Vol. 194: 143-158, 2000 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published March 17

Trophic ecology of the family Artedidraconidae (Pisces: Osteichthyes) and its impact on the eastern Weddell Sea benthic system

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ABSTRACT: The family Artedidraconidae comprises small, endemic Antarctic fishes, known as plunderfish, mostly distributed in the High Antarctic region. To study the diet of these specialised benthic feeders, stomach contents of the 11 most abundant species in the eastern Weddell Sea were examined. Prey composition was identified to the lowest taxonomic level for peracarid crustaceans and polychaetes. Half of the food volume comprised 36 crustacean taxa (26 of which were amphipods). The other half was made up of 7 polychaete taxa and 8 other zoological groups. The diet of plunderfishes <20 cm long was found to include about 70% peracarid crustaceans, 50% of which were amphipods, mainly gammarids; the rest of their diet was mostly sessile and motile polychaetes. Individuals larger than 15 cm began to prey on other fishes, although gammarids were still a part of their diet. The size of prey ranged from 5 to 32 mm. The mean size of prey increased with predator size. Selective predation effects were observed: small prey (copepods, cumaceans, ostracods, the gammarid family Eusiridae *s.l.* and the polychaete family Phyllodocidae) were found more frequently in small predators, whereas large prey (Epimeriidae, Lysianassidae *s.l.*, Cirolanidae, Arcturidae, Crangonidae, Euphausiidae, Pycnogonida) appeared in the stomachs of predators larger than a certain size. Plunderfish prey are generally abundant in the area, but the high diversity of the diet found in the genus *Artedidraco*, compared with the genera *Dolloidraco* and *Pogonophryne*, was surprising. The present analysis is based on data concerning the distribution and abundance of predators, as well as biological knowledge regarding the most characteristic types of prey. The specialised diets of plunderfishes from different habitats and of different sizes are also compared, in order to more closely examine the feeding strategy of the family Artedidraconidae, and roughly quantify its impact on the benthic trophic web.

KEY WORDS: Benthic feeders · Artedidraconids · Trophic relationships · Amphipods · Polychaetes · Weddell Sea

INTRODUCTION

Benthic feeders are common among Antarctic coastal fish species, but, in the High Antarctic, the species feeding primarily on benthic organisms are particularly numerous (Kock 1992). In the eastern Weddell Sea, 95% of the bottom-dwelling fish belong to the perciform suborder Notothenioidei (Ekau 1990), which has adapted very well to High Antarctic conditions. Most of these species live at depths of <1000 m (Eastman 1991). The notothenioid family Artedidraconidae is well represented in the High Antarctic, where 23 of the 24 known species of the family's 4 genera have been recorded (Kock 1992). These fishes are rather small, reaching rarely more than 34 cm long (Eakin 1990). They have been the subject of a number of taxonomic studies (Eakin 1977, 1981, 1987, Eakin & Kock 1984, Balushkin 1988).

They are typical specialised benthic feeders and quite sedentary (Hubold 1991), usually remaining motionless on the substratum. These fish are commonly

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known as barbeled plunderfishes, because they have fleshy filaments, or barbels, hanging from their mouths. They typically use the sit-and-wait predation method, known as ambush feeding, catching only moving prey and ignoring those that are clearly visible but immobile (Daniels 1982, Hubold 1991). The barbel is used as a lure, and is also a tactile somatosensory organ (Janssen et al. 1993). Despite the interesting predatory methods of this endemic Antarctic family, few studies have been conducted on its feeding habits. Wyanski & Targett (1981) analysed the contents of 179 stomachs from 8 species of artedidraconids in different Antarctic areas, and found that they feed on select species, in particular on infaunal and epifaunal polychaetes, molluscs and amphipods. These authors were the first to investigate this family's feeding biology; later, Schwarzbach (1988) studied the diet of 6 species in the eastern and southern Weddell Sea, and published data on their prey spectra. Both articles showed that Artetidraconidae prey upon a wide range of zoological groups.

In the present paper, we examine the feeding biology of these benthic-feeding fish from the Weddell Sea, focusing on the importance of peracarid crustaceans and polychaetes in their diet. A detailed taxonomic study of the most characteristic prey groups has been conducted in order to determine the impact of benthos-plunderfish interactions on the ecosystem, and to estimate the degree of predation sustained by certain benthic groups.

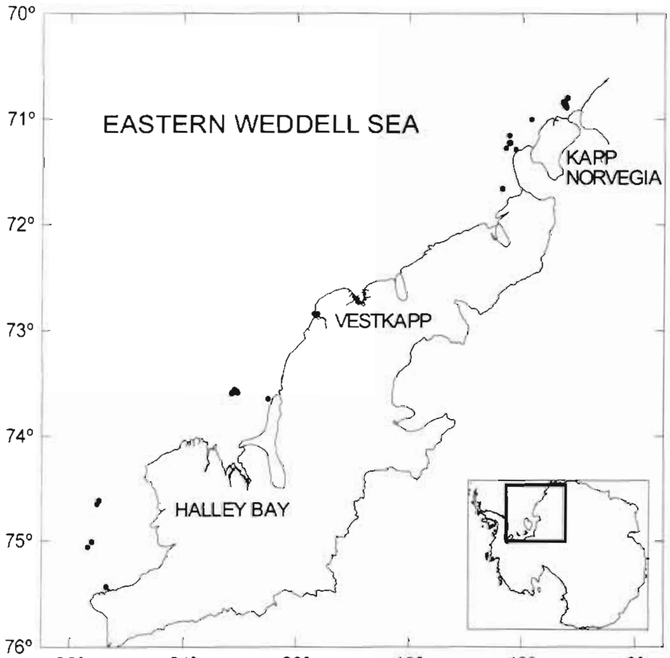

Fig. 1 Location of hauls (•) in the Weddell Sea during the ANT XV/III cruise, summer 1998

MATERIALS AND METHODS

The ANT XV/III cruise, aboard the RV 'Polarstern', was conducted in the eastern Weddell Sea (Fig. 1), from 13 January to 26 March 1998 (Arntz & Gutt 1999). Sampling was carried out using different bottom-trawling equipment (Table 1). At each station, weight, total length (rounded down to the nearest centimetre), and sex were recorded for each plunderfish caught, and the maturity stage was determined according to a 5-stage scale (Kock & Kellermann 1991).

The stomach contents of plunderfishes were analysed on board ship. The volume of total prey groups (ml) in the stomach was measured using a trophometer, a calibrated instrument consisting of several different-sized half-cylinders built into a tray (Olaso & Rodríguez-Marín 1995). The relationship between estimated volume and actual weight of the stomach contents was derived from a logarithmic model (a = 0.932735, b = 0.99324, r^2 = 0.995; $p < 0.01$). In species sensitive to pressure changes, stomach contents had been altered by regurgitation; therefore, the state of the gall bladder was examined (Robb 1992) in order to separate the empty stomachs of specimens that had regurgitated food shortly before being caught from the stomachs that were truly empty. Stomachs containing food that had been ingested during the haul itself (i.e. the gall bladder had not been exercised) were considered empty.

Fish, crustaceans and molluscs were identified by species, but other groups were combined into higher taxa. For determining prey taxa, we referred to Gon & Heemstra (1990) for fish, Barnard & Karaman (1991) and Brandt (1991) for peracarid crustaceans, Hain (1990) for molluscs, Hartmann-Schröder (1986) and Hartmann-Schröder & Rosenfeldt (1992) for polychaetes, and Sieg & Wägele (1990) for other groups. For each prey species, the following information was collected: percentage contribution to the volume of stomach contents, number of items per stomach, and state of digestion (Olaso 1990). To examine the relationship between prey size and predator size, the volume and weight of each prey were determined, and measurements of prey were taken in mm: in fish, total length, in crustaceans, total length from the apex of the head to the end margin of the telson; in the remaining prey, except for polychaetes, we measured them at their longest point. In the case of polychaetes, most of which are long and thin, we manipulated the specimens to a thickness of 10 mm, and then measured their length.

Methods used to assess the relative importance of individual prey taxa were frequency of occurrence, F; numerical percentage, N; volume percentage, V; and weight percentage, W (Hyslop 1980). To determine the

Table 1. Situation and number of hauls by bottom trawl (GSN), Agassiz trawl (AGT), epibenthic sledge (EBS), and dredge (D), during ANT XV/III in February 1998

Station	Gear	Coordinates S	Coordinates W	Depth (m)	Time (min)
71	GSN	70.4830	10.2600	291	21
78	GSN	72.5090	19.1870	390	17
220	GSN	70.5090	10.3550	254	9
222	GSN	70.5100	10.3560	250	10
82	GSN	72.5080	19.2190	406	15
84	GSN	72.5080	19.1910	393	14
263	GSN	72.5100	19.1520	386	10
95	GSN	73.3400	22.1230	893	15
120	GSN	73.3400	22.1220	877	15
100	GSN	73.3570	22.0440	442	16
97	GSN	73.3590	22.1600	644	14
123	GSN	73.3610	22.1720	654	15
150	GSN	74.3720	26.5860	734	15
154	GSN	74.3920	27.0120	576	10
167	GSN	75.0390	27.2130	406	5
168	GSN	75.2640	26.4290	230	4
165	EBS	75.0080	27.1350	398	10
128	D	73.3910	20.5960	213	37
103	AGT	73.3500	22.0700	614	9
277	AGT	71.1800	12.1500	184	10
44	AGT	70.5190	10.3380	228	3
58	AGT	70.5220	10.2900	245	10
39	AGT	70.5260	10.3190	240	10
77	AGT	71.0990	12.2920	341	10
206	AGT	71.0070	11.4250	598	15
194	AGT	71.1400	12.2760	245	10
197	AGT	71.1710	12.3600	416	5
189	AGT	71.4010	12.4320	246	8
62	AGT	70.5370	10.2820	238	8

degree of feeding specialisation of each predator group we used the Shannon-Wiener diversity index, H (Sannon & Weaver 1949):

$$H = -\sum_{i=1}^{S} P_i \ln p_i$$

where p_i is the proportion of prey taxa i in the diet, with S the total number of different prey categories consumed by the predator. We also considered evenness: $J = H/\ln S$ (Pielou 1966). This index is a measurement of the degree of uncertainty (Krebs 1972), so that the higher the diversity value, the higher the uncertainty. We were interested in comparing the feeding habits of fishes with the availability of potential food resources in their natural habitats. To do so, we used Ivlev's electivity index (Ivlev 1961), which characterises the degree of selection of a particular prey species by the predator being studied. The relationship is defined as:

$$E = (r_i - p_i)/(r_i + p_i),$$

where E is the measure of selectivity, r_i the relative abundance of prey item i in the gut (as a weight percentage of the total gut contents), and p_i is the relative abundance of same prey item in the environment (defined as a biomass percentage of total benthos in the study area; these data were taken from Brey & Gerdes 1998, Gerdes unpubl. data). We chose this index because it is generally considered to be unbiased, and relatively independent of sample size.

To compare our values of biomass and consumption with those of other authors, we carried out conversions using wet weight to dry weight and dry weight to carbon, following Jørgensen et al. (1991). In fish we assume a wet weight to carbon ratio of 10 according to Jarre-Teichmann et al. (1997).

RESULTS

We analysed the contents of 219 stomachs from 11 species of plunderfishes belonging to the genera *Artedidraco*, *Dolloidraco* and *Pogonophryne* (Table 2). These constitute nearly all of the artedidraconids collected, the most abundant species being *D. longedorsalis*, *A. orianae*, *A. skottsbergi*, *P. marmorata* and *A.*

Table 2. Artedidraconidae. Number of individuals caught and number of stomachs sampled by species

Species	Length (cm)	No. of fish caught	Total no. of stomachs	Regurgitated	% empty
Artedidraco loennbergi	7-11	20	20	1	20
Artedidraco skottsbergi	3-12	52	42		19
Artedidraco orianae	5-16	58	58		7
Artedidraco shackeltoni	5-10	11	4		50
Dolloidraco longedorsalis	9-13	215	43		19
Pogonophryne lanceobarbata	6-10	6	6		0
Pogonophryne marmorata	6-21	26	22		32
Pogonophryne phyllopogon	8-22	8	8		25
Pogonophryne barsukovi	11-21	12	12	1	42
Pogonophryne macropogon	37-37	1	1		0
Pogonophryne scotti	19-29	5	3		67
Total		414	0	2	19

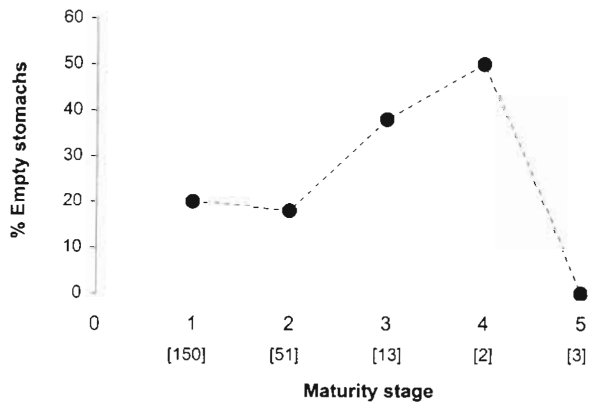

Fig. 2. Percentage of empty stomachs of the 11 artedidraconid species sampled, with regard to their maturity stage; in brackets: total no. of stomachs at each maturity stage

loennbergi. Few cases of regurgitation were observed. A total of 19% of the stomachs were empty, and only 2 of them had been regurgitated. This percentage of empty stomachs seems a little high, since other authors have reported a percentage of empty stomachs of <10% for this family (Targett 1981). However, in the present study the adults of some species (*P. marmorata*, *Artedidraco* spp.) showed very mature gonads, meaning that they were close to spawning, as can be seen in Fig. 2. It should be remembered that the state of maturity can cause an overestimation of the number of empty stomachs, since the gonad mass can occupy more than 25% of the body's total volume, and under these conditions feeding intensity usually drops. In the spawning and pre-spawning periods of other Antarctic fish species, an increase in the proportion of empty stomachs has been also observed (e.g. Duhamel & Hureau 1985, Gorelova & Shandikov 1988).

Interspecific variation in the diets of artedidraconids

Table 3 shows the diet, expressed in percentages of volume, of the 5 most abundant species of artedidraconids. *Artedidraco orianae* preyed on errant polychaetes, phyllodocids and polynoids, and on the majority of the crustacean groups, above all amphipods. It showed the highest taxonomic diversity, 4.12, and consumed different families of gammarideans, with especially noteworthy consumption of Epimeriidae. *A. skottsbergi* consumed the same percentage of amphipods as *A. orianae*, but that of polychaetes (polynoids and aphroditiids) was lower; however, its diet included other zoological groups, and also presented high taxonomic diversity. Its habits seem more benthic than those of *A. orianae*. For its part, *A. loennbergi* exhibited fewer benthic feeding habits than the 2 former species, since its prey were mostly found above the seafloor, e.g. mysids, with only 17% polychaetes; the rest of its diet comprised gammarideans. In all, its prey taxa diversity was much lower.

Dolloidraco longedorsalis were captured in a limited length range. This species consumed a high percentage of polychaetes, nearly 50%, among which we found the wide-ranging aphroditiids and the sedentary terebellids, maldanids and spionids. The species also fed on gammarids (35%), and even krill, cumaceans, isopods and other invertebrates. The taxonomic diversity was high. *Pogonophryne marmorata*'s diet was nearly 60% crustaceans, above all, large cirolanids and gammarideans and mysids. Its consumption of polychaetes was not significant. Its taxonomic diversity, 2.72, was the lowest of the family. The other species of artedidraconids caught lacked the minimum stomach contents to analyse their diets; still, we can say that while all of the prey of *Artedidraco shackeltoni* were polychaetes, these organisms were not found

Table 3. Diet of the 5 most abundant artedidraconid species (with length range). Data expressed in percentage by volume. +: value <1 %

Prey taxon	Predator species				
	Artedidraco orianae (5–16 cm)	*Artedidraco skottsbergi* (3–12 cm)	*Artedidraco loennbergi* (7–11 cm)	*Dolloidraco longedorsalis* (9–13 cm)	*Pogonophryne marmorata* (5–21 cm)
Crustacea	**58**	**59**	**77**	**46**	**97**
Amphipoda	40	41	62	36	59
Phtisicidae	7				4
Gammaridae	32	39	62	36	55
Ampeliscidae		12			
Eusiridae	4	5		7	8
Epimeriidae	16	6			30
Gammaridae undetermined	2	8	25	8	7
Iphimediidae	2				
Ischyroceridae					
Leucothoidae	1				
Liljeborgidae	1				7
Lyssianassidae			37	16	3
Oedicerotidae		3			
Phoxocephalidae	1	2		6	
Podoceridae	1				
Stenothoidae	4	1			
Synopiidae		2			
Hyperiidae	2	2			
Copepoda	1				
Cumacea		15		6	
Isopoda	10	1	6	1	21
Cirolanidae					18
Gnathiidae	+				
Isopoda undetermined	1	1	6	1	3
Munnidae	1				
Valvifera	7				
Euphausiacea	5			3	
Mysidacea			9		17
Ostracoda	2	2			
Pycnogonida	**5**				
Holothuroidea		**1**			
Mollusca		**5**			
Bivalvia		3			
Gastropoda		2			
Hirudinea	**1**				
Bryozoa		**4**			
Cnidaria		**1**		**6**	
Anthozoa				4	
Hydrozoa		1		2	
Polychaeta	**36**	**30**	**23**	**48**	**3**
Aphroditiidae				13	
Nephthyidae		7			
Maldanidae				21	
Phyllodocidae	3				
Polychaeta undetermined			23		3
Polynoidae	28	14			
Spionidae				4	
Terebellidae	6	10		10	
Stomachs with food	54	34	15	35	15
Mean replication	0.7	0.4	0.3	0.4	0.7
Mean length	11.4	8.4	9.1	10.3	11.6
No. of phyla	4	6	2	3	2
No. of taxa	28	19	4	14	10
Taxa diversity	4.12	3.72	1.53	3.50	2.72
Evenness	0.86	0.88	0.77	0.92	0.82

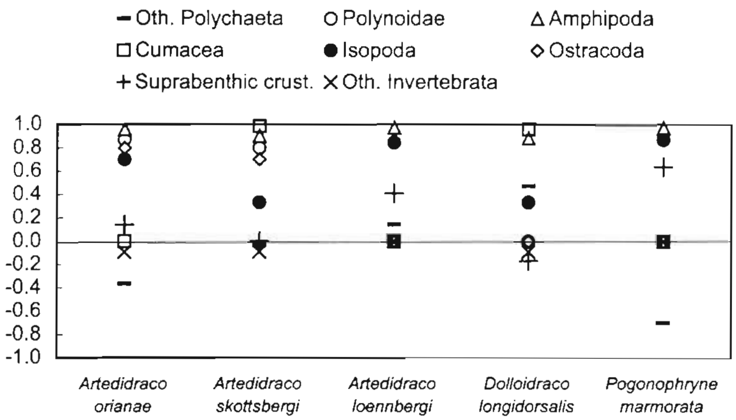

Fig. 3. Ivlev's electivity index, calculated for each prey group in the diets of the study area's 5 most abundant artedidraconid species

as food among the rest of the predators of the genus *Pogonophryne*. Only 2 fish prey were found in large specimens of *P. scotti* and *P. phyllopogon*.

Fig. 3 shows the degree of selection of the prey taxa by the 5 species of artedidraconids. All of the predator species presented active selection of amphipods. *Artedidraco orianae* and *A. skottsbergi* consumed preferably ostracods and polynoids, whereas they tended to reject other polychaetes, or preyed on them occasionally. These worms were rejected by *Pogonophryne marmorata*, and selected by *Dolloidraco longedorsalis*. Isopods presented positive values, above all in *A. orianae*, *A. skottsbergi* and *P. marmorata*, and in these 3 species we see a respective progression in the consumption of suprabenthic crustaceans from an occasional to a selected prey group. The other invertebrate groups are consumed occasionally.

Diet of the family Artedidraconidae and prey selection in the eastern Weddell Sea

With the data presented here, we aim to provide a first approximation of the degree of plunderfish predation in the benthos. Therefore, we also pooled together trophic information on the 11 species sampled from the family Artedidraconidae (Table 4). The great majority of artedidraconid prey were crustaceans (65%), followed by polychaetes (28%) and other benthic invertebrates (7%); fish did not even reach 1%. If we look at it gravimetrically, the importance of all the invertebrate groups drops, since the large size of fish prey causes them to displace 32% of the total volume. In all of the prey groups, the percentage of frequency of occurrence was very similar to the percentage in numbers. The family Artedidraconidae's high degree of benthic trophic diversification was indicated by the 8 phyla and 52 taxa found among its prey. The most important of these were gammaridean amphipods (42% by number and 27.8% by volume), and motile and sessile polychaetes. Characteristic gammarid prey were species from the families Epimeriidae (e.g. *Epimeria georgiana*), Eusiridae *s.l.* (e.g. *Prostebinggia gracilis*, *Rhachotropis* sp.), Lysianassidae *s.l.* (*Tryphosella murrayi*) and Phoxocephalidae (Table 4). In addition to amphipods, 7 other groups of crustaceans were represented in the diet, with isopods and cumaceans being found in 7% of the stomachs. More than 25% of plunderfish prey (in terms of frequency and number) were polychaetes, mostly epibenthic species, such as the epibenthic polynoids and aphroditiids, although they also consumed infaunal prey (phyllodocids and terebellids, e.g. *Begstroemia sonitki* and *Axionice spinifera*).

Fig. 4 shows that plunderfishes preferentially selected amphipods, cumaceans, isopods, ostracods and polynoids, although their mean biomass was small. In contrast, the remaining polychaetes, which were abundant, were not actively selected. Suprabenthic crustaceans (euphausiids, mysids and decapods) and other invertebrates (e.g. cnidarians, bryozoans, pantopods and molluscs) were preyed upon in proportion to their abundance.

Change of prey with predator size

In order to examine the relative impact of benthic prey in the different size-categories of plunderfishes, we determined their volume (expressed as a percentage) in the diet, by size-range (Fig. 5). In artedidraconid specimens measuring up to 20 cm, crustaceans represented about ⅔ of the food consumed, with gammarids accounting for 40% of volume, except for the 15 to 19 cm size-range. Species of Eusiridae *s.l.* were the most common prey of smaller plunderfishes, but their importance disappeared at 12 cm, while individuals from Lysianassidae *s.l.* and Epimeriidae appear in the diet of fish longer than 7 cm (Fig. 6). The genus *Epimeria*, from the latter family, became increasingly important as predator size rose. Isopods were preyed upon by all size categories of artedidraconids, their importance growing progressively with predator size. Some preys—e.g. copepods, cumaceans and the hyperiid *Themisto gaudichaudii*—appeared only in very small fish, and others appeared from a certain size on, such as euphausiids and pycnogonids. Polychaetes represented ¼ of the diet from 4 cm, with their percentage increasing gradually until it reached 39% at 12–14 cm (Fig. 5). At small sizes, there were phyllodocids, and later aphroditiids, maldanids and terebellids, with polynoids being most noteworthy. Fish

Table 4. Percentage by frequency of occurrence (*F*), number (*N*), and volume (*V*) of major food items in 219 stomachs of the 11 species of artedidraconid fish sampled

Prey taxon	% *F*	% *N*	% *V*	No. of taxa
Crustacea	63.7	65.0	45.7	36
Amphipoda	49.6	50.6	31.3	26
Aeginoides gaussi	4.6	4.7	2.6	
Ampelisca richardsoni	3.0	3.1	1.4	
Ampeliscidae undetermined	1.5	1.5	0.8	
Atyloella magellanica	0.7	0.8	0.5	
Atylopsis sp.	0.7	0.8	0.5	
Corophiidae undetermined	0.7	0.8	0.2	
Epimeria georgiana	6.0	6.1	4.4	
Epimeria grandirostris	0.7	0.8	0.4	
Epimeria macrodonta	0.7	0.8	0.6	
Epimeria sp.	3.0	3.1	7.7	
Epimeriidae undetermined	0.7	0.8	0.7	
Eusiridae undetermined	1.5	1.5	0.3	
Gammaridae undetermined	2.2	2.3	1.5	
Iphimediidae undetermined	0.7	0.8	0.5	
Leucothoe spinicarpa	0.7	0.8	0.2	
Liljeborgiidae undetermined	1.5	1.5	0.4	
Lysianassidae undetermined	1.5	1.5	0.5	
Oedicerotidae undetermined	0.7	0.8	0.4	
Paramoera sp.	0.7	0.8	0.2	
Phoxocephalidae undetermined	2.2	2.3	1.0	
Podoceridae undetermined	0.7	0.8	0.2	
Prostebbingia gracilis	1.5	1.5	0.5	
Pseudericthonius sp.	0.7	0.8	0.2	
Rhachotropis sp.	1.5	1.5	1.3	
Stenothoidae undetermined	0.7	0.8	0.6	
Synopiidae undetermined	0.7	0.8	0.1	
Torometopa sp.	0.7	0.8	0.2	
Tryphosella murrayi	0.7	0.8	0.1	
Tryphosella sp.	3.0	3.1	2.1	
Uristes gigas	0.7	0.8	0.4	
Waldeckia obesa	0.7	0.8	0.2	
Themisto gaudichaudii	3.4	3.5	0.9	
Copepoda	1.2	1.2	0.2	1
Cumacea	6.7	6.9	3.0	1
Cumacea undetermined	4.3	4.4	2.0	
Cyclaspis gigas	2.4	2.5	1.0	
Decapoda	0.6	0.6	0.6	1
Notocrangon antarcticus	0.6	0.6	0.6	
Euphausiacea	1.8	1.9	2.5	1
Euphausia superba	1.8	1.9	2.5	
Isopoda	8.0	8.1	5.6	1
Natatolana meridionalis	1.8	2.1	2.8	
Gnathia sp.	1.8	2.0	0.2	
Munna sp.	1.8	1.0	0.1	
Litarcturus bobinus	2.6	3.0	2.4	
Mysidacea	2.4	2.5	1.8	1
Antarctomysis maxima	1.8	1.9	1.4	
Mysidacea undetermined	0.6	0.6	0.3	
Ostracoda	1.8	1.9	0.7	1
Pycnogonida	**1.5**	**1.5**	**1.2**	**1**
Echinodermata	**0.5**	**0.5**	**0.1**	**1**
Holothuroidea	0.5	0.5	0.1	1
Mollusca	**2.0**	**2.1**	**1.1**	**2**
Bivalvia	0.7	0.7	0.7	1
Gastropoda	1.4	1.4	0.4	1

(Table continued on next page)

Table 4 (continued)

Prey taxon	% *F*	% *N*	% *V*	No. of taxa
Bryozoa	**1.0**	**1.0**	**0.4**	**1**
Cnidaria	**2.0**	**2.1**	**0.6**	**2**
Anthozoa	1.0	1.0	0.3	1
Hydrozoa	1.0	1.0	0.3	1
Hirudinea	**0.5**	**0.5**	**0.1**	**1**
Polychaeta	**27.3**	**27.9**	**18.8**	**7**
Aphroditiidae undetermined	2.1	2.1	0.7	1
Maldanidae undetermined	2.1	2.1	1.1	1
Aglaophamus sp.	1.0	1.1	0.6	1
Bergstroemia sotniki	3.1	3.2	1.0	1
Polynoidae	13.6	13.9	11.9	1
Spionidae	1.0	1.1	0.1	1
Axionice spinifera	1.0	1.1	1.5	1
Terebellidae undetermined	3.1	3.2	1.9	
Pisces	1.0	0.7	31.9	**1**
Notothenioidei undetermined	1.0	0.7	31.9	

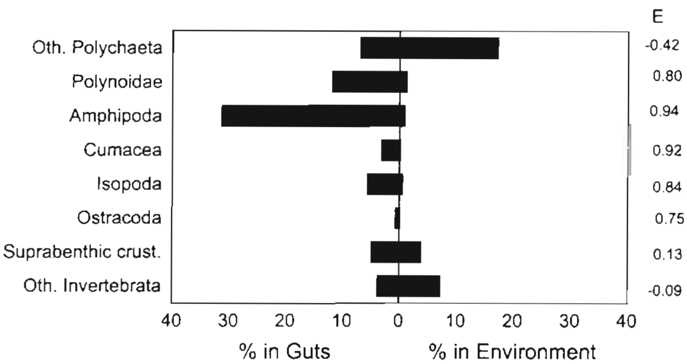

Fig. 4. Selectivity of prey groups in the family Artedidraconidae, representing the proportion of prey groups found in the gut and in the study area (*E*, electivity index)

prey began to appear from 15 cm, and from 20 cm, smaller notothenioids and large epimeriid amphipods constituted the largest portion of the plunderfish diet.

Prey size selection by artedidraconids

All species of the family Artedidraconidae feed on small prey found at the bottom or above it, i.e. they are benthic and suprabenthic feeders. The range of prey species between 8 and 18 cm is practically the same, although the shapes and forms of benthic organisms vary greatly, and we do not know exactly the margin of error caused by comparing measurements taken from such different zoological groups. However, we believe that since the majority of prey were crustaceans, this information should be included. From 18 cm, we found a slight trend for prey size to increase with predator size, which is when the artedidraconids began to consume fish, from 18 to 20 cm on. The crustacean prey found ranged from 4 to 33 mm (Table 4). The smallest prey were the copepods (4 mm), ostracods (8 mm) and cumaceans (up to 14 mm), found in the stomach contents of the smallest plunderfishes. The amphipods showed a length ranging from 4 to 22 mm, but most gammarids were small, 10 to 12 mm; they consequently seem to form the basis of the artedidraconid diet. Medium-sized prey were isopods, sea spiders, euphausiaceans, decapods and mysidaceans, the latter reaching sizes of 30 mm. Polychaetes, although they can become quite large, tended to be preyed upon only to a size of 20 mm due to their fragility and small energy value, but, since there is wide variability in the diameters of their bodies, these measurements cannot be compared with those of crustaceans. The only prey taxa larger than 30 mm were fish; a clear example of this was the case of prey in *Pogonophryne*. For crustacean prey and fish prey, the linear regression between predator length and prey length was statistically significant ($r^2 = 0.341$; $a = -24.076$; $b = 0.330$; $n = 121$; $p < 0.001$), and although the fit was not very strong, there is a gradual increase in the prey-length groups according to the predator-length.

To avoid the variation produced between the forms and measurements of the different prey groups in the benthos, we compared predator size with the individual weights of prey (Fig. 7), and found a better relationship than with the size of the prey by means of a polynomial goodness-of-fit estimate ($r^2 = 0.98$; $n = 191$; $p > 0.001$). The weight range of the crustaceans varied between 0.04 and 2.41 g; that of the copepods, cumaceans and ostracods was narrower (0.1 to 0.3 g); the weight range of the polychaetes oscillated between 0.1 and 2.36 g (Table 5).

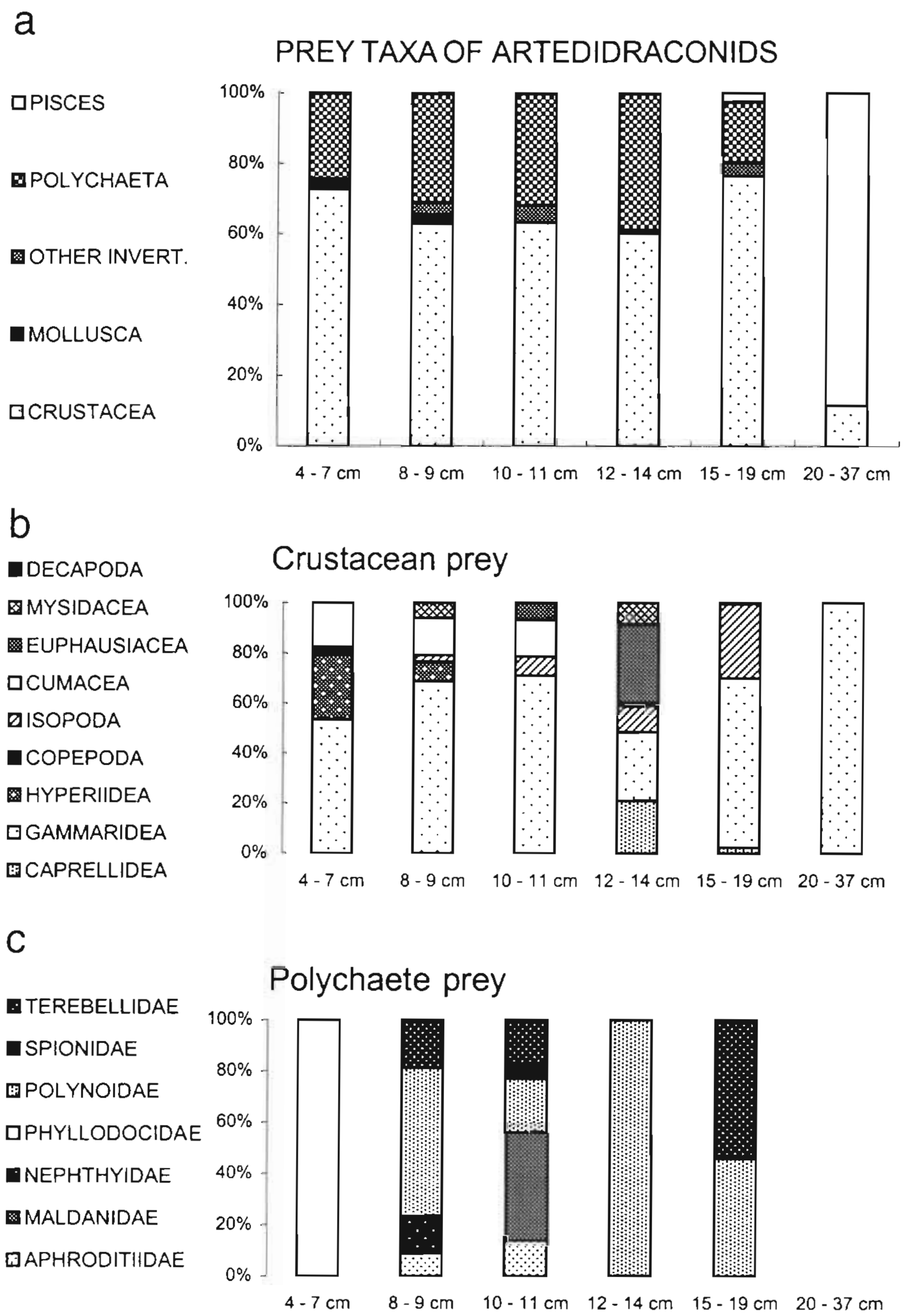

Fig. 5. Distribution of prey groups in the overall fish diet; data expressed in percentages of volume

Distribution and abundance of the eastern Weddell Sea artedidraconid fishes, and change in prey composition with depth

In our sample of plunderfishes we found that the number of artedidraconid species is greater in Kapp Norvegia and Vestkapp than in Halley Bay (Table 6). In the 200 m depth-range, a higher number of plunderfishes appeared in the Kapp Norvegia area than in Halley Bay, although in terms of weight they were more similar; the most abundant species were of the genus *Artedidraco*. In the 400 m range, the highest abundance in terms of number was found at Kapp Norvegia, whereas in weight it was lower than in the other 2 areas, the genus *Dolloidraco* being the most abundant. In the 600 m stratum, we found the highest number in Halley Bay, and once again nearly all of the catch belonged to the genus *Dolloidraco*. In Vestkapp, nearly all of the plunderfish catch also belonged to this genus. In the 800 m stratum, few plunderfish appeared, all belonging to the genus *Pogonophryne*. We were unable to sample at all depths in the 3 different study areas, but our results coincide with previous studies on the distribution of the family Artedidraconidae in the eastern Weddell Sea, in which *D. longedorsalis* was the most abundant species (Schwarzbach 1986, Hubold 1991), presenting maximum abundances at depths of 400 to 500 m, whereas the genus *Artedidraco* dominated in shallower waters (Ekau 1990).

In order to observe differences in artedidraconid feeding with depth, we examined their diets in different depth ranges. The stomachs of individuals caught at >600 m were not considered, given their scarcity. Fig. 8 shows that in the 200 m range most of the prey taxa, 42, were found; almost all of the groups of crustaceans and 8 different phyla were represented. From 400 m, crustaceans were more abundant in the artedidraconid diet, but the number of total prey taxa dropped to 25 at 400 m and to only 10 at 600 m. Nevertheless, it must be taken into account that in this last range the number of predators examined was lower. Polychaetes represented 22% of the number of prey on bottoms at 200 m, polynoids and the phyllodocid *Bergstroemia sotniki* being the most characteristic groups, although aphroditiids and nephthyids were also found. At 400 m, we found that sedentary terebellids and spionids accounted for 18%, falling to 14% on bottoms at 600 m. Regarding gammarids, we found that they were important in the diet at a depth of 400 m, but there was a higher number of taxa which were not found in stomach contents at >300 m, such as *Ampelisca richardsoni*, *Epimeria grandirostris*, and the genera *Pseudericthonius*, *Torometopa* and *Rhachotropis*. Other taxa, such as *Atyloella magellanica*, were only found in stomach contents at greater depths. *E. georgiana* was found at all depth ranges.

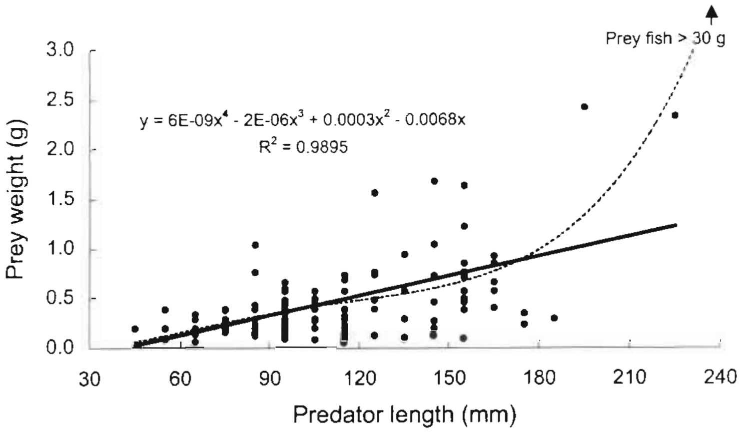

Fig. 7. Predator-prey size relationships

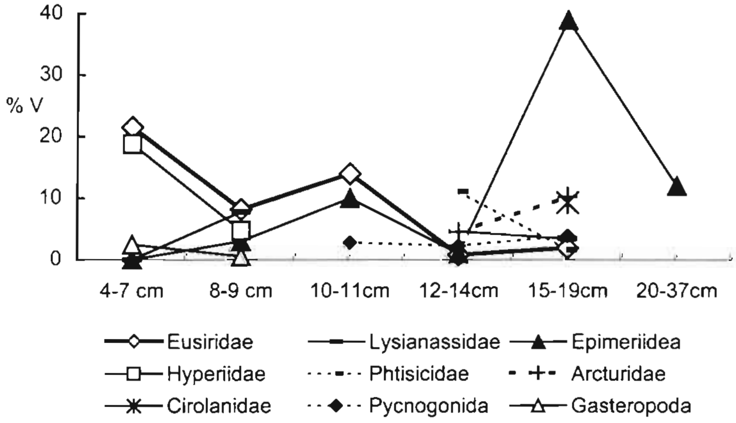

Fig. 6. Impact on amphipods, isopods and other prey in relation to predator size; data expressed in percentages of volume

DISCUSSION

Artedidraconids as benthic feeders

Artedidraconids are probably the most sedentary of Antarctic fish, remaining immobile on the substratum (Hubold 1991), and catching the prey passing by. All species of this fish family feed on small prey types found at the bottom or above it, i.e. they are specialised benthic or suprabenthic feeders. The eastern Weddell Sea shelf community exhibits a high species richness and diversity (Voß 1988, Galéron et al. 1992) and is dominated by sessile suspension feeders, such as sponges and bryozoans. This sessile epifauna, whose abundance and diversity may be related to the high sedimentation rates observed (Bathmann et al. 1991) and the frequency of dropstones as nuclei of hard substrates, provides a wide variety of habitats and microhabitats to a diverse vagile fauna of gastropods, polychaetes, pycnogonids, peracarids, ophiurids and crinoids (Ekau & Gutt 1991). In areas not covered by the sessile epibenthos, various sediment types (Gerdes et al. 1992) are colonised by sedentary polychaetes, holothurians and diverse burrowers. Some groups include a high number of species (Starmans 1993, 1997, Arntz et al. 1997), as is the case of polychaetes (Knox & Lowry 1977, Knox 1994) and peracarids, the amphipods showing a high ecological diversity

Table 5. Mean sizes and standard error (SE) of prey found in the stomach contents of plunderfishes sampled during ANT XV/III

Prey taxon		Length range (mm)	No. of prey	Length (mm) Mean	Length (mm) SE	Weight (g) Mean	Weight (g) SE
Crustacea		4–33	198	12.1	5.94	0.3	0.36
Copepoda		4–5	2	4.5	0.71	0.1	0.02
Ostracoda		6–11	3	8.7	2.52	0.3	0.15
Amphipoda		4–33	68	11.8	4.99	0.4	0.41
Gammaridea		4–33	61	11.8	4.97	0.4	0.43
Ampeliscidae	*Ampelisca richardsoni*	7–22	7	11.7	4.79	0.2	0.10
Eusiridae		11–22	11	11.4	3.80	0.2	0.19
	Atyloella magellanica			11.0		0.4	
	Atylopsis sp.			11.0		0.4	
	Paramoera sp.			9.0		0.2	
	Prosttebingia gracilis	8–9	2	8.5	0.71	0.2	0.00
	Rhachotropis sp.	12–22	4	14.5	5.00	0.3	0.31
Epimeriidae		8–33	17	13.9	7.40	0.6	0.71
	Epimeria georgiana	8–14	10	12.0	1.20	0.3	0.11
	Epimeria grandirostris			8.0		0.3	
	Epimeria macrodonta	12–33	2	22.5	14.85	1.4	1.36
	Epimeria sp.	10–32	4	21.8	7.19	1.2	1.11
Ischyroceridae	*Pseudericthonius* sp.			9.0		0.2	
Leucothoidae	*Leucothoe spinicarpa*			12.0		0.2	
Liljeborgiidae		10–11	2	10.5	0.50	0.2	0.04
Lysianassidae		8–13	9	9.6	2.79	0.3	0.19
	Tryphosella murrayi			4.0		0.1	
	Tryphosella sp.	9–13	4	11.3	1.19	0.3	0.24
	Uristes gigas			10.0		0.3	
	Waldeckia obesa			11.0		0.2	
Stenothoidae	*Torometopa* sp.			8.0		0.2	
Caprellidea		6–23	4	14.6	6.34	0.5	0.31
Phtisicidae	*Aeginoides gaussi*	6–23	4	14.6	6.34	0.5	0.31
Hyperiidea		6–13	3	9.3	3.51	0.2	0.11
Hyperiidae	*Themisto gaudichaudii*	6–13	3	9.3	3.51	0.2	0.11
Isopoda		6–24	11	14.7	5.81	0.4	0.42
Cirolanidae	*Natatolana meridionalis*	20–24	2	22.0	2.83	1.3	0.42
Gnathiidae	*Gnathia* sp.	6–8	2	7.0	1.41	0.1	0.03
Munnidae	*Munna* sp.			12.0		0.1	
Arcturidae	*Litarcturus bobinus*	15–21	5	17.6	3.01	0.5	0.16
Cumacea		9–18	11	13.8	2.90	0.3	0.11
	Cyclaspis gigas	9–15	4	13.0	2.71	0.3	0.15
Decapoda				22.0			
Crangonidae	*Notocrangon antarcticus*			22.0			
Euphausiacea		13–21	8	20.0	2.83	0.7	0.67
Mysidacea		12–33	5	26.8	8.87	0.4	0.17
	Antarctomysis maxima	25–33	4	30.5	3.70	0.4	0.20
Pycnogonida		10–18	3	14.7	4.16	0.5	0.14
Polychaeta		6–22	56	10.5	3.72	0.4	0.38
Nephthyidae	*Aglaophanus virginis*			8.0		0.5	
Terebellidae	*Axionice spinifera*	12–20	4	15.5	3.70	0.7	0.36
Maldanidae		7–9	3	8.0	1.00	0.3	0.31
Phyllodocidae	*Bergstroemia sotniki*	9–11	3	10.0	5.07	0.3	0.10
Polynoidae	*Polyeunoa laevis*	9–22	13	12.2	3.34	0.8	0.60
Aphroditiidae		13–15	2	14.0	1.41	0.3	0.02
Spionidae				7.0		0.1	

and the highest species richness (De Broyer & Jazdzewski 1993, 1996).

Polychaetes and amphipods are a trophic resource for many Antarctic benthic fish species (Gon & Heemstra 1990, Kock 1992). Previous studies by Wyanski & Targett (1981) and Schwarzbach (1988) show that plunderfish feeding is completely benthic, and that they prey on a wide variety of peracarids and polychaetes, rejecting other organisms with a higher biomass, such as suspension-feeders and some detriti-

Table 6. Numbers and weight of artedidraconid specimens found at different depths of the Weddell Sea during the ANT XV/III cruise. Data are expressed as number of individuals per trawling hour or grams per trawling hour

Depth (m)	Kapp Norvegia			Vestkapp			Halley Bay		
	No. of indiv.	Weight (g)	No. of predator species	No. of indiv.	Weight (g)	No. of predator species	No. of indiv.	Weight (g)	No. of predator species
200	218	2122	8				30	2370	1
400	102	354	5	32	1544	5	48	2141	2
600				19	2593	4	126	2810	1
800				2	1764	1	8	1779	2

vores. Their preferred prey are those most readily available, due to their behaviour, size and abundance. The wide variety of bottom organisms available, and, on the other hand, the much shorter production cycle and the much lower secondary production in the water column of the High Antarctic compared with more northern neighbouring areas, could have caused the evolution of these specialised benthic feeders (Kock 1992). Ross (1986) points out that there are other, not very well-known factor, which might be equally important, such as the wide variety of microhabitats.

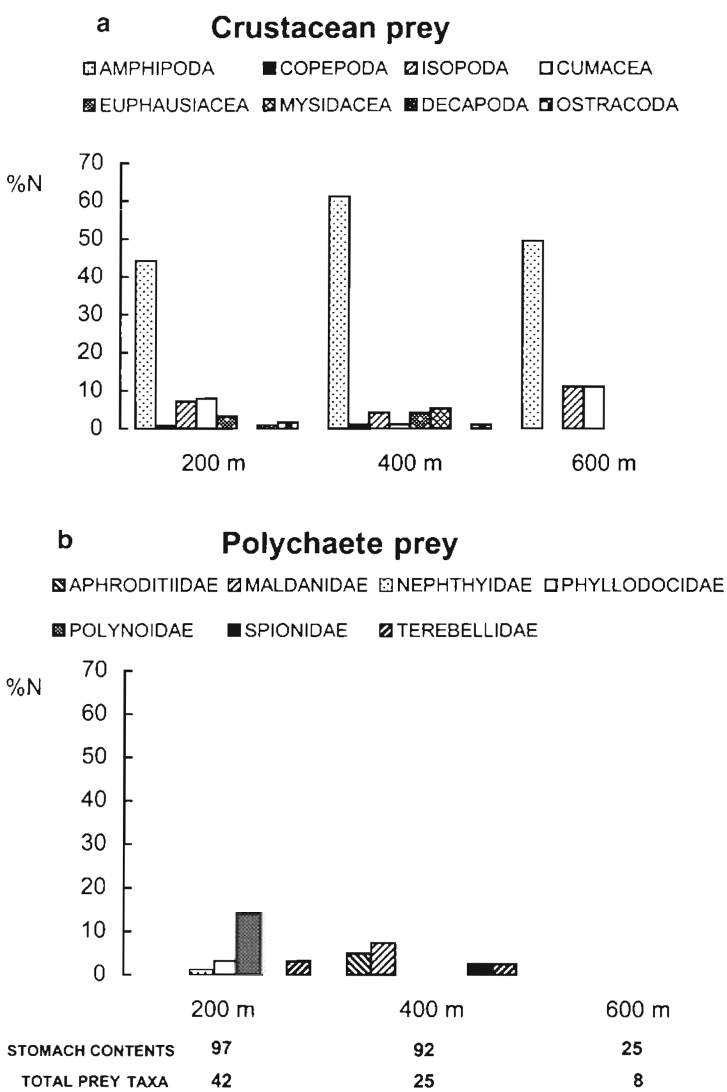

Fig. 8. Differences in plunderfish feeding with depth; data expressed in number percentages

Our detailed taxonomic determination of peracarid and polychaete prey enabled us to observe that plunderfishes prey on motile and sessile polychaetes, some groups of invertebrates, and nearly all crustacean groups. The most striking aspect was the high number of gammarid taxa consumed, mainly Eusiridae, Lysianassidae and Epimeriidae. These 3 families, along with the Stenothoidae and the Iphimedidae, are the most speciose and abundant amphipod families in the eastern Weddell Sea benthos. The absence of the common Iphimedidae in the stomach contents is noteworthy, and might be due to the repelling effect of the strong body ornamentation of teeth and spines exhibited by many iphimedids. The importance of the Eusiridae, Lysianassidae and Epimeriidae in the artedidraconid diet varies according to the predator's size-range. Kock (1992) reported that prey size increases with predator size, and that predating distance also increases. We observed a relationship which shows that there is a tendency for prey weight to rise with predator size, although the weight range of prey taxa remained almost invariable among plunderfishes measuring 5 to 17 cm long. In any case, we found that small fish mostly prey on animals that tend to be smaller than 10 mm, including organisms that swim in the water column, e.g. copepods, ostracods, hyperiids, eusirids, and motile polychaetes that live in the first layers of sediment, e.g. phyllodocids and nephtyids. Plunderfishes larger than 12 cm consume walking prey—which can reach 20 mm (e.g. epimeriids, pycnogonids and arcturid isopods) and even 30 mm (e.g. swimming euphausiids, decapods and mysids)—and motile and sessile polychaetes found under and on the surface of the sediment (e.g. maldanids, polynoids, aphroditiids and terebellids).

These data on measurements of plunderfish prey confirm and expand upon the results reported by Kock (1992), who determined that the size of artedidraconid prey tends to be small, exceeding 5 cm only in those species that prey on other fish, such as the *Pogonophryne* species, whose prey can be larger than 20 cm. In spite of these reservations, the mean prey size is probably a determining factor in the maximum size of these fishes, as already indicated for other Antarctic species by Burchett et al. (1983).

Prey selectivity

Although the High Antarctic benthos can be rich and diverse in terms of biomass and species richness (Dell 1972, Arnaud 1974, Knox & Lowry 1977, White 1984, Jazdzewski et al. 1992), only a limited part of this benthos can serve as food for fish, because large suspension-feeders are the dominant group in terms of biomass, with sponges sometimes accounting for 90% (Arnaud 1977, Voß 1988). On the eastern Weddell Sea shelf, the surface area covered by the invertebrate benthos falls progressively from Kapp Norvegia, where it can cover 90% of the floor, to Halley Bay, where it covers <10% (Ekau & Gutt 1991), affecting the distribution of the artedidraconids, which camouflage themselves among the sponges, bryozoans and hydrozoans. According to Gerdes et al. (1992), along the entire shelf, polychaetes, isopods, gammaridean amphipods and cumaceans show occurrence frequencies >94%, although they constitute only 5.5% of the total biomass. Data from Brey & Gerdes (1998) and Gerdes (unpubl.) indicate that all of the prey groups consumed by artedidraconids represent 24.1% of the total biomass of the benthos. However, we found that prey selectivity was inversely proportional to overall environment biomass, as shown in Fig. 4. Nearly all of the peracarids were strongly preferred as prey, whereas much more abundant prey, such as non-polynoid polychaetes, were only consumed by chance, but were rarely chosen. This could be explained by the general morphological characteristics of artedidraconids, which are specialised for catching small motile prey, such as peracarids, and therefore a highly important aspect of prey selection is the plunderfish's ability to detect them.

Our data on the abundance of these plunderfishes and those of other authors (Schwarzbach 1988, Ekau 1990) do not cover the family's entire distribution area in the eastern Weddell Sea, but it can be observed that artedidraconid biomass and the number of individuals decreases with latitude. These authors found no relationship between the distribution of the benthic biomass and water depth; however, we observed that at shallower depths, the trophic spectrum was more diversified, whereas moving deeper, i.e. around 400 m, there was more predation on gammarids and less on polychaetes, with the number of prey taxa falling progressively towards 800 m. Like Kock (1992) and Ekau (1990), we found that fish of the genus *Artedidraco* were distributed down to 300 m, with the highest numbers at around 200 m; the genus *Dolloidraco* had its maximum abundance at 400 m, and *Pogonophryne* was distributed from 400 m. We also observed that the prey consumed at different depths (Fig. 8) were related to the respective selectivity and diet of the 3 genera: *Artedidraco* at 200 m, *Dolloidraco* at 400 m and *Pogonophryne* at 600 m (see Table 3, Fig. 3). Therefore, these changes in artedidraconid foraging habits with depth seem mainly due to the specific diets of the genera *Artedidraco*, *Dolloidraco* and *Pogonophryne*, the maximum abundances of which occur where survival conditions are optimal, since the taxonomic composition of the invertebrate fauna also contributes to the number of feeding niches (Eastman & Grande 1989). *Artedidraco* species prey on small peracarids and polynoids. *A. skottsbergi* forages on more phyla, 6, than any other species in the family Artedidraconidae, while *A. orianae* is the one which feeds more on different taxa, particularly gammarideans. *D. longedorsalis* is a major worm feeder, as previously reported by Schwarzbach (1988), and the diversity of its diet is quite high. In contrast *P. marmorata* rejects polychaetes and selects mysids, isopods and gammarideans of large size.

Impact of artedidraconids on the eastern Weddell Sea benthos

The trophic interactions between artedidraconids and the small mobile benthos are determined by their proportions of biomass, annual production, and consumption. Gerdes et al. (1992) found in these waters a macrozoobenthic biomass ranging between 124 and 1640 mg m^{-2} and Brey & Gerdes (1998) observed that the biomass decreases from 26.83 g C m^{-2} in the 100 to 300 m stratum to 0.16 g C m^{-2} in the 1500 to 4300 m stratum. Likewise the community production decreases accordingly with depth from 4.83 to 0.09 g C m^{-2} yr^{-1}. Using data obtained from these authors in a depth ranging from 135 to 550 m, we find that the estimated biomass for the plunderfish prey groups is 3.2 g C m^{-2}, with low values in peracarids (0.12 g C m^{-2} in amphipods, as the most significant one) and 0.17 g C m^{-2} in polynoids, while other polychaetes have a much higher wet biomass, 2.16 g C m^{-2} (Brey & Gerdes 1998, Gerdes unpubl. data). But the entire High Antarctic system has low productivity. In the benthos, the production proportion ranges between 0.8 and 0.1 g C m^{-2} (Brey & Clarke 1993). Schalk et al. (1993) showed that the southeast shelf of the Weddell Sea has a mean annual macrobenthic production of 0.3 to 7.5 g C m^{-2}.

The estimated fish biomass in the eastern Weddell Sea, calculated with the swept-area method, is approximately 0.91 t km^{-2} (Ekau 1990). If we take into account the fact that in our sample artedidraconid fish represented 5.6% of the total number and 1.3% of the total weight of demersal fishes, we can see that only 10 kg km^{-2} were found, i.e. 0.01 g m^{-2}, or expressed another way 0.001 g C m^{-2}. In this area, for demersal fishes, Ekau (1990) estimated the production at only 0.03 g C m^{-2} yr^{-1} and Hubold (1992) at 0.04 g C m^{-2} yr^{-1}. In order to estimate consumption by plunderfishes, we need to know their mean stomach content, digestion time, and daily feeding rates. But the digestion time in Antarctic fish is long, approximately 48 to 96 h (Crawford 1978, Montgomery et al. 1989), depending on the nature of the prey, size of food, and ambient temperature; in addition, when the period is longer than 24 h, it is very difficult to detect feeding rhythms and intensity (Tarverdiyeva 1972). Also, due to their sit-and-wait predation method, these fishes do not always eat when they have already digested their previous prey. The feeding rates of Antarctic fish are low, barely reaching 2% of body weight per day (Kock 1992), so it is not surprising for these Antarctic fish to have such a low productivity level.

Artedidraconids caught during the ANT XV/III survey had a mean wet weight of 15 g and a mean size of 108 mm, we can thus estimate the density to be 1 fish per 1500 m^2. Using this data we can approximately calculate the value of the fish-benthos in the eastern Weddell Sea. Therefore, if plunderfishes present a density of 0.01 g m^{-2} and have a food intake of 2% of their body weight during the year, and we weight the percentage data by the volume of the overall plunderfish diet (Table 4), the elimination rate per day of the benthos by plunderfish is 0.2 mg C m^{-2} (0.1 mg C m^{-2} for amphipods, 0.04 mg C m^{-2} for isopods, 0.04 mg C m^{-2} for polynoids and 0.01 mg C m^{-2} for other polychaetes, as the most important prey groups); that it is to say that the plunderfish would consume 73 mg C m^{-2} yr^{-1}. According to Brey & Gerdes (1998) and Gerdes (unpubl. data) we assume a mean motile macrobenthic production of 1.7 mg C m^{-2} in the study area (specifically 118 mg C m^{-2} for amphipods, 130 mg C m^{-2} for other crustaceans and 1270 mg C m^{-2} for other polychaetes), of which 4% is consumed by the plunderfish.

However, precise calculations cannot be made; the present data indicate a first approximation of this fish family's consumption of the mobile benthos. Despite these limitations, we can see that the difference between the production of this mobile macrobenthos and the amount consumed by artedidraconids provides evidence that this food resource is used by other predators. In Jarre-Teichmann et al. (1997) and Arntz et al. (1994) there are examples of different species of amphipods, isopods, decapods, polynoids and aphroditiids feeding on other polychaetes and crustaceans. Olaso (1999) found only a 10% biomass of benthic prey in the notothenioids from the eastern Weddell Sea, with the exception of the plunderfish and some *Trematomus* species, but some species of this genus may also prey on the motile macrobenthos (Schwarzbach 1986, 1988), although to a lesser degree than the artedidraconids. Therefore the estimations of Schalk et al. (1993) can be considered acceptable; they propose that if the ecological efficiency of these fish is about 5% (Everson 1970), 0.6 g C m^{-2} of benthic production is required in order to maintain the current mass of demersal fishes.

In the present study we also observed some qualitative aspects of the biological processes that occur in these specialised trophic relationships. On the other hand, the morphological characteristics of the fish belonging to the most abundant families of notothenioids (Nototheniidae and Channicthyidae) enable them to prey upon a wider variety of prey, and of larger size than the small amphipods and polychaetes found in the motile macrobenthos. However, since this type of prey is not always accessible, and low temperatures require fish to limit energy expenditure on predation, specialised feeding on the mobile benthos is not always manifest (Schwarzbach 1988). On the contrary, artedidraconids exploit amphipods and polychaetes because they can sit and wait for a long time under deficient consumption conditions, thus they actually exploit only a limited part of this resource.

Acknowledgements. The authors gratefully acknowledge the help of A. Brandt, C. Gambi and B. Hilbig, for identification of isopods and polychaetes. This work was conducted under the SCAR EASIZ Programme, and was supported by the Alfred Wegener Institute, by the Spanish Antarctic Programme, and by the Belgian programme Scientific Research in the Antarctic-Phase IV.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

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Submitted: February 22, 1999; Accepted: September 20, 1999
Proofs received from author(s): February 22, 2000