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Feeding and ecomorphology of three clupeoids in the North Aegean Sea

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Abstract

This study examines the feeding habits of anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*) and round sardinella (*Sardinella aurita*). The results are combined with previously published information on feeding-related morphological features (i.e. mouth area, intestine length and tail area) in order to explore morphological affinities between species and the effect of ecomorphology on their co-existence. These species were mainly zooplanktivorous and no dietary differences were found with sex and season. Anchovy preyed mainly on Crustacea larvae, whereas sardine and round sardinella on Copepoda. In the majority of cases (>90%), the individual fractional trophic level of all species ranged between 3.0 and 3.5, classifying them as omnivores with preference to animals. The feeding-related morphological features differed between anchovy and the two other species, whereas only intestine length differed between sardine and round sardinella. The fact that the diet and morphology of round sardinella show a greater resemblance to those of sardine further supports the hypothesis that round sardinella is a particulate feeder, as is sardine. Hence the three species tend to exploit the same food resources differently throughout the year. Thus, they make best use of the environment and its resources, in order to avoid competition and achieve optimum feeding conditions throughout their life cycles.

Keywords: *Engraulis encrasicolus, Sardina pilchardus, Sardinella aurita*, seasonal feeding, diet, ecomorphology.

Introduction

The small pelagics European anchovy [*Engraulis encrasicolus* (L., 1758)], European pilchard or sardine [*Sardina pilchardus* (Walbaum, 1792)] and round sardinella (*Sardinella aurita* Valenciennes, 1847) are distributed throughout the Mediterranean Sea (Froese & Pauly 2012: www.fishbase.org), and are highly commercial, both in terms of landings and economic value (e.g. Dulčić, 1997; Stergiou *et al*., 1997; Bellido *et al*., 2000; Tsikliras *et al*., 2005a). The populations of small pelagics are characterized as 'wasp-waist', being considered as crucial components of pelagic ecosystems (Cury *et al*., 2000). They exercise both top-down and bottom-up control on food webs (Cury *et al*., 2000), since they constitute the intermediate link in the flow of energy from lower to higher trophic levels (e.g. Tudela & Palomera, 1997; Palomera *et al*., 2007; Lomiri *et al*., 2008; Preciado *et al*., 2008; Espinoza *et al*., 2009; Coll & Libralato, 2012).

With respect to their diet and feeding habits, available studies refer to adult feeding in the Atlantic (e.g. anchovy: Plounevez & Champalbert, 1999; sardine: Varela *et al*., 1988; round sardinella: Pham Thuoc & Szypuła, 1973; Nieland, 1982), the Baltic Sea (anchovy: Schaber *et al*., 2010), the western Mediterranean (e.g. anchovy: Tudela & Palomera, 1997; Plounevez & Champalbert, 2000; Bacha & Amara, 2009), the central Mediterranean (e.g. anchovy: Borme *et al*., 2009; round sardinella: Lomiri *et al*., 2008), the eastern Mediterranean (e.g. anchovy: Nikolioudakis *et al*., 2012; round sardinella: Madkour 2012) and the Black Sea (e.g. anchovy: Mikhman & Tomanovich, 1977; Sirotenko & Danilevskiy, 1977; Budnichenko *et al*., 1999). Information is also available on larval feeding (anchovy: Conway *et al*., 1998; Tudela *et al*., 2002; sardine: Dulčić, 1999; Munuera Fernández & González-Quirós, 2006; Voss *et al*., 2009; Morote *et al*., 2010; Borme *et al*., 2013; round sardinella: Moreno & Castro, 1995; Morote *et al*., 2008). As regards the Greek seas, the only studies concerning their diet are those of Petrakis *et al*. (1993), Sever *et al*. (2005) and Nikolioudakis *et al*. (2011, 2012) on sardine, Catalán *et al*. (2010) on larval anchovy, and Tsikliras *et al*. (2005b) on seasonal diet of round sardinella. Yet, the feeding habits of these three species have never been examined in a comparative manner and in relation to their ecomorphology.

In this report, we explored whether the feeding habits of these three small pelagic species, combined with ecomorphology and trophic position, affect their coexistence and potential competition, especially in the light of climate change that favours the expansion of round sardinella to northern latitudes (e.g. Tsikliras *et al*., 2005a, b; Sabates *et al*., 2006; Lomiri *et al*., 2008). To this end we: (a) studied the diet and the feeding habits of anchovy, sardine and round sardinella in the Northern Aegean Sea, their main fishing ground in Greek waters (e.g. Stergiou *et al*., 1997; 2011), (b) used published information on feeding related morphometrics in order to evaluate the effect of morphometry on diet, and (c) compiled the available literature on their feeding habits and used it to calculate their fractional trophic levels throughout their distribution range. Such information is of great importance for understanding the role and position of these species in the ecosystems, as well as interspecific competition for the same food resources (e.g. Cunha *et al*., 2005; Tsikliras *et al*., 2005b; Garrido *et al*., 2007).

Materials and Methods

Samples were collected from the N Aegean Sea with purse-seiners, using artificial light, on a seasonal basis (spring 2001-winter 2006). In the case of round sardinella, additional samples from professional gillnets, set in the same area and during the same time period, were used. The fish were preserved in 10% formalin and total length (TL, 0.1 cm) was measured at the laboratory; sex was determined by visual examination of the gonads. The digestive tract was removed and stomachs were isolated. For each stomach separately, the contents were analyzed, using a stereomicroscope and the vacuity coefficient (VC) was estimated as the percentage of empty stomachs. Each food item was identified to the lowest possible taxonomic level. Subsequently, each food category was weighed (0.001 g) and its weight was expressed as a percentage of total stomach content (Hyslop, 1980), since quantitative approaches in diet analyses (i.e. estimation of weight and/or volume of food items) are more appropriate for estimating fractional trophic level (τ) (e.g. Stergiou & Karpouzi, 2002). The presence of phytoplankton was recorded using a microscope but was not weighed due to the small quantities found. An extended account on samplings and stomach content analysis is given in Karachle & Stergiou (2008). Additionally, τ per individual per species (τ_i) was estimated using TrophLab (Pauly *et al*., 2000) and the mean values were tested for differences between species (t-test, Zar, 1999).

The following equation was used for the estimation of τ_i (Pauly *et al*., 2000):

$$\tau_i = 1 + \sum_{j=1}^{G} DC_{ij} \times \tau_j ,$$

where DC_{ij} is the weight contribution of prey item j in the diet of stomach i; τ_j is the trophic level of prey item j and G is the number of prey species included in stomach i.

The matrix of the percentage weight contribution of each prey category per species/season/sex was constructed (11columns x 64 rows). This matrix was then transformed to a triangular one, using the Bray-Curtis similarity index, and subjected to clustering (group-average linking) and multi-dimensional scaling (MDS) multivariate techniques (Field *et al*., 1982). SIMPER analysis (SIMilarity PERcentages) was used to identify the food items responsible for the formation of groups (Clarke & Gorley, 2001).

Finally, in order to explore the effect of morphology on dietary preferences between the three species, the relationships of morphologic characteristics related to feeding [i.e. mouth area (MA), intestine length (GL) and tail area (TA)] with TL were compared with analysis of covariance (ANCOVA, Zar, 1999). The above mentioned relationships have been presented elsewhere (MA: Karachle & Stergiou, 2011; GL: Karachle & Stergiou, 2010a; TA: Karachle & Stergiou, 2012).

Finally, three on-line databases (i.e. Web of Science, Scopus and Google Scholar) were used in order to collect previously published data on the feeding habits of the three species. The following information was tabulated: (a) study area and time period, (b) length measurement and range, (c) number of stomachs examined, (d) method of stomach content analysis, and (e) main food items. Based on the reported diet composition, τ was estimated whenever possible, using the corresponding routine of TrophLab (Pauly *et al*., 2000) (i.e. the "Diet composition" routine, when volumetric or weight data were available, and the "Food item" routine, when frequency or numerical data were presented by the original authors).

Results

Overall, the stomach content of 759, 752 and 230 individuals of anchovy, sardine and round sardinella, respectively, was examined. The size of the specimens ranged between 6.7 and 16.2 cm [mean ± standard error (SE) = 11.4 ± 0.05 cm; median = 11.7 cm] for anchovy, between 7.6 and 16.7 cm (mean ± SE = 12.7 ± 0.05 cm; median = 12.7 cm) for sardine, and between 8.4 and 23.9 cm (mean ± SE = 17.2 ± 0.21 cm; median = 16.7 cm) for round sardinella. The number of empty stomachs was higher for round sardinella (VC = 68.7; Table 1) than that for anchovy and sardine (VC = 31.5% and 51.1%, respectively; Table 1).

For anchovy, VC displayed the highest and lowest values in autumn (42.4%) and spring (25.1%), respectively (Table 1). This species included 45 different food items in its diet, with Crustacean larvae [53.3%; dominant larval groups: Brachyura and Euphasiacea (Table 1, Fig. 1)] being the most important taxon, in terms of weight contribution.

For sardine, VC displayed the highest value in spring

(58.6%) and the lowest in autumn (41.1%) (Table 1). Forty three different food items were identified in the stomach contents, with Copepoda being the most numerous. Copepoda (42.9%) and Brachyuran larvae (39.9%) had the highest % weight contribution to the overall diet of sardine (Table 1, Fig. 1).

Round sardinella displayed high VC values, ranging from 64.3% in summer to 80.0% in autumn (Table 1). The analysis of the stomach contents revealed 31 different food items, and Copepoda had again the highest contribution. Overall, in the diet of round sardinella, Copepoda (50.0%) and Appendicularia (22.1%) displayed the highest % weight contribution (Table 1, Fig. 1).

The difference of feeding habits between the sexes was rather small in all species (Table 2).

The range of the estimated τ_i was 2.0-4.5 [mean ± standard deviation (SD): 3.17 ± 0.30] for anchovy, 2.66-4.5 (mean ± SD: 3.11 ± 0.29) for sardine and 3.0-4.5 (mean ± SD: 3.27 ± 0.34) for round sardinella (Fig. 2). For anchovy, the majority (91.7%) of τ_i values ranged between 3.00 and 3.45, with only six values (1.2%) below 3.00 and 37 values (7.1%) above 3.45 (Fig. 2). Accordingly, for sardine 93.8% of τ_i values ranged between 3.00 and 3.40, with only three values (0.8%) being below and 20 values (5.4%) above this range (Fig. 2). For round sardinella, the majority of τ_i values (91.7%) ranged between 3.00 and 3.53, with only six values (8.3%) exceeding this range (Fig. 2). The mean τ_i differed significantly (ANOVA: $p < 0.01$) between the three species.

Cluster analysis revealed the formation of four groups, at the 25.20% level of similarity (Fig. 3): (a) Group I consisted of round sardinella in summer, (b) Group II consisted of sardine and anchovy in summer, (c) Group III consisted of sardine in winter and round sardinella in spring and autumn, and (d) Group IV consisted of sardine in autumn and spring and anchovy in spring, autumn and winter. Food items responsible for the dissimilarities among the four groups according to

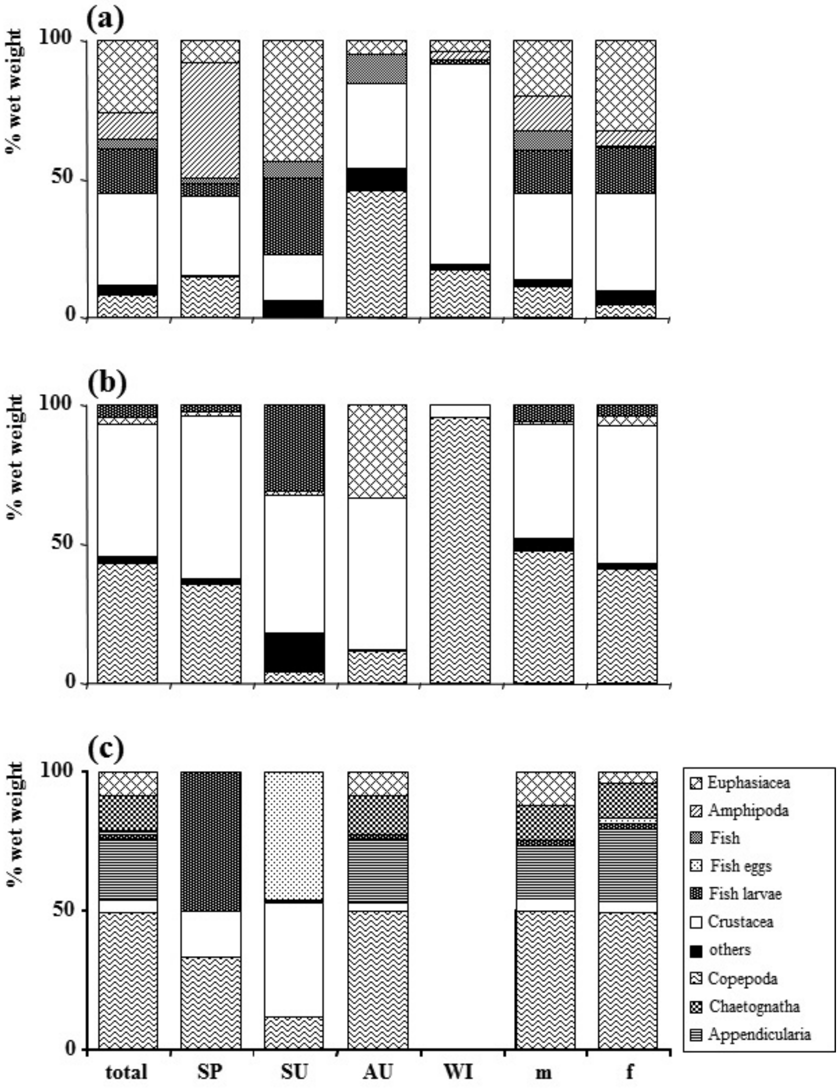

Fig. 1: Main prey items of (a) the European anchovy (*Engraulis encrasicolus*), (b) sardine (*Sardina pilchardus*), and (c) round sardinella (*Sardinella aurita*), totally, in spring (SP), summer (SU), autumn (AU), winter (WI), males (m) and females (f) from the N-NW Aegean Sea, Greece, spring 2001- winter 2006.

Table 1. Food items and their contribution (expressed as % wet weight) per season for *Engraulis encrasicolus, Sardina pilchardus* and *Sardinella aurita,* N-NW Aegean Sea, Greece, spring 2001- winter 2006. SP=spring; SU=summer; AU=autumn; WI=winter; N.i.=not identified/digested; N=number of individuals; VC=vacuity coefficient; TL=total body length; τ ± SE=fractional trophic level ± standard error. Asterisk (*) denotes presence of a food item in the diet with a percentage of <0.1.

TAXA	*Engraulis encrasicolus*					*Sardina pilchardus*					*Sardinella aurita*			
	SP	SU	AU	WI	Total	SP	SU	AU	WI	Total	SP	SU	AU	Total
Detritus		3.4			**1.9**		1.8			**0.2**				
Microalgae														
Bacillariophyceae								*		*				
Pennales														
Dinophyceae						*				*				
Prorocentrum spp.						*				*				
Ageiosperma														
Phanerogama		*			*	*				*				
Cymodocea spp.						*				*				
Polychaeta														
larvae												*	*	*
n.i. Polychaeta													0.1	**0.1**
Mollusca														
Heteropoda	*	0.4	7.9		**0.3**	*				*			0.1	**0.1**
Bivalvia														
Bivalvia larvae	*	*			*	*	*	*		*				
Cephalopoda		0.8			**0.4**									
Crustacea														
Cladocera														
Evadne spp.	*	*	0.1	*	*		0.1	0.1	*	*	16.7	2.0	*	**0.1**
Penillia spp.	*	*	0.1	*	*	*				*				
Podon spp.			0.1	*	*									
Ostracoda	*	*		*	*	*	0.1	3.8	0.1	**0.2**		0.1	*	*
Copepoda														
Acartia spp.	2.8	*		0.2	**0.6**	1.3		*	*	**0.9**			5.0	**4.8**
Anomalocera patersoni	2.1				**0.4**									
Candacia spp.	3.8	0.2		*	**0.9**								2.0	**1.9**
Candacia armata	*	*			*	*	3.7		*	**0.4**				
Candacia simplex		*			*									
Centropages spp.	*				*	1.4	*			**0.9**			*	*
Centropages typicus	*				*									
Clausocalanus spp.								*		*				
Coryaeus spp.	*			*	*	*			0.1	*			*	*
Corycaeus limbatus						*				*				
Corycella spp.	*			*	*	*		0.1	*	*		*		*
Euchaeta hebes														
Harpacticoidea						*				*				
Isias spp.	*				*							*		*
Microsetella spp.	*			*	*							*		*
Nanocalanus minor								*		*				
Oithona spp.						*				*				
Oncea spp.	*		0.1	0.1	*	*	*	*	0.1	**0.1**		*	*	*
Sapphirina spp.	*	*			*	*			*	*			*	*
Sapphirina bicuspidata		*			*									

(continued)

(continued) **Table 1**

TAXA	*Engraulis encrasicolus*					*Sardina pilchardus*					*Sardinella aurita*			
	SP	**SU**	**AU**	**WI**	**Total**	**SP**	**SU**	**AU**	**WI**	**Total**	**SP**	**SU**	**AU**	**Total**
Sapphirina migromaculata		*			*									
Temora stylifera	*	0.4		*	**0.2**	*	0.2	4.3	*	**0.2**		*		*
n.i. Copepoda	5.8		45.7	17	**5.8**	32.9		7	95.4	**40.4**	33.3	14.3	42.8	**43.3**
Stomatopoda														
Squilla spp. larvae		0.6		*	**0.3**		*			*			0.1	**0.1**
Euphasiacea														
Zoa *Euphausia brevis*							*			*				
larvae	4	43.3	5.1	3.8	**25.1**	1.3	1.8	33.3	0.2	**2.6**			9.0	**8.6**
n.i. Euphasiacea	4	0.4		*	**1.0**	0.1	*			**0.1**			0.2	**0.2**
Decapoda														
Brachyura														
Zoa														
Corystes crassivelanus							*			*			*	*
Eriphia spinifrons	*	*			*	0.5		*		**0.3**		*		*
Maja squinado								*		*				
Portunus puber	1.9	0.1		*	**0.5**	1	0.1	1.8	*	**0.8**			*	*
Metazoa														
Ethusa mascarone		*	0.1		*		*			*				
Macropodia spp.	*	*		0.2	**0.1**	*				*				
Portunus puber	19.2	11.7	25.5	65.3	**26.8**	51.6	9.3	47.3	0.9	**37.8**			0.7	**0.7**
Other Decapoda larvae	6.7	*	0.1	*	**1.4**	1.5		*	*	**1**		0.1	0.5	**0.5**
Mysidacea	*	0.7	0.1	0.6	**0.5**	*				*		*	0.8	**0.8**
Amphipoda	41.8		0.2	3.5	**9.3**	0.5		0.1		**0.3**			0.7	**0.7**
Isopoda	*	*			*			1.8		**0.1**				
Crustacea larvae												37.1		**0.6**
n.i. Crustacea	0.9	3.5	5.1	6.1	**3.7**	3.5	39.6		3.1	**6.7**				
Chaetognatha		*		0.2	*	*	*			*			13.3	**12.8**
Chordata –Urochordata														
Appendicularia	*	*		1	**0.2**	*	0.1	0.2	*	*		0.2	23.0	**22.1**
Chordata –Vertebrata														
Pisces														
eggs	*				*	1.8	0.9	*	*	**1.3**		46.0	*	**0.8**
larvae	4.4	27.7		1.5	**16.1**	2.4	30.8			**4.5**	50.0		1.7	**1.8**
Arnoglossus spp.		0.5			**0.3**									
Engraulis encrasicolus		2.2			**1.2**									
Sardina pilchardus		3.3			**1.8**									
n.i. Pisces	2.1	0.2	10.1		**0.6**									
Others														
eggs	*	*	0.1	*	*	*			*	*			*	*
various	0.3	0.5		0.6	**0.5**	*	11.5	0.1		**1.1**		*	*	*
N	179	243	33	304	**759**	227	199	146	180	**752**	45	129	50	**230**
TL range (cm)	8.6-16.2	10.3-16.0	8.5-14.0	6.7-14.1	**6.7-16.2**	7.6-15.8	7.9-16.7	9.7-16.4	10.4-16.5	**7.6-16.7**	12.1-23.9	8.4-23.7	12.7-21.9	**8.4-23.9**
TL mean ± SE (cm)	11.5±0.09	12.0±0.06	13.0±0.17	10.7±0.09	**11.4±0.05**	12.2±0.10	13.0±0.10	12.9±0.12	12.7±0.10	**12.7±0.05**	17.0±0.56	16.3±0.25	19.9±0.20	**17.2±0.21**
VC (%)	25.1	35.8	42.4	30.6	**31.5**	58.6	50.8	41.1	50.0	**51.1**	64.4	64.3	80.0	**68.7**
τ ± SE[1]	3.19±0.35	3.58±0.53	3.22±0.34	3.11±0.30	**3.38±0.44**	3.12±0.29	3.56±0.52	3.12±0.32	3.00±0.06	**3.14±0.29**	3.58±0.57	3.71±0.57	3.19±0.32	**3.20±0.32**
τ ± SE in FishBase[2]					**3.10±0.45**					**3.10±0.19**				**3.40±0.45**

[1] values from Karachle & Stergiou (2008)

[2] values from FishBase (Froese & Pauly, 2012)

Table 2. Food items and their contribution (expressed as % wet weight) per sex for *Engraulis encrasicolus*, *Sardina pilchardus* and *Sardinella aurita,* N-NW Aegean Sea, Greece, spring 2001- winter 2006. N.i.=not identified/digested; N=number of individuals; VC=vacuity coefficient; TL=total body length; τ ± SE=fractional trophic level ± standard error. Asterisk (*) denotes presence of a food item in the diet with a percentage of <0.1.

TAXA	*Engraulis encrasicolus*		*Sardina pilchardus*		*Sardinella aurita*	
	♂	♀	♂	♀	♂	♀
Detritus	1.3	2.5	0.6			
Microalgae						
Bacillariophyceae				*		
Pennales						
Dinophyceae			*	*		
Prorocentrum spp.						
Ageiosperma						
Phanerogama						
Cymodocea spp.		*		*		
Polychaeta						
larvae					*	*
n.i. Polychaeta					0.1	
Mollusca						
Heteropoda	0.4	0.2		*	0.1	0.2
Bivalvia						
Bivalvia larvae	*		*	*		
Cephalopoda		0.9				
Crustacea						
Cladocera						
Evadne spp.	*	*	*	*	0.1	*
Penillia spp.	*	*		*		
Podon spp.	*					
Ostracoda	*	*	0.4	0.1	*	0.1
Copepoda						
Acartia spp.	1.2	*	*	1.2	3.4	7.1
Anomalovera patersoni		0.9				
Candacia spp.					*	5.0
Candacia armata	1.6	0.1	0.9	0.1		
Candacia simplex						
Centropages spp.	*		*	1.3	*	
Centropages typicus		*				
Clausocalanus spp.				*		
Corycaeus spp.	*	*	*	*		*
Corycaeus limbatus						
Corycella spp.	*	*	*	*	*	
Euchaeta hebes						
Harpacticoidea			*	*		*
Isias spp.		*				
Microsetella spp.	*	*			*	
Nanocalanus minor			*	*		
Oithona spp.				*		
Oncea spp.	*	*	0.1	*	*	*
Sapphirina spp.	*	*	*	*		*
Sapphirina bicuspidata						
Sapphirina migromaculata						
Temora stylifera	0.4	*	0.1	0.3		*
n.i. Copepoda	8.0	3.5	46.4	38.0	46.9	37.3
Stomatopoda						
Squilla spp. larvae	0.3	0.1		*	*	0.2
Euphasiacea						
Zoa *Euphausia brevis*				*		
larvae	18.1	32.7	0.7	3.4	11.6	3.7
n.i. Euphasiacea	1.8	0.1	0.3		0.2	0.2
Decapoda						
Brachyura						
Zoa						
Corystes crassivelanus				*	*	
Eriphia spinifrons	*	*		0.5		*
Maja squinado			*	*		
Portunus puber	0.7	0.2	0.3	1.0	*	*
Metazoa						
Ethusa mascarone	*	*	*			
Macropodia spp.	*	0.1		*		
Portunus puber	26.7	26.8	26.1	42.5	0.8	0.4

(continued)

(continued) **Table 2**

TAXA	***Engraulis encrasicolus***		***Sardina pilchardus***		***Sardinella aurita***	
	♂	♀	♂	♀	♂	♀
Other Decapoda larvae	2.3	0.6	3.5	*	*	1.2
Mysidacea	0.1	1.0	*		0.8	0.7
Amphipoda	13.0	5.5	1.2	*	0.6	0.9
Isopoda	*	*		0.1		
Crustacea larvae					1.0	*
n.i. Crustacea	1.1	6.4	9.3	5.6		
Chaetognatha	0.1	*	*	*	12.7	12.9
Chordata –Urochordata						
Appendicularia	*	0.5	*	*	19.4	26.5
Chordata –Vertebrata						
Pisces						
eggs	*	*	1.5	1.2	0.1	1.9
larvae	15.6	16.7	6.1	3.9	1.7	1.9
Arnoglossus spp.	0.5					
Engraulis encrasicolus	2.3					
Sardina pilchardus	3.4					
n.i. Pisces	0.8	0.4				
Others						
eggs	*	*	*	*		*
various	0.4	0.6	2.3	0.6	*	*
N	389	370	391	361	147	83
TL range (cm)	7.2-16.2	6.7-14.8	7.6-16.5	8.0-16.7	8.4-23.7	8.9-23.9
TL mean ± SE (cm)	11.5±0.07	11.3±0.08	12.6±0.07	12.7±0.05	17.5±0.26	16.8±0.36
VC (%)	28.0	35.1	56.3	45.4	68.0	69.9
τ ± SE[1]	3.40±0.43	3.36±0.45	3.16±0.30	3.14±0.29	3.18±0.32	3.23±0.34

[1] values from Karachle & Stergiou (2008)

SIMPER analysis are given in Table 3.

For the same TL, the MA for anchovy was larger than that of sardine and round sardinella, whereas GL and TA were smaller for anchovy compared to those of sardine, and in sardine smaller than that of round sardinella (Fig. 4). The GL-TL relationships (Fig. 4) of the three species differed significantly (ANCOVA: all cases $p < 0.01$). In the case of MA-TL and TA-TL relationships (Fig. 4)

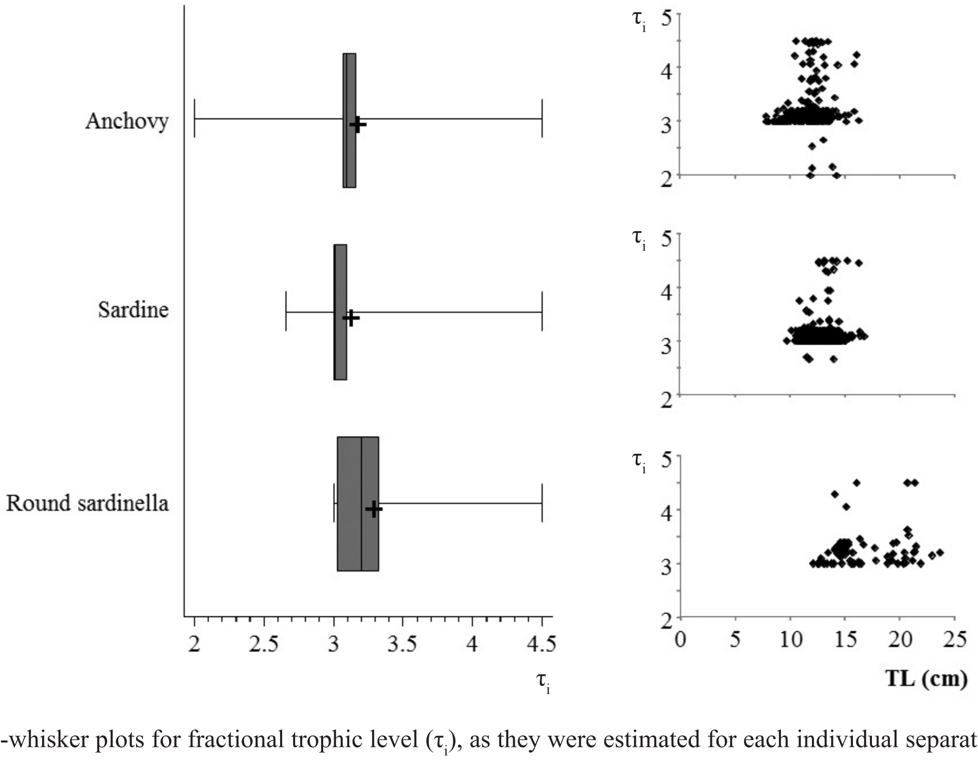

Fig. 2: left: Box-whisker plots for fractional trophic level (τ_i), as they were estimated for each individual separately, for anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*) and round sardinella (*Sardinella aurita*) from the N-NW Aegean Sea, Greece, spring 2001- winter 2006. The central box indicates the range of values representing the 50% of cases around the median (vertical lines); the whiskers (horizontal lines) show the range of the values and the cross (+) indicates the mean value. Right: relation of estimated τ_i and individual total length (TL).

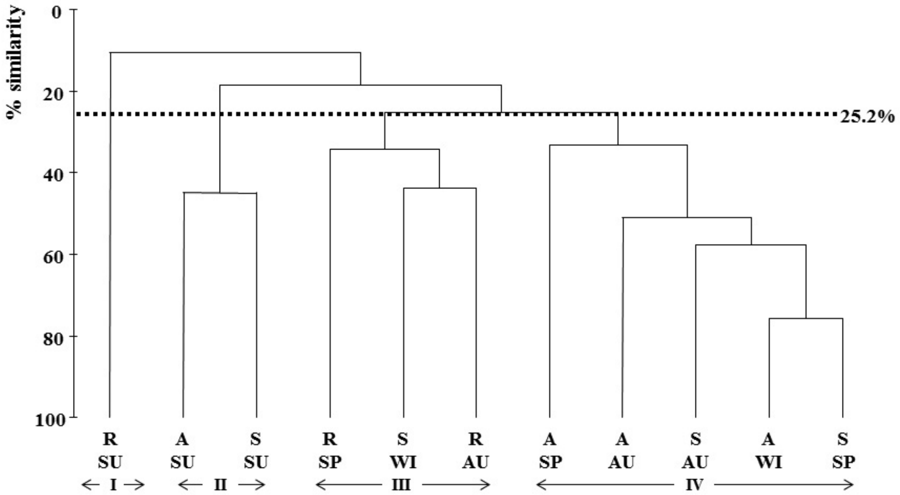

Fig. 3: Cluster analysis for anchovy (*Engraulis encrasicolus*: A), sardine (*Sardina pilchardus*: S) and round sardinella (*Sardinella aurita*: R), based on their seasonal feeding habits (data from Table 1), from the N-NW Aegean Sea, Greece, spring 2001- winter 2006. AU=autumn, WI=winter, SP=spring, SU=summer.

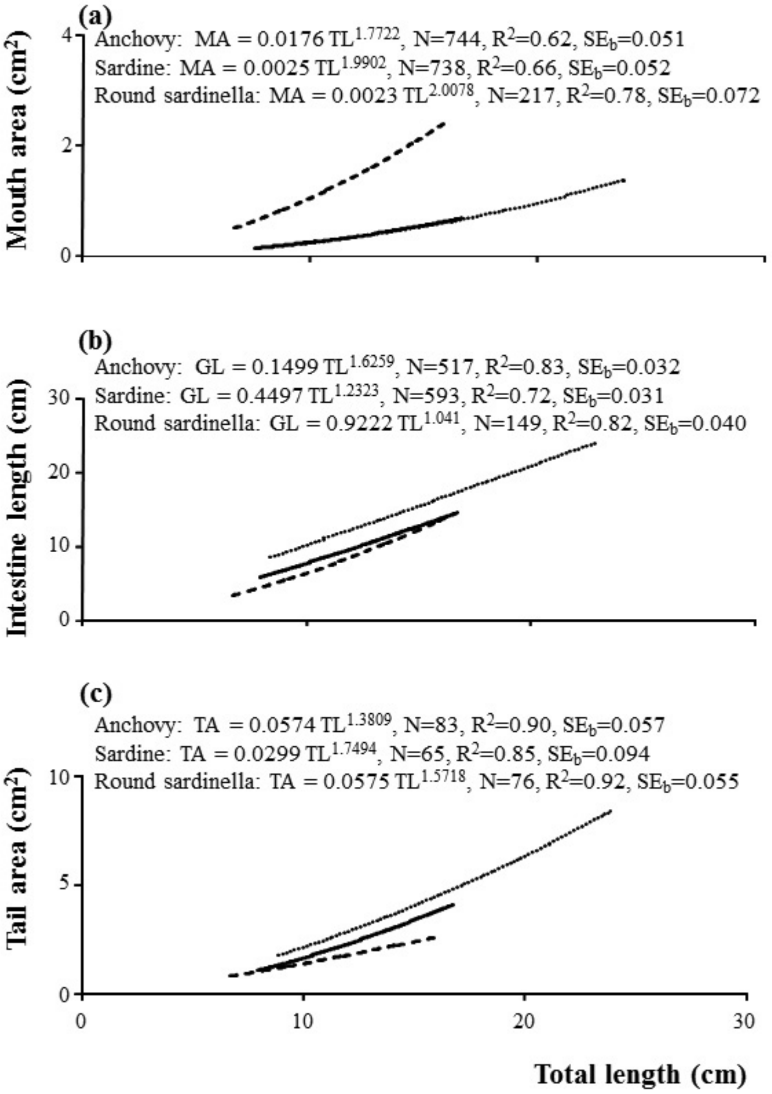

Fig. 4: Relationships of total length (TL) and (a) mouth area (MA; from Karachle & Stergiou 2011), (b) intestine length (GL; from Karachle & Stergiou 2010a) and (c) tail area (TA; Karachle & Stergiou 2012) for anchovy (*Engraulis encrasicolus*: dashed line), sardine (*Sardina pilchardus*: solid line) and round sardinella (*Sardinella aurita*: dotted line). N=number of individuals, R^2=coefficient of determination, SE_b=standard error of slope b.

Table 3. Simper analysis results. SIM=mean similarity; DISSIM= mean dissimilarity. The average contribution (%) in the formation of groups of each prey item is given in parenthesis. Groups as those in figure 3. n.i.= not identified.

	Group I		Group II		Group III		Group IV	
Group II	DISSIM=99.40		SIM=44.92					
	fish eggs	(22.94)	fish larvae	(61.69)				
	Decapoda larvae	(18.69)	metazoa *Portunus puber*	(20.71)				
	fish larvae	(14.73)						
	Euphasiacea larvae	(11.36)						
	n.i. Crustacea	(10.85)						
Group III	DISSIM=84.88		DISSIM=85.98		SIM=37.35			
	fish eggs	(27.13)	n.i. Copepoda	(33.26)	n.i. Copepoda	(97.68)		
	n.i. Copepoda	(25.28)	fish larvae	(15.04)				
	Decapoda larvae	(21.88)	Euphasiacea larvae	(12.73)				
	fish larvae	(10.16)	n.i. Crustacea	(11.93)				
Group IV	DISSIM=88.29		DISSIM=78.86		DISSIM=74.80		SIM=47.64	
	fish eggs	(25.87)	metazoa *Portunus puber*	(19.84)	metazoa *Portunus puber*	(27.58)	metazoa *Portunus puber*	(62.88)
	metazoa *Portunus puber*	(23.69)	fish larvae	(17.50)	n.i. Copepoda	(25.10)	n.i. Copepoda	(23.31)
	Decapoda larvae	(21.03)	n.i. Copepoda	(13.74)	fish larvae	(11.45)		
			Euphasiacea larvae	(13.22)				
			n.i. Crustacea	(12.22)				

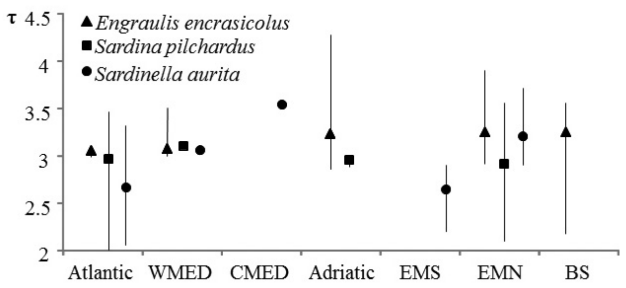

Fig. 5: Mean values of trophic level (τ) for anchovy *(Engraulis encrasicolus:* ▲), sardine *(Sardina pilchardus:* ■) and round sardinella *(Sardinella aurita:* ●), as estimated according to the relevant literature (for details see Table 4), in its various distribution areas. Vertical lines indicate τ range. WMED=West Mediterranean, CMED=Central Mediterranean, EMS=East Mediterranean South, EMN=East Mediterranean North, BS=Black Sea.

there was a significant difference between anchovy and the two other species (ANCOVA: all cases $p < 0.01$), whereas no significant difference was found between sardine and round sardinella (ANCOVA: $p = 0.8309$ and 0.0911, for MA-TL and TA-TL relationships respectively).

Information on the diet of the three species was found for 139 data sets, the majority of which concerned anchovy (68 data sets; Table 4) mainly in the Black and Azov Seas (26 data sets; Table 4), followed by round sardinella (43 data sets; Table 4). In half of the cases (70 data sets) sample size was not reported (Table 4). The estimated τ values ranged from 2.18 ± 0.16 to 4.28 ± 0.74 (mean ± SD= 3.135 ± 0.30) for anchovy, from 2.00 ± 0.00 to 3.56 ± 0.52 (mean ± SD=3.058 ± 0.28) for sardine and 2.05 ± 0.03 to 3.71 ± 0.57 (mean ± SD=2.935 ± 0.39) for round sardinella (Table 4, Fig. 5). Finally, no variations were recorded between larval and adult τ, in all three species (Table 4).

Discussion

In this study, we examined the feeding habits by season and sex, for anchovy, sardine and round sardinella in the N Aegean Sea. Sardine in the study area included both phytoplankton and zooplankton in its diet, with Copepoda being the dominant food item in terms of weight. These results are in accordance with previous studies on sardines (e.g. Varela *et al*., 1988; Petrakis *et al*., 1993; Cunha *et al*., 2005; Sever *et al*., 2005; Espinoza *et al*., 2009). Anchovy, on the other hand, fed almost exclusively on zooplankton. With the exception of the Black Sea populations of anchovy that, in most cases examined, included phytoplankton in their diets (e.g. Mikhman & Tomanovich, 1978; Bulgakova, 1993; Budnichenko *et al*., 1999); anchovy in the Mediterranean (Tudela & Palomera, 1997;

Table 4. Feeding habits of *Engraulis encrasicolus*, *Sardina pilchardus* and *Sardinella aurita,* according to the relevant literature. SP=sampling period; LM=length measurement; LR=length range (in cm); N=number of individuals; TL=total length; FL=fork length; τ ± SE=fractional trophic level ± standard error (estimated in the present study by the authors); F = frequency of occurrence; N= numerical percentage; W = percentage by weight; V = percentage by volume; VC=vacuity coefficient; IoP = index of preponderance; RA=relative abundance; IRI=index of relative importance.

Area	SP	LM	LR	N	Main prey	Method	τ±SE	Reference
Engraulis encrasicolus								
Sea of Azov	1933				Copepoda	W	3.26±0.36	Mikhman & Tomanovich (1977; data of Smirnov)
Sea of Azov	1937				Copepoda	W	3.21±0.32	Mikhman & Tomanovich (1977; data of AzCherNIRO)
Sea of Azov	1948				Copepoda	W	3.16±0.30	Mikhman & Tomanovich (1977; data of Logvinovich)
Sea of Azov	1949				Copepoda, Polychaeta	W	3.19±0.32	Mikhman & Tomanovich (1977; data of Logvinovich)
Sea of Azov	1950				Polychaeta, Copepoda	W	3.48±0.48	Mikhman & Tomanovich (1977; data of Kornilova)
Sea of Azov	1955				Mysidacea, Polychaeta	W	3.33±0.43	Mikhman & Tomanovich (1977; data of Kornilova)
Sea of Azov	1956				larvae of Cirripedia & Mollusca, others	W	3.38±0.43	Mikhman & Tomanovich (1977; data of Kornilova)
Sea of Azov	1972				larvae of Cirripedia & Mollusca	W, VC	3.25±0.40	Mikhman & Tomanovich (1977)
	1973				Phytoplankton, larvae of Cirripedia & Mollusca		2.71±0.30	
	1974				larvae of Cirripedia & Mollusca		3.36±0.42	
Black Sea	5-7/1973		8.1-13.0	405	<8.1, Copepoda	N	3.17±0.30	Sirotenko & Danilevskiy (1977)
					>8.1, Copepoda		3.17±0.30	
NW Black Sea	23-24/6/1987		7.7-13.0	200	Phytoplankton, Cladocera, Copepoda	N, W, VC	2.37±0.19	Bulgakova (1993)
	25-26/5/1988		6.2-12.5	147	Copepoda, Copepoda eggs		2.93±0.06	
	20-21/6/1989		8.7-13.0	238	Mysidacea, fish larvae		3.39±0.47	
	6-7/7/1990		7.1-12.8	188	fish larvae, Copepoda		3.56±0.50	
mouth of Ebro River, Catalan Sea	5/1994, 5/1995			311	Copepoda, Mollusca, other	RA	3.50±0.48	Tudela & Palomera (1995; 1997)
NW Adriatic	6-7/1996	SL	2.4-10.9	326	Copepoda	F	3.00±0.00	Conway *et al.* (1998)
			2.4-10.9	176	Copepoda		3.00±0.00	
Sea of Azov	1977				larvae of Cirripedia & Mollusca, Phytoplankton	W	2.97±0.34	Budnichenko *et al.* (1999; data of Lutz *et al.*)
	1978				larvae of Cirripedia & Mollusca, Copepoda		3.24±0.41	
Sea of Azov	5/1995				larvae of Cirripedia & Mollusca, Mysidacea	W	3.32±0.43	Budnichenko *et al.* (1999)
	6/1995				larvae of Cirripedia & Mollusca		3.37±0.45	
	6/1995				Copepoda		3.02±0.18	
	6/1995				larvae of Cirripedia & Mollusca, Copepoda		3.27±0.37	
	8/1995				Phytoplankton		2.18±0.16	

(continued)

(continued) **Table 4**

Area	SP	LM	LR	N	Main prey	Method	τ±SE	Reference
	10/1995				larvae of Cirripedia & Mollusca, Phytoplankton		2.84±0.35	
	6/1996				Phytoplankton, Polychaeta		2.67±0.35	
	8/1996				Polychaeta, Phytoplankton		3.01±0.43	
Bay of Biscay	5-6/1997			213	Copepoda	IoP	3.00±0.00	Plounevez & Champalbert (1999)
Gulf of Lions	8/1995	TL		279	Copepoda, Cladocera, Crustacea, Appendicularia, Mollusca, other	F, W, VC, IoP	3.40±0.44	Plounevez & Champalbert (2000)
	7/1996	TL		247	Copepoda, Cladocera, Crustacea, Appendicularia, Mollusca, other		3.40±0.44	
Catalan Sea & Gulf of Lions	7/1992		0.3-0.4	29	Copepoda	N	3.00±0.21	Tudela *et al*. (2002)
			0.4-0.8	58	Copepoda	N	3.00±0.15	
			0.8-1.16	15	Copepoda	N	3.00±0.11	
Ghazaouet, Algeria	9-12/2007	TL			Copepoda, Euphasiacea	N, F	3.00±0.12	Bacha & Amara (2009)
Benisaf, Algeria	9-12/2007	TL			Copepoda		3.00±0.10	Bacha & Amara (2009)
Bejaia, Algeria	1-12/2007	TL			Copepoda		3.00±0.07	Bacha & Amara (2009)
					winter: Copepoda		3.00±0.00	
					spring: Copepoda		3.00±0.12	
					summer: Copepoda, Gastropoda larvae		3.10±0.16	
					autumn: Copepoda		3.00±0.00	
off Pesaro, N Adriatic Sea	10/2002	TL	3.0-3.9		Bivalvia larvae, Copepoda	N, F, W, IRI	3.20±0.32	Borme *et al*. (2009)
			3.0-3.9		Copepoda		3.03±0.13	
			4.0-8.9		Bivalvia larvae, Copepoda		3.20±0.34	
			4.0-8.9		Copepoda		3.03±0.15	
			>9.0		Bacillariophyceae, Amphipoda		2.87±0.37	
			>9.0		fish larvae		4.28±0.74	
Bejaia, Algeria	1-12/2007	TL			G0: Copepoda	N, F	3.00±0.00	Bacha *et al*. (2010)
					G1: Copepoda		3.00±0.15	
					G2: Copepoda		3.00±0.10	
					G3+: Copepoda		3.00±0.15	
NE Aegean Sea	7 & 9/2003, 7 & 9/2004	SL	0.23-1.18		Copepoda	N, F	2.98±0.16*	Catalán *et al*. (2010)
					0.2-0.39: Copepoda		3.04±0.29*	
					0.4-0.59: Copepoda		2.99±0.15*	
					0.6-0.79: Copepoda		3.15±0.31*	
					0.8-0.99: Copepoda		2.92±0.03*	
					>1.0: Copepoda		3.91±0.28*	
Catalan Sea	6 & 11/2005	SL	<0.9	226	Copepoda	N, F, IRI	3.00±0.10	Morote *et al*. (2010)
				127	Copepoda		3.00±0.10	

(continued)

(continued) **Table 4**

Area	**SP**	**LM**	**LR**	**N**	**Main prey**	**Method**	**τ±SE**	**Reference**
western Baltic Sea	2006	TL	12.0-16.0	94	Bacillariophyceae, Cumacea, Copepoda, Cirripedia larvae, Amphipoda	N, F, V, VC	3.11±0.39	Schaber *et al*. (2010)
N-NW Aegean Sea	6/2001-1/2006	TL	6.7-16.2	759	Brachyura larvae, Euphasiacea larvae	W, VC	3.38±0.44**	present study
			8.6-16.2	179	*spring*: Amphipoda, Brachyura larvae		3.19±0.35**	
			10.3-16.0	243	*summer*: Euphasiacea larvae, fish larvae		3.58±0.53**	
			8.5-14.0	33	*autumn*: Copepoda, Brachyura larvae		3.22±0.34**	
			6.7-14.1	304	*winter*: Brachyura larvae		3.11±0.30**	
			7.2-16.2	389	*males*: Brachyura larvae, Euphasiacea larvae		3.40±0.43**	
			6.7-14.8	370	*females*: Euphasiacea larvae, Brachyura larvae		3.36±0.45**	
Sardina pilchardus								
Vigo, Spain	2-3/1987, 7/1988				Zooplankton, Bacillariophyceae	RA		Varela *et al*. (1988)
Vigo, Spain	2-3/1987, 7/1989				Bacillariophyceae		2.00±0.00	
La Coruña, Spain	2-3/1987, 7/1990				Zooplankton			
La Coruña, Spain	2-3/1987, 7/1991				Bacillariophyceae, Zooplankton			
Aviles, Spain	2-3/1987, 7/1992				Zooplankton, Dinophyceae			
Aviles, Spain	2-3/1987, 7/1993				Zooplankton, Dinophyceae			
Santander, Spain	2-3/1987, 7/1994				Zooplankton, Dinophyceae			
South Evvoikos Gulf	1992-1993	TL	12-16	35	Copepoda, plants, Cladocera	F, VC	3.20±0.42	Petrakis *et al*. (1993)
Canary Islands	4/1990-4/1991	TL			Copepoda	N, W, VC	3.11±0.26	Moreno & Castro (1995)
Vis Isl, East Central Adriatic	02/04/1990	SL	0.4-2.4	1429	<1.0, Copepoda nauplii	N, F	2.88±0.12	Dulčić (1999)
					1.0-1.5, Copepoda nauplii, Copepoda		3.00±0.00	
					<1.5, Copepoda, Copepoda nauplii		2.92±0.20	
Portugal	11/2002,1-5/2003,	TL	8.5-23.2	970	Copepoda, Siphonophora, fish eggs	V	3.46±0.46	Cunha *et al*. (2005)
Ismir Bay, Aegean Sea	1-12/1997	FL	9.6-14.9	365	Copepoda, Crustacea larvae	F, N, W, IRI, VC	3.08±0.25	Sever *et al*. (2005)
central Cantabrian slope, Spain	5/2000	SL	0.45-2.21	618	0.45-0.76, Copepod eggs	N	3.10±0.16	Munuera Fernandez & Gonzales-Quiros (2006)
					0.77-1.3, Copepod eggs		3.00±0.09	
					1.31-2.21, Copepodites		3.00±0.00	
German Bight, North Sea	6/2003	SL		451	Copepoda	N,W	3.08±0.21	Voss *et al*. (2010)
Catalan Sea	6 & 11/2005	SL		147	Copepoda, Tintinnida	N, F, IRI	3.10±0.24	Morote *et al*. (2010)
				145	Copepoda		3.10±0.15	
Thracian Sea, North Aegean	7/2007	TL			Copepoda	N	2.90±0.00	Nikolioudakis *et al*. (2012)

(continued)

(continued) **Table 4**

Area	SP	LM	LR	N	Main prey	Method	τ±SE	Reference
	7/2007				Bacillariophyceae, Dinoflagellata, Tintinnida		2.30±0.09	
	12/2007				Bacillariophyceae, Dinoflagellata, Copepoda		2.10±0.00	
	7/2008				Copepoda, Appendicularia		3.10±0.10	
	7/2008				Bacillariophyceae, Dinoflagellata		2.40±0.07	
	2/2009				Bacillariophyceae, Dinoflagellata, Copepoda, Tintinnida		2.30±0.11	
Gulf of Manfredonia, Adriatic Sea	2/2008	TL	2.75-4.5	217	Copepoda	N, F,VC, IRI	3.00±0.00	Borme *et al.* (2013)
N-NW Aegean Sea	6/2001-1/2006	TL	7.6-16.7	752	Copepoda, Brachyura larvae	W, VC	3.14±0.29**	present study
			7.6-15.8	227	*spring*: Brachyura larvae, Copepoda		3.12±0.29**	
			7.9-16.7	199	*summer*: Crustacea, fish larvae		3.56±0.52**	
			9.7-16.4	146	*autumn*: Brachyura larvae, Euphasiacea larvae		3.12±0.06**	
			10.4-16.5	180	*winter*: Copepoda		3.00±0.06**	
			7.6-16.5	391	*males*:Copepoda, Brachyura larvae		3.16±0.30**	
			8.0-16.7	361	*females*: Brachyura larvae, Copepoda		3.14±0.29**	
Sardinella aurita								
Aegean	1950-1951	TL	8.0-14.0	11	Copepoda, Crustacea larvae	F	2.90±0.00***	Ananiades (1952)
Aegean	1950-1951	TL	15.-21.0	11	Isopoda, Ampipoda, Schizopoda	F	3.10±0.24***	Ananiades (1952)
Aegean	1950-1951	TL	22.0-27.0	11	Crustacea, anchovy larvae, Bacillariophyceae	F	3.08±0.32***	Ananiades (1952)
NW African coasts	1970			64	Copepoda, Lamellibranchia, Ostracoda	F	3.10±0.35***	Pham Thuoc & Szypuła (1973)
Senegal (Cayar)	1977	FL	22.0-30.0	260	Copepoda, Ostracoda, Phytoplankton	W	2.96±0.23***	Nieland (1982)
Senegal (Bel Air)	1977	FL	10.0-15.0	80	Copepoda, fish eggs, Phytoplankton	W	2.90±0.25***	Nieland (1982)
Senegal (Mbour)	1977	FL	22.0-30.0	180	Phytoplankton, Copepoda	W	2.27±0.11***	Nieland (1982)
Senegal (Bel Air)	1974	FL	10.0-16.0	40	Detritus, Phytoplankton, Copepoda	W	2.05±0.03***	Nieland (1982)
Senegal (Mbour)	1974	FL	20.0-26	75	Detritus, Phytoplankton, Zooplankton	W	2.05±0.03***	Nieland (1982)
Canary Islands	4/1990-4/1991	TL			Copepoda, Appendicularia	N, W, VC	3.31±0.43	Moreno & Castro (1995)
N Aegean Sea	10/2001	TL	15.1-20.7	30	Amphipoda, other Crustacea, Copepoda	W, VC	3.08±0.29***	Tsikliras *et al.* (2005b)
	1/2002	TL	14.5-20.0	30	Copepoda, other Crustacea, Ampipoda		3.04±0.20***	
	4/2002	TL	17.0-21.5	30	Copepoda, Decapoda larvae		3.28±0.34***	
	8/2002	TL	16.0-19.4	30	Decapoda larvae, Amphipoda		3.10±0.30***	
	10/2001-8/2002	TL		8	15.0-16.0: Copepoda, Amphipoda		3.08±0.32***	
	10/2001-8/2002	TL		24	16.0-17.0: Decapoda larvae, Amphipoda		3.20±0.36***	
	10/2001-8/2002	TL		10	17.0-18.0: Amphipoda, Decapoda larvae		3.13±0.35***	
	10/2001-8/2002	TL		40	18.0-19.0: Siphonophora, Decapoda larvae		3.31±0.32***	

(continued)

(continued) **Table 4**

Area	SP	LM	LR	N	Main prey	Method	τ±SE	Reference
	10/2001-8/2002	TL		22	19.0-20.0: Copepoda		3.16±0.29***	
	10/2001-8/2002	TL		10	20.0-21.0: Copepoda, Decapoda larvae		3.21±0.34***	
	10/2001-8/2002	TL		6	21.0-22.0: Copepoda		3.26±0.37***	
Sicily	4/2004-1/2005	TL	9.3-31.5	254	Siphonophora, fish eggs & larvae, Appendicularia	F, N, W	3.54±0.52	Lomiri *et al*. (2008)
Catalan Sea	6/2005	SL	>0.8	66	Copepoda	F, N, IRI	3.10±0.16	Morote *et al.* (2008)
			≤0.8	50	Copepoda		3.00±0.10	
Port Said, Egypt	10/2009-7/2010	TL		400	Phytoplankton, Copepoda	F, N, VC	2.60±0.11	Madkour (2012)
	10/2009-7/2010	TL			8.0-9.0: Phytoplankton, Detritus, Copepoda		2.50±0.16	
	10/2009-7/2010	TL			9.0-10.0: Phytoplankton, Copepoda		2.60±0.17	
	10/2009-7/2010	TL			10.0-11.0: Phytoplankton, Copepoda		2.40±0.10	
	10/2009-7/2010	TL			11.0-12.0: Phytoplankton, Copepoda		2.50±0.09	
	10/2009-7/2010	TL			12.0-13.0: Copepoda, Phytoplankton		2.80±0.17	
	10/2009-7/2010	TL			13.0-14.0: Copepoda, Phytoplankton, Detritus		2.50±0.09	
	10/2009-7/2010	TL			14.0-15.0: Copepoda, Phytoplankton		2.90±0.10	
	10/2009-7/2010	TL			15.0-16.0: Copepoda, Phytoplankton		2.90±0.00	
	10/2009	TL			Phytoplankton, Detritus		2.20±0.09	
	1/2010	TL			Phytoplankton, Copepoda		2.60±0.11	
	4/2010	TL			Copepoda, Phytoplankton, Detritus		2.70±0.17	
	7/2010	TL			Copepoda, Phytoplankton		2.70±0.09	
N-NW Aegean Sea	6/2001-1/2006	TL	8.4-23.9	230	Copepoda, Appendicularia	W, VC	3.20±0.32**	present study
			12.1-23.9	45	*spring*: fish larvae, Copepoda		3.58±0.57**	
			8.4-23.7	129	*summer*: fish larvae, Crustacea		3.71±0.57**	
			12.7-21.9	50	*autumn*: Copepoda, Appendicularia		3.19±0.32**	
			8.4-23.7	147	*males*: Copepoda, Appendicularia, Chaetognatha		3.18±0.32**	
			8.9-23.9	83	*females*: Copepoda, Appendicularia, Chaetognatha		3.23±0.34**	

[*] τ values estimated by Catalán *et al.* (2010)
[**] τ values estimated by Karachle & Stergiou (2008)
[***] τ values estimated by Tsikliras *et al.* (2005b)

Plounevez & Champalbert, 2000; Borme *et al*., 2009) and the Atlantic (Plounevez & Champalbert, 1999) probably feeds exclusively on zooplankton. Such a contrasting difference may be attributed to the high eutrophication of the Black Sea and therefore the high abundance of phytoplankton (e.g. Yunev *et al*., 2005). Thus, the feeding preference of anchovy in the Black Sea is similar to anchovies thriving in upwelling areas (see van der Lingen *et al*., 2009 and references therein). In addition, the feeding habits and τ values of anchovy and sardine did not show great variations along the different parts of the Atlantic and the Mediterranean (Fig. 5). The diet of round sardinella in the study area included zooplankton only, as reported for this species in other areas of its northern distribution (Ananiades, 1952; Tsikliras *et al*., 2005b; Lomiri *et al*., 2008). However, in more southern areas, like Senegal and Egypt, considerable quantities of detritus and phytoplankton are also part of its diet (Nieland, 1982; Madkour, 2012), leading to lower τ values (Fig. 5), a fact probably related to the existence of upwelling in both Senegalese waters (e.g. Mittelstaedt, 1983) and air-driven upwelling in Egyptian waters (e.g. Elsayed *et al*., 1985).

All three species are planktivores and according to their 90% range of τ_i values (Fig. 2) they are classified as omnivores with preference to animal material (see Stergiou & Karpouzi, 2002) and this agrees with the classification derived from the overall τ value (anchovy: 3.38 ± 0.44, sardine: 3.14 ± 0.29, and round sardinella: 3.20 ± 0.32; Tables 1 and 4; Karachle & Stergiou, 2008). Nevertheless, for all three species there were individuals that had much higher and lower τ_i values. This is attributed to the fact that, at the time of capture, these individuals included large quantities of low (i.e. phytoplankton and detritus) or high (i.e. fish eggs and larvae) τ food items in their diet. Stomach content analysis offers 'snapshots' of diet (Stergiou & Karpouzi, 2002; Karachle & Stergiou, 2008), and this is reflected in the τ_i values. Yet, the analysis of large samples from all seasons and length ranges is a good indicator of the feeding habits and estimation of τ (Stergiou & Karpouzi, 2002; Karachle & Stergiou, 2008).

The mixed diet of sardine (i.e. phyto- and zooplankton) and the zoo-planktivorous diet of anchovy are also reflected in their intestine lengths. Species that include plants in their diet display lengthier guts than carnivorous species (e.g. Kapoor *et al*., 1975; Kramer & Bryant, 1995a, b; Karachle & Stergiou, 2010a, b), in order to achieve optimum nutrient and energy gain from the food consumed. In the study area, sardine had a lengthier intestine than anchovy (Fig. 4), a fact allowing sardine to consume and process both zooplankton and phytoplankton, the latter being a food source that is not used by anchovy, which possess a relatively shorter intestine compared to that of sardine, in the Northern Aegean Sea.

The gut of round sardinella was longer than that of the other two species despite the fact that it feeds on zooplankton and thus its gut length should have been similar to that of anchovy. Round sardinella is an opportunistic species (Tsikliras *et al*., 2005b), and in the southern areas of its distribution, such as the Senegalese (Nieland, 1982) and Egyptian Mediterranean waters (Madkour, 2012), round sardinella feeds mainly on detritus and phytoplankton. In the study area, and in the northern parts of the Mediterranean, it is a recent colonizer (e.g. Tsikliras *et al*., 2005a, b; Lomiri *et al*., 2008). Perhaps, a lengthier gut is more advantageous for the opportunistic feeding nature of round sardinella, in order to use the available food resources, especially in the light of competition with anchovy and sardine. Additionally, apart from the environmental conditions that have favoured its northward expansion (e.g. Sabatés *et al*., 2006; Tsikliras, 2008) such a morphological feature might also enhance its successful establishment in its new environment.

Information on the feeding mode exists only for anchovy and sardine. Both species display two major types of feeding strategies (Bulgakova, 1996; Tudela & Palomera, 1997; Garrido *et al*., 2007; Borme *et al*. 2009; Espinoza *et al*. 2009; van der Lingen *et al*., 2009): filter feeding and particulate feeding. Although prey size is used by both species as a criterion for the selection of the feeding mode, anchovy switches from particulate feeding to filtering as the concentration of prey increases (Bulgakova, 1996), whereas prey density does not affect the selection of feeding mode by sardine (Garrido *et al*., 2007). This shift in the feeding mode in anchovy could be favoured by the morphology of its mouth. In this study, for the same TL, mouth area of anchovy was found to be larger than that of sardine (Fig. 4), and a larger mouth gape allows the filtration of a greater volume of water, making filter feeding more profitable. On the other hand, sardine displays a more protractile mouth that might be more advantageous in the case of particulate feeding. For round sardinella, given the resemblance of mouth shape, area and position with those of sardine, one could speculate that round sardinella is also a particulate feeder, as suggested by Madkour (2012), a hypothesis that requires further investigation.

Tail area in fishes has been related to food consumption and is used for the estimation of annual food consumption per unit biomass, i.e. Q/B (Palomares & Pauly, 1989), whereas tail shape shows greater affinities between species occupying the same ecological niche (Karachle & Stergiou, 2012). Despite the fact that the tail of the three species studied here was fork-shaped, the tail area differed between anchovy and sardine, but not between round sardinella and the other two species. In the first case, for the same TL, tail area in anchovy was smaller than that of sardine (Fig. 4). This difference could be attributed to the response of anchovy to prey concentration and change of feeding mode, which is not observed in sardine (Bulgakova, 1996; Garrido *et al*., 2007). Additionally, smaller tail areas, such as that of anchovy, result in higher tail aspect ratios (the latter being negatively related to tail area: aspect ratio=squared tail height/tail area), and in turn higher aspect ratios led to higher Q/B [since aspect ratio is a factor in the numerator of the Q/B equation (Palomares & Pauly, 1989)]. Furthermore, it has been shown that particulate feeding requires higher velocities (Videler, 1993), which can be achieved with forked shape tails (Keast & Webb, 1966), such as those of the three species studied here. On the other hand, filter feeding is more costly, in terms of energy (Videler, 1993), and thus requires tails with comparatively smaller tail areas, as in the case of anchovy. Therefore, the fact that the tail area of round sardinella was similar to that of sardine further supports the hypothesis of round sardinella being a particulate feeder. Feeding intensity, as revealed in this study, differs considerably in the three species and, along with the quality of food consumed, appears to be strongly affected by the reproductive cycle and its energy demands. Anchovy in the study area reproduces from April to September (i.e. during spring and summer; Tsianis, 2003), sardine from October to April (i.e. during autumn and winter; Ganias *et al*., 2007), whereas round sardinella from May to July (i.e. during late spring and summer; Tsikliras & Antonopoulou, 2006). Additionally, anchovy (Ganias, 2003) and round sardinella (Tsikliras *et al*., 2005b) use high energy food and increase their feeding intensity during the reproductive period. Conversely, sardine tends to feed on food with a higher energy content (such as fish larvae) before its reproduction and stores this energy, as mesenteric fat, to be used later at the time of reproduction (Ganias, 2003). In accordance with our results, such differences are found because: (a) when anchovy and round sardinella display the highest VC values, sardine showed the lowest ones and vice versa; and (b) all species exhibited their highest τ values in summer (i.e. during spawning season for anchovy and round sardinella, and just before spawning for sardine), when their diet included large quantities of fish eggs (in the case of round sardinella) and fish larvae (in the case of anchovy and sardine).

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References

Ananiades, K., 1952. Quelques considérations biométriques sur l'allache (*Sardinella aurita* C. V.) des eaux grecques. *Praktika Hellenic Hydrobiological Institute*, 5, 5-45.

Bacha, M., Amara, R., 2009. Spatial, temporal and ontogenetic variation in diet of anchovy (*Engraulis encrasicolus*) on the Algerian coast (SW Mediterranean). *Estuarine, Coastal and Shelf Science*, 85, 257-264.

Bacha, M., Moali, A., Benmansour, N.-E., Brylinski, J.-M., Mahé, K. *et al.,* 2010. Relationships between age, growth, diet and environmental parameters for anchovy (*Engraulis encrasicolus* L.) in the Bay of Bénisaf (SW Mediterranean, west Algerian coast). *Cybium*, 34, 47-57.

Bellido, J.M., Pierce, G.J., Romero, J.L., Millán, M., 2000. Use of frequency analysis methods to estimate growth of anchovy (*Engraulis encrasicolus* L. 1758) in the Gulf of Cádiz (SW Spain). *Fisheries Research*, 48, 107-115.

Borme, D., Tirelli, V., Brandt, S.B., Fonda Umani, S., Arneri, E., 2009. Diet of *Engraulis encrasicolus* in the northern Adriatic Sea (Mediterranean): ontogenetic changes and feeding selectivity. *Marine Ecology Progress Series*, 392, 193-209.

Borme, D., Tirelli, V., Palomera, I., 2013. Feeding habits of European pilchard late larvae in a nursery area in the Adriatic Sea. *Journal of Sea Research*, 78, 8-17.

Budnichenko, E.V., Firulina, A.V., Bulgakova, Yu.V., 1999. Feeding conditions of Azov anchovy *Engraulis encrasicolus maeoticus* during summer-fall 1995-1996. *Journal of Ichthyology*, 39, 248-255.

Bulgakova, Yu.V., 1993. Daily feeding dynamics of the Black Sea anchovy, *Engraulis encrasicholus*. *Journal of Ichthyology*, 33 (7), 78-88.

Bulgakova, Yu.V., 1996. Feeding in the Black Sea anchovy: diet composition, feeding behaviour, feeding periodicity and daily rations (Abstract). *Scientia Marina*, 60, 283-284.

Catalán, I.A., Folkvord, A., Palomera, I., Quílez-Badía, G., Kallianoti, F. *et al.,* 2010. Growth and feeding patterns of European anchovy (*Engraulis encrasicolus*) early life stages in the Aegean Sea (NE Mediterranean). *Estuarine, Coastal and Shelf Science*, 86, 299-312.

Clarke, K.R., Gorley R.N., 2001. *PRIMER v5: User Manual/Tutorial*. PRIMER-E, Plymouth, 91 pp.

Coll, M., Libralato S., 2012. Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. *Fish and Fisheries*, 13, 60-88.

Conway, D.V.P., Coombs, S.H., Smith, C., 1998. Feeding of anchovy *Engraulis encrasicolus* larvae in the northwestern Adriatic Sea in response to changing hydrobiological conditions. *Marine Ecology Progress Series*, 175, 35-49.

Cunha, M.E., Garrido, S., Pissarra, J., 2005. The use of stomach fullness and colour indices to assess *Sardina pilchardus* feeding. *Journal of the Marine Biological Association of the UK*, 85, 1-7.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A. *et al.,* 2000. Small pelagic in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science*, 57, 603-618.

Dulčić, J., 1997. Growth of anchovy, *Engraulis encrasicolus* (L.), larvae in the Northern Adriatic Sea. *Fisheries Research*, 31, 189-195.

Dulčić, J., 1999. The diet of larval sardine, *Sardina pilchardus* (Walbaum, 1792) in the Eastern Central Adriatic. *Annals, Series Historia Naturalis*, 9 (1), 9-14.

Elsayed, A.I.W., Guelorget, O., Frisoni, G.-F., Rouchy, J.-M., Maurin, A. *et al.,* 1985. Hydrochemical, biological and sedimentological expressions of confinement in Jemsah Lagoon (Gulf of Suez, Egypt). *Oceanologia Acta*, 8 (3), 303-320.

Espinoza, P., Bertrand, A., van der Lingen, C.D., Garrido, S., Rojas de Mendiola, B., 2009. Diet of sardine (*Sardinops sagax*) in the northern Humboldt Current system and comparison with the diets of clupeoids in this and other eastern boundary upwelling systems. *Progress in Oceanography*, 83, 242-250.

Field, J.C., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*, 8, 37-52.

Froese, R., Pauly, D., 2012. *FishBase*. http://www.fishbase.org. (Accessed 31 May 2012).

Ganias, K., 2003. *Oceanographic and Biological Study of Sardine Egg Production, Sardina pilchardus (Walbaum, 1792) in Coastal Waters of Central Greece*. PhD thesis, University of Thessaly, Volos, Greece, 112 pp.

Ganias, K., Somarakis, S., Machias, A., Theodorou, A.J., 2003. Evaluation of spawning frequency in a Mediterranean sardine population (*Sardina pilchardus sardina*). *Marine Biology*, 142, 1169-1179.

Ganias, K., Somarakis, S., Koutsikopoulos, C., Machias, A., 2007. Factors affecting the spawning period of sardine in two highly oligotrophic seas. *Marine Biology*, 151, 1559-1569.

Garrido, S., Marçalo, A., Zwolinski, J., van der Lingen, C., 2007. Laboratory investigations on the effect of prey size and concentration on the feeding behaviour of *Sardina pilchardus*. *Marine Ecology Progress Series*, 330, 189-199.

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

Kapoor, B.G., Smit, H., Verighina, I.A., 1975. The alimentary canal and digestion in teleosts. *Advances in Marine Biology*, 13, 109-239.

Karachle, P.K., Stergiou K.I., 2008. The effect of season and sex on trophic levels of marine fishes. *Journal of Fish Biology*, 72, 1463-1487.

Karachle, P.K., Stergiou K.I., 2010a. Gut length for several marine fishes: relationships with body length and trophic implications. *Marine Biodiversity Records*, 3:e106.

Karachle, P.K., Stergiou K.I., 2010b. Intestine morphometrics: a compilation and analysis of bibliographic data. *Acta Ichthyologica et Piscatoria*, 40(1): 45-54.

Karachle, P.K., Stergiou K.I., 2011. Mouth allometry and feeding habits in fishes. *Acta Ichthyologica et Piscatoria*, 41 (4), 255-275.

Karachle, P.K., Stergiou K.I., 2012. *Morphometrics and allometry in fishes*. p. 65-86. In: *Morphometrics.* Wahl, C (Ed.). In Tech. Available from: http://www.intechopen.com/articles/show/title/morphometrics-and-allometry-in-fishes. ISBN: 978-953-51-0172-7

Keast, A., Webb, D., 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *Journal of the Fisheries Research Board of Canada*, 23(12), 1845-1874.

Kramer, D.L., Bryant, M.J., 1995a. Intestine length in the fishes of a tropical stream: 1. Ontogenetic allometry. *Environmental Biology of Fishes*, 42, 115-127.

Kramer, D.L., Bryant, M.J., 1995b. Intestine length in the fishes of a tropical stream: 2. Relationships to diet – the long and short of a convoluted issue. *Environmental Biology of Fishes*, 42, 129-141.

Lomiri, S., Scacco, U., Mostarda, E., Andaloro, F., 2008. Size-related and temporal variation in the diet of the round sardinella, *Sardinella aurita* (Valenciennes, 1847), in the central Mediterranean Sea. *Journal of Applied Ichthyology*, 24, 539-545.

Madkour, F.F., 2012. Feeding ecology of the round sardinella, *Sardinella aurita* (Family: Clupeidae) in the Egyptian Mediterranean waters. *International Journal of Environmental Science and Engineering*, 2, 83-92.

Mikhman, A.S., Tomanovich, L.V., 1977. The feeding of the Azov anchovy, *Engraulis encrasicholus maeoticus*. *Journal of Ichthyology*, 17, 240-244.

Mittelstaedt, E., 1983. The upwelling area off Northwest Africa – a description of phenomena related to coastal upwelling. *Progress in Oceanography*, 2 (12), 307-331.

Moreno, T., Castro, J.J., 1995. Community structure of the juvenile of coastal pelagic fish species in the Canary Islands waters. *Scientia Marina*, 59, 405-413.

Morote, E., Olivar, M.P., Villate, F., Uriarte, I., 2008. Diet of round sardinella, *Sardinella aurita*, larvae in relation to plankton availability in the NW Mediterranean. *ICES Journal of Plankton Research*, 30 (7), 807-816.

Morote, E., Olivar, M.P., Villate, F., Uriarte, I., 2010. A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the Northwest Mediterranean: influence of prey availability and ontogeny. *ICES Journal of Marine Science*, 67, 897-908.

Munuera Fernández, I., González-Quirós, R., 2006. Analysis of feeding of *Sardina pilchardus* (Walbaum, 1792) larval stages in the central Cantabrian Sea. *Scientia Marina*, 70, 131-139.

Nieland, H., 1982. The food of *Sardinella aurita* (Val.) and *Sardinella eba* (Val.) of the coast of Senegal. *Rapports et procès-verbaux des Reunions Conseil International pour l'exploration de la Mer*, 180, 369-373.

Nikolioudakis, N., Isari, S., Pitta, P., Somarakis, S., 2012. Diet of sardine *Sardina pilchardus*: an 'end-to-end' field study. *Marine Ecology Progress Series*, 453, 173-188.

Nikolioudakis, N., Palomera, I., Machias, A., Somarakis, S., 2011. Diel feeding intensity and daily ration of the sardine *Sardina pilchardus*. *Marine Ecology Progress Series*, 437, 215-228.

Palomares, M.L., Pauly, D., 1989. A multiple regression model for predicting the food consumption of marine fish populations. *Australian Journal of Marine and Freshwater Research*, 40, 259-273.

Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M. *et al.,* 2007. Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Progress in Oceanography*, 74, 377-396.

Pauly, D., Froese, R., Sa-a, P., Palomares, M.L., Christensen, V. *et al.,* 2000. *Trophlab manual*. ICLARM, Manila, 3 pp.

Petrakis, G., Stergiou, K.I., Christou, E., Politou, C.-Y., Karkani, M. *et al.,* 1993. *Small Scale Fishery in the South Euboikos Gulf.* Final Report, Contract No XIV- 1/MED-91/007. National Centre for Marine Research, Athens, Greece.

Pham-Thuoc, Szypuła, J., 1973. Biological characteristics of gilt sardine *Sardinella aurita* Cuv. et Val. 1847 from northwest African Coast. *Acta Ichthyologica et Piscatoria*, 3 (1), 19-37.

Plounevez, S., Champalbert, G., 1999. Feeding behaviour and trophic environment of *Engraulis encrasicolus* (L.) in the Bay of Biscay. *Estuarine, Coastal and Shelf Science*, 49, 177-191.

Plounevez, S., Champalbert, G., 2000. Diet, feeding behaviour and trophic activity of the anchovy (*Engraulis encrasicolus* L.) in the Gulf of Lions (Mediterranean Sea). *Oceanologia Acta*, 23, 175-192.

Preciado, I., Velasco, F., Olaso, I., 2008. The role of pelagic fish as forage for the demersal fish community in the southern Bay of Biscay. *Journal of Marine Systems*, 72, 407-417.

Sabatés, A., Martín, P., Lloret, J., Raya, V., 2006. Sea warming and fish distribution: the case of the small pelagic fish *Sardinella aurita*, in the western Mediterranean. *Global Change Biology*, 12, 2209-2219.

Schaber, M., Petereit, C., Paulsen, M., 2010. Diet composition and feeding of European anchovy *Engraulis encrasicolus* in Kiel Bight, western Baltic Sea. *Journal of Fish Biology*, 76, 1856-1862.

Sever, T.M., Bayhan, B., Taskavak, E., 2005. A preliminary study on the feeding regime of European pilchard (*Sardina pilchardus* Walbaum1792) in Izmir Bay, Turkey, Eastern Aegean Sea. *NAGA*, 28 (3 & 4), 41-48.

Sirotenko, M.D., Danilevskiy, N.N., 1977. Quantitative indices of the feeding of the Black Sea anchovy, *Engraulis encrasicholus ponticus*. *Journal of Ichthyology*, 17, 610-617.

Stergiou, K.I., Karpouzi, V.S., 2002. Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries*, 11, 217-254.

Stergiou, K.I., Christou, E.D., Georgopoulos, D., Zenetos, A., Souvermezoglou, C., 1997. The Hellenic Seas: Physics, Chemistry, Biology and Fisheries. *Oceanography and Marine Biology: an Annual Review*, 35, 415-538.

Stergiou, K.I., Karachle, P.K., Tsikliras, A.C., Mamalakis, E., 2011. *Shouting fishes: fishes from the Greek Seas – Biology, Fisheries and Management*. Patakis Publications, Athens, Greece, 358 pp.

Tsianis, D.E., 2003. *Temporal Variation of Biological Parameters of Anchovy and Sardine in NW Aegean*. MSc thesis, Aristotle University of Thessaloniki, Thessaloniki, Greece, 117 pp.

Tsikliras, A.C., 2008. Climate-related geographic shift and sudden population increase of a small pelagic fish (*Sardinella aurita*) in the eastern Mediterranean Sea. *Marine Biological Research*, 4 (6), 477-481.

Tsikliras, A.C., Antonopoulou, E., 2006. Reproductive biology of round sardinella (*Sardinella aurita*) in the north-eastern Mediterranean. *Scientia Marina*, 70 (2), 281-290.

Tsikliras, A.C., Koutrakis, E.T., Stergiou, K.I., 2005a. Age and growth of round sardinella (*Sardinella aurita*) in the northeastern Mediterranean. *Scientia Marina*, 69 (2), 231-240.

Tsikliras, A.C., Torre, M., Stergiou, K.I., 2005b. Feeding habits and trophic level of round sardinella (*Sardinella aurita*) in the northeastern Mediterranean (Aegean Sea, Greece). *Journal of Biological Research*, 3, 67-75.

Tudela, S., Palomera, I., 1995. Diel feeding intensity and daily ration in the anchovy *Engraulis encrasicolus* in the northwest Mediterranean Sea during the spawning period. *Marine Ecology Progress Series*, 129, 55-61.

Tudela, S., Palomera, I., 1997. Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea (northwest Mediterranean). *Marine Ecology Progress Series*, 160, 121-134.

Tudela, S., Palomera, I., Quílez, G., 2002. Feeding of anchovy *Engraulis encrasicolus* larvae in the northwest Mediterranean. *Journal of the Marine Biological Association of the UK*, 82, 349-350.

Van der Lingen, C.D., Bertrand, A., Bode, A., Brodeur, R., Cubillos, L.A. *et al.,* 2009. Trophic dynamics. p. 112-157. In: *Climate change and small pelagic fish*. Checkley, D., Alheit, J., Oozeki, Y., Roy, C. (Eds). Cambridge University Press, Cambridge.

Varela, M., Larrañaga, A., Costas, E., Rodríguez, B., 1988. Contenido estomacal de la sardina (*Sardina pilchardus* Walbaum) durante la campaña Saracus 871 en la plataformas Cantábrica y de Galicia en febrero de 1987. *Boletin Instituto Espanol de Oceanografia*, 5, 17-28.

Videler, J.J., 1993. *Fish swimming*. Fish and Fisheries Series 10. Chapman & Hall, London, 260 pp.

Voss, R., Dickmann, M., Schmidt, J.O., 2009. Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the German Bight, North Sea. *Oceanologia*, 51, 117-138.

Yunev, O.A., Moncheva, S., Carstensen, J., 2005. Long-term variability of vertical chlorophyll a and nitrate profiles in the open Black Sea: eutrophication and climate change. *Marine Ecology Progress Series*, 294, 95-107.

Zar, J.H., 1999. *Biostatistical analysis*. 4th Edition. Prentice Hall, New Jersey, 663 pp.