THE SEABIRD COMMUNITY OF THE PERU CURRENT, 1980–1995, WITH COMPARISONS TO OTHER EASTERN BOUNDARY CURRENTS

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SUMMARY

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We present details on the occurrence of 93 species of seabirds in the Peru Current System (PCS) during 1980–1995, including 11 species not noted previously in these waters. Data were gathered on 14 cruises occurring in both the autumn/winter and spring/summer. The avifauna is described in terms of endemic, resident and migrant species, including those originating (breeding) from both the southern and northern hemispheres. We also delineate species composition over waters of the shelf, slope and pelagic habitats, and relate occurrence patterns to various oceanographic and temporal variables. Although ocean food webs are rapidly changing because of the extractions of upper trophic levels by industrial fishing, thus making comparisons using historical data difficult, we do attempt comparisons of avifaunal composition with the other eastern boundary currents. Species structure between the PCS and the California Current is far more similar than that between the PCS and the Atlantic eastern boundary currents. The latter currents lack major contributions from storm-petrels, gulls and diving species other than pelecaniforms. We comment on the immense effect that the Sooty Shearwater *Puffinus griseus* likely has had on the structuring of seabird communities, especially those of eastern boundary currents, ocean-wide.

Key words: Benguela Current, California Current, Canary Current, community structure, ecosystem change, fish depletion, Peru Current, seabirds

INTRODUCTION

The Peru Current System (PCS), the most productive marine system in the world (Paulik 1981), hosts a diverse fauna, including one third of the world's species of seabirds (see Harrison 1983). Well-known in general terms are its seabird species composition, relative abundance and feeding behavior (Murphy 1925, 1936, 1981; Szijj 1967; Jehl 1973; Brown *et al.* 1975; Duffy 1983, 1989; Pitman 1986). During the 1960s and 1970s, its immense stocks of Anchoveta *Engraulis ringens,* the mainstay of its upper food web over prior millennia, collapsed because of overfishing and environmental stress (Murphy 1981, Pauly *et al.* 2005), leading the fishing industry to turn to other species (Pauly *et al.* 1998). As a result, breeding populations of seabirds, or at least of the guano birds, also collapsed (Duffy *et al.* 1984). Therefore, it is highly likely that the community structure of the PCS avifauna has become much altered from what it was during the earlier portion of the 20th century, when most of the foregoing work was conducted.

During 14 cruises in summer and winter 1980–1995, we collected information on the occurrence and habitat affinities of seabirds in the PCS, confining our study to the ocean lying within 370 km (200 M) of Peru and Chile. Herein, we provide abundance estimates (birds per 100 km^2) for the 93 species we encountered, documenting several species new to the region, and we describe abundance of all species in relation to season, latitude and habitat affinities as defined by ocean depth (shelf, slope and pelagic waters) and other factors. We then make comparisons with the California Current and its avifauna, which has been well studied (Ainley 1976, Wiens & Scott 1976, Briggs *et al.* 1987, Tyler *et al.* 1993, Hoefer 2000, Hyrenback & Veit 2003, Ainley *et al.* 2005, Ford *et al.* 2004), and also to the less-well-studied Benguela and Canary current avifaunas. The California Current is the Northern Hemisphere analog of the PCS, both currents being Pacific Ocean eastern boundary currents affected strongly by coastal upwelling. As well, both are lacking in coastal islands on which seabirds can breed, thus perhaps giving a numerical advantage to visiting species. The Benguela Current is the Atlantic analog of the PCS, both currents being in the Southern Hemisphere. Therefore, the Benguela and PCS avifaunas would be expected to be much more similar to one another than to the California Current, owing to adjacency of the PCS and the Benguela Current to the large and diverse sub-Antarctic avifauna. That hypothesis is the one that we are considering here.

METHODS

Study area

The study area included waters lying within 370 km of the coast of South America between 3°S and 50°S (Fig. 1). This area, owing to little survey effort, does not include the outermost portion of the PCS—that is, the portion lying west of the arbitrary cutoff of 370 km (200 M; see details, next paragraph).

The PCS begins where South Pacific Temperate Waters, flowing east along the Subantarctic Front, meet the Chilean coast between 40°S and 50°S. The flow thereafter is northward to 4°S, where waters turn northwestward toward the Galapagos Islands (Murphy 1936, Wyrtki 1967; Fig. 1). The western boundary of the PCS is not well defined, but generally consists of waters with surface salinity <35.0 ppt south of 15°S, and salinities <35.3 ppt in waters north of 15°S. Based on this information and the oceanographic data that we collected, the PCS usually extended 300–600 km offshore north of 15°S, and 150–400 km offshore south of 15°S (see also Paulik 1981). Thus, our cutoff appreciably sampled the available oceanographically-defined habitat.

The PCS "consists off several more or less independent branches" (Wyrtki 1967, Thompson 1981). It is well developed at 35°S, with formation of a strong seasonal thermocline, but at about 25°S, the PCS splits into the (inshore, shelf) Peru Coastal Current and the (offshore, pelagic) Peru Oceanic Current (or Humboldt Current). Between them, the Peru Countercurrent flows southward near to the surface and outward of the shelf break. Coastal upwelling between 35°S and 15°S is supplied by water from lower layers of the Peru Coastal Current, and Equatorial Subsurface Water, which is carried south by the Peru Countercurrent, supplies most of the upwelled water between 15°S and 5°S. Maximum upwelling in the PCS, regardless of source water, occurs during winter and may not vary appreciably with latitude (Thompson 1981), although Chilean waters are separated from Peruvian waters by a warm-water belt at 20°S (Murphy 1936, Paulik 1981).

El Niño, which definitely affects seabird occurrence patterns in the PCS (e.g. Murphy 1925, 1981), occurred in 1986/87 and 1991/92. However, variation in our annual survey effort was not sufficiently consistent from a spatial standpoint to permit us to include an assessment of El Niño effects on the seabird patterns that we observed.

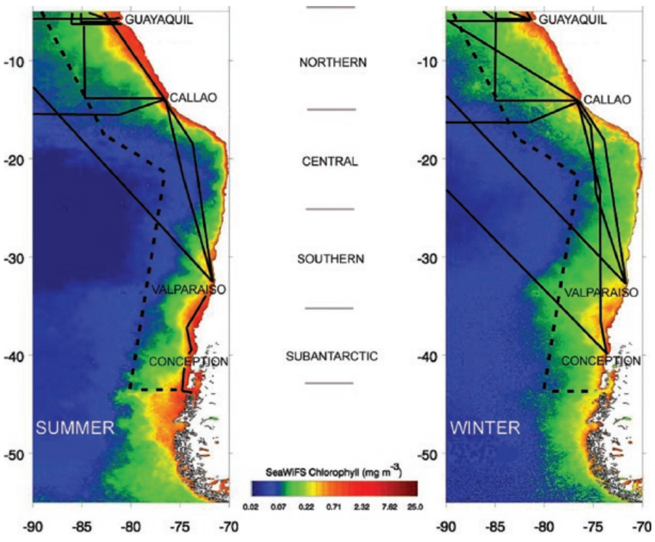

Fig. 1. Study area (dotted line indicates outer boundary), showing cruise tracks during spring/summer and fall/winter and the latitudinal partitions used for analyzing data. Tracks are shown against average chlorophyll concentrations averaged for the two seasonal periods, 1997–2002 (adapted from Montecino *et al.* 2006, compliments T. Strub). The continental shelf is roughly the same as the brightest red zone in the summer panel.

Surveys and monitoring of environmental variables

Our data were collected during 14 cruises, 1980–95 (one cruise in 1980, the remainder in 1985–1995). Surveys were conducted during spring/summer (November to January, hereafter "summer") and autumn/winter (March to August, hereafter "winter").

During daylight, whenever the ship was underway, we conducted strip surveys from the flying bridge (9–15 m above sea level), and counted all seabirds passing within a 300–600 m strip (depending on the platform height of the vessel) of the forequarter offering the best observation conditions. Strip width was calibrated after Heinemann (1981). Two observers watched simultaneously during 90% of the surveys; one or three observers watched during the remainder (see Spear *et al.* 2004). Alternating between observers, one or the other nearly constantly scanned the outer portion of the transect area with handheld binoculars for birds, especially small ones, missed with the unaided eye.

Although our surveys were continuous during daylight, we divided our effort into "transects" of 15-minute or 30-minute intervals depending on whether the vessel was transiting deeper offshore waters where attributes did not change rapidly (30 minutes = 820 transects), or waters over the shelf and slope where attributes did change quickly (15 minutes = 434 transects). Longer survey intervals in offshore waters, where birds were much less abundant, also reduced the number of segments in which zero birds were seen. At the beginning of each transect, we recorded the ship's position, speed and course. We calculated surface area of the ocean surveyed (square kilometers) as the transect period multiplied by ship speed times the width of the survey strip. We conducted 1254 survey transects for 533.8 hours, and surveyed 6563.4 km^2 of ocean, 2661.2 km^2 in summer and 3902.2 km^2 in winter (Table 1).

For each sighting, we noted behavior: resting on the water, feeding (including scavenging) or circling over a potential food source, or flying in a steady direction. For the latter behavior, we noted flight direction to the nearest 10 degrees. This information was used to correct density estimates for flux.

Data also recorded for each transect were ocean depth (meters), sea-surface temperature (degrees Celsius) and salinity (parts per thousand), thermocline depth (meters) and "strength," wind and wave direction (nearest 10 degrees), wind speed (kilometers per hour),

TABLE 1
Survey effort (ocean surveyed), by sector,[a] depth zone and season

Sector	Shelf (km^2)	Slope (km^2)	Pelagic (km^2)	Total (km^2)
Northern				
Summer	563.8 (133)	504.5 (111)	617.5 (88)	1685.8 (332)
Winter	632.2 (134)	528.2 (102)	944.3 (153)	2104.7 (389)
Central				
Summer	138.2 (23)	89.3 (16)	361.5 (59)	589.0 (98)
Winter	66.4 (16)	178.3 (37)	794.9 (144)	1039.6 (197)
Southern				
Summer	109.1 (23)	226.8 (44)	41.4 (9)	377.3 (76)
Winter	222.2 (39)	387.2 (75)	166.6 (38)	767.0 (162)
Total	1609.3 (358)	1905.3 (385)	3048.8 (511)	6563.4 (1254)

[a] Defined in Methods; Analyses.

wave height (nearest 0.3 m), and cloud cover (in eight subdivisions called "oktas"). Thermocline depth and strength were monitored every four to six hours using expendable bathythermographs (XBTs). Thermocline depth refers to the point at which the warm surface layer meets cooler water below, and temperature begins to decrease sharply. When the XBT trace lacked an inflection point, thermocline depth was recorded as 0 m (there being no thermocline). If the XBT profiles showed more than one inflection, we defined the thermocline as beginning at the depth of the strongest inflection. We measured thermocline slope as the temperature difference (nearest 0.1°C) between the thermocline boundary to a point 20 m below. A region with strong upwelling had a shallow, weak thermocline, and the reverse was true where little upwelling or mixing occurred.

Analyses

To assess seabird distributions relative to oceanographic factors, we divided the PCS into four sectors of roughly equal latitude (Fig. 1):

- the "North Sector," 3–15°S;
- the "Central sector," 15–25°S;
- the "South sector," 25–35°S; and
- the sub-Antarctic "Convergence sector" lying between 35°S and 42°30′S.

In some analyses, we combined the South and Convergence sectors. We also divided each of the sectors into three zones by ocean depth: the continental shelf, depth less than 201 m; continental slope or shelf break, 201–2000 m; and pelagic waters, more than 2000 m or more than 75 km offshore. All four latitudinal sectors were composed primarily of pelagic waters; owing to the very narrow continental shelf (only a few kilometers wide), neritic habitat was crossed only when arriving or departing ports at Guayaquil, Callao, Valparaiso and Conception. The Convergence sector and the North sector had more neritic and continental slope waters than did the other sectors (Fig. 1). Our survey effort in the three depth zones was 1819 km^2, 2055 km^2, and 2870 km^2 respectively (see Table 1 for effort by sector and season). In the Central sector, our survey effort did not cover the shelf habitat as much as it did in the others (Fig. 1).

Before estimating seabird densities, we adjusted observed (raw) numbers of birds flying in a steady direction for the effect of flight speed and direction of birds relative to ship speed and course (Spear *et al.* 1992, 2004; flight speeds from Spear and Ainley 1997; Appendix 1). Without these adjustments, densities from at-sea survey data are usually overestimated, particularly for fast-flying species. The adjustments also were required because any patterns in bird and ship direction will bias analyses. For example, if birds flew east and west at the same speed and in equal numbers, unadjusted counts from a ship transiting west would show greater numbers flying east because the observer would count more that were flying east than were flying west. Hereafter, all reports on abundances pertain to the adjusted counts ± 1 standard error.

We calculated densities for each transect by dividing the adjusted count by the number of square kilometers surveyed, and unless noted otherwise, we report densities as birds per 100 km^2 of ocean surface (where 100 km^2 is 100 blocks of 1 km^2). All birds reported are those that were seen within the survey strip (see Appendixes 2, 3). This procedure equilibrated unequal survey effort among the habitat zones. We used body mass values in Dunning (1993) and from our own studies (e.g. Spear *et al.* 2007) to estimate biomass.

We used the Stata software package (Release 3.1, 6th edition of the reference manual: StataCorp LP, College Station, TX, USA) to perform multiple regression analyses testing for relationships between bird densities (the dependent variable) and variables including season and year, and the environmental variables mentioned earlier (except for wind direction). Each independent variable was analyzed as continuous. The sample unit was one survey transect weighted for the area surveyed. Dependent variables were log-transformed to satisfy assumptions of normality (skewness/kurtosis test for normality of residuals, $P > 0.05$). Because densities included values of zero, transformations were calculated as the log (density + 1). Experimentation with various modifications [e.g. log (density + 0.5)] showed no appreciable effect of choice of modifications on *P* values. Normality was not achieved for all analyses performed, but least-squares regression analyses (ANOVA) are very robust with respect to non-normality (Seber 1977, ch. 6; Kleinbaum *et al.* 1988). Although regression analyses yield the best linear unbiased estimator relating density to independent variables, even in the absence of normally-distributed residuals, we regarded *P* values at the lower levels of significance with caution (Seber 1977, ch. 3). Therefore, to reduce the chances of type I error in ANOVAs in which normality was not achieved, we assumed significance at $P \leq 0.02$. Second- and third-order polynomials were tested for independent variables. We also used one-way ANOVAs, followed by Sidak multiple-comparison tests [an improved Bonferroni test (SAS Institute, Cary, NC, USA, 1985)], to statistically compare each habitat variable between taxa and between avifaunas.

We used principal component analysis (PCA), performed on the important habitat variables identified in the regression analyses, to delineate habitat differences between predominant species. The sample unit was each transect on which a predominant species was recorded. Thus, transects in which two or more predominant species were recorded were included in the data set more than once—that is, once for each species, together with the densities for these respective species. The PCAs were weighted by the values of log-transformed density to control for differences in the number of individuals recorded per sighting.

For each PCA, the means ± 1 standard deviation for the first and second axes were plotted, by species, to examine overlap in habitat affinities. Only the first two principal components were used, because those components explained more than 60% of the variance. We hypothesized that each important environmental factor would be expressed uniquely for a given species and that more ecologically specialized species would diverge the most (see Spear & Ainley 2007).

RESULTS

Species recorded and species abundance

We recorded 93 species of seabirds (Appendix 1). The total was composed of 18 endemics (species that breed only in the study area, 20%), 10 residents (breed in the study area and elsewhere, 11%), 41 southern hemisphere migrants (breed outside of the study area, 45%), 18 northern hemisphere migrants (18%), and 6 migrants (7%) that breed in both hemispheres. In sum, 28 species (30%) bred in the study area and 65 (70%) did not.

We classified 24 and 25 species as "regular" (density of more than five birds per 100 km^2) during summer and winter respectively (Table 2). During summer surveys, the regular species comprised 12

TABLE 2
Seabirds seen regularly in the Peru Current (species having a density[a] of five or more birds per 100 km^2) with respect to season and ordered by abundance, all sectors and habitats combined[b]

	Summer		**Winter**		**Average**	
1	Sooty Shearwater *Puffinus griseus*	209.6	Sooty Shearwater *P. griseus*	232.0	Sooty Shearwater *P. griseus*	220.8
2	Peruvian Booby *Sula variegata*	94.2	Wedge-rumped Storm-Petrel *Oceanodroma tethys*	187.7	Peruvian Booby *S. variegata*	103.1
3	Franklin's Gull *Larus pipixcan*	74.6	Peruvian Booby *S. variegata*	111.9	White-chinned Petrel *Procellaria aequinoctialis*	43.3
4	Blue-footed Booby *S. nebouxii*	38.0	Narrow-billed Prion *Pachyptila belcheri*	61.1	Wedge-rumped Storm-Petrel *O. tethys*	40.2
5	White-chinned Petrel *Pro. aequinoctialis*	30.7	Black-browed Mollymawk *Thalassarche melanophris*	57.7	Wilson's Storm-Petrel *Oceanites oceanicus*	39.3
6	Wilson's Storm-Petrel *Oceanites oceanicus*	24.0	White-chinned Petrel *P. aequinoctialis*	55.8	Black-browed Mollymawk *T. melanophris*	38.1
7	Juan Fernandez Petrel *Pterodroma externa*	22.6	Wilson's Storm-Petrel *Oceanites oceanicus*	54.9	Franklin's Gull *L. pipixcan*	37.7
8	Elliot's Storm-Petrel *Oceanites gracilis*	21.6	Peruvian Pelican *Pelecanus thagus*	50.5	Peruvian Pelican *Pele. thagus*	36.4
9	Peruvian Pelican *Pele. thagus*	20.7	Elliot's Storm-Petrel *Oceanites gracilis*	46.1	Elliot's Storm-Petrel *Oceanites gracilis*	33.7
10	Red Phalarope *Phalaropus fulicarius*	20.5	Cape Petrel *Daption capense*	30.2	Blue-footed Booby *S. nebouxii*	31.2
11	Black-browed Mollymawk *T. melanophris*	18.5	Black Tern *Childonia niger*	26.5	Narrow-billed Prion *Pac. belcheri*	30.5
12	Wedge-rumped Storm-Petrel *O. tethys*	17.8	Blue-footed Booby *S. nebouxii*	24.4	Juan Fernandez Petrel *Pt. externa*	18.7
13	Hornby's Storm-Petrel *O. hornbyi*	16.3	Southern Fulmar *Fulmarus glacialoides*	21.9	Pink-footed Shearwater *P. creatopus*	16.3
14	Pink-footed Shearwater *P. creatopus*	14.4	Kelp Gull *L. dominicanus*	18.7	Cape Petrel *D. capense*	15.2
15	Inca Tern *Larosterna inca*	11.5	Pink-footed Shearwater *P. creatopus*	17.0	Hornby's Storm-Petrel *O. hornbyi*	14.7
16	Laughing Gull *L. atricilla*	8.2	Juan Fernandez Petrel *Pt. externa*	14.8	Black Tern *C. niger*	14.2
17	King Cormorant *Phalacrocorax atriceps*	7.6	Markham's Storm-Petrel *O. markhami*	13.5	Red Phalarope *Phalaropus fulicarius*	12.9
18	Guanay Cormorant *Phalacrocorax bougainvillii*	7.4	Buller's Shearwater *P. bulleri*	13.2	Kelp Gull *L. dominicanus*	11.6
19	de Fillippe's Petrel *Pt. defilippiana*	7.4	Hornby's Storm-Petrel *O. hornbyi*	13.1	Southern Fulmar *F. glacialoides*	10.9
20	Sabine's Gull *Xema sabini*	6.7	Salvin's Mollymawk *T. salvini*	12.3	Markham's Storm-Petrel *O. markhami*	9.6
21	Pomarine Jaeger *Stercorarius pomarinus*	6.5	Stejneger's Petrel *Pt. longirostris*	9.8	Salvin's Mollymawk *T. salvini*	8.5
22	Markham's Storm-Petrel *O. markhami*	5.4	Sabine's Gull *X. sabini*	8.5	Buller's Shearwater *P. bulleri*	7.8
23	Red-necked Phalarope *Ph. lobatus*	5.3	de Fillippe's Petrel *Pt. defilippiana*	7.4	Sabine's Gull *X. sabini*	7.6
24	Stejneger's Petrel *Pt. longirostris*	5.1	Black Storm-Petrel *O. melania*	7.0	de Fillippe's Petrel *Pt. defilippiana*	7.4
25			Waved Albatross *Phoebastria irrorata*	6.1	Stejneger's Petrel *Pt. longirostris*	7.4
26					Inca Tern *L. inca*	6.0
27					Waved Albatross *Phoebastria irrorata*	5.2

[a] Calculated as averages among north, central, and southern sectors and weighted by the inverse of survey effort in each depth-defined habitat zone.

[b] See Appendix 2 for separation by habitat, and Appendix 3 for separation by sector.

Procellariiformes, five Pelecaniformes, and seven Charadriiformes, compared with 19 Procellariiformes, three Pelecaniformes, and three Charadriiformes during winter surveys. Although the number of Procellariiformes tended to increase during winter, and numbers of Pelecaniformes and Charadriiformes tended to decrease, the difference was not significant (G = 3.73, df = 2, *P* = 0.15). For summer, the regularly observed species included seven endemics, five residents and seven northern and six southern migrants; for winter, the numbers were five endemic, six resident and three northern and 11 southern migrant species. Species status ratios did not differ significantly between seasons (G = 2.91, df = 3, *P* = 0.4). The tendency for more species of northern migrants to be present during summer than winter, and vice-versa for southern migrants, also was insignificant (endemics and residents excluded: G = 2.36, df = 1, *P* = 0.12).

Of the 10 most abundant species, six were recorded on both summer and winter lists (Table 2; Figs. 2–5). In order of relative abundance (densities averaged between seasons), these were Sooty Shearwater *Puffinus griseus,* Peruvian Booby *Sula variegata,* White-chinned Petrel *Procellaria aequinoctialis,* Wilson's Storm-Petrel *Oceanites oceanicus,* Peruvian Pelican *Pelecanus thagus,* and Elliot's Storm-Petrel *Oceanites gracilis.* During summer, the species added to the 10 most abundant were, in order of abundance, Franklin's Gull *Larus pipixcan,* Blue-footed Booby *S. nebouxii,* Juan Fernandez Petrel *Pterodroma externa,* and Red Phalarope *Phalaropus fulicarius*; during winter, the four additional species were Wedge-rumped Storm-Petrel *Oceanodroma tethys,* Narrow-billed Prion *Pachyptila belcheri,* Black-browed Mollymawk *Thalassarche melanophris,* and Cape Petrel *Daption capensis.* To this list of 14 species we added the Pink-footed Shearwater *Puffinus creatopus* (the 15th most abundant species); we consider these 15 to be "predominant." These 15 predominant species—comprising one albatross, six petrels, three storm-petrels, two boobies, one pelican, one phalarope and one larid, and reflecting three endemics, five residents, two migrants from the northern hemisphere and five migrants from the southern hemisphere (Table 2)—were then considered in analyses of species' relationships to environmental variables.

Species previously undocumented in the Peru Current

We recorded 11 species that, at the time of our surveys, were unconfirmed or had not previously been reported from Peruvian or Chilean waters: Chatham Island Mollymawk *T. eremita*; Christmas *P. nativitatis,* Greater *P. gravis* and Manx *P. puffinus* shearwaters; Westland *Procel. westlandica,* Parkinson's *Procel. parkinsoni,* White-headed *Pt. lessonii,* Blue *Halobaena caerulea,* Herald *Pt. heraldica* and Kerguelen *Pt. brevirostris* petrels; and Sandwich Tern *Sterna sandvicensis.* Lack of reports of Westland and Parkinson's petrels may have been a result of confusion with White-chinned Petrels, although the bills of the former have a black nail, compared with the yellowish-green nail of the White-chinned Petrel. Westland and Parkinson's petrels are, to our knowledge, indistinguishable

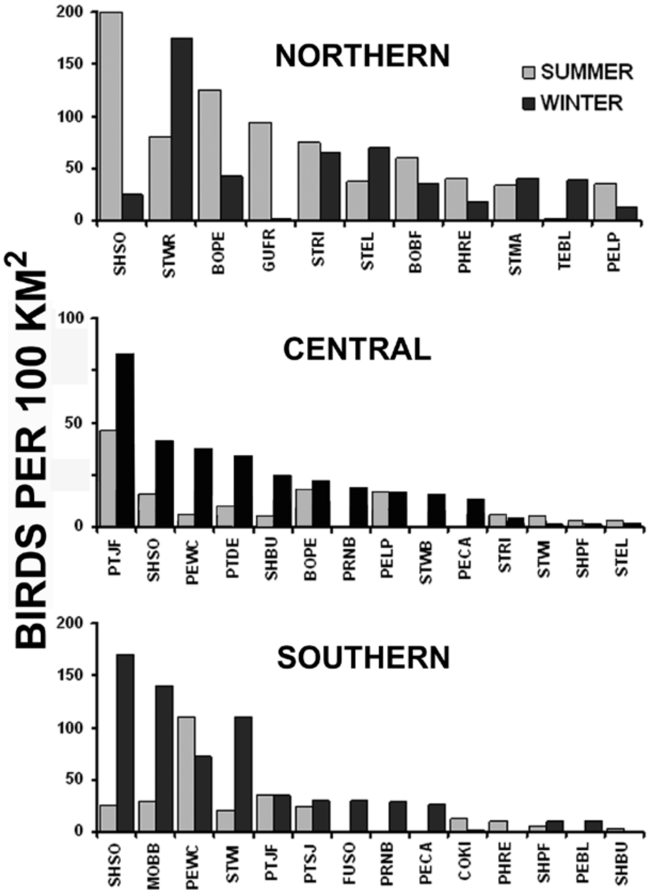

Fig. 2. Relative abundance of regularly occurring, abundant species of the Peru Current System by season and latitudinal sector. A given species had to be among the top 10 in either season to be shown. See Table 1 for sample sizes (number of survey transects), Appendix 1 for species codes, and Appendices 2 and 3 for specific details.

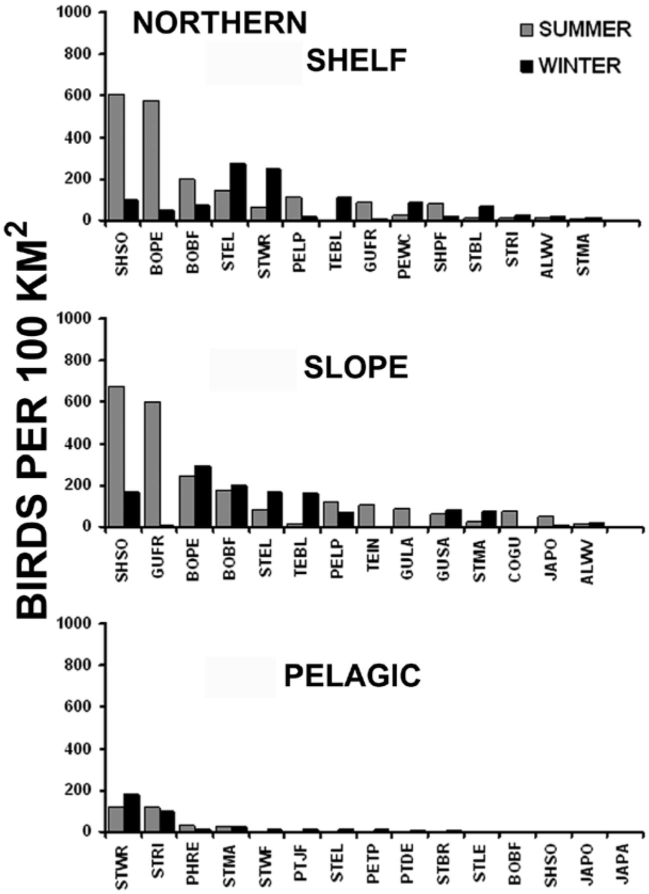

Fig. 3. Relative abundance of regularly occurring species in the northern area of the Peru Current System by season and habitat. A given species had to be among the top 10 in either season to be shown. See Table 1 for sample sizes (number of survey transects), Appendix 1 for species codes and Appendixes 2 and 3 for specific details.

in all respects except size, the latter being noticeably larger. The two also have distinct oceanographic affinities; the Parkinson's Petrel winters in large numbers in tropical waters off Central America to Ecuador; the Westland Petrel prefers cooler surface waters. Consistent with this information, we found a hiatus in the occurrence of dark-nailed *Procellaria* on the Peru coast between 12°S and 20°S, and we assumed that those seen to the north and south of that area were Parkinson's and Westland petrels respectively. Based on that assumption, Parkinson's Petrel was, in fact, frequently seen off northern Peru from 3°S to 6°S, with individuals seen to 12°32′S. Westland Petrels were occasional between 20°S and 45°S, as were Chatham Island Mollymawks *T. eremita* between 13°S and 41°S. Further details of the occurrence of these *Procellaria* and albatross species in the eastern Pacific are published in Spear *et al.* (2003, 2005).

Blue Petrels had been reported previously off Valparaiso, Chile (33°S), during July and September (Johnson 1965, Szijj 1967). These reports were considered by Jehl (1973) to be "unconvincing" because of lack of information on identification, and we also are skeptical, because sightings of these pelagic species close to the coast would be highly unusual. The Blue Petrel is easily distinguished from the similar-appearing prions and small *Pterodroma* by its prominent white terminal band on the tail, among other less distinctive differences. We recorded 24 Blue Petrels along a track between 36°35′S, 77°53′W and 41°03′S, 74°23′W, on 6 and 7 August 1995; densities at 0.165 ± 0.059 birds per square kilometer were constant along that stretch.

Szijj (1967) also reported a White-headed Petrel from 33°S and "near the Chilean coast," presumably in waters near or on the continental shelf. In view of the latter implication, and the lack of details to imply otherwise, we also question the record because this is another highly pelagic species (the record also was not included with the data given in Table 2 of the same publication). We saw two White-headed Petrels on 6 August 1995, at 36°35′S, 77°53′W and 36°46′S, 77°45′W—that is, in pelagic waters at the periphery of our study area [see Howell *et al.* (1996) for details on sightings just outside of our study area].

The dates and locations of the other newly documented species were these:

- Christmas Shearwater, 26 April 1992 (33°05′S, 74°20′W)
- Great Shearwater *P. gravis,* 19 March 1994 (48°58′S, 75°46′W)

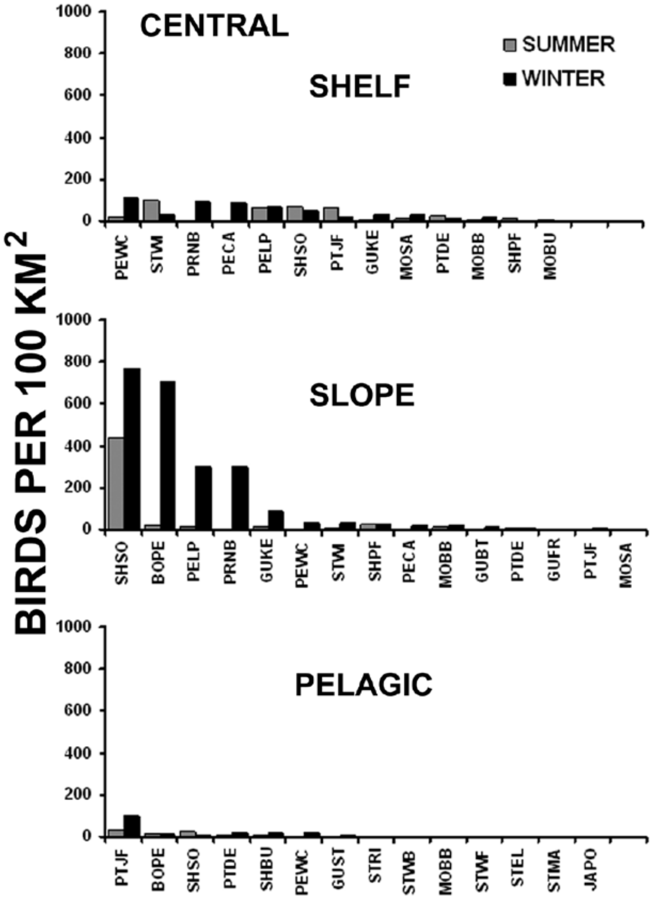

Fig. 4. Relative abundance of regularly occurring species in the central area of the Peru Current System by season and habitat. A given species had to be among the top 10 in either season to be shown. Figures were derived by summing densities across the shelf, slope and pelagic zones, and then dividing by three. See Table 1 for sample sizes (number of survey transects). See Appendix 1 for species codes. See Appendixes 2 and 3 for detailed values.

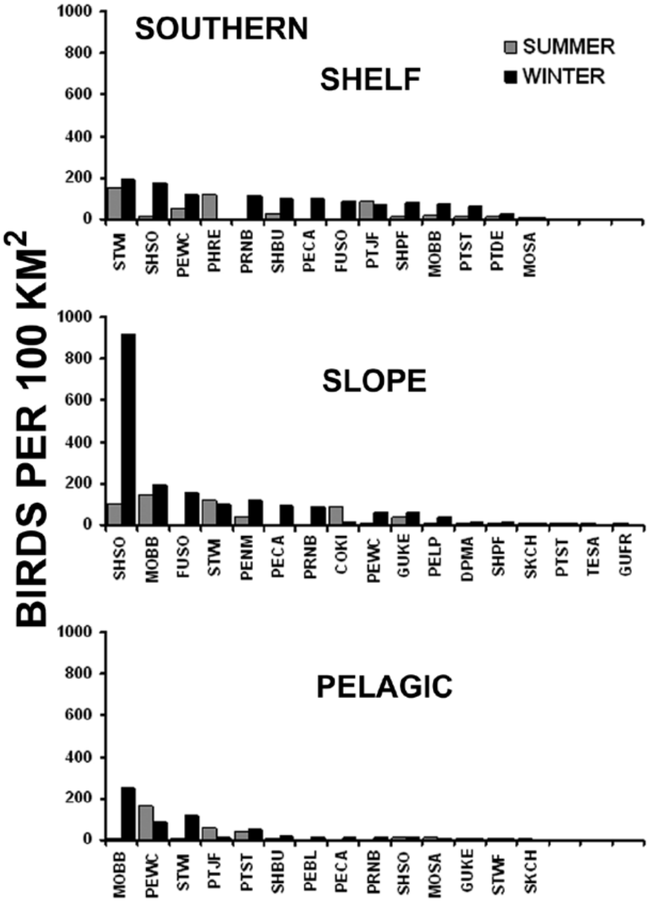

Fig. 5. Relative abundance of regularly occurring species in the southern area of the Peru Current System by season and habitat. A given species had to be among the top 10 in either season to be shown. Figures were derived by summing densities across the shelf, slope and pelagic zones, and then dividing by three. See Table 1 for sample sizes (number of survey transects). See Appendix 1 for species codes. See Appendixes 2 and 3 for detailed values.

- Two Manx Shearwaters, 3 January 1995 (33°05′S, 72°10′W)
- Two Kerguelen Petrels, 7 August 1995 (40°30′S, 74°51′W and 40°36′S, 74°47′W)
- Herald Petrel, 28 December 1992 (18°59′S, 74°46′W)
- Sandwich Tern, 8 November 1986 (5°00′S, 81°27′W)

Relationship of avian density with spatiotemporal variables

Overall, we noted a highly significant decrease in density of seabirds with increase in ocean depth, controlling for latitude [Table 3(A), Figs. 3–5]. Insignificant interactions of ocean depth with latitude and season indicated that the effect of ocean depth was similar regardless of differences in the other two variables. Density differed little with season, but increased significantly with decrease in latitude. A significant interaction was also seen between season and latitude, indicating that the relationship between density and latitude differed between seasons.

To examine the season–latitude interaction, we first analyzed the relationship between density and season separately for each of the three latitudinal sectors [Table 3(B)]. These analyses indicated that the interaction reflected higher densities during summer than during winter in the North sector, compared with higher densities during winter in the Central and South sectors. In the North sector, higher densities during summer reflected mostly the high combined abundance of Sooty Shearwater, Peruvian Booby and Franklin's Gull (Fig. 3). The latter species had moved into the region during its non-breeding period. The higher densities in winter than in summer in the Central sector was a result of high combined abundance of Sooty Shearwater, Peruvian Booby, Narrow-billed Prion and Peruvian Pelican. Only the Sooty Shearwater was highly abundant in the Central sector during summer. The higher winter densities in the South sector were mostly related to high densities of Sooty Shearwater, Black-browed Mollymawk, Southern Fulmar *Fulmarus glacialoides,* Wilson's Storm-Petrel, White-chinned Petrel and Narrow-billed Prion, all of which moved north into the region during their non-breeding period.

Analyses for the within-season effect of latitude [Table 3(C), Fig. 6] indicated a significant increase in density with decrease in latitude during summer, compared with an insignificant trend for density increase with latitude during winter.

Seabird densities over the continental shelf and slope decreased significantly from summer to winter in the North sector, but in both depth zones, densities increased significantly in winter as compared with summer in the Central and South sectors (Sidak tests: all $P < 0.05$; Figs. 3–5). In the pelagic zone, densities were significantly higher during winter in each sector except in the North sector, where densities differed insignificantly between seasons. Thus, with the exception of the pelagic zone in the North sector, the patterns in the continental shelf, slope and pelagic waters were consistent with the findings described earlier, showing, during winter, a decrease in densities in the North sector and an increase in densities in the Central and South sectors.

Densities decreased progressively from shelf to slope to pelagic waters in each zone and season except during summer in the northern and southern zones, in which densities did not differ significantly between shelf and slope waters. Densities were significantly lower in pelagic waters (Figs. 2–5).

TABLE 3
Regression analyses[a] for the effects of season, latitude and ocean depth on seabird density (species grouped) in the Peru Current, 1980–1995

			Regression coefficient[b] ± standard error	*F* value	*P* value
A	**Overall F(4,1249) = 65.24, 17.3% explained**				
		Season	0.25±0.229	1.15	0.3
		Latitude	–0.0094±0.00350	7.25	0.007
		Ocean depth	–0.00035±0.000042	210.06	<0.0001
		Season*latitude[c]	—	62.29	<0.0001
	rejected terms:				
		Season*ocean depth[c]	—	0.65	0.4
		Latitude*ocean depth[c]	—	1.71	0.2
B	**Effect of season compared by latitudinal sector (with control for ocean depth)**				
	Northern sector	Season	–0.45±0.111	16.23	<0.0001
	Central sector	Season	0.34±0.140	5.84	0.016
	Southern sector	Season	1.30±0.189	47.20	<0.0001
C	**Effect of latitude compared by season (with control for ocean depth)**				
	Summer	Latitude	–0.036±0.0054	45.54	<0.0001
	Winter	Latitude	0.0066±0.0045	2.13	0.14

[a] The dependent variable was log-birds per square kilometer. All variables were analyzed as continuous. Interactions were removed from the model before calculating values reported for the main effects. See Table 1 for sample sizes.

[b] A positive coefficient for season indicates higher density in winter than summer; negative coefficients for latitude indicate higher density in northern latitudes.

[c] Asterisk indicates interaction between these terms.

Seabird biomass over the shelf and slope showed patterns similar to those of seabird densities in relation to season (Fig. 7). That is, biomass over the continental shelf and slope decreased significantly from summer to winter in the North sector, but increased significantly in winter in the Central and South sectors (Sidak tests: all $P < 0.05$). In the pelagic zone, biomass was significantly higher in each sector during winter except in the North sector.

Like density, biomass differed little between shelf and slope during summer in the North sector (Fig. 7); it was significantly lower over the slope than over the shelf in the Central and South sectors. The summer pattern for shelf and slope waters in the South sector contrasted with that observed for density: the difference was insignificant and tended to move in the opposite direction. Seabird biomass over pelagic waters was significantly lower than that over shelf and slope in the North and Central sectors; however, and in contrast to the density relationship, pelagic biomass did not differ with that of slope biomass in the South sector. Compared with density patterns, biomass over the pelagic waters of the North and Central sectors was much lower than biomass observed over shelf and slope waters.

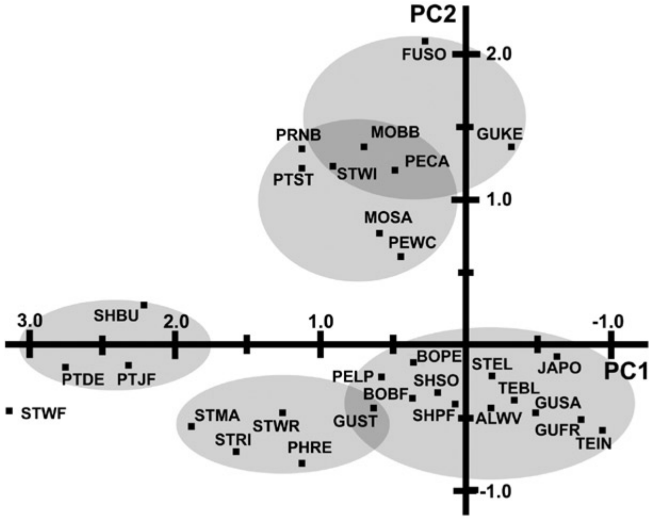

Fig. 6. Results of principal components analysis using the abundant species of the Peru Current System ordered along one axis (PC1) running from pelagic [distant from the coast (+)] to the shelf and nearshore (–), and the other axis (PC2) running from mostly year-round-occurring species present throughout the study area (–) to ones that invaded during the winter at higher latitudes (+).

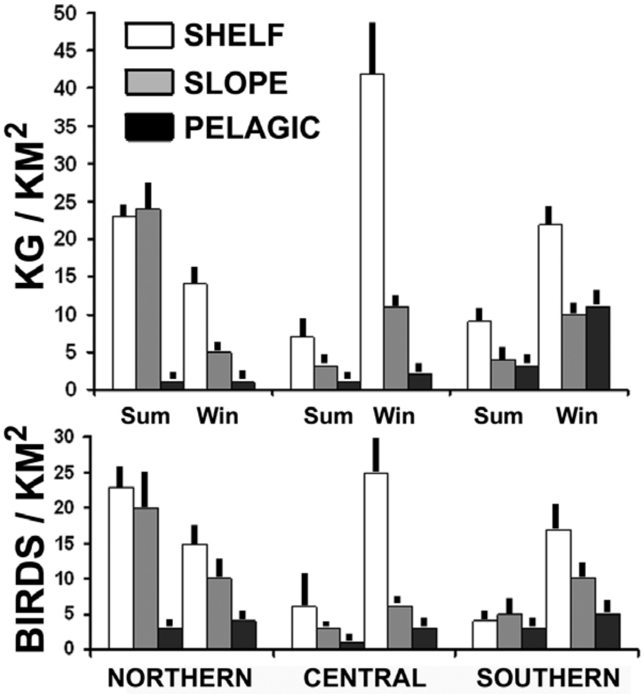

Fig. 7. Biomass (top) and densities (bottom), all species combined, by sector, season and habitat depth zone in the Peru Current System. Lines above bars are the standard error. See Table 1 for sample sizes. See Appendixes 2 and 3 for detailed values.

TABLE 4

Principal component analysis for the relationship of seabird density with spatiotemporal and oceanographic covariates,[a] compared for the 27 most abundant species of seabirds recorded in the Peru Current, 1980–1995

PC	Eigen value	Cumulative proportion	Covariate	Eigenvector PC1	Loadings PC2
A Spatiotemporal					
1	0.43	0.43	Season	0.06	0.70
2	0.28	0.71	Latitude	0.07	0.70
3	0.22	0.93	Ocean depth	0.71	–0.03
4	0.07	1.00	Distance to mainland	0.70	–0.09
B Oceanographic					
1	0.40	0.40	Sea-surface temp	0.55	–0.37
2	0.25	0.65	Sea-surface salinity	0.45	0.07
3	0.17	0.84	Thermocline depth	0.42	0.58
4	0.09	0.93	Thermocline gradient	0.52	0.32
5	0.07	1.00	Wind speed	0.29	0.64

[a] Only spatiotemporal and oceanographic data taken at locations where birds were sighted were used; analyses were weighted by bird density.

Biomass in shelf waters was significantly higher in the Central sector during summer than in other sectors during either season (Fig. 7). This finding was attributable mostly to high densities in the Central sector of larger species, including Peruvian Booby (1.35 kg) and especially Peruvian Pelican (6.9 kg). The latter species was the heaviest in the study area, with exception of Wandering *Diomedea exulans* and Royal *D. epomophora* albatrosses (approximately 9 kg). Significantly higher biomass over slope waters in the North sector during summer, as compared with other sectors during both seasons, reflected mostly the high densities in the North sector of Sooty Shearwater (0.79 kg), Peruvian Booby and Blue-footed Booby (1.45 kg). The higher biomass in pelagic waters of the South sector during winter as compared with other sectors during both seasons was mostly attributable to high densities of Black-browed Mollymawk (3.1 kg) and White-chinned Petrel (1.15 kg).

Predominant species: relationships with environmental variables

Consistent with the patterns reviewed above, the PCA using spatiotemporal and depth-defined habitats indicated an influx of sub-Antarctic and Antarctic species into the Peru Current during winter, especially in southern areas, augmenting a cluster of species that were present year-round (PC2 axis in Fig. 6, Table 4). This influx was seen against (PC1) a continuum of occurrence from pelagic offshore waters to shelf waters close to the coast. Four groups of species were evident, exhibiting a minimum of overlap. An outlier was the White-faced Storm-Petrel *Pelagodroma marina.*

Another PCA using oceanographic variables showed eight groups with generally more overlap of species than already exhibited (Fig. 8, Table 4). The species that were encountered in colder, less saline waters (PC1) were the ones in Fig. 6 that moved in over southern waters during the winter; those that occurred in warmer, more saline waters were close to the center of the axis and were mostly present year-round (or arrived from the north). This pattern was set against (PC2) species that occurred in well-mixed waters (those in Fig. 6 that occurred nearer to shore) as compared with those that occurred in stratified waters (offshore). The eight species groups were further combined into three "super groups," the two largest of which separated mostly resident, year-round occurring species from those that arrived from southern latitudes.

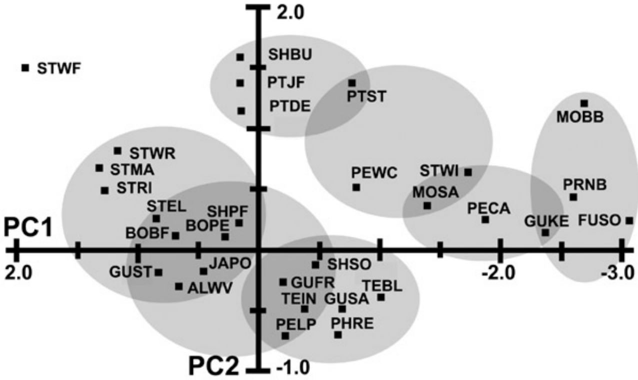

Fig. 8. Results of principal components analysis using abundant species of the Peru Current System ordered along one axis (PC1) running from warmer, saline waters (+) to colder, more dilute waters (–), and the other (PC2) running from unstratified, windy waters [strong upwelling (–)] to highly stratified, less windy waters (+).

DISCUSSION

Species composition shifted to some degree by region in accord with shifting oceanography. A very similar sort of phenomenon was described for the complex and spatially similar Benguela and Canary/Senegal upwelling systems (Brown 1979, Abrams & Griffiths 1981)—that is, upwellings from different source waters, inshore compared with offshore and countercurrents, and so on. However, only our study and Brown's attempted to tease apart regional differences in the avifauna related to current oceanographic climate. Brown thought that the differing regional species structures had to do with differences in productivity and the types of prey available. This case appears to also hold for the PCS.

Species groups in the PCS

In the analysis comparing species sorted with respect to spatiotemporal factors (Fig. 6), seabirds appeared to group by foraging guild. Although they included far fewer species in their analysis, similar sorts of functional groupings, including some of the same species, were observed by Briggs *et al.* (1987) in the California Current System (CCS). In the PCS there exists a distinct offshore group composed of Buller's Shearwater *P. bulleri* and deFilippe's *Pt. defilippiana* and Juan Fernandez petrels, all of which are species that follow predatory fish such as tuna (Spear *et al.* 2007), that are present pretty much year-round in the middle-lower latitudes. These species also grouped together on the basis of strongly stratified waters, adding Stejneger's Petrel *Pt. longirostris* in that case (Fig. 8). In the Briggs *et al.* (1987) study of the CCS, Buller's Shearwater also remained apart from most other species.

The main group of species occurred near to the origins of the two axes in both PCA analyses; this group included the classic "guano birds" (boobies, pelican, Guanay Cormorant *Phalacrocorax bougainvillii*) that feed on Anchoveta over the shelf (Fig. 6) in well-mixed, upwelling-affected waters (Fig. 8). This group was augmented by species moving into the PCS from the north (larids, jaegers) and the south (shearwaters).

The group of species that moved into the Peru Current mostly from the Antarctic and sub-Antarctic, appearing during winter (Fig. 6) and then remaining in colder, more dilute waters (Fig. 8), were mainly surface-feeding scavengers and surface seizers of prey (i.e. Salvin's *T. salvini* and Black-browed Mollymawks, Southern Fulmars, White-chinned and Pintado (Cape) petrels, Wilson's Storm-Petrels and Narrow-billed Prions).

In the PCA comparing spatiotemporal factors (Fig. 6), some storm-petrels and the Red Phalarope grouped together, mostly near the shelf break and in less-stratified water. An outlier in both analyses was White-faced Storm-Petrel, occurring in the most stratified, warmer waters far from shore. However, it is perhaps the most specialized feeder of all these species, preying largely on marine insects [*Halobates* spp. (Spear *et al.* 2007)].

Spear and Ainley (2007), in analyzing the co-occurrence (or not) of storm-petrels in the eastern Pacific, noted that disparate body size was important for species that shared the same habitat. This finding is quite obvious, too, among the groupings of all species in the PCS, being most clear in the high-latitude, surface-seizing and scavenging guild evident in both Fig. 6 (particularly positive on PC2) and Fig. 8 (negative on PC1). It is similarly obvious in the main group of species (including guano birds), with some exceptions. Among the exceptions, the two boobies group closely together, as do the Sabine's *Xema sabini* and Franklin's gulls, the Black *Childonia niger* and Inca *Larosterna inca* terns, and the Sooty and Pink-footed shearwaters. These pairings are of species similar in size. In further accord with the observations of Spear & Ainley (2007) in eastern Pacific storm-petrels, these pairings of similarly-sized species diverged by feeding methods: the groups each included a diving forager (Sooty Shearwater, Sabine's Gull, Inca Tern) and a surface forager (Pink-footed Shearwater, Franklin's Gull, Black Tern). It's not clear how the two boobies diverge, although the Blue-footed tends to be a shallower plunger (slanted approach) than does the Peruvian Booby (vertical approach, Ainley pers. obs.). The Swallow-tailed Gull *Creagrus furcatus* tended to be in subgroups separate from those with the Franklin's and Sabine's gulls, but the Swallow-tailed Gull also is much larger than either of the two former species and forages at night. Its diet must thus diverge significantly.

Comparison of avifaunas

During the past 40 years, profound changes have occurred in the species composition of the upper trophic levels of the world's oceans, including the PCS and other eastern boundary currents, and those changes have nothing to do with climate change, although effects from climate change could have had their own impacts (e.g. McGowan *et al.* 1996, 1998; Veit *et al.* 1996, 1997). The major changes have largely been a result of the removal of fish species from the upper trophic levels through marginally-controlled industrial fishing (Pauly *et al.* 1998, 2005; Myers & Worm 2003). Seabirds, though not directly taken in the fisheries, by and large could not have escaped the cascading effects that have followed (e.g. Brierley *et al.* 2001, Furness 2002, Frank *et al.* 2005, Österblom *et al.* 2006, Worm *et al.* 2006).

The fishery for Anchoveta in the PCS exhibited huge growth during the 1960s and 1970s; the stocks then collapsed by the early 1980s (Pauly *et al.* 1998). This fish was the mainstay of the diet of the Peruvian guano birds and of other species such as the Sooty Shearwater (Murphy 1925, 1936, 1981). With the collapse of that fish stock, the populations of the guano birds collapsed as well (Duffy *et al.* 1984). Our surveys were conducted in the aftermath of that calamity. Murphy (1936) did not really quantify the species composition of the entire avifauna of the PCS before the collapse, and so other than the demise of the three guano bird species—Peruvian Booby, Peruvian Pelican, Guanay Cormorant—we can only guess how the community present during our surveys compared. Along with the Sooty Shearwater, Murphy repeatedly refers to the "vast flocks" of these birds in Peruvian coastal waters.

During the period of our surveys, during summer, the shearwater ranked first, the booby second, the pelican ninth, and the Guanay Cormorant 18th in abundance. It is probable that had we surveyed more of the shelf habitat, especially in the Central sector, the rank of the latter bird would have been elevated to some degree. As it is, it appears that the Guanay Cormorant population, relatively speaking, has perhaps suffered the most from the demise of the Anchoveta. It, of course, was the least "conservative" in its breeding habits, laying multiple-egg clutches at less-than-one-year interval when conditions were right. It thus could quickly respond in a boom-or-bust sort of way to the vagaries of food availability, a phenomenon thoroughly discussed by Murphy (1925, 1981).

Other species that likely are much less abundant now than they were not so very long ago are the Humboldt Penguin *Spheniscus humboldti* and the Peruvian Diving Petrel *Pelecanoides garnotii.* For them, mining of the guano deposits in which they nest contributed to their demise. Murphy refers to the "vast" flocks in which the diving petrel was sometimes encountered. Nowadays both are listed near the top of the Red List maintained by the International Union for Conservation of Nature and Nautral Resources.

Therefore, in comparing the boundary current avifaunas, consideration has to be given not only to the timing and nature of surveys, but also to changes in marine community structure itself because of the incredible extraction of fish that has been exercised in recent decades. Effects of climate change seem almost to be a footnote. In fact, the resiliency of the community to adjust to larger-scale climate factors has likely been compromised (Worm *et al.* 2006)—that is, climate change has taken on greater importance because of the simplification of the food webs. Keeping such factors in mind, the community structure of the PCS appears to be far more similar to the CCS than to the Benguela, which should receive an influx of Antarctic and sub-Antarctic migrants similar to that seen in the PCS (Table 5).

The major difference between the PCS and CCS avifaunas, in terms of functional groups, lies in the absence of a sulid in the CCS, an aspect discussed extensively by Warheit (2002), and the relative rarity of cormorants in the CCS. Both pelecaniform groups are major players in the PCS (as well as in the Canary and Benguela currents, Table 5). Otherwise, considering the demise of penguins and diving petrels in the PCS, large and small divers are or were important to both systems. Indeed, the abundance of the Peruvian Diving Petrel in the PCS might well have once rivaled that of the Cassin's Auklet *Ptychoramphus aleuticus* now in the CCS. Similarly, the Humboldt and perhaps the Magellanic *Sphen. magellanicus* penguins were once, according to Murphy (1936), far more abundant than they were even in the early 20th century. It therefore is hard to judge whether the Common Murre *Uria aalge,* as a deep-diving species, is relatively more prevalent now in the CCS than the penguins were once in the PCS. On the other hand, the abundance of murres in the CCS may be compensating for the relatively low numbers of pelecaniforms.

Also similar between the two systems, although not obvious in Table 5, is the preponderance of medium-sized gulls, especially considering the winter avifaunas. Briggs *et al.* (1987) did not present a simple breakdown of species abundance, and Ainley's (1976) analysis is affected by the sorts of species that birding trips are want to report. However, the huge contribution of gulls, especially the California *Larus californicus,* Western *L. occidentalis,* Herring *L. argentatus* and Heerman's *L. heermani* gulls, and the Black-legged Kittiwake *Rissa tridactyla* in the CCS avifauna are clear (see Briggs *et al.*1987, Figs. 26–28; also Ainley 1976, Table 3). Some hint of this contribution is given in the data of Ford *et al.* (2004), which overestimate the summer relative to the winter avifauna (more surveys in summer). In fact, just as impressive as the lack of sulids in the CCS, is the contribution of North American medium-sized gulls to the PCS. The North American prairies and tundra, where these species breed, have no counterpart on a similar scale in South America. The migration of these gulls from inland North America to both the CCS and PCS seemingly has filled an available niche present in both systems. Similarly the movement of shearwaters, Sooty and Pink-footed, from the PCS to the CCS has filled a niche in the latter current. A diet analysis of gulls in both systems would be very interesting.

Somewhat surprisingly (at least to us), the avifaunas of the Atlantic eastern boundary currents are structured in much different ways (Table 5; see also Brown 1979, Abrams & Griffiths 1981, Crawford *et al.* 2006). A number of ecologically equivalent species are present, but in contrast to the structures of the CCS and PCS, important contributions by large and small divers, storm-petrels, and to some degree, larids (in the Benguela) are lacking, with that lack somewhat made up by a higher prevalence of pelecaniform species, especially the Cape Gannet *S. capensis* and Cape Cormorant *Phal. capensis*

TABLE 5
Percent species composition, by number, in three eastern boundary current systems

		Peru Present study	Benguela Abrams 1985	Benguela Duffy 1989	Calif S Hyrenbach & Veit 2003	Calif C Ford *et al.* 2004	Calif N Ainley *et al.* 2005
Large diver (penguin, loon, murre, puffin)		**0.3**	**0.0**	**0.1**	**1.3**	**24.3**	**13.6**
Penguin	*Spheniscus* spp.	0.3		0.1			
Albatross		**5.1**	**16.2**	**0.1**	**1.4**	**0.5**	**2.9**
Great albatross	*Diomedea* spp.	0.3	0.1				
Black-browed Mollymawk	*Thalassarche melanophris*	2.2	10.6	0.0			
White-capped Mollymawk	*T. steadi*	0.8	4.7	0.0			
Other albatross		1.8	0.6	0.0			
Large surface-feeding petrel or fulmar		**6.0**	**29.2**	**1.5**	**0.7**	**0.9**	**1.5**
Giant petrel	*Macronectes* spp.	0.2	0.2	0.0			
White-chinned Petrel	*Procellaria aequinoctialis*	3.7	22.2	1.5			
Pintado Petrel	*Daption capense*	1.2	6.7	0.0			
Southern/Northern Fulmar	*Fulmarus glacialoides*/*glacialis*	0.9	0.1			0.9	1.5
Shearwater		**23.6**	**13.0**	**0.9**	**25.1**	**49.2**	**45.5**
Sooty Shearwater	*Puffinus griseus*	20.7	10.3	0.6	21.0	48.1	43.3
Pink-footed/Greater Shearwater	*P. creatopus*/*gravis*	1.7	1.5	0.2	4.0	0.7	2.1
Buller's/Cory's Shearwater	*P. bulleri*/*Calonectris diomedea*	1.1	1.1	0.1	0.1	0.4	0.1
Little Shearwater	*P. assimilis*	0.1	0.1				
Gadfly petrel/prion	*Pterodroma*/*Pachyptila* spp.	**5.1**	**4.4**	**0.6**	**1.0**	**0.0**	**0.0**
Storm-petrel		**23.3**	**4.2**	**0.1**	**15.1**	**1.0**	**9.1**
Storm-petrel	*Oceanites*	8.7	3.4	0.0			
Other storm-petrels		14.6	0.8	0.0			9.1
Small diver (diving petrel, auklet, murrelet)		**0.1**	**0.0**	**0.0**	**3.4**	**10.5**	**15.7**
Pelican		**3.2**	**0.0**	**0.0**	**1.8**	**0.5**	**0.0**
Gannet/booby		**16.6**	**17.2**	**10.3**	**0.0**		
Cormorants		**0.8**	**11.4**	**77.4**	**0.1**	**1.6**	**0.1**
Cape/Guanay Cormorant	*Phalacrocorax capensis*/*Ph. bougainvillii*	0.6	7.5	77.3			
Other cormorants		0.2	3.9	0.1	0.1		
Phalaropes		**2.4**	**0.1**	**0.0**	**23.2**	**2.4**	**9.1**
Skuas		**0.2**	**0.1**	**0.0**	**0.0**		**0.0**
Jaegers		**1.1**	**0.3**	**0.0**	**0.1**		**0.4**
Large gulls		**0.5**	**1.7**	**2.8**	**7.5**	**5.3**	**1.4**
Kelp Gull	*Larus dominicanus*	0.5	1.7	2.8			
Medium-sized gulls		**6.4**	**0.0**	**1.1**	**0.7**	**4.0**	**0.2**[a]
Other gulls		**7.9**	**0.2**	**0.4**	**0.1**	**0.2**	**0.1**
Sabine's Gull	*Xema sabini*	0.2	0.2	0.4	0.1	0.2	0.1
Terns		**4.1**	**2.5**	**4.7**	**0.2**	**0.1**	**0.2**

[a] Would be far higher if included winter surveys (see Ainley 1976, Briggs *et al.* 1987).

(and other cormorants), and possibly petrels. As it is the Benguela has 30% fewer resident breeding species than do the PCS and the CCS (Crawford *et al.* 2006). Whether the high abundance of surface-feeding petrels in Abrams' data is real or whether it is an artifact of birds attracted to the stern-trawlers used in the surveys is not clear, nor is the reason behind the disparity between Abrams' and Duffy's data clear. Lack of island breeding habitat for the divers and lack of inland breeding habitat for the gulls are perhaps the factors involved in low abundance of those species in the Atlantic systems. The Razorbill *Alca torda* occurs (and possibly the extinct Great Auk *Pinguinus impennis* once occurred) in the very northern part of the Canary system at a yet-to-be quantified density (Brown 1979).

The ecologic importance of the Sooty Shearwater

We end this discussion with thoughts on the Sooty Shearwater. The abundance of this species in all eastern boundary currents, as well as points between (Spear *et al.* 2007), with the currents of course holding the major concentrations of seabirds outside of the Antarctic, can be viewed only as mind-boggling. Even in sub-Antarctic waters south of New Zealand, Sooty Shearwaters can be abundant during summer (e.g. Ainley *et al.* 1984). This species, through its command of trophic resources, its relatively large body mass, its rapid flight and its ability to penetrate to significant depths, likely has had an effect on the structuring of marine avifaunas far, far more than any other bird (see, for instance, observations on interactions with other species in Hoffman *et al.* 1981; Briggs *et al.* 1987; and Ainley & Boekelheide 1990, Ch. 2). As an example, it has seemingly, through interference competition, forced the similar Short-tailed Shearwater *P. tenuirostris* to overfly most of the Pacific to occupy the farther south Southern Ocean and the Bering Sea to the north during its breeding and non-breeding seasons respectively (cf. Woehler *et al.* 2006, Hunt *et al.* 1996). In terrestrial systems, we know of no species having an equivalent "ecological success," other than perhaps the rat (*Rattus* spp.). The Sooty Shearwaters is truly a remarkable seabird.

On the basis of studies in the northern CCS (Wiens & Scott 1976, Ainley *et al.* 2005; see also Briggs *et al.* 1987, Table 4), it appears that murres in waters over the northern hemisphere shelf can readily alter the Sooty Shearwater occurrence patterns. The murres are also vastly abundant, feed in flocks, can penetrate the entire shelf habitat in their diving capabilities, and, with a strategy of moving very young chicks to the food, can respond rapidly to variations in food availability (Gaston & Hipfner 2000, Ainley *et al.* 2002). These are characteristics comparable to those of the shearwater, which thus contribute to the success of both these species. As well, both species feed principally on the energy-rich mid-water schooling fish species, such as Anchovy *E. mordax* in the CCS (cf. Briggs & Chu 1987, Ainley *et al.* 1996), thus setting up a direct overlap in diet and preferred habitat.

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APPENDIX 1

Observed (raw) numbers and adjusted numbers (see Methods; Analyses) of 93 species of seabirds recorded off the Pacific coast of Peru and Chile (3°S to 50°S, and to 370 km offshore) in summer and summer, 1980–1995.

			Raw	Adjusted	Status[a]	Code[b]
	Penguins					
1	Humboldt Penguin	*Spheniscus humboldti*	74	74.0	E	PENH
2	Magellanic Penguin	*Sph. magellanicus*	97	97.0	R	PENM
	Albatross					
3	Royal Albatross	*Diomedea epomophora*	80	60.0	S	ALRO
4	Wandering Albatross	*D. exulans*	44	35.2	S	ALWA
5	Waved Albatross	*Phoebastria irrorata*	619	532.4	S	ALWV
6	Light-mantled Sooty Albatross	*Phoebetria palpebrata*	1	0.9	S	ALLM
7	Black-browed Mollymawk	*Thalassarche melanophris*	1,368	1,307.3	S	MOBB
8	Gray-headed Mollymawk	*T. chyrsostoma*	3	1.5	S	MOGH
9	Salvin's Mollymawk	*T. salvini*	404	365.0	S	MOSA
10	Chatham Island Mollymawk	*T. eremita*	27	19.5	S	MOCI
11	Buller's Mollymawk	*T. bulleri*	89	71.9	S	MOBU
	Petrels					
12	Southern Giant Petrel	*Macronectes giganteus*	106	89.6	S	GPSO
13	Northern Giant Petrel	*M. halli*	21	15.1	S	GPNO
14	White-chinned Petrel	*Procellaria aequinoctialis*	2,299	2,148.8	S	PEWC
15	Westland Petrel	*Procel. westlandica*	11	10.3	S	PETW
16	Parkinson's Petrel	*Procel. parkinsoni*	160	136.2	S	PETP
17	Cape (Pintado) Petrel	*Daption capense*	699	684.0	S	PECA
18	Southern Fulmar	*Fulmarus glacialoides*	538	518.2	S	FUSO
19	Sooty Shearwater	*Puffinus griseus*	13,361	12,180.9	R	SHSO
20	Short-tailed Shearwater	*P. tenuirostris*	50	45.0	S	SHST
21	Pink-footed Shearwater	*P. creatopus*	1029	1015.0	E	SHPF
22	Greater Shearwater	*P. gravis*	1	0.9	S	SHGR
23	Buller's Shearwater	*P. bulleri*	647	619.6	S	SHBU
24	Christmas Shearwater	*P. nativitatis*	1	1.0	S	SHCR
25	Manx Shearwater	*P. puffinus*	2	2.0	N	SHMA
26	Little Shearwater	*P. assimilis*	45	32.5	R	SHLI
27	Audubon's Shearwater	*P. lherminieri*	3	1.7	S	SHAU
28	White-headed Petrel	*Pterodroma lessonii*	2	0.7	S	PTWH
29	Juan Fernandez Petrel	*Pt. externa*	1819	1352.1	S	PTJF
30	Dark-rumped Petrel	*Pt. phaeopygia*	25	15.7	R	PTDR
31	Kermadec Petrel	*Pt. neglecta*	27	14.1	R	PTKE
32	Herald Petrel	*Pt. heraldica*	1	0.4	S	PTHE
33	Kerguelen Petrel	*Pt. brevirostris*	2	0.8	S	PTKE
34	deFilippe's Petrel	*Pt. defilippiana*	518	442.0	S	PTDE
35	Cook's Petrel	*Pt. cooki*	9	7.9	S	PTCO
36	Stejneger's Petrel	*Pt. longirostris*	373	316.0	S	PTST
37	Black-winged Petrel	*Pt. nigripennis*	6	2.4	S	PTBW
38	White-winged Petrel	*Pt. leucoptera*	4	2.1	S	PTWW
39	Broad-billed Prion	*Pachyptila vittata*	22	20.5	S	PRBB
40	Narrow-billed Prion	*Pachy. belcheri*	931	900.3	S	PRNB
41	Blue Petrel	*Halobaena caerulea*	24	19.0	S	PEBL
	Diving petrels					
42	Peruvian Diving-Petrel	*Pelecanoides garnoti*	74	68.6	E	DPPE
43	Magellanic Diving-Petrel	*Pel. magellani*	96	80.2	R	DPMA
	Storm-Petrels					
44	Wilson's Storm-Petrel	*Oceanites oceanicus*	1,566	1,711.5	R	STWI
45	Elliot's Storm-Petrel	*Oceanites gracilis*	3056	3391.1	E	STEL
46	Black Storm-Petrel	*Oceanodroma melania*	427	422.3	N	STBL
47	Markham's Storm-Petrel	*O. markhami*	1127	1168.9	E	STMA
48	Ringed (Hornby's) Storm-Petrel	*O. hornbyi*	1861	1841.9	E	STRI
49	Leach's Storm-Petrel	*O. leucorhoa*	58	63.0	N	STLE
50	Band-rumped (Harcourt's) Storm-Petrel	*O. castro*	55	47.8	S	STBR
51	Wedge-rumped (Galapagos) Storm-Petrel	*O. tethys*	4668	4766.0	R	STWR
52	Least Storm-Petrel	*O. microsoma*	2	2.0	N	STLA
53	White-faced Storm-Petrel	*Pelagodroma marina*	215	169.9	S	STWF
54	White-bellied Storm-Petrel	*Fregetta grallaria*	137	106.8	S	STWB

APPENDIX 1 *continued*

		Raw	Adjusted	Status[a]	Code[b]
Tropicbirds					
55 Red-billed Tropicbird	*Phaethon aethereus*	38	30.7	B	TRRB
56 Red-tailed Tropicbird	*Phae. rubricauda*	3	3.0	B	TRRT
Pelicans					
57 Peruvian Pelican	*Pelecanus thagus*	2,438	1,752.6	E	PELP
58 Brown Pelican	*Pele. occidentalis*	108	90.6	B	PELB
Boobies					
59 Peruvian Booby	*Sula variegata*	7,415	6,517.3	E	BOPE
60 Blue-footed Booby	*S. nebouxii*	4059	3183.7	S	BOBF
61 Masked Booby	*S. dactylatra*	48	42.4	R	BOMA
Cormorants					
62 Guanay Cormorant	*Phalacrocorax bougainvillii*	462	380.4	E	COGU
63 Olivaceous Cormorant	*Ph. olivaceus*	13	8.0	R	COOL
64 Blue-eyed Cormorant	*Ph. atriceps*	144	108.1	S	COBE
65 Magellan Cormorant	*Ph. magellanicus*	7	3.5	E	COMA
Frigatebirds					
66 Great Frigatebird	*Fregata minor*	2	2.0	B	FRGR
67 Magnificent Frigatebird	*F. magnificens*	2	1.7	B	FRMA
Phalaropes					
68 Red Phalarope	*Phalaropus fulicarius*	1083	975.0	N	PHRE
69 Red-necked Phalarope	*Phal. lobatus*	407	396.2	N	PHRN
Skuas					
70 South Polar (Maccormick's) Skua	*Stercorarius maccormicki*	32	27.0	S	SKMA
71 Chilean Skua	*Stercor. chilensis*	121	96.0	E	SKCH
72 Pomarine Jaeger	*Stercor. pomarinus*	488	442.7	N	JAPO
73 Parasitic Jaeger	*Stercor. parasiticus*	195	176.0	N	JAPA
74 Long-tailed Jaeger	*Stercor. longicaudus*	120	133.7	N	JALT
Gulls and terns					
75 Swallow-tailed Gull	*Creagrus furcatus*	346	332.5	S	GUST
76 Kelp Gull	*Larus dominicanus*	315	299.2	R	GUKE
77 Band-tailed Gull	*L. belcheri*	86	83.2	E	GUBT
78 Gray Gull	*L. modestus*	80	66.5	E	GUGR
79 Dolphin Gull	*L. scorsebii*	3	2.3	E	GUDO
80 Laughing Gull	*L. atricilla*	428	424.2	N	GULA
81 Franklin's Gull	*L. pipixcan*	3044	3749.4	N	GUFR
82 Brown-hooded Gull	*L. maculipennis*	18	15.6	E	GUBH
83 Sabine's Gull	*Xema sabini*	350	340.0	N	GUSA
84 Inca Tern	*Larosterna inca*	369	591.6	E	TEIN
85 Black Tern	*Childonia niger*	1582	1494.5	N	TEBL
86 Royal Tern	*Sterna maxima*	48	36.5	N	TERO
87 Elegant Tern	*St. elegans*	9	4.5	N	TEEL
88 Sooty Tern	*St. fuscata*	5	2.4	B	TESO
89 Sandwich Tern	*St. sandvicensis*	1	0.5	N	TESA
90 Common Tern	*St. hirundo*	141	142.8	N	TECO
91 South American Tern	*St. hirundinacea*	210	185.7	E	TESA
92 Arctic Tern	*St. paradisaea*	17	12.7	N	TEAR
93 Peruvian Tern	*St. lorata*	168	150.5	E	TEPE
Other					
Unidentified storm-petrel	*Oceanodroma* spp.	12	11.0		
Skua	*Catharacta* spp.	26	23.4		
Jaeger	*Stercorarius* spp.	7	4.9		

[a] E = endemic; R = resident (based on Duffy *et al.* 1984, Schlatter 1984); N = migrant that breeds in the northern hemisphere; S = migrant from southern hemisphere; B = migrant that breeds in both hemispheres.

[b] The abbreviation of a species as used in various figures (and in most cases the codes we used to record and analyze data).

APPENDIX 2

Abundance of seabirds seen regularly in the Peru Current (densities ≤5 birds•100 km^{-2}) with respect to four latitudinal sectors and three depth-defined habitat zones. Densities were weighted by the reciprocal of the area surveyed. In several analyses, the South sector and sub-Antarctic ("Convergence") sector were combined under "South."

	Continental shelf			**Shelf slope**			**Pelagic**		
	North sector (3°S-14.99°S)								
1	Sooty Shearwater	*Puffinus griseus*	451.3	Sooty Shearwater	*P. griseus*	406.6	Wedge-rumped Storm-Petrel	*Oceanodroma tethys*	167.7
2	Franklin's Gull	*Larus pipixcan*	381.5	Peruvian Booby	*Sula variegata*	387.7	Ringed Storm-Petrel	*O. hornbyi*	83.7
3	Peruvian Booby	*S. variegata*	259.2	Elliot's Storm-Petrel	*Oceanites gracilis*	186.0	Markham's Storm-Petrel	*O. markhami*	39.7
4	Blue-footed Booby	*S. nebouxii*	177.8	Blue-footed Booby	*S. nebouxii*	135.9	Red Phalarope	*Phalaropus fulicarius*	37.8
5	Elliot's Storm-Petrel	*Oceanites gracilis*	108.2	Wedge-rumped Storm-Petrel	*O. tethys*	129.8	Leach's Storm-Petrel	*O. leucorhoa*	6.3
6	Peruvian Pelican	*Pelecanus thagus*	78.9	Peruvian Pelican	*Pele. thagus*	61.4	Blue-footed Booby	*S. nebouxii*	5.6
7	Wedge-rumped Storm-Petrel	*O. tethys*	74.9	White-chinned Petrel	*Procellaria aequinoctialis*	51.5	Juan Fernandez Petrel	*Pterodroma externa*	5.2
8	Black Tern	*Childonia niger*	61.0	Black Tern	*C. niger*	50.4			
9	Inca Tern	*Larosterna inca*	58.9	Franklin's Gull	*L. pipixcan*	45.6			
10	Laughing Gull	*L. atricilla*	45.4	Pink-footed Shearwater	*P. creatopus*	41.6			
11	Sabine's Gull	*Xema sabini*	44.7	Ringed Storm-Petrel	*O. hornbyi*	34.9			
12	Guanay Cormorant	*Phalacrocorax bougainvillii*	27.7	Sabine's Gull	*X. sabini*	27.3			
13	Markham's Storm-Petrel	*O. markhami*	27.6	Black Storm-Petrel	*O. melania*	22.7			
14	Red-necked Phalarope	*Phal. lobatus*	27.3	Red Phalarope	*Phal. fulicarius*	21.8			
15	Pomarine Jaeger	*Stercorarius pomarinus*	27.1	Waved Albatross	*Phoebastria irrorata*	20.1			
16	Waved Albatross	*Phoe. irrorata*	26.5	Common Tern	*Sterna hirundo*	17.5			
17	White-chinned Petrel	*Procel. aequinoctialis*	24.2	Markham's Storm-Petrel	*O. markhami*	14.0			
18	Pink-footed Shearwater	*P. creatopus*	13.9	Red-necked Phalarope	*Phal. lobatus*	12.5			
19	Swallow-tailed Gull	*Creagrus furcatus*	13.3	Pomarine Jaeger	*Stercor. pomarinus*	11.9			
20	Black Storm-Petrel	*O. melania*	11.6	Inca Tern	*Larosterna inca*	8.6			
21	Peruvian Tern	*St. lorata*	10.6	Salvin's Mollymawk	*Thalassarche salvini*	8.2			
22	Parasitic Jaeger	*Stercor. parasiticus*	9.9	Band-tailed Gull	*L. belcheri*	7.1			
23	Brown Pelican	*Pele. occidentalis*	9.5	Swallow-tailed Gull	*Creagrus furcatus*	6.8			
24	Ringed Storm-Petrel	*O. hornbyi*	8.5	Long-tailed Jaeger	*Stercor. longicaudus*	6.0			
25	South American Tern	*St. hirundinacea*	8.1	Parkinson's Petrel	*Procel. parkinsoni*	5.5			
26	Long-tailed Jaeger	*Stercor. longicaudus*	5.7	Parasitic Jaeger	*Stercor. parasiticus*	5.3			
27	Parkinson's Petrel	*Procel. parkinsoni*	5.1						
28	Wilson's Storm-Petrel	*Oceanites oceanicus*	5.1						
	Central sector (15°S-24.99°S)								
1	Sooty Shearwater	*P. griseus*	737.0	Sooty Shearwater	*P. griseus*	386.4	Ringed Storm-Petrel	*O. hornbyi*	167.7
2	Peruvian Pelican	*Pele. thagus*	54.7	Peruvian Pelican	*Pele. thagus*	90.5	Wedge-rumped Storm-Petrel	*O. tethys*	83.7
3	Pink-footed Shearwater	*P. creatopus*	41.3	White-chinned Petrel	*Procel. aequinoctialis*	75.8	Juan Fernandez Petrel	*Pt. externa*	39.7
4	Pomarine Jaeger	*Stercor. pomarinus*	7.0	Pink-footed Shearwater	*P. creatopus*	69.9	Markham's Storm-Petrel	*O. markhami*	37.8
5	Franklin's Gull	*L. pipixcan*	7.0	Elliot's Storm-Petrel	*Oceanites gracilis*	65.5	Red Phalarope	*Phal. fulicarius*	17.5
6	Guanay Cormorant	*Ph. bougainvillii*	5.8	Long-tailed Jaeger	*Stercor. longicaudus*	65.0	White-faced Storm-Petrel	*Pelagodroma marina*	11.6
7	Elliot's Storm-Petrel	*Oceanites gracilis*	5.7	Wedge-rumped Storm-Petrel	*O. tethys*	22.1	deFilippe's Petrel	*Pt. defilippiana*	8.0
8				Parasitic Jaeger	*Stercor. parasiticus*	11.1	Pomarine Jaeger	*Stercor. pomarinus*	5.2
9				Pomarine Jaeger	*Stercor. pomarinus*	8.9			

APPENDIX 2 *continued*

	Continental shelf			Shelf slope			Pelagic		
	South sector (25°S-34.99°S)								
1	Sooty Shearwater	*P. griseus*	438.8	White-chinned Petrel	*Procel. aequinoctialis*	24.6	Juan Fernandez Petrel	*Pt. externa*	167.7
2	Peruvian Booby	*S. variegata*	158.4	Wilson's Storm-Petrel	*Oceanites oceanicus*	20.4	Buller's Shearwater	*T. bulleri*	83.7
3	Pink-footed Shearwater	*P. creatopus*	34.3	deFilippe's Petrel	*Pt. defilippiana*	19.1	White-chinned Petrel	*Procel. aequinoctialis*	39.7
4	Peruvian Pelican	*Pele. thagus*	7.5	Salvin's Mollymawk	*T. salvini*	15.8	deFilippe's Petrel	*Pt. defilippiana*	37.8
5	Band-tailed Gull	*L. belcheri*	5.2	Juan Fernandez Petrel	*Pt. externa*	13.8	Peruvian Booby	*S. variegata*	17.5
6				Sooty Shearwater	*P. griseus*	13.4	White-bellied Storm-Petrel	*Fregetta grallaria*	11.6
7				Pink-footed Shearwater	*P. creatopus*	7.4			
	Convergence sector (35°S-42.5°S)								
1	Sooty Shearwater	*P. griseus*	19.6	Wilson's Storm-Petrel	*Oceanites oceanicus*	155.4	Black-browed Mollymawk	*T. melanophris*	152.2
2	Pink-footed Shearwater	*P. creatopus*	9.1	White-chinned Petrel	*Procel. aequinoctialis*	71.3	White-chinned Petrel	*Procel. aequinoctialis*	85.0
3	Wilson's Storm-Petrel	*Oceanites oceanicus*	8.6	Red Phalarope	*Phal. fulicarius*	67.0	Wilson's Storm-Petrel	*Oceanites oceanicus*	69.1
4	White-chinned Petrel	*Procel. aequinoctialis*	7.9	Buller's Shearwater	*T. bulleri*	52.2	Stejneger's Petrel	*Pt. longirostris*	29.1
5	King Cormorant	*Ph. atriceps*	7.6	Juan Fernandez Petrel	*Pt. externa*	44.5	Juan Fernandez Petrel	*Pt. externa*	16.3
6	Black-browed Mollymawk	*T. melanophris*	5.4	Sooty Shearwater	*P. griseus*	42.9	Blue Petrel	*Halobaena caerulea*	9.9
7	Narrow-billed Prion	*Pachyptila belcheri*	5.0	Pink-footed Shearwater	*P. creatopus*	39.6	Sooty Shearwater	*P. griseus*	9.9
8				Black-browed Mollymawk	*T. melanophris*	35.3	Cape Petrel	*Daption capense*	6.7
9				Stejneger's Petrel	*Pt. longirostris*	28.2			
10				Southern Fulmar	*Fulmarus glacialoides*	19.5			
11				Salvin's Mollymawk	*T. salvini*	10.8			
12				Cape Petrel	*D. capense*	8.6			
13				deFilippe's Petrel	*Pt. defilippiana*	8.6			
14				Narrow-billed Prion	*Pachy. belcheri*	8.3			

APPENDIX 3

The abundance of seabirds seen regularly in the Peru Current (densities ≥5 birds•100 km^{-2}) with respect to latitudinal sectors and season. Densities (number of birds•100 km^{-2}) follow species and scientific names. Densities were weighted by the reciprocal of the area surveyed per season.

	Summer			Winter			Average		
	North sector (3°S–20°S)								
1	Sooty Shearwater	*Puffinus griseus*	427.0	Wedge-rumped Storm-Petrel	*Oceanodroma tethys*	183.7	Sooty Shearwater	*P. griseus*	240.2
2	Peruvian Booby	*Sula variegata*	261.6	Elliot's Storm-Petrel	*Oceanites gracilis*	132.4	Peruvian Booby	*S. variegata*	176.6
3	Franklin's Gull	*Larus pipixcan*	219.3	Peruvian Booby	*S. variegata*	91.6	Wedge-rumped Storm-Petrel	*O. tethys*	118.4
4	Blue-footed Booby	*S. nebouxii*	113.3	Black Tern	*Childonia niger*	76.0	Franklin's Gull	*L. pipixcan*	110.9
5	Elliot's Storm-Petrel	*Oceanites gracilis*	62.9	Blue-footed Booby	*S. nebouxii*	70.1	Elliot's Storm-Petrel	*Oceanites gracilis*	97.7
6	Peruvian Pelican	*Pelecanus thagus*	61.3	Sooty Shearwater	*P. griseus*	53.2	Blue-footed Booby	*S. nebouxii*	91.7
7	Wedge-rumped Storm-Petrel	*O. tethys*	53.0	Ringed Storm-Petrel	*O. hornbyi*	39.7	Ringed Storm-Petrel	*O. hornbyi*	43.3
8	Ringed Storm-Petrel	*O. hornbyi*	46.8	Markham's Storm-Petrel	*O. markhami*	39.4	Black Tern	*C. niger*	40.8
9	Inca Tern	*Larosterna inca*	34.3	White-chinned Petrel	*Procellaria aequinoctialis*	33.8	Peruvian Pelican	*Pele. thagus*	40.2
10	Laughing Gull	*L. atricilla*	24.3	Sabine's Gull	*Xema sabini*	24.5	Markham's Storm-Petrel	*O. markhami*	27.7
11	Red Phalarope	*Phalaropus fulicarius*	23.9	Black Storm-Petrel	*O. melania*	20.2	White-chinned Petrel	*Procel. aequinoctialis*	26.2
12	Pink-footed Shearwater	*P. creatopus*	22.5	Peruvian Pelican	*Pele. thagus*	19.1	Sabine's Gull	*X. sabini*	22.2
13	Guanay Cormorant	*Phalacrocorax bougainvillii*	21.9	Waved Albatross	*Phoebastria irrorata*	17.7	Inca Tern	*Larosterna inca*	17.5
14	Sabine's Gull	*X. sabini*	19.8	Pink-footed Shearwater	*P. creatopus*	11.8	Red Phalarope	*Phal. fulicarius*	17.3
15	Pomarine Jaeger	*Stercorarius pomarinus*	19.4	Swallow-tailed Gull	*Creagrus furcatus*	11.1	Pink-footed Shearwater	*P. creatopus*	17.2
16	White-chinned Petrel	*Procel. aequinoctialis*	18.5	Red Phalarope	*Phal. fulicarius*	10.6	Waved Albatross	*Ph. irrorata*	15.1
17	Markham's Storm-Petrel	*O. markhami*	15.9	Wilson's Storm-Petrel	*Oceanites oceanicus*	8.1	Laughing Gull	*L. atricilla*	12.5
18	Red-necked Phalarope	*Phal. lobatus*	15.7	Red-necked Phalarope	*Phal. lobatus*	7.1	Black Storm-Petrel	*O. melania*	12.2
19	Waved Albatross	*Ph. irrorata*	12.5	Peruvian Tern	*Sterna lorata*	7.0	Pomarine Jaeger	*Stercor. pomarinus*	11.4
20	Common Tern	*St. hirundo*	9.3	Juan Fernandez Petrel	*Pterodroma externa*	6.9	Red-necked Phalarope	*Phal. lobatus*	11.4
21	Parasitic Jaeger	*Stercor. parasiticus*	7.3	Salvin's Mollymawk	*Thalassarche salvini*	6.7	Guanay Cormorant	*Ph. bougainvillii*	11.3
22	Long-tailed Jaeger	*Stercor. longicaudus*	7.1	Parkinson's Petrel	*Procel. parkinsoni*	6.6	Swallow-tailed Gull	*Creagrus furcatus*	7.3
23	Black Tern	*C. niger*	5.6	Cape Petrel	*Daption capense*	5.8			
24				South American Tern	*St. hirundinacea*	5.5			
	Central sector (20°S–35°S)								
1	Sooty Shearwater	*P. griseus*	289.5	Peruvian Booby	*S. variegata*	56.6	Sooty Shearwater	*P. griseus*	154.4
2	Pink-footed Shearwater	*P. creatopus*	25.0	Juan Fernandez Petrel	*Pt. externa*	26.8	Peruvian Booby	*S. variegata*	30.2
3	Juan Fernandez Petrel	*Pt. externa*	8.0	Sooty Shearwater	*P. griseus*	19.3	Juan Fernandez Petrel	*Pt. externa*	17.4
4	deFilippe's Petrel	*Pt. defilippiana*	6.6	White-chinned Petrel	*Procel. aequinoctialis*	16.9	Pink-footed Shearwater	*P. creatopus*	14.0
5	Wilson's Storm-Petrel	*Oceanites oceanicus*	5.0	deFilippe's Petrel	*Pt. defilippiana*	11.3	White-chinned Petrel	*Procel. aequinoctialis*	9.6
6				Buller's Shearwater	*T. bulleri*	9.2	deFilippe's Petrel	*Pt. defilippiana*	9.0
7				Salvin's Mollymawk	*T. salvini*	5.8			

APPENDIX 3 *continued*

	Summer			Winter			Average		
	South/Convergence sector (35°S–50°S)								
1	White-chinned Petrel	*Procel. aequinoctialis*	38.9	Black-browed Albatross	*T. melanophris*	70.7	Black-browed Mollymawk	*T. melanophris*	52.1
2	Black-browed Mollymawk	*T. melanophris*	33.5	Wilson's Storm-Petrel	*Oceanites oceanicus*	66.4	Wilson's Storm-Petrel	*Oceanites oceanicus*	47.6
3	Wilson's Storm-Petrel	*Oceanites oceanicus*	28.7	White-chinned Petrel	*Procel. aequinoctialis*	40.7	White-chinned Petrel	*Procel. aequinoctialis*	39.8
4	Red Phalarope	*Phal. fulicarius*	23.6	Sooty Shearwater	*P. griseus*	22.9	Sooty Shearwater	*P. griseus*	22.9
5	Juan Fernandez Petrel	*Pt. externa*	23.2	Stejneger's Petrel	*Pt. longirostris*	18.7	Stejneger's Petrel	*Pt. longirostris*	14.2
6	Sooty Shearwater	*P. griseus*	22.8	Buller's Shearwater	*T. bulleri*	18.6	Juan Fernandez Petrel	*Pt. externa*	14.0
7	Guanay Cormorant	*Ph. bougainvillii*	14.4	Pink-footed Shearwater	*P. creatopus*	15.1	Red Phalarope	*Phal. fulicarius*	13.0
8	Stejneger's Petrel	*Pt. longirostris*	9.7	Southern Fulmar	*Fulmarus glacialoides*	10.5	Buller's Shearwater	*T. bulleri*	11.0
9	Magellanic Penguin	*Spheniscus magellanicus*	7.5	Narrow-billed Prion	*Pachyptila belcheri*	6.3	Pink-footed Shearwater	*P. creatopus*	9.6
10				Cape Petrel	*D. capense*	6.0	King Cormorant	*Ph. atriceps*	7.8
11							Southern Fulmar	*F. glacialoides*	5.2
12							Magellanic Penguin	*S. magellanicus*	5.0