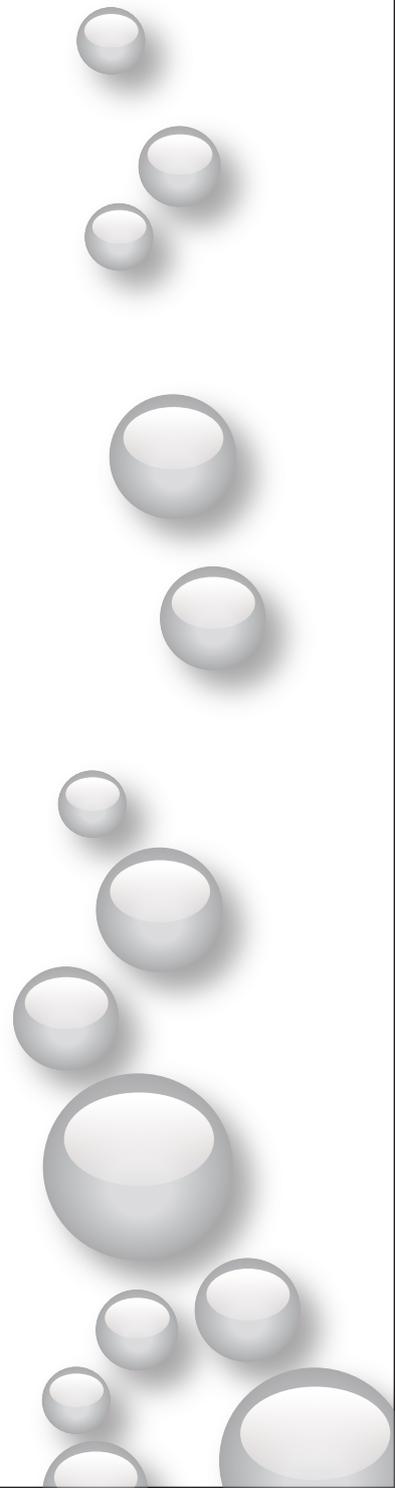


Paper 2



Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal

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Running title: Behavioural ecology and oceanography

Abstract

Highly resolved general circulation models (GCMs) now generate realistic flow fields, and have revealed how sensitive larval drift routes are to vertical positioning in the water column. Sensible representation of behavioural processes then becomes essential to generate reliable patterns of environmental exposure (growth and survival), larval drift trajectories and dispersal. Existing individual-based models (IBMs) involving larval fish allow individuals to vary only in their attributes such as spatial coordinates, and not in their inherited behavioural strategies. Here, we illustrate the interaction between short-term behaviour and longer-term dispersal consequences applying a model of larval cod drifting in a GCM, and show how variations in swimming behaviour influence temporal temperature exposure and dispersal. We discuss methods to include behavioural traits in bio-physically coupled models. First, we need to understand the causes and survival value of behaviours of larval fish, framed in terms of behavioural ecology. Second, we need practices to address how drift and dispersal of offspring are generating spawning strategies (timing and location) of adults, using life history theory. Third, the relative importance of local growth and mortality versus the need to drift to particular areas depend strongly on the mobility of organisms at the time of settling, or the spatial fitness-landscape. We recommend modelling practices that use transparent and mechanistic processes in growth, mortality, behavioural abilities, and drift; apply behavioural strategies or rules that allow true variability between individuals, and include an evolutionary selection procedure to assess fitness consequences along drift trajectories and the settlement location. The field of ‘individual-based ecology’ provides sound methods to approach this interface between evolutionary theory and physical oceanography.

Keywords: behavioural rules, larval ecology, individual-based models, general circulation models, predation, habitat selection

Introduction

The sea is a constantly moving habitat, structured and governed by physical processes. For fish and other marine organisms, this provides strong constraints and limitations to dispersal and habitat choice, but it also harbours opportunities. Organisms can exploit eddies and circular current systems for retention within an area (e. g. Sinclair 1988), or hitch-hike with tidal or vertically sheared currents flowing in desirable directions (Harden Jones et al. 1979). Mature adults of many species swim long distances to release their fertilized eggs, and let currents transport the developing early life stages to favourable nursery areas (Harden Jones 1968).

In this paper, we argue that the integration of larval behaviour with general circulation models is a key step forward to improve our understanding of larval survival, growth and dispersal. We do not intend to review or synthesize the vast field of individual-based modelling in larval fish ecology. Instead, we wish to argue why *behaviour* is the central mechanism that links these traits together, despite how restricted the behavioural repertoire of larvae may seem. There are primarily two lines of argument leading to this conclusion. First, compared to adult fish, the outcome of larval behaviour is more tightly connected to physical oceanography. Larvae distributed only a few meters apart in the vertical can end up in totally different geographical areas (Hinckley et al. 1996, Hare et al. 2005, Vikebø et al. 2005), which leaves a large scope for behaviour to influence dispersal as well as the environment for growth and mortality along the drift trajectory. Second, feeding opportunities and predation risks are spatially correlated for pelagic fish larvae. This is driven by the exponentially decaying vertical profile of light – the key determinant for encounter rates with both predators and prey (Aksnes & Giske 1993). Larvae can control their exposure to light through vertical positioning, and thus effectively influence their own survival and growth. Besides these two main arguments, larval ecology has far-reaching implications for the life history strategies of adults. The best spawning sites regarding larval drift patterns, growth and survival may require

extensive spawning migrations at the adult stage, potentially conflicting with alternative ways to use energy and time.

An unfolding of larval fish ecology therefore requires an approach integrating physical oceanography and behavioural ecology, interpreted in the perspective of life history theory. Using individual-based models rich in mechanistic detail, one can focus at the individual and let ecology emerge from individual processes; an approach recently termed *individual-based ecology* (Grimm and Railsback 2005). For larvae, this would include processes such as temperature-dependent growth and starvation, encounter rates with prey and predators that depend on e. g. light and turbulence, and various adaptive behavioural strategies. When scaling up to populations, this perspective views ecology as emerging from individuals and their processes. New patterns that can be compared with data then arise at the population level (Grimm et al. 2005), for example temporal and spatial distributions, growth variation between years and areas, and what can be considered good spawning sites and times.

Present use of individual-based models in oceanography is hampered by the lack of individual variability in behaviour (genotypes), and by the absence of fitness as the criterion to model natural selection processes among alternative behavioural strategies. It is often tempting to simply impose behaviour on individuals, or to implement caricatures of observed behaviours in models, making them more descriptive and less explanatory. The assumption of fixed individual behaviour (for instance habitat selection (they follow prescribed trajectories)) has some drawbacks: 1) the modeller determines to a large extent how growth and mortality rates should be traded against each other; 2) the larvae cannot respond behaviourally to changes in the environment; 3) the potentially conflicting objectives of short-term optimisation of growth and mortality versus long-term drifting in particular directions cannot be studied; and 4) it is impossible to predict how environmental change may alter behaviour through natural selection unless individual variability and heritability are included. The aim of this paper is to clarify some methodological concepts and

promote the use of evolutionary individual-based models in conjunction with general circulation models to address the ecology of early marine life stages.

Larval ecology has a strong tradition in dealing with mechanisms: from miniature biomechanics and behaviour, via influence from physical environmental variables and oceanography, to the capabilities and constraints of sensory systems.

Mechanistically rich representations, including behaviour and life histories, are essential to capture interactions between environmental variability and recruitment success, or to understand the ability of fish in general to adapt to environmental change and human activities such as harvesting (Jørgensen et al. 2006). A largely unutilized potential is, however, that existing individual-based models of larval fish and zooplankton do not include larval behavioural strategies as adaptive traits, nor do the models analyse evolutionary implications. This paper has three sections. First, we present the role of behaviour for marine larvae in a drift phase, and how this constrains adult life history strategies. In the second part, we focus on concepts that can promote an evolutionary interpretation of active movements by drifting marine larvae. In the third part, we discuss candidate modelling frameworks and some recommendations for future research.

1. The importance of behaviour for growth, mortality and dispersal

Larval behaviour does not imply cognition or rationally made decisions. Larvae simply execute genetically pre-programmed responses to internal states or external stimuli. Since there are always small variations in genetic predispositions between individuals and since behavioural traits are heritable (Plomin et al. 2000, Cousyn et al. 2001, Fitzpatrick et al. 2005), individuals encoded to perform behaviour that benefits their growth or survival will simply increase in numbers over the generations (Fisher 1930, Dawkins 1976). In this way, evolution leads to behavioural adaptations to the prevailing conditions. Consequently, the answer to the first question is yes: we would indeed expect that larvae have behaviour, and of a type that appears rational to a human observer.

We first identify two important effects of behaviour. Vertical positioning influences 1) immediate growth and mortality rates and 2) large-scale and long-term drift and dispersal. These two effects are not independent – priorities for one will influence the other.

1.1 Mortality and growth emerge from larval behaviour

The pelagic realm is characterised by strong environmental gradients in the vertical. Light may be the most influential physical variable structuring both productivity and predation in the pelagic (Aksnes et al. 2004). Because light decays exponentially with depth, vertical behaviour can have tremendous effects on encounter rates with prey (spot prey in the light) and predators (hide in the dark). Habitat selection of larvae influences both growth and predation risk with a trade-off between the two: higher growth can normally be achieved only by accepting also a higher mortality. These rates must therefore be emergent properties of models, resulting from behavioural trade-offs, rather than imposed or parameterized values determined by the modeller (Grimm & Railsback 2005).

While growth is often modelled in great detail (e. g. Fiksen & Folkvord 1999, Lough et al. 2005), mortality is rarely modelled explicitly. Cohort survival is sensitive to small variations in mortality rates, and we need to include both the basic mechanisms and the environmental forcing of predation processes in models of larval fish. This is a prerequisite to understand what the trade-offs between growth and survival are, and to appreciate the role of behaviour in determining these rates.

Increased body size decreases predation risk from small and abundant predators (Bailey & Houde 1989). Growth is therefore important to fish larvae since it reduces the time spent in the most vulnerable phase (Houde 1997). In evolutionary terms, this would act as a motivation to maintain high growth rates even if this involves more exposure to predators. At the same time, increasing body size makes larvae more visible, thereby increasing their vulnerability to visual predation in the euphotic zone (Aksnes & Giske 1993). That fish larvae show ontogenetic development in depth

distribution (Leis et al. 2006) and diel vertical migration (Lough & Potter 1993) is likely a response to changing mortality patterns as body size increases.

When foraging is traded against risk of predation, more prey may not lead to higher growth rates, but instead to lower predation rates (Mcnamara & Houston 1987, Lima & Dill 1990). Such behavioural mechanisms could confound studies on the link between prey availability and larval growth rates, with implications for observation programmes trying to establish the relationship between growth and prey abundance in larval fish. As an example, larval cod tend to grow at temperature-limited rates over a range of environmental conditions in field observations (Folkvord 2005). Apparently, this contradicts the study of Beaugrand et al. (2003), which suggested a connection between zooplankton availability and recruitment success of North Sea cod. However, if feeding or growth is traded against predation risk, food abundance may not influence growth directly, but instead modify the strength of a recruiting cohort through behaviourally mediated exposure to predation (Fiksen et al. 2005). At low food availability, larval cod can maintain high growth rates either by increasing their activity level at the cost of running into ambush invertebrate predators more frequently, or by spending more time at higher light intensities where they are more likely to be detected by visually searching raptorial fish. Thus, although there is no observation of food-limited growth, low prey abundance may act through behavioural compensations and influence mortality and thereby recruitment variability.

1.2 Larval drift and dispersal

Minor displacements in the vertical may expose larvae to different flow schemes due to vertical shear. For example, particles dropped at the Northeast Arctic cod spawning grounds at 10 and 20 m depth and traced for 100 days end up hundreds of kilometres apart (Vikebø et al. 2005). This shows the potential of habitat selection in the vertical to affect large-scale dispersal. In addition, horizontal swimming does not necessarily have to compensate for displacement by currents: current strengths and directions vary in space and time, and even limited horizontal movements can associate the larvae more closely with certain current regimes. Leis et al. (2006) showed that larvae

of several coral reef fish observed in the field were swimming in directions that were significantly different from random. It is not known what cues these larvae were using for orientation, but fish larvae have also been shown to detect reef sounds and the smell of conspecifics already at presettling stages (Wright et al. 2005).

These two effects are illustrated in Fig. 1, which shows trajectories of larvae drifting for one month in fixed depths (1-30 m) when released from Moskenesgrunnen, a typical spawning site for Atlantic cod in northern Norway. The physical model and the larval growth as a function of temperature is described in Vikebø et al. (2005). The simulations show a surprisingly high potential for larvae to affect their likelihood of ending up in the Coastal Current or the Atlantic Current by swimming horizontally or vertically. Vertical positioning has a strong effect (Fig. 1), but even directional horizontal swimming at the reasonable velocity of one body length per second will significantly impact the trajectory of the larvae, and at all depths (Fig. 2a). If the swimming speed would be 3 BL/s, then horizontal movements override the effects of depth position completely in this particular region (Fig. 2b). Growth histories averaged over depths diverge for the two behaviours, swimming to the right facing the currents (north-west direction) result in the largest size (panels inserted in Fig. 2). However, this also leads larvae northwards, out of the Barents Sea.

Routine swimming speeds are in the range $0.3-0.5 \text{ BL}\cdot\text{s}^{-1}$ for a cod larvae (Skiftesvik 1992, Peck et al. 2006). Although this is much lower than the 3 BL/s used in the numerical example above, both field and lab observations suggest that other species have higher capabilities. In a study of 89 species of coral reef fish larvae in their later stages, 90% of the species could swim faster than the local currents at $13.5 \text{ cm}\cdot\text{s}^{-1}$ (Fisher et al. 2005). The most common critical swimming speeds were 2-3 times as fast, meaning that swimming could significantly affect dispersal and settlement. Coral reef fish larvae have been measured to have critical swimming speeds of $4-29 \text{ BL}\cdot\text{s}^{-1}$ (Fisher et al. 2005) and some species can swim more than 20 kms at a body length of 10 mm (Clark et al. 2005). Critical swimming speeds decrease with temperature because viscosity is higher in colder water (Fuiman & Batty 1997), which could lead

to warm-water species having higher larval swimming capabilities than species inhabiting colder waters. Observations of swimming speeds in the lab and in the field correspond well (Leis et al. 2006), and critical swimming speeds normally develop in early ontogeny while endurance develops somewhat later (Clark et al. 2005).

Direct evidence for the influence of larval behaviour comes from an impressively well-sampled study on the damselfish; a coral reef fish staying in the proximity of a home coral all its life. Surface currents transported the pelagic larvae away from the reef, but when old enough to migrate vertically they sought depths (60 m) at which directional currents would bring them back to their native reef (Paris & Cowen 2004). Studies such as this one exemplify how vertical migration can exploit ocean currents as a mechanism to influence dispersal. Other coral reef fish larvae also show ontogenetic shifts in depth, with some moving to shallower and some to deeper water as they grow larger (Leis et al. 2006). It would be interesting to know whether these depth shifts are due to changes in mortality rates or due to vertical shear and implications for drift trajectories or both.

1.3 Parental trade-offs in spawning strategies

The spatial- and seasonal variability in growth- and predation risk of fish eggs and larvae are important factors affecting the spawning strategies of adults. Spawning will, however, not necessarily take place at the optimal spawning locations. Rather, the benefits eggs and larvae will have at any particular spawning location is part of a trade-off in the parental life history strategy: How much time and investment should they invest in the spawning migration to obtain benefits for their offspring? For example, how should fish store energy over the year to produce offspring at particular times and places (Schwalme & Chouinard 1999, Varpe et al. 2005), or how much energy, predation risk and lost feeding opportunities should they invest in the spawning migration (e. g. Slotte & Fiksen 2000). The ecology of early life stages therefore provides keys to understand fish life-histories as a whole, as the spawning strategy indicates both how important location and timing are to larvae and how much adults invest in offspring quality.

2. Interpreting fitness: the evolutionary analysis

The pioneering work by Mullon et al. (2002) demonstrated how evolutionary reasoning could be combined with GCMs to understand why fish spawn in particular regions. They tested the implications of various assumptions about larval survival on adaptive spawning location of anchovies in Southern Benguela, and related their results to environmental exposure (temperature) and geographical position (the risk of drifting offshore). Larvae that survived their drift phase spawned again at their natal spawning location and at the time they were spawned themselves. By repeating this procedure for some generations, successful parental spawning strategies emerged from assumptions made in the model.

In this section, we discuss methodological extensions that may extend this approach. Having established that the inconspicuous behaviour of marine larvae can affect growth, mortality, and dispersal dramatically, the obvious question is: How can we study its fitness consequences? In this section, we suggest a composite fitness measure that incorporates *survival* until settlement, the value of settlement in a given *area*, and the value of *body size* at settlement. In addition, we recommend using individual-based models with rule-based behaviour. A further discussion of alternative methodologies for implementation of these concepts is postponed until section 3.

2.1 Behavioural rules

A behavioural strategy can be interpreted as a set of rules that determine how organisms respond to their internal and external environment; directly as fixed strategies, as part of plastic strategies, behavioural rules, or as stimuli-driven neural networks, and how they are constrained by sensory input and physiological restrictions (Giske et al. 2003, Grimm & Railsback 2005, Hutchinson & Gigerenzer 2005). For drifting larvae, a key behavioural trait is vertical positioning since growth, predation risk, and horizontal advection are all functions of depth (Fig. 2).

The ‘fixed-depth’ rule applied in our example (Fig. 1) is obviously too simplistic. Larval fish change depth preference with ontogeny and size, internal condition such as hunger (stomach fullness), and also with the daily light cycle (Lough & Potter 1993, Leis et al. 2006). This choice does not need to be conscious, but may be a genetically hard-wired response to sensory cues (instinctive behaviour).

Assuming that individuals have sensory information about growth g_z and predation rate m_z in a range of depths z , they may use this information to decide which depth to choose. We have developed a more detailed version of rule-based larval behaviour in Vikebø et al. (subm). One option is a rule that maximises the instantaneous rate of mass increase (Persson & De Roos 2003); or maximise $(g_z - m_z)$. This rule avoids the problems associated with the classical Gilliam’s rule (minimize the ratio m_z/g_z) when growth rates approach zero or become negative, as discussed in detail by Railsback et al (1999). However, it may be profitable to take higher or lower risk than specified by this rule, and individuals tend to differ in how much they emphasise growth relative to survival, i.e., how risk-sensitive their behaviour is. We can thus formulate a rule where the selected depth z_i , specific to individual i , optimises the trade-off, modulated by risk sensitivity π_i , between habitat-specific growth and mortality rate:

$$z_i = \max_z [(1 - \pi_i)g_z - \pi_i m_z] \quad 1$$

A risk-averse (fearful) individual would carry π_i values close to one, whereas a bold growth-maximiser would have π_i near zero. The strategy $0 \leq \pi_i \leq 1$ thus has a straightforward interpretation as the risk-sensitivity of an individual, while the risk-sensitivity itself may be a mathematical function affected by a number of parameters translating local information into a value of π_i . The simplest version of the rule is $\pi_i = \beta_i$, then risk-sensitivity is constant and influenced directly by a single gene. Such rules are explored in more detail in Vikebø et al. (subm). The trade-off between growth and mortality may, however, be modulated by a number of stimuli, and the

rule can easily be developed further by making π_i a function of internal states such as stomach fullness or body size.

Rules act as simple heuristics translating local information into different behaviours when environmental conditions change (Hutchinson and Gigerenzer 2005). The ideal behavioural schedule should be evolutionarily robust, meaning it should work well across environmental variability, and difficult to invade by alternative strategies. The rules should also conform to observed patterns of e. g. distributions in depth or space from field studies (Grimm et al. 2005). The ultimate test is to set up gradients in the lab to experimentally challenge rules found by models, and see if larvae are responsive as predicted. Such experiments have generated much insight in limnology (e. g. Loose & Dawidowicz 1994).

2.2 Geographical fitness landscapes

Some organisms, for instance barnacles, are sedentary after the larval drift phase and for the rest of their life. Then larval behaviour must be fine-tuned to utilise currents in finding settlement habitat. A first requirement is that the settling area provides suitable habitat for further growth and survival (Larsson & Jonsson 2006). A second effect is that the settlement area also has a strong bearing on future reproductive success due to the connectivity of spatially fragmented habitat.

Cowen et al. (2006) tracked dispersing larvae in a basin-wide study of the Caribbean using an ocean circulation model. Some reefs were highly connected, and larvae spawned there dispersed to multiple and sometimes distant reefs. Other spawning locations were reproductive dead-ends because ocean currents did not bring larvae close to any suitable settlement habitat. For species with limited mobility in their juvenile or adult stages, such a geographical picture of dispersal and settlement can be viewed as a fitness landscape: all that matters is to end up at a location where your offspring can survive and disperse to other suitable habitat. Species that are more mobile in their post-larval life should be less concerned with their spatial location, and could afford to be more focused on growth and mortality in their local

environment along the drift trajectory. If juveniles and adults were mobile enough to compensate for a poor location, the fitness landscape would still show geographical variation but would become smoother.

What Mullon et al. (2002) did was actually to use a genetic algorithm to map the geographical fitness landscape based from a few assumptions about the early life stages in anchovies. This coupling of general circulation models and habitat connectivity with evolutionary reasoning make trade-offs in larval life and in adult spawning strategies explicit. Geographical position is not everything, however, and to strengthen the link with life history evolution we need a broader perspective on what constitutes fitness.

2.3 Evaluating behavioural strategies

What criteria should be used to assess fitness of different rules or strategies? If the full life cycle including reproduction is modelled, one can use emergent fitness rather than an explicitly formulated fitness criterion (Menczer & Belew 1996, Giske et al. 1998, Strand et al. 2002). However, for models focusing on the early history it is often convenient to assess the success of individuals at a particular time or age, for example at settlement. There are different components that contribute to fitness, and below we have tried to split fitness consequences into functional categories. Let V_i denote fitness evaluated at the end of the drift phase when an individual i following strategy S_i (a rule or a set of rules) has reached a given size or developmental stage. Then:

$$V_i(S_i) = l_i \cdot f(w_i) \cdot G(x_i, y_i) \quad 2$$

The first component here is the survival until settlement l_i . The second component is a function $f(w_i)$ that describes the fitness value of size w_i at settlement. A larger body size may lead to increased competitive ability for food or shelter, or may influence

starvation or predation rates after settlement. The last component is the fitness consequences $G(x_i, y_i)$ of settling at the geographical position (x_i, y_i) . This can be found by making assumptions about habitat suitability, and should ideally include connectivity and potential for future reproduction found through an iterative schedule such as in Mullan et al. (2002). In barnacles, Pineda et al. (2006) demonstrated a time window for successful settlement. In such cases, the value of a given settlement area should include also a time dimension, i.e. $G(x_i, y_i, t_i)$.

The second and third components are in essence all assumptions of expected future reproductive value given individual state and position at the end of the drift phase. It resembles the terminal fitness function known from dynamic programming methods in behavioural ecology (e. g. Houston & McNamara 1999), which is typically a reward-function of being in a particular state at a given time. The first component of fitness is accrued survival probability l_i of a larva throughout the drift phase. Survival depends on the environment along the drift trajectory (predation and starvation) and individual risk sensitivity or behaviour. Fitness V_i is then in units of expected lifetime reproductive success for a single individual following strategy S_i .

Eq. 2 is the simplest version of a fitness function. One could envisage interaction effects between size and space for example, where a large body size gives advantages in some geographical areas compared to others. In that case the effect of size has to be accounted for together with the geographical fitness consequences, and the equation would become $V_i(S_i) = l_i \cdot G(w_i, x_i, y_i)$. For example, size-dependent swimming abilities may reduce the importance of position at settlement for larger larvae. In our larval drift example, fitness may be assessed as proportional to larval length after one month (Fig. 2). However, the fitness of high temperature in the ‘Atlantic’ drift trajectory must be weighted against the potential disadvantage of ending up in unfavourable areas, in our case in the deep off-shelf areas to the west or north of Spitsbergen. Larvae following short-term hedonic cues such as high temperature may end up as losers in a longer term. A more realistic fitness measure would include the function $G(w_i, x_i, y_i)$, but this function is not easy to determine.

3. Modelling toolbox and recommendations

A blend of four different types of models is thus recommended to analyze the fitness consequences of larval behaviour: 1) models of the environment relevant to growth and survival; 2) mechanistic representations of how ecological processes are forced by the environment (growth, predation risk, drift patterns); and 3) behavioural rules to derive adaptive responses or ‘adaptive traits’ in the terminology of Chambers (1993) and Grimm & Railsback (2005); and 4) models evaluating the success of rules in terms of fitness or components of fitness (as in eq. 2). While models of marine larvae traditionally have focused on the two first categories, we argue that the third and fourth elements are crucial to understand the coupling between environment and the success of organisms. Understanding both *how* and *why* marine organisms have adapted so intricately to their moving environment is a necessary prerequisite if we are to predict how fish populations will respond to changes in their environment and to harvesting. In the following, we will discuss requirements for such an integrated modelling effort.

3.1 Physical and ecological environment

General circulation models can generate ‘offline’ matrixes of flow- and environmental variables. As oceanographers develop libraries of such matrixes, including the representations of tidal variability, individual-based models can track a large number of individuals or particles through high-resolution three-dimensional space. With current technology such offline particle models can be executed on desktop computers on time-scales of hours.

3.2 Individual properties

When implementing an individual-based model, it is instructive to keep a distinct separation between the *strategy* that contains the rules that specify behaviour, and the bookkeeping of the *phenotype*. It has been common to describe the phenotype of an individual using an *attribute vector* $A_{i,t}$ (Chambers 1993), which contains all the

states $(\alpha 1_i, \dots, \alpha j_i)$ used to characterise the individual i at time t , such as age, weight, stomach fullness, length, and spatial co-ordinates (x_i, y_i, z_i) :

$$A_{i,t} = (\alpha 1_i, \alpha 2_i, \alpha 3_i, \dots, \alpha j_i, x_i, y_i, z_i) \quad 3$$

High mortality quickly reduces population size and deteriorates variation between individuals, which leaves the composition of the model population vulnerable to chance events (analogous to genetic drift in small populations). This can be solved using super-individuals (Scheffer et al. 1995). A super-individual represents many identical individuals, and the number of identical siblings (n_s) becomes an additional attribute:

$$A_{s,t} = (\alpha 1_s, \alpha 2_s, \alpha 3_s, \dots, \alpha j_s, x_s, y_s, z_s, n_s) \quad 4$$

Here, shown for super-individual s , the number of identical siblings n_s is reduced in proportion to the mortality rate (Scheffer et al. 1995). The number of different super-individuals in the model population and therefore the variation between them remain the same. An alternative interpretation is that n_s may represent the cumulative survival probability of individuals following strategy s . Super individuals also link IBMs to population models and allows the simulation of “true” abundances of fish populations (Huse et al. 2004).

The phenotype results from the individual’s strategy in interaction with the environment. In individual-based models this can be formalized by introducing a *strategy vector* S_i (Huse 2001):

$$S_i = (\beta 1_i, \beta 2_i, \beta 3_i, \dots, \beta j_i)$$

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where βj_i is the adaptive trait j of individual i . The traits specified by the strategy vector can for example be life-history traits or behavioural strategies that specify how individuals should live their lives or use information from their local environment. In the context of larval ecology, typical traits could be the level of risk acceptance, the onset or degree of vertical migration, or built-in responses to light or temperature to mention a few. For the simplistic example presented in Figs. 1-2, the strategy vector would be the depth selected, swimming direction, and swimming velocity. A strategy vector also makes it possible to include a multitude of stimuli in the decision rule, where sensory inputs are weighted differently (analogous to affects) within individuals (Giske et al. 2003). Locally available information can also be processed by a neural network, where the strategy vector prescribes weights for each of the connections (Huse et al. 1999, Strand et al. 2002).

The combination of attribute and strategy vectors enables most relevant characteristics of individuals to be implemented in individual-based models, and the approach also specifies how fixed parameters for a strategy translate into behavioural and phenotypical differences between individuals. The classification based on attribute and strategy vectors can be used to describe IBMs verbally even though the actual programming implementation is not vector based, as for example in object oriented programming (Maley & Caswell 1993).

3.3 Evolutionary algorithms

The strategy vector may be considered as a genotype analogous to a biological chromosome, and we are therefore interested in how evolution would shape it over time. We can also interpret the strategy vector as a phenotype, and use the same type of algorithm to find optimal or adaptive types of behaviour. There are several alternative algorithms that search for solutions that evolution would favour. The broadest distinction is between *optimization* models (e. g. Houston & McNamara

1999, Clark & Mangel 2000), which find the optimal solution to a given problem, and *search heuristics* that use different types of search algorithms to find good and robust solutions but not necessarily the optimal one

Because of the complexity of models that combine physical oceanography, drift patterns, and behaviour, exhaustive search and optimality models rarely provide a viable route. Optimization tools for finding the best possible behaviour are not available for the problem sketched in the previous sections. The reason is that a change in behaviour at any point in time will influence the future drift trajectory, and therefore one has no method for predicting the fitness consequences for the alternative behavioural options. In stead, one has to use heuristics such as genetic algorithms that simulate fast-forward evolution, or simply bombard the models with solutions more like exhaustive search. These heuristic methods can be powerful search algorithms when one simulates populations that behave according to mathematically simple rules, and where there is individual variation in the rule parameters.

One suitable and widely used option is genetic algorithms (Holland 1992, Huse et al. 1999). A genetic algorithm simulates evolution of the strategy vector by modelling a population consisting of individuals with different strategy vectors. Each generation, the individuals with highest fitness pass their strategy vector on to the next generation. The trait value is tested and improved iteratively over generations, and new variation can be introduced by processes analogous to mutation and recombination. This methodology searches for evolutionarily robust strategy vectors, for instance behavioural strategies that prevent larvae from drifting into harsh settlement regions.

4. Summary and recommendations

Selection of vertical habitat for larvae drifting in currents influence both the local short-term trade-off between growth and mortality and more strategic and long-term consequences related to the large-scale circulation regime. The importance of ending

up at particular habitats depends on the mobility of juveniles at settling. If organisms have strong swimming abilities at settlement, we expect them to prioritize growth and survival along the drift trajectory above settlement location. The procedure we have suggested here frames larval behaviour and fish spawning strategies in the tradition of evolutionary ecology, both conceptually and formally. We recommend individual-based modelling practices (Grimm and Railsback 2005) that emphasise *i*) numerous emergent properties from basic, transparent, and mechanistic assumptions on growth, mortality, behavioural abilities, and drift-processes, *ii*) behavioural strategies or rules that show variability between individuals, and *iii*) selection processes that incorporate fitness consequences along the trajectory and of settlement location. One efficient tool for such investigations is models that simulate evolution based on genetic algorithms. Such models tackle sufficient complexity and are capable of evaluating consequences of larval behaviour in flow fields and integrating effects across several time-scales. Modelling should be done in close collaboration with laboratory and field studies on larval behaviour, their abilities, constraints, and temporal and spatial distribution.

ACKNOWLEDGEMENTS

We are most grateful to D.L. Aksnes and J. Giske for their original views on mechanics and evolution in the sea, an important source of inspiration for this work. We acknowledge the Research Council of Norway for support. Thanks to T. Torgersen and S. Eliassen for discussions and comments.

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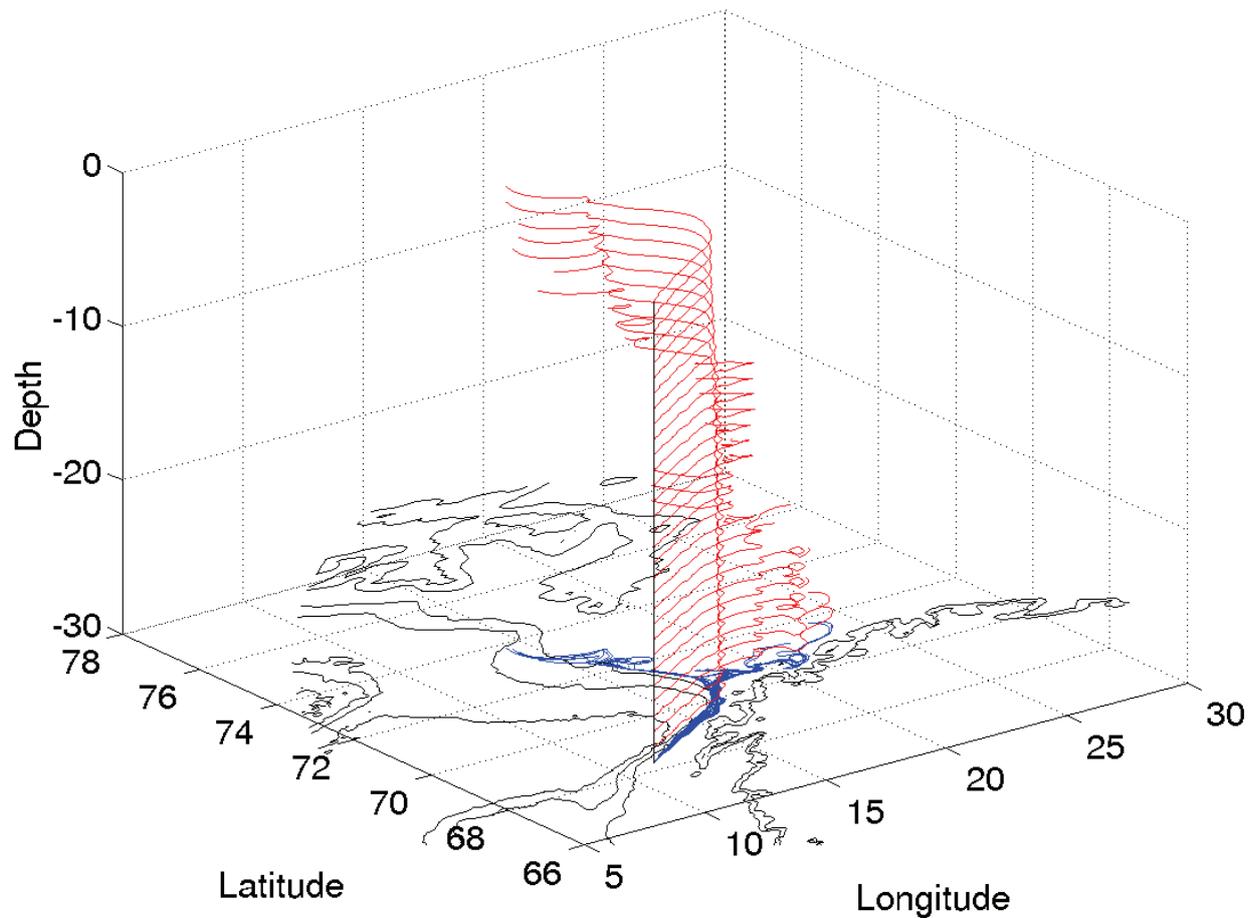


Figure 1 Drift trajectories of particles in fixed depths (0 – 30 m) over one month, The particles are released simultaneously on a fixed point at Moskenesgrunnen. The red lines show the drift trajectories in 3-D, while the blue lines are the geographical projections of the trajectories. These can be grouped in two bundles, the deep ones drifting along the coast, and the upper trajectories, drifting offshore, northwards. See Vikebø et al. (2005) for details.

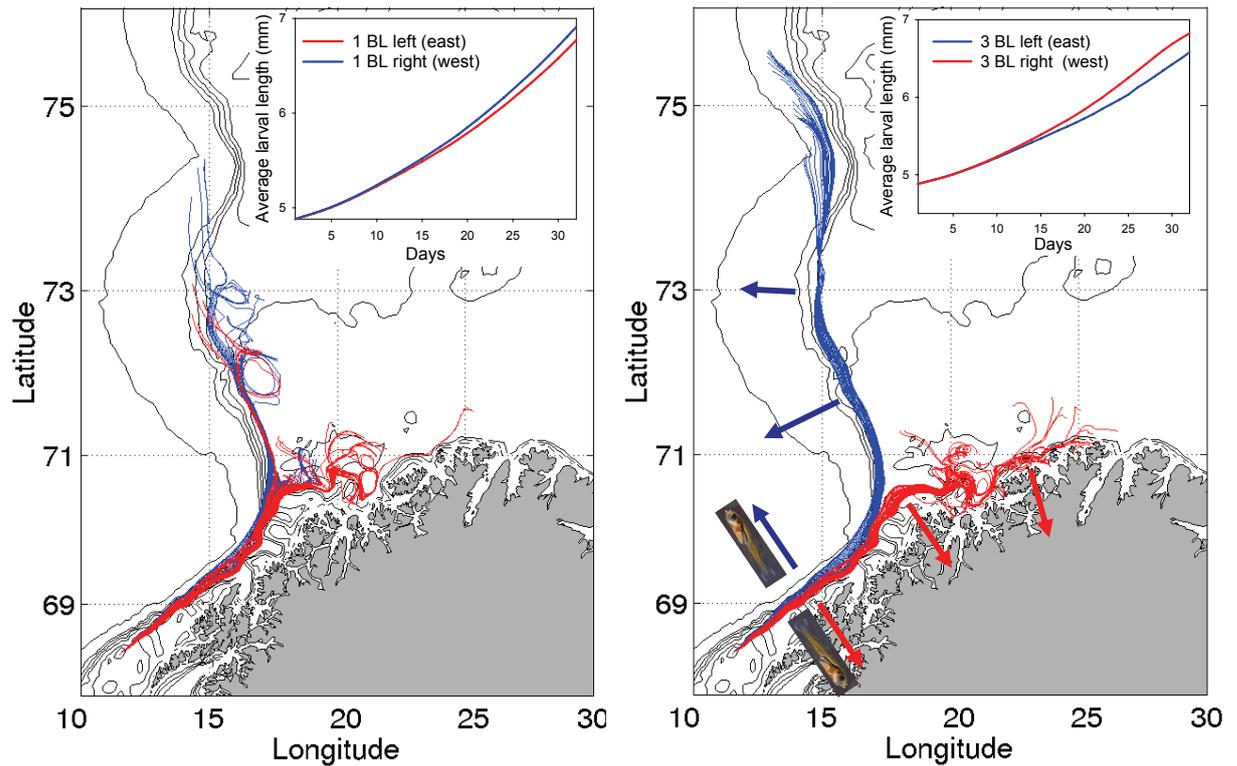
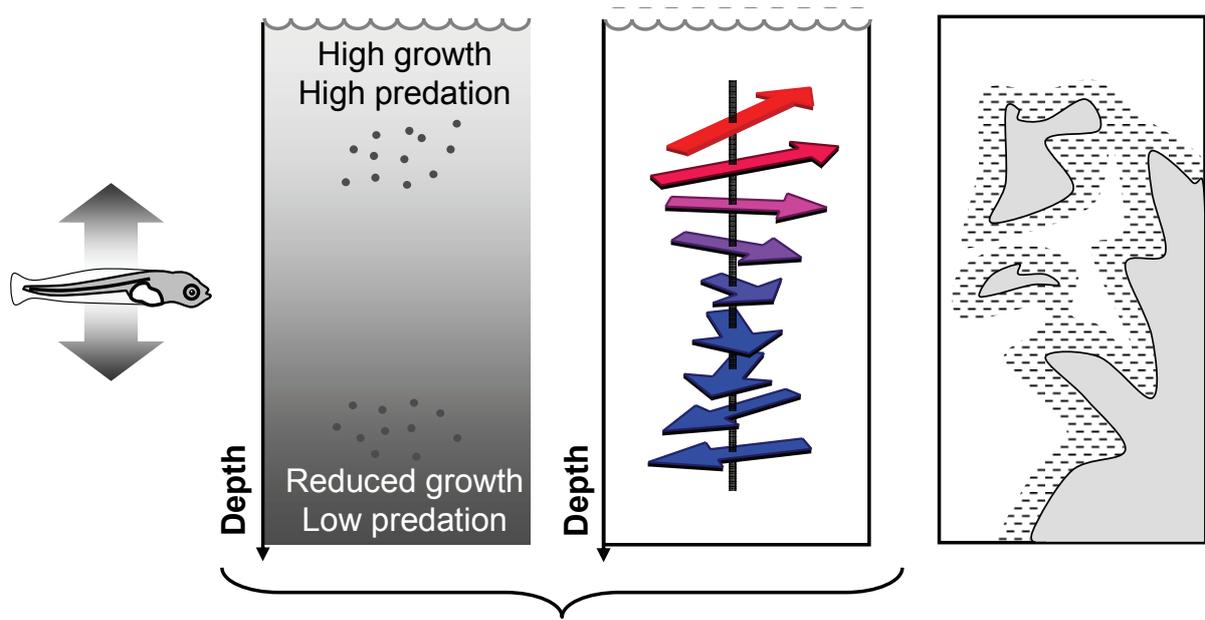


Figure 2 Drift trajectories of larvae released at Moskenesgrunnen, northern Norway, at 1st of April and one month forward in time. Each line represents one larva inhabiting a fixed depth between 1 and 30 m (one larva in each depth), blue lines are swimming constantly 90° to the right (facing the currents, mainly westerly directions); red lines are swimming constantly 90° to the left (facing the currents, mainly south-easterly directions). They swim with a velocity of either one (left panel) or three (right panel) body lengths per second. The average growth histories of the individuals are embedded in the figure. See Vikebø et al. (2005) for details.



Fitness equation:

$$V_i(S_i) = l_i \cdot f(w_i) \cdot G(x_i, y_i, t_i)$$

	Water column	Drift trajectory	Settlement area
Consequences:	Instantaneous growth and mortality	Opportunities for growth and mortality along trajectory	Opportunities for growth, mortality and reproduction in the future
Trade-off type:	Local, short-term	Strategic, medium-term	Strategic, long-term

Figure 3 This figure illustrates the local and strategic trade-offs in larval habitat selection. To the left are the classical behavioural elements of the pelagic environment, setting up a local trade-off between growth and survival. In the middle the large-scale drift consequences of local depth selection. The picture to the right illustrates the terminal settlement area when the drift phase is over. This area may also influence fitness, and should be included in the evaluation of the success of the behavioural strategy. The table refers to the symbolism introduced in the text.