Trophic ecology of a coastal fish assemblage in Portuguese waters

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The diets and trophic ecology of the dominant fish species from the marine coastal region of Aveiro (north-western Portugal) caught during a summer survey were studied. Mysids were the most important prey group for the fish assemblage analysed. As a consequence, there was a high dietary overlap between species and a low incidence of piscivory. Nevertheless, a clear segregation of trophic niches was observed, with one group (comprising the species Chelidonichthys cuculus, Callionymus lyra, Dicologlossa cuneata *and* Pomatoschistus lozanoi) *showing a stronger preference for infaunal epibenthic prey, such as polychaetes and amphipods, another group (including* Arnoglossus imperialis, Arnoglossus laterna, Chelidonichthys obscurus, Chelidonichthys lucernus, Echiichthys vipera, Pagellus acarne *and* Trisopterus luscus) *preying mostly upon suprabenthic prey, mainly mysids, and a third group (*Engraulis encrasicolus *and* Trachurus trachurus) *feeding largely on planktonic prey like copepods. Some species, including* A. imperialis, C. lyra, E. vipera, T. trachurus *and* T. luscus, *showed ontogenic diet shifts that may be related to the habitat occupied by different size-classes and/or to their ability to capture prey of different size.*

INTRODUCTION

The structure of fish communities is dependent on resource partitioning (Ross, 1986). Within a system, the coexisting species share available resources, such as food and habitat (Pianka, 1969). Trophic segregation can play an important role in structuring and partitioning fish assemblages, as food availability is a major regulator of the system (Ross, 1986). An improved knowledge of the feeding habits (diet and behaviour), trophic relationships (niche definition and predator/prey interactions) and species functional roles is, therefore, important to describe or model marine ecosystems (e.g. Macpherson, 1981; Elliott *et al.*, 2002; Metcalf *et al.*, 2008).

Awareness of the limitations of a single-species approach to fisheries management has led to global acceptance of the need to adopt a wider ecosystem approach to fisheries (EAF) assessment and management (Garcia *et al.*, 2003). In order to achieve these objectives a good understanding of marine ecosystems must be obtained, especially in relation to community interactions, including predator–prey relationships in an integrated food web (Morishita, 2008). The implementation of the Marine Strategy Framework Directive (MSFD – 2008/56/EC) requires that important elements of marine food webs are considered in order to ensure the long-term viability of ecosystem structure. Hence, information on trophic relationships may help with implementing the MSFD.

Studies on the trophic ecology of coastal fish assemblages in Portuguese waters are limited (Cabral *et al.*, 2002) and in most cases focused on single species research (e.g. Morato *et al.*, 2000; França *et al.*, 2004), with more emphasis on commercially important species (e.g. Vinagre *et al.*, 2005; Garrido *et al.*, 2008). Since data on trophic interactions are limited, the trophic structure of coastal fish assemblages is poorly understood. Studies on this subject are therefore valuable despite being, sometimes, of limited temporal and spatial coverage.

A diverse fish assemblage is present in the coastal area off Aveiro (north-western Portugal) and some species, such as *Trachurus trachurus* (Linnaeus, 1758) and *Trisopterus luscus* (Linnaeus, 1758), are very abundant, particularly during the spring/summer period, when the region is used as a nursery (Jorge *et al.*, 2002). These species, along with *Engraulis encrasicolus* (Linnaeus, 1758), *Sardina pilchardus* (Walbaum, 1792), *Scomber colias* Gmelin, 1789 and *Scomber scombrus* Linnaeus, 1758, are targeted by beach seiners, purse seiners and trawlers that operate locally, supporting the regional economy (Jorge *et al.*, 2002; Sobral, 2007).

The present work provides information on the trophic ecology of the fish assemblages in the coastal area off Aveiro and also on the feeding interactions over these nursery grounds during summer. This study was conducted to meet three objectives: (1) to describe the diet of the dominant coastal fish species during the summer; (2) to analyse ontogenic variations in diet composition; and (3) to investigate trophic relationships and niche overlap between the dominant species.

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1151

MATERIALS AND METHODS

Study area

This study was carried out off Aveiro lagoon, Portugal, in an area inshore to the 100 m isobath (Figure 1). In this region, the continental shelf is relatively wide (~60 km), gently sloping with an edge defined by the 200 m contour. The sea bottom is dominated by sandy substrates with fine sand on the inner shelf (<30 m), and coarse sand and gravel on the mid-shelf (30–80 m) (Abrantes *et al.*, 2005). The western coastline of the Iberian Peninsula is characterized by upwelling events during the summer months (June to October). For the remainder of the year, other processes such as a slope pole-ward flow and a buoyant plume become more relevant in structuring the ocean over the shelf. The coastal region is also subject to strong hydrodynamic variability associated with mesoscale structures (eddies and meanders) and transient, alongshore currents (Peliz *et al.*, 2002, 2005).

Sampling and laboratory procedures

The present study was part of a multidisciplinary campaign (NeoMAv07), including surveys for hydrology, plankton and fish. Fish sampling was conducted from 2–7 July 2007, during the morning period, using two research vessels, RV 'Noruega' and RV 'Tellina', the latter operating in shallow waters only.
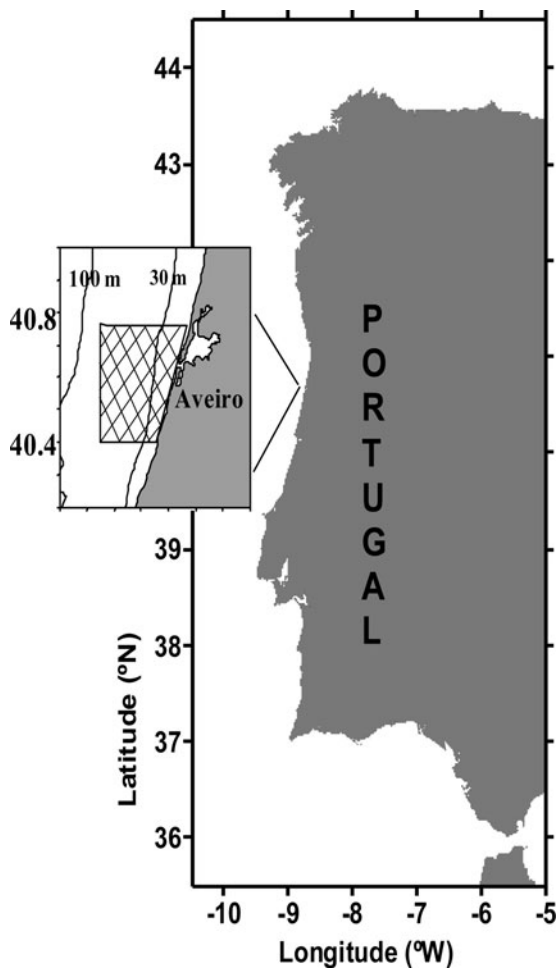

Fig. 1. Location of the sampling area in the A veiro coastal region.

Fishing was carried out to better understand the distribution and trophic ecology of the dominant fish. The summer season was selected to coincide with the recruitment period for the main fish species. A total of 14 hauls were made at depths between 10 m and 70 m, nine by RV 'Noruega' and five by RV 'Tellina' using bottom trawls with ~25 mm mesh size at the cod end. All fishes were sorted by species, weighed and grouped by size-class. The most abundant and/or the economically important fish species were selected for dietary studies. However, given their strictly planktonic diet, *S. pilchardu*s, *S. colias* and *S. scombrus* were considered in a different study (Castro, 2008). For the selected species a random sub-sample was taken from each haul and frozen for subsequent laboratory analyses, with a maximum of 150 individuals per species. Fishes were defrosted, the total length measured to the nearest milli-metre, and the stomachs and intestines were removed. Prey items were identified, using a stereomicroscope (80×), counted and weighed to the nearest 0.0001 g.

Data analysis

For dietary analyses, food items identified were grouped into 26 major taxonomic groups and the diet quantified using numerical (%N) and gravimetric indices (%W) and the frequency of occurrence (%O) (Hyslop, 1980) defined as:

$$\%N = \left(\frac{N}{NP} \right) \times 100,$$

$$\%W = \left(\frac{W}{WP} \right) \times 100,$$

$$\%O = \left(\frac{S}{SC} \right) \times 100,$$

where N and NP are the number of prey per group and the total number of prey, W and WP are the weight of each prey group and the total weight of prey, and S and SC are the number of stomachs and intestines with each prey group and the total number of stomachs and intestines with contents, respectively. These three indices were computed for the whole assemblage and also for each species in order to obtain a general overview of the trophic relationships in the study area. However, for simplicity, the subsequent analyses were made considering exclusively the frequency of occurrence (%O). This type of index is an adequate measurement when dealing with heterogeneous diets (Moreira *et al.*, 1992).

To assess diet variation with ontogeny, different size-classes were established according to the length distributions observed for each species taking into consideration the presence of different cohorts and their size at maturation ($L_{50\%}$), the latter obtained from the literature (Table 1). Only the 10 species with more than 40 individuals were used in this analysis: *Arnoglossus imperialis* (Rafinesque, 1810), *Arnoglossus laterna* (Walbaum, 1792), *Callionymus lyra* (Linnaeus, 1758), *Chelidonichthys lucernus* (Linnaeus, 1758), *Echiichthys vipera* (Cuvier, 1829), *E. encrasicolus*, *Pagellus acarne* (Risso, 1827), *Pomatoschistus lozanoi* (de Buen, 1923), *T. trachurus* and *T. luscus*. In the present work the nomenclature *Species*1 and *Species*2 was used to identify different size-classes, in length,

Table 1. Number of stomachs analysed, size-classes and respective sample size and median size of individuals, size at maturation ($L_{50\%}$) according to the literature and percentage of juveniles.

Family	Species	Abbreviation	N total	Size-classes (mm)		Median size (mm)	$L_{50\%}$ (mm)	% of juveniles
Engraulidae	*Engraulis encrasicolus*	Eenc	114	Class 1 (N)	125–140 (74)	133	111 (Millán, 1999)	0
				Class 2 (N)	141–170 (40)	148		
Gadidae	*Trisopterus luscus*	Tlus	150	Class 1 (N)	48–109 (102)	91	190 (Sobral, 1985)	100
				Class 2 (N)	110–173 (48)	125		
Triglidae	*Chelidonichthys cuculus*	Ccuc	29	–	184–265	221	140 (Moreno-Amich, 1992)	0
	Chelidonichthys obscurus	Cobs	23	–	92–112	102	125 (Muñoz *et al.*, 2003)	100
	Chelidonichthys lucerna	Cluc	150	Class 1 (N)	85–159 (56)	105	204 (Boudaya *et al.*, 2008)	91
				Class 2 (N)	160–315 (94)	179		
Carangidae	*Trachurus trachurus*	Ttra	150	Class 1 (N)	74–159 (122)	131	214 (Abaunza *et al.*, 1995)	100
				Class 2 (N)	160–210 (28)	181		
Sparidae	*Pagellus acarne*	Paca	150	Class 1 (N)	52–90 (34)	67	203 (Santos *et al.*, 1995)	100
				Class 2 (N)	91–159 (116)	106		
Trachinidae	*Echiichthys vipera*	Evip	150	Class 1 (N)	75–95 (96)	87	95 (Prista *et al.*, 2003)	61
				Class 2 (N)	96–147 (54)	105		
Callionymidae	*Callionymus lyra*	Clyr	150	Class 1 (N)	81–122 (14)	112	122 (King *et al.*, 1994)	8
				Class 2 (N)	123–250 (136)	203		
Gobiidae	*Pomatoschistus lozanoi*	Ploz	150	Class 1 (N)	36–57 (76)	55	57 (Froese & Binohlan, 2003)	41
				Class 2 (N)	58–80 (74)	61		
Bothidae	*Arnoglossus imperialis*	Aimp	41	Class 1 (N)	77–144 (23)	110	–	?
				Class 2 (N)	145–195 (18)	164		
	Arnoglossus laterna	Alat	116	Class 1 (N)	59–119 (47)	115	80 (Gibson & Ezzi, 1980)	5
				Class 2 (N)	120–164 (69)	126		
Soleidae	*Dicologlossa cuneata*	Dcun	18	–	128–180	144	165 (Jiménez *et al.*, 1998)	94
Total			1391					

in ascending order. The Spearman correlation rank test (Siegel & Castellan, 1988) was used to compare diets between different size-classes, within each species.

Correspondence analysis (CA) (Ter Braak & Prentice, 1988) was applied to evaluate the trophic structure of the fish assemblage considering the untransformed prey data of all different species/size-classes. Differences in the trophic groups identified by the CA were tested using a permutation multivariate analysis of variance (PERMANOVA; Anderson, 2001). The PERMANOVA analyses were performed using Bray–Curtis similarity on square-root transformed data. The main test and pair-wise comparisons were conducted with unrestricted permutations of the raw data.

To measure the dietary overlap among species/size-classes, the Horn index (R) was employed according to the following formula (Krebs, 1989):

$$R = \frac{\Sigma(p_{ij} + p_{ik}) \ln(p_{ij} + p_{ik}) - \Sigma p_{ij} \ln p_{ij} - \Sigma p_{ik} \ln p_{ik}}{2 \ln 2}$$

where p_{ij} and p_{ik} represent the proportion of each prey group (standardized frequency of occurrence as defined by Gunn & Milward, 1985) in species/size-classes j and k, respectively. This index ranges between 0 and 1 and significant dietary overlap is considered to occur when values are higher than 0.6 (Wallace & Ramsey, 1983).

RESULTS

Dominant prey

A total of 53 fish species belonging to 30 families were caught in the study. Thirteen of these species were chosen for trophic

analyses, with a total of 1391 fishes examined (Table 1). The majority of the individuals were juvenile.

Mysids were clearly the dominant prey for the whole fish assemblage (Table 2). Mysids were present in 34.5% of the stomachs and intestines (%O), representing 60.5% of the total prey (%N) and 49.0% of the total gut contents by weight (%W). Natantids were also important prey, especially in terms of weight and occurrence (%W = 18.2%; %O = 16.8%; %N = 14.4%). Brachyurans and teleosts represented 5.2% and 7.9% of the food by weight (%W), respectively.

Mysids were the most important prey for *A. imperialis*, *A. laterna*, *C. cuculus*, *C. lucerna*, *C. obscurus*, *E. vipera*, *P. acarne*, *P. lozanoi* and *T. trachurus* (Table 3). These supra-benthic organisms were even important in the diets of *E. encrasicolus* and *T. luscus*. Natantids were the primary food item for *T. luscus* and *Dicologlossa cuneata* (Moreau, 1881),

Table 2. Importance of each major prey group for the fish assemblage total sample, considering the frequency of occurrence and the numeric and gravimetric indices (%).

Major prey groups	%O	%N	%G
Cephalopoda	0.7	0.2	2.6
Polychaeta	4.2	1.5	4.6
Copepoda	5.4	4.4	0.1
Cumacea	3.6	1.6	0.3
Mysida	34.5	60.5	49.0
Amphipoda	7.5	4.6	1.9
Natantia	16.8	14.4	18.2
Anomura	5.8	2.1	3.2
Brachyura	5.6	1.6	5.2
Crustacea	6.6	3.7	5.6
Teleostei	4.1	1.0	7.9
Others	5.3	4.4	1.2

and also contributed in a large proportion to the diet of *A. laterna*, *A. imperialis*, *C. lyra* and *C. lucerna*. Infaunal and epibenthic prey, including polychaetes, amphipods, anomurans and brachyurans, played an important role in the feeding of *C. cuculus*, *C. lyra*, *P. lozanoi* and *D. cuneata*. Copepods and other pelagic prey prevailed in the stomach contents of *E. encrasicolus* and *T. trachurus*.

Overall, the piscivory observed in this fish assemblage was relatively low. *Chelidonichthys lucerna* was the species that consumed the highest proportion of teleosts, followed by *E. vipera* and *C. cuculus*. Gobies, *Pomastochistus* spp., were the most preyed upon fish in this assemblage.

Ontogenic changes

Five species (*A. imperialis*, *C. lyra*, *E. vipera*, *T. trachurus* and *T. luscus*) showed significant differences in the diet between the size-classes considered (Spearman rank correlations, $P >$ 0.05). All the individuals of *T. trachurus* and *T. luscus* sampled were juveniles as was the case for the majority of *E. vipera* (61%), while adult *C. lyra* predominated (only 8% were juvenile) (Table 1). For *A. imperialis* no references to the size at maturation were found in the literature and so they were not classified accordingly.

For *T. trachurus* the major differences in the diet amongst size-classes were related to an increase in prey size, as well as a greater variety of food in larger juveniles. Copepods and mysids were the most important components in the diet of smaller individuals, and although these prey were still important for individuals larger than 159 mm, larger fish showed an increased predation on teleosts (Table 3). An increased size of prey in larger specimens was also found for *T. luscus* and *E. vipera*. Mysids and natantids were present in ~70% of the stomachs of both size-classes of *T. luscus*, but amphipods, important food for individuals smaller than 110 mm, were replaced by brachyurans and anomurans in the diet of larger juveniles. In *E. vipera*, the reduced consumption of mysids from juvenile to the adult phase was balanced by a higher predation on cephalopods and teleosts by the latter. Mysids were the major prey for all sizes of *A. imperialis*, but as fish increased in size the diet showed a reduced proportion of other suprabenthic prey, like natantids and teleosts, and more infaunal and epibenthic organisms, such as polychaetes, anomurans and brachyurans. The major differences in the diet of *C. lyra* of different size-classes were likely due to an increase in prey size, and in the proportion of infaunal and epibenthic organisms, ingested by adults. Natantids were important in the diet of this species throughout life. However, for larger fishes, smaller suprabenthic prey, such as cumaceans and mysids, became less important whilst infaunal and epibenthic prey (including polychaetes, amphipods, echinoderms, bivalves, anomurans and brachyurans) became important prey taxa.

Community trophic structure

The correspondence analysis showed the presence of three distinct trophic groups in the coastal fish assemblage during this study (Figure 2). Group 1 included fish that preyed upon a large proportion of infaunal and epibenthic prey (e.g. polychaetes and amphipods), namely *C. cuculus*, *C. lyra* (*C. lyra*1 and *C. lyra*2), *P. lozanoi* and *D. cuneata*. Mysids and teleosts were less important prey for this group. Group 2 comprised *A. imperialis* (*A. imperialis*1 and *A. imperialis*2),

A. laterna, *C. obscurus*, *C. lucernus*, *E. vipera* (*E. vipera*1 and *E. vipera*2), *P. acarne* and *T. luscus* (*T. luscus*1 and *T. luscus*2). These species had diets composed mainly of suprabenthic prey, especially mysids. Group 3 contained *E. encrasicolus* and *T. trachurus* (*T. trachurus*1 and *T. trachurus*2), that fed mostly on pelagic organisms (copepods and diverse meroplanktonic organisms). The PERMANOVA main test and the subsequent pair-wise tests revealed the existence of significant differences ($P < 0.05$) between the three groups identified by the CA (Table 4).

Diet overlap

The Horn index evidenced a high dietary overlap amongst the species/size-classes, and even between fish living at different water column strata (Table 5). The high consumption of mysids was a major contributor for this high dietary overlap. *Callionymus lyra*, *D. cuneata*, *E. encrasicolus* and *T. trachurus* showed the lowest trophic overlap in the assemblage. The first two species exhibited the diets with most infaunal and epibenthic organisms of the whole assemblage while the other two were the main pelagic feeders.

DISCUSSION

The importance of mysids

Mysids played a very important role in the diet of the fish assemblages in the coastal area off Aveiro, occurring in the gut contents of all species. These findings are consistent with the results obtained by Cunha *et al.* (1997), who studied the suprabenthic communities off Aveiro (also during a summer period), and concluded that mysids were one of the most abundant organisms in the assemblage. According to Mauchline (1980), mysids are an important part of the suprabenthic community of several coastal habitats, and their daily vertical migration through the water column makes them available for several fish species that occupy different niches. Lasiak & MacLachlan (1987) stated that mysids usually form dense aggregations, making them a very important prey for fish inhabiting highly dynamic environments, as is the case of this study area. The importance of mysids in coastal food webs was also observed by Hostens & Mees (1999).

Although overlap in diets is more likely to occur when the prey identification is not undertaken to species level, the high dietary overlap observed between the fish species analysed in the Aveiro coastal area is very likely a consequence of the high abundance of mysids, their availability through the water column, and value as energetic resource (Mauchline, 1980), which makes this group highly predated on by all the fish species studied.

Piscivory

Piscivory was not common in the present study and occurred with low incidence on the species with major commercial interest. In this assemblage, *Pomastochistus* spp. were the most preyed upon fish, due to their small size and high abundance, compared to other species. The low levels of piscivory observed may have been influenced by the high abundance of

Table 3. Diet quantitative analysis of the species and respective size-classes according to the frequency of occurrence (%O) and numeric (%N) and gravimetric (%W) indices. Reference also to the percentage of empty stomachs.

Major prey groups	Abbreviation	E. encrasicolus %O	%N	%W	T. luscus %O	%N	%W	T. luscus1 %O	%N	%W	T. luscus2 %O	%N	%W	C. cuculus %O	%N	%W	C. obscurus %O	%N	%W	C. lucerna %O	%N	%W
Unidentifed organic matter	Uom	1.0	0.0	0.0	2.1	0.2	0.5	2.2	0.2	0.7	2.1	0.1	0.4							0.9	0.1	0.0
Mineral matter	Mm				2.9	0.3	0.6	3.3	0.4	0.8	2.1	0.1	0.4	30.4	3.3	22.7	8.7	0.6	0.3	4.3	0.6	0.5
Vegetable matter	Vm																					
Radiolaria	Rad																					
Gastropoda	Gast	7.6	0.6	1.2																		
Bivalvia larvae	Bivl	22.9	48.1	0.0																		
Bivalvia	Biv																					
Cephalopoda	Ceph																			0.9	0.1	0.0
Polychaeta	Pol				2.1	0.2	0.5	2.2	0.2	0.5	2.1	0.1	0.5									
Cladocera	Cla	1.0	0.0	0.0																		
Copepoda	Cop	89.5	27.2	0.2	0.7	0.1	0.0				2.1	0.1	0.0									
Cumacea	Cum																4.3	0.3	0.1	10.3	2.5	0.2
Cirripedia larvae	Cirrl	19.0	0.8	0.0																		
Mysida	Mys	41.9	11.8	28.1	70.7	42.5	25.6	68.5	47.7	31.3	68.8	36.4	20.6	43.5	60.3	15.3	100.0	97.3	96.7	60.3	61.2	16.2
Isopoda	Isso				2.9	0.3	1.8	2.2	0.3	0.9	4.2	0.2	2.5									
Amphipoda	Amph	2.9	0.1	2.4	17.9	2.6	0.4	26.1	4.8	0.8	2.1	0.1	0.1	30.4	5.7	1.1	4.3	0.3	0.9	5.2	0.9	0.2
Natantia	Nat	3.8	0.1	0.1	72.1	42.8	61.1	70.7	35.3	57.1	75.0	51.7	64.5	30.4	9.1	7.6				47.4	26.6	35.0
Anomura larvae	Anoml	17.1	6.7	2.0																		
Anomura	Anom				5.7	0.6	0.3	1.1	0.1	0.0	14.6	1.2	0.6	60.9	15.3	20.5						
Brachyura larvae	Bral	11.4	0.3	0.1																		
Brachyura	Bra	1.0	0.0	0.0	6.4	0.3	0.7	2.2	0.2	0.3	14.6	0.5	1.2	39.1	4.8	17.5	13.0	1.5	2.0	17.2	3.2	21.6
Crustacea eggs	Crustegg																					
Crustacea larvae	Crustl	5.7	0.2	0.1																		
Crustacea	Crust	21.9	2.5	10.7	20.7	9.9	7.3	21.7	10.8	6.7	18.8	8.8	7.7							1.7	0.2	0.3
Echinodermata	Echin																					
Teleostei eggs	Telegg	1.0	0.0	0.0																		
Teleostei	Tel				2.1	0.2	1.2	1.1	0.1	1.0	4.2	0.4	1.5	13.0	1.4	15.3				31.9	4.6	26.0
Empty stomachs (%)		7.9			6.7			0.0			25.0			11.5			0.0			22.7		

Major prey groups	Abbreviation	T. trachurus %O	%N	%W	T. trachurus1 %O	%N	%W	T. trachurus2 %O	%N	%W	P. acarne %O	%N	%W	E. vipera %O	%N	%W	E. vipera1 %O	%N	%W	E. vipera2 %O	%N	%W
Unidentifed organic matter	Uom	25.0	2.0	10.0	25.4	2.2	9.7	23.8	1.6	10.7	17.3	0.8	7.7									
Mineral matter	Mm	9.1	0.7	0.8	6.0	0.5	0.0	19.0	1.3	2.5												
Vegetable matter	Vm																					
Radiolaria	Rad	1.1	0.1	0.0				4.8	0.3	0.0												
Gastropoda	Gast																					
Bivalvia larvae	Bivl																					
Bivalvia	Biv										3.8	0.2	0.1	1.1	0.1	0.2	1.9	0.2	0.4			
Cephalopoda	Ceph													6.5	0.9	19.6				15.4	3.4	34.5

Continued

Table 3. Continued

Major prey groups	Abbreviation	T. trachurus			T. trachurus1			T. trachurus2			P. acarne			E. vipera			E. vipera1			E. vipera2		
		%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Polychaeta	Pol										1.9	0.1	0.4	4.3	0.6	1.0	1.9	0.2	1.0	7.7	1.7	1.0
Cladocera	Cla																					
Copepoda	Cop	33.0	13.0	0.6	29.9	0.3	0.7	42.9	45.2	0.6												
Cumacea	Cum	1.1	0.1	0.0				4.8	0.3	0.0	7.7	0.5	0.1	2.2	1.0	0.0	3.7	1.4	0.1			
Cirripedia larvae	Cirrl	2.3	3.8	0.0	3.0	5.5	0.0															
Mysida	Mys	37.5	44.5	72.0	32.8	51.4	84.7	52.4	31.0	64.0	75.0	89.4	84.6	75.3	93.8	49.4	88.9	96.8	76.2	56.4	85.2	29.2
Isopoda	Isso										1.9	0.1	0.4									
Amphipoda	Amph	3.4	0.3	0.0	3.0	0.3	0.0	4.8	0.3	0.0	23.1	5.3	1.8	2.2	0.3	0.0	1.9	0.2	0.1	2.6	0.6	0.0
Natantia	Nat										9.6	0.5	1.7	1.1	0.1	0.9				2.6	0.6	1.7
Anomura larvae	Anoml	5.7	0.5	0.0	6.0	0.5	0.1	4.8	0.3	0.0												
Anomura	Anom																					
Brachyura larvae	Bral	1.1	0.1	0.0	1.5	0.1	0.0															
Brachyura	Bra	3.4	0.4	0.1	4.5	0.5	0.1							4.3	0.7	1.1	1.9	0.2	0.1	7.7	2.3	1.9
Crustacea eggs	Crustegg	1.1	0.1	0.0				4.8	0.3	0.0												
Crustacea larvae	Crustl																					
Crustacea	Crust	43.2	11.1	13.5	32.8	8.8	14.1	42.9	17.4	15.6	9.6	3.1	4.9	2.2	0.3	0.3	1.9	0.2	0.6	2.6	0.6	0.0
Echinodermata	Echin																					
Teleostei eggs	Telegg																					
Teleostei	Tel	6.8	0.5	20.0	3.0	0.3	0.1	19.0	1.3	6.6				15.1	2.1	27.4	7.4	0.8	21.5	25.6	5.7	31.8
Empty stomachs (%)		41.3			45.1.9			25.0			65.3			38.0			43.8			27.8		

Major prey groups	Abbreviation	C. lyra			C. lyra1			C. lyra2			P. lozanoi			A. imperialis			A. imperialis1			A. imperialis2		
		%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Unidentifed organic matter	Uom	27.9	4.3	7.8	35.7	6.2	19.4	27.0	3.9	7.6	8.4	2.0	1.2									
Mineral matter	Mm	2.1	0.3	1.3				2.4	0.3	1.3	8.4	2.0	1.2	5.1	0.4	0.8				11.8	0.6	1.4
Vegetable matter	Vm										2.5	0.8	0.0									
Radiolaria	Rad																					
Gastropoda	Gast	2.9	0.5	0.3				3.2	0.6	0.3	0.8	0.2	0.3									
Bivalvia larvae	Bivl																					
Bivalvia	Biv	20.7	5.0	7.2				23.0	5.5	7.4	3.4	2.4	0.3									
Cephalopoda	Ceph	0.7	0.1	0.9				0.8	0.1	0.9				2.6	0.2	3.5				5.9	0.3	6.1
Polychaeta	Pol	48.6	11.3	21.5	35.7	6.2	19.4	47.6	11.8	21.7	9.2	2.2	6.6	5.1	0.4	2.6				11.8	0.6	4.6
Cladocera	Cla																					
Copepoda	Cop										5.9	3.8	0.1									
Cumacea	Cum	13.6	3.0	0.7	42.9	11.1	1.0	10.3	2.3	0.3	6.7	3.6	1.1									
Cirripedia larvae	Cirrl																					
Mysida	Mys	17.1	25.9	4.1	35.7	48.1	25.8	15.1	23.9	3.7	54.6	50.7	44.3	97.4	92.1	57.0	100.0	87.0	70.2	94.1	89.9	46.8
Isopoda	Isso	2.9	0.8	3.2				3.2	0.9	3.3												
Amphipoda	Amph	31.4	12.8	1.4	7.1	1.2	0.4	34.1	14.0	1.4	31.1	21.8	11.9	5.1	0.4	0.3	4.5	0.4	0.3	5.9	0.3	0.3
Natantia	Nat	38.6	14.5	3.6	42.9	27.2	5.6	38.1	13.1	3.5	6.7	2.0	19.3	46.2	5.9	12.0	54.5	8.1	17.7	35.3	4.0	7.7
Anomura larvae	Anoml																					

Major prey groups	Abbreviation	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Anomura	Anom	30.0	8.9	13.6	7.1	2.5	0.8	33.3	9.5	13.9	5.0	1.2	0.2	28.2	3.2	6.8	13.6	1.8	1.3	47.1	4.0	11.0
Brachyura larvae	Bral																					
Brachyura	Bra	37.1	10.1	27.0				41.3	11.1	27.6				7.7	0.6	5.8	4.5	0.4	0.1	11.8	0.6	10.0
Crustacea eggs	Crustegg																					
Crustacea larvae	Crustl										0.8	0.2	0.0									
Crustacea	Crust	3.6	0.6	0.5				4.0	0.7	0.5	10.1	2.0	2.2									
Echinodermata	Echin	7.9	1.5	0.7				8.7	1.6	0.7												
Teleostei eggs	Telegg																					
Teleostei	Tel													10.3	1.3	11.3	13.6	1.3	7.7	5.9	0.3	14.1
Empty stomachs (%)		6.7			0.0			7.4				20.0		4.9			0.0			11.1		

| Major prey groups	Abbreviation	A. laterna			D. cuneata		
		%O	%N	%W	%O	%N	%W
Unidentifed organic matter	Uom						
Mineral matter	Mm						
Vegetable matter	Vm	1.9	0.3	0.0			
Radiolaria	Rad						
Gastropoda	Gast						
Bivalvia larvae	Bivl						
Bivalvia	Biv						
Cephalopoda	Ceph						
Polychaeta	Pol				12.5	2.3	19.5
Cladocera	Cla						
Copepoda	Cop						
Cumacea	Cum				25.0	5.7	2.7
Cirripedia larvae	Cirrl						
Mysida	Mys	87.4	79.1	57.4	18.8	4.5	0.5
Isopoda	Isso						
Amphipoda	Amph	3.9	0.5	1.2	50.0	23.9	9.7
Natantia	Nat	44.7	15.6	28.2	68.8	56.8	44.6
Anomura larvae	Anoml						
Anomura	Anom	1.0	0.1	3.3			
Brachyura larvae	Bral						
Brachyura	Bra	18.4	2.9	2.0			
Crustacea eggs	Crustegg						
Crustacea larvae	Crustl						
Crustacea	Crust	2.9	1.6	4.7	37.5	6.8	23.1
Echinodermata	Echin						
Teleostei eggs	Telegg						
Teleostei	Tel	3.9	0.5	3.3			
Empty stomachs (%)		10.7			11.1		
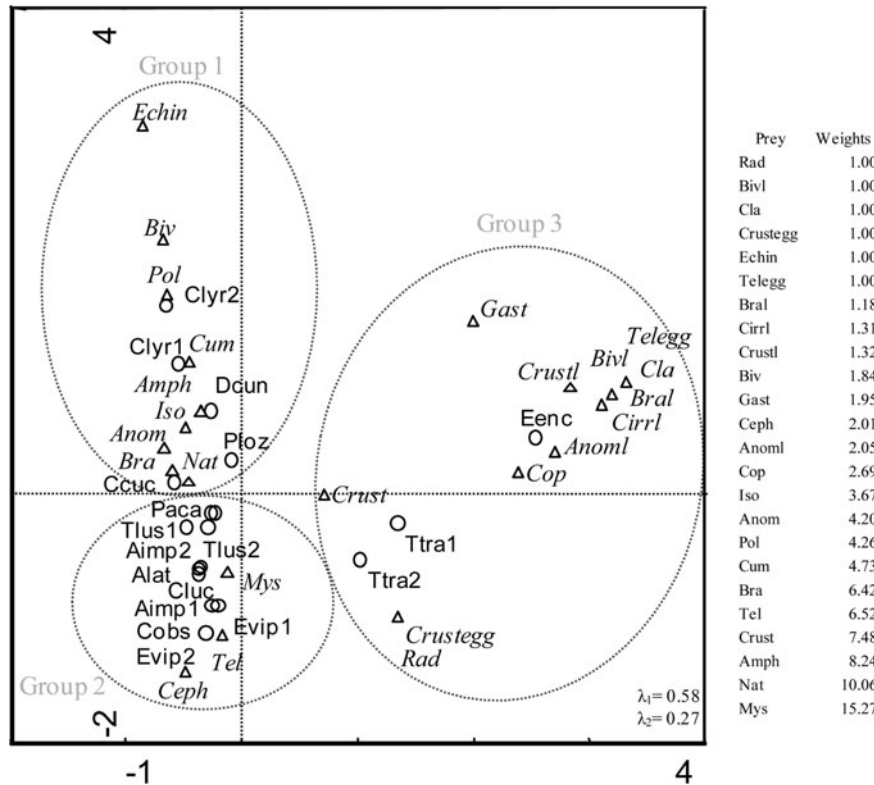
Fig. 2. Diagram of the correspondence analysis performed using the frequency of occurrence of the several species/size-classes to identify major trophic groups. Δ, prey groups; ○, species and/or size-classes (see Table 1 for the size-class details and species abbreviations and Table 3 for prey abbreviations). Eigenvalues of the first two axes (λ1 and λ2), groups formed in the diagram (Groups 1–3) and the relative weight of each prey group in the analysis are also indicated.

mysids and also by the size of the fishes studied, as many of them were juveniles.

Trophic structure

The trophic structure of the fish assemblage of the Aveiro coastal area revealed three distinct groups. Group 1, including *C. cuculus*, *C. lyra*, *P. lozanoi* and *D. cuneata*, were fishes with benthic diets that comprised polychaetes, amphipods, anomurans and brachyurans, even though mysids were also an important food resource. These findings support earlier published studies for *C. lyra* (van der Veer *et al.*, 1990; King *et al.*, 1994), *D. cuneata* (Belghyti *et al.*, 1993; Cabral *et al.*, 2002) and *C. cuculus* (Moreno-Amich, 1992). Mysids have been considered the most important prey for *P. lozanoi* (Laffaille *et al.*, 1999), which was the smallest fish in the assemblage sampled and their preference for infaunal and epibenthic items may be related to competition with the other fishes (Costa *et al.*, 2008).

Group 2 included *A. imperialis*, *A. laterna*, *C. obscurus*, *C. lucernus*, *E. vipera*, *P. acarne* and *T. luscus*. These species fed

Table 4. Results of the PERMANOVA tests performed to compare the diet (index of occurrence) of the trophic groups (1, 2 and 3) identified in the correspondence analysis.

	Groups	Pseudo-F	df	*P* (Perm)	Unique permutations
Main test	1, 2, 3	6.22	2	0.001	999
Pair-wise	1, 2	–	–	0.003	854
	1, 3	–	–	0.003	279
	2, 3	–	–	0.014	56

mainly on suprabenthic prey, including mysids. *Arnoglossus imperialis* and *A. laterna* are known to use visual stimuli to detect prey and are expected to consume more mobile organisms (Braber & de Groot, 1973). The high abundance of mysids in the diet of *A. imperialis* was also shown by Cabral *et al.* (2002), although this study also indicated that amphipods were the main prey for *A. laterna*, in contrast to the present study. It may be that the locally high abundance of mysids in the coastal area off Aveiro allows these two species to have more similar trophic preferences. Triglids such as *C. obscurus* and *C. lucerna* are active bottom dwellers and feed mostly on suprabenthic prey (Moreno-Amich, 1992; 1996; Amorim & Hawkins, 2000). Specimens of *E. vipera* preyed on several species, some of which inhabit the sediment but also others associated with the water column as observed in other Portuguese coastal areas (Vasconcelos *et al.*, 2004). This mixed feeding strategy may explain the species inclusion in Group 2. Creutzberg & Witte (1989), studying *E. vipera* in the North Sea, reported a broadly similar diet composition, but teleosts were the predominant prey. These differences may be related to prey availability on the study sites, with the high abundance of mysids off the Aveiro coast probably resulting in a lower consumption of teleosts. *Pagellus acarne* and *T. luscus*, which are more fusiform fish less associated with the sea floor, could be expected to potentially have a broader diet and capture organisms with higher mobility. However, some dependence on suprabenthic prey, as reported here, has been noted elsewhere (e.g. Hostens & Mees, 1999; Fehri-Bedoui *et al.*, 2009).

Species in Group 3 (*E. encrasicolus* and *T. trachurus*), consumed a high proportion of pelagic organisms. Although

Table 5. Results of the Horn index measuring the diet overlap among the different fish species/size-classes, using the standardized frequency of occurrence of each prey group. Values higher than 0.6 are highlighted because dietary overlap is considered to be significant above this limit (see Table 1 for size-class details and species abbreviations).

	Eenc	Tlus1	Tlus2	Ccuc	Cobs	Cluc	Ttra1	Ttra2	Paca	Evip1	Evip2	Clyr1	Clyr2	Ploz	Aimp1	Aimp2	Alat	Dcun
Eenc	–																	
Tlus1	0.42	–																
Tlus2	0.43	0.91	–															
Ccuc	0.26	0.67	0.74	–														
Cobs	0.36	0.63	0.66	0.57	–													
Cluc	0.33	0.78	0.81	0.73	0.74	–												
Ttra1	0.82	0.56	0.55	0.33	0.47	0.44	–											
Ttra2	0.70	0.55	0.55	0.37	0.51	0.55	0.92	–										
Paca	0.43	0.85	0.72	0.57	0.77	0.70	0.59	0.62	–									
Evip1	0.38	0.63	0.63	0.51	0.89	0.73	0.58	0.65	0.83	–								
Evip2	0.35	0.61	0.64	0.59	0.72	0.78	0.51	0.59	0.66	0.82	–							
Clyr1	0.26	0.68	0.63	0.47	0.54	0.68	0.29	0.35	0.69	0.53	0.50	–						
Clyr2	0.22	0.59	0.61	0.72	0.38	0.55	0.21	0.24	0.56	0.36	0.45	0.65	–					
Ploz	0.52	0.78	0.69	0.62	0.65	0.62	0.64	0.66	0.92	0.73	0.62	0.69	0.67	–				
Aimp1	0.35	0.84	0.90	0.80	0.77	0.88	0.46	0.50	0.73	0.76	0.73	0.63	0.52	0.67	–			
Aimp2	0.33	0.73	0.83	0.86	0.73	0.75	0.42	0.44	0.68	0.71	0.76	0.62	0.68	0.71	0.90	–		
Alat	0.39	0.87	0.90	0.75	0.85	0.90	0.50	0.52	0.77	0.77	0.74	0.63	0.54	0.67	0.94	0.83	–	
Dcun	0.32	0.83	0.68	0.51	0.35	0.63	0.44	0.46	0.74	0.28	0.40	0.78	0.65	0.75	0.54	0.50	0.58	–

mysids were an important food item for *E. encrasicolus,* the majority of their prey were planktonic organisms. Copepods were dominant in a diet that also included the larvae of bivalves, barnacles and decapod crustaceans. The importance of copepods in the diet of *E. encrasicolus* is consistent with previous studies (Tudela & Palomera, 1997; Plounevez & Champalbert, 1999). The highest prey diversity in the present study was observed for this species, which comprised 14 major prey groups, possibly because its feeding strategy can shift from filter feeding for smaller zooplanktonic prey to particulate feeding for larger items such as mysids (Tudela & Palomera, 1997). *Trachurus trachurus* preyed mostly upon mysids, unidentified crustaceans, copepods, and other zooplanktonic organisms. In studies conducted in deeper waters, Cabral & Murta (2002) concluded that the main items in the diet of *T. trachurus* from the Portuguese coast were copepods and euphausiids, while in the Adriatic Sea, Jardas *et al.* (2004) reported a diet comprising euphausiids, mysids, decapod crustaceans, cephalopods and teleosts. The works cited above were generally carried out in waters deeper than the present observations, and depth may account for the absence of euphausiids in the area studied, as adult euphausiids occur mainly in deeper waters (Cunha *et al.*, 1997). Additionally, the sample of *T. trachurus* in the present study comprised juveniles, in contrast to the references quoted above.

Ontogenic changes

Larger *T. trachurus*, *T. luscus* and *E. vipera* fed on larger organisms, while smaller fish predated on smaller prey, as observed elsewhere (Santos, 1989; Hamerlynck & Hostens, 1993; Cabral & Murta, 2002; Vasconcelos *et al.*, 2004). For these species the consumption of fish and in some cases decapod crustaceans, increased as fish got larger. On the contrary, dietary ontogenic changes for *A. imperialis* seemed to reflect niche shift rather than the ability to capture different sized prey. The change from large suprabenthic prey to infaunal and epibenthic organisms is, however, not in agreement with Deniel (1975), who observed that small prey like

mysids decreased as fish size increased. For adult *C. lyra*, besides the change in prey size, a niche shift from a pelagic to a benthic diet was observed, in accordance with other studies (Wheeler, 1978; King *et al.*, 1994).

Dietary ontogenic shifts may be explained by morphological changes that occur with fish growth (e.g. Castro & Hernández-Garcia, 1995). Additionally, within a geographical area, individuals of the same species but of different size-classes can occupy diverse trophic niches, feeding either on the water column or near the bottom to seek for the appropriate prey and/or to reduce predation risk (Werner & Mittelbach, 1981).

In conclusion, the present work highlighted important results concerning the coastal fish assemblage off Aveiro during summer, namely the strategies used by fish to optimize the use of resources. It also contributes to a better understanding of the marine food webs as required by the MSFD and EAF.

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