# An Ecosystem Modeling Approach to Predicting Cod Recruitment 

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#### Abstract

The NORWECOM ocean model system implemented with the ROMS ocean circulation model has been run to simulate conditions over the last 25 years for the North Atlantic. Modelled time series of volume fluxes, primary production and drift of cod larvae through their modelled ambient temperature have been analysed in conjunction with observational based VPA estimated time series of 3-year old cod recruits in the Barents Sea. Individual time series account for less than $50 \%$ of the recruitment variability, however a combination of simulated inflow of Atlantic water and primary production accounts for $70 \%$ of the variability with a 3-year lead. The prediction indicates an increased recruitment from 2007 to 2008 from about 450 to 700 million individuals with a standard error of near 150 million.


## Keywords

Ecosystem modelling, volume and larval transport, primary production, cod recruitment and prediction, Barents Sea

## 1. Introduction

A major issue in marine ecology is how food webs are controlled or regulated by their environment and human interference. This obviously has important implications for the management of marine resources, whether the issue is harvesting of marine resources or protection of species. Globally, second and third trophic level carnivorous fish such as cod are over-fished, forcing fisheries in many parts of world to harvest at lower trophic levels (Pauly et al. 1998). Moreover, the extreme variation in physical factors in northern waters, especially light, temperature, and ice cover, that occur over seasonal, inter-annual and longer timescales, cause major fluctuations at all trophic levels of the food web. Thus there is no such thing as an "ecological balance" on these time-scales. Knowledge of the ecosystem dynamics is required to make proper evaluation and prediction of the impact of fishing on a marine food web, and a fundamental challenge in this context is to determine the interaction between large natural variations and the impact of man. Due to the complexity of this challenge, it can only be explored by an extensive use of mathematical models in combination with observations.

The Norwegian modeling community has recently made significant progress in iceocean physical-chemical-biological numerical modeling (e.g., Budgell, 2005; Vikebø et al., 2005, see also Data and Methods). The modeling system includes physics from a Regional Ocean Model System (ROMS, Shchepetkin and McWilliams, 2005), three macro-nutrients ( $\mathrm{N}, \mathrm{P}, \mathrm{Si}$ ), primary production of diatoms and flagellates, and secondary production of Calanus finmarchicus, which is the main zooplankton species in the Northeast Atlantic. One of our main goals is to use these modeling activities in an ecosystem approach to marine research and management, and examples are given on how quantified knowledge of the physics and lower trophic levels impact and allow predictability of fisheries recruitment and migration.

There are many opinions about what an ecosystem approach to marine research and management, or to fisheries management, means. With respect to research, we choose to define it as an approach towards "considering the most important driving forces on and the processes within the ecosystems". While there are many important processes involved, the two main driving forces on most ecosystems related to the northern North Atlantic are climate (or the physics), and fishing. In some areas fertilization, pollution, introduction of new species and/or habitat disturbance may also be important drivers, but so far none of these are considered important in relation to the fish stocks in the Nordic and Barents seas. A simplified food web of the arctic/subarctic food web in the Barents Sea is shown in Fig. 1.

The Barents Sea ecosystem is considered relatively simple because of low species diversity and because temperature change directly or indirectly influences most species. This means that higher temperature normally is associated with increased productivity, not necessarily due to the temperature itself, but because this may be related to less ice coverage and/ or increased inflow of relatively warm Atlantic water being rich on nutrients and sometimes plankton. In spite of this, there are many processes, in particular linkages between trophic levels, which are quantitatively poorly known. Thus, it is quite problematic to consider all relevant processes and state variables in such a system. Another approach is to focus on a particular species or functional group in the ecosystem, and determine what is directly or indirectly affecting it's struggle for growth and survival. This is exemplified in Fig. 2.

Either way we end up with the same problem of several (quantitatively) poorly known processes, but the research strategy indicated in Fig. 2 may be more attractive since it focuses on the target species of interest. It is important to notice that the climate/physics is an important direct driver on all trophic levels, and indirectly through its impact at the bottom of the food chain, namely the primary production. This is demonstrated by Skogen and Moll
(2005) who show that the physics imposes varying complexity on the formulation of biological processes.

Most attempts to establish relations between the environment and fish stock dynamics have simply dealt with temperature, largely because temperature has a direct impact on biological processes and is easy to measure. However, temperature might be a proxy for other processes that may have important impacts on the ecosystem, e.g. water transports or zooplankton (Campana and Hurley, 1989; Sundby, 2000). In this paper we focus on the early life stages of northeast arctic cod, assuming that this is a critical phase for determining year class strength. We consider possible relations between:

- Physics and recruitment
- Physics and primary production and recruitment
- Physics and cod larvae drift/ growth and recruitment

Lastly we examine the predictability of cod recruitment, while acknowledging our lack of information on cod predation mortality. Similarly and unfortunately, the development of a zooplankton module has been delayed, and it may also have a significant effect on cod recruitment not captured by the above indicators.

The northeast arctic cod spawns along the Norwegian coast from mid to northern Norway during March and April (Ellertsen et al., 1989). Main spawning areas are found in the Lofoten region where 40-70\% of the eggs are spawned (Fig 3). Most of the first-feeding larvae are found in the Lofoten region in early May when they start feeding on the early naupli stages of Calanus finmarchicus. During the subsequent months of pelagic drift they are transported northeastwards to the Barents Sea, mainly by the Norwegian Coastal Current but also partly by the Atlantic Current, in the upper layer (top 30 m ). The cod gradually switch to feed upon older and larger naupli and copepodite stages (Sysoeva \& Degtereva, 1965; Helle, 1994). In June-July they are found as early juveniles ( $30-50 \mathrm{~mm}$ long) at the entrance of the

Barents Sea and the year-class strength is largely determined at this stage (Sundby et al. 1989). The largest larvae are found in the western Barents Sea and the smallest larvae in the east (Bjørke and Sundby, 1986). The same authors suggested that this was due to the larvae in the western part drifting in higher temperature waters and/or in areas with higher food abundance. Using otolith analyses, Suthers and Sundby (1993) confirmed that this was due to more rapid growth in the west, a result confirmed by modeling studies (Vikebø et al., 2005).

Temperature fluctuations have been shown to have a strong influence on year-class strengths of northeast arctic cod in various ways. Sæterdal and Loeng (1987) found that strong year classes normally occur at the beginning of warm periods in the Barents Sea. Ellertsen et al. (1989) showed that strong year classes may occur in warm years while cold years always result in poor year classes of cod, leading to the conclusion that a high temperature was a necessary but not sufficient condition for strong year classes. Ottersen and Sundby (1995) found that temperature and spawning stock biomass were equally important in the year-class formation of cod. Ottersen and Loeng (2000) observed a positive correlation between year of strong year classes and large individuals at the 0-group stage (5 months old prior to settlement out of the pelagic layer).

## 2. Data and Methods

### 2.1 Fisheries data

A time series of the 3-year old northeast arctic cod recruits in the Barents Sea is taken from ICES (2005) that reports the results of a catch-at-age analyses (VPA; Virtual Population Analysis) based on all reported catches. The estimates of the last 3-4 year-classes are considered more uncertain than earlier year-classes where the full stock cohort is used in the analysis. Recruits for 2003-2005 is therefore not used in the statistical analysis (Stiansen et al, 2005). The uncertainties in the fisheries data are not further considered.

### 2.1 Physics

The physical model is the Regional Ocean Model System (ROMS) (Shchepetkin and McWilliams, 2005). The model is 3-dimensional, baroclinic and contains a free surface. The model uses a finite difference numerical scheme with time splitting, orthogonal curvilinear coordinates in the horizontal and terrain-following coordinates in the vertical. It contains a dynamic-thermodynamic ice submodel (Budgell, 2005) that uses an elastic-viscous-plastic rheology following Hunke and Dukowicz (1997) and Hunke (2001) and ice thermodynamics based on Mellor and Kantha (1989) and Häkkinen and Mellor (1992). The model is driven by 6-hourly atmospheric forcing obtained from NCEP Reanalysis data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (http://www.cdc.noaa.gov/), including wind stress recently found to be too high especially during strong wind conditions (Budgell, pers. comm.). Some validation is presented in Budgell (2005)

### 2.3 Primary production

The NORWegian ECOlogical Model system (NORWECOM) is a coupled physical, chemical, biological model system (Aksnes et.al., 1995; Skogen et al., 1995; Skogen \& Søiland, 1998) applied to studies of primary production, nutrient budgets and dispersion of particles, such as fish larvae and pollution. The model has been validated by comparison with field data in the North Sea/Skagerrak (Svendsen et al., 1996; Skogen et al., 1997; Søiland \& Skogen, 2000 and Skogen et al. 2004, among others). These demonstrate that the model capture the typical spring bloom of diatoms and the following blooming of flagellates. It also agrees well with the seasonal cycle of nutrients and more rapid events related e.g. to coastal upwelling.

Validation is also ongoing in the Nordic and Barents seas (Skogen et al., pers. comm.).

The chemical-biological lower trophic model is coupled to the physical model through the subsurface light, the hydrography and the horizontal and the vertical movement of the water masses. The prognostic variables are dissolved inorganic nitrogen (DIN), phosphorous (PHO) and silicate (SI), two different functional groups of phytoplankton (representing diatoms and flagellates), detritus (dead organic matter), diatom tests (biogenic silica), inorganic suspended particulate matter (ISPM) and oxygen. Primary production, respiration, algal death, remineralization of inorganic nutrients from dead organic matter, self shading, turbidity, sedimentation, resuspension, sediment burial and denitrification are modelled. Phytoplankton mortality, including grazing, is everywhere and at any time assumed to be a constant fraction of the modeled phytoplankton biomass. (A more realistic mortality is assumed to be achieved when coupling to a zooplankton module is available).

Particulate matter has a sinking speed relative to the water and may accumulate on the bottom if the bottom stress is below a given threshold ( 0.064 Pa ), and resuspension takes place if the bottom stress exceeds a threshold ( 0.78 Pa ). Remineralization takes place both in the water column and in the sediments. Parameterization of the biochemical processes is taken from literature based on laboratory and mesocosm experiments, or deduced from field measurements (Aksnes et al., 1995; Pohlman \& Puls, 1994; Mayer, 1995; Gehlen et al., 1995; Lohse et al., 1995,1996).

The lower trophic model is run off-line, i.e., it is forced with the 3-day mean results from the physics model. To minimize the boundary effects on the model results, a 7 grid cell "Flow Relaxation Scheme" (FRS) zone (Martinsen \& Engedahl, 1987) is used on the open boundaries.

The incident irradiation is modeled using a formulation based on Skartveit \& Olseth $(1986,1987)$ using data for global daily downward shortwave radiation from the NCEP/NCAR reanalysis data set. The nutrient fields are reinitialised every January 1 using
typical values for winter nutrients of Atlantic Water in the Norwegian Sea (F. Rey, pers. comm), together with some small initial amounts of algae $\left(0.10 \mathrm{mgNm}^{-3}\right)$ for both diatoms and flagellates. Inorganic nitrogen is added to the system from the atmosphere as a constant value in time and space, but with double values along the coasts. In this large-scale model setup, no nutrients is added to the freshwater runoff (assumed to be unimportant for the present study).

### 2.4 Larval cod growth and distribution

The drift of cod eggs and larvae is simulated using the current and temperature fields from ROMS. Initially the physics were available only for the years 1985-1997, but later extended for the full 25 -year period. A total of 50,000 particles are released each year and tracked from 1 March to 31 September. Spawning is assumed to be normally distributed between 1 March and 30 April, with a standard deviation of 15 days. The particles are released in the spawning areas of northeast Arctic cod in the Lofoten area (70\%) and Møre (30\%) at random depths between 0 and 20 m . Depths are maintained fixed for particles throughout the simulations. Particle movement is calculated at hourly time steps by RungeKutta integration from 3D interpolation of the velocities from ROMS. A diffusion term corresponding to a Fickian coefficient of $100 \mathrm{~m}^{2} \mathrm{~s}^{-1}$ (Ådlandsvik \& Sundby, 1994; Torgersen \& Huse, 2005) is added to represent sub-grid scale physical processes.

### 2.5 Statistics

Monthly and seasonally inflows are correlated with age 3 cod recruitment, with lags of $0-6$ years (inflow preceding recruitment). Recruitment is also correlated with primary production for the total Barents Sea for the months April-August and with the total annual production. Correlations with primary production were also looked for around the spawning
areas, along early larval drift routes, and in sub-areas of the Barents Sea. The primary production and inflow time series having the highest correlations with a time lag of 0-3 years were tested in a multiple linear regression analysis using the SPLUS statistical program. The time lag of 3 years both for the inflow and the primary production were finally chosen by the authors both since it gave the best statistical results and since it represents the first year of life of the cod, which is the stage believed to be most affected by the environment.

## 3. Results and Discussion

### 3.1 Physics and recruitment

The ROMS model was run for the period 1981-2005 covering an area from about $20^{\circ}-30^{\circ} \mathrm{S}$ in the Atlantic to the Bering Strait, including the whole Arctic. Of special importance for the Barents Sea ecosystem is the inflow of relatively warm and nutrient rich Atlantic water (Fig. 4). While the annual mean total inflow typically varies around 4 Sv , the seasonal variation typically ranges from 2 to 6 Sv . From fixed current meter mooring arrays, Ingvaldsen et al. (2004) estimated net Atlantic water inflow to the Barents Sea through the Fugløya-Bjørnøya section to be 1.7 Sv during winter and 1.3 Sv during summer for the period August 1997 to July 2001. These results do not include the transports in the Norwegian Coastal Current which may be of a similar magnitude. Still, the numerical model results (including Norwegian Coastal Water) probably overestimate this inflow, although the seasonal and interannual variability seems reasonable (Budgell, 2005). This overestimation is caused by too high wind stress forcing recently found in the NCEP data (Budgell, pers. comm.). Although a positive link to the cod recruitment from the inflow during winter or spring was anticipated, no such strong links were found. Instead, a negative strong relation between the total inflow in the $4^{\text {th }}$ quarter and the recruitment of 3-year old cod 3 years later was found (Fig. 5).

At present no clear explanation for this negative relation is given, but a possible interpretation is that it is positive for the recruitment that the food for the juvenile cod becomes more stationary (with weaker currents) in areas where the cod is assumed to become stationary at the bottom. Another hypothesis could be that juvenile cod is not as stationary as assumed, and with strong flows the juvenile cod drifts too far eastward in the Barents Sea. During winter and spring it may then be hit by extremely cold bottom water formation (due to surface cooling) causing high mortality.

### 3.2 Physics and primary production and recruitment

The primary production model linked to the physical oceanography from ROMS was run for the same area and period (1981-2005). Figure 6 demonstrates the annual production for the Northeast Atlantic. Although river nutrients were not included, we believe that the variability for the larger Norwegian and Barents seas due to varying weather affecting inflow, light, stratification, turbulence and ice conditions, may be well represented (Skogen et al., in prep.). This is also based on experience and validation exercises from the North Sea (Svendsen et al., 1996; Skogen et al., 1997; Søiland \& Skogen, 2000; Skogen et al. 2004). In particular the effect of varying ice cover has a significant effect on the northern Barents Sea production due to its major effect on light penetration.

An examination of the monthly production and the recruitment shows the best relations are found in April (Fig. 7). The modelled production in large areas of the Barents Sea correlates highly ( $\mathrm{r}^{2} \approx 0.5$ ) with the recruitment (three years later). However, areas of high correlation is also found far to the south, which may indicate that this is related to the larger weather patterns influencing similarly the production over larger areas. No strong relations were found in the areas of spawning and early larval drift routs in the Norwegian Sea. About $35 \%$ of the cod recruitment variability is accounted for by the primary production of the total

Barents Sea during April, as shown in Fig. 8. It is quite logic that this early part of the spring bloom mainly of diatoms may be an important factor in the ecosystem dynamics leading to good recruitment

By combining the inflow in the $4^{\text {th }}$ quarter with the primary production in April (the same year) for the whole Barents Sea, we are able to explain about $70 \%$ of the recruitment variability of 3-year old cod (Fig. 9). Since the inflow estimates and primary production are simulations for the spawning year of the recruits, this gives a prediction of cod recruitment 3 years prior.

### 3.3 Physics and cod larvae drift/ growth and recruitment

Cod recruitment is also assumed to be affected by larval growth and drift patterns (Vikebø et al. 2005). The ambient temperature has a significant effect on larval growth rates. Although growth is also affected by food availability, lacking the necessary prey availability, we were forced only to considering the effects of ambient temperature. We found that he larvae may encounter quite drastic temperature differences (up to $4^{\circ} \mathrm{C}$ ) from year-to-year (Fig. 10), which may have a significant effect on the growth and survival rate. Initially only the 13 year period 1985-1997 were studied, and indeed we found that the average ambient temperature during the first half year of the larval drift could explain near $50 \%$ of the recruitment (3 years later). This relationship was stronger than earlier temperature-recruitment studies have shown, which basically indicated that high temperature is just a necessary condition for good recruitment (Sundby, 2000). However, when the full 25-year simulation period became available, this relation was destroyed basically by the 1983 and 2003 year-classes, with respectively relatively good/bad recruitment in spite of quite cold/warm ambient temperatures. It should be stressed that until we also are able to realistically simulate the food availability for the larvae, in particular the amounts of $C$. finmarchicus, such studies will be incomplete. A recent
simulation study (Torgersen \& Huse, 2005) has shown that 1990 was the peak year in advection of C. finmarchicus from the Norwegian Sea to the Barents Sea during the high NAO period 1988-1991. This corresponds to the year with peak in ambient temperature of cod, which again corresponds to the strongest year class of cod in the period 1985-1997.

Also the interannual variation of the amount of particles drifting into the Barents Sea was studied, but no strong relation to recruitment were found. It is assumed that with the poor model resolution of 20 km , the drift of larvae is not represented with sufficient accuracy.

### 3.4 Predictability of cod recruitment

The present basis for assessing and managing fish stocks are with few exceptions single species models where information about the environment and ecosystem is not included quantitatively. Stock assessments based on traditional tools are known not to be capable of capturing changes in abundance trends before 3-5 years after a change. Knowledge on ecosystem dynamics and its influence on fish stocks can help in assessing stock dynamics with the potential of supplying early warnings of rapid changes (Svendsen et al., 1995; Iversen et.al., 2002; Huse \& Ottersen 2003; Ottersen et al., 2002; Stiansen et al., 2002; Stiansen et al., 2005). Based on temperature observations from the Russian Kola section, survey estimates of 1-year old cod and maturing capelin biomass, Stiansen et al. (2005) have demonstrated a 2 -year prediction $\left(\mathrm{R}^{2}=0.81\right)$. This predicts a drop in recruitment from 2005 to 2006. A similar drop of about 200 million individuals is predicted from the relation with modelled inflow of water to the Barents Sea and the primary production. This 3-year prediction is seen in Fig. 11, also showing the predictions for 2007 and 2008. Note that the last years' VPA estimates (2003, 4 and 5) are quite uncertain due to the nature of VPA and have been omitted in the determination of the multiple regression model. The statistical
recruitment model equation is: $\operatorname{ModRecCod}_{t}(3 \mathrm{Y})=-240 \operatorname{Inflow}_{t-3}(4 \mathrm{Q})+40 \mathrm{PP}_{\mathrm{t}-3}($ April $)+1633$ with a residual standard error of 144 million individuals.

Huse \& Ottersen (2002) used Artificial Neural Networks (ANN) to predict recruitment and stock biomass of northeast arctic cod. Using temperature at the Kola section, capelin biomass (the main prey), and cod spawning stock biomass as input variables to the ANN, they provided a good 3-year forecast of recruitment $\left(R^{2}=0.76\right)$. Even though the aggregated time series used in ANN provide a fair predictive capability, the numerical models presented here should be capable of yielding a much better predictive capability, for example by describing the ambient temperature in a much more realistic fashion than by using fixed sections. The predictions from these new modelled time series are totally independent from the estimates by Stiansen et al. (2005). A test of the robustness of the predictions in Fig. 11 is done by retrospective runs of the regression model. This means recalculation of the model coefficients by cutting out first one, then two and up to 10 last years of the observations, and for each case re-calculating the predictions for the whole period. The results are shown in Fig. 12 demonstrating remarkable robustness which indicates the stability of the coefficients in the statistical model. This indicates that the processes leading to the variability experienced during the first 10 year are similar for the following 10 years. If this is also the case for the last years, we may assume that our predictions are realistic.

## 4. Conclusion

Recruitment is the most important indicator of fish stocks to predict since it is used in fisheries assessment and, if it can be predicted ahead of time, for early warning of rapid changes. The numerical 3-dimensional simulations presented here of the ocean circulation, hydrography, primary production and larval drift have supplied new time series of state
variables or indicators which are not available from standard monitoring programs, and their links to recruitment with 3 year predictability is promising. For example, the predicted drop in recruitment from 2005 to 2006 is a clear indication of a development that should be taken into consideration in management advice, although fortunately the present predicted drop is not considered critical. This drop was also suggested from an independent statistical model (Stiansen et al., 2005) lending further support to this new methodology. The recruitment prediction for 2008 is about 700 million with a residual standard error of 144 million.

The predictions based on the coupled information of inflow and primary production appears robust and increase our confidence in the predictions as well as the choice of explanatory variables. It is clear that the weak link in this analysis is the lack of zooplankton information, being the critical food source for the growth and thus survival of the cod larvae and juveniles. It will also strengthen the work to do the analysis further back in time, but so far such modelling simulations are not available. Still the results indicate that as long as the cod spawning stock biomass (SSB) is above about 200,000 tonnes (which has been the case for most of this period), $70 \%$ of the recruitment variability seems to be caused by natural environmental variability. For comparison ICES has set $\mathrm{B}_{\mathrm{lim}}=220,000$ being the lowest SSB assumed to have the potential of producing good recruitment.

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## References

Ådlandsvik, B. \& S. Sundby, 1994. Modelling the transport of cod larvae from the Lofoten area. ICES Mar. Sci. Symp., 198: 379-392

Aksnes, D.L., Ulvestad, K.B., Balino, B., Berntsen, J., Egge, J., and Svendsen, E. 1995. Ecological modelling in coastal waters: Towards predictive physical-chemical-biological simulation models. Ophelia, 41, 5-36.

Bjørke, H. and Sundby, S. 1986. Abundance indices and distribution of postlarvae and 0-group cod. Contribution to the third Soviet-Norwegian symposium in Murmansk, 26-30 May 1986 on The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea, 19 pp.

Budgell, W.P. (2005). Numerical simulation of ice-ocean variability in the Barents Sea region: Towards dynamical downscaling, Ocean Dynamics, DOI 10.1007/s10236-005-0008-3.

Campana SE, Hurley PCF (1989). An age- and temperaturemediated growth model for cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) larvae in the Gulf of Maine. Can J Fish Aquat Sci 46:603-613

Ellertsen, B., Fossum, P., Solemdal, P. and Sundby, S. 1989. Relations between temperature and survival of eggs and first feeding larvae of the North-East Arctic cod (Gadus morhua L.). Rapp. P.-v. Reun. Cons. int. Explor. Mer, 191:209-219

Gehlen, M., Malschaert, H., \& Raaphorst, W.R. 1995. Spatial and temporal Variability of benthic silica fluxes in the southeastern North Sea. Cont. Shelf Res., 13, 1675-1696.

Helle K. 1994. Distribution of early juvenile Arcto-Norwegian cod (Gadus morhua L.) in relation to food abundance and water mass properties. ICES Marine Science Symposia 198: 440-448.

Häkkinen S. and Mellor G.L. (1992) Modelling the seasonal variability of a coupled arctic ice-ocean system. J. Geophys Res. 97:20285-20304.

Hunke, E. (2001) Viscous-plastic sea ice dynamics with the EVP model: linearization issues. J. Comput. Phys. 170:18-38.

Hunke, E. and Dukowicz, J. (1997) An elastic-viscous-plastic model for sea ice dynamics. J. Phys. Oceanogr. 27, 1849-1867.

Huse, G. \& G. Ottersen, 2003. Forecasting recruitment and stock biomass of Northeast Arctic cod using neural networks. Scientia Marina, 67 (Suppl. 1): 325-335

Ingvaldsen, R.B., L. Asplin \& H. Loeng, 2004. The seasonal cycle in the Atlantic transport to the Barents Sea during the years 1997-2001, Continental Shelf Research, 24, 10151032.

Iversen, S.A., Skogen, M.D. \& Svendsen, E. (2002). Availability of horse mackerel Trachurus trachurus in the north eastern North Sea, predicted by the transport of Atlantic water. Fisheries Oceanography, 11: 245-250

ICES, 2005. Report of the Arctic Fisheries Working Group. Murmansk, Russia, 19-28 April 2005, ICES CM 2005/ACFM:20, 570 pp.

Lohse, L., Malschaert, F.P., Slomp, C.P., Helder, W., \& Raaphorst, W. 1995. Sediment-water fluxes of inorganic nitrogen compounds along the transport route of organic matter in the North Sea. Ophelia, 41, 173-197.

Lohse, L., Kloostechuis, H.T., Raaphorst, W., \& Helder, W. 1996.

Denitrification rates as measured by the isotope pairing method and by the acetylene inhiluition technique in continental shelf sediments of the North Sea. Mar. Eco. Prog. Ser., 132, 169-179.

Martinsen, E.A., \& Engedahl, H. 1987. Implementation and testing of a lateral boundary scheme as an open boundary condition in a barotropic ocean model. Coastal Engineering, 11, 603-627.

Mayer, B. 1995. Ein dreidimensionales, numerisches Scwebstoff-Transportmodell mit Anwendung auf die Deutsche Bucht. Tech. rept. GKSS 95/E/59. GKSSForschungszentrum Geesthacht GmbH.

NCEP Reanalysis data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, http://www.cdc.noaa.gov/

Ottersen, G., Loeng, H. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock and herring: the environmental link. Symposium on Recruitment Dynamics of Exploited Marine Populations: Physical-Biological Interactions. ICES Journal of Marine Science 57:67-85.

Ottersen, G. and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography 4 (4): 278-294.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres, F. 1998. Fishing down marine food webs. Science 279 (5352): 860-863

Pohlmann, T., \& Puls, W. 1994. Currents and transport in water. Pages 345-402 of: Sundermann, J. (ed), Circulation and contaminant fluxes in the North Sea. Berlin: Springer Verlag.

Shchepetkin, A.F. and McWilliams J.C. 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model, Ocean Modelling, 9, 347-404.

Skartveit, A., \& Olseth, J. A. 1986. Modelling slope irradiance at high latitudes. Solar Energy, 36(4), 333-344.

Skartveit, A., \& Olseth, J. A. 1987. A model for the diffuse fraction of hourly global radiation. Solar Energy, 37, 271-274.

Skogen, M.D., \& Søiland, H. 1998. A User’s guide to NORWECOM v2.0. The NORWegian ECOlogical Model system. Tech. rept. Fisken og Havet 18/98. Institute of Marine Research, Pb.1870, N-5024 Bergen. 42pp.

Skogen, M.D., Svendsen, E., Berntsen, J., Aksnes, D., \& Ulvestad, K.B. 1995. Modelling the primary production in the North Sea using a coupled 3-dimensional Physical Chemical Biological Ocean model. Estuarine, Coastal and Shelf Science, 41, 545-565.

Skogen, M.D., Svendsen, E., \& Ostrowski, M. 1997. Quantifying Volume Transports during SKAGEX with the Norwegian Ecological Model system. Cont. Shelf Res., 17(15), 1817-1837.

Skogen, M.D., Søiland, H., \& Svendsen, E. 2004. Effects of changing nutrient loads to the North Sea. Journal of Marine Systems, 46(1-4), 23-38.

Stiansen, J.E., H. Loeng, E. Svendsen, L.H. Pettersson, J.A. Johannessen, T. Furevik, N.O. Handegaard, N.O. \& O. Fredo, (2002), Climate-fish relations in Norwegian waters. Fisken og Havet nr. 12.

Stiansen, J.E., H. Loeng \& G. Ottersen, (2003), Den nordatlantiske oscillasjon (NAO) og torskerekruttering. In: L. Asplin og E. Dahl (red.), Havets miljø 2003. Fisken og havet, scernr. 2.

Stiansen, J.E., B. Bogstad, P. Budgell, P. Dalpadado, H. Gjøsæter, K. Hiis Hauge, R. Ingvaldsen, H. Loeng, M. Mauritzen, S. Mehl, G. Ottersen, M. Skogen \& E.K. Stenevik, (2005). Status report on the Barents Sea Ecosystem, 2004-2005. Fisken og havet, nr. 3-2005.

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

Sundby, S., Bjørke, H., Soldal, A.V. \& Olsen, S. 1989. Mortality rates during the early life stages and year class strength of the North-East Arctic cod (Gadus morhua L.). Rapp. P.-v. Reun. Cons. int. Explor. Mer, 191:351-358

Suthers, I. M. \& Sundby, S. 1993. Dispersal and growth of pelagic juvenile Arcto-Norwegian cod (Gadus morhua), inferred from otolith microstructure and water temperature. ICES Journal of Marine Sciences, 50: 261-270.

Svendsen, E., Berntsen, J., Skogen, M.D., Ådlandsvik, B., \& Martinsen, E. 1996. Model simulation of the Skagerrak circulation and hydrography during SKAGEX. J. of Mar. Syst., 8(3-4), 219-236.

Svendsen E., A. Aglen, S.A. Iversen, D.W. Skagen \& O. Smestad (1995). Influence of climate on recruitment and migration of fish stocks in the North Sea, p. 641-653. In R.J. Beamish (ed.) Climate Change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121

Sysoeva, TK. \& Degtereva, AA. 1965. The relation between feeding of cod larvae and pelagic fry and the distribution and abundance of their principal food organisms. International Commision for the Northwest Atlantic Fisheries. Special Publication No 6:411-416.

Søiland, H., \& Skogen, M.D. 2000. Validation of a 3-D biophysical model using nutrient observations in the North Sea. ICES J.Mar.Sci, 57(4), 816-823.

Torgersen, T. \& Huse, G. (in press) Variability in advective losses of Calanus finmarchicus. ICES Journal of Marine Science 0:00-00

Vikebø, F, Sundby, S. Ådlandsvik, B, and Fiksen, Ø. 2005. The combined effect of transport and temeprature on distribution and growth of larvae and pelagic juveniles of ArctoNorwegian cod. ICES Journal of Marine Science (In press)

## Figure captions

Fig. 1. Schematic of the typical food web in the Barents Sea
Fig. 2. Sketch of (potential) important drivers and processes affecting growth, behaviour, reproduction and mortality.

Fig. 3. Spawning and nursery grounds for the northeast arctic cod
Fig. 4. Time series of the total modelled volume transport at the entrance into the Barents Sea (in Sverdrup; $1 \mathrm{~Sv}=10^{6} \mathrm{~m}^{3} \mathrm{~s}^{-1}$ ) from January 1981 to December 2005. Monthly averages (thin pink line) and annual running mean (thick black line).

Fig. 5. Mean $4^{\text {th }}$ quarter modelled total inflow of water through the Bear Island-Fugloya section at the western entrance to the Barents Sea versus recruitment of 3-year old cod, 3 years later.

Fig. 6. Modelled annual (mean 1993-2004) total primary production (diatoms+flagellates in $\mathrm{gCm}^{-2}$. The numbered boxes indicate areas over which production was averaged to generate production time series, but only the average production of all boxes (the whole Barents Sea) were finally used.

Fig. 7. Correlation map between primary production in April and Cod (3Y) recruitment 3 years later

Fig. 8. Recruitment of 3-year old northeast arctic cod (ICES, VPA) and primary production in April (NORWECOM/ROMS) in the total Barents Sea.

Fig. 9. Statistical model of 3-year old cod recruits based on dynamically modelled inflow of water to the Barents Sea ( $4^{\text {th }}$ quarter) and primary production (for the whole Barents Sea) in April versus VPA estimates of the number of recruits (all individual p-values $<0.02$ ).

Figure 10. Modelled time series of ambient temperatures from individual years estimated from 50,000 particles released in well known spawning areas for cod starting March 1 drifting randomly in the upper 20 meters with the modelled currents and temperature fields

Fig. 11. Northeast arctic cod recruitment (numbers of 3-year-olds) from VPA estimates (dark line) compared to prediction from regression with dynamically modelled inflow of water to the Barents Sea (4 ${ }^{\text {th }}$ quarter) and primary production (for the whole Barents Sea) in April.

Fig. 12 Individual multiple regression models of recruitment based on parameter estimation by deleting from one up to ten of the last years of VPA estimates (from 2002 and backwards).


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