ICES Journal of Marine Science, 61:944–958 (2004)
doi:10.1016/j.icesjms.2004.07.018

Daily egg production of anchovy in European waters

Stylianos Somarakis, Isabel Palomera, Alberto Garcia,
Luis Quintanilla, Constantin Koutsikopoulos,
Andrés Uriarte, and Lorenzo Motos

Somarakis, S., Palomera, I., Garcia, A., Quintanilla, L., Koutsikopoulos, C., Uriarte, A., and Motos, L. 2004. Daily egg production of anchovy in European waters. – ICES Journal of Marine Science, 61: 944–958.

Since the late 1980s, the Daily Egg Production Method (DEPM) has been applied to several anchovy stocks in European waters. DEPM surveys in the Bay of Biscay were well standardized and focused on providing fisheries-independent information for stock assessment purposes. Those targeting Mediterranean stocks were largely experimental and often opportunistic, with the main aim of developing and testing the method, rather than providing estimates of spawning stock biomass (SSB) for stock assessment. Consequently, the DEPM has been applied once, twice, or a maximum of three times in certain Mediterranean areas with no among-area standardization. Different techniques for several aspects of the method have been used in the Mediterranean, and the parameters estimated vary greatly among stocks and year of application. Evidence is provided that variability in biological production among sub-basins and/or years, a characteristic of Mediterranean Sea, may directly affect anchovy egg production. The daily specific fecundity of anchovy stocks can vary greatly among years, areas, or seasons in response to changing environmental and trophic regimes. When the correlation between regression-derived estimates of daily egg production and associated estimates of daily specific fecundity for anchovy in the Mediterranean, the Bay of Biscay, and upwelling areas are compared, a significant isometric relationship emerges for the Mediterranean and the Bay of Biscay, implying density-dependent use of spawning habitat. In upwelling areas, estimates of daily egg production are relatively high for a narrow range of generally low daily specific fecundities. There is a strong linear relationship between anchovy SSB and spawning area in European waters that does not differ significantly between the Bay of Biscay and the Mediterranean Sea.

Keywords: anchovy, Bay of Biscay, Daily Egg Production Method, *Engraulis encrasicolus*, Mediterranean Sea.

Received 9 March 2004; accepted 14 July 2004.

S. Somarakis and C. Koutsikopoulos: University of Patras, Department of Biology, Laboratory of Zoology, 26500, Patra, Greece. I. Palomera: Departament de Recursos Marins Renovables, Institut de Ciències del Mar (CMIMA–CSIC), Passeig Marítim de la Barceloneta, 37–49, 08003 Barcelona, Spain. A. Garcia and L. Quintanilla: Instituto Espanol de Oceanografia (IEO), Centro Oceanografico de Malaga, Puerto Pesquero s/n, 29640, Fuengirola, Malaga, Spain. A. Uriarte and L. Motos: AZTIMAR–AZTI Marine Research Unit-Herrera kaia, Portualdea z/g, 20110 Pasaia, Gipuzkoa, Basque Country, Spain. Correspondence to S. Somarakis: tel: +30 2610 997521; fax: +30 2610 996100; e-mail: somarak@upatras.gr.

Introduction

The spawning stock biomass (SSB) of an exploited species is an important variable in fisheries management. Egg production surveys provide a method of estimating it that is independent of any commercial catch data, and have become important because of heightened demands for fishery-independent information (Hunter and Lo, 1993).

The Daily Egg Production Method (DEPM) is an ichthyoplankton-based method for estimating the SSB of pelagic schooling fish such as anchovy and sardine. It is applicable to batch-spawning species with indeterminate annual fecundity, and was developed in the late 1970s at the Coastal Division of the Southwest Fisheries Science Center in La Jolla, California (Parker, 1980; Lasker, 1985). Since then, it has been applied to a variety of small pelagic stocks in different ecosystems around the world, as well as to Atlantic mackerel (Alheit, 1993; Hunter and Lo, 1993, 1997; Priede and Watson, 1993). Both number and type of application continue to increase. Besides biomass estimation, application of the DEPM provides regional time-series on important biological variables of fish stocks, which can lead to new insights into their reproductive biology, particularly when such variables can be compared among species and stocks, or habitats and seasons (Alheit, 1993).

The DEPM is based on the model

$$SSB = P_0 A/(R/W)SF$$

where SSB is the spawning biomass in area A, P_0 the daily egg production at zero age per unit of sea surface area, W the average weight of a mature female, S the fraction of mature females spawning per day, F the batch fecundity, A the area size, and R is the female fraction of the biomass (sex ratio).

Since the late 1980s, the DEPM has been applied to several European anchovy, *Engraulis encrasicolus*, stocks in the Mediterranean Sea and the Bay of Biscay (Table 1, Figure 1). Here we present a synthesis of these applications, contrast different methodologies, and highlight peculiarities of European anchovy habitats in respect of application of the DEPM. Finally, we examine the extent to which different DEPM parameters vary among stocks and/or years.

Methods

DEPM application characteristics, and the relevant biology of European anchovy

Different DEPM estimates of SSB for European anchovy by area, month, and year are summarized in Table 1. Most of these estimates can be considered as total biomass, because the species matures on completion of its first year of life. In the Mediterranean, the length at first maturity is about 11 cm (Demir, 1965; Sinovcic, 1978; Giraldez and Abad, 1995; Basilone *et al.*, 2003; Palomera *et al.*, 2003). In the Bay of Biscay, all one-year-old anchovy >10 cm are sexually mature (Cort *et al.*, 1976; Lucio and Uriarte, 1990). Therefore, during the peak spawning season, most recruits are mature (Motos, 1996; Somarakis, 1999).

Most DEPM surveys have been conducted in May and June (Table 1). The reproductive period of anchovy in the Mediterranean lasts from spring to autumn, usually from

Table 1. Estimates of spawning stock biomass (SSB, t) for anchovy in the Mediterranean Sea and the Bay of Biscay. CVs in parenthesis.

Region	Year	Application code	Month	SSB	References
Catalan Sea	1990	CAT90	May	4 199 (0.26)	1, 2
Catalan Sea & Gulf of Lions	1993	CAT93	July	30 849 (0.30)	2, 3, 4
Catalan Sea & Gulf of Lions	1994	CAT94	May–June	52 557 (0.36)	2, 4, 5
Ligurian & Tyrrhenian Seas	1993	LIG93	July	5 829 (0.36)	2, 3, 4
Sicilian channel	1998	SIC98	June–July	13 224 (0.22)	6, 7, 8
Sicilian channel	1999	SIC99	June	3 010 (0.36)	6, 8, 9
Sicilian channel	2000	SIC00	June–July	2 851 (0.46)	10
SW Adriatic	1994	ADR94	July	8 129 (0.24)	11
Central Ionian Sea	1999	ION99	June	5 588 (0.33)	12, 13
Central Aegean Sea	1999	CAE99	May–June	6 273 (0.44)	12, 13
NE Aegean Sea	1993	NAEe93	June	14 002 (0.34)	14, 15, 16, 17
NW Aegean Sea	1993	NAEw93	June	9 030 (0.38)	14, 15, 16, 17
NE Aegean Sea	1995	NAEe95	June	10 282 (0.22)	16, 17, 18, 19
NW Aegean Sea	1995	NAEw95	June	8 948 (0.36)	16, 17, 18, 19
Bay of Biscay	1987	BB87	June	29 365 (0.48)	20, 21
Bay of Biscay	1988	BB88	May	63 500 (0.31)	20
Bay of Biscay	1989	BB8905	May	11 861 (0.41)	22
Bay of Biscay	1989	BB8906	June	10 058 (0.55)	22
Bay of Biscay	1990	BB9005	May	97 237 (0.17)	23
Bay of Biscay	1990	BB9006	June	77 254 (0.19)	23
Bay of Biscay	1991	BB91	May	19 276 (0.14)	24
Bay of Biscay	1992	BB92	May	90 720 (0.20)	25
Bay of Biscay	1994–1998	BB94–98	May	51 000–101 000	26, 27, 28

[1]Palomera and Pertierra (1993); [2]Palomera (2001); [3]Garcia *et al.* (1994); [4]Garcia and Palomera (1996); [5]Palomera (1995); [6]Mazzola *et al.* (2000); [7]Quintanilla *et al.* (2000); [8]Quintanilla and Garcia (2001a); [9]Quintanilla and Garcia (2001b); [10]Quintanilla and Garcia (2002); [11]Casavola (1998); [12]Machias *et al.* (2000); [13]Somarakis *et al.* (2002); [14]Tsimenides *et al.* (1995); [15]Somarakis and Tsimenides (1997); [16]Somarakis (1999); [17]Somarakis (in press); [18]Tsimenides *et al.* (1998); [19]Somarakis *et al.* (1997); [20]Santiago and Sanz (1992); [21]Sanz *et al.* (1992); [22]Motos and Santiago (1990); [23]Motos and Uriarte (1991); [24]Motos and Uriarte (1992); [25]Motos and Uriarte (1993); [26]Motos *et al.* (1995); [27]Motos *et al.* (1998); [28]Uriarte *et al.* (1999).

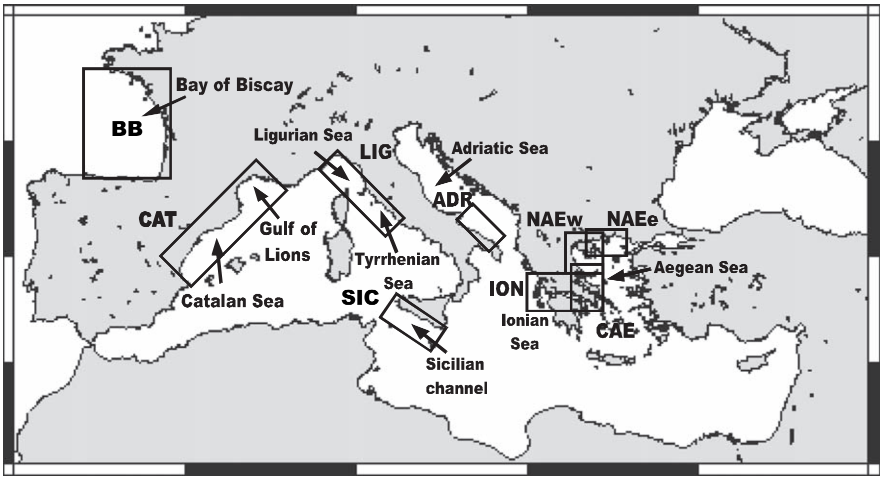

Figure 1. Areas of application of the Daily Egg Production Method to *Engraulis encrasicolus* in European waters.

May to October, and rarely from March to December (Demir, 1965; Chavance, 1980; Palomera 1992; Somarakis, 1993; Regner, 1985, 1996; Giraldez and Abad, 1995; Garcia and Palomera 1996). Results of monthly egg surveys (Palomera, 1992; Somarakis, 1993) indicate that reproduction peaks during June in both the NW and NE Mediterranean. However, in most of the Mediterranean, the gonosomatic index (GSI) is high from May to July (Figure 2). Bay of Biscay anchovy appear to spawn earlier and for a shorter period, peaking in May and June (Motos, 1996), months also associated with spawning in GSI records (Figure 2: Sanz and Uriarte, 1989; Lucio and Uriarte, 1990).

The timing of seasonal peak spawning and the location of the spawning grounds are generally associated with months/areas of high productivity, and specifically with conditions favourable for adult feeding (e.g. zooplankton maxima, riverine outflows, upwelling areas, fronts; Regner, 1985; Valencia *et al.*, 1988; Palomera, 1992; Somarakis, 1993, 1999; Garcia and Palomera, 1996; Motos *et al.*, 1996; Somarakis *et al.*, 2000). In the Mediterranean, areas of increased productivity and conditions favourable for larval survival (Agostini and Bakun, 2002) are generally few, spatially restricted, and limited to northern areas. The main concentrations of anchovy in the Mediterranean are therefore located in the Catalan Sea/Gulf of Lions, in the Adriatic, and in the northern Aegean Sea, with most other areas inhabited by small and highly variable stocks (e.g. the Sicilian channel, Garcia-Lafuente *et al.*, 2001; Quintanilla and Garcia, 2002). In the Bay of Biscay, spawning is triggered by the onset of thermocline formation caused by the relaxation of wind, and the warming of surface waters during spring. There, anchovy spawning appears to be associated with river plumes, shelf break fronts, and oceanic eddies (Koutsikopoulos and Le Cann, 1996; Motos *et al.*, 1996).

Principal characteristics of the ichthyoplankton surveys in European anchovy DEPM applications are summarized in Table 2, and those of the corresponding adult surveys (which have generally been conducted concurrently with the respective egg surveys) in Table 3. DEPM applications in the Bay of Biscay have been carried out routinely for assessment purposes since 1987. In the Mediterranean, they were largely experimental, based on opportunistic funding, with the main aim of developing and testing the method,

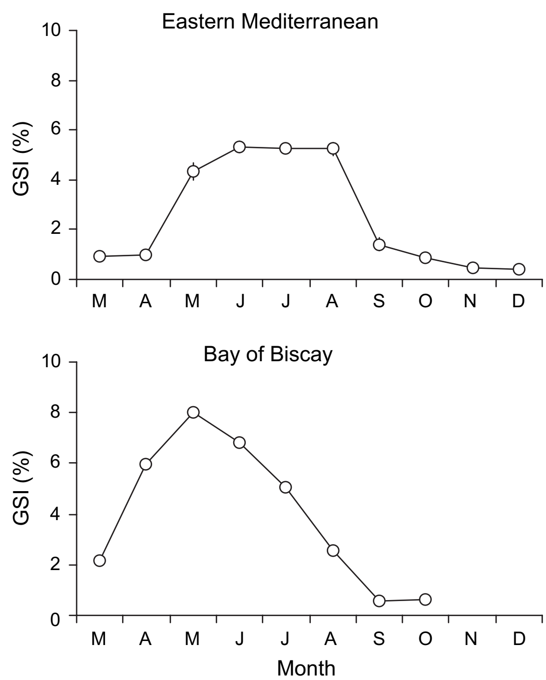

Figure 2. Monthly evolution of anchovy gonosomatic index in the central Aegean Sea (eastern Mediterranean), and the Bay of Biscay. Data from Sanz and Uriarte (1989), Lucio and Uriarte (1990), and Machias *et al.* (2000).

rather than to provide SSB estimates for stock assessment. Consequently, the method has been applied only once or twice in each Mediterranean area, though three successive attempts to apply it were made for Sicilian channel anchovy (Table 1). Although a standard protocol for implementation has been suggested for the DEPM (Lasker, 1985), a characteristic of its application to European anchovy has been that several aspects of the method have been modified in an effort to adapt to the specifics of target stocks and, on some occasions, in response to budget limitations.

All applications have been based on the modification of Parker's model (Parker, 1980) by Stauffer and Picquelle (Stauffer and Picquelle, 1980), and the parameter-estimation procedures described in Picquelle and Stauffer (1985). The latter included: (i) the fitting of an exponential mortality model to the abundance of eggs on their age, to derive the daily egg production; (ii) stratification of survey area into negative and positive strata, when applicable; (iii) plankton station weighting proportional to the representative area; (iv) use of the ratio estimator for adult parameters and their variances (Equation 5 in Picquelle and Stauffer (1985)); (v) the fit of a linear model regressing batch fecundity on ovary-free weight; (vi) bias correction for spawning fractions when oversampling active spawning females.

Ideally, a DEPM application should include the entire spawning area, and be conducted during peak spawning (to increase precision in estimating the spawning fraction). Also, because it is the average fish that is of interest, sampling density should parallel fish density (Hewitt, 1985; Smith and Hewitt, 1985a). The CAT90, ADR94, and applications in the NE Aegean Sea (NAEe93, NAEe95) did not cover the entire spawning area of their respective stocks. Instead, they covered a particular (and distinct) spawning hotspot. Hence, the resultant SSB values (Table 1) are underestimates of the total SSB of the respective stocks. Moreover, adult sampling in the CAT90, the northern Aegean Sea (NAEe93, NAEw93, NAEe95, NAEw95), and the first two applications in the Bay of Biscay (BB87, BB88) was opportunistic, based on commercial rather than research samples. They were therefore representative of fishery catches, rather than the age structure and spatial distribution of the stocks. Adult fish were taken by observers at sea and preserved immediately after capture to fix the gonads.

The vertical distribution of anchovy eggs and larvae is generally restricted to the upper water column, concentrations peaking in the upper 20 m (Palomera, 1991; Motos *et al.*, 1997; Conway *et al.*, 1998; Olivar *et al.*, 2001; Coombs *et al.*, in press). However, subsurface peaks are often distinct, depending on local physical conditions (Motos and Coombs, 2000; Boyra *et al.*, 2003). Plankton sampling in all DEPM applications included at least the 0−100 m layer. With the exception of the northern Aegean Sea (NAEe93, NAEw93, NAEe95, NAEw95), where bongo nets were used, all ichthyoplankton surveys

Table 2. Egg survey characteristics of the Mediterranean and Bay of Biscay anchovy DEPM applications.

Code	Survey area (km^2)	Positive area (km^2)	Plankton sampler	Mesh size (mm)	Tow	Sampling grid (nautical miles)	Number of stations
CAT90	17 081	8 095	CalVET (0.05 m^2)	0.15	Vertical	4 × 10	126
CAT93	44 554	33 012	CalVET (0.05 m^2)	0.15	Vertical	5 × 5	430
CAT94	42 085	31 692	CalVET (0.05 m^2)	0.15	Vertical	6 × 10; 3 × 10	334
LIG93	15 424	8 221	CalVET (0.05 m^2)	0.15	Vertical	5 × 5	172
SIC98	13 295	5 329	CalVET (0.05 m^2)	0.15	Vertical	4 × 4; 2 × 2	253
SIC99	5 878	2 692	CalVET (0.05 m^2)	0.15	Vertical	4 × 4	107
SIC00	11 812	4 505	CalVET (0.05 m^2)	0.15	Vertical	4 × 4; 2 × 2	215
ADR94	14 790	9 244	CalVET (0.05 m^2)	0.335	Vertical	7 × 7	88
ION99	12 362	12 362	WP2 (0.255 m^2)	0.2	Vertical	8 × 8; 4 × 8	87
CAE99	8 604	8 604	WP2 (0.255 m^2)	0.2	Vertical	8 × 8; 4 × 8	77
NAEe93	9 354	9 354	Bongo (0.6 m)	0.25	Oblique	5 × 10	61
NAEw93	8 042	8 042	Bongo (0.6 m)	0.25	Oblique	5 × 10	50
NAEe95	9 354	9 354	Bongo (0.6 m)	0.25	Oblique	5 × 10	61
NAEw95	8 042	8 042	Bongo (0.6 m)	0.25	Oblique	5 × 10	50
BB87	34 934	23 850	CalVET (0.05 m^2)	0.15	Vertical	3 × 15; 5 × 15	196
BB88	59 840	45 384	CalVET (0.05 m^2)	0.15	Vertical	3 × 15	358
BB8905	37 930	17 546	CalVET (0.05 m^2)	0.15	Vertical	3 × 15	317
BB8906	27 917	27 917	CalVET (0.05 m^2)	0.15	Vertical	3 × 15; 3 × 7.5	437
BB9005	79 759	59 757	CalVET (0.05 m^2)	0.15	Vertical	3 × 15; 3 × 7.5	635
BB9006	69 471	69 471	CalVET (0.05 m^2)	0.15	Vertical	3 × 15; 3 × 7.5	536
BB91	84 032	24 264	CalVET (0.05 m^2)	0.15	Vertical	3 × 15; 3 × 7.5	538
BB92	92 782	67 796	CalVET (0.05 m^2)	0.15	Vertical	3 × 15; 3 × 7.5	617
BB94−98	51 000−83 000	28 000−73 000	PairoVET (0.01 m^2)	0.15	Vertical	3 × 15; 3 × 7.5	295−697

Table 3. Adult survey characteristics of the Mediterranean and Bay of Biscay DEPM applications. N_h is the number of females used in measurements of batch fecundity (BF).

Code	Samples	Fishing gear	Number of adult samples	Sampling times	Postovulatory follicle (POF) categories	BF measurements	N_h	Remarks
CAT90	Commercial	Purse-seine, Bottom trawl	18	24 h	Day 1	Non-hydrated	18	Sampling was opportunistically representative of fishing grounds
CAT93	Research	Pelagic trawl	26	07:30–22:30	Day 1	Hydrated	60	
CAT94	Research, Commercial	Pelagic trawl, Purse-seine	26	24 h	Day 1 + Day 2	Hydrated	60	Sampling was restricted to Spanish waters
LIG93	Research	Pelagic trawl	8	07:30–22:30	Day 1	Hydrated	25	
SIC98	Research	Pelagic trawl	17	06:00–24:00	Day 1 + Day 2	Hydrated	67	
SIC99	Research	Pelagic trawl	11	08:00–22:30	Day 1 + Day 2	Hydrated	30	
SIC00	Research, Commercial	Pelagic trawl, Pair trawl	19	05:00–24:00	Day 1 + Day 2	Hydrated	81	
ADR94	Research, Commercial	Pelagic trawl, Pair trawl, Purse-seines	45		Day 1	Hydrated	89	
ION99	Research, Commercial	Pelagic trawl, Purse-seines	18	23:00–05:00	Day 1	Hydrated	58	
CAE99	Research, Commercial	Pelagic trawl, Purse-seine	23	20:00–05:00	Day 1	Hydrated	45	
NAEe93	Mainly commercial, few experimental	Purse-seine, Pelagic trawl	28	22:00–05:00	Day 0 + Day 1	Hydrated	25	Sampling was opportunistically representative of fishing grounds
NAEw93	Mainly commercial, few experimental	Purse-seine, Pelagic trawl	17	22:00–05:00	Day 0 + Day 1	Hydrated	43	Sampling was opportunistically representative of fishing grounds
NAEe95	Mainly commercial, few experimental	Purse-seine, Pelagic trawl	14	22:00–05:00	Day 0 + Day 1	Hydrated	70	Sampling was opportunistically representative of fishing grounds
NAEw95	Mainly commercial, few experimental	Purse-seine, Pelagic trawl	15	22:00–05:00	Day 0 + Day 1	Hydrated	15	Sampling was opportunistically representative of fishing grounds
BB87	Commercial	Purse-seine	35	Night	Day 1	Hydrated	62	Opportunistic sampling
BB88	Commercial	Purse-seine	82	Night	Day 1	Hydrated	167	Opportunistic sampling
BB8905	Research, Commercial	Pelagic trawl, Purse-seine	35	24 h	Day 1	Hydrated	111	
BB8906	Research, Commercial	Pelagic trawl, Purse-seine	13	24 h	Day 1	Hydrated	158	
BB9005	Research, Commercial	Pelagic trawl, Purse-seine	49	24 h	Day 1	Hydrated	194	
BB9006	Research, Commercial	Pelagic trawl, Purse-seine	46	24 h	Day 1	Hydrated	131	
BB91	Research, Commercial	Pelagic trawl, Purse-seine	29	24 h	Day 1	Hydrated	50	
BB92	Research, Commercial	Pelagic trawl, Purse-seine	31	24 h	Day 1	Hydrated	122	
BB94-98	Research, Commercial	Pelagic trawl, Purse-seine	28–60	24 h	Day 1 + Day 2	Hydrated	73–121	

utilized vertical tows of CalVET, PairoVET, or WP2 nets (Table 2).

Regression estimates of daily egg production

Estimating daily egg production (Table 4) generally involved the fitting of an exponential mortality model to a data set of egg abundance-at-age (Picquelle and Stauffer, 1985). Many applications used an automated procedure for the assignment of age to eggs (the STAGEAGE program of Lo (1985), as modified by Motos (1994)). The age was calculated on the basis of a temperature-dependent model of anchovy development rate (Motos, 1994), station surface temperature, peak spawning time, and time of tow.

In areas of high surface temperature, such as the eastern Mediterranean, the duration of the egg stage is generally short, and eggs can also be easily grouped into ''spawning nights'' manually; the distribution of eggs over the different developmental stages form distinct groups (one or two), with unrepresented stages separating each group (Somarakis *et al.*, 2002).

According to Motos (1994), the rate of development of *E. encrasicolus* eggs is slower than that of *E. mordax* (Lo, 1985), but similar to that of *E. encrasicolus* off southern Africa, a species formerly known as *E. capensis* (Valdés *et al.*, 1987). In both the Atlantic and the Mediterranean, fish exhibit a diel spawning cycle (Regner, 1985; Somarakis, 1993, 1999; Motos, 1996, and references therein). Data from histological analysis of ovaries, as well as the presence of newly fertilized eggs in the plankton in relation to time of day, indicate that, during anchovy DEPM surveys, most spawning is between 22:00 and 02:00, peaking around midnight (Garcia *et al.*, 1994; Motos, 1996; Somarakis, 1999; Quintanilla *et al.*, 2000). Hence, in all applications here, peak spawning time was assumed to be midnight (00:00; Table 4).

When fitting an exponential mortality model for small, patchily distributed stocks and/or when egg incubation temperatures are high, there is usually a scarcity of positive egg data, resulting in the estimate of egg mortality being not significantly different from zero (Hunter and Lo, 1997;

Table 4. Regression estimation of daily egg production. P_0 is the daily egg production (eggs m^{-2}), and Z the instantaneous rate of mortality. CVs in parenthesis.

Code	P_0	Z	Daily peak spawning	Surface temperature (°C) range	Assumed incubation temperature	Ageing of eggs	Yolk-sac stages used
CAT90	57.16 (0.29)	0.56 (0.44)	0:00	17.6–19.6	0–20 m	STAGEAGE	No
CAT93	64.30 (0.15)	1.09 (0.26)	0:00	13.3–22.5	0–20 m	STAGEAGE	No
CAT94	61.53 (0.21)	0.47 (0.26)	0:00	15.2–22.0	0–20 m	STAGEAGE	No
LIG93	49.87 (0.22)	0.86 (0.34)	0:00	18.9–22.5	0–20 m	STAGEAGE	No
SIC98	65.55 (0.21)	1.63 (0.33)	0:00	18.5–22.5	0–10 m	STAGEAGE	No
SIC99	43.99 (0.26)	1.24 (0.40)	0:00	18.4–22.7	0–10 m	STAGEAGE	No
SIC00	34.98 (0.15)	2.07 (0.20)	0:00	16.3–25.8	0–10 m	STAGEAGE, Manually	No
ADR94	50.11 (0.16)	0.55 (0.12)	0:00			STAGEAGE, Manually	No
ION99	8.88 (0.24)	0.52 (0.36)	0:00	18.7–25.6	5 m	Manually	Yes
CAE99	13.29 (0.39)	0.53 (0.48)	0:00	18.2–22.8	5 m	Manually	Yes
NAEe93	109.22 (0.27)	0.17 (0.36)	0:00	16.7–23.5	5 m	STAGEAGE, Manually	Yes
NAEw93	87.19 (0.33)	1.26 (0.39)	0:00	18.4–25.0	5 m	STAGEAGE, Manually	Yes
NAEe95	25.21 (0.23)	0.52 (0.40)	0:00	21.6–24.7	5 m	STAGEAGE, Manually	Yes
NAEw95	19.75 (0.26)	0.54 (0.47)	0:00	22.4–25.5	5 m	STAGEAGE, Manually	Yes
BB87	92.20 (0.32)	0.26 (0.78)	0:00	15.0–18.0	10 m	STAGEAGE	No
BB88	110.40 (0.21)	0.18 (0.68)	0:00	15.0–18.0	10 m	STAGEAGE	No
BB8905	41.60 (0.27)	0.18 (0.99)	0:00	15.0–18.0	10 m	STAGEAGE	No
BB8906	29.60 (0.30)	0.94 (0.41)	0:00	19.0–22.0	10 m	STAGEAGE	No
BB9005	75.60 (0.20)	0.49 (0.39)	0:00	15.0–18.0	10 m	STAGEAGE	No
BB9006	104.20 (0.13)	0.62 (0.31)	0:00	15.5–18.5	10 m	STAGEAGE	No
BB91	51.00 (0.22)	0.22 (0.65)	0:00	13.5–18.0	10 m	STAGEAGE	No
BB92	85.40 (0.14)	0.22 (0.65)	0:00	15.5–19.0	10 m	STAGEAGE	No
BB94–98	53.80–99.20	0.11–0.30	0:00	13.0–19.0	10 m	STAGEAGE	No

Somarakis *et al.*, 2002). Problems with the fit of the mortality model become more serious when the number of plankton stations is inadequate, as was the case in the northern Aegean Sea (NAEe93, NAEw93, NAEe95, NAEw95). In the latter applications, the egg abundance-at-age data were considered insufficient for estimating egg mortality and daily egg production (Tsimenides *et al.*, 1995; Somarakis and Tsimenides, 1997; Somarakis *et al.*, 1997). Therefore, those estimates were revised (Somarakis, 1999, in press) using a method similar to the CAE99 and ION99 applications in the central Aegean and Ionian Seas (Somarakis *et al.*, 2002). To increase the number of age categories for constructing mortality curves, Somarakis *et al.* (2002) assumed that the mortality rate was the same for eggs and yolk-sac larvae, and included both in single embryonic mortality curves. Regression parameter estimates are similar for the egg data set and the egg plus yolk-sac larva data set. However, in the latter case, the precision of the regression estimates is substantially higher (Somarakis *et al.*, 2002).

Temperature-dependent duration curves exist for two stages of anchovy yolk-sac larvae (Somarakis *et al.*, 2002), for YSI (larvae with unpigmented eyes), and for YSII (larvae with brown pigment traces or brownish eyes), calculated by Regner (1985) from laboratory experiments in the Adriatic Sea. These two stages of yolk-sac larvae are generally easily identified in plankton collections, because yolk-sac larvae rarely lose their eyes during sampling and preservation.

Spawning frequency estimation

In all DEPM applications, spawning frequency (S), the fraction of mature females spawning each night, was estimated histologically by the postovulatory follicle (POF) method (Hunter and Macewicz, 1985). Some studies used females with Day 1 POFs for estimating S (Table 3). Others used two daily classes of POF, either Day 1 and Day 2 (CAT94, SIC98, SIC99, SIC00, BB94–98), or Day 0 and Day 1 (NAEe93, NAEw93, NAEe95, NAEw95). Actively spawning anchovy (Day 0 females) are oversampled prior to or during the hours of spawning (Picquelle and Stauffer, 1985; Santiago and Sanz, 1989; Uriarte *et al.*, 1999). Hence, the fraction of Day 0 females is not generally used for spawning frequency estimates. Its use in northern Aegean Sea applications was justified by the fact that the fractions of Day 0 females did not differ significantly from Day 1 females when samples were collected outside the daily spawning period (after 04:00; Somarakis, in press).

Results

The estimated DEPM parameters for anchovy in European waters are summarized in Tables 4 and 5. They are characterized by high inter-regional and interannual differences, especially within the Mediterranean Sea. Estimates of daily egg production in the spawning area range from 8.88 to 110.40 eggs m^{-1} (Table 4), the spawning frequency from 0.06 to 0.36, the relative fecundity (the fraction F/W) from 226 to 646 eggs g^{-1} of mature female, and the daily specific fecundity (DSF = FSR/W) from 18 to 109 eggs g^{-1} of spawning stock (Table 5).

In comparing the correlation between daily egg production in the spawning area and the corresponding daily specific fecundity in the Mediterranean and the Bay of Biscay, and for other anchovy species in upwelling areas (Table 6), an isometric relationship emerges for European anchovy (Figure 3). The relationships for the Mediterranean ($\log[P_0] = 0.33 + 0.90 \log[DSF]$; $r^2 = 0.60$, $p = 0.001$) and the Bay of Biscay ($\log[P_0] = -0.77 + 1.20 \log[DSF]$; $r^2 = 0.30$, $p = 0.065$) do not differ statistically (ANCOVA; slope $F = 0.17$, $p = 0.680$; intercepts $F = 0.61$, $p = 0.442$), and the pooled model has a slope that equals 1 (t-test, $p > 0.05$), explaining about 61% of the variation in the data. For the Bay of Biscay alone, the relationship is only marginally significant ($p = 0.065$), a finding that can be attributed to the low variability of the daily specific fecundity parameter in that area during peak spawning (Figure 3, Table 5). In upwelling areas, daily egg production is relatively higher for a narrow range of small DSF values.

There is a strong relationship between the SSB and the spawning area (SA; positive strata) for anchovy (Figure 4) in both the Bay of Biscay and the Mediterranean Sea. The separate linear relationships for these two regions do not differ significantly (ANCOVA; slope $F = 0.42$, $p = 0.523$; intercepts $F = 1.32$, $p = 0.263$), and the intercept in both cases is not significantly different from zero ($p > 0.05$). The corresponding separate zero-forced models for the Mediterranean and the Atlantic are:

Mediterranean; $SSB = 1.18SA$; $r^2 = 0.79$, $p < 0.001$
Bay of Biscay; $SSB = 1.28SA$; $r^2 = 0.83$, $p < 0.001$

These results do not change if Mediterranean applications that did not cover the entire spawning grounds of the respective stocks (CAT90, ADR94, NAEe93, NAEe95) are excluded from the analysis.

Discussion

Methodology

DEPM surveys in the Bay of Biscay were well standardized and focused on providing information for stock assessment purposes, whereas those for Mediterranean stocks were largely experimental and often opportunistic. Different techniques, in several aspects of the method, have been used in the Mediterranean, and the parameters estimated vary greatly among stocks and year of application.

Adult sampling in certain Mediterranean applications, as well as in the first two applications in the Bay of Biscay, was based exclusively on commercial rather than research samples and, therefore, was representative of the commercial fishery catch rather than of the age structure and spatial

Table 5. Adult parameter estimates of European anchovy DEPM applications. R is the sex ratio by weight, W the average weight of mature females (g), F the batch fecundity, S the spawning fraction, RF the relative fecundity (RF = F/W, eggs g^{-1}), and DSF is the daily specific fecundity, the number of eggs produced per gramme weight of the population (DSF = FSR/W). CVs in parenthesis.

Code	R	W	F	S	RF	DSF
CAT90	0.54 (0.09)	14.3 (0.04)	8 006 (0.02)	0.36 (0.10)	562	109
CAT93	0.64 (0.05)	14.3 (0.07)	4 958 (0.11)	0.31 (0.13)	347	69
CAT94	0.59 (0.19)	22.9 (0.06)	7 039 (0.02)	0.21 (0.20)	307	38
LIG93	0.63 (0.05)	14.2 (0.07)	4 894 (0.10)	0.32 (0.11)	345	70
SIC98	0.59 (0.12)	15.2 (0.07)	4 835 (0.16)	0.14 (0.12)	319	26
SIC99	0.55 (0.10)	14.1 (0.08)	5 871 (0.11)	0.17 (0.10)	417	39
SIC00	0.62 (0.08)	18.9 (0.04)	8 379 (0.06)	0.20 (0.28)	443	55
ADR94	0.55 (0.05)	18.6 (0.03)	11 866 (0.03)	0.16 (0.08)	639	57
ION99	0.53 (0.07)	15.6 (0.05)	9 428 (0.08)	0.06 (0.26)	604	19
CAE99	0.47 (0.09)	15.8 (0.03)	4 725 (0.06)	0.13 (0.21)	300	18
NAEe93	0.51 (0.05)	24.9 (0.03)	12 451 (0.05)	0.29 (0.21)	500	74
NAEw93	0.60 (0.05)	20.9 (0.03)	10 474 (0.04)	0.26 (0.20)	502	78
NAEe95	0.51 (0.08)	25.6 (0.03)	7 781 (0.06)	0.15 (0.11)	303	23
NAEw95	0.61 (0.03)	22.7 (0.03)	5 128 (0.10)	0.13 (0.23)	226	18
BB87	0.54 (0.06)	33.8 (0.03)	15 904 (0.06)	0.32 (0.18)	470	81
BB88	0.52 (0.05)	29.2 (0.01)	15 783 (0.05)	0.29 (0.07)	540	81
BB8905	0.54 (0.07)	29.7 (0.01)	12 977 (0.04)	0.26 (0.1)	438	62
BB8906	0.51 (0.12)	23.7 (0.06)	15 307 (0.07)	0.17 (0.23)	646	55
BB9005	0.53 (0.04)	19.7 (0.06)	7 039 (0.05)	0.28 (0.04)	357	52
BB9006	0.58 (0.11)	17.1 (0.02)	8 993 (0.03)	0.30 (0.06)	525	90
BB91	0.59 (0.05)	22.6 (0.04)	11 761 (0.05)	0.23 (0.12)	520	68
BB92	0.56 (0.03)	17.9 (0.03)	9 246 (0.13)	0.25 (0.3)	517	72
BB94−98	0.53−0.56	16.8−28.2	7 200−15 000	0.21−0.23	430−530	53−68

Table 6. Worldwide anchovy DEPM parameters used in comparisons with the European anchovy. P_0 is the daily egg production in the spawning area (eggs m^{-2}), and DSF is the daily specific fecundity (eggs g^{-1}).

Year	Region	Species	P_0	DSF	References
1984	South	*Engraulis*	389.40	40.08	1
1985	Africa	*encrasicolus*	326.50	50.35	
1986			487.60	25.27	
1987			303.70	26.46	
1988			313.70	22.65	
1989			174.00	37.86	
1990			354.00	21.08	
1980	California	*Engraulis*	221.60	30.28	2, 3, 4
1981		*mordax*	159.20	33.03	
1982			66.40	32.53	
1983			111.00	24.35	
1984			75.80	42.43	
1985			95.40	37.00	
1981	Peru	*Engraulis*	474.00	45.39	4, 5
1985		*ringens*	60.18	17.88	
1990			302.40	13.69	
1994			380.00	20.32	

[1]Shelton *et al.* (1993); [2]Lasker (1985); [3]Bindman (1986); [4]Lo (1997); [5]Hunter and Lo (1997).

distribution of the stocks. Indeed, purse-seine samples in the northern Aegean Sea were biased with regard to mean female weight, because fishers actively selected schools of bigger fish (in deeper water) because of the higher price bigger fish attract (Tsimenides *et al.*, 1998). However, as

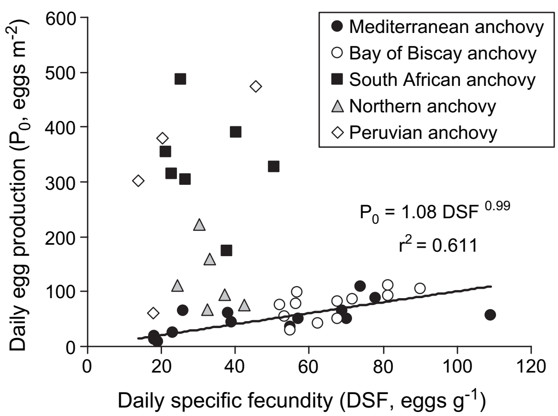

Figure 3. Plot of daily egg production on daily specific fecundity from several DEPM applications around the world. The strong isometric relationship for the European anchovy applications (Mediterranean and Bay of Biscay) is clear.

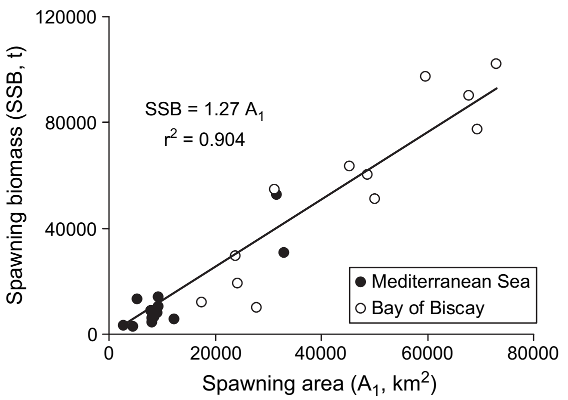

Figure 4. Linear regression of spawning stock biomass on spawning area for European anchovy (Mediterranean and Bay of Biscay) DEPM applications.

pointed out by Motos and Uriarte (1991), the DEPM is quite insensitive to inadequate adult sampling, as long as there are no substantial differences in the W/F ratio, spawning frequency, and sex ratio among different age groups. For Bay of Biscay anchovy at least, no such differences exist during peak spawning (Motos, 1996), validating the adult sample protocol generally used in the area (and occasionally in certain Mediterranean applications), i.e. a composite of research vessel pelagic trawl samples plus opportunistic commercial purse-seine samples. In the northern Aegean, the linear regressions of batch fecundity on ovary-free weight had intercepts not significantly different from zero, indicating that relative fecundity (eggs g^{-1}) did not change with fish size or age during the respective DEPM surveys (Maraveya *et al.*, 2001). In contrast, adult parameters are age-dependent in northern anchovy, *Engraulis mordax* (Parrish *et al.*, 1986). The dependence of relative batch fecundity and spawning fraction on size or age for different European anchovy stocks and different environments deserves further investigation, because it can have great impact on both parameter accuracy and population reproductive potential.

Early surveys in the northern Aegean were based on oblique rather than vertical plankton tows. Oblique bongo tows have been criticized in terms of their suitability for DEPM assessments (Somarakis and Tsimenides, 1997). However, in a recent comparison of replicate WP2 vertical (mouth area 0.255 m^2, mesh size 0.200 mm) and bongo oblique (mouth diameter 0.6 m, mesh size 0.250 mm) tows, no significant between-gear differences were found in the mean abundance of anchovy eggs. Variance for the vertical tows was 7 times higher than for the oblique tows (Tzanatos *et al.*, 2001). In Californian waters, Picquelle and Hewitt (1983) found that the CalVET net and the CalCOFI bongo net yielded consistent and compatible estimates of ichthyoplankton production.

The use of small-volume vertical plankton tows increases substantially the number of samples that can be collected for a given cost, reducing substantially the standard error of the regression estimates of daily egg production. In the Bay of Biscay, the vertical sampler was changed from a CalVET to a PairoVET net (two nets of twin CalVETs per tow; Smith *et al.*, 1985) in 1994, because increasing the effective sampling area from 0.05 to 0.1 m^2 reduced the sampling errors for 3-day-old anchovy eggs by about 33% (Uriarte and Motos, 1998).

In the eastern Mediterranean applications, both eggs and yolk-sac larvae were included in the mortality curves, to derive the daily egg production. It was assumed that the mortality rate was the same for eggs and yolk-sac larvae, as discussed in Hunter and Lo (1997) and Somarakis *et al.* (2002). The addition of yolk-sac larvae ''anchors'' the end of the mortality curve and substantially improves the precision of the estimate of daily egg production (Hunter and Lo, 1997). This allows efficient estimation of daily egg production and the rates of instantaneous mortality when egg stages are undersampled, i.e. if it is not possible to take adequate samples for budgetary reasons, or when the distribution of adults and their spawn are patchily distributed. The latter is the usual situation at low biomass (Lo *et al.*, 1996).

In areas of high surface temperature ($>20°C$), the duration of the egg stage is generally very short (<2 days), and the eggs from previous nights' spawning at a station are clustered in one or two daily cohorts (Somarakis *et al.*, 2002). The existence of only one or two cohorts of eggs in the samples greatly ''reduces'' available data points in the egg data set, which, in addition, consists mainly of patchily distributed <1-day-old eggs (Smith and Hewitt, 1985b; Hunter and Lo, 1997). The use of yolk-sac stages is therefore a useful option to increase the precision of estimates of daily egg production when sea temperatures are high.

All DEPM applications in European waters used the postovulatory follicle method to estimate spawning frequency. In general, the precision of the estimate of spawning frequency can be improved if more than one daily class of spawners can be identified in the samples, and subsequently combined to produce a composite estimate of spawning fraction (Uriarte *et al.*, 1999; Quintanilla *et al.*, 2000, Quintanilla and Garcia, 2001a, b, 2002; Ganias *et al.*, 2003). A requisite of such combination is that different spawners' classes have the same statistical distributions (Ganias *et al.*, 2003; Somarakis, in press).

The rate of POF degeneration has been described for Bay of Biscay anchovy, and has been calibrated experimentally in bait tanks (Motos, 1996). However, no such information is available for anchovy in the Mediterranean. The morphology of POFs should therefore be studied in detail in relation to time of collection, daily spawning period, and existing descriptions of POFs for other anchovy stocks or species. Interannual or regional differences in temperature regimes and their effect on the rate of POF degeneration should be addressed by analysing vertical profiles of temperature taken at the same time and in the same area (Ganias *et al.*, 2003).

DEPM parameters

The most prominent characteristic of the estimated DEPM parameters for anchovy in European waters is their high inter-regional and interannual variability, especially in the Mediterranean Sea (Tables 4, 5, Figure 3). This variability can be attributed to the diversity of methodology applied, and standardization problems (Quintanilla and Garcia, 2001c), but most of it probably reflects natural variability in reproductive parameters. The latter can occasionally change within the same spawning season, as shown for the second of the two years of double surveys (1989−1990; Tables 4, 5) conducted experimentally in the Bay of Biscay (Motos and Uriarte, 1991).

Differences in biological production among sub-basins or among seasons/years, which are prominent at least in the Mediterranean (Stergiou *et al.*, 1997; Agostini and Bakun, 2002), may directly influence anchovy egg production. Indeed, the trophic environment of reproducing stocks could directly impact anchovy reproductive effort, as shown by applications in the northern Aegean Sea. In comparing the DEPM parameters between 1993 and 1995 in relation to various environmental parameters and somatic condition, Somarakis (1999, in press) showed that adult food availability (mesozooplankton) was higher in 1993, when waters were significantly cooler and fresher, and, concurrently, female anchovy were in better condition, producing numerous eggs at a higher frequency (short interspawning interval; Figure 5). Those observations were consistent with a ration-related reproductive tactic of European anchovy (Somarakis, 1999, in press; Somarakis *et al.*, 2000). Based on those findings and observations on interannual variations in the abundance of larvae of anchovy and mesopelagic species in the plankton (Somarakis, 1999; Somarakis *et al.*, 2000; Somarakis and Maraveya 2001), short-lived planktivorous pelagic fish in the Mediterranean are classified as ‘‘income breeders’’ (*sensu* Stearns, 1992), spawning soon after energy for egg production becomes available. Income breeders might be characterized by substantial, ration-related variations in batch fecundity and spawning frequency, as observed for anchovy in the northern Aegean (Somarakis *et al.*, 2000; Somarakis, in press).

The energy allocated to multiple spawning in many small pelagic fish is derived primarily from feeding, rather than from energy reserves (Milton *et al.*, 1994; Wang and Houde, 1994). In other cases, spawning is related both to dietary intake and the nutritional status of the fish (Milton

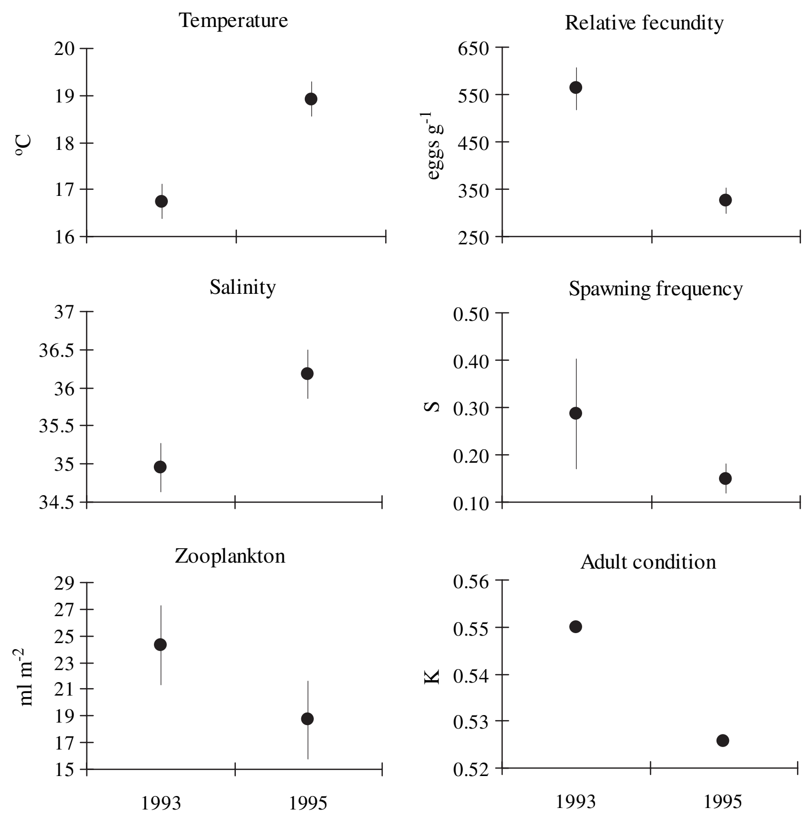

Figure 5. Northwestern Aegean Sea DEPM applications (NAEe). Averages and 95% confidence intervals for upper water column (0−40 m) temperature and salinity, zooplankton displacement volumes (0.250-mm mesh bongo net), relative fecundity, spawning frequency, and female somatic condition in 1993 and 1995. Redrawn from Somarakis (1999, in press).

et al., 1994). In Californian anchovy, *Engraulis mordax*, up to 70% of the energy stored in the previous feeding season is used for reproduction (Hunter and Leong, 1981). In eutrophic areas anchovy might find enough food to store energy for future use, in contrast to less productive or oligotrophic areas, where prey fields might not allow for significant surplus energy storage during winter, and fish can only allocate energy to reproduction during the period of maximum prey production.

Some marked inter-regional or interannual differences in anchovy reproductive parameters were observed in the more southern Mediterranean areas, such as the central Aegean and Ionian Seas (CAE99 and ION99), or the Sicilian channel (SIC98, SIC99, SIC00). These areas are inhabited by small stocks of anchovy with patchy distributions. They are largely oligotrophic, receiving the influence of only small rivers or wind-driven, but highly variable, upwelling. A remarkable difference in batch fecundity was found between the central Aegean and Ionian stocks (CAE99 and ION99, Table 5) in 1999. However, the interplay of fecundity and spawning frequency seemed eventually to condition reproductive effort, because the estimates of spawning frequency showed an opposing trend (Table 5), and resulting values for daily specific fecundity were almost equal for the two seas (about 18 eggs g^{-1} of reproducing stock).

In the Sicilian channel applications, the longest time-series in the Mediterranean (three years), the estimated SSB was relatively high in 1998 (13 224 t; Table 1), but it decreased to about 3000 t in 1999 and 2000. This decline was coupled with a contraction of the spawning area and a concomitant decline in daily egg production (Tables 2, 4). It seemed to be associated with a high interannual and short-term variability in the wind and upwelling regimes, and corresponding changes in the thermal and trophic environment in the area (Quintanilla and Garcia, 2002). In response to the decrease in daily egg production and SSB, the spawning stock almost doubled its daily specific fecundity (both relative fecundity and spawning frequency increased; Table 5) from 1998 to 2000. However, in all three years of the study, a high proportion of the adult females were in an atretic or inactive state (Quintanilla and Garcia, 2002), implying that only a fraction of the potential spawning stock produced eggs in this unstable, highly variable habitat.

Relationship between daily egg production and daily specific fecundity

An overall isometric relationship between daily egg production (P_0) and daily specific fecundity (DSF) in European waters (Figure 3) implies density-dependent use of the spawning habitat by spawning anchovy. Indeed, there is a strong linear relationship between the size of the spawning stock (SSB) and the size of the spawning area (SA; Figure 4). In upwelling areas, the daily egg production is generally much higher for a narrow range of small DSF values (Figure 3). Presumably, the trophic condition and the carrying capacity of upwelling areas is much greater than the more oligotrophic European seas, supporting much higher fish biomass per unit sea surface area.

The relatively low and less variable DSF values in upwelling areas can be attributed to the lower variability in habitat conditions and the prolonged duration of pelagic fish spawning seasons in those areas (Alheit *et al.*, 1984; Whitehead *et al.*, 1988). In order to explain the high consistency of spawning fraction estimates for pelagic species in upwelling areas, Hunter and Lo (1997) introduced the ''biorhythm hypothesis'', which suggests that the frequency of spawning is relatively constant for females actively spawning, as soon as the habitat conditions (e.g. prey fields, temperature) remain about the same. In temperate European waters, the spawning season is shorter, coupled to seasonal temperatures and the short production cycle. Variability in habitat conditions seems to have a direct influence on anchovy reproductive parameters (see above).

The empirical relationships between P_0 and DSF as well as SSB and SA found in the present study suggest that European anchovy tend to maintain an upper level of spawning stock density in European waters, one that is much lower than for upwelling areas. In the Bay of Biscay (Motos *et al.*, 1996; Uriarte *et al.*, 1996, 1999), in years of low stock abundance, eggs occur spatially restricted to the main spawning centres (i.e. productive waters of the southeastern coastal areas under the influence of river outflows, such as Garonne and Adour, and over shelf-edge fronts). In years of greater abundance, eggs occur over most of the Bay. It seems likely that when biomass per unit area of the stocks in the main spawning grounds exceeds a certain threshold (most likely related to the trophic capacity of European spawning grounds), fish tend to spread over a larger area, to avoid intra-specific interactions such as trophic competition and/or egg cannibalism. Indeed, egg cannibalism, which accounts for 20–30% of total egg mortality in upwelling areas (Alheit, 1993, and references therein), has never been observed in European anchovy (Tudela and Palomera, 1997; Plounevez and Champalbert, 1999, 2000).

According to the basin hypothesis of MacCall (1990), clupeoid populations represent optimal areas or basins for reproduction. In periods of low abundance, the distribution of stocks shrinks, and spawning is practically restricted to the more favourable spawning sites. In the Bay of Biscay, the spread of anchovy over a larger area appears to be led by the bigger/older anchovy, which consistently appear in deeper sea areas located far from the coast (Uriarte *et al.*, 1996; Petitgas *et al.*, 2003).

Based on the ''ocean triad hypothesis'', and the analysis of maritime weather reports and satellite-sensed ocean colour distributions, Agostini and Bakun (2002) suggested that suitable reproductive habitats and successful anchovy populations in the Mediterranean are likely to exist in the northern Aegean Sea, the Adriatic Sea, the Catalan

Sea/Gulf of Lions, and the Alboran Sea. With the exception of the latter, which has a very narrow continental shelf, the other three areas support the largest anchovy fisheries. Furthermore, the Aegean, the Adriatic, and the western Mediterranean stocks differ substantially in genetic structure (Magoulas *et al.*, 1996). These suitable anchovy spawning habitats are spatially restricted and separated from each other by deep, extremely oligotrophic basins, which would not be likely to support anchovy feeding and reproduction. For instance, in the Aegean Sea, there is a sharp contrast in productivity between its northern and southern basin, and anchovy schools are practically absent from the latter (Stergiou *et al.*, 1997). Given the contrasting characteristics of adjacent Mediterranean basins, we believe that the expansion of spawning areas at high stock densities would not be beneficial for Mediterranean stocks. Migration of anchovy schools away from the traditional fishing/spawning grounds has seldom been reported by fishers, nor it has ever been proved by scientists. It is therefore probable that the Mediterranean anchovy stocks rarely reach spawning densities capable of triggering a significant expansion of the spawning areas.

Acknowledgements

We thank Peter Witthames of CEFAS, UK, and an anonymous referee for useful comments on the manuscript.

References

Agostini, V. N., and Bakun, A. 2002. 'Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). Fisheries Oceanography, 11: 129–142.

Alheit, J. 1993. Use of the daily egg production method for estimating biomass of clupeoid fishes: a review and evaluation. Bulletin of Marine Science, 53: 750–767.

Alheit, J., Alarcon, V. H., and Macewicz, B. J. 1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. CalCOFI Report, 25: 43–52.

Basilone, G., Patti, B., Mazzola, S., Cuttitta, A., Bonanno, A., Giusto, B., Giuseppe, S., Vergara, A. R., Sposito, P., and Patti, C. 2003. Reproductive biology aspects of the Strait of Sicily anchovy (*Engraulis encrasicolus*). Document Presented to the GFCM – SAC Subcommittee on Stock Assessment Working Group on Small Pelagic Species, Tanger, Morocco, March 2003. 10 pp.

Bindman, A. G. 1986. The 1985 spawning biomass of the northern anchovy. CalCOFI Report, 27: 16–24.

Boyra, G., Rueda, L. D., Coombs, S. H., Sundby, S., Ådlandsvik, B., Santos, M., and Uriarte, A. 2003. Modeling the vertical distribution of eggs of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*). Fisheries Oceanography, 12: 381–395.

Casavola, N. 1998. Daily egg production method for spawning biomass estimates of anchovy in the south-western Adriatic during 1994. Rapport de la Commission International pour l'Exploration Scientifique de la Mer Méditerranée, 35: 394–395.

Chavance, P. 1980. Production des aires de ponte, survie larvaire et biomasse adulte de la sardine et de l'anchois dans l'est du Golf du Lion (*Mediterranee occidentale*). Téthys, 9: 399–413.

Conway, D. V. P., Coombs, S. H., and Smith, C. 1998. Feeding of anchovy *Engraulis encrasicolus* larvae in the northwestern Adriatic Sea in response to changing hydrobiological conditions. Marine Ecology Progress Series, 175: 35–49.

Coombs, S. H., Boyra, G., Rueda, L. D., Uriarte, A., Santos, M., Conway, D. V. P., and Halliday, N. C. Buoyancy measurements and vertical distribution of eggs of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*). Marine Biology (in press).

Cort, J. L., Cendrero, O., and Iribar, X. 1976. La anchoa, *Engraulis encrasicholus* (L.), del Cantábrico. Bolletino del Instituto Espanol de Oceanografia, 220: 3–34.

Demir, N. 1965. Synopsis of biological data on anchovy *Engraulis encrasicolus* (Linnaeus) 1758 (Mediterranean and adjacent seas). FAO Fisheries Synopsis, 26(1): 1–42.

Ganias, K., Somarakis, S., Machias, A., and Theodorou, A. 2003. Evaluation of spawning frequency in a Mediterranean sardine population. Marine Biology, 142: 1169–1179.

Garcia, A., and Palomera, I. 1996. Anchovy early life history and its relation to its surrounding environment in the western Mediterranean basin. Scientia Marina, 60(Suppl. 2): 155–166.

Garcia, A., Palomera, I., Liorzou, B., Giovanardi, O., and Pla, C. 1994. Northwestern Mediterranean anchovy. Distribution, biology, fisheries and biomass estimation by different methods. Final Report of the EC FAR Project 1992–1993. Contract No. MA 3.730.

Garcia-Lafuente, J., Garcia, A., Mazzola, S., Quintanilla, L., Delgado, J., Cuttita, A., and Patti, B. 2001. Hydrographic phenomena influencing early life stages of the Sicilian Channel anchovy. Fisheries Oceanography, 11: 31–44.

Giraldez, A., and Abad, R. 1995. Aspects on the reproductive biology of the western Mediterranean anchovy from the coasts of Malaga (Alboran Sea). Scientia Marina, 59: 15–23.

Hewitt, R. P. 1985. A protocol for designing a sea survey for anchovy biomass assessment. *In* An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*, pp. 51–53. Ed. by R. Lasker. NOAA Technical Report, NMFS 36.

Hunter, J. R., and Leong, R. 1981. The spawning energetics of female northern anchovy *Engraulis mordax*. Fishery Bulletin, US, 79: 215–230.

Hunter, J. R., and Lo, N. C. H. 1993. Ichthyoplankton methods for estimating fish biomass. Introduction and terminology. Bulletin of Marine Science, 53: 723–727.

Hunter, J. R., and Lo, N. C. H. 1997. The daily egg production method of biomass estimation: some problems and potential improvements. *In* Improvements of the Daily Egg Production Method Techniques, pp. 41–69. Ed. by L. Motos. Ozeanografika, 2.

Hunter, J. R., and Macewicz, B. 1985. Measurement of spawning frequency in multiple spawning fishes. *In* An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*, pp. 79–93. Ed. by R. Lasker. NOAA Technical Report, NMFS 36.

Koutsikopoulos, C., and Le Cann, B. 1996. Physical processes and hydrological structures related to the Bay of Biscay anchovy. Scientia Marina, 60(Suppl. 2): 9–19.

Lasker, R. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA Technical Report, NMFS 36. 99 pp.

Lo, N. C. H. 1985. A model for temperature-dependent northern anchovy egg development and an automated procedure for the assignment of age to staged eggs. *In* An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*, pp. 43–50. Ed. by R. Lasker. NOAA Technical Report, NMFS 36.

Lo, N. C. H. 1997. Empirical analyses of the precision of regression estimates of daily egg production and egg mortality of pelagic fish for daily egg production method. *In* Improvements of the Daily Egg Production Method Techniques, pp. 71–89. Ed. by L. Motos. Ozeanografika, 2.

Lo, N. C. H., Green-Ruiz, Y. A., Cervantes, M. J., Moser, H. G., and Lynn, R. J. 1996. Egg production and spawning biomass of Pacific sardine (*Sardinops sagax*) in 1994, determined by the daily egg production method. CalCOFI Report, 37: 160–174.

Lucio, P., and Uriarte, A. 1990. Aspects of the reproductive biology of the anchovy (*Engraulis encrasicholus*, L. 1758) during 1987 and 1988 in the Bay of Biscay. ICES Document, CM 1990/H: 27.

MacCall, A. D. 1990. Dynamic Geography of Marine Fish Populations. Washington Sea Grant. University of Washington Press, Seattle.

Machias, A., Somarakis, S., Tsimenides, N., Magoulas, A., and Koutsikopoulos, C. 2000. Evaluation of the southern Greek anchovy stocks. Final Report. DG XIV, Project No. 97/048.

Magoulas, A., Tsimenides, N., and Zouros, E. 1996. Mitochondrial DNA Phylogeny and the reconstruction of the population history of a species: the case of the European anchovy (*Engraulis encrasicolus*). Molecular Biology and Evolution, 13: 178–190.

Maraveya, E., Somarakis, S., and Machias, A. 2001. Batch fecundity of anchovy, *Engraulis encrasicolus*, in the NE Aegean Sea. Rapport de la Commission International pour l'Exploration Scientifique de la Mer Méditerranée, 36: 299.

Mazzola, S., Garcia, A., and Garcia-Lafuente, J. 2000. Distribution, biology and biomass estimates of the Sicilian channel anchovy. Final Report, DG XIV, MED 96–052.

Milton, D. A., Blaber, S. J. M., and Rawlinson, N. J. F. 1994. Reproductive biology and egg production of three species of Clupeidae from Kiribati, tropical central Pacific. Fishery Bulletin, US, 92: 102–121.

Motos, L. 1994. Estimacion de la biomasa desovante de la poblacion de anchoa del Golfo de Vizcaya, *Engraulis encrasicolus*, a partir de su produccion de huevos. Bases metodologicas y aplicacion. PhD thesis, Universidad del Pais Vasco/Euskal Herriko Unibertsitatea, Leioa.

Motos, L. 1996. Reproductive biology and fecundity of the Bay of Biscay anchovy population (*Engraulis encrasicolus*, L.). Scientia Marina, 60(Suppl. 2): 195–207.

Motos, L., and Coombs, S. 2000. Vertical distribution of anchovy eggs and field observations of incubation temperature. Proceedings of the 6th International Symposium on Oceanography of the Bay of Biscay, San Sebastián, April 1998. Ozeanografika, 3: 253–272.

Motos, L., Metuzals, K., Uriarte, A., and Prouzet, P. 1995. Evaluación de la biomasa de anchoa (*Engraulis encrasicolus*) en el Golfo de Vizcaya en 1994. Campaña BIOMAN 94. Informe técnico IMA, AZTI IFREMER. 32 pp. + Annexes.

Motos, L., Palomera, I., Coombs, S., and Olivar, M-P. 1997. Adaptations of the vertical distribution of eggs and larvae of anchovy (*Engraulis encrasicolus*) in different spawning environments. Journal of Fish Biology, 51(Suppl. A): v–vi.

Motos, L., and Santiago, Y. J. 1990. An egg production estimate of the biomass of Bay of Biscay anchovy (*Engraulis encrasicolus*, L.) in 1989. ICES Document, CM 1990/H: 26.

Motos, L., and Uriarte, A. 1991. An egg production estimate of biomass of the Bay of Biscay anchovy in 1990. ICES Document, CM 1991/H: 26.

Motos, L. and Uriarte, A. 1992. Egg production biomass of the Bay of Biscay anchovy, in 1991. ICES Document, CM 1992/H: 23.

Motos, L. and Uriarte, A. 1993. Egg production assessment of the Bay of Biscay anchovy in 1992. ICES Document, CM 1993/H: 25.

Motos, L., Uriarte, A., Alvarez, P., and Prouzet, W. D. 1998. Assessment update for the Bay of Biscay anchovy (*Engraulis encrasicolus*, L.) spawning biomass in 1995, 1996, 1997 and preliminary results for the 1998 survey. Working Document Provided to the 1998 ICES Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy, Copenhagen, 27 September to 7 October, 1998.

Motos, L., Uriarte, A., and Valencia, V. 1996. The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus*, L.). Scientia Marina, 60(Suppl. 2): 117–140.

Olivar, M-P., Salat, J., and Palomera, I. 2001. Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. Marine Ecology Progress Series, 217: 111–120.

Palomera, I. 1991. Vertical distribution of eggs and larvae of *Engraulis encrasicolus* in stratified waters of the western Mediterranean. Marine Biology, 111: 37–44.

Palomera, I. 1992. Spawning of anchovy *Engraulis encrasicolus*, in the north-western Mediterranean relative to hydrographic features in the region. Marine Ecology Progress Series, 79: 215–223.

Palomera, I. 1995. Avaluacio de les poblacions de peix blau a la costa catalana el 1994. Final Report of Project DPM Generalitat de Catalunya.

Palomera, I. 2001. The application of the daily egg production method for spawning biomass in the Mediterranean Sea: overview. Document Presented to the GFCM – SAC Subcommittee on Stock Assessment Working Group on Small Pelagic Species, Kavala, Greece, March 2001. 8 pp.

Palomera, I., and Pertierra, J. P. 1993. Anchovy spawning biomass estimate by the Daily Egg Production Method in 1990 in the western Mediterranean Sea. Scientia Marina, 57: 243–251.

Palomera, I., Tejeiro, B., and Alemany, X. 2003. Size at first maturity of the NW Mediterranean anchovy. Document Presented to the GFCM – SAC Subcommittee on Stock Assessment Working Group on Small Pelagic Species, Tanger, Morocco, March 2003. 6 pp.

Parker, K. 1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fishery Bulletin, US, 78: 541–544.

Parrish, R. H., Mallicoate, D. L., and Klingbeil, R. A. 1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. Fishery Bulletin, US, 84: 503–517.

Petitgas, P., Massé, J., Grellier, P., and Beillois, P. 2003. Variation in the spatial distribution of fish length: a multi-annual geostatistics approach on anchovy in Biscay, 1985–2002. ICES Document, CM 2003/Q: 15.

Picquelle, S. J., and Hewitt, R. P. 1983. The northern anchovy spawning biomass for the 1982–1983 California fishing season. CalCOFI Report, 24: 16–28.

Picquelle, S. J., and Stauffer, G. 1985. Parameter estimation for an egg production method of anchovy biomass assessment. *In* An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*, pp. 7–16. Ed. by R. Lasker. NOAA Technical Report, NMFS 36.

Plounevez, S., and Champalbert, G. 1999. Feeding behavior and trophic environment of *Engraulis encrasicolus* (L.) in the Bay of Biscay. Estuarine, Coastal and Shelf Science, 49: 177–191.

Plounevez, S., and Champalbert, G. 2000. Diet, feeding behavior and trophic activity of the anchovy (*Engraulis encrasicolus* L.) in the Gulf of Lions (Mediterranean Sea). Oceanologica Acta, 23: 175–192.

Priede, I. G., and Watson, J. J. 1993. An evaluation of the Daily Egg Production Method for estimating biomass of Atlantic mackerel (*Scomber scombrus*). Bulletin of Marine Science, 53: 891–911.

Quintanilla, L. F., and Garcia, A. 2001a. Daily egg production method for estimating Sicilian channel anchovy spawning biomass in 1998 and 1999. Rapport de la Commission International pour l'Exploration Scientifique de la Mer Méditerranée, 36: 312.

Quintanilla, L. F., and Garcia, A. 2001b. 1999 Sicilian channel anchovy daily egg production spawning biomass. Document Presented to the GFCM – SAC Subcommittee on Stock Assessment Working Group on Small Pelagic Species, Kavala, Greece, March 2001. 14 pp.

Quintanilla, L. F., and Garcia, A. 2001c. Methodological, biological and environmental factors affecting the DEPM parameters in the Mediterranean anchovy. Rapport de la Commission International pour l'Exploration Scientifique de la Mer Méditerranée, 36: 311.

Quintanilla, L. F., and Garcia, A. 2002. The Sicilian channel anchovy daily egg production spawning biomass during July 2000. Document Presented to the GFCM – SAC Subcommittee on Stock Assessment Working Group on Small Pelagic Species, Rome, Italy, March 2002. 20 pp.

Quintanilla, L. F., Garcia, A., Giraldez, A., and Cuttita, A. 2000. Daily egg production estimate of the spawning biomass of the Sicilian channel anchovy during July 1998. Document Presented to the GFCM – SAC Subcommittee on Stock Assessment Working Group on Small Pelagic Species, Fuengirola, Spain, March 2000. 31 pp.

Regner, S. 1985. Ecology of planktonic stages of the anchovy *Engraulis encrasicolus* (L. 1758), in the central Adriatic. Acta Adriatica, 26: 1–113.

Regner, S. 1996. Effects of environmental changes on early stages and reproduction of anchovy in the Adriatic Sea. Scientia Marina, 60(Suppl. 2): 167–177.

Santiago, J., and Sanz, A. 1989. Egg production of the Bay of Biscay anchovy in 1987 and 1988, and spawning stock size estimates. ICES Document, CM 1989/H: 25.

Santiago, J., and Sanz, A. 1992. Egg production estimates of the Bay of Biscay anchovy, *Engraulis encrasicolus* (L.), spawning stock in 1987 and 1988. Bolletino del Instituto Espanol de Oceanografia, 8: 225–230.

Sanz, A., Motos, L., and Uriarte, A. 1992. Daily fecundity of the Bay of Biscay anchovy, *Engraulis encrasicolus* (L.), population in 1987. Bolletino del Instituto Espanol de Oceanografia, 8: 203–214.

Sanz, A., and Uriarte, A. 1989. Reproductive cycle and batch fecundity of the Bay of Biscay anchovy (*Engraulis encrasicholus* L.) in 1987. CalCOFI Report, 30: 127–135.

Shelton, P. A., Armstrong, M. J., and Roel, B. A. 1993. An overview of the application of the daily egg production method in the assessment and management of anchovy in the southeast Atlantic. Bulletin of Marine Science, 53: 778–794.

Sinovcic, G. 1978. On the ecology of anchovy, *Engraulis encrasicolus* (L.), in the central Adriatic. Acta Adriatica, 19(2): 3–32.

Smith, P. E., Flerx, W., and Hewitt, R. P. 1985. The CalCOFI Vertical Egg Tow (CalVET) Net. *In* An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*, pp. 27–32. Ed. by R. Lasker. NOAA Technical Report, NMFS 36.

Smith, P. E., and Hewitt, R. P. 1985a. Sea survey design and analysis for an egg production method of anchovy biomass assessment. *In* An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*, pp. 17–26. Ed. by R. Lasker. NOAA Technical Report, NMFS 36.

Smith, P. E., and Hewitt, R. P. 1985b. Anchovy egg dispersal and mortality as inferred from close-interval observations. CalCOFI Report, 26: 97–110.

Somarakis, S. 1993. Contribution to the study of the planktonic stages of anchovy in the Aegean Sea. MSc thesis, University of Crete (in Greek).

Somarakis, S. 1999. Ichthyoplankton of the NE Aegean with emphasis on anchovy, *Engraulis encrasicolus* (Linnaeus, 1758) (June 1993, 1994, 1995, 1996). PhD thesis, University of Crete (in Greek).

Somarakis, S. Marked interannual differences in reproductive parameters and daily egg production of anchovy (*Engraulis encrasicolus*) in the northern Aegean Sea. Belgian Journal of Zoology (Supplement) (in press).

Somarakis, S., Koutsikopoulos, C., Machias, A., and Tsimenides, N. 2002. Applying the Daily Egg Production Method to small stocks in highly heterogeneous seas. Fisheries Research, 55: 193–204.

Somarakis, S., Machias, A., Kapantagakis, A., and Tsimenides, N. 1997. Application of the Daily Egg Production Method (DEPM) for the estimation of the northern Aegean Sea anchovy stock in June 1995. Proceedings of the 5th Hellenic Symposium of Oceanography and Fisheries, 2: 43–46.

Somarakis, S., and Maraveya, E. 2001. Covariation in mean abundance of larval myctophids and zooplankton biovolumes in the NE Aegean Sea. Rapport de la Commission International Pour l'Exploration Scientifique de la Mer Méditerranée, 36: 325.

Somarakis, S., Maraveya, E., and Tsimenides, N. 2000. Multispecies ichthyoplankton associations in epipelagic species: is there any intrinsic adaptive function? Belgian Journal of Zoology, 130(Suppl.): 125–129.

Somarakis, S., and Tsimenides, N. 1997. A Daily Egg Production Method biomass estimate of the northern Aegean Sea anchovy stock. *In* Improvements of the Daily Egg Production Method techniques, pp. 133–148. Ed. by L. Motos. Ozeanografika, 2.

Stauffer, G. D., and Picquelle, S. J. 1980. Estimates of the 1980 spawning biomass of northern anchovy. NMFS, SFC, La Jolla, California, Administrative Report LJ-80–09. 41 pp.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, New York.

Stergiou, K. I., Christou, E. D., Georgopoulos, D., Zenetos, A., and Souvermezoglou, C. 1997. The Hellenic seas: physics, chemistry, biology and fisheries. Oceanography and Marine Biology: An Annual Review, 35: 415–538.

Tsimenides, N., Papaconstantinou, K., Kapantagakis, A., Machias, A., Somarakis, S., Petrakis, G., and Caragitsou, E. 1998. Development of the Greek fisheries. Final Report. EPET II/125 (in Greek).

Tsimenides, N., Somarakis, S., Magoulas, A., and Tserpes, G. 1995. Evaluation of the anchovy stocks in the Aegean Sea. Final Report. Project No. XIV1/MED/91/011.

Tudela, S., and Palomera, I. 1997. Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea (northwest Mediterranean). Marine Ecology Progress Series, 160: 121–134.

Tzanatos, E., Somarakis, S., Machias, A., Vavoulis, A., Ramfos, A., and Koutsikopoulos, C. 2001. Comparative study of the accuracy and cost of the planktonic nets bongo and WP2 in fish stock assessment. Proceedings of the 10th PanHellenic Symposium of Ichthyologists: 49–52.

Uriarte, A., and Motos, L. 1998. Sampling errors in anchovy egg abundance estimates using the Pairovet net. Journal of Plankton Research, 20: 1861–1888.

Uriarte, A., Motos, L., Alvarez, P., Santos, M., Prouzet, P., and Masse, J. 1999. Population estimates of the Bay of Biscay anchovy by the Daily Egg Production Method. Final Report to EU, Project 96/034.

Uriarte, A., Prouzet, P., and Villamor, B. 1996. Bay of Biscay and Ibero Atlantic anchovy populations and their fisheries. Scientia Marina, 60(Suppl. 2): 237–255.

Valdés, E. S., Shelton, P. A., Armstrong, M. J., and Field, J. G. 1987. Cannibalism in South African anchovy: egg mortality and egg consumption rates. South African Journal of Marine Science, 5: 613–622.

Valencia, V., Motos, L., and Urrutia, J. 1988. Estudio de la variación temporal de la hidrografía y el plancton en la zona nerítica frente a San Sebastián. Resultados abril 1986–diciembre 1987. Informes Técnicos, Departamento Agricultura y Pesca, Gobierno Vasco, 20: 80.

Wang, S. B., and Houde, E. D. 1994. Energy storage and dynamics in bay anchovy *Anchoa mitchilli*. Marine Biology, 121: 219–227.

Whitehead, P. J. P., Nelson, G. J., and Wongratana, T. 1988. FAO species catalogue. 7. Clupeoid fishes of the world (suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 2. Engraulidae. FAO Fisheries Synopsis 7. 125. 579 pp.