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Variability in retention of *Calanus finmarchicus* in the Nordic Seas

Thomas Torgersen and Geir Huse

Using a regional ocean circulation model and particle tracking, we have studied the probability of the copepod *Calanus finmarchicus* being retained within the Nordic Seas' population as a function of its initial location, its vertical migration pattern, and the interannual variability in physical forcing. Defining a retention index in terms of the number of particles remaining within the Nordic Seas divided by the initial number of particles released, we found that spatial location had the greatest effect on the retention index during the study period, 1988−1991. Variability as a result of differences in physical forcing among years and among different seasonal vertical migration patterns had smaller but similar effects. The seasonal vertical migration behaviours with the highest advective loss rates and the most sensitive to interannual physical forcing were those that ascended early and descended late from a shallow summer depth. Average retention within the Nordic Seas was 0.40 after one year in simulations with diffusion and advection, and 0.42 in simulations with advection only. The average retention at the end of the four-year sequence was 0.10 and 0.12 with and without diffusion, respectively. Particles located in the western areas of the Nordic Seas had the highest retention, while those along the Norwegian coast showed little or no retention after four years. Initial location has a larger influence on retention than interannual variability in advective fields. *C. finmarchicus* offspring tend to reside in areas different from their parents, with different probabilities of retention. This spatial variability in retention rate is also experienced as inter-generational variability by members of the population. Model results suggest that almost all of the *C. finmarchicus* that are advected into the Barents Sea originate from off the Norwegian coast. Thus, predicting *C. finmarchicus* inflow into the Barents Sea requires knowledge of their abundance on the Norwegian Shelf.

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Introduction

Life history strategies and behaviours of organisms evolve in response to the environment. The selected strategies will be those with the highest integrated fitness over the range of variability of the environment, and therefore, populations in fluctuating and static environments will evolve differently, even if the average environmental states are the same (Murphy, 1968; Schaffer, 1974). A sudden change in the environment will often be harmful to residing organisms, and this is the background for a major concern about climate changes and ecology, i.e. populations may be unable to survive, maintain productivity, or sustain their functional roles in ecosystems if they are exposed to changes in the environmental forcing.

The copepod *Calanus finmarchicus* (Gunnerus) feeds and spawns in shallow water during spring to early summer. In the Nordic Seas (Figure 1), most of the population undergoes only one generation per year (Aksnes and Blindheim, 1996). The new generation descends to greater depths in summer to overwinter (most during the fifth copepodite stage, C5). The timing of seasonal ascent is more synchronous than the summer descent, and is initiated during late winter, one to two months before the spring bloom (Østvedt, 1955; Hirche, 1996; Niehoff *et al.*, 1999). Reproduction takes place after ascent. Average realized fecundity is probably between 100 and 1000 eggs female^{-1}, corresponding to a maximum growth rate, r_{max}, of $\sim 4-6$ y^{-1} (Aksnes and Blindheim, 1996). Some individuals initiate
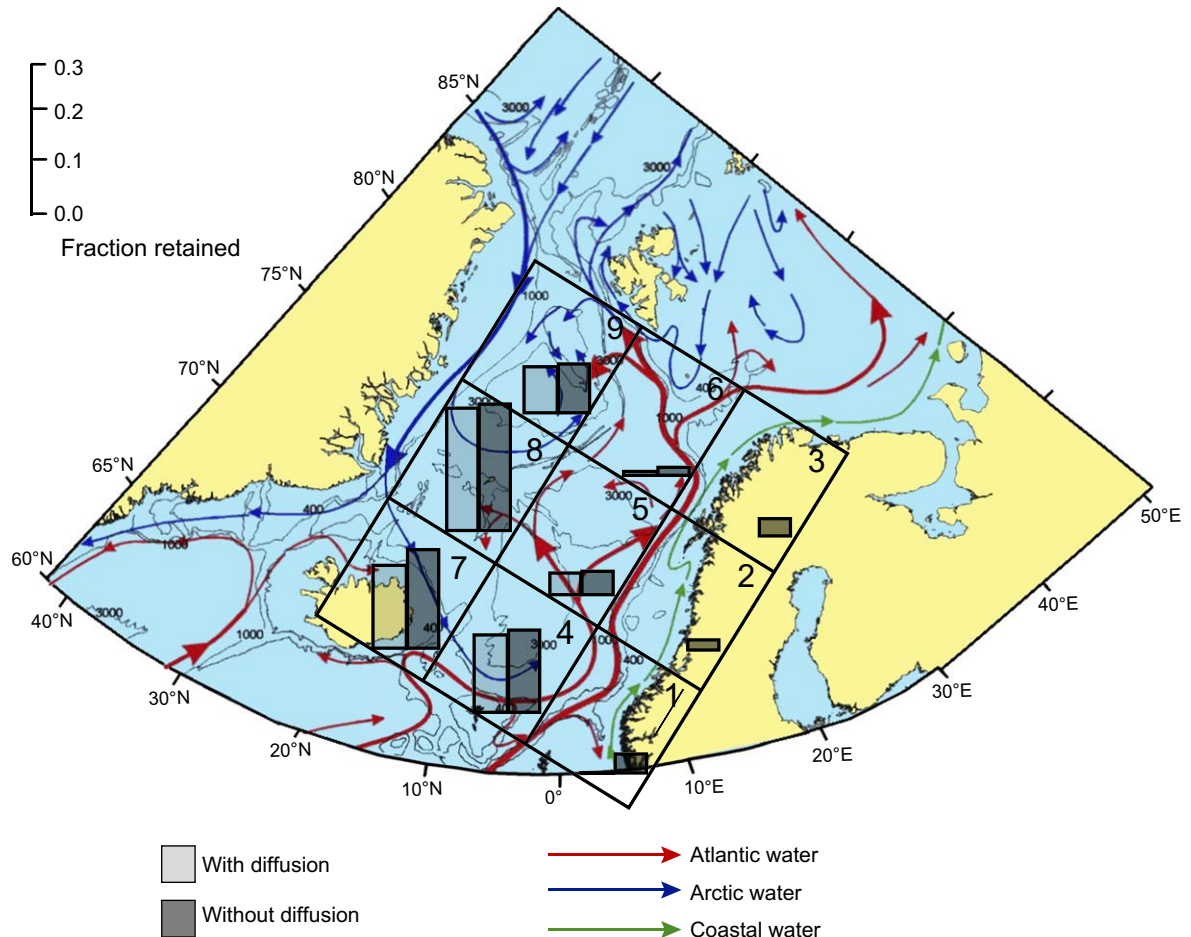
Figure 1. The nine subareas constituting the study area, overlaying a map of the Nordic Seas and adjacent areas. Proportions of individuals initiated in each subarea that are retained within the entire study area after four years (1988−1991, average of all behaviours) are shown for the simulations with and without diffusion. Main currents are indicated by arrows.

summer descent as early as May, while others are active in the upper layers throughout summer (Østvedt, 1955; Dale *et al.*, 2001). During the active period, *C. finmarchicus* are confined to the upper 100 m, and mainly above 60 m, with depth differences both between ontogenetic stages and between day and night (Tande, 1988; Dale and Kaartvedt, 2000). Over-wintering *C. finmarchicus* are typically associated with the cold, and virtually predator free, Arctic Intermediate Water (AIW). Therefore, the over-wintering depth varies strongly within the Nordic Seas (Kaartvedt, 1996, and references therein). In the Atlantic domain, east of the Polar Front, where warm Atlantic Water (AW) overlays the AIW, *C. finmarchicus* are mainly found below 500 m, while they concentrate in the upper 300 m in the Greenland Sea Gyre, where the AIW extends to the surface (Østvedt, 1955; Hirche, 1991; Richter, 1994; Dale *et al.*, 1999).

C. finmarchicus is by far the most abundant mesozooplankton species in the Nordic Seas. Early developmental stages are prey for the larvae of many commercially

important fish populations in the North, Norwegian, and Barents Seas. Late copepodites and adults are the main prey of adults of several dominant fish populations, including the Norwegian spring-spawning herring (*Clupea harengus* L.) and mackerel (*Scomber scombrus* L.).

The mean near-surface circulation in the Nordic Seas is shown in Figure 1. In the eastern areas, the upper layers are dominated by AW, entering the Nordic Seas from the south, through the Faroe−Shetland Channel and across the Iceland−Faroe Ridge. In the western area, in the Iceland and Greenland Seas, the entire water column is dominated by water of Arctic and polar origin, entering by the East Greenland Current. The upper layer flow into the Nordic Seas is around 10−15 Sv (1 Sv = 10^6 m^3 s^{-1}), the Atlantic influx being about an order of magnitude higher than that of Arctic and Polar waters (Blindheim, 2004). One branch of the AW flows into the Barents Sea. Most of the AW branching to the west of Spitsbergen cools and sinks, and forms part of the deep water of the Nordic

Sea Basins. The circulation in the Nordic Seas is largely cyclonic. Water circulates in connected gyres in the Norwegian, Lofoten, and Greenland Basins, and the main transport out of the Nordic Seas occurs close to the bottom, across the sill in the Denmark Strait, and across the Iceland–Scotland Ridge. There is also some upper layer transport out of the Nordic Seas through the East Greenland Current. Assuming that the water exchange with adjacent seas is restricted to the upper 500 m, a 12 Sv exchange as suggested by Aksnes and Blindheim (1996) corresponds to an annual water renewal rate of 0.29. For particles that are not homogenously distributed, like zooplankton, advective loss rates may deviate strongly from this value.

C. finmarchicus has two main populations, residing in the sub-polar gyre and in the Nordic Seas (Conover, 1988; Aksnes and Blindheim, 1996; Melle *et al.*, 2004). These populations are not isolated but rather there is active exchange of individuals between them. The reproductive rates of the *C. finmarchicus* are, however, much higher than the exchange rates. Therefore, even if this flux of individuals was of importance on evolutionary time scales, influencing population genetics, its direct ecological significance is modest (Aksnes and Blindheim, 1996; Bucklin *et al.*, 1996).

For *C. finmarchicus* that are advected out of the Nordic Seas, the probability of having descendants being repatriated is low. Those that are transported to the north into the Arctic are lost without any plausible return route. Those that enter the North Sea are unable to overwinter there due to the shallow bottom depth, which results in a potentially high predation risk from visual predators as well as high flushing rates. Consequently, the North Sea population is replenished each spring by advection from the over-wintering stocks off the shelf edge. Those that are transported south through the East Greenland Current or the deep overflow have a very small probability of being transported back to the Nordic Seas. Integrated water renewal rate of the sub-polar gyre has been estimated at $0.12 \, \mathrm{y}^{-1}$ (Aksnes and Blindheim, 1996), so the repatriation rate of *C. finmarchicus* lost to this area should be very low. Those entering the Northwest Atlantic through the East Greenland Current would have to enter the sub-polar gyre first in order to re-enter the Nordic Seas. Hence, being advected out of the Nordic Seas can be viewed as mortality relative to the local population. Irrespective of whether the lost individuals thrive and reproduce in other areas, their contribution to the Nordic Seas' population will be zero (Iles and Sinclair, 1982; Eiane *et al.*, 1998).

The realized fitness of organisms depends partly on strategy (genes) and partly on chance (stochasticity). *C. finmarchicus*' probability of being lost from the population by being advected out of the Nordic Seas domain will vary between years and within the spatial domain. Advection varies with depth, and Bryant *et al.* (1998) found that seasonal vertical migration was instrumental in maintaining self-sustaining, basin-scale populations of *C. finmarchicus*.

Timing of the seasonal vertical migration and summer and winter depths may have significant effects on the risk of disappearing from the population.

Owing to the currents and gyres in the Nordic Seas, a *C. finmarchicus* individual will tend to reside and develop in a place other than its parents did'. Therefore, both the spatial and temporal variabilities of the advection probability may act as inter-generational variability.

The effects of spatial and temporal variabilities on zooplankton retention can only be studied effectively through ocean model simulations. We use a particle-tracking model to quantify and compare the spatial and interannual variabilities in retention of *C. finmarchicus* in the Nordic Seas, and to evaluate to what extent retention is determined by the seasonal vertical migration pattern. Furthermore, we monitor the variability in particle inflow to the Barents Sea, which is one of the main sinks for *C. finmarchicus* in the Nordic Seas.

Model description and simulations

Current vectors from a physical ocean model were used to move particles, representing *C. finmarchicus*, around the Nordic Seas.

The physical model

Particles were advected using currents from a Princeton Ocean Model (POM) simulation (Blumberg and Mellor, 1987; Ådlandsvik and Sundby, 1994; Asplin *et al.*, 1998). This model solves the primitive equations numerically by the finite difference method. In the vertical, terrain-following sigma-coordinates are used. For vertical mixing, a Mellor–Yamada level 2.5 turbulence closure scheme is used (Mellor and Yamada, 1982). The most important modification from the standard POM version is the use of the flow relaxation scheme as an open boundary condition. The implementation in POM is documented in Engedahl (1995).

The model domain covers the Nordic, Barents, and North Seas. The horizontal resolution is 20 km and the number of grid cells is 208×120. In the vertical, 14 sigma-levels are used. For the present simulations, we used a 148×105 grid subset (Figure 1) of the larger model. The initial description of sea surface elevation, currents, salinity, and temperature was taken from a diagnostic climatology produced by the Norwegian Meteorological Institute (DNMI) and Institute of Marine Research (Engedahl *et al.*, 1998). At the open boundaries, this was complemented by four tidal constituents. The meteorological forcing was taken from the hindcast archive of "www.met.no" (Eide *et al.*, 1985). Freshwater run-off from 47 rivers was included. More details on the model set-up and validation are provided by Asplin *et al.* (1998) and Ådlandsvik *et al.* (2004).

Particle tracking

C. finmarchicus were represented as particles with seasonal patterns in vertical distribution, which varied among simulations (Figure 2, Table 1). *C. finmarchicus* overwinter at depth, ascend in early spring for reproduction, and die after an intense reproductive period. Subsequently, their offspring grow until the C5 stage, and then descend to overwinter. Alternatively, the offspring mature and commence reproduction in the same year in which they were born, and then it is the second generation that descends for over-wintering. Since we simulated a vertical distribution trajectory over a year starting 1 January and ending 31 December, we actually simulated at least two half-lives. Thus, the descending individual in autumn could be regarded as the offspring of the same individual ascending in spring. Simulations were run over four years, and at the beginning of the year particles were initiated in the final position of the previous year. *C. finmarchicus* has ontogenetic changes in vertical distribution from nauplia to C5 stages. However, these changes are small in magnitude relative to the migrations related to over-wintering. They are likely to have a minor effect on transport, and were therefore disregarded.

Horizontal movement of *C. finmarchicus* along the x-axis can be described by:

$$\frac{dx}{dt} = u(x, y, z, t) + d \qquad (1)$$

where u is the advection velocity of the water in the x direction, x and y are the horizontal positions of the particles in the domain, z is depth, t is time, and d is a diffusion term. The advection velocity was calculated by 3D linear interpolation of velocity components in the surrounding grid points. Movement was calculated in a similar fashion along the y-axis. Advection was implemented in an Euler forward way, where the interpolated velocity at the particle position at the start of the time-step was used for the duration of the time-step. Simulations were performed with and without a diffusion term added. Simulations with diffusion are
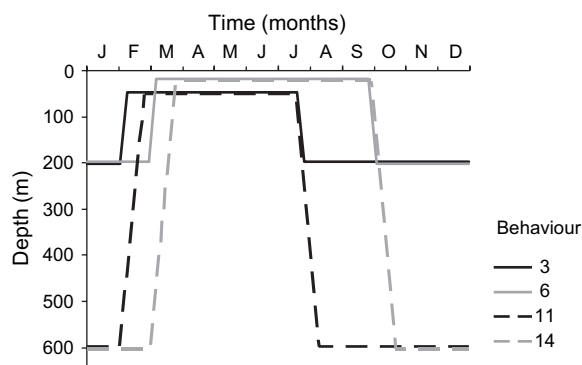
Table 1. Model variables and the fraction of individuals retained in the study area after one year (using average of different forcing years) and four years (using the observed windforcing for each year), with diffusion.

Behaviour	Winter depth (m)	Summer depth (m)	Ascent day	Descent day	After 1 y	After 4 y
1	200	20	32	200	0.36	0.04
2	200	20	32	270	0.32	0.02
3	200	50	32	200	0.39	0.09
4	200	50	32	270	0.38	0.08
5	200	20	60	200	0.39	0.07
6	200	20	60	270	0.35	0.04
7	200	50	60	200	0.42	0.12
8	200	50	60	270	0.41	0.12
9	600	20	32	200	0.40	0.08
10	600	20	32	270	0.36	0.05
11	600	50	32	200	0.43	0.13
12	600	50	32	270	0.42	0.12
13	600	20	60	200	0.44	0.12
14	600	20	60	270	0.39	0.07
15	600	50	60	200	0.47	0.17
16	600	50	60	270	0.45	0.16

considered more representative of the actual physical forcing of the Nordic Seas by mimicking sub-grid physical processes, but simulations without diffusion were run for direct comparison with the results of Bryant *et al.* (1998). Diffusion was implemented as a random walk, where the diffusion velocity d in Equation (1) was drawn at random from a normal distribution with standard deviation corresponding to an eddy diffusion coefficient of $100 \text{ m}^2 \text{ s}^{-1}$ (Ådlandsvik and Sundby, 1994). Movement was simulated at hourly time-steps, but the advection model was based on daily current vectors. Individuals were not allowed on land. To avoid accumulation of individuals in enclosed nearshore areas, individuals in squares next to a shore square were moved to a randomly chosen square in the neighbourhood, including the eight surrounding squares and the one currently occupied. If a land square was chosen, the process was continued until a sea square was found. This procedure will tend to underestimate the retention of *C. finmarchicus* in Norwegian coastal areas, but for the present purpose, individuals moving from the Nordic Seas to Norwegian fjords were considered lost from the oceanic population. Overall, this land avoidance procedure reduced the retention index by only up to 5% compared with not using it. The retention index is the number of particles retained after a given time interval divided by the initial number of particles.

In our simulations, 2000 particles were released on 1 January in randomly chosen cells within each of nine subareas in the Nordic Seas (Figure 1). This spatial resolution allowed us to identify large-scale differences in retention, as well as to address specific spatial patterns. The ocean circulation model was run with forcing for 1988−1991, a period of fairly high values of the North Atlantic Oscillation

Figure 2. Examples of simulated seasonal vertical migration patterns.

(NAO) Index (Hurell, 1995; Jones *et al.*, 2001). A high NAO index corresponds to increased westerly winds and generally warmer conditions in the Nordic Seas. There was also some variation in the NAO Index, with 1988 and 1991 having lower values ($\sim$1), and 1989 and 1990 the highest values at 5 and 4, respectively. Ideally, years with negative NAO values should have been included to contrast the high NAO years, but these were not available to us at the time of this work. Since *C. finmarchicus* has a one-year life cycle in the Nordic Seas, retention rates and variability after one year are of obvious interest. However, simulations with a one-year horizon might induce a strong bias against particles initiated in the periphery of the study area, since these need a shorter time to be transported out of the region. Therefore, all simulations were run for four years.

We ran the model both repeating the same physical forcing in each of the four years and with the forcing fields for each of the four different years in sequence in order to separate the effects of the interannual variability in physical forcing from the influence of spatial variability on the retention rate. The model was run with $2^4 = 16$ different seasonal vertical migration patterns, varying in winter depth, summer depth, day of ascent, and day of descent (Table 1, Figure 2). The two values for each variable were chosen both to be representative and to cover much of the variability, as reviewed in the introduction. However, the observed variability in the behaviour of *C. finmarchicus* in the Nordic Seas is slightly greater than that covered in the simulations. During winter, particles remained at their winter depth. When bottom depths over continental shelves and slopes were shallower than the winter depth, particles were placed 1 m above the bottom. On the ascent day, they moved upwards with a vertical velocity of 1 m h^{-1} (Carlotti and Wolf, 1998). Their descent towards the winter depth was with the same vertical speed.

Retention was defined as the fraction of the initial particles remaining in the entire study area. Below, we present the variability in retention in terms of the coefficient of variance, CV, which is the standard deviation (s.d.) divided by the average. We investigated how variability in retention depended upon where the particles were released, the physical forcing, and their vertical migration behaviour. Since retention varied by orders of magnitude between subareas, and also between years and behaviours, the arithmetic mean of CV can be misleading (e.g. between behaviour CV may be very high in subareas with very low retention). Therefore, averages of CVs were weighted by the retention index.

Results

Averaged over all behaviours, subareas, and forcing years, the retention index was 0.40 after one year in the simulations with diffusion and 0.42 in the ones without diffusion. The average retention at the end of the four-year sequence

(1988−1991) was 0.10 and 0.12 with and without diffusion, respectively. Total retention through the four-year sequence with diffusion is shown in Figure 3. Average retention after four years with the same environmental forcing each year was 0.09 and 0.11 with and without diffusion, respectively, almost identical to that after the four-year sequence using the observed forcing.

Retention varied the greatest with initial subarea and less owing to interannual climate variability (forcing year) and behaviour. Individuals initiated in the western subareas had the highest retention index (Figure 1). Simulations with diffusion yielded zero retention of particles released in subarea 3 off northern Norway, and close to zero in subareas 1 and 2 off southern and mid-Norway after four years, respectively. The simulations without diffusion yielded some, but still very little, retention of particles released in these three subareas. The following results are from simulations with diffusion.

Average retention from simulations with spatial and temporal variabilities for each of the 16 behaviours is shown in Figure 4. Retention varied strongly among different subareas (Figures 1 and 4), and, integrated over all 16 behaviours, CV was 1.15 after the four-year sequence. The difference in retention between forcing years was about half of that among subareas (Figures 4 and 5). After four years (with the same forcing year within each simulation) and integrating over all 16 behaviours, between forcing year CV for the entire study area was 0.50. The year 1988 had the highest retention, 3.4 times higher (after four years) than 1991, the year with the lowest retention.

Total retention within the study area varied significantly with behaviour (Figures 4 and 5). After the four-year sequence, the behaviours with the highest (15 and 16) and lowest (2) retention indices differed by a factor of 8.2 (Table 1), and the inter-behaviour CV was 0.48. Behaviour 2 had a shallow over-wintering depth, early ascent to a shallow summer depth, and a late descent (Table 1). In general, behaviours with long periods at their summer depth were also more sensitive to interannual climate variability than other behaviours (behaviours 2, 6, 9, 10, and 14; Table 1,
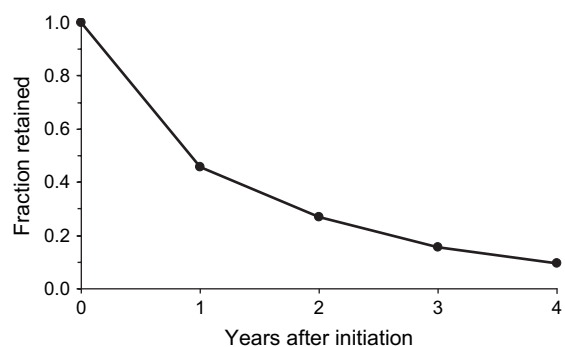

Figure 3. Retention within the study area through the four-year sequence from the simulations with diffusion. Average of all behaviours.
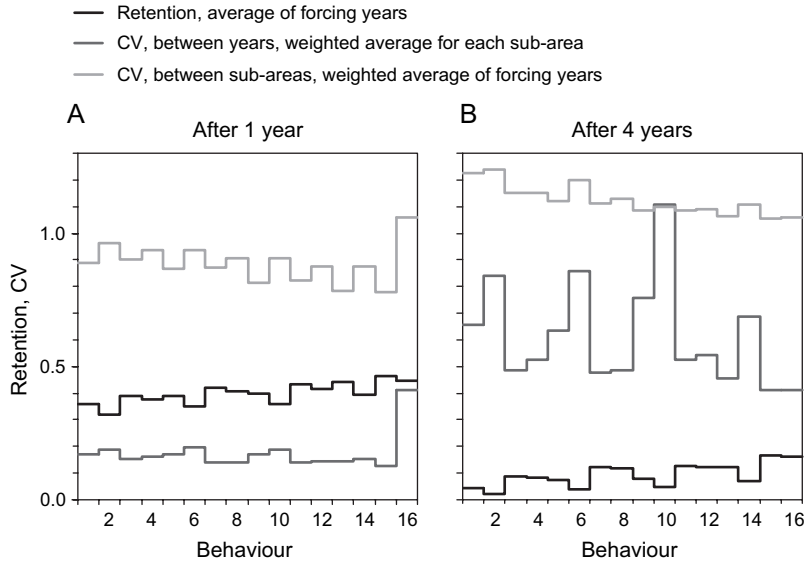
Figure 4. Retained fractions after (A) one year and (B) four years (simulations with the same forcing year for four consecutive years) with variability among years and among subareas for all behaviours. Between years, CVs were calculated first for each of the nine subareas, and then the average CV was weighted for retention. In the same way, among subareas, CVs were calculated first for each of the four forcing years, and the average CV was then weighted for retention. Simulations were run with diffusion.
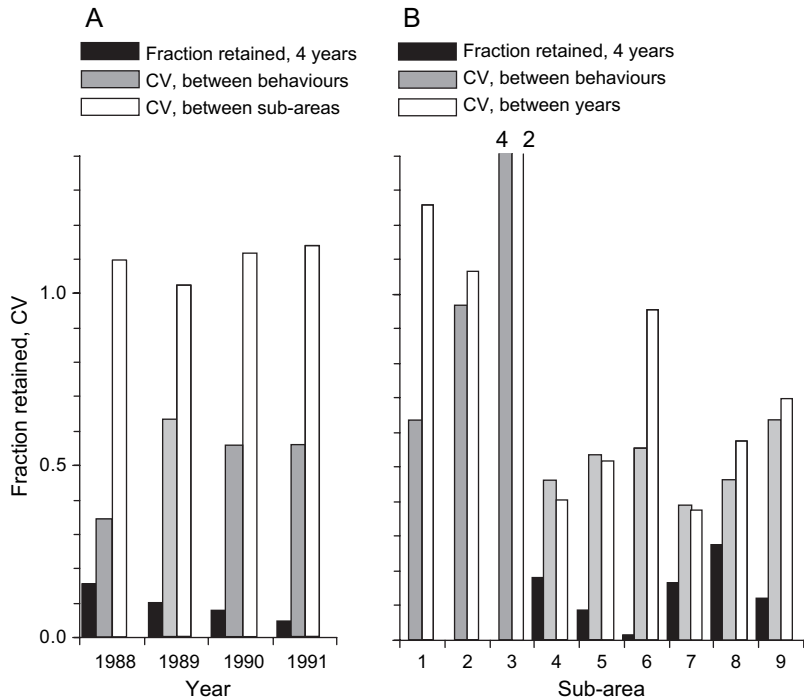

Figure 5. (A) Retained fractions (average of all forcing years and behaviours) after four years for each of the nine subareas with variability between behaviours (averaged over all four forcing years) and between years (averaged over all 16 behaviours). (B) Retained fractions (average of all subareas and behaviours) after four years for each of the four forcing years with variability between behaviours (averaged over all nine subareas) and between subareas (averaged over all 16 behaviours). Simulations are the same as shown in Figure 4.

Figure 4). Variability between behaviours was less sensitive to initial subarea. However, retention of particles that descended late was slightly more sensitive to initial subarea than that of other behaviours. Generally, the subareas with the smallest retention had the highest variability, but subarea 8 was rather sensitive to behaviour in spite of its generally high average retention. After four consecutive years with the same forcing year, inter-behaviour variability was considerably lower when forced with flow fields from 1988 (Figure 5A) compared with any of the other years.

Particles retained within the Nordic Seas drifted between subareas and after four years, particles from the same initial subarea were spread over different subareas (Table 2). The final distribution of retained particles between subareas differed partly from the retention indices based on initial subareas (Table 2). The clearest differences were that subareas 5 and 9 had high final densities of particles compared with the retention indices of these subareas, while subareas 4 and 7 had low final densities compared to the retention indices.

A large proportion of the lost particles were transported into the Barents Sea. Variability in this transport largely follows that of loss rates from the Nordic Seas. During the four-year sequence, 22% of the initial particles were advected into the Barents Sea. Averaging over years with different physical forcing, 23% of the initial particles were lost to the Barents Sea within the first year. After four years with the same forcing-year within each simulation, the average fraction lost was only marginally higher than after one year, at 0.24. Thus, most of the particles transported into the Barents Sea entered during the first year and came from subareas 1—3 (Figure 6A). Advection into the Barents Sea was highest in 1990 and lowest in 1988 (Figure 6B). The same behaviours that had a high probability of being lost from the Nordic Seas had a high probability of ending up in the Barents Sea (Figure 6C). The transport of particles into the Barents Sea is more sensitive to their distribution within the Nordic Seas than to behaviour or interannual climate fluctuations (Figures 6 and 7).

Discussion

The model transport of particles between subareas illustrates how *C. finmarchicus* is likely to have little population structure within the Nordic Seas. Thus, the Nordic Seas is considered the appropriate scale to study their retention and population closure. Our results suggest that *C. finmarchicus* experience greater inter-generational variability in risk of being lost from the Nordic Seas population owing to their variation in spatial location through transport by the mean currents than from the interannual variability in advective fields. The retention indices of the subareas are averages over large areas, and retention rates within each of these subareas are certainly not homogenous. Thus, the actual geographical variability in advective loss risk within the Nordic Sea could be even higher than outlined here. To the extent that behaviour has influence on advective loss risk, *C. finmarchicus* might have evolved behaviours that are robust against strong temporal variability in advection.

Contributions from processes on sub-grid scales will be lost in the output from the pure advection model. The diffusion term increases the loss from the study area compared with the pure advection model. Diffusion tends to move individuals that were initially entrapped in cyclonic gyres into export paths, such as that along the Norwegian coast. Hence, the slightly higher retention observed in the simulations without diffusion is to be expected.

The estimated overall retention estimates in this study are similar to those of Bryant *et al.* (1998), who, with a non-diffusive advection model, estimated retention indices of 0.52 and 0.11 after one and five years, respectively. Aksnes and Blindheim (1996) estimated the renewal rate of the water in the upper 500 m of the Nordic Seas to be 0.29 y^{-1}, corresponding to a retention index of 0.75 y^{-1}. Our estimated annual retention of 0.40 y^{-1} corresponds to a loss rate of 0.92 y^{-1}, significantly higher than the estimated water renewal rate. However, advection is generally stronger in shallow water, and since plankton spend much of

Table 2. Number of *C. finmarchicus* retained after the four-year sequence, sorted by initial and terminal subareas. Init and term are, respectively, the initial and terminal abundance of individuals in each subarea relative to initial number.

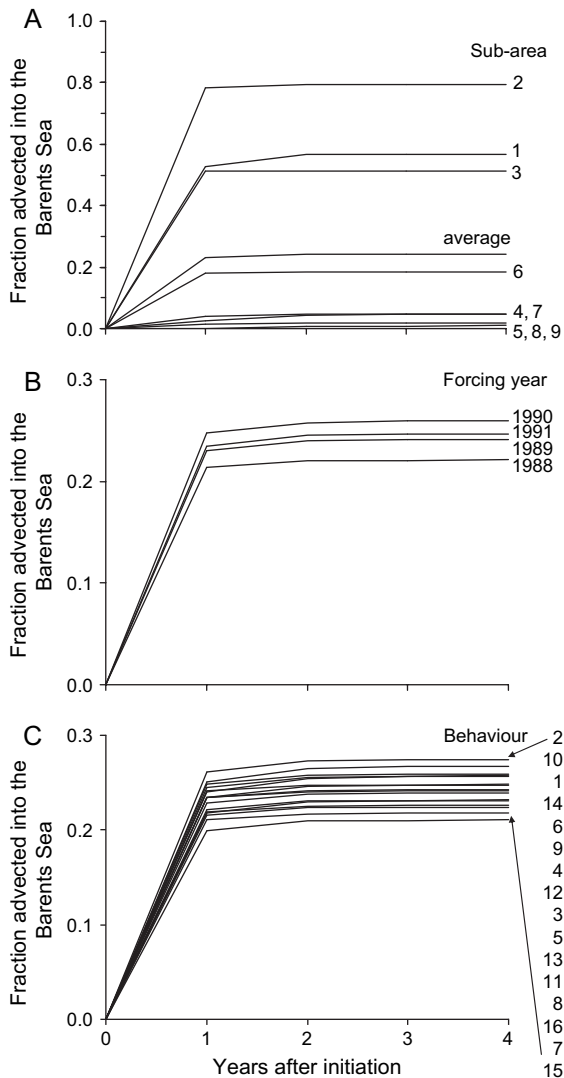|						Initial subarea					
		1	2	3	4	5	6	7	8	9	Term
Terminal subarea	1	0	0	0	9	12	0	14	21	13	0.00
	2	0	0	0	10	3	0	8	16	6	0.00
	3	0	0	0	0	1	0	1	0	0	0.00
	4	4	0	0	462	195	19	469	752	218	0.07
	5	5	0	0	875	180	41	885	1 403	421	0.12
	6	2	0	0	334	51	27	375	668	202	0.05
	7	3	0	0	130	60	7	179	306	101	0.03
	8	26	2	0	2 054	874	78	2 464	3 546	1 628	0.33
	9	14	0	0	1 939	342	84	2 161	2 798	970	0.26
	Init	0.00	0.00	0.00	0.18	0.05	0.01	0.21	0.30	0.11	0.10

Figure 6. Transport into the Barents Sea after four years (A) by subarea (average of all forcing years and behaviours), (B) by year (average of all subareas and behaviours), and (C) by behaviour (average of all forcing years and subareas). Simulations were run with diffusion and with each of the forcing years for four consecutive years.

their time there, they are expected to experience stronger advection out of the area than those based on the depth-averaged estimates. Hence, differences between average water renewal rates and advective loss rates of organisms with vertical migration are to be expected. It should be noted that the subareas with the lowest retention also tended to have higher initial densities of particles. The 2000 particles were distributed in the part of the subareas that were not covered by land, resulting in higher initial particle density in the subareas in which much of the area was covered with land, which is the case for subareas 1–3 and 7. Since initial particle density varies, a direct comparison between
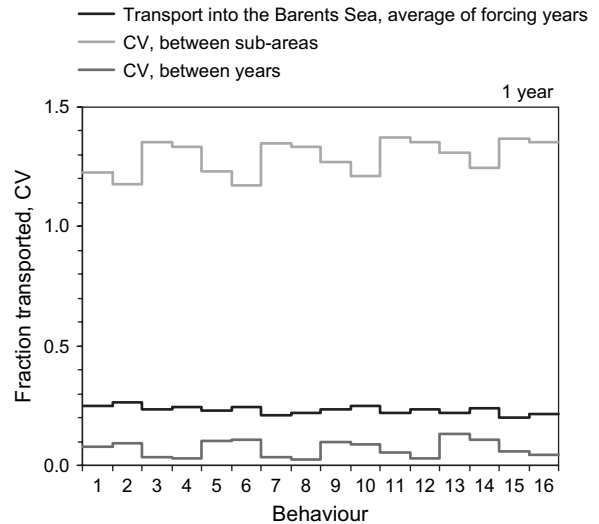

Figure 7. Fraction of individuals transported into the Barents Sea after one year with variability between years and between subareas for all behaviours. Transported fraction is the average of all forcing years, subareas, and behaviours. Between years, CVs were calculated from averages of the entire study area and all behaviours. Between subareas, CVs were calculated from averages of all forcing years and all behaviours. Simulations were run with diffusion.

particle loss rates and water renewal rates might be somewhat biased.

There was pronounced variability in retention between different behaviours. However, the birth and death rates of *C. finmarchicus* in the Nordic Seas are higher than advective loss rates, and probably more important in shaping their behaviour (Aksnes and Blindheim, 1996). It is worth noting that *C. finmarchicus*, remaining in very shallow waters throughout summer, which correspond to areas of high growth and high predation, also have high advective losses from the Nordic Seas (Eiane *et al.*, 1998). Since the generally higher rates of mortality, growth, and reproduction will vary spatially within the Nordic Seas, predicting the large-scale horizontal distribution of *C. finmarchicus* from our particle tracking results alone is not possible. We note, however, that the areas predicted to retain particles in our study correspond well with those from the simulations of Bryant *et al.* (1998). The greatest biomasses of *C. finmarchicus* are also typically found in these areas (Melle *et al.*, 2004). This suggests that the spatial pattern of our estimated retention reflects the actual pattern of *C. finmarchicus*.

Our results suggest that while transport of *C. finmarchicus* into the Barents Sea depends partly upon its behaviour and climate variability, almost all particles transported into the Barents Sea were from the Norwegian Shelf within the first year. Therefore, to predict *C. finmarchicus* inflow into the Barents Sea, one needs to determine the *C. finmarchicus* abundance on the Shelf. The rapid loss (within the first year) of particles initially placed off the Norwegian coast

corresponds well with the simulated *C. finmarchicus* trajectories previously described by Pedersen *et al.* (2001). They found that particles initially off southern Norway in an area corresponding to our subarea 1, generally were advected northwards, and travelled distances sometimes exceeding 1600 km in 180 days.

Other aspects of the environment, besides advection that affect *C. finmarchicus*, include non-uniform predator and prey distributions and temperature fields. *C. finmarchicus* are therefore advected between areas with different growth and mortality profiles. For *C. finmarchicus*, the spatial variability in these environmental parameters will act as temporal variability in a way similar to that of the risk of advective loss. Therefore, we suggest that plankton living in advective, spatially variable systems are most likely to be pre-adapted to temporal fluctuations, and consequently might be robust with regard to climatic changes. Also, in order to better predict distributions of *C. finmarchicus*, spatially resolved growth and mortality rates must also be applied. These issues will be addressed in future studies.

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