Feeding ecology and abundance of two sympatric skates, the shortfin sand skate *Psammobatis normani* McEachran, and the smallthorn sand skate *P. rudis* Günther (Chondrichthyes, Rajidae), in the southwest Atlantic

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The diet, feeding strategy, and abundance of *Psammobatis normani* and *P. rudis* in the southwest Atlantic was investigated to determine whether the species are segregated by habitat or dietary preference. The two coexist along the Argentine continental shelf, but there are differences in abundance. The most important prey for *P. normani* were crustaceans (mainly crabs and isopods) and, to a lesser extent, polychaetes, whereas *P. rudis* fed almost exclusively on crustaceans (mainly isopods, crabs, and gammarids), and fish and polychaetes contributed less to the diet. This suggests that *P. normani* and *P. rudis* are secondary consumers (trophic level <4). The two species fed on similar taxa, but in slightly different proportions according to region. However, an ANOSIM test failed to reveal significant differences in their diets. Circumstantial evidence of food competition is suggested, because the two species attain similar adult size and there are no notable morphological differences between them. Interspecific competition may be reduced by the use of distinct feeding behaviour and by the abundance of prey especially along shelf-break fronts. The use of standard ecological indices of similarity and multivariate techniques to calculate dietary overlap is evaluated.

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Introduction

Skates are significant predators in benthic and demersal communities, preying mostly on fish and invertebrates (McEachran and Musick, 1975; Ajayi, 1982; Ebert *et al.*, 1991; Ellis *et al.*, 1996; Orlov, 1998). Skate bycatch in the demersal fisheries of Argentina is considerable (Cedrola *et al.*, 2005); indeed, most skates were discarded until the early 1990s. However, this situation has changed recently, commercial landings increasing from 300 t in 1991 to 14 856 t in 1998 (Cousseau *et al.*, 2000). The generally low fecundity, slow growth, and late maturity typical of most skate species indicates that they are particularly sensitive to fishing pressure and overexploitation (Walker and Hislop, 1998), and fishing pressure could lead to changes in the structure and function of benthic and demersal communities (Stevens *et al.*, 2000).

The skate fauna in Argentine waters comprises at least 23 species (Cousseau *et al.*, 2000; Diaz de Astarloa and Mabragaña, 2004). Despite their local diversity, relatively few studies have been carried out on their feeding habits. The diet and feeding ecology of just three species, the beaked skate *Dipturus chilensis*, the sand skate *Psammobatis extenta*, and the Patagonian skate *Bathyraja macloviana*, were recently investigated (Lucifora *et al.*, 2000; Kohen Alonso *et al.*, 2001; Braccini and Perez, 2005; Mabragaña *et al.*, 2005; Scenna *et al.*, 2006).

The genus *Psammobatis* is common in South American waters (Menni, 1972; McEachran, 1983; De Carvalho and Figueiredo, 1994; Menni and Stehmann, 2000). It has eight species, seven of which are present in the southwest (SW) Atlantic. Among congeners, *P. rudis* and *P. normani* have the widest distributions, occurring in the SW Atlantic and SE Pacific, from 60 m to ca. 200 m (McEachran, 1983; Pequeño and Lamilla, 1993; Mabragaña and Cousseau, 2004). Published biological information for both is limited to their reproductive biology (Sanchez and Mabragaña, 2002; Mabragaña and Cousseau, 2004), length–weight relationships, and length frequencies (Cedrola *et al.*, 2005). A qualitative description of their diet off southern Patagonia was made by Sanchez and Mabragaña (2002).

Both species are common off southern Patagonia, but they are found also over the northern Argentine continental shelf (ACS) (Sanchez and Mabragaña, 2002). These water masses are characterized by the presence of several marine fronts, which enhance primary and secondary production (see references in Acha *et al.*, 2004). The shelf-break front is a permanent feature of the edge

of the shelf; their inner boundary lies between the 90 m and the 100 m isobaths. There is also another frontal zone off southern Patagonia, around Islas Malvinas (Acha *et al.*, 2004). The concentration of benthic and pelagic prey along frontal zones is important for several species of teleosts, seabirds, and marine mammals (Acha *et al.*, 2004), but its importance to skates is unknown.

One of many mechanisms facilitating species coexistence is resource partitioning, whereby coexisting consumer species reduce their level of shared prey to avoid deleterious effects of competition (see references in Wilson and Richards, 2000). As *P. rudis* and *P. normani* attain similar adult size and inhabit the ACS (Mabragaña and Cousseau, 2004), the main goal of this work was to investigate possible mechanisms of their coexistence, using diet, feeding strategy, and overlap analyses to determine whether they partition either their habitat or type of diet.

Material and methods
Data collection
Skates were collected from nine research cruises carried out by the National Institute for Fisheries Research and Development (INIDEP) in three regions of the SW Atlantic: northern (off Uruguay and the Argentine Province of Buenos Aires, 34–41°S), central (north Patagonia, 41–48°S), and southern (southern Patagonia, 48–55°S) (Figure 1). Each region was divided into shallow (<100 m) and deeper sites (>100 m), allowing for comparisons of sites by oceanographic and biological condition (Acha *et al.*, 2004, and references therein). The research cruises were carried out between 1998 and 2001 and were designed for
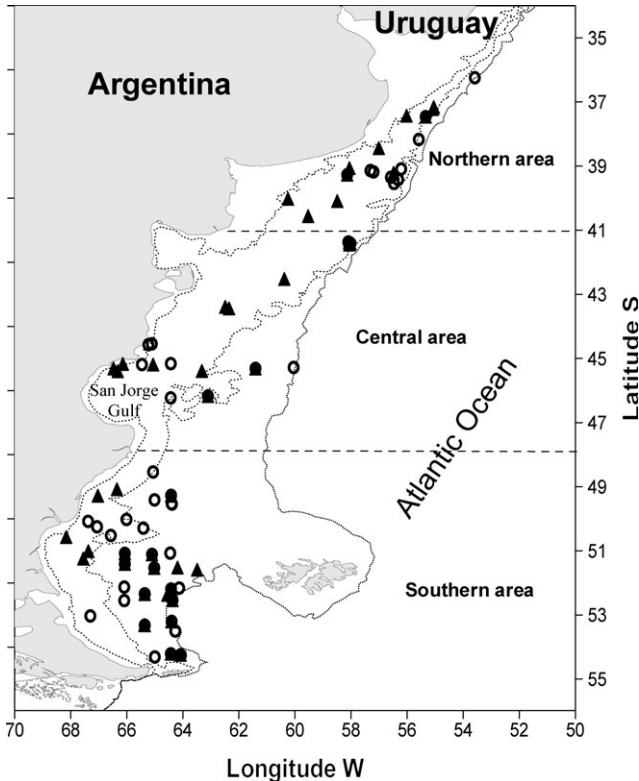

Figure 1. The study area showing the position of trawl stations. Solid triangles represent positive trawls for *Psammobatis normani*, and open circles positive trawls with *P. rudis*. The three areas are divided by dotted lines.

the assessment of demersal fish stocks, especially Argentine hake (*Merluccius hubbsi*) and hoki (*Macruronus magellanicus*). Skates (182 *P. normani* and 148 *P. rudis*) were captured using a bottom trawl (200 mm mesh in the wings and 120 mm in the codend, vertical height 4 m, horizontal opening 15 m). Tow duration was 30 min. Additional specimens were obtained from commercial trawlers. Total length (TL) and disc width (DW) of each skate were measured to the nearest millimetre (mm), and weight to the nearest gramme (g), and the sex of each animal was recorded. Stomachs were frozen and analysed ashore.

Density analysis
Data obtained from two research cruises during 2001 were used to estimate densities of the two species. The total mass of each species caught in each trawl was recorded, and the density of each was calculated as $D_i = C_i/a_i$, where D_i is the density (by weight), C_i the catch in t, and a_i the swept area in square nautical miles (distance of trawling × distance between net wings) in fishing haul i.

Because of significant departures from normality and homogeneity of variances, a non-parametric analysis of variance (ANOVA) (Kruskal–Wallis test), followed by a Dunn's multiple comparisons test (Zar, 1984), was used to determine whether the densities of skate differed significantly among species, sites, or depths.

Diet
Prey items of each skate species were identified to the lowest taxon possible, counted, and weighed (wet) to the nearest 0.01 g. We recorded percentage frequency of occurrence (%F), percentage by weight (%W), and percentage by number (%N) of prey. We assessed prey importance using the alimentary index (IA), calculated for each prey category i as the product of %F_i and %W_i (Lauzanne, 1975 in Rosecchi and Nouaze, 1987), and expressed as a percentage, where

$$\%IA = \frac{100 IA_i}{\sum_{i=1}^{n} IA_i},$$

and n is the total number of food categories considered at a given taxonomic level (Griffiths, 1997). We considered excluding information on numerical percentage contribution in this analysis because it gives no information on energy flow, is biased towards small prey items (e.g. amphipods and isopods), and there are practical difficulties in estimating numbers when prey items have undergone considerable digestion (i.e. soft bottom invertebrates such as polychaetes are usually found fragmented in stomach contents) (Hyslop, 1980; Wallace, 1981; Griffiths, 1997). However, we decided to provide estimates of numerical abundance to facilitate comparison with other studies using this metric.

Prey items were assigned to 12 prey categories to facilitate intra- and interspecific comparison of the diet. For ontogenetic comparisons, individuals of each species were divided into two size classes based on a calculated average size at 50% maturity for males and females, after Mabragaña and Cousseau (2004). To assess sample size sufficiency, randomized prey curves were generated using 100 resamplings; this technique plots the cumulative number of stomachs analysed against the cumulative number of prey taxa (or prey categories) encountered.

Trophic level (TR) was calculated to determine the position of both skates within the foodweb. Trophic level of each skate j (TR_j) was calculated after Cortés (1999) as $TR_j = 1 + (\sum P_i \times TR_i)$, where TR_i is the trophic level of each prey item and P_i the proportion of each prey item in the diet of skate j. Trophic level of prey items was obtained from Ebert and Bizarro (in press).

Feeding strategy

To obtain information on feeding strategies in terms of specialization (a narrow dietary niche width) and generalization (a broad dietary niche width), we used the graphic method proposed by Amundsen *et al.* (1996), which incorporated prey-specific biomass into Costello's (1990) analysis. This parameter is defined as the percentage a prey taxon constitutes of all items in only those predators in which the actual prey occurs, or in mathematical terms:

$$P_i = \left(\sum B_i / \sum B_{ti}\right) \times 100,$$

where P_i is the prey-specific biomass of prey i, B_i the stomach content (weight) of prey i, and B_{ti} the total stomach contents of only those predators with prey i in their stomach. This value is then plotted against frequency of occurrence on a two-dimensional graph. As stated by Amundsen *et al.* (1996), "Differences in feeding strategies are related to the between- and within-phenotype contributions to the niche width. In a population with a high between-phenotype component, different individuals specialize on different resources type, whereas in population with a high within-phenotype component, most of the individuals utilize many resources types simultaneously."

Diet overlap

Schoener's diet overlap index (Schoener, 1970) was used to measure the diet overlap between species, sex, size classes, and areas. According to Wallace and Ramsey (1983), overlap values >0.6 should be considered biologically significant. Similarity in the composition of the diet between species and sites was determined by a non-parametric multivariate analysis and an analysis of similarities (ANOSIM) test (Clarke and Warwick, 2001). The %IA of each prey category was calculated for each skate species based on pooled data for each site (trawl). The ANOSIM test was used to search for differences in the diet between areas and species. This permutation test analyses differences between replicates within sites contrasted with differences between sites, computing an R-statistic under the null hypothesis "no differences between sites". R falls between -1 and 1, so R is ~0 if the null hypothesis is true and $R = 1$ if all replicates within sites are more similar to each other than are replicates from different sites. Classification (CLUSTER, group average sorting of the Bray–Curtis similarity measure based on %IA data), ordination (multidimensional scaling, MDS, on the above similarity matrices), and ANOSIM were performed using the PRIMER software (Clarke and Warwick, 2001).

Morphology of jaws

A sample of jaws (46 *P. normani* and 34 *P. rudis*) was dissected to describe the dentition and to assess whether they might be influencing differences in prey type ingested by the skates. A parametric ANOVA (Zar, 1984) was used to compare the number of rows of teeth on upper and lower jaws between species (both are considered to be fixed factors).

Results

Abundance patterns

Psammobatis normani and *P. rudis* were found at similar depth, from 60 to 200 m, but with some differences in abundance (Figure 2 and Table 1). Densities of *P. rudis* were greater at southern sites than at northern sites at depths >100 m, whereas
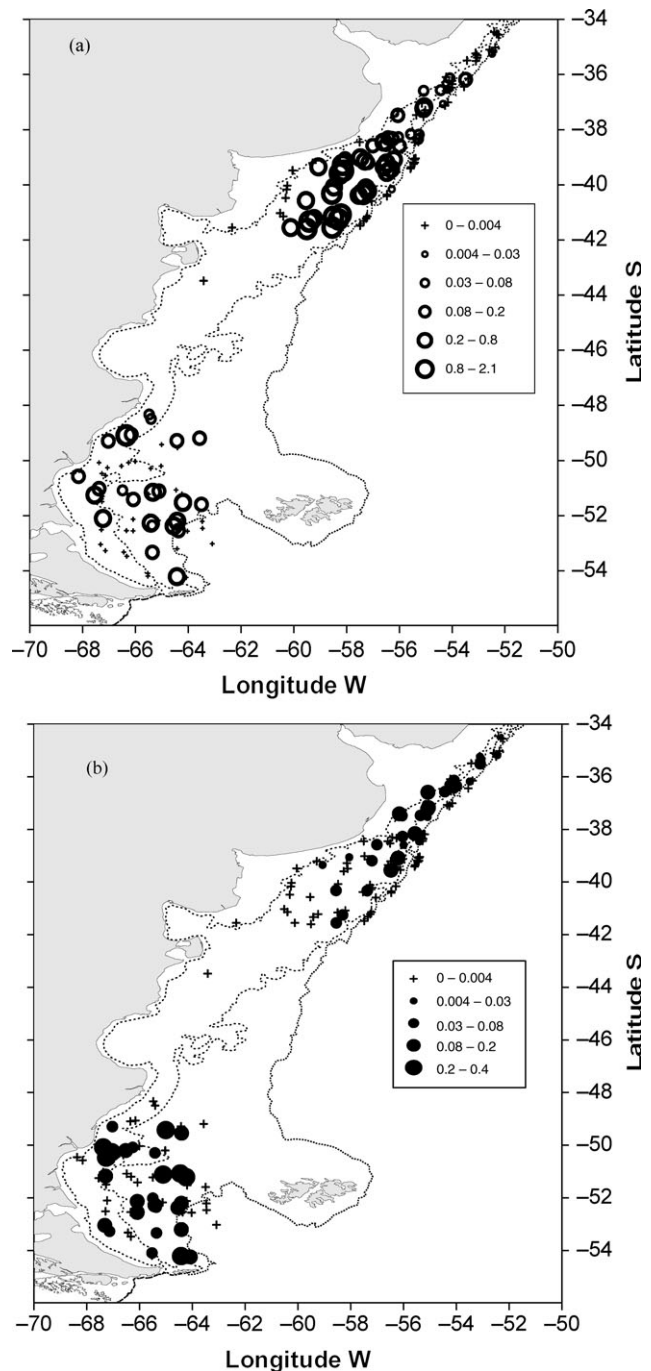

Figure 2. Study area showing estimated densities (t per square nautical mile) of (a) *Psammobatis normani,* and (b) *P. rudis* from two research cruises in 2001. Plus signs represent trawls with no catch.

Table 1. Relative densities of *Psammobatis normani* (Pn), and *P. rudis* (Pr) in the study area expressed in t per square nautical mile.

Area	Average densities (<100 m)		Average densities (>100 m)		Number of trawls	Positive trawls	
	Pn	Pr	Pn	Pr		Pn	Pr
Northern	0.32[C] (0.42)	0.02[AB] (0.04)	0.01[A] (0.02)	0.005[A] (0.01)	107	51	32
Southern	0.04[AB] (0.08)	0.05[AB] (0.08)	0.13[BC] (0.22)	0.08[BC] (0.11)	61	24	28

Values in parenthesis correspond to 1 s.d. Different letters indicate that differences are significant at $p < 0.01$ (Dunn's multiple comparisons test).

densities of *P. normani* were greater at northern sites <100 m and at southern sites >100 m (Table 1).

Diet

All sample sizes except that for the central area for *P. rudis* were adequate for diet comparisons, because the cumulative curves reached an asymptote (Figures 3–5). Schoener's diet overlap index between males and females of both skate species were relatively high (>0.8), indicating a high level of similarity between diets, so diet composition data for both sexes were pooled for subsequent analyses.

Psammobatis normani ($n = 182$) ranged from 241 to 580 mm TL. All contained food. Five major zoological groups, comprising 26 prey items, were found (Table 2). The most important prey groups, in terms of %IA, were crustaceans (85.04%) and polychaetes (14.89%). The former includes decapods and isopods (Serolidae) as main items. Other prey items occasionally found in the diet were fish, salps, and cephalopods. Diet composition between the two size classes was similar (Table 3). The Schoener index showed a high degree of dietary overlap between both categories (SI = 0.83). Only the %IA of serolid isopods differed

between class I (3.42%) and class II (19.27%) (Table 3). Overall, trophic level of *P. normani* was 3.65 (northern 3.59, central 3.55, and southern 3.97).

Psammobatis rudis ($n = 148$) ranged from 267 to 531 mm TL, and 93.2% contained food. Four major zoological groups, comprising 24 prey items, were found (Table 2). Crustaceans (96.44%) were the most important prey in terms of %IA, and included isopods, crabs, and amphipods as major items. Fish, polychaetes, and molluscs were occasionally included. Diet composition between the two size classes considered was slightly different. The Schoener index showed moderate diet overlap (SI = 0.57). Gammarids, crabs, and polychates were consumed mostly by class I, and isopods (Arcturidae and Cirolanidae) and fish preferably by class II (Table 3). The overall trophic level of *P. rudis* was 3.95 (northern 3.74 and southern 4.06).

Feeding strategies

The plots of feeding strategy for *P. normani* indicated a tendency for population specialization towards crustaceans and, to a lesser degree, polychaetes (Figure 6a). Crabs, worms, serolids, and amphipods made a large contribution to the diet and were consumed using a mixed feeding strategy, with varying degrees of specialization and generalization among individual skate (Figure 6b). In contrast, feeding strategy plots for *P. rudis* indicated a clear tendency to specialize on crustaceans (Figure 7a), preying on gammarids, isopods, crabs, and other crustaceans using a mixed feeding strategy at an individual level (Figure 7b).

Interspecific comparisons and regional trends

Both skates fed on similar prey, but they appeared in slightly different proportions according to the region analysed (Table 3). This was reflected in the global test of ANOSIM ($R = 0.098$, $p < 0.05$), which indicated no significant difference between the diets of the two species. This trend was evident also in the ordination (Figure 8a) and classification (Figure 8b) analysis, in which only a few sampling sites were clustered together. In contrast, the Schoener index revealed no biologically significant overlap between species (SI = 0.39).

Crabs were important prey of *P. normani* in northern (*Libidoclea granaria* and *Leucippa pentagona*) and central (*Peltarium spinosulum* and *L. granaria*) areas (Table 3), whereas in the south, they were replaced by small crustaceans such as serolids and gammarids. Polychaetes were in similar proportions in northern and southern regions. The ANOSIM test reflected these differences between northern and southern areas ($R = 0.447$, $p < 0.001$), and between central and southern areas ($R = 0.631$, $p < 0.001$). Differences between northern and central areas were not significant ($R = -0.021$, $p > 0.05$). These regional trends were reflected in the ordination analysis (Figure 9a). Finally, the Schoener index suggested a relatively limited overlap between
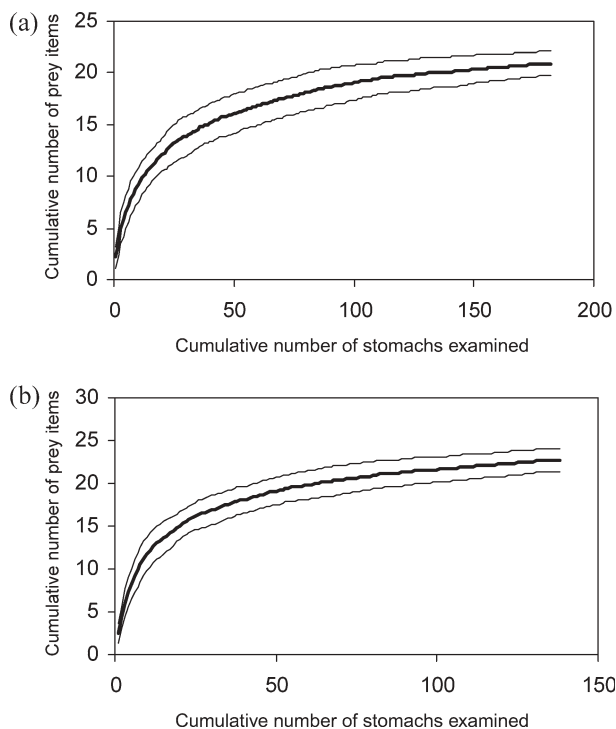
Figure 3. Cumulative prey curves (mean ± s.d.) for all prey items collected from (a) *Psammobatis normani*, and (b) *P. rudis* stomach samples as a function of sample size, generated from 100 resamplings.
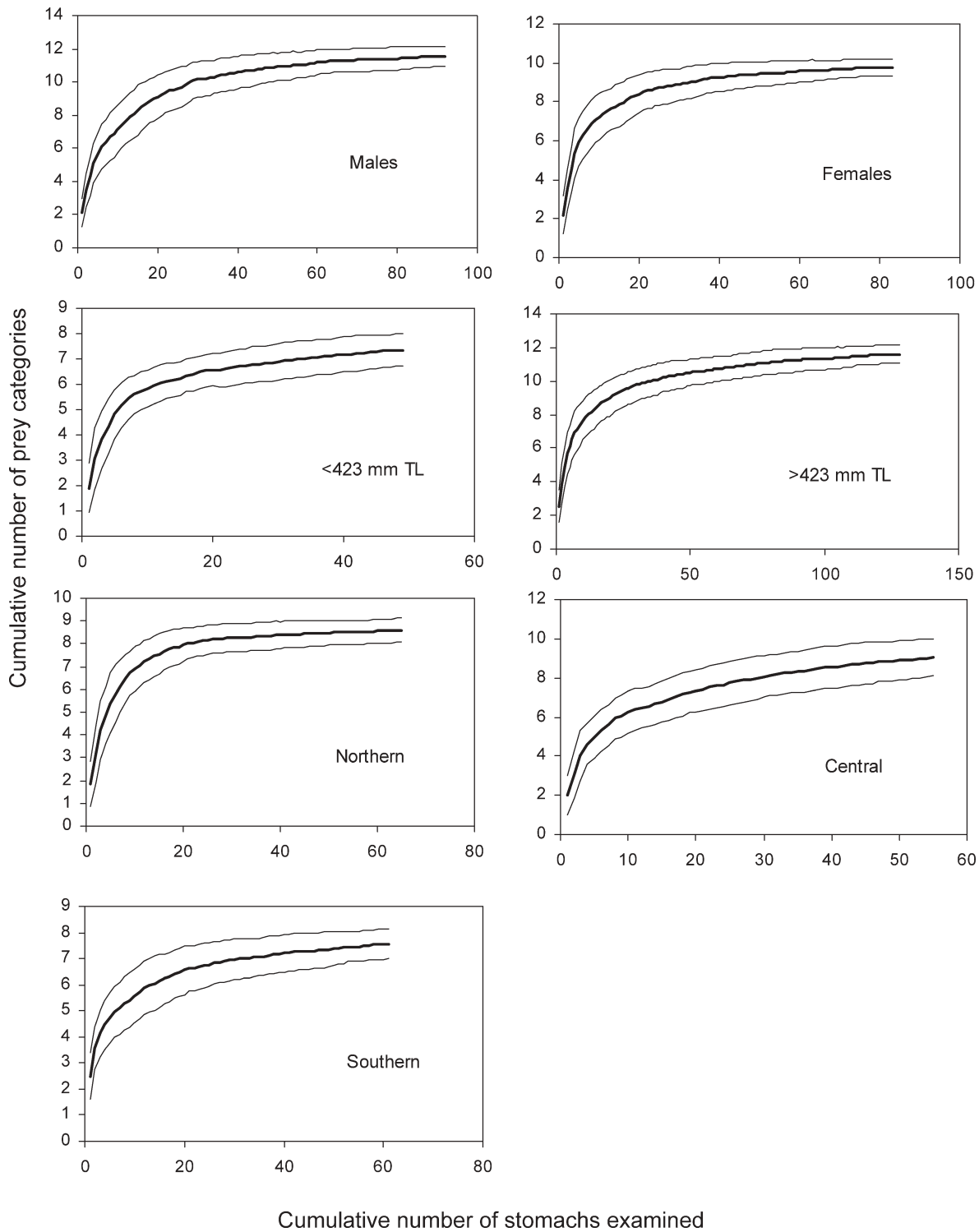
Figure 4. Cumulative prey curves (mean ± s.d.) of prey categories as a function of sample size used in the comparative analysis of the diet of *Psammobatis normani* generated from 100 resamplings.

northern and southern areas (SI = 0.4), northern and central areas (0.51), and especially central and southern areas (SI = 0.05).

The diet of *P. rudis* was relatively consistent over the regions analysed (Table 3). In the northern area, crabs (*L. granaria* and *Peltarium spinosulum*) and gammarids were the most important prey, but they were less important in the southern region, where

isopods were also one of the major items ingested (Table 3). The MDS plot (Figure 9b) and the ANOSIM test ($R = 0.104$, $p > 0.05$) reflected similar diets in northern and southern areas. In contrast, the Schoener index (SI = 0.49) suggested a low degree of overlap between areas. Low sample size in the central area prevented comparisons of that area with the other regions.
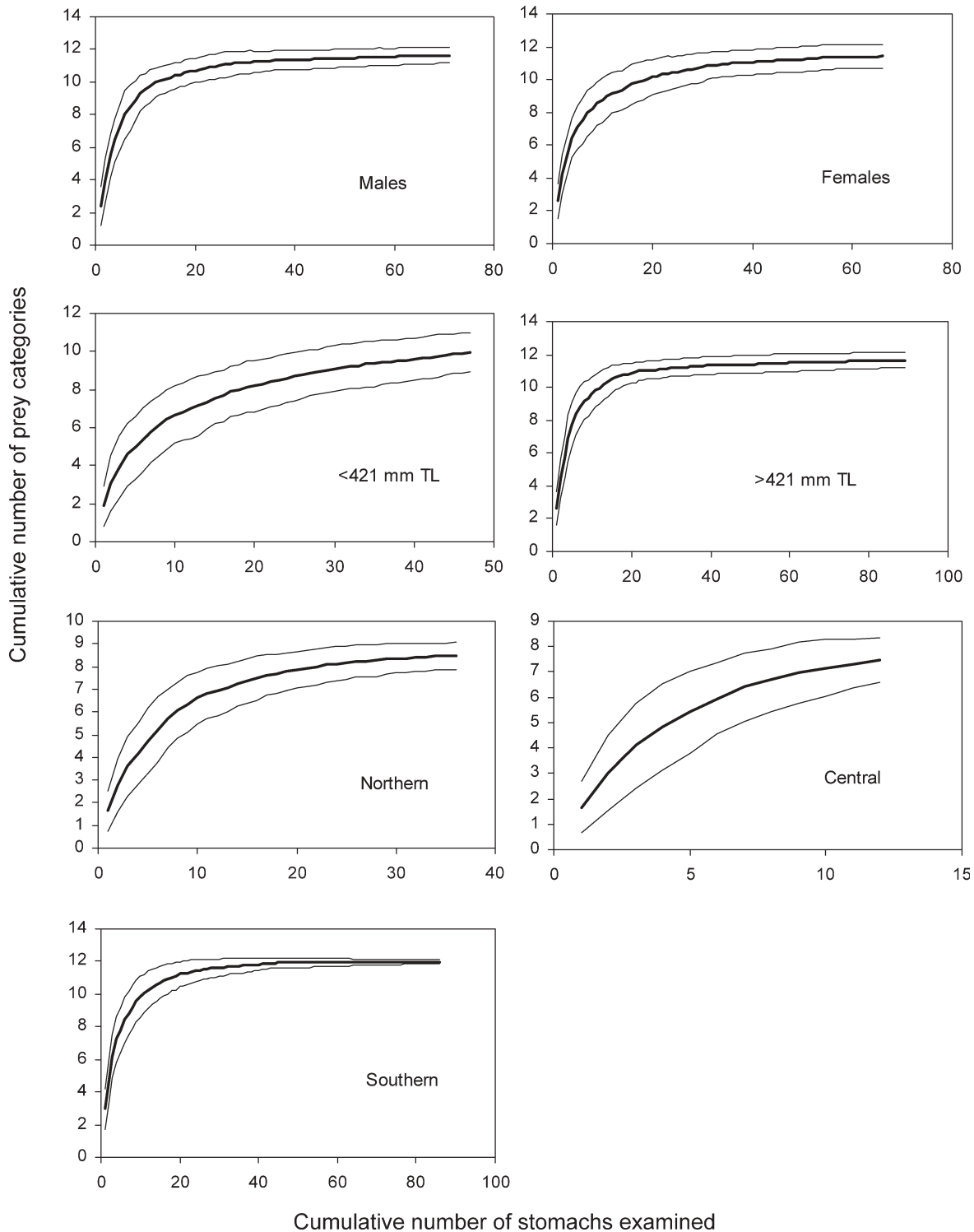
Figure 5. Cumulative prey curves (mean ± s.d.) of prey categories as a function of sample size used in the comparative analysis of the diet of *Psammobatis rudis* generated from 100 resamplings.

Dentition and morphology of jaws

Tooth morphology of both species was similar. Females and juveniles of both species have rounded cusp teeth, whereas mature males have pointed cusps. The ANOVA test ($F = 102.45$, $p < 0.0001$) indicated that the median number of teeth differed significantly

between species, *P. normani* having more teeth than *P. rudis* (40.5 vs. 34; Tukey test, $p < 0.05$). Moreover, *P. normani* showed differences in the number of teeth in upper and lower jaws (39.4 vs. 41.5), whereas in *P. rudis*, both jaws had a similar number of teeth (33.5 vs. 34.5) (Tukey test, $p < 0.05$).

Table 2. Stomach contents of *Psammobatis normani* and *P. rudis* from the study area, presented as percentage frequency of occurrence (%*F*), abundance (%*N*), wet weight (%*W*), and percentage of the Alimentary index IA (%*F* × %*W*) for each prey taxon (%IA).

Taxon	%F	%W	%N	IA	%IA
Psammobatis normani					
Osteichthyes	**2.75**	**1.23**	**0.31**	**3.37**	**0.04**
Raneya sp.	1.10	0.95	0.13	1.04	0.04
Genypterus blacodes	0.55	0.14	0.06	0.08	<0.01
Fish remains	1.10	0.14	0.13	0.15	<0.01
Thaliacea	**2.20**	**0.72**	**1.88**	**1.59**	**0.02**
Salpidae	2.20	0.72	1.88	1.59	0.06
Crustacea	**92.86**	**74.17**	**79.03**	**6 887.62**	**85.04**
Pleoticus muelleri	11.54	3.45	2.00	39.83	1.53
Artemesia longinaris	2.20	0.13	0.25	0.28	0.01
Munida spp.	2.75	1.92	2.75	5.27	0.20
Peltarium spinosulum	18.13	19.30	2.82	349.88	13.43
Libidoclea granaria	14.84	11.55	3.44	171.29	6.57
Leucippa pentagona	7.14	4.17	1.50	29.79	1.14
Lithodidae	2.20	2.78	0.63	6.11	0.23
Brachyura	2.75	2.01	0.38	5.52	0.21
Majidae	1.65	0.80	0.19	1.31	0.05
Amphipoda	34.62	4.90	35.11	169.54	6.50
Serolidae	36.81	14.56	14.27	536.05	20.57
Cirolanidae	14.29	3.67	3.07	52.42	2.01
Arcturidae	8.24	3.37	11.83	27.78	1.06
Macrochiridotea spp.	0.55	0.02	0.06	0.01	<0.01
Stomatopoda	1.10	0.37	0.13	0.40	0.01
Lepidomorpha	1.65	0.22	0.31	0.36	0.01
Crustacean remains	3.30	1.03	0.38	3.41	0.13
Polychaeta	**52.20**	**23.10**	**18.64**	**1 205.64**	**14.89**
Unidentified Polychaeta	52.20	23.05	18.59	1 203.05	46.17
Mollusca	**0.85**	**0.01**	**1.10**	**0.78**	**0.13**
Loligo spp.	0.55	0.54	0.06	0.30	0.01
Octopus spp.	0.55	0.24	0.06	0.13	<0.01
Psammobatis rudis					
Osteichthyes	**23.91**	**7.60**	**4.12**	**181.81**	**2.16**
Fish remains	18.12	5.26	2.83	95.27	4.94
Nototheniidae	5.07	2.38	1.15	12.09	0.63
Spratus fueguensis	1.45	0.21	0.18	0.3	0.01
Crustacea	**97.10**	**83.70**	**90.80**	**8 127.08**	**96.44**
Austropandalus grayi	13.04	6.82	2.13	88.92	4.61
Pleoticus muelleri	3.62	4.41	0.71	15.98	0.83
Artemesia longinaris	0.72	0.62	0.09	0.45	0.02
Munida spp.	9.42	5.31	1.77	50.02	2.59
Leucippa pentagona	7.97	6.49	1.51	51.73	2.68
Peltarium spinosulum	8.7	4.81	1.42	41.79	2.17
Libidoclea granaria	5.07	5.66	0.97	28.71	1.49
Majidae	2.17	1.52	0.35	3.31	0.17
Brachyura	1.45	0.75	0.18	1.08	0.06
Lithodidae	0.72	0.14	0.09	0.1	<0.01
Amphipoda	43.48	9.95	45.79	432.52	22.42
Arcturidae	33.33	12.58	23.12	419.31	21.74
Cirolanidae	32.61	11.81	6.99	385.13	19.96
Serolidae	22.46	5.59	3.99	125.47	6.50
Stomatopoda	0.72	0.51	0.09	0.37	0.02
Ostracoda	0.72	0.45	0.09	0.33	0.02
Crustacean remains	10.87	5.76	1.42	62.57	3.24
Polychaeta	**19.56**	**5.03**	**3.86**	**98.45**	**1.17**
Unidentified Polychaeta	19.56	5.19	3.9	101.64	5.27
Mollusca	**5.8**	**2.83**	**0.70**	**16.42**	**0.19**
Octopus spp.	3.62	1.89	0.44	6.85	0.35
Loligo spp.	1.45	0.82	0.18	1.19	0.06
Semirrosia tenera	0.72	0.21	0.09	0.15	0.01
Others	**4.35**	**0.84**	**0.53**	**3.64**	**0.04**
Unidentified	4.35	0.84	0.53	3.75	0.19

Continued

Discussion

Psammobatis normani and *P. rudis* were found along the ACS from 60 to 200 m deep at similar relative densities except in the northern area deeper than 100 m, where *P. normani* was dominant. Although reliable data on the presence and relative densities in the central area were not available for our study, Cedrola *et al.* (2005) recorded larger catches of *P. normani* than *P. rudis* in a Patagonian red shrimp fishery in the San Jorge Gulf (in the central area, Figure 1), and relative densities of the first species were similar to those estimated for other areas in the present study. Therefore, both skates sympatrically inhabit most areas of the ACS, with some differences in abundance.

The most important prey items of *P. normani* were crustaceans (mainly crabs and isopods) and to a lesser extent polychaetes, whereas *P. rudis* fed almost exclusively on crustaceans (mainly isopods, crabs, and gammarids), with fish and polychaetes contributing less to the diet. Both skates are mainly benthophagous. The fish found in stomachs were mostly benthic and of low motility, and the occasional presence of planktonic organisms in the stomach contents of *P. normani* can be explained by the occasional near-bottom aggregations of those organisms (Colombo *et al.*, 2003; Costello and Mianzan, 2003). Regional variation in the groups of crustaceans consumed was observed in both species. In the northern area, crabs were the main group eaten, whereas in the southern area, isopods and amphipods were the most important. Crabs and isopods are widely distributed over the shelf (Boschi *et al.*, 1992), but the lack of quantitative data on their abundance precludes an assessment of prey selectivity or changes in the diet in response to prey availability by these two species of skate.

Generally, partial spatial segregation, differences in feeding behaviour, and good prey availability facilitate the coexistence of sympatric species (McEachran *et al.*, 1976; Platell *et al.*, 1998; Wetherbee and Cortés, 2004). Our results suggest that *P. rudis* and *P. normani* do not partition their habitat in the SW Atlantic, because both species coexist over the ACS. In terms of feeding behaviour, *P. normani* displayed a tendency to prefer crustaceans, and polychaetes to a lesser degree, whereas *P. rudis* took crustaceans almost exclusively. Both skate species displayed a mixed feeding strategy, with an intermediate situation between high between-phenotype and high within-phenotype contribution to niche width. This was reflected in the prey use over the ACS. For both species, the proportions of different prey differed more at the southern stations than at northern ones. The northern

Table 3. Stomach contents of *Psammobatis normani* and *P. rudis* from the study area, presented as a percentage of the alimentary index (%IA) of prey categories for different areas, sexes, and sizes classes.

Prey group	Total	Northern	Central	Southern	Males	Females	<423 mm	>423 mm
Psammobatis normani								
Fish	0.09	0.40	0.01	0	0.24	0.01	0.03	0.12
Crabs	44.62	46.62	91.10	1.86	42.99	45.20	46.20	43.18
Shrimps	1.28	3.18	1.32	0	0.82	1.43	1.85	1.06
Anomurans	0.14	0	1.29	0	0.05	0.34	0.05	0.14
Gammarids	4.58	1.16	0.05	14.91	3.77	5.92	5.47	4.23
Cirolanids	1.42	0.59	3.44	0.35	0.58	3.10	3.30	0.92
Serolids	14.49	3.26	0.35	44.66	18.77	11.75	3.42	19.27
Arcturids	0.75	0	0	4.44	1.37	0.29	0.05	1.18
Other crustaceans	0.05	0.03	0.10	0	0.03	0.02	0.02	0.05
Polychaetes	32.52	44.52	2.27	33.75	31.29	31.91	39.56	29.76
Squid	0.02	0	0.07	0.02	0.03	0.02	0.05	0.01
Salps	0.04	0.24	0	0	0.07	0.02	0	0.08
Total number	182	76	44	62	88	94	53	129

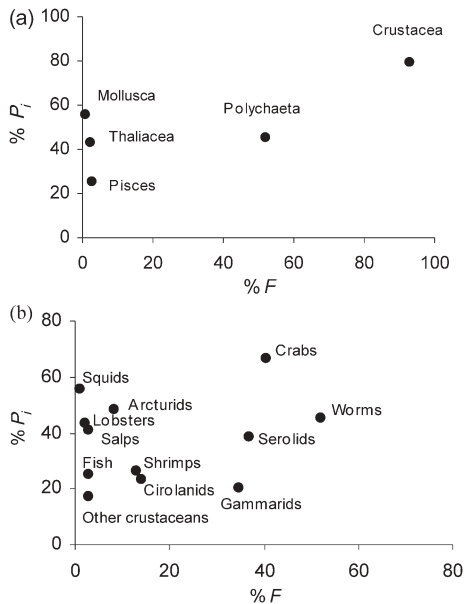|							<421 mm	>421 mm
Psammobatis rudis								
Fish	7.59	3.42	–	9.65	9.29	6.11	1.60	10.99
Crabs	22.13	56.69	–	12.44	20.62	23.68	36.77	17.82
Shrimps	8.33	3.71	–	3.42	9.99	7.08	8.85	7.17
Anomurans	2.02	1.34	–	2.07	1.57	1.59	0.04	3.39
Gammarids	17.49	15.84	–	17.53	25.03	11.37	28.12	11.36
Cirolanids	15.57	6.16	–	18.32	7.66	23.70	8.65	17.57
Serolids	5.07	5.89	–	4.69	4.73	5.40	5.35	4.63
Arcturids	16.95	0.02	–	29.59	16.31	16.87	3.86	23.27
Other crustaceans	0.06	0	–	0.02	0.07	0.05	0	0.12
Polychaetes	4.11	6.82	–	1.29	3.55	3.80	6.76	2.28
Squid	0.69	0.12	–	1.00	1.19	0.36	0	1.40
Total number	138	36	–	90	66	72	48	89

Figure 6. Feeding strategy plot for *Psammobatis normani*. Contribution of prey groups expressed as percentage of prey-specific biomass. (a) Major zoological groups, and (b) prey categories.
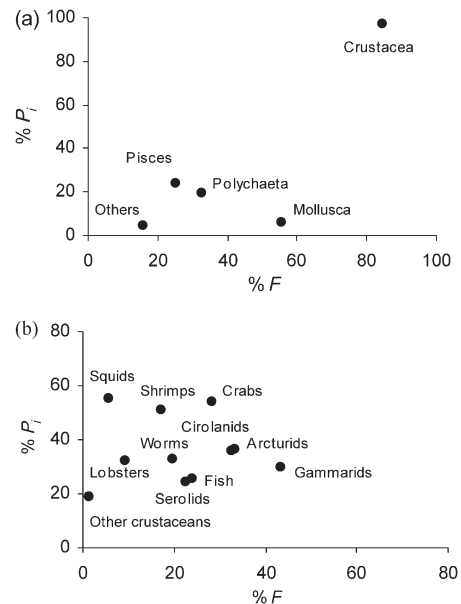

Figure 7. Feeding strategy plot for *Psammobatis rudis*. Contribution of prey groups expressed as percentage of prey-specific biomass. (a) Major zoological groups, and (b) prey categories.
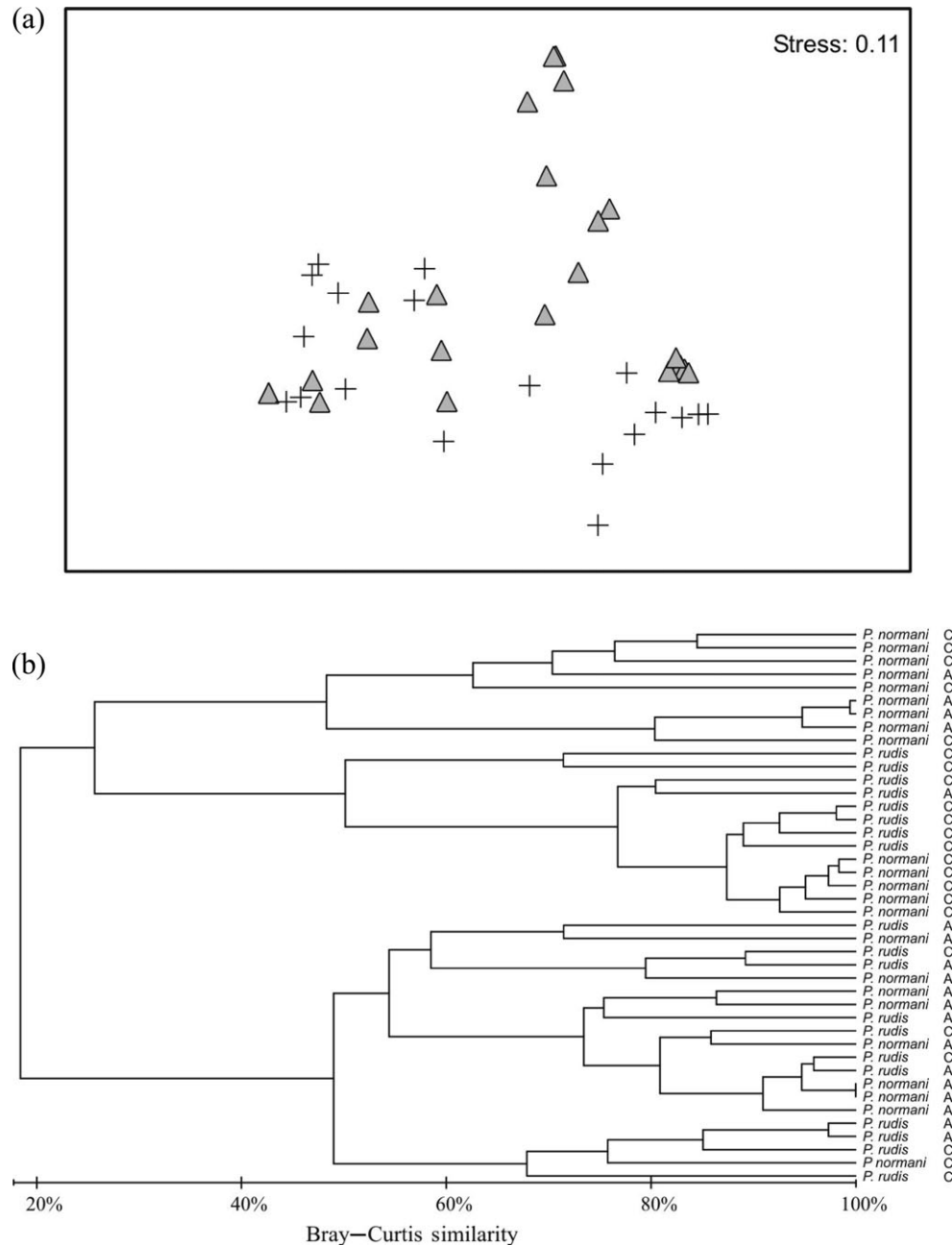
Figure 8. Feeding patterns of *Psammobatis normani* and *P. rudis* in the ACS. (a) MDS ordination of stations using %IA of prey categories. (b) CLUSTER, using group average linking on Bray–Curtis species similarity of %IA of prey categories (pooled for all individuals by species at each sampling station). Triangles, *P. normani*; plus signs, *P. rudis*; A, northern stations; C, southern stations.

area corresponds to the inner boundary of the Argentine shelf-break front, a zone of high productivity, where high concentrations of prey are exploited by a large number of species (Acha *et al.*, 2004). Therefore, greater availability of benthic prey in the northern area could reduce dietary competition between the two species, whereas in the southern area, coexistence could be achieved by the use of different prey proportions, so reducing competition.

McEachran *et al.* (1976) found that differences in the shape of the mouth and the number of tooth rows may be related to skate food habits, species with a less arched mouth and a greater number of tooth rows having a preference for infauna. An exhaustive

description of *P. rudis* tooth morphology was given by Herman *et al.* (1995). They found sexual heterodonty in adults and ontogenetic heterodonty in males, as we found here for *P. normani* and *P. rudis*. Mature males and females of both species had similar diets in this study; so sexual heterodonty in these species is probably related to reproductive behaviour, as postulated by McEachran (1977). Moreover, although *P. normani* has more rows of teeth than *P. rudis*, both species prey on epibenthic and infaunal organisms, with no particular preference.

One way to understand the ecological role of skates in the ecosystem is to estimate their trophic level (TR). Recently, this parameter was calculated for 60 skate species, including several on the
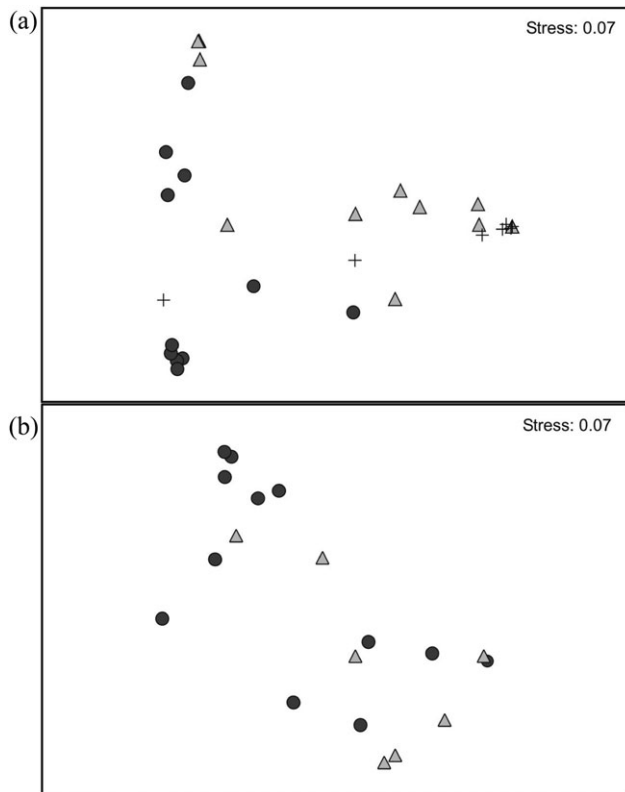
Figure 9. Feeding patterns of (a) *Psammobatis normani*, and (b) *P. rudis* in relation to the region of the ACS analysed. MDS ordination of stations using %IA of prey categories. Triangles, northern area; plus signs, central area; filled circles, southern area.

ACS. Values ranged from 3.48 to 4.22, and the values were generally correlated with the TL of predator (Ebert and Bizarro, in press). Earlier studies on the diet of skates over the ACS, based on quantitative analysis, revealed that larger species such as *D. chilensis* generally preyed on fish and squids (Lucifora *et al.*, 2000; Kohen Alonso *et al.*, 2001), occupying apex positions in the food chains (TR = 4.22). Small species have a mixed diet, based primarily on crustaceans and secondarily on polychaetes such as *P. extenta* (Braccini and Perez, 2005), with a TR of 3.85, or based mainly on polychaetes such as *B. macloviana* (Mabragaña *et al.*, 2005; Scenna *et al.*, 2006), with a lower TR (3.66). Values of TR estimated for *P. normani* and *P. rudis* were higher than expected considering their small size and their carcinophagous diet. On the other hand, although there were no clear differences in the diet of *P. normani* and *P. rudis*, values of TR were different (3.65 vs. 3.95). Differences are mainly attributable to the high TR value for the category "amphipods" (which includes amphipods and isopods), and because these values represent the average TR in the ACS. TR values are similar when calculated by area, and increased from northern to southern areas, possibly reflecting changes in trophic chains from temperate to colder water of Subantarctic origin.

Standard ecological indices of similarity have been used traditionally to calculate dietary overlap among elasmobranch species. More recently, other powerful analyses, including the use of multivariate analysis, have been used to analyse feeding ecology (Platell *et al.*, 1998; Braccini and Perez, 2005; Mabragaña *et al.*, 2005; Lucifora *et al.*, 2006; Rinewalt *et al.*, in press). Here,

we present results from the use of both techniques in the analyses, and there are notable differences in results and interpretation. Do the diets of *P. rudis* and *P. normani* overlap? According to the Schoener index, the degree of overlap is less than 0.6, suggesting no biologically significant difference. However, according to the ANOSIM test and ordination techniques, diets are similar. In the same way, geographical differences in diet observed in *P. rudis* using the Schoener index were not observed using ANOSIM or the ordination approach. Multivariate techniques search for differences between groups of samples, comparing every pair of samples (hence providing more detail), and the results are supported statistically. Therefore, they give a better picture of prey use. On the contrary, traditional indices such as the Schoener index compare just two groups (species, areas, etc.) and show the degree of overlap between the groups considered. Indeed, the "0.6 threshold overlap value" is arbitrary and does not have any statistical support. To improve the accuracy and precision of diet comparisons, the use of statistically supported tools instead of classical methods is recommended.

Acknowledgements

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