Feeding ecology of the transparent goby *Aphia minuta* (Pisces, Gobiidae) in the northwestern Adriatic Sea

MARIO LA MESA [1], DIEGO BORME [2], VALENTINA TIRELLI [2], ELENA DI POI [3],
SARA LEGOVINI [2] and SERENA FONDA UMANI [3]

[1] ISMAR-CNR, Istituto di Scienze Marine, Sezione di Ancona, Largo Fiera della Pesca 60125, Ancona, Italy.
E-mail: m.lamesa@ismar.cnr.it
[2] OGS, Istituto Nazionale di Oceanografia e di Geofisica Sperimentale, Dipartimento di Oceanografia Biologica, Via A.
Piccard 54, 34014 S. Croce, Trieste, Italy.
[3] Dipartimento di Biologia, Università di Trieste, Via Valerio 28/1, 34127 Trieste, Italy.

SUMMARY: The feeding ecology of the transparent goby *Aphia minuta* was examined in spring (May 2003) in the coastal waters off Comacchio, in the northwestern Adriatic Sea. Stomach content analysis indicated *A. minuta* to be a planktivorous species, feeding exclusively on pelagic invertebrates. The diet composition was dominated by the calanoid copepods *Acartia clausi* and *Temora longicornis*, followed in decreasing order of importance by other copepods (especially calanoids and *Oncaea* spp.) and larvae of decapods, polychaetes and bivalves. *A. minuta* exhibited a generalistic feeding strategy with a relatively broad niche width. Abundant taxa in the environment, such as *A. clausi* and *T. longicornis*, were seldom selected, whereas rare taxa, such as larvae of polychaetes and decapods, were highly selected. According to the observed ontogenetic shift in diet, small-size individuals relied preferentially on juvenile *T. longicornis* and *Oncaea* spp., whereas large-sized specimens consumed preferably *A. clausi* and calanoids. The positive relationship found between prey and fish size may help to mitigate the intraspecific competition for food resources.

Keywords: diet, feeding selectivity, transparent goby, copepods, Adriatic Sea.

RESUMEN: ECOLOGÍA ALIMENTARIA DEL GÓBIDO TRANSPARENTE *APHIA MINUTA* (PISCES, GOBIIDAE) EN EL NOROESTE DEL MAR ADRIÁTICO. – En el presente trabajo se estudió la dieta del góbido transparente *A. minuta* durante la primavera (Mayo 2003) en el nor-oeste del Mar Adriático (Comacchio). El análisis del contenido estomacal mostró que *A. minuta* es una especie planctívora, que se alimenta exclusivamente de invertebrados pelágicos. Los copépodos calanoides *Acartia clausi* y *Temora longicornis* constituyeron las presas dominantes seguidas, en orden de importancia decreciente, de otros copépodos (calanoides y *Oncaea* spp.), larvas de decápodos, poliquetos y bivalvos. *A. minuta* evidenció una estrategia alimentaria generalista y un nicho trófico amplio. Los taxones abundantes en el medio natural, *A. clausi* y *T. longicornis*, fueron raramente seleccionados, en cambio taxones poco frecuentes, como larvas de poliquetos y decápodos, estuvieron seleccionados positivamente. Atendiendo al cambio en la dieta a lo largo de la ontogenia, los ejemplares de talla pequeña se alimentaron preferentemente de juveniles de *T. longicornis* y *Oncaea* spp., mientras los ejemplares de talla mas grande consumían preferentemente *A. clausi* y calanoides. La relación positiva observada entre el tamaño de la presa y del depredador podría contribuir a atenuar la competencia intraespecífica por los recursos alimenticio.

Palabras clave: dieta, selectividad alimentaria, gobio transparente, copepodos, mar Adriático.

INTRODUCTION

The transparent goby *Aphia minuta* (Risso, 1810) is a small, neritic pelagic species with a wide distribution, occurring in the northeast Atlantic from Gibraltar to Norway and the Baltic Sea and throughout the Mediterranean to the Black Sea and Azov Sea (Tortonese, 1975). Despite its small size, this species is the seasonal target of a small-scale artisanal fishery in the western and central Mediterranean (mainly off

Spain and Italy), yielding locally more than one hundred tons per fishing season (La Mesa *et al.*, 2005).

A. minuta forms a monotypic genus within the family Gobiidae, one of the largest groups of fish which inhabit inshore marine, estuarine and freshwater environments (Miller, 1986). Unlike most Mediterranean gobies, which are generally benthic, the transparent goby has pelagic habits for most of its life cycle (Iglesias *et al.*, 1997), sharing this feature with two other gobies, the crystal goby *Crystallogobius linearis* and Ferrer's goby *Pseudaphya ferreri*. Interestingly, all three species exhibit a pattern of larval characters also into adulthood, such as the scarcity of melanophores, the persistence of the swimbladder and the possession of a short, straight alimentary canal. From an ecological perspective, this was tentatively explained as an adaptation to pelagic or semipelagic life or, more likely, to a planktivorous behaviour of these species (Miller, 1973, 1989).

The transparent goby exhibits some peculiarities in several other biological characteristics, such as reproduction, longevity, growth rate and life cycle (reviewed in La Mesa *et al.*, 2005). It is characterised by a lifespan of less than one year, an early achievement of sexual maturity through progenesis and a semelparous kind of reproduction displayed in a prolonged breeding season, and a sudden death of breeders soon after spawning (Iglesias *et al.*, 1997; La Mesa, 1999; Caputo *et al.*, 2000, 2002). During the life cycle of this species, three main ontogenetic phases have been described: planktonic larval stages hatch from demersal eggs and inhabit inshore from late spring to early autumn (pelagic phase), so juveniles gather in schools in shallow waters during winter (aggregated phase); in spring, finally, adults migrate offshore exhibiting a dispersed distribution close to the bottom (demersal phase) (Martínez-Baño *et al.*, 1993; Iglesias and Morales-Nin, 2001; La Mesa *et al.*, 2005).

Compared to the exhaustive information available on the biology of *A. minuta*, data on its feeding habits are still very scarce and frequently anecdotal, indicating roughly copepods, cirripede and mysid larvae as the main component of its diet (Hesthagen, 1971; Miller, 1986). Only recently have qualitative data on feeding habits of *A minuta* been reported from the Black Sea, where it feeds on small copepods, sharing this food resource with Baltic sprat and Azov anchovy (Chesalin *et al.*, 2004).

In order to fill this gap, the present paper reports for the first time a thorough description and quan-

titative data on the feeding ecology of this species. On the basis of the stomach content analysis and zooplankton abundance at sea, we were able a) to identify the main prey items, b) to provide insight on food preferences and feeding selectivity, and c) to assess ontogenetic changes in diet composition, considerably improving current knowledge of the feeding ecology of *A. minuta*.

MATERIALS AND METHODS

Study area and sampling

The study was conducted in the northwestern Adriatic Sea off Comacchio (locality Po di Goro, south of the Po River delta) across a transect roughly perpendicular to the coast (Fig. 1). The survey was carried out from 17 to 20 May 2003 on the Italian RV *G. Dalla Porta*, which was equipped with a BIOSONIC DT 600 echosounder used to detect fish aggregation during sampling activities. Fish were sampled with a small-meshed semipelagic trawl, with a 4 mm codend mesh size, hauled at a speed of approximately 3.0 knots and for 30 minutes. The net was also equipped with a temperature/depth recorder (VEMCO MINILOG TD). Overall, 15 hauls were carried out along the transect between 7 and 30 m depth, covering the entire daily cycle of 24 hours. Immediately after capture, all specimens were immediately preserved in a 4% formaldehyde–sea water solution for further analysis. At the end of each haul (11 out of 15), zooplankton samples were collected using a WP2 net (200 μm mesh size) equipped with an open-closing system and a flowmeter. The plankton net was towed horizontally at the same depth as previous fish trawling. On board, samples were then stored in buffered 4% formaldehyde-sea water solution for further analysis.

Laboratory methods

In the laboratory, each fish specimen was measured in length to the nearest mm (total length, TL), wet-weighed with an accuracy of 0.01 g (total weight, TW) and sexed under a stereomicroscope. For dietary analysis, fish were dissected and the stomach content analysed under a stereomicroscope at 70x magnification. Prey items were identified, when possible, to the species level (Rose, 1933; Trègouboff and Rose, 1957), counted and measured. When items were
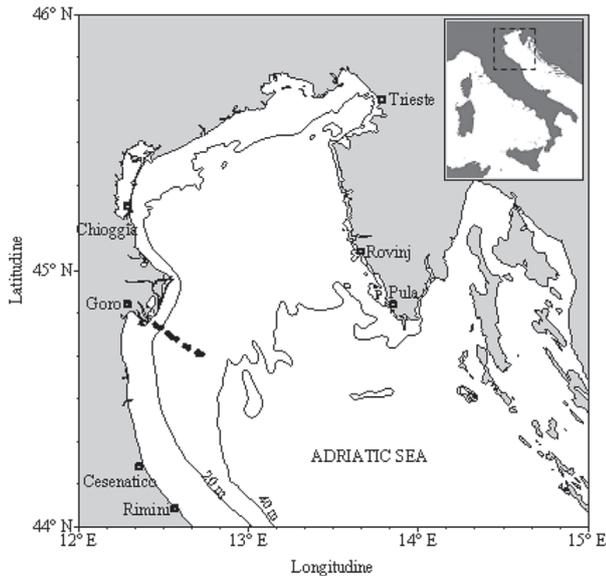
FIG. 1. – Study area, showing sampling stations (●) along the transect.

damaged, only heads were counted. Copepods were not sexed or distinguished in developmental stages; however, the size of the specimens of *Temora longicornis* found in stomach content was similar to that of juvenile stages of this species. The prosome length (PL) of all copepods or the maximum dimension of other zooplankters was measured using an ocular micrometer, with an accuracy of 14 μm. The original size of incomplete prey was estimated from whole undamaged individuals captured in zooplankton samples. To determine the weight of prey, dry weight (DW) values were calculated for copepods from PL-DW regressions (see Table 1). For the genus *Oncaea*, DW was derived from carbon content weight reported for three size classes, assuming C = 40% DW (following Kiorboe and Sabatini, 1994) (Table 1). The same relationship was applied to estimate the weight of larvae of polychaetes. For other

prey, such as larvae of bivalves and decapods, DW was evaluated following a standard procedure (Postel *et al.*, 2000) (Table 1). Finally, to estimate the abundance of mesozooplankton in the environment, we used the beaker subsampling technique as described by Van Guelpen *et al.* (1982).

Data analyses

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 percentage of frequency of occurrence (%O), was calculated as summarised in the following formula:

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

The dietary diversity or niche width of the species was calculated using the Shannon-Wiener diversity index $H' = - \sum_i p_i (\ln p_i)$, where p_i is the percentage by number of the ith prey in the sample. Furthermore, the Pielou's evenness index $J' = H' / \ln n$, where H' is the Shannon-Wiener diversity index and n is the number of prey taxa, was calculated to measure how evenly fish rely on food resources (Marshall and Elliot, 1997).

To assess the feeding strategy and phenotype (or individual) contribution to niche width, a modification of the Costello method was applied to the whole data set of prey categories identified (Costello, 1990; Amundsen *et al.*, 1996). The prey-specific abundance, defined as the percentage in number of a prey taxon calculated taking into account only those

TABLE 1. – Regressions and assigned values of dry weight (DW in μg) of prey in *A. minuta*. PL = prosome length.

Prey	Formula		Source
Acartia clausi	log DW = 2.71 log PL – 7.28		Cataletto and Fonda Umani, 1994
Temora longicornis	log DW = 3.06 log PL – 7.68		Hay *et al.*, 1991
Calanoida species	log DW = 2.71 log PL – 7.28	from *Acartia clausi*	Cataletto and Fonda Umani, 1994
Copepoda species	log DW = 2.23 log PL – 5.49		White and Roman, 1992
Oncaea spp.			
(280-350 μm)	1.275*	from *Oncaea curta*	Sautour and Castel, 1995
(420-490 μm)	1.8*	from *Oncaea venusta*	Sautour and Castel, 1995
(560-700 μm)	6.45*	from *Oncaea mediterranea*	Sabatini and Kiørboe, 1994
Polychaeta larvae	5.670*		this study
Bivalvia veliger	3.758		this syudy
Decapoda larvae	27.798		this study

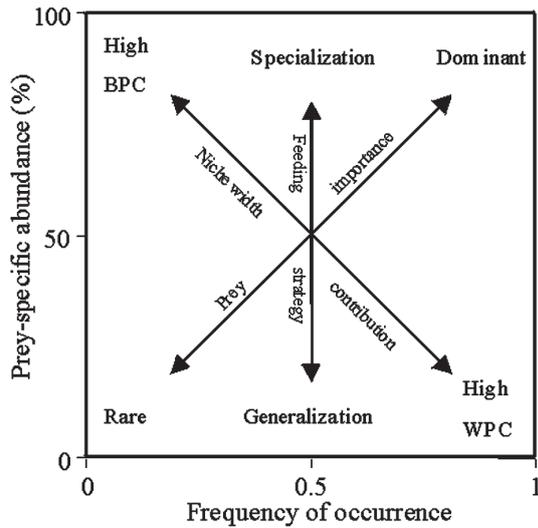* dry weight values obtained from carbon dry mass, assuming C = 40 % dry weight

FIG. 2. – Modified Costello graph showing explanatory axes (modified from Amundsen *et al.*, 1996).

predators in which the prey category actually occurs, is plotted against the frequency of occurrence, providing a two-dimensional graph (Amundsen *et al.*, 1996). In mathematical terms, the prey-specific abundance is expressed as follows:

$$P_i = (\Sigma_i\, S_i / \Sigma\, S_{ti})\, 100$$

where P_i is the prey-specific abundance of prey i, S_i the stomach content comprised of prey i, and S_{ti} the total stomach content in only those fish with prey i in their stomachs. The resulting plot provides information on prey importance, feeding strategy and niche width contribution inferred through the position of prey categories in the diagram (Fig. 2). In detail, the diagonal axis running from the lower left to the upper right of the diagram represents a measure of prey importance, with dominant prey at the upper end and rare or less important prey at the lower end. The axis running from the upper left to the lower right indicates the contribution of between- and within-phenotype (or individual) components to the niche width, with a high between-phenotype component at the upper end and a high within-phenotype component at the lower end. Finally, the vertical axis represents the feeding strategy of the predator in terms of specialisation (upper part of diagram) or generalisation (lower part). Further details are given in Amundsen *et al.* (1996).

Ontogenetic and sex-related changes in diet were assessed using a multivariate analysis of data. A Bray-Curtis coefficient similarity matrix was obtained from the whole data set, constituted of numerical abundance of prey categories in the stomach con-

tent of 243 fish, excluding specimens with an empty stomach. A non-metric multidimensional scaling (MDS) was applied to the pairwise similarity matrix to order fish in a two-dimensional plane, according to their relevant diet similarity. Sex and fish size were "superimposed" on the MDS plot to see the relevant pattern of distribution. As no difference of food preferences was found between sexes, fish were pooled in 1 mm size classes, and the mean numerical abundance of each prey category in each fish size class was calculated. This enabled the distribution points to be identified more readily on the ordination plot. To determine relevant contributions of each prey category to fish distribution in the two-dimensional plot, an analysis of dissimilarity was carried out using the SIMPER routine. Finally, a one-way statistical analysis (ANOSIM routine, test R) was performed to test the null hypothesis (i.e. no statistical difference in diet between groups). R-statistic values close to unity indicate a very different dietary composition between groups, whereas values close to 0 indicate a strong similarity. All statistical analyses were performed using the PRIMER software package developed at the Plymouth Marine Laboratory (Clarke and Warwick, 1994; Clarke and Gorley, 2001).

Finally, to assess the relationship between stomach content and the abundance of potential prey in the environment obtained from WP2 net, the Ivlev selection index (E) (Ivlev, 1961) was calculated for each prey category in different diel time:

$$E = (r_i - p_i)\,(r_i + p_i)^{-1}$$

where r_i is the relative abundance of prey category i (percentage stomach content by number, %N) in the stomachs of *A. minuta* and p_i is the abundance of that prey in WP2 samples in the environment. E ranges from -1 to +1, negative and positive values indicating respectively avoidance or positive selection for a prey category. Zero values indicate no selective feeding at all. The departure of sex ratio of *A. minuta* from unity was tested by means of the chi-square test for goodness of fit (Sokal and Rohlf, 1995).

RESULTS

Fish sample

Overall, 338 *A. minuta* specimens were available for the stomach content analysis, being on average 20
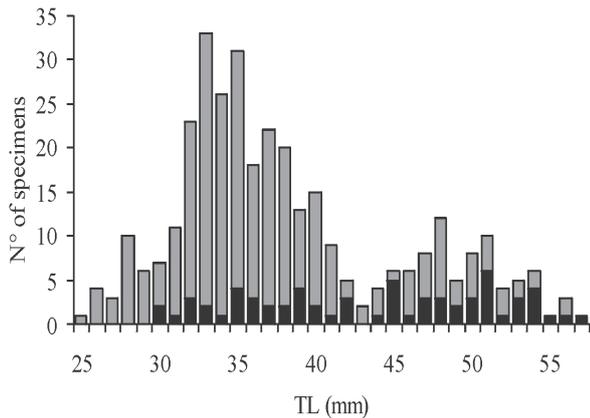
FIG. 3. – Length frequency distribution of females (■) and males (■) *A. minuta* from coastal waters off Comacchio.

specimens each haul. Applying the chi-square test for goodness of fit, the sex ratio differed significantly from 1:1 (273 females vs. 65 males, df = 1, P<0.001). The length-frequency distribution of pooled sexes was bimodal, with well-defined modes at 33 and 48 mm TL (Fig. 3). The two modes probably represented two main cohorts of age 0+ fish, derived from two different spawning events (see La Mesa, 1999). Females were slightly smaller than males, ranging from 25 to 56 mm TL and from 0.04 to 1.32 g. Males ranged from 30 to 57 mm TL and from 0.11 to 1.63 g. Applying the potential equation $TW = aTL^b$, the relationship between TL (mm) and total weight TW (g) of fish was calculated for each sex and the whole sample and is summarised in the following equations:

$$TW = 1.74 * 10^{-7} TL^{3.95} \quad n = 273, r^2 = 0.97, \text{females}$$
$$TW = 1.01 * 10^{-7} TL^{4.09} \quad n = 65, r^2 = 0.98, \text{males}$$
$$TW = 1.48 * 10^{-7} TL^{3.99} \quad n = 338, r^2 = 0.98, \text{whole sample}$$

No sex-related difference was found in the allometric coefficient (b) (F-test, P>0.1), and both sexes exhibited a significant positive allometric growth (i.e. b>3).

Diet composition

A total of 338 stomachs was examined. Empty stomachs occurred in 28% of both males and females. As a result, diet composition was investigated in 196 females and 47 males. Number of prey items per stomach ranged between 1 and 53 (mean 4.9). Eight different taxa of prey were identified, all of them consisting exclusively of pelagic organisms (Table 2). The calanoid copepods *Temora longicornis*

TABLE 2. – Diet composition of *A. minuta* from the northwestern Adriatic Sea. N%, numerical percentage; DW%, weight percentage; O%, frequency of occurrence; IRI, index of relative importance; IRI%, IRI percentage

Prey category	N%	DW%	O%	IRI	IRI%
Copepods					
Acartia clausi	30.0	26.4	40.3	2273.7	36.7
Temora longicornis	34.8	41.0	30.9	2339.4	37.7
Oncaea spp.	2.6	0.9	10.7	37.4	0.6
other calanoids	11.8	4.2	28.0	449.2	7.2
other copepods	9.4	7.9	27.2	471.0	7.6
Decapods larvae	3.9	17.8	18.9	411.3	6.6
Polychaetes larvae	7.2	1.6	25.1	220.9	3.6
Bivalves larvae (veliger)	0.3	0.2	0.4	0.2	0.0

and *Acartia clausi* represented overwhelmingly the main prey of the transparent goby, both as numerical (respectively 34.8 and 30.0%N) and weight percentage (41.0 and 26.4%DW) of diet, as well as for IRI values (respectively 37.7% in *T. longicornis* and 36.6% in *A. clausi*). Other taxa of prey, such as larvae of polychaetes and decapods, calanoids and unidentified copepods, represented secondary prey, accounting for 3.6-7.6%IRI. Poecilostomatoid copepods of the genus *Oncaea* were eaten in small amounts (0.6%IRI), but rather frequently (10.7%O). Conversely, larval stages of bivalves (veliger) were found in a single stomach. Niche width (H') and evenness (J') calculated for the whole fish population were respectively 1.63 and 0.78.
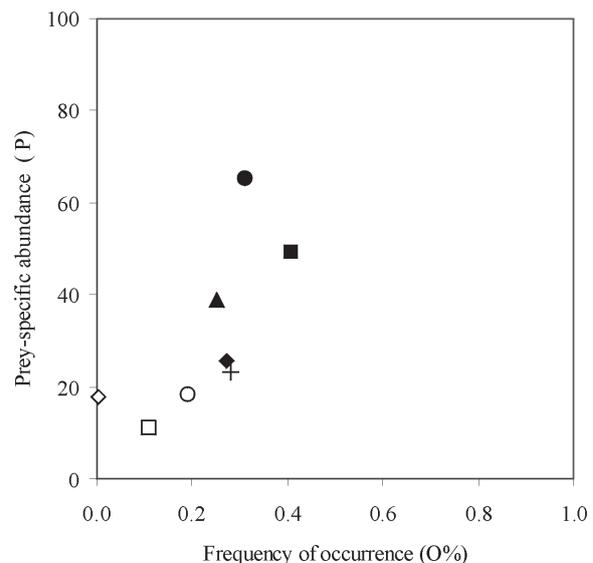

FIG. 4. – Graphic representation of diet composition of *A. minuta* according to the Costello method. *T. longicornis* (●); *A. clausi* (■); polychaetes larvae (▲); other copepods (◆); calanoids (+); decapods larvae (○); *Oncaea* spp. (□); bivalves larvae (◇).

Feeding strategy

The feeding pattern observed in the population of *A. minuta* is summarised in the modified Costello plot (Fig. 4). Considering the prey importance axis (see Fig. 2), *A. minuta* diet was mostly based on rare species which were eaten occasionally and in relative small amounts, such as copepods like *Oncaea* spp. and calanoids and larvae of polychaetes, bivalves and decapods, except for *T. longicornis* and *A. clause*, which tended to be dominant prey. The population of *A. minuta* can be considered as a generalist predator with a relatively broad niche width, but consisting also of some specialised individuals which feed widely on *T. longicornis* and *A. clausi* (i.e. prey with a high prey-specific abundance and low frequency of occurrence). These specialised fish shift the feeding strategy of *A. minuta* towards a higher between-phenotype contribution to the utilisation of the resource gradient or niche width (Fig. 2 and 4). In other words, the partitioning of food resources in a generalist predator such *A. minuta* is assured by some individuals specialised in feeding on few but abundant prey (see Table 3).

TABLE 3. – Mean abundance (specimens m⁻³) of zooplankton taxa collected off Comacchio in May 2003. SD = standard deviation

| Taxa		Mean abundance	SD
Hydrozoa	Anthomedusae	<1	<1
Gastropoda	larvae unidentified	11	15
Bivalvia	larvae unidentified	9	13
Polychaeta	*Tomopteris* spp.	<1	1
	larvae unidentified	1	3
Branchiopoda	*Evadne nordmanni*	40	38
	Evadne spinifera	2	3
	Podon intermedius	2	4
	Podon polyphemoides	10	12
Ostracoda	larvae unidentified	<1	<1
Copepoda	*Acartia clausi*	1728	1242
	Calanus helgolandicus	3	6
	Centropages typicus	4	7
	Diaixis pygmoea	20	19
	Temora longicornis	300	254
	Clauso-Paracalanidae	936	828
	Oithona cf. *nana*	221	360
	Oithona cf. *plumifera*	284	245
	Oncaea spp.	60	64
	Euterpina acutifrons	<1	1
	cf. *Tigriopus*	1	1
	Harpacticoida	1	2
Cirripedia	larvae unidentified	4	7
Decapoda	larvae unidentified	6	6
Isopoda	adult unidentified	<1	<1
Appendicularia	*Oikopleura* spp.	57	42
Teleostea	*Engraulis encrasicolus* eggs	8	14
	eggs unidentified	1	3
	larvae unidentified	1	2
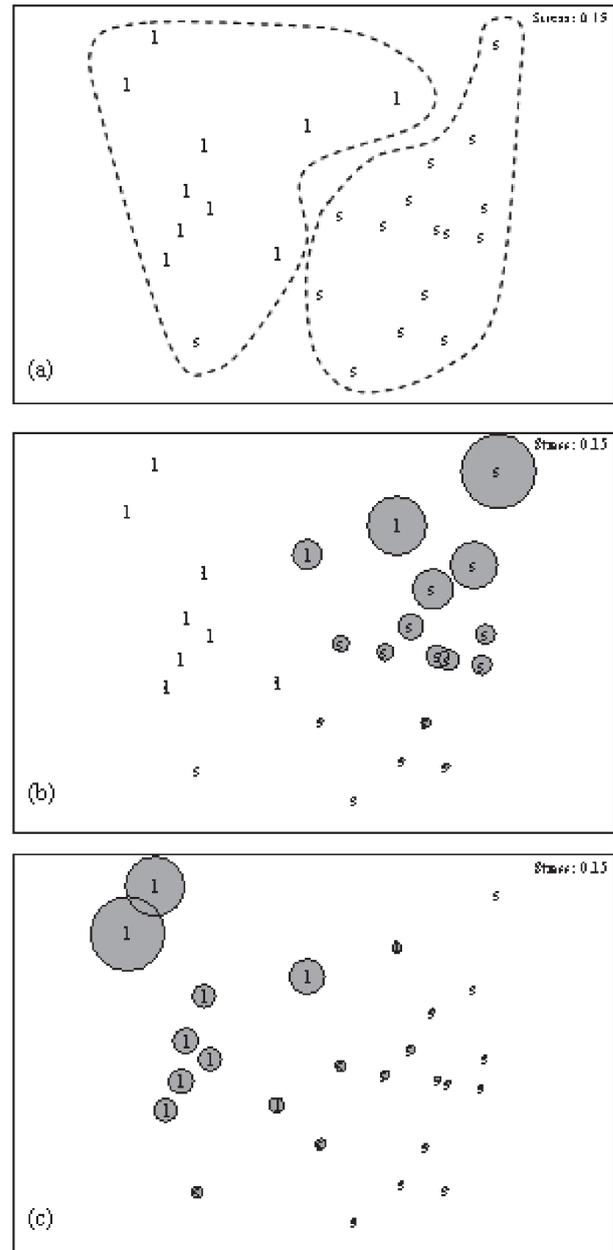
FIG. 5. – MDS analysis of pair-wise similarity matrix derived from numerical abundance of prey categories in each fish size class. (a) MDS plot, s = small fish (≤43 mm TL); l = large fish (>43 mm TL); bubble plots, showing *T. longicornis* (b) and *A. clausi* (c) abundance values superimposed on the relevant MDS ordination plot.

Ontogenetic changes in diet

The ordination plot of the non-metric multi-dimensional scaling applied to the average numerical abundance of prey calculated for each fish size class is presented in Figure 5. The stress value of the ordination was 0.15, which indicates a good representation of diet similarities among fish size classes in a two-dimensional scale (Clarke and Warwick, 1994).
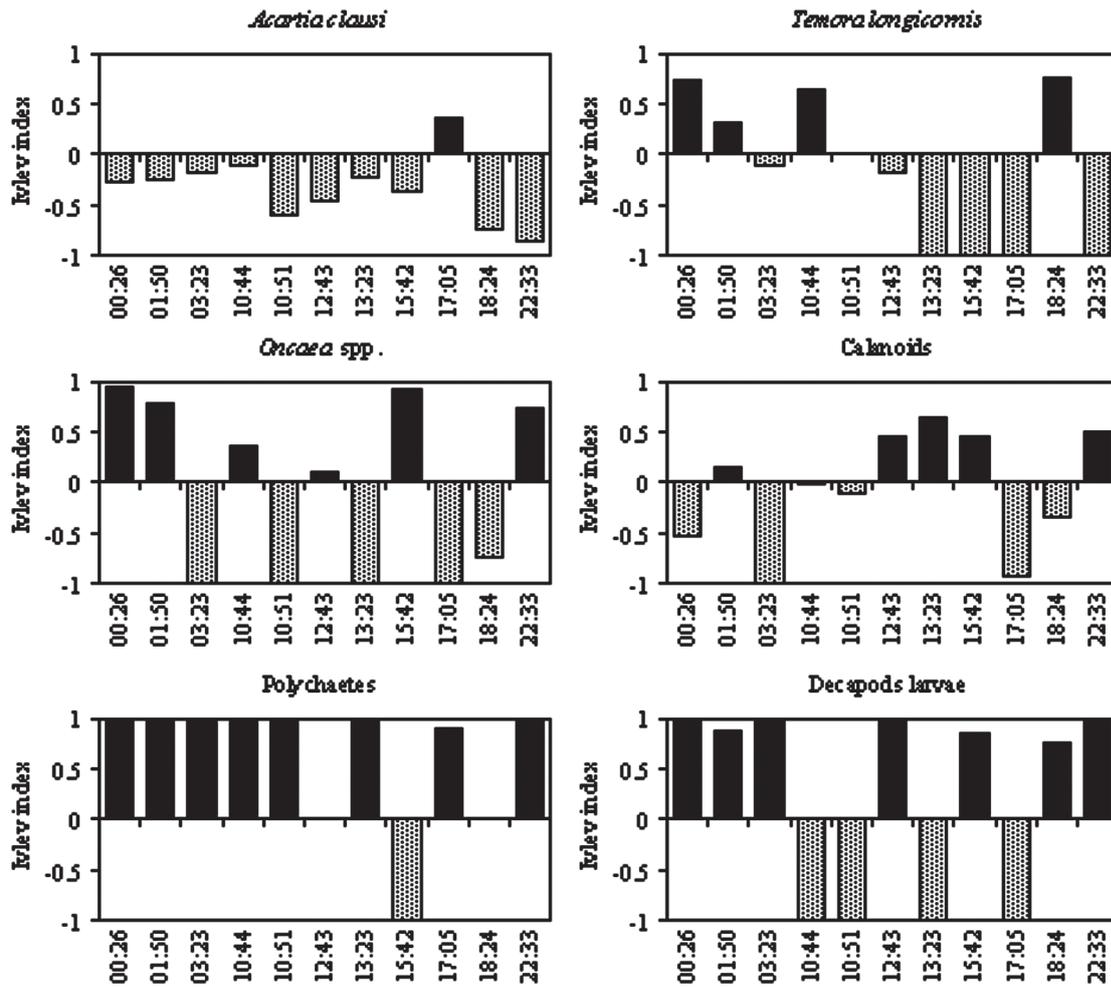
FIG. 6. – Daily pattern of Ivlev selection index (E) for each selected prey categories. The time of day (hh:mm) is on the x-axis.

Fish size was the most important explanatory variable (see above), reflecting distinct ontogenetic shifts in diets. Assigning a threshold size of approximately 43 mm TL, which separated the length frequency distribution into two main cohorts, small fish (25-43 mm TL) and large fish (44-57 mm TL) tended to cluster together in the ordination plot (Fig. 5a), at an arbitrarily chosen similarity level of 45%. Applying the SIMPER routine, most of the diet dissimilarity between small and large fish was due to the copepods *T. longicornis* and *A. clausi*, whose pooled relative contributions to average dissimilarities accounted for 67%. In particular, *T. longicornis* was preferably eaten by small fish (Fig. 5b), whereas *A. clausi* tended to be consumed mostly by large fish (Fig. 5c). As for the other prey categories, larvae of polychaetes and decapods and unidentified copepods were consumed in comparable amounts between the two fish groups; in contrast, other calanoids were preferably eaten by large fish, whereas *Oncaea* spp.

were almost exclusively confined to a small fish diet. On the basis of a univariate measure of niche width, small fish fed on more numerous and evenly distributed prey categories (H' = 1.63, J' = 0.84) than large fish (H' = 1.49, J' = 0.76).

Finally, the pattern of diet similarities observed in the MDS plot ordination was supported by ANOSIM results. The difference in diet between small (25-43 mm TL) and large fish (44-57 mm TL) was statistically significant, attaining an R value of 0.59 (P<0.001), thus allowing the rejection of the null hypothesis.

Prey selectivity

The Ivlev index (E) was calculated for six prey categories found both in the stomach content of *A. minuta* and in mesozooplankton samples from 11 hauls carried out during the 24 h period (Fig. 6). Though *A. clausi* represented numerically the most abundant item in the mesozooplankton samples

(46%), neither diel feeding periodicity nor preferential selection was observed for this copepod, which showed generally low negative values of E (Fig. 6). On the other hand, there was a significant positive selection for *T. longicornis* during night and early morning and at dusk. Interestingly, this copepod was completely absent in the stomach content of *A. minuta* in the afternoon (E = -1), possibly when other prey such as polychaetes and calanoids were preferred (Fig. 6). The genus *Oncaea*, despite its low numerical abundance in the environment (1-2%), was selectively consumed by *A. minuta*, but without any apparent diel trend. Other calanoids were preferentially selected only in the mid-hours of day (Fig. 6). In contrast, cyclopoid copepods (mainly *Oithona* spp.), which represented approximately 13% of mesozooplankton samples, were completely absent from the stomach content of *A. minuta*. A possible explanation could be that they are too thin and transparent to be easily detected and preyed on by the fish. Alternatively, it could be hypothesised that they were rapidly digested, but we discarded such a hypothesis because we found well preserved specimens of *Oithona* spp in gut content of other pelagic fish.

A strong positive selection was observed almost at any time for larvae of polychaetes (E = 1), which were seldom found in the environment in very small amounts (see Table 2). Similarly, decapod larvae were positively selected from dusk through night (Fig. 6), although they can be considered a rare component of mesozooplankton (they were always less than 1% in number). Summarising, *A. minuta* generally tended to be more selective at dusk and throughout the night, relying preferably on large prey such as *T. longicornis* and larvae of polychaetes and decapods.

In order to evaluate prey size selectivity in *A. minuta*, all prey were arbitrarily pooled in 70 μm size classes. Prey size ranged between 140 and 1500 μm, showing a bi-modal frequency distribution at 630 and 910 μm (Fig. 7), which corresponded mainly to juvenile *T. longicornis* and adult *A. clausi*, respectively (on the basis of literature data). A wide gap was found between prey of 1120 μm and the larger prey size class (1470 μm), composed of large decapod larvae. Comparing the relative frequency of prey size observed in large and small fish (see the previous paragraph), although the two fish size groups relied on the same range of prey size, the frequency of prey smaller than 700 μm was higher in small fish than in large fish, and vice versa for prey larger than 700 μm (Fig. 7).
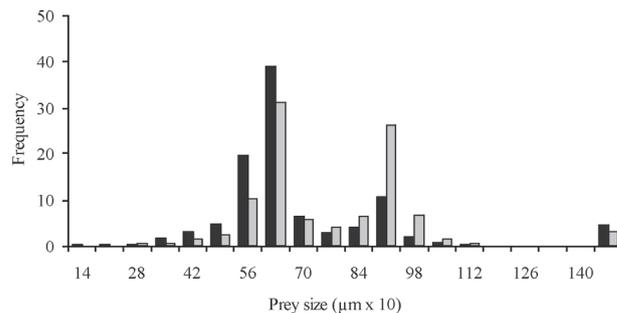

FIG. 7. – Length frequency distribution of prey in the stomach content of *A. minuta*. Small fish (≤43 mm TL) (■); large fish (>43 mm TL) (▪).

DISCUSSION

The northern Adriatic is the shallowest and most dynamic area of the Adriatic Sea. The coastal circulation is strongly influenced by the considerable, but pulsing freshwater outflow from the Po River which spreads at the surface, generating a plume during the stratified periods (spring to summer) (Grancini and Cescon, 1973). In autumn-winter the mixed coastal waters are confined in a narrow belt, and the frontal system clearly separates neritic, eutrophic waters from offshore oligo-mesotrophic waters, producing two ecologically different environments (Franco, 1984; Fonda Umani *et al.*, 1994).

As previously reported in the literature (Fonda Umani, 1996) and confirmed by the present results, the mesozooplankton community in the estuarine and coastal areas of the northern Adriatic Sea is characterised by low diversity and high abundance, with a clear prevalence of copepods (Fonda Umani, 1996; Fonda Umani *et al.*, 2005). In particular, a distinct periodicity of two ecological associations was observed, a late spring-summer association characterised by *A. clausi* and *T. longicornis* and an autumn-winter association characterised by *Temora stylifera* and *Oncaea* sp. (Hure *et al.*, 1980; Fonda Umani *et al.*, 1994; Cataletto *et al.*, 1995; Fonda Umani, 1996; Miralto *et al.*, 2003). The overwhelming dominance of *A. clausi* in summer was also reported from other eutrophic areas of eastern Adriatic, such as the Vranjic Basin and Mali Ston Bay (Lučić and Onofri, 1990; Vidjak *et al.*, 2006).

The neritic waters of this highly productive environment (Fonda Umani *et al.*, 1992; Pugnetti *et al.*, 2005) are inhabited by the transparent goby. *A. minuta* is indeed one of the few gobiid species in the Mediterranean Sea that spend most of their life cycles in the water column (Iglesias *et al.*, 1997). In agree-

ment with previous results from the central Adriatic Sea (La Mesa, 1999), the population of the transparent goby observed during the present study in late spring (May) off Comacchio consisted of two main cohorts. Samples were collected in concomitance with the offshore migration and dispersal of adults forming the demersal phase, which is more vulnerable to semipelagic trawling (La Mesa *et al*., 2005).

Despite the closer link with the bottom that characterises the demersal phase, however, the diet of *A. minuta* was still totally pelagic, indicating an active search for food confined to the water column. *A. minuta* can be considered to be a generalist feeder, with a relatively broad niche width composed of several rare prey caught occasionally. On the other hand, part of the population fed largely on abundant prey in the environment, like the copepods *T. longicornis* and *A. clausi*. Such feeding behaviour probably mitigates the intraspecific competition for food resources.

An additional step towards a successful food partitioning within the population of *A. minuta* was that of the ontogenetic changes in diet observed in our samples. Indeed, the two main fish cohorts mentioned above (and separated by a threshold size of 43 mm TL) exhibited different feeding habits, in relation to both size and type of prey. Although both fish groups relied roughly on the same taxa of prey, small fish tended to consume mainly small prey like juvenile *T. longicornis* and *Oncaea* spp., whereas large-sized fish preferably tended to consume large prey like *A. clausi* and calanoids. In other words, the intraspecific competition is mitigated by taking different amounts of the same prey, rather than by taking different prey. Summarising data on diel prey selection inferred from Ivlev index, *A. minuta* was more selective at dusk and throughout the night. Moreover, abundant taxa, such as *A. clausi* and *T. longicornis*, were negatively or poorly selected, whereas rare taxa, such as larvae of polychaetes and decapods, were positively selected.

Several other small pelagic planktivorous fish, such as juveniles of *Engraulis encrasicolus*, *Sardina pilchardus* and *Sprattus sprattus*, could be potential competitors of the transparent goby, as all inhabit the coastal environment in the northern Adriatic Sea. Comparing the stomach content of these species, they largely relied on the same prey, such as *A. clausi* and *T. longicornis*, which dominated the mesozooplankton community in spring (Tičina *et al*., 2000; Borme, 2006; present study). Similarly, the main food

items of *A. minuta* in the Black Sea were the copepods *A. clausi* and *Pseudocalanus elongatus*, species largely preyed on by *Sprattus sprattus balticus* and *Engraulis encrasicolus maeoticus* (Budnichenko *et al*., 1999; Chesalin *et al*., 2004). Nevertheless, unlike the transparent goby, it has been noted that sprat, anchovy and possibly pilchard were not able to find food during night as successfully as they were during daytime (Tudela and Palomera, 1995; Tičina *et al*., 2000; Borme, 2006).

Hence, two main factors could interact to mitigate the interspecific food competition. The first could be that *A. clausi* and *T. longicornis* are so abundant in the environment that they actually did not represent limited food resources. Secondarily, diel feeding rhythm differed among the potential competitors, providing an alternative way of food partitioning, at least in time.

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