Feeding strategies of *Atherina boyeri* (Risso 1810) in a freshwater ecosystem

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Summary

This study investigates the adaptation of certain feeding strategies by a population of *Atherina boyeri* inhabiting a freshwater ecosystem (Lake Trichonis, Greece) and links feeding habits with ecosystem interactions, using stomach content analysis and food availability. The use of Ivlev's electivity index (E) revealed the selection of different prey categories in respect to size, species and even gender. *A. boyeri* showed positive selection for larger zooplankters such as adult copepods and the egg-bearing females of *Eudiaptomus drieschi* ($0.53 < E < 0.92$ and $0.24 < E < 0.99$, respectively) or the cladocerans *Diaphanosoma orghidani* and *Daphnia cucullata* ($0.25 < E < 0.53$ and $0.23 < E < 0.37$, respectively) in spring and/or summer. In contrast, the fish totally avoided rotifers and copepod nauplii, while showing negative selection for smaller prey items like copepodites ($-1.00 < E < -0.14$). A shift to larger prey was recorded as age increased. Larger specimens showed cannibalistic behaviour by consuming larvae of *A. boyeri* and the endemic, threatened, fish *Economidichthys trichonis*. The results provide certain indications that, through selective predation, *A. boyeri* is able to affect zooplankton abundance and community composition, the vertical distribution and migration of crustaceans and the abundance of other fish species, However, more research on the dynamics and feeding ecology of *A. boyeri* and other fish species is necessary.

Introduction

The big-scale sand smelt, *Atherina boyeri* (Risso 1810), is a small, short-lived, euryhaline species that is common in the Mediterranean Basin and adjacent areas, and in the northeast Atlantic (Quignard and Pras, 1986). This species inhabits mainly coastal and estuarine ecosystems, while in some cases it can also form dense populations in freshwater bodies (Moretti et al., 1959; Francisco et al., 2008). Moreover, the euryhaline character of this species has led to its introduction into lakes and reservoirs for stock enhancement purposes (Economidis et al., 2000; Innal and Erk'akan, 2006) or its accidental transfer into freshwater bodies, where it can rapidly increase its abundance and dominate in the ichthyofauna (Küçük et al., 2009).

There have been numerous studies regarding the feeding habits of *A. boyeri* in marine and brackish environments (Danilova, 1991; Trabelsi et al., 1994; Gisbert et al., 1996; Bartulovic et al., 2004; Vizzini and Mazzola, 2005), and freshwater ecosystems (Moretti et al., 1959; Mantilacci et al., 1990; Rosecchi and Crivelli, 1992; Chrisafi et al., 2007). The species has been found to feed mainly upon planktonic or/and benthic invertebrates (mostly crustaceans) depending on their abundance, and it has been characterized as a generalist and opportunistic predator (Bartulovic et al., 2004).

A population of *A. boyeri* inhabits Lake Trichonis (Western Greece), having been naturally introduced into this ecosystem from the sea via river channels during past centuries. Nowadays, the species is dominant in the fish community and has great commercial importance, as it is the main source of fishing revenues from the lake (Leonardos, 2001). This population of sand smelt was found to be genetically divergent compared to the populations inhabiting other adjacent marine areas of western Greece (Klossa-Kilia et al., 2007) and belongs to the 'lagoon' or 'lake' type of *A. boyeri*, which possibly corresponds to a valid species awaiting formal description (Kraitsek et al., 2008). Consequently, having been introduced naturally into Lake Trichonis, *A. boyeri* cannot be considered a typically exotic species in this ecosystem.

However, one could suggest that, by inhabiting Lake Trichonis for many centuries and being the dominant fish species and the most important planktivorous predator, this population of *A. boyeri* has probably adapted certain feeding strategies (such as opportunism or prey selection), which may affect and regulate the abundance and distribution of its prey as well as its own abundance. It may also exercise several effects on other fish populations. In the only previous research on the diet of *A. boyeri* in Lake Trichonis, Chrisafi et al. (2007) reported that the species relied solely on zooplankton for its energy demands and was considered an opportunistic predator. However, this paper as well as all published studies concerning the feeding of *A. boyeri*, was based on stomach content data without relating these findings to food availability to investigate the existence of actual food preference.

The present study provides some aspects on the feeding strategies adapted by *A. boyeri* in Lake Trichonis, utilizing both stomach content data and *in-situ* zooplankton composition and availability. Specific aims were to investigate: (i) the dietary preferences of *A. boyeri* in respect to season, ontogenetic stage and prey availability, (ii) the existence of selective predation by this species, and (iii) the possible consequences of prey selection adaptation on the regulation of its own abundance, as well as the abundance and distribution of its prey. Considering that several recorded cases of intentional or accidental introduction of *A. boyeri* into freshwater ecosystems exist without assessment of their ecological impacts, the present study provides some interesting aspects on the effects of such practices.

Materials and methods

Study area

Lake Trichonis is a deep Mediterranean lake with a mean depth of 30.5 m and a maximum depth of 57.0 m (Fig. 1).
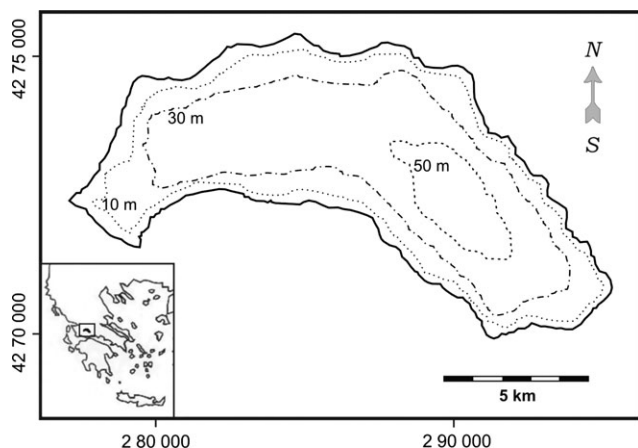
Fig. 1. Map of Lake Trichonis Greece

The lake occupies an area of 98.6 km^2 and is situated in western Greece at an altitude of 18 m a.s.l. It is a warm monomictic lake, exhibiting a long period of thermal stratification; previous studies have classified it as oligotrophic to mesotrophic (Doulka and Kehayias, 2008). Lake Trichonis is the largest natural lake in Greece and is of significant ecological and economical importance. It is included in the NATURA 2000 network of protected areas and is very rich in fish species, most economically important of which is the *Atherina boyeri* Risso, 1810 (Leonardos, 2001).

Field methods

Fish were sampled during an annual cycle between April 2006 and March 2007. Twelve monthly samplings were conducted using a purse seine net (mesh size 6 mm) in various sites of the lake with depths between 10 and 15 m. Total sample size consisted of 590 *A. boyeri* specimens. Fifty specimens were randomly selected from each of the twelve catches, except in February 2007, when only 40 specimens were obtained. All fish specimens were immediately preserved in 4% formaldehyde solution to minimize post-capture digestion.

Along with the fish samplings, three replicates of zooplankton samples were also collected from the same sites, with vertical hauls from the bottom to the surface using a Hydro-Bios plankton net (40 cm diameter, 100 cm long, 50 μm mesh size). These samples were also fixed in 4% formaldehyde solution. Water volume sampled by the net in each haul was calculated by the length of the hanging rope and the surface of the mouth area of the net.

Laboratory methods

For each fish specimen, total length (TL) and mouth gap opening were measured to the nearest 0.01 mm using a digital caliper, while gender was determined macroscopically (or in a few cases microscopically). All prey items from the stomach content were identified under a stereoscope to the lowest taxonomic level possible, given the degree of digestion. Quantification of stomach contents for abundance calculations was based on the number of identifiable specimens and the 'remains', the latter being composed of eyes, legs, telson, etc.

Data analysis was carried out using the numerical method where the number of individuals in each food category was expressed as a percentage of the total number of food items. Frequency of occurrence (% *F*) was calculated as the

percentage of stomachs containing prey category *i* over the total of non-empty stomachs (Hyslop, 1980).

The identification and abundance estimate (ind L^{-1}) of organisms in the zooplankton samples were made in three 1.5 ml subsamples for each replicate counted on a Sedwick-Rafter cell (Doulka and Kehayias, 2008). The monthly abundance values were calculated as the mean value of the replicate counts for each month.

To estimate variation in feeding habits as a function of size, the specimens were separated into four length classes: L_1: TL < 50 mm (n = 39), L_2: 50.1 < TL < 70 mm (n = 164), L_3: 70.1 < TL < 85 mm (n = 223) and L_4: TL > 85.1 mm (n = 164). Length class size boundaries correspond to total length at the 0+ to 3+ age groups of *A. boyeri* in Lake Trichonis (Leonardos, 2001). The influence of the predator's body size on the seasonal diet composition was analyzed using Correspondence Analysis (CA) on square-root transformed data (ter Braak, 1994).

The diet overlap among size groups and between genders was estimated using Schoener's (1970) similarity index:

$$\alpha = 1 - 0.5 \sum |p_{ij} - p_{ik}|$$

where p_{ij} is the proportion of resource *i* consumed by group *j* (e.g. males) and p_{ik} is the proportion of resource *i* consumed by group *k* (e.g. females). Zero value indicates no overlap, while 1 represents complete overlap. The index value is generally considered biologically significant when it exceeds 0.6 (Wallace, 1981).

To estimate prey selection, Ivlev's electivity index (*Ei*) (Ivlev, 1961) was calculated from the mean percentage of prey items found in the stomach contents and the water, as follows:

$$E_i = (p_i - P_i)(p_i + P_i)^{-1}$$

where p_i is the percentage of food item *i* in the diet, and P_i is the percentage of food item *i* in the water.

To determine the feeding strategy along the annual cycle, the modified Costello graphical method (Amundsen et al., 1996) was used. According to this method, the prey-specific abundance (*Pi*), which is defined as the percentage of a prey item over the total of prey items in only those predators in which the actual prey occurs, is plotted against the frequency of occurrence (*Fi*) on a two-dimensional graph. Information on prey importance and feeding strategy of the predator is provided by the distribution of points along the diagonals and axes of the diagram (Amundsen et al., 1996; Caiola et al., 2001).

Statistical analysis was performed with SPSS 17 software for Windows on log(x + 1) transformed values. Differences in the fish larvae consumption between male and female specimens were investigated with the chi-square (χ^2) test. The null hypothesis was that fish larvae consumption was equal for male and female specimens. Correlations between predator and prey body measurements were investigated using Pearson's correlation coefficient.

Results

Diet composition and variation

Stomach content analysis of 590 *A. boyeri* specimens identified thirteen different prey categories, belonging to four major groups: crustaceans (copepods, cladocerans, amphipods),

molluscs (Bivalvia), insects (including Chironomidae larvae) and Pisces (teleost fish larvae). In general, copepods and especially the calanoid *Eudiaptomus drieschi* (Poppe and Mràzek, 1895) were the dominant prey (Table 1). Larvae of *A. boyeri* and *Economidichthys trichonis* (Economidis and Miller 1990) were identified frequently in the gut content. No rotifers and copepod nauplii were found as prey items, while a few specimens of *Alona* sp. (Baird 1843), Chironomidae larvae and amphipods were found occasionally. The large numbers of calanoid copepod eggs recorded in the stomach contents suggest the consumption of egg-bearing females, the number of which was estimated based on the average number of eggs per female found in the zooplankton samples in each sampling period.

Stomach content analysis indicated that the diet of *A. boyeri* varied temporally. Copepods and especially *E. drieschi* prevailed among prey items in winter and spring, accounting for 74.8–87.4% of the stomach contents, respectively. The cyclopoid *M. albidus* (Jurine 1820) had the highest contribution in August (47.5%). Among the cladocerans, *Diaphanosoma orghidani* (Negrea 1982) had higher contribution in summer (63.4% in June), *Bosmina longirostris* (Muller 1785) in December 2006 (29.9%), while *Daphnia cucullata* (Sars 1862) participated in the fish diet mainly in spring. *Dreissena polymorpha* (Pallas 1771) larvae were present in the stomach contents almost throughout the year, having their greatest proportion in March (59.7%). Fish larvae participated in the diet of *A. boyeri* during autumn and early winter while during the same period, the other prey categories contributed to the taxon's diet to a lesser extent.

Correspondence Analysis biplots indicated the correlation of certain prey items with the predator's body size among seasons (Fig. 2). In most cases the Eigenvalues of CA axis 2 and 3 explained 86.6–97.7% of variance in the stomach content. The first four CA axes explained 96.7–99.0% of total variability (Table 2). The relative scattering of the prey items to the influencing factor (in this case the total length of *A. boyeri*) showed that especially in autumn and winter the consumption of fish larvae and *E. drieschi*, respectively, was strongly related to predator size. Additionally, niche overlap results shown in Table 3 indicate that the species does not consume the same prey type throughout its lifespan. Indeed, considering the entire sampling period, L_1 specimens fed mostly on *D. orghidani* (58.8%), while the diet of the other ontogenetic stages (L_2, L_3 and L_4) comprised mainly *E. drieschi* (Fig. 3). The contribution of cyclopoid copepods was more conspicuous in the diet of the three older ontogenetic stages, especially in summer, while in winter L_1 and L_2 specimens fed mostly on *B. longirostris* and *D. polymorpha* larvae (Fig. 3). Fish larvae had a higher participation in the diet of the older L_3 and L_4 stages, especially in autumn.

A total of 608 fish larvae were found in the stomach contents of 105 specimens of *A. boyeri*. Chi square tests indicated that there was no statistically significant difference in the number of larvae found in the stomach contents between male and female specimens (χ^2 test, P > 0.05). Total body length measurements were attained for 366 partially digested fish larvae. Pearson's correlation coefficient indicated a positive correlation between predator's mouth gap and larvae length ($r = 0.306$, n = 366, P < 0.01), while there was a linear regression between them (Fig. 4). Thus, preying on fish larvae by *A. boyeri* seems to be a matter of size, since the predator's mouth gap is analogous to larvae body length.

Table 1
Diet composition per number of prey items in *A. boyeri* stomach contents throughout the sampling period (April 2006–March 2007), Lake Trichonis. (Monthly contribution of cladoceran and copepod species given as percentages within their communities)

| Prey	April	May	June	July	August	September	October	November	December	January	February	March	Total
Alona sp.	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4
B. longirostris	3.98	0.00	4.85	12.86	0.63	2.94	2.92	83.33	100.00	99.18	35.71	7.55	2315
C. pulchella	1.04	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	49
D. cucullata	92.86	68.26	1.65	0.33	0.00	0.00	0.00	0.00	0.00	0.00	7.14	26.42	5597
D. orghidani	1.23	31.71	93.22	86.76	82.17	97.06	97.08	16.67	0.00	0.45	57.14	66.04	11 792
L. kindti	0.90	0.03	0.13	0.00	17.20	0.00	0.00	0.00	0.00	0.36	0.00	0.00	346
Total cladocerans	3671	2993	7450	2092	1733	34	548	6	405	1101	14	53	20 100
E. drieschi (adults)	94.59	77.59	91.17	99.95	33.77	97.97	95.94	61.54	55.02	88.76	99.61	90.35	108 215
E. drieschi (copepodites)	4.59	0.01	0.00	0.00	0.19	0.00	2.16	0.00	0.37	0.96	0.02	1.08	1915
M. albidus (adults)	0.73	22.40	8.83	0.05	55.55	2.03	1.29	34.62	44.36	9.53	0.32	8.58	12 541
M. albidus (copepodites)	0.06	0.00	0.00	0.00	9.92	0.00	0.43	3.85	0.25	0.49	0.04	0.00	861
M. varicans (adults)	0.03	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.26	0.00	0.00	159
M. varicans (copepodites)	0.00	0.00	0.00	0.00	0.42	0.00	0.09	0.00	0.00	0.00	0.01	0.00	27
Total copepods	27 256	11 174	3183	2000	5667	295	1159	52	807	55 947	8565	7614	123 719
D. polymorpha larvae	0	84	276	78	459	8	362	2	123	1475	2829	11 361	17 057
Insect larvae	0	0	0	3	2	4	2	0	1	0	3	2	17
Amphipods	0	11	1	3	5	0	1	0	0	0	0	0	21
Fish larvae	0	14	49	11	5	143	353	10	18	0	0	5	608
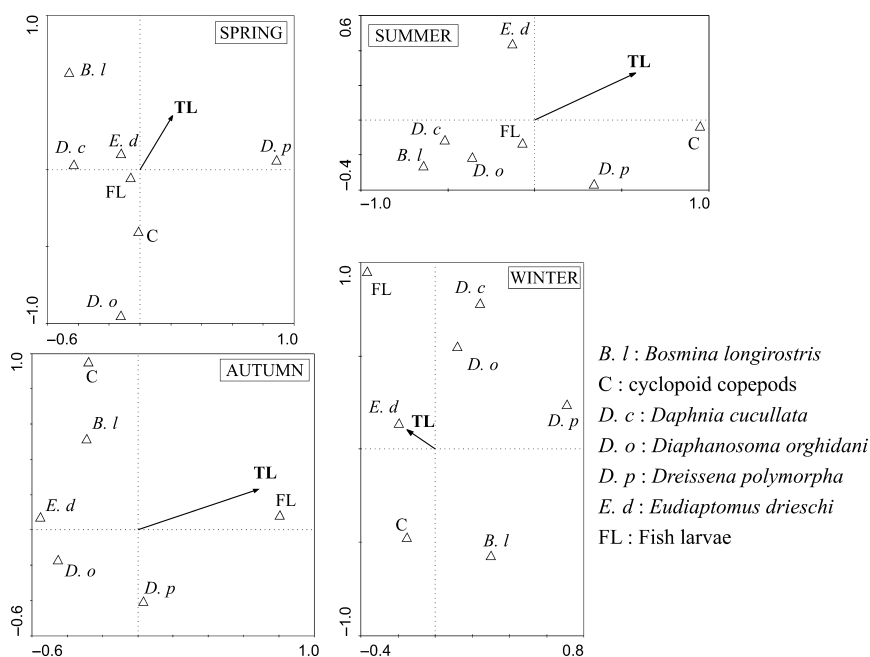
Fig. 2. CA ordination diagrams with most important prey items (white triangles) and total length of *A. boyeri* (arrow) as the influencing factor, per season

B. l : *Bosmina longirostris*
C : cyclopoid copepods
D. c : *Daphnia cucullata*
D. o : *Diaphanosoma orghidani*
D. p : *Dreissena polymorpha*
E. d : *Eudiaptomus drieschi*
FL : Fish larvae

Table 2
Eigenvalues and cumulative percentage variance of total lengths for first four CA axes, *A. boyeri* stomach contents per season

	Spring				Summer				Autumn				Winter			
CA Axis	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Eigenvalues	0.637	0.418	0.157	0.087	0.497	0.356	0.126	0.081	0.662	0.272	0.183	0.164	0.434	0.250	0.199	0.108
Cumulative percentage variance of species-environment relation	2.3	46.5	86.6	96.7	19.2	92.1	97.7	99.0	92.0	93.7	96.6	96.8	0.0	17.2	23.5	98.0

Table 3
Dietary niche overlap of *A. boyeri* by gender and length class

Month	♀–♂	L_1–L_2	L_1–L_3	L_1–L_4	L_2–L_3	L_2–L_4	L_3–L_4
APR	0.996*	0.96*	0.98*	0.88*	0.97*	0.92*	0.90*
MAY	0.95*				0.78*	0.81*	0.76*
JUN	0.94*	0.78*	0.51	0.19	0.72*	0.38	0.62*
JUL	0.82*	0.95*	0.46	0.28	0.50	0.28	0.26
AUG	0.72*				0.87*	0.58	0.69*
SEP	0.35	0.78*	0.22	0.00	0.29	0.04	0.75*
OCT	0.89*	0.86*	0.20	0.12	0.33	0.26	0.83*
NOV	0.56				0.72*	0.31	0.30
DEC	0.51	0.84*	0.73*	0.21	0.86*	0.35	0.49
JAN	0.98*				0.07	0.07	0.89*
FEB	0.90*						0.80*
MAR	0.97*				0.96*	0.81*	0.85*

*significant similarity for values of >0.60.

Prey selectivity and feeding strategies

Monthly variations in the abundance of the three most important zooplankton groups in Lake Trichonis are shown in Fig. 5a. Copepods were dominant during late winter and spring, while cladocerans were more abundant in summer. *D. polymorpha* larvae prevailed in the zooplankton community during autumn, while lower abundance was recorded during winter and spring.

The use of Ivlev's electivity index revealed certain prey preferences of *A. boyeri*. During almost the entire sampling period, the total population showed clear preference for copepods and negative preference for *D. polymorpha* larvae, except for March 2007 when the index values reversed (Fig. 5b). Positive electivity values were found for the total cladocerans but only for 6 months of the sampling period (May to July and October to December), while for the remaining 6 months negative values were recorded for this prey category. Of the different sized copepods, *A. boyeri* showed a clear preference for the larger specimens such as the adults ($0.53 < E < 0.92$), either calanoids or cyclopoids, and especially the egg-bearing *E. drieschi* ($0.24 < E < 0.99$), which were considered separately. Negative selection for the copepodites of all species was noticed (Fig. 5c). Positive selection for *D. cucullata* was recorded from April to July 2006 (Fig. 5d). After this period, either no *D. cucullata* specimens were found in the zooplankton samples (August-October), or the scarcity of this species resulted in electivity values of −1 (November–February). Positive selection for *D. orghidani* was found only between May and July and in October 2006 ($0.25 < E < 0.53$). In contrast, there was highly negative selection for *B. longirostris* in most of the sampling months ($−1.00 < E < −0.03$), except between October and December 2006 when positive values were recorded ($0.16 < E < 0.89$).

The four ontogenetic stages of *A. boyeri* showed no differences in the positive or negative diet preferences for copepods. However, the degree of positive selection for the adult copepods increased with age (Fig. 6). Negative selection for
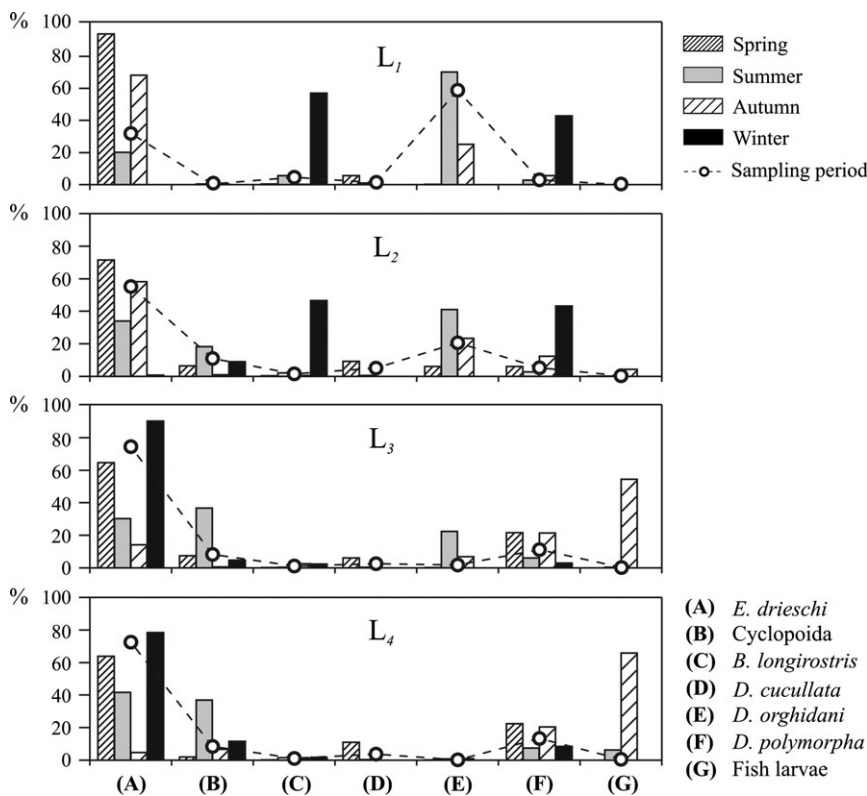
Fig. 3. Seasonal percentage contribution of main prey items in four ontogenetic stages (L_1–L_4) of *A. boyeri* diets, Lake Trichonis

(A) *E. drieschi*
(B) Cyclopoida
(C) *B. longirostris*
(D) *D. cucullata*
(E) *D. orghidani*
(F) *D. polymorpha*
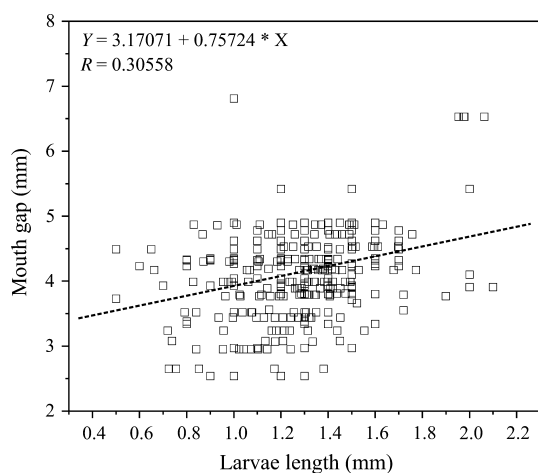(G) Fish larvae

$Y = 3.17071 + 0.75724 * X$
$R = 0.30558$

Fig. 4. Relation between total length (TL) of fish larvae recorded in stomach contents and mouth gap of predator

B. longirostris was recorded for all stages, while it was weaker for L_1 specimens. In contrast, the negative selection of *D. cucullata* by the youngest (L_1) specimens of *A. boyeri* became positive for the other three ontogenetic stages, while there was also a shift in the preference of *D. orghidani* from positive to negative with age increase (from L_1 size class to L_4).

For the entire sampling period, *A. boyeri* demonstrated a mixed feeding strategy with varying degrees of specialization and generalization on different prey items (Fig. 7). The relationship between prey specific abundance and frequency of occurrence indicated that there was some specialized predation on calanoid copepods in winter and spring. Calanoid copepods showed higher abundance and occurrence than the other prey items, being consumed by more than 60% of the fish and constituting a dominant prey. Fish larvae were most important for the *A. boyeri* diet in autumn, especially in September and November when more specialized predation occurred, even though small numbers of fish larvae were present in the stomach contents in several periods. Among the cladocerans, *D. orghidani* played an important role in the feeding of *A. boyeri* in summer. For *D. polymorpha* larvae more specialized predation occurred during spring, especially by the older (L_3 and L_4) specimens.

Discussion

In Lake Trichonis *A. boyeri* feeds exclusively on zooplankton and does not turn to benthic prey as has been reported for populations in other Mediterranean estuaries (Rosecchi and Crivelli, 1992; Trabelsi et al., 1994; Bartulovic et al., 2004). Similar findings have been recorded by Chrisafi et al. (2007) in the same area and by Mantilacci et al. (1990) in Lago Trasimeno. The present study showed that copepods, particularly the calanoid *E. drieschi*, prevailed in the diet of *A. boyeri* throughout the sampling period, in contrast to Chrisafi et al. (2007), who found the larvae of the mollusc *D. polymorpha* to be the dominant prey item, followed by *E. drieschi*. The cladocerans *D. orghidani*, *D. cucullata*, *Ceriodaphnia pulchella* (Sars 1862) and *Alona* sp. are reported here for the first time as contributing to the diet of *A. boyeri* in Lake Trichonis. In Chrisafi et al. (2007), the cyclopoid copepods were not identified to species level and it is possible that *D. orghidani* was misidentified as *Diaphanosoma brachyurum* (Lievin 1848), considering their anatomic similarities (Doulka and Kehayias, 2008).

The interrelation of stomach content with food availability indicated that *A. boyeri* practiced some specialized predation, selecting different prey categories in respect to size, species and even gender. Nevertheless, an opportunistic behaviour could be reflected regarding copepods in general, since this
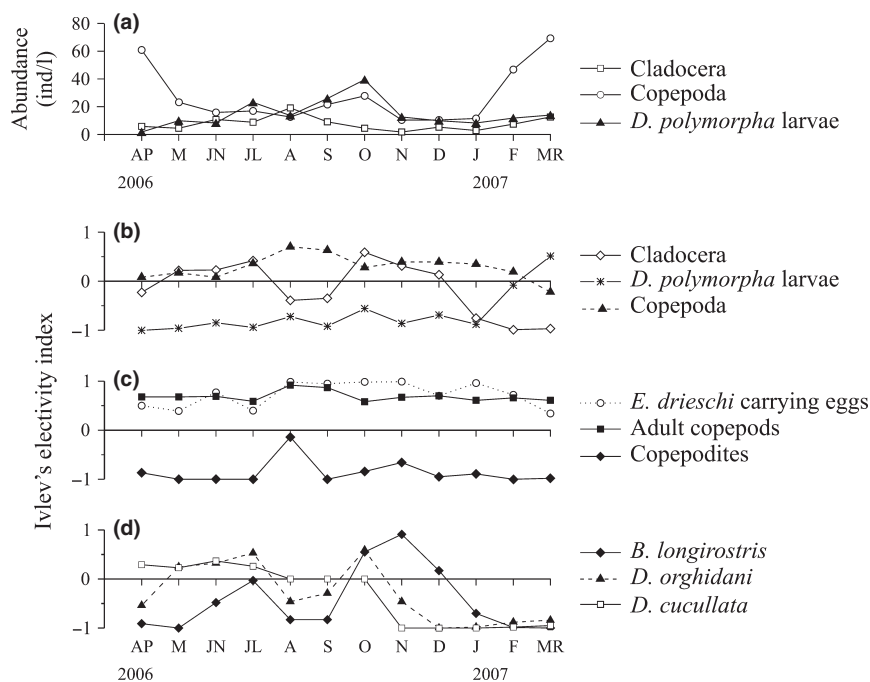
Fig. 5. Monthly variation in integrated abundance of zooplankton groups (a), Ivlev's electivity index for three most important zooplankton groups; (b) copepod community; (c) cladoceran species (d)
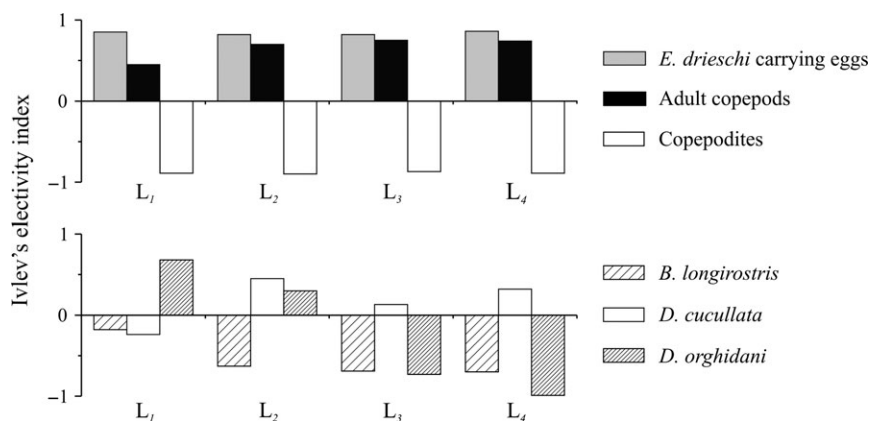

Fig. 6. Ivlev's electivity index of four ontogenetic stages (L_1–L_4) of *A. boyeri* for copepods and cladocerans during entire sampling period

dominant zooplanktonic group also prevailed in the diet. The vast contribution of copepods to the diet of sand smelt has also been reported in other areas (Scilipoti, 1998; Vizzini and Mazzola, 2002; Bartulovic et al., 2004). Cyclopoids participated considerably in the diet of *A. boyeri* only in summer, when the abundance of calanoids in the zooplankton community decreased. Considering that cyclopoid copepods have greater body-mass than the calanoids (Michaloudi, 2005), it could be suggested that during this season the sand smelt exploited cyclopoids which, although in low abundance, could provide greater energy benefits.

Small-sized prey such as rotifers and copepod nauplii were definitely not a preferred prey for *A. boyeri*, as reported also by Mantilacci et al. (1990), Rosecchi and Crivelli (1992), Bartulovic et al. (2004) and Chrisafi et al. (2007). Moreover, a clear negative selection for copepodites was recorded, although they constituted the highest proportions in the community of copepods throughout the sampling period. The body-size selection hypothesis could also explain why the large *D. cucullata* was preferred mostly by the older ontogenetic stages of *A. boyeri* which, on the other hand, showed less preference to or avoided the smaller cladocerans such as like *D. orghidani* and *B. longirostris*. According to

the foraging theory (Lazzaro, 1987), the lower mobility of small-sized organisms provides an advantage for prey capture by younger specimens. A shift to larger prey with the increase of the ontogenetic stage has been also reported by Chrisafi et al. (2007) in the same area and by Castel et al. (1977), Scilipoti (1998), Vizzini and Mazzola (2002) and Bartulovic et al. (2004) in other marine and brackish areas. Ontogenetic shifts in fish diet seem to be adaptations to maximize energy intake, thus lowering vulnerability to predation and increasing fitness (Grossman, 1980).

The larvae of *D. polymorpha* were not prevalent in the diet of *A. boyeri* nor were they preyed upon selectively, even when they were abundant in the water. The positive selection for this prey that was recorded from only late winter to early spring could probably be attributed to the maximum size of *D. polymorpha* specimens during this period (unpublished data), which leads to greater energy gains and to greater capture probability according to the foraging theory (Lazzaro, 1987).

Doulka and Kehayias (2008) reported the year-round presence of adults and egg-bearing females of *E. drieschi* and suggested that this species either has multiple reproductive periods or continuous reproduction. This fact, along with the
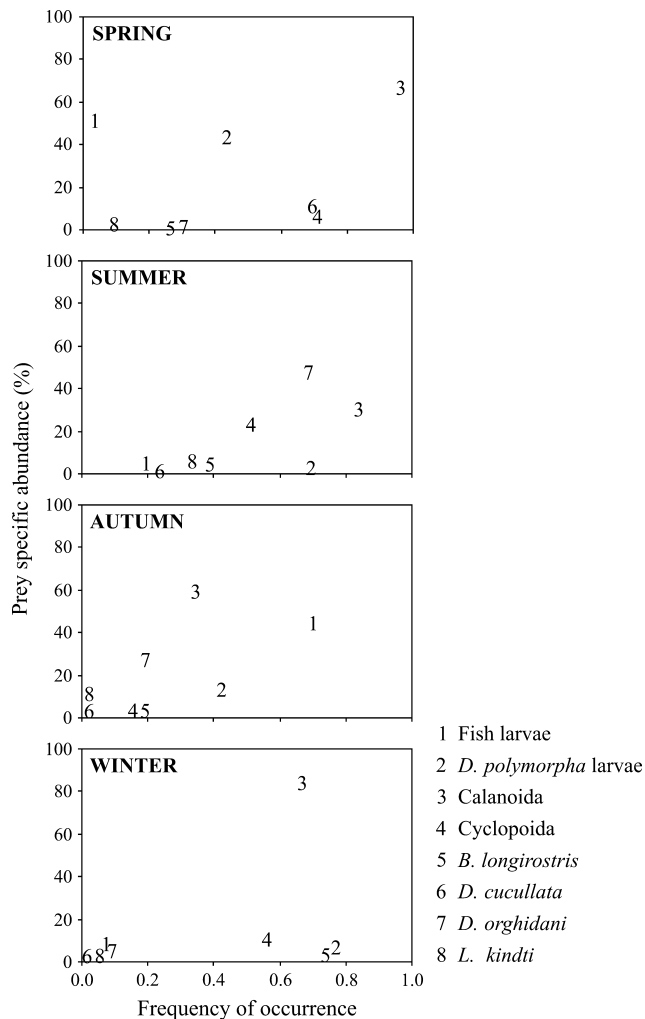
Fig. 7. Graphical analysis of *A. boyeri* feeding strategy using the modified Costello method

great preference of *A. boyeri* for *E. drieschi* adults and egg-bearing females, could form a significant ecological mechanism for the constant regulation of this dominant copepod in the lake by influencing its reproductive capacity, although its actual significance cannot be estimated with the present data-set.

Vertical distribution of zooplankton species and especially their diel vertical migration (DVM) could also affect the feeding adaptations of *A. boyeri* and explain their positive and negative selections. Lake Trichonis is a deep monomictic lake with oligo- to mesotrophic characteristics. A seasonal thermocline develops from May to November and is well established mainly between 8 and 16 m, while the water transparency fluctuates between 5 and 13 m, being greater in summer and lower in winter. Doulka and Kehayias (2011) reported that most of the zooplankton crustaceans in Lake Trichonis follow the normal DVM pattern, expressed by the ascent to surface waters during the night and descent into the thermocline or deeper in daylight. This is widely considered as an anti-predation strategy against visual predators (Liu et al., 2006). Although there are no reports on the foraging mechanisms of *A. boyeri*, the existence of selective predation by this species, at least for the larger crustaceans, is an indication that it is acting probably as a visual predator. Visual predation would be easier only above the thermocline, which is a layer of low transparency due to the high

concentration of phytoplankton and organic matter. In this sense, there should be a depth limitation in the foraging processes and thus, the vertical distribution of zooplankton species would strongly affect their selection as prey by *A. boyeri*. During most of the year, copepods distribute within the predation range of *A. boyeri* (Doulka and Kehayias, 2008, 2011), while in winter the latter would have greater difficulty reaching them, either due to lower visibility or their dispersion in the broader vertical stratum. This could also explain why *A. boyeri* turned to the mollusc larvae as an alternative prey during winter.

A. boyeri has also been reported by Chrisafi et al. (2007) to prey on fish larvae in Lake Trichonis, and by Gon and Ben-Tuvia (1983), Rosecchi and Crivelli (1992) and Bartulovic et al. (2004) in other marine or brackish areas. However, none of the above authors identified the finfish fry found in sample stomach contents. In contrast, the present results showed that *A. boyeri* preyed, at least, on the larvae of *Economidichthys trichonis* and its own fry. Preliminary results on the feeding preferences of larvae of both *A. boyeri* and *E. trichonis* in Lake Trichonis showed that specimens of similar size to those recovered from the stomach contents, also feed upon zooplankton crustaceans (unpublished data). This indicates that *E. trichonis* larvae may be potential competitors to the sand smelt population. Considering that *E. trichonis* is endemic to lakes Trichonis and Lysimachia and is considered a threatened species (Crivelli, 2006), the predation of its larvae by *A. boyeri* could be of crucial importance for its survival. It also highlights the ecological effects that a planktivorous species such as the sand smelt could exercise on other fish populations.

According to reports on the mean monthly fish catchment of *A. boyeri* in Lake Trichonis (unpublished data), its maximum abundance occurs at the end of summer and decreases as winter sets in. At the same time, the present results, being in agreement with Doulka and Kehayias (2008), showed a significant decline of the lake's zooplankton abundance after October. Therefore, in early autumn, *A. boyeri*, which is the dominant zooplanktivorous species of the lake, probably starts to face intense inter-specific competition for food. Moreover, this competition becomes greater considering that the recruited newborn specimens from the early summer reproduction period are highly abundant in early autumn (Daoulas et al., 1993; Stoumboudi et al., 1997). Thus, it could be suggested that the specialized predation of *A. boyeri* on fish larvae, especially in autumn, is an ecological adaptation of this species against food limitation. Through this behaviour, *A. boyeri* would reduce inter- and intra-specific competition by removing a number of competitors that utilize the same food sources and thus raise its energy gains for overwintering by consuming food of higher nutrient value. However, confirmation of the above hypothesis would require quantitative data on the fish larvae in the diet of *A. boyeri*, as well as data on the dietary regime of these larvae, their distribution and abundance in the lake.

In conclusion, the present study provides strong indications that *A. boyeri*, as the dominant fish species and the most important planktivorous predator in Lake Trichonis, has probably adapted specific feeding strategies (such as prey selection) to affect and regulate the abundance of its prey but also its own abundance, in some kind of co-evolution. Through selective predation, *A. boyeri* seems to be able to affect various parameters of the zooplankton in Lake

Trichonis such as:(i) community composition, (ii) abundance of the dominant copepod, and (iii) the vertical distribution and migration of crustaceans. Simultaneously it can influence the abundance of its own population (through cannibalism), as well as the abundance of other fish populations such as *E. trichonis*. However, although this study provides certain aspects on the ecological role of *A. boyeri*, more research on the dynamics and feeding ecology of this and other fish species in Lake Trichonis is required in order to clarify the specific interactions in the fish community and the significance of this predator.

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