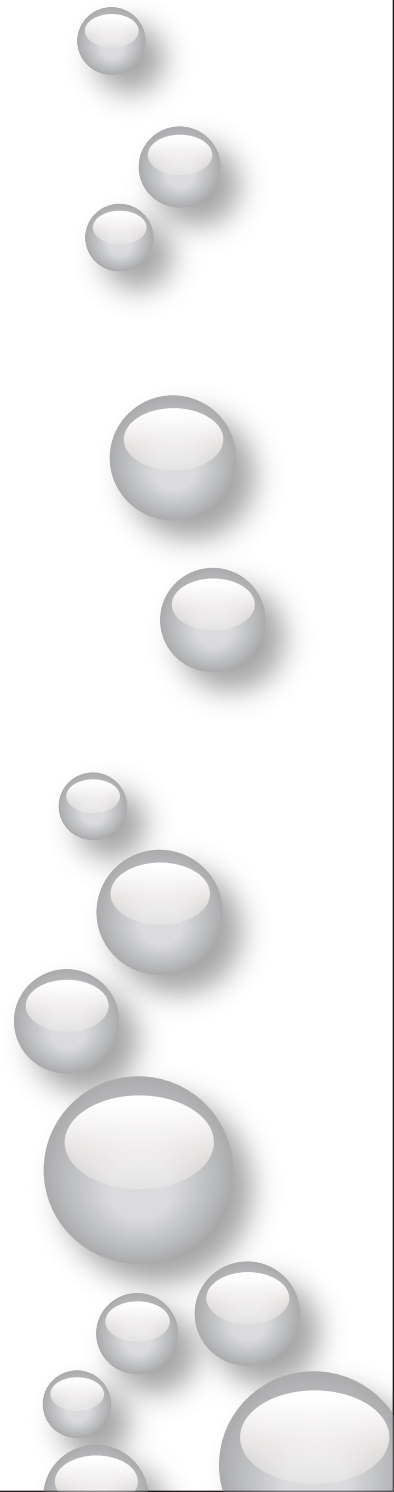


# Paper 5





# **Drift, growth and survival of larval Northeast Arctic cod with simple rules of behaviour**

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**Running title:** Adaptive depth selection in larval cod

**Abstract**

Northeast Arctic cod spawn at several locations along the Norwegian coast during March-April, with the Lofoten area as the major spawning ground. The offspring are subject to pelagic free drift from the spawning grounds to the nursery grounds in the Barents Sea, which are limited by the continental shelf edge and the polar front. Large inter-annual variations in the horizontal distribution of juveniles all the way through the early stages until settlement, with significant implications for growth and probability for survival, are highly affected by the circulation in the area. However, by vertical migration the larvae and juveniles are able to affect their drift route due to vertical variations in circulation. By allowing larvae and juveniles to choose depth according to an individual-specific risk sensitivity, we are able to investigate how this affect the resulting horizontal distribution, growth and survival. Locally, depth selection affects instantaneous mortality and growth rates, leading to higher survival through the larval period compared to larvae that were forced to stay in fixed depths. However, the strategy for depth selection also has long-term and large-scale consequences. First, since vertical behaviour interacts with ocean circulation, the strategy influences which drift trajectory a larva will follow and thereby the physical environment the larva experiences along its way. Second, the area or region where the larvae end up after the drift phase can have important consequences for later life stages.

Keywords: individual-based model, rule-based behaviour, larval fish, vertical migration, general circulation model.

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## Introduction

Marine larvae of many species have pelagic phases where they drift apparently haphazardly and arbitrarily through immense water masses. The swimming abilities of millimetre- to centimetre-sized larvae are often limited compared to ocean currents. Swimming abilities often increase throughout ontogeny (Clark et al. 2005), and may prove significant for drift if they are exerted in a non-random orientation (Leis et al. 2006). In this paper, we investigate the effects of displacements in the vertical, as vertical migrations can dramatically change the life of larvae in two important ways (Santos et al. 2006, Fiksen et al. in press). First, layered currents may bring vertically separated larvae in different directions and at different speeds. Ocean circulation models have shown that drifting particles fixed at depths only ten meters apart may end up in different oceans when spawned at times and sites typical for Northeast Arctic cod *Gadus morhua* (Vikebø et al. 2005). Second, light extinction down through the water column results in vertically distinct habitats, where the top layers have sufficient light for feeding but also for being detected by predators. Only a few tens of meters deeper, the darkness provides a safer refuge from visual predators but potentially too little light to feed. Additionally, a number of other important environmental variables such as prey density, turbulence and temperature also vary strongly in the vertical contributing to distinct vertical habitats.

Field observations suggest larvae perform diurnal vertical migrations (Ellertsen et al. 1984; Neilson and Perry 1990; Lough and Potter 1993). Several models of zooplankton and fish have interpreted such behaviour in relation to predator-prey interactions and reduction of mortality (Fiksen 1997; Strand et al. 2002; Fiksen et al. 2005). Here, we couple vertical migrations with an ocean circulation model, and evaluate the effects of vertical behaviour on ocean transport of the larvae.

The drift trajectories of eggs and larval fish depend on *i*) the time and place of spawning (Hinckley et al. 2001, Mullon et al. 2002, Huggett et al. 2003), and *ii*) the complex interaction between ocean circulation and individual behaviour throughout ontogeny (Hinckley et al. 1996, Werner et al. 1996, 2001, Hinrichsen et al. 2002, Fox

et al. 2006). In turn, this sets premises for individual growth and survival, and ultimately for recruitment to the stock and contribution to the future gene-pool.

Recent developments of ocean circulation models provide new tools for investigating how organisms are influenced by circulation patterns. However, existing individual-based models typically use fixed *ad hoc* formulations of larval depth positioning. Such imposed behaviours (*sensu* Grimm & Railsback 2005) are commonly justified from a set of observations of larval vertical distributions, and may also include observed responses to particular environmental cues such as light. The problems with this procedure are 1) that the *ad hoc* formulations are only valid for the environmental state at the time of observation – at other times there may be environmental cues that could modify or override the effect of the reference signal (Neilson & Perry 1990, Giske et al. 2003). Using observations to parameterize important flexible behaviours thus limits the prognostic value of the model when tested under new environmental conditions; and 2) the internal physiological condition of an individual typically feeds back on behavioural motivation, hunger and satiation may for example trigger different behaviours (Houston & McNamara 1999, Clark & Mangel 2000).

In addition, contemporary models of larval fish dispersal have only included individuals that vary in spatial position or physiological states. Individual differences or variability in behavioural strategies have so far been ignored (as noted by; Huse 2001, Strand et al. 2002). Behaviours such as habitat selection are adaptive traits, evolved under the constraints imposed by the physical and biological environment. A successful larva must grow, survive and end up in favourable nursery areas, and since their parents have succeeded, offspring that inherit their parents' behavioural strategies may also stand a fair chance of success (Fiksen et al. in press).

Vikebø et al. (2005) demonstrated that the vertical distribution of larval cod influenced their drift trajectory and temperature exposure, which in turn has significant implications for growth and survival. However, the model did not take active larval migrations or predation risk into consideration. In this paper we include these factors, and investigate interactive effects between behaviour and ocean

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circulation on growth, mortality, and dispersal of larval Northeast Arctic cod. We also indicate effects of spawning location by releasing larvae on two neighbouring spawning sites; one in an embayment and the other on the open shelf.

We test simple behavioural rules that use local information about growth and mortality in the water column. In the simplest version, a single parameter determines how risk sensitive the larvae are, and therefore how much they value growth and avoid mortality when they select a vertical habitat. Since currents change with depth, the vertical position has consequences for the drift trajectory the larvae follow. In this way, the behavioural strategy has both local effects on growth and mortality, as well as long-term and large-scale effects on dispersal and temperature along the drift route. Temperature will affect growth rates directly (physiological processes are faster in warmer water for the range observed in the model area). In turn this will have indirect consequences for mortality rates, since fast-growing larvae can grow through size windows where they are vulnerable to predation, and since their ability to move vertically and thereby manipulate predation rates by fish increases with size. We also explore a three-parameter version of this strategy, where the first two parameters represent risk sensitivity early and late in ontogeny, while the third parameter determines when to switch between the two behavioural strategies. Finally, we compare the two rules with non-responsive individuals (staying at a fixed depth). To assess the success of the rules, we use the accumulated mortality rate up to a given length. The rationale for this measure is that all individuals have to grow through the larval sizes to reach juvenile and adult life stages. From a life history perspective, the only reason to stop growth would be to start reproduction. We only model larval cod far below the earliest observed maturation size for this species. The success of a behavioural strategy in these early life stages can therefore be summarized as the probability with which it survives until a given size – for us limited to 18 mm as this is the maximum size where the physiological submodels remain valid.

The analysis illustrates how fitness can be improved by including adaptive habitat selection under realistic assumptions of local vertical gradients of growth and

predation risk, and the strong interaction with horizontal advection. It serves as an example of how behavioural ecology can provide methods to improve the predictive and explanatory power of individual-based models for larval fish, and provides a generic approach that may be used for fish larvae in general. Incorporating behaviour in particle-tracking ocean models represents a virtual laboratory that can prime our intuition and develop our understanding of processes and their relative importance throughout ontogeny. We are confident that this undertaking will provide hypotheses and direct future field and experimental studies. More specifically, the model also provides a set of robust behavioural rules for vertical migration of Northeast Arctic cod that can be implemented in coupled IBM and ocean models.

## **Methods and models**

### **The ocean model**

The numerical ocean model used in this study is the ROMS version 2.0 (Ezer et al., 2002; Shchepetkin and McWilliams, 2003; Shchepetkin and McWilliams, 2005, <http://marine.rutgers.edu/po/models/roms/>). The model setup is similar to Vikebø et al. (2005). Lateral boundary conditions are taken from a monthly mean climatology (Engedahl et al. 1998), while the mean daily vertical boundary conditions (air pressure, wind stress and heat flux) are taken from the NCEP/NCAR database (Kalnay et al. 1996) for the year 1985.

In Vikebø et al. (2005), the particle dispersion was run simultaneously ('online'), as a subroutine within the ocean model. However, the present exploration of behavioural strategies requires much more CPU time, and particle dispersion is therefore detached ('offline'). The Lagrangian particle-tracking model (LADIM; Ådlandsvik and Sundby, 1994) utilizes the time-dependent, daily mean current and hydrography fields from the ocean model. Multilinear interpolation provides necessary input for the dispersal of particles by use of a 4<sup>th</sup> order Runge Kutta advection scheme (Ramsden and Holloway, 1991).



The range of resolved eddies and velocity shear is proportional to the spatial resolution of the ocean model. Hence, with increasing spatial resolution the need for artificial diffusion is reduced. Ådlandsvik and Sundby (1994) used a spatial resolution of 20 km and included a random component for parameterizing a Fickian diffusion of  $100 \text{ m}^2\text{s}^{-1}$ . In the current model setup the horizontal resolution is ranging from 3.5 to 8 km moving from the upstream to the downstream boundary. We have therefore not included any artificial diffusion, though this will cause an underestimation of dispersal.

### **The individual-based model**

#### *Model organism*

The larvae are characterised by standard length  $L$  [mm], body mass  $w$  (dry weight) [mg], spatial coordinates  $(x, y, z)$ , and accrued probability of survival  $Ps$  since hatching. The attribute vector of individual  $i$  is thus:

$$A_i = (L_i, w_i, x_i, y_i, z_i, Ps_i, t) \quad 1$$

The attributes are updated by local growth, mortality and velocity field at each time increment  $t$  (one hour) of the model. Growth and mortality are driven by light, the modelled temperature-field and body size. Only horizontal velocities are considered for the advection of individuals.

It is essential for the model that growth and mortality rates emerge from habitat selection, which is specified by a behavioural rule. We used survival up to 18 mm length as fitness measure, since all individuals have to grow through this size to reach juvenile and adult life stages. We assume larvae can sense or assess growth opportunity and mortality risk in the upper 100 m water column, but they are not able

to make predictions for the future. All larvae were initialised at the same size (0.03 mg, 3.53 mm), and at a fixed depth (1 m). We released larvae at Moskenesgrunnen and in the Vestfjorden, two important spawning grounds in the Lofoten region, at times near the peak spawning period, covering 4x3 grid cells, or about 20x15 km (Fig 1). Initiating larvae with spatial variation within these cells introduce stochasticity in larval trajectories due to horizontal velocity shear.

## Submodels

**Growth:** Maximum specific growth rate  $G(w, T_z)$  is an empirical function of larval body mass  $w$  and ambient temperature  $T_z$  for larvae fed *ad libitum* and reared under laboratory conditions (Otterlei et al. 1999, Folkvord 2005). Larval cod have high growth rates, and substantial food intake is required to sustain these rates. Their visual foraging mode makes feeding highly dependent on ambient light  $I_z$  (Fiksen et al. 1998, Fiksen & MacKenzie 2002), and this may constrain growth. To include food-limited growth and additional energetic costs we add standard metabolic rate  $SMR(w, T_z)$  to the estimated growth potential, limit this by food-availability, and then subtract  $SMR$  (see Fiksen & Folkvord 1999). The standard metabolic rate of larval cod was estimated by Finn et al. (2002), and we have applied their estimate here. Additional energetic costs, such as swimming costs  $SC(w, dz)$  depending on body size  $w$  and migration distance per time  $dz$ , is subtracted from potential growth rate. The realised growth rate  $g_z$  [ $s^{-1}$ ] of a larva is thus a function of body mass  $w$ , depth  $z$  and swimming activity  $dz$ :

$$g_z(w, dz) = [G(w, T_z) + SMR(w, T_z)] \cdot (1 - e^{-10 \frac{I_z}{K_e + I_z}}) - SMR(w, T_z) - SC(w, dz) \quad 2$$

The parameter  $K_e$  (determining food limitation with light) was set to 1 as in Fiksen and MacKenzie (2002), and the coefficient 10 was chosen arbitrarily to limit growth rates at depths below  $\sim 50$  m, where zooplankton availability (prey densities and light) is normally low (we have not included prey explicitly here). Swimming costs  $SC(w,dz)$  are included as a maximum of 10% of SMR at a fixed temperature ( $7^\circ\text{C}$ ) if the larvae swim up or down at a velocity of  $1/3 L \text{ s}^{-1}$ , linearly decreasing with swimming speed or migration range ( $dz$ ). This means that specific swimming costs decrease slightly with body mass. Growth is represented more simplistically here compared to Kristiansen et al. (in press), because of the CPU-time required for the high number of particles.

**Predation:** Larval fish are subject to predation from both invertebrates and fish (Bailey & Houde 1989). Typically, vulnerability to invertebrate predators decreases with larval size as they outgrow abundant, smaller ambush and cruising zooplankton predators. On the other hand, the efficiency of piscivores is very sensitive to detection distance, which increases with light and larval size (Aksnes & Giske 1993, Aksnes & Utne 1997). Larvae may therefore become more vulnerable to fish predators with size, unless behavioural strategies such as vertical migration offset increases in encounter.

We model predation from fish and invertebrates separately, similar to Fiksen et al. (2002). Predation rate from invertebrates  $\mu_n$  [ $\text{h}^{-1}$ ] decreases with larval body length  $L$  [mm] as  $\mu_n = 0.01L^{-1.3}$ . Predation rate from fish is  $\mu_f = 0.05R^2$ , where  $R$  is the piscivore's sighting distance of a larvae depending on light and larval size, and the coefficient summarizes all factors such as e.g. fish density and escape probability (see Fiksen et al. 2002 for details). Total instantaneous mortality rate  $M_z = \mu_n + \mu_f$  is then a function of depth, surface irradiance and larval size. Little knowledge exists on how mortality risks are divided between invertebrates and fish for larvae, but this simple model captures some essential factors such as body size and light.

Light is a crucial factor for both growth and mortality rates. We model surface light as a function of latitude, day of year and time of day (Skartveit & Olseth 1988), and assume vertical light attenuation according to Lambert-Beers law with a diffuse attenuation coefficient of  $0.18 \text{ m}^{-1}$  and maximum surface irradiance of  $500 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

### Behavioural rules

Individuals follow a simple rule to select vertical position (Fiksen et al. in press.). We assume larvae have complete information about depth-dependent growth  $g_z$  and mortality  $m_z$  within the upper 100 m. The larva then decides on the next depth  $z_i^*(t)$  from:

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

where  $0 \leq \pi_i \leq 1$  is the behavioural strategy of individual  $i$  and  $\pi$  can be interpreted as the individual's risk sensitivity: low  $\pi_i$  characterises an individual always maximising instantaneous growth and high  $\pi_i$  an individual maximising instantaneous survival. Individuals with high  $\pi_i$  thus can be interpreted as being fearful and low  $\pi_i$  as being bold. The risk sensitivity of the individual thus colours its vertical behaviour, with major consequences for growth, mortality, and drift trajectory. The rule makes larval habitat selection sensitive to local environmental variability in growth and mortality rates, while the simple formulation of the strategy mimics the genetic predispositions of individuals and can be subject to natural selection over generations. We test two alternative ways of coding risk sensitivity  $\pi_i$ . The first (Rule 1) is simply a fixed genetic value  $\pi_i$  as described above. We tested the following values for  $\pi_i$ : 0, 0.01, 0.1, 0.25, 0.5, 0.75, 0.9, 0.98, 0.995, 0.997, 0.998, 0.999, 1. The second (Rule 2)

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includes two risk sensitivity parameters  $\pi 1_i$  and  $\pi 2_i$ ; one for early and one for the late part of ontogeny. A third parameter determines the size when the individual switches between the two risk sensitivities. This rule allows risk sensitivity to change ontogenetically. We tested combinations of parameter values with the same resolution of  $\pi 1_i$  and  $\pi 2_i$  as for Rule 1, and with the following values for the size at which risk sensitivity switches (in mm): 4, 6, 8, 10, 12, 14, 16, 18.

Fitness is then evaluated as the total survival probability from early larval phase to 18 mm. Within this range, all our empirical sub-models remain valid, and most larvae with positive growth will reach this size within the simulation time of 100 days (about the time it takes to reach metamorphosis).

## Results

First, we present some of the individual trajectories and dispersal of single individuals released at the same time and positions but differing in behavioural strategy. Then, we investigate emergent patterns by releasing a large number of particles with various strategies that differ in their risk sensitivities. Finally, we look at the fitness consequences that emerge from behavioural rules over the full range of possible values and with drift stochasticity resulting in variability among individuals.

### Individual trajectories and dispersal

The first numerical experiment tracked a few larvae with different risk sensitivities (Rule 1) released in Vestfjorden and at Moskenesgrunnen (see Fig. 1). The geographical dispersal trajectory of individual larvae (Fig. 2a, b) is determined by interactions between the risk sensitivity of their behaviour and ocean circulation. Larvae with low risk sensitivity ( $\pi_i = 0.01$ ) emphasise immediate growth, and tended to remain near the surface throughout the simulation period (Fig. 2c, d). The consequence of this behaviour is that they were captured by the warmer Atlantic currents (Fig. 1b), drifted towards the more central parts of the Barents Sea, and obtained high growth rates. Larvae with high risk sensitivity ( $\pi_i = 0.99$ ) went deep, grew slowly, and remained in the colder coastal current. Larvae with intermediate risk

sensitivity ( $\pi_i = 0.5$ ) tended to go deeper with time, and maybe surprisingly, decreased their range of diel migration (Fig. 2c, d). This was mainly driven by increasing day length, which influences predation risk during night, and the absence of food below 50 m, creating a narrow vertical window (30-40 m) where growth and mortality are acceptable. Larvae with intermediate risk sensitivity drifted in warm Atlantic Water (Fig. 2f) into the Barents Sea from Moskenesgrunnen, but in cold Coastal Water (Fig. 2e) when released in Vestfjorden. These different trajectories significantly affected their respective growth (Fig. 2g, h). The purely size-dependent mortality rate decreased rapidly as the larva grew, while mortality from visual predators increased due to larger size and longer days (Fig. 2i, j). This exemplifies the interaction between spawning strategy (parental decisions on timing and location of spawning) and larval behaviour. A robust larval strategy should therefore be one that functions well across the range of parental spawning strategies.

### **Emergent dispersal patterns from various risk sensitivities**

To further explore the effects of risk sensitivity (Rule 1) and spawning location, we released 50 individuals at each of 13 levels of risk sensitivity, simultaneously at the two locations. The individuals were released twice, three days before and three days after the time of peak spawning in Northeast Arctic cod, with minor spatial perturbations around the spawning grounds. The strategies covered a range of possible vertical habitats, illustrated for single individuals released at the two spawning grounds for each of the 13 levels of risk sensitivity (Fig. 3). Note that even with fixed risk sensitivity, the larvae tended to go deeper with time. The transition to deeper habitats was quite abrupt for risk-averse strategies, leading larvae below 50 m where there is no food and growth was negative. Remaining constantly at these depths lead to starvation, and such strategies consequently had low fitness. Although the general trend was to go deeper with time, this depended considerably on the growth potential in the water column. Some individuals encountered stratified water masses, which made growth sufficiently profitable near the surface to offset the increased risk associated with these habitats.

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The consequences of individual trajectories on large-scale dispersal became apparent when a large amount of individuals were released with the same risk sensitivity and at the same spawning ground (Fig. 4). First, even minor perturbations around any given release point lead to substantial spatial spread in particles after 100 days, despite the deterministic scheme of particle tracking. Second, particles originating from Moskenesgrunnen seemed to disperse more than those from Vestfjorden and tended to be more easterly distributed independent of risk sensitivity. Third, bolder, growth-maximizing individuals (low  $\pi_i$ ) tended to disperse more into the central parts of the Barents Sea from both spawning sites.

### **Fitness consequences of rules and spawning area**

At each level of risk sensitivity we tracked 50 individuals to 18 mm length, and assessed accrued probability of survival (fitness). These values are presented for the particle with maximum fitness at each level of risk sensitivity, the average of the 10% and 25% best, and the total average (Fig. 5a), for both spawning sites. This will indicate how robust the different behaviours are in a fitness perspective. Finally, this is compared to survival up to 18 mm of larvae remaining in fixed depths (Fig. 5b).

Larvae with intermediate risk sensitivity (0.5 – 0.75) had highest survival. They performed vertical behaviour, with diurnal migrations increasing towards an average depth between 30 to 50 m at late ontogeny (Fig 2c, d). Larvae with rule-based behavioural flexibility generally did better than larvae staying at fixed depths. Also, larvae from Moskenesgrunnen tended to do better than larvae from Vestfjorden in all these realisations, although less so for larvae staying at fixed depths. Note that larvae drifting at a fixed depth of 30 m achieved higher survival than larvae further up in the water column. Clearly, higher temperatures and enhanced feeding near the surface, which reduces the time needed to reach a length of 18 mm, did not compensate for the increased mortality. Larvae with a high level of risk sensitivity ( $>0.75$ ) had low (or negative) growth and were unable to reach 18 mm.

Finally, we estimated the fitness for larvae switching between two risk sensitivities at eight possible sizes (Rule 2). The maximum fitness at each risk sensitivity, the average of the 10% and 25% best, and the total average, for both spawning sites, is estimated as a function of early and late risk sensitivity (Fig. 6) for larvae switching behaviour at 6 and 16 mm (upper and lower panels respectively). For the sake of comparison with the larvae having a fixed behaviour through ontogeny, we released 50 larvae at each level of risk sensitivity (13x13x8). To assess the fitness, we extracted the 50 individuals with highest fitness ensuring that they have an optimal late (or early) behavioural strategy. Larvae changing their strategy ontogenetically did slightly better than those following Rule 1, for any size of switch. Larvae that changed their behaviour at an early ontogenetic stage emphasize growth ( $\pi_{1_i} = 0.25$ ) before shifting to a more risk-sensitive (fearful) behaviour ( $\pi_{2_i} = 0.75$ ) in order to maximize their fitness (Fig. 6a, b). However, the fitness is relatively flat across early risk sensitivity for larvae. A later switch favours more fearful strategies also during the early stage (Fig. 6c, d). The similarity between release-sites is encouraging, as it suggests that strategies may be quite robust across different spawning grounds.

## Discussion

An important topic for general population- and community ecology is to model organisms with flexible individual behaviour, motivated through individual states and environmental cues (Giske et al. 2003, Persson & De Roos 2003, Grimm & Railsback 2005). Here, we have explored two simple individual decision rules and their consequences for growth, mortality, and drift-trajectories of pelagic larval fish. The model experiments demonstrated that rules for larval vertical positioning have consequences on several scales. Locally, depth selection affects instantaneous mortality and growth rates, leading to higher survival through the larval period compared to larvae that were forced to stay in fixed depths. However, the strategy for depth selection also has long-term and large-scale consequences. First, since vertical behaviour interacts with ocean circulation, the strategy influences which drift



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trajectory a larva will follow and thereby the physical environment the larva experiences along its way. This means that the behavioural strategy, leading to a certain drift trajectory, has delayed effects for growth and survival since temperature and light conditions vary according to the particular route. Other factors, for example the spatial and vertical distribution of predators and prey, will influence growth and survival in similar ways but were not included in this model. Second, the area or region where the larvae end up after the drift phase can have important consequences for later life stages (Cowen et al. 2006). Not only does habitat type and climate vary geographically, but currents and distance can preclude the use of essential feeding and spawning sites later in life.

While the importance of vertical positioning has been realised in many coupled biophysical models (e.g. Hinckley et al. 1996, Werner et al. 1996, Fox et al. 2006), this is the first attempt to model larvae that select depths based on an inherent trade-off rule between growth and mortality in a general circulation model. This involves giving larvae an individual opportunity to respond to the processes affecting immediate growth and mortality, rather than imposing vertical distribution as an assumption of the model. We tested two simple rules, each with the full range of strategies from maximising immediate growth to maximising immediate survival, and compared these to non-responsive individuals drifting in fixed depths. Both rules gave better fitness than for fixed behaviour, where larvae remained constantly at fixed depths. Both spawning grounds favoured active vertical migration and intermediate risk sensitivity seemed to be optimal under the assumptions given here. However, it appears that Rule 2 only slightly improved fitness compared to the simpler Rule 1, where larvae use the same risk sensitivity throughout. Larvae that emphasized growth before changing to intermediate risk sensitivity at an early ontogenetic stage were the most successful ones.

Both growth and mortality depend on complex processes that link the physical environment and the distribution of predators and prey with behaviour and internal physiology. These processes must necessarily be simplified in models, and our results

are likely to be sensitive to a number of parameters used in the different submodels. Especially, the benefit of behaviour is tightly linked to how mortality is modelled. Behaviour influences light exposure and therefore encounter rates with visual predators, but does not affect predation from invertebrates, which we have modelled as a purely size-dependent mortality that is high for small larvae and declining with size (McGurk 1986). Predation from invertebrates and fish are comparable at a larval length of about 9 mm, and above this length fish predation dominates. That fish predation plays a major role is supported by the strong indications that pelagic fish are regulating recruitment success of cod (Köster & Möllmann 2000, Swain & Sinclair 2000). Both herring and capelin are abundant in the drift routes of Northeast Arctic cod and are known to forage on cod larvae.

The purely size-determined mortality rate in our model is lower than in the empirical model compiled by McGurk (1986) for larvae <13 mm and slightly higher for larger larvae. Sundby et al. (1989) estimated the average daily mortality rate to about 0.2, which is about four times higher than the mortality rate applied here (and thus also four times higher than the mortality rate from McGurk (1986) for 13 mm larvae). However, survival probabilities from hatching to 15 mm on the order of  $10^{-2}$ , is probably too high given that the mean annual egg production is around 1-2 million eggs per female (Kjesbu et al. 1996). The motivation for vertical behaviour is largely determined by the strength of predation from invertebrates relative to predation from fish. Increasing the invertebrate predation rate ( $\mu_n$ ) would make fish predation, the only depth-dependent component of mortality, less important. Larvae that grow faster would have higher survival probabilities, increasing the reward on rapid growth. Simulations (not shown here) indicate that the optimal  $\pi_i$  is then shifted to the left (from  $\pi_i = 0.5-0.75$  to  $0.25-0.5$ ) favouring larvae with a shallower vertical distribution and with average depths between 20 – 40 m in late ontogeny. Drifting at a fixed shallow depth will then result in a comparable fitness to individuals with active vertical migration, because exposure to higher mortality rates during early ontogeny in order to shorten this vulnerable stage becomes a good strategy. However, very little

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is known about the distribution of risk among visual and non-visual predators, and only more process-oriented field studies can improve our knowledge on this.

We have assumed that growth is a function of temperature and light, ignoring both spatial and temporal variability in prey distribution. The main prey items for larval cod are nauplii and copepodite stages of *Calanus finmarchicus*, and the production and abundance of these in turn depend on factors such as female abundance and primary productivity. These prey are also known to perform diel vertical migration; differences in vertical distribution between day and night of up to 20 m have been observed (Tilseth & Ellertsen 1984). Future refinements of the present analysis will be to include zooplankton models or assimilate data on prey abundance and distribution.

In this study we initialised larvae at hatching although Northeast Arctic cod has an egg stage lasting up to 3 weeks. The transport of eggs is purely a function of egg density and ocean physics (Sundby 1997). The actual density of the eggs, including the chorion membrane and the amount of yolk and buoyant fat, may have evolved as a trade-off between predation risk and advection consequences of vertical positioning due to density gradients. Incorporating drifting eggs explicitly would perhaps change the initial dispersal of eggs and could therefore precondition initial larval distribution differently than what is presented here.

Another complicating factor we have ignored is the fitness-consequences of drifting off to unfavourable settling habitats (Fiksen et al. in press). Although little is known about what determines the quality of settling areas, it might be possible to combine spatial data from 0-group surveys (Dingsør 2005) with data on later stages from winter cruises to derive information about how fitness depends on geographical position at settling (Dingsør 2006).

Observations on vertical migration by cod larvae and the corresponding distribution patterns are limited, but those described in literature indicate that diel migration is a dominant feature, depending on larval size and the general ocean conditions

(Ellertsen et al. 1984; Neilson and Perry 1990; Lough and Potter 1993). Lough and Potter (1993) reported that Atlantic cod larvae on Georges Bank of size >6-8 mm were capable of regulating their depth as long as vertical mixing was low. The ability to control their depth and the extent of diel migration increased with larval size, while the mean daily depth increased throughout ontogeny until they settled close to the seabed. Similarly, Ellertsen et al. (1984) observed diel migrations in first-feeding Northeast Arctic cod larvae. The larvae concentrated between 5-10 m during night and spread out between 5-35 m during day. The strong interaction between vertical positioning and horizontal ocean transport documented in this study suggests that further field observations of vertical distribution and its change with ontogeny should be a priority of future surveys. If possible, parallel recordings of other individual characteristics in the field, such as stomach fullness, swimming direction and speed, and activity level, could also guide firstly the further development of models coupling behaviour with oceanography, and subsequently our understanding of the ecology of early life stages.

The current analysis must be viewed as an initial exploration and an example of how simple behavioural rules can be used in combination with ocean models to study the interaction between local and strategic trade-offs in larval fish behaviour. We have only looked at two potential spawning grounds, and strategies may be very different when drift trajectories from further spawning grounds are included. A complete analysis of behavioural strategies would therefore need to take the whole geographical spawning range into account. To evaluate the success of a strategy, one should also assess parental spawning strategies including migration costs, and repeat the analysis with physical forcing for several years to investigate environmental effects. More specifically, our next steps will be to adjust the model domain in order to include all spawning grounds, put inter-annual variations on the lateral boundaries, and include vertical distribution of eggs (Thygesen and Ådlandsvik, in press).

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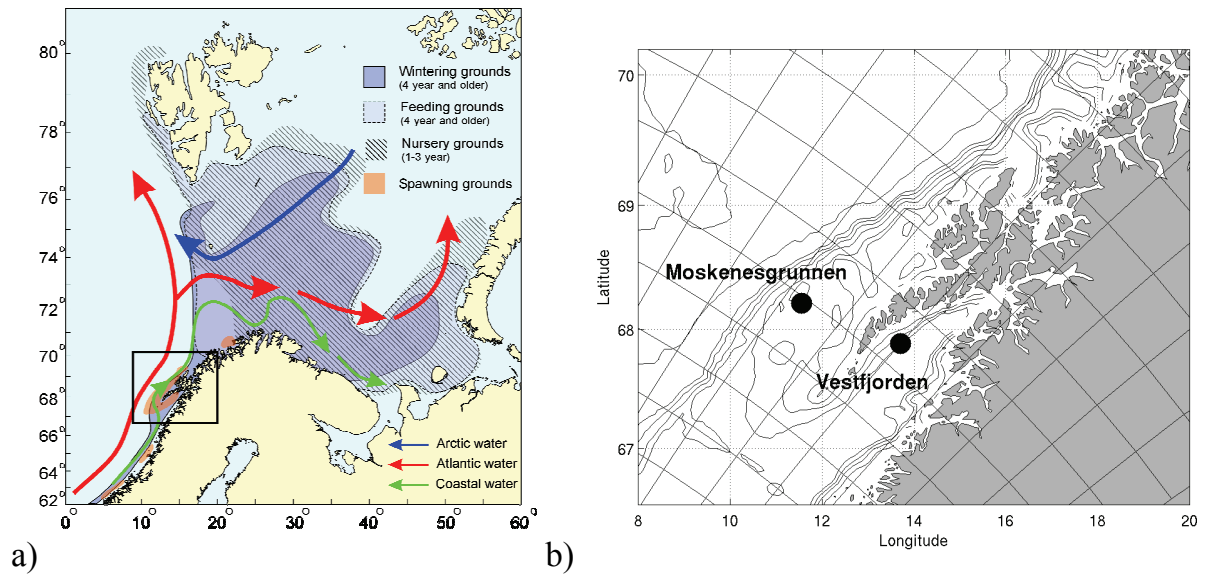
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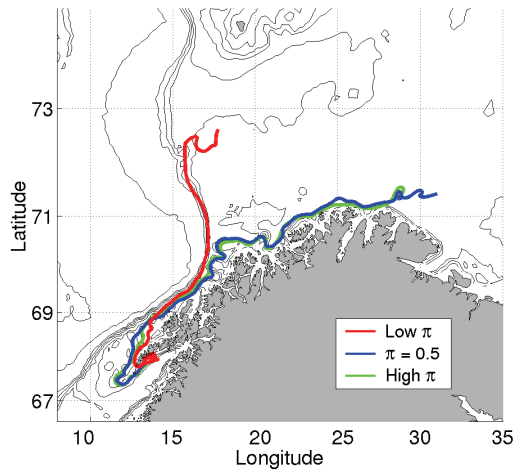
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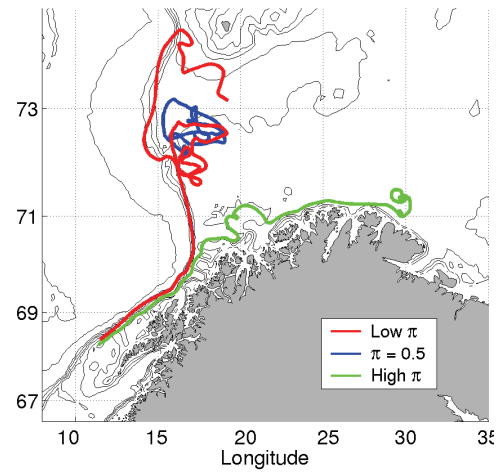
**Figure 1** (a) Spawning and nursery grounds of Northeast Arctic cod in relation to different water masses. (b) The two spawning grounds included in this study.

## Vestfjorden

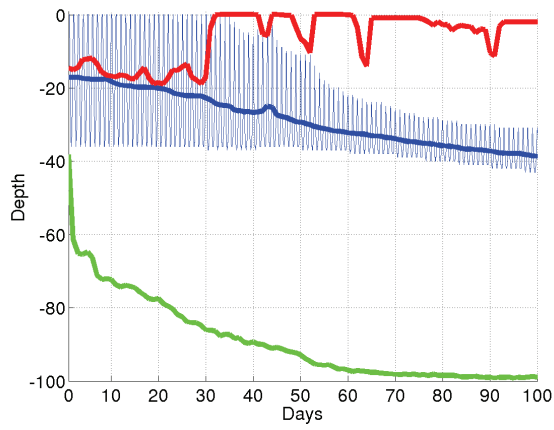


a)

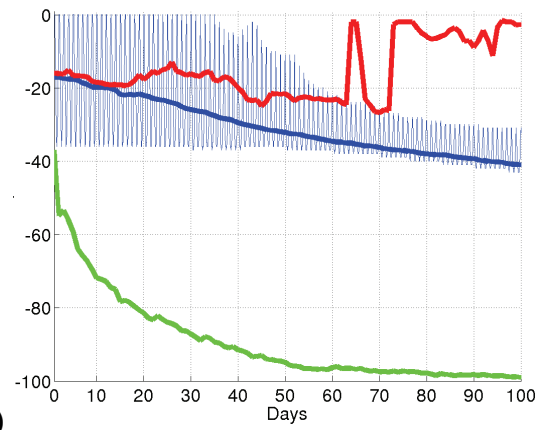
## Moskenesgrunnen



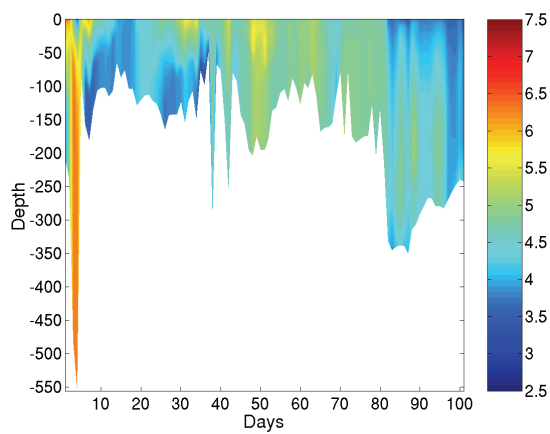
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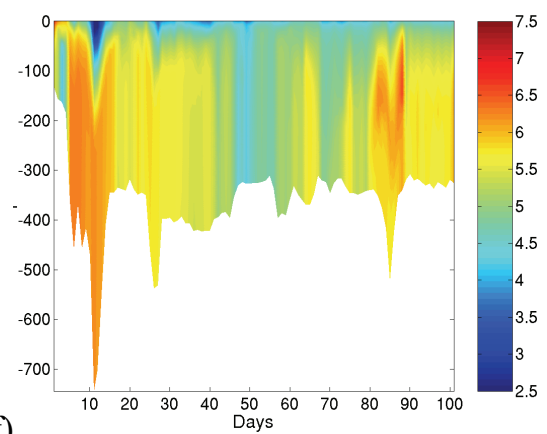
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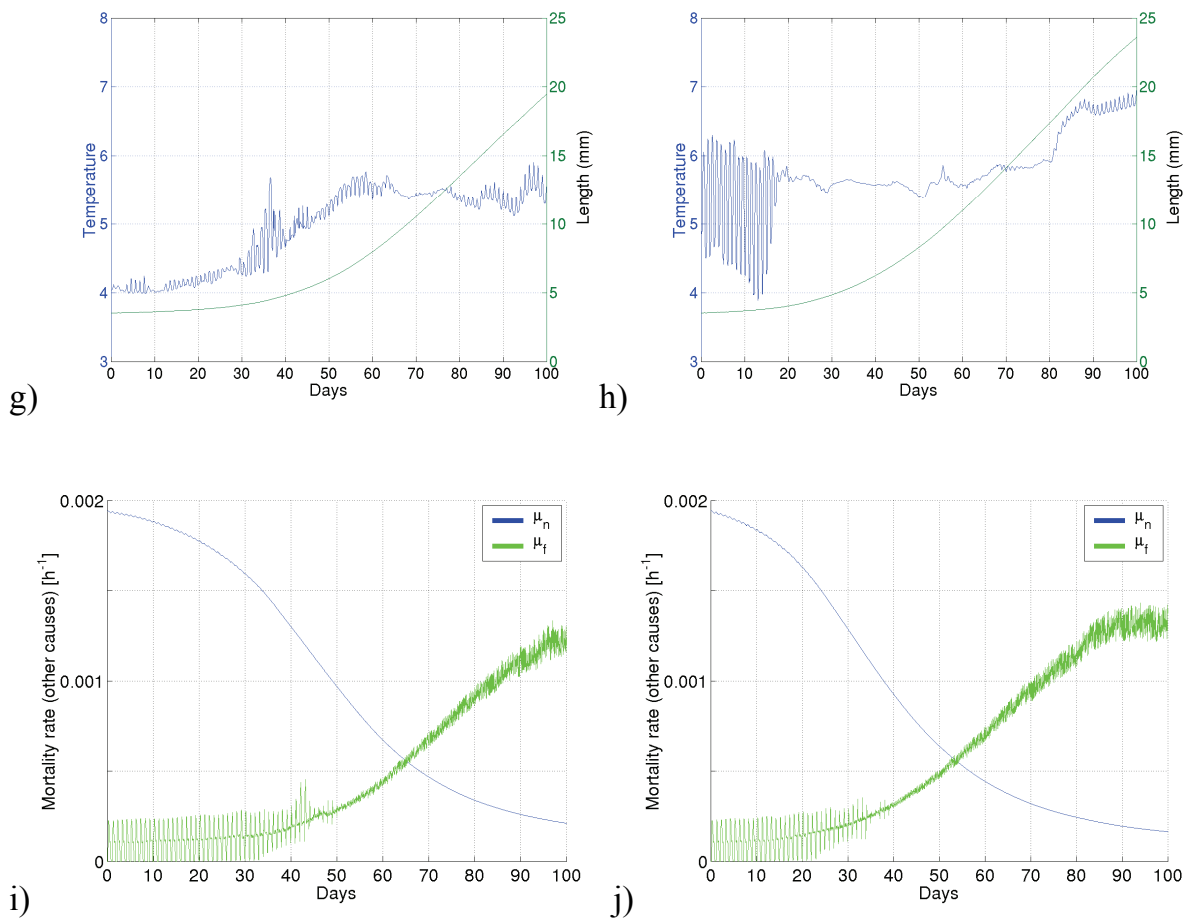
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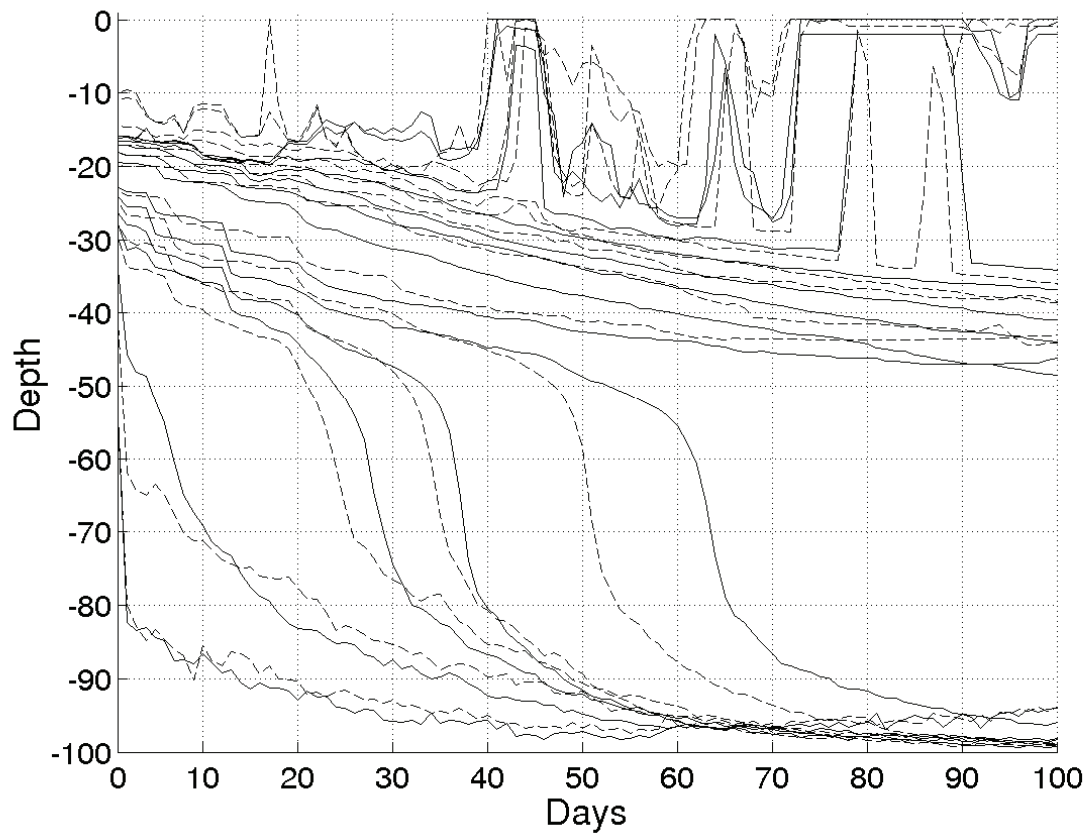
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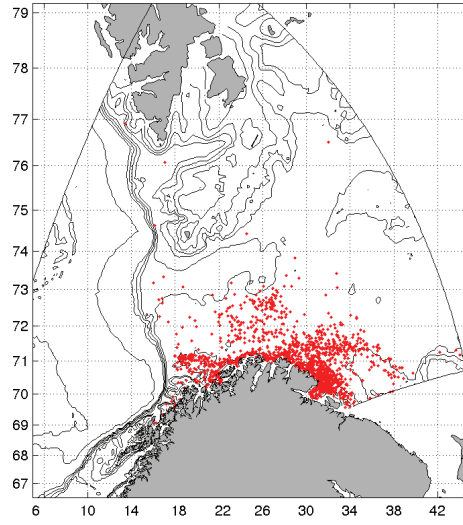
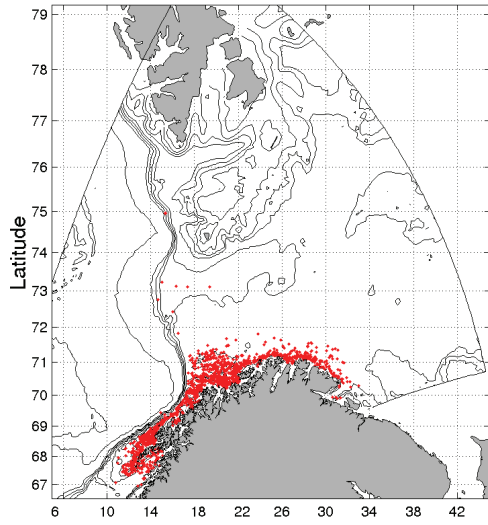
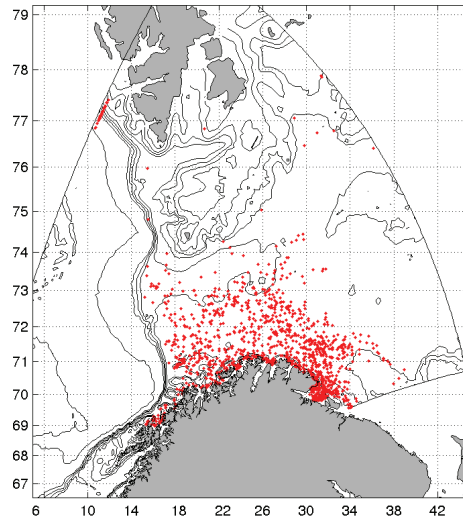
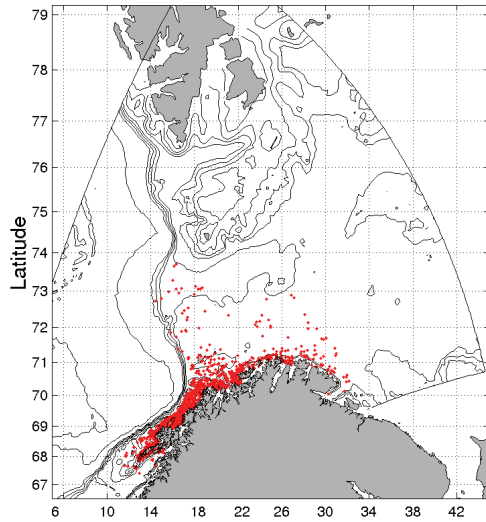
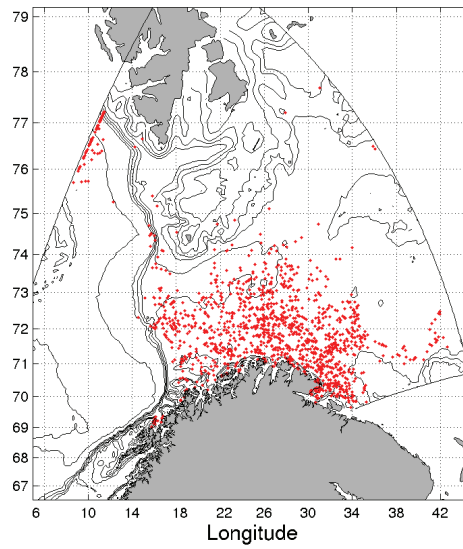
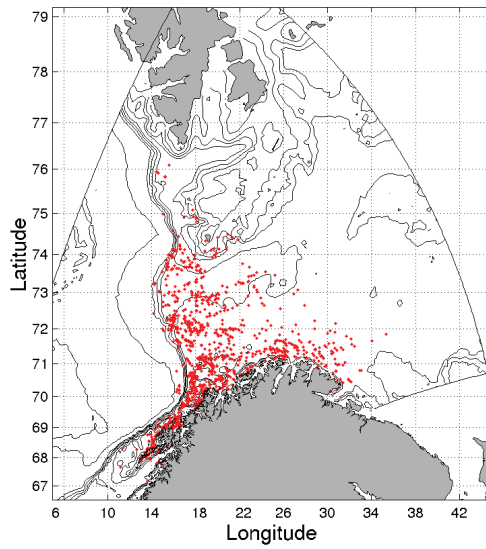
**Figure 2** An illustration of (a, b) dispersal, (c, d) daily mean depth, and (e, f) temperature profiles along the drift-trajectory of larvae released in Vestfjorden (left panels) and at Moskenesgrunnen (right panels). Dispersal and mean daily vertical depth for single individuals using Rule 1 for three strategies of risk sensitivity are included ( $\pi_i = \{0.01, 0.5, 0.99\}$ ). Depth is shown with hourly resolution for  $\pi_i = 0.5$  (to illustrate diel migration patterns), but only mean daily depth for  $\pi_i = 0.01$  and 0.99. Fearful larvae (high  $\pi_i$ ) give immediate survival high priority, migrate deeper, and drift closer to the coast. Also included are hourly ambient temperature (g, h), growth history (g, h) and mortality rates (i, j) from fish ( $\mu_f$ ) and invertebrates ( $\mu_n$ ). Temperature and growth histories are influenced by the vertical temperature profile at any point along the drift trajectory, the risk sensitivity of the strategy, and all elements of the light-environment and predation risk.



**Figure 3** Mean daily vertical positioning for single larvae released at the same time and place in Vestfjorden (broken lines) and Moskenesgrunnen (solid lines) for 13 values of  $\pi_i$  (0, 0.01, 0.1, 0.25, 0.5, 0.75, 0.9, 0.98, 0.995, 0.997, 0.998, 0.999, 1). Increasing risk sensitivity ( $\pi_i$ -value) takes larvae deeper and in addition they go deeper with time due to increasing size (risk from visual predators) and longer days.

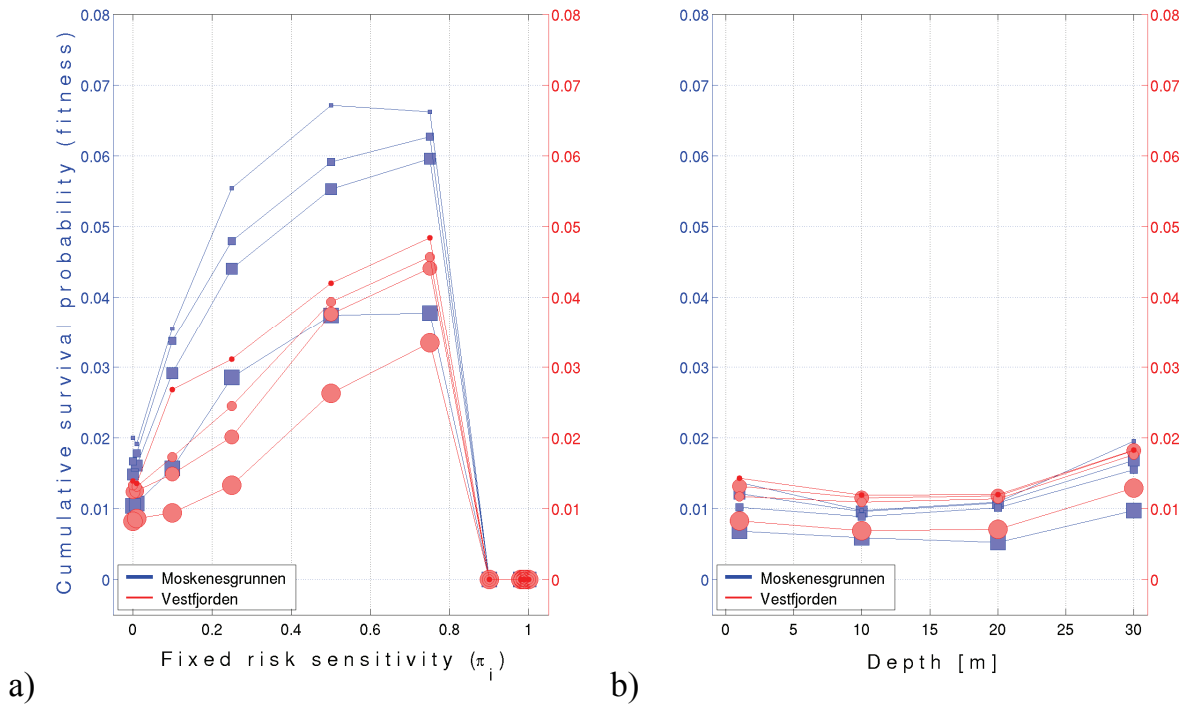
## Vestfjorden

## Moskenesgrunnen

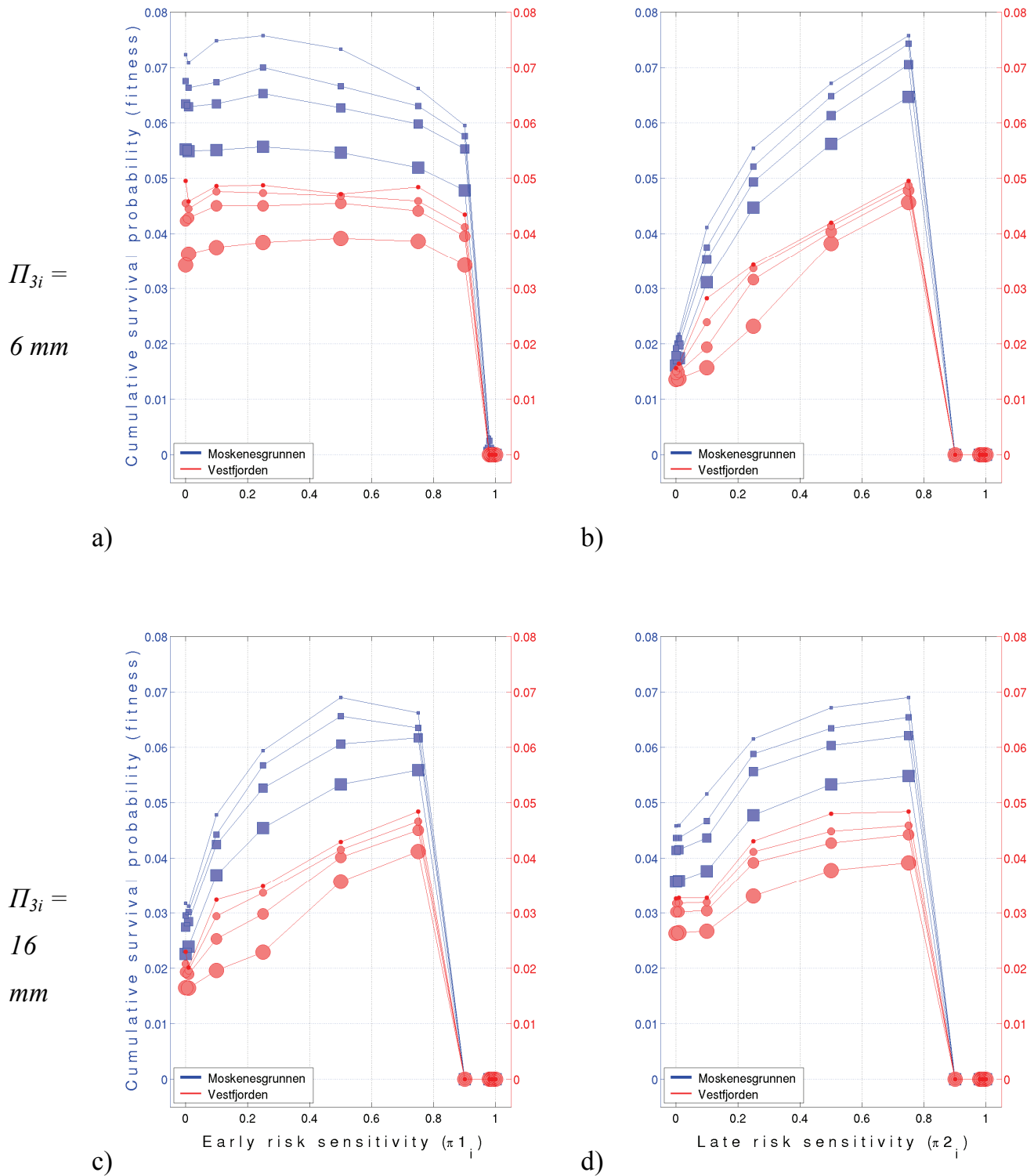
 $\pi_i = 1$  $\pi_i = 0.5$  $\beta_i = 0$ 



**Figure 4** This figure illustrates dispersal-effects of larval risk sensitivity. Each point represent the position of one larva after 100 days of drift from Vestfjorden (left panels) and Moskenesgrunnen (right panels) for  $\pi_i$  equal 1 (risk averse, upper panels), 0.5 (median risk-sensitivity, middle panels) and 0 (lower panels). For each level of risk sensitivity 50 individuals were released at the same time and place, with variability in drift paths introduced by minor spatial and temporal perturbations at the release point.



**Figure 5** Comparison of fitness consequences for larvae drifting from two spawning locations with various attitudes to risk using Rule 1 (a) and staying at fixed depths (b). Larvae from Moskenesgrunnen are indicated by blue squares and from Vestfjorden by red circles. There are four curves for each of the spawning grounds indicating the single most successful larvae, the top 10%, 25% and the average over all larvae (indicated by increasing size in circles and squares). Fitness is measured as accumulated survival probability of larvae when they reach the length of 18 mm.



**Figure 6** Comparison of fitness consequences of strategies that vary in risk sensitivity using Rule 2. Results are shown for two spawning locations (Moskenesgrunnen by blue squares and Vestfjorden by red circles). The panels show fitness consequences of changing strategy at 6 mm (a, b) and 16 mm (c, d); left panels are early risk sensitivity and right panels late risk sensitivity. Fitness is measured as accumulated survival probability of larvae at the length of 18 mm.