INTRODUCTION

Ecologists are gradually realizing the importance of behavior in understanding both patterns of growth and deaths in individuals, populations, and even ecosystems (Schmitz 2010). It has long been known that zooplankton can be behaviorally responsive to their predators, and adjust their vertical migration strategy depending on which predators are most abundant and dangerous (Ohman 1990, Frost & Bollens 1992). Larval fish are immature and vulnerable, initially highly susceptible to predation, and have received less attention for their behavioral repertoire. One may conclude that chance is the dominant factor for their success, or instead that evolutionary adaptations and behaviors become even more important due to this vulnerability. Certainly, field observations do suggest that fish larvae of various species perform diel-vertical migration (Lough & Potter 1993, Santos et al. 2006), but the mechanisms and trade-offs are rarely quantified. Although abilities of cognition and scope for behavior are low in larvae, they steadily increase with ontogeny, and should not be ignored in our understanding of larval fish.

Three behavioral traits have received attention from larval fish modelers: 1) diet selection, 2) activity level or swimming speed and 3) habitat (typically depth) selection. These behaviors are all included in various models of larval fish. With focus on our own research, we divide modelling efforts between rule-based and optimal approaches, and discuss how behavioral flexibility and spatial distribution during the early life history of fish, mainly applied to cod larvae, can be modelled. The methods and their theoretical foundations are generally well known and developed in the field of behavioral ecology, but may be new to anyone with no training in evolutionary ecology (or economics, where similar methods are often applied). We also highlight some of the key lessons and predictions from our models developed over the last decade.

THEORY AND MODELS

Diet selection and predation risk

The theory of diet selection and optimal foraging theory (OFT) are among the oldest behavioral theories with a sound evolutionary basis (Stephens et al. 2007). Prey selection, which essentially is the behavioral decision to ignore a potential prey that has been detected, makes sense (i.e. maximizes the rate at which food is consumed) if the energetic value of the particular prey item is low, the handling time is long, or the probability of capture is low relative to the expected return if the prey is ignored (Charnov 1976). It may intuitively appear suboptimal to ignore prey which has been detected, but it can easily be shown that the loss of time searching for better prey in some situations offsets the value of handling and consuming a prey of low value. In fact, the cost of not doing so can be substantial (Visser & Fiksen 2013). As an example, the general increase in prey size with larval size (Miller et al. 1988) is rooted in this theory.

An organism may have a spectrum of alternative prey in its environment, and if detected each has profitability (energy ingested per time) defined as the product of energetic value*capture success/handling time. Thus, there will be a particular range of prey that is profitable to include in the diet, and only the prey within this range should be pursued (e.g. Visser & Fiksen 2013). This theory has been applied extensively and elegantly in larval
Individual-based models and vertical migration of larval fish

Individual-based models (IBMs) represent a novel approach to think about ecology in general (Grimm & Railsback 2005, Grimm et al. 2005), and are frequently applied to understand and model evolutionary and behavioral processes (Railsback et al. 1999, Huse & Ellingsen 2008, Railsback & Harvey 2011). Some of the IBMs now developed integrate across multiple biological levels, from genetics to behavior and population dynamics (Giske et al. 2013, Giske et al. 2014). These are powerful tools, but can be challenging to develop and analyze when individuals can adapt or evolve over generations. Obviously, no truly evolutionary larval fish models exist, since they only cover a short period of the life cycle. The approach taken to model behavior in larval fish IBMs is typically referred to as ‘rule-based’ – where the larva follows a prescribed rule in how it responds to a particular stimuli. This rule can be either a simple environmental cue, but most often is based on either growth or mortality rates as perceived from one or several cues. The most classical rule is Gilliam’s rule (Gilliam & Fraser 1987) where at any moment in time, an organism is assumed to behave to maximize the difference between growth and mortality (or specifically, the ratio of growth rate/mortality rate). In an environmental gradient, this assumes that a larva can assess growth and mortality in its ambient environment and alternative adjacent locations, and move to the habitat with the highest growth-mortality difference. There are several discussions on the validity of this fitness measure in the literature (Railsback & Harvey 2002, Persson & De Roos 2003), and it is certainly not a perfect measure in all situations. Nevertheless, it does capture some essential elements of fitness, as both growth and predation are included and traded off against each other. For larval fish, the importance of growing fast out of a vulnerable size range is one of the issues that this rule may miss.

We explored the emergent spatial distribution and fitness (defined as survival probability to a given size) in larval cod using a range of behavioral rules in Kristiansen et al. (2009). Rules were all using information about either growth and mortality or foraging and mortality; but we also tried out different ‘personality traits’ to the rule, where the larva could place more or less weight on growth (‘bold’ larvae) or predation (‘fearful’ larvae). This risk-seeking or risk-averse element could also depend on stomach fullness, such that the larvae become more risk seeking and increase their ability to find food if the stomach is running empty, which may be common in nature (Pearre 2003). We performed simulation competitions between the alternative rules, and compared their success in a vertical water column with a day-night cycle. We found a substantial difference in survival (several orders of magnitude) between the random movement and all of the rule-based behaviors, with evolved rules outperforming random or uninformed behavior in all cases. This points at the importance of using a reasonable behavioral algorithm in larval fish models, which aim at quantifying how larval fish recruitment is affected by environmental factors.
An important property of IBMs is that they easily integrate with general circulation models (GCMs). This can be done using stored offline flow-fields (velocity vectors) generated by ocean models, and then let particles be moved in space within these fields (Vikebø et al. 2007). These models must contain a rule of behavior or migration of the larvae, either assuming random, fixed depth or some inherent responses to local cues. The drift trajectories and dispersal of the larvae can be quite sensitive to the chosen rule (Fiksen et al. 2007). An interesting question is how larvae may be adapted to a particular circulation system and utilize the vertical shear of currents and vertical positioning in the water column to increase retention or to end up in favorable nursery areas. The vertical positioning required to drift into favorable nursing grounds may be in conflict with the immediate need to forage or avoid predators. Particle tracking in GCM-flow fields can reveal these potential trade-offs, and suggests how personality traits or individual affinities to particular cues may evolve in these settings (Fiksen et al. 2007, Vikebø et al. 2007). A substantial number of IBMs have been developed and applied on top of large-scale marine ecosystem models or climate projections (e.g. Hinrichsen et al. 2003, Dawel et al. 2008a, Hinrichsen et al. 2012, Kristiansen et al. 2014), and there is an increasing awareness of the interaction between behavior and spatial dispersal.

Optimality models and habitat selection

Optimality models are first and foremost a thinking tool, an instrument to investigate what will happen if an organism is perfectly adapted to the environment, as a sort of null-hypothesis. Optimality models for larval fish assume that the individual behaves in a way that maximizes its fitness, which we have equalled to ‘maximize probability of survival to a given size’. We calculate the best route through a vast space of possible trajectories through state-space (depth, stomach fullness, size) and time (a number of day-night cycles), and find the optimal behaviors for each possible combination. Then, we follow individual larvae through time and space to visualize the strategies that lead to high fitness (Fiksen & Jørgensen 2011, Fouzai et al. 2015). Thus, we implicitly assume that larvae have fully adapted their behavior to a given environmental setting, which is obviously an optimistic assertion. Young larvae have limited cognition and behavioral repertoire, and this can be included as constraints in the models. In reality, individual behavior is driven by cues from the external environment (temperature, light, chemicals, etc.) or the internal physiology (gut fullness, energy reserves), while optimality models simply assume that organisms have the information needed with certainty (but stochasticity is commonly added). Consequently, the models overestimate the abilities of animals to navigate and take advantage of all loopholes in their environment.

On the other hand, ignoring behavioral plasticity completely, even in larval fish, is a more unlikely starting point. Organisms are able to assess their environment and adjust their behavior accordingly – and these can evolve faster than we often realize. For instance, mayfly nymphs adopted a new diel activity pattern shortly after brown trout were introduced to New Zealand (Mcintosh & Townsend 1994), and the activity level and diet of grasshoppers depend on whether its spider predator is an ambush or cruising species (Schmitz et al. 2008). A larval fish will not be able to live up to the optimality assumption, but it is reasonable to expect that it has evolved the ability to both sense and take advantage of gradients in its environment to some degree, and that these abilities increase rapidly during ontogeny.

Comparing IBMs and optimality models – and how they might be combined

While IBMs assume the larval behavior is naïve or rigid, and probably underestimate the prudence of larvae, optimality models are overly optimistic about what an individual may know about the local environment and the near future. Lack of behavioral responses is a well-known limitation for IBMs, and various suggestions for how to deal with this problem exist in the literature (e.g. Hutchison & Gigerenzer 2005, Railsback & Harvey 2013). For instance, the IBM-rules do not drive larvae to fill up their stomachs before the night or to leave the surface soon enough to migrate out of the dangerous depths at dawn, and modelled larvae therefore grow less or are eaten more often than they would if they planned ahead within the diel cycle. We should expect that even larval fish could be equipped with inherent responses that optimize diel periodicity in behavior if the benefits are substantial. In our models (Kristiansen et al. 2009) the lack of prudence caused larvae to be trapped in risky daylight in early morning where they encountered fish predation, and a loss of growth due to empty stomach during the night. Railsback & Harvey (2013) suggested a method to deal with such problems by allowing individuals to look into the future and use some information in their immediate decisions, but so far this has not been tried on larval fish.

Clearly both optimality models and IBMs have their pros and cons, and it should be possible to combine the best of both by using an optimality model as a benchmark for the IBM (Sainmont et al. 2015). This would mean to first find the behavior as a larva grows over time using dynamic programming, and then use the results to compare how close to this optimum one can get with rule-based modelling in exactly the same vertical, time-varying environment. Ideally, a robust rule should yield reasonable survival chances relative to the optimum in a range of different environmental settings. In any case, such benchmarking of rules against an optimum could be
WHAT HAVE WE LEARNED FROM THESE MODELS?

There are a number of lessons to be drawn from these models, some of which were recently summarized in an attempt to reframe some of the classical hypotheses on recruitment success in fish in the context of behavioral ecology (Jørgensen et al. 2014). One key point was that larvae are in a constant trade-off situation between growth and survival modulated with behavior (migration between habitats). Our models (e.g. Fiksen & Jørgensen 2011) suggest that a classical growth-mortality trade-off perspective can unify several of the hypotheses of recruitment processes which have emerged within fisheries oceanography.

Cod recruitment success has been found to be strongly associated with food abundance (Beaugrand et al. 2003), but at the same time cod larvae appear to grow at maximum temperature-limited rates, regardless of food abundance (Folkvord 2005). These studies might look like contrary findings, but from an optimality model we see that food abundance has relatively little implication in growth, but profound effect on survival (Fiksen & Jørgensen 2011). The reason is that costs of increasing the duration of the larval stage make it profitable to accept increased predation risk to maintain high growth and keep the larval stage short. As food abundance increases, the larva can take advantage by moving to safer habitats or by using other behavioral strategies. The model predicts that the benefits of survival from higher prey availability extend far beyond the level of food required to maintain satiated growth rates, and points to a stronger link between prey and recruitment than in models which do not explicitly include a foraging-predation trade-off. It also suggests that the correlation between prey availability and growth rates may be difficult to establish, as an important fraction of the benefit of more food shows up in survival rates which are much more difficult to estimate.

Similarly, higher temperatures can reduce development time, but the increased metabolism comes with a predation cost that is not trivial unless the trade-offs are made explicit. The mix of high temperature and low prey availability is detrimental not because of the risk of starvation, but because of the predation cost incurred while foraging to meet the higher metabolic demand (Fouzai et al. 2015). Vertical temperature gradients represent an opportunity for larvae to move into the right temperature regime given the food supply, but on the other hand, this can drive them into less favorable temperatures by the spatial gradient in predation risk.

In these optimality models, external temporal changes are limited to the daily light cycle. However, the model framework also allows inclusion of seasonal and yearly cycles. Behaviors related to such periodicity are often termed ‘routines’, which can be understood as adaptations to the periodicity of their environment, including annual and diel routines (McNamara & Houston 2008). These models are powerful tools to develop detailed predictions and hypotheses of the diel routines of larvae. For diel migration, the prediction is that a shift from no or limited to extensive diel migration should be abrupt at a size depending on turbidity, predator abundance and prey availability. Activity should peak in the morning and evening, to ensure the gut is operating at its capacity through the diel cycle.

WHAT REMAINS TO BE DONE?

The models we have worked on so far are theoretical, and the environment schematic. The next step is to move theoretical predictions into the sea and use data available from monitoring and field campaigns. Field surveys with detailed information of larval distribution over time are scarce, but exist (e.g. Munk et al. 1989). Detailed sampling of the environmental and biological drivers over a diel cycle are very valuable to testing and further developing models of space use in larval fish. Although we are aware of the challenges involved, observations of potential predators are desirable, and as seen from our models, at least equally important as the environmental variables in understanding what drives variability in larval recruitment success.

Another wish is more experiments that place larvae in gradients of environmental variables – light, temperature, food, cues of predators – to see if or at what stage they start to respond to gradients. Experiments which give fish a choice are rare, but do exist (Sogard & Olla 1996, Vollset et al. 2009, Vollset et al. 2013), and they are needed to develop our understanding of the capabilities and priorities of larval fish. Hopefully, the models will also stimulate discussions around patterns or absence of patterns that the models are deriving, and stimulate a productive and scientific cycle of theory and observations.

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