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Modelling growth of larval anchovies including diel feeding patterns, temperature and body size

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A reliable representation of physiology in models of larval fish is essential to understand how environmental factors affect growth rates. In particular, individual-based models of larval fish typically contain detailed bioenergetic modules that couple energy intake, temperature and body conditions to growth. These modules rely on experimental studies for their formulation and parameterization, although for many species this information is still scattered and a constraint to model development. Here, we develop a bioenergetic model including gut flow, assimilation efficiency and metabolic costs of Engraulis mordax larval anchovy based on available experimental work and field observations, and use it to investigate individual growth under different daily feeding rations and frequencies, and temperature. At satiated feeding and similar temperature-conditions, the model predicts growth rates comparable to field estimates of E. encrasicolus (but higher than observed for E. japonicus), suggesting E. encrasicolus grow near their physiological, temperature-limited rates in the field.

INTRODUCTION

In many upwelling ecosystems, anchovy or sardine are the main predators on zooplankton (Bakun, 1998) connecting lower and higher trophic levels (Cury *et al.*, 2000). Due to the high fishing pressure on anchovy (Palomera *et al.*, 2007) and low stock recruitment in some places (Uriarte *et al.*, 1996), many studies have focused on developing individual-based models (IBMs) in order to understand how physical or biological factors affect larval anchovy survival (Mullon *et al.*, 2003; Parada *et al.*, 2003; Allain *et al.*, 2007).

These models require algorithms for growth processes. Growth can be formulated quite simply as a function of ingested energy or matter, or it can be developed into a detailed bioenergetic account of physiological processes (Kristiansen *et al.*, 2007; Peck and Daewel, 2007). Growth in larval fish is particularly difficult to model, as they develop quickly and associated fundamental growth parameters change with age (Kiørboe, 1989). In addition, growth is a variable that can be influenced by individual fish behaviour, such as habitat selection (warmer waters, more prey) and ingestion rates (prey search activity), which are often traded off against survival probability (Fiksen *et al.*, 2007; Vikebø *et al.*, 2007). An important element of bioenergetic modelling is to define the scope that any particular individual has for growth, and how behaviour affects growth rate. Models which include gut fullness as a state variable are a convenient way to incorporate both constraints (Peck and Daewel, 2007), feeding history and behaviour (Lough *et al.*, 2005; Kristiansen *et al.*, 2007). Gut fullness, in particular, as a state variable is important in larvae with high gut turnover rates, as in anchovies. Explicit representation of the gut enable studies of how environmental grain or patchiness of prey influence growth processes and behaviour. A detailed physiological model has not been developed for anchovy

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larvae, but in this study we use available laboratory studies to develop an IBM.

Here we develop a model of growth processes in larval anchovy, based mainly on information from the Northern anchovy *Engraulis mordax*. In the past, *E. mordax* was a popular experimental organism, cultured to understand their growth (Kramer and Zweifel, 1970; O'Connell and Raymond, 1970; Lasker *et al.*, 1970), physiology (Theilacker, 1987), feeding success and swimming behaviour (Hunter, 1972, 1977), the capacity to sustain starvation and the size vulnerability to predation (Folkvord and Hunter, 1986). Methot and Kramer (Methot and Kramer, 1979) found similar growth rates in field-caught and in cultured, food satiated larvae in the same temperature domain. Håkanson (Håkanson, 1993) studied their nutritional condition and their growth in the California current. These studies provide a rich source of information which can be used to formulate and calibrate the model.

The model includes day length as an environmental input parameter influencing larval foraging, body size and gut fullness (state variables). We explore the model with a sensitivity analysis. To validate the model, we compare laboratory and field data with growth rates from the model at different ingestion rates, temperature and day length (foraging period). The model is developed to quantitatively assess how ingestion rates, temperature and day length (feeding intervals) affect larval anchovy.

METHOD

General structure of the model

The model simulates growth of larval anchovy from basic biological principles, using existing experimental work for calibration. Larval state variables include body mass (or length) and gut fullness in units of dry mass (Fig. 1). The growth potential, or growth when food is supplied in excess, is derived from empirical observations over the temperature range from 13 to 22°C for larvae between 4 and 8 mm. The model runs with hourly time steps.

Our model of gut flow is simple and similar to the one used by Kristiansen *et al.* (Kristiansen *et al.*, 2007) for larval cod. Growth depends on digestive and metabolic processes, body size and temperature. The philosophy of our approach is that experimentally, one can determine accurately the food-satiated growth *potential* under various temperatures. The growth potential reflects long-term selection pressures on optimal growth rates (Folkvord, 2005), and as long as ingestion rates are high, the larvae will grow at these rates [equation (2)]. This is a simple and accurate physiological constraint on growth rates, which is necessary to avoid "overfeeding" (Peck and Daewel, 2007).

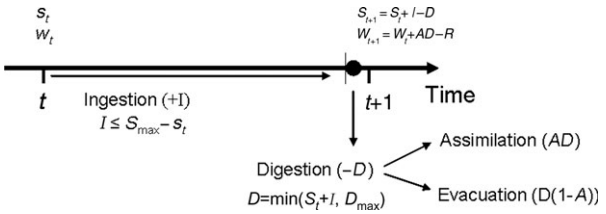

Fig. 1. The representation of the gut flow (Kristiansen *et al.*, 2007) between time step t and $t+1$, with the state variables gut fullness (s_t) and body weight (w_t). The gut fullness at the end of a time step s_{t+1} depends on the gut fullness s_t at the beginning of the time step and on the ingested I and digested D mass during the time step t. The maximum ingestion per hour is limited by gut capacity [S_{max}, equation (3)]. If the stomach content is more than that required for the maximum growth rate, then not all the stomach content is digested [equation (1)] because the maximum mass digestion depends on temperature (through g and R, see Kristiansen *et al.*, 2007): $D_{max} = (gw + R)/A$, where g is the growth potential [equation (9)], R metabolic cost [equation (6)] and A assimilation efficiency [equation (5)].

Within each time increment, the gut fullness, s_t (μg), is first filled as a result of ingestion, I (μg), and then reduced due to digestion (Fig. 1). The relationship between growth and ingestion is then simply a matter of mass balance (Kristiansen *et al.*, 2007). Body mass is updated every hour, and food entering the gut is assumed to be available for digestive processes immediately. If the stomach content after ingestion (s_t+I) (Fig. 1) does not sustain maximum growth rate and respiration then all mass in the gut is digested, otherwise digestion is limited by temperature, D_{max}. Then digestion can be expressed as:

$$D = \min(s_t + I, D_{max}) \quad (1)$$

D_{max} (μg) equals the mass required to sustain the maximal growth potential (respiration included) in each time step (Fig. 1) (Kristiansen *et al.*, 2007). If the mass digested does not sustain maximum growth and respiration, growth is reduced from the maximum rate and becomes negative under low gut fullness. Then the growth in mass in each time step is expressed as (Kristiansen *et al.*, 2007):

$$\frac{dw}{dt} = DA - R \quad (2)$$

Here R is the routine respiration rate, A the assimilation efficiency (see below), D the digestion, w the dry weight of the larva and t the time.

For the derivation of growth potential (g), we assume that anchovy larvae do not feed in darkness (Conway *et al.*, 1998) and rapidly evacuate gut contents (Theilacker, 1987). Therefore, biomass accumulation takes place during daylight hours, and the scaling of this process from field and laboratory data has to take day length into account.

Bioenergetics

We have adapted the bio-energetic model of larval cod described in Kristiansen *et al.* (Kristiansen *et al.*, 2007) to anchovy larvae using the laboratory experiments by Theilacker (Theilacker, 1987). In the experiments by Theilacker (Theilacker, 1987), larvae of *E. mordax* were maintained in tanks at a constant temperature (15.5°C) and photoperiod (12 h/12 h) under various conditions of prey type and prey concentration. The initial prey at an age of 3 days was a naked dinoflagellate of ~50 μm diameter, and 2 days later the larvae were fed with larger prey items, rotifers from 74 to 159 μm width and between 0.1 and 0.47 μg dry weight. We used the results of Theilacker's experiments with 2 (second experiment) and 25 (third experiment) rotifers/mL during 14 days to parameterize assimilation efficiency and standard metabolism.

The gut capacity ($S_{\max}$) is the maximum amount of food (mass) in the gut in fractions of body mass. The gut capacity of a larva with body mass w (μg) is determined from the data (Fig. 2) on maximum consumption $C_{\max}$ (μg) in Theilacker (Theilacker, 1987):

$$S_{\max} = \frac{C_{\max}}{w} = 0.04 + w^{-1.00745}, \quad (n = 6, \mathrm{SE} = 0.0174) \tag{3}$$

The minimum value observed by Theilacker (Theilacker, 1987) is 0.045 and we assume gut capacity approaches 4% with increasing size. In larval cod, the gut capacity is 5–6% (Lough *et al.*, 2005). Note that this is in terms of prey dry mass in the gut relative to larval dry body mass, valid for the particular prey type used in the experiment. In addition, the model assumes that the upper ingestion limit of the larvae is the gut capacity ($I \leq S_{\max} - s_l$), because the data available suggest that an anchovy larva needs about 2 h to fill the gut (Theilacker, 1987).

Assimilation efficiency (A) is the fraction of ingested energy available for growth and routine respiration after losses through defecation and specific dynamic action. We estimated this from data on ingestion, growth and respiration in Theilacker (Theilacker, 1987):

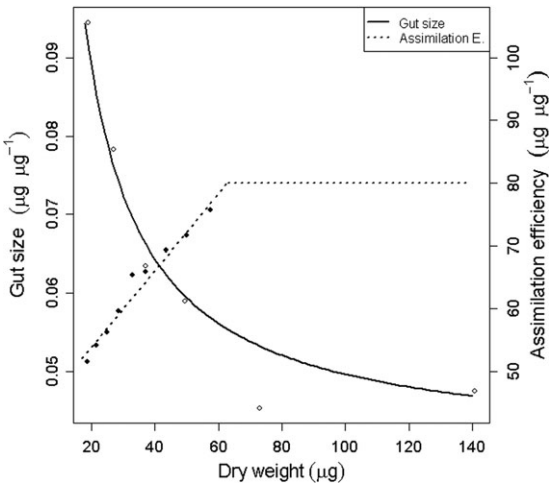

Fig. 2. The percentage in dry weight (μg) of gut capacity equation (3) (solid line) and assimilation efficiency equation (5) (dotted line) for larvae with different weights. Points are the gut size (open points) and the assimilation efficiency (filled points) from the experiment of Theilacker (Theilacker, 1987).

$$A = \frac{\Delta w + k \times R_{\mathrm{cal}}}{I} \tag{4}$$

Here, Δw is the growth rate in μg dw day^{-1}, R_{cal} is the respiration rate in cal day^{-1}, I is the food consumption in μg day^{-1} and k is the calorific value of a unit of larval tissue, 185.2 μg dw cal^{-1} (Govoni *et al.*, 1986; Theilacker, 1987). At increasing ingestion rates, gut flow increased while assimilation efficiency decreased (Theilacker, 1987). At low prey densities (2 rotifers/mL), the assimilation efficiency was higher than at high prey densities (25 rotifers/mL). This tendency has also been observed in Pacific herring larvae (Boehlert and Yoklavich, 1984). We interpret the decrease in assimilation under high ingestion/egestion rates as luxury consumption with little implication for growth rates, and in the model we assume constant and high assimilation efficiency, depending only on body mass [equation (5) and Fig. 2]. The assimilation efficiency increases proportionally to body mass (gut development) until larvae reach 60 μg dw and then it is fixed at 0.8 (Govoni *et al.*, 1986).

$$A = \begin{cases} 0.417 + 0.0061w, & w < 60 \\ 0.8, & w \geq 60 \end{cases} \tag{5}$$

This means that specific ingestion required to obtain maximum growth rate decreases with size until 60 μg dw. Assimilation efficiency and gut capacity also depend on prey type and quality, because the ratio between volume and weight changes with prey type.

These change as the larvae shift to different prey, but this is not included in this model.

Routine metabolism is determined from allometric scaling and a Q_{10} relationship (Rose *et al.*, 1999). Theilacker (Theilacker, 1987) estimated the routine respiration rate in cal day^{-1} at 16°C. We converted this to units of μg dry weight day^{-1} using a factor of 185.2 μg dw cal^{-1} (0.0054 cal/μg), which is the caloric value of larval anchovy (Theilacker, 1987). We use the same Q_{10} (2.2) as in *Anchoa mitchilli* larvae (Houde and Schekter, 1983):

$$R = 0.187w^{0.834}\mathrm{e}^{\frac{(T-16)\ln(Q_{10})}{10}} \quad (6)$$

Temperature-limited (food satiated) growth

We assume the growth estimated in Theilacker (Theilacker, 1987) at 15.5°C (in the third experiment), as an increase in standard length SL (mm) with age t (days) [equation (7)], represents the growth potential or the food satiated, temperature-limited growth of the larvae:

$$\mathrm{SL} = 3.06\mathrm{e}^{0.06t} \quad (7)$$

We used the data compiled by Methot and Kramer (Methot and Kramer, 1979) to find an expression for growth potential (mm mm^{-1} day^{-1}) as a function of temperature (T). The data represent the growth rate of 8 mm northern anchovy larvae (*E. mordax*) at different temperatures, from 13 to 22°C, obtained from a series of laboratory experiments (Kramer and Zweifel, 1970; Sakagawa and Kimura, 1975; Hunter, 1976; Theilacker, 1987) and some field samples (Methot and Kramer, 1979) (Fig. 3A). To parameterize the growth potential, it is assumed that (i) the maximum growth rate of a larva at 15.5°C is 0.06 (mm mm^{-1} day^{-1}) (Theilacker, 1987), (ii) the influence of temperature on the instantaneous growth rate is independent of body size as observed for *A. mitchilli* (Jung and Houde, 2004) and larval herring (*Clupea harengus*) (Fiksen and Folkvord, 1999) and (iii) that the relationship between the temperature and the instantaneous growth rate is linear in this temperature range:

$$g_l(T) = 0.06 + 0.00544(T - 15.5) \quad (n = 16,\ r^2 = 0.55,\ P \leq 0.001) \quad (8)$$

Using the length–weight relationship in Theilacker (Theilacker, 1987), growth rate in terms of mass g_w (μg dw (μg dw)$^{-1}$ day^{-1}) is:

$$g_w(T) = 0.1896 + 0.0171(T - 15.5) \quad (9)$$

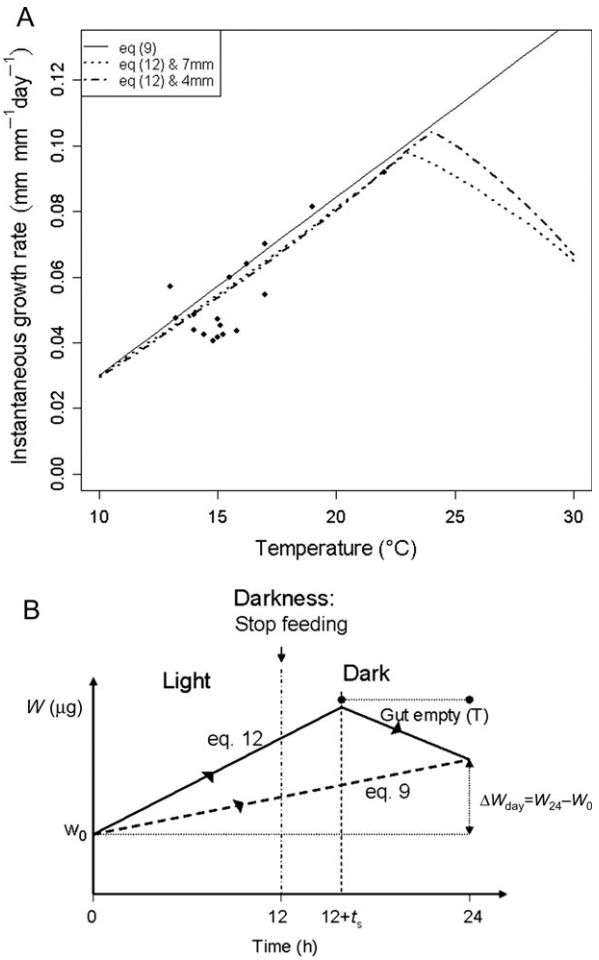

Fig. 3. (**A**) The continuous line is the calculated growth rate per day (mm mm^{-1} day^{-1}) at different temperatures (°C) calculated based on equation (9). The discontinuous and dotted lines are the modelled growth rate per day for a 7 and 4 mm larva calculated by equation (12) as the short-term growth potential and 12 h of daylight. The dots represent data, compiled from different laboratory experiments (Hunter, 1976, Kramer and Zweifel, 1970, Sakagawa and Kimura, 1975, Theilacker, 1987) and some field studies (Methot and Kramer, 1979). (**B**) The lines (arrows) represent the changes in body mass (excluding gut content) with time calculated by equation (9) (discontinuous line) and equation (12) (continuous line). Feeding takes place for the first 12 h, and 12+t_s is the time when the gut is empty, and body mass starts to decrease. See text for details.

However, these are growth rates averaged over 24 h, while our intention is to model growth also within the daily cycle. Larval anchovy inhabit regions with strong differences in day and night feeding opportunities, and all biomass accumulation occurs during daytime. This implies that the short-term growth potential g_h (=hourly growth rate; g_w/24), defined as the ability of the larvae to assimilate matter when there is prey available in the digestive system, is substantially higher than the averaged daily growth rate in equation (9) (Fig. 3B). The data in Fig. 3A are taken from regions and experiments

where larvae can feed between 12 and 14 h day^{-1}; for simplicity, we assume all of them are from the same day length (12 h). Then, equation (9) is the potential growth rate averaged over 12 h of feeding and 12 h of not feeding, after metabolic costs during both day and night. Therefore, the larvae must assimilate matter at a higher rate [equation (9)] during the 12 h of feeding. The short-term assimilation potential [μg dw (μg dw)$^{-1}$ h^{-1}] is the body mass increase over 12 foraging hours plus the metabolic loss during night (Fig. 3B). The laboratory experiments suggest that larvae can fill their guts in about 2 h at 16°C (Theilacker, 1987) and we assume that under optimal conditions they can fill the gut in 1 h. When the larva stops feeding at dusk (after 12 h of daylight), the larva continues to assimilate matter into somatic tissue for as long as there is food in the gut (Fig. 3B). The time considered to clear the gut (t_s) is temperature-dependent and will affect the slope of the short-term growth potential (i.e. g_h) to some degree (Fig. 3B). When the gut is empty, the body mass decreases due to metabolic loss [R_t, see equation (6)]. The total increase in body mass over one day (ΔW) can thus be expressed as:

$$\Delta w = g_h w_0 (12 + t_s) - \sum_{t=12+t_s}^{24} R_t \qquad (10)$$

where w_0 is the weight at the start of daylight and feeding. The short-term growth potential g_h is unknown and as a consequence also t_s and total respiration costs. To simplify, we assume $\sum R_t$ are equal to basic metabolic cost, R_0 (depending on body mass, w_0, and temperature) over the time, with an empty gut:

$$g_w w_0 = g_h w_0 (12 + t_s) - R_0 (12 - t_s) + e(R_t) \qquad (11)$$

The term $e(R_t)$ reflects the error introduced by not knowing the exact body mass to calculate respiration rate during the period with an empty gut. In addition, s_t remains unknown. Solving equation (11) for potential growth rate when gut content is not limiting, we get:

$$g_h = \frac{g_w}{12} + \frac{R_0 f(T)}{12 w_0} \text{ where}$$
$$f(T) = 12\frac{(12 - t_s)}{(12 + t_s)} - \frac{t_s g_w w_0 + 12 e(R_t)}{R_0 (12 + t_s)} \qquad (12)$$

Here, $f(T)$ is a function summarizing the unknowns, t_s and $e(R_t)$. To find the potential mass accumulation during daytime (g_h), we used available data on growth in larval anchovy as a function of temperature (Fig. 3A). By iteration, we found a linear expression of $f(T)$ that minimized the difference between body mass increase over 1 day (24 h, 12 h of night/12 h of daylight) predicted by the model and the data [equation (9)]. This function is $f(T) \approx 0.9T - 10$. In deriving this expression (and in running the model), the model gives the same results using body mass in the previous time step w_{t-1} and R_{t-1} instead of w_0 and R_0. To implement the model, we used equation (12) (first part), equation (6) (R_0) and insert the expression for $f(T)$. This procedure then give us an expression for how fast a larva can possibly grow if it has unlimited access to food, at least over a short-time period of 1 h.

RESULTS AND DISCUSSION

Growth efficiency

The growth efficiency is estimated with different Q_{10} values to see the sensitivity of the model to this parameter. The growth efficiency is calculated per day as the ratio between maximum growth rate [equation (9)] and the ingestion rate required to sustain the maximum growth rate (D_{max}) (Fig. 1) (Kristiansen *et al.*, 2007). When Q_{10} is equal to 2.2, the growth efficiency has an optimum value at 17°C for all size groups, but this is sensitive to the actual Q_{10} (Fig. 4). The decreases in efficiency at lower and higher temperatures result from differences in temperature-dependencies in growth potential (linear, [equation (9)] and respiration

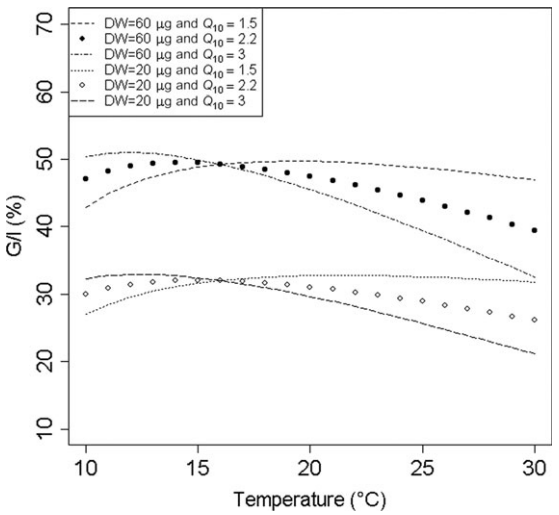

Fig. 4. The growth efficiency (growth/ingestion) at different temperatures for a larva of 20 (open points) and 60 μg dry mass (filled points) ($Q_{10} = 2.2$), under food satiation. The lines represent the sensitivity of growth efficiency under different Q_{10} values ($Q_{10} = 1.5$ and 3) and larval weight.

[exponential, equation (6)]). The change in efficiency optimum (Fig. 4) in temperature for Q_{10} values (1.5 and 3.0) is caused by the respiration function [equation (6)]. Growth efficiency is also size-dependent mainly due to the reduced assimilation efficiency of smaller larvae.

Larval growth and day length

Anchovy larvae only feed during the day and 30 min after the sunset the gut is empty (Conway *et al.*, 1998). Normally, larvae feed mainly during the day and assimilate and digest during the night, but anchovy larvae have little food in the gut during night. Therefore, Conway *et al.* (Conway *et al.*, 1998) suggested that anchovy has a different growth strategy than larvae of most other species. The short-term growth potential [equation (12)] expresses the ability of larvae to assimilate matter when there is prey available in the digestive system. With the introduction of the short-term growth potential in the model, the larvae only feed during daylight hours, but they maintain a positive growth rate in darkness until the gut is empty (Fig. 5). The high short-term growth potential at high temperatures implies faster digestion rates and higher metabolic loss during the night.

Growth potential increases with day length, as the time with empty gut and negative growth during night decreases (Fig. 6). The optimal temperature in terms of growth, however, is independent of day length when the gut is filled up once every hour (Fig. 6). At high temperature, larval growth is restricted by a maximum ingestion rate of one gut volume per hour. To grow at temperature-limited rates, higher ingestion rates are

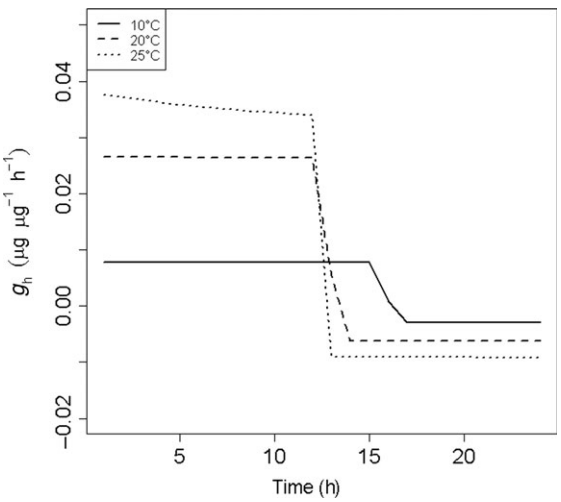

Fig. 5. The short-term growth potential (µg µg^{-1} h^{-1}) with only feeding for 12 h of day length and no feeding during the night at different temperatures (10, 20 and 25°C).

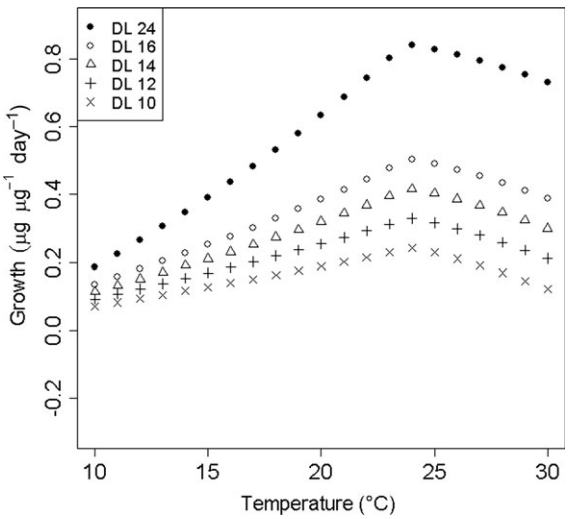

Fig. 6. The instantaneous growth rate (µg µg^{-1} day^{-1}) at different temperatures with satiated feeding during daylight (DL) hours (10, 12, 14, 16 and 24 h) and no feeding during night.

required. This also means that growth at high temperatures may become limited by prey handling times.

Suthers and Sundby (Suthers and Sundby, 1996) showed that the high growth variability in juvenile cod was influenced by the day length. At 70° north, the light intensity is higher than necessary for feeding during 24 h, so without any clouds the potential volume searched after food increases. As a consequence, their consumption can be 50% greater than at 45° north. Nevertheless, their model estimated that a 50% increase in feeding time increased the growth only 33–40% due to cloud cover and physiological limits. Bagarinao and Hunter (Bagarinao and Hunter, 1983) suggested that the anchovy larvae in Southern California have enough light to feed during at least from 11 to 16 h day^{-1}, but it is not known if the 45% increase in day length leads to a 45% increase in growth. It might be that the growth is physiologically limited as in juvenile cod. Under food satiation during 24 h, the growth predicted by our model was equivalent to equation (9).

Model validation

The predicted daily growth rates under 12 h of feeding are similar to experiments in Theilacker (Fig. 7A) both under food satiation (25 rotifers/mL) and under food limitation (2 rotifers/mL). This is not a proper validation, as the same experiments are used in the parameterization of the model, but it is reassuring that the model matches these data as well. In the food-limited case, the larval daily ration was the same quantity of food as in the low-food experiment of Theilacker (2 rotifers/mL) (Fig. 7A, inserted figure).

The growth rates estimated by our model were compared with some field data from the Bay of Biscay and cultured *E. encrasicolus* larvae. Sampling of larval anchovy (*E. encrasicolus*) was carried out on surveys in the south-eastern part of the Bay of Biscay (limited to 3°35'W and 45°40'N) in July 2003 (Cotano, unpublished data), June 2004 (Cotano *et al.*, 2008) over grid stations distributed in transects perpendicular to the coastline and at 3 stations on a cross-shelf transect off-shore San Sebastian (43°17'N, 1°58'W) during May, June and September 2000 (Cotano, unpublished data). The larvae were caught at surface temperatures between 16 and 22°C, but the food conditions probably vary within the Bay of Biscay (Zarauz *et al.*, 2007). The larvae from laboratory experiments were maintained at four different temperatures (17.5, 19.5, 20.5 and 22.5°C) and photoperiod (16 h/8 h) (Aldanondo *et al.*, 2008). Data from laboratory experiments show lower growth rates than the larvae from the sea (*E. encrasicolus*) sampled in the Bay of Biscay (Fig. 7B). Clearly, the larvae were not growing at their maximum capacity in the laboratory, so the model predictions are best compared with the field data. The larva is initiated at day 4 (20 μg) and is placed in 16 or 22°C, with 12 or 16 h of day length for 26 days, the outer limits for larvae in the field. The model predictions compare well with the field data until the larvae reach ~500 μg dry mass (Fig. 7B). After this size, the field data indicate larvae stop growing, a potential artefact due to increasing gear avoidance with size (Piccinetti *et al.*, 1982; Somarakis *et al.*, 1998; Morse, 1989). Alternatively, it could also be a consequence of a trade off between growth and predation risk from behaviours such as diel vertical migration and schooling. Laboratory measurements indicate that schooling behaviour begins between 10 and 11 mm (Hunter and Coyne, 1982) and this is linked to vertical migration behaviour (Hunter, 1981). The analysis of vertical distribution in the sea shows diel vertical migration of *E. encrasicolus* larvae >6 mm (Palomera, 1991; Olivar *et al.*, 2001; Sabatés *et al.*, 2007).

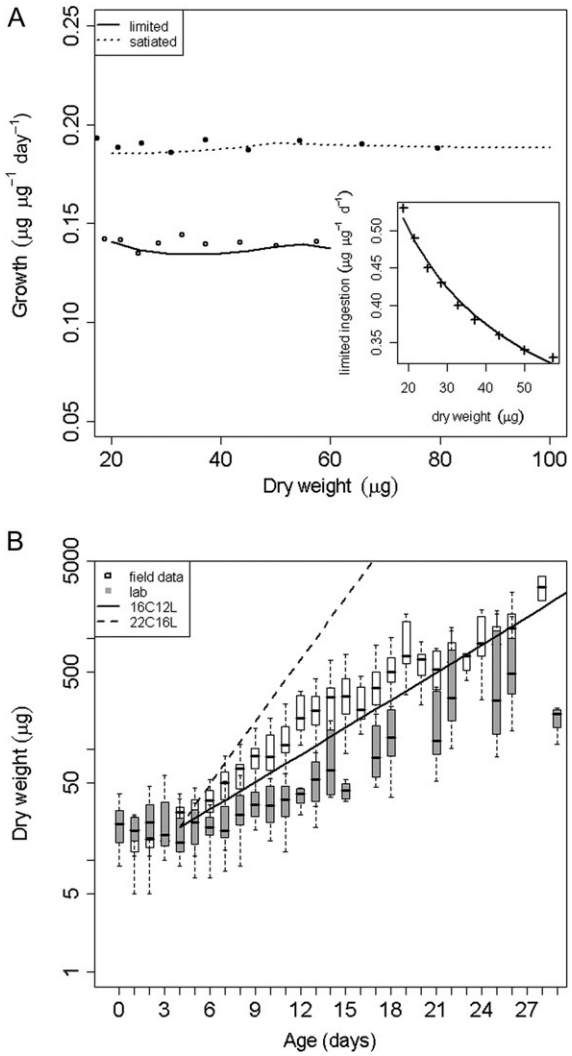

Fig. 7. (**A**) The points are the specific growth rate (μg μg^{-1} day^{-1}) for larvae with different weights from both experiments of Theilacker, with satiated (25 rotifers/mL) (filled points) and limited ingestion (2 rotifers/mL) (open points). The dotted line is the modelled growth rate (μg μg^{-1} day^{-1}) at 16°C under food satiation and 12 h of daylight for larvae with different weights and the continuous line represents the same estimation but with a food limited ingestion. The limited ingestion is estimated from the experiment of Theilacker (2 rotifers/mL) (crosses) (inserted panel) with the daily specific ingestion rate given by $ing = 179.5\ w^{-0.42}$, $r^2 = 0.98$. (**B**) The box plots are the weight at age of larval anchovies estimated from field data in the Bay of Biscay sampled during 2004 (Cotano *et al.*, 2008), 2003 and 2000 (unpublished data) (white box plot) and from laboratory experimental data (Aldanondo *et al.*, 2008) (grey box plot). The lines are the modelled body mass of satiated larvae at different temperatures (16 and 22°C) and day lengths (12 and 16 h).

Growth as a function of larval size, temperature and ingestion rate

We ran the model with fixed ingestion rates per hour over 24 h, which then summarizes into a daily ration (here without the daily feeding cycle), defined as the amount of prey mass ingested per larval body mass per day. Fast growing fish larvae may consume prey mass in the order of its own body mass per day (Hunter, 1972). With no food, the larva has a negative growth rate, and loss rates increase with temperature due to respiration costs (Fig. 8A). If growth is food-limited (Fig. 8B), the optimum temperature and growth are lower for smaller larvae with lower assimilation efficiency [see equation (5)].

Under satiating food conditions, the size-specific growth potential for larval *E. mordax* increases linearly with

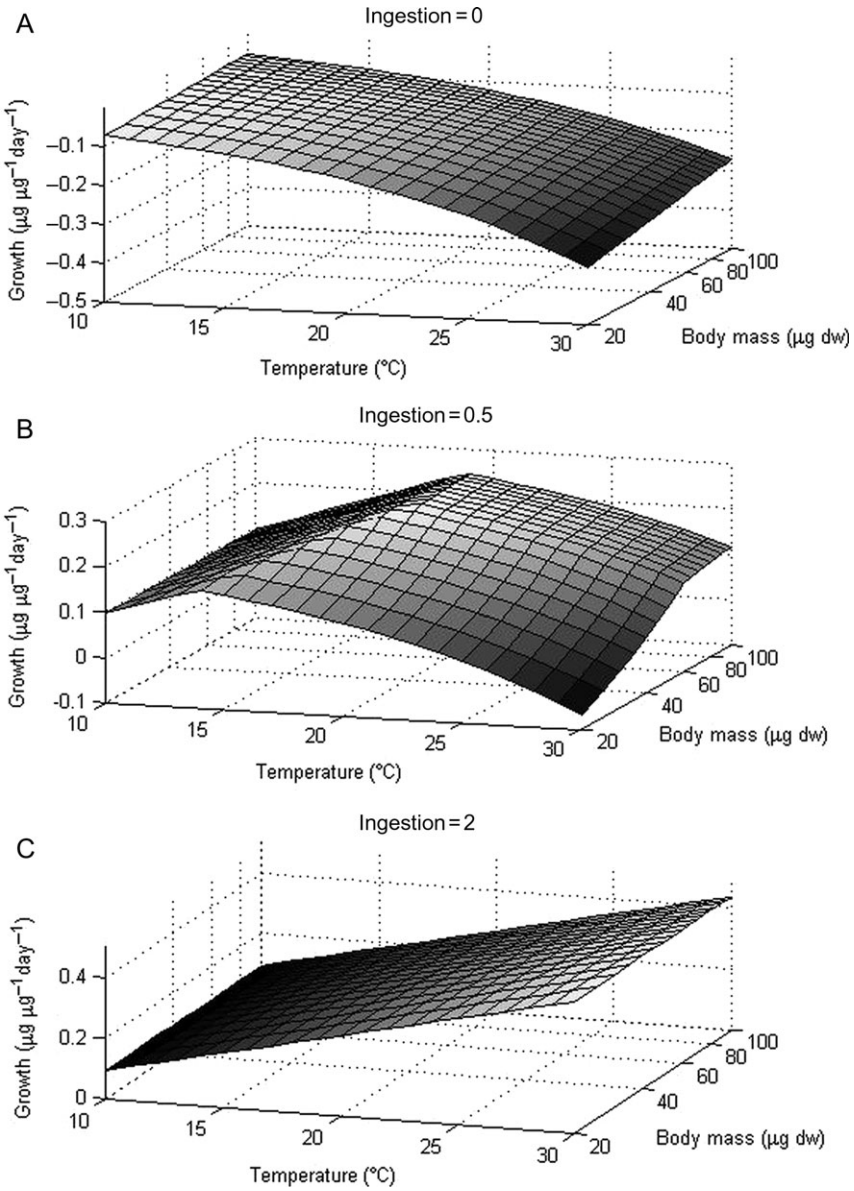

Fig. 8. Growth rates as a function of size, temperature and ingestion rates. Panels show the growth rates for three different ingestion rates (**A**) 0, (**B**) 0.5, (**C**) 2 μg μg^{-1} day^{-1} for different temperatures (10–30°C) and body mass (20–100 μg) without the inclusion of the day–night feeding cycle in the model.

temperature up to 30°C (Fig. 8C), although laboratory estimates (Methot and Kramer, 1979) above 22°C are lacking, and probably other processes (cellular, enzymatic) will be limiting at these temperatures. In our model, 1°C rise in temperature means an increase in growth potential of 0.0171 (μg dw (μg dw)$^{-1}$ day^{-1}), which is quite similar to estimates by Houde and Zastrow (Houde and Zastrow, 1993) for herring (0.0169 μg dw (μg dw)$^{-1}$ day^{-1}). However, these authors did not find a linear effect of temperature on growth in species from upwelling regions (*Engraulis* sp.), but in the upwelling regions the food and temperature are not independent and the low food abundance can be related to high temperatures. Regner (Regner, 1980) carried out an experiment to study post-larval anchovy (*E. encrasicolus*) growth at three temperatures, but the growth at the highest temperature was lower which could be due to insufficient prey availability. Regner (Regner, 1980) modelled the temperature as a linear function and in his model a 1°C rise in temperature yielded 0.0048 increase in growth potential (mm mm^{-1} day^{-1}), or 0.015 μg dw (μg dw)$^{-1}$ day^{-1} [conversion using the length–weight relationship from

Theilacker (Theilacker, 1987)]. However, experimental studies (Ryland and Nichols, 1967; McCormick *et al.*, 1972; Elliott, 1975a; Brett, 1979) typically show a dome-shaped relationship between temperature and growth rate, with a sharp decrease beyond optimal temperatures. The mechanisms behind this decrease in growth rate may relate to factors such as limitations in circulation capacity (oxygen supply to combustion), enzymatic efficiency and excessive metabolic costs at hyper optimal temperatures (Jobling, 1994). Still, the optimum temperature of larval anchovy is unknown, as no dedicated laboratory rearing experiments have been conducted to determine this.

Internal energy budgets

How is ingested material divided among egestion, respiration and growth at different temperatures? First, ignoring the day–night feeding cycle, the minimum ration required to maintain maximum growth rate increases exponentially with temperature for all larvae (Fig. 9A and B), driven by higher respiration costs and growth potential with temperature. At temperatures beyond 20°C, the larvae need to ingest very high rations to achieve the maximum growth rate. For example, a 20 μg larva needs to ingest prey equivalent to its own body mass per day at 20°C. The ration required decreases with size and 100 μg larvae need only 60% per day (Fig. 9A and B). Including the day–night feeding cycle, the growth potential levels off at temperatures above 24°C for small (Fig. 9C) and 23°C (Fig. 9D) for larger larvae. The larvae will have empty guts at night, and this limits growth at high temperatures because the food intake per hour is limited to one gut filling.

Intermittent feeding: time intervals between gut filling events and growth

During darkness, larval anchovy do not feed, and may go with empty guts for several hours during night, while in patchy food environments, larvae may encounter high food concentrations at various time-scales. Our model can realistically reproduce effects of intermittent

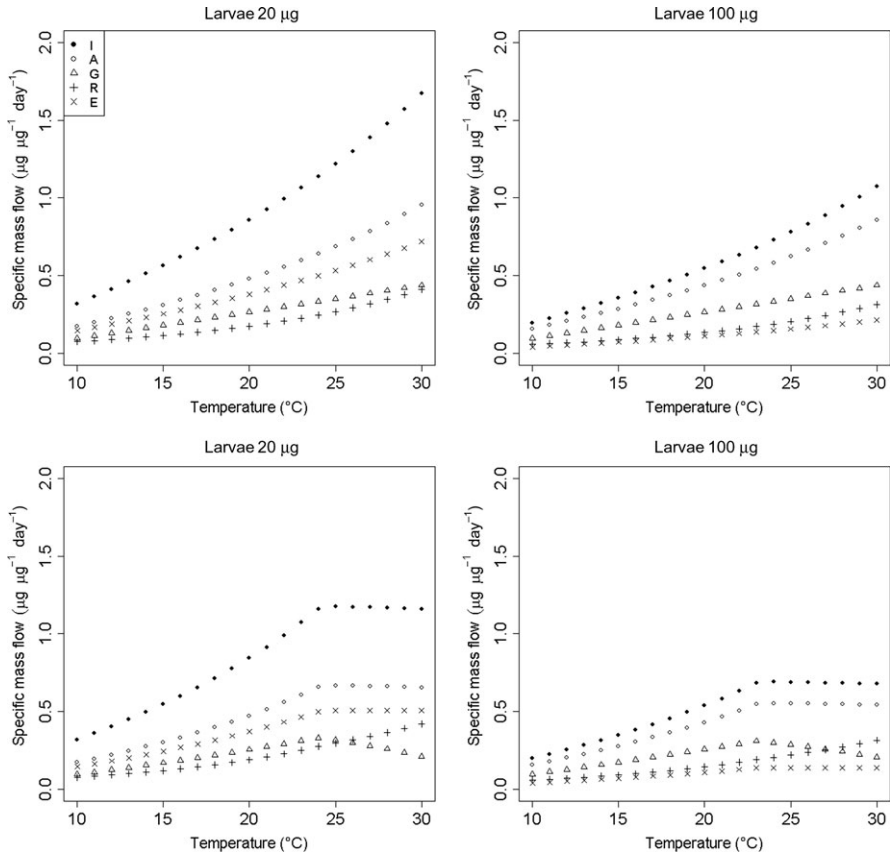

Fig. 9. The specific flow mass used in ingestion (*I*), Assimilation (*A*), growth (*G*), respiration (*R*) and evacuation (*E*) at different temperatures by a larva of 20 (**A** and **C**) and 100 μg dw (**B** and **D**) under satiated ingestion with feeding during 24 h (A and B) [equation (9)] and 12 h (C and D) [equation (12)].

feeding assuming that the larva can fill the gut in 1 h (Fig. 10A). Theilacker (Theilacker, 1987) found that under good foraging conditions, anchovy larvae can fill their stomach in 2 h, while Hunter (Hunter, 1972) suggested half an hour. We ran the model with gut filling intervals of 2 h which means that the larvae fill their guts to the gut capacity every second hour with no feeding in-between. With 12 h of daylight, filling the gut every second hour yields almost the same growth as filling the gut every hour (Fig. 10A) below 16°C, while an interval of 3 h limits the growth rate quite strongly above 13°C.

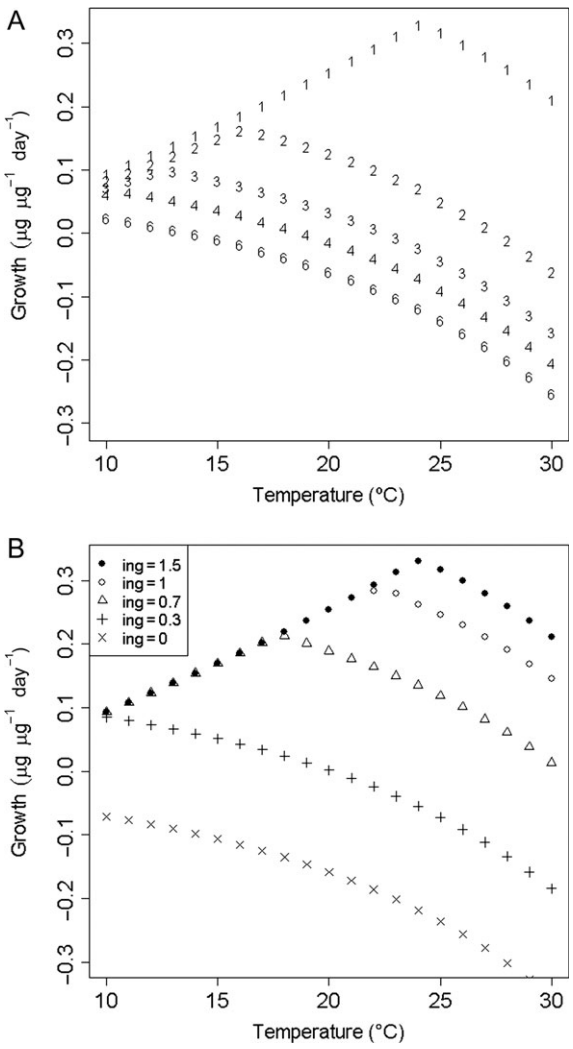

Fig. 10. (**A**) Specific growth rate at different temperatures for different time intervals between gut filling events. The numbers are the frequency of feeding, every 1, 2, 3, 4, and 6 h. (**B**) The modelled growth rate ($\mu g.\mu g^{-1} day^{-1}$) for a larva of 20 μg dw at different temperatures with 12 h of feeding. The symbols are the modelled growth with different daily ingestion rates (fractions of body mass, 1.5, 1, 0.7, 0.3, 0).

The optimal temperature and growth rate decrease when the ingestion rate is reduced (Fig. 10B). The decrease in specific growth rate of a starving larva with temperature has a concave shape (Fig. 10B). The growth rate decreases at temperatures higher than the optimum. The rate at which the growth falls is higher at elevated ingestion rates. This is because higher ingestion rates yield higher optimal temperature so the respiration cost at temperatures above the optimal is also higher.

With a decrease in ingestion rate, or under intermittent feeding, the optimum temperature and maximal growth rate decrease (Fig. 10A and B). This pattern is also found in brown trout *Salmo trutta* (Elliott, 1975b) and young sockeye salmon *Onchorynchus nerka* (Brett *et al.*, 1969). The specific respiration cost increases exponentially with temperature, but decreases with body mass [equation (6)]. As a consequence, the specific ration needed to grow at maximal rates also increases exponentially with temperature as was shown for adult brown trout by Elliott (Elliott, 1976). Observations indicate that an increase in ingestion is related to increased gut evacuation rates (Laurence, 1971; Elliott and Persson, 1978; Govoni *et al.*, 1986). In walleye pollock specific evacuation rate may decrease with size (Yamashita and Bailey, 1989). However, since assimilation efficiency varies with ingestion, it is difficult to use estimates of evacuation as validation or calibration of the model.

Comparison between the growth rates data from *Engraulis* species and the model at food satiated condition

We compiled, from a number of different field locations, estimates of growth of anchovy larvae with ambient temperature (Table I). The growth predicted by the model at satiated conditions for each temperature was compared with observed growth of anchovy larvae and temperatures (Fig. 11). Our modelled growth rate (mm/day) at unlimited consumption of a 7 mm larva (100 μg) is in the upper range of the data. In *E. japonicus*, the growth rate increases linearly until a peak and after this it decreases abruptly as in brook trout (McCormick *et al.*, 1972), indicating a physiological growth optimum at about 21–22°C (Takasuka and Aoki, 2006; Takasuka *et al.*, 2007) similar to the optimal temperature estimated by our model (assuming ingestion is maximally one gut size volume per hour).

On the other hand, Methot (Methot, 1981) reported an increase in growth of *E. mordax* larvae from 0.43 (January) to 0.55 mm/day (June) off Southern California with 12 and 16 h of day length, respectively (Bagarinao and Hunter, 1983). During those 2 months

Table I: Anchovy larval growth studies

Species	Year	Region	Model	Growth rate (mm/day)	Size (mm)	Age (days)	*T* (°C)	Reference
Engraulis encrasicolus		Adriatic (Laboratory)	G	1.15[a]			21.3	(Regner, 1980)
	1977	Adriatic (Laboratory)	L	0.6[a]			19.02	(Regner, 1980)
	1977	Adriatic (Laboratory)	L	0.8[a]			21.3	(Regner, 1980)
	1977	Adriatic (Laboratory)	L	0.7[a]			24.05	(Regner, 1980)
		North Atlantic (Estuaries)	L	0.4			16–19	(Re, 1987)
	1985	Catalan Sea	G	0.89[a]	3.9–23.4	2–19	20	(Palomera *et al.*, 1988)
	1992	Gulf of Lions	E	0.61[a]	4.0–22.5	1–21	16.5	(Garcia *et al.*, 1998)
	1992	Catalan Sea	E	0.49[a]	5.5–19.0	1–19	18	(Garcia *et al.*, 1998)
	2001	North Catalan Sea	L	0.56	3.4–22.0	1–22.5	19	(Sabatés *et al.*, 2007)
	2003	South Catalan Sea	L	0.68	4.8–13.7	3–17	20	(Palomera *et al.*, 2007)
	2003	South Catalan Sea	L	0.86	7.4–20.1	4–19	23	(Palomera *et al.*, 2007)
	2003	South Catalan Sea	L	0.59	8.1–22.7	6–29	25	(Palomera *et al.*, 2007)
	1991	Northern Adriatic Sea	G	0.94[a]	2.8–35.4	1–36	23	(Dulcic, 1997)
Engraulis mordax	1976/77	Southern California Bight	G	0.33[a]–0.47[a]			13–16	(Methot and Kramer, 1979)
		(North Pacific) Laboratory		0.45[a]			17	(Kramer and Zweifel, 1970)
		Laboratory		0.58[a]			17	(Kramer and Zweifel, 1970)
		Laboratory		0.77[a]			22	(Kramer and Zweifel, 1970)
		Laboratory		0.68[a]			19	(Sakagawa and Kimura, 1975)
		Laboratory		0.48	4.0–7	5–14	15.5	(Theilacker, 1987)
		Laboratory	G	0.53[a]			16.2	(Hunter, 1976)
Engraulis ringens	1995	Central Chile	L	0.4–0.57	5.6–20.7	3–35	11.1–13.5	(Hernandez and Castro, 2000)
	1995	Central Chile	G	0.5	5.6–20.7	3–35	11.1–13.5	(Hernandez and Castro, 2000)
		Central Chile		0.45	5.0–20.0		12.5	(Herrera *et al.*, 1985)
Anchoa mitchilli	1984	North Carolina	L	0.25–0.51	0.25–0.51	1–36	20–25	(Fives *et al.*, 1986)
	1979	Biscayne Bay	L	0.56	6–12	6–19	29	(Leak and Houde, 1987)
	1980	Biscayne Bay	L	0.43	5–13	5–23	24.4	(Leak and Houde, 1987)
	1980	Biscayne Bay	L	0.47	5–13	3–19	28.1	(Leak and Houde, 1987)
	1980	Biscayne Bay	L	0.5	6–13	6–16	30.7	(Leak and Houde, 1987)
	1988	Mesocosm Chesapeake Bay L.	E	0.63	12.5–14.8	NAN	26.1	(Cowan and Houde, 1990)
	1987	Great South Bay	L	0.58	2–15	2–15	22.4	(Castro and Cowen, 1991)
	1988	Great South Bay	L	0.56	2–15	2–15	24.4	(Castro and Cowen, 1991)
	1983	Chesapeake Bay	L	0.52–0.72	3–13	2–17	25.2–26.8	(Rilling and Houde, 1999)
Engraulis anchoita	1995	Brazilian Southeastern Bight	B	0.5	10–20	5–31	17–29	(Castello and Castello, 2003)
	1995	Brazilian Southeastern Bight	B	0.4	8–21	2–37	18–25	(Castello and Castello, 2003)
Engraulis japonicus	1990–2004	western North Pacific	B	0.1–0.5	6–60	6.4–34.3	14–27	(Takasuka *et al.*, 2007)

Model is the method used to estimate the growth: G-Gompertz, L-Linear, E-Exponential, B-back calculated from otolith.
[a]At size = 8 mm.

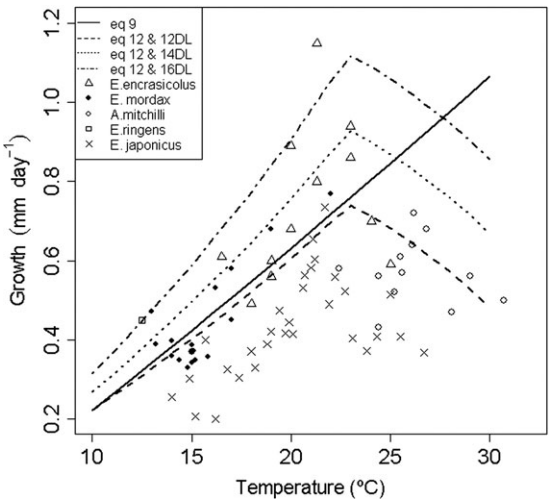

Fig. 11. Some field estimates of growth rate (mm/day) as a function of temperature. The lines are the estimated growth rate for a 7 mm (100 μg dw) larva under food satiated ingestion and different day lengths (12, 14 and 16 h). The symbols are the reported growth rate at each temperature for different anchovy species and studies: *E. encrasicolus* (Dulcic, 1997; Palomera *et al.*, 2007), *E. mordax* (Kramer and Zweifel, 1970; Sakagawa and Kimura, 1975; Hunter, 1976; Methot and Kramer, 1979; Theilacker, 1987), *A. mitchilli* (Leak and Houde, 1987; Cowan and Houde, 1990; Castro and Cowen, 1991; Rilling and Houde, 1999), *E. ringens* (Herrera *et al.*, 1985) and *E. japonicus* (Takasuka *et al.*, 2007).

in 1979, the larvae were found at 16°C (Bagarinao and Hunter, 1983; Methot, 1983). For the same scenario, our model estimates 0.44 and 0.65 mm/day growth rates for a 7 mm satiated larva (Fig. 11). Further, the mean growth rates in our model and those reported from the field in *E. mordax* and *E. encrasicolus* are quite close (Fig. 11), suggesting that these larvae may be growing near their physiological maximum rates. The mean growth rates of *E. japonicus* are lower than in our model, particularly at temperatures >23°C. Takasuka and Aoki (Takasuka and Aoki, 2006) showed that the relationship between larval *E. japonicus* growth rates and environmental factors varied between regions. In some regions, the factor that best explained the growth rates was the SST and in others the SST and food availability. The growth rate of *A. mitchilli* is close also to the rate predicted by our model; however, this species belongs to a different genus. More data are required to make any comparison with *E. ringens* and *E. anchoita*, preferably from controlled laboratory experiments where temperature and food-effects can be disentangled.

Uncertain or unknown parameters in the model

The temperature dependency in metabolism (Q_{10}) of anchovy larvae is poorly known. Houde and Zastrow (Houde and Zastrow, 1993) showed that Q_{10} was 1.95 for marine fish larva in general. For *A. mitchilli* larva, it was 2.2 (Houde and Schekter, 1983), for larval Atlantic mackerel (*Scomber scombrus*) 1.7 (Giguere *et al.*, 1988) and for larval Atlantic cod *Gadus morhua*, Q_{10} is between 2.4 and 2.6 (Finn *et al.*, 2002).

The G/I changes through ontogeny, but the value for small larvae are well within the range of reported values for larvae, 11–46% (Theilacker and Dorsey, 1980; Houde and Schekter, 1983; Theilacker, 1987). The G/I value for larvae larger than 60 μg dw was about 50% (Fig. 4), which is a bit higher than the maximum reported for other larvae (46%). The actual growth efficiency, in terms of growth per unit ingested mass depends also on the prey quality, and on potential differences between natural and cultured food used in the laboratory. A more detailed model where prey energy digestibility and energy density is included may better represent this change.

The model assumes a maximum ingestion of one gut volume per hour and this can be a limitation for our model at temperatures higher to 23°C (Fig. 11). At high temperatures, the required ingestion rate to have the maximum growth rate is higher than one gut volume per hour. Introduction of temperature dependent gut evacuation rates directly as a driver of digestion would also increase the required feeding (Lough *et al.*, 2005; Peck and Daewel, 2007), but the only data available are from Theilacker (Theilacker, 1987). Theilacker (Theilacker, 1987) estimated that at 16°C larval anchovy feeding on rotifers could empty their guts in 1.15 hours and 2.73 hours for copepod diets.

Further, we may expect that larvae will not be able to grow at g_h [equation (12)] for an extended period of time; other limiting factors, perhaps at the cellular level, may limit growth if food is supplied during a full 24 h light period. The model is, therefore, only valid for normal day–night fluctuations in feeding.

Additional experiments are necessary for a better understanding of the physiology of anchovy larvae at a smaller time scales to know the short-term growth potential, the metabolic cost during day and night, and the effect of different day lengths on growth.

Prospects

Numerous bioenergetics models have been developed to understand and compare energy allocation in larvae of different fish species (Houde and Schekter, 1983; Tucker, 1989; Yamashita and Bailey, 1989; Parra and Yufera, 2001; Cunha *et al.*, 2007). Rose *et al.* (Rose *et al.*, 1999) developed an IBM for *A. mitchilli* using daily time steps, as the model was developed to integrate over long time

scales. One day is a long time step to analyse bioenergetics in larval fish. It is not possible to include variables like gut fullness (Kristiansen *et al.*, 2007; Peck and Daewel, 2007), or the influence of day length or foraging frequency at this time scale. With the more explicit representation of energy flow, our model opens the possibility of a range of behavioural and environmental analyses.

The intermediate trophic level of anchovy makes it a very important species for the ecosystem due to their role connecting the lower and upper trophic levels (Rice, 1995; Cury *et al.*, 2000). However, little is known about the considerable fluctuations in the recruitment which depend on the larval and juvenile survival. A high growth rate means a higher survival probability in the field due to their capability to sustain starvation, to find food or to escape from predation (Cushing, 1990). The temperature (Houde, 1989), light (Blaxter, 1986; Suthers and Sundby, 1996) and prey availability (Cushing, 1990) are the most important factors affecting larval growth. Nevertheless, actually the only growth models available for *Engraulis* larvae come from the otolith and larval size relationship. Statistical age-size models do not allow exploration of the effect of interactions between prey availability, temperature and light on growth. Therefore, the potential effect of transport to different environments in anchovy larval growth remains difficult to understand. Our bioenergetic model can reproduce the growth rate at different temperatures, ingestion and day length, so this model coupled with a foraging model (Lough *et al.*, 2005) might allow investigation of the changes in larval growth under different environmental conditions such as prey size spectra and light intensity. The similar growth between *E. encrasicolus* in the field and the one estimated by our model based on *E. mordax* data suggests that with small variations the model could be applied to different anchovy species.

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