

Articles

DEMOGRAPHIC AND BREEDING PERFORMANCE OF A NEW KELP GULL *LARUS DOMINICANUS* COLONY IN PATAGONIA, ARGENTINA

DEMOGRAFÍA Y DESEMPEÑO DE LA REPRODUCCIÓN EN UNA NUEVA COLONIA DE GAVIOTA COCINERA *LARUS DOMINICANUS* EN LA PATAGONIA, ARGENTINA

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SUMMARY.—Understanding the processes involved in the establishment and persistence of new seabird colonies is important for improving conservation and management strategies. Over the past few decades, kelp gull *Larus dominicanus* numbers have increased in Patagonia, Argentina, and new colonies have been reported. We studied a recently established colony to analyse aspects of its population dynamics and breeding biology. The number of breeding pairs at Punta Loma increased from 13 to 233 in the seven years after the colony was established (2004-2011) and the number of chicks fledged per nest was low (< 1 chick per nest) compared to that of other long-established kelp gull colonies in the region. Modelled estimates of abundance assuming closed population dynamics for the Punta Loma colony were lower than observed (70% lower or more), suggesting that the observed growth cannot be explained by local productivity alone. Immigration from other colonies was likely to be the main factor responsible for the observed growth, being considerably higher than local recruitment. This study constitutes the first characterisation of demographic processes occurring during the initial years following colony establishment in kelp gulls. The main findings include rapid population growth driven by immigration and poor breeding performance potentially linked to a high proportion of young breeders. Our results highlight the key role of source-sink dynamics on the growth and persistence of new seabird colonies.

Key words: Patagonia, population growth, productivity, recruitment, seabirds.

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RESUMEN.—La comprensión de los procesos involucrados en el establecimiento y la persistencia de nuevas colonias de aves marinas es importante para mejorar las estrategias de manejo y conservación. Durante las últimas décadas, los números de gaviota cocinera *Larus dominicanus* en Patagonia, Argentina, se han incrementado y se han formado nuevas colonias. Estudiamos una colonia establecida recientemente para analizar aspectos de su dinámica poblacional y biología de reproducción. El número de parejas reproductoras en Punta Loma se incrementó de 13 a 233 en los siete años posteriores al establecimiento de la colonia (2004-2011) y el número de pollos independizados por nido fue bajo (< 1 pollo por nido) en comparación a otras colonias más antiguas de la región. Las estimaciones de abundancia obtenidas de un modelo que asume una dinámica poblacional cerrada para la colonia de Punta Loma fueron menores que las observadas (70% menores o más), sugiriendo que el crecimiento observado no puede ser explicado únicamente por productividad local. La inmigración desde otras colonias fue posiblemente el principal factor responsable del crecimiento observado, siendo considerablemente mayor al reclutamiento local. Este estudio constituye la primera caracterización de los procesos demográficos que ocurren durante los primeros años desde el establecimiento de una colonia en gaviotas cocineras. Los principales resultados incluyen un rápido crecimiento poblacional favorecido por la inmigración y un pobre rendimiento reproductivo potencialmente asociado a una elevada proporción de reproductores jóvenes. Nuestros resultados resaltan el papel clave de la dinámica de tipo fuente-sumidero en el crecimiento y persistencia de colonias nuevas de aves marinas.

Palabras clave: aves marinas, crecimiento poblacional, Patagonia, productividad, reclutamiento.

INTRODUCTION

Global change scenarios occurring during the last few decades are challenging the ability of species to adapt to a rapidly changing environment. Perturbations in coastal areas, alterations in prey distribution and abundance (i.e. prey depletion or anthropogenic food sources), and climate change, have the potential to change seabird breeding distributions (Camphuysen and Garthe, 2000; Ainley and Divoky, 2001; Erwin *et al.*, 2003; Chambers *et al.*, 2005). Distributional shifts of long-existing breeding sites and the establishment of colonies in new areas have been reported for many seabird species (Van Eerden and Gregersen, 1995; Kildaw *et al.*, 2005; Skórka *et al.*, 2005; Crawford *et al.*, 2008). The formation of new colonies at previously unoccupied sites is one of the characteristic processes of metapopulation dynamics and various models have highlighted the importance of this process in the persistence of metapopulations (Hanski and Gaggiotti, 2004). However, relatively few studies have

examined the demographic dynamics of new seabird colonies (Martínez-Abraín *et al.*, 2001; Oro and Ruxton, 2001; Kildaw *et al.*, 2005; Coulson and Coulson, 2008; Lenda *et al.*, 2010; Pyk *et al.*, 2013).

The connectivity among colonies through dispersal of individuals plays an important role in the viability of seabird populations, allowing the formation of colonies in new sites and the recolonisation of locally extinct colonies (Hanski and Gaggiotti, 2004). Natal and breeding dispersal are key parameters in the population dynamics of new colonies as they can have a great influence on their growth rates (Inchausti and Weimerskirch, 2002; Cam *et al.*, 2004; Lewison *et al.*, 2012). Seabird colonies can grow at high rates in their initial years and this population growth can be driven mainly by recruitment of individuals from other colonies, as demonstrated for some gull species (Crawford *et al.* 1999; Oro and Ruxton, 2001; Kildaw *et al.*, 2005; Skórka *et al.*, 2005; Neubauer *et al.*, 2006).

The kelp gull *Larus dominicanus* is widely distributed in the southern hemisphere

(Burger and Gochfeld, 1996). In Patagonia, Argentina, the kelp gull is the most abundant gull species (Yorio *et al.*, 1999). Along 1,800 km of coastline in northern Patagonia, Lisnizer *et al.* (2011) estimated a total population of 72,000 breeding pairs, with 10 new colonies recorded and an annual growth rate of 2.7% between 1994 and 2008. An increase in the kelp gull population may have negative effects on other coastal species through predation, competition for breeding sites and kleptoparasitism, and their activity at or near cities may result in hazards to aircraft and threats to human health (see review in Yorio *et al.*, 2005). Knowledge of kelp gull demographic and reproductive parameters is essential to implement appropriate management actions. Moreover, information on the colonisation dynamics of new sites and transfer processes (i.e. immigration, emigration) within the metapopulation is crucial for improving conservation and management strategies (Oro, 2003; Lenda *et al.*, 2010), being particularly relevant under this population increase scenario. We analysed aspects of the population dynamics and breeding biology of kelp gulls at a recently established colony in Patagonia. Our objectives were to: (1) estimate reproductive parameters, (2) analyse the rate of population change, and (3) examine the roles of immigration and local recruitment on population growth of this new colony.

MATERIALS AND METHODS

Study area

The Punta Loma Protected Area (42° 49' S, 64° 53' W) is located 15 km from the city of Puerto Madryn, Chubut, Argentina. Kelp gulls first nested there in 2004 (E. Dames, pers. comm.). The colony is at the top of a sedimentary cliff. Vegetation in the nesting area consisted of isolated shrubs, mainly *Suaeda divaricata*, *Lycium chilense* and *Atriplex lampa*.

Breeding performance

During the breeding seasons of 2006 and 2007 we visited the colony every two to three days from mid-September to early February and collected information on timing of nest initiation, laying dates, clutch sizes, hatching success, and number of chicks fledged per nest. We monitored 116 nests in 2006 and 119 nests in 2007, which were individually marked with numbered tags. We marked eggs with a felt-tip pen and chicks at hatching with individually labelled fibre-tape bands that were replaced by both metal and plastic rings when chicks were 25 days old. Before hatching, we surrounded the study area with a 60-cm-high fence to prevent chicks from moving too far from their nests and to facilitate the counting of chicks. The fence was kept in place until the end of the breeding season. We recorded hatching success (chicks hatched/eggs laid), fledging success (chicks fledged/chicks hatched) and number of chicks fledged per nest with eggs laid. Fledging was defined as chicks surviving to 28 days of age, corresponding to the age when chicks are highly mobile, but not yet flying. Sample sizes of the different variables analysed may differ due to the loss of nests and because a few inaccessible nests (e.g. located on cliff ledges or steep slopes) were not included in the fenced area. Means are presented with standard errors. We used non-parametric statistics as underlying parametric assumptions were not met, except in the analysis of the proportion of nests with eggs. In all cases, we considered tests as significant at $P < 0.05$.

Age at first breeding

From 2006 to 2008, we marked a total of 141 chicks (34, 65 and 43 chicks in 2006, 2007 and 2008, respectively) with plastic rings with unique four-letter combination

codes. From 2007 to 2011 breeding seasons, we resighted ringed birds at the Punta Loma colony to determine the age of first breeding. We observed the colony during one hour twice a week from two locations at the periphery of the colony and recorded the ring code of each ringed bird sighted together with breeding behaviour (incubation, parental care) within or at the periphery of the colony.

Demographic aspects

From 2004 to 2011, we conducted nest counts during late incubation (mid-November) to estimate the yearly abundance of breeding pairs. We considered nests active if they contained an egg or chick or if there were signs of recent use, such as fresh nesting material. We estimated the population growth rate using log-linear regression of counts against time based on an exponential model of population growth $N_t = N_0 \times e^{rt}$, where the slope of the regression line corresponds to the population growth rate (Caughley, 1977).

To determine if the observed population growth could be explained in the absence of immigration, we modelled nest abundance under the assumption of a closed population. We used a deterministic exponential growth model based on the following vital rates: Estimated nests_(t) = (Breeders_(t) + Locally-born recruits_(t)) / 2, where Breeders_(t) = Breeders_(t-1) × $S_{(breeders)}$, and Locally-born recruits = Nests_(t-3) × Productivity × $S_{(recruits)}$. The term Breeders_(t) denotes the number of breeding birds in current year (t), derived from the annual count of active nests in the case of the first modelled year. The term t-3 refers to the years to first breeding, three years being the youngest age of breeding for ringed chicks at the Punta Loma colony (see Results). 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). $S_{(breeders)}$ denotes survival of birds older than one year of age (0.84, IC_{95%}: 0.77–0.89, Altwegg *et al.*, 2007). $S_{(recruits)}$ denotes survival of birds at minimal recruitment age, and is the product of first-year survival (0.44, IC_{95%}: 0.35–0.54, Altwegg *et al.*, 2007) times $S_{(breeders)}$ ². Division by two in the estimated nests formula converts individual estimates into nest estimates, assuming a 1:1 sex ratio. We estimated mean annual productivity based on the mean number of chicks fledged per nest in 2006 and 2007 (0.48 chicks/nest; see Results). We assumed 100% philopatry. This assumption together with that of minimal age at first breeding was to maximise the estimate of locally born recruits. We also estimated colony growth rate considering immigration in the two years prior to the first possible recruitment of locally born individuals (2005 and 2006). Numbers of breeding birds in these two years were derived from the number of breeding pairs observed at the colony in each of these years. Immigration for 2005 and 2006 was calculated as the difference between the number of observed breeders in a given year and surviving breeders from the previous year (assuming no locally born recruits in those years). To assess possible variability in survival, given the lack of information for the local population, we replicated the analysis using the minimum and maximum confidence interval values for the previously mentioned survival estimates (first year survival = 0.44 IC_{95%}: 0.35–0.54; >1 year survival = 0.84 IC_{95%}: 0.77–0.89; Altwegg *et al.*, 2007). Thus, we obtained three nest abundance and population change estimates for each model. Finally, to assess the relative roles of immigration and local recruitment, we incorporated into the analysis the possible immigration of individuals from other colonies into the Punta Loma population. We estimated the immigration required to support the observed colony growth during the study period using the formula: Net migration_(t) = Total re-

$\text{cruits}_{(t)} - \text{Locally-born recruits}_{(t)}$, where $\text{Total recruits}_{(t)} = (\text{Nests}_{(t)} - (\text{Nests}_{(t-1)} \times S_{(\text{breeders})})) \times 2$. Values are reported as means \pm SE.

RESULTS

Breeding performance

The first nests were built on 17 September 2006 and 3 October 2007, and the first eggs were recorded on 20 September 2006 and 5 October 2007. The last eggs were laid on 16 December 2006 and on 26 November 2007. Thus, the laying periods spanned ~ 12 weeks in 2006 and 7 weeks in 2007, resulting in a different laying pattern of first eggs between seasons (Kolmogorov-Smirnov test, $P < 0.0001$). The median laying date was 31 October in 2006 ($N = 116$) and 4 November in 2007 ($N = 119$). The number of eggs per nest ranged from 1 to 4, although only one four-egg clutch was recorded. Mean clutch sizes were 2.62 ± 0.05 ($N = 108$) in 2006 and 2.44 ± 0.06 ($N = 118$) in 2007 (table 1). Clutch-size did not differ between

seasons (Mann-Whitney U-test, $U = 6092.5$, $P = 0.17$). The proportion of nests with eggs was significantly lower in 2006 than in 2007 (88.5 vs. 97.5%, respectively, $\chi^2_1 = 6.43$, $P = 0.01$).

The first chicks were recorded between 7 and 8 November in both years, and the last eggs hatched 54 and 46 days later in 2006 and 2007, respectively. Thus, the pattern of hatching of first eggs differed between years (Kolmogorov-Smirnov test, $P = 0.036$). However, median hatching dates were similar, being 29 November in 2006 and 1 December in 2007 ($N = 62$ and 75 nests, respectively). Hatching success was 0.60 ± 0.05 ($N = 73$ nests) in 2006 and 0.64 ± 0.04 ($N = 86$ nests) in 2007 being similar in both years (Mann-Whitney U-test, $U = 3049.0$, $P = 0.76$). Breeding pairs hatched on average 1.53 ± 0.14 chicks ($N = 72$ nests) in 2006 and 1.63 ± 0.11 chicks ($N = 87$ nests) in 2007. Fledging success was 0.22 ± 0.04 ($N = 45$ nests) in 2006 and 0.41 ± 0.05 ($N = 70$) in 2007, being significantly different between years (Mann-Whitney U-test, $U = 1211.0$, $P = 0.035$). The number of chicks fledged per nest with eggs laid was 0.30 ± 0.07 ($N = 81$) in 2006 and 0.65 ± 0.10 ($N = 89$) in 2007. Pairs raised at least one chick in 26.5% of the nests ($N = 68$) in 2006, and in 42.7% of the nests ($N = 89$) in 2007.

TABLE 1

Clutch size of kelp gulls at Punta Loma (Argentina) during 2006 and 2007.

[*Tamaños de puesta de gaviotas cocineras durante 2006 y 2007 en Punta Loma (Argentina).*]

| | 2006 | 2007 |
|-----------------|-----------------|-----------------|
| 1-egg clutches | 3 (2.78%) | 11 (9.32%) |
| 2-egg clutches | 35 (32.41%) | 45 (38.14%) |
| 3-egg clutches | 70 (64.81%) | 61 (51.69%) |
| 4-egg clutches | 0 | 1 (0.85%) |
| Mean \pm s.e. | 2.62 ± 0.05 | 2.44 ± 0.06 |
| <i>N</i> | 108 | 118 |

Age at first breeding

First breeding was recorded at four years of age for birds ringed in 2006 (2 birds, 5.9% of birds ringed that year), and at three years of age for birds ringed in 2007 and 2008 (1 bird of each cohort, 1.5% and 2.4% of birds ringed in 2007 and 2008, respectively).

Colony growth

The number of breeding pairs at Punta Loma increased from 13 in 2004 to 233 in

2011 (fig. 1), with the rate of growth varying during the study. The number of breeding pairs increased at a relatively high rate during the first three years (2004-2006: $\lambda = 2.88$), but showed a mean decreasing trend during the following three years (2006-2009: $\lambda = 0.88$). The number of breeding pairs increased again during the last two study years, although at a lower rate compared to the first period (2009-2011, $\lambda = 1.73$; fig. 1).

Model results indicated that the observed population growth during the seven years

cannot be explained by local recruitment alone (fig. 2). Assuming that the Punta Loma colony behaved as a closed population, estimated abundances showed a decreasing trend during the study period (model a: $\lambda = 0.92$). Calculations using this closed population model provided an estimated number of nests for the last year of our study (2011) that was 97% lower than that observed. In addition, the closed population analysis allowing only two immigration pulses in years prior to the first possible recruitment of locally

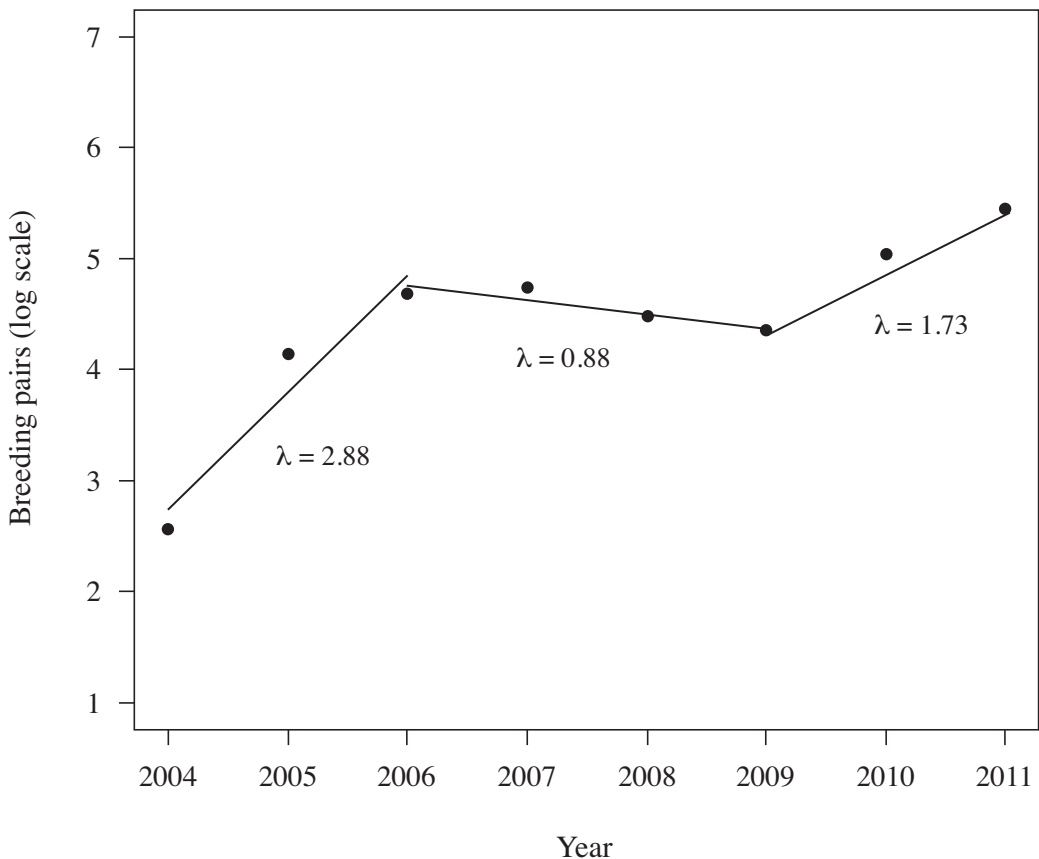


FIG. 1.—Breeding pairs observed (logarithmic scale) and estimated population growth rate during three periods in the kelp gull colony at Punta Loma (Argentina).

[Parejas observadas que nidificaron (en escala logarítmica) y tasa estimada de crecimiento poblacional durante tres periodos en la colonia de gaviotas cocineras en Punta Loma (Argentina).]

born gulls indicated that the estimated number of nests in the last study year was 72% lower than actually observed (fig. 2). This last model indicated an increasing trend (model b: $\lambda = 1.15$), but with a lower growth rate than that observed.

These results were consistent with the population growth rate estimated by the models where survival estimates were replaced by the lowest and highest values of the considered parameters confidence interval. Population growth rates (λ) considering

just one founder group (model a) were 0.84 and 0.98 for minimum and maximum survival values, respectively. Growth rate estimates for the model considering two immigration events in the two years after the colony was first established (model b) were 1.07 and 1.21 for minimum and maximum survival values, respectively. In summary, both models with variable survival estimates showed that the Punta Loma colony could not have attained the observed growth rate just by local production.

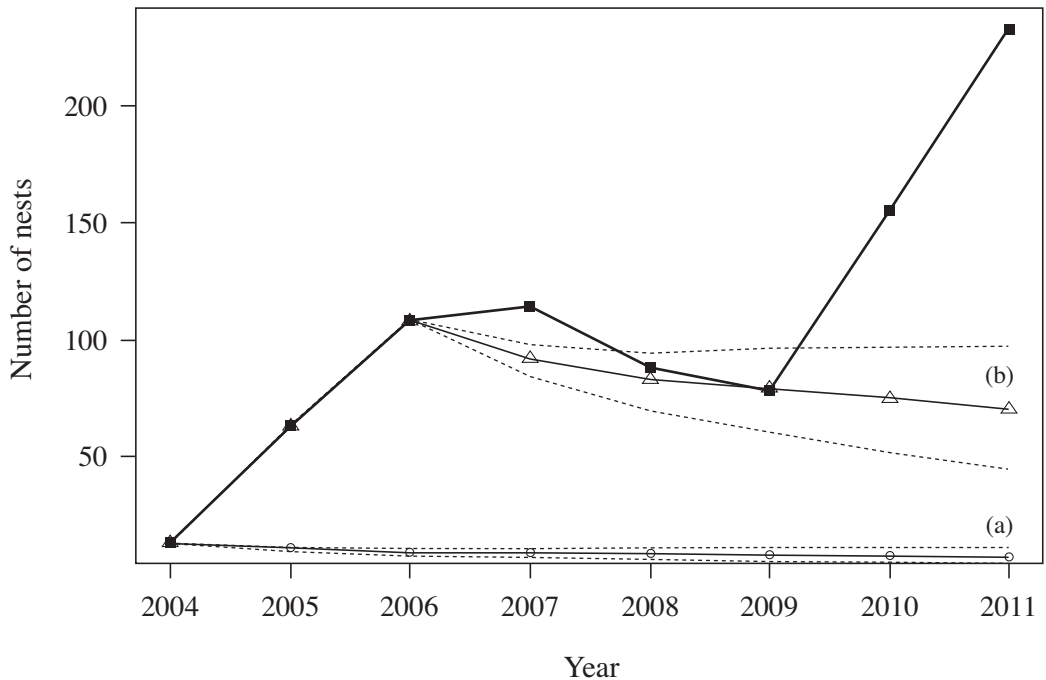


FIG. 2.—Observed nest abundance in the colony of kelp gulls at Punta Loma (Argentina) (full squares) and estimated nest abundances considering (a) a closed population without immigration (empty circles) and (b) two immigration pulses prior to the first possible recruitment event of locally-born individuals (empty triangles). Dotted lines indicate the estimations considering minimum and maximum survival values (see text).

[Número de nidos observados en la colonia de gaviotas cocineras en Punta Loma (Argentina) (cuadrados negros) y número estimado de nidos considerando (a) una población cerrada sin inmigración (círculos vacíos) y (b) dos pulsos inmigratorios antes del primer evento de posible reclutamiento de individuos nacidos localmente (triángulos vacíos). Las líneas de puntos indican estimaciones considerando valores de supervivencia máxima y mínima (véase texto).]

Local recruitment and immigration

Recruitment of breeders was relatively high, with the exception of 2008 and 2009 when there was no or very low recruitment (table 2). Model results showed that the mean number of annual recruits required to sustain the observed population growth at the Punta Loma colony was 83 ± 28 birds. Results for the same analysis using minimum and maximum survival values were consistent with this pattern (94 ± 29 birds and 75 ± 28 birds, respectively). The mean estimated number of chicks fledged during our study was 51 ± 11 per year, and the mean estimated number of locally born recruits (chicks surviving to recruitment age) was 12 ± 3 per year (table 2). Mean estimated net migration, calculated as the difference between total and locally-born recruits, was 76 ± 28 per year, with a median of 74 birds per year and a peak of up to 192 immigrant birds in 2011.

DISCUSSION

Laying dates, clutch sizes, and hatching success at the Punta Loma colony were within the ranges of those recorded at two other long-established colonies in the region (Malacalza, 1987; Yorio *et al.*, 1995; Yorio and García Borboroglu, 2002). The onset of laying was similar to that at the Punta León colony, one of the largest kelp gull colonies in the region located 50 km south of Punta Loma (late October to early November; Malacalza, 1987; Yorio *et al.*, 1995). Clutch size and hatching success were similar to those at the Punta León and Isla Vernacci Sudoeste colonies, the latter one located 300 km south of Punta Loma (clutch size: 2.3-2.5 eggs per nest, hatched eggs per nest: 1.70-2.07; Yorio *et al.*, 1995; Yorio and García-Borboroglu, 2002). However, the number of chicks fledged per nest was lower at the Punta Loma colony (1.05-1.21 at Punta León and 0.84-

TABLE 2

Annual number of estimated fledged chicks and recruits at the kelp gull colony of Punta Loma (Argentina) (estimates assume 100% philopatry).
[Número anual de volantes y reclutamientos estimados en la colonia de gaviotas cocineras en Punta Loma (Argentina) (las estimas asumen el 100% de filopatría).]

| Year | Years since colony establishment | Breeding pairs | Fledged chicks | Locally-born recruits | Net migration | Total recruits |
|------|----------------------------------|----------------|----------------|-----------------------|---------------|----------------|
| 2004 | 0 | 13 | 6 | 0 | 26 | 26 |
| 2005 | 1 | 63 | 30 | 0 | 104 | 104 |
| 2006 | 2 | 108 | 52 | 0 | 110 | 110 |
| 2007 | 3 | 114 | 55 | 2 | 45 | 47 |
| 2008 | 4 | 88 | 42 | 9 | -25 | -16 |
| 2009 | 5 | 78 | 37 | 16 | -8 | 8 |
| 2010 | 6 | 155 | 74 | 17 | 162 | 179 |
| 2011 | 7 | 233 | 112 | 13 | 192 | 206 |

0.86 at Isla Vernacci Sudoeste; Yorio *et al.*, 1995; Yorio and García-Borboroglu, 2002). The lower breeding success is consistent with the individual quality hypothesis (Kildaw *et al.*, 2005). It proposes that low quality individuals that are poor competitors in well established colonies may benefit by breeding at new sites. Individual quality may be correlated with age, and several studies in many bird species have shown that breeding success is higher in older individuals (see reviews in Saether, 1990; Hamer *et al.*, 2002). Thus, the lower productivity at the Punta Loma colony, compared to other old-established colonies, suggests that it may consist of a higher proportion of young and first-breeders. Studies in new colonies of gulls, terns, and cormorants reported that they were mainly composed by young breeders (Coulson and White, 1956; Tims *et al.*, 2004; Hénau *et al.*, 2007).

Previous research on kelp gull populations in South Africa reported that the age of first breeding was four years old (Crawford *et al.*, 2000), although some birds may breed at three years of age (Whittington, 2007). Our study provides the first information on the age of first breeding for kelp gull populations in South America, and results are consistent with those from South Africa. Different factors can affect the age of first breeding in birds, such as availability of food and mates and the abundance and density of breeders (Becker and Bradley, 2007). Lower nest densities may allow younger individuals to hold breeding territories (Lavers *et al.*, 2008). Several seabird studies have shown that low breeding densities, such as those resulting from significant events of adult mortality (i.e. culling or oil spills) allow young birds to enter the breeding population (Duncan, 1978; Coulson *et al.*, 1982; Porter and Coulson, 1987; Votier *et al.*, 2008). This compensatory recruitment is promoted by low competition levels at colonies with a reduced number of birds.

Several studies of new seabird colonies have shown high rates of increase in breeding

numbers during the first years after colonies were established (e.g., Porter and Coulson, 1987; Hénau *et al.*, 2007; Pyk *et al.*, 2013). The Punta Loma kelp gull colony increased from 13 to 233 pairs in seven years, a similar trend to that recorded during the first three years at the Isla Ezquerra colony established in northern Patagonia in 2003 (from 12 to 42 pairs; Lisnizer *et al.*, 2011). Similarly, a new kelp gull colony at Robben Island, South Africa, increased from 4 to 480 breeding pairs during the first 10 years (Calf *et al.*, 2003; Crawford *et al.*, 2009). Similar and higher rates of increase have been reported for new colonies in other gull species. For example, Oro and Ruxton (2001) reported that a new colony of Audouin's gull *Larus audouini* grew at a rate of 44% during the first decade, Kildaw *et al.*, (2005) reported relatively high growth rates (> 30%) in new kittiwake *Rissa tridactyla* colonies during the first years, and Skórka *et al.* (2005) found that a new colony of caspian gulls *Larus cachinnans* increased by 78% in 10 years. These high growth rates observed were mainly explained by immigration from other breeding locations; other factors influencing this process were low nesting density, habitat quality, and low predation (Kildaw *et al.*, 2005; Skórka *et al.*, 2005; Crawford *et al.*, 2009). Studies of gannet and gull colonies indicate that both natal and breeding dispersal can contribute to high growth rates of new colonies (Oro and Ruxton, 2001; Kildaw *et al.*, 2005; Coulson and Coulson, 2008; Pyk *et al.*, 2013). Future studies should assess the differential contribution of breeding and natal dispersal to recruitment processes at this newly established Punta Loma colony. Three- and four-year old individuals ringed as chicks at the Punta León colony were observed prospecting at the Punta Loma colony, suggesting that recruitment of first breeders from other breeding locations is occurring at our study colony (N. Lisnizer, pers. obs.). In addition, a bird ringed as a breeder in Punta

Loma was recorded in the two following years breeding at the Punta León colony (N. Lisnizer, pers. obs.). Continuity in the ringing and resighting efforts of kelp gulls will allow the unravelling of these processes in the future.

Our results suggest that immigration was important in the growth of the new kelp gull colony at Punta Loma, which is consistent with other studies of the demographic behaviour of new seabird colonies (Oro and Pradel, 1999; Martínez-Abraín *et al.*, 2001; Oro and Ruxton, 2001; Kildaw *et al.*, 2005; Skórka *et al.*, 2005; Coulson and Coulson, 2008). When compared to observed results, models under the assumption of a closed population predicted a lower population growth rate and size. Furthermore, our analysis suggested that the observed population growth could not have been attained even considering two initial immigration pulses in years prior to the first possible recruitment event of locally born individuals. Population growth results were consistent when we performed the same analysis using different survival values, suggesting that the survival values used were acceptable for this population. Further studies using estimated survival values for the local population and annual breeding success values should allow a better understanding of immigration and recruitment processes in the study colony.

In summary, the kelp gull colony at Punta Loma showed an increase in breeding pairs since it was first established, but productivity was low compared with long-established kelp gull colonies in the region. Recruitment of breeders from other colonies was likely to be the main factor responsible for the observed growth, being considerably higher than local recruitment during most years of our study. This study contributes to the understanding of the local dynamics of a recently established seabird colony, and highlights the importance of source-sink processes in its maintenance and growth.

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BIBLIOGRAPHY

- AINLEY, D. G. and DIVOKY G. J. 2001. Seabird responses to climate change. In, J. H. Steel, S. A. Thorpe and K. K. Turekian (Eds.): *The Encyclopedia of Ocean Sciences*, pp. 2669-2677. Academic Press. San Diego.
- ALTWEGG, R., CRAWFORD, R. J. M., UNDERHILL, L. G., MARTIN, A. P. and WHITTINGTON, P. A. 2007. Geographic variation in reproduction and survival of kelp gulls *Larus dominicanus vetula* in southern Africa. *Journal of Avian Biology*, 38: 580-586.
- BECKER, P. H. and BRADLEY, J. S. 2007. The role of intrinsic factors for the recruitment process in long-lived birds. *Journal of Ornithology*, 148: S377-S384.
- BURGER, J. and GOCHFELD, M. 1996. Family Laridae (gulls). In, J. del Hoyo, A. Elliott and J. Sargatal (Eds.): *Handbook of the Birds of the World*, Volume 3 (Hoatzin to Auks), pp. 572-623. Lynx Edicions. Barcelona.
- CALF, K. M., COOPER, J. and UNDERHILL, L. G. 2003. First breeding records of kelp gulls *Larus dominicanus vetula* at Robben Island, Western Cape, South Africa. *African Journal of Marine Science*, 25: 391-393.
- CAM, E., ORO, D., PRADEL, R. and JIMÉNEZ, J. 2004. Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture-recapture models. *Journal of Animal Ecology*, 73: 723-736.

- CAMPHUYSEN, C. J. and GARTHE, S. 2000. Seabirds and commercial fisheries: population trends of piscivorous seabirds explained? In, M. J. Kaiser and S. J. de Groot (Eds.): *The Effects of Fishing on Non-target Species and Habitats: Biological, Conservation and Socioeconomic Issues*, pp. 163-184. Blackwell Science. Oxford.
- CAUGHLEY, G. 1977. *Analysis of Vertebrate Populations*. Wiley. New York.
- CHAMBERS, L. E., HUGHES, L. and WESTON, M. A. 2005. Climate change and its impact on Australia's avifauna. *Emu*, 105: 1-20.
- COULSON, J. C. and COULSON, B. A. 2008. Measuring immigration and philopatry in seabirds: recruitment to black-legged kittiwake colonies. *Ibis*, 150: 288-299.
- COULSON, J. C. and WHITE, E. 1956. A study of colonies of the kittiwake *Rissa tridactyla*. *Ibis*, 98: 63-79.
- COULSON, J. C., DUNCAN, N. and THOMAS, C. 1982. Changes in the breeding biology of the herring gull *Larus argentatus* induced by reduction in the size and density of the colony. *Journal of Animal Ecology*, 51: 739-756.
- CRAWFORD, R. J. M., DYER, B. M. and UPFOLD, L. 2000. Age at first breeding and change in plumage of kelp gulls *Larus dominicanus* in South Africa. *African Journal of Marine Science*, 22: 27-32.
- CRAWFORD, R. J. M., SHANNON, L. J. and WHITTINGTON, P. A. 1999. Population dynamics of the African penguin *Spheniscus demersus* at Robben Island, South Africa. *Marine Ornithology*, 27: 139-147.
- CRAWFORD, R. J. M., TREE, A. J., WHITTINGTON, P. A., VISAGIE, J., UPFOLD, L., ROXBURG, K. J., MARTIN, A. P. and DYER, B. M. 2008. Recent distributional changes of seabirds in South Africa: is climate having an impact? *African Journal of Marine Science*, 30: 189-193.
- CRAWFORD, R. J. M., UNDERHILL, L. G., ALTWEGG, R., DYER, B. M. and UPFOLD, L. 2009. Trends in numbers of kelp gulls *Larus dominicanus* off western South Africa, 1978-2007. *Ostrich*, 80: 139-143.
- DUNCAN, N. 1978. The effects of culling herring gulls *Larus argentatus* on recruitment and population dynamics. *Journal of Applied Ecology*, 15: 697-713.
- ERWIN, R., ALLEN, D. and JENKINS, D. 2003. Created versus natural coastal islands: Atlantic waterbird populations, habitat choices, and management implications. *Estuaries and Coasts*, 26: 949-955.
- HAMER, K. C., SCHREIBER, E. A. and BURGER, J. 2002. Breeding biology, life histories, and life history-environment interactions in seabirds. In, E. A. Schreiber and J. Burger (Eds.): *Biology of Marine Birds*, pp. 217-262. CRC Press. Boca Raton.
- HANSKI, I. and GAGGIOTTI, O. E. 2004. *Ecology, Genetics, and Evolution of Metapopulations*. Academic Press. San Diego.
- HÉNAUX, V., BREGNBALLE, T. and LEBRETON, J.-D. 2007. Dispersal and recruitment during population growth in a colonial bird, the great cormorant *Phalacrocorax carbo sinensis*. *Journal of Avian Biology*, 38: 44-57.
- INCHAUSTI, P. and WEIMERSKIRCH, H. 2002. Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *Journal of Animal Ecology*, 71: 765-770.
- KILDRAW, S. D., IRONS, D. B., NYSEWANDER, D. R. and BUCK, C. L. 2005. Formation and growth of new seabird colonies: the significance of habitat quality. *Marine Ornithology*, 33: 49-58.
- LAVERS, J. L., JONES, I. L. and DIAMOND, A. W. 2008. Age at first return and breeding of razor-bills *Alca torda* on the Gannet Islands, Labrador and Machias Seal Island, New Brunswick. *Waterbirds*, 3: 30-34.
- LENDA, M., ZAGALSKA-NEUBAUER, M., NEUBAUER, G. and SKÓRKA, P. 2010. Do invasive species undergo metapopulation dynamics? A case study of the invasive caspian gull, *Larus cachinnans*, in Poland. *Journal of Biogeography*, 37: 1824-1834.
- LISNIZER, N., GARCÍA-BORBOROGLU, P. and YORIO, P. 2011. Spatial and temporal variation in population trends of kelp gulls in northern Patagonia, Argentina. *Emu*, 111: 259-267.
- LEWISON, R., ORO, D., GODLEY, B., UNDERHILL, L., BEARHOP, S., WILSON, R. P., AINLEY, D., ARCOS, J., BOERSMA, P., GARCÍA-BORBOROGLU, P., BOULINIER, T., FREDERIKSEN, M., GENOVART, M., GONZÁLEZ-SOLÍS, J., GREEN, J. A., GRÉMILLET,

- D., HAMER, K. C., HILTON, G. M., HYRENBACH, K. D., MARTÍNEZ-ABRAÍN, A., MONTEVECCHI, W. A., PHILLIPS, R. A., RYAN, P. G., SAGAR, P., SYDEMAN, W. J., WANLESS, S., WATANUKI, Y., WEIMERSKIRCH, H. and YORIO, P. 2012. Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research*, 17: 93-121.
- MALACALZA, V. E. 1987. Aspectos de la biología reproductiva de la gaviota cocinera *Larus dominicanus* Lichtenstein, en Punta León (Chubut, Argentina). *Physis*, 45: 11-17.
- MARTÍNEZ-ABRAÍN, A., ORO, D. and JIMÉNEZ, J. 2001. The dynamics of a colonization event in the European shag: the roles of immigration and demographic stochasticity. *Waterbirds*, 24: 97-102.
- NEUBAUER, G., ZAGALSKA-NEUBAUER, M., GWIAZDA, R., FABER, M., BUKACIŃSKI, D., BETLEJA, J. and CHYLARECKI, P. 2006. Breeding large gulls in Poland: distribution, numbers, trends and hybridisation. *Vogelwelt*, 127: 11-22.
- ORO, D. 2003. Managing seabird metapopulations in the Mediterranean: constraints and challenges. *Scientia Marina*, 67: 13-22.
- ORO, D. and PRADEL, R. 1999. Recruitment of Audouin's gull to the Ebro Delta colony at metapopulation level in the western Mediterranean. *Marine Ornithology*, 180: 267-273.
- ORO, D. and RUXTON, G. D. 2001. The formation and growth of seabird colonies: Audouin's gull as a case study. *Journal of Animal Ecology*, 70: 527-535.
- PORTER, J. M. and COULSON, J. C. 1987. Long-term changes in recruitment to the breeding group, and the quality of recruits at a kittiwake *Rissa tridactyla* colony. *Journal of Animal Ecology*, 56: 675-689.
- PYK, T. M., WESTON, M. A., BUNCE, A. and NORMAN, F. I. 2013. Establishment and development of a seabird colony: long-term trends in phenology, breeding success, recruitment, breeding density and demography. *Journal of Ornithology*, 154: 299-310.
- SAETHER, B.-E. 1990. Age-specific variation in reproductive performance in birds. *Current Ornithology*, 7: 251-283.
- SKÓRKA, P., WÓJCIK, J. D. and MARTYKA, R. 2005. Colonization and population growth of yellow-legged gull *Larus cachinnans* in southeastern Poland: causes and influence on native species. *Ibis*, 147: 471-482.
- TIMS, J., NISBET, I. C. T., FRIAR, M. S., MOSTELLO, C. and HATCH, J. J. 2004. Characteristics and performance of common terns in old and newly-established colonies. *Waterbirds*, 27: 321-332.
- VAN EERDEN, M. R. and GREGERSEN, J. 1995. Long-term changes in the northwest European population of cormorants *Phalacrocorax carbo sinensis*. *Ardea*, 83: 61-79.
- VOTIER, S. C., BIRKHEAD, T. R., ORO, D., TRINDER, M., GRANTHAM, M. J., CLARK, J. A., MCCLEERY, R. H. and HATCHWELL, B. J. 2008. Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *Journal of Animal Ecology*, 77: 974-983.
- WHITTINGTON, P. A. 2007. Further notes on age of first breeding, plumage and biometrics of kelp gulls in South Africa. *African Journal of Marine Science*, 29: 299-302.
- YORIO, P., BERTELOTTI, M. and GARCÍA-BORBOROGLU, P. 2005. Estado poblacional y de conservación de gaviotas que se reproducen en el litoral marítimo argentino. *Hornero*, 20: 53-74.
- YORIO, P., BERTELOTTI, M. and QUINTANA, F. 1995. Preference for covered nest sites and breeding success in kelp gulls *Larus dominicanus*. *Marine Ornithology*, 23: 121-128.
- YORIO, P., FRERE, E., GANDINI, P. and CONWAY, W. 1999. Status and conservation of seabirds breeding in Argentina. *Bird Conservation International*, 9: 299-314.
- YORIO, P. and GARCÍA-BORBOROGLU, P. 2002. Breeding biology of kelp gulls *Larus dominicanus* at Golfo San Jorge, Patagonia, Argentina. *Emu*, 102: 257-263.

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