

Research Article

The introduced green crab (*Carcinus maenas*) as a novel food resource for the opportunistic kelp gull (*Larus dominicanus*) in Argentine Patagonia

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Abstract

Introduced species are one of the main threats to biological diversity, but they can also facilitate native species through mechanisms such as trophic subsidy. We quantified the diet of breeding kelp gulls (*Larus dominicanus*) and their consumption of the introduced green crab (*Carcinus maenas*) at five colonies located along over 600 km of coastline in Patagonia, Argentina, and analyzed differences in consumption rates among breeding locations. Results based on pellet analysis (n = 961 pellets) showed that kelp gulls consumed green crabs during most or part of the breeding cycle at all study locations (0–73.9%, depending on location, year and breeding stage). Green crab consumption differed among breeding locations, with lower consumption further from the reported location of first Argentinean introduction (Golfo San Jorge, Chubut, Patagonia) in 1999–2000. Despite kelp gulls regularly consumed green crabs at most breeding locations, this invasive species was not an important component in their diet. Both stomach content and stable isotope analyses from breeding kelp gulls indicated that the main prey were fish such as Argentine anchovy and Argentine hake (*Engraulis anchoita* and *Merluccius hubbsi*, respectively) and squat lobster (*Munida gregaria*). At Isla Vernaci Este and Punta Tombo, green crabs were found in only one stomach of all kelp gull age classes sampled (incubating adults (n = 42), young chicks (n = 75), and old chicks (n = 105)). Based on carbon and nitrogen isotopic values from blood samples from incubating adults (n = 54), Bayesian mixing model outputs showed that green crabs contributed 7.3–23.9% to the overall diet. The study showed that the relatively recent introduction of green crabs supplements the available prey base of a widely distributed and abundant predator, the kelp gull, at least during its breeding season in a large coastal sector of central Patagonia. The extent to which the kelp gull in coastal Patagonia may be shaping the establishment, abundance, and population dynamics of the introduced green crab is still unknown and will require further research.

Key words: seabirds, predator-prey interactions, upper trophic level predators, intertidal prey, facilitative interactions, trophic subsidy, trophic ecology

Introduction

The introduction of alien species is one of the main threats to biological diversity, as it can result in changes in species interactions and the functioning

of natural communities. In coastal and marine environments, invasive exotic species can have negative effects at the species, community and ecosystem levels (Ruiz et al. 1997; Grosholz 2002). However, a growing number of studies have shown that species introductions can also result in neutral or even positive effects on native organisms (Rodríguez 2006; Carlsson et al. 2009; Goodenough 2010; Pintor and Byers 2015). Alien species can facilitate native species through mechanisms such as habitat modification, pollination, competitive release, predatory release and trophic subsidy (Rodríguez 2006). Native predators, for example, may adapt to feed on introduced prey when these became relatively abundant and thus obtain fitness benefits from this novel food resource (Carlsson et al. 2009). Avian predators, in particular, have been regularly recorded taking advantage of introduced prey, not only in aquatic but also in terrestrial ecosystems (Tablado et al. 2010; Speziale and Lambertucci 2013; Bertolero and Navarro 2018).

Many exotic species have been reported along coastal marine environments of Argentina, including the green crab (*Carcinus maenas* Linnaeus, 1758) (Orensanz et al. 2002; Schwindt 2008). The invasive green crab has successfully colonized several coastal regions worldwide, including the Atlantic and Pacific coasts of North America, South Africa, Australia and Japan (Cohen et al. 1995; Compton et al. 2010; Carlton and Cohen 2003; Thresher et al. 2003). In Argentina, it was first recorded on the coast of Golfo San Jorge, Chubut, between 1999 and 2000 and has since expanded north throughout a large coastal sector (Hidalgo et al. 2005; Vinuesa 2005; Torres and González-Pisani 2016). At the global level, the green crab is considered a threat to native coastal biodiversity due to its predation on molluscs, crustaceans and other invertebrates (Grosholz et al. 2000; McDonald et al. 2001), and it has been listed among 100 of the world's worst invasive alien species (Lowe et al. 2004). At the regional level, it has been argued that the green crab represents a threat to the integrity of coastal ecosystems in southern South America and for the economies of fishing communities in that region (Hidalgo et al. 2005). Among other consequences, the impacts of invasive species such as the green crab on coastal invertebrate assemblages may translate into negative effects on upper trophic level organisms, like birds that depend on intertidal prey (Grosholz 2002). On the other hand, studies in different regions of the Northern Hemisphere, where the green crab is either native or introduced, show it is a regular prey of many native birds (Klassen and Locke 2007), including several gull species (Dumas and Witman 1993; Moreira 1999; Ellis et al. 2005). This suggests that birds in coastal Patagonia may be consuming this exotic crab, and thus the recent invasion may result in direct positive effects on upper trophic level predators.

The kelp gull (*Larus dominicanus* Lichtenstein, 1823) is the most abundant and widely distributed gull in the Southern Hemisphere, nesting

in South America, Africa, New Zealand, Australia, sub-Antarctic islands and Antarctic Peninsula (Burger and Gochfeld 1996). In Argentina, its breeding population in coastal areas was estimated at over 100,000 breeding pairs (Yorio et al. 2016). Like most *Larus* gulls, the kelp gull is a generalist and opportunistic species that, in coastal Patagonia, feeds on a wide variety of prey obtained from natural and anthropogenic environments (Bertellotti and Yorio 1999; Yorio et al. 2013; Marinao et al. 2018). Natural prey consumed by kelp gulls breeding along the Patagonian coast include mostly fish and marine invertebrates, including several species of molluscs and native crabs (Yorio and Bertellotti 2002; González-Zevallos et al. 2017). Our goals were to determine if the kelp gull takes advantage of the green crab as a novel food item, and if so, to quantify the relative contribution of this novel food source to their diet composition during the breeding season. To achieve this goal, we (1) quantified the diet of breeding kelp gulls and their consumption of the green crab at five colonies located along 600 km of the Chubut coast, and (2) analyzed differences in kelp gull diet and green crab consumption among breeding locations. Given its generalist and opportunistic feeding habits, we expected that breeding kelp gulls would prey upon the green crab. We also expected that the contribution of this exotic prey would be higher in colonies within Golfo San Jorge, closer to the location where the green crab was reportedly introduced. Knowledge of the role that the green crab plays in the trophic ecology of upper trophic level predators, such as the widespread and abundant kelp gull, will contribute to a better understanding of the ecological effects of the introduction and expansion of this invasive species on Patagonian coastal ecosystems.

Materials and methods

Study area

We analyzed kelp gull breeding diet at five sites located along ~ 600 km of coastline in the Province of Chubut, Argentina (Figure 1). Locations selected were Punta Tombo (44°02'28"S; 65°12'36"W), Isla Blanca Mayor (44°46'22.61"S; 65°39'43.34"W), Isla Buque (45°03'20"S; 65°37'28"W), Isla Gaviota (45°05'57"S; 65°57'57"W) and Isla Vernaci Este (45°10'52"S; 66°29'23"W). Four of the five study locations are included within marine protected areas. Punta Tombo is included in the provincial protected area of the same name. Isla Buque, Isla Gaviota and Isla Vernaci Este are located in the northern sector of Golfo San Jorge and are included within the Patagonia Austral Marine Park, a protected area under the joint administration of the federal and provincial governments. In the study area, kelp gulls start laying eggs during the first half of November, eggs start hatching in late November to early December and chicks start fledging in January (Bertellotti and Yorio 1999; Yorio and García Borboroglu 2002; P. Yorio, *unpubl. data*).

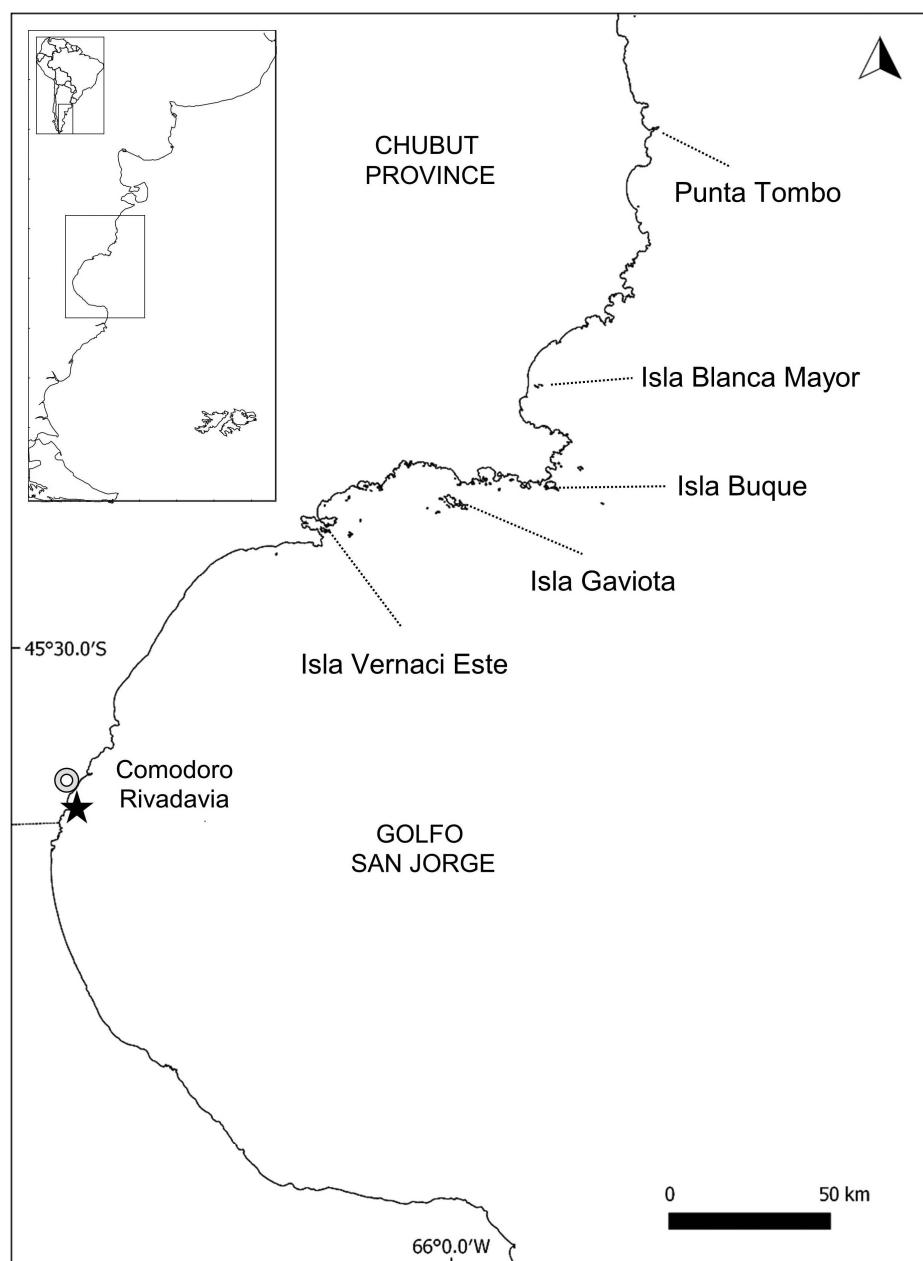


Figure 1. Study area with location of kelp gull colonies at Punta Tombo, Isla Blanca Mayor, Isla Buque, Isla Gaviota and Isla Vernaci Este, Argentina.

Conventional diet analysis

We studied the composition and temporal variation of the kelp gull diet using regurgitated pellets and stomach content samples obtained using the water offloading technique (Barrett et al. 2007). We randomly collected pellets from around nests during visits made to the colonies (see Tables S1–S3 for sample sizes and stages of the breeding cycle sampled at each location). During each visit, we noted the general breeding status of nests and divided the breeding cycle into four stages: pre-laying, incubation, young chicks (< 15 days of age), and old chicks (> 15 days of age). We distinguished young and old chicks by size and the degree of plumage development (P. Yorio *unpubl. data*). We collected samples at Isla Vernaci

Este and Punta Tombo between October and December in 2016 and 2017, covering the pre-laying, incubation and chick stages, and at the colonies of Isla Blanca Mayor, Isla Buque and Isla Gaviota during early December in 2017, corresponding to the incubation stage.

In 2016 and 2017, we obtained stomach content samples from incubating adults and chicks at Isla Vernaci Este and Punta Tombo (see Table S4 and S5 for sample sizes). We captured adult individuals using a leg-noose and chicks by hand (only one chick per nest, the largest in the brood) and obtained stomach content samples using the water offloading technique. We flushed individuals with seawater between one and three times until the water was clear, indicating the stomach was empty, using a 4.0 mm surgical catheter attached to a 60 ml syringe. We drained samples through a 0.5 mm mesh sieve and preserved them in 70% ethanol for later analysis.

Back in the laboratory, we dissected each pellet and stomach content sample in a tray under a dissecting microscope ($\times 15$ magnification) and identified food remains to the lowest taxonomic level possible using fish otoliths and cranial bones, crustacean shell fragments and chelae, mollusc shell fragments, polychaete mandibles and chetae, and insect remains. We identified prey items with the aid of published information (Boschi et al. 1992; Gordillo 1995; Gosztanyi and Kuba 1996) and a reference collection. We classified prey remains that were too degraded to be confidently identified to species level as “unidentified prey”.

We calculated the frequency of occurrence (the percentage of sampling units containing a particular prey type) for each prey type obtained from pellet and stomach content samples (Duffy and Jackson 1986). Since many prey individuals were incomplete and most diagnostic prey parts encountered in samples were too eroded for subsequent analysis, we could not conduct a numerical analysis nor estimate the contribution by mass of prey species. For this analysis, we grouped prey into ten categories: fish, crustaceans, mollusks, polychaetes, echinoderms, insects, birds (egg remains, feathers, and chick bones), fishery discards (demersal and benthic prey), urban refuse (chicken and lamb bones, fruit pits, paper, plastic, and glass), and vegetable material (grass and algae). We also grouped pellet samples into the four stages of the breeding cycle defined above: pre-laying, incubation, young chicks and old chicks. As different prey species in each pellet or stomach content sample are not independent from each other, we tested for differences in the frequency of occurrence of prey types between breeding stages and years using the analysis of similarities procedure (ANOSIM) with the PRIMER 6.1.6 package (Clarke and Gorley 2006). We constructed a similarity matrix of the samples using the Bray-Curtis similarity coefficient (Clarke and Gorley 2006), and employed similarity percentages (SIMPER) to determine the prey species that contributed most to the dissimilarities between groups (Clarke 1993; Clarke and Warwick 2001).

Stable isotope analysis

During 2017, we obtained whole blood samples (0.5–1 mL) from the brachial vein of randomly selected kelp gull adults during the late incubation stage at Punta Tombo ($n = 20$), Isla Buque ($n = 14$) and Isla Gaviota ($n = 20$). Whole-blood samples integrate the isotopic composition of the prey ingested by an individual during approximately a month before the sample is collected (Hobson and Clark 1992). We captured adult gulls at their nests using leg-nooses. We preserved blood samples in 70% ethanol, as this procedure is recommended when freezing is not possible and has been shown to have no significant effects on blood isotopic signatures (Hobson et al. 1997). In order to keep the parameters to be estimated to a minimum (see Phillips et al. 2014), only the main prey species contributing to kelp gull diet assessed through conventional diet analysis in this study were selected to be used in the isotopic mixing models (see Results; Table 1). These were Argentine anchovy (*Engraulis anchoita* Hubbs & Marini, 1935), Argentine hake (*Merluccius hubbsi* Marini, 1933), banded cusk eel (*Raneya brasiliensis* Kaup, 1856), squat lobster (*Munida gregaria* Fabricius, 1793 – *gregaria* ecotype; Pérez-Barros et al. 2008), mussel *Perumytilus purpuratus* (Lamarck, 1819), and green crab. We pooled *a priori* demersal fish prey (Argentine hake and banded cusk eel) in a fishery discard category (average stable isotope value: $\delta^{13}\text{C} = -17.21 \pm 0.47\text{‰}$, $\delta^{15}\text{N} = 16.98 \pm 0.58\text{‰}$). Demersal species are normally unavailable to surface-feeding kelp gulls, and coastal fisheries regularly discard both prey species. Information on the isotopic composition of main prey came from samples taken at Punta Tombo and Golfo San Jorge during this study. We obtained fish prey and squat lobsters from the discarded fraction of coastal fisheries and gathered mussels and green crabs by hand in intertidal environments; samples were kept frozen until analysis. Back in the laboratory, we processed prey samples and extracted muscle tissue from fish and invertebrates. We extracted lipids from Argentine anchovy samples using chloroform–methanol (2:1) (Post et al. 2007). We dried all tissue samples at 60 °C over 24 h and then ground them in a micro-mortar. We set a sub-sample of 1 ± 0.2 mg in a tin capsule for stable isotope analysis. Sample analyses were performed by the Stable Isotope Facility of the University of California, Davis (USA). Stable isotope abundance is expressed using standard δ notation relative to carbonate Vienna PeeDee Belemnite and atmospheric nitrogen. The internal laboratory standards used were Bovine Liver, USGS-41 Glutamic Acid, Nylon 5 and Glutamic Acid. Observed analytical errors were 0.14‰ and 0.19‰, for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively.

We analyzed the relative contribution of the different prey to the isotope mixture using Bayesian mixing models within the R package SIAR (Parnell and Jackson 2013) following the guidelines suggested by Phillips et al. (2014). Before running the isotopic mixing models, we conducted the

sensitivity analysis proposed by Smith et al. (2013) to evaluate the feasibility of the proposed isotopic mixing polygon. As there are no diet-tissue discrimination factors (DTDF) available for the kelp gull, we used the average values of fractionation between prey and whole blood of four seabird species following Ceia et al. (2014). We report means \pm 1 SD.

Results

General diet composition

Results based on regurgitated pellet analysis at the Isla Vernaci Este and Punta Tombo colonies showed that kelp gulls fed on a wide trophic spectrum throughout the breeding season, with variable contributions from the different food categories depending on the location and stage of the breeding cycle. In all cases, the main prey categories were molluscs and crustaceans, followed by fish (Tables S1 and S2). Diet composition at Isla Vernaci Este comprised at least 34 different types of prey, although 70.6% and 61.8% of these prey types occurred in less than 5% of the samples during 2016 ($n = 197$ pellets) and 2017 ($n = 175$ pellets). During 2016, the mussel *P. purpuratus* showed the highest frequency of occurrence across all stages (80.6, 51.9 and 64.8% in the pre-laying, incubation and young chick stages, respectively; $n = 62, 81, \text{ and } 54$ pellets, respectively). During 2017, the mussel *P. purpuratus* showed the highest frequency of occurrence in the pre-laying stage (70.3%; $n = 74$) while the green crab showed the highest frequency of occurrence in young chicks (52.5%, $n = 101$). The analysis of pellets from Isla Vernaci Este showed that diet composition differed significantly among breeding stages in 2016 (One-way ANOSIM, Global $R = 0.058$, $P < 0.02$). Significant differences were found between the pre-laying and incubation stages (One-way ANOSIM, Global $R = 0.091$, $P < 0.001$) and between the pre-laying and young chick stages (One-way ANOSIM, Global $R = 0.059$, $P < 0.002$), while diet composition was similar between the incubation and young chick stages (One-way ANOSIM, Global $R = 0.023$, $P = 0.11$). The prey types designated by SIMPER as contributing most to the observed difference in diet composition were the mussel *P. purpuratus*, the green crab and the mussel *Mytilus edulis* (pre-laying and incubation = *P. purpuratus*: 19.5%, green crab: 18.2%; pre-laying and young chick = *P. purpuratus* 18.1%, green crab: 12.5%, *M. edulis*: 10.3%). During 2017, diet composition differed significantly between the pre-laying and young chick stages (One-way ANOSIM, Global $R = 0.181$, $P < 0.001$). The prey species that contributed most to the observed differences, as designated by SIMPER, were the mussel *P. purpuratus* and the green crab (19.2%, 16.6%, respectively). Significant differences between study years were found in diet composition during the young chick stage (One-way ANOSIM, Global $R = 0.099$, $P < 0.001$), while diet composition during the pre-laying stage was similar between years (One-way ANOSIM, Global $R =$

−0.005, $P = 0.590$). The prey types designated by SIMPER as contributing most to the observed difference in diet composition between years were the mussel *P. purpuratus* and the green crab (17.8% and 16.8%, respectively).

Diet composition at Punta Tombo comprised at least 31 different types of prey, although 51.6% and 45.2% of these prey types showed percentages of occurrences smaller than 5% during 2016 ($n = 174$ pellets) and 2017 ($n = 223$ pellets). During 2016, the mussel *P. purpuratus* showed the highest frequency of occurrence during the pre-laying stage (66.2%; $n = 65$) while the squat lobster was the most frequent during the incubation and both chick stages (49.2%; $n = 65$, 43.2%; $n = 44$ and 65.0%; $n = 60$ pellets, respectively). During 2017, prey with the highest frequency of occurrence were the crab *Leucippa pentagona* (H. Milne Edwards, 1834) in the pre-laying stage (35.2%; $n = 71$), the mussel *P. purpuratus* in the incubation stage (21.2%; $n = 85$), Argentine anchovy in the young chick stage (35.8%, $n = 67$), and squat lobster in the late chick stage (57.1%; $n = 70$). Diet composition at Punta Tombo colony based on pellets was significantly different among breeding stages (Two-way crossed ANOSIM, Global $R = 0.164$; $p < 0.001$), and also for each of the pairwise comparisons ($R < 0.164$, $P < 0.001$). Prey species that contributed most to these differences, as designated by SIMPER, were squat lobster, the mussel *P. purpuratus*, and the crab *L. pentagona* (14.6–34.6%, 11.2–14.9%, and 11.9–13.8%, respectively).

The analysis of pellets obtained at additional locations during the incubation stage in 2017 indicated that crustaceans were the most frequent prey category at Isla Blanca Mayor (44.3%) and Isla Gaviota (83.3%), while molluscs were the most frequent category at Isla Buque (44.9%) (Table S3). The crab *L. pentagona* (24.3%), the polychaete *Aphrodita longicornis* (Kinberg, 1856) (34.7%) and the green crab (79.2%) were the most frequent prey recorded in Isla Blanca Mayor, Isla Buque and Isla Gaviota, respectively.

Results based on adult stomach content samples obtained at Isla Vernaci Este from incubating adults during 2016 and 2017 showed that fish were the most represented prey, while crustacean was the most frequent food category in old chicks sampled in 2016 (Table S4). Argentine anchovy and Argentine hake (fishery discards) were the most frequent prey in adults (37.5 and 25.0%, respectively in 2016, and 12.5 and 56.3% in 2017, respectively; both $n = 16$). The squat lobster was the most frequent prey in old chicks (95%; $n = 20$), followed by Argentine anchovy (50.0%). Diet composition based on adult stomach content samples during the incubation stage was significantly different between years (One-way ANOSIM, Global $R = 0.097$, $P < 0.02$). The prey types designated by SIMPER as contributing most to the observed difference were Argentine hake, unidentified fish and Argentine anchovy (19.1%, 17.9% and 12.7%, respectively). At Punta Tombo, fish was the most frequent food category in stomach contents of incubating adults and of both young and old chicks (Table S5). Argentine anchovy was in all cases the most frequent prey item, together with the squat lobster in the old

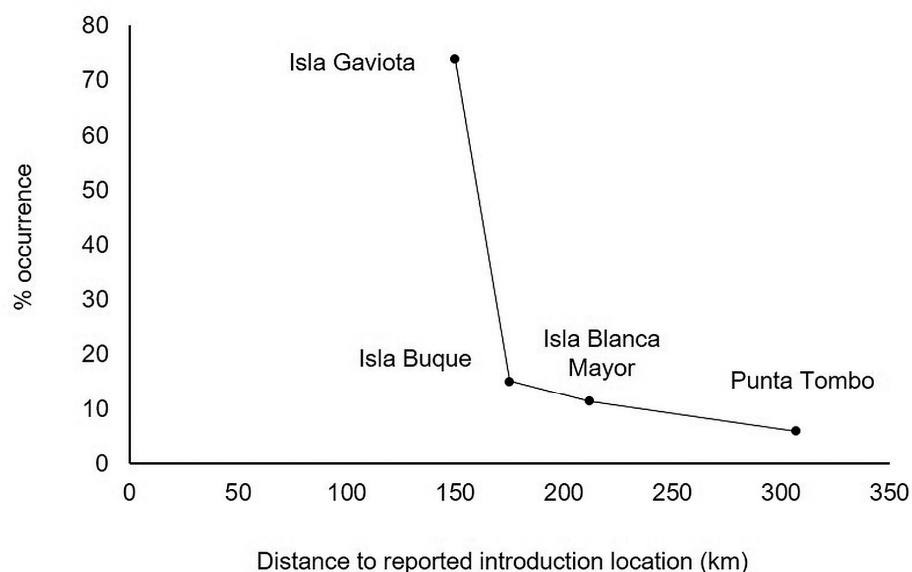


Figure 2. Frequency of occurrence (%) of green crab recorded in kelp gull pellets during the incubation stage of 2017 as a function of the distance to the location in Golfo San Jorge, Chubut, where it was reportedly introduced.

chick stage in 2016 (Table S5). Analyses of similarity also showed significant differences in the diet based on stomach content samples between chick stages (Two-way crossed ANOSIM, Global $R = 0.088$; $p < 0.001$). The prey types designated by SIMPER as contributing most to the observed differences between the two chick stages were Argentine anchovy (34.2%), squat lobster (26.7%) and Hymenoptera (11.2%).

Contribution of the green crab to kelp gull diet

Pellet analysis indicated that at Isla Vernaci Este, kelp gulls consumed green crabs in both study years and at all of the analyzed stages of the breeding cycle, in variable frequency depending on the breeding stage (Table S1). The frequency of occurrence was highest during the incubation stage in 2016 (46.9%, $n = 81$) and during the young chick stage in 2017 (52.5%, $n = 101$), although it should be noted that data could not be gathered in the incubation stage during this latter year (Table S1). At Punta Tombo, the green crab was not recorded during the pre-laying, incubation and young chick stages of the 2016 breeding season, but was recorded in the late chick stage (Table S2). In 2017, green crabs were not recorded in kelp gull pellets in the pre-laying stage but were found in relatively low frequencies in the incubation and both chick stages (Table S2). Frequencies of occurrence of green crabs in pellets collected during the incubation stage of 2017 at Isla Blanca Mayor, Isla Buque and Isla Gaviota were 11.4, 14.3 and 79.2%, respectively (Table S3). The consumption of green crabs during the incubation stage in 2017 at the four colonies for which we had information differed among locations, with a larger contribution in Isla Gaviota and a lower consumption the further from the location in central Golfo San Jorge where the species was reportedly introduced (Figure 2). The number of green

crab individuals per pellet varied between one and seven, with a mean per pellet of 1.60 ± 1.01 ($n = 117$) in Isla Vernaci Este, 2.58 ± 1.57 ($n = 19$) at Isla Gaviota, 2.14 ± 1.29 ($n = 14$) at Isla Buque, 1.13 ± 0.35 ($n = 8$) at Isla Blanca Mayor, and 1.5 ± 0.97 ($n = 10$) at Punta Tombo.

At Isla Vernaci Este, green crabs were not found in stomach content samples from incubating kelp gull adults ($n = 16$) or old chicks ($n = 20$) in 2016 and were present in only one incubating adult stomach content sample in 2017 ($n = 16$) (Table S4). At Punta Tombo, no green crabs were recorded in stomach content samples from any of the analysed individuals irrespective of age class and year (Table S5).

In the colonies of Isla Gaviota and Isla Buque within Golfo San Jorge, $\delta^{13}\text{C}$ values of kelp gull individuals varied between -19.7‰ and -13.2‰ , while $\delta^{15}\text{N}$ values varied between 13.7‰ and 21.2‰ (Figure 3A). In Punta Tombo, $\delta^{13}\text{C}$ values of kelp gull individuals ranged between -18.5‰ and -16.8‰ , while $\delta^{15}\text{N}$ values varied from 16.0‰ to 18.9‰ respectively (Figure 4A). Mixing polygon sensitivity analyses (using 1500 iterations) showed that isotopic values of most individual samples (Golfo San Jorge: 92%; Punta Tombo: 95%), given the DTDF and prey isotopic values used, were included in more than 95% of the simulated mixing polygons, validating the proposed mixing models (Figures 3B and 4B, respectively). Based on the isotopic values corresponding to potential main prey (Table 1) and kelp gull individuals of the three analyzed colonies, the Bayesian mixing model output showed that the estimated contribution of the different main prey varied among colonies (Figure 5). Green crabs had a relatively low contribution to kelp gull diet composition (7.3 ± 4.8 , 10.0 ± 6.8 and $23.9 \pm 3.7\%$ for Isla Gaviota, Isla Buque and Punta Tombo, respectively; Figure 5).

Discussion

Our results confirm that the kelp gull is a predator with a wide trophic spectrum during the breeding season, as recorded in previous studies at the same and other locations in Argentine Patagonia (Yorio and Bertellotti 2002; Yorio et al. 2013; González-Zevallos et al. 2017; Marinao et al. 2018). Kelp gulls consumed the green crab to a different degree during most or part of the breeding cycle at all study locations. Kelp gulls have a generalist and opportunistic feeding ecology, being able to include novel food resources during the breeding season as evidenced by their use of a wide variety of food items obtained in urban environments and derived from fishing and agricultural activities (Bertellotti and Yorio 1999, 2000; Marinao et al. 2018). Therefore, it is not unexpected that they would take advantage of the green crab, which is now widely dispersed along the coasts of Chubut (Schwindt et al. 2018; P. Yorio *unpubl. data*). Similar plasticity in the use of food resources has been recorded during the non-breeding period (Silva et al. 2000; Yorio and Giaccardi 2002; González-Zevallos et al. 2011),

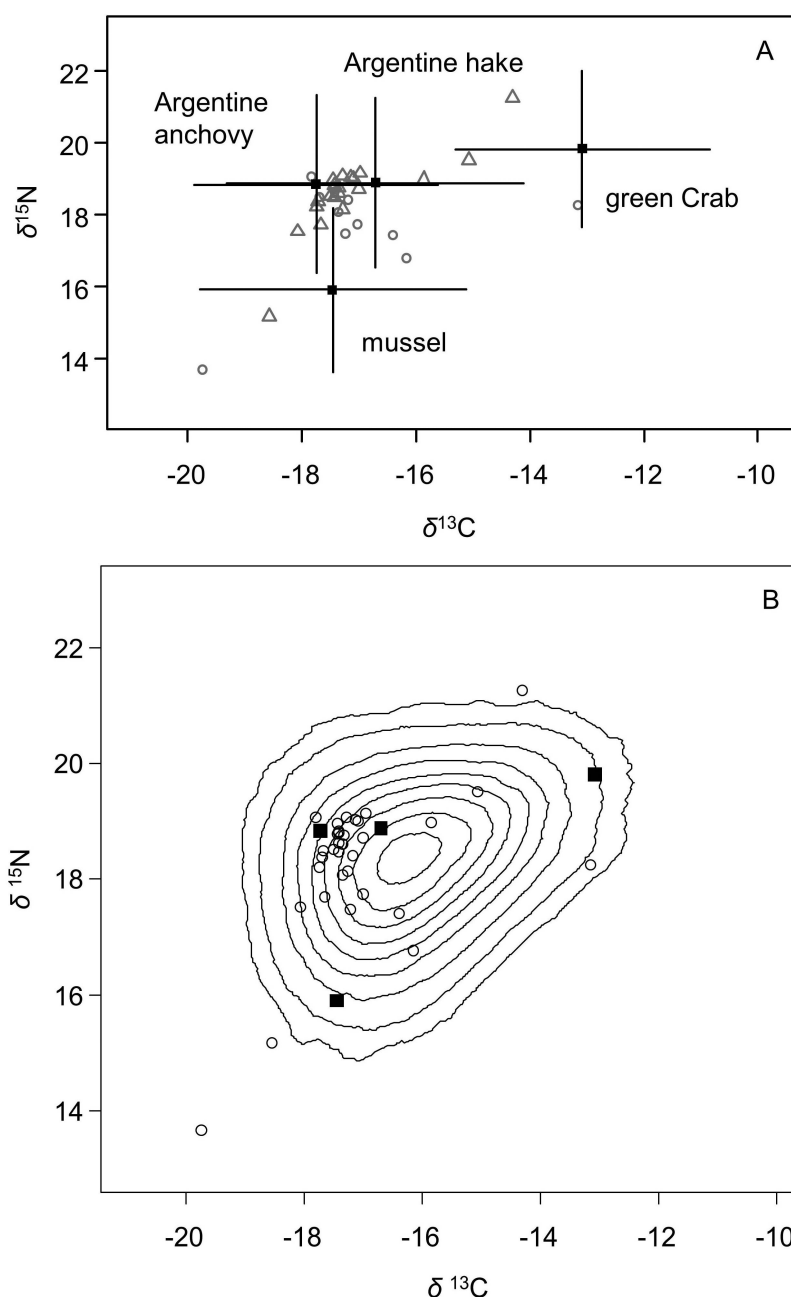


Figure 3. Dual stable isotope plot of $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) showing the isotopic values of kelp gull whole blood during the incubation period of 2017 and their potential prey in colonies within Golfo San Jorge, Chubut, Argentina. (A) Isotopic mixing diagram. Triangle: adult kelp gulls from Isla Gaviota; circle: adult kelp gulls from Isla Buque; solid squares: potential prey values corrected for fractionation (values are means and error bars \pm SD). (B) Simulated mixing region for the biplot in A. The positions of individual kelp gulls (open circles) and the average source values (solid squares) are shown. Probability contours are at the 5% level (outermost contour) and at every 10% level.

and future studies should assess the extent of kelp gull predation upon green crabs during the fall and winter months.

Native predators may rapidly modify their behaviour and adapt to feed effectively on exotic prey via existing phenotypic plasticity (Carlsson et al. 2009), and this should be more likely in generalist and opportunistic birds such as many gull species. Several gull species in other regions worldwide also take advantage of the introduced green crab and other invasive invertebrates.

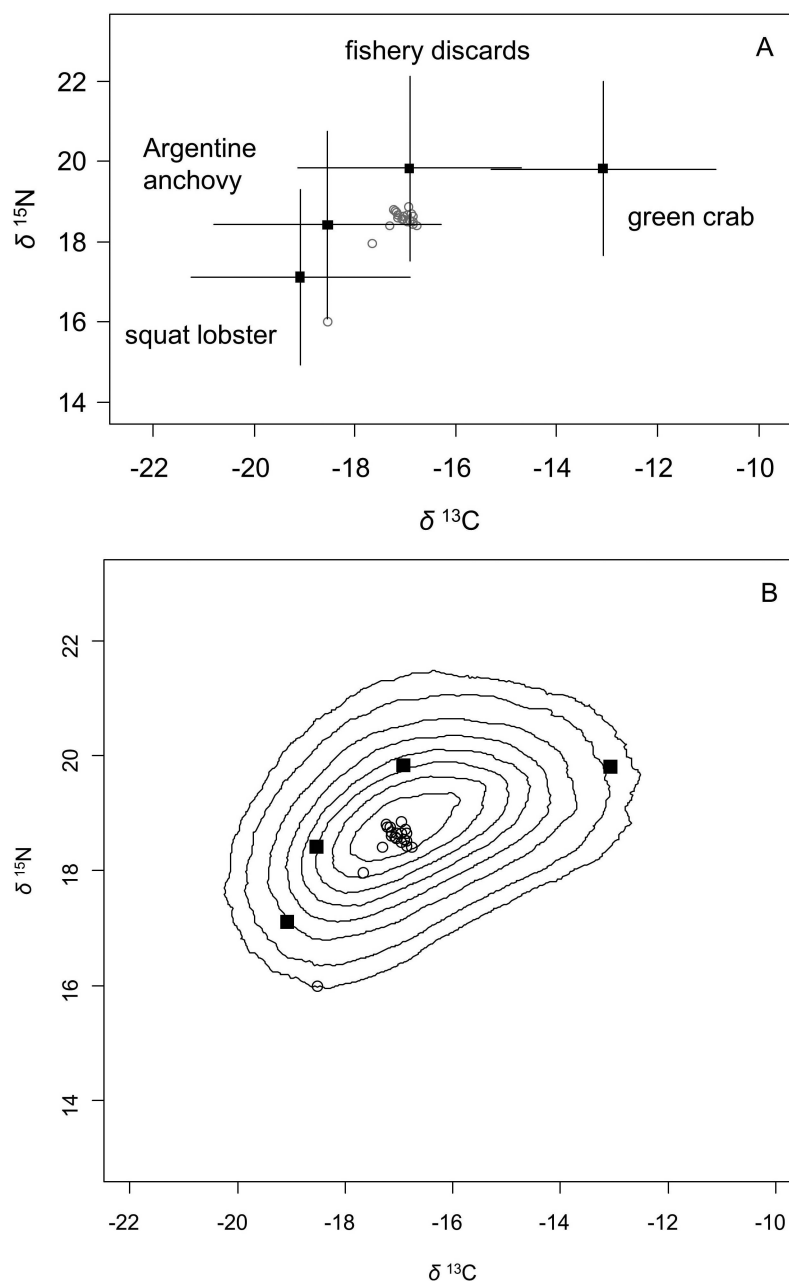


Figure 4. Dual stable isotope plot of $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) showing the isotopic values of kelp gull whole blood during the incubation period of 2017 and their potential prey in Punta Tombo, Argentina. (A) Isotopic mixing diagram. Circles: adult kelp gull; solid squares: potential prey values corrected for fractionation (values are means and error bars \pm SD). (B) Simulated mixing region for the biplot in A. The positions of individual kelp gulls (open circles) and the average source values (solid squares) are shown. Probability contours are at the 5% level (outermost contour) and at every 10% level.

For example, introduced green crabs in eastern United States are preyed upon by breeding herring gulls (*Larus argentatus* Pontoppidan, 1763), great black-backed gulls (*L. marinus* Linnaeus, 1758) and laughing gulls (*Leucophaeus atricilla* Linnaeus, 1758) (Rome and Ellis 2004; Washburn et al. 2013). In Europe, the invasive signal crayfish (*Pacifastacus leniusculus* Dana, 1852) is consumed by lesser black-backed gulls (*Larus fuscus* Linnaeus, 1758) (Mortimer et al. 2012), and the Pacific oyster (*Crassostrea gigas* Thunberg, 1793) is preyed upon by herring gulls (Cadee 2001). Similarly,

Table 1. Stable isotope values of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) of kelp gull main prey at Golfo San Jorge and Punta Tombo selected for the stable isotope mixing models. Values are expressed as means (\pm SD).

		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Golfo San Jorge			
Argentine anchovy (<i>Engraulis anchoita</i>)	(n = 10)	-18.04 ± 0.36	15.98 ± 0.73
Argentine hake (<i>Merluccius hubbsi</i>)	(n = 30)	-17.00 ± 0.83	16.03 ± 0.64
Green crab (<i>Carcinus maenas</i>)	(n = 10)	-13.38 ± 0.49	16.97 ± 0.42
Mussel (<i>Perumytilus purpuratus</i>)	(n = 3)	-17.75 ± 0.60	13.06 ± 0.56
Punta Tombo			
Argentine anchovy (<i>Engraulis anchoita</i>)	(n = 10)	-18.84 ± 0.52	15.57 ± 0.60
Fishery discards*			
Argentine hake (<i>Merluccius hubbsi</i>)	(n = 30)	-17.27 ± 0.46	16.86 ± 0.57
Banded cusk eel (<i>Raneya brasiliensis</i>)	(n = 10)	-17.00 ± 0.46	17.36 ± 0.42
Green crab (<i>Carcinus maenas</i>)	(n = 10)	-13.38 ± 0.49	16.97 ± 0.42
Squat lobster (<i>Munida gregaria</i>)	(n = 5)	-19.38 ± 0.43	14.27 ± 0.44

* See Methods for average value included in the stable isotope mixing model.

the North American crayfish (*Procambarus clarkii* Girard, 1852) is consumed by Audouin's gulls (Oro et al. 1996) and by lesser black-backed gulls, slender-billed gulls (*L. genei* Brème, 1839), and black-headed gulls (*L. ridibundus* Linnaeus, 1766) (Tablado et al. 2010). Further information on predator-prey relationships during the early stages of the invasion by green crabs in coastal Patagonia are needed to adequately understand how kelp gulls have adapted to take advantage of this novel food resource.

Despite evidence that kelp gulls regularly consumed green crabs at most breeding locations, this invasive species was not an important component in their diet. Stomach contents from incubating kelp gulls indicated that fish were their main prey. Pellet analysis, in contrast, showed a relatively low contribution of fish prey and a relatively high consumption of green crabs at some breeding stages and locations, but pellet analysis may over-emphasize the presence of prey types with indigestible hard parts, such as crabs (Duffy and Jackson 1986; Barrett et al. 2007). In addition, the analysis of pellets often underestimates the contribution of fish relative to stomach content analysis and stable isotope estimates (Weiser and Powell 2011; Marinao et al. 2018). Despite the limitations inherent to pellet analysis, several studies have demonstrated that it provides results that reflect diet composition (e.g. Annett and Pierotti 1989) and that are valuable for detecting both seasonal changes and geographic differences (Johnstone et al. 1990; Mariano-Jelicich and Favero 2006). Moreover, as they represent the presence of prey with indigestible hard parts well, they should be a good indicator of green crab consumption. Stable isotope analysis of samples from Golfo San Jorge indicated a relatively low contribution of green crabs to kelp gull diet, but samples at the Punta Tombo colony indicated a moderate contribution contrary to expectations given their relative low presence in pellets. Further studies should test if these stable isotope results reflect the relative consumption of green crabs well or they are an artifact of the analytical methods used.

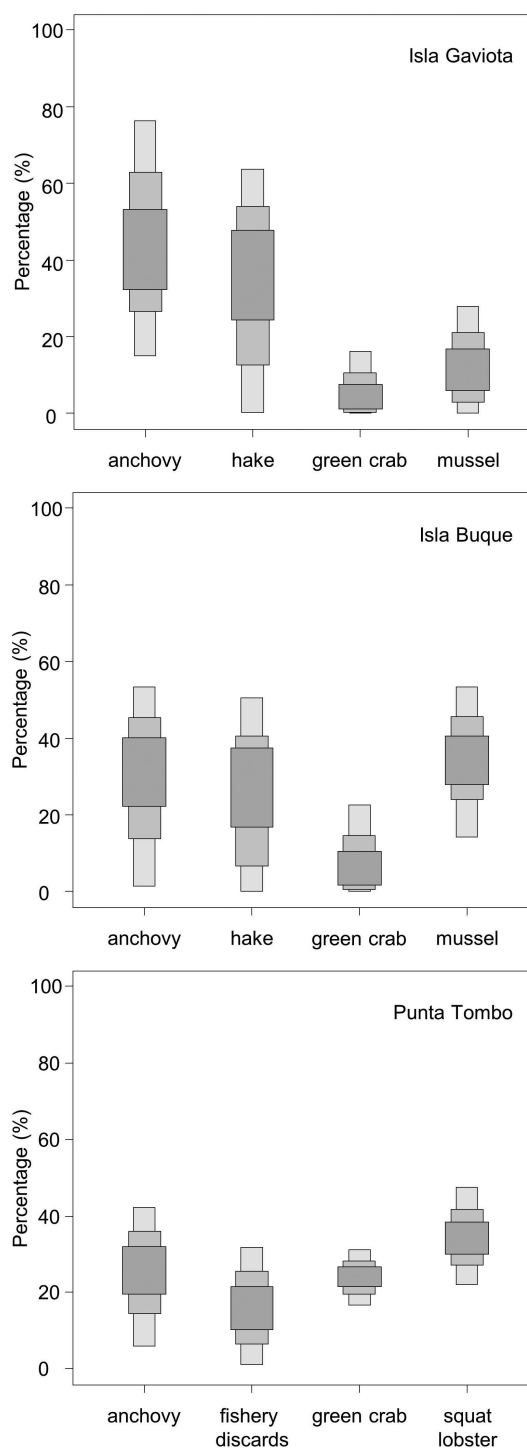


Figure 5. Results of SIAR Bayesian isotope mixing models (50%, 75% and 95% credibility intervals) showing the estimated prey contributions to the diets of kelp gull from Isla Gaviota (n = 20), Isla Buque (n = 14), and Punta Tombo (n = 20), Argentina, during the incubation period of 2017.

Our results based on pellet analysis show that the consumption of green crabs differed among breeding locations, with a higher contribution in the diet of incubating kelp gulls at Isla Gaviota than at other sites. As expected, these results show a pattern of lower consumption further from the location in central Golfo San Jorge where the species was reportedly introduced, with relatively little consumption at the more northern

location, Punta Tombo. The green crab was first recorded in 2001 along the shores of Rada Tilly (45°56'00"S; 67°32'00"W) and Comodoro Rivadavia (45°52'00"S; 67°30'00"W), located on the central coast of Golfo San Jorge (Vinuesa 2005) and it was recorded in 2003 in Camarones Bay (44°54'S), just north of Golfo San Jorge (Hidalgo et al. 2005). Based on size frequency distributions and temperature conditions in the area, Hidalgo et al. (2005) proposed that the species was introduced to Argentina in 1999 or 2000. Since then, the green crab has expanded over 1,000 km along the coastline of Chubut Province reaching Golfo Nuevo (42°46'S), where it was recorded in 2015 (Torres and González-Pisani 2016). Introduced species are more likely to become alternative prey for native predators as they become established and more abundant (Rodríguez 2006), and it is likely that green crab availability in more northern colonies has not reached levels that are profitable for kelp gulls to consume. Unfortunately, there is no information on the patterns of distribution and abundance of the green crab along the invaded coastal area. As the abundance of the invasive species should depend on the time since its successful settlement in a given area, green crab consumption by kelp gulls will likely increase in the future, so monitoring their diet composition could provide valuable information on green crab invasion patterns. Also, over fifty kelp gull colonies are distributed within the current known distributional range of the green crab (Lisnizer et al. 2011), only five of which were visited to assess green crab consumption during this study. Therefore, it would be valuable to quantify green crab use by kelp gulls at additional locations to better understand the spatial pattern of this trophic interaction. However, further studies should include a more thorough analysis using complementary methods to pellet analysis, as the mentioned pattern is not as clear when considering the information derived from stable isotope analysis. In addition, it should be noted that the observed differences in green crab consumption among locations could also be influenced by other factors determining differential green crab abundance, including habitat characteristics, wave exposure, other predators, competitors, and prey availability.

Our study shows that the relatively recently introduced green crab supplements the available prey base of a widely distributed and abundant predator, the kelp gull, at least during the breeding season in a large coastal sector of central Patagonia. Regardless of the possible benefits of green crabs as novel prey, we cannot rule out that its successful invasion will result in changes in trophic interactions and negative effects on the prey base of kelp gulls in coastal Patagonia. The green crab is a generalist predator in intertidal and subtidal areas, and it can cause declines in native bivalve and crab populations (Grosholz et al. 2000). Hidalgo et al. (2007) showed that green crabs along coastal Patagonia feed on slow-moving and sessile animals, including the foundation species *Perumytilus purpuratus*,

and argued that successful invasion by the green crab could result in its removal, which would in turn affect intertidal community composition. Kelp gulls regularly feed in rocky environments (Gatto et al. 2008) where one of the dominant intertidal invertebrates is the mussel *P. purpuratus* (Adami et al. 2018), and our diet results show that this invertebrate may be a significant component of the diet during some stages of the breeding cycle, particularly at Isla Vernaci Este. However, green crab consumption by kelp gulls may also reduce the predation intensity on mussels by this introduced species, and thus further studies are needed to understand both the direct and indirect effects of kelp gull predation on green crabs in the recently invaded coastal area.

The use of intertidal areas by foraging birds is largely determined by the distribution and abundance of prey (Goss-Custard 1970; Ribeiro et al. 2004). Throughout their distributional range, green crabs show a differential pattern of vertical distribution and mobility depending on size and sex and inhabit intertidal and subtidal areas (Aagaard et al. 1995; Rewitz et al. 2004; Smallegange et al. 2009). Previous studies have shown that kelp gulls in Golfo San Jorge forage mostly in exposed rocky and mud intertidal substrates feeding exclusively by pecking (Gatto et al. 2008). Therefore, green crabs preyed upon by kelp gulls were likely obtained through direct capture along exposed intertidal areas. Unfortunately, we lack information on the distribution and activity patterns of green crabs in the study area. Native predators can provide biotic resistance to invasion by limiting the distribution and abundance of introduced prey population (de Rivera et al. 2005). Similarly to other gull and coastal bird species (Edwards et al. 1982; Good 1992; Ellis et al. 2005), kelp gulls have the potential of reducing the abundance of crabs and affecting the upper limit of prey distribution, particularly given their main foraging strategy when exploiting shoreline habitats and their high population numbers (> 100,000 breeding individuals in the study sector; Lisnizer et al. 2011). The extent to which the widespread and abundant kelp gull in coastal Patagonia may be shaping the establishment, abundance, and population dynamics of the introduced green crab is still unknown and will require further research.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Frequency of occurrence (%) of prey items in pellets collected at the Isla Vernaci Este kelp gull colony, Argentina, during the pre-laying, incubation and young chick stages of 2016 and 2017.

Table S2. Frequency of occurrence (%) of prey items in pellets collected at the Punta Tombo kelp gull colony, Argentina, during the pre-laying, incubation, young chick and old chick stages of 2016 and 2017.

Table S3. Frequency of occurrence (%) of prey items in pellets collected at the Isla Blanca Mayor, Isla Buque and Isla Gaviota kelp gull colonies, Argentina, during the incubation stage of 2017.

Table S4. Frequency of occurrence (%) of prey items in stomach content samples of kelp gull adults during incubation and chicks during the old chick stage collected at the Isla Vernaci Este kelp gull colony, Argentina, in 2016 and 2017.

Table S5. Frequency of occurrence (%) of prey items in stomach content samples of kelp gull adults during incubation and chicks during the young and old chick stages collected at the Punta Tombo colony, Argentina, in 2016 and 2017.

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