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Feeding habits and trophic level of round sardinella (*Sardinella aurita*) in the northeastern Mediterranean (Aegean Sea, Greece)

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Four seasonal samples of round sardinella, *Sardinella aurita* Valenciennes, 1847, were collected onboard the purse-seine fleet (October 2001-August 2002, 30 individuals per season) in the northern Aegean Sea. Samples were immediately fixed with 10% formaldehyde solution. The total length (TL, cm) was measured and prey items in the stomach contents were identified to large taxonomic groups. The vacuity index, the percentage gravimetric composition and the trophic level were estimated. The percentage of empty stomachs varied seasonally and among size classes. Crustaceans (copepods, amphipods, decapod larvae and other) were the main prey, followed by siphonophores, phytoplankton and fish larvae. The percentage gravimetric composition of the diet varied seasonally. Copepods were the most abundant prey item in the winter and spring, while decapod larvae and amphipods were most abundant in the summer and autumn, respectively. The trophic level ranged between 3.04 (winter) and 3.28 (spring), and increased asymptotically with size ($Troph_{\infty} = 3.31$, $K = 0.018$). Based on the composition of its diet, round sardinella may be characterized as an omnivorous fish with preference for animal prey. In addition, information on the diet composition of round sardinella in other areas of its distribution, was collected and trophic levels were calculated. They ranged between 2.05 in Senegalese waters and 3.33 in the waters surrounding the Canary islands. The between-area variations in trophic levels are discussed.

Key words: diet, feeding ecology, round sardinella, Aegean Sea.

INTRODUCTION

The feeding preferences of fish species are important in classic ecological theory, mainly in identifying feeding competition (Bacheler *et al.*, 2004), structure and stability of food webs (Post *et al.*, 2000), omnivory (Pimm & Lawton, 1978) and assessing predator-prey functional responses (Dörner & Wagner, 2003). Despite the wealth of papers on fish feeding (for Mediterranean fishes see review by Stergiou & Karpouzi, 2002), comparisons of feeding preferences and interactions across populations, species and ecosystems, are rare. Additionally, the key role of feeding studies for fisheries biology and ecology and, more importantly, for fisheries management, was uncovered only the last decade with the use of trophic level in predicting the effects of fishing on the balance of marine food webs (Pauly *et al.*, 1998). The trophic level, which for marine animals ranges between 2 (for herbivores/detritivores) and 5.5 (for specialised predators of marine mammals), expresses the relative position of an animal in the food webs that nourish them (Pauly *et al.*, 2000). Thus, understanding of the food web structure of the Mediterranean fishes may serve as a basis for the maintenance of trophic level balance in the Mediterranean Sea, thereby preventing the fishing-induced trophic level decline (Stergiou & Karpouzi, 2002) within an

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ecosystem context of fisheries management (e.g. Browman & Stergiou, 2004).

Round sardinella, *Sardinella aurita* Valenciennes, 1847, is a middle-sized pelagic fish recently established in the northern Aegean Sea (Tsikliras, 2004). Its global landings, accounting for more than 0.5% of the total marine captured production, largely fluctuate from year to year (FAO, 2000). Its landings from the Greek seas steadily increase since 1990, having reached 2734 metric tons in 2002 (Stergiou *et al.*, 2004). Round sardinella, together with the sympatric European sardine, *Sardina pilchardus*, and European anchovy, *Engraulis encrasicolus*, make up about 40% of the Greek marine captured production (Stergiou *et al.*, 2004). There is evidence, however, that these closely related species compete for resources, especially for space and food, at certain stages of their life cycles (Palomera & Sabatés, 1990).

Besides the early work by Ananiades (1952), the feeding habits of round sardinella have never been studied in the Mediterranean Sea (Stergiou & Karpouzi, 2002). Thus, its position in the food web has never been evaluated, except that it is the main prey of several large cetacean and teleostean predators (Tsikliras *et al.*, 2004 and references therein). By contrast, information on the feeding habits of round sardinella exist for the northwest African coast (Pham-Thuoc & Szypuła, 1973), the Senegal waters (Nieland, 1982) and the waters surrounding the Fuji islands (Wang & Qiu, 1986). Finally, Moreno & Castro (1995) have studied the feeding of juvenile round sardinella off the Canary islands.

The aims of the present work are: (a) to study the feeding habits of round sardinella in northern Aegean Sea, by body size class and season, (b) to identify the nature of its feeding ecology (i.e., specialist or generalist), (c) to estimate its trophic level, and (d) to compare its diet in northern Aegean Sea with that of other populations throughout its distribution.

MATERIALS AND METHODS

Stomach contents of round sardinella were examined seasonally (October 2001, January 2002, April 2002 and August 2002). Samples were collected onboard the commercial purse-seine fleet of the northern Aegean Sea. Thirty specimens were randomly collected from each seasonal sample, immediately fixed in 10% formaldehyde solution buffered with seawater, measured (total length, TL, mm) and weighed (total weight, TW, g). The total length of the fish examined ranged between 14.5 and 21.5 cm. The fixation of the fish and the stomach contents causes an overall increase in weight (Anderson & Neumann, 1996). This problem was overcome with consistency in the procedures (time of sampling, duration of preservation) followed for all samples.

The stomachs were removed and the wet content was weighed. Prey items were identified to large taxonomic groups, counted and weighed to the nearest 0.01 g. In order to evaluate variations in food habits as a function of size and age, round sardinella specimens were separated into five length classes. The stomach content analysis was based on the recommendations provided by Stergiou & Karpouzi (2002) regarding the frequency of sampling, number of samples, method of analysis and size specificity of diet. The quantitative importance of different prey in the diet was expressed using two indices (Hyslop, 1980; Bowen, 1996): (a) the vacuity index (the percentage of empty stomachs, VI), and (b) the percentage gravimetric composition (the wet weight of each prey item, as a percentage of the total weight of the stomach contents in a sample, Cw). Finally, the diversity of prey items in the stomach contents was expressed using the Shannon-Wiener (H′) and Simpson (D′) diversity indices (Krebs, 1994).

The trophic level (TROPH) was estimated per season and per length class as follows (Pauly *et al.*, 2000):

$$TROPH_i = 1 + \sum_{j=1}^{G} DC_{ij} \times TROPHj,$$

where $\mathrm{TROPH_j}$ is the fractional trophic level of prey j, DC_{ij} represents the fraction of j in the diet of i, and G is the total number of prey species.

The TROPH of round sardinella in the study area was estimated from Cw using the quantitative routine of TrophLab (Pauly *et al.*, 2000). The relationship between TROPH and the mid point of each length class considered here was quantified using the following equation (Cortés, 1999):

$$TROPH_{L_i} = TROPH_{L\infty}(1 - e^{-KL_i}),$$

where $\mathrm{TROPH_{L\infty}}$ is the asymptotic TROPH and K is the rate at which $\mathrm{TROPH_{L\infty}}$ is approached.

Finally, TROPH values were also estimated for other round sardinella stocks based on published diet composition data (central-southern Aegean Sea: Ananiades, 1952; NW African coast: Pham-Thuoc & Szypuła, 1973; Senegalese waters: Nieland, 1982;

South Fujian-East Guangdong waters: Wang & Qiu, 1986; Canary islands: Moreno & Castro, 1995), also using TrophLab. For these cases, TROPH was estimated using the quantitative routine when gravimetric abundances of prey were available and the qualitative routine when data was expressed as frequency of occurrence of prey.

RESULTS

Thirty-three out of 120 stomachs examined were empty (27.5%). The percentage of empty stomachs varied with season and size. The vacuity index was highest in autumn (VI = 36.6%) and lowest in summer (VI = 16.6%) (Table 1). The length class of 21-22 cm TL was characterized by the highest VI and the 16-17 cm TL class by the lowest one (33.3 and 20.8%, respectively) (Table 2).

Prey items were grouped in eight different taxa (Table 1). Crustaceans (copepods, amphipods, decapod larvae and others) were the main prey, followed by siphonophores, phytoplankton and fish larvae. The percentage composition of the diet varied seasonally (Table 1, Fig. 1), with copepods being the main prey in winter and spring, decapod larvae in summer, and amphipods in autumn. Amphipods were generally dominant in size classes smaller than 18 cm TL and copepods in those larger than 19 cm TL (Table 2, Fig. 2). The mean number of prey items per stomach also varied seasonally, between 2.25 (winter) and 3 (autumn), and with size class, between 2 (for 15-16 cm TL) and 3.25 (for 17-18 cm TL).

The diet was more diverse in spring (H′ = 1.63, D′ = 0.77) and less so in winter (H′ = 1.05, D′ = 0.57) (Table 1). With respect to length classes, diversity was highest at the 18-19 TL class, whereas diet was less diverse at smaller and larger sizes (Table 2).

The TROPH of round sardinella in the northern Aegean Sea ranged between 3.04 (winter) and 3.28 (spring) (Table 1) and increased with size (Fig. 3). The relationship between TROPH and size (TL, cm) was asymptotic:

$$TROPH_{Li} = 3.31(1\text{-}e^{-0.018Li}),$$
$$SE_{TROPH\infty} = 0.11,$$
$$SE_K = 0.005,\ r^2 = 0.38.$$

The diet compositions of round sardinella in other areas of its distribution, as reported by the original authors, are summarised in Table 3. The estimated

TABLE 1. Round sardinella, northern Aegean Sea, 2001-2002. Percentage contribution of prey groups to the seasonal diet, vacuity index (VI, %), size range and mean size (TL, cm), mean stomach content weight (g), mean number of prey items per stomach and trophic level (Troph ±SE), the Shannon-Wiener (H′) and Simpson (D′) diversity indices

	Season			
Prey	Autumn	Winter	Spring	Summer
Crustacea				
Copepoda	18.84	58.92	33.75	6.59
Mysidacea	1.45	2.05	–	8.25
Amphipoda	36.23	10.96	3.75	38.46
Decapod larvae	10.14	0.68	27.50	39.56
Other	30.43	26.71	18.75	6.59
Siphonophora	–	–	6.25	–
Fish larvae	–	–	3.75	–
Phytoplankton	2.91	0.68	–	0.55
Unidentified	–	–	6.25	–
Number of stomachs	30	30	30	30
Empty stomachs	11	9	8	5
VI (%)	36.6	30.0	26.6	16.6
Length range (TL, cm)	15.1-20.7	14.5-20.0	17.0-21.5	16.0-19.4
Mean TL (cm)	18.10	17.98	19.71	16.93
Mean stomach content weight (g)	0.11	0.08	0.12	0.16
Mean number of prey items per stomach	3.00	2.25	2.60	2.80
TROPH ± SE	3.08±0.29	3.04±0.20	3.28±0.34	3.10±0.30
H′	1.44	1.05	1.63	1.33
D′	0.74	0.57	0.77	0.69

TABLE 2. Round sardinella, northern Aegean Sea, 2001-2002. Percentage contribution of prey groups to the diet per length class (TL, mm), vacuity index (VI, %), mean stomach content weight (g), mean number of prey items per stomach, trophic level (Troph ±SE), and the Shannon-Wiener (H′) and Simpson (D′) diversity indices

	Length class (TL, cm)						
Prey	15-16	16-17	17-18	18-19	19-20	20-21	21-22
Crustacea							
Copepoda	33.34	12.50	–	13.05	56.48	29.27	55.00
Mycidacea	11.11	19.22	7.58	13.55	10.33	–	–
Amphipoda	33.33	24.57	44.07	11.04	8.04	24.39	–
Decapod larvae	–	32.04	28.44	20.32	11.71	29.27	–
Other	22.22	11.67	14.22	14.94	8.27	17.07	25.00
Siphonophora	–	–	–	22.58	–	–	–
Fish larvae	–	–	–	–	5.17	–	–
Phytoplankton	–	–	5.69	4.52	–	–	–
Unidentified	–	–	–	–	–	–	20.00
Number of stomachs	8	24	10	40	22	10	6
Empty stomachs	2	5	3	13	5	3	2
VI (%)	25.0	20.8	30.0	32.5	22.7	30.0	33.3
Mean stomach content weight (g)	0.07	0.13	0.17	0.10	0.09	0.20	0.08
Mean number of prey items per stomach	2	2.42	3.25	2.5	2.33	2.33	3
TROPH ± SE	3.08 ±0.32	3.20 ±0.36	3.13 ±0.35	3.31 ±0.32	3.16 ±0.29	3.21 ±0.34	3.26 ±0.37
H′	1.31	1.54	1.35	1.86	1.37	1.37	0.56
D′	0.72	0.78	0.70	0.84	0.65	0.75	0.38

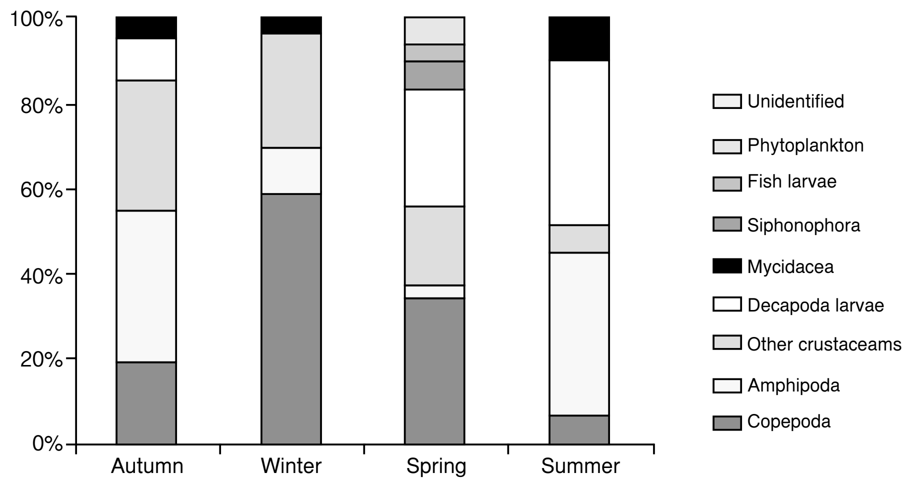

FIG. 1. Round sardinella, northern Aegean Sea, 2001-2002. Variation in diet based on percentage gravimetric composition as a function of total length (TL, cm).

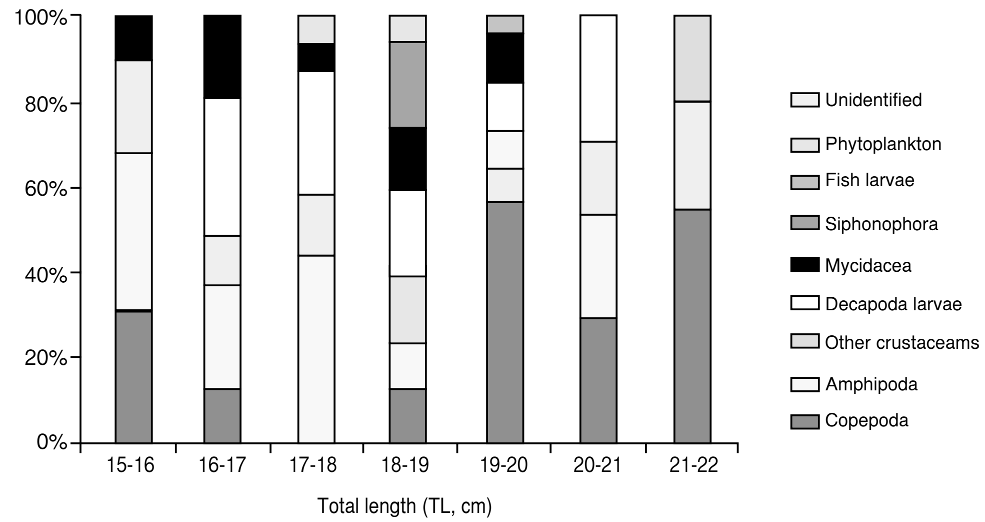

FIG. 2. Round sardinella, northern Aegean Sea, 2001-2002. Seasonal variation in diet based on percentage gravimetric composition.

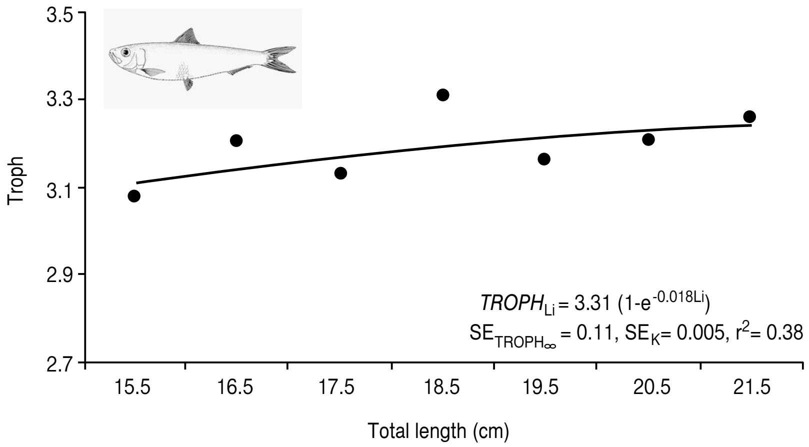

FIG. 3. Round sardinella, northern Aegean Sea, 2001-2002. Relationship between trophic level (TROPH) and total length (TL, cm, midpoint length class).

TROPH values ranged between 2.05 in Senegalese waters and 3.33 in the waters surrounding the Canary islands.

DISCUSSION

In the present work, we studied the feeding habits and estimated the TROPH of round sardinella in the northern Aegean Sea. In addition, we estimated its TROPH in other areas of its distribution based on published diet composition data. The VI, which is an inverse indication of feeding intensity, was lower in summer and spring when spawning takes place (June-July: Tsikliras, 2004). During spawning, a resource demanding function, fish need more energy input to meet the requirements of reproduction (Froese & Pauly, 2000). By contrast, VI was higher in winter, when the growth rate of round sardinella is minimal (Tsikliras *et al.*, 2005). Pham-Thuoc & Szypuła (1973) have also reported a higher VI during winter and a lower one during the summer months. The relatively low numbers of prey items per stomach is interesting given that the species is a small pelagic one. We believe that this is partly due to the low taxonomic resolution of prey analysis, whereas the oligotrophy of the eastern Mediterranean Sea (Stergiou *et al.*, 1997) might also play a role.

TABLE 3. Feeding habits (data drawn from the literature) and trophic level (Troph) and its standard error (SE) (estimated by the present authors) for round sardinella in several areas of its distribution. Year: sampling year; Upwelling: "–" indicates no upwelling, "yes" indicates upwelling during the study of diet composition, "no" indicates cessation of existing upwelling during the study of diet composition; N: sample size; Method: method use for expressing stomach content - F: frequency of occurrence, W: percentage gravimetric composition (expressed as Cw); Length range: length range of specimens examined - TL: total length, FL: fork length; Prey: list of prey items reported by the original authors

Area	Year	Upwelling	N	Method	Length range	Prey	Cw	TROPH	SE	Reference
Aegean	1950-1951	–	11	F	8-14 cm TL	Copepoda		2.90	0.00	Ananiades (1952)
						crustacean larvae				
Aegean	1950-1951	–	11	F	15-21 cm TL	Isopoda		3.10	0.24	Ananiades (1952)
						Amphipoda				
						Schizopoda				
Aegean	1950-1951	–	11	F	22-27 cm TL	Crustaceans		3.08	0.32	Ananiades (1952)
						Anchovy larvae				
						Diatoms				
						meduses				
						Siphonophora				
NW African coast (15-24A N and 15-17A W)	1970	Yes	64	F		Copepoda		3.10	0.35	Pham Thuoc & Szypula (1973)
						Cyclopoidae				
						Euphosiidae				
						Herpacticoidea				
						Lamellibranchia				
						Ostracoda				
						Gastropoda				
						Echinodermata				
						fish eggs				
Senegal (Cayar)	1977	Yes	260	W	22-30 cm FL	Copepoda	60	2.96	0.23	Nieland (1982)
						Ostracoda	11			
						Dinoflaggelata	10			
						Diatoms	8			
						Bivalvia	3			
						fish eggs	3			
						other zooplankton	4			
Senegal (Bel Air)	1977	Yes	80	W	10-15 cm FL	Copepoda	65	2.90	0.25	Nieland (1982)
						fish eggs	10			
						Dinoflagellata	20			
						Diatoms	5			

cont.

TABLE 3 (cont.). Feeding habits (data drawn from the literature) and trophic level (Troph) and its standard error (SE) (estimated by the present authors) for round sardinella in several areas of its distribution. Year: sampling year; Upwelling: "–" indicates no upwelling, "yes" indicates upwelling during the study of diet composition, "no" indicates cessation of existing upwelling during the study of diet composition; N: sample size; Method: method use for expressing stomach content - F: frequency of occurrence, W: percentage gravimetric composition (expressed as Cw); Length range: length range of specimens examined - TL: total length, FL: fork length; Prey: list of prey items reported by the original authors

Area	Year	Upwelling	N	Method	Length range	Prey	Cw	TROPH	SE	Reference
Senegal (Mbour)	1977	Yes	180	W	22-30 cm FL	Phytoplankton	76	2.27	0.11	Nieland (1982)
						Copepoda	20			
						other	3			
						zooplankton fish eggs	1			
Senegal (Bel Air)	1974	No	40	W	10-16 cm FL	Detritus	90	2.05	0.03	Nieland (1982)
						Phytoplankton	5			
						Copepoda	4			
						Cladocera	0.5			
						other zooplankton	0.5			
Senegal (Mbour)	1974	No	75	W	20-26 cm FL	Detritus	90	2.05	0.03	Nieland (1982)
						Phytoplankton	5			
						Zooplankton	5			
Canary Islands	1990-1991	No	40	W	Juveniles	Copepoda	44.3	3.33	0.40	Moreno & Castro (1995)
						Appendicularians	28.0			
						fish eggs	17.5			
						Decapoda	3.3			
						Mollusca	3.1			
						Ostarcoda	2.2			
						fish larvae	1.5			
South Fujian-East Guangdong	1979-1980	–	191	W	3.8-15.9 cm					Wang & Qiu (1986)

Our results indicate that round sardinella feeds mainly on zooplankton and crustaceans. According to the classification of fishes in functional groups based on their TROPH (Stergiou & Karpouzi, 2002), round sardinella is an omnivorous species with preference to animal prey. Similar feeding habits have been reported for round sardinella in other areas of its distribution, with the percentage composition of diet varying with area and season (Table 3). It is noteworthy that in Senegal waters round sardinella is an omnivore with preference to plant material (TROPH = 2.05, see Table 3). By contrast, from Table 3 it seems that TROPH increases with the intensity of the seasonal upwelling. It is generally known that upwelling of deep nutrient rich water reaching the surface alters the structure and composition of food webs and enhances productivity (Mann & Lazier, 1996). Although one would expect that an opportunistic species would take advantage of the abundant phytoplankton in upwelling systems, this seems not to be the case for round sardinella. The latter, which can be partially explained by its preference for animal prey, requires further studies.

Round sardinella has a flexible adaptive strategy resulting from its demographic plasticity (Cury & Fontana, 1988). This adaptability is also apparent from its diet, with its feeding habits being adjusted to the specific requirements of the species and the prevailing environmental conditions (Table 3). Thus, in upwelling areas, diet composition varies with the intensity of upwelling and round sardinella switches prey and feeds on prey positioned lower in the food web (e.g. detritus) when zooplankton availability is low during the seasonal cessation of upwelling (Nieland, 1982). Thus, its TROPH decreases (Table 3). Likewise, in other areas, such as the central-southern Aegean Sea, Senegalese and Fujian waters, round sardinella also feeds lower in the food web but on phytoplankton (Ananiades, 1952; Nieland, 1982; Wang & Qiu, 1986), which also leads to a decrease in TROPH (Table 3). Feeding lower in the food web, combined with the occasional feeding on fish eggs and larvae results in high between-area TROPH variability, from 2.05 (Senegal, mainly phytoplankton and detritus) to 3.33 (Canary islands, high percentage of fish eggs and larvae) (Table 3).

Seasonal differences in diet composition may be due to the capability of the species in adjusting its diet on the seasonally oscillating prey abundance (Nieland, 1982). The diet differences among size classes are probably due to the energy requirements, which vary according to the developmental stage. Indeed, during ontogeny, fish often change their diet mediated by allometric, morphological changes (Karpouzi & Stergiou, 2003), thus being able to exploit sequentially a series of prey sizes ranging from phytoplankton and small zooplankton to much larger prey (Wootton, 1998).

Diet composition is also useful for assessing the trophic competition among species provided that prey resources are limited. In the case of round sardinella, there is a possibility of antagonism with the European sardine and European anchovy, the TROPH of which in the Mediterranean Sea is 3.15 and 3.43, respectively (Stergiou & Karpouzi, 2002), i.e. both belong to the same functional group with round sardinella. All these three pelagic species have similar feeding habits in the northern Aegean Sea feeding on copepods in the winter and spring. Despite the fact that anchovy feeds selectively on copepods in winter and spring, it generalizes its diet and feeds upon more diverse prey items in summer (northern Aegean Sea: Kallianiotis & Torre, unpublished data; Mediterranean Sea: Stergiou & Karpouzi, 2002). The same also holds for the European sardine, which, although it generally feeds on copepods (Stergiou & Karpouzi, 2002), becomes selective in summer and autumn (Tsikliras, unpublished data). Diet differentiation among closely related species is an evolutionary mechanism aiming to avoid trophic overlapping. This ensures the least possible feeding antagonism.

The predation of round sardinella on fish eggs and larvae (Ananiades, 1952; Moreno & Castro, 1995; see also Table 3) may affect the demographic rates of the round sardinella stock itself (if cannibalism is observed), as well as of other stocks (e.g. anchovy, Ananiades, 1952; Moreno & Castro, 1995). Hence, the feeding preferences of carnivorous species may (under certain conditions, i.e. when important ichthyoplankton biomass is consumed), control the net reproductive output, recruitment and biomass of other species and ultimately contribute to the regulation of the local populations. However, in the northern Aegean Sea, one of the most important spawning and fishing grounds of the Greek Seas (Stergiou *et al*., 1997), predation by round sardinella on fish eggs and larvae is of limited nature.

In conclusion, the results of the present study and data from other areas show that round sardinella is an omnivorous, opportunistic feeder with trophic level that changes with body size, season, geographic, area and upwelling intensity.

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