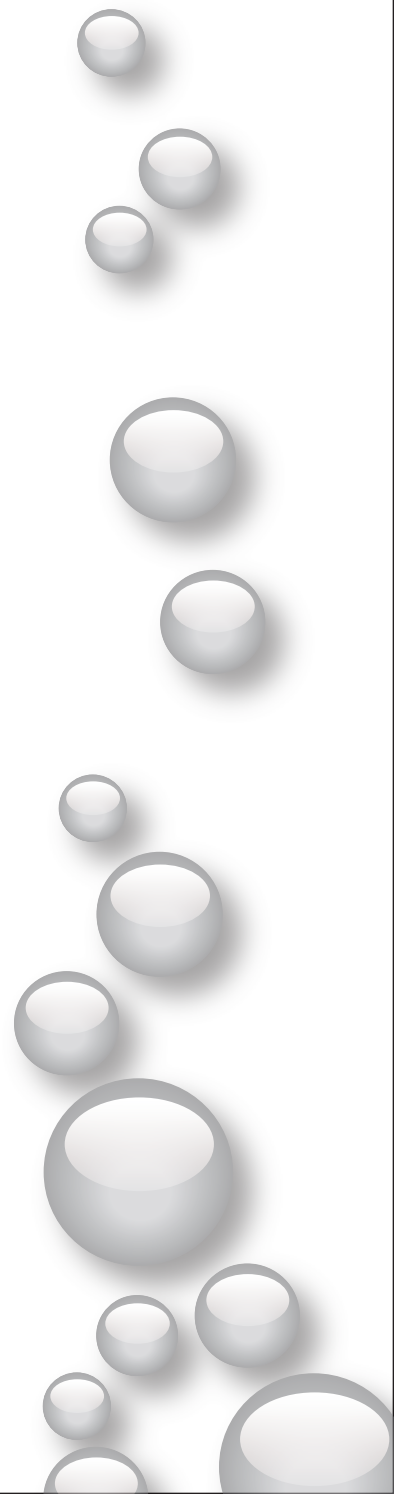


Paper 3



Trading risk and growth: exploring behavioral rules of larval cod on Georges Bank

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Running title: Vertical behavior in individual-based models

Abstract

A challenge to contemporary fisheries oceanography is to include larval behavior, and in particular, vertical habitat selection in biophysical models. Pelagic gradients of light, temperature, prey and turbulence determine growth, survival and drift trajectories of larval fish, and model predictions are thereby sensitive to the implemented vertical distribution and behavior of larvae. We explore five rules for habitat selection of larval cod (*Gadus morhua*) on Georges Bank for May 1993 and 1994. An individual-based model was applied to this ecological setting to analyze emergent feeding, growth, and mortality patterns from different rules of vertical behavior. The rules define risk-sensitivity of larvae as a strategy maximizing difference between growth (or feeding) and mortality rate, while some rules makes risk sensitivity an explicit function of stomach fullness. The performance of the rules varies with larval size, but individuals adapting to rule-based behavior outperformed random behavior. Any of the simple rules tested proved to be tentative suggestions for a simple algorithm for implementing vertical behavior in individual-based models.

Keywords: behavioral heuristics, individual-based model, larval cod, vertical behavior, growth, predation

Introduction

One current challenge for ecology in general is to make inferences at the population level from properties of individuals (DeAngelis & Rose 1992, Grimm & Railsback 2005). A particular challenge is to include individual behavior and plasticity into population and community level models (e. g. Dill et al. 2003, Persson & De Roos 2003, Fiksen et al. *subm.*). For larval ecology in marine systems, one challenge is to go from modeling passively drifting particles in ocean circulation models to larvae with adaptive and realistic behavior under environmental heterogeneity (Fiksen et al. *subm.*). Given the limited sensory and cognitive abilities of larvae and their restricted potential for swimming, the behavior has to be specified by simple rules that use only local information and lead to movements over short distances. These qualities would also make it easy to implement such rules for particles in ocean circulation models, and would thus enable simulations of large numbers of individuals that inhibit behavior for investigating distribution patterns, spawning areas, mortality, and growth rates (Vikebø et al. *subm.*). What would such a simple rule look like? What kind of information is available to the larva? How can rules be formulated and evaluated as functions or algorithms? And how will emergent behavior affect growth, mortality, drift and potentially the predicted recruitment variability?

In this paper, we investigate some candidate rules in an environment based on data from the Georges Bank. The data contain vertical profiles of zooplankton distribution (4 species by 13 stages), temperature, and turbulence, for May 1993 and 1994 (Lough et al. 2005). These data are forcing a foraging and bioenergetics model for larval cod (*Gadus morhua*) (Fiksen & MacKenzie 2002, Kristiansen et al. *in press*). A vital part of the model is the mechanistically formulated encounter rate with both predators and prey to assess feeding, growth, and mortality, and how these properties scale through ontogeny (Fiksen & MacKenzie 2002). By comparing simple one-parameter rules, we evaluate candidate rules from their combined effects on growth and mortality on fitness.

We examine five rules that use local information about instantaneous mortality rate and either instantaneous growth or ingestion rate as cues to govern vertical behavior. The first rule is a modified version of Gilliam's rule (Gilliam & Fraser 1987), trading off immediate *growth* and *mortality* rates. A single parameter π then defines how risk-sensitive a larva is. Larvae with low risk-sensitivity will accept more exposure to their predators, but may also elevate growth rates since feeding and predation rates are both influenced by light and therefore correlated. One important but often neglected source of information is the individual's own internal state (Houston & MacNamara 1999). The second rule therefore lets risk-sensitivity depend on stomach fullness: one should expect satiated larvae to be more sensitive to risk than hungrier ones (Dill & Fraser 1984). Rules 3, 4, and 5 are similar to Rules 1 and 2 except that the trade off is between *ingestion* and mortality rate. All rules are tested for the full range of values for different larval size and environmental settings in search for *robust* solutions. Robust rules yield high success and adequate behavior through consecutive size-classes in a wide range of environments.

Materials, models and methods

Purpose

The purpose of this model is to evaluate the importance of strategic behavior of larval fish in terms of accrued mortality between ontogenetic stages. The analysis focuses on the robustness of the rules, in particular how sensitive performance of alternative rules is to environmental variability and larval body size. An important aim is to explore alternatives for including behavioral plasticity in spatially explicit models of larval fish.

Structure

We evaluate the consequences of simple behavioral rules for larval cod using a comprehensive data set of zooplankton distribution and the physical environment. We simulate growth, feeding, and predation from invertebrates and visual predators for

larval cod between 6 and 18 mm body length. Individuals choose depth according to a simple rule that uses local information to optimize the trade-off between predation and feeding or growth. Prey distribution, size-structure and abundance and physical forcing are based on data collected during Georges Bank surveys in May 1993 and May 1994 (Lough et al. 2005). Visual predation is modeled mechanistically from predator-prey encounter processes (Fiksen & MacKenzie 2002), whereas non-visual predation (invertebrates) is a purely size-specific function (McGurk 1986).

Each larva i is characterized by a strategy vector S_i specifying its behavioral strategy, and an attribute vector $A_{i,t}$ containing individual states, updated every time-step t .

Individual states - the attribute vector

Each larva is characterized by the dynamic state variables length SL [mm], body mass w [mg dry weight], stomach fullness s [between 0 and 1; proportion of maximum capacity], depth position z [m], and accrued probability of being alive at time t , $PS_{i,t}$:

$$A_{i,t} = \{ SL_{i,t}, w_{i,t}, s_{i,t}, z_{i,t}, PS_{i,t} \} \quad 1$$

Processes and fitness

The processes determining $A_{i,t}$ include prey encounter and capture success, encounter rate with piscivorous (visual predation), size-dependent mortality (non-visual predation), starvation, metabolism and growth. A behavioral rule determines the continuous choice of depth (habitat), and each process is in turn driven by environmental variables such as light, turbulence, and temperature at that depth. The details of these processes are described in Fiksen and Mackenzie (2002) and Kristiansen et al. (in press).

Behavioral rules and the strategy vector

The behavioral rules assume that the larvae have information about ingestion-, growth-, and mortality-rates in the vertical range within their swimming ability during one time step. The larvae use this information to select depth based on a trade-

off between growth- and mortality rate (Rules 1 and 2) or ingestion- and mortality rate (Rules 3, 4, and 5). Rules 2, 4 and 5 also use information about the individual's stomach fullness.

Individuals follow a simple heuristic to select vertical position (Fiksen et al. *subm.*) defined by the strategy vector S_i . This makes larval behavior sensitive to local environmentally driven variability in growth and mortality rates. A simple formulation of the strategy (one or two parameters) mimics the genetic predispositions of individuals subject to natural selection over generations.

Rule 1: fixed trade-off between growth- and mortality rate

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

$$z^*(t) = \max_z [(1 - \pi_i)g_z - \pi_i m_z] \quad 2$$

where $0 \leq \pi_i \leq 1$ is the behavioral strategy of individual i and can be interpreted as the individual's risk-sensitivity: low π_i maximizes instantaneous growth and high π_i maximizes instantaneous survival. The risk-sensitivity of the individual thus determines its vertical behavior, with major consequences for growth and mortality (this model) as well as drift trajectory (Vikebø et al. *subm.*). Since the rule is 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 rate

Rule 2 uses the individual's stomach fullness $s_{i,t}$ as a modifier of risk sensitivity. More hungry larvae should be expected to take higher risks to feed. Thus, the rule uses information about both the individual's internal state and the external environment. This is implemented by making π_i in eq. 2 a function of stomach fullness $s_{i,t}$, which will vary over time t depending on foraging success: $\pi_{i,t} = s_{i,t}^{\beta_i}$. The strategy vector is now $S_i = \{\beta_i\}$. A set of risk-sensitivities $\pi_{i,t}$ as a function of stomach fullness

and β_i is shown in Fig. 1a. Lower values of β makes larvae more fearful (higher π) for any given stomach fullness.

Rule 3: Fixed trade off between ingestion and mortality rate

Larval fish may be more concerned with avoiding an empty stomach than to maximize immediate growth rate. To ensure stomach is kept busy, it may be more efficient to adjust behaviors to trade ingestion rate against predation risk:

$$z^*(t) = \max_z [(1 - \pi_i)F_z - \pi_i m_z] \quad 3$$

Ingestion rate F_z is the expected specific biomass consumed within one hour at that depth constrained by idle stomach capacity. The strategy vector for Rule 3 is a fixed value $S_i = \{\pi_i\}$ for each individual, as in Rule 1.

Rule 4: Trade-off between ingestion and mortality with 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; including a threshold value on stomach-fullness STV and fear :

$$\pi_{i,t} = \begin{cases} \left(\frac{s_{i,t} - STV}{1 - STV} \right)^{\beta_i}, & s_{i,t} > STV \\ 0 & , s_{i,t} \leq STV \end{cases} \quad 4$$

This π then enters eq. 3, determining the trade-off between risk and food intake.

When stomach fullness is below the stomach threshold value STV , the larva completely ignores risk (have no fear) and maximize ingestion rate (Additional Fig here?).

Rule 5: Sigmoid trade-off between ingestion and mortality rate

Rule 5 assumes a sigmoid relationship between the stomach fullness and risk sensitivity $\pi_{i,t}$. The function is determined by its inflection point \hat{s} and the slope parameter μ :

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

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This strategy is determined by two parameters, $S_i = \{\mu_i, \hat{s}_i\}$, and the best strategy set can be found by an exhaustive search in the parameter space.

Forcing data and environment

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 survey included continuous sampling of larvae, zooplankton, and environmental data (Fig. 2) of high quality and spatio-temporal resolution. The zooplankton data includes the most important prey species for larval cod on the Georges Bank (Kane 1984); *Pseudocalanus* spp., *Oithona similis*, *Centropages typicus*, and *Calanus finmarchicus*; all divided into 13 different developmental stages.

Initialization and simulation protocol

The larvae were initialized with empty stomachs at 15 m depth. The model tracked each individual from its initial size and until it was 0.5 mm longer. For each length increment, replicate simulations were started every second hour of the day and the survival probability averaged to remove effects of the day-night cycle. In addition, zooplankton distributions and environmental data, available for four different days each year, were iterated in four shuffled sequences, and at four different start hours. This was done to test robustness of strategies across environmental variation. The simulations were also repeated with fixed environmental data between simulations to test the sensitivity of rules to variability in environment. All simulations were performed with data from both 1993 and 1994. This procedure provided us with the potential for analyzing model behavior between years, across environmental variation, and throughout ontogeny to seek robust solutions potentially valid for different environmental settings, although for a fixed predator density.

Submodels

Growth: The details of the bioenergetics growth model are described in Kristiansen et al. (in press) where growth and foraging of larval cod were modeled and compared to data from an extensive mesocosm rearing experiment (Folkvord et al. 1994). Stomach fullness is a function of ingestion and digestion. Mass flowing through the alimentary system supplies growth up to a maximum growth potential (Folkvord 2005), and standard metabolic costs (SMR, Finn et al. (2002)) are subtracted. Both growth and metabolic costs are functions of body mass and temperature. As in Lough et al. (2005), active metabolic rate is increased by a factor of 2.5 for larvae > 5.5 mm and 1.4 for $SL \leq 5.5$ mm when light level exceeds a threshold value of $0.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Batty 1987). Assimilation efficiency is a size-dependent function increasing from 0.6 for small larvae (5.0mm) to 0.8 for larger larvae (11 mm) (Buckley & 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 is included as a maximum of 10% of SMR at arbitrary fixed temperature (7°C) if the larva swims up or down at its maximum velocity, and scaled proportionally for shorter vertical displacements. Swimming velocity is a function of larval size (Peck et al. 2006).

Mortality: We model mortality from fish and invertebrates separately and similar to Fiksen et al. (2002) and Vikebø et al. (subm.). Predation rate from invertebrates m_n [h^{-1}] decrease with larval body length SL based on the estimate from McGurk (1986): $m_n = 0.01 \cdot SL^{-1.3}$. Predation rate from fish is $m_f = 0.05 \cdot R^2$, where R is the light- and prey size-dependent perception distance of the piscivorous (the coefficient 0.05 summarizes all factors such as fish density and escape probability; see Fiksen et al. 2002 for details). Total instantaneous predation rate $m_z = m_n + m_f$ is thus a function of depth, surface irradiance, and larval size.

If food intake is low, growth may be negative. If the body mass w to SL ratio drops below 75% of the expected value, an additional mortality component m_s (0.0036 h^{-1}) is included.

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

$$\frac{m}{\Delta SL} = \sum_{t=t_0}^{t=H} [m_p(t, SL, z) + m_n(SL) + m_s(w, SL)] \quad 6$$

where the stage duration H is the number of time steps (hours) needed to grow 0.5 mm longer (depending on growth rate). This fitness measure makes the trade-off between growth (reduced stage duration H) and mortality components explicit.

Results and discussion

The behavioral strategies regulate vertical positioning with consequences for instantaneous mortality and growth rate. The main objective here is to assess the importance of including behavioral rules in models of larval fish. Therefore, we start by presenting behavior and fitness emerging from the five rules and from random vertical movements (Fig 3). Then, we proceed by 1) testing the robustness of the rules under daily and annual environmental variability, 2) investigating how optimal parameter values for each of the rules change as larvae grow, and 3) comparing daily cycles of behavior, growth and mortality to observed distributions.

The fitness value of vertical behavior

We tested the rules relative to larvae moving randomly in the water column (Fig. 3). All rules predicted larvae to go deeper in the water column with size (Fig 3a). The simplest rules, Rule 1 and 3 predicted the deepest distribution of the larvae, while the more complex Rules 4 (two parameters STV and β) and 5 (sigmoid, μ and \hat{s}) predict larvae to be higher up in the column for all size groups. All rules do markedly better than the randomly moving larvae (Fig. 3b). The effect of behavior is strongest for small and large larvae, since larvae in the intermediate size range have higher

inherent growth potential (Folkvord 2005) and shorter stage duration (H). Overall, the probability of survival from 6 to 18 mm was 0.005 % for Rule 1, 0.009 % for Rule 2, 0.004 % for Rule 3, 0.005 % for Rule 4, 0.005 % for Rule 5, and $4 \cdot 10^{-9}$ % for random behavior. The differences between the rules in their success are minor, suggesting that the additional complexity of rules 4 and 5 are not necessary. The cost of growing more slowly appears to be eliminated by lower mortality rates.

The smallest size groups of larvae (<8mm) are restricted to forage on nauplii and early stages of copepodites (Fig. 2), with varying degree of capture success (Caparroy et al. 2000, Fiksen & MacKenzie 2002). Small larvae are also visually limited as the eye is still under development (Fiksen et al. 1998). Foraging of small larvae is therefore limited to the upper parts of the water column. The modeled mortality rates are quite homogenous for small larvae in this layer (Fig. 2). Larvae behaving according to Rules 1-3 chose habitats where foraging can take place during day (~40 m), but ascend during evening and night. Contrary, individuals following Rule 4 and 5 are more risk seeking, and are located in the upper 10–30 m (Fig 3a). This results in enhanced growth rates, but also increased predation risk from fish. Larvae situated deeper in the water column, grow slower, are less prone to perils, but the time spent growing between ontogenetic stages increases (Fig. 3c). It thus seems like there are two equally fit behavioral solutions: high growth rates and short development time (Rules 4 and 5), or reduced growth rate and prolonged development (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 comparing the rules performance in day-specific prey fields. 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 (Fig. 4, left panels). Fitness or accrued mortality per length interval, however, shows only minimal differences across days (Fig. 4, 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. Individuals select depths by trading off foraging with starvation and mortality rates, and emergent behavior differ, but their performance is more comparable, indicating robustness to inter-annual environmental variation.

The robustness of rules throughout ontogeny

How much will the best performing parameter values vary with size? Both predation risk and growth rate vary with size, so the best parameters should be expected to change with size. A rule where parameters fluctuate much throughout development is not very realistic, and may represent an overfitting to the environmental setting. A robust rule is characterized by a wide fitness plateau around the optimal parameter value (reducing the cost of errors) and little or a systematic change through ontogeny. If the behavior or ‘psychology of fear’ is determined by the genetic code, then such robust rules, which may develop systematically through ontogeny, is more likely to evolve in real organisms.

For Rule 1, where growth rate is traded directly against mortality rate, large differences in fitness (eq. 6) emerge from different values of π (Fig. 5 a, b), particularly for the smallest larvae. The relationship between strategy, behavior and fitness is easy to interpret for Rule 1 and Rule 3, since state-dependence is ignored. Low values of π mean that larvae are geared for rapid growth, with little fear of predation. Larvae larger than 12 mm are less sensitive to the value of π , and $\pi \sim 0.1$ performs well across all size increments. For Rule 3, where feeding is the cue instead of growth, the plateau around the best value is broader, meaning the rule is more robust (Fig. 5 c, d). The main criteria for success is that small larvae (<12 mm) should be risk seeking (avoid $\pi > 0.5$), and ensure high feeding rates (low π).

Interpretation of Rules 2 and 4 is more intricate (Fig. 6). Here, the gene β translates an internal cue, stomach fullness, into risk-sensitivity π (Fig. 1a). For Rule 2 (Fig 6 a,

b), fitness varies erratically over a wide range of β , suggesting the rule is not very robust. No pattern with size is apparent.

Rule 4 has two parameters, and both of these may vary with larval size (Fig 6 c, d; Fig 7). We parameterized this Rule through a simple trial and error procedure, where we first found fitness to be relatively flat for β -values in the range 0-3 for different *STV*-values. Then, we kept β fixed ($\beta = 1$), and tested the full range of *STV*-values across all size-increments (Fig. 7). This revealed a trend for the best *STV* with larval size. A curve was fitted to the best values, and then this was used to find optimal β -values in each size class (Fig 6). The best β -values remained around 1 for all size increments, confirming the robustness, or low importance of β in this rule. In fact, this suggest that Rule 4 could be reduced to a simple one-parameter rule ($\beta=1$, 'hockey-stick function'), as in Fig 7. For this rule, it appears that the threshold value is the important factor, and larvae will always become highly motivated for feeding when stomach is empty. With this response in place, the exact shape of the transition to lower motivation to feeding is not important, except possibly that taking too much risk at high stomach fullness has a cost (high values of β , Fig 6, c, d).

The sigmoid Rule 5 also has two parameters, and the best values was found trough a similar iteration process. 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. We therefore chose $\hat{s} = 0.7$ as a baseline value, and present fitness of larvae where this value is fixed and combined with different slope values μ for all size classes (Fig. 1 b). Fitness remained quite homogenous across larval sizes and years (Fig. 8), and a slope of 5 is used as baseline parameter. This rule appears to be quite similar to Rule 4; if one parameter (\hat{s}) is set sensibly, the other is less important.

Predicted and observed larval diel distribution

The emerging behavior from Rules 2, 4 and 5 move individuals to safer habitats when stomach fullness increases. These rules triggers swimming towards surface waters and stimulate foraging before all stomach content has been digested and absorbed. A functional response between hunger (stomach fullness) and risk sensitivity provided promising results, and is biologically logical (Dill & Fraser 1984, Munk 1995, Skajaa et al. 2004).

We applied Rule 4 to study how 7 and 15 mm larval cod behave over one diel cycle, given their ability to forage and grow in the environmental conditions on Georges Bank in May 1993 (Fig. 9). The larvae perform diel vertical migration pattern (Fig 9a), avoiding strong light during day to minimize mortality while keeping stomach fullness high (Fig. 9b). The 7 mm larva remained between surface and 40 m depth, while 15 mm larva descended deeper, to 50–60 m (Fig. 9a), still keeping its stomach full. This difference is driven by the size-dependence in predation rates, with higher influence of visual predation for the larger 15 mm larva. Predation (Fig. 9c) and growth (Fig. 9d) rates depend strongly on larval depth selection. The predation risk peaks in the morning, since the larvae have empty stomachs and have high motivation to feed (Fig. 9c).

How does the modeled vertical distribution compare to observations of larval cod made at Georges Bank by Lough et al. (2005)? Comparing Figs. 3 and 10, it seems like Rules 3 and 4 are more in line with observations on depth distribution than Rules 1, 2 and 5. Most of the individuals were located in the upper 40 m regardless of size and time of day (Fig 10). Large (6-13mm) individuals are more widely distributed than the smallest larvae. During afternoon and evening (15-21h), larvae are distributed more evenly in the upper 40 m of the water column. Differences between the model and field observations may be related to the actual predation field on the Georges Bank being different from the modeled scenario. Our invertebrate and fish predator abundance and efficiency are assumed, and small changes in these (or in e. g. turbidity, see Fiksen et al. 2002) would change the predicted behavior. Also, under

natural settings shoals of fish may enter and cause strong episodic events (Garrison et al. 2000).

General discussion

Evolution is a process played out in large numbers where variation between individuals that affect survival or reproduction will influence which genes are passed on to the next generation (Dawkins 1976). Over time, organisms will adapt to the prevailing environmental conditions, but adaptation does not necessarily mean that optimal or perfect solutions are found. Optimal behavior often requires perfect information and great cognitive skills; two characteristics that are unrealistic and moreover rely on costly investments.

In a variable environment, behavioral rules have to perform well across the type of variation that an individual typically encounters. A strategy that works well across environmental variation, or when information is lacking or uncertain, is called a *robust* strategy (Grimm and Railsback 2005). In this paper we have explored simple strategies and tested how well they tackle the trade-off between growth and survival when the environment varies (daily and inter-annual variation) and throughout ontogeny (all size-related processes vary).

Simple rules of thumb are sometimes over-fitted, perhaps especially when found by optimization. To be optimal in one environment, the strategy often performs worse than other strategies under different environmental conditions, in turn leading to reduced robustness. At the same time, this means that robust strategies seldom are optimal in any specific environment; rather they are fairly good across many environments. A second reason that rules are seldom truly optimal is that the selection gradient for further improvements vanishes between a good strategy and one that is only marginally better.

Coupled bio-physical models (Hinrichsen et al. 2002, Mullon et al. 2002, Vikebø et al. 2005) provide a virtual laboratory to study the interactions between processes and their effects on early life history of larval fish, and to follow individual eggs and

larvae along drift routes in a realistic physical environment. The drift models track the local environment along the drift route, and may even incorporate larval behavior. A prerequisite for the latter is that the behavior is easy to calculate; otherwise simulations and analysis becomes an immense and incomprehensible task. Drift models are therefore in need of candidate simple behavioral rules that larva can follow along drift trajectories, and as they drift these rules may incorporate local information or respond to the larvae's internal state.

These model developments also generate new questions. If the realized drift trajectory has fitness consequences, for example by affecting integrated survival, temperature, and food ingestion along the trajectory, or the value of final settlement area, larvae should be expected to evolve adaptations to these factors (Fiksen et al. *subm.*). But what are the behavioral abilities and constraints of the larvae? And however restricted, the swimming ability of larvae is sufficient to select among a range of vertical positions. In turn, as this study shows, a simple rule for habitat selection may greatly influence growth and predation rate. In the following, we discuss *i*) behavioral changes with size and environmental conditions, and *ii*) vertical behavior of modeled larval cod in relation to field observations.

i) Behavioral change with size and environment. Larger larvae are less susceptible to invertebrate predation (Bailey & Houde 1989) through increased locomotive abilities (Bailey & Batty 1984). That is one reason why larvae should take high risks and grow quickly to larger sizes. Although exceptions may occur if mortality increase with size (Pepin et al. 2003), for most situations 'bigger is better' (Leggett & Deblois 1994, Hare & Cowen 1997). In our model, larvae will become less vulnerable to invertebrate predation as they grow, therefore the value of rapid growth will decrease with size. In addition, they will become more vulnerable to visual predators simply because they grow larger and become more visible. However, this does not mean that the predation risk will increase with size, because, depending on their behavioral strategies (the parameters or 'genes'), they will continuously adjust their behavior depending on growth (or feeding) and mortality risk. Any environmental change

affecting m , g or F will also change π and feed back on habitat selection and realized growth and mortality. Thus, the predictions from models with this kind of behavioral flexibility will differ considerably from those with no or fixed behavior.

ii) Behavior of modeled and sampled larvae at the Georges Bank. Eggs and larvae drift southwest with ocean currents from the spawning sites at the Northeast Peak, along the Eastern flank of Georges Bank, before the survivors enter the nursery grounds. Survival through this larval pelagic phase is modified by the presence and abundance of both prey and predators. Horizontal displacement takes place indirectly through vertical behavior. The chaotic, wind generated, horizontal current system near the surface may be avoided by shifting vertical position, entering a new habitat where predation and prey composition may be different from the surface layer (Werner et al. 1993). Lough and Potter (1993) sampled night and day vertical distribution of larval cod and haddock along the drift routes and found that the majority of larvae in the size range 2–5 mm were distributed at 15 m depth in stratified water columns (off-bank areas deeper than 60 m) and 35 m depth in well-mixed water columns (on-bank areas). They also observed diel migration for 9–13 mm larvae, initiated around 6–8 mm, with mean day and night depths of 40–60 m and 10–40 m respectively. The data in Fig. 10 are less clear on any diel patterns, suggesting that the distribution pattern may vary over time. The rules differ in their prediction of vertical positioning, and the model did not exactly match the observed larval distribution, but a range of environmental factors ignored by the model (predator distribution, abundance and turbidity variations) may cause this discrepancy.

Vikebø et al. (2005) showed how small vertical displacements may alter the drift pattern of larvae, thereby making it difficult to compare observed and modeled distributions. It has also been observed that at least larger larvae perform diel vertical migrations (Lough & Potter 1993, Leis et al. 2006), and implementing vertical behavior into coupled bio-physical models may increase the reliability of the modeled dispersal and early life history of fishes. We have shown that survival may increase

drastically when larval cod use simple rules for habitat selection based on cues from the environment and its internal state.

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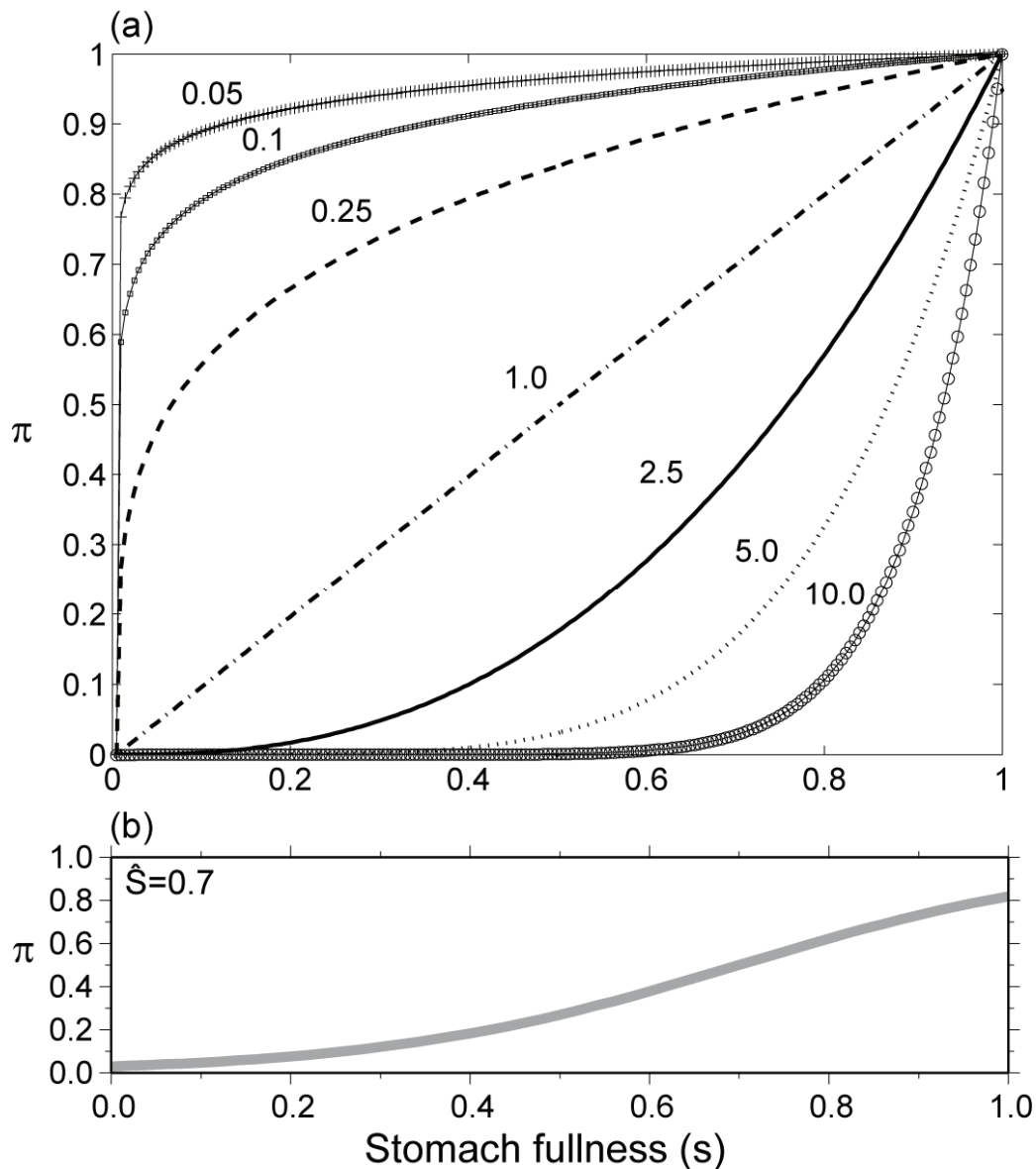


Figure 1 a) Risk sensitivity π or fear increase as stomach fullness s increases (Rule 2). The relationship between stomach fullness and increased risk sensitivity is a function of β (values from 0.05 – 10 are shown). Larvae with low β values are risk sensitive (high π , or fear) even with little food in the stomach, while larvae with high β values accept risk at higher levels of stomach fullness. b) The lower panel shows the optimal response between stomach fullness and fear from Rule 5 ($\mu=5$, $\hat{s}=0.7$).

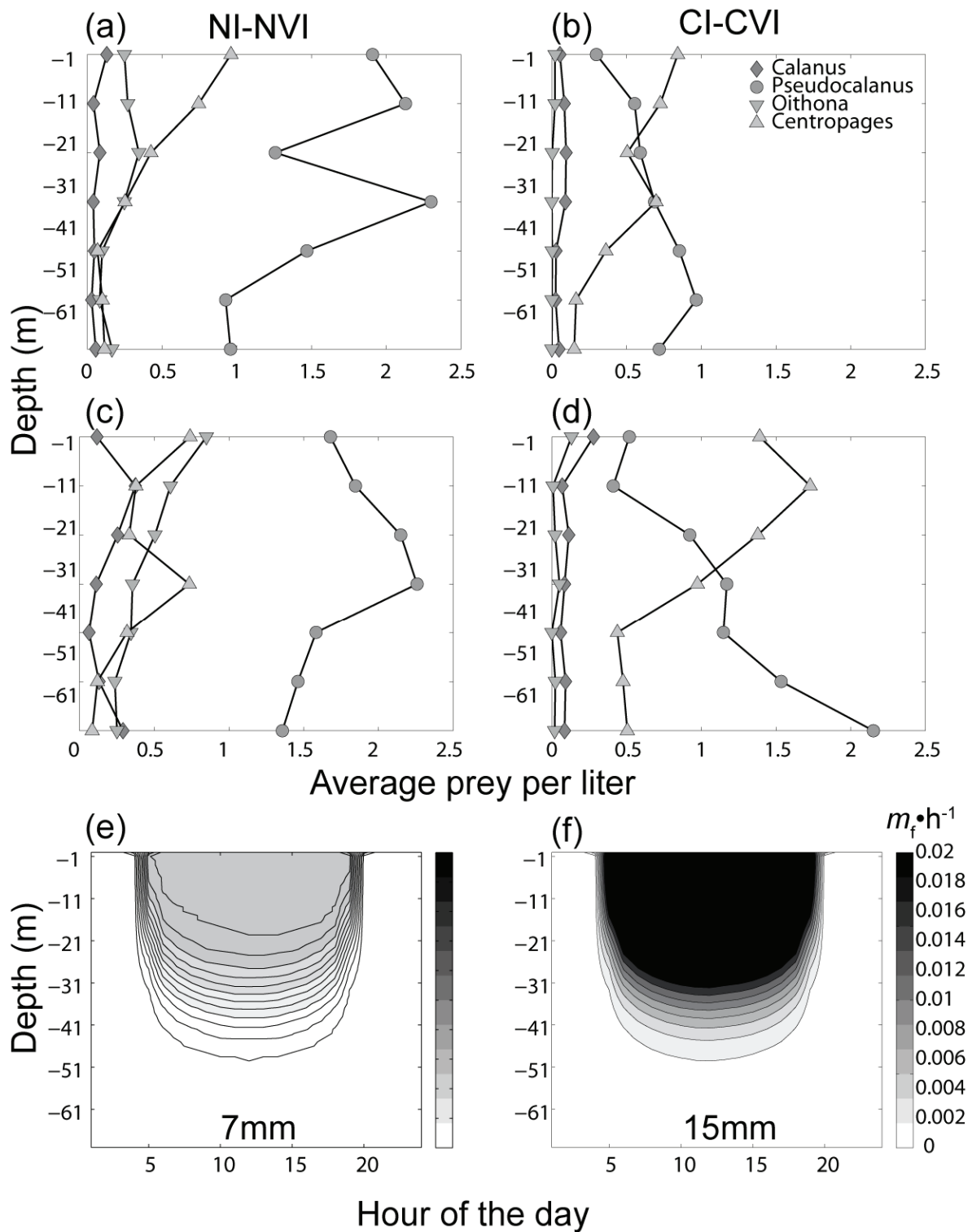


Figure 2 Averaged vertical prey distribution of four species, a) and c) show nauplii stages, b) and d) show copepodite stages; observed on Georges Bank in 22-27 May 1993 and 1994 (Lough et al. 2005). The bottom panel illustrate modeled visual predation rate over the diel cycle on 7 mm (e) and 15 mm (f) larvae.

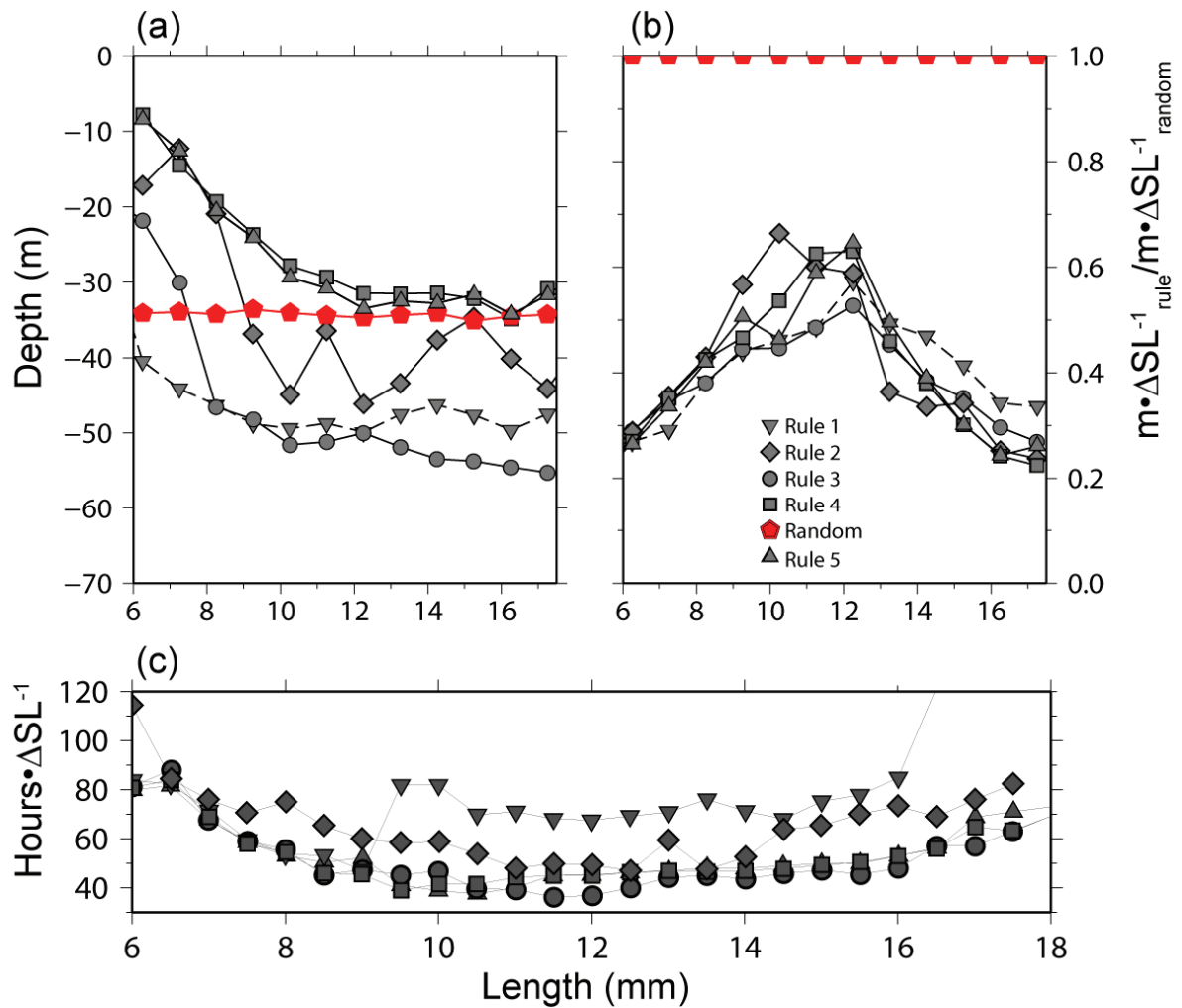


Figure 3 Performance of specific rules (Rules 1-5) relative to vertical movement which is purely random (red lines; average over 100 simulations). The choice of depth for every time step is random, but vertical movement is limited to maximum swimming distance from previous position in the random case. Left panel (a) shows the average depth between ontogenetic stages for Rule 1-5 and random, while right panel (b) shows how well the rules perform relative to the random movement, expressed in accrued mortality. Values below 1.0 indicate an improved survival between two ontogenetic stages compared to random behavior. Lower panel (c) shows the time (hours) used to grow between size-stages for each rule.

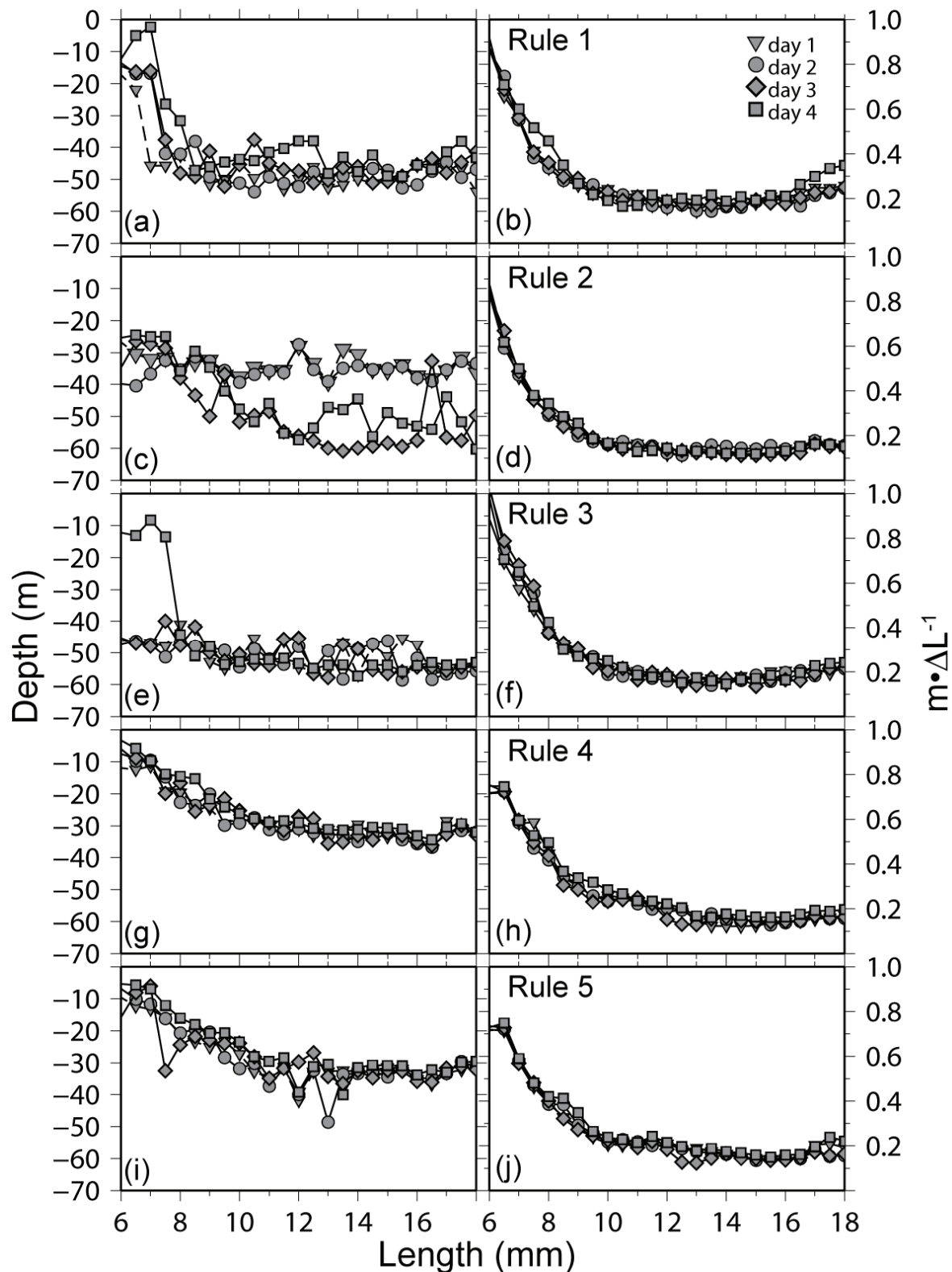


Figure 4 Averaged depth (left panels) and accrued mortality rates (right panels) for Rule 1 (a, b), Rule 2 (c, d), Rule 3 (e, f), and Rule 4 (g, h) between ontogenetic stages using a specific prey day repeatedly. This was done for 4 different days (22-25 May 1993) and demonstrates the minor effect of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

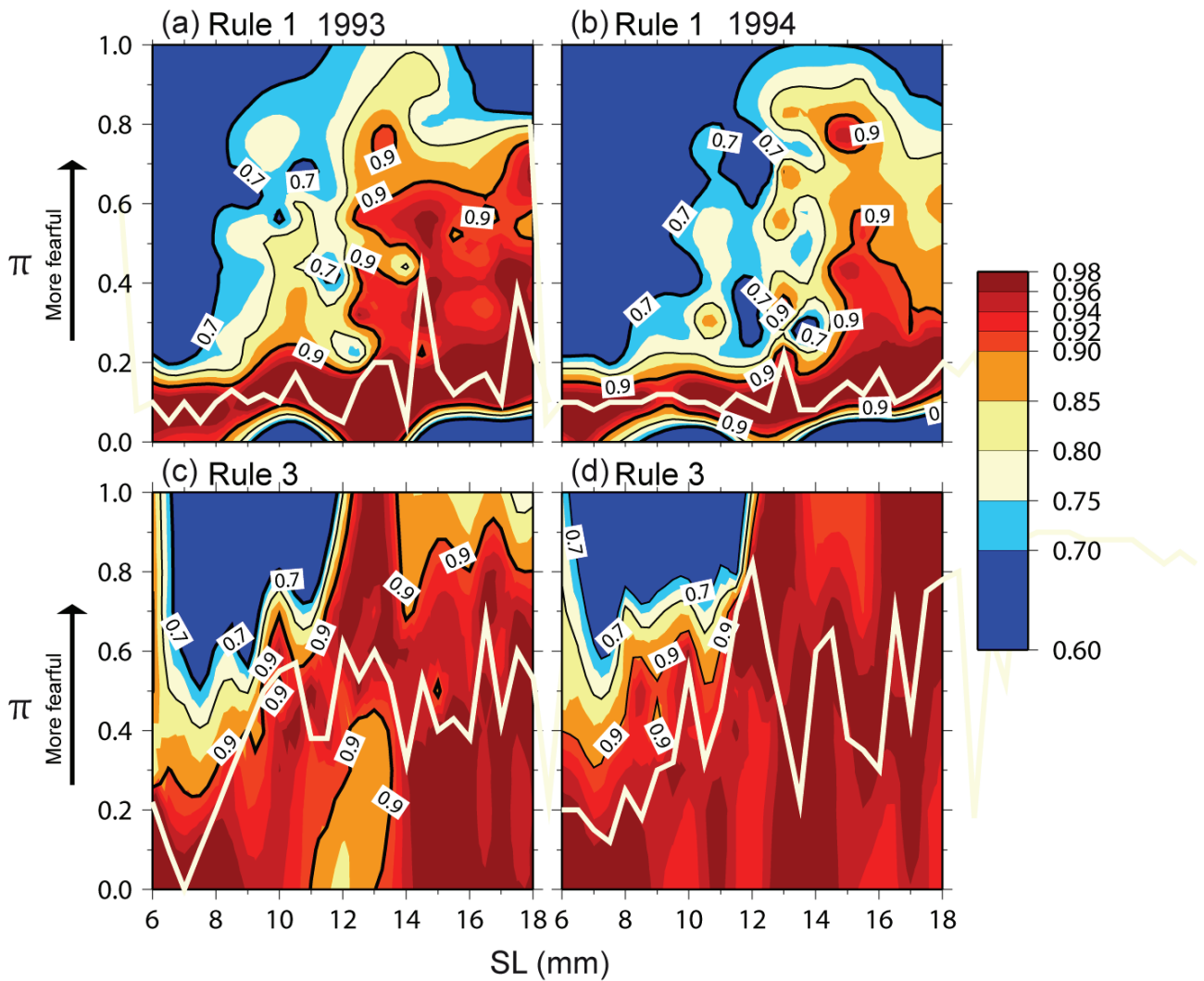


Figure 5 Landscape of accumulated mortality for 0.5 mm length increment for different values of π using growth rate (Rule 1; $\max_z[(1-\pi)g - \pi m]$) as trade off to mortality rate (upper panels) for two different years 1993 (a) and 1994 (b). The lower panels shows the trade off between ingestion rate and mortality (Rule 3; $\max_z[(1-\pi)F - \pi m]$) for years 1993 (c) and 1994 (d). The mortality (fitness) is normalized against the best solution within each size class, therefore range is [0 1]. White line denotes the optimal solution at each length increment.

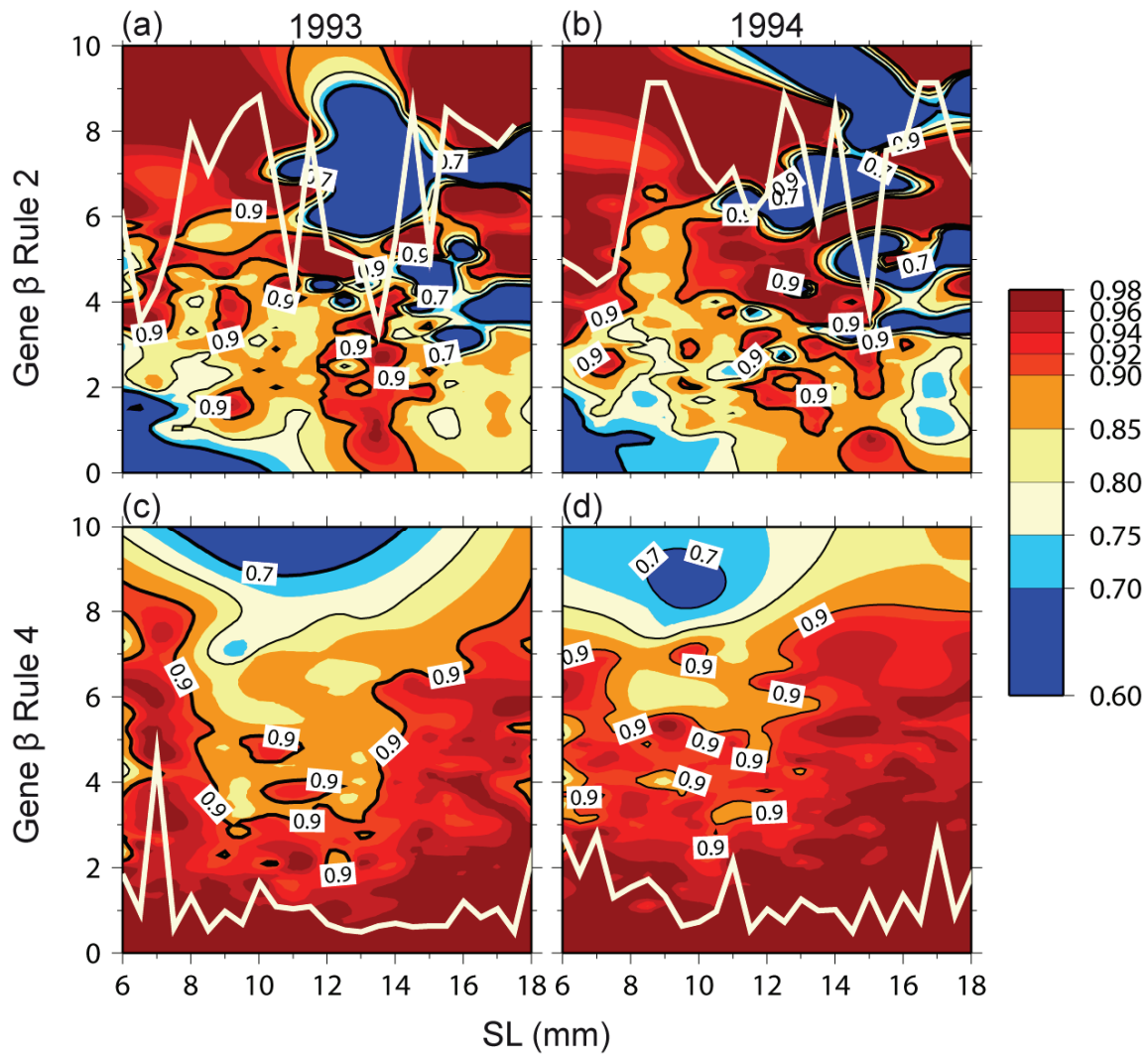


Figure 6 Landscape of accumulated mortality for different values of β using Rule 2 (upper panels) and Rule 4 (lower panels). For Rule 2 the risk sensitivity (fear) π depends on stomach fullness s and β as $\pi = s^\beta$, and for Rule 4 as $\pi = [(s-STV)/(1-STV)]^\beta$, where stomach threshold value is decreasing with size (see Fig. 7). The mortality (fitness) is normalized against the best solution within each size class, therefore range is [0 1]. White line denotes the optimal solution at each length increment.

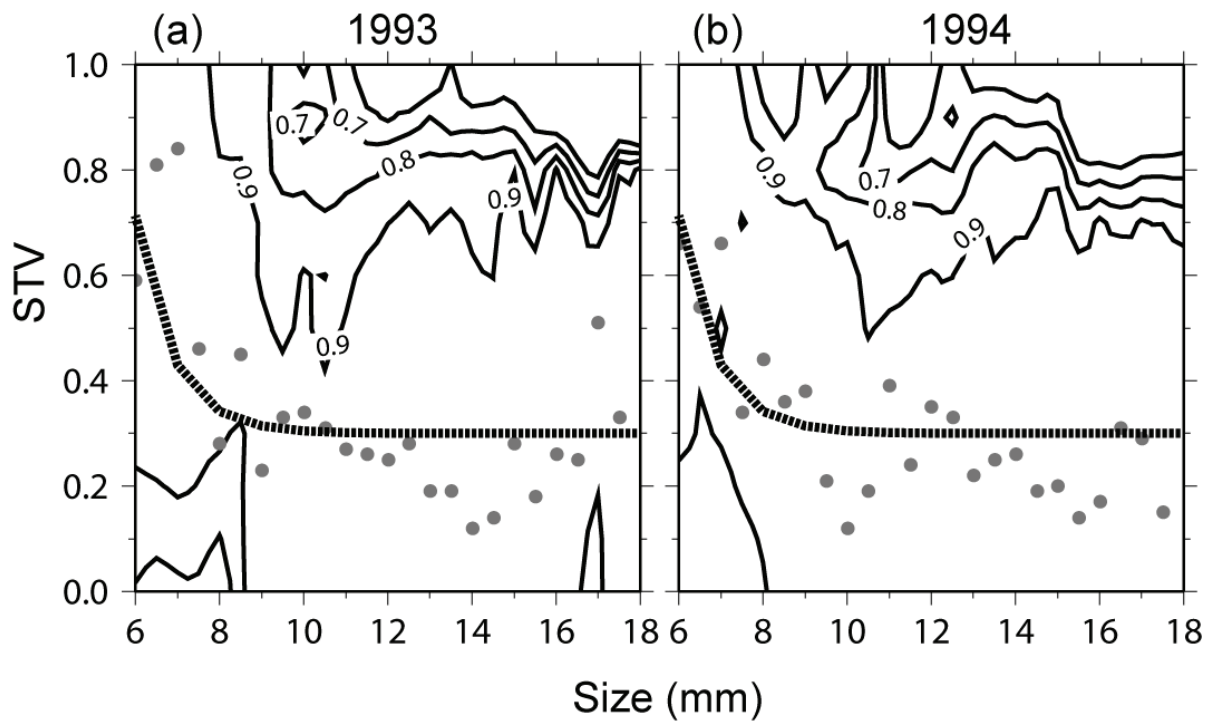


Figure 7 Fitness of individuals with different stomach threshold values (STV) given a fixed $\beta = 1$ (see Fig 6). Increased stomach threshold values indicate a more risk prone strategy, and clearly the best strategy becomes less risk prone as larvae increase in size (dots indicate best STV within each size class). The fitted line is the function $STV(SL) = 0.3 + 10^3(1 + SL \cdot e^{SL})^{-1}$, which is implemented as baseline in Rule 4.

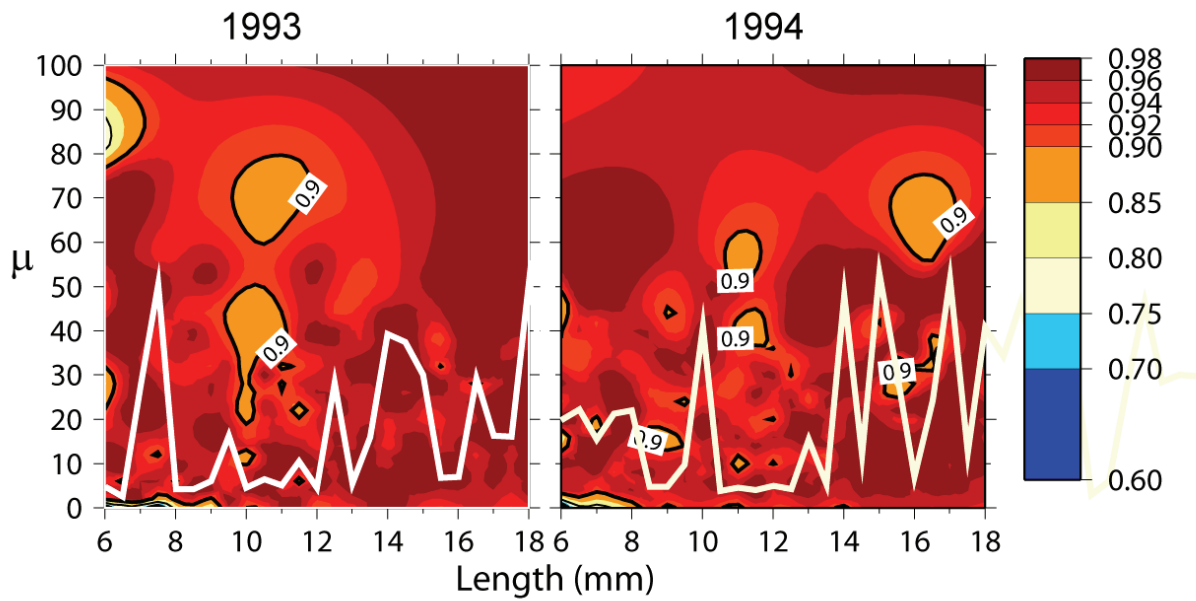


Figure 8 The relationship between stomach fullness (s) and risk sensitivity π (fear) is expressed as a sigmoid, two-parameter function (Rule 5). Using the half saturation point $\hat{s} = 0.7$, we estimated fitness using a variety of slopes (μ , 0-100). Fear (π) will always increase with stomach fullness (see eq. 5). The mortality (fitness) is normalized against the best solution within each size class, therefore range is [0 1]. White line denotes the optimal solution at each length increment.

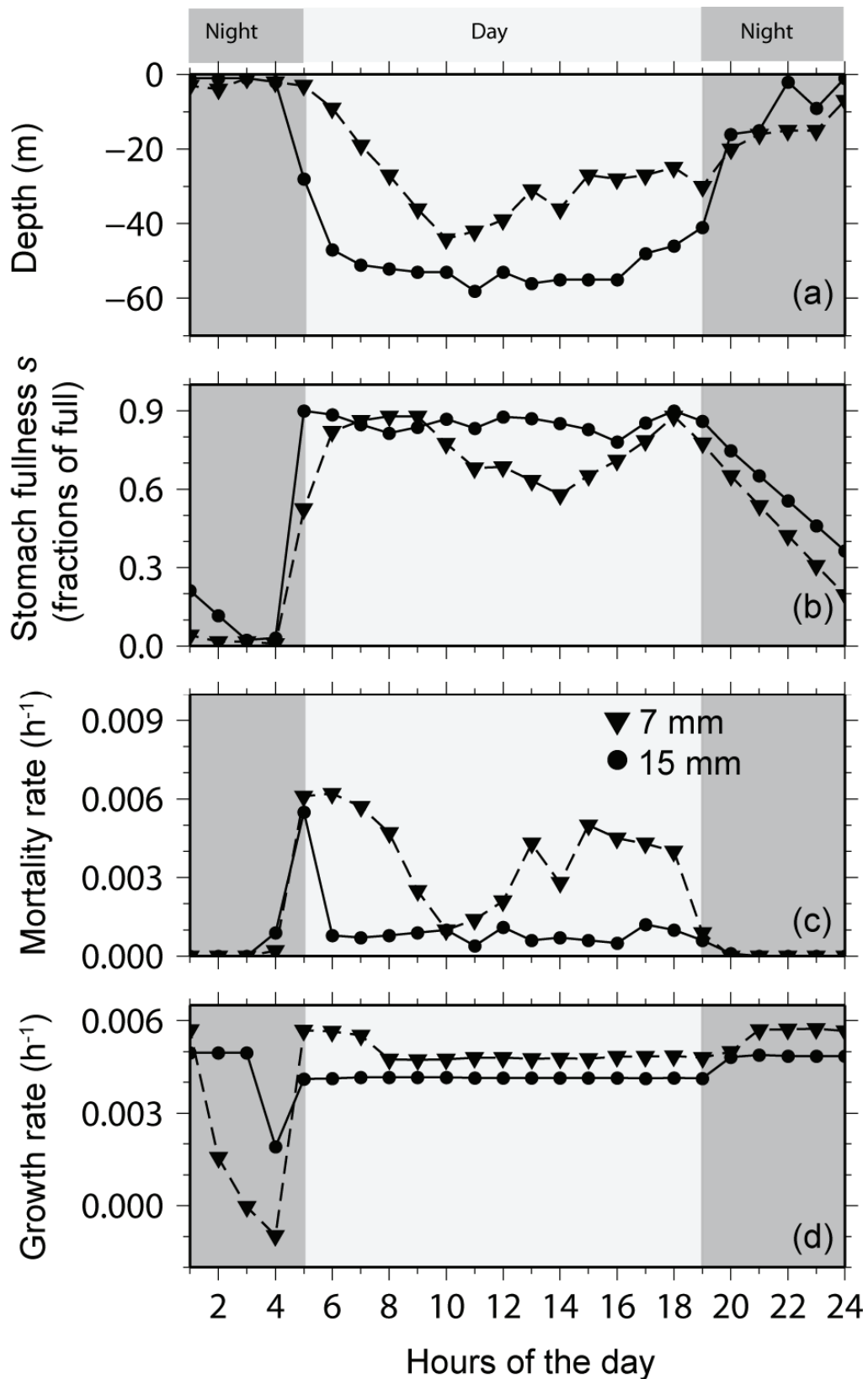


Figure 9 Emergent behavior of 7 and 15-mm larvae following Rule 4. Results are displayed for a 24 hour time period with a spin-up period of 13 hours. The panels show vertical position (a), stomach fullness (b), predation rate from piscivores (c) and growth rate (d). Environmental conditions measured from 22nd – 23rd of May 1993, and predation from fish as in Fig 2 e, f. We applied Rule 4 with baseline parameters.

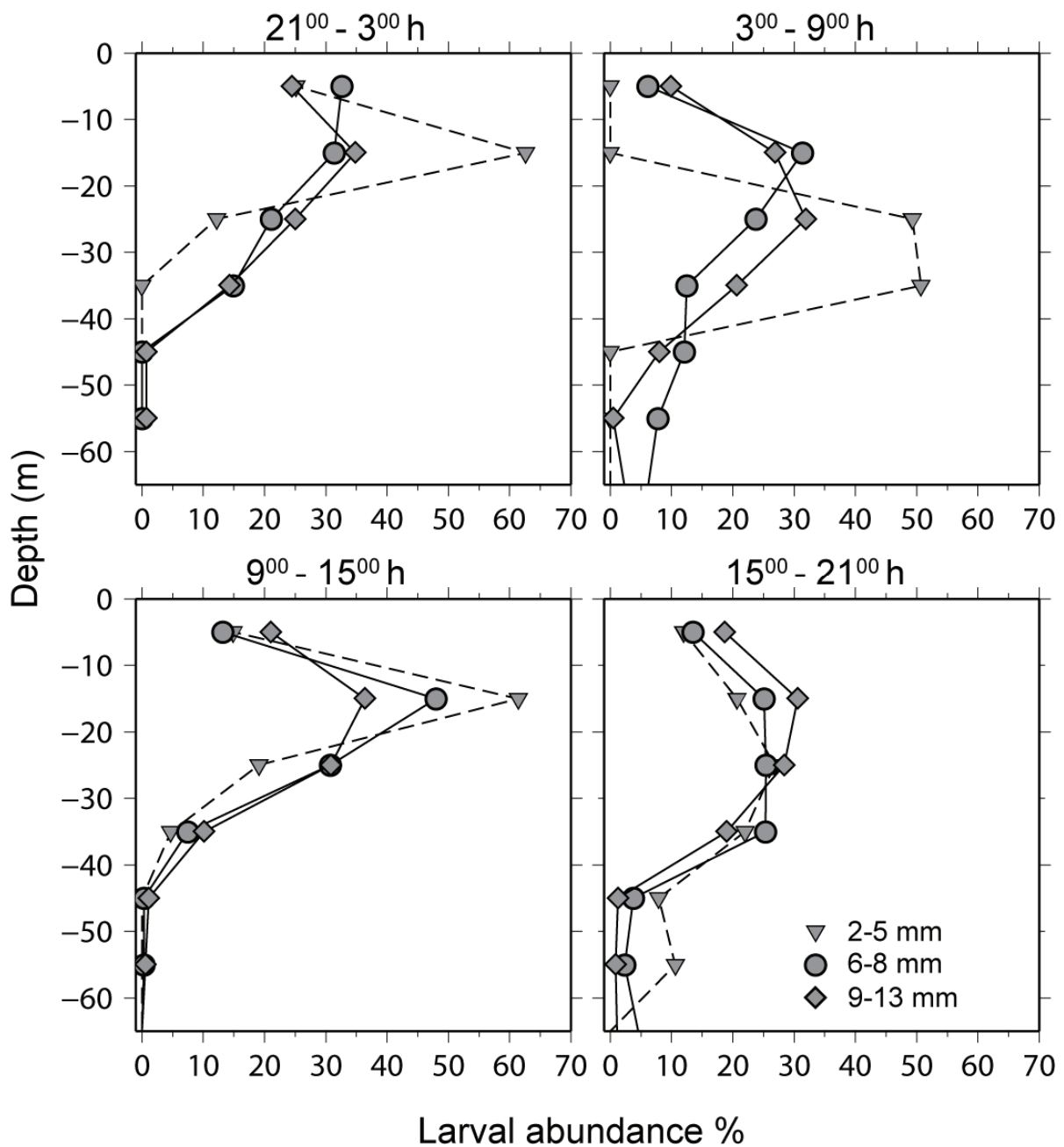


Figure 10 Averaged observed vertical distribution of larval cod and haddock divided into size categories in May 1993 and 1994 on the Georges Bank (Lough et al. 2005). Values were split into 6 hour time periods to explore the differences between day and night distributions.