



Effects of temperature and food availability on larval cod survival: a model for behaviour in vertical gradients

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ABSTRACT: Recruitment success in living marine resources is variable due to high survival variability of early life stages. Improving our understanding of how environmental and ecological factors mechanistically interact and influence larval fish growth and survival is necessary to better predict year-class strength and expected physiological and behavioural responses to climate warming. We use a state-dependent optimality model for the behaviour of larval Atlantic cod *Gadus morhua* to analyse trade-offs related to growth and survival. Temperature-dependent maximum growth rates and vertical profiles of temperature and stochastic prey availability are used as inputs within a mechanistic modelling framework that finds optimal behavioural strategies of vertical migration and foraging activity. The fitness criterion used is maximization of survival probability until the larvae reach a given body size (15 mm). Detailed descriptions of predation, physiology, growth and survival of larval cod emerge from simulations of the optimal strategies. The model shows that the effect of temperature on survival is complex. Increasing temperature may lead to faster growth and higher survival, but only when there is sufficient food. In poor food environments, higher temperatures make larvae more susceptible to predation as they take higher risks to satisfy their metabolic costs. Overall, these results suggest that larval Atlantic cod, especially those from warmer-water stocks, may experience reduced survival and recruitment in climate-change scenarios that predict both elevated temperatures and reduced food supply.

KEY WORDS: Larval cod · Optimal behaviour · Growth · Recruitment · Optimality model · Trade-off

INTRODUCTION

Climate change is an important driver of structure and dynamics in marine populations and ecosystems (Johnson et al. 2011). It can affect ecosystem productivity, phenology, species distributions and abundance (Perry et al. 2005). For a century, fisheries scientists have discussed the relation between climate variability and productivity in marine fish. Environmental variation has been shown to cause significant fluctuations in the biomass production of fish stocks through various effects on recruitment (Hjort 1914, Cushing 1982, Drinkwater & Myers 1987, Stenseth et al. 2004, Drinkwater 2005), or pro-

cesses influencing adult growth, survival and reproduction (Kjesbu et al. 2014).

There are several mechanisms, e.g. match or mismatch between first feeding larvae and their prey or predators (Cushing 1973, 1975, Anderson 1988, Bailey & Houde 1989), and retention processes during oceanic drift between spawning and nursery areas (Sinclair 1988), which may influence recruitment variability (Houde 2008). Furthermore, early life stages are likely to be more sensitive to environmental variability than later larvae and early juveniles. Relatively small changes in food abundance or temperature conditions can positively or negatively impact the behaviour and survival of larval stages (Pörtner &

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Peck 2010). As a result of behavioural plasticity and selection, species may shift distribution and modify their depth ranges, or move to more suitable areas (Perry et al. 2005).

Temperature (Ottersen et al. 2001, Pörtner & Peck 2010, Vollset et al. 2013) and prey abundance (Cushing 1990, Beaugrand et al. 2003, Houde 2008) are often considered the most influential environmental factors affecting fish larval growth and survival. Temperature can directly influence rates of digestion, gut evacuation, swimming activity and metabolic rates, with implications for growth energetics (Otterlei et al. 1999, Peck et al. 2006). There are not only direct effects of temperature on fish larvae, but also indirect effects via lower trophic levels (Behrenfeld et al. 2006). Prey availability has been recognized as an important environmental factor for survival of larval stages (Hjort 1914, Cushing 1975, Miller et al. 1988, Buckley & Durbin 2006, Fiksen & Jørgensen 2011). Most fish larvae feed primarily on zooplankton, so changes in the availability, size, quality or seasonal timing of these may affect larval survival (Beaugrand et al. 2003, Pitois & Fox 2008, Overland et al. 2010, Kristiansen et al. 2014). The exponential increase in metabolic rate with temperature will require larvae to increase their food intake, in order to gain enough energy to sustain basic functions as well as maintain survival and growth (Brett 1971). Whether such a compensation is possible depends on several mechanisms, and restricted food abundance may cause (1) slower growth and poor nutritional condition, that in turn may reduce swimming capability of larvae and increased susceptibility to predation (Houde 2008); or (2) increased risk-taking behaviour to sustain high growth rates, resulting in higher predation (Fiksen & Jørgensen 2011, Jørgensen et al. 2014). As climate change is predicted to cause both ocean warming and altered productivity of plankton communities (Brander 2010, Doney et al. 2012), understanding the complexity of interaction between temperature and food availability is important for predicting effects of climate change on the behaviour and physiology of early life stages, as well as their implications for survival, growth, recruitment and stock productivity (Kristiansen et al. 2014).

Recent attempts at evolutionary modelling of early life stages and recruitment processes have focused on developing mechanistic models that allow the incorporation of behavioural strategies (such as swimming speed and depth selection) with their consequences for survival and fitness (Fiksen et al. 2007, Fiksen & Jørgensen 2011, Jørgensen et al. 2014). From these, one can formulate simple rules whereby

larval behaviour can be implemented in coupled biophysical individual-based models (IBMs) (Vikebø et al. 2007, Kristiansen et al. 2009, 2014). Biophysical IBMs link ecological mechanisms and evolution with physically coupled ecosystem models, which have become frequently used to advance the understanding of the effects of the biotic or abiotic environment on fish early life stages (Peck & Hufnagl 2012). These methods allow complex interactions between environmental and individual processes, and may include consequences for larval foraging success, predator–prey dynamics, growth, and population abundance and distribution (Peck & Hufnagl 2012).

Our modelling study (1) analyses the interactions between temperature and prey availability, and their effects on larval growth and survival; (2) identifies key processes and associated behavioural trade-offs whereby larvae maximize survival across different scenarios of temperature and prey density; and (3) highlights key factors that will help link environmental variability to larval survival and recruitment success in marine ecosystems.

METHODS

General overview of the model

Our study is based on a detailed state-dependent optimality model for the behaviour of larval Atlantic cod *Gadus morhua* in a water column with environmental gradients. The model is described briefly in the next paragraphs; please refer to Fiksen & Jørgensen (2011) for a more detailed description. In this study, we have expanded the model to include (1) vertical gradients of temperature and stochastic food availability, and (2) a more detailed routine for determining light conditions depending on day of year, latitude and cloud cover. The model is parameterized for larval Atlantic cod, but many of the resulting predictions can be generalized to species having pelagic larval stages that share the relevant characteristics of flexible behaviour, trade-offs between growth and survival, and high mortality rates.

Vertical gradients of temperature and prey availability were used as inputs, and in this environment, the model describes encounters with food and predators mechanistically. These determine bioenergetics, growth and survival (Fiksen & Jørgensen 2011). In this study, larval body size receives special attention. This does not mean that other traits (e.g. body condition) are not important, but mortality processes are strongly dependent on larval fish size (McGurk

1986). Indeed, predation mortality from visual predators is higher for larger larvae as they become more visible and more easily detected. Predation risk from invertebrates is also size-dependent, and is highest for small larvae because of their limited escape capabilities (Bailey & Houde 1989).

The model includes gut content and body size as individual state variables and finds the optimal time variable and state-dependent behavioural strategy for vertical migration and foraging behaviour. The fitness criterion of the model is to maximize probability of survival up to a given body size (15 mm), and was found using dynamic programming techniques (Houston & McNamara 1999, Clark & Mangel 2000). Using the optimal strategies, we simulated a population of individuals within a stochastic environment starting from first-feeding larvae at a body length of 5 mm and continuing until they reached 15 mm. This is the length at which metamorphosis from the larval to the juvenile stage starts in cod (Pedersen & Falk-Petersen 1992) and the larvae become less vulnerable to predators. It is also safely within the length range at which the growth function we use remains valid (Folkvord 2005). This provides detailed individual- and population-level descriptions of foraging, predation, growth, behaviour, physiology and survival.

Environment

The model environment is a 1-dimensional water column, 100 m deep, divided into 2 m depth intervals. Vertical gradients of temperature and stochastic normal prey density distribution were used as input to the model (Fig. 1b). Light conditions I_b vary with time of the day, depending on depth z and surface light I_0 (Fig. 2). Surface light I_0 was calculated using a HYbrid Coordinate Ocean Model (HYCOM) (Bleck 2002) according to time of day, latitude (56°N), cloud cover fraction (0.5) and day of the year (Day 100). The cloud cover fraction (0.5) was chosen based on the cloud climatology data covering the Scandinavian region where the mean fractional cloud cover at latitude 56°N during April is around 50% (Karlsson 2003). Day 100 (10 April) was chosen based approximately on cod spawning (late March) and how long the larvae take to hatch (around 20 d, e.g. Iversen & Danielssen 1984). Light decays with depth at a diffuse attenuation coefficient k , related to chlorophyll concentrations in the water column (Fig. 2) (see Woźniak et al. 2003 for details). Prey density was specified in terms of biomass per volume sea water (Kristiansen et al. 2007). As larval prey encounter rates are size-de-

pendent, we assumed that prey size changes proportionally to larval size and is always 5% of larval length (Munk 1997). Prey density followed a normal distribution, with a deep prey maximum set to 30 m (Fig. 1b). To account for environmental variability in food availability, prey densities varied stochastically between 50 and 150% of their mean values, as well as every hour, with a standard deviation equal to 2 mg dry mass m^{-3} . Thus, when the value of prey density is 5 mg dry mass m^{-3} , the range is 2.5 to 7.5 mg dry mass m^{-3} , and when it is 15 mg dry mass m^{-3} , the range is 7.5 to 22.5 mg dry mass m^{-3} (Fig. 1c).

State variables and fitness

Larvae are characterized by the dynamic state variables body size l (mm) and gut fullness g (in fractions of full) (Fig. 1a). As vertical movements are constrained by the larval swimming ability, vertical position z (m) and time of day h (hour) were included as additional state variables. All state variables were updated every time step (hour) to account for behavioural and environmental effects on foraging success and physiology.

Optimal depth selection z^* and foraging activity a^* for each combination of state variables were found using dynamic programming (Houston & McNamara 1999, Clark & Mangel 2000). The optimization target is to find the behavioural strategy of vertical position z in the water column and foraging activity a that, over time, maximizes the probability of survival up to a given body size l_{max} equal to 15 mm, regardless of the time period they take to reach that size. Thus, our fitness measure V is the probability that a larva of a given length and state will survive until size l_{max} .

To determine the optimal sequence of depth position and foraging activity that maximizes fitness, the program works backwards from a terminal state at time h_{max} for which the relationship between state and fitness is known. Mathematically, we set the terminal fitness V at time step h_{max} to 0 if the larvae have not reached maximum size l_{max} (thus assuming that they die if they never manage to reach the target size of 15 mm), while the fitness of a larva that achieves maximum size l_{max} will be 1 regardless of when it reaches that size:

$$\begin{aligned} V(l, g, z, h_{max}) &= 0, \text{ for all } l < l_{max} \\ \text{and } V(l_{max}, g, z, h) &= 1, \text{ for all } h \end{aligned} \quad (1)$$

For all other state combinations the dynamic programming keeps track of the probability that a larvae will successfully survive to length l_{max} . We then iter-

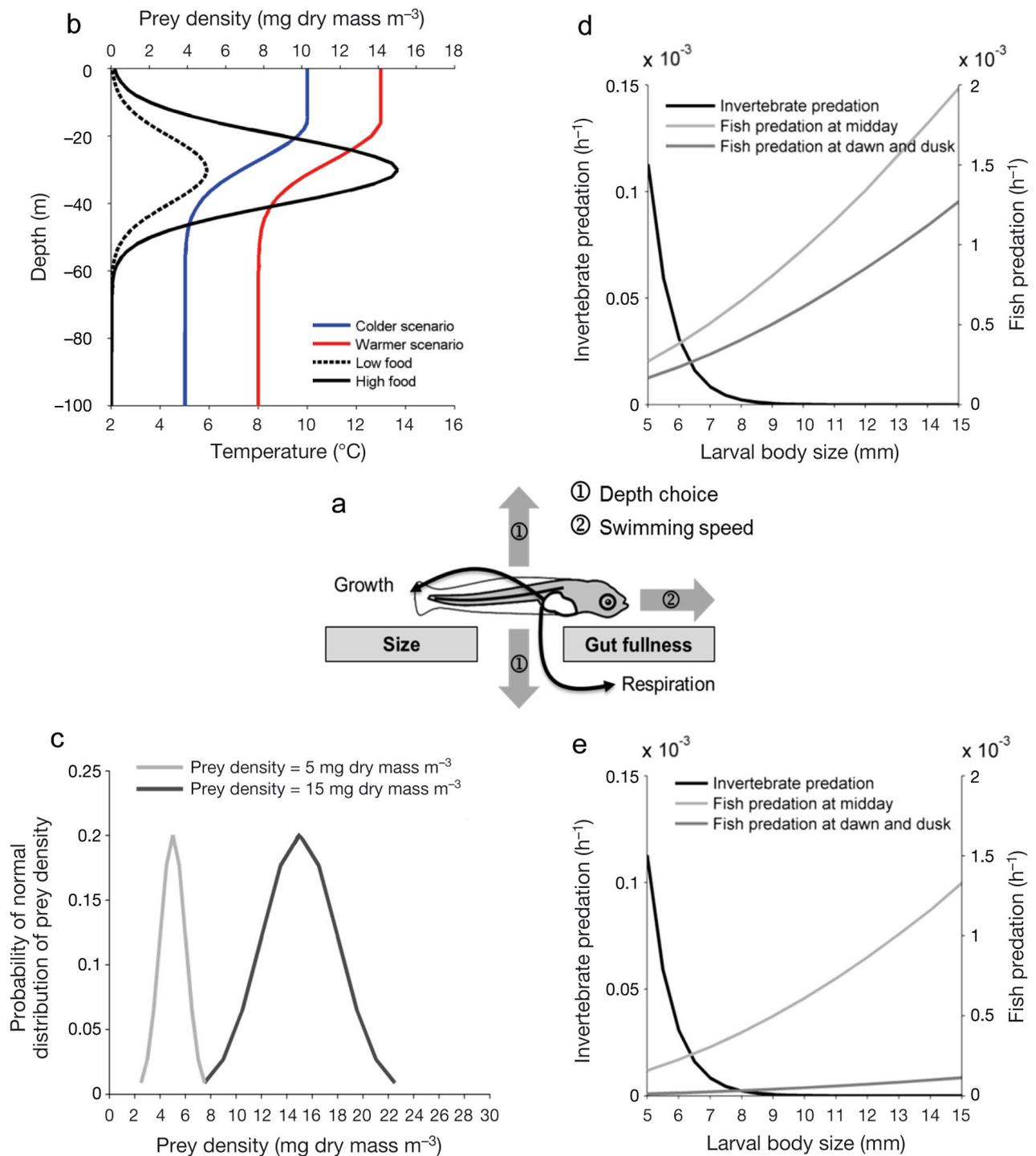


Fig. 1. (a) Schematic overview of our model approach, which includes larval fish behaviour (depth selection and swimming speed) and dynamic state variables (size and gut fullness). (b) The environment is vertically resolved with varying temperature and prey density; key scenarios are indicated. (c) Change in prey density every hour with a standard deviation of $2 \text{ mg dry mass m}^{-3}$. When the prey density value is equal to $5 \text{ mg dry mass m}^{-3}$ (low food scenario), the range is $2.5\text{--}7.5 \text{ mg dry mass m}^{-3}$ and when it is equal to $15 \text{ mg dry mass m}^{-3}$ (high food scenario), the range is $7.5\text{--}22.5 \text{ mg dry mass m}^{-3}$. (d,e) Change in rates of predation by invertebrates and fish with larval body size, time of day and depth position of (d) 20 m and (e) 40 m. Invertebrate predation rate declines rapidly with increasing larval fish size. Risk of predation by visual predators (fish) increases as larvae become larger. Due to light levels, depth position and time of the day, predation risk from fish is higher at midday than at dawn and dusk, and in shallow compared to deep habitats

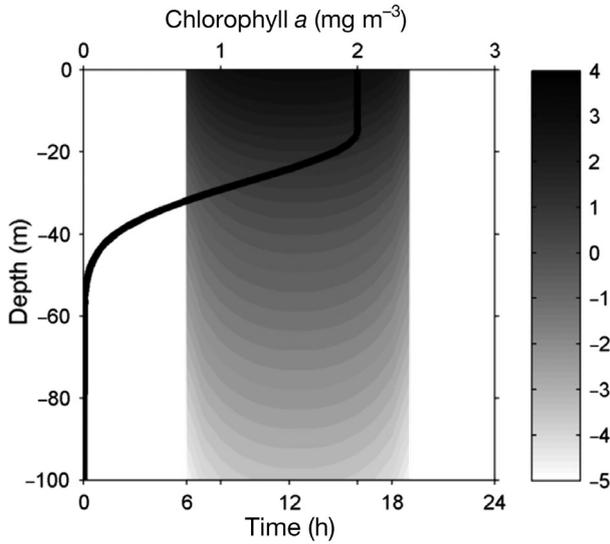


Fig. 2. Contour plot of light attenuation ($\mu\text{mol photons s}^{-1} \text{m}^{-2}$) with depth (\log_{10} scale). The line represents the vertical profile of chlorophyll a (mg m^{-3}) in the model, which affects light attenuation above the background absorption of seawater

ated backwards in time within each day (backward from $h_{\text{max}} = 24$ until $h = 0$) to find the fitness function (V) for all states. For each combination of the 3 states (body size l , gut fullness g , vertical position z) and for every time of day h , the model finds the behavioural strategies of new foraging activity a and depth z' that maximize expected survival until length l_{max} :

$$\max_{z', a} \left[\sum_E p(E) \cdot P(l, z', a, h | z, E) \cdot V(l', g', z', h+1) \right] \quad (2)$$

Here $p(E)$ is the probability of being in food environment E ; the prime sign indicates the new state value in the next time step, so l' , g' and z' are new states at time $h+1$ given E ; P is thus the probability of survival between h and $h+1$ and depends on size, starting depth and vertical migration distance ($z - z'$), activity and time of day. We repeated the iteration over a number of days, assuming that the initial fitness on a given day (d) is the same as at the end of the previous day: $V_{d+1}(l, g, z, 24) = V_d(l, g, z, 0)$. In effect, this assumes no constraints on growth rate.

If the gut runs empty, our model assumes the larvae will shrink, which in turn will have a survival cost because the lost weight has to be regained. The high predation rates typical of

fish larvae have a significant cost, but beyond this, starvation is not included as an explicit process. The state dynamics g' and l' are driven by bioenergetics as explained below in 'Growth and bioenergetics'.

For each day, the optimal behavioural strategies of new depth z'^* (l, g, z, h) and activity level a^* (l, g, z, h) were stored for each state combination (10 length categories, 11 gut states, 50 depth intervals and 24 time steps). We continuously compared the results between consecutive days. During the first diel cycles, the optimal depth selection and foraging activity matrix will change daily but the optimal strategies eventually converge and become independent of the initial terminal reward function and horizon time (Houston & McNamara 1999).

The 2 matrices of optimal depth selection z'^* and foraging activity a^* were stored and the model was then run forward in time to simulate the behaviour of several individuals from 5 to 15 mm body length.

Larval foraging processes

Larval foraging activity in this model is based on previous work by Fiksen & MacKenzie (2002) (for full details, please see Kristiansen et al. 2007, 2009, Fiksen & Jørgensen 2011). The feeding component of the model mechanistically simulates the encounter and capture of prey by larval cod. Encounter rates of larvae with their prey are functions of larval size, prey density and prey size. Encounters during each time step (1 h) were computed as the product of searched volume (light-dependent, in m^3) and prey density (depth-dependent, in prey m^{-3}) (Fig. 3a,b). Searched volume depends on larval swimming speed and prey detection distance. Swimming capability increases with the length of the larva and the actual swimming behaviour was determined by the optimal

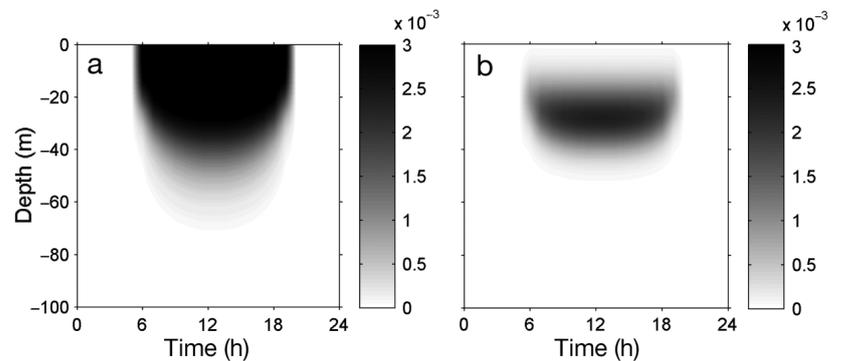


Fig. 3. Contour plots of (a) volume searched ($\text{m}^3 \text{h}^{-1}$) and (b) prey encountered (mg h^{-1}) by a larvae during 1 time step (1 h), shown for all depths and times of day. The difference is due to prey being distributed around a mean depth of 30 m

strategy. Prey detection distance, or visual range of the larvae, depends on larval and prey size, prey contrast and image area, light intensity and optical properties of the water (see Aksnes & Utne 1997, Huse & Fiksen 2010). A Holling disk foraging model is used to calculate the ingestion rate of encountered prey; assuming a capture probability of 0.2 and a prey handling time of 1 s required for the larvae to pursue, capture and consume the prey (Fiksen & MacKenzie 2002). Maximum ingestion is limited by gut capacity, with maximum energy content of the gut set to 6% of the total body mass in accordance with the upper limit of ingested material used by Lough et al. (2005).

Growth and bioenergetics

The details of the bioenergetics growth model have been described by Kristiansen et al. (2007, 2009). The model was parameterized with data from field and extensive laboratory rearing experiments on coastal larval cod carried out Otterlei et al. (1999) and Folkvord (2005). In short, gut fullness is dynamic and depends on ingestion and digestion of prey. Digestion supplies energy for metabolic costs (Finn et al. 2002), with any surplus used for growth up to a maximum growth potential, which increases with temperature and peaks at intermediate larval sizes (Folkvord 2005). This is used to find g' and l' in Eq. (2).

In the model, limited food availability will prevent the larvae from achieving their growth potential and temperature-dependent maximum. Within each time increment, the gut is filled as a result of feeding and food is assumed to be immediately available for digestive processes. If the food available for digestion does not sustain maximum growth and respiration costs, growth is reduced from the maximum rate and may become negative under low gut fullness. We assumed a constant assimilation efficiency (A) of 0.75 (Kjørboe 1989).

Predation mortality

The mechanistic representations of larval predation by fish and invertebrates have been described in detail by Fiksen & Jørgensen (2011). Predation by invertebrates is highest for the smallest larvae and decreases rapidly with increasing larval size (McGurk 1986, Bailey & Houde 1989) (Fig. 1d,e). The model distinguishes between cruising invertebrates, whose effectiveness is independent of light and lar-

val activity, and ambush predators that lie still and for which larval motion will affect encounter rates. Predation rates of visual predators, mainly fish, follow the same mechanistic relationships as encounters between larvae and their prey, and depend on perception distance of the piscivore predators, their swimming velocity and abundance, ambient light level and larval body size (Fiksen et al. 2002) (Fig. 1d,e). Visibility to fish predators increases with increasing larval size. However, the probability of being encountered and eaten can be modified behaviourally by descending to deeper and darker habitats (Fig. 1e). We assumed a constant fish density value of 10^{-5} (number of fish per m^3) in all model simulations.

Simulations

For each combination of temperature and prey density we first found the optimal behaviour for vertical migration and activity for all states, depths and time of the day. Thereafter, we simulated a population of 10000 individuals who follow the optimal strategy and vary in the stochastic feeding environment, starting from first-feeding larvae at a body length of 5 mm and continuing until they reach a size of 15 mm. During these simulations we recorded internal states (gut fullness and body size), habitat choice, behaviour and survival of each individual. Population-level patterns were quantified as mean and variance among the 10000 individuals according to the stochastic feeding environment. Our main objective is to explore how interactions between temperature and food availability may influence behaviour, growth, and survival of larval cod. We therefore present results for a 2-by-2 factorial design of low or high food (5 and 15 mg dry mass m^{-3}) combined with low or high temperature (5 versus 8°C) (Fig. 1a). The model is written in Fortran and the source code is available in the Supplement at www.int-res.com/articles/suppl/m529p199_supp/.

RESULTS

Growth and survival in relation to temperature and food availability

Larval growth generally increased with temperature (Fig. 4a) but showed almost no response to prey density. This was in contrast to survival, which increased with both temperature and prey density

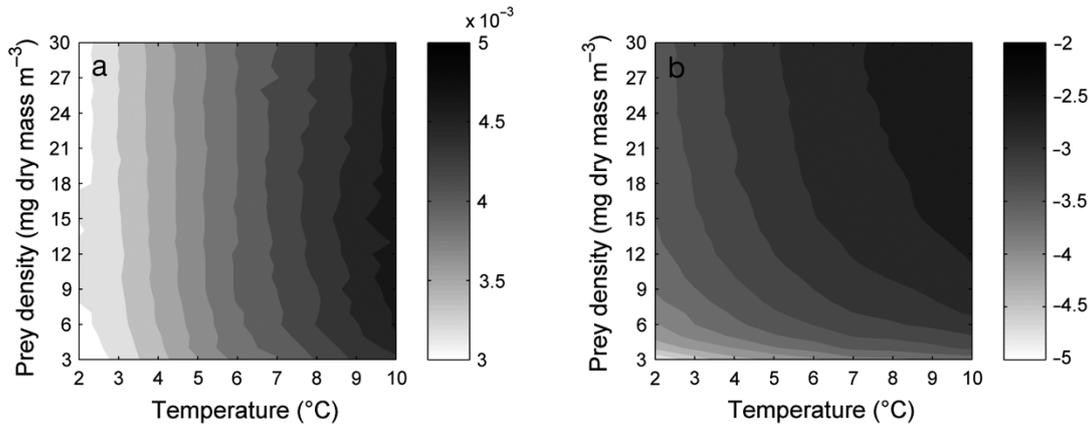


Fig. 4. Contour plots illustrating (a) mean growth rate (mm h^{-1}) and (b) probability of survival (\log_{10} scale) for 5 to 15 mm larval cod with all combinations of temperature and food availability. For growth rate (a), the contour lines are almost parallel to the y-axis. This implies that growth increases with temperature, while prey density only exerts marginal influence. For survival (b), the contour lines are neither parallel to the temperature axis nor to the prey density axis, indicating that higher temperatures and more food both contribute to higher survival. Exceptions are situations of high food abundance (above $15 \text{ mg dry mass m}^{-3}$), where the main effect is due to temperature, and very low food availabilities, which are unfavourable regardless of temperature

(Fig. 4b). The discrepancy between these 2 plots is due to behavioural compensation, by which larvae maintain high feeding rates to sustain temperature-dependent maximum growth even though it involves higher instantaneous rates of predation when food abundance is low. Evolutionarily, this can be selected for because it shortens the exposure to high predation rates that larvae experience. Thus, over the duration of larval development it may lower the overall risk of predation up to 15 mm, even though the instantaneous predation rate can be higher at any given size (Jørgensen et al. 2014).

Food availability had the most pronounced effect on survival when there was little food ($<6 \text{ mg dry}$

mass m^{-3}), and there was a moderate effect of food up to $\sim 15 \text{ mg dry mass m}^{-3}$. Above that, increased food still had a positive effect on survival but numerically the effect was not so strong (Fig. 4b). With high food availability, survival probability became more dependent on temperature, and prey density had a less significant influence on the survival of larval cod.

An interesting prediction from this model is that larva grew faster in warm water at both high and low food abundance (Fig. 5a), while survival was substantially higher in the cold high-food situation than in the warm low-food scenario (Fig. 5b). This happened despite the shorter stage duration at warm temperatures.

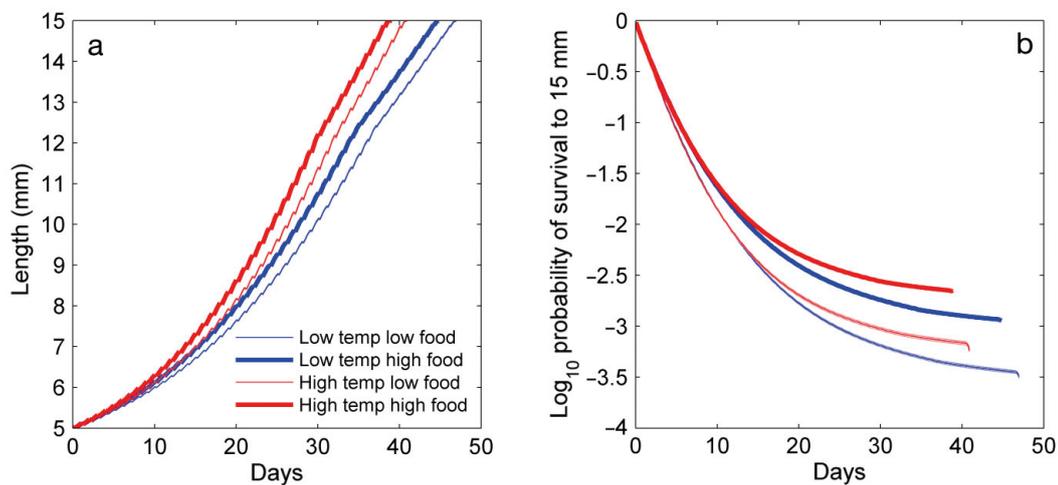


Fig. 5. (a) Growth and (b) probability of survival (\log_{10} scale) for 5 to 15 mm larval cod under different scenarios of low ($5\text{--}10^\circ\text{C}$) and high ($8\text{--}13^\circ\text{C}$) temperature with low ($5 \text{ mg dry mass m}^{-3}$) and high ($15 \text{ mg dry mass m}^{-3}$) food availability. Vertical profiles for temperature and food are shown in Fig. 1b

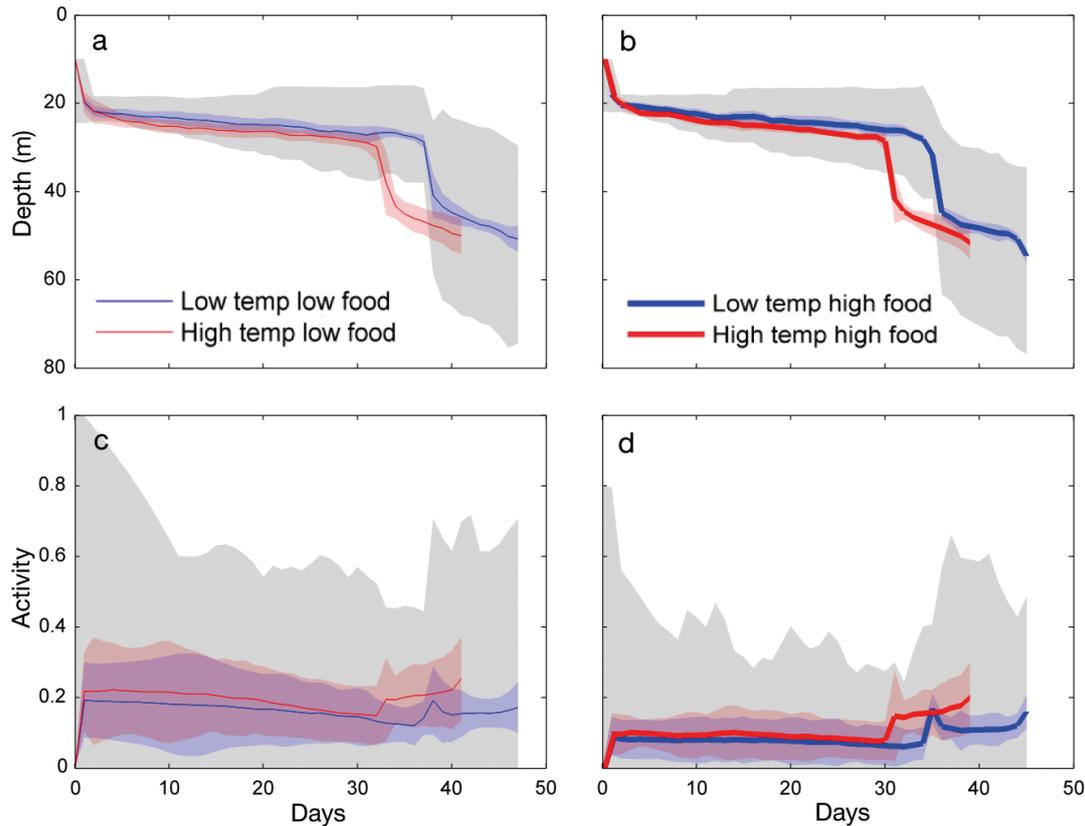


Fig. 6. Daily mean (a,b) depth selection and (c,d) swimming activity for a larva growing from 5 to 15 mm body length under different scenarios of temperature and food availability. Grey shading represents the minimum and maximum hourly depth distribution and swimming activity of larval cod in scenarios of low temperature (5–10°C). The lines denote population mean values and the red and blue shading shows the standard deviation range within the population due to food stochasticity. Left: larvae at low food abundance (5 mg dry mass m⁻³); right: larvae at high food abundance (15 mg dry mass m⁻³)

Behavioural ontogeny

Generally, the first-feeding larvae remained close to the surface in all scenarios (Fig. 6a,b). Small larvae stayed above the thermocline where it was warm and easy to find food until they reached 12 mm (ca. 30 d after hatching); their vertical migration was generally shallow and of low amplitude. As the larvae grew larger, their optimal diel vertical migrations became deeper and they searched more actively for food in warmer waters (Fig. 6c,d).

When larvae exposed to differences in food availability at the same temperatures were compared, low food larvae were more active, and variation between individuals within the population was larger (Fig. 6).

Behavioural trade-offs related to foraging activity

A more detailed examination of the diel patterns of depth selection, foraging activity, gut fullness, growth and predation illustrates how the optimal responses

varied with larval size and time of day, and between the different scenarios of temperature and food abundance (Figs. 7 & 8). Common for all scenarios was that small larvae (7 mm body length, Fig. 7) remained near the surface and were active during the day (Fig. 7). Due to their small size, they were not as vulnerable to visual predators and could remain closer to the surface while feeding. Small larvae had to be more active to fill their guts and sustain fast growth, which involved greater risk of predation from invertebrates. Survival was maximized by staying just above the mixed layer, where prey densities were high. Light enabled food encounters to become more frequent and warm temperatures favoured growth.

Larger larvae (13 mm body length, Fig. 8) were found deeper in all scenarios of temperature and food availability compared with their smaller counterparts. At dusk and dawn, larger individuals were found even deeper in warmer water (Fig. 8). During the day time, individuals descended to deeper and darker habitats at depths below 40 m to avoid visual predation. Large larvae had more extensive diel ver-

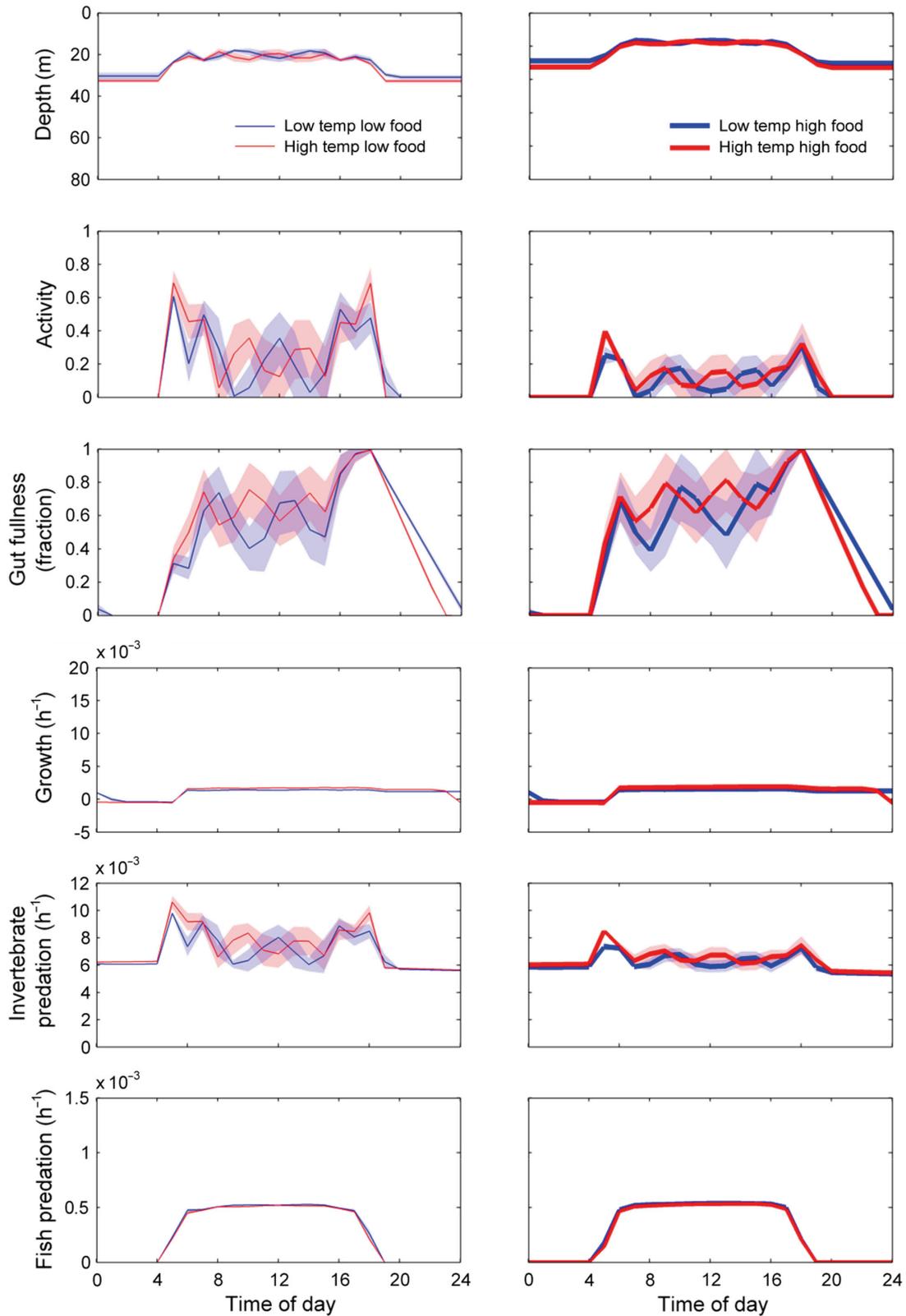


Fig. 7. Detailed depth selection, foraging activity, gut fullness, growth, and predation by invertebrates and fish for small larvae (7 mm) over a 24 h cycle. The lines denote population mean values and the red and blue shading shows the standard deviation range within the population due to food stochasticity. Left: larvae at low food abundance ($5 \text{ mg dry mass m}^{-3}$); right: larvae at high food abundance ($15 \text{ mg dry mass m}^{-3}$)

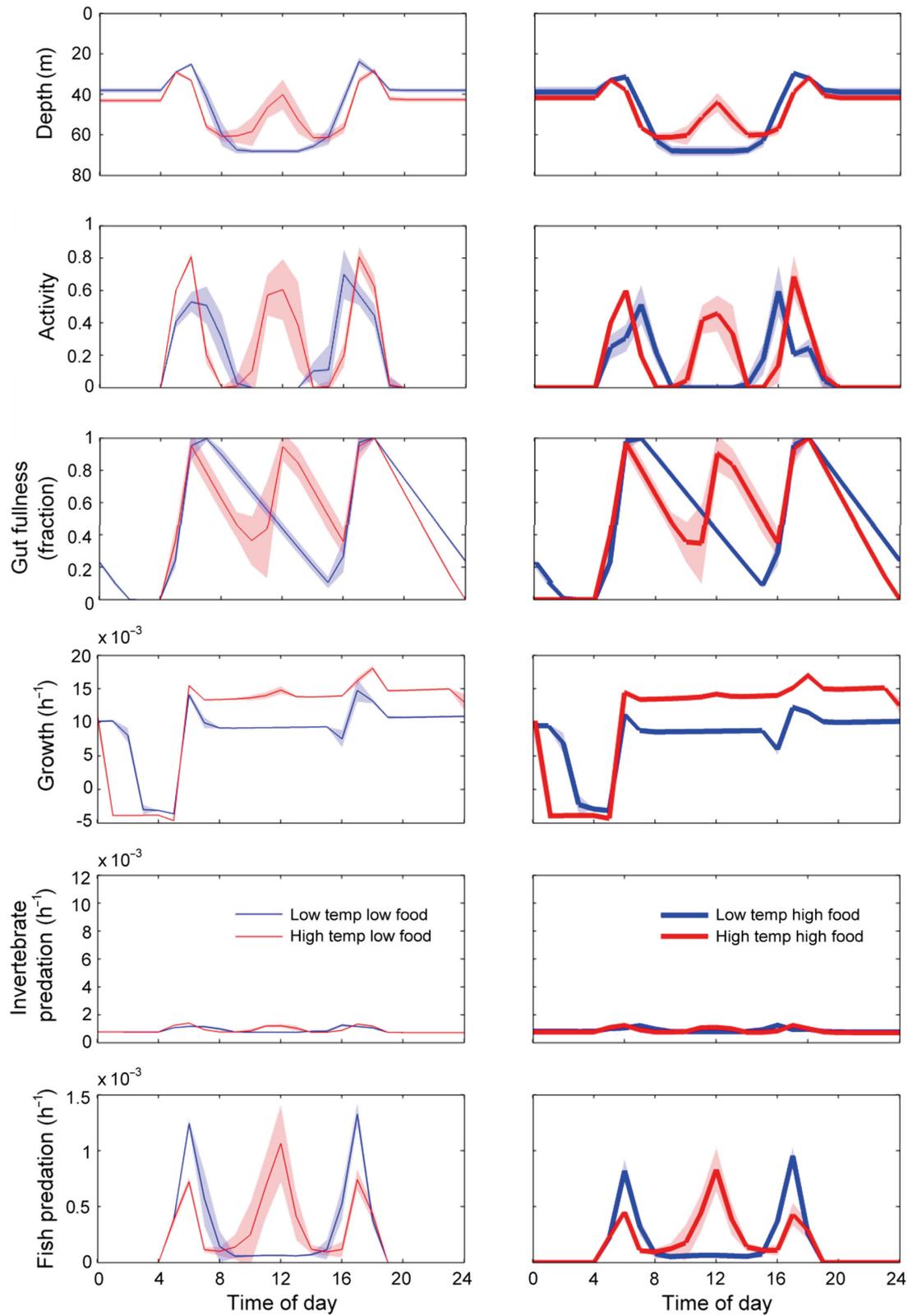


Fig. 8. Detailed depth selection, foraging activity, gut fullness, growth, and predation by invertebrates and fish for large larvae (13 mm) over a 24 h cycle. The lines denote population mean values and the red and blue shading show the standard deviation range within the population due to food stochasticity. Left: larvae at low food abundance ($5 \text{ mg dry mass m}^{-3}$); right: larvae at high food abundance ($15 \text{ mg dry mass m}^{-3}$)

tical migrations compared to small larvae. They were also more active at dusk and dawn, migrating up to the mixed layer at dusk to feed and speed-up growth in warmer waters and down to safer habitats at dawn to hide from fish predators. In all scenarios of temperature and food availability, predation rates from invertebrates were lower compared to small larvae, which were more susceptible to this type of predator (Fig. 7). Again, larvae were more active searching for food at low prey density, and their foraging activity levels increased under high temperatures. An extra trip to the surface around midday for a supplementary meal was made to secure a full gut in the evening and to maintain rapid growth, even though it involved higher risk from fish predators (Fig. 8).

DISCUSSION

The model showed that water temperature had a significant impact on larval growth and stage duration, but also that food availability exerted a comparatively strong effect on survival. Overall, larval cod grew more rapidly and need less time to reach 15 mm at higher temperatures. However, fast growth and short stage duration will not always enhance survival; it strongly depends on food availability. In particular, the model predicted that a combination of warmer water and reduced food availability may result in a higher metabolic rate. The consequent increased food requirement increased risk-taking behaviour, resulting in higher predation mortality and lower survival. Another way to describe this is that higher temperatures will enhance survival through shorter stage duration, but only if there is sufficient food to sustain high growth rates. The processes and mechanisms that affect larval survival and recruitment variability have been and still are a major focus in fishery research. Indeed, a variety of recruitment hypotheses have been proposed (Houde 2008). In particular, the 'growth-mortality' hypothesis (Anderson 1988) acknowledges that growth and survival processes are intricately linked in determining recruitment success, and underscore predation as the major source of mortality during early life stages. The 'growth-mortality' framework indicates that larger (Miller et al. 1988, Bailey & Houde 1989, Leggett & Deblois 1994), faster developing (Chambers & Leggett 1987, Houde 1987, 1997), and faster growing (Takasuka et al. 2003, 2004) individuals are less vulnerable to predation and more likely to survive. These hypotheses all relate in various ways to our model. In isolation, our model predicted that increasing temperatures lead to faster

growth, faster development, and shorter stage duration. According to the 'growth-mortality' hypothesis, this increase in growth rate translates directly into higher survival and thereby better recruitment. This concept is widely accepted in fisheries oceanography, with previous studies showing a link between recruitment of Atlantic cod and ocean temperatures, concluding that climate warming will lead to better recruitment in cold-water stocks (DeYoung & Rose 1993, Planque & Frédou 1999, Drinkwater 2005). Nonetheless, from our model results, including the role of food abundance and risk-sensitive foraging illustrated how the positive effect of temperature on survival becomes dependent on the availability of prey. This may appear to contradict observations of larvae growing at their maximum physiological rate regardless of food availability in the field (Folkvord 2005). However, increased survival in favourable food conditions can be mediated through behavioural responses, and the ability of larvae to make adjustments in vertical positioning and activity level to optimize feeding and predation risk (Fiksen & Jørgensen 2011, Jørgensen et al. 2014). Our results also support recent predictions (Kristiansen et al. 2014) of the effects of climate change on larval cod across different areas of the North Atlantic. Kristiansen et al. (2014) suggested that reduced food availability and increased temperatures under climate change will have a negative effect on larval survival throughout the range of cod in the North Atlantic. In their model, Kristiansen et al. (2014) assumed a starvation probability if the larva had less than 30% gut fullness. This caused higher starvation rates in their scenarios for ocean warming because guts were emptied at night, which occurred more frequently in warm water where digestion rates are higher. Our model predicted similar trends of reduced larval survival in a warmer ocean but only under reduced prey densities. The model did not consider a physiological starvation risk but only mortality from predation.

In ectotherms, metabolic demands rise with temperature, which consequentially requires increased food consumption to sustain basal metabolic processes (Buckley et al. 2004). This triggers more foraging activity, which increases predation rates and in turn allows for evolutionary selection towards shorter stage duration, and this chain of causation is supported by empirical evidence (Johnson & Belk 1999). Early life stages of fish are known to be sensitive to changes in temperature due to their developmental constraints and insufficient capacity for energy storage (Pörtner et al. 2006). Increased metabolic rates may force them to take more risks to feed and satisfy

their metabolic requirements (Killen et al. 2011). Earlier laboratory studies have also shown that, under limited food conditions, larval cod increase their swimming activity (Munk 1995) and are more likely to enter more risky areas inhabited by predators (Skajaa et al. 2003). Others have found some evidence of a trade-off between foraging and predator avoidance behaviour in juveniles of a marine damselfish, *Pomacentrus chrysurus* (Lienart et al. 2014). Consistent with our predictions, they suggested that under limited access to food, individuals were more susceptible to higher temperatures and may take greater risks under predation threats to satisfy their metabolic demands.

The choice of vertical migration strategy determines the larvae's exposure to light and therefore both feeding efficiency and predation risk from visual predators. Larvae descended to deeper water to hide in dark and safe habitats and only fed at dusk and dawn. Warmer waters increased metabolic demands, and the larvae required an extra trip to shallow waters to have a supplementary meal around midday (Fig. 8). Thus, high growth rates could be maintained through behavioural flexibility, but fast development and short stage duration could only be achieved by increasing food searching activity and risk-taking behaviours. Pearre (2003) reviewed the literature on vertical distribution of zooplankton in nature, with an emphasis on prey availability and their need to balance hunger and predator avoidance. Indeed, hungry individuals tended to migrate upward to near-surface waters even in daylight to feed and return to deep waters once satiated to hide from predators. This behaviour has been observed in zooplankton communities, using acoustic or vertically stratified net tow data as well as gut fullness of individuals in various depths. For instance, Pierson et al. (2013) found that the gut contents of marine copepods, *Calanus pacificus* and *Metridia pacifica*, in Dabob Bay were consistently higher in individuals migrating downward than in those migrating upward.

The degree to which Atlantic larval cod will be affected by climate change depends on how both temperature and food availability will change. The worst case scenario would be ocean warming in combination with large reductions of prey densities. This integrated effect of climate change would have negative effects on larval survival. If food availability is only mildly reduced, unchanged or even increased, then our model and our scenarios suggest positive effects for larval cod. Similar results have been found for adult North East-Arctic (NEA) cod by Holt & Jørgensen (2014). Assuming that the food availability in

the Barents Sea remains constant, these authors have suggested that global warming will have a positive effect on the NEA cod stock. Holt & Jørgensen (2014) developed a detailed state-dependent energy allocation model, which uses aerobic scope as a key constraint. They predicted that increasing temperature will lead to higher growth and fecundity rates but also to higher risk acceptance in foraging behaviour to achieve energetic requirements. Thus, adaptation to climate warming and meeting physiological needs may be achieved through a behaviourally mediated trade-off with survival.

Changes in growth and mortality rates may also be sensitive to local adaptations, for example, associated with depth positioning. Larvae can migrate between shallow and deep waters to adjust their feeding and predation risk, and also between areas, to choose a preferred thermal habitat (Perry et al. 2005). Biotic and abiotic environmental factors also vary widely across the different regions of the North Atlantic, so larval cod responses to changes in temperature and food availability might differ from one region to another. For instance, Beaugrand et al. (2003) suggested that increasing temperature since the mid-1980s in the North Sea has triggered changes in the plankton community. Reduced *C. finmarchicus*, an important prey of cod larvae, is proposed as the primary reason for the reduced survival and recruitment of cod in the North Sea. In contrast, the increase in phytoplankton and zooplankton production from resultant warm water inflow into the Barents Sea is seen as the reason why cod do well in this region (Drinkwater 2006, Dalpadado et al. 2012, Kjesbu et al. 2014).

Our approach has been largely qualitative, and was an attempt to clarify the mechanisms that link environmental variability to larval survival and recruitment success. Our study did not account for changes in prey species composition or quality, which may have implications for growth and survival of larval cod (Beaugrand et al. 2003, Heath & Lough 2007). Furthermore, in our simulations, we did not account explicitly for possible changes in abundance or depth distribution of predators, which in reality could change widely and may change the fitness landscape for larvae. Despite these shortcomings, the present study has highlighted how behaviour, growth and survival of larval cod may change under different scenarios of temperature and food availability. Overall, our model predicted that despite the positive influence of warmer water on larval growth and stage duration, food availability may strongly modify the effects temperature, with consequences for larval survival and therefore recruitment.

Acknowledgements. We thank D. L. Aksnes, J. Giske, S. Eliassen and R. E. Holt for valuable comments and discussions, 3 anonymous reviewers for constructive feedback, and the Nordic Centre for Research on Marine Ecosystems and Resources under Climate Change 'NorMER' for financial support.

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