

Application of a bioenergetics growth model for European anchovy (*Engraulis encrasicolus*) linked with a lower trophic level ecosystem model

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Abstract A bioenergetics model is implemented for European anchovy (*Engraulis encrasicolus*) and applied to the north-eastern Aegean Sea (eastern Mediterranean Sea). The model reproduces the growth of anchovy in a one-way linked configuration with a lower trophic level (LTL) ecosystem model. The LTL model provides densities for three zooplankton functional groups (heterotrophic flagellates,

microzooplankton and mesozooplankton) which serve as available energy via consumption for the anchovy model. Our model follows the basic structure of NEMURO.FISH type models (North Pacific Ecosystem Model for Understanding Regional Oceanography for Including Saury and Herring). Several model parameters were specific for the Mediterranean or the Black Sea anchovy and some others were adopted from related species and NEMURO.FISH due to lack of biological information on *E. encrasicolus*. Simulation results showed that the fastest growth rate occurs during spring and the slowest growth rate from August to December. Zooplankton abundance during autumn was low implying that decreased prey density lead to a reduction in anchovy weight, especially for the age-3 class. Feeding parameters were adjusted to adequately fit the model growth estimates to available weight-at-age data. A detailed sensitivity analyses is conducted to evaluate the importance of the biological processes (consumption, respiration, egestion, specific dynamic action, excretion and egg production) and their parameters to fish growth. The most sensitive parameters were the intercept and exponent slope of the weight-dependent consumption and respiration process equations. Fish weight was fairly sensitive to temperature-dependent parameters.

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Introduction

European anchovy (*Engraulis encrasicolus*) is one of the most important pelagic species in the Mediterranean (Leonart & Maynou, 2003). The northern Aegean Sea anchovy stock, influenced by the outflow of Black Sea waters (BSWs), is one of the largest stocks in the eastern Mediterranean constituting a key fisheries resource in this area (Somarakis et al., 2006). The integration of environmental factors with biological attributes and fishery knowledge has been recognised as a needful task in order to improve the understanding of the mechanisms that drive the pelagic fishery resources variability in the Mediterranean Sea (Giannoulaki et al., 2005). From an ecosystem perspective, small pelagic fish play a key role in connecting the lower and upper trophic levels marine ecosystems, due to their significant biomass at mid-trophic levels (Bakun, 1996).

Several fish models have been developed with different characteristics in terms of orientation, objectives and perspectives. For a detailed review of the current modelling approaches in fisheries, we propose the paper of Plagányi (2007). During the last few years, various food web models have been published emphasizing the importance of linking lower trophic levels (LTLs) with higher trophic levels (HTLs) for exploring the environment and fishing effects on ecosystems (Travers et al., 2007). For example, Bryant et al. (1995) proposed the development and analysis of a fish module within the nutrient-based ecosystem model ERSEM (Baretta et al., 1995). NEMURO.FISH (Ito et al., 2004; Megrey et al., 2007; Rose et al., 2007) has been developed for saury (*Cololabis saira*) and herring (*Clupea harengus*) through linking a LTL biogeochemical model with a HTL fish population–bioenergetics model. Oguz et al. (2008) developed a one-dimensional coupled model of LTL and anchovy population dynamics to analyse the mechanisms of sharp biomass transitions of anchovy and gelatinous zooplankton in the Black sea. Individual-based models (IBMs) offers also a promising approach for modelling population and community dynamics contributing to our understanding of recruitment processes in marine fish populations (Miller, 2007). The consequences of global warming on capelin distribution and population dynamics through an IBM model linked with a biophysical ocean model were

investigated by Huse & Ellingsen (2008), whilst a two-dimensional IBM model coupled with fish bioenergetics was developed to simulate migration and growth of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific (Okunishi et al., 2009).

Working in this framework, an attempt to develop a model that can efficiently represent the growth of a pelagic fish in a Greek marine system by bringing together a LTL food web model with a fish growth model is presented. More specifically, a complex LTL (Princeton Ocean Model–European Regional Seas Ecosystem Model, POM–ERSEM) was linked with a bioenergetics model for European anchovy following the NEMURO.FISH modelling approach (Ito et al., 2004; Megrey et al., 2007). The present LTL model provides concentrations of three zooplankton groups (heterotrophic flagellates, microzooplankton and mesozooplankton), which serve as the available energy intake via consumption for the anchovy model. In addition, the anchovy habitat temperature that significantly affects the fish growth is also based on the LTL model simulated hydrodynamics. The model performance is explored through validation and sensitivity tests.

Materials and methods

Study area

Although the Aegean Sea is characterized as an overall oligotrophic environment, there is significant spatial variability with the northern Aegean Sea being a more productive area compared to the southern. The water column in the northern part is highly stratified, consisting essentially of three layers. The upper layer (0–100 m) is a mixture of BSW and Levantine Intermediate Water (LIW) with a 20-m thick surface layer of modified BSW. Below this (100–400 m), a layer of warm and saline layer of Levantine origin (LIW) is found. The deeper layer is composed of very dense northern Aegean Deep water (NADW). The northern Aegean is characterized by an overall cyclonic circulation, overlaid with several transient and semi-permanent eddies, such as the anticyclone surrounding the Samothraki and Imvros islands (Zervakis & Georgopoulos, 2002). A prominent characteristic is the brackish water inputs from N. Aegean rivers (Fig. 1) and the Black Sea which

significantly influence both the hydrology and ecology of the area. The depth of the euphotic zone varies between 80 and 100 m, whilst nutrient (nitrates and phosphates) concentrations in the surface layer are similar to the southern Aegean with nitrate levels (0–200 m) varying between 0.05 and 1.6 μM and phosphate 0.02–0.08 μM . The seasonal variability is low with a small increase in nutrients during March related to winter mixing.

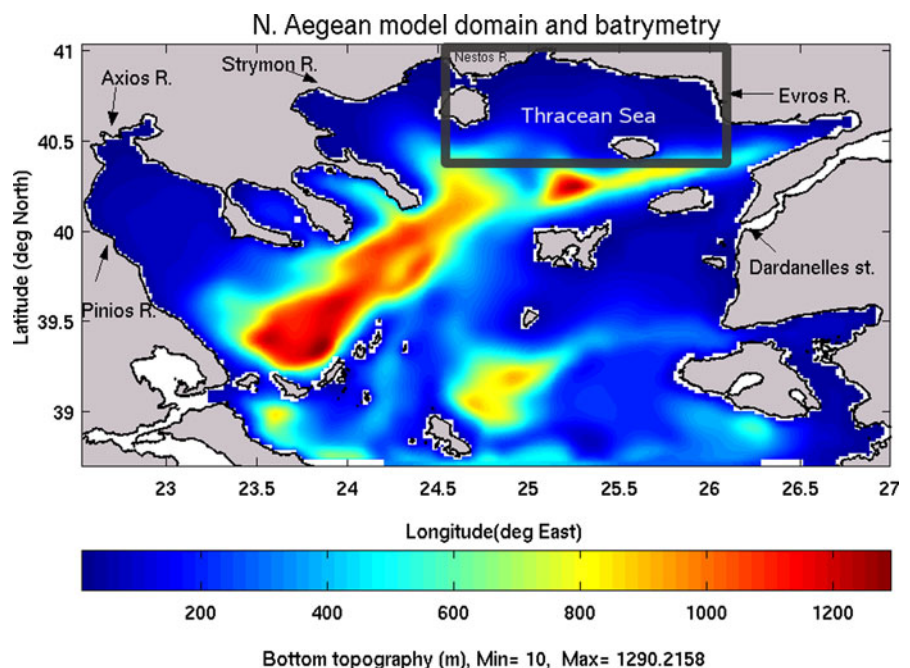
Field studies (Lykousis et al., 2002; Siokou-Frangou et al., 2002) show that the partitioning of carbon among the different plankton compartments is not a broad-based pyramid, where autotrophic biomass overwhelms that of heterotrophs as the ratio of heterotrophs/autotrophs is 0.9–2.0 indicating the importance of microheterotrophs (Bacteria, Heterotrophic Nanoflagellates and Ciliates). Autotrophic biomass values (integrated to 100 m) range between 1,072 and 2,568 mg C m^{-2} with small size cells ($<3 \mu\text{m}$) dominating (80%). Most of the biomass (49–56%) is due to the picoplankton fraction (0.2–1.2 μm), whilst the ultraplankton fraction (1.2–3.0 μm) accounts for 18–23% and the nano + microplankton fraction ($>3.0 \mu\text{m}$) for 20–33%. Heterotrophs play a significant role in the northern Aegean Sea with biomass values ranging from 1,847 to 2,421 mg C m^{-2} with the upper 50 m layer exhibiting higher

values. Bacteria constitute the largest fraction of this biomass (59–69%) whilst in terms of mesozooplankton, copepods are the most abundant. The relatively high abundance of cladocerans and appendicularians, which are organisms able to exploit the available small autotrophs and heterotrophs, indicate rather efficient trophic relationships within the food web. There are significant export fluxes of particulate organic carbon from the euphotic zone comprising a mixture of plankton cell and faecal pellets to depths of $>1,500 \text{ m}$; which implies a rapid and close relationship between benthic/pelagic coupling (Siokou-Frangou et al., 2002).

Lower trophic level ecosystem model

The zooplankton biomass values and temperature that are used as input to the fish model are provided by a 3-D coupled physical–biogeochemical model that is implemented in the northern Aegean area (model domain shown in Fig. 1). The model simulated zooplankton and temperature 3-D fields are averaged over a representative area (indicated in the box of Fig. 1) in the Thracian Sea, which is a well-known habitat for anchovy in the N. Aegean (Somarakis et al., 2007) and therefore was chosen as the study area. The hydrodynamic model is based on the

Fig. 1 Study area: northern Aegean Sea. Model domain and bathymetry. SA Samothraki Island, IM Imvros Island. The indicated *black box* represents the Thracian Sea area over which the 3D-LTL model output is averaged



Princeton Ocean Model (Blumberg & Mellor, 1983), which is a primitive equation, sigma-coordinate circulation model embedded with a Mellor–Yamada 2.5 turbulence closure sub-model (Mellor & Yamada, 1982) that is used to compute vertical mixing coefficients. POM (<http://www.aos.princeton.edu/WWW/PUBLIC/htdocs.pom>) is a widely spread community model with numerous applications. In the N. Aegean it has been applied by Kourafalou & Barbopoulos (2003), Kourafalou & Tsiaras (2007) whilst it is also implemented in the Aegean Sea as part of the operational ‘POSEIDON’ forecasting system (Nittis et al., 2006; Korres et al., 2002). The biogeochemical model is based on ERSEM II (Baretta et al., 1995) and has been implemented at sub-basin (Aegean–Levantine), shelf and coastal areas of the eastern Mediterranean (Petihakis et al., 2002; Triantafyllou et al., 2007; Petihakis et al., 2009). Furthermore, a basin–scale Mediterranean coupled model (POM–ERSEM) is operational as part of the ‘POSEIDON’ forecasting system (www.poseidon.ncmr.gr).

The coupled physical–biogeochemical model of the N. Aegean sea has a horizontal resolution of $1/10^\circ$ (~ 10 km), and 25 bottom following sigma levels resolved in the vertical, whilst the integration time step is set to 10 min. A logarithmic distribution allows a finer resolution at the layers close to the surface. Thus, in the area of interest (Fig. 1) the vertical resolution varies from 0.5 m near the surface to 5 m at mid-depth.

Coupled physical–biogeochemical model climatological simulations were performed using high-resolution (6 h, $1/10^\circ$) atmospheric forcing provided by the operational HCMR (Hellenic Centre for Marine Research) ‘POSEIDON’ system model (Papadopoulos et al., 2002).

For the biology, a complex pelagic system is used with state variables describing four autotrophic and four heterotrophic plankton groups, dissolved and particulate organic matter and the essential dissolved inorganic nutrients (nitrate, phosphate, ammonia and silicate). Biotic groups are distinguished not by species, but by their functional role in the ecosystem using size as the major characteristic. Both physiological (ingestion, respiration, excretion, egestion, etc.) and population processes (growth, migration and mortality) are included whilst biologically driven carbon dynamics are coupled to the chemical dynamics of nitrogen, phosphate, silicate and oxygen with

dynamically varying ratios. Autotrophs are light limited, competing with heterotrophic pelagic bacteria for nutrients with the latter acting as remineralisers. Nutrient uptake is controlled by the difference between the internal nutrient pool and external nutrient concentration. Heterotrophs exploit phytoplankton and bacteria as well as smaller heterotrophic groups. In the absence of fish predators a sigmoid density-dependent loss function (Edwards & Yool, 2000) is adopted for zooplankton, parameterising top-predator mortality. Finally, the benthic–pelagic coupling is described by a simple first order benthic return module, which includes the settling of organic detritus into the benthos and diffusional nutrient fluxes into and out of the sediment.

Fish model

In order to describe the growth of an individual anchovy, the bioenergetics modelling approach was adopted. Bioenergetics models have been increasingly employed to analyse the mechanisms of changes in fish growth (Ursin, 1967; Stewart et al., 1983; Kitchell et al., 1997). These models are based on balanced energy equations in which growth is represented as the difference between consumption and energy losses such as respiration, specific dynamic action (SDA), egestion, excretion and egg production (EGG). Following the basic structure of NEMURO.FISH type bioenergetics models (Ito et al., 2004; Megrey et al., 2007) the specific growth of anchovy was calculated as weight increment per unit of weight per day

$$\frac{1}{W} \cdot \frac{dW}{dt} = [C - (R + F + SDA + E + EGG)] \cdot \frac{CAL_z}{CAL_f}, \quad (1)$$

where W is the fish wet weight (g-fish), t is the time (days), C is the consumption, R is the respiration (or losses due to metabolism), F is the egestion (or losses due to faeces), SDA is the specific dynamic action (or losses due to energy costs for food digestion), E is the excretion (or losses of nitrogenous excretory wastes) and EGG is the egg production (or losses due to reproduction). Components of the energy budget (C , R , SDA , F , E and EGG) are in units of $\text{g zooplankton g fish}^{-1} \text{ day}^{-1}$, which are converted to g fish g

fish⁻¹ day⁻¹ by using the ratio of CAL_z is the caloric equivalent of zooplankton (J g zooplankton⁻¹) to CAL_f is the caloric equivalent of fish (J g fish⁻¹).

A fixed energy density coefficient for zooplankton was adopted, with a value of CAL_z = 2,580 J g zooplankton⁻¹ for marine copepods (Laurence, 1976). The scientific interest in energy density of fish has lately increased due to its use in bioenergetics models. Improper or constant values can have misleading effects on model results (Stewart & Binkowski, 1986). In this work, we used a length-based energy density coefficient CAL_f for anchovy based on experiments. Particularly, Tirelli et al. (2006) showed that the energy density for *E. encrasicolus* exhibits a rather wide range from 2,667 to 7,022 J g fish⁻¹, following a linearly increasing energy density pattern for fish lengths between 40 and 90 mm and a more variable pattern for lengths >90 mm. Based on these measurements, the following average values were chosen

$$\text{CAL}_f = \begin{cases} 3120, & \text{if length} < 40 \text{ mm} \\ 3520, & \text{if } 40 \leq \text{length} < 60 \text{ mm} \\ 4048, & \text{if } 60 \leq \text{length} < 90 \text{ mm} \\ 5150, & \text{if length} \geq 90 \text{ mm} \end{cases} \quad (2)$$

As fish shows notable biological differentiations (feeding preferences, habitat selection, reproduction capacity and length–weight relationship) during its growth, anchovy's life cycle was divided into four different stages according to length: embryonic (egg + yolk-sac larvae) stage (<3.5 mm), larval (3.5–38.0 mm), juvenile (38–105 mm) and adult (105–165+ mm) stages (Table 1).

The duration of the embryonic stage was estimated by temperature-dependent curves calculated from laboratory experiments in the Adriatic Sea (Regner, 1996). These curves show an inverse relationship between developmental time (days) and temperature (°C). In the northern Aegean sea, the water temperature at which anchovy eggs are released favour a rather short embryonic duration of approximately

Table 1 Life stages of anchovy adopted in the bioenergetics model

Stage	Length (mm)	Age (days)
1. Embryonic	<3.5	0–5
2. Larval	3.5–38	6–76
3. Juvenile	38–105	77–364
4. Adult	105–165+	365–1,205

5 days, whilst the mean growth rate of larvae was estimated to approximately 0.5 mm day⁻¹ (Somarakis & Nikolioudakis, 2007). This means that anchovy larvae need almost 70 days in order to become juveniles. The juvenile stage lasts until anchovy reach maturity at approximately 105 mm total length with the completion of its first year of life (Somarakis et al., 2006).

The growth of anchovy reproduced by the bioenergetics model is calculated as wet weight per day. However, as anchovy's life stage definition is based on length, a length–weight relationship is required. Such relationship in fishes usually changes significantly at important ontogenetic thresholds such as metamorphosis (from larva to juvenile) and onset of sexual maturity (Fuiman & Werner, 2002). In anchovy, these thresholds occur at about 38 (Somarakis, 1999) and 105 mm (Somarakis et al., 2006), respectively. A standard length–weight relationship was calculated [$\log(\text{wet weight}) = a + b * [\log(\text{length})]$] using data from 120 larvae (length range: 3.1–21.2 mm) collected during June 1995–1996 (Somarakis, 1999), 605 juveniles (43–104 mm) collected during June 2007 (unpublished data) and 1,792 adults (105–157 mm) collected during 2006 in the north-eastern Aegean Sea (Somarakis et al., 2007). Indeed, these relationships had significantly different slopes ($b = 3.34, 3.00$ and 3.79 for larvae, juveniles and adults, respectively, F test = 217.72, $P < 0.0001$).

In order to obtain a relationship that could describe all three ontogenetic stages, a piecewise allometric regression was fitted to the data using non linear regression

$$y = b_0 + b_1x + b_2(x - d_1)(x \geq d_1) + b_3(x - d_2)(x \geq d_2), \quad (3)$$

where y and x are the fish wet weight and length, respectively (log-transformed), b_0 is the y -intercept, b_1 is the slope of the function for the larval stage, b_2 is the slope change for the juvenile stage, d_1 is the inflexion point at which the slope changes (fixed at 38 mm, i.e., $d_1 = \log[38]$), b_3 is the subsequent slope change for the adult stage and d_2 is the corresponding length for this slope change (fixed at 105 mm, i.e., $d_2 = \log[105]$) (see also, Somarakis & Nikolioudakis, 2007). Equation 3 with estimated parameters $b_0 = -6.1158$, $b_1 = 3.576$, $b_2 = -0.616$ and $b_3 = 0.7137$ (Fig. 2), explained the data very satisfactorily in terms of the amount of variance ($r^2 = 0.998$) and the

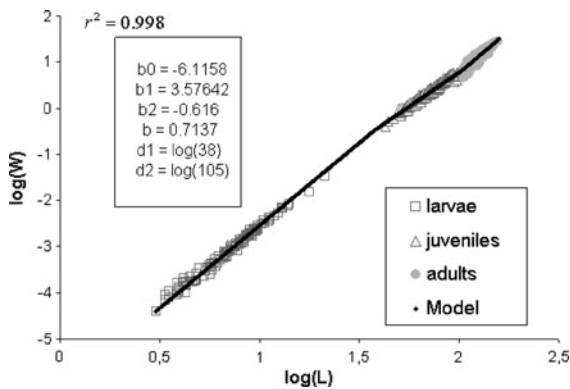


Fig. 2 Fitted piecewise allometric log-transformed relationship between weight in g (W) and length in mm (L), (3)

properties of the residuals (normally distributed, homoscedastic).

Due to the limited available data, values for *E. encrasicolus* from the Black Sea (Oguz et al., 2008) and for *E. capensis* from South Africa (James & Findlay, 1989; James & Probyn, 1989; James et al., 1989) were used for the parameterization of the growth model. However, it must be noted that according to recent studies concerning *E. capensis* (Huggett et al., 2003; Van der Lingen et al., 2006), *E. encrasicolus* and *E. capensis* must be considered as a single species (*E. encrasicolus*). Further data gaps were filled with parameter values from related species (Vasquez, 1989; Luo & Brandt, 1993; Rose et al., 1999) and NEMURO.FISH model (Ito et al., 2004; Megrey et al., 2007).

Consumption

Daily consumption rate (C) is described as the proportion of a maximum consumption rate C_{\max} modelled as a function of fish weight and water temperature:

$$C_{\max} = a_c W^{b_c} f_C(T), \quad (4)$$

where a_c is the maximum consumption rate of 1 g anchovy at the optimal temperature for consumption ($\text{g prey g fish}^{-1} \text{ day}^{-1}$), b_c is the exponent for the weight dependence of the consumption and $f_C(T)$ is a temperature-dependent function for consumption.

The adopted temperature-dependent function of maximum consumption, often used for warm water

species, was taken from Kitchell et al. (1997) using the auxiliary terms V , S , Y , X :

$$f_C(T) = V^X e^{X(1-V)}, \quad (5)$$

$$V = \frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} \quad (5a)$$

$$S = (\ln Q_c)(T_{\max} - T_{\text{opt}}) \quad (5b)$$

$$Y = (\ln Q_c)(T_{\max} - T_{\text{opt}} + 2) \quad (5c)$$

$$X = \frac{S^2(1 + (1 + 40/Y)^{1/2})^2}{400}, \quad (5d)$$

where T_{\max} is the maximum temperature for consumption (approximated by the upper lethal temperature), T_{opt} is the optimum temperature for consumption, Q_c is the slope estimate and T is the ambient temperature. Although this equation was originally applied to yellow perch and walleye, the function has been also applied to other warm water species (Luo & Brandt, 1993; Rose et al., 1999). The values of a_c and b_c in (4) are provided by Luo & Brandt (1993) and Oguz et al. (2008), respectively, (Table 2). The value Q_c in (5b–5c) was set to 2.2 for the larval stage (Luo & Brandt, 1993) and slightly increased to 2.4 for juvenile–adult stage in order to avoid underestimation of temperature limitation at low temperature values.

Studies in the northern Aegean Sea (Somarakis & Nikolioudakis, 2007) have shown that larval anchovies significantly prefer waters of high temperature (21.5–23.5°C at 10 m depth). Although we recognize that these observations are not directly associated with optimal consumption rates, it is acceptable to assume that optimal temperature T_{opt} for larval consumption lies within this range (set to 23°C, Table 2). Following the same argument as in Ito et al. (2004), for the determination of maximum temperature T_{\max} for larval stage (set 32°C in this study), a value higher than the maximum sea surface temperature reported in the northern Aegean Sea (29°C in Giannoulaki et al., 2008) was set. This is important in order to avoid underestimating consumption at higher temperatures.

Juvenile anchovies in the northern Aegean sea are generally found in shallow waters inhabiting depths around the thermocline (ANREC, 2006) with reported mean temperature for these depths, 17–18°C (Isari et al., 2008). Adult anchovy exhibit high feeding activity below the thermocline during

Table 2 Symbols, parameter identification, and parameters values used to implement the bioenergetics model (1) for anchovy (*Engraulis encrasicolus*) in the eastern Mediterranean

Symbol	Parameter identification	Parameter value
Maximum consumption (C_{\max}) (Eqs. 4, 5)		
a_c	Intercept for consumption	0.41
b_c	Exponent for consumption	-0.31
Q_c	Slope for temperature dependence	2.22 ^a , 2.4 ^{b,c}
T_{opt}	Optimum temperature (°C)	23 ^a , 17 ^{b,c}
T_{max}	Maximum temperature (°C)	32 ^a , 32 ^{b,c}
Respiration (R) (Eq. 7)		
a_r	Intercept for respiration	0.024
b_r	Exponent for respiration	-0.34
Q_{10}	Control parameter	2.22
T_m	Mean annual mean temperature	18 ^a , 15 ^{b,c}
Activity (A) (Eqs. 8, 9)		
d_r	Coefficient for R for swimming speed U	0.022
a_A	Intercept U (<12.0°C)	2.0
a_A	Intercept U (≥12.0°C)	12.25 ^a , 11.98 ^b , 14.21 ^c
a_A	Intercept U (≥12.0°C) (during low feeding activity)	9.97 ^c
b_A	Coefficient U for weight	0.27 ^a , 0.33 ^b , 0.27 ^c
c_A	Coefficient U vs. temperature (<12.0°C)	0.149
c_A	Coefficient U vs. temperature (≥12.0°C)	0.0
Egestion (F) (Eq. 10)		
a_F	Proportion of food egested	0.15 ^a , 0.126 ^{b,c}
Specific dynamic action (S) (Eq. 11)		
a_{sda}	Specific dynamic action coefficient	0.10
Excretion (E) (Eq. 12)		
a_e	Excretion coefficient	0.415
b_e	Proportion of food excreted	0.01
Egg production (EGG) (Eq. 13)		
a_{egg}	Proportion of consumption for reproduction	0.19
Multispecies functional response (Eq. 6b)		
v_{11}	Vulnerability of z6 to larval stage	0.5
v_{12}	Vulnerability of z6 to juvenile stage	0.0
v_{13}	Vulnerability of z6 to adult stage	0.0
v_{21}	Vulnerability of z5 to larval stage	1.0
v_{22}	Vulnerability of z5 to juvenile stage	0.5
v_{23}	Vulnerability of z5 to adult stage	0.5
v'_{23}	Vulnerability of z5 to adult stage (during low feeding activity)	1.0
v_{31}	Vulnerability of z4 to larval stage	0.0
v_{32}	Vulnerability of z4 to juvenile stage	0.5
v_{33}	Vulnerability of z4 to adult stage	1.0
K_{11}	Half-saturation constant for z6 to larval stage	0.035
K_{12}	Half-saturation constant for z6 to juvenile stage	0.4
K_{13}	Half-saturation constant for z6 to adult stage	0.3
K_{21}	Half-saturation constant for z5 to larval stage	0.035

Table 2 continued

Symbol	Parameter identification	Parameter value
K_{22}	Half-saturation constant for z5 to juvenile stage	0.15
K_{23}	Half-saturation constant for z5 to adult stage	0.082
K'_{23}	Half-saturation constant for z5 to adult stage (during low feeding activity)	0.082
K_{31}	Half-saturation constant for z4 to larval stage	0.3
K_{32}	Half-saturation constant for z4 to juvenile stage	0.025
K_{33}	Half-saturation constant for z4 to adult stage	0.072

^a Egg–larval stage

^b Juvenile stage

^c Adult stage

daytime, migrating to the upper layers (above the base of the thermocline) at dusk, just after the daily afternoon feeding peak, and remain in the warmer surface waters during the night (ANREC, 2006; Palomera et al., 2007). Giannoulaki et al. (2005) reported that during summer adult anchovy is positively associated with bottom depth temperatures of 14–16°C in the North Aegean Sea. Based on these observations, the optimum temperature for consumption of both juveniles and adults was set to 17°C, whereas the corresponding maximum temperature was set to 32°C. All related values are summarized in Table 2.

The curve of temperature dependence of C_{\max} for larval, juvenile and adult stages is a rising function up

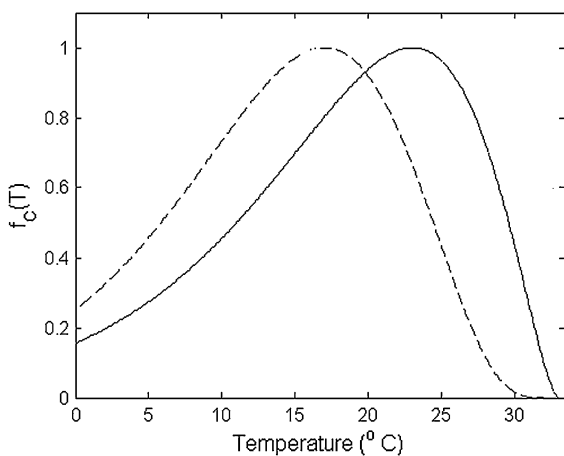


Fig. 3 Effect of temperature function (5) on consumption; larval stage (continuous line), juvenile–adult stages (dashed line)

to 1.0 at optimal temperature T_{opt} , then dropping to zero at a maximum temperature T_{max} (Fig. 3).

Realized consumption of an organism is modelled by a functional response equation which describes the relationship between available prey densities and those consumed by a predator. In the fish model, the daily consumption C of each life stage of anchovy (C_i , g prey g fish⁻¹ day⁻¹) is determined as the sum of its consumption rates for each prey type j through a type II functional response equation for multiple prey types (Rose et al., 1999; Megrey et al., 2007)

$$C_i = \sum_{j=1}^3 C_{ij}, \quad (6a)$$

$$C_{ij} = \frac{C_{\max}(\text{PD}_{ij}v_{ij}/K_{ij})}{1 + \sum_{k=1}^3 (\text{PD}_{ik}v_{ik}/K_{ik})}, \quad (6b)$$

where C_{\max} is the maximum consumption rate (g prey g fish⁻¹ day⁻¹), PD_{ij} the density of prey type j ($j = 1$ for heterotrophic flagellates, $j = 2$ for microzooplankton and $j = 3$ for mesozooplankton) (g prey m⁻³) to life stage i , v_{ij} the vulnerability of prey type j to stage i (dimensionless) and K_{ij} is a half-saturation constant (g prey m⁻³) for life stage i feeding on prey type j . Keeping to the terminology of ERSEM the three prey types are denoted in the model as z6 = heterotrophic flagellates, z5 = microzooplankton and z4 = mesozooplankton.

Although the abovementioned prey types are characterized as heterotrophic flagellates, microzooplankton and mesozooplankton in reality each type comprises a much wider range of organisms which have the same functional role defined mainly by the corresponding prey–predator relations. Thus, the

smaller prey size organisms ($j = 1$) includes not only heterotrophic flagellates, but also small ciliates and early life stages of bigger animals such as micro and mesozooplankton that forage on the same food source and are themselves preyed upon by the same predator. The second prey type the microzooplankton ($j = 2$) includes ciliates and metazoan zooplankton. The last prey type ($j = 3$) includes mainly mesozooplankton.

Apportioning the prey types, anchovy follows a size-selected pattern as it grows, selecting predominantly the largest prey particles through a biting feeding mode, whilst it uses a filter feeding mode on smaller prey sizes (Plounevez & Champalbert, 2000). Similar feeding behaviour has been shown for other *Engraulis* species (Hunter & Dorr, 1982). Although fish foraging can be rather complex it is reasonable to assume that there is a preference for particular organisms related to their size and shape and that under starvation fish will exploit other less preferred food sources.

Stomach content analysis in fish from various regions (Adriatic Sea, northwestern Mediterranean) (Conway et al., 1998; Tudela et al., 2002) shows that anchovy larvae target mainly copepod eggs, copepodites, and particularly nauplii. A recent study by Rossi et al. (2006) using fatty acids as trophic markers, indicated that small anchovy larvae also consume ciliates and flagellates that would not be detected in gut contents analysis. Hence in this application, anchovy larvae were assumed to feed mainly on prey type $j = 2$ ($v_{21} = 1.0$) and partially on the smaller $j = 1$ ($v_{11} = 0.5$).

With regard to juvenile stage, there is a lack of information on diet composition, so it is assumed that juvenile anchovy initially prey on microzooplankton and afterwards they can also exploit mesozooplankton. Thus, a partial vulnerability scheme (preference factor) has been adopted with juveniles exploiting mainly mesozooplankton ($j = 3$) ($v_{32} = 0.5$) and microzooplankton ($j = 2$) ($v_{22} = 0.5$).

Although the diet of adult fish is composed of large mesozooplankton prey items such as big copepods, other organisms such as mysids decapod larvae, fish-eggs and fish-larvae can be also found in their stomachs (Tudela & Palomera, 1997, 1999). In an attempt to represent the feeding behaviour of the adult anchovy, both biting and filter feeding modes were used. Thus, it is assumed that adults exploit big zooplankton ($j = 3$) using biting feeding, and at the

same time exploit smaller animals ($j = 2$) through filter feeding with a partial vulnerability ($v = 0.5$).

James & Findlay (1989) noted that filtering may be of importance for adult anchovy whenever there are no large particles or when feeding activity is low. Since Tudela & Palomera (1997) have noted that the feeding behaviour of *E. encrasicolus* is similar to the feeding behaviour of *E. capensis*, it is assumed that below a zooplankton threshold concentration of $z_{4th} < 0.1 \mu\text{molNI}^{-1}$, anchovy switches its feeding mode to filter feeding with complete vulnerability (1.0) on smaller microzooplankton. The choice of the threshold mesozooplankton value is chosen in way to avoid severe weight loss (more than 50%).

During the approximately 5 days embryonic stage the anchovy does not feed externally as it is nourished solely by its yolk reserves. As the increase in weight during the embryonic period is trivial, a fixed weight is considered.

Feeding half-saturation constants were calibrated during the implementation of the model in order to acquire correspondence between modelled and observed fish growth. Vulnerability constants were assigned according to the feeding preferences of anchovy's life stages described above. Values of vulnerabilities and half-saturation constants are presented in Table 2.

Since zooplankton densities in the LTL model are calculated in mol NI^{-1} they were converted to $\text{g wet weight m}^{-3}$ (in order to be compatible with the fish model energy rates) by multiplying with the term:

$$\frac{14\text{g N}}{\text{mol N}} \frac{1\text{ g dry weight}}{0.07\text{ gN}} \frac{1\text{ g wet weight}}{0.2\text{ g dry weight}} \frac{10^3\text{ l}}{\text{m}^3} = 10^{-6}\text{ g wet weight m}^{-3}.$$

Respiration

Respiration rate is modelled as an allometric function of body weight, water temperature and fish activity level:

$$R = a_r W^{b_r} f_R(T) A, \quad (7)$$

where a_r is the standard (with no motion) respiration rate of a 1 g anchovy at the optimal temperature for respiration and b_r is the exponent for the weight dependence of respiration. Since there are no laboratory data for respiration of *E. encrasicolus* the parameters a_r and b_r used by Oguz et al. (2008) in the

Black Sea were adopted. The $f_R(t)$ is a Q_{10} temperature relationship, $f_R(T) = e^{\frac{\log_e(Q_{10})(T-T_m)}{10}}$ with $Q_{10} = 2.22$ for all life stages (Rose et al., 1999) and annual mean depth-based water temperature T_m (set to 18°C for the larval stage at 0–40 m and to 16°C for other stages at 0–100 m of the water column) (Isari et al., 2008).

Term A is an activity parameter accounting for respiration due to increased metabolic costs and in particular swimming. The energetic cost of activity is an exponential function of swimming speed described by

$$A = e^{d_r U}, \quad (8)$$

where U is the swimming speed and d_r is an exponent for swimming speed given by James & Probyn (1989). Swimming speed (U) expressed in units of cm s^{-1} , depends on anchovy weight and temperature by the following equation:

$$U = a_A W^{b_A} e^{(c_A T)}. \quad (9)$$

Taking into account that the mean swimming speed whilst feeding in biting mode is 2.41 times the body length (James & Findlay, 1989) and using the weight–length relationship (3), values a_A , b_A for each life stage are estimated considering that the coefficient for temperature dependence of the swimming speed is zero ($c_A = 0$). When water temperature drops below 12.0°C a single value for a_A and b_A and c_A is adopted for all stages (Table 2).

In addition, *E. encrasicolus* regulates swimming speed according to prey sizes (Van der Lingen et al., 2006). The swimming speed is significantly lower in filter feeding mode (1.69 ± 0.591 body length s^{-1}) than in biting feeding mode since filter feeding energetic costs increase at rising swimming speeds (James & Findlay, 1989). In the model, an average value of 1.69 body length s^{-1} was chosen for the filter feeding mode below the previously defined zooplankton threshold. Sensitivity analysis tests were performed to evaluate the importance of swimming speed assumptions on fish weight.

Egestion

Egestion accounts for the portion of the energy of ingested material that is not assimilated and is released back to the environment as unused faeces

(Valiela, 1995). In the model, egestion is modelled as a direct proportion of consumption:

$$F = a_f C, \quad (10)$$

where C is the consumption, a_f is the proportion coefficient of egestion adopted from James et al. (1989). The latter authors estimated that 12.62% of the nitrogen (N) ingested from a zooplanktonic diet is not assimilated. In general, the assimilation efficiency is lower in larval clupeoids than in juveniles and adults due to immaturity of the digestive system (Blaxter & Hunter, 1982). For this reason, a slightly increased value for the larval stage was used, $a_f = 0.15$.

Specific dynamic action

SDA is a component of the total respiration, defined as the energy cost of assimilation and storage of products of digestion, in the deamination of amino acids and for the synthesis of nitrogenous excretory products (Tytler & Calow, 1985). SDA is considered as a constant proportion of assimilated energy

$$\text{SDA} = a_{\text{sda}}(C - F), \quad (11)$$

where a_{sda} is the SDA coefficient, C is the consumption rate and F is the egestion rate. A single value for all stages was adopted from Luo & Brandt (1993).

Excretion

Excretion (E) is a part of the energy budget that represents the elimination of nitrogenous products such as urea and uric acid (Valiela, 1995) and is described by a linear relationship related to the assimilated ration (James et al., 1989)

$$E = a_e(C - F) + b_e \quad (12)$$

The units of E adopted by James et al. (1989) are $\text{mg N g-fish}^{-1} \text{ dry wt}^{-1} \text{ day}^{-1}$ with parameter values $a_e = 0.415$, $b_e = 0.475$. Assuming that 1 mg wet weight of zooplankton contains 0.015 mg N (Gorsky et al., 1988) and considering that dry weight of anchovy is 32.01% of wet weight (Tudela & Palomera, 1999), excretion (E) can be converted to the current model units ($\text{g zooplankton g fish}^{-1} \text{ day}^{-1}$) with parameters: $a_e = 0.415$, $b_e = 0.01$. For the conversion the following term is applied:

$$\frac{\text{mg N}}{\text{g fish dry wt} \cdot \text{day}} = \frac{66.66 \text{ mg} - \text{zooplankton}}{3.124 \text{ g} - \text{fish wet wt} \cdot \text{day}}$$

$$\cdot \frac{1 \text{ g}}{1,000 \text{ mg}} = 0.021 \text{ g} - \text{zooplankton g}$$

$$- \text{fish}^{-1} \text{ wet weight day}^{-1}.$$

Egg production

The spawning of anchovy in the northern Aegean Sea starts in May, peaks in June and gradually decreases to September (Somarakis et al., 2006). Estimates of spawning frequency (the ratio of spawning females to all mature females) in June ranged from 0.34 to 0.44 (Somarakis et al., 2007), implying that reproduction occurs every 2–3 days, on average. According to the monthly evolution of the gonadosomatic index of anchovy in the Aegean Sea (Somarakis et al., 2006), it is assumed that spawning frequency is normally distributed, with spawning taking place every 4–5 days in July and almost every 5–6 days in May and August. This gives an estimated total number of 28 annual egg batches. It is also assumed that age 1 fish group starts to spawn later than older fish as they are not fully mature in May. Thus, 22 was set as the number of annual egg batches for age-1 class and 28 for age-2 and age-3 classes. Anchovy is considered to be an income breeder, which means that energy allocated to reproduction comes primarily from food intake, rather than from energy reserves (Somarakis et al., 2004). Therefore, in the bioenergetics model, EGG is assumed to be proportional to the consumption $\text{EGG} = a_{\text{egg}}C$. (13)

The mean wet weight of an anchovy egg was considered 27.7 μg (Somarakis, 1999). The batch fecundity Fec (mean number of eggs per mature female) generally depends on weight by a relationship of the form $\text{Fec} = f \cdot W$, where f is the numbers of eggs g female⁻¹. Setting $f = 450$, (Somarakis, 2005), the total daily number of eggs produced by each female becomes, $\text{Fec} = 450 \cdot W$.

The total daily weight of eggs, $\text{EGG}_{\text{weight}}$ (g egg day⁻¹) released per day, assuming an average spawning interval of 3.5 days, is

$$\text{EGG}_{\text{weight}} = 7.91 \mu\text{g} \cdot 450 \cdot W \quad (14)$$

Using the calorie content of egg, $\text{CAL}_{\text{egg}} = 5,600 \text{ J g egg}^{-1}$ (Valdés, 1993) and zooplankton CAL_z , the EGG is calculated

$$\text{EGG} = 3.56 \cdot 10^{-3} \text{ g} \frac{\text{CAL}_{\text{egg}}}{\text{CAL}_z}$$

$$= 0.0077 \text{ g zooplankton g fish}^{-1} \text{ day}^{-1}$$

Since the daily food ingestion (g-prey day⁻¹) of anchovy in the Mediterranean is estimated to approximately 4% of its wet weight (Plounevez & Champalbert, 2000), the daily consumption is $C = 0.04 \text{ g-zooplankton g-fish}^{-1} \text{ day}^{-1}$. Evaluating the ratio EGG to C , the coefficient, $a_{\text{egg}} = 0.19$ is estimated.

Sensitivity analysis

A number of sensitivity analysis experiments involving most of the bioenergetics model parameters were performed whilst the relative importance of input parameters to the model's performance was evaluated by using a traditional one-parameter-at-a-time analysis. Each parameter was separately varied $\pm 10\%$ and the simulation was rerun with one of the parameters changed whilst the others were kept at their nominal values. Parameters, such as optimum and maximum temperatures for consumption and respiration were varied by $\pm 1^\circ\text{C}$. Following, the change in model output between the standard simulation and the sensitivity outcome indicated the importance of each parameter.

More precisely, as a sensitivity measure, a sensitivity index $S_A(p_s)$ developed by Kitchell et al. (1997) and subsequently applied in several models (Stewart et al., 1983; Luo & Brandt, 1993) was used. The aim was to relate a change in an input parameter to a change in the growth output, as calculated by the model, subject to the new parameter value:

$$S_A(p_s) = \frac{\Delta A}{A_s} \cdot \frac{p_s}{\Delta p},$$

where p_s and Δp are the nominal and input deviation of parameter values, whilst A_s and ΔA are the nominal and output deviation response measure due to Δp . $S_A(p_s)$ was calculated as the normalized change in the output of the response measure for each change made in a model input parameter. If S is zero, A does not change with parameter p ; if the parameter

index is $S(A, p) = 1$ it means that a 10% change in parameter p_s causes a 10% increase in the output response, whilst if $S(A, p) = -1$, then a 10% change in p_s causes a 10% decrease in A . Simulated weight with $|S_A(p_s)| > 1$ demonstrates a high sensitivity to the parameter change, whereas values of $|S_A(p_s)| < 1$ indicate moderate to low sensitivities.

Design and analysis of simulations

In this application, the HTL model was one-way linked to the LTL. The averaged over the study area of Thracian Sea zooplankton biomasses simulated by the 3D POM-ERSEM model were used as forcing prey biomass for the fish model. The absence of high frequency temporal and spatial in situ data on biotic parameters does not allow a detailed validation of the model. However, measured values of key parameters during MATER (Mass Transfer and Ecosystem Response) and ANREC (Association of Physical and Biological processes acting on Recruitment and post-Recruitment of Anchovy) projects were compared against model results (Table 3). Considering the significant model uncertainties related to river and BSW nutrient inputs (climatological inputs are adopted) as well as the important horizontal variability characterizing the North Aegean area, results are reasonably close to measured values, particularly for lower heterotrophs and mesozooplankton.

LTL model results exhibit a phytoplankton spring bloom (not shown) with chlorophyll values around $0.27\text{--}0.3 \text{ mg m}^{-3}$. Since the ERSEM model does not directly parameterize migration of zooplankton, the vertical distribution of the zooplanktonic functional groups is related to food availability (Fig. 4). Thus, at the surface layers during spring when nutrients start becoming available small phytoplankton due to their favourable size, are the first to bloom initiating a parallel response from their predators (Fig. 5). As nutrients become more and more available and with small phytoplankton being controlled by predation, larger cells take over. Considering the wide difference between prey–predator growth rates for large phytoplankton–zooplankton there is a significant time lag and as a result the bloom continues. Eventually, the large zooplanktonic predators benefiting from the available food sources start to control both autotrophic and heterotrophic production.

As nutrients are used up and the system moves into summer with a stratified water column, primary production is confined close to the thermocline (50 m, see Fig. 5) where available light is combined with deep water nutrients. A similar pattern is exhibited by bacteria which are rather strong competitors to phytoplankton over nutrients.

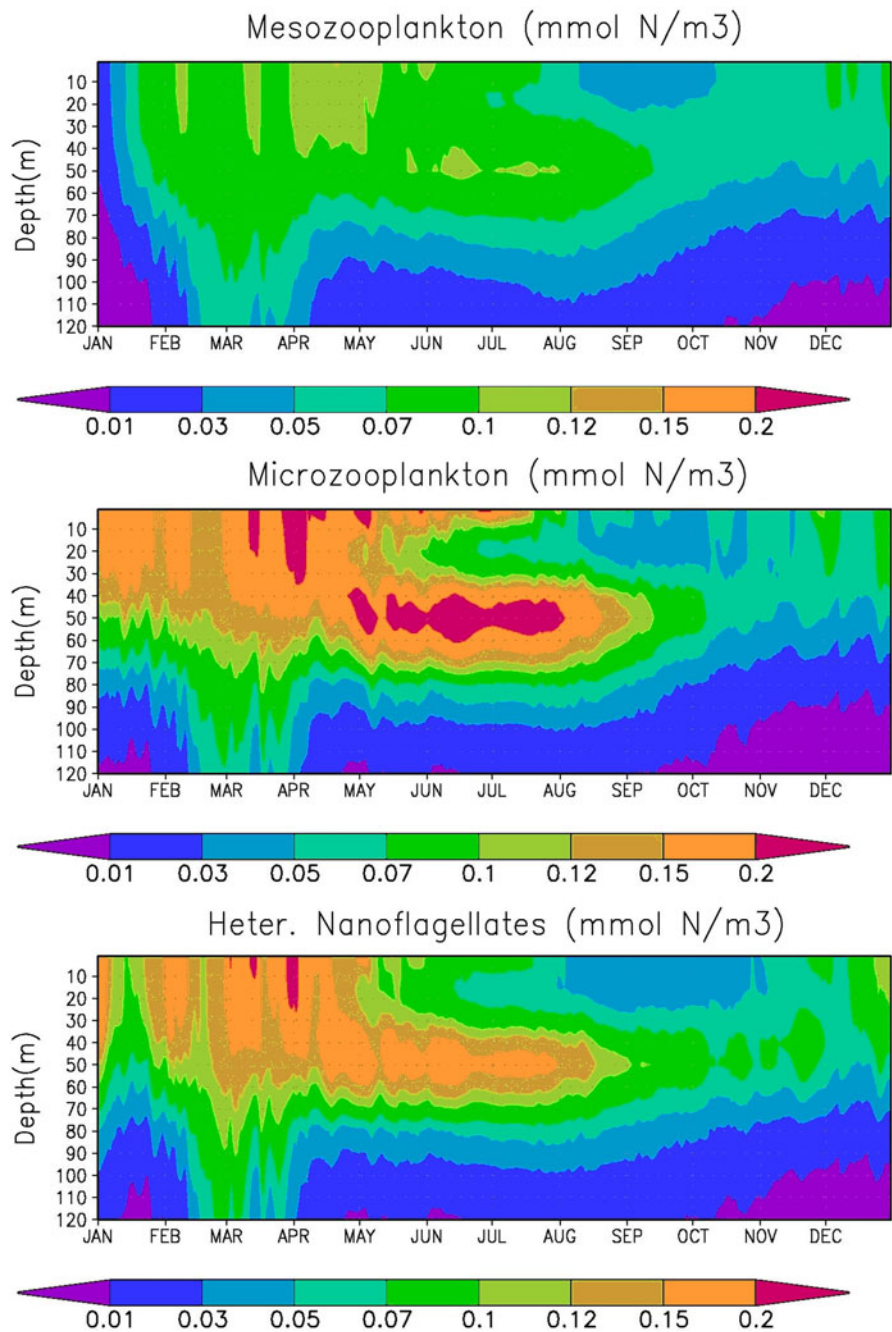
As mentioned before, since top down control is not taken into account by this modelling effort, the phytoplankton downward transport is also followed by all zooplankton groups. Considering that anchovy filter-feeds at the surface layers and exhibits particulate

Table 3 N. Aegean in situ parameters against model simulated monthly mean values, averaged over the sampling areas

MATER Siokou-Frangou et al. (2002)	March 1997		September 1997			
	In situ	Model	In situ	Model		
Phyto (mg C/m ²)	1,621 ± 426	2,605	1,072 ± 227	853		
Bacteria (mg C/m ²)	1,406 ± 327	984	1,471 ± 273	810		
Mesozoo (mg C/m ²)	424 ± 165	508	207 ± 38	266		
Heterotrophs (mg C/m ²)	1,847 ± 364	1,931	2,127 ± 225	2,054		
PP (mg C/m ² /day)	1,406 ± 362	816	253 ± 70	190		
BP (mg C/m ² /day)	48 ± 31	206	60 ± 11	90		
ANREC Isari et al. (2006, 2007)	July 2003		September 2003		July 2004	
	In situ	Model	In situ	Model	In situ	Model
Mesozooplankton (mg C/m ³)	3.44	4.50	1.90	3.06	5.60	3.80

The ANREC (Isari et al., 2006, 2007) sampling area almost matches the Thracian Sea area, indicated in Fig. 1, whilst MATER sampling stations (indicated as NA in Siokou-Frangou et al., 2002, Fig. 1) cover a much wider area

Fig. 4 Seasonal yearly variation of the zooplankton group biomasses derived from the 3D-LTL ecosystem model for depths 0–120 m, averaged over the Thracian Sea box area (as indicated in Fig. 1); mesozooplankton concentration, microzooplankton concentration and heterotrophic flagellates concentration

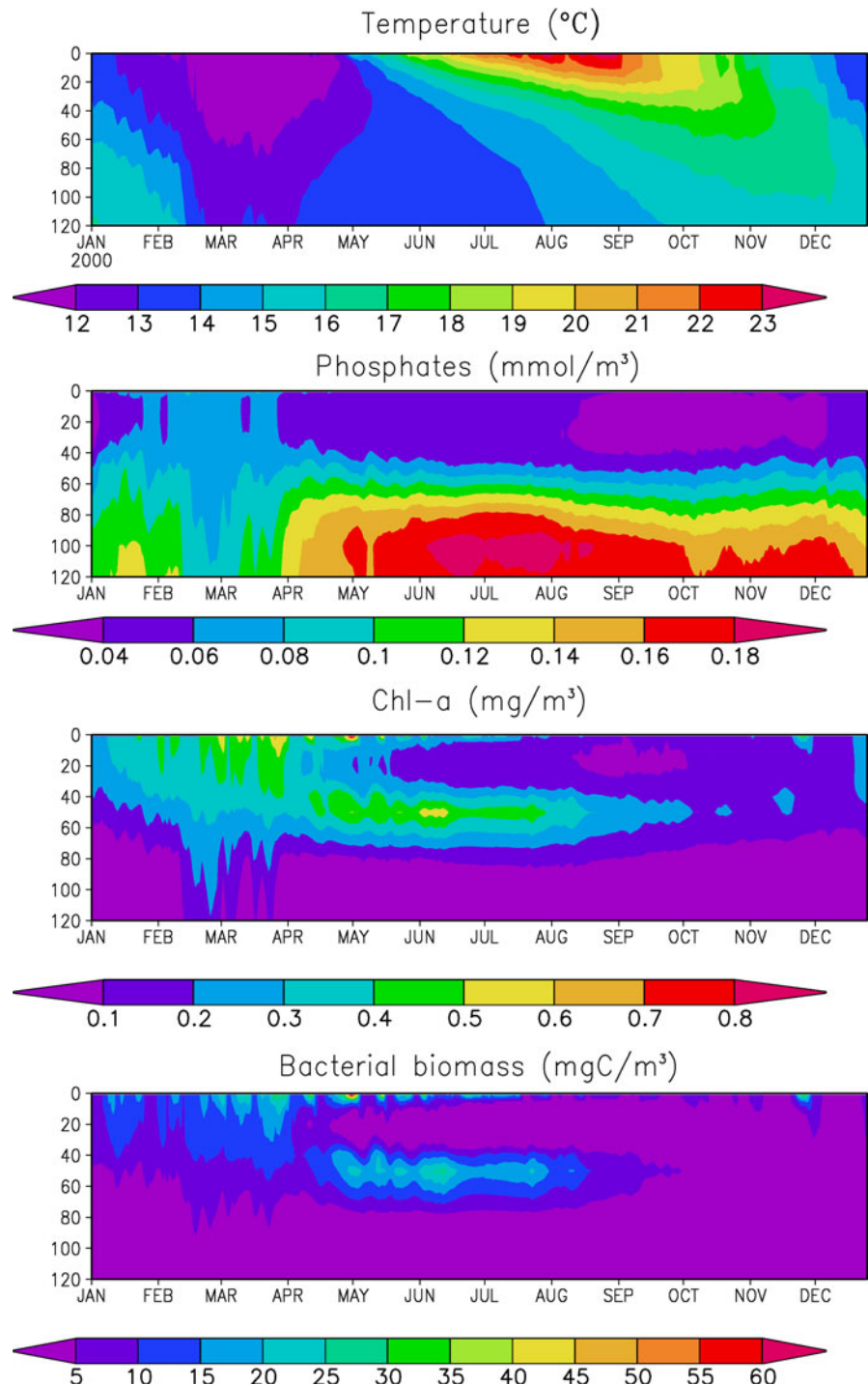


feeding at the thermocline, one would probably expect a vertical differentiation of zooplankton. As large animals cannot be taken up by filter feeding and smaller ones exhibit particulate feeding, they should be distributed at the surface layer and thermocline, respectively.

LTL-fish model linking assumptions

Anchovy experiences different depth histories throughout its life time according to its diurnal vertical migration pattern, the prey availability and the surrounding environment. Different fixed depth

Fig. 5 Seasonal yearly variation of selected variables derived from the LTL ecosystem model for depths 0–120 m; water temperature (°C), phosphate concentrations, Chl-*a* concentrations and bacterial concentrations



intervals in the water column were adopted for each life stage, following known anchovy habitat conditions. The maximum zooplankton concentration within this depth interval and the corresponding

mean temperature is then taken from the LTL model, assuming that anchovy prefer areas with maximum food availability. Since, the maximum value of each zooplankton type can be found in different depths

during the day, fish may experience varying temperatures. Thus, a mean daily temperature value of the water layers that the fish can visit according to its life stage was considered.

Analysing the habitat conditions for each life stage, as spawning takes place during night at the upper layers, anchovy larvae are generally surface distributed and restricted above the thermocline (0–20 m) (Palomera et al., 2007; Somarakis & Nikolioudakis, 2007). Thus, for the larval stage, zooplankton and water temperature values from the 0 to 20 m water layer are provided following the prescribed rationale. The available food from 20 to 40 m has been supplied to the juvenile stage based on the hypothesis that juveniles usually concentrate in shallow waters (mostly <50 m) inhabiting depths around the thermocline when waters are thermally stratified (ANREC, 2006; Tirelli et al., 2006). Adult anchovies accomplish diurnal vertical migrations, staying below the thermocline during daytime whereas during the night are scattered in the upper water column layers (Plounevez & Champalbert, 2000; ANREC, 2006). Therefore, for the adult stage,

prey availability and water temperature values are used from the 35 to 80 m layer during the day and from the 20 to 40 m layer during night to force the fish model. At the sensitivity analysis section, multiple simulations with different depth histories have been conducted to investigate a possible optimal trajectory for fish weight.

Model results

The simulated anchovy weight and length as fit to the mean weight and length estimates (○, ×) of age-1, age-2 and age-3 classes are shown in Fig. 6. Starting the model run at the 1st of June, model results show a moderate increase for age-1 class wet weight from June to December where anchovy passes through larval and juvenile stage (Fig. 6, upper panel). Pre-adult anchovy after a continuous growth from January to June reaches about 7.63 g weight and 107 mm length with the completion of the first year of life. At the start of age-2 class, fish manages to maintain its weight during the 3 month spawning season from June to September. After that, anchovy

Fig. 6 Simulated anchovy weight (*upper panel*) and length (*lower panel*) of anchovy, as fit to available weight-at-age and length-at-age estimates (○) (Machias et al., 2000; ANREC, 2006; Somarakis & Nikolioudakis, 2007). For further comparisons, observations (×) from other Mediterranean areas (western and central Mediterranean) are also shown (Pertierra et al. 1997; Basilone, 2004, 2006)

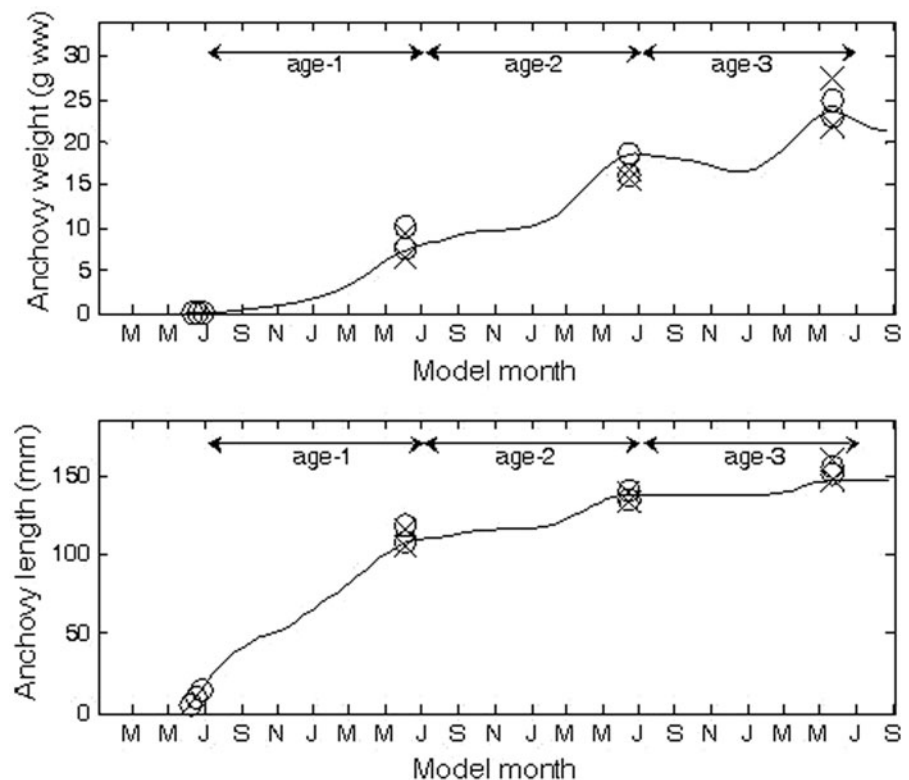


Fig. 7 Monthly variation of the mean growth rates (g ww/day)

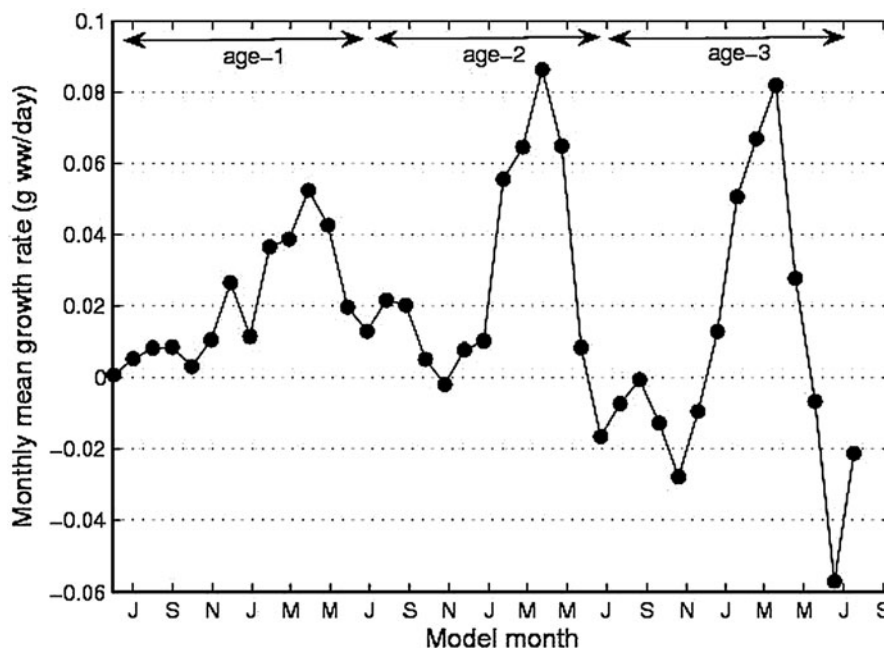


Table 4 Mean values for two seasonal periods for zooplankton groups as calculated from the zooplankton profile of Fig. 4

	Mean values for March–July	Mean values for August–December
Mesozooplankton	0.084	0.049
Microzooplankton	0.138	0.068
Heter. flagellates	0.118	0.054

The averaged values were estimated from depth 0 to 80 m

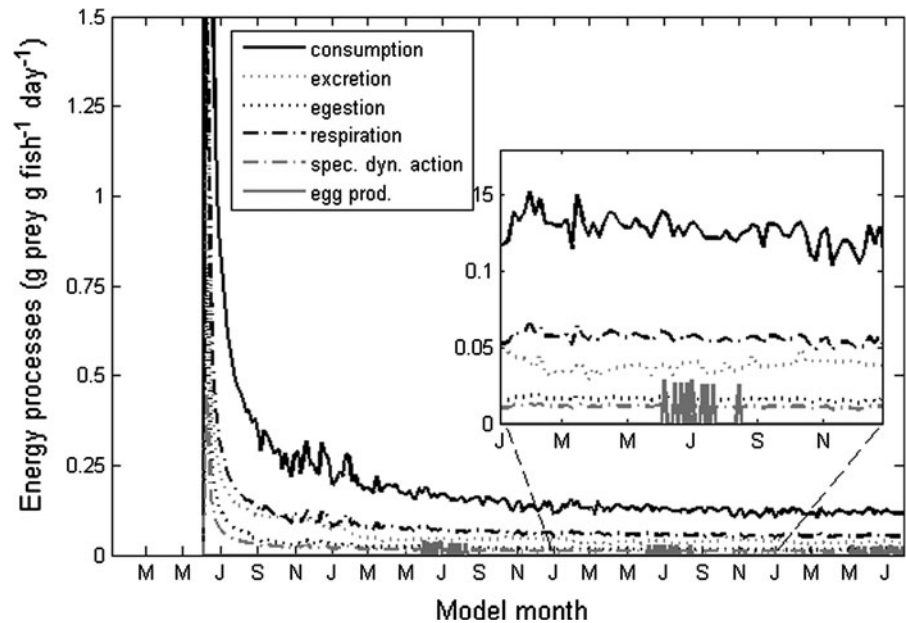
exhibits a slow growth rate ($0.0062 \text{ g ww/day}^{-1}$) from August to December (Fig. 7). In spring bloom season, anchovy grow again rapidly. At the end of the second year, anchovy weight is 18.6 g and its corresponding length is 137.4 mm. The age-3 class is characterized by a negative average growth rates (Fig. 7) which occurs mainly after the end of the second spawning activity period from August to December causing a 7.62% reduction on weight. On the contrary, anchovy weight follows a rapid average growth rate ($0.05073 \text{ g ww/day}^{-1}$, Fig. 7) in spring where fish is reaching the weight of 23.84 g and length 147.3 mm at the end of third year. Model run indicates that anchovy weight for age-3 fish increased 25.83% for the period of March–June. The corresponding mean monthly growth rates for this period are increased 0.05–0.08 (Fig. 7).

The variation of mean values for the three zooplankton groups during March–July and September–January periods are shown at Table 4. We point out the 41.7% reduction of mesozooplankton and 50.7% of microzooplankton values during August–December period compared to March–July period.

Maximum growth rates are realized during spring when zooplankton densities are highest. On the other hand, the decrease of zooplankton levels from August to December (Fig. 4, Table 4) induces a similar decrease in the anchovy growth rate that is followed by a decrease in the fish weight. Juvenile weight remains almost static during September–October, whereas in older fish (especially in age-2+ and age-3+ class), weight starts to decrease immediately after the end of the summer spawning season. These results can be attributed to the low zooplankton abundance levels influencing anchovy consumption rates. Activity respiration is an important component of the model, increasing the energy demands for the older ages especially during summer–autumn warmer periods.

When analysing model results, a prominent characteristic is that the most significant term in the bioenergetics model is consumption which is closely coupled to zooplankton density, following its variation. Thus, highest consumption levels are reached

Fig. 8 Simulated energy processes: consumption (black-solid), respiration (black, dash-dot), excretion (grey-dot), egestion (black-dot), specific dynamic action (grey, dash-dot) and egg production (grey-solid)



during spring and are reduced from August to December (Fig. 8).

In addition, temperature also plays an important role in consumption especially during winter where anchovy growth rates were often negative at the highest water temperatures, increasing both consumption and respiration processes (there is a greater effect on the latter).

The model consumption rate (Fig. 8, black line) can be expressed as percentage of anchovy weight increase per day by multiplying to CAL_z/CAL_f ratio (Eq. 2). This gives an annual mean daily consumption rate of 6% for the adult anchovy which lies in reasonable agreement with the estimates (3.6–3.9%) of Plounevez & Champalbert (2000) for daytime consumption.

Sensitivity results

The sensitivity measure $S_A(p_s)$ at 1st of June for the yearly weight outputs age-1, age-2 and age-3 classes were calculated by varying each parameter with $\pm 10\%$, as mentioned above (Table 4). Temperature inputs of $\pm 1^\circ\text{C}$ for consumption and respiration were changed separately for each life stage.

The intercept for maximum consumption (a_c), the standard respiration (a_r), the exponents for weight dependence of consumption and respiration (b_c) and

(b_r) and the proportion of excretion (a_e) had the highest overall sensitivities. As shown in Table 5, variations of the above parameters result in a net increase of ~ 5 g fish weight. On the other hand, the proportion of flagellates ($z6_{var}$), the intercept a_A (larval) and proportion of energy allocated to reproduction (a_{egg}) displayed the lowest sensitivities (Table 5). A general feature common to the majority of simulations is that the maximum sensitivities for various parameters were noted for older ages. High priority should be given to better estimates of the most sensitive parameter for future improvements in the model.

Moderate sensitivities of the $z4_{var}$ and $z5_{var}$ parameters indicate that microzooplankton and mesozooplankton changes of 10% are low and do not have a significant effect on anchovy weight. However, the sensitivities of prey density depend on the choice of the value of the half-saturation constants. Sensitivity of zooplankton caloric content affected the annual growth by 12% for young age-1. Also, it is important to note that the adjusted half-saturation parameters exhibited a high sensitivity measure on yearly anchovy growth.

Evaluation of the temperature parameters T_{opt} , T_{max} and T_r sensitivities on fish growth, showed that T_{opt} and T_r in the adult stage exhibited the highest sensitivity on age-2 and age-3 (Table 6). In general,

Table 5 Summary of sensitivity measures $S_A(p_s)$ for model parameters used to simulate yearly weight (1st of June) of anchovy for age-1, age-2 and age-3 classes

Parameters	Weight (age-1)		Weight (age-2)		Weight (age-3)	
	+10%	-10%	+10%	-10%	+10%	-10%
a_c	5.78	-4.31	7.33	-5.68	7.49	-6.02
b_c	-0.48	0.41	-3.10	5.53	-3.96	7.86
Q_c	-0.60	0.67	-0.49	0.65	-0.47	0.64
a_r	-2.91	7.71	-3.96	10.91	-4.26	11.40
b_r	-0.09	-0.33	2.53	-3.04	3.81	-3.96
Q_r	0.18	-0.25	0.26	0.90	0.28	-0.34
a_f	-0.06	0.09	0.01	0.05	0.03	0.03
d_r	-0.90	1.07	-1.77	2.25	-2.11	2.83
c_A	-0.12	0.12	-0.13	0.16	-0.15	0.17
$z4_{var}$	0.67	-0.69	0.09	-0.17	-0.10	0.01
$z5_{var}$	0.33	-0.23	0.56	-0.48	0.60	-0.55
$z6_{var}$	0.15	-0.11	0.06	0.00	0.04	0.02
a_{sda}	-0.93	1.16	-1.22	1.41	-1.28	1.46
a_e	-3.00	4.11	-3.87	5.30	-4.07	5.54
b_e	-0.49	0.52	-0.93	1.05	-1.11	1.27
a_{egg}	0.00	0.00	-0.09	0.09	-0.16	0.16
a_A (larval)	-0.05	0.03	-0.01	0.01	0.00	0.00
a_A (juvenile)	-0.84	0.92	-0.20	0.22	-0.06	0.06
a_A (adult)	0.00	0.00	-0.87	0.93	-1.15	1.28
CAL_z	1.14	-1.13	0.66	-0.73	0.30	-0.37

The model was run and parameter values were changed by $\pm 10\%$ of their nominal values. Parameter values are defined in Table 2

$z4_{var}$ proportion of mesozooplankton variation $z4$, $z5_{var}$ proportion of microzooplankton variation $z5$, $z6_{var}$ proportion of flagellates variation $z6$, a_A (larval) intercept of swimming speed for larval stage (particulate feeding), a_A (juvenile) intercept of swimming speed for juvenile stage particulate feeding), a_A (adult) intercept of swimming speed for adult stage (particulate feeding), CAL_z energy density of zooplankton

temperature parameters (T_{max}) had a low sensitivity measure for changes of $\pm 1^\circ\text{C}$.

Sensitivity results not only provided significant information on the relative importance of the various parameters on the models performance, but also illustrated the need for experimental data, especially focusing on the optimal temperature parameter for juveniles and adults.

The importance of swimming speed and feeding behaviour alterations of adult stage during the low feeding period were examined by performing two

Table 6 Estimation of sensitivity measure $S_A(p_s)$ for temperature-related parameters on yearly end-point of anchovy weight (1st June) for age-1, age-2 and age-3 classes

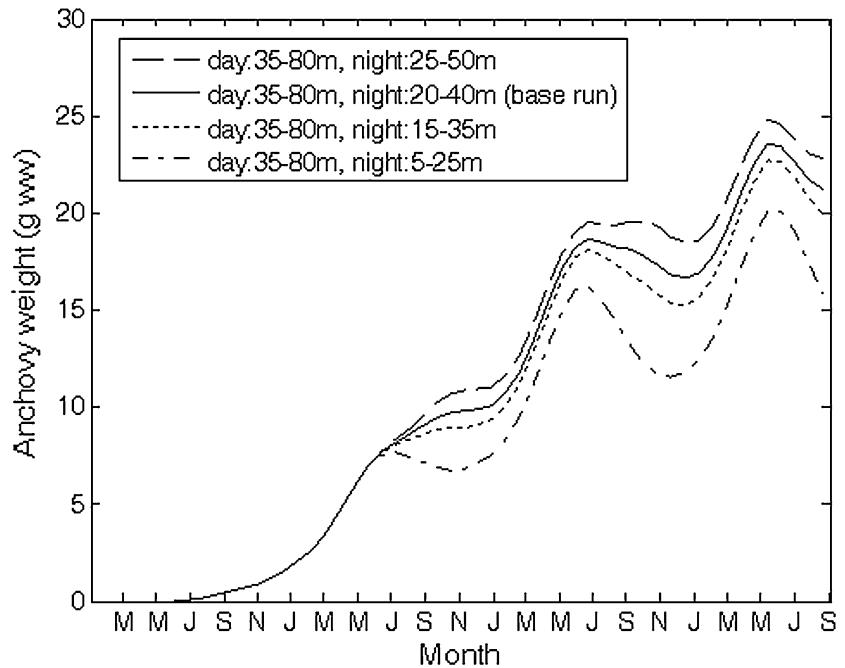
Parameter	Weight (age-1)		Weight (age-2)		Weight (age-3)	
	+1°C	-1°C	+1°C	-1°C	+1°C	-1°C
T_{opt} (larval)	-0.24	0.30	-0.05	0.09	-0.02	0.02
T_{opt} (juvenile)	-2.24	1.56	-0.56	0.37	-0.15	0.11
T_{opt} (adult)	0.00	0.00	-2.19	1.37	-2.65	1.67
T_r (larval)	0.37	-0.24	0.10	-0.04	0.03	-0.01
T_r (juvenile)	4.20	-3.67	0.96	-0.95	0.25	-0.27
T_r (adult)	0.00	0.00	5.09	-4.34	5.63	-5.29
T_{max} (larval)	0.02	-0.03	0.03	0.01	0.01	0.01
T_{max} (juvenile)	0.02	-0.03	0.02	0.01	0.01	0.01
T_{max} (adult)	0.02	-0.03	0.02	0.01	0.01	0.01

The model was run with parameter values changed by $\pm 1^\circ\text{C}$ of the nominal value. The optimal and maximum temperature sensitivities of consumption and respiration processes are combined with larval, juvenile and adult stage

more experiments. In the first experiment, it was assumed that the vulnerability on microzooplankton $z5$ remained partial ($v_{23} = 0.5$) for all periods of growth. This assumption caused an extra reduction on anchovy weight up to 22% for older age classes. In the second experiment, holding the filter feeding related swimming speed to levels associated with the biting feeding mode resulted in an annual fish growth decrease of up to ~ 6 g fish (37%).

Finally, several simulations were conducted with different depth histories for the adult stage only, as larval and juvenile stage depth histories indicated no significant sensitivities. In this sensitivity test, the aim is to investigate how the depth-based habitat selection of anchovy affects its weight. Thus, prey availability and water temperature values were provided to the adult stage from selected depth intervals following the diurnal movements. The multiple weight trajectories for the several depth ranges are shown in Fig. 9. The simulations indicate no significant differentiations for the various trajectories during the period March–July. On the contrary, during the summer–autumn stratified period, weight decreases more rapidly as anchovy shifts to shallower layers (Fig. 9: 5–25 m during night; dashed dotted line). The specific depth selection is associated with food availability but also with warmer temperature values. As primary production and consequently

Fig. 9 Weight simulations for selected depth histories during daytime. Following the adult's diurnal movements within its habitat conditions, the different lines represent the ensemble of weight trajectories in association with the base run (*solid line*) after providing the adult stage with zooplankton and water temperature values from the depths indicated in the legend



zooplankton shift to deeper layers (Figs. 4, 5), the trajectory with the deeper depth range (Fig. 9: 25–50 m during night; dashed line) appears as the most favourable concerning anchovy weight. The seasonal variability of temperature also has an impact on fish growth as lower temperature values noticed for 25–50 m during summer–autumn (Fig. 5) have a positive effect on anchovy weight. Regarding the relation of anchovy distribution with hydrographic regimes, Giannoulaki et al. (2005) indicated a higher probability of occurrence for anchovy in deeper surface and upper mixed layers showing no especial selection for warm waters. This argument seems to coincide with our model behaviour. However, more experiments are required to support these assumptions.

Discussion

The northern Aegean Sea is an important area with great scientific interest attracting studies on oceanography, ecology and fisheries. In this article, a bioenergetic model was one-way linked with the LTL ecosystem model (POM–ERSEM) integrating biological information of anchovy with environmental factors for the northern Aegean area. The

bioenergetics model has successfully simulated the weight of European anchovy indicating a seasonal evolution with stationary or negative variation mainly during autumn. Seasonality in weight and length has also been noticed for anchovy in an effort to link the fish resources with environmental conditions in the Bay of Biscay (Pecquerie et al., 2009) and Black sea (Oguz et al., 2008). The spawning activity of anchovy in Aegean Sea did not cause a negative growth rate on anchovy weight, implying that the increased zooplankton levels from March to August in the Aegean sea, which coincide with the spawning period, are adequate to support the reproduction energy demands. In case of age-2 and age-3 classes, fish weight continued to increase during reproduction period although the growth rates were smaller (Fig. 4). This seems to be in consistence with anchovy's reproduction strategy to spawn during the period of maximum prey production (Somarakis et al., 2004). In addition, Wang & Houde (1994) showed that *Anchoa mitchilli* mean weight increased during the spawning season by 26%. Another notable feature from the model's sensitivity performance is the importance of the two feeding modes. The alternations from bite to particulate feeding with a parallel reduction in swimming speed during low prey levels,

possibly is an adjustive behaviour of anchovy in order to maximize energy gains and avoid starvation. However, direct observations of such fish behaviour are particularly difficult. James & Findlay (1989) indicated a lower swimming speed of Cape anchovy during filter feeding compared to bite-feeding, which is consistent with our model results. However, similar studies on other species show either lower (Batty et al., 1990) or higher (Pepin et al., 1988; Gibson & Ezzi, 1992) swimming speed during filter feeding.

From the overall study of the model, we note that the biomass of zooplankton prey is a dominant factor in the anchovy bioenergetics' response. Simulated weight showed fastest growth rates during spring and slower growth during autumn following the variation of zooplankton prey availability. In addition, growth was fairly sensitive to temperature-dependent parameters. In the model, the caloric content of zooplankton was assumed to be fixed and the caloric content of anchovy was assumed to depend only on the life stage. However, in natural conditions, seasonal variation of the caloric content of both fish and zooplankton may play an important role in influencing fish weight (Stewart & Binkowski, 1986).

It must be noted that estimates of mean size-at-age in the Mediterranean (including the western and central Mediterranean, see Fig. 6) are relatively higher than similar values available from the Black Sea (Oguz et al., 2008 and references therein). This can be explained in terms of genetic differences (the Black Sea anchovy stock is genetically distinct from Mediterranean stocks, e.g. Magoulas et al., 1996) and lower sizes-at-maturity of the Black Sea anchovy. It has been reported that young-of-the-year, 55–65 cm in length, and 1.2–2.4 g in weight, i.e. two–three months old anchovy, may spawn towards the end of the spawning period in the Black Sea (Lisovenko & Andrianov, 1996). In contrast, in most areas of the Mediterranean, anchovy matures at around 11 cm, with the completion of the first year of life (Somarakis et al., 2004).

Due to the lack of adequate field observations and laboratory experiments for the European anchovy in the Mediterranean, a number of model parameters concerning energy processes were adopted from related species. Although significant effort was directed to minimize this, it is possible that uncertainties were introduced into the model results by these assumptions. New research is needed on those

parameters that have major effects on fish growth as indicated from the sensitivity analysis. This will help to increase the reliability of the existing models and to the development of more complex simulation tools. Another important consideration in this study is that the half-saturation constants were adjusted in order to fit model results to observed values. Therefore, independent data is needed to completely validate the model without reliance on the observed wet weight values. Particularly, data on observed consumption rate would significantly add to the model consistency. As mentioned above pinpointing knowledge gaps, hopefully will contribute towards targeted future research (field and laboratory) which will ultimately help the development of more robust models.

Model set up was also exposed to the uncertainty concerning the linkage of the LTL to the fish model. Due to its one-way link, the zooplankton biomasses are not reduced by anchovy predation, so there was no feedback into the dynamics of ERSEM. The importance of two-way linkage has been emphasized as a necessary step towards a dynamic interaction of the ecosystem components (Travers et al., 2007). For this reason, a study to include the perspective of a two-way coupling with the LTL model is the main priority for future work.

The implementation of the anchovy model demonstrates that NEMURO.FISH type bioenergetic models are sufficiently general to be considered as useful tools for the understanding fish growth in relation to environmental parameters and LTL forcing. The present work has to be considered as the beginning for the development of a broader model scheme that describes the full life cycle of anchovy in the three-dimensional space. The incorporation of a population dynamic model by including reproduction and mortality (natural and fishing) processes and the link with an IBM model in the framework of a spatially explicit 3D scheme will allow simulations of the entire anchovy stock providing a useful tool to examine the impact of climate change on the HTLs of the marine ecosystems (Megrey et al., 2007; Travers et al., 2007). This work is in progress and will be published elsewhere.

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