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A unifying framework for marine ecological model comparison

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Abstract

The complex network of the marine food chain with all the details of the behavior of individuals and the interactions with physical processes cannot be included into one generic model. Modelling requires simplification and idealization. The reduction of complex problems to simpler, but tractable problems are guided by the questions being addressed. Consequently, a variety of different models have been developed with different choices of state variables, process formulations, and different degree of physical control.

In the last decade a multitude of studies were based on biogeochemical models, population models, and individual based models. There are now models available that cover the full range from individual based models, to population models, to biomass models, to combinations thereof. The biological model components are linked to physical models ranging from 1d water column models to full 3d general circulation models.

This paper attempts to develop an unifying theoretical framework that elucidates the relationships among the different classes of models. The theory is based on state densities, which characterize individuals in an abstract phase space. Integration of the state densities over spatial or biological variables relates population densities, abundance or biomass to individuals.

1. Introduction

In the last few decades the theoretical investigation of the marine ecosystem based on mathematical models has developed into an important branch of research. Many processes in marine ecosystems involve physical–chemical–biological interactions. Consequently, modellers of marine systems strive for integrated models, linking physical, chemical and biological model components.

Food webs are complex systems, which can simply be sketched as a flux of material from nutrients to phytoplankton to zooplankton to fish. Phytoplankton communities consist of a spectrum of microscopic single-cell plants, microalgae. Microalgae in marine or freshwater systems are mostly primary producers, which build up organic compounds directly from carbon dioxide and the

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nutrients dissolved in the water. The captured matter and energy is passed along to components of the aquatic food chain through the consumption of microalgae by secondary producers, the zooplankton. Zooplankton encompass various size classes of early stages to adults. The zooplankton are eaten by fish, which are caught by man. In the food web there are individuals (cells, copepods, fish) at different trophic levels that mediate the flux of material. The individuals have biomass and form populations that interact up, down and across the food web. There is a further pathway for the nutrients: (i) release of dissolved nutrients by respiration from cells or animals, or (ii) mineralization of detritus, which comprises dead cells or animals as well as egested substances. Mineralization of such organic material by microbial activity provides recycled nutrients that again fuel the primary production.

It is obviously impossible to include the full food web and the full range of controlling physical processes into one generic model. Therefore it is reasonable and necessary to reduce the complexity of nature with models. The degree of idealization achieved by isolating parts of the food chain, truncating upper and/or lower trophic levels by effective parameterizations, and simplification of controlling physics depends on the problem at hand. Hence, there are a variety of model types. A theoretical framework is desirable to categorize the different models and show how they are related to each other.

To be specific, we use the term 'biological model' for theoretical descriptions based on differential equations that capture individual behavior or food web dynamics linked to physical processes. We confine this discussion to predictive models, which compute future states of marine systems from given initial states and are driven by internal dynamics and external forces and fluxes.

Physical quantities, such as light, temperature, current, and turbulence, as well as chemical quantities, such as nutrients, can be described by continuous functions changing in space and time. Biological models can look at a set of individuals or state variables, such as the abundance of a population or biomass concentrations representing functional groups: all in order to answers specific questions. Individual-based models treat individuals as unique and discrete entities, while state variables are considered as continuous functions changing in space and time. Intuitively we would expect that a theoretical description of long living taxa, such as fish, that may migrate over large distances in the ocean, require an individual-based treatment, while the description of plankton blooms require statistically averaged state variables, which do not resolve single cells.

The question, whether individual based modelling can unify ecological theory, was raised by Huston et al. (1988); see for review also Grimm (1999). In the present study, we look for an unifying theoretical concept that connects the different classes of models, comprising individual-based models, population models, biomass models and combinations thereof. The paper will show that different models have the same theoretical roots but can be formulated by branching out to isolate certain aspects of the food web dynamics and ignoring or simplifying links to other parts. The theoretical approach adopts methods developed in statistical physics, see for example Klimontovich (1982).

We do not intend to provide an overview or comprehensive list of all models described in the literature. Attempts to compile overviews of the numerous models were presented by, e.g., Fransz et al. (1991), DeAngelis and Gross (1992), Totterdell (1993), Grimm (1999), Carlotti et al. (2000), and Moll and Radach (2001).

2. State density and phase space

The state of an individual, be it a phytoplankton cell, a copepod or a fish, can be characterized by the location in the physical space, $\vec{r}_{\mathrm{ind}}(t)$, and by the mass, $m_{\mathrm{ind}}(t)$. More parameters can be added to describe the biological state, when required. However in the following we restrict the considerations to the parameter 'individual mass' and an index to indicate species. We define an abstract 'phase space' that has the four dimensions, (x, y, z, m). Individuals occupy points in the phase space that change their locations with time due to physical motion and growth, moving along a trajectories.

The state density for one individual can be defined as

$$\varrho_{\mathrm{ind}}(\vec{r},t,m)=\delta(\vec{r}-\vec{r}_{\mathrm{ind}}(t))\delta(m-m_{\mathrm{ind}}(t)). \quad (1)$$

A system of N individuals of a species represents a cloud of points in the phase space for every moment, t. The cloud will change its shape with time. We can write the state density for a many-individuals system as sum of the state densities of all individuals

$$\varrho(\vec{r},t,m)=\sum_{i=1}^{N}\varrho_i(\vec{r},t,m)=\sum_{i=1}^{N}\delta(\vec{r}-\vec{r}_i(t))\delta(m-m_i(t)). \quad (2)$$

This approach is adopted from the statistical theory of many-particle systems (Klimontovich, 1982). The total number and biomass of all individuals follows from

$$N=\int \mathrm{d}\vec{r}\,\mathrm{d}m\,\varrho(\vec{r},t,m),$$

and

$$m^{\mathrm{total}}=\int \mathrm{d}\vec{r}\,\mathrm{d}m\,m\varrho(\vec{r},t,m).$$

An example of the phase space for the two dimensions, z and m, is sketched in Fig. 1. The change of the locations of the individuals in the phase space is governed by the dynamics of the flow field and the individual motion, as well as the growth of the individuals. Let $\vec{v}(\vec{r},t)$ be the vector of the water motion and $\vec{v}_{\mathrm{s}}(\vec{r},t)$ be the vector the individual's motion relative to the water, then it follows that the location of an individual is specified by

$$\vec{r}_i(t)=\int_0^t \mathrm{d}t'(\vec{v}(\vec{r}_i(t'),t')+\vec{v}_{\mathrm{s}}(\vec{r}_i(t'),t')). \quad (3)$$

To describe the growth of individuals we can consider the example of the development of a copepod from the egg to the adult stage, as governed by an equation of the type

$$\frac{\mathrm{d}}{\mathrm{d}t}m_i=(g-l)m_i^p, \quad (4)$$

where the rate g stands for ingestion and l for losses. The rates, g and l, must be prescribed as functions of environmental parameters such as light, temperature, food, level of turbulence etc., and p is an allometric exponent smaller than unity. The allometric exponent follows from experimental data and reflects that older stages ingest smaller amounts of food in relation to their body mass than the younger stages. The allometric scaling can equivalently described by a linear dependence on the mass m, but with stage dependent rates

$$\frac{\mathrm{d}}{\mathrm{d}t}m=(g_j-l_j)m, \quad (5)$$

where the index 'j' refers to different stages of the life cycle. In the following we use the form (5), but drop the index 'j' for simplicity where this is possible.

While the mass (or size) of copepods can change by two order of magnitude, the mass of plankton cells varies during a life cycle by a factor two or less.

In principle we can split the state density into densities for each group of species as,

$$\varrho=\varrho^{\mathrm{cells}}+\varrho^{\mathrm{copepods}}+\varrho^{\mathrm{fish}}.$$

Using the property of the δ-function,

$$\int_{m_b}^{m_a}\mathrm{d}m\,\delta(m-m_i)=1 \quad \text{for} \quad m_a\leqslant m_i\leqslant m_b$$

or 0 otherwise,

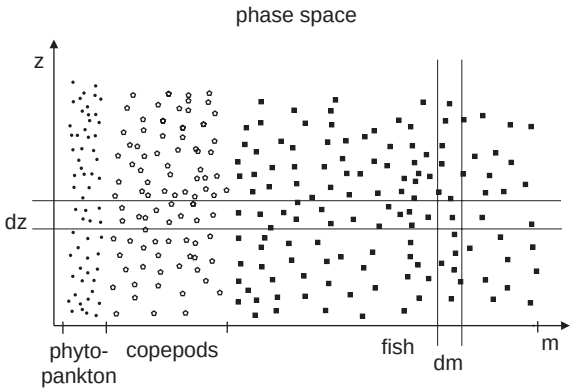

Fig. 1. Illustration of the concept of the phase space for the two-dimensional (z,m) example. Each point refers to one individual. As biological parameters the mass of the individuals is chosen.

it appears that by integration over the variable, m, from a minimum to a maximum mass, m_a and m_b, we can isolate different parts of the system and obtain abundance or biomass of species or aggregated groups. Thus the introduction of state densities provides an unifying concept where population or biomass models emerge from (very many) individuals.

3. Models of individuals

Individual-based models (IBM's) have been constructed for a wide range of organisms, starting from the level of individual cells to copepods and fish, (see, e.g., Grimm, 1999, for an overview). Individual-based models consider the details of one or more individuals during its or their life cycles. The dynamical signature of individuals involve genetically coded properties and phenotypic aspects, which develop in response to environmental conditions. The development is governed by Eqs. (3) and (5). In order to calculate the integrals in (3) we need information on the velocity field that can be provided by a circulation model that runs on-line or by archived current data.

The equation (3) allows the computation of the trajectories of individuals. Sometimes this is called a 'Lagrangian' approach, although the velocity field is usually calculated in the Eulerian mode with Ocean General Circulation Models (OGCM's). Turbulent noise can be related to the turbulent viscosities calculated in the circulation model or may be introduced as a random-walk variable, implying that single trajectories are not exactly reproduced in different simulations.

For individuals with long lifetimes (e.g., one year or more) and a well established ontogenetic migration (*Calanus finmarchicus*) such models are useful to explore and understand the migration patterns, (Miller et al., 1998). The models can become very complex when behavior must be built in, for example by a set of **if** .. **then** statements that switch between options of behavior in response to environmental signals. This implies knowledge of the physical features and prey fields for individual 'particles'.

The trajectories of the individuals define their locations and past history to the present moment. This information can be used to determine the past and present conditions for light, food, temperature, etc. The integration of the growth equation requires the numerical values of the physical control parameters as well as nutrient or prey fields, which can either be prescribed as continuous distributions, e.g., nutrients or phytoplankton, or as discrete food items. For example, if we wish to model individual copepods that ingest phytoplankton, we can assume a maximum grazing, which is set by genetic properties, say $g^{\max}$, and a modification due to food limitation, where the food is expressed as phytoplankton concentration, P, e.g.,

$$g(P) = g^{\max}(1 - \exp(-I_{\mathrm{v}}P), \tag{6}$$

with I_{v} being the Ivlev parameter. Similarly, the loss rate can be related as a certain percentage of the ingestion.

Modelling one specific individual covers the life span of just that individual. Reproduction and mortality of individuals can be involved when many individuals form populations. In the phase space, cell division or egg laying means that new individuals are created while mortality means annihilation of existing individuals. Technically reproduction and mortality can be introduced as 'creation' and 'annihilation operator' acting on the state density of the system and increase or reduce the number of individuals. For example, mortality can be represented by multiplying the state density with a factor, which removes some individuals. This factor can be produced by a random number generator that is either one or zero, and that is somehow related to the life history (nutrition, age, etc.) (Batchelder and Williams, 1995). Alternatively, mortality can be expressed by predation acting top-down. This involves predator–prey interaction.

Reproduction can be described by a 'creation operator' acting on the state density and, e.g., allowing matured female copepods to lay an amount of eggs, depending on their life history, quality of food and other factors. For phytoplankton cells, a creation operator can mimic primary production by increasing the number of cells due to cell divisions, which is controlled by external factors such as light (irradiance), temperature and

nutrient concentration. For example, we can prescribe primary production by an operator Π, which depends on continuous physical fields (e.g., light, temperature etc.) and a continuous nutrient field, e.g., nitrate. These fields are functions of time and space. For a limiting nutrient, say nitrogen, we can use a Michaelis–Menten formula, with a half-saturation constant k_{NO_3}. Then the uptake rate R is given by

$$R(\vec{r},t) = f(I,T)R^{\max}\frac{NO_3}{k_{NO_3}+NO_3}, \tag{7}$$

where the irradiance I, the temperature T, and the nitrate concentration, NO_3, are functions of $\vec{r}$ and t. The growth equation for phytoplankton cells is then,

$$\frac{d}{dt}m = (R-l)m,$$

with the initial mass m_0. The growth stops if the division mass $m_{div} \approx 2m_0$ has been reached. At this stage the cell divides and two cells start with m_0. Thus, the mass of cells cycles between m_0 and m_{div}. A primary production operator can now be constructed by

$$\Pi = \frac{1}{\Delta t}\,\theta(m-m_{div}).$$

The step function is one for cells of a mass close to the division mass, and zero otherwise. Applying $\Pi(\vec{r},t)$ onto the state density of an ensemble of phytoplankton cell amounts to

$$\Pi(\vec{r},t)\rho^{phyto} = \frac{1}{\Delta t}\sum_{i=1}^{N^{phyto}}\theta(m-m_{div}) \times\delta(\vec{r}-\vec{r}_i(t))\delta(m-m_i(t)).$$

For cells of a mass m smaller than the division mass the right hand side vanishes, while for cells of a mass close to the division mass the step function is one and new cells are created. The product $\theta(m-m_{div})\delta(m-m_i(t))$ is equal to $\delta(m-m_i(t))$ for $m_i \geqslant m_{div}$ but zero for $m_i < m_{div}$ i.e.

$$\Pi(\vec{r},t)\rho^{phyto} = \frac{1}{\Delta t}\sum_{i=1}^{N^{phyto}_{new}}\delta(\vec{r}-\vec{r}_i(t))\delta(m-m_i(t)),$$

where $N^{phyto}_{new} \leqslant N^{phyto}$. Obviously, $N^{phyto} = N^{phyto}_{new}$ means that all cells have divided.

If we wish to consider individual phytoplankton cells as food items for copepods we have to deal with IBM's of phytoplankton and copepods, with the corresponding state densities, $\varrho^{phyto}(\vec{r},t,m)$ and $\varrho^{cop}(\vec{r},t,m)$,

$$\varrho^{phyto}(\vec{r},t,m) = \sum_{i=1}^{N^{phyto}}\delta(\vec{r}-\vec{r}_i(t))\delta(m-m_i(t)), \tag{8}$$

$$\varrho^{cop}(\vec{r},t,m) = \sum_{k=1}^{N^{cop}}\delta(\vec{r}-\vec{r}_k(t))\delta(m-m_k(t)). \tag{9}$$

A grazing operator can be introduced to remove (annihilate) plankton cells. Obviously, there are three necessary conditions for the ingestion of food items: (i) Cells must stay in a finite search volume around each of the copepod, to allow them to capture the food item. (ii) A sufficient difference in size between prey and predator is required to ensure that the food item is edible for the copepod. (iii) The prey species must be appropriate for the predator. Since we considered only the mass co-ordinate in the phase space to characterize biological properties, we use the individuals mass as measure of their size. Then the grazing operator can be constructed as

$$\Gamma = \sum_{k=1}^{N^{cop}}\Gamma_k.$$

where

$$\Gamma_k(\vec{r},m) = -\frac{1}{\Delta t}\,\theta(|\vec{r}-\vec{r}_k|-\varepsilon_k)\theta((m_k-\Delta m_k)-m).$$

Here $\vec{r}$ is the position of the potential food item, $\vec{r}_k$ is the position of a copepod, and ε_k is the radius of the search volume. The search radius may depend on the properties of the specific copepod and the level of turbulence in the volume element that affects the contact rate as well as the dispersal of the 'particles', see e.g., Rothschild and Osborn (1988). If the difference in size of prey and predator is characterized by Δmk, it follows that only food items with $m \leqslant (m_k - \Delta m_k)$ can be ingested. These properties are sketched in Fig. 2. The application of the grazing

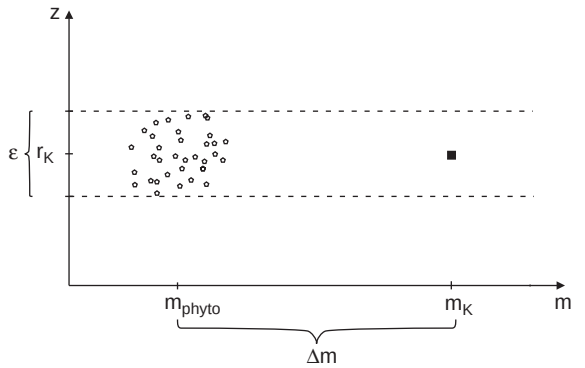

Fig. 2. Illustration of the concept of search volume and size differences relevant for the predator–prey interaction for a two-dimensional phase space. The predator of the mass m_k at the location r_k can capture food items in a search volume of the diameter ε. The prey items must have a mass smaller than $(m_k - \Delta m)$.

operator gives

$$\begin{aligned}\Gamma\varrho &= \Gamma(\vec{r},m)\varrho^{\text{phyto}}(\vec{r},t,m)\\ &= \sum_{k=1}^{N^{\text{cop}}}\sum_{i=1}^{N^{\text{phyto}}}\Gamma_k(\vec{r}_i,m^{\text{phyto}})\delta(\vec{r}-\vec{r}_i(t))\delta(m-m_i^{\text{phyto}})\\ &= -\frac{1}{\Delta t}\sum_{k=1}^{\Delta N^{\text{phyto}}}\delta(\vec{r}-\vec{r}_k(t))\delta(m-m_k^{\text{phyto}}),\end{aligned}$$

i.e., ΔN^{phyto} cells are removed due to grazing.

The ingested food drives the growth of the copepods. Let v be the number of ingested cells, then the ingested mass per time interval be vm^{phyto}. The grazing rate in (5) is relative to the mass of the grazer, m_k^{cop}, and can then be expressed as,

$$g \approx \frac{1}{\Delta t}\frac{vm^{\text{phyto}}}{m_k^{\text{cop}}}.$$

Thus, the predator–prey interaction involves ingestion of prey items, growth of predators, and mortality of prey. If food items are abundant, it is clear that only a certain number, $v^{\max}$, of cells are ingested in the time interval Δt. This can be related to the maximum grazing rate for continuously distributed food, (6), as

$$g^{\max} \approx \frac{1}{\Delta t}\frac{v^{\max}m^{\text{phyto}}}{m_k^{\text{cop}}},$$

i.e.,

$$v^{\max} \approx g^{\max}\Delta t\frac{m_k^{\text{cop}}}{m^{\text{phyto}}}.$$

In principle, we can construct predation operators for fish, which includes feeding on zooplankton but also on smaller fish (multi-species interaction, cannibalism), in a similar manner.

4. State variable models

If the number of individuals per unit of volume becomes very high, then the question which specific individual dies or lay eggs is more important than the fact that a certain percentage dies or contributes to the reproduction. Similarly, for very many phytoplankton cells it is unimportant which specific cell divides or dies. For many-individuals system it is reasonable to consider the dynamics of averages over very many cells or animals and to assume that a certain percentages of the total number of cells divides or dies. This averaging amounts to population or biomass models.

4.1. Population models

Populations consist of many individuals of the same species or functional group. In population models the state variable is abundance $n(\vec{r},t)$, i.e. number of cells or animals per unit of volume. Changes in abundance can be obtained by integrating a model of many individuals and taking averages from time to time. This amounts to a demographic model (Caswell and John, 1992). Another way is to introduce the population density, σ, for a certain parcel of water, ΔV. The population density is related to the state density by

$$\sigma(m,t,\vec{r}_{\Delta V}) = \frac{1}{\Delta V}\int_{\Delta V}\mathrm{d}\vec{r}\,\varrho(\vec{r},m,t), \tag{10}$$

where $\vec{r}_{\Delta V}$ is the location of the parcel in the sense of the theoretical fluid dynamics. In the following we drop the subscript in $\vec{r}_{\Delta V}$, and use $\vec{r}$ to refer to the location of the parcel. Then $\sigma(m,\vec{r},t)\,\mathrm{d}m$ is the number of individuals in the mass interval $(m, m+\mathrm{d}m)$ in a considered parcel. For a Lagrangian

parcel of fluid, moving with the flow, the number of individuals is controlled by birth and death rates as well as by active motion, swimming or sinking, of the individuals, which enables them to leave or enter the parcel. Let us consider first species that change their mass during their life span only within a small interval of mass, i.e. $\mathrm{d}/\mathrm{d}t\, m \approx 0$. Then we have for the population density for a parcel of fluid

$$\frac{\mathrm{d}\sigma(m,\vec{r},t)}{\mathrm{d}t} + \nabla\cdot\vec{v}_{\mathrm{s}}\sigma(m,\vec{r},t) = (\beta-\mu)\sigma(m,\vec{r},t), \tag{11}$$

where the birth rate, β, is related to effective growth rates of the average individual cell, $\beta \approx (g-l)$, and μ is the mortality rate. Active motion, swimming or sinking, of the average individual is described by a species-specific velocity, $\vec{v}_{\mathrm{s}}$. The Eulerian description amounts to the consideration of a fixed element of volume, ΔV. The change of the population density in the fixed volume is also affected by the fluxes of individuals through the borders of the volume element, i.e.

$$\frac{\partial\sigma(m,t,\vec{r})}{\partial t} + \nabla\cdot[\vec{v}+\vec{v}_{\mathrm{s}})\sigma(m,t,\vec{r}] - \nabla A\nabla\sigma(m,t,\vec{r}) = (\beta-\mu)\sigma(m,t,\vec{r}),$$

where $\vec{v}$ is the motion of water and A is the diffusivity. The state variable 'abundance', i.e. the number of individuals per unit volume, ΔV, follows from (10) as

$$n(\vec{r},t) = \int_{m_{\min}}^{m_{\max}} \mathrm{d}m\,\sigma(m,t,\vec{r}). \tag{12}$$

The dynamics of the abundance in a parcel of fluid, i.e. the change of the state variable with time, driven by birth and death rates as well as fluxes through the surfaces of the parcel, follows from (11) and (12) as

$$\frac{\mathrm{d}n(\vec{r},t)}{\mathrm{d}t} = (\beta-\mu)n(\vec{r},t) + \nabla\cdot\vec{v}_{\mathrm{s}}n(\vec{r},t), \tag{13}$$

or, in the Eulerian description,

$$\frac{\partial n(\vec{r},t)}{\partial t} + \nabla\cdot[(\vec{v}+\vec{v}_{\mathrm{s}})n(\vec{r},t)] - \nabla A\nabla n(\vec{r},t) = (\beta-\mu)n(\vec{r},t). \tag{14}$$

Note that the effective growth rates and swimming or sinking speeds apply for average individuals in a statistical sense. It is not necessary to assume that all individuals behave identically.

The links to the lower and upper part of the food web are truncated, i.e. they are parameterized by rates but are not computed from dynamical equations of state variables that represent the lower and upper parts of the food web. Consequently, the rates must be prescribed. This model type is in particular useful to look at problems such as advective transports of populations (e.g., Woods and Barkmann, 1994).

4.2. Biomass models

For studies of material fluxes through the food web biomass models are appropriate. Examples of biomass models are the biogeochemical model of Stigebrandt and Wulff (1987) for the central Baltic Sea or the model of Fasham et al. (1990), which typifies JGOFS models (JGOFS - Joint Global Ocean Flux Studies). The biomass concentration follows from the population density in a similar manner as the abundance (12),

$$B(\vec{r},t) = \int_{m_{\min}}^{m_{\max}} \mathrm{d}m\, m\sigma(m,t). \tag{15}$$

We restrict the theory in this section to species within a narrow mass interval. The equations for the biomass of a population follows from (13) by multiplication with the individual mass, m, i.e., $B = n\cdot m$. We consider the example of phytoplankton with the biomass concentration P, which is expressed by the amount of the limiting nutrient, e.g., nitrogen. With the help of Redfield ratio for living cells, the biomass of the state variable can be related to one of the chemical elements, which serve as 'model currency'. Then the dynamical change of P in a parcel of water can be written as,

$$\frac{\mathrm{d}P}{\mathrm{d}t} = (R-\mu)P - l_{\mathrm{P,NO_3}}P + \nabla\cdot\mathbf{v}_{\mathrm{P}}P, \tag{16}$$

where R is the growth rate describing the gain of biomass, $l_{\mathrm{P,NO_3}}$ is the transfer rate at which biomass is lost through respiration, and NO_3 denotes the nutrient concentration. The notation, $l_{\mathrm{P,NO_3}}$, can read as 'loss of phytoplankton to

nutrients'. The growth rate, R, is in general a function of intrinsic properties of the cells, light, temperature, and nutrients. Since nutrients are usually rapidly depleted, we may use for the limiting nutrient the Michaelis–Menten uptake formula (7). The advantage of a biomass model is that the model can be constraint by conservation of mass in a straightforward manner. The dynamics of the nutrient NO_3 can be explicitly taken into account by a state variable of the nutrient concentration, which may be denoted by NO_3. The temporal change of NO_3 is controlled by the nutrient uptake by phytoplankton and respirational release,

$$\frac{\mathrm{d}NO_3}{\mathrm{d}t} = -RP + l_{P,NO_3}P.$$

The mortality rate, μ, in (16) comprises natural mortality and zooplankton grazing. This amounts to the replacement of μP by $gZ + l_{P,D}P$, where g is a grazing (ingestion) rate, Z the bulk zooplankton, and $l_{P,D}$ prescribes the natural mortality of phytoplankton, read as loss of phytoplankton to dead material, the detritus, D. The bulk zooplankton biomass follows from (15), where the integration runs from the mass of eggs to the maximum mass of adults. Nutrients bound in dead material, the detritus, can be recycled by microbial mineralization. This can be included in the model by rewriting the equations for NO_3 and P, and adding dynamical equations for detritus, D, and zooplankton, Z,

$$\frac{\mathrm{d}NO_3}{\mathrm{d}t} = -RP + l_{P,NO_3}P + l_{Z,NO_3}Z + l_{D,NO_3}D, \tag{17}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} + \nabla\cdot\vec{v}_P P = RP + l_{PD}P - gZ - l_{P,D}P, \tag{18}$$

$$\frac{\mathrm{d}Z}{\mathrm{d}t} + \nabla\cdot\vec{v}_Z Z = gZ - l_{Z,D}Z - l_{Z,NO_3}Z, \tag{19}$$

$$\frac{\mathrm{d}D}{\mathrm{d}t} + \nabla\cdot\vec{v}_D D = l_{P,D}P + l_{Z,D}Z - l_{D,NO_3}D, \tag{20}$$

where $\vec{v}_P$, $\vec{v}_Z$, and $\vec{v}_D$ are the velocities of phytoplankton, zooplankton and detritus due to sinking or swimming. In the Eulerian framework the equations amount to advection–diffusion equations with reaction terms for every state variable . Let S stand for the state variables, (NO_3, P, Z, D) then

$$\frac{\partial}{\partial t}S + \nabla\cdot(\vec{v}+\vec{v}_S)S - \nabla\cdot A\nabla S = \text{biological dynamics } (S), \tag{21}$$

where 'biological dynamics (S)' stands for the right hand sides of (17)–(20). This is a consistent closed set of equations, which is usually denoted as NPZD-model.

The sub-grid or small scale processes are effectively accounted for by the eddy diffusivity A. Advection and turbulent diffusion transport and redistribute nutrients and plankton in vertical and horizontal dimensions. We note that in the general structure of the biological terms, right hand sides of (17)–(20), consist of state variables multiplied by rates. The dimension of the process rates is one over time. Similarly, the terms on the left hand side of (21), $\nabla\cdot(\vec{v}+\vec{v}_S)$ and $\nabla\cdot A\nabla$ are rates with dimension of t^{-1}. The rates determine the relative importance of the different physical or biological processes for the dynamical changes of the state variable, $(\partial/\partial t)S$. The advection–diffusion equation (21) represents the linkage between the biology and the circulation model (ocean general circulation model—OGCM), which computes the current, $\vec{v}$, and the diffusivity, A, for every grid point.

Eqs. (17)–(20) give an illustrative example of a biomass model with highly aggregated state variables. It can be shown that this model is the simplest choice to describe annual cycles of nutrients and plankton of systems like the Baltic Sea in a consistent manner (see Fennel, 1995). If we add Eqs. (17)–(20), we find for the sum of the state variables

$$\frac{\mathrm{d}}{\mathrm{d}t}(NO_3 + P + Z + D) = \nabla\cdot(\mathbf{v}_P P + \mathbf{v}_Z Z + \mathbf{v}_D D).$$

In a water parcel, the total mass, expressed through the limiting nutrient, is conserved, apart from the active movement, swimming or sinking of the quantities described by the state variables. Thus, the law of conservation of mass provides

a direct check for consistency of the model formulation.

An interesting property of this biomass model is that although we have more equations than for a population model, there are less requirements to prescribe rates externally. For example the nutrient uptake depends on the nutrient concentration, which changes dynamically in time and space. These changes are consistently computed in the model. More complex models can reduce the demands for the prescription of changing rates by data sets.

This type of model can be expanded to a higher degree of process resolution in a straightforward manner. For example, several nutrients and functional groups of phytoplankton were considered explicitly in Gregoire et al. (1998), Neumann (2000), Neumann et al. (2002), Savchuk (2002). A model with very many state variables is the European Regional Seas Ecosystem Model, (ERSEM); see Baretta (1993) and Baretta-Bekker et al. (1997).

5. Life cycle resolving state variable models

While for autotrophic species the cell size varies only by a factor of two, the body size of zooplankton varies over two orders of magnitude during the life cycle. The variations are even larger for fish. In the following we use the example of copepod models. If the development of individuals during their life cycle needs to be considered, then the bulk variables for zooplankton must be refined. For copepods, which develop over several stages, the bulk biomass is not simply related to bulk abundance because the individual mass may vary by two orders of magnitude. One way is to involve zooplankton stages through several size classes without resolution of the developmental stages. However, a more sophisticated approach should describe the development explicitly.

5.1. Stage resolving population models

Population models of copepods aim at the description of the dynamics of the number of individuals per unit of volume in the different stages. During their development the copepods propagate through several stages from eggs, nauplii, copepodites to adults. The 'propagation speed' is given by a growth equation of the type (4) or (5). A sketch of a propagating cohort is drawn in Fig. 3. The total abundance is

$$n(t,\vec{r}) = \int_{m_e}^{X_a} \mathrm{d}m\sigma(m,t,\vec{r}),$$

where m_e is the mass of eggs and X_a the upper limit of the mass of the adults. The temporal changes of the population density in a parcel of water and a mass interval is then, instead of (11), given by

$$\frac{\mathrm{d}}{\mathrm{d}t}\sigma(m,t,\vec{r}) + \nabla\cdot\vec{v}_s\sigma(m,t,\vec{r}) + \frac{\partial}{\partial m}\left[\sigma(m,t,\vec{r})\frac{\mathrm{d}m}{\mathrm{d}t}\right] = (\beta-\mu)\sigma(m,t,\vec{r}).$$

The term $\partial/\partial m(\sigma(m,t,\vec{r})\mathrm{d}m/\mathrm{d}t)$ follows from the consideration that the number of individuals, which enter a certain interval of mass and propagate through it, must be equal to the number of individuals that leave the interval minus those, which died (and plus newborns if the reproduction occurs in that interval). The birth rate is now restricted to the mass interval of adults. Only female adults which have reached a prescribed maturation mass can lay eggs. In the Eulerian mode the changes of the population density in a

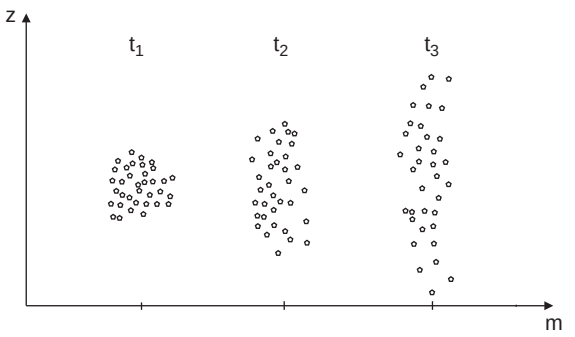

Fig. 3. Illustration of the propagation of a cohort in the two-dimensional phase space (z,m). The cloud of points indicating the individuals is shown for three moments.

fixed element of volume is

$$\frac{\partial\sigma(m,t,\vec{r})}{\partial t}+\nabla\cdot[(\vec{v}+\vec{v}_s)\sigma(m,t,\vec{r})]+\frac{\partial}{\partial m}\left[\sigma(m,t,\vec{r})\frac{dm}{dt}\right]-\nabla\cdot A\nabla\sigma(m,t,\vec{r})=(\beta-\mu)\sigma(m,t,\vec{r}).$$

This is a 'von Foerster' type equation combined with the equation of continuity. This approach allows, in conjunction with a growth equation and a reproduction term, the description of developing cohorts in space and time. An attempt to use this equation to model copepods was presented by Bryant et al. (1997), where a growth equation of the type (4) and prescribed the phytoplankton from data sets were used. The advective transport was provided by archived data, which were computed with a circulation model.

For simplicity we consider aggregated state variables of the model-copepod: eggs, nauplii, copepodites 1 and 2, and adults. The corresponding numbers of individuals per unit of volume are $n_e, n_n, n_{c_1}, n_{c_2}$ and n_a. For a certain stage, j, the individual mass, m, is confined to the interval $X_{j-1}\leqslant m\leqslant X_j$, where X_{j-1} and X_j are the molting mass of the previous and the current stage.

Next we ignore, for the moment, the spatial dependencies and we define population density functions, $\sigma_j(m,t)$, for the different stages, by

$$n_j(t)=\int_{X_{j-1}}^{X_j} dm\sigma_j(m,t). \tag{22}$$

To find an equation for the population density, σ_j of a certain stage, j, we can use (22), (without the spatial terms, for simplicity),

$$\frac{dn_j}{dt}=\int_{X_{j-1}}^{X_j}\frac{d\sigma(m)}{dt}dm=-\mu_j n_j+\sigma_j\frac{dm}{dt}\bigg|_{m=X_{j-1}}-\sigma_j\frac{dm}{dt}\bigg|_{m=X_j},$$

or, equivalently,

$$\frac{d\sigma_j}{dt}=-\mu_j\sigma_j+T_{(j-1),j}\sigma_j\delta(m-X_{j-1})-T_{j,(j+1)}\sigma_j\delta(m-X_j), \tag{23}$$

where $T_{(j-1),j}\sigma_j\delta(m-X_{j-1})$ and $T_{j,(j+1)}\sigma_j\delta(m-X_j)$ prescribe the rates at which individuals of the stage $j-1$ are transferred to the stage j, and individuals of the stage j molt into the stage $j+1$, respectively. Actually the transfer terms are, e.g. for $m\approx X_{j-1}$,

$$T_{(j-1),j}\sigma_j\delta(m-X_{j-1})\approx\frac{\Delta m}{\Delta t}\sigma_j\delta(m-X_{j-1}),$$

where $\Delta m\sigma_j$ is by definition the abundance of copepods having a mass close to the molting mass, while Δt is the time interval of the molting. This can be calculated from (5) as

$$\frac{1}{\Delta t}=\frac{(g_j-l_j)}{\ln\dfrac{X_{j-1}+\varepsilon}{X_{j-1}-\varepsilon}},$$

where ε defines the width of the molting interval, centered at $m=X_{j-1}$.

The dynamical equations for n_j follows from (22) and (23) as,

$$\frac{dn_j}{dt}=-\mu_j n_j+T_{(j-1),j}\sigma_{j-1}(X_{j-1})-T_{j,(j+1)}\sigma_j(X_j). \tag{24}$$

The problem is now to express the transfer rates by the known state variables, n_{j-1} or n_j and other available parameters.

A simple approach is $T_{j,(j+1)}\sigma_j(X_j)\sim n_j/D_j$, where the D_j's are observed stage duration times (Belehradek formulas). Then the corresponding equations for the number of individuals can be written as

$$\frac{d}{dt}n_e=q_e-\mu_e n_e-\frac{1}{D_e}n_e, \tag{25}$$

$$\frac{d}{dt}n_n=\frac{1}{D_e}n_e-\mu_n n_n-\frac{1}{D_n}n_n, \tag{26}$$

$$\frac{d}{dt}n_{c_1}=\frac{1}{D_n}n_n-\mu_{c_1}n_{c_1}-\frac{1}{D_{c_1}}n_{c_1}, \tag{27}$$

$$\frac{d}{dt}n_{c_2}=\frac{1}{D_{c_1}}n_{c_1}-\mu_{c_2}n_{c_2}-\frac{1}{D_{c_2}}n_{c_2}, \tag{28}$$

$$\frac{d}{dt}n_a=\frac{1}{D_{c_2}}n_{c_2}-\mu_a n_a, \tag{29}$$

where q_e prescribe the abundance of newborns per time. The advection and turbulent diffusion can be

included again by replacing $\mathrm{d}/\mathrm{d}t\, n_j$ by the Eulerian derivative. This type of model was for example used by Wroblewski (1982) and Gupta et al. (1994). A stage-resolving individual-based population model was linked to circulation by using archives of modelled advection in Miller et al. (1998) and Lynch et al. (1998).

5.2. Population models linked to individual development

A more refined approach, which employs the evolution of the mean individual mass to control growth and the onset of molting, i.e. the transfer to the higher stages, was proposed by Carlotti and Sciandra (1989), and Carlotti and Nival (1992). In our notations the model are equations are

$$\frac{\mathrm{d}}{\mathrm{d}t} n_e = q_e - \mu_e n_e - \tau_{en} n_e, \tag{30}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} n_n = \tau_{en} n_e - \mu_n n_n - \tau_{nc_1} n_n, \tag{31}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} n_{c_1} = \tau_{nc_1} n_n - \mu_{c_1} n_{c_1} - \tau_{c_1c_2} n_{c_1}, \tag{32}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} n_{c_2} = \tau_{c_1c_2} n_{c_1} - \mu_{c_2} n_{c_2} - \tau_{c_2a} n_{c_2}, \tag{33}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} n_a = \tau_{c_2a} n_{c_2} - \mu_a n_a, \tag{34}$$

in conjunction with a growth equation for the mean individual mass, $\bar{m}$ similar to (4) or (5). Here the transfer is no longer prescribed by empirical rates but computed in the model. The transfer is controlled by the 'growth speed', $\mathrm{d}\bar{m}/\mathrm{d}t$, multiplied by a filter function, $f(X_{j-1}-\varepsilon, \bar{m})$, which behaves like a smoothed switch-on function and activates the molting in a molting interval $(X_{j-1}-\varepsilon, X_{j-1}+\varepsilon)$. This can be done in a consistent manner for a coherent cohort, where the individuals develop more of less synchronously.

This type of model is very useful for species with long life cycles, say one year or more, such as *C. finmarchicus* (Lynch et al., 1998). Analytical fish stock assessment models are also population models combined with models of individual growth (weight at age) (see, e.g., Gulland, 1974; Horbowy, 1996).

However, for copepods with substantially shorter generation times and continuous egg laying we have to deal with several overlapping cohorts. For such a system the mean individual mass is an average of all stages and a dynamic equation of the mean individual is no longer well defined.

5.3. Stage-resolving biomass models

For the case of several cohorts of copepods within different stages, a consistent models description can be achieved by including both abundances and biomass state variables in a stage-resolving manner (Fennel, 2001). The dynamical equation for the stage-dependent biomass can be found by a combination of (5) and (23). Multiplying (5) by σ_j and (23) by m and adding the results it follows

$$\begin{aligned}\frac{\mathrm{d}m\sigma_j}{\mathrm{d}t} = & -\mu_j m\sigma_j + T_{(j-1),j} m\sigma_j \delta(m - X_{j-1}) \\ & - T_{j,(j+1)} m\sigma_j \delta(m - X_j) \\ & + (g_j - l_j) m\sigma_j. \end{aligned} \tag{35}$$

Since the biomass in a stage j is given by

$$Z_j(t) = \int_{X_{j-1}}^{X_j} \mathrm{d}m m\sigma_j(m,t),$$

the equation set for the stage dependent biomass follows as

$$\frac{\mathrm{d}}{\mathrm{d}t} Z_e = \tau_{ae} Z_a - \tau_{en} Z_e - \mu_e Z_e, \tag{36}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} Z_n = \tau_{en} Z_e + (g_n - \mu_n - l_n) Z_n - \tau_{nc_1} Z_n, \tag{37}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} Z_{c_1} = \tau_{nc_1} Z_n + (g_{c_1} - \mu_{c_1} - l_{c_1}) Z_{c_1} - \tau_{c_1c_2} Z_{c_1}, \tag{38}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} Z_{c_2} = \tau_{c_1c_2} Z_{c_1} + (g_{c_2} - \mu_{c_2} - l_{c_2}) Z_{c_2} - \tau_{c_2a} Z_{c_2}, \tag{39}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} Z_a = \tau_{c_2a} Z_{c_2} + (g_a - \mu_a - l_a) Z_a - \tau_{ae} Z_a, \tag{40}$$

where the transfer between the contiguous stages is given by the rates,

$$\tau_{j-1,j} = f(X_{j-1} - \varepsilon, \bar{m}) \frac{(g_j - l_j)}{\ln \dfrac{X_{j-1} + \varepsilon}{X_{j-1} - \varepsilon}}, \tag{41}$$

with $j = (e, n, c_1, c_2, a)$. In (36) and (40), the rate τ_{ae} occurs that can be read as 'transfer of adults to eggs'. This term can be prescribed with the filter function $f(\langle m \rangle_a, \bar{m})$, where $\langle m \rangle_a$ is a maturing mass that must be reached before the individuals can start to lay eggs. The number of eggs produced per day can then be related to the food ingested.

The dynamics of the state variables is controlled by transfer rates, $\tau_{j,j+1}$, grazing rates, g_j, loss rates, l_j, and mortality rates μ_j. Note that in (41) the mean mass appears as a control parameter, similarly as in the theory of Carlotti and Sciandra (1989). The simplest way to define the mean mass of individuals in a certain stage is $\bar{m} = Z_j/n_j$. This implies that we need also the equations for the abundance, i.e.,

$$\frac{\mathrm{d}}{\mathrm{d}t} n_e = \frac{1}{m_e} \tau_{ae} Z_a - \mu_e n_e - \tau_{en} n_e, \tag{42}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} n_n = \tau_{en} n_e - \mu_n n_n - \tau_{nc_1} n_n, \tag{43}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} n_{c_1} = \tau_{nc_1} n_n - \mu_{c_1} n_{c_1} - \tau_{c_1 c_2} n_{c_1}, \tag{44}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} n_{c_2} = \tau_{c_1 c_2} n_{c_1} - \mu_{c_2} n_{c_2} - \tau_{c_2 a} n_{c_2}, \tag{45}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} n_a = \tau_{c_2 a} n_{c_2} - \mu_a n_a. \tag{46}$$

The mortality rates, μ_j, and transfer rates, $\tau_{j,j+1}$, are the same as in (36) to (40). This type of model connects elements of individual-based models with population and biomass models (Fennel, 2001). This model applies for the development of both single cohorts or overlapping cohorts with continuous egg laying. The price is a substantially larger number of state variables.

The physical transport and mixing can again be included by replacing the total time derivations at the right hand sides of the equations by the Eulerian advection–diffusion terms. An application of this model embedded into a three-dimensional ecosystem model was presented by Fennel and Neumann (2003).

6. Summary and conclusions

In natural marine food webs there are individuals (cells, copepods, fish), forming populations, having biomass, and interacting up, down and across the food web. To understand and quantify these processes, it is necessary to reduce the complexity with models. Simplifications result in a variety of different models for individuals, populations and biomass. Different models are motivated by specific questions.

Individual-based models consider individuals as basic units and can study individual behavior and the effects of genetic variations among individuals during their life cycles. For systems of very many individuals, the question which specific individual grows faster than others or which one dies is less important than the fact that a certain percentage of the biomass increases or is removed by mortality. Thus for many-individuals systems it is reasonable to consider the dynamics of averages over very many cells or animals.

State-variable models use statistical averages of very many individuals in volume elements of the phase space. State variables are abundance (numbers per unity of volume) or concentrations of biomass and nutrients. In population and biomass models the process rates are averaged and individual variations are discarded. Biomass models are directly constrained by the conservation of mass. This is important for the calculation of budgets and fluxes of matter, in particular, for model integrations over many years. Thus, although individuals are basic units of the ecosystem, it is not always necessary to resolve individual properties. State-variable models are theoretically consistent, provided the state variables are well-defined, observable quantities.

The question, how a theoretical concept can be formulated, which in a consistent way links individual-based models and state variable models, was addressed in the literature; see for example DeAngelis and Gross (1992) and Grimm (1999).

In this study we presented a method towards the development of an unifying theory. By introducing a phase space and state densities of individuals, we could show that the biological dynamics amounts to creation or annihilation of individuals in the phase space. We also could show that these processes can be described by creation- or annihilation operators acting on state densities. As examples we used the cell division and predator-prey interaction. For very many individuals, the average over infinitesimal water parcels (in the sense of fluid dynamics) defines population densities that are related to abundance or biomass concentration in a well defined manner. The link to physics, in particular water motion including turbulence and motion of the individuals relative to the water, follows in a natural way by introducing the population density as integral over a volume element. This volume element can either be considered as a Lagrangian parcel of water, moving with the flow, or a fixed Eulerian cell. The dynamics of water motion in the volume element is governed by the equations of the fluid dynamics, which establish the link between circulation models and the biological components. With the aid of this method it can be determined how state variables are related to individuals. This amounts to a unified approach where population and biomass models emerge from individuals.

This paper is not intended to solve specific practical modelling problems but presents a theoretical study that aims at elucidating the linkage of the different types of models.

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