



Appendicularian ecophysiology. II. Modeling nutrition, metabolism, growth and reproduction of the appendicularian *Oikopleura dioica*

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ABSTRACT

A model has been developed to simulate the growth of an individual appendicularian (*Oikopleura dioica*) from egg to spawning. This model uses a new set of experimental data presented in a companion paper in this volume and estimates growth rates and generation times as well as clearance rates, house and fecal pellet production and reproductive capacity at different temperatures and food concentrations. According to the model outputs, the weight of a single house represents 11.5% of the individual's total weight, a lower value than previously estimated. The relative weight of one fecal pellet varies as a function of food concentration. The model also confirms that the minimum food concentration for growth is about 20–30 $\mu\text{g C l}^{-1}$ and that growth is maximal for a 100 $\mu\text{g C l}^{-1}$ feeding concentration. The limits of the growth optimum in relation to food concentration and temperature can be considered as a first description of the fundamental ecological niche of appendicularians. This model can be used both for predicting (1) the impact of *in situ* observed populations on the pico- and nanosetton and (2) the production of large aggregates. These two pieces of information are often needed for large-scale biogeochemical models.

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1. Introduction

Appendicularians are characterized by short life cycles and high growth rates (Hopcroft and Roff, 1995). They produce a substantial quantity of large particles, as discarded houses and fecal pellets (Gorsky and Fenaux, 1998; López-Urrutia and Acuña, 1999; Sato et al., 2001; Sato et al., 2003), which mediate the flux of biogenic carbon to the deep ocean and seafloor (Dagg and Brown, 2004; Alldredge, 2004; Robison et al., 2005). Due to their efficient filtering system, appendicularians can significantly alter the community structure of small autotrophs and heterotrophs by consuming more than 60% of the total suspended particles in seawater (López-Urrutia et al., 2003b; Scheinberg et al. 2005).

Appendicularians are difficult to study *in situ*. Sampling methods often lead to high mortalities and/or stress, which bias quantification of the ecological importance of appendicularians, notably their production of biogenic matter. Nevertheless, reliable estimates of filtration rates and production of houses and fecal pellets can be determined in the laboratory for some epipelagic species. Unfortunately, these data are difficult to extrapolate directly to the natural environment. One of the ways to estimate the impact of appendicularians on particulate matter cycling is the modeling of their physiology.

Different modeling approaches have been proposed for the species *Oikopleura dioica*. Touratier et al. (2003) developed a detailed

individual-based representation of the major biological processes responsible for metabolic balance. López-Urrutia et al. (2003a) used a simpler approach focusing on growth in response to various environmental parameters. Alldredge (2004) modeled the production of discarded houses. Aksnes et al. (2006) used a developmental model to estimate the growth of *O. dioica*.

Recent experimental results (Lombard et al., 2005, 2009-this volume) revealed lower oxygen consumption rate and higher egg weight for *O. dioica* than previously measured. It has also been demonstrated that respiration does not vary with food concentration and that assimilation efficiency is not constant and decreases with increasing food concentration. Furthermore, maturation and spawning size are not constant but vary with the ambient food concentration and temperature.

In order to predict the role of appendicularians in water column geochemistry, we propose an energetic balance model of their life cycle, validated experimentally on *O. dioica*, one of the five most abundant appendicularian species (Fenaux and Dallot, 1980; Hopcroft and Roff, 1995; Nakamura et al., 1997; Fenaux et al., 1998; López-Urrutia et al., 2004a). *O. dioica* has been successfully cultured in the laboratory (Paffenhöfer, 1973; Fenaux and Gorsky, 1985; Sato et al., 2001; Troedsson et al., 2002) and a complete data set is available for modeling its growth, nutrition, respiration, house and fecal pellet production, and reproduction in relation to temperature and food concentration.

Using new experimental data presented in a companion paper (Lombard et al., 2009-this volume) concerning morphological characteristics, reproduction, and simultaneous measurements of growth and clearance rates in different food concentrations, the model presented here proposes to predict the impact of appendicularians on the transformation

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Table 1
Oikopleura dioica. Variables of the metabolic balance model.

Symbols	Description	Units
Forcing variables		
<i>T</i>	Temperature	°C
State variables		
<i>x</i>	Carbon concentration of the food particles	µg C l ⁻¹
<i>Sb</i>	Carbon weight of the structural biomass of the appendicularian	µg C
<i>G</i>	Carbon weight of the appendicularian gonad	µg C
<i>H</i>	Cumulative carbon weight of the produced houses	µg C
<i>R</i>	Cumulative carbon weight of the respiration	µg C
<i>Dh</i>	Cumulative carbon weight of the food particles trapped in the houses	µg C
<i>Fp</i>	Cumulative carbon weight of the fecal pellets content	µg C

and fate of suspended particles. The model simulates gonad biomass, structural biomass and house evolution during an appendicularian's entire life cycle and its impact on suspended matter (respiration, secretion, aggregation).

2. Material and methods

2.1. Model conception and hypotheses

The life cycle of *O. dioica* may be characterized by four events: fertilization, hatching, tail shift and spawning (Fenaux, 1976). Organogenesis continues after hatching and the tail and trunk increase in size (Fenaux, 1998). The larva secretes its first house rudiment around the trunk and, after the shift of the tail, the individual inflates its house and begins its filtering activity. In this study, we assume that the entire life cycle can be characterized by larval development followed by a phase of somatic growth and gonad maturation. The larval phase begins with egg fertilization and ends when the larva starts to feed (shift of the tail and expansion of the first house). Following the larval stage, two distinct phases can be distinguished: first, a period during which the body size increases concomitantly with a slow development of the gonads, followed by a second phase, a period of active gonad maturation without noticeable growth of the trunk (Troedsson et al., 2002; Lombard et al. 2009-this volume). The partial overlapping of these contiguous stages (Lombard

et al., 2009-this volume) was represented in the model by assuming a progressive change in the allocation of assimilated matter between structural biomass and gonad tissue. Gonad maturation ends with the release of gametes, followed by the death of the appendicularian.

The model represents the life cycle of an individual appendicularian controlled by temperature and food availability. Temperature (*T*) acts as a forcing variable, whereas food concentration (*x*) is both a state and a forcing variable, since it can be partially controlled during the time course of experiments. Algal concentrations, appendicularian weights and particles resulting from their feeding activities are expressed in carbon units. An appendicularian is represented by its total carbon weight (*Wa*), divided into structural biomass (trunk and tail, *Sb*) and gonad (*G*) weights. The other state variables represent different forms of carbon loss from the beginning of the life cycle: respiration (*R*), fecal pellet egestion (*Fp*), house secretion (*H*), and food detritus trapped inside of the house (*Dh*). Symbols and units of the variables are listed in Table 1.

Only assimilated food contributes to the increase of the body weight (Fig. 1). The fraction of the filtered particles that is not ingested (*Dh*) is lost when an appendicularian discards its house (Flood and Deibel, 1998). Similarly, the portion of the ingested food that is not assimilated is released as fecal pellets (*Fp*). As the metabolic reserves stored in appendicularians are low (Deibel et al., 1992), we consider that assimilated matter is directly invested in houses, gonads and structural biomass. We are assuming that, except for house secretion, the only energetic expense for the body and the gonads is respiration.

Since the influence of the size of food particles on filtration is only partially known (Flood and Deibel, 1998; Fernández et al., 2004), the model does not consider the influence of particle size on filtration efficiency. The model is based on the physiological balance of one individual for which the body weight increases in relation to the rates of food intake (assimilation) minus metabolic losses (houses secretion and respiration). Model parameters and equations are given in Tables 2 and 3.

2.2. Larval stage

The weight of the appendicularian (*Sb*) is initially equal to the egg weight (0.038 µg C, Lombard et al., 2009-this volume). During embryonic development, the gonad weight remains very low and is not measurable. Here we use 2% of the total weight as initial value for

Table 2
Oikopleura dioica. Model parameters, descriptions and units.

Symbols	Description	Values	Units
<i>r1</i>	Respiration rate at 0 °C during the development phase	0.07276 ^a	µg C µg C ⁻¹ d ⁻¹
<i>r2</i>	Respiration rate at 0 °C during the growth phase	0.1086 ^a	µg C µg C ⁻¹ d ⁻¹
<i>t10</i>	10th root of the Q10 coefficient for respiration	1.08717 ^a	wd
<i>a</i>	Exponent of the allometric equation for respiration at 0 °C	0.75 ^a	wd
<i>h0</i>	House secretion rate at 0 °C during the development phase	0.022	µg C µg C ⁻¹ d ⁻¹
<i>th</i>	First house deployment threshold	0.153 ^b	wd
<i>t10_f</i>	10th root of the Q10 coefficient for filtration	1.06 ^c	wd
<i>kf</i>	Half-saturation constant for the filtration	150 ^d	µg C l ⁻¹
<i>b</i>	Exponent of the allometric equation for filtration at 0 °C	0.9 ^d	wd
<i>f</i>	maximum food intake for filtration at 0 °C	3.7 ^{c,d}	µg C µg C ⁻¹ d ⁻¹
<i>imax</i>	Maximum fraction of food not ingested	0.85	wd
<i>amax</i>	Maximum fraction of food not assimilated	0.9	wd
<i>ka</i>	Half-saturation constant for the assimilation	130 ^d	µg C l ⁻¹
<i>ki</i>	Half-saturation constant for the ingestion	200 ^e	µg C l ⁻¹
<i>fh</i>	Fraction of assimilated food allocated to houses secretion	0.35	wd
<i>p1</i>	Fraction of assimilated food allocated to gonad during growth phase	0.13	wd
<i>b1</i>	Exponent of the Holling type III relationship for the gonad matter allocation increase after hatching	2	wd
<i>k1</i>	Half-saturation constant for the gonad matter allocation increase after hatching	0.06	wd
<i>b2</i>	Exponent of the Holling type III relationship for the gonad matter allocation increase during maturation	6	wd
<i>k2</i>	Half-saturation constant for the gonad matter allocation increase during maturation	0.32	wd
<i>St</i>	Spawning threshold	0.76 ^d	wd

wd: without dimension.

Sources: ^aLombard et al. (2005); ^bSato et al. (2001); ^cBroms and Tisselius (2003); ^dLombard et al. (2009-this volume); ^eAcuña and Kiefer (2000).

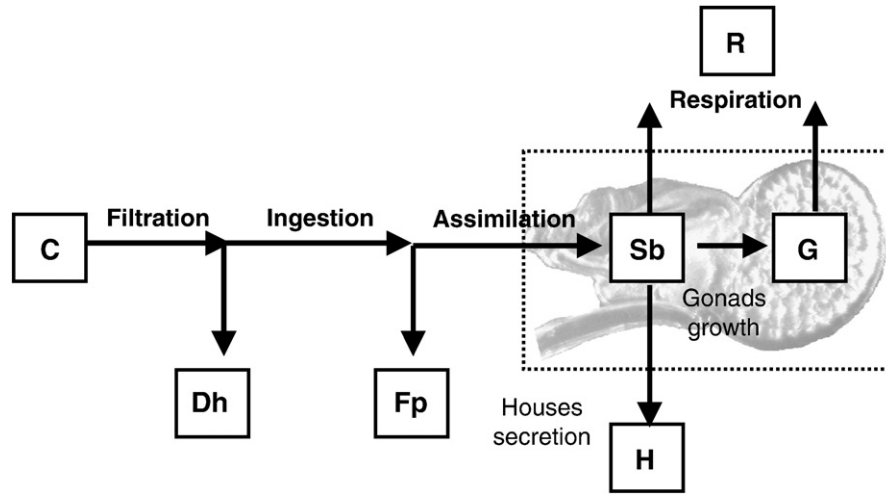


Fig. 1. *Oikopleura dioica*. Conceptual schema of the metabolic balance model. Symbols and units of the different variables are described in the Table 1.

G. The other state variables, except food particle concentration (x), are set to zero. During embryogenesis and the larval stage the individual energy expense due to respiration and secretion of the first house leads to a negative growth rate. Respiration rate of *O. dioica* in relation to size, filtration activity and temperature has been described in Lombard et al. (2005). They showed that the respiration rate of anesthetized appendicularians was only 33% lower than in active animals. Eggs are motionless and the larva is often immobile. We assume the respiratory activity of an inactive larva as 67% of the value measured for active individuals (Lombard et al., 2005), and that the respiratory quotient ($\text{CO}_2:\text{O}_2$) is 0.87 (Mayzaud et al., 2005). The respiration rate ($rtot$) of larvae as a function of their carbon weight (Wa) and temperature (T) can be expressed using the following allometric relationship:

$$rtot = r1 t10^T Wa^a. \quad (1)$$

The fraction of carbon respired by Sb and G are defined, respectively by:

$$r_G = rtot(G/Wa) \text{ and } r_{Sb} = rtot(Sb/Wa). \quad (2)$$

The secretion rate (h) of the first house can be similarly described by the following allometric relationship:

$$h = h0 t10^T Sb^a. \quad (3)$$

This relationship is a simplification and implies that houses can be produced immediately after egg fertilization, whereas their secretion actually begins when the organs of the larva are completely formed (Fenaux, 1998). Unfortunately, only few data are available on the timing of this event in *O. dioica*. The individual is considered to enter the growth phase as soon as the weight of the secreted house reaches a critical fraction (th) of the appendicularian weight (Wa). This threshold corresponds to the weight of the newly secreted house [$15.3 \pm 4.8\%$ of the appendicularian carbon weight, Sato et al. (2001)]. According to Troedsson et al. (2002) at the temperatures of 15 °C and 20 °C, 50% of animals proceed from egg to development of the first house in 15 and 11 h, respectively, after fertilization. Consequently, the parameter $h0$ is calibrated in such manner that the state variable H reaches the threshold $H > th Wa$ in 15 h for 15 °C and in 11 h for 20 °C.

2.3. Growth

As soon as the young appendicularian inflates its first house, it is able to filter seawater and increase its weight. In the model, we assume that the processes of carbon acquisition (filtration, ingestion and assimilation) and associated metabolic expenses (respiration, house secretion) act independently from the allocation of matter to the gonads. This assumption allows calibration of the growth rate without considering the gonad maturation process, which is calibrated afterwards.

The total amount of filtered food (F) is a function of individual weight (Wa), temperature (T) and food concentration (x) (Acuña and Kiefer, 2000; Broms and Tiselius, 2003; Selander and Tiselius, 2003; Tiselius et al., 2003; Fernández et al., 2004; Lombard et al., 2009-this volume):

$$F = f Wa^b t10_f^T \frac{x}{kf + x} \quad (4)$$

where $t10_f$ is the 10th root of the Q_{10} coefficient estimated by Broms and Tiselius (2003). kf and b were calculated in Lombard et al. (2009-this volume), and f is a scaling factor deduced from Lombard et al. (2009-this volume) using the $t10_f$ value at 15 °C. The clearance rate (C $\text{l ind}^{-1} \text{d}^{-1}$) was calculated as follows:

$$C = \frac{F}{x}. \quad (5)$$

The fraction of the filtered food not ingested, which accumulates in houses, is lost when the appendicularian abandons the old house and inflates the new one. Gorsky et al. (1984) and Gorsky and Palazzoli

Table 3

Oikopleura dioica. Differential equations of the model for developmental and growth phases.

Derivative	Development phase	Growth phase
$D(x)/dt =$	0	$-F$
$D(Dh)/dt =$	0	$F(1 - i)$
$D(Fp)/dt =$	0	$I(1 - ae)$
$D(Sb)/dt =$	$-r_{Sb} - h$	$A - r_{Sb} - fhA - fgA$
$D(G)/dt =$	$-r_G$	$fgA - r_G$
$D(H)/dt =$	h	fhA
$D(R)/dt =$	$r_G + r_{Sb}$	$r_G + r_{Sb}$

Variables and parameters are defined in the Tables 1 and 2. For calculation of flux F , see Eq. (4); i , see Eq. (6); I , see Eq. (7); a , see Eq. (8); A , see Eq. (9); fg , see Eqs. (11) and (12); r_G and r_{Sb} , see Eqs. (1) and (2) for developmental phase or 10 and 2 for growth phase; h , see Eq. (3).

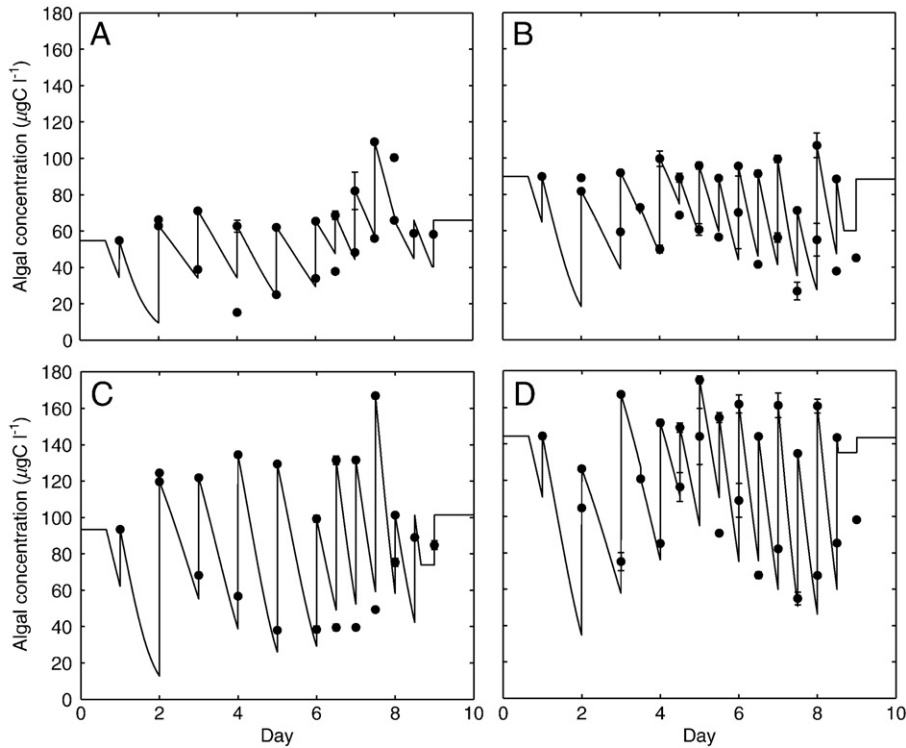


Fig. 2. Algal concentration ($\mu\text{g C l}^{-1}$). Comparison between experimental observations and outputs of the model over the life cycle of four *Oikopleura dioica* populations fed with four different algal concentrations.

(1989) found that 25 to 37% of the food collected by *O. dioica* remains in discarded houses. More recently, Acuña and Kiefer (2000) showed that the fraction of food filtered and effectively ingested decreases with increasing algal concentrations. We assume here that the ingestion efficiency (i) is dependent only on the food concentration following a Michaelis–Menten relationship:

$$i = 1 - i_{\max} \frac{x}{ki + x}. \quad (6)$$

The ingestion rate (I) is:

$$I = iF. \quad (7)$$

The assimilation efficiency (ae) (i.e., the assimilated fraction of the ingested food), decreases with increasing food concentration (Lombard et al., 2009–this volume), and can be calculated as follows:

$$ae = 1 - a_{\max} \frac{x}{ka + x}. \quad (8)$$

The assimilation rate (A) can be thus considered as:

$$A = ael. \quad (9)$$

A fraction fh of the assimilated food serves for house elaboration, whereas the remaining is used for somatic and gonadal growth.

The rates of respiration associated with the gonad and structural biomass maintenance are calculated as for the larval stage (Eqs. (1) and (2)), by using the $r2$ parameter corresponding to the respiration of an active appendicularian (Lombard et al., 2005).

$$rtot = r2t10^T Wa^a. \quad (10)$$

The onset of maturation is related to the ratio between the gonad and the total body volume (Lombard et al., 2009–this volume), and

corresponds to an increase in gonad growth. Thus, we assumed that the fraction of assimilated food that is allocated to the growth of the gonads (fg) is dependent on the index of maturity (mi) following an empirical Holling type III relationship:

$$mi = \frac{G}{Wa} \quad (11)$$

$$fg = p1 \frac{mi^{b1}}{mi^{b1} + k1^{b1}} + (1 - fh - p1) \frac{mi^{b2}}{mi^{b2} + k2^{b2}}. \quad (12)$$

The first part of the Eq. (12) takes into consideration the observation that immediately after hatching, only a small amount of energy is allocated for gonad maturation and almost all the assimilated carbon is used for the somatic growth and house secretion (Troedsson et al., 2002). After this phase, a $p1$ fraction of the assimilated carbon is used for the gonad growth. The second part of the equation represents the maturation phase of the appendicularian: when mi reaches a threshold corresponding to the $k2$ parameter, all the assimilated food, except the fh fraction allocated for house secretion, is invested in gonad maturation. This formulation simulates the progressive and opposite development of the structural biomass and gonads without complicating the model with fixed thresholds. Parameters of the Eq. (12) were calibrated to reproduce the gonad growth evolution observed by Troedsson et al. (2002) and Lombard et al. (2009–this volume).

We hypothesize that, as all the assimilated food is invested in gonads during maturation, the respiratory losses associated with the structural biomass are sufficient to explain the observed autolysis of the trunk during the maturation process (Fenaux and Gorsky, 1983).

Spawning is a short process that occurs when the weight of the gonads exceeds 70% of the total body weight (Lombard et al., 2009–this volume). Therefore, we assume that reproduction occurs when the G/Wa ratio reaches a higher value than the St threshold. At this

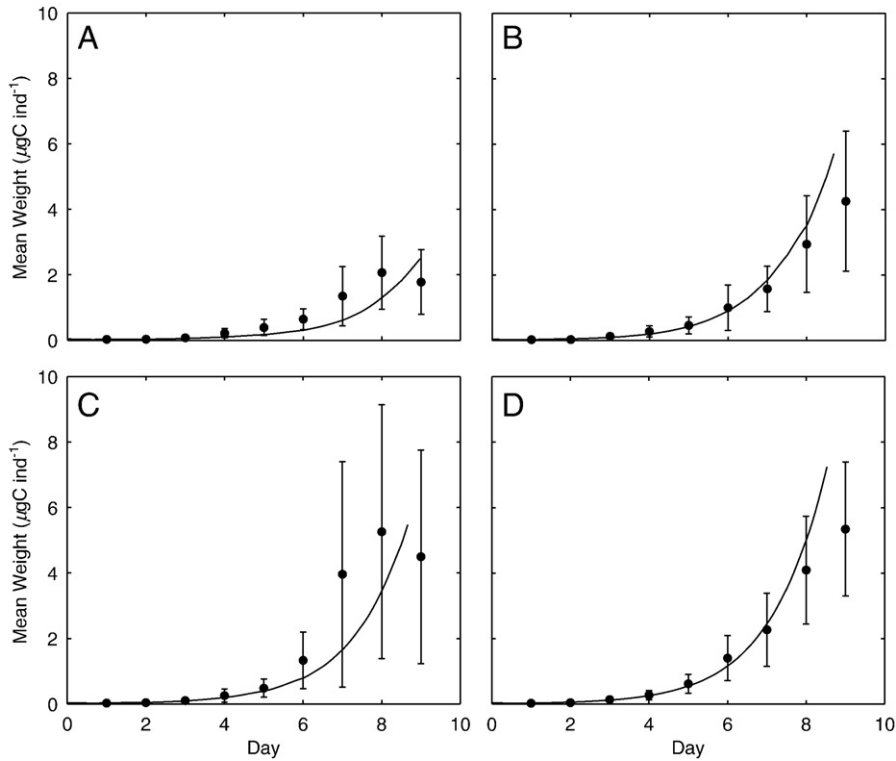


Fig. 3. Same as Fig. 2 but comparing the mean appendicularian weight ($\mu\text{g C ind}^{-1}$) experimentally observed with W_a simulated by the model.

time, the gonads (G) are converted into gametes, and the weight of the structural biomass is set to zero (death of the animal).

The system of differential equations (Table 3) was solved using the Euler integration method with a short time step (0.001 d). After

simulations of 10 days, the cumulative difference between an exponential curve corresponding to the maximal rate integrated and mathematically solved is only 0.02%, which is a reasonable value for the integration error (data not showed).

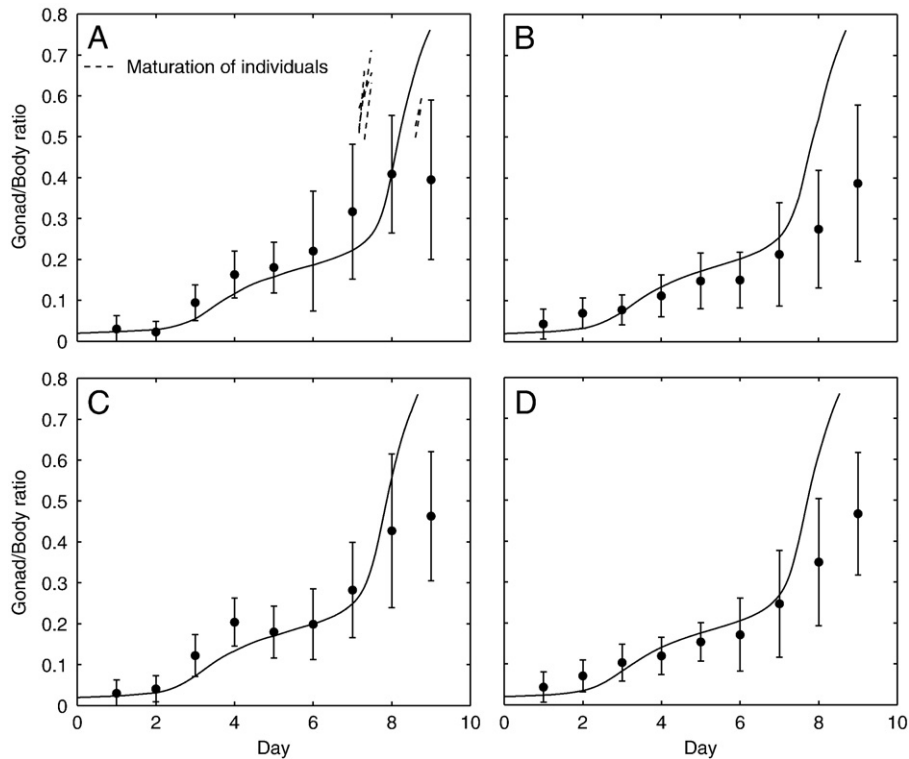


Fig. 4. Same as Fig. 2 but comparing the ratio between gonad and total body weight experimentally observed with the maturation indicator m_i (G/W_a) simulated by the model. Dotted lines in Fig. 4A represent the maturation of isolated appendicularians.

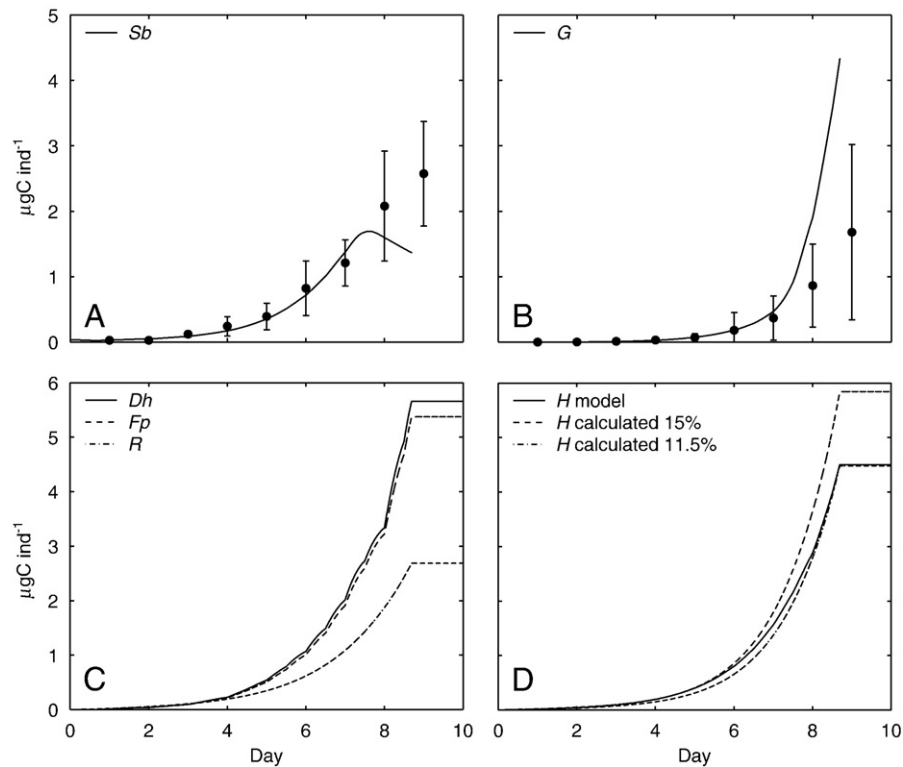


Fig. 5. Total outputs of the *Oikopleura dioica* model for data from the population fed with algal concentrations $\approx 100 \mu\text{g C}$ (Figs. 2C, 3C and 4C). (A) Carbon weight of the structural biomass, (*Sb*) and (B) of the gonad (*G*) compared with experimental observations. (C) Cumulative carbon weight of the detritus accumulated in houses (*Dh*) of fecal pellets (*Fp*), and of carbon lost by respiration (*R*). (D) Cumulative carbon weight of houses produced by appendicularians compared with two empirical calculations assuming that the weight of one house represent respectively 15% and 11.5% of the appendicularian carbon mass.

2.4. Calibration and analyses

The parameters r_1 , r_2 , t_{10} , a , th , t_{10f} , kf , b , f , ka , ki and St originate from the literature (Table 2). The other parameters were identified by comparing model outputs to experimental observations using a least square minimization method (Nelder–Mead simplex method). Parameters involved in somatic growth were determined first, followed by those related to maturation.

Model calibration was based on four experimental data sets (Lombard et al., 2009–this volume) for which the greatest number of variables was simultaneously measured (trunk and gonad volumes, clearance rate, algal concentrations at the beginning and end of the incubations and appendicularian density). After calibration, model simulations were compared with experimental results. Model simulations were considered to be correct if model simulation and experimental results were not significantly different at the 95% confidence level.

Model sensitivity was analyzed in regard to the mean growth rate within a large range of food concentrations and for different size classes (Fig. 11D). Parameters controlling the appendicularian growth were varied by $\pm 10\%$, and deviation from the standard simulation was averaged for all the conditions tested.

3. Results and discussion

3.1. Calibration

The model correctly simulated algal consumption, appendicularian growth, and the fraction of the body weight contributed by the gonads in the four populations (Figs. 2, 3 and 4, Table 5). The considerable fluctuations of the food concentration (Fig. 2) result from daily readjustments of the algal concentration. Two inadequacies were nevertheless observed. The first is due to underestimation of the algal concentration during the first 2 days (Fig. 2). This may be explained by

insufficient control of the experimental beakers during the period between spawning and the beginning of filter feeding. In order to avoid stress and minimize mortality during this key period, the young appendicularians were not transferred to fresh seawater until they developed their first houses and the detritus could have stimulated bacterial growth. The second bias was observed for the last-day simulation of the gonad:body ratio, for which the model overestimates the gonad proportion (Fig. 4). This result is due to the fact that the model applies to one individual, whereas the data represent an average population, in which maturation of individuals is not synchronized. A few individuals mature rapidly and spawn earlier than the others (Fig. 4A). After release of their gametes, appendicularians die. Then the mean gonad proportion of the population remains low due to the spawning of earliest mature animals and does not correctly represent the maturation process of individual organisms.

The model outputs (Fig. 5) show that appendicularians grow exponentially. Consequently, the losses of carbon accumulated during the somatic growth phase in houses and associated detritus, respiration, and fecal pellets also increases exponentially. For these experimental conditions, the amount of detritus accumulated in old houses (*Dh*) is of the same order of magnitude as the production of fecal pellets (*Fp*). The amount of respired carbon is two-fold lower than the amount of carbon aggregated in discarded houses or fecal pellets. Respiration rate represents, therefore, only a small amount of the carbon loss. Indeed, compared to the respiration carbon losses, appendicularians produce 5.7 times more C detritus in the form of large particles ($Fp + H + Dh$), and only 23% of the filtered food is used for the appendicularian growth. During gonad maturation, decrease in the appendicularian structural biomass is due to respiration, which dominates the metabolic balance. The total production of houses is very similar to the value calculated using the following equation (Fenaux, 1985; Sato et al., 2001):

$$dH = 0.15Wa24((0.033T) - 0.3). \quad (13)$$

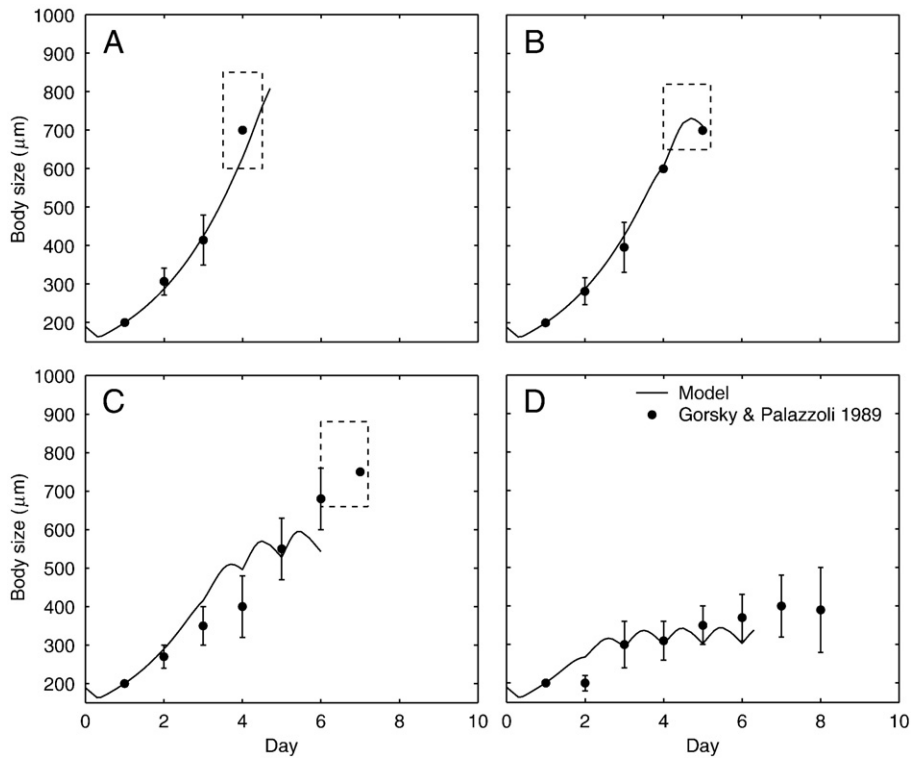


Fig. 6. Model validation on the entire life cycle. Comparison of the model-simulated trunk size with experimental observations from Gorsky and Palazzoli (1989) at 23 °C and with four different appendicularian densities. The number of appendicularian present in 1 L were 10 individuals (A), 20 (B), 50 (C) and 200 (D). Living *Oikopleura dioica* were daily transferred into fresh seawater. To keep a constant population density, dead individuals were removed and replaced by others growing in similar conditions. The dotted square represent the spawning limits of the different populations represented by the first and the last quartiles of the mature animals sizes and by the time at which 25 and 75% of the population had spawned.

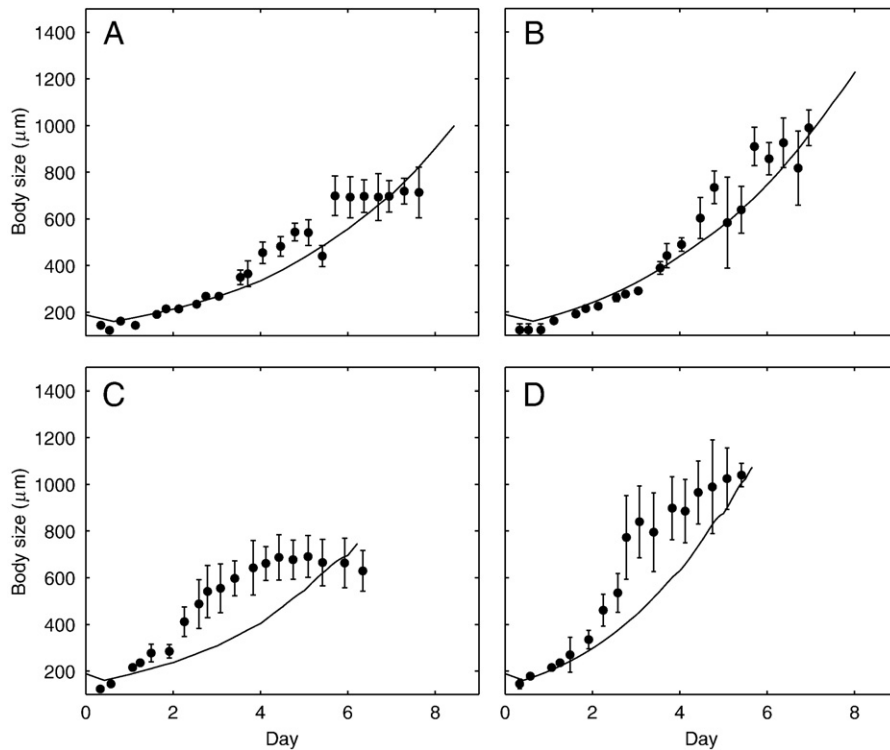


Fig. 7. Model validation on the entire life cycle. Comparison of the model-simulated trunk size with experimental observations from Troedsson et al. (2002) at 15 °C (A, B) and 20 °C (C, D) with low (A, C) and high (B, D) food concentrations. The growth rate of *Oikopleura dioica* fed with two food concentrations was estimated for populations maintained at 15 and 20 °C in 6-litre beakers. During the 6 days of the experiment, the number of appendicularians was 600, 300, 150, 110, 80 and 50. Appendicularians were transferred every day into fresh seawater complemented with algal culture. Initial food concentration was restored 12 h after each transfer (Troedsson, pers. comm.). We estimated the carbon content of the algal mixture (*Isochrysis galbana* and *Chaetoceros calcitrans*) using the cell volume-to-carbon conversion factor given by Mullin et al. (1966). We also assumed a background food concentration of 30 µg C l⁻¹, consistent with the particle concentration of the seawater used to grow the appendicularians.

Table 4
Oikopleura dioica. Experiments used to validate the model in relation to physiological processes.

Source	Interaction studied	Feeding regime	T (°C)	V (l)	x (µg C l ⁻¹)	Wa (µg C)	t (d - 1)
Fenaux (1985)	House production rate vs. T °C		13–23	0.1	150	1.08	0.5
López-Urrutia and Acuña (1999)	Gut passage time vs. food concentration	<i>I. galbana</i>	15	0	40–360	1	0
		<i>Tetraselmis suecica</i>	15	0	40–361	1	0
		<i>Chlorella</i> sp	15	0	40–362	1	0
	Gut passage time vs. temperature	<i>I. galbana</i> or <i>Chlorella</i> sp	13.5–21	0	60	1	0
		<i>I. galbana</i>	10–20	0	30	1	0
Acuña and Kiefer (2000)	Filtration rate vs. food concentration	<i>I. galbana</i>	10–20	0	250	1	0
		<i>I. galbana</i> (new houses)	15	0.02	1–3200	5.41	0.03
		<i>I. galbana</i> (average houses)	15	0.02	1–1600	5.41	0.03
Selander and Tiselius (2003)	Filtration rate and fecal pellets production rates vs. food concentration	<i>I. galbana</i>	20	0.16	0–700	0.26	0.5

The data for temperature, experimental volume, food concentration (x) and appendicularian weight (Wa) used to initiate the model were obtained from the indicated study and length of the model simulation is the same as for the experimental incubation (t).

The experimentally observed cumulative house production during the 8.7 days of simulation (Eq. (13)) is only 20% higher than the house production simulated by the model. Using a house:body weight ratio of 11.5% (Eq. (13)) instead of the $15.3 \pm 4.8\%$ given by Sato et al. (2001), this difference decreases to 0.55%, indicating that the actual weight of the house relative to body weight could be lower than 15%. The model-estimated ratio remains, however, within the standard deviation estimated by Sato et al. (2001).

3.2. Validation

As the discrepancies between model and data for small individuals are better depicted by size than by weight, we have chosen to validate the model on the basis of the trunk size variation measured for two independent studies conducted in different conditions of food and temperature (Gorsky and Palazzoli, 1989; Troedsson et al., 2002, Figs. 6 and 7). The weight values calculated by the model were converted to trunk size using the size-to-weight conversion factor given by King et al. (1980). Our model, calibrated with experiments conducted at 15 °C (Lombard et al., 2009-this volume) with four different food regimes, correctly reproduces the growth rates obtained at 23 °C for the different appendicularian densities (Gorsky and Palazzoli, 1989, Fig. 6, Table 5). The negative variations of size, which occur in denser populations (200 individuals in 1 L), reflect the strong depletion of food before its renewal, a period during which respiration exceeded food assimilation. The

increase in generation time (i.e., the time elapsed from egg production to spawning) due to food limitation is correctly simulated for the three experiments in which reproduction could be observed (Fig. 6 A, B and C). For high population densities, the model predicts that reproduction occurs in day 6 when the appendicularian body reaches 320 µm. This was not observed experimentally (Fig. 6 D) and may be due to the high mortality rate in the experiments with high appendicularian concentrations (compensated by introduction of new appendicularians). Another possibility is that the small mature animals were not identified (a female of this size would produce only 4.5 eggs according to the model) among the numerous appendicularians.

We also compared our model to the data reported by Troedsson et al. (2002). The growth rate of *O. dioica* is well-simulated for different growing conditions, with only a significant deviation appearing from day 3 to 5 at 20 °C when concentrations of food were low (Fig. 7, Table 5). The generation time was also consistent, except at 15 °C. The longer life cycle simulated in 15 °C is probably due to the fact that after day 6, the remaining appendicularians were not abundant enough to follow the complete reproductive cycle of the cohort.

3.3. Validation of physiological processes

The experimental conditions used to validate the physiological rates of the model are listed in Table 4. Response of the filtration rate

Table 5
Oikopleura dioica. Results for the tests comparing the model results with experimental observations (Figs. 2–10).

Data	Source	Figure	Test model ≠ data	Data	Source	Figure	Test model ≠ data
Algal concentration	Lombard et al. (2009-this volume)	Fig. 2A	ns	Filtration rate	Acuña and Kiefer (2000)	not showed	*
		Fig. 2B	ns			not showed	ns
		Fig. 2C	ns			not showed	ns
		Fig. 2D	ns			not showed	ns
Body weight	Gorsky and Palazzoli (1989)	Fig. 3A	ns	House production rate	Selander and Tiselius (2003)	not showed	ns
		Fig. 3B	ns			Fig. 8A	ns
		Fig. 3C	ns	Fecal pellet production rate ^a	Selander and Tiselius (2003)	not showed	ns
		Fig. 3D	ns		Selander and Tiselius (2003)	Fig. 8B	***
		Fig. 4A	ns		Gut passage time ^a	López-Urrutia and Acuña (1999)	Fig. 9A
Gonad/body ratio	Gorsky and Palazzoli (1989)	Fig. 4B	ns	Fecal pellet production rate ^b	Selander and Tiselius (2003)	Fig. 9B	***
		Fig. 4C	ns			Fig. 9C	***
		Fig. 4D	ns			Fig. 9D	***
		Fig. 4E	ns			Fig. 9E	***
Body size	Troedsson et al. (2002)	Fig. 6A	ns	Gut passage time ^b	López-Urrutia and Acuña (1999)	Fig. 9F	***
		Fig. 6B	ns			Fig. 8B	ns
		Fig. 6C	ns			Fig. 9A	ns
		Fig. 6D	ns			Fig. 9B	ns
Body size	Troedsson et al. (2002)	Fig. 7A	ns	Fig. 9C	ns		
		Fig. 7B	ns	Fig. 9D	*		
		Fig. 7C	*	Fig. 9E	ns		
		Fig. 7D	*	Fig. 9F	ns		
Lifetime length	López-Urrutia et al. (2003a)	Fig. 10A	ns				

For each data set, we have checked the significance of the differences between data and model simulations (i.e., model = data). ns: not significantly different. *Significantly different at $p = 0.05$. **; $p = 0.01$. ***: strongly different with $p = 0.001$.

^a Fecal pellet production rate simulated by the model assuming that the weight of one fecal pellet is a constant fraction of the individual weight.

^b FPR simulated assuming that the weight of one fecal pellet depends on the food concentration (Eq. (14)).

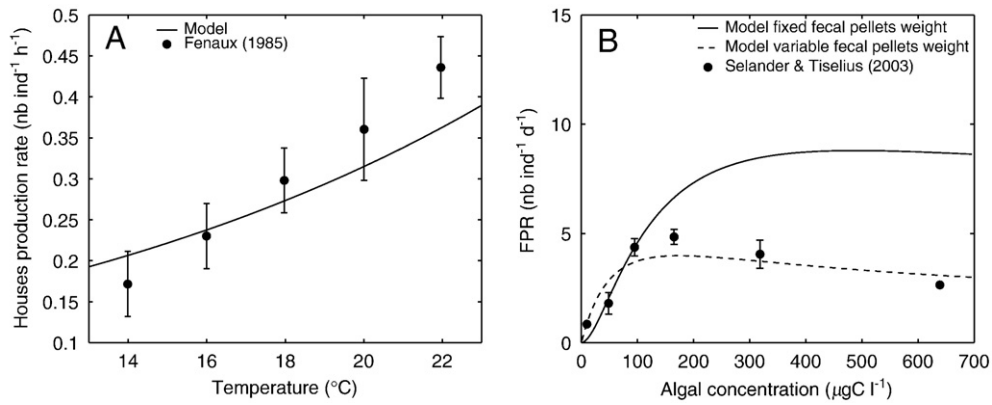


Fig. 8. (A) Temperature effect on *Oikopleura dioica* house production rate. Comparison between model outputs and experimental observations from Fenaux (1985). (B) Algal concentration effect on *Oikopleura dioica* fecal pellets production rate (FPR). Comparison between experimental observations from Selander and Tiselius (2003) and model output. The output of the model in relation to the carbon content of fecal pellets is calculated in fecal pellet number using two different transformations. The first transformation considers that the weight of one fecal pellet represents a fixed part of the appendicularian weight, whereas the second transformation assumes that the weight of a fecal pellet is dependent on appendicularian weight and food concentration (Eq. (14)). Experimental conditions used to initialise the model were listed in Table 4.

to the food concentration is adequately simulated for four growing conditions differing by temperature and individual size (data not showed, Table 5). In all cases, the model predictions were comparable with observations. Filtration, ingestion, assimilation and respiration rates were precisely measured during experiments and these data were used to calibrate the related functions of the model. The other processes (house production rate, fecal pellets production rate, gut passage time) were measured in other studies (Fenaux, 1985; López-Urrutia and Acuña, 1999; Selander and Tiselius, 2003). These data were not used to calibrate the related functions, but were used for the validation. These relationships were calibrated by optimizing the fit between the model outputs and the observed increase of the appendicularian weight. Consequently, the agreement of the model outputs with the measured productions of houses, fecal pellets and the gut passage time provides indirect evidence that the functional hypotheses concerning the regulation of the metabolic balance were correct.

On the basis of a house vs. individual mean weight ratio of 11.5% (see above), the model correctly simulates the effect of temperature on the production of houses (Fig. 8A, Table 5).

To compare the measured number of fecal pellets produced per individual and per day (FPR), the simulated production values (F_p) expressed in $\mu\text{g C ind}^{-1} \text{d}^{-1}$ were converted following two hypotheses developed for copepods, but never previously tested for appendicularians: (1) the weight of one fecal pellet (f_w) is a constant fraction (1.75%) of the individual weight (Dagg and Brown, 2004) and (2) the weight of fecal pellets depends on the food concentration according to the following Michaelis–Menten relationship (Dagg and Walser, 1986; Bochsansky and Deibel, 1999).

$$f_w (\mu\text{gC fecal pellets}^{-1}) = 0.0651 W_a \frac{x}{203 + x} \quad (14)$$

Parameter values were obtained using a least square minimization method between experimental observations and model outputs. The gut passage time (GPT) was estimated from FPR assuming that the gut of *O. dioica* always contains 2.87 fecal pellets (López-Urrutia and Acuña, 1999).

When using the first conversion method, modeled FPR and GTP do not agree with experimental data, with FPR and GTP are overestimated by the model in the highest and lowest food concentrations respectively, and GTP underestimated for highest concentrations (Figs. 8B and 9, Table 5). The model is significantly improved when the effect of food concentration on f_w is taken into account (Figs. 8B and 9, Table 5). This result may indicate that the weight of appendicularian fecal pellets depend on the food concentration, as observed for copepods (Dagg and Walser, 1986; Urban-Rich et al., 1998).

3.4. Generation time

Behavior of the model was explored by simulating the *O. dioica* life cycle in different food concentrations and temperatures. Generation times predicted by the model for two different food concentrations and various temperatures are in agreement with available data (Fig. 10A, López-Urrutia et al., 2003a). Nevertheless, the model slightly overestimates the generation time compared with observations for two possible reasons: (1) the model predicts the generation time of *O. dioica* (i.e., the time elapsed from egg production to spawning), whereas most studies focused on the development time (i.e., the time elapsed from hatching to spawning) without taking into account the embryonic phase; and (2) the overestimation was partly due to the fact that the model was designed to simulate the growth of the whole population without omitting the last few animals of the cohort (what is often the case), which are generally the largest and can be significant in terms of egg production.

When compared to the strong effect of temperature, the influence of food concentration on the generation time is small. The model predicts that the shortest generation time occurs at a food concentration of about $100 \mu\text{g C l}^{-1}$ (Fig. 10B). Fig. 10B shows that the generation times increase with increasing or decreasing food concentration around this optimal food range. In the model, the length of the life cycle is governed by the relative importance of somatic and gonad development, directly induced by the balance between assimilation and respiration rates. When both processes accelerate, maturation accelerates also, and the generation time shortens. This result occurs when the temperature increases. On the contrary, if the assimilated food quantity decreases (in the case of limitation or excess of food) and respiration losses relative to the appendicularian weight remain stable, maturation slows down and generation time increases.

3.5. Growth pattern

Growth rate, mature appendicularian size, and potential egg production calculated from the gonad weight show an optimum value within the food range of $50\text{--}200 \mu\text{g C l}^{-1}$ (Fig. 11 ABC), but decrease in higher food concentrations. This can be explained by a decrease in filtration, ingestion and assimilation efficiency observed in high food concentrations. The maximum growth rate is reached at higher temperatures, whereas the maximum trunk sizes and egg production are obtained in lower temperatures. This temperature-dependent difference in size is related to the difference in the Q_{10} estimations between filtration and respiration (parameters t_{10f} and t_{10r}). If these two parameters were identical, the size for reproduction would remain unchanged, whatever the temperature. The growth rate

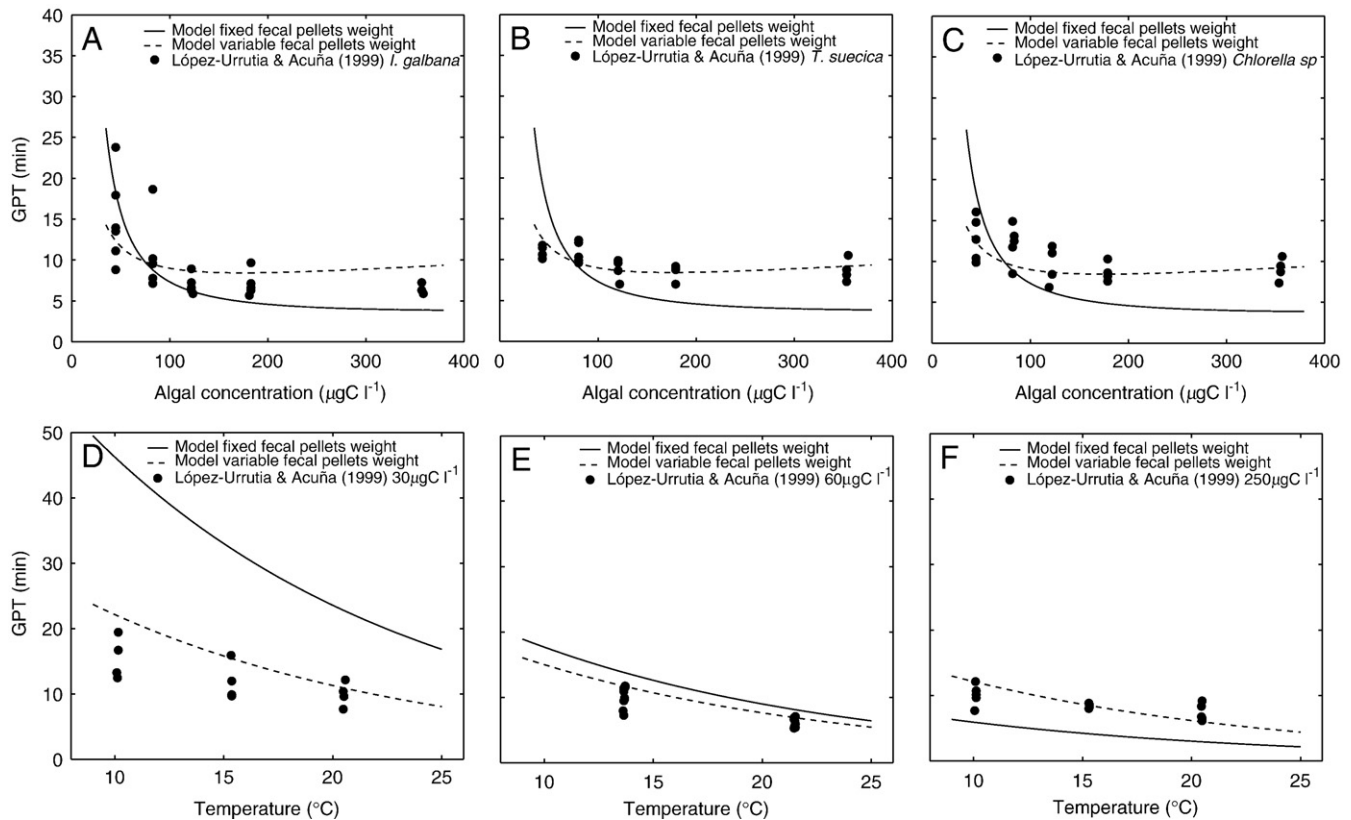


Fig. 9. Effect of temperature and algal concentration on *Oikopleura dioica* gut passage time (GPT). Comparison between experimental observations and model outputs. The GTP output of the model was calculated from the carbon weight of the fecal pellet content using two different transformations. The first transformation considered that the weight of one fecal pellet represents a fixed part of the appendicularian weight, whereas the second transformation assumes that the weight of a fecal pellet is dependent on appendicularian weight and food concentration (Eq. (14)). Experimental conditions used to initialise the model are listed in the Table 4.

estimated by the model also provides an indication on the limits of temperature and food concentration in which the growth balance is positive. The model suggests the existence of an optimal food concentration centered on a rather low value of $100 \mu\text{g C l}^{-1}$, as well as the existence of a threshold food level under which growth cannot be sustained. These outcomes are in agreement with previous studies (Acuña, 2001; López-Urrutia et al., 2003a), according to which appendicularians are able to grow and survive in feeding conditions corresponding to oligotrophic environments. The subsistence food concentration remains in the range ($20\text{--}30 \mu\text{g C l}^{-1}$) of the values provided in previous models (López-Urrutia et al., 2003a).

The model shows that the food ranges for an optimal growth rate are not the same for small ($200\text{--}400 \mu\text{m}$ body size) and large ($>800 \mu\text{m}$) appendicularians (Fig. 11D). Small animals, at a given food concentration, have a potentially higher growth rate than large ones. Growth rate of small appendicularians is also much more affected by the food availability than that of large individuals. This is due to the difference in the allometric exponent between respiration and filtration (parameters a and b) and explains why large appendicularians are able to maintain a higher growth rate in wider food ranges. This result also suggests that growth of the early development stages is critical for the survival of appendicularian populations in sub-optimal environments. The assumption that small appendicularians are more sensitive to food limitation than larger ones was already noted in a previous modeling study (López-Urrutia et al., 2003a).

3.6. Ecological niche

An ecological niche can be defined as a measure of species fitness in a multidimensional space of environmental conditions (Levins, 1968). Therefore, the calculated food and temperature ranges in which *O. dioica*

is able to develop (Fig. 11 A) partially determine the fundamental ecological niche breadth of this appendicularian in relation to these two parameters. Nevertheless, the ecological niche breadth defined by our model has to be considered with caution, as mortality is not considered. Growth rate of populations in natural environments is generally reduced by mortality and predation; therefore, the ecological niche breadth of appendicularians should be narrower than predicted from individual growth observations. Assuming the high mortality rates recorded experimentally (Paffenhöfer, 1973; Lombard et al., unpublished data), and knowing the high natural predation exerted on appendicularians (Sommer et al. 2003; López-Urrutia et al., 2004b; Purcell et al., 2004; Stibor et al., 2004), this model certainly overestimates the extent of the *O. dioica* ecological niche. This outcome is supported by the fact that, despite the very high growth rate of *O. dioica* predicted by our model and experimentally observed (Hopcroft and Roff, 1995; Troedsson et al., 2002; Lombard et al., 2009-this volume), these organisms are less frequent in the plankton than copepods, which have lower growth rates (Peterson et al., 1991; Hirst and Bunker, 2003). In order to improve the estimation of the ecological niche breadth, the model should be adapted for appendicularian population dynamics. Unfortunately, in situ estimates of fertilization success, natural mortality, and predation, which are needed for simulating appendicularian population dynamics, are lacking.

3.7. Model improvement

3.7.1. Sensitivity

Model sensitivity was analyzed on a standard simulation of instantaneous growth rate in relation with appendicularian size and food concentration (Fig. 11D) and for a 10% variation of each parameter (Table 6).

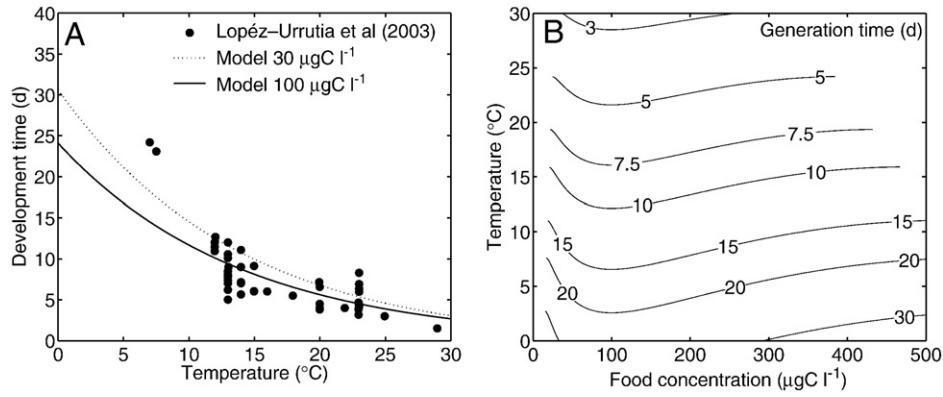


Fig. 10. *Oikopleura dioica* model pattern. Effect of temperature and food concentration on the generation time predicted by the model. (A) Comparison of the model generation times in two different food concentrations and various temperatures with experimental or in situ observations (data compilation from López-Urrutia et al., 2003a). (B) Generation times predicted by the model for different temperatures and food concentrations.

The model is most sensitive to the parameters controlling the effect of temperature (t_{10} and t_{10r}) because the variation introduced with these parameters is raised to the power of the temperature. Variations higher than 10% were obtained for b , f , i_{max} or a_{max} . A precise estimation of these parameters is therefore crucial to understand appendicularian physiology.

3.7.2. Improvements

Future improvements of the model should begin with the nutritional quality index of ingested particles. This adjustment was not feasible here because most of the data were acquired without indication concerning the food quality or its nitrogen content. In addition, the numerical conversions of algal food, Chl *a* or cell biovolume to carbon are sources of potential bias for the model

validation. Bacteria present during experiments, rarely measured, could constitute a significant food source (Fernández et al., 2004). Thus, to improve the model calibration in future studies, it will be crucial to systematically measure carbon content of the food or bacterial content together with the traditional measurements of Chl *a*, and algal concentrations or biovolumes.

Determination of the size range of particles effectively retained by appendicularians should also be more precise. As the upper size limit of *O. dioica*'s retention efficiency remains experimentally undetermined and as feeding experiments are conducted mostly with small algae, it was not critical to take into account the food particle sizes at this stage of the model validation. However, taking in account the upper and lower limits of retention efficiency will certainly increase the applicability of the model to natural conditions.

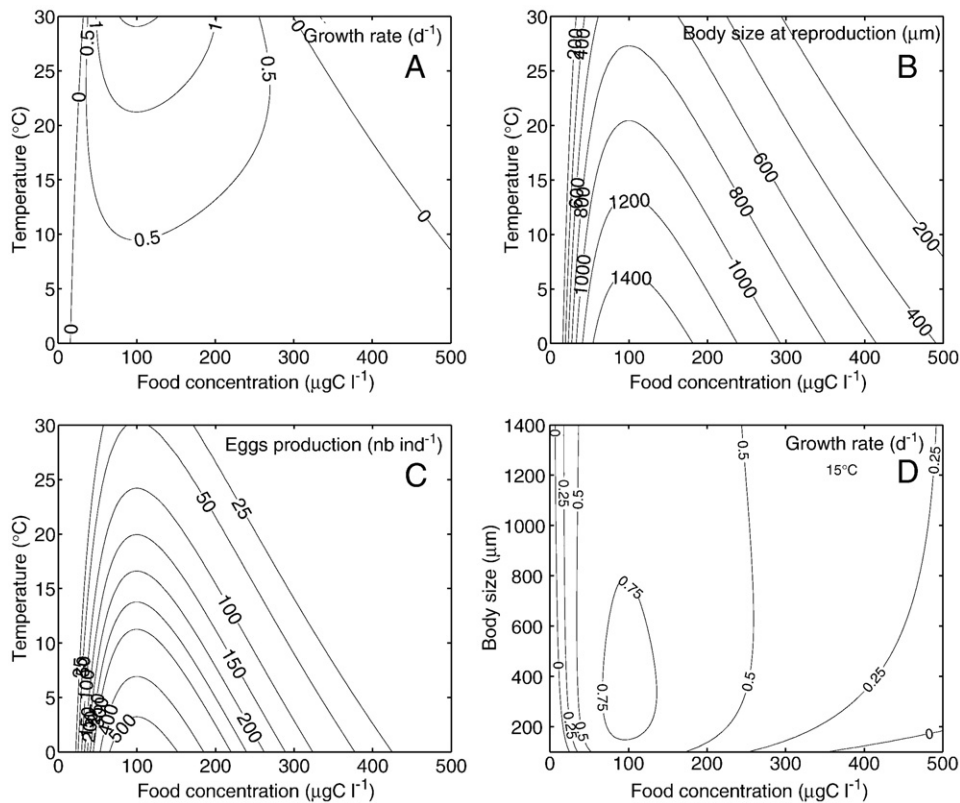


Fig. 11. *Oikopleura dioica* model pattern. (A) Temperature and food concentration effect on the growth rate, (B) the body size at the reproduction and (C) the egg number produced by reproductive females. (D) Effect of appendicularian size and food concentration on the growth rate at 15 °C.

Table 6
Oikopleura dioica. Model sensitivity in relation to a $\pm 10\%$ variation of parameters controlling the growth rate when compared to a standard simulation (Fig. 11D).

Symbols	Description	Values	Sensitivity (% deviation)	
			– 10%	+ 10%
r_2	Respiration rate at 0 °C during the growth phase	0.11	9	9
t_{10}	10th root of the Q_{10} coefficient for respiration	1.09	73	307
a	Exponent of the allometric equation for respiration at 0 °C	0.75	3	3
t_{10_f}	10th root of the Q_{10} coefficient for filtration	1.06	154	598
k_f	Half-saturation constant for the filtration	150	8	7
b	Exponent of the allometric equation for filtration at 0 °C	0.9	25	27
f	Maximum food intake for filtration at 0 °C	3.7	19	19
i_{max}	Maximum fraction of food not ingested	0.85	19	19
a_{max}	Maximum fraction of food not assimilated	0.9	31	31
k_a	Half-saturation constant for the assimilation	130	9	9
k_i	Half-saturation constant for the ingestion	200	8	7
f_h	Fraction of assimilated food allocated to house secretion	0.35	10	10

In order to keep the model formulation as simple as possible, we have assumed the Q_{10} parameters for the filtration and respiration processes to be constant. However, some studies indicate that the Q_{10} may be temperature-related (Champalbert and Gaudy, 1972; Mayzaud, 1973; Conover, 1978). Only in a few investigations was the Q_{10} determined for appendicularians and only for the temperature range from 10 to 25 °C. Therefore, the gain obtained with a more complex model including a variable Q_{10} would be minor. At this stage, however, we can consider that the model correctly simulates the temperature effect on *O. dioica* in the range 10–29 °C. Above and below this range, due to the scarcity of observational data, the model is not validated. Despite this, the model reveals that the difference between the Q_{10} functions used for filtration and respiration is a key factor for the growth response of appendicularians under different food and temperature conditions. The difference between the t_{10_f} and t_{10} parameters acts on the temperature regulation of mature appendicularian size, whereas the allometric exponents (parameters a and b) determine the optimal growth capacity at different stages of the life cycle, as well as the effect of food limitation.

4. Conclusion

The model presented here agrees with observations for growth rates and generation times measured at different food conditions and temperatures (Gorsky and Palazzoli, 1989; Troedsson et al., 2002; Lombard et al., 2009–this volume) and for the underlying processes taken individually, such as filtration, production of houses and fecal pellets, and gut passage time (Fenaux, 1985; López-Urrutia and Acuña, 1999; Acuña and Kiefer, 2000; Selander and Tiselius, 2003). As a result, the model validates some functional hypotheses and appears to confirm that the weight of fecal pellets is generally a saturating function of the food concentration as observed for copepods (Dagg and Walser, 1986; Urban-Rich et al. 1998). The model allowed us to estimate the carbon content of the house as 11.5% of the total body C, in the lowest range of the value given by Sato et al. (2001; $15.3\% \pm 4.8$). Moreover, from simulations under various environmental conditions, we can define the general growth pattern (growth rate, maximum size, and egg production) of *O. dioica* and make a first estimation of the ecological niche of this appendicularian. The model also confirms that the minimum food concentration for growth is about 20–30 $\mu\text{g C l}^{-1}$ and that the growth is optimal for a 100 $\mu\text{g C l}^{-1}$ feeding concentration.

Moreover, as this model reproduces in a relative complete way the appendicularian impact on its environment and notably on the carbon fluxes (filtration, ingestion, assimilation, particles production, respiration), it can also predict the impact of *in situ* observed *O. dioica* populations on the consumption of small particles (algae, bacteria), production of large particles (discarded houses, fecal pellets) and remineralization (respiration). Outputs of this model can be included in a general framework of modeling studies (i.e., Legendre and Rivkin,

2005) in order to estimate the contribution of appendicularians to carbon fluxes in the ocean.

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