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Impacts of physical-biological factors during egg stages

Mari Skuggedal Myksvoll

Dissertation for the degree of *Philosophiae Doctor* (PhD)
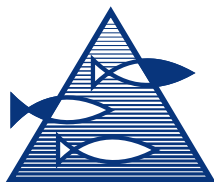Geophysical Institute, University of Bergen, Norway

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Outline

This thesis consists of an introduction and four papers. The introduction provides a scientific background of the population structure of Atlantic cod stocks in Norwegian Waters and the research history of fjord dynamics (Section 1). Section 2 states the motivation for the study and the most important results from the papers. A discussion follows focusing on the implications of the present results (Section 3) and perspectives for future research are stated in Section 4.

- **Paper I: Retention of coastal cod eggs in a fjord caused by interactions between egg buoyancy and circulation pattern**
  Myksvoll, M.S., Sundby, S., Ådlandsvik, B. and Vikebø, F. (2011)
  Marine and Coastal Fisheries, **3**, 279-294.

- **Paper II: Importance of high resolution wind forcing on eddy activity and particle dispersion in a Norwegian fjord**
  Myksvoll, M.S., Sandvik, A.D., Skarðhamar, J. and Sundby, S. (2012)
  Submitted to Estuarine, Coastal and Shelf Sciences

- **Paper III: Effects of river regulations on fjord dynamics and retention of coastal cod eggs**
  Myksvoll, M.S., Sandvik, A.D., Asplin, L. and Sundby, S. (2012)
  Manuscript

- **Paper IV: Modeling dispersal of eggs and quantifying connectivity among Norwegian Coastal cod subpopulations**
  Myksvoll, M.S., Jung, K.-M., Albretsen, J. and Sundby, S. (2012)
  Manuscript

Abstract

Norwegian Coastal cod form a stationary population of Atlantic cod (*Gadus morhua* L.) consisting of several genetically separated subpopulations. A small-scale differentiation in marine populations with pelagic eggs and larvae is made possible by local retention of early life stages in coastal regions. A numerical model was implemented for a part of the northern Norwegian coast with 800 m horizontal resolution, in addition to two fjord systems with higher resolution; Folda in Nordland and Porsangerfjorden in Finnmark. The model results were used to simulate connectivity and retention of cod eggs among coastal regions and fjords. The cod eggs in Folda attained a subsurface vertical distribution, avoiding the surface and causing retention. River regulations caused by hydroelectric power production alters the seasonal runoff cycle and reduced the retention of cod eggs in Folda. The dispersion of planktonic organisms in Porsangerfjorden is highly affected by the local wind and varies with resolution on the atmospheric forcing in the model. Coastal spawning areas have intermediate connectivity of early life stages between neighboring areas. High retention of eggs in fjords combined with strong homing to spawning areas indicate that fjord subpopulations may be described as a metapopulation.

Acknowledgements

Mari S. Myksvoll

Bergen, January 2012

An invisible red threat connects those who are destined to meet,
regardless of time, place, or circumstance.
The thread may stretch or tangle,
but it will never break.

Contents

1 Background

1.1 Population dynamics of cod (*Gadus morhua* L.)

Atlantic cod stocks (*Gadus morhua* L.) are distributed along the continental shelves on both sides of the North Atlantic from 40°N to 80°N (Sundby, 2000). The Norwegian coast is populated by two different cod stocks, the Arcto-Norwegian cod (ANC) and the Norwegian Coastal cod (NCC). The two stocks are managed separately with respect to quotas (Aglen, 2009), but there are still disagreements whether they make up one large population or possibly several non-interbreeding groups (Nordeide *et al.*, 2011). Rollefsen (1933) used otholits to determine the age of cod and started using variations in growth zones to differentiate between ANC and NCC. Several studies through the years have tried to confirm a genetic difference between the two populations by using different genetic markers, like haemoglobin (HbI) (Jørstad, 1984), mitochondrial DNA (Árnason & Pálsson, 1996), nuclear DNA (PanI) (Fevolden & Pogson, 1997; Pogson & Fevolden, 2003) and allozymes (Mork & Giæver, 1999). The results by Jørstad (1984) supported the existence of a genetic difference between ANC and NCC, but other studies have shown that haemoglobin is unreliable in studies of genetic population structure (Mork & Sundnes, 1985). Fevolden and Pogson (1997) suggest that oceanic and coastal populations of cod are more independent than suggested earlier and significant heterogeneity exists among different fjord populations. However, Westgaard and Fevolden (2007) acknowledge that PanI locus is non-neutral and affected by environmental forces. Nevertheless, the two populations have very different life-history and are therefore called oceanic migratory population (ANC) and coastal stationary population (NCC).

The main spawning areas of ANC are at the Lofoten archipelago and Møre, in addition to specific areas along the Norwegian coast (Sundby & Nakken, 2008). The eggs and larvae then drift northwards along the coastline towards the feeding areas in the Barents Sea (Bergstad *et al.*, 1987; Vikebø *et al.*, 2005). When they reach maturity they migrate back to the Norwegian coast to spawn, a distance up to 1500 km. Currently the population of ANC is large, above the long term average, and the spawning stock biomass is increasing (Bogstad, 2011). The NCC spawns several places along the Norwegian coast and specifically inside the fjords (Jakobsen, 1987). The juveniles show only short migrations and will most probably spawn in the same fjord as their nursery grounds. The overall spawning stock biomass of NCC is currently very low, while large variability exists between nearby fjords and coastal regions (Berg & Albert, 2003). The recruitment of NCC is not in phase with ANC which indicates different re-

cruitment mechanisms between the two populations (Berg & Pedersen, 2001). Knutsen *et al.* (2007) found high densities of cod eggs in sheltered fjord habitats, which indicate retention of early life stages that can support a small-scale population structure. Jorde *et al.* (2007) found genetic differences between samples less than 30 km apart, suggesting significant variability between neighboring fjords. Knowledge of subpopulations is especially important for management purposes. If a group of distinct stocks is considered to be one large stock, the growth and harvest potential will be overestimated, and may in some cases lead to sudden collapse and slow recovery (Sterner, 2007).

Marine populations have traditionally been regarded as open, meaning that the offspring is freely spreading and mixing over large geographical regions (Cowen *et al.*, 2000). However, studies have revealed that specific behavior adapted to circulation patterns oppose dispersion, like for example larvae that avoid the surface layer to enhance local retention (Cowen *et al.*, 2006; Ciannelli *et al.*, 2010). Asplin *et al.* (1999) argued that species have specialized their spawning depth and the specific gravity of eggs to reduce dispersal of early life stages. In Chesapeake Bay larval retention is strongly linked to the physical conditions within the estuarine turbidity maximum, which is strongly affected by variations in wind and freshwater discharge (North & Houde, 2006). North *et al* (2008) found that larval swimming behavior had greater influence on transport success than interannual variation in circulation.

The vertical distribution is an important variable controlling the transport and dispersion of cod eggs, and is determined by the specific gravity of eggs relative to the local density profile. The ANC eggs have a neutral buoyancy between 29.5 and 33.0 (equivalent to salinity) according to Solemdal and Sundby (1981), which means they are lighter than the surrounding water in Vestfjorden and are pelagically distributed (Sundby, 1983). Pelagic eggs have highest concentration at the surface, exponentially decreasing downwards and are mainly influenced by wind-induced mixing (Sundby, 1991). Stenevik *et al.* (2008) measured specific gravity of NCC eggs from several places along the Norwegian coast, including Tysfjord in the inner part Vestfjorden, where the neutral buoyancy was ranging between 30.6 and 34.1 (equivalent to salinity). In an estuarine environment with low surface salinity these eggs attain a subsurfacevertical distribution, having a specific gravity higher than the mixed layer in the fjords and lower than the bottom layer. The subsurface pelagic eggs have highest concentration at the pycnocline, fairly insensitive to variations in turbulence but more dependent on the local salinity profile (Sundby, 1991). The distribution of cod eggs relative to the vertical current structure is especially important in areas with strong vertical gradients, like in fjords and coastal regions.

1.2 Fjord dynamics

Pritchard (1952) defined an estuary as a semi-enclosed coastal body of water having a free connection with the open sea and containing a measurable quantity of sea salt. Fjords are a special type of estuary, as they are elongated indentures of the coastline containing a relatively deep basin with a shallow sill at the mouth, generally U-shaped in cross section and carved out by glaciers (Pritchard, 1967). The hydrography inside the fjord represents a balance between the high salinity coastal water and the freshwater discharge (Saelen, 1967), whereas atmospheric variability holds the potential to modify the balance. When river input dominates over tidal input the estuarine circulation develops (Dyer, 1997). The fjord can be divided into three layers; a thin brackish layer, an intermediate layer and a deep basin layer below the sill (Stigebrandt, 1981), as seen in Fig. 1. The surface layer is generated by the river input near the head of the fjord, mixed with saline water and pushed out of the fjord due to the pressure difference. On
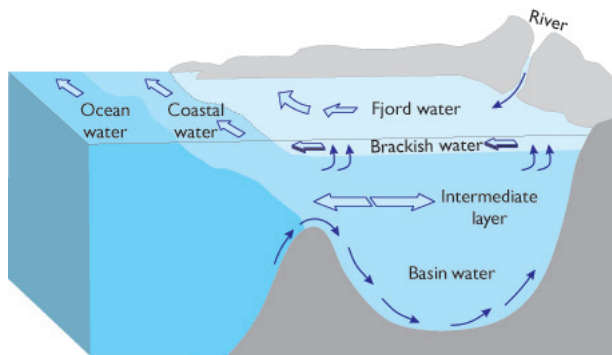
Figure 1: Schematic view of water exchange processes in a simplified fjord.
(Aure *et al.*, 2007)

the interface between the brackish layer and the intermediate layer is a strong velocity shear, resulting in wave formation and breaking causing salty water being mixed into the surface layer. As a result the salinity of the brackish layer gradually increases downstream. The amount of water being mixed into the upper layer depends on the energy available for mixing, which is mainly supplied by wind stress, tidal energy and internal waves. A compensating current is generated below and directed into the fjord (Gade, 1976). The circulation in the intermediate layer is fluctuating, varying with tidal forces and the density structure at the coast. The intermediate circulation can often be an order of magnitude greater than the estuarine circulation (Stigebrandt, 1990; Aure *et al.*, 1996). The circulation below sill level is weaker and the basin water

can be stagnant for longer periods with episodic inflows (Gade & Edwards, 1980). Vertical mixing below sill level is driven by breaking of internal waves (Stigebrandt, 1976), tides and local wind (Stigebrandt & Aure, 1989), which reduces the density and is an important precondition for renewal of bottom water. Frequent seaward winds during winter cause upwelling and lift the deep water outside of the sill causing an inflow, which usually occurs every year (Skreslet & Loeng, 1977). Also northerly winds aligned with the coast outside the fjord can cause coastal upwelling and induce deep water renewal (Klinck et al., 1981; Asplin et al., 1999).

According to Sælen (1967) river runoff is the major driving mechanism controlling both circulation and hydrography, while Svendsen and Thompson (1978) argue that wind stress is the most important forcing for the surface circulation, and stratification works to trap the wind response to the near-surface layer. Svendsen (1995) provides a description of both processes, since the importance of freshwater supply and wind stress vary in different fjords, and therefore suggests a classification depending on runoff related to the surface area of the fjord. In a fjord with large river runoff compared to surface area, the runoff is most important for the upper circulation. While in a fjord with little runoff compared to the surface area, the wind stress controls the upper circulation. Since the river runoff has large seasonal variations, the balance between the forces varies during the year. Malangen fjord in northern Norway is an example of the first case, and is stratified almost all year round. Porsangerfjord represents the second case except for a few months in the summer season when runoff is particularly high and influences the surface circulation (Cushman-Roisin et al., 1994).

The use of numerical models in coastal regions have accelerated during the last decades. As computer resources has become available, 3D applications of fjord systems have emerged with sufficiently high horizontal and vertical resolution. The first fjord simulations in Norway were done with idealized coastline, constant depth and simplified forcing (Cushman-Roisin et al., 1994; Asplin, 1995; Leth, 1995). These simplified approaches provided valuable insight to how the fjord circulation responded to local and non-local wind causing coastal upwelling/downwelling (Asplin et al., 1999). Eliassen et al. (2001) used realistic coastline and bathymetry in a numerical study of Skjerstadfjorden in northern Norway which significantly improved the complexity of the circulation, but the results were still limited by idealistic wind forcing. Ellingsen et al. (2004) used a high-resolution numerical model to evaluate the importance of river discharge on fjord circulation in the Trondheim Fjord. Skogen et al. (2009) used a high resolution wind field (3 km) to force a numerical model covering Hardangerfjorden in western Norway and showed the importance of boundary conditions, as the fjord-coast water exchange was sufficiently large to reduce the effect of fish farming on eutrophication. Numerical

modeling of estuaries has also been done in Scottish sea lochs (Amundrud & Murray, 2009), Chesapeake Bay (North & Houde, 2004; Li *et al.*, 2005), Hudson River estuary (Warner *et al.*, 2005), Lunenburg Bay of Nova Scotia (Sheng *et al.*, 2009), Columbia River estuary (MacCready *et al.*, 2009) and the Broughton archipelago on the western Canadian coast (Foreman *et al.*, 2009). However, the dynamics of estuaries are quite different than fjords, particularly due to large bottom depth in fjords. Still many of the challenges of high resolution coastal modeling are similar, like adequate atmospheric forcing, boundary conditions and turbulence closure schemes.

2 The present study

2.1 Motivation

The motivation for this thesis was to evaluate the importance of the vertical distribution on horizontal transport of cod eggs. The vertical distribution of cod eggs depends on the egg specific gravity relative to the local density profile. Small differences in egg specific gravity have been observed between ANC and NCC. We wanted to investigate whether these observed differences would cause a difference in the vertical distribution of eggs between ANC and NCC, or if the local density structure was more important. The physical environment in Vestfjorden, where ANC is spawning, is very different from the estuarine environment inside the fjords, where NCC is spawning. We chose to study the Folda fjord system in Nordland county, close to Vestfjorden. This is a typical Norwegian fjord with deep basins, complex topography and large freshwater discharge compared to the surface area of the fjord. The estuarine circulation is expected to develop in such a fjord, associated with strong surface outflow and low-saline surface layer. The potential for dispersal is therefore large, and planktonic organisms need to avoid the low-saline layer to counteract dispersal. In addition, Porsangerfjorden in Finnmark county was included in the study. This is a very different fjord than Folda, mainly due to its wide, rectangular shape and low freshwater discharge compared to the surface area of the fjord. The surface circulation is therefore assumed to be mainly controlled by wind and tidal forcing. In addition, the NCC population in Porsangerfjorden has declined during the last few decades and we wanted to investigate the potential for egg dispersion in a fjord with low river runoff.

The vertical distribution of cod eggs in Folda is assumed to be controlled by the surface salinity, which in turn is controlled by the river runoff. This fjord system has been highly affected by hydroelectric power production causing significant modifications to the seasonal pattern of river runoff. And we wanted to investigate whether

river regulations could impact the vertical and horizontal distribution of cod eggs.

To study the interaction between egg specific gravity and fjord circulation, the Regional Ocean Modeling System (ROMS) was implemented for the Folda fjord system and Porsangerfjorden. The output from the ocean circulation model was used as input to a particle-tracking model of cod eggs with a dynamical vertical distribution. The combination of these two models provides the possibility to study variations in vertical distribution caused by local salinity structure and investigate the corresponding impact on horizontal transport. In addition, was the ROMS model implemented for a coastal region covering the Folda fjord to quantify transport of cod eggs between neighboring fjords and connectivity among coastal populations.

2.2   Main results

- High river runoff in the narrow fjord system of Folda gives rise to low surface salinity, causing the cod eggs to be negatively buoyant at the surface. The cod eggs therefore attain a subsurface vertical distribution which reduces the horizontal dispersal and increase local retention.

- High resolution atmospheric forcing is necessary to provide realistic wind pattern in both wide (Porsangerfjorden) and narrow (Folda) fjords. Realistic wind variability provide a better representation of eddy activity, which increase retention of planktonic organisms.

- River regulations caused by hydroelectric power production alters the seasonal runoff cycle and reduced the retention of cod eggs in Folda.

- Medium retention of cod eggs at the coast imply medium connectivity between neighboring coastal cod populations and low connectivity between between fjord and coastal populations.

3   Discussion

The results in this thesis are only based on simulations of cod eggs, while the following discussion will include the larval stages too. What is known about vertical distribution of cod larvae is that they avoid the upper 5-10 m of the water column (Ellertsen *et al.*, 1984; Ellertsen *et al.*, 1989; Sundby & Fossum, 1990). The consequence of a subsurface larval distribution is a considerable reduction in spatial dispersion. It is therefore likely that the distribution pattern described for cod eggs will continue also for cod larvae.

Dispersing eggs will continue to spread out and eggs that are retained will continue to be retained as larvae. The discussion here includes therefore both cod eggs and larvae hereby referred to as early life stages. There are of course limitations in this approach, but it is likely that the error done would be of the same order as the uncertainty that do exists in dispersal modeling of cod larvae due to uncertainty in vertical distribution.

3.1 Fjord dynamics

The estuarine circulation was originally described for shallow estuaries, where a two-layer structure is applicable. A lot of research has been done in so-called salt wedge estuaries with high river input. Some of the results obtained in these systems have provided the basis for our knowledge of fjord systems as well. It is therefore important to emphasize that not all results from shallow estuaries are applicable to deep Norwegian fjords. The bathymetry of a fjord is fundamentally different from an estuary i.e. deep basins, steep boundaries and shallow sills, which substantially influences both the hydrography and dynamics in fjords.

The traditional description of the estuarine circulation includes a low-saline surface outflow and a compensating inflow below. According to Gade (1986) is the brackish upper layer growing in density, thickness and velocity as it approaches the open ocean. The increasing density and thickness is explained by admixed seawater, often in a ratio exceeding 5 to 1. Sælen (1967) estimated the low-saline outflow to be between 2 and 6 times as large as the freshwater supply. For preservation of continuity the inflowing seawater must therefore have an upward velocity component. The process causing mixing of seawater into the surface layer is usually named entrainment. Kundu and Cohen (2004) define entrainment as the process drawing surrounding fluid across a boundary layer by frictional forces. In Dyer (1997) the entrainment is associated with breaking of progressive interfacial Holmboe waves. The consequence is that extra volume is injected to the upper layer and thickness will increase downstream. It is possible to apply this knowledge of entrainment to estuarine circulation by turning the argument around; if the thickness of the low-saline layer increases downstream then entrainment is the most important mixing process. However, none of the model results or observations forming the basis for these four papers show larger depth of low-saline layer downstream. Data from Folda show that the depth of the 32-isohaline is exactly the same in the inner and outer part of the fjord, both from model and observations. But the surface salinity increases steadily from the inner to outer part, which implies that salt is mixed into the upper layer but no extra volume is added. Mixing caused by turbulent diffusion has exactly this effect (Dyer, 1997). Instabilities develop as Kelvin-

Helmholtz waves, and as these waves break they mix equal volumes of water between the two layers and is therefore a two-way process. Salt is mixed into the upper layer but there is no net exchange of water, which matches what we have observed in the fjords. Since there is no net exchange of water, there cannot be an upward velocity component only an upward flux of salt. The fjord basin is a large reservoir of high salinity water. Removal of salt from the deeper layers providing increasing salt content in the surface brackish layer ($\sim$ 10m) is distributed over the whole water column ($>$ 200m). The total effect on circulation in the lower layers is therefore not measurable and masked by other processes.

As research in fjords has progressed, the knowledge of the circulation in the intermediate layer has changed dramatically. Gade (1986) claimed that the intermediate water, occupying the zone between the compensation current and the sill, is most often quiescent. This is in large contrast to results by Stigebrandt (1990) and Aure *et al.* (1996) showing that the inflow in the intermediate layer, caused by density fluctuations in coastal water, is the dominating mode of water exchange being an order of magnitude greater than inflow associated with the estuarine circulation. Recent research has therefore turned focus more towards understanding the fjord-coast water exchange, and less on the so-called compensation current. This is illustrated in Fig. 1 where the circulation in the intermediate layer is shown to be strong and can be directed both into and out of the fjord.

3.2   Population dynamics of cod (*Gadus morhua* L.)

The cod populations inhabiting the Norwegian waters are separated in two units for management purposes, the Arcto-Norwegian cod (ANC) and the Norwegian Coastal cod (NCC). The ANC is also known by other names such as Northeast Arctic cod, which is the official name used by ICES, or Barents Sea cod (Sundby & Nakken, 2008). Studies of genetical variances and migration patterns have revealed that the NCC population is not as homogeneous as previously assumed. Also considering the results obtained in this thesis, it is more convenient to divide the NCC into a migratory and a stationary component. The stationary component (fjord cod) spawns inside the fjords and stays within a small geographical area throughout its life span. The migratory component (coastal cod) spawns in the coastal region and makes short migrations along the coastline. However, the migrations of coastal cod are of much smaller scale than the oceanic cod (ANC). The three cod populations are shown within their corresponding geographic region in Fig. 2. The figure is a sketch of the Norwegian coastline including two fjords and marking the outermost islands by the baseline, with the continental
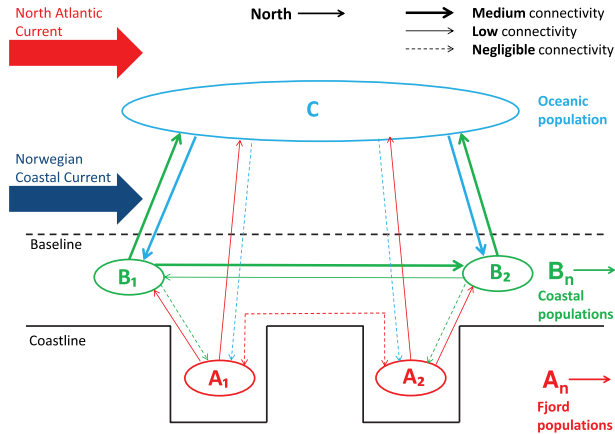
Figure 2: Mixing potential between different cod populations for early life stages.

shelf offshore. The Norwegian Coastal Current and the Norwegian Atlantic Current are the most important dynamic features in this region. The arrows between the subpopulations indicate possible transport routes by early life stages contributing to mixing between the populations. Red lines are transport from fjord cod, green lines transport from coastal cod and blue lines transport from oceanic cod. The line style indicates the magnitude of transport between the corresponding subpopulations; bold lines show medium connectivity, thin lines show low connectivity and dashed lines show negligible connectivity as indicated in the results from the papers in this thesis and the results from Vikebø *et al.* (2005; 2007; 2011).

High retention of early life stages within fjords gives rise to the assumption that fjord subpopulations (A_1, A_2,..., A_n) have low connectivity with the coastal and oceanic populations. In addition, the probability of eggs and larvae to be transported into the neighboring fjord is even less. Combining this information with the knowledge of tagging experiments from fjords showing a small home range for both juveniles and mature adult (Jakobsen, 1987; Espeland *et al.*, 2007; Knutsen *et al.*, 2011), it is very likely that neighboring fjord subpopulations can develop significant genetic differences.

The retention of cod eggs in the coastal zone is weaker than inside the fjords, giving rise to medium connectivity between a coastal cod population (B_n) and the neighboring population to the north (B_{n+1}). However, transport to the neighboring population in the south is lower, due to the northwards flow of the Norwegian Coastal Current. Due to medium retention of coastal cod offspring near the spawning ground,

Table 1: Possible connectivity for early life stages between cod populations.

From **fjord** cod:			From **coastal** cod:			From **oceanic** cod:	
A_n	$\to A_{n+1}$	low/negligible	B_n	$\to B_{n+1}$	medium	$C \to A_n$	negligible
A_{n+1}	$\to A_n$	negligible	B_{n+1}	$\to B_n$	low	$C \to B_n$	medium
A_n	$\to B_n$	low	B_n	$\to A_n$	low/negligible		
A_n	$\to C$	low	B_n	$\to C$	medium		

the possibility for mixing with oceanic cod is also intermediate. Large horizontal mixing caused by meanders and eddies in the coastal current leads to the assumption that the exchange of eggs and larvae between the oceanic and the coastal populations are of the same amplitude. For fjords with considerable freshwater discharge the possibility for pelagic eggs floating at the surface to be transported inwards is negligible, therefore the transport from both coastal and oceanic cod towards fjord cod is negligible.

A structure of separated local cod populations can be sustained through several processes during a cod's life span, besides retention of early life stages as discussed here. After about 5 months of pelagic drift, the juveniles settle to the bottom as they reach a size of 50-80 mm and is named 0-group cod. The juveniles may have specific preferences to habitat selection, time of settling and migration routes. If juveniles choose sheltered fjords instead of exposed coastal banks, the settling strategy will support a local population structure as is observed. As the cod mature they will either migrate towards a distant spawning ground (Godø, 1984) or spawn in the vicinity of their nursery ground (Neat *et al.*, 2006). Svedäng (2010) found no evidence that juveniles remain nearby nursery area in Kattegat, but found clear evidence for non-random migrations towards spawning grounds. Many studies have confirmed that cod possess strong homing, meaning a large percentage returns to the same spawning ground year after year. Svedäng *et al.* (2007a) claims that natal homing is so strong that it is the prime stock-separating mechanism. This generated a discussion on the term 'natal homing', which should include information about dispersal during the ichthyoplanktonic phase not only tagging of juveniles and adults (Bradbury & Laurel, 2007). Showing actual natal homing is particularly difficult for marine species as it requires tracking of individuals from fertilization to spawning or the use of natural natal tags (Svedäng *et al.*, 2007b). Nevertheless, the existence of true natal homing holds the potential to counteract dispersion during early life stages. However, the first choice of spawning ground and the initiation of homing behavior is not well known. Impulse to return to natal spawning ground can be triggered by social transfer of migratory behavior or it is imprinted at early life stages (Svedäng *et al.*, 2007a).

To provide a hypothesis regarding natal homing; I argue that it is unlikely for a single cod to find its way back home to the fjord where it was fertilized, if it was transported out of this fjord during the planktonic phase. However, it is more likely that a cod is able to find its way back to the place where it first settled to the bottom. As the cod migrates from this location it would be able to backtrack the route, which is probably easier than backtracking a passively drifting trajectory. But this would not be valid for the oceanic cod (ANC), spawning in Lofoten and the offspring settles 5 months later in Barents Sea. Therefore, the social transfer of migratory behavior is probably very important for long transport routes (Svedäng *et al.*, 2007a). If the homing behavior is not imprinted in the early life stages, a larvae from a fjord spawning population that is transported out of the fjord will become a coastal or an oceanic cod. The large oceanic population then acts as sink where all individuals not adapted to the fjord environment ends up, and will then develop considerable genetic diversity. The oceanic population has proven to be resilient against heavy fishing pressure and through climate variations, and is currently in good conditions partly due to good management. The fjord cod population is more specialized, which means they are adapted to the local environment and susceptible to external changes.

There has been many speculations regarding the reasons for the decline of the Norwegian Coastal cod population (Aglen *et al.*, 2011), especially high fishing intensity has caused a major decrease in local populations. In addition, the human impact on the coastal marine environment has increased through expanding aquaculture, mining and hydroelectric power production etc. This means that there is a spatial conflict as the human impact in the fjords increases. It is therefore probable that the recruitment failure of NCC is caused by the total effect of anthropogenic influence in the coastal zone.

4 Future perspectives

In modeling studies, such as the papers in this thesis, it is always important to evaluate the model results against observations. However, the comparison is challenging due to scarcity of observations both in time and space. A limited number of CTD stations is available from a limited number of Norwegian fjords and mainly from the summer and autumn seasons. The cod spawning season occurs during March and April, when there are hardly any observations. A comprehensive survey early in spring is needed to form basis for a good model evaluation. Such a survey should include CTD stations in all of the fjord branches, current measurements, egg sampling and buoyancy measurements.

Especially the egg sampling should be repeated through the spring in order to investigate the spawning season of fjord cod. The spawning season of oceanic cod (ANC) has been thoroughly explored but field data is missing for coastal and fjord cod. Especially since it is hypothesized that fjord cod has adapted its spawning behavior to the local environment (Otterå *et al.*, 2006).

Related to model evaluation, the model results from Helgeland in Paper IV is probably limited by the boundary conditions obtained from a 4 km model. The optimal setup would be to run the entire Norwegian coast with 800 m horizontal resolution. This still requires more computational resources but will probably become manageable soon. This will improve the representation of the Norwegian Coastal Current in the northern part of Norway, and also improve the boundary conditions to the fjord models.

Through the years many papers have investigated genetic differences between oceanic (ANC), coastal (NCC) and fjord (NCC) cod populations without being able to come to any conclusions (Nordeide *et al.*, 2011). As new techniques emerge, it will soon be possible to map the whole DNA sequence of cod which hopefully bring the research field towards a consensus regarding populations dynamics of cod. Concerning gene flow, the results from this thesis show that transport of early life stages from fjord cod to coastal and oceanic cod is much more likely than the opposite way.

The model simulations in this thesis include only specific years, and it would be especially interesting to expand the work to include several years. In such a way it would be possible to study the interannual to decadal variability of transport of cod eggs. In addition it will soon be possible to do regional downscaling of future climate scenarios as the next generation of climate models for the IPCC Fifth Assessment Report is available.

Paper III in this thesis shows that the environmental differences caused by river regulations may be considerable. These kind of changes have occurred gradually because the power stations were not all built at the same time, and therefore the changes might have been masked by other processes happening at the same time. More research is needed to investigate these changes further, in particular through comparison with observations during winter/spring and including impact studies on primary production, zooplankton abundance and fish recruitment. These kind of studies should be performed in several fjords to ensure that the observed effects is not caused by local conditions.

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