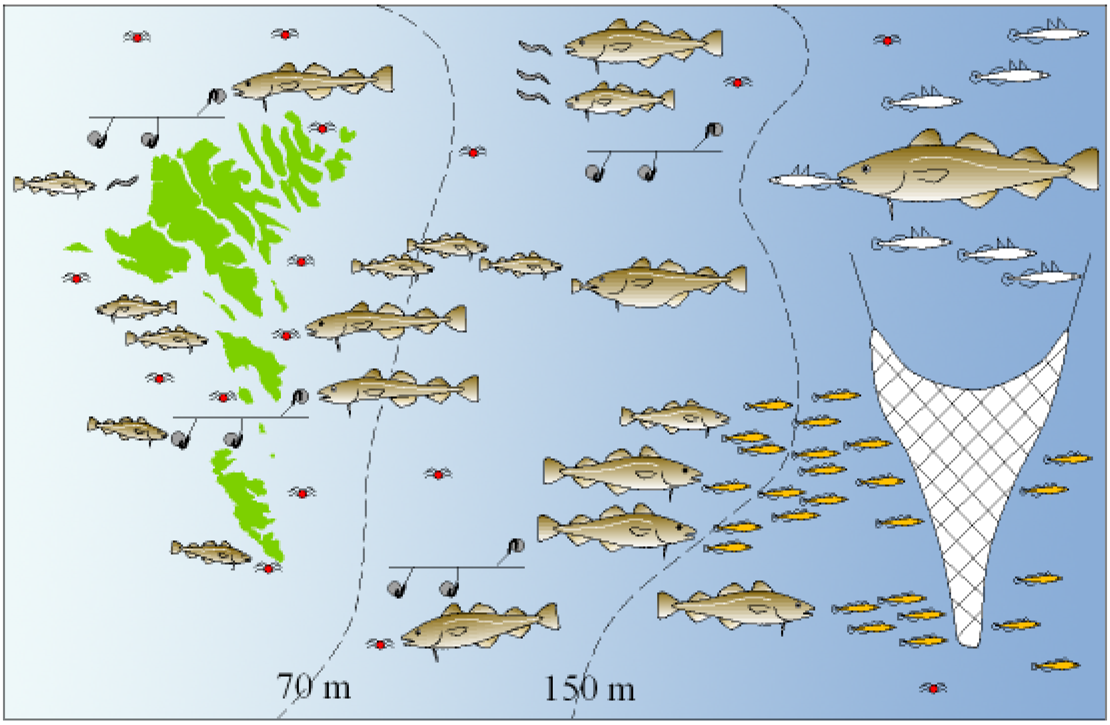
# The near-collapse of the Faroe Plateau cod (*Gadus morhua* L.) stock in the 1990s: The effect of food availability on spatial distribution, recruitment, natural production and fishery

**Petur Steingrund**



**Dr. Philos. thesis**

Department of Biology
University of Bergen
Bergen, Norway
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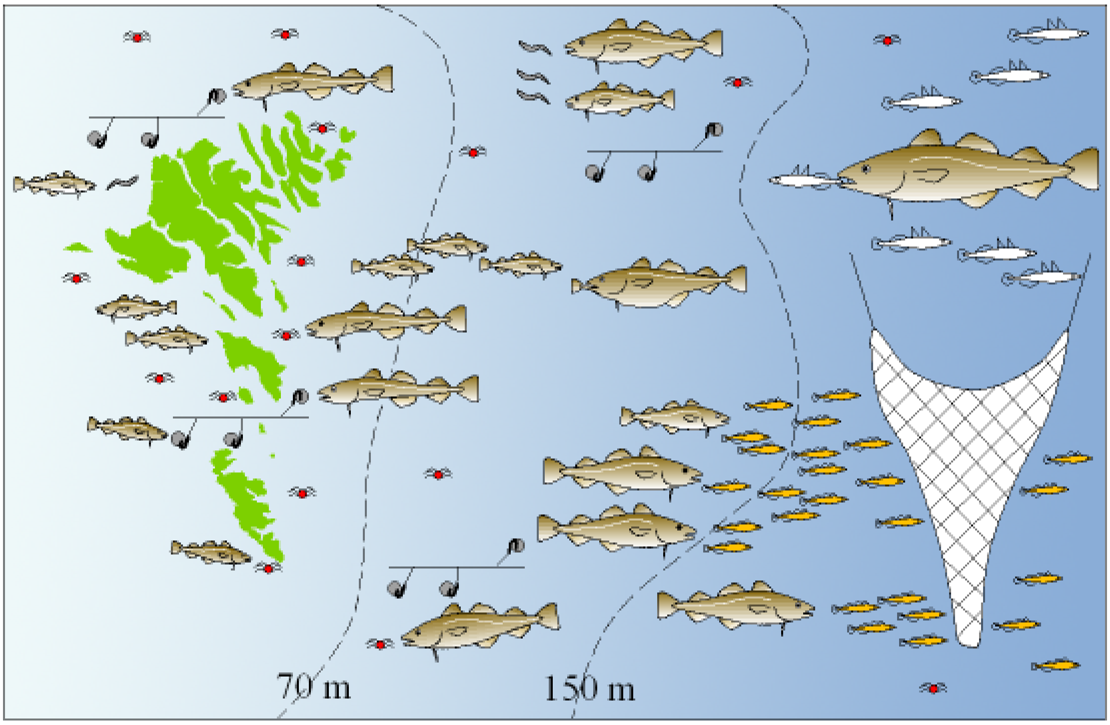

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# Contents

## Acknowledgements

I grew up in a home where fish and fisheries were a daily theme of discussions. My father, Julius Steingrund, is a former fisherman and skipper and had fished at the Faroes, Iceland and Greenland during the period from 1945-1973. Then he went on land and worked in quality control on the local fish factory, P/F Lynfrost, in Runavík, Faroe Islands. He retired in 2007 at the age of 80 years. I began to work in the factory during my summer vacation from the school in 1979 when I was 14 years old. I worked in the fish factory during the summertime in 1980-1983 and for one whole year from the summer of 1984 to the summer of 1985.

My late mother, Kristina Steingrund, encouraged me throughout all my childhood to take an education in biology. In 1985, I went to Bergen, Norway, to study at the University of Bergen. My 'career' in fisheries biology began when I went to the Department of Fisheries Biology to find out whether I should take a master's degree in fisheries biology. The very pleasant meeting with Gunnar Nævdal and Olav Dragesund resulted in a five-year-long study on cod behaviour under the supervision by Anders Fernö.

After I completed my master's degree in 1993, I moved back to my home country, the remote Faroe Islands, which are barely visible on the map and located between Iceland, Scotland and Norway. After teaching biology and chemistry for two years, I began work at the Faroese Fisheries Laboratory (FFL). This period was characterised by many unresolved questions and 'mysteries' surrounding the Faroe cod. The stock size of cod had been exceptionally low during 1991-1994, but suddenly, in 1995-1996, they were plentiful again, and nobody was able to give any answer, how this could happen so quickly. My director, Hjalti í Jákupsstovu, handed me the task of resolving this issue. Neither one of us had any idea of the work that would need to be done in order to solve the the multitude of mysteries facing us.

During one of my first cruises with the research vessel, *Magnus Heinason*, I began to analyse cod stomachs. This was not done for a number of years. I soon discovered that cod in deep waters had much larger stomach content than cod in shallow waters. I went up to the skipper and told him my findings and asked him why more cod did not move to deeper waters. I expected a thorough answer from this very experienced man, but got instead this answer: 'This is what you are supposed to find out'.

Parts of the work have been supported by grants from Føroyagrunnurin, Eik banki and Føroya Banki – which is especially acknowledged. My thanks also go to my director, Hjalti í Jákupsstovu, for giving me the best circumstances to do my job and to all the staff on FFL and on the research vessel – nobody mentioned and nobody forgotten. Also thanks to Dánjal Petur Højgaard for many inspiring discussions. Thanks to Vilhjálmur Thorsteinsson for all his kindnesses and for showing me the very interesting results from the Icelandic Data Storage Tags. Special thanks to Anders Fernö for his inspiring input and discussions. My warmest thanks go to my wife, Tórunn, for her great support and to our three lovely children.

# Abstract

1. This thesis aims to explain why there was a near-collapse of the Faroe Plateau cod stock in the 1990s and why it recovered so quickly. Contrary to what local people on the Faroes believe, these fluctuations were not explained by large-scale migrations between, e.g., Icelandic and Faroese fishing grounds, but rather by local processes on the Faroe Plateau. When cod were in poor condition they moved towards land and hampered the survival of 1-year-old cod, probably by displacing 1-year-old cod to normal cod-depths where they were cannibalised. The survival of 2-year-old cod was, however, positively correlated with the total contemporary biomass of age 3+ cod, probably caused by reduced predation mortality or enhanced foraging, up to an abundance of around 100 thousand tonnes of age 3+ cod, above which there was a sharp decline.

2. There was no negative correlation between the stock size of cod and the individual growth rate. Cod seemed to be reluctant to enter the food-rich deep waters (> 150 m) indicating that the shallower areas had to be ‘filled up’ first before cod moved to deep waters. Cod in shallow waters fed on sandeels, juvenile Norway pout and benthic crustaceans, whereas cod in deep waters mostly fed on adult Norway pout and Blue whiting. Cod in good condition tended to have a larger stomach content than slim cod, and, in deep waters, there was a positive correlation between feeding success and local cod density.

3. Cod tended to be caught on longlines when in poor condition, coinciding with a low feeding on natural prey organisms and a more pronounced feeding migration. Hence, the total fishing mortality, which was overall very high, tended to vary negatively with the individual growth rate.

4. The information in 1-3 indicated that a low ecosystem productivity during the late 1980s combined with a high fishing mortality were the main reasons why the cod fishery nearly collapsed in the 1990s. The recovery was likely caused by favorable environmental conditions and a low fishing mortality. A simulation study strongly suggested that the cod fishery on the Faroe Plateau is **not** sustainable and that the stock will probably collapse in the future. An immediate reduction of the fishing mortality of 40-60% could reverse the negative trend and result in an optimal harvesting. However, the common belief among Faroese fishermen / local people in the existence of large-scale migrations of fish, and a reluctance to accept short-term reductions in catch rates, may represent major obstacles in rebuilding the Faroe Plateau cod stock.

## Extended abstract

Annual cod catches at Faroes fluctuated regularly between 20 and 40 thousand tonnes for almost a century (except during the Second World War). The collapse of the cod fishery in 1990-1994 was neither foreseen by fisheries scientists nor local people. When the collapse was recognised as a fact, fisheries scientists predicted a slow recovery of the cod stock. The cod stock on Faroe Plateau, however, had fully recovered already by 1996 after only three years. The scientific advice relied on the assumption that recruitment of young fish to the fishery was dependent upon spawner abundance and that year class strength was determined during the pelagic larval phase in accordance with traditional views on cod recruitment processes. The mismatch between the scientific advice and the observed development of the cod stock caused a crisis in many respects. The collapse in the cod fishery contributed to a national economic crisis in the Faroes. At the same time, there was a credibility crisis between the advisory bodies (ICES, Faroese Fisheries Laboratory) and the fisheries managers/local people.

This thesis attempts to provide answers to the many questions that arose in connection with the collapse of the cod fishery. Several new investigations were initiated. A time series on phytoplankton production was initiated in 1990 and stomach content investigations of cod, haddock and saithe and a tagging program of cod were initiated in 1997. In addition, logbook data from Faroese longliners and trawlers were analysed.

A clue about a cause for the fluctuations in the cod stock was obtained in the late 1990s when a positive correlation was found between phytoplankton production and recruitment/growth of cod and haddock. This thesis presents additional information about the effect of the phytoplankton production on the behaviour and population dynamics in Faroe Plateau cod. The traditional view that cod recruitment was determined at the pelagic larval stage had to be abandoned, since no relationship was found between 0-group indices and subsequent recruitment to the fishery. The basic feature seemed to be food availability and feeding behaviour in cod. Cod in Faroese waters fed upon benthic crustaceans and fish with the proportion of fish increasing with increasing cod size. The stomach content was two times greater in deep waters (> 150 m), which reflected the high availability of prey (Norway pout and Blue whiting) in deep waters on Faroe Plateau. Cod in good condition had around 70% more food in their stomachs than cod in poor condition. There was also a positive correlation between stomach content of fish (Norway pout and Blue whiting) and cod density during the feeding season.

Food availability had a marked influence on the migration pattern of cod. Cod showed a strong fidelity towards both spawning and feeding areas. Cod spawned in three locations on the Faroe Plateau in during March to mid April. After the return to the feeding areas in April-May, the cod in poor condition selected shallower waters and *vice versa*. Cod in good condition were presumably better to catch deeper located mobile fish (Norway pout). Cod in poor condition seemed to move to shallower waters to feed on benthic organisms.

The movement of cod into shallow waters had a pronounced negative effect on the survival of juvenile (1-year-old) cod during the summertime and subsequent recruitment to the fishery the following year. Cod moving into the nursery areas of 1-year-old cod close to land either predated directly on juvenile cod or displaced them to deeper areas where they were cannibalised. The interannual variability in recruitment 1984-2006 was rather precisely (R-square > 0.8) explained by $R = aB/C + d$. That is, recruitment of 2-year-old cod (R) was directly proportional to the total stock biomass (B) and inversely proportional to the abundance of cannibalistic cod (age 3+) close to land (C) adjusted by a small constant (‘d’). B is the *contemporary* biomass of age 3+ cod at the time of

recruitment to the fishery (as 2 year-olds) and not the spawning stock two years before. B is thus a highly untraditional measure for stock size in stock – recruitment relationships. The effect of B seemed to level off when the age 3+ biomass exceeded 100 thousand tonnes, and turned into a negative relationship for larger stock sizes. For most years, the dynamics of R was dominated by the large variations in C, but B became important when stock sizes were extremely low, as now in 2008. Cod tend to be in shallow waters when stock sizes are extremely low and the model predicts extremely poor future recruitment unless food availability increases considerably (high phytoplankton production) causing cannibalistic cod to move out from land. How B affects recruitment requires future research. B seemed be a proxy for general group benefits (more efficient feeding or predation avoidance) rather than a proxy for fecundity or spawning success.

Recruitment and subsequent individual growth are the cornerstones in natural production in cod (numbers x individual growth). A close positive relationship was found between phytoplankton production and production in cod. Two main ecological pathways were suggested: (1) phytoplankton – zooplankton – zooplanktovorous fish – cod, and (2) phytoplankton (sinks to the bottom) – benthic decompositors – benthic crustaceans – cod. Cod were in both cases in the fourth trophic level. The relative contribution of the two pathways was not investigated. The relationship between phytoplankton production and cod production was hypotesized to be so strong because of the great variation in phytoplankton production. The variation in the cod fishery in the 1980s and 1990s could thus be explained by the link between phytoplankton production and cod production, but the cod production since 2000 seemed also to be influenced by low stock sizes and impared recruitment.

The feeding in cod also influenced strongly the fishing mortality. Between 30 to 65% of the total cod catches were taken by longliners in shallow waters with the rest taken by trawl deeper than 150 m. The variation in fishing mortality seemed to be linked to the catchability with longlines, i.e. slow growth – high catchability with longlines, and no migration between shallow and deep waters. The situation for cod was either ‘good’ or ‘bad’, i.e., high recruitment and growth and low fishing mortality when phytoplankton production was high and *vice versa*. The production of cod on Faroe Plateau, i.e. subsequent catch, is optimized by keeping the stock size high, which leads to the highest long-term recruitment of cod and the best utilization of the rich deepwater fish resources.

The main findings for Faroe cod may be summarised in this way: When ecosystem productivity is low (low food availability), cod will grow slowly and be in poor condition and distributed in shallow waters where cod with poor swimming ability feed inefficiently on slowly-moving benthic crustaceans, are caugth by longlines, and predate on/displace juvenile cod, which in turn leads to poor recruitment. In contrast, when ecosystem productivity is high, cod will grow fast, be in good condition and distributed in deeper waters where they feed efficiently on fast-moving fish, are caught by trawl, and interfere little with juvenile cod, which gives good recruitment if the concurrent stock size of cod is high enough.

The ‘mysterious’ development of the Faroe Plateau cod stock in the 1980s and 1990s may be summarised as follows. The immigration/emigration rate of cod between, e.g., Icelandic and Faroese waters is less than 1 out of 1000, and the stock development of Faroe Plateau cod must then be explained in terms of the local conditions. In the period 1988-1992, the phytoplankton production on the Faroe Shelf (< 130 m depth) was likely very low, causing exceptionally low recruitment and growth of cod. The productivity in the deeper areas was presumably also exceptionally low. The high phytoplankton production in 1993-1995 led to extraordinary good recruitment and rapid growth. The rapid ‘build-up’ of cod was, however, not detected at once by the fishery in 1994. Cod had not yet entered the deep waters (> 150 m) where the trawlers operated and the catchability with longlines in shallow waters was low because of high availability of natural food. In 1996, the phytoplankton production index was low which led to a reduced food availability and an increased catchability with longlines. At the same time, cod from the strong 1992- and 1993 year-classes had entered the deep waters in great numbers. The combined effect of a high abundance and high catchability, for both longlines and trawl, presumably caused the cod catches to increase spectacularly in 1996. This was incorrectly interpreted as a large-scale immigration of cod from foreign areas by the local population.

The findings for Faroe cod were also put into a larger perspective. The recruitment model is, to my knowledge, one of the most precise recruitment models for any cod stock in the North Atlantic. It is in sharp contrast to traditional views on cod recruitment where the link between spawning stock biomass – survival of pelagic larvae – and subsequent recruitment dominates. The distribution pattern of Faroe cod, moving towards land when food availability was low, seems to be a new finding. It is in contrast to the common 'rule' that cannibalism is proportional to year-class strength, i.e., large year classes have a wide spatial distribution and a high overlap with adult cod resulting in increased cannibalism. It is argued that also year-class strength in other cod stocks could be determined later than the 0-group stage and that cod distribution is a crucial factor.

In contrast to some other cod stocks, cod on the Faroe Plateau were generally distributed shallower than the bulk of potential food organisms and this mismatch is crucial. The spatial distribution of adult cod was viewed as an outcome of larval drift/settlement – a result of spawning location and ocean currents – and subsequent redistribution of juvenile/adult cod. There is presumably an 'inertia' in the redistribution because cod may need to adapt to other prey/predators and temperatures/depths. Such combined niche/habitat shifts were probably hampered by short term factors such as lack of information, behavioural adaptations to novel prey/predators and swimbladder physiology. Long-term factors, such as morphological changes in, e.g., muscle cells and metabolic pathways, as well as genetic factors are discussed.

A novel, and yet poorly established finding, was that large-scale hydrographical conditions (the strength of the North Atlantic Subpolar Gyre) affected ecosystem productivity over the deep (> 150 m) areas on the Faroe Plateau, i.e., that a weak gyre (high 'gyre index') leads to rich food availability. The Subpolar Gyre probably also effected the areas east of Newfoundland. There seemed to be a negative relationship between primary production on the Faroe Shelf and the gyre index since 1960. A notable exception occurred during 1988-1992 when both indices were low and presumably caused the 'near collapse' in the Faroe Plateau cod stock. While the stock development of Faroe Plateau cod during the 1980s, 1990s and 2000s was adequately described by processes acting on top of ecosystem productivity, the fluctuations in ecosystem productivity (inner and outer areas) seems to represent the next challenge.

The Faroe Plateau cod may now experience a collapse with the lowest stock size for 100 years. A simulation study shows that the cod fishery on the Faroe Plateau is not sustainable and that the cod stock may collapse in the future. An immediate reduction of the fishing mortality of 40-60% could reverse the negative trend and result in an optimal harvesting.

## Extended abstract in Faroese – samandráttur á føroyskum

Toskaveiðan undir Føroyum lá støðugt millum 20 túsund og 40 túsund tons í nærum eina øld (uttan undir seinna heimsbardaga). Tá toskaveiðan fór heilt niður um 10 túsund tons fyrst í nítiárunum kom tað sum ein skelkur bæði fyri fiskifrøðingar og fólk annars. Tá tað varð staðfest, at toskastovnurin var sera illa fyri fyrst í nítiárunum, varð hildið fyri vist, at tað fór at taka langa tíð at byggja hann uppaftur. Kortini gingu bert umleið trý ár til toskastovnurin var í hæddini í 1996. Fiskifrøðiliga ráðgevingin bygdi á ta áskoðan, at tilgongdin var tengd at støddini á gýtingarstovninum og at árgangsstyrkin var avgjørd longu tá toskaynglið var uppi í sjónum, nakað sum var í samsvari við vanliga fiskifrøðiliga áskoðan. Munurin millum ráðgevingina og veruleikan førdi á mangan hátt til eina kreppu. Fiskaloysið virkaði við til eina fíggjarkreppu í Føroyum. Samstundis misti fólk trúvirðið á ta fiskifrøðiligu ráðgevingina.

Henda ritgerð roynir at svara teimum mongu spurningunum, sum stungu seg upp í sambandi við fiskaloysið. Nógvar nýggjar kanningar vórðu settar í verk. Ein kanning av gróðri varð sett í verk í 1990, og magakanningar av toski, hýsu og upsa, og ein merkingarroynd við toski vóru settar í verk í 1997. Haraftrat vórðu skipsdagbøkur frá føroyskum línuskipum og trolarum kannaðar.

Síðst í nítiárunum kom ein greið ábending um, hví toskastovnurin hevði uppført seg so løgið í nítiárunum. Eitt greitt positivt samband varð funnið millum gróður í sjónum og tilgongd/vøkstur hjá toski og hýsu. Henda ritgerð viðger víðari ta stóru ávirkan, sum ein ójavnur gróður hevur á atferð hjá toski og eisini sveiggini í toskastovninum. Tann siðbundna fiskifrøðiliga áskoðanin, at árgangsstyrki hjá toski er avgjørd longu sum larvur, mátti vrakast, tí einki samband varð funnið millum yngultøl og árgangsstyrki hjá toski. Nøgd av føði og atferð hjá toski vístu seg at hava grundleggjandi týdning. Magakanningarnar vístu, at toskur át krabbadýr og fisk, og at parturin av fiski øktist so hvørt sum toskurin vaks. Stórur munur var millum grunn og djúp (> 150 m) økir, har magainnihaldið var tvær ferðir størri, og komst tað av teirri stóru mongd av hvítingsbróðri og svartkjafti. Feitur toskur át umleið 70 % meira enn slánar. Eisini var meira av fiski (hvítingsbróðri og svartkjafti) í maganum hjá toski, sum varð fingin í "stórum hálum" í august.

Nøgd av føði hevði stóra ávirkan á ferðingina hjá toski. Toskurin var støðufastur, bæði tá tað galt gýtingarøki og føðsluøki (har toskur livir, tá hann ikki gýtir), soleiðis at tann einstaki toskurin brúki sama gýtingarøki og sama føðsluøki ár undan ári. Toskur gýtti á trimum økjum (á Norðhavinum, vestan fyri Mykines og í Sandshavinum) í mars-miðjan apríl, og eftir at hann varð farin "heimaftur" í apríl-mai, valdu slánar at fara á grunt vatn og øvugt. Feitur toskur var helst betri førur fyri at fáa fatur á skjóttsvimjandi fiski so sum hvítingsbróðri. Raktoskur fór møguliga grynri fyri at eta botndýr.

Ferðingin hjá slánum móti landi hevði heilt greitt eina ringa ávirkan á yvirliving hjá 1-ára gomlum smáfiski um summarið og harvið tilgongd til fiskiskapin árið eftir. Annaðhvørt ótu slánarnir smáfisk nær landi ella eisini stygdu slánarnir smáfiskin út á djúpari vatn, har teir vórðu etnir av toski. Til bar at rokna tilgongdin av toski (1984-2006) neyvt út eftir hesum frymli: $R = aB/C + d$. Hetta vil siga, at tilgongd av 2 ára gomlum smáfiski ($R$) stóð í einum beinleiðis sambandi við samlaða toskastovnin ($B$) og í einum øvugtum sambandi við tosk nær landi ($C$), og justerað við einum lítlum konstanti ($d$). Legg til merkis, at $B$ er tann verandi biomassin av trý ára gomlum toski og eldri, tá smáfiskarnir (2 ára gamlir) koma inn í fiskiskapin og ikki gýtingarstovnurin tvey ár áðrenn. $B$ er harvið eitt sera óvanligt mát at seta í samband við eina komandi tilgongd. Ávirkanin av $B$ á tilgongd flataði út, tá biomassin av trý ára gomlum toski og eldri fór upp um 100 túsund tons, og gjørdist negativ, tá stovnurin var enn størri. Vanliga var tað broytingar í $C$, sum avgjørdu gongdina í $R$ í størstan mun, men $B$ gjørdist týdningarmikið, tá toskastovnurin var sera illa fyri, eitt nú í 2008. Við tað at toskur hevur lyndi til at halda seg grunt, tá lítið er til av honum, sigur frymilin, at tilgongdin í framtíðini kann gerast sera vánalig, um ikki gróðurin í sjónum økist munandi og toskurin fer út frá landi. Júst hvussu B ávirkar tilgongd má kannast nærri í framtíðini. B sær út til at vera eitt mát fyri bólkafyrimunir í breiðari merking (toskur fær fatur á meira føði í felagsskapi og er ikki so útsettur fyri rovdjórum) heldur enn eitt mát fyri væleydnaða gýting.

Tilgongd og vøkstur hjá toski avgera náttúrliga framleiðslu hjá toski (tal av toski faldað við vøkstri hjá tí einstaka toskinum). Eitt tætt samband varð funnið millum gróður í sjónum og framleiðslu av toski. Orkan frá gróðrinum (plantuplankton) kundi fara til tosk tveir vegir: (1) plantuplankton – djóraplankton – fiskur – toskur, og (2) plantuplankton (søkkur á botn) – niðurbrótarar á botni – krabbadýr á botni – toskur. Toskur var í báðum førum í fjórða liði í føðiketuni. Tað varð ikki kannað, hvør av hesum vegum var meira týdningarmikil. Sambandið millum gróður og tosk var so greitt, tí gróðurin var so ójavnur ár undan ári. Av stórum týdningi var hetta, at sveiggini í toskastovninum í áttati og nítiárunum fylgdu gróðrinum. Men kortini var tann náttúrliga framleiðslan av toski eftir ár 2000 minni enn gróðurin bendi á, og kom tað helst av, at tilgongdin av toski var darvað av teirri lítlu toskanøgdini.

Nøgd av náttúrligari føði hevði eisini eina stóra ávirkan á veiðitrýstið á tosk. Legg til merkis, at “veiðitrýst” í fiskifrøðiligari merking ikki sigur nakað um nøgd av skipum ella húkum í sjónum, men bert, hvussu *lutfallið* er millum veiðu og stovn. Føroyski fiskiskapurin er í stuttum soleiðis, at millum 30 og 65 % av toskaveiðuni kemur frá línuførum, sum royna grynri enn 150 metrar, meðan restin kemur frá trolarum, sum royna djúpari. Veiðitrýstið á tosk var tengt at veiðievnunum hjá línu soleiðis at toskur tók línu í størri mun, tá hann vaks seint, og øvugt, og hetta kom ikki av eini ferðing millum djúp og grunn økir. Harvið hevði toskurin annaðhvørt “góð” ella “ring” ár. Tey góðu árini var nógv til av føði og bæði tilgongd og vøkstur vóru góð og øvugt. Tann náttúrliga framleiðslan av toski á føroyska landgrunninum, tvs. langtíðar veiða, er størst, tá toskastovnurin verður hildin stórur, sum førir til ta størstu langtíðar tilgongdina av toski og frægast ger brúk av teimum stóru nøgdunum av føði á djúpum vatni.

Úrslitini í hesi ritgerð viðvíkjandi toski undir Føroyum kunnu heilt stutt samanfatast soleiðis: Tá lítið er til av føði (vegna vánaligan gróður í sjónum) veksur toskur seint, er klænur og heldur til á grunnum vatni. Hann svimur seint og roynir eftir besta førimuni at eta krabbadýr, og hann tekur ofta línu. Slánarnir nær landi hava eina ringa ávirkan á livilíkindini hjá smáfiski og tilgongdin verður tí ring. Tá nógv er til av føði er støðan tann beint øvugta. Toskur veksur skjótt, er væl fyri, og fer út frá landi at eta hvítingsbróður og nebbasild. Toskurin verður í størri mun fingin í troli og hann hevur ikki ringa ávirkan á smáfisk. Hetta gevur góða tilgongd undir teirri fortreyt, at nóg nógv er til av vaksnum toski.

Tann markháttliga gongdin í føroyska toskastovninum í áttati- og nítiárunum kann samanfatast soleiðis. Ferðingin hjá toski millum havumráðir er so lítil (umleið 1 av 1000), at hon ikki ávirkar føroyskan tosk stórvegis, og tí má útgangsstøði takast í viðurskiftunum á føroyska landgrunninum. Í 1988-1992 var gróðurin í sjónum (< 130 m dýpi) sera vánaligur, sum førdi til sera vánaliga tilgongd, lítlan vøkstur og harvið sera lítlan toskastovn. Tað eru eisini ábendingar um, at sera lítið var til av føði á teimum ytru leiðunum. Gróðurin var góður í 1993-95, sum førdi til serstakliga góða tilgongd og vøkstur hjá toski. Menn varnaðust tó ikki tær stóru nøgdirnar av toski beinanvegin (í 1994). Toskurin var ikki enn farin út á tær djúpu leiðirnar (> 150 m), har trolararnir vóru, og línan á grunnum vatni fiskaði illa, tí nógv var til av náttúrligari føði hjá toski. Í 1996 var gróðurin vánaligur, sum førdi til smærri nøgdir av føði hjá toski og at línan nú fór at fiska væl. Harumframt vóru árgangirnir frá 1992 og 1993 at finna á djúpum vatni, har trolararnir royndu. Hetta gjørdi alt, at veiðan í 1996 gjørdist størri, enn nakar hevði droymt um frammanundan. Fólk hildu tað vera eina innrás av toski frá øðrum havumráðum enn tí føroyska.

Granskingarúrslitini fyri føroyskan tosk vórðu eisini sett í eitt størri høpi. Frymilin viðvíkjandi tilgongd av føroyskum toski er, mær kunnugt, ein tann neyvasti fyri toskastovnar í Norðuratlantshavi yvirhøvur. Frymilin er í sterkari andsøgn til siðbundna fiskifrøðiliga hugsan um tilgongd av toski, har mesti denturin verður lagdur á sambandið millum gýtingarstovn – yvirliving hjá toskalarvum – og tilgongd til fiskiskapin nøkur ár seinni. Tað, at toskur fer nær landi, tá hann er rak, er helst eitt nýtt og annars ókent fyribrigdi. Tað stendur í andsøgn til ta vanligu "regluna" um, at kannibalisma fylgir árgangsstyrki hjá toski, tvs. at stórir árgangir eru meira spjaddir og harvið í størri mun blandast við størri tosk og verða etnir. Ritgerðin rør framundir, at árgangsstyrki hjá øðrum toskastovnum væl kann hugsast at verða avgjørd seinni í lívinum enn fyrsta liviár og at útbreiðslan hjá toski má takast við, tá metast skal um árgangsstyrkina.

Mótvegis øðrum toskastovnum helt toskur á føroyska landgrunninum seg vanliga grynri enn føðin, og hesin ójavni hevur avgerandi týdning. Útbreiðslan hjá toski var sædd sum eitt úrslit av, hvar toskaynglið tekur botn – veldst um gýtingarøki og havstreymar – og hvussu toskurin síðan broytir sína útbreiðslu gjøgnum lívið. Tað er helst ein "trekleiki" í hesi broyting av útbreiðsluøki, tí toskur noyðist at laga seg til aðra føði/rovdjór og annan sjóvarhita/dýpi. Tað, at fara á nýggjar leiðir kann vera tarnað av viðurskiftum so sum manglandi vitan, tillaging í atferð til annan fong og rovdjór og viðurskifti viðvíkjandi sundmaganum. Langtíðar tillaging so sum broytingar í t.d. vøddakyknum og stoffskiftisringrásum, umframt arvalig viðurskifti, eru eisini viðgjørd í ritgerðini.

Ógvuliga nýggj og fesk granskingarúrslit vórðu tikin við í ritgerðina. Tað snúi seg um, at viðurskifti í havstreymum sunnan fyri Føroyar høvdu ávirkan á føðina hjá toski á djúpum vatni (> 150 m). Tá tann "subpolari meldurin" er lítil (stórt "meldurvísital"), er nógv til av føði og øvugt. Sama fyribrigdi tykist vera galdandi fyri leiðirnar eystan fyri Newfoundland. Í føroyskum øki var tað tó eitt øvugt samband millum meldurvísitalið og gróðurin í sjónum á innaru leiðum (< 130 m dýpi) eftir 1960. Eitt undantak var tó í tíðarskeiðnum 1988-1992, tá bæði vísitølini vóru lág og førdi hetta helst til fiskaloysið fyrst í nítiárunum. Gongdin í toskastovninum við Føroyar kann greinast væl, bara ein veit, hvussu føðslunøgdin er á grunnum og djúpum vatni við føroyar. Fyri at skilja sveiggini í fiskiskapinum við Føroyar enn betri, er tað næsta stigið at skilja betri, hví føðslunøgdin á innaru og ytri leiðum (árligar broytingar í gróðri og meldurvísitali) sveiggjar soleiðis, sum hon ger.

Tað er ein møguleiki fyri, at eitt toskaloysi kann koma á føroyska landgrunninum, tí toskastovnurin nú í 2008 helst er hin minsti í 100 ár. Útrokningar vísa, at toskafiskiskapurin á føroyska landgrunninum er ikki burðardyggur og at toskastovnurin kann fara niður í einki í framtíðini. Ein bráfeingis niðurskurður í veiðitrýstinum á 40-60 % kann venda gongdini og føra til eina burðardygga veiðu.

# Introduction

## Philosophy of this thesis

Many phenomena in biology are complex and related to many factors. Furthermore, these factors may change over the course (time span, spatial range, or level) of the phenomenon in question. In addition there may be correlated phenomena that may make it difficult to distinguish causes and effects.

Fish recruitment is a good example. Year-class strength, and subsequent recruitment to the fishery, varies considerably year to year and several factors may affect recruitment variability. Some obvious, almost axiomatic, factors are the size of the spawning stock and food availability for first-feeding larvae, but additional survival bottlenecks may be found during the demersal O-group stage or as juveniles. Year-class strength will ultimately be a result of 1) survival through all these bottlenecks, 2) the relative importance of each bottleneck, and 3) which crucial factors are involved, which may vary between cod stocks / ecosystems. Furthermore, the importance of survival bottlenecks/factors may depend upon the size of the cod stock (decimated or not). There may, in addition, be correlated phenomena. For example, higher-than-average temperatures in cold waters affect recruitment positively, but it is difficult to tell whether it is a direct effect of temperature *per se* or an indirect effect of higher food availability (Ottersen and Loeng, 2000).

When predicting future year-class size, it may be a risky approach to rely on only a few indicators, as illustrated for Faroe Plateau cod. Only spawning stock biomass and O-group indicies were monitored during the 1970s-1980s. There seemed to be a positive relationship between spawning stock biomass and O-group indices and also a positive relationship between O-group indicies and subsequent recruitment. This indicated that year-class strength was determined at the pelagic O-group stage, which was in line with traditional theories and findings. Satisfaction with the the current state-of-the-art was probably the reason why no alternative life stages or factors were investigated. In the second half of the 1980s, the spawning stock was high and there were quite high O-group indices. It was predicted that the future for the cod stock looked bright, but instead the cod stock fell dramatically and contributed to a serious national economic crisis in the Faroes. Realising the misleading advice and the low state of the cod stock, as well as the low O-group indicies in 1991-1993, the scientific advice for the mid-1990s became very pessimistic. However, the cod stock showed a marked recovery and was apparently in excellent shape by 1995-1996. This caused a serious credibility crisis between local people / fisheries managers and the advisory bodies (ICES and the Faroese Fisheries Laboratory).

The Faroe cod example shows that the quality of the advice may become very poor when too few indicators are considered. Therefore, several new investigtions were initiated in the 1990s under the new philosophy that different angles and datasets had to be explored in order to understand and predict the development of the cod stock. The present thesis is a result of, and complies with, the new philosophy.

# Cod in general

## Evolution and distribution during palaeontological time

The spatial separation of the Atlantic and Pacific Ocean during palaeontological time has had a great influence upon the evolution of cod. Of special importance is the fact that the Atlantic and Pacific Ocean have been connected a few times (the Bering Sea was open and the Arctic was free of ice), allowing fish to migrate between them. Both Atlantic cod (*Gadus morhua*) and Pacific cod (*Gadus macrocephalus*) descend from an Atlantic lineage that invaded the Pacific at least 3.5 million years ago. An Atlantic lineage invaded the Pacific a second time some 2 million years ago which led to the evolution of the morphologically distinct Alaska pollock (*Theragra chalcogramma*). A Pacific lineage invaded the Atlantic during the last interglacial period, ca. 100 thousand years ago, founding the Greenland cod (*Gadus ogac*), who is better suited to the cold Arctic climate than either Pacific cod or Atlantic cod (see Bigg *et al*., 2008, and references therein).

The Last Glacial Maximum, ca. 21 thousand years ago, was one of the coldest events during the Quaternary period. The global sea level fell by 120-135 m, and the advance of ice sheets into the Polar regions, as well as frequent invasions of icebergs causing abrupt climate changes and extensive shelf floor scouring, made most continental shelves in the North Atlantic inhabitable for cod (see Bigg *et al*., op. cit., and references therein). For example, the North Sea and the Baltic Sea were inhabitable, as well as the Norwegian coast and the Barents Sea. The viable places for cod were located in a narrow strip along the European shelf extending into the Bay of Biscay. Importantly, the areas around the Faroes and South-Iceland were then viable places for cod. In the Northwest Atlantic, the viable places were located in a narrow strip from Newfoundland to the Gulf of Maine (Bigg *et al*., op. cit.). In line with these suitable refugia for cod, genetic evidence suggests that cod populations on either side of the North Atlantic survived the Last Glacial Maximum, i.e., the American and European populations. The Icelandic cod population seems to be younger than American/European populations, and likely founded by European populations during the last interglacial period. Cod at Greenland, however, seems to be founded from Icelandic populations after the Last Glacial Maximum (Bigg *et al*., op. cit.). Faroe cod therefore seems to belong to cod populations with the longest evolutionary history. It must, however, be stressed that Bigg *et al*. (2008) did not deal with the question where and when cod populations actually were present during paleontological times, but only their potential distribution.

## Distribution, density, growth and genetics in relation to temperature

Atlantic cod (*Gadus morhua*, L.) is a valuable commercial fish species that is distributed along the temperate and polar coastal areas and slopes on both sides of the North Atlantic Ocean. Cod occupy and thrive in water temperatures ranging from -1 to 19 $^{o}$C with mean annual temperatures fluctuating between 1 and 11 $^{o}$C (Sundby, 2000). The optimum temperature for growth depends upon fish size and ranges from 14.3 $^{o}$C (50 g fish) to 5.9 $^{o}$C (5000 g fish) (Björnsson and Steinarsson, 2002). Hence, Faroe cod live at nearly optimal temperatures (6-11 $^{o}$C). There is a marked difference in the hydrography between the Northwest and Northeast Atlantic Oceans. Broadly stated, the warm water (> 4$^{o}$ C) in the Northeast Atlantic flows above the cold bottom waters (< 4$^{o}$ C), while the opposite is observed in the Northwest Atlantic (ICES, 2005). In addition, the hydrography in the Northwest Atlantic is much more variable (Robichaud and Rose, 2004).

This variation in hydrography has implications for cod migration, where cod in the Northwest Atlantic have a much more variable migration pattern than in the Northeast Atlantic. In an extensive review, Robichaud and Rose (2004) grouped cod migration patterns into four types: sedentary (S), accurate homers (AH), inaccurate homers (IH) and dispersers (D). Overall, the sedentary pattern was most common on both sides of the North Atlantic. Accurate homers were restricted to the Northeast Atlantic while inaccurate homers/dispersers were more common in the Northwest Atlantic. Faroe Plateau cod were grouped as ‘accurate homers’ while Faroe Bank cod were ‘sedentary’.

Robichaud and Rose (2004) also found that sedentary groups were smaller than migratory groups and interpreted migratory behaviour to be an adaptation towards abundance, i.e. abundant cod groups need to be migratory in order to keep their abundance high. They suggested that the highly migratory behaviour of cod in cold waters could explain the (albeit weak) negative relationship between occupied temperature (individual growth) and carrying capacity for cod in the habitat since the migratory behaviour could allow cod to utilse the high food resources in cold waters.

Broadly stated, with increasing temperature / declining latitude, there is 1) a tendency towards faster individual growth (Table 1; Brander, 1995; Dutil and Brander, 2003; Michalsen *et al*., 1998), 2) earlier sexual maturity (Hutchings, 2005), 3) higher condition factor (Dutil *et al*., 1999; Lloret and Rätz, 2000; Rätz *et al*., 2000; Rätz and Lloret, 2003; Salvanes *et al*., 2004), and 4) smaller maximal size, i.e. a gradient from ‘survivors’ towards ‘reproducers’ (Goodwin *et al*., 2006). For many fish species, natural mortality increases with increasing growth rate and temperature, although ecology and phylogeny may also be important (Griffiths and Harrod, 2007). Faroe Plateau cod are ‘in the middle’ of other cod stocks (Rätz *et al*., 2000). The density of cod seems to increase with decreasing temperature / increasing latitude (Table 1), as does the carrying capacity for cod (Myers *et al*., 2001). The increased density of cod with decreasing temperature is accompanied by a decreasing diversity of fish species (Frank *et al*., 2007; Rose, 2005). While cod in the Irish Sea represent a minority of the bottom fish biomass, they represent the majority of the bottom fish biomass in cold regions (Robichaud and Rose, 2004). Species diversity also declines with increasing depth (Rose, 2005).

Table 1. Grouping of 23 offshore cod populations in relation to the 4 °C contour (mean annual temperature at 100 m depth, Sundby, 2000) according to spawning and nursery areas. Density in kg/ha was obtained from Brander (2007), and growth production in g/capita from Dutil and Brander, 2003. Three levels of maximum stock size, S: < 100 thousand tonnes, M: < 1000 thousand tonnes, L: > 1000 thousand tonnes, based on Brander (2007) and Werner *et al.*, (1999), or by half maximum annual landings, based on ICES, 2006b. Migration pattern is obtained from Robichaud and Rose, 2004: S: Sedentary. AH: Accurate homers, IH: Inaccurate homers, D: Dispersers. Inshore populations (not shown) are often sedentary.

| **Group** | **Cod stock in the NW Atlantic** | **Size** | **Cod stock in the NE Atlantic** | **Size** | **Max. density (kg/ha)** | **Growth prod. (g/capita)** |
|---|---|---|---|---|---|---|
| **Group 1** | | | | | | |
| Spawn. at < 4 °C | E. Nwfdland / Lbdor | L | | | 53 | |
| Juven. at < 4 °C | N. Grand Bank | M | | | | 321 |
| | S. Grand Bank | M | | | 17 | |
| Variable | S. Newfoundland | M | | | 40 | |
| hydorgraphy | N. G. St. Lawrence | M | | | 68 | 271 |
| | S. G. St. Lawrence | M | | | 31 | 238 |
| S, IH or D | | | | | | |
| **Group 2** | | | | | | |
| Spawn. at > 4 °C | Greenland | L | | | | |
| Juven. at < 4 °C | | | Barents Sea | L | 41 | 502 |
| Var. hydr. | | | Iceland* | L | 73 | 689 |
| AH | | | | | | |
| **Group 3** | | | | | | |
| Spawn. at > 4 °C | E. Scotian Shelf | M | | | 41 | 360 |
| Juven. at > 4 °C | W. Scotian Shelf | S | | | | 785 |
| | Gulf of Maine | S | | | | |
| Stable | Georges Bank | M | | | 5 | 1264 |
| hydrography | | | Faroe Plateau (AH) | M | 43 | 855 |
| | | | Faroe Bank | S | 29** | |
| Mostly sedentary | | | Norwegian coast | M | | |
| populations | | | Skagerrak/Kattegat | M | | |
| | | | W. Baltic | M | | 687 |
| | | | E. Baltic | L | 50 | 377 |
| | | | North Sea (IH) | L | 22 | 1990 |
| | | | W. Scotland (IH) | S | | 1849 |
| | | | Irish Sea | S | 6 | 1861 |
| | | | Celtic Sea | S | 2 | 2477 |

* The Icelandic ecosystem is divided into a warmwater southern / western part and a coldwater northern / eastern part. In contrast to the other cod stocks, which, in broad terms, live in either cold (0-4 °C) or warm water (4-12 °C), the Icelandic cod stock has access to both cold and warm water, i.e., could be placed 'in-between' group 2 and 3. Another special feature is that eggs/larvae may drift from Iceland to Greenland and a return spawning migration also may happen (Buch *et al.*, 1994).

** Based on unpublished results.

There is also a latitudinal cline in genetic properties. The frequency of the hemoglobin allele HbI(1) increases with increasing temperature in the Northeast Atlantic Ocean, while such an increase is less pronounced in the Northwest Atlantic. Faroe cod and cod at Iceland/Greenland are also dominated by the 'coldwater' allele (Sick, 1965; Jamieson and Birley, 1989; Dahle *et al.*, 2006; review in Imsland and Jónsdóttir, 2003). There is also a marked variation at the Pantophysin I (*Pan* I) locus. The frequency of the Pan I$^{A}$ allele seems to increase with increasing temperature / decreasing depth. There also seems to be a differentiation into inshore (high PanI$^{A}$ frequency) and offshore (low PanI$^{A}$ frequency) cod populations (Beacham *et al.*, 2002; Fevolden and Pogson, 1997;

Dahle *et al*., 2006; Imsland and Jónsdóttir, 2003; Jónsdóttir *et al*., 2003; Case *et al*., 2005; Pampoulie *et al*., 2006; Sarvas and Fevolden, 2005). The PanI frequencies also seem to be stable over life cycle (Karlsson and Mork, 2003; Sarvas and Fevolden, 2005) and time (Nielsen *et al*., 2007). Faroe Plateau cod have a rather special combination of genetic traits, as they mainly possess the 'coldwater' hemoglobine allele (Hb-I(2)) and the 'warmwater' $\text{PanI}^{\text{A}}$ allele. A highly significant heterogeneity between areas has also been found at the LDH-B (Lactate DeHydrogenase orthologue B) locus (Mork and Giæver, 1999; Magnussen, 1996).

Some studies have linked the latitudial cline in genetic properties of cod to environmental factors like temperature (see introduction in Zakhartsev *et al*., 2004a), but the main focus of genetic studies has always been on stock identification, i.e., the need to classify populations of cod to their mother stock. The underlying goal has been to define cod stocks unambigously so that proper stock assessments could be made. Stock assessments rely critically on the assumption that migration to or from other areas is negligible. There has traditionally been less focus on how and why genotypic or phenotypic traits are correlated with environmental factors. It should also be noted that the field of stock identification has been rather controversial because different genetic markers may give different results (see e.g. Pogson *et al*., 1995).

A final note on cod distribution is worthwile. Generally, fish in the North Atlantic Ocean spawn at higher temperatures than their feeding area (Rose, 2005). In coldwater cod stocks (Group 1 in Table 1), the juveniles grow up in cold areas, often close to land (e.g., Bogstad *et al*., 1994), while the spawning occurs at the boundary between the cold-water masses and the underlying warm-water masses. In 'warm-water' cod stocks (Group 3 in Table 1), both juvenile and adult cod are located in warm water. The populations of cod that spawn in warm water and the juveniles grow up in cold waters (Group 2 in Table 1), i.e., the spawning and feeding areas are not close together, undertake the longest migrations (note, however, that E/Newfoundland cod also migrate long distances). Of special importance is that Icelandic cod and Barents Sea cod gradually move towards warmer water during ontogeny (Pálsson and Thorsteinsson, 2003; Nakken and Raknes, 1987; Ottersen *et al*., 1998). The situation is the reverse for Faroe cod: Faroe cod gradually move to colder and deeper water (Tåning, 1943).

### Susceptibility of cod stocks to collapse

Coldwater cod stocks in Northwest Atlantic Ocean (Group 1 in Table 1) have been much more vulnerable to collapse than cod stocks in the Northeast Atlantic. Nearly all coldwater cod stocks in the Northwest Atlantic were reduced to very low levels in the beginning of the 1990s and all showed the same temporal trends, which was in accordance with seawater temperature fluctuations (Brander, 2007). Cod stocks in the Northeast Atlantic have been much more resilient to collapse but shown different temporal trends. The Icelandic cod stock has been quite stable over time (1970s – today), while the cod stock in the Barents Sea has has fluctuated much more. Some cod stocks in the Northeast Atlantic are reduced to low levels (abeit not collapsed), for example, North Sea cod, Eastern Baltic cod and Irish Sea cod (Brander, 2007). The Faroe Plateau cod stock has been quite close to collapse both in 1991-1994 and now (2008) (ICES, 2008a).

The 'near collapse' of cod at the Faroes in the 1990s caused a national economic crisis. The development of the stock in 1990-1996 was unexpected and revealed huge gaps in the knowledge of cod biology at the Faroes and also caused a credibility crisis between fisheries biologists and the people on the Faroes. The stock assessment methods were, however, in line with what was used for other cod stocks and were founded on traditional views on cod population dynamics, which are outlined below.

The processes that control the population dynamics in cod, like any other fish species, are recruitment, individual growth, mortality and migration (Pitcher and Hart, 1982). Recruitment and individual growth represent input to the population while mortality (natural death or fishing) is an output. Migration may act as an input or an output. These, fairly different, processes are discussed briefly in the following sections.

Recruitment is the input of young fish to the fishable stock. In a life history context, cod may be classified as 'survivors'. Cod are characterised by long-lived repeated spawners producing a 'small' amount of offspring per spawning, and recruitment is strongly density-dependent (Goodwin *et al*., 2006). After spawning, the eggs float pelagically and hatch after 1 week to 3 months, depending on temperature (Sundby, 2000). The larvae get their nutrition from the yolk sac the first week or so and then begin exogenous feeding. The mortality of eggs and larvae is enourmous and may be as high as several percent per day (Sundby *et al*., 1989). The temporal and spatial matching between the first-feeding larvae and abundance of food organisms (Copepod eggs and nauplii) is crucial for larval survival (Brander *et al*., 2001; Cushing, 1995) and is often considered as the most important bottleneck in year-class strength determination. Predation on eggs and larvae is also important. Recruitment variability in Baltic cod has been successfully modeled by egg/larval mortality and predation (Köster *et al*., 2001; Köster *et al*., 2005). Density-dependent processes may operate later at the O-group stage (Fromentin *et al*., 1997) and most researchers believe that year-class strength in cod is finally determined before the 1-group stage (Myers and Cadigan, 1993). There are also other important findings: For example, recruitment is stimulated by lower-than-average temperatures in warm areas and higher-than-average temperatures in cold areas (Planque and Fredou, 1999). Sundby (2000) proposes that advection of *Calanus finmarchicus* from the North Atlantic Subpolar Gyre onto the shelves, where it serves as food for cod, may be the unifying mechanism explaining the relationship between temperature and cod recruitment. Beaugrand *et al*. (2003), exporing this relationship in more detail, showed that plankton abundance, as well as composition, were of importance for cod recruitment in the North Sea. Relationships between fish recruitment and environmental factors were reviewed in Myers (1998), and few of these theories withstood the test of time. Cannibalism may also regulate year-class strength considerably at the 0-2 group stage (Bogstad *et al*., 1994). Cannibalism, which may be as high as an average year class (Daan, 1983), tends to vary in accordance with year-class strength (Bogstad *et al*., 1994; Neuenfeldt and Köster, 2000; Uzars and Plikshs, 2000) and may, therefore, not be a problem for predicting purposes because the perception of the relative size of incoming year classes may be unchanged. Overall, it has proven difficult to explain recruitment variability in cod and in most cases there has been a very poor fit between spawning stock biomass (SSB) and subsequent recruitment (Myers *et al*., 1996), which partially may be due to the fact that SSB may not adequately reflect potential fecundity (Marshall and Frank, 1999; Marteinsdóttir *et al*., 2000). Canadian coldwater stocks and cod at Greenland show, however, a strong positive relationship between SSB and recruitment (Myers *et al*., 1996). There is a high temporal autocorrelation in the data series, making firm statistical conclusions impossible (Drinkwater, 2002), as other factors could affect both the SSB and recruitment. In conclusion, recruitment is characterised by a high complexity, wherein both local processes (e.g., the size of the spawning stock) and regional processes (e.g., windfield over the North Atlantic Ocean, see Sundby, 2000) may work together. The main question seems to be the identification of the most limiting bottleneck in the process from spawning to recruitment, which is often thought to be at the egg/larval stage (Rotschild, 2000).

The other main factors affecting cod population dynamics are individual growth, mortality and migration. Individual growth of juvenile and adult cod may be a function of temperature, food and genetics, although growth is a highly complex process (Imsland and Jónsdóttir, 2003). A strong positive correlation has been found between average weight-at-age of cod stocks and temperature (Brander, 1995). Food is also an obvious factor (Björnsson and Steinarsson, 2002), and the optimum growth rate depends on fish size as well as food ration. The optimum temperature for growth decreases with decreasing food ration (see references in Chouinard and Swain, 2002 and Pálsson and Thorsteinsson, 2003) and increasing fish size (Björnsson and Steinarsson, 2002). There is also evidence that growth is influenced by genetics. For example, strains of cod from the Faroe Plateau and the Faroe Bank reared under identical conditions had different growth rates (Fjallstein and Magnussen, 1996). Differential selection of either fast or slow growing individuals in commercial fisheries also affects genetics of spawners and growth properties in its offspring (Sinclair *et al.*, 2002a). Mortality of juvenile or adult cod may be split into fishing mortality and other mortality (natural mortality, ICES, 2007). Fishing mortality is often assumed to be a linear function of fishing effort ($F = qE$), where the catchability, $q$, is assumed to be constant (Godø, 1994), although it is known that it may vary (ICES, 2007). Natural mortality may vary according to, e.g., predation pressure or starvation (ICES, 2005), and is often set as a constant (e.g., 0.2) since no data are available to give more detail. Alternatively, natural mortality may be estimated in multispecies models (see references in Floeter and Temming, 2003). Migration at the juvenile or adult stage has been extensively studied during the last century (Robichaud and Rose, 2004), mainly with the objective to define or separate cod stocks (e.g., Bagge and Steffensen, 1989). As a consequence, studies of cod migrations have been traditionally quite descriptive and the factors that influence cod migration have received less attention, although transplantation experiments have elucidated some factors affecting migration (Robichaud and Rose, 2004).

## Faroe cod

### Study area

The Faroe Islands is situated approximately midway between Iceland, Norway and Scotland. The plateau around the Faroe Islands (Faroe Plateau) is around 40,000 square kilometers within the 500 m isobath (Figure 1), which is a small area, compared to other fishing grounds. Three banks are located south-west of the Faroe Plateau: Faroe Bank, Bill Bailey Bank and Lousy Bank (not shown in Figure 1), all being considerably smaller than the Faroe Plateau.

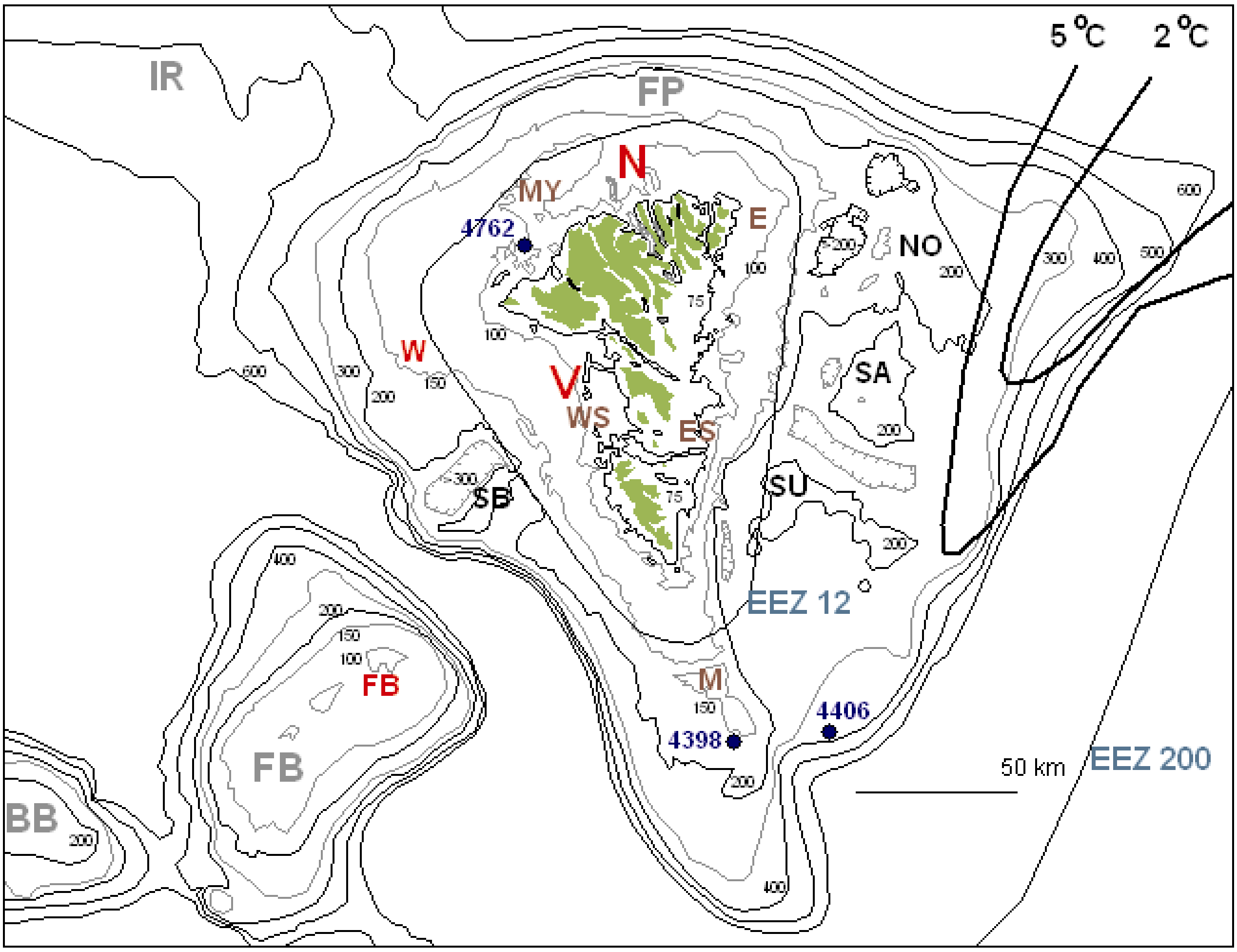

Figure 1. The study area that comprises the Faroe Plateau (FP) and the Faroe Bank (FB). The Icelandic Ridge (IR) and Bill Bailys Bank (BB) are also shown. Less pronounced banks are: Nólsoyarbanki (NO), Sandoyarbanki (SA), Suðuroyarbanki (SU), and Skeivibanki (SB). Good fishing grounds for cod in March (spawning time) are shown in red: Norðhavið (N), Vágahavið (V), west of the island Mykines (W), and on the Faroe Bank (FB). Good fishing grounds other parts of the year (brown) include: Mýlingsgrunnur (MY), east of Fugloy (E), east of Sandoy (ES), Munkagrunnur (M), and west of Sandoy (WS). Temperature contours (2 and 5 °C) are shown describing the frequent entrance of cold, low salinity water onto the eastern part of the Faroe Plateau. The 12 and 200 nautical EEZ are also shown. The labels '4762', '4398', and '4406' indicate the recapture positions of individual cod that were tagged with Data Storage Tags.

The bottom topography of the Faroe Plateau is fairly different in the various directions from the Faroes. The main fjords on the Faroes are located in the eastern part of the islands and the largest shallow areas are also found east of the Faroes (50-75 m). The medium-depth (75-150 m) areas are, however, largest west of the Faroe Islands and the deepest areas (150 - 400 m) are, by far, largest east of the Faroes. The slopes at a depth of 400-600 m are fairly steep, especially north and west of the Faroes.

The Faroe-Iceland Ridge extends from the Faroe Plateau to south-east Iceland, and is 300-550 m deep. The Faroe-Shetland channel is located south-east of the Faroes and the Faroe Bank channel (both around 800 m deep) south-west of the Faroes. Thus, the Faroes may be regarded as a bridge between the North Sea and Iceland with the only gateways to the Arctic seas being the Faroe-Shetland channel and the Faroe Bank channel.

The hydrography is dominated by the warm Atlantic water covering depths shallower than about 500 m whereas cold Arctic water dominates (Hansen, 1985; Hansen and Østerhus, 2000) the deeper areas, separated by a well-defined termocline (Meinke, 1978). The warm Atlantic water extends deeper west of the Faroes than to the east. In very broad terms, warm Atlantic water flows in a north-easterly direction, while the Arctic water flows in a south-westerly direction (Hansen and Østerhus, 2000). More specifically, the warm Atlantic water flows anticyclonically around the Faroes, and also around the Faroe Bank (Hansen, 1992; Simonsen, 1999; Gaard and Hansen, 2000). The cold Arctic water flows in a south-easterly direction along the slopes east of the Faroes and finally through the Faroe-Shetland channel and further through the Faroe Bank channel. There is occasionally some overflow of Arctic water across the Faroe-Iceland ridge (Meinke, 1978). There are occasional intrusions of cold water onto the eastern part of the Faroe Plateau (Hansen *et al.*, 1988). The temperature seems to be most stable in the northern part of the Faroe Plateau, less stable in the southern part and may be highly variable on the slope, as indicated by Figure 1 and Figure 2. These hydrographical features seem to be of great importance, as they seem to affect cod distribution and feeding (discussed below).

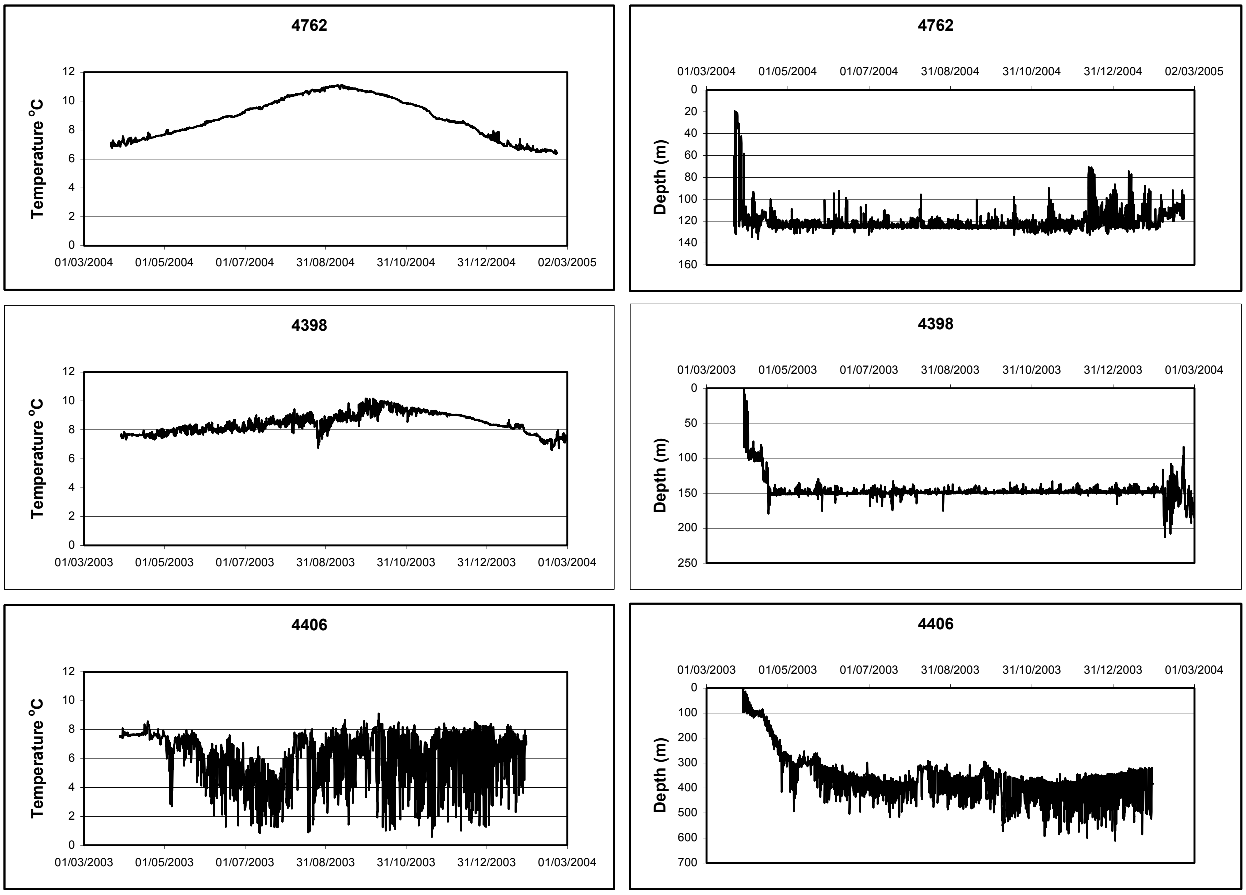

Figure 2. Temperature-depth profiles for three selected cod tagged with Data Storage Tags in March 2003 and March 2004, showing typical shallow-warmwater occupation (Tag 4762 and 4398) and highly atypical occupation close to thermal fronts in deep waters (Tag 4406) over nearly 12 months. Note different scales for depth profiles. See recapture positions in Figure 1.

In addition to the main anticyclonical current around the Faroes (and the Faroe Bank separately) there are strong tidal currents leading to uniform temperatures / salinities at depths < 130 m (the

Faroe Shelf) throughout the year (Hansen, 1992; Gaard *et al.*, 1998; Hansen *et al.*, 1998). A termocline separates the water masses on the Faroe Shelf from the outer water masses (Gaard *et al.*, 1998; Larsen *et al.*, 2002), which may be slightly thermally stratified horizontally (Hansen, 2000).

The temperature of the Atlantic water masses around Faroes varies seasonally from 6 to 10 $^{o}$C (Smed, 1952). Faroe Bank is normally 1-2 $^{o}$C warmer than the Faroe Plateau (Nielsen *et al.*, 2007). The temperature on the Faroe Plateau may, during winter, be up to 2 $^{o}$C colder than the surrounding water masses, while it may be up to 1 $^{o}$C warmer during summer (Hansen, 2000). The deep-water masses (500-600 m) of Arctic origin are characterised year-round by temperatures close to 0 $^{o}$C (Hansen, 2000).

The exchange rate of the Faroe Shelf water masses in spring, which is on the order of 2-3 months (Gaard, 2003), seems to be crucial for the phytoplankton production on the Faroe Shelf. The phytoplankton community on the Faroe Shelf is different from the outer areas (Gaard, 1996) and when the exchange rate is low, the phytoplankon production becomes high and *vice versa* (Eliassen *et al.*, 2005, Hansen *et al.*, 2005). It is believed that a low exchange rate keeps the algae in the euphotic zone (above the critical depth), while a high exchange rate flushes the algae below the critical depth. There is a large interannual variation, a factor of 5, in the phytoplankon production on the Faroe Shelf.

## Life history in Faroe Plateau cod

Faroe cod undertake a spawning migration towards the two most important spawning sites 'Norðhavið' (north of the Faroes) and 'Vágahavið' (west of the Faroes) at depths of 90-140 m. Spawning occurs from February to April with peak spawning in the late half of March. After spawning, cod from 'Norðhavið' disperse all around the Faroe Plateau (Tåning, 1940), but this information is not available for the 'Vágahavið'. The eggs float pelagically with the currents clockwise around the Faroes and hatch after 2-3 weeks. After the yolk sac has been absorbed (1 week), the larvae feed on eggs and nauplii of *Calanus finmarchicus* (Gaard and Reinert, 2002; Gaard and Steingrund, 2001). In July-August, the 3-5 cm long larvae settle to the bottom, usually close to land in shallow waters (Joensen and Tåning, 1970). The juveniles feed on a variety of benthic crustaceans and grow fast – especially on the Faroe Bank (Magnussen, 2007). Faroe Plateau one-year-old juveniles are 20-35 cm long. They are quite stationary (Strubberg, 1916; Strubberg, 1933), which also applies to reared cod that were released into fjords (Fjallstein and Jákupsstovu, 1999). This is a critical period of their lives because the year class strength seems to be determined at the 1-group stage (see later). One-year-old cod are mainly distributed shallower than 100 m, but can occasionally be found down to 300 m. Juvenile cod presumably move down to the traditional fishing grounds (80-140 m) during their second winter, in line with cod off western Scotland (Hawkins *et al.*, 1985). Faroe Plateau cod become sexually mature at an age of 3-4 years (ICES, 2007). The fishing mortality is normally quite high (0.4-0.8) and is mainly excerted on the ages 3-7. Hence, few individuals become older than about ten years.

## Broad ecological niches on the Faroe Plateau

A number of fish species inhabit waters around the Faroes. Around 200 fish species (Mouritsen, 2007) have been recorded, but only 10-20 % of them are frequently found. The fish fauna is dominated by temperate / boreal species in the warm water layers (above 500 m depth), while Arctic fish species are found in the cold water masses at depths greater than 500 m.

The fish species of greatest ecological importance are: Blue whiting, Norway pout, sandeels, saithe, cod, haddock, whiting, tusk, ling, redfish (*Sebastes spp.*), lemon sole, plaice, Atlantic halibut, Greenland halibut, herring and mackerel (Faroese Fisheries Laboratory, unpublished data).

Two broad ecological pathways exist in Faroese waters. In the Faroe Shelf area, the local phytoplankton production (Gaard, 1996) serves as food for neritic plankton species (Gaard, 1999), as well as the production of *Calanus finmarchicus* (eggs and later individual growth). Sandeels and juvenile Norway pout are important predators on zooplankton in the Faroe Shelf area, and are in turn preyed upon by saithe and cod. A part of the phytoplankton production (as well as zooplankton production) sinks to the bottom and serves as food for a variety of benthic feeders, including many benthic crustaceans and polychaets. The second pathway is based on plankton (krill), which is advected from the deep Norwegian basin (Melle *et al.*, 2004). Blue whiting, large Norway pout, redfish and saithe presumably prey on krill and other plankton (see Pálsson, 1983 for Icelandic waters). Saithe and cod also feed on large Norway pout and Blue whiting (Du Buit, 1982).

Four broad ecological niches can be defined for juvenile and adult fish that have direct relevance to cod. The first is based on sandeels and small Norway pout in shallow (< 150 m) pelagic waters. Small saithe are the typical owners of such a niche, but also whiting. The second is based on benthic crustaceans and polychaets in shallow waters and this niche is primarily occupied by haddock and small cod. The third is based on large Norway pout and Blue whiting in deep waters and is occupied by large cod, large saithe, whiting and many other fish species. The fourth niche is based on various flatfish species in shallow waters and is mainly occupied by very large cod.

## Habitat use and morphological adaptations

Faroese fishermen often claim that slender cod are of 'Icelandic' origin, whereas a more bulky body form characterizes typical Faroese cod. This may not be true because there seems to be a connection between habitat use and morphology in cod at the Faroe Plateau. Cod in deep waters (> 300 m) have a larger size-at-age and lower condition factors than cod in shallower waters (unpublished material), coinciding with higher food availability in deep waters (see later). These differences may not be due to temperature effects, as there is little difference in temperature between shallow and deep areas (Hansen, 2000). Cod in deep waters feed on mobile fish such as Norway pout and Blue whiting (Du Buit, 1982), which may require more swimming activity than the feeding on benthic crustaceans in shallow waters (Rae, 1967). The more slender body form of deepwater cod could be an adaptation to greater swimming activity, i.e., the fish are able to swim at a faster speed because their body length is greater for a given body mass, and swimming speed is positively related to body length (Videler, 1993). Pelagic ('limnetic') three-spined sticklebacks and Arctic charr also have a more slender body form than their 'benthic' counterparts (Blake *et al.*, 2005; Law and Blake, 1996; Malmquist *et al.*, 1992).

## Groundfish fishery at the Faroes

Formerly, the groundfish fishery (1900-1950s) at the Faroes was dominated by British trawlers (Jones, 1966; Jákupsstovu and Reinert, 1994). They usually exploited the shallow waters (< 200 m) and there were no area restrictions (on either spawning or feeding grounds). The fishermen primarily targetted cod and various flatfish species such as Atlantic halibut (*Hippoglossus hippoglossus*), lemon sole (*Microstomus kitt*) and plaice (*Pleuronectes platessa*). Other fish species, like haddock and saithe were less frequently landed.

In the 1960s, other nations also fished at the Faroes, e.g., Germany and France. At this time, more fish species were landed, haddock in the 1950s and saithe in the 1970s. Area restrictions were introduced in 1959 and 1964 (Nolsøe, 1963). In 1977, the EEZ was extended to 200 nautical miles and Faroese vessels replaced the foreign fleets. In the 1980s, the trawlers were allowed to fish in shallow waters (< 200 m) along with longliners.

The groundfish fishery at the Faroes nowadays (1990-2008) can be divided very broadly into a longline fishery for cod and haddock in shallow waters (< 150 m) and a trawl fishery for saithe (pair trawlers) and deepwater species such as redfish and Greenland halibut (single trawlers) in deep waters (> 150 m). The current structure of the groundfish fishery has been regulated by law since the mid-1990s (in connection with the effort management system), but was largely present in the 1980s also (although some trawlers were allowed to fish in shallower waters). Some of the smaller longliners use jigging part of the year (spawning time). There is also a gillnet fishery for monkfish (> 380 m depth) and for Greenland halibut (> 500 m depth). Some small trawlers are allowed to trawl for flatfish in shallow waters during the summertime. Also, some deepwater single trawlers are allowed to catch a small quota (in tonnes) of cod and haddock in shallow waters. For more details, the reader is referred to ICES (2007).

### Management of the groundfish fishery at the Faroes

Before 1950s, there was almost no restriction in the groundfish fishery at the Faroes. The only restriction was, in all practicality, the 3 nautical mile fishery limit, as small Faroese boats operated inside the fishery limit whereas British trawlers normally worked the fishing grounds outside the fishery limit. In the 1960s-1970s, the fishery limit was extended, leading to an exchange of the fishing fleets exploiting Faroese waters. Spawning area restrictions were introduced in the 1970s and extended in the 1980s. In 1994, a quota system was implemented, but it was replaced in 1996 by an effort management system (ICES, 2008a).

The effort management system builds on the assumption that fishermen will catch the fish species (cod, haddock or saithe) that is most abundant. It would mean that stocks that are low would be protected automatically. Another idea is that the fishing effort should be kept constant over time, i.e., the fishing effort should not be regulated on a yearly basis. If the fishing effort is set at the correct level then the variation in the fishery would reflect natural variations in the environment and the fishery would be sustainable over time. Also, it would not be necessary for precise scientific advice, because stock sizes would be reflected in the fishery anyway. This was a consequence of the poor scientific advice provided in the 1990s. The means used to regulate the fishing effort are the number of fishing licenses, the number of fishing days and area restrictions.

In retrospect, several of the assumptions / ideas were not realized (see Jákupsstovu *et al.*, 2007). A large price differential between fish species led to high exploitation of cod even though the stock size was low. Also, the number of fishing days has, according to ICES and Faroese Fisheries Laboratory, been too high, although the number of fishing days has been reduced by around 20% since 1996. The reduction of fishing days should be viewed in light of the fact that too many fishing days were allocated from the beginning. Ideally, there should be a program that monitored the (gear) efficiency over time, but that was not done.

### The crisis in the 1990s

For almost a century, Faroe cod had shown a remarkable stability in terms of annual catch (Figure 3). People had the impression that the cod stock was so robust that fishing would have but little effect on cod population dynamics. However, by 1994 there was opposing evidence (Jákupsstovu and Reinert, 1994). Over a long period of time, Faroe cod did show a decreasing trend, although trends in annual catches were absent (Figure 3). Recruitment also showed a decreasing trend (Figure 4). The 'near collapse' of the Faroe Plateau cod stock in 1991-1993 and the rapid recovery in 1994-1996 precipitated a major crisis on many levels. The low catches contributed to a severe national economic crisis with the direct consequence that around 10% of the population at the Faroes (4-5,000 out of 48,000) emigrated to other countries (mainly Denmark). The poor fit between the predicted and the observed development of the cod stock caused a credibility crisis between the advisary body (ICES and the Faroese Fisheries Laboratory) and the Faroese fisheries managers, as well as ordinary local citizens of the Faroes. This disconnect between predicted and observed cod development also brought into question the valitity of the assumptions behind the assessment methods. These assumptions are discussed below.

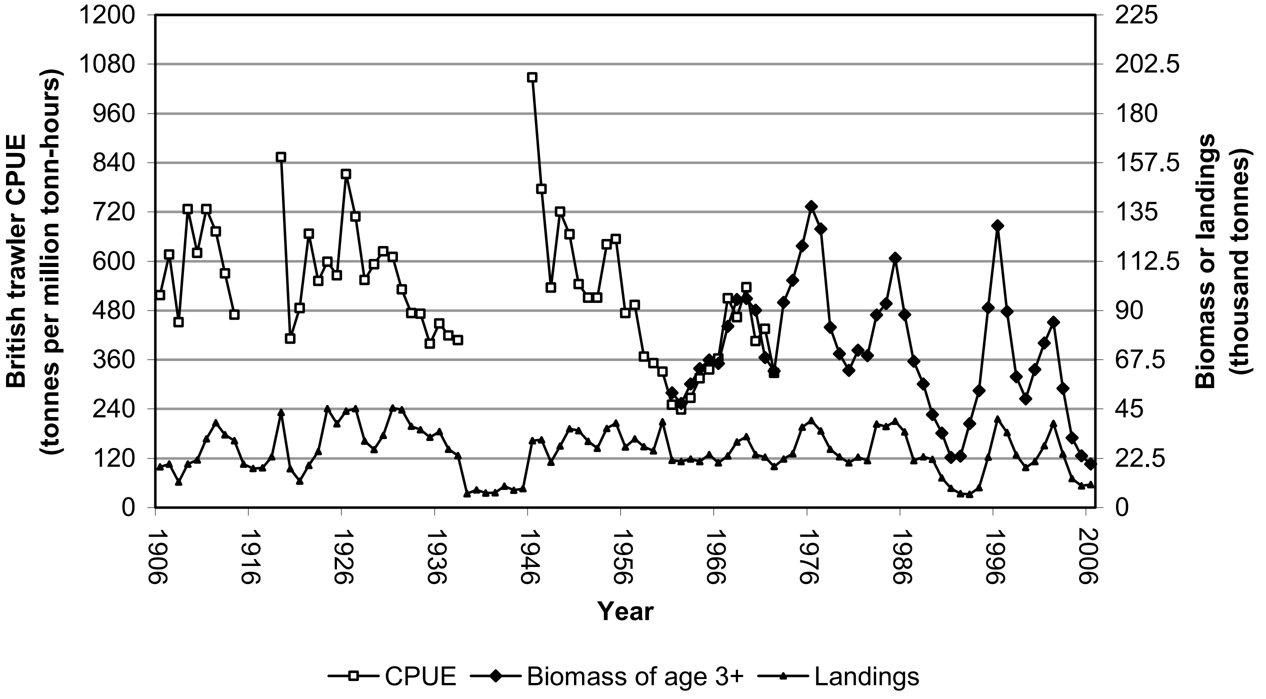

Figure 3. Faroe Plateau cod biomass, landings and British CPUE (catch per unit effort) (1906-2007). From ICES, 2008a.

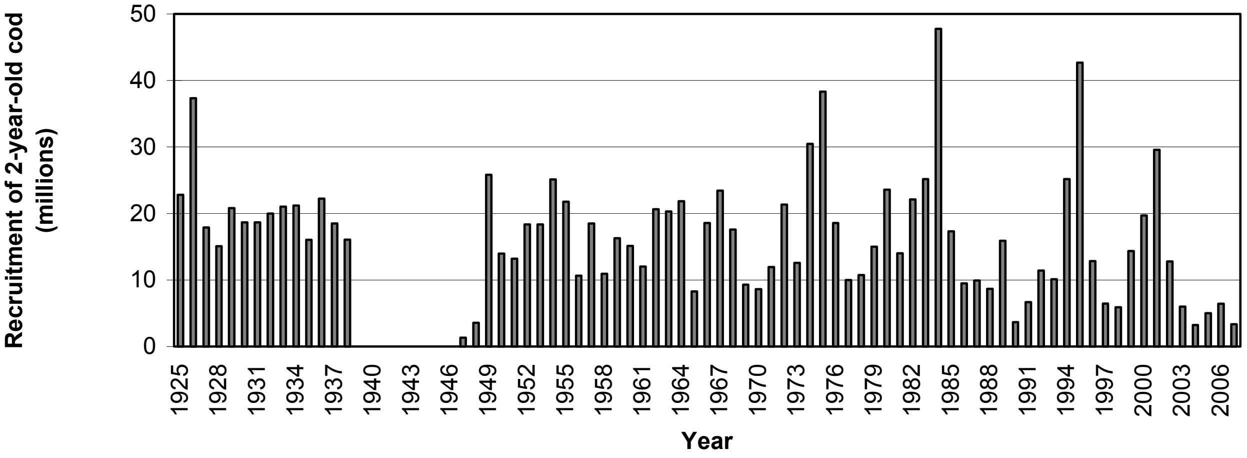

Figure 4. Faroe Plateau cod recruitment (1925-2007). The recruitment is either taken directly from the XSA-estimate (1961-2007) or estimated from a regression between recruitment and cpue year t+1 – cpue year t + catch year t. The catch prior to 1961 was scaled by 0.92 in order to separate the Faroe Plateau catch from the total catch where catches from the Faroe Bank were included.

During the 1980s, the assessment of cod was based on catch-at-age and bottom trawl survey indices (as it still is). The assessment gave reliable results back in time, but could be imprecise for the 2-3 latest years in the assessment. For example, the assessment in May 1993, having the time series 1961-1992 available, would give precise stock estimates for 1961-1989, but not necessarily for 1990-1992. The uncertainty could be in the order of +/- 30%.

Short-term predictions were therefore made that were based on current estimates of stock size, strength of incoming year classes and fishing mortality. The main source of error was the strength of incoming year classes, which were normally assumed to be of ‘average’ strength. By assuming average recruitment for future year classes, a stock projection was made several years into the future that was based on highly uncertain assumptions. The stock size was very low in 1992, as well as the O-group indices for 1990-1992, and the prediction of the stock sizes in 1993-1995 was, therefore, very pessimistic and would imply a near-collapse of the cod fishery.

However, the cod fishery at the Faroes rose from 10 thousand tonnes in 1994 to 40 thousand tonnes in 1996, which showed that the cod stock had fully recovered. The quota system, which was implemented in 1994, was abandoned in 1996 when the effort management system was introduced. The reason was partly that the quotas were far too low compared with the catch rates. The rapid recovery of the cod fishery came as a big surprise to local people, as well as to the advisory body (ICES and the Faroese Fisheries Laboratory). Local people claimed that the rapid recovery was caused by large-scale emigration of cod from foreign areas, e.g., from Icelandic waters. The Faroese Fisheries Laboratory claimed, on the other hand, that the recruitment had been high, for some unknown reason (the relationship between O-group indices and recruitment had broken down).

Strange observations about cod population dynamics in 1990-1996 were evident some years later when converged stock estimates and estimates of fishing mortality became available. The 1992-1993 year classes were far larger than predicted and contributed significantly to the large catch in 1996. Older year classes, which, during the crisis in 1991-1994, had been estimated to be weak and were seldom caught, now turned up in numbers much greater than expeced. The fishing mortality also increased substantially from 1994-1996. These phenomena were observed in the catch curves. Catch curves are the number of fish fished of a cohort during its life and they normally increase the first 2-3 years (from age 2 to age 4-5) and then decrease exponentially. Such a pattern was observed for the entire time period from 1961-1990. In the 1990s, many of the catch curves showed a spectacular increase in 1996 and could be bimodal (the 1987 year class) or steadily increasing until age 7 (the 1989 year class). Most catch curves showed also an increase from 1995 to 1996 that only should be observed for the incoming 1992-1993 year classes (ICES, 2008a).

These strange observations suggested that too little was known about cod at the Faroes. It was difficult to tell what relationship or factor should be explored. Because local fishermen on the Faroes explained the events as a large-scale emigration of cod from other areas, such an observation could be worth investigating. Unfortunately, no tagging experiments were performed prior to or during the crisis, so no observations about cod migration were available. The Icelanders had tagged cod since 1991, but very few of them were recaptured in Faroese waters. This would indicate that there had not been a large-scale emigration from Icelandic waters. As a result a tagging program was initiated in 1997. There were also other important gaps. For example, there was very little information about the feeding of cod, i.e., almost no stomach analyses had been done. Some stomachs were sampled in the 1990s (Homrum, 2007; Nicolajsen, 1993), but the last comprehensive stomach investigations were done in the 1970s (Du Buit, 1982) and in the 1950-60s (Rae, 1967). From these data, it would be impossible to deduce what had happened during the 1990s and a stomach sampling program was, therefore, also initiated in 1997.

### A clue why these strange observations happened

The poor recruitment in the late 1980s has been linked to strong westerly winds that were hypothesized to carry cod eggs / larvae out of the anticyclonical circulation (Hansen, 1992, Hansen *et al*., 1994), but this view was later abandoned. Also, Brander and Mohn (2004) did not find any relationship between recruitment variability and the North Atlantic Oscillation (NAO) for Faroe Plateau cod (although they found this for other cod stocks, see also Stige *et al*., 2006). In the late 1990s, however, the time series on phytoplankton production had been 10 years and a close positive correlation was observed between phytoplankton production and recruitment, as well as individual weights of cod and haddock. When the phytoplankton production was high, recruitment of cod and haddock was high and the fish were also larger than normal. The signal was also discernible for seabirds (Gaard *et al*., 2002).

There was a discrepancy between the biomass of the standing stock of zooplankton and the corresponding production (production of zooplankton biomass per time). In years with low primary production, the standing stock of zooplankton was high and dominated by *Calanus finmarchicus* that was advected onto the Faroe Shelf from the surrounding oceanic environment (Gaard and Hansen, 2000). On the other hand, small-sized neritic copepod species (*Acartia longiremis* and *Temora longicornis*) dominated in years with high primary production (Gaard, 1999). The abundance and size composition of zooplankton indicated that the production of zooplankton followed the phytoplankton production, both interannually and seasonally (Gaard, 2000; Gaard, 2003; Debes *et al*., 2008). The production of copepod eggs and nauplii seemed to be crucial for fish because it determined sandeel and probably also Norway pout year-class strength. Hence, the variations in phytoplankton production lead to variations in the food available for fish and seabirds. This represented a valuable clue for futher research.

## Objective

The objective in this thesis was to investigate why the scientific perception of stock size – and therefore the advice – in the 1990s turned out to be so wrong. It was hoped that a better understanding of the driving forces would increase the quality of future advice and that these findings could apply to other cod stocks.

In order to achieve this objective – and since it was not clear *a priori* what should be looked for – all the newly available time series were investigated: 1) the stomach investigations, 2) the tagging experiments, 3) the longliner logbook data and 4) the pairtrawler logbook data. Samples for genetic studies were also taken.

## Papers

**Paper I**: Steingrund, P., Hansen, B., and Gaard, E. 2005. Cod in Faroese waters. In: ICES Cooperative Research Report *Spawning and life history information for North Atlantic cod stocks* (ed. K. Brander), pp. 50-55. ICES, Copenhagen, 2005.

**Paper II**: Steingrund, P., Reinert, J., Henriksen, A., Pedersen, M., and Reinert, R. (ms). Diet and habitat use of cod (*Gadus morhua*) at the Faroes influenced by prey density, cod density, size, and condition.

**Paper III**: Joensen, J.S., Steingrund, P., Henriksen, A., and Mouritsen, R. 2005. Migration of cod (*Gadus morhua*): tagging experiments at the Faroes 1952-65. Fróðskaparrit (Annales Societatis Scientarum Færoensis), 53: 100-135.

**Paper IV**: Steingrund, P., and Mouritsen, R. (ms). Faroe Plateau cod (*Gadus morhua* L.) distribution and migration during 1997-2006.

**Paper V**: Steingrund, P., Mouritsen, R., Reinert, J., and Gaard, E. (ms). Recruitment in Faroe Plateau cod (*Gadus morhua* L.) hampered by cannibalism at age 1 but positively related to the contemporary abundance of age 3+ cod at age 2. ICES Journal of Marine Science. (Submitted).

**Paper VI**: Steingrund, P. and Gaard, E. 2005. Relationship between phytoplankton production and cod production on the Faroe shelf. ICES Journal of Marine Science 62: 163-176.

**Paper VII**: Steingrund, P., and Ofstad, L.H. (ms). Density-dependent distribution of Atlantic cod (*Gadus morhua* L.) into deep waters on the Faroe Plateau. ICES Journal of Marine Science. (Submitted).

**Paper VIII**: Steingrund, P., and Clementsen, D.H.J. (ms). Negative relationship between food abundance and catchability of cod (*Gadus morhua*) with longlines on the Faroe Plateau. Fisheries Research. (Submitted).

**Paper IX**: Steingrund, P., Ofstad, L.H., and Olsen, D. 2003. Effect of recruitment, individual weights, fishing effort, and fluctuating longline catchability on the catch of the Faroe Plateau cod (*Gadus morhua* L.) in the period 1989-1999. ICES Marine Science Symposia 219, 418-420.

**Paper X**: Jákupsstovu, S.H. í, Reinert J., and Steingrund P. 2004. Cod in Faroese Waters. 10th Norwegian – Russian Symposium, Bergen 2003. 16 pp.

**Paper XI**: Pampoulie, C., Steingrund, P., Stefánsson, M.Ö., and Daníelsdóttir, A.K. 2008. Genetic divergence among East Icelandic and Faroese populations of Atlantic cod provides evidence for historical imprints at neutral and non-neutral markers. ICES Journal of Marine Science, 65: 65-71.

## Summary of papers

**Paper I**. Cod in Faroese waters.
The paper describes the physical environment in Faroese waters and the spawning and early life history of Faroe Plateau cod. It gives additional information about stock discreteness, individual growth, migration pattern, diet and maturation of cod. The relationship between cod recruitment and phytoplankton production is also treated. Some of these aspects were also raised for Faroe Bank cod.

**Paper II**. Diet and habitat use of cod (*Gadus morhua*) at the Faroes influenced by prey density, cod density, size, and condition.
Based on stomach analyses (1997-2006), the diet of Faroe Plateau cod is described by cod size, depth, area, cod condition and cod density. The proportion of fish in the diet increased with size. In shallow waters, cod preyed upon several epibenthic crustacean species, as well as sandeels, small Norway pout and small haddock. In deep waters, cod preyed mostly upon only one crustacean species and larger Norway pout and Blue whiting. The stomach content was 2-3 times higher in deep waters (> 150 m) than in shallow waters. Cod in good condition had 1.7 times higher stomach content than cod in poor condition. There was a positive relationship between cod density and stomach content of fish in deep waters during the feeding season. Cod on the Faroe Bank stayed in shallow waters in accordance with the low food availability in the deep waters there.

**Paper III**. Migration of cod (*Gadus morhua*): tagging experiments at the Faroes 1952-65.
Based on tagging experiments (1952-1965), the migration pattern of small cod (< 60 cm) on the Faroe Plateau is described. The data revealed that medium-sized cod (55-65 cm, recaptured on traditional cod fishing grounds), usually originated from shallower depths in the same area, but a notable proportion (15-30%) came from other areas on the Faroe Plateau.

**Paper IV**. Faroe Plateau cod (*Gadus morhua* L.) distribution and migration during 1997-2006.
Based on tagging experiments (1997-2006), the migration pattern of cod (all sizes) on the Faroe Plateau was described. The data revealed migration to the two main spawning areas and a return migration to the feeding areas. The paper highlights the fidelity towards spawning areas, as well as feeding areas. Tentative migration routes are outlined and the paper also highlights the poor overlap between the distribution of cod (shallower than 150 m) and the main prey of cod (deeper than 150 m).

**Paper V**. Recruitment in Faroe Plateau cod (*Gadus morhua* L.) hampered by cannibalism at age 1 but positively related to the contemporary abundance of age 3+ cod at age 2.
Based on various data sources, a recruitment model is developed for Faroe Plateau cod that explains more than 80% of the recruitment variability during 1984-2006. According to the model, recruitment of 2-year-old cod (R) is proportional to the contemporary abundance of older cod (age 3+) (B), and inversely related to the abundance of predatory cod close to land (C) the previous summer, i.e., $R = aB/C$. C varied inversely with primary production, as cod moved out from land when condition was high. Cannibalism seemed to be an important survival bottleneck of 1-year-old cod during the summer (the 1/C term). It was proposed that there was another survival bottleneck at the 2-group stage (the B term).

**Paper VI**. Relationship between phytoplankton production and cod production on the Faroe shelf.
Based on nutrient data and stock assessment data, a positive relationship between phytoplankton production and cod production is demonstrated. Broad trophic pathways from phytoplankton to cod

are indicated and why such a relationship between phytoplankton and cod exists. The paper also indicates that the year class strength of cod is determined rather late in life, i.e., at the 1-group or early 2-group stage.

**Paper VII**. Density-dependent distribution of Atlantic cod (*Gadus morhua* L.) into deep waters on the Faroe Plateau.
Based on logbook data and stock assessment data, a positive relationship is found between the distribution of cod cohorts into deep waters (> 150 m) and the abundance of cod in shallow waters. Cod appear to select deep waters at an age of 4-5 years depending on how many 3 / 4-year-old cod are present in shallow waters at the same time. The abundance of cod in deep waters peaks at age 7-8 and decreases thereafter.

**Paper VIII**. Negative relationship between food abundance and catchability of cod (*Gadus morhua*) with longlines on the Faroe Plateau.
Based on logbook data and stock assessment data, a negative relationship is found between the individual growth of cod and the catchability with longlines. The reason seems to be that cod in poor condition prefer longline bait over natural prey. Because the longline cod fishery is important on the Faroes, the large fluctuations in longline catchability affect the total fishing mortality accordingly. The implications for fisheries management are briefly discussed.

**Paper IX**. Effect of recruitment, individual weights, fishing effort, and fluctuating longline catchability on the catch of the Faroe Plateau cod (*Gadus morhua* L.) in the period 1989-1999.
Based on logbook data and stock assessment data, an attempt is made to explain the fluctuations in the annual catches of Faroe Plateau cod during 1989-1999. Further, an attempt is made to explain how much of the fluctuations are due to varying recruitment, growth, fishing effort and catchability with longlines, as well as how much of the catch that could not be explained by these factors.

**Paper X**. Cod in Faroese Waters.
Based on various data sources, the paper describes the cod stocks in Faroese waters and briefly discusses various biological aspects. The cod fishery during the last century is briefly described and the current major fishing fleets are described. The effort management system (that was introduced in 1996) is described as well as benefits/drawbacks of the system.

**Paper XI**. Genetic divergence among East Icelandic and Faroese populations of Atlantic cod provides evidence for historical imprints at neutral and non-neutral markers.
Based on genetic sampling of cod at Iceland and the Faroe Plateau, a genetic comparison is made of the two cod populations spawning at the Faroes and at seven locations at South and East Iceland. No differences were found between the cod sampled at the two Faroese spawning areas or between cod sampled at the Faroese and East Icelandic locations. However, there were genetic differences between the East Icelandic / Faroese populations and the populations at South Iceland. The limited genetic divergence between Faroese and East Icelandic cod could be due to the dispersal of Icelandic cod eggs/larvae to Faroese waters or due to the recent origin of cod populations in both areas after the last Ice Age. The low frequency of the $\mathrm{PanI}^{B}$ allele indicated that feeding in deep and cold waters at the Faroes was limited.

# Synoptic discussion

## Structure of the synoptic discussion

The usual way of structuring a synopsis would be to follow the life cycle in cod, i.e., start with spawning and proceed with eggs / larvae, juveniles and adults. I have, however, elected to use a cause and effect structure. I start with feeding, because feeding seems to influence the distribution / migration in Faroe Plateau cod. In turn, the distribution of adult cod seems to determine year-class strength, which is not primarily determined at the pelagic larval stage – often regarded as the crucial stage – but rather at the juvenile stage (1-group). I then proceed to discuss natural production in cod (numbers x individual growth), which is highly influenced by annual variability in year-class strength. Natural production in cod is the basis for fishery and fisheries management, which, therefore, are outlined afterwards. Finally, I compare the insights obtained for Faroe cod with other cod stocks.

The structure of the discussion is strongly influenced by the lack of any relationship between the spawning stock biomass and subsequent recruitment. The year-class strength seems to be determined at the 1-group demersal stage by factors other than the spawning stock biomass. This does, however, not mean that the spawning stock size plays no role. Ultimately, there exists a lower limit of the spawning stock at which point the year-class strength will be seriously hampered. Faroe Plateau cod seems, however, to have been above this lower limit during the whole time period of fisheries investigations (since the beginning of the 1900s), which justifies the structure adopted in this thesis.

## Determinants of Faroe cod production

### Feeding of cod in general

The food of cod is very diverse, and there are marked differences between cold (< $4^o$ C) and warm areas. Cod in cold areas feed on capelin, Clupeidae, sandeels, Arctic shrimp and pelagic crustaceans, while cod in warm areas feed on Clupeidae, Gadidae, sandeels and benthic crustaceans (Dalpadado and Bogstad, 2004; Daan, 1983; Kikkert, 1993; Hüssy *et al.*, 1997; Jaworski and Ragnarsson, 2006; Hanson and Chouinard, 2002; Høines and Bergstad, 1999; Lee and Khan, 2000; Link and Garrison, 2002; Morris and Green, 2002). Faroe Plateau cod resemble the 'warmwater' group and feed on sandeels, Norway pout and a variety of benthic crustaceans (Du Buit, 1982; Nicolajsen, 1993; Rae, 1967).

### Feeding in cod and other gadoids at the Faroes

The feeding niches / habitat used by cod are more complex than for haddock and saithe. Haddock, which has largely the same distribution as cod, feeds on benthic organisms such as polychaets and small crustaceans (Du Buit, 1982; unpublished material). Of special importance for cod is the fact that haddock apparently feed fairly efficiently on small benthic crustaceans, that later become an important part of the diet of juvenile cod. Except for sporadic feeding in the upper water column at great depths (150-200 m), as judged by the presence of *Parathemisto spp.* in the stomachs (unpublished material), haddock are a typical bottom feeder on small benthic organisms.

Saithe, on the other hand, feed on pelagic crustaceans (krill) and pelagic fish (Norway pout and Blue whiting) in deep water (150-500 m, unpublished data). Saithe is a good swimmer, which may be a prerequisite for feeding on mobile fish and plankton. In shallow waters (< 150 m) saithe also feed on sandeels. Of special importance for cod is the fact that cod and saithe partially compete for the same food resources in deep waters.

Consistent with previous studies (Rae, 1967; Du Buit, 1982), the latest findings suggested that cod in shallow waters (< 150 m) fed on large epibenthic crustaceans, such as squat lobsters (*Galathea spp.*), swimming crabs (Portunidae), *Hyas spp.*, hermit crabs (*Pagurus bernhardus* and *P. pubescens*) and various shrimp (Pandalidae) (Paper II). Occasionally, other large organisms were taken such as *Aphrodite aculeata* (Polychaeta) and Bivalvia. Brittle stars (Ophiuroidea) sometimes comprised a large part of the diet, especially in the shallowest waters (< 100 m) (Paper II). Of fish species, sandeels (Ammodytidae) were of special importance (Rae, 1967; Paper II). Sandeels feed on pelagic crustacean plankton during the day and hide in the sediments during the night (Temming *et al.*, 2004), as well as during the winter (October-March). Cod presumably feed on sandeels when they are buried in the sediments (as whiting in the North Sea, Temming *et al.*, op. cit.) or when they are about to enter or leave the sediments. However, the abundance of sandeels varies considerably inter-annually and is highest when phytoplankton production is high. When scrutinizing Rae (1967), one gets the impression that the abundance of sandeels in the 1950s was higher than today and did not vary as much inter-annually as has been observed since 1997 (Paper II). Cod also fed on small Norway pout, especially during the August-September period, when the 0-group of Norway pout was distributed in shallow waters (Paper II).

Cod smaller than about 30 cm fed almost exclusively on benthic crustaceans, but by the time they were 30-40 cm long they were able to catch fish such as sandeels and Norway pout. The proportion of fish in the diet increased during ontogeny and crustaceans were rarely found in cod that were larger than 80 cm (Paper II), which is in line with studies of cod in other areas (Pálsson, 1994).

Cod in deep waters (150-300 m) fed to a large extent on Norway pout (Paper II). These cod were larger (typically 60-90 cm) and much more infrequent than in shallow waters (Paper IV). Small haddock (< 20 cm) were also frequently found in the stomachs. In March, they ranged as the second most important prey (Paper II), which is in line with Rae (1967). The stomach fullness was typically around double of what was found in shallow waters (Paper II) and the length-at-age of these cod was also greater than for shallow water cod (Paper II). The benthic habit was, however, not abandoned as these cod frequently fed on the benthic crustacean *Munida spp.* (another squat lobster).

Cod in very deep waters (300-500 m) fed almost exclusively on Blue whiting (Paper II). These cod were quite large (70-100 cm) and very infrequent (Paper IV). The food items were typically quite large (15-30 cm long) and the stomach fullness up to three times of what was found in shallow waters (Paper II). Benthic crustaceans were rarely eaten (Paper II). Very large cod (> 100 cm) seemed to abandon feeding on Blue whiting or Norway pout in deep waters and fed instead on various flatfish species (Paper II).

The feeding behaviour in cod may be deduced from the stomach content. In shallow waters, cod may feed in close proximity to the ocean floor. The morphology of cod also seems to be adapted to a benthic mode of life. The upper jaw is longer than the lower jaw and cod are able to sense potential food organisms in the sediments by the barbel and the two special fin rays of the two pelvic fins (Mattson, 1990). Cod search along the bottom with the barbel and the special fin rays in contact with the bottom (Brawn, 1969). Food organisms (i.e., bait) that release odours may be found by cod that are moving slowly around and can be captured without intense swimming activity. Cod may also be able to sense food organisms by use of the barbel or fin rays (Brawn, 1969; Mattson, 1990). Some organisms are, however, not detected until they move, even if visible to the human eye

(Steingrund and Fernö, 1997). Some prey are quite stationary and can presumably be caught without difficulties, like *Hyas coarctatus*, which presumably relies on crypsis. Hermit crabs, a very important food item in Loch Torridon, Scotland (Hawkins *et al.*, op. cit.), are probably also easy to identify, and small items were swallowed whole (with gastropod shell) (unpublished material). Large individuals presumably need to be shaken out of the shell first (Brawn, 1969). Other prey items may be more active, requiring greater swimming activity by cod. These include swimming crabs, squat lobsters, shrimp and especially fish. Cod are rapid swimmers over short distances (Steingrund and Fernö, 1997) and have a high manoevrability, but are less adapted to prolonged swimming (Martinez *et al.*, 2004; Soofiani and Hawkins, 1982; Soofiani and Priede, 1985).

The feeding behaviour of cod in deep waters (> 150 m) is probably not much different from their feeding behaviour in shallow waters. In deep waters, most cod still fed on benthic crustaceans, albeit only on one species (Paper II), and the fish were presumably caught when they were close to the bottom. On the other hand, it is known that at least one cod, tagged with a data storage tag, spent the night at a depth of 300 m (3-6 °C). The cod spent the day at a depth of 400-600 m (1-2 °C) from June 2003 to January 2004 (Figure 2). This indicates that not all cod spend all their time in close association with the bottom, at least not when they are close to the transition layer between the warm Atlantic water and the cold Arctic water (at about 500 m depth). It seems reasonable to assume, however, that the feeding on mobile fish (Norway pout and Blue whiting) requires more energy than feeding on benthic organisms.

Interestingly, the condition factor of cod had a marked influence on the stomach content (Paper II). (The relationship is unlikely to be the reverse, i.e., high feeding success leads to high condition factor, because the build-up of a high condition factor needs successful feeding during several weeks and not only during the last one-two days before the individual was caught.) Well-fed fish may have a higher feeding motivation, since their digestive capacity may be up to 29 times higher than a starving cod (Blier *et al.*, 2007) and well-fed cod may also have a higher rate of protein turnover and energy expenditure (Jobling, 1994; Couture *et al.*, 1998). The fact that the condition factor influenced the feeding efficiency on all prey organisms indicates that the swimming capacity of cod is of crucial importance. There is a stong positive correlation between the condition factor of cod and the swimming capacity (Martinez *et al.*, 2003; Martinez *et al.*, 2004). Since cod may pursue their prey only for a few seconds (Steingrund and Fernö, 1997), an endurance-exhaustion strategy is unlikely. Rather what is more probable is a predating strategy based on short bursts of activity. This strategy may have been used by cod in shallow waters (< 150 m) when feeding on sandeels and crustaceans, since those cod grew more slowly and yet had a higher condition factor than cod that were located deeper (Paper II). A high condition factor, i.e. a large cross-sectional area of the muscles and therefore force (Schmidt-Nielsen, 1983), should provide a rapid acceleration. The apparent need to gain length, rather than condition, in order to feed efficiently on fish in deep waters (Paper II) indicates that these cod swam more steadily and needed a larger swimming stroke (Videler, 1993). Cod in good condition could, alternatively, be dominant individuals and have larger home ranges than cod in poor condition or be able to scrounge for resources produced by other individuals (Beauchamp *et al.*, 1997).

Feeding success in Faroe Plateau cod also seemed to be related to prey density (Floeter and Temming, 2003; Paper II). The density of prey fish was estimated by the number of fish smaller than 23 cm that were caught in the survey trawl. In addition, feeding success depended on the density of cod, either because competition increases with increased predator density (Milinski, 1986) or because cooperation is more efficient with increased predator density (Brown and Laland, 2006). The relative importance of prey density and cod density on feeding success was investigated by grouping the stomach investigations in Paper II into three levels of prey fish densities and three levels of cod densities (Table 2). Feeding success increased with prey fish density when prey fish density was very low, but not when prey fish density was above this low threshold (Table 2). Feeding success increased with cod density when cod density was low (and prey fish density high), whereas feeding success decreased when cod density was high (and prey fish density low) – and no relationship was found at intermediate cod densities (Table 2). Cod fed little during spawning in March (PFI = 0.30, Table 2), and, if the March investigations were omitted from the considerations in Table 2, there was no effect resulting from prey fish density or cod density when they were on a medium level (in August shallower than 150 m depth). However, there was a positive effect on feeding success resulting from cod density when cod density was halved and prey fish density was doubled (in August deeper than 150 m, Table 2).

Table 2. Feeding rate of Faroe Plateau cod on fish as measured by the stomach partial fullness index (PFI). PFI is related to prey fish density (numbers per trawl hour) and cod density (kg per trawl hour) and their variability (coefficient of variation, CV). The PFI is defined in the text.

| **Feeding success in relation to:** | **Low prey fish density** Geomean 3.4 fish per trawl hour, CV 135% | **Medium density** 89-102/hour, CV 49 – 57% | **High density** 199/hour, CV 44% |
|---|---|---|---|
| **Low cod density** Geomean 40 kg per trawl hour, CV 38 – 47% | Not available. | March > 150 m depth.<br>Spawning migration.<br>PFI = **1.07**.<br>No relationship with prey density or cod density. | August > 150 m.<br>No spawning.<br>PFI = **1.28**.<br>No relationship with prey density, but **positive** relationship with cod density. |
| **Medium density** 78 kg/h, CV 32% | Not available. | August < 150 m.<br>No spawning.<br>PFI = **0.57**.<br>No relationship with prey density or cod density. | Not available. |
| **High density** 302 kg/h, CV 36% | March < 150 m.<br>Spawning migration or spawning activity.<br>PFI = **0.30**.<br>**Positive** relationship with prey density and **negative** with cod density. | Not available. | Not available. |

In the paragraph above, stomach fullness was presented as a function of local cod density, and this raises the question of cause and effect, i.e., whether shoaling enhances feeding or is a result of successful feeding. Shoaling is often regarded as a trade-off between feeding (Brown and Laland, 2006) and predator avoidance (see introduction and references in DeBlois and Rose, 1995; Sogard and Olla, 1997). Shoal structure may be more compact in response to predation threat while shoals of cod might spread out (upward from the bottom accompanied by reduced density) in response to feeding opportunities. There might be a reversal of shoal structure at very high prey densities (DeBlois and Rose, 1995), i.e., when food demands are fullfilled and the predation aspect of group formation, therefore, could become more important.

The question is whether the occasional large aggregations of cod in deep waters (> 150 m) at the Faroes (> 1000 kg per trawl hour) reflected an aggregative response of already satiated individuals that, e.g., were attempting to minimise predation threat. This seems, however, unlikely because the general predation threat from sea mammals in Faroese waters seems to be low, compared to Canadian waters where the observations of DeBlois and Rose (1995) were made. It is also hard to imagine that cod in Faroese waters aggregate in such large shoals only to minimise predation threat. Alternatively, shoaling may actually enhance feeding success (Temming *et al.*, 2004; Temming *et al.*, 2007) in addition to the well-known effect to reduce predation threat, i.e., two goals achieved at the same time. If this is correct, then it would be advantageous to increase the abundance of cod in deep waters by, e.g., reducing fishing effort in deep waters because the natural production of cod would be increased. The potential seems quite large because the areas of > 150 m depth are larger than the shallow areas. Table 2 indicates that the density of cod in the deep water areas is only half that of the shallow areas, whereas the prey density is double, i.e., four times more prey per cod in deep waters.

In summary, cod feed most efficiently when they are in good condition and are present in high densities. Their feeding success presumably relies on speed and/or acceleration and some sort of group benefit – but these factors may not be relevant for very large cod. Very large cod (> 100 cm) could be too large to get the necessary acceleration to catch highly mobile prey such as Norway pout and Blue whiting. Also, since individual cod may prefer to school with other cod of similar size (Hoare *et al.*, 2000), the average density of very large cod could be too low to permit the formation of schools. Therefore, it was not unexpected that some of these very large cod undertook a combined feeding / niche shift and moved to shallower waters where they preyed on other fish, especially flatfish. Flatfish often rely on crypsis (Endler, 1991) and also hide by covering themselves with sediments (Godø, 1994). Cod may use their traditional bottom feeding behaviour (Brawn, 1969) to search for these hidden flatfish. Flatfish comprised around half the diet of very large cod (Paper II), presumably because very large cod were strong enough to grasp, hold and ingest these slippery, disc-shaped fish. The question remains whether a smaller proportion of very large cod would undertake this niche / habitat shift if their abundance were higher.

Hence, while haddock and saithe undertake no or only one combined feeding / niche shift during ontogeny (as juveniles-adults), cod may undertake two such niche shifts, i.e., occupying three niches in total. Put most simply, cod need to feed like a haddock when small (bottom feeding on small prey) and like a saithe when large (pelagic fish feeding). Some very large cod also need to change their feeding habit from pelagic fish feeding to bottom feeding in shallower waters on large prey, which could be regarded as the typical feeding niche for cod.

### Distribution and migration in cod at the Faroes

The feeding habits of cod seemed to have important consequences for the distribution and migration of cod. Before these consequences can be treated in more detail, a word on the general distribution and migration pattern of cod is necessary.

The northern spawning area was the most important spawning location and the migration routes from it extended virtually all around the Plateau (Figure 6 in Paper IV). Some of the migration routes (mainly large cod) extended also into deep waters, often through gateways with high relief. The spawning area south-west of the Faroes was of secondary importance and migration routes extended through the areas west of the Faroe Islands. There were also gateways to deep waters from this spawning area. The chart of the migration routes (Figure 7 in Paper IV) should be interpreted as follows: As cod move away from their spawning areas, some might stop their migration at a certain point on the migration route and hold to that place until the next spawning. The migration routes are, thus, in reality broader and more diffuse than indicated on the chart. Broadly speaking, the migration routes of cod on the Faroe Plateau are simple in the areas east of the Faroes and complex in the West and South. In the east, all cod move northwards towards the northern spawning area and back again after spawning. In the west and south, cod move to one of three alternative spawning areas. Some migration routes are through sounds where deep (100 m) trenches are located, and it is possible that cod migrate through these trenches, as observed in the Gulf of Maine (Gröger *et al.*, 2007). The size of the migrating groups in Faroese waters is not known. Investigations off Eastern Canada suggested that group size may range from small (Comeau *et al.*, 2002) to very large (Rose, 1993).

The bottom topography on the Faroe Plateau is such that the fjords and the shallow areas (< 75 m), i.e., the nursery areas of juvenile cod, are located in the east, whereas the areas typically occupied by medium-sized cod (50-70 cm) are located west of the Faroes (Figure 1). There are, therefore, some distributional shifts towards the west of juvenile cod (1- to 3-year old, Paper III; Paper IV).

When cod reach an age of 3-4 years (55-60 cm), they become sexually mature. They have, by then, adopted the typical spatial and depth distribution of cod. The densest concentrations of cod were found north and west of the Faroe Islands at depths less than 150 m (Paper IV). During ontogeny, the distribution of cod extended deeper and southwards. By age 7+ (> 80 cm long), cod were found in the largest concentrations on the rich and deep feeding areas east of the Faroe Islands. At even greater sizes (age 9+, > 95 cm), they seemed to return to shallower waters. The temperature declines slightly from north to south and into deeper waters (Figure 2). Laboratory experiments indicate that small Icelandic cod (50 g) grow fastest at high temperatures (14.3 $^{o}$C), while large cod (5000 g) grow fastest at 5.9 $^{o}$C at unlimited food rations (Björnsson and Steinarsson, 2002). If ration is limited, cod prefer lower temperatures (see Pálsson and Thorsteinsson, 2003). These distributional shifts of cod on the Faroe Plateau may be consistent with a migration towards more optimal temperatures for growth, and Blanchard *et al.* (2005) had success with a similar approach when modeling the spatial distribution of 1- to 2-year-old cod in the North Sea. However, the temperature differences between the various spatial areas occupied by cod are rather small on the Faroe Plateau. Therefore, it is uncertain whether the observed match between migration and temperature is coincidental in the Faroes and actually caused by other factors. Paper IV explores whether there was a net migration southwards during ontogeny, without reaching any firm conclusion.

The distribution of cod may be regarded as a result of the initial settling locations (Rindorf and Lewy, 2006) and active movement later in life. The migration pattern can probably not be deduced from the spatial distribution, at least not with sufficient detail. Extensive tagging experiments have revealed the overall migration pattern. The taggings were mainly based on conventional tags, which normally give a reliable picture of fish migrations (Bolle *et al.*, 2005; but see Gröger *et al.*, 2007). Broadly speaking, cod on the Faroe Plateau used the same spawning areas and feeding areas over successive years. This means that a cod that feeds, e.g., east of the Faroes will migrate to the northern spawning area (Norðhavið) and return to the same feeding area (east of the Faroes) after spawning. Site fidelity and migration route familiarity is also described for cod in Placentia Bay, Newfoundland (Windle and Rose, 2005) and in Gilbert Bay, Labrador (Green and Wroblewski, 2000), which shows that Faroe cod are not exceptional in this respect. The size of the home ranges of juvenile cod in a coastal area of Newfoundland has been estimated at 2.1 ha (Cote *et al.*, 2004), and adult coastal cod in Southern Norway are estimated to have home ranges of 27 ha (Espeland *et al.*, 2007). Juvenile cod in Loch Torridon, Scotland, occupied home ranges of 1 ha (Hawkins *et al.*, 1985).

When comparing the distribution of cod and the distribution of important prey fish (Norway pout and Blue whiting) on the Faroe Plateau (Paper II, Paper IV), an astonishing feature is evident: Cod were distributed in shallow waters, while the food was distributed in deep waters, i.e., the spatial overlap between cod and important prey (Norway pout and Blue whiting) was very poor. The distribution of cod apparently matched best the distribution of sandeels and benthic crustaceans, which were abundant in shallow waters. Before possible explanations are considered, the migration routes to deep waters will be described.

Even though cod are quite stationary with respect to feeding areas, they, nevertheless, move deeper through ontogeny (except very large cod that partially return to shallower waters). The selection of feeding area and depth occurs during post-spawning migration, as indicated by the depth dynamics of a number of cod tagged with data storage tags, i.e., a large variation in depth during April-May and much less variation during the feeding season in June-December (Steingrund, 1999; Paper V; Figure 2). The conventional taggings also indicate that cod migrate to their former feeding area first and then 'evaluate' whether they should change feeding depth or not. This mechanism has important consequences for colonisation of the deep waters. As evidenced by the distribution of cod, the majority of medium-sized cod were distributed north and west of the Faroe Islands, while the rich feeding areas were located in deep waters east of the Faroe Islands. The taggings showed that cod in the north and west seldom migrated to the eastern areas.

In order to reach the rich, deepwater resources east of the Faroes, cod need to migrate along complex and long migration routes. Cod to the east had the shortest migration route, which probably was a straight line into the deep waters. The 'gateways' to deep waters were normally located in high-relief areas, which could be a result of the tendency of cod to prefer high-relief areas to plain areas (Cote *et al.*, 2004). Cod to the north probably migrated northwards onto the slope and moved eastwards (this migration route was not presented in Paper IV). Cod in the west probably moved onto the slope first and then southwards to the Munkagrunnur area (south of the Faroes) and north-eastwards along the slope. Hence, the Munkagrunnur area could be a transitory end station for cod before they moved to the deep areas east of the Faroes. The distribution and migration pattern outlined above describes the average situation. There were, however, important year-to-year differences in the distribution and migration pattern of cod on the Faroe Plateau. Two different phenomena will be discussed in the following section, one concerns the migration pattern in shallow waters and the other the migration to deep waters.

The first phenomenon (Phenomenon 1) is that cod in shallow waters (< 150 m) on the Faroe Plateau moved deeper when they were in good condition and *vice versa*. When the condition factor was low, up to 28 % of the cod moved from traditional fishing depths (110 m) to an area close to land (Paper V) where the depth was less than about 75 m, and many cod were observed close to harbours and were fished in substantial numbers. Although not investigated in detail, there seemed to be no effect of sex, as both sexes seemed to be equally well represented in the movement towards land. In contrast, when cod were in good condition, very few cod migrated towards land. The mechanism(s) behind the inward / outward migration of cod is poorly known. If the feeding on Norway pout, located deeper than 120 m depth, requires much swimming activity, which, in turn, may be positively correlated with condition (Martinez *et al.*, 2003; Martinez *et al.*, 2004), then slim cod may feed more efficiently on benthic crustaceans close to land than on mobile fish in deeper waters. Also, as food became scarcer, dominant individuals probably expanded their home ranges / territories so that inferior competitors lost ground and became 'floaters' (Milinski and Parker, 1991) that moved towards land.

The second phenomenon (Phenomenon 2) was that cod moved to deep waters (> 150 m) when the competition for shallow water resources was strong (Paper VII). Actually, the distribution of cod on the Faroe Plateau seemed to match the spatial distribution of sandeels (Paper II). Since saithe distribution matched well the distribution of Norway pout (unpublished data), there could exist a resource partitioning (Milinski and Parker, 1991) between cod and saithe. However, some cod, especially large cod, moved to deep waters and there also seemed to be differences between year-classes. The depth-distribution of a year-class seemed to be determined at an age of 4-5 years and depth increased with increasing abundance of 3- to 4-year-old cod. Phenomenon 2 may be regarded as a range expansion when abundance is high (Robichaud and Rose, 2006). The logic for considering 3- to 4-year-old cod was that they were very abundant and were distributed shallower than 4-to 5-year-old cod, i.e., they ‘pushed’ the 4- to 5-year-old cod outwards. Although not investigated specifically, it seemed likely that the movement to deep waters occurred just after spawning (i.e., in April-May). It is not unreasonable to surmise that slim 4- to 5-year-old cod (that had just spawned) lost the competition for shallow water resources against 3- to 4-year-old cod where at least some of them (30 %) were immature and often had a higher condition factor and could be stronger competitors.

This bears a similarity to guarded resoures that cannot be monopolized when the number of intruders is high (Chapman and Kramer, 1996). The stationary habit of cod in shallow waters could prevent them from encountering, or otherwise being informed about, the rich food resources in deep waters. They would probably need to rely more on public (Valone and Templeton, 2002) rather than private information (Bergen *et al.*, 2004). Fish may acquire information about the diet of other fish by the scents emitted from their faeces (Morell *et al.*, 2007). However, all the cod on the spawning grounds, which represent a mixture of cod from shallow and deep waters, could have excreted faeces originating from the deep waters. Results from Data Storage Tags indicated that most cod made short visits (a few days) to deep waters (> 150 m) during their post-spawning migration, and could thus get some information about the deepwater food resources. Alternatively, site fidelity, rather than lack of information, could explain the reluctance of cod to enter deep waters. There are several benefits to keeping restricted home ranges, including knowledge of food distribution, cooperative feeding (Brawn, 1969) and less aggressive actions against unfamiliar conspecifics (see Warburton, 2003). The presence of occasional rich feeding opportunities may not be a sufficient stimulus to attract cod from nearby home ranges. Free-ranging cod in a small Icelandic fjord were artificially fed substantial quantities of herring and capelin during a 17-month feeding experiment (Björnsson, 2002). Only around half of the local cod population in the fjord were attracted to the three feeding stations and cod from three nearby areas located 16, 6 and 3 nautical miles away, respectively, seemed not to migrate to the feeding stations. The author suggested that limited home ranges of immature cod could explain the results.

It is difficult to point to a specific feeding strategy or theory that explains Phenomenon 2 unequivocally. Cod may use a win-stay, lose-shift strategy (Nowak and Sigmund, 1993; Posch, 1999): If resources are sufficient in shallow waters then stay, else move to deep waters. Optimal foraging theory may also partly account for the observed pattern. According to the marginal value theorem (Charnov, 1976), a patch should be exploited for a longer time, if travel costs are high (Hart, 1993). Travel costs when moving to deep waters are likely high. If cod are risk averse, i.e., they do not maximise net food intake, but instead minimise the risk of starvation (Hart, 1993), they could avoid the deep water habitats, because there could be higher spatial and temporal variability in food reward.

Predation threat may affect fish distribution (Milinski, 1993), even though the predation act may be infrequent (Houston and McNamara, 1997). The effect of predation threat should be greatest on small fish, and the distribution of juvenile cod close to land at the Faroes, away from adult cod, could be regarded as a response to predation threat. Small bluegill sunfish were found in cover, whereas larger individuals, no longer vulnerable to predation, left the cover in order to exploit richer feeding patches on benthos (Werner *et al*., 1983). Laboratory experiments have shown that fish move away from potential predators on very small spatial scales (Nordeide and Svåsand, 1990; Nødtvedt *et al*., 1999). Large scale displacements of fish in response to predation threat in the field may be infrequent, at least in a Norwegian fjord (Nøttestad *et al*., 2004). Predation threat in Faroese waters is poorly known. A number of seabirds feed on fish in shallow waters. A small population of grey seals breed on special locations and feed in shallow waters on various fish species of less than 30 cm length, including cod (Mikkelsen *et al*., 2002). There is also anecdotal evidence that porbeagle sharks patrol the shallow areas, as they are caught occasionally by hooks. Regarding the deeper waters, hooded seals may migrate into deep Faroese waters and prey on fish (Folkow and Blix, 1999). There are also a number of whale species, the fin whale and mink whale, which have been observed in great numbers (Skov *et al*., 2002). The relative predation threat in shallow versus deep waters is not known. Evidence suggests, however, that the predation threat is not important for cod distribution. The predation threat is supposedly greatest in April-September when the great whales are present in Faroese waters and less during the rest of the year. It would thus be expected that cod should be distributed in shallower waters in April-September than during the rest of the year, but that seems not to be the case (Figure 2).

To the author's knowledge, Phenomenon 1 appears not to have been described for other cod stocks. Chouinard and Swain (2002), which seems to be the only work considering condition and distribution in cod, found a rather complex pattern in condition and length-at-age with depth in Southern Gulf of St. Lawrence. When abundance was low, condition was uniform over shallow and intermediate depths (< 100-125 m), but when abundance was high, condition was highest in the shallowest waters and declined steadily to 100 m depth. Condition was always low in deep waters. Length-at-age, which showed a different pattern than condition, followed temperature closely, i.e., greater or longer length-at-age in the shallowest waters, shorter at intermediate depths and again longer length-at-age in deep waters. The authors suggested that cod could choose between high benefit (food) – high cost (temperature) in shallow areas, or low benefit – low cost in deep waters. The authors had several problems when interpreting their results, for example, that the actual food availability by depth was unknown and that there could be a mixing of different cod populations. Also, the effect of sub-lethal hypoxia on cod swimming behaviour and distribution (Dutil *et al*., 2007; Herbert and Steffensen, 2005) was not considered. There was apparently no (negative) relationship between condition and depth occupation as in Faroese waters (Phenomenon 1). It seems clear, however, that more cod in Southern Gulf of St. Lawrence were displaced to poor-quality habitats when abundance was high, which is somewhat similar to Phenomenon 2. For demersal juvenile cod in Placentia Bay, Newfoundland, Robichaud and Rose (2006) found that distribution was density-dependent, i.e., range expansion / contraction with high / low abundance, which was also discernible for age 2 cod in S. Labrador (Anderson and Gregory, 2000). This mechanism, which is widely observed for marine fishes (Casini *et al*., 2005; see references in Robichaud and Rose, 2006), bears similarities with Phenomenon 2 in Faroese waters and is simpler, as there was no interaction between cohorts.

The existence of two, apparently dissimilar, distribution mechanisms (Phenomena 1 and 2) in Faroese waters may be a consequence of the migratory habits in cod. Cod in Faroese waters are fairly stationary (Paper IV) and seldom move more than 10 nautical miles from the place where they are tagged (Paper III). The movement to shallower / deeper waters with a low / high condition factor (Phenomenon 1) may be regarded as a distributional adjustment (within the area where the individual home ranges in cod are located), not a habitat shift. The movement to deep waters

(Phenomenon 2) may, however, be regarded as a true niche/habitat shift in which the original habitat is abandoned. While individual characteristics / abilities (condition factor and presumably swimming ability) seem to be crucial for the distribution within the home ranges (Phenomenon 1), competition for shallow water resources (food, space) seems to be crucial for the colonisation of deep waters (Phenomenon 2).

Fish distribution may be regarded as the outcome of the interplay between various abiotic and biotic factors, and is, therefore, a highly complex process (Giske *et al.*, 1998). Cod tend to avoid very low (sub-zero) temperatures, as observed by the southward migration of Labrador cod (deYoung and Rose, 1993; Rose *et al.*, 2000) and cod at Greenland (Jensen, 1939) (see also Castonguay *et al.*, 1999). Cod also avoid water with low salinity (ICES, 2005) or low oxygen content (Claireaux et al., 2000; see Dutil *et al.*, 2007). Biotic factors such as prey abundance (Pálsson and Thorsteinsson, 2003), intraspecific competition (Anderson and Gregory, 2000; Robichaud and Rose, 2006), and probably predators may also be decisive for cod distribution. Abiotic and biotic factors may also interact and shape cod distribution. When examining the spatial distribution of cod in the Southern Gulf of St. Lawrence, Swain (1999) found that shifts in cod distribution during the feeding season appeared to be more closely linked to density-dependent changes in environmental preferences (seeking cooler waters when food ration was low) than to density-independent responses to changing environmental conditions (avoiding extremely low temperatures). Pálsson and Thorsteinsson (2003) came to a similar conclusion when investigating the depth-distribution of cod at Iceland.

Alternatively, the factors affecting cod distribution may be grouped into physical, physiological and behavioural categories. The transport of eggs / larvae by oceanic currents is a physical process and may determine the spatial distribution of cod juveniles (Ottersen *et al.*, 2002). In this thesis, cod stocks are grouped into three broad categories (see Table 1). While the larvae / juveniles are passively carried by oceanic currents, larger juveniles and adult cod have sufficient swimming capability to withstand oceanic currents. Adult cod may be constrained by physiological factors, such as swimbladder physiology. Cod are able to tolerate a 25% reduction and 50% increase in swimbladder volume, termed the free vertical range (FVR, Arnold and Greer Walker, 1992), and vertical migrations of cod and other fish often comply with the FVR (Stensholt *et al.*, 2002). Therefore, a cod acclimated to, e.g., a 100 m depth, is able to move between 80 and 155 m depth without difficulties. In order to move beyond this vertical range, cod need to adjust the amount of gas in the swimbladder. Cod tagged with Data Storage Tags are able to descend by, on average, 10 meters per day for 1-30 days (Koij van der *et al.*, 2007). Thus, they need around twenty days to acclimate from a 100 m depth to a 300 m depth. Within the free vertical range, cod may be constrained by behavioural factors, such as the presence of familiar conspecifics (Morell *et al.*, 2007) or knowledge / adjustments to the home range in general. The latter depends on spatial learning abilities, which may vary between populations (habitats) of three-spined sticklebacks (Girvan and Braithwaite, 1998). Phenomenon 1, where cod seek deeper waters when they are in good condition and *vice versa*, seems to be constrained by behavioural factors only. Phenomenon 2, the distribution of cod into deep waters, may be constrained by behavioural factors, as well as swimbladder-physiological factors. Thus, the reluctance of Faroe Plateau cod to move to deep waters suggests that depth / temperature adaptation is a very important limiting factor in cod distribution and migration (see later).

The following discussion explores briefly the linkages between the migratory behaviour of Faroe Plateau cod with the financial crisis in the beginning of the 1990s. Contrary to popular belief, there is very little evidence for the 'large-scale migration' hypothesis. Tagging experiments show that cod are confined to the Faroe Plateau (99.9%, Paper III, unpublished data). Hence, a large-scale emigration of cod seems very unlikely, but, unfortunately, no taggings were performed in the 1980s. A migration in the opposite direction also seems unlikely. A few cod migrated from Icelandic waters to the Faroes (Jónsson, 1996), and from the North Sea (Bedford, 1966, see also Paper III), but there is, nevertheless, scant evidence that cod of foreign origin migrate to the Faroes in substantial numbers, although Tåning (1943) speculated whether some cod from the strong 1922 and 1924 year classes of cod at Greenland had migrated to the Faroes. Although cod of Icelandic origin typically inhabit the Faroe-Iceland Ridge (ICES, 2006a), genetic evidence suggests that migration of foreign cod to Faroe Plateau was very limited. As mentioned earlier, Faroe Plateau cod have a rather unique combination of hemoglobin and *Pan*I frequencies, compared to neighboring cod stocks and a large-scale immigration to Faroese waters in the mid 1990s should be expected to change these frequencies dramatically. On the contrary, there was no difference in HbI(1) frequencies between 1999 (0.07, unpublished data) and former values (0.06 in Sick, 1965), i.e., no immigration from the North Sea where the frequencies are around 0.5-0.7 (Sick, 1965). Also, a *Pan*I$^{A}$ frequency of 0.88 in September 1997 is considerably higher than 0.21 on the Faroe-Iceland Ridge (Case *et al.*, 2005), which renders an immigration of Icelandic cod very unlikely.

## Recruitment in Faroe Plateau cod

The feeding habits of adult cod seemed to be decisive for the migration pattern / distribution of adult cod over the shallow areas on the Faroe Plateau, which in turn affected the survival of 1-year-old cod (Paper V). This finding is controversial with respect to traditional recruitment theory (see Introduction), where, e.g., the spatial and temporal match between cod larvae and its food is considered crucial for recruitment success (Brander *et al.*, 2001) and where there tends to be a positive relationship between larval growth – inversely related to predation mortality – and subsequent recruitment (Campana, 1996). For Faroe cod, there was no relationship between the mean age in the spawning stock and subsequent recruitment two years later (Paper V). While a diverse spawning stock may likely lead to higher individual spawning success (Rowe *et al.*, 2007) in Faroe Plateau cod, this factor did not show up in terms of the abundance of pelagic 0-group juveniles three months later or recruitment at age 2. Similarly, a successful spawning event east of Newfoundland did not lead to increased recruitment (Smedbol *et al.*, 1998). A positive relationship between the 0-group index and recruitment (as 2-year-olds) was apparent in the 1970s and 1980s (Jákupsstovu and Reinert, 1994), but the relationship broke down in the 1990s, eventually leading to a fairly weak, but statistically significant, correlation (R = 0.42, Paper V) for the 1982 – 2004 period (Figure 5).

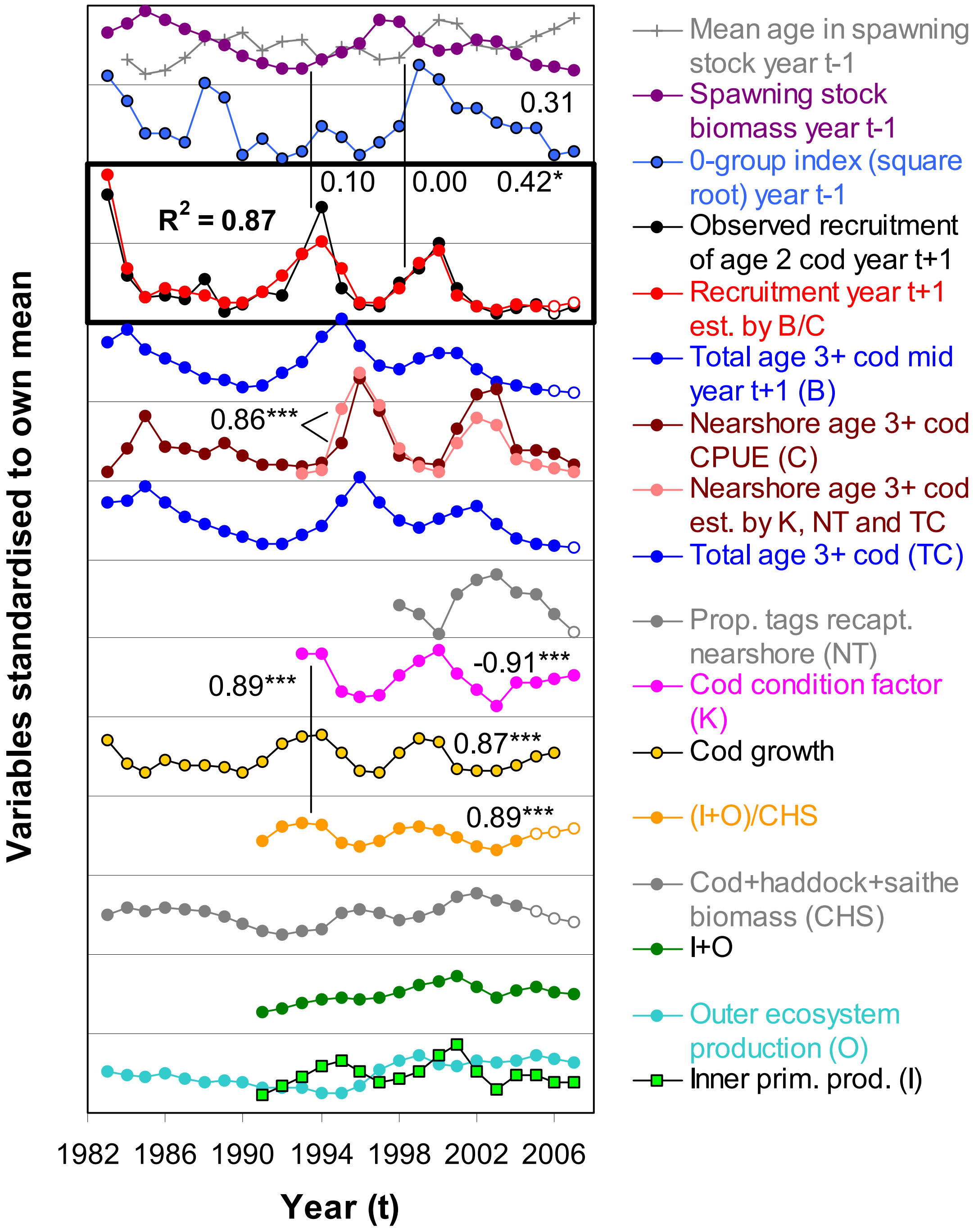

Figure 5. Interannual variation in recruitment of Faroe Plateau cod investigated by two approaches. The 'traditional' approach starts from above and includes relationships between spawning stock characteristics and subsequent recruitment to the fishery two years later. An alternative approach starts at the bottom of the chart where ecosystem productivity (inner and outer areas) and fish biomass (cod, haddock and saithe) determine individual growth of cod, which in turn determines the extent of cannibalism. The recruitment model incorporated cannibalism and stock size of cod and is highlighted by a bold frame. Correlation coefficients are shown between adjacent variables or indicated with lines. * p < 0.05, ** p < 0.01, *** p < 0.001, no star: p > 0.05.

A great improvement was noted, however, when recruitment variability was coupled with the feeding habits and movement of adult cod (Figure 5, Paper V), i.e., that cod moved towards land occasional years. This observation is not new, according to Landt (1800, p. 221): 'After spawning, it happens in occasional years that cod move into the fjords, where they are called *Landfish*, and are usually fished in great numbers' (my translation). Paper V suggests that these 'Landfish' are in poor condition, and they also have a special name in Faroese: 'slánur' (skinny cod). It is common knowledge among Faroese fishermen that the occurrence of skinny cod close to land is 'a bad sign' regarding future cod catches. In contrast, cod in good condition moved outwards from land (Paper V) and fed more on fish than otherwise (Paper II). This behaviour is beneficial for cod, as cod may grow faster on a fish diet than a crustacean diet (Björnsson and Bombaxe, 2004). This presumably created good survival opportunities for 1-year-old cod during the summer, resulting in a strong recruitment to the fishable stock some months later (Paper V, Figure 5). Interestingly, the summer period coincides with maximal seasonal growth rates in juvenile cod in Loch Torridon, a fjordic sealoch on the west coast of Scotland (Hawkins *et al*., 1985) and may be expected to coincide with maximal seasonal movement activity. The mortality on 1-year-old cod caused by cannibalism during the March-August period was estimated at 0-1.5 (on average 0.44). This is 'in the middle' of what is found elsewhere (Pedersen and Pope, 2003): Barents Sea (1.0), Sørfjord (1.5), North Sea (0.4-0.5), Western Baltic Sea (0.1) and Eastern Baltic Sea (0.1-0.2). Where cod populations are very low, other fish species may become important predators on juvenile cod, such as Grey gurnard in the North Sea (Floeter *et al*., 2005).

It is difficult to elucidate the 'where and whens' regarding the cannibalism. It could occur in the nears-shore waters, but a small stomach sample indicates that this might not be the case (no cannibalised 1-group cod found in 45 stomachs), i.e., similar to what has been shown for Icelandic fjords (Bogstad *et al*., 1994). Alternatively, adult cod close to land could displace 1-year-old cod to typical cod-depths (100-150 m) where they are cannibalised. The mortality caused by cannibalism is known to be high enough in typical cod-depths to regulate year-class strength (Paper V). Further support is gained from the fact that 1-year-old cod distribute themselves deeper on the Faroe Plateau in years when age 3+ cod are most prominent in shallow waters and *vice versa* (Paper VI).

The regulating effect of cannibalism on year-class strength could be valid for other areas. The cannibalism in Faroese waters constituted 1.9% in weight per stomach, which was lower than in Arcto-Boreal systems (Barents Sea, Iceland, and Newfoundland), and in the North Sea where it was on the order of 4-6% (Bogstad *et al*., 1994), although lower cannibalism was observed in the North Sea in 1991 (Kikkert, 1993) than in 1981 (Daan, 1983). Cannibalism in the Baltic may be considerable some years (Neuenfeldt and Köster, 2000). A common observation is that cannibalism increases with an increasing encounter rate between adult and juvenile cod, which may happen if the spatial overlap between them is increased. Thus, a positive relationship between cannibalism and year-class strength is often observed, as well as between cannibalism and the size of the adult stock (Bogstad *et al*., 1994; Neuenfeldt and Köster, 2000).

Cannibalism in the Faroe area may regulate year-class strength in a different manner than in the areas mentioned above. Although cannibalism in Faroese waters seemed to be related to the overlap between adult and juvenile cod, i.e., the same as for the other areas, the year-classes seemed not to be regulated according to their initial size, since no relationship was observed between the 0-group index and recruitment at age 2. In the other areas mentioned above (except Newfoundland), there seemed to be a positive relationship between 0-group abundance and VPA abundance at age 3, and that cannibalism was most prominent for good year classes and least for weak year classes, i.e., the relative strength of the year classes was similar. Therefore, the estimate of year-class strength at the 0-group stage may probably be used in future projections, although cannibalism may be in the same order of magnitude as the size of an average year-class (Daan, 1983; Bogstad *et al*., 1994).

During the work undertaken with regard to Paper V in which recruitment models were investigated, the two main factors in the cod recruitment models were cannibalism and food availability. The author had long favoured a model (Model 1 in Figure 6) in which recruitment was a function of food availability and cannibalism. The model was intuitive, as it stated that recruitment was positively influenced by food availability (phytoplankton production used as a proxy for food availability in higher trophic levels) and negatively by the abundance of cod close to land (cannibalism). The model was, however, not able to explain the most recent data points when cod biomass was extremely low. In 2006-2007, there was some uncertainty as to whether or not this discrepancy was due to imprecise assessments. Now (in 2008) it seems, however, quite likely that the 2003-2004 year classes are considerably weaker than predicted by the Model because the fish are now 4-5 years old and their abundance should be reliably estimated in the Faroese groundfish surveys (in March and August 2008). Thus, a new recruitment model was developed that took into account the stock size of cod in addition to cannibalism (Model 2 in Figure 6):

$$R_t = aB_t/C_{t-1} + d \qquad \text{(recruitment model)}$$
$$r^2 > 0.8,\ p < 0.001,\ n = 23\ (1983\text{-}2005)$$

where recruitment (R) at age 2 year (t) was directly proportional to the ratio between the total biomass of cod (B = age 3+) and cannibalism (C = CPUE of age 3+ cod close to land) *the previous summer* ('a' and 'd' were constants). In other words: many age 2 cod enter the fishery in years when the abundance of older cod (age 3+) is high and when few predatory cod were found in the nursery areas of juvenile cod (age 1) close to land the previous summer. The predatory group of cod in the nursery areas ($C_{t-1}$) consisted of age 3+ cod, which should not be confused with age 3+ cod over the entire Faroe Plateau in the recruitment year ($B_t$). It should also be stressed that the abundance of cod in the nursery areas did not fluctuate in exactly the same way as the total abundance of cod on the Faroe Plateau, although there was a positive correlation between them. Food availability is incorporated indirectly in the recruitment model, as C tends to vary inversely with food availability. The recruitment model was able to account for the weak 2003-2004 year classes, as well as all year classes back to 1982 (all available data points). Forcing the Model through origo made little difference (Model 3 in Figure 6, Paper V).

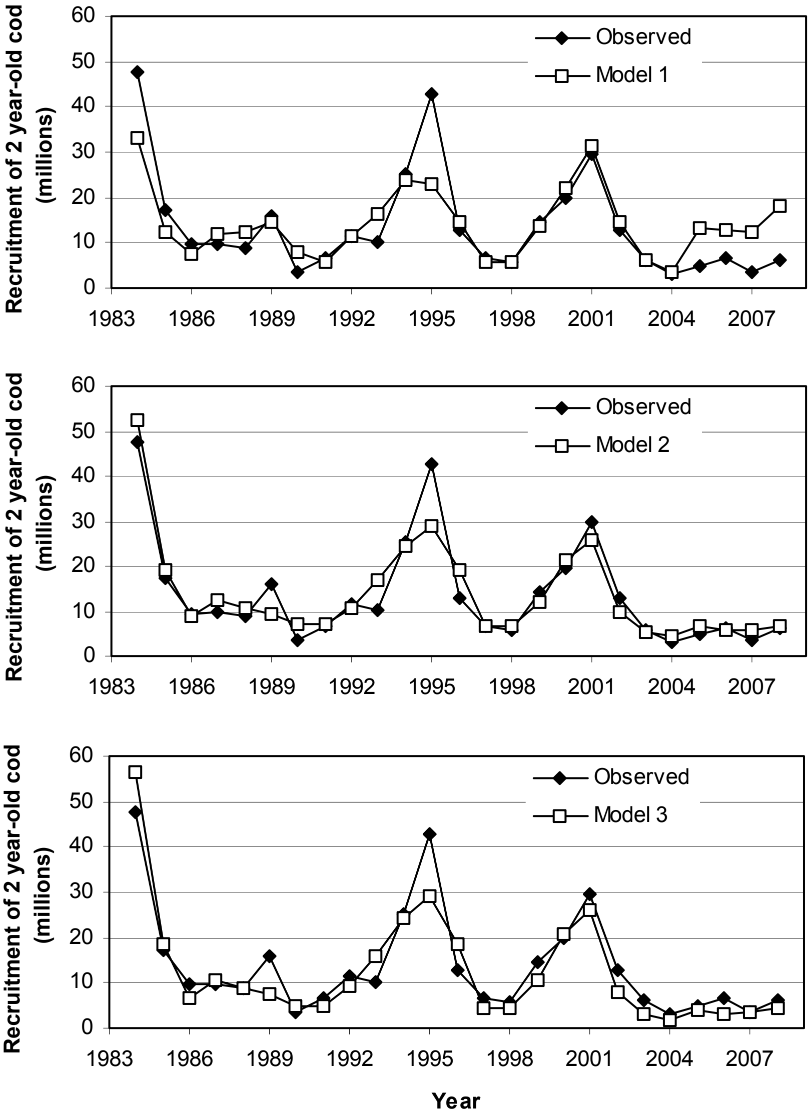

Figure 6. Three different models predicting recruitment of Faroe Plateau cod from phytoplankton production (P) (May-June), catch per unit effort (CPUE) of cod close to land (June-October), and stock size of cod. The observed values of recruitment are obtained from stock assessments. The CPUEs for the two first years were estimated from catch figures only.

Model 1: $\mathrm{Log}(R_{t+1}) = a + b*\mathrm{Log}(\mathrm{average}(P_{t-1}, P_t)) + c*\mathrm{Log}(\mathrm{CPUE}_t)$. The model was fitted for the period 1991-2003, and 't' denotes year. P in 1989 was set to the 1990 value, and P in 1983-1988 was set to the average P for 1990-2007.

Model 2: $R_{t+1} = a\ B3+_{t+1} / \mathrm{CPUE}_t + d$. The model was fitted for the 1983-2005 period. Model 2 is the same as the model in Figure 5.

Model 3: $R_{t+1} = a\ B3+_{t+1} / \mathrm{CPUE}_t$., i.e., forced through zero.

The term 'B' in the recruitment model deserves attention. Very importantly, B is *not* a proxy for the amount of spawning products (two years before the recruitment of 2-year-old fish), but rather the *contemporary* abundance of older cod (age 3+), i.e., all cod on the entire Faroe Plateau that are at least one year older than the recruiting year-class in the recruitment year (at age 2). Using the spawning stock biomass in the recruitment model decreases the fit to the observed data considerably (Paper V). It seems quite likely that juvenile cod need to associate with older conspecifics in order to learn foraging skills, migration routes and how to avoid predators, which highlights the importance of 'loss of culture'. The recruitment model indicates that juvenile cod will not survive in areas where no older cod are present and that this may explain variations in recruitment better than variations in the spawning stock biomass (or other related indices of spawning success). At some low point, however, the shortage of spawning products will ultimately take over and limit future recruitment. The joining of juvenile and adult cod, either directly in groups or merely being present in the same area, presumably occurs after the time when juvenile cod have surpassed a critical size where they no longer are in danger of being cannibalised, i.e., they are larger than 50% of the length of adult cod (Bogstad *et al*., 1994). In Faroese waters, this threshold is reached during the second winter of the juvenile's life (Paper I). The critical period for cannibalism (June-October at age 1) and the critical period for joining the adult cod stock (say, October at age 1 to June at age 2) are, therefore, quite close to each other. The recruitment model actually performed best when B was set at B3+ in summer-autumn in the year of recruitment at age 2.

Some support for B is gained from other cod stocks. B seemed to perform better than the spawning stock biomass for cod at Iceland and in the Barents Sea (Paper V). Also, the disappearance of two year classes of cod off Newfoundland in the beginning of the 1990s, when the contemporary abundance of cod was very low, may be taken as supportive evidence, although other explanations exist (Shelton and Lilly, 2000). The positive effect of B seemed to level off at a stock size of Faroe Plateau cod of around 100 thousand tonnes, and turned into a negative relationship at larger stock sizes (Paper V). Cod were probably in poor condition and moved towards land and hampered the survival of 1-year-old cod. It is also possible that the survival of 2-year-old cod was hampered by cannibalism at typical cod-depths.

A word on year-class strength and variability is worthwile. A dome-shaped function was fitted through the R – B relationship (Figure, 7; Paper V), and it was found that the ratio between the points and the modeled values seemed to be independent of B. The ratio was low when the growth rate of cod was low and *vice versa* (Figure 8), i.e., the environmental variability on recruitment was reflected by this ratio. In order to get the actual recruitment, the recruitment ratio had to be multiplied by the model values. This implies that the recruitment in Faroe Plateau cod is strong when the B is large (but not over 120 thousand tonnes) and that the recruitment varies most when it is strong, i.e., when B is around 100 thousand tonnes. Very importantly, it means that several years with favorable environmental conditions are needed to rebuild a depleted cod stock whereas only one or two years are needed if the stock is in good shape. This is because a strong recruitment is only achieved when the environmental conditions are favorable *and* the stock size is large. These findings are, to some extent, in line with Brander (2005) who showed that recruitment variability in cod was more influenced by environmental factors (NAO) when spawning biomass was low. (If Brander (2005) had used the contemporary biomass, instead of the spawning stock biomass, his study would perfectly match the findings in Paper V.) The findings in Paper V are probably not in line with Anderson *et al*. (2008) who proposed that fishing increases abundance variability through changed demographic parameters (e.g., increased individual growth rate), since the growth rate of Faroe Plateau cod seems to be virtually independent of stock size.

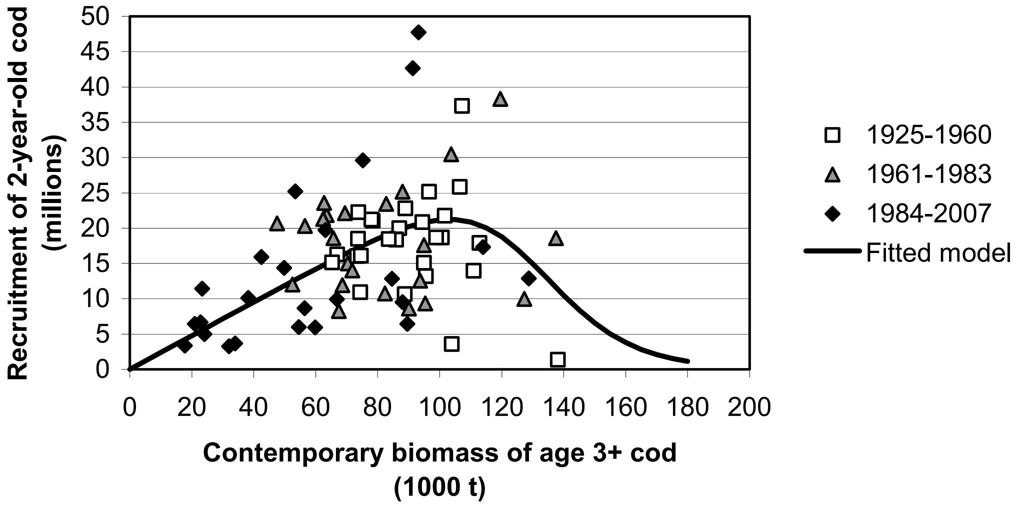

Figure 7. Recruitment (R) of 2-year-old cod vs. contemporary biomass of cod (B) three years and older. The model R = *a*B/(1+exp(*d**(B/*m*-1))) was fitted to the points, were *a*, *d*, *m* were fitted constants. The 1925-1960 period was not covered by the analytical assessment, in contrast to the 1961-2007 period. The abundance of predatory cod close to land was known for the 1984-2007 period.

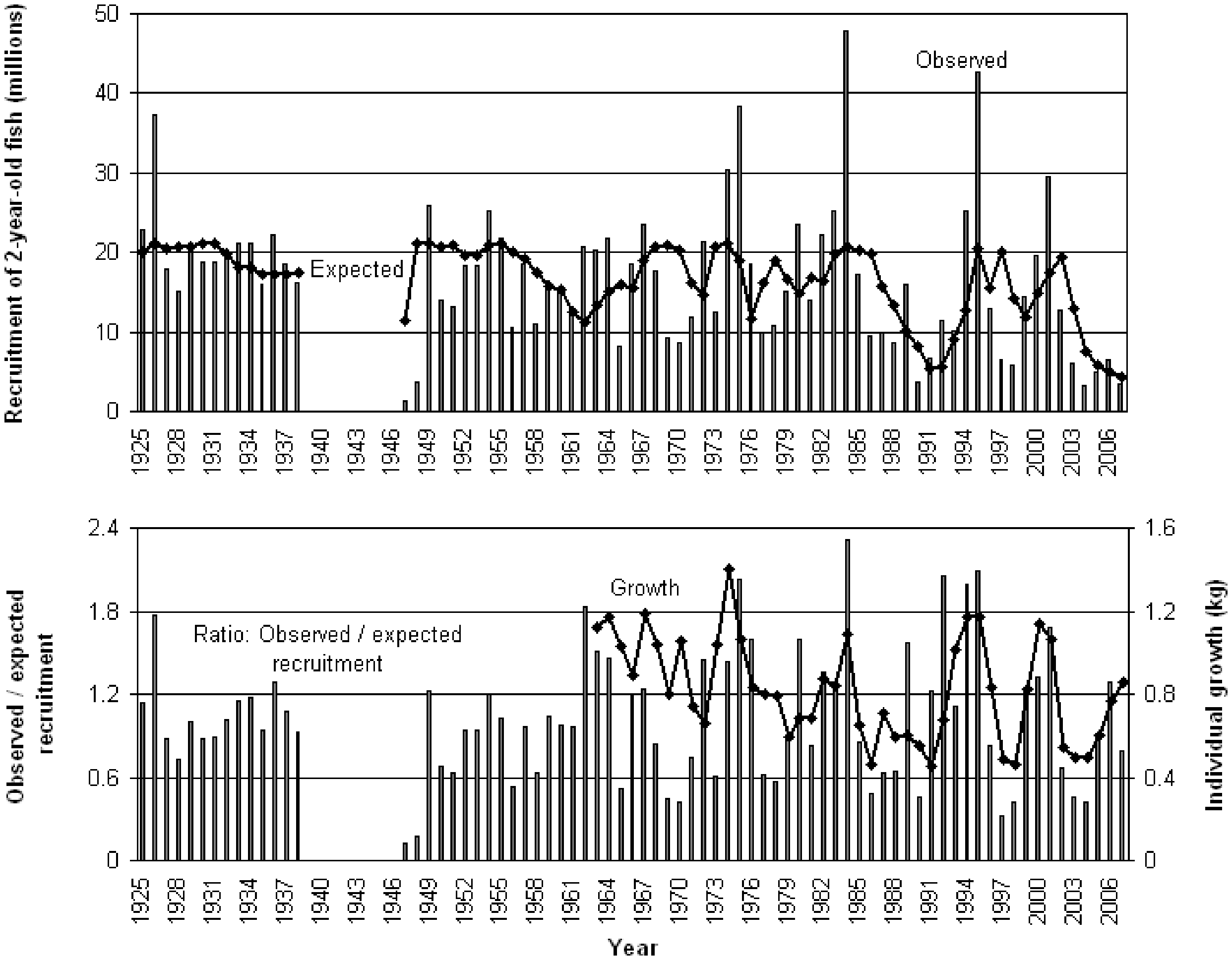

Figure 8. The upper panel shows the observed recruitment variability for Faroe Plateau cod back to 1925 (bars) as well as the values expected by the model in Figure 7 (line). The lower panel shows the ratio between the observed vs. expected values (bars) compared with the annual individual growth (over two years, see text) (line).

## Production in Faroe Plateau cod

Until now the author has merely stated that the cod are in good condition some years and in bad condition during other years, but has not gone into detail as to why. Below is an attempt to outline a link between phytoplankton production and cod condition and production, which seems to explain the variation in the cod fishery at the Faroes.

Phytoplankton production varies by a factor of 5 on the Faroe Shelf ecosystem and is the input to higher trophic levels (see Introduction). There seems to be at least two broad ecological pathways from phytoplankton to cod (Paper VI):

1) Phytoplankton → zooplankton → sandeels or other zooplankton predators →cod.
2) Phytoplankton → benthic organisms (mainly crustaceans) → cod.

Pathway 1 may be regarded as a pelagic pathway. Phytoplankton is eaten by zooplankton in the (upper) water column, which leads to production of copepod eggs and nauplii. Copepod eggs and nauplii are just the right size to be ingested by fish larvae (Gaard and Steingrund, 2001). Larvae of sandeel and Norway pout (along with a number of other fish larvae) prey on copepod eggs and nauplii, and consequently there seems to be a positive relationship between phytoplankton production and recruitment of sandeels the same year (unpublished results). Sandeels are an important food source for cod, and the survival of 1-year-old cod (during summer-autumn) seems to be linked to sandeel abundance. Norway pout grow up in the shelf area (< 130 m) and gradually migrate to deeper waters (> 150 m) with increasing size (unpublished data). Hence, Norway pout may 'transfer' energy from the Faroe Shelf down to deeper waters.

Pathway 2 may be regarded as a benthic pathway. Phytoplankton sinks to the bottom or is preyed upon by benthic filter feeders. A variety of benthic decompositors presumably eat the phytoplankton that sinks to the bottom, which, in turn, are preyed upon by a number of benthic organisms, including many crustaceans (*Galathea spp*., *Pagurus spp*., Portunidae), which are an important food source for small cod. Steingrund and Gaard (Paper VI) should, therefore, have divided the 'benthic organisms' into at least two trophic levels 'benthic decompositors' and 'crustaceans'. Hence, cod may actually be in the fourth trophic level, rather than in the third as was suggested in Paper VI. The relative importance of Pathways 1 and 2 were not assessed in Paper VI.

Large annual variations in the phytoplankton production created large annual fluctuations in the food abundance for cod, both in the Faroe Shelf area (< 130 m) and in deeper waters (> 150 m). These fluctuations were also evident in the individual growth and condition factor of cod. There was, however, the puzzling enigma that phytoplankton variability lagged *behind* cod growth by around one year and not *vice versa*, and there was no evident explanation for this discrepancy. Very recently (in 2008), however, it has become clear that the productivity of the outer areas has to be taken into account. This is a largely unexplored field of research and the author will, therefore, only deal with it briefly.

The phytoplankton production index (Paper VI) only deals with the Faroe Shelf area (shallower than about 130 m, corresponding to around 10,000 square kilometres), whereas the outer areas (out to the 500 m depth contour and around 30,000 square kilometres) were not considered. The productivity over the outer areas on the Faroe Plateau seems to be related to the hydrographical dynamics of the water masses south-west of the Faroe Islands. The upper-layer circulation in the northeastern North Atlantic is largely governed by the dynamics of the Subpolar Gyre and the Subtropical Gyre, and the hydrographic (temperature / salinity) characteristics west of the British

Isles depends on the relative water mass contribution from each of these two gyres (Hátún *et al.*, 2005). When the Subpolar Gyre is strong, the water masses around the Faroes will be colder and fresher than normal, while the opposite is observed when the Subpolar Gyre is weak and retracted to the west (Hátún *et al.*, 2005). The temporal dynamics of the Subpolar Gyre is rather slow and is characterised by decadal-scale variability: the gyre was weak in the 1950s and 1960s, strong in the mid-1970s, weak in the beginning of the 1980s and especially strong in the beginning of the 1990s and especially weak after 1996. It has recently been discovered that saithe biomass in Faroese waters covaries well with the dynamics of the Subpolar Gyre, i.e., a strong gyre leads to a low saithe biomass around four years later (Steingrund and Hátún, 2008). Too-low temperatures in 'strong gyre years' cannot be the causal mechanism, because the temperatures are, nevertheless, always higher than 5 $^{o}$C in most parts of the Faroe Plateau (Paper I). This renders other mechanisms, for example, food availability, much more likely than temperature *per se*. Phytoplankton abundance in the Iceland-Faroe region, represented by a so-called Phytoplankton Color Index again derived from the Continuous Plankton Recorder (CPR) survey (Reid *et al.*, 1998), tends to vary negatively with the strength of the Subpolar Gyre (Hjálmar Hátún, Faroese Fisheries Laboratory, personal communication).

Assuming that the strength of the Subpolar gyre is related to productivity over the outer areas on the Faroe Plateau, the author transferred the 'gyre index' (Steingrund and Hátún, 2008), which had both positive and negative values, to a 'true' index with only positive values, where zero would represent zero production. The author assumed that the variability was 3 (max:min) by looking at Figure 2 in Reid *et al.* (1998). The index was scaled in such a way that it could be compared directly with the phytoplankton production index for the Faroe Shelf area, and was allocated low values when Subpolar Gyre was strong and *vice versa*. The revised gyre index does not necessarily reflect annual variability in phytoplankton production, but probably variability in production at higher trophic levels.

Natural production of fish depends upon ecosystem productivity (Paper VI), and Table 3 shows how cod, haddock and saithe production depends upon the primary production over the Faroe Shelf (inner area on the Faroe Plateau), and the revised gyre index (outer area), as well as the sum of both. The productivity over the inner areas relates most closely to fish production (cod, haddock and saithe and combinations of them), but the total productivity (I+O) relates most closely to saithe production (Figure 9). Since the young ages of fish contribute most to production (Paper VI), it seems reasonable that cod and saithe depend upon the productivity over the inner areas, where the juveniles grow up. Saithe seems, however, to utilise the deeper areas to such a degree that the production of saithe correlates best with the total ecosystem productivity. Haddock juveniles are distributed in deep waters (100-200 m depth), while adult haddock have a similar distribution as cod (mostly shallower than 150 m). This could explain why haddock production, in addition to inner productivity, also correlates reasonably well with total ecosystem productivity. Interestingly, the sum of cod, haddock and saithe production correlates best with productivity over the inner areas, indicating that there is competition between the species for food resources – what one fish species looses may be utilised by other species.

Table 3. Correlation between fish production and ecosystem productivity over the inner areas (I), outer areas (O), and their sum for the years 1990-2005. Bold values are significant at the 5% level.

| | Cod | Haddock | Saithe | C+H+S | C+H | C+S | H+S |
|---|---|---|---|---|---|---|---|
| Correlation with I | **0.66** | **0.70** | **0.65** | **0.80** | **0.77** | **0.79** | **0.73** |
| Correlation with O | -0.31 | 0.11 | 0.46 | 0.06 | -0.11 | 0.01 | 0.27 |
| Correlation with I+O | 0.32 | **0.60** | **0.77** | **0.65** | **0.52** | **0.61** | **0.72** |

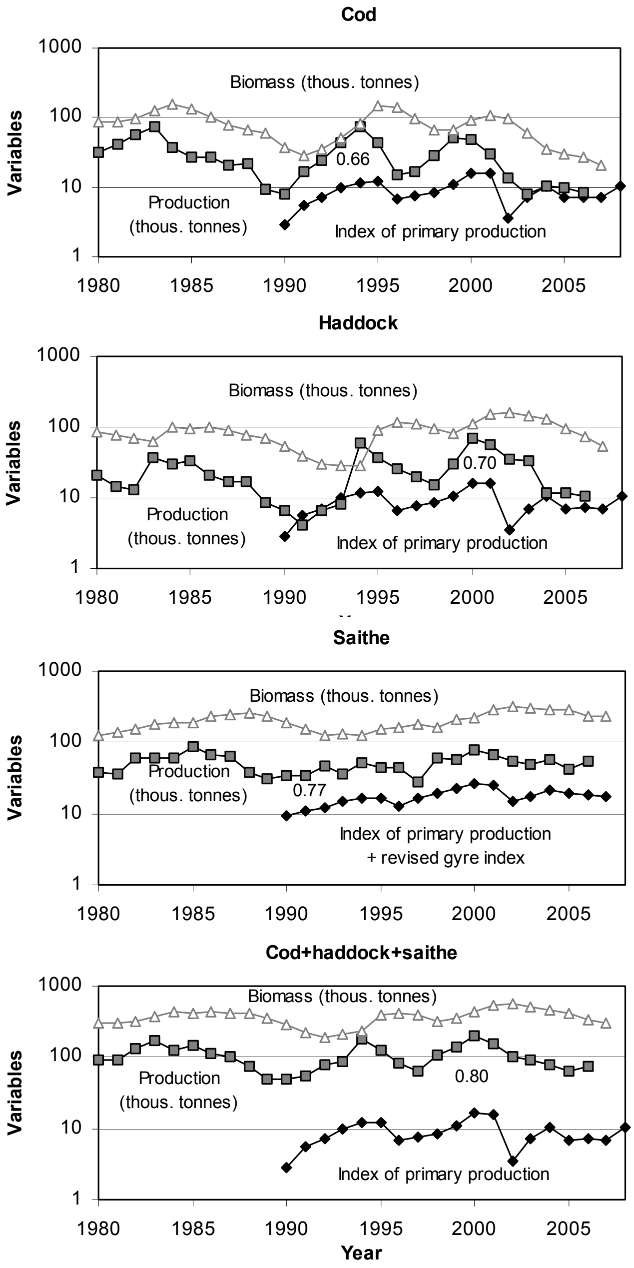

Figure 9. Relationship between the index of primary production (+ revised gyre index) and population parameters for cod, haddock, saithe and combined values. The coefficient of correlation between primary production and fish production is shown.

The total ecosystem productivity (P = I+O) should be a proxy for total food production on the Faroe Plateau, which was available for fish (plus seabirds, as well as marine mammals, but ignored here). Fish biomass is dominated by cod (C), haddock (H) and saithe biomasses (S), and 'food per kg fish' (P/B) should, thus, be proportional to (I+O) / (C+H+S). This was supported by the fact that there was a very high positive correlation between P/B and individual cod growth or condition factor (Paper V, Figure 5), indicating that the Faroe Plateau ecosystem behaves as an isolated unit, and that the revised gyre index is a reliable proxy for food availability over the outer areas on the Faroe Plateau. The relationship between P/B and cod growth was fairly insensitive to the exact scaling, and variability, of the revised gyre index.

The close positive relationship between ‘food per kg fish’ and individual growth of cod is intuitively appealing and is expected in situations where the food and the fish are well mixed in time and space. However, fish are only partially mixed in space: Cod and haddock tend to occupy the shallow areas (< 150 m depth); saithe occupies the deeper areas. There are also differences in diet between cod, haddock and saithe (Du Buit, 1982). The ‘food per kg fish’ – cod growth relationship – could, neverteless, be maintained because the food of cod (crustaceans and fish such as Norway pout, Paper II) is shared with haddock and saithe. Haddock eat crustaceans, while saithe eats Norway pout.

### An attempt to answer the main question in this thesis

The information gathered so far is sufficient to provide an answer to the main question in this thesis: ‘Why did the Faroe Plateau cod stock decline so much in the beginning of the 1990s and why did it recover so quickly in the mid-1990s? ’

When explaining cod recruitment, the following four tools are at hand: the phytoplankton production in the Faroe Shelf area (< 130 m depth), the revised gyre index as a proxy for productivity over the outer areas, the total fish biomass (cod + haddock + saithe), and the stock size of cod (age 3+) (Paper V, Figure 5). In 1989-1991, both production indices were low, leading to low ‘food per kg fish’, and, therefore, poor individual cod growth. Cod moved towards land and hampered recruitment (at age 2) by cannibalism at age 1. When the stock size attained low levels, it too hampered recruitment in 1992-1993, which led to record low catches of cod. However, the phytoplankton production increased to high levels in 1993-1995, whereas the gyre index stayed low. This led to a low biomass of saithe and a very high ‘food per kg fish’, and, consequently, very rapid individual cod growth. The rapid growth caused cod to move out from land leaving cannibalism on a minimum, but recruitment was not maximal until the adult cod population (age 3+) had reached high levels in 1995. This led to the high catches in 1996-1997.

In retrospect, the Faroese Fisheries Laboratory could not have foreseen the development of the cod stock, because the analysis tools were not available. No one understood the relative importance of both the phytoplankton production index and the gyre index. Also, interactions between fish species were unknown (e.g., saithe influence both ‘food per kg fish’ and cod growth). The importance of the concurrent biomass of age 3+ cod, rather than the spawning stock, two years before recruitment, is also a quite recent discovery.

The subsequent development of the cod stock can be explained by the same analysis tools. The phytoplankton production index was low in 1996-1997 and, together with a high fish biomass (dominated by cod), led to little ‘food per kg fish’. Cod moved again towards land and hampered recruitment, which led to a moderately low stock size of cod in 1999-2000. Phytoplankton production was high in 1999-2001, but the revised gyre index had also attained high values. This led to increased amounts of food and great numbers of fish (saithe), but ‘food per kg fish’ was not as high as in the mid-1990s. Cod moved out from land and recruitment was above average in 2000 and 2001. The cod stock peaked again in 2001-2002. However, in 2002 and onwards, a ‘dangerous’ situation arose: Phytoplankton production stayed low, whereas the revised gyre index maintained record highs. The abundance of saithe reached record high levels in 2001-2005, leading to extremely little ‘food per kg fish’ and extremely low recruitment of cod. The cod stock declined in 2007-2008 to the lowest level ever observed.

Although the phytoplankton production index has increased again now in 2008 and the revised gyre index, as well as saithe biomass, seems to have decreased somewhat, the situation remains serious because the stock size (age 3+) of cod is at record low levels and this hampers recruitment. After all, the lowest biomass (age 3+) in the beginning of the 1990s was around 30,000 tonnes, while the estimate in 2007 was around 20,000 tonnes. Since recruitment is directly proportional to cod biomass (but also inversely proportional to the density of cod close to land), every thousand tonnes of cod count heavily when the stock is at such a low level. Unless the phytoplankton production is high in 2009, and preferably in 2010 as well, there is a risk that the cod stock may collapse.

Fluctuations in biomass, however, are not what are observed by local people or fishermen, but rather the size of the catch itself. Hence, the following section deals with the catch and the catchability of cod.

## Harvesting Faroe cod production

### Cod fishery and fishing mortality

For clarity, the author has not dealt with variation in fishing mortality, although fishing mortality varies substantially between years and also between fishing gears and depths. Below is an outline of the link between cod feeding habits and fishing mortality (Paper VIII, Paper IX).

Cod are fished mainly with longlines (in shallow waters < 150 m) and trawl (in deep waters). The share between longliners and trawl is not constant over time, but varies between years. When cod are growing slowly, up to 65% of the cod catch may be taken with longlines, whereas the longliner share may drop to around 30% when cod are growing fast (ICES, 2007). The longliner share of the cod catch correlates positively with the overall fishing mortality of cod (ICES, 2008a). In other words: when cod are in poor condition (poor phytoplankton production and slow growth), the fishing mortality is high. When cod are in good condition, the fishing mortality is low. Therefore, the annual variations in overall fishing mortality seem to be coupled with the longline fishery. As the effort of the longliners has been kept fairly constant during the effort management system (1996 to present, Paper X), the variations in the fishing mortality of cod must be coupled with the catchability of longlines (and not variations in the effort of longliners).

The catchability of longlines may vary greatly (by a factor of three) between years and seems to be linked to the feeding habits of cod. When cod are in good condition, they are presumably able to catch mobile fish such as Norway pout and concentrate on fish feeding in slightly deeper waters than normal. As longlines are closely associated with the bottom, few cod are taken by longlines. When cod are in poor condition, they seem to switch to a benthic feeding mode (Brawn, 1969) and concentrate on benthic crustaceans and other benthic organisms, as indicated by the higher proportion of crustaceans in the stomachs (Paper II). In addition, they move to slightly shallower waters (Paper V) and become more available to longlines set by small longliners. When cod are in shallow waters, they may be better able to detect objects on the bottom and may thus spot longline bait from greater distances. Longline bait creates a plume of odours (Engås and Løkkeborg, 1994; Vabø *et al.*, 2004). The detection threshold (detection of odours) is probably not affected by feeding motivation, but the response threshold could decrease with increasing feeding motivation leading to a larger ‘active space’ of longlines (Engås and Løkkeborg, 1994; Løkkeborg, 1994) and a higher catchability. These observations are similar to those found for tuna off French Polynesia that were attracted to areas with high food abundance and preferred natural prey over longline bait when the natural food was distributed in dense patches (Bertrand *et al.*, 2002). However, when little alternative food is available, there seems to be a positive relationship between hunger (feeding demand) and the ingestion rate of bait, as observed for sablefish in laboratory experiments (Stoner and Sturm, 2004) and juvenile cod in the wild (Hawkins *et al*., 1985).

The catchability fluctuations with longlines were observed over a large depth range (50-200 m) (Paper VIII) and were most clearly discernible for medium-sized cod (60-80 cm, 4-7 years old, ICES, 2007; Paper VIII). Medium sized cod normally have lower condition factors than smaller or larger cod and are 'in between' two feeding niches (Paper II): benthic feeding on crustaceans (normally adoped by small cod) and feeding on mobile fish (adopted by large cod). Hence, medium-sized cod may switch more often between feeding niches / diets than other cod. Because medium-sized cod represent the bulk of the fishable stock, they dominate the overall fishing mortality in cod.

The variation in the fishing mortality of cod should, in theory, also be affected by fluctuations in the catchability of trawl. Cod in good condition, which moved to slightly deeper waters, could be more available to trawl, but this effect (Phenomenon 1, see earlier) was not detected in Paper VII. However, another mechanism was detected (Phenomenon 2) and is already outlined under the heading 'distribution and migration in cod at the Faroes'. Again, medium-sized cod (59-69 cm, 4-5 years old) were the key players, and they moved to deep waters (> 150 m) when the competition for shallow water resources was high and *vice versa*. This gave rise to 'shallow' and 'deep' year classes, although the bulk of all cohorts was distributed in fairly shallow waters (< 200 m). As the abundance of cod in deep waters (> 150 m) normally was very low, a small or moderate movement of cod from shallow to deep waters leads to a marked increase in the *relative* abundance of cod in deep waters and a higher catchability of trawl. However, the effect on the overall fishing mortality of cod was small.

The catchability fluctuations of longlines and trawl have important consequences for the cod fishery on the Faroe Plateau. The very steep increase in cod catches from 1993 to 1996 can broadly be explained by three factors that all worked in concert (Paper IX): increased recruitment, increased growth and increased fishing mortality.

The fact that recruitment, growth and fishing mortality are coupled on the Faroe Plateau represents a problem for the management of the stock. Times are either 'good' (high primary production, recruitment and growth and low fishing mortality) or 'bad' (low primary production, low recruitment and high fishing mortality), but seldom are they 'average'. In order to keep a constant fishing mortality, huge regulation of the fishing effort would be necessary, which, however, is not possible. The only solution could be to reduce the fishing effort to a point so that the stock could withstand the bad times, allowing fishing mortality to fluctuate between years.

The coupling of recruitment, growth and fishing mortality also represents a problem in the sense that the perspective gap between fisheries biologists and fishermen may be difficult to close. The ups and downs in the primary production are separated by 2-4 years. There is also a time lag from recruitment to fishery of 2-3 years, i.e., a big year class (age 2) will show up in the fishery 2-3 years later (age 4-5). Therefore, the catches of cod tend to be highest in bad times (when the primary production, recruitment and growth is low) and *vice versa*. Simply stated, even though biologically times are bad, what fishermen observe is plenty of fish. It is a difficult task for fisheries biologists to explain to fishermen and local people concerned about the state of the fishery that times may be bad even though the catches are considerable.

### Is the cod fishery managed in an optimal way?

How should the cod stock at the Faroes be managed in order to get the highest catch rates over time? There are different opinions about this matter among local people in the Faroes and fisheries biologists. In order to fully understand the controversy, it is necessary to outline the views that exist.

One long-held view among Faroese fishermen is that 'fish are migratory' and 'have to be caught when they are available'. The view is actually two statements ('migration' and 'exploitation'). The 'migration' hypothesis is a result of fishermen's experience and is based on variable short-time catch rates. This viewpoint is presumably a sum of what was experienced for different fish species in a variety of fishing areas (Faroes, North sea, Iceland, Greenland, Canada, Barents Sea) and was developed over a long period of time many years ago. Therefore, it may reflect findings for large fish stocks, rather than for today's decimated fish stocks (Myers and Worm, 2003). 'Migratory' may actually reflect a fine spatial scale, as fishermen in the Faroes in days of old used small, open boats and a small movement of fish vertically or horizontally could mean all or nothing. The second part of the view ('exploitation') is, for the fishermen, a logical consequence of the 'migratory' view. The assumption is that fish do not accumulate spatially, but disperse when density becomes too high. The 'exploitation' or 'catch them when you can' view is commonly held by fishermen, local people and politicians. It is also a convenient view for fishermen, as it means that there should be no restrictions on their fishing effort.

An alternative hypothesis was introduced about ten years ago. The Icelandic biologist Jón Kristjánsson gained strong support among Farose fishermen and managers (politicians) for his 'reduce fish density and fish more' hypothesis (see e.g., Kristjánsson, 2004 and www.mmedia.is/~jonkr). Using his background as a freshwater ecologist, he claimed that many fish stocks at the Faroes were too large and suffered from food shortages. He claimed that both recruitment and individual growth would increase, if the stocks were reduced by higher fishing effort (both the cod and haddock stocks were in good shape in 1998).

One aim of this thesis is to put new and objective evidence into the discussion so that local people are able to adopt their own opinion. The view that 'fish cannot be accumulated in the sea' can apparently be rejected. There exist stock assessments for cod, haddock and saithe in Faroese waters since 1961 and they do show marked annual variations, as do numerous fish stock assessments in other areas. The argument by Jón Kristjánsson that the stock size of cod was not especially high after the Second World War is quite simply wrong, as shown by long-term catch per unit effort series for British trawlers (1924-1972). On the contrary, the cod stock in 1946 was nearly 200 thousand tonnes (ICES, 2007; Figure 3), which is the highest value for a century.

The 'migratory' hypothesis (applied to cod at the Faroes) can also be rejected. Tagging experiments over the course of a century show that cod very seldom (about 1 out of 1000) move between fishing areas (e.g., between Faroese and Icelandic waters) (Jónsson, 1996; Paper III). Actually, cod at the Faroes seems to show a pronounced site fidelity, both with regard to spawning and feeding areas. Cod that are moved experimentally from one place to another will often migrate back to the former place (unpublished data). Data Storage Tags also show that individual cod may occupy a depth range as narrow as 20 meters (95% confidence interval) during several months (June-October) in the feeding season (Paper V; Figure 2). We are, therefore, left with the fact that cod on the Faroe Plateau are restricted to the Faroe Plateau and that the natural production of cod is based upon the food resources here.

The ‘reduce density and fish more’ hypothesis can also be rejected. I have previously argued that a decreased stock size will result in poorer recruitment. Regarding individual growth, a striking feature is that cod are mainly distributed in shallow waters (< 150 m), whereas important fish prey (Norway pout and Blue whiting) are distributed in deep waters (> 150 m) on the Faroe Plateau. A high fishing effort would decrease the distributional overlap between cod and their fish prey, as the cod stock would be reduced and mainly feed in shallow waters. The overlap between cod and their prey could be increased, if fishing mortality were reduced by, e.g., a reduction in the number of fishing days or increased ‘closed’ areas. Hence, the stock size would be higher and the average size of cod larger. More fish would enter the deep waters because the competition for shallow water resources would be high. Aggregated cod would probably also catch prey fish in deep waters more efficiently.

The ‘reduce density and fish more’ hypothesis raises other concerns. Fishing may lead to maturation at an earlier age / smaller size, which may lead to reduced yield (Law, 2000). Although this is a complex issue (Olsen *et al.*, 2004; Sinclair *et al.*, 2002a; Sinclair *et al.*, 2002b), the tendency of fisheries to remove the largest individuals is believed to cause earlier maturation because late-maturing individuals will be caught before they have reproduced (Law, 2000), which may lead to genetic changes (Hutchings, 2004). While no development in maturity-at-age over time (1982-2008) is observed for Faroe Plateau cod, the weight-at-age decreased from 3.5 kg in 1961 (4 year-old cod) to 2.0 kg in 1990-2007, although fluctuations around this trend were observed (ICES, 2008a; Jákupsstovu and Reinert, 1994). Reduced length-at-maturity may hamper individual growth because less energy is used for somatic growth. In addition, cod will presumably utilise the deep waters to a lesser extent because of the smaller size. Although the effects of this fisheries-induced genetic selection on long-term yield at the Faroes are not quantified, yet it seems clear that a high fishing effort may hamper future landings.

Indeed, the effect of different levels of fishing mortality on the stock development and production of the Faroe Plateau cod stock needs to be quantified. Of paramount importance is the fact that the recruitment seems to be hampered at low stock sizes (Figure 8), although the causal relationship is poorly known. The recruitment since the 1920s has shown a decreasing trend, along with the decreasing trend in the stock size (Figure 9). However, the ratio between the observed recruitment and the biomass-modeled recruitment has remained fairly constant and fluctuated in a cyclical way (Figure 9), probably in accordance with cod growth and fluctuating environmental conditions. The recruitment ratio was high during 1980-84, while it was low during 1986-88 and 1990. Overall, though, it was not worse during the 1980s than any other decades since World War II. The same argument applies to the 2000s. *Hence, the low stock size in the beginning of the 1990s, and now in 2008, seems to be a result of a too high fishing mortality*. The recovery in 1995-96 was preceded by five years (1991-1995) with a high recruitment ratio, the longest ‘good’ period since the 1920s. The recruitment ratio was ‘average’ during 2005-2007, and it seems, therefore, unlikely that the cod stock will recover quickly.

An attempt is made to quantify the future outlook for Faroe Plateau cod by modeling the recruitment, individual weights, and fishing mortality as a function of cod growth (Table 4). The average growth rate (half individal weight increase of four cohorts over two years) was set to 0.788 kg (average during the 1983-2006 period). The growth rate was assumed to follow a sinus function of amplitude of 0.361 kg with a period of 7.23 years (six lows and seven peaks during the 1961-2007 period, i.e., 6.5/47 = 7.23). The timing of the sinus function was random, so that the start in 2008 could represent the beginning of a low, a peak or any other part of the sinus function. The rest of the growth-development until year 2109 was determined from the initial value in 2008.

Table 4. Settings when modeling the outlook for Faroe Plateau cod. The recruitment was first modeled as a function of age 3+ biomass (Rmodel) as in Figure 8 ($a = 0.238$, $d = 9.185$, $m = 129$), and then the R/Rmodel ratio was modeled as a function of the individual growth of cod (G). G, year y, was measured as the annual weight increase from year y-1 to year y+1, averaged for four cohorts 2 to 4 years, 3-5, 4-6 and 5-7 years. G also affected the weight and fishing mortality (F) in the way shown in the table. The time-lag (in years) from G to the variable in question is also shown.

| Variable | Period | Age | Intercept | Slope | Lag (yrs) | Correl. | P-value |
|---|---|---|---|---|---|---|---|
| Recruitm. (millions) | 1994-2006 | 2 | -0.511 | 2.010 | 1 | 0.94 | 0.00000 |
| Weight | 1984-2007 | 2 | 0.724 | 0.420 | 1 | 0.73 | 0.00002 |
| (kg) | | 3 | 0.956 | 0.847 | 1 | 0.76 | 0.00001 |
| | | 4 | 1.265 | 1.376 | 2 | 0.75 | 0.00001 |
| | | 5 | 1.620 | 1.946 | 2 | 0.86 | 0.00000 |
| | | 6 | 2.659 | 1.574 | 2 | 0.73 | 0.00002 |
| | | 7 | 4.139 | 0.927 | 1 | 0.42 | 0.03136 |
| | | 8 | 3.701 | 3.335 | 0 | 0.71 | 0.00004 |
| | | 9 | 4.769 | 3.969 | 0 | 0.65 | 0.00032 |
| | | 10+ | 6.923 | 3.368 | 0 | 0.52 | 0.00644 |
| F | 1997-2006 | 2 | 0.121 | 0.000 | 1 | 0.35 | 0.32574 |
| (average of ages | | 3 | 0.301 | 0.000 | 1 | 0.33 | 0.35204 |
| 3-7 years) | | 4 | 0.655 | -0.318 | 0 | -0.61 | 0.06128 |
| | | 5 | 1.166 | -0.822 | 1 | -0.88 | 0.00086 |
| | | 6 | 1.464 | -0.972 | 1 | -0.91 | 0.00029 |
| | | 7 | 1.432 | -0.668 | 1 | -0.60 | 0.06518 |
| | | 8 | 1.384 | -0.645 | 1 | -0.62 | 0.05732 |
| | | 9 | 2.086 | -1.655 | 1 | -0.68 | 0.02931 |
| | | 10+ | 2.086 | -1.655 | 1 | -0.68 | 0.02931 |

The results of the exercise are shown in Tables 5, 6 and Figures 10, 11. It appears that fishing mortalities of 0.9 times the level in 1997-2006, or higher, are not sustainable in the long run. A very slow recovery occurs at F-factor 0.8, while reductions of 40-60% of the fishing mortalites (F-factors 0.4-0.6) are needed to rebuild the stock at a faster rate. The annual catch will then be a few thousand tonnes less the first three years, while it will be increasingly higher afterwards (Figure 11). The fishing mortality in 2007 was probably 10% higher than the average level for the 1997-2006 period, based on Steingrund (2008). With such a high fishing mortality rate, the average annual catch during the following 100 years will be only 1200 tonnes, and there is a 80% probability that it will be less than 2127 tonnes (Table 5). The highest average catch (23511 tonnes) is expected at an F-factor of 0.6 (Table 5). After the stock has fully recovered, the highest average annual catch is expected to be slightly above 26000 tonnes at an F-factor of 0.7, while the F-factor of 0.5 gives 24500 tonnes of fish that are around 0.5 kg heavier. A simpler model, where the fishing mortalities-at-age and individual weights-at-age were kept constant (same growth every year), indicated that the F-factor should be reduced by approximately 0.1 more than what was indicated in the original exercise.

Table 5. Results from 200 simulations of the future development of Faroe Plateau cod the following 100 years as a function of different levels of fishing mortalities.

| Measure | F-factor | Biomass (t) | Recruitm. | Catch (n.) | Catch (t) | Weight (kg) |
|---|---|---|---|---|---|---|
| Average | 1.1 | 3091 | 774 | 528 | 1237 | 2.36 |
| | 1 | 5651 | 1410 | 894 | 2127 | 2.40 |
| | 0.9 | 16320 | 4052 | 2368 | 5733 | 2.44 |
| | 0.8 | 59345 | 14047 | 7692 | 19289 | 2.51 |
| | 0.7 | 77286 | 16482 | 8680 | 23060 | 2.65 |
| | 0.6 | 87371 | 16641 | 8293 | 23511 | 2.82 |
| | 0.5 | 96324 | 16164 | 7497 | 22874 | 3.03 |
| | 0.4 | 105555 | 15402 | 6473 | 21454 | 3.28 |
| SD | 1.1 | 5493 | 1557 | 937 | 2185 | 0.06 |
| | 1 | 6590 | 1899 | 1046 | 2472 | 0.07 |
| | 0.9 | 7894 | 2706 | 1183 | 2795 | 0.09 |
| | 0.8 | 27901 | 8979 | 3664 | 9152 | 0.10 |
| | 0.7 | 31233 | 9777 | 3415 | 9280 | 0.15 |
| | 0.6 | 32693 | 9892 | 2868 | 8594 | 0.21 |
| | 0.5 | 33280 | 9788 | 2274 | 7588 | 0.27 |
| | 0.4 | 32421 | 9310 | 1676 | 6323 | 0.32 |
| Min | 1.1 | 9 | 1 | 1 | 3 | 2.18 |
| | 1 | 192 | 28 | 27 | 69 | 2.20 |
| | 0.9 | 4522 | 627 | 604 | 1556 | 2.21 |
| | 0.8 | 9140 | 1161 | 1135 | 2980 | 2.23 |
| | 0.7 | 10769 | 1252 | 1193 | 3247 | 2.25 |
| | 0.6 | 12765 | 1360 | 1227 | 3434 | 2.27 |
| | 0.5 | 14669 | 1465 | 1232 | 3564 | 2.29 |
| | 0.4 | 16817 | 1587 | 1198 | 3280 | 2.31 |
| Max | 1.1 | 37389 | 12367 | 6289 | 14749 | 2.50 |
| | 1 | 41322 | 13335 | 6533 | 15541 | 2.56 |
| | 0.9 | 45635 | 14377 | 6831 | 16469 | 2.63 |
| | 0.8 | 113644 | 33529 | 14463 | 36939 | 2.74 |
| | 0.7 | 133226 | 37027 | 13805 | 38716 | 2.93 |
| | 0.6 | 147345 | 38160 | 12491 | 38208 | 3.17 |
| | 0.5 | 155409 | 38130 | 11082 | 35470 | 3.54 |
| | 0.4 | 159929 | 38087 | 9540 | 31991 | 3.94 |
| Probability (%) of being below | | | | | | |
| | | 5651 | 1410 | 894 | 2127 | 2.40 |
| | | | (any year) is the following: | | | |
| | 1.1 | 82.1 | 83.2 | 80.4 | 80.4 | 73.6 |
| | 1 | 66.5 | 68.8 | 65.8 | 65.5 | 66.3 |
| | 0.9 | 2.1 | 13.4 | 4.5 | 3.0 | 42.5 |
| | 0.8 | 0.0 | 0.3 | 0.0 | 0.0 | 11.8 |
| | 0.7 | 0.0 | 0.2 | 0.0 | 0.0 | 1.3 |
| | 0.6 | 0.0 | 0.1 | 0.0 | 0.0 | 0.9 |
| | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 |
| | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 |

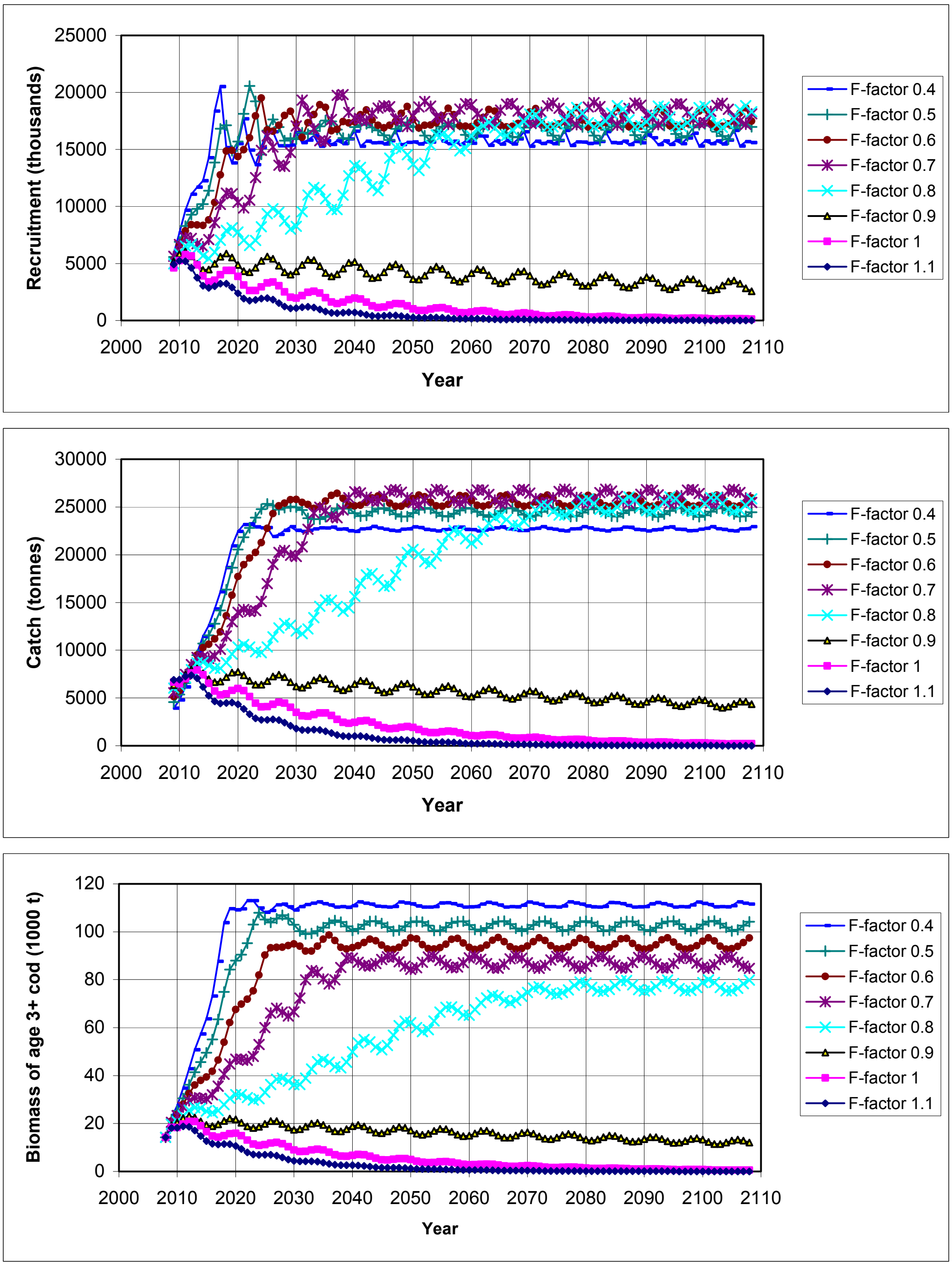

Figure 10. The average result from 200 simulations of the future development of Faroe Plateau cod the following 100 years as a function of different levels of fishing mortalities.

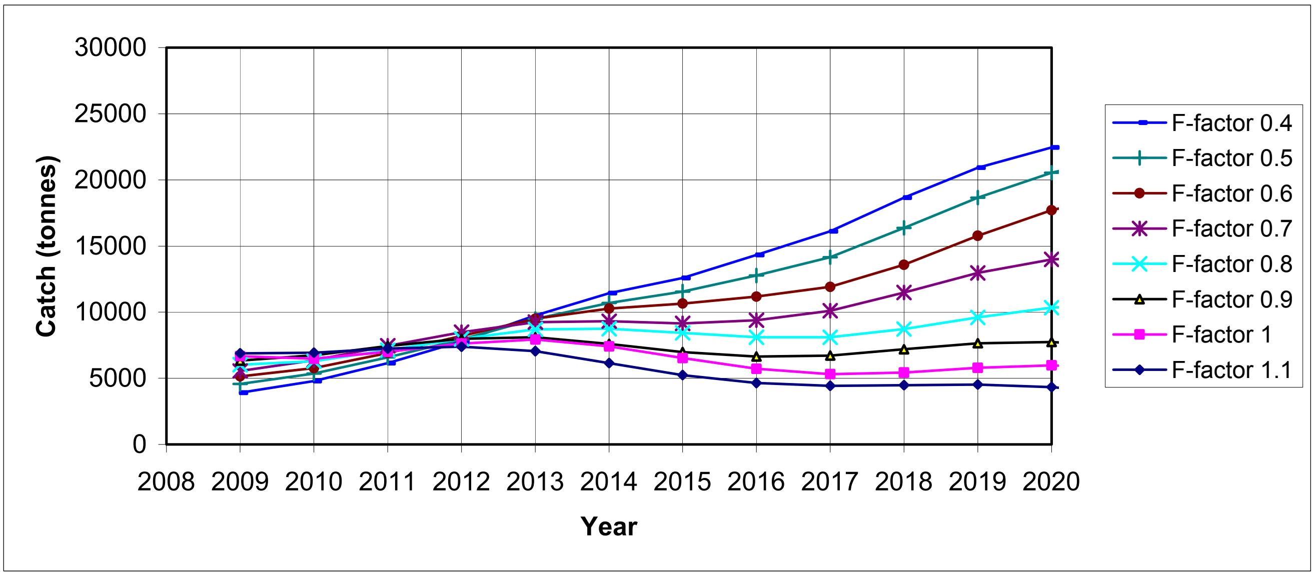

Figure 11. The average result from 200 simulations of the future development of Faroe Plateau cod the following 100 years as a function of different levels of fishing mortalities. The catch to 2020 is shown.

Table 6. Results from 200 simulations of the future development of Faroe Plateau cod the following 100 years as a function of different levels of fishing mortalities. The results from the period 2077-2106 are shown, when the variables were in equilibrium.

| Measure | F-factor | Biomass (t) | Recruitm. | Catch (n.) | Catch (t) | Weight (kg) |
|---|---|---|---|---|---|---|
| Average | 0.8 | 77169 | 17814 | 9942 | 25164 | 2.54 |
| | 0.7 | 87251 | 18126 | 9743 | 26130 | 2.69 |
| | 0.6 | 94715 | 17589 | 8930 | 25578 | 2.86 |
| | 0.5 | 102504 | 16736 | 7919 | 24436 | 3.08 |
| | 0.4 | 111153 | 15720 | 6762 | 22686 | 3.35 |
| SD | 0.8 | 22965 | 9299 | 3070 | 7525 | 0.10 |
| | 0.7 | 26432 | 9795 | 2864 | 7709 | 0.14 |
| | 0.6 | 28318 | 9914 | 2423 | 7231 | 0.19 |
| | 0.5 | 28750 | 9831 | 1878 | 6269 | 0.23 |
| | 0.4 | 27425 | 9335 | 1341 | 5037 | 0.26 |
| Min | 0.8 | 45730 | 6053 | 5560 | 14852 | 2.39 |
| | 0.7 | 54054 | 6503 | 5774 | 16321 | 2.43 |
| | 0.6 | 59316 | 6705 | 5541 | 16145 | 2.47 |
| | 0.5 | 66394 | 6902 | 5188 | 16035 | 2.56 |
| | 0.4 | 76245 | 7156 | 4770 | 15707 | 2.78 |
| Max | 0.8 | 113644 | 33529 | 14463 | 36939 | 2.74 |
| | 0.7 | 130552 | 36524 | 13779 | 37861 | 2.91 |
| | 0.6 | 142542 | 37880 | 12327 | 36687 | 3.13 |
| | 0.5 | 151534 | 38081 | 10561 | 34067 | 3.41 |
| | 0.4 | 156681 | 36651 | 8826 | 30763 | 3.72 |

Even though it is impossible to forecast the actual stock development into the future, because it depends on unknown environmental productivity, the simulation study strongly suggests that the cod fishery on the Faroe Plateau is *not* sustainable. The recovery of the cod stock in the beginning of the 1990s was preceded by as many as five 'good' recruitment years. The fishing mortality was low, partly because of the much blamed quota system, which was in charge during the 1994-1996 period. It is probably unrealistic to expect that there will come another five-year period with a high recruitment ratio in the near future. However, even if it does, the simulation exercise shows that the cod stock may collapse in the future anyway. This will have devastating effects on the Faroese fishing industry and the society as a whole. It is probably unrealistic to expect that the long-term environmental productivity will become better. The only option for the Farose managers seems to be to reduce the fishing effort substantially (by 40-60%) and to accept a reduction of the catches of 2000-6000 tonnes per year until 2012.

The pessimistic forecast is mainly due to the stock-recruitment relationship (Figure 7), and the crucial question is whether Figure 7 shows a causal relationship that will hold in the future. Interestingly, fishery biologists based their advice in the early 1990s on a relationship (spawning stock – recruitment) that looked very much the same as Figure 7, but turned out not to hold. Only time will show whether the new stock-recruitment relationship will hold, and a warning signal may be that there seems to be plenty of small-sized cod (30-40 cm, 1-year-old) close to land now in autumn 2008. Hence, it will probably soon become evident whether the new stock-recruitment relationship holds or not. If it holds, then the 2007 year class will become less than around 10 million fish at the 2-group stage. If the 2007 year class turns out to be larger than, say, 20 million fish (and the recent stock size is not seriously underestimated) then the new stock-recruitment relationship should probably be revised, as well as the pessimistic future forecast.

## Putting the findings for Faroe cod into a larger perspective

### Introduction

Are the findings for Faroe cod relevant for other cod stocks and do they increase our understanting about cod population dynamics? The author will now try to put the Faroese findings into a broader perspective at the following levels: ecosystem, population dynamics, individual behaviour, physiology, and biochemistry / genetics. As the discussion moves from one level to the next, only the most important topics will be considered, as when looking at an object in a microscope and increasing the magnification gradually.

### Ecosystem level

Traditionally, assessments of fish stocks only considered single species, but there has been a growing awareness of the fact that an adequate treatment of a fish stock needs to include information about the ecosystem where the stock is located (ICES, 2005), especially because ecosystems are subject to change over time (Alheit *et al.*, 2005). The abundance of food is of special importance, which in turn may rely on the productivity and state of the ecosystem (Paper VI). The food abundance for cod may be directy related to the production of phytoplankton, which seems to be the case for the Faroe Shelf ecosystem (Paper VI), and that the share for cod may be fairly equal between years. However, there are indications that cod production over the last years has been lower than expected from the phytoplankton-cod production relationship (Figure 9). Annual variations in cod production closely followed annual variations in recruitment, which, in turn, was adequately modeled by stock size and cannibalism. The low stock size in recent years seems to have hampered recruitment and, in turn, cod production. Still, there seems to be a direct relationship between phytoplankton production and production of cod + haddock or cod + saithe, indicating that other fish species may 'take over' what cod loose (Figure 7), as outlined below.

An interannually varying production of cod may be caused by a varying share of the total food production that is utilized by cod, rather than variations in the overall ecosystem productivity. Under this scenario, the productivity of the ecosystem may, in principle, be constant, but the cod production may fluctuate widely. This seems to be the case for several cod stocks in the Northwest Atlantic, which have been decimated for a number of years now while the production of other organisms has increased considerably, i.e., a reorganization of the food web in the ecosystem, often termed a ‘regime shift’ (Bundy and Fanning, 2005; Savenkoff *et al*., 2007a). In broad terms, the ecosystem has changed from a demersal-feeder-dominated system to a pelagic-feeder-dominated system (Bundy, 2004; Cascadden *et al*., 2001; Choi *et al*., 2004). The abundance of small pelagic fish and Arctic shrimp has increased considerably, while the abundance of cod has decreased dramatically, and the increased competition for food may limit cod recruitment (Bundy and Fanning, 2005). Buch *et al*. (2004) also observed large changes in Greenlandic waters and attributed these changes mostly to climatic effects, although they also mentioned the released predation by cod on Arctic shrimp. A shift to a pelagic-feeder-dominated system also seems to apply to the warm North Sea and the Baltic Sea (Alheit *et al*., 2005; Casini *et al*., 2005; Heath, 2005; Kempf *et al*., 2006), and is, therefore, not only restriced to cold areas. This might also partially apply to the Faroe Plateau where the abundance of saithe (bentopelagic) has increased relative to haddock and cod (benthic) over the last fourty years (ICES, 2007). Overall, there has been a marked reduction in the production of predatory fish species during the last 100 years in the North Atlantic Ocean (Christensen *et al*., 2003). One important reason seems to be that cod prey on both pelagic fish and benthic crustaceans (Essington and Hansson, 2005; Daan, 1983; Kikkert, 1993; Pálsson, 1994) and may ‘control’ the ecosystem while abundant. It remains to be seen whether these findings confound the negative causal link between cod recuitment and the abundance of pelagic fish in the Southern Gulf of St. Lawrence (Swain and Sinclair, 2000). It also remains to be seen how this affects the coupling between individual growth and genetics (Hutchings, 2004; Olsen *et al*., 2004).

The Faroese case, where the cod production is determined by the phytoplankton production (Paper VI), is an example of a ‘bottom-up’controlled ecosystem. There are also ‘top-down’ controlled ecosystems where the abundance of predators determines the production of their prey (Reid *et al*., 2000). It was a long-held view that ‘top-down’ ecosystems were constricted to some freshwater lakes and that all coastal marine ecosystems were ‘bottom-up’ controlled. A high species-diversity is characteristic of ‘bottom-up’ controlled ecosystems, while a low species-diversity applies to ‘top-down’ controlled ecosystems (Frank *et al*., 2007). It is now realised that species-poor coldwater coastal ecosystems are often ‘top-down’ controlled (Frank *et al*., 2007), for example, at the Northeast coast of Canada (Frank *et al*., 2005). It has been proposed that the warming of the North Atlantic in the 1920s and 1930s caused a regime shift that was ‘bottom-up’ controlled (Drinkwater, 2006). Such a shift was in the opposite direction of the cold-induced regime shift in the 1980s, as described by, e.g., Bundy (2004). In a purely ‘bottom-up’ controlled system, the predation on each trophic level is high and from a variety of organisms. Removing one predator does not change the function of the ecosystem because there are other predators that may ‘take-over’ and the trophic pyramide maintains its shape. If the predation pressure (high in the trophic pyramid) is reduced, it may cause imbalances in the trophic structure. The shape of the trophic pyramid may be altered and there may be a ‘cascading’ effect down through the pyramid (Frank *et al*., 2005), e.g., high cod abundance, low abundance of zooplanktivorous fish, high zooplankton abundance, low phytoplankton abundance and high levels of nutrients (nitrate). The characterisation of ‘cold’ ecosystems as ‘top-down’ controlled and ‘warm’ ecosystems as ‘bottom-up’ controlled (Frank *et al*., 2005) may, however, be too simple, as, e.g., the pelagic fish food web in the North Sea is ‘bottom-up’ controlled while the benthic fish food web is ‘top-down’ controlled (Heath, 2005).

The productivity in an area may also depend upon production elsewhere in addition to local production (Sundby, 2000). A high inflow of warm, zooplankton-rich, Atlantic water into the Barents Sea is an example. The inflow of food into the Barents Sea may thus depend both on the phytoplankton production in the Norwegian Sea, as well as the strength of the North Atlantic

Current. A high inflow of Atlantic water is associated with a good recruitment of cod (Sundby, 2000). Sundby (2000) proposes that advection of *Calanus spp*. from the deep waters in the Nordic seas (Norwegian Sea) could boost recruitment / production of cod, which inhabit the fringes of the *Calanus spp*. distribution.

Recent research suggests that large-scale hydrographical conditions in the North Atlantic may have a profound influence on fish stocks. The strength of the North Atlantic Subpolar Gyre (Hátún *et al*., 2005) seems to be of particular importance for Faroe saithe (Steingrund and Hátún, 2008), but also Faroe Plateau cod (Paper V). When the Subpolar Gyre is strong, the region from East Newfoundland to the area south of Iceland is characterised by colder and fresher water masses. When the Subpolar Gyre retracts westwards, the temperature and salinity in the northeastern North Atlantic Ocean increases (Hátún *et al*., 2005). This is also accompanied by a higher primary production in the Iceland-Faroe region, as indicated by higher near-surface chlorophyll concentrations observed with the Continuous Plankton Recorder survey (Hjálmar Hátún, Faroese Fisheries Laboratory, personal communication). The strong Subpolar Gyre in the late 1980s, i.e., presumably poor primary production, coincided with several decimated fish stocks on the Faroe Plateau and on the Faroe Bank (ICES, 2008a).

The primary production in East Newfoundland waters might be affected in a similar way by the Subpolar Gyre (Hjálmar Hátún, Faroese Fisheries Laboratory, personal communication), and many fish stocks were, in fact, decimated at the same time there (see Drinkwater (2002)). The collapse of Northern cod (NAFO subdivisions 2J3KL) coincided with the minimum stock size of Faroe Plateau cod (1991-1993). In fact, there seems to be a close relationship between the strength of the Subpolar Gyre (index provided by Hjálmar Hátún, Faroese Fisheries Laboratory) and recruitment / spawning stock biomass of Northern cod (Figure 12) (supplementary material in Shelton *et al*. ( 2006)). There is also a high correlation between the gyre index and temperature (see indices of cooling in Drinkwater (2002)), but, in contrast to temperature, the gyre index was not only low but record low for the period 1991-1994. Hutchings and Myers (1994) argued that temperatures were not especially low during the collapse of Northern cod, and that temperature-induced mortality, therefore, could not be responsible for the collapse. Hence, it seems easier to explain the collapse of Northern cod in terms of extremely low ecosystem productivity rather than extremely low temperatures.

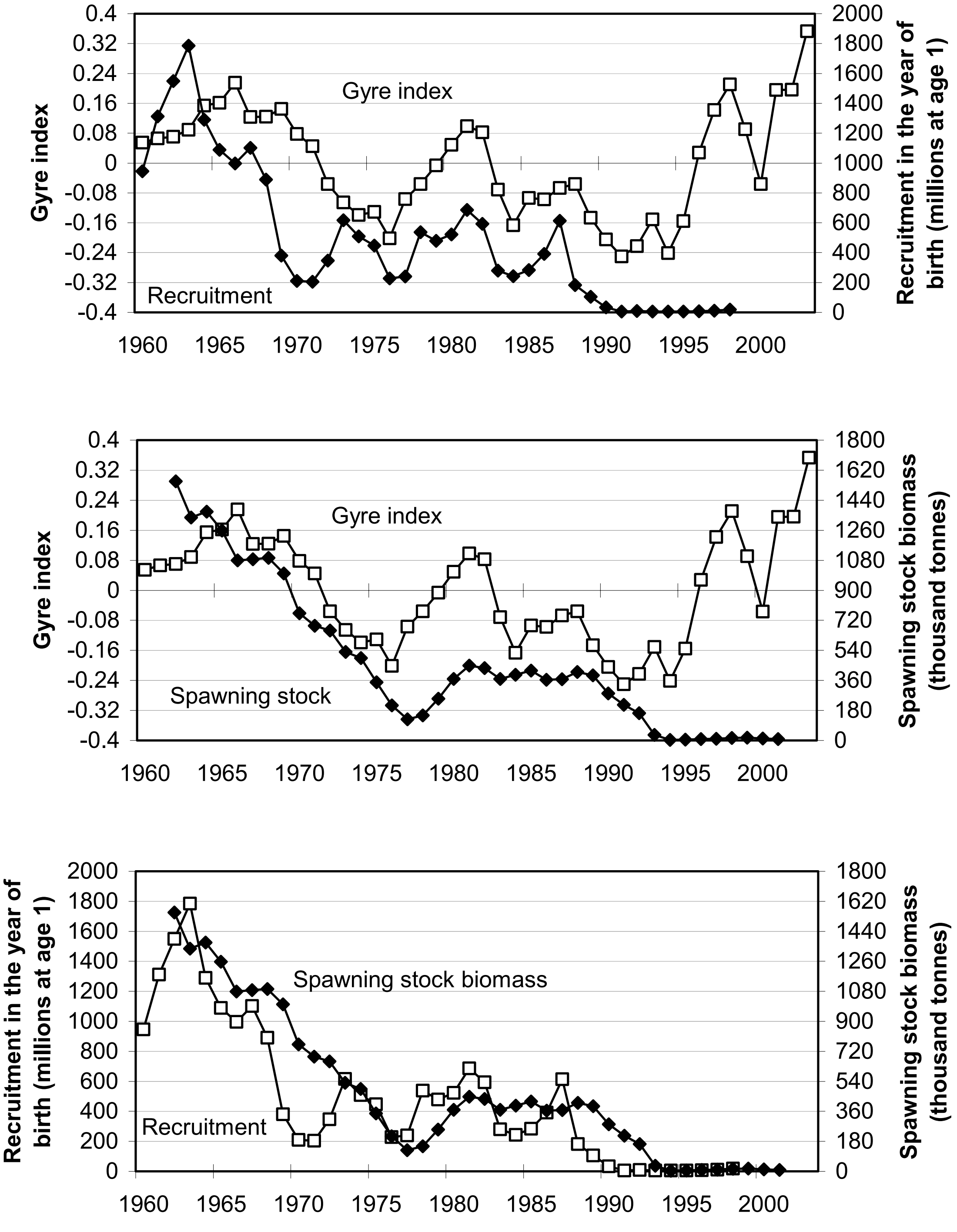

Figure 12. Temporal development of the Subpolar Gyre, and recruitment and spawning stock biomass of Northern cod, eastern Canada (2J3KL). Note that the gyre index, as presented here, is low when the Subpolar Gyre is strong and *vice versa*.

A positive relationship between cod recruitment and productivity is not a novel discovery. For example, Sutcliffe *et al.* (1983) proposed that recruitment was positively related to salinity conditions, which were used then as a proxy for productivity (more saline – more productivity). The mechanism (a north-south conveyor belt food-chain) was, however, not confirmed by subsequent work, where upwelling events near Hamilton Bank seemed more likely (Drinkwater and Harding, 1995). Myers *et al.* (1993) modified the recruitment – salinity relationship by including the (positive) effect of the spawning stock biomass. The relationship between recruitment and productivity seems likely, because cod were in very poor condition prior to the collapse (Smedbol *et al.*, 2002; Dutil *et al.*, 1999). Paper V also shows that this was not unique to Canadian cod stocks, but the effects of a strong Subpolar Gyre were discernible as far away as at the Faroes. However, the recruitment – salinity relationship was abandoned when additional years of very low recruitment and high salinity became available (Hutchings and Myers, 1994; Shelton and Atkinson, 1994). This may have been too hasty a rejection, because one limiting factor (ecosystem productivity during the period 1960s-1980s) may have been replaced by another (stock size or spawning stock size) in the 1990s, which is exactly the situation for Faroe Plateau cod now in 2008 and predicted by the Faroese recruitment model. This kind of argument has been applied for cod off Newfoundland (Rose, 2004).

Whereas there seems to be a positive relationship between the gyre index and recruitment in Northern cod, the opposite seems to apply for Faroe Plateau cod (Figure 13). The explanation might be that the primary production over the shallow areas (Faroe Shelf), which regulates recruitment and growth in Faroe Plateau cod (Paper VI), is negatively related to the gyre index. Variability in phytoplankton production is a complex field and is outside the scope of this thesis, but it should be noted that NAO-like atmospheric forcing also affects phytoplankton production (Skogen *et al.*, 2007). Both cod stocks could be influenced in a similar way by ecosystem productivity over their respective feeding / nursery areas. It remains, however, to be established whether there is a causal relationship between the strength of the Subpolar Gyre and ecosystem productivity, or whether this covariability is due to direct air-sea interaction.

There was plenty of Blue whiting in the deep waters (> 150 m) during the 1997-2006 period, coinciding with an especially weak Subpolar Gyre. Homrum (2007) did not find a single Blue whiting in cod stomachs sampled in January 1991 when the Subpolar Gyre was very stong. At slightly lower levels of the Subpolar Gyre (in September 1978), Du Buit (1982) did find abundant Blue whiting in cod stomachs collected in the deep waters around the Faroe Bank. Hence, the food availability in the deep waters may not always stay so high as observed in the 1997-2006 period (Paper II). If food availability in deep waters is impaired at gyre indices less than –0.16 (not a problem in 1975-76 at values of –0.13 and –0.20, but maybe a problem in 1991 at a value of –0.25), then this has happened in only six out of 47 years

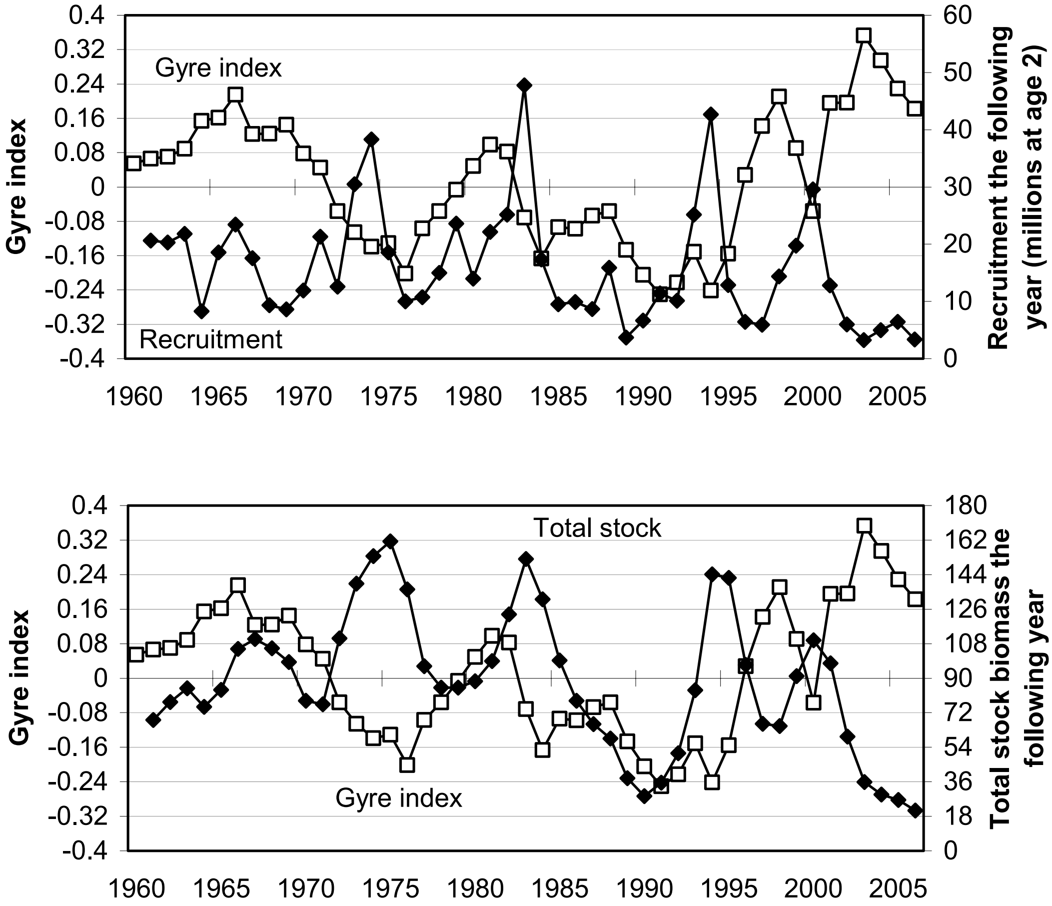

Figure 13. Temporal development of the strength of the Subpolar Gyre, and recruitment and total stock biomass of Faroe Plateau cod. The gyre index is obtained from an ocean general circulation model (see text) 1960-1992 and direct satellite altimetry measurements of sea surface height 1993-2006, which are scaled to the former part of the series, based on an overlap during 1993-2003. Note that the gyre index, as presented here, is low when the Subpolar Gyre is strong and *vice versa*.

The link between the Subpolar gyre and ecosystem productivity is fairly new and unexplored and is not treated in detail here. If correct, it suggests that the mysterious development of Faroe Plateau cod during the 1980s and 1990s was caused by the spectacular development of the productivity over the inner and outher areas, respectively. While the stock development of Faroe Plateau cod seems fairly well explained in Paper V and Figure 5, the temporal and spatial development of ecosystem productivity seems to be a much larger mystery.

## Cod population dynamics

The production of cod depends very much on the population dynamics of cod that, like other fish species, is determined by four processes: recruitment, individual growth, mortality (fishing and natural mortality) and migration. Starting with individual growth, it is remarkable that there is either no relationship or a positive relationship between cod density and individual growth (Brander, 2007), i.e., growth is not better when density is low. This could be explained by a positive relationship between food abundance (productivity of the ecosystem) and growth / recruitment, for example, by a positive relationship between capelin abundance and cod growth in Icelandic waters (Stéfansson *et al.*, 1998) and in the Barents Sea (Dalpadado and Bogstad, 2004; Hjermann *et al.*, 2004). It is also possible that food consumption by these cod stocks depends more on the abundance of cod (increased feeding with increasing cod abundance) than on food availability (e.g., Heath, 2005). This would indicate that there is food in excess in the system that is not utilised, probably explaining why the cod stocks in Canadian waters (Rose, 2004), Iceland (ICES, 2008a) and in the Barents Sea (ICES, 2008b) were much higher in former times than today.

The life history of cod needs to be considered in order to explore the nonexisting relationship between density and individual growth, especially because the spatial and temporal overlap between cod and its food is crucial for consumption and production. Cod aggregate at special spawning sites and the eggs / larvae drift with the currents to the nursery areas of juvenile cod. Spawning and nursery areas may be located far away from each other (Barents Sea cod) or close to another (Faroe Bank cod) depending on the ocean currents. As cod grow larger, they may move to other areas to feed (feeding areas) exemplified by Barents Sea cod, which have a more south-westerly distribution in warmer water when they grow larger (Nakken and Raknes, 1987; Ottersen *et al.*, 1998). In winter, cod may move to special overwintering areas exemplified by cod stocks in the Northwest Atlantic that overwinter in warm Atlantic water at the slopes of the continental shelves (ICES, 2005). Mature cod probably need to occupy warm water for gonad maturation (Kjesbu *et al.*, 1998). It is evident that cod may not be able to fully utilise all the available food because of reduced feeding opportunites in relation to overwintering or spawning migration. The juveniles may not adjust their position optimally in relation to prey availabilities because of limited migratory capacity. Hence, exploited populations of cod, which often are much smaller than virgin populations (Myers and Worm, 2003), may not be able to fully utilise the food resources, which in turn may benefit other fish species.

The underutilised food in the system may be evident from spatial variations in individual growth. If cod were able to adjust their distribution to food patches according to the Ideal Free Distribution (Fretwell and Lucas, 1970), there should be no spatial differences in individual growth, which, however, does not seem to be the case (Chouinard and Swain, 2002; but see Hughes and Grand, 2000). Icelandic cod seems to grow slowest in cold, deep waters where the density is highest and most rapidly in warm, shallow waters where the density is low (Imsland and Jónsdóttir, 2003; Pálsson and Thorsteinsson, 2003; Björnsson and Pálsson, 2004). This situation could arise from fish selecting cold temperatures when abundance is high (Hughes and Grand, 2000). In Faroese waters, however, the situation seems to be quite different: cod grow slower in shallow waters where density is highest and more rapidly in deep waters where food abundance is high (Paper II). There may only be a 1-2 °C difference in temperature between shallow and deep waters at the Faroes (Paper I). Hence, temperature or depth seem ulikely causes for these observations, which rather could be explained by inertia in migratory behaviour. Icelandic cod grow up in the cold areas north-west to north-east of the country (Björnsson and Pálsson, 2004; Pálsson, 2004) and the most rapid growth of cod occurs in the warm areas in the south-west (Jónsdóttir *et al.*, 2002). Faroe Plateau cod, on the other hand, grow up in shallow waters close to land and gradually move to deeper waters during ontogeny (Paper IV). The coupling between cod genetics and growth in Jónsdóttir *et al.*, (2002), i.e., that $\mathrm{PanI}^{A}$ cod grow faster than $\mathrm{PanI}^{B}$ cod, may, therefore, be confounded by other variables (differences in cod density).

A lack of density-dependent growth may lend support to the traditional view that year-class strength is determined at the larval stage. However, it is important to keep in mind that the amount of young fish entering the fishery (recruitment) is a result of several bottlenecks from spawning to recruitment, and that the importance of these bottlenecks may vary temporally, as well as spatially. There seems to be little doubt that mortality at the larval stage is a decisive factor, which may be coupled with food abundance, e.g., temporal match between cod spawning and local abundance of eggs / nauplii of *Calanus finmarchicus* (see Sundby, 2000). The finding that cod stocks in the Northwest Atlantic have a much lower fecundity than cod stocks in the Northeast Atlantic (May, 1967) may be one explanation for the strong positive relationship between the size of the spawning stock and subsequent recruitment for coldwater Canadian cod stocks (Group 1 in Table 1). There are, however, cases where sufficient spawning in coastal waters did not result in increased recruitment (Smedbol *et al*., 1998).

The case with Faroe Plateau cod shows, however, that there is a need to be aware of factors operating later in life. The degree of cannibalism in Faroese waters was by no means exceptionally high (1.9% by weight of total stomach content), compared with the Barents Sea and Iceland (Bogstad *et al*., 1994), the North Sea (Daan, 1983; Kikkert, 1993) and the Baltic Sea (Neuenfeldt and Köster, 2000). Normally, cannibalism increases with year-class strength (Bogstad *et al*., 1994; Neuenfeldt and Köster, 2000), which may give the false impression that year-class strength is determined at the larval / early juvenile stage, because there will be a positive relationship between 0-group abundance and recruitment, shown, e.g., in Bogstad *et al*. (1994) and Helle *et al*. (2000). The difference between cannibalism in Faroese waters compared with the other areas seems to be that cannibalism was not related to year-class strength, but rather to ecosystem productivity in relation to total fish biomass ('food per kg fish') (Paper V, Figure 5). A similar feature was observed in the Barents Sea where the 0-group indices were high for a couple of cod year-classes in the mid 1980s, which later were heavily cannibalised (Bogstad *et al*., 1994; Hjermann *et al*., 2004; Nakken, 1994).

There may exist a need to verify that the processes believed to control cod recruitment are correct, and two examples will be discussed briefly. Helle *et al*. (2000) investigated several abundance indices of larval / juvenile cod in the Barents Sea and found that year-class strength was established after 3 months, as cod post-larvae abundance was highly correlated with survey abundance indices of age 2 and age 3 cod. However, there was a poor relationship between the post-larvae index and recruitment at age 3 estimated from Virtual Population Analysis (which gives the 'sum' of what is caught of a year-class throughout its life, corrected for natural mortality). This indicates that year-class strength may be further regulated later in life (e.g., through cannibalism, Bogstad *et al*., 1994; Hjermann *et al*., 2004) although other possibilities exist (see Helle *et al*., 2000).

The other example considers Sundby's (2000) proposal that advection of Calanus from deep waters onto the shelves boosts cod recruitment in various regions in the North Atlantic Ocean. Advection of *Calanus spp*. into the systems would be expected to affect a number of trophic stages and could act in a similar way as an increase in local phytoplankton production. The beneficial effect of *Calanus spp*. advection could thus affect all stages in the life cycle of cod and other fish species through a general increase in food abundance. Hence, it is necessary to verify that the main bottleneck in the determination of year-class strength is the feeding of cod larvae on *Calanus spp*. eggs / nauplii and not any other correlated events later in life.

### Cod behaviour

The year-class strength of Faroe Plateau cod seems to be determined by events later in life, and presumably has a strong behavioural component. When food abundance for adult cod was low, there was a low survival of 1-group cod, accompanied by a movement of adult cod closer towards land into the core areas of juvenile 1-group cod (Paper V).

The movement of cod towards land (Phenomenon 1) when food was scarce may be restricted to the Faroe Plateau and may relate to the homogenious water masses (temperature) over the main distributional area of cod (0-150 m). In the absence of termoclines, cod may move according to food opportunities: if slim cod are not able to catch highly mobile prey in deep waters (100-150 m) they may make it better in shallow waters (50-100 m) catching slowly moving benthic prey.

The movement of cod into deep waters on the Faroe Plateau (Phenomenon 2), where food seemed to be plentiful, seemed to follow another principle: The shallow areas had to be 'filled up' first. The main constraint seemed to be physiological/biochemical costs associated with a change in depth, as well as other costs. The Faroe Plateau seems to offer a unique possibility to study effects of depth adaptation of fish because the temperature is so homogenious with depth down to around 500 m. For many other areas, the water masses are much more stratified, and temperature and depth may often vary together. Apparently, the total cost associated with a change in depth was high enough to prevent cod to colonise the deep waters. It could both represent direct physiological costs, e.g., filling gas into the swimbladder (Arnold and Greer Walker, 1992), as well as increased risk of predation and the cost associated with learning to catch new prey. A trade-off between growth and mortality, e.g., moving to dangerous areas where growth is high, is observed in a variety of animals and situations (Biro *et al.*, 2007; Gilliam and Fraser, 1987; see Werner, 1988 and references therein; Damsgård and Dill, 1998).

It is a complex issue to relate migration to various trade-offs or constraints because it is implicitely assumed that fish have the ability to compare the options. In the case of long-distance migrations (several nautical miles) fish may only have adequate information about the current location and very limited or out-of-date information about alternative sites. For example, cod may undertake short migrations (a few days) to the deep waters at the Faroes just after spawning and then return to shallower waters where they stay during the rest of the feeding season (Figure 2). The short experience from deep waters may also be misleading regarding, e.g., predation risk because whales and seals may be more frequent during summer than in April (Skov *et al.*, 2002). The movement to other areas may, therefore, be hampered by a lack of information rather than the unsuitability of alternative sites. A related issue is the 'loss of culture' where migration patterns may be lost due to a lack of experienced older individuals. For example, the traditional migration of cod towards the overwintering areas at the slopes in Newfoundland waters ceased as the Northern cod stock collapsed (Rose *et al.*, 1995; Rose *et al.*, 2000).

The positive correlation between feeding intensity and condition as well as with local density of cod may fit well into the observations on cod in Canadian waters. A dramatic redistribution of cod occurred in Canadian waters during the late 1980s (Rose *et al.*, 2000) when several cod stocks collapsed and when temperatures were exceptionally low, a controversial issue treated in Hutchings (1996) and Rose *et al.* (2000). The condition of cod was low, at least in the Northern Gulf of St Lawrence (Dutil *et al.*, 1999), and Northern cod migrated southwards towards higher temperatures (deYoung and Rose, 1993; Kulka *et al.*, 1995). Cod were also found in even higher densities (hyperaggregation) than normal, and the decline in stock size was accompanied by area reductions rather than density reductions (O'Driscoll *et al.*, 2000; Rose and Kulka, 1999). Natural mortality increased (Sinclair, 2001), and the fishing mortality was also extremely high (ICES, 2005). Although these issues are highly controversial (Kulka *et al.*, 1995), it is proposed that these observations may be linked by a positive relationship between feeding success and the two variables, swimming ability and group size. There is a strong positive correlation between temperature and swimming ability (He, 1991; Videler, 1993). Fish are able to acclimatize to low temperatures by various physiological mechanisms (Guderley, 2004), but such acclimatisations may require several weeks (Zakhartsev *et al.*, 2004a), while acclimatisation is limited in cases of sudden temperature change (see later). Cod may be less able to feed on mobile fish when temperatures are low. Capelin may avoid such low temperatures (Marchand *et al.*, 1999), except in connection with spawning (Davoren *et al*., 2006). The fact that capelin also seem to move southwards (ICES, 2005; O'Driscoll *et al*., 2000) would make life even worse for cod. Hence, cod in poor condition - and presumably low swimming ability (Martinez *et al*., 2003) - went towards higher (but still low) temperatures where they might have compensated for the poor swimming ability by hyperaggregating so that they were able to feed efficiently (Pitcher *et al*., 1982) and/or avoid predation by, e.g., seals. Hence, the findings for Faroe and Canadian cod taken together suggest that feeding success is positively correlated with condition / swimming ability / temperature / group size, although this single piece of evidence should not be overemphasised when dealing with the fate of Canadian cod.

The temperatures were also low in the mid-1970s and mid-1980s without any collapse. This evidence is often used as an argument that the collapse was only caused by overfishing (Hutchings and Myers, 1994; Myers *et al*., 1996), rather than a combination of fishing and adverse climatic conditions (ICES, 2005). Since cod feeding may correlate positively with stock size – as indicated earlier by the absence of a relationship between cod density and individual growth – stock size may be of vital importance for recovery when temperatures rise to normal. The stock sizes in mid-1970s and mid-1980s were low, but somewhat higher than in 1990 and might have been above a critical minimum threshold. There was a regime shift in Canadian waters in the 1990s after the collapse of the cod stocks and there might be a critical stock size of cod that turns the ecosystem into a new state that may prevent cod from recovering because vital niches for cod are then occupied by other organisms. As shown by Savenkoff *et al*. (2007b) cod played a key role in the ecosystem by preying on both pelagic and benthic organisms. A nearly complete removal of cod might have actually caused the regime shift. If cod of offshore origin have to form the basis of a future recovery, as proposed by Beacham *et al*. (2002), the future for many cod stocks in Canadian waters looks bad. It has also been proposed that fishery-induced changes in genetic properties, along with reduced size and age of maturity, cause lower survival of adult cod, as well as lower hatching success, thus leading to a slow or negligible recovery of cod stocks (Hutchings, 2005). This argument, however, does not take into account the trophic considerations considered above. This complexity demonstrates that the collapse and recovery of the Canadian cod stocks involves a multitude of factors and to delineate the importance of each is a formidable task.

Recruitment dynamics is a central theme when stock collapses are considered (Figure 14). Little is known about recruitment dynamics in Canadian waters (ICES, 2005; but see Swain and Sinclair, 2000). The Faroese recruitment model states that year-class strength is proportional to the total biomass of the adult cod stock offshore and inversely related to predation (cannibalism) in nearshore waters. If recruitment in Canadian waters is regulated in the same way, then the 'second bottleneck' (when joining the adult population) might be stronger in Canadian waters than at the Faroes. The migratory behaviour of Canadian cod stocks is much more diffuse than for cod stocks in the Northeast Atlantic (Robichaud and Rose, 2004; Table 1) and is related to the more variable hydrographical conditions in the Northwest Atlantic (Robichaud and Rose, 2004). This indicates that Canadian cod move more than cod stocks in the Northeast Atlantic. Canadian cod may also be more dependent upon group formation than, e.g., Faroe Plateau cod, since the stock size reduction of Northern cod was accompanied by area reductions (Rose and Kulka, 1999), as opposed to Faroe Plateau cod where density reductions are observed (unpublished data). The formation of groups in connection with movement may be a good strategy to avoid predators, since movement may decrease camouflage and increase predation risk considerably (Endler, 1991). The virtual absence of older cod groups in the beginning of the 1990s could have increased the predation mortality on the 1986-1987 year classes by, e.g., seals (see Chouinard *et al*., 2005; Duplisea, 2005).

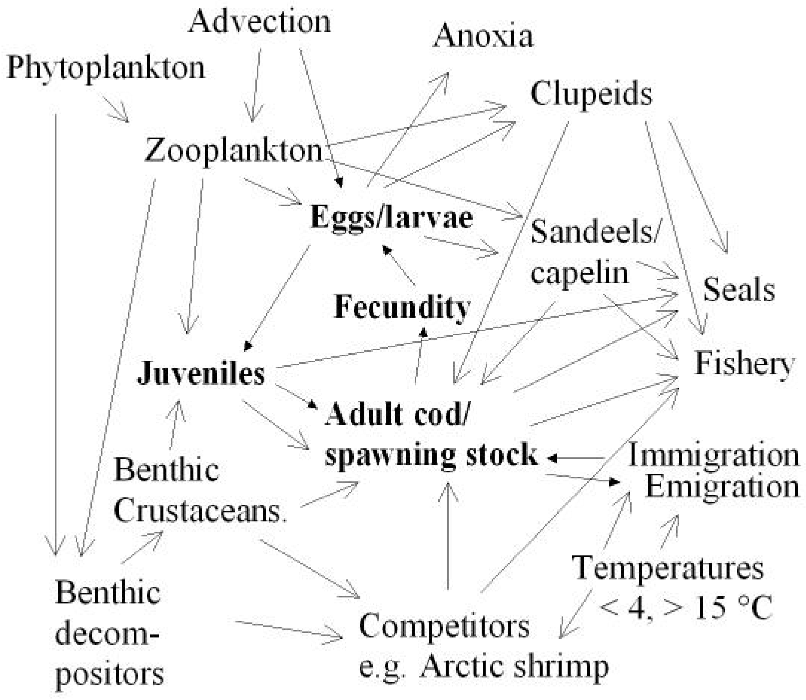

Figure 14. A conceptual framework for cod population dynamics. The life cycle in cod is highlighted in bold and connected with arrows having solid ends. Import (advection, immigration) or export (emigration) of cod is also indicated by arrows with bold ends. The other arrows indicate trophic relationships, causes of death (anoxia) or recruitment boosting (advection).

A link between temperature conditions and migration seems to be common (Robichaud and Rose, 2004) and is observed very clearly for Icelandic cod (Pálsson and Thorsteinsson, 2003). Icelandic cod are one of the few cod stocks that have access to both warm and cold waters (Table 1). Pálsson and Thorsteinsson (2003) noted that cod in shallow, warm waters (> 5 $^{o}$C, < 200 m) had a fairly stationary behaviour, just like Faroe Plateau cod in Figure 2, whereas cod in deep, cold waters showed a distinct migratory behaviour, similar to Cod 4406 in Figure 2. Pampoulie *et al.* (2008) found that shallow-water cod predominantly had the PanI$^{A}$ allele, while deep-water cod carried the PanI$^{B}$ allele, i.e., there seemed to be a genetic component involved. The difference in migratory behaviour seemed not to be caused by a widely different diet, e.g., shallow-water cod feeding on benthic crustaceans and deep-water cod feeding on fish, as shallow-water cod also preyed on fish (capelin in March) (Jaworski and Ragnarsson, 2006). Pálsson and Thorsteinsson (2003) hypothesized that the movement of cod to cold waters could reflect energy saving since the optimal temperature for growth is lower when food ration is low. This is similar to the approach taken by Chouinard and Swain (2002) when explaining the observation that high abundance of cod (and presumably low feeding) is often found in cold water in the Southern Gulf of St. Lawrence.

The virtual absence, at the same time, of stable and food-rich hydrographic fronts may explain the fact that very few cod exhibit deep-water migratory behaviour in Faroese waters (Figure 2). The food-rich, deep waters (300-500 m depth) on the eastern side of the Faroe Plateau are normally quite warm (> 5 $^{o}$C), but 'tongues' of cold water may enter from the North (Figure 1). These tongues seem to be irregular (Hansen, 1988) and there is no permanent polar front, except in waters deeper than about 500 m where large Blue whiting (20-35 cm, unpublished data) may be found on the warm side of the front. They may be difficult to catch and the cost associated with cold water adaptation may make the polar front (at 500 m depth) an unfavorable place for Faroe cod. Also, cod staying at the 300-500 m depth need to be prepared for sudden changes in temperature and presumably tolerate temporarily reduced swimming ability and increased predation risk. This may partially explain the low abundance of cod in deep waters and the virtual absence of migratory deep-water behaviour in Faroe cod. However, as noted earlier, the fact that Faroe cod 'begin' their life in warm shallow water, as opposed by Icelandic cod, also seems to be an important explanation.

### Physiological, biochemical and genetic factors causing an inertia in cod distribution

A vital part of the argumentation in this thesis has been based on physiological, biochemical and probably genetic constraints, i.e., that cod are not free to move to any location. Some of these factors are discussed below.

A change in depth causes the swimbladder in cod to expand / compress in relation to reduced / increased hydrostatic pressure, since the swimbladder obeys Boyle's law. Cod can tolerate a reduction of around 25% and an increase of around 50% in hydrostatic pressure (Arnold and Greer Walker, 1992). This would prevent cod from moving rapidly to widely different depths (Stensholt *et al.*, 2002). It would require excretion / production of oxygen gas from / into the swimbladder in order to change depth, which seems to be possible for cod provided some days (or a few weeks at most, Koj *et al.*, 2007) and the energy required to move between the locations. However, other physiological constraints may be involved.

Hydrostatic pressure (Sebert, 2002) may affect vital rates in aquatic animals (Hochachka and Somero, 1973), but this finding seems to be largely neglected in the literature of fisheries biology. Both hydrostatic pressure and temperature may have important effects on enzymatic processes, although the direction of the effect may be different. While temperature normally speeds up enzymatic processes, hydrostatic pressure may either slow down or speed up enzymatic processes, and interactions between temperature and hydrostatic pressure also exist (Hochachka and Somero, 1973).

Fish may use three strategies to cope with changes in hydrostatic pressure or temperature. The 'Qualitative' strategy implies a change in the stereostructure of enzymes / proteins, while the 'Quantitative' strategy refers to increased concentrations. The third or 'Modulative' strategy denotes the use of other molecules to modulate the stereostructure of enzymes / proteins (Hochachka and Somero, 1973; Somero, 2004). Only the Modulative strategy may be useful in case of sudden changes in hydrostatic pressure or temperature and seems also to be important in connection with slower changes in hydrostatic pressure, as the concentration of TMAO increases with increasing depth in many aquatic organisms (Somero, 2003), including cod (Love, 1975; Love *et al.*, 1974).

Apparently, there are high costs associated with acclimatization to a different depth, since, e.g., the concentration of TMAO needs to be increased or decreased. Cod may not be willing to undertake great changes in depth, e.g., from 100 to 500 m, when first acclimatized to a certain depth. This could partially explain the finding that shallow-water cod (< 200 m, Pálsson and Thorsteinsson, 2003) normally stay in shallow waters while deep-water cod stay in deep water. This also complies well with the finding that the spawning areas of shallow-water Icelandic cod (around 50 m depth at Loftstaðahraun) are located shallower than the spawning areas of deep-water cod (around 280 m depth at Kantur) (Jónsdóttir *et al.*, 2002). Figure 2 shows examples of steady depth occupancy by Faroe Plateau cod.

While the costs associated with, e.g., the increase / decrease of certain organic osmolytes (e.g., TMAO) may be considerable, the costs associated with the formation / removal of organelles should be even higher. The mitochondria seem to be the weak link in temperature acclimatization, since their efficiency as energy producers in the cells relates directly to temperature (Guderley, 2004). The only way to compensate for the loss of efficiency per mitochondrium seems to be an increase in the number of mitochondria (mitochondrial proliferation) (Guderley, 2004; Pörtner, 2002a), which, however, leads to 'proton leak' and a higher standard metabolism (Pörtner, 2002b; Sylvestre *et al.*, 2007). Cod acclimatized to a certain temperature may, thus, not be willing to change temperature. Indeed, Stensholt (2001), when analysing temperature-depth recordings from Data Storage Tags, found that migrating Northeast Arctic cod tended to migrate along stable thermal paths, as was also found for Northern cod (DeBlois and Rose, 1995). Laboratory experiments have also demonstrated that cod tend to avoid temperature changes (Claireaux *et al.*, 1995).

Nevertheless, cod are often observed to undertake rapid changes in both temperature and depth when feeding close to thermal fronts (Pálsson and Thorsteinsson, 2003; Stensholt, 2001; Figure 2). Cod apparently accept short time changes in temperature / depth during feeding, as was also observed in the laboratory by Claireaux *et al.* (1995). This could be a 'high gain-high cost' strategy, and polar fronts are normally associated with high food abundance (see Marchand *et al.*, 1999). Marchand *et al.* (1999) found that the aggregations of capelin close to thermal fronts were driven by the poor tolerance of cold water (< 2 $^{o}$C), rather than high concentrations of food for capelin. It may thus be speculated that large groups of cod may force capelin to enter cold water where capelin may be more vulnerable to reduced mobility than cod, an idea proposed by Vilhjálmur Thorsteinsson (Marine Research Institute, Reykjavík, Iceland, personal communication). If this is correct, then it might shed further light onto the fact that cod in Faroese waters seldom feed close to thermal fronts (although a single example is given in Figure 2), because the prey fish in deep waters is the considerably larger Blue whiting, which may have a higher swimming capacity than capelin. The sustained swimming speed of capelin is around 50 cm/s at 5 $^{o}$C (Behrens *et al.*, 2006), corresponding to 0.6-1.0 body lengths per second for cod, which is below the critical swimming speed of cod (Martinez *et al.*, 2003). Such a lifestyle close to thermal fronts would be expected to demand steady routine swimming activity since cod need to follow the thermal fronts which may move back and fourth relative to the ground. It must be assumed that the majority of the temperature / depth changes observed just reflect a 'hold station' behaviour of cod relative to moving thermal fronts rather than actual pursuit of prey.

When scrutinizing Cod 4406 in Figure 2, it seems clear that the depth variability is much greater on the cold side of the (presumably horizontal) front than on the warm side. Thus, this individual might have been quite inactive at night when it always was located in warm shallower waters than during the day when it was in cold, deep water. A similar behavioural feature was observed in the laboratory by Claireaux *et al.* (1995). This could be related to the need of the fish to digest food in warm water, or to speed up gonad development while feeding on the cold side of the front.

There may, however, also be a relationship between fish movement and temperature. Fish may rely on aerobic oxidation of fat when swimming slowly, (see the introduction in Martinez *et al.* 2003 and references therein) and only use the low-twitch red muscles (Altringham and Ellerby, 1999; Videler, 1993). During gradually higher activity, fish must rely more on anaerobic processes where the main energy source is glucose in the white muscles (see Martinez *et al.*, 2004). Whereas cod are able to compensate for the slowing effect of temperature on aerobic respiration, they seem less able to compensate for the loss of anaerobic scope, as also observed in other organisms (Zakhartsev *et al.*, 2004a, Zakhartsev *et al.*, 2004b). The reason may partly be that the vital enzyme, Lactate

DeHydrogenase (LDH), in the glycolytic pathway is inhibited. As with low temperature, high hydrostatic pressure may inhibit the function of glycolytic enzymes (Hochachka and Somero, 1973). Importantly, aerobic and anaerobic respiration may inhibit each other, i.e., enzymes associated with the aerobic respiration may block the function of enzymes in the anaerobic respiration and *vice versa* (Hochachka and Somero, 1973), and for individual cod there might well be a trade-off between stamina and the ability to use glycolytic locomotion (Reidy *et al*., 2000). Hence, cod may be able to maintain, or even increase, aerobic metabolic capacity when acclimatizing to cold temperatures, with the consequence of a higher standard metabolic rate (Sylvestre *et al*., 2007), but seem not to be able to maintain anaerobic metabolic capacity (Martinez *et al*., 1999).

There seems to be a link between the migration pattern and genetics. Pampoulie *et al*. (2008) found that the shallow-water cod described in Pálsson and Thorsteinsson (2003) most frequently had the $PanI^A$ allele while the deep-water cod possessed the $PanI^B$ allele. In Faroese waters, the frequency of the $PanI^B$ allele was very low (Paper XI). This is in accordance with the observation that only one out of about 140 cod tagged with Data Storage Tags on the Faroe Plateau exhibited deep-water behaviour (Cod 4406 in Figure 2), while the rest exhibited shallow-water behaviour. The pantophysin protein is involved in trafficking membrane vesicles in the cells and may in some cases be associated with glucose transport (Brooks *et al*., 2000; see Días *et al*., 2007; Hall *et al*., 2006), and it may be speculated whether the pantophysin protein is the biochemical link between cod migration pattern, anaerobic / aerobic scope and genetics.

It may be asked whether Faroe cod have the wrong genotypes, i.e., $PanI^A$ and not $PanI^B$ alleles, to exploit the favorable deep-water resources. The frequency of the PanI genotypes seems to be established early in life and does not seem to change during an individual's life (Karlsson and Mork, 2003; Sarvas and Fevolden, 2005) or through time (Nielsen *et al*., 2007). The feeding conditions in frontal areas in Faroese waters seem to be poor and there are also $PanI^B$ cod in the neighborhood at the Faroes-Iceland ridge (Case *et al*., 2005), which could be expected to invade Faroese waters, if there were rich feeding conditions associated with thermal fronts. Such a migration seems to be very limited according to tagging experiments (ICES, 2007), although $PanI^{BB}$ homozygotes are occasionally found in Faroese waters (Nielsen *et al*., 2007). Thus, Faroe Plateau cod do not seem to possess the wrong genetic properties.

## Remaining issues and future research

The phytoplankton production index is valid for the shallow parts (< 130 m) on the Faroe Shelf whereas a modified gyre index seemed to correlate well with the phytoplankton production over the outer areas. A strong positive correlation was found between the subpolar gyre index and the total biomass of saithe (lagged four years behind) and the causal mechanism was proposed to be food availability (Steingrund and Hátún, 2008). Future research should focus on the relationship between these two indices of productivity and how they might be used as a basis for future ecological models for the Faroe Plateau.

The large 1993 year-class was considerably stronger than predicted by the recruitment model (43 vs. 30 million), which is a part of the 'mysterious' cod that 'came back' in the mid-1990s. Scientists know very little about the inner areas of Faroese waters and whether factors other than the abundance of adult cod affect juvenile survival. Also, juvenile cod (0/1-group) may be found down to 300 m depth, and it may be speculated whether such 'deep-water' cod may have made an important contribution to the 1993 year-class, either because of abnormal current patterns or unusually low predation mortality (the biomass of most fish species in 1993 was low). A similar version of this hypothesis was originally formulated by Hjalti í Jákupsstovu (Faroese Fisheries Laboratory, personal communication), which is in line with Svedäng and Svensson (2006). Also, cod recruitment depends upon total fish biomass (Figure 5), which represents a gap in current knowledge, as mechanisms controlling haddock and saithe recruitment and growth are poorly known. Hence, it is unknown whether a high fishing effort on saithe, for example, could proportionally increase cod recruitment.

The recruitment model indicated that recruitment was hampered by a distributional overlap between juvenile and adult cod. It would be important to investigate the cannibalistic behaviour of cod in more detail, i.e., where and when and how, to identify the best proxy for cannibalism, for example, distributional overlap and/or shortage of alternative food. The recruitment model also indicated that recruitment was positively related to total stock size, and it was proposed that juvenile cod had to ‘join’ adult cod in order to obtain feeding benefits and reduced predation. A crucial step forward would be to evaluate whether this was a real spatial joining into shoals / groups, or just the random presence of juvenile cod in the same area as adult cod. Fine-scaled sampling, as well as direct camera observations, may be useful. Such studies could also reveal whether the B/C in the recruitment model merely reflected the inverse of the spatial overlap between juvenile and adult cod, i.e., that there was only one survival bottleneck for juvenile cod (the ‘cannibalistic’ bottleneck during the summer at age 1) and not a second bottleneck at age 2.

Individual growth slows down with decreasing temperature, but cod density, as well as recruitment, nevertheless, seems to be highest in the cold areas (Table 1, see Sundby, 2000 and references therein). Sundby (2000) tried to explain these findings by the fact that *Calanus finmarchicus*, an important food organism for cod post-larvae, is distributed in cold waters, but the temperature distribution of cod was lower than for *Calanus finmarchicus*, contradicting this explanation somewhat. Robichaud and Rose (2004) noted that the carrying capacity for predatory fish species tended to be rather constant across temperatures and that cod constituted the main (only) predatory fish species in cold waters. Frank *et al.* (2007) and Rose (2005) found that the fish species diversity decreased with decreasing temperature. This leads to the hypothesis that year-class strength in cod may be influenced by species diversity, e.g., by competition for resources by other fish species, a hot topic in connection with global warming, which should be investigated in future studies.

This thesis notes that the stationary habit of shallow, warm-water cod and the migratory habit of deep, cold-water cod (Pálsson and Thorsteinsson, 2003; Pampoulie *et al.*, 2008) probably had a genetic / physiological basis and a behavioural basis. Cold-water cod may have a higher aerobic-to-anaerobic metabolic scope and warm-water cod a lower aerobic-to-anaerobic scope. This hypothesis is based on general biochemical considerations and needs more study. An alternative explanation concerns the hypothesis that food concentration is higher in shallow waters, which would allow cod to be more stationary and hold specific home ranges. The existence and importance of each of these two alternatives needs to be investigated. One method of investigation would be to use a tagging program with data-storage-tags that included genetic mapping of all tagged fish. Laboratory studies could elaborate the behavioural differences between cod stocks / genetic strains.

## Management considerations

The fact that the stock estimates for 2007 (ICES, 2008a) were the lowest observed during a century is a critical situation because there is a realistic risk that the stock might collapse in the near future. Even though the primary production was higher-than-average in 2008, and stays high in 2009-2010, there is a high probability that the cod stock will become commercially extinct in the future, because the current fishing mortality is too high. The effort management system was implemented in 1996 (ICES, 2008a) and the number of fishing days has been reduced by around 20% in the period from 1997-2007. This has likely not been sufficient to account for increased gear efficiency, which, for the longliners, seems to be on the order of 5-7% per year (Steingrund, 2008). The number of fishing days was decreased by 10% for the fishing year September 2008 to August 2009.

Such a small reduction may seem strange to non-Faroese readers, and is a much less cautious approach than that adopted by, e.g., the Canadian fisheries managers, during the 1980s and 1990s (e.g., Hutchings and Myers, 1994). However, it must be borne in mind that the current view among Faroese people is that ‘fiskur hevur stert’ (fish are mobile). This implies that the amount of fish caught is regarded to be dependent on the fishing effort, because the fish are caught on the way from, e.g., Iceland to Norway or *vice versa*. Under this paradigm there is little hope that Faroe cod will be managed in a sustainable way in the future.

# Conclusions

The locations of spawning areas likely evolved to maximize larval survival. The eggs / larvae of cod drift passively with the currents, and the early juveniles settle in the nursery areas. During ontogeny, cod progressively undertake active movements, where they usually occupy feeding areas that are more or less spatially separated from the nursery areas. The location of the feeding areas may vary between cod cohorts and depend upon a variety of factors, such as the proximity to the nursery areas, prey abundance and composition (newly settled cod prey on benthic crustaceans, but fish comprises an increasing proportion of the diet with increasing size), individual capabilities to capture prey (cod in good condition may be able to catch fish more efficiently), competition from conspecifics of the same or other cohorts (wider distribution with increasing overall stock size), interspecific competition (lower competition in cold areas with low species diversity of fish), acclimatization to new temperatures / depths, and probably also the distribution of predators. Sexually mature cod also need access to warm temperatures for gonad maturation, which may induce a 'warmer' distribution of adult cod compared with juveniles or the selection of spatially distinct overwintering / maturing areas. Hence, the distribution / movement pattern in cod is a highly complex process and each stock / population has its own migratory pattern. Generally though, cold-water cod stocks tend to move more than warm-water cod stocks.

Year-class strength in cod, and subsequent recruitment to the fishery, may vary by a factor of ten and is a highly complex process that invokes the fecundity of the spawning stock, as well as the survival through several 'bottlenecks' from eggs / larvae to early juveniles. Traditionally, the survival bottlenecks at the larval stage have been considered to be most important. Future recruitment in Faroe Plateau cod was predicted on the basis of the spawning stock size and 0-group indices in the 1980s and 1990s, but this approach failed to account for recruitment variablity, which led to a credibility crisis between the advisory body (ICES and Faroese Fisheries Laboratory) and local people / fisheries managers. Instead, recruitment variability (R) at age 2 was found to be positively related to the total stock size (B) at age 2, and negatively related to predation by cod (cannibalism, C) at age 1.

$$R = aB/C + d \qquad \text{recruitment model}$$

In other areas, cannibalism tends to be positively related to year-class strength since the distributional overlap between juveniles and adults is increased with increasing year-class strength. Hence, year-class strength may be predicted already at the 0-group stage. However, cannibalism in Faroe Plateau cod was not correlated with year-class strength because the distributional overlap between juvenile and adult cod was not related to year-class strength. The distributional overlap between juvenile and adult cod was best explained by the behaviour of adult cod, which moved into the nursery areas close to land when food availability was low and out from land when food availability was high, which varied according to ecosystem productivity. In the absence of strong temperature / depth gradients, it was hypothesized that a behavioural mechanism concerning the ability of adult cod to catch its prey was most likely. When food availability was high, cod were in good condition, had presumably a high swimming capacity and moved deeper in order to catch the deeper-located Norway pout. When food availability was low, cod seemed to move to shallower waters where they presumably could rely more on less mobile benthic crustacean prey. The distributional pattern of cod on Faroe Plateau may not be applicaple to other areas where, e.g., strong clines in temperature are present. However, the recruitment model may be valid for cod stocks other than Faroe cod even though the dynamics of 'C' are different. Year-class strength might be determined at the 0-group stage, if there is a positive relationship between cannibalism and year-class strength, but not otherwise. This begs further investigations as to when year-class strength is determined.

The ‘redistribution’ of cod during ontogeny after settlement may be subject to inertia, because costs might be associated with habitat shifts. These might be behavioural costs associated with prey finding and capture, unfamiliar conspecifics or heterospecifics, and poor knowledge about predation risk and hiding places. In the case of temperature / depth changes cod must spend time and energy on acclimatization, which could involve the modification of the amount of gas in the swimbladder, changes in enzyme concentrations and modulatory substances, and even the production / removal of cell organelles (mitochondria) in the case of large changes in temperature. As a consequence, the distribution of cod might not match food abundance and the majority of cod in a cod stock / population – probably closest to the settlement locations – could be in poor condition, while a minority of cod, having tolerated one or more habitat shifts, could be in good condition and have a high growth rate. A lower fishing mortality, and consequently a larger cod stock, could ‘force’ a higher proportion of cod to undertake habitat shifts and the natural production of cod could be increased, depending on the extra mortality associated with habitat shifts, which, however, is rarely seen.

Cod stocks at high temperatures seem to be quite resilient to fishery-induced collapses, whereas cold-water cod stocks have been much more vulnerable. This might depend upon temperature, which in consequence might determine cod behaviour and catchability with fishing gears. At high temperatures, cod might have a high swimming capacity, especially anaerobic sprint swimming capacity. The dominant predator on cod might be cod itself (cannibalism) and cod could manage to avoid and escape predators with little use of group formation. A reduction in the overall stock size of cod seems to be accompanied by a reduction in density rather than range, unless stock size is extremely low. This could decrease the catchability and ‘protect’ the cod stock from potential collapses.

Cold-water cod stocks could face a very different situation. As temperature declines, the mobility of cod is reduced, especially anaerobic sprint swimming. Cod presumably also try to stay in locations where they have access to both warm and cold waters, since food abundance tends to be high at temperature fronts. Temperature fronts are dynamic and such ‘frontal cod’ presumably must swim continuously to stay close to the fronts. The combination of the presence of homothermic mammalian predators and presumably easily detected moving cod with poor sprint capacity could imply group formation by cod in order to mitigate predation threat and mortality. This could explain the reduction in range rather than density in declining cold-water cod stocks. It may also explain the high vulnerability to collapse, since the density and, therefore, catchability may remain unchanged or even be increased.

The presumably higher dependence upon group protection in cold waters may add a new dimension as to which factors affect recruitment variability in cod. Spawning stock – recruitment relationships are positive for cold-water cod stocks, but there is no relationship for warm-water cod stocks. It is traditionally believed that the lower fecundity of cold-water cod stocks, combined with the presumably higher mortality of eggs / larvae, accounts for this observation. However, the apparent disappearance of the moderately large 1986-1987 year-classes of Northern cod after 1990, when the cod stock was severely decimated, indicates that other processes may operate as late as at age 3-4 years. This corresponds to the time when juvenile cod attain the same spatial distribution as adult cod and it may be speculated that the virtual absence of adult cod prevented an efficient use of group protection, leading to a high predation by marine mammals. The abundance of seals increased from the mid-1980s and is believed to have caused the increased natural mortality of Northern cod, but this effect might have been exaggerated with the declining cod stock and the lesser group protection. This might also explain the slow or even lacking recovery of cold-water cod stocks. Further insights could be gained from future studies on the apparent recovery of the cod stock at Greenland.

The remarkable recovery of the cod fishery on the Faroe Plateau in 1995-1996 was presumably caused by the increased phytoplankton production in 1993-1995, which led to good recruitment and rapid growth in 1994-1995. The catchability was low, as cod from the strong 1992-1993 year classes had only partially entered the deep waters where the trawlers operated and cod in shallower waters apparently had a low tendency to be caught on longlines because the availability of natural food organisms was high. In 1996, substantial numbers of cod from the 1991/1992-year-classes were 'pushed' into deep waters by the especially strong 1993-year-class, which caused a remarkable increase in the trawl fishery. At the same time, the phytoplankton production had fallen and food shortage was evident in shallow waters, leading to a substantially higher catchability with longlines, which caused the spetacular increase in the longliner cod catch in 1996. Thus, the mysterious 'comeback' of cod in 1996 was largely a result of increased recruitment, growth and catchability.

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