

DIET OF IMPERIAL CORMORANTS (*PHALACROCORAX ATRICEPS*) AND ROCK SHAGS (*P. MAGELLANICUS*) BREEDING SYMPATRICALLY IN PATAGONIA, ARGENTINA

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Resumen. – Dieta del Cormorán Imperial y del Cormorán Cuello Negro reproduciendo en simpatria en Patagonia, Argentina. – Se analizó la dieta del Cormorán Imperial (*Phalacrocorax atriceps*) y del Cormorán Cuello Negro (*P. magellanicus*), especies que reproducen simpátricamente en Caleta Malaspina, Patagonia, Argentina, con el fin de explorar una potencial partición de alimento entre ambas especies. Sesenta y cuatro regurgitados de contenidos estomacales se colectaron durante la temporada reproductiva de 1999 en dos colonias separadas por 2,2 km. Ambas especies compartieron la mayoría de los ítem presa identificados, principalmente peces y crustáceos. Sin embargo, la dieta del Cormorán Imperial fue más diversa en tanto que el Cormorán Cuello Negro mostró un mayor grado de especialización. Si bien el Cormorán Cuello Negro consumió casi exclusivamente peces bentónicos, el Cormorán Imperial también incorporó en su dieta peces pelágicos. Entre los peces, *Notothenia* sp., seguida por *Helcogrammoides cunningghami*, predominó en la dieta de ambas especies de cormoranes. Por su parte, el Cormorán Imperial también consumió ejemplares de *Engraulis anchoita* y *Merluccius hubbsi*. La distribución espacial de las muestras de dieta mostró un claro solapamiento en los recursos alimenticios utilizados por ambas especies de cormoranes, como así también una convergencia en la composición de peces de la dieta. El solapamiento observado en la composición de la dieta concuerda con un solapamiento relativo de las áreas de forrajeo de ambas especies reportado en estudios previos, lo que podría estar reflejando una buena disponibilidad de alimentos en el área de estudio. Los mecanismos de una posible segregación ecológica que resultó en las diferencias observadas en la dieta de ambas especies podrían haberse originado a partir de diferencias en las estrategias de buceo y comportamiento de forrajeo de ambas especies.

Abstract. – We analyzed the diet of Imperial Cormorants (*Phalacrocorax atriceps*) and Rock Shags (*P. magellanicus*) breeding sympatrically at Malaspina Inlet, Patagonia, Argentina, in order to assess food partitioning between them. Sixty-four regurgitations were collected during the 1999 breeding season on two colonies separated by 2.2 km. Both species shared many of the identified prey items, mainly fish and crustacean. However, Imperial Cormorants fed on a wider variety of preys than Rock Shags did. Moreover, the latter preyed mainly on benthic fish whereas Imperial Cormorants also consumed pelagic fishes, thus foraging in

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most of the water column. Among fish, *Notothenia* sp., followed by *Helcogrammoides cunninghami*, predominated in the diet of both cormorants, whereas Imperial Cormorants also preyed on *Engraulis anchoita* and *Merluccius hubbsi*. The spatial distribution of diet samples showed a clear overlap in the food resources used by both cormorants as well as a convergence in the fish composition of the diet. The observed overlap in the diet was in concordance with the relative overlap in the foraging areas used by both species, as reported in previous studies, thus probably reflecting good food availability in waters surrounding Malaspina Inlet. Therefore, the mechanisms of a possible ecological segregation that resulted in the documented differences in the diet of both species could have arisen from a combination of dissimilarities in diving strategies and foraging behavior. Accepted 22 August 2008.

Key words: Argentina, cormorants, diet, *Phalacrocorax atriceps*, *Phalacrocorax magellanicus*, sympatric species.

INTRODUCTION

Imperial Cormorants (*Phalacrocorax atriceps*) and Rock Shags (*P. magellanicus*) are widely distributed species along the Patagonian coast of Argentina and their breeding areas overlap at many locations (Yorio *et al.* 1998, Frere *et al.* 2005). Like all cormorants, they are foot-propelled pursuit-divers that feed mainly inshore on fish and invertebrates (Wanless *et al.* 1992, Punta *et al.* 1993, 2003a; Malacalza *et al.* 1997, Quintana 1999, 2001; Frere *et al.* 2005, Quintana *et al.* 2007). Diet studies throughout their distribution range are scarce and mainly based on a single species at a single colony (Malacalza *et al.* 1997, Gosztonyi & Kuba 1998; but see Punta *et al.* 2003a). Published information has emphasized diving patterns (Quintana 1999, Wilson & Quintana 2004, Quintana *et al.* 2007) and feeding locations (Quintana 2001, Sapoznikow & Quintana 2003). At most breeding localities, both species occur in the same colonies (Punta 1989, Yorio *et al.* 1998, Punta *et al.* 2003b, 2003c). Based on pellet casts and regurgitates of adult birds from six different colonies, Punta *et al.* (2003a) analyzed the diet of both species and quantified the food partitioning at Bahía Bustamante by pooling samples from all colonies. Here we present novel data on the diet of both species from two nearby colonies in Patagonia.

To study food partitioning between these two species of cormorants in a small area is relevant given that Imperial Cormorants and

Rock Shags breeding at Malaspina Inlet showed an overlap in their foraging areas (Sapoznikow & Quintana 2003). This study complements the previous assessment of the feeding performance and the use of feeding areas of both species during the breeding season analyzed by means of radio-telemetry at Malaspina Inlet (see Sapoznikow & Quintana 2003).

The objectives of the present study were: 1) to analyze the diet of Imperial Cormorants and Rock Shags nesting sympatrically in two nearby islands at Malaspina Inlet, Chubut; 2) to compare and complement the results with those previously obtained at other Patagonian locations, and 3) to assess food partitioning between two species sharing foraging grounds.

METHODS

Study area. Fieldwork was conducted at Malaspina Inlet (45°11'S, 66°30'W), Bahía Bustamante, Chubut, Argentina (Fig. 1). This is an Inlet of 34 km², with a maximum width of 4 km and a length of 10 km (Herrera 1997). During 15 days of the 1999 breeding season, we collected regurgitates from Imperial Cormorants and Rock Shags nesting in two mixed colonies in Isla Vernacci Este, at the mouth of the inlet, and Isla Vernacci Oeste inside the inlet, which are separated by 2.2 km. For both species of cormorants, sampling occurred during the last week of incuba-

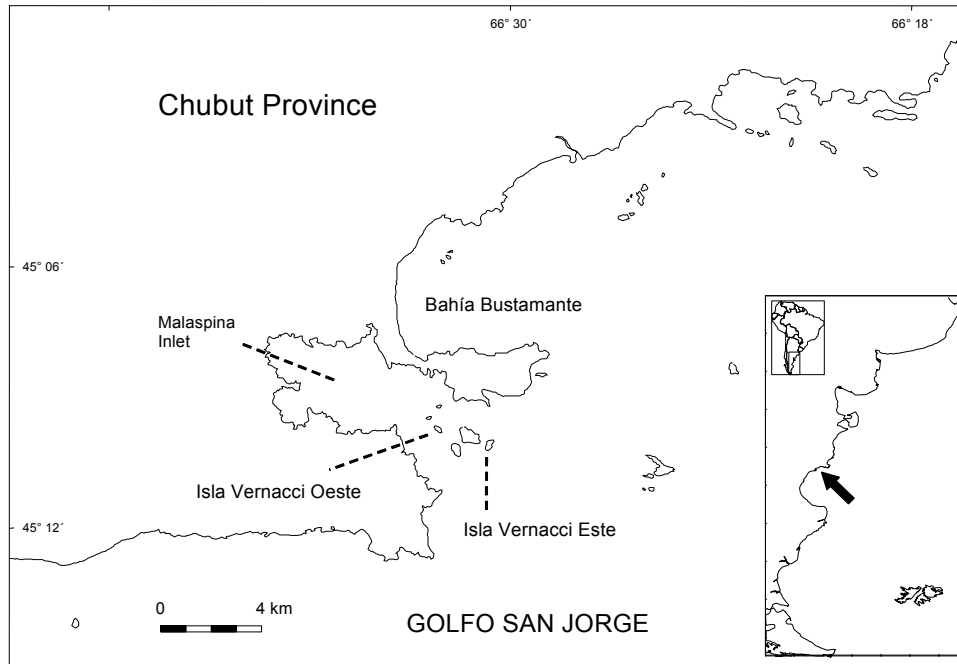


FIG. 1. Study area. Islands Vernacci Este and Vernacci Oeste at Malaspina Inlet, Chubut, Argentina.

tion or the first ten days of the chick-rearing period.

Sampling and processing. We sampled the diet of adult breeders and described the composition of recently ingested material regurgitated during the handling of birds for other research purposes. Individuals were shaken to obtain the total of the stomach content. Each regurgitate was placed in a plastic bag and returned to the lab in a cooler. Once there, samples were frozen until examination. A total of 64 regurgitates, 47 of Imperial Cormorants and 17 of Rock Shags, were analyzed. Regurgitations, fixed in 10% formalin during 3–4 days, were stained with alizarin red solution following Gosztanyi (1984) to ease the recognition and separation of bony or calcified materials (Gosztanyi & Kuba 1996). Regurgitates were sorted into prey classes up to the lowest taxonomic level possible, under a binocular micro-

scope (10X). Fish remains from digested specimens were identified to species or genus level by comparing the bony structures with a reference guide (Gosztanyi & Kuba 1996). The same procedure was followed to classify invertebrate material (Boschi *et al.* 1992). We did not use otoliths for fish identification. Because most bones and otoliths were eroded, no attempts were made to calculate prey length and fresh mass.

Analysis. To describe the diet, the percentage of occurrence of each prey species found in the regurgitates was calculated for both cormorant species. The percentage of occurrence of major prey groups in the samples (fishes, crustaceans, cephalopods, tunicates and polychaetes) was calculated for both species of cormorants, and for each island.

The Shannon-Weaver index (Shannon & Weaver 1949) was used to characterize diet

TABLE 1. Prey consumed by Imperial Cormorants and Rock Shags at Malaspina Inlet during the 1999 breeding season determined by the analysis of regurgitations. Sample size in parenthesis.

Prey taxa	Frequency of occurrence (%)	
	Imperial Cormorant (47)	Rock Shag (17)
Fishes	97.8	100
<i>Notothenia</i> sp.	57.4	100
<i>Helcogrammoides cunninghami</i>	40.4	29.4
<i>Engraulis anchoita</i>	29.8	—
<i>Merluccius hubbsi</i>	23.4	—
<i>Odontesthes smitti</i>	14.8	—
<i>Ribeiroclinus eigenmanni</i>	8.5	5.9
<i>Raneya brasiliensis</i>	6.4	—
<i>Agonopsis chilensis</i>	4.3	—
<i>Bovichtys argentinus</i>	4.3	—
Mixinidae	4.3	—
<i>Acanthistius brasilianus</i>	2.1	—
<i>Austrolycus laticinctus</i>	2.1	—
<i>Sebastes capensis</i>	—	5.9
Zoarcidae	—	5.9
Crustaceans	61.7	29.4
<i>Peisos petrunkewitchy</i>	23.4	—
<i>Austropandalus grayi</i>	14.9	—
<i>Peltarion spinosolum</i>	10.6	—
<i>Munida</i> sp.	6.4	—
<i>Alpheus puapeba</i>	4.3	29.4
<i>Pleoticus muelleri</i>	4.3	—
<i>Campylonotus vagans</i>	4.3	—
<i>Betaeus</i> sp.	2.1	—
<i>Nauticaris magellanica</i>	2.1	—
Isopod Genus <i>Edotia</i>	2.1	—
Amphipod Gammaridae	2.1	—
Cephalopods	21.3	11.7
Tunicates	10.6	5.8
Polychaetes	4.3	—

diversity in fish and crustacean preys, which were the two most important categories in the samples. To test for differences in fish and crustacean diversity among regurgitates of both species, we used the Hutchenson's t-test for the Shannon index (Hutchenson 1970,

Zar 1999). We also tested for differences in total prey groups, and in the fish portion of the diet of both species using a multivariate analysis with the PRIMER 5 package. First, we generated a Bray-Curtis similarity matrix (Bray & Curtis 1957) to assess similarities in prey group composition between samples, using non-parametric multi-dimensional scaling (MDS). A stress coefficient was calculated for each ordination representing the extent to which the relationship between the samples was adequately represented in two dimensions (stress values < 0.1 indicate a good representation of the data) (Clarke & Warwick 2001). We tested for significant differences in diet composition between species using a multivariate analysis of similarities (ANOSIM) (Clarke & Warwick 2001), which is analogous to a univariate ANOVA. This procedure uses the Bray-Curtis similarity matrix to compute a test statistic R. R is standardized so that a value of one means that all the samples within a group are more similar than any sample from the other group. R is approximately zero if there are no differences between the groups, reaching its maximum when all between-group dissimilarities are greater than all within-group dissimilarities. Statistical significance was determined by comparing the sample R with those produced by randomly assigning samples to groups. When 95% of the random arrangements had higher values than the sample, we considered values significant (Clarke 1993, Clarke & Warwick 2001).

RESULTS

Analysis of regurgitates showed that fish constituted the main component of the diet of Imperial Cormorants and Rock Shags at Malaspina Inlet, followed by crustaceans and cephalopods. Tunicates and polychaetes were occasional (Table 1).

The diet composition based on the main

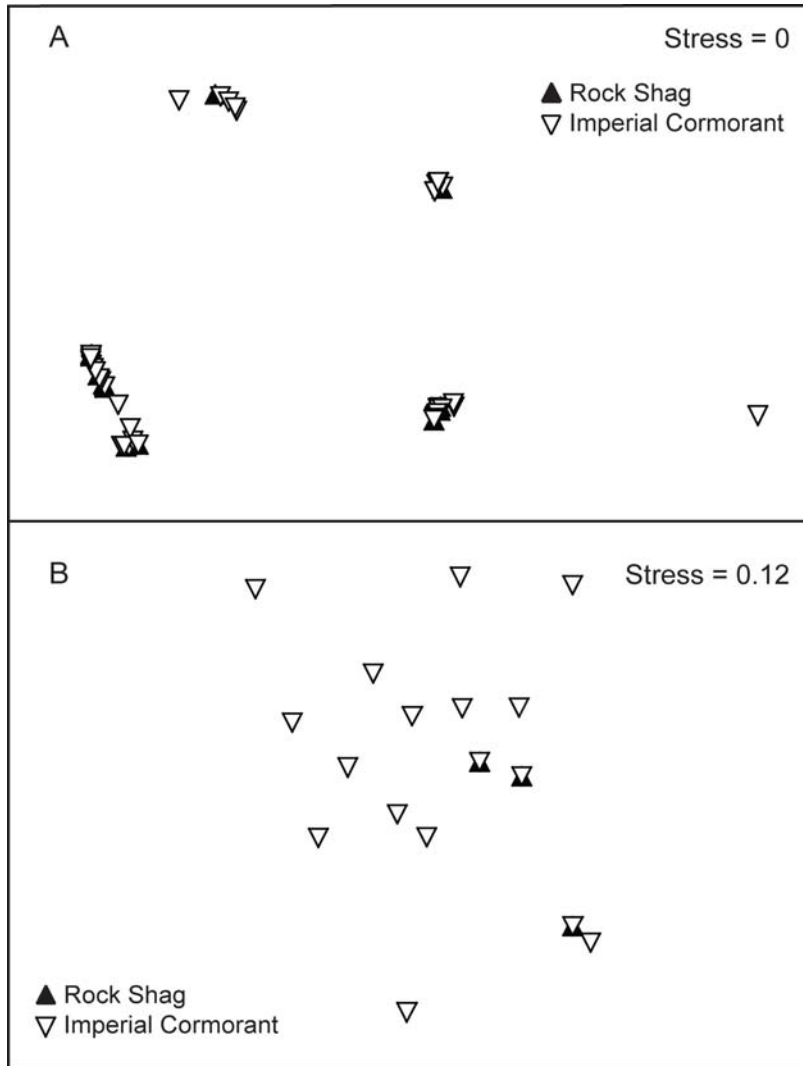


FIG. 2. Two-dimensional grouping of diet samples from Imperial Cormorants and Rock Shags according to A) Prey type (fishes, crustaceans, and cephalopods), and B) Fish species, obtained from the multidimensional non-metric scale method based on the Bray-Curtis matrix. Each triangle represents one regurgitate.

prey groups (fishes, crustaceans and cephalopods) showed a high overlap between the two species. The spatial distribution of the samples, obtained through the Bray-Curtis matrix, showed a clear overlap in the composition of the diet of both cormorants (Fig. 2A). In addition, the R-value obtained was low, also

suggesting an overlap in food resources (ANOSIM, $R = -0.004$, $P > 0.05$).

During the study period, the fish composition of the diet of both cormorants also converged (ANOSIM, $R = 0.15$, $P > 0.05$). However, the spatial distribution of the samples evidenced a wider dispersion for the diet

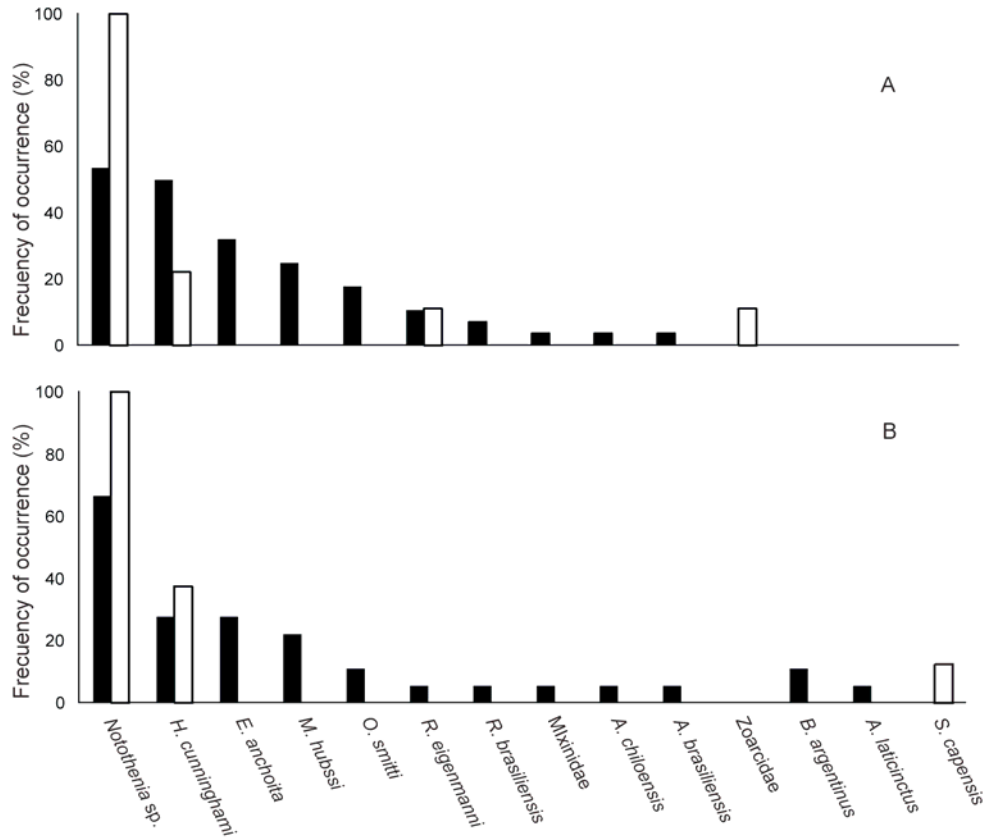


FIG. 3. Percentage of occurrence of fish prey in regurgitates from A) Imperial Cormorants (N = 28, black bars) and Rock Shags (N = 9, white bars) at Vernacci Este, Malaspina Inlet, Chubut, Argentina; and B) Imperial Cormorants (N = 19, black bars) and Rock Shags (N = 8, white bars) at Vernacci Oeste, Malaspina Inlet, Chubut, Argentina.

samples of the Imperial Cormorant, containing the total distribution of Rock Shag samples (Fig. 2B). For both species, *Notothenia* sp. (rock cod) was the most frequent prey item (58 and 100% for Imperial Cormorant and Rock Shag, respectively), followed by *Hellogrammoides cunninghami* (Cunningham's triplefin; 41 and 29% for Imperial Cormorant and Rock Shag, respectively) (Table 1). The rest of the fish species were recorded in lower frequencies (Table 1).

In addition, *Engraulis anchoita* (anchoita), *Merluccius hubbsi* (Argentine hake), and *Odontes-*

thes smitti (silverside) also made up a large component of Imperial Cormorant's diet. In total, Imperial Cormorant's diet consisted of 12 fish species whereas Rock Shag's diet consisted of 5 fish species. When analyzing fish prey by species by island, we found that Imperial Cormorants from Vernacci Este fed on 10 different fish species, whereas Rock Shags incorporated only 3 fish prey (Fig. 3A). *Notothenids* and *H. cunninghami*, both benthic species, appeared frequently in the diet of both cormorants. Imperial Cormorants also incorporated high proportions of *E. anchoita*,

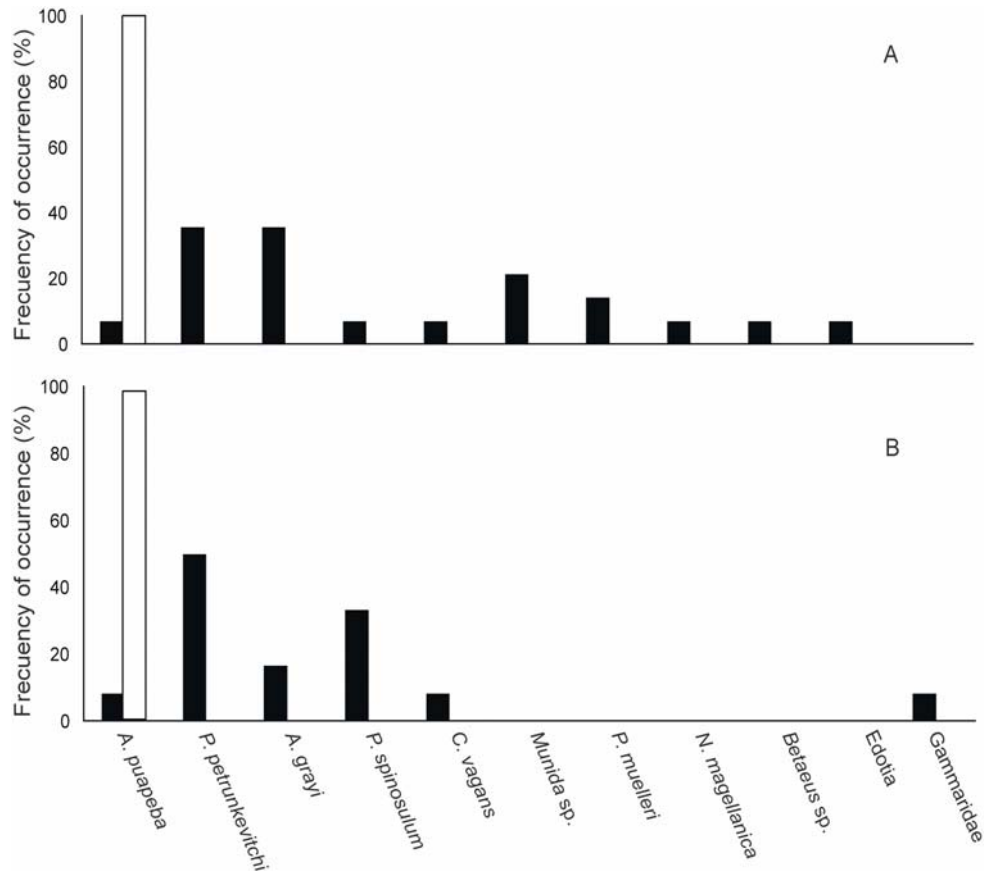


FIG. 4. Crustacean percentage of occurrence in regurgitates from A) Imperial Cormorants (N = 14, black bars) and Rock Shags (N = 1, white bars) at Vernacci Este, Malaspina Inlet, Chubut, Argentina; and B) Imperial Cormorants (N = 12, black bars) and Rock Shags (N = 4, white bars) at Vernacci Oeste, Malaspina Inlet, Chubut, Argentina.

a mesopelagic fish not recorded in the diet of Rock Shags in either of the two colonies. The third fish prey for Rock Shags was Zoarcidae fish, found exclusively and sporadically in samples from Vernacci Este (Fig. 3A). On the other hand, in Vernacci Oeste, Imperial Cormorants fed on 12 fish species, being *Notothenis* the most frequent prey, and *E. anchoita* and *H. cunninghami* the second most frequent species. Rock Shags at Vernacci Oeste preyed on three fish species, *Notothenia* sp., *H. cunninghami*, and *Sebastes capensis* (the latter appeared

exclusively in Rock Shags from Vernacci Oeste; Fig. 3B). Crustaceans were included in the diet of both cormorants, showing a similar pattern to the one observed for fish. Imperial Cormorants incorporated 11 species of crustaceans whereas Rock Shags only one: *Alpheus puapeba* (Figs 4A and 4B). Imperial Cormorants showed a higher diversity of the main preys ingested (fishes and crustaceans) when compared to Rock Shags (Corrected Shannon index: 2.44 (\pm 0.007) and 1.09 (\pm 0.02) respectively, Hutchenson's t-test $P < 0.05$).

DISCUSSION

Despite sharing some of the identified preys during the studied breeding season, Imperial Cormorant fed on a wider variety of prey species than Rock Shags, and this difference held after accounting for differences in sample size. Moreover, Rock Shags fed mainly on demersal-benthic fish species whereas Imperial Cormorants also incorporated pelagic fish species in their diet. These results agree with those previously obtained by Punta *et al.* (2003a) for the same cormorants at Bahía Bustamante, Chubut, Argentina.

Several studies have documented that using different methods for sampling diets can lead to different estimations of prey abundance in the diet of cormorant species, when numerical frequency is considered (Casaux *et al.* 1997, Seefelt & Gillingham 2006). However, in terms of presence and absence (percentage of occurrence) of prey groups, the non-lethal method of regurgitate collection and analysis seems to be appropriate and practical in assessing cormorant diet. Used in combination with information available on foraging ecology and prey availability, these data could provide useful information about the relationships between different cormorant species and their prey. Unfortunately, due to the advanced degree of digestion of the samples, no measurements of their fish prey length and mass were undertaken.

Among fish, *Notothenia* sp. predominated in the diet of cormorants in both islands, followed by *H. cunninghami* and, in the case of Imperial Cormorants, also by *E. anchoita* and *M. hubbsi*. Other fish species were much less frequent in the diet. Imperial Cormorants do have greater diversity of crustaceans in the diet. Despite Rock Shag including only one crustacean prey in their diet (*A. puapeba*), this crustacean was present in all 17 Rock Shag regurgitates, suggesting it is an important/common prey for these shags. However, it is

important to mention that part of the remains of secondary preys (crustaceans, cephalopods, etc.) found in the regurgitations could come from fish stomachs (Casaux *et al.* 1997). In a feeding trial, a captive Imperial Cormorant fed exclusively with fish produced pellets in which algae and mandibles of polychaetes were found (Casaux *et al.* 1995). In our case, the *A. puapeba* remains found in the samples of Rock Shag could be an indirect prey from the stomach of the fish *Notothenia* sp.

The main dietary difference between species was the wider variety of fish species exploited by the Imperial Cormorants, including in their diet, pelagic fish in addition to those demersal-benthic species shared with Rock Shags. This difference between species may be due to the small sample size in the case of Rock Shags, and/or temporally restricted sampling (one breeding season) given that Punta *et al.* (2003a) found a greater diversity for Rock Shag's diet at Bahía Bustamante during an extended 1992–1994 sampling period, and even greater when analyzing pellets than regurgitates.

Given that shags are opportunistic feeders (Craven & Lev 1987, Keller 1995), differences in the composition of the diet may also reflect different prey availability around the studied colonies. Sapoznikow & Quintana (2003) studied Imperial Cormorants and Rock Shags breeding in the same colony during the same season, and reported a two-dimensional overlap in their foraging areas, being lower at Vernacci Este than at Vernacci Oeste. Thus, dissimilarities in the composition of the diet of both species could not be explained by the above hypothesis of differing prey availability. Rather, the differences in diet composition between species could be explained by differences in the diving depths used and the foraging strategies displayed by both cormorants.

Among closely related species such as the Imperial Cormorant and the Rock Shag, overlap in the diet may be expected (Ridoux

1994), but mechanisms of ecological segregation such as differences in diving strategies, prey sizes, and foraging behavior may be more efficient in reducing this overlap than foraging exclusively on different prey species. Diving data of both species at Malaspina Inlet showed that Imperial Cormorants (mean body weight 2.3 kg; Svagelj & Quintana 2007) routinely dive deeper than 20 m (attaining maximum depths of 70 m), and for longer periods than other cormorant species (Quintana *et al.* 2007). Rock Shags, in contrast, are smaller birds (mean weight 1.5 kg; Quintana *et al.* 2003) and usually dive in shallow waters, primarily exploiting the first 10 m of the water column, with dives that rarely exceed 1 min (Quintana 1999, 2001; Quintana *et al.* 2002, Sapoznikow & Quintana 2003, Frere *et al.* 2005, in press).

An overlap in the diet may also reflect good feeding conditions near Malaspina Inlet, and could explain the relative diet (this study) and foraging areas overlap (Sapoznikow & Quintana 2003) as a result of both species feeding on abundant food resources during the 1999 breeding season. However, there is not enough information to address the hypothesis of overlapping due to good feeding conditions in the studied area. Further information about prey abundance and distribution is needed in order to interpret patterns of resource overlap between species. Finally, our study highlights the idea that in the Patagonian coast of Argentina, the Rock Shag is more of a specialist, whereas the Imperial Cormorant seems to be more of a generalist with a wider trophic spectrum including both fish and crustacean.

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