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ORIGINAL PAPER

Andrea Raya Rey · Adrián Schiavini

Inter-annual variation in the diet of female southern rockhopper penguin (*Eudyptes chrysocome chrysocome*) at Tierra del Fuego

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Abstract Inter-annual variation in the diet of female southern rockhopper penguins (*Eudyptes chrysocome chrysocome*) at Staten Island was studied during the early chick-rearing period to investigate the components of the diet and highlight some points of the possible food web in the study area. Gregarious crustaceans, small juveniles of squid and octopus, fish larvae and juvenile fish dominated the diet. There was a high degree of variability in the relative contribution of the different prey taxa during the three seasons studied. Overall, crustaceans were by far the most abundant in terms of number. Cephalopods contributed less to numbers, while fish was the least represented of the prey item in 2 years. Inter-annual variation in the proportion of prey items consumed was apparent only for some prey species: *Thysanoessa gregaria*, *Gonatus antarcticus*, *Themisto gaudichaudii*, *Harpagifer bispinis* and *Salilota australis*. These data suggest variability in the prey resources at sea during the study period and a subsequent opportunism of this penguin species to exploit what is differentially available. In terms of the food web in the area, we suggest an apparent relationship in the availability between *T. gaudichaudii* and *G. antarcticus*, and between *T. gaudichaudii* and *H bispinnis*. These relationships emphasise the importance of understanding food web interactions, especially those involving multiple trophic levels, when determining the role of upper-trophic level predators in marine systems.

Introduction

Penguins are the dominant component of the seabird communities in the Southern Ocean, in terms both of biomass and prey consumption (Croxall and Lishman 1987). North of 55°S, crested penguins (*Eudyptes* spp.) are the most widespread and abundant penguin species, having a circumpolar distribution with the largest numbers in the South-western Atlantic Ocean. Over much of their range the populations of *Eudyptes* penguins have undergone considerable declines, with populations of the once most numerous rockhopper declining by up to 90% in some locations (Cunningham and Moors 1994; Bingham 1998; Pütz et al. 2001). A crucial part of determining the possible causes of these declines is to examine the role of penguins in the marine ecosystem, in particular the composition of the diet and how this reflects local prey abundance or changes in prey distribution and abundance arising from oceanographic changes (Cunningham and Moors 1994). The largest concentrations of rockhopper penguins in South America are in Tierra del Fuego, and surveys undertaken recently at Staten Island estimated a population of 174,000 pairs of southern rockhopper penguin (*Eudyptes chrysocome chrysocome*) with 96% of the population located in one area, Franklin Bay. This population seems to be stable or increasing (Schiavini 2000). Conceivably, such substantial numbers of predators may have a major impact on the marine resources around the island.

Diet studies of top predators in the South-western Atlantic ocean are important not only to evaluate what they preyed on, but also to know about the marine resources of an area poorly studied. The study of the diet could contribute to the identification of at least some elements and relationships of the food web in the study area.

All the previous studies of the diet of rockhopper penguins indicated that they are opportunistic feeders and that they generally relied on macrozooplankton, crustaceans and to a lesser extent squid and fish (Horne 1985; Croxall et al. 1985; Brown and Klages 1987; Klages et al. 1988; Klages et al. 1989; Hull 1999; Clausen 2001; Clausen and Pütz 2002). However, there is evidence that squid is of greater importance in the diet of

A. R. Rey (✉) · A. Schiavini
Consejo Nacional de Investigaciones Científicas y Técnicas,
Centro Austral de Investigaciones Científicas,
Houssay 200, 9410 Ushuaia, Tierra del Fuego, Argentina
E-mail: arayarey@ciudad.com.ar
Fax: +54-2901-430644

this species in waters around the Falkland Islands than elsewhere (Clausen and Pütz 2002). Hull (1999) found no substantial differences in general composition, in terms of prey taxa, of the diet between breeding seasons and between stages of the breeding season. However, there was inter-annual variation in the proportion of the different prey items in the stomach contents. An unidentified euphausiid, fish larvae and *Loligo gahi* were the main prey of the southern subspecies at the Falkland Islands (Clausen 2001). In the eastern subspecies (*Eudyptes c. filholi*) at Marion and Macquarie Islands, crustaceans formed the predominant prey in terms of frequency of occurrence, mass and numbers. Fish appeared less important and squid were of negligible significance (Horne 1985; Brown and Klages 1987; Klages et al. 1988, 1989; Cooper et al. 1990; Ridoux 1994). The differences in diet probably reflect differences in local prey distribution and abundance.

Staten Island, together with Macquarie Island, represent the southernmost breeding range of rockhopper penguins. Staten Island is influenced by the meeting of the Pacific, Atlantic and the Southern Ocean. This complex mix of oceanography features might be reflected in the zooplankton composition. Feeding ecology studies at Staten Island revealed that southern rockhopper penguins forage as far as 20 km from their colony (Schiavini and Raya Rey 2004). Relatively little is known about the zooplankton composition in terms of diversity and relationships between species in this area.

The aim of this study was to investigate the various components of the diet of female southern rockhopper penguins in waters around Staten Island during the chick-rearing period of 3 consecutive years. Also, we try to highlight some local relationships between prey species in this environment.

Materials and methods

Sampling took place at a small colony containing c 200 nests at Punta Tello, Franklin Bay, Staten Island (54°50′S, 64°40.5′W), during the early stages of the brooding periods (29 November–13 December) of three consecutive breeding seasons of 1999–2000, 2000–2001 and 2001–2002.

Sampling collection

Birds were captured at the nest after the display with their partner prior to delivering the food to their chicks. They were weighed, sexed using bill depth and length (Hull 1996), and samples collected using water-offloading (Wilson 1984). Birds were flushed until clear water was obtained. After sampling, each bird was marked on the breast feathers to ensure that no bird was sampled more than once. Diet samples were drained and preserved in 4% formalin buffered with borax during the first season and with 70% ethanol during the other two. In the laboratory, total sample weight was noted prior to sorting into the main components: fish, squid and crustaceans. Large and entire prey items were separated from the whole sample after which one-eighth subsamples were taken at random and the results extrapolated to determine the overall composition.

Sample sorting

Identification of crustaceans was based on our reference collection (Laboratorio EcoPT CADIC), and following the keys in Guglielmo and Ianora (1997), Vinogradov (1999) and Gibbons et al. (1999). Entire crustacean bodies and pairs of eyes were counted to estimate the number of individuals consumed. Total lengths of any undigested crustaceans were measured using a microscope fitted with an eyepiece graticule. *Euphausia* sp. comprised both *E. vallentini* and *E. lucens*, as it was very difficult to identify to species level due to the degree of digestion.

Cephalopods were identified and their number assessed from lower beaks, using our reference collection, Falkland Conservation reference collection, Falkland Islands, and Clarke (1986). Beaks were present as loose beaks (free), in buccal masses or in buccal masses with crowns, and were categorized according to their degree of erosion using the following criteria of Hull (1999): (1) removed from buccal mass; (2) free in the sample with no evidence of erosion; (3) free in the sample with some evidence of erosion; and (4) free in the sample with severe erosion.

Fish were identified from whole specimens, otoliths and cranial bones using our reference collection and following Fischer and Hureau (1985) and Williams and McEldowney (1990).

Diet was described in terms of frequency of occurrence, percentage by number and percentage by mass, to allow for the various biases of each of the individual approaches (Hyslop 1980; Duffy and Jackson 1986). Composition by number was assessed using lower beaks from cephalopods, numbers of individual crustaceans and otoliths and cranial bones from fish. The original mass of prey items ingested was estimated by using regression equations for squid beak size [lower rostral length (LRL)] and body length of euphausiids (anterior edge of eyeball to tip of telson) to body mass (Clarke 1986; Ridoux 1994). It was not possible to assess the relative proportion by mass of the whole diet, as the reconstructed mass of fish could not be calculated because appropriate relationships of mass and the length of the cranial bones and/or the small otoliths were not available.

For the reasons mentioned above, we present an assessment of the diet mass only for crustaceans and cephalopods. This was made to highlight at least partially the real contribution of each prey species/taxon to the diet without the underestimation of small prey using the percentage by number analysis.

Data analysis

The quantity of food brought ashore was compared between years using one-way analysis of variance (ANOVA) and Tukey's multiple comparison. Dietary composition was assessed using frequency of occurrence, percentage by number and by mass when possible (crustaceans and cephalopods). To examine inter-annual variability in diet composition, the numerical frequency of individual prey species was compared between years with ANOVA and multiple comparisons and the frequency of occurrence of each prey item was compared using χ^2-test.

The Shannon–Weaver's diversity index (H) was calculated for each year and differences in diet diversity between years were assessed using ANOVA. The degree of digestion for the different prey items was compared between years using also the χ^2-test. Differences in length frequency of the lower beaks of cephalopods and standard length of crustaceans were assessed with one-way ANOVA and Kruskal–Wallis test when variances were not homogeneous and t-test for 2 years in the case of *Moroteuthis ingens* and *Thysanoessa gregaria*.

Table 1 Numbers of stomach contents collected, mean mass of female southern rockhopper penguins (*Eudyptes chrysocome chrysocome*) and mass content for each year. Mass given as mean ± SD

	1999	2000	2001
Stomach contents (n)	20	11	20
Mean mass of female (kg)	2.48 ± 0.16	2.30 ± 0.24	2.44 ± 0.15
Mean mass stomach contents (g)	131.43 ± 55	203.64 ± 142.3	150.34 ± 64.9

Results

Mass of diet samples

A total of 51 stomach contents was collected during the study period from female rockhopper penguins during the early chick-rearing period. The mass of samples did not vary significantly between years ($F_{2,48} = 0.98$, $p = 0.381$) (Table 1). The weight of stomach contents represented on average 5.6, 8.7 and 6.4% of the body weight of the adult birds during the three seasons.

Overall composition

Cephalopods occurred in all the samples in 1999 while crustaceans and fish occurred in 95 and 80% of the samples, respectively. In 2000, crustaceans and fish occurred in all samples while cephalopods were present in 91%. In 2001, the three prey groups occurred in all samples. Over the three seasons a total of 101,671 prey items from 15 taxa (species or species group) were identified and comprised three species of crustaceans, six species of cephalopods, and six fish taxa (Table 2).

Crustaceans were the main prey category by numbers, with *T. gregaria* and *E. vallentini* outnumbering

Table 2 The composition by number and percentage of the different prey items in the female rockhopper penguin diet

Taxa	1999		2000		2001	
	n	Percentage	n	Percentage	n	Percentage
Crustaceans	24,588	90.6	27,492	80.5	33,524	82.9
Amphipods						
Hyperiidae						
T. gaudichaudii	2,336	8.6	5,160	15.1	960	2.4
Euphausiids						
E. vallentini	7,434	27.4	9,508	27.9	14,123	34.9
T. gregaria	14,817	54.65	8,036	23.5	18,441	45.6
Not identified	0		4,788	14.0	0	
Cephalopods	1,709	6.3	5,405	15.0	2,201	5.4
Gonatidae						
G. antarcticus	614	2.26	4,752	13.9	1,030	2.5
Onychoteuthidae						
M. ingens	80	< 0.5	8	< 0.5	436	1.1
Loliginidae						
L. gahi	12	< 0.5	37	< 0.5	10	< 0.5
Ommastrephidae						
Martialia hyadesi	1	< 0.5	0		0	
Sepiolidae						
Semirossia	1	< 0.5	0		2	< 0.5
Todarodes filippovae	2	< 0.5	0		0	
Octopodidae						
E. megalocyathus	999	3.68	608	1.8	723	1.8
Fish	818	3.01	1,237	3.6	4,697	11.6
H. bispinis	789	2.91	766	2.2	4,304	10.6
S. australis	28	< 0.5	454	1.3	152	0.4
A. chiloensis	0		6	< 0.5	0	
Myctophids	1	< 0.5	16	< 0.5	20	< 0.5
S. fuegensis	0		0		221	0.6

Table 3 The composition by mass (g) and number (n) of the crustaceans and cephalopods part of the diet of female rockhopper penguins. Percentages by number refer only to crustaceans and cephalopods in the diet

	1999		2000		2001	
	g (%)	*n* (%)	g (%)	*n* (%)	g (%)	*n* (%)
T. gaudichaudii	86.7 (4)	2,336 (9)	205.6 (7)	5,160 (16)	40.4 (2)	960 (3)
E. vallentini	134.5 (7)	7,434 (28)	115.8 (4)	9,508 (29)	305.7 (15)	14,123 (40)
T. gregaria	303.4 (15)	14,817 (56)	9.8 (0)	8,036 (24)	318.1 (16)	18,441 (52)
Eupahusiids, not identified		(0)	86.7 (3)	4,788 (15)		(0)
G. antarcticus	67 (3)	614 (2)	1,373.5 (46)	4,752 (14)	54 (3)	1,030 (3)
M. ingens	278.7 (14)	80 (0)	(0)	8 (0)	312.9 (16)	436 (1)
L. gahi	456.4 (23)	12 (0)	733 (25)	37 (0)	687 (34)	10 (0)
E. megalocyathus	673 (34)	999 (4)	466 (16)	608 (2)	282 (14)	723 (2)

Themisto gaudichaudii (Table 2). In terms of biomass, cephalopods made a greater contribution to the diet than crustaceans (Table 3) with *Enteroctopus megalocyathus*, *L. gahi* and *Gonatus antarcticus* contributing most depending on the year. The difference in contribution of numbers and biomass is exemplified by *L. gahi* which contributed less than 1% in terms of numbers, but more than 20% in terms of biomass over the 3 years.

Crustaceans were numerically dominant in all years (80–90% of prey items), cephalopods contributed 6% in 1999, 15% in 2000 and 5% in 2001 while fish formed 3% of the diet in 1999 and 2000 but increase to 12% in 2001 (Table 2).

Crustaceans

Among the crustaceans, Euphausiids were the most important in terms of number with *T. gregaria* the most numerous in 1999 and 2001, and *Euphausia* sp. in 2000. The hyperiid amphipod *T. gaudichaudii* was the second most important item after the euphausiids in terms of numbers in 1999 and 2000 (8.6 and 15.1%, respectively; Table 2).

Based on the standard length, most of the crustaceans found in the diet were adults (Fig. 1). The mean size of *T. gregaria* did not differ between 1999 and 2001 (*t*-test: *t*-value 1.94, $p > 0.05$). Individuals from *Euphausia* sp. were smaller in 2000 (Fig. 1) compared with the other 2 years (ANOVA $F_{2,172} = 6.2$, $p = 0.01$, Tukey comparisons). *T. gaudichaudii* were smaller in 1999 (Fig. 1)

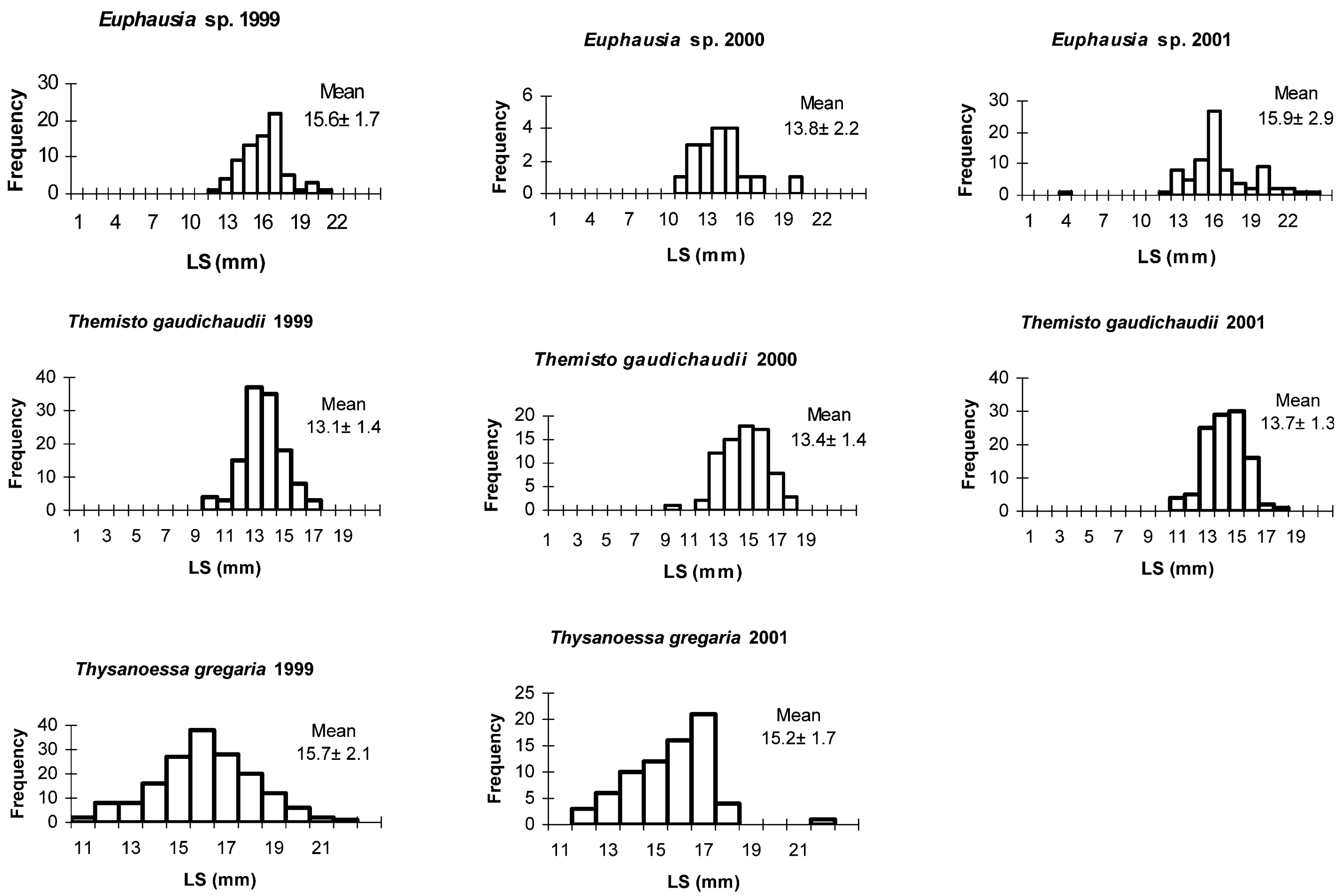

Fig. 1 Length frequency distribution of crustaceans taken by female southern rockhopper penguins (*Eudyptes chrysocome chrysocome*) in the different years

compared with 2001 (ANOVA $F_{2,308} = 6$, $p = 0.01$, Tukey comparisons), but the same size that the ones in 2000. Crustacean larvae and juvenile stages were also found in the samples, but were presumed to be fish and cephalopod prey that was ingested secondarily by penguins as they were usually found in association with the flesh of fish and squid.

Cephalopods

Among the lower beaks of cephalopod, 30% were present inside buccal masses or crowns and would therefore have been ingested relatively recently, while 50% of the beaks were loose but without erosion. Significant differences were found when comparing the degree of digestion of cephalopods within a year. *Gonatus antarcticus* was the most digested cephalopod species alone in 1999 and together with *E. megalocyathus* in 2001, while *L. gahi* was the most digested in 2000 ($\chi^2_6 = 156.8$; $\chi^2_4 = 87.5$; $\chi^2_6 = 148.9$, all $p = 0.01$, 1999, 2000 and 2001, respectively; Fig. 2). Significant inter-annual differences were also found in the degree of digestion of each cephalopod species. *Gonatus antarcticus* was more digested in 1999 while *L. gahi* and *Enteroctopus megalocyathus* were found more digested in 2000. Finally, *M. ingens* and *L. gahi* were also more digested in 2001.

The frequency distribution of LRL from cephalopods recovered in the 2000 differed somewhat from the distribution in 1999 and in 2001 (Fig. 3). Sizes of *L. gahi* consumed in 2000 were smaller than from the other 2 years (ANOVA $F_{2,56} = 10.63$, $p = 0.01$, Tukey comparisons). By contrast, sizes of *E. megalocyathus* (Fig. 3) were higher in 2000 compared with the other 2 years (Kruskal–Wallis $H = 403.61$, $p = 0.01$). Beak sizes of *M. ingens* (Fig. 3) were higher in 1999 compared with the ones found in 2001 (*t*-test *T*-value 3.78, $p = 0.01$). In 2000, we found only one specimen in the subsample. The size of *G. antarcticus* was positively related to numbers of this species consumed ($R^2 = 0.8$, $p < 0.01$), while the opposite was found for *L. gahi* ($R^2 = 0.66$, $p < 0.01$). We found no relationship between the other species with the years.

Fish

Harpagifer bispinnis was the most numerous fish during the three seasons and it formed more than the 90% of the fish in the diet in 1999 and 2001, but only 62% in 2000 when *Salilota australis* contributed 37% to the fish diet.

Diversity and patterns of variability

The diversity indices showed statistical difference between years ($F_{2,48} = 9.31$, $p = 0.01$): mean diversity index 0.045, 0.094 and 0.043 for 1999, 2000 and 2001, respectively. The higher value in 2000 was presumably due to the much greater contribution to the diet of *Euphausia* sp., *G. antarcticus* and *S. australis*.

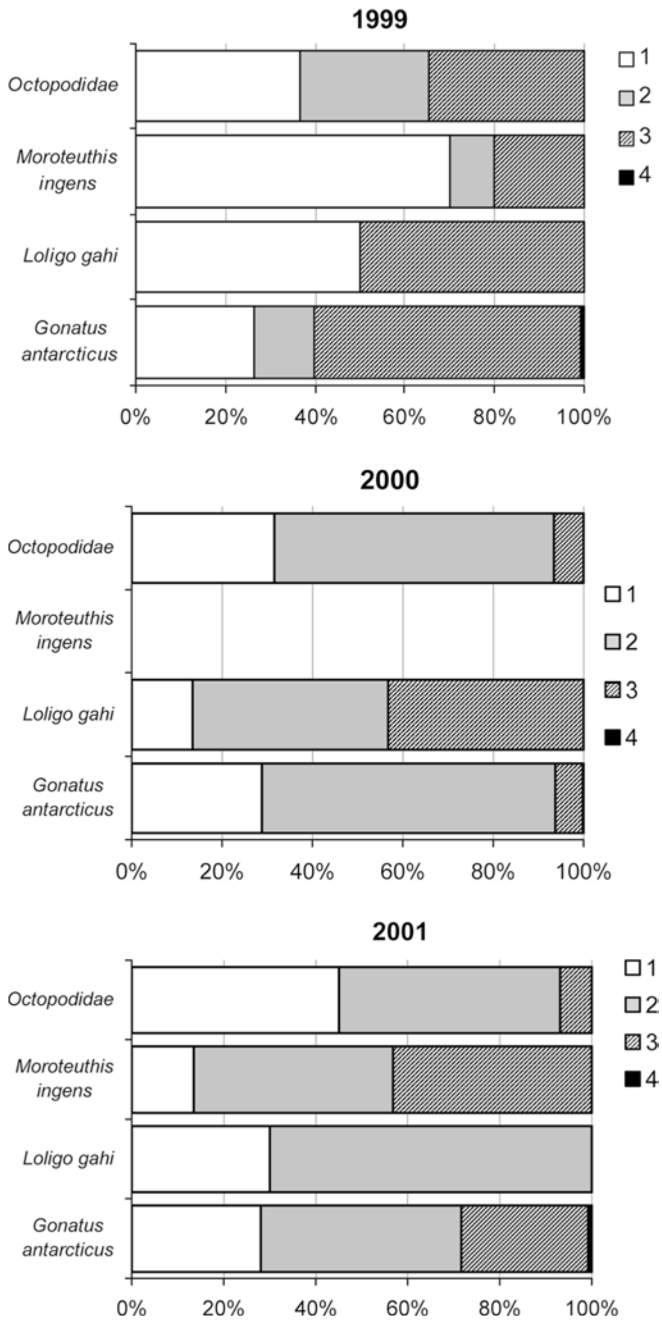

Fig. 2 Lower beaks of cephalopods taken by female rockhopper penguins classified as: *1* removed from buccal mass or crown, *2* loose without erosion, *3* loose with some evidence of erosion, *4* loose with serious damage

Frequency of occurrence of the main prey items showed significant difference between years ($\chi^2_{18} = 36.8$, $p < 0.05$) as did the numbers of the prey species that contributed more in term of percentage to the diet in any year of the study ($F_{6,350} = 8.32$, $p < 0.01$). An evaluation of the inter-annual variation in the proportion of each prey item separately revealed that five showed statistical difference: *G. antarcticus*, *M. ingens*, *T. gregaria*, *Euphausia* sp. and *S. australis* ($F_{2,47} = 2.72$, 3.33, 2.52, 4.52 and 3.94, respectively, $p < 0.01$).

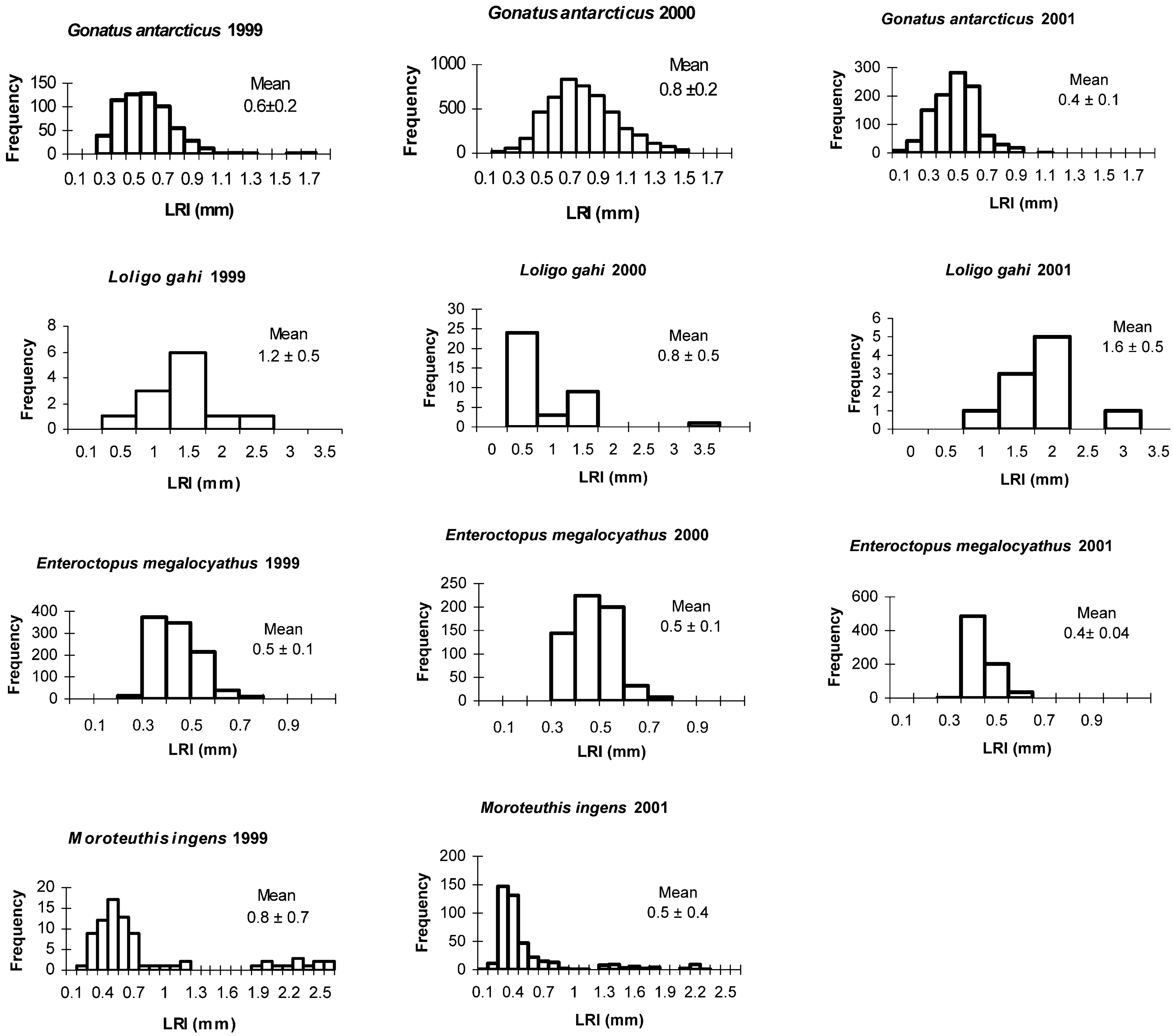

Fig. 3 Length frequency distribution of LRL from cephalopod beaks in the diet of female rockhopper penguins in the different years

Analyzing the standardized proportion (as numbers of prey items relative to the total number of prey item for each year), *G. antarcticus*, *S. australis* and *Euphausia* sp. presented a similar pattern, with a peak in 2000 (Fig. 4) while *M. ingens* and *T. gregaria* showed the inverse pattern.

Discussion

Summary of findings

Southern rockhopper penguins at Staten Island fed on a range of cephalopods, fish and crustaceans in each of the 3 years of the study. Unfortunately, the highly digested nature of the diet samples made it impossible to determine the relative contribution by mass of the fish component compared with the other components. However, the consistent collection methodology did allow detailed inter-annual comparison of the occurrence of the different prey taxa. Based on the results, the diet composition differed each of the 3 years studied. Therefore, rather than describing a "typical" diet in any one year, from which changes can be measured, it may be more appropriate to describe the diet as being highly variable (at least at a prey species level). These changes in diet composition probably reflect changes in the marine zooplankton composition within the foraging range of the penguin colony.

On average, female rockhopper penguins brought ashore 5–10% of their body weight as stomach content. This is a similar load to that found in the southern rockhopper penguins at Beauchene Island, Falkland Island (Croxall et al. 1985) and also in other penguin

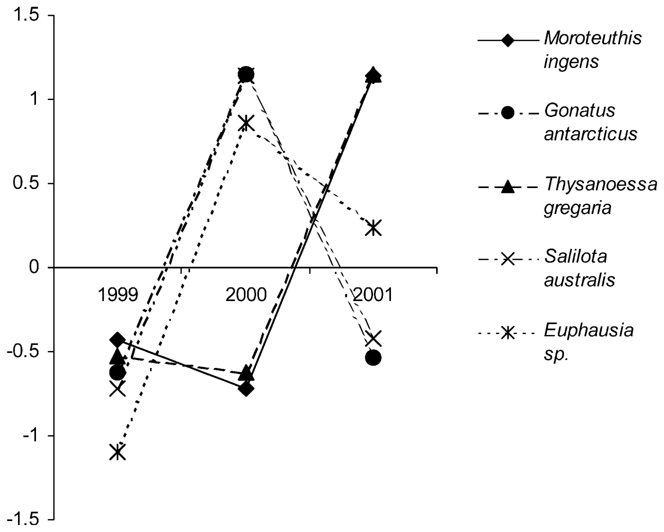

Fig. 4 Changes in the proportion of the major prey items in the diet of female rockhopper penguins in 1999, 2000 and 2001. Proportions are given as number of prey items relative to the total number in each year and all values are standardized

species, especially during the first weeks after hatching (Croxall and Lishman 1987; Hull 1999).

Southern rockhopper penguins at Staten Island seem to feed opportunistically on shoaling or swarming zooplanktonic prey, as previous studies have indicated for other localities (Croxall et al. 1985; Hull 1999). The diet found in this study is similar to that reported for other locations, which all exhibit a reliance on crustaceans and fish, although at Staten Island we found a relatively large consumption of cephalopods. Clausen and Pütz (2002) found a similar pattern of variation between years for southern rockhopper penguin in the Falkland Islands, showing that, in terms of mass, fish dominated the diet from 1995 except for the 1997-1998 season, while from 1988 to 1994, crustaceans and some squids were the most important items. We cannot compare our results directly as we could not assess the contribution by mass of fish. However, the general patterns appear similar and there is no particular bias towards fish, cephalopods and crustaceans.

Characteristics of prey taxa

To better understand the feeding and foraging ecology of southern rockhopper penguins at Staten Island it is important to consider the biology of the key prey taxa. Particularly important is how changes in the diet composition might reflect changes in the abundance and/or distribution of these taxa in the ocean or changes in the foraging behavior of the penguins.

The crustaceans found in the diet have a circumpolar distribution and are associated with subantarctic waters, although *T. gaudichaudii* is present also in Antarctic waters. The euphausiids and the hyperiid amphipod recorded in this study are found in interspecific swarms or swarms within close vicinity to each other having been caught together in net samples (Dadon and Boltovskoy 1982; Tarling et al. 1995). All of them are found at depths up to 100 m and are known to migrate vertically to the surface at night. Whilst we were not able to distinguish between *E. vallentini* and *E. lucens* due to the high level of digestion, we suspect that the majority of these were *E. vallentini* based on the known distribution of both species. Euphausiids are relatively large and frequently dominate zooplankton communities, especially over the continental shelf and in regions of high environmental productivity. Diets are broad and range from dinoflagellates, diatoms and tintinnids to fish eggs and larvae, as well as detritus. Euphausiids are not only prey for fish but they can also be significant predators on fish larvae, and are thought to exert considerable predatory impact on mesozooplankton populations (Gibbons et al. 1999). Moreover, *T. gaudichaudii* is the most common and abundant hyperiid amphipod in the Southern Ocean (Jazdzewki 1982). The results of the present study also highlight the role of *T. gaudichaudii* in the trophic chain of the Southern Ocean, as indicated by Bocher et al. (2001), who described the links between *T. gaudichaudii* and squid, fishes, birds and marine mammals in the Indian Ocean.

The Magellan plunderfish *H. bispinis* is a littoral coastal fish and inhabits waters around Staten Island (Gon and Heemstra 1990). Its diet has been described for the South Shetland Archipelago (Duarte and Moreno 1981) and for the Antarctic Region (Wyanski and Targett 1981). It is a sit-and-wait feeder that consumes primarily amphipods, preying on actively moving organisms which occur either in the water column close to the bottom or actually on the bottom sediments. It was occasionally found whole in prey samples, usually measuring 3 cm, and if it had been possible to estimate its mass it might have made it a major dietary component. *Salilota australis* and *Sprattus fuegensis* inhabit the Patagonian shelf and are associated with the Falkland (Malvinas) current. Indeed, Ehrlich et al. (1999) found densities of 102–1,000 and 11–100 larvae per 10 m^{-2} of *S. fuegensis* and *Agonopsis chiloensis*, respectively around Staten Island.

The most commonly consumed cephalopods were *G. antarcticus*, *M. ingens* and *E. megalocyathus*. Most of the squid beaks were transparent and very small in size indicating juvenile cephalopods, with only a few *L. gahi*, and *M. ingens* of commercial length. In this study, we found small numbers of highly eroded beaks suggesting that cephalopods were consumed close to the colony, especially if we took into account that most of them were very small in size, and would not be retained in the stomach for very long periods (Croxall et al. 1985). The wide range of degree of erosion must also indicate that cephalopods were widely almost homogeneously distributed in waters around Staten Island. Also, the differences found for each species between years suggests inter-annual spatial variation in the cephalopod distribution. There was some evidence that suggests that the most consumed items were also the largest. Larger individuals of *G. antarcticus* were taken in 2000, when its numbers were the highest. It is interesting to note that in 2001, when fish was the second most important item in terms of numbers, the sizes of cephalopods were the smallest for all the species except *L. gahi*. There is no information available on the distribution and abundance of these species in the study area. However, it is known that these mid- to deep-water species are present in the subantarctic zone (Rodhouse et al. 1992, 1996). Small specimens of *G. antarcticus* were found in great numbers in the polar frontal zone although this is generally a poor area for squid (Rodhouse et al. 1992). Moreover, the same study found that early life cycle stages (paralarvae and juveniles) of cephalopods are generally found in association with the major oceanographic features of the southwest Atlantic Ocean. Inter-annual variability in the physical system could thus have profound effects on the abundance of a year class of species whose life cycles are adapted to these features.

The oceanography of Staten Island

The oceanography of the waters around Staten Island (Fig. 5) is only described in very broad terms; waters around Staten Island are included into the Subantarctic Zone, with the Subantarctic Front occurring close to the south and east of Staten Island (Orsi et al. 1995). Local oceanography includes waters from the Antarctic Circumpolar Current as well as waters affected by continental discharges and tidal fronts (Sánchez and Ciechomski 1995; Bertelotti et al. 1996; Piola and Rivas 1997). To the east of Staten Island (60 nm) waters are influenced by a close shelf breakfront, an area recognized to be of high productivity (González et al. 1997). As a result, the coastal waters off Tierra del Fuego and Staten Island have a large biomass of zooplankton and ichthyoplankton (Sabatini et al. 1999; Sánchez and Ciechomski 1995).

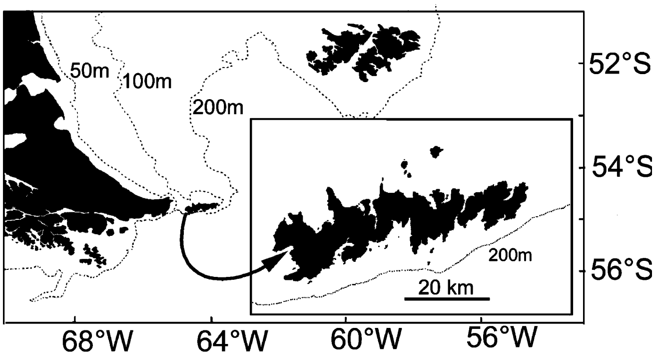

Fig. 5 Location of the study site, southern portion of the SW Atlantic Ocean

Factors influencing inter-annual variability

Inter-annual variation in the proportion of prey items consumed was apparent only for some prey species, with a higher proportion of *T. gregaria* in 1999, *G. antarcticus* and *T. gaudichaudii* in 2000 and *H. bispinis*, *Euphausia* sp. and *T. gregaria* in 2001. These data suggests variability in the prey resources at sea during the study period and a non-specialized diet of this penguin. It would appear that this generalist behavior is reflected in the many differences in diet between sites (Croxall et al. 1985; Hull 1999; Tremblay and Cherel 2003), which probably relate to broad-scale differences in inshore prey availability or abundance.

No single factor emerges as an explanation of changes in the diet between the 3 years of the study. There is some evidence that in 2000, when diet samples were more digested based on the unidentified crustaceans (Table 2), the digestion of cephalopods (Fig. 2) and fish (data not shown), and there was also a greater diversity, penguins might have been spending more time at sea, perhaps foraging over a greater area. A possible reason for these changes in diet composition could be the high degree of oceanic mixing that occurs in this region producing changes in the availability of the different taxa. We found some evidence of prey taxa showing linked changes in their relative contribution to the diet.

When the composition by number of *H. bispinis* was low, that of *T. gaudichaudii* was high and vice versa, suggesting a relationship between these two species. A potential explanation for this relationship could be a competitive interaction in numbers of the amphipods controlled by the predator. At the South Shetland Archipelago, the amphipod prey of *H. bispinis* was the dominant zooplankton species only in those seasons when the density of *H. bispinis* was low (Duarte and Moreno 1981). It is known that *H. bispinis* feeds on amphipods from the suborder Gammaridea which inhabit the intertidal zone. However, the diet of juveniles which live in shallow waters throughout the water column is not known. Rockhopper penguins feed on juveniles and larvae of this species so amphipods from the suborder Hyperiidea could be eaten by this fish at this stage.

Although there is little information on the diet of the squid present in the stomach contents, it is known that most of these species rely on crustaceans particularly in the early life history stages (Rodhouse et al. 1996). In 2000, the composition by mass of crustaceans was small compared with both 1999 and 2001. In contrast, the composition by number and mass of cephalopod was extremely high. This suggests a predator-prey relationship similar to the one found for *H. bispinis* and *T. gaudichaudii*. It is known that *G. antarcticus* feeds on *T. gaudichaudii* (Rodhouse et al. 1996). By contrast, with the predator–prey relationship found for *H. bispinis*, their frequency by number varied together depending on the year.

In terms of the food web in the area, we suggested a relationship in the availability between *T. gaudichaudii* and *G. antarcticus*, and between *T. gaudichaudii* and *H. bispinnis*. Also, we found that some species varied together, for example *S. australis* with *G. antarcticus* and *M. ingens* with *T. gregaria*. These could be predator–prey relationships or they could be independent of each other, but responding differently to the same factors, the ones that do not co-vary or responding in the same way as the ones that vary together. These relationships highlight the importance of understanding food web interactions, especially those involving multiple trophic levels, when determining the role of upper-trophic level predators in marine systems. The complexity of the marine food web of the region indicates the need for detailed information not only on the foraging locations of penguins, but also from independent assessments of the zooplankton composition in those areas.

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