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ICHTHYOPLANKTON SPATIAL DISTRIBUTION AND SPECIES RICHNESS OF THERMAIKOS AND CHALKIDIKI GULFS (NORTH AEGEAN SEA) DURING SUMMER

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SPATIAL DISTRIBUTION
SPECIES RICHNESS
ICHTHYOPLANKTON
AEGEAN SEA
FISH LARVAE
THERMAIKOS
CHALKIDIKI

ABSTRACT. – The spatial distribution and species richness of ichthyoplankton have been investigated using samples from two commercially important fishing areas of the North Aegean Sea (Thermaikos and Chalkidiki Gulfs, East Mediterranean Sea) in June 2004, 2005 and 2006. A total of 62 taxa were identified in this study something which is in agreement with other relevant studies of a wider spatial scale in the East and West Mediterranean Sea. The horizontal distribution of fish larvae was spatially segregated. Epipelagic, mesopelagic and demersal taxa occupied different geographical areas. Species richness and larvae abundance were significantly positively correlated with depth. Three ecological indicators, total taxa abundance, species richness and Shannon-Wiener diversity, were used to measure the diversity of the two areas. The relationship between environment and ichthyoplankton was tested with permutational multivariate analysis of variance using seven environmental factors as predictors. Topography and the physicochemical factors salinity and depth-integrated chlorophyll-a constitute the main factors affecting species richness of our study area. Analysis of similarities showed significant differences between the biocommunities in the span of the three years. The Chalkidiki area showed higher species richness and Shannon-Wiener diversity than the Thermaikos area, something, which is probably due to the different characteristics of water masses and also due to the variety of benthic habitats that Chalkidiki offers. Notably, in the Thermaikos Gulf, European anchovy and Round sardinella exhibited a strong domination pattern while mesopelagic larvae abundance and occurrence was higher at the deeper Chalkidiki area. Physicochemical parameters affected biodiversity by creating favorable conditions for adult spawning.

INTRODUCTION

Ichthyoplankton studies are important in fisheries biology. They contribute to a better knowledge of an area's ichthyofauna biodiversity (Siapatis *et al*. 2000). An ichthyoplankton sample can contain the early life stages of a wide spectrum of fish taxa whose adults may belong to different ecological niches. Biodiversity metrics provide insight on the status of an assemblage or community at a point in time (Marshall *et al*. 2019). In fisheries science, ichthyoplankton has been used as an index of ecological quality reflecting environmental impacts and for stock management (Edwards *et al*. 2010).

Horizontal distribution of early development stages of fish larvae can reflect the spawning bathymetry of adults (Somarakis *et al*. 2002) as they adapt to the pelagic environment. Furthermore, the variability of physical processes such as changes in temperature and salinity, fronts and currents and biological processes affect the distribution and survival of fish larvae (Olivar *et al*. 2010). Horizontal distribution studies have shown that inshore larval assemblages have a different composition to offshore ones (Sabatés 1990a). Diversity of adult fish habitats, bathymetry, primary production, stratification of the water column and currents interact with each other and in combination with other factors form the final distribution patterns of fish larvae (Sabatés *et al*. 2007). Fish larvae spatial distribution patterns show differences between species (Hernández-Miranda *et al*. 2003). These patterns may be due to biological or physical mechanisms and this in itself constitutes a subject of research (Hernández-Miranda *et al*. 2003).

The relation of biodiversity to habitat complexity is a crucial subject in ecology (Gratwicke & Speight 2005). Furthermore knowledge of underlying mechanisms behind biodiversity spatial distribution is important in predicting the effects of anthropogenic activities on the marine environment (Navarro *et al*. 2015). Relatively high species richness and larval fish abundances have been recorded in the past near areas that mesoscale oceanographic features that enhance biological productivity (Rodríguez *et al*. 2013). The niche differentiation concept suggests that a more heterogeneous environment could support more species through partitioned niche space (Yang *et al*. 2015). However, the mechanisms leading to the increase in β-diversity with increasing productivity remain largely unknown; most studies to date have been correlational (Chase 2010). Topography and environmental variables affect ichthyoplankton diversity patterns (Sabatés & Olivar 1996, Giannoulaki *et al*. 2013). The factors that cause variation in β-diversity represent one of the most important, but poorly understood, influences on global variation in biodiversity (Chase 2010).

Most fish species are spawn during spring and summer in the Mediterranean Sea (Sabatés 2004, Siapatis & Somarakis 2007, Somarakis *et al*. 2011a) and thus this period is suitable for studying the distribution and biodiversity patterns (Sabatés *et al*. 2007). While the north Aegean Sea (Eastern Mediterranean) has been studied before as far as ichthyoplankton assemblages or fisheries are concerned, studies on biodiversity are scarce. This is the first study focusing on ichthyoplankton distribution and species richness of the Thermaikos and Chalkidiki Gulfs and the first study of ichthyoplankton diversity in the northern Aegean Sea. The aim of our study was: (1) to identify possible existing patterns regarding the distribution of larvae, (2) to spatially locate the richer marine areas in terms of biodiversity, using the most common ecological indicators, and (3) to interpret any existing biodiversity patterns using physical and biological data.

Study area

The Thermaikos and Chalkidiki Gulfs are located in the north Aegean Sea (East Mediterranean Sea) (Fig. 1). Thermaikos is a shallow and wide gulf with a deeper outer part (the average depth is 50 m). Chalkidiki consists of Toronaios and Sygkitikos Gulfs with a narrow shelf with steep slopes and great depths (the average depth is > 200 m). Five rivers enrich the western part of the Thermaikos Gulf with low salinity waters and nutrients forming a complex estuary. Estuaries are productive ecosystems, providing a diverse range of habitats and supporting fish biodiversity (Tsikliras *et al*. 2009). They serve as reproduction fields and shelters for juveniles or adults (Gillanders & Kingsford 2002).

In the Chalkidiki Gulfs, an influx of freshwater from the east results in low-salinity surface waters extending across the Northern Aegean during summer, as a result of flows from the Dardanelles Strait (Hyder *et al*. 2002). These low salinity surface water masses move to the north along the coast and exit Chalkidiki Gulfs at their southwestern part (Fig. 2). Strong north winds affect the movement of this water. A strong but time-dependent anticyclone is centered on the mouth of Singitikos Bay (Olson *et al*. 2007). Thermaikos and Chalkidiki are usually treated as a single fishing area by Greek Authorities. It is the second most productive fishing area in Greece (after the Thracian Sea) and it is mainly fished by purse seiners and trawlers (Hellenic Statistical Authority, 2016 Press Release).

MATERIALS AND METHODS

Ichthyoplankton samples were collected during three surveys conducted in 15-20 June of 2004, 13-21 June of 2005 and 6-16 June of 2006 by the R/V "Philia" of Hellenic Center of Marine Research. A grid of 13 stations was sampled (Fig. 1). The distance between stations was 10 nautical miles. A 60 cm bongo with 250 and 500 μm mesh nets was used as proposed by Smith & Richardson (1977). Tows were diagonal from surface to bottom or to maximal depth of 200 m while the velocity of the vessel was 2-2.5 kn. Samples were preserved in 4 % formaldehyde and boric acid solution. A CTD Seabird Electronics 25 was used to obtain temperature, salinity and chlorophyll-a profile data (with 1 m vertical resolution) from surface to bottom or to maximal depth of 200 m at a denser grid of 46 stations (Fig. 1).

We analyzed samples from the 250 μm net at the laboratory. Larvae were sorted and identified to the lowest possible taxonomic level using the ichthyoplankton database (Siapatis & Chilari 2003). Eschmeyer's Catalog of Fishes (Fricke *et al*. 2020) was used for the scientific names of taxa as it is more complete and is updated recently as far as nomenclature data (Updated in

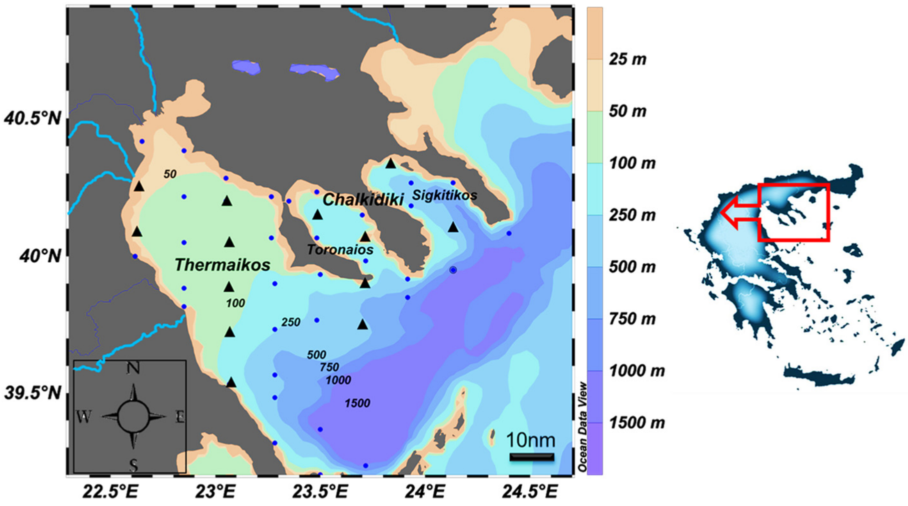

Fig. 1. – Bathymetric map of the study area. Ichthyoplankton stations are marked with black triangles and CTD stations with blue dots.

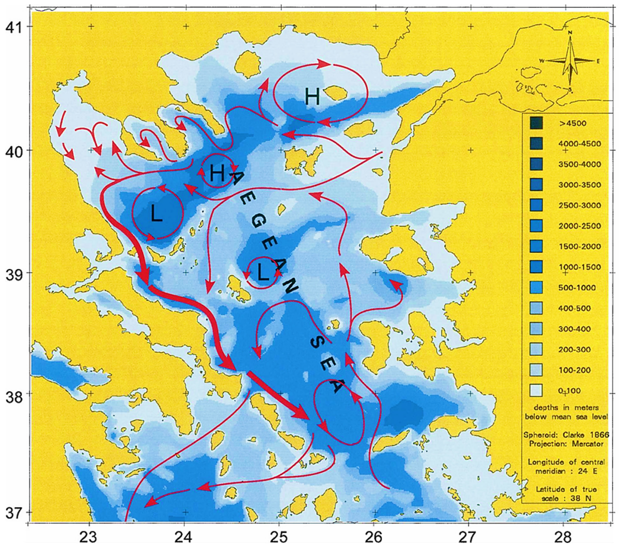

Fig. 2. – A schematic of the general circulation of the Aegean Sea. Figure copied and modified from Olson *et al*. (2007). © American Meteorological Society. Used with permission.

3 August 2020). For data comparability purposes, tow depth was used to transform larvae counts to abundance per 10 m^2.

PRIMER-e v6 software (Clarke & Gorley 2005) was used to calculate the following ecological indicators: number of taxa (species richness, S), individuals number (N) and Shannon-Wiener biodiversity index ($H' = -\sum_{i=1}^{R} p^i \ln p^i$) (logarithm base e) for each year and each area. Different indices measure different aspects of the partition of abundance between species (Hill 1973). We used the combination of these indicators to describe biodiversity patterns of our study area as they represent different diversity orders (Jost 2006). Species richness is more sensitive to rare species while Shannon index weighs all species by their frequency (Jost 2006). For the estimation of individuals' number and Shannon-Wiener index we used the maximum available information from larvae taxonomy. Ecological indicators were calculated without taking into consideration rare taxa (we considered as rare all taxa that appeared at only one station during each sampling period). Their presence can be considered random and may affect ecological indicators presented in this study.

The relationship between environment and ichthyoplankton diversity was studied with Permutational multivariate analysis of variance (PERMANOVA), to test the effect of environmental factors on the most representative of the ecological indicators (Anderson 2001). A distance matrix was computed from the raw dataset using sums of squared Euclidean distances according to the formula: $SS_w = \sum_{i=1}^{a} \sum_{j=1}^{n} \sum_{k=1}^{p} \{y_{ijk} - \text{mean}(y_{i.k})^2\}$. A pseudo F-ratio was calculated to test the multivariate hypothesis with the formula: $F = [SS_a / (a-1)] / [SS_w / (N-a)]$. A P-value was calculated with the formula: $P = \textit{number of } F_\Pi \geq F \,/\, \textit{total number of } F_\Pi$, according to Anderson 2001.

Three indicators (Species richness, larval abundance and Shannon diversity index) were used as measures of diversity to compare areas (Chalkidiki, Thermaikos), years (2004, 2005 and 2006), proximity to coast (close 0-3 km, medium 3-10 km and far > 10 km), oceanic zones (neritic/oceanic), temperature (low < 20.78 °C, high > 20.78 °C), salinity (low < 35.53, high > 35.53) and depth-integrated chlorophyll-a (low < 3.74 $mg.m^{-3}$, high > 3.74 $mg.m^{-3}$). Median of the three years was the boundary used to categorize temperature, salinity and depth integrated Chl-a in two categories in order to perform PERMANOVA: high and low. Sampling stations were categorized in two distinctive areas those of Thermaikos and Chalkidiki. Two of the stations were located at the boundary of the two areas (Fig. 1). We finally categorized them at Chalkidiki area due to their great depth, which was a common feature of all Chalkidiki stations. Fluorescence data integrated over the depth of the euphotic layer were used to calculate depth-integrated chlorophyll-a ($DIchla = \int_0^{eu} [chla] z dz$) (Morel & Berthon 1989). The neritic zone was considered as the shallow part of the study area from zero to 200m depth and the oceanic zone as the deeper part from 200m to the bottom. Larval abundance data were log-transformed to reduce the importance of the most dominant taxa.

The method of backward elimination of variables was used for the PERMANOVA (Zar 2010). Because the number of observations was restricted (13 stations × three years), the number of factors we could use for the PERMANOVA was limited. For this reason, we tested two factors at a time with the hypothesis H_0 that there are no differences between them (i.e., temperature and salinity, salinity and chlorophyll-a, etc.). At first, the physicochemical factors (chlorophyll-a, salinity, temperature) were tested in pairs and with their interaction as a new factor. The topographic factors (area, proximity to coast, oceanic zones) were tested with the same procedure. If the interaction between the two factors was found to be significant, a new PERMANOVA was run with the interaction included in the model (Zar 2010). All possible combinations of factors were tested and those factors presenting weak effects on the dependent variables were eliminated from the model. Finally, we tested the interaction between topography and physicochemical factors. This procedure was repeated until we concluded to the most important environmental factors that could interpret best the ecological indicators. PAST v3.25 software was used to carry out PERMANOVA (Hammer *et al*. 2001).

Analysis of similarities (ANOSIM) was used to test the hypothesis H_0 that the similarities between areas and years are equal. A ranked dissimilarity matrix from the biological data for each year and a test statistic R were computed for this purpose according to Clarke (1993).

We investigated the impact of depth on the ecological indicators and on abundance. A simple regression model was used relating the total abundance from each category (epipelagics, demersal and mesopelagics) with depth. We used the square-root transformation for all the dependent variables which showed heteroscedasticity, especially for species richness, as their variances were proportional to the means (Zar 2010). For the calculation of epipelagic, demersal and mesopelagic abundance, we used only the most dominant taxa (as they represented the majority of larvae abundance) and for depth descriptor, we used the tow depth. Taxa were categorized in groups based on adults' habitat according to Somarakis *et al*. (2011b). Groups consisted of the most common taxa: epipelagic, demersal and mesopelagic.

Abundance and environmental data were used to construct maps with the aid of SURFER 8® software (Golden Software 2002) and Ocean Data View 5.2.0 software (Schlitzer 2016). The krigging method (Krige 1951) was used to avoid overlapping and enhance low values. Maps of the three ecological indicators were constructed in order to get a more precise spatial view of subareas that persistently presented high diversity.

RESULTS

In total 62 taxa were identified, belonging to 40 families, while 32 taxa occurred in all the three sampling periods (Table I). The majority of larvae were identified at species level (52 species, 5 genera, 5 families). The sampling recorded 45 taxa belonging to 31 families in 2004, 42 taxa belonging to 31 families in 2005 and 49 taxa belonging to 34 families in 2006. Five unique species found in 2004 (*Uranoscopus scaber*, *Pagrus pagrus*, *Mullus barbatus*, *Parablennius gattorugine* and *Vinciguerria attenuata*) were not present in 2005. Seven unique species found in 2006 (*Lepadogaster candollei*, *Callanthias ruber*, *Buglossidium luteum*, *Parophidion vassali*, *Uranoscopus scaber*, *Pagrus pagrus* and *Lepidopus caudatus*) were not present in 2005. From the total number of taxa identified in all the three years, 26 are commercially important in Greece (e.g., *Engraulis encrasicolus*, *Sardinella aurita*, *Trachurus mediterranaeus*, etc.).

In 2004, the samples were dominated by larvae of epipelagic taxa followed by larvae of mesopelagic and demersal taxa. *Engraulis encrasicolus* (28.9 %), *S. aurita* (24.3 %) and *Ceratoscopelus maderensis* (14.6 %) were the most abundant larvae and only 0.36 % remained unidentified. In 2005, a change in taxa composition was observed. Mesopelagic taxa dominated and epipelagic and demersal taxa followed. *Ceratoscopelus maderensis* (25.08 %) and *Hygophum benoiti* (15.96 %) were the most abundant larvae and *E. encrasicolus* (13.51 %) and *S. aurita* (11.64 %) followed. A small percentage remained unidentified (3.38 %). In 2006 larvae of epipelagic taxa dominated and larvae of mesopelagic and demersal taxa followed. *Engraulis encrasicolus* (54.28 %), *S. aurita* (16.91 %) and *C. maderensis* (4.18 %) were the most abundant larvae.

Total larvae abundance of Thermaikos was noticeably higher in 2004 and 2006 mainly due to the strong presence of two epipelagic taxa (*E. encrasicolus* and *S. aurita*) (Fig. 3, Table I). Lower abundances were recorded in Thermaikos in 2005 and this can be attributed to the lower presence of the epipelagics *E.encrasicolus* and *S. aurita*. Among taxa groups, epipelagics followed a different pattern to demersal and mesopelagic taxa as regarding abundance (Fig. 3). More specifically, epipelagic taxa were less abundant in 2005, while demersal and mesopelagic taxa were recorded at lower abundances in 2005 and at even lower abundances in 2006. As far as their horizontal distribution is concerned, epipelagics were mainly dominant in the west Thermaikos Gulf (Fig. 4A), mesopelagics in the deep Chalkidiki (Fig. 4B) and demersal taxa in the shallows stations of the east Thermaikos Gulf (Fig. 4C).

Environmental data showed differences over the three year's period. Average surface salinity (20 m) was lower in 2004 and average surface temperature (20 m) was lower in 2006 (Fig. 5). Lower sea surface temperatures were recorded in 2006 across the Thermaikos and Chalkidiki Gulfs (Fig. 6C). Horizontal distribution of sea surface salinity showed lower values mainly in 2004 in the west Thermaikos Gulf near the estuaries (Fig. 6D) and in 2006 in the east Chalkidiki area (Fig. 6F). Surface chlorophyll-a showed higher values in 2004 and 2006 mainly in the west Thermaikos Gulf, close to the river estuaries (Fig. 6G-I).

The two areas showed different characteristics in the three ecological indicators (Table II). More specifically,

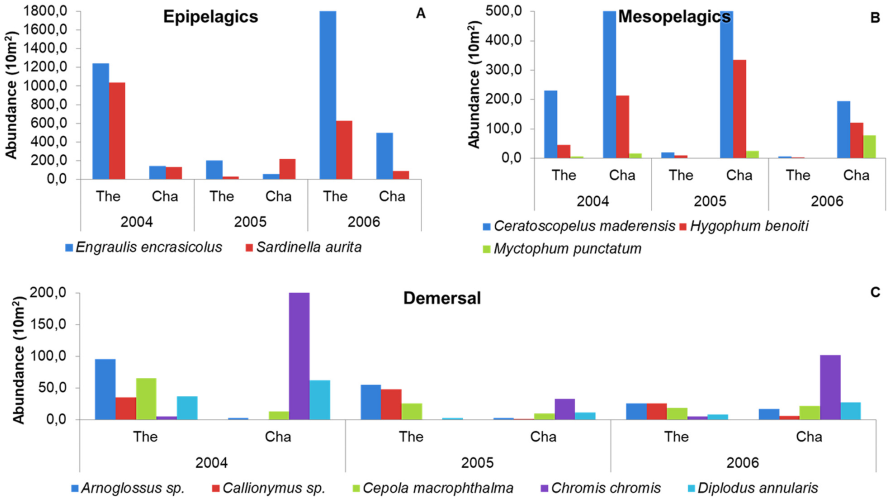

Fig. 3. – Abundances of the most dominant taxa between the three years.

Table I. – Larvae taxonomy with average abundance values (number of individuals per 10 m^2) and occurrence (%) calculated for the total number of stations of each area. [Epipelagic = E, Mesopelagic = M, Benthopelagic = B].

				Abundance						Occurrence %						
				2004		2005		2006		2004		2005		2006		
Order	Family	Taxon	Author	The	Cha	The	Cha	The	Cha	The	Cha	The	Cha	The	Cha	Habitat
Anguilliformes	Nettastomatidae	*Facciolella oxyrhynchus*	Bellotti, 1883						1.0						16.7	B
Argentiniformes	Argentinidae	*Argentina sphyraena*	Linnaeus, 1758		14.4		2.8		5.4		33.3		33.3		50.0	B
Aulopiformes	Paralepididae	*Lestidiops jayakari*	Boulenger, 1889	0.7	12.8		9.3		8.9	14.3	50.0		66.7		66.7	M
Aulopiformes	Paralepididae	*Lestidiops sphyrenoides*	Risso, 1820		0.7						16.7					M
Aulopiformes	Paralepididae	*Arctozenus risso*	Bonaparte, 1840				6.9						16.7			M
Beloniformes	Belonidae	*Belone belone*	Linnaeus, 1761			2.3						14.3				E
Clupeiformes	Clupeidae	*Sardinella aurita*	Valenciennes, 1847	1035.8	133.0	29.4	218.3	627.2	85.9	100.0	100.0	42.9	50.0	100.0	100.0	E
Clupeiformes	Engraulidae	*Engraulis encrasicolus*	Linnaeus, 1758	1244.6	142.6	202.4	57.2	1824.6	496.0	100.0	100.0	100.0	83.3	100.0	100.0	E
Gadiformes	Gadidae	*Micromesistius poutassou*	Risso, 1827					0.8						14.3		B
Gadiformes	Macrouridae		Bonaparte, 1831		1.0						16.7					B
Gadiformes	Merlucciidae	*Merluccius merluccius*	Linnaeus, 1758						1.2						16.7	B
Gobiesociformes	Gobiesocidae	*Lepadogaster candollei*	Risso, 1810					4.1						28.6		B
Myctophiformes	Myctophidae	*Benthosema glaciale*	Reinhardt, 1837	0.7					9.9	14.3					33.3	M
Myctophiformes	Myctophidae	*Ceratoscopelus maderensis*	Lowe, 1839	230.7	535.1	19.4	521.5	5.8	195.3	100.0	83.3	71.4	100.0	14.3	100.0	M
Myctophiformes	Myctophidae	*Diaphus holti*	Tåning, 1918	6.3	0.7	1.3	7.3	3.1	2.2	14.3	16.7	14.3	16.7	14.3	33.3	M
Myctophiformes	Myctophidae	*Diaphus rafinesquei*	Cocco, 1838		4.2						16.7					M
Myctophiformes	Myctophidae	*Hygophum benoiti*	Cocco, 1838	45.5	214.0	9.7	335.1	2.3	121.9	71.4	83.3	42.9	83.3	28.6	83.3	M
Myctophiformes	Myctophidae	*Lampanyctus crocodilus*	Risso, 1810	1.0	4.7		5.6		2.2	14.3	50.0		33.3		33.3	M
Myctophiformes	Myctophidae	*Lampanyctus pusillus*	Johnson, 1890			1.1						14.3				M
Myctophiformes	Myctophidae	*Lobianchia dofleini*	Zugmayer, 1911	1.5	8.4	1.1	4.7		8.7	14.3	66.7	14.3	33.3		66.7	M
Myctophiformes	Myctophidae	*Myctophum punctatum*	Rafinesque, 1810	5.7	17.3	1.8	25.9	0.8	77.7	28.6	66.7	14.3	83.3	14.3	83.3	M
Ophidiiformes	Ophidiidae	*Parophidion vassali*	Risso, 1810	0.5		0.6		1.0	1.0	14.3		14.3		14.3	16.7	B
Perciformes	Apogonidae	*Apogon imberbis*	*Linnaeus, 1758*		0.7		2.1		2.0		16.7		33.3		33.3	B
Perciformes	Blenniidae	*Parablennius gattorugine*	Linnaeus, 1758	3.0	2.7		0.9			42.9	50.0		16.7			B
Perciformes	Callanthiidae	*Callanthias ruber*	Rafinesque, 1810		2.1				4.0		16.7				50.0	B
Perciformes	Callionymidae	*Callionymus* sp.	Linnaeus, 1758	35.5	1.0	47.9	1.7	26.4	6.0	100.0	16.7	85.7	16.7	85.7	66.7	B
Perciformes	Caproidae	*Capros aper*	Linnaeus, 1758			1.3						14.3				B
Perciformes	Carangidae	*Trachurus mediterraneus*	Steindachner, 1868	109.8	4.3	9.6	5.4	18.9	10.0	100.0	50.0	57.1	33.3	71.4	50.0	E
Perciformes	Cepolidae	*Cepola macrophthalma*	Linnaeus, 1758	65.8	13.0	26.0	10.0	18.9	22.3	100.0	100.0	100.0	50.0	71.4	66.7	B
Perciformes	Gobiidae		Cuvier, 1816	217.9	45.1	65.8	42.3	52.7	45.2	100.0	100.0	100.0	83.3	100.0	83.3	B
Perciformes	Labridae	*Coris julis*	Linnaeus, 1758	15.3	21.4	5.1	39.0	4.0	17.7	71.4	83.3	42.9	100.0	14.3	100.0	B
Perciformes	Labridae	*Symphodus* sp.	Rafinesque, 1810	8.4	19.9	1.9	10.3	3.0	14.0	57.1	83.3	28.6	33.3	14.3	83.3	B
Perciformes	Mugilidae		Jarocki, 1822			13.3		14.8				28.6		71.4		B
Perciformes	Mullidae	*Mullus barbatus*	Linnaeus, 1758		3.3		2.4	10.7	8.1		50.0		16.7	28.6	66.7	B
Perciformes	Pomacentridae	*Chromis chromis*	Linnaeus, 1758	5.7	216.7		33.1	5.0	101.9	42.9	100.0		50.0	14.3	100.0	B
Perciformes	Scombridae	*Scomber colias*	Gmelin, 1789	40.1	0.6	3.5	5.5	82.5	1.8	71.4	16.7	42.9	33.3	85.7	16.7	E
Perciformes	Serranidae	*Epinephelus* sp.	Bloch, 1793						0.9						16.7	B
Perciformes	Serranidae	*Serranus cabrilla*	Linnaeus, 1758	7.3	8.3	1.9	2.1		8.9	71.4	66.7	28.6	33.3		83.3	B

Table I. – Continued.

Order	Family	Taxon	Author	Abundance						Occurrence %						Habitat
				2004		2005		2006		2004		2005		2006		
				The	Cha	The	Cha	The	Cha	The	Cha	The	Cha	The	Cha	
Perciformes	Serranidae	*Serranus hepatus*	Linnaeus, 1758	114.0	15.7	55.8	4.9	35.8	25.9	100.0	50.0	71.4	33.3	85.7	100.0	B
Perciformes	Serranidae	*Anthias anthias*	*Linnaeus, 1758*						1.0						16.7	B
Perciformes	Sparidae	*Diplodus annularis*	Linnaeus, 1758	37.3	62.4	3.4	11.5	9.0	27.6	71.4	83.3	14.3	50.0	14.3	83.3	B
Perciformes	Sparidae	*Diplodus vulgaris*	Geoffroy Saint-Hilaire, 1817		1.5				1.2		16.7				16.7	B
Perciformes	Sparidae	*Pagellus acarne*	Risso, 1827						1.2						16.7	B
Perciformes	Sparidae	*Pagellus erythrinus*	Linnaeus, 1758						4.4						16.7	B
Perciformes	Sparidae	*Pagrus pagrus*	Linnaeus, 1758	2.3					7.7	42.9					50.0	B
Perciformes	Trachinidae	*Trachinus draco*	Linnaeus, 1758	0.4	1.0	0.6	4.3	0.7		14.3	16.7	14.3	33.3	14.3		B
Perciformes	Trichiuridae	*Lepidopus caudatus*	Euphrasen, 1788						1.2						16.7	B
Perciformes	Uranoscopidae	*Uranoscopus scaber*	Linnaeus, 1758	0.5			2.1			14.3						B
Perciformes	Scombridae	*Auxis rochei*	Risso, 1810	15.9	16.4	7.2	2.4	25.3	30.3	57.1	83.3	28.6	16.7	57.1	66.7	E
Pleuronectiformes	Bothidae	*Arnoglossus* sp.	Bleeker, 1862	95.6	3.0	55.1	2.9	26.1	17.3	100.0	33.3	100.0	33.3	71.4	100.0	B
Pleuronectiformes	Soleidae		Bonaparte, 1833			1.2						14.3				B
Pleuronectiformes	Cynoglossidae	*Symphurus nigrescens*	Rafinesque, 1810						1.0						16.7	B
Pleuronectiformes	Soleidae	*Buglossidium luteum*	Risso, 1810		0.7			2.8			16.7			28.6		B
Scorpaeniformes	Scorpaenidae	*Scorpaena* sp1	Linnaeus, 1758	0.8						14.3						B
Scorpaeniformes	Scorpaenidae		Linnaeus, 1758	0.4	0.8	1.5	1.2			14.3	16.7	28.6	16.7			B
Scorpaeniformes	Triglidae	*Eutrigla gurnardus*	Linnaeus, 1758			1.2						14.3				B
Scorpaeniformes	Triglidae	*Lepidotrigla cavillone*	Lacepède, 1801	1.3		1.5			0.9	28.6		28.6			16.7	B
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	Cocco, 1838	1.0	12.2				0.9	14.3	50.0		16.7		16.7	M
Stomiiformes	Gonostomatidae	*Cyclothone braueri*	Jespersen & Tåning, 1926	0.8	36.6	0.6	29.5	0.8	12.2	14.3	50.0	14.3	66.7	14.3	50.0	M
Stomiiformes	Sternoptychidae	*Maurolicus muelleri*	Gmelin, 1789	1.4	6.8		14.0		33.0	14.3	50.0		50.0		83.3	M
Stomiiformes	Stomiidae	*Stomias boa*	Risso, 1810		1.0		3.1		9.1		16.7		33.3		33.3	M
Zeiformes	Zeidae	*Zeus faber*	Linnaeus, 1758				1.2		0.9				16.7		16.7	B

species richness varied over the three year's comparison 9 and 27 taxa in Chalkidiki and between 7 and 20 taxa in Thermaikos. The species' richness of Thermaikos was significantly higher in 2004 in comparison with 2005 and 2006 (Kruskal-Wallis test, p-value 0.0036). The Shannon index was significantly higher in 2004 and 2005 in comparison to 2006 (p-value 0.0032). Abundance was significantly lower in 2005 in comparison with 2004 and 2006 (p-value 0.0016). As far as the Chalkidiki area is concerned, no significant differences were observed over the three years when we compared the three ecological indicators. Horizontal distributions of the three ecological indicators showed that higher species richness was recorded at the majority of stations of Chalkidiki, higher larval abundances were recorded mainly in Thermaikos and higher Shannon index values were recorded at oceanic stations near the limit of the shelf, although this had not been evident in 2005 (Fig. 7).

The logarithmic-X model fitted better when we tested the correlation of depth with total larvae abundance. Table III shows the relationships of the three ecological indicators and the abundance of the most dominant epipelagic, mesopelagic and demersal taxa with depth. The single regression model indicated that species richness and the Shannon index were significantly positively correlated to depth although the relationships were weak. Epipelagics and mesopelagics were also significantly correlated to depth. However demersal abundance and total abundance were negatively correlated to depth with no significant correlation.

While many factors significantly affected the ecological indicators, the combination of physicochemical and topographic factors (and especially the factors year, area and combination) significantly affected ecological indicators for all of the possible combinations tested (Table IV). Of the three years, 2004 and

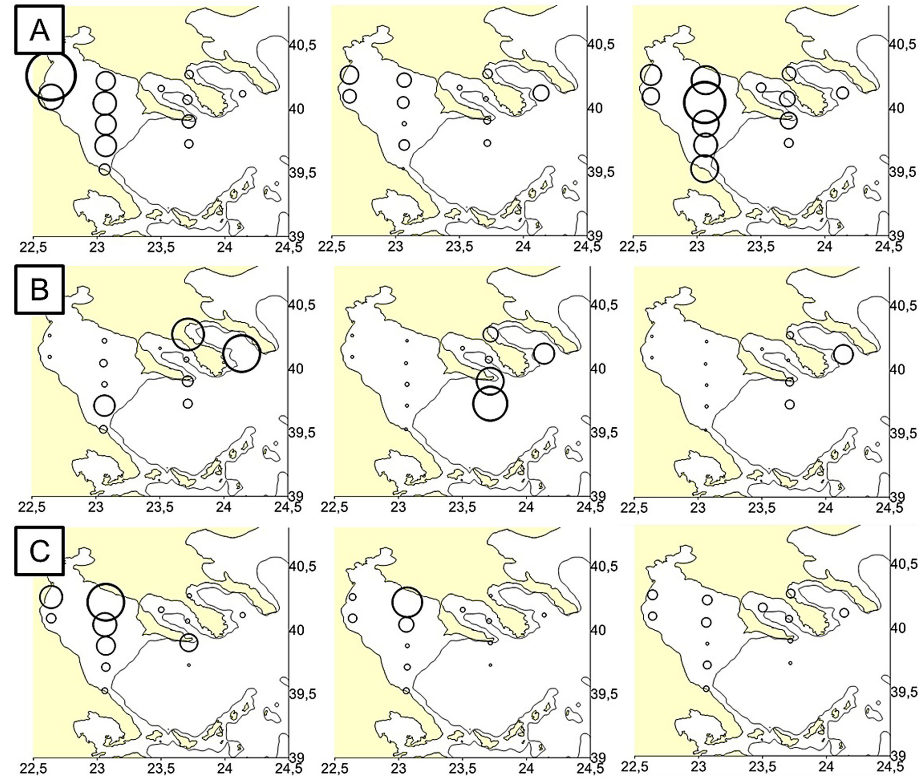

Fig. 4. – Horizontal distribution of ichthyoplankton abundance for the different taxa groups; epipelagics (**A**) mesopelagics (**B**) and demersal (**C**) for the three years (2004-left, 2005-middle and 2006-right). The contour of 200 m is present.

Table II. – Descriptive statistics of the three ecological indicators.

	Species number						Abundance						Shannon index					
	Chalkidiki			Thermaikos			Chalkidiki			Thermaikos			Chalkidiki			Thermaikos		
	2004	2005	2006	2004	2005	2006	2004	2005	2006	2004	2005	2006	2004	2005	2006	2004	2005	2006
Minimum	12	9	13	11	7	7	450.3	303.7	530.4	966.6	93.6	843.4	1.5	1.3	1.7	1.0	1.2	0.6
Maximum	24	22	27	20	11	11	2590.3	2453.8	2230.2	7665.2	854.8	5233.1	2.3	1.9	2.4	2.0	1.9	1.1
Median	18.0	11.5	22.0	14.0	9.0	9.0	1632.3	1509.0	1225.1	2411.8	469.5	2300.7	1.8	1.7	2.0	1.2	1.7	1.0
25 percentile	12.0	9.0	15.3	11.0	7.0	8.0	662.1	404.3	762.6	1929.6	154.2	1427.0	1.6	1.5	1.8	1.0	1.4	0.6
75 percentile	23.3	18.3	25.5	18.0	11.0	11.0	2285.9	2161.8	2174.2	3181.8	540.4	4292.1	2.0	1.8	2.3	1.7	1.8	1.1

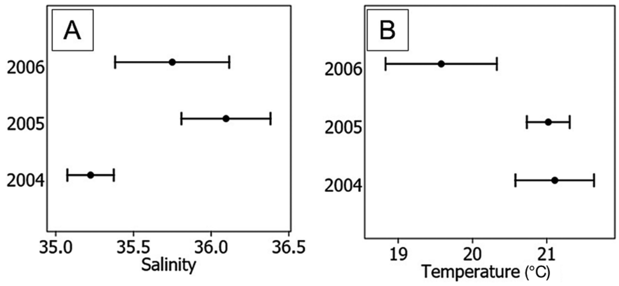

Fig. 5. – Comparison of the average sea surface values (20 m) of salinity (**A**) and temperature (**B**) between the three years. Whiskers represent the standard errors with the 95 % intervals.

Table III. – Results of the simple regression model that was used to represent the relationship between depth and the dependent variables.

Dependent variable	Intercept	Slope	P-Value	R-squared
Demersal	16.37	–2.53	0.506	0.02
Epipelagics	81.29	–27.58	0.018	0.14
Mesopelagics	–49.87	32.45	0.000	0.40
Species number	0.41	1.64	0.000	0.33
Shannon index	0.55	0.34	0.003	0.21
Abundance	47.47	–4.55	0.674	0.00
Model used				
Square root-Y model: Y = [a + b*sqrt(X)]^2				
Independent variable				
Tow Depth				

2006 presented significantly higher species richness than 2005. Chalkidiki presented significantly higher species richness and Shannon index than Thermaikos did. Thermaikos had a significantly higher total larvae abundance mainly due to the epipelagics *E. encrasicolus* and *S. aurita*. Differences were detected between high and low levels of surface salinity (0-20 m) for species' richness and between high and low levels of DIChl-a for the Shannon index and larval abundance (Table IV). On the other hand,

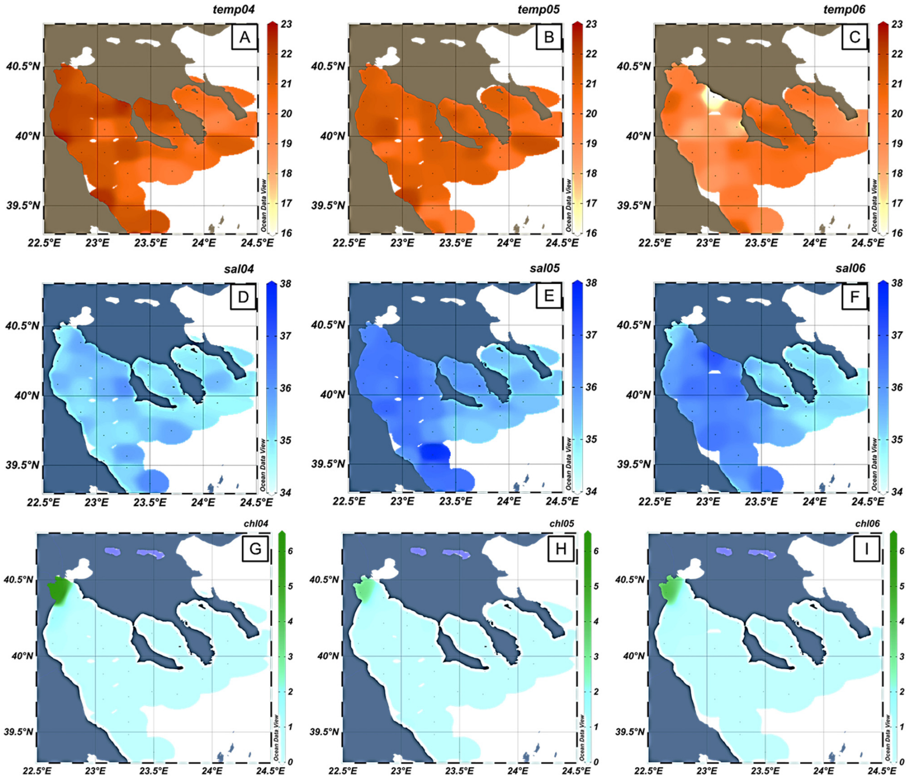

Fig. 6. – Horizontal distribution of surface temperature (20 m)(**A**, **B** and **C**), surface salinity (20 m) (**D**, **E** and **F**) and surface chlorophyll-a (20 m) (**G**, **H** and **I**), in 2004 (A, D and G), 2005 (D, E and F) and 2006 (G, H and I).

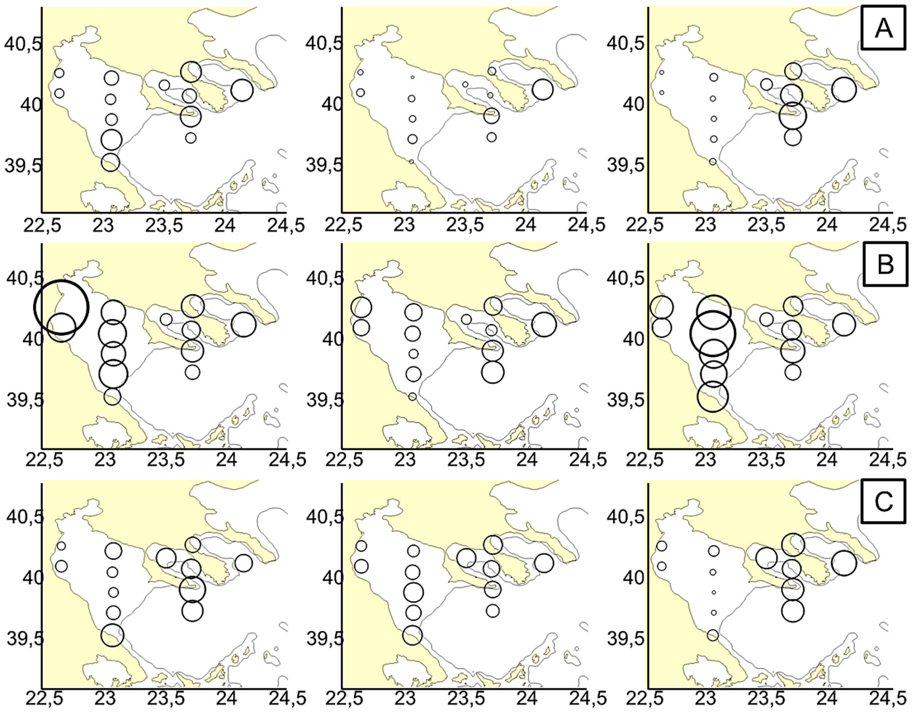

Fig. 7. – Horizontal distribution of species richness (**A**), total abundance (**B**) and Shannon diversity index (**C**) for the three years (2004-left, 2005-middle and 2006-right).

surface temperature did not seem to have a significant effect on species' richness or abundance. The same results were obtained when testing the ecological indicators for differences between environmental factors with and without counting the rare species (Table IV). ANOSIM showed significant differences between areas (R = 0.42, p-value = 0.0001) and years (R = 0.22, p-value = 0.0003). Significant differences were also found when the comparison was done without counting the rare taxa (R = 0.27, p-value = 0.0002 and R = 0.17, p-value = 0.0025, respectively).

Table IV. – Results of the PERMANOVA to test the effect of environmental factors on the ecological indicators. the = Thermaikos, cha = Chalkidiki, Species number = Species richness, log (N+1) = logarithm base e of the abundance, H (log e) = Shannon diversity index logarithm base e. * Ecological indicators calculated without taking into consideration taxa that appeared at only one station during each sampling period.

Index	Source	Sum of sqrs	df	F-Ratio	P-Value	Sig.*	Result	Index	Source	Sum of sqrs	df	F-Ratio	P-Value	Sig.*	Result	Index	Source	Sum of sqrs	df	F-Ratio	P-Value	Sig.*	Result
Species number*	year	167.13	2	7.924	0.002	*	2004, 2006 > 2005	log(N+1)*	year	2.22	2	10.925	0.000	*	2004, 2006 > 2005	H (log e)*	year	0.26	2	1.475	0.211		
	area	292.35	1	27.723	0.000	*	cha > the		area	0.00	1	0.020	0.884				area	2.83	1	31.965	0.000	*	cha > the
	Interaction	86.27	2	4.090	0.008	*			Interaction	1.15	2	5.657	0.002	*			Interaction	1.63	2	9.176	0.000	*	
	oceanic/neritic	250.15	1	10.796	0.000	*	oceanic > neretic		oceanic/neritic	0.27	1	0.854	0.262				oceanic/neritic	0.89	1	3.599	0.026	*	oceanic > neretic
	distance	167.76	2	3.620	0.009	*	far, close > medium		distance	0.10	2	0.163	0.788				distance	0.93	2	1.896	0.069		
	Interaction	–288.84	2	–6.233	0.892				Interaction	–3.86	2	–6.061	0.969				Interaction	–2.22	2	–4.515	0.352		
	DIChl-a	4.01	1	0.233	0.608				DIChl-a	0.28	1	1.995	0.143				DIChl–a	0.38	1	1.936	0.151		
	salinity	328.67	1	19.144	0.000	*	low > high		salinity	1.07	1	7.663	0.006	*	low > high		salinity	0.63	1	3.216	0.067		
	Interaction	–39.82	1	–2.319	0.237				Interaction	0.47	1	3.343	0.012	*			Interaction	–0.26	1	–1.299	0.132		
	salinity	328.67	1	328.670	0.000	*	low > high		salinity	1.07	1	6.925	0.009	*	low > high		salinity	0.63	1	2.838	0.084	*	low > high
	temperature	9.44	1	9.438	0.419				temperature	0.14	1	0.922	0.310				temperature	0.00	1	0.015	0.892		
	interaction	–19.25	1	–19.251	0.086				interaction	0.08	1	0.533	0.049	*			interaction	–0.80	1	–3.567	0.431		
Species number	year	175.54	2	6.883	0.002	*	2004, 2006 > 2005	log(N+1)	year	1.72	2	7.303	0.002	*	2004, 2006 > 2005	H (log e)	year	0.19	2	1.064	0.321		
	area	312.10	1	24.474	0.000	*	cha > the		area	0.37	1	3.136	0.078				area	3.81	1	42.505	0.000	*	cha > the
	Interaction	125.53	2	4.922	0.005	*			Interaction	0.51	2	2.159	0.036	*			Interaction	1.35	2	7.545	0.001	*	
	distance	171.41	2	3.408	0.013	*	far, close > medium		distance	0.17	2	0.283	0.644				distance	1.54	2	3.477	0.011	*	far, close > medium
	oceanic/neritic	315.88	1	12.562	0.001	*	oceanic > neretic		oceanic/neritic	0.03	1	0.103	0.684				oceanic/neritic	1.73	1	7.843	0.001	*	oceanic > neretic
	Interaction	–294.90	2	–5.864	0.960				Interaction	–3.93	2	–6.356	0.865				Interaction	–2.26	2	–5.105	0.327		
	salinity	381.89	1	19.637	0.000	*	low > high		salinity	0.46	1	2.459	0.099	*	low > high		salinity	1.04	1	4.304	0.032	*	low > high
	temperature	5.03	1	0.259	0.590				temperature	0.06	1	0.310	0.557				temperature	0.00	1	0.000	0.994		
	Interaction	–33.59	1	–1.727	0.125				Interaction	–0.55	1	–2.966	0.356				Interaction	–1.23	1	–5.070	0.797		
	DIChl-a	6.60	1	0.325	0.539				DIChl-a	0.82	1	4.027	0.042	*	low > high		DIChl–a	0.77	1	5.937	0.014	*	low > high
	salinity	381.89	1	18.785	0.000	*	low > high		salinity	1.04	1	5.158	0.022	*	low > high		salinity	0.46	1	3.547	0.052		
	interaction	–66.05	1	–3.249	0.450				interaction	–0.64	1	–3.156	0.441				interaction	0.74	1	5.716	0.004	*	

DISCUSSION

In total 62 taxa of larvae were identified in the Thermaikos and Chalkidiki areas, a similar number compared to relevant studies of a wider spatial scale in the North Aegean Sea (Somarakis *et al*. 2002, Somarakis *et al*. 2011a, Isari *et al*. 2008, Koutrakis *et al*. 2004) and in the West Mediterranean Sea (Sabatés 1990a, Sabatés & Olivar 1996). The western to eastern gradient regarding fish diversity of the Mediterranean Sea (Coll *et al*. 2010) does not seem to find application to ichthyoplankton species richness (Table V). Ichthyoplankton species richness across the Mediterranean (Table V) does not seem to follow a similar eastward decrease. The North Aegean Sea larval richness is comparable to other areas of the north Mediterranean Sea and longitude does not seem to affect spatial patterns of larvae species richness.

Late spring-summer is ideal for studying spatial distribution and biodiversity because it is a transitional period regarding reproduction strategies of many fish. It marks the end of the reproduction of many winter spawners (e.g., *Buglossidium luteum*, *Trachurus trachurus*) and the beginning of summer spawners (e.g., *Serranus cabrilla*, *Cepola macrophthalma*) (Somarakis *et al*. 2011a, Sabatés & Olivar 1996). Summer coincides with the spawning peak of many fish species such as *E. encrasicolus* (Somarakis *et al*. 2011a, Palomera & Sabatés 1990), *C. maderensis*, *H. benoiti*, *S. shepatus* and C. *macrophthalma* (Sabatés 1990a). This temporal coincidence of spawning has multiple ecological extensions. Taxa composition is similar to the results of other studies with early spring to summer samplings with bongo nets in the north Aegean Sea (Somarakis *et al*. 2002) and the western Mediterranean Sea (Sabatés 1990a). This is also evident in mesozooplankton species composition (Siokou-Fragkou *et al*. 2009). Their results show that the majority of taxa have been identified at the species level and only a minority of them has been identified at the genera/family level. Consequently, both the results described in the literature as well as our results are comparable because a relevant taxonomic effort has been used.

Table V. – List of previous ichthyoplankton studies conducted at the Mediterranean Sea with bongo nets during summer. A large number of fish species found in present study is common with previous studies of the West Mediterranean Sea.

Authors	Net	Mesh size	No samples	Tow depth (m)	Season	Area	Number of taxa	Common taxa
Alemany *et al.* (2006)	Bongo	333 µm	25	0-100	June	Balearic archipelago (Wmed)	52	63.5 %
Olivar *et al.* (2010)	Bongo	300 µm	9	0-200	June	Catalan coast (NW Med)	62	41.9 %
Sabates & Olivar (1996)	Bongo	300 µm	44	0-200	May and June	Catalan coast (NW Med)	29, 31, 36	65.5 %
López-Sanz *et al.* (2011)	Bongo	300 µm	32	0-20	May-June, July-August	Medes islands (NW Med)	28	57.1 %
Álvarez *et al.* (2012)	Bongo-40	335 µm	3	50-80	March to August	Southern Mallorca (Wmed)	58	74.1 %
Sabates (1990a)	Bongo	300 µm	264	0-200	April to October	Catalan coast (NW Med)	45	71.1 %
Zarrad *et al.* (2013)	Bongo	335 µm	71	0-100	June and July	Eastern coast of Tunisia (Ionian Sea, S Med)	68	63.2 %
Cuttitta *et al.* (2016)	Bongo-40	200 µm	124	0-100	July	Gulf of Sirte (S Med)	66	43.9 %
Isari *et al.* (2008)	Bongo	250 µm	24	0-200	Mainly June	North Aegean Sea (E Med)	59	74.6 %
Somarakis *et al.* (2011) (a)	Bongo	250 µm	144	0-120	Summer	North Aegean Sea (E Med)	57	80.7 %
Somarakis *et al.* (2011) (b)	Bongo	250 µm	125	0-200	Summer	Central Aegean and Ionian seas (E Med)	74	67.6 %
Siapatis & Somarakis (2007) (SHF)		Several nets		0-200	All year	Aegean Sea (E Med)	105	60,0 %
Present study	Bongo	250 µm	39	0-200	Summer	North Aegean Sea (E Med)	62	

Sabatés *et al.* (1990a) found that the peak of spawning for many common species of the present study is during June and July. It is possible that a synchronization of the spawning period of many fish exists between the East and West Mediterranean Sea. Demersal and mesopelagic taxa showed low abundances in 2006. It is possible that the onset of the spawning season was delayed for these species due to the low average sea surface temperature that was recorded during the sampling of 2006 (Fig. 5). The effects of temperature on the onset of the spawning period have been studied in the past (Jansen & Gislason 2011, Wright & Trippel 2009). Somarakis *et al.* (2011a) support the idea of similar covariation of summer spawners with temperature on the onset of the reproductive period. Interannual differences of epipelagic species abundances were more related with primary productivity whereas mesopelagic and demersal species were more related with temperature and the onset of the spawning period. Different species may use different environmental factors as signals to initiate seasonal behaviors (Asch 2013). Over the three years, common species as well as unique species were found. Although these unique species were equally distributed between the two study areas, their presence significantly affected species' richness when we compared them over the three years. It is possible that trophic conditions of the greater north Aegean Sea area in 2005 were poor, as shown by the environmental data collected during the three years, and this environmental state affected spawning intensity of adults. The year of 2005 was poorer, in terms of species richness, due to the absence of these unique species. All of them have been reported before as summer spawners (Siapatis & Somarakis 2007, Somarakis *et al.* 2011a, Koutrakis *et al.* 2004). Especially *Vinciguerria attenuata* has probably extended its spawning season in the Aegean Sea, as past reviews report its spawning season from December to February (Siapatis & Somarakis 2007).

Differences between the two study areas regarding distribution reflect the preference of adults for a specific habitat. All taxa groups appeared at spatially segregated habitats during all of the three years and few species of larvae were found far from adults' habitats. More specifically larvae of epipelagic taxa were most abundant in the shallow Thermaikos whereas larvae of mesopelagic taxa were most abundant at the deeper Chalkidiki area. The distribution of demersal taxa, (they were mainly located at shallow stations), is also explained by the preference of adults for a specific habitat. Adults of many demersal species usually live in shallow areas below 100 m (Loris & Rucabado 1990, Smith 1981). Myctophids have low fecundity rates, migrate from deeper layers to shallower ones for feeding and for spawning (Catul *et al.* 2011) and this behavior of spatial and temporal separation from other species is a good strategy that helps them survive. This observation suggests mainly two conclusions: firstly, adults' habitat is a strong factor regarding spatial patterns of fish larvae and secondly, spatial patterns seem to be related to different spawning strategies of adults. Results of other research generally agrees with the presence of fish larvae close to the adults' habitat and with the heterogeneous spatial distribution of larvae (Sabatés 1990a, b).

Regarding biodiversity, PERMANOVA showed that Chalkidiki presented a higher species richness and Shannon diversity index when compared with Thermaikos, despite the lower sampling effort of the former (only 6 stations in contrast to 7 stations at Thermaikos). Chalkidiki offers a variety of habitats (oceanic and close to the coast) and thus attracts multiple taxa groups; mesopelagic and demersal taxa coexist near the narrow Chalkidiki shelf and explain its richness. It is possible that the complex topography of Chalkidiki provides adult fish and other marine organisms — which can be prey for fish — with many habitats for protection, and this attracts them, providing them with favorable conditions for reproduction. Such positive relationships between complex environments and species diversity have been reported in numerous reviewers in the past (Shmida & Wilson 1985, Bell *et al.* 2000, Stein *et al.* 2014, Pinha *et al.* 2017, Witman *et al.* 2004, etc.). Gratwicke & Speight (2005) interpret the distinctive spatial patterns of species richness as habitat complexity, with more complex areas having more species than less complex ones. Habitat heterogeneity can create different niches across localities thus increasing β-diversity by favoring different groups of species as part of deterministic processes (Chase 2010). Relative high species richness and diversity values have been justified in the past due to the spatial overlapping of larvae of neritic and oceanic species (Rodríguez *et al.* 2013), which is a feature of the Chalkidiki topography. On the other hand, Thermaikos is characterized by spatially distinct habitats which are separated by a wide continental shelf. The environmental heterogeneity hypothesis, i.e., "more heterogeneous environments would be expected to support a greater number of species" (Bell *et al.* 2000, Stein *et al.* 2014, Yang *et al.* 2015) seems to be more applicable in our case study as the Mediterranean Sea has the capacity to hold a high number of species, proportionally to the great variety of its marine habitats.

The exclusion of rare species in our analysis (ANOSIM and PERMANOVA) has not impacted our outcomes regarding biodiversity. Their presence or absence does seem to have any effect neither on the existing differences among biocommunities nor on the relationship between environment and diversity. Although their role regarding biodiversity seems to be weak, they have a significant role in identifying unique biocommunities (Cao *et al.* 2001). Each researcher shall decide whether they are important in assessment studies, in predictive models or in pattern analyses (Cao *et al.* 2001).

Distribution and biodiversity are also affected by environmental forcing (Bertrand *et al.* 2008, Sabatés 1990a, Sabatés & Maso 1990). Higher species richness values were recorded in 2004 in the Thermaikos Gulf, where salinity was lower. It is possible that low salinity waters from the western Thermaikos Gulf, where the estuaries of five rivers are located, and low salinity waters from the open Aegean Sea coming from the Dardanelles Strait (Hyder *et al.* 2002) enriched with nutrients our study area and this enhanced zooplankton production (Zervoudaki *et al.* 2006), which is food for fish larvae. Probably, an upwelling event took place in the Thermaikos Gulf during 2006 and enhanced local productivity. Larvae of Myctophidae family (mesopelagics) were present at shallow stations of Thermaikos, away from the deep Chalkidiki area, which is the natural habitat of their adults. It is possible that hydrography contributed to the enrichment of Thermaikos with mesopelagic taxa through horizontal transportation. Despite this possible horizontal transportation of larvae, species richness of Thermaikos was still significantly lower than species richness of Chalkidiki. *Lobianchia dofleini*, *Myctophum punctatum*, *H. benoiti* and *C. maderensis* are known to spawn during the year (Siapatis & Somarakis 2007). Sabatés & Olivar (1996) found *C. maderensis* larvae mainly at deep stations (> 200 m) while they were present (but less abundant) at shallow stations as well.

Higher surface chlorophyll-a in the western Thermaikos Gulf were recorded in 2004 and 2006, during the years that epipelagic taxa abundances were high (*E. encrasicolus* and *S. aurita*). Their adults are planktivorous (Nikolioudakis *et al.* 2014) and prefer Thermaikos Gulf for its high primary and secondary production. Despite the connectivity of the two study areas, physicochemical factors seem to significantly affect the reproductive effort intensity of *E. encrasicolus* and, therefore, affect the total abundance of larvae (Somarakis *et al.* 2004). Sudden changes in larval abundance of small pelagic species such as *E. encrasicolus* and *S. aurita* are more likely related to the adult reproductive output as they have the ability to produce great numbers of eggs in a short period (Somarakis *et al.* 2011a). This temporal coincidence of chlorophyll-a, which is an indirect indication of the trophic condition of an ecosystem, with the high abundances of the epipelagic larvae, is probably related to a mechanism of larvae coincidence with their food. Such coincidences between fish larvae and their food have been reported in the past (Lasker 1981, Sabatés *et al.* 2007) and it is possibly related with the stable ocean hypothesis and the successful larval feeding (Lasker 1981). However, the investigation of this coincidence should take place over a longer period of time to establish the degree of abiotic factors effect on species richness.

To conclude, ichthyoplankton spatial distribution studies provide niche modeling scientists with necessary data and their cost-effective approach to conservation. Furthermore, they can provide useful information regarding biodiversity hotspots of the greater north Aegean Sea area, thus helping us select and place emphasis on the conservation of specific sites. The study of ecological indicators in dynamic ecosystems (such as estuaries) can give us a reference point which to compare with less dynamic and more pressed areas. Monitoring diversity in different areas or periods can be a useful tool to determine the human impact and the ecosystem resilience. Despite the overlapping in species' functional roles in an ecosystem, the role of every species in a community structure (Halpern & Floeter 2008) and ecosystem functioning (Stuart-Smith *et al.* 2013) is unique. Thermaikos and Chalkidiki are two well-segregated areas regarding taxa groups' habitat in which species spatial overlapping and larvae dispersal may exist. It is interesting to observe the role of Thermaikos as a nursery ground or as a fish spawning habitat in the future and the way that great environmental changes may affect larvae abundance at this semi-closed ecosystem as compared to the wider north Aegean Sea area.

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REFERENCES

Alemany F, Deudero S, Morales-Nin B, López-Jurado JL, Jansá J, Palmer M, Palomera I 2006. Influence of physical environmental factors on the composition and horizontal distribution of summer larval fish assemblages off Mallorca island (Balearic archipelago, western Mediterranean). *J Plankton Res* 28(5): 473-487.

Álvarez I, Catalán IA, Jordi A, Palmer M, Sabatés A, Basterretxea G 2012. Drivers of larval fish assemblage shift during the spring-summer transition in the coastal Mediterranean. *Estuar Coast Shelf Sci* 97: 127-135.

Anderson MJ 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26(1): 32-46.

Asch RG 2013. Interannual-to-Decadal Changes in Phytoplankton Phenology, Fish Spawning Habitat, and Larval Fish Phenology. Univ California, San Diego: 288 p.

Bell G, Lechowicz MJ, Waterway MJ 2000. Environmental heterogeneity and species diversity of forest sedges. *J Ecol* 88(1): 67-87.

Bertrand A, Gerlotto F, Bertrand S, Gutiérrez M, Alza L, Chipollini A, Díaz E, Espinoza P, Ledesma J, Quesquén R, Peraltilla S 2008. Schooling behavior and environmental forcing in relation to anchoveta distribution: an analysis across multiple spatial scales. *Prog Oceanogr* 79(2-4): 264-277.

Cao Y, Larsen DP, Thorne RSJ 2001. Rare species in multivariate analysis for bioassessment: some considerations. *J N Am Benthol Soc* 20(1): 144-153.

Catul V, Gauns M, Karuppasamy PK 2011. A review on mesopelagic fishes belonging to family Myctophidae. *Rev Fish Biol Fish* 21(3): 339-354.

Chase JM 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328(5984): 1388-1391.

Clarke KR 1993. Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18(1): 117-143.

Clarke KR, Gorley RN 2005. PRIMER: Getting started with v6. PRIMER-E Ltd: Plymouth, UK.

Coll M, Piroddi C, Steenbeek J, Kaschner K, Lasram FBR, Aguzzi J, Ballesteros E, Bianchi CN, Corbera J, Dailianis T, Danovaro R 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PloS ONE* 5(8): e11842.

Cuttitta A, Bonomo S, Zgozi S, Bonanno A, Patti B, Quinci EM, Torri M, Hamza M, Fatah A, Haddoud D, El Turki A 2016. The influence of physical and biological processes on the ichthyoplankton communities in the Gulf of Sirte (Southern Mediterranean Sea). *Mar Ecol* 37(4): 831-844.

Edwards M, Beaugrand G, Hays GC, Koslow JA, Richardson AJ 2010. Multi-decadal oceanic ecological datasets and their application in marine policy and management. *Trends Ecol Evol* 25(10): 602-610.

Fricke R, Eschmeyer WN, Van der Laan R Eds 2020. Eschmeyer's catalog of fishes: genera, species, references. (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 5 Oct. 2020.

Giannoulaki M, Iglesias M, Tugores MP, Bonanno A, Patti B, De Felice A, Tsagarakis K 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. *Fish Oceanogr* 22(2): 69-89.

Gillanders BM, Kingsford MJ 2002. Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. *Oceanogr Mar Biol: Ann Rev* 40: 233-309.

Golden Software 2002. Surfer 8 Golden Software Inc. Golden-CO 80401 USA

Gratwicke B, Speight MR 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J Fish Biol* 66(3): 650-667.

Halpern BS, Floeter SR 2008. Functional diversity responses to changing species richness in reef fish communities. *Mar Ecol Prog Ser* 364: 147-156.

Hammer Ø, Harper DA, Ryan PD 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol Electron* 4(1): 9.

Hellenic Statistical Authority, Press Release Sea Fishery Survey by Motor-Propelled Vessels 2016. Piraeus, 28 Sep. 2017: 12 p.

Hernández-Miranda E, Palma AT, Ojeda FP 2003. Larval fish assemblages in nearshore coastal waters off central Chile: temporal and spatial patterns. *Estuar Coast Shelf* S 56(5-6): 1075-1092.

Hill MO 1973. Diversity and evenness: a unifying notation and its consequences. *J Ecol* 54(2): 427-432

Hyder P, Simpson JH, Christopoulos S, Krestenitis Y 2002. The seasonal cycles of stratification and circulation in the Thermaikos Gulf Region of Freshwater Influence (ROFI), northwest Aegean. *Cont Shelf Res* 22(17): 2573-2597

Isari S, Fragopoulu N, Somarakis S 2008. Interannual variability in horizontal patterns of larval fish assemblages in the northeastern Aegean Sea (eastern Mediterranean) during early summer. *Estuar Coast Shelf Sci* 79: 607-619.

Jansen T, Gislason H 2011. Temperature affects the timing of spawning and migration of North Sea mackerel. *Cont Shelf Res* 31(1): 64-72.

Jost L 2006. Entropy and diversity. *Oikos* 113(2): 363-375.

Koutrakis ET, Kallianiotis AA, Tsikliras AC 2004. Temporal patterns of larval fish distribution and abundance in a coastal area of northern Greece. *Sci Mar* 68(4): 585-595.

Krige Danie G 1951. A statistical approach to some basic mine valuation problems on the Witwatersrand. *J South Afr Inst Min Metall* 52 (6): 119-139.

Lasker R 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. Marine fish larvae: morphology, ecology and relation to fisheries: 81-87.

López-Sanz À, Stelzenmüller V, Maynou F, Sabatés A. 2011. The influence of environmental characteristics on fish larvae spatial patterns related to a marine protected area: The Medes islands (NW Mediterranean). *Estuar Coast Shelf Sci* 92(4): 521-533.

Loris D, Rucabado J 1990. Pomacentridae. *In* Quéro JC, Hureau JC, Karrer C, Post A & Saldanha L Eds, Check-List of the Fishes of the Eastern tropical Atlantic (CLOFETA). JNICT, Lisbon; SEI, Paris; and UNESCO, Paris. Vol 2: 842-850.

Marshall KN, Duffy-Anderson JT, Ward EJ, Anderson SC, Hunsicker ME, Williams BC 2019. Long-term trends in ichthyoplankton assemblage structure, biodiversity, and synchrony in the Gulf of Alaska and their relationships to climate. *Progr Oceanogr* 170: 134-145.

Morel A, Berthon JF 1989. Surface pigments, algal biomass profiles, and potential production of the euphotic layer: Relationships reinvestigated in view of remote-sensing applications. *Limnol Oceanogr* 34(8): 1545-1562.

Navarro J, Coll M, Cardador L, Fernández ÁM, Bellido JM 2015. The relative roles of the environment, human activities and spatial factors in the spatial distribution of marine biodiversity in the Western Mediterranean Sea. *Prog Oceanogr* 131: 126-137.

Nikolioudakis N, Isari S, Somarakis S 2014. Trophodynamics of anchovy in a non-upwelling system: direct comparison with sardine. *Mar Ecol Prog Ser* 500: 215-229.

Olivar MP, Emelianov M, Villate F, Uriarte I, Maynou F, Alvarez I , Morote E. 2010. The role of oceanographic conditions and plankton availability in larval fish assemblages off the Catalan coast (NW Mediterranean). *Fish Oceanogr* 19(3): 209-229.

Olson DB, Kourafalou VH, Johns WE, Samuels G, Veneziani M 2007. Aegean surface circulation from a satellite-tracked drifter array. *J Phys Oceanogr* 37(7): 1898-1917.

Palomera I, Sabatés A 1990. Co-occurrence of *Engraulis encrasicolus* and *Sardinella aurita* eggs and larvae in the northwestern Mediterranean. *Sci Mar* 54: 61–67.

Pinha GD, Tramonte RP, Bilia CG, Takeda AM 2017. Differences in environmental heterogeneity promote the nestedness of Chironomidae metacommunity in Neotropical floodplain lakes. *Acta Limnol Bras* 29.

Rodríguez JM, Alvarez I, López-Jurado JL, Garcia A, Balbín R, Álvarez-Berastegui D, Torres AP, Alemany F 2013. Environmental forcing and the larval fish community associated to the Atlantic bluefin tuna spawning habitat of the Balearic region (Western Mediterranean), in early summer 2005. *Deep Sea Res* Part I: Oceanogr Res Pap 77: 11-22.

Sabatés A 1990a. Distribution pattern of larval fish populations in the Northwestern Mediterranean. *Mar Ecol Prog Ser* 59: 5-82.

Sabatés A 1990b. Changes in the heterogeneity of mesoscale distribution patterns of larval fish associated with a shallow coastal haline front. *Estuar Coast Shelf Sci* 30:131-140.

Sabatés A 2004. Diel vertical distribution of fish larvae during the winter-mixing period in the Northwestern Mediterranean. *ICES J Mar Sci* 61(8): 1243-1252.

Sabatés A, Masó M 1990. Effect of a shelf-slope front on the spatial distribution of mesopelagic fish larvae in the western Mediterranean. *Deep-Sea Res* 37: 1085-1098

Sabatés A, Olivar MP 1996. Variation of larval fish distributions associated with variability in the location of a shelf-slope front. *Mar Ecol Prog Ser* 135: 11-20.

Sabatés A, Olivar MP, Salat J, Palomera I, Alemany F 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Prog. Oceanogr* 74(2-3): 355-376

Schlitzer R 2016. Ocean data view http://odv.awi.de.

Shmida AVI, Wilson MV 1985. Biological determinants of species diversity. *J Biogeogr:* 1-20.

Siapatis A, Chilari A 2003. Database of ichthyoplankton from the Greek Seas. Proceedings of the 7th Congress on Oceanography and Fisheries, Book of Abstracts: 192 p.

Siapatis A, Somarakis S 2007. Early Life History of Fish. SoHelFI, 2007, State of Hellenic Fisheries. C Papaconstantinou, A Zenetos, V Vassilopoulou, G Tserpes Eds. HCMR Publ: 466 p.

Siapatis A, Caragitsou E, Kavadas S, Papaconstantinou C 2000. The contribution of ichthyoplankton studies to the better knowledge of the fish fauna in the Thermaikos Gulf and Thracian Sea. Proceedings 6th Congress on Oceanography & Fisheries, Chios, 2nd vol.: 78-85.

Siokou-Frangou I, Christaki U, Mazzocchi MG, Montresor M, d'Alcalá MR, Vaqué D, Zingone A 2009. Plankton in the open Mediterranean Sea: a review. *Biogeosci Discuss* 6(6).

Smith CL 1981. Serranidae. *In* Fischer W, Bianchi G & Scott WB Eds, FAO Species Identification Sheets for Fishery Purposes. Eastern Central Atlantic; fishing areas 34, 47 (in part). Depart Fish Oceans Canada & FAO. Vol 4: pag var.

Smith PE, Richardson SL 1977. Standard techniques for pelagic fish egg and larval surveys. FAO Fish Tech Pap 175: 100 p.

Somarakis S, Drakopoulos P, Filippou V 2002. Distribution and abundance of larval fishes in the northern Aegean Sea-eastern Mediterranean in relation to early summer oceanographic conditions. *J Plankton Res* 24: 339-357.

Somarakis S, Palomera I, Garcia A, Quintanilla L, Koutsikopoulos C, Uriarte, A, Motos L 2004. Daily egg production of anchovy in European waters. *ICES J Mar Sci* 61(6): 944-958.

Somarakis S, Ramfos A, Palialexis A, Valavanis VD 2011a. Contrasting multispecies patterns in larval fish production trace inter-annual variability in oceanographic conditions over the NE Aegean Sea continental shelf (eastern Mediterranean). *Hydrobiologia* 670: 275-287.

Somarakis S, Isari S, Machias A 2011b. Larval fish assemblages in coastal waters of central Greece: reflections of topographic and oceanographic heterogeneity. *Sci Mar* 75(3): 605-618.

Stein A, Gerstner K, Kreft H 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol Lett* 17(7): 866-880.

Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE, Baker SC, Thomson RJ, Stuart-Smith JF, Hill NA, Kininmonth SJ, Airoldi L, Becerro MA 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501(7468): 539.

Tsikliras AC, Koutrakis ET, Sylaios GK , Kallianiotis AA 2009. Summer distribution of fish larvae in northern Aegean Sea. *JMBA* 89(6): 1137-1146.

Witman JD, Etter RJ, Smith F 2004. The relationship between regional and local species diversity in marine benthic communities: a global perspective. *Proc Nat Acad Sci* 101(44): 15664-15669.

Wright PJ, Trippel EA 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish Fish* 10(3): 283-304.

Yang Z, Liu X, Zhou M, Ai D, Wang G, Wang Y, Chu C, Lundholm JT 2015. The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. *Sci Rep* 5: 15723.

Zar JH 2010. Biostatistical Analysis, 5th edition. Pearson Education Upper Saddie River, New Jersey, USA.

Zarrad R, Alemany F, Rodriguez JM, Jarboui O, Lopez-Jurado JL, Balbin R 2013. Influence of summer conditions on the larval fish assemblage in the eastern coast of Tunisia (Ionian Sea, Southern Mediterranean). *J Sea Res* 76: 114-125.

Zervoudaki S, Nielsen TG, Christou ED, Siokou-Frangou I 2006. Zooplankton distribution and diversity in a frontal area of the Aegean Sea. *Mar Biol Res* 2(3): 149-168.

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