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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.

1. Introduction

Copepods are some of the most important zooplankter 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, zooplankters, 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 integers 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