

P. Østergaard · P. Munk · V. Janekarn

Contrasting feeding patterns among species of fish larvae from the tropical Andaman Sea

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Abstract Feeding habits of tropical fish larvae were analysed in a comparative study of four species (*Scorpaenodes* sp., *Carangoides* sp., *Acanthocephala* sp. and *Cynoglossus* sp.) from the Andaman Sea. We investigated morphological characteristics and their potential influence on larval feeding, and looked for common patterns in larval prey preference. Gut contents of a total of 300 larvae were examined and compared with local zooplankton composition. The feeding habits of the investigated larvae shared a number of characteristics. During ontogeny both the preferred prey size and the number of prey in the gut increased, and across all larval size classes the relative prey size spectrum stayed constant, of approximately the same magnitude for all four species. On the other hand, larval feeding also differed in a number of aspects, especially differences in the taxonomic composition of preferred prey were apparent. *Scorpaenodes* sp. preferred abundant and large prey taxa, *Acanthocephala* sp. and *Carangoides* sp. preferred large, but less common prey taxa, while *Cynoglossus* sp., which had the relatively smallest mouth size, preferred smaller sized prey groups. Hence, the findings indicate that from an offset of common characteristics, especially related to prey size preference,

larvae have their individual feeding patterns related to specific morphology and patterns of distribution.

Introduction

Prey availability and feeding success are of prime importance in the early life of fish. To maintain a high growth rate and survive to recruitment, the larvae must optimise their food intake by being effective prey searchers and predators. Defining dietary preferences for the early stages is therefore an important element in the assessment of feeding conditions and larval chances of meeting food requirements (Robichaud-LeBlanc et al. 1997). Observations on larval prey preference are mainly based on analyses of gut contents. Some larval fish may be opportunistic feeders, ingesting prey in direct proportion to their abundance in the environment, while other larval fish show preference for prey of a certain size (Scharf et al. 2000). Generally, fish larvae are very flexible and adaptive in their foraging behaviour (Munk 1992, 1995), and studies on larval feeding will have to acknowledge that prey intake is the outcome of a process influenced by a number of interacting factors, these being morphological, behavioural, physiological, as well as environmental.

A factor of prime importance in the process of prey search and capture is the morphology of the larva. Larval structure and developmental stage determine its ability to detect, approach and attack prey, while constraints such as the size of the mouth set the maximum size of prey that they can ingest (e.g. Govoni et al. 1983; Munk 1992; Young and Davis 1992; Sabatés and Saiz 2000; Scharf et al. 2000). Hence, feeding behaviour is likely to change during larval ontogeny depending on the morphological changes taking place (Sabatés and Saiz 2000). For example, during growth, mouth size will increase and larval swimming and manoeuvring abilities will improve, increasing the efficiency of foraging. However, feeding is also dependent on prey size and

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P. Østergaard · V. Janekarn
Phuket Marine Biological Center, P.O. Box 60,
83000 Phuket Province, Thailand

P. Munk (✉)
Danish Institute for Fisheries Research,
Charlottenlund Castle, 2920 Charlottenlund, Denmark
E-mail: pm@dfu.min.dk
Tel.: +45-3396-3409
Fax: +45-3396-3434

Present address: P. Østergaard
Department of Zoology, The Natural History Museum,
SW7 5BD London, England UK

morphology. With increasing size the prey improve their mobility and/or defence mechanisms (e.g. spines) (Scharf et al. 2000); hence, improvements by the predator might be counterbalanced by parallel advancement in the avoidance behaviour of the prey.

The range of prey sizes found in the gut is often used as a descriptor of the dietary breadth of a fish species. However, a range of prey sizes is a poor measure, among other reasons because it is dependent on sample size. It is more relevant to describe dietary breadth on a ratio scale, relating prey size to predator size (Ursin 1973; Pearre 1986). Pearre (1986) proposed that a ratio-based trophic niche breadth should be used in fish diet analysis, and suggested the use of the standard deviation of observations, because of its independence of sample size. He defined an index (SLH) as the standard deviation of logarithmically transformed prey size data. Based on an investigation of 43 predator–prey relationships, Pearre (1986) proposed that the ratio-based trophic niche breadth remains constant during growth of the fish and that the size spectrum of the ingested food resource cannot be increasing as larval fish grows. While the estimate of trophic niche breadth, based on stomach contents, depends on prey composition in the environment, the width of the prey preference spectra would be a more reliable measure for comparison between predator sizes, areas of sampling, etc. When considering prey preference instead, one must account for the variation in environmental prey composition and standardise indices (Pearre 1986). The hypothesis of constancy in trophic niche breadth or preference spectrum width continues to be widely debated, with several authors questioning the general applicability of this concept (e.g. Houde 1997; Pepin and Penney 1997; Gonzáles-Quiros and Anadón 2001).

As part of a larger study on the pelagic community in the Andaman Sea (Munk et al. 2004; Nielsen et al. 2004), fish larvae were sampled along a series of cross-shelf transects. The fish larvae and zooplankton sampled at one station were used in a study of feeding habits of four species, *Scorpaenodes* sp., *Carangoides* sp., *Acanthocephala* sp. and *Cynoglossus* sp. The goal of the study was to describe common patterns and variability in the larval feeding and prey preference, focusing on the relative influence of: (1) prey type and size, (2) species characteristics and (3) ontogenetic changes. Further emphasis was given the evaluation of whether size of most preferred prey is a constant ratio of larval mouth size, and whether the width of the ratio-based preference spectra is constant.

Materials and methods

Fish larvae and zooplankton samples were collected at the position 8°24'N; 97°53'E during 16 January 1999. The station was located in a cross-shelf transect of sampling stations used during previous surveys, and was selected as earlier surveys had shown this position to be

of high productivity and plankton abundances (station 18 in Munk et al. 2004). Bottom depth at the station was 69 m. Fish larvae were sampled using a net-ring of 2-m diameter, equipped with a black, 14-m-long net of 1-mm-mesh size. The net was hauled in oblique tows from the surface to 60 m depth, at the ship's speed of 3 knots and paying and retrieving the wire at speeds of 25 and 15 m min⁻¹, respectively. A flowmeter in the centre of the ring measured the volume of water entering the net. The tows were carried out every 3 h between 0500 and 2300 hours (local time). Each tow lasted around 20–30 min. All fish larvae sampled were sorted on deck and stored in 96% ethanol. Following each ring net haul, the meso-zooplankton was collected using a submersible pump (Grundfos SP 16) equipped with a 250-µm-meshed conical net. The pump was lowered from the surface to 60 m and subsequently retrieved. Samples from this net were preserved in 4% formaldehyde, and sorting of the samples took place after the cruise. For a more comprehensive description of the hydrographic data (i.e. CTD data) in the area of sampling see Nielsen et al. (2004).

In the laboratory, the fish larvae were identified to family level. From the most abundant species we chose four species of conspicuously different morphology, for detailed studies of feeding patterns. These larvae were identified to genus as follows: *Scorpaenodes* sp. (family: Scorpaenidae), *Carangoides* sp. (family: Carangidae), *Acanthocephala* sp. (family: Cepolidae) and *Cynoglossus* sp. (family: Cynoglossidae) (Fig. 1). We measured standard length (SL) and made other morphological measurements of the larvae, which might relate to the larval ability to catch and eat prey. We used body depth (BD, maximal distance from ventral to dorsal side) and mouth size (ML, length of the lower jaw/mandibula from the tip to the angle of the mandibula bone, viewed from the side). BD is related to larval swimming and manoeuvring abilities, while ML determines the maximal size of prey the individual larva is able to ingest. The measurements are illustrated in Janekarn et al. (2002). SL was measured to the nearest 0.05 mm; BD and ML were measured to the nearest 0.02 mm. After measuring the larva, the stomach was opened with fine needles and stomach contents were analysed. Predominant food items were copepods (>98% by number), and only these were considered in the further analysis. The condition of many of the copepods made taxonomic identification difficult, and identification was either non-specific (to nauplius or copepod stage) or to the following order/family groups: Calanoida/spp., Cyclopoida/Oithonidae, Poecilostomatoida/Corycaeiidae, Poecilostomatoida/Oncaeiidae and Harpacticoida/spp. The copepods were counted, and their maximum width and/or cephalothorax length were measured (to the nearest 0.02 mm). In addition, aliquots of copepods from the related net-sampled zooplankton were identified and measured following the same procedures. Only taxa observed in the gut contents were considered in the further analysis. For a more comprehensive description

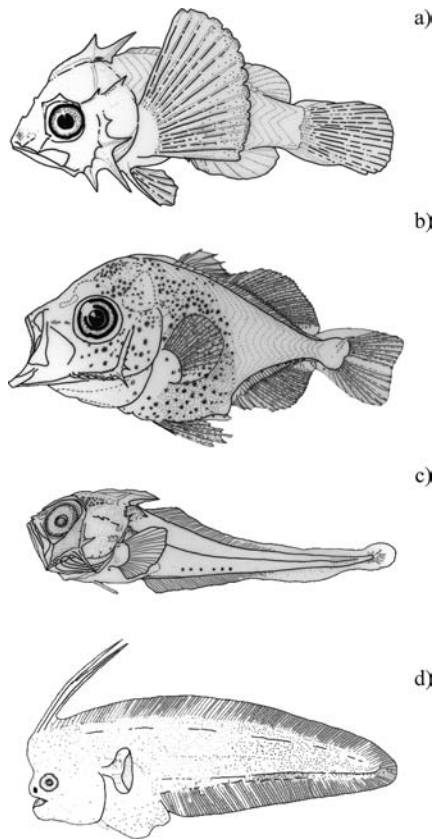


Fig. 1a–d Larvae collected from the Andaman Sea in 1999. **a** *Scorpaenodes* sp., **b** *Carangoides* sp., **c** *Acanthocephala* sp. and **d** *Cynoglossus* sp.

of the zooplankton community in the area of sampling see Munk et al. (2004) and Nielsen et al. (2004). Length and width measurements of 100 specimens from each of the identified groups of copepods as well as 100 nauplii were recorded in order to get a length–width relationship for each, which was used to estimate either width or length when only one of these measurements was available.

We compared abundance of copepods within size intervals, but the abundance of copepods declines markedly with size. To ensure reasonable abundances in the larger size intervals, we used logarithmically increasing intervals. The smallest interval was set to a midpoint of 0.050 mm, and subsequent interval midpoints were spaced \log_{10} distances of 0.1003. Hence, midpoints were 0.050, 0.063, 0.079, 0.100, 0.126, 0.159, 0.200, 0.252, 0.317, 0.400, 0.504, 0.635, 0.800, 1.008, 1.270, 1.600, 2.016 and 2.540 mm. Prey preference was quantified using Chesson's (1978) preference index α . The index, ranging from 0 to 1, is calculated as: $\alpha = (r_i/p_i) / (\sum r_i/p_i)^{-1}$ ($i = 1, \dots, m$), where r_i is the proportion of prey item i in the larval diet, p_i is the proportion of prey item i in the environment and m is the total number of prey types (size and/or taxonomic group). Neutral preference is found at $1/m$. Prey size preferences were calculated using 1-mm intervals of larval sizes. The mean of this spectrum was used as the mean prey size, whereas

the standard deviation of the spectrum was used as an estimate of the SLH-index (cf. Pearre 1986; Munk 1992, 1997). In these estimates we assumed a normal distribution of the log-scaled data (log normality). Fish larvae were pooled in a size interval of 5–10 mm in order to get sufficient data for a combined analysis of preference for prey size and taxonomy. All statistical analyses were carried out using GLM in the Statistical Analysis System, estimating significance of relationships at the 5% level.

Results

The abundance of fish larvae reached densities up to 6.7 m^{-2} . Of the four species, 89 *Scorpaenodes* sp., 80 *Carangoides* sp., 99 *Acanthocephala* sp. and 32 *Cynoglossus* sp. larvae were examined. The larvae ranged in size from 3.6 to 12.5 mm SL for *Scorpaenodes* sp. (mean: 5.8 mm), from 1.7 to 10.4 mm SL for *Carangoides* sp. (mean: 5.9 mm), from 4.0 to 23.4 mm SL for *Acanthocephala* sp. (mean: 7.9 mm) and from 4.0 to 15.0 mm SL for *Cynoglossus* sp. (mean: 6.8 mm). The four species displayed conspicuous differences in body shape and pigmentation pattern (Fig. 1). To a different degree all species showed allometric growth, apparent from the regressions of both body depth and mandibula length against standard length (Fig. 2; Table 1). Body depth was generally higher for the *Scorpaenodes* sp. and *Carangoides* sp. than for the *Acanthocephala* sp. and *Cynoglossus* sp. (Fig. 2a). Mouth morphology, measured by mandibula length, also differed among species (Fig. 2b). *Scorpaenodes* sp. had the largest relative gape size (ML in proportion to SL; $\sim 25\%$), whereas *Cynoglossus* sp. had the smallest ($\sim 10\%$). Copepods dominated the zooplankton community ($> 98.5\%$ by number). Their estimated densities varied from 1,800 to 9,300 individuals m^{-3} , depending on sampling time. The distinguished groups of copepods differed in size composition and relative abundance (Fig. 3a), as well as in morphology, expressed by their length–width relationship (Fig. 3b).

We found high feeding incidences (88–100%) during all daytime sampling sequences for all four species of larvae (Fig. 4a). All larvae had empty guts at the early morning sampling (0500 hours local time), and maximum incidence was reached at the next sampling, 2 h after sunrise. Feeding incidence declined after sunset (at 1800 hours), some larvae still had gut contents in the subsequent sample (especially *Acanthocephala* sp.), which were probably remains of food from daytime feeding. The mean number of prey in larval guts followed the increase and decline pattern described for feeding incidence. Most larvae had maximal prey number in the gut in the morning and again in the afternoon (Fig. 4b). This pattern was most obvious for *Carangoides* sp. and *Acanthocephala* sp., whereas *Cynoglossus* sp. only showed a morning peak, and *Scorpaenodes* sp., an afternoon peak. The number of large larvae with a high number of

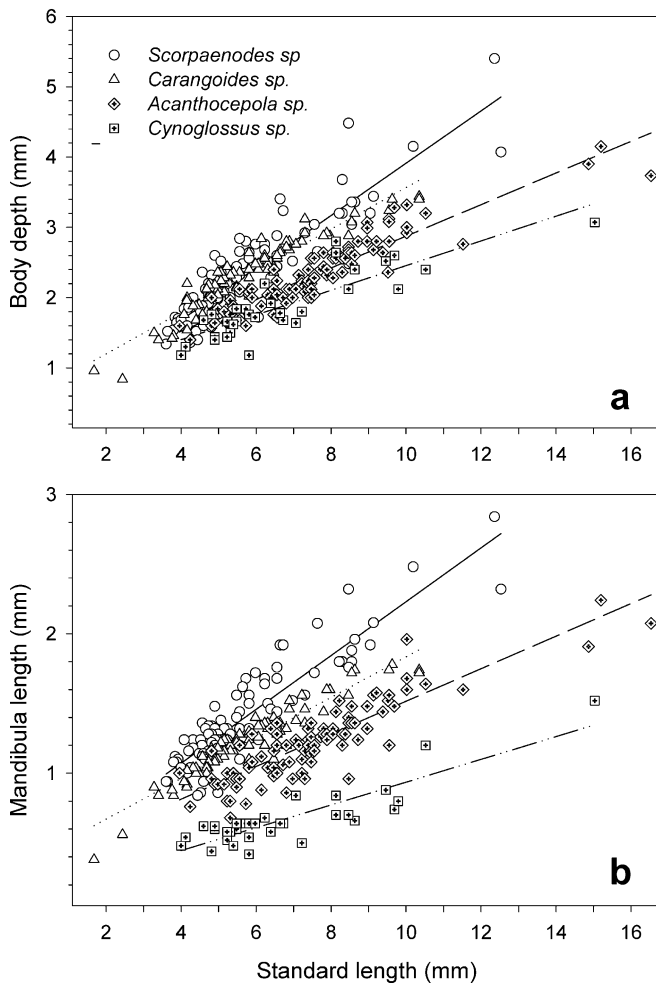


Fig. 2a, b Morphological differences in *Scorpaenodes* sp., *Carangoides* sp., *Acanthocephala* sp. and *Cynoglossus* sp.: **a** body depth as a function of standard length and **b** lower jaw length as a function of standard length. Species are indicated by *symbols* as shown in the figure, regression lines are as follows *Scorpaenodes* sp. (solid line), *Carangoides* sp. (dotted line), *Acanthocephala* sp. (broken line) and *Cynoglossus* sp. (broken line with dots)

prey in gut was evenly distributed in the samples; hence, the observations are not biased by any systematic pattern in larval mean size during the day. *Carangoides* sp. larvae generally had the largest number of prey in their guts (mean and standard deviation, 15 ± 9 prey per larva). *Acanthocephala* sp. had on average ca. 12 ± 6 prey per larva, *Cynoglossus* sp., on average 9 ± 4 prey per

Table 1 *Scorpaenodes* sp., *Carangoides* sp., *Acanthocephala* sp. and *Cynoglossus* sp. Regression of body depth and mandibula length against larval standard length (**significantly different from zero, $P < 0.01$; + and # insignificantly different from zero, $P = 0.34$ and $P = 0.06$, respectively)

	Body depth against standard length (mm)			Mandibula length against standard length (mm)		
	Intercept	Slope	r^2	Intercept	Slope	r^2
<i>Scorpaenodes</i> sp.	0.19**	0.37	0.80	0.30 ⁺	0.19	0.83
<i>Carangoides</i> sp.	0.61**	0.30	0.89	0.38**	0.15	0.90
<i>Acanthocephala</i> sp.	0.62**	0.23	0.84	0.35**	0.12	0.77
<i>Cynoglossus</i> sp.	0.70**	0.18	0.73	0.12 [#]	0.08	0.76

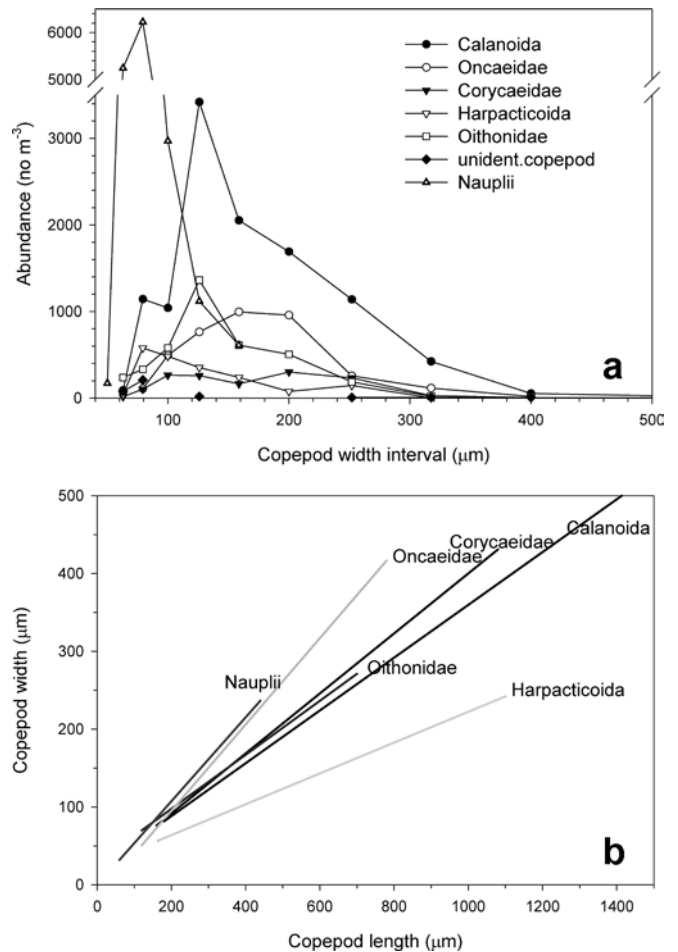


Fig. 3 a Abundance of the dominant copepod groups available to fish larvae. Data from all zooplankton net-samples are pooled. *Symbols* indicate different groups as shown in the figure. **b** Copepod length-width relations for the dominant copepod groups in the zooplankton

larva, and *Scorpaenodes* sp., 8 ± 4 prey per larva. Number of prey per larva increased during ontogeny for *Carangoides* sp., *Scorpaenodes* sp. and *Acanthocephala* sp., whereas no increase was observed for *Cynoglossus* sp. (Fig. 5).

Copepods dominated the diet of all four species. Fractions of non-copepod prey found in the guts included the following: euphausiids (0.7% by number; average width = 282 μm), chaetognaths (0.7%; average

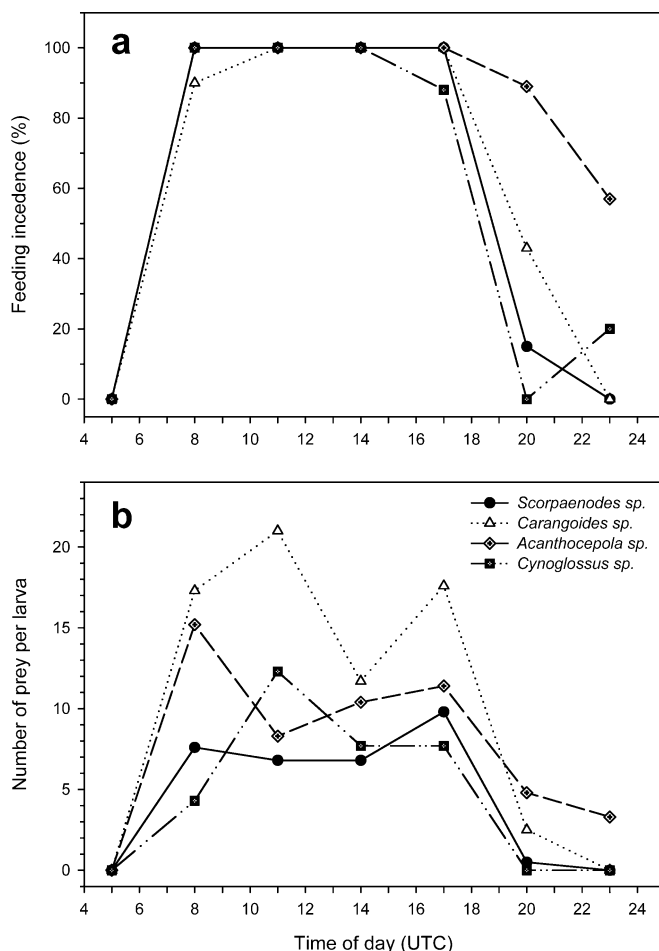


Fig. 4a, b *Scorpaenodes* sp., *Carangoides* sp., *Acanthocephala* sp. and *Cynoglossus* sp. **a** Feeding incidence, showing relationship between time of day and proportion of larvae feeding and **b** mean number of prey per larva in relation to time of day. Approximate times of sunrise (0600 hours) and sunset (1800 hours). Symbols and lines as in Fig. 2

width = 516 μ m) and gastropods (0.5%; average width = 247 μ m). Because of their small contribution to the diet of the larvae they are not considered in the present analysis. Composition of gut contents differed among species and size groups of larvae. *Scorpaenodes* sp. larvae < 7.0 mm SL had a mix of Calanoida, Oncaeiidae and Corycaeiidae in their gut (Fig. 6a). In the larger larvae (> 7.0 mm SL), calanoids dominated the gut contents (> 85%). The main prey of *Carangoides* sp. were Oncaeiidae and Corycaeiidae (between 47% and 61%) (Fig. 6b). Small *Carangoides* sp. larvae ate a mix of Calanoida, Oncaeiidae, Corycaeiidae and Harpacticoida. In the larger *Carangoides* sp. larvae (> 9.0 mm SL), however, harpacticoids were of little importance. In the guts of *Acanthocephala* sp., the main items were Oncaeiidae and Corycaeiidae (between 42% and 71%) (Fig. 6c). The diet composition for *Acanthocephala* sp. was very similar to that of *Carangoides* sp., and during ontogeny the relative importance of harpacticoids eaten by smaller larvae declined gradually. Finally, the guts of smaller larval *Cynoglossus* sp. had a remarkably high prevalence

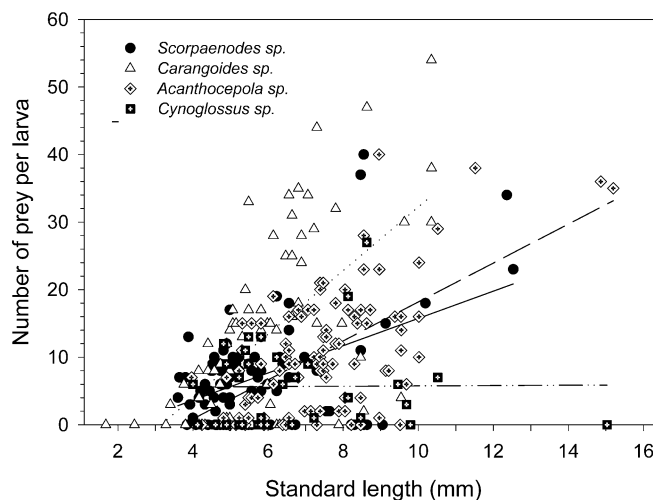


Fig. 5 *Scorpaenodes* sp., *Carangoides* sp., *Acanthocephala* sp. and *Cynoglossus* sp. Relationship between number of prey in stomach and size of larvae. Linear regressions are indicated ($P < 0.05$ for all except *Cynoglossus* sp. where $P = 0.99$). Species are indicated by symbols as shown in the figure, regression lines are as in Fig. 2

of harpacticoids (between 36% and 67%), while during ontogeny of this species the relative importance of Oncaeiidae increased (from 7% to 36%) (Fig. 6d).

In accordance with the observed variation in prey composition, mean prey size also differed among species and varied during ontogeny (Fig. 7, closed circles). The value for each mean prey width in our calculation is based on values for at least three prey entries, which may reflect data from several fish larvae. The rate of change in mean prey size (width of prey), i.e. the slopes of the regressions in Fig. 7, differed significantly among most species. In pairwise comparisons of slopes only *Carangoides* sp. and *Acanthocephala* sp. were not significantly different ($P = 0.22$), all other combinations were significant (for all: $P < 0.05$). The calculated preferences followed the same pattern and differed among species as well as changed during ontogeny (Fig. 7, open squares). Comparison between prey width in guts and preferred prey width showed that larval preference was skewed towards the larger prey sizes present in the environment. The width of the prey preference spectrum (SLH-index) was calculated for a range of larval size groups, and the change during ontogeny was investigated by linear regressions (Fig. 8). There was no significant relationship to larval size (for all: $P > 0.19$), and a covariance analysis with both larval size and species showed an insignificant species effect ($P > 0.26$). The mean SLH for all sizes and species was 0.13.

Larvae not only selected for size, but also showed differences in their preference for equally sized prey of different taxa. This was apparent when comparing size-preference curves for each taxonomic prey group for the different larvae (Fig. 9). The combined analysis of prey size and taxa requires a larger set of data than needed for separate analysis of the parameters, and we only carried out the analysis for the most abundant size group of

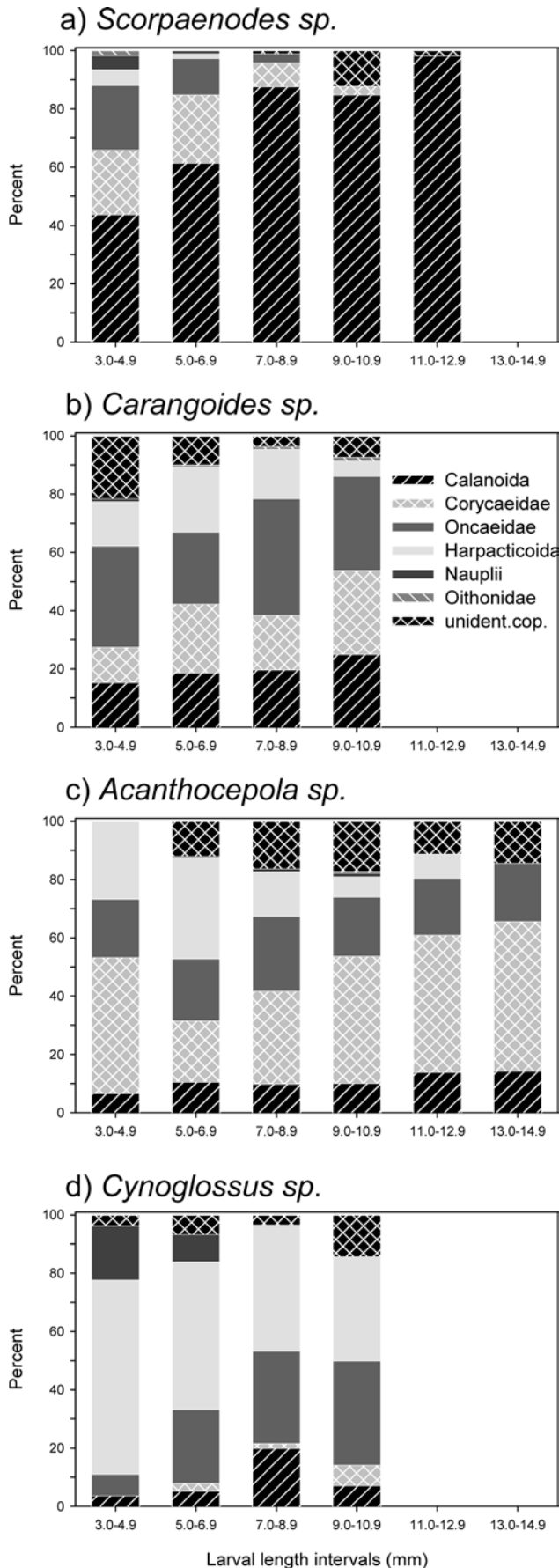


Fig. 6 *Scorpaenodes* sp. (a), *Carangoides* sp. (b), *Acanthocepola* sp. (c) and *Cynoglossus* sp. (d). Cumulative diet composition in relation to larval size class. Different *hatching of bars* illustrate prey types as indicated in panel b

larvae (5–10 mm). *Scorpaenodes* sp., which showed increasing preference for calanoids during ontogeny (Fig. 6a), preferred specimens >250 μ m (Fig. 9a), while the average size of calanoids in the zooplankton was only 140 μ m. Also *Scorpaenodes* sp. supplemented its diet with Oncaeidae and Corycaeidae, of which they preferred larger than average corycaeids. *Acanthocepola* sp. and *Carangoides* sp. showed similarities in their prey preferences. Their diet included many Corycaeidae, Oncaeidae and, in smaller larvae, also Harpacticoida (Fig. 6b, c), which were the least abundant components in the zooplankton. Besides their taxonomic preference, they also showed a clear selection for larger sized specimens of those taxa. However, *Carangoides* sp. preferred Oncaeidae of about 250–400 μ m, Corycaeidae of about 200–400 μ m and Harpacticoida of about 140–150 μ m (Fig. 9b), which were all larger than the average size of these groups in the environment, whereas *Acanthocepola* sp. preferred Oncaeidae of about 200–250 μ m, Corycaeidae of about 150–250 μ m and Harpacticoida of about 140 μ m (Fig. 9c). During ontogeny the diet of *Cynoglossus* sp. shifted from dominance of small sized nauplii to the larger sized Oncaeidae (Fig. 6d). It is obvious that of all four larvae, *Cynoglossus* sp. prefers the smallest prey (Fig. 9). In summary, the larvae did not feed on the whole spectrum of available copepod species; we observed for all larval species that the Corycaeidae and Harpacticoida were highly preferred groups in their respective size ranges, while the relative preference of Oncaeidae and Calanoida differed among larval species. Nauplii were generally of very low preference.

During ontogeny the relative size of the most preferred prey declined, both when expressed by prey width against larval mouth size and by prey length against larval length (Fig. 10a, b). The decline is significant for all illustrated comparisons (for all: $P < 0.05$), except the prey width/mouth size for *Scorpaenodes* sp. ($P = 0.78$). The relative size of preferred prey differed among species, dependent on whether the comparison was to mouth size or to larval length. For example, *Cynoglossus* sp. preferred wider prey relative to its mouth size than the other species of larvae (Fig. 10a), but it preferred smaller prey than the others in the situation when the relative prey size is expressed against larval length (Fig. 10b).

Discussion

Our study showed a series of characteristic feeding patterns as well as clear differences among the four larvae. Common to *Scorpaenodes* sp., *Carangoides* sp.,

Fig. 7 *Scorpaenodes* sp., *Carangoides* sp., *Acanthocephala* sp. and *Cynoglossus* sp. Mean and standard deviation of log-transformed prey widths in relation to mean standard length (mm) of larval groups (closed circles; regression: solid line). Most preferred prey widths in relation to mean standard length of larval groups (open squares; regression: broken line)

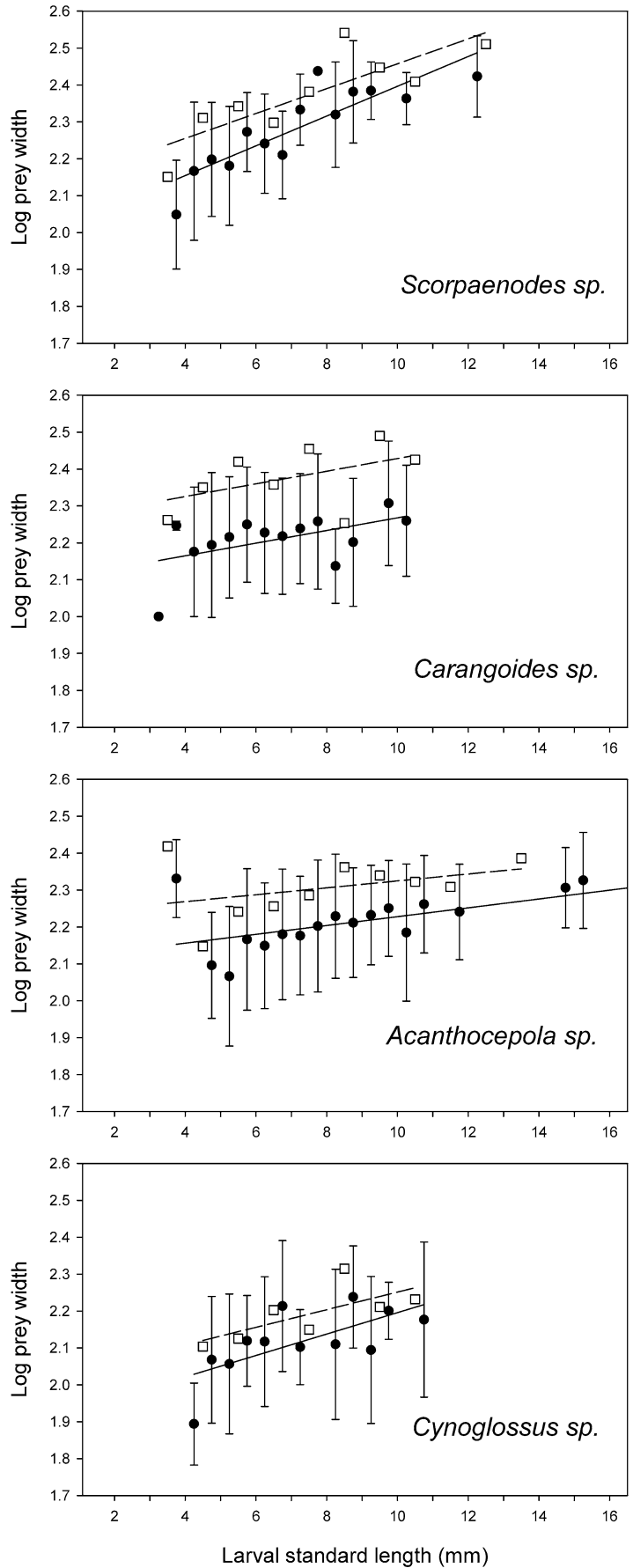


Fig. 8 *Scorpaenodes* sp., *Carangoides* sp., *Acanthocephala* sp. and *Cynoglossus* sp. The width of prey size spectra, expressed by the standard deviation of log-transformed prey width data (SLH-index) as a function of larval size. Slopes of all regressions are not different from 0 ($P > 0.19$)

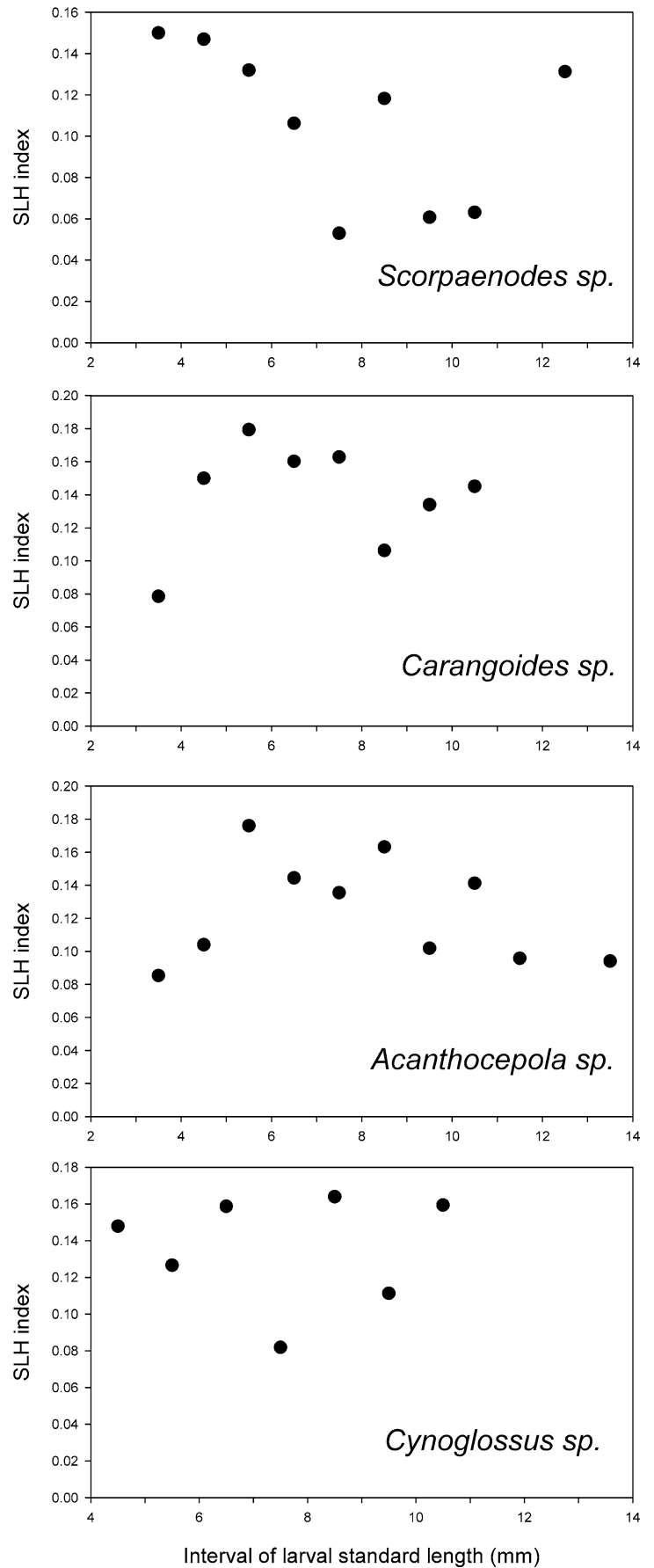
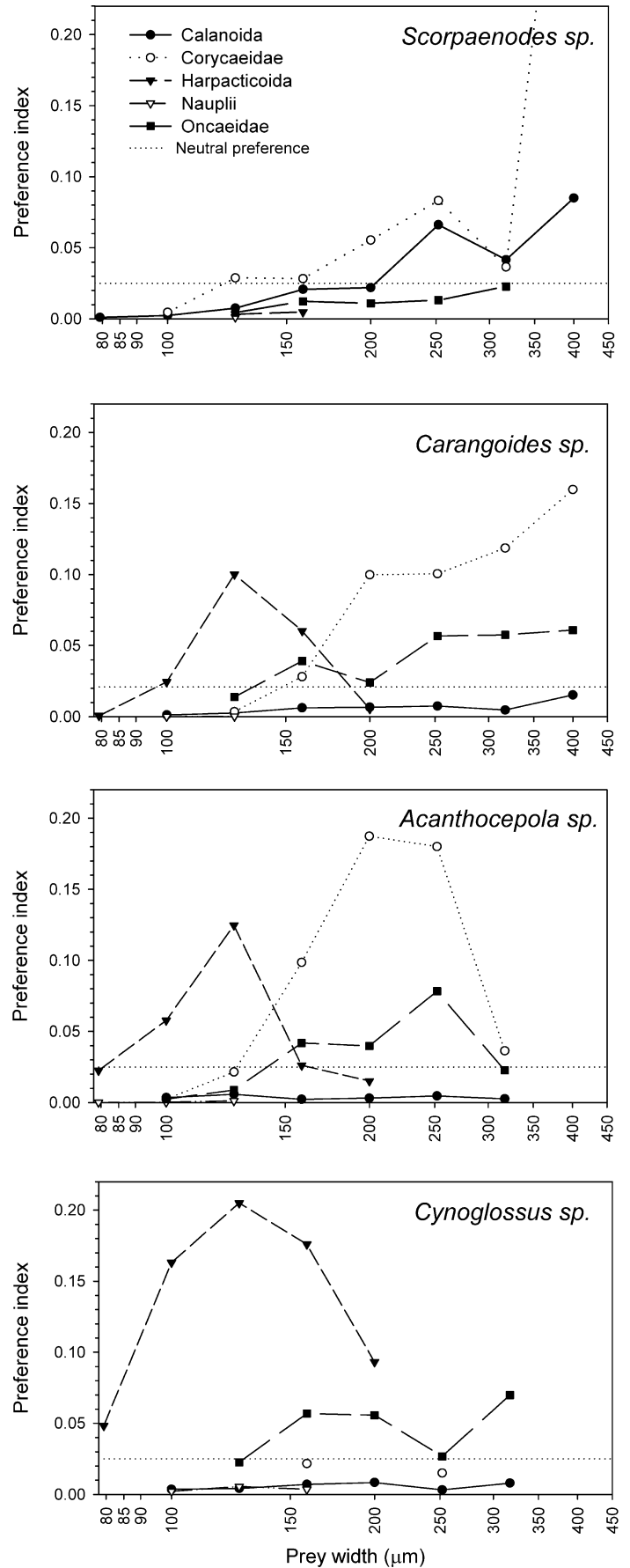


Fig. 9 *Scorpaenodes* sp., *Carangoides* sp., *Acanthocephala* sp. and *Cynoglossus* sp. Chesson index of preference along an axis of \log_{10} size intervals of prey width for fish larvae of size interval 5–10 mm. Preference for each copepod group is illustrated by separate curves. Preference values accumulate to one in each fish species. The horizontal, dotted line shows the index of neutral preference



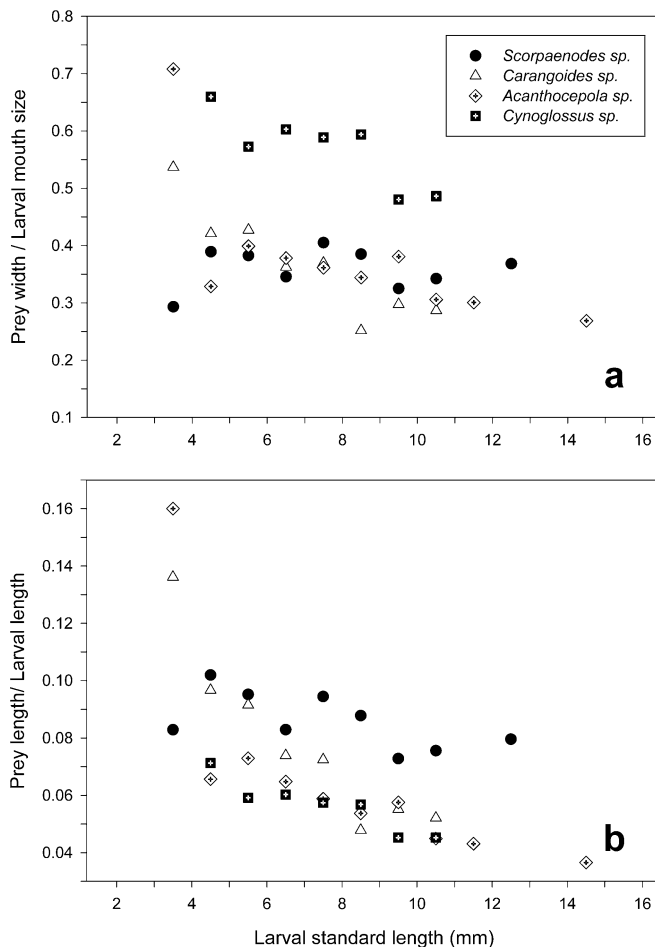


Fig. 10a, b *Scorpaenodes sp.*, *Carangoides sp.*, *Acanthocephala sp.* and *Cynoglossus sp.* **a** Width of the most preferred prey in proportion to larval mouth size as a function of larval standard length (mm). **b** Length of the most preferred prey in proportion to larval length as a function of larval standard length

Acanthocephala sp. and *Cynoglossus sp.* was an increase in preferred prey size and number of prey in gut during ontogeny. Another characteristic of larval feeding was the uniform width of the relative prey size spectrum. Our measure of the relative width (SLH-index) was not only constant across the larval sizes investigated, but was also approximately of the same magnitude (0.13) for all species. Likewise, constancy in the SLH-index during ontogeny has been observed for six different species of myctophiform larval fish (ca. 5–17 mm) from the Mediterranean (Sabatés and Saiz 2000). Scharf et al. (2000) found a constant relative width of the size preference spectrum for 18 species of juvenile and adult fish caught off the northeast coast of the United States. These fishes were mainly 60–200 mm, hence of a larger size range than in the present study. For even larger fish (> 500 mm), these authors observed a negative relationship in the SLH-index with fish size. A negative relationship in SLH was also observed in the largest larvae (7–15 mm) of blue whiting, *Micromesistius pautassou*, from the northern Spanish Coast (González-

Quirós and Anadón 2001). González-Quirós and Anadón (2001) suggested that the decrease in SLH-index in large larvae was due to a low abundance of large prey; hence, the large larvae have difficulties encountering large prey, although they would be capable of ingesting them. However, in the cited studies, the SLH calculations were based on gut contents only, and not “calibrated” against available prey by calculating preferences as in the present study. For comparative purposes the calculated widths of prey size spectra should preferably be independent of prey composition in the environment; hence, the preference-based spectrum is preferable to those directly estimated from stomach contents.

A positive relationship between average prey size and size of larvae has been reported for several species of fish larvae (e.g. Govoni et al. 1983; Kellermann 1990; Young and Davis 1990; Pepin and Penney 1997; DeVries et al. 1998; Sabatés and Saiz 2000), but the proportionality differs among species, as observed in the present study. Pepin and Penney (1997) and Sabatés and Saiz (2000) also found that even closely related species differed in the rate by which the average size of ingested prey increased during larval ontogeny. Sabatés and Saiz (2000) also found that observed difference in prey preference between species to a great extent was related to morphological differences between larval species. Obviously, the larvae of the present study differed markedly in morphology, and our analysis indicates that different feeding strategies of larvae to some extent are related to differences in larval morphology. Body depth per se does not set restrictions on the size of prey ingested, but body depth as a factor influencing swimming and manoeuvring abilities could influence feeding behaviour and hence the prey preference. For example, the two species of largest body depth, *Scorpaenodes sp.* and *Carangoides sp.*, were the species that, relative to their length, preferred the largest prey organisms. Hence, when we registered less stomach contents in *Scorpaenodes sp.* (about 8 prey per stomach) than for, e.g., *Carangoides sp.*, this was counterbalanced by the larger size and biomass of the prey items. Also the differences in findings for *Acanthocephala sp.* and *Carangoides sp.* might be related to differences in their morphology. Both their relative mouth size and body depth differed, and so did their size preference of the same prey taxa. Further, *Cynoglossus sp.*, having a relatively small mouth and body depth, was the species that preferred the smallest prey relative to its length. In summary, these findings suggest that specific feeding patterns differ among the four species of fish larvae: (1) *Scorpaenodes sp.* fed on abundant and large prey, a common prey type (calanoids) was preferred, but larger than average prey of that type was eaten. (2) *Acanthocephala sp.* and *Carangoides sp.* fed on less abundant and large prey, a less common prey type was preferred (e.g. Oncaeidae and Corycaeidae), and larger than average prey of that type was eaten. (3) *Cynoglossus sp.* fed on smaller sized prey, and both common (e.g.

nauplii) and less abundant (e.g. harpacticoids) prey were important in the diet when larger prey were less available due to restrictions of gape size and body depth. Differences in prey preference between species, and between size groups of the same species, might reduce inter- and intra-specific competition for the food resource. In this context it should be noted that a prey preference estimate based on stomach contents and integrated samples of environmental prey composition incorporates the spatial component of prey preference. Hence, it might include the behavioural aspect that a predator swims towards enhanced concentrations of a preferred prey type. Our findings of constancy in the relative niche breadth imply that during development the larvae invade new niches (of prey sizes) as they grow; hence, the competition with smaller sized larvae for the smaller sized prey is lessened. As pointed out by Krebs and Turingan (2003), the foraging of larvae is not only dependent on what the larvae are capable of ingesting, but also on the actual environmental plankton composition. Govoni et al. (1983) found that when food is abundant, diet overlap is very common. Pepin and Penney (2000) observed in their study that larval predation pressure on the zooplankton community was very low, but found that larval fish gradually shifted their diet to larger prey items, thus limiting competition. However, they also found a substantial overlap in the types and sizes of prey eaten by different species that co-occurred, and concluded that since the predation pressure on the zooplankton community was generally low there was less reason to partition resources. Accordingly, the observed overlap in prey eaten by the fish larvae *Carangoides* sp. and *Acanthocephala* sp. does not necessarily imply strong competition among these species. The density of copepods in this study ranged between 1,800 and 9,300 m⁻³ and the density of fish larvae was <6.7 m⁻² (approximately 0.1 m³ given the water depth of 69 m), which means that the number of available copepods per larva is 18,000 to 93,000. Hence, food seems to be sufficiently abundant to lessen such competition.

Despite the lack of apparent competition for food, the feeding pattern of the four larvae differed in several aspects. Differences in relative abundance of larval species across their area of distribution, as shown in the concurrent study described by Munk et al. (2004), as well as differences in size, morphology and behaviour apparently lead to differences in larval foraging strategies. The applied comparative approach has proven useful for ascertaining strategies and evaluating factors that determine prey preference and larval food intake. With the high species diversity in tropical waters the comparative information is important in the description of ichthyoplankton ecology in these waters.

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