Transfer processes drive population dynamics of kelp gull colonies in Patagonia: Implications for management strategies

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Running head: Kelp gull demography in Patagonia, Argentina

Abstract

Dispersal of individuals among breeding sites is considered as one of the key processes in seabird population dynamics. The kelp gull (*Larus dominicanus*) is the most abundant gull in coastal Argentina, although its population dynamics in the region remains poorly understood. This paper aims to address aspects of kelp gull demography along a wide coastal sector (~1800 km) in northern Patagonia to improve our understanding of population changes and contribute to the design of management strategies and monitoring programs. Modeled scenarios suggest that annual increases of 10 to 20% are high for the species, and 29% of 62 evaluated colonies presented growth rates within this high reference range. Transfer processes among colonies (e.g. source-sink) contributed to the growth of at least six kelp gull colonies. These processes have been instrumental in the growth of small, and in some cases recently established colonies, which had generally higher growth rates and were found nearby large and long-established colonies. These are the first studies of kelp gull demography in the coasts of Argentina, aimed at understanding the population dynamics of this species in a metapopulation context.

Key words: Demography, *Larus dominicanus*, seabird colonies, source-sink processes

Introduction

Dispersal processes among breeding sites can play a key role in seabird population dynamics. In particular, it has been shown that the dispersal probability of a breeding individual to another colony can be influenced by environmental conditions, such as food availability (Ainley et al. 1990; Oro et al. 2004), being this probability higher in young breeders (Oro & Pradel 1999; Oro et al. 1999; Inchausti & Weimerskirch 2002; Breton et al. 2006). In addition, it has been argued that colonies with higher productivity are more attractive to prospecting individuals (Cadiou et al. 1994) and that the resulting differential recruitment greatly determines the rate of colony growth (Danchin et al. 1998), affecting the dynamics of individual colonies (Kildaw et al. 2008). The conceptual framework provided by the theory of metapopulation dynamics is particularly suitable to the study of the demography of colonial birds, including seabirds, whose populations are spatially organized in discrete patches (colonies) connected by dispersal (Inchausti & Weimerskirch 2002; Barbraud et al. 2003; Oro 2003; Kildaw et al. 2008; Schippers et al. 2009). Several gull species, for example, present high patch colonization-extinction rates which occur as a result of individual dispersal (immigration-emigration) (Danchin & Monnat 1992; Coulson 2001; Oro 2003; Kildaw et al. 2005), favoring the study of dynamic processes which are characteristic of metapopulations.

Seabirds are long lived species inhabiting environments characterized by a high temporal variability (e.g., food availability, weather conditions). Therefore, a thorough understanding of seabird demography should be based on long-term studies (Weimerskirch 2001). However, in those cases with shorter time series or incomplete data sets, exploratory analyses incorporating population modeling tools can be valuable. These analyses can integrate and summarize available knowledge, help clarify assumptions, identify gaps, and allow the identification of parameters that deserve higher priority sampling (Hilborn & Mangel 1997; Akçakaya & Sjögren-Gulve 2000; Morris & Doak 2002).

Kelp gulls (*Larus dominicanus* Lichtenstein, 1823) are widely distributed in the southern hemisphere, breeding in South America, southern Africa, Australia, New Zealand, on the subantarctic islands, and the Antarctic Peninsula (Burger & Gochfeld 1996). Along the coast of Argentina it is the most abundant gull species, with a total population estimated at >108,000 pairs, distributed in ~140 colonies (Yorio et al. 1999; Yorio, unpublished data). Over 65% of the total population breeds in northern Patagonia (Río Negro and Chubut Provinces). The population in this area increased by 37% between 1994 and 2008, but with differences between coastal sectors, some of which experienced substantial growth in numbers while others remained stable (Lisnizer et al. 2011). Population expansion has been also reported at some coastal sectors of other South American countries (Villablanca et al. 2007) and regions in the Southern Hemisphere (Coulson & Coulson 1998; Whittington et al. 2006), suggesting that similar demographic processes may be taking place throughout its breeding range. The population expansion of the kelp gull is a matter of concern in Argentina given their potential negative effects through their predation on globally threatened species such as the Magellanic Penguin (*Spheniscus magellanicus* Forster, 1781), Olrog's Gull (*Larus atlanticus* Olrog, 1958), and White-headed Steamer Duck (*Tachyeres leucocephalus* Humphrey & Thompson, 1981) and conflicts with man, such as hazards to aviation and threats to human health as they may be carriers of Enterobacteria, particularly Salmonella (Yorio et al. 1998; Yorio et al. 2005). In particular, complaints and calls for action in coastal Argentina are frequent, but the basic information required to define management actions is still lacking.

In this paper we investigate the demography of kelp gulls breeding along a broad coastal sector (~1800 km) in northern Patagonia, in order to improve our understanding of population changes and contribute to the design of management strategies and monitoring programs. Our specific goals were to (a) analyze kelp gull demographic behavior considering the possible role that transfer processes among colonies may have in population growth, (b) examine whether colony growth rates are related to colony size and location, and (c) suggest monitoring and research recommendations based on the resulting analyses.

Material and methods

Study area

The study area included 1770 km of the mainland coast and islands from San Antonio Oeste, Río Negro Province (40°47'S, 64°53'W), south to the boundary between the Chubut and Santa Cruz Provinces (46°S) (Figure 1). The most recent kelp gull survey in the study area estimated a total of 72,600 breeding pairs distributed at 68 colonies (Lisnizer et al. 2011). We defined four coastal sectors, encompassing the whole study area (see definitions in Lisnizer et al. 2011; Figure 1).

Transfer processes among colonies

We estimated a maximum growth rate reference value (λ_{ref}) specific for the kelp gull to assess potential transfer processes among colonies and among the four defined coastal sectors. We defined this reference value as the highest population growth rate obtained analytically using the combination of highest survival and fecundity values reported for the kelp gull (see below). We then compared this maximum growth rate reference value (λ_{ref}) with the growth rate values estimated from nest counts at each kelp gull colony located along the study area and provided by Lisnizer et al. (2011). Thus, we considered those colonies with reported growth rates higher than the maximum growth rate reference value (λ_{ref}) as potential sites where the intrinsic growth might have been complemented by immigration from other colonies (source-sink processes). We used the same procedure to evaluate population growth rates by coastal sector (see above) and for the overall population in the study area.

We calculated the maximum growth rate reference value (λ_{ref}) based on a deterministic age-structured matrix population model (Caswell 2001). In this model, we assumed that all individuals of 4 years of age or older were breeders (Crawford et al. 2000), and that they bred in all years. Model parameters were:

S_1, first year survival

S_2, survival in years 2+

F, fecundity of breeders (≥4 years).

Estimates of adult and juvenile survival were not available for the region, so we used survival values estimated for kelp gull populations in southern Africa (Altwegg et al. 2007).

We used for survival values S_1 and S_2, the upper confidence interval value reported by Altwegg et al. (2007) for first year individuals and for individuals older than one year, respectively (Table I). We estimated fecundity (F) as:

$$F = \text{Breeding success} * S_2 * 0.5$$

We defined breeding success as the number of fledged chicks per breeding pair (nest). The model included only females, and we assumed a balanced sex ratio in hatchlings.

We modeled three possible fecundity scenarios based on published data on kelp gull breeding success and clutch size (Table I): (i) the 'Patagonian model' included the highest breeding success value reported for kelp gulls breeding in Patagonia as the fecundity parameter, (ii) the 'species model' included the highest breeding success value reported for kelp gulls throughout their breeding range, and (iii) the 'maximum fecundity model' included the highest median clutch size value reported for kelp gulls along their hemispheric breeding range. We considered this last fecundity scenario as very unlikely, because it assumes no egg or chick mortality. Several studies on kelp gulls show that egg and chick mortality may be substantial, reaching in some cases over 25 and 50%, respectively (Williams et al. 1984; Malacalza 1987; Yorio et al. 1995; Yorio & García-Borboroglu 2002; Prellvitz et al. 2009; Dantas & Morgante 2010; Lisnizer et al. 2014), and thus we defined this model as a hypothetical maximum fecundity scenario. We obtained the maximum growth rate reference value (λ_{ref}) from analytical eigenvalue analysis of the projection matrix A (Caswell 2001): $\underline{n}_{t+1} = \mathbf{A} * \underline{n}_t$, where $\underline{n}$ is a vector with the number of individuals in all age classes, and **A** is the Leslie matrix:

$$A = \begin{pmatrix} 0 & 0 & 0 & F \\ S_1 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 \\ 0 & 0 & S_2 & S_2 \end{pmatrix}$$

Colony demographic behavior and population growth patterns in the region

We analyzed the relationship between colony size and growth rate, and in relation to maximum growth rate reference value (λ_{ref}). We accounted for the spatial distribution of colonies by considering their grouping as part of the four pre-defined coastal sectors. These sectors were then characterized by the growth rates of colonies therein as compared to maximum growth rate reference value (λ_{ref}). For this analysis, we used the published data on size, growth rate and spatial distribution of kelp gull colonies in the study area (Table II). Our analysis included all colonies that had breeding pairs in the last survey (Lisnizer et al. 2011).

Results

Population growth and individual transfer processes

We compared the maximum growth rate reference value (λ_{ref}), defined as the range determined by the obtained values (λ_{ref}= 1.08 - 1.19), with the observed kelp gull colony growth rates (Table I, II). Sixty one percent of the colonies (38 colonies, n = 62) showed growth rates smaller than the estimated range (Figure 2). Twenty nine percent showed growth rates within the estimated range, and 10% (6 colonies, n = 62) showed growth rates higher than the maximum reference value estimated with the maximum fecundity model (λ = 1.19). These six colonies were identified as locations that may operate as sinks, receiving breeders from other colonies. Meanwhile, the growth rates by coastal sectors (Río Negro: 1.053 ± 0.015; northern Chubut: 0.991 ± 0.010; central Chubut: 0.994 ± 0.028 and southern Chubut: 1.047 ± 0.009; Lisnizer et al. 2011), as well as that for the entire studied region (1.027 ± 0.006; Lisnizer et al. 2011), were lower than the calculated maximum growth rate range.

Colony demographic behavior and population growth patterns in the region

The largest colonies (>4,000 pairs) showed growth rates close to 1, except for Quintano Island (λ = 1.18), while the smallest colonies (<400 pairs) showed growth rates between

0.83 and 1.55 (Figure 3). We did not find a statistically significant correlation between colony population size and growth rate (R = 0.055; P = 0.635). All colonies with growth rates higher than the maximum growth rate reference value (λ_{ref}) were small, ranging from 37 to 650 pairs (Coefficient of variation (CV): 0.98, n = 6) (Figure 3). Colonies with growth rates within the reference range (λ_{ref}: 1.08-1.19) showed more variable population sizes, from 79 up to 11,296 pairs, and if Quintano Island is excluded from the analysis, population size varied between 79 and 2,935 pairs (CV: 1.12; n = 17). Most colonies showed growth rates that were smaller than the reference range, and their sizes varied from 1 to 7,445 pairs (CV = 1.54; n = 38) (Figure 3).

From the coastal sector perspective, we found that the Río Negro, northern Chubut and southern Chubut sectors showed more than one colony with growth rates located within the range of reference (λ_{ref}), but only the northern and southern Chubut sectors included colonies with growth rates higher than λ_{ref} (Table II). Out of the 6 colonies with growth rates higher than λ_{ref}, five of them (Galfráscoli Islet, Galiano Norte Island, Galiano Sur Island, Vernacci Norte 2 Island, Ezquerra Island) were located within a restricted coastal sector of southern Chubut, less than 50 km apart from each other, and also less than 50 km apart from the largest colonies of this sector. The remaining colony, Punta Loma, is located in the northern Chubut sector, 15 km from the city of Puerto Madryn and less than 50 km from the largest colonies of this sector.

Discussion

Our results show that source-sink processes contributed to the growth of at least six kelp gull colonies. Highest growth rates were estimated for smaller colonies, all of them located in the proximity of larger colonies, largely with stationary population trends. The maximum growth rate reference values, estimated for the different scenarios based on known values of population parameters, suggest that an annual increase of between 10 and 20% could be considered high for the species. Twenty nine percent of the evaluated colonies showed rates of population growth within this high value reference range. Most of these colonies were located in coastal sectors where populations increased in abundance between 1994 and

2008, but two of them were located in the northern Chubut coastal sector which presented a steady trend over the study period (Lisnizer et al. 2011). At least six colonies showed values of population growth higher than the value estimated using the model of maximum fecundity, suggesting that the observed increase could have been favored by source-sink type processes, i.e., the incorporation into the breeding population of individuals from other colonies. Our method allows the detection of such extreme cases where immigration is the only factor that could explain the observed high growth. However, there are probably other colonies involved in source-sink dynamics, including those providing emigrants. It is important to mention that the estimation of the theoretical maximum lambda is based upon vital rates obtained for the South African Kelp Gull population, as survival rates are unknown for *L. dominicanus* or any related species in the study region. Taking into account the lack of information on this regard, we used the upper confidence interval value of the parameter to estimate the highest possible maximum lambda and, therefore, provide a stricter test of the existence of dispersal among colonies. Also, not introducing density dependence or sources of stochasticity in the matrix model produces high estimates of theoretical lambda with the same result on the evaluation of the role of dispersal.

The dispersal of individuals between colonies has been suggested as one of the main mechanisms of seabird population growth (Ainley et al. 1990; Martínez-Abraín et al. 2001, 2003; Breton et al. 2006). Several gull studies demonstrate the influence of these transfer processes on colony growth (Danchin & Monnat 1992; Suryan & Irons 2001; Oro 2003; Cam et al. 2004; Kildaw et al. 2005; Skórka et al. 2005). In particular, a population model developed for one of the studied colonies, Punta Loma, has suggested that immigration from other colonies was the main mechanism explaining the observed growth (Lisnizer et al. 2014). Colonies at both Punta Loma and Ezquerra Island, locations with population growth rates higher than the reference rate, have been recently established (Ezquerra Island in 2003 and Punta Loma in 2004; Lisnizer et al. 2011), indicating that dispersion and transfer of individuals between sites are factors that contribute in a substantial way to the growth of recently established colonies.

The relationship between seabird colony size and growth rate has been particularly investigated in cormorants, gannets and gulls, and in some cases it has been shown that small (and recently established) colonies tend to grow at a faster rate than larger ones (Coulson 1983; Furness & Monaghan 1987; Porter & Coulson 1987; Moss et al. 2002). Our results show that colonies with large population sizes presented stationary trends while smaller sized colonies presented both increasing and decreasing rates. Most colonies with high growth rates (particularly those higher than the calculated reference rate for the species) showed small to medium population sizes, except for the colony in Quintano Island, located in the southern Chubut coastal sector. This colony was the only breeding site with a large population size (more than 11,000 breeding pairs) and a growth rate close to the maximum limit of the reference range. Monitoring showed that kelp gulls at Quintano Island increased in abundance by 84% in about ten years (Yorio et al. 1998; Lisnizer et al. 2011). This increase may have been favored by immigration of breeders from other colonies in the region that during the same time span presented stationary or decreasing trends (Lisnizer et al. 2011).

Recruitment to small colonies of first breeding birds from other sites is a well-known phenomenon in seabirds, and several authors have suggested that the sources of these birds are the nearest colonies (Oro & Pradel 1999; Velando 1999; Inchausti & Weimerskirch 2002; Bonnaud et al. 2009). While kelp gull dispersal patterns in Argentina are still unknown, all small to medium size colonies with high growth rates were not far from large colonies. Interestingly, most colonies with high growth rates were located in San Jorge Gulf, a relatively small coastal area in southern Chubut. This sector was characterized by a high population growth considering both individual colonies and the overall population, and is where most of the new colonies established during the last two decades have been detected (Lisnizer et al. 2011). The high availability of food of anthropogenic origin (Lisnizer et al. 2011) and suitable nesting habitat (García-Borboroglu & Yorio 2004) in this coastal sector may explain the recruitment of breeders from other sites and the intrinsic growth of colonies.

As in other seabirds, dispersal of individuals between colonies and differential recruitment could have been important determinants of kelp gull population change in the study area. Although our analysis did not provide insights into the extent of these mechanisms, they provide strong evidence that transfer processes have been important determinants of the observed changes in colony size within the region, being an important part of a dynamic and interconnected system. The dispersal of individuals among colonies and the existence of differential spatial dynamics depending on population size suggest a metapopulation structure and dynamics of the kelp gull in the study region.

Kelp gulls in Argentina and throughout South America regularly feed at refuse tips, and their increased activity at or near cities may result in hazards to aircraft and threats to human health (Yorio et al. 1998; González-Acuña et al. 2006; Albarnaz et al. 2007; Rodriguez et al. 2012). As airports in coastal Patagonia, Argentina, are often located near coastal refuse tips, kelp gulls have been reported to affect airport traffic at the cities of San Antonio Oeste, Trelew, and Comodoro Rivadavia (Yorio et al. 1998). Kelp gulls have also been reported to prey upon and kleptoparasite other seabird and coastal birds, some of them globally threatened (see review in Yorio et al. 2005). In addition, studies in the Península Valdés area, Chubut Province, have shown that kelp gull attacks on right whales (*Eubalaena australis* Desmoulins, 1822) to feed on their skin and blubber have substantially increased in recent years (Sironi et al. 2009; Fazio et al. 2012). This has resulted in growing concerns about the negative effects of this interactions on whales and on the tourist business, and promoted the discussion among authorities, NGOs and research institutions in relation to the design of needed population monitoring programs and alternative culling initiatives or management practices (Sironi et al. 2009).

Our results also suggest some recommendations for population monitoring and research priorities related to potential management needs. Monitoring programs of kelp gull populations should be implemented at the regional level, covering a wide geographical area during the same year and considering not only the pre-existing colonies but also sites with suitable habitat for the establishment of new colonies. Although the regular population assessment of only key colonies is of great value, the interpretation of resulting data for demographic purposes should be done in the regional context. In addition, given the spatial and temporal dynamics of the system, a regional survey and census of all colonies should be implemented on a regular basis, at least every 3-5 years. This would allow the identification of changes in gull population trends, the redefinition of priority colonies and coastal sectors for subsequent monitoring and, if necessary, help in the design and implementation of management actions. Similarly, our results also indicate that management strategies in areas with current kelp gull-wildlife conflicts in Patagonia should avoid considering a single colony or a small region as the unit of effective management, but focus on a larger scale so as to take into account the potential connectivity among colonies. In this context it should be considered that one of the major indirect consequences of performing culling programs is the individual dispersal to other unaffected colonies (Bosch et al. 2000), and thus the population implications of this practice should be evaluated at the metapopulation level prior to its implementation. In addition, management practices aimed at minimizing the availability of urban and fishery waste for gull populations should be implemented at broad geographic scales. Furthermore, our results strongly suggest the connectivity among colonies distributed along a vast area which encompasses several Provincial jurisdictions, highlighting the complexities involved with management decisions. Thus, this larger scale approach requires the development of strategies for joint work between the authorities of the different jurisdictions involved, so as to achieve an effective management. Finally, it is essential to identify and quantify some of the key factors that may be affecting these demographic processes, such as the differential food availability in both natural and anthropogenic sources, predation, and habitat availability. In particular, it would be valuable to conduct further research on the mechanisms involved in the observed demographic processes, not only those related to the reproductive period but also those acting during the non-breeding season.

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Table I. Parameters used for the kelp gull age structured population model under three different fecundity scenarios (see text), and maximum growth rate reference values (λ_{ref}) obtained in each case.

	Patagonian model	Species model	Maximum fecundity model
Breeding success	1.21[a,b]	1.93 [c,d]	2.60 [e]
Survival [f] (S_1)	0.54	0.54	0.54
Survival [f] (S_2)	0.89	0.89	0.89
Growth rate (λ_{ref})	1.08	1.14	1.19

References: [a] Yorio et al. 1995; [b] Lisnizer et al. 2014; [c] Parmelee et al. 1978; [d] Calf et al. 2003; [e] highest clutch size value (Lisnizer et al. 2014); [f] Altwegg et al. 2007.

Table II. Position, size (number of breeding pairs) during the 2006-2008 survey, population growth rate (λ) during the period 1994-2008 and classification of colony growth rate using maximum growth rate reference value (λ_{ref}, see text) of kelp gulls colonies along the northern coast of Patagonia, Argentina. Adapted from Lisnizer et al. (2011).

Colony	Position	Size	λ	Comparison with λ_{ref} (1.08 – 1.19)
Río Negro coastal sector				
Isla Novaro	40°45'S, 64°50'W	288	1.111	=
Islotes del Canal Escondido	40°47'S, 64°47'W	265	0.979	<
Islote La Pastosa	41°25'S, 65°02'W	2935	1.075	=
Islote Redondo	41°26'S, 65°01'W	941	1.009	<
Islote de los Pájaros	41°27'S, 65°02'W	1163	1.066	<
Northern Chubut sector				
Isla Primera de Caleta Valdés	42°21'S, 63°37'W	1917	1.096	=
Islote Notable	42°25'S, 64°31'W	4044	0.975	<
Punta Pirámide	42°35'S, 64°17'W	453	1.027	<
Punta Delgada	42°43'S, 63°38'W	106	1.003	<
Playa La Pastosa	42°50'S, 63°59'W	682	1.089	=
Punta Loma *	42º82'S, 64°47'W	88	1.556	>
Punta León	43°04'S, 64°29'W	5813	0.981	<
Central Chubut sector				
Punta Tombo	44°02'S, 65°11'W	6457	1.006	<

Punta Gutiérrez	44°24'S, 65°16'W	338	0.998	<
Cabo San José	44°31'S, 65°17'W	194	1.055	<
Isla Sur Cabo San José	44°31'S, 65°18'W	131	0.861	<
Isla Acertada	44°32'S, 65°19'W	249	1.093	=
Isla Cumbre	44°35'S, 65°22'W	1356	1.011	<
Southern Chubut sector				
Isla Blanca Mayor	44°46'S, 65°38'W	1463	1.021	<
Isla Blanca Menor Este	44°46'S, 65°38'W	15 [2]	1.019	<
Isla Blanca Menor Oeste	44°46'S, 65°39'W	287 [2]	1.005	<
Isla Moreno	44°54'S, 65°32'W	35	0.83	<
Isla Sola	44°58'S, 65°33'W	641	0.98	<
Isla Aguilón del Norte	45°00'S, 65°34'W	42	1.029	<
Isla Arce	45°00'S, 65°29'W	786	0.978	<
Península Lanaud	45°03'S, 65°35'W	688	1.031	<
Isla Leones *	45°03'S, 65°36'W	78	0.954	<
Isla Buque	45°03'S, 65°37'W	1323	1.025	<
Isla Pan de Azúcar	45°04'S, 65°49'W	1822	1.008	<
Islotes Arellano	45°03'S, 65°51'W	182	1.125	=
Islotes Massa	45°02'S, 65°51'W	30	0.885	<
Islote Laguna	45°02'S, 65°53'W	523	1.01	<
Islote Galfráscoli	45°02'S, 65°51'W	37	1.198	>

Islote Puente	45°02'S, 65°50'W	118	1.063	<
Islote Luisoni	45°02'S, 65°51'W	102	1.12	=
Isla Patria	45°03'S, 65°51'W	596	1.046	<
Isla Blanca	45°03'S, 65°58'W	1	0.833	<
Isla Tova	45°06'S, 66°00'W	152	0.873	<
Isla Tovita	45°07'S, 65°57'W	263	1.051	<
Isla Gaviota de Complejo T-T	45°06'S, 65°58'W	1873	1.023	<
Isla Este	45°07'S, 65°56'W	981	1.024	<
Isla Sur	45°07'S, 65°59'W	724	1.117	=
Islotes Goëland	45°05'S, 66°03'W	550	0.975	<
Isla Pequeño Robredo	45°07'S, 66°06'W	439	1.029	<
Isla Gran Robredo	45°08'S, 66°03'W	1110	1.09	=
Isla Felipe	45°04'S, 66°19'W	836	1.045	<
Isla Ezquerra *	45°04'S, 66°20'W	42	1.518	>
Isla Galiano Norte	45°05'S, 66°24'W	654	1.209	>
Isla Galiano Central	45°06'S, 66°25'W	317	1.164	=
Isla Galiano Sur	45°06'S, 66°25'W	317	1.254	>
Isla Isabel Norte	45°07'S, 66°30'W	227	1.086	=
Isla Isabel Sur	45°07'S, 66°30'W	144	1.076	=
Isla Ceballos	45°09'S, 66°22'W	1911	1.054	<
Isla Vernaci Este	45°11'S, 66°29'W	2762	1.09	=

Isla Vernaci Norte 1	45°11'S, 66°30'W	260	1.098	=
Isla Vernaci Norte 2	45°11'S, 66°30'W	628	1.526	>
Isla Vernaci Oeste Noroeste *	45°11'S, 66°30'W	79	1.111	=
Isla Vernaci Sudoeste	45°11'S, 66°31'W	7445	1.016	<
Isla Vernaci Noroeste	45°10'S, 66°31'W	455	1.185	=
Isla Vernaci Oeste	45°11'S, 66°31'W	106	1.06	<
Isla Viana Mayor	45°11'S, 66°24'W	1819	1.116	=
Isla Quintano	45°15'S, 66°42'W	11296	1.183	=

* Colonies established between years 1995 and 2008.

Figure 1. Study area in the northern coast of Patagonia, Argentina. Arrows indicate the boundaries of defined coastal sectors.

Figure 2. Kelp gull colony growth rates along the northern coast of Patagonia (1994-2008) and range of maximum growth rate reference values (framed). Only colonies with breeding pairs in the last survey were analyzed (see text).

Figure 3. Relationship between colony size (number of pairs from the last survey) and growth rate (1994-2008) of kelp gulls in the four different coastal sectors in the northern coast of Patagonia. Data extracted from Lisnizer et al. (2011). Dashed lines show the maximum growth rate reference extreme values (λ_{ref}). Full symbols indicate colonies established during the study period.