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ECOSYSTEMS AND SUSTAINABILITY

Contrasting multispecies patterns in larval fish production trace inter-annual variability in oceanographic conditions over the N.E. Aegean Sea continental shelf (Eastern Mediterranean)

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Abstract The response of larval fish communities of the northeastern Aegean Sea (NEA) to interannual environmental changes is analyzed using data from four ichthyoplankton surveys covering the NEA continental shelf during June 1993, 1994, 1995, and 1996. Waters were significantly cooler, less saline and richer in zooplankton in 1993 and 1996 ('cold' years) than in 1994 and 1995 ('warm' years). A comparison of monthly SST series (1993–1997) between the NEA, the Marmara Sea, and the Western Black Sea revealed high correlations and similar trend components among these areas implying that oceanographic conditions over the NEA (and observed inter-annual differences) were most likely dominated by the properties and relative amount of Black Sea water inflow in the NEA. The relative composition of the larval fish community was significantly related to the 'cold/warm' regime and larval diversity was higher during the warm years. Larvae of the small-sized pelagic species, such as anchovy (*Engraulis encrasicolus*), and most mesopelagic fishes were relatively more abundant during the cold, zooplankton-rich years. Larvae of the middle-sized pelagics (*Sardinella aurita*, *Scomber japonicus*, *Trachurus mediterraneaus*, *Auxis rochei*) and certain benthopelagic species exhibited an opposite trend, i.e., they were more abundant during the warm years or absent during the cold years. Most of these species are known to be typical summer spawners (e.g., *Serranus cabrilla*, *Lisa saliens*, *Trachinus draco*, and *Symphurus nigrescens)*. Co-variation in larval fish production might be indicative of similar responses among species to changing physical and/or trophic regimes.

Keywords Ichthyoplankton · North Aegean Sea · Black Sea water

Introduction

Variability in recruitment of fish stocks is primarily determined by inter-annual changes in oceanographic conditions. These may act directly on adults, affecting the spatiotemporal pattern of egg production, timing and duration of spawning (e.g., Ganias et al., 2007; Stratoudakis et al., 2007), geographical distribution of spawning habitats (e.g., Planque et al., 2007; Bernal et al., 2007), fecundity and spawning

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frequency (e.g., Somarakis et al., 2004; Somarakis, 2005), and/or on developing eggs and larvae, determining their drift, development, growth, and survival (e.g., Heath, 1992, Allain et al., 2007).

As climate impacts on marine ecosystems and synoptic-scale recruitment processes are difficult to address experimentally, the comparative method is the best way to improve our knowledge on the reaction of ecosystems and populations embedded in them to physical forcing. The existence, scale, and interspecies relationships of repeated patterns may yield valuable insight into the nature of the processes driving recruitment variability (Koslow, 1984; Koslow et al., 1987; Cohen et al., 1991; Myers et al., 1997; Hsieh et al., 2005; Mueter et al., 2007). Furthermore, multispecies patterns may provide basic information required to devise effective multispecies and ecosystem fishery management strategies (Ludwig et al., 1993; Christensen, 1996).

The importance of multispecies ichthyoplankton investigations for our understanding of fish reproductive strategies has been often emphasized in recent years (Moser & Smith, 1993; Somarakis et al., 2000). According to Frank & Leggett (1983), multispecies larval fish associations are adaptive and result from similar responses among species to the pelagic environment. In that sense, covariation in the abundance of larvae of different fish species in the plankton might indicate similarities in patterns of egg production and subsequent recruitment for these species (Somarakis et al., 2000). Long-term inter-annual trends in larval abundance mostly reflect trends in adult biomass (Hsieh et al., 2005). Short-term fluctuations are generally considered to be related to episodes of high or low reproductive output or geographical shifts due to animal movement (Moser et al., 2000; Hsieh et al., 2005).

This paper extends a previous, 2-year, study (1995 and 1996) on epipelagic fish larvae in the northeastern Aegean Sea (Somarakis et al., 2000), to examine multispecies trends in mean abundance for the entire larval fish community during early summer from 1993 to 1996 (4 years). In the early 1990s, the northeastern Aegean Sea (NEA) experienced marked inter-annual fluctuations in oceanographic conditions that were recorded during the anchovy ichthyoplankton surveys in the region (Somarakis, 1999, 2005; Somarakis et al., 2000, 2002). This has afforded a unique opportunity to investigate the response of larval fish communities to dramatic environmental changes.

The NEA is the most important area of the eastern Mediterranean in terms of fisheries production (Stergiou et al., 1997). It has a relatively wide continental shelf and receives the direct influence of the cooler, less saline, Black Sea water (BSW) that significantly enhances the productivity of the area (Isari et al., 2006, 2007, and references therein). The structure and physical characteristics of the water column in the NEA are primarily determined by the seasonal and interannual variability in the amount of BSW entering into the Aegean Sea (Poulos et al., 1997; Zervakis & Georgopoulos, 2002). The advection of BSW induces high hydrological and biological complexity that is directly reflected in the structure, composition, and distribution of the assemblages of holoplankters (Isari et al., 2006, 2007). However, the formation of assemblages of early fish larvae is primarily determined by the bathymetric and spatial distribution of adults (Somarakis et al., 2002; Isari et al., 2008).

Horizontal distribution patterns of larval fishes over the broader area of the northern Aegean Sea (including NEA) have been described by Somarakis et al. (2002) for the June 1995 and June 1996 surveys. The focus here is on inter-annual changes in overall abundance of different species and in relative composition of the larval assemblage in relation to changes in the abiotic and biotic environment. Time series of mean SST over the study area are compared with those of Bosporus (Marmara Sea) and the Black Sea in order to provide the first evidence that oceanographic conditions in the Black Sea directly influence the NEA.

Materials and methods

Ichthyoplankton data

Larval fishes were collected during four surveys carried out during 7–11 June 1993, 19–23 June 1994, 15–22 June 1995, and 6–14 June 1996 in the northern Aegean Sea (Eastern Mediterranean). Samples from a grid of 36 plankton stations spaced every 10 nautical miles are analyzed here (Fig. 1). These stations were sampled in all years, except, for two (stations 39 and 58) which were not sampled in 1994 due to time

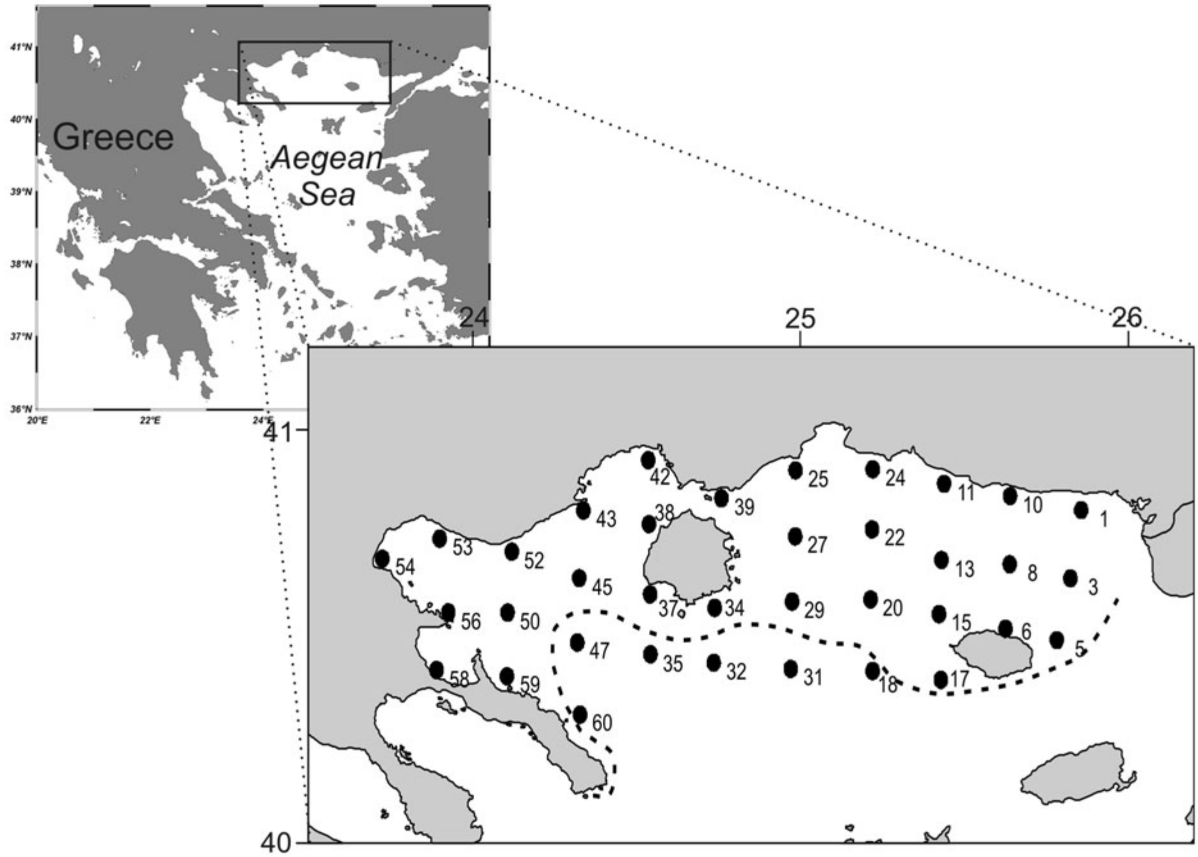


Fig. 1 Topography and sampling grid of the surveyed area. *Dotted line*: the 200 m isobath

constraints. Hydrographic sampling (temperature and salinity profiles) was also performed at each station using a Seabird 19 CTD profiler.

A 60-cm bongo-net sampler was used to sample ichthyoplankton. Mesh sizes on the sampler were 335 and 250 μm. Tows were double-oblique from within 5 m of the bottom to the surface or from 120 m depth to the surface at deep stations. Catches were standardized to numbers per square metre using information on maximum tow depth and volume of water filtered. More details are provided in Somarakis et al. (1998). Immediately after collection, samples were preserved in 5% borax-buffered formalin.

In the laboratory, larvae from the 0.250-mm mesh net were sorted and identified to the lowest possible taxonomic level. Zooplankton displacement volume (ZDV), which can be considered a rough index of zooplankton production (Smith & Richardson, 1977), was measured for each sampling site from the catch of the 0.250-mm mesh net. ZDV values were standardized to ml m^{-2}.

Analysis of variance was performed on $[\log_{10}(x + 1)]$ transformed abundance values to test for differences in abundance of dominant larval taxa (i.e., those with frequency of occurrence > 10% in at least two surveys) between years. The Student–Newman–Keuls (SNK) test was used to define homogenous groups.

The ($\log_2$) Shannon–Wiener information index (H') and Pielou's evenness index (J') were calculated to assess the diversity of the larval fish in the samples. Only larvae identified to the species level were used for these indices.

A taxon-by-sampling site matrix, expressed as abundance values (ind. m^{-2}), was subsequently analyzed using non-metric multidimensional scaling (NMDS) (Field et al., 1982; Clarke & Warwick, 1994). Data were transformed using the $[\log_{10}(x + 1)]$

transformation and similarities were computed using the Bray-Curtis similarity index. 'Outlier' samples (e.g., samples biasing or dominating the ordination, often compressing the distribution of the remaining sites) were removed from the data set to obviate problems associated with such outliers (Gauch, 1982; Hosie & Cochran, 1994). These three outlier samples, collected in 1994, were identified by prior exploratory data analysis using group-average clustering (Hosie & Cochran, 1994; Somarakis et al., 2002).

Ordination scores produced by the NMDS were compared to various environmental parameters using multiple regression analysis in order to determine which of these parameters were significantly related to the larval assemblage compositions (Kruscal & Wish, 1978; Hosie & Cochran, 1994). In the regression analysis the NMDS scores were treated as the independent variables and each environmental parameter as the dependent variable. The rationale for selecting this method (vs. other methods, e.g., canonical analysis, non-parametric methods) is described in Somarakis et al. (2002). Regression lines and their directions were plotted in the NMDS graphs according to Kruscal & Wish (1978): The direction of maximum correlation of each regression line is at an angle φ_r with the rth MDS axis. The direction cosine, or regression weight c_r, of that angle is given by the formula:

$$c_r = b_r / \sqrt{b_1^2 + b_2^2}$$

where b_1 and b_2 are the coefficients from the multiple regression $a + b_1x_1 + b_2x_2$, and x_1 and x_2 are the scores in the first and second MDS axis, respectively. The parameters examined were latitude (Lat), longitude (Lg), distance from the coast (CD), haul depth (HD) and ZDV, as well as temperature (T) and salinity (S) of the upper water column (means for the 0–40 m layer).

Satellite data

The hydrological and biological properties of waters in the NEA are highly influenced by Black Sea Water (e.g., Isari et al., 2006). In order to better understand whether the inter-annual differences in the biotic and abiotic environment observed in this area (e.g. differences in temperature) are affected by BSW, i.e., reflect processes in the Black Sea, we examined monthly time series of sea surface temperature for the study area, the Marmara Sea and the Black Sea, covering the period 1993–1997. Satellite images of sea surface temperature (SST) distribution (in °C) were downloaded from the German Aerospace Agency's (DLR, Germany) online EOWEB data archive (eoweb.dlr.de:8080) derived from the Advanced Very High Resolution Radiometer (AVHRR) datasets on a spatial resolution of 1.3 km.

These monthly averaged datasets were processed as regular grids under a Geographic Information Systems (GIS) environment using ArcInfo GRID software (ESRI, 1994). The mean monthly values for the period March 1993–December 1997 were estimated for the western half of Black Sea (west of 34°E parallel), Marmara Sea and the northeastern Aegean Sea (north of the 40°N parallel).

A seasonal-trend decomposition procedure based on Loess (STL) was used for the decomposition of time-series into trend, seasonal, and remainder components, as described by Cleveland et al. (1990). The trend component represents a low frequency variation in the data together with non-stationary, long-term changes in level. The seasonal component represents the variation in the data at or near the seasonal frequency, while the remainder component is the remaining variation beyond that in the seasonal and trend component. The STL was implemented in Brodgar software (www.brodgar.com). The time-series frequency was set to 12 since monthly time-series were used. The 'periodic' value was selected for the Loess window trend and seasonal, which means that mean values per month are taken. For the trend and seasonal degree, a linear regression model was selected to be used by the Loess algorithm.

Results

The water column in the NEA presented typical early-summer conditions in all years. A seasonal thermocline was coupled with a strong halocline, separating the upper 40 m of the water column from the colder and more saline deeper layer (Fig. 2). Mean thermocline depth was at ~18 m and mean thermocline temperature range was 9°C during all years. In 1993 and 1996 (hereafter referred to as 'cold' years), temperature in the upper 100 m was about 2°C lower than in 1994 and 1995 (hereafter referred to as 'warm'

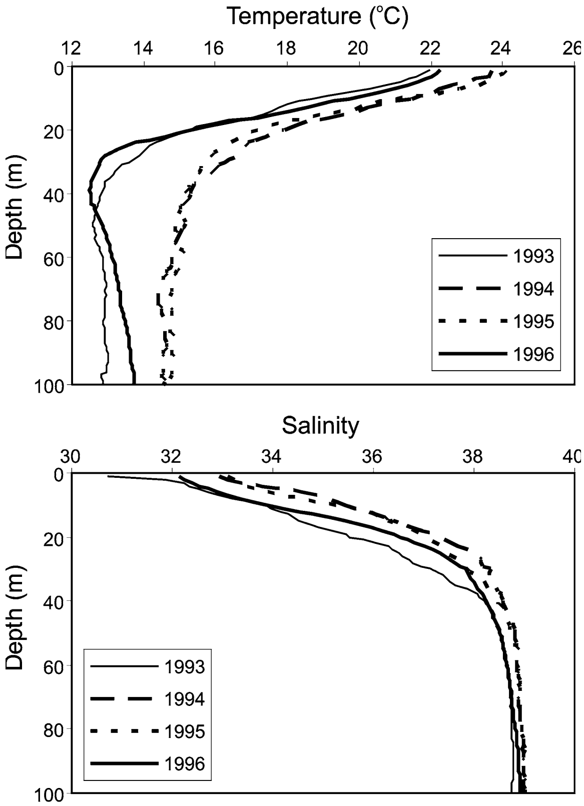


Fig. 2 Average profiles of temperature and salinity for the four surveys

years) (Fig. 2). The warm-cold pattern was also apparent in the mean SST values of the study area (NEA), Sea of Marmara (SM) and western Black Sea (WBS), which exhibited interannual patterns similar to in situ CTD measurements (Fig. 3A).

Mean salinity values increased sharply from the surface to 40 m depth and were lower in 1993 and 1996 (Fig. 2). Analysis of variance indicated that mean temperature and salinity of the upper water column (0–40 m) was significantly higher in 1994 and 1995 (Fig. 4, left panel; $F = 66.00$, $P < 0.0001$ and $F = 23.60$, $P < 0.0001$ for temperature and salinity, respectively). Mean ZDV was significantly higher during the cold years, especially in 1996 (Fig. 4, left panel; $F = 11.54$, $P < 0.0001$).

The analysis of mean monthly SST time series for NEA, SM, and WBS showed high linear correlations between NEA and both SM and WBS (Fig. 3B). The trend component of the three SST time series (Fig. 3C) exhibited similar general pattern with an increasing part from March 1993 to spring–summer 1994 and a decreasing part thereafter until spring–early summer of 1996.

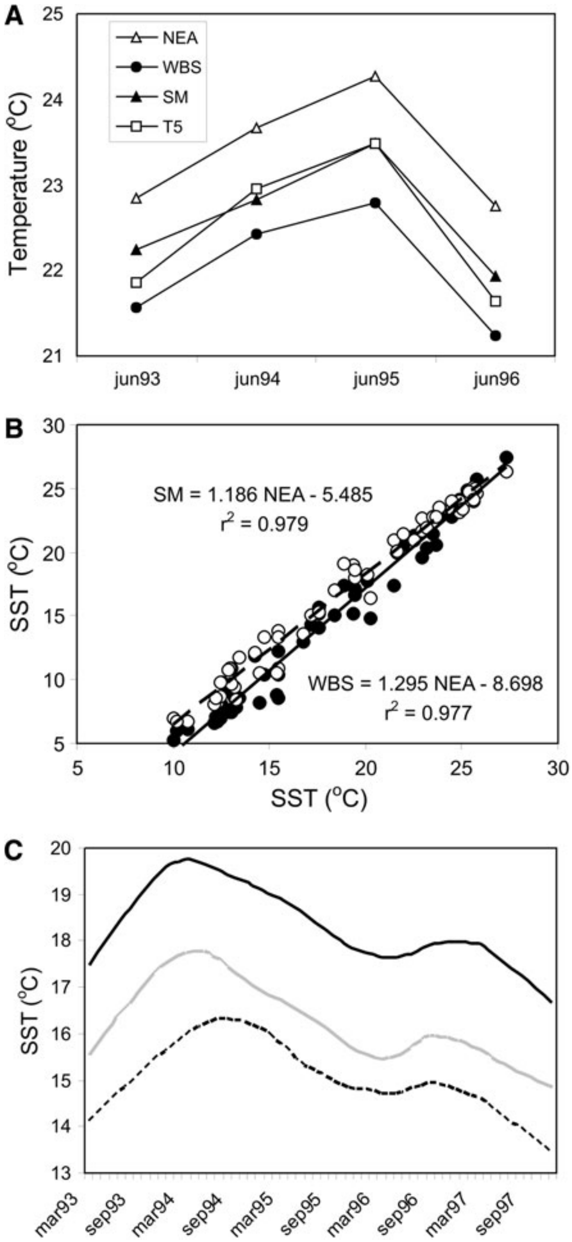
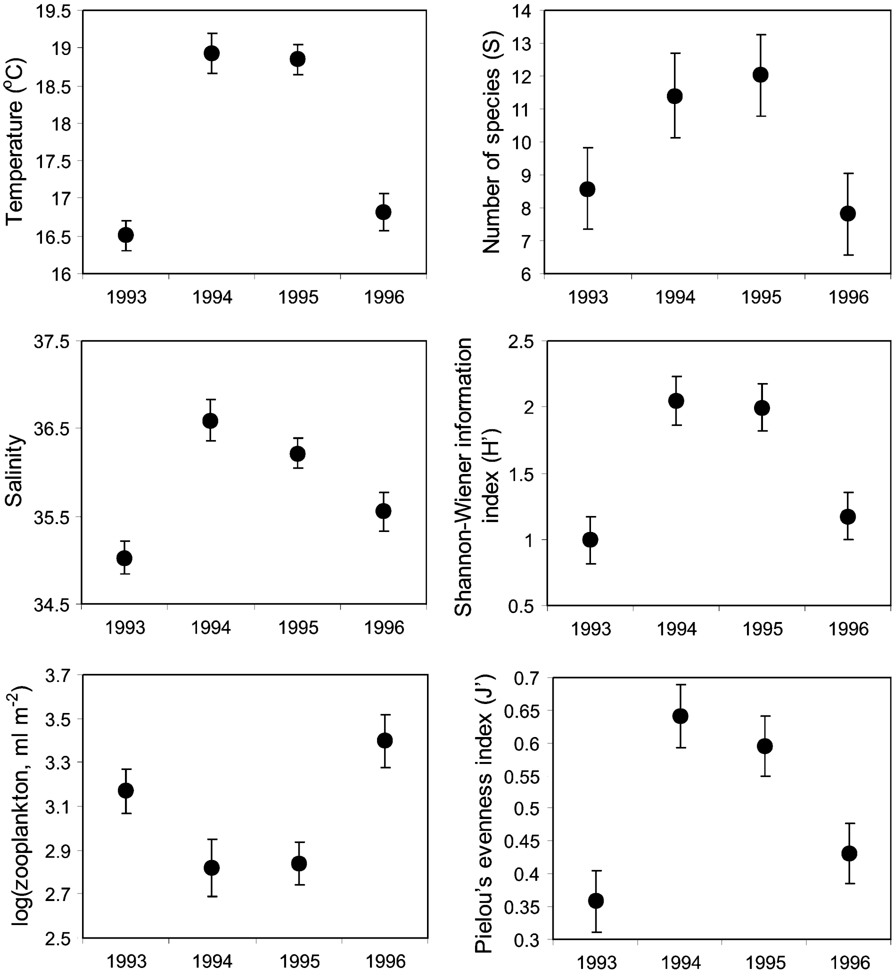


Fig. 3 **A** Plot of mean satellite SST for Western Black Sea (WBS), the Marmara Sea (SM) and the Northeastern Aegean Sea (NEA) in June 1993, 1994, 1995 and 1996. T5: mean temperature at 5 m measured during the ichthyoplankton surveys. **B** Regressions of mean monthly (March 1993–December 1997) SST in the WBS on SST in the NEA (*closed circles*) and SST in the SM on SST in the NEA (*open circles*). **C** The trend components of the SST data series in WBS (*dotted line*), SM (*grey line*), and NEA (*black line*)

Fig. 4 Means and 95% confidence intervals for temperature (0–40 m), salinity (0–40 m) and zooplankton (ZDV) (*left panel*) and selected diversity indices for ichthyoplankton (*right panel*)



A total of 57 larval taxa were identified in the collections (40 in 1993, 44 in 1994, 48 in 1995, and 41 in 1996) from which 30 taxa were common in all years (Table 1). The most common species were the small- and middle-sized pelagics, namely *Engraulis encrasicolus*, *Sardinella aurita*, *Trachurus mediterraneaus* and *Scomber japonicus*, certain mesopelagic species, e.g., *Ceratoscopelus maderensis*, *Hygophum benoiti*, *Myctophum punctatum*, *Maurolicus muelleri*, and the benthopelagics *Serranus hepatus*, *Callionymus* spp., *Cepola macrophthalma*, *Arnoglossus* spp., *Serranus cabrilla*, *Mullus barbatus*, *Chromis chromis*, and *Coris julis*.

Species diversity and evenness were significantly higher during the warm, 1994 and 1995, years (Fig. 4 right; $F = 18.18$, $P < 0.0001$ and $F = 15.83$, $P < 0.0001$ for H' and J', respectively). These differences were mainly due to the high dominance of anchovy (*E. encrasicolus*) larvae (Table 1) and the lower mean number of species observed during the cold years (Fig. 4 right; $F = 5.42$, $P < 0.01$ for S). Certain species, such as *Callanthias ruber*, *Trachinus draco*, *Lepidopus caudatus*, *Parophidion vassali*, *Lisa saliens*, *Microchirus variegatus* and *Symphurus nigrescens* were collected only during the warm years.

When examining inter-annual trends in mean abundance, it was quite evident that certain species exhibited contrasting patterns between cold and warm years (Fig. 5; Table 1). Anchovy (*E. encrasicolus*), which was the most abundant species, exhibited higher mean abundance during 1993 and 1996. A similar pattern was observed for most mesopelagic species (e.g., *M. muelleri*, *H. benoiti*, *M. punctatum*, *Cyclothone braueri*, *Bentosema glaciale*, *Vinciguerria* spp., *Lestidiops* spp., *Arctozenus risso*, *Argyropelecus*

Table 1 Frequency of occurrence (N%) and mean abundance values (ind. m^{-2}) of larval fish taxa identified in the collections (June 1993–1996)

Taxa	1993		1994		1995		1996		*P*
	N%	ind. m^{-2}	*N%*	ind. m^{-2}	*N%*	ind. m^{-2}	*N%*	ind. m^{-2}	
Sardinella aurita	44	10.87^{b}	67	19.80^{a}	94	35.38^{a}	56	6.80^{b}	*
Engraulis encrasicolus	100	301.04^{a}	89	$110.12^{b,c}$	100	80.52^{c}	100	$187.12^{a,b}$	*
Cyclothone braueri	11	0.88	11	0.14	22	0.17	11	0.96	ns
Argyropelecus hemigymnus	17	0.30					3	0.04	
Maurolicus muelleri	31	1.34^{a}	14	$0.34^{a,b}$	11	0.15^{b}	22	$1.06^{a,b}$	*
Vinciguerria spp.	17	0.50	14	0.27	14	0.15	19	1.03	ns
Stomias boa boa			6	0.05	8	0.07	8	0.12	
Glossanodon leioglossus							3	0.12	
Bentosema glaciale	17	0.37	11	0.19	17	0.20	22	1.24	ns
Ceratoscopelus maderensis	53	4.10	56	16.77	58	17.54	61	18.01	ns
Diaphus holti			3	0.03	6	0.05			
Hygophum benoiti	58	13.26	31	4.67	44	5.98	39	12.50	ns
Lampanyctus crocodilus	11	0.18	19	0.75	31	0.39	19	0.63	ns
Lobianchia dofleini	14	0.58	14	0.20	28	0.61	14	0.47	ns
Myctophum punctatum	44	4.14	19	1.62	31	2.08	33	5.45	ns
Lestidiops spp.	11	0.24	8	0.13	8	0.10	22	0.55	ns
Arctozenus risso	3	0.04					3	0.12	
Macrouridae					3	0.04			
Merluccius merluccius	3	0.05			3	0.02	6	0.09	
Anthias anthias			6	0.05					
Callanthias ruber			14	0.14	11	0.07			ns
Epinephelus spp.	3	0.04	8	0.14	3	0.03			
Serranus cabrilla	19	0.34^{c}	67	2.76^{a}	58	1.46^{b}	17	0.45^{c}	*
Serranus hepatus	83	10.25^{a}	78	11.34^{a}	86	7.76^{a}	67	2.69^{b}	*
Cepola macrophthalma	75	4.54^{b}	81	8.17^{a}	81	3.53^{b}	58	2.19^{b}	*
Trachurus mediterraneus	64	5.31^{b}	75	10.74^{a}	83	$6.61^{a,b}$	69	2.75^{b}	*
Trachurus trachurus	14	0.20	25	0.26	25	0.26	14	0.17	ns
Brama brama					3	0.01			
Mullus barbatus	17	0.33^{c}	58	2.75^{a}	47	1.27^{b}	8	0.24^{c}	*
Boops boops	17	0.26			11	0.07	8	0.16	ns
Dentex dentex	6	0.08	3	0.02			3	0.03	
Pagellus erythrinus	6	0.03^{b}	44	1.09^{a}	11	0.19^{b}	19	0.26^{b}	*
sparids/centracanthids	72	$5.24^{a,b}$	78	6.77^{a}	92	$3.09^{a,b}$	61	2.40^{b}	*
Chromis chromis	22	1.64^{b}	69	4.42^{a}	72	2.51^{a}	11	1.52^{b}	*
Coris julis	50	$1.22^{b,c}$	64	6.65^{a}	64	2.12^{b}	22	0.48^{c}	*
Labridae	33	0.85	56	1.68	64	1.82	42	1.75	ns
Trachinus draco			17	0.26	8	0.05			
Uranoscopus scaber	3	0.03							
Lepidopus caudatus			8	0.11	3	0.02			
Auxis rochei			25	0.39^{b}	44	1.04^{a}	3	0.11^{b}	*
Scomber japonicus	53	$2.13^{b,c}$	61	7.62^{a}	53	$6.81^{a,b}$	33	1.56^{c}	*
Gobiidae	94	$16.09^{a,b}$	81	5.18^{c}	97	$10.03^{b,c}$	100	18.78^{a}	*

Table 1 continued

Taxa	1993		1994		1995		1996		*P*
	N%	ind. m^{-2}	*N*%	ind. m^{-2}	*N*%	ind. m^{-2}	*N*%	ind. m^{-2}	
Callionymus spp.	97	13.07^{a}	81	4.99^{b}	89	12.09^{a}	94	9.68^{a}	*
Blennius ocelaris					3	0.02			
Blenniidae	17	0.37	36	0.44	42	0.39	22	0.40	ns
Parophidion vassali			8	0.08	22	0.22			
Carapus acus	3	0.03					3	0.03	
Liza saliens			6	0.06	19	0.18			
Scorpaena spp.	3	0.05^{b}	28	0.33^{a}	14	0.11^{b}	3	0.02^{b}	*
Lepidotrigla cavillone	3	0.04	6	0.05			3	0.03	
Arnoglossus spp.	72	4.66	72	2.39	81	2.28	72	1.97	ns
Buglossidium luteum	17	0.45	8	0.17	17	0.33	14	0.99	ns
Microchirus variegatus			6	0.06	3	0.02			
Solea lascaris	3	0.04					17	0.18	
Symphurus nigrescens			3	0.02	17	0.11			
Remora remora					3	0.01			
Lophius budegassa					3	0.02			

Results for analysis of variance and SNK multiple range tests on $\log(x + 1)$ abundance of dominant species are also given

For ANOVA *P* values: * $P < 0.001$, *ns* non significant, a, b, c: SNK test homogeneous groups (a > b > c)

hemigymnus) in terms of either abundance, frequency of occurrence or both (Fig. 5; Table 1). With the exception of three species (*C. maderensis*, *Lampanyctus crocodilus*, and *Lobianchia dofleini*), all remaining mesopelagic larvae showed relatively increased abundance during the cold years, especially in 1996 when zooplankton concentration was significantly higher (Fig. 4). In contrast, larvae of middle-sized pelagics, i.e., *S. aurita*, *T. mediterraneus*, *Auxis rochei* and *S. japonicus* presented higher abundance during the warm years (1994 and 1995). A similar pattern was also observed for certain demersal species, such as *M. barbatus*, *S. cabrilla*, *C. chromis*, *C. julis* and *C. ruber* (Fig. 5; Table 1). Larvae of most remaining benthopelagic species did not present any particular between-years pattern.

Finally, the NMDS results based on larval composition data showed that samples were differentiated according to depth but also according to the ‘cold-warm’ regime (Fig. 6). It must be noted here that three samples (i.e., stations 24, 25, and 42) collected in 1994 were not used in the MDS because they were biasing the ordination. These “outlier” stations were characterized by both very low total abundance and low number of species.

Haul depth, latitude and distance from coast explained 67, 60, and 28% of the variation in the ordination, along the axia separating shallow sites (<40 m), sites of intermediate depth (>40 m and <110 m) and deeper sites (>110 m) (Table 2; Fig. 6A). In addition, temperature, salinity and zooplankton (ZDV) explained a significant amount of variation in the sense of cold (1993 and 1996) versus warm (1994–1995) years (Table 2; Fig. 6B).

Discussion

Significant inter-annual differences in temperature, salinity, and zooplankton concentration have been recorded in the NEA during the four ichthyoplankton surveys which took place in the 1990s (1993–1996). The high correlation of the SST time series among the NEA, SM, and WBS as well as the similarity of the SST trend components among the three areas indicate that the Black Sea water (BSW) might have a dominant role in determining the oceanographic regime of the NEA. Recently, Oguz et al. (2003) provided evidence that an intense warming event with ~2°C increase in the SST of the open (>200 m

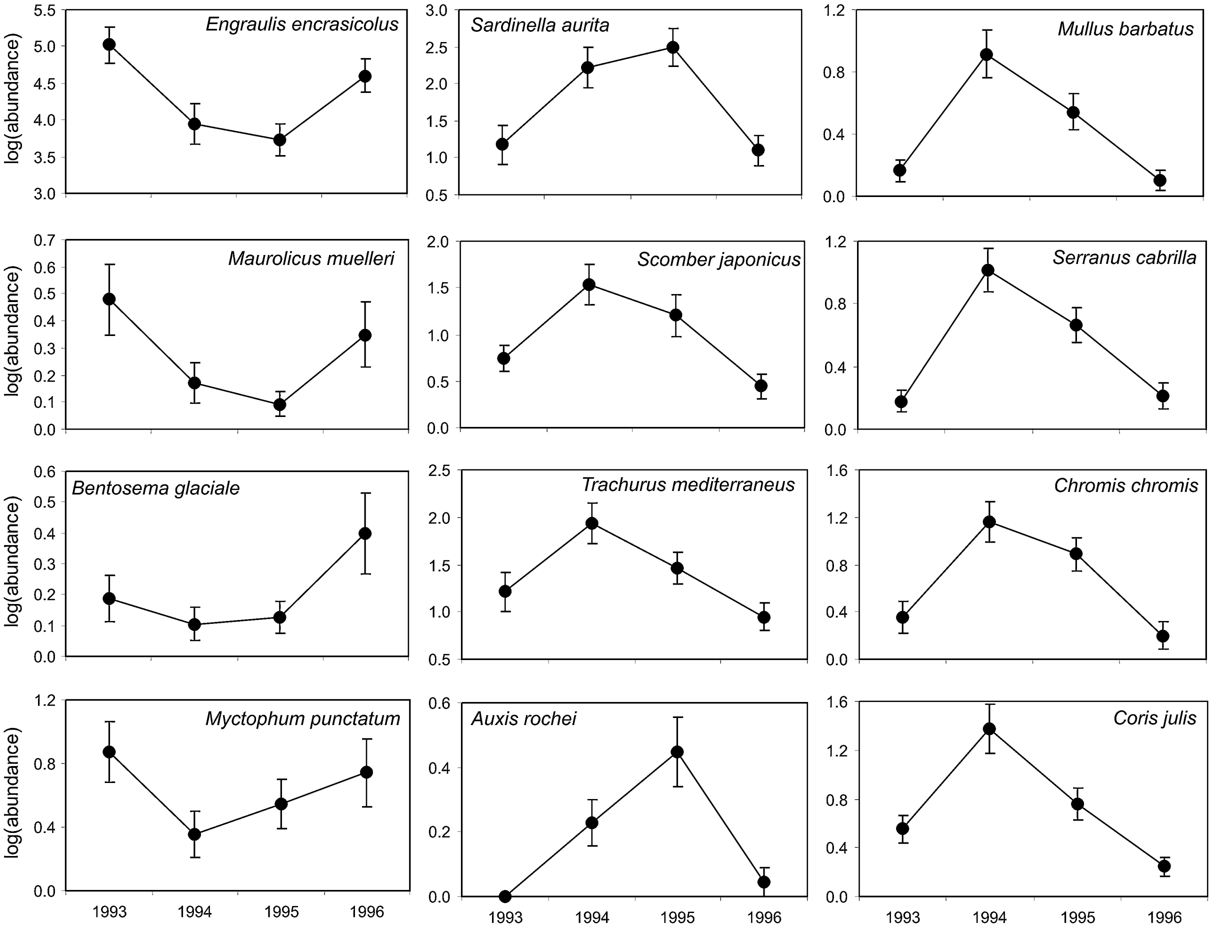


Fig. 5 Mean abundance (ind. m^{-2}) of selected larval species exemplifying among-year patterns. *Bars* indicate standard errors

depth) Black Sea took place during winters of the period 1995–1996, triggering changes in the ecological regime of the Black Sea. Furthermore, Stanev & Peneva (2002) have shown that negative anomalies in the outflow of BSW from the Bosporus Straits can result in increased salinity in the Aegean Sea. Hence, high salinity and lower productivity during the 1994 and 1995 surveys (warm years) might imply a decreased BSW influence (outflow).

Summing up, inter-annual differences in oceanographic conditions observed in this study are most likely related to changes in BSW properties and/or relative influence (e.g., amount of BSW entering into the NEA). We may hypothesize here that physical forcing affecting the Black Sea ecosystem might in turn affect the pelagic ecosystem of the Aegean Sea, a hypothesis that warrants further investigations.

Inter-annual differences in environmental conditions over the NEA were noticeably reflected in the structure and diversity of the larval fish assemblage. In the cold, less saline and richer in zooplankton regime (June 1993 and June 1996) larval diversity was significantly lower (Fig. 4). Factors determining the taxonomic composition and abundance were primarily depth-related (Fig. 6A), however inter-annual differences in temperature, salinity, and zooplankton (i.e., the cold-warm regime) were also significantly correlated with the NMDS scores (Fig. 6B).

In ichthyoplankton studies, individual species abundance among sampling stations generally exhibits high variability (in this study, coefficients of variation for dominant taxa ranged from 111 to 453%) and the number of stations feasible to sample is usually limited (here, $n = 36$). Hence, between-years

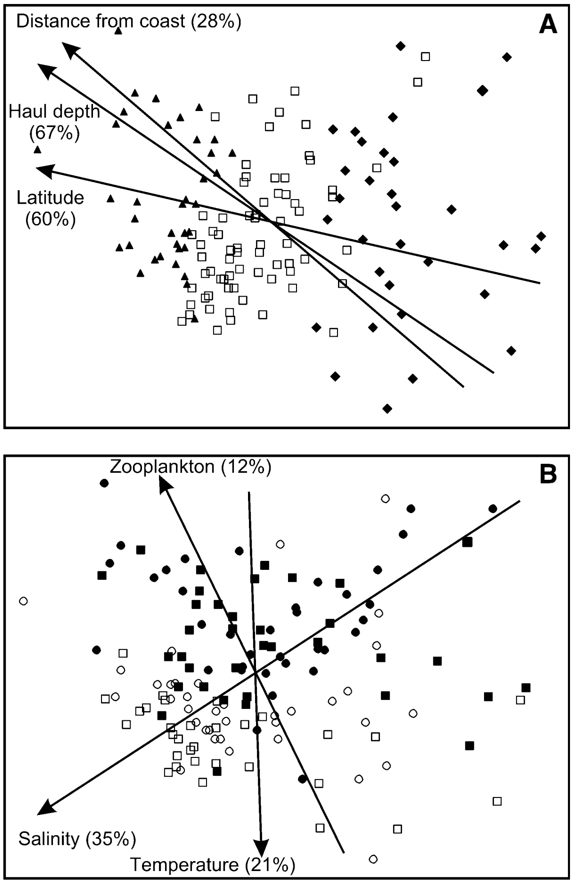


Fig. 6 Ordination plot of the comparison of sampling sites using non-metric multidimensional scaling and Bray-Curtis similarity index. **A** symbols according to station depth: *filled diamonds* < 40 m, *open squares* 40–110 m, *filled triangle* > 110 m. **B** Symbols according to sampling year (*open symbols* warm years, *closed symbols* cold years): *filled square* 1993, *open square* 1994, *open circle* 1995, *closed circle* 1996. Significant multiple regressions between ordination scores and environmental parameters are shown, as well as the fraction (%) of variance explained (see also Table 2)

Table 2 Multiple regression analysis between various environmental parameters and the NMDS scores for two-axis ordination of sampling sites

Variable	*X*	*Y*	Adjusted r^2	*F*	*P*
Haul depth	−33.44	15.32	67.15	141.0	<0.001
Latitude	0.15	−0.01	60.44	106.4	<0.001
Distance from coast	−2.62	1.25	27.9	27.7	<0.001
Temperature (0–40 m)	0.24	−1.4	21.37	19.4	<0.001
Salinity (0–40 m)	−0.78	−0.11	35.29	37.8	<0.001
Zooplankton (ZDV)	−4.84	5.17	12.49	10.9	<0.001
Longitude				2.26	>0.05

X and *Y* are the direction cosines (regression weights)

changes in mean abundance of most species are hard to be detected statistically (unless they are quite large) because the power of the Analysis of Variance and a posteriori multiple comparisons (i.e., avoiding Type II error) is low (Rotenberry & Wiens, 1985). This was especially true for mesopelagic species in this study (Table 1) because the number of stations sampled beyond the continental shelf was very low. However, despite the intrinsically low power for statistical inferences, when examining inter-annual trends in mean abundance, it was quite apparent that certain species exhibited contrasting patterns between the cold and warm years (Fig. 5; Table 1). Larvae of the small-sized species (anchovy and most mesopelagic species) were more abundant during the cold, less saline and zooplankton-rich years. A similar association of larvae of Engraulidae and Myctophidae with increased plankton production has also been reported off the U.S. northwest coast (Doyle et al., 1993). Other pelagic species, namely *S. aurita*, *T. mediterraneus*, *S. japonicus*, and *A. rochei* were more abundant during the warm regime (1994 and 1995). The same trend (higher relative abundance during the warm years) was observed for certain benthopelagic species (*M. barbatus, S. cabrilla, C. julis, and C. chromis*). Others, namely *C. ruber*, *T. draco*, *L. caudatus*, *P. vassali*, *L. saliens*, *Microchirus variegatus* and *S. nigrescens* were only collected during the warm years.

The period of spring-early summer is a transitional period in the reproduction of Mediterranean fish species (Sabatés & Maso, 1992; Sabatés & Olivar, 1996). It marks the end of the spawning season of those species that reproduce during the winter months (e.g., *Trachurus trachurus*, *Boops boops*) and the start of spawning for summer spawners (Tsikliras et al., 2010). This period coincides with the peak of spawning for anchovy (Palomera, 1992; Somarakis, 1999). There is only a single detailed study on seasonal patterns of larval fish occurrence in the Mediterranean (Sabatés, 1990). It shows that species such as *S. aurita*, *T. mediterraneus*, *S. japonicus* *και A. rochei, S. cabrilla*, *L. saliens, T. draco* and

S. nigrescens exhibit their peak abundance after the peak of anchovy and they comprise the group of the so called 'summer spawners'. The lower abundance (or absence) of these species in the NEA during the cold 1993 and 1996 years could be attributed to higher temperature thresholds for the onset of spawning in typically summer spawners.

Inter-annual differences in the abundance trends of the different larval taxa could not be explained in terms of changes in specific hydrographic structures (e.g., fronts, gyres) or currents differentially modifying the advection of larvae (Somarakis, 1999). Patterns of species distribution as well as horizontal patterns of hydrological properties (temperature, salinity, density) and inferred baroclinic currents, were very similar among years (not shown here, but see Somarakis et al. (2002) for the 'warm' June 1995 and the 'cold' June 1996). The semi-permanent anticyclones (like the Samothraki gyre) that are present in the area, always resided on the shelf and their effect on distributions could hardly be identified for pre-flexion larvae that dominate the bongo-net collections (e.g., Somarakis & Nikolioudakis, 2007).

In conclusion, the data presented here imply: (a) a temporal (inter-annual) covariation in larval production for the small-sized anchovy and mesopelagic species that is likely related to zooplankton production and (b) a similar covariation for typically summer spawners that can be explained in terms of temperature effects on the onset of the reproductive period. Larval abundances are primarily measures of the spawning biomass and reproductive effort of the adult stock, because most larvae sampled by low-speed plankton nets are in early stage of development (e.g. Somarakis et al., 1998). Since sudden changes in adult biomass would not be expected, short-term inter-annual changes in larval abundance are most likely related to adult reproductive output (Moser et al., 2000; Hsieh et al., 2005; Doyle et al., 2009). Regarding the pelagic species in this study, observed inter-annual differences have been explained in terms of the life history theory (Somarakis et al., 2000) and, specifically, the hypothesis of contrasting reproductive strategies among pelagic species (capital vs. income breeding, Stearns (1992)), coupled with differences in morphology and performance abilities of the larvae (Somarakis et al., 2000). At least for anchovy, for which concurrent adult fish sampling was carried out in June 1993 and June 1995, it has been shown that somatic condition, egg size, batch fecundity, and spawning frequency were significantly higher in 1993 (when adult prey fields -zooplankton- were higher) but spawning stock biomass was similar between 1993 and 1995 (Somarakis, 2005).

According to Frank & Leggett (1983), temporal and/or spatial covariation in the abundance of different species in the plankton implies similar inter-specific responses to the pelagic environment, i.e., co-adaptation of reproductive strategies (Moser & Smith, 1993). The synchrony in species larval abundance, similarities in links with physical and trophic variables and commonality of reproductive and early life history strategies imply common response to physical forcing and regime shifts and may explain the phenomenon of synchrony in recruitment and biomass trends among different populations (Doyle et al., 2009).

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