Ecomorphological trends in the Artedidraconidae (Pisces: Perciformes: Notothenioidei) of the Weddell Sea

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Abstract: An ecomorphological study was performed on ten species of the family Artedidraconidae, the most benthic of the suborder Notothenioidei. These species are sympatric on the shelf of the Weddell Sea. The results show that the four genera comprising the family (*Artedidraco*, *Dolloidraco*, *Histiodraco* and *Pogonophryne*) can be differentiated by just a few morphometric features of their sensory organs and mouth. The genera were also clearly defined by the composition of their diet (benthic and epibenthic), the size of their prey, and their bathymetric distribution. Comparison of the morphological and ecological data shows a very close connection between sensory organs development, the mouth and bathymetric distribution. The morphological and ecological divergence observed can be explained as the result of the rapid adaptive radiation of the artedidraconids. The results confirm that characteristics of the sensory organs and alimentary structures are very suitable for the ecomorphological study of fishes.

Introduction

The perciform suborder Notothenioidei is an especially interesting group because of its adaptation to the special conditions of high Antarctic waters. It dominates the fish community of the Weddell Sea, representing 95% of all bottom-dwelling species (Ekau 1990). The notothenioids are characterized by having evolved quickly (Bargelloni *et al.* 2000) after replacing a Tertiary fish fauna. The fish of the time were radically different from those that exist today (Eastman 1991, 1993). The evolution of this suborder is characterized by adaptive radiation (Clarke & Johnston 1996, Eastman & Clarke 1998, Bargelloni *et al.* 2000). Most studies have focused on the families Nototheniidae and Channichthyidae and on the pelagization processes (Ekau 1988, 1991, Eastman 1991, 1993, Macdonald & Montgomery 1991, Klingenberg & Ekau 1996, Montgomery & Clements 2000). The other notothenioid families, such as the Bathydraconidae, Harpagiferidae and Artedidraconidae, have been considerably less studied.

The family Artedidraconidae (barbeled plunderfishes) is composed of 20–25 endemic species from the Antarctic, distributed across four genera (*Artedidraco*, *Dolloidraco*, *Histiodraco* and *Pogonophryne*) (Balushkin & Eakin 1998). The group is characterized by the presence of a mental barbel whose morphology is species specific (Hureau 1985, Eakin 1990, Eastman 1991, Balushkin & Eakin 1998, Eastman & Eakin 1999, Eakin *et al.* 2001). The artedidraconids are the most benthic of the notothenioids and are typical macrobenthic feeders, more sedentary than other groups (Eastman 1991, Ekau & Gutt 1991, Hubold 1991). They occupy different spatial and trophic niches to the rest of the notothenioids (Olaso *et al.* 2000).

Perhaps the most interesting aspect of the group is its evolution. Phylogenetic studies, based on mitochondrial DNA, indicate a high degree of diversification in a relatively short period of time (2–8 million years [m.y.]), very possibly as a result of sympatric speciation (Bargelloni *et al.* 2000). This rapid adaptive radiation makes the artedidraconids very suitable for testing hypotheses of ecological and evolutionary change in marine organisms (Eastman 2000, Pisano & Ozouf-Costaz 2000). This group allows study of morphological, environmental and phylogenetic aspects without interference by homoplasy (Bock 1990, Ricklefs & Miles 1994).

One of the main problems in ecomorphological studies is deciding upon the most suitable morphological and ecological traits (Norton *et al.* 1995). These characters should bear a close relationship to the environmental factors that form the niche of the organisms (Bock 1990, Norton *et al.* 1995). Within the morphological characters that can be analysed, the structures related to feeding and sensory perception of the environmental stimuli, demonstrate appropriate form-function relationships (Bock & von Waehlert 1965, Laverack 1981, Blaxter 1987, Bock 1990, Winemiller *et al.* 1995).

The aim of the present study was to establish the ecomorphological relationships between sensory and alimentary structures and the environment, and to evaluate the role of environmental adaptation in the diversification of artedidraconids. This has been pointed out by Eastman (1995) as one of the high priority lines of investigation into Antarctic notothenioids. A comparative morphometric study

Table I. Species, size, depth range and number of specimens used in morphometric and trophic analyses of artedidraconids of the Weddell Sea.

species	total length range (mm)	depth range (m)	morphometric analysis number of specimens	trophic analysis number of specimens
Artedidraco loennbergi Roule	47–111	281–417	24	20
A. orianae Regan	56–161	227–360	42	58
A. shackletoni Waite	65–119	184–301	9	-
A. skottsbergi Lönnberg	35–114	184–301	30	42
Histiodraco velifer Regan	158–183	227–416	6	-
Dolloidraco longedorsalis Roule	56–132	390–583	29	43
Pogonophryne barsukovi Andriashev	168–216	440–758	14	12
P. lanceobarbata Eakin	93–150	341–659	4	4
P. marmorata Norman	52–242	211–670	29	22
P. scotti Regan	73–297	234–670	15	11

was performed on sensory and feeding structures i.e. mental barbels, the eyes, the otoliths and the mouth.

Materials and methods

The specimens were obtained during 16 trawl surveys (GSN) and 17 Agassiz trawls (AGT) at depths of 180–2000 m in the Weddell Sea during the EASIZ II cruise (see Arntz & Gutt 1999, Schröeder *et al.* 1999). The species and sample sizes used in the morphometric analyses are indicated in Table I. For each specimen a total of eight morphological measurements were made: body length, from the dentary symphysis to the end of the caudal fin (TL); mental barbel length (MBL); mouth width (MWI) distance between descending process of both premaxillae, mouth length, distance between the dentary symphysis and the tip of the descending process of the premaxilla (MLE); dissected sagitta otolith weight (OWE); maximum eye diameter (MDE); minimum eye diameter (mDE); lens diameter (LDI). The eye was excised and measured to obtain the two diameters. The lens was removed and measured. All the measures (with exception of otolith weight) were obtained by a calliper to the nearest 0.5 mm. Measurements were obtained from ten sympatric species belonging to the four genera of the family Artedidraconidae: *Artedidraco loennbergi*, *A. orianae*, *A. shackletoni*, *A. skottsbergi*, *Dolloidraco longedorsalis*, *Histiodraco velifer*, *Pogonophryne barsukovi*, *P. lanceobarbata*, *P. marmorata* and *P. scotti*. Eye and otolith measurements were taken on the left side. Specimens were classified following the identification keys of Eakin (1990), Balushkin & Eakin (1998), Eakin & Eastman (1998), Eastman & Eakin (1999).

For each species, the measurements were standardized by removing the fish body size and effects of allometry, and by adjusting all measurements to a standard fish body measurement (Lombarte & Lleonart 1993, Lleonart *et al.* 2000). The allometric relationship to total fish length (TL) was calculated by species for each morphological measurement. The standard potential equation $Y = aX^b$ was used, fitting the logarithmic transformation to homogenize the residuals. Each Y_{ij} measurement, where i is the variable and j the individual, was transformed into Z_{ij} according to

$$Z_{ij} = Y_{ij} (X_0/X_j)b_j$$

where X_j is the body length of the individual j, X_0 is the reference body length, and b_j is the allometric parameter relating the dependent variable Y_i to the independent variable X. Z_{ij} would equal Y_{ij} if the fish length were X_0. Transformation of the measurements was carried out using the mean size of the total of the groups analysed ($X_0 = 150$ mm of TL) (Lleonart *et al.* 2000). The mean morphometric measurements of every species were investigated using correspondence analysis to obtain an order of the artedidraconid species in multivariate space based on morphological features.

The depth distribution and stomach contents of the plunderfishes were analysed to determine the trophic niche of each species. To establish depth distribution, the mean density and the standard deviation were calculated from the number of individuals caught hourly in the trawl samples. Since the samples were obtained from two different trawl nets (GSN and AGT) (Arntz & Gutt 1999), the data were analysed separately.

The volume of total prey groups (ml) in the stomach was determined using a trophometer, a calibrated instrument consisting of several different sized half-cylinders built into a tray (Olaso & Rodríguez-Marín 1995). The following information was collected for each prey taxon: percentage contribution to the volume of stomach contents, and number of items per stomach (Olaso 1990, Olaso *et al.* 2000). The mean volume and weight of each prey type was determined to examine the relationship between prey size and predator size (Hyslop 1980). In order to determine the relationship between prey weight and mouth size, the mean and the standard deviation of prey weight were calculated for each species and compared to the length of the mouth (mm).

The study of the spatial and trophic niches of the artedidraconid subcommunity was performed by correspondence analysis. The depth strata (180–350 m, 351–550 m and > 550 m), chosen according to the gear used, defined the spatial distribution: Agassiz trawl (A250
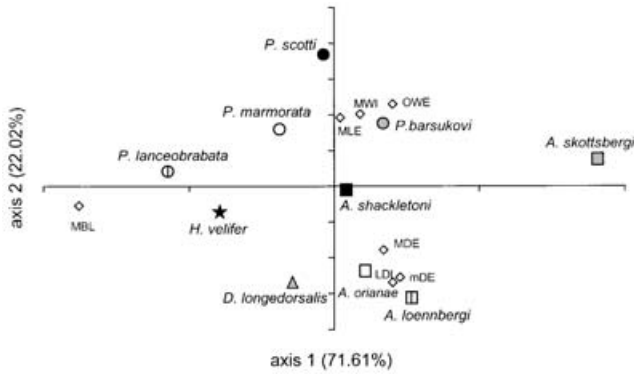
Fig. 1. Plots of the two first axes of the correspondence analyses for artedidraconid species in relation to morphology gradient. The abbreviations of the morphometric variables are indicated in Fig. 1. TL = total length, MBL = mental barbel length, MDE = maximum diameter of the eye, mDE = minimum diameter of the eye, LDI = diameter of the crystalline lens, MWI = mouth width, MLE = mouth length, OWE = otolith weight.
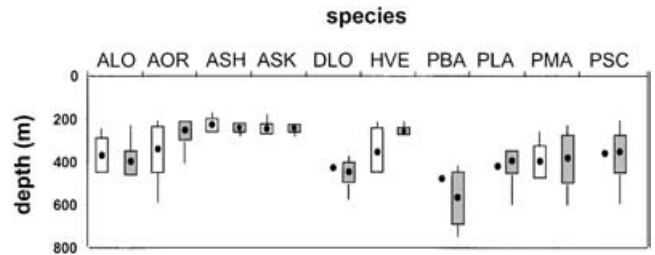

Fig. 2. Box-whisker plots of the presence of different species of artedidraconids by depth in EASIZ II Survey (Weddell Sea), based on the number of individuals per hour obtained during the EASIZ II cruise. Indicated are mean, box standard, indicates deviations and whisker minimum and maximum depth, range values. Grey boxes are data obtained from GSN trawl and white boxes data from AGT trawl. ALO = *Artedidraco loennbergi*, AOR = *A. orianae*, ASH = *A. shackletoni*, ASK = *A. skottsbergi*, DLO = *Dolloidraco longedorsalis*, HVE = *Histiodraco velifer*, PBA = *Pogonophryne barsukovi*, PLA = *P. lanceobarbata*, PMA = *P. marmorata*, PSC = *P. scotti*.

and A450) or bottom trawl (G250, G450, G650). The mean (WEI), minimum (mWE) and maximum (MWE) weight of the prey and the taxonomic composition of the diet were used to define the trophic composition of the artedidraconid species. Prey taxa were grouped in the following way: Amphipoda (Amp), Copepoda (Cop), Cumacea (Cum), Isopoda (Iso), Euphasiacea (Eup), Mysidacea (Mys), Ostracoda (Ost), Decapoda (Dec), Pycnogonida (Pyc), Mollusca (Mol), Bryozoa (Bry), Cnidaria (Cni), Polychaeta (Pol) and Osteichthyes (Ver). The trophic spectrum of all the species was also analysed, except for *Artedidraco shackletoni* and *Histiodraco velifer,* since the information collected from their stomach contents was insufficient.

To test the existence of a direct correlation between ecological and morphological data, canonical correspondence analysis (CANOCO) was performed (Ter Braak 1986) on all species except for *A. shackletoni* and *H. velifer.*

Results

Morphometry

The allometric relationship r^2 for almost all studied

Table II. Factor loadings of each morphological features in the first three axes of the correspondence analysis.

Morphological features	axis 1	axis 2	axis 3
mental barbel length	-0.1753	-0.0113	0.0051
maximum eye diameter	0.0346	-0.0362	-0.0018
minimum eye diameter	0.0465	-0.0514	0.0045
lens diameter	0.0411	-0.0547	-0.0043
mouth width	0.019	0.0402	-0.025
mouth length	0.0053	0.038	-0.0115
otolith weight	0.0416	0.0461	0.0338

variables exceeds 0.85. The results of the correspondence analysis show the first two factors to account for 93.6% of the total variability, and to separate clearly the four genera (Fig. 1). Axis 1 (71.6%) ordered the species based on the largest relative size of the mental barbel (Table II); the species with the shortest mental barbel (*A. skottsbergi*) and the largest barbel (*P. lanceobarbata*) were placed at opposite extremes. Axis 2 (22.0%) ordered the species based on the relative size of the mouth, otolith and eyes (Table II).

Histiodraco was characterized by a relatively large mouth and long barbel. *Dolloidraco* had similar morphological characteristics, with a relatively smaller mouth and relatively larger eyes than *Histiodraco*. A relatively smaller eye size and a larger mouth and otolith size differentiated *Pogonophryne*. This genus shows great variability in the mental barbel length (medium to long). *Artedidraco* was characterized by a relatively small mouth, moderate to large eyes, and short to medium barbel length. The genera *Pogonophryne* and *Artedidraco* were separated basically by the size of the mouth, which was relatively larger in *Pogonophryne* species.

Artedidraco orianae and *A. shackletoni* were characterized by the longest barbels in their genus. The species that inhabits the shallowest waters*, A. skottsbergi*, showed the smallest mental barbel and eyes. *Artedidraco loennbergi* was intermediate with respect to these structures. *Artedidraco shackletoni* and *A. skottsbergi* were separated from the rest by a relatively larger mouth size.

In the genus *Pogonophryne*, *P. lanceobarbata* had the longest barbel of the species analysed and showed a narrower mouth and proportionally smaller otoliths. The mental barbels of *P. marmorata* and *P. scotti* were of intermediate size, while *P. barsukovi* had a relatively shorter

Table III. Percentage contribution of every taxa to the volume of stomach contents in artedidraconid species of the Weddell Sea.

Species	Taxa prey													
	Copepoda	Ostracoda	Euphasiacea	Mysidacea	Cumacea	Isopoda	Amphipoda	Decapoda	Pycnogonia	Mollusca	Bryozoa	Cnidaria	Polychaeta	Osteichtya
A. loennbergi	0	0	0	9	0	6	62	0	0	0	0	0	23	0
A. orianae	1	2	5	0	0	10	41	0	5	0	0	0	36	0
A. skottsbergi	0	2	0	0	15	1	42	0	0	5	4	1	30	0
D. longedorsalis	0	0	3	0	6	1	36	0	0	0	0	6	48	0
P. barsukovi	0	0	0	0	0	34	52	0	0	14	0	0	0	0
P. lanceobarabata	0	0	0	0	0	0	100	0	0	0	0	0	0	0
P. marmorata	0	0	0	17	0	21	59	0	0	0	0	0	3	0
P. scotti	0	0	14	0	66	0	0	10	0	0	0	0	0	10

barbel. *Pogonophryne scotti* was characterized by having the largest mouth of the four species studied, the largest otolith, and by its relatively small eyes.

Depth distribution

In the Weddell Sea, artedidraconids inhabited the area studied between 180 and 800 m. However, its distribution was not homogeneous (Fig. 2). Some species had a limited depth distribution, for instance, *A. shackletoni* and *A. skottsbergi* were benthic species characteristic of the near shore and upper continental shelf (around 200 m). *Artedidraco loennbergi* also showed a restricted depth distribution (250–450 m). *Artedidraco orianae, Pogonophryne lanceobarabata, P. marmorata* and *P. scotti* had wider distributions and were found on bottoms between 200 and 600 m. *Pogonophryne barsukovi* lived at the greatest depth (between 500 and 800 m). In our data from the Weddell Sea, *Histiodraco velifer* and *Dolloidraco longedorsalis* showed a restricted depth distribution. However, data from the Ross Sea indicated a wider depth distribution for both species (Eastman & Hubold 1999, Eastman & Eakin 2001).

Food composition

Table III shows the diet of the eight most abundant species of artedidraconids expressed in percentage of main prey taxa.

Artedidraco orianae showed a prey diversity of seven different taxa: amphipods (41%), polychaetes (36%), isopods (10%), euphasiacids (5%), pycnogonids (5%), ostracods (2%) and copepods (1%). *Artedidraco orianae* can prey on the largest species of isopods and pycnogonids.

Artedidraco skottsbergi also showed a high prey diversity with eight different taxa taken: amphipods (42%), polychaetes (30%), cumaceans (15%), molluscan bivalves (5%), bryozoans (4%), ostracods (2%), isopods (1%) and cnidarians (1%). The high percentage (40%) of polychaetes, bryozoans, bivalves and cnidarians indicates that *A. skottsbergi* has more benthic feeding habits than *A. orianae*.

Artedidraco loennbergi search for prey above the seafloor, feeding on amphipods (62%) (basically lysianassids), mysids (9%) and isopods (6%), and few polychaetes (23%). Prey diversity was low at four taxa.
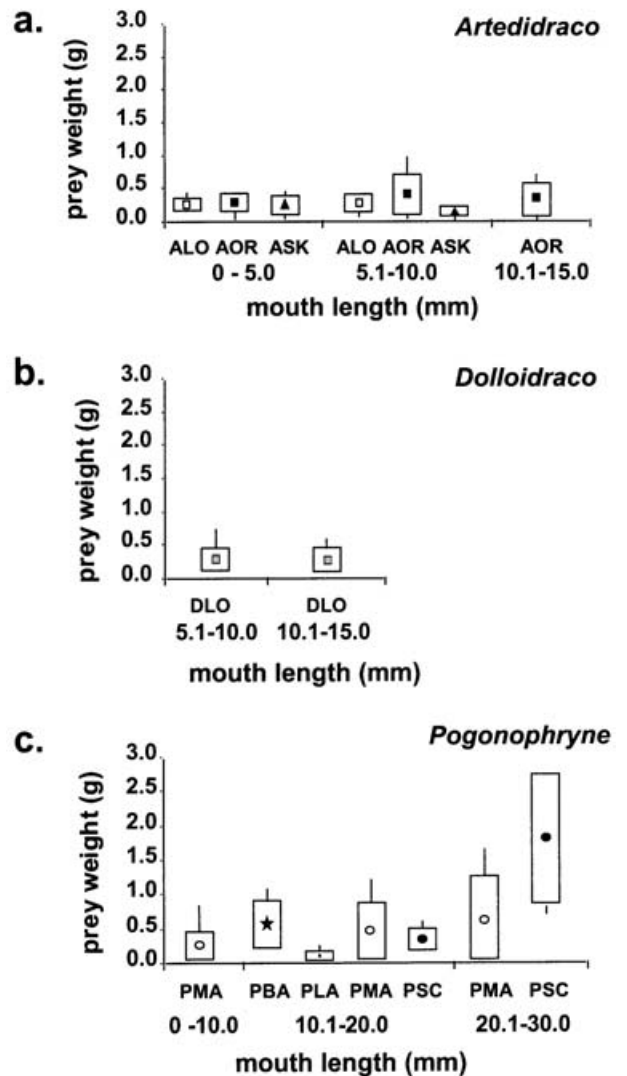

Fig. 3. Box-whisker plots of prey weight in relation to mouth length (mm) groups. The point indicates the mean data, box standard deviations and whisker minimum and maximum range values. The abbreviations for the species are indicated in Fig. 2.
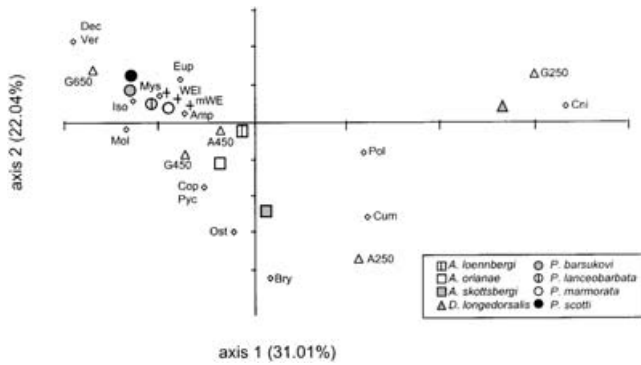
Fig. 4. Plots of the first and second axes of the correspondence analyses for artedidraconid species in relation to trophic and depth niches. Triangles indicate depth distribution, rhomboids indicate dietary data, crosses indicate prey weight. A250 = Agassiz trawl at 180–350 m, A450 = Agassiz trawl at 351 and 550 m, G250 = bottom trawl at 180–350 m, G450 = bottom trawl at 351 and 550 m, G650 = between 551 and 800 m. WEI = mean weight prey, mWE = minimum weight of prey, MWE = maximum weight of prey, Amp = percentage of Amphipods in the stomach in relation to the number of prey items, Cop = Copepoda, Cum = Cumacea, Iso = Isopoda, Eup = Euphasiacea, Mys = Mysidacea, Ost = Ostracoda, Dec = Decapoda, Pyc = Pycnogonida, Mol = Mollusca, Bry = Bryozoa, Cni = Cnidaria, Pol = Polychaeta, Ver = Osteichthya.

Dolloidraco longedorsalis consumed a high percentage of polychaetes (48%). This species also fed on amphipods (36%), cnidarians (6%) cumaceans (3%), krill (3%) and

Table IV. Factor loadings of each environmental features (depth distribution and trophic niche) in the first three axes of the correspondence analysis.

Environmental features	axis 1	axis 2	axis 3
Agassiz 150–350	-0.7363	0.4321	0.3522
Agassiz 351–550	0.0883	-0.301	-0.2569
GSN 150–350	0.1568	0.3725	-0.5681
GSN 351–550	0.0587	-0.3044	0.2786
GSN 551–750	0.6607	-0.7078	0.4524
mean prey weight	0.4498	-0.0186	0.1522
minimum prey weight	0.298	-0.1181	0.279
maximum prey weight	0.4754	0.0133	0.0658
% Copepoda	-0.2656	0.5474	-1.7076
% Ostracoda	-0.8473	0.9209	-0.4455
% Euphasiacea	0.8622	0.7703	-0.1751
% Mysidacea	-0.0922	-1.0006	-0.59
% Cumacea	-1.0029	0.8944	0.8688
% Isopoda	-0.1399	-0.6244	-0.1219
% Amphipoda	0.1103	-0.159	0.14
% Decapoda	2.2524	1.146	0.2665
% Pycnogonida	-0.2656	0.5474	-1.7076
% Mollusca	-0.4835	-0.3294	1.0513
% Bryozoa	-1.4289	1.2945	0.8166
% Cnidaria	-0.6673	0.5792	0.91
% Polychaeta	-0.5384	0.2352	-0.1664
% Osteichtyies	2.2524	1.146	0.2665

isopods (five prey taxa).

The species of *Pogonophryne* showed a low prey diversity. The most abundant species in the genus *Pogonophryne*, *P. marmorata*, preyed on four taxa: amphipods (59%), isopods (21%), mysids (17%) and polychaetes (very low at 3%). For *P. barsukovi*, food was present in six stomachs (the percentage of empty stomachs was 50%). Few stomachs were analysed and only three taxa were found: amphipods (52%), isopods (34%) and molluscs (14%).

For *P. scotti*, four prey taxa were detected. Large prey such as paramphitoids cumaceans (66%), euphasiaceans (14%), osteichthyes (10%) and decapods (10%) were recorded.

In *P. lanceobarbata*, food was present in the four stomachs analysed. The only prey found was amphipods, which were highly digested.

The comparative study of the mouth size (mouth length) and the weight of prey (Fig. 3) showed clear differences between genera. In *Artedidraco* and *Dolloidraco*, no important increase in prey size was observed with increase in mouth size. However, for the species of *Pogonophryne*, with their great size range, the larger individuals showed the capacity to catch bigger prey.

Food and depth niche analysis

The first two factors of the correspondence analysis accounted for 53.1% of the total variability, and clearly separated the three genera analysed (Fig. 4). Axis 1 (31.0% of the total variability) placed *D. longedorsalis* at one end, since this species is characterized by its living in a restricted bathymetric depth range. In addition, its diet was very different to those of the other species of the family, with a high percentage of Polychaeta and Cumacea, and including Cnidaria (Table IV). At the other end of axis 1 were located those species of the genus *Pogonophryne* characterized by having a diet of heavier prey, such as Decapoda, Isopoda, Euphasiacea, Mysidacea and Mollusca (Table IV). This genus was also characterized by its wide bathymetric distribution, reaching greater depths than the other genera. *Artedidraco* was located in an intermediate position but closer to *Pogonophryne*. Axis 2 (22.1%) placed *Artedidraco* at one end. This genus is characterized by its greater prey diversity, small prey size and a preference for shallower waters than species of *Pogonophryne* and *Dolloidraco*,

Table V. Percentage of variability in the first three axes of the canonical correspondence analysis for the two sets of data (morphological and environmental data).

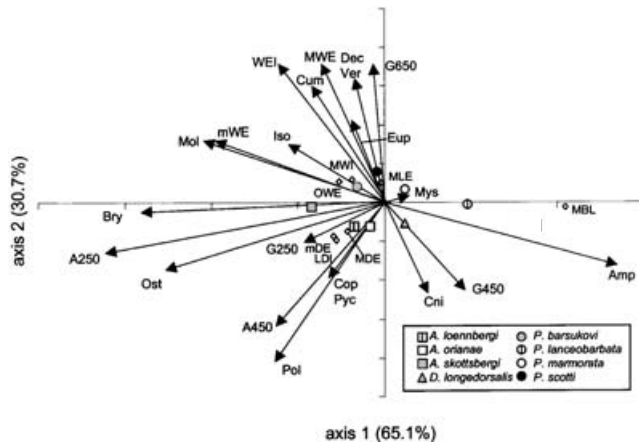| Percentage of variance	axis1	axis2	axis3
morphological data	65.1	30.7	3.6
species-environment-relation	65.1	30.7	3.6
accumulate percentage	65.1	95.8	99.4

Fig. 5. Plots of the first and second axes of the canonical correspondence analysis ordination diagram with species, morphological features (rhomboids) and environmental variables (arrows). The abbreviations for the morphological features and species are indicated in Fig. 1. The abbreviations for the environmental variables are indicated in Fig. 5.

which appear at the other end of axis 2 (Table IV).

Ecomorphological analysis

Canonical correspondence analysis showed high correspondence between ecological and morphological data, with an identical percentage of variability in the first three axes of the analysis for the two sets of data, as indicated in Table V. The canonical correspondence ordination diagram for the two first axes (95.8%) separated the genera in a fashion similar to that obtained in previous analyses (Fig. 5). *Pogonophryne* species were characterized by deeper distributions, larger prey and a relatively larger mouth and otolith. *Artedidraco* species showed a preference for the shallowest waters, small prey, and had a relatively larger eye size. *Dolloidraco longedorsalis* was characterized by an intermediate depth distribution, the consumption of small prey, and relatively large eyes and mental barbels.

Discussion

Morphological differentiation

The results confirm that in ecomorphological investigations, the morphological characters chosen for study can be restricted considerably if their functional value is considered (Norton *et al.* 1995). Characteristics related to the external sensory perception are very suitable for ecomorphological studies. The species of the family Artedidraconidae can be defined using very few morphological characters associated with the sensory organs and the size of the mouth. These results are similar to those observed in other studies that have analysed the morphological characteristics of fish communities, and

show the species are ordered into different morphological types (Winemiller 1989, Ekau 1991, Motta *et al.* 1995, Norton 1995, van de Meer *et al.* 1995, Winemiller *et al.* 1995, Klingenberg & Ekau 1996).

According to Hendry *et al.* (2000), sympatric speciation could be related to quantitative morphological changes, such as those observed in the sensory systems of artedidraconids. The morphological variability of the sensory organs are related to different environmental signal responses. As a result, a clear connection exists between the ecological niche of an organism and its sensory adaptations (Laverack 1981, Blaxter 1988). Several studies performed on other groups of notothenioids, especially from the family Nototheniidae, support this connection. A clear relationship has been observed between the anatomical arrangement of the eyes and the retinal morphology, and habitat type (pelagic or benthopelagic), bathymetric distribution and trophic niche (Meyer-Rochow & Klyne 1982, Macdonald & Montgomery 1991, Eastman 1993). Differences related to the mechanoreceptor system formed by the lateral line and the habitat type have also been observed (Ekau 1991, Coombs & Montgomery 1994, Janssen 1996). However, few studies have been performed on artedidraconids, and those reports that do exist, consider only a single species (Mac Donald & Montgomery 1991).

Mental barbels show a very disparate degree of development across the whole family, and some species can be characterized by their size and typology (Eakin 1990, Eakin *et al.* 2001). Instead, other species (*P. scotti* and *D. longedorsalis*) show a high morphological variability (Eakin *et al.* 2001, Eastman & Eakin 2001). The mental barbel has been associated with tactile inputs (Macdonald & Montogomery 1991, Janssen *et al.* 1993). This structure could be a specialization related to the benthic habitats of the family. The present analyses show a relationship between large eyes and large barbels. The morphological connection may be related to a special way of catching prey in which photoreceptors and tactile organs act together (Zimermann 1997).

With respect to eye size, the genera *Artedidraco*, *Histiodraco* and *Dolloidraco* have large eyes and lenses, and therefore their vision would seem to play a more important role than in *Pogonophryne*. The increase in the size of the eye and lens is directly related to an increase in focal length, which may confer better visual acuity or sensitivity (Fernald 1988).

The acoustic system of teleosts is based on otolithic hearing (Platt & Popper 1981) and variability in the size and shape of the otoliths has been correlated with phylogenetic position and habitat (Gauldie 1988, Paxton 2000). In artedidraconids, an inverse relationship is observed between the size of the otolith and that of the eye. This may indicated an increase in non-visual sensory capabilities as visual capabilities decrease. A similar relationship is seen in other benthic-feeding Perciformes with barbels such as the

Mullidae (Aguirre & Lombarte 1999).

Trophic specialization

The diet composition indicates that the artedidraconids species feed on prey that dwell close to the bottom. This characterizes these species as benthic and suprabenthic feeders (Olaso *et al.* 2000). Amphipods are important in the diet of nearly all artedidraconid species. In general, *Artedidraco* are less specialized in their diet, while *D. longedorsalis* shows a high degree of specialization, feeding on the smallest benthic prey such as polychaetes and cumaceans. The highest specialization is again observed in *Pogonophryne*.

Artedidraco and *Dolloidraco* are characterized by relatively small mouths and rather unspecialized diets. In these genera there was not a clear relationship between increase in mouth size (associated with an increase in body size) and prey size, which means that both genera feed on small benthic and suprabenthic organisms throughout life. However, in the *Pogonophryne* species, characterized by their large mouths, a clear relationship is observed between mouth and prey size.

Ecomorphological trends in Artedidraconidae

Analysis of the diet and the size of the prey, as well as their bathymetric distribution in Weddell Sea, show that the species analysed have different ecological niches. Comparison of the morphological and ecological data reveals a close connection between the development of the sensory organs and the mouth, and the wide-ranging ecological niches of these species.

The four genera that comprise the artedidraconids differ in their morphotypes: no morphological convergence is seen. A degree of development of the sensory organs was observed with adaptation to greater depth and specialization in diet. *Artedidraco*, which lives in shallower water, is the least morphologically differentiated group and has a less specialized diet, poorly developed barbels and medium-size eyes. *Dolloidraco* is a monospecific genus characterized by large eyes and developed barbels. In the Weddell Sea, the preferred depth-range distribution for this species was in deeper water, and it has a more specialized diet than *Artedidraco* species. *Histiodraco*, characterized by large barbels and medium-size eyes, has a similar epibenthic diet to *Dolloidraco*. Finally, the species of the genus *Pogonophryne* have small eyes, medium or large barbels, a more specialized diet, and a very wide bathymetric distribution, which, in some species such as *P. albipinna*, reaches depths of 2500 m (Eakin 1990).

The diversification of the morphological and ecological characteristics of the different genera of the artedidraconids could be associated with the rapid adaptive evolution of the group. The genetic study carried out by Bargelloni *et al.* (2000), based on mitochondrial DNA, indicates a high degree of diversification reached within a relatively short time (8–12 m.y.), very possibly by a process of sympatric or microvicariant speciation (Bargelloni *et al.* 2000). This phenomenon is very evident in the genus *Pogonophryne,* which includes more than half of the species of the family (Balushkin & Eakin 1998). The genus is characterized by species with a wide bathymetric distribution (they appear down to 2500 m) and by having a more specialized diet than the other genera of the family (Olaso *et al.* 2000). In addition, a larger morphological diversity exists within *Pogonophryne*, as indicated by Balushkin & Eakin (1998) who established five groups of species with evident morphological differences.

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