

Multispecies Ichthyoplankton associations in epipelagic species: is there any intrinsic adaptive function?

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ABSTRACT. Species composition, distribution patterns and abundance of larvae of epipelagic fishes during June 1995 and June 1996, are described in waters of the northeastern Aegean Sea (eastern Mediterranean). Significant interannual differences were found that appeared to be associated with differences in environmental conditions. In June 1996 waters were colder, less saline and richer in zooplankton, which indicated a delay in the spring-to-summer transition during that year. Concurrently, larvae of the small-sized anchovy (*Engraulis encrasicolus*) were significantly more abundant in 1996 than in 1995. This contrasted with larvae of the middle-sized pelagics: *Sardinella aurita*, *Trachurus mediterraneus*, *Scomber japonicus* and *Auxis rochei*, which were most abundant in 1995. These results indicate differences in reproductive strategies among pelagic fishes, which we discuss in terms of 'income' versus 'capital' breeding, as well as inter-specific differences in the performance abilities of the larvae. The multispecies larval association of middle-sized pelagics may be adaptive and result from similar responses among species to the pelagic environment.

KEY WORDS: *Engraulis encrasicolus*, *Sardinella aurita*, *Trachurus mediterraneus*, *Scomber japonicus*, *Auxis rochei*, reproduction, early life history.

INTRODUCTION

Most marine teleost fishes have external fertilization and complex life cycles, characterized by an early meroplanktonic larval phase. During this relatively short period of the life cycle, individuals are extremely vulnerable to starvation, predation and unfavorable transport, and it has long been realized that the larval phase may have a potentially disproportionate influence on the local abundance of adult populations (HEATH, 1992; LEGGETT & DEBLOIS, 1994).

The timing and intensity of spawning in fishes is believed to be adaptive, reflecting the phase of the mean seasonal cycle of the environment favorable for offspring survival. Hypotheses proposed to explain the need for precise timing of reproduction have emphasized the relative importance of temporal variability in either food chain processes (CUSHING, 1990), predation pressure (HEATH, 1992), physical dispersive patterns of an area (SINCLAIR, 1988) or the interaction between physical forc-

ing and conditions favorable for larval growth (CURY & ROY, 1989). Despite fluctuations in recruitment caused by environmental variability, reproductive strategies adapted to long-term average conditions of an area will result in maintenance of the local populations.

A well-known description of an adapted reproductive strategy can be found in capelin in Newfoundland coastal waters (FRANK & LEGGETT, 1982). Interestingly, the results of a subsequent study (FRANK & LEGGETT, 1983) indicated a synchronous emergence and resulting co-occurrence of capelin larvae and larvae of other demersal spawning species that led the authors to propose that multispecies larval fish associations are adaptive and result from similar responses among species to the pelagic environment. Under the general framework of multispecies approaches to the study of fish populations, 'an important consideration in larval assemblage studies is whether they have an intrinsic adaptive function' (MOSER & SMITH, 1993), as suggested by FRANK & LEGGETT (1983).

In the Mediterranean, the period of late spring-early summer, characterized by the development of the seasonal thermocline, is a transition period in the spawning of

fishes (SABATES, 1990; SABATES & MASO, 1992; SABATES & OLIVAR, 1996). It coincides with the onset of the spawning season for those species that spawn in summer. The intent of this study was directed towards an understanding of the factors that influence the timing and intensity of spawning of the eastern Mediterranean epipelagic fishes, during the period of early summer. We followed a comparative approach, which examined co-variation in their larval distribution and abundance. Interannual variability in the assemblage of epipelagic fish larvae might trace variability in physical processes and be particularly useful in highlighting shared or contrasting adaptations of species to the pelagic environment.

MATERIAL AND METHODS

Larval fishes were collected during two surveys carried out in 15-22 June 1995 and in 6-14 June 1996 in the northeastern Aegean Sea (eastern Mediterranean). Sampling was based on transects running parallel to lines of longitude and spaced 10 nautical miles apart (Fig. 1). Sampling stations were located at approximately 5 or 10 nautical mile intervals on each transect in 1995 and 1996, respectively. In 1996, five additional offshore stations were sampled. At each station, a vertical profile of salinity and temperature was taken using a Seabird 19 CTD (conductivity/temperature/depth meter).

A 60-cm bongo-net sampler was used on both cruises. Mesh sizes on the sampler were 335 and 250 microns. 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. Volume filtered was determined from a calibrated flowmeter in the mouth of each net. Maximum tow depth and volume of water filtered were subsequently used to standardize catches to numbers per m² (SMITH & RICHARDSON, 1977). More details are provided in SOMARAKIS ET AL. (1998). In the laboratory, all samples were sorted and larvae were identified to the lowest possible taxonomic level.

To provide a more powerful test for among years differences in the abundance of species, we bootstrapped

95% confidence intervals on resulting means (THORROLD & MCKINNON, 1995). We calculated 1000 bootstrapped estimates. A preliminary analysis showed that interannual differences in sampling intensity did not affect the results. Hence, results using all data are presented here.

RESULTS

Environmental conditions

The water column in the northern Aegean Sea presented typical early summer conditions in both 1995 and 1996. It was generally well stratified (Fig. 2) and characterized by a warmer, less saline, mixed surface layer, which was occasionally very shallow (e.g. transect No 8), separated by a thermo-halocline from the cold and more saline deeper layer. The mean depth of the thermocline, which was generally above 40m of depth, was 33.32m in 1995 and 25.18m in 1996. In general, the upper water column was colder and less saline in 1996 than in 1995 (Fig. 3A). Mean zooplankton displacement volume (ZDV, ml/m²), which is a rough index of zooplankton production (SMITH & RICHARDSON, 1977), was twice as much in 1996 than in 1995 (Fig. 3A).

Distribution and abundance of epipelagic fish larvae

A total of seven epipelagic species were captured during the surveys (Table 1). Larvae of the winter/spring spawning *Trachurus trachurus* were very rare in the collections, and we did not consider this species in further analysis, since early summer marks the end of its spawning period (KARLOU-RIGA & ECONOMIDES, 1997). The scombrid *Euthynnus alletteratus* was captured at a single station, in 1995. The distribution and abundance of larval anchovy, *Engraulis encrasicolus*, and larvae of *Sardinella aurita*, *Scomber japonicus*, *Auxis rochei* and *Trachurus mediterraneus* are presented in Fig. 4. In general, their distribution was wide, particularly over the outer continental shelf, but there were marked differences in both frequency of occurrence (Fig. 4, Table 1) and abundance (Fig. 3B, Fig. 4) between 1995 and 1996. Larvae of *S.*

TABLE 1

Epipelagic larval species collected during June 1995 and June 1996 in the northeastern Aegean Sea. %P = % of positive stations. A = mean abundance (larvae/m²).

Species	1995		1996	
	%P	A	%P	A
<i>Sardinella aurita</i> Valenciennes, 1847	93.44	43.03	56.10	7.91
<i>Engraulis encrasicolus</i> (Linnaeus, 1758)	100	99.65	100	186.54
<i>Trachurus trachurus</i> (Linnaeus, 1758)	11.48	0.16	12.20	0.15
<i>Trachurus mediterraneus</i> (Steindachner, 1868)	86.89	7.07	65.85	3.17
<i>Auxis rochei</i> (Risso, 1810)	44.26	0.82	4.88	0.13
<i>Euthynnus alletteratus</i> (Rafinesque, 1810)	1.64	0.03	-	-
<i>Scomber japonicus</i> Houttuyn, 1782	65.57	6.59	34.15	1.45

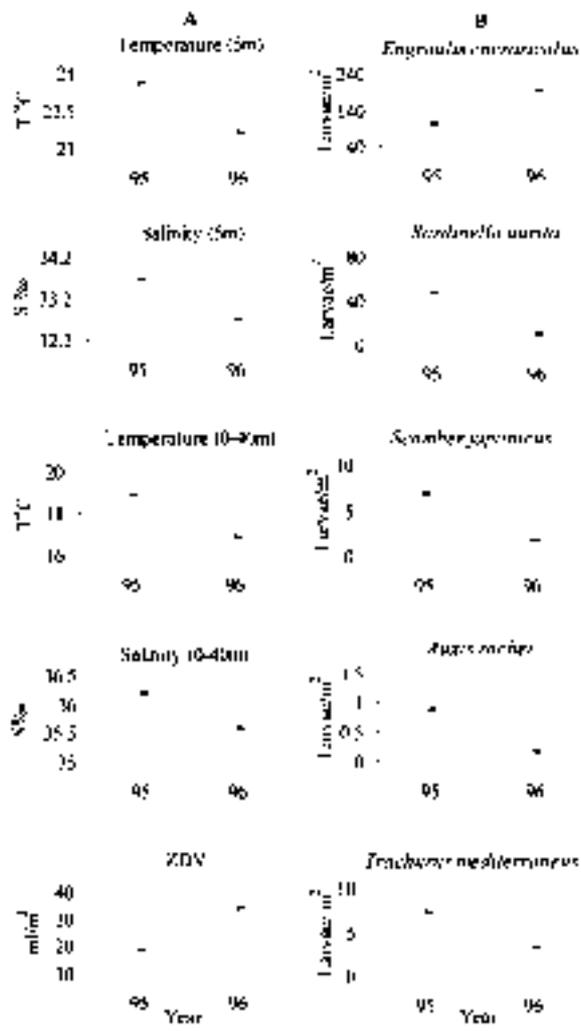
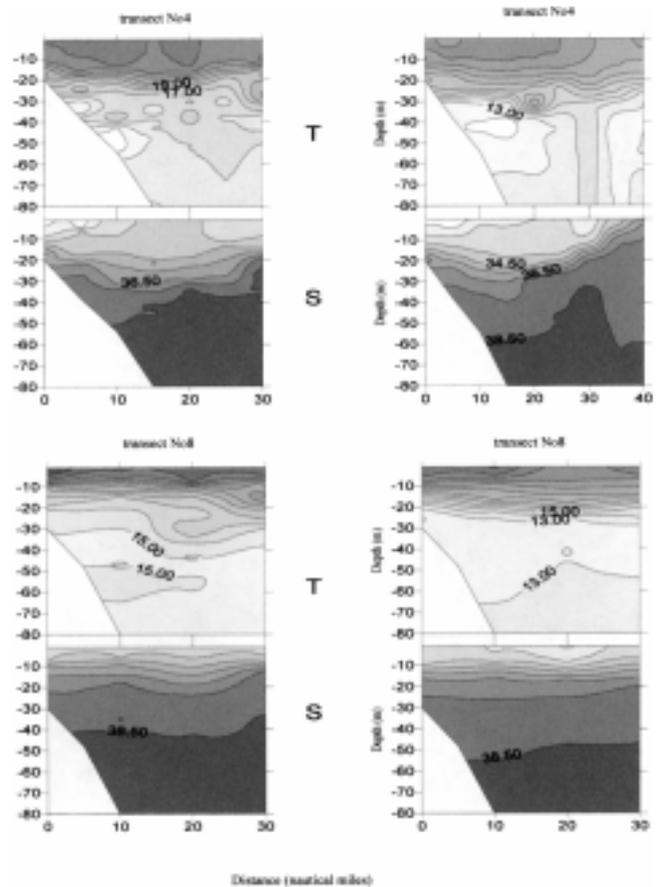
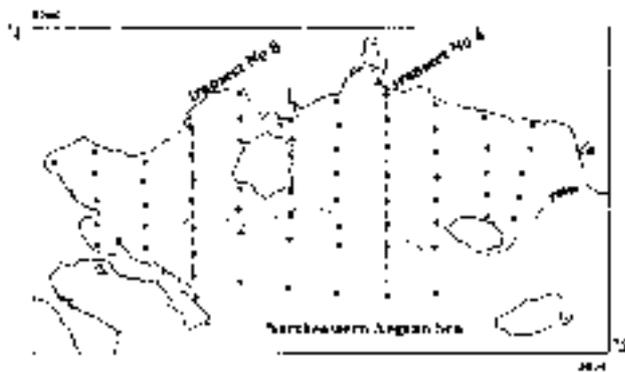


Fig. 1 (upper left). – Map of the study area showing the location of sampling stations. Black cycles = stations sampled both in 1995 and 1996. Open cycles = stations sampled only in 1995. Crosses = offshore stations sampled only in 1996.

Fig. 2 (upper right). – Vertical sections (transect No 4 and No 8 in Fig. 1) of temperature (T) and salinity (S). Isolines are contoured for every 1°C temperature and 1 psu salinity.

Fig. 3 (lower left). – Means and 95% confidence intervals for 1995 and 1996. (A) Surface (5m) and upper water column (0-40m) temperature and salinity. Zooplankton displacement volumes (ZDV). (B) Abundance of epipelagic fish larvae.

Fig. 4 (lower right). – Distribution and abundance of epipelagic fish larvae. Diameters of disks are proportional to the logarithms of abundance.

aurita, *S. japonicus*, *A. rochei* and *T. mediterraneus* were more frequent and their abundance was significantly higher in 1995 than in 1996. On the contrary, the abundance of *E. encrasicolus* was higher in 1996 (Fig. 3B).

DISCUSSION

Substantial interannual differences were found in this study: In June 1996, waters were colder, less saline and richer in zooplankton, a fact indicating a delay in the spring-to-summer transition. Concurrently, larvae of the small-sized anchovy (*E. encrasicolus*) were significantly more abundant in 1996 than in 1995. In contrast, the larvae of the middle-sized pelagic fishes (*S. aurita*, *T. mediterraneus*, *S. japonicus* and *A. rochei*) were most abundant in 1995.

Studies in the Western Mediterranean (SABATES, 1990; SABATES & MASO, 1992; SABATES & OLIVAR, 1996) have shown that early summer coincides with the onset of the reproductive season of summer spawning fishes. These include the middle-sized pelagic species: *S. aurita*, *T. mediterraneus*, *S. japonicus* and *A. rochei*. The same period is characterized by the maximum spawning intensity for anchovy (PALOMERA, 1992; SOMARAKIS & TSIMENIDES, 1997).

According to FRANK & LEGGETT (1983), temporal and/or spatial covariation in the occurrence of larvae of different species in the plankton might reflect co-adapted reproductive strategies. For multiple spawning species, such as the Mediterranean pelagic fishes, covariation in spawning intensity, i.e. synchronous increases or decreases in batch fecundity and/or spawning frequency, resulting in concerted variations in the abundance of their larvae in the plankton, might also be adaptive, whereas contrasted variations might indicate alternative reproductive tactics. We hypothesize that small-sized pelagics have different reproductive tactics to middle-sized pelagics, which might be associated with differences in the performance abilities of their larvae.

Applying the terminology of life history evolution (STEARNS, 1992), we may label planktivorous short-lived small pelagic species as 'income breeder', spawning soon after energy for egg production becomes available. These species are characterized by substantial, ration-related short-term variations in batch fecundity and spawning frequency (PEEBLES ET AL., 1996). For example, reproductive studies of the Greek anchovy stocks (SOMARAKIS & TSIMENIDES, 1997; SOMARAKIS ET AL., 1997, unpublished data) indicate marked spatio-temporal variations in batch fecundity and spawning frequency, resulting in higher egg and larval abundance values when zooplankton biovolumes are much higher. Presumably, adult and/or larval prey densities are also higher. Because of the inherent interdependence between copepod life stages, income breeding may be seen as a seasonal fine-tuning of reproductive effort according to offspring survival probabilities (PEEBLES ET AL., 1996).

Longer-lived middle-size pelagics may be labeled as 'capital breeders', exhibiting a longer delay in their fecundity response, i.e., they use increased plankton production to acquire energy reserves and subsequently reproduce, thus their larvae are more likely to encounter lower prey fields.

If our hypothesis is reasonable, larvae of the middle-sized pelagics are expected to have higher performance abilities than larvae of anchovy. We provide some evidence of this in the next paragraphs.

The larvae of clupeoids (such as *E. encrasicolus* and *S. aurita*) are characterized by an elongate body, small fins, and a small terminal mouth. They are dependent on small sized, abundant and patchy prey, their swimming abilities are poorly developed, and they are capable of searching a small volume of water for food (HEWITT, 1981; HUNTER, 1981; BLAXTER & HUNTER, 1982). The size of prey eaten, as well as swimming speeds increase with size. WALLINE (1987) has estimated similar growth rates for *E. encrasicolus* and *S. aurita* larvae in the coastal waters of Israel. However, the latter are much bigger than anchovy (e.g. yolksac larvae of *S. aurita* are 40% bigger than *E. encrasicolus*, unpublished data) and presumably enjoy a substantial advantage in food searching and predator avoidance (MILLER ET AL., 1988).

In comparison to clupeoid species, larvae of scombrids (e.g. *Scomber japonicus*, *Auxis* spp.) and carangids (e.g. *Trachurus* spp.) share different morphologies and life history traits. Their body rapidly changes from an elongate shape to a deep body form with jaws and large eyes. They have fast growth rates (e.g. HUNTER & KIMBRELL, 1980; USHIDA, 1981; unpublished data), well developed swimming abilities, feed on increasingly large-sized, rare prey, and are capable of searching a large water volume for food (HUNTER & KIMBRELL, 1980; HEWITT, 1981; MATSUURA & HEWITT, 1995).

To sum up, larvae of the middle-sized pelagics have potentially superior performance abilities to larvae of the anchovy, the latter most probably increasing their chances of survival in low prey density - high temperature waters.

The existence of differences in the reproductive and early life history characteristics of epipelagic species has ecological but also management implications. From the fisheries perspective, factors affecting recruitment of the small-sized pelagic fishes might be substantially different from those affecting the middle-sized ones. Thus, there might be differences in the variability of the respective recruitment and subsequent catch rates, entailing separate management perceptions.

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