

DENSITY-DEPENDENT MIGRATORY WAVES IN THE MARINE PELAGIC ECOSYSTEM

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Abstract. The migration of large aggregations of animals that sweep through the landscape is a phenomenon with large consequences in many ecosystems. It has been suggested that such migrations are mediated by resource depletion. Under this hypothesis it has been shown that simple foraging rules may generate density-dependent migratory waves (DDMW) in which the speed and amplitude increase with animal abundance. We tested these predictions on a 32-year data set of the spatial distribution of the two youngest age groups of a small pelagic schooling fish, the capelin (*Mallotus villosus*), by the end of their annual feeding migration in the Barents Sea. Our data suggest that the two age groups divided the Barents Sea by forming migratory waves that moved in opposite directions. The aggregation and spatial displacement of these waves increased with increasing age-specific abundance. However, possibly through social interactions, migratory pattern was modified by the abundance of the other age group.

Key words: animal movement; area-restricted search; Barents Sea; capelin; gregarious behavior; *Mallotus villosus*; migration; pelagic schooling fish; spatial distribution.

INTRODUCTION

Massive migration of gregarious animals is a common phenomenon with large consequences in many ecosystems. Commonly, the species involved fluctuate markedly in abundance, gregariousness, and migratory pattern. Peaks in abundance are often associated with increased gregariousness and migratory behavior, resulting in more or less regular episodes of massive migration. Species with such variable migratory and gregarious behavior are found in many different ecosystems and make a highly diverse group, including, e.g., the desert locust (*Schistocerca gregaria*; Collett et al. 1998, Babah and Sword 2004), sea urchins (*Strongylocentrotus droebachiensis*; Bernstein et al. 1983, Scheibling et al. 1999), African wildebeest (*Connochaetes taurinus*; Musiega and Kazadi 2004), and pelagic schooling fishes such as herring (*Clupea harengus*; Ferno et al. 1998, Corten 2001) and capelin (*Mallotus villosus*; Gjøsæter 1998, Carscadden et al. 2001, Fauchald and Erikstad 2002).

Animal movement and migration may be initiated and guided by a spatial gradient in food or other environmental factors (Johnson et al. 1992, Wiens et al. 1993). A group of gregarious animals will, however, by their own aggregated spatial distribution, create a spatial gradient in prey with higher levels of resources towards the outer edges of the aggregation. At high densities, the result may be a spontaneously initiated

directional migration. The direction of such migrations may be random or it may depend on inherited or learned preferences or initial spatial heterogeneity in the environment. According to foraging theory, an individual should respond to spatial heterogeneity in a limiting resource by adjusting its turning rate and searching speed as a response to local resource density (Kareiva and Odell 1987). More specifically, an individual should increase its turning rate and reduce its speed in response to increased density of the resource. This behavior has been termed “area-restricted search,” with which the forager will concentrate its search activity in profitable areas with high resource levels. During a feeding migration, individuals that are at the head of the movement will, according to this theory, slow down when they experience high densities of food. In contrast, individuals that lag behind will speed up because they move through areas that are already depleted of food. Wilson and Richards (2000) showed that these simple principles will result in resource-mediated, density-dependent group formations. In their model, dense aggregations that swept through the habitat were formed under high densities. In the following, we term this phenomenon “density-dependent migratory waves” (DDMW). When a gregarious animal undertakes a directional feeding migration we expect, according to the DDMW theory, that the spatial distribution of individuals will form a front that is oriented perpendicular to the direction of the movement (e.g., Sword 2005). The aggregation of animals along the front should depend on the gradient in food density. When the gradient in food density is steep, differences in search pattern across the front should increase and the animals should be more

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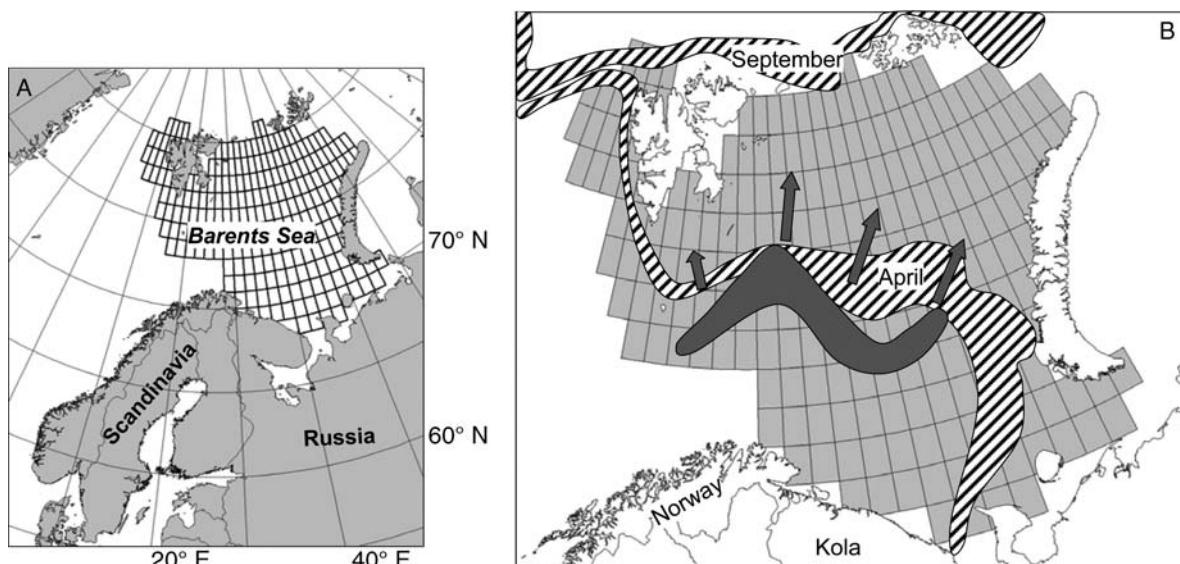


FIG. 1. (A) Study area and (B) major feeding migration of capelin in the Barents Sea. The geographical grid (1° latitude \times 2° longitude) in which capelin were found at least once during the study period (September) from 1972 to 2003 is indicated. (B) The shaded area is the main position of capelin in June before the start of the feeding migration (redrawn from Ozhigin and Luka [1985]). Arrows indicate direction of major feeding migration in late summer and fall. Hatched areas are the mean position of ice edge (25–50% ice cover) in April (maximum extent) and September (minimum extent) from 1989 to 2003. Ice data are from Cavalieri et al. (2004).

aggregated towards the frontal edge. When the gradient is formed by consumption, the spatial distribution of a gregarious, migrating species should be density-dependent. Under high abundance the depletion of food is great, the velocity of the migration should be high, and the animals should be more aggregated along the front (*sensu* Wilson and Richards 2000). In other words, the spatial distribution of the migrating animals should form a wave with speed and amplitude increasing with animal abundance.

We tested the predictions of the DDMW theory on a multiyear data set on the spatial distribution of capelin in the Barents Sea. Capelin is a small, short-lived, pelagic schooling fish, removes a considerable amount of the secondary production in the Barents Sea (Dalpadado et al. 2001, Gjøsæter et al. 2002b, Dalpadado et al. 2003), and is an important food item for herring (Gjøsæter and Bogstad 1998), cod (*Cadhus morhua*), seabirds, and marine mammals in the area (Hamre 1994, Sakshaug et al. 1994). Partly as a consequence of natural predation and harvesting, the abundance of capelin has fluctuated considerably in the last three decades (Gjøsæter and Bogstad 1998). In winter and spring, the northern and eastern parts of the Barents Sea are covered by ice (Fig. 1). The melting of sea ice during summer is followed by a bloom in primary and secondary production. From a central position in the Barents Sea in June, capelin make a feeding migration into the previously ice-covered waters during late summer and fall (Ozhigin and Luka 1985, Gjøsæter 1998; Fig. 1). Data on the spatial distribution of capelin were gathered in September, by the end of the yearly

feeding migration, and before the capelin return to the wintering areas in the central part of the Barents Sea (Gjøsæter 1998, Gjøsæter et al. 1998). Earlier studies have shown a negative relationship between the abundance of zooplankton and capelin in the Barents Sea (Gjøsæter et al. 2002b, Dalpadado et al. 2003). This has been attributed to grazing pressure, and we predicted accordingly that the migration of capelin should follow a DDMW. Specifically, we predicted that capelin should migrate faster and farther and have a more aggregated spatial distribution during years of high capelin abundance compared to years of low abundance.

METHODS

Data on abundance, distribution, and demographic parameters of capelin were gathered during the annual scientific cruises in the Barents Sea during September from 1972 to 2003 (Gjøsæter et al. 1998). The cruise tracks are laid out by regularly spaced east–west transects, with a distance of ~ 55 km between transects. Data from these cruises are used in stock assessments (Gjøsæter et al. 2002a), and the cruises are intended to cover the entire stock of capelin in the Barents Sea. The geographical distribution of capelin was measured acoustically, and otoliths (i.e., ear stones) were used to age individuals and construct age frequency distributions. Biological samples were taken by a pelagic trawl at regular intervals and whenever the characteristics of the echogram changed. When capelin were present in the catches, the length, mass, age, sex, and other characteristics were recorded for a subsample of 100 individuals.

Sampling methods are described in detail in Gjøsæter et al. (1998).

Geographical grid, age groups, and abundance

The Barents Sea was divided into a grid defined by 1° latitude \times 2° longitude. The density of capelin from each age group was assigned to the grid cells based on the acoustic and biological samples (Gjøsæter et al. 1998). The study area was defined by the subset of grid cells in which capelin had been found at least once during the study period (Fig. 1). Five age groups of capelin were recorded during the cruises. The two oldest age groups were not present in all years. When present, the spatial distribution of the four oldest age groups was similar, while the spatial distribution of the youngest age group differed markedly from the others. We therefore present the results of the analyses of the two youngest age groups separately (1-yr-old capelin, age group 1; 2-yr-old capelin, age group 2). Numerically they represented on average 84% of all capelin recorded. The abundance of capelin for each age group and year was calculated from the density estimates from the grid. The abundance of the two age groups fluctuated markedly (Fig. 2). Abundance estimates were \log_{10} -transformed in all analyses.

Spatial displacement and spatial gradients

To investigate the interannual variation in spatial displacement, we calculated the center of the mass of the distribution (CMD) for each age group and year. The coordinates (X , Y) of a CMD was calculated as $(\sum_i x_i N_{i,j} / \sum_i N_{i,j}, \sum_i y_i N_{i,j} / \sum_i N_{i,j})$, where x_i , y_i is the position of the midpoint of grid cell i in the X and Y directions of a stereographic projection and $N_{i,j}$ is the estimated number of capelin of age group j in grid cell i . The age-specific main direction in the displacement between years was found by a principal component analysis (PCA) with the X and Y coordinates of the CMDs as variables. We used the value along the principal axis as a measure of yearly displacement. Assuming that the feeding migration starts from approximately the same position along the principal axis each year (cf. Fig. 1), the yearly displacement in CMD is a proxy for the speed of the feeding migration. The DDMW predicts that the speed of the migration should increase with increasing density. We tested this prediction by analyzing the relationship between the spatial displacements in CMDs and the total abundance of each age group in multiple regressions.

Under a directional feeding migration, we expected the spatial distribution to be nonstationary. Specifically, under a DDMW the animals at the frontal edge should have a lower speed than the animals that lag behind. The density of animals should accordingly increase in the migratory direction with the highest density at the front of the migration. To test for such spatial trends in density, we performed multiple regression analyses for each year with the density within all nonzero grid cells as

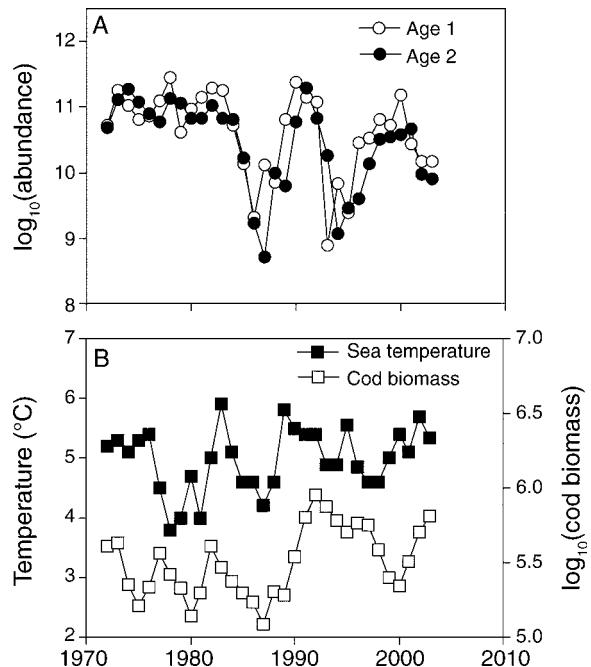


FIG. 2. (A) Estimated total number of individuals of 1-yr-old (age group 1; open circles) and 2-yr-old (age group 2; solid circles) capelin within the study area from 1972 to 2003. Note the \log_{10} scale. (B) Temperature and the spawning stock biomass (SSB; 1 metric ton = 1000 kg) of cod in the following year from 1972 to 2003 (data from Anonymous [2004]).

the dependent variable and the X and Y coordinates as independent variables. Densities were \log_{10} -transformed to meet the assumption of normality.

Spatial structure

To measure the spatial aggregation of an age group within a year, we calculated the spatial autocorrelation in densities between neighboring grid cells. If capelin has an aggregated spatial distribution and grid cells are smaller than the scale of aggregation, the correlation between neighboring cells should be large. We used Moran's I as a measure of spatial autocorrelation (Legendre and Fortin 1989, Fauchald et al. 2000). Densities were $\log_{10}(\text{density} + 1)$ -transformed. The variance in the log-transformed density increased with increasing total abundance for both age groups. This might bias the correlation coefficients. To keep the variance in density constant between years, irrespective of total abundance, the data were standardized to mean zero and standard deviation equal to one before entering the analyses. We predicted that a directional migration would affect the spatial orientation of the large-scale patches of capelin. Specifically, we predicted the spatial distribution to form a band that was oriented perpendicular to the direction of the migration. To inspect such direction dependencies, we calculated Moran's I index between neighbors in the four directions (south–north, southwest–northeast, east–west, and northwest–south-

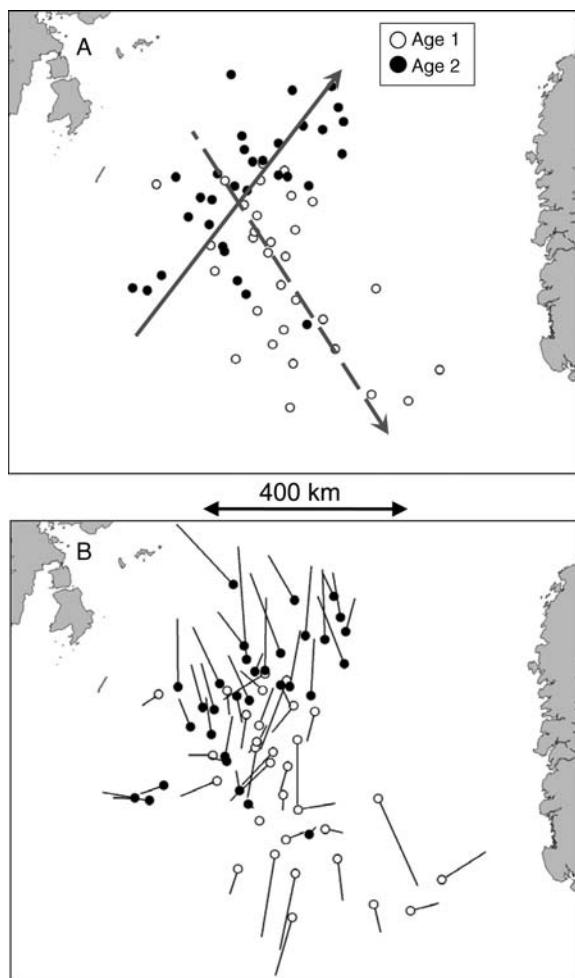


FIG. 3. Spatial distribution, principal displacement axes, and density gradients of 1- and 2-yr-old capelin (age groups 1 and 2, respectively). Circles are the center of the mass of the distribution (CMD) of 1-yr-old (open circles) and 2-yr-old (solid circles) capelin from 1972 to 2003. (A) Dashed and solid arrows show principal displacement axes of the positions of the CMDs for age group 1 and age group 2, respectively. (B) Lines show the direction and strength (length of the lines) of the spatial gradient in densities (see Results: *Spatial displacement and gradients*) for each year.

east) separately. According to the DDMW theory, the aggregation of animals should increase with total abundance. We tested this prediction by analyzing the relationship between the spatial autocorrelation and the total abundance of each age group in multiple regressions.

Sea temperature, competition, and predation

It has been suggested that the spatial distribution of capelin in the Barents Sea is determined by sea temperature (Gjøsaeter 1998). Specifically, ocean climate might affect the position of the start of the feeding migration and the migration length. Ocean climate was accordingly included as a confounding variable in the

analyses. The climate fluctuations of the Barents Sea are partly determined by the advection of warm Atlantic water and partly by teleconnections of large-scale atmospheric climate anomalies (Ottersen and Stenseth 2001, Ingvaldsen et al. 2004). These climatic drivers cause marked and synchronous differences in sea temperature between years. The “Kola section” is a monthly, long-term data series of sea temperatures along a fixed transect (33.5° E and 70.5°–72.5° N, 0–200 m depth) that capture the climatic anomalies of the Barents Sea (Ottersen and Stenseth 2001). We used Kola section data from September (Bochkov 1982) to investigate the effect of sea temperatures on the spatial distribution of capelin. Using temperature data from other months or data on the percentage of ice cover (data from Cavalieri et al. [2004]) gave similar results and did not alter our conclusions.

Competition between the two age groups might be an important factor that affects their spatial distribution. Due to their larger size, age group 2 might for example dominate age group 1, and a high abundance of age group 2 might consequently have an impact on the spatial distribution of age group 1. To control for such effects, we included the abundance of the other age group in the analyses.

Predation pressure might affect the spatial distribution and migration of capelin. Abundance of predators should accordingly be included as a confounding variable in the analyses. Cod is the major predator on capelin (Bogstad and Gjøsaeter 2001), and the abundance of this predator has varied considerably the last decades (Anonymous 2004; Fig. 2). We used the estimated spawning stock biomass of cod (Anonymous 2004) the following spring as a measure of predation pressure during the feeding migration of capelin.

RESULTS

Spatial displacement and gradients

The centers of the spatial distribution for each year and age group are shown in Fig. 3A. One-year-old capelin had generally a more southerly and easterly distribution than 2-yr-old capelin. Mean differences in the positions of CMDs between age groups 1 and 2 were in the east direction 64 km (120, 9; 95% CL) and in the north direction –166 km (–136, –197). The main direction of the spatial displacements, as defined by the principal axis from the PCA analysis (Fig. 3A), ran in a northwest–southeast direction for age group 1. This axis explained 69% of the variation in the position of the CMDs. For age group 2, the principal axis ran in a southwest–northeast direction and explained 78% of the variation (Fig. 3A).

The spatial gradients in density for each year and age group were investigated by multiple regressions with density within the grid cells as the predictor variable and the X and Y coordinates of the grid cells as explanatory variables. The estimated coefficients for X and Y reflect the direction and strength of the spatial gradients in

TABLE 1. Multiple regression analyses of the yearly displacement in the distribution of 1- and 2-yr-old capelin (age groups 1 and 2, respectively).

Factors	Spatial displacement, CMD (km)				Distance, CMD (km)	
	Age group 1		Age group 2		From age group 1 to age group 2	
	Estimate (95% CL)	$P > t $	Estimate (95% CL)	$P > t $	Estimate (95% CL)	$P > t $
Intercept	0.0 (-41.0, 41.0)	1.000	0.0 (-35.0, 35.0)	1.000	222.5 (189.7, 255.4)	0.000
Abundance						
Age group 1	167.2 (70.7, 263.7)	0.002	-87.8 (-170.2, -5.4)	0.046	144.8 (67.7, 222.0)	0.001
Age group 2	-231.6 (-321.8, -141.4)	<0.001	217.2 (140.2, 249.2)	<0.001	-141.1 (-213.2, -68.9)	0.001
Environment						
Temperature	-113.1 (-196.6, -29.6)	0.013	68.1 (-3.2, 139.4)	0.072	-105.8 (-172.6, -39.1)	0.004
Cod standing stock biomass	173.4 (-21.9, 368.7)	0.093	12.2 (-154.5, 179.0)	0.887	133.6 (-22.6, 289.7)	0.105

Notes: Independent variables are total abundance of the two age groups (\log_{10} -transformed), sea temperature ($^{\circ}\text{C}$), and the spawning stock biomass of cod in 1000 tons [1 metric ton = 1000 kg] (\log_{10} -transformed). Independent variables were standardized to mean equal to zero. Spatial displacement, CMD is the position in kilometers of the center of the mass of the distribution (CMD) along the principal displacement axis (cf. Fig. 3A). Distance, CMD is the distance in kilometers between the CMDs of the two age groups. Statistics indicating fit for the models with all factors included are: spatial displacement, age group 1, $R^2_{\text{adj}} = 0.48$, $F_{4,27} = 8.05$; spatial displacement, age group 2, $R^2_{\text{adj}} = 0.56$, $F_{4,27} = 10.96$; distance from age group 1 to age group 2, $R^2_{\text{adj}} = 0.54$, $F_{4,27} = 10.20$. Data were gathered during the annual scientific cruises in the Barents Sea during September from 1972 to 2003.

density. The mean estimate for the increase in \log_{10} density (original data in number per square kilometer) per kilometer in the east direction were -0.14 (-0.41 , 0.12) $\times 10^{-3}$ for age group 1 and -0.35 (-0.55 , -0.15) $\times 10^{-3}$ for age group 2. Mean estimates in the north direction were -0.81 (-1.20 , -0.43) $\times 10^{-3}$ and 1.28 (0.91 , 1.66) $\times 10^{-3}$ for age groups 1 and 2, respectively. Accordingly, the spatial gradients of the two age groups ran, on average, in different directions (Fig. 3B); while the densities of 1-yr-old capelin mainly increased southward, the densities of 2-yr-old capelin increased toward the northwest.

Abundance and spatial displacement

We used multiple regressions to investigate the relationships between the displacement of the two age groups along their principal axes and their total abundance, sea temperature, and biomass of cod (Table 1). There was a positive correlation between the abundance of the two age groups ($R^2 = 0.52$). These two variables were therefore analyzed both alone and together in the models. The directions of the axes are as shown in Fig. 3A.

For age group 1, we found a negative relationship between the displacement along the principal axis and temperature, meaning that age group 1 was found further to the northwest in warm years (Table 1). Increased biomass of cod was marginally associated with a displacement in the southeast direction. We found strong relationships between the displacement of age group 1 and the abundance of the two age groups. However, these relationships worked in opposite directions (Table 1, Fig. 4A, B). When entered alone, there was no significant relationship between the displacement of age group 1 and its own abundance ($P = 0.78$).

However, the displacement of age group 1 was negatively related to the abundance of age group 2 ($P = 0.004$; Fig. 4A). When this effect of age group 2 on displacement of age group 1 was controlled for, the relationship between the displacement of age group 1 and its own abundance became significantly positive (Table 1, Fig. 4B). Accordingly, age group 1 was displaced to the southeast when its own abundance was high. However, that displacement was heavily influenced by the abundance of age group 2, for which abundance was positively associated with a displacement to the northwest.

For age group 2, there was a marginally positive relationship between the displacement along the principal axis and temperature (Table 1). We found no significant relationship between the displacement and the biomass of cod. Like age group 1, there were strong but opposite relationships between the displacement and the abundance of the two age groups (Table 1; Fig. 4C, D). When entered alone, there was a significant positive relationship between the displacement of age group 2 and its own abundance ($P < 0.001$; Fig. 4C). When also entered alone, the abundance of age group 1 was marginally positively related to the displacement of age group 2 ($P = 0.06$). However, when this effect of age group 2 was controlled for, the relationship between the abundance of age group 1 and displacement of age group 2 became significantly negative (Table 1, Fig. 4D). Thus, age group 2 was displaced to the northeast when its own abundance was high, while high abundance of the other age group was related to a displacement in the opposite direction. It should be noted that the abundance of age group 2 was more strongly related to the spatial distribution of both age groups than the abundance of age group 1. Thus, the distance between

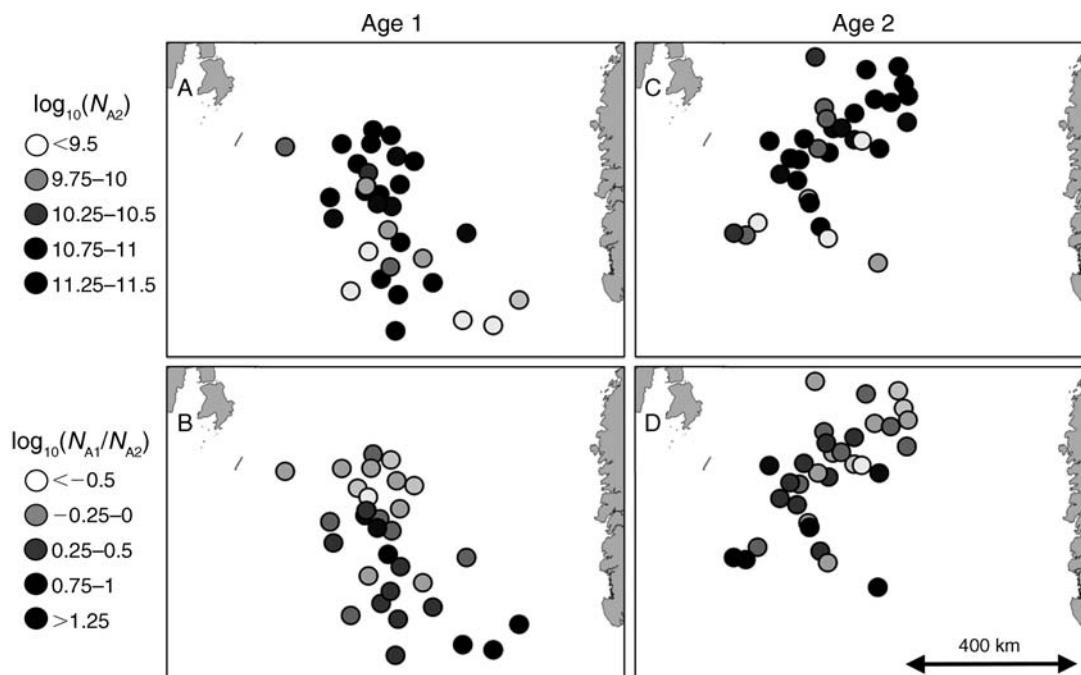


FIG. 4. Spatial distribution of the center of the mass of the distribution of (A, B) 1-yr-old capelin (age group 1, A1) and (C, D) 2-yr-old capelin (age group 2, A2). Each circle represents one year and shows the average distribution of the respective age groups in a given year (age 1 in A and B; age 2 in C and D). Shading of the circles represents the total abundance estimate (the total estimated number of capelin in the study area) for each year. The log-transformed total abundance of age 2 capelin [$\log_{10}(N_{A2})$] is shown in (A) and (C), and the log-transformed abundance of age 1 capelin relative to the abundance of age 2 capelin [$\log_{10}(N_{A1}/N_{A2})$] is shown in (B) and (D). Thus, (A) and (C) show that both age groups are displaced to the north in years of high abundance of 2-yr-old capelin. On the other hand, (B) and (D) show that both age groups are displaced to the south in years with high relative abundance of 1-yr-old capelin.

the CMDs of the age groups increased with increasing abundance of 1-yr-old capelin, while it decreased with increasing abundance of 2-yr-old capelin and increasing temperature (Table 1).

The results are illustrated in Fig. 5 in which the spatial distributions of the two age groups are shown for three selected years. In years when the abundance of age group 2 was high, both age groups migrated deep into the previously ice-filled areas in the northern part of the study area, with age group 2 in the lead (e.g., 1974; Fig. 5). In years when the abundances of both age groups were low, they were found in the central part of the study area, indicating low migratory activity (e.g., 1986; Fig. 5). When the abundance of age group 1 was high relative to age group 2, the age groups were displaced to the south and southeast, indicating a migration led by the youngest age group into the southeastern part of the study area (e.g., 1996; Fig. 5).

Abundance and spatial structure

Spatial aggregation was defined as the autocorrelation between neighboring cells. The relationship between spatial aggregation and capelin abundance, environmental variables, and the direction between neighbors was investigated in a multiple regression (Table 2). Nonsignificant interactions between direction and the

other variables were removed from the models. For both age groups, the spatial autocorrelation was positive in all directions, indicating a patchy spatial distribution. However, the autocorrelation between neighbors in the east–west direction was higher than the other directions for both age groups (Table 2, Fig. 6), suggesting that the aggregations were elongated in the east–west direction (cf. Fig. 5). It should be noted, however, that the spacing between adjacent grid cells differed depending on the direction. These differences might generate spurious direction dependencies.

For age group 1, the spatial autocorrelation (i.e., aggregation) was negatively related to cod biomass, while temperature showed a marginally positive relationship (Table 2). Age group 1 was accordingly less aggregated under high predation pressure, while it had a tendency to be more aggregated under high temperatures. Spatial autocorrelation of age group 1 was positively related to its abundance. This applied to models in which the abundance was entered alone ($P < 0.001$; Fig. 6A) and when it was controlled for the abundance of age group 2 (Table 2). Entered alone, the degree of spatial autocorrelation of age group 1 was also positively related to the abundance of age group 2 ($P < 0.001$). However, when controlling for the abundance of

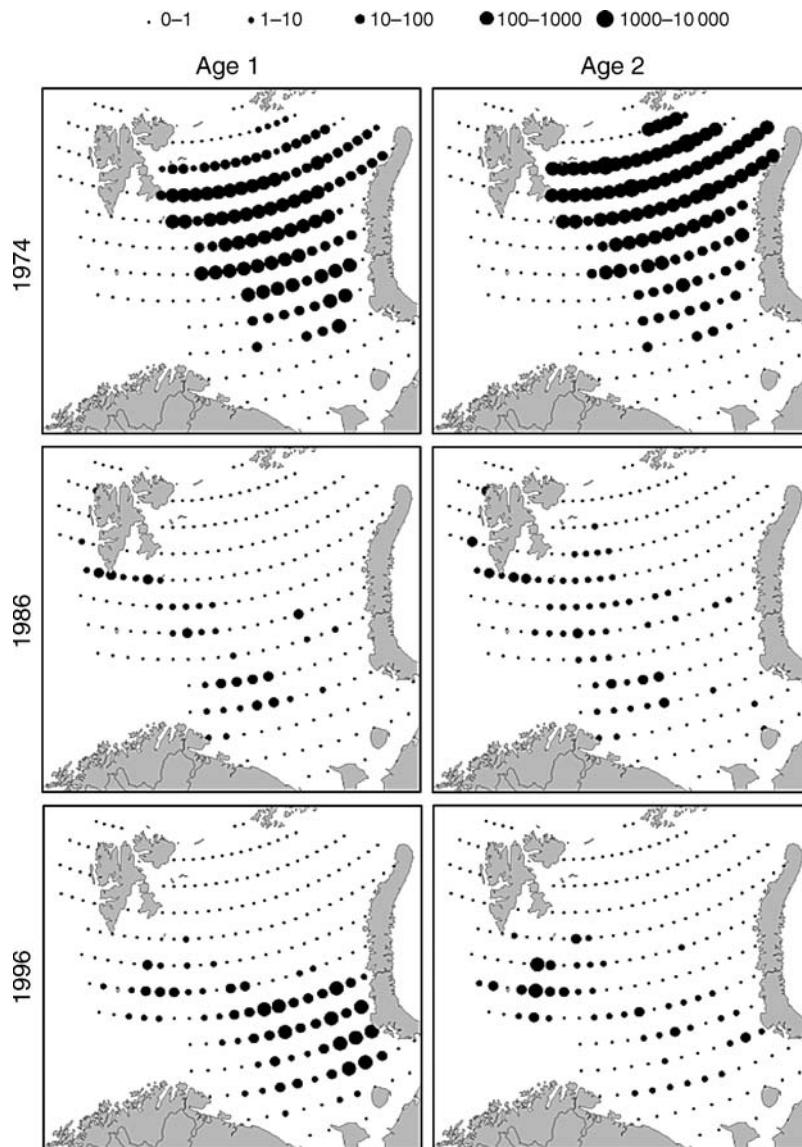


FIG. 5. Spatial distribution of 1-yr-old capelin (age group 1; left panels) and 2-yr-old capelin (age group 2; right panels) for three selected years. Circle size indicates density (no./km²). The year 1974 was one with a high abundance of both age groups, 1986 was a year with generally low abundance, and 1996 was a year with high abundance of age group 1 relative to age group 2.

age group 1, this relationship became marginally negative (Table 2).

For age group 2, we found no significant relationships between the environmental parameters and the spatial autocorrelation (Table 2). Similar to that of age group 1, the autocorrelation of age group 2 was positively related to its own abundance both entered alone ($P < 0.001$; Fig. 6B) and when controlling for the abundance of age group 1 (Table 2). When the abundance of age group 1 was entered alone, it was positively related to the autocorrelation of age group 2 ($P < 0.001$). However, when controlling for own abundance, this relationship became nonsignificant (Table 2).

The results are illustrated in Fig. 5 for three selected years. In years of high abundance (e.g., 1974 and 1996 for age group 1 and 1974 for age group 2), the age groups were aggregated in well-defined areas. In years of low abundance (e.g., 1986 for age group 1 and 1986 and 1996 for age group 2), the age groups had a more scattered spatial distribution.

DISCUSSION

This study demonstrates a strong relationship between the abundance and the spatial migratory pattern of a small pelagic schooling fish. High abundance was associated with increased aggregation and a longer, presumably faster, migratory movement. We suggest

TABLE 2. Multiple regression analyses of the spatial aggregation of 1- and 2-yr-old capelin (age groups 1 and 2, respectively); values are estimates and 95% CL of Moran's *I*, with significance levels.

Factor	Age group 1		Age group 2	
	Estimate (95% CL)	<i>P</i> > <i>t</i>	Estimate (95% CL)	<i>P</i> > <i>t</i>
Direction				
E-W	0.725 (0.695, 0.755)	<0.001	0.734 (0.701, 0.767)	<0.001
S-N	0.552 (0.509, 0.594)	<0.001	0.538 (0.491, 0.584)	<0.001
SW-NE	0.556 (0.514, 0.599)	<0.001	0.553 (0.506, 0.600)	<0.001
SE-NW	0.546 (0.503, 0.588)	<0.001	0.523 (0.476, 0.569)	<0.001
Abundance				
Age group 1	0.169 (0.134, 0.204)	<0.001	-0.029 (-0.068, 0.010)	0.143
Age group 2	-0.032 (-0.065, 0.001)	0.057	0.185 (0.149, 0.221)	<0.001
Environment				
Temperature	0.028 (-0.003, 0.058)	0.078	0.008 (-0.025, 0.042)	0.635
Cod standing stock biomass	-0.083 (-0.154, -0.012)	0.024	-0.038 (-0.116, 0.041)	0.346
		$R^2_{adj} = 0.67$		
		$F_{7,120} = 38.43$		
			$R^2_{adj} = 0.68$	
			$F_{7,120} = 39.21$	

Notes: Spatial aggregation was defined as the spatial autocorrelation (Moran's *I*) in capelin densities ($\log_{10}(\text{density} + 1)$ -transformed and standardized to mean equal to zero and standard deviation equal to one) between neighboring cells in the east-west (E-W), south-north (S-N), southwest-northeast (SW-NE), and southeast-northwest (SE-NW) directions. Other independent variables are the same as in Table 1. Nonsignificant interactions between direction and the other variables have been removed.

that this result is related to food depletion and a consequence of a behavioral response to differential food densities across the migratory front (Wilson and Richards 2000). According to the theory of area-restricted search (Kareiva and Odell 1987), fish that lag behind the movement should speed up as they move through areas of low food densities. In contrast, fish that are at the head of the movement should slow down as they experience high food densities. Increased abundance will increase the food gradient and the result is a density-dependent migratory wave in which the ampli-

tude and velocity increase with abundance (sensu Wilson and Richards 2000). Our test of the DDMW hypothesis would have benefited from two additional lines of evidence that we were unable to collect: estimates of both prey density and the rate of movement of capelin at the front and back of the aggregations. Future tests of the applicability of the DDMW hypothesis in this and other systems would benefit from such estimates.

Our suggestion that the density-dependent migratory pattern is mediated through resource depletion is supported by the fact that there is a close relationship

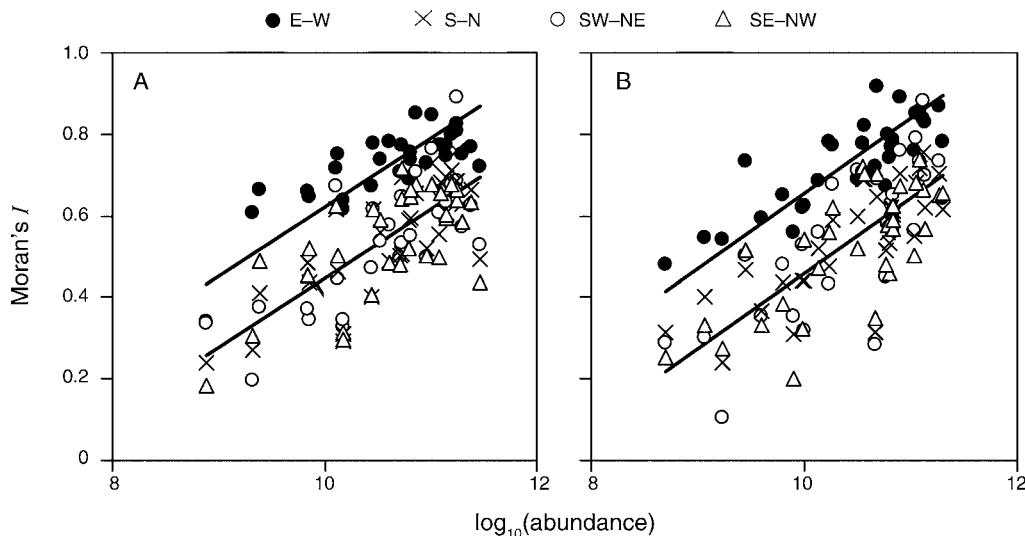


FIG. 6. Spatial aggregation as a function of capelin abundance (\log_{10} -transformed) for (A) 1-yr-old capelin (age group 1) and (B) 2-yr-old capelin (age group 2). Spatial aggregation was defined as the spatial autocorrelation (Moran's *I*) between densities of neighboring grid cells (see *Methods: Spatial structure*). Different directions between neighbors are indicated by different symbols; E-W, east-west; S-N, south-north; SW-NE, southwest-northeast; and SE-NW, southeast-northwest.

between capelin growth, capelin abundance, and zooplankton biomass (Gjøsæter et al. 2002b). Sea temperature had, as expected, an effect on the distribution of capelin (Gjøsæter 1998). This effect was, however, small compared to the density-dependent effect. Similarly, we found a weak negative relationship between the spatial autocorrelation and the biomass of the major predator in the area, indicating that high predation pressure was associated with a less aggregated spatial distribution.

Our results suggest that 1- and 2-yr-old capelin migrate in opposite directions. This conclusion is based on the two following findings. First, the spatial gradients in densities of the two age groups had opposite directions (Fig. 3A). Secondly, increased abundance of 1-yr-old capelin resulted in a displacement in the southeast direction while an increased abundance of 2-yr-old capelin was associated with a displacement in the northeast direction. A division of the Barents Sea between the two age groups may be a consequence of unbalanced competitive abilities and will probably reduce the adverse effects of intraspecific competition, especially on the younger age group. Moreover, for both age groups we found that the abundance of the other age group had an opposite effect on the spatial displacement. Furthermore, the effect of the abundance of 2-yr-old capelin on 1-yr-old capelin was stronger than vice versa. We suggest that this is an effect of dominance and schooling behavior. When yearlings are outnumbered by the older age groups, they may be led to follow the schools of older capelin northeastward and consequently be unable to initiate their southeastward migration. This is further supported by the fact that the distance between the age groups increased with increased abundance of age group 1 and decreased with increased abundance of age group 2. Corten (1999) suggested that the migratory pattern of herring, another pelagic schooling fish, is influenced by social learning by younger age groups from older age groups. Once adopted, the migration pattern tends to remain constant and changes are usually initiated by a recruiting age group that lacks the "guidance" of older herring. Similarly, our results indicate that 1-yr-old capelin have a more variable migratory pattern and that they are more influenced by the older age groups than vice versa. The large variation in age group strength suggests that the major migratory pattern of capelin may change rapidly and unpredictably. In the Barents Sea, such changes will presumably have large consequences for ecosystem dynamics.

Capelin are major consumers of the zooplankton production in the Barents Sea, and under high abundance they effectively reduce the standing stock biomass (Gjøsæter et al. 2002b). For an individual capelin it will, under such circumstances, be advantageous to be close to the front of the feeding migration. A gregarious behavior will increase the likelihood of being at the head of the migration and such behavior should accordingly be favored. This behavior will however increase the congregation of fish along the front and

consequently increase the food gradient across the front. The aggregative mechanism due to different foraging behavior across the front will consequently be reinforced. In other words, under high abundance the migratory wave might be strengthened by a mutual reinforcement between gregarious behavior and foraging pattern (Wilson and Richards 2000).

In the model of Wilson and Richards (2000), migratory waves formed when consumer abundance was increased. However, at very high consumer abundance the system collapsed and migratory waves failed to materialize. In this situation the resource gradient responsible for the migratory waves was not formed because the resource was quickly consumed and held at a low and constant density. In the Barents Sea system, seasonal sea ice dynamics (cf. Fig. 1) ensures a spatial mismatch between capelin and zooplankton each summer. This initial mismatch will inevitably result in a sharp gradient in zooplankton density under very high capelin abundance, and a DDMW might consequently be formed. In marine pelagic systems, seasonality and spatial heterogeneity might be a prerequisite for DDMWs to occur under high consumer abundance. Such massive migrations of animals may have large effects on the ecosystem. Compared to random foraging, a migratory wave will systematically exploit the available habitat and will reduce the resources to very low levels. A migratory wave is consequently a potentially highly overcompensatory mechanism and might have strong perturbing effects on populations and ecosystems.

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