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

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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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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

ctenophores that are less that 1 mg C in biomass, the adult clearance rate is adjusted empirically by

$$G_t = a(W/w2c)^{-b} \times (0.01P)^{0.65W-0.65} \quad (11)$$

where a, W and b are the same as in Eq. (10), P represents food (zooplankton) abundance (no. l^{-1}), that is estimated by dividing the food concentration F (mg C l^{-1}) by an average mass of individual copepod species assumed to be 0.0024 mg C (Kremer and Reeve, 1989). For transitional stage ctenophores that are greater than 1 mg C the clearance rate is estimated by Eq. (9).

2.2.1.3. Juvenile stage. According to Sullivan and Gifford (2004), daily rations of early tentaculate larvae can be satisfied by consumption of protistan prey formed by heterotrophic, mixotrophic and autotrophic species. Rapoza et al. (2005) showed that the relative proportion of microplankton in the diet of ctenophores that are smaller that 10 mm in size is above 80% and the contribution of microplankton to the nutritional requirements of developing larvae declines as they pass through the transitional stages from cydippid to lobate forms. Thus, the model assumed that juvenile stage ctenophores consume predominantly the microplankton prey. The juvenile clearance rate is estimated by a linear relationship developed by Sullivan and Gifford (2004):

$$G_j = 0.4 \times l + 0.1 \quad (12)$$

where, G_j is the volume cleared (l/mg dry weight day) and l is the mm length of the ctenophore that is estimated using the relationship developed by Kremer (1976):

$$l = (W/w2c)^{0.574} \times 12.3 \quad (13)$$

where W is the carbon weight of the ctenophore (mg C). In the model maximum net growth rate of the juvenile stage is limited to 4 day^{-1} following Sorokin (2002).

2.2.1.4. Assimilation efficiency. Assimilation efficiency of adult ctenophores is normally high (72%) but if they continue to feed at high food concentrations, incoming food is only partially digested and assimilation efficiency decreases substantially (Kremer and Reeve, 1989; Reeve et al., 1989). Therefore, AE is assumed to vary with food concentration according to

$$AE = 0.85 - 0.09 \ln P \quad (14)$$

where P represents food (zooplankton) abundance (no. l^{-1}). On the other hand, the assimilation efficiency of juvenile ctenophores is not known; we therefore set it to a constant rate of 75% and tested the sensitivity of the model dynamics to variations of this parameter (cf. Section 3.2).

2.2.2. Transfer rates

2.2.2.1. Adult and transitional stages. The stage resolving model requires to specify the transfer rates of biomass and abundance from one stage to the next for the development of the ctenophore. The transfer rate, T, for each of the juvenile, transitional and adult stages is defined as

$$T = g \times f \quad (15)$$

where g is the grazing rate and f is a sigmoidal function, which controls the transfer of biomass to the next stage. The transfer starts after the mean individual exceeds a certain critical value (cf. Table 1), and continues up to the reference mass (W_r) and is further modulated by the maximum mass (W_m) and the slope factor p which is taken as 4 (Stegert et al., 2007).

$$f = (W - W_r)^p) / ((W - W_r)^p + (W_m - W_r)^p) \quad (16)$$

The details of the sensitivity of transfer mechanism to the parameter values used in the transfer function (Wr_j and Wm_j) are given in Table 2.

2.2.2.2. Juvenile stage. It is observed that the eggs hatch about 24 h after release at summer temperatures (i.e. 25 °C) and the threshold temperature of 4 °C corresponds to the termination of hatching (Purcell and Sturdevant, 2001). Thus, a temperature dependent relation is developed to estimate the transfer from eggs to juveniles:

$$T_{ej} = 0.27e^{d(T-4)} \quad (17)$$

where d is the coefficient of exponential increase of hatching rate with increasing temperature taken to be 0.063, T represent temperature in °C. Contrary to Fennel (2001) and Stegert et al. (2007) the present formulation of transfer rates does not incorporate an inhibition term because ctenophores do not molt.

2.2.3. Reproduction

In the model it is assumed that all adults can reproduce, and that only 1% of ingested food is spent on reproduction right after transfer from the transitional stage (1.5 mg C) (Kremer, 1976). As the animal

Table 1
Definitions and units of variables or parameters used in the equations that describe the dynamics of *Mnemiopsis* life cycle.

Symbol	Definition	Value	Units
$w2c$	Conversion factor of ctenophore g wet weight to grams carbon weight	0.574	mg C (g wet weight)$^{-1}$
b	Exponential term representing the decrease of clearing rate with size	0.5	
a_o	Adult stage basal increase of clearing rate with temperature	0.09	l (mg d)$^{-1}$
K	Exponential term that represents the increase of clearing rate with temperature	0.05	°C^{-1}
p	Slope factor used in the transfer function		
c	Coefficient of exponential increase of transfer	0.115	
d	Exponential term that represents the increase of hatching rate at higher temperatures	0.063	
r	Basal fraction of food spent on reproduction	0.01	
R_b	Basal respiration rate	0.04	d^{-1}
R_{max}	Maximum increment above basal respiration rate	0.11	d^{-1}
μ_e	Egg mortality rate	0.99	d^{-1}
μ_j	Juvenile mortality rate	0.95	d^{-1}
μ_e	Transitional mortality rate	0.30	d^{-1}
μ_a	Adult mortality rate	0.02	d^{-1}

Table 2
Mass parameters.

Egg mass	$m_e = 0.1$ μg C	
Stage	Reference mass	Maximum mass
Juvenile	$Wr_j = 0.13$ mg C	$Wm_j = 0.15$ mg C
Transition	$Wr_t = 1.2$ mg C	$Wm_t = 1.5$ mg C
Adults	$Wr_a = 2.8$ mg C	$Wm_a = 3.10$ mg C

grows this fraction increases exponentially. The fraction of ingested food spent on reproduction is estimated following Kremer (1976):

$$T_{ae} = re^{cW/w2c}T_f \quad (18)$$

where r is a constant taken to be 0.01, c represents the coefficient of exponential increase of transfer with increasing mass which is taken as 0.115 following Kremer (1976) and W is the carbon weight (mg C) of the ctenophore.

An empirical linear temperature function is developed which is represented by the last term of Eq. (18), $T_f = -1.875 + 0.125T$, where T represents the temperature in °C. This function is based on the field observations and experiments (Shiganova, 1998; Purcell et al., 2001) that show intensive spawning occurs during late summer–autumn.

2.2.4. Loss rates

We assume that the main cause of ctenophore mass loss is respiration and organic release (Kremer and Reeve, 1989). The general ctenophore respiratory demand in the model is formulated using a Monod equation following Kremer and Reeve (1989):

$$resp = R_b + R_{max}\frac{foodno}{K_s + foodno} \quad (19)$$

where R_b is the basal respiration rate taken to be 4% of the body carbon per day and R_{max} is the maximum respiration rate (11% of the body carbon per day) and K_s is the half saturation constant (prey concentration of 30 no l^{-1}). Following Kremer and Reeve (1989) the release of organic carbon is taken to be half of the respiratory demand. Loss rates of juvenile ctenophores are not known, therefore a constant total loss rate of 6% is chosen, which is within the observed range of a large range of ctenophore sizes (Kremer and Reeve, 1989).

2.2.5. Mortality

Observations on mortality of different stages of *Mnemiopsis* are very limited. Following Kremer (1976) we have assumed that the mortality of adults (μ_a) is 2% per day and this value increases to 99% for eggs (μ_e). It is documented that the newly hatched larvae are very vulnerable and can even be largely destructed by larger copepods (Greve, 1977; Reeve, 1980; Stanlaw et al., 1981). Thus, mortality rate of juveniles (μ_j) and transition stage ctenophores (μ_t) are assumed to be 95% and 30%, respectively.

3. Results

The population model described above was initially tested with constant food and temperature conditions reported for the Black Sea (Finenko et al., 2006). A reference simulation was first established to simulate the development of a cohort of eggs without any reproduction (Section 3.1) and then the simulation was repeated with reproduction. In Section 3.2 model sensitivity to poorly constrained parameters is analyzed. The influence of temperature and food conditions on regulating ctenophore abundance and biomass is discussed in Section 3.3. Section 3.4 provides the results of model runs that are forced with time dependent *in situ* conditions.

3.1. Reference run

The reference simulation was performed at 25 °C with constant food resources of 25 mg C m^{-3} mesozooplankton and 90 mg C m^{-3} microplankton. These values base on several assumptions. They represent the maximum mesozooplankton in Sevastopol Bay (Finenko et al., 2006) and microplankton levels assumed to include microzooplankton and microphytoplankton (Finenko et al., 2006; Oguz and Velikova, 2010) that are available to *Mnemiopsis* in the region. These maximum levels are assumed to represent food levels that are not exhausted by grazing. For the reference simulation the development of 1000 eggs with an initial biomass of 0.1 mg C m^{-3} to adults was simulated. No reproduction (no production of new eggs) is considered and stage resolving biomass and abundance (Fig. 1A and B, respectively) is shown for a full generation time. A generation time here comprises the development of eggs into adults.

Without reproduction the biomass accumulates in the adult stage over time. The control of the sigmoidal transfer function (Eq. (16)) can be seen in Fig. 1A and B. The transfers are smooth although inhibition of growth during transfers was not used in contrast to Fennel (2001) and Stegert et al. (2007). The duration times of the different *Mnemiopsis* stages are variable and a full generation time, from eggs to mature adults, takes about 17 days which is consistent with observations (Sorokin, 2002). After day 35 only adults continue to exist. Without any reproduction loss the increase in adult biomass continues until day 70 and due to the influence of mortality losses, biomass starts to decrease following the decreasing trend in abundance (Fig. 1B).

Next we repeated the reference simulation including reproduction. A similar development as in the reference simulation can be seen until the adults start to produce eggs after day 17 (Fig. 2A and B). After the onset of reproduction there is a clear increase in biomass and number of individuals. The production of eggs starts at day 17 immediately followed by an increase in juvenile abundance while the increase of transition stage abundance starts on day 68 (Fig. 2B). The adult biomass in the reproduction run is lower (Fig. 2A) than in the reference simulation (Fig. 1A) because of the energy flow from adults to eggs.

3.2. Model sensitivity to internal dynamics

Many of the parameters used to formulate the growth dynamics of ctenophore stages are not well constrained by measurements. Information on feeding rates, assimilation efficiency, reproduction and transition between stages is very limited (Kremer and Reeve, 1989; Rapoza et al., 2005). Thus, we investigated the sensitivity of small ±10% changes in selected parameter values on the growth dynamics of *Mnemiopsis*.

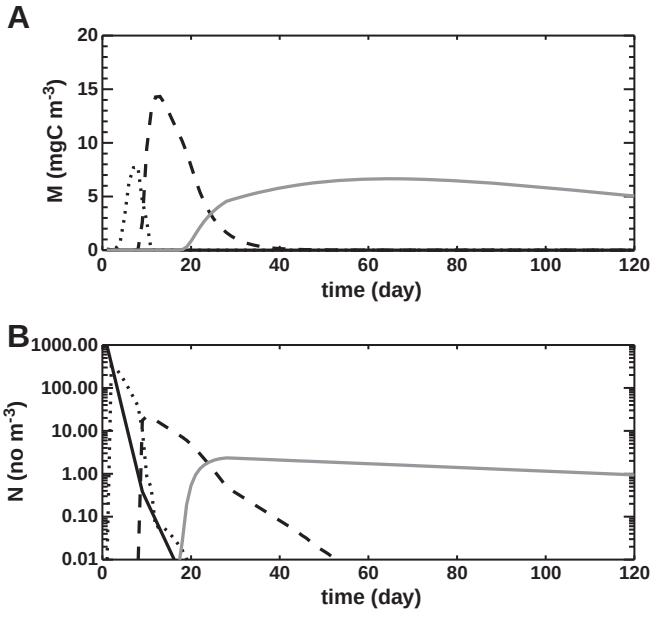

Fig. 1. Development of *Mnemiopsis* (A) biomass, M, (mg C m^{-3}) of juvenile (dotted line), transition (dashed line) and adult (solid grey line) stages and (B) abundance, N, (no. m^{-3}) of eggs (solid black line), juvenile (dotted line), transitional (dashed line) and adult (solid grey line) stages over time obtained from the reference simulation.

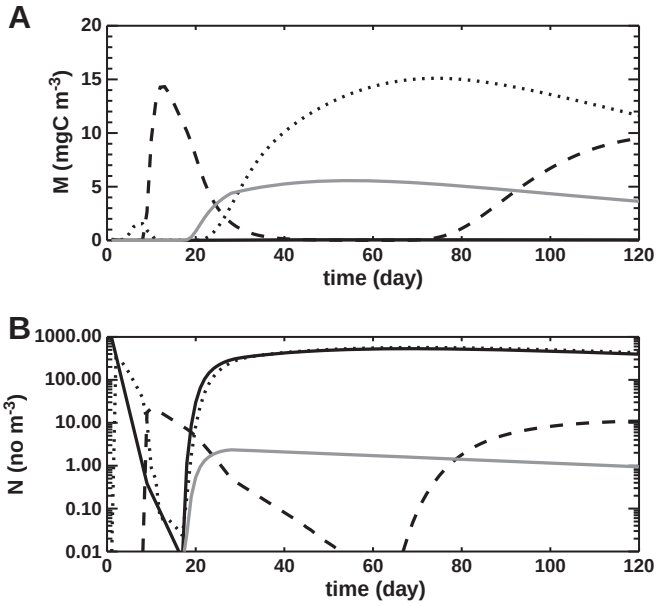

Fig. 2. Development of *Mnemiopsis* (A) biomass, M, (mg C m^{-3}) of juvenile (dotted line), transition (dashed line) and adult (solid grey line) stages and (B) abundance, N, (no. m^{-3}) development of eggs (solid black line), juvenile (dotted line), transitional (dashed line) and adult (solid grey line) stages over time obtained from the reference simulation with reproduction. To be able to show the results on the same scale juvenile biomass (dotted) is divided by 5 in panel (A).

These parameters include the assimilation efficiency (*AE*), the linear coefficient of Eq. (10) (a_o) that determines an increased feeding rate at increased temperatures, the exponential coefficient used in Eq. (9) (*K*), and the coefficient of the reproduction equation Eq. (18) (*r*). In addition, the reference mass (W_r) and maximum mass (W_m) of each stage (cf. Table 2) which influence the transfer between different stages are modified. The effect of variations in these parameters was assessed calculating yearly biomass and reproduction rates as diagnostics.

Results show that the model dynamics are most sensitive to the changes in *AE*, a_o, and *K*, with positive changes in biomass and production occurring with an increase in these parameters and vice versa while *r* and W_r of each stage have minor effects on biomass and reproduction (Figs. 3 and 4). The response of biomass is stronger than that of reproduction when *AE*, a_o or W_m is modified. Although the change in reproduction is similar in response to an increase or decrease in the parameters, the change in biomass is specifically

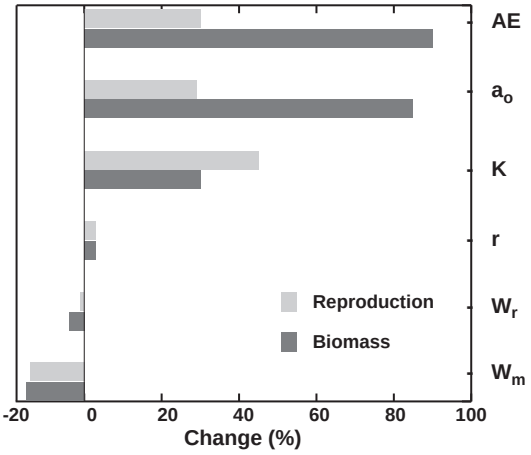

Fig. 3. Change (%) in annual integrated biomass and reproduction in response to a 10% increase in selected parameters.

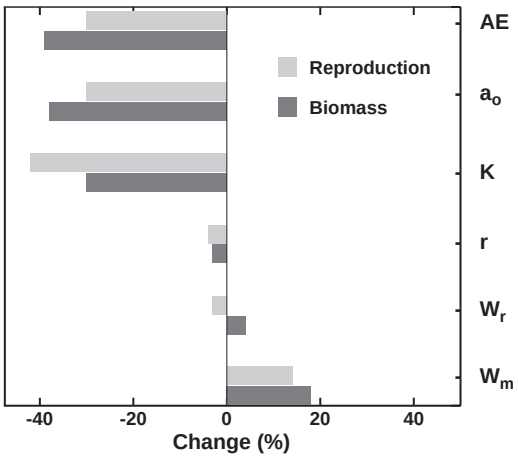

Fig. 4. Change (%) in annual integrated biomass and reproduction in response to a 10% decrease in selected parameters.

higher when *AE* or a_o is increased. This suggests that an increase in biomass is not necessarily linearly reflected in reproduction.

How changes in parameter values used in the transfer function (slope factor (*p*), reference mass (W_r) and maximum mass (W_m)) regulate the transfer mechanism is shown in further detail in Fig. 5A–C. Results for the juvenile transfer function show that reference and maximum mass are the main parameters that define the structure of the transfer. Reference mass especially regulates the timing of the

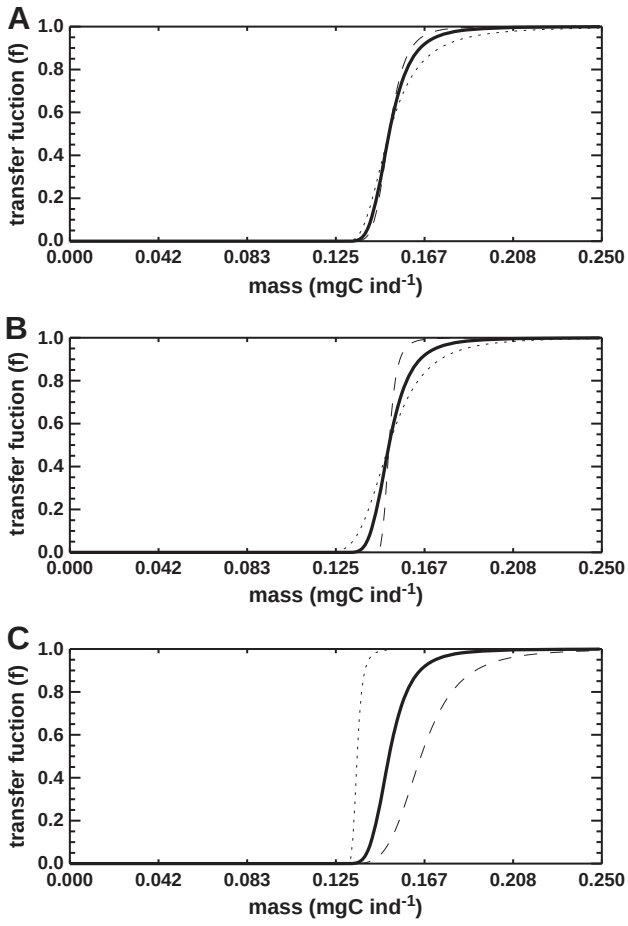

Fig. 5. Transfer function (*f*) as function of juvenile stages of individual *Mnemiopsis* biomass (mg C). Dashed and dotted lines show 10% increase and decrease, respectively, in (A) slope factor (*p*), (B) reference mass (Wr_j), and (C) maximum mass (Wm_j).

transfer initiation and maximum mass has a strong impact on the transfer rate. This is found for the transfer functions of other stages as well. Our analyses indicate that the specification of the transfer function is one of the important elements that controls the ctenophore model dynamics.

Because the temperature dependency of reproduction is based on limited observations (cf. Section 2.2.4) we also tested the model with nonlinear Q_{10} functions, $T_f = Q_{10}^{(T-23)/10}$ and $T_f = 0.03e^{(0.14*T)}$, where Q_{10} was taken as 4 following Purcell and Sturdevant (2001) and T denotes temperature in °C (Fig. 6). To test the influence of the different temperature functions on seasonal dynamics of the *Mnemiopsis* community an annual run was done. This run was different from the reference simulation in that it used a changing temperature time series to force the model (details given in Section 3.4). Model results show that when a Q_{10} type temperature function is used egg production continues even during winter months at temperatures lower then 16 °C. This results in a transfer of biomass and abundance between stages throughout the year and reduces the individual biomass especially at the beginning of spring. In turn, this reduces the reproduction success of the second year community (not shown). Field observations and experiments showed that spawning may not occur during spring below 16 °C in the Black Sea (Purcell et al., 2001).

The difference between the results of different temperature functions shows the importance of the appropriate representation of this process in the model.

3.3. Model sensitivity to external dynamics

To compare the influence of changing temperature and food concentration on ctenophore abundance and biomass, five simulation runs were performed at 10, 15, 20, 25, and 30 °C with constant food conditions as in the reference simulation, 25 mg C m^{-3} mesozooplankton and 90 mg C m^{-3} microplankton, (Figs. 7 and 8), and three runs were performed for different mesozooplankton food levels of 15, 20, 25, and 30 mg C m^{-3} and microplankton food levels of 50, 70, 90, and 110 mg C m^{-3} at 25 °C (Figs. 9 and 10).

At 10 °C only the juvenile and transition stages can develop and no reproduction occurs (Fig. 7A). Biomass of the transitional stage ctenophores is also low compared to the reference run at 25 °C (Fig. 7D). At 15 °C development time takes almost 40 days and a low level of reproduction occurs (Fig. 7B). At 20 °C reproduction starts right after day 20 and the secondary transition from the juvenile to transition stage takes place after day 60 (Fig. 7C). At 30 °C the biomass of all stages is more than three times as high compared to the reference run and development time is reduced to 15 days (Fig. 7E). Model results therefore suggest that increasing temperature favors all stages of ctenophore growth. In fact, *Mnemiopsis* biomass follows an exponentially increasing trend (Fig. 8A). This increase was also reflected on the number of eggs increased (Fig. 8B), and the number of individuals produced (Fig. 8C).

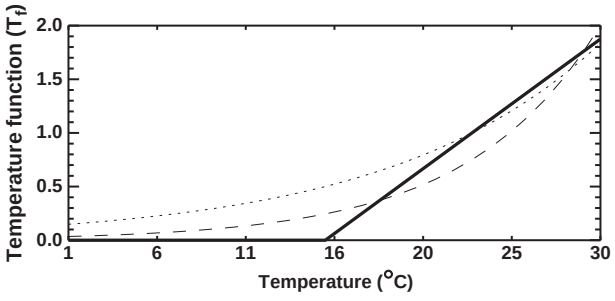

Fig. 6. Temperature function (T_f) as a function of temperature. Solid, dotted and dashed lines show the changes in temperature limitation for linear and two nonlinear Q_{10} type functions, $T_f = -1.875 + 0.125T$, $T_f = Q_{10}^{(T-23)/10}$ and $T_f = 0.03e^{(0.14*T)}$, respectively, where T represents temperature in °C.

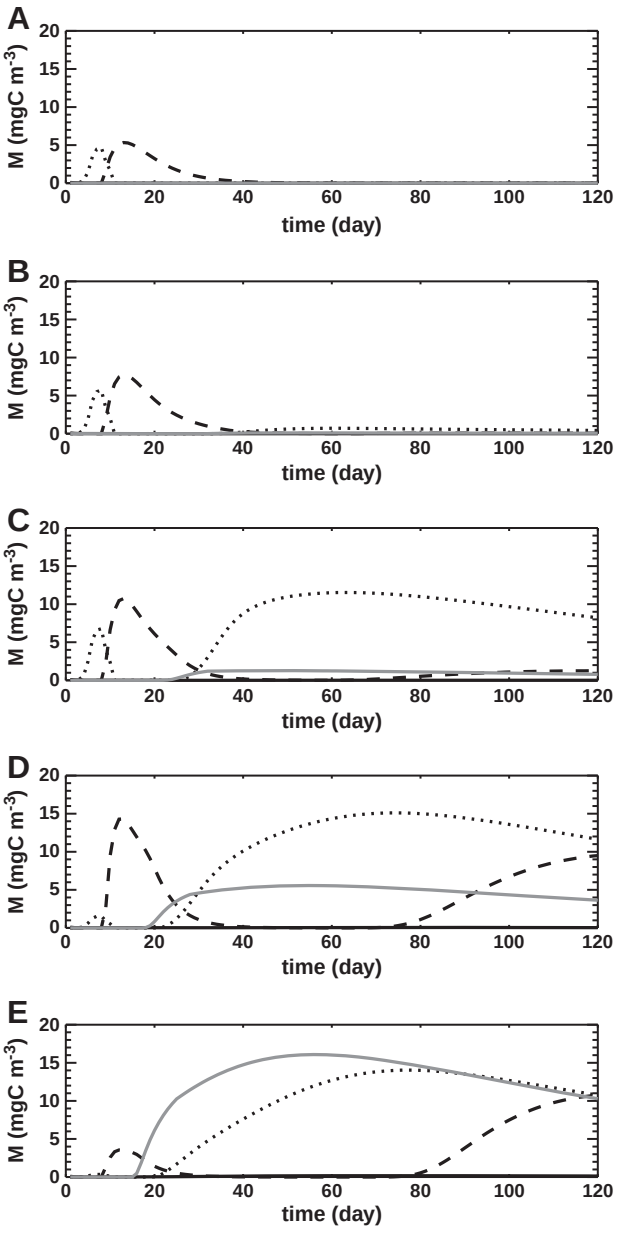

Fig. 7. Time evolution of juvenile (dotted line), transition (dashed line) and adult (solid grey line) stages of *Mnemiopsis* biomass, M, (mg m^{-3}) feeding on constant mesozooplankton food of 25 mg C m^{-3} and 90 mg C m^{-3} microplankton food at (A) 10, (B) 15, (C) 20, (D) 25, and (E) 30 °C. To be able to show the results on the same scale juvenile biomass (dotted) is divided by 5 in panel (D), while juvenile biomass (dotted) is divided by 25 and transition stage biomass (dashed line) is divided by 5 in panel (E).

The influence of low food concentrations (Fig. 9A) is similar to the influence of low temperatures (Fig. 7A), whereas high food concentrations (Fig. 9D) especially influence the biomass of transitional and adult stages. Changes in food concentrations have an intensive impact on stage development of the ctenophore. For example when mesozooplankton and microplankton levels increase to 30 mg C m^{-3} and 110 mg C m^{-3}, respectively, the secondary production of the transitional stage occurs right after day 35 (around 40 days earlier) and its biomass reaches levels that are fifteen times higher than that of the reference run.

Model results show that under increasing prey (zooplankton) conditions *Mnemiopsis* biomass follows an exponentially increasing trend (Fig. 10A) similar to the increase in temperature (Fig. 8A). This

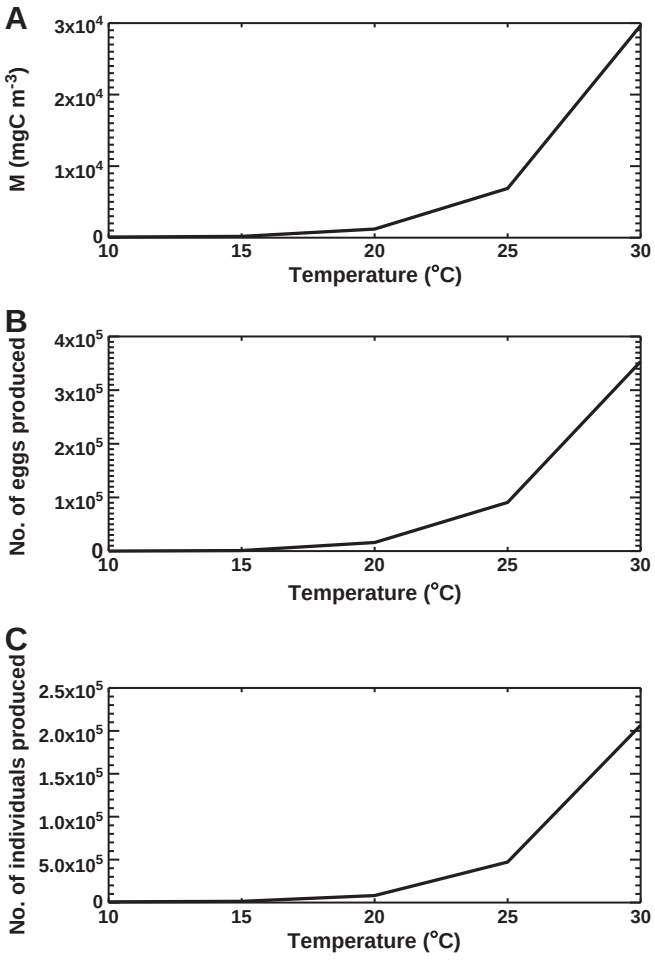

Fig. 8. Simulated change in (A) total *Mnemiopsis* biomass (mg m^{-3}), (B) number of eggs produced, and (C) number of individuals produced (transfer among stages) in 120 days under changing temperature conditions. Food conditions are the same as in the reference run (25 mg C m^{-3} mesozooplankton and 90 mg C m^{-3} microzooplankton).

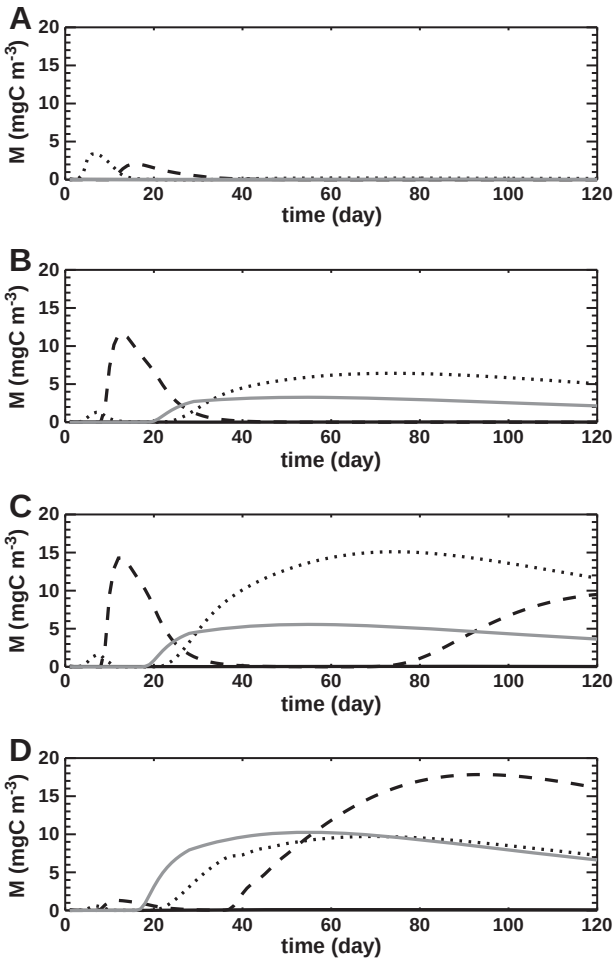

Fig. 9. Time distribution of juvenile (dotted line), transition (dashed line) and adult (solid grey line) stages of *Mnemiopsis* biomass, M, (mg m^{-3}). Comparison of simulated population development with food concentrations of (A) 20 mg C m^{-3} and 70 mg C m^{-3}, (B) 25 mg C m^{-3} and 90 mg C m^{-3} and (C) 30 mg C m^{-3} and 110 mg C m^{-3} of mesozooplankton and microplankton biomass at 25 °C. To be able to show the results on the same scale juvenile biomass (dotted) is divided by 5 in panels (A) and (B), while juvenile biomass (dotted) and transition stage biomass (dashed line) are divided by 15 in panel (C).

increase is also reflected in the number of eggs (Fig. 10B) and the number of individuals (Fig. 10C) produced. However, under low temperature this increase is almost two orders of magnitude less than the increase under high temperature. Under high temperature the increase in egg production is more pronounced at low food concentrations, however under low temperatures egg production increases only at very high food concentration levels.

In addition, the model was used to test the relative influence of mesozooplankton and microplankton levels on *Mnemiopsis* population biomass and reproduction. Results show that while decreasing the mesozooplankton and microplankton levels influence the population biomass equally, a decrease in mesozooplankton has a stronger control on reproduction (Table 3) than microzooplankton. Also, providing only mesozooplankton or only microplankton to the population was tested with the model. Results of both simulations are identical in that the growth of the population stops in both cases.

3.4. Influence of environmental forcing

In order to better assess the model performance, adaptability and to analyze the influence of environmental factors on model dynamics, the model was initialized with conditions given in the reference model run at the beginning of the year and then run with observed mixed layer depth temperature, mesozooplankton and microplankton data obtained from Sevastopol Bay. The model was run over one year to assess the seasonal dynamics of *Mnemiopsis* population (Fig. 11). The results are compared with observed *Mnemiopsis* biomass and abundance (Finenko et al., 2006).

The observed zooplankton concentrations show the zooplankton biomass after consumption by ctenophores (Finenko et al., 2006). Thus, the model was tested with observed maximum concentrations to avoid this bias and the onset of vernal *Mnemiopsis* biomass increase is controlled by means of temperature (Fig. 11A). Model results overestimate observations when forced with observed temperature and constant maximum observed mesozooplankton, 25 mg C m^{-3}, and microplankton, 90 mg C m^{-3}, concentrations (Fig. 11A–C).

Data concerning the used observations from Sevastapol Bay suggest that following the peak of *Mnemiopsis* development *Beroe ovata* started to reproduce (Finenko et al., 2006). *B. ovata*, also an invader ctenophore species, was introduced to the Black Sea during 1998 (Vinogradov et al., 2000) and is known to feed on *Mnemiopsis* in native waters (Kremer, 1976). To include the effect of such a top-down control a temporary increase in mortality has to be included in the model, which is presumed to be caused by predation. To include the potential predation pressure of *B. ovata* on *Mnemiopsis* population the mortality terms are modified to include quadratic terms:

$$\mu_e = 0.98 + 0.00002N_j^2 \quad (20)$$

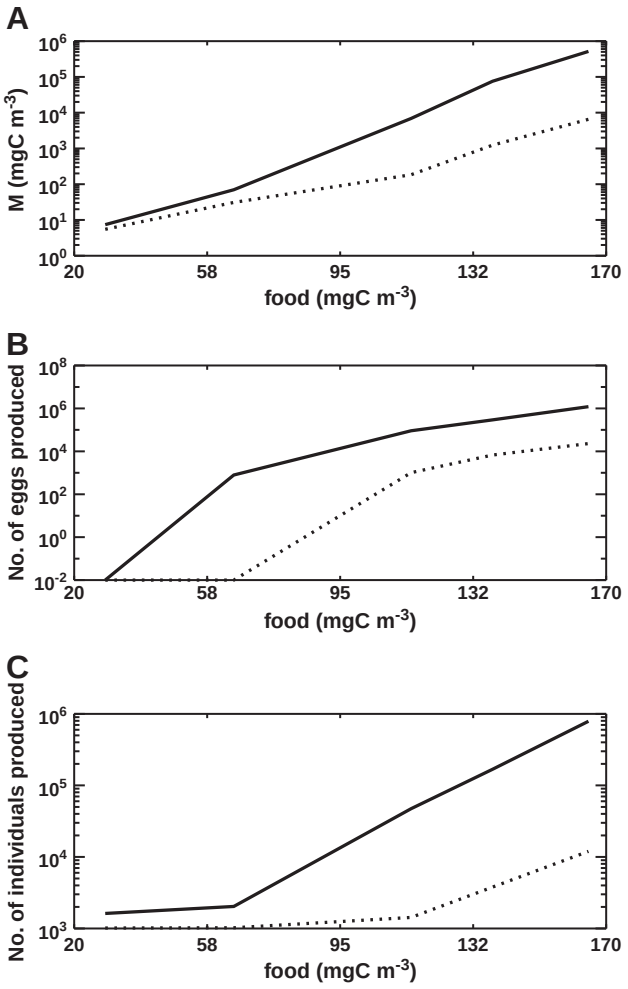

Fig. 10. Simulated change in (A) total *Mnemiopsis* biomass, M, (mg m^{-3}), (B) number of eggs produced, and (C) number of individuals produced (transfer among stages) in 120 days under changing food (mg C m^{-3}) conditions. Solid line shows the change under high temperatures (25 °C) and the dotted line shows the change under low temperatures (15 °C).

$$\mu_j = 0.93 + 0.0003N_j^2 \tag{21}$$

$$\mu_t = 0.3 + 0.003N_t^2. \tag{22}$$

Results of this simulation show that the influence of potential grazing at increased *Mnemiopsis* concentrations helps to reduce the model-data misfit (Fig. 12A–B).

It is also possible to track the change in individual ctenophore size of each stage by dividing the total biomass to the number of individuals. Individual biomass of adult stage shows that individual size reflects the changes in environmental factors (Fig. 12C). During low temperature conditions where clearing rate decreases, individual ctenophore size decreases, and this result is expected because although the mortality and transfer rates are common loss terms for stage dependent biomass and population size (Eqs. (1)–(7)) metabolic loss rate only affects biomass. These results are consistent with observations that suggest ctenophore is able to shrink during starvation periods (Reeve et al., 1989; Yousefian and Kideys, 2003).

Table 3
Change (%) in annual integrated biomass and reproduction in response to changes in mesozooplankton and microplankton levels.

Analysis	Change in biomass	Change in reproduction
10% decrease in mesozooplankton	−31%	−33%
10% decrease in microplankton	−33%	−15%

4. Discussion and conclusions

We have developed a modified form of the stage resolving approach of Fennel (2001) adopted for a ctenophore that integrates elements of biomass models and stage dependent population models. Moreover, this model uses the growth dynamics of Kremer (1976); Kremer and Reeve (1989) for 4 stages of model-ctenophore together with the dietary transitions among different stages.

4.1. General characteristics

The process-formulations of growth and development allowed the calculation of stage durations. Thus, observations of stage durations can be used to check the model formulations instead of being used as prescribed rates. Stoecker et al. (1987) showed that under optimum food conditions the body mass of *Mnemiopsis* larvae increases by factors of 3–4 in 4 days and of 15–18 in 8 days. Model results were similar to these observations (Section 3.1) and simulated *Mnemiopsis* grew by a factor of 4 during the first 4 days and of 14 during the first 8 days.

Results show that the model is most sensitive to the changes in assimilation efficiency (*AE*), the linear coefficient of Eq. (10) (a_o) that determines an increased feeding rate at increased temperatures and the exponential coefficient used in Eq. (9) (*K*). This may indicate that the model response to these parameters cannot be considered as robust which is consistent with the results of Stegert et al. (2007). It should also be noted that model equations are mostly based on laboratory studies and may not adequately reflect physiological characteristics of the ctenophore under natural conditions.

In order to check the consistency and plausibility of the model we simulated annual cycles of *Mnemiopsis* growth by using the observed food and temperature levels from Sevastopol Bay. It was problematic to use the observed mesozooplankton and microplankton data because these values represent the already grazed part of the biomass (Finenko et al., 2006). Therefore, our results indicate the response of the model to changing temperature fields. In order to realistically assess the interactions between the changing food and temperature conditions the current model should be coupled to an ecosystem model that provides changing food levels that are not modified by grazers.

4.2. Environmental effects

It is hypothesized that the only factors that appear to restrict the rapid population growth of *Mnemiopsis* are temperature, the availability of food and the presence of predators. This hypothesis is supported by observations, for example Kremer (1994) concluded that three factors determine the abundance of *Mnemiopsis*, temperature, food availability and predation mortality. Other factors such as salinity are not considered because *Mnemiopsis* is known to adapt to a wide range of salinities from 2 to 38 (Purcell and Sturdevant, 2001). To our knowledge our work is the first to include detailed ctenophore physiology that allows the influence of temperature and diet on growth dynamics. The main focus of this study was to assess the regulation of *Mnemiopsis* population by these factors.

Limited observations (Purcell, 2005) support our results that show that the abundance of *Mnemiopsis* is very sensitive to temperature variability. Additional tests done to understand the sensitivity of model stages to changing temperature conditions showed that the influence of temperature on egg production and on growth of different stages of *Mnemiopsis* equally regulated its seasonal growth

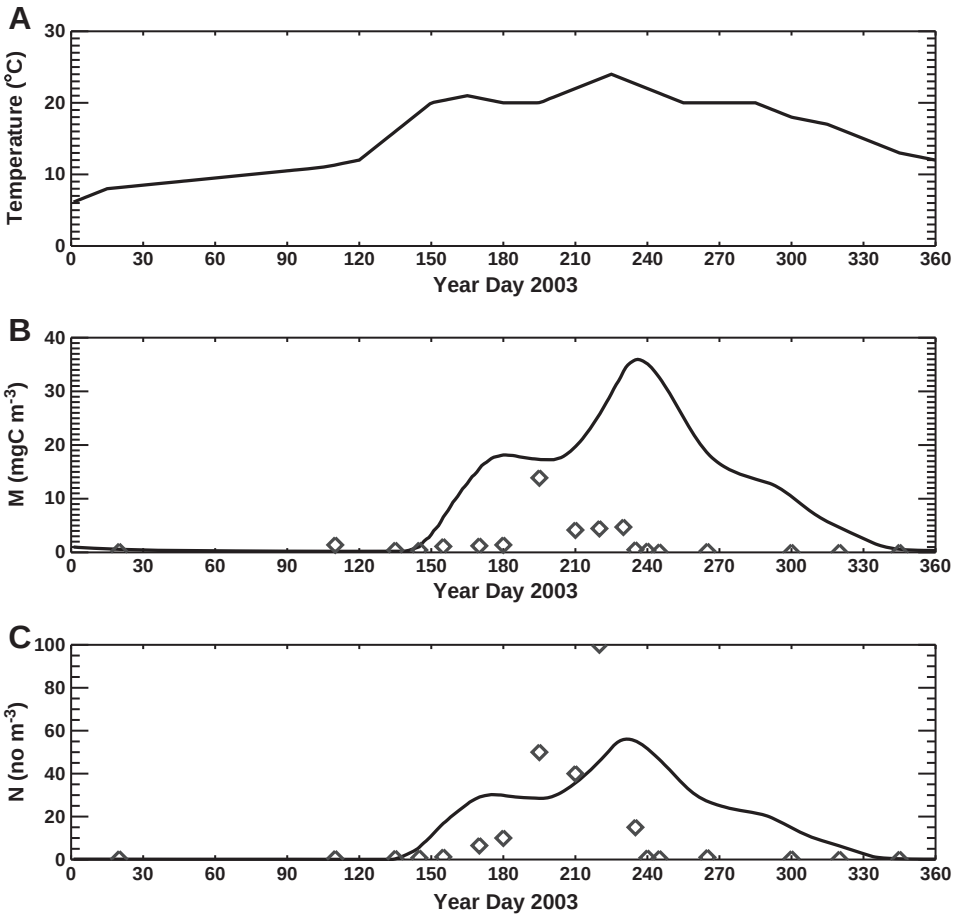

Fig. 11. Time distribution of (A) observed temperature for year 2003, (B) simulated *Mnemiopsis* biomass, M, and (C) simulated *Mnemiopsis* abundance, N. Symbols indicate *Mnemiopsis* observations obtained from Finenko et al. (2006) for the year 2003 in Sevastopol Bay.

pattern. Even when the influence of temperature on egg spawning and hatching was removed, minimum growth during the winter season was observed (not shown). These results imply a strong temperature control on all stages of *Mnemiopsis*. Also, model results that show a reduced success of the second year *Mnemiopsis* population when a Q_{10} type temperature function for reproduction is used (Fig. 6) support the hypothesis that reproduction in the Black Sea cannot occur at temperatures lower than 16 °C (Purcell and Sturdevant, 2001).

Model results agree with the observations by Anninskii and Abolmasova (2000) that high growth rates under high temperatures can only be reached if the food sources are not limited (i.e. 25 mg C m^{-3} and 90 mg C m^{-3} mesozooplankton and microplankton, respectively). The model developed further helps to quantify how under given food conditions changing temperatures can regulate transition time between stages, development time to adult reproduction, maximum growth rates and the biomass of each stage. For example, a 5 °C decrease can result in considerable decrease in biomass of all stages and can decrease the development period (Fig. 7D and E). Whereas, at a temperature of 25 °C a 40% decrease in food concentrations can result in termination of transfer between stages (cf. Fig. 9A and B). These results show that even under increasing temperature conditions it may be possible to avoid population explosion of ctenophores by controlling the levels of eutrophication which may have strong implications for degraded seas like the Black and Baltic Seas.

The introduction of invasive species can have the potential to restructure marine ecosystems. The influence of *Mnemiopsis* on different trophic levels of the ecosystem is still debated. It was previously suggested that increased feeding of *Mnemiopsis* on zooplankton prey can lead to increased levels of phytoplankton (Finenko et al., 2006; Kideys et al., 2008). Results by Sullivan and Gifford (2004) have shown that larval ctenophores occur at sufficient abundances capable of impacting prey (microplankton) populations. Model results showed that under favorable spring conditions larval *Mnemiopsis* could consume more than 2 mg of microplankton per day. These results support the conclusions by Sullivan and Gifford (2004) that understanding the processes that influence survival during early development stages can be a key to understanding the initiation and maintenance of the adult *Mnemiopsis* blooms. This shows that considering the feeding ecology of higher trophic levels as such can be a fundamental issue. Without stage resolving higher trophic level models that include dietary patterns it may not be possible to realistically link lower trophic and higher trophic level models.

Although there are observations on the influence of dietary patterns on *Mnemiopsis* (Sullivan and Gifford, 2004, 2007; Rapoza et al., 2005; Waggett and Sullivan, 2006) the response of different stages of the population to changing food sources is not known because of shortage of manipulative experiments. Model sensitivity studies show that while decreasing the mesozooplankton and microplankton levels influenced the population equally, decreased mesozooplankton had a stronger control on reproduction (Table 3). This shows the strong role of mesozooplankton in controlling the adult biomass that is capable of reproducing eggs. Also, the model was additionally tested by providing only mesozooplankton or only microplankton to the population. Results were identical in that the growth of the population stopped in both cases. Model results translate to the hypothesis that both larval and lobate stages of

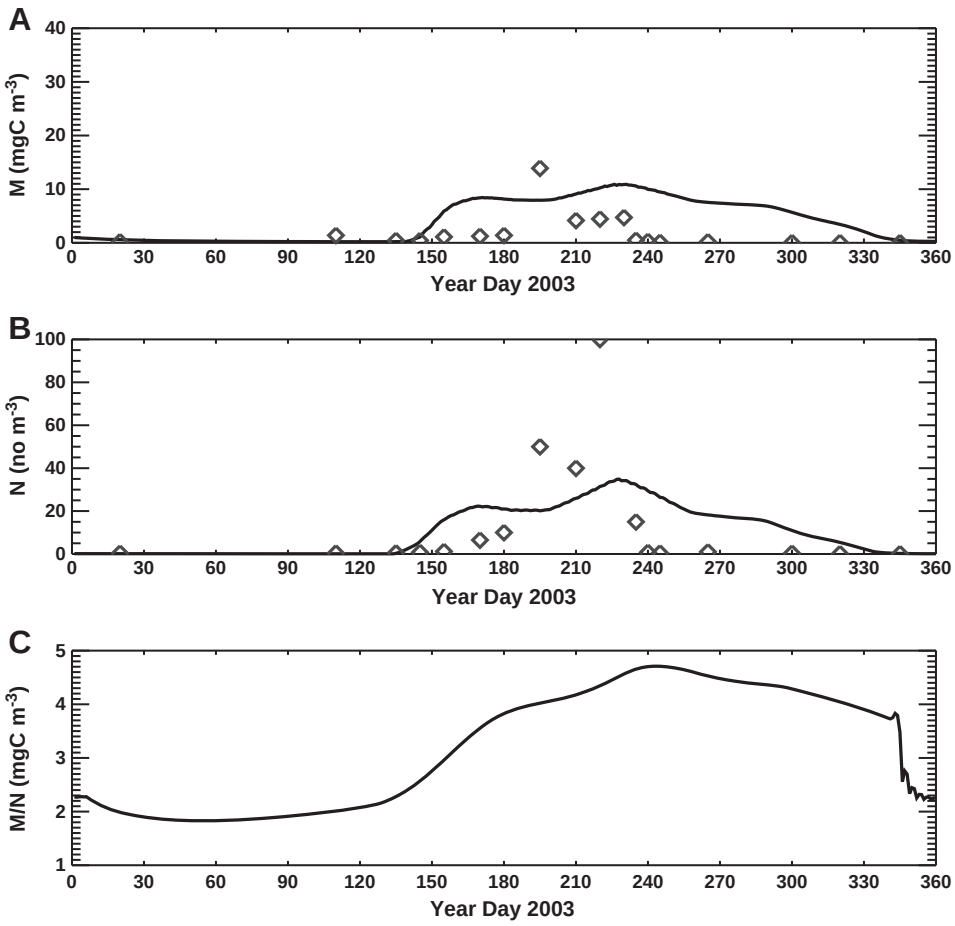

Fig. 12. Time distribution of (A) simulated *Mnemiopsis* biomass, M, (B) simulated *Mnemiopsis* abundance, N, and (C) individual biomass, M/N, of adult stage after the inclusion of potential *Beroeovata* pressure on *Mnemiopsis*. Symbols indicate *Mnemiopsis* observations obtained from Finenko et al. (2006) for the year 2003 in Sevastopol Bay.

Mnemiopsis need to encounter favorable growth conditions in the form of the right food supply for each stage in order for high overall population growth rates, as they are associated with *Mnemiopsis* blooms, to occur. A similar hypothesis has been put forward by Rapoza et al. (2005) earlier and is supported by our model results. Model results demonstrated that the relative influence of temperature and food decrease on different stages is similar, whereas an increase in food can favor transitional and adult stages over other stages. Such a differential response between stages does not occur for increased temperatures.

4.3. Future directions

The influence of climate variations and global warming on jellyfish and ctenophore species and their retrospective role on the ecosystems is still under debate (Purcell, 2005). Oguz et al. (2008b) reported that incorporation of temperature-dependent reproduction and growth characteristics of *Mnemiopsis* is needed to examine their long term population growth dynamics under changing environment and climate conditions. The 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 (IMBER, 2005; Travers et al., 2007; Rose et al., 2010) it is not possible to analyze the influence of ctenophores on different trophic levels of the ecosystem which is closely linked to the environmental factors. For example, the influence of *Mnemiopsis* on the anchovy collapse in the Black Sea is still debated. Some investigators (Kideys, 2002) linked the collapse to the excessive consumption of anchovy eggs and larvae by *Mnemiopsis*, diversion of food resources to *Mnemiopsis* and selective feeding of *Mnemiopsis* on small copepods. Oguz et al. (2008b) showed that in order to quantitatively test these hypotheses a model that includes differential feeding behavior of *Mnemiopsis* stages is needed. To achieve these goals, efforts to couple the current model with existing ecosystem models are already underway.

The current modeling effort also has strong implications on fisheries management. There are examples that long term climate driven cycles are resulting in increases of jellyfish populations (cf. reviews by Mills, 2001; Graham et al., 2001; Purcell, 2005; Purcell et al., 2007). The majority of the world's oceans are under some level of fishing pressure (Pauly et al., 1998, 2002) and jellyfish predators can additionally contribute through predation on eggs and larvae of fishes to a multitude of human induced pressure (Halpern et al., 2008). Therefore, considering that fisheries either contribute directly to increased jellyfish populations or are being impacted by jellyfish or both (e.g. Oguz et al., 2008a), newly emerging ecosystem based management schemes should incorporate jellyfish populations (Ruckelshaus et al., 2008; Pauly et al., 2009). Our stage resolving model has the structure that allows to include trophic (i.e. jellyfish–plankton and jellyfish–fish) interactions in a realistic manner.

Acknowledgments

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