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Differences between colonies and chick-rearing stages in Imperial Cormorant (*Phalacrocorax atriceps*) diet composition: implications for trophic studies and monitoring

Cynthia Ibarra,¹ Cristian Marinao,² Nicolás Suárez,² and Pablo Yorio^{2,3*}

ABSTRACT—We assessed differences in diet composition between Imperial Cormorants (*Phalacrocorax atriceps*) breeding at Isla Arce and Isla Vernaci Este, Golfo San Jorge, Argentina. Both colonies are located within the Patagonia Austral marine park, and commercial trawl fisheries operate in adjacent waters, thus knowledge of their food requirement is fundamental to assess potential conflicts and monitor interactions. We obtained stomach samples from 63 adult Imperial Cormorants during the chick-rearing period in 2014: 32 at Isla Arce and 31 at Isla Vernaci Este. We recorded 27 and 30 prey taxa in stomach samples at Isla Arce and Isla Vernaci Este, respectively, and at least 21 were common to both islands. Significant differences in diet composition in terms of importance by mass were found between young and old chick stages at Isla Arce but not at Isla Vernaci Este. Rock cod (*Patagonotothen* spp.) were dominant at Isla Vernaci Este during both chick stages (75.7% and 86.5%, respectively). At Isla Arce, rock cod, Argentine anchovy (*Engraulis anchoita*), and Argentine hake (*Merluccius hubbsi*) contributed similarly to their diet (26–33%) during the young chick stage, whereas Argentine anchovy dominated during the old chick stage (76.6%). Diet composition in terms of importance by mass was significantly different between colonies. Imperial Cormorant consumed benthic, demersal, and pelagic prey, confirming plasticity in feeding habits, but their contribution differed depending on the site and chick stage. Our results suggest that diet assessments and monitoring the potential interaction between Imperial Cormorant and fisheries should not be based on information from a single breeding stage or location, but requires the analysis of diet composition throughout the breeding cycle with a representative sampling of the 17 colonies within the marine park. Received 18 October. Accepted 19 April 2017.

Key words: Argentina, diet, Golfo San Jorge, *Phalacrocorax atriceps*, seabirds, site differences.

Diferencias entre colonias y etapas de crianza de los pichones en la composición de la dieta del Cormorán Imperial (*Phalacrocorax atriceps*): implicancias para los estudios tróficos y el monitoreo

RESUMEN (Spanish)—Evaluamos las diferencias en la composición de la dieta entre *Phalacrocorax atriceps* que se reproducen en Isla Arce e Isla Vernaci Este, Golfo San Jorge, Argentina. Ambas colonias están ubicadas dentro del parque marino Patagonia Austral y pesquerías comerciales de arrastre operan en aguas adyacentes, por lo que el conocimiento de sus requerimientos alimentarios es fundamental para evaluar potenciales conflictos y monitorear interacciones. Obtuvimos contenidos estomacales de 63 *Phalacrocorax atriceps* adultos durante el período de crianza de pichones en 2014: 32 en Isla Arce y 31 en Isla Vernaci Este. Registramos 27 y 30 ítems presa en los contenidos estomacales de Isla Arce e Isla Vernaci Este, respectivamente, y al menos 21 fueron comunes a ambas islas. Se encontraron diferencias significativas en la composición de la dieta en términos de importancia en peso entre las etapas de pichones temprana y tardía en Isla Arce pero no en Isla Vernaci Este. *Patagonotothen* spp. fueron dominantes en Isla Vernaci Este durante las dos etapas de pichones (75.7% y 86.5%, respectivamente). En Isla Arce, *Patagonotothen* spp., *Engraulis anchoita* y *Merluccius hubbsi* contribuyeron de manera similar a su dieta (26–33%) durante la etapa de pichones temprana, mientras que *Engraulis anchoita* dominó durante la etapa de pichones tardía (76.6%). La composición de la dieta en términos de importancia en peso fue significativamente diferente entre las colonias. *Phalacrocorax atriceps* consumió presas bentónicas, demersales y pelágicas, confirmando la plasticidad en sus hábitos alimenticios, pero su contribución difirió dependiendo del sitio y la etapa de pichones. Nuestros resultados sugieren que la evaluación de la dieta y el monitoreo de la interacción potencial entre *Phalacrocorax atriceps* y las pesquerías no deberían basarse en información de una sola etapa o sitio de reproducción, sino que requieren del análisis de la composición de la dieta a lo largo del ciclo reproductivo en una muestra representativa de las 17 colonias ubicadas dentro del parque marino.

Palabras clave: Argentina, aves marinas, dieta, diferencias entre sitios, Golfo San Jorge, *Phalacrocorax atriceps*.

Seabird diet composition may be affected by different sources of variation, which need to be assessed to interpret aspects of their life history and the ecology of their populations (Shealer 2002, Barrett et al. 2007). For example, seabird diet can

differ among breeding locations (Bertellotti and Yorio 1999, Liordos and Goutner 2008, Chiaradia et al. 2012), likely due to the effect of habitat characteristics on prey availability within their foraging range, or can vary along the breeding cycle in response to changes in food availability and/or individual demands (Annett and Pierotti 1989, Suryan et al. 2002, Karnovsky et al. 2008). Knowledge of seabird diet requirements is fundamental to understanding ecosystem functioning and assessing potential impacts of climate change and commercial fisheries on their populations

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(Sydeaman et al. 2001, Einoder 2009, Elliot et al. 2015).

The Imperial Cormorant (*Phalacrocorax atriceps*) is widely distributed along the southern tip of South America from central Argentina to central Chile, including the Malvinas (Falkland) Islands (Johnsgard 1993). The northern coastal sector of Golfo San Jorge, Argentina, is an important nesting area for this cormorant species, comprising about 25% of the total Patagonian breeding population, distributed at 17 colonies (Yorio et al. 1998). All these nesting sites are included within the Patagonia Austral marine park, a protected area that extends from the high tidemark to one nautical mile offshore. The area also constitutes a primary fishing ground for trawl fisheries targeting Argentine red shrimp (*Pleoticus muelleri*) and Argentine hake (*Merluccius hubbsi*; Góngora et al. 2012), and foraging breeding Imperial Cormorant often spatially overlap with operating vessels (Yorio et al. 2010b). The Imperial Cormorant is the main source of commercially harvested guano in Argentina, and this area holds several colonies that could potentially be harvested (Punta 1996). Knowledge of Imperial Cormorant diet requirements and diet variation is key to adequately interpret its interaction with trophic resources in the current context of fishing in waters adjacent to the marine protected area and the value of this cormorant species as a source of guano.

Previous studies at different locations in Golfo San Jorge indicated that the Imperial Cormorant is mainly a piscivorous species that complements its diet with marine invertebrates such as squid, crustaceans, and polychaetes (Punta et al. 1993, 2003a; Bulgarella et al. 2008; Yorio et al. 2010a). Despite those studies providing valuable information on Imperial Cormorant diet requirements, they were based on the analysis of pellets, which may provide biased results because of the loss or erosion of diagnostic prey parts during digestion or spontaneous regurgitations, which do not always allow the recovery of the whole stomach contents (Duffy and Laurenson 1983, Barrett et al. 2007). In addition, the previous studies relied on prey frequency of occurrence as a measurement of diet data, which may over-emphasize prey that occur in small numbers or persist longer in stomachs and may also over-estimate small, less significant prey in terms of biomass (Duffy and Jackson 1986).

Several prey species consumed by the Imperial Cormorant in this area are of commercial value, and some are captured and/or discarded by trawl fisheries operating in areas adjacent to their colonies (Yorio et al. 2010a, Bovcon et al. 2013).

Studies at Isla Arce, located in the northern sector of Golfo San Jorge, suggested that 3 species of commercial value, Argentine anchovy (*Engraulis anchoita*), Argentine hake, and Argentine red shrimp, may be important components of Imperial Cormorant raising chicks (Yorio et al. 2010a). Yorio et al. 2010a also showed that Imperial Cormorant diet composition was significantly different from that of birds breeding on a nearby island located north of the gulf. In this context, updating the information on Imperial Cormorant diet composition by applying methods that better assess the contribution of different prey species will improve our knowledge of its food requirement in this relevant coastal sector for economic activities and conservation. Our goals were to (1) update and obtain more accurate information on Imperial Cormorant diet composition during 2 stages of the chick-rearing period at 2 colonies located within the Patagonia Austral marine park, Golfo San Jorge, and (2) assess possible differences in diet composition between these 2 colonies.

Methods

Study area and species

The northern coastal sector of the Golfo San Jorge extends from Cabo Dos Bahías (44°55'S, 56°31'W) to Isla Quintano (45°13'S, 66°03'W), Chubut Province (Fig. 1). In this sector, the Imperial Cormorant breeds at 17 colonies consisting of 20 to 3,000 nests, totaling ~13,300 breeding pairs (Frere et al. 2005). All nesting sites are located on islands along ~100 km of coastline and are included within the Patagonia Austral marine park, a 750 km² protected area under the joint administration of the federal and provincial governments. The study was conducted at 2 Imperial Cormorant colonies located 80 km apart: Isla Arce (45°00'S, 65°34'W) at the northern end of the marine park and Isla Vernaci Este (45°11'S, 66°30'W) at its southern end (Fig. 1). The colonies consisted of 1,850 and 270 breeding pairs, respectively (PY, unpubl. data).

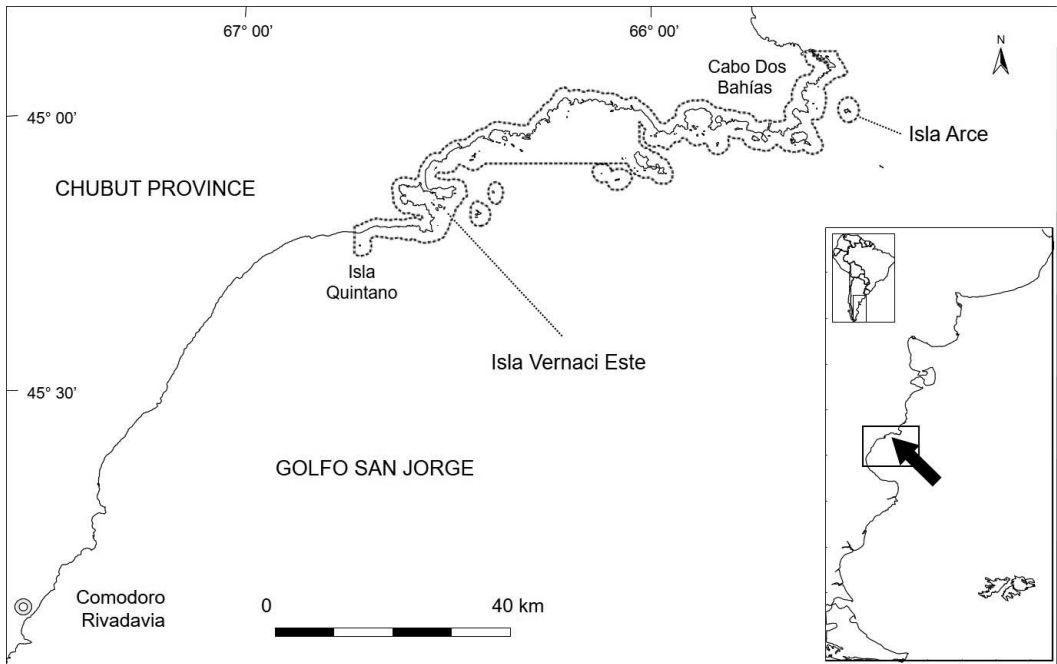


Figure 1. Study area with location of Imperial Cormorant colonies at Isla Arce and Isla Vernaci Este, Golfo San Jorge, Argentina.

Imperial Cormorants breeding in Golfo San Jorge settle at the colony site in September and start laying eggs between mid-October and mid-November depending on the season; incubation lasts about a month, and chicks start fledging at 90 days old (Punta et al. 2003b). The Imperial Cormorant is a pursuit diver that, during the chick-rearing stage, forages in different coastal habitats (Gómez-Laich et al. 2015) at an average coastal distance of 10 km (Sapoznikow and Quintana 2003, Yorio et al. 2010b). The mean maximum diving depth at Golfo San Jorge was estimated at 28 m (Quintana et al. 2007).

Diet sampling

To assess diet composition, we gathered 63 stomach samples from breeding adults during 11–16 December 2014 and 12–17 January 2015 (young and old chick stages, respectively; Punta et al. 2003b). We obtained a similar number of samples from males and females in each stage, identifying their sex based on vocalizations, which differ between sexes (Malacalza and Hall 1988). We captured individuals from peripheral and central nests with a long hook that extended from

the colony periphery to minimize disturbance. Sampled individuals were those that had recently returned from the sea, identified by their behavior toward their mate and their wet plumage. We obtained samples through induced regurgitation (Cooper 1985), which consists of holding the individual upside down over a bucket and shaking it, complemented with the massaging of abdomen and throat. We flushed a subsample of 22 individuals with sea water (Wilson 1984, Gales 1987) immediately after they regurgitated and validated that the induced regurgitation technique collects complete stomach contents (Yorio et al. 2017). For flushing, we used a 5.3 mm surgical catheter attached to a 250 mL syringe, repeating the procedure 1–3 times until the water was clear, indicating the stomach was empty. Samples obtained from each of the 2 procedures were strained through a 0.5 mm mesh sieve and preserved in 70% ethanol in separate containers. For the diet analysis we combined the samples obtained from the same individuals.

In the laboratory, we dissected each stomach content sample in a tray under a zoom binocular microscope (5–20× magnification) and identified

food remains to the lowest taxonomic level possible based on whole individuals or using diagnostic remains (fish otoliths and bones, squid beaks, crustacean chelae and carapaces, and polychaete mandibles). We identified prey items with the aid of a reference collection and published information (Boschi et al. 1992, Gosztanyi and Kuba 1996, Pineda et al. 1996, Volpedo and Echeverría 2000, Rozbaczylo et al. 2006, Bovcon and Cochia 2007). We classified prey remains too degraded to be positively identified to species level as 'unidentified prey' and excluded them from the statistical analysis. In some stomach contents we were able to identify rock cod remains as *Patagonotothen cornucola* and *N. sima*, but because discriminating between these 2 species in all samples was not possible, we reported all rock cod prey items as *Patagonotothen* spp.

We calculated frequency of occurrence (%F) and numerical importance (%N) for each prey type (Duffy and Jackson 1986). We calculated the relative importance by mass (%W) only for the main prey species, defined as those with both frequencies of occurrence >10% and numerical importance >5%. We estimated %W using a subsample of fish cranial bones and otoliths that showed low or no erosion and measured them under a zoom binocular microscope (5–20× magnifications). We then assigned the mean weight obtained for a given species to the individuals of the same species whose diagnostic parts showed high erosion and could therefore not be measured. We calculated mass of Argentine anchovy and Argentine hake by applying the equations presented in Koen-Alonso et al. (1998) and the mass of Cunningham's triplefin (*Helcogammoides cunninghami*) using unpublished equations (N. Bovcon and X. Navoa, unpubl. data). Because no linear regressions were available for the other selected species, we obtained their mass from a sample of whole individuals and used the average to estimate %W. In these cases, we obtained mass to the nearest ± 0.002 g using a digital scale.

Statistical analyses

We tested for differences between the numerical importance and importance by mass of prey obtained at both colonies and both chick stages using the analysis of similarities procedure (ANO-

SIM) 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).

Results

General description of diet composition

We captured and flushed 63 adult Imperial Cormorant, 32 at Isla Arce and 31 at Isla Vernaci Este, and identified 1,936 prey items from the stomach contents obtained, comprising at least 35 prey taxa composed of 16 fish, 12 crustaceans, 3 cephalopods, 3 polychaetes, and 1 gastropod (Table 1). In addition, some stomach samples included parasites, algae, small stones, and feathers. From the samples collected, prey species accumulation curves indicated that sampling was extensive enough to represent the prey items as indicated by all accumulation curves reaching a plateau, except for that corresponding to the large chick stage at Isla Vernaci Este. Fish were the main prey category at both islands and for both chick stages, with a numerical importance of 69.4–91.9% (Table 1). Most stomach contents (79.4%) had 2 or more different prey taxa, but 13 comprised only one fish or crustacean species. Species present in these latter samples were Argentine anchovy in 9 cases and Argentine hake, Argentine red shrimp, *Austrolycus laticinctus*, and the squat lobster (*Munida gregaria*) in one case each. The squat lobster has 2 morphs, 'gregaria' and 'subrugosa,' which have pelagic and benthic habits, respectively (Pérez-Barros et al. 2008), and both could be identified in some stomach samples.

Comparison between chick stages

At Isla Arce and during the young chick stage, the most frequent prey was the Argentine red shrimp (58.3%), followed by Argentine anchovy (33.0%; Table 1), whereas in the old chick stage the most frequent prey was Argentine anchovy (65.0%), followed by rock cod (30.0%). Prey with the highest importance by number was rock cod (36.7%), followed by Argentine hake (14.0%) during the young chick stage, and Cunningham's

Table 1. Frequency of occurrence (%F) and numerical importance of prey types (%N) recorded in stomach samples of Imperial Cormorants breeding at Isla Arce and Isla Vernaci Este, Argentina, during the chick stage in 2014.

Taxa	Isla Arce				Isla Vernaci Este			
	Young chicks		Old chicks		Young chicks		Old chicks	
	n = 12 %F	n = 221 %N	n = 20 %F	n = 724 %N	n = 20 %F	n = 723 %N	n = 11 %F	n = 268 %N
Fish	83.3	78.7	100.0	91.9	95.0	69.4	100.0	78.0
<i>Engraulis anchoita</i>	33.3	8.1	65.0	22.1	10.0	1.2	0.0	0.0
<i>Merluccius hubbsi</i>	25.0	14.0	10.0	0.4	0.0	0.0	0.0	0.0
<i>Patagonotothen</i> spp. ^a	25.0	36.7	30.0	9.3	85.0	33.6	81.8	44.8
<i>Helcogrammoides cunninghami</i>	16.7	9.0	15.0	27.9	40.0	6.5	45.5	8.6
<i>Ribeiroclinus eigenmanni</i>	0.0	0.0	0.0	0.0	40.0	6.2	45.5	11.6
<i>Leptonotus blainvillanus</i>	0.0	0.0	0.0	0.0	30.0	13.3	18.2	1.5
<i>Odontesthes smitti</i>	0.0	0.0	5.0	22.9	5.0	0.7	9.1	3.0
<i>Raneya brasiliensis</i>	16.7	3.2	10.0	0.3	5.0	0.1	0.0	0.0
<i>Sebastes oculatus</i>	0.0	0.0	20.0	2.1	30.0	1.4	18.2	1.1
<i>Agonopsis chilensis</i>	16.7	1.4	5.0	5.1	30.0	1.5	27.3	4.1
<i>Nemadactylus bergi</i>	25.0	2.3	15.0	0.7	15.0	3.0	0.0	0.0
<i>Cottopeca gobio</i>	0.0	0.0	5.0	0.1	0.0	0.0	0.0	0.0
<i>Ramnogaster arcuata</i>	0.0	0.0	10.0	0.3	5.0	0.1	0.0	0.0
<i>Austrolycus laticinctus</i>	0.0	0.0	5.0	0.1	10.0	1.0	27.3	1.5
<i>Bovichtus argentinus</i>	0.0	0.0	5.0	0.3	0.0	0.0	9.1	0.4
<i>Mixine australis</i>	0.0	0.0	5.0	0.1	0.0	0.0	9.1	0.7
Unidentified fish	25.0	4.1	5.0	0.1	20.0	0.7	9.1	0.7
Crustaceans	83.3	19.5	25.0	4.6	85.0	23.7	72.7	13.1
<i>Pleoticus muelleri</i>	58.3	5.4	0.0	0.0	0.0	0.0	9.1	0.4
<i>Nauticaris magellanica</i>	8.3	1.8	5.0	0.1	5.0	0.1	0.0	0.0
<i>Austropandalus grayi</i>	0.0	0.0	10.0	0.3	15.0	2.4	0.0	0.0
<i>Betaeus truncatus</i>	0.0	0.0	5.0	0.1	10.0	0.3	0.0	0.0
<i>Munida gregaria</i>	0.0	0.0	15.0	3.2	75.0	18.9	45.5	10.8
<i>Halicarcinus planatus</i>	8.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Carcinus maenas</i>	8.3	8.1	0.0	0.0	5.0	0.3	0.0	0.0
<i>Peltarion spinosulum</i>	0.0	0.0	0.0	0.0	15.0	0.4	0.0	0.0
<i>Eurypodius latreillei</i>	0.0	0.0	0.0	0.0	20.0	1.1	0.0	0.0
<i>Leucippa pentagona</i>	0.0	0.0	0.0	0.0	0.0	0.0	9.1	0.4
Isopod	8.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Stomatopod	0.0	0.0	5.0	0.1	0.0	0.0	0.0	0.0
Unidentified crustaceans	16.7	3.2	5.0	0.7	5.0	0.1	36.4	1.5
Cephalopods	16.7	1.4	20.0	1.1	50.0	2.4	45.5	3.7
<i>Octopus</i> sp.	16.7	0.9	20.0	1.1	35.0	1.5	45.5	3.4
Squids	0.0	0.0	0.0	0.0	15.0	0.4	9.1	0.4
<i>Doryteuthis sanpaulensis</i>	8.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Doryteuthis gahi</i>	0.0	0.0	0.0	0.0	10.0	0.4	0.0	0.0
Gastropods	0.0	0.0	0.0	0.0	15.0	1.1	0.0	0.0
<i>Ataxocerithium pullum</i>	0.0	0.0	0.0	0.0	15.0	1.1	0.0	0.0
Polychaetes	0.0	0.0	15.0	2.5	30.0	23.5	36.4	5.2
<i>Eunice</i> spp.	0.0	0.0	5.0	0.1	20.0	1.5	36.4	1.5
<i>Nereis</i> spp.	0.0	0.0	10.0	2.3	20.0	1.5	18.2	2.2
Polynoidae	0.0	0.0	0.0	0.0	15.0	0.6	27.3	1.5
Unidentified prey	8.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0

^a Includes *P. cornucola* and *P. sima*; see text in Methods.

triplefin (27.9%), followed by silverside (*Odontesthes smitti*; 22.9%) and Argentine anchovy (22.1%) during the old chick stage (Table 1). Diet composition in terms of prey numerical impor-

tance varied significantly between both chick stages (one-way ANOSIM, Global $R = 0.19$; $P = 0.008$). The prey species that contributed most to these observed differences, as designated by

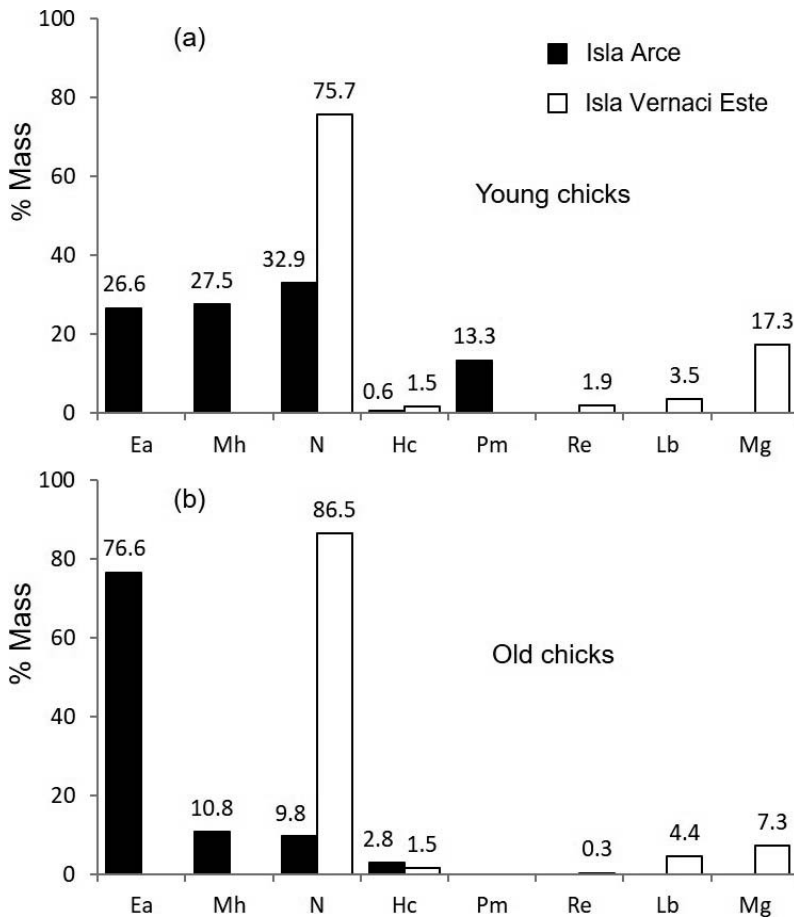


Figure 2. Importance by mass (%) of main prey species recorded in stomach samples of Imperial Cormorants feeding their chicks at Isla Arce and Isla Vernaci Este, Argentina, during the (a) young and (b) old chick stages in 2014 (Isla Arce: $n = 12$ and 20, respectively, and Isla Vernaci Este: $n = 20$ and 11, respectively). Ea: *Engraulis anchoita*, Mh: *Merluccius hubbsi*, N: *Patagonotothen* spp., Hc: *Helcogrammoides cunninghami*, Pm: *Pleuotus muelleri*, Re: *Riberoclinus eigenmanni*, Lb: *Leptonotus blainvillanus*, Mg: *Munida gregaria*.

SIMPER, were Argentine anchovy (33.2%) and rock cod (16.2%). During the young chick stage, values of importance by mass of rock cod, Argentine anchovy, and Argentine hake were 26–33%, whereas during the old chick stage, Argentine anchovy was the dominant prey (76.6%; Fig. 2). Significant differences in diet composition in terms of importance by mass were found between chick stages (one-way ANOSIM, Global $R = 0.213$; $P = 0.004$). The prey contributing most to these differences, as designated by SIMPER, was Argentine anchovy (53.6%).

At Isla Vernaci Este, the most frequent prey in both the young and old chick stages was rock cod

(85.0 and 81.8%, respectively; Table 1). Rock cod was also the prey of highest numerical importance in both the young and old chick stages (33.6% and 44.8%, respectively), followed by squat lobster (18.9%) and *Riberoclinus eigenmanni* (11.6%) in the young and old chick stages, respectively (Table 1). Diet composition in terms of numerical importance did not vary significantly between chick stages (one-way ANOSIM, Global $R = 0.006$; $P = 0.423$). Rock cod was the dominant prey in terms of importance by mass in both the young and old chick stages (75.7% and 86.5%, respectively; Fig. 2). No significant differences were found in terms of importance by mass

between stages (one-way ANOSIM, Global $R = 0.008$; $P = 0.394$).

Comparison between colonies

We recorded 27 and 30 prey taxa at Isla Arce and Isla Vernaci Este, respectively (Table 1). At least 21 prey taxa were common to both colonies. The Argentine hake, channel bull blenny (*Cottoperca gobio*), crab (*Halicarcinus planatus*), isopods, stomatopods, and the inshore squid (*Doryteuthis sanpaulensis*) were found only at Isla Arce, whereas the deep-bodied pipefish (*Leptonotus blainvillaeus*), a clinid (*Ribeiroclinus eigenmanni*), crabs (*Peltarion spinosulum*, *Eurypodius latreillei*, and *Leucippa pentagona*), a gastropod (*Ataxocerithium pullum*), a patagoninan longfin squid (*Doryteuthis gahi*), and polychaetes of the family Polynoidae were only found at Isla Vernaci Este.

Diet composition in terms of numerical importance differed significantly between colonies (2-way crossed ANOSIM, Global $R = 0.432$; $P < 0.001$). The prey species contributing most to these observed differences, as designated by SIMPER, were the rock cod (27.3%), Argentine anchovy (15.3%), and squat lobster (12.4%). In terms of importance by mass, the rock cod was the dominant prey at Isla Vernaci Este during both the young and old chick stages (75.7% and 86.5%, respectively). At Isla Arce, rock cod, Argentine anchovy, and Argentine hake contributed similarly to their diet (26–33%) during the young chick stage, whereas Argentine anchovy dominated during the old chick stage (76.6%). Diet composition in terms of importance by mass was significantly different between colonies (2-way crossed ANOSIM, Global $R = 0.424$; $P < 0.001$). The prey species contributing most to these differences, as designated by SIMPER, were the rock cod (36.4%), Argentine anchovy (33.8%), and Argentine hake (10.3%), together accounting for >80% of the observed differences.

Discussion

Our results show that the Imperial Cormorant is mainly piscivorous at both breeding locations, agreeing with previous studies conducted at Golfo San Jorge (Punta et al. 1993, 2003a; Bulgarella et al. 2008; Yorio et al. 2010a) and at other locations

along the coasts of Patagonia (Malacalza et al. 1994, Gosztonyi and Kuba 1998, Ferrari et al. 2004) and Malvinas (Falkland) Islands (Michalik et al. 2010). Cormorants also consumed other prey species, such as crustaceans, cephalopods, and polychaetes, as reported in the studies mentioned earlier. The species accumulation curves showed that the total number of prey species recorded reached a plateau, except for that corresponding to the old chick stage at Isla Vernaci Este, so those results must be interpreted with caution given the relatively small sample size.

The trophic spectrum included benthic prey (e.g., *Patagonotothen* spp., *H. cunninghami*, *R. eigenmanni*, and *M. gregaria* ‘subrugosa’ morph, among others), pelagic prey (e.g., *E. anchoita* and *R. arcuata*), and demersal prey (e.g., *M. hubbsi*), confirming their opportunism and plasticity in feeding habits. This plasticity has been previously reported in the Imperial Cormorant (Punta et al. 2003a, Ferrari et al. 2004, Harris et al. 2016) and other cormorant species (e.g., Crawford et al. 1985, Velando and Freire 1999, Morgenthaler et al. 2016), and it has been argued that such flexibility in cormorant foraging helps maximize food intake given their limited diving time when in cold waters (Grémillet et al. 1998).

Four prey species were not recorded in previous Imperial Cormorant diet studies at Golfo San Jorge: the fish *Leptonotus blainvillaeus* and crabs *Eurypodius latreillei*, *Leucippa pentagona*, and *Carcinus maenas*, although their contribution to cormorant diet was relatively low. Note that *C. maenas*, documented during the young chick stage at both study colonies, is an introduced and invasive species first reported in the northern Golfo San Jorge in 2003 (Hidalgo et al. 2005) that has expanded its distribution during the last decade (P. Baron, CESIMAR-CONICET, 2017, pers. comm.). Our results include this introduced species in coastal food webs and show its potential as food for higher trophic level predators that forage in subtidal habitats within the gulf.

Previous studies on the diet of Imperial Cormorant breeding at Golfo San Jorge have quantified prey composition based on their frequency of occurrence obtained from pellet analysis (Punta et al. 1993, Bulgarella et al. 2008, Yorio et al. 2010a), except for one study that also included the importance by mass of ingested prey based on the analysis of spontaneous regurgitations (Punta

et al. 2003a). In the present study, the relative contribution of different prey to the Imperial Cormorant diet differed depending on the measurement used. Some prey showed relatively high frequencies of occurrence and numerical importance, such as *M. gregaria*, *P. muelleri*, *H. cunninghami*, and *R. eigenmanni*. Because of their small size or presence in large numbers in just a few stomach contents, however, these prey had low importance by mass and therefore a low contribution to Imperial Cormorant diet. This finding highlights the value of determining the mass of prey consumed in addition to other metrics to adequately assess the contribution of different prey. For example, a previous study based on prey frequency of occurrence at Isla Arce suggested that Argentine red shrimp, a key fishery resource in the area, had a relevant contribution to Imperial Cormorant diet during the chick rearing period (47% and 51% during the young and old chick stages, respectively; Yorío et al. 2010a). In the present study, however, Argentine red shrimp showed a similar contribution in terms of frequency of occurrence during the young chick stage (58%) but an importance by mass of only 13%, suggesting that its relevance to Imperial Cormorant diet may have been overestimated in the previous study. An inadequate quantification and interpretation of diet data may lead to inappropriate recommendations in the context of fisheries and ecosystem based management. Also note that the analysis of stomach contents provides information from only the last feeding event (Karnovsky et al. 2012) and may not adequately reflect diet composition if the temporal variability in food availability is high during the study period.

The Argentine anchovy is a pelagic species that forms dense shoals and shows high mobility in search of food (Pájaro 2002), thus constituting a less predictable prey than less mobile benthic prey. This mobility may also partly explain the low frequency of Argentine anchovy in Imperial Cormorant diet at the colony of Isla Vernaci Este compared to that observed in previous studies along the same coastal sector (Punta et al. 1993, Bulgarella et al. 2008). Because sampling time was limited, the opportunistic exploitation of Argentine anchovy by breeding Imperial Cormorant at Isla Vernaci Este was possibly not reflected in the data. Therefore, future evaluations should complement conventional diet methods with stable isotope

analysis to determine the contribution of main prey consumed during a longer time span (Bond and Jones 2009).

Three of the prey species found in Imperial Cormorant diet in this study (Argentine hake, Argentine red shrimp, and Argentine anchovy) have commercial value. The first 2 are the target of trawl fisheries operating in Golfo San Jorge (Góngora et al. 2012) in areas adjacent to all Imperial Cormorant colonies (Yorio et al. 2010b). The Patagonian stock of Argentine anchovy, however, is exploited only occasionally, although there is current interest in further developing a fishery targeting this fish in provincial waters (N. Bovcon, Universidad Nacional de la Patagonia, 2017, pers. comm.). Of the 3 prey species, only Argentine anchovy made an important contribution to Imperial Cormorant diet in this study, and only at Isla Arce. Trawl fisheries also generate large numbers of discards because of the low selectivity of their fishing gear. The bycatch of hake and shrimp fisheries in central and northern Golfo San Jorge includes at least 90 species of fish and invertebrates (Bovcon et al. 2013). Of these, at least 16 species were documented as prey of Imperial Cormorants in this study. Imperial Cormorant has been recorded feeding on discards around fishing vessels operating in the waters of northern Golfo San Jorge (González-Zevallos and Yorío 2006, González-Zevallos et al. 2011), but determining whether the prey species identified in their diet came from fishing discards or were obtained through direct capture is not possible. Future studies should assess the relationship between Imperial Cormorant diet composition throughout their breeding season and the catches from fishing operations in northern Golfo San Jorge.

Imperial Cormorant diet composition at Isla Arce differed between the 2 stages of the chick rearing period, mainly because of the increased consumption of Argentine anchovy and, to a lesser extent, a reduction in the contribution of rock cod. This dietary difference could be due to a change in the availability and abundance of prey throughout the breeding season, as observed in other cormorant and seabird species (Lehikoinen 2005, Karnovsky et al. 2008, Liordos and Gouter 2008). An alternative but not mutually exclusive explanation is that changes in diet composition result from the increase in energy demands of

growing nestlings (Grémillet et al. 1996). The increase in the consumption of Argentine anchovy could be a result of its higher energy density relative to other fish and invertebrate prey identified in Imperial Cormorant diet (González-Miri and Malacalza 1999, Ciancio et al. 2007).

Diet also differed between colonies, both in overall species composition and in the contribution of main prey consumed, likely reflecting the ability of Imperial Cormorant to take advantage of prey available in each area. The 2 study islands are separated by ~80 km and located at different distances from the mainland, and thus breeding cormorants may be foraging in areas with different environmental characteristics and prey availability. Differences in diet composition between nearby colonies should be expected in opportunistic cormorants with relatively small foraging ranges, particularly during the breeding season when they behave as central place foragers. Spatial variations in diet at relatively small scales, even smaller than the present study, have been previously reported for Imperial Cormorant in the northern sector of Golfo San Jorge (Yorio et al. 2010a) and in other diving seabirds (Wanless and Harris 1993, Velando and Freire 1999, Lescroël et al. 2004, Clausen et al. 2005). Despite the possible differences in marine habitats and prey availability between sites, both colonies could be similarly affected by trawl fisheries, which operate along the entire coastal sector. Our results on the dietary differences between stages of the reproductive cycle and breeding sites suggest that the assessment and monitoring of the interaction between Imperial Cormorant and fisheries cannot be based on information from a single breeding stage and location but will require the analysis of diet requirements throughout the breeding cycle with a representative sampling of the 17 colonies located within the marine protected area.

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