Ibis (2004), **146**, 438–453

Feeding ecology of the Common Tern *Sterna hirundo* in a wintering area in southern Brazil

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The wintering diet of Common Terns *Sterna hirundo* was studied by using 714 pellets collected on roosting sites at the mouth of the Lagoa dos Patos and on adjacent coastal beaches, in Rio Grande do Sul, southern Brazil, from March 1999 to February 2000. A total of 12 340 individual prey items of 35 different food types was found. Fish was the most important food type in the diet, constituting 32% by number and 93% by mass. Insects contributed 67% by number but only 3% by mass. The main food types were sciaenid fishes *Paralonchurus brasiliensis*, *Micropogonias furnieri*, *Cynoscion guatucupa* and *Macrodon ancylodon*. Several of these are important commercial species; fisheries potentially impact food availability to the terns, and terns may contribute significantly to the natural mortality of these fishes. Clupeiform fishes, the urophycid fish *Urophycis brasiliensis* and flying ants (*Camponotus* sp.) were also important. Species composition of the diet (food types), both by number and by mass, differed significantly between months. Prey sizes ranged in length from 12.7 mm to 217.4 mm. The average estimated total length of fish taken was 77.7 mm, but the mean differed significantly among prey species. The importance of demersal sciaenids to the diet of the Common Tern, a surface predator, may be explained by their association with aquatic predators, especially adult Bluefish *Pomatomus saltatrix* and Striped Weakfish *Cynoscion guatucupa*, and the Franciscana Dolphin *Pontoporia blainvillei*, which drive these fish to the surface. The occurrence of flying ants in the diet was related to offshore winds, which carried these insects out to sea. The occasional high availability of insects possibly changed the cost/benefit relationship of several food types, causing diet changes. The high number of prey species, the temporal variations in the composition of the diet and the wide range of prey sizes are evidence of the high dietary plasticity of the Common Tern, at wintering areas in southern Brazil.

Among seabirds, terns are particularly sensitive to food scarcity because their energy reserves are small, the time needed for foraging is long (especially during the chick-rearing period), their foraging methods are energetically expensive and their foraging range is limited (Frank & Becker 1992). Pearson (1968) studied three tern species in Britain and asserted that these species were close to the limits of their physical ability to acquire food, spending between 40 and 94% of daylight time, during the chick-feeding period, in foraging activities. Thus, the availability of food close to breeding sites is of key importance to the reproductive success of terns (Courtney & Blokpoel 1980). Food availability near roosting sites is essential during other times of the annual cycle of terns and other seabirds, such as the premigratory fattening period and the wintering period (Wooller *et al*. 1992). However, studies on the diets of seabirds are generally carried out at breeding colonies when the birds return to feed their chicks (Shealer 1998). An example of this is the Common Tern *Sterna hirundo*, a cosmopolitan species, which breeds in the Northern Hemisphere and winters in the Southern Hemisphere (Burger & Gochfeld 1991). The feeding ecology of this species has been studied in breeding colonies in Europe and North America (e.g. Erwin 1977, Cramp 1985, Frank 1992, Granadeiro

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et al. 2002). The Common Tern has a high degree of foraging plasticity. This is indicated by its high prey diversity, and by its use of a variety of feeding methods, which include picking up food from the ground, feeding on fishery discards at sea, kleptoparasitism and, most commonly, surface feeding on the water (Kirkham & Nisbet 1987, Blokpoel *et al*. 1989, Oro & Ruiz 1997, Walter & Becker 1997, Nisbet 2002). The species forages in freshwater habitats, in estuaries and at sea at varying distances from the shore (Becker *et al*. 1997). The use of several feeding strategies is a response to the uncertainty of locating food in a varying environment (Erwin 1977).

Juvenile Common Terns use wintering grounds in northern Brazil, Trinidad, Guyana and Suriname (Blokpoel *et al*. 1982, 1984, Hays *et al*. 1999). Adults winter in southern Brazil and Argentina in large flocks, and these locations are the most important wintering grounds for adult Common Terns in South America (Hays *et al*. 1997, Bugoni 2001, Sapoznikow *et al*. 2002). Studies of feeding ecology in the wintering areas are needed to assess the interactions between this piscivorous bird and the local fisheries, and to identify the food base that must be maintained in the wintering areas for the conservation of the species.

A large part of the food of raptors (owls, falcons and hawks), shorebirds (sandpipers) and seabirds (cormorants, gulls and terns) consists of indigestible non-nutritive material such as hair, bones, claws, teeth, mollusc shells, carapaces of crustaceans, eye lenses, scales and otoliths of fishes, and beaks of squids. The undigested components of the meal are compacted into pellets in the proventriculus or the gizzard. They are then covered with a layer of mucus secreted by the proventriculus, and are egested. The production of pellets and their regular egestion from the proventriculus directly through the mouth is thought to be a shortcut method aimed at obviating the passage of such material through the intestine (Duke *et al*. 1976). Food remains in the pellet can be identified as to prey species and can be counted and measured to provide estimates of the number and size of the ingested prey items. Pellets are therefore much used as a source of data on the food and feeding of seabirds, although the method has been criticized (Jobling & Breiby 1986, Suter & Morel 1996). Disadvantages of the method are: under-representation of very small prey and of prey without hard diagnostic parts; under-estimation of prey sizes owing to erosion of otoliths, cephalopod beaks and bones; and uncertainty regarding the number of pellets produced each day by the individual bird (Jobling & Breiby 1986, Johnstone *et al*. 1990, Brugger 1993, González-Solís *et al*. 1997). Advantages are that large samples of pellets are easily collected, and that this collecting has little or no negative effect on the birds (Duffy & Laurenson 1983, Duffy & Jackson 1986, Zijlstra & van Eerden 1995). Pellets are particularly useful for the study of differences in feeding between geographical areas, between seasons of the year and between individuals, especially when the birds feed on fishes with large otoliths, which are little affected by digestion (Duffy & Jackson 1986, Furness & Monaghan 1987); more reliable results are obtained when birds feed on fish with large and rigid otoliths, which are less vulnerable to digestion (Suter & Morel 1996, Jahncke & Rivas 1998).

The diet of Common Terns wintering in Brazil was studied for the first time in 1999 and 2000 by pellet analysis. The results of this study are reported in the present paper.

METHODS

The pellets were collected at roosting places on beaches and mudflats at the mouth of the Lagoa dos Patos (32°08′S, 52°05′W) and on the nearby 100-km ocean beach, part of a barrier beach stretching about 220 km south and 400 km to the north of the inlet (Fig. 1). The lagoon mouth is about 500 m wide, and on each side a pier, about 4 km long, extends into the ocean. The roosting sites in the lagoon mouth were situated on the seaward beach of a sand spit 2 km long, running into the lagoon mouth from the shoreward end of the northern pier. This locality is known as the Pontal Sul and Common Tern flocks consisting of several hundred or thousand individuals (up to 10 000) are found from October to March (Bugoni 2001). In southern Brazil wintering Common Terns average 4.8 years of age, the youngest being 1.4 years old (Hays *et al*. 1997). So, results presented here reflect the diet of adult and subadult birds.

From March 1999 to February 2000, a total of 714 pellets was collected, 563 at the Pontal Sul and 151 on the ocean beach. We collected fresh pellets, most still with a layer of mucus; pellets tended to disintegrate within a few hours, depending on wind conditions and moisture when on mudflats. Common Terns roosted mostly in mixed-species flocks, which included one or more of the following: Kelp Gull *Larus dominicanus*, Brown-hooded Gull *L. maculipennis*, Trudeau's Tern *Sterna trudeaui*, South American

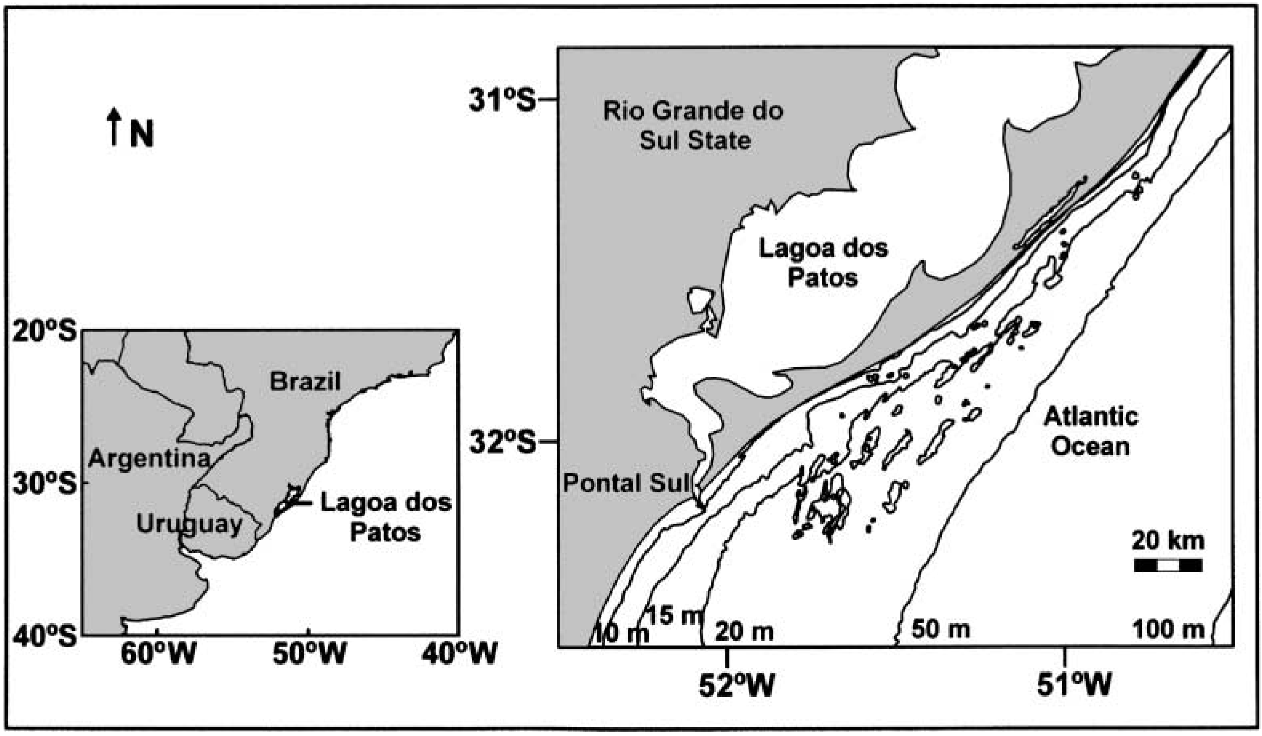

Figure 1. Study area in southern Brazil where pellets of Common Terns were collected in 1999 and 2000.

Tern *S. hirundinacea*, Royal Tern *S. maxima*, Cayenne Tern *S. eurygnatha* and Amazon Tern *S. superciliaris*. The longest and shortest diameters of each pellet were measured with callipers, and the pellet was placed in a paper envelope. The typical size, shape and texture of Common Tern pellets were determined from material obtained from monospecific flocks. With the use of the criteria thus established (see Results section), Common Tern pellets were distinguished from the larger and/or differently shaped pellets of the gulls. Pellets of the other tern species mentioned above are similar in appearance to those of Common Terns. Therefore, in multispecies flocks of terns, pellets were collected in flocks with more than 800 Common Terns and fewer than 10 terns of other species, and away from the marginal zone of the roosting area where, in such flocks, the other tern species tended to position themselves.

In the laboratory the pellets were dried in an oven at 60 °C for 1 h and then weighed, and stored individually in plastic bags with naphthalene as an insect repellent. The pellets were analysed under a dissecting microscope. In each pellet the prey remains were identified to the lowest taxon possible. A prey taxon present in the pellet is termed a 'food type', and for each food type an individual animal represented in the pellet is termed a 'prey'. Fish were identified using otoliths, scales, opercular bones and the hypural bone according to criteria in Corrêa and Vianna (1992), Naves (1999) and by comparison with a reference collection of otoliths. The number of fish prey was determined from the maximum number of either hypural bones or the number of pairs of otoliths, opercular bones and eye lenses.

Cephalopod beaks were identified according to Santos and Haimovici (1998) and Santos (1999) and the number of cephalopod prey was determined from the maximum number of either upper or lower beaks of each species in the same pellet. Crustacean remains occurred as the rostra of shrimps and claws of crabs and were identified through comparison with a reference collection. The minimum number of crustacean prey was determined by counting shrimp rostra and pairing the claws of crabs. Insects occurred as chitinous body parts and were identified by reference to Roth (1970) and Carrera (1989). The number of insect prey was determined by pairing mouth parts, eyes and, in the case of beetles, also elytra.

Prey remains were measured with the ocular micrometer of the microscope. In fishes, measurements were made of the sagitta otolith. For each otolith the length, width and the index of digestion (ID) were recorded, the latter accorded a four-point scale as follows: ID (0), no sign of wear or digestion; ID (1), otolith edges slightly worn but sulcus acusticus still well defined; ID (2), otolith edges very worn, sulcus acusticus becoming vague; ID (3), sulcus acusticus worn away. For details on anatomy and terminology of fish otoliths see Kalish *et al*. (1995). For cephalopod beaks, the upper (URL) and lower (LRL) rostral length in *Loligo* squids and upper (UHL) and lower (LHL) hood length in the *Argonauta* octopus were measured. For details on anatomy and terminology of cephalopod beaks we follow Clarke (1986). The body length and mass of each fish and cephalopod prey were calculated by means of the equations listed in Table 1. The prey sizes thus obtained were within the size range of the sample from which these equations were derived. Only measurements of otoliths ID (0) and ID (1) were used for calculation of body size and body mass of the prey. When a pair of otoliths of a prey was present, the mean of the measurements of both otoliths was used. Otolith width was used when otolith length could not be measured because of breakage of the rostrum. For fish identified to species level but without measurable otoliths present, and for fish not identified to species level, the mean of the prey mass calculated for the other fish prey in the corresponding taxon was assigned as an estimate of its body mass. For crustacean prey the average body mass in summer of *Artemesia longinaris* (2.0 g), the most common marine shrimp in coastal waters of the study area (Haimovici & Mendonça 1996), was used. An estimated body mass of 0.07 g was assigned to ants and 0.2 g to other insects, these values being the mean fresh body mass of 14 honey

Table 1. Otolith-length and length/body mass relationships of juvenile fishes and cephalopods taken by the Common Tern *Sterna hirundo* in southern Brazil.

Species	Total length × Otolith length	Body mass × Total length	Total length × Otolith width
Fish			
Brevoortia pectinata[a]	TL = 5.6187 + 44.875OtL	$M = 0.0000224TL^{2.79379}$	–
Anchoa marinii[a]	TL = –2.15 + 28.271OtL	$M = 0.0000027TL^{3.146719}$	TL = –20.53 + 54.546OtW
Engraulis anchoita[a]	$TL = 35.355345OtL^{1.0309666}$	$M = 0.0000076TL^{2.9566755}$	$TL = 64.55592OtW^{1.236113}$
Lycengraulis grossidens[a]	$TL = 38.106486OtL^{1.080817}$	$M = 4.2407473(10^{-7})TL^{3.5467624}$	$TL = 55.756704OtW^{1.5481124}$
Urophycis brasiliensis[c]	TL = –22.65 + 24.254OtL	$M = 2(10^{-7})TL^{3.7386}$	TL = (72.294OtW) – 23.186
Porichthys porosissimus[c]	TL = –8.335 + 26.734OtL	$M = 6.1769(10^{-6})OtL^{3.0948}$	–
Jenysnsia lineata[a]	$TL = 38.658233OtL^{0.9465327}$	$M = 0.0000012TL^{3.571191}$	–
Atherinella brasiliensis[a]	$TL = 31.932036OtL^{1.1347503}$	$M = 3.8638877(10^{-7})TL^{3.605203}$	$TL = 54.4346OtW^{1.193502}$
Prionotus punctatus[a]	$TL = 24.812663OtL^{1.1901627}$	$M = 0.0000025TL^{3.2740894}$	–
Ctenosciaena gracilicirrhus[c]	TL = –0.543 + 20.37OtL	$M = 5.242(10^{-6})TL^{3.19}$	–
Cynoscion guatucupa[a]	$TL = 12.719507OtL^{1.22121}$	$M = 0.0000028TL^{3.2433257}$	–
Macrodon ancylodon[b,c]	TL = –6.412 + 18.451OtL	$M = 1.633(10–6)TL^{3.3014}$	TL = –14.52 + 45.226OtW
Menticirrhus sp.[a]	$TL = 16.842076OtL^{1.288075}$	$M = 0.0000063TL^{3.088628}$	–
Micropogonias furnieri[a]	$TL = 16.434024OtL^{1.158209}$	$M = 0.0000019TL^{3.3303687}$	–
Paralonchurus brasiliensis[a]	$TL = 15.631357OtL^{1.192579}$	$M = 8.8310686(10^{-7})TL^{3.458188}$	$TL = 22.707827OtW^{1.9636747}$
Stellifer rastrifer[a]	$TL = 15.042305OtL^{1.4217153}$	$M = 7.2182324(10^{-7})TL^{3.597134}$	–
Umbrina canosai[c]	TL = –68.42 + 33.49OtL	$M = 1.09(10^{-5})OtL^{3.044}$	–
Mugil sp.[a]	$TL = 23.33166e^{0.3448573OtL}$	$M = 0.000048TL^{2.702358}$	$TL = 18.34138e^{0.8412142OtW}$
Trichiurus lepturus[b,c]	TL = –171.424 + 176.718OtL	$M = 2.141(10^{-8})TL^{3.477}$	–
Peprilus paru[c]	TL = –1.173 + 19.384OtL	M = –1.794 + 0.08934TL	–
Symphurus jenynsi[c]	–	M = –13.82 + 0.1923TL	–
Cephalopods			
Loligo sanpaulensis[d]	$ML = 13.546e^{1.211URL}$	$M = 0.3408e^{2.766URL}$	–
	$ML = 13.173e^{1.109LRL}$	$M = 0.2768e^{2.659LRL}$	
Argonauta nodosa[e]	$CM = 4.9237UHL^{1.2933}$	$M = 0.0377UHL^{3.4949}$	–
	$CM = 9.5338LHL^{1.2314}$	$M = 0.2593LHL^{3.1856}$	

TL: total length; M: body mass; ML: mantle length; OtL: otolith length; OtW: otolith width; LRL: lower rostral length; URL: upper rostral length; LHL: lower hood length; UHL: upper hood length. Measurements are given in mm and body mass in g. – indicates lack of data. [a]Naves (1999); [b]Haimovici and Velasco (2000); [c]M. Haimovici (Laboratório de Recursos Pesqueiros Demersais e Cefalópodes, FURG, unpubl. data); [d]Santos and Haimovici (1998); [e]Santos (1999).

bees and 21 unidentified beetles, respectively, weighed for this purpose and of a body size similar to that of the insects found in the pellets.

Variables were determined as follows, for each food type:

1 FO, frequency of occurrence in the pellets, i.e. number of pellets with occurrence of the food type;
2 FO%, relative frequency of occurrence, i.e. FO as a percentage of the total number of pellets examined;
3 N, number of prey counted in the pooled sample of pellets;
4 N%, numerical proportion in the diet, i.e. N as a percentage of the total number of prey of all food types in the pooled sample;
5 M, total mass of all prey in the pooled sample;
6 M%, proportion by mass in the diet, i.e. M as a percentage of the total mass of all prey of all food types in the pooled sample;
7 IRI, index of relative importance.

IRI was calculated according to Pinkas *et al.* (1971), but modified as follows: IRI = (N% + M%)FO%. In the original expression, as used by Pinkas *et al.* (1971), volume of prey is used instead of mass. In the present case, as the volume of the prey could not be determined, mass was used. This is justified by the fact that the mass of ingested animal food is proportional to its volume (Diamond 1983). In addition, the use of mass instead of volume is a better measure of the contribution of the food type to the diet in terms of energy content.

The hypothesis that the body length of prey differed between food types was tested by a Kruskal–Wallis test (Zar 1999). The monthly variation of the relative proportion by number (N%) and mass (M%) of selected fish food types was tested by a *G*-test (Sokal & Rohlf 1987).

RESULTS

The pellets of Common Terns were oval in shape. Pellet lengths averaged 15.4 mm (range 8.9–32.0 mm, sd = ±3.5 mm). Pellet width averaged 10.4 mm (range 7.0–19.0 mm, sd = ±1.8 mm). The dry mass of the pellets averaged 0.3 g (range 0.06–1.0 g, sd = ±0.2 g), with 77% of the sample between 0.2 and 0.4 g (668 pellets weighed). Fresh pellets were coated with a thin layer of transparent mucus. The pellets were light grey when consisting of fish remains, and black or brown when consisting of insect remains. Fish remains occurred in about 90% of the pellets, mostly sagitta otoliths, vertebrae, opercular bones, hypural bones and teeth or tooth plates. Undigested fish tails complete with fin, scales and flesh occurred frequently, about once in every seven pellets; there was usually one tail in a pellet (Table 2).

Table 2. Frequency of occurrence (FO%) of the main fragments of prey and other items found in 714 pellets of Common Tern in southern Brazil.

Prey fragments and other items	FO%
Fish	
Sagitta otolith	89.4
Asteriscus otolith	21.3
Lapillus otolith	17.9
Eye lens	21.2
Hypural bone	70.9
Scale	81.8
Vertebra	91.2
Teeth	58.7
Opercular bone	19.2
Undigested fish tail	15.1
Other	
Feather	95.7
Cephalopod beak	6.3
Anthropogenic debris	0.6
Mollusc shell	0.7
Wood fragment	0.3

Tern feathers were the most common item, occurring in 96% of the pellets. Feathers occurred as thin and flexible barbules, white in colour and about 1 cm in length, but this varied, or several barbules adhering to a thin piece of white feather shaft. From the size and texture of these items, they were identified as fragments of downy feathers. The numbers of such fragments ranged from 10 to 100 per pellet, but contributed negligibly to the volume of the pellet. Occasional items included squid beaks, anthropogenic debris (plastics, nylon fibre), mollusc shell fragments and wood fragments. Mollusc shell remains, feathers, anthropogenic debris and wood fragments were excluded as food types in the analysis of the pellets.

In the 714 pellets, 12 340 prey were found, of which 4003 were fishes, 8251 insects, 69 cephalopods and 17 crustaceans. Of the total of 41 food types, 27 were fishes, two cephalopods, six insects and six crustaceans (Table 3). Of the total prey, 3752 were identified to species level and 8588, or 70% of the total, to the level of genus or some higher taxon. This high proportion of unidentified prey is almost entirely due to the 8251 insect prey, of which none was identified to species, but 7963 to the genus level. Of the fish prey, 92% were identified to species level (Table 4). Most clupeiform fish were only identified to family (Engraulididae) or class, owing to the difficulty of identifying the small, fragile and highly

Table 3. Composition of diet and Index of Relative Importance (IRI) of the Common Tern in southern Brazil.

	Frequency of occurrence		Number		Mass		
Food types	FO	FO%	N	N%	M	M%	IRI
Fish							
Brevoortia pectinata	4	0.56	5	0.04	6.64	0.03	0.04
Anchoa marinii	5	0.70	7	0.06	6.64	0.03	0.07
Engraulis anchoita	12	1.68	18	0.15	44.28	0.22	0.63
Lycengraulis grossidens	13	1.82	14	0.11	92.99	0.47	1.06
Unidentified Engraulididae	40	**5.60**	108	0.88	408.81	2.07	16.50
Unidentified Clupeiformes	54	**7.56**	81	0.66	251.48	1.27	14.60
Unidentified Ariidae	10	1.40	19	0.15	90.44	0.46	0.85
Urophycis brasiliensis	70	**9.80**	87	0.71	945.37	4.78	**53.78**
Porichthys porosissimus	16	2.24	19	0.15	117.34	0.59	1.66
Jenynsia lineata	2	0.28	4	0.03	2.21	0.01	0.01
Atherinella brasiliensis	11	1.54	20	0.16	8.86	0.04	0.32
Prionotus punctatus	1	0.14	1	0.01	0.57	< 0.01	< 0.01
Ctenosciaena gracilicirrhus	2	0.28	2	0.02	8.86	0.04	0.02
Cynoscion guatucupa	126	**17.65**	227	1.84	830.24	4.20	**106.54**
Macrodon ancylodon	111	**15.55**	171	1.39	813.96	4.11	**85.58**
Menticirrhus sp.	5	0.70	9	0.07	79.70	0.40	0.33
Micropogonias furnieri	193	**27.03**	534	4.33	3183.69	**16.09**	**551.96**
Paralonchurus brasiliensis	467	**65.41**	2498	**20.24**	11169.48	**56.45**	**5016.29**
Pogonias cromis	16	2.24	34	0.28	158.78	0.80	2.42
Stellifer rastrifer	10	1.40	10	0.08	53.14	0.27	0.49
Umbrina canosai	10	1.40	17	0.14	48.71	0.25	0.54
Unidentified Sciaenidae	46	**6.44**	58	0.47	270.86	1.37	11.84
Mugil sp.	3	0.42	5	0.04	2.21	0.01	0.02
Trichiurus lepturus	2	0.28	2	0.02	5.72	0.03	0.01
Peprilus paru	2	0.28	2	0.02	4.43	0.02	0.01
Symphurus jenynsi	4	0.56	4	0.03	26.57	0.13	0.09
Unidentified fishes	35	4.91	47	0.38	223.72	1.13	7.42
Cephalopods							
Loligo sanpaulensis	44	**6.16**	67	0.54	281.17	1.42	12.08
Argonauta nodosa	2	0.28	2	0.02	0.38	< 0.01	< 0.01
Insects							
Camponotus sp. (flying ants)	129	**18.07**	7963	**64.53**	557.41	2.82	**1216.96**
Unidentified Curculionidae (beetles)	8	1.12	17	0.14	3.40	0.02	0.18
Unidentified Coleoptera	50	**7.00**	137	1.11	27.40	0.14	8.74
Unidentified Orthoptera (grasshoppers)	2	0.28	2	0.02	0.40	< 0.01	< 0.01
Unidentified Belostomatidae (water bugs)	10	1.40	36	0.29	7.20	0.04	0.46
Unidentified insects	81	**11.34**	96	0.78	19.20	0.10	9.95
Crustaceans							
Unidentified Cirolanidae	1	0.14	1	0.01	2.00	0.01	< 0.01
Unidentified Isopoda	2	0.28	2	0.02	4.00	0.02	0.01
Artemesia longinaris (marine shrimp)	7	0.98	7	0.06	14.00	0.07	0.13
Unidentified Penaeidae (shrimp)	1	0.14	1	0.01	2.00	0.01	< 0.01
Unidentified Brachyura (crab)	4	0.56	4	0.03	8.00	0.04	0.04
Unidentified Crustaceans	2	0.28	2	0.02	4.00	0.02	0.01
	n = 714 pellets		12 340 prey		19786.26 g		

Contributions in number, mass and frequency of occurrence greater than 5% and IRI greater than 50 are highlighted in bold type.

digested otoliths of these fishes. The hypural bone was found to be useful for distinguishing between 'unidentified clupeiforms' and 'unidentified fishes'.

The estimated body mass of all prey together was 19 786 g (Tables 3 and 4). Of this total, fish constituted 95.3%, insects 3.1%, and cephalopods and crustaceans together 1.6%. In number, insects contributed

Table 4. Number of prey and food types found in 714 pellets of Common Terns in southern Brazil, and number identified to species level.

	Prey		Food types		
	No.	No. identified to species level	No.	No. identified to species level	Mass (g)
Fish	4 003	3676	27	20	18855.70
Cephalopods	69	69	2	2	281.55
Insects	8 251	0	6	0	615.01
Crustaceans	17	7	6	1	34.00
Total	12 340	3752	41	23	19786.26

66.9% and fish 32.4%. The frequency of occurrence of fish was 93.4%, and of insects 29.1%. Cephalopods and crustaceans contributed little to the diet. They occurred with frequencies of 6.3% and 2.2%, respectively, and with contributions in mass of 1.4% and 0.2%, and number 0.6% and 0.1%, respectively.

Twenty fish species, belonging to 13 families, occurred in the diet (Table 3). Four species of sciaenid fishes (*Paralonchurus brasiliensis*, *Micropogonias furnieri*, *Cynoscion guatucupa* and *Macrodon ancylodon*) and the gadoid *Urophycis brasiliensis* together contributed the bulk of the fish diet (87.9% by number, and 89.9% by mass). In the diet as a whole, these five fish species together contributed 28.5% in number and 85.6% in mass, each species with IRI greater than 50. The clupeiform fishes (*Brevoortia pectinata* to 'Unidentified Clupeiformes' in Table 3) together contributed 1.9% in number and 4.1% in mass. The winged form of the ant *Camponotus* sp. contributed 64.5% in number but only 2.8% in mass, with high IRI owing to its frequency of occurrence of 18.1% and the high number of prey items contributed (64.5%). The six food types *P. brasiliensis*, *M. furnieri*, *C. guatucupa*, *M. ancylodon*, *U. brasiliensis* and *Camponotus* ants together contributed 93.0% in number and 88.5% in mass to the diet of the Common Tern.

The total estimated body length (TL) of fish averaged 77.7 mm (range 12.7–217.4 mm) (Table 5; Fig. 2), with only 0.4% exceeding 140 mm. The difference between the TL of the five main fish species was significant (Fig. 2; Kruskal–Wallis, $H = 200.8$, $df = 4$, $P = 0.0001$). TL of less than 90 mm predominated in *P. brasiliensis*, *M. furnieri*, *C. guatucupa* and *M. ancylodon*, and TL greater than 90 mm predominated in *U. brasiliensis*. Fish smaller than 30 mm and larger than 150 mm were rarely taken. The mantle length of the squid *Loligo sanpaulensis* varied mostly between 20 and 50 mm, which is at the lower end of the range of TL of the fishes (Fig. 2). However, the mantle length does not include the head and tentacles of the squid. Total body size of this squid was estimated at 50–80 mm, similar to the sizes of the fishes predominantly taken. There are no data on the size of the insects because whole insects were not found in the pellets. Most insects taken were ants, with an estimated body length of *c.* 10 mm, much smaller than the fishes and squids taken by the birds.

The monthly variation of fish prey size is shown in Figure 3. In *P. brasiliensis* the frequency distribution of TL varied irregularly between months, but all were within the same wide range of 10 size classes from 30 to 130 mm. In *M. furnieri*, TL varied less within months, over a range of only three or four size classes, but the February fish were much larger (100–120 mm) than the fish from September and March (70–100 mm). In *M. ancylodon*, fish of 80–140 mm predominated in November, but smaller fish of 30–80 mm predominated in January and March. Presumably, this is evidence that *M. ancylodon* of 30–80 mm became accessible in large numbers only after November. All these temporal variations were statistically significant (*P. brasiliensis*, $H = 39.7$, $df = 4$, $P = 0.0001$; *M. furnieri*, $H = 68.4$, $df = 5$, $P = 0.001$; *M. ancylodon*, $H = 26.8$, $df = 2$, $P = 0.00001$).

The body mass of fish prey varied from 0.01 to 47.0 g about the mean of 4.8 g (Table 5). Fish prey greater than 15.0 g were rarely taken, and the modal mass of fish prey was less than 2.0 g (Fig. 4). This was the modal mass of three of the main fish prey species: *P. brasiliensis*, *M. ancylodon* and *C. guatucupa*. The predominant body mass of *M. furnieri* and *U. brasiliensis* was 3.0–15.0 g. The body mass of the squid *L. sanpaulensis* fell within the range of that of the fishes, mostly 1.0–8.0 g. Overall, 80% of the fish and cephalopod prey weighed less than 8.0 g.

Fish were the most frequent food type, predominating in number and mass, in all months except December, when insects occurred in 83% of the pellets

Table 5. Total length and body mass of the fishes and cephalopods found in 714 pellets of the Common Tern in southern Brazil.

	Total length (mm)			Mass (g)			
Food type	Mean	Min.	Max.	Mean	Min.	Max.	*n*
All fish	77.73	12.72	217.36	4.76	0.01	47.04	3615
Brevoortia pectinata	50.49	41.50	55.00	1.31	0.74	1.63	5
Anchoa marinii	49.34	20.47	77.00	1.00	0.04	2.33	7
Engraulis anchoita	62.52	22.68	133.50	2.51	0.08	14.63	17
Lycengraulis grossidens	93.58	25.28	138.51	6.66	0.04	16.70	14
Urophycis brasiliensis	110.24	23.43	150.32	10.86	0.26	27.54	85
Porichthys porosissimus	55.98	18.40	109.29	2.51	0.05	12.58	18
Jenynsia lineata	30.02	16.24	23.84	0.39	0.03	1.12	4
Atherinella brasiliensis	36.26	21.30	74.45	0.42	0.02	2.17	14
Prionotus punctatus	43.41	–	–	0.57	–	–	1
Ctenosciaena gracilicirrhus	–	64.64	81.96	–	3.13	6.67	2
Cynoscion guatucupa	71.47	12.72	109.98	3.66	0.01	11.69	227
Macrodon ancylodon	80.24	17.14	134.73	4.76	0.02	17.50	155
Menticirrhus sp.	73.60	19.04	141.52	8.81	0.06	27.70	9
Micropogonias furnieri	86.86	24.27	141.08	5.96	0.08	27.37	534
Paralonchurus brasiliensis	75.86	15.63	171.49	4.47	0.01	47.04	2491
Stellifer rastrifer	70.69	15.04	111.82	5.29	0.01	16.87	9
Umbrina canosai	55.49	32.05	85.63	2.90	0.42	8.33	14
Mugil sp.	28.33	23.06	42.82	0.47	0.23	1.23	5
Trichiurus lepturus	217.36	–	–	2.86	–	–	1
Peprilus paru	–	25.96	53.10	–	0.53	2.95	2
Symphurus jenynsi	–	–	–	–	4.45	8.39	2
Cephalopods							
Loligo sanpaulensis	38.89	13.55	65.46	4.19	0.34	12.42	67
Argonauta nodosa	–	7.84	9.59	–	0.16	0.22	2

Species with one or two specimens, original values are given.
n = number of prey; – insufficient data to calculate.

Table 6. Monthly variation in the diet of the Common Tern, with respect to frequency of occurrence and proportion of the diet in number and mass. Number of pellets by month is given in parentheses.

	Fish			Insects			Cephalopods			Crustaceans		
Month	FO%	N%	M%	FO%	N%	M%	FO%	N%	M%	FO%	N%	M%
November (20)	100.0	89.3	98.1	30.0	5.8	0.7	0.0	0.0	0.0	< 0.0	4.9	1.2
December (159)	70.4	4.4	17.2	83.0	95.5	77.6	6.3	0.1	5.2	0.6	< 0.0	0.1
January (297)	100.0	97.0	87.6	8.1	1.1	0.2	9.1	1.7	12.2	2.7	0.2	0.1
February (56)	100.0	94.2	91.9	3.6	2.3	0.3	7.1	3.5	7.8	1.8	< 0.0	< 0.0
March (174)	100.0	92.4	98.9	23.0	6.4	1.1	1.7	1.2	0.0	0.0	0.0	0.0

and predominated in both number and mass (Table 6). The results for December are influenced by samples obtained on 16 and 17 December 1999, when most pellets consisted entirely of the remains of winged ants. During summer, persistent onshore north-easterly winds predominate in the study area (Braga & Krusche 2000). The wind blew from the north-east with a speed of 14.4–25.2 km/h on 10–13 December 1999, then shifted to an offshore south-westerly of 7.2–32.4 km/h from 14 to 16 December before veering back to north-easterly at 7.2 km/h on the 17th and 18th (unpubl. data, Meteorological Station of Fundação Universidade Federal do Rio Grande, Departamento de Geociências). Between 14 and 16 December 1999, the mass emergence of winged ants coincided with offshore winds, and on 16 and 17 December the terns fed on ants blown out to sea in great numbers, an uncommon event that did not occur in the other months.

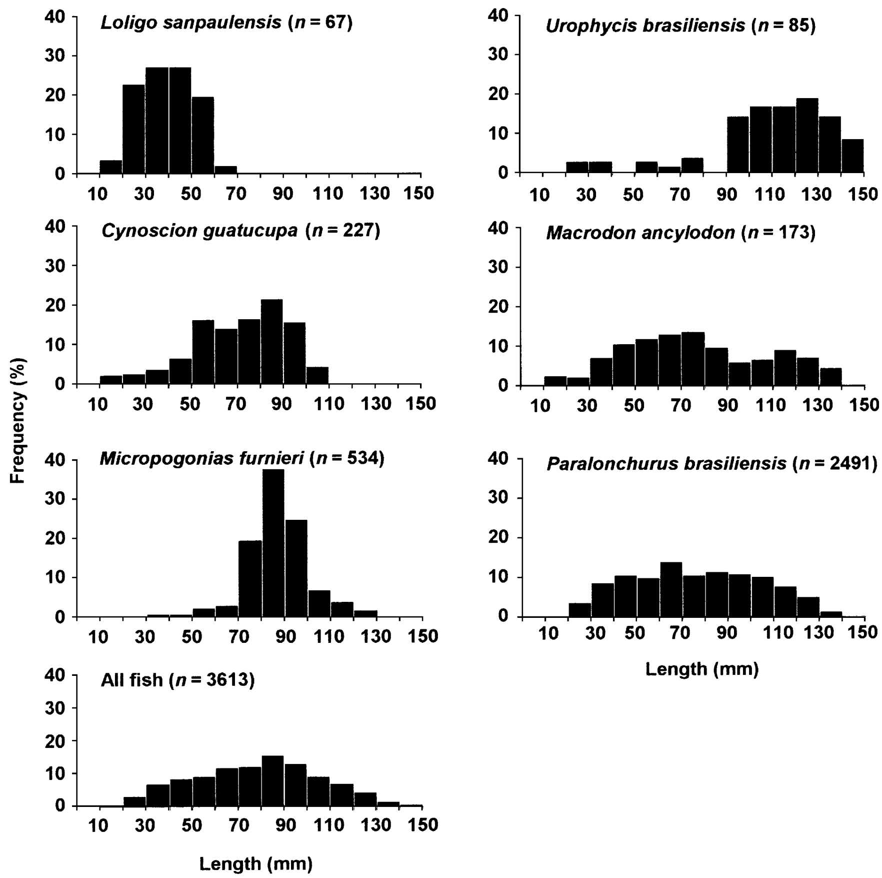

Figure 2. Size-frequency distribution of fishes (total length) and the squid *Loligo sanpaulensis* (mantle length) preyed on by Common Terns in southern Brazil.

The species composition of fish prey varied between months (Fig. 5). *P. brasiliensis* predominated strongly in December and January, *C. guatucupa* in November and *M. furnieri* in March. In February, besides *P. brasiliensis*, a large part of the fish food consisted of Clupeiforms and *M. furnieri*. These monthly differences were statistically significant, both by number and by mass (N%, G-test = 79 852; M%, G-test = 796 767; both $df = 24$ and $P < 0.0001$).

The richness in food types per pellet was low, with a mean of 2.2 types per pellet, and with 89% of the pellets containing from one to three food types (Fig. 6). The number of prey per pellet varied from one to 131, but this number varied depending on whether the terns were feeding on fish or on insects. In 584 pellets, fishes predominated and insect prey occurred in only 81 of these pellets, with a modal value of one insect per pellet (Fig. 7A). In the 584 fish pellets, the number of non-insect prey (mainly fish) was mostly one to 10, with a mean value of 6.8 (Fig. 7B). In the 128 pellets collected on 16 and 17 December 1999, non-insect prey were scarce or absent, and the number of insect prey per pellet was mostly 40–100 with modes of between 50 and 60 (Fig. 7A).

DISCUSSION

In southern Brazil the Common Tern feeds mainly on fish, as reported throughout the rest of its range (Pearson 1968, Becker *et al.* 1987, Safina 1990, Mauco *et al.* 2001, Granadeiro *et al.* 2002). Its six principal prey species are the sciaenid fishes *P. brasiliensis*, *M. furnieri*, *M. ancylodon* and *C. guatucupa*, the gadoid (= urophycid) fish *U. brasiliensis* and the squid *L. sanpaulensis*. In Argentina, the Anchovy *Engraulis anchoita*, a small pelagic fish of the continental shelf, is one of the main prey species of the Common Tern (Mauco *et al.* 2001). However, in southern Brazil, this fish is scarce during summer (Castello 1998), which explains its minor importance in the diet of the Common Tern in the study area.

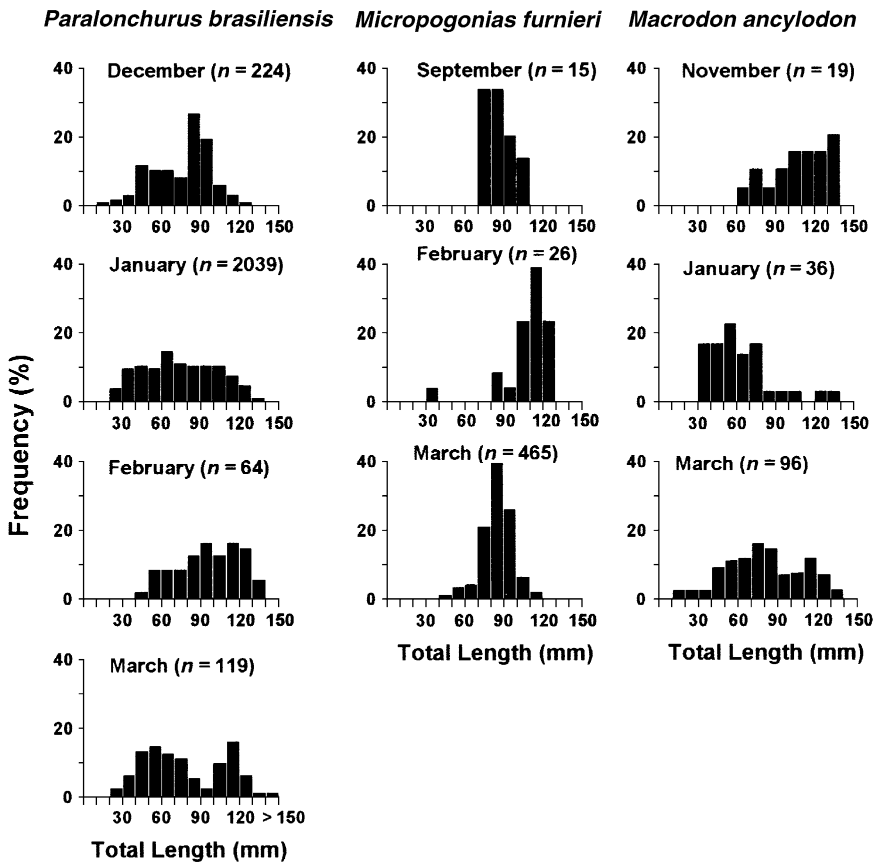

Figure 3. Monthly variation in the total length (mm) of the main fish prey in the diet of Common Terns in southern Brazil in 1999 and 2000.

Table 7. Total length (TL) and mantle length (ML) at first sexual maturity and depth of occurrence of juveniles of the main fish and cephalopod prey of Common Tern in southern Brazil.

Species	TL and ML at 1st maturity (mm)	Depth zone (m)
Paralonchurus brasiliensis[f,g]	150	< 20
Micropogonias furnieri[a,d,e,f]	200–300	< 20
Macrodon ancylodon[d,e,f]	450	< 20
Cynoscion guatucupa[e,f]	550	< 20
	M = 230	coastal
Urophycis brasiliensis[e,f]	F = 400	
	M = 45	< 60
Loligo sanpaulensis[b,c]	F = 40	

M – male; F – female.
[a]Castello (1986); [b]Haimovici and Perez (1991); [c]Andriguetto and Haimovici (1991); [d]Haimovici and Umpierre (1996); [e]Haimovici (1998); [f]Haimovici *et al.* (1996); [g]Oliveira and Haimovici (2000).

The six principal prey species occur year round on the continental shelf (Haimovici *et al.* 1996). From the comparison between prey body-sizes and adult body-sizes of the six species (Fig. 2; Table 7), it is evident that Common Terns prey mainly on small juveniles. As *M. furnieri*, *M. ancylodon*, *C. guatucupa* and *U. brasiliensis* are important fishery resources (Haimovici & Mendonça 1996, Haimovici 1998, Haimovici *et al.* 1998), the fishery affects the food availability to the terns. However, *P. brasiliensis* is the principal prey species, contributing 56% of the total diet mass, and this is not the object of a fishery.

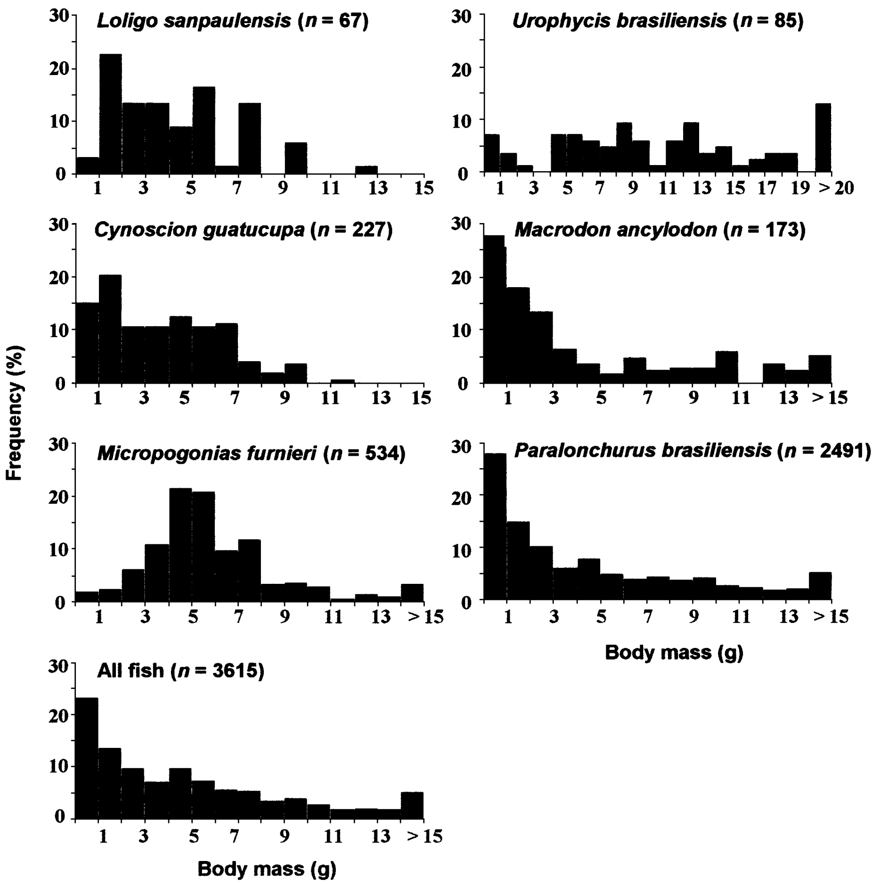

Figure 4. Body mass-frequency distribution of fishes and the squid *Loligo sanpaulensis* preyed upon by Common Terns in southern Brazil in 1999 and 2000.

This fish is a discarded bycatch of the coastal trawl fishery, but there is no information on the effects that fishing has on this food resource of the Terns (Haimovici *et al.* 1998, Oliveira & Haimovici 2000).

Typical surf zone and estuarine fishes such as *Trachinotus marginatus*, *Menticirrhus* spp. and *Mugil* spp. (Cunha 1981, Chao *et al.* 1982) were scarce or absent in the diet of the Common Tern during this study (Table 3). Juveniles of all six principal prey species occur in marine coastal waters at depths of less than 20 m, and of four of these, the juveniles are restricted to those depths (Table 7). Our data suggest that in southern Brazil Common Terns forage mainly in marine coastal waters between the surf zone and the 20-m isobath (depth contour line), which occurs between 15 and 30 km from shore (Fig. 1).

The juveniles of all six principal prey species fall within the size range eaten by Common Terns, and are discarded as a bycatch of the coastal shrimp trawl fishery (Ruffino & Castello 1992). In the years 1980–97, the trawl fishery off southern Brazil discarded between 17 000 and 30 000 tonnes of fish at sea annually (Haimovici *et al.* 1998). This means that Common Terns could feed on fishery discards. However, such behaviour is uncommon in the Common Tern in other areas (Blokpoel *et al.* 1982, Garthe 1997), and if it were common in the study area, discard feeding by such an abundant bird would be as well-known as it is for Procellarilform birds (Vooren & Fernandes 1989); this is not the case with the Common Tern. In addition, given the large quantities of discards available, such an easy feeding method would make it difficult to explain the shift to insect feeding in December 1999. It is more likely that in southern Brazil, Common Terns feed on fishes that occur naturally at the sea surface, as the bird does elsewhere throughout its range (Burger & Gochfeld 1991, Nisbet 2002).

The five main fish species (Table 7) are demersal (Haimovici *et al.* 1996) and are not expected to

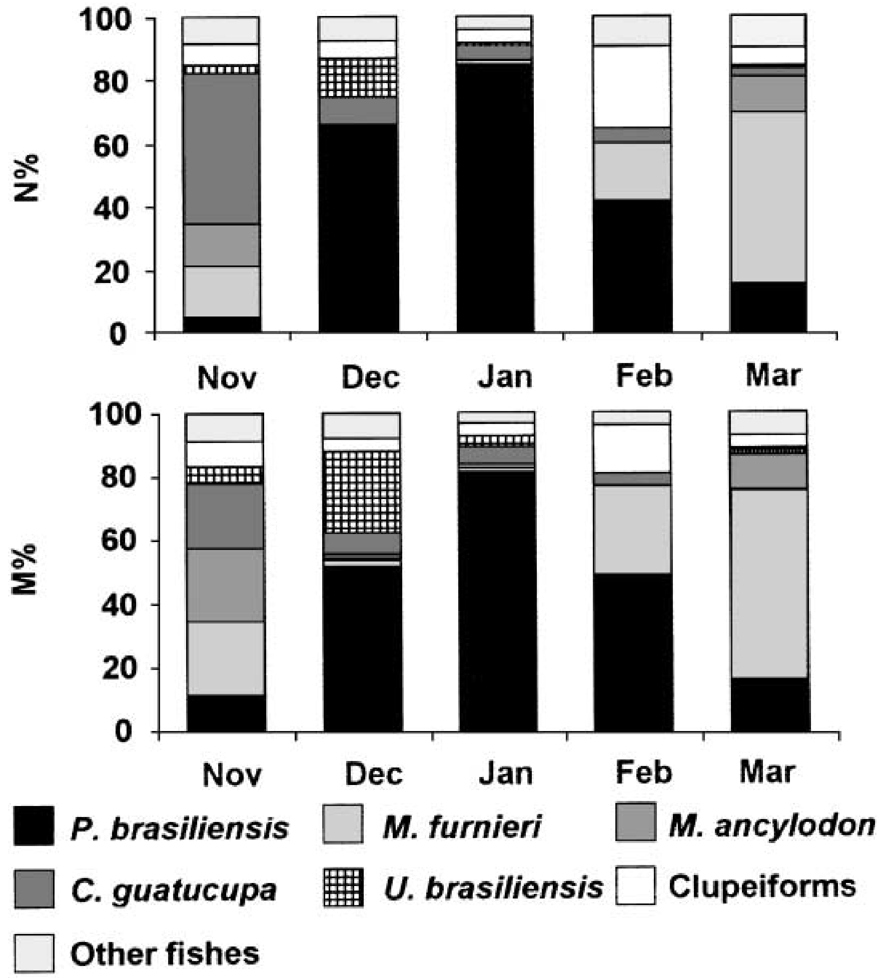

Figure 5. Monthly variation in the main fishes taken by Common Terns in southern Brazil in 1999 and 2000, by numbers (N%) and mass (M%).

occur at the surface and to be available as food for Common Terns. However, in other demersal fishes such as Cod *Gadus morhua* and Haddock *Melanogrammus aeglefinus*, the early juvenile stages (TL 6 and 10 cm, respectively) are pelagic (Muus & Dahlstrøm 1974). By analogy, the small juvenile stage of the five main fish prey species could also be pelagic and thus be available to surface-feeding Common Terns. In addition, the action of aquatic predators may make these fishes available to the Terns. In the study area, the Bluefish *Pomatomus saltatrix*, the adults of the Striped Weakfish *C. guatucupa* and the Franciscana Dolphin *Pontoporia blainvillei* feed on the same juvenile fishes as the Common Tern (Pinedo 1982, Lucena *et al.* 2000). Associations between surface schools of Bluefish and feeding bird flocks have been recorded in southern Brazil and off the east coast of the United

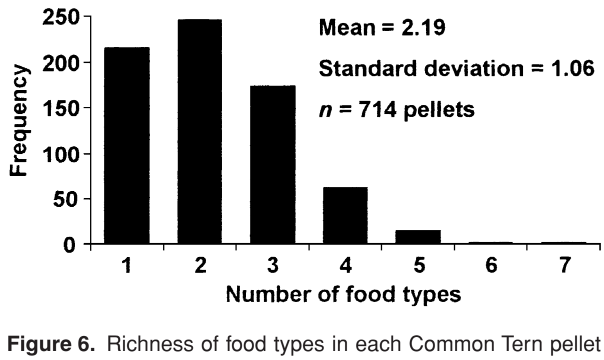

Figure 6. Richness of food types in each Common Tern pellet collected in southern Brazil in 1999 and 2000.

States (Krug 1984, Safina & Burger 1985, 1989, Safina 1990). The action of aquatic predators, which drive fish to the surface where they are preyed on by seabirds, is a widespread phenomenon (Ashmole

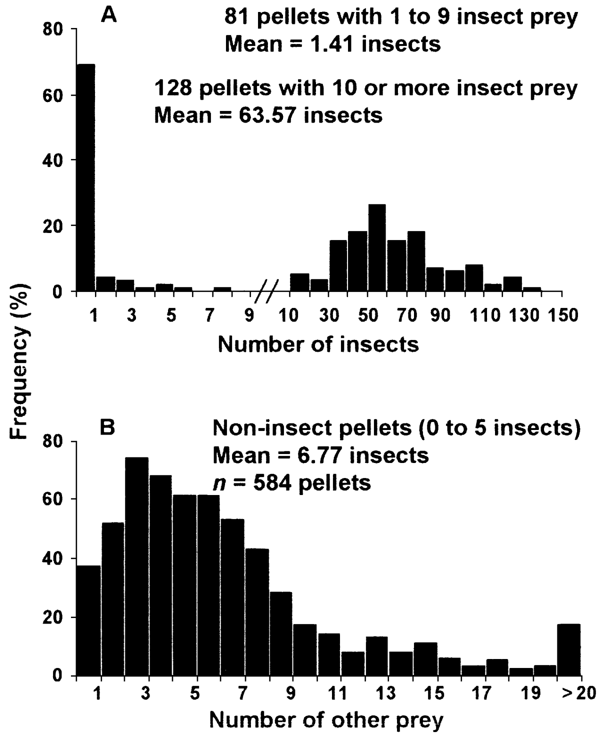

Figure 7. Relative frequency of number of prey per pellet. (A) Number of insect prey per pellet; (B) non-insect prey per pellet (fish, cephalopod and crustaceans). Pellets with six or more insects were not included in the histogram 'B'.

1968, Evans 1982, Shealer 2002), and may increase the availability of such prey to the Terns.

Pellets varied from 8.9 to 32.0 mm in length, but only from 7.0 to 19.0 mm in diameter. The difference in the variation of these two measurements presumably reflects the fact that the breadth is more constrained than the length during egestion through the oesophagus. The average dry mass of the pellets was 0.3 g, and most (99.7%) of the pellets weighed less than 1.0 g. This contrasts with the average calculated fresh meal mass of about 30 g, based on the average number of prey per pellet (6.8 g) and the average mass of preys (4.8 g). This means that about 95% of the fresh prey mass is digested in the stomach and passes to the intestine. Only the otoliths, vertebrae, teeth and pharyngeal plates of fishes, the rostra and claws of crustaceans, the beaks of squid and the mouth parts and elytra of insects remain in the stomach. Scales were also a frequent prey fragment (81.8%), but the number in each pellet was fairly small in comparison with the total number of scales in a fish prey. Even so, most (92%) fish prey and all squid were identified to the species level. This result further validates the use of pellets for the quantitative study of piscivorous bird diets (but see Duffy & Jackson 1986, Johnstone *et al.* 1990). This applies especially to terns feeding on fish that are large relative to the size of the birds, so that the hard parts of these fishes do not pass easily to the intestine, as is also seen from the fact that fish otoliths are only occasionally found in the faeces of Common Terns (L. Bugoni unpubl. data).

Fragments of downy feathers occurred in 96% of the pellets, and were the commonest item in pellets. As roosting Common Terns in the study area spend much time preening (Bugoni 2001), this suggests that birds probably ingested pieces of down that became detached from the plumage.

The high species richness of the diet (35 food types) and the average of seven prey in the 'non-insect pellets' (Fig. 7B) contrast with the average of only two different food types per pellet (Fig. 6). In part this reflects the fact that only five species of fishes together constituted 88% of the fish prey by number. The low average number of food types per pellet is also evidence that in the foraging area the main food organisms are not distributed uniformly and/or sparsely, but occur in monospecific patches, a characteristic of marine environments (Shealer 2002), and that the foraging strategy of the bird is adjusted so as to take advantage of this. The bird finds such a patch and then feeds on it to satiation or as the patch remains available. This foraging strategy reduces time and energy spent in searching for food, and implies that in a short time the bird ingests prey until satiated and then returns to the roosting beach to rest and digest the meal. Plasticity in foraging strategies is particularly important to species that feed in environments where prey distribution is ephemeral and gregarious, such as the marine environment (Erwin 1977, Becker *et al.* 1997). The above conclusions agree with the sequence of events on the roosting location as deduced from the observations of the daily cycle of birds in the area (Bugoni 2001).

The way in which the birds on 16 and 17 December 1999 abruptly switched from fish to insects as food, and then back to fish is further evidence of the exploration of food patches as a feeding strategy. The Common Tern takes insects as a minor food type throughout its range (Lemmetyinen 1973, Becker *et al.* 1987, Safina *et al.* 1990, Mauco *et al.* 2001, Granadeiro *et al.* 2002), but insects do not normally occur at high densities at the sea surface near the study area. During the study period, offshore winds and the mass emergence of flying ants coincided, as indicated by observations of dense tidal deposits of these ants on the ocean beaches. Evidently, large numbers of ants floated on the sea at that time. The terns were not seen feeding on the insects cast ashore. Either they picked the floating insects up from the sea surface or they were feeding by aerial pursuit of airborne swarms of ants, as has been observed in the Brown-hooded Gull *Larus maculipennis* in the study area (Belton 1994) and other small gulls and terns in both the Old and New Worlds. Opportunistic feeding on swarming ants and chironomids is probably common for these birds. In either case, the birds fed on insect prey patches that were dense enough for feeding to satiation and that were more easily found and exploited than the usual fish prey, in spite of the small body mass of the ants (about 0.07 g) in comparison with the average body mass of fish prey (4.76 g).

We conclude that the Common Tern in southern Brazil chooses prey patches according to an evaluation of size and 'catchability' of the prey and of density of the patch. The great variation of the size and mass of fish prey (3–15 cm, 1–15 g) is further evidence of this (Figs 2 & 4). Small prey are taken if present in patches of acceptable density, down to a size of about 1 cm, which is the estimated size class of insects taken occasionally in large numbers. The mean fish prey size of 7 cm (Table 5; Fig. 2) does not reflect a preference for this prey size, but the greater availability of prey of this size class. The size frequency distribution of fish prey reflects the composition of the available patches of prey smaller than 15 cm. The *C. guatucupa* and *M. furnieri* larger than 10 cm and *U. brasiliensis* smaller than 9 cm were scarce in the diet, and this reflects the size composition of these prey populations (Fig. 4). Small juveniles of *M. ancylodon* with modal size of 5 cm appeared in the diet in January (Fig. 3). This species spawns in spring (Haimovici 1988) and in summer the birds fed on juveniles recruited from the spawning in the previous spring. The modal progression from 5 cm in January to 7 cm in March (Fig. 3) may have been due to the body growth of these juveniles during summer. The food of the terns reflected the dynamics of the population of *M. ancylodon* in the study area.

In a breeding colony in the United States, Common Terns fed their chicks on fishes of 5–6 cm (Wagner & Safina 1989), smaller than most prey taken in the present study. This difference may reflect selection by the breeding birds of small prey sizes adequate as food for the chicks. Size of food brought to the chicks is not necessarily a measure of the prey taken as food for the adult birds.

In the 584 'non-insect pellets' the average number of non-insect prey (mostly fish) was 6.8 (Fig. 7), and the average body mass of fish prey was 4.8 g (Table 5). Therefore, the mean 'non-insect pellet' corresponds to a fish meal of the order of 30.0 g. A similar calculation for the 'insect pellets' (Fig. 7), with a mean of 63.6 insect prey per pellet (mostly flying ants) with an estimated mass of 0.07 g per prey, results in an average insect meal size of only 4.5 g. The number of insects in the diet may have been underestimated, although the fact that insect chitin is largely indigestible for most birds makes this unlikely (Krebs & Avery 1984, Castro *et al.* 1989). Another possibility is that a meal of insects with the same volume as a fish meal has a smaller mass owing to the difficulty of accommodating items such as wings and legs in the bird's stomach. This hypothesis assumes that a pellet represents a bird's meal (i.e. one pellet = one meal) and does not preclude there being two or more meals per day. However, it remains true that the 128 'insect pellets' are evidence that on those occasions the birds fed mostly or exclusively on insects.

In conclusion, in its wintering area in southern Brazil, the Common Tern feeds mostly on juvenile sciaenid fishes, but with great temporal variation in the composition of the diet in terms of prey size and species. The birds switch opportunistically from one prey species or size to another, according to the available food patches. The temporal variation in the diet is due to variation of the availability of prey species and reflects the dynamics of the prey populations. By their taking juvenile fish and not using fishery discards as a food source, the foraging of the Terns is not directly related to fishery activities. However, this does not mean that they might not have an impact on the recruitment of commercially important fish species.

We thank Fernando D'Incao, Roberta A. dos Santos and Elena Diehl for the identification of some food types. Special thanks are due to Flavio Quintana, Manuel Haimovici, Andrew W. Boyne, José C.C. Xavier and Michael Gochfeld for criticism and suggestions on this manuscript. We also thank the Fundação Universidade Federal do Rio Grande (FURG) for institutional and logistic support. The Brazilian Research Council (CNPq) provided an MSc grant to L.B.

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Received 15 May 2003; revision accepted 13 December 2003.
First published online early on 11 March 2004;
doi: 10.1111/j.1474-919x.2004.00277.x