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Modelling encounter rates and distribution of mobile predators and prey

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ABSTRACT

Marine ecosystem models often contain modules for two phytoplankton compartments (flagellates and diatoms) and two zooplankton groups (micro- and mesozooplankton). The models rarely include fish, not even as an agent in zooplankton mortality, which is often formulated as a constant rate. This mortality rate is treated as a free parameter, which can be used to tune or stabilize the model. There are major gaps in our knowledge and modelling capabilities of interactions at the higher trophic levels for example with regards to movement of fish at different scales, prey selection, and zooplankton responses to predators. Here, we argue that there are good reasons for making zooplankton mortality dependent on some key environmental variables known to affect the interaction strength between zooplankton and fish. In addition, since fish are highly mobile organisms, often moving in large groups, there is a need to better understand and model their horizontal migration and to include this in ecosystem models. We present basic models for light-dependent encounters between fish and their zooplankton prey and illustrate how predator–prey interactions can be modelled for herring–*Calanus* and cod–capelin interactions using individual-based models with super-individuals. In the latter two cases individual displacement is determined by movement behaviour and ocean circulation, and growth and mortality become emergent properties resulting from local encounters between predators and prey. Similarly movement behaviours emerge from simple adaptive rules or more complex models where behavioural strategies are evolved using a genetic algorithm. Such models are versatile and we argue that emergent mortality and growth rates resulting from adaptive behaviours and key environmental forcing are essential for realistic representation of fish–zooplankton interactions.

1. Introduction

1.1. State of the art in ecosystem modelling

The Grand challenge in marine ecosystem modelling is to achieve realistic end-to-end 3D models where the entire ecosystem is simulated from the physics all the way up through the food web (IMBER, 2005; Travers et al., 2007). Models are now beginning to emerge that cover this range with model systems such as ATLANTIS (Fulton et al., 2004) being parameterised for different ecosystems around the world. End-to-end ecosystem modelling poses a lot of challenges to modelling marine ecosystem dynamics for example related to implementation of the behavioural flexibility that typically is associated with the higher trophic levels. The traditional marine ecosystem models simulate the dynamics of nutrients, phytoplankton, zooplankton and detritus. These so-called NPZD models have been developed into more sophisticated models with several functional forms coupled as a food web (see review by Moll and Radach, 2003). These models normally contain modules for two phytoplankton compartments (flagellates and diatoms) and two zooplankton groups (micro- and mesozooplankton), or alternatively, structured models of single key species. The models rarely include fish, not even as a closure term for the zooplankton mortality, which is usually formulated as a constant rate. This mortality rate is treated as a free parameter, which can be used to tune or stabilize the model. The most common approach for including variable predation risk is to assume that it correlates with some environmental feature, such as temperature, but with little justification of underlying mechanisms.

However, there are some recent model developments where fish consumption is explicitly represented in a marine ecosystem model (Megrey et al., 2007; Werner et al., 2007). These represent innovative steps in integrating fish population dynamics with the underlying oceanography and ecological processes. Here, we point at the need to develop (1) improved representation of the actual zooplankton–fish encounter process and how this is affected by e.g. chlorophyll concentrations and (2) a more flexible, or adaptive approach to how zooplankton and fish move in space. While the first point can easily be included in existing models, the second part will require a more radical change in the way models are constructed.

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1.2. Motivation for including fish predation in zooplankton models

Among the motivations for better representation of fish predation in ecosystem models are:

- Zooplankton mortality is often poorly parameterised.
- Fish predation has the potential to structure zooplankton communities, and ecosystem functioning.
- Fish predation can be important to zooplankton population dynamics.
- Zooplankton biomass influences foraging potential of planktivorous fish and may limit fish production.
- It is important to understand how zooplankton dynamics and availability generate density-dependency in fish populations.

Fish predation is important to the structure and population dynamics of zooplankton. This is obvious in lakes where the zooplankton community structure to a large degree is dependent on the presence of planktivorous fish (Brooks and Dodson, 1965). But effects of fish predation on the zooplankton community is also seen in marine fjords (Eiane et al., 2002), and ocean areas such as the Barents Sea (Hassel et al., 1991; Skjoldal et al., 1992). Planktivorous fish also contribute substantially to zooplankton mortality in basin scale oceans such as the Norwegian Sea (Skjoldal et al., 2004), where there are negative correlations between the distribution of herring and biomass of *Calanus finmarchicus* one year later (Olsen et al., 2007). This suggests that herring predation has effects on the distribution of *C. finmarchicus* that are traceable for months in spite of the considerable advection in the Norwegian Sea (Aksnes and Blindheim, 1996; Bryant et al., 1998; Torgersen and Huse, 2005). Furthermore there can be substantial inter-annual variation in distribution and abundance of planktivorous fish, which makes it problematic to represent fish planktivory as being constant. The commercial harvest of planktivorous fish strongly affects fish mortality, which can have indirect consequences for zooplankton mortality. Another element to the fish–zooplankton interaction is the process of fishing down the food web (Pauly et al., 1998), which has made planktivorous fishes more abundant in some areas with the advent of industrialised fisheries and the large scale removal of piscivores. Consequently there are several reasons for attempting to represent fish predation in ecosystem models.

1.3. The nature of predation

Predators affect prey, obviously, by killing and eating them, but also by scaring them. The latter aspect of predation has been referred to as "the ecology of fear" (Brown et al., 1999). The former effect has direct consequences for prey population dynamics and may also have indirect consequences for other species through trophic cascades. Similarly the scaring can be a direct effect on the prey, and diel vertical migration is an example of this, or indirectly mediated behavioural effects on other species (Abrams, 1995; Dill et al., 2003; Werner and Peacor, 2003; Hölker and Mehner, 2005). Finally, over time predation tends to have a structuring effect on the ecosystem. Here Brooks and Dodsons study of lakes in New England is a classic example showing that lakes with planktivorous fish had much smaller zooplankton than lakes without fish (Brooks and Dodson, 1965). Similar examples have been seen in marine waters as well, including Norwegian fjords that differ in dominant functional predators (Eiane et al., 2002). The killing and scaring effects of predation have traditionally been addressed by contrasting modelling approaches (Rosenzweig and MacArthur, 1963; Brown et al., 1999). Most emphasis is typically put on the direct numerical consequences when predators kill and ingest prey like in the classical Lotka–Volterra model, or how environmental factors can affect and modify this process (e.g. Eggers, 1977). But within behavioural ecology the risk effects are typically modelled using optimality methods such as dynamic programming (Clark and Levy, 1988; Mangel and Clark, 1988). The first approach may be most relevant for situations where the predators are relatively mobile while the prey is immobile. However, in cases where both the predator and the prey are able to relocate, the fear of predation can be an important consequence of predator–prey interactions. While fish generally have a greater repertoire of behaviours, zooplankton can also respond to predation levels by changing their vertical positioning (e.g. Bollens and Frost, 1989). Both aspects of predator–prey interactions are therefore important for fish–zooplankton interactions and it is a challenge for models to integrate them.

1.4. Approaches for implementing fish predation in zooplankton models

Pelagic fish often have a dynamic use of space. The role of space in ecology remains elusive, and the subject has been referred to as the "*final frontier for ecological theory*" (Kareiva, 1994). Modelling the spatial- and temporal distribution of fish has traditionally been difficult due to the great computing power required, poor representation of environmental forcing and fish distribution, and a general lack of numerical methodology (Giske et al., 1998). However, computing power is ever increasing and now allows simulations of rather large ocean areas at a fine scale with fish stocks and 3D environmental description. Fish species vary in feeding strategies and efficiency and there is a general lack of parameter estimates and validated parameterisation methods. These are the challenges when approaching the issue of parameterising fish–zooplankton interaction.

Here, we argue that there are good reasons for making zooplankton mortality dependent on some key environmental variables such as light and optical properties of the water, which are known to affect the interaction strength between zooplankton and fish (Aksnes, 2007). In some cases it can be sufficient to use these environmental variables to parameterise fish predation on zooplankton implicitly without modelling the predator. But since fish can be highly mobile and often move in large groups, there is also a need to understand and model their horizontal migration and to include these in ecosystem models (Giske et al., 1998; deYoung et al., 2004). The mortality of zooplankton and the structuring effect of fish predation are the product of both feeding efficiency (environment) and the abundance of mobile predators. Fish may actively seek out productive areas with high zooplankton concentrations despite lower feeding efficiency caused by environmental factors. We therefore decompose the problem and initially present an approach for parameterising fish–zooplankton interactions based on modelling light-dependent local predator–prey encounters. Then a spatially explicit individual-based *Calanus* model with herring as a predator is presented that integrates the effects of local encounters with predator and prey distribution. However, the herring distribution in the model is static and we also examine a model of cod–capelin interactions using an individual-based model (IBM, Grimm and Railsback, 2005), where both the predator and prey are capable of substantial horizontal movement. We focus on presentation of approaches for modelling zooplankton mortality and fish foraging and predation rather than providing detailed model description and discussion, which is done elsewhere for our example models. The final approach outlined here integrates population dynamics with the "ecology of fear" and thus captures both the key aspects of predatory interactions.

2. The mechanics of fish predation and zooplankton mortality

Planktivorous fish have two foraging modes. If prey are small and present in high concentrations, fish can swim with mouths wide open and filtrate prey over their gill rakers (Gibson and Ezzi, 1985; Batty et al., 1986). However, the most common foraging mode is particulate feeding, approaching prey one by one at visual detection (Eggers, 1977). Therefore, the interaction strength between fish and zooplankton is to a large extent determined by factors involved in the encounter rate between individual fish and their zooplankton prey. This process has been studied intensively, both in the laboratory (Vinyard and Obrien, 1976; Aksnes and Utne, 1997) and theoretically (Aksnes and Giske, 1993; Eggers, 1977). The implications of this process are important for zooplankton mortality rates or predation risk (Hernandez-Leon, 2008), for structuring of aquatic zooplankton communities (Sørnes and Aksnes, 2006) and for the productivity of large commercial fish stocks (Aksnes, 2007). What are the essential elements of the interaction? How can the predator–prey interaction be stripped down to serve in ecosystem models?

The classical model of the feeding rate f of a predator searching for prey and then consuming encountered prey, is the Holling disk equation (Holling, 1966):

$$f = \frac{\beta n}{1 + h\beta n} \tag{1}$$

where β is the volume efficiently scanned for prey per time (clearance rate), n is the density of prey and h is the time it takes to capture and ingest one prey (handling time). Note that fish may also be constrained by digestion when feeding rate is high.

The clearance rate for a cruising predator depends on swimming velocity v, reactive distance R and angle of the visual field θ (Fig. 1):

$$\beta = \pi (R \sin\theta)^2 v \tag{2}$$

The reactive distance R is a key variable here, driven by complex combinations of the physical environment, and physiological, morphological and ecological characteristics of both predator and prey (Eggers, 1977; O'brien, 1979; Aksnes and Giske, 1993). The chance that a fish detects a zooplankton prey depends on (1) properties of the prey, such as body size (or image area A) and its inherent contrast against the background (C, see Utne-Palm (1999)); (2) the visual capabilities of the predator (their eye sensitivity E and adaptation to specific light levels K, see Aksnes and Utne 1997); and (3) the ambient level (and quality) of light I. The light level I at any depth is determined by the diffuse attenuation coefficient (the rate of absorption of photons, a) and surface irradiance, varying with time of day, season, and latitude. In addition, the scattering of light (c) will decay image-forming light and decrease visibility, just as fog reduces visibility in air (Fig. 1). From these elements, Aksnes and Utne (1997) elaborated a model by Eggers (1977) and Aksnes and Giske (1993) into the following expression for R:

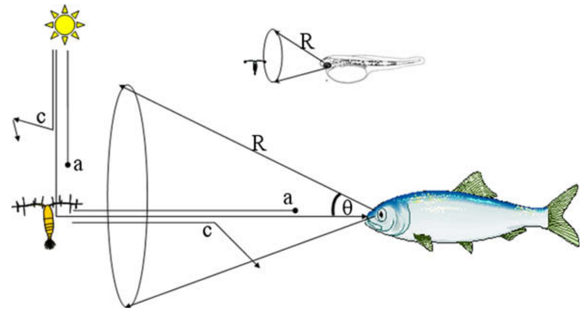

Fig. 1. Fish searching for zooplankton prey in the pelagic (modified from Fiksen et al., 2002). Down welling light is absorbed (a) or scattered (c), and is reflected from the prey, becoming image-forming light that enters the retina of the planktivore. Scattering and absorbance decays image-forming light, particularly if visual range R is long – therefore larval fish feeding rates should be less affected by high turbidity (e.g. algal blooms) because they have small R.

$$R^2 e^{(c \cdot R)} = C \cdot A \cdot E' \frac{I}{K+I}, \quad \text{or if } R <\sim 0.1 \text{ m}, R \approx \sqrt{C \cdot A \cdot E' \frac{I}{K+I}} \tag{3}$$

The approximation of R is valid when R or scattering c of image-forming light is low. For small prey, low light levels or low turbidity, the approximation will be reasonable. In fact, small fish or larval fish may be positively affected by turbidity since their visual range is little reduced (Fig. 1), while their chance of being detected by piscivores may decrease considerably (Giske et al., 1994; Fiksen et al., 2002).

Diel and seasonal variability in surface irradiance (such as lunar cycles) will influence fish feeding efficiency, and may itself have ramifications for zooplankton communities, fish recruitment and fisheries (see Hernandez-Leon, 2008). In addition, the optical properties of the water (i.e. c and a) are essential, since downwelling radiance I decays exponentially with depth according to Beer's law. Absorption of light in water is a discipline by itself (hydrologic optics, see e.g. Mobley (1994)), and here we only discuss the role of prey depth distribution, water turbidity, and the importance of phytoplankton in modifying optical properties of the waters, and therefore the interaction strength between fish and zooplankton. Very general bio-optical models of absorption $a(\lambda)$ and scattering $c(\lambda)$ do capture these factors, as detailed in Mobley (1994), and they must be spectral, since attenuation varies with wavelength λ. One particular example of Case 1 (mainly oceanic) waters, is from Morel (1991):

$$a(\lambda) = a_W(\lambda) + 0.06 a_c(\lambda) Chla^{0.65}[1 + 0.2\exp(-0.014(\lambda - 440))] \tag{4}$$

where $Chla$ is chlorophyll a concentration (mg m^{-3}), and $a_w(\lambda)$ and $a_c(\lambda)$ are spectral coefficients (=0.064 and 0.357, respectively, at 550 nm, from Mobley (1994)). Often, such bio-optical models are predictable functions of salinity and oxygen saturation of water (Sørnes and Aksnes, 2006). The spectral nature of optics introduces the question of which wavelengths are most relevant to fish vision, and ultimately, how these can be represented in 'community functions', encapsulating the diversity in visual adaptations among potential predators. This is directly comparable to defining the 'action spectra' in models of primary production, where different photosynthetic pigments can utilise different regions of the light spectra. Much work is devoted to describe and understand the diversity and ecological importance of photoreceptors in fish. Spectral sensitivity, measured from both absorbance spectra of visual pigments and experiments of reaction distance, peaked at 550 nm in *Gobiusculus flavescens*, a small littoral planktivore fish (Utne-Palm and Bowmaker, 2006), and we have assumed that this is the relevant λ for our planktivore here.

An alternative expression for light absorption at 550 nm, derived from the Baltic, is more representative for coastal waters (Wozniak et al., 2003):

$$a(550) = 0.056 + Chla(0.0506 \cdot e^{-0.606 Chla} + 0.0285). \tag{5}$$

For the beam attenuation coefficient (scattering) we suggest the model by Voss (1992)

$$c(550) = 0.0579 + 0.363 Chla^{0.57}. \tag{6}$$

With these relatively simple expressions of fish foraging we can now obtain instantaneous mortality rate M of a population of identical zooplankton prey n:

$$M = \frac{fF}{n}, \tag{7}$$

where F is the fish density. The mortality rate will depend on abundance, vertical distribution and overlap of fish and zooplankton, surface irradiance, optical properties of the water and zooplankton size.

We have parameterised this model for a herring-like planktivore feeding on a *Calanus*-like zooplankton prey (Fig. 2). We assumed fish to match the distribution of zooplankton, such that both zooplankton and fish are normally distributed around 30 and 60 m. The results illustrate the importance of vertical distribution on zooplankton mortality and fish feeding rates for a midday situation. Mortality rates are reduced by approximately one order of magnitude by the 30 m shift down in the water column (Fig. 2, left panel). Exactly how deeper distribution will influence zooplankton mortality rates depends on all elements that affect R, e. g. if light levels are high deep in the water, vertical distribution may not make a large difference since visual range saturates at high I (Eq. (3), Fig. 2, right panel).

Fish feeding efficiency (clearance rate β, Eq. (2) is much reduced in coastal compared to oceanic water (Fig. 2, right panel). Coastal waters contain more suspended organic matter, and therefore have higher light absorption even at low phytoplankton concentrations. Fish search efficiency is also strongly affected by phytoplankton, and for coastal waters, the modest concentration of 2 mg *Chla* m^{-3} implies that a given level of feeding efficiency is shifted ~20 m up in the water column relative to the clear water situation. Depending on the zooplankton distribution, this could severely reduce the overall predation pressure from fish.

The role of phytoplankton in regulating the mortality rate of zooplankton is explored in more detail in Fig. 3. Here, we have calculated the hourly mortality rate (M, Eq. (7)) of the standing stock of zooplankton at a range of *Chla*-concentrations in the upper 30 m, for coastal and oceanic waters (Eqs. (4) and (5)) and two depth-distributions of predators and prey. Clearly, both the inherent turbidity of the water and the depth distribution generates a major difference in mortality rates. In addition, increasing phytoplankton concentration will reduce zooplankton mortality rates significantly, particularly in coastal water types.

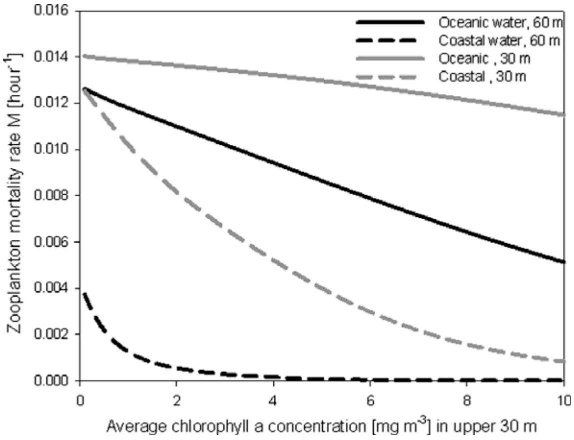

Fig. 3. The overall zooplankton mortality rate during daytime (Eq. (7)) integrated over depth for different water types (see Fig. 2). All parameters are as in Fig. 2.

3. Modelling spatial overlap between predators and prey

The classical mechanics of predation are relatively simple once the abundance and distribution of predators and prey are defined. However, in the case of migratory animals the likelihood of encounters with particular prey is likely to be highly variable over time, and this is a major gap in our knowledge of parameterisation of predator–prey interactions between fish and zooplankton. We will put particular emphasis on the spatial aspects of predator–prey interactions since this is an area that is particularly relevant for the higher trophic levels.

3.1. Vertical distribution

While the purely physical links driving fish feeding efficiency and zooplankton mortality rates should be straightforward to implement in marine ecosystem models, the issue of zooplankton vertical distribution is more problematic. Mesozooplankton are not passively distributed as a function of buoyancy and mixing, but have active ontogenetic and diel vertical migrations, often modified by environmental gradients, internal body conditions

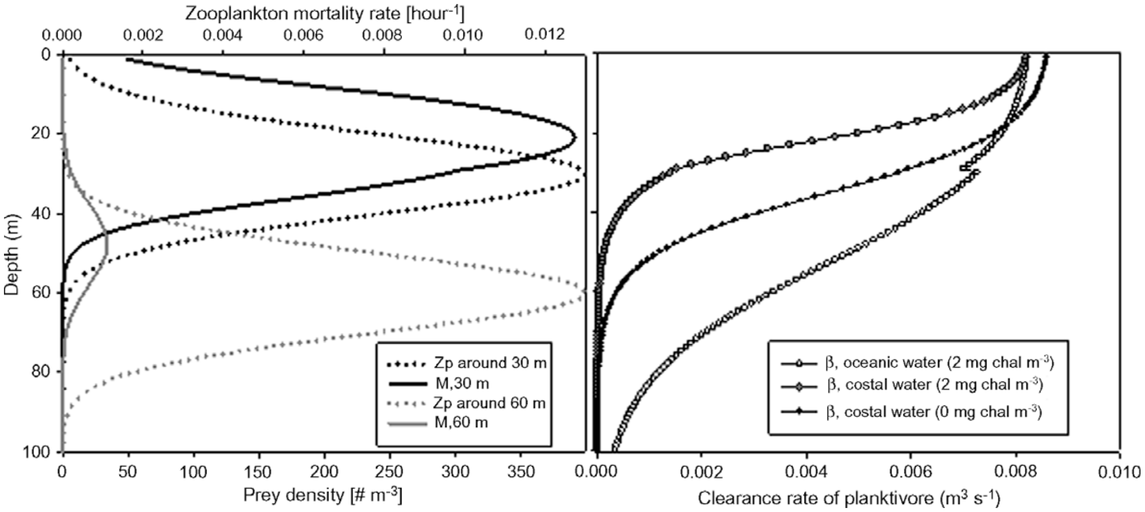

Fig. 2. Left panel: assume a population of zooplankton (*Calanus* copepodites, 2 mm long carapax, $A = 10^{-6}$ m^2) is distributed normally around 30 and 60 m depth (n_z, dotted lines), and that vertical distribution of the planktivore match the zooplankton distribution perfectly. The chlorophyll concentration in the upper 30 m is 2 mg m^{-3} and 0 below 30 m. The solid lines show mortality rate of zooplankton in each depth as calculated from Eq. (7), with 30 (black line) and 60 m as mean depth of zooplankton. Right panel: the clearance rate β of the planktivore as a function of depth for oceanic and coastal water types (a and c from Eqs. (4)–(6) and two levels of *chla*. Parameters: $I_0 = 500$ µmol photons m^{-2} s^{-1}, $F = 0.1$ herring m^{-2}, (left panel: coastal waters, 2 mg chla m^{-3}), $K = 5$ (Aksnes and Utne, 1997), $h = 2$ s, $v = 0.1$ m s^{-1}.

and the abundance of predators (Fiksen et al., 2005; Ohman, 1990; Pearre, 2003). In addition, planktivores are not passive either, and will have their own behavioural trade-offs and vertical distributions (Clark and Levy, 1988; Strand et al., 2002). As an example, fish foraging in the upper range of the copepod distribution in Fig. 2, left panel will have higher feeding rates, while zooplankton in the deeper end will have lower mortality and this could lead to relocation of both.

As shown in Fig. 3, vertical distribution will have a great effect on the predation risk of zooplankton from visual predators. In terms of implementation in ecosystem models it is important to simplify the predator–prey interaction as much as possible. It can be cumbersome to keep track of the vertical distribution of both prey and predator. Instead of modelling the predator behaviour explicitly it may be assumed that zooplankton will optimise their vertical distribution with regards to growth, survival and reproduction (Fiksen and Giske, 1995; Fiksen and Carlotti, 1998; Eiane and Parisi, 2001). A certain proportion of the predators can be assumed to overlap with the prey. A simple way to parameterise vertical distribution is therefore to use an overlap index that is 1 when the predator matches the prey distribution completely and 0 when there is no overlap. The operating predator density is then a product of the horizontal distribution of predators and the overlap index. Prey mortality can then be calculated with conventional encounter based models (Evans, 1989) that integrate density of predators and prey, the swimming velocities and reaction distance, which will be light-dependent (e.g. Rosland and Giske, 1994).

3.2. Herring–*Calanus* interactions

To exemplify the concept of modelling spatial overlap between fish and zooplankton we present a *C. finmarchicus* model where herring predation is an important source of mortality. *C. finmarchicus* is the dominant species of the mesozooplankton in the Norwegian Sea which is one of its core distribution areas (Aksnes and Blindheim, 1996; Marshall and Orr, 1952; Melle et al., 2004; Østvedt, 1955). The species is largely herbivorous and constitutes an important link between the phytoplankton and the higher trophic levels in the Norwegian Sea food chain (Aksnes and Blindheim, 1996; Melle et al., 2004). The *Calanus* is vital to many of the planktivorous fish species including Norwegian spring spawning (NSS) herring (*Clupea harengus* L.), blue whiting (*Micromesistius poutassou*, Risso), and mackerel (*Scomber scombrus* L.), which enter the Norwegian Sea during summer to utilise the abundant zooplankton resources. The herring also acts as a biological vector, a conveyor belt, of an enormous amount of lipids from the open ocean to the coastal ecosystem (Varpe et al., 2005).

A flexible IBM has been developed (Huse, 2005) to address different issues related to *Calanus* ecology. This model takes into account growth, mortality, and reproduction of *C. finmarchicus*, and uses "genes" to model its life history and behavioural strategies. The model relies on super-individuals that represent a collection of identical siblings (Scheffer et al., 1995), and the entire Norwegian Sea population of *C. finmarchicus* is thus represented by using about 30,000 super-individuals. The *Calanus* IBM includes five strategy variables ("genes", Fig. 4). The strategy variables control the over-wintering depth (OWD), and time for ascent from over-wintering (WUD), the amplitude of vertical migration (VM) which is assumed to be size dependent, the critical date for in-year maturation of C5s (AFD) and the fat soma ratio at which a C5 descends to over-wintering (FSR) (Fiksen, 2000). The *Calanus* model relies on input from an ocean circulation model, which generates temperature, advection rates and phytoplankton fields (Skogen et al., 2007). Although the model is focussing on the *Calanus*, which is modelled in great detail, it also contains an individual-based representation of the herring. However, the herring super-individuals only have a spatial position and an internal number (number of individuals represented by each super individual), and their feeding is not simulated in an explicit manner. More details about the model is given elsewhere (Huse, 2005; Samuelsen et al., 2009).

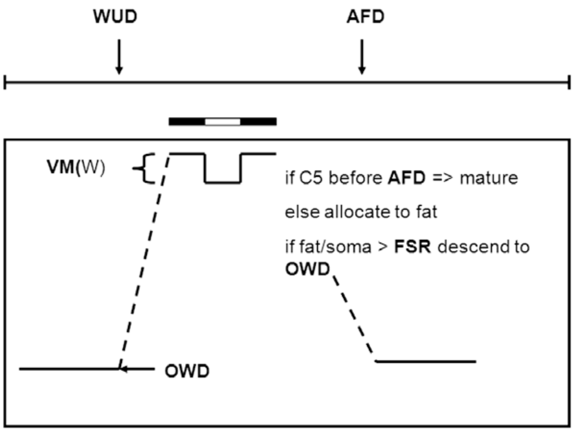

Fig. 4. The conceptual framework of the life history traits of the *Calanus* IBM. The strategy variables, whose values are evolved during a spin up simulation, are given in bold. OWD is the over-wintering depth, WUD is the date at which the over-wintering C5 starts ascent towards the surface, VM(W) gives the deepening of the *Calanus* during day as a function of their total weight (W), AFD is the date after which an individual becoming C5 will prepare for over-wintering, whereas before this date the individual will mature and try to reproduce within the season, FSR gives the fat to soma ratio at which a C5 preparing for diapauses will descend to the OWD for over-wintering.

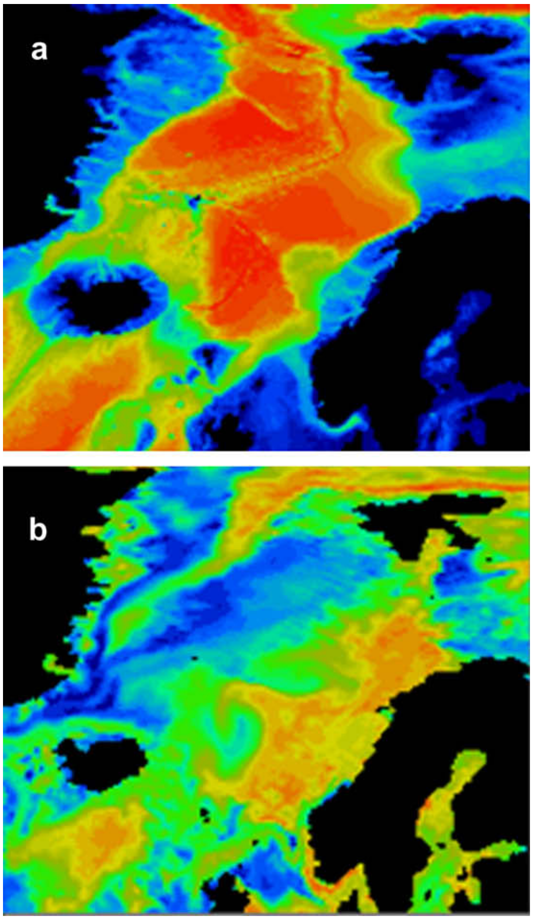

Fig. 5. The bathymetry of the *Calanus* model domain (a) and snapshot of spring phytoplankton distribution (b).

The bathymetry and a snapshot of the phytoplankton distribution during spring is shown in Fig. 5. The distribution of pelagic fish used in the present model simulations is indicated by the white square in Fig. 6a. Six simulations were performed with different assumptions about vertical distribution of the *Calanus* (see Fig. 2) and degree of vertical overlap with herring. When the *Calanus* is distributed shallowly and the overlap with herring is low (Fig. 6a), the production is high and there is only a minor effect on the distribution of *Calanus* compared to when the overlap index is high and there is a clear sign of depletion due to predation (Fig. 6b). When the *Calanus* is distributed deeper, there is a strong reduction in the production of *Calanus*, seen as a much lower second peak in the *Calanus* abundance (Fig. 7) compared to the other simulations. For the low overlap simulation (Fig. 6c) there are indications of depletion in the area where herring is distributed, the areas with depletion is much expanded when the overlap is increased (Fig. 6d). In the case when there is only non-spatially explicit mortality the *Calanus* is spread fairly evenly over the model

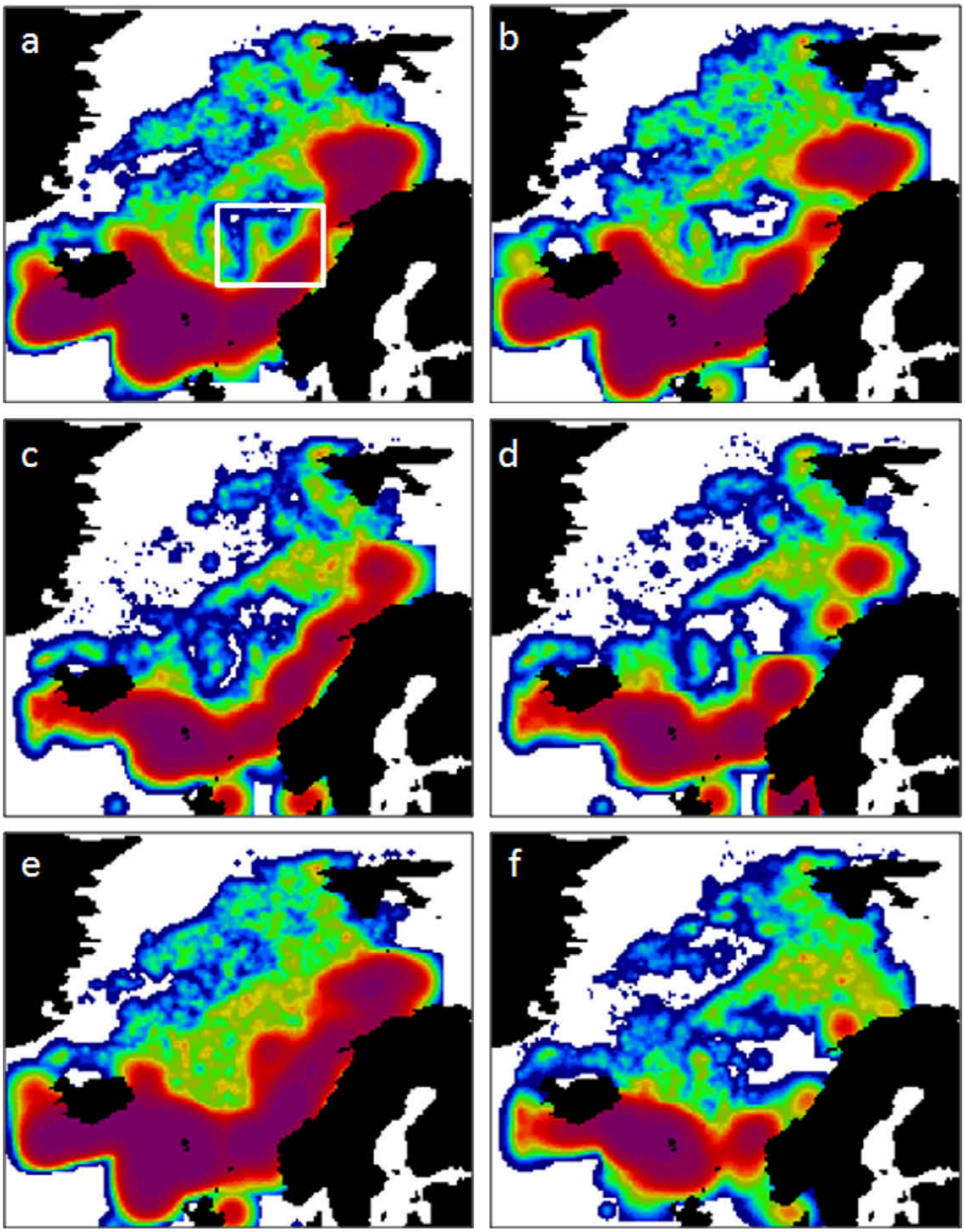

Fig. 6. Distribution of *C. finmarchicus* in early summer (day number 150) from simulations with different *Calanus* depth and vertical overlap with herring (PO). PO = 0.01 and depth 20 m (a), PO = 1, depth = 20 m (b), PO = 0.01, depth = 40 (c), PO = 1.0, depth = 40 m (d), and no spatially resolved mortality (e), PO = 1.0, night depth = 20, day depth = 40 (f). Red indicates high *Calanus* densities while blue indicates low densities, and white areas have no *Calanus*. The white square in panel a indicates the area where herring was assumed to be distributed.

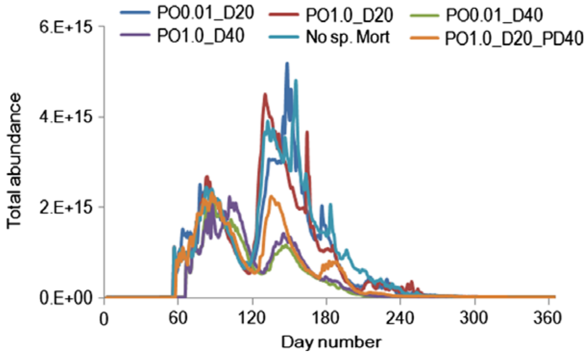

Fig. 7. Stage integrated total population abundance of the different simulations. See Fig. 6 for more explanation of the different simulations.

domain and lacks the depletion in the herring area and adjacent areas (Fig. 6e). To separate the effects of vertical distribution related to growth and predation, a final simulation was performed where the *Calanus* performed diel vertical migration between staying at 20 during night and 40 m during day with high overlap (Fig. 6f). This simulation gave a clear tendency for *Calanus* depletion in the herring area, but it is less pronounced than for the other deep simulation with high overlap (Figs. 6b and 7). The vertical dynamics of visual predation are illustrated in Fig. 2 and the present simulations illustrate the population effects of the differences in vertical distribution. There are also patterns in horizontal distribution of the *Calanus* within the "herring" distribution area. In the areas closer to the coast where the phytoplankton biomass is higher in the model (Fig. 5b), there are less signs of depletion than in the areas. Furthermore the simulations suggest that herring predation can cause depletion and thus affect the distribution of *Calanus* in the Norwegian Sea. A recent study by Olsen et al. (2007) has found that *Calanus* abundance in different areas of the Norwegian Sea is negatively related to the herring biomass in the area in the previous year. That study thus suggests that there can be "traces" of herring feeding and that these traces can be maintained for a rather long time, similar to the effect of herring predation seen in Fig. 6d. There has also been a reduction in the zooplankton abundance in the Norwegian Sea in the last decade, especially in the central parts (Anon, 2008). The feeding of the pelagic fish is therefore presently mostly associated with the fringes of the Norwegian Sea.

3.3. Cod–capelin interactions

Next we consider predator–prey interactions between cod and capelin which are both mobile and can position themselves in all three dimensions. This is studied by using an IBM with super-individuals as in the previous case, and a fine spatial resolution and short time steps to simulate the movement, growth and survival of cod (*Gadus morhua* L.) and capelin (*Mallotus villosus* Müller) in the Barents Sea. As opposed to the previous case, both the prey and the predator are represented explicitly in the model. The consumption of capelin by cod emerges from simulating encounters between the two species, and growth is calculated using bioenergetics models. We use the same basic IBM as a previous study by Huse et al. (2004), but investigate the impact of different movement rules on the spatial dynamics of the two populations and cod's consumption of capelin. Active movements can be categorised into reactive and predictive processes (Neill, 1979; Fernö et al., 1998). Reactive processes are undirected movement where the behaviour is biased by previous experiences (Neill, 1979). During feeding periods movement is dominated by turning at the presence of food patches or moving away from empty patches (Thomas, 1974), an example of reactive movement control. Predictive movement refers to movement towards relatively distant areas expected to possess favourable qualities, e.g. food or mates. As opposed to the previous study (Huse et al., 2004) where individuals were assumed to move in a predictive fashion, individuals are here allowed to respond to information about the density of the opponent (predator or prey). We investigate how such conditional rules affect the consumption of capelin by cod and the spatial dynamics of the species.

The model domain is a grid of 90 × 100 squares with a 20 km resolution. Each square is specified in terms of its temperature and zooplankton biomass. The model is initiated in fall and runs over one year (Fig. 8). Survey results are used to distribute the observed populations of cod and capelin into 20,000 super-individuals that together constitutes the entire stocks at the time of the initiation (Fig. 8). The relatively high number of super-individuals provides a highly realistic structure of the populations. Growth is calculated using bioenergetics models (Hewett and Johnson, 1992; Hansson et al., 1996) that depend on the feeding level, fish body size, temperature and activity level. Predation from cod is the greatest contributor to capelin mortality, but in addition there is starvation and fishing mortality. Cod mortality is a function of

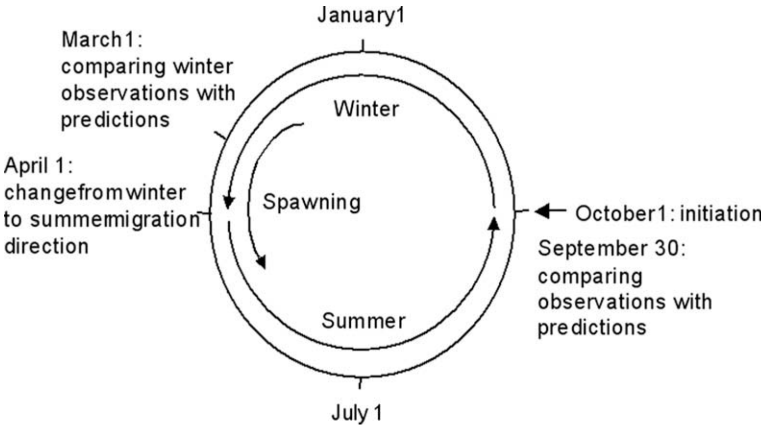

Fig. 8. The conceptual structure of the cod–capelin model. The model is initiated from observations of spatial distribution of the two stocks on October 1 and run over one year. The age, length and abundance information from the surveys are transferred into 20,000 super-individuals of capelin and cod respectively. The model predictions are compared to survey observations taken in February and September for both stocks. In addition the predicted spawning distribution of capelin is compared to observations taken in April. The movement model relies on summer and winter movement vectors and the time period for which these are used as indicated by the arrows. There is a separate movement vector for the spawning migration of the capelin. Modified from Huse et al. (2004).

Table 1
The specification of the movement rules used for simulating cod and capelin movements. The default rule is the best movement model found by Huse et al. (2004). CB and LB are the cod and capelin biomasses in a square, and CB_T and LB_T are corresponding threshold values for movement respectively.

	Capelin	Cod
0	Default	Default
1	Move towards northeast if $CB > CB_T$	Move towards northeast if $LB < LB_T$
2	Move towards fittest square within neighbourhood	Move towards fittest square within neighbourhood
3	Stay if fitness > average fitness	Stay if fitness > average fitness

fishing and starvation. For more details on the model see Huse et al. (2004).

Three different movement rules were investigated in the present study in addition to the default migration model presented by Huse et al. (2004) (Table 1). Rule 1 simulated the specific hypothesis that capelin move towards northeast to avoid cod predation (Fiksen et al., 1995) when the biomass of cod (CB) is above a threshold level (CB_T). Conversely, the cod moves towards Northeast if the biomass of capelin (LB) is below the threshold biomass (LB_T) which was set to zero for the simulation shown here. The so-called reactive search of rule 2 involves choosing the square within the neighbouring nine squares (the one presently occupied by the individual plus the eight surrounding ones) yielding the highest fitness at each time step. For capelin, the ratio of cod biomass to capelin growth rate was used as a proxy for fitness. Thus the "best" square is the one that minimises this ratio (Werner and Gilliam, 1984). For cod on the other hand we used capelin biomass as a proxy for fitness. Finally rule 3 was to stay if the fitness (as defined for rule 2) is above average for the model area or else move using the default rule from Huse et al. (2004). Each rule was tested for both species simultaneously, and for each species while the opponent used the default movement rule. In total 10 simulations, including the default simulation, were performed.

The different rules produced very different dynamics of fish movement as illustrated both by cod's predicted consumption of capelin as well as the spatial distribution of the two species and their overlap (Fig. 9). In the default simulation from Huse et al. (2004), as seen lower left panel (0/0), the average capelin consumption by cod is about 0.9 million tons. Common to all the new simulations was that when only one species was allowed

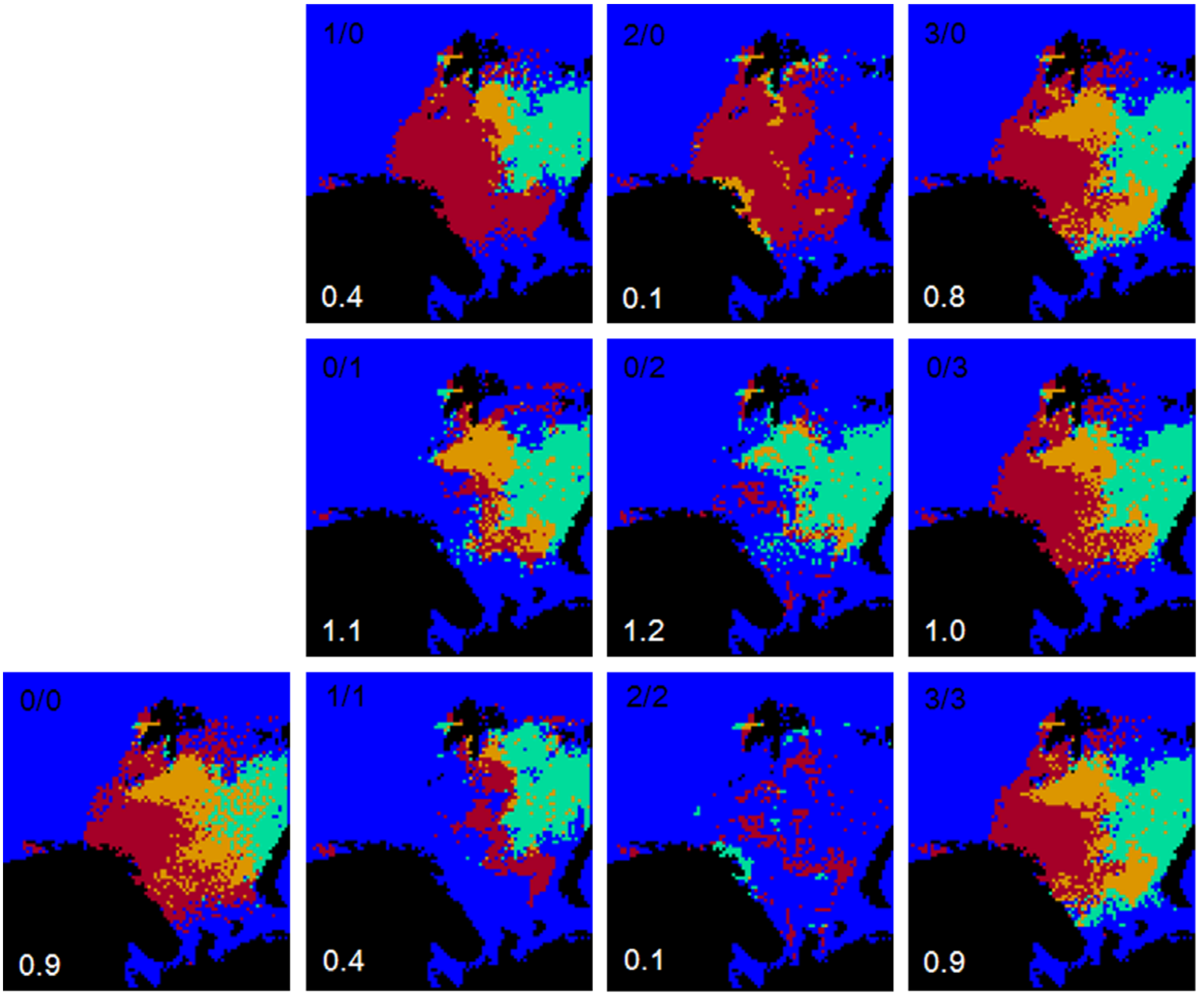

Fig. 9. The distribution of cod only (red), capelin only (green), and both species (orange) at the end of the simulation for different rules (Table 1). The number in the upper left corner of each panel gives the rule applied by capelin and cod respectively, and the value in the lower left corner gives the annual capelin consumption by cod (in million tonnes) for the simulation. The panel in the lower left corner (0/0) is the default simulation.

information about the opponent, it improved its interaction. This is seen as low levels of consumption for the simulations where only capelin was allowed information (top row) and peaks in consumption when only cod was allowed information (middle row). When both species were allowed information about the local abundance of each other, the results favoured capelin for rules 1 and 2 and was similar to the default simulation for rule 3 (Fig. 9). For rule 1 the interaction depended on the parameter giving the wariness level of the capelin (LB_T). The sensitivity of this parameter is illustrated in Fig. 10. The results show that when capelin accepts increased abundance of cod before it leaves a square, the capelin consumption by cod increases. However, since this increase in risk acceptance also makes the capelin spend more time in warm water, it also grows faster which results in an increase in capelin biomass in spite of the increased mortality (Fig. 10c). Rule 2, which relied on reactive movement only, produced very aggregated distributions (Fig. 9), and the poor fit with the default model shows that neither cod nor capelin rely purely on reactive movement. Rule 3 assumes that individuals have an idea of the average fitness of the domain and only move when the local conditions are worse than on average. When both the predator and prey apply this rule, both the distribution and consumption is fairly similar to the default simulation. This also reflects that rule 3 relied partly on the default simulation for movement.

In conclusion the simulations illustrate that implementing behaviour that is conditional on the distribution of the opponent has great impact on the spatial distribution and consumption. The approach taken here illustrates a feasible way to model dynamic interactions between predators and prey, and rules 1 and 3 in particular capture important elements of interactions between capelin and cod. Simulations based on purely reactive behaviour on the other hand do not resemble the observed spatial distribution of the cod and capelin stocks or their level of interaction determined from consumption levels. However, reactive search is a good strategy for the predator when the prey does not also employ the strategy. This is seen in the 0/2 simulations where the consumption of capelin by cod is one third higher than in the default simulation. This suggests that reactive search can be important in cases where the prey is less evasive, as in the case of the interaction between planktivorous fish and zooplankton.

4. Discussion

4.1. Implications of modelling fish predation for ecosystem models

How will the inclusion of more realistic mortality rates influence predictions from ecosystem models? One important change is that the trophic transfer from primary production to fish will not be linear. At low levels of dissolved nutrients, productivity will obviously be bottom-up regulated, and the total production of both fish and zooplankton should increase with increased nutrient supplies. However, just as self-shading will lead to negative feedback on primary production, at some point high phytoplankton concentrations will reduce foraging efficiency of fish and predation rates on zooplankton. This will limit fish production, and reduce predation on zooplankton, particularly larger forms. The production of fish as a function of nutrient supplies may be dome-shaped, where fish are prey limited at low levels and search efficiency-limited at higher levels. The nature of these processes will be important to the question of how eutrophication works on fish production. Inclusion of zooplankton–fish interactions will lead to better understanding of exactly how this will feed back on lower trophic levels and the structure of marine ecosystems. For instance, fish are generally much more efficient foragers than gelatinous invertebrates (Sørnes and Aksnes, 2004), but this is sensitive to optical properties of the water (Eiane et al., 1999; Aksnes et al., 2004). Clearly shifts in turbidity, driven by eutrophication or salinity, will have major impacts on aquatic ecosystems and their services (Aksnes, 2007), but these are not captured in contemporary ecosystem models. Similarly, lunar cycles affect fish foraging efficiency during night in low latitude regions, and this propagate into cycles of behaviour and predation on zooplankton communities (Hernandez-Leon, 2008).

In addition to the inherent environmental properties, aggregative predator responses and vertical movements of prey have strong implications for predation rate. Fish may actively seek out productive areas with high zooplankton densities, and this aggregative behaviour may alter the mortality risk to zooplankton substantially. It is therefore necessary to consider the specific behaviour of planktivorous fish in the target area when choosing how to parameterise zooplankton behaviour.

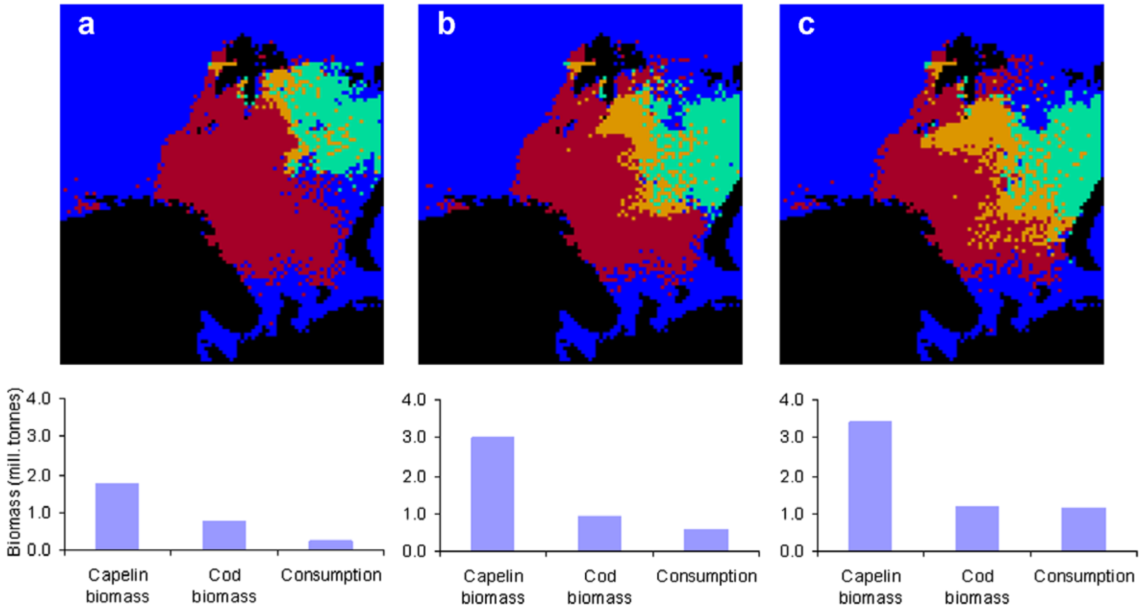

Fig. 10. The distribution of cod only (red), capelin only (green), and both species (orange) at the end of the simulation for different rules (upper panels), and capelin and cod biomass and capelin consumption (lower panels) for different values of the LB_T parameter of rule 1 (see Table 1).

Adding fish to ecosystem models is likely to result in a more realistic parameterisation of mortality, but at an increased modelling cost in terms of model complexity and need for parameterisation. Such parameterisation can help bridge the gap between ecosystem modelling and the fisheries assessment and management, and could also generate understanding or raise our consciousness of how fish production is connected to oceanography, lower trophic levels and primary productivity.

Models cannot cover everything there is to know about a particular ecosystem at the same level of detail. deYoung et al. (2004) proposed to solve this by the so-called rhomboid approach to modelling where the greatest level of detail is maintained for the target species while maintaining some level of detail for the ecosystem components immediately above and below this, and less emphasis on everything else. The balancing of where to put emphasis in model development also depends on what the goals of modelling are. If the goal is to understand the ecology of a particular species, then this is a reasonable approach (e.g. the herring–Calanus model presented above). But in case of strongly interacting species or functional groups it can also be fruitful to represent the interacting groupings with the same amount of detail (e.g. cod–capelin model).

We have suggested some elements that tie predation from fish closer to environmental variables. Naturally, zooplankton communities are also structured by predation from invertebrates (Ohman and Hirche, 2001), where relative size, turbulence and motility patterns are important in determining encounter and predation rates. For a detailed overview of the mechanics of predation among zooplankton, see Kiørboe (2008). However, mechanics are only an ingredient in food web- or ecosystem models. We will not address these issues here, only note that we expect to see an increase in agent- or trait-based approaches to community and ecosystem modelling (e.g. Woods, 2005; Bruggeman and Kooijman, 2007; Urban et al., 2008).

4.2. Modelling higher trophic levels

In studies of predator–prey interactions there has been a focus on prey behaviour while assuming predator behaviour to be unaffected by prey behaviour (Lima, 2002). This view on predator–prey interactions has historic reasons: the assumption of a constant unresponsive predator was a sensible starting point for addressing this complex problem. Also, prey species are often more amenable to observation and experimental manipulation, which has led to an emphasis on prey species. In addition to these factors, mathematical complexity has been a barrier against implementation of responsive predators (Lima, 2002). Still there have been some studies that provide predictions about predator and prey distribution. Predators tend to aggregate in areas where prey are abundant (Hassell, 1978; Sih, 1984) or easily caught, whereas prey on the other hand tend to avoid predators. These two responses can be referred to as predator and prey responses respectively. When prey are relatively immobile the predator response should dominate, yielding aggregated predator distributions (Sih, 1984). On the other hand when the prey is relatively mobile and has spatial refuges, the prey response should dominate. If both predators and prey are mobile and there are no refuges, there are no general predictions. The ability of predators to locate prey patches has been shown to be a key factor in regulating predator–prey interactions (Ellner et al., 2001). This ability depends on the complexity of the habitat, but also on the search behaviour of the predator. For example the westward migration of the Norwegian spring spawning herring in the Norwegian Sea during the feeding season is a strategy that ensures high likelihood of detecting high density food patches (Fernö et al., 1998; Holst et al., 2004). It is therefore important to improve our understanding of this element in predator–prey interactions and a close link between fieldwork, experiments and modelling will be important in this endeavour.

IBMs have been applied increasingly in ecology during the last decade (DeAngelis and Gross, 1992; Huston et al., 1988; Grimm, 1999; Grimm and Railsback, 2005). The cases presented above showed that IBMs can indeed be a valuable tool for addressing predator–prey interactions due to the readily included spatial detail and application of mechanistic sub-models. Furthermore, IBMs have the advantage of being based on the same unit as natural selection. This is important for adaptive models, as used here, where artificial evolution is used as a method for seeking good behavioural strategies (Huse, 1998; Huse et al., 1999; Strand et al., 2002). The use of adaptive modelling also allows both the predator and prey to be implemented with behavioural traits as illustrated in the cod–capelin model, a feature requested in a recent review (Lima, 2002).

Although there are many advantages associated with using emergent mortality as opposed to hard-wired mortality rates, there are some problems with the approach, particularly related to parameterisation. The number of parameters increases strongly when mortality is dependent on functional relationships and environmental features rather than fixed rates. An increased attention to modelling predation processes is therefore needed. An alternative way of parameterising predatory interactions is through size structure as in the individual-based OSMOSE model (Shin and Cury, 2001, 2004). The latter model also has spatial detail included, but operates on a much longer time step than the present models and does not take into account risk effects of predation. Nevertheless, the ability in models of having individuals adapt to the predation risk is a key issue in the study of the dynamics of animal populations in space and time. Furthermore the dynamic parameterisation of predator–prey interactions is conceptually sounder than the fixed rate assumption that has prevailed within fisheries biology for example.

5. Conclusions

There is still some way to go before we have a firm foundation for implementing fish predation on zooplankton in ecosystem models, and this represents a key step in developing end-to-end models. A key challenge is to develop generic representation of the complex spatial dynamics of fish, which is impacted by the environmental conditions and results from interplay between individual and collective decision making (Fernö et al., 1998; Corten, 2002; Huse et al., 2002). In many cases fish predation is important to the population dynamics of zooplankton and also the level of fish predation can vary markedly between years. There is management and commercial interest in planktivorous fish, and therefore several reasons for including fish predation in ecosystem models. We have discussed the dual role of predation as removing individuals from the prey population as well as impacting on the behaviour of prey. Furthermore we have illustrated how predation processes can be included in ecosystem models both on a conceptual basis and with specific implementations for herring–*Calanus* and cod–capelin. It is important to explore different avenues of incorporating fish predation in ecosystem models and we have presented both a relatively simple approach based on relating the predation mortality implicitly to environmental features and an alternative approach where the predators are modelled explicitly. In case of relatively stationary fish predators such as mesopelagic fish, the first approach is sufficient to capture the interaction, but in cases where the horizontal space use of the fish is highly dynamic, the latter explicit representation of predators is preferable.

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