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ORIGINAL PAPER

Comparative feeding patterns of early stages of mesopelagic fishes with vertical habitat partitioning

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Abstract The present study analysed the trophic ecology of the early developmental stages of four species of mesopelagic fish, the myctophids *Ceratoscopelus maderensis*, *Hygophum benoiti* and *Benthosema glaciale* and the sternoptychid *Argyropelecus hemigymnus*. These species display different morphological traits and a segregated vertical distribution throughout the water column. The study was conducted off Mallorca Island (39° N, 3° E) in the western Mediterranean, during the summer stratification period. The results indicated that feeding patterns of myctophid larvae were strictly diurnal, while in *A. hemigymnus* larvae, day and night feeding occurred. In the transformation stage of *C. maderensis*, *B. glaciale* and *A. hemigymnus*, day and night feeding was evidenced. The feeding incidence during the larval stages was low, increasing in the transformation stages, and being particularly high for *A. hemigymnus*. Although an increasing tendency in size and number of ingested prey was observed, the trophic niche breadth did not indicate a trophic specialization in any of the species analysed. Gut content analysis determined that diet composition was very similar among the four species, with the different developmental stages of copepods being the dominant prey throughout the early larval development. Nevertheless, in transformation stages of *C. maderensis* and *H. benoiti*, other preys, like ostracods, become important contributors to the diet. Despite the important physical and biological structuring of the water column, no differences in feeding success were observed for larvae occurring in the layers of higher biological production.

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Introduction

The mesopelagic fishes constitute the most abundant group of teleosteans worldwide with a ubiquitous occurrence in both temperate and tropical waters, with the greater biomass belonging to the orders Myctophiformes and Stomiiformes (Hulley 1994; Sassa et al. 2002; Gjøsaeter and Kawaguchi 1980). The adults of these species have a broad distribution in the water column, spreading from the surface to as deep as 1000 m (Gartner et al. 1997), and feeding on a wide assortment of zooplanktonic taxa (Merrett and Roe 1974; Petursdottir et al. 2008). The high biomass of these mesopelagic species and the great migratory capacity of some of them (Gjøsaeter 1981; Willis and Pearcy 1982; Roe and Badcock 1984) lead to consider this group as a significant contributor to the carbon transport from the photic zone to deeper waters (Pakhomov et al. 1996), playing an important role in marine food webs. Likewise, mesopelagic fishes are prey for diverse organisms such as large pelagic fishes of commercial interest, cephalopods, and marine birds and mammals (Walker and Nichols 1993; Hunt et al. 2005; Connan et al. 2007). Larval stages of mesopelagic fishes have a more restricted vertical distribution, living in the upper 200 m of the water column (Ahlstrom

1959; Moser et al. 1984) and with limited capacity to perform diel vertical displacements, which increases with development. In the western Mediterranean (WM), it has been observed that some myctophid larvae perform discrete migrations to the surface at daytime (Sabatés 2004), whereas the adult specimens show an opposite migratory behaviour, reaching the upper layers at night and being absent from them during daytime (Olivar et al. 2012). In contrast, the adults of some stomiiformes such as the sternoptychid *Argyropelecus hemigymnus* are non-migrants to the epipelagic waters and occur mainly at 400–600 m in the deep scattering layer (DSL) (Olivar et al. 2012).

As in other regions, the distributions of these mesopelagic fishes extend from the continental slope to open waters, where they constitute the dominant fish biomass of this typically oligotrophic system (Goodyear et al. 1972). The low primary production in the open ocean may induce the partitioning of food resources among mesopelagic fish species and within the species throughout development, involving different distributions through the water column and diverse feeding preferences (Hopkins and Gartner 1992).

The study of feeding patterns provides valuable information about the biology and ecology of organisms, and contributes to the understanding of the intra-community interactions, supplying information from the individual to a large ecosystem scale (Cailliet et al. 1996). The feeding patterns of mesopelagic fishes have been extensively studied in adults (e.g. Clarke 1978; Rissik and Suthers 2000; Watanabe et al. 2002 for myctophiformes, or Sutton and Hopkins 1996; Carmo et al. 2015; Champalbert et al. 2008 for stomiiformes); however, current knowledge about the feeding behaviour of the early stages is more limited (e.g. Conley and Hopkins 2004; Sassa and Kawaguchi 2004 for myctophiformes or Landaeta et al. 2011 for stomiiformes), but considered essential for understanding how organisms interact with each other (Pakhomov et al. 1996; Conley and Hopkins 2004). Previous investigations on larval feeding patterns of Mediterranean mesopelagic fishes included several species of myctophids (Sabatés and Saiz 2000; Sabatés et al. 2003; Bernal et al. 2013). However, there are no studies regarding the stomiiformes, and information on feeding of early stages is limited to the juvenile phases of the gonostomatid *Cyclothone braueri* (Palma 1990) and the sternoptychid *A. hemigymnus* (Bernal et al. 2015).

The analysis of the different feeding strategies of larvae of mesopelagic fishes yields information about their energy requirements, and foraging abilities (Hunter 1981). Despite the fact that feeding behaviour is characteristic of each species, differences may result in relation to the environmental features in the larval habitat (Theilacker et al. 1996) and changes in morphology with ontogenetic development. The increase in mouth size, visual specializations and swimming ability with development enhances capture of prey resources and consequently survival probabilities in oligotrophic systems (Sabatés and Saiz 2000).

Pelagic larvae are mainly visual predators (Greene 1985; Sabatés et al. 2003), for this reason it is considered that light plays a key role in prey detection (Sabatés et al. 2003). However, factors such as colour, size and swimming prey behaviour may be important to facilitate their perception and capture (Checkley 1982; Govoni et al. 1986). Prey size is likely the most determinant factor for selectivity, and it is closely associated with larval mouth width (Shirota 1970; Hunter 1981). Sabatés and Saiz (2000) indicate that both the size of the mouth and the ability to search and swim of the larval fish increases with the ontogenetic development and that individuals with larger sizes have higher success than the smaller ones.

This research addressed the study of feeding habits of the early developmental stages (larvae and transformation stages) of four abundant mesopelagic species in the western Mediterranean Sea: *Ceratoscopelus maderensis*, *Hygophum benoiti* and *Benthosema glaciale* (Myctophidae) and *A. hemigymnus* (Sternoptychidae). The larval stages of these species have different morphological characteristics and are distributed through the first 200 m of the water column showing different depth preferences (Olivar et al. 2014). In these species, the stages of transformation have a deeper distribution below 200 m (Olivar et al. 2014). The present study compares the feeding patterns of these four species throughout the early stages of development by means of the analysis of feeding incidence, diet composition, prey size spectra and selectivity. The final aim is to determine whether larvae of these species exhibit taxon-specific trophodynamic patterns in relation to their different vertical distribution, in relation to their different larval morphology, and through their early ontogeny.

Materials and methods

Sampling

The study was carried out off Mallorca Island (39° N, 3° E) (western Mediterranean) in July 2010. Fish and plankton samples were taken between the shelf break (200 m) and slope (900 m). Fish larvae were collected through stratified tows using a MOCNESS gear with a 1-m^2 mouth opening and consisting of seven nets with 333-µm mesh size. A total of 26 fixed stations (16 at daytime and 10 at nighttime) were sampled with the following depth strata: 0–25, 25–50, 50–75, 75–100, 100–125, 125–150 and 150–200 m. In some of the stations located at the slope, sampling was extended to deeper layers (200–400 m). Because of the low abundance of larvae found in the four strata between

75 and 200 m, data were combined and analysed as a single layer. The detailed analyses of fish larval distributions through the water column during the study period were the subject of a previous investigation (Olivar et al. 2014), and here, we outline the relative vertical distribution of the four species considered in this study.

The hauls were oblique, from deep to shallow layers, and the ship speed was 2–2.5 knots. The water volume filtered by each net was recorded by a flowmeter attached to the net mouth. Volume of filtered water was 200–250 m^3 for each 0–25 m strata. Zooplankton samples were preserved in 5 % buffered formalin. In the laboratory, all fish specimens were sorted and identified according to the pertinent literature and stored in 5 % buffered formalin. Identification of the species objective was performed using Tåning (1918), Sanzo (1931), Moser et al. (1984) and Olivar and Palomera (1994).

Laboratory analysis

Specimens were identified and then grouped according to their developmental stage: larvae (preflexion–flexion and postflexion, according to the notochordal flexion) and transformation (body becomes thicker and the photophores appear, but the squamation has not been developed yet) (Table 1). Specimens were measured under a microscope equipped with an ocular micrometer. Larval measurements were performed with an accuracy of 0.1 mm. Before dissection, the following measurements were recorded: standard length (SL); lower jaw length (LJL), measured from the tip to the junction with the maxilla; upper jaw length (UJL), measured from the tip of the snout to the posterior end of the maxilla; and mouth width (MW), measured ventrally as the widest distance between the posterior edge of the maxillae. Allometric relationships between mouth size and body size were determined by fitting a power function, with the slope of the function representing the allometric coefficient.

In larvae, the entire gut of each specimen was extracted. For transformation stages, dissection was performed after the oesophagus and only the stomach content considered for analysis. Preys were extracted using a fine needle, placed in a drop of 50 % glycerine-distilled water on a glass slide, and prey organisms were teased out for identification, enumeration and measurement. Each prey item in the guts was measured along the maximum cross section with a precision of 0.001 mm under a stereomicroscope (Leica MZ12, reaching 100×) using a micrometric eye piece. Identification was made to coarse taxonomic groups, except for copepods in which identification was to genus level when possible. The main identification guides were Vives and Shemeleva (2007, 2010) and Rose and Tregouboff (1957).

Table 1 Sizes (standard length) ranges of the different developmental stages for the four studied species

Species	Larvae		Transformation
	Preflexion and flexion	Postflexion	
C. maderensis	<6.9 mm	7–16 mm	>16 mm
H. benoiti	<5.9 mm	6–13 mm	>13 mm
B. glaciale	<5.9 mm	6–13 mm	>13 mm
A. hemigymnus	<9 mm (N/P)	6–9.5 mm (N/P)	>7 mm (P)

N/P without photophores, *P* with photophores

Data analysis

The feeding incidence (FI) was determined as the percentage of examined specimens containing at least one prey in the stomach (Arthur 1976) and separately for daytime and night-time.

The diet was described in terms of frequency of occurrence (%F) of a diet item in those larvae with food in their guts, and in terms of the abundance (%N), calculated as the proportion of prey items of a given category to the total number of diet items examined. The product of these two values was taken as the percentage index of relative importance of each diet item (%IRI) (Govoni et al. 1986).

For each species, the trophic niche breadth was analysed according to Pearre (1986) as the standard deviation (SD) of the log10 transformed maximum prey width versus the SL. The larvae were grouped into 0.2-mm size intervals so as to produce the maximum number of size classes containing at least three or more prey items.

Prey selectivity was calculated for the transformation specimens, which were located in the deep scattering layer. The abundance of mesozooplankton, grouped by similar taxonomic categories than those identified from gut contents, was obtained from the MOCNESS hauls (300-μm mesh size) at the same strata where specimens were taken.

Selectivity was calculated for the most common prey items in the guts, by applying the Chesson's selectivity index (Chesson 1978) as follows:

$$\alpha_i = \frac{r_i / p_i}{\sum_{i=1}^{m} r_i / p_i}$$

where r_i and p_i are the respective frequencies of a prey item in the diet and plankton, and m is the number of prey categories considered. Positive or negative selectivity were determined when the α-values ±95 % CI fell above or below the line defining the neutral α-value for selectivity, respectively.

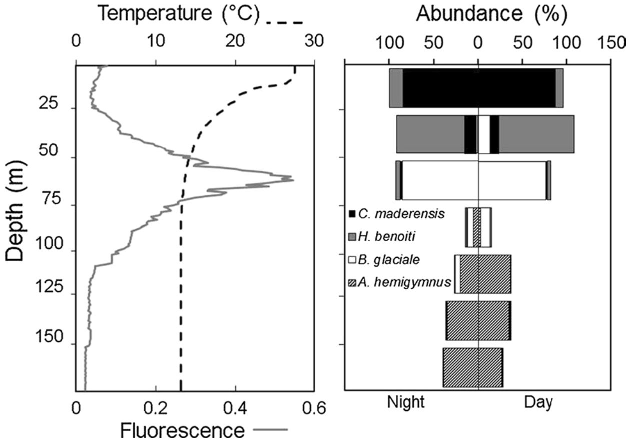

Fig. 1 Vertical profiles of temperature and fluorescence (*left graph*) and vertical distribution of *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus* (*right graph*) during the study period (July 2010) off Mallorca Island

Differences in prey number and size among developmental stages were analysed by means of one-way ANOVA. For *H. benoiti* and *B. glaciale*, whose vertical distribution was wider than for the other two species, differences were also tested among vertical depth layers and developmental stages by means of multifactorial ANOVA followed by a post hoc test. Significant differences were considered when probability was lower than 0.05. Analyses were performed using STATISTICA 11.

Results

Vertical patterns of hydrography and plankton

During the study period, July 2010, the water column was characterized by a strong stratification in the first 50 m, with a thermal gradient of ten degrees. The vertical fluorescence profiles showed a typical deep fluorescence maximum (DFM) between 60 and 80 m, with maximum copepod concentrations during the day between 50 and 75 m, associated with DFM (Fig. 1).

The larvae of the mesopelagic species considered here showed a marked vertical segregation, and no differences in the vertical pattern within species were observed between day and night. *C. maderensis* was located between the surface and 50 m depth, being particularly abundant in the first 25 m, and *H. benoiti* occurred between surface layers and 75 m, with highest concentrations between 25 and 50 m. Larvae of *B. glaciale* showed a more restricted distribution, between 50 and 100 m and those of *A. hemigymnus* displayed the deepest distribution, between 75 and 200 m (Fig. 1). Transforming stages of all the species occurred at deeper levels, between 200 and 400 m.

Feeding incidence (% FI)

A total of 1429 individuals were analysed, 81.1 % were myctophids (*C. maderensis*, *H. benoiti* and *B. glaciale*) and 18.9 % corresponded to the sternoptychid *A. hemigymnus.*

Larvae of the three myctophid species fed exclusively during daylight hours and did not have prey items in their guts during the night. Day larval feeding incidence was lower in preflexion and flexion (<5 %) than in postflexion stages (from 14.9 to 27.9 %). *B. glaciale* showed the highest feeding incidence of the three myctophids for the larval stages and *C. maderensis* the lowest values of FI (Table 2). When comparing FI among different layers, *H. benoiti* and *B. glaciale* showed the highest incidences between 50 and 75 m (35.9 and 15.1 %). For the other fish species, whose larvae were mainly located in a single layer (0–25 m depth for *C. maderensis* and 75–200 m depth for *A. hemigymnus*), comparisons between layers cannot be established. In transformation stages, myctophids showed both day and night feeding, with incidences from 25 % for day samples to 41.5 % at night.

Larvae of *A. hemigymnus* fed during both day and night, with slightly higher incidences during the day (20 vs. 8.3 %). In transformation stages, the incidence was much

Table 2 Day and night feeding incidence (FI %) by developmental stage for the four studied species

Species	Larvae				Transformation	
	Preflexion and flexion		Postflexion			
	% FI day	% FI night	% FI day	% FI night	% FI day	% FI night
C. maderensis	2.8 (176)	0 (40)	14.9 (47)	0 (40)	25 (20)	47.1 (18)
H. benoiti	3.3 (246)	0 (30)	23.7 (190)	0 (30)	38.5 (13)	–
B. glaciale	4.2 (144)	0 (34)	27.9 (43)	0 (34)	41.5 (41)	41.7 (12)
A. hemigymnus	20 (45)	4.8 (62)	15.2 (33)	8.3 (24)	87.5 (64)	81.4 (43)

Numbers in parenthesis indicate the total number of analysed specimens

– no data

higher, reaching 87.6 % during the day and 81.4 % at night (Table 2).

Prey size spectra

In the four species, mouth size (measured as maximum width or length of both jaws) showed a faster growth rate than body length (positive significant allometry of each mouth measurement relative to the standard length) (Table 3). In all developmental stages, *C. maderensis* and *H. benoiti* were the species with the smallest mouths. Mouth size of *B. glaciale* and *A. hemigymnus* was similar during larval stages but, at transformation, *A. hemigymnus* was the species with wider mouth size (Fig. 2).

In *C. maderensis*, *H. benoiti* and *A. hemigymnus,* the number of prey items per gut increased from the preflexion–flexion to the transformation stages always being significantly higher during transformation, with a maximum of five ingested prey per individual in larvae and 12 in transformation individuals. Conversely, there was no relationship between the prey number and development in *B. glaciale* (Fig. 3a).

Maximum prey widths ranged from 50 to 550 µm for larval stages and from 58 to 1200 µm for transformation. The early developmental stages of the two species with smaller mouths, *C. maderensis* and *H. benoiti,* ingested prey with mean sizes from 100 to 115 µm; mean prey size for *B. glaciale* was 140 and 250 µm for *A. hemigymnus*. Prey size increased with development in the three myctophids, with significant differences for the transformation stages of *H. benoiti* and *B. glacial*e. In *A. hemigymnus,* the size of ingested prey increased from preflexion to postflexion stages, with a significant decrease in the transformation stage. It should be noted that the average prey size of transformation stages of *A. hemigymnus* was significantly lower than for the three studied myctophids (Fig. 3b).

Table 3 Parameters of the allometric relationships between mouth width (MW), upper jaw length (UJL), lower jaw length (LJL) and standard body length (SL) for the four studied species

Species	*n*	r	a	b	95 % CIb
C. maderensis					
MW	324	0.98	0.35	1.33	0.03
UJL	324	0.99	0.53	1.41	0.02
LJL	324	0.99	0.57	1.41	0.02
H. benoiti					
MW	495	0.94	0.36	1.33	0.04
UJL	495	0.97	0.54	1.41	0.03
LJL	495	0.98	0.59	1.38	0.03
B. glaciale					
MW	285	0.94	0.65	1.20	0.05
UJL	285	0.97	0.85	1.33	0.04
LJL	285	0.98	0.97	1.29	0.03
A. hemigymnus					
MW	510	0.93	0.37	1.47	0.05
UJL	510	0.92	0.58	1.55	0.06
LJL	510	0.93	0.67	1.51	0.05

n number of measured individuals, *r* correlation coefficient, *a* intercept, *b* slope (allometric coefficient), 95 % *CIb* 95 % confidence interval of the slope

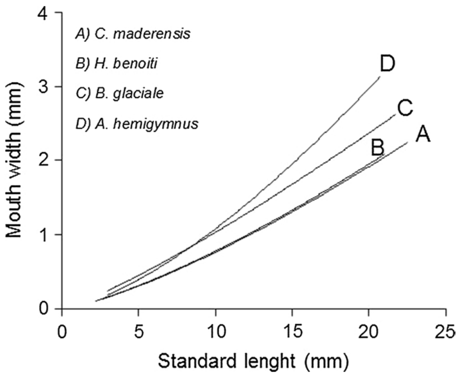

Fig. 2 Relationship between body length (standard length) and mouth width for *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus* (fitting parameters given in Table 3)

Comparison between layers of the water column, larvae of *H. benoiti* and *B. glaciale* showed the highest number of prey per gut at 50–75 m (Fig. 4), although differences were not significant. Prey size did not show significant differences among layers and stages within the same species (Fig. 5).

Though maximum prey size increased with body size from early larvae to transformation stage, trophic niche breadth showed no significant trend towards feeding size specialization for any of the species throughout their development (Fig. 6).

Diet

In *C. maderensis*, copepodite stages and the calanoid *Paracalanus* were important prey during larval stages, reaching indices of relative importance (IRI) higher than 80 %. Higher prey diversity was observed in transformation stages, and therefore, the relative importance values of different prey items did not exceed 23.3 %, with ostracods being the prey with the highest contribution (Table 4).

Copepod nauplii and copepodites were the most important prey in preflexion and flexion larvae of *H. benoiti*, with 73 % IRI and 22.5 % IRI, respectively. In postflexion larvae, copepodites represented the 40.2 % and adult *Calanus* and *Paracalanus* the 11 and 36 %, respectively. During

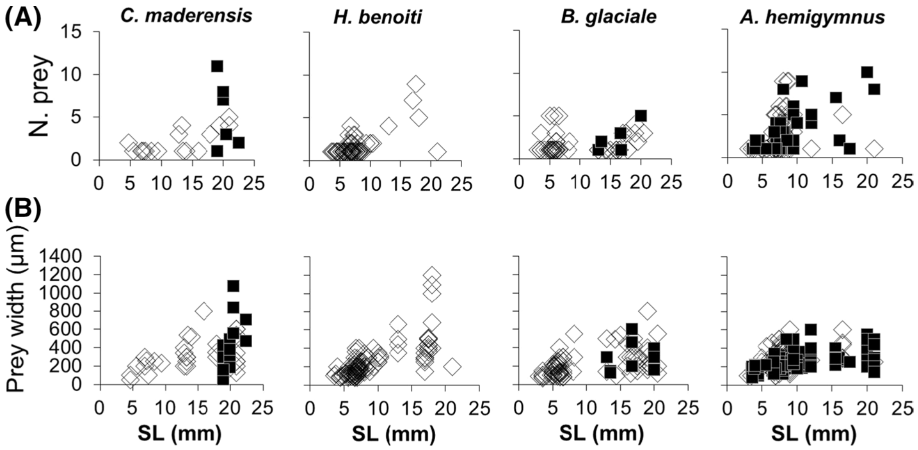

Fig. 3 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*, variation in the number of prey ingested (**a**) and prey width (**b**) along development. *Filled black symbols* denote night samples and *empty symbols*, day samples

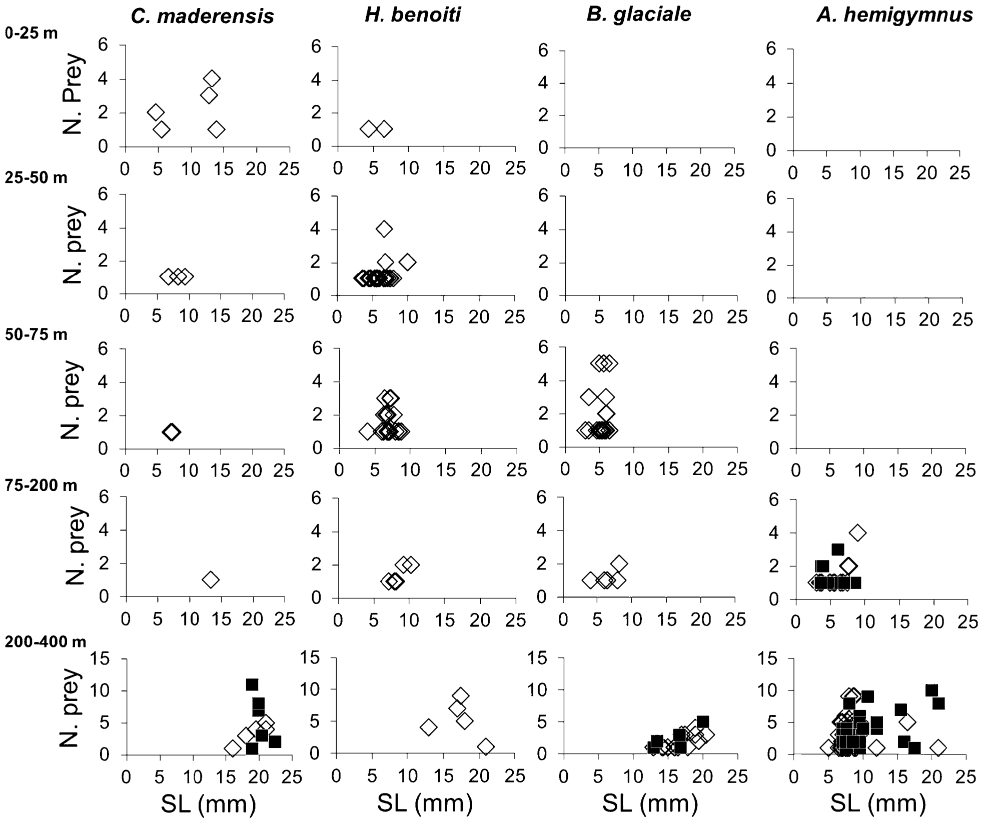

Fig. 4 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*, variation in the number of prey ingested along development. Each file shows the results for the different layers of the water column, 0–25, 25–50, 50–75, 75–200 and 200–400 m. *N. prey* number of prey, *SL* standard length. *Filled black symbols* denote night samples and *empty symbols*, day samples

transformation, copepodites and ostracods were the main prey categories, both with a rate of 39.5 % (Table 4).

In preflexion and flexion larvae of *B. glaciale*, the highest indices of relative importance corresponded to copepod nauplii and copepodites, 61.1 and 24.7 %, respectively. However, in postflexion stages, copepod eggs and copepodites were the most important prey, with IRI values of 43.4 and 19.3 %, respectively. In transformation stages, copepodites represented 66 %, followed by the copepod *Calanus* with 21.5 % (Table 4).

In preflexion and flexion *A. hemigymnus,* the most common and abundant prey were copepod nauplii and copepodites, both with IRI of 33 %, followed by crustacean eggs and calanoid copepods of genus *Paracalanus* with 17.7 and 14.76 %, respectively. In postflexion stages, the main prey was calanoid of the genus *Calanus* with 47.4 %, followed

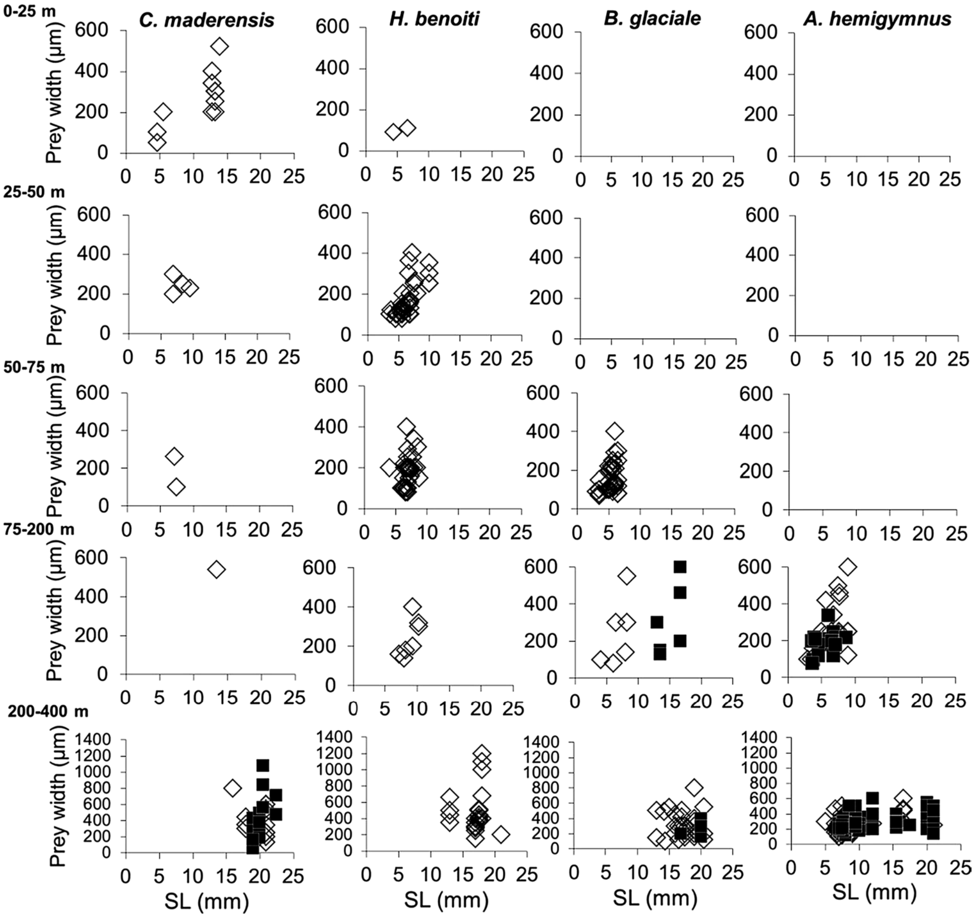

Fig. 5 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*, variation in the ingested prey width along development. Each file shows the results for different layers of the water column, 0–25, 25–50, 50–75, 75–200 and 200–400 m. *SL* standard length. *Filled black symbols* denote night samples and *empty symbols*, day samples

by copepodites and ostracods, both with 21.1 % IRI. In transformation stages, copepodites represented 59.8 %, followed by calanoid copepods of the genera *Calanus* and *Paracalanus* with 13.7 and 9.7 %, respectively (Table 4).

The most notable results for the selectivity analysis performed for the transformation stages was the positive selection for large copepods (>200 µm), being significant for most of the species, except for *H. benoiti*. Additionally, *B. glaciale* showed negative selectivity for copepods of the genus *Oncaea*, and *A. hemigymnus* for *Calanus* and ostracods (Fig. 7).

Discussion

Based on the results of our study, it is interesting to note that feeding patterns are very similar for the several species studied, despite their different morphological features and its occurrence at different depths in the water column.

Fish larvae are usually visual predators that feed, primarily during daylight hours (Hunter 1981). Most myctophid larvae fit this diel pattern (Sabatés and Saiz 2000; Sassa and Kawaguchi 2005; Rodríguez-Graña et al. 2005; Bernal et al. 2013). In the present study, larvae of the myctophids *C. maderensis*, *H. benoiti* and *B. glaciale* showed exclusively day feeding, independent of their vertical distribution, while in transformation stages they fed both during day and night. The nocturnal feeding is a common pattern in adult myctophids (Sassa et al. 2002; Yatsu et al. 2005; Takagi et al. 2009). However, there are no studies addressed to the feeding rhythms during transformation stages, although some previous investigations included these phases within the juveniles (Watanabe et al. 2002; Bernal et al. 2015). Our results indicate that transformation phases of the different species of myctophids did not have a defined feeding pattern, as individuals with stomach contents appeared in both day and night samples. It is likely that this apparent lack of diel pattern was due to the fact that this is a transitional phase between the larval and adult stages, which occupy different habitats and have well-defined and opposite circadian rhythms. The larval stage is characterized by a strictly epipelagic planktonic life, and therefore, its feeding routine is highly influenced by light. However, adults occur mainly at the mesopelagic zone during the day and migrate at night to the epipelagic region for feeding and forage. The fact that transformation stages occur at both day and night in the 200–400 m layer, showing always feeding content in their guts, suggests that they

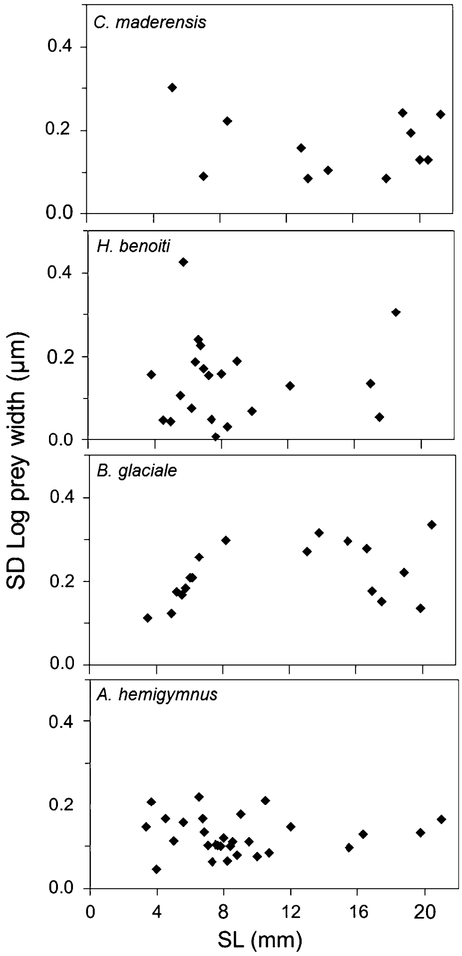

Fig. 6 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus.* Trophic niche breadth, expressed as SD log of prey width, plotted against standard length

must feed at this layer. The switch of habitat in the transformation stage to a dim zone, where day and night variations are barely detectable, probably requires some learning and adaptation times before the adult migrating patterns are achieved.

There are a few studies on larval feeding of the Sternoptychidae *A. hemigymnus*. In general, these investigations provide average fish sizes (Kinzer and Schulz 1988) or size intervals (Mauchline and Gordon 1983), but do not differentiate between developmental stages. To define the early developmental stages of this species is necessary to consider the degree of curvature of the notochord and the presence/absence of photophores. By itself, the size is a poor descriptor of the state of development. Previous investigations on juveniles and adults of *A. hemigymnus* indicated that feeding could take place both during the day and at night, with this pattern being common to other species of the family (Merrett and Roe 1974; Hopkins and Baird 1985). The present results pointed out to the same pattern for larval stages of *A. hemigymnus*, since dim light conditions below 75 m depth, where these larvae dwell, does not seem to be a limitation for feeding. Possibly the particular features of its eyes, the elliptical shape and upwards projection from the early stages of development (<7 mm SL), increase their visual field and contribute to a good perception of potential prey in its low-light environment (Weihs and Moser 1981). Furthermore, it is likely that this species develop rod photoreceptors associated with vision in low light intensities from early stages as it has been reported in larvae of other mesopelagic and deep dwelling species (Bozzano et al. 2007). However, the contribution of non-visual senses to prey detection cannot be disregarded as fish larvae frequently employ more than one sensory modality in prey detection (Pankhurst 2008).

Feeding incidence provides information related to feeding success/catchability (Arthur 1976; Blaxter 1971; Zaika and Ostrovskaya 1972). Feeding incidence values observed in this study for *H. benoiti*, *B. glaciale* and *A. hemigymnus* were quite low for the larval stages, although similar to previously documented for larvae of other fish species (Coombs et al. 1992), and for other myctophids (Balbontín et al. 1997) and sternoptychids (Landaeta et al. 2011). However, feeding incidence for *C. maderensis* was extremely low, despite the large number of individuals dissected for this species (>300). This fact was probably related to their gut morphology (short and straight) influencing the amount and retention of gut content in larval fishes (Arthur 1976). In general, larvae with more complex guts (with several compartments or looped guts) typically exhibit greater feeding incidence than larvae with straight guts (Govoni et al. 1983), which suggests that prey retention and, therefore, the assessment of feeding success may be a consequence of the digestive tract morphology (Canino and Bailey 1995).

Prey size spectra

The fast mouth growth rate in relation to that of body length observed in all the studied species is a common tendency for larvae of many fish species (Sabatés and Saiz 2000; Rodríguez-Graña et al. 2005; Morote et al. 2008), and it is related to a fast development of the buccal structure and to the improvement of swimming, prey detection and catchability. In previous studies on fish larvae, both mesopelagic and neritic species, it has been pointed out that the number and size of the ingested prey increases along with development resulted from the improvement of larval foraging skills (González-Quirós and Anadón 2001; Conway et al. 1994; Voss et al. 2009). In our study, these tendencies were observed in *C. maderensis* and *H. benoiti*; however, no variations were detected in the

Table 4 Diet of *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*

	C. maderensis			*H. benoiti*			*B. glaciale*			*A. hemigymnus*		
	Pre and flex[a]	Post[b]	Trans[c]	Pre and flex[a]	Post[b]	Trans[c]	Pre and flex[a]	Post[b]	Trans[c]	Pre and flex[a]	Post[b]	Trans[c]
Copepod eggs				3.6	4		12.6	43.4		0.9		0.1
Copepod nauplii	9.1			73	5.5	0.8	61.1	10.8	1.4	33	5.3	
Copepodites		83.1	13.1	22.5	40.2	39.5	24.7	19.3	66	33	21.1	59.8
Calanoida												
Acartia			0.4		0.1							0.1
Calanus		6.8	0.4		11.1	7.3		4.8	21.5		47.4	13.7
Centropages			5.8									
Clausocalanus			0.4						0.34			
Paracalanus	81.8	6.8	3.3		36.1	3.2	0.5	10.8	0.34	14.7		9.7
Pleuromamma			1.5						0.34			
Cyclopoida												
Oithona				0.9	1		0.5					
Harpacticoida												3.4
Microsetella sp	9.1								1.3			1.8
Poecilostomatoida												
Oncaea			5.8						5.4			0.3
Copepod indeterminate		1.7	9.1			7.3		4.8	1.3		5.3	3.4
Crustaceans eggs						0.8	0.5			17.7		0.1
Tintinnids			0.4									
Appendicularians			17.8		1							
Cladocerans			5.8									
Euphausiids			13.1									
Ostracods			23.3			39.5		4.8	0.34	3.7	21.1	7.2
Foraminifera								1.2	0.34			
Indeterminate prey									1.35			0.2

Index of relative importance (%IRI) determined for each developmental stage

[a] Preflexion and flexion stages

[b] Postflexion stage

[c] Transformation stage

number of prey for *B. glaciale*. Interestingly, the size of prey ingested by transforming *A. hemigymnus* does not increase with development as was observed for the other species The distinct morphology of the transformation stages with a very deep body suggests that their movements must be more costly than those of the species with more hydrodynamic shapes, such as myctophids, making *A. hemigymnus* less efficient in capturing prey. The analysis of trophic niche breadth showed no tendency, indicating no trophic specialization by size with development in any of the analysed species. This result has been observed in larvae of many fish species (Pearre 1986; Sabatés and Saiz 2000; Catalán et al. 2011), although in the literature, there are some exceptions to this rule for other species which seem to specialize in particular prey size ranges (Morote et al. 2008, 2011; Murphy et al. 2012; Llopiz 2013).

Diet

In summer, the Mediterranean Sea is characterized by a strong stratification and the presence of a DFM below the thermocline (Estrada 1996). Associated with these maximum production layers, important biomass zooplankton concentrations (Alcaraz et al. 2007), particularly different copepod stages, have been reported (Sabatés et al. 2007; Olivar et al. 2014). In spite of this important structuration, larvae of the four species showed a strong vertical segregation along the first 200 m of the water column, with only *B. glaciale*, and partially *H. benoiti* coinciding with the DFM. For these two species, slightly higher feeding incidence and number of ingested prey at the DFM layer were observed; however, these differences were not significant. These results suggest that, in the study zone, mesopelagic fish larvae would

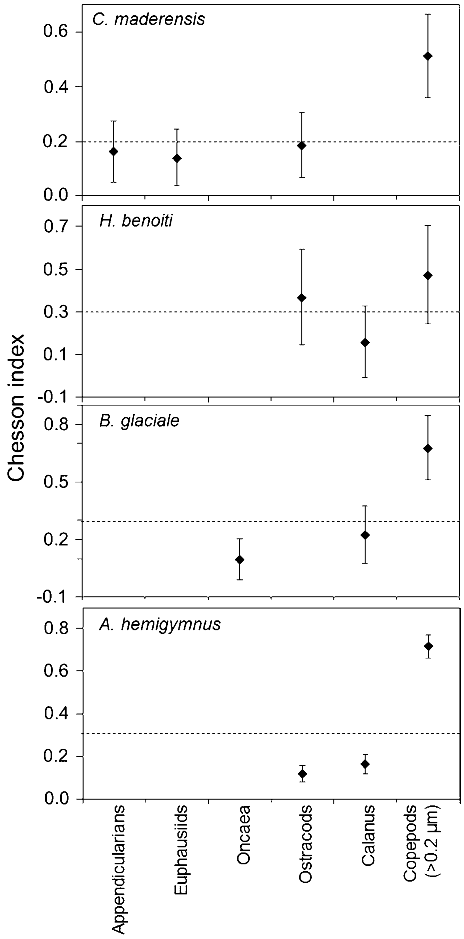

Fig. 7 Mean Chesson's α values (±95 % confidence interval) for the most common prey items in transformation specimens of *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*. Values above the *dashed line* indicate positive selection

encounter favourable trophic conditions in a wide range of depths and food by itself would not be the determinant limiting factor in the vertical structuring shown by these four species. Therefore, vertical distribution should be the result of a combination with other factors, such as light (Sabatés et al. 2003), thermal preferences (Haldorson et al. 1993) or capability to cross the thermocline (Perry and Neilson 1988). As in many species of teleosts, myctophid larvae feed mainly on copepod nauplii, small copepodites and species of copepods of small size (Sabatés et al. 2003; Sassa and Kawaguchi 2005; Bernal et al. 2013). Adults are also second-order consumers within the pelagic system (Pakhomov et al. 1996), with crustaceans being the most important group in their diet. This includes calanoid copepods, euphausiids, amphipods, mysids and decapods (Gorelova 1975; Kinzer and Schulz 1985; Pakhomov et al. 1996; Bernal et al. 2015). The diets of larvae of the four species studied are very similar to previously observed. Gut content analysis of *C. maderensis*, *H. benoiti* and *B. glaciale* indicated that copepods, the most abundant group of the zooplankton (in its different stages), were the most frequent prey in the early larval stages (preflexion–flexion), with elevated indices of relative importance. In transformation stages, the most abundant prey were copepodites, which were positively selected, although ostracods were also fairly well represented, mainly in *C. maderensis* and *H. benoiti*. Ostracods tend to be highly visible because of its relatively thick and opaque body. In addition, their escape response is to withdraw into their carapace and sink, whereas copepods quickly dart off in unpredictable directions (Conley and Hopkins 2004), which may contribute to a more successful capture of ostracods.

Studies performed in different geographical areas indicate that *A. hemigymnus* is a zooplanktivorous species whose diet, from juvenile to adult stages, consists primarily of copepods and ostracods (Merrett and Roe 1974; Mauchline and Gordon 1983; Hopkins and Baird 1985, Carmo et al. 2015, for the Atlantic ocean, and Bernal et al. 2015, for the Mediterranean Sea). In our study, we found that larval diet was also based on different stages of copepods and ostracods even from the larval stages, but this last prey was not important during the transformation stages. It is worth mentioning that the presence of ostracods in the larval diet of this species, and its low contribution in those of myctophids, could be related to the higher concentrations of ostracods below 75 m (Olivar et al. 2014), where the larvae of *A. hemigymnus* dwell.

In summary, the present study indicates that larvae of the myctophids *C. maderensis*, *H. benoiti* and *B. glaciale* are visual predators with daylight feeding rhythms, while the sternoptychid *A. hemigymnus*, with a deeper vertical distribution, is able to feed at both daytime and night-time. In transformation stages of *C. maderensis*, *B. glaciale* and *A. hemigymnus*, located in the mesopelagic region, not defined day and night feeding rhythms could be stablished. Diet composition in the different species was fairly similar along their development, with crustaceans being the most important prey, particularly the different developmental stages of copepods. The vertical segregation along the water column shown by these four species and the lack of higher feeding success at the layers of maximum food concentration suggest that food by itself would not be the determinant factor in their vertical structuring.

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