

Diet of *Engraulis encrasicolus* in the northern Adriatic Sea (Mediterranean): ontogenetic changes and feeding selectivity

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ABSTRACT: Ontogenetic variation in the diet of *Engraulis encrasicolus* (L.) was examined in the northern Adriatic Sea, off the River Po delta, by stomach contents analysis. Anchovy (10 to 130 mm total length) were collected during a 1 wk cruise in October 2002. Feeding activity was mainly diurnal in all the length classes: stomach fullness, calculated for each 10 mm size class, was always higher during the day than at night, with maximal values measured for the 40 to 49 and 50 to 59 mm size classes. All analysed life stages of *E. encrasicolus* had a strictly zooplanktivorous diet based on a few species of copepods. The principal prey of *E. encrasicolus* were small-sized copepods, measuring about 0.2 to 0.3 or 0.5 to 0.6 mm in prosoma length. The copepods *Euterpina acutifrons* and *Oncaea* spp. dominated anchovy diet during the day, both in terms of frequency, number and biomass, in all anchovy size classes. During the night, bivalve larvae were also important dietary items, with *Oncaea* spp. and *E. acutifrons* making up >69% of total prey number for all anchovy size classes. Within the considered size range, the dimensions of particles does not seem to be a limiting factor in food selection, and no relationship was found between anchovy length and the maximal dimension of ingested prey. Ivlev's electivity index confirmed that European anchovy was able to select specific food items and preferred small copepods such as *E. acutifrons* and *Oncaea* spp., and bivalve and decapod larvae.

KEY WORDS: Anchovy · Late larvae · Stomach contents · Prey selection · Zooplankton

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INTRODUCTION

European anchovy *Engraulis encrasicolus* (Linnaeus, 1758) is a coastal pelagic species of the Engraulidae family distributed across the eastern Atlantic and the Mediterranean, Black and Azov seas (Whitehead et al. 1988). *E. encrasicolus* is one of the major components of Mediterranean fisheries, where it is heavily exploited by purse seine vessels and pelagic trawlers. The Adriatic Sea, occupying about 5% of the Mediterranean Sea, produced about 13 000 tonnes of anchovy, equal to 19% of the entire Mediterranean production of this species in 1991 (Stamatopoulos 1993).

The importance of small pelagic fish, and anchovy in particular, in the Adriatic Sea food web was recently

pointed out by Coll et al. (2007). They highlighted the importance of medium-low trophic levels, such as sardine and anchovy, in the functioning of the ecosystem due to their role in capturing energy and making it available to the higher trophic levels. Moreover, anchovy was found (Coll et al. 2007) to be one of the keystone species within the Adriatic ecosystem when applying the index proposed by Libralato et al. (2006) based on the total mixed trophic impacts of the food web.

Fish abundance and production is critically dependent on both trophic linkages and environmental conditions (e.g. Christensen & Pauly 2004). *Engraulis encrasicolus* is characterized by a short life-span, and interannual fluctuations in its abundance could be important and more evident in comparison with other species.

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Several studies on *Engraulis* species have demonstrated that anchovy can feed by filtering or particulate feeding (O'Connell 1972, James 1987, James & Findlay 1989, van der Lingen 1994, Bulgakova 1996, van der Lingen et al. 2006, 2009). The ability to switch between these feeding modes makes anchovy highly opportunistic and flexible foragers, which are able to maximize their energy intake through employing the feeding mode most appropriate to a particular food environment. Given this ability, the diet of anchovy, which is generally comprised of mesozooplanktonic prey, may also include smaller particles such as phytoplanktonic cells (King & Macleod 1976, Mikhman & Tomanovich 1977, Bulgakova 1996). The feeding behaviour of anchovies and the resulting variability or breadth in their food intake make field and laboratory studies regarding selectivity the only means of predicting their diet in any particular ecosystem.

Robert et al. (2008) recently pointed out the importance of carrying out field studies coupling fish gut contents analysis and prey availability assessment. In fact, the knowledge of prey availability is essential in order to understand the relative importance of food categories and to assess prey selectivity. Moreover, Robert et al. (2008) stressed the importance of obtaining high taxonomical resolution in the identification of prey in selectivity studies, this being mandatory to identify the key prey species to consider, rather than the entire prey field, for assessing any relationship between fish and their trophic environment.

Current knowledge concerning the trophic ecology of *Engraulis encrasicolus* is primarily limited to studies carried out on adults (Black Sea, Bulgakova 1996; Azov Sea, Budnichenko et al. 1999; Catalan Sea, Tudela & Palomera 1995, 1997, Palomera et al. 2007; Bay of Biscay, Plounevez & Champalbert 1999; Gulf of Lions, Plounevez & Champalbert 2000), although assessments of the diets of larval stages have been conducted in the Western Mediterranean (Tudela et al. 2002) and the Adriatic Sea (<10 mm; Regner 1971, Conway et al. 1998, Coombs et al. 2003). However, knowledge concerning the trophic ecology of juveniles from silvering to pre-spawning stage is still lacking.

The present study focuses on the diet of late larvae and juvenile anchovy to complete missing information on feeding ecology of *Engraulis encrasicolus* and provide the basis for future investigation of the trophic ecology of this species in the Adriatic Sea. For this purpose, a multidisciplinary investigation was conducted, coupling fish stomach contents analysis and contemporary plankton net sampling. The simultaneous capture of late larvae, juveniles and adults during a 1 wk cruise carried out near the River Po delta provided the opportunity to examine anchovy diet with the aims of (1) determining the major components of the diet,

(2) examining anchovy feeding patterns in relation to ontogenesis, (3) identifying feeding periodicity, and (4) studying food selectivity.

MATERIALS AND METHODS

Study area. The study area was located in the north-western Adriatic Sea, near the Po River delta (off Pesaro), across a transect nearly perpendicular to the coast (Fig. 1). The northern Adriatic spans from the continental northern border to the -100 m contour line: it features an extremely shallow mean depth of ca. 30 m and a weak depth gradient along the major axis together with a strong annual thermal variation (8 to 25°C at the sea surface; Poulain et al. 2001). Freshwater inputs in this region represent nearly 20% of the entire Mediterranean's inputs (Mariotti et al. 2002). Shallow depths and gentle sea-bottom slope greatly affect the hydrology of the basin, reducing the time of water mass exchange, which may occur over a few months. Stormy winds from the NE and SE allow water mixing, thus enhancing the recirculation of the nutrients. All these characteristics create a highly productive system (Buljan 1964, Franco 1973, Fonda Umani et al. 1992, Fonda Umani 1996) which makes this basin one of the richest in the Mediterranean, producing about 85% of the total Italian landings of small pelagic fish (Cingolani et al. 2003). Moreover, anchovy spawning in the Adriatic Sea, although widespread, is generally quantitatively more important in the northern areas and, in particular, in the study area around the Po river delta (Piccinetti 2001).

Fish sampling. The survey was carried out aboard the RV 'G. Dalla Porta' from 20 to 23 October 2002. The vessel was equipped with an echo sounder (BIOSONIC DT 600) which was used to detect fish aggregations during sampling. Fish were sampled by a semipelagic trawl net equipped with a fine-meshed cod-end (mesh length 5 mm, ISO 1107), towed at an approximate speed of 3.0 knots for 30 min. The net was also equipped with a temperature/depth recorder (VEMCO MINILOG TD). Overall, 11 tows (Table 1) were carried out along the transect, but only 4 (Tows 1, 3, 7 and 9) landed an adequate number of specimens of a wide size range. Only the samples from these tows were considered in the present study. Anchovy were captured both during the day and night (Table 1) in a near-shore position (Fig. 1). Adult and juvenile fish were randomly sampled from every haul, immediately frozen at -20°C to stop digestive processes and preserved at the same temperature until laboratory analysis. Early developmental stages were immediately fixed in 10% buffered formaldehyde. The term 'late larva' refers to individuals with completed yolk sac resorption (\approx 10–39 mm); 'juveniles' are individuals in

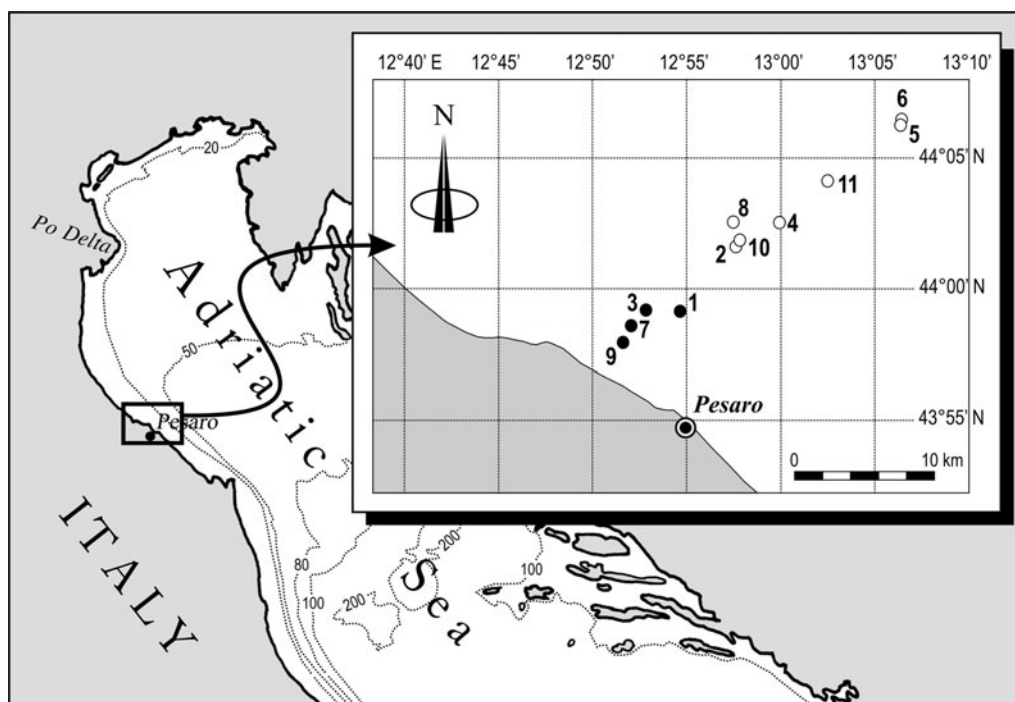


Fig. 1. Location of the sampling stations where anchovy *Engraulis encrasicolus* were captured, off the coast of NE Italy in October 2002. (●) tows where anchovy diet was studied; (○) tows where anchovy diet was not studied. Bathymetry is shown (m)

which silvering had already started (≈ 40 – 89 mm) and individuals >90 mm total length are considered 'adults' (Sinovčić 1999).

In the laboratory, fish total length (TL), to the nearest 0.1 mm, and fish wet weight, to the nearest 0.0001 g, were measured for each individual. Since larvae undergo shrinkage due to fixation in formaldehyde, their length was converted into real length at sea by applying the correction factor of 1.03 previously obtained for *Engraulis mordax* (Theilacker 1980).

Table 1. Sampling information for anchovy trawls and zooplankton tows. Times indicate the start of hauls and refer to GMT+1. Sampling depth indicates where both anchovy and zooplankton were collected. *: hauls considered for diet analysis

Tow	Date	Latitude (°N)	Longitude (°E)	Depth (m)	Time	Sampling depth (m)
1*	20/10/02	43° 59.16'	12° 54.64'	13	00:43	10
2		44° 01.68'	12° 57.72'	23	04:25	10
3*		43° 59.20'	12° 52.85'	13	10:45	10
4		44° 02.54'	12° 59.91'	23	17:05	22
5	21/10/02	44° 06.28'	13° 06.35'	55	00:16	28
6		44° 06.48'	13° 06.42'	55	08:13	53
7*		43° 58.59'	12° 52.06'	13	20:35	10
8		44° 02.55'	12° 57.46'	23	23:04	18
9*	23/10/02	43° 57.95'	12° 51.61'	13	13:10	10
10		44° 01.87'	12° 57.83'	23	15:04	20
11		44° 04.15'	13° 02.49'	45	16:51	40

Mesozooplankton sampling and analyses. Zooplankton sampling took place immediately after fish trawling. Net hauls were taken using a WP-2 standard net (0.25 m² opening, 200 μ m mesh size) equipped with an opening-closing system, a depth sensor and a flowmeter. The plankton net was towed horizontally for 2 to 3 min at the depth of the previous fish sampling. On board, samples were then stored in a buffered 4% formaldehyde-seawater solution. Taxonomical analyses were performed on subsamples of at least 1000 individuals. Individuals of each identified taxon were counted and their relative abundances in different hauls were calculated as individuals per cubic meter. Organisms were identified to the lowest taxonomical level possible.

The species *Oithona nana*, *O. similis*, *O. plumifera* and *O. setigera* were grouped as *Oithona* spp. Similarly, the genera *Paracalanus*, *Ctenocalanus*, *Clausocalanus* and *Parvocalanus* were classified as the 'Clauso-Paracalanidae' group.

Stomach content analyses. For dietary analyses, 663 fish were dissected and the digestive tract of at least 10 anchovies for each 10 mm size class

per single tow were removed and preserved individually in 4% buffered formaldehyde. The stomach content was defined as the material contained in the pyloric and cardiac stomachs, while the content of the intestine was discarded to reduce bias caused by different rates of digestion and gut passage times (Berg 1979, Hyslop 1980). Regurgitation during sampling was not observed since no food was found in the oesophagus. In late larvae, where the stomachs were not yet developed, the entire digestive tract was examined, from oesophagus to anus.

Dissection took place under a stereo-microscope and the entire stomach content of each fish was washed out on a Petri dish and examined individually (at 70 to 90× magnification). Prey items were identified, if possible, to species level, counted and measured. Diatoms, dinoflagellates and other microplankton were also identified. When items were damaged, only heads were counted. The prosoma length of all copepods or the maximum dimension of other zooplankton was measured using an ocular micrometer, with a precision of 14 µm. The original size of incomplete prey was estimated from whole individuals captured in zooplankton samples.

The dry weight of the total stomach content was mathematically reconstructed on the basis of literature references or direct measurements (Table 2). The contribution in terms of weight of dinoflagellates, tintinnids and diatoms was not considered because of their low abundance and their comparatively insignificant weight.

To compare the feeding intensity of individual fish of different sizes, the fullness index (F) was calculated as:

$$F = [SCW/(BW - SCW)] \times 1000$$

where SCW is the stomach content dry weight (g) and BW the fish body dry weight (g). Gonad weight was not considered in this fullness index because the majority of fish were sexually immature individuals or, if mature, they were at the end of their reproductive cycle and gonads were not evident. Wet weight of fish analysed for diet were transformed to dry weight using the relationship ($DW = 0.2607 \times WW$; $r^2 = 0.97$) obtained by drying 234 individuals (TL = 40.5 to 128.7 mm). For the day/night ratio of fullness index, the fullness index was calculated for each 10 mm fish size class, separately for day and night samples.

Mean values of the numerical abundance and dry weight of prey found in stomachs were calculated for each 10 mm anchovy size class. Since the data were not normally distributed (Kolmogorov-Smirnov test with Lilliefors' correction), the non-parametric 1-way ANOVA (Kruskal-Wallis test) was used to evaluate sig-

nificant differences between fish samples in terms of prey number per fish and stomach content dry weight per fish.

A cluster analysis based on similarity in feeding habits was applied on an anchovy size class–prey consumed matrix, using the Primer v.5 package (Clarke & Warwick 2001), to evaluate possible clustering of samples between anchovy size classes and time of catch. The matrix was made up of 22 anchovy groups (12 size classes from nocturnal and 10 size classes from diurnal tows) and all taxa of prey consumed. The mean value of prey abundance in each size class was used. The Bray-Curtis coefficient of similarity (Bray & Curtis 1957) and the group-average method of linkage was applied to $\log_{10}(x+1)$ -transformed data. All specimens of each group, or cluster, obtained from the cluster analysis were used for analysis of the diet, except for empty stomachs which were not used to calculate the frequency of occurrence.

The dietary analysis was carried out using both numerical and gravimetric methods, calculating number and weight of each prey item as well as the frequency of occurrence (Hyslop 1980, Cortés 1997). The index of relative importance (IRI, Pinkas et al. 1971), which incorporates the relative contribution of a food item to total stomach content by number (%N) and by weight (%DW), as well as the percent frequency of occurrence (%O), was calculated as:

$$IRI = (\%N + \%DW) \times \%O$$

To verify if any size-related selection of food occurs in anchovy, prey identified in stomach contents and mesozooplankton obtained by net-plankton sampling were grouped into 0.1 mm size classes. Size-frequency histograms were constructed for prey eaten by each group of fish identified by cluster analysis (anchovy sized 30 to 39 and 40 to 104 mm) and were subsequently compared with those of the plankton from the environment.

Finally, to assess the relationship between stomach contents and the abundance of potential prey in the sea, Ivlev's selection index (E ; Ivlev 1955) was calculated for each prey category separately for day and night samples:

$$E = (r_i - p_i)/(r_i + p_i) - 1$$

where r_i is the relative abundance of prey category i (%N) in the stomachs of *Engraulis encrasicolus* and p_i is the abundance of that prey in the horizontal net-plankton samples. E ranges from -1 to $+1$; negative and positive values indicate avoidance or positive selection for a prey category, respectively. A zero value indicates neutral selectivity.

Table 2. Dry weight (DW) of *Engraulis encrasicolus* prey and morphometric relationships used to calculate DW (μg). For certain prey, DW was obtained by conversion of their carbon content (CW/DW) or directly measured. n: number of specimens weighed; \emptyset : diameter; CW: carbon weight (μg); PL: prosome length (μm); L: total length (μm). Superscripts ^a and ^b refer to sources

Prey item	DW	Regression (length–DW)	C/DW (%)	n	Source
Gastropoda larvae		DW = 0.6 ^a	31.25 ^b		Sautour & Castel (1995) ^a , James (1987) ^b
Bivalvia veliger	3.758	Mean		740	La Mesa et al. (2008)
Polychaeta larvae	5.670	Mean		114	La Mesa et al. (2008)
<i>Evadne</i> spp. (ref. Cladocerans)		DW = 3.946L ^{2.436}			James (1987)
<i>Penilia avirostris</i>	1.2	Mean			Fonda Umani et al. (1979)
<i>Podon poliphemoides</i>	1.6	Mean			Fonda Umani et al. (1979)
<i>Evadne</i> spp. eggs (ref. copepods and euphausian eggs)		lnDW = 0.0143 \emptyset – 3.381			van der Lingen (2002)
Ostracod juveniles	6.035	Mean		94	Present study
<i>Acartia clausi</i>		logDW = 2.71logPL – 7.28			Cataletto & Fonda Umani (1994)
<i>Calanus helgolandicus</i>		logDW = 2.691logPL – 6.883			Hay et al. (1991)
<i>Calocalanus pavo</i> <i>Nannocalanus minor</i> <i>Paracalanus</i> spp. (ref. <i>P. parvus</i>)		logDW = 2.738logPL – 6.934			Hay et al. (1991)
<i>Centropages kroyeri</i> <i>C. typicus</i>		logDW = 2.451logPL – 6.103			Hay et al. (1991)
<i>Temora longicornis</i>		logDW = 2.815logPL – 7.181			Hay et al. (1991)
<i>Temora stylifera</i>		logDW = (2.71logPL – 3.685)/1000			Razouls (1981)
Clauso-Paracalanidae in October (ref. <i>P. parvus</i>)		logDW = 2.738logPL – 6.934			Hay et al. (1991)
Clauso-Paracalanidae in May (ref. <i>Acartia clausi</i>)		log DW = 2.71logPL – 7.28			Cataletto & Fonda Umani (1994)
<i>Oithona similis</i>		CW = (9.4676 \times 10 ⁻⁷)PL ^{2.16a}	40 ^b		Sabatini & Kjørboe (1994) ^a , Kjørboe & Sabatini (1994) ^b
<i>Copilia</i> spp. <i>Corycaeus speciosus</i> <i>Corycaeus</i> spp. <i>Clytemnestra rostrata</i>		lnDW = 1.96lnPL – 11.64			van der Lingen (2002)
<i>Oncaea</i> spp.	1.34	Mean		1000	Present study
<i>Euterpina acutifrons</i>		DW = (1.389 \times 10 ⁻⁸)PL ^{2.857}			Ara (2001)
<i>Microsetella rosea</i> Other harpacticoids (ref. <i>M. norvegica</i>)		CW = (2.65 \times 10 ⁻⁶)PL ^{1.95}	40		Uye et al. (2002)
Copepod nauplii (ref. <i>Acartia</i> nauplii)		logDW = 2.848logL – 7.265			Durbin & Durbin (1978)
Copepod copepodites (ref. <i>Acartia</i> copepodites)		logDW = 3.095logPL – 8.195			Durbin & Durbin (1978)
Cirripeda larvae Decapod nauplii		CW = 0.67 ^a	39.97 ^b		Sautour & Castel (1995) ^a , James (1987) ^b
Decapod larvae	27.798	Mean		61	La Mesa et al. (2008)
Macruran larvae (ref. euphausians)		DW = 1.9(L/1000) ^{3.19}			James (1987)
Isopods (ref. harpacticoids)		lnDW = 1.96lnL – 11.64			Chisholm & Roff (1990)
Amphipods	1181	Mean		2	Present study
Invertebrate eggs			40		Present study
<i>Sagitta</i> spp. (ref. <i>Sagitta elegans</i>)	1430				Omori 1969
<i>Engraulis mordax</i> eggs	30				Hunter & Dorr (1982)
<i>Engraulis encrasicolus</i> larvae		DW = (6 \times 10 ⁻¹⁵)L ^{4.13}		100 (r ² =0.9654)	Present study

The mean values of the numerical abundance and dry weight of prey found in the stomachs were calculated for each 10 mm size class. There were no significant differences between samples from the nocturnal Tows 1 and 7 (Kruskal-Wallis test: $p = 0.436$ for prey number stomach⁻¹, $p = 0.402$ for stomach content DW), nor for diurnal Tows 3 and 9 ($p = 0.505$ for prey number stomach⁻¹, $p = 0.894$ for stomach content DW). On the contrary, differences were significant between night and day samples ($p = 0.017$ for prey number stomach⁻¹, $p = 0.031$ for stomach content DW).

In the following analyses, samples were pooled together (Tows 1 and 7 as nocturnal; Tows 3 and 9 as diurnal).

The clustering of fish groups on the basis of mean prey number per stomach provided the dendrogram shown in Fig. 4. The borderline of cluster definition was arbitrarily set at 57.5% similarity and this resulted in a division of the dendrogram into 8 fish clusters. Diurnal and nocturnal samples were never present in the same cluster. Groups n1 and n2 differed considerably from other clusters and referred to fish sized 10 to 19 mm and 20 to 29 mm, respectively, with almost empty stomachs at night (n). During the day (d), anchovies of these sizes (clusters d1 and d2) consumed some prey and were more similar to adjacent clusters. These dimensions characterized late-larval individuals whose digestive tracts were not yet completely formed, as observed during dissection. A more defined stomach was observed in anchovy 30 to 39 mm TL (clusters 3n and 3d), and this, coupled with the finding of a larger number of prey, suggesting an increased ingestion capacity. Anchovy between 40 and 120 mm TL included juveniles and adults and formed 2 clusters only (4n and 4d), clearly separating diurnal and nocturnal samples.

Feeding selection

Prey dimensions ranged between 70 μm and 38.6 mm. No relationship was found between anchovy TL and maximal prey size, since larvae and juveniles fed on the same plankton size classes as adults (Fig. 5). As a consequence, mouth width did not seem to be a limiting factor for the smallest anchovies when compared to adults.

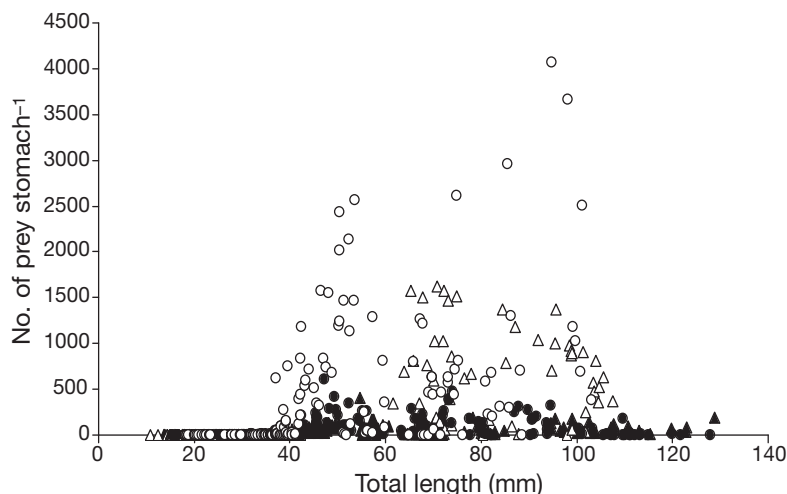


Fig. 2. *Engraulis encrasicolus*. Number of prey per stomach relative to total length of anchovy in each trawl. Tows 1 (\blacktriangle) and 7 (\bullet) were nocturnal tows and Tow 3 (\triangle) and 9 (\circ) were diurnal tows

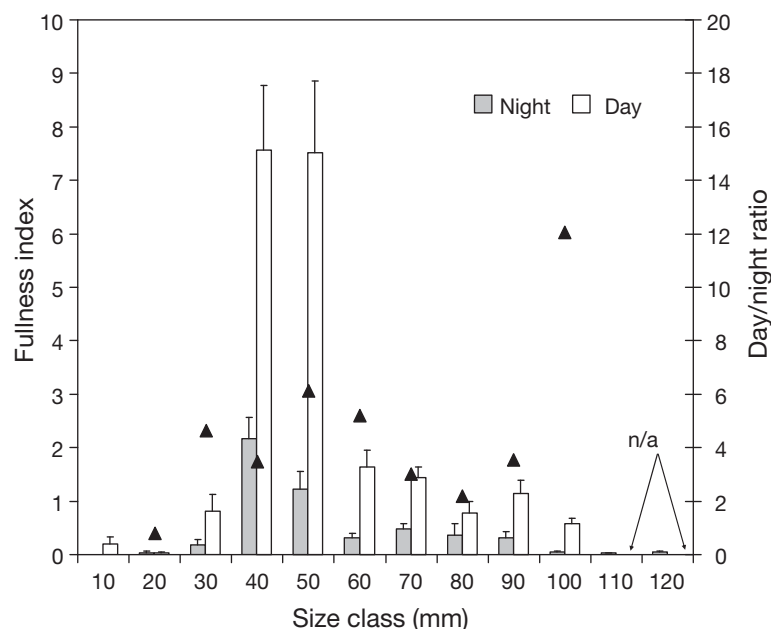


Fig. 3. *Engraulis encrasicolus*. Fullness index (F) for anchovy. Size classes are in 10 mm increments. Mean values (\pm SE) at night and day and the day/night ratio (\blacktriangle) are presented. n/a: data not available for day sampling

The size frequency of planktonic organisms in the field and of the prey recovered in the stomachs presented 2 main, non-overlapping, peaks (Fig. 6): the highest size frequencies of mesozooplanktonic organisms at sea were 0.3 to 0.4 and 0.6 to 0.7 mm, while that of prey recovered in the stomachs were 0.2 to 0.3 and 0.5 to 0.6 mm. This pattern was observed during both day and night. The prosoma length of *Oncaea* spp. (0.21 to 0.28 mm) and the total length of *Euterpina acu-*

tifrons (0.49 to 0.56 mm), the main prey items of anchovy during the considered period, were within the range of the peaks of prey dimensions.

Ivlev's selection index was used to describe the selection of the food items among the planktonic organisms present in the environment (Fig. 7). The species composition of zooplankton (ind. m⁻³) from horizontal plankton-net tows is presented in Appendix 1, Table A2. Copepods represented the main component of the mesozooplankton. Calanoids were characterized by *Temora stylifera* and other species of the families Clausocalanidae and Paracalanidae. *Euterpina acutifrons* and the genus *Oncaea* were the most abundant species of Harpacticoids and Poecilostomatoids, respectively. Cyclopoids were represented by *Oithona plumifera* and *Oithona nana*. The most representative cladocerans were *Penilia avirostris* and *Evadne nordmanni*. The meroplankton community was dominated by ophioplutei and bivalve veligers.

During night feeding, selection was positive for bivalves, ostracods, *Oncaea* spp., *E. acutifrons* and *Microsetella rosea* in all the size groups of anchovy. As length increased (juvenile and adult anchovy), *Corycaeus* spp. and decapod larvae were also positively selected, while polychaete larvae were negatively selected. During day feeding, selection was positive for *Oncaea* spp., *E. acutifrons* and *M. rosea* in all size groups. Decapod larvae were positively selected only by late larvae and bivalves only by adults. Clauso-Paracalanidae copepods were very abundant at sea (Table A2), but they were poorly selected by anchovy of all size groups. Some planktonic organisms, despite being very abundant in the environment, were never found in the stomach contents. This was the case for

ophioplutei, siphonophores, appendicularians and doliolids, which numerically constituted altogether 43.73 and 35.11 % of net-plankton at night and day, respectively.

DISCUSSION

Diet composition

In the present study we present for the first time a description of the diet of juvenile stage of *Engraulis encrasicolus*. Our results show that all analysed life stages of *E. encrasicolus* had a strictly zooplanktivorous diet based on a few species of copepods. The diets of juveniles and adults were dominated by small copepods, both in terms of number and biomass. Among copepods, *Euterpina acutifrons* and *Oncaea* spp. appear to be of particular importance. A shift in prey importance was noted during the growth of individuals (from 30 to 39 mm to >40 mm), with diurnal IRI values of *E. acutifrons* decreasing from 78.5% (late larvae) to 48.26% (juveniles) and 43.92% (adults) and *Oncaea* spp. increasing from 14.6% (late larvae) to 45.45% (juveniles) and 37.16% (adults). The genus *Oncaea* has been previously described as particularly important for anchovy diet (Tudela & Palomera 1997, Plounevez & Champalbert 1999, 2000, Sciolis 2000, Tanaka et al. 2006). Of particular interest is the importance of bivalve larvae in the nocturnal anchovy diet, as shown both by IRI and Ivlev's selection index in all anchovy ontogenetic stages (Table A1, Fig. 7). In the Adriatic Sea, the abundance of bivalves is very important, as is evident from the abundance of bivalve larvae presented in the results on zooplankton composition, mainly at the stations where anchovy was caught. This increases our knowledge on the feeding plasticity of *E. encrasicolus*, as this result has not been reported for other areas where anchovy diet has been studied (e.g. Gulf of Lions, Catalan Sea, Bay of Biscay).

A zooplanktivorous diet was reported in most investigations carried out on the genus *Engraulis* (*E. ringens*, Konchina 1991; *E. mordax*, Koslow 1981, Chi-

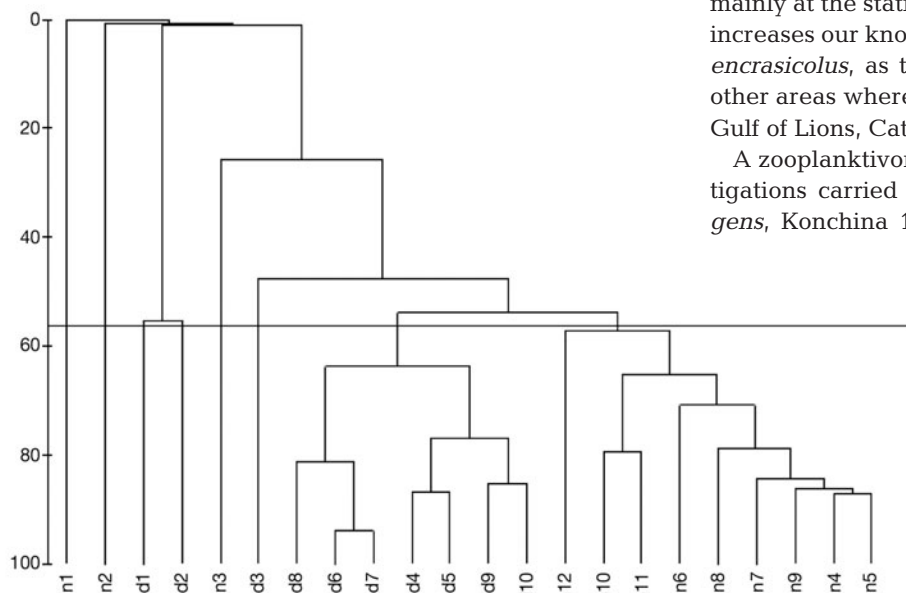


Fig. 4. *Engraulis encrasicolus*. Dendrogram resulting from the analysis of the anchovy size class–prey consumed matrix. n: night; d: day. Size classes 1 to 12 correspond to 10 mm intervals, i.e. size class 1 is 10 to 19 mm, 2 is 20 to 29 mm and so on until 12, which is 120 to 129 mm. Horizontal line is the borderline of cluster definition (arbitrarily set at 57.5% similarity)

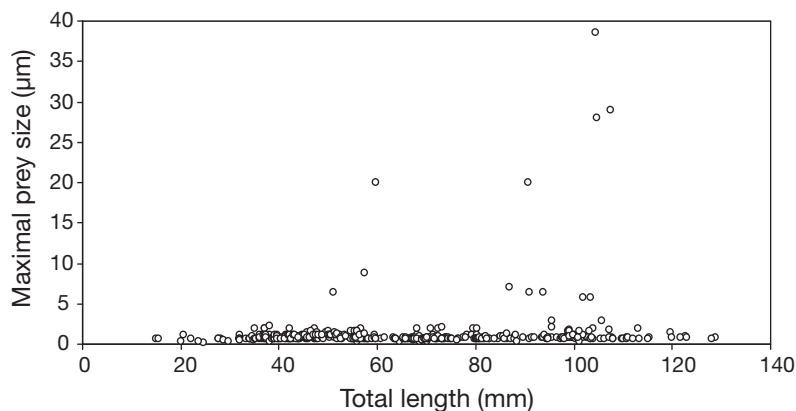


Fig. 5. *Engraulis encrasicolus*. Maximal prey size (μm) versus anchovy total length (mm)

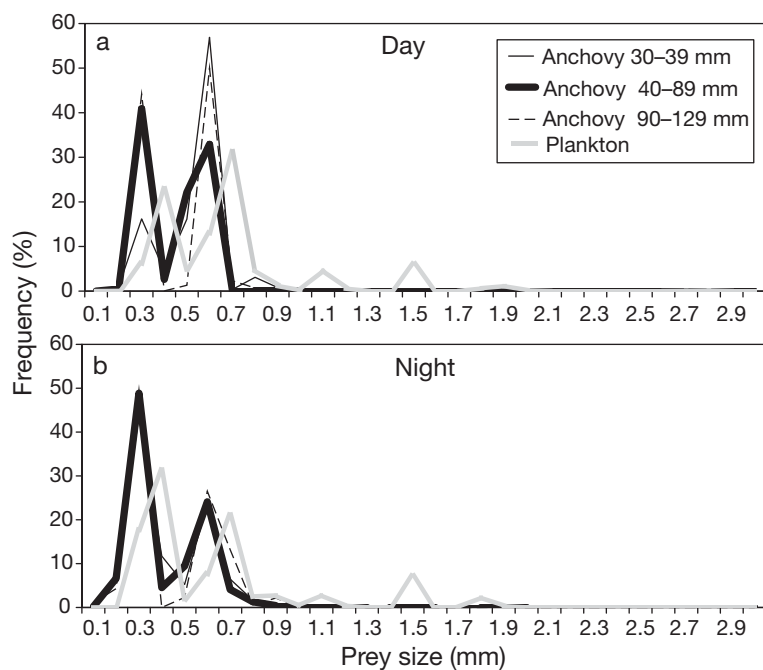


Fig. 6. *Engraulis encrasicolus*. Length frequency of plankton specimens from the environment (grey line) and from stomach contents of late larvae (30 to 39 mm, black line), juvenile (40 to 89 mm, thick black line) and adult (≥ 90 mm, dotted line) anchovy (a) during the day and (b) at night

appa-Carrara & Gallardo-Cabello 1993; *E. anchoita*, Angelescu & Anganuzzi 1981; *E. capensis*, James 1987; *E. encrasicolus*, Bulgakova 1996, Mikhman & Tomanovich 1977, Tudela & Palomera 1997, Plounevez & Champalbert 1999, 2000; *E. japonicus*, Tanaka et al. 2006). Conversely, James (1987) observed large diatoms (e.g. *Rhizosolenia*, *Pleurosigma* and *Coscinodiscus*) in the gut contents of *E. capensis*. King & Macleod (1976) showed that specimens of *E. capensis* were zooplanktivorous in the larval stages, but they progressively became phytoplanktivorous, eating mostly diatoms. The change in diet occurred at 80 mm TL and

was probably due to the development, during growth, of a more efficient filtering system, with a decreasing porosity among branchial spines, allowing the retention of smaller food particles. Some studies on anchovy adults from the Black and Azov seas have shown that diet could include microphytoplankton (Mikhman & Tomanovich 1977, Bulgakova 1996) and tintinnids (Ferreira & Ré 1993). In accordance with these authors, Budnichenko et al. (1999) observed that 87% of *E. encrasicolus maeoticus* stomach contents comprised microphytoplankton (*Coscinodiscus* spp.), while mesozooplankton was rare.

Recently, Rossi et al. (2006), using fatty acids as trophic markers, observed that prymnesiophycean fatty acids were transferred to anchovy larvae in the NW Mediterranean. Since these phytoplanktonic cells are mainly represented by nanoflagellates, probably too small to be efficiently eaten by anchovy larvae, the authors suggested that the microalgae are most likely ingested by the fish via naked and non-naked protozoan prey which have consumed the algae. This means that microzooplankton could be an intermediate trophic step between phytoplankton and anchovy larvae. Fukami et al. (1999), who carried out an experimental study on the identification of naked protozoans in fish larvae, reported the presence of flagellate-like cells 5 μm in size and ciliate-like cells 20 to 30 μm in size in the gut contents of several species of fish larvae, but they did not observe any protists in the gut contents of *Engraulis japonicus*. In the present study, predation on naked protozoans by anchovy late larvae (≥ 30 mm) could not be excluded, although few tintinnids and dinoflagellates were observed. This finding appears to minimise the importance of a direct microzooplankton–anchovy late larvae trophic link in the northern Adriatic Sea.

Although our study area is known as one of the most productive in the Adriatic Sea (Degobbi et al. 2000, Totti et al. 2000), phytoplankton (diatoms and dinoflagellates, mainly belonging to the genera *Coscinodiscus* and *Protoperdinium*) was observed in less than one-sixth of the analysed gut contents and always in very low concentrations (1 to 46 phytoplankton cells stomach⁻¹). According to James (1987), small food particles could have been accidentally taken up during particulate feeding. Moreover, other observations, made in the same area in spring and year-round in the

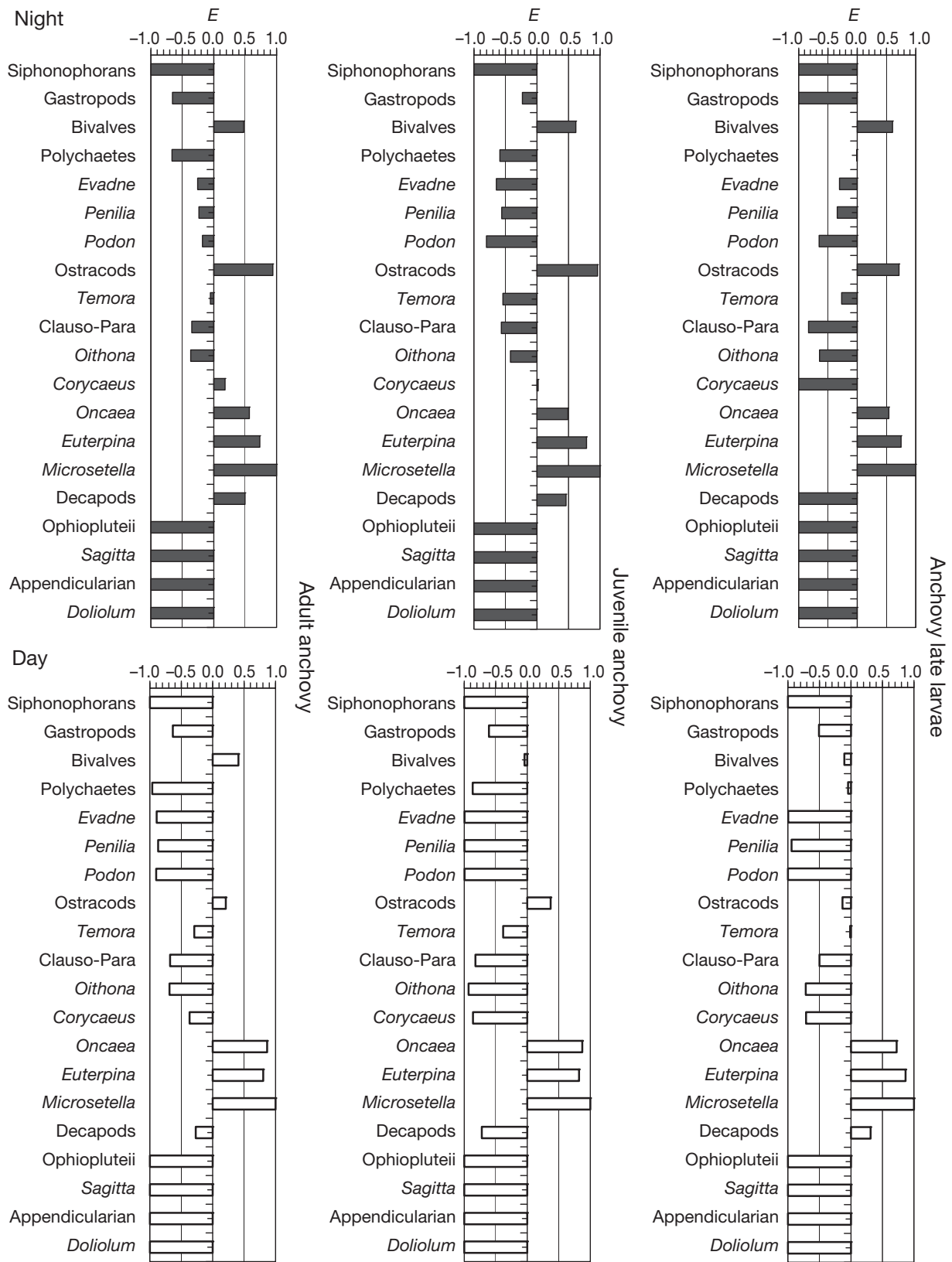


Fig. 7. *Engraulis encrasicolus*. Ivlev's selection index (*E*), calculated for anchovy late larvae (30 to 39 mm), juveniles (40 to 89 mm) and adults (≥ 90 mm) during the day (white bars) and at night (black bars). Clauso-Para: Clauso-Paracalanidae

Gulf of Trieste (Italy), confirm that phytoplankton is not abundantly present in the diet of European anchovy (D. Borme unpubl. data).

The cladoceran *Penilia avirostris* has been indicated as an important component of the diet and the ecology of *Engraulis encrasicolus* in the Adriatic Sea (Štirn 1969, Specchi et al. 1999). Štirn (1969) proposed that this cladoceran was the pivotal link of a short and very efficient trophic chain with the diatom *Nitzschia* spp. as the primary producer, the phytoplanktivorous *P. avirostris* as the primary consumer and anchovy as its predator. Specchi et al. (1999) confirmed this hypothesis, verifying the synchronism between the occurrence of the cladoceran and the appearance of anchovy in the Gulf of Trieste (northern Adriatic). In contrast, Ogawa & Nakahara (1979) found that high concentrations of cladocerans could produce unfavourable effects on the feeding activity of small planktivores. In the present study, *P. avirostris* was found in stomach contents mainly at night (Table A1), but it never represented an important prey even if it was abundant at sea, especially in the area where anchovy were caught (>3000 individuals m^{-3} ; Table A2).

Diel and ontogenetic variation in feeding

Significant differences in anchovy diet were found between diurnal and nocturnal catches. Feeding activity of *Engraulis encrasicolus* was mainly diurnal, in accordance with previous reports (Tudela & Palomera 1995, 1997, Plounevez & Champalbert 1999, 2000). However, the analysis of gut contents revealed the presence of recently ingested prey even at night, suggesting that some nocturnal feeding activity exists. Dietary indexes, based on stomach contents analyses measured in larvae of various species, show significant diel variability, with activity generally higher during the day and peaks at dusk and dawn (Last 1978, Kane 1984, Blaxter 1986, McLaren & Avendaño 1995, McLaren et al. 1998).

The results obtained from the cluster analysis confirmed the differences between day and night samples. Moreover, the size classes 10 to 19, 20 to 29 and 30 to 39 mm appeared to be more differentiated than size classes from 40 to 130 mm, which presented more similar diets, suggesting that juveniles and adults do not have large differences in diet composition. Differences between the smallest size classes are probably mainly related to the amount of food eaten and in particular to the low feeding activity measured in the smallest late larvae. Anchovy ranging between 10 and 29 mm TL have incomplete development of the digestive tract which comprises an indistinct cylinder. The amount of ingested prey notably increased at total lengths between 30 and 39 mm, when the formation of the

stomach begins, allowing for the storage of greater quantities of food. Individuals between 40 and 60 mm, whose tegument pigmentation and stomach were already complete, had maximal levels of stomach replenishment, particularly related to their body mass (F index in Fig. 3). The fact that anchovy of this size presented high values of both prey number and fullness index is probably due to higher metabolic needs.

Feeding selection

Within the considered size range of the present study, the dimension of particles does not seem to be a limiting factor in food selection: late larvae and juveniles were able to ingest prey whose dimensions were similar to those ingested by adults, and no relationship was found between anchovy length and the maximal size of ingested prey. The principal prey of *Engraulis encrasicolus* were small-sized copepods measuring about 0.2 to 0.3 or 0.5 to 0.6 mm in prosoma length.

Although by WP2 net sampling we obtained an incomplete planktonic spectra and could not consider plankton patchiness, some considerations about feeding selectivity are possible. The sizes of prey ingested were different from those of the most frequent mesozooplanktonic organisms in the field (Fig. 6), suggesting a discrimination of food particles by anchovy in all size classes. Ivlev's selection index (Fig. 7) confirmed that European anchovy late larvae, juveniles and adults were able to select specific food items and preferred small copepods such as *Euterpina acutifrons* and *Oncaea* spp. Even if the WP2 net may have underestimated the presence of small copepods at sea (e.g. Munk et al. 2003), the numerical dominance of these 2 small copepods observed in anchovy gut contents (Table A1) support Ivlev's selection index results. Further proof that feeding did not occur through indiscriminate filtration is that despite the extremely high concentrations of siphonophores, ophiopluteii, chaetognats, appendicularians and doliolids in the environment, these organisms were completely avoided by anchovy.

Several laboratory studies have shown that fish feeding on small particles (as small pelagic fishes) have 2 different feeding behaviours: filter-feeding, essentially non-selective, and particulate-feeding, which allows the selection of food on a dimensional basis (e.g. Gibson & Ezzi 1985, James & Findlay 1989, van der Lingen 1994). Feeding mode essentially depends on the dimensions and density of prey; generally, species showing this feeding plasticity, filter when high concentrations of small food particles (e.g. phytoplankton or zooplankton of small dimensions) are present and use oriented suction on larger prey. The ability to

switch from one feeding type to the other is surely an advantage in the marine environment inhabited by clupeids, where food is patchily distributed and fish must cope with complex spatial and temporal variations in food density and dimensions. Filtering was observed in *Engraulis mordax* (Konchina 1991) and in *E. capensis* (Gibson & Ezzi 1990) in the presence of small prey, while raptorial feeding occurred in the presence of large prey independently of food concentration. James & Findlay (1989) reported that South African anchovy *E. capensis* switched from filter feeding to particulate feeding at a threshold prey size of 700 μm . Similarly, Bulgakova (1993) found that in *E. encrasicolus*, inert organisms such as phytoplankton and copepod eggs were ingested through filtering, while large and fast-swimming prey, such as adult copepods and fish larvae, were caught by biting. Recently, van der Lingen et al. (2006), in a review on *E. encrasicolus* and *Sardinops sagax* in the southern Benguela, pointed out that anchovy feed predominantly by particulate feeding, feeding inefficiently on phytoplankton and deriving the bulk of their dietary input from large zooplankton (anchovy showing higher weight-standardized clearance rates than sardine for prey >580 μm). All these studies were carried out on adult stage fish, but our results strongly suggest that similar behaviour may also occur in juveniles.

During the sampling period, the mesozooplankton community was dominated by several copepod species of small sizes and by cladocerans (Table A2). Nevertheless, *Oncaea* spp. and *Euterpina acutifrons* were preferred by anchovy, suggesting that these species were more vulnerable to anchovy predation. The observed preference of European anchovy for a few copepod species of small sizes might be related to (1) the abundance of copepod species of small sizes in the Adriatic Sea (Kamburska & Fonda Umani 2006), and (2) species-specific behavioural (e.g. swimming patterns, patchy distribution) and/or physical characteristics (e.g. colour, bioluminescence) of the prey.

The importance of well-defined prey items means that fish attention is focused on particular prey types. James & Findlay (1989) showed that on a short temporal scale, anchovy seem to 'learn' to discriminate between different food targets. The authors hypothesized that *Engraulis capensis* acquires target-images to search. This idea came from the observation, under experimental conditions, that the reaction distance and the efficiency in catching food particles tend to increase after offering consecutively the same prey type. Anchovy probably filter planktonic organisms, but only when they encounter an adequate patch of prey; in other words, the fish filters solely when it is energetically convenient to switch from biting on single prey to indiscriminate filtering. The shape of the stomach, with the

corpus of the stomach extending backwards into a caecum, whose size is highly variable, may sustain this hypothesis. Attempts have been made to interpret such variation in terms of diet, and it has been suggested, for example, that the presence of a large caecum in active predaceous swimmers, such as *Scomber* spp. (Suyehiro 1941), may be correlated with their capacity to attack shoals of fish and consume large quantities of prey in a short time. This explanation may also be applied to anchovy when the consistent number of ingested prey recovered in the present study is considered.

Future research should focus on extensive sampling which considers both seasonal and spatial variation of the relationship between small pelagic diet and ambient mesozooplankton composition. Small copepods seem to be a fundamental trophic link for anchovy in the Adriatic Sea. Therefore, insights into the behaviour and ecology of small copepods would be of great importance in understanding the drivers of feeding strategies of small pelagic fish species.

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Appendix 1. Dietary indexes (Table A1) and zooplankton species composition in the environment (Table A2)Table A1. Dietary indexes obtained at night and during the day. Total stomach contents by number (N), frequency of occurrence (O), weight (DW) and index of relative importance (IRI) calculated for prey items in anchovy size classes. Late larvae: 30 to 39 mm; juveniles: 40 to 89 mm; adults: ≥ 90 mm total length (TL). n: number of anchovy analysed; indet.: indeterminate

	TL 30–39 mm				TL 40–89 mm				TL > 90 mm			
	O (%)	N (%)	W (%)	IRI (%)	O (%)	N (%)	W (%)	IRI (%)	O (%)	N (%)	W (%)	IRI (%)
NIGHT												
Gastropoda												
Gastropoda pediveliger					6.43	0.17	0.12	0.01	3.70	0.06	0.03	<0.01
Bivalvia												
Bivalvia veliger	77.78	25.10	48.94	43.34	91.81	26.18	38.19	40.22	79.63	17.60	20.88	24.86
Polychaeta												
Polychaeta larva	11.11	0.40	1.19	0.13	10.53	0.11	0.24	0.03	3.70	0.08	0.15	0.01
Cladocera												
<i>Evadne</i> spp.	77.78	4.86	3.35	4.81	40.35	1.97	0.93	0.80	62.96	5.40	2.18	3.87
<i>Penilia avirostris</i>	55.56	6.07	3.78	4.12	56.73	3.50	1.63	1.98	57.41	7.67	2.90	4.92
<i>Podon</i> spp.	11.11	0.40	0.34	0.06	11.11	0.21	0.13	0.03	29.63	1.33	0.67	0.48
<i>Evadne</i> eggs					35.09	3.00	0.44	0.82	7.41	1.58	0.19	0.11
Ostracoda												
Ostracoda juveniles	11.11	0.40	1.27	0.14	58.48	3.41	7.98	4.53	35.19	2.19	4.16	1.81
Copepoda												
Copepoda nauplius	55.56	2.43	0.09	1.05	33.92	1.77	0.05	0.42	9.26	1.47	0.03	0.11
Copepoda copepodita	11.11	0.40	0.02	0.04	5.26	0.09	<0.01	<0.01				
Calanoida												
<i>Temora stylifera</i>	33.33	1.62	5.12	1.69	38.60	0.83	5.01	1.53	55.56	2.52	11.28	6.22
Clauso-Paracalanidae	11.11	0.40	3.79	0.35	43.27	1.22	2.56	1.11	42.59	2.13	4.45	2.27
Cyclopoida												
<i>Oithona</i> spp.	22.22	0.81	0.25	0.18	35.67	1.53	0.41	0.47	20.37	1.74	0.58	0.38
Poecilostomatoida												
<i>Corycaeus</i> spp.					19.88	0.36	0.28	0.09	20.37	0.50	0.34	0.14
<i>Oncaea</i> spp.	55.56	29.15	20.27	20.66	93.57	25.46	13.26	24.66	94.44	31.41	13.29	34.25
Harpacticoida												
<i>Clytemnestra rostrata</i>					1.17	0.01	0.02	<0.01	1.85	0.03	0.04	<0.01
<i>Euterpina acutifrons</i>	88.89	22.27	10.50	21.92	91.23	26.56	9.34	22.29	87.04	20.70	6.45	19.17
<i>Microsetella rosea</i>	33.33	1.21	0.39	0.40	39.18	1.22	0.37	0.43	24.07	0.61	0.17	0.15
Harpacticoida indet.					5.85	0.06	0.03	<0.01	1.85	0.03	0.01	<0.01
Cirripedia												
Cirripedia nauplius	22.22	0.81	0.70	0.25	9.94	0.13	0.08	0.01	9.26	0.14	0.07	0.02
Cirripedia cypris					0.58	0.01	<0.01	<0.01				
Decapoda												
Macrura larva					0.58	0.02	9.04	0.04				
Decapoda nauplius					0.58	0.01	<0.01	<0.01	1.85	0.03	0.01	<0.01
Decapoda zoea+mysis					6.43	0.07	0.80	0.04	5.56	0.08	0.73	0.04
Isopoda												
Isopoda indet.					1.17	0.02	0.06	<0.01	11.11	0.25	0.37	0.06
Amphipoda												
Amphipoda indet.					1.75	0.02	8.49	0.10	3.70	0.08	30.95	0.93
Bacillariphyceae												
<i>Coscinodiscus</i> spp.					4.09	0.04		<0.01	3.70	0.08	30.95	0.93
Dinoflagellida												
<i>Ceratium</i> spp.									7.41	0.83		0.05
<i>Dynophysis caudata</i>					1.17	0.01						
<i>Phaeocystis</i> spp.					2.92	0.04						
<i>Protoperdinium claudicans</i>	11.11	0.40		0.03	2.34	0.02						
<i>Protoperdinium conicum</i>					4.68	0.06		<0.01	1.85	0.03		<0.01
<i>Protoperdinium depressum</i>	33.33	3.24		0.81	34.50	1.31		0.31	12.96	1.16		0.12
<i>Protoperdinium divergens</i>					2.34	0.04		<0.01				
<i>Protoperdinium mediterraneum</i>					0.58	0.01		<0.01				
<i>Protoperdinium oblongum</i>					0.58	0.01		<0.01	1.85	0.03		<0.01
<i>Protoperdinium steinii</i>					1.75	0.02		<0.01				

(Table A1 continued on next page)

Table A1 (continued)

	TL 30–39 mm				TL 40–89 mm				TL > 90 mm			
	O (%)	N (%)	W (%)	IRI (%)	O (%)	N (%)	W (%)	IRI (%)	O (%)	N (%)	W (%)	IRI (%)
Tintinnida												
<i>Stenosemella ventricosa</i>									1.85	0.17		<0.01
Other												
Invertebrate eggs					9.36	0.51	0.52	0.07	1.85	0.08	0.06	<0.01
n	9	58	58	58	171	180	180	180	54	59	59	59
DAY												
Gastropoda												
Gastropoda pediveliger	4.35	0.28	0.39	0.02	25.00	0.21	0.31	0.07	29.63	0.19	0.04	0.06
Bivalvia												
Bivalvia veliger	17.39	1.36	3.71	0.70	61.00	1.53	4.45	2.08	96.30	4.00	1.50	4.51
Polychaeta												
Polychaeta larva	21.74	0.56	2.30	0.49	28.00	0.04	0.20	0.04	11.11	0.01	0.01	<0.01
Cladocera												
<i>Evadne</i> spp.	2.17	0.04	0.04	<0.01	10.00	0.04	0.04	<0.01	66.67	1.05	0.13	0.67
<i>Penilia avirostris</i>	6.52	0.44	0.38	0.04	2.00	0.02	0.02	<0.01	70.37	1.04	0.12	0.70
<i>Podon</i> spp.					7.00	0.01	0.01	<0.01	44.44	0.23	0.04	0.10
<i>Evadne</i> eggs	4.35	0.24	0.07	0.01	14.00	0.06	0.02	<0.01	44.44	0.29	0.01	0.11
Ostracoda												
Ostracoda juveniles	4.35	0.08	0.35	0.01	36.00	0.23	1.07	0.27	74.07	0.16	0.10	0.16
Copepoda												
Copepoda nauplius	8.70	0.44	0.04	0.03	18.00	0.06	<0.01	0.01	22.22	0.06	<0.01	0.01
Copepoda copepodita	17.39	0.32	0.02	0.05	3.00	0.01	<0.01	<0.01				
Calanoida												
<i>Acartia clausi</i>					1.00	<0.01	0.01	<0.01	7.41	0.01	<0.01	<0.01
<i>Calanus helgolandicus</i>					1.00	<0.01	0.10	<0.01	3.70	<0.01	0.04	<0.01
<i>Centropages kroyeri</i>	2.17	0.04	0.41	0.01								
<i>Centropages typicus</i>					4.00	0.01	0.08	<0.01				
<i>Nannocalanus minor</i>									7.41	0.01	0.01	<0.01
<i>Temora stylifera</i>	21.74	1.00	12.58	2.33	49.00	0.46	6.87	2.04	85.19	0.56	0.88	1.05
Clauso-Paracalanidae	36.96	2.23	7.15	2.74	55.00	0.65	2.64	1.03	92.59	1.28	1.06	1.84
Cyclopoida												
<i>Oithona</i> spp.	15.22	0.48	0.17	0.08	20.00	0.10	0.04	0.02	55.56	0.54	0.14	0.32
Poecilostomatoidea												
<i>Copilia quadrata</i>									11.11	0.01	0.02	<0.01
<i>Corycaeus speciosus</i>									3.70	0.01	<0.01	<0.01
<i>Corycaeus</i> spp.	10.87	0.20	0.43	0.05	34.00	0.09	0.15	0.05	81.48	0.54	0.12	0.46
<i>Oncaea</i> spp.	52.17	17.90	17.46	14.56	94.00	41.64	43.24	45.45	96.30	39.96	5.34	37.16
Harpacticoida												
<i>Clytemnestra rostrata</i>					3.00	0.01	0.02	<0.01	11.11	0.02	0.01	<0.01
<i>Euterpina acutifrons</i>	80.43	73.50	50.15	78.51	95.00	53.63	35.54	48.26	96.30	48.73	4.79	43.92
<i>Microsetella rosea</i>	8.70	0.24	0.12	0.02	70.00	0.91	0.57	0.59	88.89	0.87	0.08	0.72
Harpacticoida indet.	10.87	0.20	0.19	0.03	13.00	0.04	0.03	<0.01	25.93	0.05	0.01	0.01
Cirripedia												
Cirripedia nauplius									7.41	0.02	<0.01	<0.01
Cirripedia cypris									3.70	<0.01	<0.01	<0.01
Decapoda												
Macrura larva					1.00	<0.01	0.10	<0.01	7.41	0.01	0.39	0.03
Decapoda nauplius					1.00	<0.01	<0.01	<0.01	3.70	<0.01	<0.01	<0.01
Decapoda zoea+mysis	8.70	0.20	4.03	0.29	8.00	0.02	0.36	0.02	22.22	0.05	0.13	0.03
Amphipoda												
Amphipoda indet.					2.00	<0.01	2.57	0.03				
Echinodermata												
Ophiuroidea juveniles					1.00	<0.01						
Chaetognatha												
<i>Sagitta</i> spp.					1.00	<0.01	1.56	0.01				
Teleostea												
<i>Engraulis encrasicolus</i> larva									11.11	0.03	85.02	8.05
Bacillariphyceae												
<i>Coscinodiscus</i> spp.	8.70	0.28		0.02	20.00	0.24		0.03	33.33	0.24		0.07
Dinoflagellida												
<i>Phaeocystis</i> spp.									3.70			
<i>Protoperdinium depressum</i>					2.00	<0.01		<0.01	3.70	0.02		<0.01
Other												
Invertebrate eggs					2.00	0.01	0.01	<0.01	7.41	0.02	<0.01	<0.01
Pollen grains					1.00	<0.01						
n	46	74	74	74	100	105	105	105	27	27	27	27

Table A2. Zooplankton species composition (ind. m⁻³) from horizontal plankton-net tows

Taxa	1	2	3	4	Tow 5	7	9	10	11
Foraminiferida									
<i>Globigerina bulloides</i>	0	3	0	0	0	0	0	0	0
Hydrozoa									
<i>Obelia</i> spp.	0	0	0	0	13	0	0	0	0
Siphonophora indet.	4350	267	2928	72	162	1183	1659	64	141
Hydrozoa indet.	669	5	251	2	13	370	261	4	42
Gastropoda									
<i>Creseis acicula</i>	0	0	42	0	0	24	0	0	0
Gastropoda pediveligera	223	33	753	15	30	299	41	30	203
Bivalvia									
<i>Bivalvia veligera</i>	3681	41	1213	79	50	8438	343	37	131
Polychaeta									
Polychaeta larvae	112	30	460	11	84	968	137	30	91
Nemertea									
<i>Nemertea pilidia</i>	0	8	0	0	0	0	14	0	3
Cladocera									
<i>Evadne nordmanni</i>	12270	360	14097	79	19	4410	576	12	7
<i>Evadne spinifera</i>	0	147	0	0	2	12	329	0	0
<i>Evadne tergestina</i>	669	3	1213	2	0	382	946	0	0
<i>Penilia avirostris</i>	15951	989	10792	26	37	8211	3004	5	3
<i>Podon intermedius</i>	446	25	0	2	4	72	14	1	0
<i>Podon polyphemoides</i>	2789	41	3012	2	6	418	1015	7	20
Ostracoda									
Ostracoda indet.	0	0	84	4	0	131	14	0	3
Copepoda									
<i>Acartia clausi</i>	112	25	84	13	47	24	411	0	16
<i>Calanus helgolandicus</i>	0	3	167	0	2	0	234	0	3
<i>Calocalanus pavo</i>	112	8	42	2	26	0	0	21	42
<i>Centropages typicus</i>	223	3	0	0	4	24	14	0	3
<i>Centropages kroyeri</i>	0	3	0	0	0	0	0	0	0
<i>Diaixis pygmoea</i>	223	0	0	0	0	0	14	0	0
<i>Eucalanus elongatus</i>	0	71	0	11	11	0	0	0	13
<i>Mecynocera clausi</i>	223	3	0	15	17	0	0	2	16
<i>Nannocalanus minor</i>	112	0	84	26	37	0	0	1	10
<i>Temora stylifera</i>	4685	104	335	42	41	765	617	90	3
Clauso-Paracalanidae	5800	300	2844	193	316	1745	2332	192	882
Calanoida copepodita	446	128	335	180	35	0	69	99	258
Cyclopoida									
<i>Oithona</i> cf. <i>nana</i>	4685	22	669	61	78	430	261	49	422
<i>Oithona</i> cf. <i>plumifera</i>	1785	33	1506	114	179	430	261	65	732
Poecilostomatoida									
<i>Copilia quadrata</i>	0	0	0	2	0	0	14	1	3
<i>Corycaeus</i> spp.	446	63	753	9	32	227	357	21	10
<i>Oncaea</i> spp.	15951	104	1631	116	54	992	1029	100	82
<i>Sapphirina</i> spp.	0	0	0	4	0	0	0	0	0
Harpacticoida									
<i>Clytemnestra rostrata</i>	0	0	0	0	2	0	0	0	7
<i>Euterpina acutifrons</i>	5466	25	2886	7	32	765	2016	32	20
<i>Microsetella rosea</i>	0	0	0	0	4	0	0	1	0
Harpacticoida indet.	112	0	0	2	0	0	0	0	3
Cirripedia									
Cirripedia nauplii	0	0	0	0	4	0	0	15	10
Decapoda									
Decapoda larvae	0	22	84	13	24	72	14	5	7
Phoronida									
Phoronidea actinotrocha	0	3	0	0	0	12	14	0	0
Echinodermata									
Ophiuroidea pluteii	54658	629	11838	485	657	6143	9203	510	732
Stelleroidea bipinnariae	112	0	0	31	37	24	14	36	0
Chaetognatha									
<i>Sagitta</i> spp.	1673	150	376	198	172	1028	1262	114	173
Urochordata									
Appendicularia indet.	4462	139	962	329	345	598	590	248	422
Thaliacea									
<i>Doliolum</i> spp.	12270	1033	4559	51	63	1506	1070	74	422
<i>Thalia</i> spp.	0	14	0	2	15	0	0	4	0
Urochordata larvae	0	0	2	2	0	0	0	0	0
Osteichthyes									
Teleostea eggs	0	0	125	0	0	72	0	0	0
Teleostea larvae	112	3	0	0	7	0	0	0	7