

Trophic relationships in a Mediterranean deep-sea fish community: partition of food resources, dietary overlap and connections within the benthic boundary layer

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ABSTRACT: Food resource partitioning and some trends in the feeding ecology of 13 species of fishes inhabiting the slope of the Catalan Sea (western Mediterranean) were examined. Specimens were collected from 1987 to 1991, using bottom trawls at depths between 1000 and 2250 m. Prey selection was also examined in relation to data collected in the same area on 2 potential prey compartments for fish, the benthopelagic macrofauna—suprabenthos or hyperbenthos—and the megafaunal decapod crustaceans. Thus, the possible connections with prey availability within the benthic boundary layer (BBL) were also analysed. The size of available food resources was the most important factor responsible for food resource partitioning, both by depth stratum and season. The importance of the variable predator size is also evidenced. Most of the deep-sea demersal fish species inhabiting the Catalano-Balearic slope often consumed a variety of available resources in their diets, mainly comprising suprabenthos, but also infauna or planktonic prey. Thus, the BBL macrofauna constitute an important part of the available food exploited, with the range of the prey consumed increasing for the largest predators. A significant trend to increase dietary H' values within the depth interval where each species attained its maximum abundance was observed. Some (positive) prey selection upon certain prey groups was detected depending on the fish species: sharks, *Alepocephalus rostratus* and *Nettastoma melanurum* preferentially preyed on decapods, siphonophores and pyrosomids; *Polyacanthonotus rissoanus*, macrourids, *Lepidion lepidion* and *Cataetix alleni* preyed upon suprabenthic peracarid crustaceans; and only *Bathypterois mediterraneus* preferentially consumed copepods, the numerically dominant group in the bathyal BBL. Resource partitioning was high among the fish assemblage analysed in relation to the generally low dietary overlap values recorded. Overall, dietary overlap values among fish species decreased with increasing depth.

KEY WORDS: Resource partitioning · Dietary overlap · Interaction prey-predator · Deep sea ecology · Western Mediterranean

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INTRODUCTION

Trophic relationships are fundamental to understanding biological interactions in animal communities. Segregation and competition between species

may be the result of combinations of several niche aspects (distribution, diet, etc.), one of which may possibly be preponderant over the others. In deep sea environments, testable hypotheses have been proposed. Dietary overlap among coexisting species is generally held to be low, even in deep-sea communities in which available food resources are considered

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scarce (Grassle & Sanders 1973, Macpherson 1981, Blaber & Bulman 1987, Gage & Tyler 1991), whereas in deep-sea decapods, the lower diversity of available prey items probably increases dietary overlap (Cartes 1998a).

In their original definition within a community, guilds consist of groups of species that exploit relatively distinct packages of resources (Jaksic 1981). Furthermore, recognition of such guilds, even if the clusters can be objectively defined, does not necessarily imply any functional role within the community dynamics. Even so, the fact remains that this will still impose some structure on competitive interactions within the community as a whole, with members of each guild interacting strongly with each other, but only relatively weakly with members of other clusters (Putman 1994). The resource partitioning between species may be indicative of the degree of organisation of animal communities, and can be related with the concept of competition among species. *A priori*, the importance of competition may be enhanced in deep-sea fish communities due to the (relatively) high environmental stability (Gage & Tyler 1991). Both predation and prey availability are factors which may influence interspecific competition. Predation may act either by lowering demand for resources or removing higher competitors (Caswell 1978, Mittelbach 1986, Putman 1994). In the Mediterranean deep sea, predation is not expected to maintain densities of fish populations under a theoretical threshold to avoid competitive interactions, because of the scarce role of fish as prey in this particular environment (non-existence of an ichthyofagous guild as in shallower waters: see Macpherson & Roel 1987). Similarly, the generally recognised low food availability, particularly in oligotrophic regions such as the deep Mediterranean (Carpine 1970, Thiel 1983, Pérès 1985), may also contribute to enhance competitive exclusion among species.

Studies on both resource partitioning and prey selection in deep-water communities are limited. Data are available for fish in the Atlantic sea (Sedberry & Musick 1978, Mauchline & Gordon 1986, 1991, Mahaut et al. 1990, Bergstad 1991, Crabtree et al. 1991) and in the Tasmanian sea (Blaber & Bulman 1987). In the Mediterranean, these studies correspond to fish from the continental slope (Macpherson 1981) or to deep-water decapod crustaceans (Cartes 1998a,b).

Studies on the deep-sea fish assemblages in the Catalan Sea below a depth of 1000 m and their depth size trends were carried out by Stefanescu et al. (1992b, 1993). Feeding habits were extensively studied by Carrassón et al. (1992, 1997) and Carrassón & Matallanas (1998, 2001, 2002). The need for a more complete description of the community structure and

of the interspecific relationships within that community were the primary motivation for the present work, the second being the possible involvement of the availability of prey in the trophic chains.

This paper primarily concerns interspecific relationships, analysing on a spatial and temporal scale the feeding habits and dietary overlap of fish species in relation to food availability, selection of prey and other parameters of trophic ecology. We further discuss their possible significance in interspecific competition.

MATERIALS AND METHODS

Data from a total of 3189 specimens belonging to 13 species (Table 1) collected between 1000 and 2250 m depth were examined. All material was collected from the continental slope of the Catalan Sea (western Mediterranean) using semi-balloon otter trawls, between 1987 and 1991, as described in previously published papers (Stefanescu et al. 1992a, Cartes et al. 1994a, Sardà et al. 1994).

The specimens were measured to the nearest mm (standard length = SL, total length = TL) and dissected for analysis of stomach contents. The composition of the diet was analysed in 1690 individuals with foreguts containing food (Table 1). Particular aspects on the processing of foregut samples were given previously and descriptions of the diets of most of the species have already been published (Carrassón et al. 1992, 1997, Carrassón & Matallanas 1998, 2001, 2002).

Diets have been expressed as percentage abundance (%N) by prey item for each species, and trophic interactions between species were analysed according to depth interval and season. Although the percentage of the index of relative importance (%IRI) was used in previous studies on dietary description (Carrassón et al. 1992, and references cited therein), here we used %N to compare with densities of prey in the milieu. Samples were not collected in winter; in spring, samples are available for only 2 species. Zonation in fish communities has previously been established on the slope in the Catalan Sea (Stefanescu et al. 1993). According to Stefanescu et al. (1993), 2 depth strata were established (middle slope: 1000 to 1425 m; lower slope: 1425 to 2250 m); moreover, a further division of the lower slope around the 1800 m isobath was made because of the availability of data on benthopelagic macrofauna down to this level.

Prey items were separated into a total of 52 categories (Table 2a). Only prey categories that occurred in 1% or more, in terms of %N of the predator stomachs, qualified for inclusion.

Fish species and their prey items (expressed as %N) were grouped in a data matrix according to depth strata.

tum and season. Factorial correspondence analysis (FCA) (Benzecri 1973) was applied to this data matrix comprising fish species and prey groups. Predator size was included as the illustrative nominal variable in the analysis. FCA ordines predator and prey species simultaneously along a set of ordination axes. Predators with similar scores on these axes have similar diet composition. Prey items with similar scores have a similar pattern of occurrence among the predator diets. Normally, only the first 2 or 3 axes have an ecological meaning. A hierarchical cluster analysis was simultaneously performed because this method served to define predator groups (trophic guilds) better than the

FCA. The SPAD program was used to run FCA and cluster analysis.

The percentage of empty foreguts (V: vacuity coefficient) was calculated for each species at each depth stratum. The trophic diversity of prey calculated in terms of mean %weight of prey items (H' : Shannon index) and the food intensity index (Ki) (Yasuda 1960) calculated using the average of the index of the amount of food eaten per fish, were also determined to disclose any overall depth-related patterns. A non-parametric Kruskal-Wallis test (Sokal & Rohlf 1979) was applied to each set of values (V, H' , Ki) for all 3 depth strata.

Table 1. Fish species examined in the present study. Size, the range of length values: SL = standard length, TL = total length; Nt, total number of specimens analysed; N, number of foreguts with food examined at every depth and season; Depth, intervals of depth analysed: 1 = 1000 to 1425 m specimens, 2 = 1425 to 1800 m, 3 = 1800 to 2250 m; Season: p = spring, s = summer, a = autumn; for *Centroscymnus coelolepis*: i = immature specimens, m = mature specimens

| | Size (mm) | Nt | Everted stomachs | Empty stomachs | Stomachs with food | Code | N | Depth | Season |
|--------------------------------------|--------------|------|---------------------|-------------------|-----------------------|------|-----|-------|--------|
| <i>Alepocephalus rostratus</i> | 95–385 SL | 430 | 0 | 312 | 118 | a1p | 34 | 1 | p |
| | | | | | | a1s | 19 | 1 | s |
| | | | | | | a2s | 51 | 2 | s |
| | | | | | | a3s | 14 | 3 | s |
| <i>Bathypterois mediterraneus</i> | 44–181 SL | 305 | 0 | 23 | 282 | b1s | 94 | 1 | s |
| | | | | | | b2s | 84 | 2 | s |
| | | | | | | b2a | 11 | 2 | a |
| | | | | | | b3s | 93 | 3 | s |
| <i>Nettastoma melanurum</i> | 452–740 TL | 6 | 0 | 0 | 6 | n1a | 6 | 1 | a |
| <i>Polyacanthothonus rissoanus</i> | 110–210 TL | 326 | 0 | 123 | 203 | p1s | 19 | 1 | s |
| | | | | | | p1a | 22 | 1 | a |
| | | | | | | p2s | 64 | 2 | s |
| | | | | | | p2a | 60 | 2 | a |
| | | | | | | p3s | 38 | 3 | s |
| <i>Chalinura mediterranea</i> | 80–340 TL | 191 | 28 | 40 | 123 | m2s | 40 | 2 | s |
| | | | | | | m3s | 83 | 3 | s |
| <i>Coelorhynchus labiatus</i> | 99–216 TL | 43 | 28 | 4 | 11 | cl2s | 11 | 2 | s |
| <i>Coryphaenoides guentheri</i> | 47–217 TL | 626 | 132 | 76 | 418 | r2s | 189 | 2 | s |
| | | | | | | r2a | 10 | 2 | a |
| | | | | | | r3s | 219 | 3 | s |
| <i>Trachyrhynchus trachyrhynchus</i> | 122–430 TL | 149 | 141 | 3 | 5 | t1 | 5 | 1 | |
| <i>Lepidion guentheri</i> | 196–525 SL | 13 | 4 | 3 | 6 | lg3s | 6 | 3 | s |
| <i>Lepidion lepidion</i> | 40–315 SL | 617 | 195 | 99 | 323 | l1s | 214 | 1 | s |
| | | | | | | l2s | 75 | 2 | s |
| | | | | | | l2a | 5 | 2 | a |
| | | | | | | l3s | 29 | 3 | s |
| <i>Cataetyx alleni</i> | 33–128 SL | 358 | 65 | 187 | 106 | c1s | 35 | 1 | s |
| | | | | | | c1a | 24 | 1 | a |
| | | | | | | c2s | 28 | 2 | s |
| | | | | | | c2a | 19 | 2 | a |
| <i>Centroscymnus coelolepis</i> | 194–614 TL | 86 | 0 | 32 | 54 | o3si | 44 | 3 | s |
| | | | | | | o3sm | 10 | 3 | s |
| <i>Galeus melastomus</i> | 102–610 TL | 39 | 0 | 4 | 35 | g1p | 6 | 1 | p |
| | | | | | | g1s | 22 | 1 | s |
| | | | | | | g1a | 7 | 1 | a |
| Total | | 3189 | 593 | 906 | 1690 | | | | |

Table 2. (a) Prey groups used in the data matrices for the study of the trophic interactions between species (FCA). (b) Benthopelagic taxa used for the study of prey selectivity

| Code | Prey items | Code | Prey items |
|------------|-------------------------------|------|-----------------------------------|
| (a) | | | |
| FO | FORAMINIFERA | Ja | <i>Janirella</i> sp. |
| SI | SIPHONOPHORA | TA | TANAIDACEA |
| GA | GASTROPODA | Cu | Cumacea unid. |
| BI | BIVALVIA | Cy | <i>Cyclaspis longicaudata</i> |
| CE | CEPHALOPODA | Pl | <i>Platysympus typicus</i> |
| Po | Polychaeta unid. | Ma | <i>Makrokyllindrus</i> sp. |
| Af | Aphroditomorpha | My | Mysidacea unid. |
| Eu | Eunicidae | Bo | <i>Boreomysis arctica</i> |
| Hy | <i>Hyalinoecia</i> sp. | Pa | <i>Parapseudomma</i> sp. |
| Fl | Flabelligeridae | EP | EUPHAUSIACEA |
| Gl | <i>Glycera</i> sp. | De | Dec. unid. |
| Pe | Pectinoridae | Dn | Dec. Nat. unid. |
| CC | Cop. Calanoida | Pm | <i>Pasiphaea multidentata</i> |
| Ag | Amph. Gam. unid. | Ae | <i>AcanthePHYra eximia</i> |
| Ly | Lysianassidae | Ap | <i>AcanthePHYra pelagica</i> |
| Br | <i>Bruzelia typica</i> | Pn | <i>Pontophilus norvegicus</i> |
| Ps | <i>Pseudotiron bouvieri</i> | Dm | Dec. Mac. Rept. unid. |
| Rh | <i>Rhachotropis</i> spp. | Cm | <i>Calocaris macandreae</i> |
| El | <i>Eusirus longipes</i> | DA | DEC.ANOMURA |
| Oe | Oedicerotidae | Py | <i>Pyrosoma atlanticum</i> |
| AH | AMPH. HYPERIIDEA | Os | Osteichthyes unid. |
| Is | Isopoda unid. | Ba | <i>Bathypterois mediterraneus</i> |
| Gn | <i>Gnathia</i> sp. | No | <i>Notolepis rissoi</i> |
| Mu | <i>Munnopsurus atlanticus</i> | Mm | <i>Mora moro</i> |
| Ey | Eurycopidae unid. | Mo | Moridae |
| Il | <i>Ilyarachna</i> sp. | Ch | <i>Chauliodus sloani</i> |
| (b) | | | |
| sip | SIPHONOPHORA | jan | <i>Janirella</i> sp. |
| pol | POLYCHAETA | tan | TANAIDACEA |
| coc | Copepoda Calanoida | cyc | <i>Cyclaspis longicaudata</i> |
| lys | Lysianassidae | pla | <i>Platysympus typicus</i> |
| bru | <i>Bruzelia typica</i> | bor | <i>Boreomysis arctica</i> |
| pse | <i>Pseudotiron bouvieri</i> | par | <i>Parapseudomma</i> sp. |
| rha | <i>Rhachotropis</i> spp. | eup | EUPHAUSIACEA |
| eus | <i>Eusirus longipes</i> | pas | <i>Pasiphaea multidentata</i> |
| oed | Oedicerotidae | ace | <i>AcanthePHYra eximia</i> |
| amh | AMPH. HYPERIIDEA | acp | <i>AcanthePHYra pelagica</i> |
| gna | <i>Gnathia</i> sp. | pon | <i>Pontophilus norvegicus</i> |
| mun | <i>Munnopsurus atlanticus</i> | cha | CHAETOGNATHA |
| eur | Eurycopidae unid. | pyr | <i>Pyrosoma atlanticum</i> |
| ily | <i>Ilyarachna</i> sp. | cyc | <i>Cylothone braueri</i> |

Data on benthopelagic macrofauna, the so-called suprabenthos or hyperbenthos (Mees & Jones 1997), were collected in the Benthic Boundary Layer (BBL) in the same area between 1991 and 1992, down to a depth of 1800 m. The suprabenthic Macer-GIROQ sledge was used. This gear collects the fauna distributed between about 0.1 to 1.5 m above the bottom (Cartes et al 1994b); benthos (e.g. non-natatory infauna) was not sampled by this method. Therefore, for comparison between prey groups and available trophic resources, only the benthopelagic organisms have been considered in the diet of fish. Details on gears and sampling procedures, depths and seasons,

as well as descriptions of the composition and abundance of the organisms of the BBL, were given previously (Cartes et al. 1994b, Cartes & Sorbe 1995, 1997, 1999). Data on the abundance of decapods, captured with the same OTSB-14 used for fish, were also available from the same sampling cruises (Cartes & Sardà 1992).

Prey selectivity was determined considering both the relative abundance of suprabenthos (BBL) and decapod crustaceans. Prey were grouped into the same taxa (Table 2b) that were established for the BBL fauna, with the objective of establishing a subsequent comparison in terms of food selectivity between prey groups and available prey in the environment. For the BBL, the analysis was carried out for each of the 2 bathymetric levels sampled (1000 to 1425 and 1425 to 1800 m) and the 2 seasons (summer and autumn). For the decapods, it was carried out for the 3 bathymetric levels sampled (1000 to 1425, 1425 to 1800 and 1800 to 2250 m) and the 2 seasons (summer and autumn); 11 specimens of *Centroscymnus coelolepis* captured at 1800 m (5 in summer and 6 in autumn) were included in the 1425 to 1800 m depth interval.

A linear index of food selection (Strauss 1979) was used to obtain food selectivity for each prey:

$$L = r_i - p_i$$

where r_i and p_i are the relative proportions of a prey item in the diet and habitat, respectively. This index ranges from -1 to +1, with positive values indicating preference and negative values avoidance or inaccessibility, while 0 (or close to 0) is the expected value for random feeding. This

index, like the most commonly used Ivlev index (Ivlev 1961), does not take into account the different digestion times for each type of prey.

In addition to the calculation of L for each prey of suprabenthos, we also proposed a general index of prey selectivity $GS = \sum L_i$. This is made up of the sum of the selectivity indexes of all the prey consumed by each predator. Subsequent comparisons of GS among predators provide us with a global view of how fish are distributed in the water column close to the sea bed (the first 1.5 m sampled by the sledge) as a function of the prey exploited (being considered as more or less benthopelagic).

Affinities between fish diets were calculated using the quantitative Schoener index (Schoener 1974). A 1-way ANOVA and post hoc Scheffé comparisons were used to compare dietary overlap among fish species, within each depth stratum considered.

RESULTS

FCA analysis

At the 1000 to 1425 m depth stratum, the first 3 factors of FCA accumulated 50.78% of the total variance. Factors 1 and 2 (representing the first and second axes) explained 19.75 and 16.20% of variance, respectively (Fig. 1). Large (cephalopods, osteichthyes) and small prey (calanoid copepods, isopods) had positive and negative values, respectively, along the first axis. The pelagic *Pyrosoma atlanticum* had a highly positive value and the Decapoda Anomura a highly negative value along the second axis.

The following groups could be defined following a cluster analysis: Class 1: *Alepocephalus rostratus* of spring (alp) clearly separated into the positive part of Axis 2 due to the consumption of *Pyrosoma atlanticum* and gastropods; Class 2: *Alepocephalus rostratus*, *Lepidion lepidion* and *Bathypterois mediterraneus* of summer, and *Trachyrhynchus trachyrhynchus* (a1s, l1s, b1s, t1) separated into the negative part of Axis 1 and slightly positive into the Axis 2, characterised by the preferential consumption of calanoid copepods and *Boreomysis arctica*; Class 3: *Cataetyx alleni* and *Polyacanthonotus rissoanus* of summer and autumn (c1a, c1s, p1a, p1s) separated into the negative parts of Axes 1 and 2, consuming *Parapseudomma* sp., isopods and polychaetes; Class

4: *Nettastoma melanurum* of autumn (n1a) separated into the negative part of Axis 2 and the positive part of Axis 1, consuming prey such as Decapoda Anomura and *Acanthephyra eximia*; Class 5: *Galeus melastomus* of all seasons (g1p, g1s, g1a) was defined perfectly by Axis 1, due to the consumption of cephalopods and *Pasiphaea multidentata*, among others.

At the lower slope between 1425 and 2250 m, the first 3 factors of FCA accumulated 52.05% of the total variance (Fig. 2). As in the preceding case, Factor 1 was characterised by large prey (mainly of planktonic origin or swimming prey) in the positive part of the plot (e.g. cephalopods: 38.2% of total variance in the axis and osteichthyes: 10.6%), while small preys (calanoid copepods) were found in the negative part. Prey which mainly contributed to the inertia explained by Axis 2 were gastropods (17.9%), siphonophores (9.7%) and *Pyrosoma atlanticum* (8.2%) in the negative part and cephalopods (15.6%) in the positive part (Fig. 2a). Axis 3 is clearly characterised by calanoid copepods (Fig. 2b), with a contribution of 46.8% to the total inertia. The illustrative variable predator size clearly shows how Axis 1 separates the large size predators into the positive part, while the rest (medium and small size) are separated into the negative part.

Six classes were defined: Class 1: *Alepocephalus rostratus* (a2s, a3s) is perfectly characterised by Axis 2 in the negative part due to the importance of gastropods, siphonophores and *Pyrosoma atlanticum* in its diet. Class 2: *Lepidion guentheri* (lg3s) is perfectly separated in the positive part of Axis 1 due mainly to the consumption of *Acanthephyra eximia* and also of *Bathypterois mediterraneus*. Class 3: *Centroscymnus coelolepis* (o3si, o3sm) is characterised in the positive part of Axes 1 and 2 above all by the preferential con-

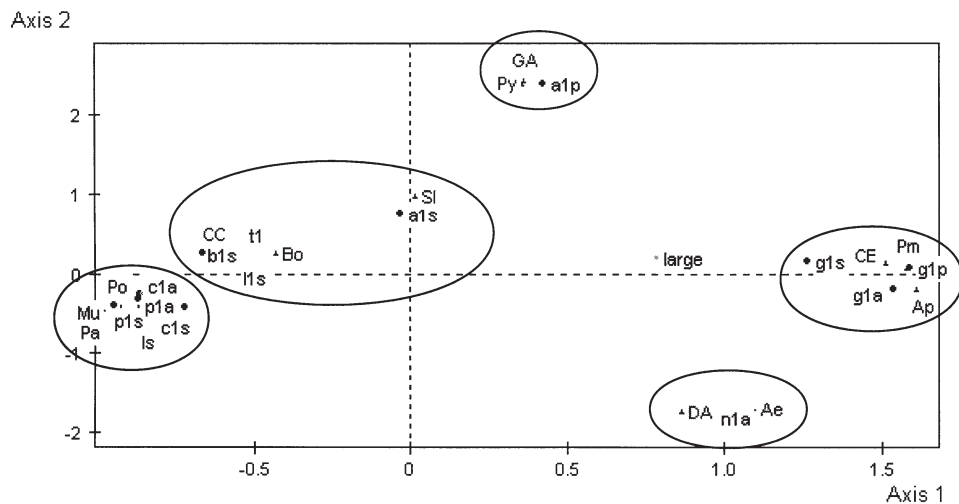


Fig. 1. Factorial correspondence analysis for the fish species and their prey items on the middle slope area (1000 to 1425 m) in the season studied. See Tables 1 & 2 for an explanation of the codes used

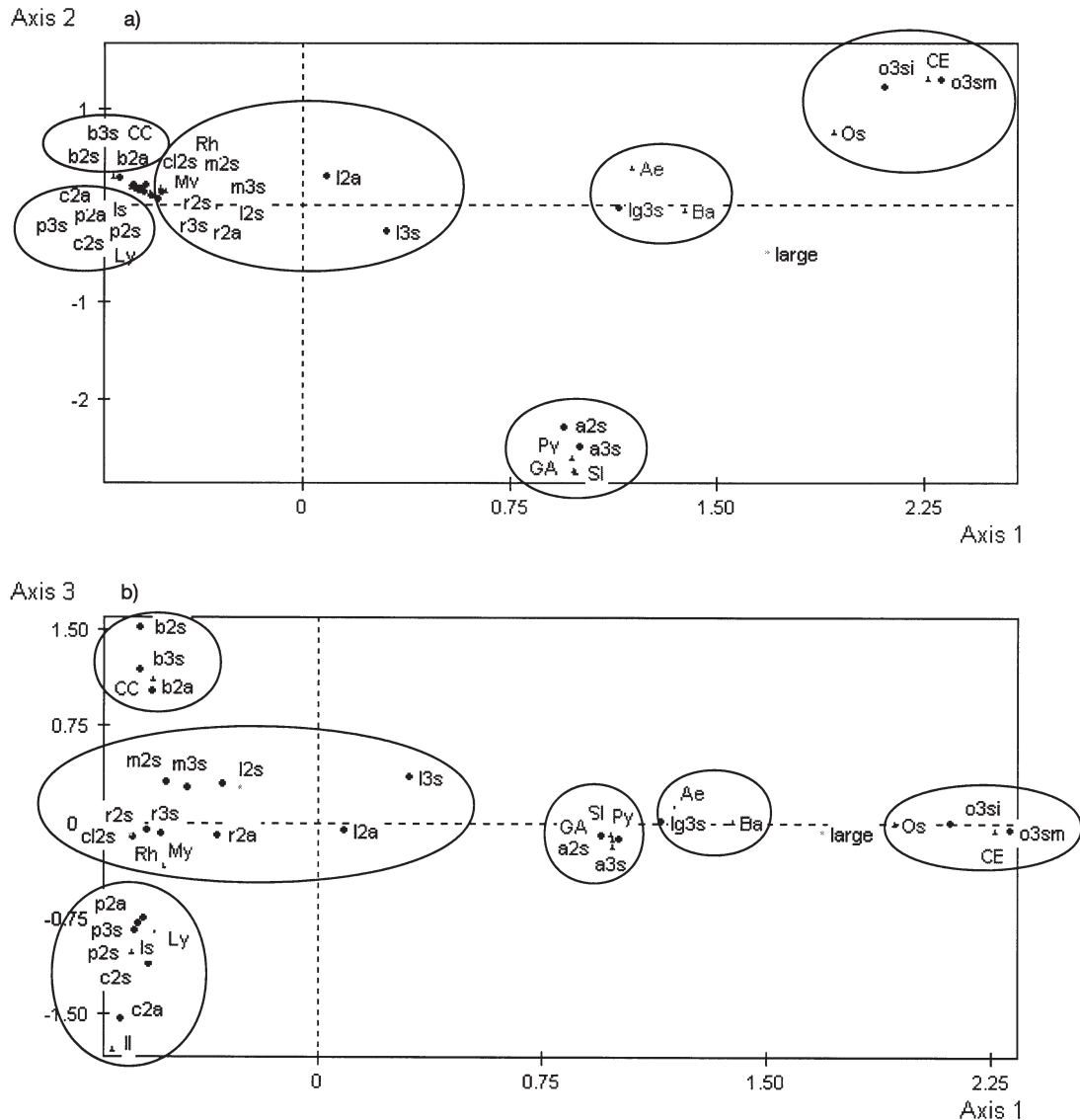


Fig. 2. Factorial correspondence analysis for the fish species and their prey items in the lower slope area (1425 to 2250 m) in the season studied: (a) along the first 2 ordination axes; (b) along the first and third ordination axes. See Tables 1 & 2 for an explanation of the codes used

sumption of cephalopods and osteichthyes. Class 4: *Chalinura mediterranea*, *Lepidion lepidion*, *Coelorhynchus labiatus* and *Coryphaenoides guentheri* (m2s, m3s, l2s, l2a, l3s, cl2s, r2s, r2a, r3s) are characterised in the negative part of Axis 1 by prey such as mysids and *Rhachotropis* spp. It is the class that is least characterised by the plot. Within the class, *C. guentheri* (r2s, r2a, r3s) is seen to be separated from the other 3 predators. Class 5: *Cataetyx alleni* and *Polyacanthonotus rissouanus* (c2s, c2a, p2s, p2a, p3s) are well characterised by the negative part of Axes 1 and 3, this being determined by the prey isopods *Ilyarachna* sp. and *Lyssianasidae*. Class 6: *Bathypterois mediterraneus* (b2s, b2a, b3s) was perfectly characterised in the neg-

ative part of Axis 1 and the positive part of Axis 3 by the preferential consumption of calanoid copepods.

Trends in H' , V and K_i

No general significant bathymetric trends in H' , V and K_i (Fig. 3) were found ($p > 0.10$, non-parametric Kruskal-Wallis test). More specific trends in H' , V and K_i are, however, interesting to note: (1) higher significant H' values (χ^2 , $p < 0.05$) were detected at the centre of gravity (c. o. g.) of the bathymetric distribution of species (Fig. 3). K_i do not have significant differences in the c. o. g. A lesser variation in V with depth (Fig. 3)

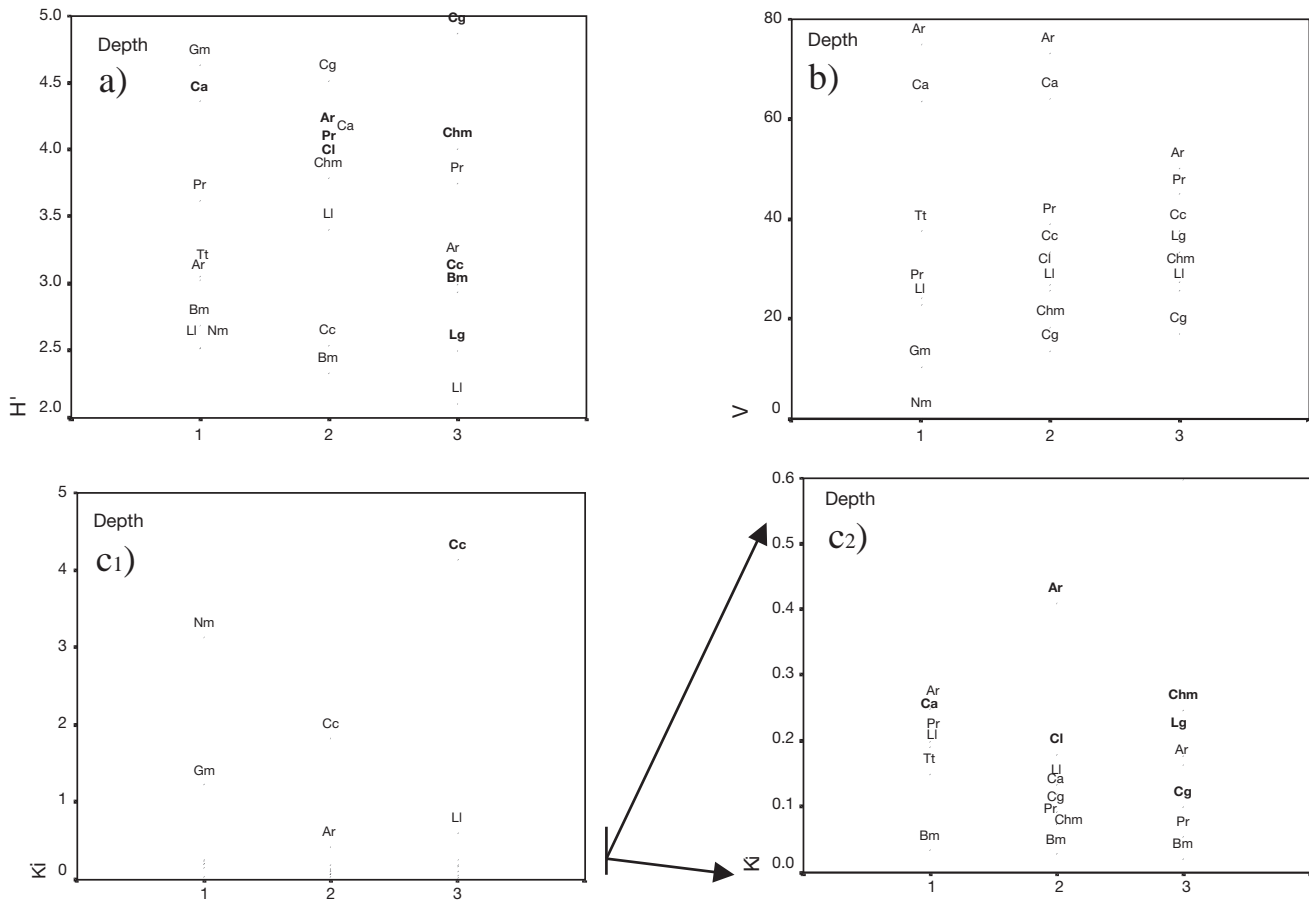


Fig. 3. (a) Trophic diversity (H'), (b) Vacuity coefficient (V), and (c₁, c₂) food intensity index (Ki) for all species considered by depth: 1 = 1000 to 1425 m, 2 = 1425 to 1800 m, 3 = 1800 to 2250 m. (c₂) The first 0.6 Ki units in detail. In bold when the highest H' and Ki values were detected at the centre of gravity of the bathymetric distribution of species. See Table 3 for significance of species codes

was observed (test for homogeneity of variances of Levene, $p < 0.05$); and (2) most species present at more than 1 depth stratum had the highest V at their deepest habitat (χ^2 , $p < 0.05$).

Prey selectivity

Although results on prey selectivity should be interpreted with caution, the following conclusions were reached. (1) Negative values of L predominated over positive (which may imply that prey selection by fish is generally low); and (2) absolute positive values were lower than negative ones (Mann-Whitney test, $p < 0.001$) (Tables 3 & 4). This presumable bias in the L results may be a consequence of sampler bias in different groups at least at 2 different levels: (1) both the Macer-GIROQ sledge and the OTSB-14 basically collected benthopelagic animals distributed between 0 and 2 m above the bottom (in other words, infauna and

macroplankton are not well sampled with the sledge); and (2) it is likely that the size spectra of the well-sampled taxa do not coincide with the size spectra exploited by our fish, copepods probably being a clear example of this latter limitation. As a consequence, the value of the results obtained on prey selectivity basically make sense when we compare results between species or within a gradient (e.g. depth or season) and not in absolute terms of preferential prey exploitation by predators.

Despite these considerations, some differential preferences for certain prey groups were found. Thus, sharks, *Alepocephalus rostratus* and *Nettastoma melanurum* preyed preferentially on decapods, siphonophores and pyrosomids (in comparison to other fish); *Polyacanthonotus rissoanus*, macrourids, *Lepidion lepidion* and *Cataetyx alleni* preyed upon peracarid crustaceans (gammaridean amphipods, isopods, cumaceans and mysids); and only *Bathypterois mediterraneus* preferentially consumed copepods, despite the

Table 3. Food selectivity of fish on benthopelagic prey (Strauss index L): comparison between relative proportions of prey items in the gut and the environment (captured by MaceR-GIROQ sledge) respectively, for (a) 1000 to 1425 m and (b) 1425 to 1800 m depth. Fish: Cc, *Centroscymnus coelolepis*; Gm, *Galeus melastomus*; Ar, *Alepocephalus rostratus*; Bm, *Bathypterois mediterraneus*; Nm, *Nettastoma melanurum*; Pr, *Polycanthonothus tissoanus*; Chm, *Chalinura mediterranea*; Cl, *Coelorthynchus labiatus*; Cg, *Coryphaenoides guentheri*; Tt, *Trachyrhynchus trachyrhynchus*; Ll, *Lepidion lepidion*; Ca, *Cataetx alleni*. GS = $\sum L_i$. * = less than ± 0.001

| Prey items | Summer | | | | | Autumn | | | | | | |
|--------------------------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| | Gm | Ar | Bm | Pr | Ll | Ca | Gm | Nm | Pr | Tt | Ca | |
| (a) 1000–1425 m | | | | | | | | | | | | |
| Siphonophora | 0.016 | 0.316 | -0.002 | -0.002 | 0.021 | -0.002 | -0.002 | -0.002 | -0.002 | 0.023 | -0.002 | -0.002 |
| Polychaeta | * | * | 0.020 | 0.080 | 0.073 | 0.071 | -0.008 | -0.008 | 0.154 | 0.090 | 0.166 | 0.166 |
| Copepoda Calanoida | -0.926 | -0.813 | -0.170 | -0.926 | -0.589 | -0.873 | -0.571 | -0.571 | -0.571 | -0.206 | -0.571 | -0.571 |
| Lysianassidae | -0.001 | 0.045 | 0.028 | -0.001 | 0.035 | 0.035 | -0.006 | -0.006 | 0.082 | 0.091 | 0.081 | 0.081 |
| <i>Bruzelia typica</i> | * | * | * | * | 0.003 | * | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 |
| <i>Pseudotiron bouvieri</i> | * | * | * | 0.011 | * | 0.018 | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 |
| <i>Rhachotropis</i> spp. | -0.007 | -0.007 | 0.002 | -0.007 | 0.014 | 0.082 | -0.077 | -0.077 | 0.011 | -0.077 | -0.034 | -0.034 |
| <i>Eusirus longipes</i> | * | * | * | * | 0.001 | 0.035 | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 | 0.085 |
| Oedicerotidae | -0.008 | -0.008 | -0.006 | -0.008 | 0.002 | 0.010 | -0.047 | -0.047 | -0.047 | -0.047 | -0.003 | -0.003 |
| Amph. Hyperiidea | 0.108 | -0.001 | * | -0.001 | 0.013 | -0.00 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 |
| <i>Gnathia</i> sp. | * | * | 0.003 | 0.011 | 0.006 | * | -0.001 | -0.001 | 0.014 | 0.023 | 0.086 | 0.086 |
| <i>Munnopsurus atlanticus</i> | -0.001 | -0.001 | -0.001 | 0.194 | -0.001 | -0.001 | -0.031 | -0.031 | 0.014 | -0.031 | -0.031 | -0.031 |
| Eurycopidae unident. | * | * | * | 0.023 | 0.007 | 0.125 | -0.017 | -0.017 | -0.017 | -0.017 | 0.026 | 0.026 |
| <i>Ilyarachna</i> sp. | -0.002 | -0.002 | * | 0.067 | 0.003 | 0.034 | -0.007 | -0.007 | -0.007 | -0.007 | 0.080 | 0.080 |
| <i>Janirella</i> sp. | * | * | * | 0.057 | 0.002 | * | -0.001 | -0.001 | 0.014 | -0.001 | 0.042 | 0.042 |
| Tanaidacea | * | * | 0.003 | * | 0.003 | 0.018 | * | * | * | * | * | * |
| <i>Cyclaspis longicaudata</i> | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 | -0.021 | -0.021 | -0.021 | -0.021 | -0.021 | -0.021 |
| <i>Platysympus typicus</i> | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.003 | -0.003 | -0.003 | -0.003 | -0.003 | -0.003 |
| <i>Boreomyis arctica</i> | 0.010 | -0.008 | 0.024 | -0.008 | 0.034 | -0.008 | -0.058 | -0.058 | -0.058 | 0.040 | -0.058 | -0.058 |
| <i>Parapseudomma</i> sp. | * | * | 0.001 | 0.230 | 0.014 | 0.071 | -0.002 | -0.002 | 0.145 | -0.002 | -0.002 | -0.002 |
| Euphausiacea | 0.052 | 0.043 | -0.002 | -0.002 | 0.003 | -0.002 | 0.056 | -0.003 | -0.003 | -0.003 | -0.003 | -0.003 |
| <i>Paspiphaea multidentata</i> | 0.091 | * | * | * | 0.002 | * | 0.059 | * | * | * | * | * |
| <i>Acanthephyra eximia</i> | 0.018 | * | * | * | 0.002 | * | 0.029 | 0.182 | * | * | * | * |
| <i>Acanthephyra pelagica</i> | 0.018 | * | * | * | * | * | 0.294 | * | * | * | * | * |
| <i>Pontophilus norvegicus</i> | * | * | * | * | 0.003 | 0.018 | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 |
| <i>Chaetognatha</i> | -0.003 | -0.003 | -0.003 | -0.003 | -0.002 | -0.003 | -0.010 | -0.010 | -0.010 | -0.010 | -0.010 | -0.010 |
| <i>Pyrosoma atlanticum</i> | 0.018 | 0.023 | * | * | 0.006 | * | * | * | * | 0.049 | * | * |
| <i>Cyclothone braueri</i> | -0.001 | 0.022 | -0.001 | -0.001 | -0.001 | -0.001 | -0.005 | -0.005 | -0.005 | -0.005 | -0.005 | -0.005 |
| GS | -0.622 | -0.400 | -0.109 | -0.290 | -0.352 | -0.378 | -0.438 | -0.697 | -0.320 | -0.122 | -0.183 | -0.183 |

Table 3 (continued)

| Prey items | Summer | | | | | | Autumn | | | | | | | | |
|-------------------------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| | Cc | Ar | Bm | Pr | Chm | Cl | Cg | Li | Ca | Cc | Bm | Pr | Cg | Li | Ca |
| (b) 1425–1800 m | | | | | | | | | | | | | | | |
| Siphonophora | -0.005 | 0.067 | -0.005 | -0.005 | -0.005 | -0.005 | -0.005 | 0.006 | -0.005 | -0.003 | -0.003 | -0.003 | -0.003 | -0.003 | -0.003 |
| Polychaeta | -0.002 | -0.002 | * | 0.079 | 0.105 | 0.092 | 0.073 | 0.021 | 0.146 | -0.005 | 0.014 | 0.083 | 0.092 | -0.005 | 0.112 |
| Copepoda Calanoida | -0.688 | -0.658 | 0.216 | -0.670 | -0.387 | -0.515 | -0.594 | -0.481 | -0.677 | -0.538 | -0.067 | -0.532 | -0.465 | -0.384 | -0.538 |
| Lysianassidae | * | 0.020 | 0.002 | 0.074 | 0.018 | 0.053 | 0.007 | 0.015 | 0.193 | * | 0.019 | 0.145 | 0.024 | * | * |
| <i>Bruzelia typica</i> | -0.004 | -0.004 | -0.003 | -0.004 | -0.004 | 0.009 | 0.015 | * | 0.007 | -0.003 | -0.003 | 0.003 | 0.046 | -0.003 | -0.003 |
| <i>Pseudotiron bouvieri</i> | * | * | * | 0.037 | 0.012 | * | 0.122 | 0.003 | 0.034 | -0.009 | -0.009 | 0.022 | 0.064 | -0.009 | -0.009 |
| <i>Rhachotropis</i> spp. | -0.001 | -0.001 | -0.001 | 0.073 | 0.087 | 0.105 | 0.038 | 0.032 | -0.001 | -0.053 | -0.053 | 0.042 | -0.004 | 0.024 | 0.006 |
| <i>Eusirus longipes</i> | * | * | * | 0.006 | * | 0.013 | 0.002 | * | * | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 |
| Oedicerotidae | -0.002 | -0.002 | -0.002 | -0.002 | 0.004 | 0.038 | 0.008 | 0.013 | 0.032 | -0.074 | -0.074 | -0.061 | -0.074 | -0.074 | -0.074 |
| Amph. Hyperidea | -0.002 | -0.002 | -0.002 | -0.002 | -0.002 | -0.001 | -0.001 | 0.020 | -0.002 | -0.004 | -0.004 | 0.006 | -0.004 | 0.073 | 0.055 |
| <i>Gnathia</i> sp. | -0.001 | -0.001 | -0.001 | 0.030 | -0.001 | -0.001 | 0.002 | 0.003 | 0.067 | -0.009 | -0.009 | 0.004 | -0.009 | -0.009 | -0.009 |
| <i>Munropsurus atlanticus</i> | -0.002 | -0.002 | -0.002 | 0.011 | 0.004 | -0.002 | 0.001 | -0.002 | 0.010 | -0.004 | -0.004 | -0.004 | -0.004 | -0.004 | -0.004 |
| Eurycopidae unident. | * | * | * | 0.049 | * | * | 0.040 | 0.026 | 0.057 | -0.012 | -0.012 | -0.012 | -0.012 | -0.012 | 0.164 |
| <i>Ilyarachna</i> sp. | -0.001 | -0.001 | -0.001 | 0.018 | -0.001 | 0.012 | -0.001 | -0.001 | 0.079 | -0.012 | -0.012 | -0.012 | -0.012 | -0.012 | 0.164 |
| <i>Janirella</i> sp. | * | * | * | 0.148 | 0.018 | * | 0.019 | * | * | * | * | 0.019 | 0.024 | * | * |
| Tanaidacea | * | * | 0.006 | * | 0.012 | 0.026 | 0.028 | 0.003 | * | * | * | * | 0.073 | * | * |
| <i>Cyclaspis longicaudata</i> | -0.016 | -0.016 | -0.015 | -0.016 | -0.016 | -0.016 | 0.011 | -0.016 | -0.016 | -0.044 | -0.044 | -0.044 | 0.029 | -0.044 | -0.044 |
| <i>Platysympus typicus</i> | -0.026 | -0.026 | -0.026 | -0.026 | -0.026 | -0.026 | -0.013 | -0.026 | -0.026 | -0.016 | -0.016 | -0.016 | -0.016 | -0.016 | -0.016 |
| <i>Boreomyia arctica</i> | -0.075 | -0.075 | -0.064 | -0.075 | 0.020 | -0.075 | -0.073 | 0.136 | -0.075 | -0.051 | 0.025 | -0.051 | 0.023 | -0.051 | -0.051 |
| <i>Parapseudomma</i> sp. | * | * | * | 0.049 | 0.006 | 0.080 | 0.020 | 0.011 | 0.023 | -0.002 | -0.002 | 0.011 | -0.002 | -0.002 | -0.002 |
| Euphausiacea | -0.001 | 0.019 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.008 | -0.008 | -0.008 | -0.008 | -0.008 | -0.008 |
| <i>Pasiphaea multidentata</i> | * | 0.031 | * | * | * | * | 0.001 | * | * | * | * | * | * | * | * |
| <i>Acanthephyra eximia</i> | -0.002 | -0.002 | -0.001 | -0.002 | -0.002 | -0.002 | -0.002 | 0.009 | -0.002 | 0.141 | -0.002 | -0.002 | -0.002 | 0.075 | -0.002 |
| <i>Acanthephyra pelagica</i> | 0.167 | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Pontophilus norvegicus</i> | -0.001 | -0.001 | -0.001 | -0.001 | 0.010 | -0.001 | 0.003 | 0.013 | -0.001 | * | * | * | * | * | 0.117 |
| <i>Chaetognatha</i> | -0.005 | -0.005 | -0.005 | -0.005 | -0.005 | -0.005 | -0.005 | -0.005 | -0.005 | -0.006 | -0.006 | -0.006 | -0.006 | -0.006 | -0.006 |
| <i>Pyrosoma atlanticum</i> | * | 0.082 | * | * | * | * | * | 0.004 | * | * | * | * | * | * | * |
| <i>Cyclothone braueri</i> | * | * | * | * | * | * | * | * | * | -0.006 | -0.006 | -0.006 | -0.006 | -0.006 | -0.006 |
| GS | -0.668 | -0.580 | 0.097 | -0.236 | -0.155 | -0.222 | -0.307 | -0.217 | -0.165 | -0.707 | -0.190 | -0.404 | -0.240 | -0.466 | -0.321 |

Table 4. Food selectivity of fish on decapod prey (Strauss index L). The sampling method used was the OTSB-14 trawl. Fish: Cc, *Centroscymnus coelolepis*; Gm, *Galeus melastomus*; Nm, *Nettastoma melanurum*; Pr, *Polyacanthonotus rissoanus*; Chm, *Chalinura mediterranea*; Cg, *Coryphaenoides guentheri*; Tt, *Trachyrhynchus trachyrhynchus*; Lg, *Lepidion guentheri*; Ll, *Lepidion lepidion*; Ca, *Cataetyx alleni*. * = prey that does not exist in the environment at this depth

| Prey items | 1000–1425 m | | | | | | | | | | 1425–1800 m | | | | | 1800–2250 m | | | | | | | | | | | | |
|-------------------------------|-------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|-------------|--------|--------|--------|--------|-------------|--------|--------|--------|--------|--------|----|----|-----|----|----|--|--|
| | Summer | | | | | Autumn | | | | | Summer | | | | | Autumn | | | | | | | | | | | | |
| | Gm | Ll | Ca | Gm | Nm | Tt | Ca | Cc | Chm | Cg | Ll | Ca | Ca | Cc | Ll | Ca | Cc | Chm | Cg | Ll | Ca | Cc | Pr | Chm | Cg | Ll | | |
| Dec. Natantia | -0.311 | -0.555 | -0.548 | -0.201 | -0.307 | -0.555 | -0.579 | -0.436 | -0.591 | -0.597 | -0.573 | -0.602 | -0.403 | -0.469 | -0.428 | -0.418 | -0.631 | -0.632 | -0.643 | -0.313 | -0.468 | | | | | | | |
| Sergestidae | 0.042 | -0.009 | -0.012 | 0.012 | -0.015 | 0.010 | -0.015 | -0.011 | -0.011 | -0.007 | -0.011 | -0.011 | -0.012 | -0.012 | -0.012 | -0.009 | -0.009 | -0.009 | -0.009 | -0.009 | -0.009 | | | | | | | |
| <i>Sergestes arcticus</i> | -0.003 | -0.001 | -0.003 | -0.010 | -0.010 | -0.010 | -0.010 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.002 | -0.002 | -0.002 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | | | | | | | |
| <i>Sergia robusta</i> | 0.045 | -0.009 | -0.009 | -0.005 | -0.005 | -0.005 | -0.005 | -0.010 | -0.010 | -0.010 | -0.010 | -0.010 | -0.009 | -0.009 | -0.009 | -0.008 | -0.008 | -0.008 | -0.008 | -0.008 | -0.008 | | | | | | | |
| <i>Acanthephyra eximia</i> | -0.077 | -0.093 | -0.095 | -0.012 | 0.143 | -0.039 | -0.039 | -0.356 | -0.356 | -0.356 | -0.345 | -0.356 | -0.088 | -0.154 | -0.231 | -0.260 | -0.435 | -0.426 | -0.435 | -0.213 | -0.298 | | | | | | | |
| <i>Acanthephyra pelagica</i> | 0.014 | -0.005 | -0.005 | 0.265 | -0.006 | -0.006 | -0.006 | 0.160 | -0.007 | -0.007 | -0.004 | -0.004 | -0.014 | -0.014 | -0.014 | 0.042 | -0.011 | -0.011 | -0.011 | -0.011 | -0.011 | | | | | | | |
| <i>Pasiphaea multidentata</i> | 0.082 | -0.007 | -0.009 | 0.050 | -0.005 | -0.005 | -0.005 | -0.004 | -0.004 | -0.003 | -0.004 | -0.004 | -0.006 | -0.006 | -0.006 | -0.003 | -0.003 | -0.003 | -0.003 | -0.003 | -0.003 | | | | | | | |
| <i>Pontophilus norvegicus</i> | -0.141 | -0.138 | -0.123 | -0.189 | -0.189 | -0.189 | -0.189 | -0.105 | -0.093 | -0.101 | -0.090 | -0.105 | -0.135 | -0.135 | -0.017 | -0.009 | 0.006 | -0.009 | -0.006 | -0.009 | 0.005 | | | | | | | |
| Dec. Reptantia | -0.380 | -0.394 | -0.310 | -0.360 | 0.068 | -0.338 | -0.343 | -0.398 | -0.380 | -0.390 | -0.383 | -0.364 | -0.454 | -0.454 | -0.337 | -0.354 | -0.354 | -0.352 | -0.354 | -0.354 | -0.341 | | | | | | | |
| <i>Calocaris macandreae</i> | -0.007 | 0.009 | 0.064 | -0.059 | -0.059 | -0.035 | -0.059 | -0.002 | -0.002 | 0.009 | -0.002 | -0.002 | -0.007 | -0.007 | -0.007 | * | * | * | * | * | * | | | | | | | |
| Polychelidae | -0.048 | -0.048 | -0.048 | -0.052 | -0.052 | -0.052 | -0.198 | -0.198 | -0.198 | -0.198 | -0.198 | -0.198 | -0.134 | -0.134 | -0.134 | -0.305 | -0.305 | -0.305 | -0.305 | -0.305 | -0.291 | | | | | | | |
| <i>Munida tenuimana</i> | -0.320 | -0.335 | -0.338 | -0.306 | 0.057 | -0.306 | -0.306 | -0.198 | -0.180 | -0.191 | -0.198 | -0.198 | -0.318 | -0.318 | -0.318 | -0.049 | -0.049 | -0.049 | -0.049 | -0.049 | -0.049 | | | | | | | |
| <i>Geryon longipes</i> | -0.022 | -0.041 | -0.041 | -0.025 | -0.025 | -0.025 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.001 | -0.002 | -0.002 | -0.002 | * | * | * | * | * | * | | | | | | | |

fact that the latter are the numerically dominant group in the bathyal BBL (Table 3). Of these results, the preference for peracarids is probably the most realistic because this is most likely to be the best sampled taxa using suprabenthic sledges.

Some prey also seemed to be more abundant in stomach contents than in the environment. This was the case of Lyssianasidae, a preferential prey among all fish excluding only *Nettastoma melanurum* (maximum L of 0.193 by *Cataetyx alleni* in summer), *Pseudotiron bouvieri*, a preferential prey in summer (maximum L of 0.122 by *Coryphaenoides guentheri*), and isopods, preferred by *Polyacanthonotus rissoanus* and *C. alleni* (L of 0.194) etc. This confirms that peracarids are less biased than other taxa using suprabenthic sledges.

Other comparative trends can also be evidenced. Thus, siphonophores *Platysympus typicus* and *Acanthephyra eximia* were less selected as the depth increased (Table 3), while selection of *Rhachotropis* spp. increased (Mann-Whitney tests, $p < 0.05$). By season, higher L values were generally recorded in summer than in autumn for most peracarids (e.g. for *Pseudotiron bouvieri*, *Rhachotropis* spp., *Eusirus longipes*, Oedicerotidae, Eurycopidae, *Munnupsurus atlanticus*, *Ilyarachna* sp., *Cyclaspis longicaudata* and *Parapseudomma* sp.), while some prey had an inverse trend (e.g. *Acanthephyra eximia*) (Mann-Whitney tests, $p < 0.05$). Preference for gelatinous plankton was detected in summer by *Alepocephalus rostratus*. The maximum negative values of GS were reported for sharks.

Concerning decapods, L was also negative in many cases and positive (although low) values of L were reported for large predators (sharks). Some prey species, such as *Acanthephyra eximia*, were more preferred in autumn by *Galeus melastomus* and *Centroscymnus coelolepis*, both in relation to the sledge (Table 3) and the OTSB (Table 4) results.

Dietary overlap

On the whole, the results for dietary overlap between species were low (Table 5). The lowest values were recorded between benthopelagic-feeder species (*Alepocephalus rostratus*, *Bathypterois mediterraneus*, *Galeus melastomus* and *Centroscymnus coelolepis*), while the highest values were obtained for those species preying on more benthic (or suprabenthic) prey and located nearest each other in the FCA plots (*Polyacanthonotus rissoanus*, *Chalinura mediterranea*, *Coryphaenoides guentheri*, *Lepidion lepidion* and *Cataetyx alleni*).

By depth, a significant decrease in dietary overlap was detected in summer (ANOVA: $F = 5.687$, $p < 0.01$).

Table 5. Dietary overlap (Schoener index) between the species of the 3 depths considered. See the Table 3 legend for species codes. For *Centroscymnus coelolepis*: Cci = immature specimens, Ccm = mature specimens

| | 1000–1425 m | | | | | | | | | | | |
|-----|-------------|--------|--------|--------|------|------|------|------|--------|------|------|------|
| | Bm | Summer | | | Ca | Gm | | Pr | Autumn | | Gm | |
| | | Pr | Ll | | | | | Tt | Ca | | | |
| Ar | 0.34 | 0.18 | 0.51 | 0.30 | 0.34 | Nm | 0.12 | 0.12 | 0.07 | 0.32 | 0.24 | |
| Bm | | 0.15 | 0.60 | 0.22 | 0.15 | Pr | | 0.32 | 0.46 | 0.22 | | |
| Pr | | | 0.35 | 0.37 | 0.11 | Tt | | | 0.30 | 0.24 | | |
| Ll | | | | 0.43 | 0.32 | Ca | | | | 0.18 | | |
| Ca | | | | | 0.19 | | | | | | | |
| | 1425–1800 m | | | | | | | | | | | |
| | Bm | Pr | Summer | | Cl | Ll | Ca | | Autumn | | Ca | |
| | | | Chm | Cg | | | | Pr | Cg | Ll | | |
| Ar | 0.10 | 0.13 | 0.15 | 0.16 | 0.21 | 0.22 | 0.13 | Bm | 0.28 | 0.32 | 0.30 | 0.14 |
| Bm | | 0.09 | 0.41 | 0.19 | 0.34 | 0.34 | 0.11 | Pr | | 0.49 | 0.45 | 0.46 |
| Pr | | | 0.50 | 0.55 | 0.57 | 0.43 | 0.58 | Cg | | | 0.36 | 0.28 |
| Cm | | | | 0.53 | 0.69 | 0.67 | 0.39 | Ll | | | | 0.27 |
| Cg | | | | | 0.58 | 0.48 | 0.39 | | | | | |
| Cl | | | | | | 0.56 | 0.49 | | | | | |
| Ll | | | | | | | 0.39 | | | | | |
| | 1800–2250 m | | | | | | | | | | | |
| | Bm | Pr | Chm | Summer | | Lg | Ll | Cci | Ccm | | | |
| | | | | Cg | | | | | | | | |
| Ar | 0.13 | 0.15 | 0.17 | 0.21 | 0.31 | 0.31 | 0.16 | | | 0.26 | | |
| Bm | | 0.24 | 0.45 | 0.36 | 0.07 | 0.15 | 0.04 | | | 0.05 | | |
| Pr | | | 0.43 | 0.53 | 0.09 | 0.19 | 0.06 | | | 0.07 | | |
| Cm | | | | 0.48 | 0.16 | 0.32 | 0.09 | | | 0.08 | | |
| Cg | | | | | 0.16 | 0.24 | 0.09 | | | 0.14 | | |
| Lg | | | | | | 0.40 | 0.40 | | | 0.29 | | |
| Ll | | | | | | | 0.20 | | | 0.15 | | |
| Cci | | | | | | | | | | 0.69 | | |

Dietary overlap was significantly lower at 1800 to 2250 m than at 1425 to 1800 m (post hoc Scheffé test). No significant differences were found in autumn between the 1000 to 1425 and 1425 to 1800 m depth ranges.

DISCUSSION

Feeding guilds

The size of available food resources was the factor most responsible for food resource partitioning among bathyal fish in the Catalan Sea both by depth stratum and season. At the depth strata analysed, all large predators, perhaps excluding only *Trachyrhynchus trachyrhynchus* (sharks, *Nettastoma melanurum*, *Lepidion guentheri* and *Alepocephalus rostratus*), were clearly separated from the medium-sized and smaller predators. The importance of the variable predator size is also evidenced when it is included as an illustrative nominal variable in the FCA. Other factors, such as the

trophic level of predators (not considered here), also influence the trophic organisation of the deep Catalan sea fish assemblages (Cartes & Carrassón unpubl. data).

Mauchline & Gordon (1985) have classified fish into 3 trophic groups on the basis of dietary diversity and the number of prey-items per meal, from Group I with the lesser values to Group III with the greatest. As macrourids of the NE Atlantic Ocean (Mauchline & Gordon 1985), Mediterranean macrourids belong to Group III, having the most diverse diets and the greatest mean number of prey items per meal. By contrast, *Nettastoma melanurum*, *Lepidion guentheri* and *Centroscymnus coelolepis*, species having a low diverse diet and few items per meal ($N_p < 1.9$), belong to Group I. This is also the case of the shark *Etmopterus spinax*, represented below 1000 m by large individuals with a specialised diet based exclusively on cephalopods (Carrassón et al. 1992). Other species represented by large specimens below 1000 m in the Catalan Sea (e.g. *Mora moro* and *Phycis blennoides*) might also be within this category. Although only preliminary data are available on their diet, *Mora moro*,

for example, prey on large Natantian decapods, fish and cephalopods (Carrassón et al. 1997, authors' unpubl. data on intestinal contents). The remainder of the species studied are included in Group II, which comprises both pelagic and demersal feeder species with more diverse diets than Group I, although still consuming relatively few items per meal.

Species-by-species comparisons reveals, however, some differences between the trophic strategies of Mediterranean and Atlantic deep fish. Among the most notable differences, *Centroscymnus coelolepis* consumes fewer prey items in the deep Mediterranean than in the deep Atlantic (Mauchline & Gordon 1985), probably related with the clearly lower size exhibited by Mediterranean individuals, a trend widely reported for other deep Mediterranean fish such as *Polyacanthonotus rissoanus* and macrourids (Stefanescu et al. 1992a). *C. coelolepis* reaches a TL of over 110 cm in the Atlantic while it hardly reaches 60 cm in the Catalan sea. The deeper waters occupied by this species in the Mediterranean (Carrassón et al. 1992) might also contribute to the observed changes in its feeding strategy in this area.

Changes in the trophic guild of species may depend not only on biological features (e.g. size) but also on possible spatio-temporal changes in the ecological interactions between species. Hence, at the middle slope, *Trachyrhynchus trachyrhynchus* is in the same trophic guild as the benthopelagic feeders *Lepidion lepidion* (the dominant species; Stefanescu et al. 1993), *Bathypterois mediterraneus* and *Alepocephalus rostratus* of summer. These are possible competitors of *T. trachyrhynchus*, which increases its size with depth below 1000 m (Stefanescu et al. 1993), becoming a more benthopelagic feeder (Carrassón & Matallanas 2002). Possible competitors of *T. trachyrhynchus* at upper- and mid-slope levels to 800 m (*Gnathophis mystax* and *Lepidorhombus boscii*; Macpherson 1981), have also disappeared below 1000 m. Similarly, *L. lepidion*, which is still important in biomass up to 2000 m, was trophically included with macrourids in a different feeding guild at 1425 to 2250 m depth than at shallower depths. Macrourids are increasingly dominant in number at maximum depths in the Catalano-Balearic Basin (Stefanescu et al. 1993).

Overall, the deep-sea demersal fish species inhabiting the Catalano-Balearic slope often consumed a variety of available resources in their diets, mainly comprising suprabenthos, but also infauna or planktonic prey. A few, albeit dominant species in terms of biomass, exploited the plankton compartment (e.g. *Alepocephalus rostratus*, preferentially at 1000 to 1425 m), while infauna (e.g. polychaetes and bivalves) was also important in the diet of a variety of species (e.g. *Cataetys alleni*, *Polyacanthonotus rissoanus* and

most macrourids). Although at a whole fish-assemblage level, benthos (suprabenthos included) had slightly greater importance in the energetic requirements of fish than plankton resources, bathyal fish exploited 2 different trophic pathways in the Catalan Sea area.

Prey selectivity and trophic diversity

Large predators may have higher displacement ability within the BBL, with size and swimming activity probably being correlated variables. In a previous study on decapods, where it was not possible to consider prey and predator size as variables, the vertical distribution of food resources near the seabed was considered the most important factor determining resource partitioning in this taxa (Cartes 1998a). Large fish species often showed a strong preference for swimming prey (e.g. natantian decapods, euphausiids, siphonophores and pyrosomids), most of them too large to be adequately sampled with the Macer-GIROQ sledge (0.5 mm mesh size). Therefore, prey selectivity was overestimated (positive values of L) for these prey (see also Cartes 1998b). Prey selectivity on decapods consumed by fish are, however, in many cases negative when decapods and fish were simultaneously collected with an OTSB-14 bottom trawl (Cartes & Sardà 1992). Calanoid copepods are the most abundant benthopelagic taxa in the environment (Cartes 1998b), but the only fish species that preferentially preys on this prey is *Bathypterois mediterraneus* (especially at 1425 to 1800 m), and to a lesser extent *Lepidion lepidion* (at 1000 to 1400 m). Other demersal fish select prey of a relatively larger size (>3 mm) than copepods. The small size of fauna collected with the Macer-GIROQ sledge is reflected in the selectivity indexes obtained (both L and GS, the sum of the selectivity indexes L). *Bathypterois mediterraneus* was in all the depth strata the species presenting the highest L values, which is explained by the fact that this species selects copepods, which are well sampled with the sledge. By contrast, the GS had always high negative values for large predators (*Nettastoma melanurum*, *Galeus melastomus*, *Centroscymnus coelolepis* and *Alepocephalus rostratus*), due to the low consumption of small prey collected with the sledge. Among decapod crustaceans, the other dominant taxa of megabenthos in the area, L was also low for Calanoids, in spite of their dominance in the environment (Cartes 1998a). In summary, the small-sized fish dominant on the Catalan Sea slope seem to select prey in the water-sediment interface of the BBL (ca. 0 to 1.5 m above the bottom). Also, as occurs in the NE Atlantic (Mauchline & Gordon 1991), the largest predators increase the

range of the prey exploited with a parallel increase in the average swimming capacity of their prey.

We did not find significant depth-related changes in the dietary diversity of bathyal fish, either at the level of the whole assemblage or families (e.g. macrourids). However, most species showed an increase in H' associated with the depth interval where they attained their maximum abundance, the so-called c. o. g. (as defined by Stefanescu et al. 1992a). Thus, species may find better trophic requirements in the depth range where they attain their highest densities, a consequence of their adaptative success in the milieu. The only exception to this trend was *Lepidion lepidion*, with higher H' deeper than its c. o. g. (1000 to 1425 m). *L. lepidion* is the only species in the deep Mediterranean below 1000 m in which a bigger-deeper phenomenon has been reported (Stefanescu et al. 1992b). We interpret that higher sizes (and also higher feeding intensity), related to wider size spectra of prey consumed, may favour the reproduction of this species at greater depths.

In the deep Mediterranean, large demersal fish with high energy requirements (e.g. *Trachyrhynchus trachyrhynchus*, *Mora moro* and *Phycis blennoides*) prevail at the middle slope to 1400 m, being progressively substituted with depth by smaller (*Coryphaenoides guentheri* and *Chalinura mediterranea*) and/or probably less active species (Stefanescu et al. 1992b), such as *Bathypterois mediterraneus*. The adoption of a less active trophic behaviour could thus be interpreted as a result of lower food availability in oligotrophic areas. Although the dominant small-sized fish below 1400 m (especially at 1800 to 2250 m) all capture small-sized organisms distributed uniformly throughout the space, different trophic strategies can be identified. Thus, *B. mediterraneus* have a stenofagous diet based on copepods, while *C. guentheri* (the second-most abundant species after *B. mediterraneus*) presents a more euryphagous diet centred on the epibenthos and endobenthos. *C. guentheri* prey preferentially on copepods (Gordon & Duncan 1987) in the NE Atlantic, where this species is dominant at 2250 m (Mauchline & Gordon 1984, Gordon & Mauchline 1990). Therefore, its diet is more similar to that of the dominant species in the deep Mediterranean Sea (*B. mediterraneus*) than to their own close species in these waters. *C. guentheri*, and macrourids in general, are more active predators than benthic chlorophthalmids; Priede et al. (1990), using acoustic transmitters, did not observe in macrourids evidence of a 'sit and wait' foraging strategy of the kind that occurs in *Bathypterois*.

A general trend, also coinciding with that of decapod crustaceans in the same area (Cartes 1998a), was the increase of V (% of empty stomachs) with depth for most species. As in the case of decapods, this trend

could also be explained as a consequence of the food resources impoverishing with depth in the Catalan Sea or generally in the deep Mediterranean, documented for meiofauna (Stora et al. 1999, Cartes et al. 2002), macrobenthos (Pérès 1985) and suprabenthos (Cartes 1998b, Cartes et al. in press).

Dietary overlap and resource partitioning

All discussion on the possible influence of resource partitioning on competition is often controversial and even speculative. High overlap values between species were uncommon in marine communities, indicating that on the whole species did partition the available resources (Grassle & Sanders 1973, Macpherson 1981, Blaber & Bulman 1987, Cartes 1998a). In deep-sea communities, dietary overlap is generally low, also suggesting low species interaction. However, in the case of biological interactions between pairs of deep species in a similar trophic guild, high dietary overlap (60% of diet affinity) has been documented both for decapod crustaceans (Cartes 1998a) and for sharks (Carrassón et al. 1992), with segregation of species depending on size or depth. In the present study, at a whole taxocenosis level, low dietary overlap values were generally recorded, implying high resource partitioning; this coincides with results for decapod assemblages in the same area (Cartes 1998a). However, possible interactions between pairs (or groups) of species were also observed. Therefore, *Bathypterois mediterraneus* evidence some possible competition for food along the deep slope below 1000 m only with *Lepidion lepidion* at the middle slope (dietary overlap 0.60), decreasing progressively at the lower slope when depth increases. *B. mediterraneus* is the most abundant fish, with an increasing dominance on the lower slope assemblages of the NW Mediterranean (Stefanescu et al. 1993, Morales-Nin et al. 1996). Its microphagous feeding habits, with a 'sit and wait' feeding strategy and other biological features such as its hermaphroditism (which may double its reproductive potential), are additional arguments to explain its success in colonising great and low productive depths. This same strategy seems to be very successful in the Bahamas, where other *Bathypterois* species dominate, in contrast to the temperate regions of the deep Atlantic, where more active foraging feeding fish prevail (Crabtree et al. 1991). Two distinct patterns seem thus to occur in less productive deep areas (Bahamas and the western Mediterranean) and in more eutrophic areas of the Atlantic Ocean (Sulak 1982, Anderson et al. 1985). Such trends between more/less productive areas are also possible when comparing different depth ranges (e.g. the middle and lower

slope) subject to a decrease in productivity when depth increases.

Throughout the depth range studied, *Cataetys alleni* and *Polyacanthonotus rissoanus* belong to the same trophic group, both being euryphagous with a diet based on small-sized organisms. The increase in dietary overlap observed at 1425 to 1800 m between these 2 species suggest a higher food competition, and could cause the disappearance of *C. alleni* below 1800 m. The bathymetric centres of distribution (c. o. g.) also tended to be different, reinforcing the dietary differences as a means of niche separation. As Brown (1975) suggested, indirect evidence of interspecific competition comes from inverse correlations of predator abundance. This trend has been described by other authors for other species (Roughgarden 1974, Macpherson 1981).

Another general trend in the deep Mediterranean fish assemblages was a decrease in dietary overlap among species with increasing depth. A detailed analysis of the overlap between pairs of common species, however, demonstrates that this trend is not general. According to Gascon & Legget (1977) and Keast (1978a), dietary overlap increases as food availability decreases. This is observed for species of predators of similar size, and the overlap between *Bathypterois mediterraneus* and the macrourids *Coryphaenoides guentheri* and *Chalinura mediterranea* increases slightly with depth. The trend is parallel to that of deep-water decapods of the zone in which it has been suggested that the lower diversity of available prey items at 1300 to 2200 m depth may increase overlap (Cartes 1998a). Nevertheless, the presence of large benthopelagic fishes such as *Lepidion lepidion* at 1800 to 2250 m, *L. guentheri*, *Centroscymnus coelolepis*, etc., means that overlaps tend to be lower at deeper than shallower depths. This could be due to the fact that these species may have access to a wider variety of benthopelagic prey, as already suggested by other authors (Zaret & Rand 1971, Keast 1978b, Macpherson 1981).

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