

## Diet of Neotropic cormorant (*Phalacrocorax brasilianus*) in an estuarine environment

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**Abstract** The diet of the Neotropic cormorant (*Phalacrocorax brasilianus*) was studied by analysing 289 regurgitated pellets collected from a roosting site at Lagoa dos Patos estuary, southern Brazil, between November 2001 and October 2002 (except April to June). In total, 5,584 remains of prey items from 20 food types were found. Fish composed the bulk of the diet representing 99.9% by mass and 99.7% by number. The main food items were White croaker (*Micropogonias furnieri*) (73.7% by frequency of occurrence, 48.9% by mass and 41.2% by number), followed by Catfish (Ariidae) and anchovies (Engraulidae). In Lagoa dos Patos estuary the generalist Neotropic cormorant fed mainly on the two most abundant demersal fishes (White croaker and Catfish), which accounted for the low niche breadth calculated. The total length of all fish preyed varied from 27.2 to 318.3 mm ( $113.5 \pm 48.0$  mm), and preyed White croakers' size differed between months. Neotropic cormorants seem to prey on most abundant class sizes of White croaker instead of selecting similar prey size throughout the time. However,

temporary changes in diet in terms of food items, abundance and prey size were detected, revealing a high ecological plasticity of the species. Individual daily food intake of Neotropic cormorants estimated by pellets and metabolic equations corresponded to 23.7 and 27.1% of their body mass, falling in the range of other cormorant species. Annual food consumption of the population estimated by both methods was 73.4 and 81.9 tonnes, comprising mainly immature and subadult White croaker and Catfish which are commercially important. Temporal variations in diet composition and fish size preyed by Neotropics cormorants, a widespread and generalist species, suggest shifts according to fluctuations in the abundance of prey. The plasticity of this cormorant is also revealed by their ability to adjust feeding behaviour in response to temporal or local changes in the environment, from a generalist at the species level to a specialist at the individual or local population level.

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### Introduction

Marine organisms differ greatly in their ability to cope with environmental changes, either natural or anthropogenic. In a continuum, species could benefit from changes by expanding their range and increasing population or decreasing in numbers down to the extinction point. Feeding plasticity is of great adaptive value for animals coupling with environmental changes, as have been shown for a range of species. For instance, the Antarctic bottom-dwelling fish (*Trematomus hansoi*) showed extreme feeding plasticity, switching its feeding habits at the time of fishery operations (Pakhomov 1998); and the Spitting cobra (*Naja nigricollis*) and Black forest cobra (*N. melanoleuca*)

showed changes in the composition of diet from one habitat to another (Luiselli et al. 2002). On their turn, birds have shown a wide range of strategies to deal with different changes (reviewed in Newton 1998). For instance, seabirds in the North Atlantic and Barents Sea had responded differently to the decline of pelagic fish stocks: surface-feeding Kittiwakes (*Rissa tridactyla*) had difficulty in finding enough food, while pursuit diving Common guillemots (*Uria aalge*) and Puffins (*Fratercula arctica*) fared better (Barrett and Krasnov 1996; Carscadden et al. 2002). Similarly, gulls (*Larus* spp.) and Great skua (*Stercorarius skua*) increased in population size following the availability of fish discharges from vessels, but changed their foraging effort from scavenging to predation on seabirds, after the decline of discharges (Carscadden et al. 2002; Votier et al. 2004). Optimal foraging theory predicts that an organism will maximize its food intake rates; however, their ability to cope with changes in food availability differs greatly among species, and not all species are able to deal efficiently with changes in food resources (Barrett and Krasnov 1996; Carscadden et al. 2002). In addition, predator responses can occur either in the short term, by changing prey species, foraging areas or delaying breeding season (Barrett and Krasnov 1996; Votier et al. 2004; Watanuki et al. 2004), or in the long term, by changing trophic level or distribution areas (Thompson et al. 1995; Newton 1998). In this study we investigate monthly variations in the prey species and prey size of the generalist Neotropic cormorant (*Phalacrocorax brasilianus*) and how they deal with variations in prey abundance.

The Neotropic cormorant lives in both freshwater and marine environments (Harrison 1985), and they occur from southern USA to southern South America (Telfair and Morrison 1995). It is one of the most widely distributed cormorants in Americas, one of the most numerous seabird species in South America, and is remarkably versatile in its use of habitats (Telfair and Morrison 1995). However, many aspects of its life history such as nutrition and energetics, seasonal diet and population dynamics require further study (Telfair and Morrison 1995; Kalmbach et al. 2001). Neotropic cormorants are primarily generalists during breeding season, taking the most readily available prey, particularly the fish that are most abundant (Telfair and Morrison 1995). They feed in protected bays and nearshore waters along the coast by pursuit-diving from the water surface, using their feet for propulsion (Humphrey et al. 1988; Telfair and Morrison 1995). Despite dietary studies being restricted to breeding season and based on short-term data (reviewed by Telfair and Morrison 1995), the species is known to have flexible foraging techniques, i.e. they are opportunistic rather than selective predators (Humphrey et al. 1988; Quintana et al. 2004). For instance, the Neotropic cormorant in Peru prey mainly on Peruvian

anchovy (*Engraulis ringens*) (Jordán 1967), and in Santa Fé, inland Argentina, they prey mainly on fish from open waters and some crustacean species (Beltzer 1983). In central Chile the Neotropical cormorant fed mainly upon demersal fish and one crustacean species, but the study was based on only 38 regurgitates and no data about size of fish (Kalmbach et al. 2001), which is necessary to understand the ecological role of piscivorous predators on particular prey species, are available. In Galveston Bay, USA, 1,064 regurgitates were collected, with fish comprising the most of diet, and shrimp were the only invertebrate prey (King 1989). Thus, food requirements and diet based on large sample sizes and a large temporal data set are not available for Neotropic cormorants in their distribution areas. The lack of detailed data on the diet of the widespread, abundant and generalist Neotropic cormorant preclude a clear understanding of their ecological role and capacity to adjust to changing resources.

Fish constitute the bulk of the cormorants' and shags' diet, which are large waterbirds with cosmopolitan distributions in marine, coastal and freshwater ecosystems (Barrett et al. 1990; Kirby et al. 1996; Neuman et al. 1997; Grémillet et al. 2000; Nelson 2005). Their abundance in some areas raises concerns about the impacts on fish stocks of economic value (Kirby et al. 1996), in commercial fisheries and aquaculture systems, such as the predation of cormorants on Catfish in the USA (Glahn and Stickley 1995), and predation upon sport fishing resources in North America (e.g. Ross and Johnson 1995). Cormorants displace daily from colonies or nocturnal roosting sites to feeding grounds, which limits their foraging range. For instance, 90% of radio-tracked foraging trips of Neotropic cormorants in Argentina were within 2.5 km of the colony (Quintana et al. 2004). As a consequence of their limited foraging radius, large body size and abundance, cormorants could severely impact local fish stocks, as shown by Birt et al. (1987) in Double-crested cormorants (*Phalacrocorax auritus*) in Canada. Detailed study of diet and calculations of daily food intake of the Neotropic Cormorant are valuable information for the understanding of their role in the local environment. A range of energetic and dietary approaches have been carried out to estimate seabird energy requirements and number of different fish species consumed, as well as comparison of seabird prey consumption and fishery captures (Adams et al. 1991; Furness and Cooper 1982; Derby and Lovvorn 1997).

In the Lagoa dos Patos estuary in southern Brazil, Neotropic cormorant is present in all months, with spring (October to December) and summer (January to March) populations in the mouth of Lagoa dos Patos estimated at 1,400 birds (V. Barquete et al., submitted). Monthly variations in number are poorly understood because they

have variable breeding seasons in the area, their breeding grounds were not fully located and their local or migratory movements are not clear. However, based on plumage characteristics the population is composed of post-breeding adults migrating from colonies away from the estuary and immature birds that stay year-round in the area. The Lagoa dos Patos estuary is an important feeding and developmental ground for several fishes and crustaceans (Castello 1986) and sustains a commercially important fishery targeting several species. Seagrass (*Ruppia maritima*) beds occur extensively during spring and summer in shallow lagoon waters, which contain large numbers of juvenile fish and act as shelter for adult fish (Seeliger 1998a, b). These are also important foraging grounds for other cormorant species elsewhere (Dorfman and Kingsford 2001).

This study was carried out in 2001–2002 at a major nocturnal roosting site of Neotropic cormorant in Lagoa dos Patos, southern Brazil, aiming to (1) determine species composition, size and body mass of prey species in the diet; (2) identify monthly variations in the composition of diet; and (3) estimate the quantity of food ingested by cormorants, individually and at the population level. This was the first approach in studying their overlap with fishery activities.

## Materials and methods

### Study area and sampling

Lagoa dos Patos is located between 30°30'S–50°36'W and 32°12'S–52°05'W near Rio Grande city; it is connected to the Atlantic Ocean by a narrow natural channel bordered in the southern portion by artificial jetties 20 km long and 0.5–3 km wide (Asmus 1998). It is the world's largest choked lagoon (Seeliger 2001), with the estuarine section at the southern part of the lagoon spanning an area of 971 km<sup>2</sup> or around 10% of the total area, with influx of seawater (Asmus 1998), mean depth of 5 m with large shallow banks <5 m and maximum depth of 18 m (Calliari 1998).

Regurgitated pellets ( $n = 289$ ) were collected from November 2001 to October 2002 (except April to June), on the base of a power tower at Pontal Sul area located at mouth of Lagoa dos Patos estuary (32°08'S; 052°05'W, Fig. 1). Pellet sampling was performed weekly when navigation to the tower was possible using a small boat. Only fresh pellets, i.e. wet and covered by mucous, were collected in the morning, after birds had departed to feeding grounds. Pellets were collected from both non-breeding adults and immature birds based on plumage characteristics but roosting in mixed flocks. There was no way to recognize pellets from immature or adult birds, but

similar food requirements were assumed to occur. Previous studies on non-breeding adult and immature free-living cormorants elsewhere demonstrated that they typically regurgitate one pellet per day, usually just before dawn and before leaving for fishing grounds (Telfair and Morrison 1995; Zijlstra and van Eerden 1995). However, cormorants kept in captivity and being fed on anchovies which have typically fragile otoliths, produce one pellet in 55% of days (Jahncke and Rivas 1998). In the area we have data on pellet production for other species, namely the Common tern (*Sterna hirundo*) that produce two pellets per day (Bugoni et al. 2005). However, the time gap between feeding and egestion is related to metabolic rates and body mass, with larger birds having lower digestive transit (Duke et al. 1976), which corroborate data on other cormorants egesting pellets daily (Jordán 1959; Johnstone et al. 1990; Russell et al. 1995). During the breeding period in autumn (April to June) when they move to inland areas (V. Barquete et al., submitted) only 117 and 317 birds on average were counted in the roosting site, and no pellets were collected, preventing comparisons during those months.

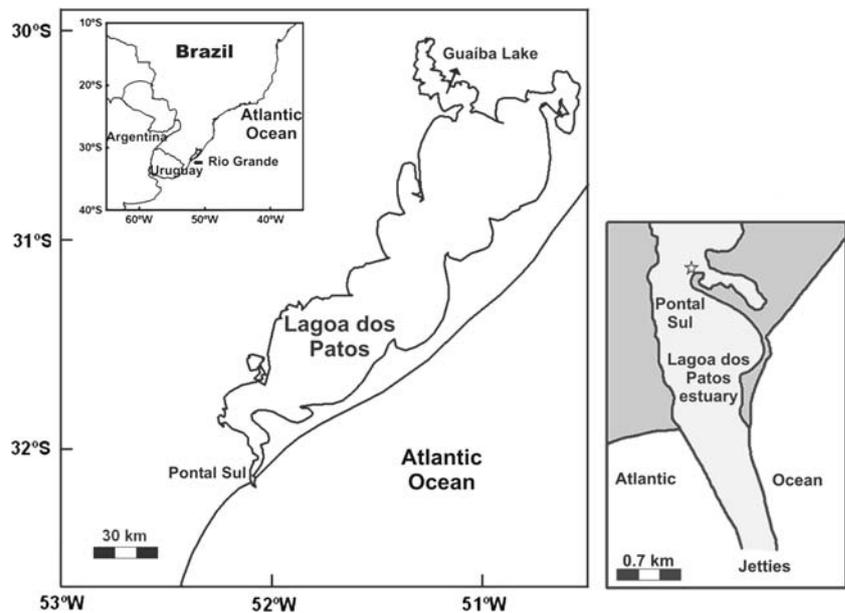
### Diet analysis

Pellets were individually stored and frozen until processing. Pellet analysis consisted of defrosting in water and liquid soap (4 l of water: 3 ml of liquid soap) for 24 h according to Neuman et al. (1997). After this they were washed in flowing water using a sieve with mesh of 0.125 mm.

After removing the mucous, all remains were analysed under a dissecting microscope. Fish were identified through *sagitta* and *lapillus* otoliths, and scales according to Corrêa and Vianna (1992) and Naves (1999), and by comparison with reference collections at the Department of Oceanography at Fundação Universidade Federal do Rio Grande (FURG). Otoliths were sorted by species, paired and counted, and the number of eye lense pairs assessed. The largest number of otoliths pairs or eye lenses was assumed to represent the number of fish in the pellet.

The length of *sagitta* otoliths (from the rostrum tip to the caudal end) was measured using the ocular micrometer of the microscope. An Index of Digestion (ID) according to Bugoni and Vooren (2004) was given for each *sagitta* otolith, where: ID (0), no sign of wear or digestion; ID (1), otolith edges slightly worn but *sulcus acusticus* still well defined; ID (2), otolith edges extremely worn, *sulcus acusticus* becoming vague; ID (3), *sulcus acusticus* worn away. *Sulcus acusticus* is a longitudinal depression in the middle of the otoliths surface and can vary on morphology according to species (Corrêa and Vianna 1992). For details

**Fig. 1** Lagoa dos Patos estuary in southern Brazil with location of the nocturnal roosting site of the Neotropic cormorant (*Phalacrocorax brasilianus*). Star tower, roosting site of Neotropic cormorant



on anatomy and terminology of fish otoliths, see Kalish et al. (1995). Regarding Catfish, only *lapillus* otoliths were recovered from pellets and identified as Catfish according to Reis (1982), but no regression was available to estimate total length (TL) and body mass (BM) because the three Catfish species in the estuary have *lapillus* otoliths not identifiable at the species level and those species have different life traits, which precludes the calculation of a general regression for the family. Only otoliths with ID (0) and (1), which accounted for 50.6% of the otoliths, were used to estimate the TL and BM of fish consumed by Neotropic cormorants, using allometric equations in Table 1. Total length and BM of fish were calculated using the mean length of the right and left otoliths. For fish with broken otoliths or digested with ID (2) and (3), corresponding to 49.4% of otoliths, or when an equation was not available, the mean of the prey BM calculated for the other fish prey in the corresponding taxon was assigned as an estimate of its BM. For ‘unidentified fish’ the mean BM of all fish was used for calculating the ingested food and contribution by mass and Index of Relative Importance (IRI). For shrimp found in samples the mean BM of juvenile male and female of Pink shrimp (*Farfantepenaeus paulensis*), the most common shrimp in the estuary, was used (D’Incao and Calazans 1978). The BM of fish and shrimp ingested by cormorants was named ‘reconstructed mass’.

Invertebrates in the pellets of cormorants could be derived from secondary or indirect consumption (Johnson et al. 1997). In this study, invertebrates were not considered part of the cormorant’s diet, with the exception of the Pink shrimp found in pellets without any other prey

remains, which were therefore ingested intentionally by cormorants.

#### Data analysis

A prey taxon present in the pellet is termed a ‘food item’, and for each food item an individual animal represented in the pellet is termed as ‘prey’, according to Bugoni and Vooren (2004). The importance of each food item in the diet was reported as frequency of occurrence absolute (FO) in pellets and relative (FO%), contribution by number ( $N$  and  $N\%$ ), and contribution by reconstructed mass ( $M$  and  $M\%$ ). Additionally, we calculated the IRI modified from Pinkas et al. (1971) by Bugoni and Vooren (2004) where

$$\text{IRI} = (N\% + M\%) \cdot \text{FO}\% \quad (1)$$

Niche breadth ( $B$ ) was calculated from Levins’ equation

$$B = \left( \sum p_i^2 \right)^{-1} \quad (2)$$

where  $p_i$  is the proportion of mass contribution of each food item, standardized as

$$[B_S = (B - 1/n - 1)] \quad (3)$$

where ‘ $n$ ’ is the number of food items; with values near ‘one’ meaning that all food items were used in similar proportions, while values near ‘zero’ means that one or a few categories were used with high frequency and many with low frequency (Krebs 1989).

**Table 1** Otolith-length and length/body mass relationships of juvenile fishes consumed by Neotropic cormorant (*Phalacrocorax brasilianus*) in southern Brazil

Fish	TL × OtL (range of OtL)	Body mass × TL (range of fish TL)
<i>Micropogonias furnieri</i> <sup>a</sup>	TL = 16.434024·OtL <sup>1.158209</sup> (1.7–12.5)	BM = 0.0000019·TL <sup>3.3303687</sup> (30–300)
<i>Lycengraulis grossidens</i> <sup>a</sup>	TL = 38.106486·OtL <sup>1.080817</sup> (0.44–5.12)	BM = 4.2407473 × 10 <sup>-7</sup> ·TL <sup>3.571191</sup> (33–245)
<i>Menticirrhus</i> sp. <sup>a</sup>	TL = 16.842076·OtL <sup>1.288275</sup> (1.56–13.4)	BM = 0.0000063·TL <sup>3.088628</sup> (35–470)
<i>Mugil</i> sp. <sup>b</sup>	TL = 23.33166·(e <sup>0.3448573OtL</sup> ) (0.78–8)	BM = 0.000048·TL <sup>2.702358</sup> (22–313)
<i>Mugil platanus</i> <sup>b</sup>	TL = 46.315·OtL–5.8946 (0.5–8.2)	BM = 41.782·OtL <sup>1.0005</sup> (0.08–1612.5)
<i>Jenynsia multidentata</i> <sup>a</sup>	TL = 38.658233·OtL <sup>0.9465327</sup> (0.44–2.46)	BM = 0.0000012·TL <sup>3.571191</sup>
<i>Mugil curema</i> <sup>b</sup>	TL = 35.299·OtL + 1.3516 (0.9–3.4)	BM = 36.652·OtL <sup>0.8729</sup> (0.2–1.18)
<i>Trachinotus marginatus</i> <sup>b</sup>	TL = 45.12246·OtL <sup>1.22121</sup> (0.49–2.04)	BM = 0.000857·TL <sup>2.533267</sup>
<i>Brevoortia pectinata</i> <sup>a</sup>	TL = 5.6187 + 44.875·OtL (0.6–2.7)	BM = 0.0000224·TL <sup>2.79379</sup> (31–105)
<i>Stellifer rastrifer</i> <sup>a</sup>	TL = 15.042305·OtL <sup>1.4217153</sup> (1.8–4.9)	BM = 7.2182324 × 10 <sup>-7</sup> ·TL <sup>3.597134</sup> (32–150)
<i>Anchoa marini</i> <sup>a</sup>	TL = –2.15 + 28.271·OtL (1.44–4)	BM = 0.0000027·TL <sup>3.146719</sup> (35–115)
<i>Cynoscion guatucupa</i> <sup>a</sup>	TL = 12.719507·OtL <sup>1.22121</sup> (1.3–11)	BM = 0.0000028·TL <sup>3.2433257</sup> (21–252)
<i>Engraulis anchoita</i> <sup>a</sup>	TL = 35.355345·OtL <sup>1.0309666</sup> (1.8–4.8)	BM = 0.0000076·TL <sup>2.9566755</sup> (62–180)
<i>Paralonchurus brasiliensis</i> <sup>a</sup>	TL = 15.631357·OtL <sup>1.192579</sup> (2.2–9.5)	BM = 8.8310686 × 10 <sup>-7</sup> ·TL <sup>3.597134</sup> (32–227)
<i>Odontheistes argentinensis</i> <sup>b</sup>	TL = 39.71408·OtL <sup>1.1932243</sup> (0.4–7)	BM = 0.0000079·TL <sup>2.9644835</sup> (23–421)
<i>Pomatomus saltatrix</i> <sup>b</sup>	TL = 17.959854·OtL <sup>1.255077</sup> (2.9–15.7)	BM = 0.000015·TL <sup>2.9232217</sup> (72–594)

Range of OtL and TL used for calculations are given below equation. Values are given as mean

TL total length (in mm), BM body mass (in g), OtL Otolith length (in mm)

Sources: <sup>a</sup>Naves (1999); <sup>b</sup>M. Haimovici (Laboratório de Recursos Pesqueiros Demersais e Cefalópodes, FURG, unpublished data)

The Kruskal–Wallis test was used to test monthly variation in TL of the White croaker (*Micropogonias furnieri*) in the diet of Neotropic cormorant (Zar 1999). Monthly variation in the proportion of the main food items was tested by  $\chi^2$  test (Zar 1999). Data were analysed through Statistica for Windows v. 5 and BioEstat software (StatSoft, Inc 1995; Ayres and Ayres 1998).

Individual daily food consumption ( $C_d$ ) of the Neotropic cormorant was estimated by the equation for Field Metabolic Rate (FMR) from Ellis and Gabrielsen (2002), obtained from 45 studies on 37 seabird species from different latitudes:

$$\text{FMR} = 16.69 \cdot m^{0.651} \quad (4)$$

where 'm' is the birds' body mass in grams, in this study assumed to be 1,568 g, corresponding to the mean body mass of 47 Neotropic cormorants from Guaíba Lake, in the northern portion of Lagoa dos Patos, southern Brazil (C. Monteiro, unpublished data; Monteiro et al. 2006).

A caloric content of fish of 5.9 kJ g<sup>-1</sup> was used, corresponding to the content of teleost fish (clupeiform and non-clupeiform) in Wiens and Scott (1975). Clupeiform and non-clupeiform fish have different caloric contents, but both groups were found in the Neotropic cormorants' diet. Assimilation efficiency was assumed to be 80% based on measurements of captive Double-crested cormorants (Dunn 1975; Brugger 1993).

Average monthly consumption ( $C_m$ ) of the population in Lagoa dos Patos estuary was estimated as follows:

$$C_m = C_d \cdot t \cdot n \quad (5)$$

where  $C_d$  = individual daily food consumption (in g);  $t$  = length of a given month, i.e. 28, 30, or 31 days;  $n$  = mean number of individuals in the area during a given month.

The mean parameter 'n' was obtained monthly through weekly censuses performed from November 2001 to October 2002 at the same location used for pellet collecting. Censuses were carried out by direct counts according to Bibby et al. (1993), using 10 × 50 mm<sup>2</sup> binoculars and a 12–36 × 50 mm<sup>2</sup> telescope. The observer was located on the southern margin of the channel, approximately 800 m from the tower, and counted birds every 30 min from 15:00 h until dusk, defined here as the moment when there was not enough luminosity for counts. The Neotropic cormorants were present in high abundance from September to February (1,099–1,390 birds); and low abundance from April to July (117–557 birds). March and August were months with intermediate abundance (833–870 birds). Early censuses of the Neotropic cormorants were carried out on the south margin of Lagoa dos Patos estuary on 6, 8 and 9 November 2001, and no flock was found at dusk along the borders. Thus, the power tower at Pontal Sul is the main nocturnal

roosting site in the area and holds virtually the whole population in the lower estuarine area. No other species of seabird used the tower as a night roosting site, which is also free of terrestrial predators. Mean monthly consumption ( $C_m$ ) was estimated for the 12-month period based on censuses and annual consumption calculated as the sum of monthly consumptions.

## Results

A total of 5,584 preys were found in 289 pellets, of which 5,566 were fish and 18 crustaceans (Table 2). Mean number of ingested prey per pellet was  $19.32 \pm 26.35$ , varying between 1 and 173. We identified a total of 20 food types, belonging to 10 fish families and one crustacean family

(Table 2). Niche breadth calculated from the Neotropic cormorant diet was  $B_s = 0.056$ .

The reconstructed mass from 289 pellets resulted in 107680.68 g of food, with an average mass of  $372.28 \pm 379.83$  g per pellet ( $n = 289$ ), a minimum of 0.82 g and maximum of 3446.59 g. Fish constituted the bulk of the reconstructed mass (99.84%), and crustaceans only 0.16%. Fish were also the most important item by frequency of occurrence (98.96%, Table 2). Remains of 19 fish species were found in the pellets. The White croaker was the main prey species. Other important food items were Catfish (Ariidae), the Atlantic sabretooth anchovy (*Lycengraulis grossidens*), unidentified Characiidae, Kingcroaker (*Menticirrhus* sp.), Mulletts, unidentified fish and anchovies (Table 2). Anchovies had proportionally small otoliths, which were more severely affected by digestion. Similarly,

**Table 2** Composition of the diet of the Neotropic cormorant (*Phalacrocorax brasilianus*) in Lagoa dos Patos estuary, southern Brazil, in 2001–2002

Food items	FO	FO%	N	N%	M	M%	IRI
<b>Fish</b>							
<i>Micropogonias furnieri</i>	213.00	<b>73.70</b>	2303.00	<b>41.24</b>	52653.83	<b>48.90</b>	<b>6643.61</b>
Ariidae	126.00	<b>43.60</b>	575.00	<b>10.30</b>	13804.00	<b>12.82</b>	<b>1007.89</b>
<i>Lycengraulis grossidens</i>	24.00	<b>8.30</b>	260.00	4.66	2390.03	2.22	<b>57.10</b>
<i>Menticirrhus</i> sp.	17.00	<b>5.88</b>	93.00	1.67	2900.79	2.69	25.64
<i>Mugil</i> sp.	20.00	<b>6.92</b>	128.00	2.29	912.68	0.85	21.73
Characidae	19.00	<b>6.57</b>	70.00	1.25	1666.00	1.55	18.41
<i>Mugil platanus</i>	11.00	3.81	15.00	0.27	3394.96	3.15	13.02
<i>Jenynsia multidentata</i>	4.00	1.38	88.00	1.58	589.60	0.55	2.94
<i>Mugil curema</i>	3.00	1.04	10.00	0.18	739.30	0.69	0.90
<i>Trachinotus marginatus</i>	5.00	1.73	10.00	0.18	111.87	0.10	0.49
<i>Brevoortia pectinata</i>	5.00	1.73	7.00	0.13	33.59	0.03	0.27
<i>Stellifer rastrifer</i>	3.00	1.04	3.00	0.05	77.30	0.07	0.13
<i>Atherinella brasiliensis</i>	3.00	1.04	3.00	0.05	71.40	0.07	0.12
<i>Anchoa marinii</i>	3.00	1.04	6.00	0.11	2.93	<0.01	0.11
<i>Cynoscion guatucupa</i>	4.00	1.38	4.00	0.07	6.80	0.01	0.11
<i>Engraulis anchoita</i>	2.00	0.69	3.00	0.05	8.63	0.01	0.04
<i>Paralanchurus brasiliensis</i>	1.00	0.35	1.00	0.02	23.50	0.02	0.01
<i>Odontesthes argentinensis</i>	1.00	0.35	1.00	0.02	21.20	0.02	0.01
<i>Mugil gaimardianus</i>	1.00	0.35	1.00	0.02	7.13	0.01	0.01
<i>Pomatomus saltatrix</i>	1.00	0.35	1.00	0.02	83.20	0.08	0.03
Unidentified fish	142.00	<b>49.13</b>	755.00	<b>13.52</b>	17921.40	<b>16.64</b>	<b>1482.10</b>
Unidentified anchovies	53.00	<b>18.34</b>	1225.00	21.94	10045.00	<b>9.33</b>	<b>573.39</b>
Unidentified clupeiforms	3.00	1.04	3.00	0.05	23.88	0.02	0.08
Unidentified sciaenids	1.00	0.35	1.00	0.02	23.00	0.02	0.01
Fish total	286	<b>98.96</b>	5566	<b>99.68</b>	107512.02	<b>99.84</b>	<b>19744.60</b>
<b>Crustacean</b>							
<i>Farfantepenaeus paulensis</i>	17.00	5.88	18.00	0.32	168.66	0.16	2.82

Contribution is expressed as frequency of occurrence absolute (FO) and relative (FO%), contribution by number absolute (N) and relative (N%), contribution by mass absolute (M) and relative (M%) and Index of Relative Importance (IRI). Contributions over 5% and IRI over 50 are highlighted in bold. In FO% the total is over 100% because two or more different items frequently occur in the same pellet

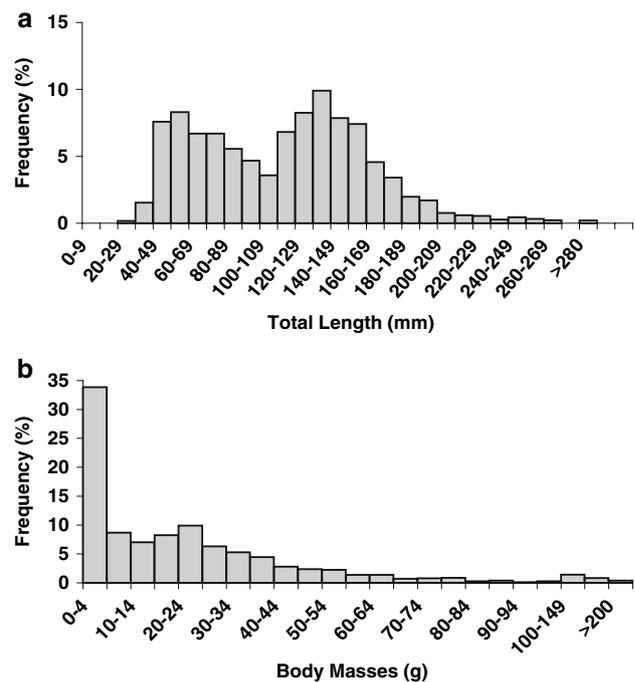
'unidentified fish' (13.5% by number) were fish whose otoliths were affected by digestion, precluding identification. The only crustacean found was the Pink shrimp, occurring in low number in February, March and September (Table 2).

The average TL of all fish was  $113.49 \pm 48.01$  mm which varied from 27.19 to 318.31 mm. Overall, 94.65% of fish had TL between 30 and 190 mm, and modal classes were 50–60 and 130–140 mm. The same modal classes were found for the White croaker, which had TL varying between 27.19 and 304.91 mm (Table 3; Figs. 2, 3).

Significant monthly variation of the TL was verified for White croaker (Kruskal–Wallis,  $H = 428.9$ ,  $df = 8$ ,  $P < 0.001$ ,  $n = 1,819$ ) (Fig. 3). White croakers ingested by Neotropical cormorants from July to September were smaller than in the other 6 months.

Mean BM of fish in the diet of the Neotropical cormorants was  $23.75 \pm 34.09$  g, with a minimum of 0.11 and a maximum of 356.43 g. Small fish less than 5 g dominated the diet (34.13%). White croaker and Atlantic sabretooth anchovy had a modal BM of between 0 and 5 g, with a frequency of occurrence of 33.86 and 62.17%, respectively. The modal BM of Kingcroaker was 15–20 g, with 24.13% of fish corresponding to this class (Table 3).

Despite 19 fish species occurring in the diet of the Neotropical cormorant reported here, only White croaker and



**Fig. 2** Size class frequencies of the total length (TL) and body mass (BM) of the White croaker (*Micropogonias furnieri*) ( $n = 1,819$ ), the main prey of Neotropical cormorant (*Phalacrocorax brasilianus*) from November 2001 to October 2002 (except April to June) in the estuary of Lagoa dos Patos, southern Brazil

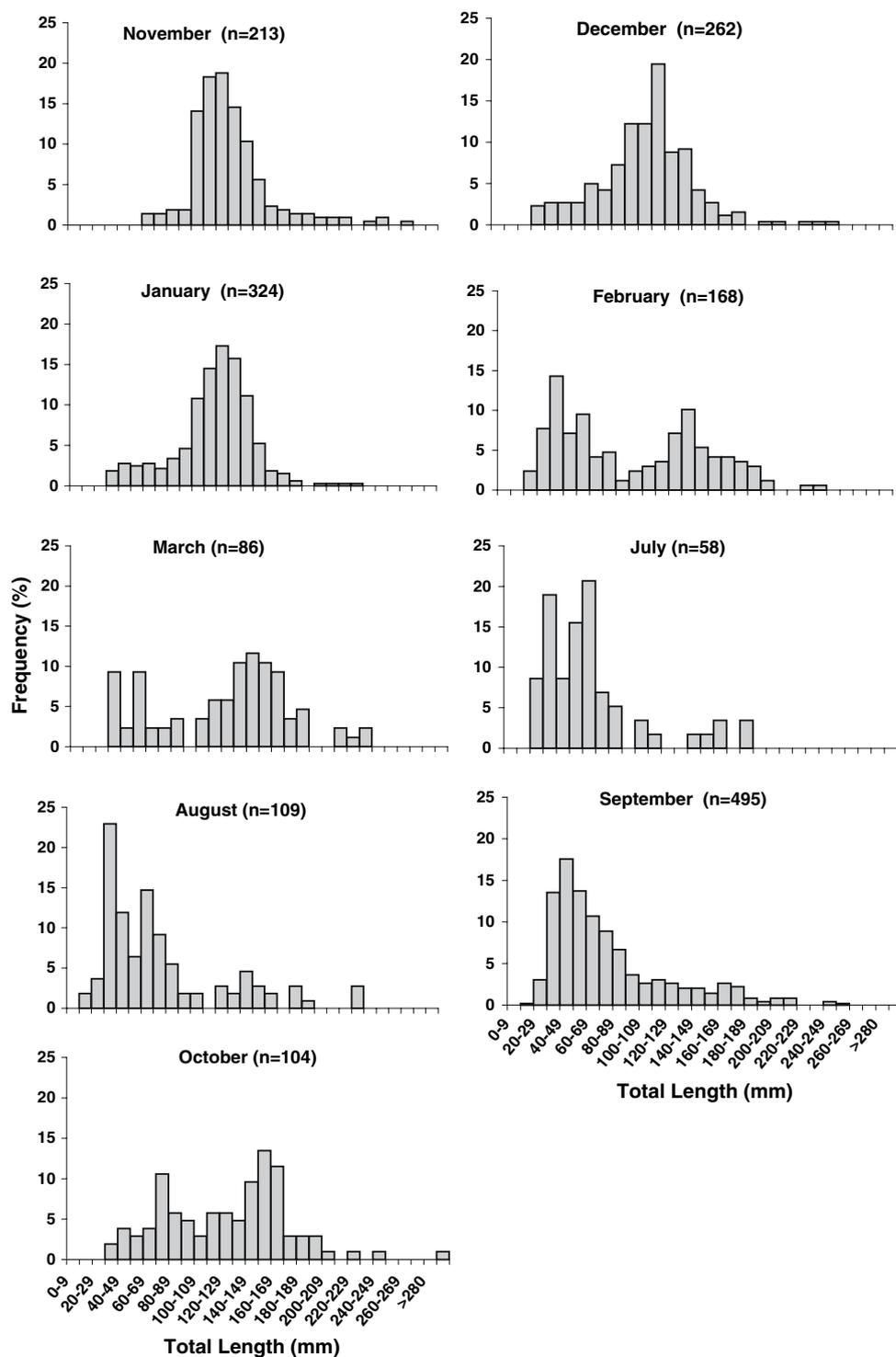
**Table 3** Total length and body mass of fish ingested by Neotropical cormorant (*Phalacrocorax brasilianus*) in Lagoa dos Patos estuary, southern Brazil in 2001–2002

Food items	Total length (mm)				Body mass (g)				n
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	
<i>Micropogonias furnieri</i>	113.45	47.25	27.19	304.91	22.86	30.42	0.11	356.43	1,819
<i>Lycengraulis grossidens</i>	102.12	35.85	50.60	184.35	9.16	10.77	46.04	0.46	51
<i>Menticirrhus</i> sp.	135.86	39.30	72.32	227.64	31.17	29.04	3.48	120.23	29
<i>Mugil</i> sp.	76.30	22.81	43.40	150.20	7.13	7.53	1.28	36.59	20
<i>Mugil platanus</i>	244.79	58.78	149.26	318.31	226.34	47.68	140.05	292.76	12
<i>Jenynsia multidentata</i>	77.14	6.22	72.74	81.54	6.69	1.90	5.34	8.04	2
<i>Mugil curema</i>	80.52	20.37	57.83	100.19	73.94	16.75	55.24	90.04	7
<i>Trachinotus marginatus</i>	103.70	11.91	89.00	115.50	11.17	3.18	7.44	14.39	5
<i>Brevoortia pectinata</i>	80.56	6.46	70.69	86.39	4.80	1.02	3.29	5.76	5
<i>Stellifer rastrifer</i>	100.87	79.49	44.66	157.07	25.76	35.55	0.62	50.90	2
<i>Anchoa marinii</i>	46.62	1.82	44.50	48.74	0.48	0.06	0.42	0.55	4
<i>Cynoscion guatucupa</i>	60.79	–	–	–	1.71	–	–	–	1
<i>Engraulis anchoita</i>	76.60	7.06	68.52	81.57	2.88	0.74	2.04	3.41	3
<i>Paralanchurus brasiliensis</i>	140.37	–	–	–	23.53	–	–	–	1
<i>Odontheistes argentinensis</i>	147.32	–	–	–	21.15	–	–	–	1
<i>Pomatomus saltatrix</i>	202.83	–	–	–	83.24	–	–	–	1
Total	113.49	48.01	27.19	318.31	23.75	34.09	0.11	356.43	1,963

For species with one or two specimens all values are given

– Insufficient data to calculate, *SD* standard deviation, *n* number of prey

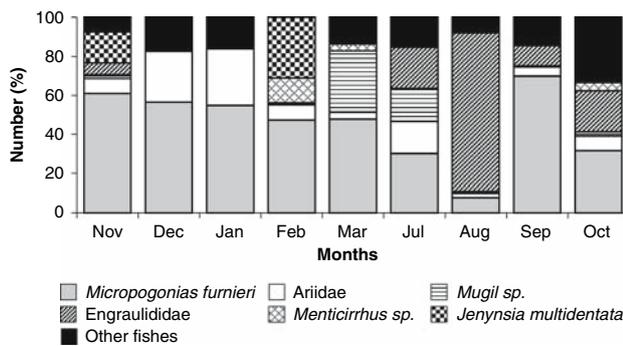
**Fig. 3** Monthly variations in total length (TL) of the White croaker (*Micropogonias furnieri*) ingested by Neotropic cormorant (*Phalacrocorax brasilianus*) from November 2001 to October 2002 (except April to June) in the estuary of Lagoa dos Patos, southern Brazil



Catfish were recorded during all sampling months. White croaker was the main food item in most months except August and October. In August, anchovies were the main food items; and in October, several species were dominant (Fig. 4). Significant monthly variation in the diet composition, by number, was verified in the diet ( $\chi^2 = 5738.01$ ,  $df = 48$ ,  $P < 0.001$ ,  $n = 5,558$ ). Large differences between

expected and observed values for White croaker and anchovies present in August and September determined this statistical result.

The FMR estimated for the Neotropic cormorant was  $2007.37 \text{ kJ day}^{-1}$ , and daily consumption ( $C_d$ ) was estimated at  $425.29 \text{ g}$ , or  $27.12\%$  of their body mass. Monthly food consumption of the population was estimated to



**Fig. 4** Monthly variations by relative number of the main food items in Neotropical cormorant (*Phalacrocorax brasilianus*) diet from November 2001 to October 2002 (except April to June) in the estuary of Lagoa dos Patos, southern Brazil

average 11.08 tonnes, with a peak of 18.33 tonnes in January. Annual consumption was estimated at 132 tonnes. Otoliths and other prey remains recovered in pellets resulted in a reconstructed meal of  $372.28 \pm 379.23$  g (23.74% of the Neotropical cormorant body mass) and, assuming that each bird produces one pellet per day, the annual food consumption estimated by this method was 119 tonnes, 10.36% lower when comparing with the energetic estimation.

## Discussion

### Diet composition

Fish were the main food items preyed by Neotropical cormorants, similar to other *Phalacrocorax* species (Trayler et al. 1989; Harris and Wanless 1993; Ross and Johnson 1995; Suter and Morel 1996; Casaux et al. 1997; Jahncke and Goya 1997; Casaux et al. 1998). Neotropical cormorants in USA and Chile also feed extensively on fish (Morrison et al. 1977; Kalmbach et al. 2001). The immature Neotropical cormorant's diet in USA was 98.3% by number and 97.8% by mass composed of fish (Morrison et al. 1977). Similarly, only six fish species comprised 79% of the diet by number and 78% by mass in an estuary in Texas (King 1989). In both studies *Penaeus* shrimps were the only invertebrate found. Mollusc shells and crustaceans found in the diet of other cormorant species were treated as secondary consumption by other authors (Barrett et al. 1990; Johnson et al. 1997). The occurrence of these items and fragments of insects in the Neotropical cormorant's diet could be explained by the diet of their main prey (White croaker and Catfish) because crustaceans, gastropods and insects are important prey of these fishes (Araújo 1984; Figueiredo and Vieira 1998). Invertebrates also compose a small proportion of the Neotropical cormorant diet in other

areas (reviewed by Telfair and Morrison 1995; Kalmbach et al. 2001).

Neotropical cormorant is a generalist species throughout their distribution area, using a wide range of habitats and food items (Telfair and Morrison 1995), and could also be considered as a generalist species in the present study in terms of prey use because 20 food items were found in the diet, but few food items were used in high frequency, which accounted for the low niche breadth value of  $B_s = 0.056$ . Niche value alone is not informative, because hiding monthly differences and not taking into account the diet in other places. Blaber and Wassenberg (1989) in Australia found Levin's niche breadth of  $B_s = 0.27$  (54 food items) and  $B_s = 0.26$  (27 food items) for Pied (*Phalacrocorax varius*) and Little pied (*P. melanoleucos*) cormorants, respectively, which was explained by cormorants feeding on discharges from the unselective trawling fishery. Jahncke and Goya (1997) found niche breadth of  $B_s = 0.061$  (53 food items) for Guanay cormorant in Peru, similar to the low value found in this study. Despite the large differences in the number of food items in both studies (53 vs. 20), one and two items composed the bulk of Guanay and Neotropical cormorant diet, respectively. The Neotropical cormorant in Lagoa dos Patos preyed upon a few abundant species during all months, but switched their diet composition and relative prey abundance on a monthly basis, probably reflecting their availability in the lagoon where only ten species comprising 94% of catches in trawling sampling (Vieira 2006). As generalist predators, the diet of cormorants and shags in general and the Neotropical cormorant in particular appear to reflect the higher composition of prey available in the environment (Jahncke and Goya 1997; Watanuki et al. 2004). This is particularly evident in Neotropical cormorant in Texas whose diet was composed of abundant fish available (Telfair et al. 1982; Telfair and Morrison 1995; and in the present study Vieira 2006).

Generalist species are often both widely distributed and abundant. They also are often plastic in their ecology, both spatially and temporally, in response to variation in resources (Gregory and Isaac 2004). On the other hand, individual specialization is a widespread phenomenon in animals and particularly well documented in seabirds. Black-browed albatrosses (*Thalassarche melanophris*) exhibited a striking degree of site fidelity, returning to the same region, as well as remarkable consistency in the chronology of their movements, in consecutive years (Phillips et al. 2005). In Crozet shags (*Phalacrocorax melanogenis*), Cook et al. (2006) found consistency in individual daily activity patterns and diving profiles over time. Individuals displayed fidelity to the time of first daily trip to sea and also a strong fidelity to depth ranges day after day, suggesting foraging area fidelity, a behaviour that could help increase foraging efficiency, thanks to the

memorization of the bottom's topography and the habits of its fauna. But we also suggest that a generalist (species level) could behave as a specialist in a particular place or period (local population).

Among fish found in the Neotropic cormorant diet in the present study, the White croaker and Catfish were the most abundant species in deep waters and the channel sampled by shrimp trawling by Vieira (2006), with the former probably being the species with larger biomass (Vieira et al. 1998). On the other hand, shallow water communities of 1.5 m in depth were dominated by the Brazilian silverside (*Atherinella brasiliensis*), and the Mullet (*Mugil platanus*) (Garcia et al. 2001), corroborating previous information of birds feeding predominantly in deep waters inside the estuary. The main food items taken are benthic fishes in spite of mesopelagic ones (anchovies) present for several months and dominating in August, suggesting a flexible feeding strategy of the Neotropic cormorant (Quintana et al. 2004), a characteristic of other cormorants (e.g. Watanuki et al. 2004). Unfortunately, detailed data on monthly abundance of potential prey species in Lagoa dos Patos are not available, limiting comparisons. Feeding plasticity appears to be an important factor determining the year-round abundance of Neotropic cormorant in Lagoa dos Patos, making it the dominant piscivorous bird in biomass at the estuary (authors' personal observation), and a behavioural characteristic which makes it less vulnerable to changes in fish community structure.

#### Fish size

Neotropic cormorants in Lagoa dos Patos prey on fish of similar sizes (50–100 mm) to fish preyed in the Paraná River (Beltzer 1983), and in the USA, where about 90% were <80 mm (Telfair and Morrison 1995). In Lagoa dos Patos, abundant deep-water fish had TL below 100 mm (Vieira 2006). Neotropic cormorants appear to choose their prey according to abundance as well as the trade-off in capturing several small or a fewer large prey. Therefore, 300 mm in TL suggests a limit of fish that could be swallowed by the species. Figueiredo and Vieira (1998) classified White croakers as juveniles (30–90 mm), subadults (90–210 mm) and adults (>210 mm). Size classes of White croakers preyed by Neotropic cormorants were juveniles and subadults with total length varying along the studied months. This can be explained by the White croaker being multiple-spawner with a long spawning period (November to July), generating several new cohorts during the spawning season (Castello 1986). Despite several cohorts simultaneously present in the area, the abundance of different cohorts is expected to vary in the environment, and in the diet of the generalist Neotropic cormorant.

Juvenile and subadults of White croaker, Banded croaker (*Paralonchurus brasiliensis*), King weakfish (*Macrodon ancylodon*) and Kingcroaker (*Menticirrhus americanus*) are abundant in Lagoa dos Patos estuary (Vieira et al. 1998; Vieira 2006). Adults of White croaker and Catfish are also found in the area (Vieira et al. 1998), but their large size (up to 736 mm; Haimovici and Velasco 2000) precludes predation by cormorants. These fishes and other species such as the Atlantic sabretooth anchovy, Catfish and Marini's anchovy (*Anchoa marinii*) are abundant year-round in the channel and the adjacent areas (Vieira et al. 1998). White croaker and Catfish were the only species that occurred in all months in the Neotropic cormorant diet, with the former being dominant in most months. Unidentified Engraulididae fish (anchovies) were numerically important in August with high IRI in comparison with other food items. Juvenile Atlantic anchovies (*Engraulis anchoita*) are found in the estuary only in autumn (April to June) and winter (July to September) (Vieira et al. 1998), coinciding with the occurrence of a high number in the Neotropic cormorant diet. On the other hand, Marini's anchovy and Atlantic sabretooth anchovy are species occurring year-round in the estuary (Vieira et al. 1998) and could also be present in high number in August. Overall, Neotropic cormorants' diet relies on abundant demersal Sciaenids and Catfish in the area throughout the year, but they can switch to pelagic anchovies when they are abundant during winter, which is a plastic behavior identified in other cormorant species (Watanuki et al. 2004).

#### Food consumption and fisheries

Daily food consumption for the Cape cormorant (*Phalacrocorax capensis*), the European shag (*P. aristotelis*), the Double-crested cormorant and the Imperial shag (*P. atriceps*) were estimated to be 18, 17, 20 and 31% of their body mass, respectively (Furness and Cooper 1982; Johnstone et al. 1990; Brugger 1993; Casaux et al. 1995). Individual daily food ingestion of Neotropic cormorants estimated here by pellets was 372.28 g or 23.74% of their body mass, and according to the metabolic equations was 425.29 g of food, or 27.12% of the body mass. Values found by both methods fell within the range expected for cormorants and estimated in studies using different techniques, considering the several assumptions and limitations of both methods. Using pellets to study the daily consumption of prey could be biased (Barrett et al. 1990) if birds egest pellets more than once each day (Johnstone et al. 1990; Bugoni et al. 2005), or the number and size of fish could be underestimated due to partial or total otolith digestion or otoliths passing through the digestive tract (Jobling and Breiby 1986; Barrett et al. 1990; Casaux et al.

1998). However, pellets are widely used in cormorant and other seabirds' diet studies because it is a non-lethal method causing minimal disturbance, and large numbers of pellets can be collected, making spatial and temporal comparisons possible (Duffy and Jackson 1986; Zijlstra and van Eerden 1995; Casaux et al. 1998). Metabolic approaches also have limitations. For instance, Boyd (2002) had shown that uncertainty in the measurements of metabolic rates led to bias in the quantity of food consumed by Macaroni penguins (*Eudyptes chrysolophus*) and Antarctic fur seals (*Arctocephalus gazella*). However, in spite of limitations of both methods, estimating food consumption is central to define the ecological role of top predators (Boyd 2002), and could be done adequately by using complementary approaches, as carried out in the present study. Taking into account the daily food ingestion and mean body size of fish prey, an estimated 16 to 18 fish are eaten per day per cormorant. When birds prey upon fish of small size it is reasonable to suppose that they increase the number of preyed items, in order to supply the minimum energetic requirement, an issue that should be more specifically addressed in the future. Although values change according to month, following variations in fish body size and cormorant energetic requirements (Grémillet et al. 1995), it gives a rough estimation of the role of Neotropic cormorants as fish predator.

The artisanal fishery in Rio Grande do Sul State, southern Brazil, targets teleosts predominantly inside Lagoa dos Patos estuary and the adjacent oceanic coast. In the estuary, White croaker is the single most important species caught by this fishery followed by Catfish (Reis et al. 1994), the most important species consumed by Neotropic cormorants. Landings of White croaker and Catfish from these estuarine fisheries in 2004 were 1,930 and 74 tonnes, respectively (IBAMA/CEPERG 2005). On the other hand, estimated annual consumption of fish by Neotropic cormorants based on pellet reconstruction and energetic was 119 and 132 tonnes, respectively, of which 61.65% by mass were White croaker and Catfish. Thus, taking into account the monthly variations in abundance (116–1,390 birds), an estimated 73.4 to 81.9 tonnes of White croaker and Catfish were consumed per year by Neotropic cormorants, representing 3.7–4.1% of the annual landings of White croaker and Catfish by artisanal fishery. The minimum size of White croaker and Catfish that could be landed by fishermen is 350 and 400 mm, respectively (Regulation IBAMA No. 171/98), while the cormorants' diet is composed of juvenile and subadult White croakers. Fisheries and cormorants target fish of different sizes. Barrett et al. (1990) suggest that predation of European shags and Great cormorants (*P. carbo*), upon small Cod (*Gadus morhua*) and Saithe (*Pollachius virens*) in Norway could affect the recruitment of young fish in these two

important commercial fisheries, limiting the build up of the stocks during years of low stock size. Capture rates of fish by the artisanal fishery in Lagoa dos Patos estuary have been decreasing since 1980 (Reis et al. 1994), and are primarily attributed to overexploitation of stocks from fishing pressure. These include some illegal techniques, such as pair bottom trawl and bottom trawl for shrimp that kill undersized fish (Reis and Castello 1996). Fish stocks management for the area need to consider the potential impact of avian predators, of which the Neotropic Cormorant seems to be the most important.

The composition of the Neotropic cormorant diet was essentially piscivorous, but varied by number, mass and frequency of occurrence of species, as well as fish size over 9 months. The generalist Neotropic cormorant fed mainly upon the two most abundant demersal fishes. Temporal changes in cormorant diet may reveal its ecological plasticity to a changing environment. From our study it is obvious that this estuarine population when migrating to breed in inland freshwater areas shift food items. In the study area we have shown that they change diet composition and prey size monthly, even changing from bottom (Sciaenids/Catfish) to pelagic (Clupeids) species. Thus, Neotropic cormorants could be characterized as a generalist (and/or plastic) in which a group of individuals in a particular place (Lagoa dos Patos) behave as a specialist in given months, but change their diet temporally adjusting to changes in the prey availability. The direct or indirect impacts of Neotropic cormorants on fish stocks should be taken into consideration in future studies for both fishery management and cormorant conservation.

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