

Research

Dying from the lesser of three evils: facilitation and non-consumptive effects emerge in a model with multiple predators

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Prey modify their behaviour to avoid predation, but dilemmas arise when predators vary in hunting style. Behaviours that successfully evade one predator sometimes facilitate exposure to another predator, forcing the prey to choose the lesser of two evils. In such cases, we need to quantify behavioural strategies in a mix of predators. We model optimal behaviour of Atlantic cod *Gadus morhua* larvae in a water column, and find the minimal vulnerability from three common predator groups with different hunting modes; 1) ambush predators that sit-and-wait for approaching fish larvae; 2) cruising invertebrates that eat larvae in their path; and 3) fish which are visually hunting predators. We use a state-dependent model to find optimal behaviours (vertical position and swimming speed over a diel light cycle) under any given exposure to the three distinct modes of predation. We then vary abundance of each predator and quantify direct and indirect effects of predation. The nature and strength of direct and indirect effects varied with predator type and abundance. Larvae escaped about half the mortality from fish by swimming deeper to avoid light, but their activity level and cumulative predation from ambush predators increased. When ambush invertebrates dominated, it was optimal to be less active but in more lit habitats, and predation from fish increased. Against cruising predators, there was no remedy. In all cases, the shift in behaviour allowed growth to remain almost the same, while total predation were cut by one third. In early life stages with high and size-dependent mortality rates, growth rate can be a poor measure of the importance of behavioural strategies.

Keywords: consumptive effects, dynamic programming, facilitation, multiple predators, non-consumptive effects, optimal behaviour, predator–prey interactions, trait mediated indirect effects

Introduction

Predator–prey interactions structure ecological communities, and understanding the nature and strength is a central challenge for ecologists. The most obvious way predators affect prey populations is through consumption, which reduce the abundance of prey. In turn, such direct ‘consumptive effects (CEs)’ can influence growth and reproduction of the prey population through released density dependence (Preisser and Bolnick 2008),

and the population dynamics of a predator–prey species pair can become intricately linked (Paine 1969). Both predator and prey can be studied using optimal foraging theory, which paints a dynamic picture as it predicts how individuals strive for the optimal balance between fitness gains from feeding versus potential fitness losses from exposure to predators (Lima and Dill 1990, Schmitz et al. 2004). Tradeoffs between feeding and exposure to predators can cause strong and diverse indirect effects on entire ecosystems, through changes in behaviour or habitat choice (Schmitz 2010, Schmitz et al. 2017), morphology (Grant and Bayly 1981), and other phenotypic traits (Preisser et al. 2005, 2007, Schmitz 2010). When predation risk influences fitness correlates (e.g. behaviour, growth and survival) of the prey, it is often referred to as ‘non-consumptive effects (NCE),’ since prey need not be eaten for it to be adversely affected by the predator (Abrams 2007, Peacor and Werner 2008, Peckarsky et al. 2008). A telling example is the study conducted on snowshoe hare *Lepus americanus* which showed that perceived predation risk alone is sufficient to reduce adult female survival and the number of her offspring – even though the period of exposure to predators was ended at birth (Macleod et al. 2018). These changes in prey traits can furthermore influence the interaction of the prey with other species, prey resources or predators of the prey, causing trait-mediated indirect effects (TMIEs) on these other species (Abrams 2007, Peacor and Werner 2008). For instance, Schmitz and Suttle (2001) have shown that sit-and-wait spiders cause grasshoppers to move from nutritious grass to less nutritious but safer herbs, and that this predator-induced habitat change in prey led to a positive TMIE on grass, and a negative TMIE on herbs.

Several reviews conclude that non-consumptive effects represent a numerically important component of predator–prey interactions and food-webs dynamics. The meta-analysis by Preisser et al. (2005) and the review by Creel and Christianson (2008) indicate that non-consumptive effects are often as strong or stronger than the consumptive effects of a predator, and cascading effects through multiple trophic levels have been documented from decline and recovery of the largest carnivores (Ripple et al. 2014).

While most predator–prey theory assumes that all predator species act the same and elicit qualitatively similar anti-predator behavioural responses in their prey, the nature and strength of non-consumptive effects may vary with the predator’s presence and abundance, its hunting mode and its habitat use (Schmitz 2010, Schmitz et al. 2017). Typical responses of prey to the presence of a predator include hiding more, moving less and changing habitats (Sih 1992, Peckarsky 1996, Stoks et al. 2003, Miller et al. 2014).

Often, non-consumptive effects are easier to identify when exposing the prey first to one predator, then another predator species, and contrasting the prey’s behaviour between the two situations. For example, the freshwater snail *Physella gyrina* is consumed by two predators that elicit different behavioural responses. When exposed to the pumpkinseed sunfish, which is a visual predator hunting in the water column, the snail

selected covered habitats to hide. In the presence of crayfish, an ambush predator waiting under rocks and other substrates, the snail moved to the water surface (Turner et al. 1999, Bernot and Turner 2001). In a grassland system, the grasshopper *Melanoplus femurrubrum* suffers predation from three predatory spiders with different hunting modes: *Pisaurina mira* (sit-and-wait); *Rabidosa rabida* (sit-and-pursue); and *Phidippus rimator* (actively hunting) (Schmitz and Suttle 2001). Here, the grasshoppers could avoid the first two by changing habitat from grasses to herbs, but did not change behaviour in the presence of the actively hunting spider, which was found everywhere.

In nature, prey are rarely exposed to one predator at the time, but are threatened simultaneously by several predator species (Soluk 1993, McIntosh and Peckarsky 1999, Griffen 2006). When these predators differ in their mode of foraging, the prey face a complex tradeoff, whereby avoiding one predator type may increase the risk of running into another (Matsuda et al. 1993). For example, in the snail example above each predator could be avoided by changing habitat, but the presence of both would put the snail at great risk. Varying the mix of predator abundance can alter such tradeoffs, and the combined effects of a community of predators cannot be predicted from the effect each species has in isolation (Sih et al. 1998, Bolker et al. 2003). As the abundance of one predator increases, this may lead to a change in behaviour that facilitates the susceptibility to other predators, an example of a trait-mediated indirect effect. Such complications are integral to a coherent understanding of predator–prey dynamics, with consequences for community structure and ecosystem function.

We know that TMIEs occur, but how strong are they, exactly? To assess the relevance of behavioural plasticity, we need to be explicit about environment, processes, state-dependence, behavioural options and tradeoffs. Here, we model optimal prey responses to multiple predators in the pelagic, upper layers of the open ocean up to 100 m depth, which is not a homogenous environment with nowhere to hide, as one might initially believe, because of vertical and diurnal variation in light. In this system, tradeoffs are particularly strong, and we model an organism with a limited behavioural repertoire: fish larvae about one centimeter long that can move up and down in the water column and influence their encounter rate with food by swimming slowly or not at all. In our study species, Atlantic cod *Gadus morhua*, the larvae drift with the currents to the nursery grounds, and although larvae are abundant, the ocean is big and each larva far apart so there is weak or no density dependence during this stage.

In addition to its simplicity, this system also has applied value because predation is believed to be the major cause of mortality for most early life stages (Houde 1987, Bailey and Houde 1989) and therefore having huge effects on the biomass and yield of commercially important fish stocks. Conceptual work by Bailey and Houde (1989) and others (Folkvord and Hunter 1986, Greene 1986, Anderson 1988,

Miller et al. 1988, Fuiman 1994) has suggested that larger and faster growing larvae are less vulnerable to predation and more likely to survive. However, larger larvae may be more vulnerable under some circumstances (Cowan et al. 1996, Paradis et al. 1996, Fuiman et al. 2005), and fast growth requires food for which foraging can be risky (Abrams 1991). Cowan and Houde (1992) pointed out that the relationship between size and mortality may change with predator type, the larvae's swimming speed, and behaviour of both predators and larvae. In addition to size-related escape responses, larvae may also reduce mortality risk by hiding in deeper and darker waters at certain times of the day to avoid visual predators during their peak performance, with the consequence that foraging activity is reduced (Clark and Levy 1988, Engström-Öst and Lehtiniemi 2004, Jørgensen et al. 2014).

The analysis of how all these factors interact to form predator-prey interactions and indirect effects is complicated. First, the mechanics of search, encounter and predation determine interaction strength between predators and prey, and may change with size and ontogeny. Second, since animals tend to be adapted to their natural environment, we can expect that prey have evolved flexible behaviours that make use of available loopholes in the environment. These behaviours would, over time and space, increase foraging and survival in ways that can, at least as a first approximation, be studied by optimization conditional on internal body states such as hunger. In this context, a key question is how behaviour can navigate the landscape of fear from multiple, functionally different predator types.

To assess how three functional predator types influence the behaviour of fish larvae, we hypothesize that 1) larval fish respond more strongly to predators that pose the greatest risk, and 2) predators with complementary hunting modes (ambush and fish predators) benefit from the presence of each other and the multiple predator interaction would result in facilitation between them.

Here, we develop a general model of optimal behaviour, growth and survival of larval fish exposed to ambush and cruising invertebrates and visually hunting fish. We use it to assess if larvae can effectively adjust behaviour to avoid specific predatory modes; to quantify the relative importance of consumptive, non-consumptive and trait-mediated indirect effects; to map the scope for behaviour to reduce overall predation; And to investigate how variable composition of predator communities affect overall predation rates.

Model description

We use a state-dependent optimality model which describes the physiological and ecological mechanisms of feeding, growth and predation of larval Atlantic cod *Gadus morhua* in a vertical environment structured by gradients in light that vary strongly with time of day [see Fouzai et al. (2015) and Fiksen and Jørgensen (2011) for a detailed description of

the model]. This model is formulated and parameterized for larval Atlantic cod, but many of the mechanisms and the resulting predictions are relevant for other small organisms in the pelagic that are characterized by flexible behaviour, tradeoffs between growth and survival, and high mortality rates from predation. For this study we have expanded the model of Fouzai et al. (2015), briefly described below, with a process-based encounter rate model for ambush, cruising and fish predators. The model finds the optimal behaviour given body size, depth and time of day, and from the optimal behavioural strategy we quantify growth and predation mortality of larvae between 5 and 15 mm body length. The key driver is variation in the abundance of three functionally different types of predators: 1) ambush invertebrates, that sit-and-wait for approaching fish larvae (but do not encounter those that sit still). They are most effective on smaller larvae that move and swim a lot; 2) cruising invertebrates, such as jellyfish, that eat larvae in their search path (regardless of light or the movement of the larvae). They are most efficient on smaller larvae that have limited escape abilities; and 3) fish, visually hunting predators for which the larvae can hide in deep, dark waters. Fish are most dangerous for larger larvae as they form a larger visual image, particularly in daylight and near the surface.

We vary the relative dominance of each type of predator to find optimal larval behaviour and to quantify vulnerability to changing predator compositions.

Environment and fish larvae

The spatial landscape is a 100 m deep water column (resolution 2 m) in which light intensity varies with depth and time of day. The model assumes a spatially homogenous distribution of zooplankton prey with temporal stochasticity (15 ± 2 mg dry mass m^{-3} , standard deviation). Prey biomass was converted to abundance using typical prey mass and length for each larval size category. Temperature was set to 8°C throughout the water column, and both prey and temperature were fixed across all simulations.

Larvae are characterized by three dynamic state variables: body size; gut fullness; and vertical position. The depth position and foraging activity that maximize survival probability to a given body size (15 mm) were found for each hour and for each combination of individual state using dynamic programming (Houston and McNamara 1999, Clark and Mangel 2000; for details of this model see Fouzai et al. 2015). Submodels for the physical and biological processes for encounter, capture success, ingestion, assimilation, metabolism and growth are described in Fiksen and MacKenzie (2002), Kristiansen et al. (2007), Kristiansen et al. (2009) and Fiksen and Jørgensen (2011). Briefly, larvae search visually for zooplankton and have higher foraging success higher in the water column during day. Survival depends on habitat choice and activity level of the larvae, and, importantly, the time it takes to reach the target size of 15 mm.

The three predators

An extension from earlier models is that we have split predation into three modes following the conceptual classification based on hunting, detection and capture strategies developed in the seminal paper by Bailey and Houde (1989). Larvae are now subject to predation from (Fig. 1): ambush predators that quietly wait for their prey to swim into their zone of capture (e.g. chaetognaths and large crustaceans); cruising predators that move constantly and search a fixed volume per unit time (e.g. jellyfish, euphausiids); and visually searching predators (fish) where ambient light and size of the visual target are most important detection and capture.

The encounter rates E (s^{-1}) between fish larvae and ambush (E_A) and cruising (E_C) predators are based on the Gerritsen and Strickler (1977) model of randomly moving predators encountering their randomly swimming prey in a three dimensional space. The expected encounter rate is found by combining the detection distance (R) with relative swimming speeds of both the predator (V_p), the larvae (V_L) and the density of the predators (A_p):

$$E_A = \pi \times R^2 \times A_A \times \frac{V_A^2 + 3 \times V_L^2}{3 \times V_L}, \text{ for ambush predators (1)}$$

$$E_C = \pi \times R^2 \times A_C \times \frac{V_L^2 + 3 \times V_C^2}{3 \times V_C}, \text{ for cruising predators (2)}$$

where V_A , V_C and V_L are the swimming speeds ($m s^{-1}$) of ambush and cruising predators and larval fish, respectively, and A_A and A_C are the abundance of ambush and cruising predators (m^{-3}). The prey detection distance of the predator R is proportional to its length:

$$R = a \times L_p \quad (3)$$

where L_p is the size of predator (m), which was set to $L_A = 30 \times 10^{-3} m$ for the ambush predator and $L_C = 50 \times 10^{-3} m$ for the cruising predator (see Table 1 for description and value of a). The swimming speeds of predators (V_p) are also length-dependent:

$$V_p = b + c \times L_p^d \quad (4)$$

where b , c and d are parameters specific to each predator type (Table 1). For these predators, encounter rates go up the faster the larvae swim, and the effect is strong for ambush predators (Fig. 1a) while negligible for cruising predators (Fig. 1b).

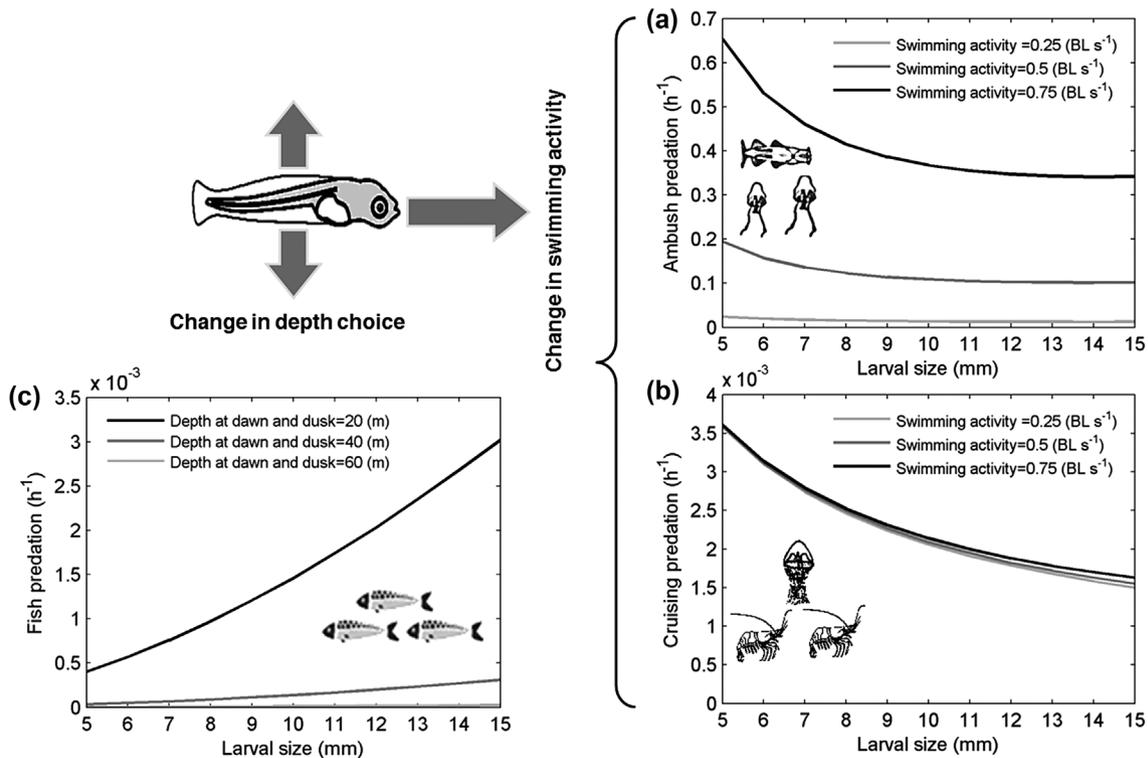


Figure 1. Mechanisms of larval vulnerability to different types of predators to a given change in the swimming activity for ambush and cruising predators and the depth choice and light levels for fish predators. Predation risk from all predator types are size dependent through encounter rates and capture success. (a) Effectiveness of ambush predators is sensitive to larval swimming speed, but not (b) to cruising predators because their swimming velocity is much larger while (c) the risk of encountering a fish predator depends on depth position and ambient light levels. Predation may increase or decrease with size depending on relative predator abundances and larval behaviour.

Table 1. Values of the parameters in equations of encounter radius, swimming speed and susceptibility (Eq. 2–4 respectively) adapted from Paradis et al. (1999).

Equation	Parameter	Fish larvae	Ambush predator	Cruising predator
Encounter radius	<i>a</i>		0.5 ^w	0.5 ^w
Swimming speed	<i>b</i>	0 ^x	0 ^y	1.2 ^y
	<i>c</i>	1 ^x	1.16 × 10 ⁻⁶ ^y	0.4 ^y
	<i>d</i>	1 ^x	1.22 ^y	1 ^y
Susceptibility	<i>g</i>		-6.1 ^z	-3 ^z
	<i>h</i>		-2.1 ^z	-0.8 ^z
	<i>l</i>		0.6 ^z	0 ^z

^wCowan et al. 1996

^xWare 1975

^yCowan and Houde 1992

^zParadis et al. 1999

The encounter rate (E) between a fish larva and a fish predator (E_F) is modelled mechanistically as a function of visual range of the fish (R_F), their swimming velocity (V_F which was set to 0.1 m s⁻¹) and abundance (A_P m⁻³):

$$E_F = 0.5 \times \pi \times R_F^2 \times V_F \times A_P \quad (5)$$

The fish predator (a piscivore) visual range or prey detection distance (R_F) is a function of larval contrast against the background, the visual sensitivity of the predatory fish and ambient light intensity and water clarity. Note that the visibility of the larvae to a fish predator increases with larval body size, but decreases if the larvae migrate to deeper and darker habitats (Fig. 1c). In a fixed light environment, the risk to be eaten from fish will be proportional to the squared larval length. We have explained the details of visual predation elsewhere (Fiksen and Jørgensen 2011), and use exactly the same model and parameters here. We assume that visual predators have a uniform probability of appearing anywhere in the water column, swim much faster than the fish larva and capture the larva with certainty at encounter.

Once a prey is encountered, capture probability (S) is an empirical function of relative larval and predator body lengths (Paradis et al. 1996):

$$S_p = e^{g + b \times \ln \frac{L_p}{L_A} + i \times \left(\ln \frac{L_p}{L_p} \right)^2} \quad (6)$$

where g , b and i are predator-specific parameters (Table 1) and L_p is L_A or L_C , for ambush and cruising predators, respectively. For fish, it is assumed that $S_F = 1$, i.e. that capture is always successful once a larval prey is encountered. The mortality rate of the larvae is defined as the product of the encounter rate (E_P) and susceptibility to capture if encountered (S_p) for each predator type, and the sum of these mortality rates is the total mortality rate experienced by the fish larvae.

Simulation protocol

The model was used to find optimal behaviour in shifting predator communities to quantify consumptive, non-consumptive and trait-mediated indirect effects of each predator type. We did this in three steps.

- 1) We calibrated predator densities so that the larva had equal predation mortality from each of the three predators when considered over the entire growth range modelled, from 5 to 15 mm body length. A second requirement was that total predation mortality should equal the value estimated from field data by McGurk (1986) (for 1 cm larval fish ≈ 0.16 day⁻¹). An iterative procedure with gradual adjustments of predator densities and new model runs was required. This default situation is referred to as the 'balanced scenario' where each of the three predator types caused a third of the total predation mortality.
- 2) Abundance was then increased for one predator and reduced for the two others to quantify effects on mortality from each predator type when assuming static behaviour. We multiplied predator abundances from the balanced scenario with factors of (80/33) and (10/33), respectively, so that if behaviours remained identical to the balanced scenario, each predator would now cause 80%, 10% and 10% of the total mortality. Assuming static behaviour provides a baseline against which to quantify the role of adaptive behaviour in this system. In a subsequent analysis, we ran the model for more gradual changes in predator communities and recorded predation mortality assuming static behaviour from the balanced scenario. This was repeated so that each of the three predators in turn was the dominant one.
- 3) Of course, adaptive (optimal) larval behaviour can change predation rates experienced. We performed a full model simulation to find optimal behavioural responses of the fish larvae to the new composition of the predator community. By simulating this strategy in a population, we estimated the emergent mortality given adaptive larval responses. By comparing this emergent mortality

to proportional mortality expected from the numerical scaling of predator abundance alone (assuming the same behavioural strategy as in the balanced scenario), we could quantify consumptive, non-consumptive and trait mediated indirect effects of each predator given adaptive behavioural changes. To find the emergent optimal behaviour (vertical migration and foraging strategies) we ran the backward optimization algorithm for each predator composition and stored the optimal strategy vectors for all state combinations (Houston and McNamara 1999, Clark and Mangel 2000; see details in Fouzai et al. 2015). Thereafter, we simulated 1 million individuals that followed these optimal strategies through the larval stage and under stochastic prey density, while we recorded internal states (size and gut fullness), habitat choice, activity and predation rates from each predator type.

The model is written in Fortran and the source code is available in the Supplementary material Appendix 1.

Results

To quantify the importance of adaptive behaviour in this system, we compare predation rates assuming static behaviour (the same depth selection and swimming activity strategies as in the balanced scenario) with that from adaptive behaviour optimized to one dominant predator (Fig. 2). In terms of integrated predation rates while growing from 5 to 15 mm length, the default balanced scenario by definition resulted in the same contribution from each of the predators (the same integrated area under the curves in Fig. 2a, e, i). There was no effect of behaviour from increasing cruising predator density (lines for static and adaptive behaviour are on top of each other in Fig. 2c, g, k).

With ambush predators dominating (Fig. 2b), adaptive behaviour could reduce predation from ambush predators, but lead to an increase in predation from fish (Fig. 2j). Similarly, in a fish-dominated scenario, predation from fish was reduced (Fig. 2l) whereas ambush predators became more successful (Fig. 2d). The trait-mediated indirect effects

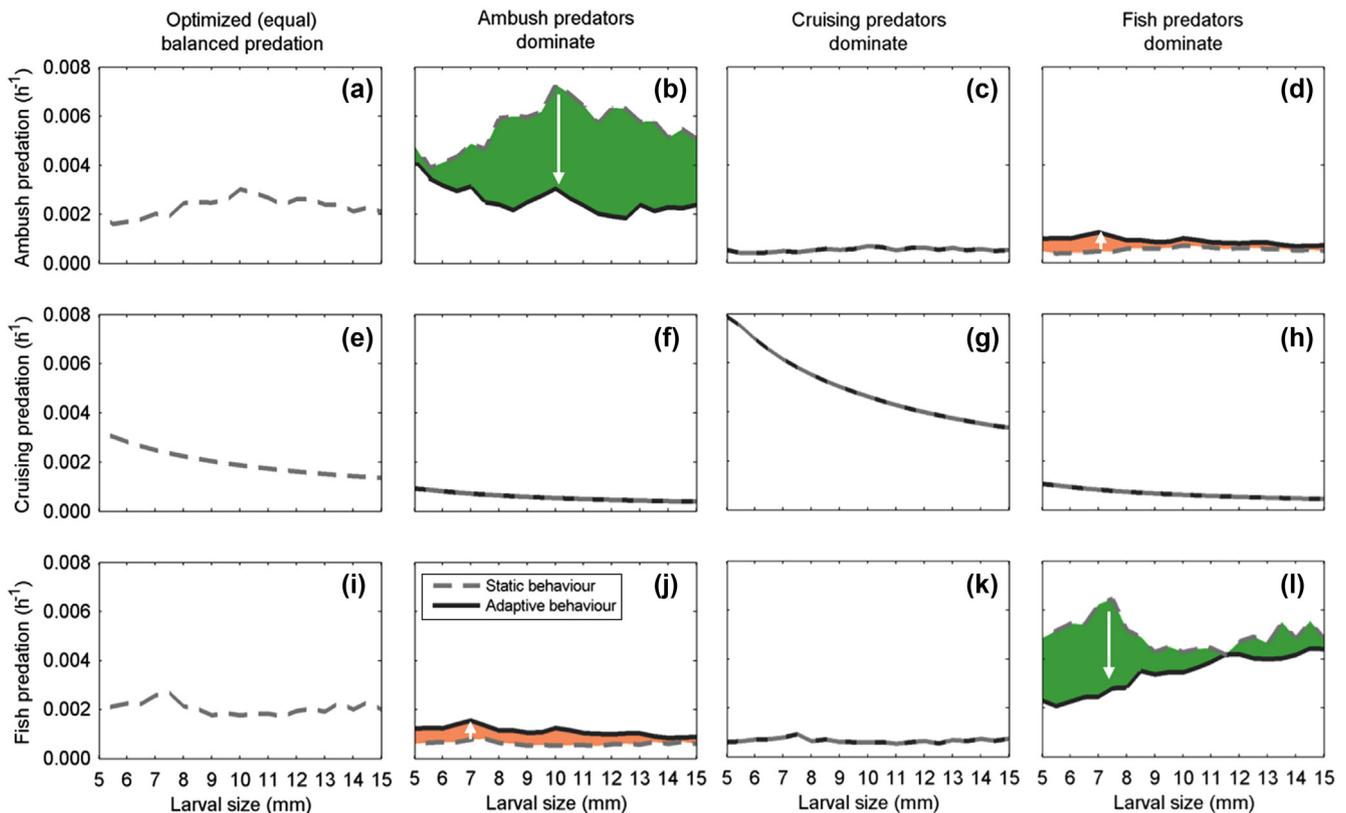


Figure 2. Predation mortality rates with static and adaptive behaviour. Predation rates on cod larvae from ambush (a–d), cruising (e–h) and fish (i–l) predators with static behaviour (predation directly proportional to predator density considering same behaviour as in the optimized balanced scenario; dashed line) and with adaptive behaviour (the emergent mortality with adaptive optimal behaviour; whole line) as a function of larval length under different predator compositions. The 1st column is the balanced predation scenario with equal (33%) contribution to predation from each predator. The 2nd to 4th columns are predator compositions dominated by ambush, cruising and fish predators, respectively. Green and orange areas with white arrows indicate the reduction (avoidance) and the increase (facilitation), respectively, in emergent predation rate (due to adaptive behaviour) relative to what would be expected if predation was proportional to increase in predator density.

are visible as the extra (and size-dependent) predation from fish (Fig. 2j) and ambush predators (Fig. 2d) due to the relative increase of ambush and fish predators, respectively. When increasing in abundance, these predators make their own life harder because they induce a behavioural response in their prey, but facilitate feeding for the other predator types.

The size-dependency of the predation processes (Fig. 1) has been estimated in laboratory experiments with limited scope for behaviour such as vertical migration. However, assuming larvae can behave optimally in natural environment, these relationships, except for cruising predators (Fig. 2e–h), take a very different shape (comparing Fig. 1 and Fig. 2). For ambush and fish predators, both the absolute level and the size-dependency were sensitive to the predator mix. For example, when cruising invertebrates or fish predators dominated, ambush predation did not change with size at all (Fig. 2c–d). Similarly, when ambush or fish predators dominated, the size-dependency of predation could even take opposite slopes from the balanced scenario (Fig. 2a versus b, and Fig. 2i versus l, respectively).

The three common predator foraging modes in pelagic ecosystems induced different behavioural counterplays in fish larvae that attempted to reduce predation risk. Overall,

the predator community had minor effect on optimal growth rates throughout larval ontogeny (Fig. 3a–c). The mortality rate of larval stages was generally high, and any delay in growth had high survival costs. Fish predators caused some reduction in growth, as larvae then swam deeper to avoid light, encountered less food, and required a few more days to reach 15 mm (Fig. 3c, f). Against ambush predators that sit-and-wait for prey to arrive, our model predicted fish larvae to swim more slowly and instead search for food closer to the surface (Fig. 3a, d).

For these two predator types, the optimal behaviour reduced predation from that specific predator by as much as 50%, but the behavioural change caused a simultaneous increased exposure to the predation strategies of other predators (facilitation), so the overall reduction in mortality was about one third (Fig. 4a, c). Overall, the behavioural changes are not very large, but integrated over the larval stage they have substantial effect on total predation rates. With cruising predators, the only remedy was to grow fast to shorten the duration of the exposure (Fig. 3b), which can be seen as higher activity levels than with ambush predators (Fig. 3h versus g) and more exposure to light than with fish predators (Fig. 3e versus f).

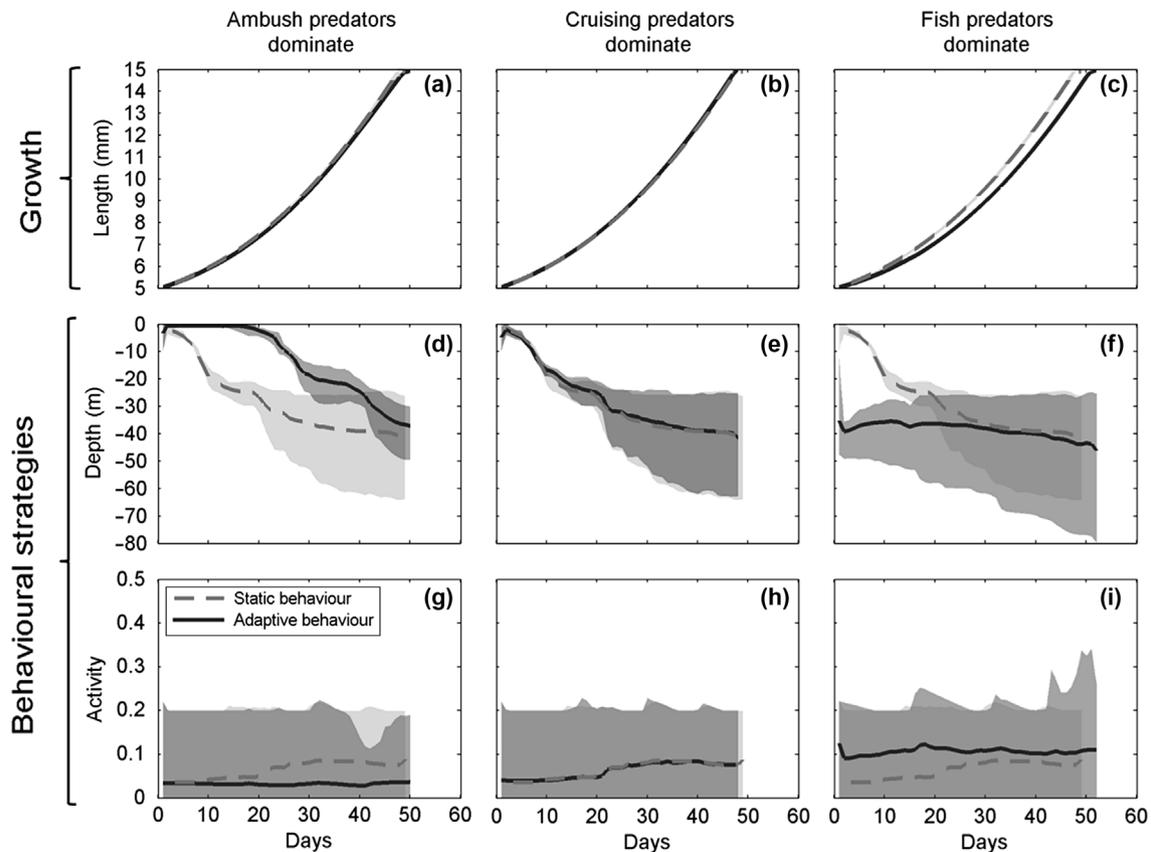


Figure 3. Daily mean larval growth and behaviour (depth selection and swimming activity) under 1) balanced predator community densities mix (dashed lines) and 2) predator community densities mix equal to 80% for each of the dominant predator types and 10% for others predators types (whole lines). Light and dark grey shades represent the minimum and maximum hourly length, depth distribution and swimming activity of the larva in case 1 and 2 respectively. Stage duration is differing between predator regime.

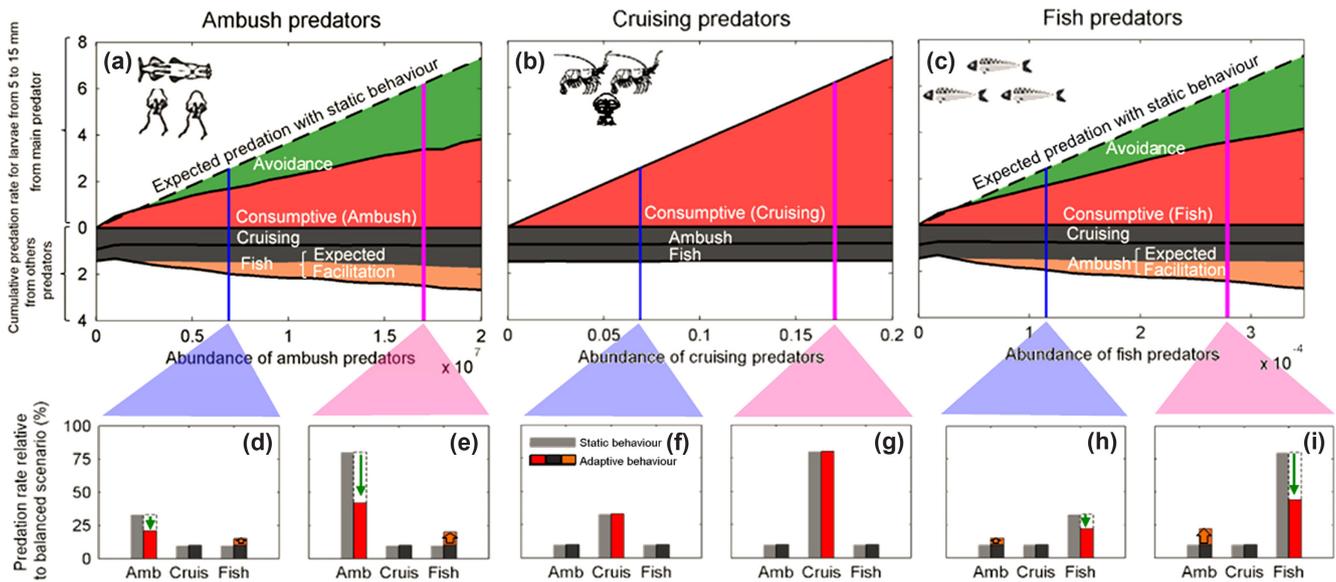


Figure 4. Change in proportional and emergent predation mortality as a function of predator abundance. Upper panels (a–c) show cumulative predation mortality (for larvae from 5 to 15 mm) from a specific (primary) predator (ambush (a), cruising (b) and fish (c)) under different predator abundances. The secondary predators (cruising and fish (a), ambush and fish (b) and ambush and cruising (c)) are fixed at low, 10% of scaled, abundances. Dashed lines are expected primary predator mortalities rates proportional to change in abundance (with static behaviour), while whole black lines represent emergent mortality (with adaptive behaviour). Corresponding bar plots for low (d, f and h) and high (e, g and i) primary predator densities show proportional (light grey) and emergent (dark grey) predation mortality relative (%) to the balanced predation scenario for all predator types. Red and dark grey shading is the emergent predation mortality (consumptive effect) (with adaptive behaviour) directly associated with the main and others predators respectively, while orange shading is predation mortality increase (facilitation) by other predators due to adaptive behaviour (trait-mediated indirect effect mediated by direct non-consumptive effects on larval traits). Green shading is the difference between proportional (mortality with static behaviour) and emergent (mortality with adaptive behaviour) predation mortality (avoidable predation). Orange and green arrows indicate positive and negative change, respectively, in emergent predation rate (due to adaptive behaviour) relative to what would be expected if predation was proportional to increase in predator abundance.

To quantify primary predator consumptive effects (larval mortality rate from the primary predator) and trait-mediated indirect effects (change in predation rate from secondary predators as the dominant predator increases in abundance mediated by direct non-consumptive effects on larval traits), we first varied predator abundance including adaptive behaviour (Fig. 4). Increasing ambush and fish predator abundances yielded decelerating total consumption rates due to behavioural change, but also induced extra mortality from the other predator (fish and ambush predators respectively; Fig. 4a, c). This quantifies the trait-mediated indirect effect where fish larvae ended up being eaten by fish predators because they attempted to escape ambush predators, and vice versa (Fig. 4a, c). For cruising predators, predation risk scaled linearly with predator abundance (Fig. 4b).

The relative contribution of consumptive effects was larger than trait-mediated indirect effects for ambush and fish predators, and the added trait-mediated indirect effects was about $\frac{1}{4}$ of the consumptive effect (Fig. 4e, i). Adaptive behaviour reduced the total predation rate by about one third compared to static behaviour, except at low predator densities.

Discussion

Ecological theory often rely on sweeping assumptions, producing broad and general patterns for interactions between organisms. However, to assess the relevance of behavioural plasticity in any given system, we need to capture key drivers and explicit mechanisms, environment and physiology. As an example, the size-dependency in prey vulnerability is predicted to be more sensitive to prey behaviour and foraging mode of the dominant predators than to the mechanics of size-dependent encounter and capture processes. Our detailed, mechanistic model quantify the relative effects of consumptive (CE), non-consumptive (NCE) and trait-mediated indirect effects (TMIEs) in different predator communities. Central to the model is the assumption of optimal, adaptive behaviour concerning two traits (depth selection and swimming activity of fish larvae) given mechanistic models of predator-specific encounter rates and capture processes. By treating the model as a numerical laboratory, we could quantify not only the change in predation given altered predator communities, similar to what can be observed in experiments, but also the magnitude of the mortality that could be avoided by comparing adaptive behaviour to the

hypothetical situation of no behavioural change. As hypothesized, the potential of avoiding predation from an abundant predator was substantial, but simultaneously led to higher exposure to another predator. Indeed, the antipredator behaviour response of the prey to the most abundant predator increases the encounter frequency with other predators which became more successful. Here conflicting demands on the antipredator behaviour have caused facilitation between predators and led to more captures from the less abundant one (trait-mediated indirect effects).

On the other hand, NCEs from predation typically cause lower growth rates, but this was not evident in this model. If total predation pressure is high, the fitness costs of increased stage duration prevent this strategy. In our system, the functional differences of predators still open a loophole where behaviour can act to increase survival. If ambush predators dominate, they can change habitat and maintain high feeding rates with less movement. If fish dominate, they can go darker, but move more actively to maintain growth rate almost at the same level.

When ambush predators are important, prey should minimize their movements to avoid running into this type of predators. Such behavioural change has been observed, for instance by Soluk and Collins (1988) for stonefly *Agettina* larvae which responded to the presence of sculpins (sit-and-wait predators) by significantly decreasing the time spent moving on sides and tops of rock and by reducing movements in general. Recently, Kenison et al. (2017) demonstrated that rusty crayfishes *Orconectes rusticus* were able to detect and respond to hellbender salamanders *Cryptobranchus alleganiensis* (sit and wait predators) by reducing their activity and increasing refuge use.

If fish predators are dominant, our model predicts that larvae should switch behavioural strategy and hide in deeper and darker habitats. Engström-Öst and Lehtiniemi (2004) found that pike larvae were able to differentiate between levels of threat and reduce swimming and foraging activity with increased predator exposure. Also, Martin et al. (2010) showed that behavioural responses of juvenile roach *Rutilus rutilus* were highly dependent on the hunting modes of its predator: northern pike *Esox lucius* (an ambush predator that occupies structured habitats) versus European perch *Perca fluviatilis* (a roving predator that forages in structured and unstructured habitats). They suggested that roach select their habitat in response to the alternative foraging strategies of these predators. For instance, roach selected open-water habitat when exposed to ambush predators, but entered a more structured habitat when presented to roving predators.

Animals often tailor their habitat use and foraging activity to anticipated risk (Lima and Dill 1990, Schmitz et al. 2004). Recently, Miller et al. (2014) found that grasshopper mortality and use of space was sensitive to hunting mode of the predator – grasshoppers showed a flexible and adaptive behaviour when exposed to different predator foraging strategies. Naturally, grasshoppers and fish larvae are very different organisms and they may not be comparable.

One may reasonably question how accurately individual fish larvae may sense a large and dynamic environment, and whether they can tailor their behaviours to fluctuations in the predator community. It is more likely that there can be local adaptations to area-specific differences in the predation community, or that natural selection may cause shifting behavioural strategies over generations in response to shifting predator communities. Recently, Wisenden et al. (2016) found that swimming performance and skeletal ossification of the larvae on one side, and brood defense by the parents on the other side, differed across populations of convict cichlids *Amatitlania siquia* (a freshwater fish). They demonstrated that larval morphological development, antipredator behaviour and parental care had coevolved with site-specific ecological differences. They suggested that these differences reflect population variation in selection on antipredator capability and thus local adaptation to different habitat conditions. On the other hand, Skajaa et al. (2003) showed that cod larvae, older than three weeks, were able to sense cues from predators and make tradeoffs between foraging activity and antipredator behaviour, so at some point during ontogeny these capabilities may develop.

The strength of consumptive, non-consumptive and trait-mediated indirect predator effects depend on foraging, predator densities and several environmental factors (Schmitz et al. 2004, Lehtiniemi 2005, Preisser et al. 2007, Peacor and Werner 2008). Behaviours to avoid one predator's foraging mode may conflict with the avoidance of other complementary hunting types, and therefore facilitate risk from the other predator (Soluk and Collins 1988, Soluk 1993, Eklöv and Vankooten 2001, Fiksen et al. 2005, Carey and Wahl 2010). An adaptive strategy for the prey is to respond behaviourally to the predator that presents the highest risk, a 'hierarchy control' (McIntosh and Peckarsky 1999). Hierarchy control applies when one predator presents significantly higher predation risk than another. In the optimality model, larvae modified their anti-predator behaviours to better avoid and escape the most risky source, which changed with body size. In addition, the relative importance of non-consumptive and trait-mediated indirect effects can change with environmental factors (Peacor and Werner 2008). For example, the relative magnitude of the NCE on growth rate depends on the time prey spends foraging, which is conditional on prey availability and temperature.

Multiple predators can have non-additive effects on prey survival. In a review, Sih et al. (1998) found that risk-reducing effects were frequently observed in natural communities. Indeed, many prey species can change habitat or alter behaviour (e.g. decreasing foraging activity) in response to one or multiple predators, which in turn result in reducing the overall risk of predation (Vance-Chalcraft and Soluk 2005, Carey and Wahl 2010). This mechanism could explain the overall risk reduction predicted when fish or ambush predators were dominant in the system.

Despite the growing body of evidence of the importance of multiple predator, non-consumptive and trait-mediated

indirect effects in terrestrial and freshwater systems, these processes are poorly represented in marine ecosystem models. The predictive ability of these models would benefit from incorporating adaptive anti-predator prey behaviour and different behavioural strategies of prey (such as activity and habitat selection). Furthermore, larval fish suffer from high predation rates, and predation is an important driver of fish stock recruitment variability.

We have modelled the mechanisms of predator–prey interactions including multiple predators and variable predator communities. An illustrative example of how predators can benefit from each other is the collaborative hunting of groupers *Plectropomus pessuliferus* and moray eels *Gymnothorax javanicus* on coral reefs (Bshary et al. 2006). Although these species are competitors for the same prey, certain individuals have been observed to cooperate during hunting, with the moray searching inside the reef and the grouper waiting just outside, leaving prey with no alternative for escape. Similar behaviours, or more simply a spatial affinity between predators having complementary detection or capture modes, may have implications for survival of prey and can drive more elusive patterns of predator–prey and predator–predator interactions (Schmitz et al. 2017).

In conclusion, the present study quantifies the benefits of antipredator responses in a complex landscape of risk posed by multiple predators. We based our predictions on a detailed, rich and concrete account of spatial environmental gradients, foraging processes, physiology, internal state and optimal behavioural decisions. For a small fish, we found that the overall benefit of relatively minor behavioural changes can cut predation rates from a particular predator in half, and the total predation rate by one third, even with minor offset of growth rates. This latter prediction could only appear in a model with two alternative behavioural options. An effect on survival of this magnitude will likely lead to strong selection pressures on behaviour, whereby fish larvae and other pelagic organisms evolve a behavioural repertoire tailored to the local predator community.

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Supplementary material (available online as Appendix oik-05631 at <www.oikosjournal.org/appendix/oik-05631>). Appendix 1.