Isotopic niches of fishes in coastal, neritic and oceanic waters off Adélie land, Antarctica

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Abstract

We used the stable isotope method to investigate the ecological niches of Antarctic fishes, with $\delta^{13}C$ and $\delta^{15}N$ as proxies of fish habitats and dietary habits, respectively. Muscle isotopic signature was measured for each of 237 delipidated tissue samples from 27 fish species collected offshore Adélie Land, East Antarctica. Overall, $\delta^{13}C$ values ranged from $-25.3‰$ to $-18.2‰$, thus allowing characterizing of the fish habitats, with inshore/benthic species having more positive $\delta^{13}C$ signatures than offshore/pelagic ones. No clear difference in the $\delta^{13}C$ values of pelagic fishes was found between species living in neritic and oceanic waters. Overall, the $\delta^{15}N$ signatures of neritic pelagic and epibenthic fishes encompassed ~ 1.0 trophic level ($3.1‰$), a higher difference than that ($1.4‰$) found within the oceanic assemblage. Fishes with the lowest and highest $\delta^{15}N$ values are primarily invertebrate- and fish-eaters, respectively. The isotopic niches of fishes illustrate the different mechanisms allowing coexistence, with most fishes segregating at least by one of the two niche axes ($\delta^{13}C$ and $\delta^{15}N$). Muscle isotopic values also document interindividual foraging specialization over the long-term in coastal benthic fishes, but not in more offshore pelagic species. Finally, the $\delta^{15}N$ signatures of fishes overlap with those of penguins and seals, indicating that seabirds and marine mammals share the upper levels of the Antarctic pelagic ecosystem with some large fish species. In conclusion, the concept of isotopic niche is a powerful tool to investigate various aspects of the ecological niche of Antarctic fishes, thus complementing the use of other conventional and non-conventional approaches.

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1. Introduction

Understanding habitat selection and use in fish is time- and resource-consuming, often requiring the collection of large numbers of individuals and various sampling methods to characterize habitat preferences. Although stomach content analysis provides insight into prey items and foraging habitats, it only represents a limited area of actual habitat selection. Within that context, measuring the isotopic niche of animals is a powerful complementary tool to the conventional means investigating various dimensions of their ecological niche (Newsome et al., 2007). The basic isotopic concept is that an animal's chemical composition is directly influenced by what it consumes. Consumers are enriched in ^{15}N relative to their food and consequently stable-nitrogen isotope measurements (δ^{15}N) serve as indicators of a consumer diet and trophic position. By contrast, stable carbon signatures (δ^{13}C) vary little along the food chain and, in the marine environment, δ^{13}C values are mainly used to indicate the foraging habitats of predators, including fish. The stable isotope method provides some key advantages (Hobson, 2009). Firstly, they provide information on assimilated and not just ingested food. Secondly, they can provide an unbiased estimate of trophic level and habitat, because they are not hampered by the shortcoming of biases associated with conventional approaches. Thirdly, they provide time-integrated information that represents days to months of the consumer life depending on the tissue chosen. For example, the isotopic signature of white muscle is representative of the fish isotopic niche during the months preceding sampling (Herzka, 2005).

Over the last 15 years, stable isotopes have become a powerful tool for ecological studies on fish (Dufour and Gerdeaux, 2001), including their trophic relationships (Sherwood and Rose, 2005), resource partitioning within communities (Duponchelle et al., 2005), individual specialization (Beaudoin et al., 1999) and migrations (Nakamura et al., 2008). Surprisingly, there has been no research on the isotopic niches of Antarctic fishes, with limited isotopic information being provided by predators' and food web investigations (Rau et al., 1992; Table 1). The objective of this study was thus to test the use of stable isotopes to better define the ecological niches of Antarctic fishes, including their habitats (δ^{13}C) and dietary habits (δ^{15}N). We focused on fishes collected during the Collaborative East Antarctica Marine Census (CEA-MARC) that took place off Adélie Land, East Antarctica, during the austral summer 2007–2008.

Little is known about the foraging ecology of fishes from Adélie Land, the two available contributions being those of Hureau (1970) and Koubbi et al. (2007) that detailed the diet of four nototheniid species.

Based on the scientific literature on fish biology and on isotopic gradients in aquatic environments, we did the following predictions about the isotopic niches of Antarctic fishes.

1. Fish δ^{13}C values should decrease in the following order coastal > neritic > oceanic species, because δ^{13}C signature of particulate organic matter decreases from inshore to offshore waters (Hill et al., 2006), including Antarctic waters (Trull and Armand, 2001) (prediction 1).
2. Muscle δ^{13}C values should be higher in benthic than in pelagic species, because benthic organisms are ^{13}C-enriched when compared to pelagic ones (France, 1995; Kaehler et al., 2000) (prediction 2).
3. The δ^{13}C signature of fish caught in northern waters should be higher than that of southern species, because marine plankton δ^{13}C, and thus consumer δ^{13}C, varies with latitudes in oceanic waters (Rau et al., 1982), including the Southern Ocean (Trull and Armand, 2001; Cherel and Hobson, 2007; Jaeger et al., 2010b; Quillfeldt et al., 2010) (prediction 3). The latitudinal δ^{13}C gradient results from the annular structure of the Southern Ocean worldwide, with water masses and fronts with different physical and biological characteristics encircling the Antarctic continent (Orsi et al., 1995).

The Southern Ocean is here defined as the marine area south of the Subtropical Front, and the Antarctic Zone (Antarctic waters) as the area south of the Antarctic Polar Front.

2. Material and methods

Most fishes were collected during the Census of Antarctic Marine Life (CAML, International Polar Year Project 53) and its component program CEA-MARC. Its key focus was a major ship-based research program to study the marine organisms and oceanography of the waters north of Adélie Land and George V Land in the austral summer of 2007–2008. Specifically, neritic and oceanic fishes were caught using beam trawls and pelagic trawls (international young gadoid pelagic trawl, IYGPT, and rectangular midwater trawl, RMT) during the RSV *Aurora Australis* and TRV *Umitaka Maru* cruises, respectively. Coastal

Table 1
Literature isotopic values of fish from Antarctic waters (south the Polar Front). Scientific names, systematic order and feeding habitats followed Gon and Heemstra (1990) and Eastman (1993).

Species	Feeding habitat	Locality	Size/age	Tissue	Delipidation	n	δ13C (‰)	δ15N (‰)	C:N	References
Petromyzontidae										
Geotria australis	Pelagic (parasitic)	South Georgia	ni	Muscle	Yes	11	−22.3 ± 2.1	8.5 ± 0.6	ni	Anderson et al., 2009
Paralepididae										
Notolepis coatsi	Mesopelagic	Australian Sector	ni	ni	No	1	−25.8	7.1	ni	Wada et al., 1987
Myctophidae										
Electrona antarctica	Mesopelagic	Australian Sector	ni	ni	No	1	−27.1	7.5	ni	Wada et al., 1987
Zoarcidae										
Lycodichthys dearborni	Benthic	McMurdo Sound	ni	Muscle	No	1	−23.6	13.2	3.3	Burns et al., 1998
Lycodichthys sp.	Benthic	Antarctic Peninsula	ni	Muscle	No	5	−24.2 ± 0.5[a]	10.6 ± 0.7[a]	3.5 ± 0.1[a]	Mincks et al., 2008
Nototheniidae										
Dissostichus eleginoides	Epibenthic & pelagic	South Georgia	ni	Muscle	Yes	3	−21.8 ± 0.7	11.4 ± 0.1	ni	Anderson et al., 2009
Dissostichus mawsoni	Epibenthic & pelagic	McMurdo Sound	ni	Muscle	No	5	−28.9 ± 0.6[a]	13.5 ± 0.2[a]	7.2 ± 1.2[a]	Burns et al., 1998
Gobionotothen gibberifrons	Benthic	Antarctic Peninsula	ni	Muscle	No	3	−24.9 ± 0.9[a]	10.1 ± 0.7[a]	4.5 ± 0.0[a]	Dunton, 2001
Lepidonotothen squamifrons	Benthic	South Shetland Islands	ni	Muscle	Yes	7	−23.6 ± 0.6	12.1 ± 0.5	3.1 ± 0.1	Polito et al., 2009
Lepidonotothen larseni	Benthic/semipelagic	South Georgia	ni	Muscle	Yes	6	−16.0 ± 0.3	14.5 ± 0.2	ni	Anderson et al., 2009
		Bouvet Island	ni	Muscle	No	10	−26.2 to −21.0	8.0 to 9.9	ni	Jacob et al., 2006
Notothenia coriiceps	Benthic	Antarctic Peninsula	ni	Muscle	No	5	−20.4 ± 0.5[a]	12.0 ± 0.3[a]	4.7 ± 0.3[a]	Dunton, 2001
Pagothenia borchgrevinki	Cryopelagic	McMurdo Sound	Small adults	Whole body	Yes	2	−25.7, −24.7	10.4, 11.4	ni	Krahn et al., 2006
		McMurdo Sound	ni	Muscle	No	3	−25.5 ± 0.5[a]	11.0 ± 0.2[a]	3.7 ± 0.4[a]	Burns et al., 1998
Patagonotothen guntheri	Semipelagic	South Georgia	ni	Muscle	Yes	8	−22.0 ± 0.6	9.0 ± 0.3	ni	Anderson et al., 2009

Species	Habitat	Location	Stage	Tissue	Predator stomach	n	δ13C	δ15N	δ34S	Reference
Pleuragramma antarcticum	Pelagic	Adélie Land	Juveniles	Stomach contents[b]	Yes	5	−24.7 ± 0.4	10.6 ± 0.3	3.8 ± 0.2	Cherel, 2008
		McMurdo Sound	ni	Muscle	No	4	−28.3 ± 0.4[a]	10.9 ± 0.2[a]	6.4 ± 0.6[a]	Burns et al., 1998
		Prydz Bay	Juveniles	Muscle	Yes	10	−24.3 ± 0.3	9.6 ± 0.4	ni	Hodum and Hobson, 2000
		Prydz Bay	Adults	Stomach contents[b]	Yes	13	−23.9 ± 0.7	10.7 ± 1.2	ni	Hodum and Hobson, 2000
Trematomus bernacchii	Benthic	Davis station	ni	Muscle	Yes	10	−14.4	15.2	ni	Hall-Aspland et al., 2005a
		Elephant Island	ni	ni	ni	1	−23.4	10.4	2.5	Wada et al., 1987
Trematomus loennbergii	epibenthic	McMurdo Sound	ni	Muscle	No	2	−26.8, −24.5	10.3, 13.4	3.5, 4.3	Burns et al., 1998
Trematomus newnesi	Semipelagic	McMurdo Sound	Small adults	Whole body	Yes	2	−26.0, −24.3	10.1, 11.2	ni	Krahn et al., 2006
		Mawson station	Juveniles	Stomach contents[b]	Yes	10	−20.0 ± 1.1	9.0 ± 0.9	ni	Tierney et al., 2008
Nototheniids sp.		Antarctic Peninsula	ni	Muscle	No	5	−24.9 ± 0.3[a]	10.7 ± 0.3[a]	3.5 ± 0.1[a]	Mincks et al., 2008
Harpagiferidae										
Harpagifer antarcticus	Benthic	Antarctic Peninsula	ni	Muscle	No	5	−20.7 ± 0.5[a]	11.8 ± 0.2[a]	4.5 ± 0.2[a]	Dunton, 2001
Bathydraconidae										
Parachaenichthys georgianus	Benthic	South Georgia	ni	Muscle	Yes	1	−18.3	11.9	ni	Anderson et al., 2009
Channichthyidae										
Chaenocephalus aceratus	Benthic	Antarctic Peninsula	ni	Muscle	No	4	−24.9 ± 0.1[a]	11.0 ± 0.6[a]	4.3 ± 0.0[a]	Dunton, 2001
Champsocephalus gunnari	Pelagic	South Georgia	ni	Muscle	Yes	16	−20.7 ± 0.5	9.3 ± 0.3	ni	Anderson et al., 2009
Chionodraco hamatus	Benthic	Prydz Bay	ni	Muscle	Yes	8	−22.5 ± 0.3[a]	12.6 ± 0.3[a]	ni	Hall-Aspland et al., 2005b
Chionodraco rastrospinosus	Benthic	Antarctic Peninsula	ni	Muscle	No	5	−25.9 ± 0.1[a]	7.6 ± 0.2[a]	3.4 ± 0.1[a]	Mincks et al., 2008
Pseudochaenichthys georgianus	Pelagic/ semipelagic	South Georgia	ni	Muscle	Yes	5	−20.1 ± 0.2	11.0 ± 0.7	ni	Anderson et al., 2009

Abbreviation, ni: no information. Values are means ± SD.

[a] Means ± SE.

[b] Samples collected from predators' stomach contents.

species were caught at and near the French station of Dumont d'Urville using various gears, including handlines, bottom longlines, trammels and dredges during 2007 and at the beginning of 2008.

Fish identification relied on their external features, using published guides (Gon and Heemstra, 1990) and our own reference collection. Each individual fish was measured (standard length, SL), and a piece of its white muscle was sampled and kept in 70% ethanol until analysis. After being dried in an oven at +50 °C, muscle samples were ground to a fine powder and lipids were extracted using cyclohexane. The low C:N ratio of the delipidated samples allowed comparison of the carbon isotopic signature without any deleterious effect due to different lipid contents among individuals and species (see discussion below). Relative abundance of ^{13}C and ^{15}N were determined using an Isoprime (Micromass) continuous-flow isotope-ratio mass spectrometer. Results are presented in the usual γ notation relative to PeeDee belemnite and atmospheric N_2 (Air) for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors < 0.15‰ and <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Data were statistically analyzed with SYSTAT 12 (statistical significance: $P < 0.05$). Values are means ± SD.

3. Results

The stable isotopic signature of white muscle from 237 individuals belonging to 27 fish species were analyzed in the present work, thus increasing considerably the number of individuals ($n = 177$) and species (24) of Antarctic fish for which isotopic data were available in the scientific literature (Table 1). Noticeably, we looked at 20 species of fish that were not previously investigated isotopically in Antarctic waters (Table 2). Overall, the $\delta^{13}C$ values of fish white muscle encompass a 7.1‰ difference, from −25.3‰ (*Chaenodraco wilsoni*) to −18.2‰ (*Notothenia coriiceps*), while $\delta^{15}N$ values encompass a 4.2‰ difference, from 9.2‰ (*Protomyctophum bolini*) to 13.9‰ (*Artedidraco skottsbergi*) (Table 2). Such a large range in isotopic signatures indicates that fish foraged in various habitats where they fed on different prey.

3.1. Isotopic niches of coastal and neritic fishes

According to their size (Gon and Heemstra, 1990), the coastal and neritic fishes investigated in the present study were large juveniles, subadults and adult specimens (Table 1). In Adélie Land, the 12 species of coastal and neritic fishes were segregated by both their $\delta^{13}C$ and $\delta^{15}N$ muscle values (Kruskal−Wallis, H = 141.00 and 119.97, respectively, both $P < 0.0001$). Noticeably, three species (*N. coriiceps*, *Trematomus bernacchii* and *T. pennellii*) showed more positive $\delta^{13}C$ values (from −19.3 to −18.2‰) than the remaining nine species (from −25.3 to −22.3‰) (Fig. 1, upper panel). Otherwise, the 12 fish species fed along a continuum of $\delta^{15}N$ values amounting to 3.1‰, from 10.3‰ (*C. wilsoni*) to 13.4‰ (*Chionodraco hamatus*).

Resource partitioning of related species belonging to the same family was investigated. The two bathydraconids did not show statistically different isotopic signatures (*t*-tests, $t = 0.57$ and 0.56, $P = 0.575$ and 0.583 for $\delta^{13}C$ and $\delta^{15}N$, respectively), but the three channichthyids segregated by both their $\delta^{13}C$ and $\delta^{15}N$ values (ANOVA, $F_{2,20} = 38.39$ and 51.76, respectively, both $P < 0.0001$). Post-hoc Tukey Honest Significant Difference multiple comparison tests indicate that *C. hamatus* and *Cryodraco antarcticus* had identical isotopic niches that nevertheless differed from that of *C. wilsoni*. Overall, nototheniid fishes segregated by both their habitats ($\delta^{13}C$) and trophic positions ($\delta^{15}N$) ($H = 98.52$ and 87.65, respectively, both $P < 0.0001$). Tukey tests indicate that the seven species differed by at least one isotopic niche axe, with only *Trematomus eulepidotus* and *Pleuragramma antarcticum* showing a complete overlap in their $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 1, upper panel).

Adult *P. antarcticum* were collected using both bottom and pelagic trawls (*Aurora Australis* and *Umitaka Maru* cruises, respectively). Fish size was not statistically significant among the two groups (SL: 155 ± 19 and 165 ± 14 mm, $n = 12$ and 18, respectively; *t*-test, $t = 1.64$, $P = 0.113$), but muscle $\delta^{13}C$ and $\delta^{15}N$ values of individuals caught at the bottom were higher than those of fish caught in the water column ($\delta^{13}C$: −24.3 ± 0.3 and −25.1 ± 0.3‰, $\delta^{15}N$: 10.8 ± 0.6 and 10.1 ± 0.6‰; $t = 7.55$ and 3.16, $P < 0.0001$ and $P = 0.004$, respectively).

3.2. Isotopic niches of oceanic fishes

According to their size (Gon and Heemstra, 1990), the oceanic fishes investigated in the present study were subadult and adult specimens (Table 1). The seven species of oceanic fishes were segregated by both their $\delta^{13}C$ and $\delta^{15}N$ values (Kruskal−Wallis, $H = 49.30$ and 29.15, respectively, both $P < 0.0001$). Two species (*Cyclothone microdon* and, to a lesser extent, *Cynomacrurus piriei*) showed more positive

Table 2
Isotopic signatures of fish from Adélie Land, Antarctica. Age was estimated using standard length (SL, Gon and Heemstra, 1990).

Species	Fishing gears	Depths (m)	Age	n	SL (mm)	δ¹³C (‰)	δ¹⁵N (‰)	C:N
Bathylagidae								
Bathylagus antarcticus	Pelagic trawl	500–2000	Subadults	3	79 ± 24	−23.3 ± 0.2	10.9 ± 0.2	3.25 ± 0.05
Bathylagus sp.	Pelagic trawl	1000	Subadults/adults	17	95 ± 30	−23.6 ± 0.4	10.2 ± 0.8	3.41 ± 0.04
Gonostomatidae								
Cyclothone microdon	Pelagic trawl	1000–2000	Adults	9	45 ± 5	−21.0 ± 0.4	10.2 ± 0.5	3.27 ± 0.03
Anotopteridae								
Anotopterus vorax	Pelagic trawl	200	Adult	1	1015	−23.2	8.9	3.22
Myctophidae								
Electrona antarctica	Pelagic trawl	500–1000	Subadults/adults	15	66 ± 13	−24.5 ± 0.8	9.4 ± 0.5	3.28 ± 0.02
Gymnoscopelus bolini	Pelagic trawl	1000	Subadult	1	250	−20.8	11.2	3.30
Gymnoscopelus braueri	Pelagic trawl	1000	Subadults/adults	5	121 ± 37	−24.0 ± 1.2	9.7 ± 0.9	3.28 ± 0.12
Krefftichthys anderssoni	Pelagic trawl	200	Adult	1	59	−24.0	8.1	3.35
Protomyctophum bolini	Pelagic trawl	0–2000	Subadults	13	40 ± 3	−23.0 ± 0.5	9.2 ± 0.5	3.23 ± 0.01
Macrouridae								
Cynomacrurus piriei	Pelagic trawl	1000	Subadults	5	339 ± 29	−22.1 ± 1.0	10.6 ± 0.7	3.19 ± 0.02
Oneirodidae								
Oneirodes notius	Pelagic trawl	1000	Adult	1	194	−22.3	12.2	3.21
Nototheniidae								
Notothenia coriiceps	Handline, bottom longline	5–36	Subadults/adults	18	202 ± 29	−18.2 ± 1.2	12.8 ± 0.4	3.16 ± 0.05
Pleuragramma antarcticum	Benthic & pelagic trawls	263–878	Subadults/adults	40	145 ± 34	−24.7 ± 0.4	10.4 ± 0.6	3.22 ± 0.08
Trematomus bernacchii	Handline, benthic trawl, dredge	10–81	Juveniles/adults	21	130 ± 45	−19.3 ± 1.4	12.4 ± 1.0	3.17 ± 0.05
Trematomus eulepidotus	Benthic trawl	211	Juveniles/subadults	5	175 ± 67	−24.2 ± 0.4	10.6 ± 0.5	3.19 ± 0.06
Trematomus hansoni	Handline, bottom longline, trammel	36–80	Subadults/adults	7	202 ± 31	−22.3 ± 1.3	12.1 ± 0.5	3.12 ± 0.04
Trematomus lepidorhinus	Benthic trawl	421	Subadult	1	155	−24.2	10.3	3.06
Trematomus newnesi	Dredge	ni	Juveniles/adults	5	89 ± 36	−23.2 ± 0.6	11.0 ± 0.3	3.15 ± 0.01
Trematomus pennellii	Handline, trammel, benthic trawl	36–80	Juveniles/subadults	27	73 ± 28	−19.2 ± 1.1	11.9 ± 0.7	3.11 ± 0.05
Artedidraconidae								
Artedidraco skottsbergi	Benthic trawl	ni	Subadult	1	83	−20.6	13.9	3.31
Bathydraconidae								
Gymnodraco acuticeps	Handline, benthic trawl	18–211	Subadults/adults	8	249 ± 29	−23.0 ± 1.0	12.9 ± 0.9	3.13 ± 0.01
Racovitzia glacialis	Benthic trawl	263–546	Subadults/adults	8	209 ± 34	−22.8 ± 0.4	12.7 ± 0.6	3.14 ± 0.02
Channichthyidae								
Chaenodraco wilsoni	Pelagic trawl	50–200	Juveniles	11	120 ± 30	−25.3 ± 0.4	10.3 ± 0.8	3.40 ± 0.05
Chionodraco hamatus	Benthic trawl	460–544	Subadults/adults	7	297 ± 29	−24.1 ± 0.1	13.4 ± 0.6	3.17 ± 0.02
Cryodraco antarcticus	Benthic trawl	421–460	Large juveniles	5	170 ± 25	−24.0 ± 0.3	12.5 ± 0.3	3.10 ± 0.05
Dacodraco hunteri	Pelagic trawl	500	Juvenile	1	144	−24.7	13.1	3.37
Gempylidae								
Paradiplospinus gracilis	Pelagic trawl	1000	Juvenile	1	355	−22.5	9.8	3.26

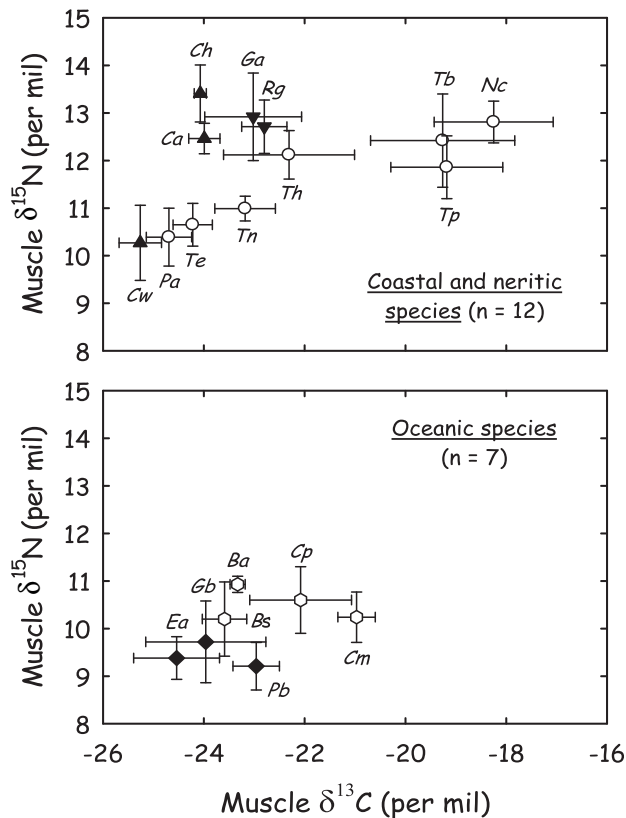Abbreviation, ni: no information. Values are means ± SD.

Fig. 1. Stable carbon and nitrogen isotope values of white muscle of coastal and neritic (upper panel) and oceanic (lower panel) fishes from Adélie Land, Antarctica. Abbreviations, *Ba*: *Bathylagus antarcticus*, *Bs*: *Bathylagus* sp., *Ca*: *Cryodraco antarcticus*, *Ch*: *Chionodraco hamatus*, *Cp*: *Cynomacrurus piriei*, *Cm*: *Cyclothone microdon*, *Cw*: *Chaenodraco wilsoni*, *Ea*: *Electrona antarctica*, *Ga*: *Gymnodraco acuticeps*, *Gb*: *Gymnoscopelus braueri*, *Nc*: *Notothenia coriiceps*, *Pa*: *Pleuragramma antarcticum*, *Pb*: *Protomyctophum bolini*, *Rg*: *Racovitzia glacialis*, *Tb*: *Trematomus bernacchii*, *Te*: *Trematomus eulepidotus*, *Th*: *Trematomus hansoni*, *Tn*: *Trematomus newnesi*, *Tp*: *Trematomus pennellii*. Values are means ± SD.

$\delta^{13}C$ values (from −22.1 to −21.0‰) than the remaining species (from −24.5 to −23.0‰) (Fig. 1, lower panel). Otherwise, the seven species fed along a continuum of restricted range of $\delta^{15}N$ values amounting to 1.7‰, from 9.2‰ (*P. bolini*) to 10.9‰ (*Bathylagus antarcticus*). The three myctophids segregated by their $\delta^{13}C$, but not their $\delta^{15}N$ values (H = 18.71 and 1.67, P < 0.0001 and = 0.435, respectively), with Tukey tests showing that *Electrona antarctica* and *P. bolini* differed by their $\delta^{13}C$ values (P < 0.0001).

4. Discussion

4.1. Lipid removal and $\delta^{13}C$ values

The lowest $\delta^{13}C$ values of individual fishes from Adélie Land were in the range from −25.5 to −26.0‰.

These values are noticeably higher than the carbon signature of some Antarctic fishes from previous investigations. Those very low $\delta^{13}C$ values are consistently associated with high C:N ratios (Rau et al., 1992; Table 1), thus indicating a large lipid effect lowering the fish carbon signature, because C:N is positively related to lipid content in animal tissues (Post et al., 2007) and lipids are depleted in ^{13}C when compared to proteins and carbohydrates (DeNiro and Epstein, 1977; Tieszen et al., 1983). Lipid content varies with tissue-type, nutritional status, age, individual and species, and these variations have the potential to introduce considerable bias into biological interpretation of $\delta^{13}C$ signatures. In the present study, lipid extraction leads to an homogenization of C:N mass ratios, with all values being in the range 3.1−3.4 (Table 2). Such low C:N values indicate low lipid contents that do not influence the $\delta^{13}C$ signatures (Post et al., 2007). We therefore recommend firstly to extract lipids from fish muscle (or, alternatively, to mathematically normalize $\delta^{13}C$ values using C:N mass ratios of the samples; Post et al., 2007); secondly to monitor the sample C:N ratios to check chemical extraction, and thirdly to include routinely the C:N ratios together with $\delta^{13}C$ and $\delta^{15}N$ values in published works. Consequently, previous $\delta^{13}C$ values from non-delipidated samples with associated high C:N ratios or with no indication of their C:N values cannot be used to define accurately the foraging habitats of fish and their food sources and trophic pathways (e.g. Pakhomov et al., 2006; Table 1).

4.2. Isotopic niches of Antarctic fishes

4.2.1. Predictions 1 & 2

The isotopic investigation highlights two main features within the Antarctic fish assemblage: firstly, three species segregate from the other fishes by their high muscle $\delta^{13}C$ values, and secondly, there is a large overlap in the low $\delta^{13}C$ values of neritic and oceanic fishes (Fig. 1). *N. coriiceps*, *T. bernacchii* and *T. pennellii* are shallow benthic species (Gon and Heemstra, 1990). Noticeably, *N. coriiceps*, which is the coastal species with the most restricted depth range (0−30 m; Hureau, 1970), showed the most positive $\delta^{13}C$ value. The species thus illustrates well the horizontal (inshore/offshore) and vertical (benthic/pelagic) isotopic gradients in the marine environments and it can be considered as a coastal end-point for the combination of both gradients in Adélie Land. Two other fish species were also collected in coastal waters, but both *Gymnodraco acuticeps* and *Trematomus hansoni* presented lower

$\delta^{13}C$ values than the three former species. All the five species have a benthic life style and feed primarily on benthic prey (Hureau, 1970; Gon and Heemstra, 1990; La Mesa et al., 2004). However, *G. acuticeps* and *T. hansoni* also include pelagic items in their diet (Hureau, 1970; Eastman, 1985), thus explaining their lower carbon signatures that are intermediary between benthic and pelagic ones (e.g. *G. acuticeps* in Fig. 2). In the same way, the intermediate $\delta^{13}C$ value of *Trematomus newnesi* is in agreement with the semipelagic life style of the species (Gon and Heemstra, 1990).

P. antarcticum is by far the dominant midwater fish over the Antarctic shelf (Gon and Heemstra, 1990). Accordingly, its $\delta^{13}C$ signature is low, which is a consistent characteristic of pelagic organisms from high-Antarctic waters (Cherel, 2008). Interestingly, $\delta^{13}C$ values were slightly higher in specimens caught in bottom than in pelagic trawls, which agrees with adult *P. antarcticum* living in the deep and occasionally feeding near the bottom (Eastman, 1985). As expected, other pelagic species also show $\delta^{13}C$ values $< -24‰$ (*C. wilsoni* and *Dacodraco hunteri*; Eastman, 1993; La Mesa et al., 2004), and their low $\delta^{13}C$ signatures confirm that epibenthic species (*C. hamatus*, *Cryodraco antarcticus*, *Trematomus eulepidotus* and *T. lepidorhinus*; Gon and Heemstra, 1990; La Mesa et al., 2004) feed mainly on pelagic prey. Finally, the
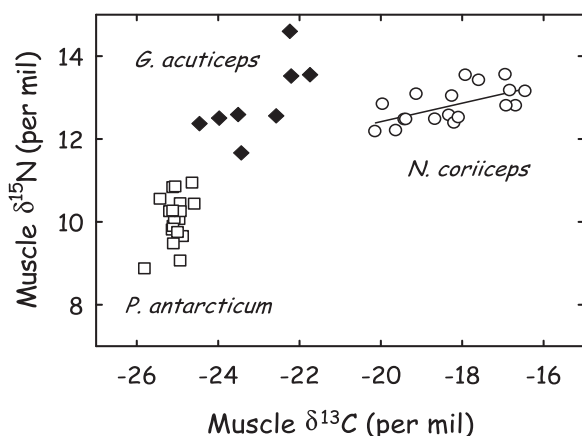

Fig. 2. Stable carbon and nitrogen isotope values of individuals from three representative fish species from Adélie Land, Antarctica. *Notothenia coriiceps*, *Gymnodraco acuticeps* and *Pleuragramma antarcticum* illustrate a benthic species feeding on benthic prey, a fish species feeding on both benthic and pelagic prey, and a pelagic species feeding on pelagic prey, respectively. *Notothenia coriiceps* and *Gymnodraco acuticeps* are two species showing large interindividual variations in their food and feeding ecology (see text). The linear regression between $\delta^{15}N$ and $\delta^{13}C$ values of *N. coriiceps* underlines the positive link between carbon and nitrogen baseline levels that characterize the different fish benthic micro-habitats and/ or diets ($y = 0.22x + 16.89$, $R^2 = 0.367$, $F_{1,16} = 9.25$, $P = 0.008$).

$\delta^{13}C$ values of neritic and oceanic fishes overlap greatly in the pelagic environment. For example, the two commonest Antarctic pelagic species, *P. antarcticum* over the shelf and *E. antarctica* in the oceanic domain have identical $\delta^{13}C$ values. These data do not agree with the little available information on baseline levels showing that $\delta^{13}C$ values of particulate organic matter are higher in neritic waters than in adjacent oceanic waters (Trull and Armand, 2001).

4.2.2. Prediction 3

Baseline oceanic $\delta^{13}C$ value, and thus consumer $\delta^{13}C$ signatures, decreases toward higher latitudes (Trull and Armand, 2001; Cherel and Hobson, 2007; Jaeger et al., 2010b; Quillfeldt et al., 2010). Accordingly, $\delta^{13}C$ values of myctophids (*E. antarctica*, *Gymnoscopelus braueri* and *P. bolini*) are lower off Adélie Land than off Kerguelen Islands that are located further north (Cherel et al., 2010). In the Southern Ocean, the isotopic latitudinal change more likely occurs stepwise in frontal regions (François et al., 1993; Trull and Armand, 2001). Hence, lower $\delta^{13}C$ values are expected from fishes collected south than north of the Southern Boundary and the Southern Antarctic Circumpolar Current Front (SACCF), which are close together in the sampling area (Orsi et al., 1995). These two fronts were located at $\sim 64°S$ offshore Adélie Land and influenced the pelagic fish community structure during the CEAMARC surveys (Koubbi et al., 2010). Indeed, *E. antarctica* had lower $\delta^{13}C$ values that all the other oceanic species of which most (if not all) individuals had been caught north of $64°S$. A notable exception is *P. bolini*, because most individuals were collected south of the SACCF, but they retained relatively high $\delta^{13}C$ values. Since the stable isotope integrates the fish feeding ecology over the long-term, the most likely explanation of that discrepancy is a recent migration of *P. bolini* across the SACCF. The single specimen of *Paradiplospinus gracilis* showed the same pattern: it was caught south of the SACCF, but its isotopic $\delta^{13}C$ signature indicates a past feeding ecology north of it. Such latitudinal movements within the Southern Ocean were recently described using stable isotope signatures of various animals, including squids, seabirds and marine mammals (Cherel and Hobson, 2005; Cherel et al., 2009; Jaeger et al., 2010a).

4.2.3. Trophic ranges and trophic structure

Overall the $\delta^{15}N$ signatures of Antarctic pelagic and epibenthic fishes encompassed ~ 1.0 trophic level (3.1‰), a higher difference than that (1.4‰) found

within the oceanic assemblage. These $\delta^{15}N$ ranges are relatively small when compared to the trophic structure of communities elsewhere (Al-Habsi et al., 2008; Revill et al., 2009). Nevertheless, Antarctic neritic fishes with low $\delta^{13}C$ values can be broadly grouped according to their high and low $\delta^{15}N$ signatures (Fig. 1), which correspond to diets mainly based on fish and crustaceans, respectively (Gon and Heemstra, 1990). Oceanic fishes have low $\delta^{15}N$ values that are consistent with a crustacean diet (e.g. myctophids; Hopkins and Torres, 1989; Gon and Heemstra, 1990), but some species presented unexpectedly high $\delta^{15}N$ signatures for invertebrate feeders (e.g. *Bathylagus* spp, *Cyclothone microdon* and *Cynomacrurus piriei*; Gon and Heemstra, 1990; Geiger et al., 2000; Gaskett et al., 2001). Those fishes are all deep-dwelling species (Gon and Heemstra, 1990; Moteki et al., 2009) and their high $\delta^{15}N$ values can be related to the higher $\delta^{15}N$ in zooplankton with increasing depth, a feature that is explained by more trophic steps between deep-sea consumers and food web base or/and by a ^{15}N enrichment of the source material at depth (Laakmann and Auel, 2010).

Fish isotopic niches illustrate the different mechanisms allowing coexistence. Noticeably, fishes of the family nototheniids pointed out the importance of both different habitats ($\delta^{13}C$) and diets ($\delta^{15}N$), with all species segregating by at least one isotopic niche axis. Two exceptions are the epibenthic *T. eulepidotus* and the pelagic *P. antarcticum* that presented identical isotopic signatures, thus underlining a limitation of the isotopic method that cannot segregate species living in different environments but feeding on the same prey. The relatively low $\delta^{15}N$ value of *P. antarcticum* is nevertheless in agreement with a diet based on omnivorous crustaceans, e.g. the ice krill *Euphausia crystallorophias* (Gon and Heemstra, 1990; Cherel, 2008).

4.2.4. Isotopic generalists and specialists

All the five shallow-living species (*G. acuticeps*, *N. coriiceps*, *T. bernacchii*, *T. hansoni* and *T. pennellii*) showed large variances in their isotopic signatures. Since muscle tissue integrates the individual feeding habits over months preceding sampling, high variances indicate long-term interindividual differences in the fish foraging ecology (e.g. *N. coriiceps*, a species that is known to feed both on algae and invertebrates; Hureau, 1970). This biological characteristic was recently described in other coastal benthic predators from the Southern Ocean (Bearhop et al., 2006). At the species and population levels, the five fishes are considered as trophic generalists and opportunist feeders (Gon and Heemstra, 1990; La Mesa et al., 2004). Their isotopic signatures complete the picture by showing that these generalist populations are composed of specialist individuals that forage in different micro-habitats and/or on different food types, a common but still underestimated feature of many animal populations (Bolnick et al., 2003). Noticeably, it is in agreement with the complex mosaic of habitats that characterizes the coastal benthos of Antarctica (Thrush et al., 2010). In contrast, isotopic variances were smaller in pelagic species (e.g. *P. antarcticum* in Fig. 2), a feature that is probably related to the more homogeneous pelagic than benthic environment in coastal and neritic waters.

4.3. Fishes within the Antarctic trophic web

The $\delta^{13}C$ signatures of air-breathing predators living in Antarctica, including Adélie Land, were all very negative (Hodum and Hobson, 2000; Zhao et al., 2004; Cherel, 2008; authors' unpublished data) thus indicating that they prey almost exclusively upon pelagic organisms. The only exception is the slightly more positive $\delta^{13}C$ value of Weddell seals (authors' unpublished data), which, accordingly, is known to include some benthic prey in its diet (Burns et al., 1998). Consequently, most of the Antarctic neritic fishes are not preyed upon by any of the seabirds and marine mammals, because they belong to the endemic suborder Notothenioidei, which is principally a benthic group (Eastman, 1993; La Mesa et al., 2004).

$\delta^{15}N$ signatures of two key macrozooplanktonic species and of three diving top predators highlight two main features about the trophic position of Antarctic fishes within the pelagic ecosystems off Adélie Land (Fig. 3). Firstly, fish $\delta^{15}N$ values are well above ($\geq$one trophic level) those of the mainly herbivorous Antarctic krill *Euphausia superba* and omnivorous ice krill, thus showing that all pelagic fishes are strictly carnivorous. Secondly, a major result of the present work is the complete overlap between the $\delta^{15}N$ signatures of fish with those of penguins and seals, indicating that the so-called top predators (seabirds and marine mammals) share the upper levels of the trophic web with some large fishes, including channichthyids. Indeed, the lowest and the highest $\delta^{15}N$ values correspond to species feeding mainly on crustaceans (myctophids and Adélie penguin) and on fish (icefishes, and emperor penguin and Weddell seal), respectively (Gon and Heemstra, 1990; La Mesa et al., 2004; Cherel, 2008). Depending on species, other
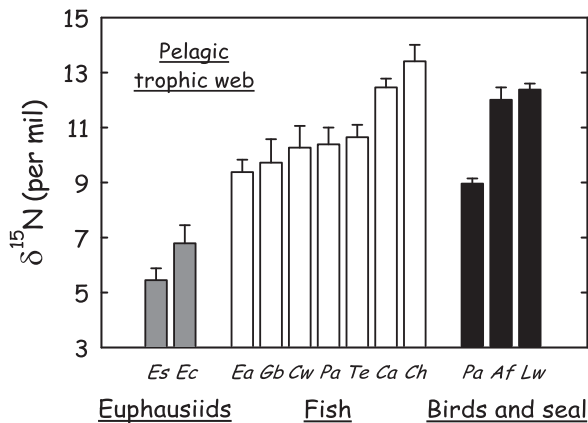
Fig. 3. Stable nitrogen isotope values of whole euphausiids (gray), white muscle of pelagic fishes (e.i. $\delta^{13}C \leq -24‰$) (white) and blood of adult air-breathing diving vertebrates (black) from Adélie Land, Antarctica (data from Cherel, 2008; authors'unpublished data; this study). Abbreviations, *Af*: *Aptenodytes forsteri* (emperor penguin), *Ca*: *Cryodraco antarcticus*, *Ch*: *Chionodraco hamatus*, *Cw*: *Chaenodraco wilsoni*, *Es*: *Euphausia superba* (Antarctic krill), *Ec*: *Euphausia crystallorophias* (ice krill), *Lw*: *Leptonychotes weddellii* (Weddell seal), *Pa*: *Pleuragramma antarcticum*, *Ea*: *Electrona antarctica*, *Gb*: *Gymnoscopelus braueri*, *Pa*: *Pygoscelis adeliae* (Adélie penguin), *Te*: *Trematomus eulepidotus*. Values are means ± SD.

seabirds and marine mammals also prey upon crustaceans and fish in Adélie Land and elsewhere, with euphausiids, and *P. antarcticum* and *E. antarctica* playing pivotal roles in the nutrition of top predators in the high-Antarctic (Ridoux and Offredo, 1989; Ainley et al., 1991; La Mesa et al., 2004; Smith et al., 2007).

4.4. Conclusions

To our knowledge, this work is the first detailed isotopic investigation on Antarctic fishes. Overall, the isotopic niches are in general agreement with the known life-styles, habitats and diets of fish collected off Adélie Land and from elsewhere in Antarctica. The isotopic data however add substantial information to the knowledge of fish in Antarctic waters, e.g. their importance as top predators in the pelagic ecosystem, and the level of individual specialization within populations. Nevertheless, the isotopic method suffers from some limitations. Firstly, the isotopic signature does not allow prey identification at the species level. Secondly, a thorough interpretation of the isotopic niches necessitates a good knowledge of the isotopic gradients occurring within the consumers' foraging areas (Cherel et al., 2008). Thirdly, overlaps between the different gradients can lead to strong misinterpretation of foraging origins (Cherel and Hobson, 2007). Consequently, the method is at its most powerful when combined with other conventional (e.g. food analysis, morphological and anatomical adaptations) and non-conventional (habitat modeling, lipids as trophic markers) approaches. Importantly, it bypasses the problems of empty stomachs (e.g. channichthyids, *Acanthodraco dewitti*; La Mesa et al., 2004) and of post-capture feeding in nets. For Antarctic fish, the method is probably best used to investigate community structure and poorly known species (e.g. artedidraconids, bathydraconids), including rarely caught fish (e.g. *D. hunteri*, *Gvozdarus svetovidivi*; Gon and Heemstra, 1990; La Mesa et al., 2004). Finally, more isotopic information is needed on ontogenic changes and on other species (including the large *Dissostichus mawsoni*) and areas to better understand the ecological role of fishes in Antarctic waters.

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