Journal of Marine Systems 87 (2011) 55–65

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Control mechanisms on the ctenophore *Mnemiopsis* population dynamics: A modeling study

B. Salihoglu *, B.A. Fach, T. Oguz

Institute of Marine Sciences, Middle East Technical University, P.O. Box 28, Erdemli 33731, Mersin, Turkey

ARTICLE INFO

Article history:
Received 29 July 2010
Received in revised form 28 February 2011
Accepted 2 March 2011
Available online 9 March 2011

Keywords:
Ecosystems
Modeling
Mnemiopsis
Ctenophore
Jellyfish
Developmental stages
Food availability
Temperature effects
Black Sea

ABSTRACT

A comprehensive understanding of the mechanisms that control the ctenophore *Mnemiopsis* blooms in the Black Sea is gained with a zero-dimensional population based model. The stage resolving model considers detailed mass and population growth dynamics of four stages of model-ctenophore. These stages include the different growth characteristics of egg, juvenile, transitional and adult stages. The dietary patterns of the different stages follow the observations given in the literature. The model is able to represent consistent development patterns, while reflecting the physiological complexity of a population of *Mnemiopsis* species. The model is used to analyze the influence of temperature and food variability on *Mnemiopsis* reproduction and outburst. Model results imply a strong temperature control on all stages of *Mnemiopsis* and that high growth rates at high temperatures can only be reached if food sources are not limited (i.e. 25 mg C m^{-3} and 90 mg C m^{-3} mesozooplankton and microplankton, respectively). A decrease of 5 °C can result in considerable decrease in biomass of all stages, whereas at a temperature of 25 °C a 40% decrease in food concentrations could result in termination of transfer between stages. Model results demonstrate the strong role of mesozooplankton in controlling the adult ctenophore biomass capable of reproduction and that different nutritional requirements of each stage can be critical for population growth. The high overall population growth rates may occur only when growth conditions are favorable for both larval and lobate stages. Current model allows the flexibility to assess the effect of changing temperature and food conditions on different ctenophore stages. Without including this structure in end-to-end models it is not possible to analyze the influence of ctenophores on different trophic levels of the ecosystem.

1. Introduction

The invasion of marine habitats by gelatinous species is of major ecological concern worldwide due to the detrimental implications for native ecosystem structure and function, often resulting in the collapse or even extinction of native populations (Moller, 1984; Purcell and Grover, 1990; Cohen and Carlton, 1998; Brodeur et al., 1999; Purcell and Arai, 2001; Lynam et al., 2005). The cumulative effects of mounting shipping traffic, global warming, ocean acidification, eutrophication, and exploitation of marine living resources have recently favored their spreading, settlement and sometimes domination of local food webs (Mills, 2001; Byers, 2002). Among gelatinous organisms, the ctenophore *Mnemiopsis* is of special interest as it is a highly opportunistic species with a rapid linear growth rate and high reproduction ability under a wide range of environmental conditions. The native habitat of *Mnemiopsis* is the eastern coastal waters of the North and South American continents (Burrell and Van Engel, 1976; Kremer, 1979, 1994; Deason and Smayda, 1982; Deason, 1982; Purcell and Sturdevant, 2001). It has been introduced into the Black, Marmara, and northern Aegean Seas following the early 1980s (Vinogradov et al., 1989; Studenikina et al., 1991; Shiganova, 1998; Shiganova et al., 2001). Its invasion has been extended into the Caspian Sea a decade later (Kideys, 2002; Finenko et al., 2006), and more recently to the North Sea and the Baltic Sea (Faasse and Bayha, 2006; Javidpour et al., 2006; Boersma et al., 2007; Oliveira, 2007; Riisgard et al., 2007; Viitasalo et al., 2008). *Mnemiopsis* heavily regulates zooplankton communities and planktivorous fish populations particularly during the warm half of the year and therefore exert profound influence on the functioning of marine ecosystems (Kremer and Nixon, 1976; Deason, 1982; Shiganova, 1998; Mutlu and Bingel, 1999; Finenko and Romanova, 2000; Shiganova et al., 2001).

To our knowledge, no explicit individual based population dynamics model is available for making a comprehensive analysis of the role of environmental factors on the growth and reproduction characteristics of ctenophore species in general and *Mnemiopsis* in particular. For example, although *Mnemiopsis* tolerates a wide range of temperature conditions (Burrell and Van Engel, 1976; Baker, 1973) and the optimum population and biomass growths occur at temperatures above 20 °C (Kremer et al., 1986; Reeve et al., 1989), it is not clear from the available observations how populations of the

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* Corresponding author. Tel.: +90 324 521 2150; fax: +90 324 521 2327.
E-mail address: baris@ims.metu.edu.tr (B. Salihoglu).

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doi:10.1016/j.jmarsys.2011.03.001

early life stages can grow nonlinearly at lower spring transitional temperatures between 10 and 20 °C. Similarly, there is no clear understanding on how early their life history and feeding characteristics differ from those of the adult stage because early stages of *Mnemiopsis* selectively ingest protistan prey whereas adult lobate individuals utilize a diverse variety of metazoan prey including copepods, fish egg and larvae and veliger larvae (Sullivan and Gifford, 2004; Rapoza et al., 2005). In order to further our conceptual understanding of the *Mnemiopsis* growth dynamics, the present study offers the development of a relatively simple, zero-dimensional individual-based biomass and population dynamics model (cf. Section 2) and then explores the role of changing temperature and food conditions using the environmental setting of the Black Sea (cf. Section 3). The last section discusses the implications of model findings and possible future outlook of the model implementation.

2. Model structure

2.1. Life history characteristics of Mnemiopsis

Three distinct life history stages in the development of *Mnemiopsis* larvae have been identified (Sullivan and Gifford, 2004). Upon hatching, *Mnemiopsis* larvae exhibit a classic cydippid morphology in the tentaculate stage. Larvae then enter a transition stage at 5.0 mm (~0.15 mg C) possessing both tentacles and small oral lobes. Finally, tentacle bulbs resorb the tentacles during the lobate stage. Approximately 15 days after hatching young ctenophores begin to propagate when reaching a size of 30 mm which corresponds to approximately 3 mg C biomass (Sorokin, 2002). Therefore, in our model *Mnemiopsis* population is represented by four stages; egg, juvenile, transitional and adult. Adult specimens spawn every 10–20 days releasing 100–10,000 eggs each time. Their fecundity depends on food supply and temperature. Average dry weight of an egg is 0.0005 mg, with 2% of organic carbon content (Reeve et al., 1989) which is taken as 0.0001 mg C per egg in the model. Embryonic development takes about 1 day at 23 °C (Sorokin, 2002). The size of the hatched larvae is 0.3–0.4 mm and its biomass remains comparable to the egg and, thus is assumed to be 0.0001 mg C in the model.

2.2. Stage resolving Mnemiopsis life cycle model

Our stage resolving ctenophore model combines a modified form of the stage resolving approach of the Fennel (2001) zooplankton model which includes the *Mnemiopsis* growth dynamics of Kremer (1976) and Kremer and Reeve (1989). The four stages of model-ctenophore include different growth characteristics of egg (e), juvenile (j), transitional (t) and adult (a) stages. The dietary patterns of the different stages follow observations by Rapoza et al. (2005); Waggett and Sullivan (2006); Sullivan and Gifford (2007) which are given in detail in Section 2.2.1.

The state equations for the stage-dependent biomass M in mg C m^{-3} are expressed by

$$\frac{\partial M_e}{\partial t} = T_{ae}M_a - T_{ej}M_e - \mu_e M_e \tag{1}$$

$$\frac{\partial M_j}{\partial t} = T_{ej}M_e + \left(g_j - \mu_j - l_j\right)M_j - T_{jt}M_j \tag{2}$$

$$\frac{\partial M_t}{\partial t} = T_{jt}M_j + (g_t - \mu_t - l_t)M_t - T_{ta}M_t \tag{3}$$

$$\frac{\partial M_a}{\partial t} = T_{ta}M_t + (g_a - \mu_a - l_a)M_a - T_{ae}M_a. \tag{4}$$

The time dependent dynamics of biomass changes are controlled by the transfer rate T_{ij} from stage i to stage j, grazing rate, g, metabolic loss rate, l, and mortality rate, μ. The first term on the right hand side of Eq. (1) denotes the single source term for the egg stage which is the transfer from adults. Second and third terms show the transfer to the juvenile stage and the mortality of eggs, respectively. Equations for the juvenile, transitional and adult stages (Eqs. (2)–(4), respectively) include grazing of zooplankton as extra source terms and metabolic losses as extra loss terms. We assume that the main metabolic losses of ctenophores are respiration and organic release (Kremer and Reeve, 1989). The way in which these rates are included in the model equations is presented in detail in the following subsections. The corresponding equations for the temporal population changes read:

$$\frac{\partial N_j}{\partial t} = T_{ej}N_e - \mu_j N_j - T_{jt}N_j \tag{5}$$

$$\frac{\partial N_t}{\partial t} = T_{jt}N_j - \mu_t N_t - T_{ta}N_t \tag{6}$$

$$\frac{\partial N_a}{\partial t} = T_{ta}N_t - \mu_a N_a - T_{ae}N_a \tag{7}$$

where N denotes the number of individuals in m^{-3}. Number of individuals that are transferred from one stage to the next (e.g., N_j in Eq. (6) and N_t in Eq. (7)) is estimated by dividing the total biomass by the maximum biomass of the corresponding stage (M/W_m).

2.2.1. Grazing rates

The grazing rates define the amount of ingested food per day in relation to the biomass of an individual ctenophore of any stage. Daily carbon grazing g (day^{-1}) is included in the model following the empirical relation by Kremer (1976):

$$g_i = G_i \times F \times 73 \times AE_i \tag{8}$$

where i denotes the stage of the ctenophore, G is the volume cleared (l/mg dry weight day), F is the food (zooplankton) concentration (mg C l^{-1}), 73 is to convert carbon weight to dry weight, and AE represents the assimilation efficiency.

2.2.1.1. Adult stage. Kremer (1976) and Kremer and Reeve (1989) suggested an empirical relationship for the clearing rate of adult *Mnemiopsis* that is independent of prey concentration but rather a function of temperature and organism size.

$$G_a = a(W/w2c)^{-b} \tag{9}$$

where, G_a is the volume cleared (l/mg dry weight day) and W is the carbon weight of the ctenophore (mg C), $w2c$ is the factor used to convert gram wet weight of the ctenophore to mg carbon weight and is assumed to be 0.574 mg C (g wet weight)$^{-1}$. The negative exponential coefficient b shows the trend for decreasing weight-specific clearing rate with size and taken as 0.5 following Kremer (1976). Temperature dependence of the clearance rates is defined by a.

$$a = a_o e^{KT} \tag{10}$$

where, a_o and K are the constants and T is the temperature. The value of K (0.05 °C^{-1}) is equivalent to a feeding rate Q_{10} of 1.7 and, a_o is taken as 0.09 and 0.08 l mg^{-1} day^{-1} for transitional and adult stages, respectively.

2.2.1.2. Transitional stage. Kremer and Reeve (1989) showed that for smaller ctenophores (<18 mm or <1 mg C) there is a considerable effect of food concentration on the clearance rate. Thus, for transitional stage