

Individual-based model of the phenology of egg-bearing copepods: Application to *Eurytemora affinis* from the Seine estuary, France



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ABSTRACT

This study presents a non-spatial and temperature-dependent population model to better understand the population dynamics of the copepod *Eurytemora affinis* in the Seine estuary. The proposed individual-based model (IBM) allows each life-stage, or group of stages, to be represented and considers the differences in development rates and mortality caused by temperature and predation. The biological functions of the model were selected and calibrated to ensure realistic development at the temperatures recorded in the Seine estuary. The effect of temperature on development time and clutch size (CS) were obtained indirectly by fitting equations to the durations of stages observed in the laboratory at various temperatures and to CSs observed in the field. The degree-day approach was used to consider temperature variations. Mortality from predation was parameterized using the observed abundance of key predators. The proposed model successfully reproduces the life-history timing of the *E. affinis* population observed in the Seine estuary. The IBM approach was also used to simulate the development of the *E. affinis* population over several years at various temperatures with unlimited food conditions and no density dependence. The results confirm that the proposed model captures the role of temperature and predation in driving the seasonal population dynamics of *E. affinis* in the Seine estuary. This tool could be applied to any other egg-bearing copepods or could be used to test various *E. affinis* development scenarios in estuaries. This study also provides examples showing increasing temperatures and predation pressure shifts.

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1. Introduction

Copepods are some of the most important zooplankton in marine and inland waters, because they are an intermediate link between phytoplankton and higher trophic levels (Kimmel et al., 2006; Marques et al., 2007; Martinho et al., 2007). Their pivotal role in food webs makes the adaptive responses of these organisms to pollutants and global changes important to the entire ecosystem, from fish and other consumers to phytoplankton and other prey (Dam, 2013). Their rapid generation and suitability for experimental manipulation make copepods an excellent indicator of anthropogenic (e.g., pollution) and climate changes. In this context, population dynamic studies can be useful management tools for ecosystem protection. Because the basal state (i.e., the control)

must be defined before assessing the effect of any hazard on a population, individual based models (IBMs), such as this one, are useful in these types of studies.

Most ecological models of aquatic ecosystems assume that all individuals within a trophic compartment are identical (Batchelder et al., 2002). Therefore, these models are based on average population behavior. However, zooplankton, similar to other organisms, exhibit unique physiological and behavioral traits and act and react in a different ways (Bundy et al., 1993; Carlotti and Sciandra, 1989; Carlotti and Nival, 1992; Carlotti et al., 1997; Devreker et al., 2004, 2007; Doall et al., 1998; Gurney and Middleton, 1996; Souissi and Ban, 2001). Calanoid copepods undergo several developmental stages before reaching adulthood and each stage, or group of stages, exhibits different mortality rates (Beyrend-Dur et al., 2009; Kawabata, 1995), feeding habits (Kawabata, 1987), predation pressures (Aaser et al., 1995; Kawabata, 1991), and swimming behavior (Dur et al., 2010; Schmitt et al., 2011). Therefore, each stage, or group of stages, should be separately modeled using different parameters and processes (Souissi and Ban, 2001). This

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individual variability of different traits results in properties emerging at a population level that traditional ecological models cannot detect. Because these properties are important, more IBMs have been developed in the last few decades (Grimm, 1999).

Laboratory experiments can be used to isolate the effects of one cause on basic individual dynamics. IBMs are used to investigate interactions between intrinsic individual characteristics and extrinsic or environmental forces, and the effects of these interactions on population dynamics (Batchelder and Williams, 1995). Therefore, both laboratory experiments and modeling approaches should be used to investigate the complex interactions and processes that may affect population dynamics. Although researchers have recently developed several copepod IBMs, most have used different approaches and focused on free-spawning copepods (Souissi et al., 2004). However, the reproductive strategy of egg-bearing copepods is different to that of free spawners and should be accurately modeled. The reproduction of free spawners can be modeled as a continuous process, while egg-bearing copepod reproduction must consider two additional processes. An egg-bearing female cannot produce a new clutch of eggs until the previous clutch has hatched or felt. A female also requires time to produce a new egg sac after the extrusion of the last egg. This is referred to as latency time (LT). This increases the time required for the egg production rate. This study presents an IBM that considers the whole life cycle of egg-bearing copepods. The model is calibrated for *Eurytemora affinis* and the selected life cycle representation is based on the model developed for another calanoid—*Centropages abdominalis* (Souissi et al., 2004). The proposed model refines a previous model for the same species (Souissi et al., 2005). In the new model, the life cycle integrates the reproductive cycle of egg-bearing females (Dur et al., 2009). It also considers the effects of seasonal temperature variations on development time and reproduction, and seasonal variations in top-down control.

Researchers agree that temperature is the most important abiotic factor that regulates the growth rate of the developmental stages and reproductive potential of copepods (Durbin and Durbin, 1981; Isla and Perissinotto, 2004; Lawrence et al., 2004; Mallin, 1991; Peterson, 2001; Sullivan and MacManus, 1986; Sullivan et al., 2007; Sun et al., 2008). Temperature is one of the most important factors affecting the annual dynamics of *E. affinis* in the Seine estuary (Devreker et al., 2010). Therefore, introducing seasonal variability is essential for developing a reliable tool to simulate the effects of various scenarios (involving natural or anthropogenic forces) on the population structure and biomass of *E. affinis*.

The literature agrees that stage-specific mortality is important when studying or modeling the demography of copepods (Bi et al., 2011; Eiane and Ohman, 2004; Jiménez-Melero et al., 2013; Ohman and Wood, 1995; Souissi and Ban, 2001). The inherent uncertainty when estimating mortality in the field limits all modeling approaches. Models such as this one allow the effects of this parameter on population dynamics to be modeled. Predation is the principal source of field mortality of non-food limited copepods (Aaser et al., 1995; Fulton, 1982, 1985; Hairston and Twombly, 1985; Hirst et al., 2010; Ohman and Wood, 1995; Saunders and Lewis, 1987). Predators are sensitive to the swimming abilities of their prey (Meng and Orsi, 1991) and their effect on the prey population is different from early to late developmental stages and over time. Studies on the diet of several predators in the Seine estuary (including the decapod *Palaemon longicornis*, the goby *Pomatoschistus microps*, and the mysid *Neomysis integer*) have shown that *E. affinis* is a major component of their diets (Mouny, 1998). *E. affinis* is also the principal prey of *Crangon crangon* in this estuary (Rybarczyk and Elkaim, 2003).

The *Mobidyc* simulation platform was used to build the model. The platform is designed for amateur computer users (Ginot et al., 2002; Souissi et al., 2004, 2005). The multi-agent architecture

defines different agents (e.g., each developmental stage or groups of aggregated stages) as autonomous objects that perceive and react to their environment. Thus, *Mobidyc* can predict the development of a cohort by considering individual variability within a population. To contribute to better communication of this type of model, the model description follows the overview, design concepts, and details protocol proposed by Grimm et al. (2006, 2010). The modeling calibration was reinforced by the results obtained from the Seine-Aval program (Mouny, 1998; Devreker et al., 2004, 2007, 2009) and by experience accumulated by studying this species for over a decade (unpublished data on the life cycle of *E. affinis* collected by Souissi and colleagues).

The main purpose of the presented model is to produce an accurate life-history timing of the *E. affinis* population in the Seine estuary over several years. The simple model considers the effect of two significant population dynamic factors that affect calanoid copepods on an individual level: temperature and predation. The proposed model was then used to test the sensitivity of seasonal *E. affinis* population patterns to temperature and seasonal predation patterns.

2. Material and methods

2.1. Purpose

The stochastic IBM developed in this study provides insights into how biotic and abiotic environmental factors, and their variations affect the dynamics of the *E. affinis* population in the Seine estuary in France. The population dynamics of the calanoid copepod were simulated on a pluri-annual scale. The effects of temperature and predation timing on these dynamics were then evaluated.

To achieve this, four sets of simulations were conducted. Each set fulfilled a different purpose.

- Set 1 observed the development of each stage during a 1-year simulation.
- Set 2 investigated the variation in the number of individuals and the amount of biomass over 4 consecutive years.
- Set 3 evaluated the seasonal dynamic response to a temperature increase.
- Set 4 investigated the effects of predator phenology on copepod dynamics. It examined how changing the timing of nauplii and adult survival alters the model output in a 1-year simulation.

2.2. Entities, state variables, and scales

The *Mobidyc* platform is based on an all-agent architecture that makes using the platform simple and simplifies the concept of the model (Ginot et al., 2002). Of the various agents, those labeled “cells” represent the discrete space of the environment. The model developed in this study does not consider any spatial dimension. The following sections present the entities defined by the model. These entities are divided into two main predefined groups in *Mobidyc*: located agents, or animats, and non-located agents (Ginot et al., 2002).

2.2.1. Located agents—Animats

The animats in this model represent the different life stages of *E. affinis* (Fig. 1). Some developmental stages, including the first three and last three naupliar stages (N1 to N3 and N4 to N6), were combined to facilitate computation without affecting the model results (Souissi and Ban, 2001). The animats represent individuals undergoing developmental stages or groups of stages (for simplicity, this paper refers to both developmental stages and groups of stages as stages). Differentiating between males and females is necessary

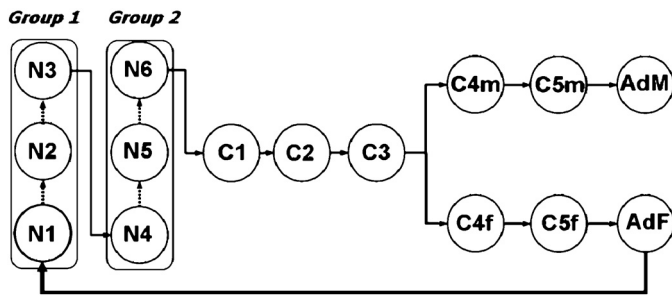


Fig. 1. Conceptual scheme of the *E. affinis* life cycle. The larval stages (nauplii) are included in two groups—N1 to N3 and N4 to N6 (modified from Souissi et al., 2005). Sex was differentiated from the fourth juvenile stage. The arrows represent the molting and metamorphosis processes. The thicker arrow linking adult females and the first naupliar group depicts the reproduction process described by Dur et al. (2009) (see their Fig. 1).

because the fourth copepodite stage (Stage C4) shows clear development time differences (Devreker et al., 2007). These low-level entities in the model are characterized by their number, n ($n = 1$ represents an individual), and their localization (not considered by this model). This model considers the duration of each stage with the attribute “duration” for the larval and juvenile stages, and the attribute “longevity” for the adult life span. The model incorporates several additional attributes to accurately model the life cycle (Table 1).

E. affinis belongs to a group of copepods that carry their eggs in masses. Thus, the reproduction process is relatively complex and constitutes a multi-phase cycle (Dur et al., 2009). This model integrates the different phases in the model developed by Dur et al. (2009). The animats representing adult females were credited with 10 more reproduction process characteristics (Table 1).

The model includes several additional attributes to model the effects of temperature variation on the life cycle (Table 1). These are *degreeday* and *ddlong* for the larval and juvenile stages and for the adult life span, respectively. The proposed model modified the reproduction process described by Dur et al. (2009) to integrate the temperature variation effect. Thus, the entities representing adult females exhibit several additional attributes (Table 1).

2.2.2. Non-located agents

The non-located agents in this model store constant values, reducing the number of attributes carried by the animats and decreasing the required computation time (see Ginot et al., 2002 for further information). The proposed model includes several non-located agents, and each one contains constant values for a certain process (Table 2).

ParamDev reflects the post embryonic development of an individual throughout various life stages. *ParamSur* shows the survival probability of each life stage. *ParamRepro* stores all constants associated with the reproduction process. *ParamWeight* stores the average weight at different stages.

2.2.3. Environment

The highest hierarchical level of the model considers environmental fluctuations by using another non-located agent: *Envi*. This entity refers to the overall environment, and its attributes are the forces that drive the behavior and dynamics of the located agents. In the basic version of the model, this agent only uses one attribute to define the temperature (*Envi_temperature*).

2.2.4. Spatial and temporal resolution

The model represents time with fixed duration discrete time steps. Simulation experiments were conducted on variable durations based on the experiment objectives. However, the time step was 6 h for all simulations. This model does not consider the spatial dimension.

2.3. Process overview and scheduling

At each discrete step, the various agents perform their tasks in the following sequence.

- *Envi*
 - Computes the temperature at each time step (*DefT*).
- *ParamDev*
 - Defines the mean residence time at each developmental stage, and the longevity of adults, depending on the temperature. This agent also defines the value of the shape of the gamma distribution parameter (α) used to introduce individual variability (*InfluTemperature*).
- *ParamRepro*
 - Defines the average clutch size (CS) depending on the temperature (*TempEffectCS*).
 - Computes the mean value of the embryonic development time (EDT) and LT, and the scale parameters of the gamma distribution (β) for each reproductive parameter (EDT, LT, and CS) in relation to temperature (*TempEffect*).
- *ParamSurv*
 - In the first step, this agent defines the survival rate of the different developmental stages for the entire duration of the simulation, except that of the naupliar stages and adult stages (*DefProbSurv*).

Table 1
Animat attributes used to define the life cycle of *E. affinis*.

Attribute	Owner	Dimension	Definition
Duration	N1N3–C5	[days]	Time required to pass in the following stage
RequireDD	N1N3–C5	[° days]	Energy required to pass in the following stage
degreeday	N1N3–C5	[° days]	Energy accumulated by an individual
Longevity	Adults	[days]	Life span of an adult
maxDD	Adults	[° days]	Energy threshold value over which an adult dies
ddlong	Adults	[° days]	Energy accumulated by an adult
Randssex	C3	None	Intermediate, used to assign a random real between 0 and 1
Sexstate	C3	None	Intermediate, used to define the type of sex in the C4 stage
Ovigerous	Adult fem.	None	Intermediate, used to define the ovigerous state of a female
Clutchsize	Adult fem.	None	Clutch size (number of eggs/clutch/female)
EmbryoDT	Adult fem.	[days]	Embryonic development time.
latencyTime	Adult fem.	[days]	Time between hatching and the production of a new clutch
rddedt	Adult fem.	[° days]	Energy required for the embryonic development
rddlt	Adult fem.	[° days]	Energy required for the production of a new clutch
ddedt	Adult fem.	[° days]	Energy accumulated for the embryonic development
ddlt	Adult fem.	[° days]	Energy accumulated for the production of a new clutch

Table 2
Attributes of each non-located agent used to define the life cycle of *E. affinis*.

Attribute	Owner	Definition
mdX	ParamDev	Mean stage duration for egg to C5 stages and life span in adult stage
alX	ParamDev	Intermediate, used to define the variability around mean stage duration for the stage X
btX	ParamDev	Intermediate, used to define the variability around mean stage duration for the stage X
sexratio	ParamDev	Proportion of females molting from C3 to C4
pSurvX	ParamSurv	Survival probability in the stage X
mdEDT	ParamRepro	Mean embryonic development time of eggs
mdLT	ParamRepro	Mean latency time between hatching and laying of a new clutch
mdCS	ParamRepro	Mean size of a clutch (number of eggs)
alEDT	ParamRepro	Intermediate, used to define the variability around mean embryonic development time
alLT	ParamRepro	Intermediate, used to define the variability around mean latency time
alCS	ParamRepro	Intermediate, used to define the variability around mean clutch size
btEDT	ParamRepro	Intermediate, used to define the variability around mean embryonic development time
btLT	ParamRepro	Intermediate, used to define the variability around mean latency time
btCS	ParamRepro	Intermediate, used to define the variability around mean clutch size
wX	ParamWeight	Mean weight in μg of dry weight of the stage X

- In the second step, this agent computes the survival rate of individuals in the naupliar stages and adult stages over the year (*SurvSeasonVar*). These stages are considered separately to test the effects of predation on phenology.
- Animats: Eury

The tasks performed by an individual depend on its development stage. Some tasks are common to all stages, whereas others are unique to a certain stage.

- Each female completes the tasks described in Dur et al. (2009). This model is slightly different because it uses degree-days. A female produces an egg sac containing a definite number of eggs (CS) after reaching a certain number of degree-days (representing the LT). A female stays ovigerous until it reaches the number of degree-days associated with the EDT. At this point, the eggs hatch and the female becomes non-ovigerous again and begins accumulating degree-days for the LT.
- Each stage, from N1 to N3 to C5, completes the following individual tasks:
 - Tests its survival in relation to the survival probability of the stage (*Survive*).
 - Defines the number of accumulated degree-days required to molt or perform metamorphosis (*DDNeed*).
 - Updates the number of accumulated degree-days (*CalcDegreeDay*).
 - If the required number of degree-days is reached, the molt occurs (*Molting*). The C3 stage molts to the C4F or C4M stage based on the sexual state (*MoltingM-MoltingF*).
- Every adult male simultaneously completes the following tasks:
 - Tests its survival in relation to the survival probability of all adult males (*Survive*).
 - Defines the maximal quantity of heat it can accumulate (*DDmax*).
 - Updates the quantity of heat accumulated (*CalcDegreeDay*).
 - If the quantity of heat accumulated exceeds the threshold value, it dies (*Die*).

2.4. Design concepts

Basic principles—In this model, temperature affects the development time and CS. To determine the effects of temperature on development time and longevity, we used the empirical relationship described by Bělehrádek (1935) and adopted the concept of equiproportional development, that is, each developmental stage occupies a constant proportion of the total time required to reach

maturity (Corkett et al., 1986). The model includes the result of regular temperature changes (i.e., seasonal variation) on the growth period considering the degree-day approach. This approach assumes that individuals require a certain amount of heat (normally expressed as degree-days) to molt. Demographic analyses based on degree-days have achieved good predictability for populations in variable temperature conditions (Ryoo et al., 1988) and in the field (Jones et al., 1997). This study hypothesizes that temperature and CS are positively correlated up to an optimal value, above which the production wanes or even ceases, as observed in several populations of *E. affinis* (Escaravage and Soetaert, 1993; Hirche, 1992; Peitsch, 1992). Another important hypothesis considered when developing the model is that predation is the most important cause of mortality for the nauplii and adult stages of *E. affinis*.

The proposed IBM implements these relationships and concepts at the input level and uses submodels to observe the emergence of population dynamics related to temperature and predation.

Emergence—Population dynamics emerge from the behavior of individuals, but the life and reproductive cycle of an individual are described by simple empirical and stochastic rules. To understand the effects of demographic processes (at the population level) on the emerging patterns, the parameterization of the model was simple as possible.

Adaptation—Female fecundity depends on temperature. Temperature influences CS, LT, EDT, and female longevity (FL). It is assumed that this representation of the reproductive process indirectly affects individual fitness.

Objectives—Individual fitness is determined by the individual survival rate, adult longevity, female hatching success, CS, latency, and embryonic development duration. Although the results of fitness variations at higher levels can be quantified, this study does not address this.

Sensing—It is assumed that individuals know the quantity of heat accumulated, their sex when determined at C4, their ovigerous state (for females), and that they must fulfill their specific tasks. Individuals also indirectly sense temperature because the values of the parameter used for the reproduction process and the duration or longevity are randomly drawn into gamma distributions selected in relation to the temperature.

Interactions—This model does not consider interactions between individuals. It assumes that the time required for a male to anchor his spermatophore to a female is included in the LT duration. The model does not consider mating limitations or failed egg fertilization.

Stochasticity—The model introduces two types of random fluctuations. Individual survival is determined by drawing randomly from a uniform probability density function at each time step (cf,

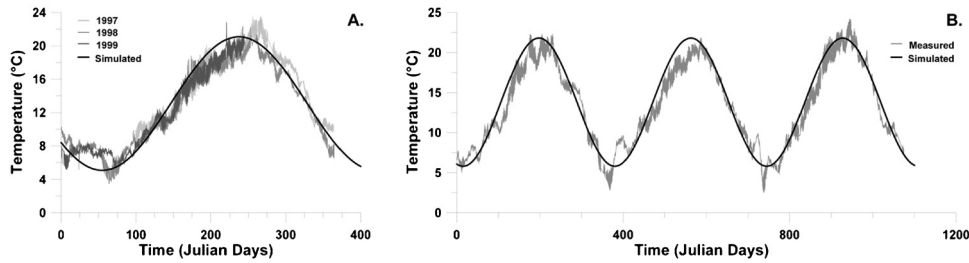


Fig. 2. (A) Comparison between simulated seasonal temperature variations (in black) and seasonal temperature variations measured by the MAREL estuarine station at Honfleur from 1997 to 1999. (B) Comparison between simulated temperatures (in black) and temperatures measured by the MAREL station from 2001 to 2003 (in gray). The simulated values were obtained with $T_m = 13$, $T_a = 16$, and $\delta = 55$ (Eq. (1)).

“survive” in Section 2.7). Each individual is also randomly assigned a duration for a stage or life span, and a new LT, EDT, and CS for each clutch. The values of these parameters were obtained from the gamma distributions—parameter β , which is related to temperature (see Section 2.7).

Observation—The number of individuals in each developmental stage is counted at each time step. This procedure allows cohort development to be described.

2.5. Initialization

All simulations began on 1 January, with 50 newly molted adult females. For all simulations, the survival of the juvenile stages (copepodite) was fixed at 100% day⁻¹, except for the C3 stage survival, which was set at 95% day⁻¹. These survival values were selected based on laboratory-observed values (Devreker et al., 2007). All simulated experiments were repeated 10 times (10 replicates) to consider the output variability produced by the same set of parameters and initial conditions.

For simulation sets 3 and 4, the parameter values for the equations defining the environment (i.e., the effects of temperature and predation on survival during the adult and naupliar stages) were varied between simulations.

For simulation set 3, the value of the average annual value (T_m , Eq. (1)) was increased from 13 °C to 14 °C in 0.25 °C increments.

For simulation set 4, the repetitions considered one group at a time: first the nauplii and then the adults. The sensitivity to predation pressure was tested by varying the value of the time-lag coefficient in the equation defining the mean survival rate per stage (shown in Section 2.6). The time lags tested varied in 10-d increments from 170 d to 230 d for the naupliar stages and from 245 d to 305 d for the adult stages. The smallest and largest values corresponded to a 1-month-early and 1-month-late appearance of predators, respectively.

2.6. Input

2.6.1. Temperature

Temperature is the first input in the proposed model, and demographic parameters depend on this parameter. To consider this influence, the following equation was used to simulate seasonal temperature variations:

$$T = T_m - \frac{T_a}{2} \cos\left(\frac{2\pi}{365}(t - \delta_T)\right), \quad (1)$$

where T is the value of temperature at time t , T_m is the mean annual temperature, T_a is the maximal amplitude of the temperature variation, t is the time (measured in units equal to the time step used for the simulations), and δ_T is the time-lag coefficient (in days) between the day with the lowest temperature and the first day of the year.

The values of these equation parameters were calibrated to ensure that the simulated values and those recorded by the

autonomous MAREL buoy at Honfleur (frequency 0.1 min⁻¹) in the Seine estuary (Dur et al., 2007, see Fig. 2) were similar. The temperature recorded at the MAREL buoy at Honfleur fluctuates from 4 °C to 23 °C in a year, and there is little evidence of significant inter-annual variability (Fig. 2A). The simulation did not consider tide cycle or turbulence variability (Fig. 2). This is justified because temperature only has an effect during periods exceeding tide cycles (Dur et al., 2007).

2.6.2. Adult and naupliar survival rate

The main predators of *E. affinis* appear during spring and summer (Fig. 3A and D) or during fall (Fig. 3B and C), and are dominated by *N. integer* (Mouny, 1998), which feeds preferentially on copepod nauplii (Aaser et al., 1995) and increases its predation activity when the temperature increases (Winkler and Greve, 2004). We simulated the survival of *E. affinis* naupliar stages (N1 to N3 and N4 to N6) so that it was in antiphase with the density of its predators (Fig. 3E). The adults were shifted slightly relative to the larval stages (Fig. 3F). This decreases adult survival with increasing temperature (Fig. 3F), as shown by another calanoid study (Rhyne et al., 2009). The following equation was used:

$$S = S_m - \frac{S_a}{2} \cos\left(\frac{2\pi}{365}(t - \delta_S)\right), \quad (2)$$

where S is the survival rate at time t , S_m is the mean annual survival, S_a is the maximal amplitude of the survival variation, t is the time (measured in units equal to the time step used for the simulations), and δ_S is the time-lag coefficient (in days) between the day with the lowest survival and the first day of the year. The values of S_m , S_a , and δ_S used in this study were 75, 25, and 200 and 70, 25, and 275 for the naupliar and adult stages, respectively. This equation was integrated with the task used to define the survival rate at each stage (i.e., *DefprobSurv*), carried by the non-located agent, *ParamSurv*.

2.6.3. Representation of individual variability

This study models individual variability with a gamma density function (GDF) appropriate to this species (Beyrend-Dur et al., 2009; Devreker et al., 2007). The asymmetry of the GDF is characterized by two parameters: the shape parameter (α) and the scale parameter (β). These parameters should be identified for the entire set of durations from the development stages and for the reproductive parameters (i.e., EDT, LT, and CS). As in Dur et al. (2009), this study adopts the method described by Souissi (2006) to separate the contribution of an extrinsic factor from the intrinsic variability. We used data obtained at two temperatures (10 °C and 15 °C) and two salinities (5 and 25) (Devreker et al., 2007, 2009) to estimate the values of α and β .

We used the gamma cumulative function, *gamcdf*, included in the curve fitting toolbox in MATLAB R2009b® (The Mathworks Company, Inc.) to obtain the smaller least mean square non-linear value and the confidence intervals of the gamma distribution parameters

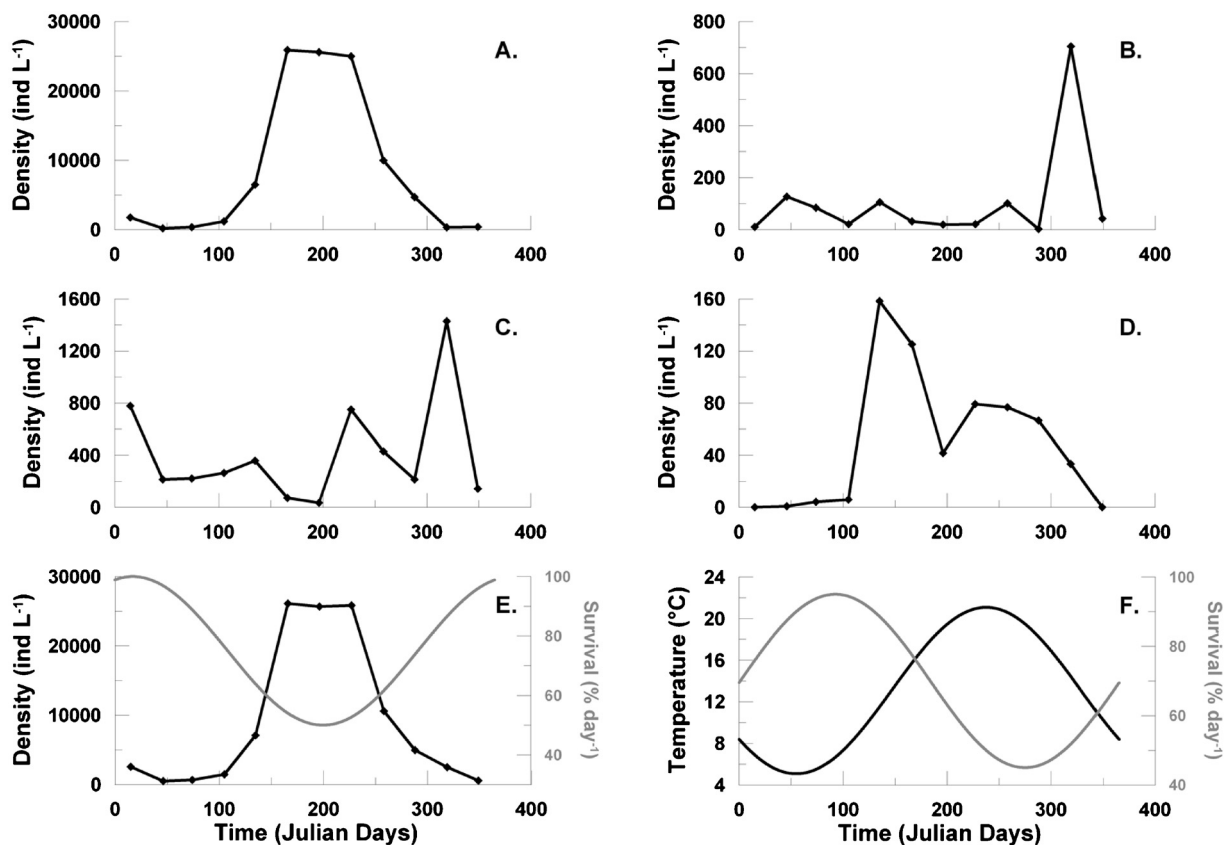


Fig. 3. Annual variations in the density of *E. affinis* predators in the Seine estuary: *N. integer* (A), *P. microps* (B), *P. longicornis* (C), and *C. crangon* (D) (data from Mouny, 1998 were used). The variation in total predator density (black line) is compared with the simulated seasonal variation of the survival rate of naupliar stages (gray line) (E). The simulated seasonal temperature variation (black line) is compared with the seasonal variation in the adult survival rate (gray line) (F).

(α and β). Fig. 4 and Table 3 show the fitting results and gamma parameter values, respectively.

2.6.4. Individual biomass

The non-located agent *ParamWeight* introduces the mean biomass of each stage or group of stages into the model. We obtained the average weights by combining data from the literature, particularly from Mouny (1998) and Gasparini (1997). Table 4 shows these data. The weight of the groups of stages (N1 to N3; N4 to N6) corresponds to the average values observed for each of the stages included in a group.

Table 3

Gamma distribution parameter values of the various durations included in the model. The R^2 values reflect the fitting accuracy.

Parameter	GDF parameters (confidence bound)		R^2
	α	β	
E.D.T. ^a	65.46 (63.02; 67.91)	0.0153 (0.0147; 0.0158)	0.989
LT. ^b	0.9346 (0.9063; 0.9629)	1.338 (1.281; 1.395)	0.989
C.S. ^c	12.54 (10.34; 14.74)	0.1708 (0.1315; 0.21)	0.996
dN1N3	177.7 (152.6; 202.7)	0.0056 (0.0048; 0.0063)	0.961
dN4N6	53.13 (48.16; 58.1)	0.0188 (0.0171; 0.0206)	0.969
dC1	14.92 (13.62; 16.21)	0.0653 (0.0595; 0.0710)	0.981
dC2	14.45 (13.18; 15.72)	0.0679 (0.0618; 0.0739)	0.981
dC3	23.3 (21.36; 25.25)	0.0423 (0.0387; 0.0459)	0.984
dC4f	24.91 (19.47; 30.36)	0.0401 (0.0312; 0.0489)	0.972
dC4m	13.63 (12.5; 14.75)	0.0740 (0.0678; 0.0802)	0.987
dC5f	49.37 (39.99; 58.75)	0.0200 (0.0162; 0.0238)	0.971
dC5m	98.42 (81.32; 115.50)	0.0101 (0.0083; 0.0118)	0.963
lAdf	14.58 (11.72; 17.44)	0.0713 (0.0572; 0.0854)	0.976
lAdm	18.82 (17.22; 20.43)	0.0551 (0.0503; 0.0598)	0.986

^a Embryonic development time.

^b Latency time.

^c Clutch size.

2.7. Submodels

We used a macroinstruction combination to describe the various tasks and individual specific behaviors (Table 5).

2.7.1. InfluTemperature–TempEffect

We used the common equation in Bělehrádek (1935) to represent the influence of temperature on the clutch mean development time and LT:

$$\text{Mean Duration}_X = \lambda_X (T - T_{0X})^\delta. \quad (3)$$

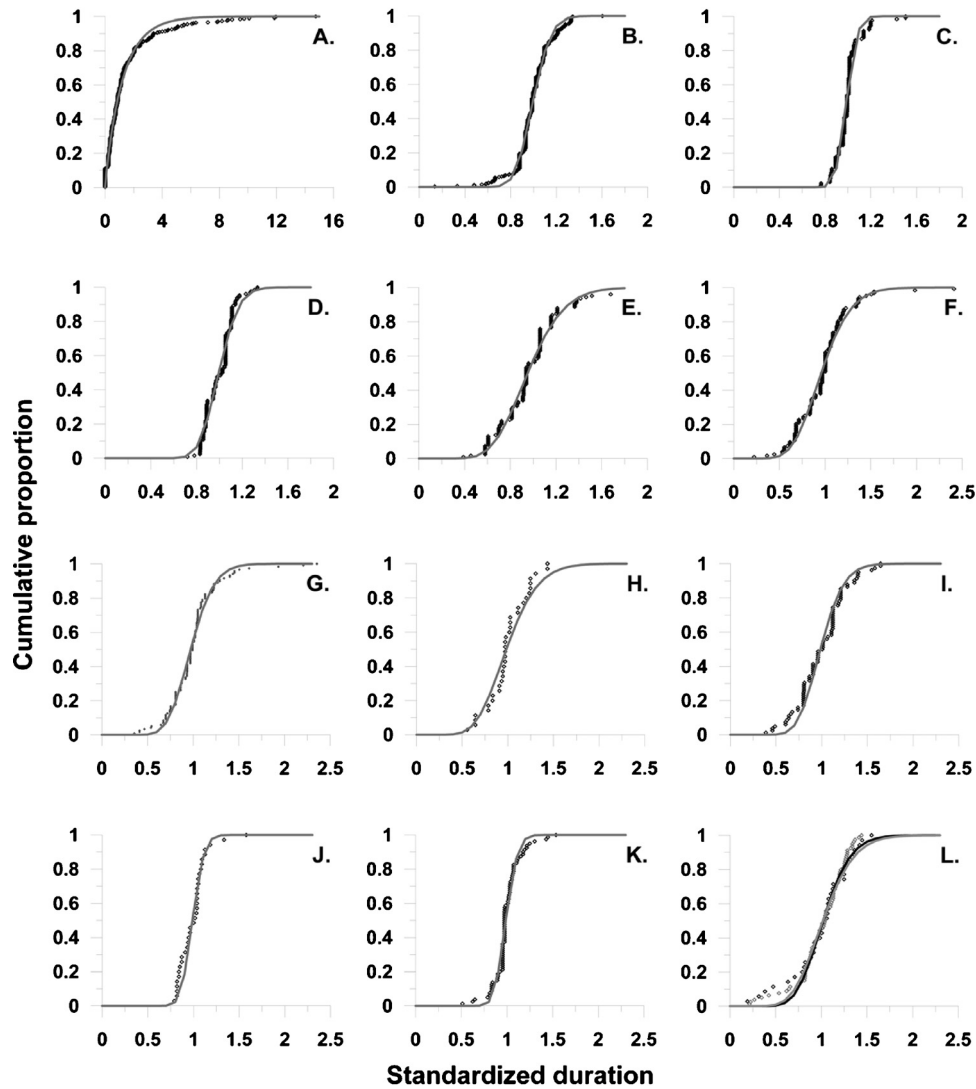


Fig. 4. Cumulative proportions of the duration of LT (A) and EDT (B) and of the development of N1N3 (C), N4N6 (D), C1 (E), C2 (F), C3 (G), C4 females (H), C4 males (I), C5 females (J), C5 males (K), and adults (L). The observed data (black diamonds) are plotted above the values predicted by the model $gamcdf [x/\alpha\beta]$ (gray lines). For the adult stages, the diamonds reflect the observed data and the continuous line reflects the simulated data (black for males and gray for females). Table 6 shows the values of α and β for each parameter.

To calibrate this effect, we considered the hypothesis that all parameters expressed in time follow Eq. (3). Based on the equiproportional rule in Corkett et al. (1986), we assumed that δ was constant between stages or group of stages. Fig. 5 shows the relationship between mean duration and temperature and Table 6 presents the values of the parameters λ , T_0 , and δ .

Table 4

Mean individual weights (in micrograms of dry weight) for the various stages of the life cycle of *E. affinis*. Data were gathered from Mouny (1998) and Gasparini (1997).

Stage	Dry weight (μg)
N1-N3	0.11
N4-N6	0.27
C1	0.98
C2	1.63
C3	2.32
C4f	3.18
C4m	3.18
C5f	8.41
C5m	6.30
Adf	11.10
Adm	9.95

We multiplied the values of gamma distribution parameter β by the estimated mean value of the duration determined at the local temperature. This procedure defines the gamma distribution (now incorporated in *MobidyC*), within which the values of the development and reproduction parameters at a given temperature are randomly sorted per individual. All other parameters were constant, and only β was modified to fit the different durations at a given temperature.

2.7.2. TempEffectCS—Effects of temperature on CS

The relationship between temperature and mean CS in this study and its parameterization are similar to those reported in Dur et al. (2009).

2.7.3. Survive

The mean survival values were defined through task *DefprobSurv* of the non-located agent, *ParamSurv*. The predefined task, *Survive*, introduces individual survival variability for any individual during a time step. For a high survival rate in stage X (e.g., $ParamSurv_X = 95\% \text{ day}^{-1}$), the probability of drawing a random number larger than $ParamSurv_X$ is low. Thus, the individual is more likely to survive than die at each time step.

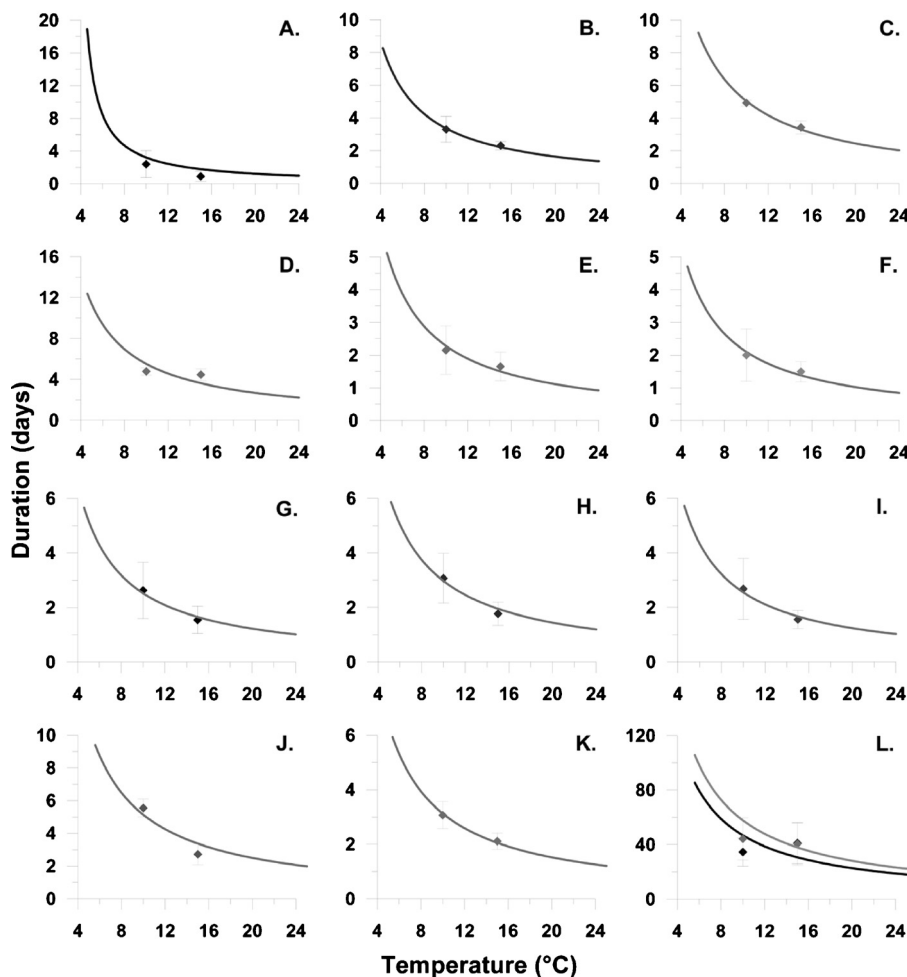


Fig. 5. Relationships between temperature and LT (A), embryonic development time (B), and the development time for N1N3 (C), N4N6 (D), C1 (E), C2 (F), C3 (G), C4 females (H), C4 males (I), C5 females (J), C5 males (K), and adults (L) using the Bélehradek equation (1935).

2.7.4. Cohort development

This study uses several tasks to represent the development of individuals from the first group of larval stages to the adult stage.

The first task, *DDNeed*, works only when an agent enters a new stage. This task defines in two steps the value of attribute *RequireDD* that the agent must reach to molt in the next stage. The first step defines the duration required in the stage by randomly selecting a value by using the specific gamma distribution function. The second step integrates the effects of temperature variation. This is based on the assumption that each life stage requires a specific quantity of heat, expressed in degree-days ($^{\circ}\text{D}$), to complete its development. This quantity of heat, stored in *RequireDD*, is defined as the product of the duration and temperature when the computation is performed (Table 5). This *DDNeed* task initializes the value of *degreeday* accumulated by the individual (Table 5).

The second task, *CalcDegreeDay*, then estimates and updates the *degreeday* value accumulated at each time step. For the degree-day accumulation, this study uses the popular summation model developed by El messoussi et al. (2007).

The *Molting* task defines the transfer between two successive stages. Transfer to the next stage is conducted after the individual has gathered a sufficient quantity of energy. This condition is also imposed for molting in C4F or C4M, with an additional condition defining the sex, that is, in which C4 stage the C3 individual should molt (i.e., C4F or C4M). This additional condition is associated with the sex ratio, which is fixed at 0.5 (M:F) and stored in the non-located agent, *ParamDev*.

2.7.5. Temperature variation effect–degree-day approach

The temperature variation effect was integrated by transforming the duration into a quantity of energy expressed in degree-days ($^{\circ}\text{D}$). This quantity is defined as the product of the duration, randomly provided by the specific gamma distribution function, and the temperature when the computation is performed.

Each located agent must be given two new attributes to estimate this quantity of energy. Some tasks were also added to integrate the degree-day approach. The following submodel section presents a description and explanation of these tasks.

2.7.6. Reproduction

We modified the series of tasks used to simulate reproduction in Dur et al. (2009) to fit the degree-day approach (Table 5). When an individual enters the adult female stage (*ddlong*=0), it performs task *DefImpTime*. This task introduces individual variability in longevity and LT, and allocates the value of the maximal energy a female can accumulate (*maxDD*) and the energy required for the LT (*rddlt*).

In the proposed model, *DDcumul* (equivalent to *Timecumul* in Dur et al., 2009) updates the energy accumulated by the adult female, its current embryonic development, and latency values (i.e., *ddlong*, *ddedt*, and *ddlt* in Table 5).

The female produces an egg mass after reaching the threshold value of energy accumulated during the LT (*ddlt* \geq *rddlt*). As the results of egg production, the *EggProduct* task modifies the ovigerous status (i.e., *my_ovigerous*=1) and defines the CS. The

Table 5
Definitions of the tasks used to integrate the influence of temperature variation on the life cycle.

Task	Type	Setting
InfluTemp	Mathscript	ParamDev_mdX: = $\lambda X (\text{Envi_Temperature} - T_0)^{-1.04}$ ParamDev_btX: = ParamDev_mdX $\times \beta X$
TempEffectCS	Mathscript	ParamRepro_meanCsize: = $(T/T_0 \times X^h)^{\sigma}$
TempEffect	Mathscript	ParamRepro_mEDT: = $\lambda \text{EDT} (\text{Envi_Temperature} - T_0 \text{EDT})^{-1.04}$ ParamRepro_mLT: = $\lambda \text{LT} (\text{Envi_Temperature} - T_0 \text{LT})^{-1.04}$ ParamRepro_btEDT: = ParamRepro_mEDT $\times \beta \text{EDT}$ ParamRepro_btLT: = ParamRepro_mLT $\times \beta \text{LT}$
Survive	Generate	*Automatically conducted by MobidyC, it works as my_randSurv = randomReal(0,1) my_stateSurv = ParamDev_psurvAdf-my_randSurv if true (my_survivalstate < 0) then I am dying The automation avoids the creation of the attributes randSurv and stateSurv.
DDNeed	Generate (Modify) Conditional)	if true my_age: = 0; my_duration: = RandomGamma [ParamDev_alX, ParamDev_btX] my_requireDD: = my_duration $\times \text{Envi_Temperature}$ my_degreeday: = 0 endif
CalcDegreeDay Molting	Mathscript Predefine (Metamorphosis)	my_degreeday: = (Envi.Temperature \times Simulator.timestep) + my_degreeday if true my_degreeday \geq my_requireDD Then 100% molt into the next stage
Die	Predefine (Die)	if true my_ddlong \geq my_maxDD Then I die
DefImpTime	Mathscript	if true (my_ddlong = 0) my_longevity = randomGamma(ParamDev_alAdf, ParamDev_btAdf) my_latencyTime = randomGamma(ParamRepro_allT, ParamRepro_btLT) my_maxDD = Envi.Temperature \times my_longevity my_rddlT = Envi.Temperature \times my_latencyTime endif true
DDCumul	Mathscript	if true ((my_ovigerous = 0) and (my_ddlt = 0)) my_latencyTime = randomGamma(ParamRepro_allT, ParamRepro_btLT) my_rddlT = Envi.Temperature \times my_latencyTime endif true my_ddlong = (Simulator.timeStep \times Envi.Temperature) + my_ddlong my_ddedt = (Simulator.timeStep \times Envi.Temperature) + my_ddedt my_ddlt = (Simulator.timeStep \times Envi.Temperature) + my_ddlt
EggProduct	Mathscript	if true (my_ddlt > my_rddlT) my_ovigerous = 1 my_clutchsize = randomGamma(ParamRepro_alCS, ParamRepro_btCS) my_ddedt = 0 my_ddlt = 0 my_rddlT = 1000 my_EmbryoDT = randomGamma(ParamRepro_alEDT, ParamRepro_btEDT) my_rddedt = my_EmbryoDT \times Envi.Temperature endif true
Reproduce	Predefined	if true ((my_ddedt \geq my_rddedt) and (my_ovigerous = 1)) Then ParamRepro_hatchingsucces% of my_clutchsize will reproduce in N1N3
InitPostRepro	Predefine (PostAction)	my_ovigerous = 0 my_clutchsize = 0 my_rddedt = 1000 my_ddedt = 0 my_ddlt = 0

Table 6
Results of the calibration of parameters λ , T_0 , and δ in Eq. (3) reflecting the influence of temperature on life cycle traits.

Stage X	λ	T_0	δ	Duration at 10 °C (days)		Duration at 15 °C (days)	
				Estimated values	Observed values	Estimated values	Observed values
LT	22.86	3.4	-1.04	3.21	2.40	1.79	0.90
EDT	36.80	0	-1.04	3.36	3.30	2.20	2.30
N1-N3	55.34	0	-1.04	5.04	4.93	3.31	3.44
N4-N6	60.48	0	-1.04	5.51	4.78	3.62	4.46
C1	25.04	0	-1.04	2.28	2.15	1.50	1.65
C2	23.01	0	-1.04	2.10	2.00	1.38	1.49
C3	27.69	0	-1.04	2.52	2.63	1.66	1.55
C4f	32.59	0	-1.04	2.97	3.07	1.95	1.77
C4m	27.98	0	-1.04	2.55	2.68	1.67	1.56
C5f	56.35	0	-1.04	5.13	5.55	3.37	2.72
C5m	34.29	0	-1.04	3.12	3.07	2.05	2.11
Adf	633.7	0	-1.04	57.79	44.22	37.9	40.54
Adm	512.2	0	-1.04	46.71	34.54	30.64	41.4

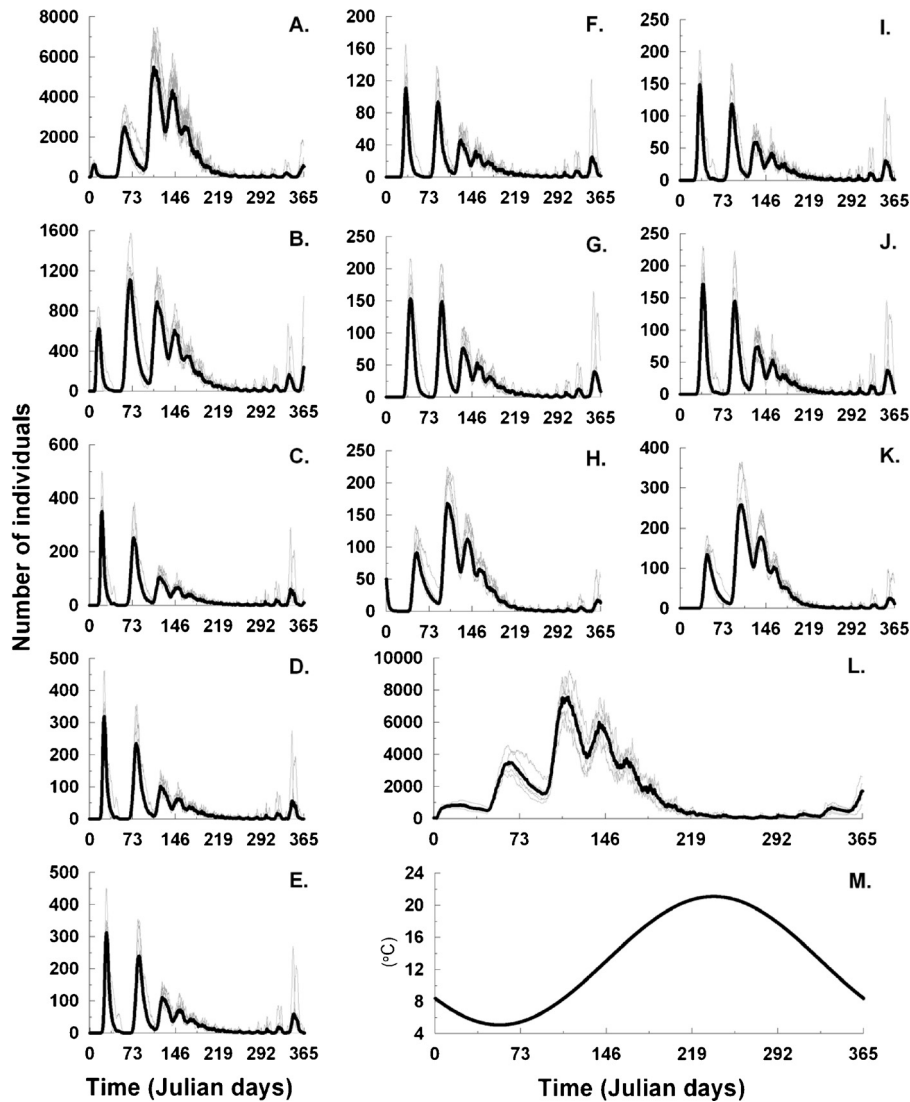


Fig. 6. Seasonal variations in the number of *E. affinis* individuals for N1N3 (A), N4N6 (B), C1 (C), C2 (D), C3 (E), C4 females (F), C5 females (G), adult females (H), C4 males (I), C5 males (J), adult males (K), the entire population (L), and temperature (M). This figure shows the 10 replicates (in gray) and the mean value of these replicates (in black) for each stage. The seasonal temperature variation is also presented.

CS is determined by randomly selecting a value from a gamma probability density function (shape parameter = α ; scale parameter = $\beta \times mCS_T$; Table 3). With mCS_T , the mean CS is determined at the local temperature by *TempEffectCS*.

To prevent a female from producing any other egg masses while carrying one, *EggProduct* sets the value of *rddlt* to 1000 and the value of *ddlt* to 0. It then sets the quantity of energy required for embryonic development (*rddedt*).

The task, *Reproduce*, manages the last step in the reproduction process (i.e., the hatching of eggs and emergence of nauplii; Table 5). Several conditions are required for this task to operate. The female must be ovigerous (*my.ovigerous* = 1) and the value of attribute *ddedt* must exceed the threshold value provided by *rddedt*. When these conditions are met, a certain percentage of eggs (i.e., hatching success) hatch and create new individuals in the first naupliar stage (N1 to N3). Hatching success remains constant (100%) in the proposed model.

As a female is no longer ovigerous after *Reproduction*, several attribute values are redefined. This is completed by the post-action task, *InitPostRepro*. This task reinitializes the *ovigerous*, *clutchsize*, and *ddlt* attributes to 0. *InitPostRepro* changes the values of *rddedt* and *ddedt* to avoid any errors in the model (Table 5).

2.7.7. Die

Using degree-days also requires the adult *Die* task to be modified. This task now requires a maximal quantity of energy to be accumulated (*maxDD* for *AdM* or *ddlong* for *AdF*), after which the individual dies (Table 5).

3. Results

3.1. Simulation set 1

The results produced by the proposed model exhibit considerable variation in the total number of individuals produced during the first 150 d (Fig. 6). Even if a population does not seem to reach equilibrium, certain areas of variation are expected: a peak in one stage is always followed by a peak in the next stage. This model accurately reproduces the different development of males and females. The maximal number of males appear a few days before the maximal number of females. For example, the first peaks appear after 46 d and 51 d of simulation for males and females, respectively. Several cohorts were produced: the first group of nauplii appeared after 3 d and the second appeared 45 d later. The period

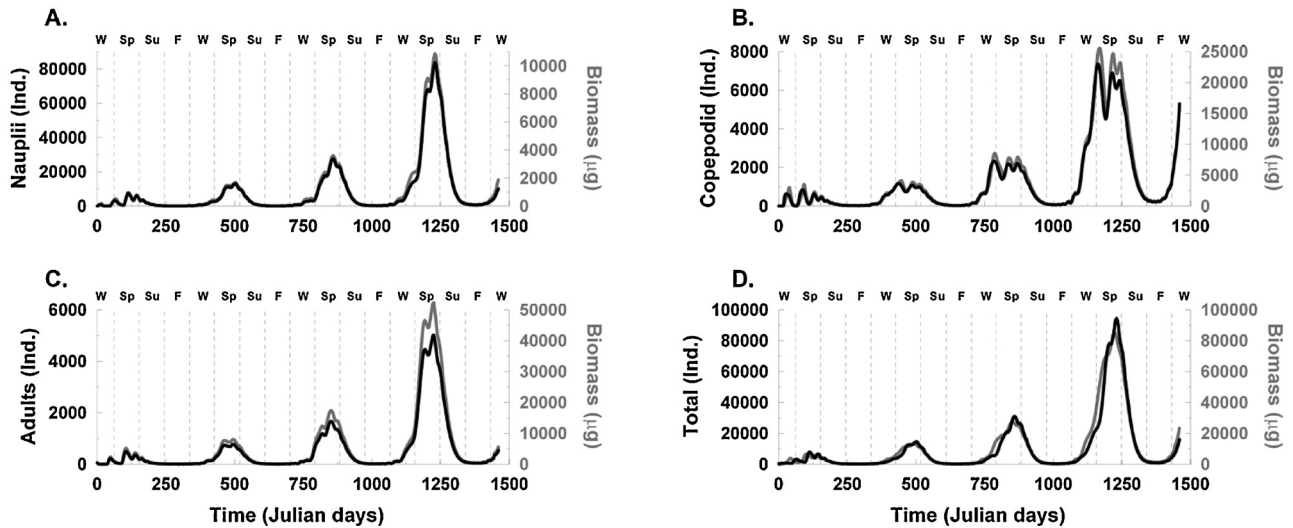


Fig. 7. Average seasonal variations in the number of *E. affinis* nauplii (A), copepodid (B), and adults (C), and all three stages (D) of the 10 replicates (in black) and their corresponding biomass (in gray). Discontinuous lines show the seasonal boundaries mentioned at the top of each delimited area, with W, Sp, Su, and F representing winter, spring, summer, and fall, respectively.

between two generations decreases as the temperature increases, resulting in closer peaks during spring. However, once the survival rate decreases in spring, fewer individuals are produced in each generation. The low survival rate in summer creates a population composed of a few individuals. However, sufficient individuals exist to maintain the population and begin increasing at the end of the year, although low temperatures limit their development and production.

The population dynamics obtained from these results show that maximal abundance occurs at the end of spring (114 d) and decreases during summer, which is in agreement with in situ conditions.

3.2. Simulation set 2

The population dynamics over four consecutive years were summarized by considering the total number of individuals in the larval (nauplii), juvenile (copepodite), and adult stages (Fig. 7A–C). The biomass of each group of stages was computed by multiplying the mean weight of the stage by the number of individuals in the stage (Fig. 7). Similar patterns of population increases during spring and decreases during summer were observed for all simulated years (Fig. 7D). A slight shift in nauplii phenology was observed from the first to the second year. The second-year nauplii produced by the first-year over-wintering adults appeared slightly earlier (at the end of December; Fig. 7A), and more of them survived for longer. This resulted in higher individual densities in the spring during the second year (Fig. 7D).

A slight lag appeared between the abundance and biomass curves. The total biomass increased during the first 45 d, whereas the population abundance began decreasing after day 15 of the simulation. At the time of the biomass peak, the population consisted of approximately 500 individuals. Despite this low number, the adults represented a mass equivalent to a large number of larvae. The biomass decreased as the proportion of adults in the population decreased because of death (Fig. 7C and D).

Despite slight discrepancies, the abundance and biomass curves exhibit similar kinetics. The discrepancies are caused by the large biomass created by the late stages and adults, despite their low numbers.

3.3. Simulation set 3

An increase in the mean annual temperature changed several aspects of the dynamics (Fig. 8). It increased the total abundance. The annual mean population size (N) increased exponentially with temperature from 1738 to 16604 individuals ($N = 2.10^{-10} e^{2.272 \times T}$, $r^2 = 0.994$, where T is temperature). An increase in mean annual temperature also produced more generations. A mean annual temperature change of 13 °C and 14 °C produced four and six successive generations, respectively. Temperature caused a forward shift in *E. affinis* phenology from 6 h to 5 d. As temperature increased, all cohorts appeared earlier. However, the time shift between two temperatures was not constant from one peak to the next peak. For example, when the first peak at 13.25 °C appeared 5 d before the peak at 13 °C, the second peak at 13.25 °C only appeared 1 day earlier than the peak at 13 °C.

3.4. Simulation set 4

The naupliar survival rate with $\delta_S = 200$ d shows that 5 of the 10 simulated populations were maintained for the entire 2-year simulation (Fig. 9). The remaining 50% did not last more than 300 d. When δ_S increased to 210 d and 220 d, the percentage of the simulated population that was maintained throughout the 2-year simulation reached 60% and 70%, respectively. The 2-year average also increased from 5.46×10^3 to 8.43×10^3 and 20.77×10^3 individuals for a δ_S of 200 d, 210 d, and 220 d, respectively. A postponed

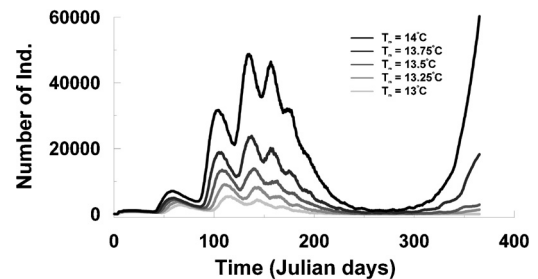


Fig. 8. Seasonal variations in the whole *E. affinis* population after a 1-year simulation of different temperature regimes. The mean annual temperatures— T_m in Eq. (1)—of the temperature regimes are different.

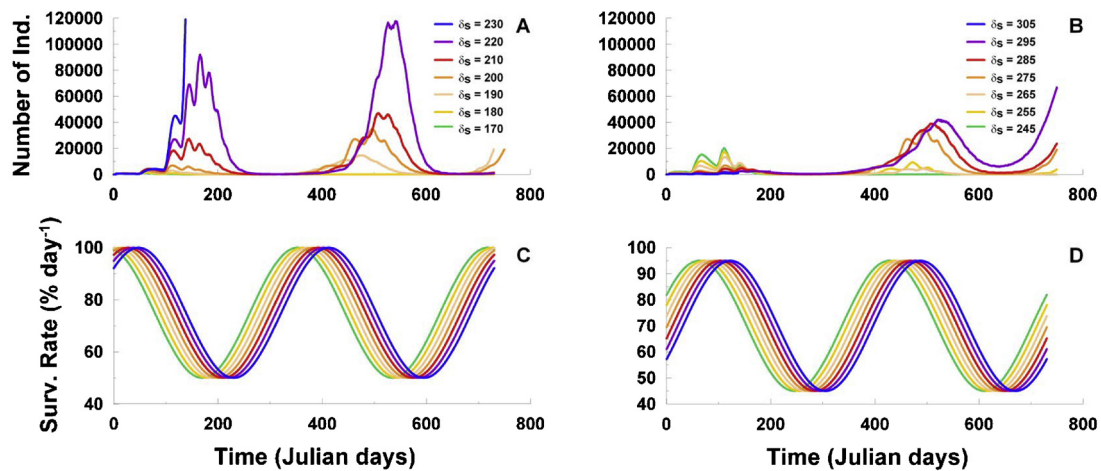


Fig. 9. Two-year seasonal variations in the number of *E. affinis* individuals for six representations of the seasonal survival probability of the naupliar (A) and adult stages (B). The figure also shows seasonal variations in the survival probability for nauplii (C) and adults (D).

survival cycle ($\delta_S = 230$ d) resulted in a population explosion during the first spring at approximately 160 d. Conversely, when the minimal survival rate occurred earlier in the year ($\delta_S = 180$ d), 50% of the simulated populations collapsed after 175 d. A delayed maximal survival rate increased the total abundance. The means from the first 175 d of simulation were 0.37×10^3 , 0.57×10^3 , 2.71×10^3 , 3.19×10^3 , 8.92×10^3 , and 20.81×10^3 individuals for the first six survival delay conditions (Fig. 9A).

Unlike the nauplii, the early appearance of the adult survival peak ($\delta_S = 245$ d, 255 d, and 265 d) positively affected total abundance during the first year (Fig. 9B). However, although the population abundance during the first year increased as the maximal survival rate appeared earlier, it also collapsed faster in the second year. The increase in total abundance during the first year was nevertheless relatively low, with the annual mean abundance increasing from 1522.8 to 3296.5 individuals with $\delta_S = 275$ d and $\delta_S = 245$ d, respectively. When a delay negatively affects the total abundance for the first year, it exhibits a positive effect during the second year. A 10 d to 20 d postponed survival cycle resulted in a larger and more delayed spring peak during the second year. Thus, maximal abundances of 34.85×10^3 , 39.08×10^3 , and 66.62×10^3 individuals appeared on the 495th, 507th, and 750th days of simulation with $\delta_S = 275$ d, 285 d, and 295 d, respectively. However, when the delay was exceptionally large ($\delta_S = 305$ d), the population was not maintained throughout the 2-year simulation.

4. Discussion

4.1. Model development and working hypothesis

Many factors influence copepod dynamics including temperature, food, predation, competition (Mauchline, 1998), and mating capacity (Kjørboe, 2006). In the present model, only the main driving forces in the Seine estuary that exhibit strong seasonal variability were considered, that is, predator pressure and temperature. This top-down perspective is based on the assumption that *E. affinis* from the Seine estuary is omnivorous and food is unlimited. Several populations of *E. affinis* feed on a wide variety of food, including phytoplankton and particulate matter (Tackx et al., 1995), protozoan microplankton (Jiménez-Melero et al. 2013; Merrel and Stoecker, 1998), and rotifers (Feike and Heerkloss, 2009). The non-food limited hypothesis is valuable for the Seine estuary, where the reproduction of *E. affinis* is observed annually (Ben Radhia-Souissi, 2010). Copepod survival may depend on the presence and quality of food (Hart, 1996; Koski et al., 1998). Based on the non-food

limited hypothesis and the capacity of *E. affinis* to adjust its feeding activity depending on turbidity (Gasparini and Castel, 1997), we are confident in setting the survival of copepodite stages (other than C3) to the maximum. Modifications to the hypotheses (i.e., applying the model to other *E. affinis* populations or to other species) could be easily integrated into the current model using the *MobidyC* platform. For simplification, we removed the effect of food for the Seine estuary, which seems to be a realistic assumption (Souissi, unpublished data).

To integrate the effect of temperature variations, we considered that an individual requires a certain quantity of heat to molt in the next stage (i.e., the degree-day approach). The IBM provides a good representation of the succession of developmental stages (or group of stages) and total population dynamics. The degree-day approach, therefore, provides a good estimate of the developmental time of the copepod, *E. affinis*.

The predation dynamics are implicitly considered by the seasonal variation of mortality of naupliar and adult stages. This was a simplification; we did not directly model predator interactions or predator dynamics. More precisely, this study ignores the interaction between predators and different adult stages, even though they differ in their responses to predation (Kawabata, 1991; Mahjoub et al., 2011). These model simplifications were essential because suitable data on seasonal variation in the gut content of the main *E. affinis* predators are unavailable. Moreover, introducing the effect of a main predator, such as Mysids, requires an adequate model of the population structure (in size or stages) and predator density to be developed. Predation efficiency depends on the size ratio of prey to predators (Winkler and Greve, 2004) and the abundance of predators (Hansson et al., 2001). Nevertheless, the sensitivity of the *E. affinis* population to the seasonality of predation pressure was tested in simulation set 4 by shifting the seasonal cycle of naupliar and adult stage survival.

This study shows that the proposed modeling approach can be used to gain important insights into the seasonality of *E. affinis*, and egg-carriers in general.

4.2. Representation of the seasonality of the *E. affinis* population

This model indicates that the peak of abundance of *E. affinis* occurs in May and decreases consistently until reaching a minimum in early September (simulation set 1). These results confirm in situ observations of the same population from the Seine estuary (Mouny, 1998) and other European populations from the Elbe and Westerschelde estuaries (Escaravage and Soetaert, 1995; Köpcke,

2004; Peitsch et al., 2000). In this study, the generation time obtained during the low-temperature season is similar to the 50 d of total development observed for the same species at a temperature of approximately 5 °C (Escaravage and Soetaert, 1995; Vijverberg, 1980).

Mouny (1998) observed at least four successive generations of *E. affinis* during the spring of 1997. We found that the time lag between the C1 and adult maximums was approximately 30 d in early spring and 10 d in late spring. This decrease in time lag is associated with a temperature increase, which leads to faster development. In the Seine estuary, the population shift toward early spring observed by Devreker et al. (2010) during 2005 was related to the cooler temperatures at the end of winter (i.e., February). This model seems to confirm this hypothesis.

The proposed model only provides concordant results for the estuarine population of *E. affinis* from nearby geographical regions. Populations from lower latitudes exhibit maximal abundance in early spring (David et al., 2005; Heinle and Flemer, 1975) mainly because of differences in seasonal temperature variations. However, this may also be caused by physiological differences derived from genetic differences between these European populations (Winkler et al., 2011). These differences arise from divergent evolutionary histories or phenotypic plasticity, as observed in a recent comparison of trans-Atlantic populations of *E. affinis* (Beyrend-Dur et al., 2009; Ben Radhia-Souissi, 2010; Devreker et al., 2012). These findings make a specifically calibrated model necessary for studying a given population, at least when the divergence between populations is clear. Alekseev and Souissi (2011) recently described a new species within the complex *E. affinis*, as defined by Lee (1999). This new species, originating in the United States of America, recently invaded the Baltic Sea and seems to be a better competitor than the local *E. affinis* population (Sukhikh et al., 2013). The IBM approach developed here could be used to investigate the possible interaction between these two divergent populations.

4.3. Model sensitivity to temperature increases

Global warming may affect the annual mean and amplitude of temperatures (Qian et al., 2011). This study shows that global warming may increase mean annual temperatures, as modeled by parameter T_m in Eq. (1). To investigate how global warming affects the dynamics of *E. affinis*, we simulated a low-temperature increase (simulation set 3). This scenario is realistic, because global warming could lead to a similar temperature increase in the Seine estuary (Moisselin et al., 2002; Ducharne et al., 2009). The clear pattern observed in all simulation runs indicates that an increase in mean annual temperature from 13 °C to 14 °C positively affects the overall population. Although this beneficial effect increases the population size, it may cause density-dependence effects, impairing the population growth rate (Sibly and Hone, 2002).

The results of simulation set 4 show that the adult and first developmental stage survival rates are critical parameters inherent to the population seasonality of *E. affinis*. Environmental characteristics, such as mean annual temperatures and predator seasonality, are critical parameters that affect these survival rates and vary because of global change. According to the general laws suggested by Hirst and Kiørboe (2002), a temperature increase may affect the mortality of *E. affinis*, subsequently affecting the predator dynamics and shifting its seasonality. The results of this study partially confirm the finding that global change can affect population seasonality (Edwards and Richardson, 2004). For a long-term variation in parallel with global warming (i.e., a temperature increase of 0.9 °C), Edwards and Richardson (2004) found that the phenological response of many zooplankton taxa to climate change includes an earlier abundance peak (10 d for copepods), except for copepods with peaks in spring and autumn (i.e., those with

bimodal cycles). However, changes in copepod phenology are not only linked to temperature increases, but can also result from eutrophication (Seebens et al., 2007). The temperature effect can change the environment trophic status, which affects spring and autumn blooms (Seebens et al., 2007). These changes in abundance of key copepod species may affect other trophic levels, as observed in Chesapeake Bay (Kimmel et al., 2006) and southern European estuaries (Marques et al., 2007; Martinho et al., 2007).

4.4. Vulnerability of the total population: Adult and naupliar stage survival

The results from simulation set 4 emphasize the importance of time-dependent mortality rates to the temporal dynamics and maintenance of *E. affinis* populations. Analyzing high-frequency time series data of an oceanic free-spawner produced a similar conclusion (Ohman and Hirche, 2001).

Investigating these scenarios allowed us to analyze the implications of the mortality of various developmental stages on the overall population dynamics. Assuming that the copepodite survival is 100% (except C3), overall population dynamics similar to those observed in the field were obtained. Therefore, copepodite mortality in the field should not be important. Despite inter-species differences in mortality rates over their life spans, copepods exhibit low mortality rates in the early copepodite stages (Ohman and Wood, 1995; Eiane and Ohman, 2004). Eiane and Ohman (2004) estimated negligible losses for late naupliar-early copepodite stages of *Calanus finmarchicus*, *Pseudocalanus elongatus*, and *Oithona similis*. They attributed this low mortality rate to the vertical migration of late developmental stages to avoid predators.

This approach can also help address difficulties that arise from limited or incomplete information on the predator-prey relationship. When predator-prey interactions involve several life stages, the dynamics of the system become complex (Souissi and Nival, 1997). The analysis in this study suggests that nauplii survival is important to *E. affinis* population dynamics and emphasizes that nauplii act as a bottleneck in copepod population dynamics (Santer and Lampert, 1995). Conversely, the adult stage is the most critical stage that significantly affects extinction probabilities. Copepod mortality can also be non-consumptive because of starvation, environmental stresses, disease, pollution, injuries, parasites, and harmful algal blooms (Burns, 1985; Byron et al., 1984; Carpenter et al., 1974; Delgado and Alcaraz, 1999; Ianora et al., 1987; Kimmerer and McKinnon, 1990). In the proposed model, mortality includes death from predation and non-consumptive mortality. However, the model does not consider advection, which is important for estimating nauplii disappearance. The late developmental stages of *E. affinis* can maintain themselves within a specific region in several estuaries (i.e., the maximal turbidity zone; Schmitt et al., 2011), but losses caused by advection affect early developmental stages. However, this loss is yet to be quantified. Thus, the current results are conservative with regards to the need of proper predation closure term to accurately model the seasonality of planktonic production cycles (Ohman and Wood, 1995). These results also emphasize that understanding predator feeding preferences more precisely is important, as stated by Hirst et al. (2010). Although copepod females are more prone to predation because they are larger than males, they are also more able to escape (Kiørboe, 2008). However, whether visual predators prefer female prey to male prey depends on the predator itself. Certain predators prefer feeding on females (e.g., Baltic herring *Clupeaharengus membras*; Sandström, 1980; Viitasalo et al., 2001), whereas others have no significant preferences, such as sticklebacks (e.g., *Gasterosteus aculeatus*; Vuorinen et al., 1983) and larval striped bass (*Morone axatilis*; Meng and Orsi, 1991). However, ovigerous females experience a higher predation risk (Mahjoub

et al., 2011). Studies on several copepod species have suggested that males exhibit higher mortality rates (Hirst et al., 2007; Ohman et al., 2002) and are up to 32 times more likely to die than females (Hirst et al., 2010). In the proposed model, the mortality rate is the same for males and females. Future investigations with this model should include the effects of sex-dependent mortality on population dynamics.

Whereas adult copepods may be prone to predation because they are large, *E. affinis* nauplii are prone to cannibalism because they are small and soft-bodied. *E. affinis* cannibalism may significantly affect its population dynamics, regulating population size when abundance exceeds a threshold (Heerkloss et al., 1993). Nevertheless, in the field, nauplii remain in the surface layer longer (Schmitt et al., 2011) and are therefore more likely to drift with the tidal current. This limits the effects of cannibalism. Ueda et al. (2010) used a similar suggestion to explain the shallow depth positioning of *Pseudodiaptomus inopinus* and *Sinocalanus sinensis* early nauplii stages in the Chikugo River estuary, Japan. In the Seine estuary, density-dependence is negligible and was ignored by the model. If the model is applied to other species, the decision to ignore the density-dependence effect requires a pre-analysis of the biology of the studied species.

Generally, proper estimates of mortality, its sources, and seasonal variations are necessary to quantitatively address the population dynamics of any copepods.

4.5. An adequate tool for diverse areas of study

This version of the model ignores mate limitation, which can be observed in estuaries (Choi and Kimmerer, 2009) and may strongly influence reproduction (Dur, 2009). Further information on mate limitation can improve the behavior parameterization of the model and provide insights into the effects of mate limitation at a population level.

Even if some submodels should be improved or developed, the results of this study are promising. The IBM accounts for all development stages and can simulate population development over several years. Accounting for all development stages is extremely important from an ecotoxicological perspective, because it allows sensitivity to toxins to be associated with the age and stage of an individual (Rand et al., 1995). Therefore, Mooij et al. (2003) concluded that an individual-based approach is the most appropriate method of studying emerging properties in ecotoxicology. Future studies could explore this topic, but it requires the correct representation and quantification of the accumulation process of a toxin. However, the structure of the model makes changing or adding supplemental submodels easy, which could, for example, represent a process of bioaccumulation. By modeling pollution-induced mortality (i.e., death at a certain dose of bio-accumulated product), the model can be used to assess the effect of introducing fertilizers or pesticides at certain times of year. More generally, when emerging research programs (such as the one conducted in the Seine estuary) develop adequate parameterization to link the effects of pollution to the different life traits of *E. affinis* (or any other copepod), this IBM can be used for several ecotoxicological and risk assessment applications.

The proposed model can also be generalized to any egg-bearing copepod species. Recent individual-based experiments conducted on *Arctodiaptomus salinus* in Spain (Jiménez-Melero et al., 2007, 2012) and *Pseudodiaptomus annandalei* in Taiwan (Beyrend-Dur et al., 2011) have provided excellent data that could be integrated into this IBM. Proper calibration of the model for these species from different ecosystems could enable the comparative study of specific adaptations or differential responses to global warming.

Laboratory and in situ data were obtained to accurately access parameter values before sensitivity tests were conducted by this

study. A fairly narrow uncertainty range was determined for most of the data. However, this was not the case for mortality, and manual calibration of mortality was mainly conducted. We are aware that more meaningful parameter selection is required for IBM calibration. Further applications of this model should include the recently developed approach of combining sensitivity analysis and calibration (i.e., pattern-oriented parameterization; Beaudoin et al., 2008).

5. Conclusion

This model is different from previous modeling efforts because it explicitly incorporates the specific reproductive cycle of egg-bearing copepods. The results show that variable temperature and predation affect the demography of the species. The model provides valuable insights into population structure (i.e., different developmental stages) and population dynamics variations. This study also shows that the model can be used to answer a wide range of fundamental questions on the population dynamics of any egg-bearing copepods. Nevertheless, more comprehensive information on the life history of the species and its interaction with the environment are required to produce a more realistic simulation model. Therefore, we suggest that an IBM should be developed that incorporates food dependence, mate limitation, and stage dependent mortality to better represent the studied species. In polluted environments (such as estuaries), this modeling approach can be used to assess the impact of pollution at a population level.

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