Scientia Marina 72(2)
June 2008, 393-401, Barcelona (Spain)
ISSN: 0214-8358

The feeding ecology of *Aphanius fasciatus* (Valenciennes, 1821) in the lagoonal system of Messolongi (western Greece)

IOANNIS LEONARDOS

Biological Applications and Technology Department, University of Ioannina, 45110 Greece. E-mail: ileonard@ uoi.gr

SUMMARY: The Mediterranean toothcarp *Aphanius fasciatus* (Valenciennes, 1821) is a small-sized omnivorous estuarine fish. Its diet is dominated by juveniles of shrimps (*Palaemon adspersus*), Isopods, Branchiopoda, Bivalvia, eggs of invertebrates, mosquitoes (adults and larvae) and diatoms. An ontogenetic diet shift with an increase in mean prey size with fish length was observed. Smaller fish feed on planktonic prey (e.g. copepods, ostracods, nauplii of *Artemia*), while larger fish prefer larger and more benthic preys (e.g. ampipods, Bivalvia). The diet of *A. fasciatus* shows a high degree of seasonal variation, with a reduction in the feeding activity during the periods of adverse environmental conditions (winter and autumn). It is a well-adapted estuarine fish, its feeding mode and preferences depending on the preys that are available. Its feeding strategy is characterised by specialisation in different resource types (aquatic invertebrates and mosquitoes) and a high between-phenotype contribution (BPC) to niche width, with specialised individuals showing little or no overlap in resource use.

Keywords: *Aphanius fasciatus*, feeding strategy, intraspecific variation, feeding ecology, lagoon.

RESUMEN: Ecología alimentaria de *Aphanius fasciatus* (Valenciennes, 1821) en el sistema lagunar de Messolongi (Grecia occidental). – El fartet sudeuropeo *Aphanius fasciatus* (Valenciennes, 1821) es un pez de pequeño tamaño, omnívoro, que habita en zonas estuarinas. Su dieta está constituida principalmente por juveniles del camarón *Palaemon adspersus,* isópodos, braquiópodos, bivalvos, huevos de invertebrados, mosquitos (huevos y larvas) y diatomeas. Se observó un cambio ontogénico en la dieta, incrementándose de la talla media de las presas con la longitud del pez, de manera que los ejemplares de menor tamaño se alimentan de presas planctónicas (ej. copépodos, ostrácodos, nauplii de *Artemia*), mientras que los de mayor tamaño prefieren presas más grandes y con mayor afinidad bentónica (ej. anfípodos, bivalvos). La dieta de *A. fasciatus* muestra una marcada variación estacional, con una reducción en la alimentación durante los períodos de adversas condiciones ambientales (invierno y otoño). Se trata de una especie estuarina bien adaptada, sus preferencias y forma de alimentación dependen de las presas disponibles. La estrategia de alimentación de *A. fasciatus* se caracteriza por la especialización en distintos tipos de recursos (invertebrados acuáticos, mosquitos) y una elevada BPC (between phenotype component*)* respecto a la amplitud del nicho, con individuos especializados entre los que el solapamiento en el uso del recurso es escaso o nulo.

Palabras clave: *Aphanius fasciatus,* estrategia alimentaria, variación intraespecífica, ecología alimentaria, laguna.

INTRODUCTION

The Mediterranean toothcarp, *Aphanius fasciatus* (Valenciennes, 1821), is distributed in the coastal zone of the central and eastern Mediterranean (Whitehead *et al.*, 1986). It is a small fish (total length usually less than 6 cm) (Leonardos and Sinis 1999) with external sexual dimorphism and a relatively short lifespan (less than 7 yrs). It is among the most eurythermal and euryhaline species in the Mediterranean Sea, resisting water temperature ranges of 4 to 40ºC and able to reproduce in a salinity range of 10 to 80 psu (Leonardos, 1996). It spawns in batches from April to July, laying up to 500 eggs in each successive spawning act, and reaches sexual maturity within a few months (at a total length of less than 2 cm) (Leonardos and Sinis, 1998).

Aphanius fasciatus originally inhabited a wide range of lowland waters but its distribution is now reduced to brackish and hypersaline waters in salt marshes and coastal lagoons. From a conservation perspective, the populations of *A. fasciatus* have declined dramatically, in many cases even to extinction, due to problems such as brackish-water habitat degradation, pollution of continental and coastal waters, destruction and reduction of salt-works, and introduction of exotic fishes (Bianco, 1995). As a consequence, it has been listed in Annexes II and III of the "Bern Convention", relative to the conservation of wildlife and the natural environment in Europe (Council of Europe, 2000) and in Annex II of the 'Fauna–Flora-Habitat' Directive 92/43/EEC concerning conservation of natural habitats and wild flora and fauna of the European Union (Council of Europe, 1992). Furthermore, *A. fasciatus* was recently listed in the International Union for Conservation of Nature and Natural Resources Red Data Book of endangered species (Baillie and Groombridge, 1996), where it was qualified as "Least Concern", namely a species that has been evaluated against the criteria and does not qualify for Critically Endangered, Endangered, Vulnerable or Near Threatened.

The aim of this study is to provide qualitative and quantitative information on the feeding strategy of *A. fasciatus* with special emphasis on seasonal, habitat and ontogenetic variation in diet.

MATERIALS AND METHODS

Study area

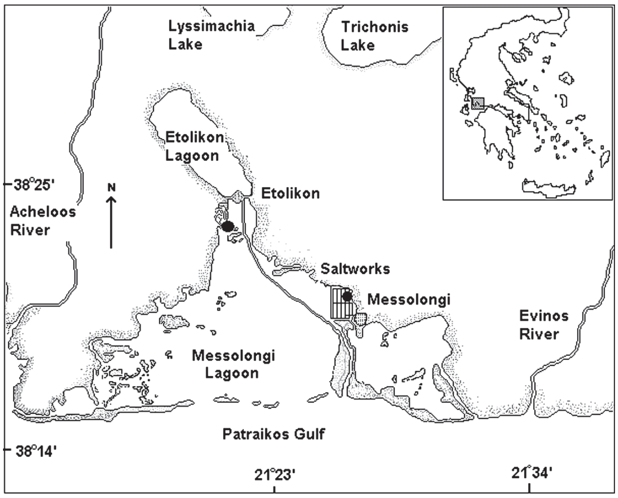

FIG. 1. – Map of the Messolongi Lagoon. The dots indicate the sampling stations.

The present study was carried out at two sites of the Messolongi coastal lagoon system (Fig. 1), one of the largest in the Mediterranean, with a surface area of about 150 km^2 and a mean depth of less than 1 m. In the lagoon sampling site, during the study period the salinity varied between 9.2 (January) and 28 (September) and water temperature from 5ºC (January) to 37ºC (August). The bottom of the lagoon was covered by dense submerged meadows of *Zostera marina* and *Cymodea nodosa* and floating mats of *Enteromorpha intestinalis*, and occasionally aggregations of *Cystoseira barbata*, *Feldomania globifera* and *Cladofora echinus* are found. The shore of the lagoon, which is occasionally flooded, was covered by species of the genus *Salicornia* and *Arthrocnemum*, whereas in places supplemented by inflows of freshwater there are dense aggregations of *Phragmites australis*. It is an eutrophic system according to the concentrations of total nitrogen, total phosphorus and chlorophyll-*a* (Leonardos, 1996).

At the Saltworks sampling site the salinity ranged from 19 (January) and 80 (July) and water temperature from 4ºC (January) to 40ºC (July). The coastal zone was covered mainly by *Arthrocnamum macrostaphylum, Atriplex portulacoides, Salicornia europea* and *Sueda maritima*. Macrophyte coverage was open where the dominant species was *Ruppia maritima*, and dense at one end of the lagoon (the farthest from the sea), where the dominant species was *Phragmites australis*. Lagoon banks were covered by *Juncus maritimus* Lam. and *Atriplex portulacoides*.

At the Lagoon site, in addition to *A. fasciatus*, eight other fish species occurred: *Atherina boyeri, Liza aurata, Liza saliens, Chelon labrosus, Liza ramada*, *Mugil cephalus, Gambusia affinis, Syngnathus abester* and *Anguilla anguilla*. At the Saltworks site, *A. fasciatus* was the dominant species, but during the winter months, when the salinity was lower, some specimens of *L. aurata* and *A. boyeri* were also found.

Field and laboratory methods

Fish were sampled monthly at both sampling sites using a fry fishing drag net with mesh size of 2.5 mm and a length of 15 m from March 1996 to February 1997. The *A. fasciatus* captured were rinsed in fresh water and immediately placed in neutralised formalin (4%) until examination. In the laboratory fish total length (TL) was measured to the nearest mm. Body weight (NW) was measured to the nearest 0.1 mg after removal of the intestines and gonads. Sex was determined from external characteristics and confirmed by gonad examination. Age was determined from scales that were taken from the left side of the body, between the posterior end of the pectoral fin and the anterior end of the dorsal fin. Full guts were removed and food items found in the first third of the gastrointestinal tracks (excluding the rectum) were identified to the lowest taxonomic level possible and counted under dissecting microscope. The volume of each food category was estimated to the nearest 0.00025 mm^3 using a Neubauer counting chamber and later transformed to biomass using a conversion of 0.27 mg of dry weight/mm^3 (Lindegaard, 1992; Alcaraz and Garcia-Berthou, 2007).

Diet analysis

The seasonal feeding activity pattern was assessed through the analysis of the seasonal variation in the percentage of empty guts. To determine the importance each food category to the diet of *A. fasciatus* percent number (%N), percent volume (%V) and frequency of occurrence (%F) were calculated. Percent number (%N) is the number of individuals of a food category divided by the total number of individuals and expressed as a percentage, after pooling the gut contents of all fish. Percent volume (%V) is the equivalent index applied to volume data. Frequency of occurrence (%F) is the percentage of guts in which a food category was present (Hyslop, 1980). In order to provide a balanced, general picture of the importance of food categories that combines the effects of these indices, the index of relative importance (IRI) (Pinkas *et al.*, 1971) expressed as a percentage (Cortés, 1997) was used:

$$\mathrm{IRI} = \%\mathrm{F} \times (\%\mathrm{N} + \%\mathrm{V});$$
$$\%\mathrm{IRI} = (\mathrm{IRI}/\textstyle\sum \mathrm{IRI}) \times 100.$$

Diet diversity (for each fish) was measured with the complement of Simpson's index (D) calculated as:

$$D = 1 - \sum_i \frac{n_i(n_i - 1)}{N(N-1)},$$

where n_i is the number of individuals of prey type i, and N is the total number of prey (Hulbert, 1971).

To determine the feeding strategy of *A. fasciatus*, the modified Costello graphical method (Amundsen *et al.*, 1996) was used. In this method, the prey-specific abundance (Pi), defined as the percentage a food category comprises of all food items in only those predators in which the actual food category occurs is plotted against the frequency of occurrence on a two-dimensional graph. The prey specific abundance was calculated according to the following equation: $Pi = (\sum Si/\sum Sti) \times 100$, where Pi is the prey-specific abundance of food category i, and Sti the total stomach content in only those individuals with prey i in their stomach. Information about prey importance and feeding strategy of the individual can be obtained by examining distributions of points along the diagonals and axes of the diagram. The prey importance is represented in the diagonal from lower left (rare prey) to upper right (dominant prey); the feeding strategy is represented in the vertical axis from bottom (generalisation) to top (specialisation); and the relationship between feeding strategy and the between- or within-phenotype contributions to the niche width is represented in the diagonal from lower right, which represents a high within-phenotype component (WPC), to upper left, which means a high between-phenotype component (BPC). A population with a narrow niche must necessarily be composed of individuals with narrow and specialised niches. A population with a broad niche may, on the other hand, consist of individuals with either narrow (high BPC) or wide (high WPC) niches.

To analyse seasonal and intraspecific differences in diet, the samplings were categorised into seasons (winter=Dec–Feb; spring=Mar–May; summer=Jun–Aug; autumn=Sep–Nov). The R x C independence G-test was performed in order to analyse differences in the seasonal feeding activity.

Analysis of covariance (ANCOVA) was performed to compare the diet diversity and total food category items in gut content and volume of gut contents among sampling sites, seasons and sex using age as covariates. The most complex model was used by the introduction of all possible interactions. The general linear model was simplified by removing the non-significant interactions, in order to increase the statistical power of the remaining sources of variation. When the covariate was non-significant it was removed from the model and an analysis of variance (ANOVA) was used instead.

Correspondence Analysis (CA) was used in order to describe the main sources of diet variation separately for number and IRI%data. CA is an ordination method that reduces a species X sample matrix to a few dimensions explaining most of the variation. CA is a suitable multivariate method for community ecology and is better than the traditional procedure of a priori pooling food categories, which is a method based usually on taxonomic rather than on ecological criteria (Garcia-Berthou, 1999). All the alimentary tracks containing food were used in the analysis and then correlation analysis and ANOVA of the resulting scores were used to interpret the dimensions in term of the measured features of the samples (age, sampling site, season and sex).

RESULTS

Seasonal variation of vacuity index

The seasonal variation in the percentage of empty alimentary tracks reflected a marked discontinuity in *A. fasciatus* feeding activity. The percentage of empty alimentary tracks was significantly higher in winter in Messolongi Lagoon and in autumn at the Saltworks.

In Messolongi Lagoon, the seasonal percentages of empty alimentary tracks were 35% in winter, 33% in spring, 15% in summer and 29% in autumn (G-test=9.77, df=3, P=0.02), while at the Saltworks they were 27% in winter, 28% in spring, 11% in summer and 37% in autumn (G-test=15.36, df=3, P=0.001).

Overall composition of the diet

A total of 27 food categories, mainly invertebrates, were found in the gut contents of *A. fasciatus* (Table 1). The diet was mostly based on Crustacea (Isopoda, Ostracoda, Copepoda, Decapoda), Mollusca (Gastropoda, Bivalvia), Diatoma and Algae. The main food items were littoral invertebrates, particularly Isopoda (Sphaeromatidae and Idoteidae), Copepoda, Decapoda (juveniles of *Palaemon adspersus*), Branchiopoda (Artemia), Insecta (adults and larvae of mosquitoes), Gastropoda, Bivalvia, invertebrates and fish eggs (Table 1, Fig. 2).

Regarding the percent number, the most important food categories for *A. fasciatus* in Messolongi Lagoon were diatoms (*Nitzchia* sp., *Chaetoceros* sp., and *Gymnodinium* sp.), shrimps (juveniles of *Palaemon adspersus*), bivalves (mainly larvae of the species *Abra ovata, Cerastoderma lamarcki, Mytilaster minimus*, *Parvicardium exiguum, Loripes*

Table 1. – Diet of *Aphanius fasciatus* in Messolongi Lagoon and Saltworks: %Number, %Volume and Frequency of occurrence of the main food components.

	Messolongi Lagoon			Saltworks		
	%F	%N	%V	%F	%N	%V
Algae	1.15	0.53	1.97	0.26	0.06	0.37
Diatoms	34.48	41.40	0.69	42.67	45.10	0.90
Plant debris	6.40	1.59	10.65	1.03	0.25	2.01
Crustacea: Ostracoda	3.94	3.47	3.62	0.51	4.90	6.09
Crustacea: Copepoda	5.09	0.61	1.28	5.40	4.29	10.65
Crustacea: Isopoda: Sphaeromatidae	0.99	2.04	6.64	5.66	0.25	1.07
Crustacea: Isopoda: Idoteidae	0.66	1.18	4.04	7.97	0.06	0.30
Crustacea: Isopoda (other)	2.30	0.16	1.45	0.26	7.35	31.05
Crustacea: Branchiopoda: *Artemia*	2.79	0.49	0.31	0.26	7.29	9.62
Decapoda: Shrimp (*P. adspersus*)	0.99	10.70	32.74	11.57	0.18	0.76
Amphipoda	17.24	0.29	0.55	0.77	0.00	0.00
Crustacea (other)	0.82	1.67	2.44	0.00	0.37	0.64
Insecta: Mosquito (adults)	3.94	1.22	5.02	10.28	2.88	11.26
Insecta: Mosquito (larvae)	0.82	0.37	0.68	8.48	7.60	9.44
Molusca: Gastropoda	0.33	1.27	8.93	0.51	0.98	4.25
Molusca: Bivalvia	4.76	16.29	8.36	3.86	4.35	2.38
Molusca other	13.14	0.08	0.85	5.66	0.12	1.52
Hydrozoa: Siphonophora	0.99	0.29	0.30	5.91	1.53	1.90
Fish eggs	5.42	2.69	4.08	2.57	1.35	2.42
Invertebrate eggs	48.11	13.19	2.47	40.62	10.97	2.47
Other	1.48	0.45	2.93	0.26	0.12	0.91
Stomachs analysed	859			526		
Stomachs containing food	609			389		
Total number of prey in gut content	3749			2204		

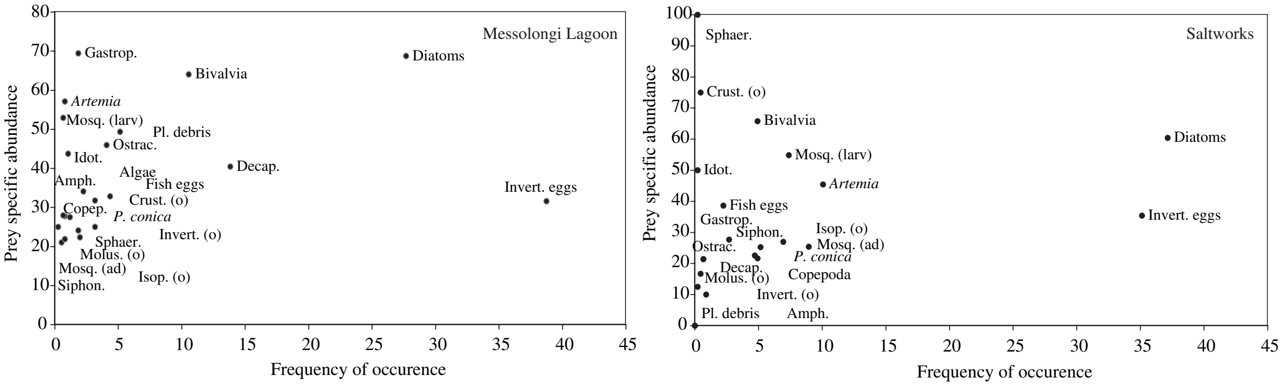

FIG. 2. – Relationship among prey specific abundance (Pi) and Frequency of occurrence (% Fi) of food categories of *Aphanius fasciatus* diet. Plots based on the modified Costello graphical method (Amundsen *et al*., 1996). Food categories described are the most important in diet. (Gastrop.= Gastropoda, Mosq. (larv) = Mosquito larvae, Pl. debris = Plant debris, Ostrac. = Ostracoda, Idot. = Idoteidae, Decap. = Decapoda, Amph.=Amphipoda, Invert. eggs= Invertebrate eggs, Crust. (o)= Crustacea (other), Copep.= Copepoda, *P. conica*=*Pirinella conica*, Invert. (o) = Invertebrates (other), Sphaer. = Sphaeromatidae, Molusc (o) = Molusca (other), Mosq. (ad)= Mosquito (adults), Isop. (o)= Isopoda (other), Siphon. = Siphonophora.

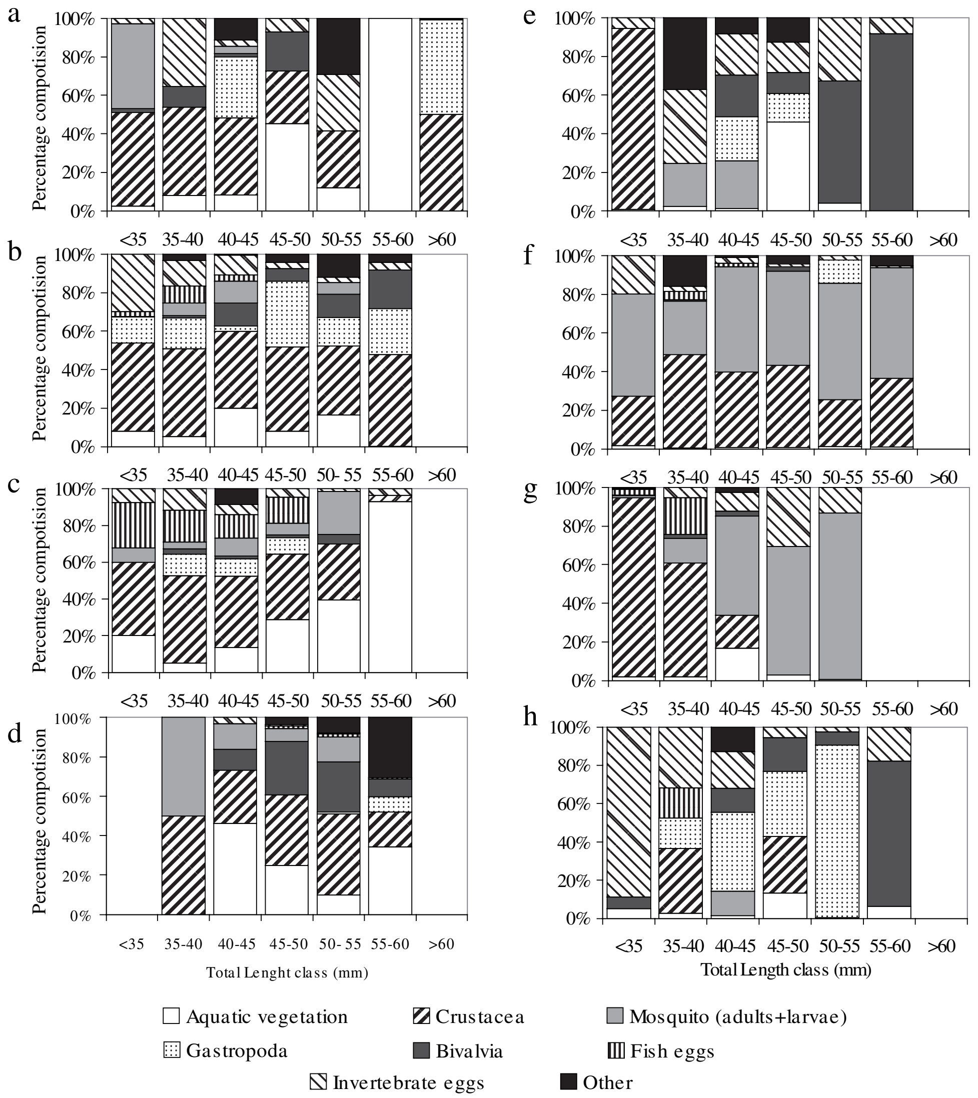

FIG. 3. – Ontogenetic, seasonal and habitat variation in the diet of *Aphanius fasciatus*. Data are the percentage of alimentary content volume averaged for 5 mm-length classes. (Messolongi Lagoon: a, winter; b, spring; c, summer; d, autumn. Saltworks: e, winter; f, spring; g, summer; h, autumn).

lacteus, Venerupis aurea and *Mytillus galloprovincialis*), gastropods (mainly the species *Gibbula adriatica, Haminea navicula Atys jeffreysi* and *Hydrobia ventrosa*) and eggs of invertebrates and fish (mainly *A. fasciatus, Atherina boyeri and Gobius* sp.). At the Saltworks, diatoms (*Nitzchia* sp. and *Chaetoceros* sp.), invertebrate eggs, mosquitoes (larvae and adults), Artemia *sp.* and eggs of *A. fasciatus* were the most important food category for *A. fasciatus*.

Feeding strategy

A similar feeding strategy pattern was followed by *A. fasciatus* at both sampling sites (Fig. 2). The relative importance of the prey eaten was highly dependent on season, size of toothcarp and habitat variation (Fig. 3). Diatoms of the genus *Chaetoceros*, *Gymnodinium* and *Nitzchia* were important at both sampling stations, with more than half the fishes showing a high contribution. The predators that consumed diatoms were mainly small-sized young-of-the-year (YOY). Small-sized specimens also consumed small particles of plant debris as well as invertebrate eggs. Large specimens of the family Sphaeromatidae were found spontaneously.

Diet variation

From the correspondence analysis of %IRI the first two dimensions (Fig. 4) explained 90% of the variance. There was a significant seasonal effect (ANOVA, $F_{3,1058}=5.39$; P=0.001) on the first dimension scores. On the right part of the axis were food categories consumed during the summer such as crustaceans (especially isopods of the families Idoteidae and Sphaeromatidae and juveniles of the shrimp *Palaemon adspersus*), Ostracoda and plant debris. On the left of the first dimension, the preys consumed during autumn included Amphipoda, Gastropoda, nauplii of brine shrimp (*Artemia* sp.), adults and larvae of mosquito, bivalves, various molluscs and algae. The scores of the second dimension varied significantly with the sampling station (ANOVA $F_{1,1060}=19.23$; P<0.001), with mosquito larvae and Gastropoda, mainly *Pirinella conica,* on the surface being consumed at the Saltworks, and bivalves and plant debris on the bottom being consumed in the Messolongi Lagoon.

The results of CA for prey number were quite similar. They distinguished on the left of CA1 the largest preys (amphipods, bivalves, isopods of the families Sphaeromatidae and Idoteidae, various species of gastropod and especially *Pirinella conica*), which dominated especially in the gut contents of large-sized fishes (age >2 years). On the right of the first dimension, the smallest prey included Ostracoda, isopods and copepods consumed from small-sized specimens (age <2 years).

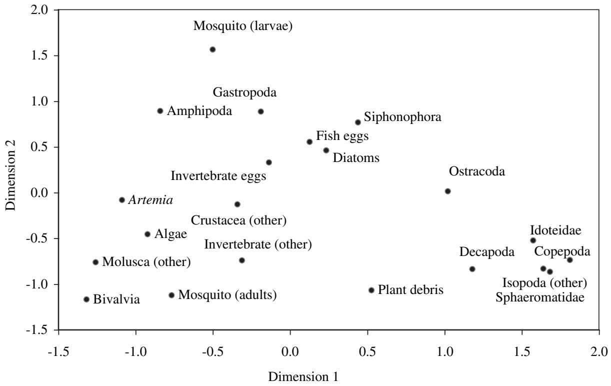

FIG. 4. – Correspondence analysis of gut contents (prey number) of *Aphanius fasciatus*: food category scores for the first and second dimensions.

Habitat and intraspecific variation in diet

The overall diversity of the prey consumed by *A. fasciatus* was significantly dependent on age, showing that larger specimens had wider dietary breadth. It was significantly higher in Messolongi Lagoon (D=0.39±0.012) than at the Saltworks (D=0.35±0.014) but was not significantly dependent upon season or sex. However, the interaction of sampling station with season was statistically significant (Table 2). The overall diversity of *A. fasciatus* was

TABLE 2. – ANCOVA results of the dietary descriptors of *Aphanius fasciatus*

Variable (source of variation)	df	F	P
Simpson index of Diversity D			
Age	1, 971	5.98	0.015
Sampling Station	1, 971	13.60	0.000
Season * Sampling station	3, 971	4.92	0.002
Number of prey items			
Season	3, 1384	20.05	0.000
Sex	1, 1384	5.30	0.021
Season * Sampling station	3, 1384	16.04	0.000
Region * sex	1, 1384	4.37	0.037
Volume of gut content			
Age	1, 775	95.64	0.000
Season	3, 775	12.39	0.000
Sampling station * Sex	1, 775	8.98	0.003
Season * Sampling station * Sex	3, 775	5.45	0.001

negatively correlated with the total stomach volume content (Spearman's rho =-0.218; P<0.001), showing that prey diversity was expanded in cases in which stomach fullness was reduced.

In contrast, the number of different food categories in gut contents was not related significantly to age or sampling station. Moreover, it varied seasonally, decreasing from winter to autumn and varied between sexes, with females consuming more prey items than males (Table 2). The volume of gut content of *A. fasciatus* increased significantly with age. Significant differences were also found in relation to season, while there was no significant relation of the gut content volume with sex (Table 2).

DISCUSSION

The diet of *A. fasciatus* comprises food of both animal and plant origin. Its pattern of feeding on animal prey is characterised by the consumption of only a few prey types, especially crustaceans and molluscs. The most common prey in the diet of *A. fasciatus*, by number and occurrence, were diatoms, juveniles of the shrimp *Palaemon adspersus* and bivalves. An ontogenetic diet shift and among-habitat variation in diet appeared as a result of different prey availability (e.g. the presence of the branchiopod Artemia and the higher abundance of mosquitoes at the Saltworks).

A similar feeding pattern has been observed in other *Aphanius* species (Alcaraz and Berthou, 2007; Al-Daham *et al*., 1977; Haas, 1982) and other cyprinodontiform fish such as *Fundulus luciae* (Kneib, 1978) and *Valencia hispanica* (Caiola *et al*., 2001) that exhibit a diet based only on the consumption of invertebrates. Diet based on invertebrates has been found in two other species, *Fundulus heteroclitus* (Kneib, 1986) and *Gambusia holbrooki* (Crivelli and Boy, 1987; Garcıa-Berthou, 1999). Observations in the laboratory show that *A. fasciatus* feeds preferentially on living mobile prey that are caught with its teeth and then gulped. The projection of the lower jaw beyond the upper jaw allows it to feed on preys that are on the surface of the water (i.e. chironomids and mosquitoes), while the projection of its upper jaw over the lower jaw allows it to feed on benthic organisms.

The maximum percentage of empty guts occurred in winter in Messolongi Lagoon (35%) and in autumn at the Saltworks (37%). This is attributed to the reduction in the feeding intensity during the winter as the result of the influence of the lower water temperature in the Messolongi Lagoon and the extreme increase in water salinity that occurred in early and late autumn at the Saltworks. It is well documented that environmental parameters, such as temperature and salinity, have a negative effect on the feeding intensity of fish because they cause a distress or brake of feeding (Williams and Williams, 1991; Stoner, 2004). Temperature and salinity are among the most important factors governing the metabolism in ectothermic fishes (Fry, 1971; Yan *et al*., 2004). Indeed, the pause in growth and the formation of annual rings in the scales of *A. fasciatus* occur during low winter temperatures (Leonardos *et al*., 1996). Moreover, false rings were observed in specimens collected at the Saltworks in early autumn, coinciding with the salt harvest (Leonardos, 1996). The higher prey consumption in spring and summer, as emerged from the study of the volume and number of food categories in gut content, may be a consequence of greater food availability and higher energy requirements for growth and reproduction. Fish had more food in their stomachs during summer and autumn, coinciding with an increased growth rate for the species (Leonardos *et al*., 1996), than in winter and spring. The increased stomach fullness of smaller fish compared to larger ones could be associated with the increased energetic needs of small specimens, which show the highest growth rates during the first year of their life (Leonardos *et al*., 1996).

The wider dietary diversity in larger specimens, as expressed by the Simpson diversity index, could reflect the ability of large specimens to utilise a wider range of habitat resources, both on the trophic level (diet composition) due to their increased morphological adaptations (mainly mouth width), and on the spatial level (distribution) due to their greater mobility and hence dispersal rate. The overall dietary breadth of the species in the study area appeared to expand in cases in which stomach fullness was reduced. The greater dietary diversity observed in winter and autumn could be attributed to the possibly decreased availability of particular prey during those seasons, which would force *A. fasciatus* to switch to other preys that might be readily available. According to Eggers (1977), the diet breadth increases with decreasing prey density. There is a marked variation in the diet of adult and immature individuals. Bigger fish consume more and larger prey items and have a wider diet range because they can consume preys that are not available for small fish. There is a general trend for prey size to be correlated with their energetic value. It is possible that larger fish try to maximise energy intake by increasing the consumption of larger prey (Grossman *et al*., 1980). These differences might reflect a combination of increasing mouth size and an improved ability to handle prey and to swim faster (Gerking, 1994; Platell and Potter, 1998). Differences in diet pattern between individuals with different lengths are related to the decrease in intraspecific competition (Caiola *et al*., 2001; Helfman, 1978; Grossman *et al*., 1980). Indicative of this strategy are the ontogenetic differences observed in the feeding pattern of *A. fasciatus* (Fig. 3)

An important parameter of the feeding ecology of *A. fasciatus* is the feeding on fish eggs, and especially the cannibalistic behaviour observed in spring and summer at the Saltworks. This intraspecific predation may be regulated by natural selection and be under genetic control. Cannibalism occurs as a by-product of normal feeding behaviour and is controlled by environmental factors such as changes in temperature and salinity and expansion of habitat, and by alternative food availability. Fish benefit both phenotypically (nutritional gain) and genotypically (contribution to future gene pools), whereas the eggs consumed lose phenotypically because they die (Valdes Szeinfeld, 1993). Accordingly, it has been proven that in the adverse environmental conditions that occurred at the Saltworks the fish could interrupt the reproductive process and absorb the oocytes (Leonardos and Sinis, 1998). Egg cannibalism could therefore evolve when the future benefits of offspring consumption outweigh the loss of present reproduction. Rohwer's (1978) hypothesis leads to a prediction that filial cannibalism should increase as parental energy reserves decrease. Cannibalism is a mechanism for density-dependent regulation of fish populations (Cushing, 1977). The resources from both egg cannibalism and atresia can be allocated for growth of the organism or for maintaining homeostasis, in this case osmotic regulation.

On analysing the diet composition (Fig. 2), it emerges that *A. fasciatus* has a generalised diet strategy and a narrow niche width. However, the analysis of the feeding strategy by the modified Costello method (Amundsen *et al*., 1996) suggests quite the opposite, implying that different individuals specialise in different resource types. This is attributed to the distinction between the niche of individuals and that of the whole population. A population with a broad niche may consist of individuals with either narrow or wide niches or a combination of both (Amundsen *et al*., 1996). The studied population of *A. fasciatus* from Messolongi lagoon showed a high between-phenotype contribution to niche width (variation in resource use between individuals) that consisted of specialised individuals with little or no overlap in resource use. It seems that this strategy is suitable for avoiding intraspecific competition.

The feeding strategy of *A. fasciatus* should be classified in general as specialist, but it may sometimes prey on occasional resources. A number of studies have suggested that the strategy of an individual fish may be density-dependent or conditional on levels of intraspecific competition (Ward *et al*., 2006). The same feeding strategy is followed by another Cyprinodontiform fish endemic to the Iberian Peninsula, *Valencia hispanica* (Caiola *et al*., 2001).

By specialising on a particular resource or prey type, an individual is likely to become more effective at foraging in that particular niche. A consequence of this is that by specialising on a particular type of prey, an individual may become less able to feed effectively on different preys, especially if the required foraging skills vary between different prey types. The extent of individual feeding specialisation in a population depends on an array of different ecological, behavioural and physiological factors. Important among these are the rate at which foragers encounter a given prey type, the value of that prey type and the anti-predator defences of the prey (Ward *et al*., 2006). Ultimately, it seems that specialisation yields greater benefits than a generalist approach, so it is likely to be selected.

ACKNOWLEDGEMENTS

I wish to thank A. Kokkinidou for her help in field work and V. Moutsaki for the linguistic improvement of the text. The comments of Dr. A. Tsikliras greatly improved the manuscript. Finally, I would like to thank the anonymous referees for their constructive comments on the manuscript.

REFERENCES

Al-Daham, N.K., M.F. Huq and K.P. Sharma. – 1977. Notes on the ecology of fishes of genus *Aphanius* and *Gambusia affinis* in Southern Iraq. *Freshw. Biol.,* 7: 245-251.

Alcaraz, C. and E. Garcia-Berthou. – 2007. Food of an endangered cyprinodont (*Aphanius iberus*): ontogenetic diet shift and prey electivity. *Environ. Biol. Fish.,* 78: 193-207.

Amundsen, P.A., H.M. Gabler and F.J. Staldvik. – 1996. A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *J. Fish Biol.,* 48: 607-614.

Baillie, J. and B. Groombridge. – 1996. *IUCN Red List of Threatened Animals. IUCN Publications Service Unit*, Cambridge, UK.

Bianco, P.G. – 1995. Mediterranean endemic freshwater fishes of Italy. *Biol. Conserv.,* 72: 159-170.

Caiola, N., M.J. Vargas and A. de Sostoa. – 2001. Feeding ecology of the endangered Valencia toothcarp, *Valencia hispanica* (Actinopterygii: Valenciidae) *Hydrobiologia*, 448: 97-105.

Council of Europe. – 1992. *Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Flora*. *Off. J.E.C.*, Ser. L 206: 7-50.

Council of Europe. – 2000. *The Bern Convention*. http: //www.nature.coe.int/ english/cadres/bern.htm [access date: 11/7/2002].

Crivelli, A.J. and V. Boy. – 1987. The diet of the mosquitofish *Gambusia affinis* (Baird & Girard) (Poeciliidae) in Mediterranean France. *La Terre et la Vie, Rev. d'Ecol. Appl.,* 42: 421-435.

Cortés, E. – 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. Fish Aquat. Sci.,* 54: 726-738.

Cushing, D.H. – 1977 Observations on fish shoals with the ARL Scanner, *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* 170(1977): 15-20.

Eggers, D.M. – 1977. The nature of prey selection by planktivorous fish. *Ecology*, 58: 46-59.

Fry, F.E. – 1971. The effects of environmental factors on the physiology of fish. In: W. S. Hoar and D. J. Randall (eds.), *Fish Physiol.*, pp 1-99. New York Academic Press.

Garcıa-Berthou, E. – 1999. Food of introduced mosquitofish: ontogenetic diet shift and prey selection. *J. Fish Biol*., 55:135-147.

Gerking, S.D. – 1994. *Feeding Ecology of Fish*. San Diego, CA: Academic Press.

Grossman, G.D., R, Coffin and P.B. Moyle. – 1980. Feeding ecology of the bay goby (Pisces: Gobidae). Effects of behavioural, ontogenic and temporal variation on diet. *J. Exp. Mar. Biol. Ecol.,* 44: 47-59.

Haas, R. – 1982. Notes on the ecology of *Aphanius dispar* (Pisces, Cyprinodontidae) in the Sultanate of Oman. *Freshwater Biol.,* 12: 89-95.

Helfman, G.S. – 1978. Patterns of community structure in fishes: summary and overview. *Envir. Biol. Fish*, 3: 129-148.

Hulbert, S.H. – 1971. The nonoconcept of species diversity: a critique and alternative parameters. *Ecology*, 52: 577-586.

Hyslop, E.J. – 1980. Stomach contents analysis: a review of methods and their application. *J. Fish. Biol.*, 17: 411-429.

Kneib, R.T. – 1978. Habitat, diet, reproduction and growth of the spotfin killfish, *Fundulus luciae*, from a North Carolina Salt Marsh. *Copeia*, 1: 164-168.

Kneib, R.T. – 1986. The role of *Fundulus heteroclitus* in Salt Marsh Trophic Dynamics. *Am. Zool.,* 26: 259-269.

Leonardos, I. – 1996. *Population dynamics of* Aphanius fasciatus *(Nardo, 1827) in Messolongi and Etolikon Lagoons*. PhD thesis. Aristotelian Univ. of Thessaloniki 197 pp. (In Greek).

Leonardos, I. and A. Sinis. – 1998. Reproductive strategy of *Aphanius fasciatus* Nardo, 1827 (Pisces: Cyprinodontidae) in the Messolongi and Etolikon lagoons (W. Greece) *Fish. Res.*, 35:171-181.

Leonardos, I. and A. Sinis. – 1999. Population age and sex structure of *Aphanius fasciatus* Nardo, 1827 (Pisces: Cyprinodontidae) in the Messolongi and Etolikon lagoons (W. Greece). *Fish. Res.*, 40: 227-235.

Leonardos, I., A. Sinis and D. Petridis. – 1996. Influence of Environmental factors on the population dynamics of *Aphanius fasciatus* (Nardo, 1827). (Pisces: Cyprinodontidae) in the Lagoons Mesolongi and Etolikon (W.Greece). *Israel J. Zool.,* 42: 231-249.

Lindegaard, C. – 1992. Zoobenthos ecology of Thingvallavatn: vertical distribution, abundance, population dynamics and production. *Oikos*, 64: 257-304.

Pinkas, L.M., S. Oliphant and I.L. Iverson. – 1971. Food habits of albacore, bluefin tuna and bonito in Californian waters. *Calif. Fish. Game,* 152: 1-105.

Platell, M.E. and I.C. Potter. – 1998. Distributions, size compositions and diets of two abundant benthic ambush-feeding teleosts in coastal waters of south-western Australia. *J. Mar. Biol. Assoc. UK*., 78: 587-608.

Rohwer, S. – 1978. Parent cannibalism of offspring and egg raiding as a courtship strategy. *Am. Nat.*, 112: 429-440.

Stoner, A.W. – 2004. Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. *J. Fish Biol*., 65: 1445-1471.

Valdes Szeinfeld E. – 1993. The energetics and evolution of intraspecific predation (egg cannibalism) in the anchovy *Engraulis capensis. Mar. Biol*. 115: 301-308.

Ward, A.J., M.M.Webster and P.J. Hart. – 2006. Intraspecific food competition in fishes. *Fish Fish.*, 7: 231-261.

Whitehead, P.J., M.L. Bauchot, J.C. Hureau, J. Nielsen and E. Tortonese. – 1986. *Fishes of the North-Eastern Atlantic and the Mediterranean, Vol. 2.* UNESCO, Paris.

Williams, M.D. and W.D. Williams. – 1991. Salinity tolerances of four species of fish from the Murray-Darling River system. *Hydrobiologia*, 210: 145-160.

Yan, M, Z. Li, B. Xiong and J. Zhu. – 2004. Effects of salinity on food intake, growth, and survival of pufferfish (*Fugu obscurus*). *J. Appl. Ichthyol.*, 20: 146-149.

Scient. ed.: P. Martín.
Received April 17, 2007. Accepted February 12, 2008.