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Diet composition and feeding habits of fish larvae of two co-occurring species (Pisces: Callionymidae and Bothidae) in the North-western Mediterranean

L. Sánchez-Velasco

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Larval diet and feeding habits of the marine fish *Callionymus* sp. and *Arnoglossus laterna* larvae, two species co-occurring in the Catalan Sea (May, 1992), were compared. For the *Callionymus* sp. larvae, the dominant prey were *Oithona* spp. and *Oncaea* sp. copepodites, and with less frequency, *Paracalanus* sp. copepodites. For *A. laterna* larvae, the diet was composed only of *Paracalanus* sp. copepodites. Copepod nauplii were not important in the diet of these two species, although they were the most abundant zooplankter in the area. As larvae of both species grew, the size and number of prey increased. This tendency was more obvious in *Callionymus* sp. larvae, which reflected a greater prey diversity during all their early ontogeny. An analysis of covariance showed prey size increased with larval size in both species, but the prey consumed by *Callionymus* sp. larvae was larger than prey of *A. laterna*, corresponding to the larger mouth size ($p<0.001$). The results of this study show that these co-occurring species have different feeding strategies.

Key words: fish larvae, diet composition, feeding habits, Catalan Sea, north-western Mediterranean.

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L. Sánchez-Velasco: Centro Interdisciplinario de Ciencias Marinas, Laboratorio de Plancton y Ecología Marina. Playa El Conchalito s/n, C.P. 23000, La Paz, Baja California Sur, México: tel: 52 112 25344; fax: +52 112 25322; e-mail: lsvelasc@vmredipn.ipn.mx

Introduction

One of the most important influences on the survival of fish larvae is the availability of suitable food, and knowledge of their feeding behaviour is necessary for an understanding of the factors that affect the mortality of the larvae in the wild and the subsequent year-class strengths of the adult fish (Last, 1980).

Feeding strategies of fish larvae are complex. Moreover, they depend on the food availability in areas defined by mesoscale hydrographic structures (Iles and Sinclair, 1982). Some factors, such as the physiological and morphological features of the larvae, and their innate preferences, play important roles. Perception, recognition, capture, and digestibility of prey influence the apparent selection of food (e.g. Hunter, 1972; Govoni *et al.*, 1986; Fortier and Harris, 1989).

In the north-western Mediterranean, fish-larval distribution and abundance have been studied in relation to hydrographic factors (e.g. Palomera and Sabatés, 1990; Sabatés, 1990; Palomera, 1992), from which the need to understand the trophic processes that affect larval survival have been recognized. Studies focused on fish-larval feeding are scarce in this area (Sánchez-Velasco and Norbis, 1998).

The *Callionymus* sp. (probably *C. maculatus*) and the *Arnoglossus laterna* larvae form about the 50% of the ichthyoplankton community along the Catalan coast in the early spring. Even though the fish larvae of these two species are morphologically different, they are located on the continental shelf and slope, showing a high degree of spatial coexistence in the slope zone (Sabatés, 1990; Sabatés and Olivar, 1996).

The aim of this work is to describe and compare the feeding habits of *Callionymus* sp. and *Arnoglossus laterna*, two co-occurring fish larvae species in the Catalan Sea, when they spawn in great abundance. Feeding incidence, diet composition, and changes in diet through the different growing stages are discussed in relation to morphological features of the larvae and their prey.

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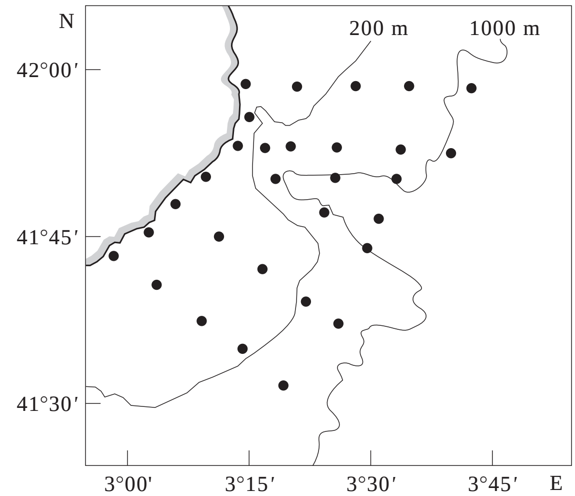

Figure 1. Location of the study area and sampling stations.

Table 1. Length distribution and feeding incidence of *Callionymus* sp. larvae collected in the Catalan Sea (May 1992). Daylight hours were from 6:30 to 20:30. *Post-flexion larvae.

Length interval (mm)	*Callionymus* sp.			
	Number of larvae analysed		Larvae with food (%)	
	Day	Night	Day	Night
2	106	35	74.3	62.9
3	111	34	94.5	79.4
4*	81	13	98.8	98.8
5	27	7	100.0	100.0
6	8		100.0	
7	1	1	100.0	100.0
Total	334	90	89.7	71.1

Materials and methods

Field methods

The study area is in the northern part of the Catalan Sea (north-western Mediterranean) (Fig. 1). Sampling was made aboard the R/V ‘‘García del Cid’’ during 14 to 20 May 1992 (cruise PRIM I). Macro and micro-zooplankton were obtained in each station almost simultaneously. Macro-zooplankton samples were collected using a bongo net with a mouth diameter of 60 cm and 300-μm mesh size. Oblique tows were made from just above the bottom to the surface in the shallow waters or from 200 m depth to the surface at 2 kt. A Juday-Bogorov net with a mouth diameter of 39 cm and 300-μm mesh size was also used to collect macrozooplankton samples. These hauls were horizontal at 10-, 40-, and 80-m depth using opening-closing devices and all nets were equipped with general oceanic flowmeters. Micro-zooplankton samples were collected with a conical net of mouth diameter of 14.5 cm and a mesh size of 60 μm again using opening-closing devices. Vertical hauls were made from 40- to 25-m depth (subsurface level) and from 25 m to the surface (surface level). The volume of water passing through the net during each haul was calculated multiplying the area of the mouth by the sampling distance. Each sample was fixed immediately after capture with a 5% formaldehyde solution buffered with sodium borate.

Laboratory analysis

All *Callionymus* sp. and *Arnoglossus laterna* larvae caught in good condition were examined. Standard length (SL) (tip of the snout to tip of the notochord) and length of the lower jaw (tip of the lower jaw to angle end) of each larvae was measured using a dissecting microscope with an ocular micrometre. The gut of each larvae were separated and opened lengthwise with electrolytically sharpened needles of tungsten. The prey items were identified to the lowest possible taxon and measured transversally. The stage of digestion was assigned to each prey according to the following criteria: (1) low, when it was found practically intact; (2) medium, when only the carapace, or part of it, was found sufficiently preserved to enable it to be recognized; (3) high, when it had lost its original shape and had a highly digested carapace. The relation between the prey stage of digestion and its position in the larval gut was checked.

In order to identify the most abundant plankters in this study site, micro-zooplankton samples were identified to the lowest possible taxa and counted.

Data analysis

The percent frequency of occurrence (%FO) and percent of total number (%n) of prey ingested by larvae in each size group were calculated for each food category. An estimate of the relative importance of each food category was obtained by multiplying %FO by %n (Laroche, 1982).

Analysis of covariance (ANCOVA) was used to compare selected morphometric relationships between larvae and their prey both after fixation. Morphometric data were log-transformed [Ln(X+1)] to homogenize variances. The normality of data was verified with the Kolmogorov–Smirov test (Sokal and Rohlf, 1979). An ANCOVA was applied for each pair of variables: (a) standard length of larvae and lower jaw length; and (b) lower jaw length and prey width. In both, larvae from 3- to 6.99-mm SL with identifiable prey in their guts were considered.

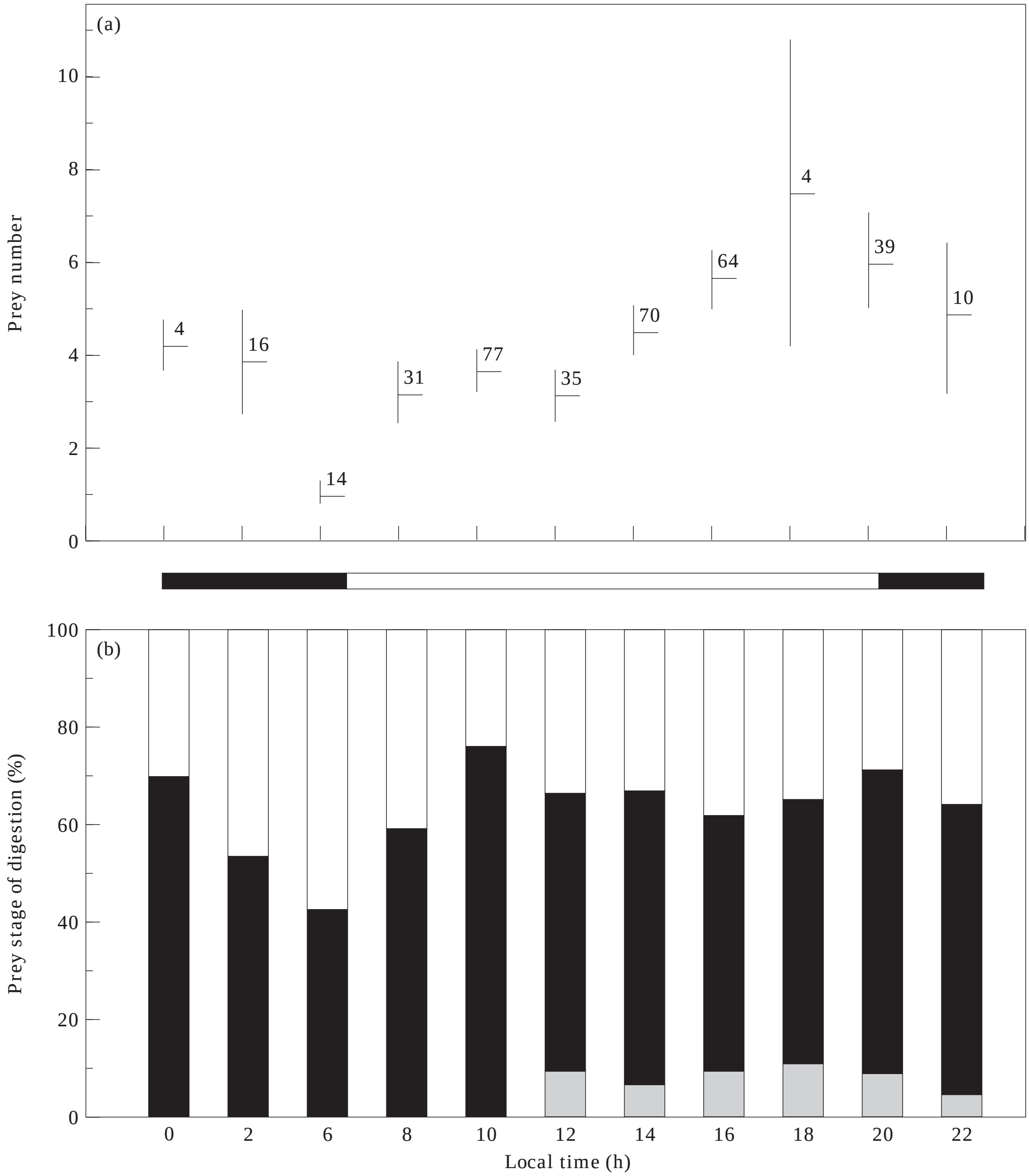

Figure 2. Feeding in relation to daily cycle of *Callionymus* sp. (n = 361) larvae collected in the Catalan Sea (May 1992). Daylight hours were from 6:30 to 20:30. (a) Mean and standard deviation of prey consumed by larvae. (b) Accumulated percentage of stage of digestion of prey consumed by larvae: low (▨); medium (■); high (□). Note: larvae at 4 h were not collected.

Results

Feeding incidence and diel feeding patterns

Callionymus sp. larvae had a high feeding incidence: 89% during the daylight hours (6:30 to 20:30 local time) and 71% during the night. The feeding incidence increased as the larvae increased in size, to more than 98% in larvae at the post-flexion stage (>4 mm) (Table 1). The number of prey eaten per larva fluctuated between 1 to 14 and the average consumption increased at sunset. The medium stage of digestion was greatest during the day (Fig. 2).

The feeding incidence of *A. laterna* larvae was relatively low, only 28% during daylight and 18% during the first part of the night (Table 2). No food was found in the guts between 22:00 and 04:00 h. The number of prey

Table 2. Length distribution and feeding incidence of *Arnoglossus laterna* larvae collected in the Catalan Sea (May 1992). Daylight hours were from 6:30 to 20:30. *Post-flexion larvae.

Length interval (mm)	*Arnoglossus laterna*			
	Number of larvae analysed		Larvae with food (%)	
	Day	Night	Day	Night
3	39	1	7.7	100.0
4	97	19	20.6	21.1
5	129	23	23.3	15.0
6	76	24	38.2	8.3
7	68	24	42.6	0.0
8*	34	13	35.3	23.1
9	9	2	22.2	0.0
10	4	4	25.0	50.0
11	2	6	50.0	50.0
12	1	4	100.0	0.0
13				
14				
15	1		100.0	
Total	460	120	28.0	18.3

consumed per larva fluctuated between 1 and 5, with increased average consumption during sunrise and sunset. The medium stage of digestion was the most common (Fig. 3).

No relation was found between the position of prey in the gut and the stage of digestion.

Diet composition

The relative importance index (Laroche, 1982) shows the diet composition between the species analysed was very different. The *Callionymus* sp. larvae fed from a wide variety of prey dominated by copepodites of *Oithona* spp. (probably *Oithona helgolandica*) and *Oncaea* sp. (probably *Oncaea subtilis*). In contrast, *A. laterna* larvae only consumed *Paracalanus* sp. copepodites (probably *Paracalanus parvus*) (Table 3).

Diet diversification throughout larval development

Even from the smallest sizes, larvae of *Callionymus* sp. had a very diversified diet, feeding on the *Oithona* spp. copepodites and on a smaller scale the *Oncaea* sp. For post-flexion larvae, consumption of *Oncaea* sp. copepodites increased and to a lesser extent *Paracalanus* sp. copepodites, but these larvae continued consuming copepodites of *Oithona* spp. (Fig. 4). Larvae of *A. laterna* only feed on *Paracalanus* sp. copepodites during early ontogeny (Fig. 5).

Prey size and number

The size and number of prey consumed increased as larval size increased in both species. The number of the prey consumed by larvae of *Callionymus* sp., however, was higher than *A. laterna* larvae (Figs 6 and 7).

Morphometric relationships between larvae and their prey

ANCOVA indicated that the relationship of the standard legnth (SL) of the larvae and lower jaw length was significantly different between the two species analysed ($p<0.001$). The jaw length was bigger in the *Callionymus* sp. larvae. Also, the size of prey consumed was significantly larger in these larvae ($p<0.001$) (Table 4).

Micro-zooplankton composition in the study area

Copepod nauplii were the most abundant zooplankter in the area in both levels, followed by *Oithona* spp., *Paracalanus* sp., *Centropages* sp. and *Oncaea subtilis* copepodites (Table 5).

Discussion

Feeding incidence and diel feeding patterns

The larvae of *Callionymus* sp. and *A. laterna* have different feeding habits in relation to the daily cycle. The high feeding incidence of *Callionymus* sp. larvae can be associated with a looped gut, which reduces the amount of regurgitation on capture as in the other perciform species (e.g. Arthur, 1976; Sánchez-Velasco and Norbis, 1998). The presence of prey with a medium stage of digestion during daylight and dark hours shows that these larvae can feed at any time. That larvae of *Callionymus* sp. have food in their guts during the night differs from the general diel feeding pattern of fish larvae (Hunter, 1981). However, there are records of the night-time feeding (e.g. Sumida and Moser, 1980; Watson and Davis, 1989), possibly by perceiving the prey's movements. For the *Callionymus* sp. larvae, the increasing number of consumed prey at sunset will increase the presence of prey in the gut of the captured larvae during the night. A relatively slow digestion process and long gut-transit rates, which can be up to 8 h according to Theilacker and Dorsey (1980), also influences the presence of food during the night.

The low feeding incidence of *A. laterna* larvae is difficult to understand since the shape of their gut is similar to other flatfish larvae that showed efficient food retention (e.g. Last, 1978; Jenkins, 1987). It is possible the low feeding incidence of *A. laterna* larvae is related to other aspects of their feeding habits, such as the reduced number of prey eaten, prey consumption limited

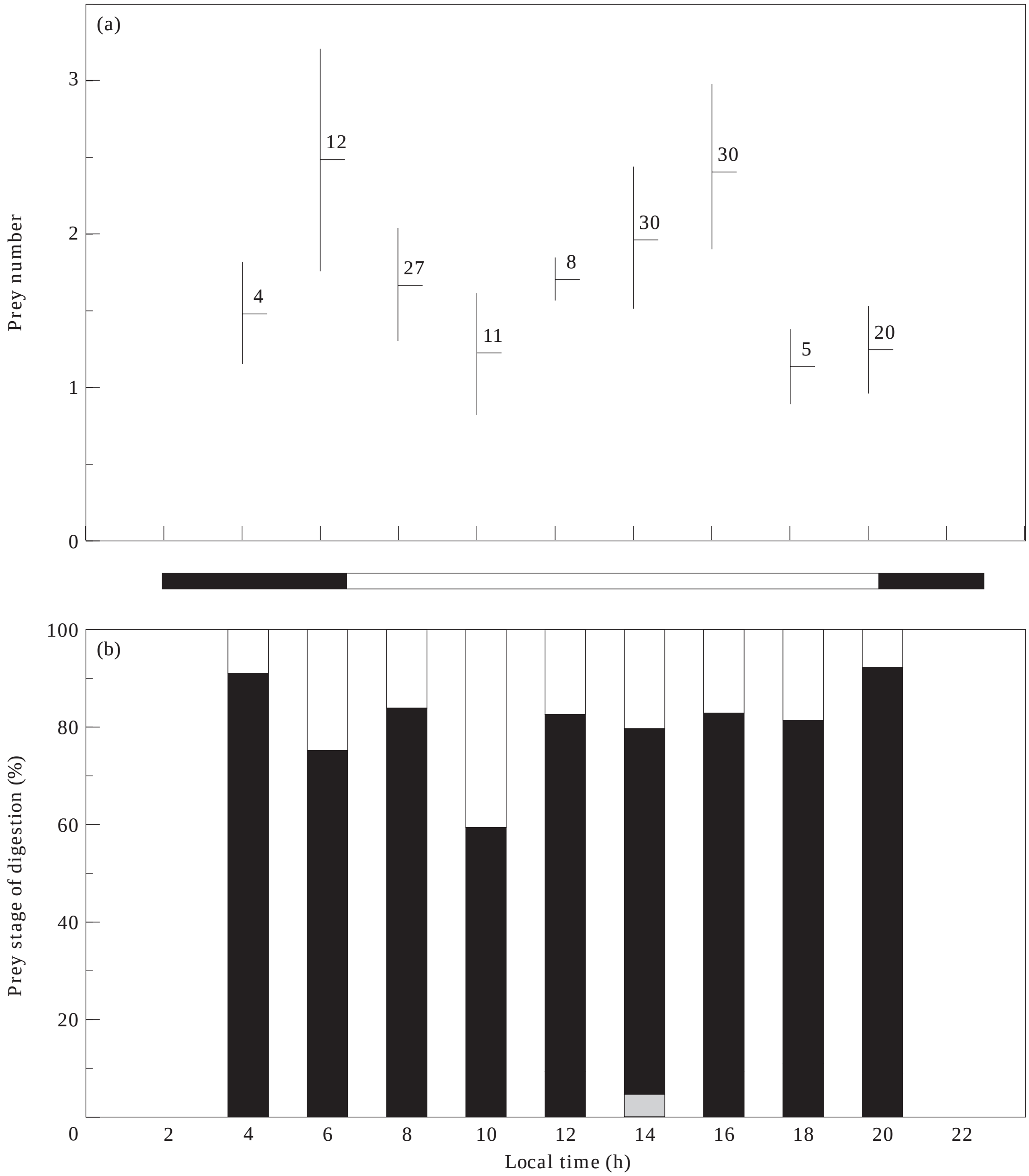

Figure 3. Feeding in relation to daily cycle of *Arnoglossus laterna* (n = 147) larvae collected in the Catalan Sea (May 1992). Daylight hours were from 6:30 to 20:30. (a) Mean and standard deviation of prey consumed by larvae. (b) Accumulated percentage of stage of digestion of prey consumed by larvae: low (□); medium (■); high (□).

to daylight hours, and also to the composition of the diet.

Diet composition

The *Callionymus* sp. and *A. laterna* larval diets were mainly composed of dominant species of copepodites in the area (e.g. *Oithona* spp. *Oncaea* sp., *Paracalanus* sp.). In spite of these two fish species feeding mainly on copepodites, strong difference in the diet composition was observed. It is interesting that *A. laterna* larvae only consumed *Paracalanus* sp. copepodites during their early ontogeny. This condition could be related to the sensory capacity of the larvae, but to date this has not been

Table 3. Diet composition of *Callionymus* sp. and *Arnoglossus laterna* larvae collected in the Catalan Sea (May 1992), expressed as percent frequency of occurrence (F%) in larval guts, percent of the total number (n%) of items in the diet, and the product (F × n) which was used as an index of relative importance. The number of larvae examined is given in brackets.

	Callionymus sp. (361)			*Arnoglossus laterna* (147)		
Prey items	n%	F%	F × n	n%	F%	F × n
Calanoid copepod eggs	2.9	6.6	19.3	2.6	4.1	10.9
Copepod nauplii	2.7	7.4	20.2	6.4	10.3	66.1
Copepodites *Microsetella* sp.	8.0	19.0	152.0	2.6	4.1	10.9
Copepodites *Oithona* spp.	37.5	60.7	2276.8			
Copepodites *Oncaea* sp.	23.2	47.3	1097.9			
Copepodites *Paracalanus* sp.	12.6	26.9	340.2	88.0	86.9	7644.3
Copepodites *Centropages* sp.	0.5	1.6	0.9	3.0	4.1	12.4
Copepodites unidentified	1.6	4.9	8.1			
Cirripedia	0.2	0.8	0.2			
Evadne nordmanni	3.7	2.5	9.2			
Podon intermedius	0.8	2.2	1.8			
Cladocera unidentified	2.1	4.9	10.4			
Pelecypoda	3.7	7.4	27.2			
Gastropoda	0.3	1.1	0.3			

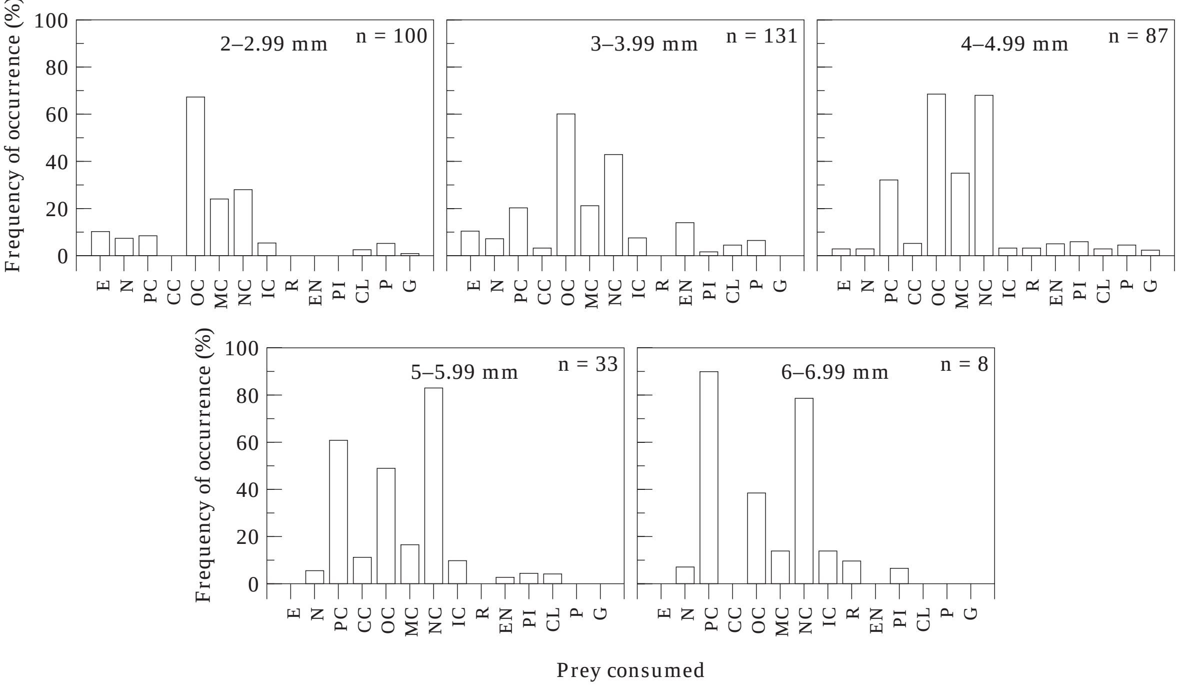

Figure 4. Frequency of occurrence of prey items in relation to size class of *Callionymus* sp. larvae collected in the Catalan Sea (May 1992). n, number of larvae examined. E = calanoid copepod eggs; N = copepod nauplii; PC = *Paracalanus* sp. copepodites; CC = *Centropages* sp. copepodites; OC = *Oithona* spp. copepodites; MC = *Microsetella* sp. copepodites; NC = *Oncaea* sp. copepodites; IC = calanoid copepodites unidentified; R = Cirripedia; EN = *Evadne nordmanni*; PI = *Podon intermedius*; CL = Cladocera unidentified; P = Pelecypoda; G = Gastropoda.

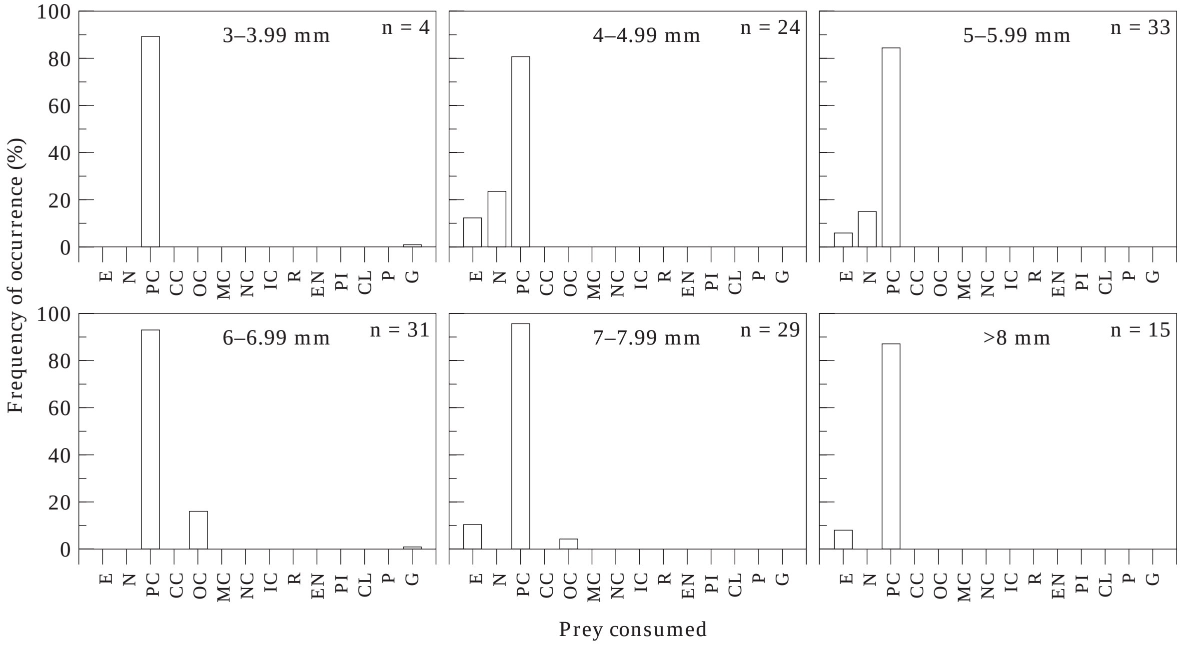

Figure 5. Frequency of occurrence of prey items in relation to size class of *Arnoglossus laterna* larvae collected in the Catalan Sea (May 1992). n, number of larvae examined. E = calanoid copepod eggs; N = copepod nauplii; PC = *Paracalanus* sp. copepodites; CC = *Centropages* sp. copepodites; OC = *Oithona* spp. copepodites; MC = *Microsetella* sp. copepodites; NC = *Oncaea* sp. copepodites; IC = calanoid copepodites unidentified; R = Cirripedia; EN = *Evadne nordmanni*; PI = *Podon intermedius*; CL = Cladocera unidentified; P = Pelecypoda; G = Gastropoda.

studied. Appelbaum and Schemmel (1983), Appelbaum *et al.* (1983) and Livingston (1987) analysed the sensory capacity of juveniles and adults of flatfish species. They noted a high sensory specialization related to feeding. After metamorphosis, fish became more active at night and they developed more chemosensory and mechanosensory organs, *Arnoglossus* being one of the most developed genera.

Differing from *A. laterna* larvae, the *Callionymus* sp. larvae tended to consume more cyclopoid copepods (*Oithona* spp. and *Oncaea* sp.) than calanoid copepodites (*Paracalanus* sp.). This behaviour was also observed in larvae of *C. lyra* from the North Sea (Last, 1980).

Copepod nauplii were not an important component in the diet of the fish larvae analysed in this study, even though they were significantly dominant in the planktonic environment. This contrasts with the composition of the diet of the majority of marine fish larvae which consume copepod nauplii at different frequencies, because of their great abundance in the environment as well as their appropriate size as food for fish larvae (e.g. Arthur, 1976; Turner, 1984; Watson and Davies, 1989).

The absence of copepod nauplii in the diet of *A. laterna* and *Callionymus* sp. larvae contrasts with the diet composition recorded in larvae of two sparid species found during the same survey (Sánchez-Velasco and Norbis, 1998), although they were located closer to the coast. These sparid species consumed copepod nauplii at different frequencies during their development, showing that components of the larval fish assemblages in the Catalan Sea have different diet compositions.

Changes in diet with size

Callionymus sp. and *A. laterna* larvae showed changes in diet during their early ontogeny. As larvae grow, the proportion of larger items in the diet increases. This shift may be associated with the increase of their energetic requirements (e.g. Blaxter, 1969; Hunter, 1981).

That *Callionymus* sp. larvae eat significantly larger prey than the *A. laterna* larvae could be related to their morphology, especially the mouth size, which functions as a ''filter'' to determine prey size (Chao and Musick, 1977). The jaw dimensions of *Callionymus* sp. larvae are larger than *A. laterna* larvae corresponding with the results.

To analyse morphometric relationships between the larvae and their prey, it is important to consider the problems of shrinkage in the net and after fixation, which will affect the jaw dimensions and the size of both larvae and the prey consumed. The degree of shrinkage

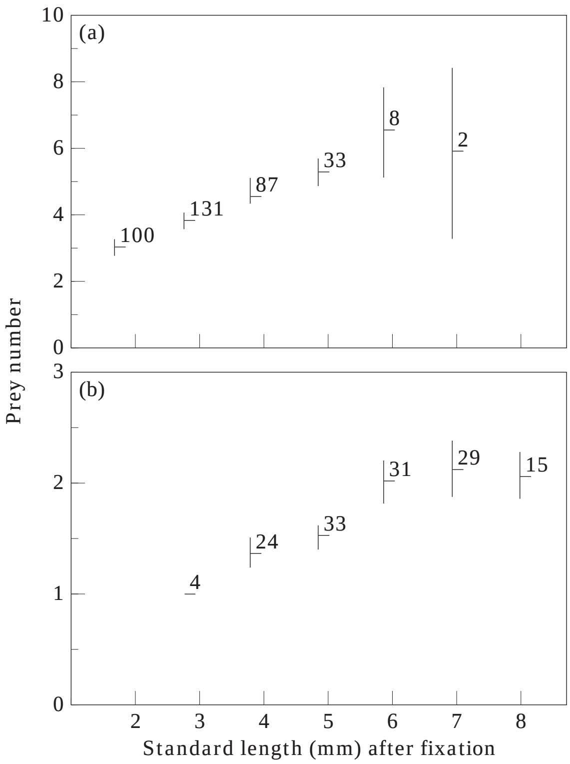

Figure 6. Mean and standard deviation of prey number consumed by (a) *Callionymus* sp. larvae and (b) *Arnoglossus laterna* larvae collected in the Catalan Sea (May 1992) in relation to standard length (mm) after fixation. Values beside data points indicate number of larvae examined.

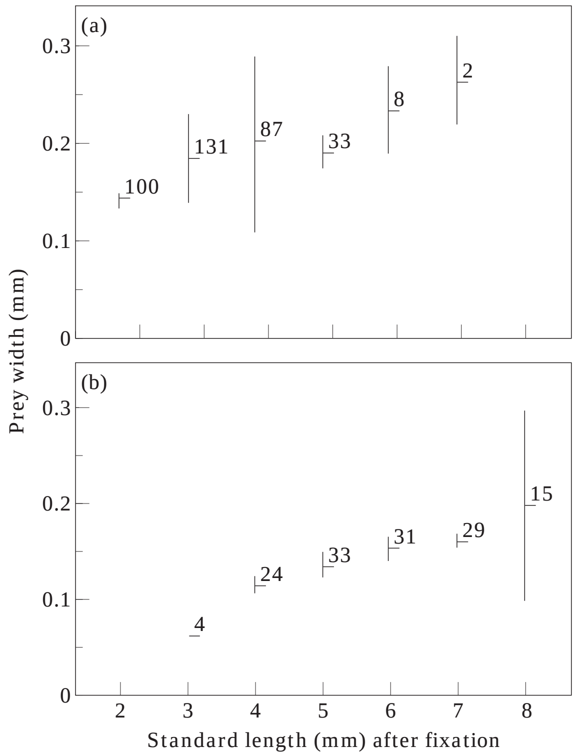

Figure 7. Mean and standard deviation of prey width consumed by (a) *Callionymus* sp. larvae and (b) *Arnoglossus laterna* larvae collected in the Catalan Sea (May 1992) in relation to standard length (mm) after fixation. Values beside data points indicate number of larvae examined.

varies with the species, type and strength of preservative, the time between death and preservation, and the size of the fish (Theilacker, 1980; Butler, 1992). It was not possible to do these analyses of fresh material and indeed, there was no way of checking shrinkage within the net before fixation. It was considered best, therefore, for all measurements to be made on fixed material where relative proportions were unlikely to be affected.

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Table 4. Results of ANCOVA comparing some morphometric relationships between *Callionymus* sp. and *Arnoglossus laterna* larvae and their prey. Samples collected in the Catalan sea (May 1992). SL, standard length (mm); LJL, lower jaw length (mm); PW, prey width (mm). Values were transformed in Ln (X + 1).

	Regression values		Analysis of covariance (ANCOVA)				
Cases analysed	y-intercept	Slope	d.f.	Sum of squares	Mean square	F-ratio	Significance level
SL/LJL			1	14.73	14.73	537.20	$p < 0.001$
Callionymus sp.	− 1.46	1.02					
Arnoglossus laterna	− 2.58	0.71					
LJL/PW			1	1.84	1.84	21.76	$p < 0.001$
Callionymus sp.	− 1.43	0.79					
Arnoglossus laterna	− 1.62	0.26					

Table 5. Most abundant and frequent micro-zooplankton taxa collected in the Catalan Sea (May 1992). Abundance was expressed as number of organisms. X, mean abundance; %F, percentage of occurrence in 31 sampling stations.

	Surface level (from 25 m of surface)		Subsurface level (from 40 to 25 m)	
Taxa	X	%FR	X	%FR
Copepod nauplii	7570.4	100.0	4409.4	100.0
Copepodites *Oithona* sp.	1250.8	100.0	1105.7	97.7
Copepodites *Paracalanus* sp.	996.8	95.1	904.5	97.7
Copepodites *Centropages* sp.	402.7	100.0	162.6	70.0
Pelecypoda veliger	134.8	92.6	82.9	81.4
Microsetella sp.	123.4	97.5	104.5	95.4
Oncaea subtilis	66.2	82.9	23.3	67.4
Centropages sp.	53.5	80.4	30.7	65.1
Evadne nordmanni	38.4	78.0	4.9	25.6
Aglaura hemistona	38.1	68.2	13.7	58.1
Gastropoda veliger	37.8	92.6	29.5	86.1
Copepodites *Acartia* sp.	26.5	78.1	20.2	69.7

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