

Variability of copepods as seen in a coupled physical–biological model of the Baltic Sea

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A key factor for the survival of fish larvae is the availability of prey (nauplii and copepodites) at the right time, place, and quality. This depends on several physical and biological processes and factors which can be studied theoretically by means of coupled physical–biological models with a stage-resolving zooplankton component. This study is based on an advanced ecosystem model of the Baltic Sea (ERGOM) with an increased resolution of the zooplankton stage variable. The model zooplankton consists of five stages: eggs, nauplii, two aggregated groups of copepodites, and adults. Food availability and temperature control the transfer processes, such as reproduction, hatching, and moulting. A simulation of the annual cycle is used to explore theoretically the temporal and spatial development of the various stages in relation to the physical forcing and the food web interactions. The dynamic equations for the “model copepod” were guided by *Pseudocalanus*; however, the model amounts to a stage-resolving description of aggregated zooplankton state variables. The effects and implications of increased process resolution are highlighted by comparisons of stage-resolving model runs and simulations with a single bulk-zooplankton variable.

Keywords: copepods, coupled biological–physical models, nauplii dynamics, stages.

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Introduction

Progress in theoretical understanding and quantitative description of marine ecosystems, and their responses to changes in physical forcing or nutrient input, can be achieved by coupling ocean circulation models and chemical–biological models. Model equations of General Ocean Circulation Models follow directly from fundamental principles, such as conservation of momentum, energy, and mass. Although the biological processes have to obey the basic physical laws, it is a theoretical challenge to find appropriate mathematical formulations which govern food web dynamics.

Many marine ecosystem models truncate the food chain at the level of zooplankton, either including grazing implicitly in phytoplankton mortality, e.g. Fransz and Verhagen (1985), Stigebrandt and Wulff (1987), and Humborg *et al.* (2000), or by a bulk-zooplankton state variable which provides grazing pressure on the phytoplankton, e.g. Wroblewski (1977), Aksnes and Lie (1990), Aksnes *et al.* (1995),

Fasham *et al.* (1990), Broekhuizen *et al.* (1995), Fennel and Neumann (1996), and Neumann (2000). The feedback to the lower trophic levels is established directly by respiration and exudation rates or through the detritus pathway, where material is transferred to detritus by excretion and mortality, and recycled to the nutrient pool. These models have been applied in studying fluxes of matter among the state variables, in understanding and quantifying carbon fluxes in the ocean, in studying eutrophication in coastal seas, and in examining the mesoscale distribution of nutrients and plankton in response to the circulation patterns.

Model studies of fish recruitment require stage-resolving descriptions of zooplankton in order to address size-selective feeding of larvae, juvenile, and adult fish. They should involve growth, development, and reproduction of copepods, food web interactions, and physical control through advection and small-scale turbulence.

A model of zooplankton biomass including several species and stages was developed by Vinogradov *et al.* (1972). Stage-resolving population models

were used by Wroblewski (1982), Gupta *et al.* (1994), and Lynch *et al.* (1998). Individual-based modelling of population dynamics has been considered, for example by Batchelder and Miller (1989) and Miller and Tande (1993). Such an individual-based population model was linked to circulation by using archives of modelled advection (Miller *et al.*, 1998). These population models used experimental data of stage duration as prescribed parameters, which depend on temperature and are known as Belehradek formulas (e.g. Corkett and McLaren, 1978).

An integration of mean individual properties and population dynamics was proposed by Carlotti and Sciandra (1989), where the equations for the numbers of individuals have been linked to the evolution of the mean individual mass, \bar{m} , that in turn obeys an equation of the type

$$\frac{d}{dt}\bar{m}(t) = (g(t) - l(t))\bar{m}^p \quad (1)$$

Here g and l prescribe growth and losses, and p is an allometric exponent, which generally is less than unity. The transfer and mortality rates needed in the population model are not prescribed by data, but controlled by the development of the “mean individual”. Moulting occurs only if the critical moulting mass, X_c , is approached (see Carlotti and Sciandra (1989) and Carlotti and Nival (1992) for a detailed description). Attempts to couple this type of model to 1-D (one-dimensional) water column models including phytoplankton dynamics were presented by Carlotti and Radach (1996) in Eulerian fashion and by Carlotti and Wolff (1998) in a Lagrangian ensemble theory. Models incorporating phytoplankton production and population dynamics as described by a von Foerster equation (see Murray, 1993) for the population density in conjunction with growth of the mean individual mass, as in Equation (1), have been embedded in flow fields in Lagrangian fashion by Heath *et al.* (1997) and as a spatially distributed array of boxes in an Eulerian approach by Bryant *et al.* (1997). A variety of existing zooplankton models was recently reviewed by Carlotti *et al.* (2000).

In the present article we aim to integrate a stage-resolving zooplankton model (Fennel, 2001) into a 3-D Baltic Sea ecosystem model (Neumann, 2000). The model system consists of a circulation model and an embedded chemical-biological model which describes the dynamics of nutrients, phytoplankton, stage-resolved zooplankton, and detritus. The explicit description of the food web allows, in principle, simulation of the survival conditions of larvae, i.e. timing and location of nauplii abundance, and has the potential also to simulate, among other issues, the effects of food quality.

The model

This study is based on an advanced 3-D ecosystem model of the Baltic Sea, which is described in some detail in Neumann (2000) and Neumann *et al.* (2002). The biological component of the model consists of nine state variables. The phytoplankton functional groups are diatoms, flagellates, and cyanobacteria; the nutrients are ammonium, nitrate, and phosphate. Moreover, detritus and oxygen (hydrogen sulphate as negative oxygen) are included. The model zooplankton, which was originally introduced as a bulk biomass state variable, is described in the present study by a stage-resolving model (Fennel, 2001).

Stage-resolving model of copepod dynamics

We start with a brief outline of the copepod model of copepods. For integration of such a model into a General Circulation Model it is desirable to keep the number of state variables and hence the number of evolution equations small. The model copepod develops through five stages: eggs, nauplii, copepodites 1 and 2, and adults. The nauplii stages are merged into one state variable “model nauplii” and the copepodites stages are aggregated into the state variables “model copepodites 1 and 2”, and partly into “model adults”. The corresponding stage-dependent biomass variables per unit volume are Z_e , Z_n , Z_{c1} , Z_{c2} , and Z_a . The corresponding numbers of individuals per unit volume are N_e , N_n , N_{c1} , N_{c2} , and N_a .

We assume that the numbers of individuals per unit volume is high enough that the state variables behave like continuous functions and, hence, the dynamics can be expressed by differential equations.

Population density and state variables

The state variables Z_i and N_i ($i = e, n, c_1, c_2, a$), are related to the population density, $\sigma(m, t)$, of individuals of mass m . Thus $\sigma(m, t)dm$ is the number of individuals in the interval $(m, m + dm)$ at time t . The total zooplankton biomass and the total number of individuals are related to $\sigma(m, t)$ as:

$$Z_{\text{tot}} = \int_{m_e}^{x_a} \sigma(m) m dm \quad \text{and} \quad N_{\text{tot}} = \int_{m_e}^{x_a} \sigma(m) dm,$$

where m_e is the egg mass and x_a is the maximum mass of mature adults.

The dynamics of $\sigma(m)$, i.e. its changes over time, are controlled by losses due to mortality and gains through production of new eggs:

$$\frac{d}{dt}\sigma = -\mu\sigma + T_{ae}\sigma\delta(m - m_e) \quad (2)$$

where T_{ae} is an egg rate, prescribing the transfer of mass from adults to eggs, and $\delta(m - m_e)$ is the Dirac delta-function. For stage, i , the individual mass (m) is confined to the interval $X_{i-1} \leq m \leq X_i$, where X_{i-1} and X_i are the moulting mass of the previous and the current stages, respectively. The biomass (Z_i) and number of individuals (N_i) are:

$$Z_i = \int_{X_{i-1}}^{X_i} \sigma(m) m dm \quad \text{and} \quad N_i = \int_{X_{i-1}}^{X_i} \sigma(m) dm \quad (3)$$

Owing to the growth of the individuals the distribution density $\sigma(m, t)$ will propagate along the m -axis with the "propagation speed" ($\frac{d}{dt}m$), which is controlled by growth (grazing minus losses) according to

$$\frac{d}{dt}m_i(t) = (g_i(t) - l_i(t))m_i \quad (4)$$

where m_i refers to the mass within a certain stage, i.e., $X_{i-1} \leq m \leq X_i$. Contrary to (1), we use stage-dependent rates for grazing, $g_i(t)$, and losses, $l_i(t)$, to avoid an allometric exponent different from unity.

For the population density (σ_i) of stage i , it follows similar to (2) that:

$$\frac{d}{dt}\sigma_i = -\mu_i\sigma_i + T_{(i-1),i}\delta(m - X_{i-1}) - T_{i,(i+1)}\delta(m - X_i) \quad (5)$$

where $T_{(i-1),i}\delta(m - X_{i-1})$ and $T_{i,(i+1)}\delta(m - X_i)$ prescribe the rates at which individuals of stage $i-1$ are transferred to stage i , and individuals of stage i moult into stage $i+1$, respectively.

The dynamical equations for Z_i and N_i follow from (3), (4), and (5) as

$$\begin{aligned} \frac{d}{dt}Z_i &= \int_{X_{i-1}}^{X_i} \left(\frac{d\sigma_i}{dt} m + \frac{dm}{dt} \sigma_i \right) dm \\ &= (g_i - l_i - \mu_i)Z_i + T_{(i-1),i}X_{i-1} - T_{i,(i+1)}X_i \end{aligned} \quad (6)$$

and

$$\frac{d}{dt}N_i = \int_{X_{i-1}}^{X_i} \frac{d\sigma_i}{dt} dm = -\mu_i N_i + T_{(i-1),i} - T_{i,(i+1)}. \quad (7)$$

In order to prescribe the transfer among the stages, filter functions are introduced that decrease the growth and activate the transfer if a substantial part of the population in a certain stage has approached the moulting mass. This can be accomplished by comparing the mean individual mass $\bar{m} = Z_i/N_i$ with the maximum mass (X_i) represented by the moulting mass. We choose a Fermi function, which provides a representation of the step-function with a smooth transition,

$$f(\bar{m}_i, X_i) = \frac{1}{1 + \exp\left(\frac{\kappa}{X_i}(\bar{m}_i - X_i)\right)}. \quad (8)$$

In a statistical sense, the function (8) provides the connection of the individual level to the bulk biomass of the stage. The function drops from unit to zero if the mean individual mass ($\bar{m} = Z_i/N_i$) of a stage approaches the moulting mass X_i . The grazing rate (g_i) will be multiplied by this function.

At the same time, a transfer rate to the next stage must be activated. Noting the property of the Fermi functions, $f(x, y) = 1 - f(y, x)$, the transfer rates ($T_{i,i+1}$) can be defined as:

$$T_{i,i+1} = g_i f(< m >_i, m_i), \quad (9)$$

where g_i is the grazing rate and $f(< m >_i, \bar{m}_i)$ is a highpass filter function, which ensures that the transfer to the next stage does not start before the mean individual mass, \bar{m} , exceeds a value $< m >_i$. We chose $< m >_i$ to be smaller than the moulting mass of the corresponding stages. Moreover, because the transitions in real systems are not as sharp as indicated by the δ functions in (5), we modify the transfer terms in (6) as $T_{i,i+1}X_i \approx T_{i,i+1}Z_i$, where, because of the highpass filter property of $T_{i,i+1}$, these terms are activated only for values of Z_i close to X_i (see Fennel (2001) for more details).

Then the equations for the stage-dependent biomass can be written as

$$\begin{aligned} \frac{d}{dt}Z_e &= T_{ae}Z_a - T_{en}Z_e - \mu_e Z_e, \\ \frac{d}{dt}Z_n &= T_{en}Z_e + (g_n - l_n - \mu_n)Z_n - T_{nc_1}Z_n, \\ \frac{d}{dt}Z_{c_1} &= T_{nc_1}Z_n + (g_{c_1} - l_{c_1} - \mu_{c_1})Z_{c_1} - T_{c_1c_2}Z_{c_1}, \\ \frac{d}{dt}Z_{c_2} &= T_{c_1c_2}Z_{c_1} + (g_{c_2} - l_{c_2} - \mu_{c_2})Z_{c_2} - T_{c_2a}Z_{c_2}, \\ \frac{d}{dt}Z_a &= T_{c_2a}Z_{c_2} + (g_a - l_a - \mu_a)Z_a - T_{ae}Z_a. \end{aligned} \quad (10)$$

The dynamics of the state variables are controlled by transfer rates ($T_{i,i+1}$), growth rates (g_i), loss rates (l_i), and mortality rates (μ_i), where $i = (e, n, c_1, c_2, a)$. The process rates are specified below. The corresponding equations for the number of individuals are,

$$\begin{aligned} \frac{d}{dt}N_e &= \tau_{ae} - \mu_e N_e - \tau_{en}, \\ \frac{d}{dt}N_n &= \tau_{en} - \mu_n N_n - \tau_{nc_1}, \\ \frac{d}{dt}N_{c_1} &= \tau_{nc_1} - \mu_{c_1} N_{c_1} - \tau_{c_1c_2}, \end{aligned} \quad (11)$$

$$\frac{d}{dt}N_{c_2} = \tau_{c_1c_2} - \mu_{c_2}N_{c_2} - \tau_{c_2a},$$

$$\frac{d}{dt}N_a = \tau_{c_2a} - \mu_aN_a - \tau_{ac}.$$

The mortality rates (μ_i) are the same as in Equation (10). The transfer rates ($\tau_{i,i+1}$) are closely related to $T_{i,i+1}$, i.e. $\tau_{i,i+1} = T_{i,i+1}Z_i/X_i$.

Use of the filter functions (8) and (9) implies that both biomass variables and number of individuals are needed to compute the mean mass of the individuals for each stage. The interfaces for the integration of the two sets of biological equations, (10) and (11), into the circulation model are advection-diffusion equations, one for each state variable. An attractive feature of including the biomass state variables is the explicit conservation of mass in the model. Population models are not constrained in such an easy way because there is no law for the conservation of the number of individuals.

Process descriptions and parameter choices

In order to specify our model copepod, we follow Fennel (2001) and focus on *Pseudocalanus*, which is an important copepod in the Baltic. The mass parameters listed in Table 1 were derived from Baltic Sea data (Hernroth, 1985). However, coupled models require that other species, such as *Acartia*, with different life cycles be taken into account by means of aggregated, stage-resolving state variables. Since most of the process descriptions are outlined in Neumann (2000) and Fennel (2001), we confine the discussion to the extension developed in the present model.

The grazing rates, which describe the amount of ingested food per day in relation to the biomass, are formulated in terms of modified Ivlev expressions:

$$g_i(P) = \beta_i(1 - \exp(-I_i^2 P_{\text{sum}}))f(\bar{m}, X_i) \quad (12)$$

Table 1. Mass parameters.

Egg mass	$m_e = 0.1 \mu\text{gC}$		
Stage	Moulting mass	Maturation mass	Mean mass
Nauplii	$X_n = 0.3 \mu\text{gC}$	—	$\langle m \rangle_n = 0.22 \mu\text{gC}$
Copepodites 1	$X_{c1} = 0.8 \mu\text{gC}$	—	$\langle m \rangle_{c1} = 0.6 \mu\text{gC}$
Copepodites 2	$X_{c2} = 2 \mu\text{gC}$	—	$\langle m \rangle_{c2} = 1.6 \mu\text{gC}$
Adults	—	$X_a = 3 \mu\text{gC}$	$\langle m \rangle_a = 2.6 \mu\text{gC}$

Table 2. Grazing rates (β_i) at different temperatures, Ivlev constants (I_i^2), and mortality rates (μ_i).

Stage	β_i (0°C) d^{-1}	β_i (10°C) d^{-1}	β_i (15°C) d^{-1}	$I_i^2 10^{-3}$ $\text{mmol C}^{-2} \text{m}^{-6}$	$\mu_i \text{d}^{-1}$
Eggs	—	—	—	—	0.2
Nauplii	0.5	0.93	1.3	2.5	0.033
Copepodites 1	0.35	0.66	0.9	4.7	0.05
Copepodites 2	0.25	0.47	0.64	7	0.05
Adults	0.12	0.22	0.31	10.1	0.025

where P_{sum} is the food concentration, i.e. $P_{\text{sum}} = P_d + P_f + P_c$, (P_d diatoms, P_f flagellates, P_c cyanobacteria), the I_i 's are stage-dependent Ivlev constants, and f is the Fermi function (8). The maximum grazing rate, β_i , depends on the temperature through an Eppley factor, $\beta_i = b_i \exp(aT)$, with $a = 0.063 (\text{°C})^{-1}$. The numerical values of the involved parameters are listed in Table 2. The decrease of β_i for the higher stages reflects that older stages with more body mass ingest a smaller amount of food, in relation to their body mass, than the younger stages. Moreover, we have included a lower preference of cyanobacteria (Müller-Navarra *et al.*, 2000) by a factor $(P_d + P_f + \frac{1}{2}P_c)/P_{\text{sum}}$, which for simplicity is not included in (12).

The ingested food is partly used for growth and partly for the metabolism of the animals. About 35% of the ingestion is lost as egestion, 10% as excretion, 10% by respiration, and 15% is needed for the moulting processes (see Corkett and McLaren, 1978). These losses are expressed by the rates $l_i = 0.7 g_i(P, T)$ for ($i = n, c_1, c_2$) and $l_a = 0.8 g_a(P, T)$ for the adults ($i = a$). Note that these rates depend on temperature and food through the grazing rates (g_i).

The transfer rates involve moulting, egg laying, and hatching. The rate of reproduction (T_{ac}), describes the egg production of the female adults after reaching the maturation mass. We assume that half of the adults are female and 30% of the ingested food is transferred into egg biomass.

$$T_{ac} = (\frac{1}{2}) 0.3 g_i.$$

Then the number of new eggs per day is given by $\tau_{ea} = T_{ac} Z_a/m_e$. This approach implies that the egg-rate depends on food availability and temperature through the grazing rates, but ignores the discontinuous release of clutches of eggs with time intervals of a couple of days; see, e.g., Hirche *et al.* (1997). The transfer from eggs to nauplii (hatching) is set by the embryonic duration at low temperatures, about 10 days (Corkett and McLaren, 1978). The effect of temperature is accounted for by an Eppley factor:

$$T_{en} = h \theta (T - T_0) \exp(a(T - T_0)),$$

with $h = 0.124 \text{ d}^{-1}$. The involved step-function, $\theta(x)$, ($\theta(x) = 1$ for $x > 0$ and $\theta(x) = 0$ for $x < 0$) implies that the model eggs hatch to model-nauplii only for temperatures exceeding the threshold, $T_0 = 2.5^\circ\text{C}$.

The model food chain is truncated at the level of zooplankton and mortality involves both death rates and predation by planktivorous fish. The choice of mortality rate is difficult because the basic factors are poorly known. In the literature, stage-dependent mortalities with some seasonal variation are often used, e.g. Gupta *et al.* (1994). The typical orders of magnitude vary from $\mu \sim 0.01$ to 1 d^{-1} . In the present simulations we choose stage-dependent mortality rates. For simplicity, the mortality is held constant within each stage. The numerical values are listed in Table 2.

The performance of the model was illustrated in Fennel (2001). For example, a simulation of the development of a cohort of eggs in a rearing tank with constant food and temperature conditions can be achieved by integrating the equation sets (10) and (11). In a first phase, the egg-signal propagates through the following stages, while the total number of individuals decreases due to mortality. After a generation time of 30 days adults have developed and start to lay new eggs, and after 55 days the abundance of adults has increased significantly in response to the reproduction.

Experimental simulations

The zooplankton model outlined in the preceding section was integrated into the 3-D ecosystem model of the Baltic Sea (Neumann, 2000; Neumann *et al.* 2002) and run to simulate the production cycle over one year. We chose 1980 because of the availability of initial data as well as comprehensive sets of forcing data. The model was driven with meteorological data from the ERA 15 project (<http://wms.ecmwf.int/research/era/Era-15.html>), and with river run-off, nutrient loads and atmospheric nutrient deposition provided by the Baltic Environmental Database of the University of Stockholm (<http://data.ecology.su.se/Models/bed.htm>). The initial distributions of temperature and salinity fields were taken from a climatological data set (Janssen *et al.*, 1999). Initialization of the biogeochemical state variables was accomplished with the help of an existing initialization run (Neumann *et al.*, 2002).

Since there are no data available for a proper initialization of the copepod distribution, we chose an evenly distributed background population of overwintering copepods of 2400 ind m^{-3} . The seed population starts to lay eggs in response to the model-generated phytoplankton spring bloom. Although the model parameterization was guided by *Pseudocalanus* data compiled for the Baltic (Hernroth, 1985), we consider this as a "model

copepod" which comprises several species implicitly. In particular, *Acartia* is included, although these are characterized by smaller mass (Hernroth, 1985) and their life cycle is characterized by overwintering of dormant eggs resting at the bottom in the shallower areas. It is assumed that the dormant eggs of *Acartia* commence hatching at the same time as *Pseudocalanus* starts to lay eggs. The model copepod develops both in colder and warmer areas, where the state variables refer to *Acartia* in the nearshore regions and to *Pseudocalanus* in the offshore areas and below the seasonal thermocline. Thus, the state variables may refer to different species at different locations.

In this article we explore the dynamics of the model zooplankton. For a discussion of the biogeochemical aspects of the model simulation, see Neumann (2000) and Neumann *et al.* (2002). The most effective way to present the results of the simulations is by animation, showing the development of the state variables in time and space. Computer animation files can be obtained on request. Here we show only a selection of snapshots. A map of the Baltic is shown in Figure 1, indicating two stations and sections referred to later.

The modelled phytoplankton spring bloom (not shown) commences in the southwestern Baltic by the end of March and propagates toward the central Baltic during April and May. The seed population of adult copepods starts to lay eggs in response to the spring bloom of phytoplankton. The response patterns emerge, with some delay due to the hatching process, in the model nauplii distribution (Figure 2). With further delay, the signals propagate through the copepodite stages until the abundance of the adults showed an increase 2 months after the spring bloom (Figure 3). In the summer, the

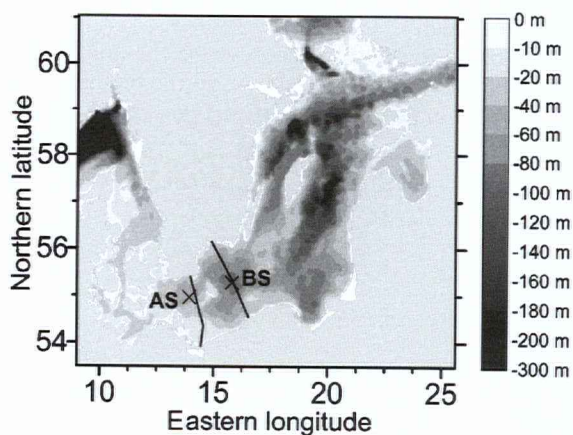


Figure 1. Map of the southwestern and central part of the Baltic Sea. The stations in the Arkona Sea (AS) and Bornholm Sea (BS) refer to the sampling locations of the Baltic Monitoring Programme and data from the indicated sections are used to compare with model results.

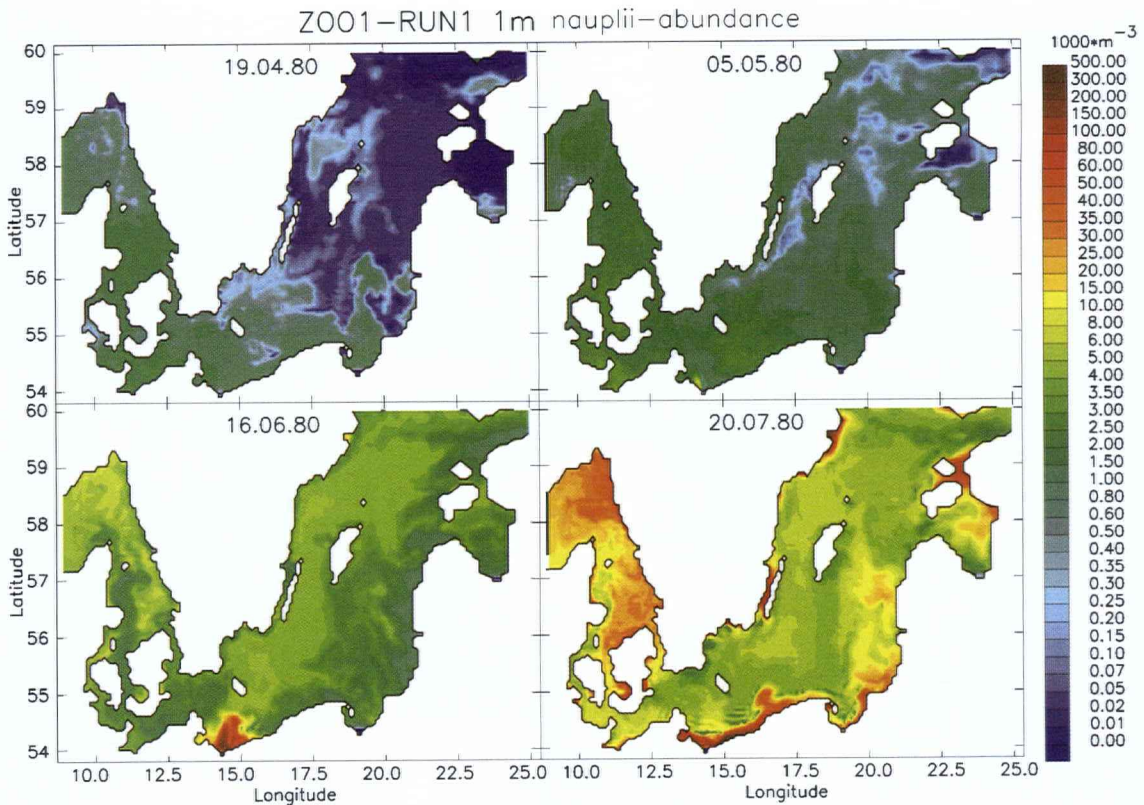


Figure 2. The development of model nauplii near the sea surface (uppermost layer, thickness 2 m).

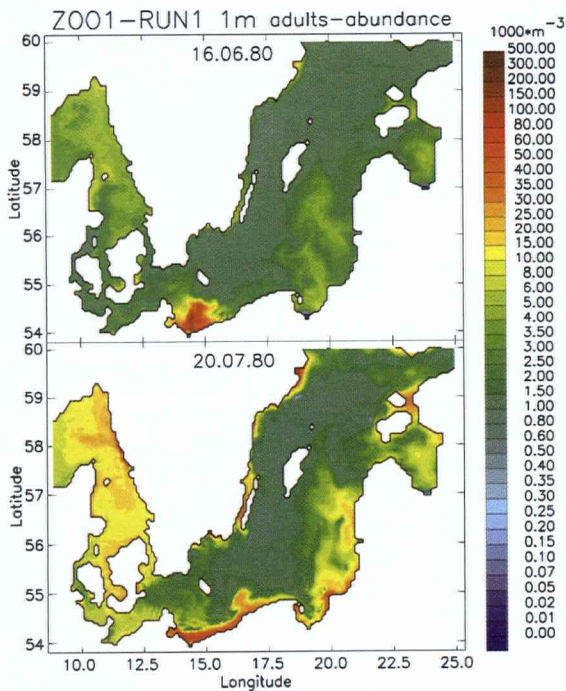


Figure 3. Development of model adults near the sea surface (uppermost layer, thickness 2 m).

abundance of all stages reaches the maximum level (Figure 4). The spatial distribution of the different stages shows similarities and differences which are due to the interplay of the mesoscale current patterns and the different temporal development of the stages.

The general development and distribution patterns are qualitatively as would be expected, but a quantitative comparison with observations is difficult due to limited observations. In order to provide a qualitative comparison, snapshots of the vertical distribution of model nauplii along sections in the Arkona Sea and the Bornholm Sea are examined (Figure 1). These sections include stations from the Baltic Monitoring Programme. An overview of the observed abundance of mesozooplankton from the monitoring programme for 1980 to 1990 has been published in the HELCOM Assessment (Helcom, 1996). The data refer to the vertically integrated bulk abundance of copepods, where stages were not resolved. The data have been compiled from three stations in the central Arkona Sea, with about 20 samples per season. These stations correspond to the central part of the model sections, as discussed below.

In the central Arkona Sea, the abundance of copepods in 1980 was 6000 ind m⁻³ for the period

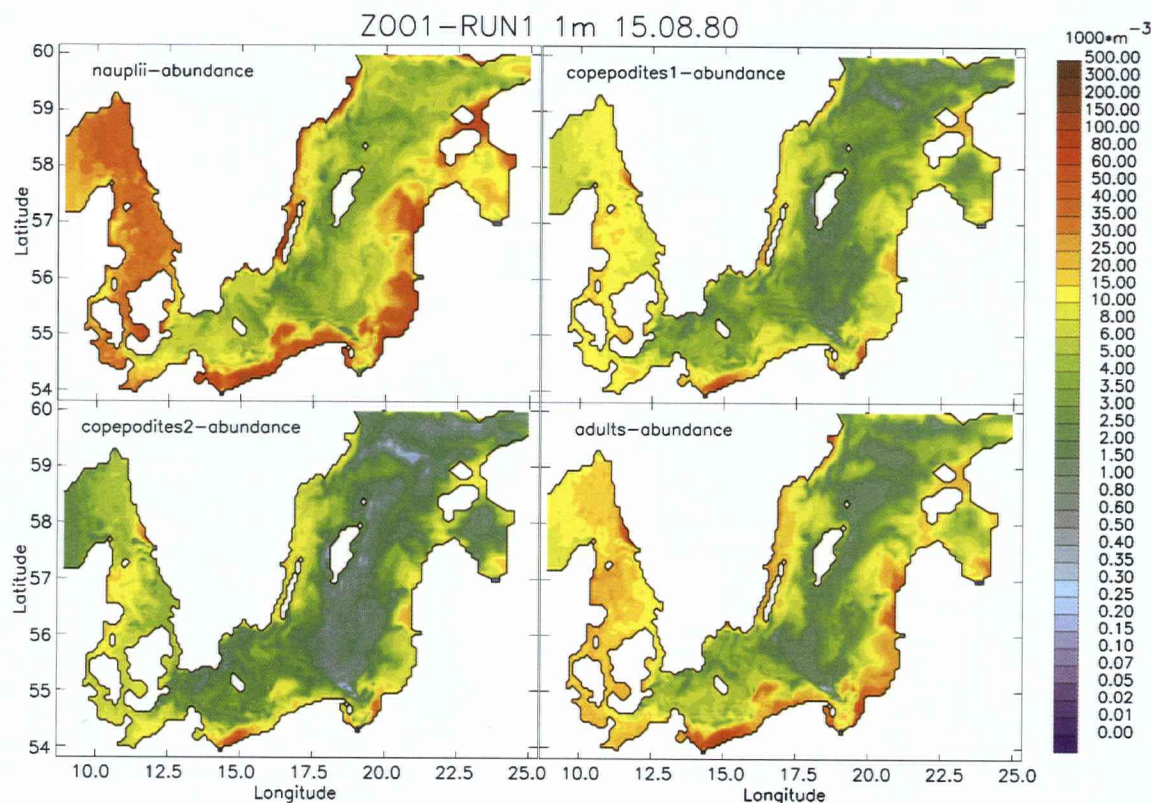


Figure 4. The summer peak of abundance of model nauplii, copepodites 1 and 2, and adults.

before the spring bloom (January to March), 15 000 ind m^{-3} for the period April and May, and 25 000 ind m^{-3} during the summer.

The simulated spring bloom maximum occurs in the central part of the Arkona Sea at the end of March. Thereafter, the concentration decreases to low summer levels. Elevated values are found in the area of the shallow bank (Oder Bank), which is influenced by the nutrient loads of the Oder river. The abundance of eggs (not shown) and nauplii (Fig. 5) responds with some delay to the chlorophyll signal (not shown).

The model-nauplii abundance, which is an important indicator for the potential survival of larvae, shows a slight increase, from 4000 to 10 000 ind m^{-3} , in the central part of the Arkona Sea and a substantial increase, from 4000 to 200 000 ind m^{-3} , in the shallow coastal area from spring to summer. This figure is qualitatively in accordance with observation in the shallow area in 1988 (Postel *et al.*, 1991). Below the surface layer the abundance is smaller and varies between 4000 and 6000 ind m^{-3} (Figure 5). Development of the model copepodite 1 follows that of the nauplii, with a delay of several weeks. The abundance of model adults increases slowly and reaches its maximum in August. The strongest signals are found in the area of the Oder Bank.

Next we examine the section through the Bornholm Sea (Figure 1). The available data from the Baltic Monitoring Programme are confined to one station in the central Bornholm Sea. Copepod abundance was compiled from 17 samples in winter, 43 samples in spring, and 63 samples in summer. For 1980, the data for the central Bornholm Sea indicate 2000 ind m^{-3} for the period before the spring bloom (January to March), 10 000 ind m^{-3} for the period April and May, and 8000 ind m^{-3} for the summer (Helcom, 1996). The observed abundance is generally higher in the Arkona Sea than in the Bornholm Sea.

In the central part of the Bornholm Sea, the model phytoplankton spring bloom (not shown) occurs in mid-April, i.e. later than in the Arkona Sea. The summer values are low and confined to the surface layer. The model eggs (not shown) and nauplii respond to the phytoplankton signal with a delay of a couple of weeks with a patchy distribution. Relative high levels appear near the eastern coast (Figure 6). The model nauplii abundance, which is an important food source for larvae, increases from spring to summer, from 4000 to 10 000 ind m^{-3} in the central part of the Bornholm Sea, while in the coastal region off Poland increased up to 40 000 ind m^{-3} . Below the surface layer, values

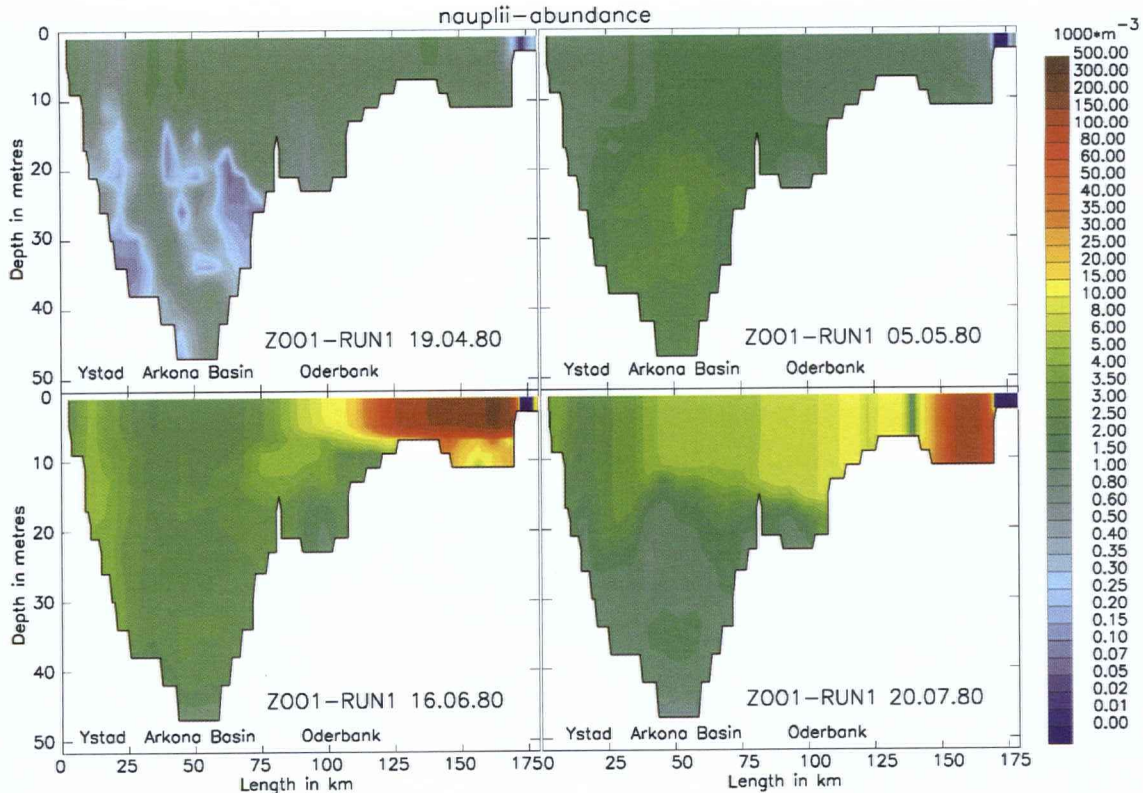


Figure 5. Development of the model nauplii along the Arkona Sea section (Figure 1).

are much smaller and exceed 2000 ind m^{-3} only in a few patches.

The response patterns of the model copepodite abundances show a similar offshore gradient. The model adults do not increase significantly before July and their maximum abundance is reached in August (not shown). The model generally reproduces the observed higher abundance in the Arkona Sea than in the Bornholm Sea.

The observational site corresponds to the central part of the model section. Contrary to observations, the model abundance of copepods is slightly higher in summer than in spring. However, this difference becomes negligible when we look at the total observed mesozooplankton, which also assumes maximum values in the summer. This implies that our model copepod ingest food, which in nature is taken by other species, in particular *Cladocera* and *Rotifera*.

In both basins, the vertical distribution patterns in the model show the strongest signals in the upper layer, while below the seasonal thermocline adults, as well as eggs and nauplii, are less abundant. This applies, in particular, to the Bornholm Sea during the summer. The reason is that the model phytoplankton in the summer season consists mainly of flagellates, with zero sinking speed, and blue greens,

with a slight buoyancy, while the spring bloom is dominated by diatoms, which sink relatively quickly Neumann (2000). Thus, the summer chlorophyll concentrates mainly in the surface layer.

The vertical motion of the model copepods is passive, i.e. driven by currents and turbulent diffusion in a similar manner as in a bulk-zooplankton description. While a background stock of adults is maintained by setting the adult mortality to zero for low abundance there is still some egg laying and hatching to nauplii, whereas the model copepodites in the deeper layers are short of food and damped by mortality. This could be amended by allowing copepods some grazing on detritus, including vertical motion, i.e. diel migration, to draw from the food in the surface mixed layer.

It is interesting to compare the stage-resolving simulations (Figure 7) with the model containing one bulk-zooplankton variable (Figure 8). Compared to the bulk-zooplankton run, the stage-resolving case displays a lower grazing pressure during the spring bloom and a higher grazing pressure in the summer. While the bulk-zooplankton reacts immediately with an increase of biomass, the overwintering adults in the stage-resolving model first increase their body mass and start to lay eggs, then have to propagate through all stages until they

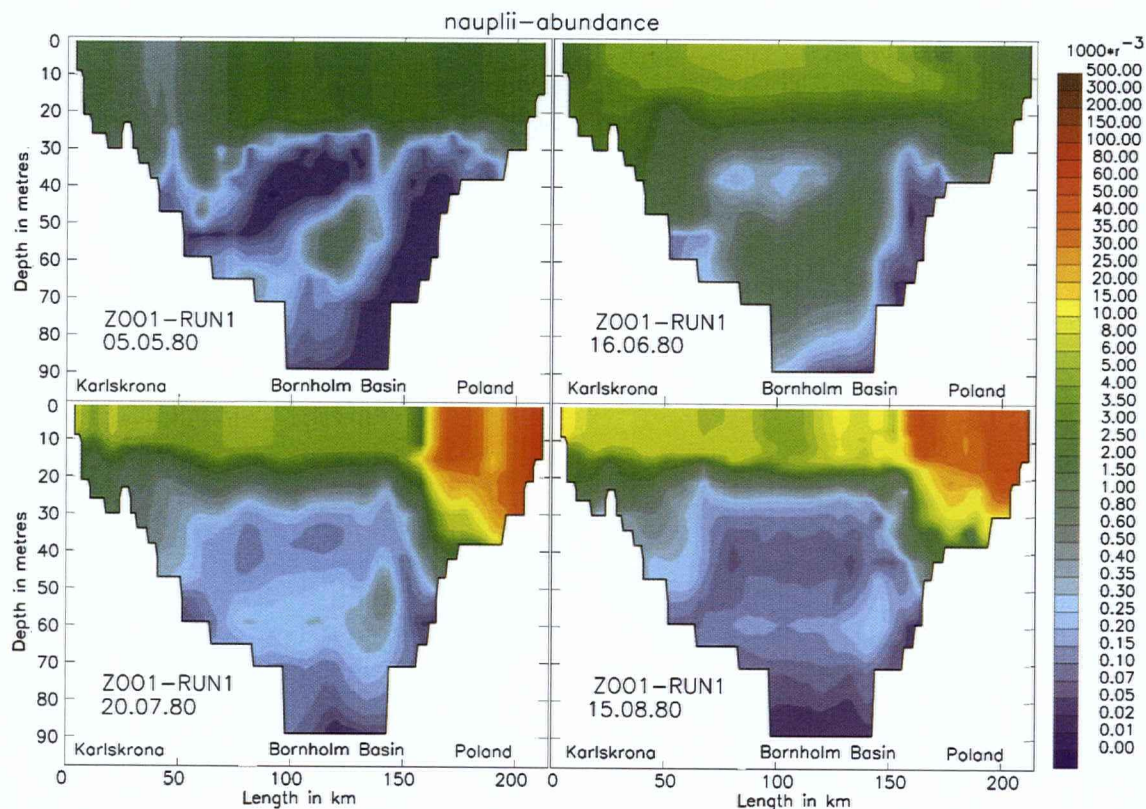


Figure 6. Development of the model nauplii along the Bornholm Sea section (Figure 1).

become adults, which then increases the reproduction. Thus a time interval of a full generation is needed before the zooplankton mass and the number of individuals increase through reproduction. The difference of both simulations is relatively small for the summer. The main deviations occur after the spring bloom.

Discussion and conclusions

The present study extends an advanced ecosystem model of the Baltic Sea in which the zooplankton biomass was considered as one aggregated bulk variable (Neumann, 2000; Neumann *et al.*, 2002) to a stage-resolving model of copepods (Fennel, 2001). The stage-resolving model combines elements of biomass models and stage-dependent population models and uses the concept of critical moulting mass (Carlotti and Sciandra, 1989). This approach allows a consistent formulation of the equations of the state variables, where abundance and biomass are based on a function of the population density, and obey von Foerster equations. In order to bridge the levels of individual and population dynamics, we introduced statistical aspects by means of the filter

functions (Fermi function). An attractive property of the present model is its ability to conserve mass distributed within the food web explicitly. Such a conservation law cannot generally be applied to population models, because there is no law of conservation of the number of individuals. Only in special cases can it be assumed that for limited time periods the total number of individuals is constant, e.g. Wroblewski (1982).

An unavoidable disadvantage of the model is the need for two sets of state variables, biomass and the number of individuals, and hence the need for two equations at each stage. This is because of the connection of individual to population and bulk biomass levels in a statistical treatment.

Formulation of the dynamic signatures of the “model-copepod” was guided by properties of *Pseudocalanus* in the Baltic. However, in order to integrate the stage-resolving model into the coupled physical-biological model, it was assumed that the model copepod comprises other copepod species (aggregated state variables), although their parameters differ from those of *Pseudocalanus*. Species such as *Cladocera* and *Rotifera* were not explicitly taken into account in the present model approach.

Although not discussed in this article, we note that the model calculates, in a consistent way, the

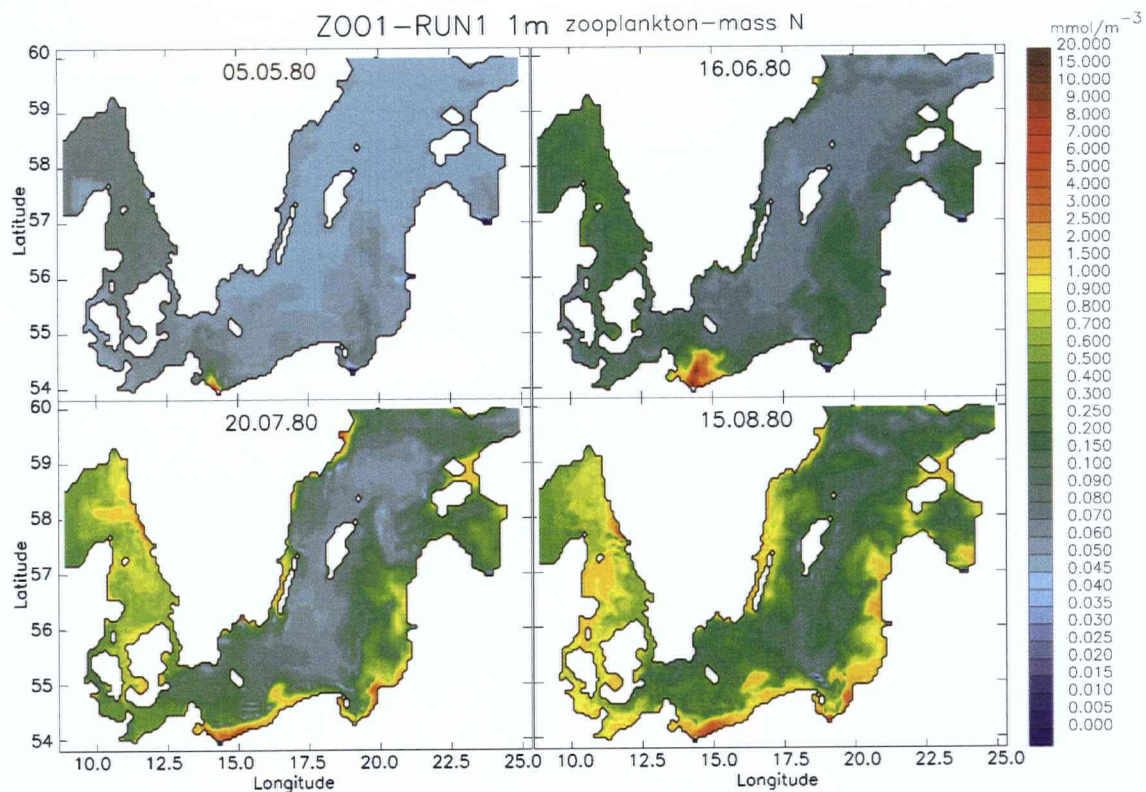


Figure 7. Development of the total zooplankton biomass near the sea surface (uppermost layer, thickness 2 m).

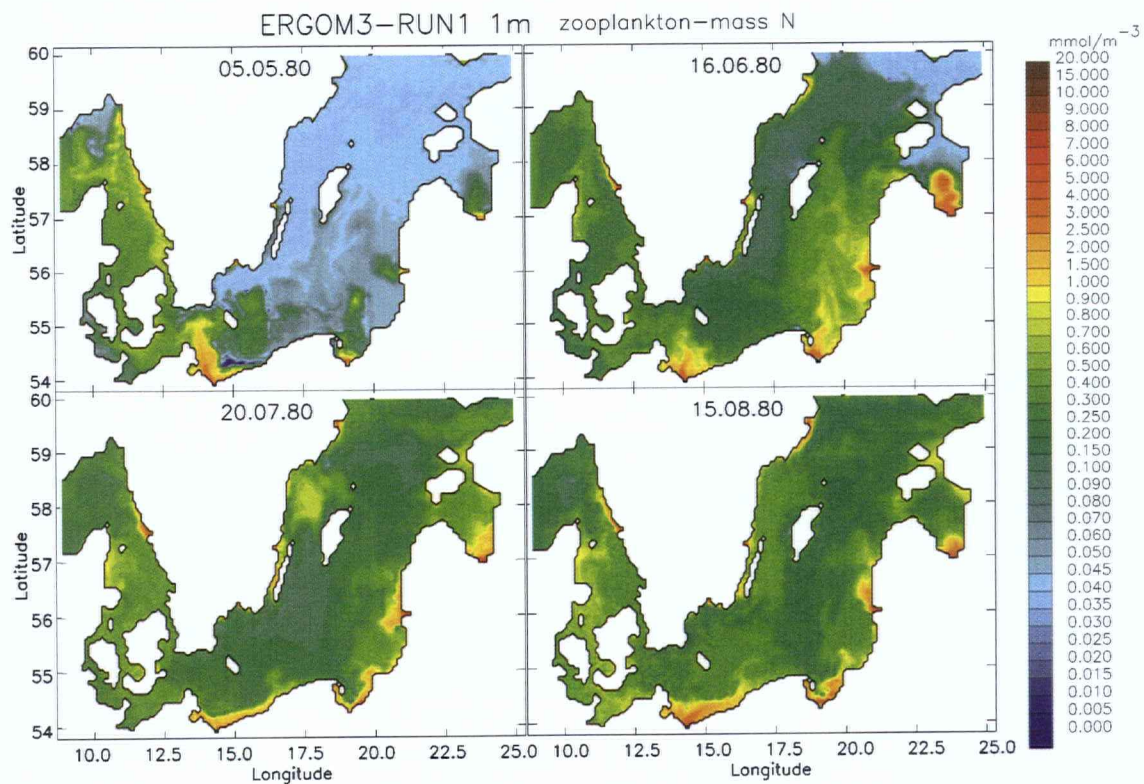


Figure 8. As Fig. 7, but for a model run with only one bulk zooplankton state variable.

food-web dynamics controlled by physics and the chemical-biological processes. It includes biogeochemistry and has the potential to simulate oxygen depletion in the bottom waters of the central Baltic Sea (Neumann, 2000; Neumann *et al.*, 2002).

The food web is truncated at the level of the zooplankton although the zooplankton mortality includes predation by planktivorous fish. Nevertheless, the model provides a basis from which to explore variations in the recruitment condition, by computing development of larvae food (distribution of nauplii) in time and space in response to climate changes or altered river loads. Inclusion of the lower trophic levels allows, for example, simulation of how signals propagate through the food web and study of the effects of food quality on reproduction.

Although the present model is complex, it still involves a substantial simplification of the real system. For example, the stage-resolving formulation used in the 3-D ecosystem model has elements of a bulk approach by its lumping together several species into the corresponding stages. The description of vertical migration of the higher stages must be improved and grazing on detritus as a low quality food resource can be included. The influence of salinity and oxygen on the physiological rates has not been considered.

This study also highlights the need for more observational data, both for model initialization and for comparison of model results with observations.

It is generally accepted that models should be as simple as is reasonable and only as complex as is necessary. This implies that the choice of model equations depends on the problem considered and involves the assumption that enhancing or reducing the complexity of a model system by parameterization is possible to a certain degree. The quality of parameterizations can only be judged by comparison with measurements and by exploring models of different complexity. The present study indicates, for example, that the spring bloom is more strongly controlled within models using bulk zooplankton parameterization and responds faster than in a stage-resolving model where the eggs have to propagate through the stages before a significant increase in the grazing pressure develops. This delay has a time-scale of a full generation at relatively low temperatures. Thus, the presented simulations provide arguments to improve parameterizations of bulk-zooplankton biomass models.

The present model study was a first attempt to include a stage-resolving zooplankton component within a full 3-D physical-chemical-biological model of the Baltic Sea. Although the simulation was made for the year 1980, the model provides the means for studying the zooplankton response to decadal hydrographical variability. However, this will be the subject of future work.

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