixed transect route (Figure 1). The transect was designed to include a range of marine habitats on the continental shelf that could be traversed in a day's cruise. The transect was divided into six legs of unequal length. The two portions parallel with the shore (Inshelf and Offshelf) were both divided into two legs in order to compare areas proximal (Inshelf East: mean distance 14.0 ± SE 0.1 km; and Offshelf East: 14.3 ± 0.3 km) and distal (Inshelf West: 14.5 ± 0.4 km; and Offshelf West: 21.6 ± 0.6 km) to the canyon at two distances offshore. The Canyon leg (16.3 ± 0.5 km) covered the water from the edge of the canyon to the deepest portion (> 200 m). The Cross-shelf leg (29.6 ± 1.0 km) ran perpendicular to the shore and the depth isobars. The outer shelf legs were truncated on two winter/spring surveys due to limited daylength and on one summer/autumn survey due to mechanical problems.

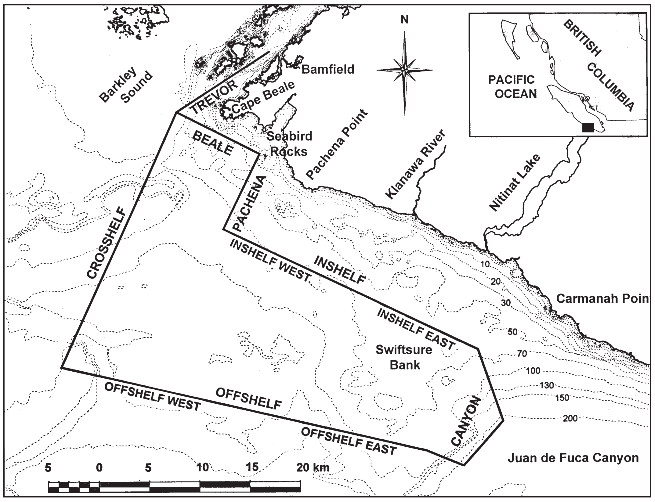

Fig. 1. Map of the study area showing the transect route. This analysis used data from the Inshelf (East and West), Canyon, Offshelf (East and West), and Cross-shelf legs. Depth isobaths are in metres.

Surveys were conducted aboard the 11 m research vessel M.V. *Alta* (eye-level 2.0-2.5 m above the sea), and occasionally from other similar vessels, and used LORAN and Global Positioning System (GPS) for navigation. Vessel speed was relatively constant (mean 14.8 km h^{-1}, range 13.0-18.5 km h^{-1}). The vessel was occasionally slowed to permit counting and identification of birds in dense flocks. Occasional deviations off-course to investigate flocks of birds were excluded from the data. All data were collected in 1-minute bins, corresponding to about 250-280 m of travel. Surveys were usually restricted to periods when the Beaufort sea state was 3 or less (winds <5.5 m s^{-1} and white-caps from breaking wavelets rare), but sometimes included brief periods of stronger winds to maintain continuity.

Sea surface temperatures (accurate to 0.1° C) were manually recorded from a hull-mounted electronic thermometer in 1993, and automatically in a flow-through system using an Endeco YSI PC600 probe linked to a computer in 1994-1996. Both systems sampled the water about 1 m below the surface. To illustrate the variations in temperature among the legs within the entire transect,

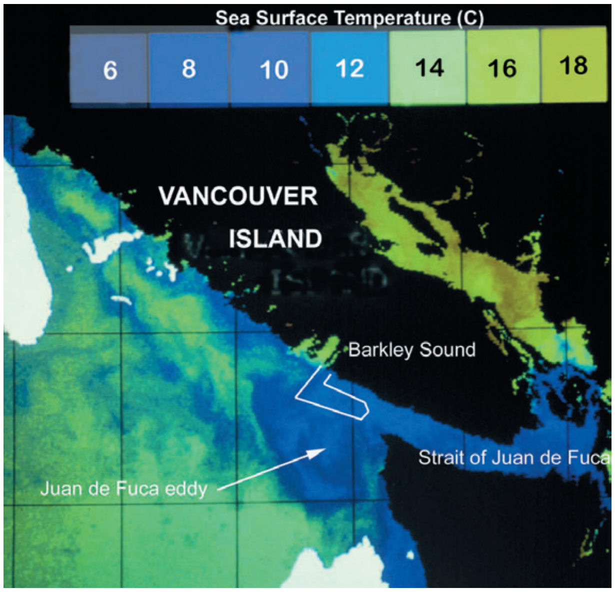

Fig. 2. Satellite image of sea surface temperature (°C) off southwest Vancouver Island on 18 August 1982. Several features typical of summer conditions can be seen, including cold, upwelled water associated with the Juan de Fuca Eddy and the plumes of colder water upwelled over the shelf. The transect route is shown.

I calculated a deviation function on each day surveyed, which was the difference between the mean temperature within each leg and the mean for the transect as a whole on that day. Positive deviations indicate warmer temperatures and negative deviations colder temperatures within the leg than for the transect as a whole.

Prey abundance was measured using a 200 kHz Furuno 600 hull-mounted sounder (approx. 1 m deep), with a paper trace recorder. Sounder traces were divided into 1 minute intervals of travel (250-280 m) and 10 m depth intervals. Within each rectangle formed by this division observers visually scored the density of prey, based on the intensity of the sounder trace, using a scale of 0 (no prey) through 9 (near-saturation; Piatt 1990). Three independent observers gave almost identical scores in tests of the same sounder traces. I then squared the score to account for the non-linear change in sounder intensity relative to prey school density (Forbes & Nakken 1972). Analysis focused on the 1-10 m depth range, as a measure of near-surface prey likely to be accessible to surface-feeding birds, and the 1-40 m range, as a measure of the overall prey abundance and the prey accessible to most diving birds. A few surveys which sampled deeper depths showed few schools of fish below 40 m, other than Pacific hake *Merluccius productus*, which were not taken by birds except as fisheries discards (Hay *et al.* 1992, AEB. pers. obs.).

I did not attempt to identify the organisms producing each sounder trace, but schooling fish (predominantly immature herring *Clupea harengus pallasi* and sand lance *Ammodytes hexapterus*) and euphausiids (predominantly *Thysanoessa spinifera* and *Euphausia pacifica*) are common in the study area within the depths sampled (Hay *et al.* 1992, Mackas & Galbraith 1992). Traces made by larger fish not taken by birds, such as salmonids and spiny dogfish *Squalus acanthias*, could usually be identified by the solitary, bold traces, and were disregarded. The interpretation of sounder traces excluded near-surface interference caused by waves and diffuse back-scatter from small plankton, but included dense schools of larger zooplankton, primarily euphausiids (Mackas & Galbraith 1992; AEB pers. obs.).

Two observers reported birds within an area 250 m ahead, and 150 m on either side of the vessel (transect width was 300 m). Data were recorded manually by a third person. Several observers took turns on duty to avoid fatigue. Densities were calculated from the area of the strip covered in each leg, on each day surveyed. To focus on birds most likely to be foraging, I considered only birds seen on the water with the exception of storm-petrels, which frequently forage on the wing. Storm-petrels on the water and flying were both included in analyses.

Birds were grouped into three foraging guilds: divers, surface-feeders, and shearwaters. Diving birds included loons, cormorants, grebes, and alcids. Surface-feeding birds included fulmars, storm-petrels, phalaropes, gulls, and jaegers. Shearwaters, which usually forage at the surface but are also accomplished divers (Burger 2001), were treated as a separate foraging guild. Separate analyses were done for the most common species (mean density >0.5 birds km^{-2} and found in at least 50% of surveys). The remaining less common species were not analysed separately, but were included in the appropriate foraging guilds. An exception was made for Marbled Murrelets *Brachyramphus marmoratus*: although uncommon it was included in the detailed analysis because it is a threatened species in British Columbia and the United States, and its seasonal use of shelf and offshore waters is poorly documented (Burger 2002b).

Seasons were defined as: winter – 16 December through 15 March; spring – 16 March – 15 June; summer – 16 June – 15 September; autumn – 16 September – 15 December (Morgan *et al.* 1991). Based on the changes in SST (see results), I pooled the winter/spring data, and the summer/fall data.

The bird and prey data presented problems for statistical analysis, because of the high variability, heteroscedacity, and occurrence of many zeroes. Logarithmic transformations (Zar 1996) did not completely eliminate these problems. Consequently, I used non-parametric Kruskal-Wallis analysis of variance to compare data from the different legs, using SPSS 10.0. Tests were considered significant if P<0.05.

RESULTS

Sea surface temperatures

Variations in SST among the six legs of the transect showed a strong seasonal pattern (Fig. 3). During winter and most of the spring there were relatively few differences in temperature among the legs, with the warmest waters often over the Canyon. From June through mid-December, however, the mean temperatures within each leg showed clear differences, often exceeding 2°C. During this period, the two legs along the inner shelf (Inshelf East and Inshelf West) and the Canyon leg had consistently colder SST than the legs on the outer shelf and the Cross-shelf leg. This was consistent with summer upwelling associated with the Juan de Fuca Eddy. The cold temperatures in the Inshelf West leg also indicated upwelling over the inner shelf, which was probably a combination of the effects of wind forcing and the eddy. To match the two seasonal temperature regimes, the prey and bird data were pooled into winter/spring and summer/autumn periods for statistical analyses.

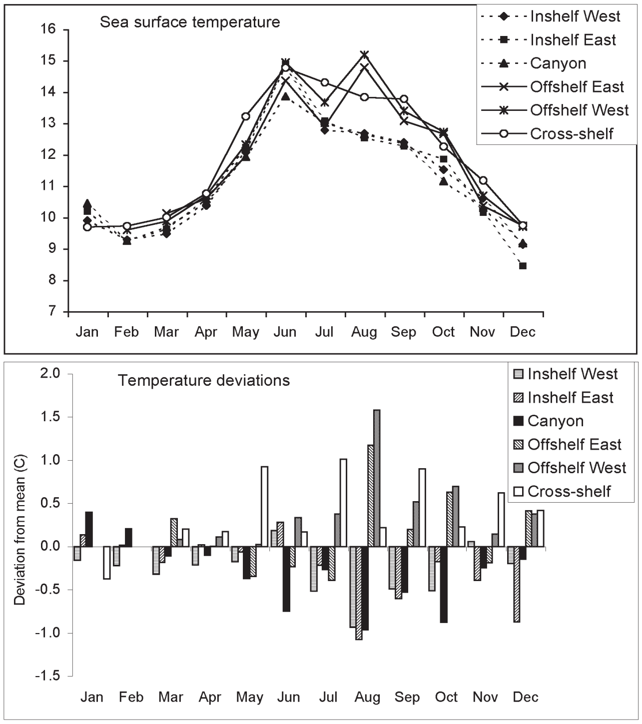

Fig. 3. Monthly variations in sea surface temperatures within each transect leg, showing mean temperatures (a), and mean deviation in temperature within each leg, relative to the mean for the whole transect on each day of survey (b). Positive deviations indicate warmer temperatures and negative deviations colder temperatures.

Prey abundance

Prey abundance scores varied seasonally, and were lowest in winter and highest in summer and autumn (Fig. 4). The greatest increases occurred in the two legs immediately adjacent to the canyon and, in autumn, in the Canyon leg itself. When prey scores were grouped into two seasons, the differences among the six transect legs were not significant in winter/spring, but were significant in summer/autumn for the 0-40 m depth range, and nearly so for the 0-10 m depth range (Table 1).

Bird densities

The bird species recorded, mean year-round densities and percentage occurrence in transects are summarised in Table 2. Seasonal trends within the transect are given elsewhere (Burger 2002a, Burger *et al.* in press.). This analysis focused on seasonal differences among the legs in the occurrence (Table 3) and densities (Table 4) of the more common species and groups.

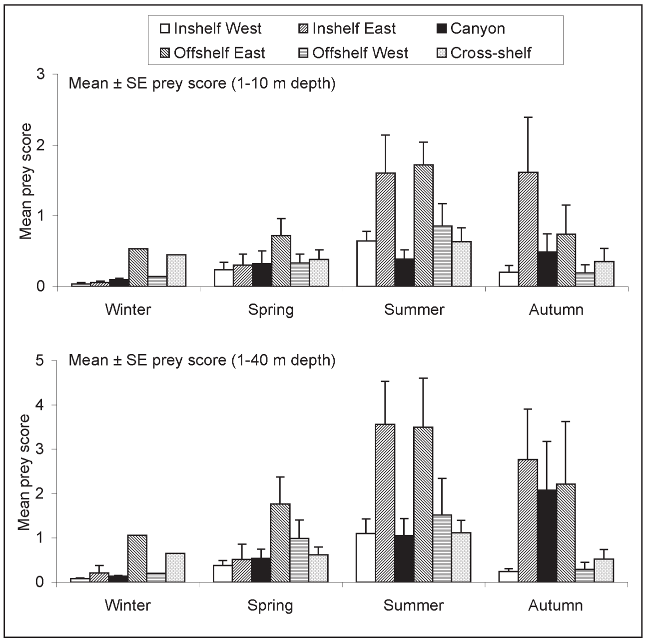

Fig. 4. Mean (± SE) of the hydroacoustic prey scores per transect leg in each season, within the near-surface 1-10 m depth range (a), and the 1-40 m depth range (b).

Loons and cormorants – Pelagic Cormorants *Phalacrocorax pelagicus*, Brandt's Cormorants *P. penicillatus* and Pacific Loons *Gavia pacifica* were uncommon on the shelf water (Table 2). They occurred in all legs (Table 3) but had higher densities in the legs nearest the shore (Table 4). Densities did not differ significantly among the legs in winter/spring but in summer/autumn there were significantly more birds in the three legs over or adjacent to the canyon (Table 4).

Common Murre *Uria aalge* – Murres were found in nearly every leg in all seasons (Tables 3) and had the highest densities among the diving birds (Tables 2 and 4). Densities were considerably higher in summer/autumn than in winter/spring, but did not vary significantly among the six legs in either of the seasonal periods. During summer/autumn, however, the highest densities occurred in the two legs immediately adjacent to the canyon (Inshelf East and Offshelf East).

Cassin's Auklet *Ptychoramphus aleuticus* – This species occurred in about half of the surveys in each leg (Table 3). Densities were higher in summer/autumn than in winter/spring (Table 4). There were no significant differences in density among the legs in winter/spring, but during summer/autumn the densities were significantly higher in the three legs over or adjacent to the canyon.

Marbled Murrelet – This species, included here because of its threatened status, was rare over the shelf during winter/spring and usually absent during summer/autumn (Tables 2-4). There were no significant differences in density among the legs, but the data were too sparse for rigorous tests.

Rhinoceros Auklet *Cerorhinca monocerata* – This species was more common over the shelf during winter/spring than summer/fall and was found in all legs (Tables 3 and 4). During winter/spring Rhinoceros Auklets had similar densities in all six legs, but during summer/autumn they were concentrated in the three legs over or adjacent to the canyon.

Shearwaters – Sooty Shearwaters *Puffinus griseus* were by far the most common shearwater in the study area followed by Short-tailed Shearwaters *P. brevirostris* and other species (Table 2). Some Short-tailed Shearwaters were undoubtedly recorded as Sooty

TABLE 1

Mean (± SE) prey scores within each transect leg, grouped into two seasons.
Prey scores for the near-surface depths (1-10 m) and for the entire sample (1-40 m) are shown.

Leg	1-10 m depth		1-40 m depth		No. of surveys	
	Winter + Spring	Summer + Autumn	Winter + Spring	Summer + Autumn	Winter + Spring	Summer + Autumn
Inshelf West	0.18 ± 0.08	0.42 ± 0.11	0.29 ± 0.09	0.67 ± 0.23	10	8
Inshelf East	0.23 ± 0.12	1.61 ± 0.44	0.42 ± 0.25	3.16 ± 0.71	7	8
Canyon	0.26 ± 0.13	0.44 ± 0.13	0.42 ± 0.17	1.56 ± 0.57	7	8
Offshelf East	0.68 ± 0.20	1.23 ± 0.31	1.65 ± 0.50	2.85 ± 0.86	6	8
Offshelf West	0.30 ± 0.11	0.52 ± 0.20	0.85 ± 0.37	0.90 ± 0.45	6	8
Cross-shelf	0.40 ± 0.10	0.49 ± 0.14	0.62 ± 0.14	0.81 ± 0.20	5	8
Kruskal-Wallis test (df = 5 for all)						
Chi-square	7.54	10.56	7.70	16.86		
P	0.184	0.061	0.173	0.005		

TABLE 2
Summary of year-round mean densities and percentage occurrence of seabird species recorded in 29 surveys made between May 1993 and December 1995 over the shelf off southwest Vancouver Island.

Taxa	Scientific name	Density (birds km^{-2})			Percentage occurrence in surveys	Maximum count
		Mean	SE	% of total		
Red-throated Loon	*Gavia stellata*	0.010	0.009	0.019	7	2
Pacific Loon	*Gavia pacifica*	0.272	0.064	0.498	69	39
Common Loon	*Gavia immer*	0.012	0.007	0.021	14	1
Loon spp.		0.094	0.050	0.172	31	35
Western Grebe	*Aechmophorus occidentalis*	0.015	0.008	0.027	14	5
Black-footed Albatross	*Phoebastria nigripes*	0.025	0.013	0.046	21	7
Northern Fulmar	*Fulmarus glacialis*	3.842	1.314	7.033	76	999
Pink-footed Shearwater	*Puffinus creatopus*	0.049	0.024	0.089	34	22
Buller's Shearwater	*Puffinus bulleri*	0.014	0.008	0.026	17	5
Sooty Shearwater	*Puffinus griseus*	10.852	2.358	19.865	83	1690
Short-tailed Shearwater	*Puffinus tenuirostris*	0.165	0.076	0.302	62	58
Fork-tailed Storm-petrel	*Oceanodroma furcata*	1.348	0.574	2.467	59	489
Leach's Storm-petrel	*Oceanodroma leucorrhoa*	0.004	0.004	0.007	3	4
Brant's Cormorant	*Phalacrocorax penicillatus*	0.342	0.170	0.626	72	160
Pelagic Cormorant	*Phalacrocorax pelagicus*	0.066	0.021	0.121	52	7
Cormorant spp.		0.010	0.004	0.019	17	3
Surf Scoter	*Melanitta perspicillata*	0.296	0.168	0.541	34	172
White-winged Scoter	*Melanitta fusca*	0.066	0.031	0.120	31	25
Black Scoter	*Melanitta nigra*	0.055	0.039	0.100	7	35
Scoter spp.		0.138	0.061	0.252	34	41
Other waterfowl*		0.337	0.187	0.617	31	173
Red-necked Phalarope	*Phalaropus lobatus*	1.192	0.889	2.182	48	902
Red Phalarope	*Phalaropus fulicaria*	0.049	0.038	0.090	10	39
Phalarope spp.		0.293	0.115	0.536	45	76
Pomarine Jaeger	*Stercorarius pomarinus*	0.031	0.013	0.058	21	9
Parasitic Jaeger	*Stercorarius parasiticus*	0.003	0.002	0.005	10	1
Jaeger spp.		0.002	0.002	0.004	7	1
Bonaparte's Gull	*Larus philadelphia*	0.012	0.008	0.022	10	7
Mew Gull	*Larus canus*	0.141	0.089	0.257	21	86
Ring-billed Gull	*Larus delawarensis*	0.006	0.004	0.011	7	4
California Gull	*Larus californicus*	16.698	7.325	30.567	79	6975
Herring Gull	*Larus argentatus*	0.288	0.185	0.527	52	184
Thayer's Gull	*Larus thayeri*	0.153	0.067	0.279	28	57
Western Gull	*Larus occidentalis*	0.041	0.009	0.076	59	5
Glaucous-winged Gull	*Larus glaucescens*	4.444	0.826	8.135	100	708
Black-legged Kittiwake	*Rissa tridactyla*	0.506	0.264	0.927	31	220
Sabine's Gull	*Xema sabini*	1.312	0.659	2.402	31	539
Gull spp.		0.586	0.249	1.072	69	171
Common Murre	*Uria aalge*	7.774	1.444	14.230	100	904
Pigeon Guillemot	*Cepphus columba*	0.030	0.013	0.055	28	10
Marbled Murrelet	*Brachyramphus marmoratus*	0.130	0.044	0.239	52	19
Ancient Murrelet	*Synthliboramphus antiquus*	0.062	0.033	0.113	17	26
Cassin's Auklet	*Ptychoramphus aleuticus*	1.937	0.737	3.546	79	686
Rhinoceros Auklet	*Cerorhinca monocerata*	0.852	0.186	1.559	93	106
Tufted Puffin	*Fratercula cirrhata*	0.038	0.025	0.070	24	5
Alcid spp.		0.037	0.017	0.067	24	11
Total birds		54.63	59.16	100.0	100	10396

* Single sightings of lone Harlequin Duck (*Histrionicus histrionicus*) and Red-breasted Merganser (*Mergus serrator*), and a flock of 31 Brant (*Branta bernicla*).

Shearwater due to difficulties in distinguishing these species. Shearwaters were rare during the winter (those identified were predominantly Short-tailed Shearwaters) but more common in other seasons (Table 3). Densities of shearwaters showed no significant differences among legs in either of the seasonal periods, but there were seasonal shifts in distribution (Table 4). During winter/spring most shearwaters were found on the outer shelf legs and the outer portion of the Cross-shelf leg. In summer/autumn, however, most were in the three legs over or adjacent to the canyon, with the highest densities in the Inshelf East leg.

Northern Fulmar *Fulmarus glacialis* – Fulmars were rare in winter and spring (Tables 3 and 4). During summer/autumn they showed no significant variation in density among the transects, but somewhat higher numbers over or near the canyon and in the Offshelf West.

Fork-tailed Storm-petrel *Oceanodroma furcata* – This species was found in low numbers year-round (Tables 2-4). During winter/spring there were no significant differences in density and many were found in the Cross-shelf leg. Densities differed among legs in summer/autumn, with most birds in the Offshelf West leg.

Gulls – Gulls were by far the most common surface-feeders. Glaucous-winged Gulls *Larus glaucescens* occurred year-round and in all legs (Table 2 and 3), with similar densities among legs in winter/spring, but significantly higher densities in the Inshelf East and Canyon legs in summer (Table 4). California Gulls *L. californicus* were rare and relatively uniformly distributed in winter/spring, but were the most common bird during the summer and autumn surveys and huge flocks were found associated with the canyon, especially in the Inshelf East leg (Table 4). Other gull species, notably Mew Gull *L. canus*, Thayer's Gull *L. thayeri*, Black-legged Kittiwakes *Rissa tridactyla* and Sabine's Gull *Xema sabini* were seasonally common, but not reported sufficiently often for detailed analysis (Table 2). Total counts of gulls, dominated by California Gulls, were relatively uniformly distributed in winter/spring but strongly concentrated in the Inshelf East and Canyon legs in summer/autumn (Table 4).

Comparison of foraging guilds

Pooled data for all diving birds and surface-feeders largely mirror the patterns of the most abundant species in each guild, namely Common Murres and California Gulls, respectively (Tables 3 and 4). Both guilds showed seasonal shifts in density and distribution, from low-density, relatively uniform distributions in winter/spring to high-density aggregations in the Inshelf East and Canyon legs, and, in the case of the diving birds, also in the Offshelf East leg (Fig. 5). Shearwaters, as described above, were concentrated over the outer shelf in winter/spring and had a distribution similar to the divers in summer/autumn (Fig. 5). The spatial distribution of seabirds overall was largely influenced by shearwaters in winter/spring and California Gulls in summer/autumn (Fig. 5, Table 4).

TABLE 3
Proportion of surveys in which each species or group of birds was recorded within each transect leg.

	Most affected by canyon and eddy											
	Inshelf West		Inshelf East		Canyon		Offshelf East		Offshelf West		Cross-shelf	
Species or group of birds	winter & spring	summer & autumn	winter & spring	summer & autumn	winter & spring	summer & autumn	winter & spring	summer & autumn	winter & spring	summer & autumn	winter & spring	summer & autumn
Diving birds												
Loons & cormorants	0.44	0.67	0.56	0.75	0.44	0.83	0.43	0.27	0.43	0.18	0.78	0.50
Common Murre	1.00	0.92	1.00	1.00	1.00	0.83	1.00	0.91	1.00	1.00	0.89	1.00
Cassin's Auklet	0.44	0.42	0.67	0.67	0.44	0.75	0.57	0.73	0.57	0.55	0.56	0.42
Marbled Murrelet	0.11	0.00	0.11	0.17	0.22	0.00	0.00	0.00	0.00	0.00	0.22	0.17
Rhinoceros Auklet	0.78	0.42	0.67	0.75	0.67	0.58	0.29	0.45	0.57	0.09	0.78	0.50
Other alcids	0.11	0.25	0.11	0.17	0.44	0.25	0.43	0.36	0.00	0.00	0.33	0.33
Shearwaters (all species)	0.78	0.92	0.56	0.92	0.56	0.83	1.00	0.91	0.86	0.91	0.89	0.92
Surface-feeders												
Northern Fulmar	0.22	0.58	0.11	0.83	0.00	0.58	0.00	0.82	0.00	1.00	0.33	0.92
Fork-tailed Storm-petrel	0.00	0.00	0.11	0.08	0.33	0.00	0.29	0.18	0.43	0.45	0.22	0.33
Other procellariiforms	0.00	0.08	0.00	0.17	0.00	0.08	0.00	0.27	0.29	0.45	0.22	0.33
California Gull	0.44	1.00	0.56	0.92	0.56	0.92	0.43	1.00	0.43	0.91	0.67	1.00
Glaucous-winged Gull	1.00	0.92	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91	1.00	0.83
Other gulls	0.67	0.75	0.67	0.75	0.78	0.67	0.29	0.82	0.57	0.64	0.78	0.75
No. of surveys	9	12	9	12	9	12	7	11	7	11	9	12

TABLE 4

Mean (± SE) densities (Birds km^2) of birds recorded within each transect leg off southwest Vancouver Island.
The data are grouped into two seasons: winter+spring (when the canyon eddy effect was absent or weak), and summer-autumn (when the effect was strongest). Densities were calculated from birds seen on the water, except for Fork-tailed Storm Petrels for which both birds on the water and flying were included. The number of surveys in each leg is given in Table 3.

			Most affected by canyon and eddy					Kruskal-Wallace test (df = 5 for all)	
Bird groups and species	Season	Inshelf West	Inshelf East	Canyon	Outshelf East	Outshelf West	Crossshelf	Chi-sq.	P
Diving birds									
Loons & Cormorants	Winter+Spring	0.24 ± 0.24	0.03 ± 0.03	0.05 ± 0.03	0.03 ± 0.03	0.00 ± 0.00	0.03 ± 0.03	1.588	0.903
Loons & Cormorants	Summer+Autumn	0.07 ± 0.07	0.30 ± 0.14	0.37 ± 0.16	0.22 ± 0.22	0.00 ± 0.00	0.01 ± 0.01	12.850	0.025
Common Murre	Winter+Spring	1.21 ± 0.33	1.98 ± 1.27	1.45 ± 0.50	4.42 ± 1.85	0.56 ± 0.23	2.65 ± 1.09	8.573	0.127
Common Murre	Summer+Autumn	6.11 ± 2.94	16.14 ± 5.52	5.90 ± 3.38	13.09 ± 6.98	5.30 ± 1.97	7.35 ± 2.21	6.494	0.261
Cassin's Auklet	Winter+Spring	0.26 ± 0.17	0.48 ± 0.13	0.22 ± 0.11	0.99 ± 0.41	0.06 ± 0.04	0.13 ± 0.06	7.065	0.216
Cassin's Auklet	Summer+Autumn	0.34 ± 0.24	10.79 ± 7.43	4.81 ± 1.99	4.85 ± 2.61	0.16 ± 0.09	0.22 ± 0.12	13.539	0.019
Marbled Murrelet	Winter+Spring	0.05 ± 0.05	0.05 ± 0.05	0.09 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.13	3.534	0.618
Marbled Murrelet	Summer+Autumn	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	4.833	0.437
Rhinoceros Auklet	Winter+Spring	0.54 ± 0.22	0.85 ± 0.37	0.90 ± 0.41	0.27 ± 0.18	0.54 ± 0.22	0.64 ± 0.33	2.659	0.752
Rhinoceros Auklet	Summer+Autumn	0.05 ± 0.05	0.20 ± 0.10	0.25 ± 0.09	0.34 ± 0.21	0.00 ± 0.00	0.04 ± 0.02	11.314	0.045
All diving birds	Winter+Spring	2.41 ± 0.71	3.39 ± 1.26	2.77 ± 0.63	5.75 ± 1.98	1.17 ± 0.28	3.66 ± 1.17	7.555	0.183
All diving birds	Summer+Autumn	6.59 ± 3.02	27.66 ± 12.23	11.53 ± 3.43	18.73 ± 8.97	5.46 ± 2.02	7.63 ± 2.23	7.606	0.179
Shearwaters									
Sooty and Short-tailed	Winter+Spring	0.75 ± 0.46	0.93 ± 0.61	0.23 ± 0.18	23.54 ± 15.92	10.63 ± 7.59	5.60 ± 3.95	6.484	0.262
Sooty and Short-tailed	Summer+Autumn	1.21 ± 0.66	27.98 ± 19.51	7.58 ± 4.97	18.55 ± 13.81	5.57 ± 2.24	1.97 ± 0.96	5.691	0.337
Surface-feeders									
Northern Fulmar*	Winter+Spring	0	0	0	0	0	0	-	-
Northern Fulmar	Summer+Autumn	0.20 ± 0.10	4.38 ± 4.02	13.69 ± 13.16	0.93 ± 0.44	3.17 ± 1.83	1.52 ± 0.95	3.558	0.615
Fork-tailed Storm Petrel	Winter+Spring	0.00 ± 0.00	0.03 ± 0.03	0.46 ± 0.33	0.31 ± 0.24	0.36 ± 0.22	6.53 ± 6.47	5.687	0.338
Fork-tailed Storm Petrel	Summer+Autumn	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00	0.08 ± 0.07	4.42 ± 2.90	0.70 ± 0.47	14.748	0.011
California Gull	Winter+Spring	0.37 ± 0.32	0.03 ± 0.03	0.03 ± 0.03	0.00 ± 0.00	0.46 ± 0.46	0.26 ± 0.13	8.959	0.111
California Gull	Summer+Autumn	1.98 ± 0.84	268.86 ± 145.76	36.45 ± 20.17	12.13 ± 4.92	6.57 ± 3.55	0.90 ± 0.40	13.781	0.017
Glaucous-winged Gull	Winter+Spring	1.23 ± 0.40	1.08 ± 0.39	1.16 ± 0.37	3.33 ± 0.90	0.91 ± 0.26	1.44 ± 0.58	5.332	0.377
Glaucous-winged Gull	Summer+Autumn	0.79 ± 0.32	16.52 ± 10.66	10.36 ± 7.28	2.77 ± 0.99	0.33 ± 0.12	0.12 ± 0.04	19.028	0.002
All gulls	Winter+Spring	2.32 ± 1.15	1.32 ± 0.41	1.43 ± 0.36	4.83 ± 2.03	5.24 ± 4.21	2.79 ± 1.15	3.135	0.679
All gulls	Summer+Autumn	3.12 ± 0.94	286.96 ± 148.94	51.16 ± 30.32	21.79 ± 6.93	10.25 ± 6.47	1.24 ± 0.40	21.251	0.001
All surface-feeders	Winter+Spring	2.32 ± 1.15	1.32 ± 0.41	1.45 ± 0.35	4.83 ± 2.03	5.30 ± 4.22	4.55 ± 1.78	4.236	0.516
All surface-feeders	Summer+Autumn	3.32 ± 1.01	291.43 ± 151.31	64.85 ± 43.27	22.78 ± 7.21	14.99 ± 6.36	2.87 ± 1.04	16.978	0.005
All birds									
All birds on water	Winter+Spring	5.50 ± 1.67	5.82 ± 1.89	4.55 ± 0.92	34.39 ± 17.83	17.44 ± 7.77	14.44 ± 5.53	10.648	0.059
All birds on water	Summer+Autumn	17.04 ± 7.48	348.93 ± 168.08	84.16 ± 43.64	62.64 ± 15.51	28.79 ± 9.59	12.79 ± 3.23	14.359	0.013
All birds on water + flying	Winter+Spring	18.94 ± 3.88	14.55 ± 2.73	13.88 ± 2.31	68.40 ± 39.79	29.92 ± 9.20	31.15 ± 11.44	8.035	0.154
All birds on water + flying	Summer+Autumn	40.38 ± 11.06	451.53 ± 201.04	139.29 ± 48.34	92.03 ± 16.27	58.25 ± 12.87	27.47 ± 5.04	14.782	0.011

* Northern Fulmar were not observed on the water during winter/spring and very few were seen flying.

DISCUSSION

Processes affecting seabirds on the shelf

Seabird distributions on the continental shelf off southwest Vancouver Island are affected by several physical and biological processes, and by fishing vessels (Martin & Myres 1969, Porter & Sealy 1981, Vermeer *et al.* 1989, Hay 1992, Logerwell & Hargreaves 1996). This study focused on upwelling processes affecting near-surface temperatures and hence SST visible on satellite images. Water temperatures recorded in the transects during the summer and autumn showed evidence of wind-induced upwelling over the inner shelf (Denman *et al.* 1981, Thomson 1981, Thomson *et al.* 1989), and upwelling associated with the large Juan de Fuca Eddy (Freeland & Denman 1982, Freeland 1992). The relatively low SST in the Inshelf East and Inshelf West legs in summer/autumn was likely the result of both processes, with decreasing influence of the Juan de Fuca Eddy in the western leg. Low temperatures in the Canyon leg were likely due to the effects of the eddy. More detailed measurements of the temperature, salinity and nutrient contents of the water are necessary to determine the origins of the cold surface water.

Aggregations of seabirds are usually associated with concentrations of prey at or near the surface, or within diving range for subsurface foragers. Currently, there are insufficient data on the diets of birds locally and the availability of prey to attempt a detailed explanation of the links between sea temperature and the distribution of seabirds and their prey off southwest Vancouver Island. Euphausiids, however, seem to be a key organism in this regard. *Thysanoessa spinifera* and *Euphausia pacifica* are the common species in this area. Off Vancouver Island, concentrations of euphausiids and other macro-zooplankton are associated with bathymetric breaks, such as the outer shelf-break zone (not sampled in this study), the edges of the larger canyons (especially the inner, northwestern slope of the Juan de Fuca canyon), and over Swiftsure Bank and other midshelf banks (Simard & Mackas 1989, Mackas & Galbraith 1992, Mackas *et al.* 1997). Concentration and advection of euphausiids has been shown to result from upwelling at canyons in this area (Mackas *et al.* 1997, Allen *et al.* 2001). Oblique upward currents carry euphausiids over the shelf edge into areas where they might become accessible to seabirds.

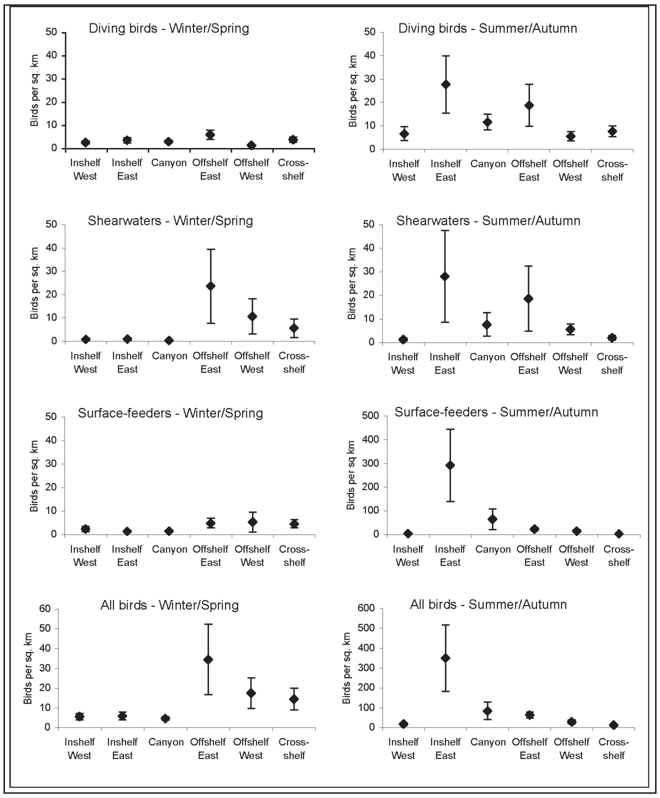

Fig. 5. Mean (± SE) densities of the three major foraging guilds (Divers, Shearwaters, and Surface-feeders) in the six legs of the shelf transects off southwest Vancouver Island in winter/spring and summer/ autumn. Note that the scale of the y-axis varies among the graphs for surface-feeders and all birds; summer/autumn densities were much higher than in winter/spring.

My study confirmed this pattern. The highest prey scores were recorded on the two transect legs immediately adjacent to the canyon. Surface swarms of euphausiids were regularly encountered in summer and autumn during this study, especially on the shelf near Swiftsure Bank and the canyon edge. These swarms were usually accompanied by large flocks of feeding seabirds, including all the common species recorded in the transects. Some larger birds were also seen to take small fish, including herring, which were attracted to the euphausiid swarms.

In contrast to the eddy effects, the cold temperatures generated near the shore by wind-induced upwelling were not associated with advection of euphausiids and other prey species from deeper ocean, and therefore showed lower prey scores and seabird densities. There is a considerable time delay for upwelled nutrients to affect higher trophic levels supporting birds. In my study area Denman *et al.* (1989) concluded that a pulse of primary productivity would take 90 days to create a peak in biomass in euphausiids and fish larvae (food for planktivores) and 270 days in 30 g fish (food for piscivores). By contrast, upwelling and advection of deep canyon water, rich in macro-zooplankton, produces a rapid increase in prey taken by birds as described above.

Seasonal changes in the sea surface temperatures and prey abundance were matched by changes in the densities and distribution of most species of seabirds, involving all the foraging guilds. During winter and spring, temperatures varied relatively little among the six legs, despite a gradual increase of about 4°C from January through June in all legs. Similarly, prey scores and densities of most seabirds showed little variation in density among the six legs in these seasons, with no statistically significant differences in any bird species or guild. In contrast, sea temperatures, prey scores and bird densities showed marked differences among the legs during summer and autumn. The two inner legs (Inshelf East and Inshelf West) and the Canyon leg were usually colder than the outer shelf legs and the Cross-shelf leg, likely due to the upwelling processes discussed above. High bird densities were not consistently associated with all the areas of low sea temperature. Bird densities within the Inshelf West leg remained low for most species and all guilds, even though this leg had consistently cold summer/autumn temperatures. Proximity to the Juan de Fuca canyon, in combination with the temperatures, seemed to provide the most optimal conditions for seabirds, within the Inshelf East and Canyon legs. Several species, especially diving birds and shearwaters, showed higher densities in the Offshelf East leg, adjacent to the canyon, even though this leg did not have consistently low SST.

Other factors affecting seabird distributions

Proximity to colonies likely affected some of the distribution patterns seen in this study. Common Murres, Rhinoceros Auklets and Glaucous-winged Gulls breed on Tatoosh Island, about 14 km southeast of the outer portion of the Canyon leg. Parrish *et al.* (1998) reported that proximity to this colony had a strong influence on densities of these three species during the breeding season, and associations with prey concentrations were evident only after controlling for distance from the colony. Proximity to Tatoosh Island might partly explain the high densities of murres and auklets near the canyon edge, although the Canyon leg itself, closest to that colony, did not contain the highest densities. Rhinoceros Auklets, Glaucous-winged Gulls, Cassin's Auklets, and Fork-tailed Storm Petrels nest on Seabird Rocks (Rodway 1991), about 8 km north of Inshelf West leg, but none of these species had high densities within this leg in any season.

Proximity to roost sites on land might partly explain the high densities of gulls within the Inshelf East leg. Many post-breeding California and Glaucous-winged Gulls, which make up the bulk of the summer/autumn flocks, roost on shore each night, and roosting flocks of hundreds to thousands of gulls are a common sight along the adjacent West Coast Trail coastline.

Many species in this study were obviously not affected by proximity to colonies or roost sites, and there were clear seasonal patterns in the abundance of these species, which migrate into the area in spring and summer. Shearwaters, fulmars, kittiwakes, and Sabine's Gulls showed similar distributions to the California Gulls and alcids, but did not breed or come ashore to roost in this area. The concentrations of alcids adjacent to and over the canyon persisted through the autumn, long after all breeding had ceased.

Using sea surface temperatures to monitor seabird concentrations

Several studies have used satellite images of surface temperatures to reliably predict where concentrations of seabirds might occur when associated with meso-scale ocean processes such as eddies, fronts, upwelling plumes and current filaments (Briggs *et al.* 1987, Haney 1989a,b). This study lacked the resources to include satellite imagery as part of the analysis, but clearly that is an important next step for explaining and tracking the distribution of seabirds off southwest Vancouver Island. Predicting the likely distribution of large aggregations of birds using remote sensing has great value in an area where there is a realistic probability of major oil spills.

This study indicates that SST alone is not a reliable indicator of prey abundance or seabird aggregations off southwest Vancouver Island. Although high prey and bird measures were associated with cold water from the Juan de Fuca Eddy in summer and autumn, the cold upwelled water of the inner shelf away from the eddy (Inshelf West) did not show these high measures of prey or birds. Conversely, the outer shelf leg closest to the eddy (Offshelf East) did not consistently show cold SST in summer and autumn, but did have high measures of prey and birds during these seasons. Clearly the interactions of bathymetry, meso-scale ocean currents and physical conditions causing concentrations of zooplankton, fish and seabirds are complex. Heating of stratified surface water might mask the effects of upwelling and enrichment. More detailed analysis of these variables is needed before satellite imagery can be used to reliably predict seabird distributions off southwest Vancouver Island.

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