Marked interannual differences in reproductive parameters and daily egg production of anchovy in the northern Aegean Sea

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ABSTRACT. In the present paper, an overview of the application of the Daily Egg Production Method (DEPM) to the northern Aegean Sea anchovy stock is presented, and reproductive parameters are compared in the framework of ambient oceanographic regimes. The DEPM was applied twice : in June 1993 and June 1995. Data collection was based on bongo-net ichthyoplankton surveys and concurrent adult surveys onboard the commercial fishing fleet. Revised, more precise estimates of the daily egg production are presented based on the inclusion of both eggs and yolksac stages in the estimation procedure (fit of single embryonic mortality curves). Remarkable between-years differences in the daily egg production, batch fecundity and spawning frequency were found. These parameters were significantly higher in June 1993 than in June 1995. In June 1993, waters were colder, less saline and richer in zooplankton compared to 1995. Adult somatic condition and egg size were also higher in June 1993 than in 1995. These findings emphasize the importance of adult prey availability in determining anchovy egg production.

KEY WORDS : *Engraulis encrasicolus*, Aegean Sea, DEPM, Reproduction

INTRODUCTION

The Daily Egg Production Method (DEPM) is an ichthyoplankton-based method for estimating biomass of fish stocks and monitoring trends in fish abundance (HUNTER & LO, 1997). It has been developed for fishes that have indeterminate annual fecundity, like most clupeoids (LASKER, 1985), and has been applied to a variety of anchovy and sardine species and stocks (ALHEIT, 1993 ; HUNTER & LO, 1997). Besides biomass estimation, the application of DEPM provides regional time series on important biological variables of fish stocks, which can lead to new insights into the reproductive biology of multiple spawning fishes, particularly when such variables can be compared and subsequently related to environmental regimes.

This paper presents an overview of the application of DEPM to the anchovy [*Engraulis encrasicolus* (Linnaeus, 1758)] stock of the northern Aegean Sea (Greece, Eastern Mediterranean). The DEPM has been applied to anchovy stocks in the Western Mediterranean (GARCIA & PALOMERA, 1996), the northern Aegean Sea (SOMARAKIS & TSIMENIDES, 1997 ; SOMARAKIS et al., 1997 ; SOMARAKIS, 1999), the central Aegean and Ionian Seas (SOMARAKIS et al., 2002) and the Sicilian channel (QUINTANILLA & GARCIA, 2001). The applications in the northern Aegean Sea were carried out in June 1993 and June 1995 and were largely experimental, based on bongo-net larval surveys coupled with concurrent adult surveys onboard the commercial purse seine fleet. Reproductive parameter estimates are compared in an effort to understand the reproductive strategy of the species.

MATERIAL AND METHODS

The biomass model

The spawning stock biomass was estimated according to the model (LASKER, 1985) :

$$B = (k \cdot P \cdot A \cdot W)/(R \cdot F \cdot S)$$

where, B = spawning stock biomass in metric tons, k = conversion factor from grams to metric tons, P = daily egg production (number of eggs per sampling unit, m^2), A = total survey area (in sampling units, m^2), W = average weight of mature females (grams), R = sex ratio (fraction of mature females by weight), F = batch fecundity (mean number of eggs per mature females per spawning), and S = fraction of mature females spawning per day (spawning frequency).

Based on the delta method, the approximate variance of the biomass estimate is a function of sample variances and covariances (LASKER, 1985) :

$$VarB \cong \hat{B}^2 (CV(P)^2 + CV(W)^2 + CV(F)^2 + CV(S)^2 + 2COVS)$$

where CV denotes coefficient of variation, and $COVS$ is the sum of terms involving covariances.

Survey description

Two oceanographic surveys were carried out during June 1993 and June 1995 in the northern Aegean Sea (eastern Mediterranean). The sampling scheme was based on transects spaced approximately ten nautical miles apart and stations located at five nautical-mile intervals on each transect (Fig. 1). The same stations (n=111) were sampled in both years. The total survey area was 17396 km^2. Plankton and hydrographic sampling (vertical profiles of temperature and salinity) were performed at each station.

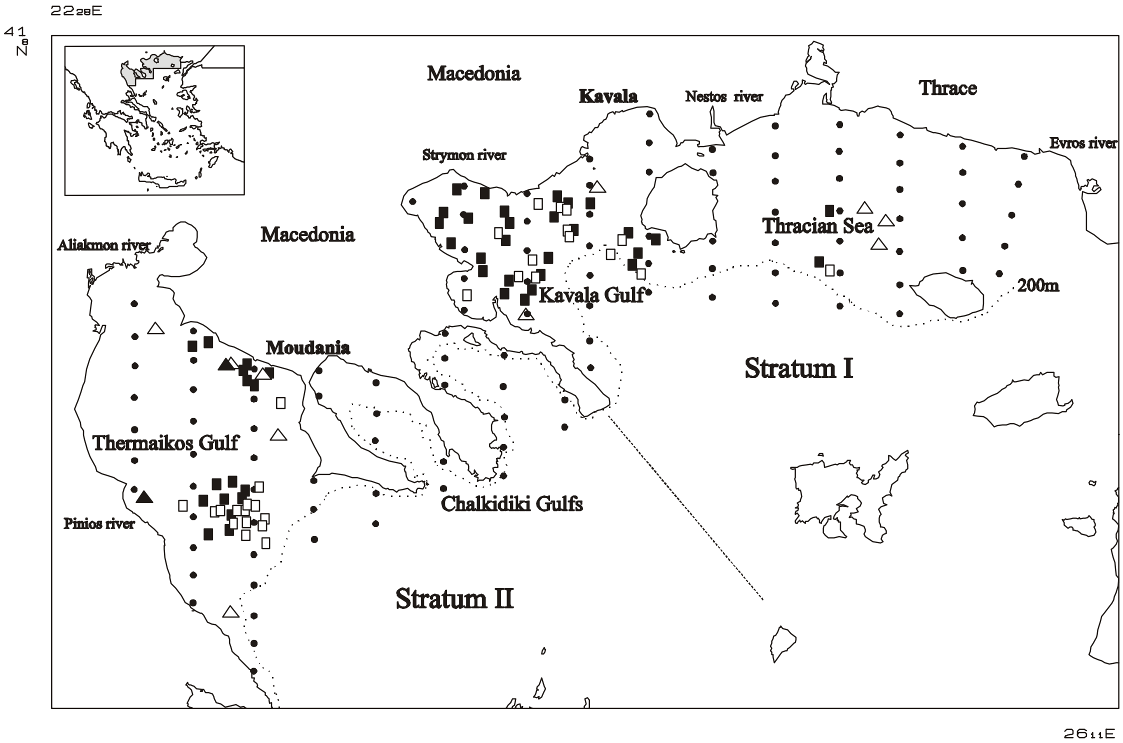

Fig. 1. – Northern Aegean Sea. Map of the surveyed area showing the location of sampling stations. ● : plankton and hydrographic samples. ■ : 1993, purse seine samples. □ : 1995, purse seine samples. ▲ : 1993, pelagic trawl samples. △ : 1995, pelagic trawl samples.

A 60-cm bongo-net sampler was used on both cruises. Mesh sizes on the sampler were 335 and 250 microns. The 0.250-mm mesh net is considered to completely retain anchovy eggs and larvae (Somarakis et al., 1998 ; Somarakis, 1999). Tows were double oblique and the volume filtered was determined by a calibrated flowmeter (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 depthmeter attached to the sampler. Maximum tow depth and volume of water filtered were subsequently used to standardize catches to numbers per m^2. More details are provided in Somarakis et al. (1998).

Adult samples were collected on board the commercial purse seine fleet of Kavala and Moudania and were representative of the fishing grounds (Fig. 1). Additional samples of hydrated females were obtained by means of a pelagic trawl operated from the research vessel "PHILIA", during the daily spawning interval (21:00-2:00). Fish were fixed onboard immediately after collection, using 15 l jars filled with 10% neutral-buffered formalin. Each sample consisted of random collection of 1.5-2 kg of anchovies.

Laboratory procedures

Anchovy eggs and larvae were sorted from the plankton samples. The eggs were staged using the eleven - stages system of Moser & Ahlstrom (1985). Yolk-sac larvae were staged into larvae with un-pigmented eyes (YSI) and larvae with traces of brown pigment or brownish eyes (YSII). Eggs and yolk-sac larvae at each developmental stage were counted and their abundance standardized to number per m^2. Zooplankton displacement volume (ZDV) was measured for each sampling site from the catch of the 0.250-mm mesh bongo net (Smith & Richardson, 1977). ZDV values were standardized to ml/m^2. At each station, the major and minor diameters of ten anchovy eggs were measured to the nearest 0.02 mm using an ocular micrometer. Egg volumes were calculated using the formula for a prolate spheroid.

Processing of an adult sample in the laboratory consisted of measuring length and weight (both total and gonad free weight), and sexing of all or at least 50 fish per sample. Correction factors were applied to convert formalin-weight to wet weight and the total weight of hydrated females was corrected for the increase in weight due to hydration of the ovaries (Somarakis et al., 2002). Relative condition factor of females (Bolger & Connolly, 1989) was calculated. The gonads of ten females per sample were randomly selected and subjected to histological analysis. All macroscopically detected hydrated or running females were measured and their gonads weighed and preserved in formalin for subsequent histological and batch fecundity analysis. The hydrated oocyte method was used for batch fecundity measurements (Hunter et al., 1985).

Spawning frequency (S), i.e., the fraction of mature females spawning per night, was assessed by the postovulatory follicles (POFs) method. The three types of POFs described by HUNTER & MACEWICZ (1985) (Day-0, Day-1, and Day-2+ POFs) were also observed in our histological preparations and were used in classifying ovaries as to the date of spawning (SOMARAKIS et al., 2002). Actively spawning anchovy (hydrated and Day-0 females) are oversampled during the hours of spawning (SOMARAKIS, 1999 ; SOMARAKIS et al., 2002 and references therein). To overcome this problem, we used samples collected outside the daily spawning interval, i.e. after 4 :00 a.m., and calculated spawning frequency based on the composite fraction of Day-0 and Day-1 spawners, to increase precision of the spawning frequency estimates (QUINTANILLA & PEREZ, 2000). Fractions of Day-0 and Day-1 spawners had the same statistical distributions after 4:00 a.m. (Wilcoxon paired sample tests, p>0.05).

Parameter estimation

Age of eggs was calculated based on a temperature dependent model of European anchovy developmental rate (REGNER, 1985), the station surface temperature (5 m), peak spawning time (midnight ; SOMARAKIS, 1999), and time of tow (LO, 1985). Procedures of ageing anchovy eggs are described in SOMARAKIS et al. (2002).

The estimation of the daily egg production generally involves the fit of an exponential mortality model to the abundance-at-age egg data set (PICQUELLE & STAUFFER, 1985). A preliminary estimate of the daily egg production for the 1993 survey, based on the egg data set (SOMARAKIS & TSIMENIDES, 1997) was problematic and highly uncertain because of inadequate numbers of positive egg data. This was mainly due to the effect of high incubation temperatures and corresponding occurrence of only single or two daily cohorts of eggs in the samples. To increase the number of age categories for constructing the mortality curves, we assumed that the mortality rate was the same for eggs and yolk-sac larvae, and we included both in single embryonic mortality curves (LO et al., 1996 ; SOMARAKIS et al., 2002). The estimate of daily production of eggs was derived by regressing the counts of embryos (eggs and yolk sac larvae) on their age using the exponential mortality model :

$$P_t = Pe^{-Zt}$$

where P_t= number of embryos at age t produced per day per m^2, t = age in days, P = daily egg production per m^2, Z= daily rate of instantaneous embryonic mortality.

We used both yolk-sac larvae stages (YSI and YSII) and calculated their duration and age from fertilization following methods described in SOMARAKIS et al. (2002). The technique to estimate *P* and *Z* was weighted non-linear least squares regression. Station weighting factors were proportional to the station representative area.

We used the ratio estimator (PICQUELLE & STAUFFER, 1985) for adult parameters *W*, *R*, *F*, and *S*. Data on the number of eggs per batch (F_{ij}) and the ovary free weight (W^*_{ij}) recorded for the hydrated females were used to fit a linear model :

$$F_{ij} = a + bW^*_{ij}$$

The regressions were forced through zero because *a* was not significantly different from zero at the 0.05 level.

RESULTS

The distribution and abundance of eggs and yolk-sac larvae are presented in Fig. 2. Higher egg concentrations were found in the Thracian Sea and Thermaikos Gulf. The surveys did not cover the entire anchovy egg and yolksac distribution. Particularly in the Thracian Sea, a significant fraction of egg and larval production seemed to extend offshore as well as in Turkish territorial waters.

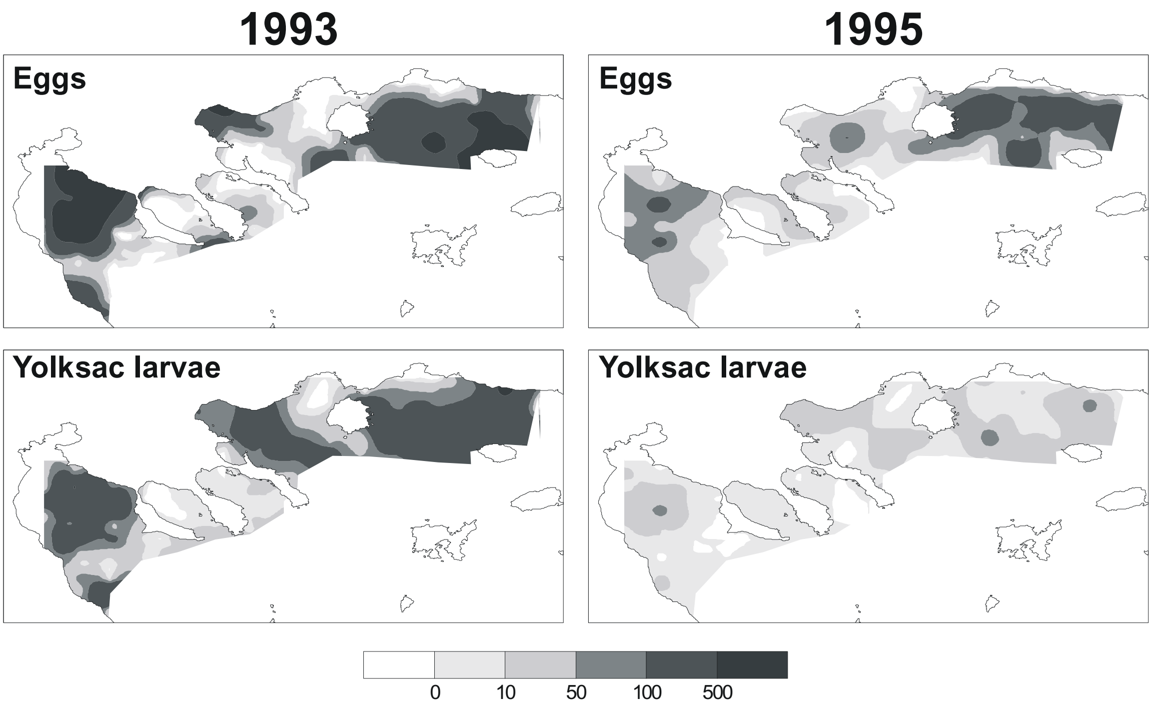

Fig. 2. – Contour maps of anchovy eggs and yolksac larvae abundance (numbers/m2) in June 1993 and June 1995.

On the basis of the egg distribution pattern and regional allocation of adult samples (Fig. 1) the surveyed area was stratified into two sub-regions : the Eastern region (Thracian Sea and Kavala - Stratum I) and the Western region (Thermaikos and Chalkidiki Gulfs - Stratum II). The DEPM was applied separately for the two strata. Statum I covered 9354 km^2 and stratum II 8042 km^2. Parameter and biomass estimates are given in Table 1.

TABLE 1

Biomass and parameter estimates of the DEPM applied to the northern Aegean anchovy stock in June 1993 and June 1995. Stratum I comprised the Thracian Sea and Kavala Gulf. Stratum II comprised the Thermaikos and Chalkidiki Gulfs (see Fig. 1). Coefficients of variation are given in parentheses.

	Stratum I (East)		Strarum II (West)	
Parameter	**1993**	**1995**	**1993**	**1995**
Daily egg Production (*P*, eggs/m^2)	109.22	25.71	87.19	19.75
	(0.27)	(0.24)	(0.33)	(0.26)
Instantaneous embryonic mortality rate (*Z*)	0.17	0.52	1.26	0.54
	(0.36)	(0.40)	(0.39)	(0.48)
Average weight of mature females (*W*, g)	24.89	25.65	20.88	22.72
	(0.03)	(0.03)	(0.03)	(0.03)
Weight specific sex ratio (*R*)	0.51	0.51	0.60	0.61
	(0.05)	(0.08)	(0.05)	(0.03)
Average batch fecundity (*F*, number of eggs)	12451	7781	10474	5128
	(0.05)	(0.06)	(0.04)	(0.10)
Fraction of mature females (*S*)	0.29	0.15	0.26	0.13
	(0.21)	(0.11)	(0.20)	(0.23)
Spawning biomass (*B*, metric tons)	14002	10282	9030	8948
	(0.34)	(0.22)	(0.38)	(0.36)

Estimates of the daily egg production (*P*) and adult reproductive parameters (*F, S*) indicated a higher spawning intensity in 1993 than in 1995. Batch fecundity (F_{ij})-on-gonad free weight (W_{ij}^*) relationships were :

<u>Stratum I</u> : 1993 : $F_{ij} = 563\ W^*_{ij}$, $r^2 = 0.63$, n=25

1995 : $F_{ij} = 325\ W^*_{ij}$, $r^2 = 0.22$, n=70

<u>Stratum II</u> : 1993 : $F_{ij} = 558\ W^*_{ij}$, $r^2 = 0.81$, n=43

1995 : $F_{ij} = 242\ W^*_{ij}$, $r^2 = 0.27$, n=15.

Analysis of covariance showed that, for each year separately, the between-strata difference in batch fecundity was not significant (P>0.05). However, the slope of the regression line (relative batch fecundity, eggs/g) was significantly higher in 1993 than in 1995 (P<0.05, Fig. 3). Spawning frequency estimates (Table 1) indicated a mean inter-spawning interval (=1/S) of 3.5 days and 3.9 days, for Stratum I and II respectively, during June 1993, and 6.7 days and 7.7 days for the same areas in June 1995.

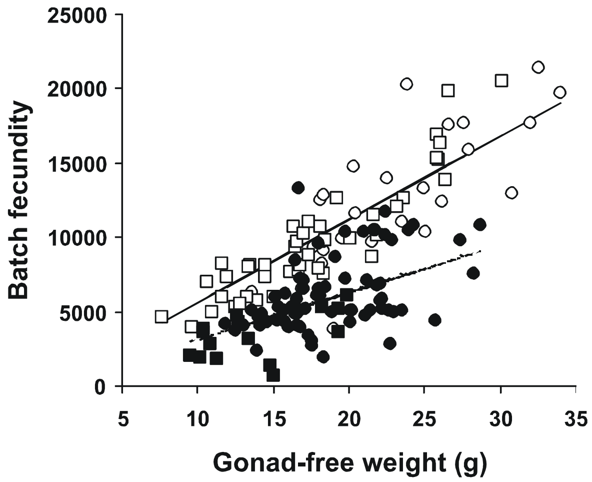

Fig. 3. – Batch fecundity (number of eggs)-on-gonad free weight relationsships. ○ : 1993, Stratum I. ● : 1995, Stratum I. □ : 1995, Stratum II. ■ : 1995, Stratum II. Zero-forces regression lines for 1993 (solid line) and 1995 (broken line) are also drawn.

Mean egg size and somatic condition of adult females were also significantly higher (t-tests, p<0.05) in June 1993 than in 1995 (Fig. 4). Concurrently, waters were colder, less saline and richer in zooplankton during 1993 than in 1995 (p<0.05, Fig. 4).

DISCUSSION

The applications of the DEPM to the northern Aegean Sea anchovy stock were largely experimental, based on data from bongo-net larval fish surveys and opportunistic adult sampling on board the commercial fleet (Somarakis & Tsimenides, 1997). A concurrent total biomass survey carried out by acoustic methods during June 1995 (Machias et al., 1997), gave the estimates of 26671 (CV=0.19) and 17929 metric tons (CV=0.15) for the eastern and the western stratum respectively. The surveyed area during the DEPM applications did not cover the entire spawning area of the anchovy stock, thus, the calculated biomass values are underestimates of the total spawning biomass of this stock. However, sampling procedures and subsequent laboratory and analytical methods were identical between 1993 and 1995 and allowed the between-year comparison of the estimated parameters. The robustness of the DEPM to opportunistic adult sampling is discussed elsewhere (Somarakis & Tsimenides, 1997).

In comparing the DEPM parameters between 1993 and 1995 in relation to various environmental and fish parameters, we observed that adult food availability (mesozooplankton) was higher in the cooler and fresher waters of 1993 (Fig. 4). Concurrently, female anchovies were in better condition, producing numerous large-sized eggs at a higher spawning frequency (short interspawning interval). These observations are consistent with a ration-related reproductive tactic in anchovy (Somarakis et al., 2000).

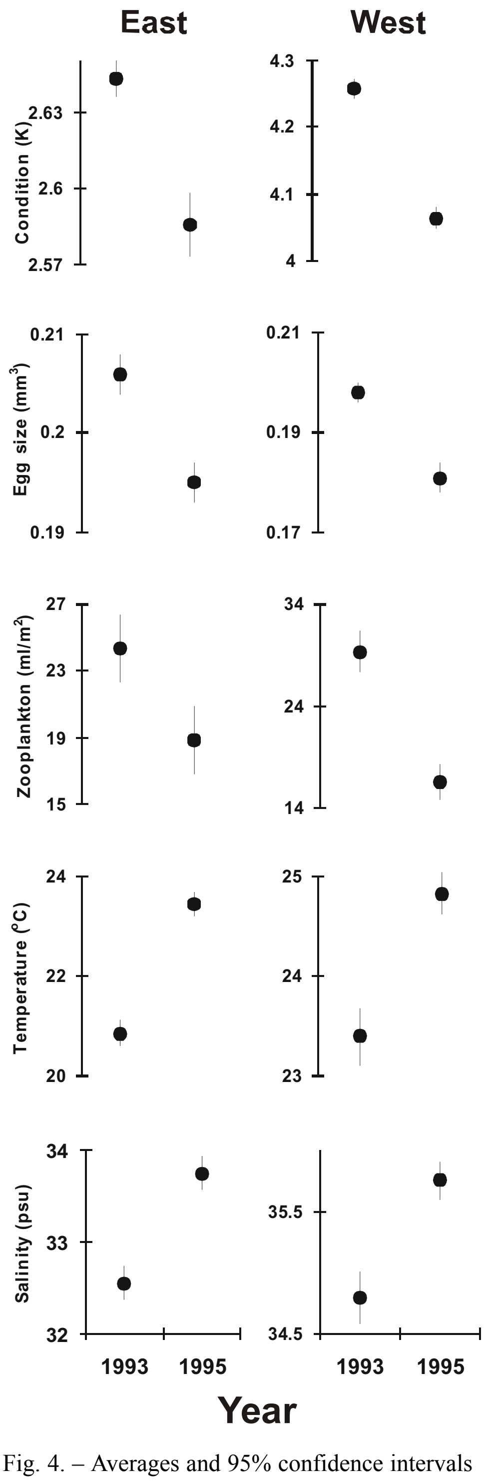

Fig. 4. – Averages and 95% confidence intervals per area (East: Stratum I – West: Stratum II) and year (1993-1995) for relative condition factor (K), mean egg size, zooplankton displacement volume, surface temperature (5 m) and surface salinity (5 m).

In short-living multiple spawning fishes, adults may spawn in direct response to temperature and photoperiod, however, there are examples that minimum forage be required for the onset of spawning, despite ample fat stores (Blaxter & Hunter, 1982). Several studies indicate a ration-related variation in size-specific fecundity or interspawning interval (e.g. Bagenal, 1973 ; Bailey & Almatar, 1989 ; Tsuruta & Hirose, 1989). In south-African pilchard, females spawn an increased number of eggs in response to better fish condition, irrespective of temperature (Le Clus, 1992). Energy allocated to multiple spawnings is derived primarily from feeding rather than from energy reserves in many small pelagic fishes (e.g. Wright, 1990 ; Wang & Houde, 1994). In other cases, spawning is related to both dietary intake and nutritional status of the fish (e.g. Milton et al. 1994). A link between adult forage and spawning is reasonable because of the high energetic cost of frequent spawnings and the fact that areas suitable for planktivorous adults are also suitable for the planktivorus larvae (Blaxter & Hunter, 1982). Recently, Peebles et al. (1996) showed that bay anchovy's egg and subsequent larval production is related to adult as well as larval prey availability. They suggested that hatching larvae are likely to be associated with elevated nauplius densities because of the inherent interdependence between copepod life stages.

Applying the terminology of life history evolution (Stearns, 1992), Somarakis et al. (2000) labeled planktivorous short-lived small pelagic species, such anchovies, as 'income breeder', spawning soon after energy for egg production becomes available. These species are characterized by substantial, ration-related variations in batch fecundity, spawning frequency, and, probably, in egg size. In multiple-spawning fish, batch fecundity does not necessarily increase to compensate for smaller egg sizes (Le Clus, 1992).

The DEPM applications to the northern Aegean Sea anchovy stock are the first to be made in the eastern Mediterranean. The comparison of parameter estimates in relation to environmental regimes highlights the importance of inter-annual variations in the oceanographic habitat in controlling anchovy egg production.

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