

# A length-based hypothesis for feeding migrations in pelagic fish

Leif Nøttestad, Jarl Giske, Jens Chr. Holst, and Geir Huse

**Abstract:** We evaluated the costs and benefits of long-distance horizontal migration by pelagic planktivores, Atlantic herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*), mackerel (*Scomber scombrus*), and capelin (*Mallotus villosus*) in the Norwegian and Barents seas using a numerical model and tested model predictions against field observations. Specifically, we considered (i) energetic costs as a function of body size, water currents, swimming speed, and distance, (ii) time costs as a function of speed and distance, and (iii) energetic gain in terms of differences in food intake between areas. The model demonstrates how body size restricts large-scale horizontal migration patterns. Model and field results suggest that the extent of migration will increase with increasing body length. The model predicts that long-distance migration costs may exceed energy intake for fish <20 cm, due to increased hydrodynamical drag with decreasing fish size. Field results suggest that migration distance is a function of length, weight, and age. Food abundance and distribution, current speed and direction, and differences in day length at boreal latitudes are believed to be the major driving forces influencing large-scale migration distance, direction, and timing in pelagic planktivores. Northwards latitudinal rather than longitudinal feeding migrations are explained by the improved feeding opportunities with increased day lengths.

**Résumé :** Nous avons évalué les coûts et les avantages de la migration horizontale à longue distance de poissons pélagiques planctivores, à savoir le hareng (*Clupea harengus*), le merlan bleu (*Micromesistius poutassou*), le maquereau (*Scomber scombrus*) et le capelan (*Mallotus villosus*), dans la mer de Norvège et la mer de Barents. Nous avons comparé les prévisions obtenues d'un modèle numérique et d'un modèle fondé sur les observations aux valeurs observées sur le terrain. Plus précisément, nous avons examiné (i) les dépenses énergétiques en fonction de la taille, du courant, de la vitesse de nage et de la distance, (ii) les dépenses de temps en fonction de la vitesse et de la distance et (iii) le gain énergétique en fonction des écarts de la consommation alimentaire entre les zones. Le modèle montre comment la taille limite la migration horizontale à grande échelle. Le modèle et les résultats obtenus sur le terrain portent à croire que l'importance de la migration s'accroît avec la longueur du poisson. Selon le modèle, les coûts d'une migration sur une longue distance peuvent être supérieurs à l'énergie absorbée chez les poissons de moins de 20 cm de longueur, étant donné que la traînée hydrodynamique s'accroît à mesure que la taille du poisson décroît. Les résultats obtenus sur le terrain indiquent que la distance de migration est fonction de la longueur, du poids et de l'âge. L'abondance et la répartition de la nourriture, la vitesse et la direction du courant de même que la durée du jour, différente sous les latitudes boréales, semblent constituer les principales forces qui influent sur la distance, la direction et le moment des migrations à grande échelle chez les planctivores pélagiques. Les migrations d'alimentation en direction des latitudes nordiques plutôt qu'en longitude sont expliquées par les meilleures possibilités d'alimentation découlant de jours plus longs.

[Traduit par la Rédaction]

## Introduction

Large-scale horizontal migrations (>1000 km occurring over several months) have evolved in response to predictable oceanic features such as frontal areas where food is expected to be abundant, overwintering areas where conditions are favourable for energy saving and survival, and spawning areas where partners are expected to be found and conditions for

spawning as well as larval drift routes are benign (Harden Jones 1968; Fernö et al. 1998). But migrations are energetically demanding (Weihs 1987; Jobling 1994), with smaller fish incurring greater swimming costs than larger fish (Videler 1993). High energetic costs may be offset by swimming in the same direction as the transporting tide (Weihs 1978; Metcalfe et al. 1990; Castonguay and Gilbert 1995) or by taking advantage of favourable coastal (Nøttestad et al. 1996) and oceanic (Thomson et al. 1995; Walter et al. 1997) currents. This energy saving could confer a selective advantage by increased allocation to growth and reproduction and by reducing starvation risk (Harden Jones 1984).

For long-distance migrators with distinct spawning and feeding seasons, time use may be as equally important as energy use in an environment with short feeding durations. During the summer, day length increases the further north the fish travel, thus potentially increasing the feeding duration for pelagic visual predators. In situations with similar

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concentrations of food everywhere, the visual predator would benefit energetically from staying in areas where the day length is longest, unless the uniform concentration of prey is sufficiently high to maximize energy ingestion or growth even for shorter daylight periods.

All horizontally migrating planktivorous fish species in the Nordic Seas, Atlantic herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*), mackerel (*Scomber scombrus*), and capelin (*Mallotus villosus*), are larger than the nonmigratory planktivores, the northern lightfish *Benthoosema glaciale*, and the lightfish *Maurollicus muelleri* (Skjoldal et al. 1993). We therefore hypothesize that fish length may be a vital parameter for long-distance horizontal migration for pelagic fish, as fish length strongly influences the costs of swimming.

This paper focuses on the energetic cost–benefit relationship in long-distance migration in pelagic fish. In particular, we focus on time, size, and current constraints. Migration is hence analysed for its value in growth enhancement, which is likely to be an important motivation for migration in the Northeast Atlantic, since the productive time span for food of planktivorous fishes is very short (Skjoldal et al. 1993; Fernö et al. 1998). A numerical model was developed that analyses time and energy costs and benefits of migration for different sized fish, and this model was applied to invoke predictions about migration direction, routes, and physical and hydrodynamical constraints. Field data collected from Atlantic herring, blue whiting, mackerel, and capelin were then used to test the model predictions.

## Material and methods

### Model of migration

#### Energy minimization

The energetic costs of horizontal migration is a function of distance traveled ( $D$ ), swimming speed ( $U$ ), and energetic costs of swimming at speed  $U$ . Cost of locomotion (swimming) can be approximated by calculating the power ( $P$ ) required to overcome drag. Power needed to overcome the drag of a moving object increases with the length of the object and with its swimming speed. For sockeye salmon (*Oncorhynchus nerka*) >10 cm, Ware (1978) used the empirical relationship

$$(1) \quad P = a_1 L^\alpha U^\beta$$

where  $a_1$ ,  $\alpha$ , and  $\beta$  are coefficients and  $L$  is fish length (all symbols used in all equations are explained in Table 1). Standard metabolism of a fish may be expressed from fish length (Brett 1964):

$$(2) \quad z = a_2 L^\gamma.$$

However, cost of migration must also consider water movements. If we denote the average directional speed of the current by  $u$  and the total travel speed by  $U_T$ , we have  $U_T = U + u$  (current speed may be positive or negative, but to migrate in the right direction,  $U + u > 0$ ). Following Ware (1978), we may express optimum cruising speed ( $U^*$ ) as the speed where cost (sum of standard metabolic rate and power output) per distance travelled is minimum. By solving

$$(3) \quad \frac{d\left(\frac{U_T}{z + P}\right)}{dU_T} = 0$$

we obtain an expression for the most cost-effective cruising speed depending on fish length and water current:

$$(4) \quad U^* = \left[ \frac{a_1 L^\alpha \left( \beta + \frac{u}{U^*} - 1 \right)}{z} \right]^{-\frac{1}{\beta}}$$

(an asterisk is used to indicate the optimum value of a parameter under energy minimization). We assume that fish may assess the current speed, but if fish are unable to do so, the estimated  $U^*$  (eq. 4) would tend to be underestimated, and consequently, the migration cost would be underestimated. For each fish species, a weight–length function  $W = a_3 L^b$ , where  $W$  is body wet weight, can be described. The energy cost per body mass during cruising at optimal speed in a current can be expressed as

$$(5) \quad \frac{C^*}{W} = \frac{P^* + z}{W}$$

where  $P^*$  is found from eq. 1 by use of  $U^*$  and where  $C^*$  ( $= P^* + z$ ) is total energy costs at optimum speed. The cost per distance is  $C^*/U^*W$ , and the minimum total energy ( $E^*$ ) use for migrating the distance  $D$  is

$$(6a) \quad E^* = \frac{DC^*}{U^* + u}.$$

The most cost-efficient time for this migration ( $T_m^*$ ) is

$$(6b) \quad T_m^* = \frac{D}{U^* + u} = \frac{E^*}{C^*}.$$

$U^*$  is optimal only in the sense of energy efficiency. For long-distance migrating fish in a highly seasonal environment, time use may be as equally important as energy use. This is not considered here but would tend to increase swimming speed.

Given that the main purpose of the migration away from the spawning area in spring and summer is increased feeding (Skjoldal et al. 1993; Fernö et al. 1998), the energetic cost must be offset by an energetic gain (ultimately to reduce time to maturation and increase survival and fecundity). We will analyse this decision under two different assumptions: (i) that fish at the spawning grounds decide to make a horizontal migration to a distant feeding area or (ii) that feeding fish on a daily basis decide whether to remain for another day or swim towards a less food deprived area.

Fish in the first scenario must also cover the cost of the return migration. Thus, swimming a distance  $D$  from an area with feeding rate  $F_1$  and standard metabolic cost  $z_1$  to feed in an area with feeding rate  $F_2$  and standard metabolic cost  $z_2$  and then back again during the time period  $T$  is energetically beneficial if

$$(7a) \quad F_2 T_f - 2PT_m - z_2 T > F_1 T - z_1 T$$

where  $T$  is total time and  $T_f$  is the time available for feeding ( $T - 2T_m$ ). The feeding season in the Norwegian Sea is usually from April to August (Skjoldal et al. 1993; Fernö et al. 1998), about  $T = 5$  months. Note that eq. 7a assumes no swimming cost (but still standard metabolic costs  $z$ ) for fish that choose to remain on the spawning grounds during the feeding season. If we further assume equal standard metabolic costs for the two localities (i.e., no temperature effects, as in eq. 2), we have a metabolic benefit of migration to a distant feeding area when

$$(7b) \quad F_2 > \frac{F_1 T(U^* + u) + 2DP}{T(U^* + u) - 2D}.$$

**Table 1.** Symbols used in the equations in the text.

Symbol	Explanation	Value	Units
	Length – swimming cost allometry exponent	1.42 <sup>a</sup>	
	Swimming speed – swimming cost allometry exponent	2.42 <sup>a</sup>	
	Length–metabolism allometry exponent	2.47 <sup>b</sup>	
$a_1$	Swimming cost allometry constant	$5.18 \times 10^{-3a}$	
$a_2$	Length–metabolism allometry constant	$1.47 \times 10^{-5b}$	
$a_3$	Length–weight allometry constant	Species specific	
$b$	Length–weight allometry exponent	Species specific	
$C$	Total energy cost		J·s <sup>-1</sup>
$C/W$	Energy cost per body weight		J·g <sup>-1</sup> ·s <sup>-1</sup>
$C/(UW)$	Energy cost per distance		J·g <sup>-1</sup> ·m <sup>-1</sup>
$c$	Conversion factor from energy contents to wet weight of prey	1800	J·g wet weight <sup>-1</sup>
$D$	Horizontal migration distance		m
$E$	Energy use by migrating distance $D$		J
$F_i$	Feeding rates at site $i$		J·s <sup>-1</sup>
$L$	Fish body length		cm
$N_i$	Prey concentration at site $i$		Individuals·m <sup>-3</sup>
$P$	Power needed to overcome the drag of a moving object		J·s <sup>-1</sup>
$R_i$	Feeding rations at site $i$		g wet weight prey·g wet weight fish <sup>-1</sup> ·day <sup>-1</sup>
$r$	Sensory range of fish		m
$s_f$	Part of the diel cycle that is allocated to feeding		s
$T$	Time available for migration and feeding = $T_f + T_m$		s
$T_f$	Time available for feeding		s
$T_m$	Migration time		s
$U$	Individual swimming speed		m·s <sup>-1</sup>
$U_T$	Total travel speed = $U + u$		m·s <sup>-1</sup>
$u$	Average directional speed of the current		m·s <sup>-1</sup>
$W$	Fish weight		g
$W_{\text{prey}}$	Prey weight		g
$z, z_i$	Standard metabolism of the fish (at site $i$ )		J·s <sup>-1</sup>

**Note:** Symbols with an asterisk in equations refer to parameter values under optimal cruising speed  $U^*$ .

<sup>a</sup>Ware (1978).

<sup>b</sup>Brett (1964).

If the current speed and direction experienced by the fish are constant during migration (feeding and spawning migration), then we may exclude  $u$  from eq. 7b. On the other hand, if the fish may take advantage of horizontal or vertical variation in  $u$ , e.g. in a horizontal gyre or in a vertical countercurrent system (Harden Jones 1957, 1963, 1965, 1968; McCleave et al. 1984), this behaviour may be of great biological importance by saving travel time and travel costs and increasing feeding time.

The daily feeding ration  $R$  can be expressed from the instantaneous feeding rate  $F$  by

$$(8) \quad R_i = \frac{F_i s_f}{Wc}$$

( $i = 1$  or  $2$  as in eqs. 7a and 7b) where feeding rate is scaled against the weight of the fish, the energy concentration of the prey ( $c$ ), and the fraction of the day spent feeding ( $s_f$ ). Minimum required daily increase in ration to offset the cost of migration can now be calculated from eq. 7b. If day length increases along the feeding migration route, then a smaller increase in  $F_2$  is needed to obtain a sufficiently high  $R_2$  to facilitate migration.

The second scenario describes the choice for an individual that shall decide whether to migrate a smaller distance  $D$  to feed there for today or remain where it is for at least one more day. Standard metabolic costs may be considered constant over this distance. If we further assume that migration time is at the expense of feeding

time, we may express a different criterion for horizontal migration based on eq. 7a:

$$(7c) \quad F_2 > \frac{F_1 T(U^* + u) + DP}{T(U^* + u) - D}$$

That is, migration will occur if feeding rate at area 2 can replace energy lost due to migration. Note that eq. 7c does not assume that the fish will have to reserve energy for the return migration. Neither is the cost of a countercurrent ( $-u$ , metres per second) in the homing migration included.

If feeding rate approaches stomach capacity, the feeding motivation for further migration will cease. Feeding rate will depend on a series of factors, including sensory range of the fish ( $r$ ), food concentration ( $N$ ), swimming speed of the predator ( $U$ ), and prey size ( $W_{\text{prey}}$ ) (Giske and Salvanes 1995; Aksnes and Utne 1997). To obtain an encounter-limited feeding at a rate of  $F$  (joules per second), a predator will need a concentration (individuals per cubic metre) of

$$(9) \quad N_i = \frac{F_i}{\pi r^2 (U + u) c W_{\text{prey}}}$$

Both  $U$  and to a smaller extent  $r$  are length dependent (sensory range will predominantly be depth dependent, Aksnes and Utne 1997). Although swimming speed under feeding ( $U$ ) will differ

from optimum cruising speed  $U^*$ , size differences will probably remain. Optimum swimming speed is twice as high for a 50-cm fish as for a 10-cm fish and three times as high if  $u = 0.5 \text{ m}\cdot\text{s}^{-1}$ . Hence, a 10-cm fish will probably need more than twice the prey concentration to achieve the same feeding rate  $F$  as a 50-cm fish.

Current speed ( $u$ ) in the Northeast Atlantic between 55°N and 80°N and from 5°W to 15°E including the main 20- to 50-km branch of the strong Atlantic current was calculated by taking average speed and direction for every 1°N from available field data (Poulain et al. 1996) and model simulations (E. Svendsen and M. Skogen, Institute of Marine Research, Bergen, Norway, personal communication). The average current speed in a northerly direction during the period from April to August from 1993 to 1996 was estimated by vector analysis. Arrays indicating current speed and direction were vectored into a north–south and east–west component. From this contribution the northern component was calculated.

### Field sampling

Model predictions were tested using acoustic and trawl data for four Atlantic species (Atlantic herring, blue whiting, mackerel, and capelin) collected from scientific cruises on R/V *Johan Hjort* and R/V *G.O. Sars*. The goal of these surveys was to estimate the abundance of commercially important pelagic species over a broad geographical range (Anonymous 1996a, 1996b; Monstad et al. 1996; Fernö et al. 1998; Gjøsæter 1998). Thus, these data sets are ideal for testing our model predictions. For Norwegian spring-spawning Atlantic herring, data are from April–May (spring feeding) and July–August (late-summer feeding) 1993–1996 cruises. Data were used to calculate overall migration distances and to determine geographic patterns of length, weight, and age. Average lengths ( $\pm$ SE) for every 1.0°N from 62°N to 80°N and between 5°W and 15°E were calculated from subsamples ( $N = 100\text{-trawl}^{-1}$  in 146 trawl hauls). The distance that an individual shoal migrates was not available from the data set. Thus, we assumed that spawning is limited in space and time for each species; this has been shown to be a good approximation (Fernö et al. 1998). Atlantic herring (as well as blue whiting, mackerel, and capelin) have reasonably defined spawning sites (Fig. 1). Although variations in spawning locations do exist both within and between years (Dragesund et al. 1997; Gjøsæter 1998), the majority of spawning is concentrated within a small geographical location providing a core spawning site from which to estimate migration distance. Moreover, all species in this study have a pronounced south–north migration pattern. The end result is a data set from which we can estimate migration distance and the relationship between length and latitude.

A similar procedure was applied to blue whiting, mackerel, and capelin. Data from July–August 1993–1996 (late-summer feeding) were applied for blue whiting, while data from July–August 1991, 1993, 1995, and 1996 (late-summer feeding) and September–October 1990–1992 (most northern extent of the migration) were applied for mackerel and capelin, respectively. The time periods chosen for each species reflect maximum spatial coverage. Capelin in the Barents Sea ecosystem achieve the most northerly extent of their migration later than Atlantic herring, blue whiting, and mackerel studied in the Norwegian Sea. This information is used to include only those data from the feeding period where these species are distributed furthest to the north. The years used represent periods when population size was high and long-distance feeding migration was pronounced for each species applied in the analysis.

For Atlantic herring, we have also included a westerly migration during the feeding migration in addition to the pronounced northerly migration (Misund et al. 1997). Atlantic herring migrate to the polar front area in the western part of the Norwegian Sea (Fig. 1), where they feed during late spring and early summer. Later, they swim further north. This migration pattern is not as pronounced as for blue whiting and mackerel in the Norwegian Sea. Capelin prefer the productive areas connected to the Arctic ice edge during

summer feeding, giving a more pronounced northward feeding migration. Thus, in blue whiting, mackerel, and capelin, we have only incorporated a northerly migration pattern from the spawning sites. Again, this is believed to represent conservative minimum values on migration distance for each length group and species. A simplistic northward migration route may nevertheless reveal important aspects of long-distance migration. Repeated surveys over subsequent years also indicate this to be appropriate (Anonymous 1996a).

## Results

### Model simulations

#### *Assumption 1. Long-distance migration*

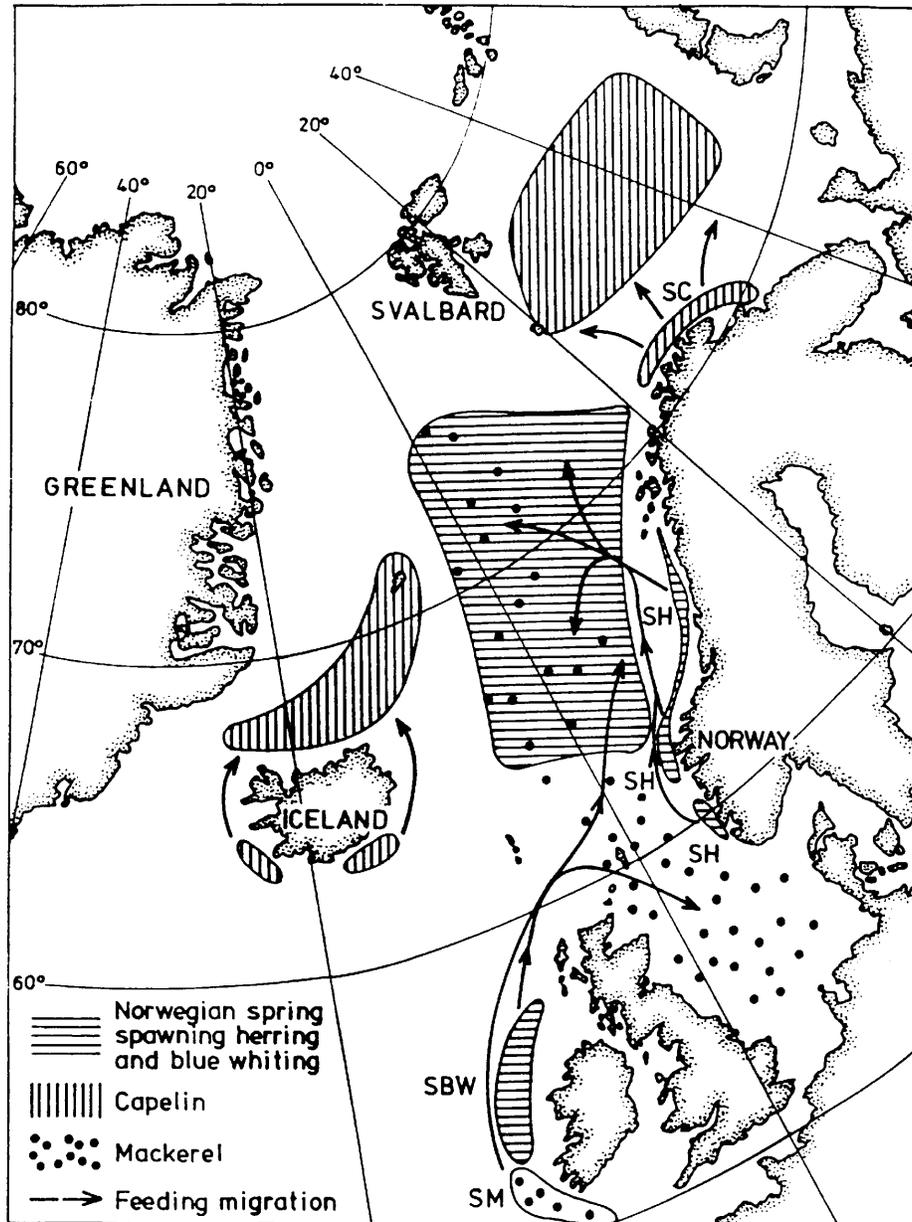
The migration model predicts a decrease in swimming cost per body mass with increasing size of fish, so that the most optimal swimming speed is size dependent (cf. Ware 1978; Videler 1993). Effects of current speed override size effects at high currents in the swimming direction, while size differences are maximized for the expensive countercurrent swimming (Fig. 2). The time needed to swim  $D = 500 \text{ km}$  will be length dependent in the absence of water currents, while strong currents in the swimming direction reduce differences in migration time between sizes (Fig. 3).

Minimum ration to offset a horizontal migration does not vary significantly among species. Figure 4 is based on length–weight relationships for Atlantic herring ( $a_3 = 6.9 \times 10^{-3}$ ,  $b = 3.04$ ) but on sockeye salmon data in eqs. 1 and 2. The parameters  $a_3$  and  $b$  were also measured from the other three species, with only small differences found in swimming costs. The maximum difference between species in minimum ration to offset migration was found to be 6% between 10-cm capelin and mackerel at low  $R_1$  and  $u = 0$ . The increase in minimum ration to initiate an energetically beneficial feeding migration of  $2D = 1000 \text{ km}$  is about 40–65%, without help from currents, for fish <20 cm (Fig. 4). However, if fish use prevailing currents ( $u = 0.5 \text{ m}\cdot\text{s}^{-1}$ ), without the penalty of a countercurrent spawning migration, the minimum increase in ration to initiate a feeding migration is only 15% and essentially independent of fish size (Fig. 4).

#### *Assumption 2. Short daily migrations*

Daily decision to migrate will depend on body size, water currents, day length, and expected differences in feeding rates (Fig. 5). (The nonlinearities in Fig. 5 appear when  $F_1$  is close to standard metabolic demands  $z$ . At such very low feeding rates, the small amount of energy required to transport the fish 1 km is big relative to the low  $F_1$ .) Food competition in a large resident population will drive  $F_1$  to the left in Fig. 5, so that a smaller absolute difference between  $R_2$  and  $R_1$  will initiate a migration (eq. 7a). Although any food density  $N$  gives twice as high  $F_1$  for a 50-cm than for a 10-cm fish (eq. 9), this advantage is counteracted by the far higher energy demands of the larger fish. Smaller individuals, with both smaller stomachs and lower swimming speed, will experience satiation at far lower feeding rates (measured as joules per second) than larger fish. As the initial food density in a virgin area decreases due to feeding, the larger fish will experience nonsatiating food concentration and thereby food competition first. Large individuals can therefore be expected to continue their swimming towards areas

**Fig. 1.** Migration patterns of pelagic fish in the Northeast Atlantic. Atlantic herring, blue whiting, and mackerel migrations are shown for the Norwegian Sea, while capelin migration is shown for both the Barents Sea and Icelandic stocks. Different shading and symbols used to indicate feeding migration, feeding area, spawning migration, and spawning area for each species. Spawning areas: SH, Atlantic herring; SBW, blue whiting; SM, mackerel; SC, capelin. Migration data collected from Gjørseter (1980), Loeng (1981), FAO (1983), Ozhigin and Luka (1984), Monstad (1990), Holst and Iversen (1992), Røttingen (1992), Vilhjálmsson (1994), Walsh et al. (1995), Anonymous (1996a, 1996b), and Monstad et al. (1996).



with more food and for longer days of feeding opportunity before the smaller fish experience any competition, creating a size-dependent horizontal migration. Following currents will reduce the size-dependent difference in feeding rates needed for migration.

Since longer days give visual predators more time to feed, migration will be directed northward if the food gradients change in the same manner in all directions away from the present feeding area (compare Figs. 5A and 5B with Figs. 5C and 5D). Expectations with increasing day length are far more reliable than expectations with feeding rates

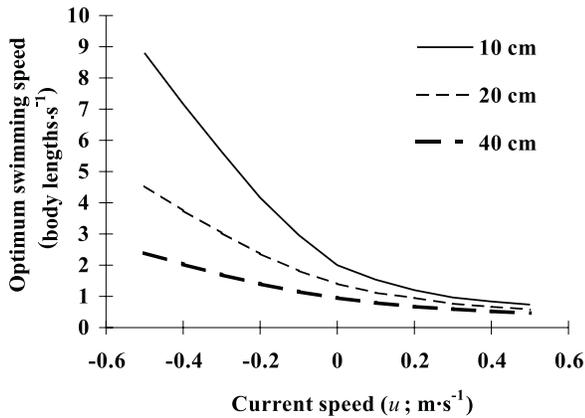
and currents. The predictable seasonal northward propagation of phytoplankton and zooplankton production present in the Northeast Atlantic during the feeding season may also influence the migration pattern of pelagic planktivores.

#### Model predictions

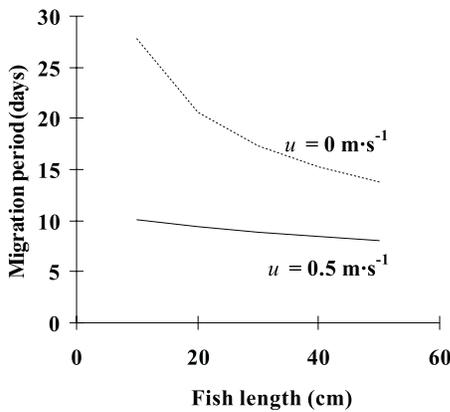
Based on the model results, three predictions emerge as follows.

- (1) Due to time constraints, visual predators under equal feeding conditions (given that food concentration is sufficiently low to impact feeding rate) will migrate pole-

**Fig. 2.** Swimming speed for which energy cost per distance travelled is minimum for various sizes of fish as a function of current speed  $u$ .



**Fig. 3.** Duration ( $T_m$ ) to migrate 500 km, swimming at optimal migration speed  $U^*$ , as a function of fish length  $L$  and current velocity  $u$ . Current speed may override size effects on days used for a 500-km migration at the most energy-efficient swimming speed.



wards in the feeding season to obtain longer days and feeding periods. This will apply to areas with pronounced latitudinal variation in day length and in particular to 40–70°N or S.

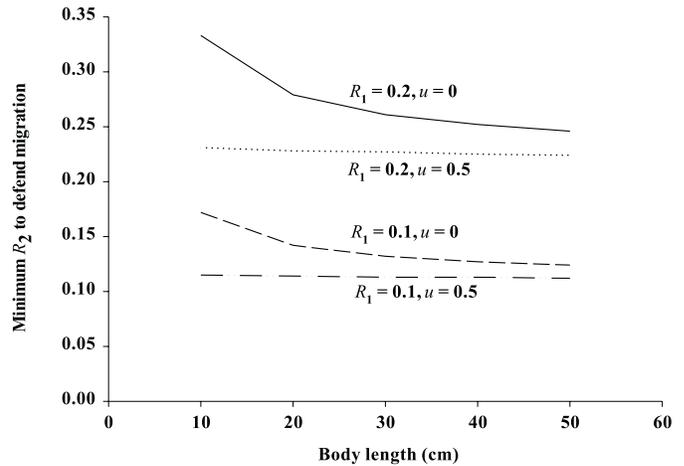
- (2) Larger individuals will experience food competition at higher food concentrations than smaller fish and will therefore benefit most from continual horizontal (northwards) feeding migration during summer. We therefore expect to find the average size of the individuals in a species to increase northwards.
- (3) Consistent variation in current speed  $u$  in the vertical or transverse to the direction of migration may enable individuals to utilize different migratory routes in feeding migrations and in the spawning migrations. This will benefit smaller individuals more than larger ones and will counteract some of the strongest size selection in prediction 2.

**Field data**

*Length-dependent migration*

Average fish length increased significantly with latitude

**Fig. 4.** Minimum food ration  $R_2$  at the destination to initiate a migration given food ration  $R_1$  at the present location and average current speed  $u$ .



for Atlantic herring, blue whiting, mackerel, and capelin (Fig. 6). Fish length ( $\pm$ SE) increased  $0.71 \pm 0.28$ ,  $1.01 \pm 0.08$ ,  $0.99 \pm 0.10$ , and  $0.50 \pm 0.05$  cm for each 1°N for Atlantic herring, blue whiting, mackerel, and capelin, respectively.

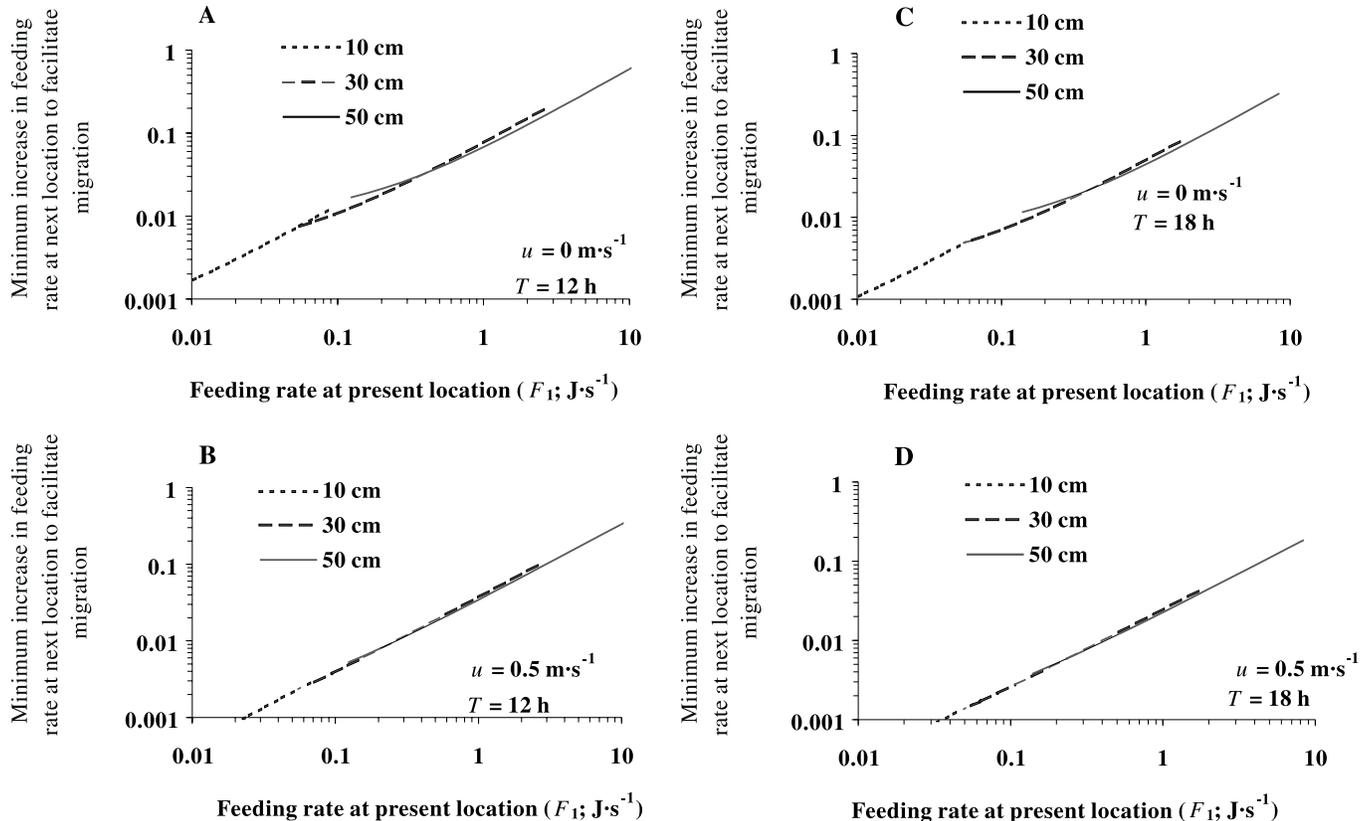
*Currents*

Current speed in April–July 1990–1993 at 1°N intervals from 55°N to 80°N and from 5°W to 15°E in the Northeast Atlantic is given in for depths of 20 and 250 m (Fig. 7). The chosen current depths are directly related to average migration depth for the selected species during the feeding period. We assume a migration depth for Atlantic herring, mackerel, and capelin to be around 20 m, while the migration depth for blue whiting is at about 250 m depth. Based on acoustic measurements, visual observations, and biological samples, there should be a good approximation between applied current depth and migration depth.

**Discussion**

Feeding migrations may be looked upon as opportunistic. The hunt for food drives pelagic fish in a northerly and northwesterly direction during spring and summer for several reasons: (i) inter- and intra-specific competition is forcing fish to move to new feeding areas (Wootton 1990), (ii) the zooplankton production cycle is initiated in the south and propagates northwards during spring and summer (Mann and Lazier 1991), thus forcing pelagic planktivorous fishes to follow the production of zooplankton, and (iii) prolonged day length increases the feeding period for visually feeding planktivorous fish, providing increased energy ingestion and energetic benefits (Suthers and Sundby 1996). Since day length increases significantly when heading north in boreal waters, fish may decide to swim towards north rather than west, even though the food concentration may be similar in other areas. However, Atlantic herring have a pronounced westerly migration pattern towards the polar front area during spring and early summer (Misund et al. 1997). This may be linked to higher phytoplankton and zooplankton produc-

**Fig. 5.** Energetic motivation to initiate small-scale migration to a new feeding area. The fish may at sunrise decide to stay where it is and feed all day ( $T = 12$  or  $18$  h of daylight) or migrate at optimum speed to a new area  $D = 1$  km away and feed there for the remaining hours of daylight ( $T_f = T - T_m^*$ ). If the difference in feeding rates ( $F_2 - F_1$ ) between these locations is above a threshold defined by the line for each fish size (eq. 7c), then horizontal migration is energetically profitable. The threshold for migration is lowest at long days and swimming with a current (Fig. 5D). Differences between size-classes are most pronounced in the absence of a following current (Figs. 5A and 5C).



tion in the polar front areas in the western part of the North-east Atlantic, where relatively warm Atlantic water mixes with colder Arctic water (Blindheim 1989; Fernö et al. 1998). There may be different plausible explanations for northward migrations in boreal waters during the summer feeding period. Random dispersal of fish within the Atlantic current system could be another explanation. Nevertheless, based on our field data on length-dependent migration pattern and model results, we strongly argue that food, together with favourable current and light conditions, predominantly influences the active migration pattern for pelagic fish.

### Prediction 1

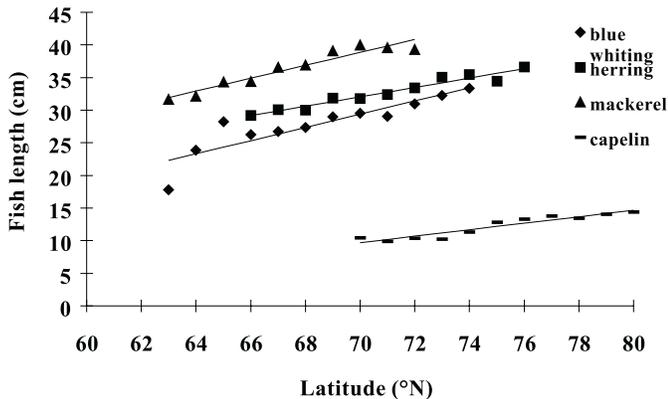
The field data for the Atlantic species support the first prediction that fish in general should swim northwards during summer to obtain longer days and thus more time to feed compared with areas further south. One should note that expectations with increasing day length are far more reliable than expectations with feeding rates and currents. A predictable seasonal northward propagation of phytoplankton and zooplankton production present in the Northeast Atlantic during the feeding season may also influence the migration pattern of pelagic planktivores. Highly productive polar front areas in the mixed region between Atlantic and Arctic water masses in the western part of the Norwegian Sea slightly modify this picture (see Fig. 1). Atlantic herring prefer to

feed in polar front areas during part of the summer feeding as opposed to blue whiting and mackerel in the Norwegian Sea. This may result in a more western distribution of Atlantic herring, at least when food is abundant in the polar front area. Nevertheless, Atlantic herring have a pronounced northward migration pattern during the feeding season, without considering their extensive western migration route. In all species, our estimates of length-dependent migration are most probably significantly underestimated and conservative.

### Prediction 2

The longest individuals of each species were consistently found furthest to the north. This supports the second prediction and relates to the greater swimming efficiency of longer fish as well as to the higher sensitivity to food concentrations. Pacific herring in British Columbia do not seem to migrate outside the continental shelf area (D. Hay, Department of Fisheries and Oceans, Victoria, B.C., personal communication), suggesting that they may be too small (<22 cm) to beneficially undergo such long-distance migrations. In addition to swimming more efficiently, large fish generally have greater fat reserves than small fish so that the capability for long-distance feeding migrations should increase with size (Videler 1993). It is possible that small fish cannot store or expend sufficient energy to travel long distances. Larger fish

**Fig. 6.** Latitudinal variation in average length of Atlantic herring, blue whiting, mackerel, and capelin. The linear equation  $y = ax + b$  and values of the correlation coefficient  $R^2$  for each species are as follows: Atlantic herring,  $y = 0.73x - 18.17$  ( $R^2 = 0.94$ ,  $n = 4696$ ); blue whiting,  $y = 1.01x - 41.56$  ( $R^2 = 0.79$ ,  $n = 5969$ ); mackerel,  $y = 0.99x - 30.61$  ( $R^2 = 0.92$ ,  $n = 4002$ ); capelin,  $y = 0.50x - 25.23$  ( $R^2 = 0.90$ ,  $n = 5905$ ). Data are from scientific cruises in 1990, 1992, 1993, 1994, and 1996 (Institute of Marine Research, Bergen, Norway).

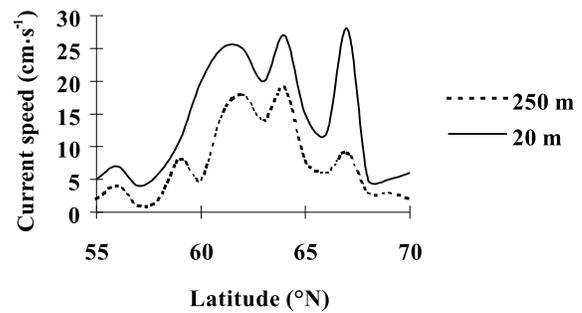


may swim longer distances at suboptimal swimming speeds without losing much energy, while smaller fish are much more sensitive to swimming speed energetics. Trump and Leggett (1980) predicted that with respect to distance, larger fish will have higher optimal swimming speeds and lower minimum specific energy expenditures and will experience smaller energetic penalties for swimming at speeds other than the optimal. Larger fish seem to benefit first by leaving an area with food competition (Fig. 5), so larger fish will then first occupy new and possibly highly productive feeding areas. Competition between species may also be important during the feeding season and influence migration patterns. In practice, Atlantic herring, blue whiting, and mackerel are competing for the same food resources (Fig. 1), thus creating an interspecific competition for zooplankton in the Norwegian Sea (Fernö et al. 1998).

### Prediction 3

The general size-specific migration shown in this study may be closely connected to the prevailing current system of the Norwegian and Barents seas. Adult planktivores rarely swim against the prevailing currents (Harden Jones 1968). A recent report on near-surface circulation of the Nordic seas by Poulain et al. (1996) gives the highest resolution and most detailed description of circulation patterns including the Norwegian and Barents seas. From the Faeroe–Shetland channel, Atlantic water will spread towards the northeast. The current spreads outside Stad (62°N), and the easterly border of the current follows the continental edge north along the continental slope. After spawning, Atlantic herring, blue whiting, and mackerel seem to associate with strong currents ( $>40 \text{ cm}\cdot\text{s}^{-1}$ ) up to 66–67°N, where the flow changes direction towards the west/northwest. Interestingly, after detailed tracking of Atlantic herring schools during the whole feeding period in 1995 and 1996, the Atlantic herring headed westward after reaching 66–66.30°N (Anonymous 1996a; Poulain et al. 1996). Not surprisingly, Atlantic her-

**Fig. 7.** Average current speed in the northern direction from April to July 1990–1993 at 20 and 250 m depth from 5°W to 15°E.



ring and possibly blue whiting and mackerel take advantage of the strong current flowing north and then westward to the polar front areas. Passive advection requires current speeds in the range of  $10\text{--}20 \text{ cm}\cdot\text{s}^{-1}$ , which is possible in the Continental Slope Current (Hansen and Jákupsstovu 1991). Weihs (1978) demonstrated that substantial (40–90%) energy savings can be achieved by migrating fish that move at a constant velocity relative to the bottom where both fish and tide are moving in the same direction. Presently, there exists no evidence on how pelagic fish navigate in the ocean, apparently without any external reference points such as the bottom or the coastline (see Harden Jones 1968). One challenge for future science is whether or how pelagic fish assess the current speed (“ground speed” versus “through-the-water speed”) and how these aspects may influence our understanding and quantification of fish migration. More synoptic field data on variation in the current system compared with the migration routes on proper spatiotemporal scales are required in order to establish how and to what extent fish may take advantage of the current system. However, field data from Poulain et al. (1996) and simulation models support the hypothesis that consistent variation in current speed may enable individuals to use different migratory routes in feeding migrations and in spawning migrations.

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