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Modeling rule-based behavior: habitat selection and the growth-survival trade-off in larval cod

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Environmental variation can cause significant fluctuations in the survival of larval fish and plankton. Understanding these fluctuations is critical for developing more accurate fisheries models, which are needed for both scientific and socioeconomic research. Growth, survival, and dispersal of marine planktonic larvae rely strongly on their behavior. Larval fish change their vertical positioning due to strong vertical gradients in light, temperature, predation pressure, and prey availability. Here, we explore how various behavioral rules predict vertical distribution, growth, and survival of larval cod (*Gadus morhua*) in a numerical model. The rules determine the trade-offs between larval growth, feeding rate, and predation rate, including their dependence on gut fullness and body mass. We evaluated the survival through size classes for different rules and random behavior and compared model predictions with observed larval distribution patterns. The rules predicted the correct average depth position with larval size, but failed to predict the timing of the observed vertical distribution pattern. However, model simulations revealed significant increases in survival for larval and juvenile cod with active behavior compared with larvae with random behavior. Behavior was important across all sizes of fish, and this study illustrates the value or added information of incorporating behavior in biophysical models. *Key words:* behavioral heuristics, diel vertical migration, individual-based model, larval cod, trade-off. *[Behav Ecol 20:490–500 (2009)]*

Abundance of many marine populations varies considerably between years because survival of the progeny is affected by biotic and abiotic conditions (Stenseth and Mysterud 2002; Stenseth et al. 2003). Such differences occur under natural climate variability, with strong consequences for the biomass production of marine organisms (Cushing 1990; Platt et al. 2003). However, under human-induced pressures such as fishing (Hsieh et al. 2008) and climate change, these impacts may increase in strength (Brander 2007). A key component of predicting responses to these impacts is the successful prediction of survival through early life stages where mortality rate typically reach 0.1 day^{-1} (Houde 1987; Sundby et al. 1989). In spite of the importance of behavior in determining survival rates, few biophysical models (but see, e.g., Strand et al. 2002) incorporate behavior (Leis et al. 2006).

An increase or decrease in stratification affects the properties of the water column, such as the vertical distribution of light, supply of nutrients from deeper waters, temperature, phytoplankton, and zooplankton (Hays et al. 2005). Changes in environmental forcing (e.g., wind, light, turbulence, temperature, and prey concentration) may lead to adverse growth conditions that are unfavorable for recruitment. Consequently, planktonic organisms that rely on phytoplankton and zooplankton as food resources will be affected by changes in the spatial and temporal distribution of prey abundance.

However, individuals can modify their behavior to move into more favorable conditions for growth or survival. Because the pelagic environment offers limited structure for larval fish to escape predation, vertical behavior may serve the purpose for reducing encounters with visual predators (Lima and Zollner 1996). Still, movement to greater depths also translates to less light for locating and capturing food. Consequently, habitat selection mediates trade-offs between feeding, digestion, growth, and mortality from predators in a structured environment.

The movement ability of fish larvae is usually low compared with ocean current velocities in temperate waters, but not in tropical waters (Clark et al. 2005; Fisher et al. 2005; Leis 2007). Previous research showed that local decisions on the choice of vertical position have long-term effects on cumulative transport and dispersal patterns (Fiksen et al. 2007; Vikebø et al. 2007). Currents are often vertically stratified, and once larval fish choose particular depths, they will follow different current movements (Vikebø et al. 2007). Therefore, a complete understanding of the full life cycle of fish requires connecting survival and dispersal of the early life stages with spawning migrations and their relative costs in terms of energy and time at the adult life stages (Jørgensen et al. 2008).

Most models of larval fish are detailed with respect to physiology and predator–prey interactions, but not behavior, although it is known to be important (Leis et al. 2006). Accounting for behavior in models requires knowledge on foraging, behavioral, and landscape ecology to account for spatial and temporal gradients that may influence survival and growth of an individual (Lima and Zollner 1996). How an individual behaves is often motivated by hunger (Skajaa et al. 2003) or satiation and may change with size throughout ontogeny. Such state dependence has generally been studied with models that rely on optimality approaches (e.g., Houston and McNamara 1999). An alternative is to use individual-based models (IBMs), which can incorporate phenotypic differences among individuals and enable researchers to explore how varying environmental properties may affect individual survival and behavior. Behavioral differences among individuals will further create emergent properties at the population level (DeAngelis and Gross 1992; Grimm et al. 2006), such as differences in weight and length (Folkvord and Otterå 1993; Folkvord et al. 1994; Gallego and Heath 1997) that can be studied and compared with observations.

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An IBM can be used to simulate large fish populations where individual behavior is specified by simple rules. Such rules can be made state dependent by responding to information about the individual's physiological state or cues for the external environmental (Railsback and Harvey 2002). A key challenge is to derive and apply rules that are consistent with observed behavioral patterns and evolutionary principles. Several techniques have been applied to achieve these goals, for example, combining several separate cues into actions through genetic algorithms with neural networks (Huse et al. 1999) and "hedonic tones" (Giske et al. 2003). More simple rules are often based on growth and mortality rates directly (Persson and De Roos 2003), assuming these can be estimated.

Here, we explored a set of possible behavioral rules that larval fish may follow in a spatially structured environment. We used field data from Georges Bank (Northeast coast of USA) to drive the model and compared the emergent patterns from our model with observations of larval fish from the same location. Our IBM contained 1) a detailed physiological model of the internal states and processes of individuals' digestion and growth, 2) functional ecological interactions between individuals and their environment including predators and prey, and 3) a behavioral strategy or rule of thumb unique to each individual based on immediate spatial growth/ingestion and predation rates. We tested five behavioral rules that regulated the movement and positioning of larval fish in the vertical water column in our IBM. Behavior was formulated as a rule-specific relationship between the internal states of the larvae and the environment. All of these rules were tested under fluctuating environmental forcing and for a range of larval sizes. Using this approach, we were able to explore adaptive behavior under environmental heterogeneity and to suggest behavioral rules with a mathematically simple formulation that can be included in coupled biological–physical marine ecosystem models.

METHODS

The methods follow the standard protocol suggested by Grimm et al. (2006).

Purpose

We evaluated the behavioral rules of larval cod (*Gadus morhua*) in terms of accrued mortality between ontogenetic stages or size intervals, including their robustness to environmental variability. The work presented here is a step toward implementing behavioral plasticity in spatially explicit models of larval fish. Behavior is typically modeled as if it were only determined by phenotype, disregarding genotype and using fixed rules (Grimm et al. 2006). In our approach, individuals used state-dependent behavioral strategies or rules of thumb, based on local and immediate sensory information, to govern behavior (Giske et al. 2003; Hutchinson and Gigerenzer 2005).

Structure

The candidate rules were evaluated in an environment based on data from Georges Bank (41.5°N, −67.5°E) May 22–27 in both 1993 and 1994 (Lough et al. 2005). The data contained vertical profiles of zooplankton abundance and size structure (4 species by 13 stages), temperature, and turbulence, all of which were necessary parameters for our larval cod (*G. morhua*) foraging and bioenergetics model (Fiksen and MacKenzie 2002; Kristiansen, Fiksen, et al. 2007; Kristiansen, Lough, et al. 2007). In the model, individuals moved vertically according to simple rules that used local information to optimize the trade-off between predation risk and growth. We also tested rules that used feeding rather than growth rates. Predation from fish was modeled mechanistically from predator–prey encounter processes (Fiksen and MacKenzie 2002) using ambient light level as an input variable. Nonvisual predation (tactile or ambush invertebrates) was modeled as a purely size-dependent process (Fiksen et al. 2002). Finally, the evaluation of behavioral strategies was based on fitness considerations. Here, we equated fitness with the probability of surviving from one size class to the next.

Study species

Atlantic cod (*G. morhua*) is a commercially important fish species that lives in relatively discrete stocks along the European coast from the Bay of Biscay to the Barents Sea, around Iceland, on the east and west coast of Greenland, and from Cape Hatteras to Ungava Bay along the east coast of USA and Canada (ICES 2005). We focused on the Georges Bank cod stock, which is primarily a resident population (ICES 2005). Spawning takes place at the Northeast Peak on Georges Bank during November to May, with peak spawning during February and March (ICES 2005). Eggs and larvae drift southwesterly with the currents toward the Great South Channel, before they enter the nursery grounds on the Georges Bank plateau during summer (Lough and Bolz 1989). The first few months of their life, the eggs and larvae are drifting with the prevailing currents, and the larvae have the ability to migrate vertically (Lough and Potter 1993). Bottom settlement occurs when the larvae are around 40 mm (Lough and Potter 1993).

Environmental data

Surveys conducted by US-GLOBEC on Georges Bank in May 1993 and 1994 (Lough et al. 2005) and models of turbulence fields (Naimie 1995, 1996) provided environmental forcing to our model. The surveys included sampling of larvae, zooplankton, and environmental data (Figure 1) of high quality and spatio-temporal resolution. The zooplankton data included the most important prey species for larval cod on Georges Bank (Heath and Lough 2007; Kane 2007), *Pseudocalanus* spp., *Oithona similis*, *Centropages typicus*, and *Calanus finmarchicus*; all divided into 13 different developmental stages.

Individual states—the attribute vector

Each larval individual i is characterized by an attribute vector $A_{i,t}$ (Chambers 1993) and a strategy vector S_i (Huse 2001). The attribute vector contains the state variables standard length l (mm), body mass w (mg dry weight), gut fullness s (proportion of maximum capacity; between 0 and 1), current depth position z (m), and accrued probability of surviving until time t, $p_{i,t}$:

$$A_{i,t} = \{l_{i,t}, w_{i,t}, s_{i,t}, z_{i,t}, p_{i,t}\}. \quad (1)$$

Processes and fitness

States were updated every time increment (1 h); $A_{i,t}$ thus depends on prey encounter, capture success, ingestion rate, encounter rate with piscivores, size-dependent mortality, starvation, metabolism, and growth. The behavioral rule determined hourly depth position (habitat selection), and each process was in turn driven by ambient environmental variables such as light, turbulence, and temperature. A detailed description of these processes is found in Fiksen and MacKenzie (2002) and Kristiansen, Fiksen, et al. (2007).

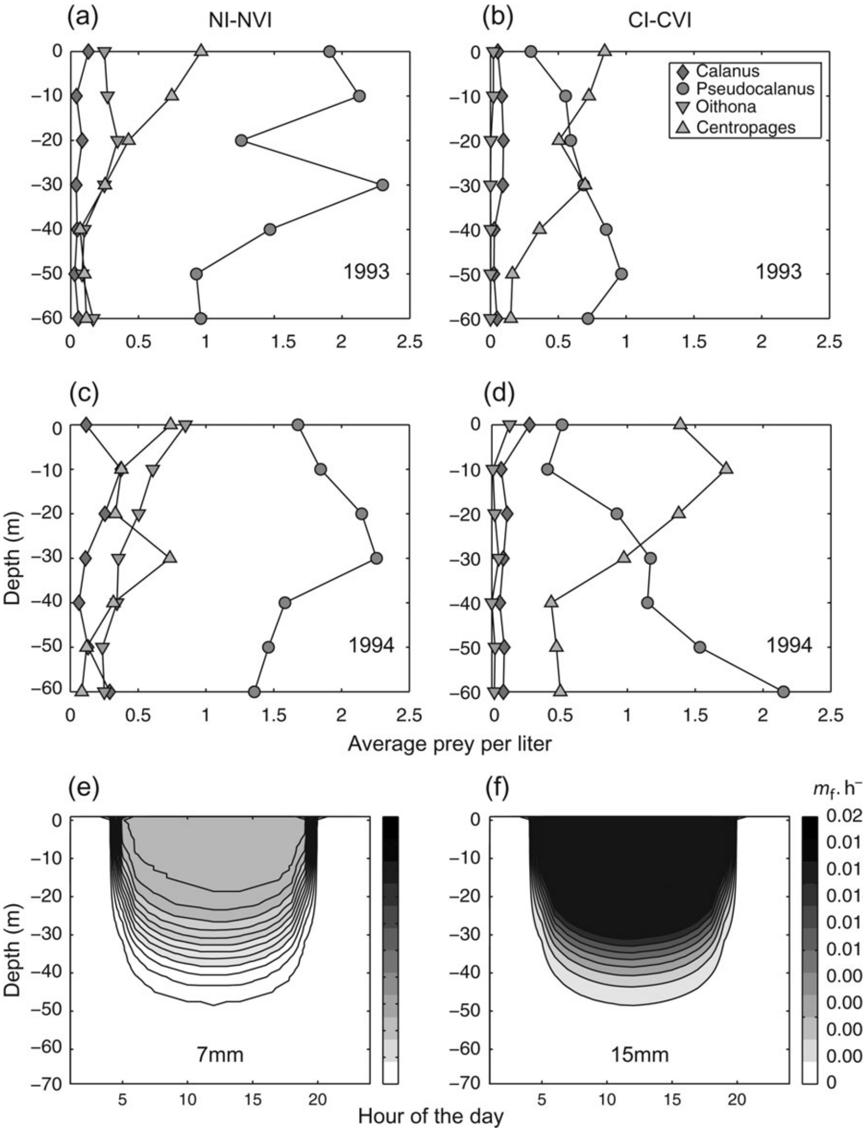

Figure 1
Averaged vertical distributions of four prey species for cod larvae as observed on Georges Bank in May 22–27, 1993 (a,b) and 1994 (c,d) (Lough et al. 2005). Panels (a) and (c) show nauplii stages (NI–NVI), panels (b) and (d) show copepodite stages (CI–CVI). The bottom panel illustrates the modeled visual predation rate over the diel cycle for cod larvae of 7 mm (e) and 15 mm (f).

Behavioral rules and the strategy vector

We examined five rules that used local information about instantaneous mortality rate and either instantaneous growth or ingestion rate as cues to govern vertical behavior. Rule 1 was a modified version of Gilliam's rule (Gilliam and Fraser 1987) based on immediate "growth" and "mortality" rates. A single parameter π defined the risk sensitivity of each larva (Figure 2a). Larvae with low risk sensitivity accepted more exposure to predators but also increased growth rates because feeding and predation rates were both positively influenced by light. One important but often neglected source of information is the individual's own internal state (Houston and McNamara 1999). Risk sensitivity in Rule 2 (Figure 2b) therefore depended on gut fullness with satiated larvae assumed to be more risk averse than hungrier ones (Dill and Fraser 1984). Rules 3 and 4 (Figure 2a and c) were similar to Rules 1 and 2, except that the trade-off was between "ingestion" and mortality. Rule 5 (Figure 2d) used a sigmoid function to trade-off ingestion rate and mortality. All rules were tested for the full range of values for different larval size and environmental settings in search for "robust" solutions or parameter combinations giving high survival under various environmental conditions and for a range of sizes of fish. The behavioral rules assumed that the larvae have information about ingestion-, growth-, and mortality-rates in the vertical range within their swimming ability during one time step (1 h).

A strategy vector $S_i\{\beta_j\}$ represents a set of (j) adaptive traits for an individual (i) such as individual life history or behavioral strategies (Fiksen et al. 2007). Here, the strategy vector represented the simple one- or two-parameter formulation of the strategy or genetic predispositions of behavior that has evolved from natural selection over generations.

Rule 1: fixed trade-off between growth and mortality

Rule 1 was modified from Gilliam's rule and implies a fixed trade-off between growth and survival. The larva chose depth $z_i{}^*(t)$ from:

$$z^*(t) = \max_z[(1-\pi_i)g_z - \pi_i m_z], \tag{2}$$

where m_z and g_z are mortality and growth rates at depth z, respectively. The parameter $\pi_i \in [0,1]$ was the behavioral strategy of individual i and can be interpreted as the individual's risk sensitivity: low π_i maximized instantaneous growth and high π_i maximized instantaneous survival. The risk sensitivity of the individual thus determined its vertical behavior, with major consequences for growth and mortality. Because the

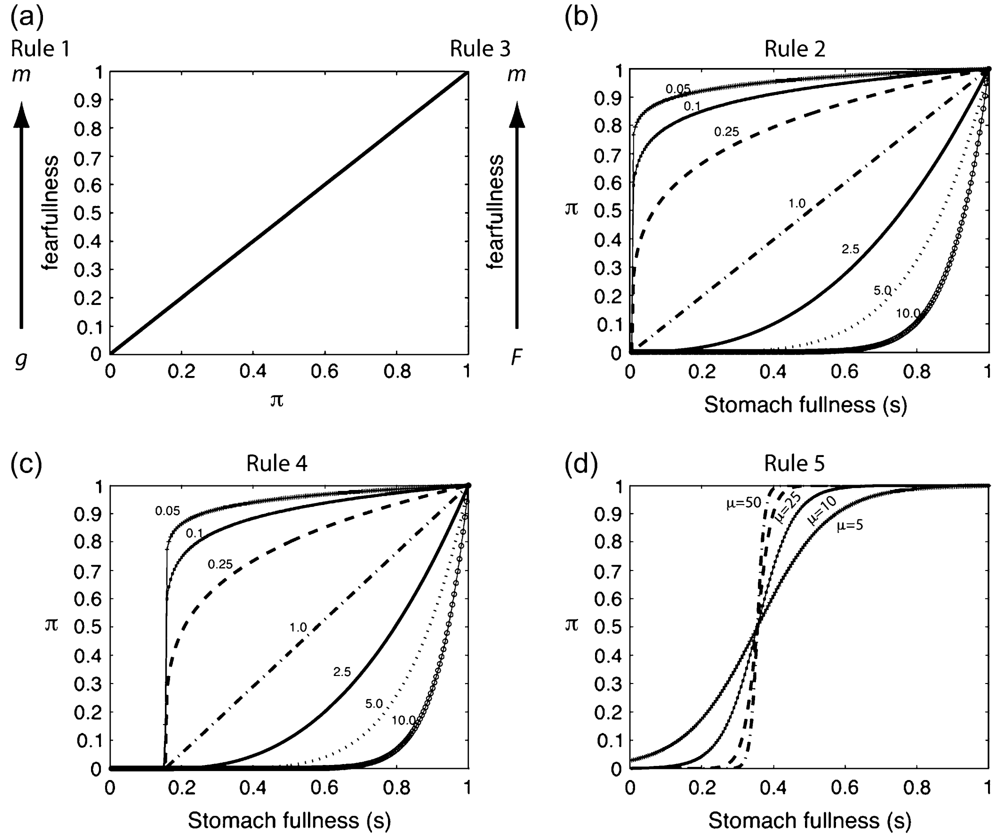

Figure 2
Examples of the 5 different rules of behavior: a) combined figure for Rule 1 and Rule 3. Rule 1 (left): risk sensitivity is a constant between 0 and 1, and behavior is a fixed trade-off between growth (*g*) and survival (implemented as mortality rate *m*). An increase in π increases fearfulness, reduces mortality, and decreases growth. Rule 3 (right): risk sensitivity is a constant between 0 and 1, and behavior is a fixed trade-off between ingestion rate (*F*) and survival. b) Rule 2: risk sensitivity π increases as stomach (gut for small larvae) fullness *s* increases with a curvature specified by β (values from 0.05–10 are shown). Larvae with low β values are risk sensitive (high π, or fear) even with little food in the gut, whereas larvae with high β values accept risks also at higher levels of gut fullness. c) Rule 4: risk sensitivity π increases as stomach fullness increases above a threshold value T ($T = 0.3$ in this example). The stomach threshold is implemented as a size-dependent function in the simulations. d) Rule 5: a sigmoid relationship between stomach fullness and π, described by the position of the midpoint and the steepness μ (the lines shown are $\mu = 5$, $\mu = 10$, $\mu = 25$, and $\mu = 50$, for $= 0.7$).

rule was defined by a single parameter, the strategy vector S_i of individual i is simply $S_i = \{\pi_i\}$.

Rule 2: state-dependent trade-off between growth and mortality
Rule 2 used the individual's gut fullness $s_{i,t}$ as a modifier of risk sensitivity. Hungrier larvae were assumed to take higher risks when feeding. Therefore, the rule used information about both the individual's internal state and the external environment. This relationship was implemented by making π_i in Equation 2 a function of gut fullness $s_{i,t}$, which varied over time t depending on foraging success: $\pi_{i,t} = s_{i,t}^{\beta_i}$. The strategy vector was $S_i = \{\beta_i\}$. A set of risk sensitivities $\pi_{i,t}$ as a function of gut fullness and β_i is shown in Figure 2b. Lower values of β enhanced larval fearfulness (higher π) for any given gut fullness.

Rule 3: fixed trade-off between ingestion and mortality
Larval fish may be more focused on maximizing ingestion than immediate growth rate, as this may lead to higher gut fullness in evenings and maintain growth through night. In Rule 3, ingestion rate is traded against mortality:

$$z^*(t) = \max_z[(1-\pi_i)F_z - \pi_i m_z]. \tag{3}$$

Ingestion rate F_z is the expected specific biomass consumed within 1 h at depth z constrained by gut capacity. The strategy vector for Rule 3 was a fixed value $S_i = \{\pi_i\}$ for each individual, as in Rules 1 and 2.

Rule 4: state-dependent trade-off between ingestion and mortality with stomach threshold
The number of potential rules that fish may use to determine their behavior is exhaustive. In addition to the relatively simple Rules 1–3, we tested a more complex Rule 4, which included a threshold value on gut fullness T. When stomach fullness was below T, ingestion had maximum priority:

$$\pi_{i,t} = \begin{cases} \left(\frac{s_{i,t}-T}{1-T}\right)^{\beta_i}, & s_{i,t} > T, \\ 0, & s_{i,t} \le T. \end{cases} \tag{4}$$

This π was then used in Equation 3, determining the trade-off between survival and food intake. When gut fullness was below the threshold value T, the larva completely ignored risk (has no fear) and maximized ingestion rate. The strategy vector $S_i = \{\beta_i\}$ was determined by the parameter T and β that regulated the dependence between stomach fullness and level of risk exposure.

Rule 5: sigmoid trade-off between ingestion and mortality
Rule 5 assumed a sigmoid relationship between the gut fullness and risk sensitivity $\pi_{i,t}$. The inflection point $\hat{s}$ and the slope parameter μ determine the function:

$$\pi_{i,t} = \frac{1}{1 + e^{-\mu(s-\hat{s})}}. \tag{5}$$

This strategy is determined by two parameters, $S_i = \{\mu_i, \hat{s}_i\}$, and the best strategy was found through an exhaustive search for optimal parameter combinations. Combining different values of $\hat{s}$ (the inflection point, where $\pi = 0.5$) systematically with values of μ in the range −1.5 to 100, we found that fitness remained quite flat for values of $\hat{s}$ in the range 0.5–0.9, with optimal value of $\hat{s} = 0.7$ as a baseline value.

Initialization and simulation protocol

To parameterize the five rules, we conducted an exhaustive search for a wide range of parameter combinations. For each rule, the larvae were initialized with empty guts at 5-m depth and modeled forward in time for 24 h. To avoid effects of the initialization states, we then reset the size of the larvae to the initial start value, while information on gut content and depth was used to restart the simulation and logging of data began. The model tracked each individual from its initial size until it was 0.5 mm longer. For each such length increment, replicate simulations were started every sixth hour of the day. In addition, zooplankton distributions and environmental data, available for 4 different days each year, were simulated in four shuffled sequences repeated until all larvae had reached the next length category. Survival probabilities were averaged over all these simulations to average effects of the day–night cycle, remove environmental dependencies, and to test robustness of strategies across environmental variation. The simulations were also repeated with fixed environmental data (data from a specific day were repeated in loop) between simulations to test the sensitivity of rules to variability in environment. This combination of procedures enabled us to analyze model behavior for larval and juvenile cod size 6–18 mm across naturally occurring environmental variation between days and years, to seek robust solutions potentially valid for different environmental settings, although for a fixed predator density. We examined the larval size range from 6 to 18 mm, because this was the size range where the physiological submodels are valid.

Figures resulting from parameterization and sensitivity testing of the rules for different size classes and environmental conditions are given as an online supplementary text.

Submodels

Growth

The details of the bioenergetics growth model are described in Kristiansen, Fiksen, et al. (2007) where growth and foraging of larval cod were modeled and compared with data from an extensive mesocosm rearing experiment (Folkvord et al. 1994). Gut fullness is a function of ingestion and digestion. Mass flowing through the alimentary system supplied growth up to a maximum growth potential (Folkvord 2005), and standard metabolic costs SMR (Finn et al. 2002) were subtracted. Both growth and metabolic costs were functions of body mass and temperature. As in Lough et al. (2005), active metabolic rate was increased by a factor of 2.5 for larvae of standard length (SL) >5.5 mm and 1.4 for SL ≤ 5.5 mm when light level exceeded a threshold value of 0.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Batty 1987). Assimilation efficiency was a size-dependent function increasing from 0.6 for small larvae (5.0 mm) to 0.8 for larger larvae (11.0 mm) (Buckley and Dillmann 1982).

Larval feeding processes were modeled with light-dependent prey encounter rates and prey-capture success as in Fiksen and MacKenzie (2002). The cost of vertical movements was included as a maximum of 10% of SMR at fixed temperature (7 °C) if the larva swims up or down at its maximum velocity and scaled proportionally for shorter vertical displacements. Swimming velocity was a function of larval size (Peck et al. 2006).

Mortality

We modeled mortality from fish and invertebrates separately, similar to Fiksen et al. (2002) and Vikebø et al. (2007). Predation rate from invertebrates m_n (h^{-1}) decreased with larval body length SL (McGurk 1986): $m_n = 0.01 \cdot l^{-1.3}$. Predation rate ($\text{h}^{-1}$) from fish was $m_f = 0.05R^2$, where R was the perception distance of the piscivore predators, depending on light level and larval size. Note that the coefficient 0.05 summarizes all factors such as fish density and escape probability (see Fiksen et al. 2002 for details), but we had no information on fish abundance or efficiency, and the value was chosen arbitrarily (same value as in Fiksen et al. 2002) and kept constant in all model realizations. Total instantaneous predation rate $m_z = m_n + m_f$ was thus a function of depth, surface irradiance, and larval size (Figure 1e and f). If food intake is low, growth may be negative. If the body mass w to l ratio dropped below 75% of the expected value an additional mortality component m_s (0.0036 h^{-1}) was included.

Fitness measure

We defined our fitness measure as accrued mortality per length interval $m/\Delta\text{SL}$:

$$\frac{m}{\Delta \text{SL}} = \sum_{t=t_0}^{t=H} \left[m_f(t, \text{SL}, z) + m_n(\text{SL}) + m_s(w, \text{SL}) \right], \qquad (6)$$

where the stage duration H was the number of time steps (hours) needed to grow 0.5 mm longer (depending on growth rate). The best behavioral rule minimizes left-hand side of Equation 6.

RESULTS

Model simulations revealed a significant increase in survival rate for larval and juvenile cod with active behavior compared with larvae with random behavior. The importance of behavior was robust with changing environment.

The fitness value of habitat selection in larval and juvenile cod

We tested five different behavioral rules relative to a null rule where larvae moved randomly in the water column (Fig. 3). All rules predicted larvae to go deeper with size (Figure 3a and e). The simplest rules, Rules 1 and 3 predicted the deepest distribution of the larvae, whereas the more complex two-parameter Rules 4 (T and β) and 5 (sigmoid, μ and $\hat{s}$) predict larvae to be higher up in the column for all size groups. All rules did markedly better than the randomly moving larvae (Figure 3b and f). The effect of behavior was strongest for small and large larvae, because larvae in the intermediate size range have higher inherent growth potential (Folkvord 2005). Intermediate-sized larvae experienced minimum stage duration, which further minimized the exposure to predation for both random and active vertical behavior and minimized the effect of active decision making. Overall, the probability of survival from 6 to 18 mm in 1993 and 1994, respectively, was 0.013% and 0.037% for Rule 1, 0.023% and 0.072% for Rule 2, 0.05% and 0.13% for Rule 3, 0.08% and 0.22% for Rule 4, 0.08% and 0.23% for Rule 5, and 3×10^{-7}% and 1×10^{-5}% for random behavior.

Our analyses indicate that survival probabilities were roughly three times higher in 1994 compared with 1993, primarily due to differences in zooplankton abundance and distribution. In addition, these results emphasize the importance of behavior because each rule was markedly better than the random strategy, ranging from 3700-fold to 267 000-fold higher probability of surviving from 6 to 18 mm. The cost of growing more slowly can be compensated by lower mortality rates, as larvae larger than 11 mm showed both faster- and slower-growing strategies than the random strategy but still had lower mortality rates.

We also found that there were marked differences between the strategies, where the best strategy (Rule 5) was 5-fold better than Rule 1 in the 2 years, respectively. Rule 4 was almost as good as Rule 5, whereas the other strategies had lower fitness, indicating that an extra parameter led to enhanced performance. Finally, using ingestion rate rather than growth

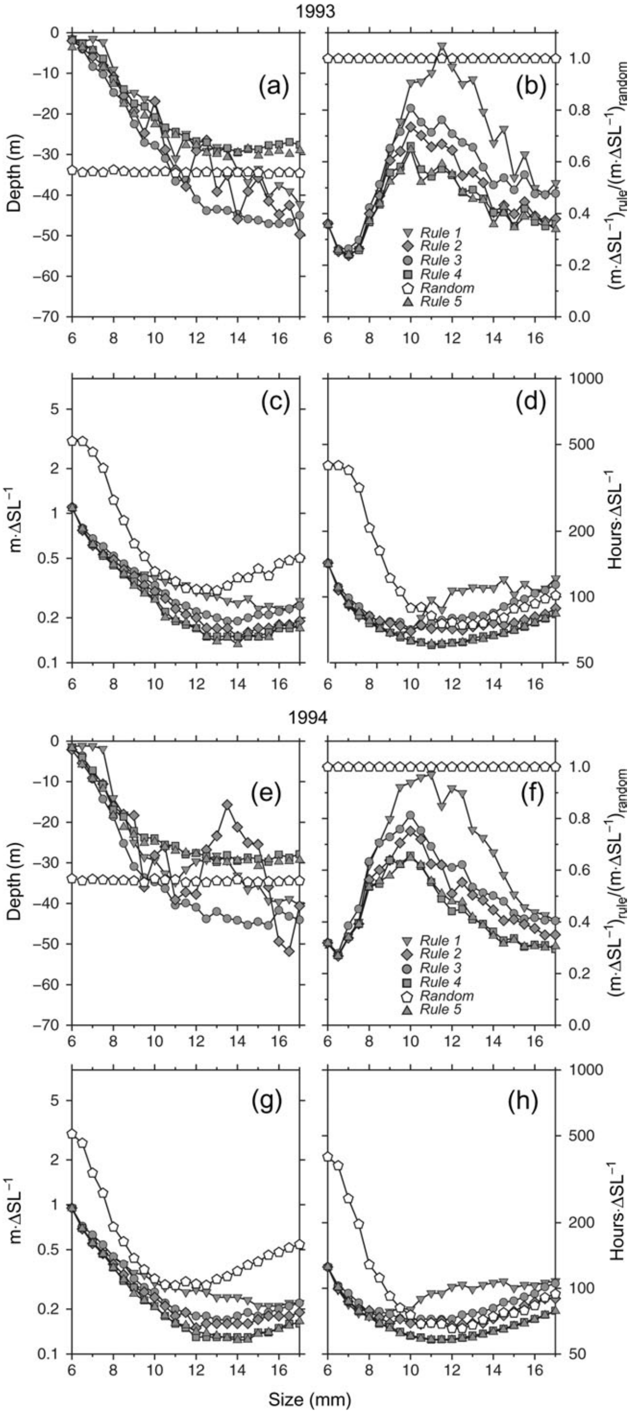

Figure 3
Performance of five rules (gray symbols) for vertical behavior in cod larvae compared with random vertical movements (open symbols; each data point is averaged over 100 simulations). For random movements, the selected depth for every time step is random, but vertical displacements are limited to maximum swimming distance from previous position in the random case. Panels (a)–(d) show simulations using environmental conditions for 1993 and panels (e)–(h) for 1994. (a,e) Modeled average daily depth for each ontogenetic stage. (b,f) Performance (fitness) of each rule relative to random movement, expressed as accrued mortality per 0.5-mm growth interval. Here, values below 1.0 indicate that survival is improved relative to random behavior. (c,g) Modeled mortality rate (*m*) experienced for each growth interval. (d,h) The time (hours) used to grow from one interval to the next.

improved performance, as Rule 3 was 2.5- to 3-fold better than Rule 1.

The smallest size groups of larvae (<8 mm) are restricted to forage on nauplii and early stages of copepodites (Figure 1), with varying degrees of capture success (Caparroy et al. 2000; Fiksen and MacKenzie 2002). Small larvae are also visually limited because the eye is still under development (Ellertsen et al. 1980). Feeding ecology of small larvae was therefore limited to the upper parts of the water column. The modeled predation rates from fish were quite homogenous in this layer (Figure 1). Larvae behaving according to Rules 1–3 chose habitats where foraging can take place during the day (~40 m) but ascended during evening and night. On the contrary, individuals following Rules 4 and 5 were more risk seeking and were located in the upper 10–30 m (Figure 3a and e). This vertical positioning not only resulted in enhanced growth rates but also increased predation risk from fish (3c and g). Larvae situated deeper in the water column grew slower, were less prone to visual predation, but the time spent growing between ontogenetic stages increased (Figure 3d and h). Therefore, our analyses suggest that there are two behavioral solutions: high growth rates and short development time (Rules 4 and 5) or reduced growth rate and prolonged development (Rules 1 and 3), and although both these options were better than random behavior, Rules 4 and 5 were markedly better than Rules 1 and 3.

Robustness under environmental variation

The performance of behavioral rules may differ between environments. As the observed prey fields for each day were quite different (Lough et al. 2005), we can assess robustness by their sensitivity or robustness prey fields varying on a daily basis. The rules were compared using optimal parameter values for each rule for each size class. Differences in prey availability between days are reflected in the behavior and variation in average depth position for same-sized larvae (Figure 4 and Supplementary Figure 1, left panels). Fitness or accrued mortality per length interval, however, shows only minimal differences across days (Figure 4 and Supplementary Figure 1, right panels). Larvae respond to the specific prey distribution and abundance each day by altering behavior and navigating in the growth and mortality profiles in that particular environment. Behavior differs among individuals, but their performance is more comparable, indicating robustness-to-environmental variation.

Predicted and observed larval diel distribution

Rules 2, 4, and 5 led individuals to seek safer habitats as gut fullness increases. In Rules 4 and 5, the trade-off between ingestion and mortality triggered swimming toward the surface to forage before all gut content had been digested. This coupling between hunger (gut fullness) and risk sensitivity is well known from experimental studies on fish (Dill and Fraser 1984; Munk 1995; Skajaa et al. 2004).

We applied Rules 2 and 4 to study how 7- and 15-mm larval cod behaved over one diel cycle, given the environmental conditions on Georges Bank in May 1993 (Figure 5). The larvae following Rule 4 performed diel vertical migration (Figure 5b), avoided strong light during the day to minimize mortality, while keeping gut fullness high (Figure 5d). The 7-mm larvae remained between surface and 30-m depth, whereas 15-mm larva descended deeper, to 40–50 m (Figure 5b), still keeping their guts full. This difference was driven by size dependence in predation rates, with a higher influence of visual predation for the larger 15-mm larvae. Predation (Figure 5f) and growth (Figure 5h) rates depended strongly on larval

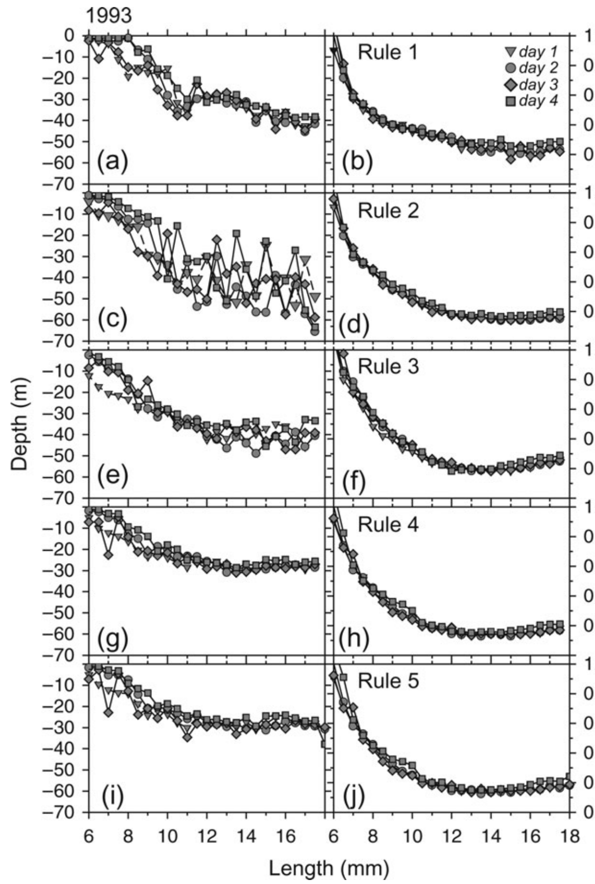

Figure 4
Averaged depth (left panels) and accrued mortality rates (right panels) for Rule 1 (a,b), Rule 2 (c,d), Rule 3 (e,f), and Rule 4 (g,h) between ontogenetic stages using a specific prey day repeatedly. This was done for 4 different days (May 22–25, 1993) and demonstrates the minor effect of prey variability (abundance, distribution, and size structure) on the performance of each rule.

depth selection. The predation risk peaked in the morning because the larvae had empty guts, and high motivation to feed, and because they had no foresight and were trapped in risky light exposure due to limited swimming abilities (Figure 5f).

Larvae following Rule 2 optimized a trade-off between growth and survival. Both 7- and 15-mm larvae stayed at depths where feeding and growth were high during the day (Figure 5a), but did not move up or down during dusk and dawn to maximize ingestion. Instead high growth rate (Figure 5g) was attained through gut reserves (Figure 5c). This resulted in a sharp decline in gut fullness and growth during the night. Still, the mortality experienced for larger individuals (15 mm) following Rule 2 was slightly less than by individuals subject to Rule 4 (Figure 5e and f). Probability of survival through 24 h for 7- and 15-mm larva was 90.3% and 97.8% for Rule 2, and 90.4% and 96.4% for Rule 4. There is a trade-off between growing fast, which reduced the total stage duration, and the exposure to predators. Observations in natural conditions suggest that fast growth is favored (Meekan et al. 2006), relative to slow growth (Houde 1987, 1997; Hare and Cowen 1997), although exceptions occur (Pepin et al. 2003).

The observed vertical distributions suggest that larval movements followed a diel pattern but not as explicit as our model predicted (Figure 6). We found that our modeled depth distribution with time was significantly equal to the observed for the size classes 2–5 mm (χ^2: 29.2, $P = 0.00001$) and 6–8 mm (χ^2: 18.3, $P = 0.0001$), but was not significantly equal for the 9–13 mm (χ^2: 6.8, P=0.08) size class. The diel pattern created by the use of behavioral Rule 4 was apparent in our population simulations (Figure 7). We modeled the distribution of three size groups 2–5, 6–8, and 9–13 mm, where each cohort consisted of 1000 individuals. Initial variation in size and gut fullness for individuals following Rule 4 resulted in a vertical distribution of the individuals within each cohort. Each size group had preferred depth ranges that may change with their gut fullness. The 9- to 13-mm larvae showed diel migration, moving from 40- to 45-m depth during the day to the surface at night, whereas the two smaller size groups were located further up in the water column. The smallest individuals were located in the upper 10 m during night and day (Figure 7).

DISCUSSION

A good behavioral rule has to perform well across the environmental variation an individual fish typically encounters. We formulated simple behavioral strategies for larval cod and tested how the trade-off between growth, ingestion, and survival changed with different environmental conditions (daily and interannual variation) and ontogeny (Figures 3, 4, and Supplementary Figure 1). Our results suggest that emergent behavior such as diel vertical migration and its consequences for survival are dependent on the mathematical formulation of the rule, the number of parameters, and the information that is used as input to the rule. Even simple rules of behavior may greatly influence growth, feeding, and predation rate. In general, the use of individual state dependence (e.g., gut fullness) and local environmental conditions (e.g., Rules 4 and 5) performed better than rules without such information (e.g., Rules 1 and 2) (Figure 3). Including state dependence in behavioral rules adds information on the gut fullness of the larvae to the immediate local conditions. This enables larval fish to start searching for food before running out of energy reserves (e.g., empty stomach), which has important consequences for their behavior and survival.

Any environmental change affecting mortality, growth, or ingestion will also change the optimal strategy and thereby habitat selection and realized growth and mortality. Thus, predictions will differ between models that implement or omit active behavior. Active behavior may differ between individuals and with the environmental conditions in a dynamic manner based on cues. Although the cues used by larval cod for habitat selection are not known, we have assumed that the larvae can assess growth and mortality rates in a local area reasonably accurately. We also assume that these cues integrate a variety of environmental variables. To include the effect of genetic and phenotypic differences between individuals in the model, any bias in the assessment of growth and mortality could easily be incorporated as a stochastic deviate between the true and the perceived risk, growth, or feeding rate at any habitat.

Because there are many size-dependent factors that affect larval growth and mortality, general rules based on assessed risk and growth must be sensitive to both external and internal cues, and they may change throughout ontogeny. Larger larvae are generally less susceptible to invertebrate predation (McGurk 1986; Bailey and Houde 1989) because they have better locomotory abilities (Bailey and Batty 1984; Peck et al. 2006). In contrast, larger larval fish may also become more vulnerable to visual predators as a result of their increased visibility (Aksnes and Giske 1993). Although there are exceptions where overall mortality increases with size (Pepin et al. 2003), the combined effect of invertebrate and visual predation generally equates to "bigger is better" (Leggett and Deblois 1994; Hare and Cowen 1997).

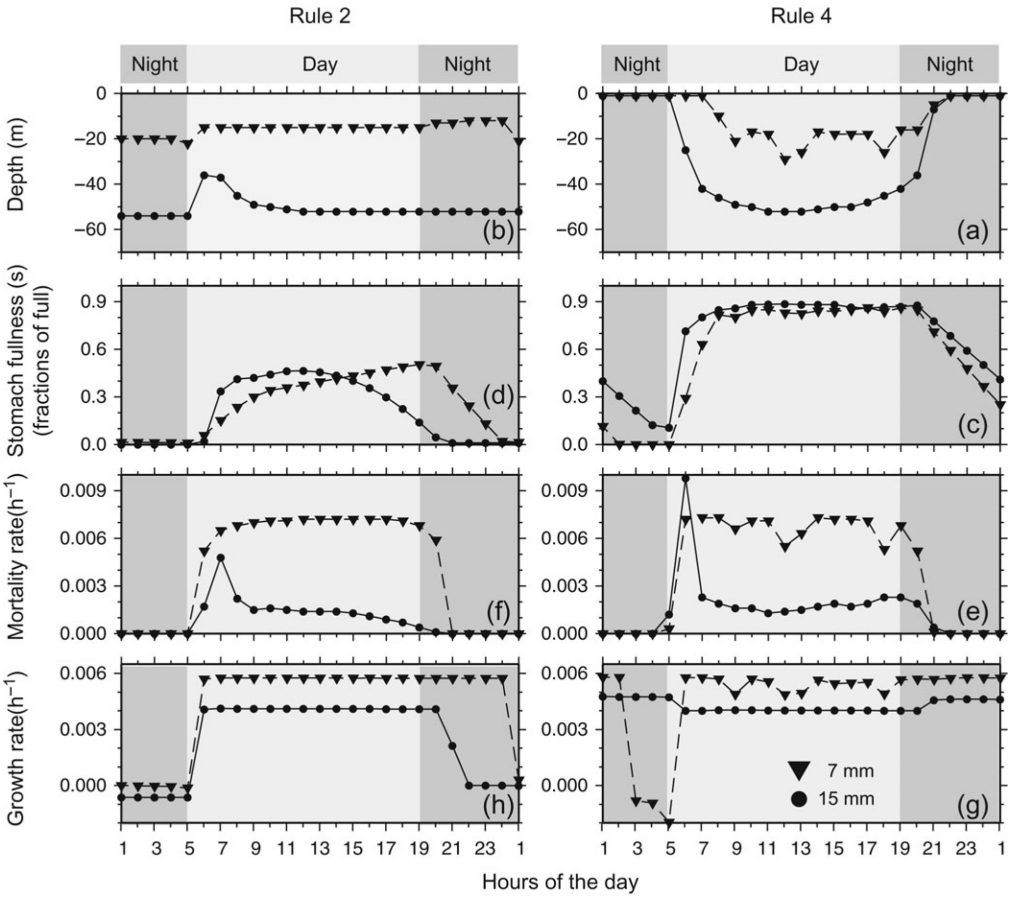

Figure 5
Emergent behavior for 7- and 15-mm larvae following Rule 2 (left column) and Rule 4 (right column). Results are displayed for a 24-hour (h) time period with a spin-up period of 48 h. (a,b) Vertical position (*m*), (c,d) gut fullness (*s*), (e,f) predation rate (h^{-1}) from piscivores, and (g,h) growth rate (h^{-1}). Environmental conditions were measured from 22nd to 23rd of May 1993, and predation from fish as in Figure 2e and f.

When we compared field observations with our model results (Rule 5: trading feeding and survival using a two-parameter model [μ_i, $\hat{s}_i$]) the modeled behavior resulted in a very distinct diel migration pattern, whereas the observed distributions did not reveal such a clear pattern (Figure 6). Our model simulations predict a behavioral pattern that always moves the larvae to their optimal vertical position in the water column. Although the swimming distances we used are conservative compared with observations for cod larvae (Peck et al. 2006), the model may allow the larvae to move too far in the water column. These differences may especially influence the largest individuals (9–13 mm), where our model fails to reproduce observations.

Our approach to modeling behavior is based on theoretical assumptions that have been simplified, and it is obvious (Figure 6) our model could not capture all aspects of larval fish distribution patterns. For example, prey distribution is important for behavior and is only resolved on a vertical scale of 10 m in the model. Patchy distributions of prey separated in thin layers may develop into areas where high feeding rates are achievable for the larvae (Tilseth and Ellertsen 1984; Skreslet 1989; Davis et al. 1992). These patches may lower larval motility and thereby susceptibility to predators, while at the same time sustaining ingestion at or close to maximum. Our time resolution of zooplankton and larval fish distribution is 6 h between samples, which may be too coarse to identify important zooplankton behavior such as diel migration (Lampert 1989). If larval fish follow the zooplankton movement, the vertical observations of larval cod may also be affected, and the sampling time scale may not resolve the actual dynamics of the systems.

In addition, the modeled predation pressure and its spatial distribution may not accurately describe Georges Bank. The abundance of invertebrate and fish predators were not assessed in the field, and changes in these variables would alter the predicted mortality rates and thereby the behavior of the larvae. Further, episodic or rare events may occur when large shoals of predators enter the Georges Bank and overlap with the drift trajectories of the larval fish (Garrison et al. 2000). Cod cannibalism may also affect the survival dynamics. In laboratory experiments Puvenandran et al. (2008) found larvae as small as 9 mm preyed on 5- to 7-mm larvae; 15-mm juveniles were the greatest threat to recently hatched larvae. The highest incidence of cannibalism by pelagic juveniles could occur during strong water column stratification when larvae and copepod prey are concentrated in narrow layers. Also, the turbidity level in the modeled water column is only depth dependent and did not change with the abundance and dynamics of phytoplankton layers. This implies that the modeled irradiance does not account for phytoplankton abundance, which may have a shading effect in the water column and consequently influence larval visibility to predators and larval feeding (Fiksen et al. 2002).

Vertical migration also has long-term effects on drift trajectory and thereby on the dispersal of larval fish the first few months after hatching. On Georges Bank, drift of eggs and larval stages of cod and haddock to off-bank areas may result in mass starvation and decreased recruitment (Lough and Bolz 1989; Werner et al. 1993). Off-bank drift is strong in the surface layer because of the chaotic, wind-generated, horizontal current system. However, the surface layer may be avoided by moving deeper in the water column. The larvae enter a new habitat through vertical displacement where predation and prey composition may be different from the surface layers

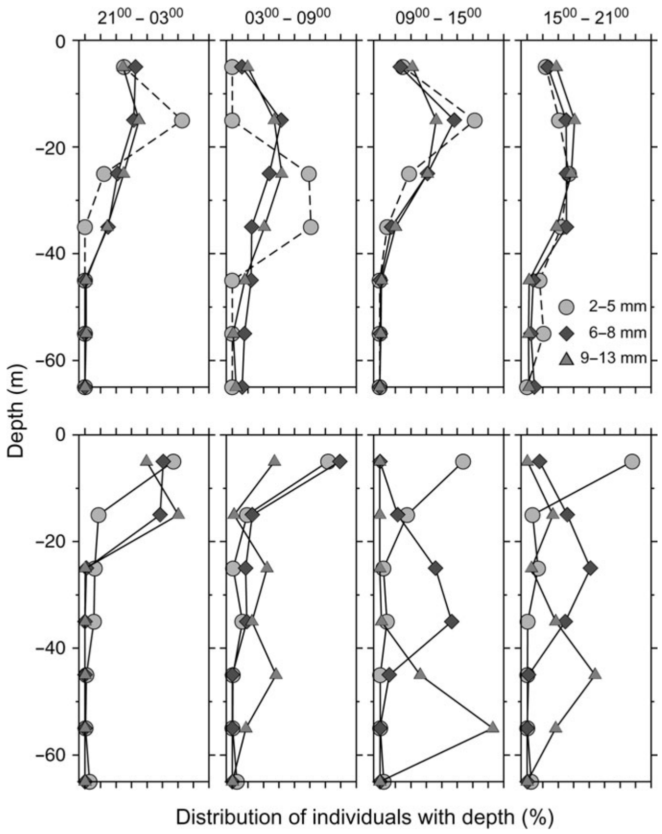

Figure 6
Upper rows show time-averaged observed vertical distribution of larval cod divided into size categories, averaged over observations made in May 1993 and 1994 on Georges Bank (Lough et al. 2005). Values were split into 6-h time periods to explore the differences between day and night distributions. Lower rows show the accumulated vertical distribution of 1000 simulated individuals over 24 h, where individuals range in size from 6 to 8 mm.

(Werner et al. 1993). When Lough and Potter (1993) sampled night and day vertical distribution of larval cod along the typical drift routes, they found that the majority of larvae in the size range 2–5 mm were distributed at 15-m depth in stratified water columns. Lough and Potter (1993) also observed diel migration of larvae sized 9–13 mm, with mean day and night depths of 40–60 and 10–40 m, respectively. These daily migrations were initiated when the larvae were

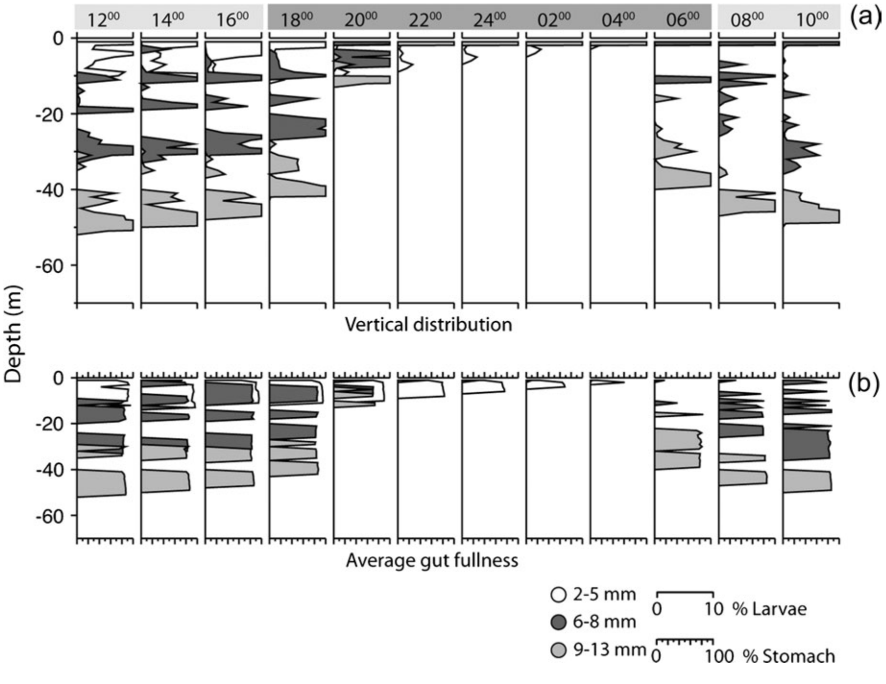

Figure 7
Modeled vertical distribution (a) and average gut fullness at depth (b) for three cohorts of larvae following Rule 4 for three size categories: 2–5 mm (light gray), 6–8 mm (dark gray), and 9–13 mm (medium gray). Each simulated cohort consisted of 1000 individuals that were all able to move independently of each other for 48 h (hours 24–48 shown here).

6–8 mm, revealing that larval cod exhibit diel vertical migration already early in their life history.

When we compared the results of Lough and Potter (1993) with our predictions of how cod are distributed by depth (Figure 6), we found that a distinct migration pattern was difficult to identify in the model. Diel migration may be influenced by a number of local factors not included in the model. For example, research on red drum larvae suggests that optimal behavior may not necessary be heritable (Dill et al. 2003), an assumption that we make in our modeling exercise. In addition, different conditions may favor different behavioral traits (Meekan and Fortier 1996). If so, then good behavioral rules limited to certain types of local information may not exist and other formulations or additional information should be considered.

Our model represents a key shift away from modeling larvae as passively drifting particles in ocean circulation models to incorporating adaptive and realistic behavioral responses in a heterogeneous environment (Fiksen et al. 2007). Given the limited sensory and cognitive abilities of larvae and their restricted potential for swimming, we propose their behavior may be reasonably well captured by simple rules that incorporate data on environmental conditions. These findings are critical for the development of computationally practical, more accurate drift models, which can be used to investigate distribution patterns, spawning areas, mortality, and growth rates (Vikebø et al. 2007).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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