Modeling the impact of climate variability on Black Sea anchovy recruitment and production

CEREN GÜRASLAN^{*}, BETTINA A. FACH AND TEMEL OGUZ

Institute of Marine Sciences, Middle East Technical University, Erdemli, 33731, Mersin, Turkey

ABSTRACT

The connection of climate variability with anchovy spawning and recruitment in the Black Sea in particular, and other ecosystems in general, was studied using a two-way coupled lower trophic level and anchovy bioenergetics model. Climate variability was represented by a 50-yr time series of daily temperature and vertical mixing rates with stochastic variations. Temperature was found to be the dominant factor influencing early life stages and hence population dynamics of Black Sea anchovy as marked by a high correlation of anchovy egg production and recruitment success in response to changes in temperature. Each decrease of 2°C in summer mean temperatures resulted in a delay in the timing of egg production of between 12 and 19 days. Water temperatures in the spawning season had a greater influence than the number of available spawning females on the intensity of egg production. Anchovy recruitment was similarly influenced by temperature, with decreased temperatures resulting in a significant delay in the onset of peak recruitment during the fall by 21-38 days. Also, recruitment numbers in December decreased by about 20% with decreasing temperatures. The impact of temperature on production was slightly diminished by the impact of vertical mixing. The strong linkage of climate variability with anchovy spawning and recruitment has an important prediction potential for short-term anchovy stock estimations, which may serve fisheries management purposes.

Key words: anchovy bioenergetics model, anchovy recruitment, climate impact, stochastic temperature variability

*Correspondence. e-mail: ceren@ims.metu.edu.tr Received 9 June 2013

Revised version accepted 4 June 2014

436

INTRODUCTION

Many of the largest fisheries today in the world's oceans are based on small pelagic fish species such as anchovy and sardine. Anchovies are small saltwater forage fish belonging to the Engraulidae and Anchoa families. Of those, Anchoveta or the Peruvian anchovy (*Engraulis ringens*), the European pilchard (*Sardina pilchardus*), the Japanese anchovy (*Engraulis japonicus*), and the European anchovy (*Engraulis encrasicolus*) are distinctive in the world's catch and are harvested for human consumption. The European anchovy supports intense fisheries in the Mediterranean Sea (Plounevez and Champalbert, 2000) and Black Sea (Chashchin, 1996; Daskalov, 2003), where it constitutes the main fisheries resource.

Environmental factors are known to influence population dynamics of small pelagic fish species via regulation of egg survival and hence recruitment success (Lasker, 1975; Crawford et al., 1987; Cury and Roy, 1989; Bakun, 1996; Schwartzlose et al., 1999; Takahashi and Watanabe, 2004a,b; Palomera et al., 2007; Houde, 2008). Such factors may include input of nutrients into the surface water through mixing, offshore egg and larval transport, and water column stability (Peterman and Bradford, 1987; Bakun and Parrish, 1991; Borja et al., 1996; Tsai et al., 1997; Cole and McGlade, 1998; Painting et al., 1998; Guisande et al., 2001, 2004; Lloret et al., 2004). Changes in vertical mixing rates of the water column have been shown to explain 70% of the variance in the recruitment index of the Bay of Biscay anchovy (Borja et al., 1996). However, ambient temperature is known to be a critical factor affecting marine fauna, particularly the reproduction biology of clupeid species (Blaxter and Hunter, 1982; Tsuruta and Hirose, 1989; Imai et al., 1998; Funamoto et al., 2004). Anchovy is a thermophilic species known for its higher vulnerability to temperature fluctuations as compared with other species sharing the same trophic level such as sardine (Lluch-Belda et al., 1991). Cushing (1996), on the other hand, suggests that the variation in recruitment numbers is linked to spawner availability and is therefore regulated by exploitation of the existing stock. However, as in the case of the Black Sea anchovy, the intense fishing activity during the 1980s did not lead to a collapse of the anchovy fishery until the alien ctenophore (*Mnemiopsis leidyi*) invaded the whole system in 1989 (Oguz, 2005).

Anchovy has undergone significant fluctuations in standing stock size over the past five decades due to regional climate variability, intensive fishing activity, increased anthropogenic nutrient input from rivers, and, as in the case of the Black Sea, introduction of the alien ctenophore species Mnemiopsis leidyi (Oguz, 2005). Observations imply that not only humanrelated activities but also environmental variations may play a critical role in controlling anchovy production. There is evidence of a strong relationship between regional climatic variations such as those influenced by the North Atlantic Oscillation (NAO) and anchovy stock fluctuations in the Black Sea (Niermann et al., 1999; Oguz, 2005; Oguz et al., 2006; Oguz and Gilbert, 2007) and other areas such as in the Mediterranean, where anchovy oscillations have been related to climatic variations (Grbec et al., 2002; Katara et al., 2011), and recently the Western Mediterranean Oscillation index (Martin et al., 2012).

European anchovy abundance in the North Sea has fluctuated greatly in the past (Aurich, 1953) and periods of high abundance seem to coincide with warm phases of the Atlantic Multidecadal Oscillation (AMO) indicating the high impact of climate variability on anchovy dynamics (Petitgas et al., 2012). In the Pacific, the Japanese anchovy (E. japonicus) also has shown multi-decadal fluctuations, as opposed to sardine population dynamics, which are related to interdecadal North Pacific ocean/climate variability (Yasuda et al., 1999; Yatsu et al., 2005). Such regime shifts have been observed not only in the North Pacific (Takasuka et al., 2008) but also in the California Current and Humboldt Current systems and a relationship with climatic regime shifts has been suggested (Lluch-Belda et al., 1989; Kawasaki, 1991; Chavez et al., 2003).

It has been shown that decadal scale climate variability of either natural or human origin can trigger regime transitions that may not only harm a resource but also have eventual economic effects (Steele, 1998). Additionally, within a period of favorable environmental conditions, the fishing stress, although very heavy, may sustain a high catch; whereas under adverse environmental conditions, the same level of fishery may lead to a stock collapse (Hofmann and Powell, 1998; Oguz, 2005).

Bioenergetics models of anchovy have been applied to different regions such as Chesapeake Bay (Wang *et al.*, 1997; Rose *et al.*, 1999), the northern Aegean

© 2014 John Wiley & Sons Ltd, Fish. Oceanogr., 23:5, 436-457.

Sea (Politikos *et al.*, 2011), the Gulf of Lions (Pethybridge *et al.*, 2013), the Bay of Biscay (Pecquerie *et al.*, 2009), the coast off Peru (Xu *et al.*, 2013) and the Black Sea (Oguz *et al.*, 2008a). The use of such models gives an insight into the life cycle dynamics and shows that human impact coupled with environmental variability may initiate strong perturbations in marine ecosystems including the collapse of commercially valuable fish stocks such as anchovy in the Black Sea (Oguz *et al.*, 2008a,b).

To understand the extent of the impact of climateinduced drivers on anchovy fecundity the present study analyzes the way an anchovy population responds to environmental variability in the form of changing water temperature and water column mixing. We investigate whether high frequency fluctuations in temperature decrease fecundity rates, as well as the recruitment rates of anchovy and if so, to what extent. Of particular interest is to determine the times of the year when anchovy are particularly vulnerable to temperature changes (such as the spawning season) and how strongly this influences the entire population. In addition, we investigate how effective increased mixing rates that may occur simultaneously with lower temperatures, are in enhancing nutrient flux to increase anchovy survival and possibly counteract temperature effects. These questions are elaborated using a onedimensional coupled model of the lower trophic level that is two-way coupled with an anchovy population dynamics model. Here, two-way coupling means that the lower trophic level influences anchovy population dynamics and vice versa. Although this theoretical study on how a recruitment system reacts to stochastic climate variability is designed for the Black Sea, its results may also be applicable to other systems.

Below, we first describe the model setup, followed by a presentation of model findings. We describe the seasonal variations of anchovy survival and recruitment in response to three different scenarios over 1 yr. We then examine interannual variability and the relationship between anchovy reproduction, recruitment and spawner numbers under varying environmental conditions. The model results are discussed and summarized in the Discussion and Conclusions sections.

MATERIALS AND METHODS

Model description

The anchovy bioenergetics and lower trophic level models are two-way coupled (details may also be found in Oguz *et al.*, 2008a). This modeling system has previously been tested and validated for the Black Sea (Oguz *et al.*, 2008a,b). The one-dimensional (1-D)

ecosystem model of the lower trophic level represents the euphotic zone, assumed to be 50 m deep, with two layers: a surface mixed layer with daily variations and a subthermocline layer. A third layer below the euphotic zone provides nutrients to the euphotic zone via mixing. For further details we refer to Oguz *et al.* (2008a).

The anchovy bioenergetics (life-cycle dynamics) model (also described in Oguz et al., 2008a) tracks each individual spawner's progeny through developmental stages (such as hatching, yolk-sac larvae, early larvae, late larvae, juvenile, young of the year (YoY) and adult stages (age 0+, 1+, 2+ and 3+). Each model year begins in June and one model year takes 360 days to complete. Female adult anchovy start spawning on 1 June and the spawning season lasts until the end of August (90 days). Anchovy spawning in the model, i.e., egg production, is dependent on water temperature in the mixed layer, population density and weight of adult females, which connects egg production with food availability to adult anchovy and recruitment. With the application of such density dependency it is possible to assess the impacts of year-to-year climate variability. Spawning takes place in the mixed layer when the water temperature exceeds 20°C (Niermann et al., 1994; Kideys et al., 1999; Satilmis et al., 2003). All eggs spawned on the same day are assumed to belong to the same cohort. Recruitment in the model is defined as the surviving larval and juvenile stages which grow to 6.0 cm in length, also defined as the length at first maturity. Mortality of anchovy due to fishing, or natural mortality (including predation, grazing by gelatinous carnivores on anchovy eggs and larvae), and basal losses, i.e., senility, parasitic losses and food starvation, are included. The fishing season in the model lasts from the 1 October to 15 March (165 days) every year, corresponding to more than 80% of the total annual yield (Prodanov et al., 1997).

The model was run with the same parameter setting as in Oguz *et al.* (2008a) for moderate eutrophication levels and moderate gelatinous predation on anchovy,

 Table 1. Input parameter set for the moderate eutrophication set-up of the model.

Input parameters	Value
Source layer nitrate concentration Predation mortality	3.0 mmol m^{-3} $2.0 \times 10^{-4} \text{ m}^{3} \text{ day}^{-1}$ $0.5 \times 10^{-3} \text{ day}^{-1}$
Fishing pressure	0.3 yr^{-1}

fyr⁻¹: fishing year, is defined as daily fishing rate applied over 165 days of fishing activity during 1 year.

the details of which can be found in Table 1. With this model setup, model anchovy experience positive weight growth from the beginning of summer to winter (from June to January) as a result of availability of fodder zooplankton, which is triggered by increased primary production (see Oguz *et al.*, 2008a; Fig. 6). During winter, scarcity in food limits the weight growth. As a result, weight growth slows down and finally leads to weight loss during the period from January to the end of May. In addition, as individuals grow older, they divert increasingly more energy to building up body tissues for reproduction.

Model forcing

Forcing files for the baseline simulation of the model include time series of daily values of mixed layer depth, total mixing rate, temperature and photosynthetically available radiation (PAR) spanning 1 yr (Fig. 1). These files were derived from observations representing the mean climatology of the Black Sea (Altman et al., 1987; Efimov and Timofeev, 1990; Oguz et al., 1992, 1996, 1999). In particular, the mixed layer depth in the euphotic zone shallows to 15 m in summer and the water remains stratified until October (Fig. 1a). During winter, vertical mixing destabilizes the water column and the mixed layer deepens to a maximum depth of 45 m until mid-March. The total vertical mixing rate is close to 0.01 day⁻¹ during summer, increasing to 0.04 day^{-1} in January through March (Fig. 1b). Total mixing here is defined as the sum of daily diffusion rate and daily vertical entrainment rate between the two layers of the euphotic zone. The mixed layer temperature increases to 24°C in September and cools down to 7°C in March, thereby describing a sinusoidal pattern (Fig. 1c) that was fitted with a regression equation following Rose et al. (1999) as follows:

$$T = \alpha_0 - \alpha_1 \cos(0.01745 \, \text{day}) - \alpha_2 \sin(0.01745 \, \text{day})$$
(1)

where day is day of the year and α_0 , α_1 , α_2 are constant parameters with the values of 15.5, 0.1, and 8.5, respectively. The subthermocline temperature remains constant (7°C) throughout the year. PAR starts at 210 m² W⁻¹ on 1 June and reaches its maximum of 300 m² W⁻¹ on 15 August (Fig. 1d). The following 4 months, the PAR values decline down to 20 m² W⁻¹ on 15 December and then remain at this value during winter. This set of input files was used to assess the impact of seasonal variation of temperature on anchovy production.

Following this, interannually varying temperature and vertical mixing rates time series for long-term

Figure 1. Model forcing for the baseline simulation derived from mean climatologic conditions for the Black Sea. Annual cycle for daily (a) mixed layer depths (m) (Oguz *et al.*, 1996), (b) total mixing rates (day⁻¹) (Oguz *et al.*, 1999), (c) mixed layer temperatures (°C) (Altman *et al.*, 1987), and (d) photosynthetically available radiation (PAR; W m⁻²) (Efimov and Timofeev, 1990).

model runs of 65 yr (15-yr spin up followed by a 50-yr simulation) were created by first repeating the above temperature cycle (Fig. 1c) for 15 yr to account for model spin-up. By creating white noise for 50 simulation years and adding it to the values of the three coefficients $(\alpha_0, \alpha_1, \alpha_2)$ of Eqn (1), a 50-vr stochastic time series of temperature was generated to mimic climatic variations (Fig. 2a). This randomly generated noise is an anomaly that translates to different temperature and mixing rates during each respective year but when summed up over the total of 50 yr gives no deviation from the mean climatological conditions (Fig. 2c). The white noise was created using the Box-Muller method in the form of normally distributed, pseudorandom numbers with a mean of 0 and a standard deviation of 1. In this way winter temperature variations of $\pm 1^{\circ}$ C were created (Fig. 2c) that are well within observations of natural variability in winter sea surface temperatures in the Black Sea due to climatic teleconnections, such as the North Atlantic Oscillation of around approximately 1.8°C (Oguz, 2005b). A similar procedure was also applied to the mixing rate cycle (Fig. 2b); however, the noise had a reversed sign so that higher temperatures corresponded to lower total mixing rates and vice versa, such as during years 12–16 and 25–36 (Fig. 2b,c).

The response of the Black Sea anchovy population (spawners, recruitment and eggs) to seasonal and interannual changes in temperature and mixing was then studied with three different simulations that commenced after a 15-yr model spinup:

- 1 Temperature-only simulation: the model is forced with the 50-yr time series of changing temperature
- © 2014 John Wiley & Sons Ltd, Fish. Oceanogr., 23:5, 436-457.



input (Fig. 2a), while the reference cycle is used repeatedly for the total mixing rate time series.

- 2 Mixing-only simulation: the model is forced with the changing 50-yr mixing rate time series (Fig. 2b), while the reference cycle is used repeatedly for the temperature time series.
- **3** Temperature and mixing simulation: the model is forced with both 50-yr time series of changing temperature and mixing rate (Fig. 2a,b).

RESULTS

Seasonal variation

Temperature simulations. Throughout the spawning season, there may be a daily temperature difference of $\pm 2^{\circ}$ C between the years with minimum and maximum temperature distribution with respect to the baseline year (Fig. 3a,b). Simulations show that the differences between these three temperature cycles influence the start dates of spawning, spawning intensity, and recruitment success of the anchovy (Fig. 3e,f, dashed and dotted lines). The baseline yearly temperature variation (Fig. 3a,b; solid lines) and total mixing rates (Fig. 3c,d; solid lines) illustrates the start of egg production on 1 July at around 6600 eggs m^{-3} (Fig. 3e, solid line). Egg numbers increase gradually during this time to 10 260 eggs m^{-3} on 30 August. By mid-August, the mean length of all cohorts reaches 6.0 cm, indicating the beginning of recruitment (Fig. 3f, solid line). Recruitment peaks at 11 063 ind. m^{-3} on December 17th (Fig. 3f, solid line). After this time the anchovy population starts to decrease, as the anchovy



Figure 2. Stochastic 50-yr time series of (a) temperature (°C) and (b) total mixing rate (day^{-1}) serving as model forcing for long-term simulations, (c) winter temperature anomaly (°C) and (d) total mixing rate anomaly (day^{-1}) .

are subjected to winter conditions and food shortage. In May, when the conditions improve, the stock abundance rises again.

There is a considerable change in the onset of spawning, as the start of egg production is delayed by 12 days in the reference simulation compared with the maximum temperature year (Fig. 3e, dashed line), and by another 19 days in the minimum temperature year (Fig. 3e, dotted line). In addition, there is a 13 and 14.5% difference in the number of eggs that survive and recruit to the population at the end of the spawning season between the years of maximum, baseline, and minimum temperature years with 11.8×10^3 , 10.26×10^3 and 8.77×10^3 ind. m⁻³, respectively (Fig. 3e).

A similar effect of temperature is seen in the recruitment numbers. It takes until August for recruitment to start in all simulations. However, in early September recruit numbers in the maximum temperature year start increasing rapidly to 12.55 ind. m^{-3} on 9 December (Fig. 3f, dashed line). The onset of rapid increase in recruits is delayed by 21 days for the reference simulation (Fig. 3f, solid line) and by another 38 days for the minimum temperature year (Fig. 3f, dotted line). Consequently, the maximum number of recruits is lower in

Figure 3. Model input: seasonal variations of temperature (°C) during (a) the spawning season (June-September), (b) the course of a year for minimum (dotted line), maximum (dashed line) and baseline (solid line) years. Seasonal variation of total mixing rate (day^{-1}) during (c) the spawning season, and (d) the course of a year for minimum (dashed line), maximum (dotted line) and baseline (solid line) years. Model output: variations of (e) eggs (no. $m^{-3} yr^{-1}$) during the spawning season and (f) recruits (ind. $m^{-3} yr^{-1}$) over the course of 1 yr, for minimum, maximum and baseline years of temperature only simulation. Variation of (g) eggs (no. $m^{-3} yr^{-1}$) during the spawning season and (h) recruits (ind. $m^{-3} yr^{-1}$) over the course of 1 yr, for minimum, maximum and baseline years of the temperature and mixing simulation.

mid-December at 11.1 and 8.3 ind. m^{-3} for the reference and minimum temperature simulations, respectively. This recruitment is due to the availability of mesozooplankton in autumn that reaches a maximum in December. Subsequently, due to food limitation in winter, the population decreases down to 4.61, 3.84 and 2.68 ind. m^{-3} at the end of the simulation (May) in the maximum, reference, and minimum temperature simulations, respectively (Fig. 3f).

Mixing simulations. Because the total mixing rate is high in winter only, changes in total mixing exert no influence on egg production (not shown here), which takes place from June to September. However, mixing plays a role in nutrient cycling which slightly increases food availability for anchovy during winter (November–March) and therefore promotes recruitment before December with peak biomass values in recruitment of around 10.5, 11.1 and 11.5 ind. m^{-3} in the minimum, baseline, and maximum total mixing year, respectively.

Temperature and mixing simulations. When both temperature and total mixing vary between years, egg

© 2014 John Wiley & Sons Ltd, Fish. Oceanogr., 23:5, 436-457.



production during the spawning season is the same as for the temperature-only simulation (Fig. 3g, solid line) as mixing does not change in summer. However, the recruitment variability is responding to both (temperature and total mixing) effects, as they are operating simultaneously when the 0+ age group grows during winter. The combination of the two effects results in a population size of recruits for the year of maximum temperature accompanied with a minimum total mixing of 12.13 ind. m^{-3} (Fig. 3h, dashed line) which is slightly lower than the population size in the temperature-only simulation for the year of maximum temperature (Fig. 3f, dashed line). This is a consequence of the additional effect introduced by low mixing, which supplies fewer nutrients into the mixed layer and therefore results in less food for larvae to feed on. In the year of minimum temperature accompanied with maximum total mixing, the peak recruitment number in December is 8.85 ind. m^{-3} (Fig. 3h, dotted line), which is slightly higher than for the minimum temperature simulation. Apparently, the maximum total mixing effects contribute to effects caused by the lowest temperature increasing nutrient availability and hence food for anchovy larvae, and therefore increasing recruitment above the value of the minimum temperature year simulation (Fig. 3f, dotted line).

Interannual variation

The above simulations clearly indicate the importance of both temperature and total vertical mixing for anchovy dynamics. To understand the effect of interannual variations of both on anchovy and the dynamics behind it, we first describe the effect of interannual variability of the temperature and mixing simulation on the lower trophic level compartments, before detailing the response of anchovy below. The lower trophic level model consists of five compartments: nitrate, phytoplankton, microzooplankton, mesozooplankton, and gelatinous predators.

Lower trophic level. Simulations with temperature alone show that colder winter temperatures regulate nutrient supply indirectly since they increase the depth of the mixed layer; as a result the deeper mixed layer facilitates a higher addition of nutrients into the mixed layer, increasing available nitrate there. When both environmental factors are considered simultaneously (Fig. 4a,b), the indirect effect of temperature and the comparatively small direct effect of changes in total mixing combine, leading to a decrease in nitrate from approximately 526 to 506 mmol N m⁻³ between vears 12 and 16 (Fig. 4c). Between years 25 and 36, a period of abrupt temperature decrease and total mixing increase cause nitrate concentrations to rise from 510 mmol N m⁻³ to approximately 530 mmol N m⁻³. Model phytoplankton directly reacts to changes in nitrate concentration such that in between years 12 and 16, when temperature is increasing and corresponding mixing rates are decreasing, phytoplankton decreases from 1252 to 1234 gC m^{-2} (Fig. 4d) and varies from 1234 to 1256 gC m⁻² between years 25 and 36. Microzooplankton (Fig. 4e) reacts to the combined influence of temperature and total mixing with a 1-yr delay. Hence, its biomass decreases between years 13 and 17, from 78.5 to 70.5 gC m⁻², and later increases between years 26 and 37 from 72.5 to 77.5 gC m⁻². In mesozooplankton (Fig. 4f), the bottom-up effect of temperature and mixing is not clearly evident because predation on mesozooplankton by gelatinous carnivores and anchovy is an important factor determining biomass (Fig. 4f,g). Thus, mesozooplankton abundance increases when there is reduced predation pressure by gelatinous carnivores and decreases as grazing pressure increases. Mesozooplankton biomass decreases from 277 to 255 gC m⁻² between years 12 and 16 and increases from 257.5 to 287.5 gC m⁻² during years 25–36 (Fig. 4f).

The gelatinous predator shows strong temperature dependence because it is not limited by predation in the model and the total mixing forcing acts here to counteract the temperature effect. Thus, during years 12–16, when temperature increases and total mixing decreases, gelatinous carnivore biomass values increase from 167.5 to 185 gC m⁻² and decrease from 181 to 158 gC m⁻² in years 25–36 (Fig. 4g).

Higher trophic level. Temperature simulation: Anchovy egg production (Fig. 5b) is directly related to interannual temperature variation as it follows the same variability pattern as the lowest winter temperature (Fig. 5a). This is due to the fact that low winter temperatures also mean low summer temperatures in this temperature time series (see Fig. 2a,c). For example, during the period in which the lowest temperature increases from 6.36 (year 12) to 7.66°C (year 16) the summer temperatures during the spawning season increase from 21.8 to 26.4°C and the egg population almost doubles from 361 to 686 ind. m^{-3} (Fig. 5b). Thus, a 4.4°C increase in summer temperature over half a decade led to the egg numbers increasing by approximately 90%. In the period of a decrease in summer temperature from 25.6 to 21.1°C (between years 25 and 36), egg numbers decrease by 56%, from 640 to below 282 ind. m^{-3} .

Anchovy recruitment numbers are also highly correlated with temperature (Fig. 5c). For the abovementioned period of temperature increase, recruitment numbers increase from 1.13 (year 12) to 2.12 (year 16) ind. m^{-3} , which amounts to an 87% recruitment increase corresponding to a winter temperature increase of 1.3°C. On the other hand, a 1.31°C decrease in winter temperature (between years 25 and 36) causes the recruitment numbers to decline from 1.99 to 1.0 ind. m^{-3} , a decrease of 49%.

Spawner numbers, which here represent female adults that constitute 50% of the total population, also vary directly in proportion to the temperature variations (Fig. 5d). During the temperature increase period, spawners rise from 1.7 ind. m^{-3} (year 12) to 2.15 ind. m^{-3} (year 16). Thus an increase in winter temperature of 1.3°C, results in an increase of 24% in the number of spawners. During the period of temperature decrease, the number of spawners decreases by approximately 24%, from 2.11 ind. m^{-3} (year 25) to 1.60 ind. m^{-3} (year 36).

Mixing simulation: Changes in total mixing influences anchovy egg production only very slightly (not

Figure 4. Temperature and mixing simulation. Model input in the form of (a) lowest winter temperature (°C) and (b) total mixing rate (day^{-1}) at the end of February. Model output: interannual variability of euphotic layer (c) total annual nitrate concentration (mmol N m⁻³), euphotic zone integrated total annual (d) phytoplankton (gC m⁻²), (e) microzooplankton (gC m⁻²), (f) mesozooplankton (gC m⁻²) and (g) gelatinous carnivore biomass (gC m⁻²) variations. Straight line represents the result of the baseline simulation.



© 2014 John Wiley & Sons Ltd, Fish. Oceanogr., 23:5, 436-457.



Figure 5. Temperature simulation. Model input: interannual variation of (a) lowest winter temperatures (°C) at the end of February. Model output: interannual variability of total annual anchovy (b) eggs, (c) recruits and (d) spawner population (ind. m^{-3} yr⁻¹). Straight line represents the result of the baseline simulation.

shown here) when the intensity of mixing is either very high or considerably low. Recruits and spawner numbers are directly influenced by total mixing variations, owing to the fact that they are feeding during December, which corresponds to the onset of intense winter mixing, and increased mixing in the model translates to greater food availability to the anchovy. Both are positively correlated with the total mixing rate variations, which means when total mixing is intensified, spawners, and so recruitment numbers, increase in the same year without any delay in timing. However, the influence of mixing alone is small compared with the temperature simulation: recruitment numbers decrease by 7% and spawners by 5% when total mixing rates decrease by approximately 17% between years 12 and 16. In the period of abrupt changes in total mixing (years 25–36), the recruitment biomass increases by 7%, from 1.625 to 1.750 ind. m⁻³, and spawners increase by 5% due to the 20% increase in the total mixing rate during this time. This effect is small compared with the influence of temperature variations.

The influence of total mixing on egg production in the model is minimal and indirect. It takes 1 yr for egg numbers to respond to changes in total mixing because mixing is effective in winter and influences nutrient

Temperature and mixing simulation: When both the temperature and total mixing time series (Fig. 6a,b) are input in the model, it is again seen that temperature effects dominate the egg production levels (Fig. 6c), although the results deviate slightly from the egg numbers given in the temperature simulation (Fig. 5b). The reason for these slight differences is the indirect effect of total mixing rates effective from the previous year. For example, in the period of temperature increase (accompanied by total mixing decrease) from years 12–16, egg numbers increase by 92%, from 358.3 to 687.1 eggs m⁻³ (Fig. 6c). Within the period of temperature decrease (or total mixing increase) from years 25–36, the egg numbers decrease by 56%, from 644.39 to 284.79 eggs m⁻³.

The main factor influencing recruitment to the population is also temperature. The inclusion of total mixing counteracts the effects of temperature slightly, reducing the biomass in years of warm winters, but increasing the biomass in years of cold winters due to a deepening of the mixed layer, which causes increased nutrient upwelling and hence food supply to recruits. This means that, for the recruitment population, variation (Fig. 6d) is less than in the temperature simulation (Fig. 5c). Therefore, between years 12 and 16, the recruitment increases by 70%, from 1.21 to 2.05 ind. m⁻³, whereas during years 25-36, the recruitment decreases by 44%, from 1.74 to 1.09 ind. m^{-3} (Fig. 6d).

The interannual variation of spawners responds directly to the effects of both temperature and total mixing in the same year. Spawners are mainly affected by temperature. The total mixing effect slightly counteracts the temperature effect, but not as much as in the case of recruits. In addition, spawners also include adults of other year-classes that carry the temperature signal of previous years. The resulting time series shows slightly smaller variations of spawners in this simulation (Fig. 6e) compared with the temperatureonly simulation (Fig. 5d). In the period of temperature increase (or total mixing decrease) between years 12 and 16, a 20% increase in the number of spawners from 1.77 to 2.12 ind. m^{-3} is seen. Within the period of abrupt temperature decrease (or total mixing increase), from years 25 to 36, the spawner numbers also decrease abruptly by 21%, from 2.08 to 1.64 ind. m^{-3} .

Anchovy reproduction and recruitment

The above simulations show that temperature exerts a greater influence than total mixing on the interannual variations in the abundance of eggs, recruits and spawners. To better understand the egg production and recruitment success in relation to climate variability, a correlation analysis was carried out.

It can be seen that there is a linear relationship between the egg production numbers and the total number of recruits of the same year in the temperature simulation, and a correlation $(r^2 = 0.88)$ is found (Fig. 7a). In the temperature and total mixing simulation this determination coefficient (r^2) is higher, 0.93 (Fig. 7d). This indicates that anchovy recruits benefit from increased mixing and hence higher food availability in cold winters, as already shown in the above sections on seasonal and interannual variations (Figs 3h and 6d), while reduced mixing in warmer winters decreases their numbers. Hence, the decrease in recruitment numbers due to the opposing effects of temperature and mixing causes an increased correlation in the number of eggs versus recruitment in the temperature and mixing simulation (Fig. 7d).

The relationship between the total number of spawners and the total number of eggs under different environmental scenarios reveals that the correlation $(r^2 = 0.99)$ is significant (99%) in the temperature simulation (Fig. 7b) but decreases to 94% in the temperature and total mixing simulation (Fig. 7e). This demonstrates that temperature is the dominant influence on spawners, and that decreased recruitment variation in the temperature and mixing simulation does not affect spawners.

The correlation coefficient between spawners and recruits is 84% when temperature influence alone is considered (Fig. 7c), and 78% for the temperature and mixing simulation (Fig. 7f).

To explore whether the influence of changes in mixing, which take place during winter, on anchovy recruitment numbers is indeed related to food availability to anchovy and not some other mechanism, mesozooplankton biomass was correlated with both environmental influences. Temperature alone is negatively correlated to mesozooplankton in the temperature-only simulation ($r^2 = 0.79$, Fig. 8a) because of a smaller nutrient supply to the mixed layer in warmer years, as well as increased abundances of anchovy and gelatinous carnivores in warmer years (Fig. 4f,g) that graze on them. The mixing rate is positively correlated in the mixing-only simulation ($r^2 = 0.91$, not shown); however, the mesozooplankton biomass changes only a little in the mixing-only simulation. In the temperature

Figure 6. Temperature and mixing simulation. Model input: interannual variation of (a) lowest winter temperatures (°C) and (b) total mixing rates (day^{-1}) at the end of February. Model output: interannual variability of total annual anchovy (c) eggs, (d) recruits and (e) spawners population (ind. m^{-3} yr⁻¹). Straight line marks result of the baseline simulation.



© 2014 John Wiley & Sons Ltd, Fish. Oceanogr., 23:5, 436-457.



Figure 7. Correlation analysis of total annual (a) eggs versus recruitment, (b) eggs versus spawners and (c) recruitment versus spawners for the 50-yr temperature simulation. Correlation analysis of total annual (d) eggs versus recruitment, (e) eggs versus spawners and (f) recruitment versus spawners for the 50-yr temperature and mixing simulation (ind. $m^{-3} yr^{-1}$).

and mixing simulation, both environmental effects combine, and cold temperatures in winter cause the mixed layer depth in the model to increase, intensifying the nutrient supply from the source layer in addition to increased mixing, resulting in a high positive correlation of total mixing rate maxima with mesozooplankton biomass ($r^2 = 0.84$, Fig. 8b) and increased zooplankton biomass with increased mixing rates.

Furthermore, anchovy recruits are negatively correlated to mesozooplankton ($r^2 = 0.73$, Fig. 8c) as anchovy is feeding on mesozooplankton in the model. A higher negative correlation, which explains 95% of the variation, is found between mesozooplankton and gelatinous predator production (Fig. 8d), which can be explained by the predator–prey relationship of both compartments (see Fig. 4f,g). It should be noted that the mesozooplankton bloom in the model occurs in summer, with a second smaller bloom in winter, as observed in the Black Sea (Oguz *et al.*, 2001). During the summer spawning season, adult anchovy compete with gelatinous carnivores for this food source, whereas during winter, anchovy recruits compete with gelatinous carnivores at a time when food is essential for their development. The above analysis clearly shows that gelatinous predators may influence anchovy population dynamics through competition for food.

Next, a regression analysis between the spawners of 1 yr (n) and egg numbers produced by these spawners in the following year (n + 1) was calculated for both the temperature simulation (Fig. 9a) and the temperature and mixing simulation (Fig. 9b). This was done to investigate further whether there is a relationship between this year's spawners (12 months starting 1 June) and next year's egg production. Neither analysis shows any correlation, indicating that no such relationship exists.

In an effort to analyze the control spawner numbers have over the seasonal egg production of anchovy,



50-yr model output of available spawners during different time periods of the model year were correlated with the total number of eggs produced during the spawning season (Fig. 10). However, relationships between the number of spawners of the current (*n*) model year at the beginning of the spawning season (1 June) (Fig. 10a), during the entire spawning season (June– September) (Fig. 10b) and during winter of the previous (n-1) model year (December–March) (Fig. 10c) with current (*n*) year's egg production showed no correlation for any of the selected time intervals.

When the 50-yr mean summer (*n*th yr) and mean winter (n-1th yr) temperatures were regressed against the total number of eggs produced in each (*n*th) year during the spawning season, results indicated a high correlation explaining 98% of the variance for the summer temperatures, which are incidentally the temperatures anchovy encounter during the spawning season (Fig. 11a) and no correlation with winter temperatures (Fig. 11b).

Comparing temperature variability (Fig. 12, \bullet) with variability within the different age classes of anchovy in the temperature-only simulation showed that the variability in the anchovy recruitment (age

Figure 8. Regression analysis of (a) temperature maxima (°C) versus total annual mesozooplankton production in the temperature only simulation (gC m⁻³ yr⁻¹). (b) Total mixing rate maxima (day^{-1}) , total annual recruitment (c) (ind. $m^{-3} yr^{-1}$), and (d) gelatinous carnivore biomass (gC $m^{-3} yr^{-1}$) versus mesozooplankton production (gC m⁻³ yr⁻¹) of the temperature and mixing simulation.

0+) group (Fig. 12, $\mathbf{\nabla}$) directly matches the maximum summer temperature signal of the same (nth) year. This means that the years with lower temperatures generate years with a lower recruitment population, and the years with higher temperatures promote higher recruitment. When older age groups are considered, the temperature signal can still be tracked in the stock, but there is a delay timing equal to the year-class age. For example, the 1-yr adult stock (Fig. 12, \blacklozenge) carries the temperature signal of the previous (n-1th) year, during which it is apparently more vulnerable to temperature variations. As a result, the temperature signal translates to the 1st year-class numbers with a delay in timing of 1 yr. The same applies to the following age classes, where 2-yr-old adults (Fig. 12, +) match the temperature signal (n-2nd yr) they are subjected to when they were in the recruitment stage. The age 2+ group reacts to changes in the temperature signal with a delay of 2 yr. Similarly, in the age 3-class adults (Fig. 12, \bullet) the temperature signal (*n*-3rd yr) can be tracked with a 3-yr delay. One reason for continuously higher numbers of age 3+ than age 2+ is because the age 3+ population includes all anchovy that are of age 3 or older. Another reason for lower population



Figure 9. Regression analysis of number of current (*n*th) year total annual spawners versus next (n + 1th) year eggs for 50 yr of (a) temperature simulation and (b) temperature and mixing simulation (ind. m⁻³ yr⁻¹).

Figure 10. Regression analysis of number of total current (*n*th) year spawners (including age 0+, 1+, 2+ and 3+) at (a) the beginning of the spawning season (June 1st), (b) during the spawning season (June–September) and (c) during the following (n + 1th) years of winter (December–March) versus total egg production (*n*th yr) in the spawning season of the temperature and mixing simulation (ind. m⁻³ yr⁻¹).



nth yr. Temperature [Jun-Sept] (°C)

(n-1)th yr. Temperature [Dec-Mar] (°C)

numbers in the age 2+ than age 3+ year-class is that fishing mortality accounts for higher losses in age 2+ year-class, whereas for age 3+, senility (i.e., natural mortality) accounts for more than fishing mortality.

mixing simulation.

The propagation of the temperature signal through anchovy age-classes over time causes a curious phenomenon in that even though total eggs and recruitment numbers are increasing significantly (90 and

Figure 12. Time series of summer temperature maxima (°C) at the end of August (\bullet) and total number of the whole anchovy population (\blacktriangle), total number of adult anchovies (\bigcirc), as well as total numbers of anchovies in age classes 0+ (\blacktriangledown), 1+ (\bullet), 2+ (+), and 3+ (\bullet) of the temperature-only simulation (ind. m⁻³ yr⁻¹).



87%, respectively) during times of temperature increase (e.g., years 12–16) the total population of adult anchovy (1+ to 3+ year-class) actually decreases slightly by 6% (Fig. 12, \bigcirc), mainly owing to a decrease in the age 1+ year-class (and to a lesser extent the age classes 2+ and 3+), which is a consequence of the decrease in temperature from years 11 to 12. This decrease in the adult population is also the reason that spawner numbers, although dominated by the 0+ year-class, do not react as strongly to environmental changes compared with recruits or eggs (Figs 5c,d and 6d,e).

Interannual variation in egg and recruitment numbers over the 50-yr simulations is 2.3- and 2.1-fold, respectively. Model-simulated total anchovy abundance varies by 1.8-fold.

DISCUSSION

In the present study we investigate how changes in water temperature and water column mixing, as they naturally occur between different years, impact anchovy population dynamics. Model results show that temperature exerts a strong control over the lower trophic level by contributing directly to lower trophic level compartment metabolic rates and by promoting bottom-up control. On the other hand, total mixing is seen to induce a smaller response by most compartments of the lower trophic levels.

In the nitrate compartment, colder winters result in higher nitrate concentrations by enabling higher entrainment of nutrients into the euphotic zone through formation of a deeper mixed layer, a physical process observed in the Black Sea. When the model is forced with the effects of both temperature and total mixing, both factors combine, enhancing nutrient entrainment even more, acting as a bottom-up control on the lower trophic level compartments. The response given by the rest of the Lower Trophic Level (LTL) (biota) is more complex. Phytoplankton growth is influenced by temperature but benefits more from changes in winter mixing, so that this group reacts immediately to changing environmental conditions. However, it takes several months until the bottom-up control reaches the phytoplankton and microzooplankton level. This influence is then added to the current direct effects of temperature and total mixing. Thus the model results for phytoplankton show that its biomass reacts to environmental changes not only at the beginning of summer but throughout the summer season, whereas microzooplankton biomass shows a slightly delayed reaction to these changes, with temperature changes being of greater importance than mixing changes. Observations from the Black Sea

(Oguz, 2005b) confirm these dynamics. In the 1980s, a strong phytoplankton biomass increase was correlated with a sharp decline in winter temperature values. This was caused by an increased rate of nutrient supply from the chemocline, leading to higher spring phytoplankton production during cold winters.

In mesozooplankton, the bottom-up direct effect of temperature diminishes due to the on-going predatorprev interactions between mesozooplankton and gelatinous carnivores as well as anchovy. Winter mixing in combination with temperature effects increases mesozooplankton production. In the LTL model, gelatinous carnivores control mesozooplankton, as the gelatinous predator does not undergo food saturation. Thus, mesozooplankton biomass only increases when there is a lack of grazing pressure by the gelatinous carnivore, and decreases with higher gelatinous carnivore biomass and hence additional grazing pressure. The above-described dynamics of the lower trophic level model are consistent with available observations from the Black Sea and have been analyzed in detail by Oguz et al. (2001).

The gelatinous predator shows strong temperature dependence because it is not limited by predation in the model and total mixing forcing acts to counteract the temperature effect. Therefore, although warm temperatures promote anchovy production, they also limit anchovy abundance because of increased food competition with gelatinous carnivores. Similar prey–predator relationships as a result of climate-induced variations were also identified for the sprat–cod interactions, which constitute the majority of the fish species in the Baltic Sea ecosystem (Köster *et al.*, 2001).

Seasonal variations

As expected, model simulations of seasonal variation showed that temperature strongly controls egg production through regulation of the onset of spawning activity, daily survival rates and egg abundance during the spawning season. When summer temperatures increased by 2°C relative to the minimum temperature simulation, the beginning of the spawning season shifted to start 19 days earlier, and a further increase of 2°C caused spawning to commence an additional 12 days earlier. Further, higher summer temperatures increased both recruitment numbers and the timing of their appearance, as temperature significantly influences anchovy larval survival rates. This effect then translated into anchovy recruiting to the population 38 and 21 days earlier with each 2°C increase in summer temperatures, and the peak number of recruits in December increasing by 25 and 13%, respectively, with respect to the minimum temperature simulation. The assumption of a 2°C temperature variability is in line with observations of natural variability in sea surface temperatures in the Black Sea due to climatic teleconnections, such as the North Atlantic Oscillation (NAO). From 1980 to 1995 a total approximately 1.8°C decrease in the basin-averaged, winter (December–March) mean sea surface temperature (SST) was observed with respect to the long-term trend, which coincided with the strong positive phase of the NAO (Oguz, 2005b). Similarly, warm SSTs dominated the 1960s during a negative phase of the NAO (Oguz, 2005b).

The influence of both mixing and temperature showed that mixing has an influence on the early developmental stages of anchovy, as mixing is a winter phenomenon (November–March) and slightly increases/decreases food availability for anchovy during that time in cold/warm years. Recruitment numbers are affected by mixing, its effect counteracting the temperature influence. It should be noted that turbulence is not incorporated in this model due to its complexity, although it may influence anchovy population and weight growth. Anchovy are visual feeders, thus the turbulence level is expected either to promote or to suppress the feeding behavior of anchovy, which may also have serious consequences for the resulting predator-prey dynamics (Megrey and Hinckley, 2001).

Houde (1987) suggested that in the early life history of marine fishes, cohort-specific survival rates are closely related to the 'transition length', the length at which weight growth rate exceeds the instant mortality rate and after which biomass growth starts increasing progressively. In the model presented here, the transition length was 6.0 cm and marked the length at which anchovy in the model are counted as recruits to the population. For further information on the influence of environmental factors determining interannual variations of day-age until anchovy reach this transition length, we refer to Oguz *et al.* (2008a; Figs 4–6).

Interannual variations

Modeling 50-yr interannual variations of temperature and mixing confirmed the sensitivity of egg production to temperature. Mixing had no significant effect on egg production since this process is taking place at a time in summer when mixing is very low and only indirectly influences egg production through slightly increasing spawner numbers. Anchovy recruitment biomass and spawners also respond strongly to interannual changes in temperature. The addition of mixing counteracts the temperature effects, resulting in decreased recruitment variability that follows temperature, but with a weaker signal. This is observed for spawners as well, but to a lesser extent. Temperature is the dominant influence for spawners because, in addition to newly recruited anchovy (age 0+), the spawner group also includes individuals of adult age classes that are influenced by environmental conditions of previous years (Fig. 12). In addition, recruits have higher feeding rates in the model than do older anchovy, which translates into a better utilization of food. Such higher feeding rates for recruits have been observed in Black Sea anchovy (Unsal, 1989; Ozdamar *et al.*, 1991; Uckun *et al.*, 2005; Samsun *et al.*, 2006). However, survival of recruits and spawners in the model is more dependent on temperature than on the bottomup supply of nutrients induced by changes in mixing rates.

The finding of the model therefore indicate that temperature variability may impose a serious control over anchovy egg production and larval survival rates, by increasing individual fecundity and larval survival. This may be the main cause of variation in anchovy recruitment. Observational studies connecting environmental conditions with growth show that growth rates are higher where the temperatures are higher (Zenitani, 1995; Takahashi and Watanabe, 2004a; Itoh et al., 2011; Bonanno et al., 2013). Although the Argentinian anchovy (Engraulis anchoita) recruitment success is explained by variations in food availability for the larvae (Marrari et al., 2013), growth rates for the Japanese anchovy (E. japonicus) are found to be more vulnerable to temperature variation than to nutrient availability (Takahashi and Watanabe, 2005). This is due to the dependency of feeding rates and metabolism on temperature (Houde, 1989). Another reason for increased growth and survival chances for anchovy larvae in habitats where higher mean temperatures are observed is an increase in avoidance of predators with increase in their body size (Methot and Kramer, 1979; Palomera et al., 1988; Houde, 1989; Dulcic and Kraljevic, 1996; Wang and Tzeng, 1999).

The relationship between small pelagic fish production and temperature in the Black Sea is also evident in observations (Shulman *et al.*, 2009) and is in line with modeling studies for other seas; the recent anchovy expansion in the North Sea was shown to be dependent on increased summer warming that consequently increases local anchovy production (Petitgas *et al.*, 2012). Similarly, Pethybridge *et al.* (2013) found temperature to be the major influence on anchovy growth and fecundity in the North-western Mediterranean Sea. A similar trend was observed in the Baltic Sea, where a close link between sprat recruitment and 45-yr climate variations has been observed (MacKenzie and Köster, 2004). Low temperatures affect sprat recruitment abundance via controlling the individual fecundity levels (Grauman and Yula, 1989), regulating egg and larval survival chances (Grauman and Yula, 1989; Ojaveer, 1998; Nissling, 2004).

Regression analysis

The dominant influence of temperature compared to mixing can also be seen in the regression analyses of spawner versus egg biomass where a correlation of 99% was found in the temperature-only simulation and 94% when mixing was included. When eggs versus recruitment numbers were regressed in order to identify the survival chances of produced eggs in response to environmental variability, the recruitment success was 88% for the temperature simulation and 93% for the temperature and mixing simulation. In cold years, the deepening of the mixed layer released available nutrients into the water column that caused phytoplankton and subsequently zooplankton growth, which increased the resources available for consumption by feeding larvae and thus resulted in enhanced recruitment success through bottom-up food supply during winter (Fig. 8c). This scenario was reversed in warm years. Recruitment versus spawner relationship produced 84 and 78% correlations for the temperature simulation and temperature and mixing simulation, respectively. This result is mainly due to the ratio of recruitment stock in the total spawners as well as the higher feeding rates of recruits compared to older anchovy (Unsal, 1989; Ozdamar et al., 1991; Uckun et al., 2005; Samsun et al., 2006) resulting in more efficient utilization of food in winter. Total spawners include individuals of other age classes, which have been influenced by the environmental conditions of previous years (Fig. 12). Anchovy recruitment stages were seen to be more sensitive to environmental conditions compared to older age classes, which has also been shown for anchovy in the North-west Mediterranean Sea (Pethybridge et al., 2013) and supports the theory that earlier life stages are more vulnerable to climate change effects than the older age classes (Riinsdorp et al., 2009). The results of the regression analyses agree well with those calculated by Wang et al. (1997) with an individual based model for Chesapeake Bay anchovy using varying density dependent growth rates.

More importantly, the regression analysis between the number of spawners at the beginning of the spawning season, during the entire spawning season, and during winter with egg production showed no correlation for any of the selected time intervals (Fig. 10) but did

show a 98% correlation with mean summer temperatures (Fig. 11a). These results indicate that the amount of eggs produced in a given year is not dependent on the current stock of anchovy available, but rather on the prevailing temperature conditions during the spawning season of that year. This is in contrast to an earlier theory on recruitment that relates recruitment success to the number of available spawners (Cushing, 1996). However, MacKenzie and Köster (2004) have found similarly that the spawner availability, whilst important, is a secondary contributor to egg production in Baltic sprat.

Long-term recruitment variability

The model results further reveal the critical importance of temperature in driving long-term recruitment variability, indicating that cooler years (with cold winters and cool spawning seasons) result in lower recruitment, while in warmer years (with mild winters and warm spawning seasons) the recruitment success is higher. This agrees with reports of the anchovy stock variations in the Black Sea corresponding to fluctuations in the NAO (Niermann et al., 1999; Oguz, 2005b; Oguz et al., 2006; Oguz and Gilbert, 2007), which however may have also been influenced by increased fisheries activity within the same time frame (Oguz, 2005b; Oguz and Gilbert, 2007). This tendency has also been found in the North Sea (Petitgas et al., 2012) and Baltic Sea, where the analysis of 45 years of Baltic Sea observations implied a high consistency between sprat recruitment and large-scale climatic variations (i.e., NAO) and even estimates of potential recruitment and landing abundance possible for the following years (MacKenzie and Köster, 2004). Biological responses to such decadal-scale climate variations in the form of oscillations may provide the most accurate estimates for longer-term climate change effects (Trathan et al., 2007). Long-term changes in environmental variability therefore have the potential to modify anchovy population dynamics and with it ecosystem dynamics, as well as predator-prey interactions. In the Baltic Sea example, sprat are the major predators of cod ichthyoplankton and therefore warm atmospheric indices can cause a regime transition towards high sprat abundance while leading to a decreased population growth of cod (Köster et al., 2001; Mac-Kenzie and Köster, 2004). Lehodey et al. (2003) showed with multi-trophic level modeling that the production of tropical tuna such as, skipjack (Katsuwonus pelamis) and yellowfin (Thunnus albacares) and subtropical tuna, albacore (Thunnus albacares) are regulated remarkably under control of climate indices such as ENSO and the Pacific Decadal Oscillation.

© 2014 John Wiley & Sons Ltd, Fish. Oceanogr., 23:5, 436-457.

Observations suggest a positive relationship between the Western Mediterranean Oscillation index of a particular year and the landing-per-unit-effort of 1st year-class sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) of the following year, in the last 30 yr in the north-western Mediterranean (Martin *et al.*, 2012). This study shows that the climate index is positively correlated to landing-per-unit-effort of both fish species the following year, which is the time period necessary for larvae to grow into 1st year-class as adults (Martin *et al.*, 2012).

For fisheries assessment, it is important to determine the extent of the variability of fish stocks (Mac-Kenzie and Köster, 2004). In the North Pacific Ocean, the switchbacks in the polarity of low frequency Pacific Decadal Oscillation that occurred in 1925, 1947 and 1977 are found to be closely related with the shifts in Alaskan salmon production (Mantua *et al.*, 1997). Environmental variations are also shown to drive recruitment variability in highly exploited stocks of northern cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae, eastern oyster (*Crassostrea virginica*) and Antarctic krill (*Euphausia superba*; Hofmann and Powell, 1998).

Recent studies turned their attention to the compelling evidence that links climate impacts with the development of fish, recruitment and also population dynamics and therefore point to the need for models as a useful tool to assess climate-induced effects on fish production (Megrey *et al.*, 2007). Bioenergetics modeling of fish as done in this study is a powerful approach for its capability of simulating the fish life history dynamics under environmental variations (Megrey *et al.*, 2007) and has a great potential to be used in fisheries management (Hinrichsen *et al.*, 2011).

CONCLUSIONS

In this modeling study it was found that anchovy are most sensitive to temperature variations in their early life stages (eggs, larvae and recruitment) and temperature variability is thus the main cause in varying recruitment. In addition, recruitment success is highly dependent on temperature variations and the temperature effects explicitly drive the variations of the adult age classes in the early life stages, more so than the effect of temperature on nutrient supply or metabolic rates. The temperature influence proliferates in the anchovy stock through age classes from year to year. However, the overall effect on the entire stock at once is hard to resolve by traditional, current management based approaches. Under such circumstances, future yield estimations can be anticipated considering individual anchovy age groups, with the time lag it requires for the environmental effect to propagate to a certain age.

Further results indicate that changes in total mixing affect lower trophic levels minimally. Total mixing counteracts temperature to slightly diminish the lower trophic level reaction to temperature only, as low mixing is limiting the nutrient supply in the model.

In conclusion, considering the intense fisheries pressure, today's management strategies should aim to develop approaches integrating both the ecosystem processes and variability in the environmental conditions (Hofmann and Powell, 1998). Although in this model the environmental forcing is limited to daily temperature and total mixing rate variations, the multi-trophic-level modeling approach is sensitive enough to link the anchovy population response with the environmental variability through a lower trophic level model. However, evaluation of the environmental effects alone is difficult in marine ecosystems that are impacted by heavy fishing activity (Mertz and Myers, 1994). The influence of intense exploitation may overlay the effects caused by environmental variations (Hofmann and Powell, 1998).

ACKNOWLEDGEMENTS

We thank Prof. Ferit Bingel and four anonymous reviewers for constructive comments on an earlier version of this manuscript. This research was partially funded by the European Commission programs MEE-CE (Contract No. 212085) and PERSEUS (Contract No. 287600).

REFERENCES

- Altman, E.N., Gertman, I.F. and Golubeva, Z.A. (1987) Climatological Fields of Temperature and Salinity in the Black Sea. Sevastopol, Ukraine: Rep., State Oceanogr. Inst., Sevastopol Branch, 109 pp (in Russian).
- Aurich, H.J. (1953) Verbreitung und Laichverhältnisse von Sardelle und Sardine in der südöstlichen Nordsee und ihre Veränderingen als Folge der Klimaänderung. *Helgol. Wiss. Meer.* 4:175–204 (in German).
- Bakun, A. (1996) Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. San Diego, CA: University of California Sea Grant, incooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico, 323 pp.
- Bakun, A. and Parrish, R.H. (1991) Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. *ICES J. Mar. Sci.* 48:343–361.
- Blaxter, J.H.S. and Hunter, J.R. (1982) The biology of the clupeoid fishes. Adv. Mar. Biol. 20:1–223.

- Bonanno, A., Zgozi, S., Cuttita, A. et al. (2013) Infulence of environmental variability on anchovy early life stage (Engraulis encrasicolus) in two different areas of the Central Mediterranean Sea. Hydrobiologia 701:273–287.
- Borja, A., Uriarte, A., Valencia, V., Motos, L. and Uriarte, A. (1996) Relationships between anchovy (*Engraulis encrasicolus*) recruitment and environment in the Bay of Biscay. Sci. Mar. 60(Suppl. 2):179–192.
- Chashchin, A.K. (1996) The Black Sea populations of anchovy. Sci. Mar. 60:219–225.
- Chavez, F.P., Ryan, J., Lluch-Cota, S.E. and Niquen, M. (2003) From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. Science 29:217–221.
- Cole, J. and McGlade, J. (1998) Clupeoid population variability, the environment and satellite imagery in coastal upwelling systems. *Rev. Fish Biol. Fish.* **8:**445–471.
- Crawford, R.J.M., Shannon, L.V. and Pollock, D.E. (1987) The Benguela ecosystem. Part IV. The major fish and invertebrate resources. Oceanogr. Mar. Biol. 25:353–505.
- Cury, P. and Roy, C. (1989) Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* **46:**670–680.
- Cushing, D.H. (1996) Towards a Science of Recruitment in Fish Populations. Oldendorf/Luhe: Ecology Institute, 175 pp.
- Daskalov, G.M. (2003) Long-term changes in fish abundance and environmental indices in the Black Sea. Mar. Ecol. Prog. Ser. 255:259–270.
- Dulcic, J. and Kraljevic, M. (1996) Weight–length relationships for 40 fish species in the eastern Adriatic (Croatian waters). *Fish. Res.* 28:243–251.
- Efimov, V.V. and Timofeev, N.A. (1990) Investigation of the Black Sea and Azov Sea Heat Balance, Technical Report. Sevastopol, Ukraine: Ukr. Acad. of Sci, 237 pp.
- Funamoto, T., Aoki, I. and Wada, Y. (2004) Reproductive parameters of Japanese anchovy, *Engraulis japonicus*, in two bays of Japan. *Fish. Res.* **70**:71–81.
- Grauman, G.B. and Yula, E. (1989) The importance of abiotic and biotic factors in the early ontogenesis of cod and sprat. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* **190**:207–210.
- Grbec, B., Dulcic, J. and Morovic, M. (2002) Long–term changes in landings of small pelagic fish in the Eastern Adriatic – possible influence of climate oscillations over the Northern Hemisphere. *Clim. Res.* 20:241–252.
- Guisande, C., Cabanas, J.M., Vergara, A.R. and Riveiro, I. (2001) Effect of climate on recruitment success of Atlantic Iberian sardine (Sardina pilchardus). Mar. Ecol. Prog. Ser. 223:243–250.
- Guisande, C., Vergara, A.R., Riveiro, I. and Cabanas, J.M. (2004) Climate change and abundance of the Atlantic Iberian sardine (Sardina pilchardus). Fish. Oceanogr. 13:91– 101.
- Hinrichsen, H.H., Dickey-Collas, M., Huret, M., Peck, M.A. and Vikebø, F.B. (2011) Evaluating the suitability of coupled biophysical models for fishery management. *ICES J. Mar. Sci.* 68:1478–1487.
- Hofmann, E.E. and Powell, T.M. (1998) Environmental variability effects on marine fisheries: four case histories. *Ecol. Appl.* 8:23–32.
- Houde, E.D. (1987) Fish early life history dynamics and recruitment variability. Am. Fish. Soc. Symp. 2:17–29.
- Houde, E.D. (1989) Comparative growth, mortality and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fish. Bull.* 87:471–495.

- Houde, E.D. (2008) Emerging from Hjort's shadow. J. Northwest Atl. Fish. Soc. 41:53-70.
- Imai, C., Kajitori, K., Tajima, Y., Nakamura, M., Uchiyama, M. and Yamada, H. (1998) Biomass estimation of Japanese anchovy stock in the Honshu-Pacific waters by the egg production method using sea surface temperature information. *Bull. Jap. Soc. Fish. Oceanogr.* 62:356–368 (in Japanese with English Abstract).
- Itoh, S., Saruwatari, T., Nishikawa, H. et al. (2011) Environmental variability and growth histories of larval Japanese sardine (*Sardinops melanostictus*) and Japanese anchovy (*Engraulis japonicus*) near the frontal area of the Kuroshio. Fish. Oceanogr. 20:114–124.
- Katara, I., Pierce, G.J., Illian, J. and Scott, B.E. (2011) Environmental drivers of the anchovy/sardine complex in the Eastern Mediterranean. *Hydrobiologia* 670:49–65.
- Kawasaki, T. (1991) Effects of global climatic change on marine ecosystems and fisheries. In: Climate Change: Science, Impacts and Policy. Proc. Second World Climate Conference. J. Jager & H.L. Ferguson (eds) Cambridge: Cambridge University Press, pp. 291–299.
- Kideys, A.E., Gordina, A.D., Bingel, F. and Niermann, U. (1999) The effect of environmental conditions on the distribution of eggs and larvae of anchovy (*Engraulis encrasicolus L.*) in the Black Sea. ICES J. Mar. Sci. 56(Suppl.):58–64.
- Köster, F.W., Hinrichsen, H.H., St. John, M.A. et al. (2001) Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. Can. J. Fish. Aquat. Sci. 58:1534–1556.
- Lasker, R. (1975) Field criteria for survival of anchovy larvae: the relation between in shore chlorophyll maximum layers and successful first feeding. *Fish. Bull.* **73:**453–462.
- Lehodey, P., Chai, F. and Hampton, J. (2003) Modelling climate–related variability of tuna populations from a coupled ocean–biogeochemical–populations dynamics model. Fish. Oceanogr. 12:483–494.
- Lloret, J., Palomera, I., Salat, J. and Sole, I. (2004) Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north–western Mediterranean). Fish. Oceanogr. 13:102–110.
- Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T. et al. (1989) Worldwide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci. 8:195–205.
- Lluch-Belda, D., Hernandez-Vazquez, S. and Schwartzlose, R.A. (1991) A hypothetical model for the fluctuation of the California sardine population (*Sardnops sagax caeru-lea*). In: Long-Term Variability of Pelagic Fish Populations and Their Environment. T. Kawasaki, S. Tanaka, Y. Toba, A. Taniguchi (eds) New York: Pergamon Press, pp. 293–300.
- MacKenzie, B.W. and Köster, F.W. (2004) Fish production and climate: sprat in the Baltic Sea. Ecology 85:784–794.
- Mantua, N.J., Hare, S.R., Zhang, J., Wallace, J.M. and Francis, R.J. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* 78:1069–1079.
- Marrari, M., Signorini, R.S., McClain, C.R. et al. (2013) Reproductive success of Argentine anchovy, Engraulis anchoita, in relation to environmental variability at the midshelf front (Southwestern Atlantic Ocean). Fish. Oceanogr. 22:247–261.
- Martin, P., Sabatés, A., Lloret, J. and Martin-Vide, J. (2012) Climate modulation of fish populations: the role of Western

Mediterranean Oscillation (WeMO) in sardine (Sardina Pilchardus) and anchovy (Engraulis encrasicolus) production in the north-western Mediterranean. *Clim. Change* **110**:925–939.

- Megrey, B.A. and Hinckley, S. (2001) Effect of turbulence on feeding of larval fishes: a sensitivity analysis using an individual-based model. ICES J. Mar. Sci. 58:1015–1029.
- Megrey, B.A., Rose, K.A., Klumb, R.A. et al. (2007) A bioenergetic-based population dynamics model of pacific herring (*Clupea harengus pallasi*) coupled to a lower trophic lever nutrient plankton – zooplankton model: description, calibration and sensitivity analysis. Ecol. Model. 202:144– 164.
- Mertz, G. and Myers, R.A. (1994) The ecological impact of the Great Salinity Anomaly in the northern North–west Atlantic. *Fish. Oceanogr.* **3:**1–14.
- Methot, R.D. Jr and Kramer, D. (1979) Growth of northern anchovy (Engraulis mordax), larvae in the sea. Fish. Bull., U.S. 77:413–423.
- Niermann, U., Bingel, F., Gorban, A. et al. (1994) Distribution of anchovy eggs and larvae (*Engraulis encrasicolus Cuv.*) in the Black Sea in 1991 and 1992 in comparison to former surveys. *ICES J. Mar. Sci.* 51:395–406.
- Niermann, U., Kideys, A.E., Kovalev, A.V., Melnikov, V. and Belokopytov, V. (1999) Fluctiations of pelagic species of the open Black Sea during 1980–1995 and possible teleconnections. In: Environmental Degredation of the Black Sea: Challenges and Remedies, Vol. 56. S. Besiktepe, U. Unluata & A. Bologa (eds) NATO ASI Series–B: Environmental Security, Dordrecht, The Netherlands: Kluwer Academic Publishers, pp. 147–174.
- Nissling, A. (2004) Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea – implications for stock development. *Hydrobiologia* **514**:115–123.
- Oguz, T. (2005b) Black Sea ecosystem response to climatic variations. Oceanography 18(2):122–133.
- Oguz, T. and Gilbert, D. (2007) Abrupt transitions of the topdown controlled Black Sea pelagic ecosystem during 1960– 2000: evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. *Deep-Sea Res. I* 54:220–242.
- Oguz, T., La Violette, P.E. and Unluata, U. (1992) The upper layer circulation of the Black Sea: its variability as inferred from hydrographic and satellite observations. J. Geophys. Res. 97:12569–12584.
- Oguz, T., Ducklow, H., Malanotte-Rizzoli, P., Tugrul, S., Nezlin, N.P. and Unluata, U. (1996) Simulation of annual plankton productivity cycle in the Black Sea by a one-dimensional physical-biological model. J. Geophys. Res. 101:16585– 16599.
- Oguz, T., Ducklow, H., Malanotte-Rizzoli, P. *et al.* (1999) A physical–biochemical model of plankton productivity and nitrogen cycling in the Black Sea. *Deep-Sea Res. I* **46:**597–636.
- Oguz, T., Ducklow, H.W., Purcell, J.E. and Malanotte-Rizzoli, P. (2001) Modeling the response of top-down control exerted by gelatinous carnivores on the Black Sea pelagic food-web. J. Geophys. Res. 106:4543–4564.
- Oguz, T., Dippner, J.W. and Kaymaz, Z. (2006) Climatic regulation of the Black Sea hydro–meteorological and ecological properties at interannual–to–decadal time scales. J. Mar. Syst. 60:235–254.
- © 2014 John Wiley & Sons Ltd, Fish. Oceanogr., 23:5, 436–457.

- Oguz, T., Salihoglu, B. and Fach, B. (2008a) A coupled plankton–anchovy population dynamics model assessing nonlinear controls of anchovy and gelatinous biomass in the Black Sea. *Mar. Ecol. Prog. Ser.* **369**:229–256.
- Oguz, T., Salihoglu, B. and Fach, B. (2008b) Invasion dynamics of the alien ctenophore *Mnemiopsis leidyi* and its impact on anchovy collapse in the Black Sea. J. Plankton Res. 30:1385– 1397.
- Ojaveer, E. (1998) Influence of long-term climate fluctuations on marine organisms: preliminary results. In: Climate Change Studies in Estonia. T. Kallaste & P. Kuldna (eds) Tallinn, Republic of Estonia: Stockholm Environment Institute Tallinn, International Institute for Environmental Technology and Management Ministry of the Environment, pp. 85–104.
- Ozdamar, E., Khiara, K. and Erkoyuncu, I. (1991) Some biological characteristic of European anchovy Engraulis encrasicolus L. in the Black Sea. T. Tokyo Univ. Fish. 78:57– 64.
- Painting, S.J., Hutchings, L., Hugger, J.A., Korrubel, J.L., Richarson, A.J. and Verheye, H.M. (1998) Environmental and biological monitoring for forecasting anchovy recruitment in the southern Benguela upwelling region. *Fish. Oceanogr.* 7:364–374.
- Palomera, I., Morales-Nin, B. and Lleonart, J. (1988) Larval growth of anchovy, *Engraulis encrasicolus*, in the Western Mediterranean Sea. Mar. Biol. 99:283–291.
- Palomera, I., Olivar, M.P., Salat, J. et al. (2007) Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Prog. Oceanogr.* 74:377–396.
- Pecquerie, L., Petitgas, P. and Kooijman, S.A.L.M. (2009) Modeling fish growth and reproduction in the context of the Dynamic Energy Budget theory to predict environmental impact on anchovy spawning duration. J. Sea Res. 62:93–105.
- Peterman, R.M. and Bradford, M.J. (1987) Wind speed and mortality rate of a marine fish: the northern anchovy (Engraulis mordax). Science 235:354–356.
- Pethybridge, H., Roos, D., Loizeau, V., Pecquerie, L. and Bacher, C. (2013) Responses of European anchovy vital rates and population growth to environmental fluctuations: an individual–based modeling approach. *Ecol. Model.* 250:370– 383.
- Petitgas, P., Alheit, J., Peck, M.A. *et al.* (2012) Anchovy population expansion in the North Sea. *Mar. Ecol. Prog. Ser.* **444:**1–13.
- Plounevez, S. and Champalbert, G. (2000) Diet, feeding behaviour and trophic activity of the anchovy (*Engraulis encrasicolus* L.) in the Gulf of Lions (Mediterranean Sea). Oceanol. Acta 23:175–192.
- Politikos, D., Triantafyllou, G., Petihakis, G. et al. (2011) Application of a bioenergetics growth model for European anchovy (*Engraulis encrasicolus*) linked with a lower trophic level ecosystem model. *Hydrobiologia* 670:141–163.
- Prodanov, K., Mikhailov, K., Daskalov, G. et al. (1997) Environmental management of fish resources in the black sea and their rational exploitation. GFCM Stud. Rev. 68:1– 178.
- Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Mollmann, C. and Pinnegar, J.K. (2009) Resolving the effect of climate change on fish populations. *ICES J. Mar. Sci.* 66:1570–1583.
- Rose, K.A., Cowan, J.H., Clark, M.E. Jr, Houde, E.D. and Wang, S.B. (1999) Simulating bay anchovy population dynamics in the mesohaline region of Chesapeake Bay using

an individual-based approach. Mar. Ecol. Prog. Ser. 185:113-132.

- Samsun, O., Samsun, N., Kalayci, F. and Bilgin, S. (2006) A study on recent variations in the population structure of European anchovy (*Engraulis encrasicolus* L., 1975). in the southern Black Sea. Ege Univ. J. Fish. Aquat. Sci. 23:301–306.
- Satilmis, H.H., Gordina, A.D., Bat, L. et al. (2003) Seasonal distribution of fish eggs and larvae off Sinop (the southern Black Sea) in 1999–2000. Acta Oecol. 24:S275–S280.
- Schwartzlose, R.A., Alheit, J., Bakun, A. et al. (1999) Worldwide large–scale fluctuations of sardine and anchovy populations. S. Afr. J. Mar. Sci. 21:289–347.
- Shulman, G.E., Ozturk, B., Kideys, A.E., Finenko, G.A. and Bat, L. (2009) Trophic Relationships and Food Supply of Heterotrophic Animals in the Pelagic Ecosystem of the Black Sea, Vol. 2. Istanbul: Black Sea Commission Publications, 308 pp. ISBN 978-605-89206-0-6.
- Steele, J.H. (1998) Regime shifts in marine ecosystems. Ecol. Appl. 8:33–36.
- Takahashi, M. and Watanabe, Y. (2004a) Growth rate dependent recruitment of Japanese anchovy, *Engraulis japonicus*, in the Kuroshio-Oyashio transitional waters. *Mar. Ecol. Prog. Ser.* 266:227–238.
- Takahashi, M. and Watanabe, Y. (2004b) Developmental and growth rates during metamorphosis of Japanese anchovy *Engraulis japonicus* in the Kuroshio-Oyashio transitional waters. Mar. Ecol. Prog. Ser. 282:253–260.
- Takahashi, M. and Watanabe, Y. (2005) Effects of temperature and food availability on growth rate during late larval stage of Japanese anchovy (*Engraulis japonicus*) in the Kuroshio-Oyashio transition region. *Fish. Oceanogr.* 14:223–235.
- Takasuka, A., Oozeki, Y., Kubota, H. and Lluch-Cota, S.E. (2008) Contrasting spawning temperature optima: why are anchovy and sardine regime shifts synchronous across the North Pacific? Prog. Oceanogr. 77:225–232.
- Trathan, P.N., Forcada, J. and Murphy, E.J. (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 362:2351–2365.
- Tsai, C.F., Chen, P.Y., Chen, C.P., Lee, M.A., Shiah, G.Y. and Lee, K.T. (1997) Fluctuation in abundance of larval anchovy environmental conditions in coastal waters off south– western Taiwan as associated with the El Niño-Southern Oscillation. Fish. Oceanogr. 6:238–249.
- Tsuruta, Y. and Hirose, K. (1989) Internal regulation and reproduction in Japanese anchovy (*Engraulis japonica*) as related to population fluctuation. *Can. Spec. Publ. Fish. Aquat. Sci.* **108:**111–119.
- Uckun, D., Akalin, S. and Togulga, M. (2005) Investigations of the age and growth of anchovy (*Engraulis encrasicolus* L., 1958) in Izmir Bay. *Ege Univ. J. Fish. Aquat. Sci.* 22:281– 285.
- Unsal, N. (1989) Karadenizdeki hamsi baligi Engraulis encrasicolus (L. 1758) nin yas-boy-agirlik iliskisi ve en kucuk av buyuklugunun saptanmasi uzerinde bir arastirma [A study on age- length-weight relationship and determination of the smallest catching size of anchovy, Engraulis encrasicolus (L.) in the Black Sea]. Su urunleri dergisi. [J. Aquat. Prod.] 3:17–28 (in Turkish, abstract in English). Source: ASFA 1 Biological Sciences & Living Resources. Access. no 2331373.
- Wang, Y.T. and Tzeng, W.N. (1999) Difference in growth rates among cohorts of *Encrasicholina punctifer* and *Engraulis*

japonicus larvae in the coastal waters off Tanshui River Estuary, Taiwan, as indicated by otolith microstructure analysis. *J. Fish Biol.* **54:**1002–1016.

- Wang, S.B., Cowan, J.H. Jr, Rose, G.A. and Houde, E.D. (1997) Individual–based modeling of recruitment variability and biomass production of bay anchovy in mid. Chesapeake Bay. J. Fish Biol. 51(Suppl. A):101–120.
- Xu, Y., Chai, F., Rose, K.A., Niquen, C.M. and Chavez, F.P. (2013) Environmental influences on the interannual variation and spatial distribution of Peruvian anchovy (*Engraulis ringens*) population dynamics from 1991 to 2007: a three–dimensional modeling study. *Ecol. Model.* 264:64–82.
- Yasuda, I., Sugisaki, H., Watanabe, Y., Minobe, S.S. and Oozeki, Y. (1999) Interdecadal variations in Japanese sardine and ocean/climate. *Fish. Oceanogr.* 8:18–24.
- Yatsu, A., Watanabe, T., Ishida, M., Sugisaki, H. and Jacobson, L.D. (2005) Environmental effects on recruitment and productivity of Japanese sardine Sardinops melanostictus and chub mackerel Scomber japonicus with recommendations for management. Fish. Oceanogr. 14:263–278.
- Zenitani, H. (1995) Analysis of lipid components for determining the nutritional condition of sardine larvae Sardinopsis melanostictus. Fish. Sci. 61:725–726.