How does a generalist seabird species use its marine habitat? The case of the kelp gull in a coastal upwelling area of the Humboldt Current

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The distribution of kelp gulls (*Larus dominicanus*) was studied by ship-based transect counts in the SE Pacific Ocean off Chile, South America. Some 96–98% of the kelp gulls were in a band less than 20 km from the coast, mainly near the breeding colony on Pájaros Island and the City of Coquimbo. Abundance did not change significantly among years, but was influenced significantly by distance to land. Principal component analysis yielded two components that jointly explain 53% of the standardized variance. The first (explaining 36% of the variance) includes distance to the nearest coast and water depth, the second (17%) associates with the presence of fishing vessels. The results suggest that the stability of the summer distribution of kelp gulls is generated by the large and semi-permanent offer of food at fish markets and city sewage works, as well as the location of the breeding colonies. Further analysis on other temporal scales (seasonal, decadal) associated with reproductive or non-reproductive changes within the population and/or ENSO cycles will be necessary to confirm the multiscale stability of the pattern described.

Keywords: Chile, generalist, habitat use, kelp gull, *Larus dominicanus*, opportunist, seabirds, upwelling zone.

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Introduction

Over the past two decades, several studies have attempted to elucidate the at-sea patterns of distribution and behaviour of seabirds in relation to hydrographic variables and human activities (e.g. Haney and McGillivary, 1985; Briggs *et al.*, 1987; Tasker *et al.*, 1987; Ryan and Moloney, 1988; Hunt, 1990; Camphuysen *et al.*, 1995). Some have suggested that at-sea aggregations of seabirds are more correlated to hydrographic features (e.g. fronts and upwelling areas) than to the activity of fishing vessels (Skov and Durinck, 2001). Colony location is another factor that strongly influences the at-sea distribution of seabirds (e.g. Schneider and Hunt, 1984; Wilson *et al.*, 1995). Weichler *et al.* (2004) conducted a study of seabirds in the Humboldt upwelling ecosystem in northern Chile and found that the occurrence of feeding flocks was the variable that had the greatest influence on the distribution pattern of endemic seabirds that are specialist feeders (grey gull *Larus modestus*, Humboldt penguin *Spheniscus humboldti*, Peruvian booby *Sula variegata*, Guanay cormorant *Phalacrocorax boungainvillii*). They also found that seabird distribution is explained only to a minor extent by the presence of fishing vessels and hydrographic features, but that the occurrence of feeding flocks is mostly related to schools of pelagic fish, especially anchovy, sardine, and mackerel, which feed near fronts and cold water and nutrient-rich upwelling zones (Arntz and Fahrbach, 1991).

Although most of the information supports the general hypothesis that seabird distribution is correlated with hydrographic features and productivity, in some species, the expected pattern varies because of factors such as feeding behaviour, morphology, and bioenergetics. This suggests that the direct role of upwelling processes in determining seabird distribution patterns should be interpreted with care. Gulls (Laridae) are seabirds in which this situation has been observed. They are food generalists and include in their diet items of different origin, from natural and anthropogenic sources. Among the latter, domestic refuse, discards, and other fishery waste are common components of the diet of several species of gull. The availability and predictability of these food resources has been proposed as the most likely explanation for the increase in gull populations at some places in Europe (Furness and Monaghan, 1987; Oro *et al.*, 1995; Garthe *et al.*, 1996; Oro, 1996) and South America (Gandini and Frere, 1998; Yorio and Caille, 1999; Bertellotti *et al.*, 2001).

The kelp gull (*Larus dominicanus*) has a widespread distribution in the southern hemisphere, breeding in southern Africa, Australia, New Zealand, the sub-Antarctic islands, the Antarctic

Peninsula, and the coast of southern South America (Harrison, 1985). In Chile, it breeds along the entire coast, mainland and islands, in a great array of environments (Murphy, 1936; Johnson, 1965; Simeone and Bernal, 2000). Its food spectrum is broad and includes intertidal invertebrates (Bahamondes and Castilla, 1986; Hockey and Steele, 1990; Steele and Hockey, 1995; Bertellotti and Yorio, 1999), rodents (Ruiz and Simeone, 2001), eggs and chicks of their own (Fordham and Cormack, 1970; Burger and Gochfeld, 1981) and other species (Emslie *et al.*, 1995; Yorio and Quintana, 1997), and fishery discards and waste (Fordham, 1967; Bertellotti *et al.*, 2001; Yorio and Giaccardi, 2002).

Previous studies of the kelp gull in Chile suggest that it has a coastal distribution, related to the availability of food at fish markets and city dumps (Ludynia *et al.*, 2005), and around coastal fishing vessels (Weichler *et al.*, 2004). However, we do not know how stable is its pattern of distribution, or the influence on distribution of anthropogenic and environmental factors. In northern Chile, the kelp gull breeds at many coastal and offshore islands in colonies ranging from 40 to 2000 pairs (Simeone *et al.*, 2003). In addition, it breeds every year on buildings near the fishing harbour and fish factories in Coquimbo city (Kotzerka, 2002; pers. obs.). Data for northern Chile and Coquimbo indicate that it has a generalist diet, including items of anthropogenic origin, and that the gulls breeding on offshore islands feed mainly on intertidal organisms and olives, whereas birds breeding or resting near fishing ports used these as their main feeding grounds (Ludynia *et al.*, 2005). Based on this information, we hypothesize that: (i) the at-sea distribution patterns of kelp gulls during summer is stable both in time (i.e. between successive breeding seasons) and space, as a result of constancy in the availability of food mainly from anthropogenic sources; (ii) the at-sea abundance of kelp gulls is a function of the coastal border, where food is found in a predictable amount and availability for the mainly intertidally feeding birds, the location of the colonies, and the fishing vessels providing discards and offal at sea. To test these hypotheses, we studied on an interannual basis the spatio-temporal patterns of abundance of kelp gulls at sea. We further determined the influence of some environmental features, including physical (distance to shore, distance to colonies, water depth, sea surface temperature), biological (abundance of feeding flocks, chlorophyll), and anthropogenic variables (presence of fishing vessels) on the distribution and abundance of the kelp gull in northern central Chile (30°S).

Material and methods

The work was conducted in January of 1999, 2002, 2003, and 2004 (Table 1). The study area, referred to here as the Coquimbo Coastal System (CCS), is located in central Chile, between Chañaral Island (29°03′S) and Punta Lengua de Vaca (30°17′S; Figure 1). Kelp gulls nest on all islands within the area, with the largest colonies on Pájaros 1 Island (2000 pairs) and Chañaral Island (500 pairs; Simeone *et al.*, 2003). Approximately 50 pairs breed near the Guayacan fishing harbour in Coquimbo city, where they feeds on fishery waste (Kotzerka, 2002). During the study period, most adult gulls were raising chicks, but some were still incubating eggs.

Table 1. Sampling effort deployed during SCC cruises.

Year	Observation days at sea (and cruise date)	Effective exploration time (h)	Area studied (km^2)
1999	8 (14–29/01)	49.0	470
2002	7 (17–24/01)	47.2	357
2003	7 (25/01–01/02)	54.9	421
2004	7 (17–23/01)	52.5	434

The method used for counting birds at sea was the same as utilized previously in the area by Luna-Jorquera *et al.* (2000) and Weichler *et al.* (2004). Counting was done on board an 18 m oceanographic vessel. Transects, both parallel and perpendicular to the coastline, extended up to 50 km offshore and covered an area annually of 357–470 km^2 (Table 1). Sea surface temperature, recorded automatically with a fast-response digital Squirrel® thermometer, was taken at 1 min intervals during the transects, except during 1999. The sensor was calibrated against a mercury thermometer. Feeding flocks and working fishing vessels were noted up to a radius of 5 km from the vessel, using the method described by Heinemann (1981).

Kelp gulls (including adults, immatures, and juveniles) were counted from the highest platform and to both sides of the vessel, on transects 300 m wide. Within the transect, birds resting on the sea were counted directly, and flying birds were counted using the snapshot method that minimizes double counting (Tasker *et al.*, 1984). The final count for resting birds was corrected using the methods developed by Buckland *et al.* (1993). We applied a half-normal function with a cosine adjustment available within the DISTANCE 4.0 software (Laake *et al.*, 2002). Correcting factors ranged between 1.2 and 1.8. Kelp gulls following the vessel were counted when they approached for the first time. All seabird observations were summarized at 10-min intervals, using vessel speed, geographic position, and transect width (2 × 300 m) to calculate their density (Tasker *et al.*, 1984). In addition, behavioural information was recorded (except during 1999) including associations with other species and flight directions (Camphuysen and Garthe, 2004). During the observation period, we noticed that kelp gulls were coming and going from the city of Coquimbo. Therefore, we used an angle–angle correlation analysis to determine the potential influence of the location of the city on the flight direction of the birds.

A non-parametric two-way ANOVA was used to compare the distribution and abundance among years (Scheirer *et al.*, 1976). ANOVA factors were year (1999, 2002, 2003, and 2004) and distance from the coast (0–10, 10–20, 20–30, >30 km offshore). The number of data per cell was balanced using a random selection function (Zar, 1984).

The joint influence of environmental variables over the distribution of kelp gulls was evaluated by principal component analysis (PCA), using data from 2002, 2003, and 2004; 1999 data were excluded because some variables were not concurrently recorded along the tracks. The following variables were considered: (i) depth of the water column, (ii) nearest distance from the coast, (iii) distance from the nearest large breeding colonies (defined as Chañaral Island and Pájaros 1 Island; Figure 1), (iv) sea surface temperature, (v) number of feeding flocks (the number of birds of different species feeding together on pelagic fish) in a 5 km radius from the vessel, and (vi) number of fishing vessels either in fishing operations or carrying fish in a 5 km radius. Only components with eigenvalues >1.0 were included in the model (Briggs and Chu, 1986; Garthe, 1997). Bird abundance was $\log_{10}(X_i + 1)$-transformed to stabilize its variance (Briggs and Chu, 1986).

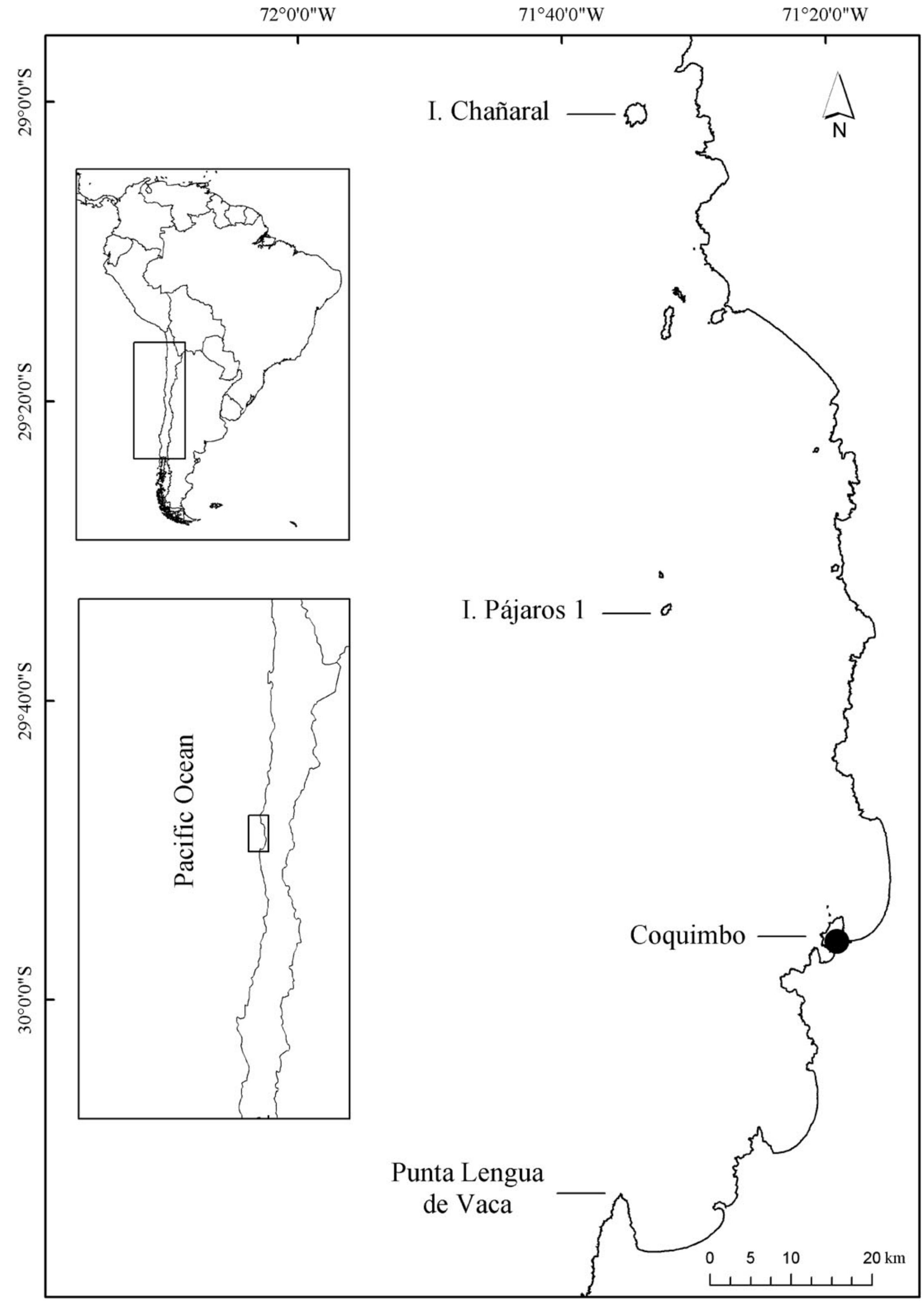

Figure 1. Geographic location of the study area off the Chilean coast, showing the main nesting sites for kelp gulls within the SCC, Chañaral Island and Pájaros 1 Island.

Abundance grids were generated for each cruise through kriging interpolation (Rossi *et al.*, 1992; Gonzalez and Marín, 1998). The size of the grid cell (16 km^2) represents a compromise between statistical accuracy (considering that data were recorded at intervals of nearly 1 km^2) and spatial resolution. Spearman correlation matrices were calculated to analyse distributional patterns among cruises and between bird abundance and distance to breeding colonies.

We also studied the potential relationship (regression analysis) between the biological spatial structure of the coastal ocean, using

Table 2. Mean, standard deviation (s.d.) and maximum abundance (birds km^{-2}) of kelp gulls during the four cruises within the SCC.

Cruise	Mean ± s.d.	Maximum
1999 ($n = 327$)	1.07 ± 4.88	64.13
2002 ($n = 300$)	1.94 ± 13.12	171.21
2003 ($n = 352$)	0.91 ± 2.28	29.14
2004 ($n = 327$)	1.90 ± 3.80	26.02

Table 3. Two-way non-parametric ANOVA for bird abundance as a function of year and distance from the coast.

Source	d.f.	*h*	*p*-value
Year	3	6.43	>0.05
Distance	3	80.37	<0.001
Year × distance	9	4.96	>0.75

satellite chlorophyll (s-chlorophyll) as index, and bird distribution. Images of s-chlorophyll for all sampling dates were obtained from NASA (http://oceancolor.gsfc.nasa.gov). Always we used level 3-weekly composite images. Data for 1999 and 2002 corresponded to 9-km binned SeaWiFS images, and for 2003 and 2004, we used 4-km binned MODIS/Aqua images. A preliminary analysis of SeaWiFS/MODIS images for 2003 and 2004 showed no significant differences in terms of spatial structure between satellites. All images were rectified under ERDAS 8.6 to a common reference (UTM) using a Chilean coastline coverage. Rectified images were then converted to Arc/Info grid files and loaded into ARCVIEW 3.3, along with the bird abundance grids. All grids, birds and s-chlorophyll, were sampled using a point-coverage of randomly located sampling points for the overlapping area among all images.

Results

The mean abundance of kelp gulls in the CCS fluctuated between 0.91 birds km^{-2} in 2003 and 1.94 birds km^{-2} in 2002. The highest value for a single cell (171 birds km^{-2}) was recorded during 2002 (Table 2). The two-way ANOVA showed that abundance did not change significantly ($p > 0.05$) among years and that there is a significant influence of distance to coastline on bird abundance (Table 3). Indeed, 96–98% of the kelp gulls were in a band of <20 km from the coast of the mainland, mainly near Pájaros 1 Island and the city of Coquimbo (Figure 2). The spatial analysis suggests that this pattern is stable (Table 4). Moreover, kelp gull abundance was inversely proportional to distance from the colony, the mainland, and the water column depth (Table 5). Therefore, kelp gulls tend to be more abundant in shallow water close to the coast and near Pájaros 1 Island (Figure 2).

The regression analysis between s-chlorophyll and kelp gull abundance showed that although there seems to be a significant relationship between these variables for 1999, 2002, and 2004 ($F_{1,149}$; $p < 0.05$), the regression explained always <10% of the dependent variable (Figure 3). The relationship was not significant for 2003, so satellite chlorophyll does not seem to be a good predictor of kelp gull distribution.

PCA showed that the environmental variables studied can be reduced to two components that jointly explain 53% of the standardized variance (Table 6). The most important variables for the first component (explaining 36% of the variance) are distance to the nearest coast and water depth. The second component (17% of the variance) is mainly associated with the number of fishing vessels. The loadings for each factor, when plotted, clearly show that kelp gull abundance is positively associated with the presence of fishing vessels, and negatively related to distance from the coast and the colony, and depth (Figure 4).

Finally, the angle–angle correlation analysis showed that 47% of all kelp gulls recorded had a flight direction correlated with

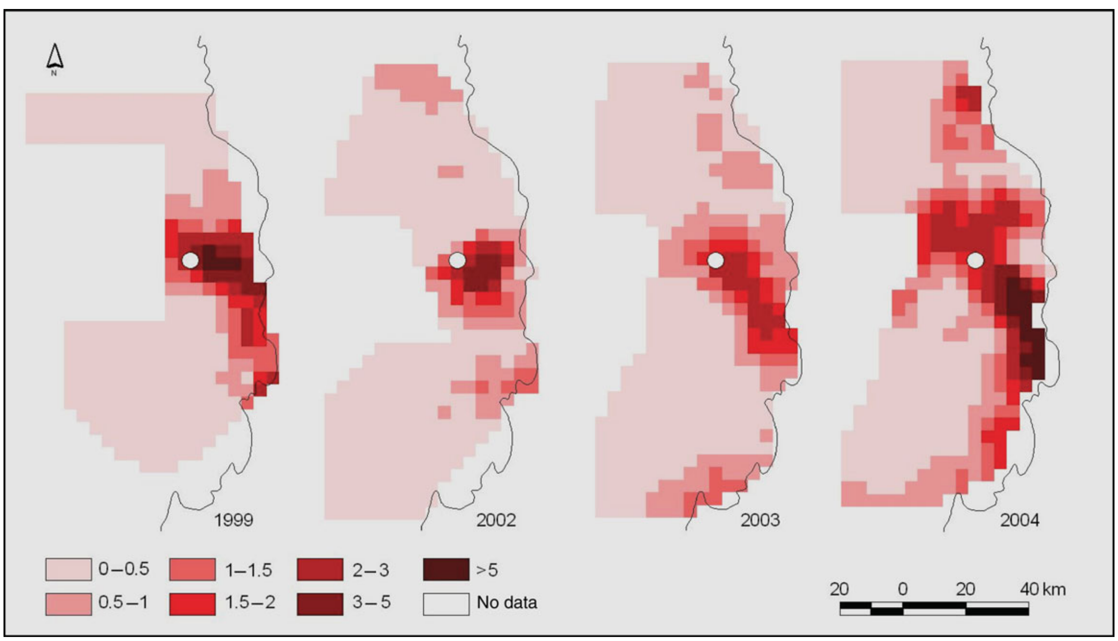

Figure 2. Spatial distribution of kelp gull abundance (birds km^{-2}) in the SCC. Grids were generated by kriging of 10-min interval points. The white dot shows the location of Pájaros 1 Island.

Table 4. Spatial correlation values (r_s) of the abundance of kelp gulls derived from a comparison among all grids from the four SCC cruises.

Year	1999	2002	2003	2004
1999	–	*266*	*271*	*270*
2002	0.65	–	*374*	*362*
2003	0.80	0.64	–	*416*
2004	0.72	0.58	0.77	–

All values were significant at $p < 0.01$. Values in italics show the number of grid cells compared for each pair of years.

Table 5. Spatial correlation values (r_s) among kelp gull abundance and environmental variables.

Parameter	1999 ($n = 311$)	2002 ($n = 394$)	2003 ($n = 446$)	2004 ($n = 422$)
Distance from the coast	−0.73	−0.71	−0.79	−0.75
Water depth	−0.70	−0.63	−0.75	−0.74
Distance to the nearest large colony	−0.71	−0.35	−0.37	−0.43

All values were significant at $p < 0.01$.

the location of the city of Coquimbo, where sewage is dumped and there are several fish markets ($p < 0.001$; Table 7). Earlier and additional observations revealed large numbers of kelp gulls feeding on food and fishery discards within the city area.

Discussion

We studied aspects of the distribution and behaviour of kelp gulls at sea in the CCS during four summers (1999, 2002, 2003, and 2004). Our results show that their distributional pattern within the CCS is stable, with kelp gulls abundant near the coast and around nesting colonies. Colony location as a determinant of distribution of seabirds has been documented previously (Schneider and Hunt, 1984; Wilson *et al.*, 1995; Garthe, 1997). The mechanistic explanation offered by those authors is that birds behave as central location foragers during the reproductive season. Although it is not possible to determine the reproductive condition of birds during counts at sea, ancillary observations showed that breeding birds were raising chicks in the whole area during our periods of observation, especially at Pájaros 1 and Chañaral Islands.

The land-sea pattern revealed here (i.e. gull abundance inversely proportional to distance from the coast and water depth) has been reported for other *Larus* species. Briggs *et al.* (1987), studying the upwelling waters of the California Current, show that the density of *L. occidentalis* varies inversely with the land-sea gradient. Garthe (1997), studying several species in the North Sea, showed that the gradient is the main determinant of abundance in areas with plenty of food. For *L. dominicanus*, previous studies have shown that its main abundance is in neritic waters, where coastal upwelling generates low temperature and high production of plankton (Acuña *et al.*, 1989). Alternatively, we propose that within the CCS, the abundance of kelp gulls in high-production areas is not causally related to feeding from the marine foodweb, as suggested for other seagulls (O'Driscoll *et al.*, 1998; Hoefer, 2000). Indeed, contrary to other endemic seabirds within the study area (e.g. Peruvian booby, Peruvian diving petrel, Humboldt penguin; Luna-Jorquera *et al.*, 2003), kelp gulls obtain most of their food from anthropogenic rather than from natural sources.

Similar to previous studies elsewhere (Abrams, 1983; Ryan and Moloney, 1988; Bertellotti and Yorio, 2000) and in the same study area (Weichler *et al.*, 2004), we found that fishing vessels influence the distribution of kelp gulls at sea. Significant numbers of kelp gulls, as revealed by the PCA (component 2), were observed following fishing vessels in Coquimbo, as previously reported in

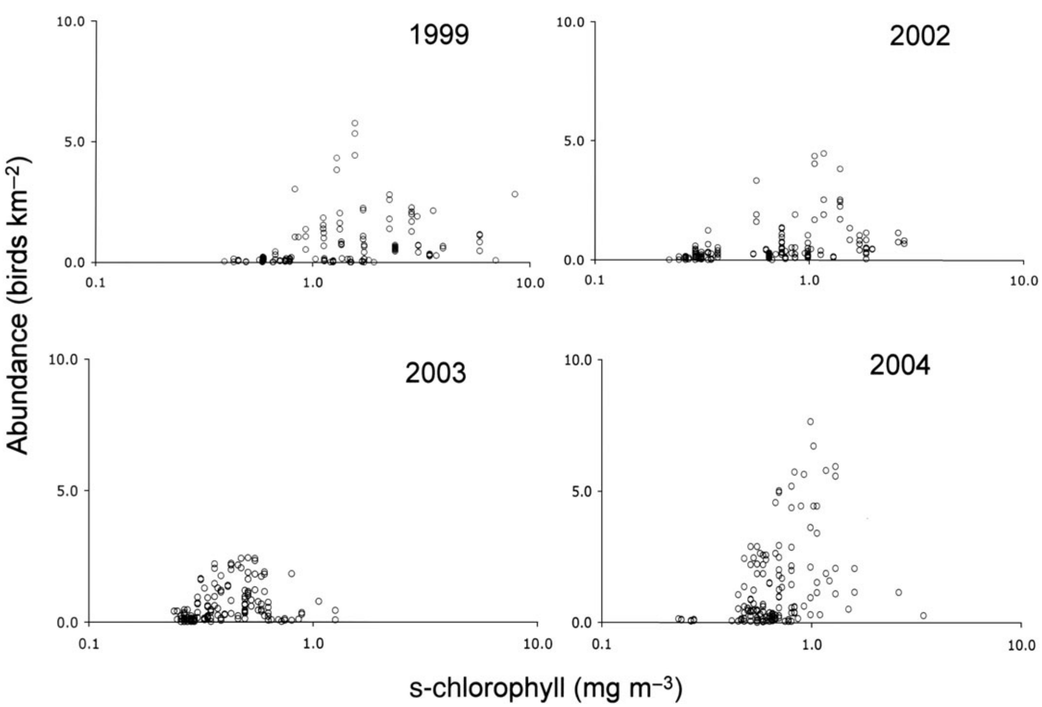

Figure 3. Scatterplot of s-chlorophyll and kelp gull abundance for the 4 years of observations.

Table 6. Results from the PCA.

Variable	Component 1	Component 2
Kelp gull abundance (log $x + 1$)	−0.55	0.58
Distance to coast	0.90	0.20
Water column depth	0.89	0.19
Distance to nearest colony	0.51	0.19
Sea surface temperature	0.46	0.22
Presence of feeding flocks	−0.12	−0.31
Presence of fishing vessels	−0.34	0.79
Variance explained (%)	36	17

Loadings for the first two principal components are shown (for eigenvalues >1.0).

the study area for this species and for Franklin's (*L. pipixcan*) and grey (*L. modestus*) gulls (Weichler *et al.*, 2004). Weichler *et al.* (2004) also found that fishing activities influence bird behaviour, but they suggested that the effects of this factor on kelp gull distribution seems to be less remarkable than reported elsewhere. It is likely, however, that their results were influenced by the large number of species (24) and different factors they included in their analysis. We found that the distribution pattern of kelp gulls was stable over the four summers and that fishing activities were responsible for 17% of the variance in distribution patterns at sea. The greater explanatory power of distance from the coast found here suggests that kelp gulls may seek food at the coast rather than by following fishing vessels. This is supported by observations of kelp gulls feeding at the harbour and refuse sites, and by Kotzerka (2002) and Ludynia *et al.* (2005), who report that garbage and fish discards are important food items in the diet of the birds.

The stability and predictability of food sources can be a crucial factor determining, in turn, the stable spatio-temporal patterns of kelp gulls. This finding contrasts with that for other species of seabird that have diets mainly of fish and other natural items, which generally have greater variability in their distribution patterns (pers. obs.). Although uncertainty and biases are often associated with spatial ecology studies (Stine and Hunsaker,

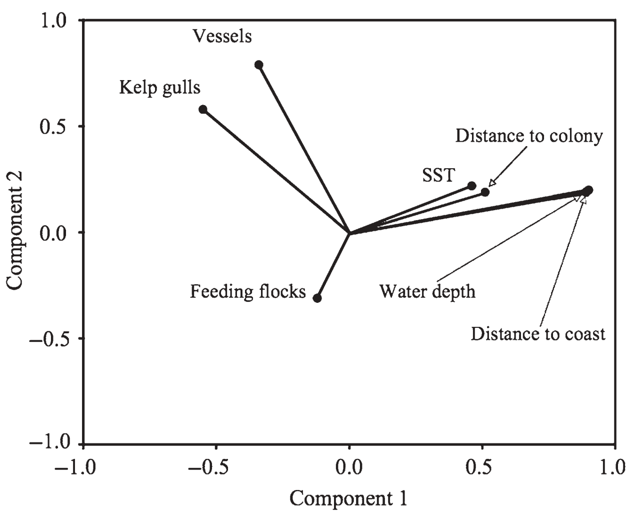

Figure 4. Plot of the loadings of the main two components obtained from PCA.

Table 7. Results of the angle-angle correlation analysis (r_{aa}) between the direction towards/from Coquimbo city and the flight direction of kelp gulls during 2002, 2003, and 2004.

2002 ($n = 92$)	2003 ($n = 1\,714$)	2004 ($n = 1\,121$)
0.49	0.27	0.45
$p < 0.001$	$p < 0.001$	$p < 0.001$

2001), the information obtained here from oceanographic cruises allowed us to establish spatial relationships between kelp gull abundance and environmental variables. Indeed, our results and those from others within the same area (Kotzerka, 2002; Weichler *et al.*, 2004; Ludynia *et al.*, 2005) suggest that the stability of the summer distribution pattern of kelp gulls is generated by the location of the breeding colonies and the large and semi-permanent availability of food at fish markets and city sewage plants. As has been demonstrated for other generalist seabird species (e.g. Votier *et al.*, 2004; Whittington *et al.*, 2006), the extra supply of food results in an exacerbated increase in the size of kelp gull populations. As a consequence, the kelp gull is gradually extending its breeding and resting sites from islands to the mainland and buildings in Coquimbo city (Kozertka, 2002; pers. obs.). This is similar to the situation observed in the Eastern Cape of South Africa, for example, where the population of kelp gulls has increased by 71% since 1982 (Whittington *et al.*, 2006). It has been demonstrated before that large populations of scavenging seabirds or marine mammals could have negative effects on other seabird species (Votier *et al.*, 2004), especially for endemic species facing conservation problems. A similar situation has been observed in the Benguela ecosystem, where the Cape fur seal population has burgeoned and is now preying on five threatened or near-threatened seabird species (David *et al.*, 2003). Observations at several islands in northern Chile show that kelp gulls prey on chicks of Peruvian boobies and Humboldt penguins. Additionally, recent observations at Isla Choros, the last large colony in Chile (Simeone *et al.*, 2003) of the globally endangered Peruvian diving petrel, show that kelp gulls prey on the chicks of that species too. Further analysis on other temporal scales (seasonal, decadal) associated with reproductive or non-reproductive changes within the population and/or *El Niño*/Southern Oscillation (ENSO) cycles are necessary to confirm the multiscale stability of the patterns we have described. Moreover, considering the increasing need for ecosystem-based management in the Humboldt Current system (see outlook in Thiel *et al.*, 2007), it is crucial to identify the importance of discards, offal, waste, and refuse as food sources for seabird populations favouring generalist seabirds while, at the same time, increasing pressure on the populations of some endemic specialists.

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