

Distribution and abundance of larval fish in the northern Aegean Sea—eastern Mediterranean—in relation to early summer oceanographic conditions

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*Two ichthyoplanktonic surveys were conducted during June 1995 and 1996 along the northern Aegean Sea coast with the aim of describing species composition, abundance and distribution patterns of the assemblages of fish larvae and their relationships to oceanographic regimes. The upper water column was generally cooler, fresher and richer in zooplankton during June 1996. The mean abundance of larvae of the small-sized pelagic fish (anchovy and most mesopelagics) was higher in 1996. In contrast, larvae of the middle-sized pelagics (*Sardinella aurita*, *Trachurus mediterraneus*, *Scomber jaconicus* and *Auxis rochei*) were more abundant in 1995. The eastern part of the surveyed area (NE Aegean Sea) was colder and less saline during both years because of the influence of Black Sea and riverine waters. In the colder June 1996, larvae of many ‘summer spawners’, e.g., the middle-sized pelagics, were present infrequently and at very low numbers in the NE Aegean Sea. Cluster analysis using the Bray–Curtis similarity index revealed well-defined groups of stations and assemblages of larvae. Ordination scores derived from non-metric multidimensional scaling were compared by multiple regression with various parameters and the analysis showed that taxonomic composition and abundance was primarily explained by bathymetry. In the cooler June 1996, a significant amount of variation in ordination scores was related to longitudinal differences in temperature, salinity and the width of the continental shelf. The membership of station and species groups defined by the cluster analysis differed between 1995 and 1996 and reflected interannual differences in the distribution and abundance of component species. Spatial and temporal spawning patterns of adults played the key role in the formation of assemblages of early larvae.*

INTRODUCTION

Spawning times and locations of fish species are generally believed to have evolved so that the meroplanktonic early-life stages emerge into an environmental regime that is suitable for their survival (Cushing, 1969). Favourable larval habitats have been defined by both their biological (e.g. high abundance of food, low abundance of predators) and physical (e.g. circulation patterns promoting retention or transport to nursery areas) characteristics (Heath, 1992). However, the environmental conditions at the time of egg and larval development may differ from

year to year, due to variation in the environmental characteristics, changes in the timing of emergence of eggs and larvae or a combination of both (Page and Frank, 1989). Variation in the oceanographic environment on an annual scale may cause interannual changes in both the distributional range of the adult fish and the features of their spawning environment such as timing, duration and location of spawning (Doyle *et al.*, 1993). The patterns of distribution of the spawning products are initially set by the adults, but a combination of physical and biological factors (such as water movement and temperature, distribution and abundance of prey and predators) act directly

on larvae to influence their distribution, abundance, growth and survival (Heath, 1992). Examining spatial and temporal patterns in distribution and abundance of ichthyoplankton in relation to oceanographic conditions may provide insight into the adaptation of spawning strategies to the prevailing physical and biological processes as well as into the effect of the variability in these processes on year-class strength.

Under the more general multispecies framework in the study of fish populations, a recent approach to investigating ichthyoplankton spatial patterns has been to identify larval fish assemblages and relate their occurrence and variability to the biology of the component species and to the pelagic ecosystem in which they occur (Moser and Smith, 1993). An important consideration in assemblage studies is whether larval fish associations are adaptive and result from similar responses among species to the pelagic environment (Frank and Leggett, 1983; Somarakis *et al.*, 2000).

This paper presents results of the first broad-scale multispecies ichthyoplankton investigation in the eastern Mediterranean. It involves the definition of early summer larval fish communities in the northern Aegean Sea, their composition, the dominant or indicator species, the major distribution patterns, both across and along the continental shelf, and, where possible, the principal characteristics of the water column that control these patterns. Late spring to early summer is a transition period in the spawning of Mediterranean marine fish: summer spawners start their spawning season and ichthyoplankton is at maximum abundance and species diversity (Sabates, 1990a; Sabates and Maso, 1992; Sabates and Olivar, 1996).

The northern Aegean Sea (Figure 1) connects with the Black Sea through the Bosphorus Straits, the Marmara Sea and the Straits of Dardanelles. It has the widest continental shelf and is the most productive region of the Aegean Sea (Stergiou *et al.*, 1997). The combination of brackish water inflow from the Dardanelles (Black Sea water – BSW) and discharge from a series of large rivers in the inner shelf (Figure 1) are the predominant factors affecting the structure of the water column in the area (Zervakis *et al.*, 2000). The circulation is mainly determined by the surface inflow from the Dardanelles, which, under the influence of the prevailing wind patterns, shifts above or below the island of Lemnos, creating various thermohaline fronts and gyres (Poulos *et al.*, 1997). During summer, the BSW follows a southwestward route due to the Etesians (summer northerly winds), whereas during autumn, winter and spring, it enters the Thracian Sea by following a northwestward route through the strait between the islands of Lemnos and Imvros. This stream feeds the Samothraki anticyclonic gyre, an almost permanent

feature that can be detected throughout most of the year (Poulos *et al.*, 1997; Stergiou *et al.*, 1997). The northern Aegean continental shelf is the most important area for the Hellenic fisheries, however, it has rarely been studied (Stergiou *et al.*, 1997).

METHOD

Sample collection and analysis

Larval fish were collected during two surveys carried out in 15–30 June 1995 and in 6–21 June 1996 in the northern Aegean Sea (eastern Mediterranean). The sampling scheme was based on transects spaced approximately 10 nautical miles apart and stations located at 10 nautical-mile intervals on each transect (Figure 1). The same stations ($n = 64$) were sampled in both years, except that in 1996, five additional offshore stations were sampled in the eastern part of the study area (Thracian Sea and Kavala Gulf).

A 60 cm bongo-net sampler was used on both cruises. Mesh sizes on the sampler were 335 and 250 μm . Tows were double oblique and the volume filtered was determined by a calibrated flow meter (Hydrobios) in the mouth of each of the nets. The depth of the sampler could be monitored onboard at any time during the tow by means of a recording depth meter attached to the sampler. Maximum tow depth and volume of water filtered were subsequently used to standardize catches to numbers per square metre. More details are provided in Somarakis *et al.* (Somarakis *et al.*, 1998).

In the laboratory, larvae from the 0.250 mm mesh net were identified to the lowest possible taxonomic level. Larvae were sorted into yolk-sac larvae and post-yolk-sac larvae, then counted and measured. Zooplankton displacement volume (ZDV) was measured for each sampling site from the catch of the 0.250-mm mesh bongo net (Smith and Richardson, 1977). ZDV values were standardized to ml m^{-3} .

In the present paper, the focus is on post-yolk-sac larvae rather than the total ichthyoplankton. Fish embryos (egg and yolk-sac larvae) of Mediterranean fish are still poorly known and incompletely identified in plankton collections. Less than 40% of the eggs and yolk-sac larvae of the species identified as post-yolk-sac larvae in this study have been adequately described (Filippou, 1997). Furthermore, many species (e.g. gobiids, *Chromis chromis* etc.) have demersal eggs though their planktonic larvae are prominent members of the ichthyoplankton.

Hydrographic data and geostrophic analysis

Hydrographic data were collected on a denser grid of 144 and 147 stations in 1995 and 1996 respectively. A SBE-19

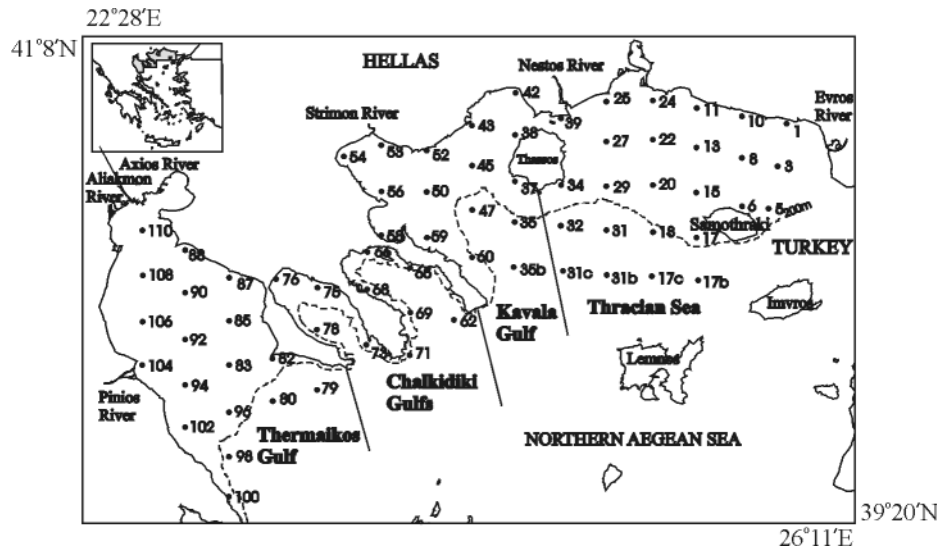


Fig. 1. Map of the survey area showing the location and labels of ichthyoplankton sampling stations, as well as the toponyms mentioned in the text. The survey area can be divided into four sub-regions (Thracian Sea, Kavala Gulf, Chalkidiki Gulfs and Thermaikos Gulf) based on topographic and hydrographic characteristics. In June 1996, the sampling transects in the eastern part of the area were extended by 10 nautical miles and five additional stations were sampled (17b, 17c, 31b, 31c and 35b).

Seacat internally recording CTD (Conductivity-Temperature-Depth) has been used and the resulting temperature and salinity profiles had a vertical resolution of 1 metre. Circulation patterns potentially influence the distribution of larval fish assemblages, however, the surface circulation for the surveyed area was poorly known. In order to overcome this limitation, we have obtained a first estimate of the surface geostrophic flow field during the time the cruises were held by exploiting the relevant information present in the density profiles. This was accomplished with standard geostrophic analysis, i.e. geostrophic currents were estimated assuming a balance between the horizontal pressure gradient and the Coriolis force (e.g. Pond and Pickard, 1983; Reiss *et al.*, 2000):

$$f\bar{v} = \frac{\partial D}{\partial x}, f\bar{u} = -\frac{\partial D}{\partial y}$$

where f is the Coriolis parameter, u and v are the eastward and northward components of the velocity and D is the dynamic height defined as:

$$D = \int_P^{P_2} \frac{dp}{\rho(p)}$$

where p is the pressure and ρ is the water column density.

The steps taken were the following: First we evaluated the dynamic height at a particular depth relevant to a predefined depth (the limits of integration) for each hydrographic station, then we applied Kriging objective analysis in order to obtain a smooth dynamic height field and

finally we differentiated horizontally this field which in turn yielded the flow field at this depth. A drawback of this method is that the inferred currents include only the baroclinic component relevant to the predefined depth. This predefined depth for our case was taken to be 50 m. This is justified as follows: most of the shelf area ranges from 50 to 100 m, thus most of our stations were included in this analysis. Furthermore, due to the influence of the riverine and Black Sea outflows, most of the vertical shear in the flow field is present in the upper layer (Theocharis and Georgopoulos, 1993). Therefore the baroclinic currents relevant to the depth of 50 m are expected to be the most energetic, and in any case to give a qualitative picture of the poorly known surface circulation of the area.

Multivariate analysis

The inclusion of a taxonomic category in the community analysis was based on the criterion of identification to species or type (Cowen *et al.*, 1993). Sampling sites were compared first to define areas with similar species composition. The species by sampling site matrix, expressed as abundance values (number of individuals per m²), was analysed using both cluster analysis and non-metric multidimensional scaling (NMDS) (Field *et al.*, 1982; Clarke and Warwick, 1994). Data were transformed using the $\log_{10}(x + 1)$ function to enhance the contribution of the less abundant species. Hierarchical agglomerative clustering was carried out first using the Bray–Curtis similarity

index coupled with group average linkage. This technique has been proved appropriate for delineating groups of sites with distinct community structure in a large number of ecological studies (Clarke and Warwick, 1994).

Following cluster analysis, the data sets were further subjected to NMDS ordination. Prior to ordination, ‘outlier’ sample sites identified by cluster analysis were removed from the data set to obviate problems associated with such outliers, e.g. biasing or dominating the ordination, often compressing the distribution of the remaining sites (Gauch, 1982; Hosie and Cochran, 1994). NMDS ordinations may be arbitrarily rotated and so axes are not labelled.

Ordination scores derived from NMDS were subsequently compared by multiple regression analysis with various parameters to determine which of these parameters may best explain the larval distributions (Kruskal and Wish, 1978; Hosie and Cochran, 1994). The parameters examined were latitude, longitude, distance from the coast, tow-depth, temperature and salinity.

Regression analysis involved treating each parameter as the dependent variable and the NMDS scores for each axis as the independent variables (Kruskal and Wish, 1978). In contrast to other methods (canonical analysis, non-parametric methods [e.g. (Clarke and Ainsworth, 1993)], this technique is not based on an *a priori* ecological hypothesis, it is not affected by parameter inter-correlations, and does not remove the variance explained by previously used variables (Karakassis and Eleftheriou, 1997; Grioche *et al.*, 1999). By comparing the coefficient of determination of each parameter, the variable that explained best the larval distribution could be determined. Regression lines and their directions were plotted in the corresponding NMDS graphs using the technique described by Kruskal and Wish (Kruskal and Wish, 1978).

The direction of maximum correlation of each regression line is at an angle ϕ_r with the r th MDS axis. The direction cosine, or regression weight, c_r , of that angle is derived from 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 axes.

Sampling site groups determined by the analysis were further analysed to define abundance indicator species. These comprised species that distinguish a group by their higher abundance. Only dominant species, defined as those with mean abundance >0.5 individuals per m² in at least one group of sampling sites, were used. To provide a more powerful comparison of differences in species abundance, we bootstrapped 95% confidence intervals on resulting means (Thorrold and McKinnon, 1995). We calculated 1000 bootstrap estimates. Parametric tests (i.e. analysis of variance) were not used because the data did not meet the required assumptions.

Inverse analysis of the data sets to define dominant species affinities also involved cluster analysis with Bray–Curtis index and group average linkage. Dominant species were used and data were standardized according to Field *et al.* (Field *et al.*, 1982).

RESULTS

Environmental conditions

The water column in the northern Aegean Sea presented typical spring to early summer conditions during both years (Figure 2). It was generally well stratified and the

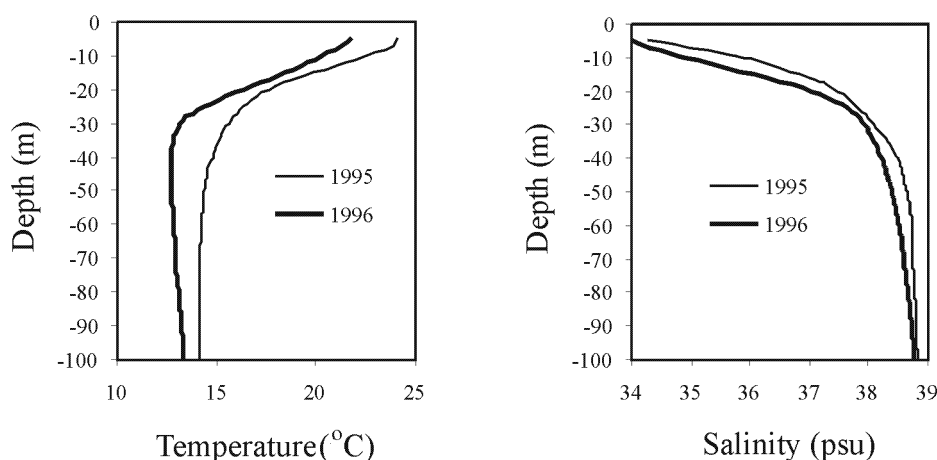


Fig. 2. Average water column properties during June 1995 and June 1996.

Table I: Northern Aegean Sea. averages and standard deviations (SD) for temperature and salinity at 5 m and at the thermocline. Averages and standard deviations for zooplankton displacement volumes (ZDV) are also given

	June 1995		June 1996	
	Average	SD	Average	SD
Temperature (°C)				
5 m	24.1	1.5	21.8	1.1
Thermocline	21.0	2.4	17.7	2.1
Salinity (psu)				
5 m	34.3	1.3	33.6	1.3
Thermocline	36.5	1.2	36.5	1.1
ZDV (ml m ⁻³)	0.29	0.17	0.62	0.38

thermocline was located at a mean depth of 14 m in 1995 and 18 m in 1996. The upper water column was generally cooler and less saline in 1996 than in 1995 (Figure 2, Table I). Mean zooplankton displacement volume [which can be considered a rough index of zooplankton production (Smith and Richardson, 1977)] was twice as much in 1996 as in 1995 (Table I).

The horizontal distribution of surface temperature and salinity showed a consistent pattern in the two years (Figure 3). Lower salinities were observed at the inshore sites of the Thracian Sea and Kavala Gulf, which receive the freshwater influence from three large rivers (Evros, Nestos and Strimon rivers; Figure 1). The Thracian Sea, influenced by the Lemnos–Imvros stream (see below), was generally cooler and less saline than the rest of the surveyed area. Due to mesoscale variability, the thermocline depth varied, having a tendency to move upward in cyclonic areas and downward in anticyclonic areas. Hence, horizontal patterns of the upper column temperature conditions were better depicted when means (e.g. mean temperatures in the 0–20 m layer) or temperatures at isopycnal surfaces were examined. On the isopycnal surface of $\sigma_t = 26$ (Figure 4), which was the approximate mean density of the pycnocline, the distribution of temperature showed two regimes: the cold (and fresher) tongue of mainly Black Sea and riverine waters in the Thracian Sea and Kavala Gulf, and the warmer, more saline waters in Thermaikos, Chalkidiki Gulfs and the area south of the island of Thassos. In June 1995 (Figure 5), the circulation appeared to be cyclonic overall and the predominant feature in the West was a well-defined cyclonic gyre located at the entrance of Thermaikos Gulf.

In the east, the main feature was the Lemnos–Imvros stream resulting from the BSW outflow from the Dardanelles. The stream bifurcated as it moved north-west and one section fed a large anticyclone, at the same time as the other, in a cyclonic movement, returned in a southward direction. The circulation in the Kavala Gulf was mainly anticyclonic. Mean surface geostrophic velocities were low (of the order of 5 cm s⁻¹). In June 1996, surface circulation was more anti-cyclonic (Figure 5). The Lemnos–Imvros stream was again present; however, its northwestward and then southward propagating cyclonic components were stronger. The circulation in the Thermaikos Gulf was unsettled with no clearly recognizable features apart from an anticyclone at the entrance.

Taxonomic composition and abundance

A total of 77 taxa were identified (70 taxa in 1995 and 65 in 1996). Fifty-six taxa were present in both years' collections (Table II).

Larvae of small-sized, short-lived pelagic species, such as the anchovy (*Engraulis encrasicolus*), and the mesopelagic fish (e.g. *Cyclothone braueri*, *Maurollicus muelleri*, *Vinciguerria* spp., *Benthosema glaciale*, *Myctophum punctatum* and *Lestidiops jayakari*) were more abundant in 1996 than in 1995. Larvae of middle-sized pelagics (i.e. *Sardinella aurita*, *Trachurus mediterraneus*, *Auxis rochei* and *Scomber japonicus*) were less abundant and/or frequent in the 1996 collections.

With some exceptions (e.g. callionymids), the abundance of larvae of most demersal species was similar between the two years. However, certain of them (e.g. *Chromis chromis*, *Mullus* spp.) occurred more frequently (in many stations) in 1995 compared to 1996 (Table II). Some

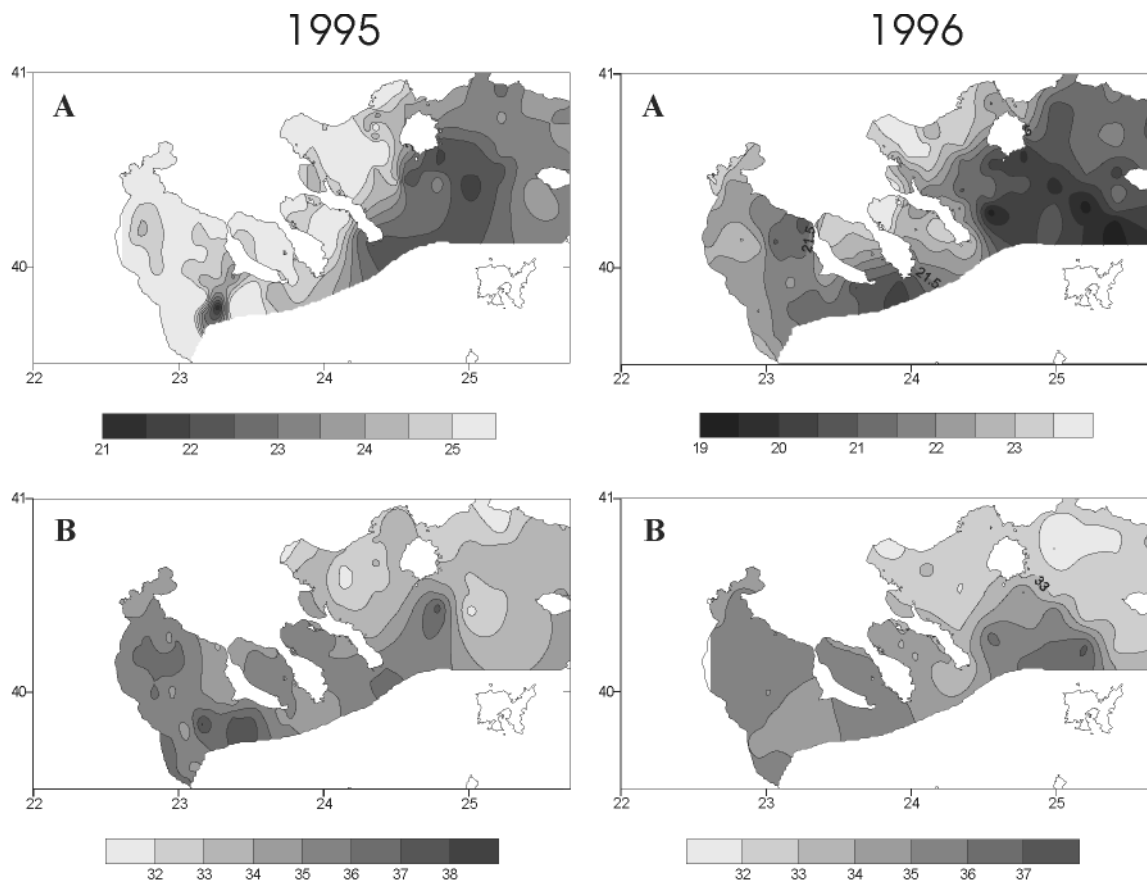


Fig. 3. Contour maps of surface (5 m) temperature (A) and salinity (B) during June 1995 and June 1996.

typical summer spawners, such as *Apogon imberbis* and *Symphurus nigrescens* were quite common in 1995 but absent in 1996.

Individual species distributions

Distribution and abundance maps of several species, exemplifying between-year similarities and differences, are given in Figures 6, 7 and 8. Several species, such as *Buglossidium luteum*, *Arnoglossus* spp. (Figure 6), *Engraulis encrasicolus*, *Callionymus* spp., *Cepola rubescens*, *Serranus hepatus*, Labridae I and the mesopelagic species (Figure 6) did not show any marked interannual differences in their horizontal distribution (although their abundance might have been different between the two years, e.g. the abundance of most mesopelagics). Several other species, specifically the middle-sized pelagics [*Sardinella aurita* (Figure 7), *Trachurus mediterraneus* (Figure 8), *Auxis rochei* (Figure 7) and *Scomber japonicus* (Figure 8)] and the demersals [*Mullus* spp. (Figure 7), *Chromis chromis* (Figure 8) and *Serranus cabrilla*], showed a peculiar distribution in 1996, being almost absent or present infrequently and at low

numbers in the eastern part of the surveyed area (Thracian Sea and Kavala Gulfs). Furthermore, the abundance of these species was particularly high in the Gulfs of Chalkidiki and the offshore sites of the Thermaikos Gulf in 1996 (i.e. at sites where the abundance of mesopelagic larvae was also very high).

Comparison of sampling sites

Cluster analysis of sampling sites produced four distinct cluster groups in 1995 at the 45% similarity level and three groups in 1996 at the 44% similarity level (Figure 9). There were two distinct outlier stations in 1995 and one outlier station in 1996 (Stn 45 and Stn 88 in 1995 and Stn 34 in 1996). These stations had peculiar species compositions (i.e. exceptionally high abundance of one or two rare species). The NMDS ordinations, excluding outlier stations, showed that the station groups identified in cluster analysis were quite distinct (Figure 10). In 1995, Groups 1a and 1b comprised inshore stations, Group 2 were predominantly continental shelf stations, whereas Group 3 were outer-shelf and off-shelf sites (Figure 9).

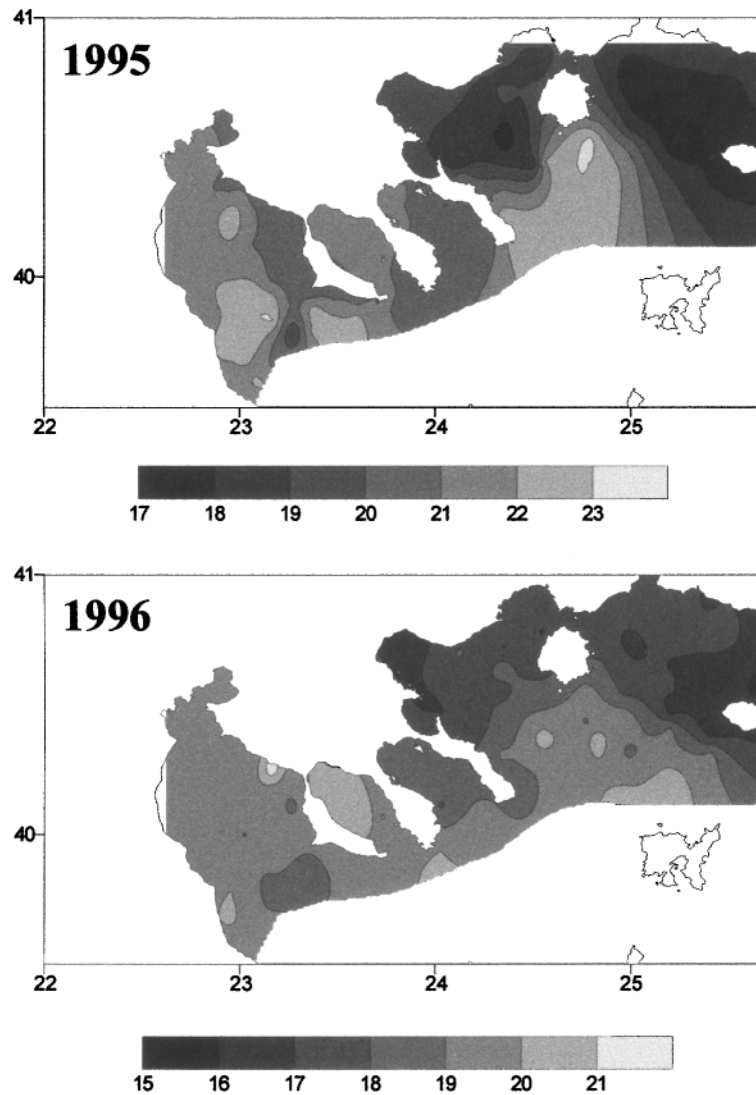


Fig. 4. Contour maps of temperature on $\sigma_t = 26$ during June 1995 and June 1996.

Similarly, in 1996, Group 1 comprised inshore stations, Group 2 comprised the majority of continental shelf stations and Group 3 comprised mainly outer-shelf and off-shelf sites (Figure 9). Fourteen stations belonging to Group 2 in 1995 were clustered in Group 3 in 1996. For example, all sites in the Chalkidiki Gulfs (where the continental shelf is quite narrow) were clustered within the 'off-shore' group in 1996 (Group 3).

Depth explained 74% and 82% of the variation of the data in the respective 1995 and 1996 NMDS ordinations (Table III, Figure 10). In contrast to 1995, all parameters examined in 1996 explained an amount of the variation in the NMDS ordination at a significant level (Table III).

Based on relative angles of intersection, variables could be grouped into: (a) Depth, (b) Latitude and Salinity, mainly explaining the contrast of Group 1 which was characterized by the lowest salinity values (Figure 3) and, (c) Longitude, Distance from coast and Temperature. The latter two sets of variables, particularly the last one, seemed to mainly explain within-station group variability in species composition and abundance, which was related to longitudinal differences in temperature, salinity and width of the continental shelf (Figures 1, 3 and 4), and was mainly due to the peculiar distribution patterns of certain species, such as the middle-sized pelagics (Figures 7 and 8).

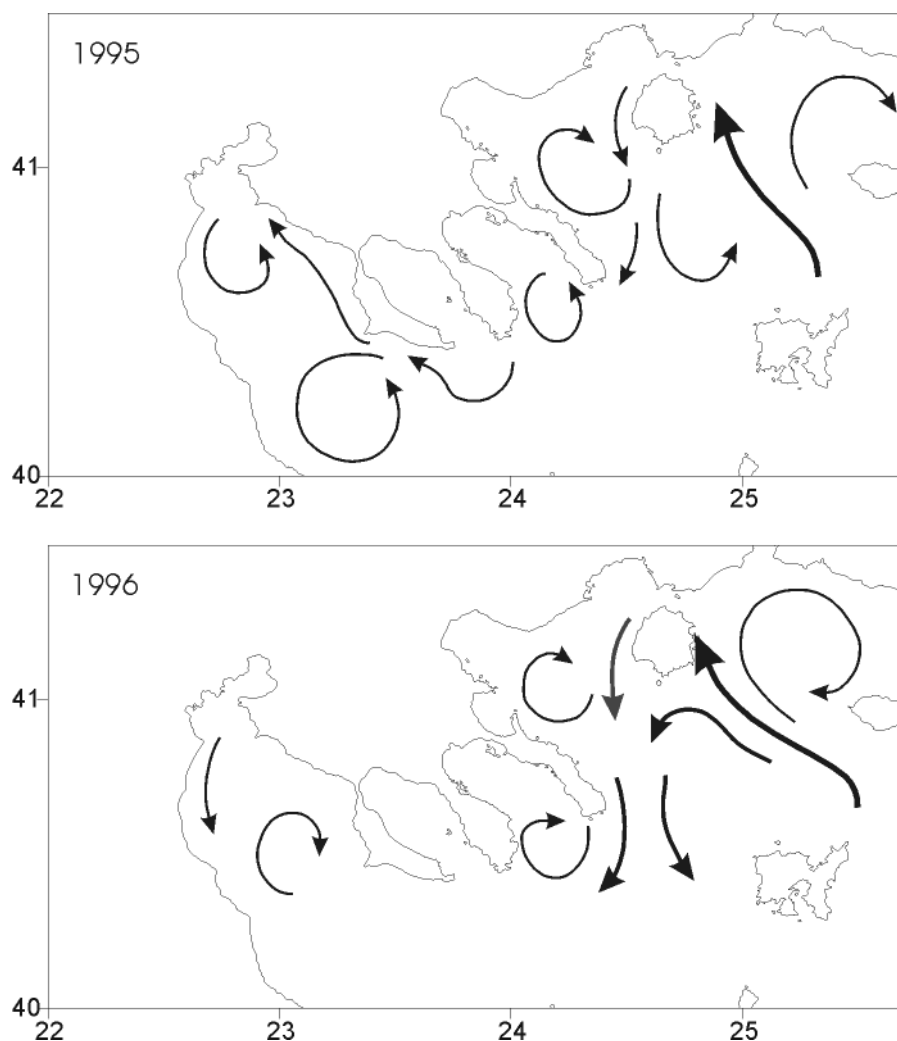


Fig. 5. Patterns of surface circulation (inferred baroclinic currents at 5 m relevant to the depth of 50 m) during June 1995 and June 1996. The thickness of lines is indicative of the strength of estimated geostrophic velocities.

Abundance indicator species

The inshore group of stations, Group 1b, identified in 1995 differed from Group 1a, in having low abundance of *Callionymus risso* (Table IV). Some species abundant in Group 1a, such as *Buglossidium luteum* and *Cepola rubescens*, were not captured in Group 1b. Furthermore, Labridae II was collected only in the Group 1b (Table IV). The latter was a small group of stations ($n = 4$) and was not used in any of the subsequent comparisons.

Patterns common to both years (Tables IV and V)

The inshore sites (Group 1a in 1995 and Group 1 in 1996) were generally characterized by the presence of the flatfish *Buglossidium luteum*. The callionymid

Callionymus risso characterized both Group 1 and Group 2, whereas *Arnoglossus laterna* was the abundance indicator of Group 2. Mesopelagic fish larvae, such as *Cyclothone braueri*, *Cerato scopelus maderensis*, *Hygophum benoiti*, *Lampanyctus crocodilus*, *Lobianchia dofleini* and *Lestidiops jayakari*, characterized the ‘offshore’ sites (Group 3). Mesopelagic species, the scombrids *Scomber japonicus* and *Auxis rochei* and the callionymid *Callionymus maculatus*, were absent from Group 1 in both years. The clupeoids *Sardinella aurita* and *Engraulis encrasicolus*, the serranids *Serranus* spp., the near-shore species *Chromis chromis* and *Coris julis*, the carangid *Trachurus mediterraneus*, the mullids *Mullus* spp. and the cepolid *Cepola rubescens* were found in lower numbers in Group 1.

Table II: List of larval fish taxa identified in the bongo-net collections (June 1995, June 1996—Northern Aegean Sea)

Order	Family	Larval taxa	1995		1996		
			N%	N° m ⁻²	N%	N° m ⁻²	
Clupeiformes	Clupeidae	<i>Sardinella aurita</i>	84	19.27	52	28.21	
	Engraulidae	<i>Engraulis encrasicolus</i>	97	44.14	100	115.90*	
	Gonostomatidae	<i>Cyclothone braueri</i>	19	0.47	32	2.33*	
	Sternoptychidae		<i>Argyropelecus hemigymnus</i>			6	0.09
			<i>Maurollicus muelleri</i>	11	0.15	35	1.98*
		Photichthyidae	<i>Vinciguerria</i> spp.	17	0.21	36	2.64*
		Stomiidae	<i>Stomias boa</i>	9	0.06	13	0.15
		Argentinidae	<i>Glossanodon leioglossus</i>			4	0.06
Scopeliformes	Myctophidae	<i>Benthoosema glaciale</i>	13	0.14	33	1.86*	
		<i>Ceratoscopelus maderensis</i>	59	21.90	70	72.40*	
		<i>Diaphus holti</i>	8	0.07	7	0.10	
		<i>Hygophum benoiti</i>	47	10.89	54	35.33*	
		<i>Lampanyctus crocodilus</i>	25	0.63	33	1.65	
		<i>Lobianchia dofleini</i>	31	0.61	29	1.42	
		<i>Myctophum punctatum</i>	34	1.97	45	8.92*	
	Paralepididae	<i>Lestidiops jayakari</i>	14	0.18	32	0.94*	
		<i>Lestidiops sphyrenoides</i>	3	0.02	6	0.06	
		<i>Notolepis rissoi</i>			6	0.12	
Anguilliformes	Congridae	<i>Ariosoma balearicum</i>	2	0.01			
Gadiformes	Macrouridae	<i>Coryphaenoides</i> sp.	2	0.02			
	Merlucciidae	<i>Merluccius merluccius</i>	2	0.01	7	0.17*	
Zeiformes	Zeidae	<i>Zeus faber</i>	2	0.01	1	0.01	
Perciformes	Serranidae	<i>Callanthias ruber</i>	17	0.18	7	0.10	
		<i>Epinephelus</i> sp.	3	0.02	1	0.02	
		<i>Serranus cabrilla</i>	58	1.08	41	1.50	
		<i>Serranus hepatus</i>	88	7.56	74	5.12	
	Apogonidae	<i>Apogon imberbis</i>	20	0.24			
	Cepolidae	<i>Cepola rubescens</i>	72	3.21	54	2.22	
	Carangidae	<i>Trachurus mediterraneus</i>	89	7.46	71	3.74	
		<i>Trachurus trachurus</i>	13	0.12	12	0.16	
	Bramidae	<i>Brama brama</i>	2	0.01			
	Mullidae	<i>Mullus</i> spp.	41	0.83	22	0.80	
	Sparidae	<i>Boops boops</i>	9	0.06	9	0.16	
		<i>Dentex dentex</i>	3	0.02	3	0.03	
		<i>Pagrus pagrus</i>	22	0.25	19	0.29	
		Sparidae I	9	0.06	1	0.03	
		Unidentified sparids or centracanthids	81	2.78	68	6.22	
		Pomacentridae	<i>Chromis chromis</i>	77	4.49	38	8.68
		Labridae	<i>Coris julis</i>	64	1.97	49	3.15
Labridae I	52		0.90	45	2.00*		
Labridae II	3		0.04				
Labridae III	3		0.02				
	Labridae IV	6	0.04	6	0.06		

Table II: continued

Order	Family	Larval taxa	1995		1996		
			N%	N° m ⁻²	N%	N° m ⁻²	
	Trachinidae	<i>Trachinus draco</i>	6	0.04	3	0.03	
	Trichiuridae	<i>Lepidopus caudatus</i>	9	0.07	1	0.01	
	Scombridae	<i>Auxis rochei</i>	45	0.63	17	0.76	
		<i>Euthynnus alletteratus</i>	3	0.05	3	0.03	
		<i>Scomber japonicus</i>	45	2.27	23	0.68*	
	Gobiidae	<i>Gobius paganellus</i>	19	0.26	30	0.30	
		Gobiidae I	11	0.13	14	0.18	
		Gobiidae II			3	0.26	
		Gobiidae III	3	0.02			
		Gobiidae IV	5	0.11			
		Gobiidae V			1	0.01	
		Unidentified gobiids	97	9.99	94	17.82*	
		Callionymidae	<i>Callionymus lyra</i>	2	0.01		
			<i>Callionymus maculatus</i>	22	0.38	41	1.40*
			<i>Callionymus risso</i>	78	8.26	61	4.31*
	Blenniidae	<i>Blennius ocellaris</i>	3	0.02			
		Blenniidae I	14	0.16	16	0.25	
		Blenniidae II	16	0.11	6	0.06	
		Blenniidae III	2	0.01			
		Blenniidae IV			1	0.02	
	Ophidiidae	<i>Parophidion vassali</i>	16	0.12	1	0.02	
	Carapidae	<i>Carapus acus</i>	3	0.02	9	0.10	
	Mugilidae	<i>Liza saliens</i>	11	0.26	7	0.10	
Scorpaeniformes	Scorpaenidae	<i>Scorpaena porcus</i>	17	0.18	6	0.06	
		<i>Scorpaena scrofa</i>	3	0.03	1	0.02	
	Triglidae	<i>Lepidotrigla cavillone</i>	3	0.03	7	0.11	
Pleuronectiformes	Bothidae	<i>Arnoglossus laterna</i>	63	1.38	52	1.75	
		<i>Arnoglossus thori</i>	47	0.84	43	1.13	
	Soleidae	<i>Buglossidium luteum</i>	9	0.15	9	0.54	
		<i>Microchirus variegatus</i>	3	0.02			
		<i>Solea lascaris</i>			7	0.07	
	Cynoglossidae	<i>Symphurus nigrescens</i>	13	0.18			
Echeneiformes	Echeneididae	<i>Remora remora</i>	2	0.01	3	0.04	
Lophiiformes	Lophiidae	<i>Lophius budegassa</i>	2	0.01			

N% = per cent of positive stations (frequency of occurrence). N° m⁻² = mean abundance (larvae m⁻²). Asterisks indicate non-overlapping 95% bootstrapped confidence intervals for mean abundance in 1995 and 1996.

Between-year differences (Tables IV and V)

Most between-year differences involved a sort of ‘shift’ or ‘spreading’ of taxa from Group 2 to Group 3. Thirteen more species were abundance indicators of Group 3 in 1996. They comprised four mesopelagic taxa (*Maurolicus muelleri*, *Vinciguerria* spp., *Benthosema glaciale* and *Myctophum punctatum*), the middle-sized pelagics

(*Sardinella aurita*, *Trachurus mediterraneus*, *Scomber japonicus* and *Auxis rochei*), two near-shore species (*Chromis chromis* and *Coris julis*) and three shelf taxa (*Serranus cabrilla*, *Mullus* spp. and *Arnoglossus thori*). The anchovy, *Engraulis encrasicolus*, as well as the demersals *Serranus hepatus* and *Cepola rubescens* were abundance indicators of Group 2 only in 1995.

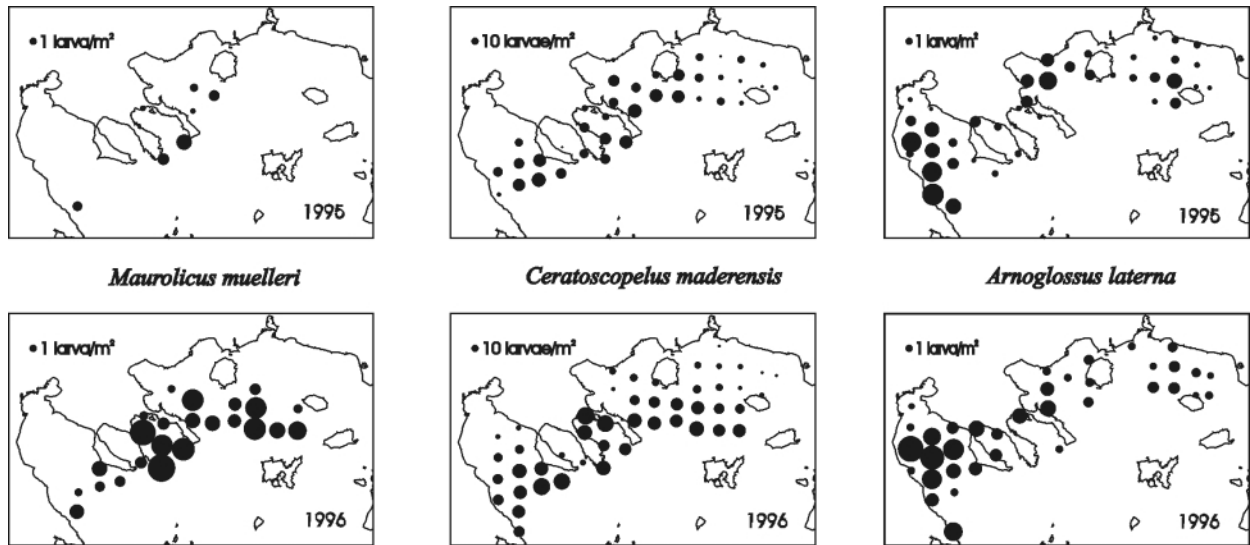


Fig. 6. Distribution and abundance of selected species of fish larvae exemplifying similar horizontal distribution patterns in June 1995 and June 1996. Diameters of discs are proportional to the logarithm of abundance.

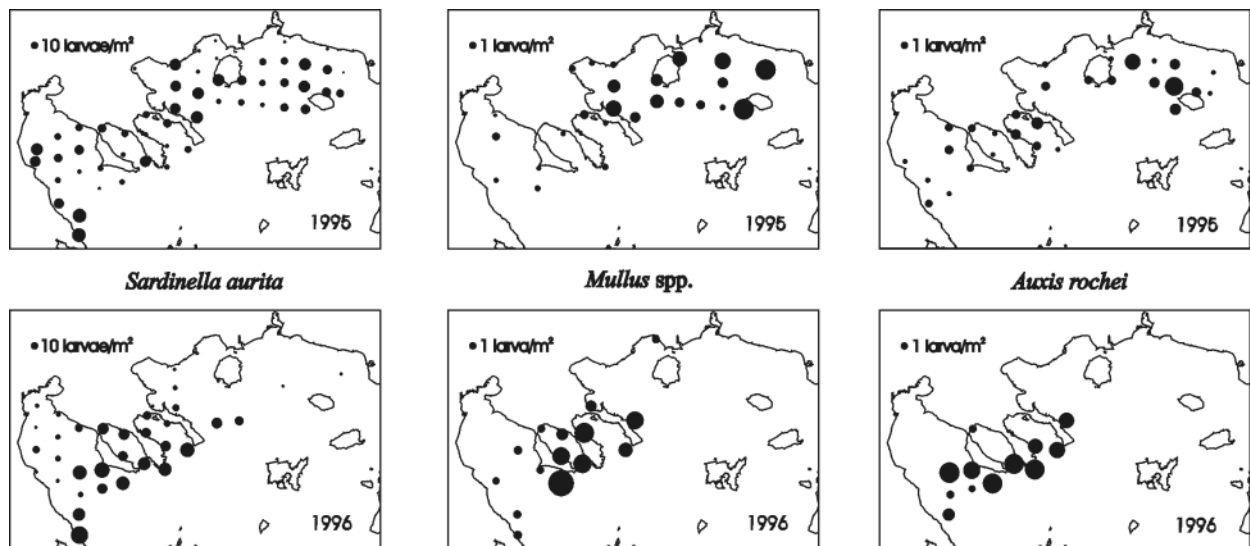


Fig. 7. Distribution and abundance of selected species of fish larvae showing extremely low frequency of occurrence in the eastern part of the surveyed area during June 1996. Diameters of discs are proportional to the logarithm of abundance.

Larval assemblages

Four groups of species were defined in 1995 and three groups in 1996, at the 22% similarity level (Figure 11). They generally corresponded to the station groups identified in the cluster analysis of sampling sites.

Group A₂ in 1995 and Group A in 1996 comprised *Buglossidium luteum*, which was an indicator of the inshore group of stations (Group 1a and Group 1 in 1995 and 1996 respectively). Group A₁ in 1995 comprised Labridae II which was only found in the station Group 1b (Table IV). *Arnoglossus laterna*, which was the indicator of

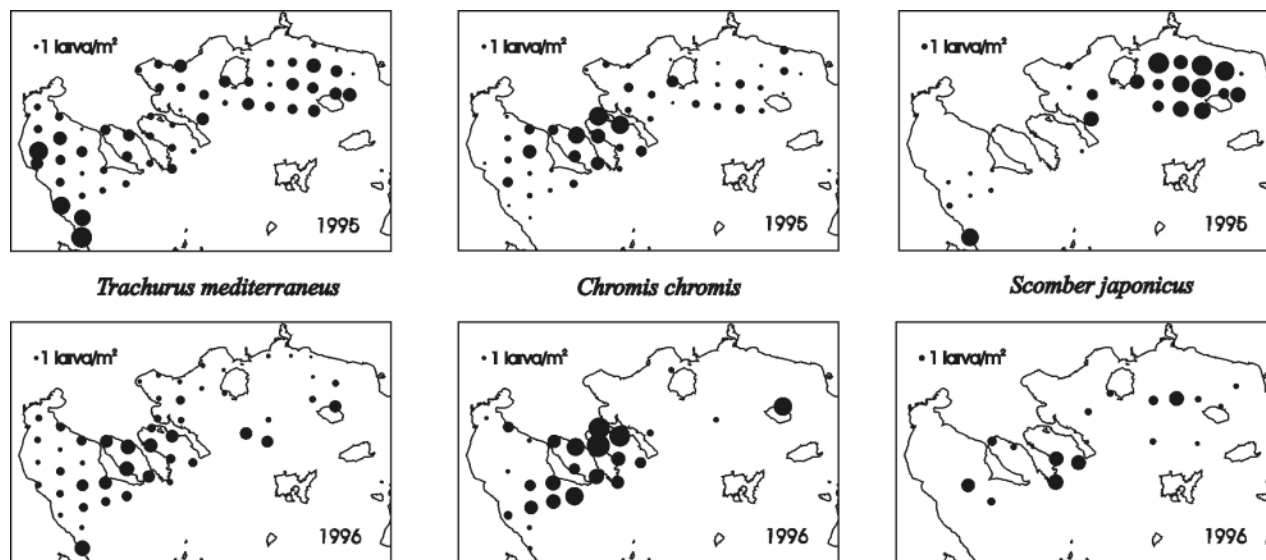


Fig. 8. Distribution and abundance of selected species of fish larvae showing low frequency of occurrence and abundance in the eastern part of the surveyed area during June 1996. Diameters of discs are proportional to the logarithm of abundance.

Table III: Multiple regression analysis between various parameters and NMDS scores for two-axis ordination of sampling sites

Variable	1995					1996				
	X	Y	Adj. R ²	F	P	X	Y	Adj. R ²	F	P
Latitude	0.713	-0.701	0.173	7.392	**	0.425	0.905	0.381	21.687	***
Longitude			0.000	0.336	ns	0.930	0.368	0.302	15.530	***
Temperature			0.056	2.523	ns	-0.977	0.211	0.205	9.609	***
Salinity	-0.495	0.869	0.170	7.260	**	-0.548	-0.836	0.513	36.258	***
Tow depth	-0.709	0.705	0.737	81.130	***	0.704	-0.710	0.815	149.021	***
Coast distance			0.058	2.882	ns	0.995	-0.100	0.307	15.849	***

X, Y are direction cosines (regression weights). For ANOVA P values: * P < 0.05; ** P < 0.01; *** P < 0.001; ns, not significant.

station Group 2, together with other shelf-dwelling species were clustered in species Group B, whereas mesopelagic larvae, indicators of station Group 3, such as *Hygophum benoiti*, *Cyclothone braueri*, *Lampanyctus crocodilus* and *Lobianchia dofleini*, were clustered in species Group C. Group B comprised 14 species in 1995 but seven species in 1996, whereas Group C comprised 11 species in 1995 and 19 species in 1996. Eight species (*Mullus* spp., *Arnoglossus thori*, *Chromis chromis*, *Serranus cabrilla*, *Auxis rochei*, *Scomber japonicus*, *Sardinella aurita* and *Trachurus mediterraneus*) had ‘moved’ from Group B in 1995 to Group C in 1996.

DISCUSSION

The largest differences in larval fish assemblages during both years were found in the cross-shelf (onshore/off-shore) location of sampling sites, the greatest contrast being roughly between the two sides of the shelf break at 150–200 m. Depth was the most important determinant of taxonomic composition and abundance. These results are consistent with other ichthyoplankton studies on continental shelves around the world (Richardson *et al.*, 1980; Young *et al.*, 1986; Sabates, 1990a; Moser *et al.*, 1993).

Despite the fluid nature of the pelagic environment (Doyle *et al.*, 1993), zonal distributions are a regular

Table IV: June 1995. Mean abundance of dominant larval species in station groups defined in the cluster analysis

Larval taxa	Station groups (Cluster analysis)			
	1b	1a	2	3
<i>Sardinella aurita</i>	0.39	0.53	33.93**	3.69*
<i>Engraulis encrasicolus</i>	20.53	10.51	71.28*	11.67
<i>Cyathothone braueri</i>	0	0	0.07	2.48*
<i>Vinciguerria</i> spp.	0	0	0.17*	0.67*
<i>Ceratoscopelus maderensis</i>	0	0	14.93*	78.10**
<i>Hygophum benoiti</i>	0	0	5.68*	42.98**
<i>Lampanyctus crocodiles</i>	0	0	0.31*	2.56**
<i>Lobianchia dofleini</i>	0	0	0.50*	1.93**
<i>Myctophum punctatum</i>	0	0	2.25*	4.15*
<i>Lestidiops jayakari</i>	0	0	0.03	0.91*
<i>Callanthias ruber</i>	0	0	0.05	0.90*
<i>Serranus cabrilla</i>	0	0.05	1.52*	1.23*
<i>Serranus hepatus</i>	1.34	3.27	11.85*	2.20
<i>Cepola rubescens</i>	0 ¹	1.08	5.36*	0.47
<i>Trachurus mediterraneus</i>	0.25 ¹	1.61	12.00*	3.47
<i>Mullus</i> spp.	1.00	0.11	1.12*	0.74*
<i>Chromis chromis</i>	0.25	0.71	7.14*	2.40
<i>Coris julis</i>	0 ¹	0.52	2.25*	3.56*
Labridae I	0.49	1.85*	0.67*	0.18
Labridae II	0.67	0	0	0
<i>Auxis rochei</i>	0.25	0	1.03*	0.30
<i>Scomber japonicus</i>	0.25	0	3.94*	0.56
<i>Callionymus maculatus</i>	0	0	0.30*	0.75*
<i>Callionymus risso</i>	0.58 ¹	16.45*	8.97*	0.34
<i>Arnoglossus laterna</i>	0.14 ¹	0.93	2.05*	0.33
<i>Arnoglossus thori</i>	0 ¹	0.33	1.14	0.86
<i>Buglossidium luteum</i>	0 ¹	0.74*	0.02	0

Double asterisk (**) indicates that the group abundance is higher than groups marked with single asterisk (*) or no asterisk and its 95% bootstrapped confidence intervals do not overlap with other groups. Single asterisk indicates that the group abundance is higher than the group with no asterisk and its 95% bootstrapped confidence intervals do not overlap with that group. The Group 1a is only compared with Group 1b. ¹ indicates non-overlapping confidence intervals of the inshore Groups 1a and 1b.

feature of continental coasts (Young *et al.*, 1986; Moser *et al.*, 1993). In general, (i) shelf and oceanic (offshore) assemblages occur (often separated by a narrow 'transitional' assemblage). (ii) The transition from shelf to oceanic assemblage generally parallels the 200 m contour. However, it may vary in position with time from near the coast to well out over the continental shelf, which may be due to temporal variation in the circulation patterns (Richardson *et al.*, 1980), the amount of riverine input (Thorrold and McWilliams, 1996) and the location of hydrodynamic barriers (e.g. the shelf-slope front [Sabates

and Olivar, 1996]). (iii) The shelf group split into mid-shelf and inner-shelf subgroups. (iv) Stability of the bathymetric zonal structure seems to depend on the width of the continental shelf (Sabates, 1990a; Young *et al.*, 1986) or on unusual mesoscale circulation patterns (Sabates and Maso, 1992).

In the western Mediterranean (off the Catalan coast), Sabates (1990a) analysed samples collected with a 40-cm bongo sampler and found that the spatial distribution of fish larvae followed a basically conservative pattern, which, with certain seasonal variations, was

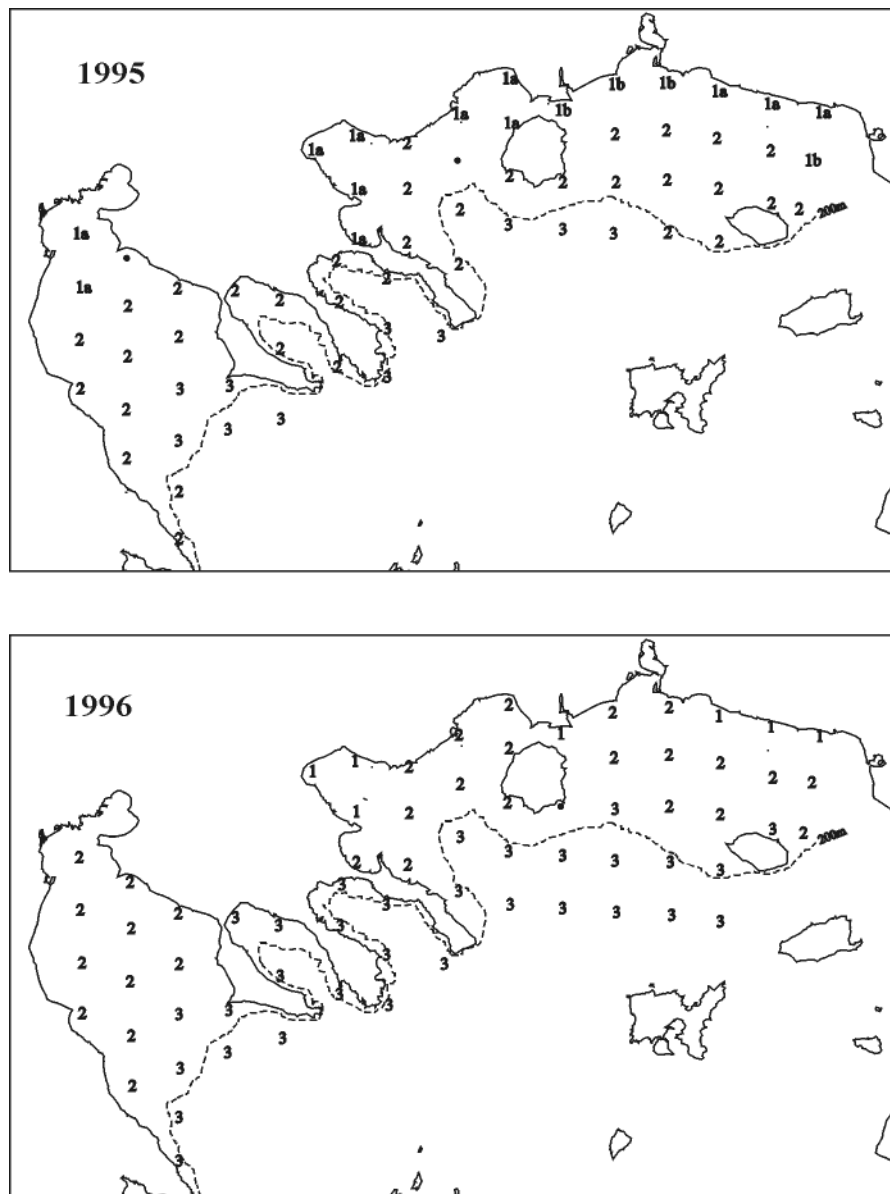


Fig. 9. Geographic distribution of station Groups defined by cluster analysis. • indicates ‘outlier’ sampling sites not grouped in the cluster analysis.

consistent over the course of the year and was characterized by a gradual ‘inshore–offshore’ gradient of species composition and abundance. Larval assemblage definition was mainly affected by shelf topography, adult habitat, behaviour, spawning locality and spawning period. The distribution pattern of fish larvae off the Catalan coast (collections were presumably dominated by young preflexion larvae) did not generally seem to be affected by advection processes (i.e. it was

more related to topography). Present data from the eastern Mediterranean reveal a general pattern similar to Sabates’. Sampling sites were distributed along a primary depth continuum (reflecting adult spawning bathymetry) and main differences were quantitative (levels of abundance) rather than qualitative (presence/absence). The estimated baroclinic currents, which were expected to give a rough picture of the poorly known surface circulation of the study area, did

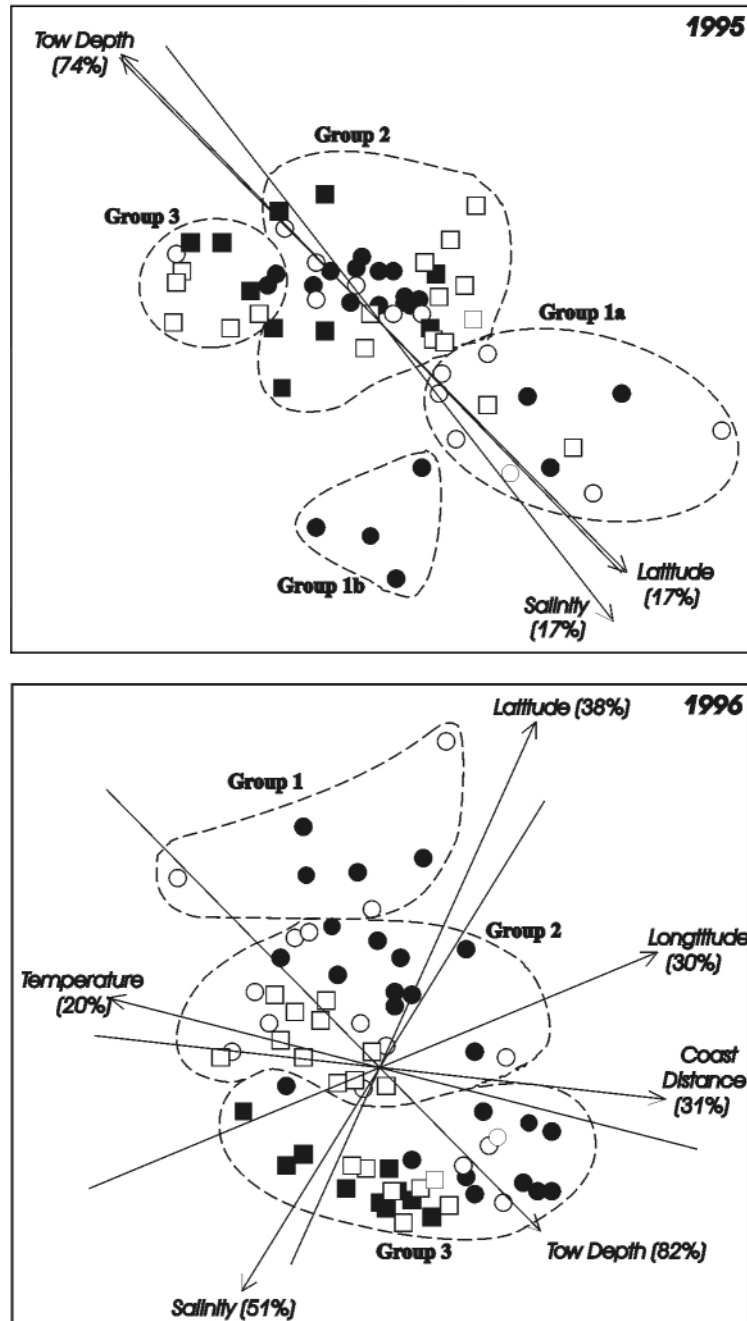


Fig. 10. Ordination plots of the comparison of sampling sites using non-metric multidimensional scaling and Bray–Curtis similarity index. Respective cluster groups are superimposed. Significant multiple regressions between ordination scores and environmental parameters are shown, as well as the fraction (%) of variance in the larval fish data explained by the parameters (see Table III). Stress values are 0.11 and 0.12 in 1995 and 1996 respectively. ●, Thracian Sea; ○, Kavala Gulf; ■, Chalkidiki Gulfs; □, Thermaikos Gulf (see Figure 1).

not seem to be related to patterns in the broad-scale larval distribution. The lack of ‘unusual’ distributions [e.g. similar to those occasionally described in the western Mediterranean (Sabates, 1990b; Sabates and Maso, 1990, 1992; Sabates and Olivar, 1996)], together

with the presumably young age of the larvae collected (mostly preflexion stages), suggest that the spatial patterns we have observed mainly reflect the spawning localities of adults.

The onshore-to-offshore transition and membership of

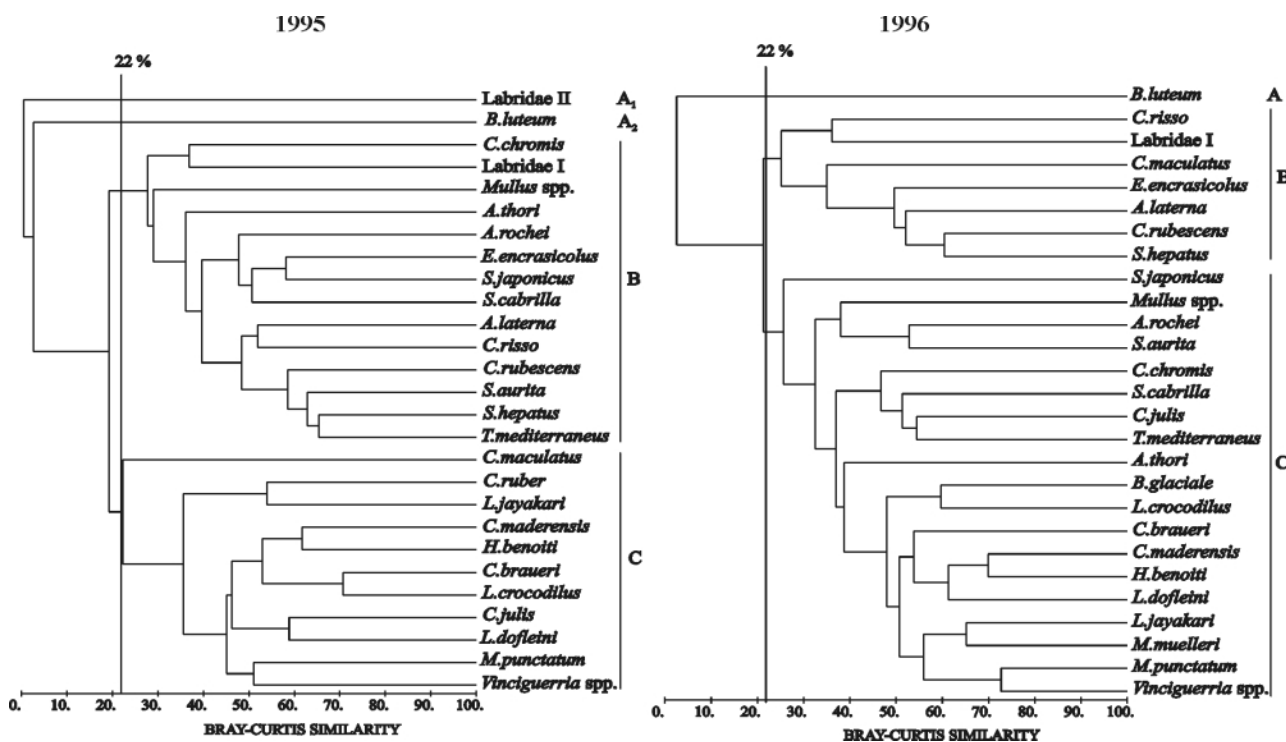


Fig. 11. Dendrograms of the cluster analysis comparing dominant species.

the respective assemblages seemed to be influenced by (i) the width of the continental shelf, (ii) the relative abundance of mesopelagic larvae and (iii) the relative offshore diffusion of larvae of the shelf-dwelling species. More sites were clustered in the ‘offshore’ group of stations (Group 3) in 1996 and larvae of many shelf species had increased abundance in Group 3 and/or were clustered within the ‘offshore’ Group of species (Group C) in 1996. A larger amount of riverine input (Thorrold and McWilliams, 1996) and lower temperature (longer incubation times) in 1996 were likely to have increased the offshore diffusion of shelf-spawned larvae. Indeed, larvae of most coastal and shelf species found in the present study are distributed in the upper thermocline layer, which may explain their wide cross-shelf distribution (Olivar and Sabates, 1997). However, a closer inspection of the species distribution and abundance maps (some of them are shown in Figures 5, 6 and 7), showed that interannual differences in the ‘onshore’-‘offshore’ station and species clusters and station abundance indicator species were mainly due to sampling sites in the narrow-shelved Chalkidiki Gulfs, which were characterized by a high abundance of larvae of both shelf and mesopelagic species in 1996.

There were marked differences in the abiotic and biotic

environment between 1995 and 1996. Colder, less saline waters in 1996 had substantially higher zooplankton displacement volumes (Table I). As shown from an analysis of meteorological and sea surface temperature data (Somarakis, 1999), these differences were related to a cooler and rainier winter in 1996. Larvae of small pelagic and mesopelagic fish showed a higher abundance in 1996, when zooplankton biovolumes were substantially higher. A similar association of larvae of Engraulidae and Myctophidae with increased plankton production has been reported off the northwest coast of the USA (Doyle *et al.*, 1993).

Multivariate analysis essentially identifies concerted variation in multispecies distributions (Rakocinski *et al.*, 1996). Different taxa must have consistently similar patterns for assemblages to be identifiable and have patterns (Leis, 1993). However, as emphasized by Leis, the lack of pattern in assemblages does not imply lack of pattern for individual taxa. The primary depth-related source of variation in multispecies distributions (Figure 10), masked peculiar regional distribution and abundance of certain species in 1996 (Figures 7 and 8), which seemed to be related to longitudinal differences in abiotic factors (temperature and salinity).

In both years’ surveys, the distribution of temperature

Table V: June 1996. Mean abundance of dominant larval species (larvae m^{-2}) in station groups defined in the cluster analysis

Larval taxa	Station groups (Cluster analysis)		
	1	2	3
<i>Sardinella aurita</i>	0	2.00*	60.18**
<i>Engraulis encrasicolus</i>	8.95	157.61*	102.52*
<i>Cyclothone braueri</i>	0	0	5.22*
<i>Maurolicus muelleri</i>	0	0.04	4.42*
<i>Vinciguerria</i> spp.	0	0	5.93*
<i>Benthoosema glaciale</i>	0	0.18	4.01*
<i>Ceratoscopelus maderensis</i>	0	6.57*	157.15**
<i>Hygophum benoiti</i>	0	0.78*	78.73**
<i>Lampanyctus crocodiles</i>	0	0.08	3.65*
<i>Lobianchia dofleini</i>	0	0	3.21*
<i>Myctophum punctatum</i>	0	0.07	19.91*
<i>Lestidiops jayakari</i>	0	0.11	2.03*
<i>Serranus cabrilla</i>	0	0.23*	3.07**
<i>Serranus hepatus</i>	0	5.56*	5.91*
<i>Cepola rubescens</i>	0.15	1.89*	3.08*
<i>Trachurus mediterraneus</i>	0.62	1.76*	6.40**
<i>Mullus</i> spp.	0	0.18*	1.62**
<i>Chromis chromis</i>	0	0.57*	18.90**
<i>Coris julis</i>	0	0.51*	6.46**
Labridae I	2.09	2.18	1.84
<i>Auxis rochei</i>	0	0	1.71*
<i>Scomber japonicus</i>	0	0.34*	1.18*
<i>Callionymus maculatus</i>	0	1.55*	1.64*
<i>Callionymus risso</i>	14.57*	5.10*	1.38
<i>Arnoglossus laterna</i>	0.25	2.91*	1.04
<i>Arnoglossus thori</i>	0.14	0.35	2.11*
<i>Buglossidium luteum</i>	4.98*	0.08	0

Double asterisk (**) indicates that the group abundance is higher than groups marked with single asterisk (*) or no asterisk and its 95% bootstrapped confidence intervals do not overlap with other groups. Single asterisk indicates that the group abundance is higher than the group with no asterisk and its 95% bootstrapped confidence intervals do not overlap with that group.

showed two regimes: the cold (and fresher) tongue of mainly Black Sea and riverine waters in the Thracian Sea and Kavala Gulf; and the warmer, more saline waters in Thermaikos and Chalkidiki Gulfs. In the generally cooler 1996, larvae of several summer spawning species, i.e. the middle-sized pelagics and certain demersals, were absent or occurred infrequently and at very low densities in the Thracian Sea and Kavala Gulf. The latter may be attributed to a temperature-related delay in the onset of the spawning period for summer spawners in the eastern part of the survey area. These species had not spawned or had just started to spawn at low intensities in the cooler eastern

part of the continental shelf. It is known from the Western Mediterranean (Sabates and Maso, 1992; Sabates and Olivar, 1996) that summer spawners start their reproductive period during the transitional period of spring/early-summer. These include the middle-sized pelagics *Sardinella aurita*, *Trachurus mediterraneus*, *Scomber japonicus* and *Auxis rochei* and the demersal species, such as *Serranus cabrilla*, *Trachinus draco* and *Symphurus nigrescens* [Table 1 in (Sabates, 1990a)].

This is, to our knowledge, the first broad-scale, multi-species ichthyoplankton study in the eastern Mediterranean. It suggests that the spatial and seasonal spawning

patterns of adult fish play the key role in the formation of assemblages of early larvae. Interannual variability in assemblage structure and distribution, particularly during the transition period of early summer, may reflect variability in meteorological, physical and biological processes and be particularly useful in highlighting shared or contrasting adaptations of species to the pelagic environment.

ACKNOWLEDGEMENTS

The authors would like to thank the captain and the crew of R/V 'Philia', as well as our colleagues A. Machias, M. Giannoulaki, L. Manousakis, A. Kapantagakis, S. Kiparissis and I. Kostikas for their assistance during the research cruises. This study was partly supported by the Ministry of Research and Development of Hellas as part of the project 'EPET 125, II/94—Development of the Hellenic Fisheries'.

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Received on 19 May, 2001; accepted on 3 December, 2001

