

Structure and distribution of the slope fish community in the vicinity of the sub-Antarctic Prince Edward Archipelago

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Abstract

Demersal fish community structure, distribution and trophic relationships on the slope (depth range 200–1500 m) of the sub-Antarctic Prince Edward Islands and surrounding sea rises were investigated during a pilot survey conducted in April 2001 onboard fishing vessel *MV Iris*. A total of 56 fish taxa were collected during the survey, of which 44 were identified to the species level, seven to the genus level and five to the family level. Among the identified taxa, 36 constituted new records for the area investigated. Total catch per unit effort (cpue) during the survey ranged from 1.1 to 241.2 individuals h^{-1} . Both average fish diversity and total cpue positively correlated with trawling depth. Overall, mean sampling depth and near-bottom temperature explained 56% of total fish cpue. Hierarchical cluster analysis identified three distinct fish assemblages with pronounced dominant species. Major shifts in fish community composition occurred at 500–600 m and 800–900 m depth strata and could probably be a result of physical and biological vertical zonation. Analysis of the diet of selected fish species showed that they were generalist feeders, consuming predominantly pelagic, including epipelagic, meso- and benthopelagic, prey. Diets of six species and nitrogen stable isotope signatures of 22 species revealed that with a few exceptions most fishes occupied the fourth trophic level and were tertiary consumers. Wide variability in carbon isotopic signatures is discussed with respect to alternative, *e.g.* possible importance of high Antarctic and chemoautotrophic *v.* photoautotrophic sub-Antarctic primary production, organic matter sources at the base of deep-sea food webs.

Introduction

Intensive commercial fishing in the Southern Ocean began at the end of 1960s, with most important fishing areas concentrating over the shelves and continental slopes of South Georgia, the South Orkney and the Kerguelen Islands (Kock, 1992; Knox, 1994). Unfortunately, on many occasions, commercial fishing in the Southern Ocean was initiated before studies on target species were conducted to assess the potential impact of fishing on their populations. This resulted in overexploitation of several Antarctic fish populations and in some places led to the 'commercial extinction' of valuable fish stocks (Everson, 1984; Kock, 1992; Knox, 1994). Furthermore, it has also been documented that potentially exploitable fish stocks may undertake irreversible changes in case of environmental shifts and overfishing (Kock, 1992; Cushing, 1995). There is, therefore, a need to gain a deeper understanding of the structure and functioning of the Antarctic ecosystem overall and demersal fish communities in particular as a basis for the future management of potential living resources.

The Prince Edward Islands (PEIs), including Marion and Prince Edward Island, are an isolated sub-Antarctic archipelago situated *c.* 2000 km south-east off the South African coastline. Rising steeply from depths of >3000 m,

the islands are separated by a shallow saddle, which varies between 45 and 260 m in depth (Pakhomov & Chown, 2003). The PEIs are relatively young, thin-soiled volcanic islands with terrestrial and nearshore communities strongly influenced by the allochthonous input of energy and nutrients from the surrounding seas (Pakhomov & Chown, 2003). The islands seasonally accommodate >2 million top predators, including flying seabirds, penguins and seals, support commercially exploited demersal fish populations and attract migrating whales to rich feeding grounds (CCAMLR, 1996).

Although 55 species of benthic and benthopelagic fishes are known for the area from Bouvet to Kerguelen-Heard Islands (Duhamel *et al.*, 1983), currently only 44 fish species have been recorded from the shelf area of the PEIs and on surrounding seamounts (Gon & Klages, 1988; Gon & Heemstra, 1990; Pakhomov *et al.*, 2001). Among the recorded taxa, several fish species, *e.g.* the grey notothen *Lepidonotothen squamifrons* (Günther) and the Patagonian toothfish *Dissostichus eleginoides* Smitt are of potential commercial value. A legal, exploratory fishery on the Patagonian toothfish commenced in 1996 (Pakhomov & Chown, 2003). Unknown numbers of fishing vessels, however, have been illegally exploiting Patagonian toothfish stocks prior to 1996, resulting in a near-collapse of this potentially highly lucrative fishery (B. Watkins, pers. comm.). To date, however, there is no information on fish stocks or even fish community structure on the shelf and continental slope of the PEIs and surrounding areas because of the absence of systematic bottom-fish surveys in the area. The fish stocks may, however, be substantial, judging from the Patagonian toothfish fishery and appearance of grey notothen juveniles in the diet of selected species of penguins on Marion Island (Adams & Klages, 1989; Brown *et al.*, 1990).

The main aims of this paper are two-fold: firstly, to provide information on the structure and distribution of the slope demersal fish community in the vicinity of the PEIs, and secondly, to obtain information on the general biology and diets of selected fish species in the South African Exclusive Economic Zone around the PEIs.

Materials and methods

Data for this study were collected during an exploratory cruise to the proximity of the PEIs onboard fishing vessel MV *Iris*, belonging to the commercial company *Irvine & Johnson* based in Cape Town, South Africa. This cruise took place mostly within the South African Exclusive Economic Zone around the PEIs during April and May 2001, while the actual bottom trawling survey was completed between 13 and 30 April 2001 (Fig. 1). In total, 52 trawls between 200 and 1500 m depth (Appendix) were carried out at a speed of 5.6–6.5 km h⁻¹ (3.0–3.5 knots) using a commercial bottom Arrow trawl, which is a bucket-designed trawl for scooping fishes off mountain slopes. The trawl had a wing-span of 33 m, headline height of 9 m vertical and a cod-end mesh-size of 112–115 mm. The footrope was a rockhopper type fitted with 0.533 and 0.610 m rubber discs. Temperature was recorded using a net-mounted sensor for each tow.

The area of investigation was large (Fig. 1) and >90% of the survey area was deeper than the maximum depth that the survey vessel was able to trawl (>1500 m). Furthermore, the region above the 1500 m isobath in the proximity of the PEIs was not contiguous, but rather scattered over a number of seamounts. As the exact number, size and position of those seamounts were unknown, bottom trawlings were possible on only a fraction of the area above the 1500 m isobath. Due to the paucity of bathymetric data for the area of investigation, it was impossible to develop a rigorous survey design. As a consequence, mostly downhill tows covering the maximum possible depth range and trawl distance were carried out. Therefore, this survey should be considered as a pilot study aimed at, for the first time, obtaining information on fish community structure and biology of selected species in this area. The mean sampling depth was calculated as arithmetic mean of start and end depths.

Community analysis

Onboard, fishes were identified to the lowest possible taxonomic level and counted. For comparative purposes, a modified catch per unit effort (cpue, individuals h⁻¹) was calculated scaling the number of collected specimens to 1 h of sampling time. Community structure was analysed using the Plymouth Routines in Multivariate Ecological Research (PRIMER) programme designed by Clarke & Warwick (1994) according to the procedure described in Field *et al.* (1982). The true mesopelagic groups, families Myctophidae and Bathylagidae, were excluded from the

analysis. Log-transformed [$\log_{10}(x+1)$] fish cpue values were used for hierarchical agglomerative clustering (q -type) with group-averaging linking based on the Bray–Curtis similarity measure to delineate groupings with a distinct community structure. Similarity levels were adjusted to obviously meaningful groupings rather than forcing clusters to a fixed level. Following the cluster analysis, a similarity matrix was ordinated using non-metric multidimensional scaling (NMDS) for which a stress level of <0.2 provides an adequate representation of the two-dimensional plot (Clarke & Warwick, 1994). The percentage contribution of individual species to within-group similarity and between-group dissimilarity, based on station cpue data, was determined using the similarity percentages routine (SIMPER) (Clarke & Warwick, 1994). Species contributing to $>70\%$ of the similarity were considered as consolidating species, while species cumulatively accounting for $>70\%$ of dissimilarity were considered as discriminating species. The significance levels and sources of difference between communities were tested using an ANOSIM routine (Clarke & Warwick, 1994). To compare fish communities, the Shannon–Weaver diversity indices [$H' = -\sum p_i(\log p_i)$] and Pielou evenness index [$J = H'(\text{observed}) \times (H'_{\max})^{-1}$] calculated for each station (Clarke & Warwick, 1994).

Differences in environmental parameters between clusters were investigated using one-way ANOVA, performed on data normalized by $\log_{10}(x+1)$ transformation, and Newman–Keuls multiple range tests (Zar, 1984). The relationships between fish cpue values and environmental variables were investigated using regression analysis. All analyses were carried out using STATISTICA'99 software (StatSoft Inc., Tulsa, OK, U.S.A.).

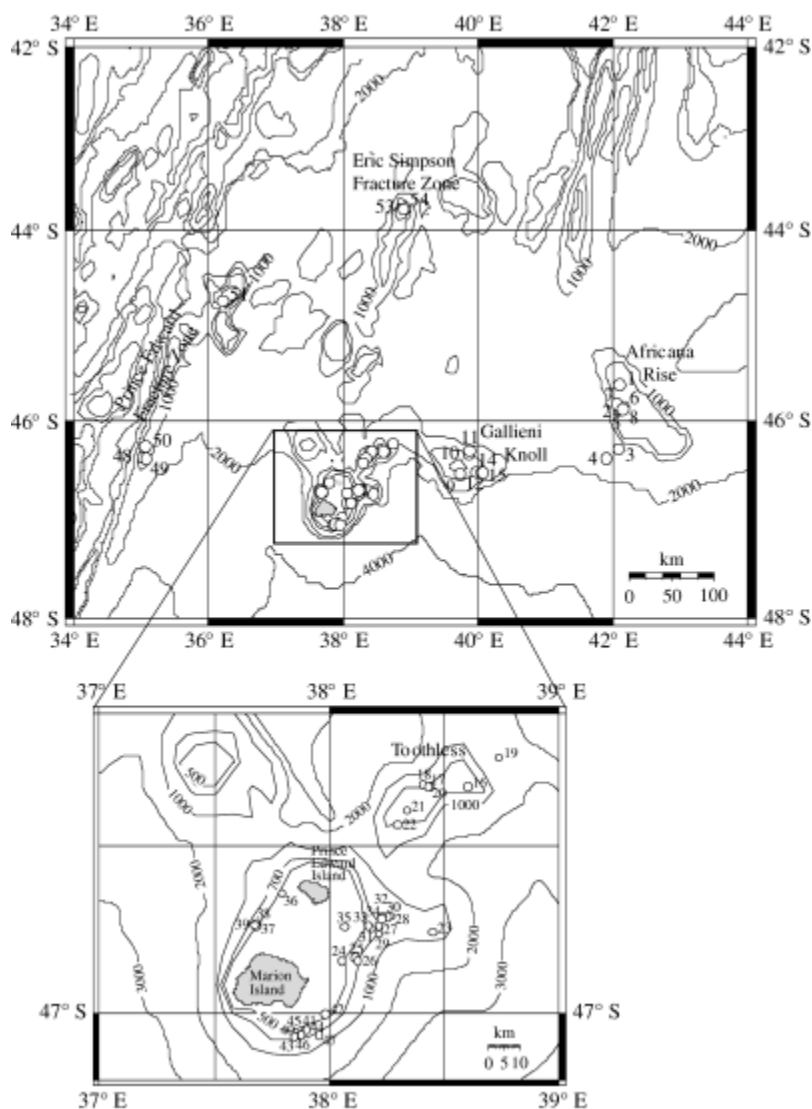


Fig. 1. Region of the bottom-fish survey with trawl number (see Appendix) in the vicinity of the Prince Edward Islands during April 2001.

Fish biology

Onboard, biological analysis was only performed for the Patagonian toothfish specimens. Patagonian toothfish were measured (total length, L_T) to the nearest 0.5 cm, weighed to the nearest 10 g and sexed. The stomach was then extracted, firstly frozen at -20°C and then preserved in 6% buffered formaldehyde seawater solution. In addition, random sub-samples of other fish species were firstly frozen at -20°C and after the cruise transferred into 6% buffered formaldehyde seawater solution for future laboratory analyses. In the laboratory, each fish was measured (standard length, L_S) to the nearest mm, weighed (M_T) to the nearest 0.1 g and stomachs removed. The stomach content of all fishes was sorted separately and prey items identified to the species or to the lowest possible taxonomic group and counted. Prey items were then blotted using a filter-paper weighed separately (M_P) to the nearest 0.1 mg. The mean percentage composition of the diet and frequency of occurrence (O_F , %) of each prey category were then calculated for each fish. The stomach fullness index, I_F , was calculated by $I_F = 100 M_P M_T^{-1}$ to investigate fish feeding intensity.

Stable isotopes

For stable isotopes, 22 fish species were collected at stations conducted on the Africana Rise (trawl numbers 5, 6 and 8), Gallieni Knoll Rise (trawl number 9), Toothless Rise (trawl numbers 16–18, 20 and 21), downstream (trawl numbers 23, 24, 30 and 47) and upstream (trawl numbers 36 and 37) of the PEIs, and at the Prince Edward Fracture Zone (trawl number 48) (Fig. 1). After collection, fishes were frozen at -20°C for storage. In the laboratory, fishes were defrosted, identified and measured for L_S . Samples of dorsal muscle tissue were collected and oven-dried for 36 h at 50°C . Subsequently, samples were crushed and homogenized with a pestle and mortar. Samples were neither decalcified nor defatted. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ determination was carried out on a Finnigan-MAT 252 stable light-isotope mass spectrometer after sample combustion in an on-line Carlo-Erba preparation unit. Merck gelatine was used as an internal standard calibrated against several International Atomic Energy Agency reference materials. Results were expressed in the standard data notation as $\delta X = 1000 \{ [R_{\text{sample}}/R_{\text{standard}}] - 1 \}$, where X = the element in question and R = the ratio of the heavy over the light isotope. Repeated analyses of homogeneous material yielded a S.D. of 0.1‰.

Results

Fish composition, density and distribution

A total of 56 fish taxa were collected during the April 2001 survey in the proximity of the PEIs (Table I). Of these, 44 taxa were identified to the species level, seven to the genus level and five to the family level. The highest number of taxa (eight) was recorded in the Myctophidae, followed by the Stomiidae (six) and Nototheniidae (five) (Table I). Paralepididae, Rajidae, Archirosettidae, Macrouridae and Moridae comprised three taxa, while other families were represented by one or two taxa (Table I). Three species, namely *Echiodon cryomargarites* Markle, *Macrourus carinatus* (Günther) and *D. eleginoides* were encountered in 46–69% of all trawls. Frequency of occurrence of *Stomias boa boa* (Risso), *Borostomias antarcticus* (Lönnberg), *Idiacanthus atlanticus* Brauer, *Icichthys australis* Jordan & Gilbert, *L. squamifrons*, *Antimora rostrata* (Günther), *Halargyreus johnsonii* Günther and *Paradiplospinus gracilis* (Brauer) ranged between 12 and 36%. The remaining taxa occurred in <10% of samples (Table I).

TABLE I. List of species caught in the vicinity of the Prince Edward Islands

Taxa	<u>Gon & Klages (1988),</u> <u>Pakhomov et al. (2001)</u>	Iris survey	
		Trawl numbers (see <u>Appendix</u>)	O_F (%)

Taxa	<u>Gon & Klages (1988), Pakhomov et al. (2001)</u>	<i>Iris</i> survey	
		Trawl numbers (see <u>Appendix</u>)	O_F (%)
Myctophidae (M)			
<i>Protomyctophum bolini</i> (Fraser-Brunner)	+		
<i>Protomyctophum normani</i> (Tåning)	+		
<i>Protomyctophum choriodon</i> Hulley	+* _		
<i>Protomyctophum tension</i> (Norman)	+		
<i>Protomyctophum</i> sp.		1, 12, 38, 41, 44	9·6
<i>Gymnoscopelus nicholsi</i> (Gilbert)	+		
<i>Gymnoscopelus braueri</i> (Lönnerberg)	+* _	16	1·9
<i>Gymnoscopelus bolini</i> Andriashev	+	16–18, 22–24, 28, 30–32, 34, 37	22·2
<i>Gymnoscopelus hintonoides</i> Hulley	+* _		
<i>Gymnoscopelus opisthopterus</i> Fraser-Brunner	+* _		
<i>Gymnoscopelus piabilis</i> (Whitley)		18, 20	3·8
<i>Gymnoscopelus fraseri</i> (Fraser-Brunner)		17, 37	3·8
<i>Gymnoscopelus</i> sp.		3, 6, 12, 14, 15, 21, 33–35, 43, 44	21·2
<i>Krefflichthys anderssoni</i> (Lönnerberg)	+		
<i>Electrona subaspera</i> (Günther)	+		
<i>Electrona carsbergi</i> (Tåning)	+		
<i>Electrona</i> sp.		3, 23, 33, 44	7·7
<i>Diaphus</i> sp.	+		
<i>Lampanyctus intricarius</i> Tåning		24	1·9
<i>Lampanyctus achirus</i> Andriashev		6, 22, 30, 37	7·7
Gonostomatidae (BP)			
<i>Vinciguerrria attenuate</i> (Cocco)	+* _		
<i>Dyplophos rebainsi</i> Krefft & Parin	+* _		
<i>Photichthys argenteus</i> Hutton		25, 30, 34, 38	7·8
<i>Cyclothone</i> sp.		17, 30	3·8
Alepisauridae (BP)			
<i>Alepisaurus brevirostris</i> Gibbs	+	24	1·9
Stomiidae (BP)			
<i>Stomias boa boa</i> (Risso)	+* _	17, 21–23, 28–30, 34, 37, 49	19·2

Taxa	<u>Gon & Klages (1988), Pakhomov et al. (2001)</u>	<i>Iris</i> survey	
		Trawl numbers (see <u>Appendix</u>)	O_F (%)
<i>Borostomias antarcticus</i> (Lönnberg)		6, 10, 21, 22, 26, 28, 29	13·5
<i>Idiacanthus atlanticus</i> Brauer		12, 20, 21, 25, 28, 36	11·5
<i>Trigonolampa miriceps</i> Regan & Trewavas		17	1·9
<i>Chauliodus sloani</i> Bloch & Schneider		4, 29, 30	5·8
<i>Malacosteus niger</i> Ayres		20	1·9
Scopelarchidae (BP)			
<i>Benthalbella macropinna</i> Bussing & Bussing		10, 16	3·8
<i>Scopelosaurus hamiltoni</i> (Waite)		10	1·9
Paralepididae (BP)			
<i>Magnisudis prionosa</i> (Rofen)	+	22	1·9
<i>Stemonosudis</i> sp.	+*		
<i>Notolepis</i> sp.		6, 16	3·8
<i>Macroparalepis</i> sp.		45	1·9
Centrolophidae (E)			
<i>Icichthys australis</i> Jordan & Gilbert		6, 10, 16, 21, 23, 27, 28, 30–34	23·1
Centrolophidae gen. sp.		54	1·9
Ceratiidae (BP)			
<i>Ceratias tentaculatus</i> Kröyer		53	1·9
Carapidae (B?)			
<i>Echiodon cryomargarites</i> Markle, Williams & Olney	+*	2, 3, 5, 6, 8, 10, 12, 15, 16, 20, 21, 23, 25, 26, 29, 30, 33, 36–38, 48, 49	46·2
Congiopodidae (B)			
<i>Zanclorhynchus spinifer</i> Günther	+	12, 42	3·8
Rajidae (B)			
<i>Raja taaf</i> Meissner		22	1·9
<i>Raja barnardi</i> Norman	+*		
<i>Raja</i> sp.	+*		
Archiropsettidae (B)			
<i>Mancopsetta maculate</i> (Günther)	+	12, 47	3·8

Taxa	<u>Gon & Klages (1988), Pakhomov et al. (2001)</u>	<i>Iris</i> survey	
		Trawl numbers (see <u>Appendix</u>)	O_F (%)
<i>Mancopsetta milfordi</i> Penrith	+	2, 34, 35, 42	7.7
<i>Pseudomancopsetta andriashevi</i> Evseenko	+	8, 47	3.8
Exocoetidae (E?)			
<i>Cheilopogon pinnatibarbus</i> <i>altipennis</i> Collette & Parin	+		
Nototheniidae (B)			
<i>Lepidonotothen larseni</i> (Lönnberg)	+	9	1.9
<i>Notothenia rossi</i> Richardson	+		
<i>Notothenia coriiceps</i> Richardson	+		
<i>Paranotothenia megellanica</i> (Forster)	+		
<i>Gobionotothen acuta</i> (Günther)	+		
<i>Gobionotothen marionensis</i> (Günther)	+		
<i>Lepidonotothen squamifrons</i> (Günther)	+	3, 12, 35–38, 41–43, 45–48	25.0
<i>Dissostichus eleginoides</i> Norman	+	2, 5–8, 12, 14–16, 18, 19, 21–23, 25, 27–35, 37–47, 53	69.2
Channichthyidae (B)			
<i>Channichthys rhinoceras</i> Richardson	+		
Harpagiferidae (B)			
<i>Harpagifer georgianus</i> Nybelin	+		
Macrouridae (BP)			
<i>Macrourus holotrachys</i> Günther	+		
<i>Macrourus carinatus</i> (Günther)		2, 4–8, 10–12, 14–23, 27–38, 44, 48, 51, 54	67.3
<i>Coryphaenoides</i> sp.		8, 25	3.8
Macrouridae gen. sp.		6, 53	3.8
Moridae (B)			
<i>Antimora rostrata</i> (Günther)	+	2, 5–8, 15, 16, 20–23, 26, 28, 30, 32, 37, 49	32.7
<i>Laemonema kongi</i> Markle & Meléndez	+	39	1.9

Taxa	<u>Gon & Klages (1988), Pakhomov et al. (2001)</u>	<i>Iris</i> survey	
		Trawl numbers (see <u>Appendix</u>)	O_F (%)
<i>Halargyreus johnsonii</i> Günther		2, 5–8, 11, 15, 16, 23, 26, 27, 49, 50, 51, 53, 54	30·8
<i>Lepidion</i> sp.	+		
Muraenolepididae (B)			
<i>Muraenolepis marmoratus</i> Günther	+		
<i>Muraenolepis orangiensis</i> Vaillant	+		
Alepocephalidae (EB)			
<i>Alepocephalus antipodiana</i> (Parrott)		2, 5–8	9·6
Anotopteridae (E)			
<i>Anotopterus pharao</i> Zugmayer		23, 54	3·8
Astronesthidae (BP)			
<i>Astronesthes boulengeri</i> Gilchrist		8, 17, 54	5·8
Bathylagidae (M)			
<i>Bathylagus tenuis</i> Kobylansky		16, 22, 23, 36, 51	9·6
Chiasmodontidae (BP?)			
<i>Dysalotus cf. alcock</i> MacGilchrist	+		
<i>Chiasmodon niger</i> Johnson		10	1·9
Halosauridae (BP)			
<i>Halosauropsis macrochir</i> Günther		7	1·9
Liparididae (B)			
Liparididae gen. sp.		16, 54	3·8
Melamphaidae (BP)			
<i>Poromitra crassiceps</i> (Günther)		5, 16	3·8
Melamphaidae gen. sp.		22	1·9
Gempylidae (BP)			
<i>Paradiplospinus gracilis</i> (Brauer)		1, 3, 6, 10, 12, 14, 15, 17, 18, 21, 23, 28, 29, 31, 33, 34, 36, 37, 38	36·5
Gadidae (B)			
<i>Physiculus</i> sp.		46	1·9
Platyroctidae (BP)			
Platyroctidae gen. sp.		20	1·9
Notacanthidae (BP)			

Taxa	<u>Gon & Klages (1988), Pakhomov et al. (2001)</u>	<i>Iris</i> survey	
		Trawl numbers (see <u>Appendix</u>)	O_F (%)
<i>Notocanthus chemnitzii</i> Bloch		15, 49	3.8

*New records added to Gon & Klages (1988) by Pakhomov et al. (2001); O_F , frequency of occurrence in trawls. Typical habitat of the group is shown in parentheses next to the family: M, mesopelagic; E, epipelagic; B, benthic; BP, benthopelagic; EB, epibenthic (according to Gon & Heemstra, 1990; Eastman, 1993).

Total cpue during the survey ranged widely from 1.1 to 241.2 individuals h^{-1} . There was no spatial pattern evident in total fish cpue distribution because latitude and longitude of trawling together accounted for <7% of cpue and fish diversity variation ($P > 0.05$). On the other hand, near-bottom water temperature and sampling depth explained c. 56% of both total fish cpue and diversity variation. The total cpue positively correlated with the trawling depth (Fig. 2). For example, average cpue increased from c. 3 individuals h^{-1} at a depth of 200–300 m to c. 93 individuals h^{-1} within the 1100–1300 m depth strata (Fig. 2). The H' were the highest, range 2.0–3.0, at depths 600–1000 m (Fig. 2). Sampling depth, however, explained only 14% of variation (multiple regression, $n = 52$, $P = 0.019$) in total fish cpue, while mean near-bottom seawater temperature decreased with depth (Fig. 2) and accounted for the largest proportion (c. 42%, multiple regression, $n = 52$, $P = 0.002$) of the cpue variation.

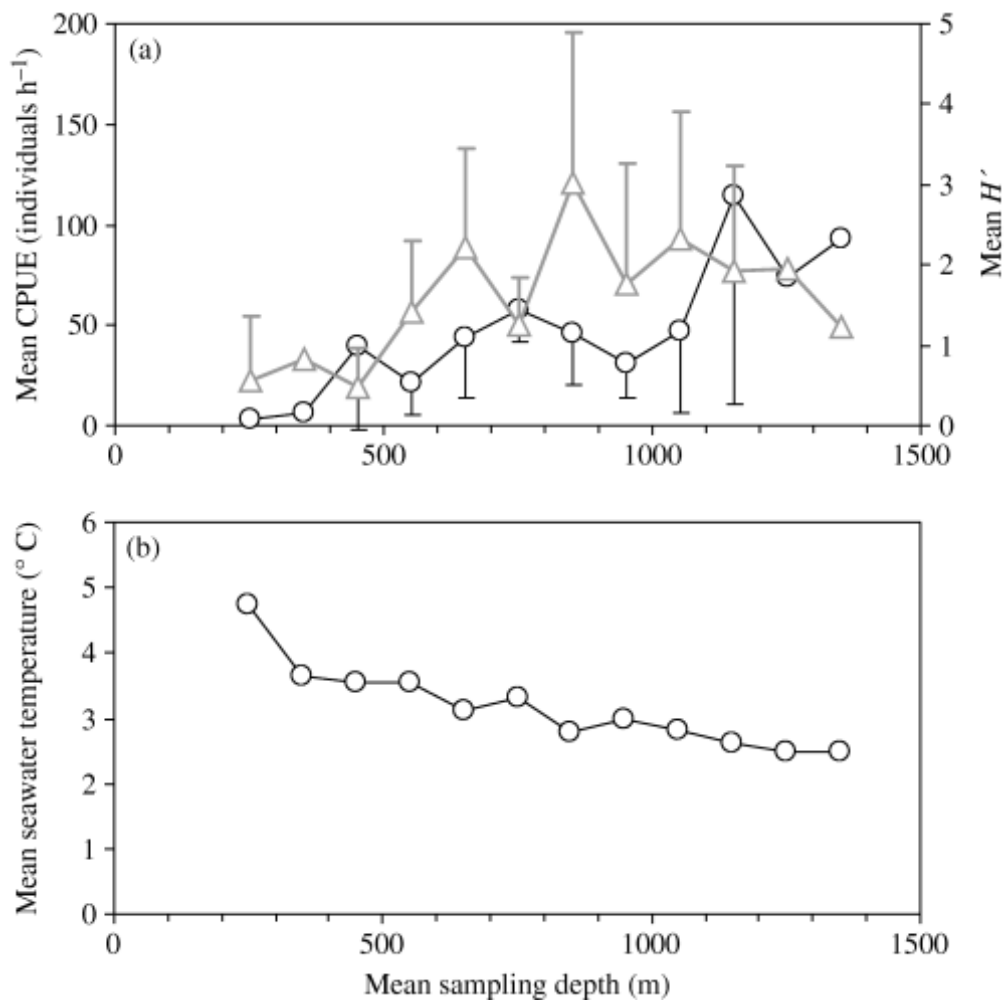


FIG. 2. (a) Depth-dependant changes in mean +S.D. cpue (\circ) and Shannon (\blacktriangle) indices and (b) mean near-bottom seawater temperature in the vicinity of the Prince Edward Islands during April 2001.

A clear taxonomic change in fish community composition occurred along the depth gradient. The Nototheniidae dominated fish communities between 200 and 500 m accounting for >70% of total fish cpue (Fig. 3). At c. 500–600 m depth, the first major shift in the fish community occurred and the Nototheniidae was essentially replaced by species of the family Macrouridae (Fig. 3). Smaller contributors were Gempylidae (up to 10%) and Carapidae (up to 22%). The next major shift in the fish community composition was observed between 800 and 900 m depth, where the proportion of the Macrouridae decreased by c. 50% due to an increasing contribution of fishes belonging to Moridae and, from a depth of 1100 m, Alepocephalidae (Fig. 3). In the deepest depth strata (1300–1400 m), species of the family Moridae predominated (c. 80%) total fish cpue, with Macrouridae and Alepocephalidae together accounting for almost 20% of total cpue (Fig. 3).

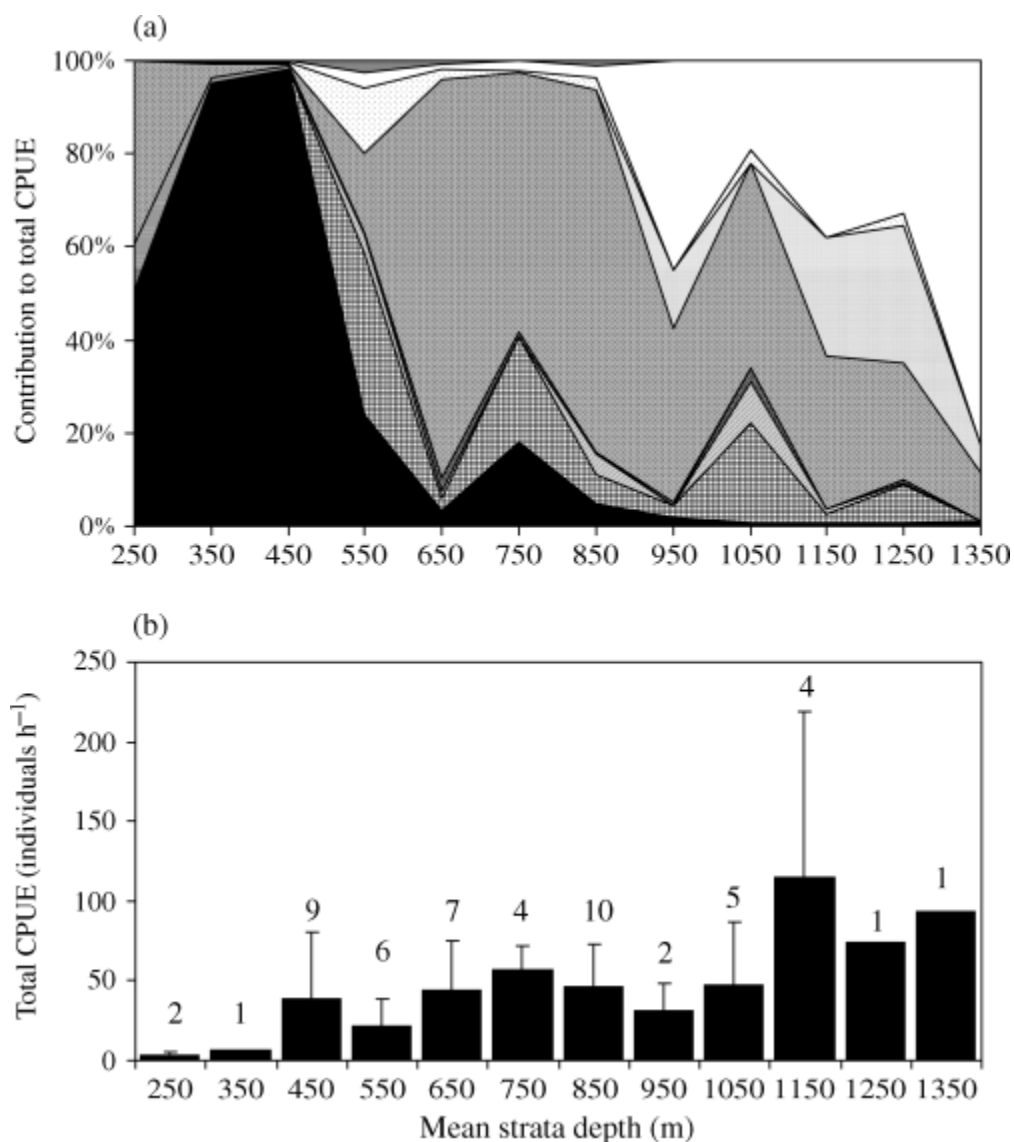


FIG. 3. (a) Fish family composition [Nototheniidae (■), Carapidae (▨), Stomiidae (▩), Centrolophidae (■), Achiropsettidae (▨), Macrouridae (▩), Alepocephalidae (□), Gempylidae (▨), Moridae (□) and Gonostomatidae (▩)] and (b) depth-dependant changes in mean +S.D. total cpue in the vicinity of the Prince Edward Islands during April 2001. Numbers above bars show sampling effort (number of trawls) within particular depth range.

The depth distribution of the most frequently sampled fish species (>20% frequency of occurrence in all trawls) is presented in Fig. 4. There were three major types of vertical distribution: (1) species abundant in depth mostly shallower than 600 m, e.g. *D. eleginoides* and *L. squamifrons* [Fig. 4(a), (d)], (2) species which are generally abundant within the depth range 600–1100 m, e.g. *M. carinatus*, *E. cryomargarites*, *Gymnoscopelus bolini* Andriashev, *P. gracilis* and *I. australis* [Fig. 4(b), (e), (f), (g), (i)] and finally (3) species which are most abundant in depth deeper than 1100 m, e.g. *A. rostrata* and *H. johnsonii* [Fig. 4(c), (h)].

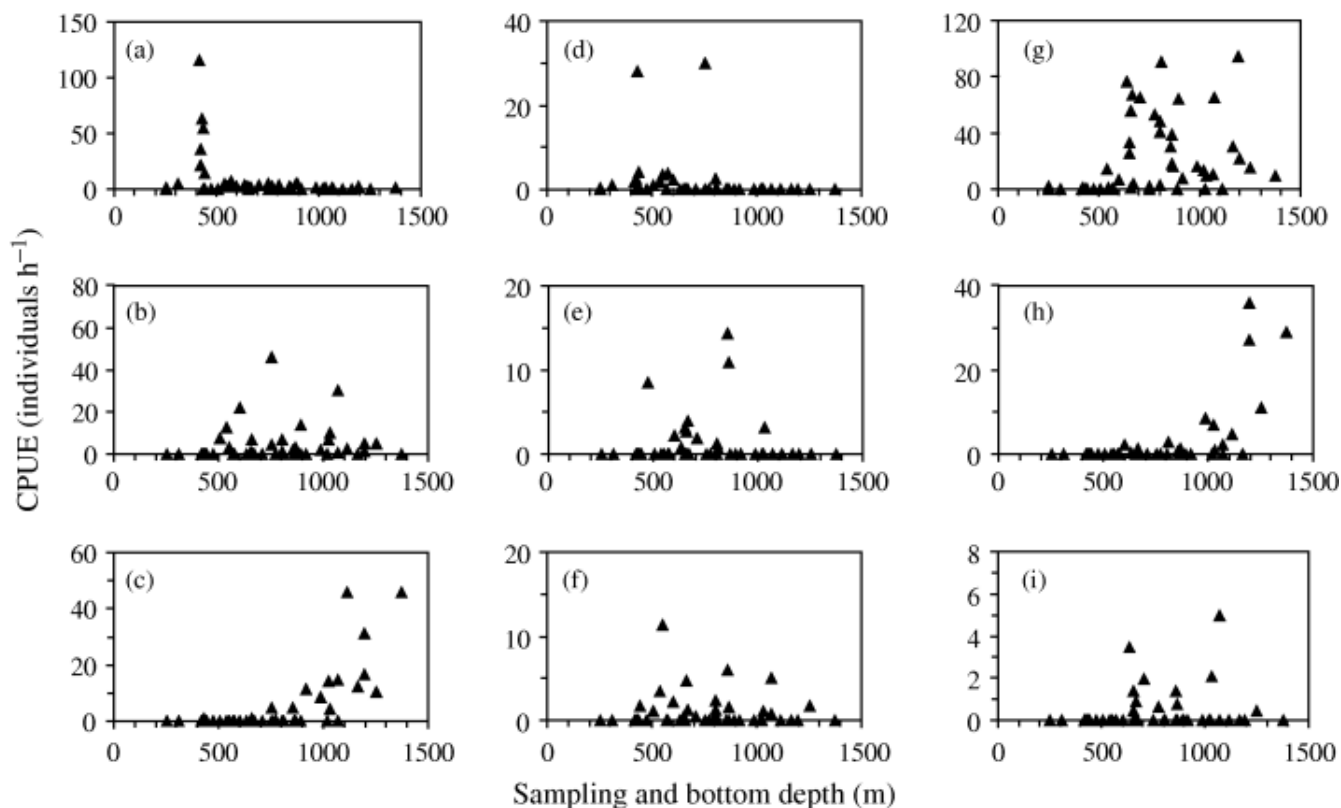


FIG. 4. Species-specific cpue changes with depth in the vicinity of the Prince Edward Islands during April 2001. (a) *Dissostichus eleginoides*, (b) *Echiodon cryomargarites*, (c) *Halargyreus johnsonii*, (d) *Lepidonotothen squamifrons*, (e) *Gymnoscopelus bolini*, (f) *Paradiplosinus gracilis*, (g) *Macrourus carinatus*, (h) *Antimora rostrata* and (i) *Ichthyos australis*.

Community structure

A hierarchical analysis revealed three major fish assemblages at the distance level of *c.* 25% and three outliers, including trawl numbers 1, 24 and 50 (Fig. 5). The one-way ANOVA (ANOSIM) showed that the identified assemblages were significantly ($n=52$, $P < 0.05$) separated from each other. Outliers coincided with the stations characterized by the lowest number of species and total cpue. Geographically, assemblage A, with the exception of one station, was located south-east of Marion Island (Fig. 1). This assemblage had 10 species and the lowest average H' (0.5) and J' (0.2) indices. It was also the shallowest assemblage, occupying depths between 372 and 519 m, with an average total cpue of 41.1 individuals h^{-1} (Table II). This community was overwhelmingly dominated by *D. eleginoides* (86.5% of total cpue), which was followed by *L. squamifrons* (only 10%).

Assemblage B included the largest number of stations (29), taxa (34) and average total cpue (51.4 individuals h^{-1}), but had intermediate H' (1.9) and J' (0.4) indices. It was also the deepest assemblage, occupying a depth range of 762–1013 m, with the lowest average seawater temperatures (Table II). Spatially, stations belonging to this assemblage were scattered over the downstream slope of Prince Edward Archipelago, as well as the slopes of

Gallieni Knoll and the Africana and Toothless rises (Fig. 1). The most prominent species in this assemblage were *M. carinatus* (57.5% of total cpue), followed by *H. johnsonii* (12.4%), *Alepocephalus antipodiana* (Parrott) (9.9%) and *A. rostrata* (8.5%) (Table II).

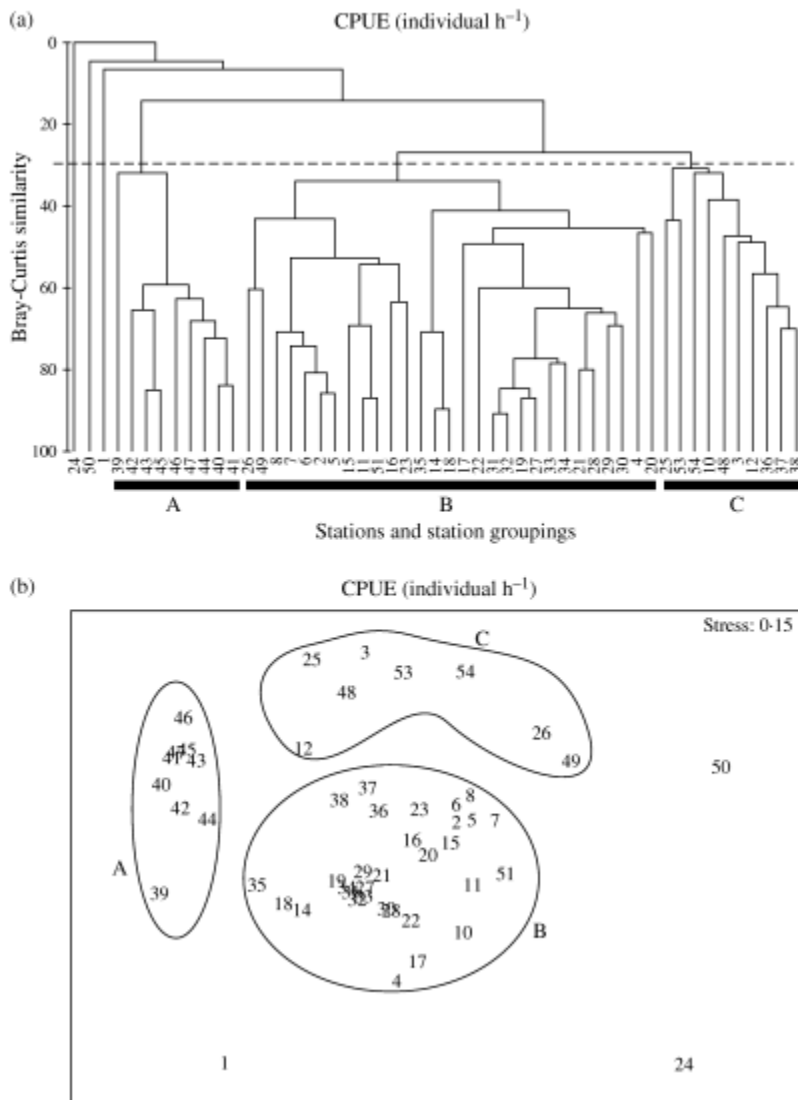


FIG. 5. (a) Dendrogram and (b) the ordination in two-dimensions using multidimensional scaling (MDS) showing the clustering of the three communities in the vicinity of the Prince Edward Islands (see Fig. 1) during April 2001 based on fish cpue.

Assemblage C was composed of stations occupied within the Prince Edward and Eric Simpson Fracture zones (trawl numbers 48, 53 and 54), between Africana and Gallieni Knoll rises (trawl numbers 3, 10 and 12) and in the upstream (trawl numbers 36 to 38) as well as downstream (trawl number 25) slopes of the Prince Edward Plateau (Fig. 1). It should be noted that six out of a total 10 trawl numbers belonging to the assemblage C had a sampling depth range >400 m (Appendix). Compared to assemblages A and B, it was characterized by an intermediate number of species (24) and depth range (567–855 m) but by the highest H' (2.0) and J' (0.6) indices. Assemblage C had the lowest average total cpue (34.8 individuals h⁻¹) and the highest seawater temperatures (Table II). Three species, *E. cryomargarites*, *M. carinatus* and *P. gracilis*, were the most abundant species accounting for 36.5, 27.3 and 7.5% of total cpue, respectively (Table II).

TABLE II. Demersal fish community structure in the vicinity of the Prince Edward Islands

	cpue		
	Mean \pm S.D. individuals h^{-1}	%	O_F
Assemblage A (n= 9)			
<i>Dissostichus eleginoides</i>	35.55 \pm 37.23	86.5	100
<i>Lepidonotothen squamifrons</i>	4.53 \pm 8.98	10.0	66.7
<i>Laemonema kongi</i>	0.22 \pm 0.66	0.5	11.1
<i>Physiculus</i> sp.	0.21 \pm 0.62	0.5	11.1
<i>Mancopsetta maculata</i>	0.14 \pm 0.41	0.3	11.1
<i>Pseudomancopsetta andriashevi</i>	0.14 \pm 0.41	0.3	11.1
<i>Macroparalepis</i> sp.	0.09 \pm 0.26	0.2	11.1
<i>Macrourus carinatus</i>	0.09 \pm 0.25	0.2	11.1
<i>Mancopsetta milfordi</i>	0.05 \pm 0.13	0.1	11.1
<i>Zanchlorhynchus spinifer</i>	0.05 \pm 0.13	0.1	11.1
Total cpue	41.1 \pm 39.6		
Range of cpue	4–117.4		
H'	0.5		
J'	0.2		
Mean minimum trawling depth (m)	372 \pm 58		
Mean maximum trawling depth (m)	519 \pm 126		
Mean seawater temperature ($^{\circ}$ C)	3.32 \pm 0.16		
<i>Electrona</i> sp.	0.43 \pm 1.29	—	11.1
<i>Gymnoscopelus</i> spp.	0.29 \pm 0.62	—	22.2
<i>Protomyctophum</i> sp.	0.18 \pm 0.36	—	22.2
Assemblage B (n= 29)			
<i>Macrourus carinatus</i>	29.54 \pm 29.43	57.5	79.4
<i>Halargyreus johnsonii</i>	6.35 \pm 12.14	12.4	38.2
<i>Alepocephalus antipodiana</i>	5.09 \pm 18.2	9.9	14.7
<i>Antimora rostrata</i>	4.36 \pm 9.48	8.5	47.1
<i>Dissostichus eleginoides</i>	1.40 \pm 1.25	2.7	64.7
<i>Echiodon cryomargarites</i>	1.17 \pm 1.90	2.3	41.2
<i>Paradiplospinus gracilis</i>	0.71 \pm 1.41	1.4	35.3
<i>Stomias boa boa</i>	0.54 \pm 1.09	1.0	26.5
<i>Icichthys australis</i>	0.50 \pm 0.88	1.0	32.3

	cpue		
	Mean \pm S.D. individuals h^{-1}	%	O_F
<i>Borostomias antarcticus</i>	0.38 \pm 1.41	0.7	17.6
<i>Chaulidotus sloani</i>	0.29 \pm 1.24	0.6	8.8
<i>Notocanthus chemnitzii</i>	0.11 \pm 0.46	0.2	5.9
<i>Idiacanthus atlanticus</i>	0.08 \pm 0.23	0.2	8.8
<i>Astronestes bouleengeri</i>	0.07 \pm 0.28	0.1	5.9
<i>Coryphaenoides</i> sp.	0.07 \pm 0.35	0.1	2.9
<i>Halosauropsis macrochir</i>	0.06 \pm 0.34	0.1	2.9
<i>Photichthys argenteus</i>	0.06 \pm 0.26	0.1	5.9
<i>Cyclothone</i> sp.	0.06 \pm 0.23	0.1	5.9
Liparididae gen. sp.	0.05 \pm 0.25	<0.1	2.9
<i>Anoptopterus pharao</i>	0.05 \pm 0.24	<0.1	2.9
<i>Mancopsetta milfordi</i>	0.05 \pm 0.14	<0.1	8.8
<i>Promitra crassiceps</i>	0.04 \pm 0.15	<0.1	5.9
<i>Trigonolampa miriceps</i>	0.04 \pm 0.22	<0.1	2.9
<i>Notolepis</i> sp.	0.04 \pm 0.14	<0.1	5.9
<i>Pseudomancopsetta andriashevi</i>	0.03 \pm 0.17	<0.1	2.9
Macrouridae gen. sp.	0.03 \pm 0.16	<0.1	2.9
<i>Benthalbella macrospinna</i>	0.02 \pm 0.12	<0.1	2.9
Melamphaidae gen. sp.	0.02 \pm 0.12	<0.1	2.9
<i>Magnisudis prionosa</i>	0.02 \pm 0.12	<0.1	2.9
Platytrichidae gen. sp.	0.02 \pm 0.12	<0.1	2.9
<i>Malacosteus niger</i>	0.02 \pm 0.12	<0.1	2.9
<i>Raja taaf</i>	0.02 \pm 0.12	<0.1	2.9
<i>Lepidonotothen squamifrons</i>	0.01 \pm 0.05	<0.1	2.9
Total cpue	51.4 \pm 45.9		
Range of cpue	4.4–241.2		
<i>H'</i>	1.6		
<i>J'</i>	0.4		
Mean minimum trawling depth (m)	762 \pm 234		
Mean maximum trawling depth (m)	1013 \pm 287		
Mean seawater temperature ($^{\circ}$ C)	2.85 \pm 0.33		
<i>Gymnoscopelus bolini</i>	1.16 \pm 2.78	—	29.4

	cpue		
	Mean \pm S.D. individuals h^{-1}	%	O_F
<i>Gymnoscopelus</i> spp.	0.42 \pm 1.11	—	20.6
<i>Lampanyctus achirus</i>	0.30 \pm 1.38	—	8.8
<i>Bathylagus tenuis</i>	0.22 \pm 0.74	—	11.8
<i>Gymnoscopelus piabilis</i>	0.12 \pm 0.43	—	5.9
<i>Electrona</i> sp.	0.06 \pm 0.25	—	5.9
<i>Gymnoscopelus fraseri</i>	0.04 \pm 0.22	—	2.9
<i>Gymnoscopelus braueri</i>	0.02 \pm 0.12	—	2.9
Assemblage C (n= 10)			
<i>Echiodon cryomargarites</i>	12.7 \pm 13.1	36.5	100
<i>Macrourus carinatus</i>	9.49 \pm 19.9	27.3	70.0
<i>Paradiplospinus gracilis</i>	2.60 \pm 3.50	7.5	60.0
<i>Dissostichus eleginoides</i>	1.93 \pm 2.23	5.5	50.0
<i>Lepidonotothen squamifrons</i>	1.45 \pm 1.37	4.2	60.0
<i>Idiacanthus atlanticus</i>	0.83 \pm 1.55	2.4	30.0
<i>Protichthys argenteus</i>	0.81 \pm 1.73	2.3	20.0
<i>Halargyreus johnsonii</i>	0.56 \pm 1.45	1.6	20.0
<i>Icichthys australis</i>	0.50 \pm 1.58	1.4	10.0
<i>Borostomias antarcticus</i>	0.50 \pm 1.58	1.4	10.0
<i>Coryphaenoides</i> sp.	0.46 \pm 1.45	1.3	10.0
Macrouridae gen. sp.	0.46 \pm 1.45	1.3	10.0
<i>Ceratias tentaculatus</i>	0.46 \pm 1.45	1.3	10.0
<i>Stomias boa boa</i>	0.44 \pm 1.40	1.3	10.0
<i>Benthalbella macrospinna</i>	0.25 \pm 0.79	0.7	10.0
<i>Scopelosaurus hamiltoni</i>	0.25 \pm 0.79	0.7	10.0
<i>Chiasmodon niger</i>	0.25 \pm 0.79	0.7	10.0
<i>Antimora rostrata</i>	0.22 \pm 0.70	0.6	10.0
Centrolophidae gen. sp.	0.19 \pm 0.31	0.6	10.0
<i>Astronestes bouleengeri</i>	0.10 \pm 0.30	0.3	10.0
Liparididae gen. sp.	0.10 \pm 0.30	0.3	10.0
<i>Anoptopterus pharao</i>	0.10 \pm 0.30	0.3	10.0
<i>Zanchlorhynchus spinifer</i>	0.05 \pm 0.16	0.1	10.0
<i>Mancopsetta maculata</i>	0.05 \pm 0.16	0.1	10.0

	cpue		
	Mean \pm S.D. individuals h^{-1}	%	O_F
Total cpue	34.8 \pm 26.1		
Range of cpue	9.4–90.5		
H'	2.0		
J'	0.6		
Mean minimum trawling depth (m)	517 \pm 221		
Mean maximum trawling depth (m)	906 \pm 160		
Mean seawater temperature ($^{\circ}$ C)	3.47 \pm 0.57		
<i>Protomyctophum</i> sp.	2.94 \pm 7.80	—	20.0
<i>Gymnoscopelus fraseri</i>	0.44 \pm 1.40	—	10.0
<i>Electrona</i> sp.	0.32 \pm 0.99	—	10.0
<i>Bathylagus tenuis</i>	0.24 \pm 0.75	—	10.0
<i>Gymnoscopelus bolini</i>	0.22 \pm 0.70	—	10.0
<i>Lampanyctus achirus</i>	0.22 \pm 0.70	—	10.0
<i>Gymnoscopelus</i> spp.	0.10 \pm 0.21	—	20.0

O_F , frequency of occurrence (%) in catches; H' , Shannon–Weaver diversity index; J' , Pielow evenness index; n , number of stations. Species belonging to the families Myctophidae and Bathylagidae are listed for each assemblage but not included in cpue and diversity indices calculations.

Ordination analysis (NMDS) produced similar results: three assemblages and three outliers, with stress = 0.15 (Fig. 5). The SIMPER, undertaken using these groupings, showed low average within-group similarity ranging in all assemblages between 25 and 35%. Three main consolidating species were identified. *Dissostichus eleginoides*, *M. carinatus* and *E. cryomargarites* accounted for 92% in the within-group similarity in assemblage A, 79% in assemblage B and 87% in assemblage C, respectively. Unlike within-group similarity, the dissimilarity levels between three assemblages were high, ranging from 90 to 95%. Discrimination was achieved mainly through species, which were absent or rare in one of the assemblage pairs. For example, *D. eleginoides*, *E. cryomargarites* and *L. squamifrons* together accounted for 81% of total (92%) dissimilarity between assemblages A and C. Furthermore, *M. carinatus*, *D. eleginoides*, *H. johnsonii*, *M. carinatus* and *L. squamifrons* together contributed 77% towards total (95%) dissimilarity between assemblages A and B. Finally, *M. carinatus*, *E. cryomargarites*, *L. squamifrons* and *H. johnsonii* were responsible for 70% of total (90%) dissimilarity between assemblages B and C.

Diet of selected species

During the survey, the Patagonian toothfish with L_T ranging from 280 to 1200 mm (mostly 450–650 mm) were caught [Fig. 6(a)]. The diets, however, were investigated from stomach contents of 118 specimens of 440–1200 mm L_T . Only 37 stomachs (31%) contained prey (Table III). In stomachs with food, the stomach I_F varied between 0.01 and 5.20%, averaging *c.* 1.9% of body wet mass (Table III). A reconstruction of a diet pattern in the feeding intensity of the Patagonian toothfish did not reveal a distinct temporal pattern, indicating that this species feeds throughout the 24 h cycle [Fig. 6(b)]. This was also confirmed by the presence of freshly consumed prey throughout

the 24 h cycle. The L_T and wet mass relationships for the Patagonian toothfish and other investigated species are presented in Fig. 7.

During April 2001 in the vicinity of the PEIs, the Patagonian toothfish preyed mainly upon squid, which contributed 61% to the fish's diet. Two species, mainly *Moroteuthis* sp. and to a lesser extent *Kondakovia longimana* Filippova, contributed c. 97% to the mass of consumed squid (Table III). The remaining 39% of the diet consisted of fishes with almost equal proportions of mesopelagic (mainly *Gymnoscopelus* spp.) and deep-sea (mainly *Stomias* spp.) taxa (Table III).

During April 2001, the diet of *L. squamifrons* of 172–223 mm L_S was more diverse than the diet of the Patagonian toothfish (Table IV). It was composed of planktonic (24% of total food bolus by mass), benthic (20%) and micronektonic (56%) prey (Table IV). *Lepidonotothen squamifrons* consumed mainly myctophiids (54% of food bolus by mass), with *Protomyctophum bolini* (Fraser-Brunner) and *Electrona carsbergi* (Tåning) dominating the diet (Table IV). Among the plankton, the most important prey items were the tunicates *Salpa thompsoni* Foxton (20%), while among the benthos, bottom-dwelling polychaetes contributed 13% to the diet of *L. squamifrons* (Table IV). Although, all stomachs investigated contained prey items, the feeding intensity of *L. squamifrons* was low with a mean I_F only just exceeding 1% of body mass (Table IV).

The diets of the remaining four species were investigated on rather limited (range six to 14 stomachs) material and are presented in Table V. The feeding intensity of all species was low ranging from 0.1 to 0.7% of body mass. Juveniles of *M. carinatus* (194–765 mm L_S) fed mainly on fishes of the Myctophidae (82% by mass), while mesopelagic mysids of the genus *Gnathophausia* (14%) and benthic crustaceans (3%) were the second and third most important prey groups (Table V). *Echiodon cryomargarites* of 260–378 mm L_S consumed mainly mesopelagic hyperiids (68%) and gonostomatiid fishes (28%), while the myctophiid *Lampanyctus achirus* Andriashev of 79–140 mm L_S preyed mainly upon epipelagic euphausiids (45%), hyperiids (30%) and copepods (11%) (Table V). Finally, almost empty stomachs of *A. antipodiana* (372–549 mm L_S) contained well-digested remains of squid (85% by mass), pyrosomes (12%) and hyperiids (3%) (Table V).

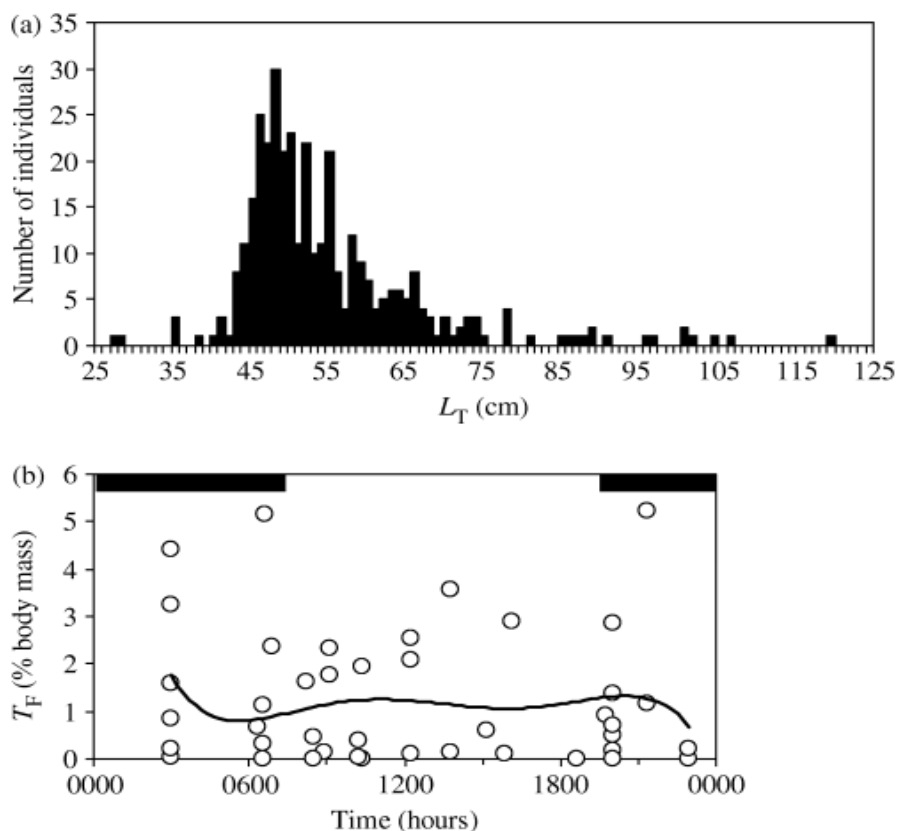


FIG. 6. (a) Total length frequency distribution ($n=357$) and (b) diet variability of stomach fullness indices of the Patagonian toothfish caught in the vicinity of the Prince Edward Islands during April 2001. Black horizontal bars, times of darkness.

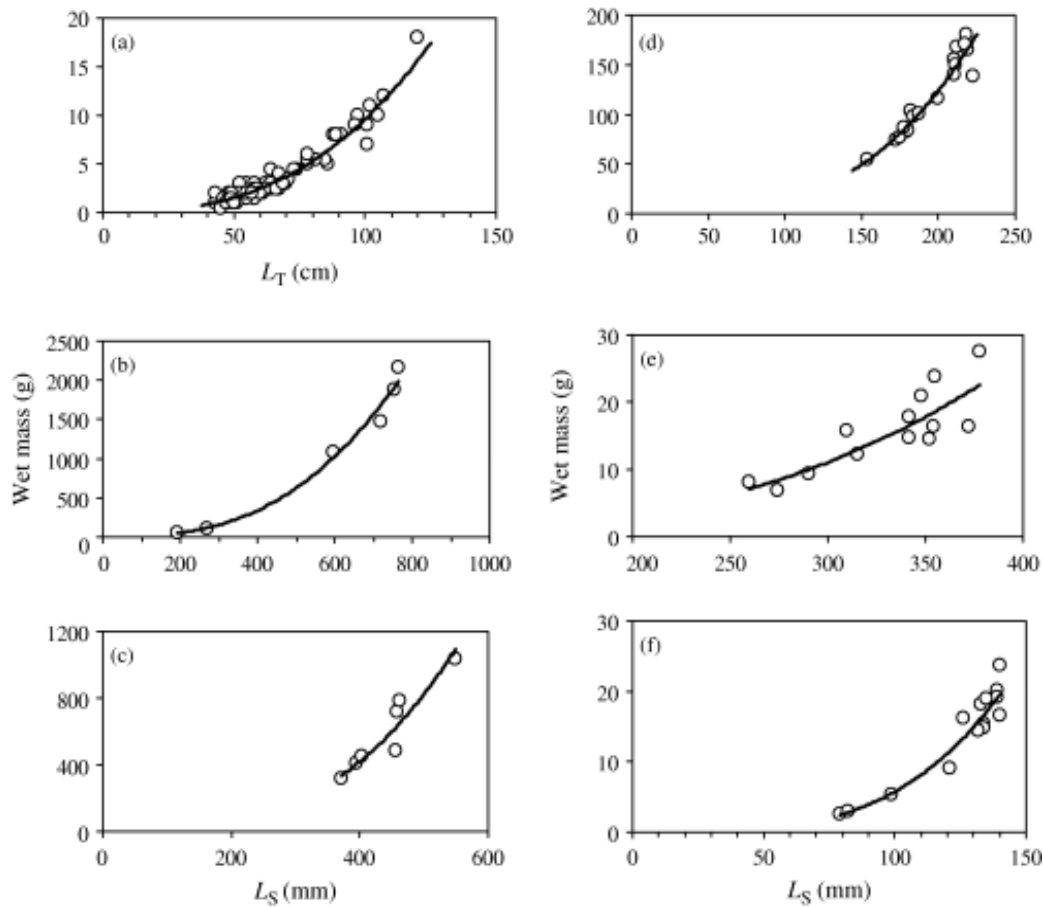


FIG. 7. Length and mass relationships of selected fish species collected in the vicinity of the Prince Edward Islands during April 2001. (a) *Dissostichus eleginoides* $y = 5E-05x^{2.6607}$ ($r^2 = 0.855$, $n = 109$), (b) *Macrourus carinatus* $y = 3E-05x^{2.7395}$ ($r^2 = 0.998$, $n = 6$), (c) *Alepocephalus antipodiana* $y = 0.0059x^{3.027}$ ($r^2 = 0.88$, $n = 7$), (d) *Lepidonotothen squamifrons* $y = 5E-06x^{3.1961}$ ($r^2 = 0.944$, $n = 18$), (e) *Echiodon cryomargarites* $y = 2E-07x^{3.101}$ ($r^2 = 0.80$, $n = 13$) and (f) *Lampanyctus achirus* $y = 3E-07x^{3.6241}$ ($r^2 = 0.97$, $n = 14$).

TABLE III. Diet of *Dissostichus eleginoides* (440–1200 mm total length) during April 2001 in the vicinity of the Prince Edward Islands

Prey items	O_F	I_M
Osteichthyes		
<i>Protomyctophum bolini</i>	5.4	0.6
<i>Electrona carsbergi</i>	8.1	2.7
<i>Gymnoscopelus</i> sp.	18.9	11.2
<i>Lampanyctus</i> sp.	2.7	0.2
Myctophidae	18.9	4.0
<i>Gonostoma</i> sp.	5.4	1.1
<i>Stomias boa boa</i>	10.8	8.7
<i>Echiodon cryomargarites</i>	2.7	0.6

Prey items	O_F	I_M
<i>Anotopterus pharao</i>	2.7	2.8
Macrouridae	2.7	0.7
Fish digested	8.1	0.7
Oegopsida		
<i>Kondakovia longimana</i> Filippova	18.9	12.0
<i>Moroteuthis</i> sp.	5.4	47.5
<i>Histioteuthis macrohista</i> N. Voss	2.7	1.2
Teuthida (digested)	8.1	0.4
Crustacea		
<i>Pasiphaea</i> sp.	2.7	0.1
Number of stomachs analysed	118	
Number of stomachs with prey	37	
I_F	1.89	
O_F , frequency of occurrence (%); I_M , contribution by mass (%); I_F , stomach fullness index (calculated using stomachs containing prey).		

TABLE IV. Diet of *Lepidonotothen squamifrons* (172–223 mm standard length) during April 2001 in the vicinity of the Prince Edward Islands

Prey items	O_F	I_M
Euphausiacea		
<i>Euphausia vallentini</i> Stebbing	5.5	0.2
<i>Euphausia</i> sp.	16.7	0.8
Hyperiididae		
<i>Themisto gaudichaudi</i> (Guerin)	5.5	<0.1
<i>Vibilia</i> sp.	22.2	1.4
<i>Cyllopus</i> sp.	11.1	0.1
Gammaridea	5.5	<0.1
Isopod		
<i>Aega semicarinata</i> Miers	5.5	3.7
<i>Exosphaeroma gigas</i> (Leach)	5.5	2.7
Ostracoda	5.5	<0.1
Copepoda	5.5	<0.1

Prey items	O_F	I_M
Decapoda (<i>Pasiphaea</i> sp.)	5.5	1.5
Echinodermata		
<i>Cucumaria kerguelensis</i> (Théel)	5.5	0.5
Polychaeta		
<i>Rhynchonerella</i> sp.	5.5	<0.1
<i>Pseudonereis anomala</i> Gravier	5.5	3.5
<i>Laetmonice producta</i> Grube	5.5	9.5
Tunicata		
<i>Salpa thompsoni</i> Foxton	72.2	20.1
Myctophidae		
<i>Protomyctophum bolini</i>	5.5	25.0
<i>Electrona carsbergi</i>	5.5	21.8
<i>Lampanyctus</i> sp.	11.1	5.0
Myctophidae scales	55.5	1.7
Oegopsida		
<i>Kondakovia longimana</i>	5.5	2.5
Number of stomachs analysed	18	
Number of stomachs with prey	18	
I_F	1.05	
O_F , frequency of occurrence (%); I_M , contribution by mass (%); I_F , stomach fullness index (%).		

TABLE V. Diets of *Macrourus carinatus* (194–765 mm standard length, L_S), *Echiodon cryomargarites* (260–378 mm L_S), *Aleptocephalus antipodiana* (372–549 mm L_S) and *Lampanyctus achirus* (79–140 mm L_S) during April 2001 in the vicinity of the Prince Edward Islands

Prey items	<i>M. carinatus</i>		<i>E. cryomargarites</i>		<i>A. antipodiana</i>		<i>L. achirus</i>	
	O_F	I_M	O_F	I_M	O_F	I_M	O_F	I_M
Copepoda								
<i>Rhincalanus gigas</i> Brady	—	—	7.7	0.8	—	—	—	—
<i>Pleuromamma</i> sp.	16.7	<0.1	—	—	—	—	—	—
Unidentified	—	—	—	—	—	—	14.3	10.9
Euphausiacea								
<i>Thysanoessa vicina</i> Hansen	—	—	—	—	—	—	28.6	14.4

Prey items	<i>M. carinatus</i>		<i>E. cryomargarites</i>		<i>A. antipodiana</i>		<i>L. achirus</i>	
	O_F	I_M	O_F	I_M	O_F	I_M	O_F	I_M
<i>Thysanoessa gregaria</i> G.O. Sars	16·7	0·2	—	—	—	—	—	—
Unidentified	—	—	—	—	—	—	35·7	30·4
Mysidacea								
<i>Gnathophausia gigas</i> Willemoes-Suhm	33·3	14·1	—	—	—	—	—	—
Hyperiididae								
<i>Themisto gaudichaudi</i>	—	—	—	—	—	—	7·1	25·4
<i>Lanceopes</i> sp.	—	—	7·7	68·3	—	—	—	—
Unidentified	—	—	—	—	14·3	3·2	7·1	4·8
Gammaridea								
Isopoda	16·7	0·7	—	—	—	—	—	—
Crustacea unidentified	—	—	23·1	1·5	—	—	21·4	12·8
Chaetognatha								
Tunicata (<i>Pyrosoma</i> sp.?)	—	—	—	—	42·9	12·3	—	—
Oegopsida	—	—	—	—	28·6	84·5	—	—
Myctophidae								
<i>Protomyctophum</i> sp.	16·7	82·4	—	—	—	—	—	—
Gonostomatidae								
<i>Cyclotone</i> sp.	—	—	7·7	11·4	—	—	—	—
Pisces unidentified	—	—	38·5	16·8	—	—	—	—
Unidentified prey	—	—	15·4	1·1	—	—	—	—
Number of stomachs analysed	6		13		7		14	
Number of stomachs with prey	4		13		6		14	
I_F	0·16		0·74		0·07		0·17	

O_F , frequency of occurrence (%); I_M , contribution by mass (%); I_F , stomach fullness index (%).

Fish trophic positions

Stable isotope signatures of nitrogen ($\delta^{15}\text{N}$) of 22 species of fish varied between 4 and 13‰, covering almost three trophic levels (Fig. 8). If pooled, data showed a slight, but not significant (multiple regression, $n=62$, $P=0\cdot095$), increase in $\delta^{15}\text{N}$ values across the body length range of 50–500 mm (Fig. 9). The $\delta^{15}\text{N}$ values of the majority of species (19 out of 22) ranged between 7 and 10‰, with a distinct mode of 8–9‰ (Fig. 10). Three trophic levels could be identified using $\delta^{15}\text{N}$ tissue values. The lowest trophic level included three species [*Electrona* sp., *Anotopterus pharao* Zugmayer and *Lepidonotothen larseni* (Lönnberg)], with a L_S generally <150 mm (Fig. 8). The highest trophic level was represented by a single species, *M. carinatus*, with a L_S > 200 mm. The intermediate trophic level was composed of a variety of species, with L_S mainly ranging between 100 and 350 mm (Fig. 8).

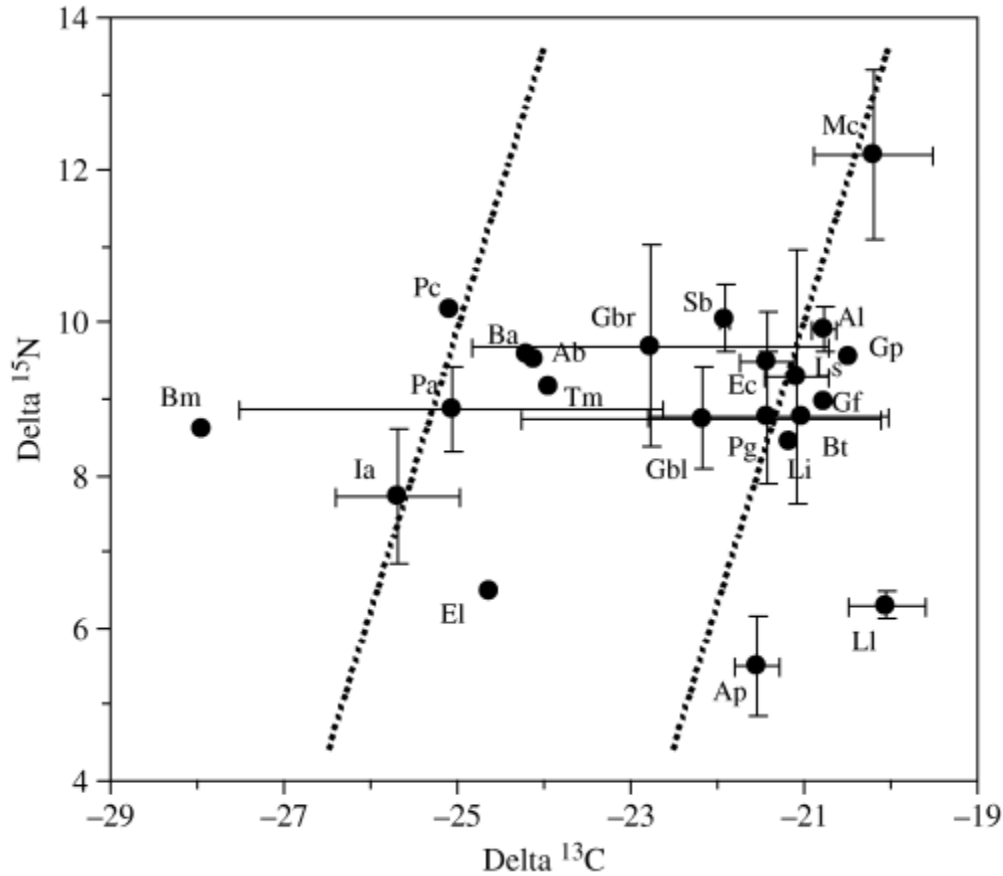


FIG. 8. Plot of mean \pm 1 S.D. isotope abundance values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in fish species collected in the vicinity of the Prince Edward Islands during April 2001. Ab, *Alepisaurus brevirostris* (standard length, L_S = 314 mm, n = 1); Al, *Aleptocephalus antipodana* (L_S = 267–319 mm, n = 2); Ap, *Anoptopterus pharao* (L_S = 144–164 mm, n = 3); Ba, *Borostomias antarcticus* (L_S = 244, n = 1); Bm, *Benthalbella macrospinna* (L_S = 291 mm, n = 1); Bt, *Bathylagus tenuis* (L_S = 134 mm, n = 1); Ec, *Echiodon cryomargarites* (L_S = 340–400 mm, n = 4); El, *Electrona* sp. (L_S = 49 mm, n = 1); Gbl, *Gymnoscopelus bolini* (L_S = 109–123 mm, n = 11); Gbr, *Gymnoscopelus braueri* (L_S = 98–198 mm, n = 6); Gf, *Gymnoscopelus fraseri* (L_S = 84 mm, n = 1); Gp, *Gymnoscopelus piabilis* (L_S = 111 mm, n = 1); Ia, *Idiacanthus atlanticus* (L_S = 347–514 mm, n = 2); Li, *Lampanyctus intricarius* (L_S = 102 mm, n = 1); Ll, *Lepidonotothen larseni* (L_S = 44–45 mm, n = 2); Ls, *Lepidonotothen squamifrons* (L_S = 154–218 mm, n = 8); Mc, *Macrourus carinatus* (L_S = 197–446 mm, n = 4); Pa, *Pseudomancopsetta andriashevi* (L_S = 104–359 mm, n = 3); Pc, *Promitra crassiceps* (L_S = 122 mm, n = 1); Pg, *Paradiplospinus gracilis* (L_S = 331–417 mm, n = 5); Sbb, *Stomias boa* (L_S = 209–232 mm, n = 2); Tm, *Trigonolampa miriceps* (L_S = 338, n = 1). possible food-chains assuming average trophic enrichment of 1‰ for carbon and 3.5‰ for nitrogen (Vander Zanden & Rasmussen, 2001).

Stable isotope signatures of carbon ($\delta^{13}\text{C}$) were extremely variable ranging between -28 and -19‰ (Figs 8 and 10), covering at least 10 trophic levels, assuming an average enrichment of *c.* 1‰ between trophic levels. Even within a single trophic level identified using $\delta^{15}\text{N}$ data, the range of $\delta^{13}\text{C}$ values was substantial (Fig. 8). The combined data revealed a significant decreasing trend (multiple regression, $n=62$, $P=0.019$) of $\delta^{13}\text{C}$ values with the body length (Fig. 9). Finally, two distinct modes in the distribution of $\delta^{13}\text{C}$ values corresponding to -24 and -21‰ were evident in the combined data set (Fig. 10).

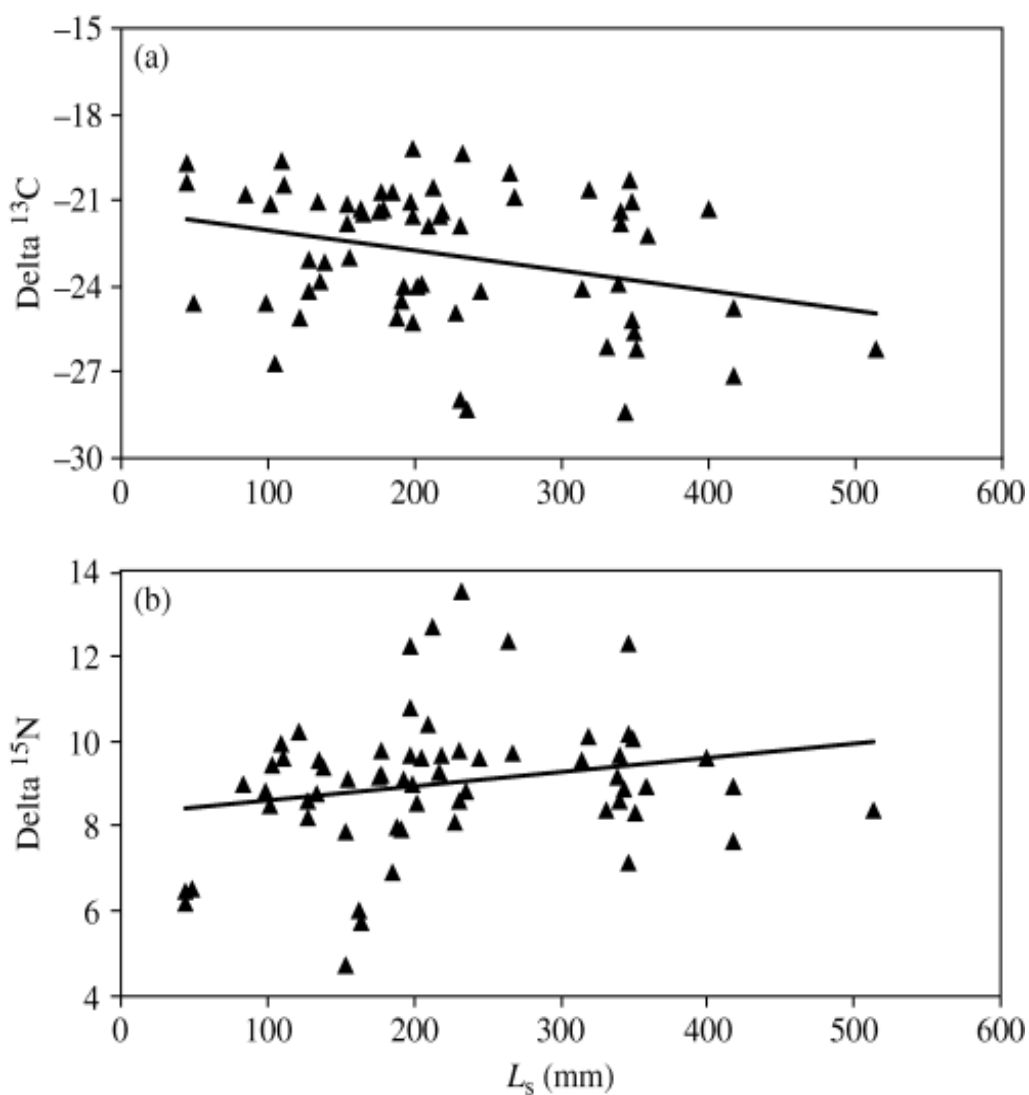


FIG. 9. Standard-length-dependant changes in (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ values based on the data from all fish species collected in the vicinity of the Prince Edward Islands during April 2001.

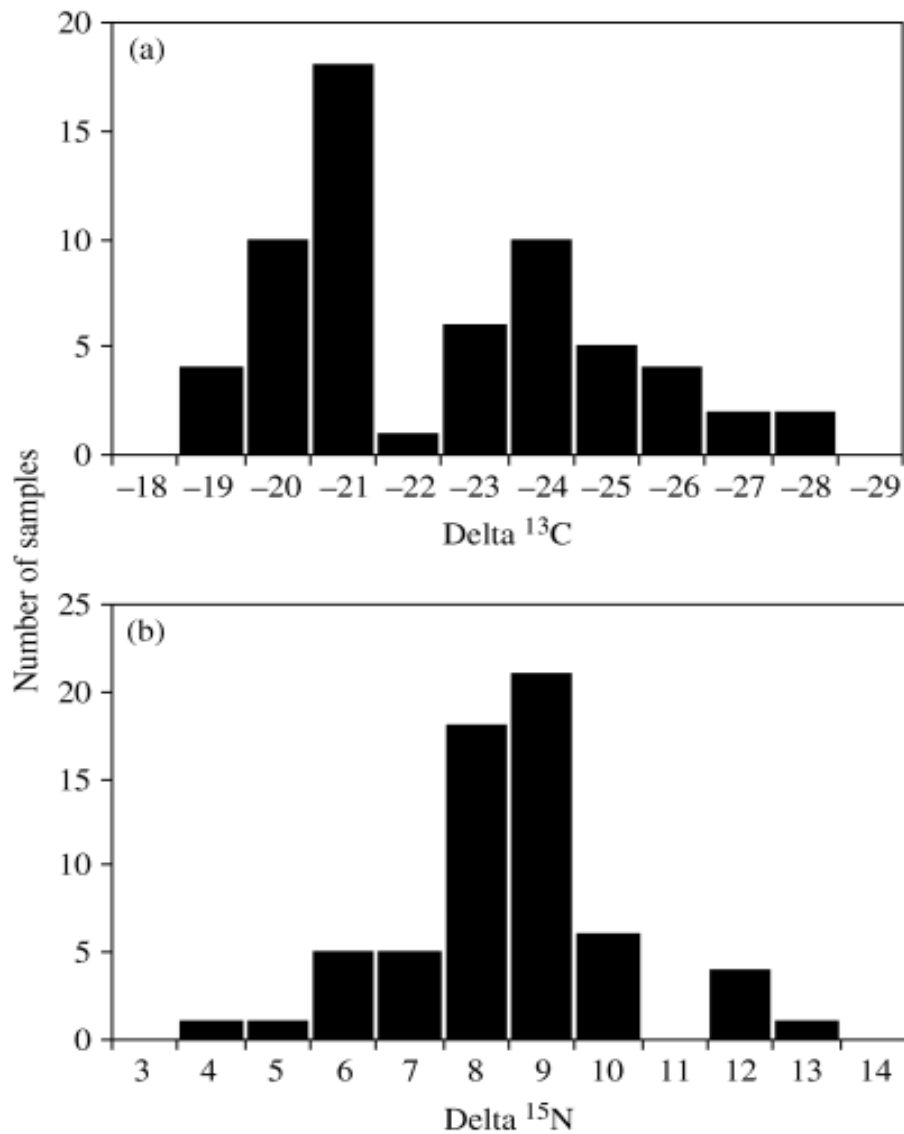


FIG. 10. Frequency distribution of (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ values based on the data from of all fish species collected in the vicinity of the Prince Edward Islands during April 2001.

Discussion

Community structure

According to [Andriashev \(1986, 1987\)](#), biogeographically, the PEIs belong to the Marion-Crozet District of the Indian-Island Province in the Kerguelen (transitional) Subregion of the Antarctic Region. Prior to the 2001 survey, the fish fauna in the vicinity of the PEIs was one of the most poorly studied compared to other islands in the southern hemisphere ([Günther, 1880](#); [Andriashev, 1971](#); [Hureau, 1979](#); [Duhamel *et al.*, 1983](#); [Gon & Klages, 1988](#); [Gon & Heemstra, 1990](#)), with only 44 fish species (including Myctophidae) having been identified (see [Table I](#)). The survey onboard MV *Iris* during April 2001 added 36 new records, increasing the total number of species to 70 (Myctophidae included), which is comparable to that found around the better-studied islands to the east (*e.g.* Crozet and Kerguelen Islands, [Hureau, 1979](#); [Duhamel & Hureau, 1982](#); [Gon & Heemstra, 1990](#)). Almost doubling in number of species found around the PEIs could be attributed to a substantial increase in the sampling depth as previous surveys largely sampled depth <600 m or used fishes or their remains recovered from stomachs of top predators on the islands ([Günther, 1880, 1887](#); [Duhamel *et al.*, 1983](#); [Gon & Klages, 1988](#)). Diversity and evenness

values observed in this study were similar to those reported from other temperate and Southern Ocean regions (Targett, 1981; Daniels & Lipps, 1982; Schwarzbach, 1988; Eastman & Hubold, 1999; Fock *et al.*, 2002). Overall, however, the total number of species recorded around the PEIs accounts for only *c.* 25% of overall species richness known to date within the Antarctic Region (Eastman, 1993).

It should be noted that the current survey was designed to sample bottom-dwelling species, although some nectobenthic fishes were also caught. Furthermore, the large mesh-size of the net (100 mm) did not allow for the collection of smaller sized species, which may well be numerous at shallow (<400 m) depths (Gon & Heemstra, 1990). The suggestion that the sampling gear may have underestimated fish diversity is supported by the fact, that only 35% (six out of 17) of the myctophid fauna (truly pelagic, small to medium size fishes) known from the PEIs were recorded during the April 2001 survey (Table I). Out of 95 species belonging to the Antarctic suborder Notothenioidei, only 10 species have previously been recorded around the PEIs and only three were encountered during the April 2001 survey (Andriashev, 1986, 1987; Eastman, 1993; Table I). This again points to limitations associated with the sampling depth (no truly shelf species) and mesh-size.

In the Antarctic region, the highest Notothenioidei species diversity has been observed within the depth range of 300–600 m (Andriashev, 1986, 1987; Eastman, 1993). The findings of this survey thus concur with previous studies, as nototheniids were most diverse and abundant within the depth range 300–500 m (Fig. 3). It has been suggested that the fish fauna of the PEIs is similar in its origin and basic structure to the fauna of the Antarctic Region proper (Gon & Klages, 1988). The sub-Antarctic islands, including the PEIs, are probably the northernmost limit of the Notothenioidei distribution and is a region where deep-water northern hemisphere fish fauna meet the Southern Ocean fauna (Andriashev, 1986, 1987; Gon & Heemstra, 1990; Eastman, 1993). Indeed, the upper slope fish fauna of the PEIs dominated by Notothenioidei was sharply replaced at 600–800 m depth by widely distributed northern hemisphere fish families including the Macrouridae, Alepocephalidae, Moridae, Carapidae and Stomiidae (Gon & Klages, 1988). Overall, the present findings indicate that relatively few families contributed to the total biomass at a particular bathymetric zone. It remains unexplained why the third and fourth most numerous families of fishes in the Antarctic Region, *e.g.* Liparididae and Zoarcidae (Eastman, 1993), were either poorly represented or absent during the April 2001 survey.

It has been documented in different regions of the world's oceans that abundance, biomass and number of species of demersal fishes decline with increasing depth (Haedrich, 1997; Gordon, 2001). On several occasions, however, at depths of 800–1000 m, on continental slopes or around seamounts in different oceans, an increase in demersal fish density and diversity has been recorded (Merrett, 1987; Merrett & Haedrich, 1997; Gordon, 2001; Fock *et al.*, 2002). The sound-scattering layer interception hypothesis, proposed by Isaacs & Schwartzlose (1965), has been applied to explain anomalies in demersal fish vertical distribution patterns. According to this hypothesis, deep-sea scattering layers composed of vertically migrating prey organisms impinge the slope at *c.* 800–1000 m, providing a rich source of food to benthopelagic fishes (Gordon & Duncan, 1985; Mauchline & Gordon, 1991; Garter *et al.*, 1997; Fock *et al.*, 2002). In the vicinity of the PEIs during April 2001, the fish density gradually increased with the increasing depth within 200–1500 m depth range. The highest cpue values, however, were recorded in the 400–500, 700–800 and 1100–1200 m depth strata (Fig. 3). The highest biodiversity was also found around these depths. Finally, although not included in the analysis, myctophids were most numerous in the depth range 500–1000 m. In the vicinity of the PEIs, strong deep-sea scattering layers have previously been observed in the depth range of 300–400 m (Perissinotto & McQuaid, 1992) and seldom within the depth range of 700–1000 m (E. A. Pakhomov, pers. obs.). These depths largely but not perfectly coincided with either total cpue increase (shallower depths) or increase in fish diversity (Figs 2 and 3), thus potentially explaining the observed distribution pattern.

It is well documented that the composition of fish assemblages normally changes with depth (Day & Percy, 1968; Haedrich *et al.*, 1980; Stefanescu *et al.*, 1992, 1993, 1994; McClatchie *et al.*, 1997; Cartes *et al.*, 2004). Various environmental variables (*e.g.* temperature, salinity and oxygen concentrations), overlying productivity and interspecific relationships have been found to affect fish community composition (Mauchline & Gordon, 1984; Snelgrove & Haedrich, 1985; McClatchie *et al.*, 1997; Jacobs *et al.*, 1998). In this study, the sampling depth only explained a small proportion of fish density variability, while temperature appeared to be the strongest environmental variable responsible for the fish density distribution. Overall, both variables appeared to be major structuring variables for fish assemblage composition (Table II).

Three communities, identified during this study, all had pronounced dominant species but only A and B occupied distinct vertical zones with specific environmental characteristics. The shallowest community (assemblage A) was

dominated by the Nototheniidae, while the deepest assemblage (B) was composed mainly of the Macrouridae. The first family is common at these depths in the Antarctic Region (Andriashev, 1986, 1987; Eastman, 1993). The last family is considered to be ubiquitous in the world's oceans, dominating (50–100% of all fishes collected) near-bottom fish fauna at a depth >1000 m (Marshall & Iwamoto, 1973; Stein & Pearcy, 1982; Haedrich & Merrett, 1990; Martin & Christiansen, 1997). Despite the strong separation between assemblages, the mid-depth assemblage (C) appeared to be an intermediate in composition. Although *E. cryomargarites* dominated in this assemblage, *M. carinatus* ranked the second by importance. The intermediate nature of the assemblage C is also reflected in the highest biodiversity observed within this depth range, possibly representing a mixture of both assemblages A and B but also an increased appearance of nectobenthic species. Presently, the status of the assemblage C is unclear, perhaps mainly due to inclusion of stations with the widest sampling range, which was clearly overlapping with the depth range occupied by assemblages A and B. As a consequence, further sampling efforts are required to assess the status of the assemblage C.

In the absence of the detailed near-bottom information, it is impossible at this stage to comment on factors leading to the increase in the contribution of nectobenthic species within the assemblage C. It is not unreasonable to suggest that the nature of the substratum, food availability and physical properties of the water could be accountable for this. In this regard, it appeared that the depth range where assemblage A was observed could largely be influenced by sub-Antarctic surface water, while the deepest assemblage B could be affected by the Antarctic intermediate water (Lutjeharms *et al.*, 1985; Lutjeharms, 1990). Indeed, the depth range occupied by assemblage C is to a large extent the domain of sub-Antarctic intermediate water (Lutjeharms *et al.*, 1985; Lutjeharms, 1990).

From the studies of the demersal fish communities in other parts of the world's ocean, the depths of community switches observed in the vicinity of the PEIs was similar to community switches in the Mediterranean Sea, North Atlantic and New Zealand and Australian coasts (Koslow, 1993; Koslow *et al.*, 1994; McClatchie *et al.*, 1997; Jacobs *et al.*, 1998; Massuti & Moranta, 2003; Cartes *et al.*, 2004). This could be a worldwide pattern driven by the similarity in the deep-sea environments. The fact that these boundaries coincide with physical boundaries may, however, suggest that identified fish assemblages may belong to the different depth-specific food web networks.

Fish trophic relationships

Whether or not the material was limited, the diets of all species investigated are presented for the first time from the proximity of the PEIs. Patagonian toothfish is widely distributed throughout the Southern Ocean and generally inhabits waters near or to the north of the Antarctic Polar Front (Gon & Heemstra, 1990). In the literature, this species is described as an opportunistic predator consuming mainly fishes and to a lesser extent cephalopods and crustaceans in its circum-Antarctic range: the Crozet and Kerguelen Islands, Ob and Lena seamounts (Chechun, 1984); South Georgia (McKenna, 1991; Tarverdieva *et al.*, 1996a; García de la Rosa *et al.*, 1997; Pilling *et al.*, 2001; Xavier *et al.*, 2002), Macquarie Island (Goldsworthy *et al.*, 2001, 2002) and Falkland Islands (García de la Rosa *et al.*, 1997; Arkhipkin *et al.*, 2003). Distinct changes in the diet with depth, body length and during different seasons have also been reported (Arkhipkin *et al.*, 2003). During April 2001, cephalopods and fishes were found to be the most important prey items, while mesopelagic and deep-sea fishes were only of secondary importance. This agrees well with the seasonal changes in the Patagonian toothfish diet around the Falkland Islands (Arkhipkin *et al.*, 2003). Overall, it appears that based on the diet composition and mercury concentration analysis presented by McArthur *et al.* (2003), Patagonian toothfish is positioned near the top of the food-chain in the vicinity of the sub-Antarctic islands (Arkhipkin *et al.*, 2003; this study). Similar to Patagonian toothfish, the macrourid *M. carinatus* appeared to be at the top of the food-chain based on the diet composition and stable isotope values (Table V and Fig. 8). The macrourids in general exhibit a range of feeding behaviours varying between benthic invertebrate and obligate fish feeding, depending on the availability of prey (Haedrich & Henderson, 1974; Pearcy & Ambler, 1974; Sedberry & Musick, 1978; Bulman *et al.*, 2002).

During April 2001 in the vicinity of the PEIs, the diet of *L. squamifrons* included a variety of prey groups, with myctophiids dominating the diet. This conforms well with the prey composition previously found in the stomachs of *L. squamifrons* sampled over the shelves and slopes of a variety of sub-Antarctic islands and seamounts (Chechun, 1984; Duhamel & Hureau, 1985; McKenna, 1991; Pakhomov, 1993; Tarverdieva *et al.*, 1996a, b).

Lepidonotothen squamifrons can, therefore, be described as an opportunistic planktophagous species, which at times complements its diet with benthos and micronektonic demersal or mesopelagic fishes.

The diets of other species investigated in the vicinity of the PEIs (Table V) are poorly studied not only in the Southern Ocean but elsewhere in the world's ocean. Overall, these fishes fed predominantly on pelagic, including epipelagic, meso- and benthopelagic, prey, which is consistent with studies on ecologically similar species (Gon & Heemstra, 1990; Pakhomov *et al.*, 1996; Bulman *et al.*, 2002).

Stable isotopes provide a powerful analytical tool allowing feeding ecology to be linked with their foraging habitats and time-integrated diets. According to nitrogen stable isotopes, most of fish species investigated in this study (Fig. 8), with the exception of small mesopelagic fishes on one side and *M. carinatus* (and perhaps Patagonian toothfish) on another, belong to tertiary consumers occupying the fourth trophic level (Wada *et al.*, 1987; Kaehler *et al.*, 2000; McArthur *et al.*, 2003). Despite the limited direct observations and literature sources, the fish diets appeared to be consistent with stable isotope measurements (Gon & Heemstra, 1990; Pakhomov *et al.*, 1996; Bulman *et al.*, 2002). Extreme variability of carbon stable isotope values, however, may indicate a greater number of food sources and trophic pathways in the deep-sea slope environment compared to the surface layers. It has been documented that at the base of the food web, carbon stable isotopes vary dramatically between nearshore *v.* offshore and between terrestrial *v.* aquatic realms (Rau *et al.*, 1982, 1989; Wada *et al.*, 1987; Kaehler *et al.*, 2000). Since wide carbon isotopic variations in demersal slope fishes could not be attributed to the above variability, it is possible to postulate that unique food pathways may be present in the deep-sea realm in the vicinity of the PEIs. Several fish species, including *I. australis*, *Benthalbella macrospinna* Bussing & Bussing, *Pseudomancopsetta andriashevi* Evseenko, *Poromitra crassiceps* (Günther) and perhaps *Alepisaurus brevirostris* Gibbs, *Trigonolampa miriceps* Regan & Trewavas and *B. antarcticus*, had similar nitrogen isotopic values with other species but surprisingly low carbon isotopic values (Fig. 8). Many variables, *e.g.* physiological state, body condition, seasonality, location and prey abundance, could affect inter- and intraspecific differences in nitrogen and carbon isotopic values. Nevertheless, differences are so pronounced that this is probably a result of substantially different sources at the base of the food web. First, the $\delta^{13}\text{C}$ anomalies could be a result of high lipid accumulation in deep-sea fishes as lipids have substantially lower $\delta^{13}\text{C}$ values relative to the whole organism (Rau *et al.*, 1982; Wada *et al.*, 1987). Second, the diets of above species may have included larger proportions of prey of a high Antarctic origin compared to the sub-Antarctic prey. It has been shown that both planktonic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ sources from the regions south of the Antarctic Polar Front are isotopically light ranging from -32.2 to -26.4‰ and from 0.6 to 9.8‰ , respectively (Rau *et al.*, 1982, 1989; Wada *et al.*, 1987). Finally, the proximity of the Southwest Indian Ridge may result in a high proportion of chemoautotrophic rather than photoautotrophic primary production to be incorporated into deep-sea food webs. In the recent study, spreading rates of $12\text{--}20$ mm year⁻¹ have been measured in the Southwest Indian ridge, suggesting the possibility for the establishment of hydrothermal vent communities in the region (Dick *et al.*, 2003). It has previously been documented that vent invertebrates are consistently isotopically lighter ($\delta^{13}\text{C}$ range is -74.3 to -10.2‰ and $\delta^{15}\text{N}$ range is -12 to 4‰ ; Conway *et al.*, 1994). The stable isotope approach postulates that deep-sea food webs in the vicinity of the PEIs could be more complicated than previously believed. Therefore, further studies, including both classic stomach content analyses and stable isotopes, are urgently required to better understand deep-sea (meso- and bathypelagic) food webs.

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