A mass-balanced pelagic ecosystem model with size-structured behaviourally adaptive zooplankton and fish

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ABSTRACT

Mesozooplankton is a highly diverse group of organisms ranging from very small to large herbivorous, omnivorous or predatory forms. However, most aquatic ecosystem models typically contain only one or two state variables which represent all mesozooplankton forms and specify their role in marine food webs. We have extended an existing mass-balanced marine ecosystem model to include a wide range of mesozooplankton size-classes and species growing from small to large, and maturing at different size. The model includes a dynamic pool of fish with a fixed mortality rate as a closure term of the model, and mechanistic expressions for fish predation. The zooplankton consumes phytoplankton and smaller zooplankton, and responds adaptively to the instantaneous local rates of growth and predation by migrating towards more profitable habitats. We run the model for long time in a stable and repetitive diel light cycle, and explore the emerging ecosystem structure and complexity. In the stable environment the presence of fish has strong structuring effects over the size-structure of mesozooplankton, but little influence on phytoplankton because the total biomass of mesozooplankton remains relatively stable over the fish cycles. The inclusion of adaptive and flexible behaviour leads to emergent effects of multiple predators; the removal of intra-guild predation among zooplankton result in low fish abundance because zooplankton spend more time in deeper habitats. The model reveals persistent spatial and cascading behavioural interactions and is a step towards a mechanistic and adaptive representation of the upper trophic levels in ecosystem models.

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1. Introduction

One of the challenges in contemporary ecosystem theory and modelling is to integrate the classical biogeochemical cycling of energy and matter with evolutionary strategies and behavioural plasticity of organisms (Schmitz, 2010). Ecosystem topology is formed by a mixture of consumptive and non-consumptive interactions such as size structure and risk-sensitive behavioural responses (Heckmann et al., 2012). Coupling adaptive risk-sensitive behaviour and size structure to ecosystem function has been pointed out as a key missing link in the integration of evolutionary and ecosystem ecology (Schmitz et al., 2008).

It is recognized that ocean ecosystem and biogeochemical models need to represent some diversity of organisms to be representative of real systems (Follows and Dutkiewicz, 2011), and so far

most progress in this 'trait-based' direction has been made in representing microbial communities. Earth system models now have started to characterize microbial organisms by a range of randomly generated traits rather than in bulk functional groups (Barton et al., 2010; Follows et al., 2007), and size-resolved ocean ecosystem models featuring mesozooplankton are now appearing (Ward et al., 2012). In models including zooplankton and fish, focus has been directed to the question of how to represent the size-resolution and life-cycles of organisms growing over orders of magnitudes from birth to maturation (deYoung et al., 2004).

Higher trophic levels such as mesozooplankton and fish are often not included in ecosystem models, but there is a growing awareness of the need to integrate the effects of climate with those of fishing, and to explore their interactions quantitatively. Ecosystem models with this aim are often referred to as end-to-end models (Fulton, 2010; Rose et al., 2010; St. John et al., 2010), and include a wide range of approaches to develop and understand fully coupled models from oceanography to fishing.

Adding representations of multicellular, stage-structured higher organisms with complex life cycles and behaviours to models of ecosystem dynamics involves a number of challenges. These organisms have swimming capabilities exceeding the vertical

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mixing, act more as risk-sensitive adaptive foragers than passive particles, grow orders of magnitude in size, and have shifting functional roles over their life cycle.

The potential of higher trophic levels to structure ecosystem functioning disproportionally relative to their low biomasses is well known in both terrestrial (Schmitz, 2010) and aquatic ecology (Frank et al., 2011; Pace et al., 1999; Verity and Smetacek, 1996). Fish may change pelagic nutrient cycles (Vanni and Layne, 1997) and in particular the presence of fish can completely alter the size-composition of zooplankton (Brooks and Dodson, 1965). The removal of planktivorous fish can be a remedy to lower phytoplankton densities in eutrophic lakes (Hansson et al., 1998). Even in large scale marine systems fisheries may have cascading effects all the way to phytoplankton and nutrient levels (Casini et al., 2008; Frank et al., 2011). Similar community shifts can also occur through physical pathways. For example, differences in light attenuation in marine fjords change the abundance and search efficiency of mesopelagic fishes (Aksnes, 2007; Aksnes et al., 2004). Such changes have implications for the whole ecosystem structure, with a switch in top predators from fish to jellyfish and corresponding shifts in zooplankton size structure (Eiane et al., 1999).

Pelagic predator–prey interactions are governed by risk-sensitive and state-dependent behaviours. The most conspicuous one is diel vertical migration which varies widely depending on community structures, the densities of predators, the environment (light in particular), and resources (Pearre, 2003). Some influential studies have shown how zooplankton can reverse their migration pattern from a normal (up during night) to an inverse cycle (up during day) if ambush invertebrates replace fish (light-dependent foragers) as the main predators (Ohman, 1990). In oceanic regions, the light cycles of moon phases govern the vertical distribution of euphausiids and propagate a strong structuring effect on small zooplankton, microbial communities and carbon-pathways in the system (Hernandez-Leon et al., 2001).

The processes listed above are essential in pelagic ecology, but very difficult to include in ecosystem models because they require both size-structure, adaptive life-histories and behavioural responses in the model (Carlotti and Poggiale, 2010; deYoung et al., 2010). At present, these elements are a major obstacle to the development of meaningful 'end-to-end' models (St. John et al., 2010).

Here we present a mass-balanced ecosystem model where focus is on the mesozooplankton group. We started out from the ecosystem model ECOSMO (Schrum et al., 2006a,b) derived to study the distribution of phyto- and zooplankton in the North Sea. We added a coupled fish compartment and extended the mesozooplankton module considerably. Organisms in this group span from about 0.1 mm to several cm in length, encompassing a functional diverse and important part of pelagic ecosystems. The mesozooplankton module is resolved in a size-matrix representing species of increasing size at maturation, each species producing eggs which grow through size-classes depending on their foraging and survival. The particular feature that each species grows from small to large is important, and makes our model different from most other size-structured ecosystem models (e.g. Baird and Suthers, 2007). Another key novelty of our model is that it allows for flexible and adaptive spatial behaviour of both zooplankton and fish predators as a function of predation risk and growth processes. Here, the model is presented in detail, and we explore and discuss how risk sensitive behaviour can be modelled in the mass-balanced framework of an aquatic ecosystem. We emphasize the methodological and technical issues more than the ecological, pointing for instance at the need for a more mechanistic foraging module to make the model more informative about natural systems.

2. Model

2.1. Model essentials

In this paper we present a marine ecosystem model with detailed size-structure and life-cycles, and adaptive behavioural responses in mesozooplankton and fish, and we analyze some of the emergent spatial dynamics and diversity patterns. We used a 1D vertical version of the ECOSMO model (Schrum et al., 2006a,b) as a starting point (Fig. 1). This is a traditional ocean ecosystem model with chemistry (N, P, and Si), phytoplankton (diatoms and flagellates), biogenic opal, micro- and mesozooplankton as bulk state variables. We have replaced the mesozooplankton compartment with a developmental stage- and species specific matrix and added fish as a dynamic biomass feeding on mesozooplankton. The new zooplankton module includes organisms with stage-structured life-cycles such as copepods and euphausiids, growing from eggs to variable reproductive size. This resolution provides the model with an emergent size-structure of the zooplankton community, structured from foraging opportunities and predation. We let all our mesozooplankton feed on a mixed diet of microzooplankton, detritus, phytoplankton, and smaller zooplankton, following the current practice in marine ecosystem models of predetermined preference functions. Fish feeds on mesozooplankton depending on their encounter rates and handling time (Holling disc), where the encounter rate is driven by prey density and detection distance through body size and ambient light. Fish are acting as optimal foragers; they ignore and do not waste valuable handling time on non-profitable prey (Visser and Fiksen, in press), and perform active prey choice among available prey. Fish (the fish biomass) move continuously towards depth locations where they increase their food intake. Similarly, mesozooplankton feed on a mixed diet, and we have developed an algorithm where zooplankton biomass within each size class moves towards surrounding habitats with higher net biomass growth rate. This frequently involves a trade-off between increasing the ingestion of phytoplankton or smaller zooplankton, which tend to be located near the surface, the risk of being eaten by fish, which see better in the higher illumination near the surface, and the risk of being eaten by larger zooplankton, which is more abundant in deeper habitats during the day. The diel cycle in radiation and the vertical gradients in productivity, light, and predators generate a spatial and temporal landscape where a diverse zooplankton community may emerge.

2.2. Model components

All the processes, variables, and parameters that enter the model are described in detail in the Online Appendix A. The model is written in C++ and the code itself is made available in the Online Appendix B. In this section, the main components and functionalities are broadly described and discussed, aiming to give sufficient overview of the model to understand the results, and limiting most details to the appendixes. Other modellers interested in running the model should be able to do this from the detailed description (Appendix A) and the source code (Appendix B).

2.2.1. Physics

The model represents a vertical water column, uniformly segmented into a number of discrete depths. The standard resolution used in the experiments is 2 m, and a total depth of 80 m. The temperature profile is kept uniform along the whole column. Sun irradiance at the surface can be either fixed to a constant value, or a fixed day–night cycle. Light transmission is limited by water turbidity and phytoplankton shading. Each depth compartment contains a whole system of the kind shown in Fig. 1, and biomass is exchanged vertically between compartments due to passive transport
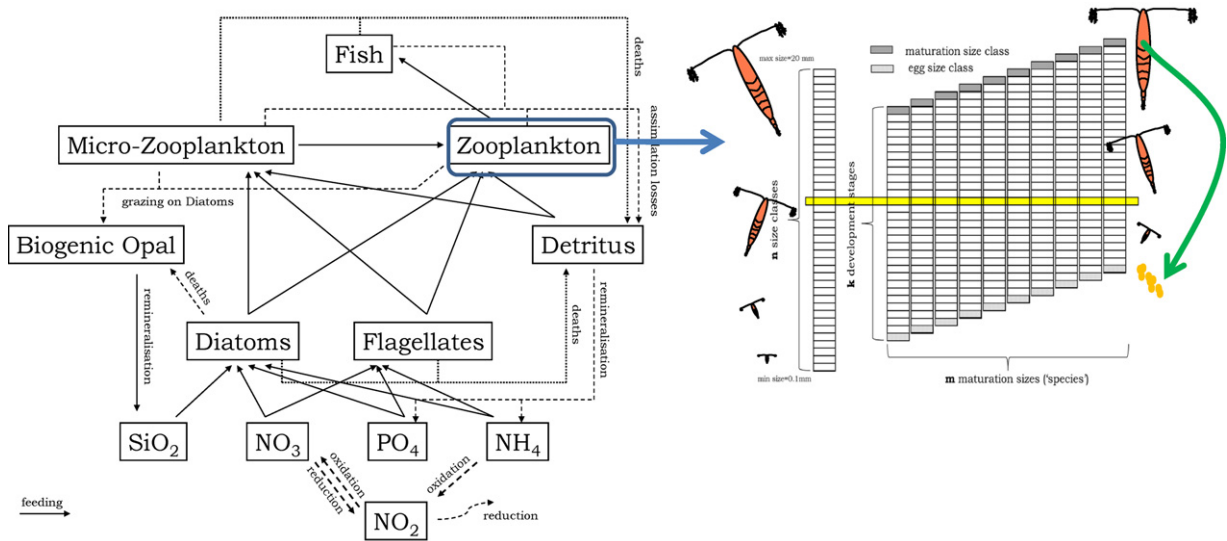
Fig. 1. An illustration of the model components, where the nutrient cycles (Si, N, and P), phytoplankton (flagellates and diatoms) and microzooplankton are from the ECOSMO model (Schrum et al., 2006a,b). The zooplankton is size-resolved in a number (56) of 'species' each with a particular egg and maturation size. Each species is divided into a set (50) of 'stages' which they have to grow through to reach maturity and start reproducing. The size class (horizontal marking) is defining the ecological role of the zooplankton size class, what it prefers to eat and its vulnerability to both fish and larger zooplankton.

(mixing) or active swimming (fish and mesozooplankton). Mixing is constant throughout the water column in most simulations in this paper, but we also tested the effect of a shallow mixed layer.

2.2.2. Nutrients

We account for three nutrient cycles: nitrogen, phosphorus, and silica as in ECOSMO. All organisms produce detritus (faecal pellets and fixed losses) and biogenic opal in the case of diatoms, which are remineralized into nutrients (nitrates, ammonia, phosphates, and silicates) and re-enter the food chain via phytoplankton uptake. Ammonia is produced by animal excretions.

2.2.3. Phytoplankton

There are two phytoplankton functional groups: flagellates and diatoms. Phytoplankton growth is limited by the availability of nutrients, light, and specific maximum growth rates similarly to most other marine ecosystem models. Microzooplankton feeds on detritus, flagellates, and diatoms according to given food preference factors and grazing rates. The nutrients and phytoplankton parts are kept as similar to the original ECOSMO model (Schrum et al., 2006a,b) as possible. One change we made was to give diatoms and flagellates the same growth and background mortality rates (in ECOSMO diatoms have higher growth potential than flagellates), to avoid differences in the resource productivity to impact the emerging size structure.

2.2.4. Mesozooplankton

Mesozooplankton is divided into a user-defined number of species and development stages within each species. The simulations here include 56 species characterized by their size at maturation, each divided into 50 development stages (from eggs to adults) of increasing size, yielding a total of 105 logarithmically distributed size classes (Fig. 1, and Appendix A). The key difference between the species is their size at maturation, defined here as the body size at which all surplus energy is diverted to egg production. As a direct consequence species also differ in their egg size and their ontogenetic size range (Fig. 1). Following each species through from egg to adult is a key element of our model. The size and species resolution allows either a single winning species, or a diversity of species coexisting over time. As a sensitivity test to the size resolution, we also collapsed the representation of the

zooplankton size-structure into three species, each with 2 size-classes, juveniles and adults (Fig. 2).

Organisms of same size across different species share allometric parameters, predators, and prey. All mesozooplankton size classes are omnivorous and can potentially feed on flagellates, diatoms, detritus, micro-zooplankton, and smaller mesozooplankton. This brings up the question of 'food-preferences' in the model (Anderson et al., 2010; Gentleman et al., 2003; Prowe et al., 2012a,b), in particular how prey selectivity among different zooplankton groups might change with size. For a predator of a given size foraging on alternative prey, food preference factors are often fixed parameters (as in ECOSMO). Alternatively, food preference factors may be a function of the local abundance of the alternative prey types, typically such that the preference for a particular kind of prey is a function of its abundance (e.g. Stock et al., 2008). This latter alternative tends to stabilize the models and prevent extinction in prey most susceptible to predation, since predators are assumed to 'switch' away from and not consume less abundant forms. However, these assumptions about prey selectivity are not substantiated by optimal foraging theory (see Visser and Fiksen, in press), and we have tested our model responses to both. In the first case, we let the preferences be independent of relative abundances ('fixed preferences'), and introduced size-dependence so that
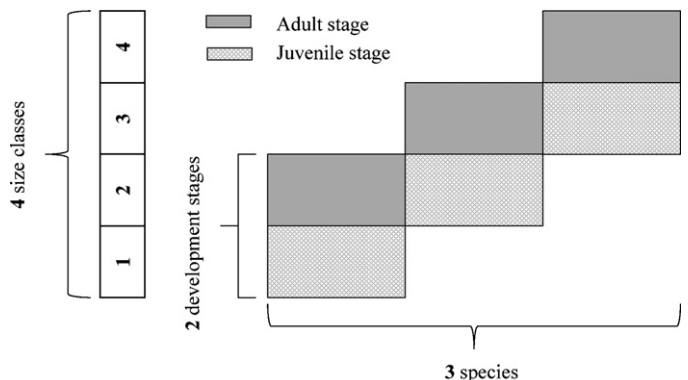

Fig. 2. Size structure of meso-zooplankton population of a simplified, lower resolution system. Each species here only have a juvenile and an adult stage.

mesozooplankton increasingly prefer diatoms to flagellates as their body size increases. In the second case, the preference for one food source increases with its relative abundance ('switching preference').

In the model, mesozooplankton have an allometric maximum ingestion rate decreasing with body size (Hansen et al., 1997). This relationship is established over many orders of magnitude (Fig. 2a in Hansen et al., 1997) but is weak within the mesozooplankton. Except for a minor fixed (0.002 day^{-1}) background mortality term all predation loss is explicitly from larger classes of zooplankton or from fish. For each species, biomass is progressively moved from eggs (the first development stage) to higher development stages according to a probabilistic rule based on the feeding history of the stage. All biomass assimilated by adults is converted into eggs with no further growth in size after maturation.

To challenge the existing population of zooplankton with immigrating life-history strategies, a small amount of biomass is added daily to the adult stage of a randomly selected mesozooplankton species. This biomass is collected from the existing mesozooplankton population, "taxing" each development stage of each species of a small amount (1% of biomass per day). This procedure simulates the dispersion of individuals in the surrounding environment (taxation) and the invasion of foreign species (random assignment of mass) while maintaining mass balance. The success of the introduced strategy or trait (size at maturation) is determined by its ability to compete under the existing conditions, in an evolutionary process.

2.2.5. Fish

Planktivorous fish is the top predator of the system. It feeds on mesozooplankton with a rate modelled from biological predator–prey encounter rates, driven by ambient light and body size, and abundance of prey (Huse and Fiksen, 2010). We assume that planktivorous fish act as optimal foragers and only include small prey in their diet when this is profitable. The rationale is that fish vary their diet to maximize food intake, and this is done by an adaptive use of time. Since capturing small prey takes time away from searching for larger more profitable prey, some of the smaller prey should be ignored to obtain optimal diet breadth (Visser and Fiksen, in press). Accordingly, we use a Holling equation for multiple prey items under the assumption of optimal foraging. Optimal foraging implies that diet breadth is determined adaptively to optimize the trade-off between available food and handling time. That is, fish hunt mesozooplankton down to the smallest size class that increases the food intake. Below that size, prey are ignored since the handling time would detract from the time required to hunt larger and more nutritious individuals. Being a visual predator, fish are most efficient in the daylight and closer to the surface. As a consequence of the above rules, larger zooplankton in more illuminated habitats (near the surface) will be more susceptible to predation from fish.

2.2.6. Swimming and risk-sensitive behaviour

All chemical and physical variables and microbes are mixed passively, but mesozooplankton and fish have swimming capabilities which dominate their distribution. Individuals move to those depths that maximize their biomass growth, avoiding altogether depths where growth is negative. The biomass growth is defined as the difference between biomass intake (feeding) and biomass loss (predation and metabolic costs). Accordingly, light and prey availability govern the fish habitat selection procedure. Large mesozooplankton species migrate towards the surface in the night where food (phytoplankton) is most abundant, protected by darkness from their visual predator. In the day, large species seek refuge from predation in deep dark waters. Medium-sized species try to find the optimal compromise between the necessity of feeding, the danger of being eaten by larger species (their main predator), and the danger coming from fish predation. The maximum swimming speed of mesozooplankton and fish is set by the user to a fixed number (set to 1 here) of body-lengths per second.

2.2.7. Model aims

Our aim is to explore how an idealistic ecosystem model with behaviourally responsive predators and prey, and explitcit representation of fish and zooplankton predation, can be constructed, and how it behaves and deviates from models of lower complexity. The settings chosen for the illustrations represent a particular set of assumptions for comparison and discussion. There are still many aspects of marine ecosystem models that need to be developed further before the level of complexity that we have added here is applicable for reliable predictive modelling (see e.g. Visser and Fiksen, in press).

3. Results

3.1. Ecosystem properties and zooplankton community structure over time

First we present some temporal properties of the model, emphasizing the emergence of size distribution among zooplankton size classes (Fig. 3A) and species diversity (Fig. 3B) under the assumption of a switching prey preference. The smallest species of mesozooplankton takes over completely (Fig. 3B), and the inclusion of risk sensitive behaviour was not sufficient to allow large zooplankton to establish or generate a diverse size-structure in the model.

We started fish at very low initial biomass levels, it builds up gradually (Fig. 3C), and eventually reach a biomass where it impacts the zooplankton abundance and community structure. Phytoplankton is controlled by grazing, free nutrients remain stable and never become limiting to growth (Fig. 3C). This pattern remains even if we reduced the vertical mixing from a standard value of 10^{-4} m^2 s^{-1} to 10^{-5} and 10^{-6} (not shown) and the phytoplankton remained grazer-limited while the productivity was reduced. All zooplankton size classes do consume phytoplankton, so the grazing pressure will be high independent of which size class dominates. Fish are not efficient predators on the smallest zooplankton forms because they are difficult to detect by vision, and thus zooplankton will always reach abundances where phytoplankton is controlled by grazers.

Periodic cohorts of zooplankton appear and graze down both phytoplankton and the smallest zooplankton stages. This involves cannibalistic predation by adults on young stages of the smallest species preventing an increase in the abundance of adults (Fig. 3A and D). The mature zooplankton are eventually eaten by fish and a new cycle starts when the eggs and juveniles are relieved from the cannibalistic predation. In model simulations without predation among zooplankton (not shown) the cycles disappear, indicating that predation from zooplankton is in fact the mechanism of this pattern.

The total biomass of mesozooplankton (Fig. 3C) remains quite stable over the fish peaks (but note the log scale), while the biomass and size structure of the zooplankton community cycles with fish abundance (Fig. 3C and D). An increase in fish biomass does not relieve the producers from their grazers; a different response from what a simple linear foodchain model would predict.

If we remove fish from the model, the large zooplankton groups become dominating (Fig. 4A and B). If we assume fixed prey preferences, the shift to larger species is slower and the diversity of species is higher (Fig. 4C and D). With more separation of resources there is less competition among size classes, and a wider range of species can coexist.
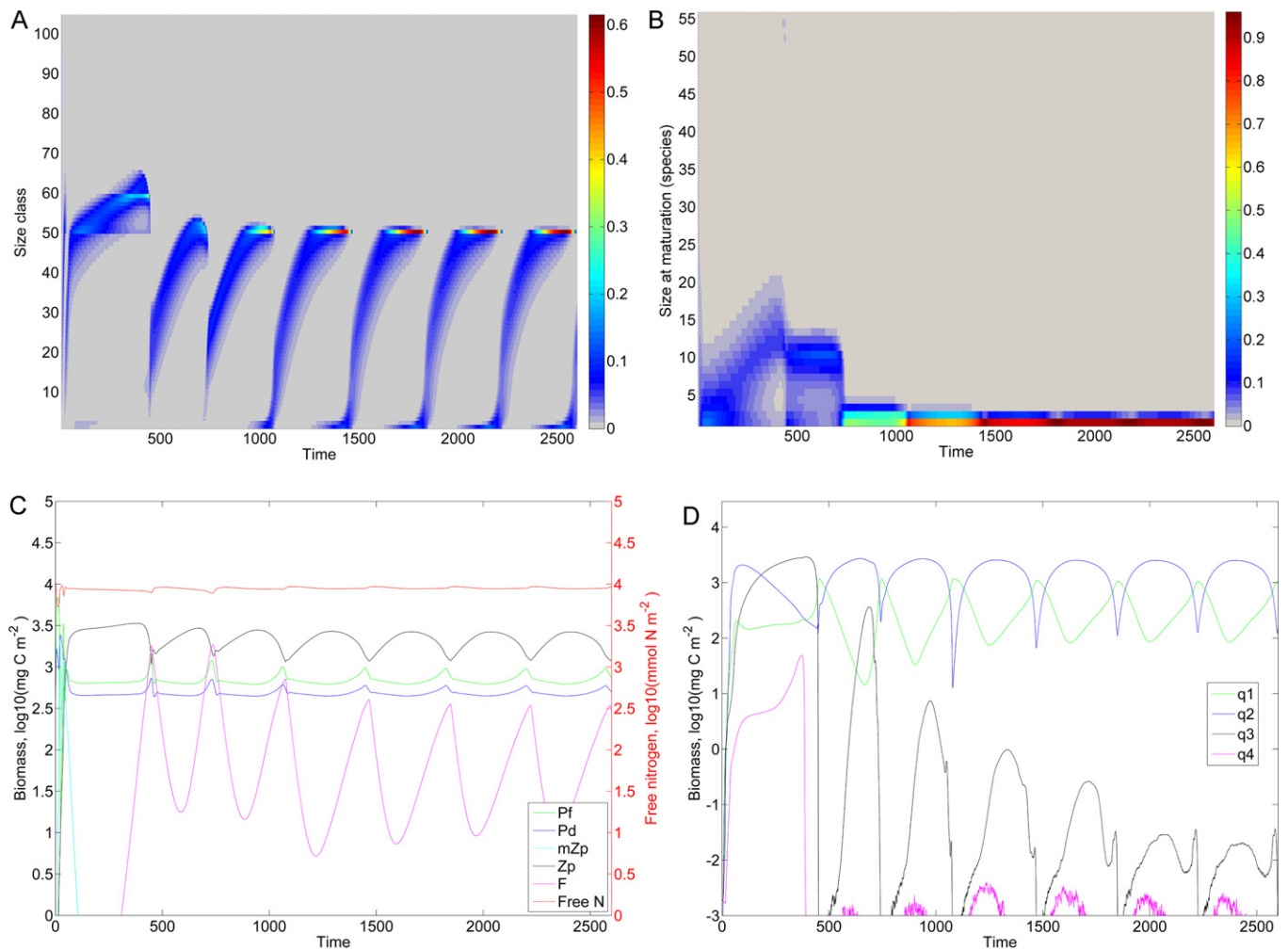
Fig. 3. Development of (A) size-classes and (B) species (class where they mature and start reproducing) structure in the mesozooplankton community over time; (C) Ecological state variables (fish *F*, flagellates *Pf*, diatoms *Pd*, microzooplankton *mZp*, mesozooplankton *Zp*, fish *F*, inorganic $NO_3 + NH_4$ *Free N*); and (D) mesozooplankton binned in 4 size groups over time (*q1* smallest, *q4* largest). The top panels show the normalized relative distribution of the biomass (the ratio B_i/B, where B_i is the biomass of species *i*, and *B* is the total mesozooplankton biomass), over all 105 size groups (in ordinate) and time (weeks, in abscissa). The temporal abundance of nitrate is averaged over the upper 30 m. The mesozooplankton population is partitioned into four broad size categories, namely *q1* representing the smallest individuals (size classes 1–27), *q2* consisting of medium-small individuals (size classes 28–53), *q3* corresponding to medium-large individuals (size classes 53–79), and *q4* grouping the largest individuals (size classes 79–105). The size groups of each category are roughly composed of predators of the immediately smaller category (e.g. *q3* individuals are predators of *q2* individuals). Panel D shows the evolution of the total biomass in these four broad size categories. Switching preference functions were used for all these results.

3.2. Diel vertical distribution and migratory behaviour

To demonstrate the behavioural repertoire represented in the model, we include a few snapshots of the vertical profiles of some of the biological groups. The spatial patterns will depend on light, phytoplankton biomass, and abundance of fish relative to the various size-groups of zooplankton. The 48-h detailed vertical images in Fig. 5 are snapshots of a particular situation towards the end of the model. The figures illustrate the emerging behaviours and spatial dynamics of some selected size classes of mesozooplankton and fish. All zooplankton consume phytoplankton which is found near the surface, reducing their abundance during the night, and other zooplankton of size roughly 10 times smaller (about 42 classes in our 105 class resolution). This means that zooplankton size class 20 is prey of a range of size classes centred on class 62, which in turn is prey of class 104 and its neighbouring classes (Fig. 5). The main predation pressure on zooplankton is given by the distribution and abundance of its zooplankton and fish predators. The spatial fitness landscape for zooplankton is formed by the difference in immediate grazing and total predation rates. This leads to a dynamic spatial game among predators and prey: small zooplankton remains near

the surface while larger forms move towards increasingly deeper waters during day to avoid predation from fish (Fig. 5).

Fish is less able to locate prey in the darkness of the depths. They are also unable to see during night and therefore do not move vertically (Fig. 5). During the day fish distribute throughout the water column to feed on zooplankton, actively selecting among the most profitable prey. The algorithm used to distribute fish maximizes specific growth, which contributes to a spatial dispersal in the water column (Appendix A). The consumption of zooplankton by fish (Fig. 5, middle panels) results from the vertical profile of light, the density of prey and fish, and the optimal foraging strategy of the fish. Note for instance that size class 41 is not included in the diet of the fish in the near surface, where the abundance of this class is high. In the surface, the encounter rate with more profitable prey (such as class 61) is sufficiently high to ignore less profitable prey to maximize food intake. Consequently, the abundance and distribution of other zooplankton will affect the predation rate from fish on potential zooplankton prey. Note also that the intermediate zooplankton (41 and 62) only are consumed by larger zooplankton during the night, when they come up to feed near the surface.
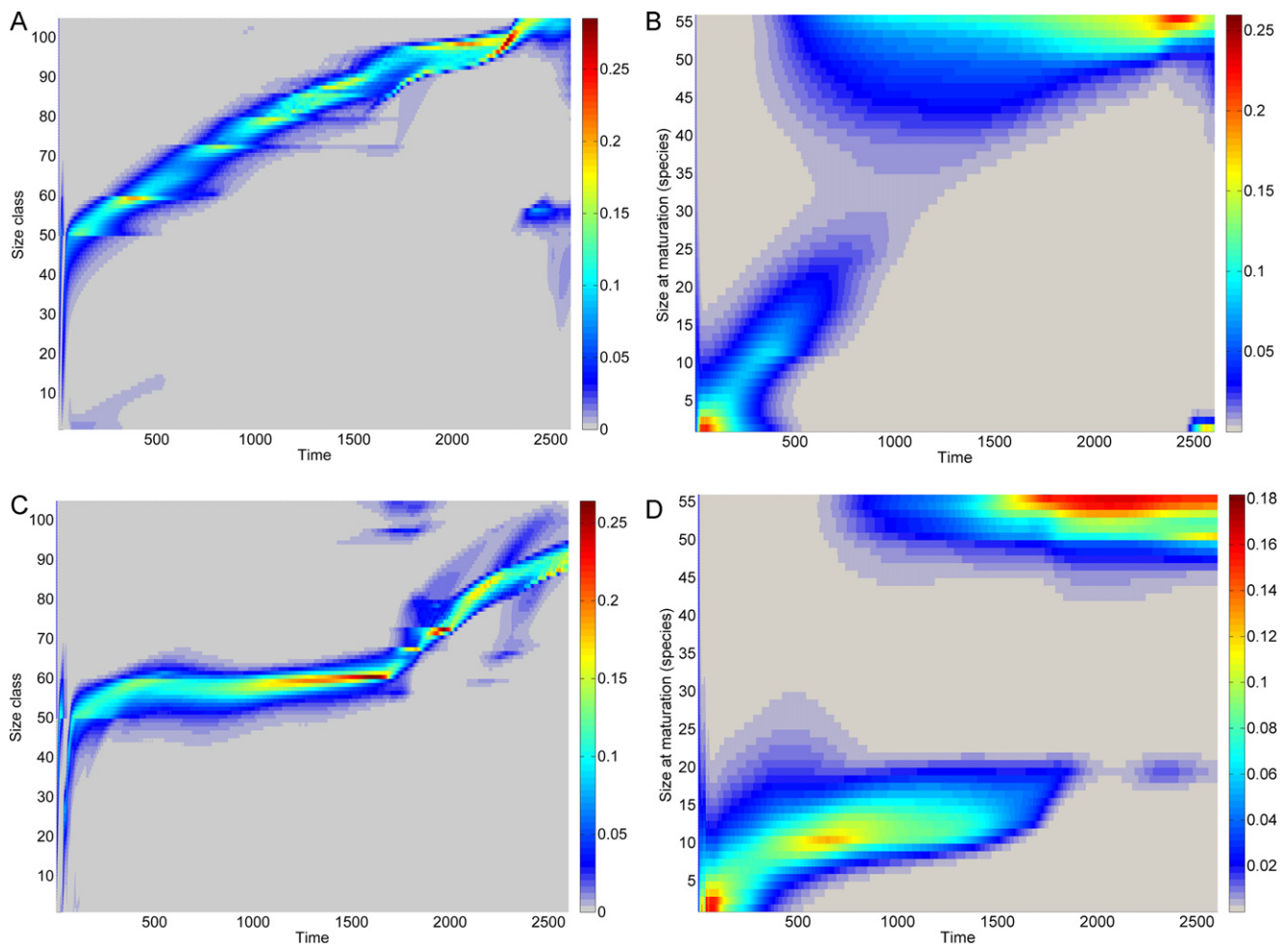
Fig. 4. The mesozooplankton size-distribution over time in terms of size-classes (left panels) and size at maturation or species (right panels) with switching (A and B) and fixed (C and D) prey preferences. These simulations did not include the fish predator. All other parameters as in Fig. 3.

One other typical pattern in the model is that larger zooplankton experience a higher mortality rate during the morning, and less in the evening. A weak example of this is evident for size class 83 (Fig. 5, middle panel), but this effect can be substantial in some configurations. Zooplankton migrating to the surface during night are 'caught by surprise' by dawn, a result of the myopic heuristics in the behavioural rule. They migrate downward, but the fraction lagging behind does not keep up with the rising sun and is eaten in the descent. This does not happen during the evening ascent, when the zooplankton return to feed on phytoplankton and smaller prey near the surface. This effect of the behavioural rule limits the ability of larger species to establish in the model when fish is present. The fish and zooplankton standing stock is not much altered if we turn off the spatial behaviour (not shown) since large species most sensitive to fish predation and dependent on vertical migration never establish when fish are included in the model.

3.3. Sensitivity to light

The growth of phytoplankton, foraging of fish, and behavioural dynamics all relate tightly to the diel light cycle. If we run the model in 24 h of daylight the primary productivity increases substantially and a stable cycle of phytoplankton emerges from fish-zooplankton predator–prey cycles (Fig. 6A). The increased productivity does increase the standing stock of phytoplankton biomass, but most of this is channelled into the fish and mesozooplankton compartments. In particular, fish benefits from the extra light, both through

the higher stock of zooplankton prey and extra hours of foraging time. The biomass of fish is more than 10 times higher under the extra light than it was under the standard day cycles (Fig. 3C). Under such light conditions nutrients become limiting for the total biomass of the system, and microzooplankton establish.

3.4. 'Switching' and 'fixed' prey preferences

We used the switching preference function in Fig. 3, and contrast this with the alternative assumption of fixed prey preferences in Fig. 6B. In periods when the community is dominated by larger zooplankton classes diatoms are cleared out, while flagellates increases in abundance. Under switching prey preferences the two phytoplankton groups will cycle in parallel and fluctuate less (Fig. 3C). Using switching or fixed preferences also made considerable difference to the zooplankton community when fish was not included (Fig. 4).

3.5. Fewer compartments and lower complexity

The model is developed with a flexible resolution of size classes and species of mesozooplankton (Figs. 1 and 2 and Appendix A). How does the model outcome depend on this resolution and complexity? With only 3 species and 4 size classes in total the model reaches a stable equilibrium with no oscillations, and microzooplankton appears (Fig. 6C). The biomass of zooplankton stabilizes at a lower level than in the comparable high-resolution
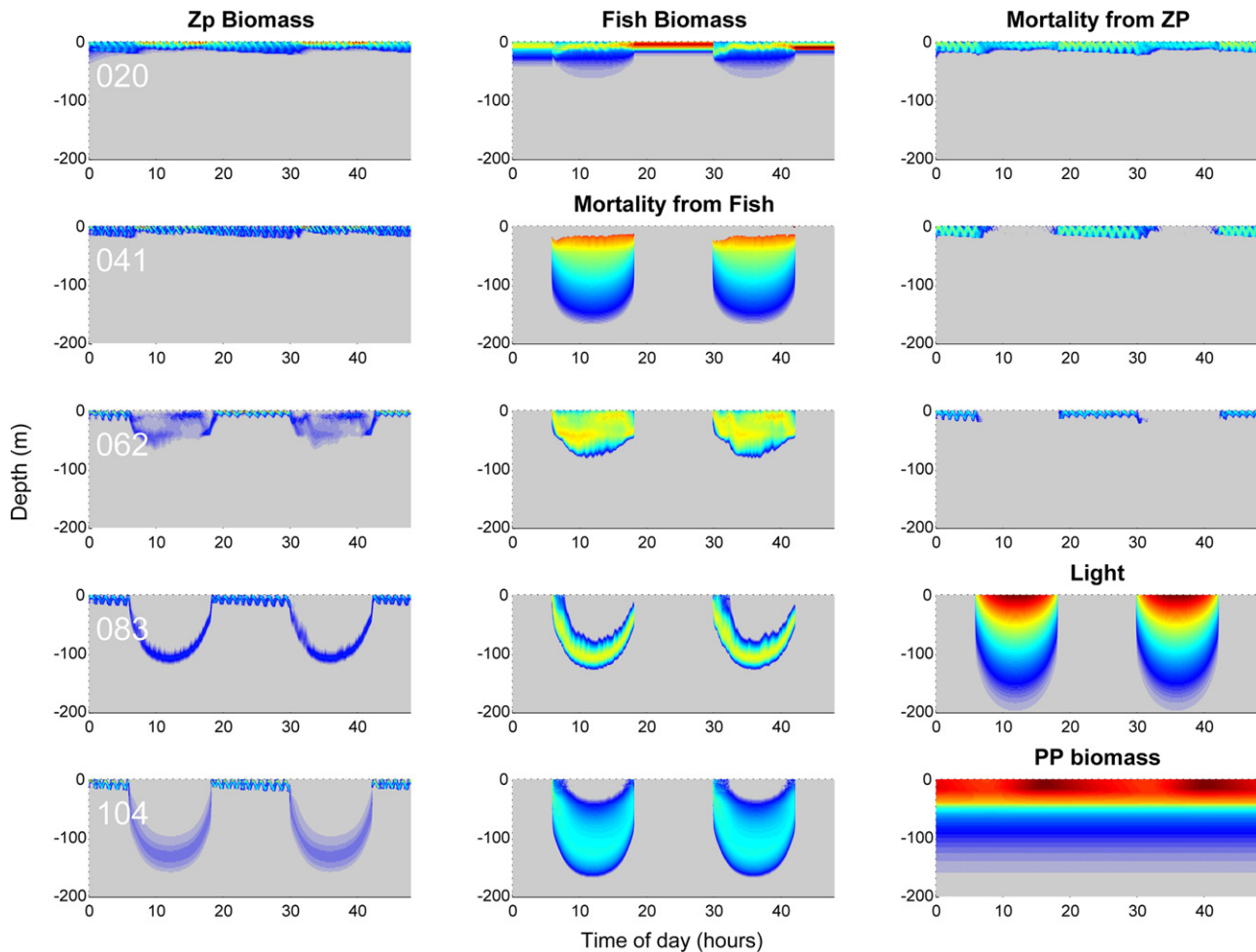
Fig. 5. Spatial patterns of biomass (colour scale of increasing density from blue to red, with densities scaled within each plot, i.e. the density of the largest zooplankton are orders of magnitude lower than the smaller) of five zooplankton size classes (left panels: 20, 41, 62, 83, and 104), the predation from fish (middle panels) and from other zooplankton (right panels); biomass consumed in $\log_{10}$ scale. The distribution of fish is in upper middle panel, and light and total phytoplankton biomass is shown in the bottom right panels. The smallest zooplankton are not susceptible to fish predation and the largest are not susceptible to zooplankton predation, and are therefore not included.

model (Fig. 3), while fish and flagellates settle at a higher level. The key point here is that the resolution of the size-classes has a strong bearing on ecosystem structure and functioning in the model.

3.6. No internal predation among zooplankton

We tested a version of the model without the internal zooplankton predation and dynamic prey preferences (Fig. 6D). In this experiment fish struggles to survive and establish. Zooplankton are threatened only by fish predation, and will spend more time away from the surface waters. In particular, medium- and small-size zooplankton can stay in dark deep waters without the threat of predation from larger species, and be less susceptible to fish compared to the simulation in Fig. 3. This illustrates the potential impact of behavioural risk-enhancement responses in structuring pelagic ecosystem models.

4. Discussion

We have presented a model where different zooplankton life-history strategies (size at maturity) compete for resources and predate each other. The size-structure of the community emerges as a result of predator–prey interactions, competition and risk-sensitive behavioural responses. A particularly novel feature is the inclusion of vertical migration driven by a continuous evaluation of risks and benefits in nearby habitats. Planktivorous fish is included as a dynamic variable, constantly moving in space and selecting prey by ignoring non-profitable size-classes in an adaptive manner. We show how such interactions and dynamics can be included in a 1D pelagic ecosystem model, and explore some of the consequences that fish predation and adaptive behaviour has on ecosystem structure. We remain cautious in extracting ecological insight from the model at the present stage as a number of questions are still unresolved. Among these is the prey-preference formulation, the diversity or trait-distribution among phytoplankton and mesozooplankton, a better representation of microzooplankton, protists and bacteria, and alternative behavioural heuristics that may increase the success of some forms (large zooplankton under fish predation).

4.1. Risk sensitive migration behaviour and diversity

The largest zooplankton never established when fish was part of the model. Including risk-sensitive behaviour therefore did not produce much difference in biomass within trophic levels, or affect significantly the size structure of the zooplankton. If organisms alter their behaviour and reduce their risk-taking as a predator becomes more abundant (risk-sensitive foraging), this is expected to reduce the vulnerability and growth of the prey, and at the
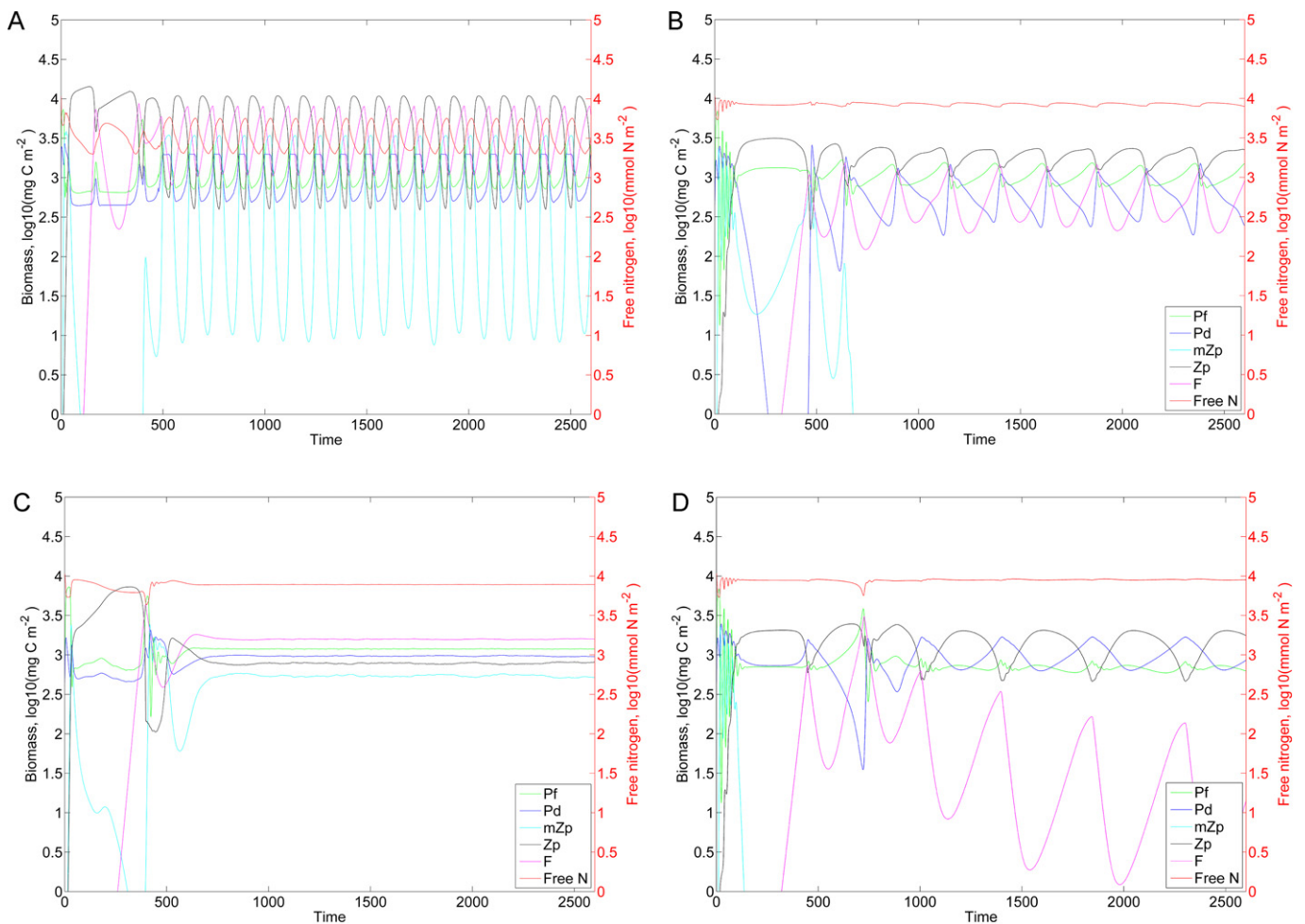
Fig. 6. The distribution among functional groups under (A) constant light 24 h a day; (B) fixed prey preferences; (C) two size classes and 3 species; (D) no internal zooplankton predation, otherwise parameters and settings as in Fig. 3 in all cases.

same time to decrease the growth rate and success of the predator (Schmitz, 2010). In theory, this could stabilize cyclic predator–prey dynamics and allow for a broader range of zooplankton species (size-at-maturation) to coexist in a given ecosystem setting. In our ocean water column the most relevant behaviour is vertical migration, where plankton regularly swim away from near surface waters during the day to hide from fish in deeper and darker waters (Pearre, 2003). Among zooplankton, large species are those that descend deepest in daytime, since they are the most easily detected by fish. As often observed in nature (Ohman, 1990), the migration of large, predatory and omnivorous zooplankton away from the surface opens space for smaller zooplankton, which are less vulnerable to fish but subject to predation from larger zooplankton. This type of behavioural cascades are often seen when multiple trophic levels interact (e.g. Romare and Hansson, 2003) and our model does capture this mechanics. In an earlier study (Fiksen et al., 2005) we took an optimality approach to behavioural cascades in a similar system of behaviourally responsive prey being chased by multiple predators. We found that more abundant zooplankton predators would push the smaller zooplankton towards the surface and make them more vulnerable to fish (but not vice versa). The present model contains similar predator–prey interactions in a dynamically coupled system, where the immediate rates and behaviours influence the densities of predators and prey. Risk enhancement from the presence of invertebrate predators occurs here, and fish almost disappear in the simulation with no intra-guild predation (Fig. 6D).

The formulation of behavioural strategies involves an entirely myopic rule – the zooplankton move towards depth with higher immediate growth-mortality ratios, with no foresight of the diel cycle. Instead of migrating down well in advance of the morning light, the zooplankton start swimming too late, and experience high death rates every morning. This is one reason why the large zooplankton predators do not establish, since they are the most susceptible to fish predation and need lower mortality rates to compensate for the longer life span. Simpler rules such as remaining within given isolumes (Dupont et al., 2009) of the migration behaviour may alleviate this problem.

4.2. The switching/non-switching prey preference

The preference functions of the zooplankton grazers have strong bearing on who are the stronger competitors and the coexistence of alternative prey (comparing Figs. 3C, 4 and 6B). Preference functions and to some degree functional responses have been revealed as 'known unknowns' in ecosystem models. They are often parameterized and chosen by convenience to stabilize models rather than to express fundamental ecological traits and behaviours (Anderson et al., 2010; Gentleman et al., 2003; Gentleman and Neuheimer, 2008). Here, we have developed a detailed and evolutionary consistent approach to fish foraging (optimal diet, adaptive spatial movement) and to elements of predation internally in zooplankton (adaptive movement). Flexible foraging modes, grazing, and diversity among primary producers are still crudely or

arbitrarily represented. The foraging of mesozooplankton on alternative shared food sources (diatoms, flagellates, detritus, and microzooplankton) is determined by rather phenomenological preferences. The formulation of functional responses under mixed diets continues to be an important, unresolved challenge for marine ecosystem models (Prowe et al., 2012a,b). The use of half-saturation coefficients is particularly problematic under multiple prey, but using more mechanistic formulations (Kiørboe, 2011) where foraging mode and activity level emerge in an adaptive manner could make ecosystem models less arbitrary (Mariani and Visser, 2010; Visser and Fiksen, in press). The influence of the preference functions should be seen as a general challenge to their use and not as an interesting ecological phenomenon.

Phytoplankton also comes with a range of strategies, and a meaningful way to structure the phytoplankton community should include their susceptibility to grazing (Verity and Smetacek, 1996; Verity et al., 2002). Under heavy grazing the slower-growing but heavily defended (morphologically, chemically or behaviourally) forms should be successful. Since phytoplankton defence mechanisms is not part of our model, grazers control the producers to a level where nutrients never becomes limiting. The cascades within the mesozooplankton species do not make any difference to this pattern, as all species are omnivorous and feed on phytoplankton. The approach suggested by Merico et al. (2009) where defence is traded off against growth capacity could be a sensible replacement for the prey preference parameterization. Structuring phytoplankton functional types along a trait-space where the trade-off is between grazing resistance (primarily from smaller zooplankton) and competitive ability (smaller cell size) is likely to restore much of the size-structure among the zooplankton, based on 'Killing the Winner' mechanisms (see Thingstad et al., 2010).

4.3. The link between lower and higher trophic levels

We have not made changes to the lower trophic levels but kept them similar to the ECOSMO model with a diatom and a flagellate functional group. In other size-based marine ecosystem models, such as the one developed by Baird and Suthers (2007), the phytoplankton, protozoans and metazoans are all size-resolved. When the predator–prey interactions depend on size throughout the system a direct link from size-structure at lower levels propagates to higher levels. The phytoplankton groups are also assumed to have similar affinities for nutrients. A more complete formulation of the phytoplankton module, including an explicit trade-off between growth and vulnerability to grazers (Smith et al., 2011), would resolve the size- and trait-structure throughout the biological compartments also below the 100 μm size (Baird and Suthers, 2007; Fuchs and Franks, 2010). Neither have we resolved size within fish, which is less critical to model output, since fish in our model consume prey in proportion to encounter rates (mainly driven by zooplankton size) and not relative size.

One challenge for a realistic representation of growth in fish and mesozooplankton is the intermittency in their feeding activity – generally the presence of a gut and storage system, which effectively allows them to grow for long periods without feeding. Representing these organisms as bulk biomasses in a cyclic and light-dependent predator–prey interaction regime does not allow them to take full advantage of the loopholes of the system, such as zooplankton grazing during the night and digesting in the deep during the day with no loss in growth. This, and several other shortcomings of the current model (migration triggers, limited trait resolution) may be solved by turning to a Lagrangian Ensemble or individual-based approach (Clark et al., 2011; Woods, 2005), but this is not without challenges either.

Most biogeochemical models ignore higher trophic levels and have a fixed closure term on primary producers or bulk herbivore grazers. Some notable exceptions to this are the NEMURO (Megrey et al., 2007; Werner et al., 2007), OSMOSE (Shin et al., 2010; Shin and Cury, 2004) and the NORWECOM (Utne et al., 2012) models. The reasons for closing ocean ecosystem models at a low trophic level are many and sensible, given the complex behaviour and life-cycle of fish. However, given the mixture of direct and indirect effects from higher trophic levels in various ecosystems (reviewed by Schmitz, 2010), it is reasonable to ask how ecological mechanisms and interactions among zooplankton and fish may affect productivity, biogeochemical cycles, and microbial communities. From a fisheries or management perspective, we also need tools to better predict how environmental change or fisheries affect ecosystem structure and productivity. Establishing mechanistic linkages between trophic levels from microbes to fish, and the more subtle indirect effects of behaviour, is a difficult but necessary step to develop reliable predictions of marine ecosystem responses.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.12.007.

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