Vertical migration in adult Atlantic cod (*Gadus morhua*)

Espen Strand and Geir Huse

Abstract: We investigate the trade-offs associated with vertical migration and swimming speed of Atlantic cod (*Gadus morhua*) using an adaptive individual-based model. Simulations with varying distribution and occurrence of prey, with and without swimbladder constraints, and visual predation were performed. Most simulations resulted in cod migrations between the bottom and pelagic zones. In simulations with high probability of encountering pelagic prey, the cod spent the daytime in the pelagic zone, moving to the bottom to feed only when no pelagic prey were encountered. At night the cod stayed in the pelagic zone to attain neutral buoyancy. In simulations with low occurrence of pelagic prey or high visual predation pressure, the cod remained at the bottom feeding on the consistently present benthic prey. If the pelagic prey occurred far above the sea floor or there were no benthic prey, the cod abandoned all bottom contact. The study thus predicts that the probability of encountering energy-rich pelagic prey is the key factor in driving vertical migration in adult cod. Buoyancy regulation is further shown to be an important constraint on vertical migration.

Résumé : Nous examinons les compromis associés à la migration verticale et la vitesse de nage chez la morue franche (*Gadus morhua*) à l'aide d'un modèle adaptatif basé sur l'individu. Nous avons procédé à des simulations comprenant des répartitions et des présences variables des proies, avec et sans contraintes sur la vessie natatoire et une prédation visuelle. Le résultat de la plupart des simulations comprend une migration des morues entre le fond et la zone pélagique. Dans les simulations avec une forte probabilité de rencontre de proies pélagiques, les morues passent la journée dans la zone pélagique et se déplacent vers le fond pour se nourrir seulement s'il ne trouvent pas de proies pélagiques. La nuit, les morues demeurent dans la zone pélagique pour maintenir une flottabilité neutre. Dans les simulations avec une faible présence de proies pélagiques ou avec une forte pression de prédation visuelle, les morues restent sur le fond à se nourrir des proies benthiques qui sont toujours présentes. Si les proies pélagiques se trouvent loin du fond de la mer ou s'il n'y a pas de proies benthiques, les morues abandonnent tout contact avec le fond. Notre étude permet donc de prédire que la probabilité de rencontrer des proies pélagiques riches en énergie est le facteur essentiel qui régit la migration verticale chez les morues adultes. Elle montre aussi que le contrôle de la flottabilité constitue une contrainte importante pour la migration verticale.

[Traduit par la Rédaction]

Introduction

Although the forces governing vertical migration in small fishes are relatively well known (e.g., Clark and Levy 1988; Giske and Aksnes 1992; Rosland and Giske 1994), the trade-offs associated with vertical positioning in larger fishes are less well understood. Fish exposed to predation from visually foraging predators tend to trade good foraging opportunities against increased survival probability by descending into darker water masses during daylight hours (Iwasa 1982; Clark and Levy 1988; Giske et al. 1994). Atlantic cod (*Gadus morhua*) larger than about 70 cm generally have few predators (Pálsson 1994) and much of their observed vertical movements is therefore unlikely to be motivated by predation risk. Adult cod are often considered to be demersal, but observations have shown that they can spend a considerable amount of time in the pelagic zone (e.g., Beamish 1966;

Rose 1993; Arnold et al. 1994). Tagging experiments have further revealed that adult cod can display both "chaotic" vertical distribution patterns and patterns that conform to a more common diel vertical migration scheme (Godø and Michalsen 2000).

Several hypotheses have been put forward to explain vertical migration in cod. The physical environment varies strongly along the vertical axis, in particular for light level and hydrostatic pressure, but often also with regards to temperature (Stensholt 2001), current speed (Arnold et al. 1994; Aglen et al. 1999), salinity, and oxygen (Neuenfeldt and Beyer 2003). The temporal and vertical distribution of different kinds of prey (Rose and Leggett 1990; Righton et al. 2001) is also likely to impact on behaviour. Last, but not least, varying internal states such as stomach fullness and swimbladder volume (Arnold and Greer Walker 1992; Strand et al. 2005) can impact on vertical positioning. Below

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we discuss these hypotheses in more detail for cod in general and the Northeast Arctic (NA) cod in particular.

The NA cod feed to a large degree on benthic and hyperbenthic prey such as polychaetes, northern shrimp (*Pandalus borealis*), and amphipods (*Paratemisto* sp.) but are also known to prey heavily on pelagic capelin (*Mallotus villosus*) and Atlantic herring (*Clupea harengus*) in the Barents Sea (Mehl 1989; Bogstad et al. 2000; Johansen 2002). Other cod stocks are also known to have a mixed diet consisting of both benthic and pelagic prey (Adlerstein and Welleman 2000; Hanson and Chouinard 2002). Although pelagic fish tend to be patchily distributed in dense schools, the demersal zone represents a more persistent and varied prey community. Pelagic fish normally have high energy content and might therefore represent a more valuable prey compared with invertebrates (Hewett and Johnson 1992). Currents may also vary strongly with depth and generally decrease with increasing depth. It has been suggested that NA cod stay very close to the bottom during times of strong current (Aglen et al. 1999). This will allow the cod to save energy because the friction in the bottom layer decreases the current to virtually zero in the lower few metres (Vogel 1994). In the North Sea, it has been shown that cod can utilise currents during horizontal migrations by moving vertically between water layers with different current velocities and directions (Arnold and Cook 1984; Arnold et al. 1994).

Digestion time associated with heavy meals of large prey may leave the cod unable to ingest prey for a prolonged period of time due to stomach limitation (dos Santos and Jobling 1992). In such cases, a diel vertical migration strategy might not be profitable, and following a large meal, vertical positioning may rather be based on maximising digestion rate and thus temperature (Rosland and Giske 1994). Other factors may indirectly constrain the behavior of cod. For example, cod has a closed swimbladder with slow gas exchange (Harden Jones and Scholes 1985). Swimbladder gas content puts restrictions on the distance and speed at which cod can change depth, as the swimbladder will be damaged or will burst if the pressure is decreased by 50%–70% (Tytler and Blaxter 1973). Maturity status may also impact on foraging behaviour, but here we will only address a period of active feeding.

Neilson and Perry (1990) conclude a review on vertical migration in fish by suggesting that vertical migration in demersal fish, formerly believed to be inconsequential, may indeed be substantial. The vertical migration of adult cod is intriguing from an assessment perspective as it causes problems for abundance estimation, which relies on the combination of bottom trawling and acoustics (Michalsen et al. 1996). Consequently, better knowledge of natural fish behaviour can be utilised in development of improved survey strategies (Godø and Michalsen 2000).

The objective of this paper is to investigate the effects of different environmental factors and internal states on the vertical positioning strategies in adult cod. It is difficult and expensive to investigate the various hypotheses through fieldwork and experiments; therefore we approach the problem from a theoretical perspective by utilising an individual-based model with artificial neural networks and genetic algorithms. This modelling concept has previously proven successful in describing both vertical and horizontal migration

in fish (Huse and Giske 1998; Huse et al. 1999; Strand et al. 2002) and calculates behaviour as the product of environmental stimuli, individual states, and evolved "synapses". It is often assumed in models that animals have complete knowledge about their environment when making decisions, as in the case of the ideal free distribution (e.g., Fretwell and Lucas 1970). For the present case with vertical migration in cod, the water column is rather deep and the visual range is limited to a few metres at the most. Consequently, a lot of the movement patterns we observe in cod in nature are actually about information gathering. Thus the assumption about complete information does not hold. This is the motivation for choosing an adaptive approach to modelling behaviour based on local information and adapted strategies, after all, animals are adaptation executers not fitness maximisers (Wright 1994).

Materials and methods

The Material and methods section is presented in accordance with the format proposed by Grimm et al. (2006) for communicating individual-based models.

Purpose

The presented model is developed to investigate how different internal states and external forces impact on the vertical migration behaviour of top predatory fish such as adult cod. In this study, vertical migration behaviour includes both vertical positioning (depth) and swimming speed. We present different simulations in order to answer the following questions. How do cod behave when they can choose from both benthic and pelagic food sources? How does the likelihood of encountering pelagic prey influence cod vertical migration? How fast should the cod swim at night (or day) in the absence (or presence) of pelagic prey? If cod is subject to predation, how does this influence vertical migration behaviour? Does the prey school's height above seabed effect cod behaviour? Does the swimbladder impose restriction on or modify the cod's behaviour? The simulation protocol (Table 1) was set up to help answer these questions.

State variables and scales

The model environment is constructed to resemble a one-dimensional water column with a depth of 300 m, divided into discrete depth intervals of 1 m. Each depth interval is characterised by hydrostatic pressure, temperature, prey abundance, and the amount of light. The first two variables are independent of time, whereas the latter two may vary with time. Each individual within the model is uniquely described by the state variables depth position and swimming speed (also referred to as behavioural variables), together with body mass, stomach fullness, and swimbladder volume. For each generation, 20 consecutive days with a time-step resolution of 10 min were simulated. Such a temporal scale allows a high resolution in the behaviour, as well as a distinction between different behavioural strategies.
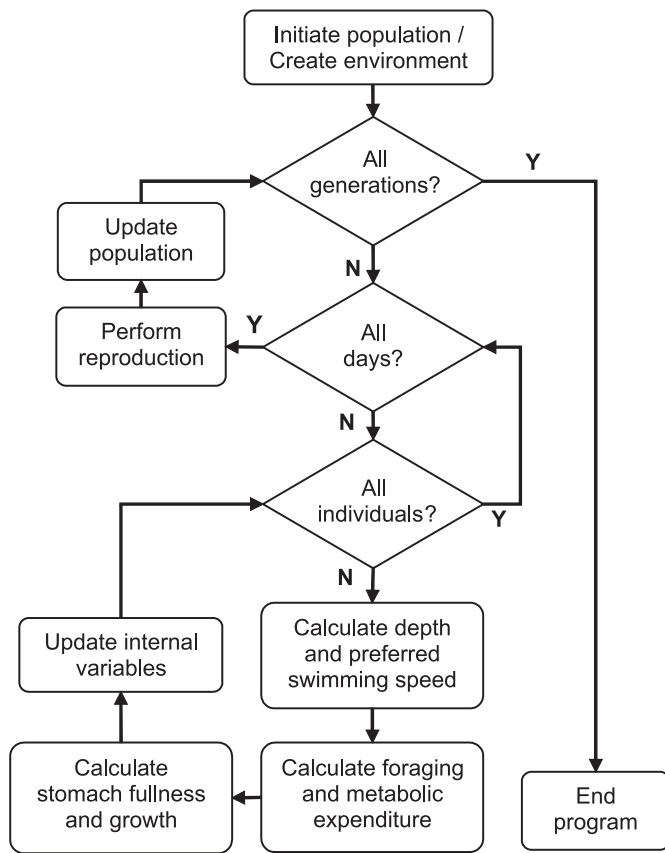
Process overview and scheduling

The model has a nested loop structure with an outermost generation loop followed by the time-step loop and an inner-

Table 1. The simulation protocol.

| Simulation no. | Factors | | | | | | |
	Benthic food	Pelagic food	Swimbladder	Predator density	Depth range of pelagic food	Frequency of pelagic prey (F_p)	Cod able to rest on bottom?
1	Yes	No	Yes	0.0000	200–250	0.00	No
2	No	Yes	Yes	0.0000	200–250	0.50	No
3	Yes	Yes	Yes	0.0000	200–250	0.50	No
4	Yes	Yes	No	0.0000	200–250	0.50	No
5	Yes	Yes	Yes	0.0035	200–250	0.50	No
6	Yes	Yes	Yes	0.0070	200–250	0.50	No
7	Yes	Yes	Yes	0.0000	200–250	0.35	No
8	Yes	Yes	Yes	0.0000	200–250	0.20	No
9	Yes	Yes	Yes	0.0000	100–150	0.50	No
10	Yes	Yes	Yes	0.0000	200–250	0.50	Yes

Note: "Yes" and "No" refer to inclusion or exclusion, respectively, in the model simulation of the factor given in the column heading.

Fig. 1. A flowchart of the model showing the scheduling of all major events and calculations. The flowchart starts with the initiation of the environment and the first population.

most individual loop. A schematic overview of the main processes and scheduling of events in presented (Fig. 1).

Design concepts

Adaptation

The model is based on the ING (individual based, neural network, genetic algorithm) modelling approach (Huse and Giske 1998; Huse et al. 1999; Strand et al. 2002) in which behaviour is evolved by simulating evolution in a population of artificial individuals (Holland 1975). Each individual carries a unique genetic string or strategy vector (Huse 2001; Huse et al. 2002) consisting of a finite number of characters, each assigned a character value. The character values are refined by a genetic algorithm (Holland 1975) by simulating hundreds of generations to find a set of character values that enables individuals to behave in manner that maximises a chosen fitness criterion. The genetic algorithm thus mimics the process of evolution by natural selection (Darwin 1859) by differentiating between the reproductive success of individuals. New genetic variability is introduced due to mutations of the strategy vector during reproduction. Maximisation of growth was chosen as a fitness criterion, as the study focuses on a feeding period. This criterion entails both maximisation of feeding rate and minimisation of energy expenditure. The character values on the strategy vector are used as weights in an artificial neural network (ANN; Rosenblatt 1958; Rummelhart et al. 1986), a simplified model of a brain, for transforming input variables to behaviour (Fig. 2). Locally obtained information about the environment and individual state (Fig. 2a) and the evolved strategy vector (Fig. 2b) are used to calculate behavioural decisions (Fig. 2c).

Emergence

The two behavioural variables, depth positioning and preferred swimming speed, emerge during a simulation as the individuals gradually become better adapted in responding to the input variables in order to maximise the fitness criterion in the simulated environment.
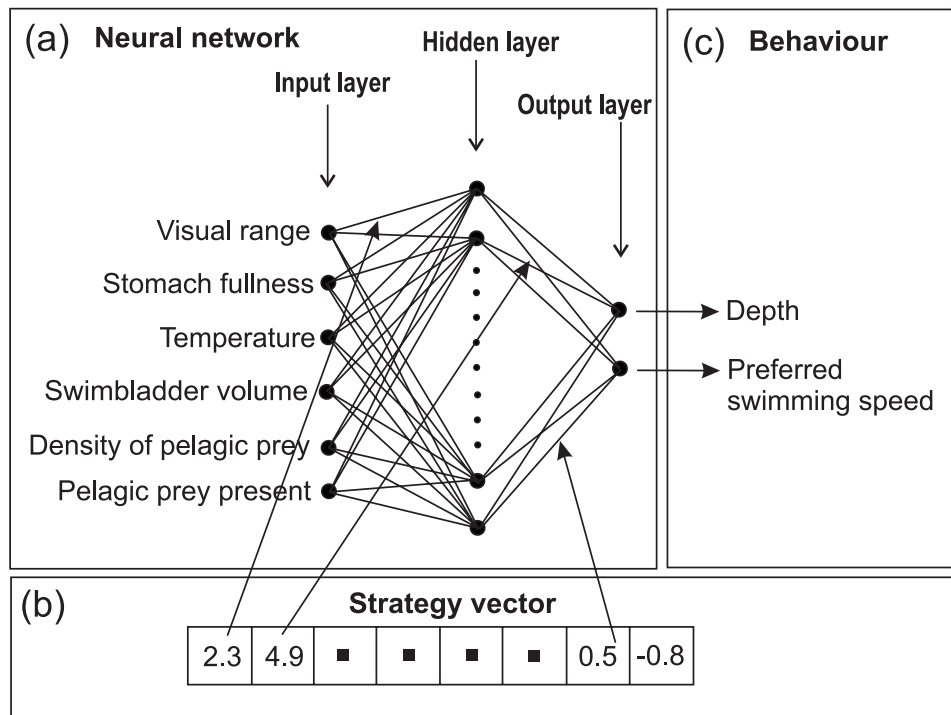
Sensing

Individuals are assumed to have knowledge of all the input variables, namely their own visual range, stomach fullness, and swimbladder volume, as well as the ambient temperature and prey density. Finally, it is assumed that individuals, after searching the whole water column in which pelagic prey potentially occur, can determine whether pelagic prey are present or not.

Interaction

It is assumed that cod are not able to any significant degree to diminish their food sources and hence no interaction between cod and their prey is included in the model. It is

Fig. 2. The neural network design. (*a*) The neural network structure and the applied input variables. (*b*) How the strategy vector codes the neural network. (*c*) Behaviour is determined in the neural network by weighting the input values with the adapted strategy vector.

further assumed that cod do not aggregate in such high densities compared with their food that intraspecific dynamics occur (Horne and Schneider 1997). This is justified by what must be perceived from a relatively stationary cod's point of view as a stochastic and ephemeral appearance of onshore-migrating pelagic prey such a capelin (Behrens et al. 2006). Furthermore, cod are not likely to aggregate in high numbers to utilise the widely distributed benthic food source.

Stochasticity

Stochasticity is a prominent feature of the model. In the model, pelagic prey occurred each day with a given probability, and if present, they appeared at a random depth between an upper and lower limit. Modelling pelagic prey in such a way mimics the ephemeral nature of migrating capelin schools and forced individual cod to actively search for prey. Whether or not prey was actually captured at any given time step was also modelled as a stochastic process (Monte Carlo simulation, e.g., Judson 1994) influenced by visual range, prey density, and cod swimming speed. Predation risk, if included in a simulation, was modelled similarly to foraging described above, but from a predator's point of view.

Observation

Depth position, swimming speed, stomach fullness, body weight, and swimbladder volume was recorded for the average population for the duration of the simulation, and individual data were recorded at every time step during the final generation.
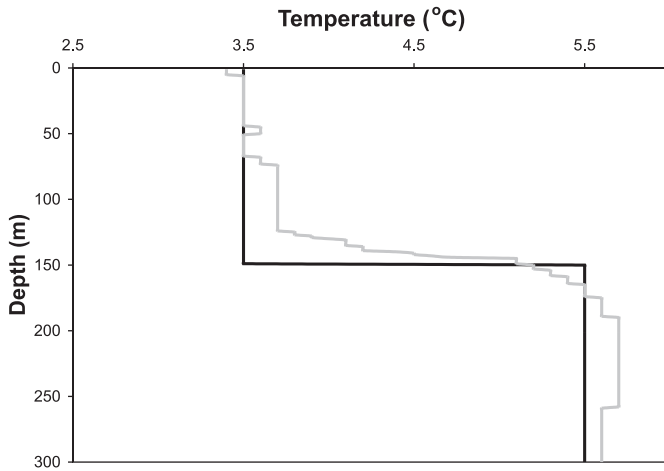
Initialization

At the beginning of a simulation, each individual in the population was assigned a random depth position of 1 to 300

and a strategy vector consisting of random values in the range –5 to 5. The numerical value of elements on the strategy vector has no explicit biological meaning but can conceptually be pictured as the signal strength between neurons in a brain. Based on the authors' modelling experience, the initial value range of the strategy vector should exceed the range of input values (all input values were normalized to the range 0 to 1). Maximum stomach capacity was set to 10% of the body weight and all individuals were initiated with a body mass of 4 kg. Initial stomach fullness was set to 5% of maximum. The body length (l) of a 4 kg cod was set to 0.76 m. Each cod was given a randomly selected starting depth at the beginning of each generation. To avoid any initialisation problems relating to the randomly selected starting depth, the cod had 10 time steps to find its preferred depth. At this time, the swimbladder volume was set so as to give the cod neutral buoyancy. Each model simulation was run for 500 generations with five replicate runs. The last generation of each replicate within one simulation experienced the same pelagic prey distribution both temporally and spatially. This was done to ensure comparability between replicates.

Input

The model environment is parameterised to resemble conditions found in the southern Barents Sea during winter (Fig. 3). This included a simplified (see reason for this below) temperature profile and the amount of surface light (Skartveit and Olseth 1988). Visual range depends on the light condition at depth and was calculated from beam attenuation, background irradiance, prey contrast, prey radius, a sensitivity threshold of eye detection of changes in irradiance, and maximal irradiance processed by the eye. Iteration was needed to solve the equation (see Aksnes and

Fig. 3. The temperature profile used in the model (solid line). The shaded line shows the actual recorded temperature profile.

Fig. 4. The calculated visual range (*r*, in metres; scale on right) of cod (*Gadus morhua*) given time of day and depth.

Utne (1997), eq. 7). The two latter parameters have, to our knowledge, never been experimentally determined for cod. These values are thus established by adjusting values from other species. The exact visual range at any depth may consequently be inaccurate, but the slope of the curve at each time step, as a function of depth, will be unaffected by the irradiance parameters (Fig. 4). Also, the density of prey was adjusted to allow reasonable foraging during the simulation period.
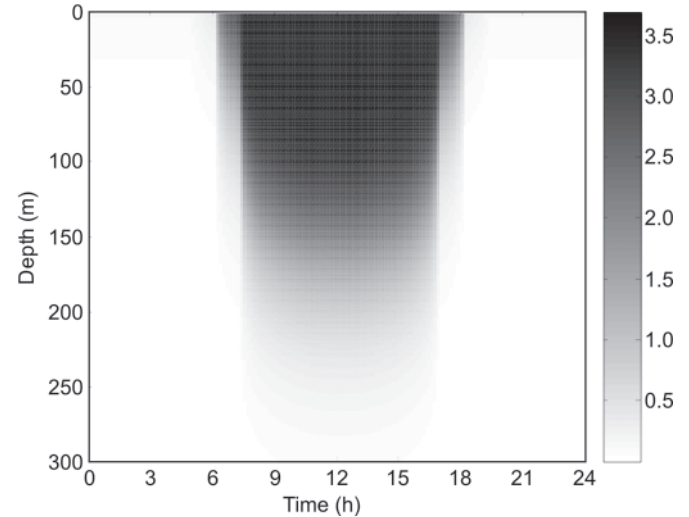
Two different prey sources are included in the model: pelagic and benthic, represented by capelin and shrimp, respectively, which are both common prey of cod (Bogstad et al. 2000). To include the dynamics of a prey item resembling schooling fish, we choose to make the presence of the pelagic prey stochastic. Either the pelagic prey was present at a high density or not present at all. The likelihood of pelagic prey being present is given by a frequency parameter (Fp), value of which was varied between simulations. The presence or absence of pelagic prey and at which depth the pelagic prey appeared is decided on a daily basis using Monte Carlo simulations (Judson 1994). The vertical extent of the school is set to 9 m (±4 m from centre). As opposed to the stochastic occurrence of the schooling pelagic prey, the benthic prey is either present at all times or not present at all (depending on the simulation setup). During daytime, the maximum density of benthic prey is found at the bottom and decreases exponentially up to 270 m. This roughly resembles the vertical distribution of shrimp (Larsen et al. 1993), a major prey of cod (Mehl 1991; Bogstad et al. 2000). At night we assumed the benthic food source to migrate upwards and spread out, and a constant density from 250 m down to the bottom was used. The depth-integrated amount of benthic prey is constant.

Submodels

Behaviour and reproduction

At the beginning of every time step, each individual decides its depth and preferred swimming speed by applying the present input values in the ANN. After several calculations within the ANN, the two output values (values between 0 and 1) are multiplied by the maximum values of the two

behavioural parameters, depth (maximum = 300) and swimming speed (maximum = 1.0 body lengths (BL)·s^{-1}). The calculations that take place in the ANN are described in detail by Huse and Ottersen (2003). The cod moves to the decided depth as long as it is within the maximum vertical migration distance (0.05 BL·s^{-1} vertical migration or 21 m for each time step). If the depth change is greater, the cod moves the maximum distance. Also, if the cod is about to move completely through a school of pelagic prey (vertically extending 9 m), it is assumed that the cod would stop in the middle of the school. If the cod, within 1 day, searches through the entire depth range where pelagic prey are expected to occur (Table 1), the ANN input variable "pelagic prey present" (Fig. 2*a*) changes from 1 to 0, thereby assuming that the cod knew that pelagic prey was not present that day.

At the end of each generation, the individuals are sorted according to the chosen fitness criterion (maximisation of growth) and the 20% best individuals produce five offspring each. During reproduction, the offspring's strategy vector is subject to mutations and this occurs with a probability of 0.07. It is common to also include recombination (mixing the strategy vector of two successful individuals) during reproduction (van Rooij et al. 1996), but we found that the model performed best with the recombination probability set to zero. By simulating numerous generations in this manner, the behavioural response to changing external stimuli and internal states will become better and better according to the fitness criterion.

Swimbladder regulation

The swimbladder dynamics are calculated using the model of Strand et al. (2005). The model is based on calculations of the swimbladder volume, the maximum rates of gas secretion and absorption (Harden Jones and Scholes 1985), and the rate of leakage through the swimbladder wall (Lapennas and Schmidt-Nielsen 1977). If the cod moves vertically faster that the swimbladder can accommodate by secretion or absorption of gases, the cod will experience a buoyant force (Archemdes' principle), working either upwards (floating) or downwards (sinking). To compensate for this force,

the cod will have to swim through the water at a tilt angle while extending its pectoral fins (Alexander 1972) to generate a positive or negative lift. The energetic cost associated with cod swimming has been estimated (Schurmann and Steffensen 1997; Webber et al. 1998; Reidy et al. 2000), and these equations are used to calculate the energetic cost of compensatory swimming needed to counteract non-neutral buoyancy. See Strand et al. (2005) for more details.

Two different swimming speeds were tracked. It was assumed that the cod modified its swimming speed to provide the necessary lift given the present swimbladder volume. This is referred to as compensatory swimming. At the same time, a preferred swimming speed was calculated using the ANN. The higher of these two swimming speeds at any time step was used to calculate the cod's activity metabolism.

Growth

A basic balanced energy budget is the foundation of the bioenergetics in this model (Hewett and Johnson 1992). This is a way to account for energy flow in an organism:

$$(1) \qquad \Delta B = C - R - S - F - U$$

where C is consumption, R is respiration, S is specific dynamic action, F is egestion, and U is excretion. Net energy gain (ΔB) is used for structural growth. The equations are fitted with parameters for cod (Hansson et al. 1996) (Table 2). The prey encounter probability (PE) was calculated by

$$(2) \qquad PE = \pi (r \sin \theta)^2 \cdot N \cdot v$$

where r is the visual range (Fig. 4), θ is the reactive half angle (Luecke and O'Brien 1981; Dunbrack and Dill 1984), N is prey density, and v is predator swimming speed (see Aksnes and Giske (1993) for details). If PE is greater than a random number picked by Monte Carlo simulation, one prey item is consumed. The same equation is applied for both benthic and pelagic food.

Stomach evacuation is based on a temperature-dependent gastric evacuation model for cod (dos Santos and Jobling 1992) with prey-specific values for capelin and shrimp. The basic evacuation model must keep track of the time that each food particle has been in the stomach, which means that all prey items must be tracked separately. This yields very time-consuming calculations. Further, if the temperature changes during evacuation, the basic model would predict a steep increase in evacuation rate if the temperature is raised or a decrease in evacuation rate if temperature is lowered (see gastric evacuation equation in Table 2). It was therefore necessary to construct some time-independent equations that could account for the stomach evacuation at different temperatures (3.5 and 5.5 °C), of different prey types (P_1 or P_2), and with varying stomach fullness (SC). For this reason, the temperature profile was simplified (Fig. 3).

Assuming that a cod at time $t = 0$ ate 0.40 kg (i.e., full stomach, 10% of body mass) of capelin (P_1) at an ambient temperature (T) of 3.5 °C, one can calculate the amount of stomach contents $SC_t(P_1, T, SC_0, t)$ as a function of temperature, initial meal size (SC_0), and time from the original equation. When fitting a 2nd-order polynomial function to these data, one would get

$$(3) \qquad SC_t(P_1, 3.5, 0.4, t) = (2 \times 10^{-5})t^2 - 0.0045t + 0.3935$$
$$(R^2 = 0.999)$$

Similar equations were constructed for initial meal sizes of 0.3, 0.2, 0.15, 0.10, and 0.05 kg prey at 3.5 and 5.5 C°. The solution to this equation, $SC_t'(P_1, 3.5, 0.4, t) = 4 \times 10^{-5} \cdot t - 0.0045$, will return the rate of evacuation at time t. To make a time-independent equation, we needed to find the time until $SC_t'(P_1, 3.5, 0.4, t)$ equals $SC_t'(P_1, 3.5, 0.3, 0)$ down to $SC_t'(P_1, 3.5, 0.05, 0)$. Then, by plotting this relationship and fitting a 2nd-order polynomial function to these data, one obtains

$$(4) \qquad t = 247.8 \, SC^2 - 307.8 \, SC + 84.0 \qquad (R^2 = 0.999)$$

Finally, by inserting this equation into the derived equation of the 0.4 kg evacuation and setting $t = 0$, one gets the instantaneous evacuation rate $ER(P_1, 3.5, SC)$ given any stomach fullness SC:

$$(5) \quad ER(P_1, 3.5, SC) = (4 \times 10^{-5})(247.8 \, SC^2 - 307.8 \, SC + 84.0)$$
$$- 0.0045$$

In this model, four such equations were made to account for both prey types at two different temperatures. Assuming that the cod will completely empty its stomach, such a simplification will give a slight overestimate of the evacuation at a late stage of evacuation, because the original equation assumes an asymptotic evacuation curve that reaches zero stomach contents at $t \rightarrow \infty$.

In the simulations in which mortality was included, the cod faced the risk of predation at every time step. To assess whether a cod dies at any given time step, we used the same encounter equation as the one used for calculating a cod's prey encounter (eq. 2) only setting $N = 1$ and $v = 1$ and multiplying this value with the cod predation risk parameter (see Table 1). If this value is greater than a randomly drawn number between 0 and 1, the cod is assumed to have died and its body mass is set to 0, giving it no chance to reproduce at the end of a generation.

Results

The results are grouped and presented to best illustrate how different external forces and internal states influence vertical migration strategy of cod.

Prey distribution

Only benthic prey present

When no pelagic prey was present (Sim1), the cod, as expected, adopted a purely benthic life style foraging solely on benthic prey (Fig. 5). The cod swam with a preferred swimming speed of 0.40 m·s^{-1} during daytime and ceased swimming during night (Table 3). The average cod stomach content was 0.3 kg (maximum stomach fullness ≈ 0.4 kg) (Fig. 6a).
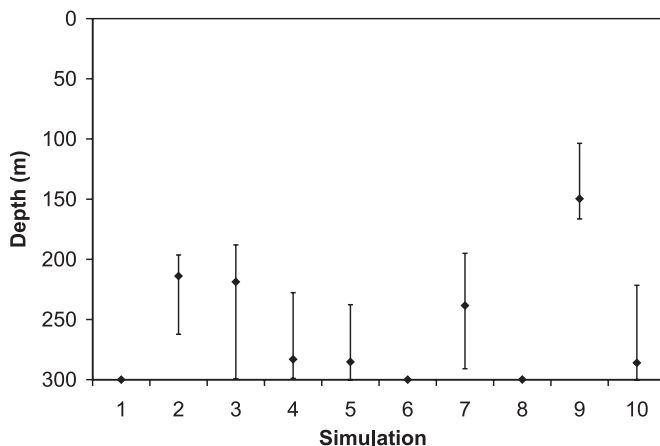
Only pelagic prey present

When no benthic prey and only pelagic prey (Sim2) was present, the cod adopted a purely pelagic way of life (Fig. 5). This strategy consisted of being almost neutrally buoyant at the top of its vertical range during night and

Table 2. Bioenergetic equations and parameters used in the model.

Description	Equation	Parameter (value) and variable (unit)
Total metabolism	$R = R(W_s) \cdot f(T) \cdot A(v)$	
Resting metabolism	$R(W_s) = \alpha \cdot W_s^\beta$	W_s = body weight (g)
		α = 0.0033
		β = –0.23
Temperature-dependent metabolism	$f(T) = e^{(R_q \cdot T)}$	T = temperature (°C)
		R_q = 0.055
Activity metabolism	$A(v) = \left(3.2 \cdot \left[\dfrac{v}{l}\right]^{1.5}\right) \cdot l^{-1} + 1$	v = swimming speed (m·s^{-1})
		l = body length (m)
Egestion	$F = F_a \cdot C$	C = consumption (g)
		F_a = 0.16
Excretion	$U = U_a \cdot (C - F)$	U_a = 0.10
Specific dynamic action	$SDA = S_a \cdot (C - F)$	S_a = 0.175

Note: Activity metabolism equation is from Strand et al. (2005). All other equations are from Hewett and Johnson (1992).

Fig. 5. Simulations 1 to 10. The mean depth position (◆) with maximum and minimum depths (bars) throughout a 20-day simulation. The data are based on the replicate that resulted in the highest average terminal weight.

descending downwards at dawn, thereby searching the water column for potential pelagic prey during the first hours of daylight. If the cod encountered prey during the morning descent, it stopped and fed throughout the period with sufficient light for visual foraging (Fig. 7b). The cod swam with an average speed of 0.36 m·s^{-1} during daytime while foraging on pelagic prey and 0.20 m·s^{-1} while searching for prey. At night the cod would swim very slowly, matching its swimming speed to counteract sinking. With a daily probability of encountering pelagic prey of 0.5, the cod had an average stomach fullness of about 0.22 kg (Fig. 6a).

Both prey types present

When both benthic and pelagic prey were present (Sim3), the cod would start descending from the pelagic zone towards the bottom at dawn (Fig. 7c). If no pelagic prey was detected during the morning descent, the cod would spend the daylight period at the bottom, foraging on benthic prey. While at the bottom, the cod were negatively buoyant and

needed to swim at 0.36 m·s^{-1} to stay above the seabed. At dusk, the cod rose off the bottom into the pelagic zone, where it would become less negatively buoyancy. If pelagic prey was encountered, the cod was found to swim with a preferred speed of 0.37 m·s^{-1}. The main diet of cod in this scenario was pelagic prey (Fig. 6a), but the consumed benthic prey would nonetheless increase the terminal weight slightly compared with Sim2 (Fig. 6b).

Variation in prey encounter probability

When the daily probability of encountering pelagic prey (Fp) was lowered from 0.5 (Sim3) to 0.35 (Sim7), there was a reduction in the total stomach fullness and consequently a lower terminal weight was realized (Fig. 6b). However, the general vertical migration pattern did not change, except that the cod spent more time at the bottom. Swimming speeds did not vary much between Sim3 and Sim7 (Table 3). However, when Fp was lowered even further (Sim8, Fp = 0.20), a change in the adapted behaviour occurred. At this probability level, the cod chose not to search for pelagic prey at all and rather stayed at the bottom throughout the simulation (Fig. 7h), producing a behavioural pattern very similar to that of Sim1 (no pelagic food).

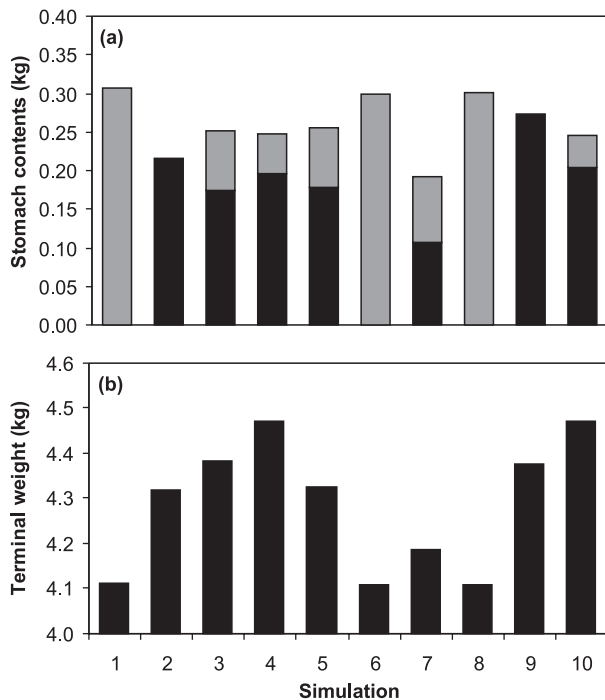### Variation in prey schools' height above the bottom

When pelagic prey schools occurred higher above the bottom, within the interval of 100–150 m (Sim9), the cod ceased performing vertical migrations, staying in the pelagic zone throughout the day, regardless of whether pelagic prey was encountered or not. When foraging higher up in the water column, the visual range of the cod was increased during daytime, resulting in an increase in the average stomach fullness of pelagic prey. However, the terminal weight did not increase as the cod did not forage on benthic prey at all (Fig. 6b). The density of the pelagic prey schools was the same for all simulations regardless of the depth at which they occurred. The increased visual range during daylight hours also resulted in a very low preferred swimming speed while foraging because the cod became satiated within the first few hours of feeding (Fig. 7j). Swimming to counteract

Table 3. Swimming speeds during day and night, with and without pelagic prey present.

	Sim1	Sim2	Sim3	Sim4	Sim5	Sim6	Sim7	Sim8	Sim9	Sim10
Day										
Pelagic prey present										
Preferred	*	**0.36**	**0.37**	**0.36**	**0.42**	**0.47**	**0.36**	**0.46**	0.00	**0.44**
Buoyancy	*	0.18	0.17	*	0.18	0.00	0.24	0.01	**0.16**	0.14
Pelagic prey not present										
Preferred	**0.40**	0.07	0.03	**0.25**	0.11	**0.47**	0.02	**0.46**	0.00	0.04
Buoyancy	0.00	**0.20**	**0.36**	*	**0.35**	0.00	**0.33**	0.01	**0.26**	**0.26**
Night										
Pelagic prey present										
Preferred	*	0.03	0.04	**0.00**	0.06	**0.02**	0.04	**0.01**	0.01	0.00
Buoyancy	*	**0.05**	**0.05**	*	**0.33**	0.00	**0.17**	0.00	**0.25**	**0.01**
Pelagic prey not present										
Preferred	**0.00**	0.01	0.03	**0.01**	0.05	**0.02**	0.01	**0.01**	0.01	0.00
Buoyancy	0.00	**0.04**	**0.06**	*	**0.34**	0.00	**0.11**	0.00	**0.27**	**0.02**

Note: The higher of the two motives for swimming is marked in bold as this value determines activity metabolism. Asterisk (*) means that no value exists or not applicable (refer to Table 1).

Fig. 6. (*a*) Average stomach contents of benthic (shaded bars) and pelagic (solid bars) food during the 20 days in the last generation. (*b*) Average terminal weight of the last generation. Data are from the replica yielding the highest terminal weight.

non-neutral buoyancy was the factor determining swimming speed (Table 3).

Swimbladder constraints

To investigate the effect of swimbladder dynamics on behaviour, we chose to run a simulation (Sim4) without including the swimbladder submodel in the main model. Instead we assumed that cod were always perfectly adjusted to the ambient pressure. This had a marked effect on behaviour. The cod adapted a strategy where it would mainly stay at the bottom, making a vertical ascent at dawn to assess if pelagic prey were present. If prey were encountered, it remained in the pelagic zone during daylight hours before descending to the bottom at dusk. If prey were not detected during the morning ascent, the cod soon returned to the sea floor and fed on benthic prey. When foraging during the day, the cod had a swimming speed of 0.36 m·s^{-2} in the pelagic zone and 0.25 m·s^{-2} in the benthic zone. During night, they almost cease swimming.

Predation risk

Predation risk for adult cod (>4 kg) is believed to be rather low. If one, however, assumes that mortality from visually foraging predators exists (i.e., seals and whales), this has the potential of changing behaviour dramatically (Fig. 8). With relatively low predator densities, the cod continued performing pelagic–benthic migrations (F_d = 0.0035; Fig. 7*e*). The average occupied depth was deeper and the average terminal weight became lower with increasing mortality risk. With a predator density of 0.005 and higher (F_d = 0.008; Fig. 7*f*), the cod stayed close to the sea floor at all times and did not pursue pelagic prey at all.
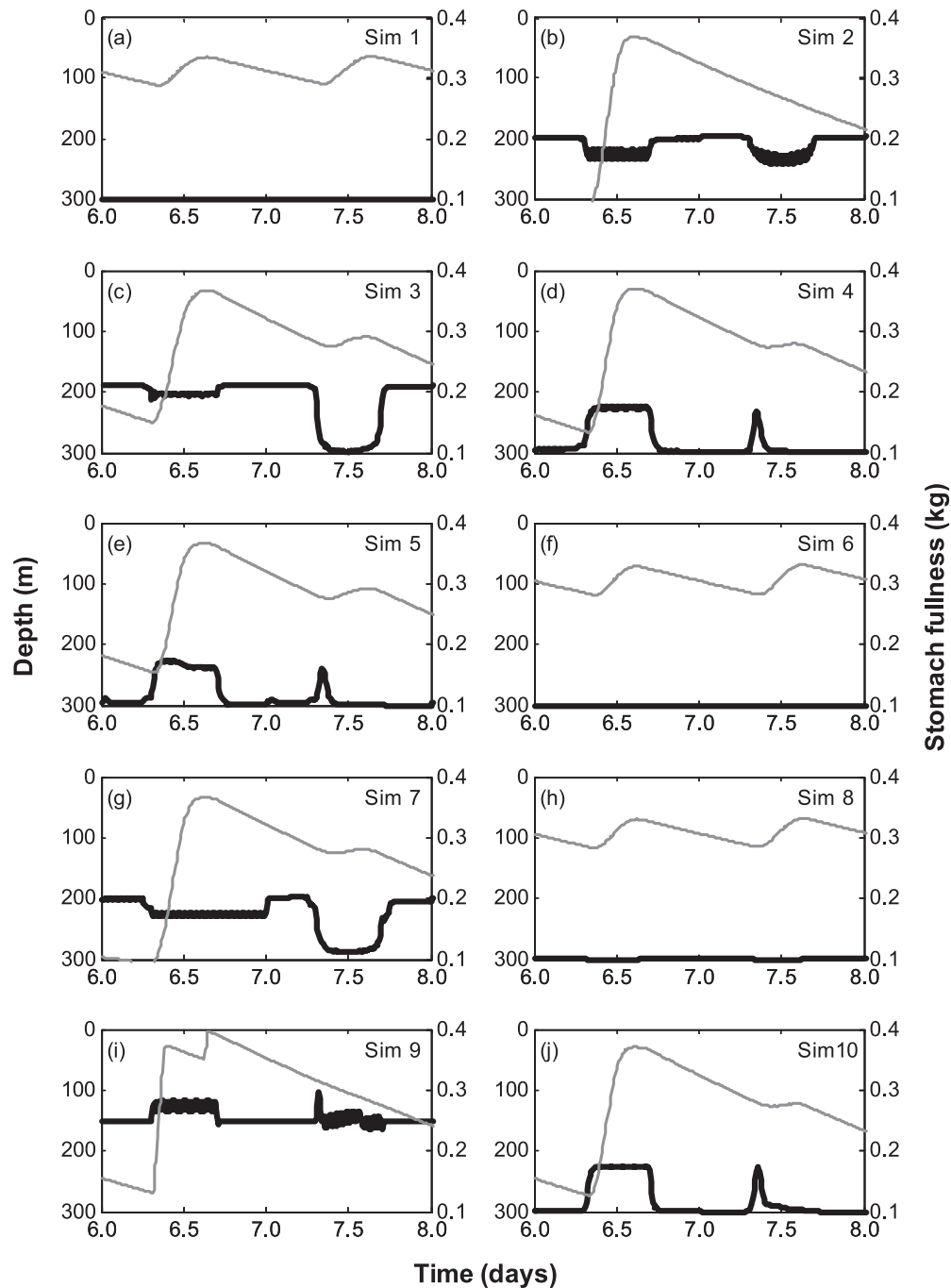
Resting at the bottom

Contrary to all other simulations, it was assumed in Sim10 that if a cod positioned itself at 300 m, it would be laying still on the bottom. This was implemented in the model by setting all swimming speeds to 0 when the cod stayed at the 300 m depth. Consequently, the cod did not need to spend energy to regulate buoyancy but was unable to forage. The results showed that cod did utilise this possibility during night. At dawn the cod would rise off the sea floor to check for pelagic prey and remain in the pelagic zone if prey was detected. If prey was not detected, the cod would soon descend towards the bottom, but not all the way to the sea floor, and forage on benthic food until dusk when it would settle on the sea floor at 300 m.

Discussion

Model predictions

The presented model simulations show that strikingly different vertical positioning strategies emerge as a result of

Fig. 7. Adapted depth profile (solid line) and stomach fullness (shaded line) in two consecutive days of the last simulated generation of simulations 1–10 (*a–j*). On day 6, pelagic food occurred if possible (*F*p > 0), whereas no pelagic food occurred in either simulation during day 7.
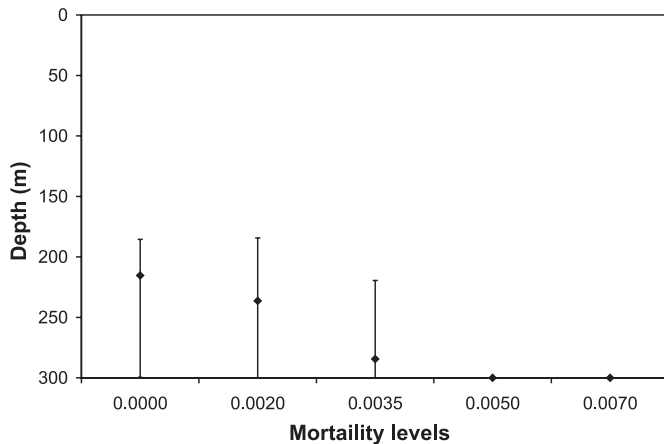

different environmental forcing and physical constraints. In general, the distribution of prey and probability of encountering prey were the most important factors in determining the vertical distribution and behaviour of cod. The simulations also yielded four specific predictions: (*i*) visually foraging piscivorous fish should swim faster during the day than at night; (*ii*) nighttime depth should be decided so as to trade off the effects of temperature and buoyancy; (*iii*) the probability of encountering pelagic prey must be sufficiently high in order for cod to perform vertical migrations; and (*iv*) if prey occur at a sufficient distance above the bottom,

the cod will abandon all association with the bottom and switch to a completely pelagic life style.

Most previous studies on vertical migration in fish have shown variation in the level of diel vertical migration, but rarely strikingly different vertical migration patterns as presented here. Such variation in vertical migration strategies resembles more the plasticity seen in zooplankton when facing different predatory regimes (e.g., Bollens and Frost 1989; Ohman 1990). The range of behavioural strategies found in our model reflects the ability of cod to switch between different prey types and conforms to the "chaotic" mi-

Fig. 8. The effect of mortality risk on behaviour. Different levels of predation pressure from visually foraging predators changed the adapted behaviour. Diamonds (◆) represent the average depth position and the vertical bars represent the maximum and minimum depth utilised by the cod throughout one simulation. The presented data are based on the replicate with the highest terminal fitness.

gration patterns often observed in this species (Godø and Michalsen 2000). Although abiotic factors such as light and hydrostatic pressure are important in constraining behaviour, the present study suggests that distribution and abundance of different prey types are the main factors in determining the vertical migration patterns of top predators such as adult cod. Below we discuss the support of the predictions with regards to observed cod behaviour, but first we address some methodological issues.

Methodology

An aspect of adaptation-based models that separates them from more classical optimisation techniques, which calculate all possible combinations and pick the optimal solution, is the importance of historic events, a feature common to all evolutionary processes. Because evolution continuously builds on existing genetic material, future evolutionary pathways depend on the present status of the population. Because all presented computer simulations were initiated with different combinations of weights, the starting point of replicate runs are different. Given that the selective pressure for a specific behaviour is relatively strong, replicate runs are likely to evolve the same behavioural solution. However, in cases where the selective pressure is relatively weak or two different strategies have similar fitness values, the dependence on initial conditions becomes stronger. Furthermore, because pelagic prey in the model were simulated to occur stochastically, many consecutive days without pelagic prey within one generation will increase the profitability of the benthic feeding strategy relative to pelagic feeding strategy. Such events may produce bottleneck effects that have consequences for future evolution. A few examples of strategy divergence were seen in the simulations, but in all cases, at least three out of the five replicates were similar, and in all 10 simulations, the majority of evolved behavioural patterns of the replicates also had highest terminal fitness.

We presently scaled the ANN output so that it produced the desired depth directly within the range of depths possible. This avoids any additional calculations and allows the direct usage of the ANN output. An alternative way of using the ANN would be to calculate a change in depth relative to the present depth (Eiane and Parisi 2001) and thus add the ANN output to the present depth. In our model setup with a constant bottom depth, these approaches are likely to produce similar results. However, in cases where the bottom depth is variable, the absolute depth output would not be appropriate because the vertical scale may be altered between time steps. In such cases, a relative depth change would be preferable.

Model assumptions

The present model did not take into account density-dependent effects, such as removal of prey following feeding. Adding density dependence would probably have forced the cod to forage on benthic prey if capelin schools had been decimated. The model does not take into account possible effects of altered prey behaviour in response to the presence of predators such as school dispersal or aggregation and whether or not the school seeks refuge in deeper water. It would be tempting to try to include such behaviour in a future model, but it would require even shorter time steps and thus more computational power than is currently available.

It has sometimes been reported that cod rest on the bottom (Mattson 1990), but the extent of such behaviour is not well known. Movement patterns of cod tracked with a stationary positioning system suggest that cod rarely sit completely still (Løkkeborg 1998). We performed one simulation in which the cod was allowed to rest on the bottom (Sim10). When a cod performs regular vertical migrations, bottom resting is shown to be a favourable strategy. However, the only cost associated with bottom resting in the model is that the cod is unable to eat benthic food while lying still on the bottom. Possible additional costs related to pumping water over the gills and increased parasitic exposure are not included in the model and could very well change the model predictions. More information on cod's potential for resting on the bottom is needed before a possible adaptive value of such behaviour can be perused in more detail.

We assumed that cod feed mainly by vision, which is in accordance with previous studies (Løkkeborg 1998). However, some studies have suggested that cod prey actively on capelin during the night (Konstantinov 1958; Turuk 1973). Several sensory mechanisms can be involved in this. Although cod may use the barbel and pectoral fins, which have taste buds, to locate and ingest prey lying at the bottom, they may rely on locating pelagic prey using olfaction and then use the lateral line organ to aid in capturing mobile prey (Bleckmann 1993). We have not included the latter, and consequently, the simulated cod are virtually unable to forage on pelagic prey at night. Bioluminescence is an additional source of light that might allow cod to feed by vision at night, but the extent of this remains uncertain. In any case, the foraging efficiency on pelagic prey is likely to be much greater during daylight than at night.

The model as presented does not include currents. However, we have run several of the simulations with a variable current profile included. It was then assumed that the cod

would have to swim at least as fast as the current to avoid being transported away from the favourable feeding area. In two such simulations, the cod adapted a behavioural strategy that resulted in, on average, a deeper depth position. During night, the cod exposed to current also had to swim faster to counteract the current. However, the slightly altered behavioural pattern did not result in any significant differences in stomach fullness and terminal weight between the otherwise identical simulations. The reason why these simulations were omitted was the lack of evidence that cod can actually detect currents while being in the pelagic zone with no fixed point of reference.

Comparing model predictions with observed cod behaviour

Cod is very plastic with regards to vertical positioning. Different behaviours have been observed between stocks (Righton et al. 2001), geographical area (Trout 1957; Konstantinov 1958), and seasons (Konstantinov 1958; Righton et al. 2001) and within a diurnal period (Godø and Michalsen 2000; Righton et al. 2001). Righton et al. (2001), for example, found that North Sea and Irish Sea cod stocks had dissimilar vertical behaviour depending on season and proposed that this behavioural variation was a response to variation in the distribution and abundance of prey. This behaviour fits very well with our model predictions. Brunel (1965) reported that Northwest Atlantic cod change their vertical migration strategy over time, emphasising two special cases: a nocturnal strategy in which the cod ascend to midwater during night and descend to the bottom during the day and a pelagic strategy in which the cod stay in midwater for an extended period of time. Both these patterns were seen in our simulations. The nocturnal strategy corresponds to the simulations in which pelagic prey occur relatively deep and often. Sim2 showed that if benthic food is unavailable, cod could shift to an entirely pelagic life style, feeding exclusively on pelagic food items. However, not only a total absence of benthic food induced such behaviour. Because cod remained pelagic during nighttime in periods with vertical migrations, encounters with pelagic prey on a daily basis would result in a purely pelagic life style over time. Also, if prey occurred higher above the bottom, the model predicted that cod would remain pelagic as long as the probability of encountering prey was high enough (Sim9). In addition to these behavioural patterns, it is well known that cod spend extended periods of time close to the bottom (e.g., Trout 1957; Løkkeborg and Fernö 1999). Its distinct morphological characters such as a well-developed barbel and prolonged soft pelvic rays show that cod is well adapted to feed on the bottom (Mattson 1990; Harvey and Batty 2002).

As a result of the slow secretion and the faster absorption of swimbladder gasses, regular vertical migrations will make cod neutrally buoyant only at the top of their vertical range (e.g., Alexander 1971; Arnold and Greer Walker 1992; Strand et al. 2005). One prediction that emerged from the present model simulations was that cod should stay in the pelagic zone at night during periods of pelagic feeding to remain neutrally buoyant and save energy. This is clearly illustrated by the difference in vertical positioning strategy seen in simulations with and without the swimbladder dynamics included (Sim3 vs. Sim4).

The nighttime depth of many vertically migrating organisms is chosen to allow feeding at times when the predation risk exerted by visual predators is small. This includes staying at the top of the vertical range during night to commence feeding at dawn in the "antipredator window" (Clark and Levy 1988). In addition, it can be advantageous to stay at the temperature maximum to maximise the digestion rate and thus increase growth (Levy 1990; Rosland and Giske 1994). In four simulations, the model predicted that cod remain pelagic during night to reduce swimming speed associated with being negatively buoyant. This strategy reduces the energy expenditure and thereby increases growth and can be seen as a complementary strategy to the "stay at the temperature maximum" during nonfeeding periods.

In the presented model, the temperature profile had a marked thermocline at 150 m where the upper water had a temperature of 3.5 °C and the bottom water had a temperature of 5.5 °C. In most simulations, because of the distribution of prey, the cod spent all their time in the warmer water. Sim9 is the simulation with the shallowest average depth position, but the average depth in periods without pelagic food lies just below 150 m even though pelagic prey occur at or above the thermocline. This shows that cod preferred staying in the warm water to maximise digestion rate and not in the cold water to minimise standard metabolic rate.

The model predicted that the swimming speed should be higher during the day than at night. This is caused by the increased encounter rate with pelagic or benthic food during daytime. Conversely, the model predicted that cod should swim slowly during the night to save energy. These predictions are supported by observations on tagged cod (Løkkeborg and Fernö 1999).

Information from data storage tags (DST) from cod often reveals rapid ascents from the bottom to high up into the water column followed by subsequent rapid descents to the bottom (Godø and Michalsen 2000). These "spikes" resemble the behavioural patterns seen in simulations 4, 5, and 10, where individuals searched the pelagic zone for prey without finding anything and returned to the bottom shortly afterwards. It seems plausible that the pattern seen in cod DSTs also reflects prey search behaviour in a similar manner to our model predictions. To a varying extent depending on season, there is a reduction in bottom trawl catches of cod during night (e.g., Konstantinov 1958; Brunel 1965; Michalsen et al. 1996). Such a decline in catch-per-unit-effort at night may indicate that cod rise off the bottom and out of range from the bottom trawl. This pattern has, however, also been related to varying effect of vertical herding during day and night (Glass and Wardle 1989; Wardle 1993). During daytime, when visual foraging opportunities are good, cod are predicted to descend to the bottom and forage if no pelagic prey are detected higher up in the water column. This could explain the increased catch during hours at which visual feeding can be performed (Engås and Soldal 1992).

Although marine mammals pose some risk, large cod, as studied here, probably have a rather low predation risk in general (Pálsson 1994). Cannibalism can be a source of high mortality for young cod (ages 1–3) in some years (Mehl 1991), and it is more pronounced when capelin is scarce (Bogstad et al. 2000). In such cases, the mortality of small cod is likely to increase close to the bottom because of the

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benthic distribution of older cod. Our model predicted that when the probability of finding pelagic prey is low, the adult cod would mainly stay at the sea floor. Such a behaviour in the real cod would possibly force young cod to occupy pelagic waters.

Foraging on schooling prey

The classic interpretation of diel vertical migration (DVM) is related to the behavioural trade-off between foraging opportunity and predation risk (e.g., Iwasa 1982; Clark and Levy 1988; Giske and Aksnes 1992). Small planktivorous fish are driven towards the surface by increased foraging opportunities higher up in the water column where the prey encounter rate generally is greater. At the same time, predation risk from visually foraging predators during daylight hours increases with decreasing depth, given a uniform predator distribution. Cod, however, might not simply increase their foraging rate by ascending from the bottom as most of their pelagic prey are highly mobile and move in schools. Instead of using a constant, time-independent density of pelagic prey, we assumed that the prey occurred in schools, the presence (or absence) of which were decided on a daily basis using Monte Carlo simulation (Judson 1994). This approach mimics the ephemeral nature of cod interactions with schooling capelin on their spawning migration towards the coast of northern Norway during February to April (Gjøsæter 1981; Dolgov 2002). Studies on spatial coherence between cod and capelin indicate that cod abundance is correlated with capelin abundance only on large scales (>15 km) and, obviously, on very small scales when cod is actively feeding on capelin (3.5 m) (Rose and Leggett 1990). Others have found no spatial coherence within a wide range of scales (Horne and Schneider 1994, 1997). Horne and Schneider (1994) reasoned that the low spatial coherence between cod and capelin could be due to cod being stomach-limited when foraging in high densities of capelin. Hence, cod did not need to actively pursue capelin over large distances, but rather act as a "sit and wait" predator. Our model implementing schooling prey is a simplification but reflects both the stochastic nature of predator–prey interactions and the observed variability in spatial coherence between feeding and nonfeeding periods (Rose and Leggett 1990). If capelin are encountered, the cod should utilise this resource as it is digested faster (dos Santos and Jobling 1992) and yields higher energetic revenue per unit weight than does benthic invertebrate food (Lawson et al. 1998). In the Barents Sea, the availability of capelin to cod will vary spatially, seasonally, and interannually. However, seasonal variation in availability of pelagic prey is likely to produce a seasonal pattern in the vertical distribution of cod (Righton et al. 2001; Stensholt 2001). The simulation results, not surprisingly, predicted that in the absence of pelagic prey, cod would only utilise the benthic food resources and hence not ascend into the pelagic zone. A similar pattern is also observed in the NA cod during times of low capelin biomass (Bogstad et al. 2000).

Implications for stock assessment and further work

Vertical migration poses challenges for abundance estimation of fish. The abundance of NA cod is measured using a combination of bottom trawling and acoustics (Godø 2003).

Cod found in the acoustic "dead zone" near the bottom are unavailable to acoustic measurements but are captured in the trawl. Conversely, pelagic cod are readily available for acoustic abundance estimation but are not captured by the bottom trawl. The vertical positioning of cod therefore potentially has a great impact on measurements of cod. Hjellvik et al. (2004) found that the acoustic abundance of fish in the Barents Sea was two times higher during the day than at night and attributed this difference to diurnal differences in vertical distribution and tilt of the fish. Although their study was based on aggregated data and not only cod, it illustrates the importance of considering fish behaviour in stock assessment. A possible extension of the present work is to provide the individuals with a target strength based on their length, swimbladder volume, and tilt and investigate how the acoustic backscattering is affected by different assumptions about the environment, season, time of day, and stock structure. In this manner, behavioural models could become useful to abundance estimation.

Acknowledgements

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