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GREENLAND INSTITUTE
OF NATURAL RESOURCES

Reproductive investment in West Greenland inshore cod (*Gadus morhua*)

Master thesis

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RESUME

In the introduction, the objective was to give an overall picture and background information about the cod (*Gadus morhua*).

The cod belongs to the family Gadidae and the genus *Gadus*. It is widely distributed throughout the North Atlantic. There are 27 populations of cod in the North Atlantic, of which the largest of those are the Norwegian-Arctic in the Barents Sea and the Icelandic.

In Greenland there are three populations of cod, but due to a lack of knowledge about their migrations pattern, these are often considered as one. The population considered in this study is the inshore cod population, which is the most important population in the fisheries in West Greenland for commercial fisheries at present. Until now, it has been described very little, in general, and not at all in regard to their spawning characteristics. The significance of the cod for the fishing industry and the local community, stress the importance for stock management. For this additional knowledge about its spawning is needed.

The cod is a so-called batch spawner, with group synchronous oocyte development, and determined fecundity, meaning that it spawns in batches throughout the spawning season, with continuous maturing of the batches, but the numbers of oocytes in the gonads being determined prior to spawning. Furthermore, the energy allocated to reproduction has a positive impact on the survival success of the oocytes and larvae. The general introduction is followed by the manuscript. The manuscript goes into detail with the reproductive investment in West Greenland inshore cod, with emphasis on the properties of fecundity and energy allocated to reproduction. The collection of data was conducted in the three areas: Nuuk, Paamiut and Qaqortoq. The study showed a significant effect of fish length on potential fecundity, and on total energy content in the gonad. The total energy content in the gonad, however, was best explained by a combination of fish length and liver index (HSI). An increase in energy content in the gonad was seen up to spawning initiation. No correlation was seen between the energy content per gram gonad and fish length, or between energy per oocyte and fish length, but the energy content per oocyte increased significantly with the oocyte size.

The results of the present study were followingly compared to the findings in other localities. While some results coincided with that of others, some were rather surprising, such as the effect of fish size on relative fecundity and egg size. The possible reason for difference in the results could be that only one spawning season is covered in this study. The reproductive potential can show great variation between

years and hence, to achieve a more accurate insight into the reproduction of inshore cod in West Greenland, data from a longer time series is needed.

RESUMÉ

I introduktionen var formålet at give et overordnet billede og baggrundsinformation om torsken (*Gadus morhua*).

Torsken tilhører familien Gadidae, og slægten *Gadus*. Den er udbredt i stor udstrækning på den nordlige halvkugle med 27 populationer. De største af disse, er den norsk-arktiske i Barentshavet og den islandske.

I Grønland findes der tre populationer, omend de betragtes som en, på grund af manglende viden om deres respektive migrationsmønstre. Populationen der beskrives i dette studie er den indenskærs torskepopulation, som på nuværende tidspunkt er den vigtigste population i fiskeriøjemed i Vestgrønland. Denne population er meget lidt beskrevet i det hele taget, og slet ikke i forhold til deres reproduktive egenskaber.

Siden torsken er så vigtig en del af det kommercielle fiskeri, er behovet for bestandsvurderinger meget stort, inklusiv viden om dens reproduktion.

Torsken er en såkaldt portionsgyder, med gruppe-synkront oocyt udvikling, og determineret fekunditet, hvilket betyder at den gyder i portioner gennem hele gydeperioden, med kontinuerlig modning af portionerne, men med antallet af oocytter i gonaden fastlagt forud for gydningen. Endvidere har energien, der bliver allokeret til reproduktionen en positiv effekt på overlevelseschancerne for oocytterne og fiskelarverne.

Efter introduktionen følger et artikeludkast, der går i detaljer med den reproduktive investering hos indenskærs torsk i Vestgrønland. Her er der lagt vægt på fekunditet og den mængde energi der allokeres til reproduktion. Indsamling af data foregik i disse tre områder: Nuuk, Paamiut og Qaqortoq.

Undersøgelsen viste en signifikant effekt af fiskelængde på potentiel fekunditet og det totale energiindhold i gonaden. Dog blev det totale energiindhold i gonaden bedst forklaret ved en kombination af fiskelængde og leverindeks (HSI). En forøgelse i energiindhold i gonaden var desuden set op til gydningsstart.

Ingen korrelation blev fundet mellem energiindhold per gram gonade og fiskelængde, og heller ikke mellem energi per oocyt og fiskelængde, men en forøgelse af energi per oocyt blev set som funktion af oocyt størrelse.

Resultaterne blev sammenlignet med resultater fra andre områder. Nogle af resultaterne var sammenfaldende med det andre har vist, mens andre viste nogle overraskende forskelle, som effekt af fiskestørrelse på relativ fekunditet og ægstørrelse. Den mulige grund til forskellen i resultater kunne være at kun en gydesæson er dækket i dette studie, og variation i reproduktivt potentiale generelt er meget stort mellem årene.

Så for at opnå en bedre viden om den indenskærs torsk i Vestgrønlands reproduktive egenskaber, er flere tidsserier nødvendige.

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Preface

This thesis describes a study on the reproductive investment of Atlantic cod (*Gadus morhua*) in West Greenland, in collaboration with Greenland Institute of Natural Resources, and under supervision of Kurt Thomas Jensen, Aarhus University, Anja Retzel and Holger Hovgaard, Greenland Institute of Natural Resources.

Data sampling took place from January 2008 to May 2008 in the fjords by Nuuk, Paamiut and Qaqortoq, and data analysis took place at the Department of Biological Science, Marine Ecology, Aarhus University, Denmark, all in collaboration with Kirstine Haidarz Olesen.

The thesis consists of a general introduction, describing the background of the study and species investigated. Furthermore, it includes a manuscript entitled “Reproductive investment in West Greenland inshore cod (*Gadus morhua*)”.

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Suna Schleiss Thomsen

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I highly value the supervision and support provided by Kurt Thomas Jensen, Anja Retzel and Holger Hovgaard, thank you for your constructive criticism and help with data. I thank Kirstine Haidarz Olesen for her help in the field and laboratory, and collaboration with data analysis. Also, thank you Frants Havmand Jensen, for your help with the statistical analysis. Thank you, Rikke Markfoged and Mikkel Boel Sørensen, I highly appreciate the help with proofreading! I owe a great thanks to the employees at Greenland Institute of Natural Resources for making me feel welcome and a part of the team, and for helping me with all of the fieldwork. The greatest appreciation goes to my friend and fellow student, Rasmus Berg Hedeholm, for his help not only with data and statistical analysis, but also for his everlasting support, inspiration and good ideas.

Lastly, I want to thank all of my friends and my family for putting up with all my whining and frustration.

INTRODUKTION

1.1 Atlanterhavstorsken

Atlanterhavstorsken tilhører slægten *Gadus* fra familien Gadidae. Indenfor samme familie findes kuller (*Melanogrammus*), hvilling (*Merlangius*) og sej (*Pollachius*), og indenfor slægten *Gadus* findes:

- Stillehavstorsken (*G. macrocephalus* T.),
- Atlanterhavstorsken (*G. morhua* L.) og
- Grønlandstorsken (*G. ogac* R.).

Atlanterhavstorsken er en populær spisefisk, den er derfor kommercielt vigtig, og spiller en stor økonomisk og samfundsmæssig rolle. Den er en del af et økosystem med flere trofiske niveauer, da den også selv er byttedyr for fx grønlandssæl (*Phoca groenlandica*), og præderer på andre fisk og invertebrater under den i fødekæden (Link and Garrison 2002).

Torskens udbredelsesområde i Atlanten strækker sig fra 35°–79°N og 95°–42°V til 36°–90°N og 42°V–69°Ø. Fra Kap Hatteras til Ungavabugten langs den Nordamerikanske østkyst, Grønlands øst- og vestkyst, omkring Island og langs Europas vestkyster fra Biscayabugten til Barentshavet, samt Østersøen og området omkring Bjørneøen (Figur 1) (ICES 2008b; Froese and Pauly 2009). Den findes i forskellige habitater, fra kystlinjer ned til kontinentalsokkelen samt i fjorde.

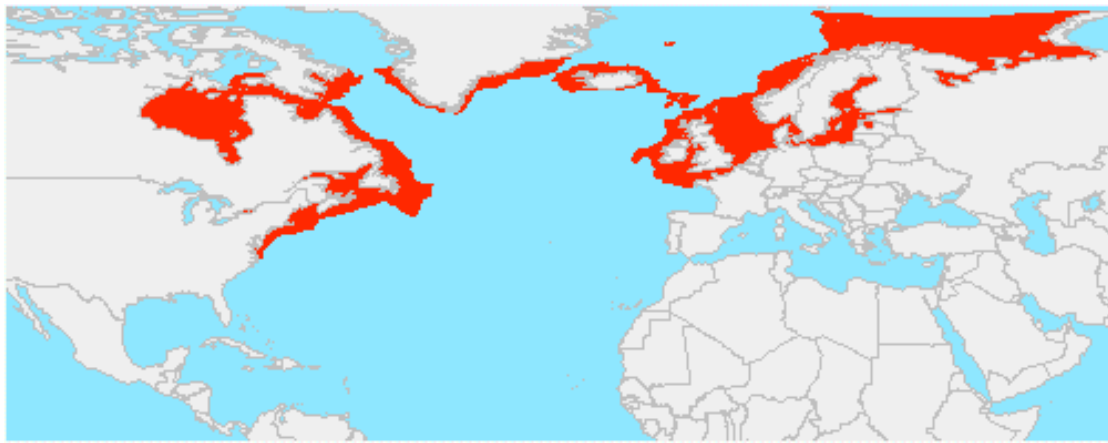
Der er ifølge Northwest Atlantic Fisheries Organisation (NAFO) og International Council for the Exploration of the Sea (ICES) 27 separate torskepopulationer fordelt over hele nordatlanten, hvoraf de største populationer i Nordatlanten er den norsk-arktiske ved Barentshavet og den islandske. 22 af disse populationer er omfattet af bestandsvurderinger (Marteinsdottir *et al.* 2005).

Bestandene er generelt faldende, og torsken er blevet rødlistet som en sårbar art (Froese and Pauly 2009). I flere områder som i Nordsøen, Østersøen, Barentshavet, Newfoundland og ved Grønland er bestanden stort set kollapsede.

1.2 Torsken i Grønland

1.2.1 Udbredelse

Torskens distribution ved Grønland er primært mellem 59°–70°N og 59°–66°N i farvandene hhv. vest og øst for Grønland, men kan variere som effekt af varmere perioder, der udvider den nordlige udbredelse (ICES 2005).



Figur 1. Atlanterhavs-torskens udbredelse givet ved FAO (<http://www.fao.org/fishery/species/2218>).

Der findes tre bestande af torsk ved Grønland, som bliver defineret ud fra deres gydeområder. Den bestand der er studeret i dette projekt er den indenskærs torsk, der gyder i de vestgrønlandske fjorde. Ud over denne er der en udenskærs bestand, der gyder i farvandene ud for både øst- og vestkysten. Den sidste bestand findes langs de grønlandske sydvestlige og sydøstlige kyster, men har islandsk oprindelse, og migrerer tilbage til Island for at gyde (Storr-Paulsen *et al.* 2004). Denne bestand kan danne grundlag for store torskeårgange i Grønland, fordi larverne bliver transporteret med Irmingerstrømmen fra Sydvestisland til Grønland, hvilket var tilfældet i 1973 og i 1984 (Hovgard 1993).

1.2.2 Populationer historisk set

Dannelse af en torskepopulation ved Sydvestgrønland i starten af 1900 tallet blev startskuddet for det kommercielle torskefiskeri, der så småt kom i gang indenskærs i 1911 med grønlandske fiskere (Hansen 1949; Storr-Paulsen *et al.* 2004). Det internationale fiskeri kom til de grønlandske farvande i 1920'erne, hvorefter det primære fiskeri flyttede udenskærs, og den indenskærs fangst blev mindre vigtig (Storr-Paulsen *et al.* 2004).

Frem til 1950 voksede torskepopulationen i Vestgrønland jævnt, og i 1950 toppede den med en biomasse på 4.1 millioner ton, men faldt hurtigt herefter, hvilket kunne tilskrives et højt fiskeritryk (Hovgard and Wieland 2008). Mængden af gydende torsk faldt ligeledes som følge af et fald i temperaturen (Drinkwater 2006). Disse faktorer, når kombinerede, resulterede i en høj mortalitetsrate for de gydende fisk, en lav rekruttering og en lav overlevelsesevne for torskelarver, og som følge heraf, en ikke længere bæredygtig bestand. På trods af dette fortsatte det høje fiskeritryk i 60'erne, hvor den årlige fangst lå på mellem 350.000 – 500.000 ton (Storr-Paulsen *et al.* 2004).

I 1990'erne kollapsede bestanden totalt, og torskefiskeriet stoppede stort set indtil for cirka 4 år siden, hvor der var tegn på ny rekruttering (Hovgard and Wieland 2008). Mens det udenskærs fiskeri var på sit højeste udgjorde det indenskærs fiskeri mindre end 10 % af den samlede fangst (Hovgard 1993). I 1990'erne under kollapset var fangsten helt nede på under 400 ton om året, et historisk lavt niveau (Hovgard and Wieland 2008), men den indenskærs fangst i dag udgør alligevel mere end 90 % af det samlede torskefiskeri ved Grønland (Storr-Paulsen *et al.* 2004).

Der har været fremgang i bestandene de seneste år. I 2006 var den samlede fangst af uden- og indenskærs torsk i grønlandske farvande på 10.000 ton, i 2007 var den steget til 17.000 ton, hvoraf 14.000 blev taget i Vestgrønland, men for at give gydebestanden de bedste forudsætninger for fremgang anbefaler ICES at der ikke fiskes direkte på torskebestanden i 2009 (ICES 2008a). Det er ligeledes blevet anbefalet at en flerårig forvaltningsplan bør udarbejdes for fiskeriet ved Grønland, for at sikre at det ikke øges før der er registreret en betragtelig stigning i biomassen og rekrutteringen til bestanden.

1.3 Udenskærs og indenskærs forhold

1.3.1 Hydrografi

De udenskærs og indenskærs fjorde er meget forskellige i deres hydrografiske forhold. De inderste fjorde påvirkes ikke særlig meget af den variation i hydrografi, der forekommer udenskærs, der påvirkes af to store havstrømme:

- Irmingerstrømmen, som medbringer varmt vand med høj salinitet.
- Den Østgrønlandske strøm, der medbringer koldt polarvand, med lav salinitet.

De to havstrømme mødes ved Kap Farvel og flyder op langs vestkysten, hvor de efterhånden bliver opblandet. Indflydelsen fra havstrømmene varierer fra år til år og mellem sæsoner, hvilket bevirker variationen. Noget af det varme højsaline irmingervand strømmer som bundvand et stykke ind i fjordene, men opblandes med det lavsaline smeltevand, der tilføres fjordene fra floder og gletschere. Inderst i fjordene, hvor havstrømmene ikke når ind, er temperaturen gennem vandsøjlen generelt stabil, mens overfladetemperaturen svinger, på grund af påvirkning af lufttemperaturen. Saliniteten ved bunden i fjordene er ligeledes stabil, men er i overfladen markant lavere om sommeren, når isen smelter.

De hydrografiske forhold har stor betydning for torskens udvikling og overlevelse. Klækningstidspunktet af æggene afhænger af temperaturen i det vandlag de flyder i, og larvernes overlevelseshastighed. Primær og sekundærproduktion bliver også påvirket af hydrografien (Smidt 1979), og siden de udgør de første led i fødekæden har de

dermed stor indflydelse på højere trofiske niveauer, inklusiv torsken. Udenskærs bliver der i løbet af vinteren og det tidlige forår tilført næring til overfladen, som følge af en vertikal opblanding af vandsøjlen. Dette medfører en god basis for en høj primærproduktion. Indenskærs er der stort set ikke nogen opblanding af vandsøjlen, og derfor er primærproduktionen generelt meget lav.

1.3.2 Økologi

Torsk er generalister i fødevalg, men i Vestgrønland udgøres mere end 57 % af dens relative fødevægt af lodden (*Mallotus villosus*), som har et højt lipidindhold. Torsken oplagrer sine energireserver i leveren, som den tærer på, hvis der er mangel på føde (Lambert and Dutil 1997a). Denne energikilde bliver også brugt af hunner i forbindelse med modning af oocytter (Kjesbu *et al.* 1991), og allokeres desuden til æggene ved gydning (jvf. Afsnit . Det er derfor vigtigt for torskens reproduktion at have en meget lipidholdig føde.

Føden påvirker ligeledes torskens kondition, som også er vist at have en betydning i dens reproduktive potentiale (Lambert and Dutil 1997b).

I et specialeprojekt om Atlanterhavstorskens fødeøkologi (Mikkelsen and Svendsen 2008) blev konditionsfaktoren (torskens vægt/længde i tredje potens) udregnet for efteråret 2006 til et gennemsnit på 0.91 for udenskærs torsk i Vestgrønland. Ifølge Lambert & Dutil (1997b) findes de højeste værdier for leverindeks og konditionsfaktor i sensommeren og om efteråret, og de laveste i gydeperioden. Resultaterne fra et andet specialeprojekt viste at den indenskærs konditionsfaktor fra december 2007 til juni 2008 (inkl. gydeperioden) var > 0.98 for hunner og > 0.96 for hanner (Haidarz *et al.* in prep.). Det indikerer at den indenskærs bestand er i bedre kondition end den udenskærs, hvilket videre kan relateres til fødeindtaget, hvor det er vist at torsk i fjordene generelt spiser mere end de der lever uden for fjordene, Tabel 1.

Table 1. Total maveindhold for Atlanterhavstorsk i Vestgrønland i forhold til længdegruppe (cm) (Revideret fra Nielsen & Andersen 2001).

Område	30–34	35–39	40–44	45–49	50–54	55–59	60–69	70–79	80–89	>90	Middel
Kyst	...	20.53	23.38	27.61	34.23	50.98	84.90	3.70	184.60	...	53.74
Fjord	...	54.79	182.20	56.21	52.60	65.17	69.71	26.69	81.14	107.20	73.56

... Ingen observationer

1.3.3 Bestandene

Forståelsen af de forskellige populationer er ikke helt komplet for forskerne. I hvor høj grad de islandske årgange påvirker den indenskærs biomasse, eller om denne kun består af rekrutter fra lokal gydning vides eksempelvis ikke (Storr-Paulsen *et al.*

2004). Ud fra fangst-genfangst forsøg, der er lavet siden midten af 20'erne, har man kunnet kortlægge torskenes migrationsmønstre, og resultaterne indikerer, at den indenskærs population forbliver hele deres liv i fjordene og langs kysterne (Hansen 1949). Derudover ser det også ud til, at der kun er en meget begrænset blanding af populationer imellem fjordene (Storr-Paulsen *et al.* 2004). Det ser ud til de indenskærs torsk forbliver i den fjord de er gydt hele deres liv, og de udenskærs torsk svømmer ind i fjordene, men ikke gyder der. Sandsynligheden for en blanding mellem de to populationer er derfor ikke stor, men der mangler dog genetisk understøttelse af denne påstand (Storr-Paulsen *et al.* 2004).

1.4 Gydning

1.4.1 Gydeområder

I 1949 konkluderede Hansen (1949) at gydningen i Vestgrønland primært fandt sted mellem 67 – 64°N. Gydningen i Nuuk Fjorden foregik især i bunden af Kapisillit fjordarmen ved bygden Kapisillit, men også i fjordarmene Qorqut og Ameralik blev der observeret gydning. Ud fra nyere undersøgelser konkluderede Hovgaard & Wieland (2008) at gydningen nu foregår mellem 66 – 62°N, men at den stadig er størst i Nuuk Fjorden og primært i Kapisillit.

1.4.2 Gydestrategier

Fisk udvikler gydestrategier som tilpasning til deres miljø, der sikrer de bedste betingelser for deres afkom. Udfaldet af strategien er desuden en funktion af populationens reproduktive potentiale, der defineres som en populations kapacitet til at producere levedygtige æg og larver.

Atlantehavstorsken, er en såkaldt portionsgyder, hvor en mængde oocytter gydes løbende i et vist antal portioner over en periode. Modsætningen er at være totalgyder, hvor alle oocytterne modnes og frigives af én omgang.

Oocytterne hos Atlantehavstorsk modnes gruppe-synkront, hvilket betyder at mindst to grupper af oocytter er til stede i ovariet på ethvert tidspunkt. Der findes to andre strategier for udvikling af oocytter, henholdsvis synkron, hvor alle oocytterne udvikler sig ens i samme tempo, og asynkron, hvor alle udviklingsstadier forekommer på samme tid, uden nogen af dem værende dominerende (Murua and Saborido-Rey 2003).

Når Atlantehavstorsken bliver reproduktionsmoden vil den gyde hvert år, hvis forholdene er gunstige. Det er observeret at gydning springes over, blandt andet som

funktion af dårlig konditionsfaktor (Jorgensen *et al.* 2006). Ligesom mange andre fisk er Atlanterhavstorsken ovipar, det vil sige at embryoet udvikler sig udenfor ovariet. Andre fisk med samme strategi som torsken er fx hellefisk (*Reinhardtius hippoglossoides*), sej (*Pollachius virens*) og rødspætte (*Hippoglossoides platessoides*) (Murua and Saborido-Rey 2003). Selve befrugtningen foregår ved at han- og huntorsken svømmer med bugen mod hinanden, mens oocytter og spermatozoer sprøjtes ud og bliver blandet sammen (Holm *et al.* 1991). Når æggene er befrugtet, flyder de op i de øverste vandmasser og opholder sig på den dybde, hvor saliniteten holder dem neutralt flydende (MacKenzie *et al.* 2000). Temperaturen har stor betydning for, hvornår æggene klækkes (Holm *et al.* 1991).

1.4.3 Fekunditet

Potentiel fekunditet er et mål for en fisks reproduktive potentiale, altså fiskens evne til at reproducere sig og bidrage til rekruttering af den fremtidige bestand. Potentiel fekunditet er defineret af Kjesbu *et al.* (1991) som det antal modnende oocytter i fisken forud for gydning.

Fekunditeten hos Atlanterhavstorsk er determineret, hvilket betyder at den samlede mængde af vitellogenesiske oocytter er bestemt forud for gydningen. Der bliver ikke produceret flere i løbet af gydesæsonen, i stedet falder antallet ved hver gydning. Modsætningen til determineret fekunditet er indetermineret fekunditet, hvor antallet af vitellogenesiske oocytter ikke er forudbestemt og udvikler sig løbende igennem gydeperioden. Denne form for fekunditet ses bl.a. hos ansjos (*Engraulis encrasicolus*) og hestemakrel (*Trachurus trachurus*) (Murua and Saborido-Rey 2003).

I naturen gyder huntorsken omkring 15 portioner (batches) på en sæson med 2 – 3 dages mellemrum. Generelt er de første portioner der bliver gydt mindre, og kvaliteten af oocytterne kan være dårligere i forhold til senere portioner, hvilket medfører at mange går til grunde (Holm *et al.* 1991). Den bedste kvalitet af oocytter fås typisk omkring femte gydeportion (Støttrup 2002).

Gydningerne varierer både hvad angår oocytternes antal, mængde, størrelse og vitalitet, afhængig af gydetidspunkt, hvor stor fisken er og om det er en førstegangsgyder. En førstegangsgyder har generelt lavere fekunditet og oocytterne er mindre end hos fisk der har gydt før. Fekunditeten stiger desuden med størrelsen af fisken, både i forhold til længde, hvilket undersøgelserne i dette studie understøtter, men også i forhold til vægt.

Holm *et al.* (1991) gjorde observationer ved Norge, der viste at kysttorsk (inklusive indenskærs torsk) havde en væsentlig højere fekunditet end Skrei (norske udenskærs

torsk). Dette kan muligvis forklares ved at kysttorsken vandrer mindre og derfor kan investere mere energi i oocyt produktion.

Temperatur påvirker, udover klækningstidspunktet, også fekunditeten af fiskene. Kjesbu *et al.* (1998) fandt at fekunditeten hos torsk var positivt korreleret til dels med den temperatur de havde oplevet forud for gydeperioden, men også med fødetilgængeligheden, hvilket betyder at temperaturen både har en direkte og en indirekte effekt. Ved en øget temperatur øges fiskens metabolisme, og derved også dens vækst. Samtidig påvirker temperaturen forekomsten af byttedyr, der så er tilgængelige for torsken.

1.4.4 Energi allokering til reproduktion

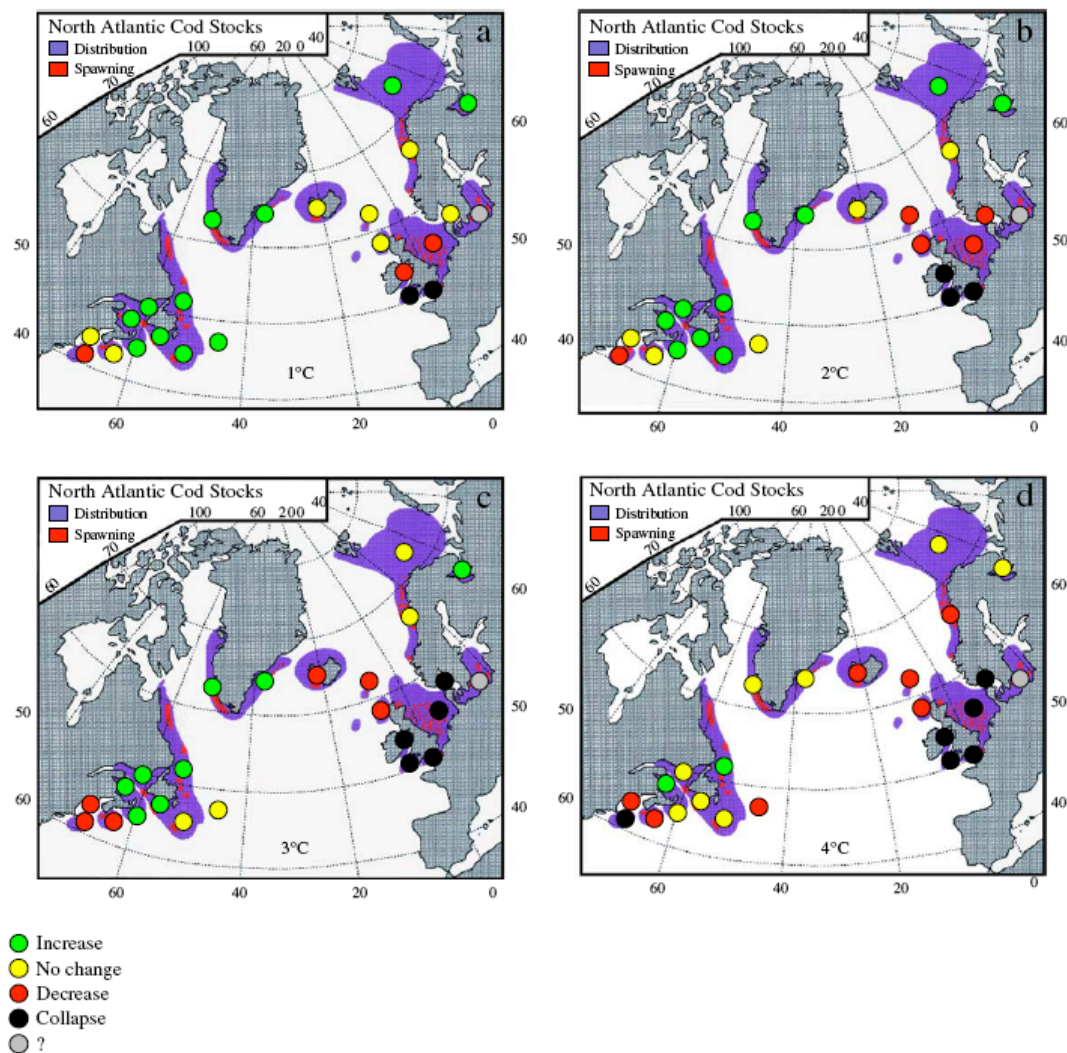
Et andet vigtigt aspekt af torskens reproduktive potentiale er, hvor meget energi der bliver allokeret til reproduktionen. Jo mere energi der bliver allokeret til æggene, des længere tid kan larverne ernære sig endogent, og er derfor ikke afhængig af den eksterne fødetilgængelighed i den periode.

Det er blevet vist at ægstørrelse er positivt korreleret med fiskens størrelse (Marteinsdottir and Steinarsson 1998), og i dette studie blev der ydermere påvist en positiv sammenhæng mellem ægstørrelsen og energiindholdet. Dette viser at større fisk allokerer mere energi til reproduktionen end en mindre fisk, en sammenhæng der understøttes ved en sammenhæng mellem det totale energiindhold i gonaden og størrelsen af fisken. Der blev desuden etableret en sammenhæng mellem fiskenes leverindeks og mængden af energi i gonaden, hvilket betyder at en fisk med en masse energi oplagret i leveren producerer mere energirige oocytter, og derved øger sandsynligheden for larvernes overlevelse.

Idet fekunditet og energi allokeret til reproduktion tilsammen giver et estimat af en torsks reproduktive potentiale, ville det være forventeligt at disse to parametre er tæt koblet, hvilket de reelt også er. Da torsk oplagrer deres energi i leveren er leverindekset et mål for, hvor meget føde har været tilgængelig for fiskene. Siden leverindekset desuden er tæt koblet til den reproduktive energiallokering, hænger kvaliteten af oocytterne sammen med, hvor meget føde der har været tilgængelig forud for gydesæsonen, som samtidig påvirker fekunditeten. Dette betyder i sidste ende at mængden af tilgængelig føde både påvirker produktionen af oocytter, samt kvaliteten af disse, og spiller dermed en vigtig rolle i populationens reproduktive potentiale.

1.5 Torsken og klimaforandringer

Torsken bliver som så mange andre dyr også påvirket af den igangværende klimaforandring. Konsekvenserne af klimaforandringer for Atlanterhavstorsken er blevet opsummeret af Drinkwater (2005) og ICES (2008b). Den største temperaturstigning vil ske i de arktiske og subarktiske områder, herunder i Grønland ifølge klimamodeller, og en stigning i havtemperaturen vil forskyde torskens udbredelse længere nordpå. Hvis temperaturen i Nordatlanten stiger med 1-4°C, vil følgende scenarier udspille sig (Figur 2):



Figur 2. Forventede ændringer i hyppigheden af torskebestande med temperaturstigninger på a: 1°C, b: 2°C, c: 3°C og d: 4°C over nuværende niveau. (Revideret fra Drinkwater 2005).

Grønland udgør det nordligste af torskens udbredelsesområde, og derfor vil en stigning på 1-3°C være gavnligt for populationerne ved Grønland, der vil blive større og ved en stigning på 4°C vil der ikke være nogen forandring. I modsætning til dette vil en stigning på blot 1°C medføre et kollaps i bestandene af torsk i de sydligste udbredelsesområder, fx Den Engelske Kanal og Det Keltiske hav.

Udover at påvirke torskens distribution vil en temperaturforøgelse påvirke deres vækstrate, den alder hvor de bliver modne, og gydetidspunkt. En varmere havbundstemperatur giver en højere vækstrate, og samtidig med en vækststigning vil maturity-at-age falde med ca. 1 år for hver 2°C temperaturstigning (Drinkwater 2005). Dette påvirker endvidere populationernes reproduktive potentiale, i og med større fisk bidrager med mere, og bestandene vil således opleve et fald i rekruttering.

Udover problemerne direkte forbundet med gydning, er der også komplikationerne set på de trofiske niveauer. Hele det økologiske samspil som torsken er tilpasset ændrer sig ikke nødvendigvis med samme hastighed niveauerne imellem, og dermed kan der opstå en negativ effekt for torskens udvikling.

På grund af den vidtrækkende betydning temperatur har på de forskellige trofiske niveauer, som fx hydrografien ved påvirkning af nedbørsforhold, og dermed også primærproduktionen, er det vanskeligt at forudse de præcise konsekvenser af klimaforandring for torsken.

Derfor er det meget vigtigt at tage hensyn til torskebestandene, og fangstregulativer bør følges så der ikke udøves uopretteligt skade på bestandene. Det er yderligere vigtigt, for at få det mest nuancerede og præcise billede, at belyse alle de økologiske interaktioner torsken indgår i, både udenskærs og indenskærs.

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Reproductive investment in West Greenland inshore Cod (*Gadus morhua*)

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Abstract.

Fecundity and energy content in gonads and oocytes were determined in sexually mature female inshore cod, *Gadus morhua*, sampled in West Greenland fjords (February to May 2008).

The potential fecundity (i.e. number of vitellogenic oocytes in the gonad), and total energy content in the gonads were positively correlated to fish length. The energy content was furthermore significantly correlated to the hepatosomatic index (HSI). An increase in energy content in the gonads up to spawning was observed. Other relations, such as fish length compared to relative fecundity, egg size and energy content per oocyte, and condition compared to potential fecundity showed no significance, probably because of a relatively small sample size.

Key words: *Gadus morhua*, fecundity, energy allocation, West Greenland inshore.

Introduction

The cod fishery in the northern hemisphere is an important part of the commercial fishery worldwide. The need for proper management of local cod stocks requires solid input data on life-history characteristics. Studies have shown that the size selective nature of commercial fishing can induce a change in size at age and thereby a decrease in maturity-at-age (Jorgensen 1990), both of which can have a significant influence on the reproductive potential of the stock of concern and thus on its dynamics and population development.

In management studies it is very important to have knowledge of a stock's reproductive potential, because it represents the ability of a fish stock to produce viable offspring that may recruit to the adult population or fishery. While fecundity does not give information on offspring viability, it does provide the starting number of potential offspring that can be produced and is therefore one of the essential components for estimating a population's reproductive potential (Trippel 1999). As it has been shown that size is positively correlated to the reproductive output of an individual fish, the population changes induced by an intense fishery may have an effect on the reproductive potential. Hence, in order to manage a population in a sustainable manner, knowledge on the reproductive potential is needed, especially seen in the light of the intense fishery of cod worldwide.

In addition to the number of eggs being important to the reproductive potential of a fish, the viability of the offspring is partly dependent on the energetic reserve provided in the egg. Hence, it has been shown that larvae from oocytes with large yolk sacs (i.e. more energy) can live longer without feeding, and are thus more likely to survive (Solemdal 1996).

Fecundity and reproductive energy allocation have been studied extensively in different spawning locations, e.g. Norway (Kjesbu 1989; Kjesbu *et al.* 1991; Kjesbu *et al.* 1996), Canada (Lambert and Dutil 1997b; Ouellet *et al.* 1997) and Iceland (Marteinsdottir and Begg 2002), and it has been established that potential fecundity is positively correlated with the size (Kjesbu *et al.* 1991; Marteinsdottir and Begg 2002) and the condition of the fish (Lambert and Dutil 1997b). Furthermore, large fish have been shown to produce larger oocytes, which in turn can contain higher amounts of energy (Marteinsdottir and Begg 2002). Hence, a size reduction in the spawning stock biomass of a population may not only reduce the quantity of the eggs spawned, but also the quality as size-at-maturity is reduced. In order to address the question of energetic investment in reproduction by cod of differing size, we present such information from inshore cod in West Greenland fjords.

In Greenland, the inshore fishery after cod have fluctuated greatly over the last decade (Storr-Paulsen *et al.* 2004), but since the collapse of the offshore population in the 1980's, the primary fishery has been in the fjords, a non-restricted fishing quota. It is therefore of great importance, for the sustainability of the population and the future inshore fishing industry, to provide a suitable assessment which will ensure a strong and continuous inshore cod population.

In this study, we have looked at the reproductive parameters fecundity and energy allocated to reproduction in inshore cod (*Gadus morhua*) in West Greenland fjords, to outline the reproductive investment of these populations. Special emphasis has been made on the importance of individual size and condition for investment in reproduction, i.e. number of oocytes and energy content allocated to reproduction. Such information can besides being essential in stock assessment also help in uncovering the importance of such a fjord area, by reflecting for example the food availability, visible in both individual growth, condition, and reproduction.

Materials and methods

Sampling

From December 2007 to May 2008 cod were sampled in the areas shown on Figure 1. The sampling took place on a regular basis, from December '07 to May '08, in different inlets of the Nuuk fjord (Figure 2).

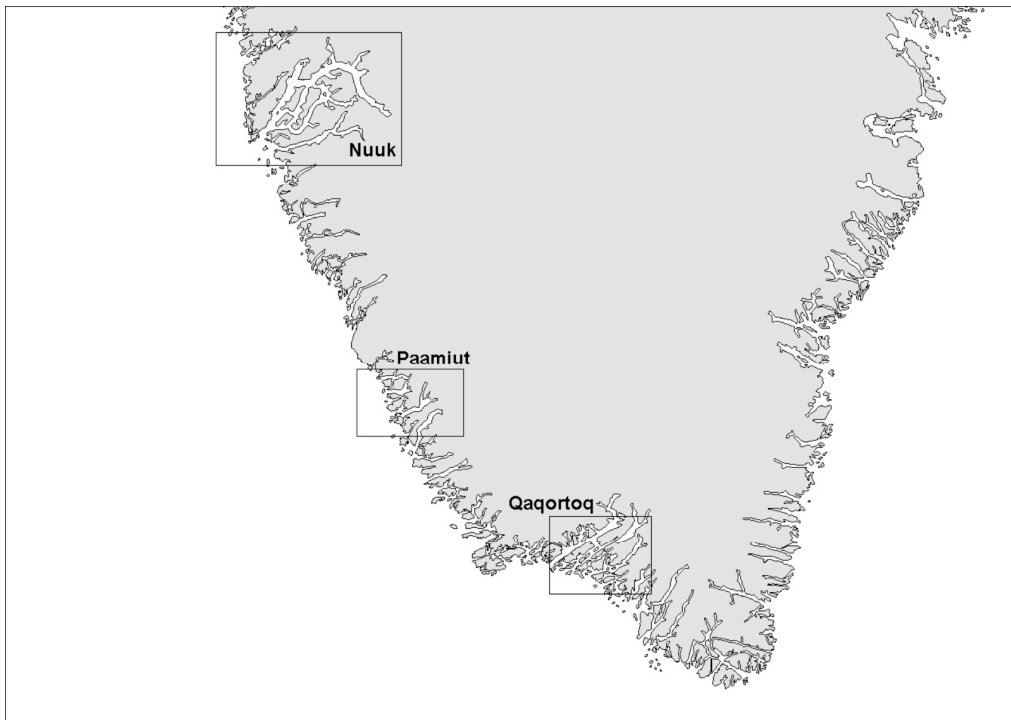


Figure 1. Map of the overall sampling area.

In addition in March samples of cod were taken in the areas of Qaqortoq (Figure 3) and Paamiut (Figure 4). The hydrographic characteristics of the three areas are shown in Table 1. The fish were caught using jigs and longlines in the Nuuk fjord while the fish from South Greenland were caught using net, jigs and longlines.

Table 1. Hydrographic characteristics of the three fjords, wherein sampling were conducted.

Location	Mean water temperature (°C)	Mean salinity (psu)
Nuuk	2,1	31,9
Paamiut	2,7	34,1
Qaqortoq	3,2	34,3

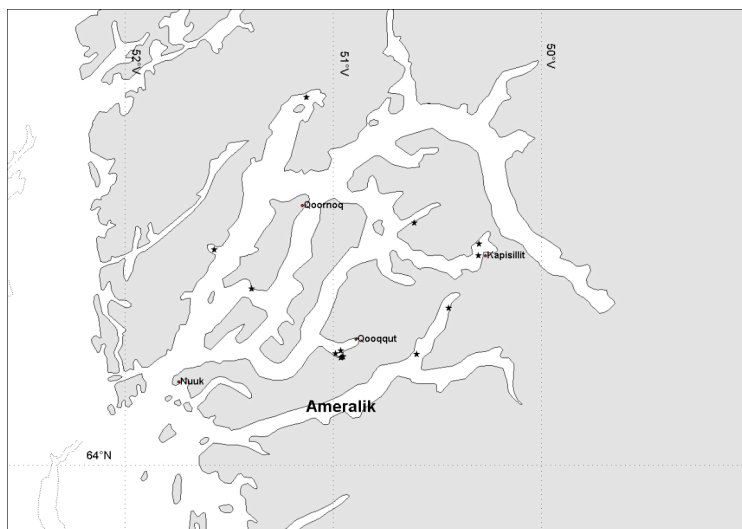


Figure 2. The sampling area in Nuuk. ● Town, ★ Catch locations

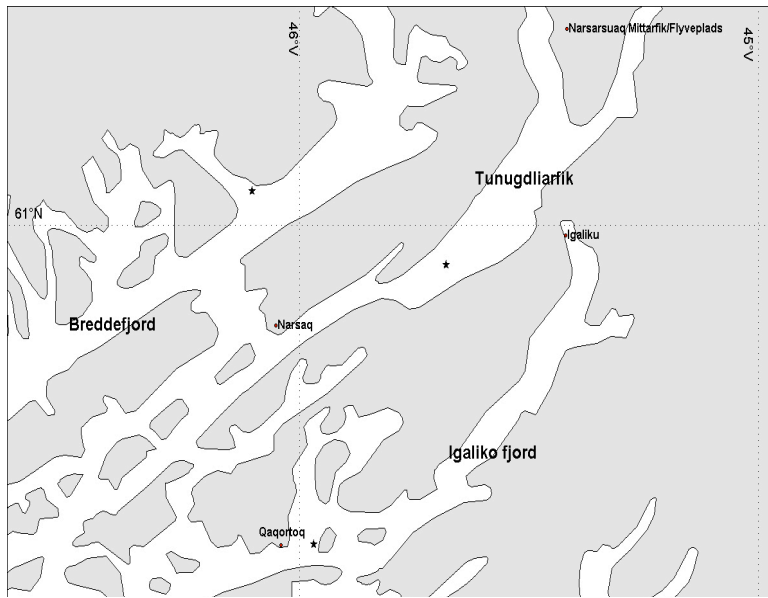


Figure 3. Sampling area in Qaqortoq. ● Town, ★ Catch locations



Figure 4. Sampling area in Paamiut. ● Town, ★ Catch locations

All fish were sexed, measured to the nearest cm (Total length, LT) and body weight (total (W_T) and gutted weight (W_{CL}), kg), liver weight (W_L), gonad weight (W_G) were recorded. Furthermore, the maturity stage (MI), using the ten-stage classification scale (Tomkiewicz *et al.* 2003) was identified, and the appurtenant indexes for liver and gonad proportional to cleaned weight, HSI and GSI were calculated.

Gonads from female cod in maturity stage four (see description of stages in Tomkiewicz *et al.* 2003) were removed for fecundity and energy analyses. Two samples of approximately 3g were taken from the middle part of the right lobe. These were frozen (-20 °C) and preserved in buffered histofomaldehyde for energy and fecundity analyses respectively.

Table 2. An overview of the fish caught, location, date, fishdata and samples taken. The numbers in fecundity and energy samples are the total number of samples (in bracket), and the numbers used for analyses. * No cleaned weight obtained.

Location	Date	Total # fish caught	# stage 4 females	Length span (cm)	Weight span (kg)	Mean HSI	Mean GSI	Fecundity samples	Energy samples
Paamiut	04/02/08	54	2	40-69	0.613-2.92	4.8	2.8	1 (1)	2(2)
Nuuk	05/02/08	63	13	39-71	0.57-4.12	4.6	5.8	8(8)	8 (8)
Paamiut	08/02/08	55	0	45-83	0.66-5.34	4.7	3.6	-	-
Nuuk	21/02/08	42	6	34-69	0.33-4.12	3.9	4.8	3 (3)	2 (2)
Nuuk	29/02/08	1	0	30	0.223	2.6	0.1	-	-
Paamiut	06/03/08	1	0	30	0.22	*	*	-	-
Paamiut	08/03/08	14	0	36-62	0.36-2.3	4.3	1.8	-	-
Paamiut	10/03/08	75	4	33-69	0.314-3.38	3.7	1.2	2 (3)	1 (1)
Nuuk	11/03/08	65	3	32-57	0.23-1.988	4.7	3.5	-	-
Qaqortoq	19/03/08	80	5	27-74	0.16-4.22	3.9	1.3	4 (4)	-
Qaqortoq	20/03/08	10	0	30-48	0.234-0.94	4.9	0.3	-	-
Nuuk	26/03/08	71	6	33-64	0.318-2.794	5.5	3.5	6 (6)	4 (4)
Nuuk	01/04/08	32	0	34-57	0.38-1.88	5.9	3.7	-	-
Nuuk	01/04/08	107	7	29-75	0.22-3.62	4.6	6.4	3 (6)	3 (3)
Nuuk	15/04/08	75	2	33-77	0.32-5.96	6.6	3.8	2 (3)	2 (2)
Nuuk	23/04/08	51	2	31-74	0.26-3.92	4.5	4.7	1 (1)	1 (1)
Nuuk	24/04/08	2	0	44-49	0.96	5.3	0.7	-	-
Nuuk	24/04/08	8	1	36-60	0.36-2.2	4.6	6.7	1 (1)	1 (1)
Nuuk	24/04/08	30	2	31-49	0.24-1.26	5.9	1.4	2 (2)	2 (2)
Nuuk	30/04/08	29	5	52-67	1.38-3.02	6.3	13.6	3 (5)	3 (3)

Energy analysis procedure

The frozen gonad samples were freeze-dried for 24 hours after which no further weight loss took place. The sample was then homogenized using a glass mortar and a subsample of 0.0471 \pm 0.06 g (Mean \pm SE) was compressed into a pellet of minimum 25 mg. This was placed in a Parr 6725 semi micro calorimeter in an oxygen-enriched atmosphere (30 atm) to ensure complete combustion. The sample was ignited by sending a current through a 10 cm NiCr fuse wire. The final energetic value was corrected for the burned wire's contribution to the heat increment. Only samples that had burned completely were used in further analysis.

Data on fecundity, water content (%) and energy density in the samples, made it possible to calculate the energy content (per gram gonad), the total energy content of the gonads as well as the energy content per egg, by simple conversion of data.

Fecundity procedure

The fecundity samples were analysed using the method described by Thorsen & Kjesbu (2001). A subsample of the preserved tissue was placed in a Petri dish, and a drop of dishwashing detergent was added to prevent the oocytes becoming attached to the water surface. The sample was placed under a microscope at 10x magnification and subsequently photographed using Deltapix photosoftware. Several pictures were taken to cover the entire Petri dish. All pictures were analyzed using ImageJ (Rasband

1997-2005). In accordance with Thorsen and Kjesbu, a roundness factor was assigned to each egg:

$$\text{Roundness} = \frac{\text{perimeter}^2}{4 \cdot 3.14 \cdot \text{area}}$$

All oocytes having roundness factor ≥ 1.20 were discarded from further analyses, as they were typically damaged oocytes or two or more oocytes in contact with each other. The perimeter and area of 150 eggs was measured.

Each oocyte in all samples had their diameter (D) calculated, and a mean diameter for all oocytes in each sample was calculated.

The oocyte density was calculated based on the equation of a power regression line in Thorsen & Kjesbu (2001). A prerequisite to do this was that the results of Thorsen & Kjesbu (2001) were similar to the results of the present study regarding oocyte size (mean diameter (μm)) in proportion to the number of oocytes per gram. For that reason a manual count was done on five of our samples, to see whether they matched the results in Thorsen & Kjesbu (2001), and all the datapoints fitted the line, so:

$$\text{Oocyte density (NG)} = 2.139 \cdot 10^{11} \cdot OD^{-2.700} (\mu\text{m})$$

where OD = oocyte diameter

Since no difference between oocyte size and number of oocytes in the ovary was seen in the two studies, the equation from Thorsen & Kjesbu (2001) was also used for calculation of the potential fecundity:

$$\text{Potential fecundity (Fp)} = \text{OW (g)} * \text{NG}$$

where OW = ovary weight and NG = oocyte density.

Statistics

All statistical analyses were performed in the program JMP (JMP® 2008). The parameters were grouped, and tested in clusters, when possible. Data was transformed when necessary. All length-weight relations were double log transformed, and tested with linear regression.

Results

In the period February to May 2008, a total of 865 cod were caught. Of these, 58 female cod were assessed as being in stage 4, and used for fecundity and energy

analyses (see Table 2). The sample size from the southern areas (i.e. Paamiut and Qaqortoq) was smaller than from the Nuuk fjord, and insufficient to do full statistical analyses on and since no statistical difference between the fjords was seen in fecundity (Students t-test, $t_{1,28} = 0.0426$, $p=0.97$) and energy content in the gonads (Students t-test, $t_{1,46}=0.223$, $p=0.82$), the fish were pooled in further analyses. A significant positive relationship was found between gonad weight and fish length (linear regression, $F_{1,46} = 64.15$, $p<0.0001$).

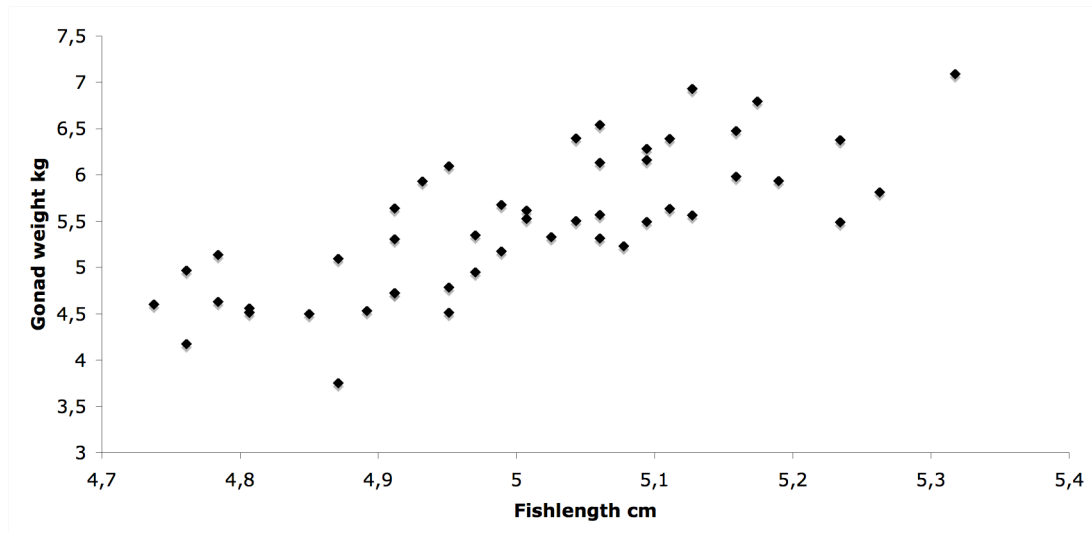


Figure 2. The relation between fish length (cm) and gonad weight (kg). Double-log transformed data.

Fecundity

Fecundity ranged from $0.06 \cdot 10^6$ to $2.03 \cdot 10^6$ across all fish sizes (Table 3), and was positively correlated with fish length (Figure 6) (linear regression, $F_{1,34}=52.36$, $P<0.0001$, $r^2=0.64$). The number of oocytes per gram gonad was on the other hand not significant (linear regression, $F_{1,34}=1.45$, $p=0.303$). Neither was there a significant correlation between oocyte diameter and fish length (linear regression, $F_{1,26} = 0.04$, $P=0.83$).

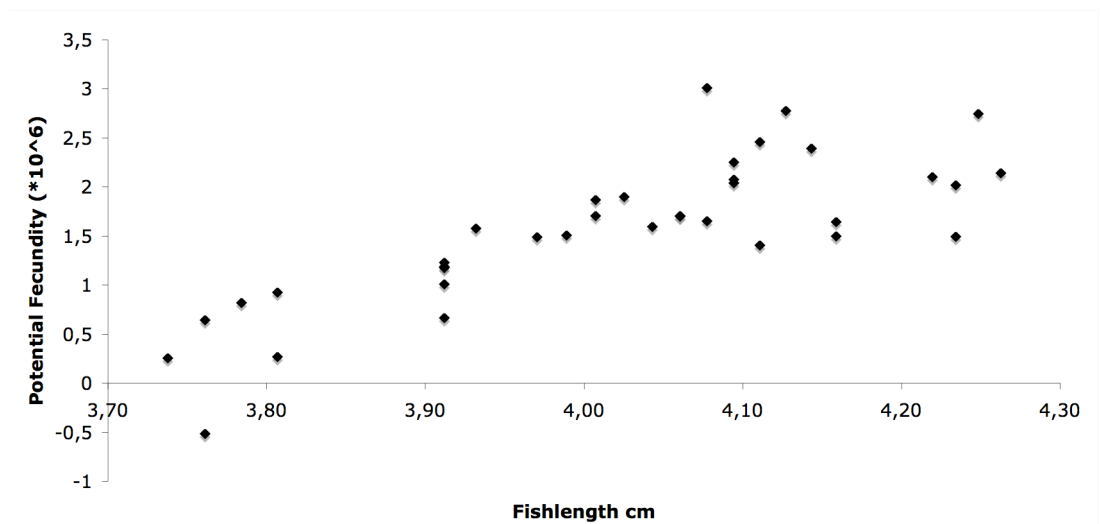


Figure 3. Fecundity in relation to fish length. Double-log transformed data.

Energy content

The amount of total energy in the gonad (E_{tot}) spanned from 66 to 3370 kJ (Table 3) and a significant positive correlation between length and total energy allocation was seen (linear regression, $F_{1,46} = 13.78$, $P=0.0006$, $r^2=0.23$) (Figure 7).

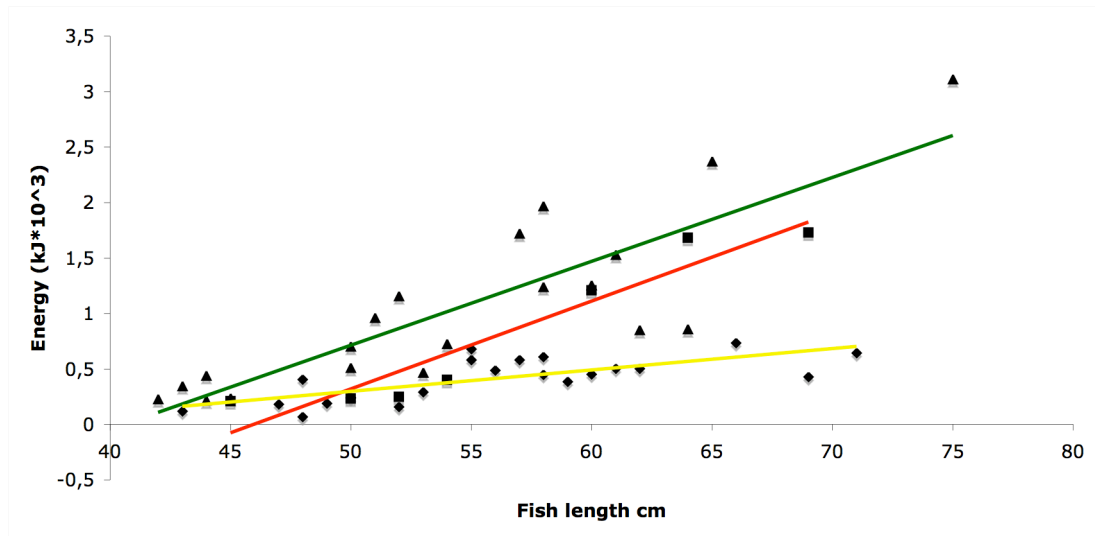


Figure 7. The total energy content (kJ) in the gonads related to fish length. ▲: Fish caught in April ■: Fish caught in March, ◆: Fish caught in February. n = 48.

The total energy content in the gonads varied between the different months (ANCOVA, $F_{5,38} = 12.67$, $P<0.0005$), with March and April not being significantly different from each other (ANCOVA, $F_{3,19} = 7.58$, $P=0.48$), but different from February. Another relationship proven significant was the total energy content as a function of the Hepatosomatic index (HSI) (linear regression, $F_{1,46} = 16.79$, $P=0.0002$) (Figure 8).

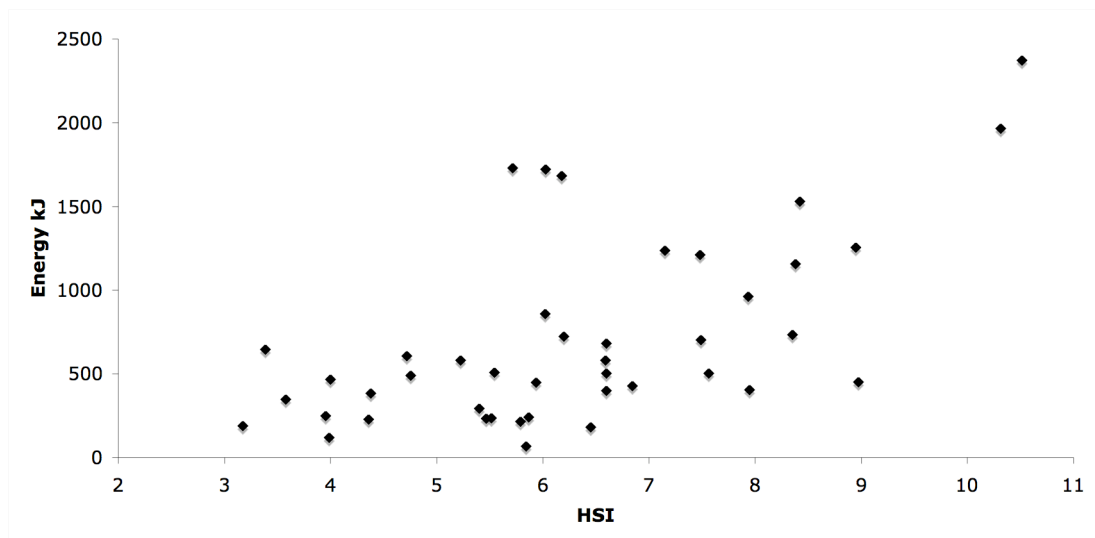


Figure 8. The total amount of energy in the gonad compared to HSI.

HSI and fish length accounted for 28 and 37 % respectively of the variation seen in the total reproductive energy content, while when tested collectively had a highly

significant effect (ANCOVA, $F_{3,39} = 13.87$, $0.0009 < P < 0.0012$), and explained 51% of the variation.

The energy content per gram gonad ranged from 20.969 to 23.261 kJ/g (Table 3), but the relation to fish weight was not significant (Spearman's correlation, $P=0.427$) (Figure 9). The same pattern was seen in energy per oocyte relationship (Figure 10). On the other hand, a positive correlation was seen between the energy content per oocyte and oocyte size (linear regression, $F_{1,26} = 391.16$, $p < 0.0001$) (Figure 11).

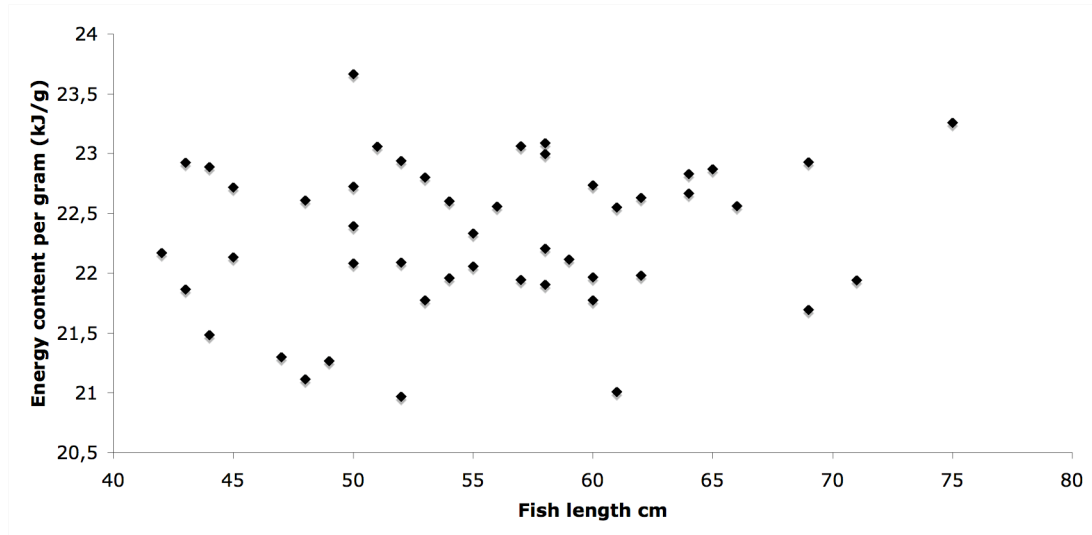


Figure 9. The relation between the energy content per gram gonad (kJ/g) and the length of the fish.

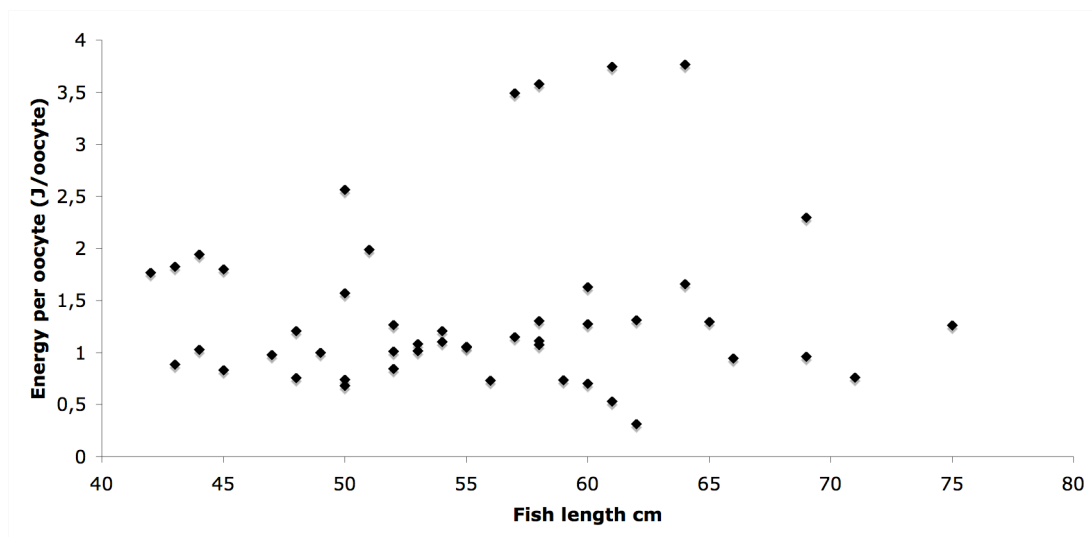


Figure 10. The energy content per oocyte compared to fish length.

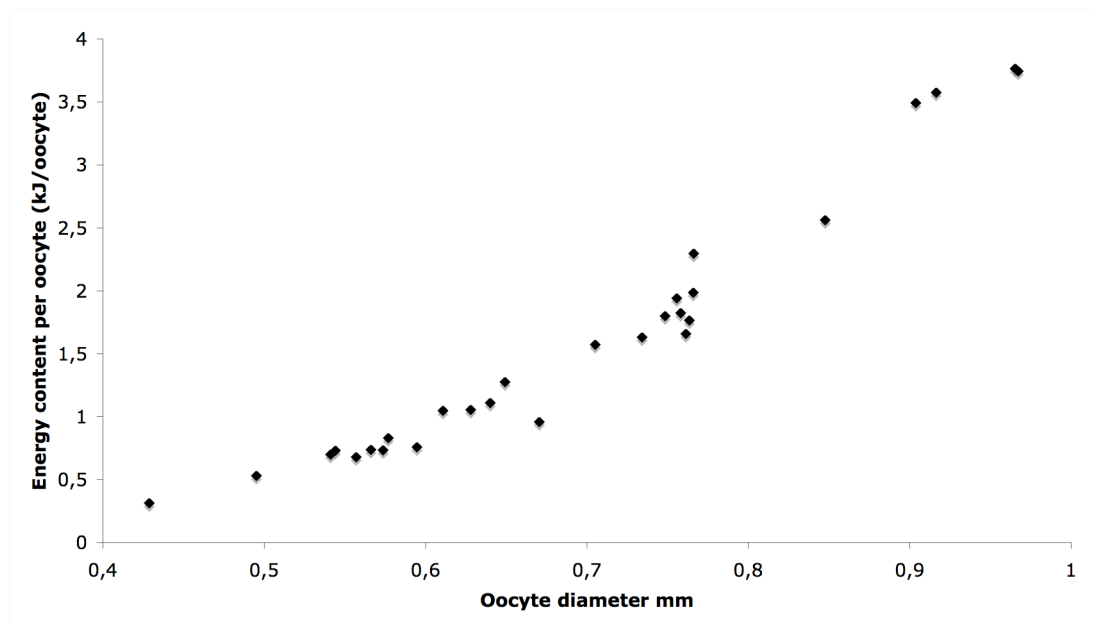


Figure 11. Energy per oocyte compared to oocyte size.

The body condition of the fish were calculated as well, and tested as independent variable against fecundity and energy content in the gonad. However, no significant relationship was found with neither fecundity (linear regression, $F_{1,27}=0.48$, $P=0.49$) nor energy content (linear regression, $F_{1,46}=0.33$, $P=0.56$).

Discussion

Fecundity

The relation between potential fecundity and fish length was significant, with 64% of the variation explained. Several studies have found similar size-specific potential fecundity, e.g. Kjesbu *et al.* (1991), who furthermore found a large individual variation in this relationship, reflected in different ovarian sizes during various stages of vitellogenesis. A large variation was also seen in this study.

Marteinsdottir & Begg (2002) examined the potential fecundity for Icelandic cod, and found it ranged from $0,23 \cdot 10^6$ to $31,7 \cdot 10^6$ vitellogenic oocytes (Table 4) and was correlated with fish length and weight. For a 70 cm fish, fecundity ranged from $0,836 \cdot 10^6$ to $1,726 \cdot 10^6$, which is comparable to our $1,56 \cdot 10^6$ for a 70 cm fish (Table 4). The potential fecundity values for different locations are shown in Table 4. To be able to compare our results to others, a power regression was made. It is seen that the potential fecundity in this study lies between those in the other areas, the highest being in the Baltic Sea cod for a similar sized fish.

Interannual variation in fecundity is generally large, with very different values of potential fecundity between years (Kjesbu *et al.* 1991; Kraus *et al.* 2000;

Marteinsdottir and Begg 2002). Krauss *et al.* (2000) found an interannual variation in fecundity of 33 %, and different studies give possible explanations for this variation. Some of the oocytes enter the circumnuclear ring phase during the postspawning

period (Woodhead and Woodhead 1965), and require limited energy for their production, thus, the number of these oocytes is more a function of fish and hence ovary size, than it is dependent on the nutritional status of the fish (Kjesbu *et al.* 1991). On the other hand, a second process controlling the annual fecundity is the number of extra oocytes entering the circumnuclear ring phase during the subsequent feeding period until vitellogenesis becomes well established. The number of the latter oocytes is thus linked to the nutritional status of the fish (Kjesbu *et al.* 1991) achieved during the feeding period following the previous spawning period. This is most likely to provide the major contribution to the yearly variation in potential fecundity of similar sized fish (Kraus *et al.* 2000). Since the results in this study are achieved within a single spawning season, it is not possible to conclude that the potential fecundity measured is at a high or low level. For that purpose, data from more spawning seasons are needed.

Another parameter influencing potential fecundity is environmental temperature, with a positive correlation between them (Kjesbu *et al.* 1998), a relationship that can be beneficial in regard to climate change and concomitant increasing temperatures. But climate change might also have negative impact on the stock's reproduction. A study made on Atlantic cod on the Scotian shelf found that temperature accounted for 52 % and 70 % of the seasonal variation of egg and larvae size, respectively, with decreasing size as temperature increased (Miller *et al.* 1995).

The number of oocytes per gram gonad showed no relation to fish length, indicating that a small fish produces the same amount of oocytes as a large fish, relatively seen. The same result was seen in Kjesbu *et al.* (1998), with samples containing only small fish (50-70 cm). In contrast, Kraus *et al.* (2000) found a significant correlation between relative fecundity and fish size. These contradictory results are possibly seen because of the different sizes of fish. The fish in Kraus *et al.* (2000) ranged to 104 cm, fish at much greater maximum length than in this study (75 cm) and 70 cm in Kjesbu *et al.* (1998).

Table 3. Estimates of fecundity and energy measurements. The results marked with * are samples where no fecundity parameters were measured, and a mean calculated from the obtained results was used.

Location	Date	Fishlength cm	Relative fecundity (numbers of oocytes/g)	Pot. fecundity (#*10 ⁶)	Energy per gram (kJ/g)	Total Energy (kJ)	Condition (K)	Energy per oocyte (J/oocyte)
Paamiut	04/02/08	66	5588.2*		22.562	733	0.85	0.945
		69	4998.7	0.44	21.693	427	0.84	0.959
Nuuk	05/02/08	48	5588.2*		21.115	66	0.9	0.754
		50	7894.5	0.33	22.396	241	1.04	0.738
		52	5588.2*		20.969	157	1.02	0.842
		53	5588.2*		21.775	293	0.95	1.013
		56	8785.5	0.67	22.559	489	0.99	0.732
		57	5588.2*		21.946	581	1.06	1.149
		58	5588.2*		22.206	449	0.95	1.073
		58	5670.8	0.55	21.906	608	1.09	1.109
		59	7618.5	0.52	22.115	384	0.79	0.735
		60	8919.3	0.80	21.776	559	0.98	0.701
		61	11339.9	1.17	21.009	621	1.16	0.532
Nuuk	21/02/08	62	16712.8	1.60	21.982	502	0.84	0.313
		71	6917.9	0.85	21.943	645	0.96	0.759
		43	5011.9	0.06			0.93	
		43	5588.2*		21.864	118	1.02	0.884
		47	5588.2*		21.299	180	0.93	0.977
		48	5588.2*		22.609	404	1.02	1.208
		49	5588.2*		21.265	189	1.18	0.997
		55	6431.7	0.65	22.335	62	1.02	1.049
		55	5965.9	0.55	22.056	685	0.99	1.056
		52	5588.2*		22.089	248	0.97	1.011
		Paamiut	10/03/08	54	5588.2*		21.959	400
68	8024.3			0.82			0.92	
69	3488.3			0.75	22.929	1264	1.03	2.296
Qaqortoq	19/03/08	53	4186.3	0.44			0.43	
		54	5500.9	0.45			1.09	
		63	4812.2	1.10			1.69	
		70	6348	1.56			1.3	
Nuuk	26/03/08	45	7502.1	0.25	22.717	912	0.97	0.832
		50	8246.2	0.34	22.083	555	1.14	0.679
		50	5855.2	0.19			2.09	
		59	7941.8	2.03			0.62	
		60	5452.4	0.95	22.735	1990	1.17	1.275
		64	1868.9	0.45	22.668	2836	1.07	3.765
Nuuk	01/04/08	50	2654.4	0.27	23.183	1137	1.16	2.563
		50	4362.4	0.32	22.727	709	0.86	1.572
		51	3491.7	0.48	23.059	887	0.98	1.986
		53	5588.2*		22.803	466	0.78	1.08
		54	5588.2*		22.603	724	0.93	1.206
		65	5588.2*		22.872	2371	1.02	1.293
		75	5588.2*		23.261	3113	0.9	1.262
		44	3620.3	0.00	22.889	1843	1.29	1.942
Nuuk	15/04/08	45	3715	0.13	22.135	616	0.89	1.801
		62	5588.2*		22.6311	2753	1.1	1.31
		44	5588.2*		21.483	216	0.85	1.027
Nuuk	23/04/08	64	3547.6	0.52	22.831	3370	0.92	1.659
		60	3913.8	0.77	21.965	317	1.02	1.629
Nuuk	24/04/08	42	3521.7	0.13	22.169	445	0.97	1.766
Nuuk	30/04/08	43	3587.7	0.19	22.927	500	0.96	1.826
		52	5588.2*		22.94	1156	1.07	1.265
		57	2232.2	0.49	23.062	1690	1.02	3.491
		58	5588.2*		23.087	1237	1.14	1.304
		58	2150	0.55	22.999	467	0.98	3.577
		61	1859.2	0.41	22.552	1213	0.94	3.744

Table 4. Potential fecundity relationships (PF= $a \cdot \text{length}^b$), and potential fecundity (*106) of a standard fish, 70, 90 and 120 cm length cod from different areas in the North Atlantic, the Baltic and the North Sea. Revised from Marteinsdottir & Begg (2002).

Geographical area	Time period	n	Length range	a	b	r ²	Fec-70 cm	Fec-90 cm	Fec-120 cm	Source
Greenland	2008	36	42-71	$3.414 \cdot 10^{-8}$	4.09	0.63	1.56	NA	NA	Present study
Gulf St. Lawrence Labrador and Newfoundland	1955–1956	43	51–140	0.38	3.5	0.83	1.090	2.628	7.192	Powles (1958) ^A
	1964	130	50–130	0.5	3.42	0.72–0.93	1.021	2.412	6.453	May (1967) Buzeta & Waiwood (1982)
Gulf St. Lawrence Newfoundland (Bonavista Bay)	1980	30	47–103	1.1	3.28	0.81	1.239	2.827	7.262	Pinhorn (1984)
Newfoundland (Trinity Bay)	1967–1968	58	65–109	0.3548	3.5	0.77	1.018	2.454	6.716	Pinhorn (1984)
Newfoundland (St. Pierre Bank)	1967–1968	78	60–108	1.778	3.13	0.78	1.060	2.327	5.726	Pinhorn (1984)
Newfoundland (St. John's)	1967, 1969, 1970	103	51–128	0.4168	3.37	0.82	0.688	1.606	4.235	Pinhorn (1984)
Newfoundland (Placenta Bay)	1966,1968	62	61–118	2.630.267	1.41	0.38	1.05	1.498	2.247	Pinhorn (1984)
Gulf St. Lawrence	1966	96	64–113	53.703	2.42	0.72	1.567	2.879	5.776	Pinhorn (1984) Lambert & Dutil (2000)
	1995	53	37–65	0.065	3.964	0.7	1.339	NA	NA	Joakimsson (1969)
Iceland	1960	42	58–94	3.42	3.071	0.525	1.586	3.432	NA	Schopka (1971)
Iceland	1967	49	54–125	0.5678	3.457	0.835	1.357	3.236	8.748	Marteinsdottir & Begg (2002)
Iceland	1995	264	67–125	0.0076	4.457	0.81	1.272	3.898	14.051	Marteinsdottir & Begg (2002)
Iceland	1996	160	57–133	0.0252	4.223	0.9	1.562	4.516	15.22	Marteinsdottir & Begg (2002)
Iceland	1997	160	67–128	0.0034	4.622	0.62	1.146	3.664	13.85	Marteinsdottir & Begg (2002)
Iceland	1998	88	59–129	0.000072	5.455	0.83	0.836	3.294	15.822	Marteinsdottir & Begg (2002)
Iceland	1999	102	59–133	0.0472	4.099	0.88	1.726	4.835	15.722	Marteinsdottir & Begg (2002)
Iceland	2000	96	63–131	0.0063	4.535	0.86	1.468	4.59	16.921	Marteinsdottir & Begg (2002)
Baltic ^B	1987	64	32–104	49.76	2.51	0.76	2.126	3.995	8.224	Kraus et al. (2000)
Baltic	1996	37	40–100	185.56	2.28	0.79	2.987	5.298	10.209	Kraus et al. (2000)
NE Arcto- Norwegian	1986	50	50–120	0.123	3.764	0.89	1.083	2.79	8.24	Kjesbu et al. (1998)
NE Arcto- Norwegian	1987	46	50–90	0.261	3.541	0.79	0.891	2.171	NA	Kjesbu et al. (1998)
NE Arcto- Norwegian	1988	49	50–125	0.0614	3.909	0.92	1.001	2.675	8.235	Kjesbu et al. (1998)
NE Arcto- Norwegian	1989	111	50–130	0.804	3.357	0.92	1.257	2.922	7.675	Kjesbu et al. (1998)
NE Arcto- Norwegian	1991	8	50–130	16.8	2.693	0.82	1.564	3.077	6.676	Kjesbu et al. (1998)
North Sea	1971–1972	92	60–110	1.29	3.29	0.82	1.517	3.468	8.935	Oosthuizen & Daan (1974)

A: Regression coefficients obtained from Buzeta & Waiwood (1982)

B: In the Baltic, years containing large females were selected from Kraus et al. (2000)

Energy content of gonads and oocytes

The energy measurements in our study were achieved by measuring a sub sample of the gonad in a bomb calorimeter. This method is not commonly used, despite its very accurate output, and the frame of reference is hence very small.

A relationship between the total energy content in the gonad and length of the fish was, as expected, found, indicating that a large fish invest more energy in the oocytes than a small fish, overall seen. Several correlations have been established between the reproductive energy allocation and offspring survival (Solemdal 1996), between egg quality and hatching success as well as larval development (Bell and Sargent 1996;

Pickova *et al.* 1997). The hepatosomatic index (HSI) has been established as being a good proxy for reproductive potential. Egg production in relation to total lipid energy originated from the liver was for example examined in Marshall *et al.* (1999), and a positive relationship between recruitment and liver weight was established, consistent with the relationship between HSI and total reproductive energy content seen in this study. It has furthermore previously been established that there is a massive influx of yolk to the cod ovary from white muscle (i.e. yolk precursors) via the liver around the time of the start of spawning (Marshall *et al.* 1999). This is consistent with the result seen in this study, with an increasing amount of energy in the gonads as spawning initiation approaches.

It is not only in cod this allocation of energy from body reserves to the gonad is seen. Rijnsdorp (1988) studied the energy allocation in female North Sea Plaice (*Pleuronectes platessa*), a fish with the same reproductive strategy as the cod (Murua and Saborido-Rey 2003), and found that an estimated 50 % of the gonad growth was subsidised from body reserves built up during the growing period.

Conceptually, the total lipid energy (TLE) is very useful because lipids represent a common “currency” linking food quality and quantity to many aspects of fish nutrition (Sargent *et al.* 1995), reproduction (Henderson *et al.* 1996; Pickova *et al.* 1997; Henderson and Wong 1998), and population dynamics (Bell and Sargent 1996). In regard to lipid reserves, Lambert & Dutil (1997) found that protein and lipid reserves used for metabolism, gonad development and spawning behaviour of fish co-vary in response with food abundance (Lambert and Dutil 1997b), findings that are supported by Jorgensen *et al.* (2006).

Another important predictor of reproductive potential is the condition of the female established in several studies (Kjesbu *et al.* 1991; Lambert and Dutil 1997b; Kjesbu *et al.* 1998; Lambert and Dutil 2000; Marteinsdottir and Begg 2002). However, we found no correlation between either energy allocated to reproduction nor fecundity and condition of the fish, indicative of a small influence of condition on the reproductive potential. This is coincident with the findings in Kraus *et al.* (2000), who found that condition had no substantial predictive power in regard to fecundity in their study.

In contrast to the significant correlation between total energy content in the gonads and fish length, the measurements of energy per gram gonad content showed no such correlation, a relationship indicative of a similar investment in reproductive energy between a small and a large fish relatively seen. The same relationship was seen in the energy content per oocyte. These two results are somewhat surprising, since it, in other studies, has been established that large fish produce larger oocytes (Kjesbu *et al.*

1991), and it here has been shown that the energy content per oocyte is positively correlated with egg size.

However, in a study made on the energy allocated to reproduction in capelin (*Mallotus villosus*), the same relationship between energy per oocyte and fish size was seen (Hedeholm *et al.* unpubl.). An explanation could be that the difference in energy contents between the oocytes is so small, that the uncertainty in the measurements diminishes the effect.

The West Greenland fjords as spawning locations

The West Greenland inshore cod populations are very sedentary, with almost no migration between different fjord systems (Storr-Paulsen *et al.* 2004). This sedentary behaviour could be an indication of an optimal area with regard to nutrition and growth, reproduction and recruitment.

Since the reproductive parameters, i.e. potential fecundity and energy allocated to reproduction are correlated with several factors, such as temperature, food availability and condition of the fish (i.e. a nutritional status) these parameters can be used as indicator of an area's suitability.

In the comparison of areas in regard to fecundity, temperature is used as a common denominator because of its influence on fecundity. The two areas most comparable in temperature are Norway and Canada. The average temperature in Norway (Vesterålen) is, because of the warm Gulf Stream, 3.4°C, while in Canada (Gulf of St. Lawrence) it is on average 5.5°C, temperatures a bit higher than in West Greenland (cf. Table 1). The fecundities (given in numbers*10⁶ oocytes) of the areas are 1.15 for Norway and 1.22 for Canada. Since temperature has shown to be positively correlated with fecundity, it would be assumed that the fecundities of these two areas would be higher than the one seen in West Greenland, but they are not. The explanation could be that the temperatures and fecundity estimates are averages taken over a period of years, and temporal variation of the reproductive potential between years have been shown to be very large. Several studies have found variation in the reproductive potential between years (Kjesbu *et al.* 1991; Kraus *et al.* 2000; Marteinsdottir and Begg 2002), because of the changing environment, and subsequent influence on the reproductive parameters.

Several studies have furthermore described the potential for annual variation in reproductive variables, as a way to increase the knowledge of temporal stability for these variables that influence reproductive potential. It has been noted that longer time series is needed to gain a profound knowledge on reproductive parameters, which exhibit interannual variation (Marteinsdottir and Begg 2002). In this study only one

spawning season is covered, which means that the reproductive potential only gives a snapshot of the reproductive characteristics of these fjords. To place this in a wider context, and gain thorough knowledge, more spawning data is needed. With a longer time series, it might also be possible to explain some of the variation seen in the patterns described here.

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