

## Abstracts from the GLOBEC Norway 2005 annual meeting

As introduced by Svein Sundby on page 1 of this Newsletter, the following abstracts provide preliminary results of the GLOBEC Norway projects ECOBE, CLIMAR and ADAPT. All GLOBEC National Programmes are encouraged to use the Newsletter to expose their research in this manner. Contact the Editors for further information.



### General aspects of the southern Barents Sea circulation

Lars Asplin, Randi Ingvaldsen, Harald Loeng and Roald Sætre  
Institute of Marine Research, Bergen, Norway

Based on historical current measurements from more than 70 locations and numerous drifting satellite-tracked buoys in the period 1970–1996, some general features of the circulation in the southern Barents Sea are summarised. Results of a three-dimensional numerical ocean model for the period September 1997–July 1999 gives further information of the current system of the area.

The main findings were:

1. The mean current speed is generally low in the Barents Sea (<0.05 m/s)
2. There exist well defined regions of one-layer (barotropic) and multi-layer (baroclinic) flow
3. The eastward flow of Atlantic water have a seasonal latitudinal variation.

The current observations from all sources indicate that on average (and the averages are based on periods from several days up to months) only moderate current speeds occur. In the upper 100m depths 55% of the current speeds were less than 0.05m/s and only 15% were above 0.1m/s. In the water depths below 100m the speeds were lower, with 72% less than 0.05m/s and 6% above 0.1m/s.

At current moorings where recordings from several vertical levels were obtained, direction differences in the vertical could be found. This indicates whether the flow is mainly barotropic or if it is mainly baroclinic. The findings were that the flow is mainly baroclinic close to the coast in the southern part and on shallow banks in the middle and northern parts of the area (Fig. 1). In the regions where the Atlantic water inflow takes place, the flow is mainly barotropic.

To assess the flow of Atlantic water eastwards into the Barents Sea from the western border, numerous passive drifting particles were seeded into the currents from the numerical model results. The particles clearly follow a more northerly track on the mean when released during summer than during winter (Fig. 2), spending a year to cover the distance of the track. The current pattern will have impact on transport both of zooplankton and fish larvae.

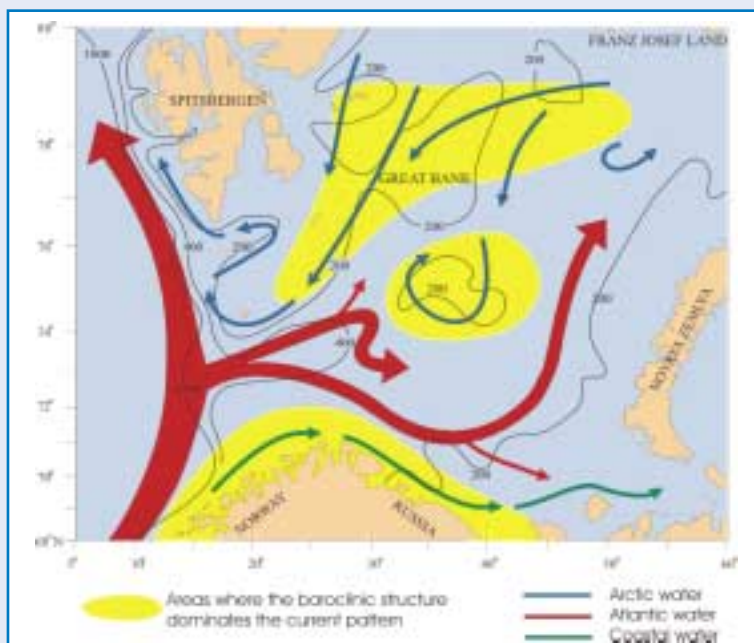


Figure 1. The general circulation of the Barents Sea with the areas of mainly barotropic and baroclinic flow.

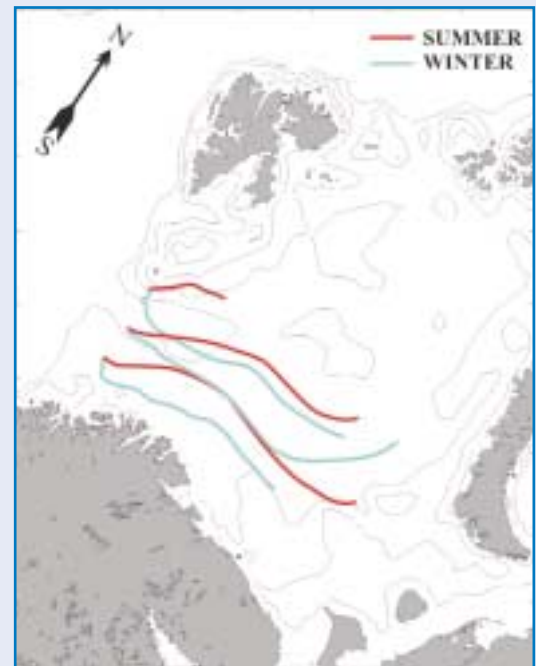


Figure 2. Seasonal variability of mean trajectories for a large number of particles advected eastwards in the Barents Sea based on currents from a numerical model simulation. The particles flow at 100m depth basically in the Atlantic inflowing water. Three release positions for particles were used, all along the transect from Norway to Bear Island.

## Feeding migration and diet of Norwegian spring spawning herring in relation to the seasonal cycle of *Calanus finmarchicus* in the Norwegian Sea

Cecilie Broms Årnes (cecilie.broms.aarnes@imr.no) and Webjørn Melle (webjoern.melle@imr.no).  
Institute of Marine Research, Bergen, Norway

The aim of this study is twofold: 1) to examine the importance of *Calanus finmarchicus* in the diet of herring (*Clupea harengus*) throughout their feeding migration in the Norwegian Sea, and 2) to study the timing of herring migration in relation to the life cycle of *Calanus finmarchicus*. The feeding ecology and distribution of herring were studied during cruises in 1995 – from the start of the feeding migration at the spawning grounds off the coast of Norway, to the main feeding area in the Atlantic and Arctic waters of the Norwegian Sea (Fig. 1). The feeding and migration have been related to differences in the seasonal cycle of production of *Calanus finmarchicus* in the different water masses obtained from acoustic mapping, stomach samples and zooplankton samples collected during the cruises.

Herring feed selectively on adults and older copepodite stages of *Calanus finmarchicus* (Fig. 2). The timing of the development of the *Calanus* population varies between water masses and herring also inhabit different water masses during their feeding season, which seems to be related to the occurrence of older developmental stages of *C. finmarchicus*.

In the beginning of the season, herring mainly feed on the overwintering population (G0) of *Calanus finmarchicus*, which concentrates towards the surface to feed and spawn during the phytoplankton spring bloom. They then switch to feed on the new generation (G1) when it has reached older copepodite stages. This switch may however not be so successful for older herring, which is in the northeastern part of the Norwegian Sea at the end of their feeding migration. The reason may be that this corresponds in time (July and August) with the descent to overwintering depths of the older stages of the G1 generation of *Calanus finmarchicus*. Simultaneously, a large part of the G1 generation has not yet reached the older stages that herring prefer to feed upon. This may explain the lower average stomach contents, more empty stomachs and a diet consisting of a wider variety of prey organisms compared with earlier in the feeding season (Dalpadado *et al.*, 2000).

### References

Dalpadado P., B. Ellertsen, W. Melle and A. Dommasnes. 2000. Food and feeding condition of Norwegian spring spawning herring (*Clupea harengus*) through its feeding migration. ICES Journal of Marine Science, 57, 843–857.

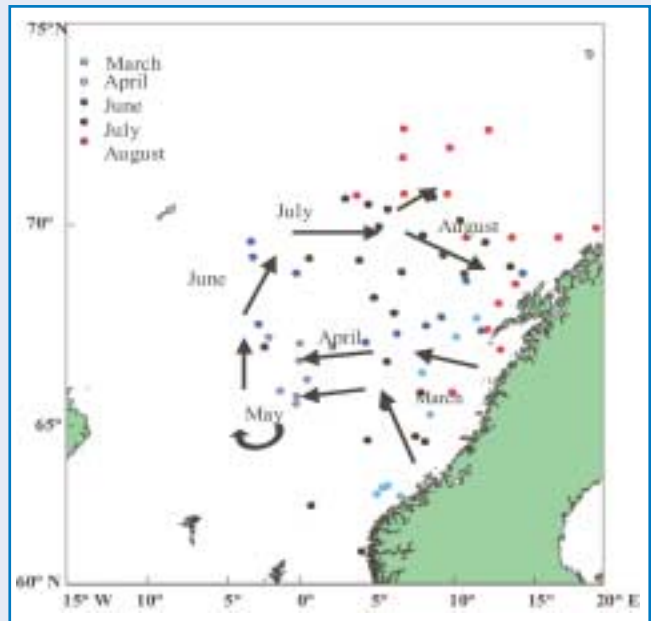


Figure 1. The feeding migration of Norwegian spring spawning herring in the Norwegian Sea from March to August 1995.

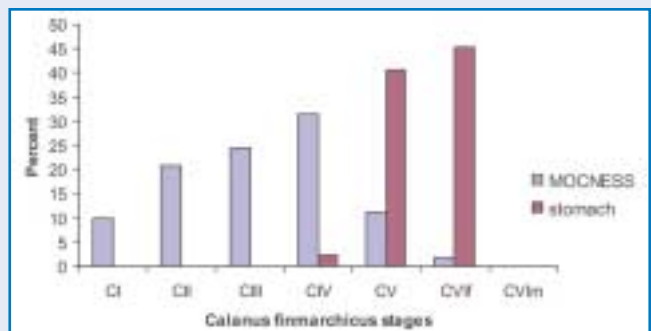


Figure 2. An example of selective feeding on adult and older copepodite stages of *Calanus finmarchicus* from trawl station 351, July 1995.

## Prey-specific gastric evacuation of Norwegian spring spawning herring (*Clupea harengus*)

Cecilie Broms Årnes (cecilie.broms.aarnes@imr.no), Webjørn Melle (webjoern.melle@imr.no) and Anders Thorsen (anders.thorsen@imr.no)  
Institute of Marine Research, Bergen, Norway

The knowledge about the emptying rate of herring is minimal because very few earlier studies of this subject have been performed on herring or with small crustacea as the main prey. Gastric evacuation rates have earlier mainly been measured based on laboratory experiments. The aim of the present study is to obtain information of gastric

evacuation rates when the herring are feeding in their natural environment.

Gastric evacuation field experiments were performed on Norwegian spring spawning herring (*Clupea harengus*) based on three catches obtained by purse-seining in Arctic/Atlantic water masses in the Norwegian Sea between

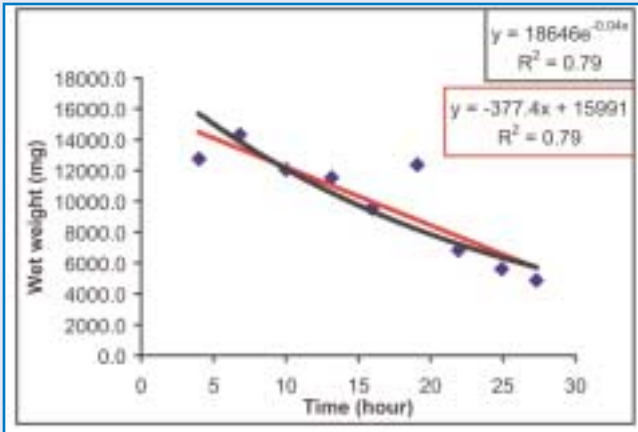


Figure 1. Gastric evacuation of the total stomach contents at station 2. Both an exponential and linear evacuation gave a good description of the data and had a high explanation value. Notice the high stomach content in the first sub-samples.

1 and 4 June 2002. After capture the herring were kept in the seine for about 24 hours, and during that time usually more than 20 individuals were sampled from the catch at time intervals of approximately three hours and frozen. The herring sub-samples were taken with gillnet stretched out in the seine. Sea surface temperature was noted at the ships sensors at the time of sampling. In the laboratory a total of 303 herring stomachs were analysed. The stomach contents were identified to the lowest taxonomic group, dried and weighed, and used to calculate the prey-specific evacuation rates.

Copepods were the main prey of herring in all three stations, amounting to 92–97% of the diet. *Calanus hyperboreus* constituted a large part of the diet owing to the strong

influence of Arctic water at the sampling stations, while *Calanus finmarchicus* constituted a smaller part. Also krill and amphipods were found in the stomachs, but usually in small amounts.

Based on earlier studies we could expect an exponential evacuation of all the different prey types. In the present study however, a linear evacuation also gave a good description of the data from the total stomach contents (Fig. 1) and from the copepods (Fig. 2). Based on the time to 90% stomach evacuation at station 2, the estimated consumption of copepods per day was 9.8 and 7.0g wet weight according to the linear and the exponential model respectively. It is difficult to draw conclusions from the krill and amphipods because of their minor contribution to the diet.

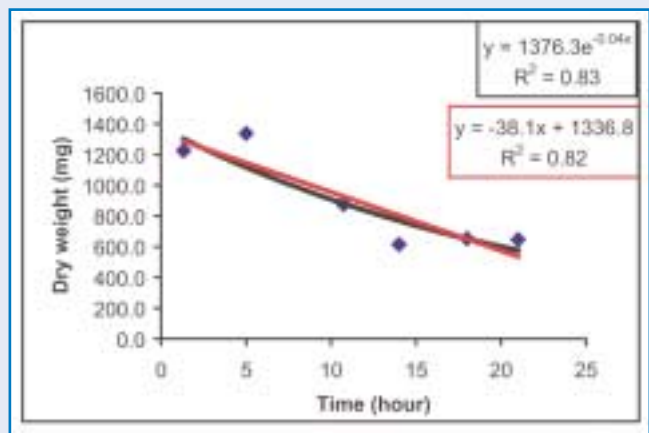


Figure 2. Gastric evacuation of copepods in the diet of herring from station 3. The copepods consisted almost entirely of *Calanus hyperboreus* and *C. finmarchicus*.

### ROMS Model for the North Atlantic and Arctic Oceans

W. Paul Budgell, Institute of Marine Research and Bjerknes Centre for Climate Research, Bergen, Norway

The ROMS (Regional Ocean Modelling System) (<http://marine.rutgers.edu/po/index.php?model=roms>) model coupled to a dynamic-thermodynamic sea ice model has been used to conduct a simulation of ocean and ice conditions in the North Atlantic and Arctic Oceans for the period 1980–2004. The model horizontal resolution is 20 km in the Arctic Ocean and Nordic Seas and 30 km in the western North Atlantic. The vertical discretization consists of 30 vertical levels in a stretched sigma (S) coordinate system that provides higher resolution in the surface mixed layer. The forcing fields used in the simulation were daily mean surface heat and momentum fluxes from the NCAR/NCEP Reanalysis data set. Sample results from the simulation from January 1, 1994 for sea surface temperature (SST) and ice concentration are shown in Figures 1 and 2 respectively. The SST image shows that, although the model is not eddy-resolving, the simulation produces Gulf Stream separation at the correct

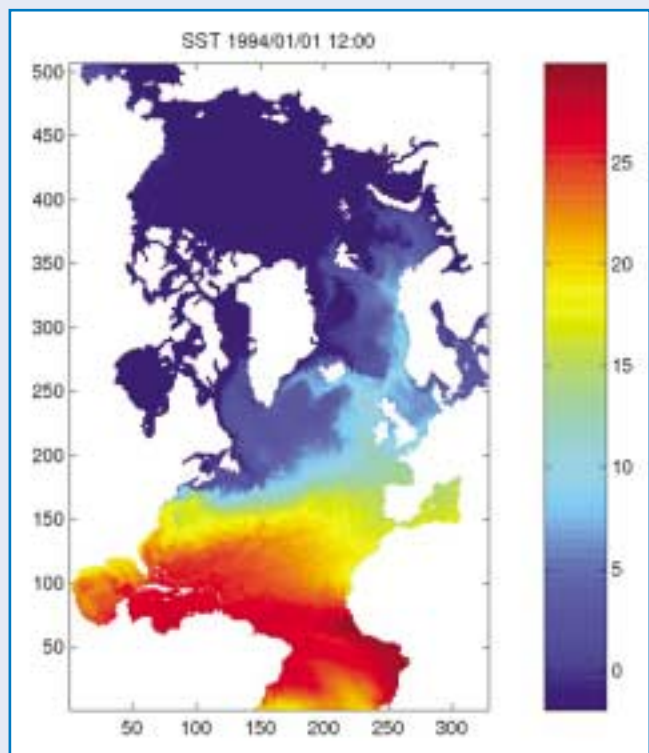


Figure 1. Simulated sea surface temperature for January 1, 1994.

location (Cape Hatteras, 35°N). The Iceland-Faeroes front is clearly visible, as is the bifurcation of the Norwegian-Atlantic Current into the West Spitzbergen Current and the Barents Sea Inflow. The ice distribution shown in Figure 2 is representative of observed January conditions.

The model results are archived as 3-day mean fields for the period of the simulation. The archived data set is currently being used to provide the circulation and hydrographic fields for off-line ecosystem (NPZ) simulations and individual-based model (IBM) simulations of zooplankton and fish larvae distributions.

Work has now begun to carry out a hindcast for the full period of the NCEP/NCAR Reanalysis, 1948–2004. The archived model results will be made available to the GLOBEC community to aid studies of the impact of decadal-scale and climatic variations in abiotic forcing on the marine ecosystem.

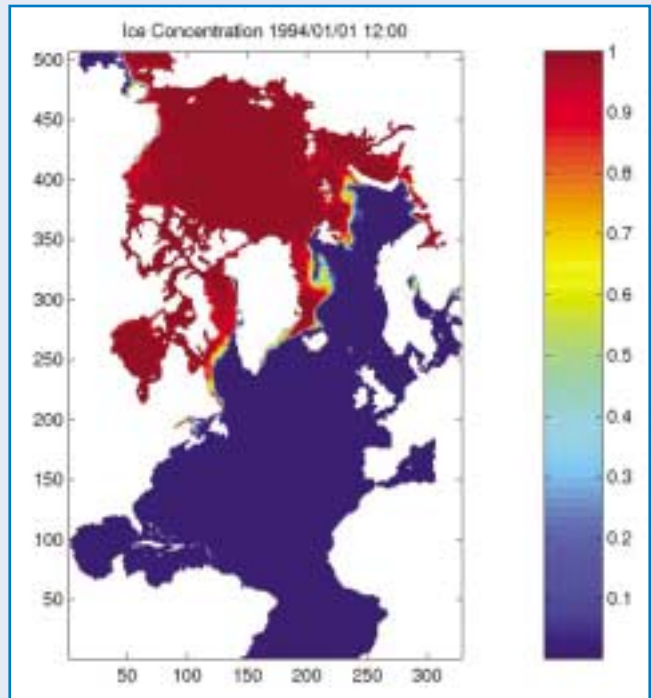


Figure 2. Simulated sea ice concentration for January 1, 1994.

### Multiple predators in the pelagic: modelling behavioural cascades

Øyvind Fiksen, Sigrunn Eliassen and Josefin Titelman, Department of Biology, University of Bergen

The behaviour of predators is rarely considered in models of predator-prey interactions, nor is it common to include multiple predators in models of animal behaviour. We introduce a model of optimal diel vertical migration in zooplankton prey facing predation from two functionally different predators, fish and other zooplankton. Zooplankton predators are themselves subject to predation from larger zooplankton, and all zooplankton face the classical trade-off between increasing growth rate and predation risk from fish towards the surface. Prey are most vulnerable to zooplankton predators at small sizes, but become more visible to fish as they grow. However, by habitat selection, prey continuously manage their exposure to different sources of risk. We analyse situations with cascading behavioural interactions of size-structured predator-prey interactions in the pelagic. In particular, we explore how vertical gradients in growth rates and relative abundance of fish and zooplankton predators affect optimal distribution patterns, growth and mortality schedules. A major model prediction is that prey susceptibility to one functional predator type depends on the abundance of the other predator. Higher abundance of zooplankton predators lead to risk enhancement from fish, minor increases in predation rate from zooplankton and unchanged prey growth rates. Increasing abundance of fish does not alter the risk from zooplankton predators, but reduce growth and development rates. Such asymmetric emergent effects may be common when prey and predators share the same spatial refuge from a common top predator. Full article in press for Journal of Animal Ecology.

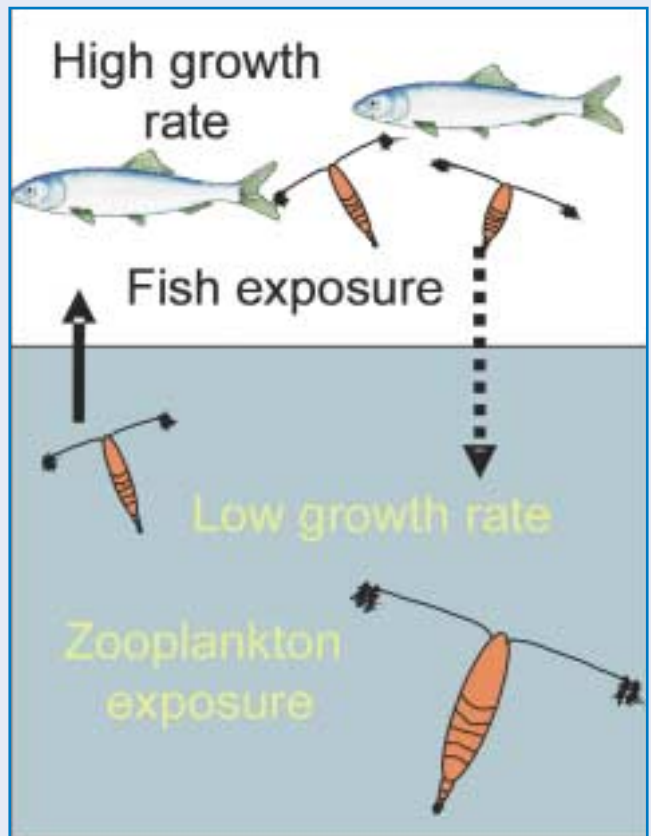


Figure 1. Size-structured predator-prey interactions.

## Artificial evolution of *Calanus*' life history strategies under different predation levels

Geir Huse, Institute of Marine Research, Bergen, Norway (geir.huse@imr.no)

Predation risk and food availability are key environmental features in shaping life history strategies and behaviour. Predation from planktivorous fish represents a major mortality source for the copepod *Calanus finmarchicus* in the Norwegian Sea. It has been suggested that high predation risk explains the prevalence of only one annual *C. finmarchicus* generation in the Norwegian Sea (Kaartvedt, 2000). This study uses an individual-based model (IBM) with artificial evolution (Strand *et al.*, 2002) to investigate the effect of varying levels of predation risk on the behaviour and life history strategy of *C. finmarchicus*.

The model consists of a 1 m vertically resolved domain [0,2000 m] and relies on light, daily temperature and phytoplankton densities taken from the NORWECOM model (Aksnes *et al.*, 1995) run for the southern Norwegian Sea. The strategies are optimised by using a genetic algorithm (Holland, 1992). The time step of the model is one hour, simulated at a day-to-day basis over the entire year and repeated 500 times to evolve good life history and behavioural traits. Life history traits including ascent day, overwintering depth, timing of fat allocation, and fat/soma ratio needed to descend to overwintering, and behavioural positioning are evolved in this manner. Active movement is calculated using an artificial neural network with information about predation risk, depth, phytoplankton density, and individual weight (Huse *et al.*, 1999).

The basic run yielded a population with two annual generations, ascent from overwintering in February–March and two waves of descent in late June and July respectively (Figs. 1A and B). In the simulation with increased predation risk, ascent is delayed by 10 days and there is pronounced diel vertical migration in the older stages (Fig. 1C). Descent was initiated in early June and only one annual generation

was produced (Fig. 1D). The overwintering depth was also much deeper in the simulation with increased predation risk compared with the basic run (Figs. 1A and C). The study shows that changing the magnitude of predation risk can have a profound effect on life history and behavioural strategies in *C. finmarchicus*, and thus supports the hypothesis that predation from planktivorous fish is important in shaping the life history of *C. finmarchicus* (Fiksen and Carlotti, 1998; Kaartvedt, 2000). The approach illustrated here (Huse, in prep.) yields a population of individuals with robust strategies that for example can be implemented in 3D biophysical ocean models.

### References

- Aksnes D.L., K.B. Ulvestad, B.M. Baliño, J. Bernsten, J.K. Egge and E. Svendsen. 1995. Ecological modelling in coastal waters: Towards predictive physical-chemical-biological simulation models. *Ophelia* 41: 5–36.
- Fiksen O. and F. Carlotti. 1998. A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. *Sarsia* 83:129–147.
- Holland J.H. 1992. *Adaptation in natural and artificial systems*. Cambridge, MA, The MIT Press.
- Huse G. In prep. Adapting the life history of *Calanus finmarchicus* under different predator regimes by artificial evolution.
- Huse G., E. Strand and J. Giske. 1999. Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evolutionary Ecology* 13: 469–483.
- Kaartvedt S. 2000. Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. *ICES Journal of Marine Science* 57:1819–1824.
- Strand E., G. Huse and J. Giske. 2002. Artificial evolution of life history and behavior. *The American Naturalist* 159:624–644.

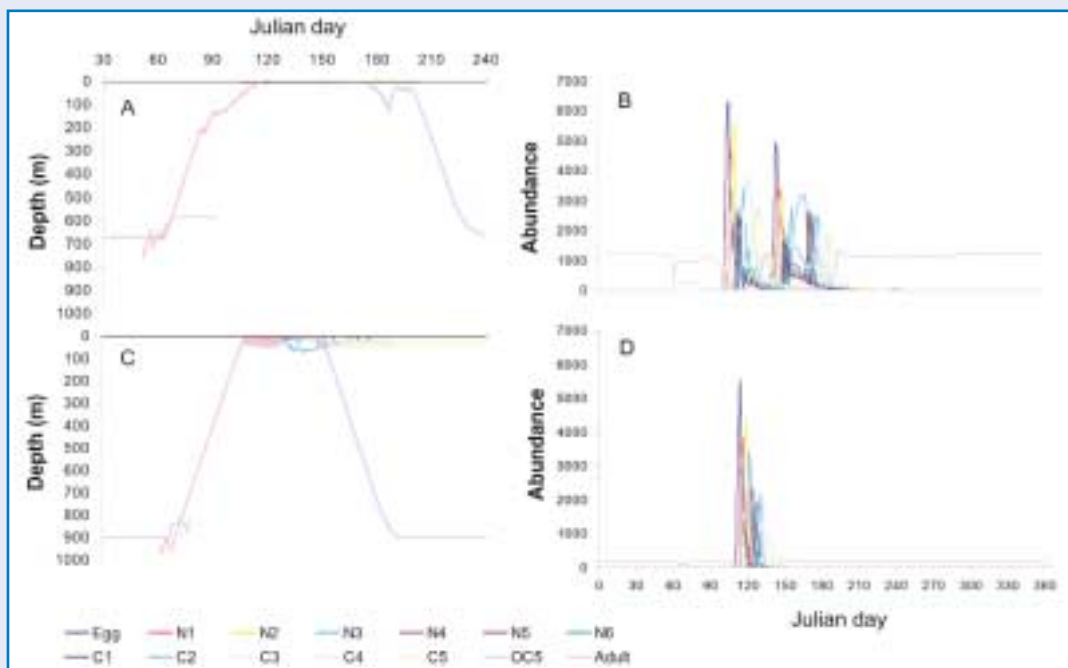


Figure 1. Simulated population dynamics in *C. finmarchicus* where life history strategies and behaviour are evolved under low (A, B) and high (C, D) predation pressure from fish. The colours indicate the different *Calanus* stages. C5 individuals were categorized as Adult upon initiating ascent from overwintering.



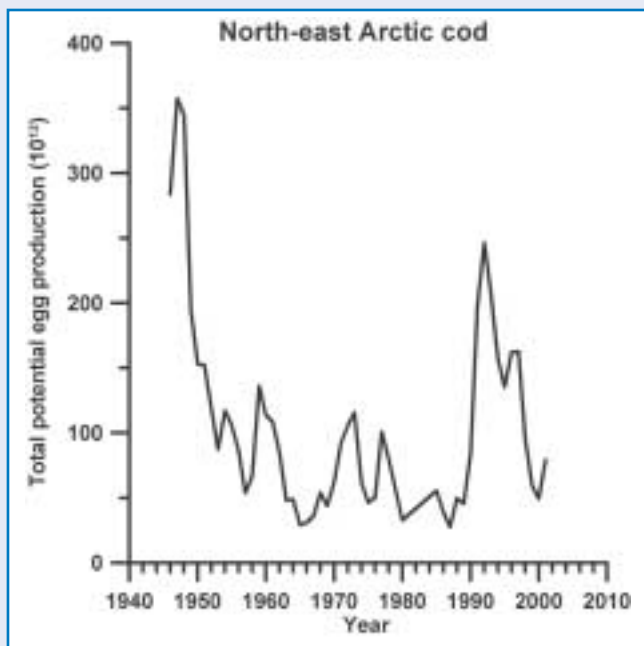


Figure 3. The reproductive potential of the North-east Arctic cod population between 1946 and 2002. Reproductive potential is measured as the total potential egg production of the stock.

at larger sizes (Marshall *et al.*, in prep). Also, since about 1990 the pattern of maturity of females has changed with the proportion of smaller fish being mature having increased considerably. These large changes give insight in to the dynamics of the stock both under high exploitation levels but also under a range of environmental conditions.

The initial step for estimating the egg production over time is to convert the population size (numbers at age) estimated by Virtual Population Analysis (VPA) (ICES, 2004a) to a population length frequency of females (Marshall *et al.*, unpublished data). Using a length-weight relationship estimated each year (Marshall *et al.*, 2004) the weight-at-length is estimated and this is converted to a relative condition factor (Scott *et al.*, in press). Fecundity for each length class is estimated from a simple relationship incorporating length and relative condition (Marshall *et al.*, in prep). Using the numbers of females and the fecundity per length class the total egg production can be estimated. In this way the historical change in the NE Arctic cod stock is presented as the change in total egg production or stock reproductive potential (Marshall *et al.*, 2003) rather than the traditional Spawning Stock Biomass used in standard stock assessments (ICES, 2004a).

The relevance of this research to the theme of climate change is that under various climate change scenarios there will be changes in the environmental factors and also in the available prey for cod (in this case principally capelin). Given a set of prey and environmental conditions it will be possible to estimate the reproductive potential of the North-east Arctic cod stock, and with incorporation of recruitment models examine the population dynamics of this species under different environmental conditions.

This research will also examine the population egg production in Arcto-Norwegian haddock (1950 to the present) and Norwegian spring spawning herring (1938 to the present).

References

Bogstad B. and S. Mehl. 1997. Interactions between cod and its prey species in the Barents Sea. In: Proceedings of the International Symposium on the role of forage fish in marine ecosystems, p.591–615. Alaska Sea Grant College Program Report No. 97–01. University of Alaska, Fairbanks.

Harðardóttir K., O.S. Kjesbu and G. Marteinsdottir. 2003. Atresia in Icelandic cod (*Gadus morhua* L.) prior to and during spawning. p.51–55. In: O.S. Kjesbu, J.R. Hunter and P.R. Witthames. (Eds.). Report on the Working Group on Modern Approaches to Assess Maturity and Fecundity of Warm- and Cold-water Fish and Squids. Institute of Marine Research, Bergen, Norway.

ICES. 2004a. Report of the Arctic Fisheries Working Group. ICES CM 2004/ACFM:28.

ICES. 2004b. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group. ICES CM 2004/ACFM:24

Kjesbu O.S. 1994. Time of start of spawning in Atlantic cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. *Journal of Fish Biology* 45: 719–735.

Kjesbu O.S., P. Solemdal, P. Bratland and M. Fonn. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 53: 610–620.

Kjesbu O.S., P.R. Witthames, P. Solemdal and M. Greer Walker. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *Journal of Sea Research* 40: 303–321.

Köster F.W., H.-H. Hinrichsen, M.A. St. John, D. Schnack, B.R. Mackenzie, J. Tomkiewicz and M. Plikshs. 2001. Developing Baltic cod recruitment models II: Incorporation of environmental variability and species interaction. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1535–1557.

Lambert Y. and J.-D. Dutil. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 815–825.

Ma Y., O.S. Kjesbu and T. Jørgensen. 1998. Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 55: 900–908.

Marshall C.T., O.S. Kjesbu, N.A. Yaragina, P. Solemdal and Ø. Ulltang. 1998. Is spawner biomass a sensitive measure of the reproduction and recruitment potential of Northeast Arctic cod? *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1766–1783.

Marshall C.T. *et al.* 2003. Developing alternative indices of reproductive potential for use in fisheries management: Case studies for stocks spanning an information gradient. *Journal of Northwest Atlantic Fisheries Science* 33: 161–190.

Marshall C.T., C.L. Needle, N.A. Yaragina, A.M. Ajjad and E. Gusev. 2004. Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1900–1917.

Marshall C.T., C.L. Needle, A. Thorsen, O.S. Kjesbu and N.A. Yaragina, N.A. In prep. Systematic bias in estimates of reproductive potential of cod stocks: Implications for stock/recruit theory and management.

Marteinsdottir G. and K. Thorarinsson. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1372–1377.

Murua H. and F. Saborido-Rey. 2003. Female reproductive strategies of marine fish species of the North Atlantic. *Journal of Northwest Atlantic Fishery Science* 33: 23–31.

Scott B.E., G. Marteinsdottir, G.A. Begg, P.J. Wright and O.S. Kjesbu. In press. Effects of population structure, condition and temporal dynamics of flexible life history traits on reproductive output in Atlantic cod (*Gadus morhua*). *Ecological Modelling*.





## Buoyancy of eggs of Norwegian coastal cod from different areas along the coast

Erling K. Stenevik (erling.stenevik@imr.no) and Svein Sundby (svein.sundby@imr.no)  
Institute of Marine Research, Bergen, Norway

According to Pogson and Fevolden (2003) the population structure of cod in northern Norwegian areas has been a controversial topic for several decades. A number of publications have suggested that there are genetic differences between coastal cod, which are stationary and spawn along the entire Norwegian coast, and north-east Arctic cod which is highly migratory and spawns mainly near the Lofoten Islands. This has led to the conclusion that they are two separate populations. There are, however, also authors who state that the genetic analyses should be interpreted with caution and that there is no clear genetic difference between migratory cod and stationary cod. Mork *et al.* (1985) suggested that the genetic differentiation of Atlantic cod, covering most of the species range, was weak. Also within the coastal cod, both genetic (Knutson *et al.*, 2003) and behavioural (Salvanes *et al.*, 2004) differences have been observed between different areas along the coast. Actually, the results presented by Pogson and Fevolden (2003) suggested that there were a higher degree of similarity between Arctic and coastal cod than among coastal cod sampled from different populations along the coast.

Salvanes *et al.* (2004) states that evolution of genetically differentiated sub-populations in species distributed over wide range of environments is likely as long as there are mechanisms ensuring local retention of early life stages (Asplin *et al.*, 1999). Vertical distribution of the eggs is one factor which will affect their transport. Because of the often strong vertical shear in circulation, eggs distributed in the upper water column will have a different transport than eggs distributed deeper. Transport in surface waters will favour advection away from spawning areas close to the shore and in fjords, while deeper eggs will have a higher degree of retention in the spawning areas. In this study, the buoyancy of eggs from Norwegian coastal cod from four localities (Porsanger, Tysfjord, Helgeland and Øygarden) along the Norwegian coast was investigated (Fig. 1). The broodstock was collected in the different areas during the spawning season in 2002 and transported to Parisvannet field station where pairs of male and female were set up in individual tanks and spawning monitored. The eggs in this experiment were collected during the spawning season in 2004. Buoyancy of the eggs was measured using a density



Figure 1. The circles indicate origins of the four groups of cod broodstock used in the experiment.

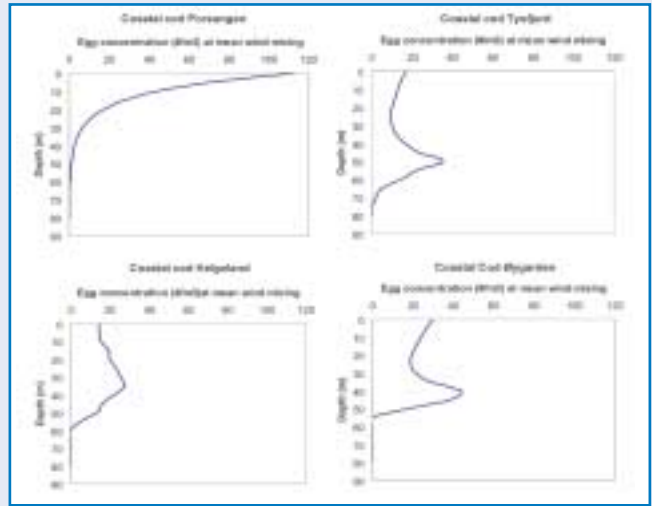


Figure 2. Modelled vertical distribution of cod eggs from the four localities at a wind speed of 6 m s<sup>-1</sup>.

gradient column and eggs from 22 families were investigated. Based on these measurements and the in situ salinity structure at the different localities, the vertical distribution of the eggs was modelled using a model developed by Sundby (1991). The results showed that there were differences in buoyancy and in vertical distribution (Fig. 2). The eggs from cod sampled in the northernmost locality (Porsanger) had high buoyancy and were mostly distributed in the upper water column similarly to eggs from north-east Arctic cod, while the eggs from the other localities were heavier and had a peak in vertical distribution at 30–50 m. The implication of this is that the eggs from Porsanger will have a higher probability of being transported away from the spawning areas and into the Barents Sea while eggs from the other localities will have a higher degree of retention. The next step will be to model the horizontal transport of the eggs using 3D modelling to better understand how the observed differences in vertical distribution will influence transport.

### References

- Asplin L., A.G.V. Salvanes and J.B. Kristoffersen. 1999. Nonlocal wind-driven fjord-coast advection and its potential effect on plankton and fish recruitment. *Fisheries Oceanography* 8: 255–263.
- Knutson H., E. Jorde, C. André and N.C. Stenseth. 2003. Fine-scaled geographical population structuring in a highly mobile species: the Atlantic cod. *Molecular Ecology* 12: 385–394.
- Mork J., N. Ryman, G. Ståhl, F. Utter and G. Sundnes. 1985. Genetic variation in cod (*Gadus morhua*) throughout its range. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1580–1587.
- Pogson G.H. and S.E. Fevolden. 2003. Natural selection and the genetic differentiation of coastal and Arctic populations of the Atlantic cod in northern Norway: a test involving nucleotide sequence variation at the pantophysin (PanI) locus. *Molecular Ecology* 12: 63–74.
- Salvanes A.G.V., J.E. Skjøeraasen and T. Nilsen. 2004. Subpopulations of coastal cod with different behaviour and life-history strategies. *Marine Ecology Progress Series* 267: 241–251.
- Sundby S. 1991. Factors affecting the vertical distribution of eggs. *ICES Marine Science Symposia* 192: 33–38.



*C. finmarchicus* was higher in the western pre-bloom area the average population production was higher in bloom water (213682 eggs m<sup>-2</sup> day<sup>-1</sup>) compared to pre bloom waters (141410 eggs m<sup>-2</sup> day<sup>-1</sup>) and post-bloom waters (78773 eggs m<sup>-2</sup> day<sup>-1</sup>). But still, the population egg production was considerable in the pre-bloom area mainly because of the high abundance of females in this area. The pre-bloom will also normally last longer than the bloom (Niehoff *et al.* 1999) increasing the importance of this period for spawning of *C. finmarchicus*.

**References**

Kaartvedt S. 2000. Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. ICES Journal of Marine Science 57: 1819–1824.  
 Niehoff B., U. Klenke, H.-J. Hirche, X. Irigoien, R. Head and R. Harris. 1999. A high frequency time series of Weathership M, Norwegian Sea, during the 1997 spring bloom: the reproductive biology of *Calanus finmarchicus*. Marine Ecology Progress Series 176: 81–92.  
 Niehoff B. and H.-J. Hirche. 2000. The reproduction of *Calanus finmarchicus* in the Norwegian Sea in spring. Sarsia 85: 15–22.

**Predator-prey encounters in turbulent waters**

H.L. Pécseli<sup>1</sup>, J. Trulsen<sup>1</sup>, J. Mann<sup>2</sup> and S. Ott<sup>2</sup>

<sup>1</sup>University of Oslo, Blindern, Norway <sup>2</sup>Risø National Laboratory, Roskilde, Denmark

With reference to studies of predator-prey encounters in turbulent waters, we demonstrate the feasibility of an experimental method for investigations of particle fluxes to an absorbing surface in turbulent flows. A laboratory experiment is carried out, where an approximately homogeneous and isotropic turbulent flow is generated by two moving grids. The simultaneous trajectories of many small neutrally buoyant polystyrene particles are followed in time. Selecting one of these to represent a predator, while the others are considered as prey, we obtain estimates for the time variation of the statistical average of the prey flux into a suitably defined “sphere of interception”. The variation of this flux with the radius in the sphere of interception, as well as the variation with basic flow parameters is well described by a simple model, in particular for radii smaller than the integral length scale, which is here in the range of 20–25 mm, while the inner scale (Kolmogorov scale) is typically 1/4 mm.

The turbulence is generated by the motion of two plastic grids, in the top and bottom of a tank with 320 x 320 x 450 mm<sup>3</sup> inner dimensions. The motions of small polystyrene particles of size 0.5–0.6 mm are followed with 4 video-cameras, and the simultaneous positions of typically 500–1000 particles recorded at time intervals of 1/25 s. By a tracking procedure it is then possible to link the positions of particles, and thus follow their individual motions in 3 spatial dimensions and in particular also to deduce their time varying velocity (Ott and Mann, 2000).

With the records of simultaneous particle trajectories being available, we can now select one to represent the predator and label all the others as prey. We then select a predetermined radius *R* in the sphere of interception, and then remove all the particles which happen to be inside this sphere. During the subsequent Lagrangian motion of the reference “predator”, we count the number of prey entering its co-moving sphere of interception between successive time steps. Each time a particle enters, it is “eaten” in the sense that it is removed from the database. By repeating the procedure, we reduce the signal-to-noise level, and obtain an estimate for the prey flux to a predator, with given radius and turbulence parameters. Experimentally obtained scaling laws with radius *R* and turbulent dissipation rate *e* are shown in Figures 1 and 2. The results agree well with simple models, which can be obtained by dimensional reasoning (Mann *et al.*, 2002).

**References**

Ott S. and J. Mann. 2000. An experimental investigation of the relative diffusion of particle pairs in three dimensional turbulent flow. Journal of Fluid Mechanics 422: 207–223.  
 Mann J., S. Ott, H.L. Pécseli and J. Trulsen. 2002. Predator-prey encounters in turbulent waters. Physics Review E 65: 026304.

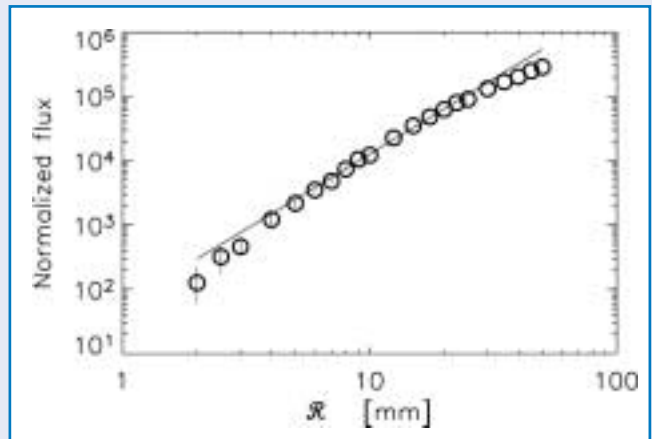


Figure 1. The normalized average prey flux to a moving predator, shown for different radii, *R*, in the sphere of interception, for fixed turbulent energy dissipation, *ε*. A theoretical *R*<sup>1.5</sup> line is inserted for reference.

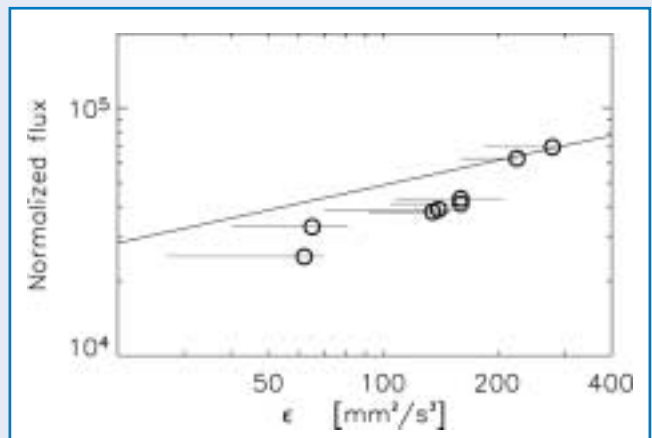


Figure 2. Variation of the normalized average prey flux to a moving predator, for fixed *R* = 20 mm, and varying *ε*, in units of mm<sup>2</sup>/s<sup>3</sup>. A theoretical *ε*<sup>1.2</sup> line is inserted for reference.



## Possible connectivity between Arcto-Norwegian cod and Norwegian Coastal cod – a model approach

Frode Vikebø (frovik@imr.no), Svein Sundby and Bjørn Ådlandsvik  
Institute of Marine Research, Bergen, Norway

There are two cod populations spawning along the Norwegian coast; the Arcto-Norwegian cod (ANC) and the Norwegian Coastal cod (CC). They are managed as two separate populations with implications on stake holders decisions regarding quotas, fishing tools, minimum catch size, fishing bans (locations and periods) etc.

ANC and CC spawn at several locations along the Norwegian coast, with the ANC eggs, on average, more buoyant than the CC eggs (Solemdal and Sundby, 1981; Kjesbu *et al.*, 1992). There is partly horizontal and temporal overlap of ANC and CC eggs on the spawning grounds in the Vestfjord, with their individual neutral buoyancies determining the vertical distribution, as the only source of vertical separation.

The slight differences in observed buoyancy of ANC eggs and CC eggs will have the potential to create differential drift patterns of the two stocks in the way that CC eggs will, on average, be transported northwards at greater depths than that of the ANC eggs. Hence, differences in mean buoyancy of eggs contribute to separate them geographically, while deviations from the mean buoyancy, which may give eggs of equal buoyancy, contribute to mix them geographically and allow exchange of individuals between respective habitats.

Simulations with a regional ocean model (ROMS – <http://marine.rutgers.edu/po/models/roms/>) indicate that particles released in the Vestfjord will diverge horizontally when they are kept fixed at different depths. Particles close to the surface are more likely to be transported into the nursery grounds of Arcto-Norwegian cod in the Barents Sea. Contrary, particles transported at deeper levels of the water column are more likely to end up along the Norwegian coast and into the fjords (Fig. 1).

Interaction between lateral mixing caused by winds and topographic effects, and the features of the local currents is the cause for this divergence. The Norwegian Atlantic Current (NwAC) flows along the continental shelf edge, bifurcating northwest of the Tromsøflaket (71°N, 18°E), with a branch entering the Barents Sea along the wedge-shaped Norwegian Coastal Current (NwCC) close to the Norwegian Coast and the other branch

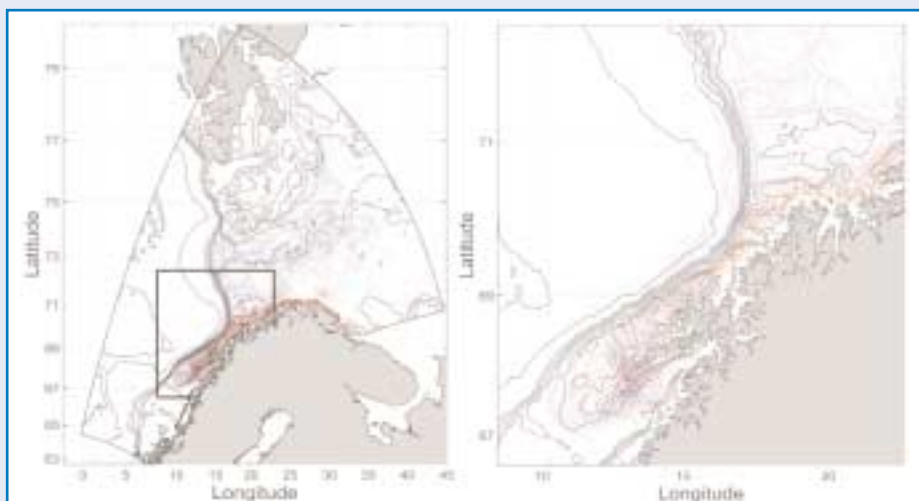
following the shelf edge towards the western Barents Sea and Spitsbergen. When particles are released at the same geographical location in the Vestfjord, the ones closer to the surface will experience the most lateral mixing and have the highest fraction of particles displaced out into the NwAC. The implication for the drift of eggs is clear; a higher fraction of eggs close to the surface will be laterally spread out into the NwAC than for eggs drifting at greater depths. This will precondition further larval drift differently and may result in CC juveniles to sense the bottom, and consequently settle to the bottom, at an earlier stage and closer to the coast than the more offshore-drifting ANC juveniles. Differences in the environmental conditions along the individual drift paths will set the premise for the later achieved individual meristic characters.

Buoyancy differences between ANC and CC eggs do exist, causing separation of ANC and CC during the period of pelagically free drift from the spawning area to the area where the juveniles settle to the bottom and become more stationary. This supports the idea that ANC and CC are two separate populations. On the other hand, the neutral buoyancy of the eggs also overlaps, causing the drift paths to overlap, enabling a potential connectivity between ANC and CC as the 0-group juveniles are mixed at the nursery grounds. Studying the simulated inter-annual 0-group distributions for eggs with neutral buoyancies representative for ANC and CC eggs would enlighten the long-term relation between separation and mixing and will be a natural line of progress for the current study.

### References

- Kjesbu O.S., H. Kryvi, S. Sundby and P. Solemdal. 1992. Buoyancy variations in eggs of Atlantic cod (*Gadus morhua* L.) in relation to chorion thickness and egg size: theory and observations. *Journal of Fish Biology* 41: 581–599.
- Solemdal P. and S. Sundby. 1981. Vertical distribution of pelagic fish eggs in relation to species, spawning behaviour and wind conditions. *ICES CM 1981/G:77* (mimeo).

Figure 1. A sample of simulated drift trajectories for larvae at different depths (1, 10, 20 and 30m) and time of hatching for a period ranging from spawning in the Vestfjord, (68°N, 14°E) until 0-group stage 1985 (4–6 months old). Drift routes ending up close to the coast are coloured red and the ones spread out into the Barents Sea are coloured blue.





the individual weight of the 0-group fish (Fig. 1). Also, the total abundance of 0-group larvae was higher in 1985 than in 1986, and the centre of biomass was further to the west. The distribution in 1985 covered a larger area than in 1986 and the average length of 0-group cod, and therefore the weight (Ellertsen *et al.*, 1989), were significantly lower in 1986 than in 1985 (Ottersen and Loeng, 2000). To what degree will the models be able to reproduce measured larval distributions? In what way will vertical distribution of larvae and juveniles affect 0-group distribution and weight? Will the time of spawning affect growth and distribution of 0-group cod?

The simulations reproduce the observed key features of 0-group cod distributions for the two years 1985 and 1986. (1) The simulated area-dependent weight distributions indicate larger larvae and juveniles in the western parts of the Barents Sea than further east, (2) the centre of gravity is more eastern in 1986 than in 1985, (3) the distributions are limited to Coastal and Atlantic Water masses and (4) prolonged transport time from the spawning ground to the nursery ground due to retention above bank structures along the shelf. This indicates that transport and temperature-dependent larval growth alone can reproduce key features of the 0-group weight distribution and concentration in the Barents Sea.

The vertical placement of larvae is shown to have a significant impact on both the later horizontal distribution and weight. Larvae drifting close to the surface are more likely to end up in the central or western Barents Sea, while larvae further down in the water column are more likely to end up close to the Norwegian coast and to the eastern Barents Sea. Earlier spawned larvae have a higher mean and standard deviation of 0-group weights and are geographically more widespread as a consequence of longer transport time and stronger winds earlier in the year. However, the temperatures experienced by the individuals and the 0-group distributions by August are both less dependent on the time of spawning than on the vertical placement of the larvae. Food availability is not considered in the model in its present form. However, this might affect the dependence of the growth on time of

spawning due to the 'match-mismatch' of prey and predators (Hjort, 1914).

Using inter-annual variations on these boundaries, in the same way as for the atmospheric forcing, is considered to be the most important factor to improve the model results. This would also enable us to estimate year-to-year variations in recruitment, as this is linked to abundance of 0-group cod (Sundby *et al.*, 1989) and their condition (Ottersen and Loeng, 2000). This is one of the topics we plan to pursue. Also, a more sophisticated individual based model where growth depends on food availability, turbulence and light, in addition to transport and temperature, is needed. This will, among other things, enable us to find the optimum behaviour concerning the trade off between feeding and favourable temperature.

**References**

Björnasson B. and A. Steinarsson. 2002. The food-unlimited growth rate of Atlantic cod *Gadus morhua*. Canadian Journal of Fisheries and Aquatic Sciences 59: 494–502.

Hjort J. 1914. Fluctuation in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Proces-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer 20: 1–228.

ICES. 1985. Preliminary report of the International 0-Group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1985. ICES CM 1985/G:75.

ICES. 1986. Preliminary report of the International 0-Group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1986. ICES CM 1986/G:78.

Otterlei O., G. Nyhammar, A. Folkvord and S.O. Stefansson. 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod: a comparative study of Norwegian coastal cod and northeast Arctic cod. Canadian Journal of Fisheries and Aquatic Sciences 56: 2099–2111.

Ottersen G. and H. Loeng. 2000. Co-variability in early growth and year-class strength of Barents Sea cod, haddock and herring: The environmental link. ICES Journal of Marine Science 57: 339–348.

Sundby S. and P. Bratland. 1987. Kartlegging av gytefeltene for norsk-arktisk torsk i Nord-Norge og beregning av eggproduksjonen i årene 1983-1985. Fisken og Havet, 1: 1–58. [In Norwegian].

**Variability in advective losses of *Calanus finmarchicus* in the Nordic Seas**

Thomas Torgersen<sup>1</sup> and Geir Huse<sup>2</sup>

<sup>1</sup>University of Bergen, Norway (Thomas.Torgersen@bio.uib.no)

<sup>2</sup>Institute of Marine Research, Bergen, Norway (geir.huse@imr.no)

Climate variability causes variability in the environment of organisms, and thereby has an effect on their growth, fecundity and survival. Planktonic organisms are transported with the currents. Therefore, as opposed to non-drifting organisms, plankton may experience the spatial variability of advective systems as temporal variability. Using a regional ocean circulation model, we have used a particle tracking model to study the spatial and inter-annual variability in *Calanus finmarchicus*' risk of being advected out of the Nordic Seas population, and the significance of seasonal vertical migration patterns. We found that spatial variability was higher than inter-annual variability during the period 1988–1991. Variability between forcing years and between different seasonal vertical migration patterns were of approximately the same size. Average retention was 40% after 1 year in simulations with diffusion and advection and 42% in simulations with advection only. The average retention at the end of a 4 year sequence was 10 and 12%

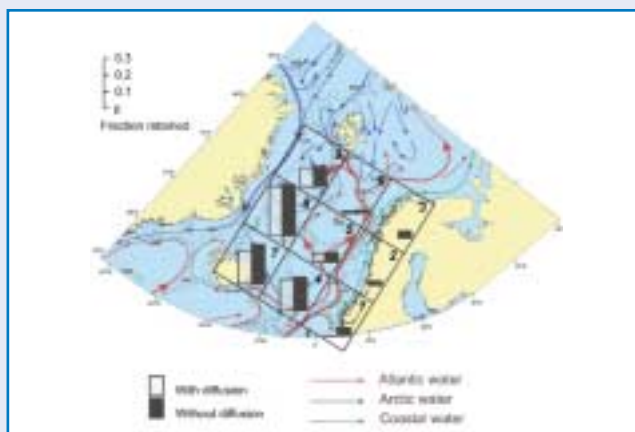


Figure 1. The model area with the 9 numbered sub-areas shown. Proportions of individuals initiated in each sub-area that are retained within the entire study-area after 4 years (1988–1991, average for all behaviours) are shown for the simulations with and without diffusion. Main currents are indicated with arrows.

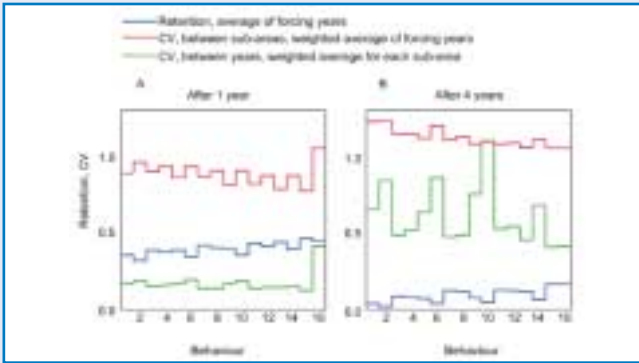


Figure 2. Retained fractions after 1 (A) and 4 (B) years with variability between years and between sub-areas for all behaviours. Simulations were run with diffusion.

with and without diffusion respectively. Individuals initiated in the western sub-areas had the highest retention. Sub-areas along the Norwegian coast showed little or no retention after 4 years. Our results suggest that *C. finmarchicus* experience larger inter-generational variability in risk of being lost from the Nordic Seas population due to the spatial variability of its domain than from the inter-annual variability in advective fields. Hence, to the extent that behaviour has influence on advective loss risk, *C. finmarchicus* should have evolved behavioural strategies that are robust towards strong temporal variability in advection.

This work was supported by the Research Council of Norway.

## The cause and the effect of the 18.6 year nodal tide in the Barents Sea

Harald Yndestad, Aalesund, University College, Norway. (hy@hials.no)

The lunar node is the intersection between the moon plane and the ecliptic plane to the sun. This intersection moves 360° in 18.6 years and causes the lunar nodal cycle (Fig. 1). A 5 degree oscillation between the planes causes an oscillating gravity force and a 18.6 year tide on the earth. This small lunar nodal tide may have an important influence on climate change dynamics.

A wavelet analysis of time series from the Barents Sea has identified a lunar nodal tide spectrum of 18.6/3=6.2, 18.6 and 18.6\*3= 55.8 years that influences Atlantic inflow to the Barents Sea. This lunar nodal spectrum is identified in the vertical tide, the Kola section temperature and salinity, Barents Sea ice extent and the NAO winter index. The phase relation between the lunar nodal cycles indicates there is the time delay of about a year from the Kola section temperature to Barents Sea ice extent and the NAO winter index. The NAO winter index has a dominant cycle of about 4\*18.6=74.4 years (Fig. 2). This cycle has the same cycle time and cycle phase as the mean 74 year cycle from ice extent in the Greenland Sea and the Barents Sea. The close relation

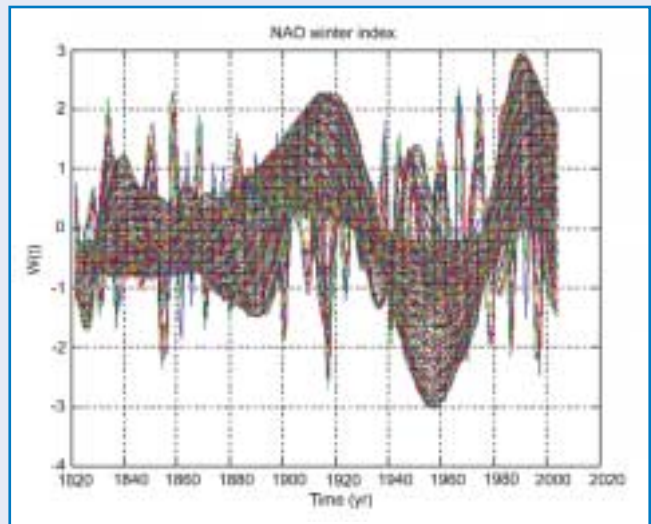


Figure 2. Wavelet spectrum of the NAO winter index that shows the dominant 74 year cycle.

between the long-term tides, Arctic ice extent and the NAO winter index indicates that the NAO winter index fluctuation has a major influence from Arctic ice extent. This indicates that Arctic ice is an isolator between the cold air and a warm sea in the winter time (Yndestad, 2004).

The identified lunar nodal cycles have a time variant phase. The identified 18.6 year cycle has a phase reversal related to a sub-harmonic cycle of 4\*18.6=74.4 years. This phase-reversal is identified in the Faroe-Shetland time series and the Barents Sea time series (Yndestad *et al.*, 2004). The phase-reversal represents a regime shift that may be caused by interference between cycles in the lunar nodal spectrum.

### References

- Yndestad H., W.R. Turrell and V. Ozhigin. 2004. Temporal linkages between Faroe-Shetland time series and Kola section time series. Theme Session M. Regime Shifts in the North Atlantic Ocean : Coherent or Chaotic. ICES CM 2004/M01.
- Yndestad, H. 2004. The lunar nodal cycle influence on the Barents Sea. Doctoral Thesis. NTNU 2004:132. Trondheim.

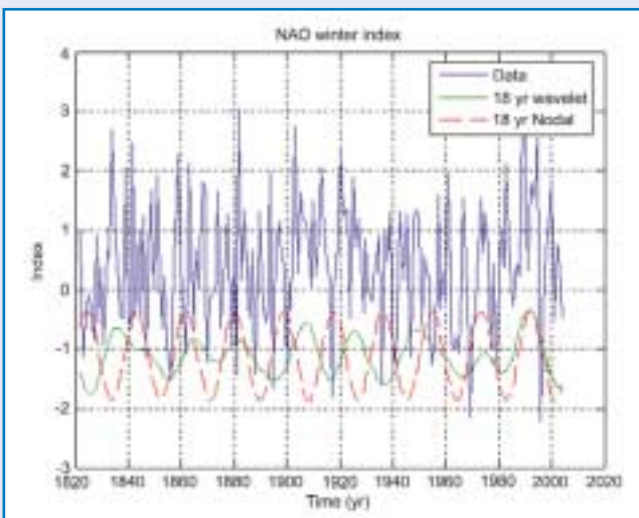


Figure 1. Time series of NAO winter index, the 18.6 yr cycle and the dominant 18-yr wavelet cycle. The 18-yr cycle has phase-reversals at about 1885 and 1960.





## What happens with the Arcto-Norwegian cod if the thermohaline circulation slows down?

Frode Vikebø (frovik@imr.no)<sup>1</sup>, Svein Sundby<sup>1</sup>, Bjørn Ådlandsvik<sup>1</sup> and Odd Helge Otterå<sup>2</sup>

<sup>1</sup>Institute of Marine Research, Bergen, Norway.

<sup>2</sup>Nansen Environmental and Remote Sensing Center, Bergen, Norway.

A reduction of the thermohaline circulation (THC) might have a strong impact on the Northeastern Atlantic ecosystem. We address this potential challenge by studying the effects of THC changes on larval drift and development of Arcto-Norwegian Cod (ANC), as several studies have shown that there is a close link between the condition of cod at the 0-group stage and the year class strength of the 3-group fish. The approach taken is that of a modelling study supported by analysis of existing data on fish stocks and climate. A regional model (ROMS) is forced by a global climate model in which the hydrological cycle of the Nordic Seas is perturbed. The impact of the anomalous circulation and ocean temperature on ANC in its habitat, as simulated by ROMS, is investigated by using an individual based model to simulate growth of the larvae and juveniles along their resulting drift paths. The Nordic Seas are dominated by the near surface inflow of warm and salt Atlantic Water (AW), driven by prevailing southwesterly winds (Furevik and Nilsen, in press) and thermohaline circulation (THC) (Broecker, 1991). That is, ocean circulation driven by density differences. The relative importance of winds versus density differences is, however, not yet clear (Hansen and Østerhus 2000; Blindheim, 2004). Because of the massive heat transport by the AW, atmospheric and oceanic cold fronts are pushed northwards giving a maximum deviation of air temperature from the latitudinal mean in the northeastern North Atlantic of about 10°C. Sediment cores have revealed that the THC has undergone major changes in the past (Sarnthein *et al.* 1994; 1995). In this regard several authors have discussed the possibility of non-linear behaviour of the THC (Manabe and Stouffer, 1988; Rahmstorf, 1994). A THC collapse is now widely discussed as one of a number of “low probability – high impact” risks associated with global warming (Integration – [www.pik.potsdam.de/~stefan/Projects/integration/](http://www.pik.potsdam.de/~stefan/Projects/integration/)). More likely than a breakdown of the THC, which only occurs in very pessimistic scenarios (Rahmstorf and Ganopolski, 1999), is a weakening of the THC by 20–50%, as simulated by many coupled climate models (Rahmstorf, 1999).

Significant changes of the THC will affect ecological processes across a broad range of temporal and spatial scales. Atlantic cod (*Gadus morhua* L.) is one of the major North Atlantic fish resources and Arcto-Norwegian cod (ANC) is the larger of these cod stocks. By existing data on ANC and

climate it has been well documented that weak year classes always occur during cold years, and that strong year classes occurs during warm years (Sætersdal and Loeng, 1987; Ellertsen *et al.*, 1989; Ottersen and Sundby, 1995; Ottersen and Loeng, 2000). This relationship between recruitment and temperature is partly, directly through feeding intensity and metabolic rates (Otterlei *et al.*, 1999), and partly, indirectly through lower trophic layers, as temperature in the Barents Sea is a proxy for the advection of zooplankton-rich AW from the Norwegian Sea and onto the shelves, e.g. the Barents Sea and the shelf off Norway (Skjoldal and Rey, 1989; Helle and Pennington, 1999; Sundby, 2000). Existing knowledge on cod and climate may be used to infer the consequences of a permanent change in the physical state of the environment occupied by cod.

A regional ocean model system (ROMS – <http://marine.rutgers.edu/po/models/roms/>) is set up for the habitat of ANC. ROMS is forced with initial- and boundary conditions from a simulation with the Bergen Climate Model (BCM), in which the hydrological cycle is perturbed, resulting in a weakened THC from 18 to 12 Sv (1Sv equals 1mill. m<sup>3</sup>/s) and a subsequent reduced inflow of AW to the Barents Sea. As a consequence, the temperature in the Barents Sea is reduced by up to 3°C. ROMS simulates transport of larvae and juveniles, while keeping a record of the individual temperature histories enabling calculation of temperature dependent growth, from spawning until settlement at the nursery grounds. Temperature-growth relations from two studies were included (Otterlei *et al.*, 1999 and Björnasson and Steinarsson, 2002). What are the qualitative and quantitative effects of a substantial reduction of the THC on growth, distribution and recruitment of ANC?

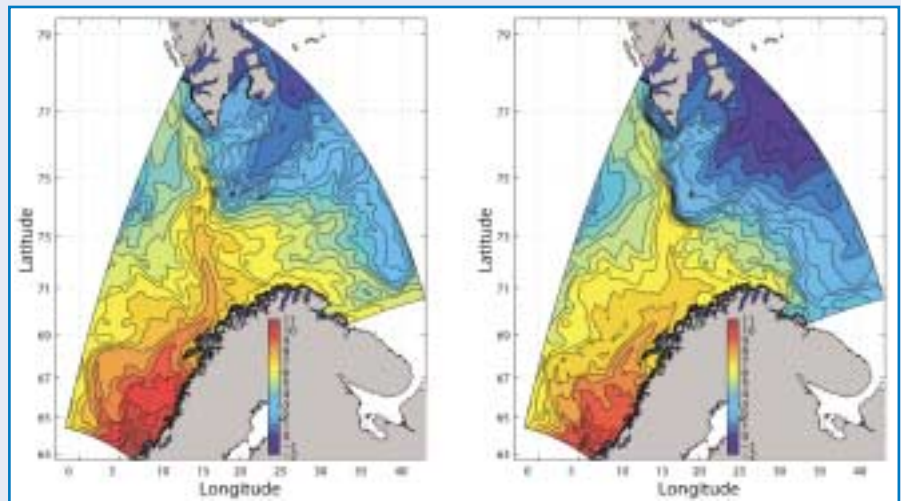


Figure 1. Temperature averaged for May, June and July at 100m depth for simulated fields with forcing fields from the BCM control run (left panel) and the BCM perturbed run (right panel).

In conclusion, the present description of a reduction in the THC by 35% results in:

- 1) An increased flow west of Spitsbergen, while the inflow to the Barents Sea is considerable reduced.
- 2) A southward and westward shift in the distribution of cod year classes from the Barents Sea onto the narrow shelves of Norway and Svalbard.
- 3) A reduced individual growth of the pelagic juveniles with a subsequent poorer year classes, most probably less than 10% of the strong year classes of today (Ellertsen *et al.*, 1989).
- 4) An increasing number of larvae and juveniles advected towards the western parts of Spitsbergen and possibly further into the Arctic Oceans where they are unable to survive.

A southward shift of the spawning areas along the Norwegian Coast will enhance this development (Sundby and Nakken, submitted).

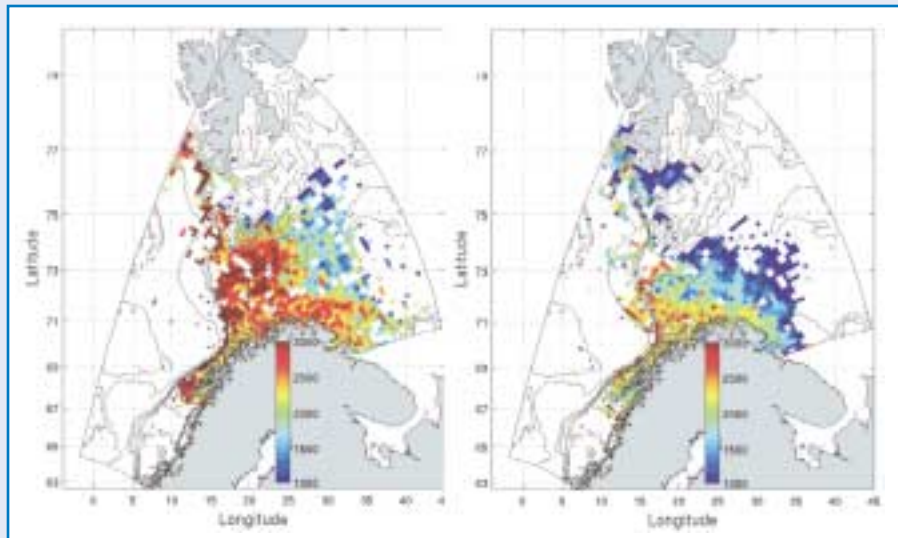


Figure 2. Simulated distribution of 0-group cod late August, 4 to 6 months old depending on time of spawning, with ocean and atmospheric forcing from the ctrl run (left panel) and +50 run (right panel). All particles are released inside the Vestfjorden, the main spawning site. The colour scale indicates wet weight in milligram.

**References**

Björnasson B. and A. Steinarsson. 2002. The food-unlimited growth rate of Atlantic cod *Gadus morhua*. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 494-502.

Broecker W.S. 1991. The great ocean conveyor. *Oceanography* 4(2): 79-89.

Ellertsen B., P. Fossum, P. Solemdal and S. Sundby. 1989. Relation between temperature and survival of eggs and first-feeding larvae of northeast Arctic cod *Gadus morhua* (L). *Rapports et Proces-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer* 191: 209-219.

Furevik T. and J.E. Nilsen. In press. Large-Scale Atmospheric Circulation Variability and its Impact on the Nordic Seas Ocean Climate – a Review. *Climate Variability in the Nordic Seas, Geophysical Monograph Series, AGU*.

Hansen B. and S. Østerhus. 2000. North Atlantic-Nordic Seas exchanges. *Progress in Oceanography* 45: 109-208.

Helle K. and M. Pennington. 1999. The relation of the spatial distribution of early juvenile cod (*Gadus morhua* L) in the Barents Sea to zooplankton density and water flux during the period 1978-1984. *ICES Journal of Marine Science* 56: 15-27.

Hjort J. 1914. Fluctuation in the great fisheries of northern Europe viewed in the light of biological research. *Rapports et Proces-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer* 20: 1-228.

ICES. 1985. Preliminary report of the International 0-Group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1985. *ICES CM 1985/G: 75*.

ICES. 1986. Preliminary report of the International 0-Group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1986. *ICES CM 1986/G: 78*.

Manabe S. and R.J. Stouffer. 1988. Two stable equilibria of a coupled ocean-atmosphere model. *Journal of Climate* 1: 841-866.

Sundby S. and O. Nakken. submitted. Spatial shifts in spawning habitats of Arcto-Norwegian cod induced by climate change.

Otterlei O., G. Nyhammar, A. Folkvord, and S.O. Stefansson. 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod: a comparative study of Norwegian coastal cod and northeast Arctic cod. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2099-2111.

Ottersen G. and H. Loeng. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock and herring: The environmental link. *ICES Journal of Marine Science* 57: 339-348.

Ottersen G. and S. Sundby. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. *Fisheries Oceanography* 4: 278-292.

Rahmstorf S. 1999. Shifting seas in the greenhouse? *Nature* 399: 523-524.

Rahmstorf S. 1994. Rapid climate transitions in a coupled ocean-atmosphere model. *Nature* 372: 82-85.

Rahmstorf S. and A. Ganopolski. 1999. Long-term global warming scenarios computed with an efficient coupled climate model. *Climate Change* 43: 247-256.

Sarnthein M., K. Winn, S.J.A. Jung, J.C. Duplessy, L. Labeyrie, H. Erlenkeuser and G. Ganssen. 1994. Changes in the east Atlantic deepwater circulation over the last 30,000 years: Eight time slice reconstructions. *Paleoceanography* 9: 209-267.

Sarnthein M., E. Jansen, M. Weinelt, M. Arnold, J.C. Duplessy, H. Erlenkeuser, A. Flatoy, G. Johannesen, T. Ganssen, S. Jung, N. Koc, L. Labeyrie, M. Maslin, U. Pflaumann and H. Schulz. 1995. Variations in Atlantic surface paleoceanography, 50-80°N: A time slice record over the last 30,000 years. *Paleoceanography* 10: 1063-1094.

Skjoldal H.R. and F. Rey. 1989. Pelagic production and variability of the Barents Sea ecosystem. In: Sherman, K. and Alexander, L.M. (Eds.) *Biomass yields and geography of large marine ecosystems. American Association for the Advancement of Science, Selected Symposium III. Wetview, Boulder, Colorado. Fisheries Research* 5: 241-286.

Sundby S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* 85: 277-298.

Sundby S. and P. Bratland. 1987. Kartlegging av gytefeltene for norsk-arktisk torsk i Nord-Norge og beregning av eggproduksjonen i årene 1983-1985. *Fisken og Havet* 1: 1-58. [In Norwegian].

Sættersdal G. and H. Loeng. 1987. Ecological adaptation of reproduction in northeast Arctic cod. *Fisheries Research* 5: 253-270.