

Distribution, abundance, habitat use and behaviour of three *Procellaria* petrels off South America

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Abstract We studied the distribution along the Pacific coast of South and Central America of three large petrels species that nest on New Zealand and subantarctic islands: white-chinned petrel (*Procellaria aequinoctialis*), Parkinson's petrel (*P. parkinsoni*) and Westland petrel (*P. westlandica*). During 15 cruises from 1980 to 1995, we conducted 1,020 hrs of surveys over 14,277 km² of ocean from the shoreline to 1500 km off the coast from Chile north to Panama, and recorded 2114, 179, and 20 individuals, respectively, of the three species. White-chinned petrels occurred throughout the study area, but were most abundant off Chile, Parkinson's petrels were most abundant along the coasts of Ecuador and Peru, and Westland petrels off southern Chile. All three species preferred waters over the continental slope, although Parkinson's petrel was abundant also over the continental shelf during the austral winter. Densities of each species were positively related to oceanographic properties that are associated with upwelling features. Abundance estimates, analyzed using generalized additive models, peaked during the non-breeding season of each species. Estimates were 722,000 White-chinned petrels during austral autumn (95% confidence interval "CI" = 349,000 – 907,000); 38,000 Parkinson's petrels during austral autumn (95% CI = 28,000 – 50,000); and 3,500 Westland petrels during the austral spring (95% CI = 2,000 – 6,400). Scavenging appeared to be the primary feeding method of *Procellaria*, a habit that would make them susceptible to mortality as a result of their regular association with commercial fishing operations, particularly the recently developed long-line fishery on the continental slope of Chile.

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INTRODUCTION

The white-chinned, spectacled, Parkinson's and Westland petrels (*Procellaria aequinoctialis*, *P. conspicillata*, *P. parkinsoni*, and *P. westlandica*, respectively) are all southern hemisphere species. The White-chinned petrel has a circumpolar distribution (Marchant & Higgins 1990) and is the most abundant of the *Procellaria*, nesting on southern archipelagos including Iles Crozet and Iles Kerguelen in the southern Indian Ocean, South Georgia Island, and islands in the New Zealand subantarctic. The spectacled petrel breeds only on Inaccessible Island of the Tristan group in the South Atlantic Ocean (estimated population 2,000 breeding birds; Enticott & O'Connell 1985; Fraser *et al.* 1988) and occurs in the Atlantic sector of the Southern Ocean from eastern South America to South Africa. Of the two, only white-chinned petrel has been observed off the west coast of South America. The Parkinson's and Westland petrels are

both endemic to New Zealand and occur primarily in the Pacific Ocean (Best & Owen 1976; Marchant & Higgins 1990) east to the Americas (Jehl 1974; Imber 1987; Pitman & Ballance 1992; Brinkley *et al.* 2000). The Westland petrel occurs also in the southwestern Atlantic Ocean (Brinkley *et al.* 2000).

These birds are difficult to census while breeding because they nest in burrows and are active at their colonies only at night. The Parkinson's and Westland petrels are especially problematic because of their scattered distribution in heavily-forested precipitous terrain (Imber 1987; Marchant & Higgins 1990), whereas the white-chinned petrel nests on subantarctic islands that are rarely visited and where any attempts at counting are infrequent (M. Imber pers. comm.).

Numbers of breeding white-chinned petrels about New Zealand have been estimated at 200,000 birds on Disappointment Island, Auckland Islands, 200,000 on Antipodes and adjacent islands, and 20,000 birds on the Campbell group (Taylor 2000). An estimate for the South Georgia archipelago is four million (Croxall *et al.* 1984), and tens to

hundreds of thousands breeding on Iles Crozet and the Kerguelen archipelago (Jouventin *et al.* 1984; Weimerskirch *et al.* 1989). Thus, there may be seven million white-chinned petrels in total (Brooke 2004).

The number of breeding Parkinson's petrels was estimated at 3 - 4,000 birds (Imber 1987; Bell & Sim 2000), and the Westland petrel was thought to number 2 - 10,000 breeding birds; both populations may be increasing (Marchant & Higgins 1990; E. Bell, pers.comm). The world population of Parkinson's petrel was estimated at 10,000 birds (Taylor 2000).

The pelagic range of Parkinson's petrels in waters off the coast of the Americas is from southern Mexico to northern Peru (Pitman & Ballance 1992), that of Westland petrels is from southern Peru to southern Chile, including extensive use of inland Chilean fjords (Brinkley *et al.* 2000; P. Scofield unpubl. data), while white-chinned petrels range from northern Peru to southern Chile (Murphy 1936). However, we are not aware of quantitative information on the distribution, abundance and habitat preferences of these species in these waters. Although Pitman

& Ballance (1992) reported the distribution and abundance (number of birds observed per 2° latitude × 2° longitude grid block) of Parkinson's petrels in the eastern Pacific, quantitative interpretation of their plot is problematic because grid blocks differed in survey effort.

Detailed information on the distribution, abundance, and behaviour of these petrels in waters off South America is now of particular interest because of the long-line fishery for the Patagonian toothfish (*Dissostichus eleginoides*) on the Chilean continental slope (Moreno 1991) and insular shelves of subantarctic islands. This fishery has caused substantial mortality of Procellariiformes (Moreno *et al.* 1996, Ryan *et al.* 1997). Indeed, many breeding populations of Procellariiformes have decreased markedly due to increased fisheries-induced mortality: after being attracted to baits, they are hooked and drowned by the long-line fisheries (Jouventin *et al.* 1984; Weimerskirch *et al.* 1987; Croxall *et al.* 1990; Murray *et al.* 1993). While there is no direct evidence that any of the three *Procellaria* species have been affected by the toothfish fishery operating off Chile, an effect could be expected

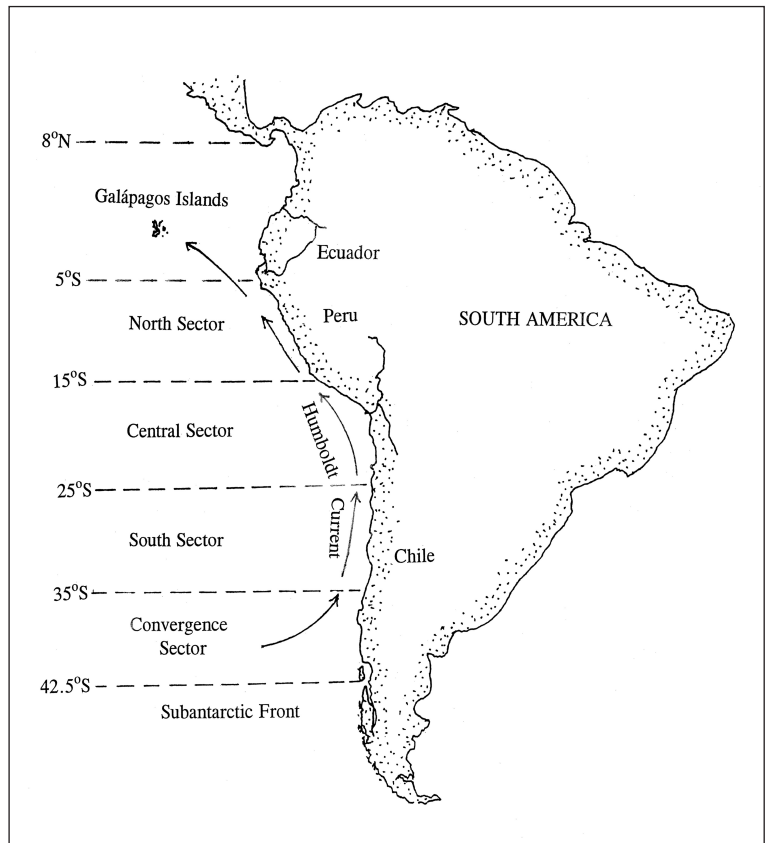


Figure 1 Study area, including designated sectors within the Humboldt Current System (from Wyrski 1967; Paulik 1981).

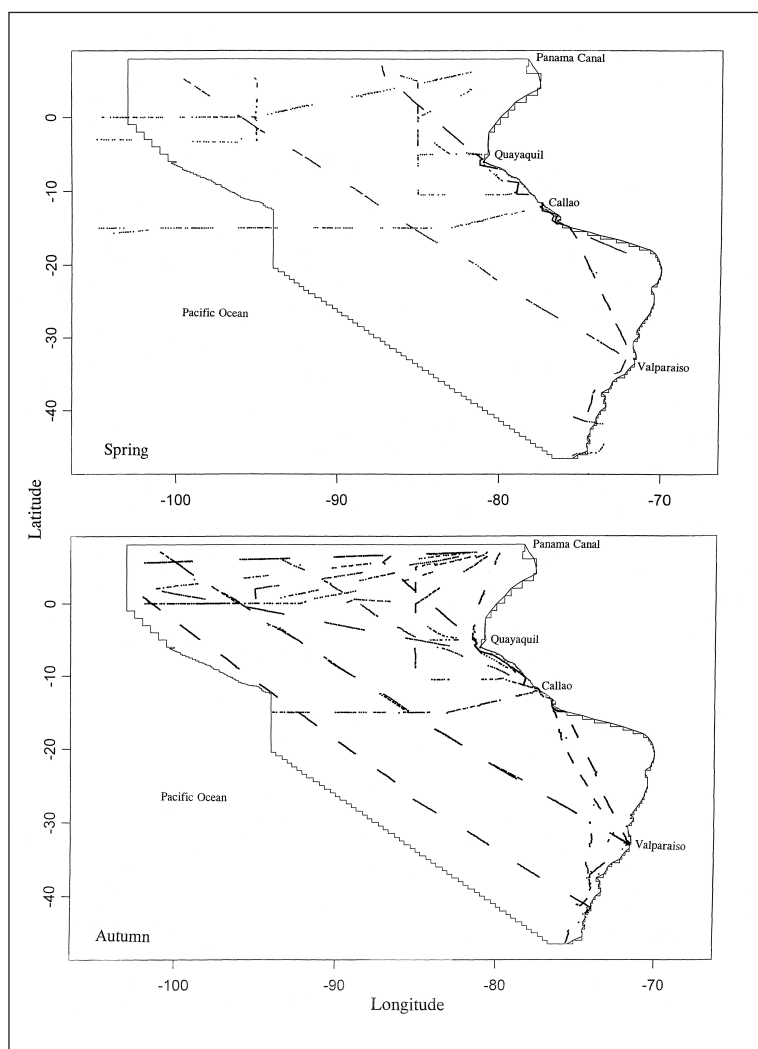


Figure 2 Survey cruise tracks within the study area during the austral spring (top) and autumn (bottom), 1980-1995. Each dot represents one survey transect. Some cruise tracks were repeated on different cruises.

if a sufficient number of these birds occurred on the fishing grounds, as these species are readily attracted to discarded offal and bycatch (Jackson 1988; Murray *et al.* 1993; Catard *et al.* 2000).

The aims of this study were fourfold: to describe quantitatively the seasonal distributions of these three petrels in waters within about 2000 km of the west coast of South America; to estimate the seasonal abundance of each species in that area based on densities (birds/km² of ocean) observed during surveys at sea; to describe petrel distributions based of the relation between petrel density and oceanographic variables; and to assess the importance of different ocean habitats (continental shelf, slope, and Pacific basin waters) as foraging areas and report on the birds' foraging methods.

BACKGROUND

Breeding chronology

The annual cycles of these petrels were reviewed by Marchant & Higgins (1990). This information is important for understanding their presence in the eastern Pacific. In summary, white-chinned petrels breed in the austral spring and summer from October to May, and Parkinson's petrels from November to June. Westland petrel breeds in the austral autumn and winter from March to November. Hereafter, all references to season refer to the austral time frame.

In accord with this chronology, adults and fledged young of white-chinned and Parkinson's petrels are expected to be most abundant at sea during winter (June to September), those of Westland petrels during spring and summer (November to

February). However, subadults, most of which remain at sea throughout the year, should show little seasonal variation.

Oceanographic characteristics of the study area

The Humboldt Current System (HCS) is the most productive of the world's five eastern boundary currents (Paulik 1981). The system begins where south Pacific temperate water, flowing east along the northern edge of the subantarctic front, meets the Chilean coast between about 40° and 50°S (Fig. 1). Thereafter, flow is northward to 5°S, where the current flows northwestward toward the Galapagos Islands (Wyrтки 1967). The western boundary of the HCS is not well defined. South of 15°S it generally consists of waters with surface salinity <35.0 ppt; to the north of 15°S salinities are <35.3 ppt. Based on this information and the oceanographic data that we collected, during this study the HCS extended 300 - 600 km offshore north of 15°S, and 150 - 300 km offshore south of 15°S (see also Paulik 1981).

The HCS consists of several independent branches (Wyrтки 1967; Thompson 1981). It is well developed at 35°S with formation of a strong seasonal thermocline. At about 25°S, it splits into the (inshore) Humboldt Coastal Current, and the (offshore) Humboldt Oceanic Current. Between them, a counter-current flows near the surface towards the south. Maximum upwelling in the HCS occurs during the austral 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). Sea-surface salinity in the HCS increases from south to north and from east to west (Wyrтки 1967). In general, sea-surface temperature is usually more uniform from south to north, compared to the increase in temperature with increase in distance from shore.

Based on the above, and to better describe distributions of the *Procellaria* relative to risk on South American fishing grounds, we divided the HCS into six sectors (Fig. 1): 1- the "Subantarctic sector" (42.50°S to 48°S); 2- the "Convergence sector," (35°S to 42.50°S); 3- the "South sector," (25°S to 35°S); 4- the "Central sector," (15°S to 25°S); 5- the "North sector," (5°S to 15°S); and 6- the "Galapagos Islands sector" (5°S to 8°N). Because Parkinson's petrel was confined to sectors 5 and 6, to describe the distribution of that species we further subdivided those two sectors (see Results).

We also recognized three habitat zones based on ocean depth: 1- the continental shelf, depth < 201 m; 2- continental slope, 201 to 2,000 m depth; and 3- pelagic or basin waters, >2,000 m depth.

METHODS

Identification

All three species are all dark (brownish black) but differ regarding bill color and body size. We distinguished white-chinned petrels from Parkinson's and Westland petrels by the lack of any dark coloration on their light gray to whitish-green bills, whereas bills of the latter two species have strongly demarcated black superior and inferior unguicorns (Marchant & Higgins 1990). We distinguishing between Westland and Parkinson's petrels by size; Parkinson's petrel is about 75% the size of Westland petrel (and white-chinned). Thus, when Parkinson's is in the company of either of the other two *Procellaria*, size is a good distinguishing feature, however, when either of the two black bill-tipped species are observed alone, identification is more difficult. In the latter situations, we relied on observation of relative size of other associated species and the more thickset structure of Westland compared to Parkinson's (see also Marchant and Higgins 1990).

Surveys and monitoring of environmental variables

We undertook 15 cruises, one in 1980 and the others in 1985-1995, in the HCS and Panama Bight between latitudes 8°N and about 50°S, and between the coast of the Americas and waters 1725 km offshore (Fig. 2). We define those waters as the "study area". We used a 1725 km cutoff for analyses of abundance and habitat preference because we observed no *Procellaria* during extensive surveys beyond that limit (see Results), and because we needed to minimize the number of surveys having density values of zero in the analyses (see Methods - Statistical analyses). Surveys were conducted during the austral autumn/winter (March to August), coinciding with the non-breeding season of white-chinned and Parkinson's petrels and the breeding season of Westland petrels, and spring/summer (November to January) when white-chinned and Parkinson's petrels were breeding, but not Westland petrels. We report seasonal results as pertaining to "autumn" or "spring" because most surveys occurred during those seasons.

These birds were infrequently attracted to our research vessels, possibly because, at our request, the ship's garbage was rarely tossed overboard during the day. With two or three observers working simultaneously, we conducted continuous strip-surveys from dawn to dusk while the ship was underway. Surveys over the continental shelf and slope (where environmental variables changed more rapidly than over deeper pelagic waters) were usually partitioned into 15 min. transect intervals, and those over pelagic waters were usually partitioned into 30 min.

transects. Exceptions included those terminated when the ship stopped at an oceanographic station. Petrels seen within a 90° quadrant on one forequarter were counted. Strip widths were 400 to 600 m, varying according to observer height above sea level, which was 12–16 m (see Spear *et al.* in press). Strip width was calibrated after Heinemann (1981) and Spear *et al.* (in press), and periodically validated with ship's radar on objects of known distance. By noting ship speed (km/hr), we calculated surface area of ocean surveyed. Within the study area, we observed for 1,020 hr and surveyed 14,277 km² of ocean: 9,688 km² during autumn and 4,589 km² during spring.

For each sighting we noted behaviour: resting on the water, feeding or circling over a potential food source, attracted to the ship, or flying in a steady direction. For the latter behaviour, we noted flight direction to the nearest 10°. We adjusted observed numbers of petrels (hereafter termed the "adjusted count") to correct for movement of transiting birds (Spear *et al.* 1992; flight speeds from Spear & Ainley 1997). For foraging individuals we noted feeding method. We recorded as "attractees" only those birds that approached from the direction extending from the 90° forequarter being surveyed (Spear *et al.* in press). Thus, we did not record birds that approached from the other side or the rear of the ship. Birds were deemed as attractees if they changed their flight direction to inspect the ship. Although ship attraction was not problematic in this study (see Results, Behaviour at sea), each attractee was given a value of 0.3. This method has been validated with acceptable results for estimating abundance of a large larid that is prone to follow ships (Clarke *et al.* 2003).

Further data recorded for each transect were ship position and course, water depth (m), sea-surface temperature (°C) and salinity (ppt), thermocline depth (m) and "strength" (see below), wind direction (nearest 10°), and wind speed (km/h). Thermocline depth and strength was monitored using expendable bathythermographs (XBTs). We define "thermocline depth" as the point where the warm surface layer met cooler water below; i.e., the shallowest inflection point as determined visually from XBT printouts plotting temperature as a function of depth. We measured "thermocline strength," or the intensity of the stratification of that layer, as the temperature difference (to the nearest 0.1°C) between the first obvious thermal inflection and a point 20 m below it. If no obvious inflection was present then the thermocline depth was recorded as zero (= at the surface). A region with strong upwelling or mixing in the water column has a shallow thermocline with little thermal stratification; the reverse is true where little mixing is occurring.

Statistical analyses

Generalized additive models

Using the programs developed by Clarke *et al.* (2003), we employed S-Plus (1997) to examine the seasonal distributions and abundance of the petrels with generalized additive models (GAMs; see Hastie & Tibshirani 1990). GAMs were used to deal with our non-random survey effort (including under-surveyed areas) in combination with the non-random distributions of the petrels. Being model-based, rather than sample-based, GAMs overcome such bias. They also capture complex nonlinear trends in density while using only a few parameters. Specifically, only four independent variables (latitude, longitude, ocean depth, and distance to the mainland) were initially included in each model. Therefore, besides increasing accuracy, with small *df* they considerably improve the precision of abundance estimates among marine biota (compared to previously used analytical procedures), which usually have extremely variable (clumped) densities over their pelagic ranges (e.g., Hunt 1990).

Modelling spatial distributions

GAMs were fitted using the observed petrel counts during each survey segment (see below) as the response variable. Segments outside the study area were excluded (Fig. 2). Based on segment position, ocean depth and distance to mainland were calculated using coastline and bathymetry data obtained from

<http://rimmer.ngdc.noaa.gov/mgg/coast/getcoast.html> and <http://iridl.ldeo.columbia.edu/SOURCES/WORLDBATH/>, respectively.

Count data are often modelled using a Poisson error structure, in which the variance is equal to the mean (McCullagh & Nelder 1989). However, when birds occur in clusters, the variance of the counts is more dispersed than implied by a Poisson distribution. Therefore, we modelled these data using the Poisson variance function and estimating a dispersion parameter, which we incorporated into the model selection procedures (e.g., Venables & Ripley 1997). Observed counts must be adjusted for bird movement and depend on the area surveyed within each segment, so we used the logarithm of the area surveyed multiplied by the bird-movement adjustment factor (which varies for each data point) as an offset. The logarithm was used because we used a log link function.

Estimation of abundance

Once fitted, a GAM provides a smooth average density surface over the area of interest, including unsampled areas. Abundance was estimated by integrating numerically under this surface. This was done by first creating a fine grid across the

study area. The fitted surface was then used to predict the average number of birds in each grid-square. Finally, abundance was estimated as the sum of the predicted numbers over all grid-squares within the study area.

Bootstrap variance estimation

To control for the correlation between counts from survey segments that were close in space and time, confidence intervals for population size were obtained using an adaptation of a moving-blocks bootstrap (Efron & Tibshirani 1993): the data are re-sampled with replacement from all possible contiguous blocks of some specified length. The block lengths were chosen by taking into account the strength of the autocorrelation between survey segments; the block must be long enough so that observations further than one block length apart are independent.

The block length used was one survey segment. The "length" of each segment was measured as the number of 0.25 - 0.5 hr transects surveyed. The re-sampling algorithm works through the data set, recreating each segment's data in turn. Generating data for a segment involved randomly selecting a segment from the survey data and randomly selecting a transect to start from within that segment. Counts for the survey transects in the original segment were then recreated in turn from the survey transects in the new segment using the semi-parametric bootstrap procedure (Davison & Hinkley 1997) described below. If the end of a segment was reached before enough transects had been re-sampled, the re-sampling was continued at the start of the next segment. For data collected in autumn, there were 374 segments of data with an average of 5.6 transects per day; for spring, these numbers were 211 and 5.0, respectively. The surface area of ocean surveyed per segment was 21.8 ± 9.0 km² in spring and 25.9 ± 10.7 km² in autumn.

A total of 199 bootstrap re-samples were generated for each data set modelled. The model was refitted to each bootstrap re-sample and a new abundance estimate obtained. The coefficient of variation (CV) of the population size estimate was calculated by dividing the sample standard deviation of the scaled bootstrap estimates by the original abundance estimate. The 95% confidence intervals (CI) were estimated using the percentile method (Davison & Hinkley 1997).

GAMs have not yet been sufficiently developed to examine interactions between two independent environmental/temporal variables. Therefore, we used multiple linear regression (Stata Corp. 1995) to examine the relationships between petrel distributions and habitat variables. Independent variables included in regression models were sea-surface temperature and salinity, thermocline

depth and strength, and wind speed. The sample unit was one 0.25 - 0.5 hr survey transect. Transects were excluded from regression analyses if there was missing data for independent variables. Details of our use of multiple regression are described in Spear *et al.* (2003).

We log-transformed petrel densities to satisfy assumptions of normality (skewness/kurtosis test for normality of residuals, $P > 0.05$). All ANOVAs were conducted using log-transformed density values (calculated as: $\log[\text{density} + 0.1] / \log[10]$), which is considered appropriate for data having a Poisson distribution (Kleinbaum *et al.* 1988). Although the residuals were not normally distributed in all analyses, we consider this unimportant because least-squares regression (ANOVA) is very robust with respect to non-normality (Seber 1977; Kleinbaum *et al.* 1988). Although they yield the best linear unbiased estimator in the absence of normally distributed residuals, P values near 0.05 must be regarded with caution (Seber 1977, Ch. 3). Therefore, we accepted significance in regression analyses at $P < 0.025$ instead of $P < 0.05$. For other analyses, significance was accepted at $P < 0.05$.

We used Sidak multiple comparison tests, an improved version of the Bonferroni test (SAS Institute, Inc. 1985), to compare each habitat variable statistically among species. We also conducted a principal components analysis (PCA) in conjunction with ANOVA to compare overall habitat use among the three *Procellaria* species on a seasonal basis. Habitat variables were the same as those used in the regression analyses. The sample size for PCA analyses was equal to the number of *Procellaria* recorded, including 570 birds in spring and 1743 in autumn. Other than providing information about seasonal differences in the responses of each petrel species, the PCA is a means of determining which of the five habitat variables were most important in affecting the *Procellaria* as a group.

To test for significant differences in overall habitat use among the three *Procellaria*, we used two one-way ANOVAs. In the first, we tested for differences among the PC1 scores of the data representing each species; in the second we compared PC2 scores among those data. We considered differences between two species to be significant if either or both of the PC1 or PC2 scores differed significantly between them.

Procellaria densities per survey transect were weighted in the regression analyses by the area surveyed to control for differences in area surveyed per transect. Densities are reported as birds/100 km², and, unless noted otherwise, were calculated as the adjusted number of birds divided by the area (km²) surveyed, multiplied by 100. Unless noted otherwise, means are reported as $\pm$ one standard

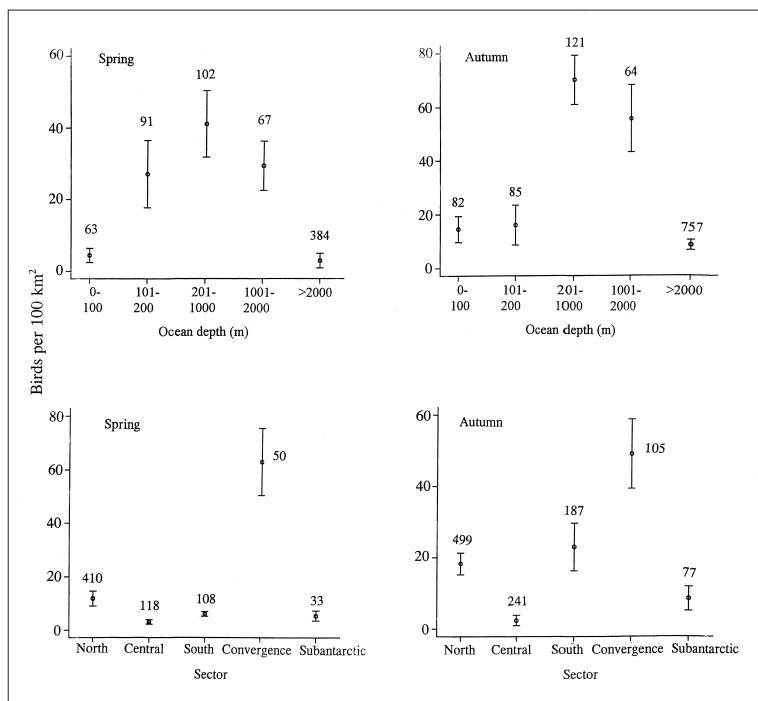


Figure 3 Densities (mean $\pm$ SE) of white-chinned petrels relative to ocean depth, latitude sector, and season within the study area. Values adjacent to means are sample sizes (number of survey transects).

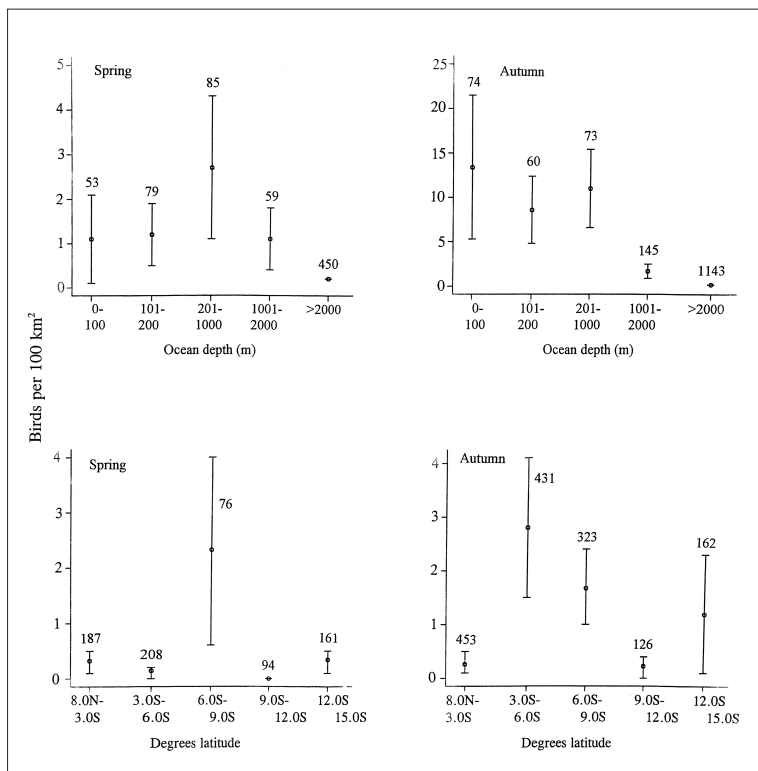


Figure 4 Densities (mean $\pm$ SE) of Parkinson's petrels relative to ocean depth, latitude, and season within the study area. Values adjacent to means are sample sizes (number of survey transects).

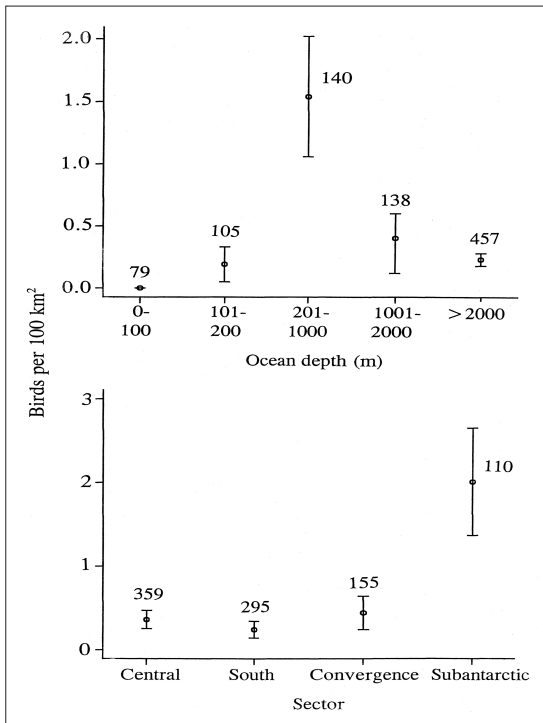


Figure 5 Densities (mean $\pm$ SE) of Westland petrels relative to ocean depth and latitude sector within their range in the study area. Values adjacent to means are sample sizes (number of survey transects). Seasons were grouped due to the low number of sightings for this species.

deviation. For brevity, hereafter we use scientific names of *Procellaria* (i.e., "*aequinoctialis*, *parkinsoni*, *westlandica*") except in tables and figures.

RESULTS

Number of sightings and distributional range

The adjusted number of recorded *aequinoctialis*, after correction for flux, was 1906.5 (raw count = 2114 birds). We did not observe this species north of 4.38°S or west of 93.95°W. We recorded 179 *parkinsoni* (adjusted count = 154.5) from 8.02°N to 13.93°S, and 20 *westlandica* (adjusted count = 16.3) between 19.65°S and 50.72°S. We recorded only three *parkinsoni* west of 95°W and none beyond 101.10°W, all near the Equator and in waters where our survey effort was greatest. We recorded no *westlandica* west of 81.70°W, and for the purpose of this study considered the sighting of a *westlandica* at 50.72°S as having occurred within the study area.

Distributions of all three species showed distinct patterns relative to ocean depth and latitude. During both spring and autumn, *aequinoctialis* occurred in significantly higher densities over the continental

slope than the shelf and basin waters (Sidak tests, all $P < 0.05$; Fig. 3); in spring *aequinoctialis* densities were also higher over the slope than basin. Significantly higher *parkinsoni* densities occurred over the continental slope than the basin during autumn and spring (Sidak tests, all $P < 0.05$; Fig. 4). Their densities were also higher over the shelf than basin in autumn, but did not differ significantly between those two zones during spring. Densities of *westlandica* were also higher over the continental slope than shelf and pelagic zones (Sidak tests, all $P < 0.05$; Fig 5; seasons grouped due to small number of sightings); density did not differ between the latter.

Latitudinally, *aequinoctialis* was most abundant in the Convergence sector, especially in spring (Fig. 3); *parkinsoni* was most abundant from 3°S to 9°S (Fig. 4); and highest densities of *westlandica* were observed in the Subantarctic sector (Fig. 5; seasons grouped due to small number of sightings).

Relationship between petrel density and environmental variables

Results of the regression analyses explained 30% of the variation in *aequinoctialis* density (Table 1). Density of *aequinoctialis* was significantly higher in the austral autumn than spring, but increased significantly with decrease in sea-surface temperature, thermocline depth and strength, and with increase in sea-surface salinity and wind speed. Significant interactions of season with sea-surface temperature and salinity, and thermocline depth and strength reflected stronger relationships of *aequinoctialis* density with sea-surface temperature and thermocline depth and strength during spring than during autumn. Similarly, there were stronger relationships with sea-surface salinity during autumn compared to spring. These results indicate a preference for stronger winds and stronger upwelling/mixing in the water column, especially during spring.

The regression analysis explained 4% of the variation in *parkinsoni* density (Table 1). Densities were significantly higher in autumn than spring, and increased significantly with decrease in sea-surface temperature and thermocline strength. A significant interaction of season with thermocline strength reflected a stronger relationship of *parkinsoni* density with thermocline strength during autumn than spring. Similar to *aequinoctialis*, these results indicate a preference among *parkinsoni* for stronger upwelling/mixing in the water column.

Oceanographic habitat compared among species

During autumn and spring, *aequinoctialis* occurred in cooler waters than did the other two species (Table 2, Fig. 6) while *parkinsoni* was found in

Table 1 Regression models to identify significant oceanographic variables associated with white-chinned and Parkinson's petrel density in the Humboldt Current; Westland petrel densities were too low to allow regression analyses. For white-chinned petrels, survey transects numbered 1509 (autumn 805, spring 704) and model variance explained = 29.8%. For Parkinson's petrels, survey transects numbered 2035 (autumn 1312, spring 723) and variance explained = 4.0%. Density, the dependent variable, was log transformed. Season was analyzed as continuous where values "1" = autumn, and "2" = spring. Quadratic terms are terms having nonlinear relationships with density; linear terms were calculated after respective quadratic terms had been dropped from the model. Asterisks denote interactions between season and independent terms. All numerator *df* = 1; ns = not significant; na = not applicable.

Term	White-chinned petrel			Parkinson's petrel		
	Coefficient sign	F-value	P-value	Coefficient sign	F-value	P-value
<i>Main effects:</i>						
Season	(-)	165.0	<0.001	(-)	11.7	<0.001
Sea-surface temp.	(-)	256.1	<0.001	(-)	6.2	<0.02
Sea-surface salinity - linear	(+)	19.8	<0.001	ns	0.9	
- quadratic				(+)	5.9	<0.025
Thermocline depth	(-)	60.7	<0.001	ns	0.6	0.4
Thermocline strength – linear	(-)	27.3	<0.001	(-)	17.3	<0.001
- quadratic				(+)	11.0	<0.001
Wind speed – linear	(+)	250.8	<0.001	ns	0.2	0.7
- quadratic	(-)	149.3	<0.001			
<i>Interactions:</i>						
Season * Sea-surface temperature	na	14.7	<0.001			
Spring	(-)	141.4	<0.001			
Autumn	(-)	28.1	<0.001			
Season * Sea-surface salinity	na	11.3	<0.001			
Spring	(+)	33.9	<0.001			
Autumn	(+)	85.0	<0.001			
Season * Thermocline depth	na	8.8	<0.01			
Spring	(-)	25.4	<0.001			
Autumn	(-)	11.4	<0.001			
Season * Thermocline strength	na	50.5	<0.001	na	11.3	<0.001
Spring	ns	0.2	0.7	ns	3.3	0.07
Autumn	(-)	37.6	<0.001	(-)	34.9	<0.001

Table 2 Ocean habitat characteristics (mean $\pm$ SD) associated with white-chinned, Parkinson's, and Westland petrels observed in the Humboldt Current, by season, 1980-1995. Values of *n* are the number of birds recorded.

Species (<i>n</i>)	Sea surface temperature (°C)	Sea surface salinity (ppt)	Thermocline depth (m)	Thermocline strength (°C change)	Wind speed (km/hr)
Autumn					
White-chinned petrel (1577)	17.6 $\pm$ 3.2	34.26 $\pm$ 1.17	26 $\pm$ 15.2	2.4 $\pm$ 0.9	19 $\pm$ 8.5
Parkinson's petrel (159)	22.9 $\pm$ 4.0	34.80 $\pm$ 0.46	24 $\pm$ 8.4	2.1 $\pm$ 1.3	19 $\pm$ 6.4
Westland petrel (7)	15.2 $\pm$ 4.6	30.77 $\pm$ 3.90	22 $\pm$ 4.9	2.0 $\pm$ 0.6	2.0 $\pm$ 0.6
Spring					
White-chinned petrel (537)	16.9 $\pm$ 1.8	34.31 $\pm$ 1.03	16 $\pm$ 12.4	3.0 $\pm$ 0.7	23 $\pm$ 8.0
Parkinson's petrel (20)	20.0 $\pm$ 1.2	34.94 $\pm$ 0.21	8 $\pm$ 10.4	2.6 $\pm$ 1.1	18 $\pm$ 7.7
Westland petrel (13)	15.2 $\pm$ 4.6	33.75 $\pm$ 1.13	19 $\pm$ 0.12.2	2.4 $\pm$ 1.9	25 $\pm$ 10.6

Table 3 Principal component (PC) analyses for the relationship between five habitat variables and the occurrence of white-chinned, Parkinson's, and Westland petrels recorded during autumn and spring in the Humboldt Current. A PC analysis was performed for each season. Table divided into two parts: (a) eigenvalues and cumulative proportions of variance explained by each, and (b) the five habitat variables with eigenvector loadings given for each season. Sample sizes are given in Table 1.

A			B				
Eigen-value	Cumulative Proportion		Habitat Variable	Eigenvector Load:			
	Autumn	Spring		Spring PC1	Spring PC2	Autumn PC1	Autumn PC2
1	0.31	0.50	Sea surf. temp.	0.54	0.46	0.44	0.61
2	0.55	0.73	Sea surf. salinity	0.70	-0.08	0.56	0.32
3	0.75	0.92	Thermocline depth	0.33	0.19	-0.54	0.34
4	0.92	0.97	Therm. strength	-0.23	0.49	-0.40	0.64
5	1.00	1.00	Wind speed	-0.20	0.71	0.21	-0.06

	Autumn			Spring		
	Low	High		Low	High	
Sea-surface temperature	PETW	PETH	PETB	PETW	PETH	PETB
Sea-surface salinity	PETW	PETH	PETB	PETW	PETH	PETB
Thermocline depth	PETW	PETB	PETH	PETB	PETH	PETW
Thermocline strength	PETW	PETB	PETH	PETW	PETB	PETH
Wind speed	PETB	PETH	PETW	PETB	PETH	PETW

Figure 6 Comparisons between white-chinned (PETH), Parkinson's (PETB), and Westland (PETW) petrels for association with five oceanic variables during austral autumn and spring. Analyses by Sidak multiple comparison test. Lines connecting species indicate insignificant differences.

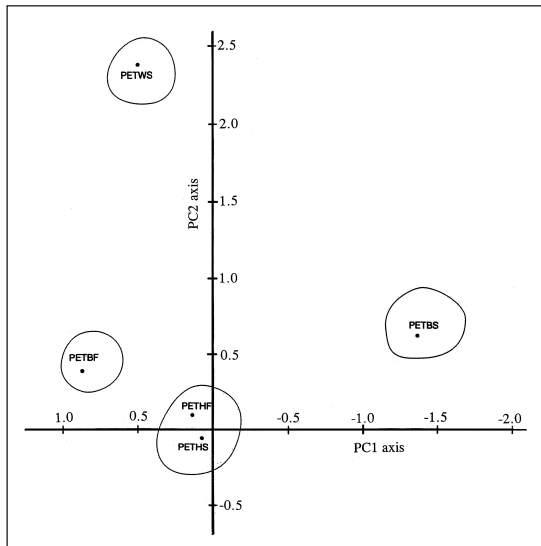


Figure 7 Principal component analysis of the relationship of five habitat variables among white-chinned, Parkinson's, and Westland petrels during autumn (F) and spring (S). See Fig. 5 for species codes. Species/season enclosed in circles are significantly different from others.

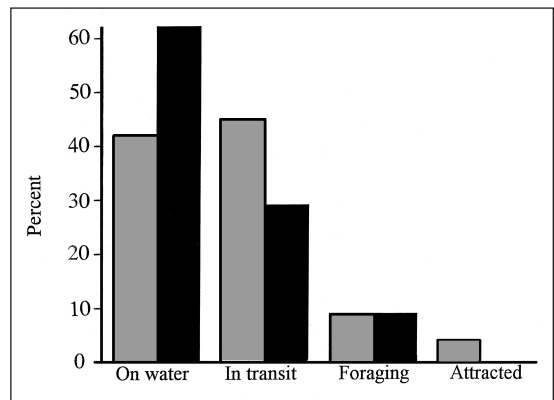


Figure 8 Behavioural allocation of white-chinned petrels (light bar) and Parkinson's petrels (dark bar) observed during at-sea surveys off the coast of South America, 1980-1995. Analyzed were the raw numbers (see Results; Numbers recorded).

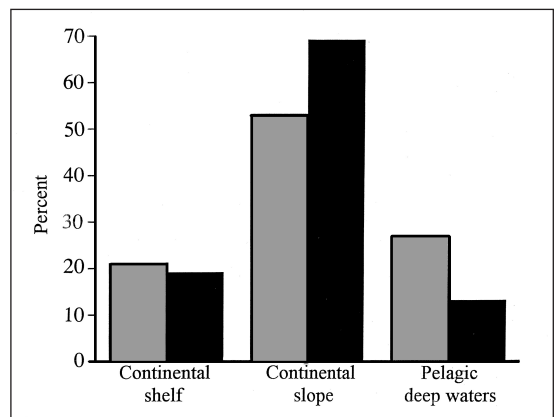


Figure 9 Proportion of feeding white-chinned Petrels (light bar) and Parkinson's petrels (dark bar) observed during at-sea surveys in different marine habitats off the coast of South America, 1980-1995. See Methods for definition of shelf, slope, and pelagic waters. Analyzed were the raw numbers (see Results; Numbers recorded).

waters of higher temperature and salinity than was *aequinoctialis* or *westlandica* during both spring and autumn. Temperature and salinity differed little between the habitats of the latter two species. In regard to thermocline depth, values differed little between the three species in autumn, although during spring, *parkinsoni* occurred where thermocline depths were shallowest, and *westlandica* and *aequinoctialis* where thermocline depths were deeper. Each species occurred in relatively mixed waters (i.e., those having low thermocline strength); thermocline strength differed little among them in either season. Wind speed did not differ among the three species in autumn. In spring *westlandica* was associated with stronger wind speed than *parkinsoni*

but wind speed did not differ between *parkinsoni* and *aequinoctialis*.

PC analyses for the autumn period, relating *Procellaria* occurrence to five more important oceanographic variables (Table 3), indicated significant differences in overall habitat use by *aequinoctialis* and *parkinsoni* (Fig. 7); the sample size of *westlandica* was too small to include in this analysis. Important oceanographic variables, in order of importance, were: PC axis 1 — sea-surface temperature and salinity; and PC axis 2 — wind speed, thermocline strength, and sea-surface temperature (Table 3). The separation of *parkinsoni* from *aequinoctialis* occurred primarily on the PC1 axis, reflecting the preferences of each species for

Table 4 Marine mammal species recorded (number of sightings and number of animals), including number of associated white-chinned (PETH) and Parkinson's petrels (PETB) during cruises within the Humboldt Current study area, 1980-1995.

Species	Sightings (n)	Animals (n)	Petrel Associations	
			PETH	PETB
Blue whale <i>Balenoptera musculus</i>	1	2	0	0
Unid. rorqual <i>Balenoptera</i> sp.	4	5	0	0
Sperm whale <i>Physeter macrocephalus</i>	7	23	0	0
Unid. pilot whale <i>Globicephala</i> sp.	12	132	4	0
False killer whale <i>Pseudorca crassidens</i>	8	90	11	1
Risso's dolphin <i>Grampus griseus</i>	6	45	2	0
Melon-headed whale <i>Peponocephala electra</i>	3	31	3	0
Killer whale <i>Orcinus orca</i>	1	8	0	0
Bottle-nosed dolphin <i>Tursiops truncatus</i>	22	361	0	0
Common dolphin <i>Delphinus delphis</i>	16	2920	0	0
Spotted dolphin <i>Stenella attenuata</i>	3	125	0	0
Spinner dolphin <i>Stenella longirostris</i>	2	200	0	0
Dusky dolphin <i>Lagenorhynchus obscurus</i>	3	725	0	0
Striped dolphin <i>Stenella coeruleoalba</i>	3	235	0	0
unid. dolphin	7	440	0	0
Bermiester's porpoise <i>Phocoena spinipinnis</i>	3	5	0	0
South American sea lion <i>Otaria flavescens</i>	72	232	11	2
South American fur seal <i>Arctocephalus australis</i>	2	2	0	0

Table 5 Food items contained in four white-chinned petrels collected off South America in August 1987 ($n = 18$ prey). Total with prey = 4. Mass of fishes and cephalopods calculated from equations in Clarke (1986) and Spear *et al.* (in review).

	Number of		Mass		Occurrence	
	prey	(%)	(g)	(%)	Frequency	(%)
Fishes	4	(22.2)	14.4	5.3	3	(75.0)
Argentinidae	1	(5.6)	8.8	3.3	1	(25.0)
<i>Nansenia</i> sp.	1	----	8.8	3.3	----	----
Melamphidae	1	(5.6)	5.6	2.1	1	(25.0)
<i>Melamphaes longivellus</i>	1	----	5.6	2.1	----	----
Unidentifiable Teleosts	2	11.1	0.0	0.0	2	(50.0)
Cephalopoda	14	(77.8)	255.0	94.7	3	(75.0)
Teuthoidea	14	(77.8)	255.0	94.7	3	(75.0)
Ommastrephidae	5	(27.8)	60.0	22.3	2	(50.0)
<i>Sthenoteuthis oualaniensis</i>	4	22.2	48.0	17.8	2	50.0
unident. Ommastrephidae	1	5.6	12.0	4.5	1	25.0
Onychoteuthidae	1	(5.6)	20.0	7.4	1	(25.0)
<i>Onychoteuthis banksii</i>	1	----	20.0	7.4	----	----
Pholidoteuthidae	1	(5.6)	25.0	9.3	1	(25.0)
<i>Pholidoteuthis boschmai</i>	1	----	25.0	9.3	----	----
Octopoteuthidae	1	(5.6)	40.0	7.4	1	(25.0)
<i>Octopoteuthis deletroni</i>	1	----	40.0	7.4	----	----
Mastigoteuthidae	2	(11.1)	70.0	26.0	1	(25.0)
<i>Mastigoteuthis</i> sp.	2	----	70.0	26.0	----	----
Cranchiidae	1	(5.6)	40.0	7.4	1	(25.0)
<i>Galiteuthis pacifica</i>	1	----	40.0	7.4	----	----
Unidentifiable Teuthoidea	3	16.7	0.0	0.0	2	(50.0)

Table 6 Results of generalized additive model analyses to estimate abundance of white-chinned, Parkinson's, and Westland petrels in the Humboldt Current; including 95% confidence intervals (95% CI), and coefficients of variation $\times 100$ (CV). Seasons given in austral time frame. Sample sizes given in Fig. 8.

Species/season	Estimate	95% CI	CV
White-chinned petrel			
Spring/Summer	238,096	211,800 – 300,237	11.5
Autumn/Winter	722,095	348,599 – 907,493	17.2
Parkinson's petrel			
Spring/Summer	12,415	6,486 – 20,520	24.3
Autumn/Winter	37,950	28,268 – 49,806	11.6
Westland petrel			
Spring/Summer	3,464	2,053 – 6,388	25.3

different sea-surface temperature and salinity regimes (Fig. 6).

During spring, overall habitat use differed significantly between each of the three species (Fig. 7). Important habitat variables were: PC1 — sea-surface salinity and thermocline depth; and PC2 — thermocline strength and sea-surface temperature (Table 3). Again, the separation of *parkinsoni* from *aequinoctialis* occurred primarily on the PC1 axis, reflecting differences between them in use of salinity and thermocline depth (Table 2). Habitat use did not differ significantly between spring and autumn among *aequinoctialis* (Fig. 7). We are puzzled by the wide separation of *westlandica* from *aequinoctialis* and *parkinsoni*, as their overall oceanographic affinities were relatively consistent (Fig. 6).

Behaviour at sea

Allocation of behaviours — resting on the water, foraging, flying in transit, and being attracted to the survey vessel, differed significantly between *aequinoctialis* and *parkinsoni* ($\chi^2 = 29.04$, $df = 3$, $P = <0.0001$; proportional differences compared among counts, not percents, Fig. 8), due to a higher proportion of *parkinsoni* recorded sitting on the water and a lower proportion in transit. A low percentage, only of *aequinoctialis*, was recorded as attracted to the survey vessels.

The proportion of birds observed feeding in three habitat zones did not differ significantly between *aequinoctialis* and *parkinsoni* ($\chi^2 = 1.85$, $df = 2$, $P = 0.4$; proportional differences compared among counts, not percents, Fig. 9). Both species fed primarily over the continental slope.

Foraging behaviour

Of 193 observations of *aequinoctialis* foraging, 64% were associated with fishing vessels, 6% attended South American sea lions, 20% were feeding on dead cephalopods floating at the surface, and 10% were attending small cetaceans; comparable figures for *parkinsoni* ($n = 16$) were 25%, 13%, 56% and 6% respectively. The frequency with which each method was sighted varied significantly between the two species ($\chi^2 = 12.57$, $df = 3$, $P = <0.01$); *aequinoctialis* foraged more frequently while attending fishing vessels while *parkinsoni* foraged primarily on dead cephalopods floating on the ocean surface. On five occasions, *parkinsoni* were scavenging cephalopods while associated with other seabirds, including: 1 waved albatross (*Phoebastria irrorata*), 1 *parkinsoni*, 1 *aequinoctialis*, 2 Markham's storm-petrels (*Oceanodroma markhami*), 9 black storm-petrels (*O. melania*), 15 Galapagos storm-petrels (*O. tethys*), 8 Elliot's storm-petrels (*Oceanites gracilis*), 2 white-bellied storm-petrels (*Fregetta grallaria*), and 1 band-tailed gull (*Larus belcheri*).

About 38% of the foraging *parkinsoni* were attending fishing vessels and South American sea lions (*Otaria flavescens*) off the coast of Peru; one was associated with false killer whales (*Pseudorca crassidens*; Table 5). No *parkinsoni* attending marine mammals was feeding.

Cetaceans with which *aequinoctialis* foraged included pilot whales (*Globicephala* sp.), false killer whales, Risso's dolphins (*Grampus griseus*), and melon-headed whales (*Peponocephala electra*; Table 4). Most of these associations involved petrels sitting on the water near relatively inactive mammals, but on three occasions the petrels were following or circling transiting animals. We did not see *aequinoctialis* eating prey when associated with cetaceans, but on three occasions we saw them gleaning pieces of flesh becoming detached from large fishes being eaten at the surface by male sea lions. We frequently observed sperm whales (*Physeter macrocephalus*) in the HCS (Table 4), but did not see associations with *Procellaria*.

Foraging *aequinoctialis* were associated with only five of the 16 species of marine mammals recorded in this study (Table 4); these mammals made up 9.6% of all mammals observed. The four cetacean species with which *aequinoctialis* were associated are all among the largest of delphinids. These species accounted for 65% of all *aequinoctialis* - mammal associations; the South American sea lion accounted for the remaining 35%. Similarly, the two species of mammals with which *parkinsoni* were associated made up only 5.8% of all mammals recorded.

Most of the associations between *aequinoctialis* and fishing vessels involved the large fishing fleet operating off central and southern Chile. The two *parkinsoni* associated with fishing vessels included one bird off Guayaquil, Ecuador and another about 75 km north of Callao, Peru.

The number of *Procellaria* we recorded scavenging cephalopods may have been negatively biased because we usually could not determine if birds sitting on the water were attending a prey item (dead squid floating at the surface are often nearly neutrally buoyant and often can not be seen) or were merely resting. On the other hand, use of other feeding methods could be determined at greater distances.

Prey of *aequinoctialis* in the HCS

The prey contained within a sample of four *aequinoctialis* collected in the HCS during winter included, by number, 22% fishes and 78% cephalopods; by mass the proportions were 5% fishes and 95% cephalopods (Table 5).

Both species of fishes included in the diet were mesopelagic (Table 6; Kawaguchi and Butler 1984;

Spear *et al.* in press.). These migrate vertically towards the ocean surface at night, and are absent from surface waters during the day. Two of the six cephalopod families are considered to be epipelagic (Ommastrephids and Onychoteuthids), however the remaining four are considered to be mesopelagic/bathypelagic (Nesis 1987).

Abundance

Our best estimate for the number of *aequinoctialis* was about 722,000 individuals in autumn and 238,000 in spring (Table 6). The 95% CIs indicated that during autumn and spring at least 349,000 and 212,000 of these birds occurred in the HCS, respectively

The estimated number of *parkinsoni* during autumn was 38,000 birds; 95% CIs indicated that no fewer than 28,300 were present during that season (Table 6). During spring, the estimated number was 12,400 *parkinsoni*, with a minimum of 6,500.

The estimated number of *westlandica* was about 3,500 birds during spring/summer (Table 6); 95% CIs indicated that numbers were not lower than 2,000 individuals. Densities of *westlandica* observed during autumn/winter were too low to assess abundance.

DISCUSSION

This paper presents the first quantitative information on the distribution and abundance of the white-chinned, Parkinson's and Westland petrels in the Humboldt Current off South America; as well as their oceanographic affinities, and detailed information on their foraging behaviour there.

Comparison of distributions and ocean habitat by season

Our surveys during the austral autumn coincided with the part of the annual cycle when most breeding adults and recently-fledged young *aequinoctialis* and *parkinsoni* should have been at their wintering areas, whereas our spring surveys coincided with the peak of their breeding season (see Methods: Breeding chronology). In contrast, our autumn surveys occurred during the breeding season of the *westlandica*, and spring surveys during their non-breeding period. Nevertheless, subadults and non-breeders are not constrained to stay within the foraging range of their colonies during the breeding season (as are breeding adults) and can be expected to occur wherever feeding conditions are favourable throughout the year.

During autumn, *aequinoctialis* was observed from Ecuador (4°S) to southern Chile (48°S), but was most abundant off the coast of Chile between 30°S and 48°S; in spring, *aequinoctialis* was confined primarily to waters south of 40°S. Our records of

westlandica occurred from 20°S to about 50°S during both spring and autumn, although that species was most abundant in waters south of 40°S in both seasons. These latitudinal distributions are similar to that observed adjacent to New Zealand breeding areas in summer, where *aequinoctialis* occur from 44°S to 55°S and *westlandica* occur from 40°S to 44°S (Imber 1976). The southern Chilean waters are on the northern side of the convergence zone between South Pacific Temperate Waters (from which the HCS originates) and the cooler waters of the Subantarctic Front.

In contrast, we observed *parkinsoni* from 8°N to 14°S, although this species was most abundant in the northern HCS between 3°S and 14°S during autumn, and from 6°S to 9°S in spring. This latitudinal distribution is more northern than observed for this species during the breeding season off New Zealand, where it occurs from 30°S to 40°S (Imber 1976). The confinement of *aequinoctialis* and *westlandica* to the convergence region is inconsistent with the more favourable feeding conditions in the northern HCS where the continental shelf and slope (areas of strongest upwelling) are much wider than in the south (Murphy 1936; Paulik 1981; and see below). Greater productivity in the north HCS, however, would explain the higher abundance of *parkinsoni* there.

All three species were associated primarily with the continental slope, although, during autumn, *parkinsoni* also was abundant over the continental shelf. Off New Zealand, this species also prefers waters over the shelf break/slope (Marchant & Higgins 1990), and is rarely sighted over shelf waters. Preference for continental slope habitat also was noted among *aequinoctialis* feeding in the Benguela Current off Africa (Enticott & O'Connell 1985; Jackson 1988), in the subantarctic Indian Ocean (Catard *et al.* 2000), and off South Georgia (Croxall *et al.* 1995); *westlandica* also occurs mostly over shelf break/slope waters of New Zealand during their non-breeding season (Marchant & Higgins 1990).

Habitat preference

Within their respective ranges in the HCS, all three *Procellaria* were associated with waters having a shallow, weaker thermocline, indicating a preference for areas of strong upwelling. Similar habitat use was found among Buller's and Salvin's albatrosses (*Thalassarche bulleri* and *T. cauta*, respectively) wintering in the HCS (Spear *et al.* 2003). *Westlandica* and *aequinoctialis* were associated with HCS waters of lower sea-surface temperature and salinity than *parkinsoni*. These results are indicative of the higher latitude coastal waters preferred by the former two species, and the lower latitude coastal waters preferred by the latter.

Foraging behaviour

Comparisons between *aequinoctialis* and *parkinsoni* indicated similar behavioural allocation to resting, foraging, and transiting in the HCS. Foraging frequency for these petrels was highest over continental slope. Thus, foraging incidence of these birds was consistent with their density distributions.

All of our observations of foraging *Procellaria* in the HCS involved scavenging birds, a result consistent with the primary feeding behaviour observed in other studies (Jackson 1988; reviewed in Pitman & Ballance 1992). Scavenging in association with commercial fishing vessels and on dead (floating) cephalopods accounted for about 80% of the foraging *aequinoctialis* and *parkinsoni* recorded, although, regarding use of fishing vessels, this result may have been biased by our frequent transits through heavily fished waters near Valparaíso, Chile. The evidence also indicated that these petrels obtained an appreciable amount of prey by associating with marine mammals, utilizing both cetaceans (about 10% of our foraging observations) and pinnipeds (6% of our foraging observations). The association of *Procellaria* with cetaceans has been documented for *parkinsoni* feeding off Central and South America (Pitman & Ballance 1992) and for *aequinoctialis* in the Benguela Current (Jackson 1988; Enticott, in Marchant & Higgins 1990). Indeed, most of the observations by Pitman & Ballance (1992) of *parkinsoni* associations with cetaceans were of birds feeding with the same four to five species of large delphinids as noted in the present study (Table 4).

Similar observations regarding scavenging in association with feeding cetaceans in the HCS were made for Buller's Albatross (Spear *et al.* 2003; see also Croxall & Prince 1994). In the Benguela Current (Enticott, in Marchant & Higgins 1990), *aequinoctialis* often associates with *Globicephala*, although the species also associates with smaller delphinids (Jackson 1988). Indeed, Jackson (1988) suggested that the tendency for *aequinoctialis* to scavenge in association with marine mammals may account for their habit of scavenging at fishing vessels.

Consistent with the results of most studies of the diet of *Procellaria* (Imber 1976; Jackson 1988; Croxall *et al.* 1995), cephalopods were an important prey (by number and mass) of *aequinoctialis* collected in the HCS. Although myctophids, thought to have been caught at night, were important prey in all three studies listed above, only one species of fish, a mesopelagic melamphaid which vertically migrates towards the ocean surface at night, was found in the *aequinoctialis* from the HCS.

All six cephalopod families recorded in the diet of *aequinoctialis* in the HCS have been reported as prey of spotted dolphins (*Stenella attenuata*) in the tropical Pacific, as well as numerous other cetacean

species in that area (Robertson & Chivers 1997). One of them, *Pholidoteuthis boschmai*, also was reported as prey of dolphinfish (*Coryphaena hippurus*) in the tropical Pacific (Olson & Galvan-Magna 2002), and five of the six families of cephalopods were observed in the diet of Galapagos petrels (*Pterodroma phaeopygia*) resident on the Galapagos Islands (Imber *et al.* 1992). In addition, one family, Octopoteuthidae, was reported as prey of a Parkinson's petrel collected while associated with bottlenose dolphins (*Tursiops truncatus*) in the eastern Pacific (Pitman & Ballance 1992).

Although Pitman & Ballance (1992) conducted many hours of observations within the waters we surveyed, they did not observe these petrels associate with South American sea lions, which are numerous in the HCS. This might have been because their attention was focused primarily on the recording of cetaceans and seabirds; they reported no pinnipeds. We are aware of only one other study documenting the use of feeding pinnipeds by *Procellariiformes*: that of *aequinoctialis* and sooty shearwaters (*Puffinus griseus*) with Cape fur seals (*Arctocephalus pusillus*) that were feeding at the surface on small fishes (myctophids) in the Benguela Current (Jackson 1988).

We also have observed (unpubl. data) sooty shearwaters, northern fulmars (*Fulmarus glacialis*) and larids (*Larus* spp.) feeding in association with California and northern sea lions (*Zalophus californianus* and *Eumetopias jubatus*, respectively) in the California Current, and northern fulmars, Laysan and black-footed albatrosses (*Phoebastria immutabilis* and *P. nigripes*, respectively) and larids with northern sea lions in the Bering Sea; in all cases the sea lions were eating large fishes (> 0.5 m; e.g., elasmobranchs, salmonids, cod, flatfish). Most instances in the Bering Sea involved sea lions and birds associated with fishing vessels that were long-lining Pacific cod (*Gadus macrocephalus*) and incidental Pacific halibut (*Hippoglossus stenolepis*), where the sea lions were taking larger fish from hooks as the lines were being retrieved. Similar to our observations in the HCS, the seabirds are attracted when a sea lion (generally a large male) brings a large fish to the ocean surface where it grasps the fish in its mouth and swings it back-and-forth to tear off chunks of flesh. Often, pieces of the prey are cast about, land on the ocean surface, and are scavenged by the seabirds.

Abundance

The CVs for the seasonal abundance estimates of *aequinoctialis*, *parkinsoni*, and *westlandica* during their respective non-breeding periods, ranged from 11% to 25%, thus indicating that the GAMs performed reasonably well in modeling the petrel distributions at sea, particularly in the case of *parkinsoni* (CV = 11%).

Abundance estimates of *aequinoctialis*, *parkinsoni*, and *westlandica* during their respective non-breeding periods were about 722,000, 38,000 and 3,500 birds, respectively. Based on the 95% confidence intervals, estimates of minimum numbers were 350,000, 28,000 and 2,000 birds, respectively. These estimates represent the average for years 1980 to 1995, because the data were grouped across years in the analyses. Thus, the HCS appears to be an important non-breeding area for all three species, particularly for *parkinsoni* and *westlandica*, as the at-sea estimates represent a large percent of, or exceed, estimates made at breeding colonies: 3 - 4,000 birds, and 2 - 10,000 birds, respectively (Imber 1987; Robertson & Bell 1984).

The majority of *aequinoctialis* estimated to occur in the HCS are likely to be birds originating from the main New Zealand colonies at Antipodes Island, and Disappointment, Adams and Enderby Islands of the Auckland Islands group (M. Imber pers. comm). More specifically, our HCS estimates of numbers of both *aequinoctialis* and *parkinsoni* for the non-breeding season are likely to be good estimates of the total populations of *parkinsoni* and the New Zealand population of *aequinoctialis*. Likewise, our breeding season estimates for the two species (12,400 *parkinsoni* and 238,000 *aequinoctialis*) are likely to be good estimates of the non-breeding populations of each. That the majority of *aequinoctialis* off Peru and Chile are non-breeders was indicated by examination of the four *aequinoctialis* that we collected during August; based on gonad condition (non-convoluted oviducts in females and very small testes in males), all had no breeding experience. In addition, Imber *et al.* (2003) concluded that immature *parkinsoni* were generally absent from the New Zealand region until 4-5 years old, and they are presumably in the eastern Pacific at that time. The same probably applies to the New Zealand population of *aequinoctialis* as both species are mostly absent from New Zealand waters from about July to September (M. Imber pers. comm). Assuming that the above is true, the number of breeding New Zealand *aequinoctialis* would have been about 484,000 birds, and that of *parkinsoni*, about 25,000.

Hence, it appears that under-estimates for numbers of *parkinsoni* may have been made at the New Zealand breeding areas, given the above discussion as well as our at-sea estimate indicating no less than 28,000 *parkinsoni* present in the HCS during the austral winter. Greater numbers of *parkinsoni* than previously indicated (e.g. Imber 1987; Taylor 2000) is likely to be due to some recovery, following eradication of cats, of the colony nesting on Little Barrier Island, but is probably primarily a result of the ongoing increase in numbers nesting on Great

Barrier Island (E. Bell & M. Imber pers. comm). Our estimate for numbers of Westland petrels in the HCS is puzzling as one would expect it to be more consistent with the size of the population from a New Zealand perspective. According to J.A. Bartle (in Adams 1998), there are about 20,000 Westland petrels ($\pm 5,000$), including breeders and non-breeders. A possible explanation for what appears to be low numbers wintering on the Pacific coast of South America could be that large numbers reside in Chilean fjords while moulting (P. Scofield unpubl. data). We did not survey those waters during this study. Nevertheless, it appears that at least 10 - 20% of the total population is using the Humboldt Current during the non-breeding season.

Potential interaction with the Patagonian toothfish fishery

Albatross and petrels are experiencing high mortality from incidental catches by long-line fisheries, and many breeding populations have decreased markedly (reviewed in Murray *et al.* 1993; Prince *et al.* 1994). As noted above, substantial numbers of both *aequinoctialis* and *parkinsoni* were seen attending fishing vessels in the HCS, and both species were readily attracted to within very close range by discarded offal. Clearly, each population is at risk from interaction with Peruvian and Chilean fisheries, a fact well documented for *aequinoctialis* and *westlandica* in New Zealand (Murray *et al.* 1993), Africa and eastern South America (Moreno *et al.* 1996; Ryan *et al.* 1997). Of particular concern is the recent development of a long-line fishery, using small (45 m maximum) vessels to catch Patagonian toothfish (*Dissostichus eleginoides*) over the continental slope (isobaths 500 to 2,000 m) of Chile (Moreno 1991) where the majority of these petrels reside. Although there is no direct evidence that these petrels are being affected by fisheries in the HCS (but see Imber *et al.* 2003), monitoring of the interaction (e.g., Moreno *et al.* 1996; Ryan *et al.* 1997) is advisable.

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