VIE ET MILIEU - LIFE AND ENVIRONMENT, 2015, 65 (2): 115-120

OPTIMALITY AND RULE-BASED MODELS FOR LARVAL FISH BEHAVIOR

Ø. FIKSEN[1*], *A. F. OPDAL*[1]

[1] *Department of Biology, University of Bergen and Hjort Centre for Marine Ecosystem Dynamics,*
P.O. Box 7803, N-5020 Bergen, Norway
Corresponding author: oyvind.fiksen@bio.uib.no

IBMS
LARVAL FISH
MODELS
OPTIMALITY THEORY
RULE-BASED BEHAVIOR

ABSTRACT. – Larval fish are small and vulnerable, but can they improve their survival chance through adaptive behavioral strategies? Most theoretical models linking larval success to environmental conditions use oceanography, the physical environment and prey supply as the sole determinants of survival and growth. Here we review our recent model developments, which are based on the assumption that larval fish are like most other animals, hungry for food, afraid of predators, and equipped with cognitive abilities to respond to and make use of gradients and fluctuations in their environment. We explain and discuss differences between individual-based models and optimality models, and summarize some key predictions. We also point at the need for experimental studies to reveal the behavioral capacities of larval fish, both in the lab and in the ocean.

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 fish models where there is a spectrum in prey size, first by Letcher *et al.* (1996), and later in a number of large-scale applications (e.g. Daewel *et al.* 2008a, Daewel *et al.* 2008b, Hinrichsen *et al.* 2012), mathematically solving a problem that occurs immediately when a larva is offered several alternative prey items. Sometimes this issue is handled by inclusion of more or less sophisticated 'preference functions', but these are not mechanistic or ecologically meaningful when the prey composition changes over time or in space.

Prey searching and selection involve an energetic cost and a feeding-predation risk trade-off. Swimming associated with either searching for food or moving to a new depth location inherently lead to higher encounter rates with both prey and predators. Movement activity therefore increases feeding rate but also make the larva more visible to predators, leading to a classical survival-growth trade-off. A similar trade-off is typically involved in habitat or depth selection of larvae, since both larvae and visual predators are dependent on light to see and find food. Light decays exponentially with depth but since the detection range of fish satiates with light, foraging and risk do not necessarily follow the same curve with depth (Giske *et al.* 1994, Fiksen *et al.* 1998, Huse & Fiksen 2010). Vertical gradients of growth and predation rates can be steep, and therefore the behavioral migration decision, even within the range attainable by larval fish, becomes an important determinant of survival and growth. The spatial aspect may often exceed differences between models with alternative formulations of processes or across typical variation in environmental parameters, and the behavioral kernel then becomes the most important element of the model.

Ideas from optimal foraging theory OFT have since its invention spilled over to other areas, such as spatial distribution and migration of animals. But this has mainly happened after OFT developed into UFT – unified foraging theory – where the risk of predation associated with foraging also became part of the equations (Mangel & Clark 1986, Houston *et al.* 1988). The ability to integrate growth and survival in a behavioral trade-off became possible with the introduction of what is called 'dynamic programming' in ecology during the 1980s. This particular method is widely used in a range of disciplines, and the relevance and application in ecology have been elaborated in detail in several textbooks (Mangel & Clark 1988, Houston & McNamara 1999, Clark & Mangel 2000). We have used it extensively to understand the rationale and importance of behaviors, such as swimming activity and depth selection in larval fish.

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 larvae 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, Daewel *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. Hutchinson & 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 a possible approach to the development and ground-truthing of proximate behavioral rules (Sainmont *et al.* 2015).

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 on 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.

ACKNOWLEDGEMENTS. – We are grateful to our many current and former colleagues at BIO and the Theoretical Ecology Group for forming and sharpening our ideas about larval fish behaviour. In particular, we are depending on C Jørgensen for his clear thinking on evolution and excellent programming skills.

REFERENCES

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC 2003. Plankton effect on cod recruitment in the North Sea. *Nature* 426: 661-664.

Charnov EL 1976. Optimal foraging - attack strategy of a mantid. *Am Nat* 110: 141-151.

Clark CW, Mangel M 2000. Dynamic state variable models in ecology: methods and applications. Oxford University Press, New York.

Daewel U, Peck MA, Kuhn W, St John MA, Alekseeva I, Schrum C 2008a. Coupling ecosystem and individual-based models to simulate the influence of environmental variability on potential growth and survival of larval sprat (*Sprattus sprattus* L.) in the North Sea. *Fish Oceanogr* 17: 333-351.

Daewel U, Peck MA, Schrum C, St John MA 2008b. How best to include the effects of climate-driven forcing on prey fields in larval fish individual-based models. *J Plankton Res* 30: 1-5.

Fiksen Ø, Jørgensen C 2011. Model of optimal behaviour in fish larvae predicts that food availability determines survival, but not growth. *Mar Ecol Prog Ser* 432: 207-219.

Fiksen Ø, Utne AC W, Aksnes DL, Eiane K, Helvik JV, Sundby S 1998. Modelling the influence of light, turbulence and ontogeny on ingestion rates in larval cod and herring. *Fish Oceanogr* 7: 355-363.

Fiksen Ø, Jørgensen C, Kristiansen T, Vikebø F, Huse G 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. *Mar Ecol Prog Ser* 347: 195-205.

Folkvord A 2005. Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models. *Can J Fish Aquat Sci* 62: 1037-1052.

Fouzai N, Opdal AF, Jørgensen C, Fiksen Ø 2015. Effects of temperature and food availability on larval cod survival: a model for behaviour in vertical gradients. *Mar Ecol Prog Ser* 529: 199-212.

Frost BW, Bollens SM 1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. *Can J Fish Aquat Sci* 49: 1137-1141.

Gilliam JF, Fraser DF 1987. Habitat selection under predation hazard - test of a model with foraging minnows. *Ecol* 68: 1856-1862.

Giske J, Aksnes DL, Fiksen Ø 1994. Visual predators, environmental variables and zooplankton mortality risk. *Vie Milieu* 44: 1-9.

Giske J, Eliassen S, Fiksen Ø, Jakobsen PJ, Aksnes DL, Jørgensen C, Mangel M 2013. Effects of the emotion system on adaptive behavior. *Am Nat* 182: 689-703.

Giske J, Eliassen S, Fiksen Ø, Jakobsen PJ, Aksnes D, Mangel M, Jorgensen C 2014. The emotion system promotes diversity and evolvability. *Proc R Soc B* 281.

Grimm V, Railsback S 2005. Individual based modeling and ecology. Princeton University Press, Princeton and Oxford.

Grimm V, Revilla E, Berger, Jeltsch F, Mooij WM, Railsback SF, Thulke HH, Weiner J, Wiegand T, DeAngelis DL 2005. U Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science* 310: 987-991.

Hinrichsen HH, Bottcher U, Koster FW, Lehmann A, St John MA 2003. Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift. *J Sea Res* 49:187-201.

Hinrichsen HH, Kuhn W, Peck MA, Voss R 2012. The impact of physical and biological factors on the drift and spatial distribution of larval sprat: A comparison of the Baltic and North Seas. *Prog Oceanogr* 107: 47-60.

Houston AI, McNamara J 1999. Models of adaptive behaviour. An approach based on state. Cambridge University Press, Cambridge.

Houston A, Clark C, McNamara J, Mangel M 1988. Dynamic models in behavioral and evolutionary ecology. *Nature* 332: 29-34.

Huse G, Ellingsen I 2008. Capelin migrations and climate change - a modelling analysis. *Climatic Change* 87: 177-197.

Huse G,, Fiksen Ø 2010. Modelling encounter rates and distribution of mobile predators and prey. *Prog Oceanogr* 84: 93-104.

Hutchinson JMC, Gigerenzer G 2005. Simple heuristics and rules of thumb: Where psychologists and behavioural biologists might meet. *Behav Process* 69: 97-124.

Jørgensen C, Opdal AF, Fiksen Ø 2014. Can behavioural ecology unite hypotheses for fish recruitment? *ICES J Mar Sci* 71: 909-917.

Kristiansen T, Jørgensen C, Lough RG, Vikebø F, Fiksen Ø 2009. Modeling rule-based behavior: habitat selection and the growth-survival trade-off in larval cod. *Behav Ecol* 20: 490-500.

Kristiansen T, Stock C, Drinkwater KF, Curchitser EN 2014. Mechanistic insights into the effects of climate change on larval cod. *Global Change Biol* 20: 1559-1584.

Letcher BH, Rice JA, Crowder LB, Rose KA 1996. Variability in survival of larval fish: Disentangling components with a generalized individual-based model. *Can J Fish Aquat Sci* 53: 787-801.

Lough RG, Potter DC 1993. Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus-aeglefinus* and Atlantic cod *Gadus-morhua* on Georges Bank. *Fish Bull* 91: 281-303.

Mangel M, Clark CW 1986. Towards a unified foraging theory. *Ecol* 67: 1127-1138.

Mangel M, Clark CW 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, N.J.

Mcintosh AR, Townsend CR 1994. Interpopulation variation in mayfly antipredator tactics - differential effects of contrasting predatory fish. *Ecol* 75: 2078-2090.

McNamara JM, Houston AI 2008. Optimal annual routines: behaviour in the context of physiology and ecology. *Phil Trans R Soc B* 363: 301-319.

Miller TJ, LB Crowder, JA Rice, EA Marschall 1988. Larval size and recruitment mechanisms in fishes - toward a conceptual framework. *Can J Fish Aquat Sci* 45: 1657-1670.

Munk P, Kiorboe T, Christensen V 1989. Vertical Migrations of Herring, Clupea-Harengus, Larvae in Relation to Light and Prey Distribution. *Environ Biol Fish* 26: 87-96.

Ohman MD 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecol Monogr* 60:257-281.

Pearre S 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol Rev* 78: 1-79.

Persson L, De Roos AM 2003. Adaptive habitat use in size-structured populations: Linking individual behavior to population processes. *Ecol* 84: 1129-1139.

Railsback SF, Harvey BC 2002. Analysis of habitat-selection rules using an individual-based model. *Ecol* 83: 1817-1830.

Railsback SF, Harvey BC 2011. Importance of fish behaviour in modelling conservation problems: food limitation as an example. *J Fish Biol* 79: 1648-1662.

Railsback SF, Harvey BC 2013. Trait-mediated trophic interactions: is foraging theory keeping up? *TREE* 28: 119-125.

Railsback SF, Lamberson RH, Harvey BC, Duffy WE 1999. Movement rules for individual-based models of stream fish. *Ecol Model* 123: 73-89.

Sainmont J, Andersen KH, Thygesen UH, Fiksen Ø, Visser AW 2015. An effective algorithm for approximating adaptive behavior in seasonal environments. *Ecol Model* 311: 20-30.

Santos AMP, Re P, Dos Santos A, Peliz A 2006. Vertical distribution of the European sardine (*Sardina pilchardus*) larvae and its implications for their survival. *J Plankton Res* 28: 523-532.

Schmitz OJ 2010. Resolving Ecosystem Complexity. Princeton University Press, Princeton and Oxford.

Schmitz OJ, Grabowski JH, Peckarsky BL, Preisser EL, Trussell GC, Vonesh JR 2008. From individuals to ecosystem function: Toward an integration of evolutionary and ecosystem ecology. *Ecol* 89: 2436-2445.

Sogard SM, Olla BL 1996. Food deprivation affects vertical distribution and activity of a marine fish in a thermal gradient: Potential energy-conserving mechanisms. *Mar Ecol Prog Ser* 133: 43-55.

Stephens DW, Brown JS, Denberg RC Y 2007. Foraging: Behavior and Ecology. University Of Chicago Press.

Vikebø F, Jørgensen C, Kristiansen T, Fiksen Ø 2007. Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. *Mar Ecol Prog Ser* 347:207-219.

Visser A W, Fiksen Ø 2013. Optimal foraging in marine ecosystem models: selectivity, profitability and switching. *Mar Ecol Prog Ser* 473: 91-101.

Vollset KW, Catalan IA, Fiksen Ø, Folkvord A 2013. Effect of food deprivation on distribution of larval and early juvenile cod in experimental vertical temperature and light gradients. *Mar Ecol Prog Ser* 475: 191-201.

Vollset KW, Fiksen Ø, Folkvord A 2009. Vertical distribution of larval cod (*Gadus morhua*) in experimental temperature gradients. *J Exp Mar Biol Ecol* 379: 16-22.

Received on February 2, 2015
Accepted on April 15, 2015
Associate editor: N Coineau