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The Scaled Subspaces Method: A new trait-based approach to model communities of populations with largely inhomogeneous density

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ABSTRACT

We present a new individual-based approach to model populations of largely inhomogeneous densities. By monitoring different populations at a spatial scale which is inversely proportional to the maximum expected concentration, the Scaled Subspaces Method solves the problem of demographic explosion of the most numerous species. It is intuitively similar to the experimental practice of changing the magnification of a microscope depending on the size-class of organisms inspected, and retains the possibility for uniform biological descriptions across scales. We use this method to simulate a pelagic microbial mixotrophic food web, where the most abundant species has population densities up to five orders of magnitude higher than the rarest species. The model generates biologically plausible and highly consistent predictions of biomass distribution across this density spectrum. Individual-based community models are affected by the possibility of artificial extinctions. We discuss theoretically and confirm experimentally this possibility, and show that this problem can be overcome through the use of large populations, genetic mutations, and periodical random reintroduction of lost species or traits. We also show that the proposed individual-based model produces the same solutions as a state-variable model of the same ecological scenario. This indicates that the predictions of the two models are independent of implementation issues, and allows using them interchangeably according to convenience. Overall, the study proves the viability of the Scaled Subspaces Method, and provides useful insights on its functioning and parameterization.

1. Introduction

Modelling biological systems often implies the representation of groups of organisms of different size, density, and behaviour. The literature can be broadly divided into two main approaches: the state-variable (Grünbaum, 1994; Woods, 2005) and the individual-based (DeAngelis and Gross, 1992; Grimm and Railsback, 2005) methods. These two approaches have a long history that has roots back in the field of fluid dynamics modelling, and are characterised by a complementary view of how to represent complex systems.

State-variable models regard populations as homogeneous aggregates, and describe the development of their density distribution (Grünbaum, 1994). According to the state-variable approach, the biological agents are whole functional groups of individuals (Woods, 2005). The dynamics of the system are usually described using differential equations that are parameterized with biological traits estimated from population averages.

Individual-based models are founded on the basic assumption that organisms are not identical, and that their diversity affects the population dynamics (DeAngelis et al., 1980, Beyer and Laurence, 1980; Adioui et al., 2003; Grimm and Railsback, 2005). In the individual-based approach, biological systems are resolved at the level of organisms, which are the agents (Woods, 2005). The diversity in individual behaviour is determined by a number of traits, some of which may be transmitted to future generations through the offspring (Huse and Giske, 1998; Giske et al., 2003). The dynamics of the system emerge from the evolution of and interactions between the single agents. The life history of each organism is described by ordinary or stochastic differential equations that determine the trajectory in space and time of a number of state parameters (DeAngelis and Gross, 1992).

The strength of the state-variable approach is its relatively low computational complexity, and the ease of representing populations of largely diverse density. For this reason, state-variable models have been most common in the literature up to now

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(Woods et al., 2005; Hellweger et al., 2007). The success of this approach is based on how well three fundamental assumptions are verified, namely, that all individuals can be represented by the average values of their traits, that they experience uniform conditions, and that the population is large enough that the effects of demographic stochasticity are negligible. Unfortunately, homogeneity in the environmental conditions of biological systems is usually encountered only at small spatial scales, which can host only small populations (Donalson et al., 2004). Other drawbacks of state-space models are that they do not consider intra-group variability, which is known to play an important role in shaping ecosystems (Grünbaum, 1994; Loreau et al., 2001; Thygesen et al., 2007). Lack of intra-group resolution also prevents the encoding and evolution of genetic traits. In the case of more complex biological models, it may also be difficult to express analytically the system processes and population behaviours (Hellweger and Bucci, 2009).

The strength of the individual-based approach is that it accounts for individual variability (Grimm and Railsback, 2005), and that the traits are explicitly represented and may be transmissible between generations (Huse and Giske, 1998; Giske et al., 2003). The individual-based approach also allows the life history of organisms to be modelled. It is most useful when intra-group diversity is important for understanding community and system dynamics, and in cases where the system dynamics can be shaped by events at a small or individual scale (e.g. a mutation event in a virus spreading model). It is also useful for representing complex processes, as the system dynamics become an emergent property of the model. The main drawback of the individual-based approach is the possibility of demographic explosion, which may quickly exhaust the available computing resources. Additionally, trait-based models need a statistical interpretation of the results.

The problem of unmanageably large populations is unavoidable when individuals of largely different size scales are to be represented. For example, in an ecosystem model simulating an area large enough to host a statistically relevant number of elephants, the number of ants would count to billions. Large numbers are also needed to simulate individuals in populations undergoing high mortality rates, such as marine larvae (DeAngelis et al., 1980; Beyer and Laurence, 1980) and plant seeds.

The simplest approach to deal with populations of largely different size is to use individual-based representations only for the target species, and use a state-variable representation for their much smaller and more numerous prey and any other relevant functional group (Megrey et al., 2007). This approach is suitable when only a single component of the ecosystem is the focus of the investigation. To study many ecologically and economically important species, whole or large parts of the ecosystem must be included at the level of individual interactions. A cost/benefit analysis is also needed to decide at which trophic levels to restrict the representation of intra-group diversity and traits (Fath and Jørgensen, 2001). In the case where ecological dynamics may impose trait changes in populations of highly varying abundances (e.g. Thingstad, 2000, Yoshida et al., 2003, Waite and Shou, 2012), a method that represents a sufficient but manageable number of individuals in each population is necessary.

To represent large numbers of organisms, some authors partition large populations into homogeneous sub-groups of organisms called 'super-individuals' (Scheffer et al., 1995; Bartsch and Coombs, 2004; Parry and Evans, 2008), 'ensembles' (Woods and Onken, 1982; Woods, 2005), or 'cohorts' (DeAngelis et al., 1993). These sub-groups act as a unit representative of several similar individuals, and become the biological agents of the model. This approach has been successful in many applications (Woods and Onken, 1982; Rose et al., 1993; Carlotti and Wolf, 1998; Thorbek and Topping, 2005; Hellweger and Bucci, 2009). However, in the super-individual approach, regular bookkeeping is needed to limit or keep the number of agents constant. This bookkeeping effort introduces computational costs, and may lead to computational artefacts that could affect biodiversity unpredictably. For instance, if the number of agents needs to be reduced, the two most similar super-individuals in the population may be merged. Alternatively, the least representative super-individual may be merged with another. Rare species are more likely to be preserved in the first case than in the second. Also, the non-uniform representativeness of the super-individuals (i.e. some super-individuals represent a large number of organisms, others only a few) can affect the model dynamics differently depending on which agent is selected for a given action.

This paper presents a new individual-based method to model functional groups of largely different size and density. The proposed approach uses a multiple scaling technique to limit the size of the individual populations that are modelled. The idea is to restrict the scale of the representation on increasingly smaller spaces as the potential for population abundance increases. Dynamics between different populations (e.g. predator–prey interactions) are resolved using the density of the individuals at the different size scales. Although first sketched by Scheffer et al. (1995), to the best of our knowledge, this method has never been implemented and tested. The Scaled Subspace Method may be more intuitive for biologists than the super-individual approach, as it reflects experimental practice, where microscope magnifications ("simulated subspaces") are adjusted to the size (and hence abundance) of the organisms studied. Also, it avoids potential artefacts due to bookkeeping and non-uniform representativeness of super-individuals.

The proposed method was devised for a pelagic microbial food web, which will be used as a case study. The major dynamics of our model are the abundances of the populations and the trait changes occurring within each population.

The agents are characterised by two traits: size and trophic mode. The difference in size amongst the various species ranges over several orders of magnitude. Because of their population heterogeneity, high numbers, high mortality rates, and non-linear biological responses, microbes are a good application case for individual-based modelling. Hellweger and Bucci (2009) cite 46 examples of individual-based models of microbial systems, ranging from simulations of marine and freshwater communities, wastewater treatment plants, biofilms, bacteria in food, and digital artefacts (e.g. computer viruses). As microbial food webs span several orders of magnitude in cell size, the scale-independent method proposed here is particularly useful to model such food webs on an individual basis.

Microbes in our model either acquire nutrients directly from the sea (*osmotrophs*), or from eating other organisms (*phagotrophs*), or they combine the two approaches in different degrees (*mixotrophs*). Mixotrophs are an interesting case study for individual-based modelling because of the large range of strategies in nature. They are also important ecologically, since they contribute significant amounts of primary production and bacterivory in marine environments (Havskum and Riemann, 1996; Zubkov and Tarran, 2008; Hartmann et al., 2012). However, due to the heterogeneity of sizes and behaviours, the modelling of mixotrophs has been so far limited to fairly broad state-space approaches.

Section 2 introduces the proposed method, whilst Section 3 presents the microbial food web model. Section 4 presents an equivalent state-variable model, and Section 5 discusses the differences between the proposed individual-based and the state-variable model. Section 6 presents the experimental results obtained using the proposed model, and compares these results with those obtained using the state-variable model. Section 7 discusses the main issues concerning the model. Section 8 concludes the paper and gives indications for further work.

2. The Scaled Subspaces Method

This section describes the proposed individual-based modelling approach.

2.1. The microbial food web

As mentioned in the introduction, we have used the Scaled Subspaces Method to model a pelagic microbial food web.

As they vie for resources, microbes can either evolve to maximise their uptake ability for dissolved nutrients (osmotrophs), or specialise in acquiring nutrients from other organisms (phagotrophs). Mixed strategies increase the capability of an organism to survive occasional shortages of one food source. As pointed out by Thingstad et al. (1996), "eating your competitor" is also a way for mixotrophs to win the struggle for resources. However, mixotrophy is assumed to imply efficiency costs due to the necessity of maintaining the double nutritional machinery (Tittel et al., 2003; Flynn and Mitra, 2009).

One strategy to avoid being eaten is to increase in size, becoming too large to be ingested by the predator(s). However, this implies an efficiency trade-off (Thingstad et al., 2010), as small cells are thought to be more efficient at gathering resources at low concentration where uptake rates are diffusion limited, whilst large cells typically require high concentrations to establish.

The study of the above trade-offs motivated the design of the individual-based model. Each agent represents one biological organism, and is characterised by two traits: the size and the foraging mode.

The main obstacle to implementing a trait-based model is the large difference in density of the various microbial species, which covers several orders of magnitude. The proposed approach was devised to solve this problem.

2.2. Scaled Subspaces Method

The idea is to follow different populations at different spatial scales, in order to constrain the maximum number of individuals per population. That is, the scale of description of the model is set at large sections of the environment (volumes) for large species, and gradually reduced to smaller volumes for increasingly smaller organisms. The members of each population are defined by a mass and diameter that varies within a given interval, whilst the trophic mode varies in the continuous interval between pure osmotrophy and pure phagotrophy.

The proposed system can be thought of as being visualized as a microscope, where the field of vision is narrowed down as smaller organisms are observed (Fig. 1).

In this particular implementation, the microbial food web is assumed to be closed, and the nutrients to be instantaneously recycled. For the sake of simplicity, the mineral nutrient pool is limited to only one element (phosphorous). The concentration δ_P of the total phosphorous present in the system is a fixed parameter, and the microbial community is partitioned into a fixed number Σ of size groups. For each group i, the population size n_i is allowed to vary from 0 to a maximum number N of organisms. In this study, N is the same for all size groups, that is, N is a fixed system parameter. Each size group i is then modelled in a subspace $volume_i$ of the overall environment so that its abundance n_i cannot exceed N:

$$volume_i = N \cdot \frac{\min mass_i}{\delta_P}, \tag{1}$$

where $minmass_i$ represents the lower bound for the mass of the members of size group i. According to Eq. (1), small organisms (those with higher potential for population abundance) are modelled in small volumes. When a population monopolises all the available phosphorous δ_P in the system, it reaches the size limit N.

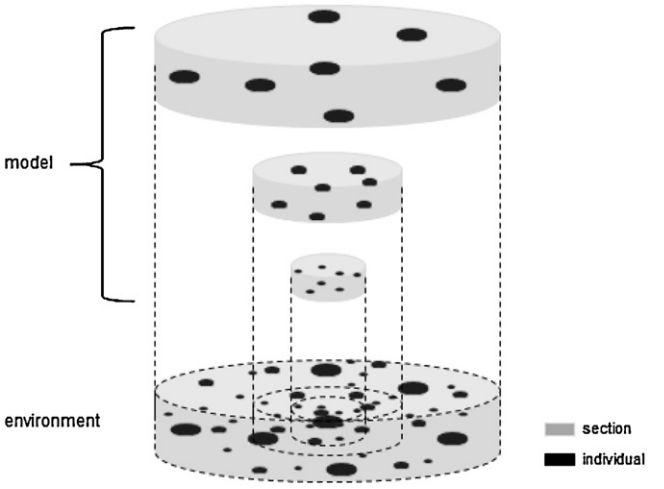


Fig. 1. Larger populations are followed in smaller regions of the overall environment in order to limit the total number of individuals modelled.

The phosphorous biomass concentration δ_i of a given size group i at any moment in time is the sum of phosphorous in all individuals, adjusted for the fraction of the total environment used by its subspace:

$$\delta_i = \frac{1}{volume_i} \sum_{j=1}^{n_i} m_{ij}, \tag{2}$$

where n_i is the population size of group i, and m_{ij} is the actual weight in phosphorous of individual j belonging to group i.

3. Microbial food web model

This section describes the model of the microbial community. The notation and equations are given in Tables 1–6.

3.1. Agents

The agents represent microbes of mass ranging from $mass_1 = 1.6 \times 10^{-8}$ to about 33 nmol P. They are assumed to be spherical (Harte, 1998), of diameter varying from $diam_1 = 0.5$ to 640 μm. They are characterised by two traits: the standard mass (typical weight in phosphorous) and trophic mode.

The standard mass of an individual belonging to size group i doubles at each successive size class, giving a logarithmic cell mass distribution:

$$mass_i = mass_1 \cdot 2^{i-1} \tag{3}$$

The diameter is calculated from the standard mass assuming spherical cells:

$$diam_i = diam_1 \left(\frac{mass_i}{mass_1} \right)^{1/3} = diam_1 \times 2^{(i-1)/3} \tag{4}$$

The actual mass of an individual is allowed to vary between $(1/2) \cdot mass_i$ and $2 \cdot mass_i$ (Fig. 2).

The feeding strategy is allowed to vary from pure osmotrophy to pure phagotrophy. For each individual, the feeding mode is encoded in a trait f_{ij}, which takes any value in the 0–1 range, where 0 denotes pure osmotrophy and 1 pure phagotrophy.

Nutrient (φ_{ij}) and prey (ψ_{ij}) uptake rates are defined by Holling type II functions with saturation at high resource concentration (Holling, 1959). The functions are given in Eqs. (5) and (6), Table 2.

Table 1
Individual agents—notation.

$diam_i$	standard diameter of individuals of size class i
f_{ij}	feeding mode of individual j of size class i
i,k,z	class
j,h	Individual
$mass_i$	standard weight of individuals of size class i
$mass_{p0}$	mass of the smallest predator
$\max UP_{ij}$	maximum P uptake rate per unit of cell mass of individual j of size class i
$\max UV_{ij}$	maximum prey mass intake rate per unit of weight of predator j of size class i
m_{ij}	weight of individual j of size class i
$minmass_i$, $maxmass_i$	minimum and maximum mass of individuals of size class i
$mutRate$	mutation rate [0,1]
r	optimal predator–prey ratio
$[v_{0i}, v_{Li}]$	range of size classes of organisms on which individuals of class i prey upon
w	width w of the bell-shaped predation curve
α_1	nutrient affinity of the smallest osmotroph
α_{ij}	nutrient (P) affinity per unit of cell mass of individual j of size class i
β_1	clearance rate of the smallest phagotroph
β_{ij}	water clearance rate for prey per unit of mass of predator j of size class i
γ_0	prey assimilation efficiency
δ_k	prey biomass density of size class k
μ	metabolic loss rate per unit of weight
π_{ik}	size preference factor of predators of group i for prey of size group k
ρ	optimal predator–prey ratio in size classes
τ	efficiency trade-off between mixotrophy and osmotrophic or heterotrophic specialization
φ_{ij}	nutrient uptake rate per unit of cell mass of individual j of size class i
ψ_{ij}	total prey biomass uptake rate per unit of mass of predator j of size class i
ψ_{ijk}	biomass uptake rate per unit of mass of predator j of size class i for prey of size group k
ω	width w of the bell-shaped predation curve in size classes
ξ	tax (% of body mass) levied on individual if reintroduction procedure is applied

Table 3
Environment and subspaces—notation.

D	number of individuals that duplicate
DIP	dissolved inorganic phosphorous in the system
$D \cdot M^-$	number of mutants lost to neighbouring classes
M^+	number of mutants acquired from neighbouring classes
$N_i = N$	maximum population size of size class i
n_a	number of individuals of class z created by reintroduction procedure.
n_i	population size of size class i.
T	total P collected from individuals if reintroduction procedure is applied.
$[p_{0i}, p_{Li}]$	range of size classes of organisms which prey upon the members of group i
$volume_i$	volume of subspace where size class i is modeled
δ_P	density of total phosphorous (P) biomass present in the system
θ^s	number of individuals dead due to starvation
θ_i^v	total biomass lost due to predation per time step
Σ	number of subspaces (one for each size group)

Fig. 3 shows the functional response curves for a pure osmotroph and a pure phagotroph.

Predators do not assimilate the whole phosphorous content of their prey. A yield (γ_0) is incorporated in Eq. (6) to account for the effects of sloppy feeding and other inefficiencies. At each time step, the total amount of waste produced by each predator per unit of biomass is obtained by considering all eaten prey (Eq. (7), Table 2). This unassimilated prey content is immediately remineralised into the dissolved inorganic phosphorous (DIP) pool.

The nutrient affinity α_{ij} and prey clearance rate β_{ij} (Eqs. (8) and (9), Table 2) define the slope of the functional response curves (Eqs. (5) and (6), Table 2) at low resource concentrations. Their decrease with the square of the cell diameter implements the size penalty postulated by Thingstad et al. (2010).

At high resource concentrations, the phosphorous and prey uptakes asymptotically approach the maximum rates $\max UP_{ij}$ and $\max UV_{ij}$. The maximum intake rates depend on the cell traits (standard mass and foraging mode), and on τ (Eqs. (10) and (11), Table 2).

The third factors on the right hand sides of Eqs. (8)–(11) reflect the decrease in resource uptake efficiency and maximum uptake rates of mixotrophs compared to osmotrophic and heterotrophic specialists (Tittel et al., 2003). The magnitude of the efficiency loss is adjusted via the parameter τ. Fig. 4 depicts the effect of τ on α_{ij} and β_{ij}.

Predators of a given size class i eat prey within a fixed range $[v_{0i}, v_{Li}]$ of size classes (Eq. (6), Table 2). They have maximum preference for individuals smaller by a diameter ratio r (ρ size classes), where r is a fixed system parameter. The preference factors $\pi_{ik} \in [0, 1]$ for predators of size class i for prey of size class $k \in [v_0, v_L]$ are

Table 2
Individual agents—equations.

$$\varphi_{ij} = \frac{\alpha_{ij} \cdot \mathrm{DIP}}{1 + (\alpha_{ij} \cdot \mathrm{DIP} / \max UP_{ij})} \tag{5}$$

$$\psi_{ij} = \gamma_0 \cdot \sum_{k=v_0}^{k=v_L} \psi_{ijk} = \gamma_0 \cdot \sum_{k=v_{0i}}^{k=v_{Li}} \left(\pi_{ik} \cdot \frac{\beta_{ij} \cdot \delta_k}{1 + (\beta_{ij} \cdot \pi_{ik} \cdot \delta_k / \max UV_{ij})} \right) \quad 0 \le \gamma_0 \le 1 \tag{6}$$

$$ds_{ij} = (1 - \gamma_0) \cdot \sum_{k=v_{i0}}^{k=v_{iL}} mass_k \cdot \psi_{ijk} \tag{7}$$

$$\alpha_{ij} = \alpha_1 \cdot \left(\frac{mass_i}{mass_1} \right)^{-2/3} \cdot \left(1 - f_{ij} \right) = \alpha_1 \cdot \left(\frac{diam_i}{diam_1} \right)^{-2} \cdot \left(1 - f_{ij} \right) \tag{8}$$

$$\beta_{ij} = \beta_1 \cdot \left(\frac{mass_i}{mass_{p0}} \right)^{-2/3} \cdot f_{ij} = \beta_1 \cdot \left(\frac{diam_i}{diam_1} \right)^{-2} \cdot f_{ij} \tag{9}$$

$$\max UP_{ij} = \max UP_1 \cdot \left(\frac{mass_i}{mass_1} \right)^{2/3} \cdot \left(1 - f_{ij} \right)^{\tau} \tag{10}$$

$$\max UV_{ij} = \max UV_{p0} \cdot \left(\frac{mass_i}{mass_{p0}} \right)^{2/3} \cdot f_{ij}^{\tau} \tag{11}$$

$$\pi_{ik} = e^{-(i-k-\rho/\omega)^2} \tag{12}$$

$$\Delta m_{ij} = \left(\psi_{ij} + \varphi_{ij} - \mu \right) \cdot m_{ij} \cdot \Delta t \tag{13}$$

$$m_{kh} = \frac{m_{ij}}{2} \cdot \frac{volume_k}{volume_i} \quad k = \left\{ i - 1, i + 1 \right\} \tag{14}$$

$$f_{mk} = f_{ij} + \delta \tag{15}$$

Table 4
Environment and subspaces–equations.

$$\theta_i^v = \left(\sum_{k=p_{0i}}^{p_{Li}} \sum_{j=1}^{n_k} mass_j \cdot \frac{\psi_{kji}}{volume_k} \right) \cdot volume_i \cdot \Delta t \quad (16)$$

$$n_i(t+\Delta t) = n_i(t) - \theta^v - \theta^s + D \cdot \left(1 - M^-\right) + M^+ \quad (17)$$

$$T = \sum_{i=1}^{\Sigma} \sum_{j=1}^{n_i} \frac{\xi \cdot m_{ij}}{volume_i} \quad (18)$$

$$n_z = \frac{T \cdot volume_z}{mass_z} \quad (19)$$

Table 5
State-variable model—notation.

i,f	size group and trophic mode of a module
$\max UV_{if}$	maximum prey mass intake rate per unit of predator mass, defined as in Eq. (11), Table 2
$[v_0, v_L]$	range of size classes on which species v_{if} preys upon
β_{if}	water clearance rate, defined as in Eq. (9), Table 2
$0 < \gamma_0$	yield
δ_{jk}	biomass density of prey of species v_{jk} θ_{ik}^v loss rate per unit of cell mass due to predation
μ	metabolic loss rate
v_{if}	state-variable model module (species)
π_{ij}	preference factor for predators of size class i for prey of class j, defined as in Eq. (12), Table 2
φ_{if}	nutrient uptake rate per unit of cell mass
ψ_{if}	prey uptake rate per unit of cell mass
ψ_{ifjk}	mass uptake rate per unit of predator weight for prey of size group j and trophic mode k

Table 6
State-variable model—equations.

$$m_{if}(t+\Delta t) = m_{if}(t) + \left(\psi_{if} + \varphi_{if} - \theta_{if}^v - \mu\right) \cdot m_{if}(t) \cdot \Delta t \quad (20)$$

$$\psi_{if} = \gamma_0 \cdot \sum_{j=v_0}^{j=v_L} \sum_{k=0}^{k=32} \psi_{ifjk} = \gamma_0 \cdot \sum_{j=v_0}^{j=v_L} \sum_{k=0}^{k=32} \left(\frac{\beta_{if} \cdot \pi_{ij} \cdot \delta_{jk}}{1 + (\beta_{if} \cdot \pi_{ij} \cdot \delta_{jk} / \max UV_{if})} \right) \quad (21)$$

$$\theta_{if}^v = \sum_{j=s}^{l} \sum_{k=2}^{32} \psi_{jkif} \quad (22)$$

distributed in bell-shaped fashion (Fig. 5) around the optimal size ratio r (Eq. (12), Table 2). Prey are consumed irrespective of their feeding mode. That is, pure phagotrophs are eaten with the same likelihood as pure osmotrophs.

At each time step, an individual gains mass according to its osmotrophic and phagotrophic intake, and loses mass due to metabolic costs at a constant rate μ (Eq. (13), Table 2). The rate of metabolic loss is assumed to be a fixed fraction of body mass across all species.

If the mass m_{ij} of an individual drops below $(1/2) \cdot mass_i$, the organism dies of starvation. In this case, all the remaining mass is immediately reconverted into the inorganic nutrient pool. If the mass reaches $2 \cdot mass_i$, the organism reproduces by duplication. In the standard case, two new cells are formed with half the mass of

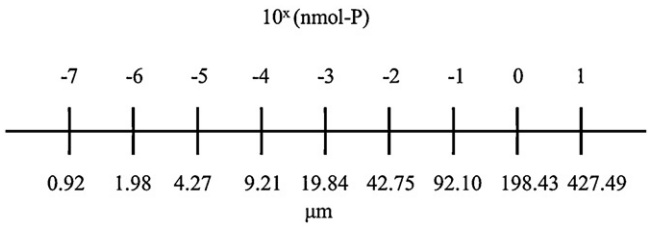


Fig. 2. Range of cell sizes (diameter) and corresponding average masses.

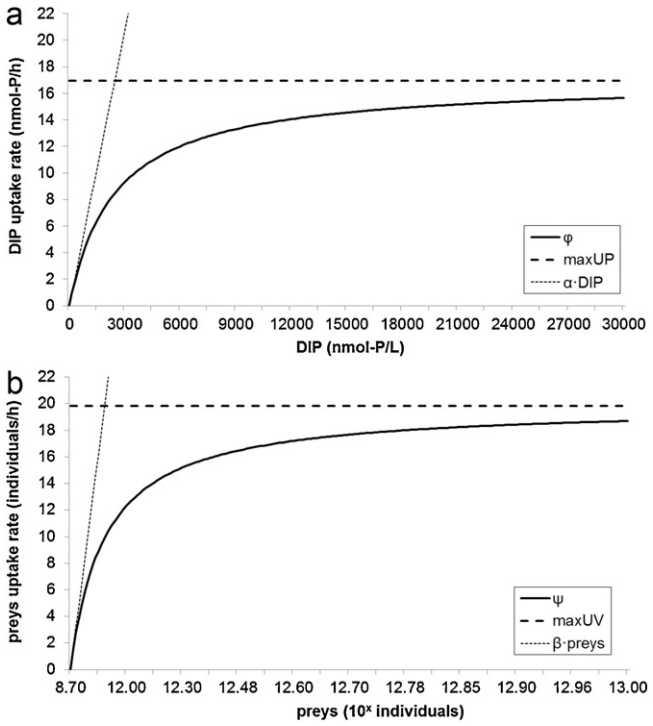


Fig. 3. Examples of food intake rates: osmotrophy and phagotrophy.

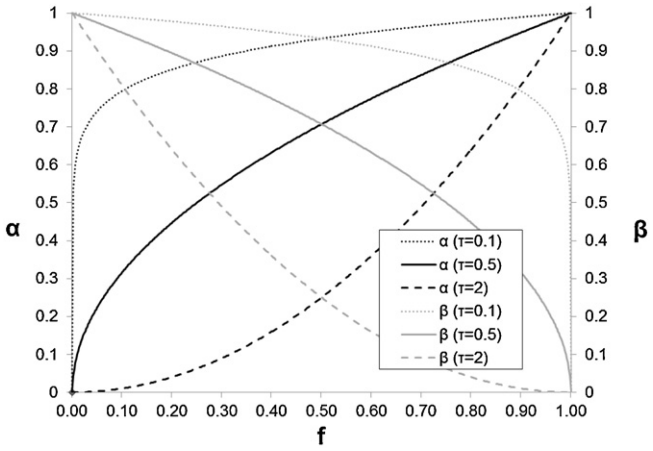


Fig. 4. Effect of parameter τ on resource use efficiency $\alpha = k \cdot (1-f)^\tau$, $\beta = k \cdot f^\tau$, $k = 1$.

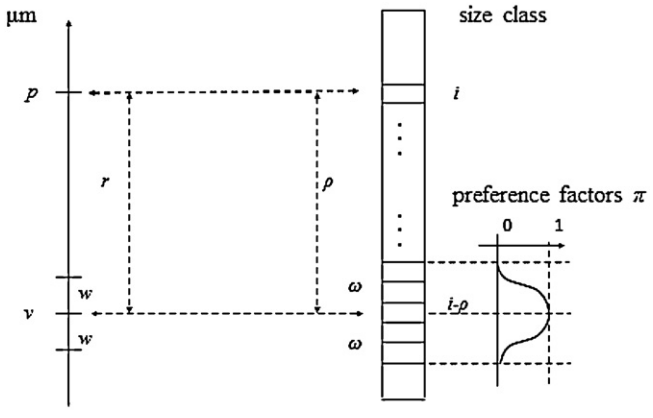


Fig. 5. Visualisation of predator–prey size and class relationship.

θ^v=0, m=0
while $(m < \theta_i^v)\&\&(n_i > 0)$
pick random integer number $r \in [0, n_i]$
remove agent r from class i
$\theta^v = \theta^v + 1$
$m = m + mass_{ir}$
$n_i = n_i - 1$

Fig. 6. Iterative procedure to calculate the number of individuals killed due to predation.

the parent cell. Namely, the new cells are initialised with a weight equal to the standard mass $mass_i$ of its size class. The new cells inherit the trophic mode of the parent. However, occasional genetic mutations may alter the traits (size and foraging mode) of the duplicated individuals.

The probability of mutation $mutRate \leq 1$ is a fixed system parameter. At every duplication event, a random number $rand \in [0, 1]$ is sampled. If $rand < mutRate$, the new individual undergoes with equal probability mutation of either the size or the feeding mode.

If a new individual undergoes a mutation in size, it will join with equal probability either the next smaller or the next larger size class (Eq. (14), Table 2). Eq. (14) accounts for the different volumes of the subspaces of origin and destination of the mutant, and scales the mass of the mutated individual up or down to keep the total phosphorous density δ_P constant.

If a new individual undergoes a mutation in trophic mode, the change δ in the parameter f_{ij} occurs within a limited range $[-\sigma, \sigma]$ from the mother trait (Eq. (15), Table 2), where σ is a system parameter (Table 7).

3.2. Subspaces

Each size group i is modelled within a sub-space of the overall environment. The volume ($volume_i$) of this sub-space is calculated as in Eq. (1), and kept constant throughout the simulation. The two main features of a subspace are its volume and the total biomass density of the hosted population.

In each time step, predation from other size classes may lead to mortality. The biomass θ_i^v of size class i eaten by predators of a particular size class follows Holling Type 2 curves (Eq. (6), Table 2). Summation over all predator classes gives the total amount eaten, θ_i^v (Eq. (16), Table 4). Individuals of a prey class are killed randomly until the number of individuals (θ^v) corresponds to the killed biomass (θ_i^v) (Fig. 6).

At the end of every time step Δt, the population size n_i of class i is updated (Eq. (17), Table 4). Eq. (17) takes into account the number of individuals dead due to starvation (θ^s) the number of new individuals created by cell duplication events (D), and the number of mutants lost to ($D \cdot M^-$) and acquired from (M^+) neighbouring classes. The size class biomass density is then recalculated as in Eq. (2).

3.3. Environment

The environment is composed of the Σ subspaces, where the different size groups and the DIP pool are modelled (one subspace for each size group). The environment is assumed to have uniform density in terms of spatial distribution of the populations and DIP content.

The DIP pool is depleted by the activity of the mixotrophs and osmotrophs, and is replenished by the excretions, detritus, and dead bodies produced by the Σ populations. The only direct interaction between populations is given by the predation of large

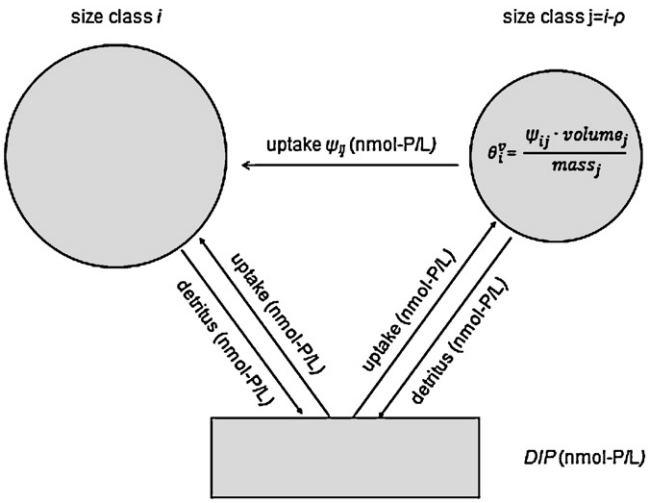


Fig. 7. Flow of biomass between two sample classes and the DIP pool. The phagotrophs and mixotrophs of size class i prey upon the individuals of class j (predator–prey ratio is ρ). The total biomass intake of the predators of class i is ψ_{ij}, corresponding to θ^v class j individual killed. Osmotrophs and phagotrophs of the two classes consume DIP. The DIP pool is refilled by the detritus, excretions, and dead bodies produced by the two classes.

individuals on smaller organisms. Fig. 7 visualises the biomass flow within the system for two sample species.

In biological systems, spatial heterogeneity allows species to survive in some areas when unfavourable conditions may lead to their extinction elsewhere. The surviving populations may then recolonise the empty niches and thrive when conditions change. An extra procedure was designed to simulate the possible reintroduction of locally extinct species.

The additional procedure introduces individuals of a randomly picked size class at fixed time steps. If conditions are favourable, the new individuals form a stable population. This process simulates occasional invasions of alien species in ecological subsystems. It works as follows: each living individual is "taxed" of a small fraction ξ of its body mass (Eq. (18), Table 4). This tax simulates the loss of individuals that moved to neighbouring regions outside of the modelled area. It is then used to create n_z new members of a randomly selected size class z (Eq. (19), Table 4), simulating the immigration of individuals from contiguous areas. The foraging mode of these new agents is randomly initialised.

4. State-variable model

To evaluate the reliability of the proposed modelling approach, two conditions need to be checked: that the predictions on the emerging food web structure are biologically realistic, and that they are not affected by computational artefacts.

Unfortunately, accurate quantitative descriptions of pelagic microbial communities are still lacking. Yet, qualitative evaluations on the plausibility of the model predictions are possible.

To ascertain the presence and extent of computational artefacts, the results of the individual-based model are compared with those of an equivalent state-variable model. If the differences are large, the results of the two models will have to be treated with caution until the issue is further resolved. If the two models yield similar predictions, the results can be assumed to be independent of implementation issues. In case the two models perform comparably, it will also be possible to use them interchangeably according to the needs.

The state-variable model is composed of a matrix of $\Sigma \times 32$ modules, dividing the food web into Σ size classes and 32 classes of feeding modes. The Σ size classes correspond one-by-one to

Table 7
Standard settings for the system parameters of the individual-based (IBM) and state-variable (SV) models.

Parameter	Symbol	Value	Model
Main loop			
total phosphorous concentration	δ_P	500 (nmol-P/L)	IBM/SV
number of size groups	N_s	32	IBM/SV
max number of individuals per group	N	10000	IBM
mass smallest individual	$mass_1$	$1.6{\cdot}10^{-8}$ (nmol-P)	IBM/SV
diameter smallest individual	$diam_1$	0.5 (μm)	IBM/SV
mass increment factor between successive size groups		2	IBM/SV
nutrient affinity smallest osmotroph (per unit of biomass)	α_0	$0.7\left(\frac{L}{h}\cdot\frac{1}{nmol-P}\right)$	IBM/SV
max uptake rate smallest osmotroph (per unit of biomass)	$\max UP_0$	$0.16\left(\frac{nmol-P}{h}\cdot\frac{1}{nmol-P}\right)$	IBM/SV
water clearance rate smallest phagotroph (per unit of biomass)	β_0	$0.0008\left(\frac{L}{h}\cdot\frac{1}{nmol-P}\right)$	IBM/SV
max prey biomass intake rate smallest phagotroph (per unit of biomass)	$\max UV_0$	$3.125\left(\frac{nmol-P}{h}\cdot\frac{1}{nmol-P}\right)$	IBM/SV
yield	γ_0	0.3	IBM/SV
mixotrophy trade-off	τ	0.3	IBM/SV
optimal predator–prey ratio	ρ	4 (6 size classes)	IBM/SV
width predator–prey size window	ω	1.26 (1 size class)	IBM/SV
mutation rate	$mutRate$	0.02	IBM
width of feeding mode mutation	σ	0.1	IBM
general loss rate	μ	0.001 (1/h)	SV
metabolic loss rate	μ	0.001 (1/h)	IBM
Initialisation procedure			
fraction of total P into DIP		0.001	IBM/SV
"noise" in mass distribution amongst classes		0.1	IBM/SV

the size classes used in the individual-based model, whilst the 32 feeding modes cover at fixed steps of 0.03125 the range from pure osmotrophy (0) to pure phagotrophy (1).

The increment of biomass is determined for each module (species) ν_{if} by the nutrient and prey uptake, loss due to predation, and metabolic losses (Eq. (20), Table 6). Analogously to the individual-based model, nutrient and prey uptake as well as loss due to predation follow Holling Type 2 functional responses (Eq. (5), Table 2, and Eqs. (22) and (23), Table 6, respectively).

The differential equation of the state-variable model (Eq. (21), Table 6) is integrated using the MATLAB ODE23 implementation of the explicit Bogacki and Shampine third-order Runge-Kutta method (Shampine and Reichelt, 1997).

5. Differences between individual-based and state-variable model

The equations defining the dynamics of the two models are the same. They differ only in the fact that in the individual-based model, they apply to one individual, whilst in the state-variable model, they apply to the whole biomass of the functional group. This difference accounts for the fact that the agents are individuals in the former and whole species (modules) in the latter.

The trait-based model discretises the biomass of one size class into several units (the agents), whilst the state-variable model discretises the trophic structure of the size classes into 32 functional groups. That is, in the state variable model, the 'feeding mode' is discretised into regularly spaced steps within each of the size classes.

The above differences can be minimised choosing large population sizes, and partitioning the functional groups of the state-variable model into finely divided classes of feeding modes. In both cases, the correct parameterization needs to trade-off representation power for efficiency.

In the state-variable model, biomass is a continuous variable for each size group. As a result, the mass content of a group may happen to drop below the mass equivalent of one organism. In this case, unless explicitly stated in the model implementation, the species does not become extinct. In the individual-based model, the biomass is discretised in individual units. Once its biomass is below $(1/2)\cdot mass_i$ it dies, and once the last individual has died, the species is lost. This dissimilarity makes the populations of the state-variable model more robust to environmental fluctuations. This is one of the fundamental differences between individual-based and state-variable representations, and is independent of the implementations chosen in this study.

The discretisation of the biomass in individual units in the individual-based model has also consequences on the effects of predator–prey interactions. That is, in a state-variable model a predator may consume an amount of mass equivalent to a fraction of a prey (e.g. a lion eats half a gazelle); the remaining fraction of prey still survives and contributes to the total biomass of its species. In an individual-based model, the partly eaten prey cannot survive, and the remains are usually discarded as detritus. As a consequence, the activity of predators has a greater impact on the prey population in individual-based models. In the proposed individual-based model, the discarded remains correspond to at most a fraction of one individual (see Eq. (16), Table 4). Even though this amount may be considered small in a large population, in a small population or over several time steps, it might lead to appreciable discrepancies between the predictions obtained using the individual-based and the state-variable model.

In the proposed study, genetic mutations are used only in the individual-based model. This feature is expected to blur the shape of the emergent population structure. It was created to promote innovation in species, and partly compensate for the likelihood of extinction events in individual-based models. Mutations may in fact reinstate extinct species, reducing the loss of population diversity in individual-based systems.

6. Experimental tests

This section describes the experimental settings and results.

6.1. Experimental settings

For the parameters of the two models, the standard setting and the dimensions are given in Table 7.

Initially, 0.1% of the total phosphorous concentration constitutes the DIP pool, and the rest is shared amongst the size groups. This scenario simulates an oligotrophic environment, which is the typical state of pelagic ecosystems.

The maximum hourly phosphorous uptake rate for the smallest osmotroph ($\max UP_0$) is set equal to one sixth of the cell's weight, yielding a duplication time of six hours in absence of food limitation. The maximum prey uptake rate for the smallest phagotroph ($\max UV_0$) is set equal to 200 individuals per cell per hour. This quantity is converted into units of prey mass per unit of predator mass as follows:

$$\max UV_0 = \frac{m_v}{m_p} \cdot 200 = \frac{m_v}{m_v \cdot 2^{\rho}} \cdot 200 = \frac{1}{2^{\rho}} \cdot 200 \quad (23)$$

where m_p and m_v are the weights in phosphorous of respectively the predator and the prey, and ρ is the size ratio of predator to prey (henceforth called predator–prey ratio).

The above values were set in accordance with experimental observations on the maximum nutrient affinity (Lignell et al., 2013) and uptake rate (Kemp et al., 1993) for pure osmotrophs, and maximum clearance rate (Lignell et al., 2013) and prey uptake rate (Vaquè et al., 1994) for pure phagotrophs. Other parameters like the mixotrophy trade-off and predator–prey ratio are at present not known precisely (Stoecker, 1998), and were set heuristically. The sensitivity of the predictions to these less understood parameters is the object of a separate study.

Four groups of experiments were run to investigate the sensitivity of the predictions to the choice of the main model parameters. In all cases, 10 independent runs were executed per model configuration. For each run, the system was let to evolve for 10 years with time steps of 5 min. At the end of the evolution period the emerging populations were monitored for one additional year, where the biomass distribution was sampled every five days. A final map of the average biomass distribution amongst size classes and feeding modes was generated for the last year. This map represents the model prediction.

The code was implemented in C++, and the tests were run on an Intel Core2 Duo CPU, 2.54 GHz speed, 4GB Ram, and Windows 7 32-bit OS. In all cases unless explicitly stated, the execution time was less than 20 min per run.

6.2. Sensitivity to initialisation procedure

The first set of experiments was designed to test the sensitivity of the model predictions to the initialisation of the microbial community. Three initialisation procedures were tested.

The first procedure (henceforth named '*deterministic–deterministic*') distributes the biomass uniformly amongst the size classes, and uniformly amongst the individuals within the size classes. That is, each agent is initialised with a weight in phosphorous equal to the class standard $mass_i$ (Eq. (3)). This uniform distribution of biomass amongst the logarithmically spaced size groups simulates the natural state of planktonic systems (Sheldon et al., 1972).

The second procedure (henceforth named '*deterministic–random*') distributes the biomass uniformly amongst the size classes, and initialises the mass of each individual randomly within the interval $[minmass_i, maxmass_i]$ Section 3.2).

The third procedure (henceforth named '*random–random*') distributes the biomass randomly amongst classes, and randomly amongst the individuals. For each class, the initial biomass is drawn with uniform probability within ±10% of δ_P/Σ.,here δ_P and Σ are respectively the total phosphorous in the system, and the number of size classes (Section 2.2).

Fig. 8 shows the statistical mean of the predictions obtained in 10 independent runs for each of the three cases. The microbial community is divided into 32 size classes (Table 1), each characterised by a specific diameter and mass (see Section 3.2 and Fig. 2). For each size class, the emergent population is grouped into 32 classes according to the feeding mode. The map represents thus a 32×32 matrix of size and foraging mode classes. The mass distribution is plotted versus the average cell mass of the size classes and the feeding mode.

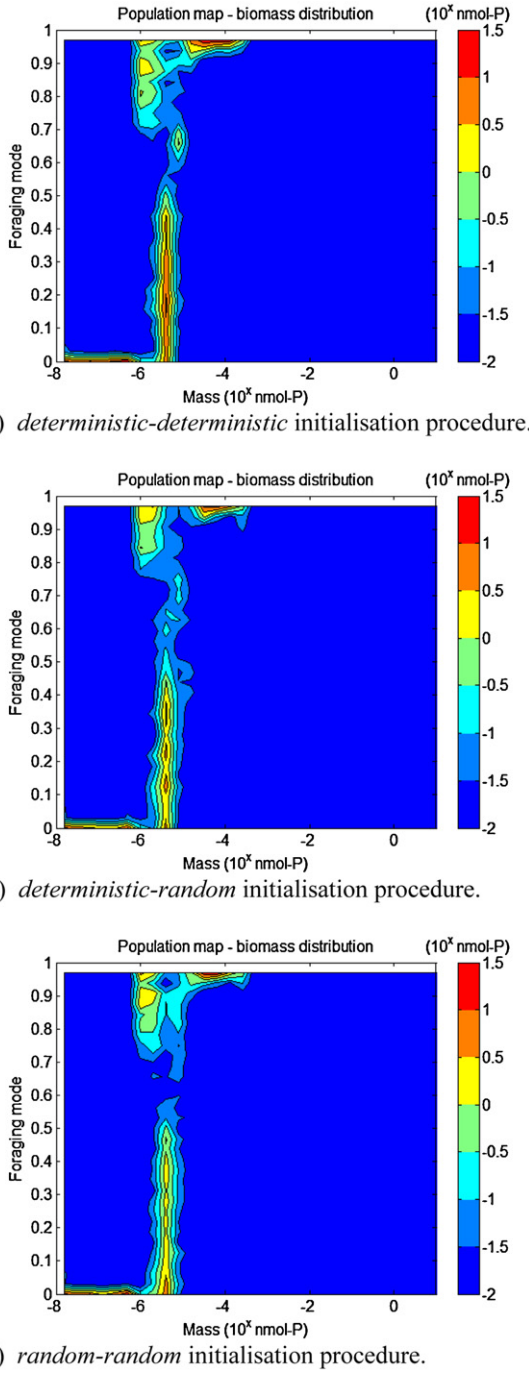


Fig. 8. Comparison of initialisation procedures. Model parameters as in Table 7.

The plots show very similar results, with stable populations of mixotrophs emerging roughly within the 2–4 μm diameter range. The evolved mixotrophic populations are in the size range of bacteria (0.2–2 μm) and nanoflagellates (2–20 μm).

Populations of pure osmotrophs emerge in a size range within the smallest allowed diameter (0.5 μm) and 3 μm circa.

Two populations of pure phagotrophs appear: one of ca. 2–3 μm diameters, and the other of ca. 4–13 μm diameters. The latter population is within the size range of dinoflagellates (5–2000 μm). The group of largest phagotrophs preys on the microbial communities in the 2–4 μm range (the predator–prey ratio was set to 4), whilst

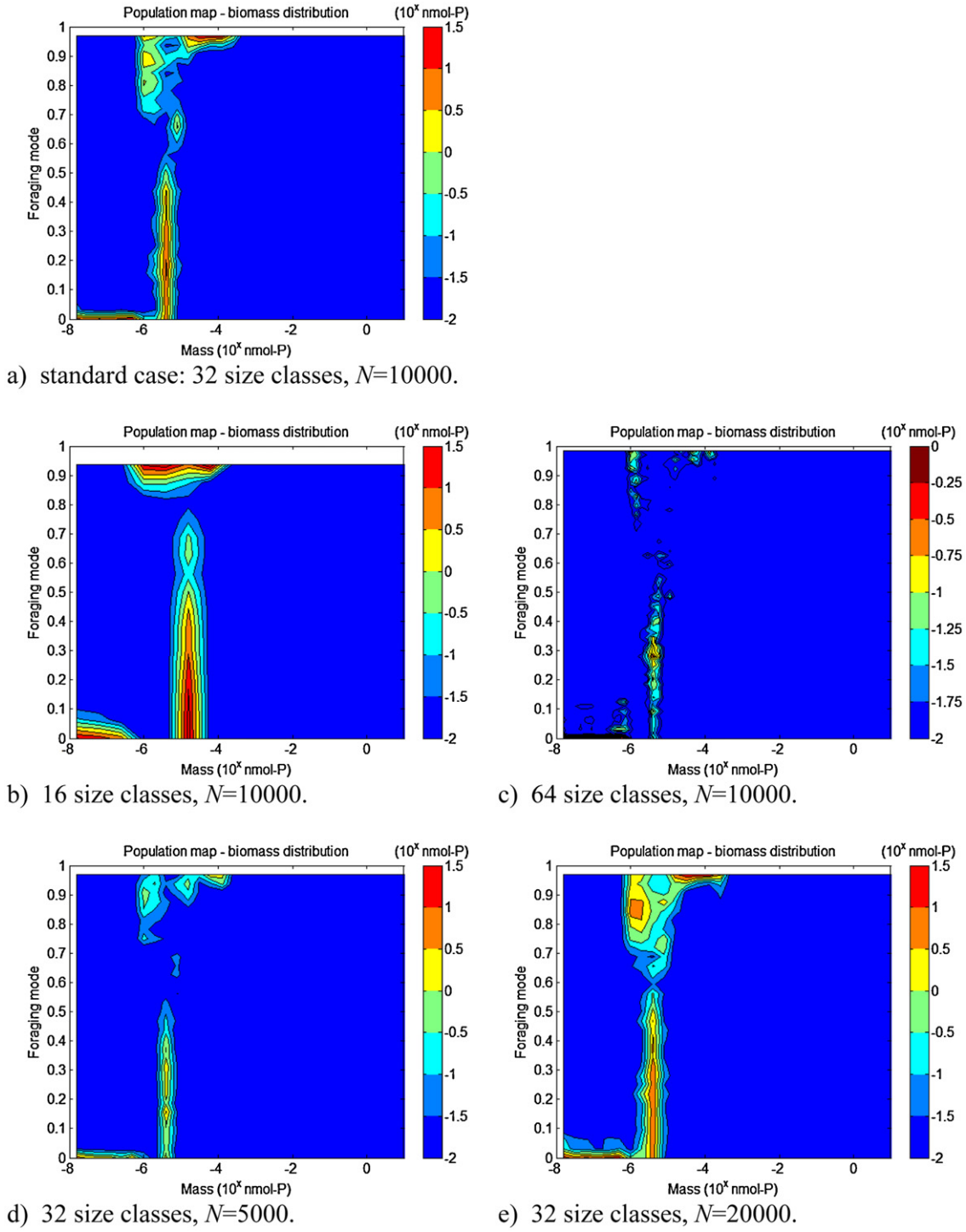


Fig. 9. Sensitivity of the results to the variation of the number and maximum population size of the size classes. Model parameters as in Table 7, the *deterministic–deterministic* initialisation procedure is used.

the population of smaller phagotrophs preys on the smallest classes of osmotrophs.

The significance of the differences between the maps of biomass distribution obtained using the three initialisation procedures was analysed pixel-by-pixel using the Mann–Whitney *U*-test. The analysis confirmed the high similarity of the results. The two most dissimilar maps were those obtained using the *deterministic–deterministic* and *deterministic–random* methods, where the biomass values differed significantly in 13 pixels (1.27% of total map).

Given the substantial equivalence of the different initialisation routines, the *deterministic–deterministic* method will be used as the standard procedure henceforth.

6.3. Sensitivity to model configuration

The second set of experiments (Fig. 9) was devised to investigate the robustness of the predictions to variations of model parameters such as the number of size classes (Σ), and the maximum class size (N).

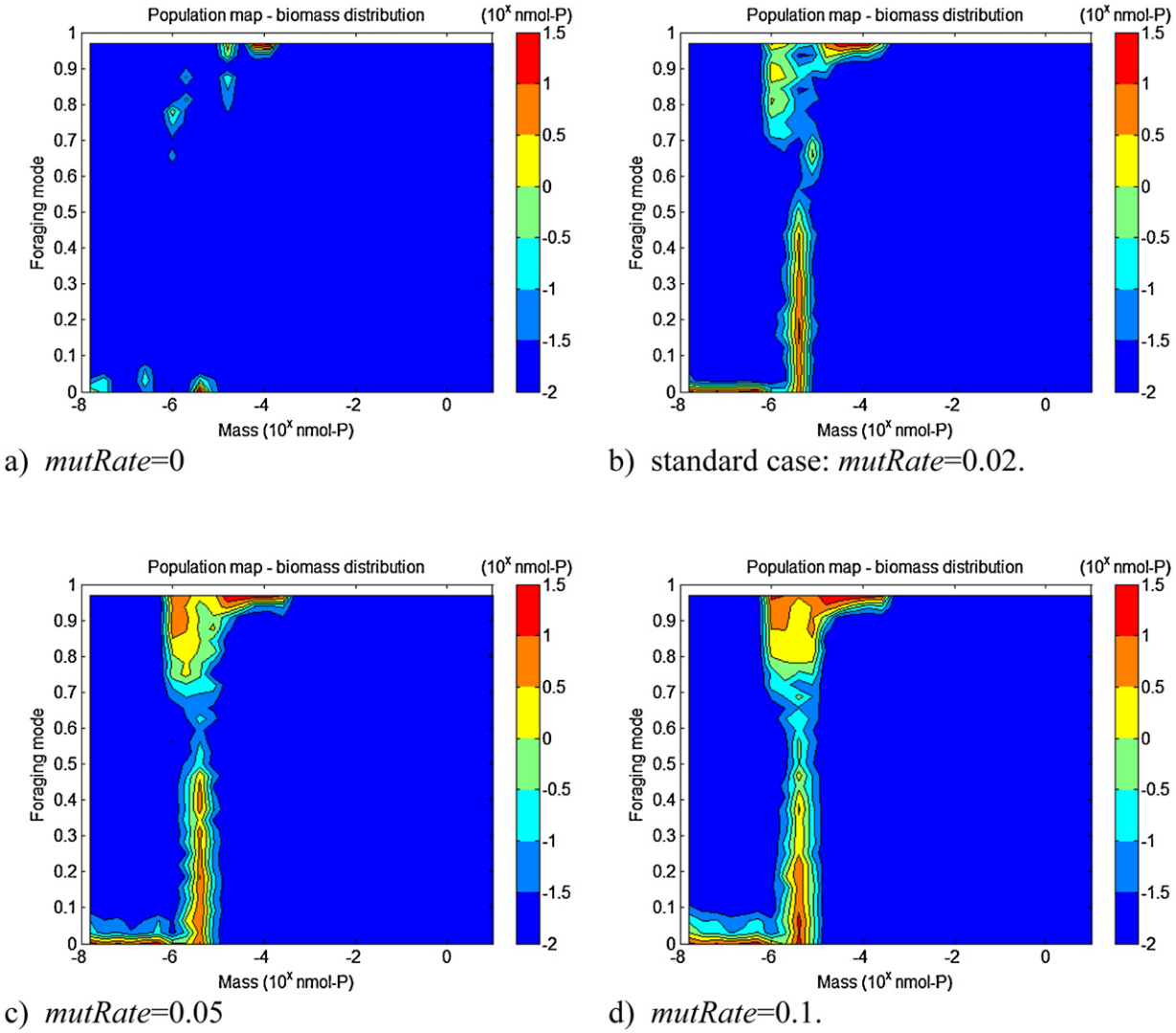


Fig. 10. Sensitivity of the results to variations of the mutation rate. Model parameters as in Table 7, the *deterministic–deterministic* initialisation procedure is used.

The emergent populations are substantially similar regardless of the number of size classes. Due to the lower resolution, the map relative to the case $\Sigma = 16$ has a better delineated shape. As Σ increases, the microbial community breaks down in an increasing number of smaller populations.

The relationship between the maximum population size N and the algorithm running time appears to be roughly linear. For example, enlarging N from 10000 to 40000 agents per size group increased the execution time from 20 min to over 90 min.

The use of larger populations reduced the risk of extinction for the individual species. This favoured the establishment of more variegate microbial communities in the tests involving the largest population sizes. A pixel-by-pixel comparison between the predictions found 43 (4.2%) significantly different pixels between the maps obtained using $N = 5000$ and $N = 10000$, 41 (4%) significantly different pixels between the maps obtained using $N = 10000$ and $N = 20000$, and 93 (9.1%) significantly different pixels between the maps obtained using $N = 5000$ and $N = 20000$. The significance tests were carried out using the Mann–Whitney U-test. The overall biomass distribution is, however, similar in all the cases, indicating also in this case robustness of the model to variations of the system parameters.

6.4. Effects of mutation and reintroduction of species

The third set of experiments was designed to assess the effects of the mutation (Section 3.2) and reintroduction (Section 3.4) procedures on the model predictions.

Mutation played a decisive role for the maintenance of population diversity (Fig. 10). Without mutation, mixotrophs disappear and the population clusters into three groups of pure osmotrophs and three corresponding groups of predators. As the mutation rate is increased, the plots show a progressively thicker band of mixotrophs establishing. The populations of pure osmotrophs and phagotrophs become also more broadly distributed.

The map obtained using the standard mutation rate (0.02) and those obtained using higher rates (0.05 and 0.1) differ significantly by 52 (5.07%) and 89 (8.7%) pixels respectively. In all the three cases, the distribution of the emergent population is similar.

If performed with sufficient frequency, the reintroduction procedure (Fig. 11) can compensate for the loss of species. However, it introduces a certain degree of 'noise' in the individual runs. The emergent biomass distribution is similar to the standard case.

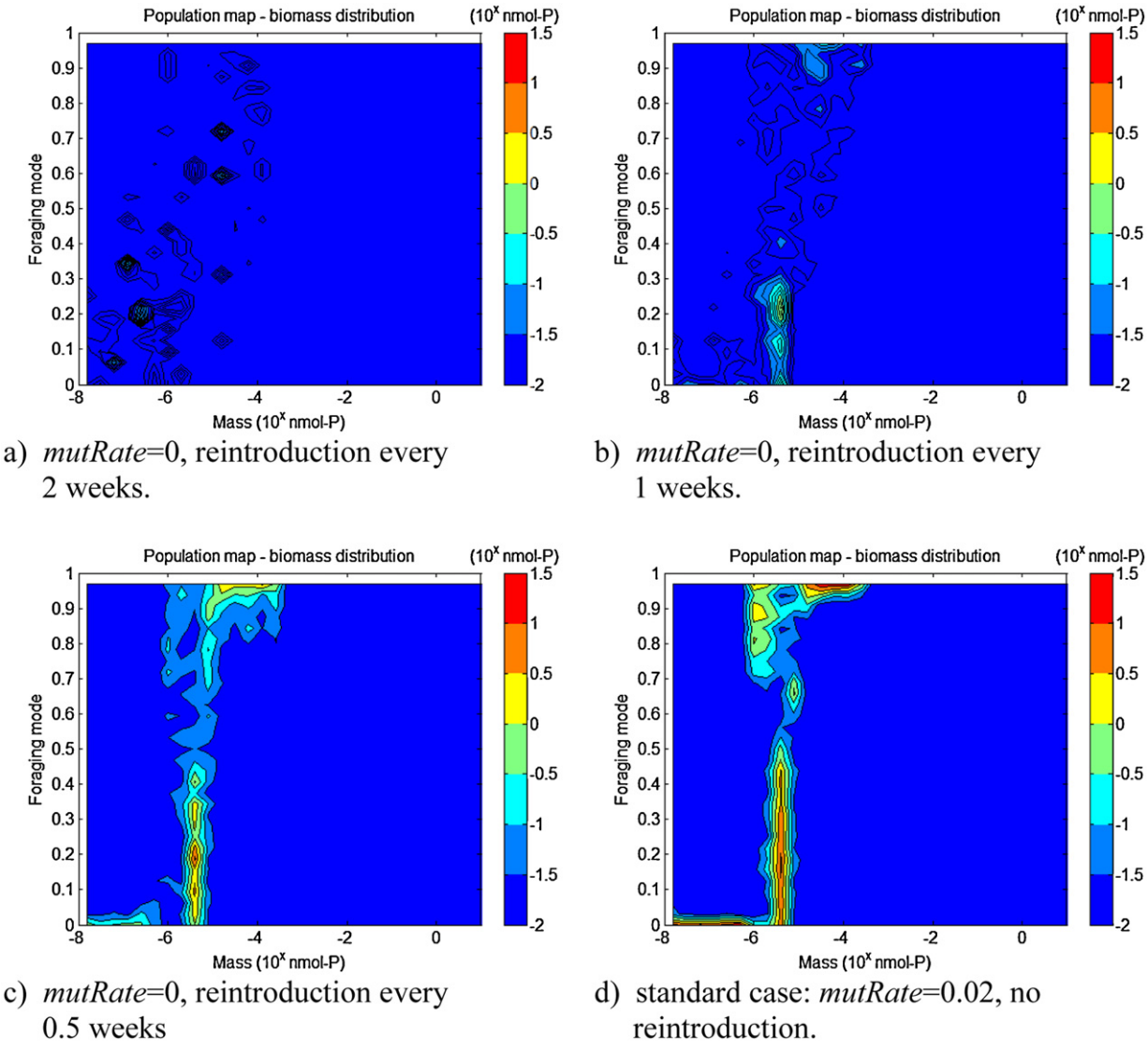


Fig. 11. Sensitivity of the results to variation of the reintroduction procedure. Model parameters as in Table 7, *deterministic–deterministic* initialisation procedure is used.

6.5. Comparison with state-variable model

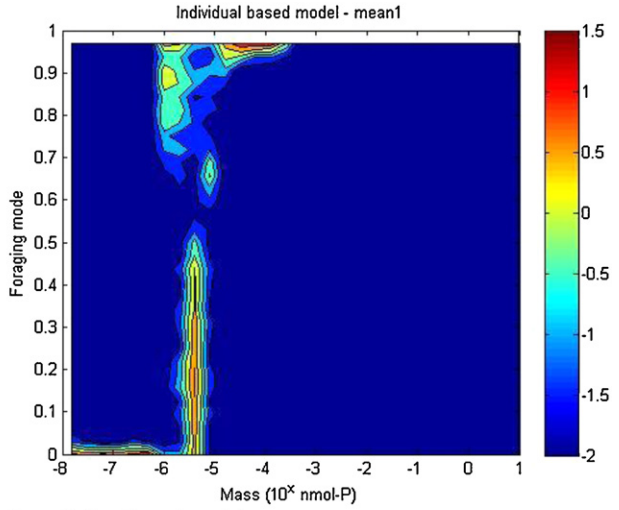
The fourth set of experiments concerns the comparison of the predictions obtained using the individual-based model with those obtained using the state-variable model. Following the results of the theoretical study presented in Section 6, the metabolic loss rate of the individual-based model was set equal to the general loss rate of the state-variable model (see Table 7). Good agreement was found between the predictions obtained using the two approaches (Fig. 12), with populations of mixotrophs, pure osmotrophs and phagotrophs emerging at the same size ranges.

7. Discussion

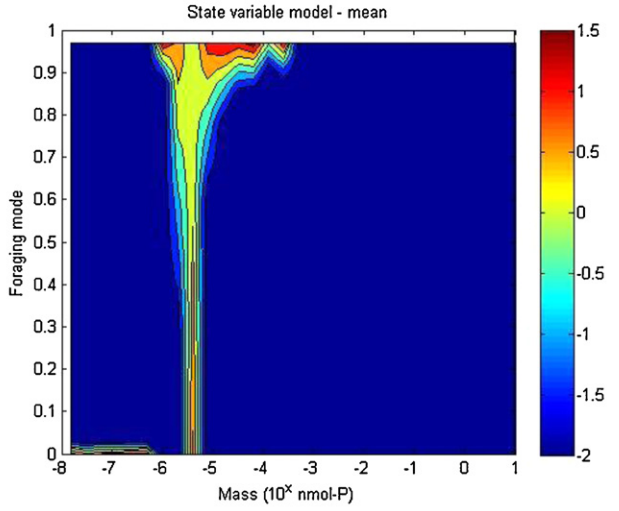
The Scaled Subspaces Method models the evolution of populations of largely diverse traits and density with the same degree of detail, eliminating the risk of demographic explosion of the most numerous species. In order to limit the population size, increasingly smaller-sized species are modelled in increasingly smaller spaces, in the same way microbiologists choose objectives of increasingly narrower field to observe increasingly smaller organisms on an optical microscope. This makes the proposed method intuitively easy to understand and visualise. Also, when we are interested in how organism strategies lead to emergent patterns in the topology of the population within the strategy plane (i.e. the cell size and trophic mode trait-space), it is important that biological representations are continuous and equally diverse over all size classes. As opposed to approaches that combine state variables and individual-based descriptions (Megrey et al., 2007), our Scaled Subspace Method allows this.

The Scaled Subspaces Method can be implemented in fast and compact software code. The effectiveness of the proposed method was demonstrated in an application of modelling a microbial food web.

Experimental evidence proved that the Scaled Subspaces Method generates consistent and realistic population distributions. It is thus a viable alternative to trait-based approaches using super-individuals (Scheffer et al., 1995; Woods and Onken, 1982; DeAngelis et al., 1993) to deal with the problem of unmanageably large populations. With respect to the latter approaches, the proposed method may be conceptually and computationally more simple, as it does not involve bookkeeping efforts (e.g. splitting and merging of super-individuals) to maintain the population within given boundaries. This also minimises the possibility of introducing computational artefacts with respect to biodiversity in the modelling results.



a) Individual-based model.



b) State-variable model.

Fig. 12. Comparison between the predictions obtained using the individual-based and state-variable models. Model parameters as in Table 7, the *deterministic–deterministic* initialisation procedure is used for both models.

There are similarities between the single individuals used in the Scaled Subspaces Method and super-individuals. Agents modelled in small subspaces implicitly represent several individuals over the whole system. In this sense, every individual in the scaled subspaces can be seen effectively as a representative of many others. However, the representativeness (i.e. how many organisms an agent represents) of each individual is constant in the Scaled Subspaces Method, whilst it varies with the stochastic events in approaches using super-individuals. In the latter, it is often the case that several similar super-individuals of highly different size (e.g. one large and several small) coexist. Without the need of constant rearranging of super-individuals, the Scaled Subspaces Method allows one to model with uniform representativeness a large number of individual types. This makes the proposed approach a good candidate for modelling biodiversity at all trophic levels. The uniform detail in the representation of the species at diverse size scales makes the Scaled Subspaces Method particularly useful to model fractal-like biological systems, where self-similarity is repeated at largely different scales (Thingstad et al., 2010).

The comparison of the predictions given by Scaled Subspaces Method with those given by an equivalent state-variable model with high resolution in organism size and foraging mode ensured the independence of the results from implementation issues. The test also gave the occasion to analyse the expected differences between trait-based and state-variable models.

The Scaled Subspaces Method implicitly assumes the environmental conditions to be spatially uniform, meaning that the focus of the model can be narrowed down to a small area without loss of generality. This was assumed for the simplified representation of the marine microbial food web used in this study. In other cases this assumption may not be true. A possible way to circumvent this problem would be to simulate the evolution of communities of species in different environments in parallel. Each species would be defined in a subspace where the environmental conditions might be considered uniform, and plausible rules of interaction should be devised for those species that are capable of migrating and operating across different subspaces. The feasibility of this solution should be weighed against the computational overheads that it would imply.

The scaling of the subspaces was here based on the total biomass in the closed system. In cases where the overall biomass varies with time, the approach is still applicable as long as the change is within reasonable bounds. In extreme cases, where the total biomass changes of several orders of magnitude, the size of the subspaces could be adjusted at periodic intervals, or when one or more populations reach a pre-set upper or lower size threshold. Such adjustments are possible as long as the fluctuations of nutrients are not too frequent. In particularly variable ecosystems, where the total biomass changes rapidly of several orders of magnitude, other approaches such as the use of super-individuals are computationally more efficient.

In general, the scaling of the subspaces may take into account other criteria than the potential for population abundance. For example, where some species have a greater potential for heterogeneity (e.g. they have more traits), the scaling of the subspaces may take into account additional or alternative considerations, such as the possibility of population diversity.

Beyond the uniformity of the environmental conditions, the only other assumption made in the Scaled Subspaces Method is that the effect of the interactions of each species with the other species and the environment can be computed from the population (biomass) density. The details of the interactions may be expressed analytically as in the proposed application, or probabilistically on an individual-to-individual basis. The trait-based paradigm allows the representation of any level of high intra-class and inter-class diversity. As long as the impact of the populations on the ecosystem can be expressed in terms of their population density, communities of species as heterogeneous as ants and elephants can be simulated.

One of the main difficulties in modelling ecosystems is to simulate a large and virtually unbound world in a limited and closed system. In this sense, closed ecosystem models are more similar to laboratory set ups than natural environments. In such kind of scenarios, with relatively small population numbers and constant environmental conditions, the extinction of all but a few species is likely. In nature, the distribution of organisms is inhomogeneous, and individuals migrate in and out of local environments. In the presented application of the Scaled Subspaces Method, we wanted to simulate mechanisms found in the open sea where abundant species disperse to neighbouring areas, and where other species enter and re-colonise local environments when conditions are favourable. As an extension for the new method, the reintroduction procedure was designed for this purpose. Mutation also plays a role in reinstating populations and balancing the overall distribution of species, since some of the offspring of the most abundant classes mutate into similar species that got extinct. Mutants occur naturally, and they may be able to colonise vacant niches. Genetic mutations, periodic reintroduction of species, and the use

of large populations were shown to be effective policies against the extinction of species in our model. Nonetheless, state-variable approaches might offer better protection from group extinctions when the populations are known to undergo large oscillations in size. In general, the maintaining of population diversity in closed and bound environments is a common problem to all individual-based discrete approaches.

Mixotrophs seem more at risk of extinction in our model than pure foraging specialists. However, this result was found to depend on the particular value chosen for the mixotrophy trade-off τ (not shown). In general, the issue of the sensitivity of the model predictions to variations of the biological parameters has not been addressed in this study. Many of the parameters listed in Table 7 and allometric relationships defined in Tables 2, 4 and 6 are only best estimates. Sensitivity to biological parameters is subject to another study, where the proposed model is used to help understand the effect of these variables on the structure of the emerging food web.

It can be argued against the biological realism of the mutation and reintroduction procedures used in this study. We believe that they are reasonably "natural" as long as open marine environments are to be modelled. The rate and extent of the mutation and reintroduction events used in this study may possibly not be biologically accurate, and the model may conceivably be parameterized more realistically. Indeed, more than suggesting a fixed set up, our tests aimed to highlight the role of mutation and reintroduction on the evolution of the ecosystem modelled.

In general, this paper presented a first documentation of the applicability and reliability of the Scaled Subspaces Method in case of microbial food webs, which are fundamental to all ecosystems. Microbial food webs are particularly well suited for the Scaled Subspace Method due to their self-similarity and different densities at many scales. The precise boundaries and details of the methods range of application need to be thoroughly investigated.

8. Conclusions and indications for further work

This paper presented the Scaled Subspaces Method, a new trait-based approach that addresses the problem of demographic explosion in models composed of populations of inhomogeneous density. The method was applied to a model of a pelagic microbial mixotrophic food web, where the population density of the species of smallest size is several orders of magnitude higher than the density of the largest species. For each size group, the individuals are monitored at different size scales. The smallest individuals are monitored at scales small enough to contain only a limited number of agents. With this we keep computational costs low, whilst still allowing equal diversification of species at all levels. Also, computational artefacts that may occur through bookkeeping and non-uniform representativeness in super-individuals, is avoided. It hence represents a beneficial alternative method to the super-individual approach for complex systems.

Experimental evidence shows that the proposed model produces biologically plausible and consistent predictions of biomass distribution in the foraging mode and cell size trait-space. Similar results were found for other settings of the biological parameters not documented in this paper. The predictions attained using the proposed individual-based model matched well those obtained using a classical state-variable model. This shows that the results are independent from computational artefacts and implementation issues, and allows using the two models interchangeably. The comparison of the two approaches was complemented by a thorough analysis of the differences between individual-based and state-variable representations.

The main issue concerns the possibility of extinction of species in the proposed method, which is inherent to all individual-based models, and does not depend on the representation method used in this study. The problem can be alleviated by simulating the creation of new individuals via genetic mutations, or by reintroduction of lost species. The frequency of the mutation or reintroduction events should take into account the need to create and support biological diversity as well as biological plausibility. Future work should investigate the relationship between the mutation and reintroduction rate and population diversity.

Using large populations helps to prevent group extinctions. However, the computational overheads of managing a large number of agents need to be taken in account when setting the size of populations. State-variable or individual-based approaches based on super-individuals might be more robust to group extinctions than the proposed method. Further work should test this hypothesis and investigate the "breaking points" (i.e. extinction events of entire groups) of the population diversity for the different approaches.

We found that mixotrophs in our model could successfully coexist with foraging specialists under a range of parameter settings. This result agrees well with the reported high abundance of mixotrophs in pelagic environments (Zubkov and Tarran, 2008; Hartmann et al., 2012). We hold that the Scaled Subspaces Method represents a novel, realistic and useful tool to the field of ecological modelling.

Acknowledgement

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