

# Multiple predators in the pelagic: modelling behavioural cascades

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## Summary

1. The behaviour of predators is rarely considered in models of predator–prey interactions, nor is it common to include multiple predators in models of animal behaviour.
2. We introduce a model of optimal diel vertical migration in zooplankton prey facing predation from two functionally different predators, fish and other zooplankton. Zooplankton predators are themselves subject to predation from larger zooplankton, and all zooplankton face the classical trade-off between increasing growth rate and predation risk from fish towards the surface. Prey are most vulnerable to zooplankton predators at small sizes, but become more visible to fish as they grow. However, by habitat selection prey continuously manage their exposure to different sources of risk.
3. We analyse situations with cascading behavioural interactions of size-structured predator–prey interactions in the pelagic. In particular, we explore how vertical gradients in growth rates and relative abundance of fish and zooplankton predators affect optimal distribution patterns, growth and mortality schedules.
4. A major model prediction is that prey susceptibility to one functional predator type depends on the abundance of the other predator. Higher abundance of zooplankton predators leads to risk enhancement from fish, minor increases in predation rate from zooplankton and unchanged prey growth rates. Increasing abundance of fish does not alter the risk from zooplankton predators, but reduces growth and development rates. Such asymmetric emergent effects may be common when prey and predators share the same spatial refuge from a common top predator.

*Key-words:* DVM, dynamic programming, emergent effects, multiple predators, zooplankton.

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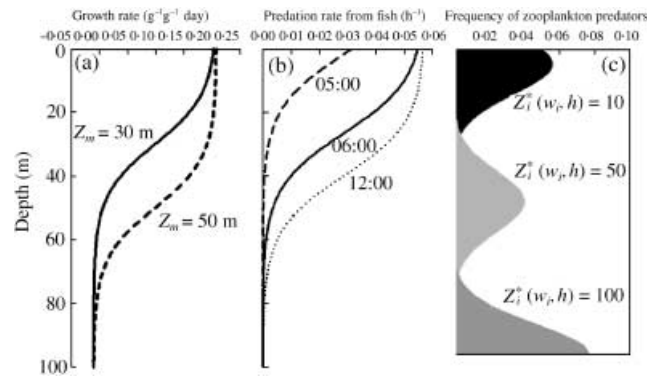
## Introduction

Predator and prey theory is biased towards one-predator–one-prey interactions (Sih, Englund & Wooster 1998). However, most prey are exposed to and responsive towards several predators, and may balance their antipredator behaviours with the relative predator abundance. It is usually not obvious how the presence of several predators affect behaviour, growth and predation risk of prey. Prey may benefit from the presence of multiple predators if these interfere with each other. Also, behavioural defence of prey to one predator may enhance the exposure to other predators. Presence of

several predators thus may increase predation rates more than the additive expectation from the predators in isolation. Recently, the need to include multiple and behaviourally responsive predators in models of animal behaviour has been emphasized (Holt & Polis 1997; Sih *et al.* 1998; Alonzo 2002; Lima 2002; Lima, Mitchell & Roth 2003).

In size-structured pelagic food webs the classification of organisms as predator or prey is determined largely by relative size. Behaviour in one size category may therefore structure the behaviour of smaller size-groups, because predators often induce behavioural or strategic changes in their prey. If these prey are important predators to smaller organisms they may in turn cause further behavioural changes, or ‘behavioural cascades’ (Romare & Hansson 2003), where the abundance of a predator at a higher trophic level leads to behavioural changes of organisms over several lower

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**Fig. 1.** Vertical profiles of growth and predation rate. (a) Growth rates with two different mixed layer depths  $Z_m$  (30 and 50 m). (b) Predation rate (from fish only) for a 5 mm prey at three different times of the day (05, 06 and 12), with  $B_F = 1 \text{ g m}^{-2}$  and light extinction at  $0.12 \text{ m}^{-1}$ . (c) The concentration of zooplankton predators  $N_i(z, w, h)$  in depth  $z$ , size class  $w_i$  at time  $h$  is defined by the total zooplankton abundance (in biomass  $B_p$  or numbers  $I_i$ ; Table 1) and a normal distribution with mean  $z_i^*(w_i, h)$  and standard deviation 7.5 m. The graph shows the depth distribution of size-classes with three different optimal depths (10, 50 and 100 m).

trophic levels. An example is when planktivorous fish induce normal (up at night, down during the day) diel vertical migration (DVM) in large predatory copepods and chaetognaths, which in turn leads to inverse DVM in their smaller copepod prey (Ohman 1990). Such observations indicate that the optimal DVM strategy depends on the presence and relative abundance of two functionally different predators.

Situations where prey responses dominate and predation rates or distribution patterns change considerably in the presence of several predators are called ‘emergent effects of multiple predators’ (Sih *et al.* 1998). In the absence of fish, large zooplankton predators may remain in the preferred habitats of their prey. In the presence of fish, large zooplankton are forced out of the illuminated habitats during the day, which reduces spatial and temporal overlap with smaller zooplankton prey. The best response of small zooplankton may then be to remain near the surface during the daytime, despite the cost of higher predation from fish. In this case, it is not obvious if prey experience risk enhancement or reduction. Behavioural interactions between predators could lead to deviations from simple additive or linear effects from the two predator types. Also, prey themselves may adjust their habitat selection in response to relative densities or efficiencies of predators, and exhibit considerable ontogenetic changes in behaviour (Titelman & Fiksen 2004).

DVM is a classic example of the trade-off between growth and predation risk (Pearre 2003). Despite the wide range of models on DVM strategies in both fish and plankton (Clark & Levy 1988; Fiksen 1997; Eiane & Parisi 2001), none of them consider behavioural cascades. However, modelling behavioural interactions in size-structured predator–prey systems with functionally different predators is challenging. In particular, if both predators and prey respond readily to the movements of each other, a game-theoretical approach is required (Iwasa 1982; Gabriel & Thomas 1988). If prey has a safe refuge or predators do not tend to follow their prey, then an optimality approach is appropriate.

Using an optimality approach, we predicted successfully ontogenetic habitat switches of different copepod species in a Swedish fjord system (Titelman & Fiksen 2004). Here, we develop a general model of DVM patterns and predation rates under multiple predators, assuming that prey behave optimally. The model predicts interaction strength between prey and its two predator types to change abruptly with their relative abundance.

## Model

The model is formulated mainly with the pelagic oceanic community in mind, where large omnivorous or predatory euphausiids, copepods and chaetognaths and smaller zooplankton grazing on microzooplankton, phytoplankton and detritus are core components. We focus on a zooplankter resembling a large copepod or euphausiid. It increases in body length from 0.5 mm at birth to 20 mm at maturity (196 discrete size-groups in 0.1 mm intervals), after which they allocate all surplus energy to reproduction. The specific growth rate  $g(z)$  varies over depth reflecting a typical situation with a well-mixed layer of warm or food-rich water above the thermocline and deeper, colder or food-deprived water where growth becomes slightly negative (Fig. 1a). We assume that all zooplankton, including both prey and predators, have a fixed habitat-specific growth rate. Larger stages act as predators (‘zooplankton predators’) on smaller stages. The planktivorous fish predator is represented as a size-structured (0.02–0.3 m) population, with equal biomass in each size category (smaller fish more abundant). Fish are inert to prey movements, and distributed homogeneously across all depths. The fish population is therefore described fully by its abundance (Table 1). Fish are cruising predators, with clearance rates determined by ambient light, prey size and search-and-capture efficiency, as described by Titelman & Fiksen (2004). The predation rate  $\mu_F(z, w_p, h)$  from fish on prey with body mass  $w_p$  in depth  $z$  at time  $h$  is a function of clearance rate  $\beta_F$ , density  $N_F$  and capture

**Table 1.** A description of variables, parameters, their dimensions and values. The subscripts *F*, *P* and *i* denote fish, zooplankton prey and zooplankton predators, respectively

Symbol	Description	Value (range)	Unit
<i>z</i>	Depth	1 (0–100)	m
<i>h</i>	Time	0.5 (0–48)	hour
<i>d</i>	Day number	1 (1–150)	day
<i>l<sub>p</sub>, l<sub>i</sub></i>	Zooplankton length class	10 <sup>-4</sup> (0.5–20 × 10 <sup>-3</sup> )	m
<i>l<sub>F</sub></i>	Fish length class	10 <sup>-2</sup> (2–30 × 10 <sup>-2</sup> )	m
<i>w<sub>F</sub></i>	Fish weight <sup>1</sup>	–	g
<i>w<sub>p</sub>, w<sub>i</sub></i>	Zooplankton weight <sup>2</sup>	–	g
<i>B<sub>F</sub></i>	Total fish abundance (biomass)	(0–1)	g m <sup>-2</sup>
<i>B<sub>P</sub></i>	Total zooplankton abundance (biomass)	(0–25)	g m <sup>-2</sup>
<i>I<sub>F</sub></i>	Number of fish in length class <sup>3</sup>	–	ind m <sup>-2</sup>
<i>I<sub>p</sub>, I<sub>i</sub></i>	Number of zooplankton in length class <sup>3</sup>	–	ind m <sup>-2</sup>
<i>J<sub>F</sub></i>	Number of fish length classes	29	–
<i>J<sub>p</sub></i>	Number of zooplankton length classes	196	–
<i>N<sub>F</sub></i>	Concentration of fish in length class <sup>4</sup>	–	ind m <sup>-3</sup>
<i>N<sub>p</sub>, N<sub>i</sub></i>	Concentration of zooplankton predator at any depth, length and time <sup>5</sup>	–	ind m <sup>-3</sup>
<i>μ<sub>F</sub></i>	Fish predation rate <sup>6</sup>	–	h <sup>-1</sup>
<i>μ<sub>p</sub></i>	Zooplankton predation rate <sup>7</sup>	–	h <sup>-1</sup>
<i>P<sub>F</sub></i>	Capture success of fish predator <sup>8</sup>	–	ND
<i>P<sub>i</sub></i>	Capture success of zooplankton predator <sup>9</sup>	–	ND
<i>β<sub>F</sub></i>	Clearance rate of fish predator <sup>8</sup>	–	m <sup>3</sup> h <sup>-1</sup> ind <sup>-1</sup>
<i>β<sub>i</sub></i>	Clearance rate of zooplankton predator <sup>9</sup>	–	m <sup>3</sup> h <sup>-1</sup> ind <sup>-1</sup>
<i>Φ</i>	Zooplankton fitness <sup>10</sup>	–	Eggs
<i>m</i>	Maximum movement range per time <sup>10</sup>	–	m
<i>z<sub>i</sub><sup>*</sup>, z<sub>p</sub></i>	Optimal depth	(0–100)	m
<i>Z<sub>m</sub></i>	Mixed layer depth	30, 50	m
<i>g</i>	Zooplankton growth rate <sup>11</sup>	(–0.01–0.2)	g g <sup>-1</sup> day <sup>-1</sup>
<i>b</i>	Zooplankton reproduction <sup>12</sup>	–	Eggs day <sup>-1</sup>
<i>k</i>	Growth-to-egg conversion efficiency <sup>12</sup>	0.1	Eggs g <sup>-1</sup>

<sup>1</sup> $w_F = l_F^3 \times 10^4$ ; <sup>2</sup>length–weight relation as for *Calanus finmarchicus* in Mauchline (1998); <sup>3</sup> $I = B/wJ$ ; <sup>4</sup> $N_F(l_F) = I_F/100$  (abundance/number of depth cells); <sup>5</sup> $N_i(z, w_p, h) = I_i \eta(z, \sigma) / l_i \eta(z, \sigma) dz$ , where  $\eta$  is a normal distribution with mean  $z_i^*(w_i, h)$  and standard deviation  $\sigma$  equal 7.5 m (see Fig. 1c); <sup>6</sup>eqn 1; <sup>7</sup>eqn 2; <sup>8</sup>Titelman & Fiksen (2004); <sup>9</sup>Svensen & Kiørboe (2000); <sup>10</sup>eqn 3; <sup>11</sup> $g(z) = 0.21/(1 + e^{0.125(z - Z_m)}) - 0.01$ , plotted in Fig. 1; <sup>12</sup> $b(w_p, z) = g(z)w_p k$ .

success  $P_F$  summed over all fish size categories (Table 1, Fig. 1b):

$$\mu_F(z, w_p, h) = \sum_{l_F=0.3}^{l_F=0.3} \beta_F(z, w_p, l_F, h) N_F(l_F) P_F(w_p, l_F) \quad \text{eqn 1}$$

Similarly, we have included an explicit model of the zooplankton predation rate  $\mu_p(z, w_p, h)$ , where clearance rate  $\beta_i$  is taken from Svendsen & Kiørboe (2000) and capture success  $P_i$  depends on predator–prey size ratio (Titelman & Fiksen 2004). The total mortality rate is the sum from all potential predators (length  $l_i$ ) larger than the focal prey of length  $l_p$  and body mass  $w_p$ :

$$\mu_p(z, w_p, h) = \sum_{l_i=l_p+0.0001}^{l_i=0.02} \beta_i(w_i, w_p) N_i(z, w_i, h) P_i(w_i, w_p) \quad \text{eqn 2}$$

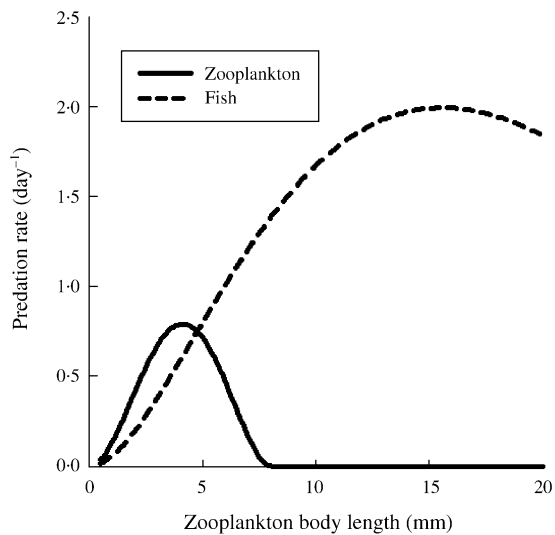
The largest zooplankton are not susceptible to predation from other zooplankton. For smaller prey, which are themselves prey of larger zooplankton, the picture is more complex, as they must balance risk from different predators against growth. To smooth the predator field, the concentration  $N_i$  of each size class of zooplankton predators is distributed normally around the optimal habitat, constrained by surface and bottom

(Fig. 1c, Table 1). The predation risk from both fish and zooplankton is highly size-dependent (clearance rate, capture success, numerical abundance of size class; see Table 1). Figure 2 shows an example of size-dependent predation rates when both prey and predators are restricted to the surface layer. Prey outgrow their zooplankton predators, but can always be consumed by at least some fish.

The optimal habitat is defined as the depth that maximizes expected future egg production, and is found by dynamic programming (Houston & McNamara 1999; Clark & Mangel 2000). Habitat selection is restricted to depths that can be reached by constant, directional swimming (assuming a swimming velocity of one body length  $s^{-1}$ ) during one time step (i.e.  $z^* \pm m$ ). The general dynamic programming equation is:

$$\Phi(w_p, z^*, h, d) = \max_{z^*-m \leq z \leq z^*+m} \left[ b(w_p, z) + e^{-\mu_F(z, w_p, h) - \mu_p(z, w_p, h)} \times \Phi(w_p + w_p g(z), z, h + 1, d) \right] \quad \text{eqn 3}$$

This equation maximizes expected lifetime reproductive output by choosing the best sequence of habitats from the present time (hour  $h$ , day  $d$ ) until the end of the season ( $d = 150$ ). The diel cycle is divided into 48



**Fig. 2.** The predation rate from fish and zooplankton predators when the model has no spatial resolution (only the surface layer) and there is no behaviour. The predation rate is low for small individuals as they are less conspicuous to both fish and zooplankton. At some size, prey outgrow their predators capture abilities. Here,  $B_p$  was reduced to  $1 \text{ g m}^{-2}$  and  $B_f$  to  $0.01 \text{ g m}^{-2}$ .

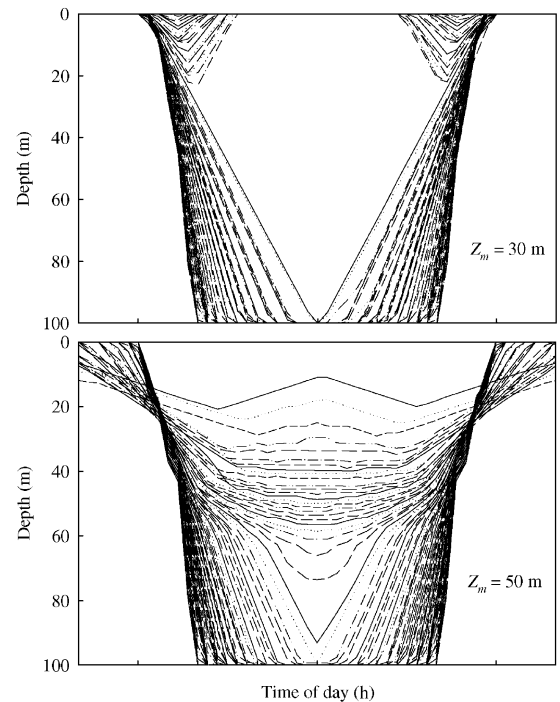
discrete time intervals. The terminal fitness value  $\Phi(w_p, z^*, 48, 150)$  equals zero, meaning that all individuals die in the end. As time to horizon decreases, animals become more risk-prone to produce as many offspring as possible before the end of the season. We therefore ran the model for more than 100 days to avoid these terminal effects. Reproduction  $b(w_p, z)$  is restricted to mature stages and is proportional to specific growth rate  $g(z)$  (Fig. 1a, Table 1). Predation from fish  $\mu_f$  and zooplankton  $\mu_p$  varies in space and time. In addition,  $\mu_p$  is formed by the habitat selections of larger zooplankton. The convergent optimal DVM strategy  $z_p^*(w_p, h, d = 150)$  is stored for analysis and presentation.

## Results

### WITH FISH PREDATORS ONLY: THE EFFECT OF GROWTH GRADIENTS

There are striking differences in the optimal strategy  $z_p^*(w_p, h)$  as the mixed layer depth increases from 30 to 50 m (Fig. 3). The deeper growth profile alters the balance between risk and growth to the point where it becomes profitable also for larger zooplankton to remain within the mixed layer during the day (Fig. 3, lower panel).

The optimal diel trajectories of different size classes are not obvious, even with only one predator type. Some intermediate size classes descend in the water column at dusk and dawn (Fig. 3). The profitability of this behaviour emerges from the diel changes in predation risk (Fig. 1b). In the early morning the risk decreases exponentially with depth. At midday, the profile is sigmoid due to light saturation in the functional response of the fish. Zooplankton must leave the mixed layer completely



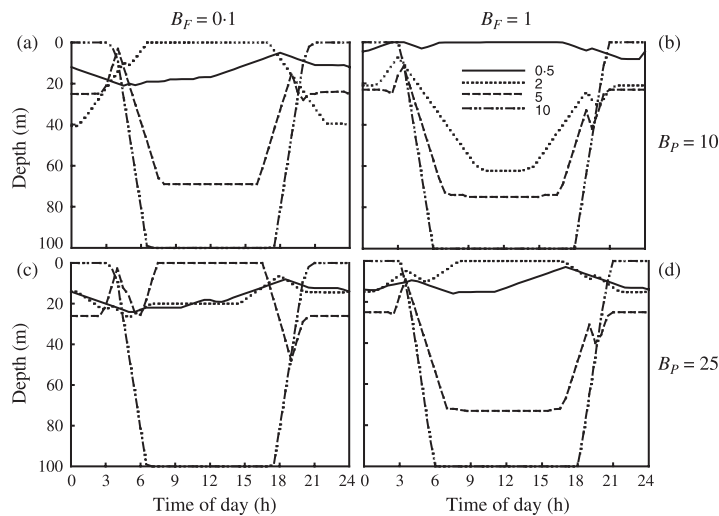
**Fig. 3.** Modelled optimal habitats over one diel cycle for all size groups (0.5–20 mm) of zooplankton when fish is the only predator ( $B_f = 0.1 \text{ g m}^{-2}$ ). Lines represent one size group structured from small to large from surface to bottom during midday. The simulations differ in their inflexion point  $Z_m$  (Table 1) of the growth function (mixed layer depth), which is 30 m in the upper and 50 m in the lower panel. The vertical growth profiles are as in Fig. 1a.

to significantly reduce predation risk at high levels of irradiance, whereas in the morning and evening they benefit from simply moving deeper into the mixed layer.

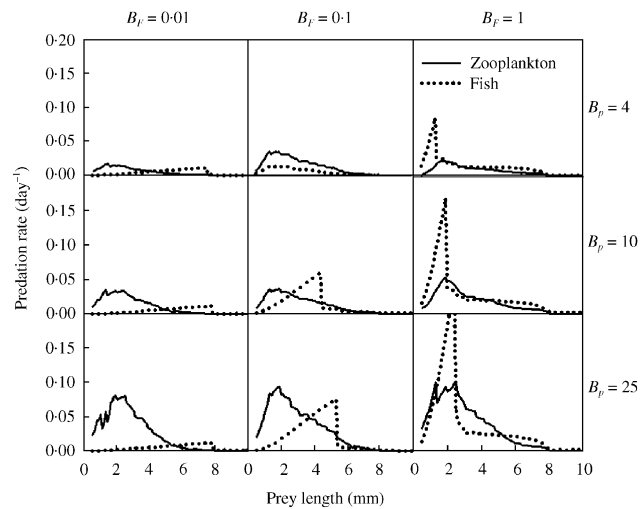
### OPTIMAL BEHAVIOUR WITH TWO PREDATORS

The picture becomes more complicated when zooplankton predators are included. In Fig. 4, we present optimal DVM strategies for four size classes at combinations of 0.1 and  $1 \text{ g m}^{-2}$  of fish  $B_f$  and 10 and 25 (wet weight)  $\text{g m}^{-2}$  of zooplankton  $B_p$ . These concentrations (Table 1) are scaled to fit with those seen typically in oceanic areas. Now, the behaviour, abundance and distribution of larger zooplankton predators also affect the emerging spatial distributions. The effects of  $B_f$  and  $B_p$  on zooplankton distribution vary with size, and there are threshold predator levels that trigger behavioural shifts that cascade down the food chain.

The largest zooplankton predators ( $> 10 \text{ mm}$ ) are vulnerable to fish, but safe from other zooplankton predators. They are efficient swimmers, and migrate between the habitat with the highest growth during the night and the safest habitat during the day. Similarly, the 5 mm prey are susceptible to visual predators, but can also be eaten by the largest zooplankton predators. Consequently, 5 mm prey migrate out of the mixed layer during the day, but avoid the deepest habitats to reduce overlap with the largest zooplankton. For the



**Fig. 4.** Predicted optimal habitats over the diel cycle for selected size-classes of prey (0.5, 2, 5 and 10 mm) under four different predator regimes: (a) low fish–low zooplankton; (b) high–low; (c) low–high and (d) high fish–high zooplankton abundance.



**Fig. 5.** Average diel rate of predation under various combinations of predator abundance. The abundance of fish  $B_F$  is 0.01 (left panels), 0.1 (middle panels) and 1  $\text{g m}^{-2}$  (right panels) and  $B_P$  is 4, 10 and 25  $\text{g m}^{-2}$  from top to bottom. Predation rates are low and constant for prey  $> 10$  mm, and are omitted from the graphs.

same reason, they avoid the maximum growth habitats near the surface at night. This pattern changes with low  $B_F$  and high  $B_P$  (Fig. 4c). The enhanced risk in deeper layers during the day, including descent and ascent, and reduced risk in the surface shift the balance towards an inverse DVM strategy. The optimal behaviour includes strategic movements to reduce temporal overlap with large zooplankton at dusk and dawn.

Smaller zooplankton ( $< 2$  mm) are more difficult to assess, as they have numerous predators behaving in different ways. The optimal strategy for these varies with predator regime (Fig. 4). The 2 mm prey do inverse DVM in the low  $B_F$ –low  $B_P$  case (Fig. 4a), but normal DVM for the high  $B_F$ –low  $B_P$  case (Fig. 4b). Under high  $B_P$  (Fig. 4c,d), this response is reversed. Migratory activity is low in both cases. The smallest prey (0.5 mm) have limited mobility ( $1.8 \text{ m h}^{-1}$ ), and migrate typically asymmetrically over the diel cycle as a response to the ascending and descending zooplankton predators. In summary, inverse, normal and no DVM

may be optimal depending on the relative abundance of predators and prevailing environmental conditions.

#### REALIZED PREDATION RATES UNDER VARIOUS PREDATOR REGIMES

Predator-induced behavioural changes typically modify both magnitudes of risk and exposure and vulnerability to other predators (Fig. 5). At low  $B_F$  ( $0.01 \text{ g m}^{-2}$ ), an increase in  $B_P$  from 4 to 25  $\text{g m}^{-2}$  increases the predation rate proportionally, without changing fish predation rate. However, at  $B_F \geq 0.1 \text{ g m}^{-2}$  emergent effects appear. In fact, an isolated increase ( $4\text{--}10 \text{ g m}^{-2}$ ) in  $B_P$  yields only minor increases in predation from these predators. Simultaneously, predation from fish increases considerably.

The exposure to fish changes markedly as zooplankton grows in size. Initiation of strong normal DVM is reflected in a conspicuous drop in fish predation (Fig. 5). This behavioural shift is delayed as  $B_P$  increases, mainly

**Table 2.** Number of days required for a 0.5 mm prey to reach the size of 1, 10 and 20 mm under various combinations of predator abundance

Size (mm)	$B_F = 0.1 \text{ (g m}^{-2}\text{)}$			$B_F = 1 \text{ (g m}^{-2}\text{)}$		
	$B_P \text{ (g m}^{-2}\text{)}$					
	4	10	25	4	10	25
1	10.3	10.9	11.8	9.7	9.9	10.3
10	75.1	70.0	70.0	102.0	98.1	95.0
20	102.0	96.9	98.1	132.0	129.9	127.0

as a result of increased danger in deeper layers during the day and the increased benefit of growing rapidly through the small and vulnerable size classes.

The emergent effect of multiple predators appears to be one-way in the case outlined here (Fig. 5). While higher  $B_P$  strongly affects the allocation of risk between predators, a corresponding increase in  $B_F$  at a given level of  $B_P$  does not affect the predation rate from zooplankton (Fig. 5).

Managing risk from several predators comes at the cost of slower growth and higher age at maturation (Table 2). More fish generate longer development times than do higher abundance of zooplankton. This is because the behavioural response to visual predators is associated more directly with growth – more normal DVM implies less time in the best habitats for growth. At higher levels of  $B_P$ , the surface is a better alternative at times when larger zooplankton predators are located below the mixed layer.

## Discussion

The model suggests that predation rates are sometimes, but usually not, proportional to the density of predators (Fig. 5), nor do they resemble the predation rate expected under the assumption of no antipredator behaviour (Fig. 2). Increasing fish abundance will lead partly to reduced rates of growth and development of their prey (Table 2) and partly to higher, but not proportionally higher, rates of mortality. The presence of two size-structured predator populations led to marked switches in the spatial distribution of size-classes as the abundance of the predators changed (Fig. 4). With only fish as predators, we demonstrated that mixed-layer depth is surprisingly important for DVM strategies of zooplankton (Fig. 3).

All animals are normally at risk of predation from several predators. In the pelagic oceanic community, most mesozooplankton may be eaten by several species with different foraging strategies: schooling fish appearing randomly at any depth or mesopelagic fishes forming ‘deep scattering layers’ in the daytime and migrating to the surface at night (Kaartvedt 2000). Other animals in the deep scattering layers are omnivores such as krill and predatory invertebrates with

considerable migration activity. Zooplankton are flexible in their migration behaviour, depending on the abundance of fish (Bollens & Frost 1989) or invertebrates (Ohman, Frost & Cohen 1983; Irigoien, Convey & Harris 2004). Our model includes many of these features: intraguild predation, flexible prey and strong spatial gradients of growth and risk. In Titelman & Fiksen (2004), we demonstrated that this approach successfully predicted ontogenetic habitat shifts in numerous marine zooplankton species.

Behavioural cascades may be important in structuring aquatic ecosystems. Wissel, Boeing & Ramcharan (2003) conducted an enclosure experiment with combinations of fish, invertebrate predators (*Chaoborus*) and various herbivorous zooplankton in high and low turbidity water. As expected, larger zooplankton did best in turbid treatments, where the predation from fish was reduced. However, small herbivorous zooplankton dominated over larger *Daphnia* in clear water treatments with *Chaoborus* but no fish. Wissel *et al.* (2003) related this to the altered distribution pattern in clear water, where the smaller herbivores concentrated nearer the surface, the larger herbivores deeper down and the invertebrate predators more evenly in the water column. Thus, the increased light may have generated a perceived feeling of risk that increased the spatial overlap between large herbivores and invertebrate predators. This behavioural response had a strong effect on the structure of the food web (Wissel *et al.* 2003). Similarly, Romare & Hansson (2003) added caged piscivores to an enclosure with planktivores (roach) and herbivores (*Daphnia*). The presence of piscivores caused planktivores to spend more time in the safer (vegetated) habitats, and this triggered large *Daphnia* to increase time spent in open waters. In this behavioural cascade herbivores had only one predator, and the planktivore had reduced efficiency in the safe habitat shared with the herbivores.

Asymmetry in predator effects should occur in any system where predator 1 consumes predator 2 and prey, and the best response to increasing threats from predator 1 for both predator 2 and prey is to hide in the same habitat. This tends to increase the spatial overlap between predator 2 and prey, and at some point it may become profitable for the prey to move back to the habitat where it is exposed to predator 1.

The prey exposure to fish predators varied with  $B_F$ ; at lower fish abundance the model predicted that zooplankton should be larger before the onset of strong DVM (Fig. 5). Therefore smaller zooplankton remain vulnerable to fish at larger sizes at low fish abundance. On the other hand, a higher abundance of zooplankton may lead to major changes in predation from fish due to the behavioural responses of prey. Such shifts in exposure between predators represent a major challenge to models, including organisms with flexible behaviour, in systems where behavioural cascades are prominent. In these systems, major changes in abundance or distribution of predators will induce behavioural changes

in their prey and transfer of energy between trophic levels will be altered.

A wide range of explanations of diel rhythms of zooplankton migration has been suggested (reviewed in Pearre 2003), and only a limited number has been addressed here. Our model suggests that the optimal positioning of zooplankton in a water column is sensitive to environmental gradients, abundance and distribution of predators. The model predicted DVM patterns to depend on mixed layer depth and the relative shapes of growth and mortality rates. When growth can be achieved at lower risk, as with a deeper mixed layer depth, the value of daytime migration decreases.

The optimality framework that we have applied here has two main limitations. First, it is difficult to incorporate a behavioural response in the predator to the defensive strategy of its prey. This implies that the model does not fully 'put predators back into behavioural predator-prey interactions' in the game-theoretical meaning of Lima (2002). Secondly, the model does not allow for environmental feedback mechanisms to operate. Thus, the consequences of behaviour of either predators or prey on population dynamics or food web structure cannot be modelled realistically (Persson & De Roos 2003). To include such processes, simulations with individual-based models including explicit genetic structure governing behavioural responses (Eiane & Parisi 2001; Strand, Huse & Giske 2002; Giske *et al.* 2003) or models with rule-based individual behaviour (Persson & De Roos 2003) may be more suitable. However, our model allows explicit solutions, and is valid when prey has safe refuges or prey responses dominates.

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### References

- Alonzo, S.H. (2002) State-dependent habitat selection games between predators and prey: the importance of behavioural interactions and expected lifetime reproductive success. *Evolutionary Ecology Research*, **4**, 759–778.
- Bollens, S.M. & Frost, B.W. (1989) Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus-Pacifcus*. *Limnology and Oceanography*, **34**, 1072–1082.
- Clark, C.W. & Levy, D.A. (1988) Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *American Naturalist*, **131**, 271–290.
- Clark, C.W. & Mangel, M. (2000) *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford University Press, New York.

- Eiane, K. & Parisi, D. (2001) Towards a robust concept for modelling zooplankton migration. *Sarsia*, **86**, 465–475.
- Fiksen, Ø. (1997) Allocation patterns and diel vertical migration: modeling the optimal *Daphnia*. *Ecology*, **78**, 1446–1456.
- Gabriel, W. & Thomas, B. (1988) Vertical migration of zooplankton as an evolutionarily stable strategy. *American Naturalist*, **132**, 199–216.
- Giske, J., Mangel, M., Jakobsen, P., Huse, G., Wilcox, C. & Strand, E. (2003) Explicit trade-off rules in proximate adaptive agents. *Evolutionary Ecology Research*, **5**, 835–865.
- Holt, R.D. & Polis, G.A. (1997) A theoretical framework for intraguild predation. *American Naturalist*, **149**, 745–764.
- Houston, A. & McNamara, J. (1999) *Models of Adaptive Behaviour*. Cambridge University Press, Cambridge.
- Irigoin, X., Convey, D.V.P. & Harris, R.P. (2004) Flexible diel vertical migration behaviour of zooplankton in the Irish Sea. *Marine Ecology – Progress Series*, **267**, 85–97.
- Iwasa, Y. (1982) Vertical migration of zooplankton – a game between predator and prey. *American Naturalist*, **120**, 171–180.
- Kaartvedt, S. (2000) Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. *ICES Journal of Marine Science*, **57**, 1819–1824.
- Lima, S.L. (2002) Putting predators back into behavioral predator-prey interactions. *Trends in Ecology and Evolution*, **17**, 70–75.
- Lima, S.L., Mitchell, W.A. & Roth, T.C. (2003) Predators feeding on behaviourally responsive prey: some implications for classical models of optimal diet choice. *Evolutionary Ecology Research*, **5**, 1083–1102.
- Mauchline, J. (1998) Advances in marine biology – the biology of calanoid copepods. *Advances in Marine Biology*, **33**, 1–710.
- Ohman, M.D. (1990) The demographic benefits of diel vertical migration by zooplankton. *Ecological Monographs*, **60**, 257–281.
- Ohman, M.D., Frost, B.W. & Cohen, E.B. (1983) Reverse diel vertical migration – an escape from invertebrate predators. *Science*, **220**, 1404–1407.
- Pearre, S. (2003) Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biological Reviews*, **78**, 1–79.
- Persson, L. & De Roos, A.M. (2003) Adaptive habitat use in size-structured populations: linking individual behavior to population processes. *Ecology*, **84**, 1129–1139.
- Romare, P. & Hansson, L.A. (2003) A behavioral cascade: top-predator induced behavioral shifts in planktivorous fish and zooplankton. *Limnology and Oceanography*, **48**, 1956–1964.
- Sih, A., Englund, G. & Wooster, D. (1998) Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, **13**, 350–355.
- Strand, E., Huse, G. & Giske, J. (2002) Artificial evolution of life history and behavior. *American Naturalist*, **159**, 624–644.
- Svensen, C. & Kiørboe, T. (2000) Remote prey detection in *Oithona similis*: hydromechanical versus chemical cues. *Journal of Plankton Research*, **22**, 1155–1166.
- Titelman, J. & Fiksen, Ø. (2004) Ontogenetic vertical distribution patterns in small copepods: field observations and model predictions. *Marine Ecology – Progress Series*, **284**, 49–63.
- Wissel, B., Boeing, W.J. & Ramcharan, C.W. (2003) Effects of water color on predation regimes and zooplankton assemblages in freshwater lakes. *Limnology and Oceanography*, **48**, 1965–1976.

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