Seabird distribution and abundance in relation to oceanographic processes in the California Current System

W. Breck Tyler,[1] Kenneth T. Briggs,[2] David B. Lewis,[1] and R. Glenn Ford[3]

[1] *Institute of Marine Sciences, University of California, Santa Cruz, CA 95060*
[2] *1411 Garrison Street, Davis, CA 95616*
[3] *Ecological Consulting, Inc., 2735 N.E. Weidler, Portland, OR 97232*

Abstract

In this paper, we present an overview of the seabird communities of the California Current System, relating large-scale patterns of abundance, distribution, and species diversity to physical and biological characteristics of the ocean habitat.

The population of seabirds that feed in waters of the California Current System during the breeding season is about 1.9 million individuals, comparable to populations in the Benguela and Senegal upwelling systems. Excluding terns and other nearshore inhabitants, 19 species have breeding populations exceeding 1000 individuals. The Common Murre *Uria aalge* is the premier breeding species, accounting for about 43% of the California Current total. Size and species composition of California Current breeding populations vary with latitude. More than 80% of the breeding seabirds nest along the coasts of Oregon and northern California in the zone of strongest and most persistent upwelling. A distinct change in faunal composition occurs in the vicinity of Point Conception.

Oceanographic conditions, species composition, and total abundance of bird populations at sea vary with latitude, season, and distance from shore. Surface waters are generally cooler, less saline, and richer in organic nutrients at higher latitudes. Latitudinal trends in seabird distribution are seasonal; in winter, average density is highest off southern California, but density is lowest there in summer. Primary production and seabird biomass are highest over the continental shelf, moderate over the slope, and lowest in deep (>2000-m) offshore waters.

Bird density at sea is highest during spring and fall migration and higher in summer than in winter. Species diversity is highest during migration and lowest in midsummer. In summer, the avifauna consists primarily of local breeders and visitors from nesting colonies in the southern and central Pacific. The Sooty Shearwater *Puffinus griseus* is the most abundant species over the shelf and slope during this season. The winter fauna consists primarily of local breeders and visitors from boreal and inland colonies; gulls and alcids are the predominant species, achieving their southernmost dispersal in this season. Year-to-year variability in the abundance, distribution, and composition of bird populations at sea results from El Niño–Southern Oscillations and other large-scale events.

The primary threats to California Current seabird populations are fisheries, floating oil, and toxic chemicals. Breeding populations are vulnerable also to colony disturbance, the introduction of nonnative predators, and habitat loss.

Résumé

Dans cette étude, les auteurs présentent un aperçu des collectivités d'oiseaux marins dans les régions du courant de Californie, en comparant les schémas, à grande échelle, d'abondance, de distribution et de diversité des espèces aux caractéristiques physiques et biologiques de l'habitat océanique.

La population d'oiseaux qui s'alimentent dans les régions du courant de Californie durant la période de reproduction compte environ 1,9 million d'individus ce qui se compare aux populations des courants ascendants de Benguela et du Sénégal. Exception faite des sternes et des autres oiseaux côtiers, 19 espèces ont une population de nicheurs supérieure à 1 000 individus. La Marmette de Troïl *Uria aalge* est l'espèce reproductrice dominante, puisqu'elle représente environ 43 % de tous les oiseaux marins du courant de Californie. La taille et la composition en espèces des populations varient selon la latitude. Plus de 80 % des reproducteurs nichent le long des côtes de l'Oregon et du nord de la Californie, là où les eaux ascendantes sont les plus vives et les plus constantes. La composition de l'avifaune subit un changement brusque près de la pointe Concepcion.

Les conditions océanographiques, la composition en espèces et l'abondance totale en mer varient selon la latitude, la saison et l'éloignement du rivage. Aux latitudes supérieures, les eaux de surface sont habituellement plus froides, moins salées et plus riches en substances organiques. Les tendances de distribution en fonction des latitudes sont des tendances saisonnières. En hiver, la densité moyenne atteint un sommet au large du sud de la Californie. En été, on y observe le phénomène contraire. La productivité primaire et la biomasse d'oiseaux marins sont supérieures au-dessus de la plate-forme continentale, moyennes au-dessus de la pente continentale et inférieures dans les eaux du large (> 2 000 m).

La densité de l'avifaune en mer atteint un sommet pendant les migrations du printemps et de l'automne. Elle est plus forte l'été que l'hiver. La diversité des espèces atteint un sommet pendant les périodes de migration et un creux au milieu de l'été. Pendant la saison estivale, l'avifaune comprend surtout des nicheurs locaux et des visiteurs provenant des colonies établies dans les régions australe et centrale du Pacifique. Le Puffin fuligineux *Puffinus griseus* est l'espèce la plus abondante, en été, au-dessus de la plate-forme et de la pente continentales. En hiver, l'avifaune comprend surtout des nicheurs locaux et des visiteurs provenant des colonies établies dans les régions boréales et dans les terres. Les espèces dominantes sont alors des mouettes, des goélands et des alcidés, des oiseaux dont l'aire de dispersion est pendant cette saison la

plus méridionale. La variabilité d'une année à l'autre de l'abondance, de la distribution et de la composition des populations en mer est attribuable à l'épisode El Niño–oscillation australe et aux autres événements climatiques de grande envergure.

Les populations d'oiseaux marins des régions du courant de Californie sont menacées d'abord et avant tout par les activités de pêche, les nappes d'hydrocarbures et les substances toxiques. Les populations de nicheurs souffrent également de la perturbation des colonies, de l'introduction de prédateurs non indigènes et de la destruction de leur habitat.

1. Introduction

Marine bird communities of the Pacific coast of North America, from Baja California (Mexico) to Washington, are structured primarily by oceanographic conditions in the California Current, an eastern boundary current. Eastern boundary currents are zones of intense upwelling, rich in temporal and spatial variability, and are highly productive, supporting some of the world's richest fisheries and large populations of marine birds (Cushing 1971; Parrish et al. 1981; Flament et al. 1985; Landry and Hickey 1989). The California Current supports almost two million nesting seabirds and at least twice that many seasonal visitors (Briggs et al. 1987, 1992). In this paper, we present an overview of the seabird communities of the California Current System (CCS), relating large-scale patterns of abundance, distribution, and species diversity to physical and biological characteristics of the ocean environment.

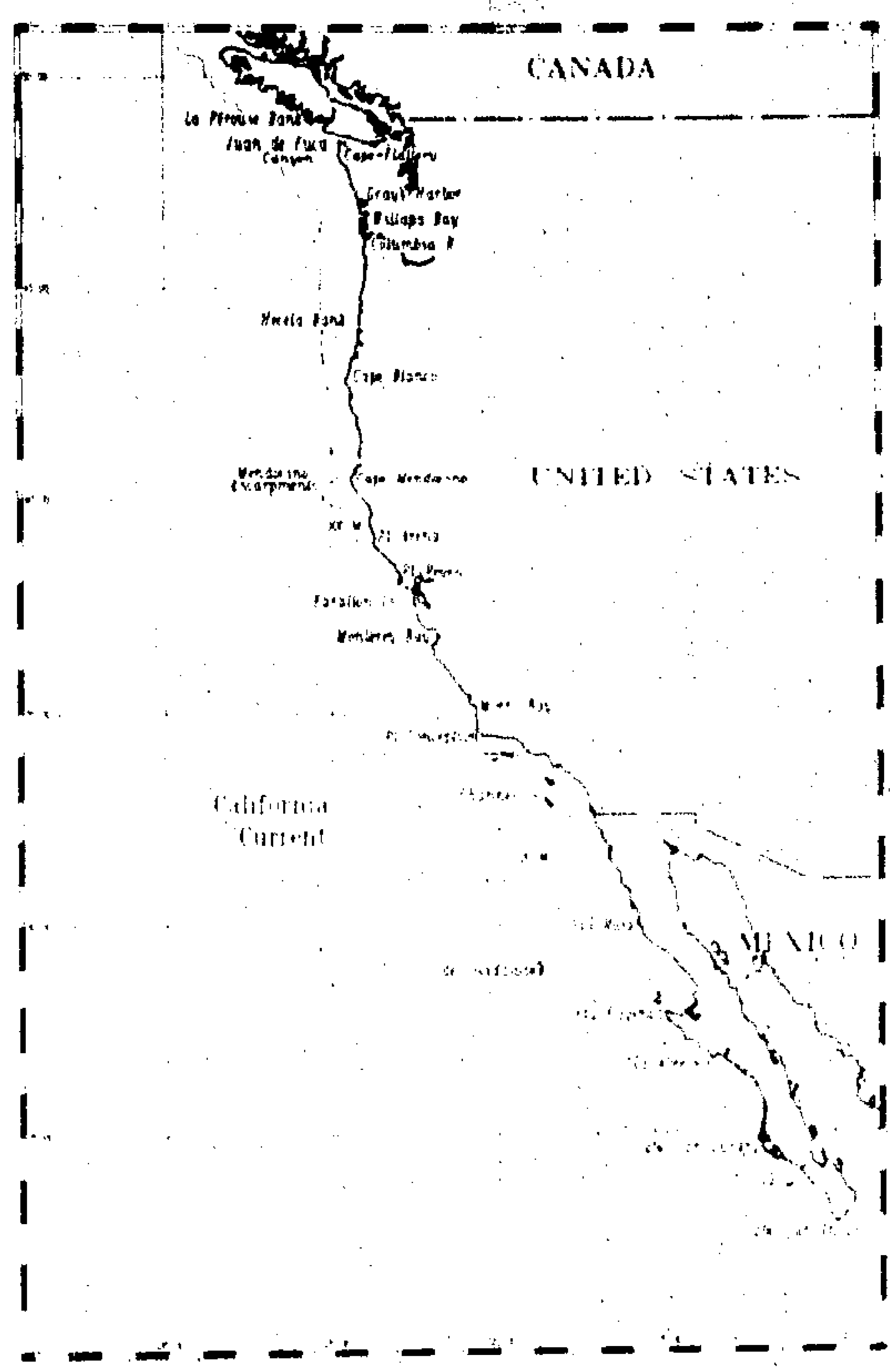
The key to understanding the relationship between seabirds and their marine habitat is knowledge of the patterns of prey distribution and abundance and of the oceanographic processes and conditions that influence these patterns. Recently, we have begun to understand that spatial and temporal variability in prey persistence and predictability should be reflected by the distribution patterns of seabirds (e.g., Briggs et al. 1987). By examining the scales over which birds aggregate, it is possible to infer which oceanographic processes are likely to be of trophic importance. It is necessary, however, to consider variability in bird distribution and community composition over a range of temporal and spatial scales (Hunt and Schneider 1987). For example, large oceanographic features like the California Current comprise numerous smaller-scale (10^0–10^2 km) processes and features that may be important to birds. The relevant time scales range from century- and decade-long events to annual, seasonal, and daily variation (Stommel 1963; Haury et al. 1978).

The seabird populations and the oceanography of the California Current have been relatively well studied. Ship and airplane surveys at sea (Briggs et al. 1987, 1992) and colony censuses (Sowls et al. 1980; Hunt et al. 1981; Ainley and Boekelheide 1990; Carter et al. 1990, 1992) have described variation over time scales of days to months or years and spatial scales of 10^0–10^2 km. By considering the results of these surveys cumulatively, we can appreciate some of the currentwide distribution patterns and the driving processes that shape them.

2. Oceanographic overview

The California Current is the eastern limb of the clockwise circulating North Pacific Gyre (Fig. 1). Fed from the north by the easterly flow of the West Wind Drift, the California Current diverges about 500 km off the coast of Vancouver, British Columbia (about 50°N latitude), and flows southwards for 2800 km before turning southwest, away from the continent, off Baja California, Mexico (about 25°N latitude).

Figure 1
Map of the California Current System



Eastern boundary currents are considered broad, slow-moving, uniform sheets of cool water, but in fact they are complex current systems. In the CCS, the main surface flow (to 200-m depth) parallels the shoreline, transporting cool, fresh, nutrient-rich, subarctic water southwards. The physical and chemical character of the surface waters changes with latitude as the subarctic water mixes with the warmer, saltier, nutrient and oxygen-limited central gyre waters from the west. Surface flow is centred 250–500 km offshore and is strongest (0.8 m/s) in spring and summer. Embedded within the flow are smaller mesoscale (10^1–10^2 km) features, such as eddies, meanders, and surface jets, which persist for a few days or up to several months (Hickey 1979; Mooers and Robinson 1984). As a result, the flow at any given spot may be faster than or even opposite in direction to the current's mean flow (Owen 1980; Simpson et al. 1984). In some areas, hydrography over the inner continental shelf is strongly influenced by freshwater outflow from large rivers (e.g., Columbia River) and estuaries (e.g., San Francisco Bay). These outflow plumes feature high turbidity due to suspended sediments and pronounced thermohaline gradients at their margins.

The second major component of the CCS is a poleward jet, the California Undercurrent, which flows all year at depths of 100–300 m over the continental slope and transports warm, salty, oxygen-poor, but phosphate-rich equatorial waters to higher latitudes. During winter, when the main southward surface flow decreases and moves farther offshore, this poleward flow surfaces and moves nearer shore. Poleward flow over the shelf is sometimes called the Davidson Current (Bolin and Abbott 1963).

The CCS is also characterized by strong upwelling, especially over the continental shelf (Hickey 1979; Huyer 1983). Equatorward wind stress leads to offshore transport of nearshore surface waters which are replaced by cold, saline, nutrient-rich waters from below (to depths of 100 m). The result is increased phytoplankton production near the surface and, where upwelled waters intrude into the warmer, stratified waters of the main current flow, the formation of structurally complex "fronts." Upwelling fronts are areas of strong horizontal property gradients thought to passively trap zooplankton used by feeding seabirds (Briggs et al. 1984, 1987). Up to 10^1 km wide and 10^2 km in length, and lasting up to several weeks, these fronts typically overlie the continental slope.

Regional variation in upwelling intensity has been discussed by Bakun and Nelson (1977), Parrish et al. (1981), and Huyer (1983). South of Cape Blanco (Oregon), mean wind direction is favourable all year, so that upwelling can occur in any month. Upwelling is most persistent and intense in midsummer between Cape Blanco and San Francisco. From Point Conception north, coastal upwelling may be reinforced seasonally by oceanic upwelling, resulting from positive curl in the wind stress field seaward of the shelf break (Chelton et al. 1982). Off the coasts of northern Oregon and Washington, mean wind stress is poleward, and thus unfavourable for upwelling, except in summer. At these latitudes, upwelling resulting from estuarine tidal flux, river runoff, and complex shelf-edge dynamics may be of greater general significance for feeding seabirds than is wind-generated upwelling (Landry and Hickey 1989; Wahl et al., this volume).

The result of these different influences is pronounced seasonal and regional variability in oceanographic conditions. Strong meridional (north–south) and zonal (east–west) gradients exist in physical and chemical properties, such as temperature, salinity, and organic nutrients. This heterogeneity is reflected in the composition, diversity, and ecology of seabirds nesting in and visiting different parts of the current system.

3. Breeding populations

The breeding population of the CCS totals about 1.9 million individuals, a figure comparable to populations in the Benguela and Senegal upwelling systems (Brown 1979; Abrams and Griffiths 1981; Duffy and Siegfried 1987). Breeding populations in the Gulf of Alaska (including coastal British Columbia) are considerably larger, but are predominated by relatively fewer species (Sowls et al. 1978).

Breeding populations in the CCS have undoubtedly varied during the last 5000–10 000 years, not only in response to climatic change but also because of human exploitation and interference (Ainley and Lewis 1974; Warheit 1990; Duffy, this volume). Still, large, stable nesting colonies are believed to form where oceanographic conditions promote abundant and predictable food resources over the long term. Thus, the present-day locations of nesting colonies provide our best estimate of long-term (decades to centuries) distribution patterns. Furthermore, the specific oceanographic conditions that support large colonies today provide a fair indication of conditions that have been important over long time scales.

Table 1
Numbers (thousands of individuals) of breeding seabirds in the California Current System. The northern California region includes colonies north of Point Conception and on San Miguel Island; the southern California region includes colonies from Point Conception south to Punta Abreojos, Baja California. P = Breeds in low numbers.

Faunal groups and species	Region: Washington	Oregon	Northern California	Southern California	Total
California Current endemic					
Black-vented Shearwater	0	0	0	14.0	14.0
Ashy Storm-Petrel	0	0	4.1	P	4.1
Brandt's Cormorant	0.6	23.0	54.0	17.0	94.6
Western Gull	—	16.4	35.9	40.0	92.3
Xantus' Murrelet	0	0	0.3	20.0	20.3
Boreal					
Fork-tailed Storm-Petrel	3.9	1.0	0.4	0	5.3
Pelagic Cormorant	2.6	12.0	11.8	2.4	28.8
Glaucous-winged Gull	16.5[a]	0	0	0	16.5[a]
Common Murre	21.4	438.1	351.0	0	810.5
Pigeon Guillemot	0.4	3.5	12.8	2.7	19.4
Rhinoceros Auklet	24.2	1.0	1.7	0	26.9
Cassin's Auklet	88.0	0.5	52.3	10.0	150.8
Tufted Puffin	23.7	5.0	1.8	0	29.0
Marbled Murrelet	2.4	2.0	1.8	0	6.2
Northeast Pacific					
Leach's Storm-Petrel	36.0	435.0	10.8	10.0	491.8
Double-crested Cormorant	2.2	3.4	7.5	4.0	17.1
Subtropical					
Least Storm-Petrel	0	0	0	15.0	15.0
Black Storm-Petrel	0	0	0	10.0	10.0
Brown Pelican	0	0	0	20.0	20.0
Total	221.9	940.9	544.7	165.1	1872.6

Sources: Washington and Oregon—Speich and Wahl 1989; Briggs et al. 1992; R. Lowe, pers. commun. Northern California and southern California—Sowls et al. 1980; Carter et al. 1990, 1992; W. Everett, pers. commun.
[a] Includes some Western Gulls and Glaucous-winged/Western hybrids.

We will focus on coastal colonies south of the U.S.–Canada border and north of Punta Abreojos, Mexico. These boundaries are somewhat arbitrary because we suspect, for example, that some birds from colonies in southern British Columbia feed in California Current waters whereas others do not. Colonies south of Punta Abreojos include Brown Pelicans *Pelecanus occidentalis* and Double-crested Cormorants *Phalacrocorax auritus*, but they also feature nesting boobies (*Sula* spp.) and Magnificent Frigatebirds *Fregata magnificens*—species that are clearly of tropical affinity.

Excluding terns, waders, and other nearshore species, the CCS breeding fauna consists of 19 species with populations of more than 1000 individuals (Table 1). Nine of these species (Fork-tailed Storm-Petrel *Oceanodroma furcata*, Pelagic Cormorant *Phalacrocorax pelagicus*, Glaucous-winged Gull *Larus glaucescens*, Common Murre *Uria aalge*, Pigeon Guillemot *Cepphus columba*, Rhinoceros Auklet *Cerorhinca monocerata*, Cassin's Auklet *Ptychoramphus aleuticus*, Tufted Puffin *Fratercula cirrhata*, and Marbled Murrelet *Brachyramphus marmoratus*) have breeding ranges centred in the boreal zone; this group accounts for almost 60% of the individuals. Five species (Black-vented Shearwater *Puffinus opisthomelas*, Ashy Storm-Petrel *Oceanodroma homochroa*, Brandt's Cormorant *Phalacrocorax penicillatus*, Western Gull *Larus occidentalis*, and Xantus' Murrelet *Synthliboramphus hypoleucus*) are endemic to the California Current, although not

Figure 2
Number (in thousands of individuals) and biomass (in thousands of kilograms) of CCS breeding birds by taxonomic group (abbreviations as follows: ALCIDS = alcids; PETR = storm-petrels; GULLS = gulls; CORMS = cormorants; PELS = pelicans; SHEAR = shearwaters)

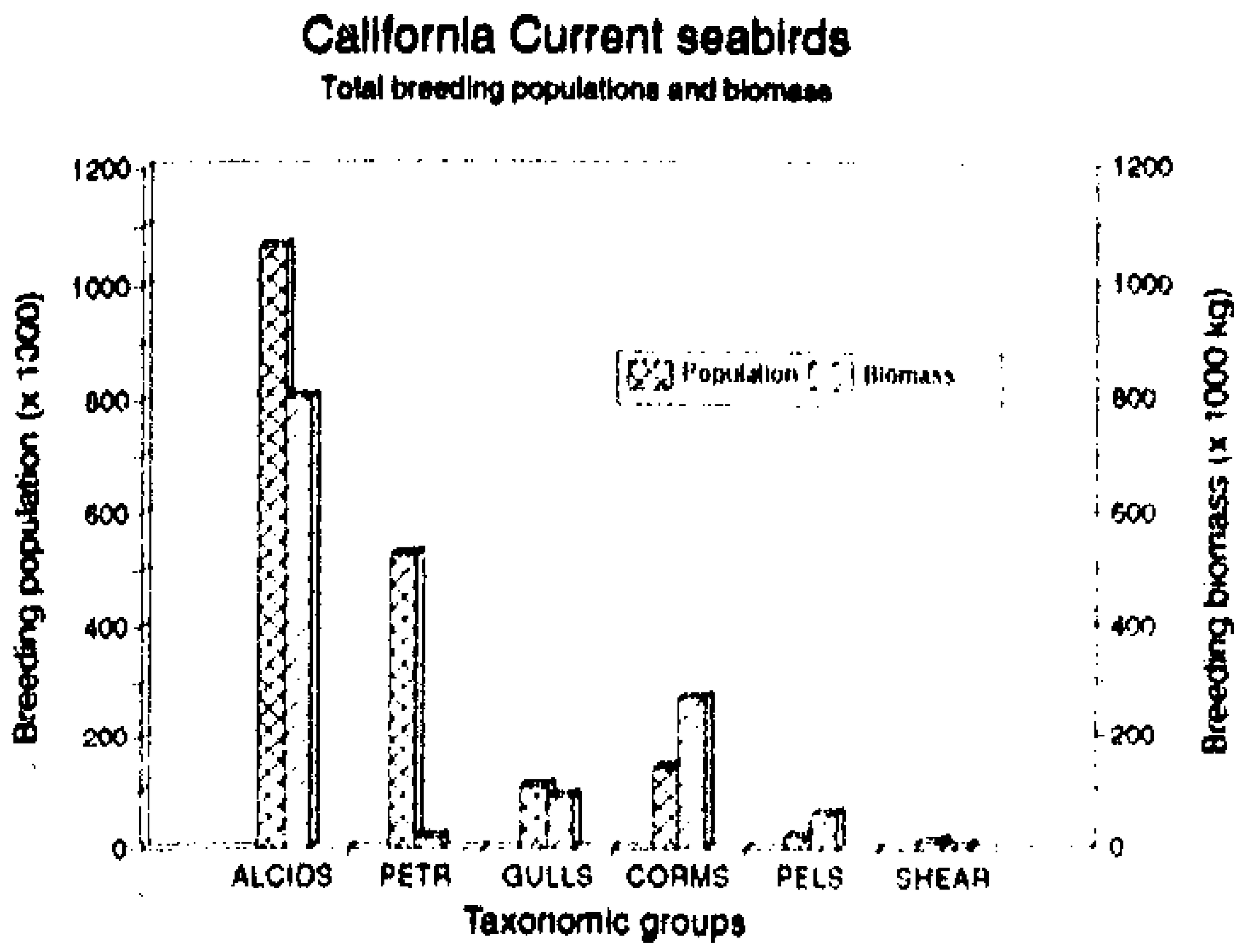


Figure 3
Number and biomass of CCS breeding birds using different feeding methods. Feeding categories are as follows: diver—feeds at depths of 3 m and below; plunger—feeds at depths of 1–3 m; surface seizer—feeds within the upper 1 m, neuston feeder—feeds only at the sea surface.

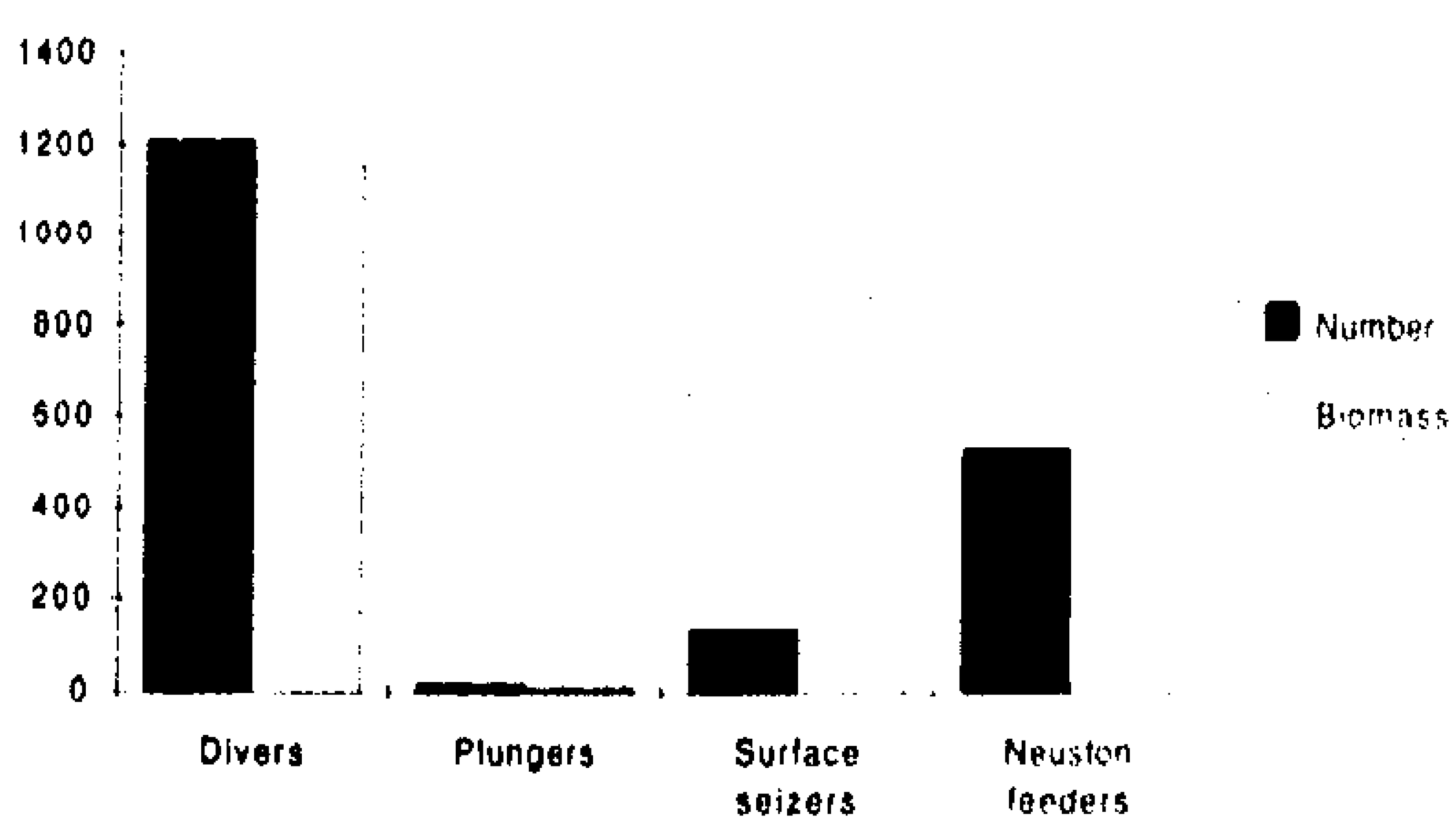


Figure 4
Number and biomass of breeding birds within subregions of the CCS (abbreviations as follows: WA = Washington, OR = Oregon, NCAL = northern California, SCAL = southern California)

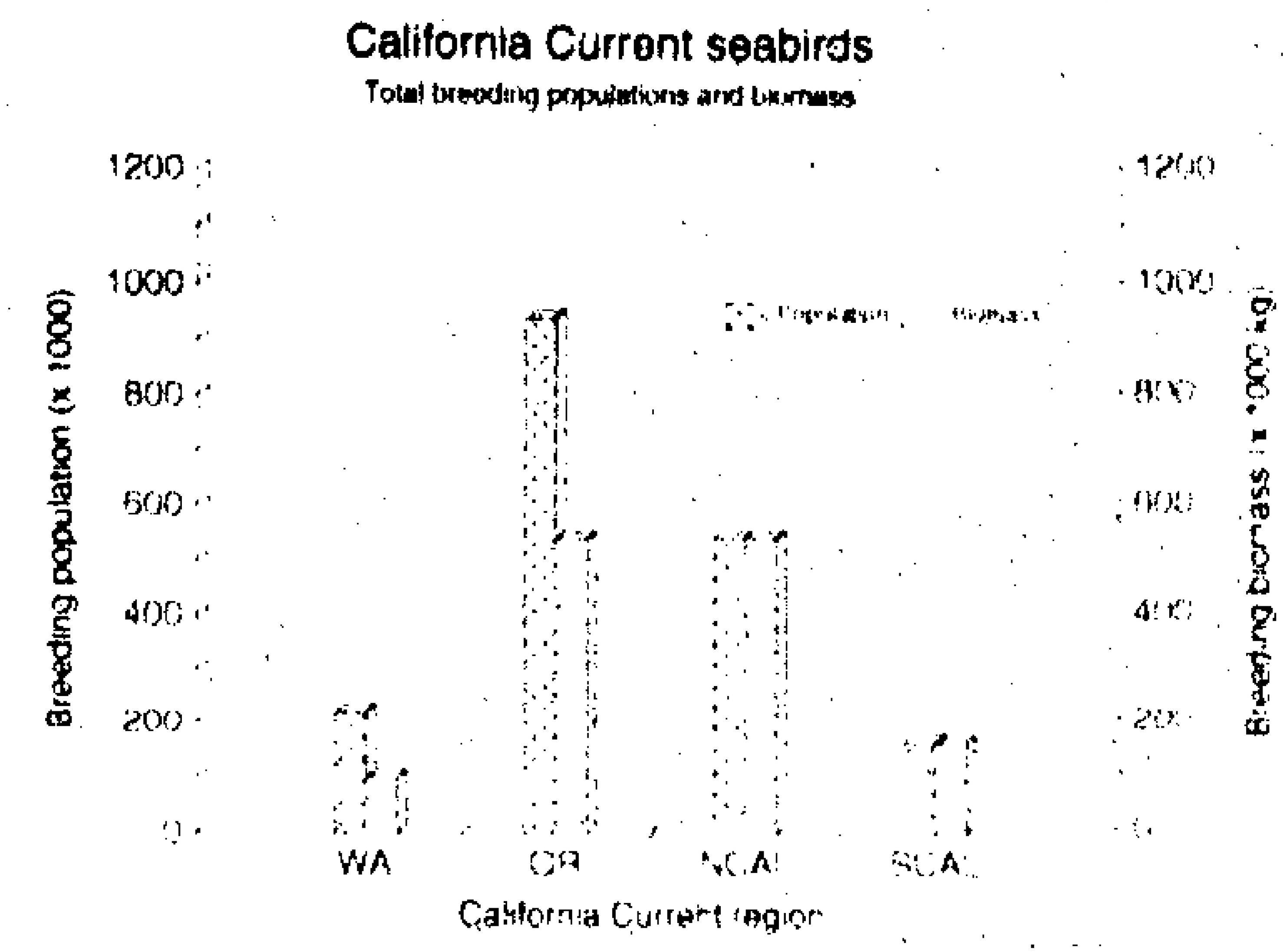
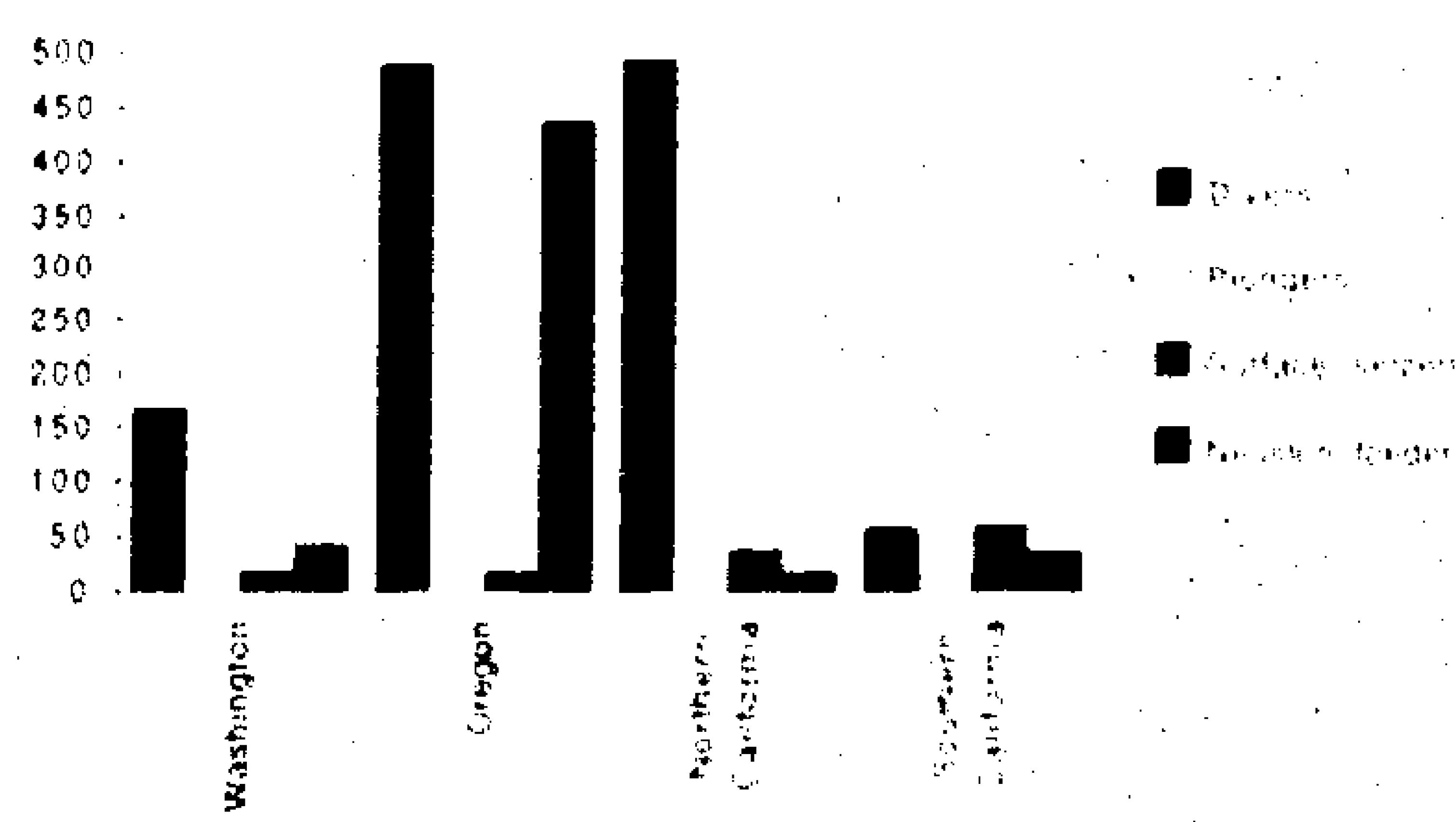


Figure 5
Feeding methods of breeding seabirds within subregions of the CCS. See Figure 4 for subregion abbreviations and Figure 3 for feeding categories.



overly numerous. Three subtropical species (Least Storm-Petrel *Oceanodroma microsoma*, Black Storm-Petrel *O. melania*, and Brown Pelican) and two species that nest throughout the northeast Pacific (Leach's Storm-Petrel *Oceanodroma leucorhoa* and Double-crested Cormorant) make up the remainder of the nesting fauna. Alcids makeup more than a third of the species and over half of the breeding population (Fig. 2). Storm-petrels also are numerous, with over 500 000 nesting birds. Several foraging methods are represented, but the breeding fauna is predominated by divers which comprise more than 65% of the population and 85% of the biomass (Fig. 3).

The Common Murre is the dominant breeding species of the CCS, accounting for 43.3% of the population (Table 1). The next four most abundant species, Leach's Storm-Petrel, Cassin's Auklet, Brandt's Cormorant, and Western Gull, in combination account for another 44.3%. No other species makes up more than 1.5% of the total.

3.1. Regional (latitudinal) variation

The size and species composition of CCS breeding populations vary significantly with latitude. In this section, we compare the nesting faunas of four regions (Fig. 1): Washington, Oregon, northern California (Point Conception north, including San Miguel Island), and southern California (Point Conception south to Punta Abreojos, Baja California).

More than half of the breeding seabirds of the CCS nest along the Oregon coast (Fig. 4, Table 1); divers and neuston-feeding storm-petrels predominate (Fig. 5). The colonies of northern California, which feature fewer storm-petrels and more cormorants, support fewer breeding individuals (30% of the CCS total) but comparable breeding biomass (Fig. 4). The colonies of Washington and southern California combined support less than 20% of the system's breeding individuals or biomass.

Oregon colonies support a nesting population of almost a million birds (Table 1). Washington colonies feature most of the same species, but only about 220 000 birds. One reason for the disparity is that Washington has only half as much outer coast and fewer colony sites, especially in the southern and central parts of the state. Also, as much as 23% of Washington's breeders nest in bays, the Strait of Juan de Fuca, and Puget Sound (Speich and Wahl 1989).

Additionally, the California Current has little influence on continental shelf waters off Washington, especially north of Grays Harbor (Hickey 1989). The shelf is relatively wide (25–60 km) and this tends to isolate nearshore waters from the nutrient-rich waters of the main southward flow. Favorite et al. (1976) described a broad region offshore of Washington as the "Dilute Domain" due to the input of fresh water from bays and rivers and low surface evaporation. Nearshore waters are also influenced strongly by estuarine outflow. Due to the inconsistency of favourable winds, the intensity and seasonal duration of coastal upwelling are much reduced north of Cape Blanco (Bakun 1973; Huyer 1983; Hickey 1989). Steep horizontal property gradients associated with the edges of upwellings ("upwelling fronts") are less prevalent here (Briggs et al. 1992), and we may speculate that convergent flow fields (a mechanism promoting passive concentration of poorly motile plankton) are also less prominent. Additionally, off central and northern Oregon, summer upwelling is restricted to a narrow band near shore due to the barrier formed by the surface plume from the Columbia River estuary (Hickey 1989); fronts seaward of the shelf are suppressed or masked by a thin film of overlying estuarine water. Shelf-edge eddies (within the main current flow), which enhance the complexity of seabird foraging habitat, are less prevalent off Washington than off California (Hickey 1989). In contrast, Parrish et al. (1981) have suggested that the shoreward transport of surface waters, which limits upwelling during most of the year, also prevents offshore dispersion of larval fish, leading to increased stocks of northern anchovies *Engraulis mordax* and other schooling fishes in shelf waters of northern Oregon and Washington.

This is not to imply that upwelling has no effect at the northern edge of the CCS. Chelton et al. (1982) have shown that annual variation in zooplankton biomass is determined mostly by the intensity of southward transport of subarctic water. Along the Washington and northern Oregon coasts, this flow strengthens (enhanced at the surface by northwesterly winds) and moves nearer to the shore coincident with the onset of seabird nesting in April and May. Although prevailing winds don't become equatorward until midsummer, short periods (2–10 days) of favourable winds, associated with large-scale weather events, produce event-scale pulses of upwelling, which enhance local primary production in late spring (Landry et al. 1989). This bloom in productivity contributes to support of nesting seabirds, even without the benefit of widespread, persistent upwelling.

Colonies in northern Washington benefit also from upwelling induced by tidal flows impinging on shelf-edge banks and canyons (Wahl et al., this volume). The coolest waters north of Cape Blanco (and, occasionally, strong thermal gradients) are found over the shelf southwest of Vancouver Island, especially at the edge of the Juan de Fuca submarine canyon, where there is strong, topographically induced upwelling. The mixture of estuarine water with nutrient-rich California Undercurrent water produces broad productive fronts over the shelf (Brinkhurst 1987; Landry and Lorenzen 1989). Morgan et al. (1991) and Briggs et al. (1992) found persistently high seabird numbers over La Pérouse and Swiftsure banks adjacent to the canyon. The warm, fresh waters of the Columbia River plume, which are advected offshore and to the south in summer, may also enhance food production and availability by contributing to thermohaline fronts at the shelf break off northern Oregon.

The largest percentage of the fauna nests from Cape Blanco to Point Conception, the zone of strongest and most persistent upwelling. Within this region, the largest colony complexes are located adjacent to promontories, such as Cape Blanco, Point Arena, Point Reyes, and Point Conception, which significantly affect upwelling (through coastal wind "jets" and topographic steering of currents). At these upwelling centres, the mesoscale (10^1–10^2 km) fronts so important to feeding birds are recurrent, somewhat predictable, and relatively persistent, lasting up to several weeks (Briggs et al. 1987). Perhaps because surface waters are transported offshore during much of the year, midwater schooling fishes such as anchovies are abundant only seasonally off northern California and do not spawn there. Instead, seabirds eat rockfish *Sebastes* spp., flatfish, squid, and micronekton such as large euphausiids and copepods (Baltz and Morejohn 1977; Chu 1984; Briggs and Chu 1986; Ainley and Boekelheide 1990).

In the southern California Bight (SCB), the wide shelf area southeast of Point Conception, nesting populations are modest. Potential nesting habitat is abundant on the eight islands and island groups, but human activities and the introduction of nonnative species have greatly reduced the number of usable sites. At this latitude, the subarctic waters of the main current flow have been diluted by the waters of the central ocean gyre, and their influence on coastal production is limited by the width (up to 200 km off San Diego) of the continental borderland (shelf and slope). Except at Point Conception, there is little persistent upwelling in the region (Huyer 1983). Circulation and hydrographic conditions in the northern SCB are controlled in part by the so-called southern California Eddy, a cyclonic flow centred over the Santa Rosa–Cortés Ridge. The area north and west of the ridge features southward surface flow and cool waters generated by upwelling at Point Conception. Nesting birds from the Northern Channel Islands and San Nicolas Island that feed in these waters eat mainly euphausiids and juvenile rockfish (Hunt et al. 1981). East of the ridge and throughout the southern part of the SCB, surface waters are warm and well stratified; the thermocline is 30–60 m deep (compared to 10–20 m off northern California).

Along the coast of Baja California, winds are favourable for upwelling all year (Huyer 1983). In January, however, the cool surface temperatures resulting from upwelling are restricted to northern Baja; south of Punta Eugenia, surface waters are warm (18°C or above). In May, wind-generated upwelling is strong along exposed coasts from San Diego to Punta Baja and from Punta Eugenia to the north side of Cabo San Lazaro. Most of the important nesting islands (including Isla Cedros, Islas San Benito, Isla Natividad, and Isla Asunçion) are located in these upwelling zones, especially over the outer shelf near Punta Eugenia (Everett 1988). Birds from these colonies most likely forage in the narrow zone of strong temperature gradients located within 30 km of shore.

The composition of the nesting fauna varies with latitude (Table 1). For example, of the nine boreal species, eight nest in the three northernmost regions (Washington, Oregon, and northern California), whereas only three (Pelagic Cormorant, Pigeon Guillemot, and Cassin's Auklet) nest in southern California. Conversely, of the eight California Current endemics and subtropical species, all nest in the southernmost region, and only two (Brandt's Cormorant and Western Gull) nest north of California. Clearly, there is a distinct difference in the nesting faunas north and south of the San Miguel Island–Point Conception area (Ainley 1976).

Dominated by divers (Fig. 5), especially alcids, the nesting fauna of the Washington coast also is transitional between that of the upwelling zone to the south and that of higher latitudes. Currentwide peaks in numbers of Fork-tailed Storm-Petrels, Glaucous-winged Gulls, Rhinoceros Auklets, Cassin's Auklets, and Tufted Puffins breed here. Higher numbers of burrow-nesting storm-petrels and auklets and lower numbers of surface-nesting murres in Washington and British Columbia likely relate in part to the type of nest habitat available (Manuwal and Campbell 1979; Varoujean and Pitman 1980; Speich and Wahl 1989).

Divers also predominate in the central upwelling region (Fig. 5). Peak populations of Common Murres, Pigeon Guillemots, and the three cormorants are found here. All inhabit the turbid waters of the continental shelf. The system's largest population of Leach's Storm-Petrels nests in this region, as does virtually the entire world population of Ashy Storm-Petrels. Leach's Storm-Petrels forage in clear oceanic and continental slope waters, whereas Ashy Storm-Petrels feed at the edges of upwellings over the outermost shelf and upper slope (Briggs et al. 1987, 1992).

In southern California, the major foraging modes are more equally represented (Fig. 5). The surface-feeding Western Gull is the most abundant nester followed by the Brown Pelican, Xantus' Murrelet, and Brandt's Cormorant (Hunt et al. 1981; Carter et al. 1992). These four species account for more than half of the nesting birds (Table 1). The four species of storm-petrels comprise one-quarter of the population but account for little of the biomass. The only breeding shearwater of the CCS, the Black-vented Shearwater, nests near the upwelling centres of Baja California (Everett 1988).

3.2. Annual variation

The strength and duration of the main flow of the California Current (i.e., the southward surface transport of subarctic waters) vary considerably from year to year, as a result of El Niño–Southern Oscillation (ENSO) and anti-ENSO events, and perhaps other basin-wide wind patterns. This fluctuation leads to CCS-wide differences in productivity and zooplankton stocks (Bernal and McGowan 1981; Chelton et al. 1982) and in seabird nesting success (Hodder and Graybill 1985; Ainley et al. 1988; Ainley and Boekelheide 1990). In years of strong southward transport, primary production is high (Smith and Eppley 1982), leading to large standing stocks of zooplankton and the schooling fishes preyed upon by seabirds. Years of weakened southward transport, especially those with strong ENSO events, are characterized by low primary and secondary production. In these years, nearshore concentrations of warm, saline water resulting from increased countercurrent flow and deep, stable thermoclines resulting from reduced surface mixing impair the upwelling of nutrients (Chelton 1980; McLain 1983).

Nesting failure resulting from reduced upwelling during years of very low southward flow has been well documented at the Farallon Islands (Ainley and Boekelheide 1990). During the 1982–83 ENSO event, sea surface temperatures averaged 1–3°C warmer than normal, and prey species such as euphausiids and juvenile rockfish, typically important to nesting birds, were absent from seabird diets. All species of alcids and cormorants suffered nesting failure. Only the Western Gull, which relied upon garbage, and the offshore-feeding Leach's Storm-Petrel raised chicks. Species-specific responses were similar for Oregon colonies (Graybill and Hodder 1985).

4. Bird populations at sea

Observations of birds at sea reveal considerable variation in relative abundance and species composition with latitude, distance from shore, and season. To address variability in distributions at sea, we use ship and airplane survey data gathered since 1975. Unfortunately, not all parts of the CCS have been equally well studied. Seabird distribution off California has received the most attention (Briggs et al. 1987) and aerial surveys were recently completed for the waters off Oregon and Washington (Briggs et al. 1992). The waters off Baja California have never been studied systematically, nor have many sections of the CCS seaward of the continental slope.

More than 100 species of marine birds have been recorded from California Current waters, of which about 40 are abundant enough to play significant roles in pelagic energy cycling (Briggs et al. 1987, 1992). Over half of these dominant species are present only seasonally as visitors from other breeding domains (Tables 2 and 3). The four species or species pairs (Sooty Shearwater, Common Murre, Cassin's Auklet, Red *Phalaropus fulicarius* and Red-necked *P. lobatus* phalaropes) that attain estimated populations greater than one million individuals reach annual peaks in different seasons.

The total number of birds supported by the CCS is unknown; however, estimates of maximum instantaneous populations are 5.5–6 million birds off California (Briggs et al. 1987) and 1.8 million birds off Oregon and Washington (Briggs et al. 1992). These numbers are comparable to those reported for the Benguela Current off Africa (Abrams and Griffiths 1981; Schneider and Duffy 1985) and higher than those for the Senegal upwelling system (Brown 1979).

4.1. Latitudinal variation

Spanning almost 25 degrees of latitude, the CCS includes a range of oceanographic, climatic, and faunal regimes. There is a pronounced north–south trend in the oceanographic character of surface waters, ignoring seasonal and local variability, waters are generally cooler, less saline, and richer in organic nutrients at higher latitudes (Reid et al. 1958, Hickey 1979; Bernal and McGowan 1981). This latitudinal thermal gradient is greatest in summer, when surface waters off southern California may be 10°C warmer than those off Washington. Moving from north to south, air temperatures and weather patterns become gradually more tropical. In general, the importance of species of boreal affinity increases with latitude, and the relative importance of subtropical species decreases (Ainley 1976).

Relative abundance and species composition of at-sea bird populations in the CCS vary considerably with latitude, but the important latitudinal trends follow distinctly seasonal cycles; for example, in winter average density increases from north to south, whereas summer populations at sea are smallest off southern California. Many northern nesting species reach their southern limit of distribution in the SCB or off Baja California during winter. In late summer, southern CCS nesters and other subtropical species disperse to the northern edge of the CCS.

4.2. Longitudinal variation

In general, longitude correlates well with distance from shore, water depth, and sea surface temperature (SST). In most of the CCS, water depth and SST increase as one moves seaward from the coastline. In the SCB, however, the shelf physiography and circulation are complex. There, deep water (>2000-m depth) occurs within 50 km of the coast (e.g., Santa Cruz Basin) and shallow water (<50-m depth) is found 150 km offshore (e.g., Tanner and Cortes banks); SST is similarly variable.

Table 2
Mean density (birds/km^2) at sea of predominant seabird species of the California Current System during July. Northern California includes waters north of Point Conception; southern California includes U.S. waters south of Point Conception.

Faunal groups and species	Oregon and Washington $\bar{x} \pm$ s.e.	Northern California $\bar{x} \pm$ s.e.	Southern California $\bar{x} \pm$ s.e.
Breeding species			
Black-vented Shearwater	0	0	0
Ashy Storm-Petrel	0	0.01 ± 0.04	0.13 ± 0.44
Fork-tailed Storm-Petrel	1.61 ± 3.44	0.17 ± 0.45	0
Leach's Storm Petrel	1.47 ± 1.87	0.84 ± 1.40	0.05 ± 0.06
Brown Pelican	0.02 ± 0.01	0.19 ± 0.42	0.08 ± 0.16
Brandt's Cormorant	0.10 ± 0.09	1.65 ± 5.56	0.02 ± 0.05
Western Gull	0.74 ± 1.34	1.01 ± 2.07	2.79 ± 5.72
Glaucous-winged Gull	0.35 ± 1.13	0	0
Common Murre	1.75 ± 3.88	5.14 ± 12.52	0.07 ± 0.25
Rhinoceros Auklet	0.11 ± 0.15	0.04 ± 0.88	0
Cassin's Auklet	1.02 ± 3.88	2.18 ± 4.70	0.07 ± 0.18
Tufted Puffin	0.31 ± 0.77	0.01 ± 0.01	0
Xantus' Murrelet	0	0	0.04 ± 0.01
Breeder total[a]	9.36	11.29	3.36
Visiting species			
Black-footed Albatross	0.61 ± 0.99	0.24 ± 0.50	0.01 ± 0.01
Northern Fulmar	2.94 ± 15.05	0.09 ± 0.12	0.01 ± 0.01
Pink-footed Shearwater	0.10 ± 0.23	1.61 ± 7.27	0.79 ± 1.06
Buller's Shearwater	0.22 ± 1.06	0.01 ± 0.01	0
Sooty Shearwater	3.13 ± 5.83	24.21 ± 66.60	6.47 ± 10.38
Phalarope spp.	0.76 ± 2.10	4.84 ± 15.50	0.01 ± 0.01
Pomarine Jaeger	0.01 ± 0.03	0.01 ± 0.03	0.01 ± 0.01
Bonaparte's Gull	0.01 ± 0.02	0	0.01 ± 0.01
Heermann's Gull	0.02 ± 0.02	0.01 ± 0.02	0.09 ± 0.27
California Gull	0.10 ± 0.18	0.01 ± 0.02	0
Herring Gull	0.01 ± 0.04	0	0
Common/Arctic Tern	0.09 ± 0.34	0.10 ± 0.46	0
Ancient Murrelet	0.03 ± 0.13	0	0
Visitor total[a]	14.98	31.53	7.40
Total[a]	24.34	42.82	10.76

Sources: Washington and Oregon—Briggs et al. 1992; northern California—Briggs et al. 1983; southern California—Briggs et al. 1981a.
[a] Includes additional species and birds not identified to species.

Table 3
Mean density (birds/km^2) at sea of predominant seabird species of the California Current System during December. Northern California includes waters north of Point Conception; southern California includes U.S. waters south of Point Conception.

Faunal groups and species	Oregon and Washington $\bar{x} \pm$ s.e.	Northern California $\bar{x} \pm$ s.e.	Southern California $\bar{x} \pm$ s.e.
Breeding species			
Black-vented Shearwater	0	0	0.09 ± 0.30
Ashy Storm-Petrel	0	0.04 ± 0.12	0
Fork-tailed Storm-Petrel	0.07 ± 0.10	0.10 ± 0.24	0
Leach's Storm-Petrel	0	0.05 ± 0.10	0
Brown Pelican	0	0	0.28 ± 0.38
Brandt's Cormorant	0.01 ± 0.05	0.10 ± 0.21	0.04 ± 0.12
Western Gull	—	0.[illegible]5 ± 0.87	0.58 ± 1.18
Glaucous-winged Gull	0.67 ± 1.11	0.[illegible]1 ± 0.20	0.01 ± 0.02
Common Murre	0.95 ± 1.90	3.54 ± 7.71	0.5[illegible] ± 1.37
Rhinoceros Auklet	0.84 ± 1.55	1.79 ± 7.5[illegible]	1.59 ± 2.24
Cassin's Auklet	0.01 ± 0.01	2.51 ± 3.06	0.18 ± 0.26
Tufted Puffin	0	0	0.01 ± 0.03
Xantus' Murrelet	0	0.01 ± 0.01	0.04 ± 0.01
Breeder total[a]	3.43	8.80	3.41
Visiting species			
Pacific Loon	0	0.09 ± 0.24	1.35 ± 4.54
Black-footed Albatross	0.09 ± 0.21	0	0.01 ± 0.01
Laysan Albatross	0.04 ± 0.09	0	0
Northern Fulmar	0.30 ± 0.32	0.46 ± 0.48	2.63 ± 9.66
Pink-footed Shearwater	0	0	0.02 ± 0.04
Sooty Shearwater	0	0	0.01 ± 0.01
Phalarope spp.	0	0.80 ± 2.12	0.10 ± 0.32
Pomarine Jaeger	0	0.05 ± 0.07	0.06 ± 0.07
Bonaparte's Gull	0	0.01 ± 0.05	0.85 ± 2.29
Heermann's Gull	0	0	0.66 ± 2.01
California Gull	0.04 ± 0.02	1.31 ± 2.57	12.74 ± 27.40
Herring Gull	1.40 ± 3.46	0.75 ± 1.53	0.21 ± 0.24
Black-legged Kittiwake	0.52 ± 0.59	1.24 ± 1.36	0.65 ± 0.88
Ancient Murrelet	0.06 ± 0.19	0	0
Visitor total[a]	4.17	6.16	19.50
Total[a]	7.60	14.96	22.91

Sources: Washington and Oregon—Briggs et al. 1992; northern California—Briggs et al. 1983; southern California—Briggs et al. 1981a.
[a] Includes additional species and birds not identified to species.

Throughout the CCS, seabird density is highest over the continental shelf, moderate over the slope, and lowest in the deep (>2000 m) offshore waters (Wahl 1984; Briggs et al. 1987, 1992; Wahl et al., this volume). Off California, for example, average density over the shelf is 18 times higher than that offshore (110 vs. 6 birds/km^2). Shelf densities are comparable to those reported for upwelling zones in other eastern boundary currents; offshore densities are similar to those reported for open ocean gyres. This trend holds during all seasons, but is least pronounced in midwinter. Off California, species diversity does not vary significantly among depth zones, but species richness does, averaging 1.5–2 times more species over the shelf (Briggs et al. 1987).

Several factors contribute to high seabird density and species richness in shelf waters. Undoubtedly because of their proximity to the mainland and nearshore islands, these waters are used by roosting and nesting birds. However, more importantly, primary production is greatest over the shelf. For example, off Washington phytoplankton biomass is 8–12 times higher in shelf waters than over the slope (Perry et al. 1989). Upwelling rarely affects waters deeper than 100 m; in deeper waters, benthic and suspended organic nutrients are below the level where they can be recycled into the photic zone. As a result of upwelling, secondary production and standing stocks of zooplankton, micronekton, and schooling fish are highest over the shelf. Additionally, the shelf has more physiographic heterogeneity, featuring variable bottom and shoreline topography, including promontories, islands, submarine banks and canyons, and variable benthic and coastal substrate. Tidal flux, river and estuarine outflow, and upwelling all contribute to hydrological heterogeneity and may serve as prey-concentrating mechanisms. The result is an abundance of seabird prey and a diversity of seabirds not found in the more homogeneous surface waters offshore.

Habitat homogeneity is maintained at much smaller scales in the east–west direction than in the north–south direction (Briggs et al. 1987, 1988a). Some seabird species (e.g., Common Murre, Cassin's Auklet, and the phalaropes) mirror this physical patterning, aggregating on relatively short (8–16 km) across-shelf scales.

4.3. Seasonal variation

Within the CCS as a whole, bird density at sea is highest during spring and fall migration and higher in summer than in winter (Briggs et al. 1987, 1992). Species richness is highest during migration and lowest in midsummer.

4.3.1. Summer

The summertime pattern of bird distribution at sea reflects that described previously for nesting colonies: that is, large numbers of birds in the central and northern regions of the CCS and relatively few in the south (Table 2). In this season, the CCS avifauna comprises primarily two major elements—the local breeders and visitors from nesting colonies in the southern and central Pacific. Visitors outnumber breeders at all latitudes, but the pattern is most pronounced from Point Conception to Cape Blanco, where the ratio is approximately 3:1.

Throughout the CCS during summer, shearwaters are the most abundant birds over the shelf and slope. The Sooty Shearwater is the dominant species at all latitudes. The Pink-footed Shearwater *Puffinus creatopus* is an order of magnitude less numerous than the Sooty Shearwater off California (Briggs et al. 1987), and even less abundant off Oregon and Washington, where the surface-feeding Buller's Shearwater *Puffinus bulleri* is more common (Briggs et al. 1992). Shearwater density off California increases in March and April and, during the June–July peak, the statewide population is estimated between 2.7 and 4.7 million birds. Shearwaters are transient and large flocks can appear anywhere, but average density is highest in the strong upwelling zone from Morro Bay to Cape Blanco. There, the birds often aggregate near or downstream from stable upwelling centres, especially those with thermohaline fronts at the seaward edge (Briggs et al. 1987). Off California, shearwaters eat primarily juvenile rockfish during the upwelling season (May–July), then switch to northern anchovies and squid (*Loligo* sp.) when upwelling decreases in August and September (Chu 1984).

Shearwaters are less abundant off Oregon and Washington in May and June, but their numbers increase in July–September, perhaps in response to seasonal concentrations of spawning anchovies in nearshore and estuarine waters (Richardson 1981; Wahl 1984; Briggs et al. 1992). The largest shearwater flocks occur off the Strait of Juan de Fuca, where tidal flux conspires with shelf-edge canyons and banks to create an important upwelling complex over the shelf (Freeland and Denman 1982). The relationship between shearwaters, summer-spawning anchovies, and the Columbia River plume is poorly understood but probably very important (Wahl et al., this volume). The plume provides vertical stability adjacent to the otherwise very hydrographically dynamic coastal zone in southern Oregon.

During summer off Oregon and Washington, the Northern Fulmar *Fulmarus glacialis* is second in abundance to the Sooty Shearwater (Table 2). Moderate fulmar density here (2.94 birds/km^2) reflects the proximity of a large nonbreeding population associated with Alaskan colonies. The hydrology and trophic structure of shelf-edge habitats off Washington are much more similar to those in southern Alaska than is the case farther south. Fulmars may also be attracted to this area to feed on offal generated by a large international trawl fishery, which is not present farther south. Black-footed Albatrosses *Diomedea nigripes* are also numerous here (0.61 birds/km^2); the location of trawlers appears to influence this species' distribution, but effects of the fishery on the size of the population in the region are unknown (Wahl and Heinemann 1979; Briggs et al. 1992).

For the most part, nesting species are found at sea adjacent to their colonies in numbers proportionate to colony size. An exception is the larger-than-expected number of Leach's and Fork-tailed storm-petrels off Oregon and Washington. Leach's Storm-Petrels, probably from the colonies near Cape Blanco, forage along the seaward side of the shelf break, while Fork-tailed Storm-Petrels, possibly from colonies in British Columbia, feed over the outer shelf (Wahl 1984; Briggs et al. 1992). Both species frequent the margins of the Columbia River plume. Also, large (10^3) feeding assemblages of Fork-tailed Storm-Petrels are seen at the margins of shelf-edge banks (e.g., La Pérouse and Swiftsure in British Columbia; Hecata–Stonewall in Oregon), where zooplankton and micronekton are known to accumulate.

Off central and northern California, breeders account for most of the population at sea, other than shearwaters (Table 2). Common Murres, Cassin's Auklets, Brandt's Cormorants, and Western Gulls exhibit average densities above 1.0 birds/km^2. The strategies by which different species exploit prey in the hydrographically dynamic upwelling zone are not well understood, but Briggs et al. (1988a) compared foraging and diet of two divers, the Common Murre and the Cassin's Auklet, nesting on the Farallon Islands. Prior to the establishment of persistent upwelling, murres ate euphausiids over the outer shelf in waters intermediate in character between recent upwellings and estuarine outflow; at the onset of upwelling, they switched to juvenile rockfish and, nearer shore, to schooling fishes (anchovies, smelt) associated with the murky waters of the estuarine outflow from San Francisco Bay. At the start of egg-laying (late March), Cassin's Auklets moved shoreward from offshore waters (where they ate mostly euphausiids) and formed dense aggregations over the continental slope. Once upwelling intensified, large numbers of birds fed on surface-swarming copepods *Thysanoessa spinifera* in the edges and cores of cold upwelling filaments of the outer shelf. Some auklets (possibly nonbreeders) captured juvenile rockfish over the shelf break, where moderately clear (optical depth 5–7 m), warm surface waters lay over a strong shallow (15–30 m) thermocline.

In the SCB, the at-sea distribution of breeding birds is determined primarily by colony location. Nesting birds (especially Cassin's Auklets and other divers) from the northern Channel Islands and San Nicolas Island and large numbers of shearwaters feed (mainly on euphausiids and juvenile rockfish) west of Point Conception, in outer Santa Barbara Channel, and along the Santa Rosa–Cortés Ridge. At these sites, cool upwelled water interacts with subtropical water forming strong surface thermal fronts (up to 0.5°C/km; Hunt et al. 1981; Briggs et al. 1988b). Among the storm-petrels, which often forage farther from their colonies than other species, Ashy Storm-Petrels frequent the edges of the major upwellings at Point Conception, Leach's Storm-Petrels inhabit clear offshore waters, and Black Storm-Petrels are most common near shore, in the southeast part of the bight (Briggs et al. 1981a).

Birds nesting on islands in the lower SCB feed in warmer surface waters primarily on the northern anchovy, the most abundant schooling fish (Hunt et al. 1981). Xantus' Murrelets, which eat larval anchovies and rockfish, forage 0.5–12.5 km west of Santa Barbara Island, the principal colony site. Nesting Brown Pelicans are almost entirely dependent on anchovies (Anderson and Anderson 1976). Anchovy population size and distribution in the SCB vary in response to large-scale oceanographic and weather patterns, but pelican nesting (timing and success) is controlled by anchovy abundance within about 20 km of the colonies during the five-month nesting season (Anderson et al. 1982). Pelicans usually begin to nest in March, but start as early as December when prey are available (Anderson and Gress 1983). For nesting adults, foraging is restricted to waters near the colonies at Anacapa Island, Islas Los Coronados, and Santa Barbara Island. Once immigration from Mexico begins (by June), pelicans forage within 40 km of shore throughout the SCB, but especially in Santa Monica Bay and eastern Santa Barbara Channel (Gress et al. 1980; Briggs et al. 1981b).

4.3.2. *Fall*

During late summer and fall, the oceanographic character of the CCS changes. Equatorward winds and upwelling are less intense and less persistent. The main surface flow weakens and moves offshore, often resolving into large eddies (100–300-km diameter), which transport clear, well-stratified oceanic waters onto the continental shelf (Reid et al. 1958; Bernstein et al. 1977; Hickey 1979; Broenkow 1982). The results are annual maxima in sea surface temperature, greater water clarity over the shelf, and deeper thermoclines, especially off central and northern California. Also, anchovies from the southern California stock migrate into the waters of the northern half of the state (Parrish et al. 1981).

During this season, birds that have nested in Mexico and southern California, including Brown Pelicans, Heermann's Gulls *Larus heermanni*, Xantus' Murrelets, and Black Storm-Petrels, achieve maximal northward dispersal. Brown Pelicans range north to British Columbia and are abundant over the shelf off central California through November (Briggs et al. 1983; Jaques et al. 1992). Large mixed flocks of storm-petrels (primarily Ashy and Black) form regularly over the submarine canyon in Monterey Bay (Stallcup 1976).

Migrants contribute to elevated density and species diversity during this season. Bonaparte's Gulls *Larus philadelphia* are abundant over the shelf during October and November, and Pomarine Jaegers *Stercorarius pomarinus* and Arctic Terns *Sterna paradisaea* are numerous over the slope (Briggs et al. 1987). After following the Fraser, Columbia, and other rivers to return to the coast from inland colonies (Wahl et al., this volume), California Gulls move south over the shelf in a broad front. The most abundant birds at sea off central and northern California during late summer and fall are the southward migrating phalaropes (Table 2). Mixed flocks of Red and Red-necked phalaropes are widespread in shelf waters, but only the Red Phalarope is numerous farther from shore (Briggs et al. 1987; Wahl et al., this volume). Density is highest over the outer shelf and slope, where flocks concentrate along the shoreward edges of surface convergences (Briggs et al. 1984). Here, as elsewhere at sea, phalaropes rely on convergences and other physical processes to concentrate zooplankton (especially euphausiids and *Calanus* copepods) near the surface (cf. Brown 1980; Haney 1985). In the CCS, optimal foraging conditions for phalaropes appear to occur downstream from active upwelling centres, where phytoplankton and zooplankton grazers have attained large populations.

Fall also marks the transition to the winter faunal regime. As the North Pacific storm track develops, shearwaters and other South Pacific nesters depart the region and southern CCS nesters withdraw to lower latitudes. Birds from inland and boreal nesting colonies arrive in the CCS and gradually disperse southwards through the season.

4.3.3. *Winter*

Average seabird density in the CCS is significantly lower in winter than in summer (Tables 2 and 3). The wintertime fauna consists primarily of visitors from northern and inland colonies, plus the local breeders. Populations of breeding species outnumber visiting populations off central and northern California. In contrast, visitors account for 85% of the birds in the SCB. Boreal nesting species, especially gulls and alcids, are most abundant at all latitudes, achieving their southernmost dispersal in this season. Shearwaters and albatrosses are scarce, and Brown Pelicans and other subtropical nesters are nearly restricted to the SCB. Conspicuous by their near absence are storm-petrels, which appear to move southwards or well offshore, possibly out to the zone of maximum southward flow.

Total bird density at sea is lowest in the north (7.6 birds/km^2), off Oregon and Washington, where breeders and visitors are present in about equal numbers. Here, alcids and boreal gulls are numerically predominant (Table 3). Rhinoceros Auklets, Herring *Larus argentatus* and Glaucous-winged gulls, and Black-legged Kittiwakes *Rissa tridactyla* are present in higher densities, relative to summer. The Common Murre is the most abundant alcid off Oregon and Washington, but average density at sea is lower than during breeding season; some murres from Oregon colonies are thought to winter on inland marine waters of Washington (Wahl et al. 1981). Numbers of Cassin's Auklets and Northern Fulmars are much reduced and puffins are absent, but a few Ancient Murrelets *Synthliboramphus antiquus* are present. Small numbers of Black-footed and Laysan *Diomedea immutabilis* albatrosses occur over the continental slope.

Most species that nest in colonies off Canada and Alaska pass quickly along the Oregon and Washington coast, en route to California where, presumably, prey availability or foraging conditions are better. Production off the coast of Oregon and Washington is much lower in winter than in summer (Perry et al. 1989). This results from several factors. There, southward transport of subarctic waters is reduced and centred far offshore, and the prevailing surface current over the shelf is the poleward-flowing Davidson Current. The tropical character of the water in this flow is confirmed by the predominance of copepods of southern affinity, species that are not present in other seasons. Prevailing winds also are poleward, contributing to coastal convergence or downwelling. Additionally, incident light in December is only half that in June, and cloud cover can reduce these winter values an additional 25% (Perry et al. 1989). Finally, the frequent storms break down frontal structure and deepen the mixed layer by 2–3 times, thereby inhibiting phytoplankton blooms. The result is low primary and secondary production, poor vertical and horizontal stratification (eliminating some physical concentrating mechanisms for bird prey), and frequently turbulent foraging conditions. In this season, bird densities off Oregon and Washington are often highest over the inner shelf and on bays and other inland marine waters (Wahl et al., this volume). The few ocean frontal boundaries found in the northern CCS in winter and spring are associated with the Columbia River plume off Washington or the tidal discharge from the Strait of Juan de Fuca (Briggs et al. 1992).

Moderately high average densities (15 birds/km^2) are found off central and northern California. Alcids predominate, especially murres and Cassin's and Rhinoceros auklets, which together comprise over 50% of the population at sea (Table 3).

Breeding species account for a larger percentage of the winter population off central and northern California than do visitors (Table 3), but this is somewhat misleading. Average densities of Cassin's and Rhinoceros auklets are higher in winter than in summer, due to immigration from northern colonies. This is also the case for murres, although in December (Table 3) populations in California have not yet been augmented by immigration. Some local nesters are relatively sedentary; for example, murres are most abundant within 50 km of colonies. Still, large concentrations of murres north of Point Arena are thought to be mainly immigrants. Murre densities are highest (averaging up to 35 birds/km^2) in the turbid waters of the continental shelf. In contrast, the two auklets are most numerous in deeper waters seaward of the shelf break.

Rhinoceros Auklets are distributed somewhat farther offshore than Cassin's Auklets, which often form dense aggregations over the continental slope (Briggs et al. 1987). Over the shelf, California, Herring, and Western gulls are numerous (Table 3). Large numbers of kittiwakes and some fulmars are present seaward of the shelf break. Phalaropes are present, but average density is much reduced from that seen in fall, and the birds are restricted to offshore waters.

In contrast with all other seasons, average bird density at sea in December peaks (more than 22 birds/km^2) in the SCB (Table 3), where productivity and prey stocks appear to be highest. The SCB is protected from most winter storms, permitting development of stratified (stable) surface waters. Midwater schooling fishes, especially anchovies, exploit this environment for spawning (Parrish et al. 1981). Newly hatched anchovy larvae are critically dependent on stable patches of phytoplankton. The combination of low vertical mixing and the influx from the south of equatorial water results in high phytoplankton production in the SCB in winter. As a result, anchovy standing stocks are higher in the SCB than elsewhere in the CCS, probably leading to enhanced feeding conditions for a variety of seabirds (Parrish et al. 1981; Hunt et al. 1981; Briggs et al. 1987).

The relatively large winter seabird population in the SCB is made up primarily of species visiting from northern and inland areas; breeders are much less numerous (Table 3). The most abundant species, the California Gull, accounts for up to 55% of the birds in the region (12.74 birds/km^2), and is ubiquitous over the shelf. Bonaparte's Gulls and local breeders such as Western Gulls, pelicans, and cormorants inhabit shallow waters along mainland and island shores. At the western edge of the SCB, the true continental margin, there are large numbers of visiting boreal species, especially Rhinoceros Auklets, fulmars, Herring Gulls, and kittiwakes. In other words, the coolest waters at the western edge of the SCB support a fauna characteristic of the Gulf of Alaska. This boreal fauna is present over the outer shelf and slope the length of the CCS to about Punta Eugenia.

4.4. Annual variation

Year-to-year variability in the abundance, distribution, and composition of bird populations at sea results primarily from ENSOs and other large-scale events. During the ENSO events of 1977–78 and 1982–83, Briggs et al. (1987) observed lower overall at-sea densities off California, higher relative percentages of warm-water species, and reduced numbers and southward dispersal by northern nesters. Annual variation in the number of birds off Washington in summer and fall also correlates with upwelling intensity (Wahl et al., this volume).

During periods of anomalous oceanographic conditions, seabirds often forage in unusual regions or habitats. For example, off California, Common Murres were 60% less numerous at sea in midwinter and they foraged unusually far from colonies during the 1982–83 ENSO (Briggs et al. 1987; Croll 1990). In Washington, southern visitors and resident species fed nearer shore during ENSO conditions, perhaps because detritus-based estuarine systems are less affected than upwelling systems (Wahl et al., this volume). Also, ENSOs may force birds to use alternative prey; for example, Fork-tailed Storm-Petrels have been seen eating crab larvae in the harbours of coastal Washington (Wahl et al., this volume). In Monterey Bay and the SCB, Western Gulls and other nearshore feeders ate pelagic red crabs (*Pleuroncodes* sp.), a tropical species, during fall 1982 (Stewart et al. 1984).

5. Conservation

At present, the primary threats to at-sea bird populations in the CCS are human fisheries, floating oil, and in a few places toxic chemicals. Breeding populations are vulnerable also to colony disturbance, the introduction of nonnative predators, and habitat loss.

Potential impacts of fisheries on seabirds include competition for prey species, incidental mortality, and changes in trophic systems. Off Washington and Oregon, the large international trawl fishery is of greatest concern. The fishery is known to influence the distribution of some seabird species; for example, California Gulls occur much farther offshore when accompanying fishing boats than they do in regions without boats (Wahl and Heinemann 1979). Although the fishery is a source of food (offal) for some species, the attraction of species from other regions might lead to increased competition for natural prey resources.

Off California, the nearshore gillnet fishery has been shown to cause considerable mortality of murres, shearwaters, and other divers (Heneman 1983; Takekawa et al. 1990). Recent legislation restricting gillnetting to deeper waters appears to have reduced the rate of mortality. In Washington, there is a gillnet fishery for salmon in inland marine waters and estuaries, which is also known to kill murres, grebes, and shearwaters (Wahl et al., this volume).

Cases where overfishing by humans has led to crashes in bird populations are well documented (e.g., Duffy et al. 1984). In the SCB, Brown Pelicans (and perhaps other species) are vulnerable to human depletion of the northern anchovy (Anderson et al. 1980; Gress and Anderson 1983). In U.S. waters, there is no longer a reduction fishery, but some anchovies are caught for bait for recreational fishing. The anchovy stock that feeds pelicans in southern California is fished by the Mexican fleet off Baja, which operates under very different regulations than those in effect in U.S. waters (Anderson and Gress 1984).

There has been only one significant oil spill (in 1969) from platforms off southern California, but transportation accidents have been common, especially off central California where barge and tanker spills have accounted for more than 40 bird mortalities since 1971 (Smail et al. 1972; Carter et al. 1990; Anderson et al. 1991). As yet, transportation accidents have been relatively infrequent in the Pacific Northwest although, following the recent "Nestucca" barge spill outside Grays Harbor, 13 000 oiled birds were recovered from beaches in Washington and British Columbia (Burger et al. 1989; Wahl et al., this volume).

Toxic chemicals have been implicated as a threat to seabirds in the SCB and elsewhere (Ohlendorf et al. 1990). In the late 1960s and early 1970s, dumping of DDT into coastal waters led to pesticide-induced eggshell thinning and nest failure of Brown Pelicans and Double-crested Cormorants at colonies in the SCB and northern Baja California (Keith et al. 1971; Gress et al. 1973). Reproduction at these colonies has improved considerably since 1980, but lingering, chronic toxicity may in part be preventing pelicans in the SCB from achieving the fledging rates seen at colonies in the Gulf of California (Gress et al. 1992). There continues to be concern about DDE and PCB residues being slowly released from sediments off Los Angeles. These compounds are known to contaminate some fish species and may still affect bird reproduction.

Some nesting colonies in the CCS have experienced population declines in recent years. In the most dramatic example, the number of Common Murres breeding on the Farallon Islands decreased by 47% during 1980–1986 (Takekawa et al. 1990). Mortality from gillnetting and oil contamination, compounded by prey shortage associated with an ENSO event, contributed to this decline (Carter et al. 1990). This case demonstrates that populations can decline significantly over short time periods when several damaging factors occur simultaneously.

Human disturbance of coastal colony islands is not currently a widespread problem in the CCS, except off Baja California (Anderson 1988). However, in the future, the risk of disturbance, development, and the introduction of exotic predators may well increase everywhere as human populations expand. In addition, threats to mainland shoreline habitat are of great concern. Logging of the old-growth forests may be contributing to population declines of Marbled Murrelets (Leschner and Speich 1989; Nelson 1991). Within the CCS, Marbled Murrelet nesting is restricted to old-growth forest within 50 km of the coast, habitat which is rapidly disappearing due to exploitation by the timber industry.

6. Conclusion

The processes which affect the day-to-day and hour-to-hour decisions of individual birds most likely operate on shorter scales than those we have dealt with here. Still, larger-scale distribution patterns reflect the summation of all the choices of all the individuals in the populations or communities as well as the overall suitability of habitats. Resolution of patterns at smaller scales will require much intensive, process-oriented work, whereas variability at large scales can only be appreciated with time series. Both are needed for the CCS as well as elsewhere. We urge that efforts be made to fill the remaining major gaps in the CCS picture; that is, the waters off Baja California and the outer waters of the current at all latitudes should be surveyed systematically. Other questions deserving attention include the following: What are the effects on seabird and prey populations of the Columbia River plume and tidal upwelling from the Strait of Juan de Fuca? What are the similarities and differences among the Cape Blanco, Point Arena/Point Reyes, Point Conception, and Punta Eugenia upwelling centres? Does thermocline depth influence the distribution or nesting success of divers in these upwelling zones? Finally, our challenge is to build on the general ecological information now available by examining the factors influencing habitat choices by individual birds and determining the costs and benefits of those choices.

7. Acknowledgements

We are indebted to the multitude of observers who gathered the data presented in this paper. We thank especially Roy Lowe and Harry Carter of the U.S. Fish and Wildlife Service and William Everett of the San Diego Natural History Museum for sharing with us their unpublished colony data. D.J. Rupiper and S.W. Turner kindly criticized our drafts. Much of the survey effort which generated the data used here was supported by the Minerals Management Service.

This is a contribution of the Institute of Marine Sciences, University of California, Santa Cruz, and Ecological Consulting, Inc.

Literature cited

Abrams, R.W.; Griffiths, A.M. 1981. Ecological structure of the pelagic seabird community in the Benguela Current region. Mar. Ecol. Ser. 5:269–277.

Ainley, D.G. 1976. The occurrence of seabirds in the coastal region of California. West. Birds 7:33–68.

Ainley, D.G.; Boekelheide, R.J. 1990. The Farallon Island seabird community: dynamics and structure in an upwelling-system community. Stanford Univ. Press, Stanford, CA. 450 pp.

Ainley, D.G.; Lewis, T.J. 1974. The history of Farallon Island marine bird populations, 1842–1972. Condor 76:432–446.

Ainley, D.G.; Carter, H.B.; Anderson, D.W.; Briggs, K.T.; Coulter, M.C.; Cruz, F.; Cruz, J.B.; Valle, C.A.; Fefer, S.I.; Hatch, S.A.; Schreiber, E.A.; Smith, N.G. 1988. ENSO effects on Pacific Ocean marine bird populations. Proc. Int. Ornithol. Congr. 19:1747–1758.

Anderson, D.W. 1988. Dose-response relationship between human disturbance and Brown Pelican breeding success. Wildl. Soc. Bull. 16:339–345.

Anderson, D.W.; Anderson, I.T. 1976. Distribution and status of Brown Pelicans in the California Current. Am. Birds 30:3–12.

Anderson, D.W.; Gress, F. 1983. Status of a northern population of California Brown Pelicans. Condor 85:79–88.

Anderson, D.W.; Gress, F. 1984. Brown Pelicans and the anchovy fishery off southern California. Pages 128–135 *in* Nettleship, D.N.; Sanger, G.A.; Springer, P.F. (eds.), Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Anderson, D.W.; Gress, F.; Mais, K.F.; Kelly, P.R. 1980. Brown Pelicans as anchovy stock indicators and their relationships to commercial fishing. Calif. Coop. Oceanic Fish. Invest. Rep. 21:54–61.

Anderson, D.W.; Gress, F.; Mais, K.F. 1982. Brown Pelicans: influence of food supply on reproduction. Oikos 39:23–31.

Anderson, D.W.; Fry, D.M.; Gress, F. 1991. Activity of California Brown Pelicans after exposure to oil and subsequent veterinary rehabilitation. Abstract in Program from Pacific Seabird Group Annual Meeting, Monterey, CA.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–71. NOAA Tech. Rep. NMFS SSRF-671. U.S. Dep. Commer., Seattle, WA.

Bakun, A.; Nelson, C.S. 1977. Climatology of upwelling related processes off Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 19:107–127.

Baltz, D.M.; Morejohn, G.V. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. Auk 94:526–543.

Bernal, P.A.; McGowan, J.A. 1981. Advection and upwelling in the California Current. Pages 381–399 *in* Richards, F.A. (ed.), Coastal upwelling. American Geophysical Union, Washington, DC.

Bernstein, R.L.; Breaker, L.; Whritner, R. 1977. California Current eddy formation: ship, air and satellite results. Science 195:353–359.

Bolin, R.L.; Abbott, D.P. 1963. Studies on the marine climate and phytoplankton of the central coastal area of California 1954–1960. Calif. Coop. Oceanic Fish. Invest. Rep. 9:23–45.

Briggs, K.T.; Chu, E.W. 1986. Sooty Shearwaters off California: distribution, abundance and habitat use. Condor 88:355–364.

Briggs, K.T.; Chu, E.W.; Lewis, D.B.; Tyler, W.B.; Pitman, R.L.; Hunt, G.L. Jr. 1981a. Distribution, numbers, and seasonal status of seabirds of the Southern California Bight. Pages 1–399 *in* Book 1, Part III. Investigators' Reports, Summary of Marine Mammal and Seabird Surveys of the Southern California Bight Area, 1975–1978. U.S. Natl. Tech. Inf. Serv. Publ. PB-81-248-205.

Briggs, K.T.; Tyler, W.B.; Lewis, D.B.; Hunt, G.L. Jr. 1981b. Brown Pelicans in Southern California: habitat use and environmental fluctuations. Condor 83:1–15.

Briggs, K.T.; Tyler, W.B.; Lewis, D.B.; Kelly, P.R.; Croll, D.A. 1983. Brown Pelicans in central and northern California. J. Field Ornithol. 54:353–373.

Briggs, K.T.; Dettman, K.F.; Tyler, W.B.; Lewis, D.B. 1984. Phalarope feeding in relation to autumn upwelling off California. Pages 51–62 *in* Nettleship, D.N.; Sanger, G.A.; Springer, P.F. (eds.), Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Briggs, K.T.; Tyler, W.B.; Lewis, D.B.; Carlson, D.R. 1987. Bird communities at sea off California: 1975 to 1983. Stud. Avian Bio. 11:1–74.

Briggs, K.T.; Ainley, D.G.; Adams, P.B.; Spear, L.B.; Ferris, L.A.; Smith, S.E. 1988a. Distribution and diet of Cassin's Auklet and Common Murre in relation to central California upwellings. Proc. Int. Ornithol. Congr. 19:983–990.

Briggs, K.T.; Ainley, D.G.; Carlson, D.R.; Lewis, D.B.; Tyler, W.B.; Spear, L.B.; Ferris, L.A. 1988b. Final report: California Seabird Ecology Study. Vol. I. Feeding ecology of California nesting seabirds. U.S. Minerals Management Service OCS Study H7-055, Pacific OCS office. Los Angeles, CA.

Briggs, K.T.; Varoujean, D.H.; Williams, W.W.; Ford, R.G.; Bonnell, M.L.; Casey, J.L. 1992. Seabirds of the Oregon and Washington OCS. 1989–1990. Pages 1–162 *in* Brueggeman, J. (ed.). Oregon and Washington marine mammal and seabird surveys. U.S. Minerals Management Service, Camarillo, CA.

Brinkhurst, R.O. 1987. Distribution and abundance of macrobenthic infauna from the continental shelf off southwestern Vancouver Island, British Columbia. Can. Tech. Hydrogr. Ocean Sci. 85.

Broenkow, W.W. 1982. A comparison between geostrophic and current meter observations in a California Current eddy. Deep-Sea Res. 29:1303.

Brown, R.G.B. 1979. Seabirds of the Senegal upwelling and adjacent waters. Ibis 121:283–292.

Brown, R.G.B. 1980. Seabirds as marine animals. Pages 1–39 *in* Burger, J.; Bolla, B.C.; Winn, H.E. (eds.), Behavior of marine animals. Vol. 4. Plenum Press, New York.

Burger, A.E. 1989. Effects of the "Nestucca" oil spill (January 1989) on seabirds along the southwest coast of Vancouver Island. Unpublished report Can. Wildl. Serv., Vancouver, B.C.

Carter, H.B.; Jaques, D.L.; Strong, C.S.; McChesney, G.J.; Parker, M.W. 1990. Seabird breeding population trends in northern and central California: 1979 to 1989. Pac. Seabird Group Bull. 17:15.

Carter, H.B.; McChesney, G.J.; Whitworth, D.L.; Lewis, D.B.; Jory, D.L. 1992. Breeding populations of seabirds in southern California. Abstract in Program from Pacific Seabird Group Annual Meeting, Charleston, OR.

Chelton, D.B. Jr. 1980. Low-frequency sea level variability along the west coast of North America. Ph.D. thesis, Scripps Institute of Oceanography, La Jolla, CA.

Chelton, D.B.; Bernal, P.A.; McGowan, T.R. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40:1095–1125.

Chu, E.W. 1984. Sooty Shearwaters off California: diet and energy gain. Pages 64–71 *in* Nettleship, D.N.; Sanger, G.A.; Springer, P.F. (eds.), Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Croll, D.A. 1990. Physical and biological determinants of the abundance, distribution and diet of the Common Murre in Monterey Bay, California. Stud. Avian Biol. 14:139–148.

Cushing, D.H. 1971. Upwelling and the production of fish. Adv. Mar. Biol. 9: 255–334.

Duffy, D.C.; Siegfried, W.R. 1987. Historical variations in food consumption by breeding birds of the Humboldt and Benguela upwelling regions. Pages 327–346 *in* Croxall, J.P. (ed.), Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge, U.K.

Duffy, D.C.; Hays, C.; Plenge, M.A. 1984. The conservation status of Peruvian seabirds. Int. Counc. Bird Preserv. Tech. Publ. 2:245–259.

Everett, W.T. 1988. Biology of the Black-vented Shearwater. West. Birds 19:89–104.

Favorite, F.; Dodimead, A.J.; Nasu, K. 1976. Oceanography of the subarctic Pacific region 1960–71. Int. North Pac. Fish. Comm. Bull. 33.

Flament, P.; Armi, L.; Washburn, L. 1985. The evolving structure of an upwelling filament. J. Geophys. Res. 90:1765–1778.

Freeland, H.J.; Denman, K.L. 1982. A topographically controlled upwelling center off southern Vancouver Island. J. Mar. Res. 4:1069–1093.

Graybill, M.R.; Hodder, J. 1985. Effects of the 1982–83 El Niño on reproduction of six species in Oregon. Pages 205–210 *in* Wooster, W.S.; Fluharty, D.L. (eds.), El Niño Norte. Washington Sea Grant Program, Univ. of Washington, Seattle.

Gress, F.; Anderson, D.W. 1983. A recovery plan for the California Brown Pelican. U.S. Fish and Wildlife Service, Portland, OR.

Gress, F.; Risebrough, R.W.; Anderson, D.W.; Kiff, L.F.; Jehl, J.R. 1973. Reproductive failures of Double-crested Cormorants in southern California and Baja California. Wilson Bull. 85:197–208.

Gress, F.; Kelly, P.R.; Lewis, D.B.; Anderson, D.W. 1980. Feeding activities and prey preference of Brown Pelicans breeding in the Southern California Bight. Annu. rep. to Calif. Dep. Fish and Game, Sacramento, CA.

Gress, F.; Anderson, D.W.; Jarman, W.M. 1992. Current status of organochlorine levels in Brown Pelicans breeding in the Southern California Bight. Abstract in Program of Pacific Seabird Group Annual Meeting, Charleston, OR.

Haney, J.C. 1985. Wintering phalaropes off the southeastern United States: application of remote sensing imagery to seabird habitat analysis at oceanic fronts. J. Field Ornithol. 56:321–333.

Haury, L.R.; McGowan, J.A.; Wiebe, P.H. 1978. Patterns and processes in the time and space scales of plankton distributions. Pages 277–327 *in* Steele, J.H. (ed.), Spatial pattern in plankton communities. Plenum, New York.

Heneman, B. 1983. Gill nets and seabirds 1983. Point Reyes Bird Obs. Newsl. 63:1–10.

Hickey, B.M. 1979. The California Current System – hypotheses and facts. Prog. Oceanogr. 8:191–284.

Hickey, B.M. 1989. Patterns and processes of circulation over the Washington continental shelf. Pages 41–115 *in* Landry, M.R.; Hickey, B.M. (eds.), Coastal oceanography of Oregon and Washington. Elsevier Series in Oceanography 47. Elsevier, New York.

Hodder, J.; Graybill, M.R. 1985. Reproduction and survival of seabirds in Oregon during the 1982–83 El Niño. Condor 87:535–541.

Hunt, G.L., Jr.; Schneider, D. 1987. Scale-dependent processes in the physical and biological environment of marine birds. Pages 7–41 *in* Croxall, J.P. (ed.), Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge, U.K.

Hunt, G.L., Jr.; Pitman, R.L.; Naughton, M.; Winnett, K.; Newman, A.; Kelly, P.R.; Briggs, K.T. 1981. Distribution, status, reproductive ecology, and foraging habits of breeding seabirds and seasonal status of seabirds of the Southern California Bight. Pages 1–399 *in* Book 2, Part III. Investigators' Reports. Summary of marine mammal and seabird surveys of the Southern California Bight area, 1975–1978. U.S. Natl. Tech. Inf. Serv. Publ. PB-81-148-205.

Huyer, A. 1983. Coastal upwelling in the California Current System. Prog. Oceanogr. 12:259–284.

Jaques, D.L.; Anderson, D.W.; Lowe, R.W. 1992. Northward range extension in California Brown Pelicans. Abstract in Program for Pacific Seabird Group Annual Meeting, Charleston, OR.

Keith, J.O.; Woods, L.A.; Hunt, E.G. 1971. Reproductive failure in Brown Pelicans on the Pacific coast. Trans. North Am. Wildl. Nat. Resour. Conf. 35:56–63.

Landry, M.R.; Hickey, B.M. 1989. Coastal oceanography of Oregon and Washington. Elsevier Series in Oceanography 47. Elsevier, New York.

Landry, M.R.; Lorenzen, C.J. 1989. Abundance, distribution and grazing impact of zooplankton on the Washington shelf. Pages 175–210 *in* Landry, M.R.; Hickey, B.M. (eds.), Coastal oceanography of Oregon and Washington. Elsevier Series in Oceanography 47. Elsevier, New York.

Landry, M.R.; Postel, J.R.; Peterson, W.K.; Newman, J. 1989. Broad-scale distributional patterns of hydrographic variables on the Washington–Oregon shelf. Pages 1–40 *in* Landry, M.R.; Hickey, B.M. (eds.), Coastal oceanography of Oregon and Washington. Elsevier Series in Oceanography 47. Elsevier, New York.

Leschner, L.; Speich, S. 1989. Report from the Marbled Murrelet Technical Committee. Pac. Seabird Group Bull. 16:55–58.

Manuwal, D.A.; Campbell, R.W. 1979. Status and distribution of breeding seabirds of southeastern Alaska, British Columbia, and Washington. Pages 73–92 *in* Bartonek, J.C.; Nettleship, D.N. (eds.), Conservation of marine birds of northern North America. U.S. Fish Wildl. Serv. Wildl. Res. Rep. 11.

McLain, D.R. 1983. Coastal warming in the northeast Pacific. Pages 61–86 *in* Pearcy, W.G. (ed.), The influence of ocean conditions on the production of salmonids in the north Pacific, a workshop. Sea Grant Col. Prog. Rep. ORESU-W-83-001. Oregon State Univ., Newport.

Mooers, C.N.K.; Robinson, A.R. 1984. Turbulent jets and eddies in the California Current and inferred cross-shore transports. Science 223:51–53.

Morgan, K.H.; Vermeer, K.; McKelvey, R.W. 1991. Atlas of pelagic birds of western Canada. Can. Wildl. Serv. Occas. Pap. No. 72, Ottawa.

Nelson, K. 1991. Report from the Marbled Murrelet Technical Committee. Pac. Seabird Group Bull. 18:14–21.

Ohlendorf, H.M. 1990. Marine birds and toxic chemicals in the temperate North Pacific. Pac. Seabird Group Bull. 17:29–30.

Owen, R.S. 1980. Eddies of the California Current system: physical and ecological characteristics. Pages 237–263 *in* Power, D. (ed.), The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Parrish, R.H.; Nelson, C.S.; Bakun, A. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

Perry, M.J.; Bolger, J.; English, D.C. 1989. Primary production in Washington coastal waters. Pages 117–139 *in* Landry, M.R.; Hickey, B.M. (eds.), Coastal oceanography of Oregon and Washington. Elsevier Series in Oceanography 47. Elsevier, New York.

Reid, J.L., Jr.; Roden, G.I.; Wyllie, J.G. 1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest. Prog. Rep. 5:27–57.

Richardson, S.L. 1981. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull. 78:855–876.

Schneider, D.C.; Duffy, D.C. 1985. Scale-dependent variability in seabird abundance. Mar. Ecol. Prog. Ser. 25:211–218.

Simpson, J.J.; Dickey, T.D.; Koblinsky, C.J. 1984. An offshore eddy in the California Current. Part I: Interior dynamics. Prog. Oceanogr. 13:5–49.

Smail, J.; Ainley, D.G.; Strong, H. 1972. Notes on birds killed in the 1971 San Francisco oil spill. Calif. Birds 3:25–32.

Smith, P.E.; Eppley, R.W. 1982. Primary production and the anchovy population in the Southern California Bight: comparison of time-series. Limnol. Oceanogr. 27:1–17.

Sowls, A.L.; Hatch, S.A.; Lensink, C.J. 1978. Catalog of Alaskan seabird colonies. U.S. Fish Wildl. Serv. FWS/OBS-78/79.

Sowls, A.L.; DeGange, A.R.; Nelson, J.W.; Lester, G.S. 1980. Catalog of California seabird colonies. U.S. Fish Wildl. Serv. FWS/OBS-80/37.

Speich, S.M.; Wahl, T.R. 1989. Catalog of Washington seabird colonies. U.S. Fish Wildl. Serv. Biol. Rep. 88:1–510.

Stallcup, R.W. 1976. Pelagic birds of Monterey Bay, California. West. Birds 7:113–136.

Stewart, B.S.; Yokum, P.K.; Schreiber, R.W. 1984. Pelagic red crabs as food for gulls: a possible benefit of El Niño. Condor 86:341–342.

Stommel, H. 1963. Varieties of oceanographic experience. Science 139:572–576.

Takekawa, J.E.; Carter, H.R.; Harvey, T. 1990. Decline of the Common Murre in central California, 1980–1986. Stud. Avian Biol. 14:149–163.

Varoujean, D.H.; Pitman, R.L. 1980. Oregon seabird colony survey, 1979. Unpublished report. U.S. Fish and Wildlife Service, Portland District Office OBS.

Wahl, T.R. 1984. Distribution and abundance of seabirds over the continental shelf off Washington. Washington Department of Ecology, Olympia.

Wahl, T.R.; Heinemann, D. 1979. Seabirds and fishing vessels: co-occurrence and attraction. Condor 81:390–396.

Wahl, T.R.; Speich, S.M.; Manuwal, D.A.; Hirsch, K.V.; Miller, C.S. 1981. Marine bird populations of the Strait of Juan de Fuca, Strait of Georgia and adjacent waters in 1978 and 1979. U.S. Dep. Commer. Interagency Energy/Environment R&D Prog. Rep. EPA-600/7-81-156.

Warheit, K.I. 1990. Evolutionary history of seabirds of the temperate North Pacific. Pac. Seabird Group Bull. 17:41.