ICES CM 2006/Q:07

Linking tagging technology and molecular genetics to gain insight in the spatial dynamics of two stocks of cod in Northeast Atlantic waters.

Kathrine Michalsen Torild Johansen and Edda Johannesen

Abstract

The Northeast Arctic cod (*Gadus morhua* L.: NEAC) is thought to be the most abundant cod stock in the North Atlantic, while the catches of the partially co-occurring Norwegian coastal cod (NCC) stocks have dramatically decreased in recent years. At the same time, reports on climate change have caused a growing concern about climate impact on life in the ocean. For effective management it is necessary to be able to partition the variability in fish populations into environmental, genetic and fisheries effects. In the present study we have combined information from molecular genetic methods and electronic data storage tags (DST) to study spatial dynamics, such as distribution, behaviour and environmental conditions experienced by individuals fish from the two cod stocks NEAC and NCC in spawning area Lofoten in the North-east Atlantic.

Keywords: molecular genetics, data storage tags (DST), distribution, behaviour, environmental conditions, Northeast Arctic cod, Norwegian coastal cod.

Contact author:

Kathrine Michalsen: Institute of Marine Research, P.O.Box 1870, Nordnes, 5817 Bergen, [Phone 55238500 Fax 55238687, e-mail; kathrine@imr.no].

Introduction

The cod along the Norwegian coast and Barents Sea are managed as two separate stocks, the Northeast Arctic cod (NEAC) and the Norwegian coastal cod (NCC). The NCC cod has been dramatically reduced in recent years and there is great concern of possible overfishing (ICES 2006). Separate quotas for the NCC has unfortunately limited effect on preventing overfishing since a mixed stock fishery with the NEAC is taking place at the spawning grounds in Lofoten. ICES has recommended no catch of NCC in recent years, but for social-economic reasons limited quotas are still given. Protected areas have been introduced to reduce the fishing pressure, but this seems only to have had a limited effect, mainly due to the short time period and restricted area involved.

A serious reduction in the abundance of a population due to fishing may result in genetic changes that could make recovery of the population difficult or slow even after periods with reduced or cessation of fisheries (Hutchings 2005). Since fish populations are heavily influenced by ocean climate, the effect of environmental conditions on its distribution is crucial in defining the constraints under which fisheries may safely operate in the long term (Nakken 1994). Effective management requires partition of the variability in fish stocks into environmental, genetic and fisheries effects. Knowledge of spatial dynamics is thus of great importance to ensure effective regulations and management plans in the future.

The indications of separating NEAC and NCC into separate groups or stocks dates back to early studies of otolith structure and life-history characteristics that revealed differences between oceanic cod and cod inhabiting coastal areas (Rollefsen 1933). Recent studies employing various DNA markers have yielded results ranging from panmixia or high gene flow across the Atlantic (Smith et al. 1989, Arnason et al. 2000) to the presence of significant population structuring on small to medium spatial scales (Dahle 1991, Dahle and Jørstad 1993, Fyhn et al. 1994, Fevolden & Pogson 1997, Hutchinson et al. 2001, Jonsdottir et al. 2001, Pogson & Fevolden 2003, Sarvas & Fevolden 2005). Similar results have been reported from the western Atlantic, where temporally stable differences between inshore and offshore cod off Newfoundland have been demonstrated (Ruzzante et al. 1996, 1997, 1999 and the Southern areas of the Northeast Atlantic between Norwegian coastal- and the North Sea cod (Knutsen et al. 2003, Hutchinson et al. 2001).

The NEAC are mainly found in the Barents Sea but display substantial migratory behaviour both within the Barents Sea and also during its spawning migrations along the Norwegian coast (Ottersen et al. 1998). The NCC is more typically found in the fjords all along the coast of Norway and display less migratory behaviour (Berg and Albert 2003). However, in the Northern Norwegian areas the distribution of the two stocks overlaps, especially during the spawning season in Lofoten. It has been shown that NEAC and NCC are separated into two populations based on gentic variation within hemoglobin (Hb; Fyhn et al. 1994, Dahle and Jørstad 1993 and references therein) and the gene marker *Pan* I (Pogson et al. 1995, Fevolden & Pogson 1997) which exhibits particularly large differences in allele frequencies between samples collected in the Barents Sea and in coastal areas of Norway. While samples of NEAC are almost fixed for the *Pan* IB allele, samples of NCC exhibit high frequencies of the *Pan* I_A allele (Fevolden & Pogson 1997, Sarvas & Fevolden 2005). This is supported when the otolith structure as characterised by Rollefsen (1933) is combined with the *Pan* I analysis (Berg et al. 2005) and microsatellites (Wennevik 2006).

It is proposed that temperature shifts exert differential influence on the different cod populations (Daan 1994, Drinkwater 2006), but most studies rely on sea surface temperature, or snapshots of temperature during a survey, or average temperatures for a specific area or month. Since population-level data from monitoring surveys might not fully reflect the dynamic behaviour of individual fish, or the temperature the cod actually have experienced, the use of electronic Data storage tags (DST's) as a proxy for temperature would provide long term, high-resolution observations of individual fish. Data from DST tags can elucidate the factors affecting fish movements and the mechanisms underpinning them, and tagging has therefore been established as the main technology in acquiring information about the movement of animals (Arnold and Dewar 2001).

It is of particular importance for management to know whether a commerisial species should be managed as one or divided into several management units and how much intermingling there is between the oceanic migratory components and stationary coastal components of a species. Previous studies on NEAC and NCC have either focused on the genetical- or the distributional aspect in isolation. By combining the two techniques we will be able to understand individual behaviour, gain insight in the spatial dynamics and improve the scientific basis for management of a complex mixed fishery of Atlantic cod in the Lofoten area.

Methods

Capture, tagging, release and recapture

In order to ensure an even spread of tagged fish between NEAC and NCC fish were tagged both in the Barents Sea, at the Bear Island and along the coast of the Lofoten peninsula, in 2003-2006. The 20 different release sits were pooled into 5 main locations (table 1). Genetic identification of the cod was conducted after tagging (see genetic identification). Electronic data storage tags (see data storage tags) and conventional tags were attached to adult cod (>45cm) to obtain information on environmental condition experienced during the time from release until recapture. A total of 742 cod were tagged with conventional tags (giving deployment and recovery positions), 390 were tagged with DSTs and 722 finclips were stored for genetic identification (Table 1).

The fish were captured by bottom trawl (less than 200 m depth), which was slowly brought to the surface. To minimise damage to the fish during capture the trawl was modified to include a PVC liner in the cod end that retained 1 m^3 of seawater. Trawl duration was limited to 15 min. The cod were transferred to a holding tank immediately after release from the codend. Gas in the body cavity caused by rupture of the swimbladder (Godø & Michalsen 2000, Nicol & Chilton 2006) was removed manually by placing the fish on their backs and gently pressing their bellies. Only fish in good condition that were able to control their depth and swam near the bottom of the tank were used. Before tagging, all individuals were placed in a shallow (30 cm) bath containing anaesthetic (0.5 % ethyl aminobenzoat) until light anaesthesia was obtained. Once fully anaesthetised as indicated by first cessation of opercular beating, most of the tags were attached through the muscles anterior to the first dorsal fin (Godø & Michalsen 2000). Some of the DSTs were inserted into the body cavity of the fish. In order to detect any adverse effects of tagging, fish were placed in a 70 cm-deep recovery tank prior to release. Upon recapture via the commercial fishery, fishermen returned the tags and information on the physical condition of the fish, date, depth and position of the recapture. Based on this it was evident that the incision had healed and no wounds could be seen. This is in accordance with a number of studies quantifying the effect of tags on fish, with special focus on natural behaviour, swimming performance and growth (see Arnold & Dewar 2001 and Righton et al. 2006 for references). The tagging was conducted under licence from the Norwegian Animal Research Authority (reference no S-2536/02) and complied with the 1974 Animal Welfare Act (supplemented by the provisions of the EU Directive 86/609/CEE).

Up to the time of writing, 66 of the tagged cod have been recaptured. 38 of these were NAC, 16 were NCC, 9 were heterozygotes (AB). For 11 of the recaptured fish genetic samples had not been taken, but 8 of these fishes were tagged in the Barents Sea during summer and are most probable from the NAC (AA) cod stock (Table 2).

Genetic identification:

The fin clips (dorsal fin) were stored in 96% ethanol for later extraction of DNA, and microsatellite and Pan I analyses. The samples were stored (4 ºC) in the laboratory in Bergen until DNA extraction, which was carried out by using Qiagen DNeasy 96 Tissue kit (Qiagen or Omega). For the present paper only Pan1 locus is analysed and we followed the procedures described by Fevolden and Pogson (1997) with slightly modified primers (unpublished).

Data Storage Tags

The Star-Oddi Data Storage Tag (DST) are small (15 mm x 46mm; 19 g in air, 12 g in water) electronic tag, representing 0.084% to 0.009% of the weight in water of the smallest and largest fish, respectively, that records depth (0 to 780 ± 2.0 m) and water temperature (-3 to 40^{o} C ± 0.003^{o} C), and can store up to 43,582 measurements per sensor (see web-site of Star Oddi (http://www.star-oddi.com/). The interval between recordings for the fish used in this study was set to 10 min, for as long as the storage capacity permitted or the fish being caught.

Distribution

Annual abundance surveys on North-East Arctic cod have been conducted at the main spawning ground in Lofoten in the period March-April, since 1982 (see Korsbrekke 1997). Trawl stations were taken at random locations along the cruise track. For each trawl station species identification from 5 fish per 5 cm length group were collected. In the present study only field observations from 1996-1999 and 2001 to 2005 had adequate number of stations to be included in our analysis. Only mature cod are included (data from maturity stages 2, defined as large gonads, viewable eggs and male gonad products and maturity stage 3, representing running gonads). The mature fish made up 85% of the total number of fish for which biological samples were taken. A distinction between North-East Arctic (NEA) and Norwegian Coastal Cod (NCC) was based on the structure of the otoliths. 77 % of the cod could with certainty to be identified to type, whereas 23 % could be identified to type with less certainty. These were pooled in the analysis.

Position of release site and recapture of the tagged cod were plotted in maps and the shortest distance between corresponding positions calculated (Table 2).

Study area and water masses

The tagged fish were released close to the most important spawning area for cod, at the traditional fishing area off the Lofoten Archipelago, Northern Norway. The area is characterized by steep slopes both above and below surface. From the coastline the depth increases gradually down to 300 m at the coastal shelf. From the offshore shelf the depth increases rapidly down to 2000 m (Saelen 1967). The fresher coastal water occupies the surface layers, with saltier Atlantic water below (Orvik et al. 1995). During winter surface cooling makes the coastal water colder than the Atlantic water. Particularly during cold and dry winters in Lofoten, the cold coastal water may extend down to depths of 200 m, while during mild winters the coastal water is much shallower (Eggvin 1936). The thickness and depth of the transition layer between cold coastal fjord water and warm saline Atlantic water also varies during the spawning season depending on the direction of the wind (Furnes & Sundby 1981).

Results

Distribution

Trawl hauls that contain spawning individuals of NEAC and NCC (already identified from their otolith structure), are seen in Figure 1. The figure can be representative for the spawning sites occupied and do illustrate quite well the extensive geographical overlap in distribution between the two cod stocks.

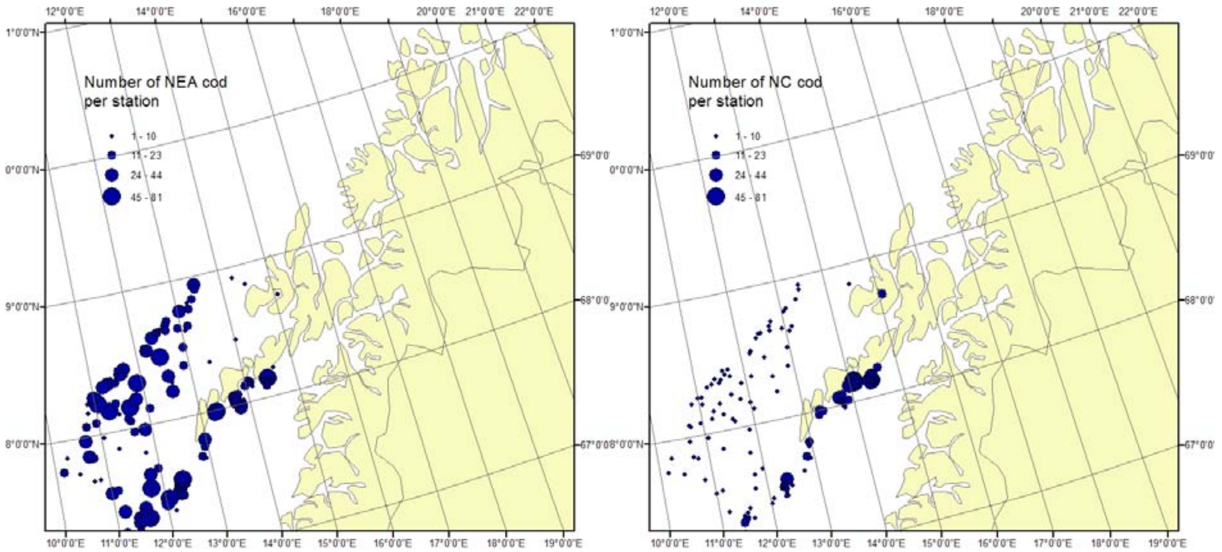

Figure 1. Number of North East Arctic cod (NEAC) and Norwegian coastal cod (NCC) per trawl station from annual abundance surveys conducted at the main spawning ground in Lofoten. Data are pooled for the years 1996-1999 and 2001-2005.

The 5 main release locations, indicated by with different colours in Figure 2 are distributed within the main distribution area for the two cod stocks. The different cod categories are distinguished by symbols and illustrate a large diversity in cod movements. Cod tagged at the two northernmost release sites during summer, do all move southwards and are recaptured close to the coast (T742, T717, T476, T446, T8446, T421). There are however one exception, a fish tagged at Bear Island (T 587) was recaptured further south and east, 4 months after release (Table 2). All of these fishes were deployed in 2003 before the procedure of collecting fin clips were established. Due to the area and time of the year the tagging was conducted, these individuals are most probably NEAC.

Fish tagged at the release site north of Lofoten have been recaptured in the Barents Sea (T699), north of the release site (T721), close to the release site (T7608) and further south (T856). All, except for one of these fishes (T7608) were identified as NEAC.

From the release sites west of Lofoten, 3 fishes were recaptured in the Barents sea (T752, T739, T2886), 2 were recaptured north of the release site, but still close to the coast (T751, T409). One of these fishes was a heterozygote (AB), while the other one was a homozygote (BB, NEAC). The DST record from this fish showed a typical pattern in both depth and temperature, which can be used to identify stock belonging to individuals where fin clips are missing. The rest of the fish tagged at this release station had migrated eastwards and were all recaptured in the Vestfjord basin.

Fish tagged at the easternmost locations were mainly recaptured close to the release site. However, 8 of the individuals had migrated out of the area and were recaptured further north. 4 of these were identified as NCC (AA), 2 as heterozygote (AB), 1 as NEAC (BB) and 1 was unidentified.

Several of the tagged fish had migrated more than 700 km from they were released until they were recaptured. The longest distance calculated between release site and recapture position was 845 km (Table 2).

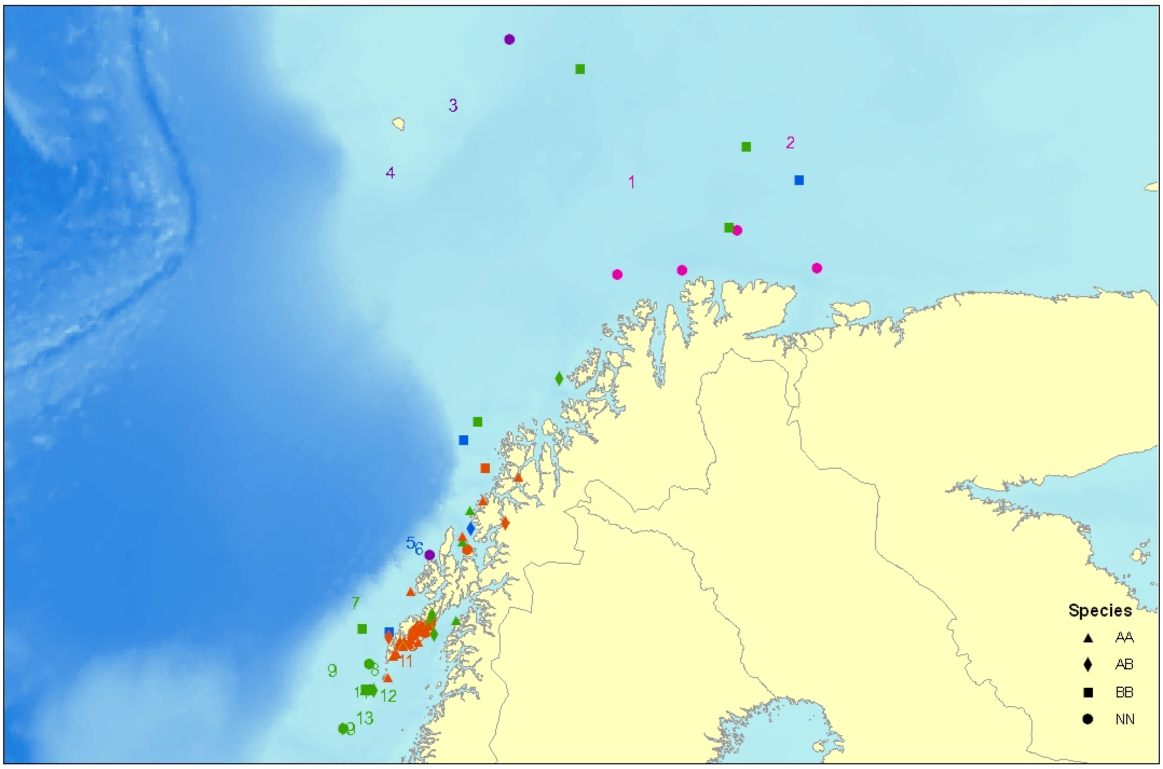

Figure 2. Release site (numbers) and recapture position (symbols) of the tagged cod. The different symbols indicate stock identification. The release sites were further grouped into 5 main geographical locations within the distribution area of cod (indicated by colours on numbers and symbols).

Behaviour of the fish and environmental conditions experienced

The data recorded by the DST confirmed that NEAC and NCC occupy different areas during summer and autumn, whereas the experienced the same temperatures (4-6 ^{0}C) during the spawning period in January to March (Figure 3).

NEAC cod experiences **lower** temperatures during the **warm summertime**, than during the **cold winter period** (Figure 3a). Within the area of distribution the mature part of the population fish, older than 8 years, will experience temperatures that range from 8 ^{o}C at the spawning grounds along the coast of Norway to down to 0 ^{o}C when they are in the northern and north-eastern feeding areas during summer. NCC, on the other hand, follow the seasonal temperature cycle in land, with higher temperatures during summer and autumn than in winter (Figure 3b).

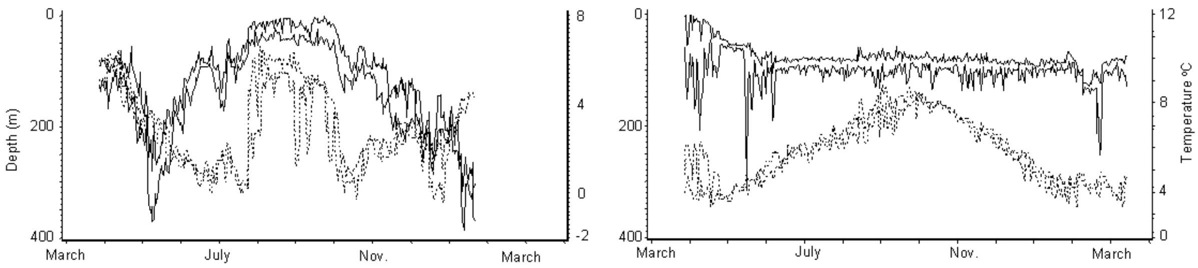

Figure 3. Maximum and minimum values of temperature (dotted line) and depth (solid line) recorded by two DST-tagged fish, which could be representative for a) NEAC and b) NCC . The cod were released and recaptured at approximately the same location, in the western part of.

Discussion

Different components or subpopulations of a species may have different productivities (e.g. Atlantic cod, Brander 1994, Ruzzante et al. 2000) and should be subjected to separate management regimes where fishing pressure is adjusted to the carrying capacity of the individual components. Managing whole populations as single units when discrete breeding units within the population exist may lead to overexploitation and depletion of the components with lowest productivity, or those who are most easily captured (Ruzzante et al., 1997). Knowledge of population structure is thus fundamental to the conservation of genetic resources and the sustainable management of exploited species. When populations are sub structured into separate breeding structures that are temporally stable, they are likely to display independent population dynamics, warranting separate management regimes.

The pantophysin locus (*Pan-1**) is the most potent locus at the moment to separate NEAC and NCC individuals in a mixed sample (Sarvas 2005). The *Pan-1* locus exhibits two alleles, A and B, genotype BB found almost exclusively in NEAC individuals while AA is the dominating allele in NCC (Sarvas 2005 and references there in). In the coastal area the *Pan-1*B* is present, but at low frequencies. The tagging program from 2003-2006 in total Therefore in combination of Pan-1* and microsatellites this will give us the possibility of excluding the “wrong” classification of the two main types. The tagged cod in the in the present report is only analysed for Pan-1 loci to get a brief review of the origin of the selected cod. Both the genetically analysis and the DST records indicate that NEAC migrate and NCC can both show non-migrating and medium-scaled migration patterns.

For further identification of the NEAC and NCC proper assignment tests is needed and then a combination of Pan-1 and microsatellites should be used to assign recaptured cod to NEAC and NCC (Wennevik 2006). At IMR we have a large database to compare the recaptured cod with baseline population from the spawning and feeding area. This will give us the possibility to test if the migration pattern observed is related to population or to genotype per se. Among the tagged and recaptured cod 176 fish showed the heterozygote genotype Pan-1*AB. Since none of these fishes were recaptured in the Barents Sea they do most likely belong to NCC. To gain further knowledge, also these fish need to be analysed by microsatellites.

Previous studies have shown that NEAC migrate from the warm spawning grounds along the coast during the winter, up to the summer feeding grounds where water temperatures may be low (Ottersen et al. 1998). In contrast, NCC, which do not undertake large-scale seasonal migrations, stay close to the coast throughout the year and therefore experience the opposite seasonal change in temperature as conditions become warmer in summer (Godø and Michalsen, 2000). However, both stocks intermingle at the spawning ground in Lofoten. The present study indicated that individuals from the two cod stocks also would experience large differences in environmental conditions. NEAC cod experiences lower temperatures during the warm summertime, than during the cold winter period, while NCC will experience the opposite temperature pattern.

In the very first acoustic recordings of fish, Sund (1935) reported that the spawning concentrations of cod in the field are observed in a 10-12 metre-thick sharply defined pelagic layer, 50-70 m below the surface. Sars (1879) also observed that spawning cod in Lofoten remained within certain depth layers, which he believed coincided with a specific temperature range, later called the transmission layer. In Lofoten, it has been reported that cod spawn in the thermocline between 4 and 6 °C and normally near the area where this layer intersects with the bottom. Longer-term hydrographic conditions, in conjunction with short-term atmospheric forcing, influence the depth of the thermocline layer and hence the depths where the spawning cod occur (Ellertsen et al. 1981; Furnes and Sundby 1981). Due to lack of relevant tools it has so far not been possible to determine whether NEAC and NCC have different environmental preferences as regards water characteristics and the time and place of spawning. Since DSTs can identify the factors that affect fish movements and the mechanisms underpinning them, tag records will in future analyses be used to investigate behavioural and environmental experience of the individual NEAC and NCC in more detail.

In summary, NEAC appear to migrate between deep, warm overwintering grounds and shallow summer feeding grounds where water temperatures may be low. In contrast, coastal cod, which do not undertake large-scale seasonal migrations, show little seasonal variation in depth distribution and experience the opposite seasonal change in temperature as conditions become warmer in summer. These seasonal differences in the habitat associations of cod, as well as the geographic differences between the northerly migratory NEAC and the NCC, may reflect differences in the factors motivating habitat selection. Martin and Jean (1964)) argued that selection of preferred temperatures appears to be the dominant force controlling cod migrations and depth distributions. However, factors other than temperature preference are likely to influence habitat selection during the summer feeding season. Lawson and Rose (2000) argued that the seasonal changes in habitat associations of cod in Placentia Bay, Newfoundland were more closely related to depth than temperature, with the shallower depths occupied in summer and early autumn a consequence of greater food availability at these depths. Similarly, Swain et al. (1998) noted that habitat choice by cod in the southern Gulf of St. Lawrence appeared to be more closely related to depth than to temperature during the feeding season in September. Further analysis is need before we can conclude how this work for NEAC and NCC.

References

Arnason, E., Petersen, P.H., Kristinsson, K., Sigurgislason, H., and Palsson, S. 2000. Mitochondrial Cytochrome B Dna Sequence Variation of Atlantic Cod From Iceland and Greenland. Journal of Fish Biology **56**: 409-430.

Berg, E. and Albert, O.T., 2003. Cod in fjords and coastal waters of North Norway: distribution and variation in length and maturity at age. ICES J. Mar. Sci., 60: 787-797

Berg, E., Sarvas, T.H., Harbitz, A., Fevolden, S.E. and Salberg, A.B., 2005. Accuracy and precision in stock separation of north-east Arctic and Norwegian coastal cod by otoloths – comparing readings, image analyses and genetic method. Marine and Freshwater Research **56 (5**): 753-762.

Dahle G 1991. Cod, *Gadus morhua* L., populations identified by mitochondrial DNA. *J. Fish Biol.* **38**, 295-303.

Dalpadado, P. and Skjoldal, H.R. 1996. Abundance, maturity and growth of the krill species Thysanoessa inermis and T. longicaudata in the Barents Sea. Marine Ecology Progress Series, 144: 175-183.

Eggvin, J. 1938. Trekk fra Nord-Norges oseanografi sett i sammenheng med torskefisket (in norwegian). Fiskeridirektoratet. Skrifter. Serie Havundersøkelser, 5: 33-46.

Ellertsen, B., Solemdal, P., Strømme, T., Sundby, S., Tilseth, S., Westgård, T. & Øiestad, V**.** 1981. Spawning period, transport and dispersal of eggs from the spawnng area of Arcto-Norwegian cod (*Gadus morhua* L.). Rapports et Proces-verbaux des Réunions du Conseil International pour l'Exploration de la Mer , 178: 260-267.

Fevolden SE, Pogson GH (1997) Genetic divergence at the synaptophysin (*Pan* I) locus among Norwegian coastal and North-east Arctic populations of Atlantic cod. *Journal of Fisheries*, **51**, 895-908.

Furnes, G. K. & Sundby, S. 1981. Upwelling and wind/induced circulation in Vestfjorden. Proceedings from Norwegian Coastal Current Symposium, Geilo, Norway. 9-12 September 1980, Volume 1, pp.152-178.

Gjøsæter, H. 1997. The Barents Sea Capelin Stock (Mallotus villosus): A brief review. In Forage fishes in marine echosystems. Proceedings of the International Symposium on the role of forage fishes in marine echosystems, pp. 469-484.

Godø, O.R. and Michalsen, K. 2000. Migratory behaviour of north-east Arctic cod, studied by use of Data Storage Tags. Fisheries Research 48: 127-140.

Hutchings, J.A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences **62**: 824-832.

Hutchinson WF, Carvalho GR, Rogers SI 2001. Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. *Marine Ecology Progress Series* **223**, 251 – 260

ICES 2006. Report of the Arctic Fisheries Working Group, Copenhagen 18-27 April 2006. ICES C. M. 2006/ACFM:25 ,584 pp.

Jakobsen, T. 1987. Coastal cod in northern Norway. Fisheries Research **5**: 223-234.

Jonsdottir, O.D.B., Danielsdottir, A.K., and Naevdal, G. 2001. Genetic differentiation among Atlantic cod (Gadus morhua L.) in Icelandic waters: temporal stability. ICES Journal of Marine Science **58**: 114-122.

Knutsen, H., Jorde, P. E., André, C. and Stenseth, N. C. (2003). Fine-scaled geographic population structuring in a highly mobile marine species: the Atlantic cod. Molecular Ecology 12, 385-394.

Konstantinov, K.G. 1967. Forecasting of the distribution of fish concentrations in the Barents Sea according to the temperature factor. Fisheries Research Board Canada. Translated Series, 1132: 28.

Lawson, G.L., Rose, G. A., 2000. Seasonal distribution and movements of coastal cod (*Gadus morhua* L.) in Placentia Bay Newfoundland. Fisheries Research, 49: 61–75.

Martin, W. R., and Jean, Y. 1964. Winter cod taggings off Cape Breton and on offshore Nova Scotia banks, 1959-62. J. Fish. Res. Board Can. 21: 215-237.

Michael E. Mann, M. E., Bradley, R.S., and Hughes, M. K. 1998. Global-scale temperature patterns and climate forcing over the past six centuries. Nature 392, 779 – 787.

Nakken, O., and Raknes, A. 1987. The distribution and growth of Northeast Arctic cod in relation to bottom temperatures in the Barents Sea, 1978-1984. Fisheries Research, 5: 243-252.

Ottersen, G. and Ådlandsvik, B. 1993. Climatological temperature and salinity fields for the Nordic Seas. Institute of Marine Research, Department of Marine Environment. Report no.8, 121.

Ottersen, G., Michalsen, K. & Nakken O. 1998. Ambient temperature and distribution of north-east Arctic cod. ICES Journal of Marine Science, 55:67-85.

Pogson GH and Fevolden SE 2003. Natural selection and genetic differentiation of coastal and Arctic population of the Atlantic cod in northern Norway: a test involving nucleotide sequence variation at the antophysin (PanI) locus. Mol. Ecol. 12:63-74.

Pogson GH, Mesa KA, Boutilier RG 1995. Genetic population structure and gene flow in the Atlantic Cod *Gadus morhua*: A comparison of allozyme and nuclear RFLP loci. *Genetics* **139**, 375 - 385.

Pogson, G.H. 2001. Nucleotide polymorphism and natural selection at the Pantophysin (Pan I) locus in the Atlantic cod, *Gadus* m*orhua* (L.). Genetics **157**: 317-330.

Pogson, G.H. and Mesa, K.A. 2004. Positive Darwinian selection at the pantophysin (*Pan*I) locus in marine Gadid fishes. Molecular Biology and Evolution **21**: 65-75.

Rollefsen, G. 1933. The otoliths of cod. Fiskeridirektoratets skrifter, serie Havundersøkelser **4**: 1-14.

Ruzzante DE, Taggart CT, Cook D 1999. A review of the evidence for genetic structure of cod (*Gadus morhua*) populations in the NW Atlantic and populations affinities of larval cod off Newfoundland and the Gulf of St. Lawrence. *Fisheries Research* **43**, 79 - 97.

Ruzzante ED, Taggart CT, Cook D, Goddard S 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. *Can. J. Fish. Aquat. Sci.* **53**, 634-645.

Ruzzante, D.E., Taggart, C.T., Cook, D., and Goddard, S.V. 1997. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: a test

and evidence of temporal stability. Canadian Journal of Fisheries and Aquatic Sciences **54**: 2700-2708.
Ruzzante, D.E., Taggart, C.T., Lang, S., and Cook, D. 2000. Mixed-stock analysis of Atlantic cod near the Gulf of St. Lawrence based on microsatellite DNA. Ecological Applications **10**: 1090-1109.
Sarvas, T.H. and Fevolden, S.E. 2005. The ScnDNA locus *Pan*I reveals concurrent presence of different populations of Atlantic cod (*Gadus morhua* L.) within a single fjord. Fisheries Research **76**: 307-316.
Smith, P.J., Birley, A.J., Jamieson, A., and Bishop, C.A. 1989. Mitochondrial DNA in the Atlantic cod, *Gadus morhua*: lack of genetic divergence between eastern and western populations. Journal of Fish Biology **34**: 369-373.
Sund, O. 1935. Echosounding in fishery research. Nature 135, p. 953.
Swain, D. P., Chouinard, G. A., Morin, R. and Drinkwater, K. F. 1998. Seasonal variation in the habitat associations of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 55: 2548-2561.Wootton, R. J. 1990. Ecology of teleost fishes. Chapman & Hall, London, UK. 404 pp.
Taylor, M.F.J., Shen, Y., and Kreitman, M.E. 1995. A population genetic test of selection at the molecular-Level. Science **270**: 1497-1499.
Wennevik, V. 2006. The application of genetic profiling and statistical assignment methods in the management of fish populations. PhD thesis, University of Bergen

Table 1.

Location	Release site no	# DST released	# conv. tag released	# DST recaptured	# conv. tag recaptured	No. of genetic samples
Barents Sea	1, 2	50	59	4	0	36
Bear Island	3, 4	55	37	3	0	40
Lofoten, North	5, 6	70	141	5	0	211
Lofoten, West	7,8,9,12,13,14,19	156	271	9	8	254
Lofoten, East	19,11,15,16,17,18,20	59	234	21	16	181
Sum		390	742	42	24	722

Table 2.

Tag no	Stock id.	release date	release site no	Recapture date	Latitude	Longitude	Distance(m)	days at sea
1611	AB	03.04.2005	16	15.04.2005	69,16	18,05	194 625	12
2602	AB	04.04.2006	18	18.04.2006	68,10	13,94	37	14
2455	AB	01.04.2004	11	16.04.2004	68,13	14,07	45 421	15
1494	AB	01.11.2004	13	30.03.2005	68,30	14,72	178 695	149
2403	AB	02.04.2004	12	15.11.2004	68,05	14,62	112 452	227
2383	AB	02.04.2004	12	10.03.2005	67,53	12,25	18 807	342
7608	AB	18.03.2004	5	12.04.2005	69,22	16,83	87 385	390
7615	AB	30.03.2004	10	24.04.2006	68,14	13,13	43 901	755
409	AB	25.03.2004	9	02.05.2006	70,67	21,69	528 636	768
1564	BB	30.03.2005	14	01.04.2005	67,56	11,99	12 931	2
1725	BB	01.04.2005	15	07.04.2005	68,14	14,07	23 744	6
4590	BB	28.03.2006	20	03.04.2006	68,14	14,06	7 365	6
4509	BB	28.03.2006	20	04.04.2006	68,15	14,10	5 388	7
1729	BB	01.04.2005	15	14.04.2005	68,12	13,94	18 214	13
856	BB	19.03.2004	6	03.04.2004	68,22	13,15	127 196	15
721	BB	19.03.2004	6	14.04.2004	70,33	17,50	166 772	26
4599	BB	28.03.2006	20	18.05.2006	69,92	17,95	246 462	51
739	bb	21.03.2004	7	02.06.2004	71,46	30,14	755 974	73
699	BB	19.03.2004	6	01.06.2004	71,50	33,48	754 411	74
2886	BB	21.03.2004	7	04.12.2004	74,17	27,88	828 367	258
751	BB	21.03.2004	7	28.02.2005	70,50	18,21	311 157	344
2707	BB	01.04.2004	11	20.03.2005	68,21	14,64	68 443	353
752	BB	21.03.2004	7	15.08.2005	72,23	32,47	858 877	512
2364	BB	03.04.2004	13	05.03.2006	67,54	12,14	41 683	701
412	BB	25.03.2004	9	05.04.2006	68,33	12,28	72 508	741
2735	NN	30.03.2004	10	30.03.2004	68,16	14,31	8 319	0
421	NN	08.02.2003	2	21.05.2003	70,42	32,25	185 082	102
587	NN	28.08.2003	4	18.12.2003	74,90	25,52	254 103	112
463	NN	08.02.2003	2	21.06.2003	71,37	30,35	149 832	133
717	NN	28.08.2003	4	26.02.2004	69,04	15,15	550 489	182
742	NN	26.08.2003	3	13.03.2004	67,54	12,13	844 739	200
446	NN	02.02.2003	1	14.10.2003	71,27	27,73	144 493	254
476	NN	02.02.2003	1	15.01.2004	71,58	25,37	135 242	347
2864	NN	23.03.2004	8	22.03.2005	67,12	11,03	97 383	364
2349	NN	03.04.2004	13	04.04.2005	67,86	12,29	77 375	366
2719	NN	30.03.2004	10	23.07.2005	68,98	16,50	137 041	480
2606	AA	04.04.2006	18	05.04.2006	69,67	19,00	271 856	1
1564	AA	03.04.2006	17	05.04.2006	68,17	14,51	7 502	2
1656	AA	01.04.2005	15	04.04.2005	68,06	13,78	9 029	3
4547	AA	28.03.2006	20	31.03.2006	68,14	14,06	7 365	3
1653	AA	01.04.2005	15	05.04.2005	68,07	13,58	7 710	4
1577	AA	01.04.2004	11	06.04.2004	68,00	13,72	25 180	5
1663	AA	01.04.2005	15	07.04.2005	68,02	13,38	11 301	6
1744	AA	01.04.2005	15	07.04.2005	68,13	13,90	17 916	6
1577	AA	03.04.2005	16	09.04.2005	67,90	13,11	54 991	6
4555	AA	28.03.2006	20	04.04.2006	68,00	13,50	36 006	7
1582	AA	03.04.2005	16	12.04.2005	68,18	14,53	15 096	9
1728	AA	01.04.2005	15	12.04.2005	68,08	13,44	12 253	11
1632	AA	03.04.2005	16	15.04.2005	68,14	14,06	6 364	12
1623	AA	03.04.2005	16	16.04.2005	67,65	12,80	83 630	13
1841	AA	26.03.2006	19	19.04.2006	68,01	13,51	146 820	24
2441	AA	01.04.2004	11	08.05.2004	68,15	14,06	47 025	37
4550	AA	28.03.2006	20	06.05.2006	68,67	14,19	53 747	39
2417	AA	02.04.2004	12	01.06.2004	68,22	14,56	123 620	60
4516	AA	28.03.2006	20	01.06.2006	67,92	13,18	52 049	65
1620	AA	03.04.2005	16	08.08.2005	69,17	16,44	144 863	127
701	AA	01.04.2004	11	20.10.2004	68,00	14,05	34 000	202
2377	AA	03.04.2004	13	20.11.2004	69,09	16,40	289 899	231
1564	AA	01.04.2004	11	06.12.2004	69,52	17,52	255 160	249
1663	AA	02.04.2004	12	28.12.2004	69,46	16,96	291 912	270
1657	AA	02.04.2004	12	10.01.2005	68,15	15,44	148 019	283
1581	AA	01.04.2005	15	22.03.2006	68,14	14,06	23 737	355
1641	AA	01.04.2004	11	11.05.2005	67,92	13,24	16 026	405
1568	AA	01.04.2004	11	09.03.2006	68,14	14,10	46 697	707
2454	AA	01.04.2004	11	16.03.2006	68,10	14,32	49 917	714
2460	AA	01.04.2004	11	23.03.2006	68,12	14,40	53 827	721