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Recruitment processes in West Greenland waters

With special focus on Greenland halibut (Reinhardtius hippoglossoides, W.)

Claus Stenberg

Dissertation for the degree philosophiae doctor (PhD)

at the University of Bergen

2007

Preface (in Danish)

At skrive en Ph.D. afhandling var slet ikke det jeg havde i mine tanker, da jeg i sin tid indleverede mit kandidat speciale. Min plan var, at komme ud at opleve verden og anvende den havbiologi og viden om fisk jeg havde lært. Det var ikke et bevidst valg, nærmere en række af tilfældige hændelser som gjorde, at den verden jeg kom ud til blev Grønland og at den fisk jeg kom til at arbejde med blev hellefisken.

Skæbnens ironi ville dog, at jeg, til trods for at jeg år forinden ville have forsvoret det, i år 2000 gik gang med et Ph.D. studium. Vi var en gruppe[1] som tilbage i efteråret 1998 ønskede at se nærmere på hydrografiske og biologiske processers betydning for variationer i rekrutteringen til reje- og fiskebestandene ved Vestgrønland. Netop denne kobling mellem havets fysik og biologi, og ikke mindst indflydelse på fiskens vé og vél, har altid fascineret mig. Vi gik i gruppen i gang med at definere forskningsprojektet RekPro og søge penge hertil. I projektet lå et Ph.D. studie til undertegnede såfremt vi fik pengene. Dét gjorde vi!

I 1999 og 2000 gennemførte vi størstedelen af feltarbejdet. Tak til RekPro-gruppen, ikke mindst Søren Anker Pedersen for nogle spændende og udbytterige togter med RV Adolf Jensen. Ph.D. studiet blev påbegyndt ved Universitetet i Bergen og en gæsteforskningsaftale med Havforsknings Instituttet blev etableret. Et NorFa mobilitets stipendium og velvillighed fra Grønlands Naturinstitut gjorde det muligt at flytte til Bergen, hvorfra jeg arbejdede i årene 2000 til 2002. Det var nogle gode og lærerige år i det norske. Ikke mindst på grund af mine inspirerende vejledere Arild Folkvord, Kjell Nedreaas, Svein Sundby og Åge Høines. Tak skal I alle have fra dansken. En speciel varm tak til Arild for hans altid store entusiasme og tro på projektet.

---

[1] Søren Anker Pedersen, Peter Munk, Torkel G. Nielsen, Benny Hansen, Lars Storm, Ninna Reuss, Louise K. Poulsen og undertegnede.

Størstedelen af dette Ph.D. studie blev gennemført under min ansættelse ved Grønlands Naturinstitut i Nuuk. At bo og arbejde i et land med så smuk en natur og så venlige mennesker, ikke mindst blandt gode kollegaer på Naturinstituttet, gjorde at min tid i det smukke land, altid vil stå som noget helt specielt for mig. Tak til jer alle "deroppe" for nogle uforglemmelige år. I perioder så I ikke meget til mig når jeg pendlede mellem Grønland, Havforsknings Instituttet, Universitetet i Bergen og Danmarks Fiskeriundersøgelser i Charlottenlund. Det var ikke altid nemt at holde en balance mellem mit ansvar for den biologiske rådgivning på hellefiskene i fjordene omkring Ilulissat, Uuummannaq og Upernavik og mine æg, larver og yngel i Ph.D.'en. Tak til min afdelingschef Helle Siegstad, som ved at give mig frihed og fritagelse fra mange af mine øvrige forpligtelser ved Naturinstituttet gjorde det hele muligt.

Afslutningen af dette Ph.D. studie har jeg gennemført ved Danmarks Fiskeriundersøgelser, Afdelingen for Havøkologi og Akvakultur i Charlottenlund (HØK). Tak til forskningchef Helge A. Thomsen for imødekommenhed og for altid at "finde plads" til mig. Også tak til HØK'erne Josianne Støttrup og Per Dolmer som opfordrede mig til at få skrevet denne afhandling færdig, og derfor accepterede mit fravær i perioder på de fælles danske arbejdsopgaver. Jonathan Carl var en stor hjælp i den sidste fase af afhandlingen, med sin flair for sproglige formuleringer af det engelske øgede han læsbarheden af denne afhandling signifikant. Tak Jonathan. Sidst, men ikke mindst en stor tak til Pia som har vist en fantastisk støtte og opbakning gennem hele Ph.D. forløbet. Ikke mindst i det sidste 1½ år hvor vores dejlige datter Nanna er kommet til.

Jeg vil slutte dette forord af med et citat fra den græske filosof Xenofanes (ca. 580 - ca. 478 f.Kr.) som jeg synes beskriver hele denne Ph.d. proces. En proces som startede med et MIK-nettræk den 22. juni 1999 kl. 8:38 på position 64°59.91N 52°40.998W:

"*Guderne åbenbarede ikke fra begyndelsen alt for os, men i tidens løb kan vi gennem vor søgen vinde bedre erkendelse. Men den absolutte sandhed har intet menneske kendt. Ej heller vil han komme til det, hverken om guderne eller om alle de øvrige ting, jeg beretter om. For selv om han tilfældigt ytrede den endelige sandhed, ville han ikke selv vide det; thi alt er kun et spind af gisninger*"

Claus Stenberg

Frederiksberg den 1. juni 2007
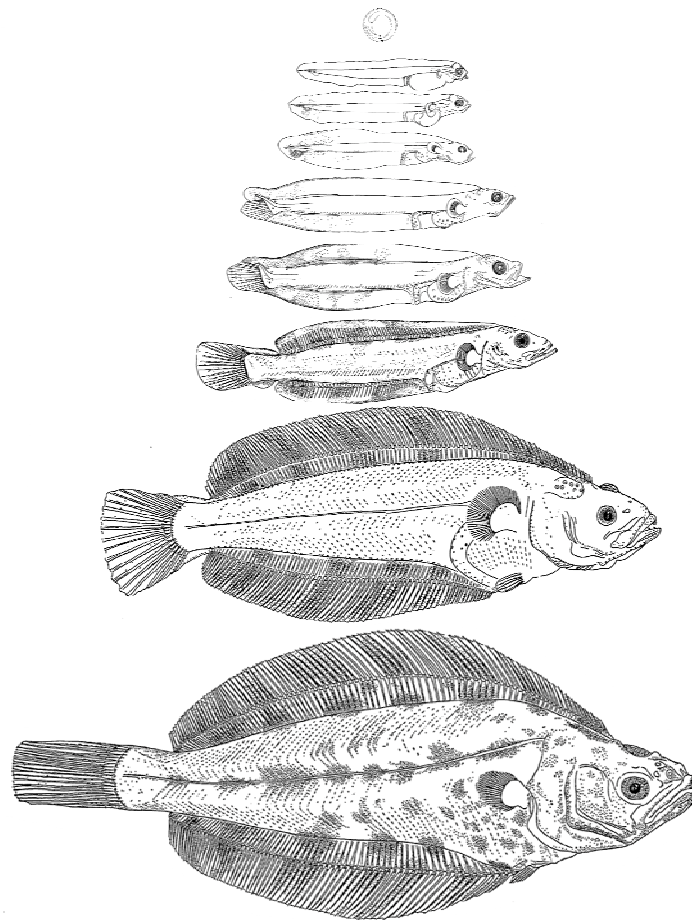
[above illustration from Smidt (1969) and Jensen (1935) showing Greenland halibut larvae development from egg to metamorphosed larvae (egg 3.8 mm; larval length 15; 16; 17; 25; 27; 32; 57 and 65 mm). Drawn by CM Steenberg, I Lieberkind and P Winter].

Contents

Scientific environment

This thesis was undertaken at the Department of Biology, University of Bergen with Professor Arild Folkvord as main supervisor and Professor Svein Sundby, Dr. Åge S. Høines and Dr. Kjell Nedreaas as secondary supervisors.

The Ph.D. study was initiated while Claus Stenberg (surname Simonsen to 2006) was employed at Greenland Institute of Natural Resources and finished while employed at Department of Marine Ecology and Aquaculture, Danish Institute for Fisheries Research, Technical University of Denmark.

The study was funded by:

- Greenland Homerule, KIIIP "Forskningspuljen" no. 05.11.03\99+1; 05.19.00/99; 05.19.00/02 and 05.19.00/04

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Introduction

Recruiting new individuals to a fish population begins with the development of the oocytes in the ovary. During development of the fish from fertilized egg to larvae to juvenile, the ontogeny, a number of processes influence the numbers that survive. Mortality in the early life stages is enormous among most marine fish species. Fecundity varies among species, but in general the number of eggs that a female fish spawn throughout its life sums up to millions. Of these, only two individuals have to survive in order to maintain population size. Thus, even small differences in mortality rate in the early life stages can have huge impact on the numbers that recruit to the population and ultimately the population size (Houde 2002).

Surviving the early life stages is basically a question of avoiding being eaten and having something to eat (Hjort 1914, Bailey & Houde 1989). In the field, predation mortality has been difficult to identify and quantify (Bailey & Houde 1989, Munk 2002, Pepin et al. 2002), but experimentally it has been demonstrated that it can be large for certain larval sizes (Folkvord & Hunter 1986, Fulford et al. 2006, Mueter et al. 2006). Evidence of differential prey availability resulting in differential growth and survival are however plentiful from both field (Kiørboe et al. 1988, Munk et al. 1995, Sundby 2000) and experimental studies (Folkvord et al. 1996, van der Meeren & Moksness 2003, Caldarone 2005). Field studies have shown that there can be a coupling between hydrodynamic and biological processes. Biological hotspots with higher productivity can emerge where hydrodynamic processes like fronts and upwelling transport nutrients up to the photic zone (Richardson 1985, Heilmann et al. 1994, Richardson & Pedersen 1998). If these processes are persistent in time and space, increased biological production can be seen at higher trophic levels and directly influence fish larvae growth and survival success (St. John & Lund 1996, Richardson et al. 2003, Munk 2007).

Hydrographic processes can also affect early life stages directly. Fish eggs and larvae have no or only limited swimming capabilities and are therefore more or less

passively transported by currents. Such egg and larval drift can be essential in maintaining population structure as it creates a triangle closure were egg and larvae drift downstream from spawning to nursery areas and subsequently adults migrate upstream to spawn (Harden Jones 1968).

In recent years there has been an increased awareness that the transition phase when larval metamorphosis to juvenile and adapts to a different habitat can be a critical phase with high mortality rates and many have argued that it may be more important than the larval phase in determining year-class strength (Beverton & Iles 1992, Van der Veer & Leggett 2005, Juanes 2007). Density-dependent settlement and habitat specific growth and mortality are probably the major factors controlling recruitment variability in the settlement phase (Gibson 1994, Iles & Beverton 2000, Juanes 2007).

Most studies on fish recruitment variability have been made in temperate water ecosystems. Thus, there is much less knowledge on higher latitude ecosystems. The present study will examine recruitment in the waters off West Greenland. This area shows marked variability in hydrographical and biological conditions and includes both polar and temperate regimes, which is reflected in the species composition and community structures (Møller & Nielsen 2000, Pedersen & Rice 2002, Munk et al. 2003, Pedersen et al. 2005).

The objective of this thesis is to examine recruitment of Greenland halibut (*Reinhardtius hipposlossoides*, Walbum) in West Greenland. However, because there are considerable connections to adjacent areas in eastern Greenland and western Canada these areas will also be included where it is appropriate. Sandeel (*Ammodytes* sp.) will also be included in the studies on larval ecology for comparative reasons. The study consists of four parts:

    I. Examine maturity development of female Greenland halibut from different areas in West Greenland in order to determine possible spawning areas and to evaluate reproduction strategies for the species.

    II. Analyse distribution and growth of Greenland halibut and sandeel larvae across the West Greenland shelf variability in biotic and abiotic factors.

Identify areas of special importance for Greenland halibut and sandeel larval growth and survival.

III. Study feeding ecology for Greenland halibut and sandeel larvae and examine if feeding conditions are optimal in central areas of fish larval distribution and at time of larval emergence.

IV. Analyse drift patterns of Greenland halibut egg and larvae from potential spawning areas around Greenland, and by use of a simple temperature growth model to predict settling place and time. Small scale spatio-temporal distribution and the settling process will be studied at Store Hellefisk Bank in West Greenland.

Abstract

The topic of this thesis is recruitment processes in Greenland Halibut (*Reinhardtius hippoglossoides*) in West Greenland waters. The focal point is Greenland halibut's early life history from oocytes in the female ovary - to larvae living in the pelagic - to juveniles on the sea bottom. These early life stages are examined in four studies:

Ovary and oocyte development in adult female Greenland halibut was studied in Davis Strait, Disko Bay and Baffin Bay. The objective of this study was to track and compare ovary development from winter to autumn from the inshore fjords of Disko Bay, Baffin Bay and the presumed spawning area in Davis Strait. Results showed that maturity was much more progressed in Davis Strait compared to the two other areas. Furthermore, almost all adult female fish in Davis Strait showed signs of maturation while only a fraction of the larger females (>80 cm length) were mature in Disko and Baffin Bay. A large proportion of the Greenland halibut in Disko and Baffin Bay did not appear to begin the maturation cycle until very late in their life history and/or were repeat spawners with a multiyear maturation cycle. Thus the observations from Disko and Baffin Bay support the theory that Greenland halibut can have a prolonged adolescent phase. The result from the study also strongly indicated that Davis Strait was the only major spawning area in West Greenland.

Larvae distribution and growth of Greenland halibut and Sandeel (*Ammodytes* sp.) was studied across the West Greenland shelf. The objective of this study was to analyse spatial distribution and growth during three periods May, June and July and relate these to cross shelf variability in biological and hydrographical conditions in order to identify areas of special importance for larval growth and survival. Results showed that in May small Greenland halibut larvae, some still with small remains of the yolk-sac, were primarily distributed offshore in Davis Strait. Their distribution coincided with their prey resources while some vagrant larvae were dispersed to areas with less food, which likely resulted in higher mortality rates. Consequently, the emergence of first feeding Greenland halibut larvae matched their prey in time and

space which is believed to be crucial for survival success at this critical stage in their development. From June to July Greenland halibut larvae gradually shifted their distribution from the bank slopes to the deeper parts of the slope near the shelf break. The lack of clear and well-defined frontal zones made it difficult to evaluate the hydrographical processes that had significance for larval distribution patterns. Greenland halibut larvae did, however, show preference for stratified water masses. Growth analysis of Greenland halibut larvae was only possible for July and showed higher growth was observed at stations positioned in frontal zones suggesting that growth was significantly influenced by the level of frontal activity. The study also included distribution and growth comparisons with sandeel. The larvae of sandeel was considerably more associated to the banks and bank slopes than Greenland halibut larvae in all three months (May-July), however in June, the two species coexisted considerably in the same areas of the cross shelf. The growth analysis showed that sandeel and Greenland halibut larvae showed opposite responses to some hydrographical conditions and prey abundance. Sandeel growth decreased with increasing frontal activity and increased with increasing prey biomass. The later observation suggests that sandeel growth was limited by food availability. Cross shelf variation in growth in Greenland halibut larvae showed that enhanced growth was observed at some stations where they were most abundant. Overall, however, there was no clear association between larval growth and larval abundances for neither Greenland halibut nor sandeel larvae. The observed patchiness in larval distribution could therefore also be a result of retention mechanisms and / or predation mortality.

The feeding ecology of pelagic Greenland halibut and sandeel larvae was studied across the West Greenland shelf. The aim of this study was to analyse and compare feeding ecology of coexisting Greenland halibut and sandeel larvae. Diet analysis and prey preference considerations were used to assess spatial variation in prey availability and feeding. The hypothesis was that feeding conditions are optimal in central areas of fish larval distribution, and that timing of larval emergence is synchronised with prey availability. The study showed that for both species copepods were the main prey items and that absolute size of preferred prey increased during

larval ontogeny. However, preferred copepod size in relation to larval length differed markedly between Greenland halibut and sandeel. In Greenland halibut the relative size of the prey declined during growth of the larvae while for sandeel the relative size of prey remained constant at a level of 2.7% of larval length. This led to a reduction in prey niche overlap between the two species as Greenland halibut and sandeel larvae increased in size. The available prey copepod biomass differed distinctly across the shelf area. In May, Greenland halibut prey density was highest in the off-shelf area in Davis Strait. In June and July, the prey rich areas for both species were mainly located on the slopes of the banks and at the shelf break area. In these areas gut fullness was higher than in neighbouring areas, suggesting that the food resource could be scarce. The feeding ecology of Greenland halibut and sandeel could explain why larval abundance indices for the two species historically have shown opposite responses to annual environmental conditions and total zooplankton occurrence.

Drift and growth of Greenland halibut from eggs throughout the pelagic larval stage was tracked from sub-population spawning areas in Davis Strait, Baffin Bay, East Greenland and West Iceland by combing drift- and individual-based egg and larval temperature dependent growth models. Model results were compared to survey results and the settling process was followed at Store Hellefisk Bank in West Greenland. The aim of this study was to evaluate spatio-temporal distribution of small first feeding and large settling larvae, and the between metapopulations. Results showed that egg and larvae can drift for long distances and that the exchange of individuals among the geographically-separated sub-populations could be important for metapopulation dynamics. Larvae from the spawning area in Davis Strait were primarily (>60%) transported to Canadian waters. Only larvae from the eastern part of the spawning area in Davis Strait remained in West Greenland. All larvae from the East Greenland spawning area were transported south of Cape Farewell and to West Greenlandic (82%) or Canadian (18%) waters. From the West Icelandic spawning areas larvae either, depending on the spatial location on the emergence first feeding larvae, drifted to East Greenland (45-53%), West Greenland (19−34%) or Northern

Iceland (21−28%) or remained (>98%) in Iceland waters. In Baffin Bay low water temperatures resulted in very slow development rates and eggs probably never hatched. The surveys showed that in West Greenland larvae settling started in August and continued in September but the settling peak period could not be determined. The study in the two areas of Hellefisk Bank showed that juveniles of age 1 and 2+ almost exclusively occurred in one area while the 0-group was equally distributed in both areas. In the area of high juvenile age 1 and 2+ abundance the condition and stomach fullness was significantly higher than in the low abundance areas. Nursery ground processes within the first year clearly restricted the successful nursery area to a more specific bottom habitat types. The concentrating of juveniles into specific nursery areas implies that juvenile densities may approach the carrying capacity of their habitats in years when settlement is high, which would dampen the annual variability in year class strength of Greenland halibut.

List of publications

Paper I Simonsen CS, Gundersen AC (2005) Ovary development in Greenland halibut (*Reinhardtius hippoglossoides*) in West Greenland waters. Journal of Fish Biology, 67: p. 1299-1317

Paper II Stenberg C, Folkvord A, Pedersen SA, Høines Å (Manuscript) Distribution and growth of Greenland halibut (*Reinhardtius hippoglossoides*) and sandeel (*Ammodytes* sp.) larvae in the sea off West Greenland: pp. 37

Paper III Simonsen CS, Munk P, Folkvord A, Pedersen SA (2006) Feeding ecology of Greenland halibut and sandeel larvae off West Greenland. Marine Biology, 149: p. 937-952

Paper IV Stenberg C, Ribergaard MH, Boje J, Sundby S (Manuscript) Drift of Greenland halibut (*Reinhardtius hippoglossoides*) egg and larvae and the settling process: pp. 46

1. Introduction

1.1 The area and its environmental conditions

The sea off West Greenland, has a varied topography that significantly influences the areas physical and biological characteristics. From Cape Farwell in the south (60°N) to Disko Bay in the north (69°N) runs a shelf area with a number of shallower banks

Fig. 1
Surface currents around Greenland. Modified from Pedersen and Smidt (2000)

with depths as shallow as 30 m. Deep channels down to more than 500 m intersect the shelf several places and divide the shelf bank systems. In area the largest of these are the Store Hellefisk Bank and the Lille Hellefisk Bank. Several large fjords systems connect to the shelf from the mainland in the East and the depth of the shelf break to the West sharply increases to more than 1000 m. A sea ridge at 66°N with a maximum depth of 600 m connects Greenland and Canada and forms a strait, the Davis Strait, between two deep basins south and north of the ridge. The basin south of the ridge is located in the Labrador Sea while north of it, is the Baffin Bay.

Temperature and saline watermass characteristics in the West Greenland Costal Current are formed in the western Irminger Sea where the East Greenland Current and the Irminger Current meets and flows southward side by side (Fig. 1). As the currents round the tip of Greenland the Irminger water ducks the Polar Water in the East Greenland Current and extensive mixing takes place. Hence, the marine shelf ecosystems of West Greenland are reflective of intermediate characteristics from the cold Polar Water masses of the Arctic region and temperate water masses of the Atlantic Ocean. The flow of water masses is to a great extent controlled by the large
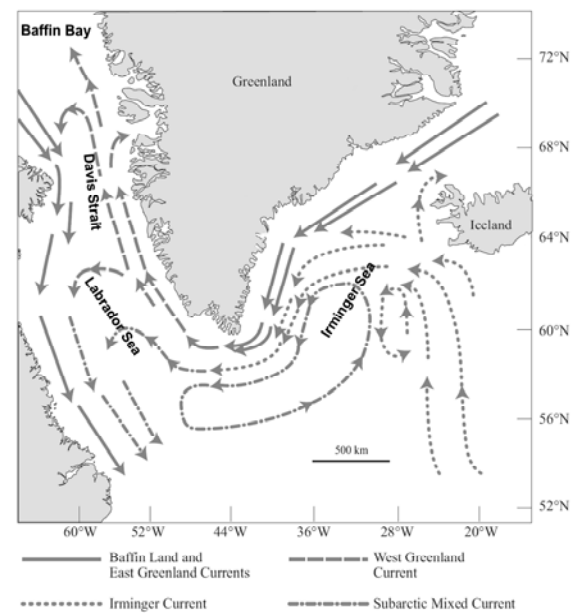
atmospheric low and high pressure systems. In the North Atlantic it is mainly the pressure difference between the subtropical and polar area that controls the North Atlantic Current. Traditionally this is described by the North Atlantic Oscillation (NAO) index which is defined as the normalized pressure difference between a station on the Azores and one on Iceland. At normal conditions the North Atlantic Current is widening with increased branching, especially for the Irminger Current when the NAO index is low (Blindheim et al. 2000). This result in increased inflow of relatively warm Iriminger water to West Greenland (Buch et al. 2004). A typical summer water mass situation over the shelf at Store Hellefisk Bank is shown in Fig. 2. The West Greenland Current with warm and intermediate salinity dominates from the coast and over the banks shelf. West of the banks, beneath the West Greenland Current flows the cores of two currents: the Polar Current at 50-100 m and the North Atlantic/Labrador Current from 200 m. These two currents are different with regard to temperature and salinity, the Polar Current has an intermediate salinity and

Fig. 2
Watermasses in a cross shelf transect of Store Hellefisk Bank at 67°35 N shown by (a) T/S plot of corresponding measurements of temperature (°C) and salinity (p.p.t.) Numbers refer to deduced water masses. (b) Contouring of combined salinity/temperature characteristics with indication of deduced water masses. Numbers correspond to indication in (a). From Munk et al. (2003)

cold temperatures while the North Atlantic/Labrador Current is warmer and has a slightly higher salinity. Further offshore towards Canada is the returning Polar Current that has been circulating around Baffin Bay and now flows southward as the Baffin Current. Depending on the distribution and extension of the "West-Ice", relatively cold and fresh ice melt is often observed in the surface at the westernmost
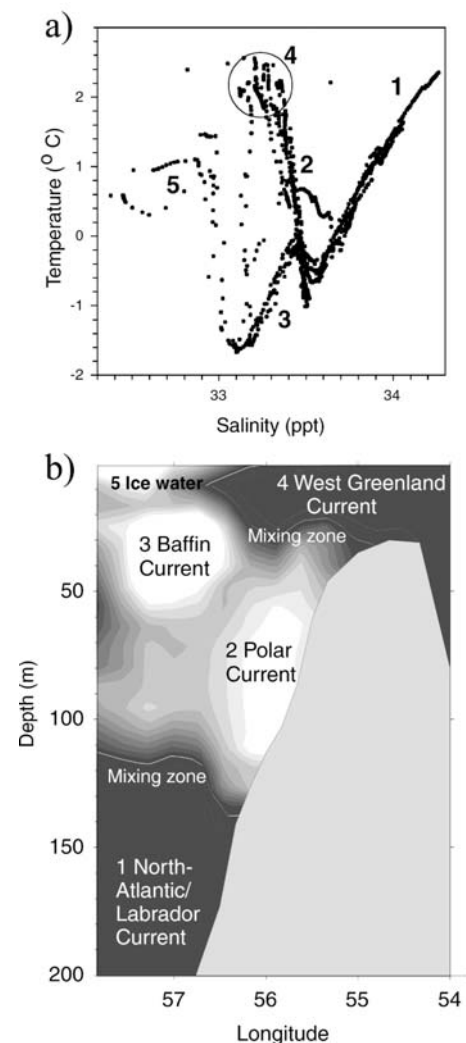
sections. Front zones can be distinguished between theses different water masses. Furthermore, hydrodynamic model simulations predict frequent upwelling fronts west of the shelf banks and to a lesser extent in the deep channels separating the banks along the West Greenland shelf from 64-67°30N (Fig. 3) (Pedersen et al. 2005).

Drift speed and direction of surface currents was followed by two satellite tracked buoys deployed east and west of Fyllas Bank on May 12 and 13. 2000 (Pedersen et al. 2002). Both buoys showed a net northward drift (Fig. 4a). The trajectories of the drifters intersected several times and showed meandering along their tracks. Occasionally eddies and gyres trapped the buoys for periods of 2-3 weeks (Fig. 4bc). Overall the drift speed was about 2-4 km day^{-1}. By September-October the buoys drifted along the shelf at Store Hellefisk Bank and Disko Bank.
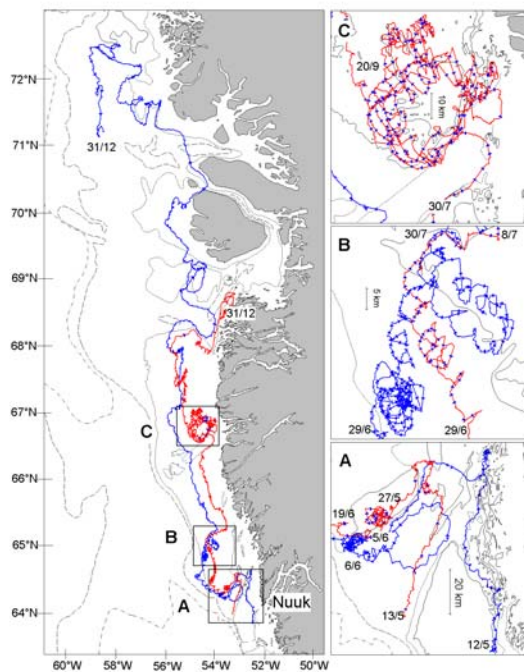
Fig. 4
Drift of the two satellite tracked SVP buoys with drogue at 30m. Blue released 12/5; red 13/5, 2000. (A): following the bottom topography (B): daily tidal induced clockwise circulation of about 5 km in diameter (C): anticyclonic circulation around bank. From Pedersen et al. (2002)
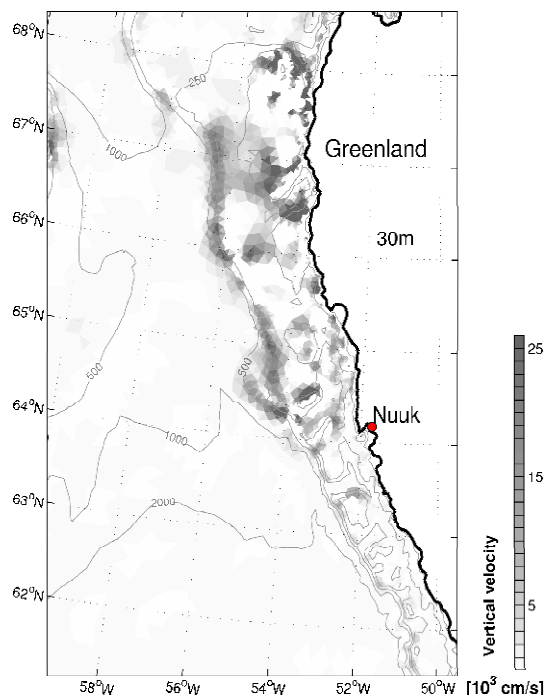
Fig. 3
Locations of potential upwelling areas calculated from the hydrodynamic model from April to October 2000. Modified from Pedersen et al. (2005).

1.2 The ecosystem

The pelagic ecosystem off West Greenland is with its position between cold Polar Water masses of the Arctic region and temperate water masses of the Atlantic Ocean high in biological species diversity and diverse in its physical environment. This greatly affects structure and function of the ecosystem.

The plankton constitutes an important part of the pelagic ecosystem. The yearly production cycle is initiated with a phytoplankton spring bloom (Fig. 5). Cushing (1975) suggested that there is a time lack before the zooplankton population is established and able to graze the phytoplankton. However, recent research has shown that copepods in West Greenland lay their eggs in winter, thereby the newly hatched nauplii can utilized the spring bloom instantly (Madsen et al. 2001, Nielsen 2005). Furthermore, grazing in the post bloom period is mainly done by protozooplankton which

Fig. 5
Generalized yearly production cycle in the Artic by Cushing (1975) and Nielsen (2005). Modified from Nielsen (2005).

ensure a lager degree of nutrient regeneration and thus a higher level of primary production throughout the summer months than previous thought (Nielsen & Hansen 1999). In the connection with the present study on Greenland halibut three plankton surveys were carried out in May, June and July. Patterns and findings from these surveys are used in the following for a general description of the succession in plankton ecology from May to July:

In May the phytoplankton community is in a typical late spring situation with diatoms dominating, while in June there is a shift to a post-bloom situation with nutrient depletion and small autotrophic are dominating the plankton (Poulsen & Reuss 2002). In the post-bloom period phytoplankton growth therefore seems dependent on regenerated nutrients or release of nutrients to the photic zone by hydrographic
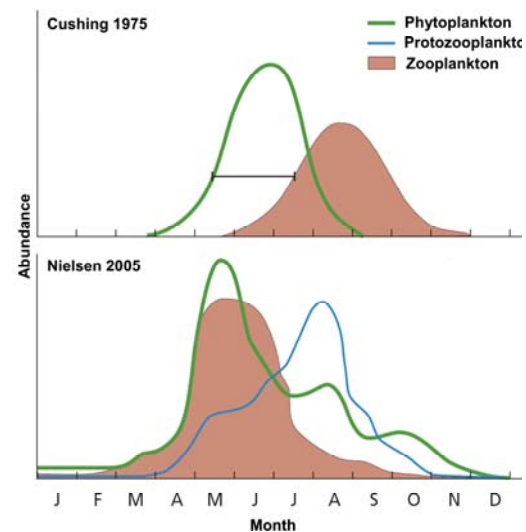
processes. The zooplankton is. in terms of biomass, dominated by the large copepodites of *Calanus spp. (C. finmarchicus; glacialis* and C. *hyperboreus)* and the smaller copepodites of *Pseudocalanus* spp., *Metridia longa*, and *Oithona* spp. comprise most of the remaining biomass. By number, bivalves larvae and relatively large copepod nauplii (>200µm) dominate the zooplankton community (>50µm) in May, whereas smaller copepod nauplii (<200µm) are dominating in June and July (Pedersen et al. 2005). The ichtyoplankton is by numbers dominated by sandeel (*Ammodytes* sp.). It constitutes 71-80% of the total catches. Other frequent observed fish larvae is Greenland halibut (*R. hippoglosoides*), American plaice (*H. platessoides*), and sculpins (*Myxocephalus* sp.). The top 10 abundance by species is illustrated in Table 1.

Table 1
Ichtyoplankton top 10 species abundance (total catch per survey) on the surveys in May, June and July.

Period	Species	no.
May	*Ammodytes sp.*	1213
	Hippoglossoides platessoides	167
	Cyclothone microdon	71
	Lumpenus sp.	71
	Aspidophoroides olriki	47
	Reinhardtius hippoglossoides	37
	Triglops sp.	33
	Myoxocephalus sp.	31
	Mallotus villosus	23
	Gadus sp.	14
June	*Ammodytes sp.*	1113
	Reinhardtius hippoglossoides	77
	Myoxocephalus sp.	76
	Hippoglossoides platessoides	51
	Triglops sp.	24
	Leptagonus decagonus	22
	Anarhichas sp.	14
	Bathylagus sp.	7
	Gadus sp.	6
	Aspidophoroides olriki	5
July	*Ammodytes sp.*	4966
	Myoxocephalus sp.	974
	Hippoglossoides platessoides	202
	Liparis sp.	186
	Triglops sp.	166
	Reinhardtius hippoglossoides	157
	Anarhichas sp.	147
	Stichaeus punctatus	127
	Lumpenus sp.	63
	Bathylagus sp.	51

Spatially, there is a gradient in the biological community structure and function of the ecosystem both latitudinal's and longitudinal's. Northwards, the component of the Irminger current in the West Greenland Costal Current is weak and the area is positioned north of the polar circle. Consequently, the environment is colder with ice cover several months each winter. The fish species are therefore dominated of more arctic species as arctic cod (*Boreogadus saida*), arctic shanny (*Stichaeus punctatus*) and the yearly succession in time displaced compared to south for all trophic levels (Pedersen & Smidt 2000, Munk et al. 2003). Southward, the area is greatly influenced by warm Atlantic Water and hence more temperate fish species as Atlantic cod is more frequent. In the east – west direction the coastal area is influenced by the

freshwater runoff and fish species as sculpins; the shelf by the West Greenland Costal Current and by solar summer stratification of water masses and the fish species sandeel on the shelf bank and larval Greenland halibut on the banks slopes (paper II). Westward, the offshore areas is influenced by the cold Baffin Current polar currents and low concentration of fish in the upper water masses except for small first feeding Greenland halibut larvae in the spring (paper II; Munk et al. 2003, Pedersen et al. 2005). In the offshore area from 700-1600 m depth adult Greenland halibut one of the most dominant fish species (Jørgensen 1998).
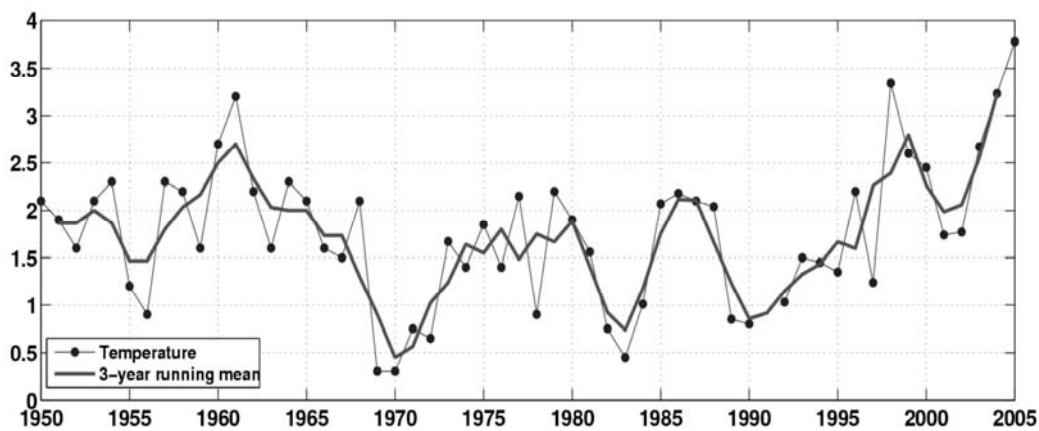
Fig. 6
Temperature at Fylla Bank (0-40 m) in the middle of June for the period 1950–2005. Running mean value (3 years) illustrated by curve.

Variations in inflow of different water masses to the West Greenland area have historical resulted in great variability in temperature conditions Fluctuations between warm and cold periods are evident looking at historic time series (Fig. 6). In periods since present to late 1990'ties, in the mid 1980'ties, from 1970-80 and 1950-68 temperatures has been above average and classified as warm periods. Total yearly landings in the commercial fishery of cod (*Gadus morhua*), redfish (*Sebastes* sp.), Greenland halibut and shrimp (*P. borealis*) show opposite trends in these different temperature regimes (Buch et al. 2004). Except for the present warm period, Greenland halibut and shrimp fishery has been high in cold periods whereas cod and redfish fishery has been high in warm periods. Cod, and partly redfish, in West Greenland is recruited from spawning areas in Iceland and East Greenland and

transported in the Irminger Current component to West Greenland (Hansen & Buch 1986). Hence, in warm periods with stronger inflow of Irminger water to West Greenland and also strong year classes at Iceland, the drift and recruitment to the West Greenland area can be extensive. The present warm period is a situation that has resulted in a low inflow of cod larvae (Ribergaard 2004). When the cod fishery was on its highest, the yearly landings reached more than 400 000 tons. Cod can therefore be an important player in the ecosystem and its absence in cold periods and especially since the 1990'ies must have changed ecosystem structure. For example predation mortality on shrimp and juvenile Greenland halibut, two frequent prey items by cod (Jensen 1935, Hansen 1949, Templeman 1973), must be much less. The lower predation mortality probably explains some of the increase in Greenland halibut and shrimp abundance that, judged from commercial landings, seems to have taken place since the 1980'ies.

2.   Biology, population structure and exploitation

2.1 Biology

Greenland halibut (*Reinhardtius hippoglossoides, Walbum 1792*) belongs to the *Pleuronectidae* family (the right eye flounders), of the *Pleuronectiformes* (the flatfishes). It is a deepwater species distributed from 200-1600 m (Jørgensen 1997a) but has been caught at depths more than 2200 m (Boje & Hareide 1993). It is mainly found in waters with temperatures from 1-4°C, but has also been observed at sub-zero temperatures down to -2.1°C (Jørgensen 1998). It has a circumpolar distribution and is found in both the Atlantic and the Pacific Oceans.
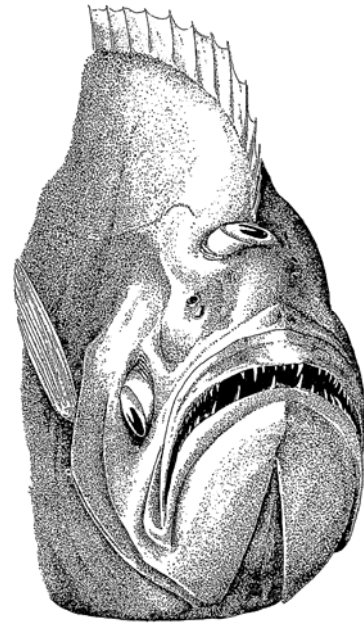
Fig. 7
Greenland halibut seen from front. From Smidt (1969)

Its morphology with the left eye positioned on the dorsal ridge of the forehead gives it an appearance of a cyclops[2] when looking straight at it (Fig. 7). The central position of the left eye in the Greenland halibut probably gives it a much wider range of peripheral vision in comparison to other flatfish where the eye has migrated completely to one side. The body shape is elongated and compressed dorsal-ventrally and muscles on both sides equally developed. Both sides are pigmented but the left blind side is slightly lighter in colour than the right side.

Its physical appearance suggests it is a vigorous swimmer that can swim in a vertical position. Vertical swimming has been observed during tagging experiments (see

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[2] In Greek mythology a Cyclops, or Kyklops (Greek Κύκλωψ), is a member of a primordial race of giants, each with a single round eye in the middle of its forehead.

Simonsen & Treble 2003), however, video analyzing of Greenland halibut behavior in front of a bottom trawl showed no sign of swimming in a vertical position (Albert et al. 2003). Even though most Greenland halibut are caught in bottom fishing gears (trawl, longline and gillnet) they have also been caught in surface drift nets (Smidt 1969) indicating that they can occur in the pelagic near the surface. Stomach analysis has also shown that the diet of Greenland halibut consists mostly of pelagic or bathypelagic organisms (Godø & Haug 1987, Pedersen 1994, Hovde et al. 2002). Thus, even though the Greenland halibut is a flatfish it does at times behave more like a round-fish.

Greenland halibut can be aged by the number of annuli structures on the sagitta otolith. Annuli can be used to estimate age up to nine years with reasonable precision (Anonymous 1997) and have been validated in Greenland halibut by length frequency data (the Petersen method) for ages up to 4 years (Bowering & Nedreaas 2001; see also paper IV for the distinct length modes for age 1 and 2). A nine year old female Greenland halibut from the NE Atlantic is about 60 cm while a female halibut of the same age from the NW Atlantic is about 57 cm (Bowering & Nedreaas 2001). Nine year old males are about 1-2 cm smaller than females of the same age. The average lifespan of males is considerably shorter than females which is typical of other flatfish species. Male Greenland halibut seldom reach more than 12 years of age or a size of 70 cm, whereas females can reach a length of more than 100 cm and have been estimated to be more than 20 years (Bowering & Nedreaas 2001)

The estimated proportion of 50% maturity at length (L_{50}) is less than 65 cm for females and less than 50 cm for males (Morgan et al. 2003). There is little variation in L_{50} throughout spawning populations in the North Atlantic with the exception of the population off Labrador –Newfoundland where L_{50}'s are about 10 cm larger for both sexes (Morgan et al. 2003).

The timing of spawning varies from winter to early spring between spawning areas throughout the North Atlantic (paper I; Sigurdsson 1977, Jørgensen 1997a, Gundersen 2003, Junquera et al. 2003, Gundersen et al. 2004). Studies of oocyte
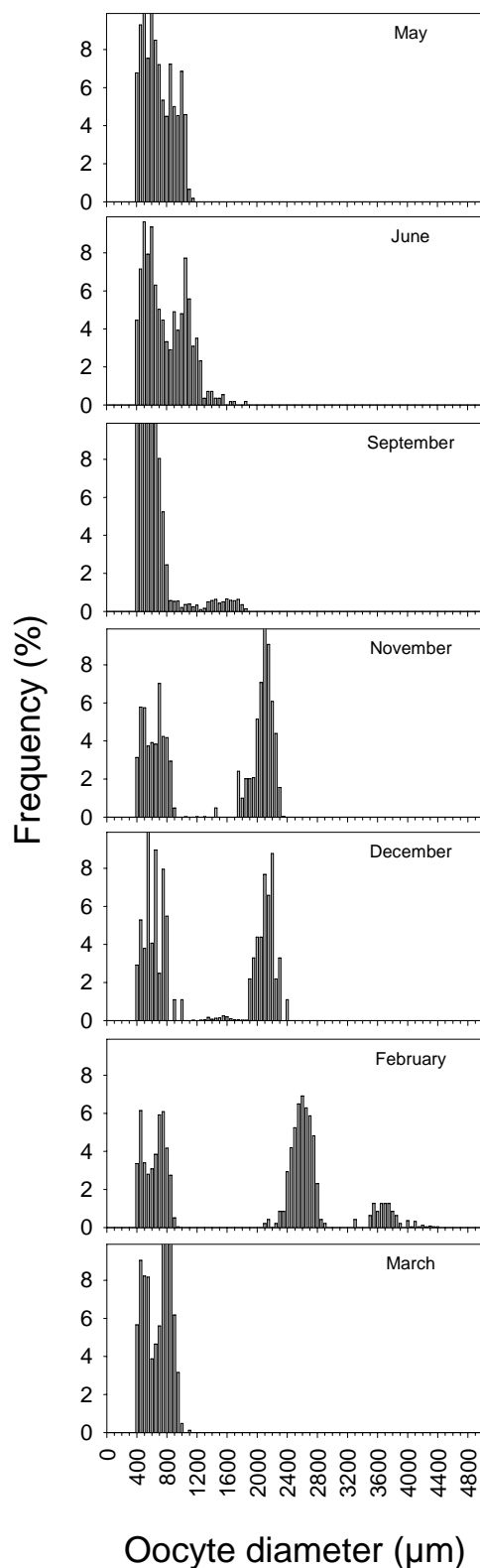
Fig. 8
Development of the oocytes in the ovaries of
Greenland halibut in Davis Strait. shown by
monthly oocytes diameter frequency (no
information from April, July, August and
October (Gundersen et al. *in prep.*)

development in West Greenland have shown that
within the single ovary oocytes can be divided into
two cohorts - a cohort of oocytes up to 1000 μm, the
developing cohort, and a cohort of oocytes larger
than 1000 μm, the leading cohort (Fig. 3 in paper I).
In the Davis Strait the leading cohort begins to
appear in September and increases in size until
February. In the inshore area in Disko Bay an
increase in oocyte size was seen from May to
August / September, and in Baffin Bay in October,
but only amongst a small fraction of the larger
specimens (>80 cm length) (paper I). This was in
striking contrast to Davis Strait were the majority of
Gr. halibut (>70 cm length) had a leading cohort of
oocytes. In addition, the ovaries from fish from the
Davis Strait were in more advance maturity stages
compared to the two other areas (paper I). These
results strongly suggest that Davis Strait is the only
major spawning area in West Greenland. In a
follow-up study it was shown that in Davis Strait
oocyte size increased until February where several
leading cohorts were seen in the population
(Gundersen et al. *in prep.*). This implies that
gametogonesis is not synchronous within the
population. In March most female fish were spent
and there were no larger oocytes in any of the
ovaries examined suggesting that spawning had
ceased.

Spawned and fertilized Greenland halibut egg has a reddish-brown membrane and a diameter of 3.8 to 4.3 mm (Smidt 1969). In a study of egg development in Greenland halibut from the Barents Sea it was observed that at hatching larvae are primitive but have a large yolk sac (Stene et al. 1998). The length of the yolk sac stage is unknown, but in Atlantic halibut (*Hippoglossus hippoglossus*) it is 305 to 395 degree-days (Pittman et al. 1990). Due to the many similarities in egg size, hatching time and development at hatching it is likely that Greenland halibut have comparable yolk stage duration.

The vertical depth distribution of the yolk sac larvae was examined by Jensen (1935) and in the present thesis (paper II). Jensen concluded that yolk sac larvae are located between 600 and 1000 m of depth and hypothesised that yolk sac larvae are bathypelagic and gradually rise towards the surface as they utilize the yolk. Even though the same areas in Davis Strait as Jensen were examined in paper II, only a few specimens were found at the 400-800 depth strata with the highest concentrations being in the surface layers (<100 m). Jensen's hypothesis, however, cannot be rejected as larvae caught in the present study were actively feeding (paper III)

indicating that they was in a more progressed ontogenetic stage than the larvae Jensen reported and would therefore, in accordance with Jensens hypothesis, also be distributed in shallower depths.

Information on summer larval distribution patterns in the waters around Greenland goes back as early as 1908 from the R/V "Tjalfe" expedition and was further strengthen by the "Norwestlant" programme in 1963. These
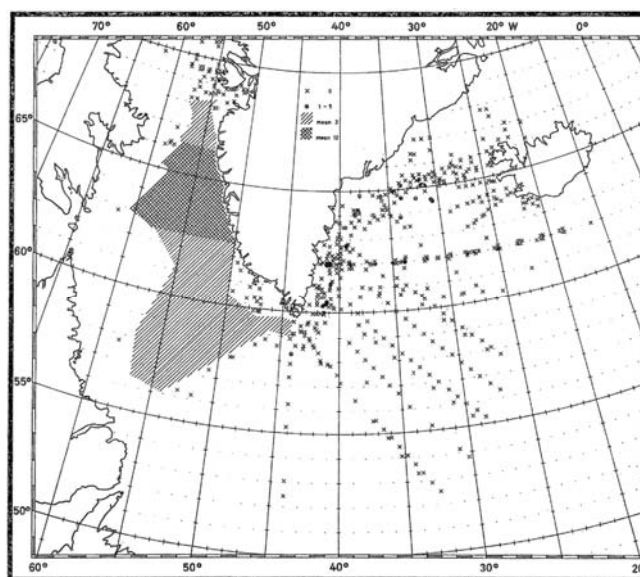

Fig. 9
Distribution of Greenland halibut larvae in the NW Atlantic. Crossed hatched area 12 larvae 30 min^{-1} haul; diagonal hatched area 3 larvae 30 min^{-1} haul; black circles few larvae (never more than 5 larvae 30 min^{-1}) and crosses no larvae. From Smidt (1969).

pioneering studies showed that Greenland halibut larval abundance was highest in West Greenland waters south of Disko Island and especially high in the Davis Strait between 62°30N and 66°15N Fig. 9 (Smidt 1969). Larvae were also caught in the Irminger Sea between Iceland and East Greenland, but only in low numbers. No ichtyoplankton tows were carried out in the sea off Baffin Island and Labrador. The western border in Fig. 9 is therefore a result of missing information. Ichtyoplankton tows was carried out in the fjords of Northwest Greenland but neither Greenland halibut egg nor larvae have ever been caught north of 68°N (Smidt 1969). Analysis of spatial distribution in the present study showed that small first feeding Greenland halibut in May were found almost exclusively offshore in Davis Strait. From June to July there was a gradual shift in larvae distribution from the bank slopes to the deeper parts of the slope near the shelf break Fig. 10) (paper II).

Fig. 10
Greenland halibut abundance (number m^{-2}) in May, June and July. (modified from paper II).

Through the summer months larval length progressively increased from 18 mm in May to 24 mm in June and 32 mm in July (Fig. 3 in paper II). Larval size is, however, not necessarily equal between areas at a given time. For example larvae in East Greenland have been observed to be 17-20 mm longer than larvae from West Greenland or the Barents Sea in the month of August (Smidt 1969, Godø & Haug 1987, Albert et al. 2002). Growth models show that differences between East and West Greenland can be explained by different temperature regimes (paper IV).

The pelagic larval phase ends when larvae metamorphose and settle. This occurs when larvae reach a size of approximately 65-70 mm (Fig. 11) (paper IV; Jensen 1935, Smidt 1969). The combined drift and temperature dependent growth model in paper IV estimates that settling occurs already in July from larvae spawned West of Iceland. In West Greenland waters larvae from spawning in Davis Strait was estimated to settle around October-November. The timing of the last settling was estimated for larvae that drifted into Canadian waters. Even though juvenile halibut have settled on the bottom, diurnal studies have shown that smaller juveniles (<15 cm length) in particular undertake pelagic migrations during the night (Jørgensen 1997b). The pelagic occurrence of juveniles has been confirmed by stomach analyses which showed the pelagic amphipod *Parathemistro* sp. was one of the most frequently observed prey in small juveniles (Haug et al. 1989, Jørgensen 1997b). In Greenlandic waters the abundance of age 1 and 2+ juvenile halibut is

Fig. 11
Right and left side view of Greenland halibut in different development stages. (a) pelagic larvae 32 mm; (b) pelagic larvae 57 mm; (c) transition to bottom stage 65 mm and (d) bottom stage 125 mm. From Jensen (1935)

especially high on Hellefisk Bank, Disko Bank and in Disko Bay in West Greenland (paper IV; Riget & Boje 1988). Juveniles have also been observed in East Greenland but densities are about an order of magnitude lower (Smidt 1969). Drift simulations have shown that juveniles on Hellefisk Bank mainly recruited from spawning in Davis Strait (paper IV). The northern part of Hellefisk Bank was surveyed monthly in July, August and September in 2002 (paper IV) and results showed that settling

began in August and increased towards September. It was, however, not possible to directly determine when the peak of settling occurred. Even though settling appears to take place over a wide area and on different bottom habitats, nursery ground processes within the first year clearly limited the recruitment success into nursery areas with specific bottom habitat types. Thus older juveniles were considerably concentrated in more specific nursery areas where individuals had significantly better condition and higher stomach fullness.

2.2 Population structure

Greenland halibut throughout the North Atlantic consist of several geographically separated populations or sub-populations. Several investigations have been carried out to determine the interactions between different populations and to what degree they can be considered discrete. These studies have considered meristic characteristics (Templeman 1970, Misra & Bowering 1984, Riget et al. 1992, Rasmussen et al. 1999), genetic variability (Fairbairn 1981, Riget et al. 1992, Vis et al. 1997), indicator parasites (Khan et al. 1982, Boje et al. 1997) and tagging data (Smidt 1969, Bowering 1984, Boje 2002). The results of these investigations varied but suggested that Gr. halibut in the areas:

1) Norwegian and Barents Sea;

2) The waters off East Greenland, Iceland and Faroe Islands;

3) Newfoundland area, Grand bank, Labrador, West Greenland;

4) The Gulf of St. Lawrence

despite having some common features could be characterised as separate "stocks". The genetic studies have, however, concluded that they are all genetically homogeneous (Fairbairn 1981, Vis et al. 1997). Greenland halibut in the North Atlantic can therefore be viewed as a metapopulation with a group of spatially separated sub-populations which interact at some level (McQuinn 1997). Studies on connectivity have mostly concentrated efforts on investigating the exchange of adults (by tagging studies), but the study in paper IV on egg and larval transport from

spawning areas in Davis Strait and Kap Bille Bank in East Greenland and West Iceland suggests that larval dispersal may be even more important. For example about 50% of the eggs and larvae from spawning in West Iceland can drift to West Greenland under certain conditions or about 20% of the eggs and larvae from spawning in East Greenland can drift to Labrador. The models to determine dispersal were relatively simple and did not include biological characteristics such as diurnal migrations patterns or stage specific vertical distribution etc. Thus including "biology" in the hydrodynamic models would strength the dispersal simulations considerably. Never the less the drift study suggested that the association of stocks due to larval dispersal was noteworthy and could be significant for local and metapopulation genetic diversity, dynamics and resiliency of sub-populations to fishery exploitation.

2.3 Exploitation

Exploitation of the Greenland halibut resource is around 60-70 000 tons in the NW Atlantic and 40-50 000 tons in the NE Atlantic per year (Fig. 12) Thus it is the largest deepwater fisheries in the North Atlantic. The fishery today is performed with longlines, gillnets and otter trawls at 600-1600 m depth. Historically the commercial fishery was developed in Ilullisat at West Greenland by Napoleon Andreasen in 1906 as a longline fishery (Smidt 1969). With the introduction of monofilament-gillnets and increased technology in the trawler fleet in the 1970´s and 80's a deepwater gillnet and trawling fishery evolved that increased the effort and landings considerably (Fig. 12).
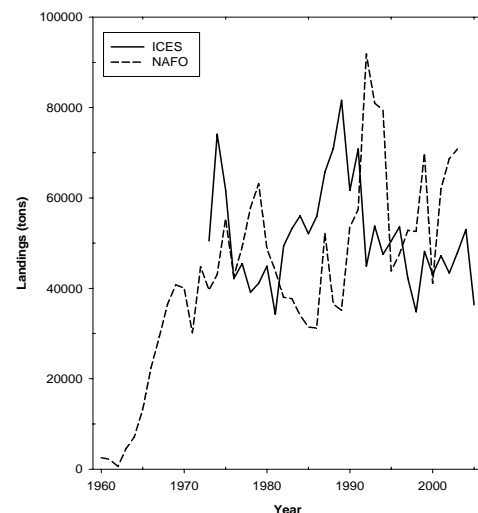
Fig. 12
Landings of Greenland halibut in NE Atlantic (ICES) and NW Atlantic (NAFO). Data: www.ices.dk and www.nafo.int.

Consequently the total stock biomass has decreased in several areas. Actions have been taken to increase regulations, however, biological information is generally insufficient, and the need for increased research activity has been expressed by all management units over the past few years. The lack of information includes e.g. knowledge on maturity, egg production, juvenile distribution, migration patterns and recruitment dynamics.

3. Recruitment processes

What determines the number of recruits from one life stage to the other is a key question in understanding fish population dynamics, and has since the question first was asked in Hjort (1914)'s "*Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research*" been researched, debated and discussed without reaching a consensus. To this day it remains one of the least understood problems in fishery science. However, it is generally agreed that the high and variable mortality during early life stages can explain much of the recruitment variability (Houde 1987, Cushing 1990, Rothschild 2000). In the following different early life history traits for Greenland halibut will be presented and different processes which influence recruitment variability will be evaluated.

3.1 Ovary and oocytes

Fecundity determines a fish's upper reproduction potential and thereby whether recruitment potential is large or small even before the egg is spawned. Fecundity of Greenland halibut is low compared to other flatfish. Estimates of eggs per female ranged from 6.4-94.4 thousand depending on body size with a mean fecundity between 18.1-28.1 thousands eggs per female (Gundersen et al. 1999, Junquera et al. 1999, Gundersen et al. 2001). This was expected as species with low fecundity are generally found in stable and predictable environments (Tyler & Sumpter 1996). Thus, the recruitment potential for Greenland halibut is considered small compared to other flatfish species.

Even though the spawning of Greenland halibut is a reoccurring annual event, it is questioned in paper I whether each individual female does actually spawn every year. The relative energy investment required for spawning is high at high latitudes or for deep water fish species, and species such as Arctic cod (*Boreogadus saida*) and orange roughy (*Hoplostethus atlanticus*) have been observed to skip spawning if in

poor condition (Bell et al. 1992, Hop et al. 1995). To maintain somatic tissue at the expense of not partaking in spawning may be a conservative strategy that long lived species such as Greenland halibut would benefit from. In Disko Bay and Baffin Bay there was supporting evidence showing that Greenland halibut had a prolonged adolescent phase or were repeat spawners with a multi-year maturation cycle (paper I). If adult female Gr. halibut do not spawn yearly, or the number of spawning individuals is regulated by biological conditions such as prey abundance, then the true spawning population biomass would be more variable than previously thought and directly coupled to the state of the ecosystem. This life history trait would thus add to recruitment variability.

3.2 Egg and yolk-sac larvae

Temperature determines the time needed for egg and yolk-sac larvae development (Pittman et al. 1990, Neuheimer & Taggart 2007). Information on temperature was used to develop a simple temperature dependent growth model to predict development time from fertilization to first feeding larvae at different spawning areas in and around Greenland (paper IV). It was found that the time needed for this development varied by more than a factor two (from 55 to more than 120 days). Thus the cumulative egg and yolk-sac larvae mortality would be relatively greater the longer the development time. This, however, was not expected to vary within areas only between areas and thus did not add to recruitment variability within sub-populations.

3.3 Pelagic larvae

Greenland halibut larvae are relatively large compared to the general ichytoplankton community. Large larvae are known to have reduced starvation and lower mortality rates due to predation (Miller et al. 1988). This aspect alone suggests reduced recruitment variability in the pelagic larvae stages of Greenland halibut.

In May model and survey results showed that small (10-18 mm long) Greenland halibut larvae were distributed offshore between 63 and 65°N in the Davis Strait (paper II and IV). Remains of yolk-sacs were observed among some of the larvae and they were believed to have just arrived in the surface waters from the bathypelagic. They were actively feeding on relatively large nauplii and copepodite stages and their distribution coincided with that of their prey (paper III). The shift from yolk to live prey is believed to be a critical stage in the early life history as larvae need to adjust to locating, catching and ingesting prey within days in order to avoid death from starvation (Hjort 1914, Cushing 1975). Consequently, a time and spatial match between the first feeding of Greenland halibut larvae and the presence of their prey are believed to have a major impact on larval mortality and thus have the potential to seriously effect year class strength in cases of a miss-match.

From June to July Greenland halibut larvae gradually shifted their distribution from the bank slopes to the deeper parts of the slope near the shelf break and showed preference for stratified water masses. Growth analysis showed an increase in growth rate with increased levels of front activity (paper II) which increases larval survival as high-growth-rate-larvae are better survivors than those with low growth rates (Meekan & Fortier 1996, Folkvord et al. 1997, Grønkjær et al. 2004). Variability in the strength and position of hydrographical fronts would thus add to recruitment variability.

Prey availability had allegedly no influence on Greenland halibut larvae growth in July (paper II). This was probably a result of their preference for relatively small prey items not predated on by other predators. The size preference of Greenland halibut larvae was either a result of preference for a specific copepod species, or the result of a prey competition where larvae shifted to other prey sizes to reduce prey size niche overlap (paper III). If larvae prefer specific species as prey then the dependence on a single prey species makes it vulnerable to the dynamics of that prey species. Such instances would add to recruitment variability. If a larvae choice of prey was more related to the effects of prey competition then any plasticity in prey size preference

would make larvae more robust to situations of food competition which in turn would reduce recruitment variability.

3.4 Settling and the juvenile stage

The study of two areas with different bottom habitats at the northern part of Hellefisk Bank (paper IV)) showed that Greenland halibut settled equally in the two areas, while age 1 and age 2+ juveniles primarily were found in one of the areas. Condition and stomach fullness was significantly higher in the areas of high abundance. These observations were interpreted as post-settlement mortality being habitat specific. The concentrating of juveniles to more specific nursery areas implies that juvenile densities may approach the carrying capacity of their habitats in years when settlement is high which would reduce recruitment variability. Such density dependent mechanisms have been described for several flatfish species and can explain why flatfish population dynamic recruitment variability is typically smaller than that experienced by other teleosts (Beverton & Iles 1992, Iles & Beverton 2000, Van der Veer & Leggett 2005).

In conclusion, juvenile Greenland halibut enters a density controlled "survival gate" when they concentrate into nursery grounds within their first year, because it is the available area of suitable nursery grounds that determines the upper threshold limits of recruits. Recruitment variability up to this threshold is thus found in the biological or physical processes that influence survival in the egg, larval and the early post settling stages.

4. Conclusion

This thesis represents a culmination of a number of studies investigating recruitment processes in Greenland halibut in West Greenland waters which have resulted in 4 scientific papers. The following is a summary of these results showing that:

- Although Greenland halibut is widespread in West Greenland waters there appears to be only one major spawning area that is positioned in Davis Strait. Some female Greenland halibut in Disko Bay and Baffin Bay show signs of seasonal maturity changes but it remains uncertain whether they undertake spawning migrations to Davis Strait or sporadically spawn locally. There is evidence supporting that Greenland halibut can have a prolonged adolescent phase or a multi-year maturation cycle.

- Greenland halibut larvae originating from spawning in the Davis Strait disperse to either the banks of West Greenland or Baffin Island and Labrador. Their drift route is determined by their spawning site in Davis Strait. Small first feeding Greenland halibut larvae are found in offshore Davis Strait in early spring. A time and spatial match of these larvae and their prey is believed to be crucial for their survival success. In June and July larvae are associated with the bank and its slopes. During these months they feed on prey of an almost constant size. This is either a result of preference for a specific copepod species, or the result of prey competition where larvae shift to other prey sizes to reduce prey size niche overlap with competing species. Larval growth rate was found to increase with increased hydrographical front activity suggesting a coupling between hydrographical processes and recruitment success.

- Greenland halibut larvae drift and are dispersed throughout their pelagic stages. The tracking of egg and pelagic larvae from sub-population spawning areas in Davis Strait, Baffin Bay, East Greenland and West Iceland showed

that egg and larvae can drift for long distances and that the exchange of individuals among the geographically-separated sub-populations can be significant. For instance up to 50% of the eggs and larvae from spawning areas in West Iceland can drift to West Greenland and about 20% of the eggs and larvae from spawning areas in East Greenland can drift to Labrador. Connectivity therefore seems noteworthy and can be significant for local and metapopulation genetic diversity, dynamics and resiliency of sub-populations to fishery exploitation.

- Juvenile Greenland halibut in West Greenland are mainly distributed on Store Hellefisk Bank, Disko Bank and in Disko Bay. The transition from pelagic larvae to the demersal juvenile stage starts in September and results from a model suggest that it continues through most of the autumn. Settling occurs on different bottom habitats but within the first year juveniles are concentrated in more specific nursery areas. This observation implies that the densities of juveniles within these nursery habitats may approach its carrying capacity in years when settlement is high, which in turn would dampen the annual variability in year class strength.

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Paper I

Ovary development in Greenland halibut *Reinhardtius hippoglossoides* in west Greenland waters

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Maturity in adult female Greenland halibut *Reinhardtius hippoglossoides* was studied in three areas in west Greenland waters: the inshore area in Disko Bay and two offshore areas, Baffin Bay and Davis Strait. The aim was to monitor maturity changes in the inshore fjords of Disko Bay over an extended period from winter to autumn and compare these findings with specimens from Baffin Bay and the presumed spawning area in Davis Strait. A significant difference in maturity level was observed in and between the three areas. In Disko Bay maturity indices increased significantly in August and September both with respect to the gonado-somatic index (I_G) and the size in the leading oocyte cohort. In the period February to May no significant changes were observed. Mature ovaries were only observed among fish >80 cm total length and only among a fraction of these large fish. Offshore areas of Baffin Bay, even though poorly sampled, showed similar signs in the maturity indices as in Disko Bay. Relative to Disko Bay and Baffin Bay, female fish in Davis Strait had more progressed maturity indices. Furthermore, almost all fish in Davis Strait showed signs of progressed maturity contrary to Disko and Baffin Bay. A large proportion of the Greenland halibut in Disko and Baffin Bay apparently did not begin the maturation cycle until very late in their life history or were repeat spawners with a multi-year maturation cycle. These observations could thus support the hypothesis that Greenland halibut have a prolonged adolescent phase. Atresia was highest in the early phases of maturation in Greenland halibut but relatively high levels of atresia were also observed in fish in more advanced maturity phase. The first was ascribed to fecundity regulation while the latter could be linked to the fish's fitness condition but it was not possible to show this with the available condition index. © 2005 The Fisheries Society of the British Isles

Key words: atresia; Greenland halibut; maturity; ovary development; spawning.

INTRODUCTION

Adult female fishes develop their ovaries prior to spawning. The development rate does, however, vary a lot from species to species (Tyler & Sumpter, 1996). In Greenland halibut *Reinhardtius hippoglossoides* (Walbaum) an arcto-boreal, deep water flatfish, the development rate of the ovaries to spawning have been questioned and the time cycle may be >1 year (Junquera *et al.*, 2003). A common

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feature for all specimens observed in spawning condition has been large ovaries and oocytes. The relative mass of the ovaries to the body mass, the gonado-somatic index (I_G), for spawning Greenland halibut has been between 18 and 25% (Fedorov, 1968) and the oocyte diameter 3·7–4·9 mm (Smidt, 1969). Female Greenland halibut with similar I_G values and oocyte diameter have been found in deep water (400–1600 m) throughout Greenland from Heimland Ridge, east Greenland (Gundersen *et al.*, 2001), to Davis Strait in west Greenland (Jensen, 1935; Smidt, 1969) and in the west Greenland fjords from Uummannaq Fjord (71° N) in the north (Smidt, 1969) to the fjords of Julianehåb Bay (60° N) in the south (Jensen, 1935; Smidt, 1969). The wide geographical distribution indicates that Greenland halibut may have several spawning grounds in Greenland waters and therefore the population dynamics and stock affiliations could be complex. The proportion of female fish with high sexual maturity indices at the places mentioned above, however, has been low. The exception is the stock in Davis Strait where the vast majority of female fish in autumn have developed ovaries (Jørgensen & Boje, 1994). During autumn Greenland halibut in this area also relocated to the deeper parts of Davis Strait which has been interpreted as a spawning aggregation (Jørgensen, 1997). Thus, even though the Davis Strait area has never been investigated during spawning, there is strong evidence that it is an important spawning area for Greenland halibut in Greenland waters. The full extent of a spawning area in Davis Strait is not known. The northern boundary may be the sea-ridge between Greenland and Canada at 67° N in Davis Strait (Jensen, 1935; Smidt, 1969) or south of there at 64° N (Jørgensen, 1997). The southern extent is not well described. Spawning, however, has been observed as far south as to the Flemish Pass off Newfoundland (Junquera & Zamarro, 1994). The sea-ridge in Davis Strait has great implications for the hydrography in the area and creates two very different deep water environments. South of the ridge bottom temperature at 1000 m depth is 3–4° C while north of the ridge is 0–1° C (Treble & Jørgensen, 2002).

Genetic studies of Greenland halibut throughout the North Atlantic have not shown any stock differentiation (Vis *et al.*, 1997). Some Greenland halibut have migrated several thousands kilometres intermixing with other populations (Bowering, 1984; Boje, 2002) and the gene flow between the different spawning stocks may be too large to develop genetically unique populations. Four separate stocks, however, have been defined based on the main distributions: 1) off eastern Canada and west Greenland, 2) eastern Greenland, Iceland and Faroe Island, 3) north-east Atlantic and 4) Gulf of St Lawrence (Morgan *et al.*, 2003). In each of these areas spawning fish and more or less well defined spawning grounds have been identified (Templeman, 1973; Sigurdsson, 1977; Bowering, 1982; Riget & Boje, 1989; Albert, 2003).

Greenland halibut in Davis Strait, Baffin Bay and the inshore fjords of north-west Greenland are both part of the eastern Canada and west Greenland stock complex. Davis Strait is believed to be a spawning ground as referred to earlier. The Baffin Bay area has until very recently been poorly studied and knowledge of sexual maturation and possible spawning grounds is strictly limited. In the inshore fjords of north-west Greenland Riget & Boje (1989) suggested that Greenland halibut here originated from the Davis Strait spawning stock. A maturity study by Jørgensen & Boje (1994) showed that the proportion of

female fish with developed ovaries was low in the fjords compared to the Davis Strait and they concluded that if spawning took place in the fjords it was insignificant. Instead it was assumed that the fjord populations were supplied by the inflow of fry and juvenile Greenland halibut from spawning in the southern Davis Strait. Studies on migration showed that when Greenland halibut entered the fjords they remained here throughout their adult life (Boje, 2002). There was thus no indication of a spawning migration back to Davis Strait. A serious shortcoming of the studies on maturity of Greenland halibut in the fjords of north-west Greenland has been that sampling took place only during February and August. In order to follow the maturation cycle sampling should have been carried out regularly throughout the year. It is therefore unknown if the sexual maturity level or proportion of mature fish were higher during other parts of the year.

This study focused on Greenland halibut in the west Greenland area and in particular the inshore fjords. The aim was to track ovary development in adult female fish in the inshore fjords of Disko Bay over an extended period from winter to autumn and compare these findings with specimens from Baffin Bay and the presumed spawning area in Davis Strait. Furthermore the occurrence of atresia was examined and compared within and between each of the three different areas studied.

MATERIALS AND METHODS

Biological samples from Disko Bay (NAFO Division 1A inshore) were collected randomly from commercial gillnet and longline catches landed to the local fish plants and from a longline research survey. The commercial fishery was conducted on three main grounds (Fig. 1) and was a mixture of gillnets and longlines. The use of baited hooks in the longline fishery could have biased the catch rate of very mature Greenland halibut as other species [cod *Gadus morhua* L. and haddock *Melanogrammus aeglefinus* (L.)] have been observed to be less attracted to bait in the spawning period (Løkkeborg *et al.*, 1989). About 50% of the annual landings, however, were taken by longlines and gillnets, which were used throughout the year (Simonsen & Boje, 1999). Spawning fish would thus occur in the catches if they were present. Sampling was conducted in the years 1998, 1999, 2001 and 2002 covering the months February to May and August to September (Table I). Fish were measured for total length (L_T) and mass (M). In the period February to May only ovaries from fish >75 cm were selected and frozen for later preservation in a 4% formaldehyde solution. In August and September only ovaries from fish >69 cm were selected and they were preserved directly in a 4% formaldehyde solution (Table I). Freezing the ovaries could have introduced bias because the chorion of smaller oocytes in particular would break thereby damaging these oocytes. Visual examination, however, confirmed that it was only small oocytes that were destroyed by the freezing process. These small oocytes were below the threshold diameter size of 300 μm used in the oocyte size analyses procedure. In total 396 ovaries were sampled from fish between 70 and 108 cm.

In the sampling programme in Baffin Bay and Davis Strait Greenland halibut were measured (L_T and M) and ovaries were removed from fish >69 cm, weighed and preserved directly in 4% formaldehyde. Samples from Baffin Bay (NAFO Division 1A) were sampled during a trawl survey in October 2001 (Jørgensen, 2002*a*). In total 13 ovaries were sampled from fish between 70 and 92 cm (Table I and Fig. 1). Davis Strait (NAFO Divisions 1 C and D) samples were collected in October and November 1998 and 2001 during a set of random stratified trawl surveys (Jørgensen, 2002*a*) and from the commercial trawl fishery (Table I and Fig. 1). A total of 135 ovaries were sampled from fish between 70 and 107 cm. Ovaries sampled in October were unfortunately badly
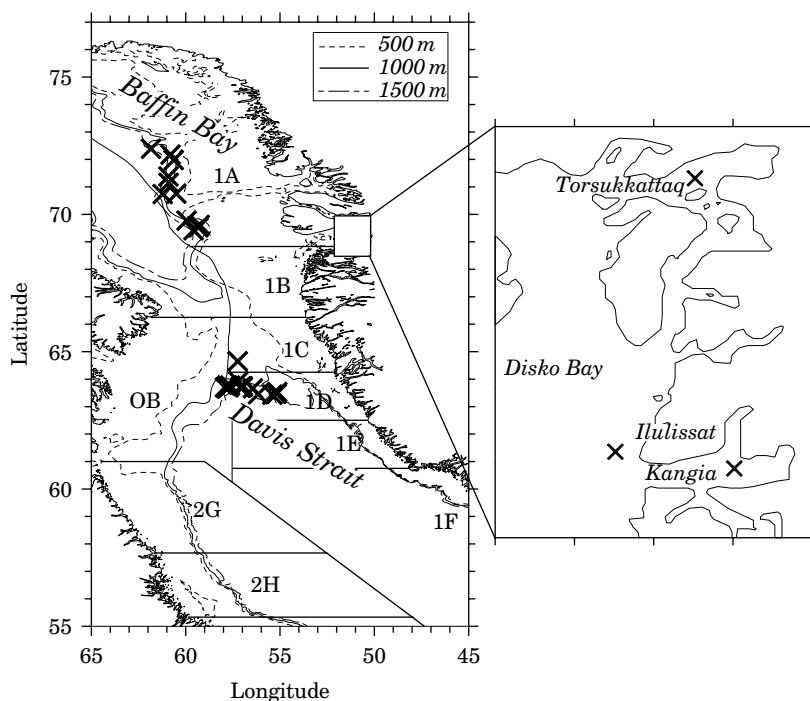
FIG. 1. Sampling area at the west coast of Greenland. Left, the entire sampling area inshore and offshore with the NAFO Division boundaries and names. Right, a close up of the inshore area in Disko Bay. ×, areas and stations where fish were sampled.

preserved and had to be discarded. The October samples were thus only used in I_G analyses.

In the laboratory frozen ovaries were defrosted and transferred to a 4% formaldehyde solution for a period of 1–2 months. All ovaries were then weighed and the mass was backcalculated to fresh mass using conversions factors: 1·34 for ovaries that had been frozen and then placed in formaldehyde and 1·10 for ovaries put directly in formaldehyde (A.C. Gundersen, unpubl. data).

In order to describe ovary development and maturation the I_G was applied on the total material while the more precise, but laborious methods of oocyte diameter measurements and histological examination were only carried out on a sub-set of the material (Table I).

The I_G was defined as the relation between the gonad mass (M_G) and M: $I_G = 100 M_G (M - M_G)^{-1}$. According to de Vlaming et al. (1982) I_G has to be validated for a species prior to application. This has, as far as is known, never been done for Greenland halibut and therefore the present samples were assessed against the following assumptions set up by de Vlaming et al. (1982): 1) linear relationship between M_G and M, 2) intercept of regression is not different from zero, 3) the relationship of ovary mass to M does not change with stage of ovary development and 4) the coefficient of variation (CV) is constant over the entire body mass range.

Oocyte diameter was measured on a sub-sample of ovarian tissue taken from the middle part of the right ovarian lobe following the procedures described in Gundersen (2003) and Thorsen & Kjesbu (2001). Only ovaries with $M_G \geq 40$ g were included. According to Simonsen & Gundersen (2002) this is the lower threshold for Greenland halibut ovaries to start the developing process. The oocyte size distribution for these fish in the population was expressed as a total monthly frequency distribution for each area. Furthermore, based on the oocyte size distribution in the individual ovary each fish was classified to a developing stage following the criteria: early developing ovary, >90% of

TABLE I. Overview of number of fish sampled divided by area, month, total length and processing method. Disko Bay was sampled in 1998 (February, March, April and May), in 1999 (March), in 2001 (August) and in 2002 (August and September). Baffin Bay was sampled in 2001 while Davis Strait was sampled in 1998 (October and November) and in 2001 (November)

Area	L_T interval (cm)	February			March			April			May			August			September			October			November		
		T	D	H	T	D	H	T	D	H	T	D	H	T	D	H	T	D	H	T	D	H	T	D	H
Disko Bay	70–79	13			72			31			11	1		33	4	4	24	1	4						
	80–89	21	4		65	5		22	1		3	2		13	6	4	5	3	6						
	>90	11	5		30	18		16	11		3	3		13	10	9	10	10	9						
Baffin Bay	70–79																			9	2	4			
	80–89																			3	3	3			
	>90																			1	1	1			
Davis Strait	70–79																			21			29	3	4
	80–89																			19			29	3	3
	>90																			12			25	5	6

T, total number of samples; D, number of ovaries where oocyte diameter analyses were carried out; H, number of ovaries where histological analyses were performed.

oocytes were <1 mm; developing ovary, >10% of oocytes were between 1 and 2 mm; late developing ovary, >10% of oocytes were between 2 and 4 mm.

Histological examination of oocytes was done on a small selection of ovaries using the same criteria as outlined above for oocyte diameter. Only ovaries preserved directly in formaldehyde were used as the cell structure of the frozen ovaries were damaged by ice crystals. Ovarian tissue was taken from the midsection of the right lobe, embedded in Technovit®, sectioned to 3 μm on a microtome and stained in tolouidine blue following the standard protocol described in Kjesbu *et al.* (1998) and adjusted for Greenland halibut by Gundersen (2003). The analysis included classification of oocytes to primary oocytes (P), early vitellogenic oocytes ($G2$) or fully vitellogenic oocytes ($G1$). Oocyte diameter was measured on $G2$ and $G1$ oocytes that were sectioned through the nucleus. The frequency of oocytes undergoing degeneration (atresia) was registered for each ovary. The occurrence of atresia was related to L_T, Fulton's condition factor (K, $K = M L_T^{-3}$), I_G and each of the three areas using multivariate ANOVA.

In statistical analyses data on mass data were $\log_{10}$ transformed while percentages data (including I_G) were arcsine transformed (Sokal & Rohlf, 1995) in order to assure normal distributions and homogeneity of variances. Statistical analyses were performed in the SAS/STAT® version 8.02.

RESULTS

ASSESSMENT OF FISH SAMPLES

There was no significant difference in L_T, M_G or the relationship between samples from the same months sampled in different years in either Disko Bay or Davis Strait (ANCOVA, $P > 0.06$) so data were broken down to month and pooled across years.

Size distributions of the fish sampled from Disko Bay were similar for the different months, except for August where they were significantly smaller (Tukey HSD, $P < 0.03$). In Davis Strait the size of sampled fish showed no difference between October and November (ANOVA, $P = 0.57$). When comparing the different areas there was no difference in size for fish sampled from Davis Strait and Disko Bay (ANOVA, $P = 0.09$) while fish sampled from Baffin Bay and Davis Strait were significantly different (ANOVA, $P = 0.02$). Fish from Baffin Bay were significantly smaller (mean 77 cm L_T) compared to both fish from Davis Strait (mean 84 cm L_T) and Disko Bay (mean 82 cm L_T) (Tukey HSD, $P < 0.04$).

VALIDATION OF I_G

The first of Vlaming *et al.*'s assumptions was met when all data were pooled as well as when the data were assigned to ovary development stage (linear regression on $\log_{10}$ transformed mass data, see Table II). The second assumption was validated for stages developing ovary and late developing ovary (*t*-test for zero intercept of linear regression, see Table II). The third assumption was met as the slope of the regression lines were not different (homogeneity of slopes test, $P = 0.22$). The fourth assumption requiring a constant CV over the entire fish mass range was not fulfilled. The CV on $\log_{10} M_G$ data declined significantly with increasing fish size (ANOVA, $P = 0.001$). Even though the assumptions for I_G were not validated in all respects, the fact that there was an overall significant

Table II. Coefficients $\pm$ s.e. for the linear regression of ovarian mass (M_G) and body mass (M) in Greenland halibut: $\log_{10} M_G = b\log_{10} M + \log_{10} a$, for all data and data where ovaries were classified to a development stage. Correlation coefficients and probability are also given. Where the assumptions (see methods) are met for the regression coefficients they are marked in bold

Ovary developing stage	n	b	a	r	P
All	543	**1·712 ± 0·125**	−4·711 ± 0·476	0·26	**<0·0001**
Early developing	39	**1·099 ± 0·119**	−2·557 ± 0·474	0·69	**<0·0001**
Developing	47	**0·551 ± 0·271**	**−0·072 ± 1·077**	0·09	**0·048**
Late developing	15	**0·877 ± 0·217**	**−0·737 ± 0·854**	0·56	**0·001**

positive correlation between ovary and body mass and that the relationship did not change with developing stages, supports the use of I_G to compare individuals in different stages of gonadal development and from different times of the year. The linear regression analysis suggested that M_G should be adjusted with a $\log_{10}$ factor between −2·6 and −4·7. This correction factor, however, was considered small and the analysis was based on a relatively limited sample size, therefore, a correction factor was not applied.

ANALYSIS OF I_G

The I_G in Disko Bay were low from February to May, varying between 0·1 and 2·5% [Fig. 2(a)]. One fish in May had a I_G of 6·3%, constituting an outlier in the data set (Dixon test, $P < 0·001$). In August and September I_G increased for some, but not all fish, to c. 3–6% [Fig. 2(a)]. The I_G increased significantly with L_T [general linear model (GLM), $P < 0·01$], and L_T and monthly slope were significantly different (homogeneity of slopes test, $P < 0·0001$), therefore a separate slope model was used to analyse for monthly difference in I_G. A significant difference was found between months (ANOVA, $P < 0·01$) with I_G in August and September being significantly higher than the earlier months (Tukey HSD, $P < 0·04$). In Baffin Bay in October most fish had a I_G of c. 1% with a single fish up to 4·7% [Fig. 2(b)]. In Davis Strait most fish had a I_G between 4 and 9% with a maximum of 13% [Fig. 2(c)].

The I_G in the three areas, (for Disko Bay only the months August and September were included) increased significantly with L_T with no difference in the rate (homogeneity of slopes test, $P = 0·10$). Using L_T as a covariate in ANOVA the difference between the three areas was highly significant (ANCOVA, $P < 0·0001$).

OOCYTE SIZE

The distribution of oocyte diameter in Greenland halibut ovaries was bimodal. One batch of oocytes at a size of c. 600 μm and a second batch of larger oocytes (typically >1200 μm) that were undergoing development (Fig. 3). These batches
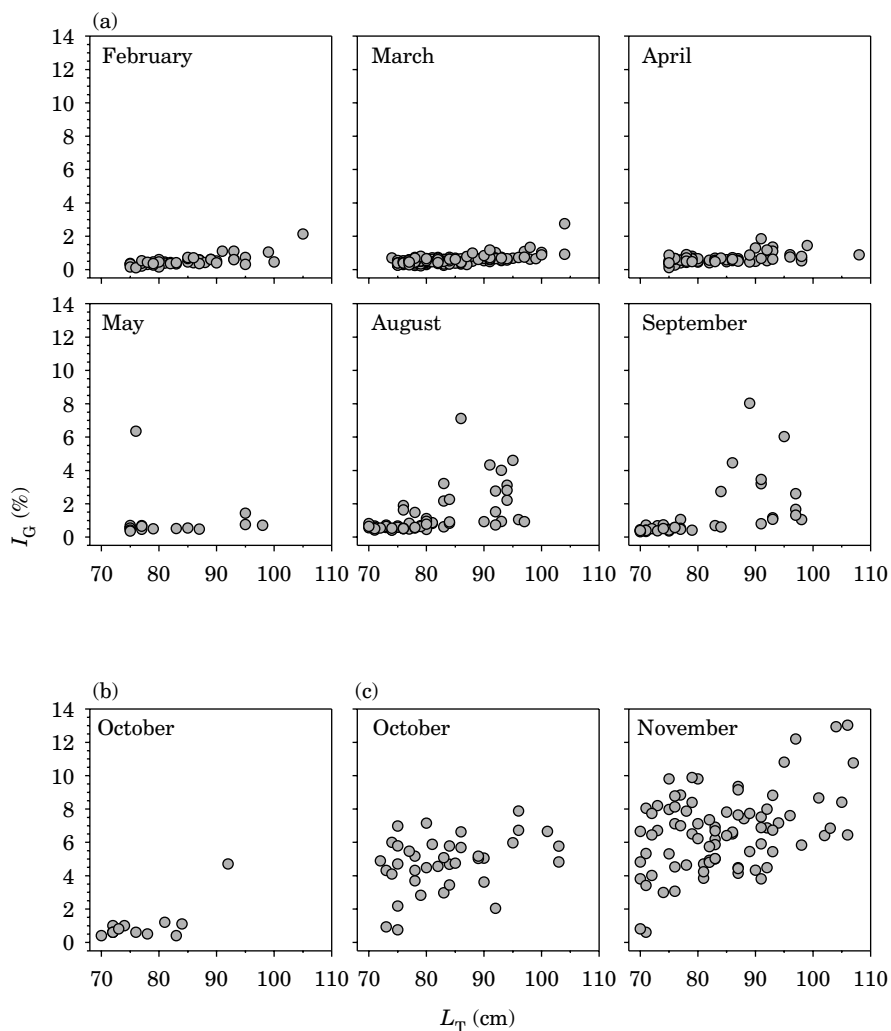
FIG. 2. Relationship between total length and gonado-somatic index for each sampled month and area: (a) Disko Bay from February to September, (b) Baffin Bay in October and (c) Davis Strait in October and November.

were respectively defined as the early developing cohort and the leading cohort. Fish with large oocytes in the leading cohort were also characterized by having a high I_G. The correlation was highly significant ($r = 0.76$, $n = 49$, $P < 0.0001$). Fish L_T had no effect on either the mean oocyte size in the early developing cohort or the leading cohort in any of the three areas (ANOVA, $P > 0.1$). Data were therefore examined for month and area effects only.

In Disko Bay from February to April almost all oocytes belonged in the early developing cohort and it was therefore difficult to distinguish a leading cohort [Fig. 3(a)]. A leading cohort was observed in May with oocytes up to 2000 µm.
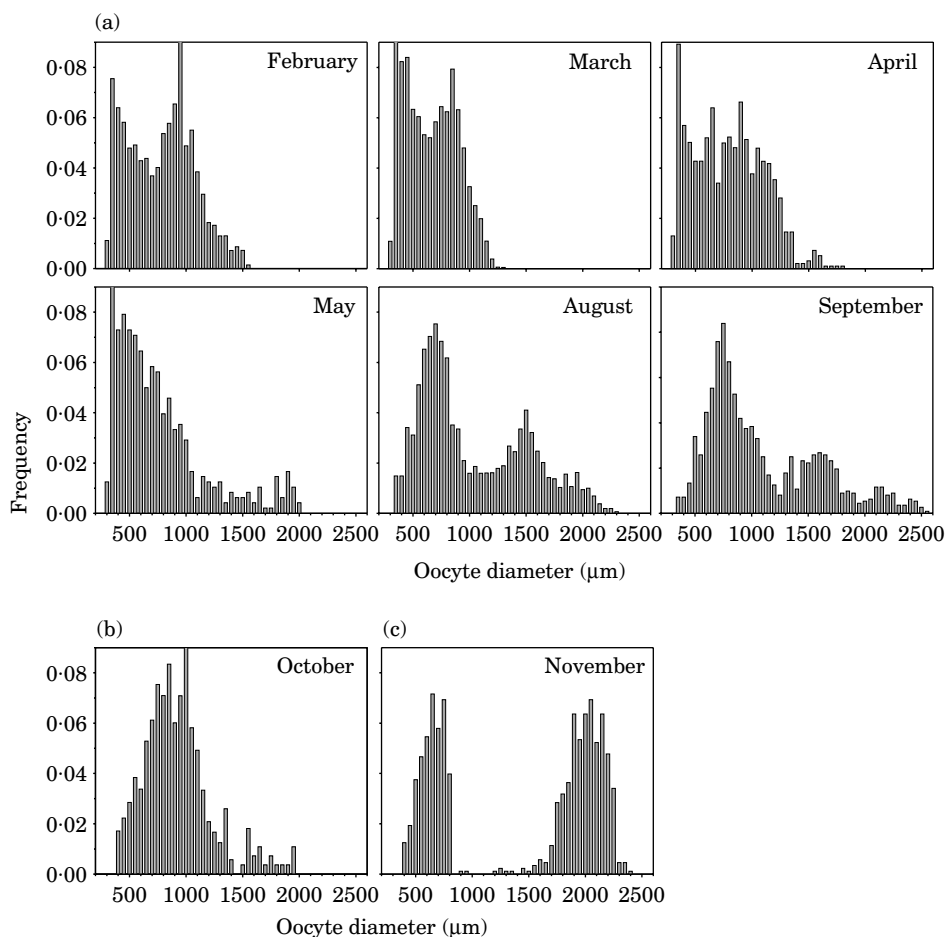
FIG. 3. Oocyte diameter frequency by month and area for Greenland halibut in (a) Disko Bay from February to September, (b) Baffin Bay in October and (c) Davis Strait in November.

The oocytes in the leading cohort, however, originated from a single female fish (with a I_G of 6·3%). There was no leading cohort in the other fish from May. In contrast to this >50% of the oocytes sampled in August and September belonged to the leading cohort. The leading cohort had two peaks that were most pronounced in September. The first peak was c. 1500 μm and the second 2100 μm. The leading cohort at the individual level, however, had only one peak. The CV for the mean oocyte size of the leading cohort (defined as oocyte >1200 μm) was 14% in August and 19% in September. The presence of two peaks indicated that oocyte development was not synchronous among the female fish in the population.

In the offshore areas in Baffin Bay in October most oocytes belonged to the early developing cohort. A single fish, however, had oocytes in the leading cohort [Fig. 3(b)]. In Davis Strait in November most oocytes were in the leading

cohort [Fig. 3(c)]. The leading cohort was well defined with one peak c. 2000 µm, even though differences in mean size of the leading cohort between individual fish were observed. The CV for the mean oocyte size in the leading cohort was 6%.

OVARY DEVELOPMENT

Classification of fish to ovary development stage showed that in Disko Bay for February to May the majority of fish were immature or early developing (Table III). The relative share of these stages was less in August and September. Also fish in the late developing stage were now observed among 5% of the fish examined (Table III). In the offshore areas in Baffin Bay in October most female fish had immature or early developing ovaries (Table III). In Davis Strait in November the majority of the female fish were classified to the late developing stage (Table III).

HISTOLOGICAL ANALYSIS

Histological analysis of the oocytes showed both early (G2) and fully vitellogenic (G1) oocytes were present in Disko Bay in August and September and offshore Baffin Bay in October as well as in November in Davis Strait (Fig. 4). Only a single fish in Baffin Bay had G1 oocytes. The G1 oocytes displayed a significantly different size range (mean diameter from 680 to 1380 µm) in Disko Bay compared to Davis Strait (mean diameter from 1710 to 2080 µm) (ANOVA, $P < 0.001$). Also the size of G2 oocytes was significantly different between the three areas (ANOVA, $P < 0.001$) with the smallest in Disko Bay (Tukey HSD, $P < 0.01$).

TABLE III. Proportion of female Greenland halibut in the different ovary development stages and total sample size. Number of immature ovaries was determined by mass while the other ovary development stages were determined from the oocytes diameter frequency (see methods)

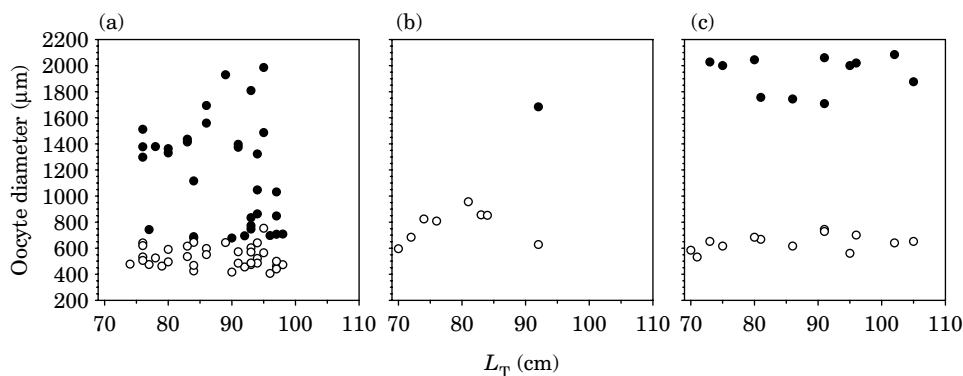|		Ovary development stage				
Area	Month	Immature (%)	Early developing (%)	Developing (%)	Late developing (%)	Total sample size
Disko Bay	February	80	4	16	0	45
	March	84	12	4	0	167
	April	83	7	10	0	69
	May	65	18	18	0	17
	August	66	9	21	5	58
	September	64	5	26	5	39
Baffin Bay	October	50	8	42	0	13
Davis trait	November[1]	15	8	0	77	17

[1]Only samples from November 2001.

FIG. 4. Mean oocyte diameter per fish for fully vitellogenic (G1) (●) and early vitellogenic oocytes (G2) (○) in relation to fish total length in (a) Disko Bay, (b) Baffin Bay and (c) Davis Strait.

ATRESIA

Atresia was seen in 35 of 58 ovaries examined. In most ovaries the per cent of oocytes in degeneration was <10%, but up to 58% was observed (Fig. 5). Samples from Disko Bay in August and September were similar (ANOVA, $P = 0.10$) and were therefore pooled. In a multivariate ANOVA the variables L_T, K, I_G and each of the three areas were related to the level of atresia. Only I_G and area were significant ($P < 0.02$). Furthermore the cross effect of area and I_G was significant ($P = 0.01$). The significant difference in the three areas was interpreted as difference in I_G associated with each area rather than an effect of area itself. The highest levels of atresia were observed in fish with I_G of $c.$ 1%. (Fig. 5).

DISCUSSION

MATURITY INDICES

The present study used several indices on the development of the ovary and its oocytes. Even though each index can be viewed separately, a close relationship obviously exists. Oocyte maturation was followed by an increase in oocyte size. Occurrence of atresia was most frequent in the early phases of gonad development and rare in the later phases. The number of oocytes in the ovary can therefore be considered relatively constant except for the early phases. The increase in oocyte size must increase mass of the ovary resulting in allometric growth. This was supported by the high positive correlation between oocyte size in the leading cohort and I_G. Furthermore, histology showed that oocytes in the leading cohort were fully vitellogenic. These findings were in agreement with other studies on sexual maturity of Greenland halibut; Albert *et al.* (2001) found that I_G increased with maturation stage and Gundersen (2003) that the oocyte size in the leading cohort as well as I_G increased towards spawning. Therefore
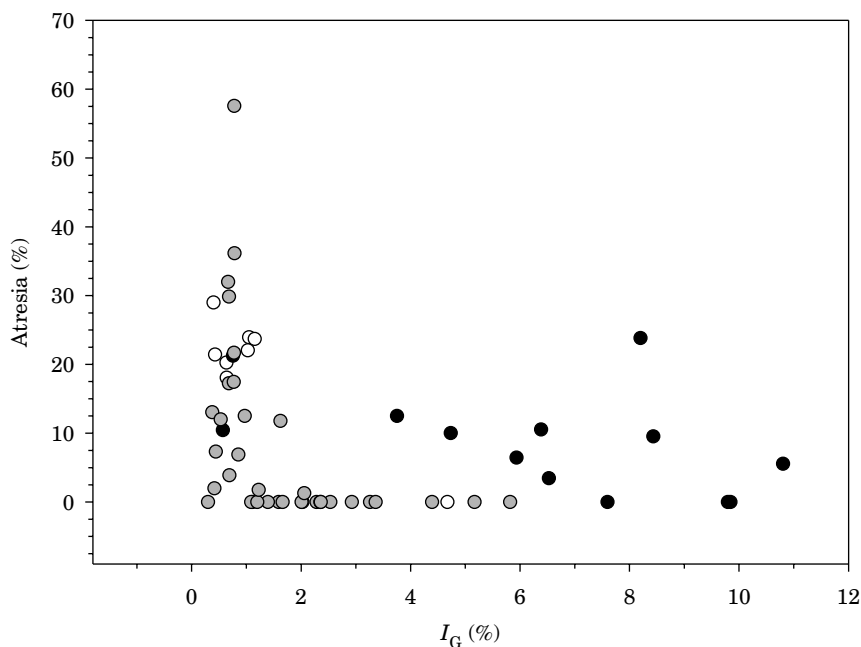
FIG. 5. Relationship between the gonado-somatic index and percentage of oocytes in the ovary affected by atresia in Disko Bay (⬤), Davies Strait (●) and Baffin Bay (○).

the different maturity indices used in the present study were all considered valid for describing the sexual maturity stage of Greenland halibut.

OVARY DEVELOPMENT

The tracking of the ovarian development in Disko Bay disclosed significant changes in August and September with a proportion of the fish having 3–6% I_G, a size in the leading cohort of 2500 µm and oocytes being fully vitellogenic. In the period February to May no significant changes were observed. As spawning is known to occur at I_G between 18 and 25% (Fedorov, 1968) and a oocyte diameter at 3·7–4·9 mm (Smidt, 1969) these fish were not in an immediately prespawning phase. Earlier studies in the fjords of west Greenland in Upernavik, Uummannaq and Disko Bay in the months February and August did not observe significant difference in I_G between the 2 months studied (Jørgensen & Boje, 1994). In Disko Bay and Upernavik I_G was low in both months. In Uummannaq increased I_G-values for some fish, but not all, were observed in some years in August while in other years in February. The present study showed that maturation process also occurred amongst the female Greenland halibut in Disko Bay. Further studies including the period September to January should be carried out in order to clarify if the proportion of fish showing signs of ovary development increased during autumn, and if the fish found in a late developing stage in September matured any further.

The offshore areas of Baffin Bay, even though poorly sampled, showed similar results for I_G, size of G1 oocytes and ovary developing stage as in Disko Bay. Compared to Disko Bay and Baffin Bay, female fish in Davis Strait were at a much more advanced maturity stage with respect to I_G, size of the G1 oocytes, number of oocytes in the leading cohort and the ovary development stage. There was a time displacement of 2–3 months between the sampling in Disko Bay and Davis Strait which could explain some of the observed difference. Studies on Greenland halibut in the Barents Sea, where the maturation has been followed over an entire maturation cycle (Gundersen, 2003), however, suggests that a 2–3 month time difference cannot explain all of the observed difference in maturity development. This could suggests that the maturation cycle in Disko Bay was not parallel to Davis Strait, but further studies with overlap in time should be carried out before any firm conclusions can be made.

The finding of more fish being in a more advanced state of maturity in Davis Strait compared to other areas in west Greenland was identical to the earlier study by Jørgensen & Boje (1994) who also found an increase in I_G in the third and fourth quarter of the year. Smidt (1969) summarized findings of females with ripe eggs in the period 1908–1960 in west Greenland and reported that only five fish had been observed. Of these, two were from Davis Strait and three from the fjords in south-west Greenland. The sexually mature fish from Davis Strait were caught in June and July while the ones from the fjords were from March to July. These observations, however, probably reflected the fishing pattern in time and space during this period rather than the actual distribution of spawning fish. In the five main distribution areas of Greenland halibut in the North Atlantic the main spawning time was between autumn and spring (Morgan *et al.*, 2003). Based on this, and on information from this study as well as the results presented by Jørgensen & Boje (1994) it is likely that spawning is taking place in Davis Strait, somewhere between late autumn and spring. Further studies actually covering this period is, however, needed in order to establish a more precise spawning time.

THE SEXUAL MATURATION PROCESS

In general a significant positive relationship between Greenland halibut length and I_G was observed which was in accordance with other studies (Jørgensen & Boje, 1994). In several fish species I_G is correlated with fish size simply because the proportional relationship between body and ovary size changes as fish grow larger (de Vlaming *et al.*, 1982; West, 1990). Increased I_G-values, however, were only observed among females >80 cm L_T in Disko Bay and Baffin Bay whereas I_G in Davis Strait was high for almost all sampled fish. Thus, the explanation for the observed differences must be found elsewhere than size alone.

One hypothesis is that larger Greenland halibut females start maturing earlier in the year compared to smaller females. This is for instance seen in herring *Clupea harengus* L. and several other fish species (Slotte *et al.*, 2000). A study on Greenland halibut in the Barents Sea showed that the large fast growing individuals started the spawning migration earlier than smaller ones (Albert, 2003). Assuming that it was the onset of the maturation that triggered this spawning migration, there must be a size related mechanism applied for Greenland halibut.

Implicit in this hypothesis is that the smaller Greenland halibut would commence maturation later in the year. This may be the explanation for findings in the Barents Sea of a second, less extensive, spawning event *c*. 6 months later than the peak spawning in winter (Fedorov, 1968; Gundersen, 2003). With the present sampling scheme this hypothesis could not be accepted or rejected for Greenland halibut in west Greenland waters.

Another hypothesis is that Greenland halibut have a prolonged adolescent phase. Junquera *et al.* (2003) suggested that there is a time lag of *c*. 4 years between the time that female Greenland halibut change from immature to mature adults and spawning occurs. Such a prolonged adolescence would especially explain the situation in Disko Bay where it was only among fish >80 cm higher I_Gs were found. Furthermore, most of the fish <80 cm in Disko Bay had small and contracted ovaries and did not appear to be repeat spawners. A considerable fraction of the specimens >80 cm in Disko Bay, however, still had low I_G and showed no or only weak signs to have begun maturity development towards spawning. Either these Greenland halibut were still in a prolonged adolescence phase or they were repeat spawners with a multi-year maturity cycle that had only just commenced. Lengthy reproductive cycles are known from several arctic species and have been suggested for Greenland halibut (Fedorov, 1971; Junquera *et al.*, 2003). Junquera *et al.* (2003) estimated that the very first maturity cycle of an individual could last up to 4 years in Greenland halibut. Greenland halibut in Davis Strait generally had higher maturity indices, including fish <80 cm, and this was interpreted as a result of spawning migration of only sexually mature fish to this area. That a spawning ground generally holds fish with higher maturity indices than surrounding areas was expected.

Thus, even though there were strong presumptions that Greenland halibut had a prolonged adolescent phase and repeat spawners a multi-year maturity cycle, the present study was not able to prove it directly. In order to do this, sampling had to cover at least a year in each of the areas investigated. Furthermore, the first hypothesis concerning a maturity time lag connected to fish size has to be rejected before the hypothesis on prolonged adolescence can be accepted.

ATRESIA

Degeneration (atresia) of oocytes can be a process that affects maturation in female fishes, either by reducing the number of maturing oocytes preparing for spawning, or actually interrupt the entire maturity process (Fedorov, 1968, 1971; Tyler & Sumpter, 1996). In the present study prevalence of atresia was highest in the early maturity phases of Greenland halibut. This is in accordance with observations made by Junquera *et al.* (1999) in the north-west Atlantic and by Fedorov (1971) in the Barents Sea. Highest prevalence of atresia in the early vitellogenic phase has been ascribed as a natural process regulating the surplus of oocytes in the early vitellogenic stages recruited into successive stages of development (Tyler & Sumpter, 1996). On the order hand atresia has also been noted to be widespread in later phases of the maturation process and associated with the available energy resources and environmental conditions, thereby regulating fecundity under sub-optimal conditions (Ma *et al.*, 1998; Bromley *et al.*, 2000; Kurita *et al.*, 2003). In the Barents Sea Greenland halibut atresia has observed to

be so intensive that spawning was completely interrupted (Fedorov, 1968, 1971). These studies, however, did not provide information on the fitness of these fish. In another study on the deepwater species Orange roughy *Hoplostethus atlanticus* Collett total atresia was seen in some large specimen with fully vitellogenic oocytes (Bell *et al.*, 1992). The authors suggested that scarcity of food, combined with the high energy cost of spawning migration triggered this reabsorption of the oocytes. Even though there was no sign of interrupted maturation in the present study atresia was still relatively high (10–20%) among some fish with higher I_G. It was expected that there was some correlation between atresia and K but most likely these K values were too approximate to discover differences at the appropriate scale. A more direct measure of the available energy resources in these fish such as liver mass or lipid content in the tissue would probably be a better measure.

THE POPULATION COMPLEX IN WEST GREENLAND

Even though a new insight has been provided into the maturation process for the female fish in west Greenland further studies are needed in order to confirm the findings and to have more extensive sampling both in time and space. The present and previous studies indicate that Davis Strait is an important spawning ground for the west Greenland and east Canada stock. Questions then arise about what is the situation regarding Greenland halibut in Baffin Bay and the inshore areas of west Greenland. Do they mature for spawning and if so what are their spawning grounds? There seems to be three possibilities: 1) they conduct a spawning migration to Davis Strait and spawn there, 2) they spawn locally and 3) they never enter a spawning phase.

The first possibility: 'Greenland halibut conduct a spawning migration to Davis Strait and spawn there'. If Greenland halibut in Baffin Bay and the inshore fjords migrate to the Davis Strait to spawn the hypothesis for multi-year vitellogenic cycle suggests that only a fraction of the fish would mature and migrate each year. No vast spawning migration is thus to be expected. Earlier studies have rejected the presence of a spawning migration from the inshore fjords to Davis Strait (Riget & Boje, 1989; Jørgensen & Boje, 1994) based on data that showed no fish tagged in the inshore area has ever been recaptured in Davis Strait (Riget & Boje, 1989; Boje, 2002). Is it to be expected, however, that these fish could be recaptured in Davis Strait given the tagging programme, the hypothesis of a prolonged adolescence and fishing pattern in Davis Strait? Fish that were tagged in the inshore area were between 31 and 100 cm L_T but with the majority of the fish between 60 and 75 cm L_T (Boje, 2002). The survival rate from tagging was estimated to be *c*. 90% (Simonsen & Treble, 2003). The majority of the tagged fish were recaptured within the first 2 years (Boje, 2002). Based on the present study Greenland halibut could be in a prolonged adolescence phase until they reach a size of *c*. 80 cm. Given the slow growth rate (Bowering & Nedreaas, 2001) most of the tagged fish that could be expected to be recaptured would not be past the prolonged adolescence phase. Furthermore, if a tagged fish did perform a spawning migration to Davis Strait it would have a low chance of being caught as Davis Strait was dominated by a trawl fishery which is known to be highly size selective with a L_{T50} at 42 cm (Huse *et al.*,

1999). Throughout the 1990s only 2–7% (calculated by data presented in Jørgensen, 2002b) of the fish landed each year were ≥80 cm [minimum estimated age for a 13 year old fish in Disko Bay (Simonsen & Boje, 2001)]. In addition to this, fishing effort in Davis Strait has been low (O.A. Jørgensen, pers. comm.) to none in the period late autumn to spring in which spawning was believed to take place. From this it is concluded that large fish undergoing a spawning migration to Davis Strait would not be expected to be caught.

The second possibility 'Greenland halibut spawn locally'. Female Greenland halibut in ripe condition have 'as mentioned earlier' been observed in the inshore fjords so local spawning is occurring but in these studies they have reached a proportion that indicated spawning on a larger scale (Jensen, 1935; Smidt, 1969; Riget & Boje, 1989). Based on the hypothesis of prolonged adolescence and multi-yearly vitellogenic cycle, large scale spawning aggregations would not be expected. In the north-west Atlantic Junquera et al. (2003) estimated that 25% of the females would spawn annually. The present study as well as earlier observations suggests that the proportion of spawning female fish in the inshore fjords would be even lower than this.

The third possibility 'Greenland halibut never enter a spawning phase'. At present the interpretation of the situation in the inshore fjords is that the majority of the Greenland halibut in the fjords remain there throughout their life and never participate in spawning (Riget & Boje, 1989; Jørgensen & Boje, 1994). If the hypothesis on prolonged adolescence is accepted it could be that Greenland halibut never reach maturation but remain in puberty throughout their life. Such a life-history strategy only seems rational if it has a trade-off. The development of the ovaries to spawn requires an energy allocation in the individual fish. The relative energy investment required has been observed to be particularly high among some fishes living in high latitudes, especially Arctic cod Boreogadus saida (Lepechin) (Hop et al., 1995). If Greenland halibut have a prolonged adolescence it suggests to that the energy available for allocation to ovary development and maturation is limited. The trade-off for not spending energy in development of the ovaries would then simply be survival at the individual level with an expectation that at some point they would have an energy surplus that could trigger the sexual maturation process. Evidence of such a strategy is seen in the orange roughy a deepwater species. Up to 45% of the adult orange roughy never migrate to the spawning area and do not initiated the maturation cycle allegedly because they have no energy surplus (Bell et al., 1992). This could suggest that energy surplus is never reached or only reached for a few of the Greenland halibut in the inshore fjords and therefore a majority of the fish never enter a spawning phase.

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Paper II

Distribution and growth of Greenland halibut (*Reinhardtius hippoglossoides*) and sandeel (*Ammodytes* sp.) larvae in West Greenland waters

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Abstract

Greenland halibut (*Reinhardtius hippoglossoides*) and sandeel (*Ammodytes* sp.) larvae were sampled along transects crossing the West Greenland shelf in May (2000), June (1999) and July (2000). In May, Greenland halibut was found offshore in Davis Strait, while sandeel was closely associated to the central parts of the banks. In June both species occurred together mostly on the banks or slopes wherefter from June to July there was a gradual shift in their distribution as Gr. halibut in particular moved to the deeper parts of the slope near the shelf break at stations with weak stratification. Otolith microstructure analysis on larvae from July showed that growth within the two species responded differently to the environmental conditions. Gr. halibut had enhanced growth while sandeel had poorer growth at high levels of frontal activity. Furthermore, sandeel growth increased with increasing prey biomass. This suggested that sandeel growth was suboptimal and limited by food availability. Cross shelf variation in growth showed that enhanced growth was observed at some

stations where G. halibut was most abundant, however in general high growth did not appear to be a prerequisite for a high larval abundance.

 Keywords: fishlarvae; distribution; fronts; shelf break; growth; otolith analysis;

Introduction

Growth and survival of fish larvae are closely linked. A prerequisite for growth is food, which for fish larvae is primarily obtained from predation on copepods (Pepin & Penney 2000, Simonsen et al. 2006). Spatial differences in availability of copepod prey in the ocean can thus result in spatial differentiated larval growth and survival (Munk 1993, Folkvord et al. 1997, Beaugrand et al. 2003). Enhanced larval growth is often seen in hydrographical fronts and upwelling areas (Kiørboe et al. 1988, Bakun 2006, Munk 2007). This coupling between larval growth and hydrographical processes is complex but it is probably driven by the physical processes in fronts and upwelling areas that 1) bring nutrients to the photic zone thereby triggering an enhanced biological production (Heilmann et al. 1994); 2) accumulate organic matter due to retention mechanisms (Franks 1992); and 3) introduce turbulence which increases the encounter rate between fish larvae and their prey (MacKenzie 2000). The physical and the derived biological processes in the ocean are therefore of crucial importance for survival of fish larvae.

Compared to temperate waters, relatively little is known in the Arctic on the coupling between hydrographical processes and recruitment success of fish larvae. Given the low energetic cost of living at cold temperatures recruitment processes for fish in arctic waters may differ from fish in temperate waters. In recent years a comprehensive research program on pelagic ecology in West Greenland waters have investigated the distribution and ecology of plankton in general and fish and shrimp larvae in particular (see Munk 2002, Pedersen & Storm 2002, Pedersen et al. 2002, Poulsen & Reuss 2002, Reuss & Poulsen 2002, Storm & Pedersen 2003, Ribergaard et al. 2004, Pedersen et al. 2005, Simonsen et al. 2006). The present study analyses

larval distribution and growth of two key fish species, the Greenland halibut (*Reinhardtius hippoglossoides*, Walbum) (hereafter referred to as Gr. halibut) and sandeel (*Ammodytes* sp.)[1]. The Gr. halibut was selected because this stock is one of the largest ground fish stocks in West Greenland and is the target species of the second most important fishery in Greenland (Anonymous 2003, Storr-Paulsen & Jørgensen 2003). The sandeel was selected because it is the most abundant genus in the ichtyoplankton (Pedersen & Smidt 2000, Munk et al. 2003), and an important prey item for fish, seabirds and marine mammals (Hansen 1949, Larsen & Kapel 1982, Munk 2002, Boertmann et al. 2004) and thus a key species in the ecosystem.

The objectives of this paper are to: 1) Analyse distributions of Gr. halibut and sandeel larvae across the West Greenland shelf; 2) Examine G. halibut and sandeel larval growth and the possible coupling to cross shelf variability in biological and hydrographical environmental conditions; and 3) Identify areas of special importance for G. halibut and sandeel larval growth and survival.

Materials and methods

Plankton and larval fish sampling

Plankton samples were collected during three cruises with RV Adolf Jensen conducted in June 1999, May 2000 and July 2000 off West Greenland between 63.30 to 66.30° N (Fig. 1). Detailed descriptions of sampling gear and methods used during the three cruises are given in other literature (Munk 2002, Pedersen & Storm 2002, Pedersen et al. 2002, Poulsen & Reuss 2002, Reuss & Poulsen 2002, Storm & Pedersen 2003, Pedersen et al. 2005, Simonsen et al. 2006). The cruises took place 21

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[1] According to Muus B (1981) In: Salomonsen (ed) Grønland Natur, p 84-85 (in danish) *Ammodytes dubius,* Reinhardt and *A. marinus*, Raitt both occur in Greenland waters, the former being the most common especially offshore and the latter generally occurring closer to the coast. In the present study we were unable to distinguish between the two species and use the genus *Ammodytes* sp

June to 1 July 1999 (hereafter referred to as the "June cruise"), 8 to 21 May 2000 ("May cruise") and 11 to 23 July 2000 ("July cruise"). Sampling took place along transects using a 4, 8 and 15 km resolution between stations. Highest resolution was used near the shelf break. In addition to the transect sampling the May cruise visited 7 stations in the fjords near Nuuk and 2 stations in Davis Strait (Fig. 1).

Distributions of Gr. halibut and sandeel larvae were investigated from catches in oblique hauls with a ring net at ship cruise speed of 3 knots. Oblique hauls were carried out from the surface to approximately 200 m depth or 5 m above seafloor. Double-oblique hauls from the surface to about 35 m depth were carried out on most, but not all stations due to time constraints. In May and July vertical larval distributions were investigated at selected stations (Fig. 1). Vertical tows were undertaken by lowering the net to the desired depth where after the vessel commenced sailing at a speed of 1.5 m sec^{-1} while the holding wire was eased off until wire length was 2.4 times the midpoint of the desired depth which kept the net within the desired depth interval. Tow distance was set to 4 times the target depth in order to reduce the "catch-noise" from retrieval of the net. At net retrieval vessel speed was reduced to under 1 m sec^{-1}. On the May cruise, samples were taken at depth intervals of; 100-200m; 200-400m; 400-800m; 800-1000m. On the July cruise samples were taken at depth intervals of; 13-25m; 25-40m; 40-55m; 55-100m. Gr. halibut and sandeel larvae were sorted immediately after net retrieval and either frozen or preserved in 96% ethanol. In the laboratory each larvae was given a number for individual identification and measured (standard length, SL). SL was corrected for shrinkage according to Simonsen et al. (2006). Larvae horizontal density was calculated as number m^{-2} ((number of fish larvae)*(filtrated water volume)$^{-1}$* (gear depth)). Larvae concentrations at vertical depth intervals were calculated as number m^{-3} ((number of fish larvae)*(filtrated water volume)$^{-1}$).

Larval age and growth

A representative number (~20) of Gr. halibut and sandeel larvae were selected per station. Sagittal otoliths (hereafter referred to as "otoliths") were extracted and

mounted convex side upwards on an object slide in thermoplastic resin (Buehler®). To elucidate microstructures otoliths were wet grinded on successively finer grades of lapping film (grade 5 to 0.5 µm) rotating 100-200 rounds per minute. Microstructures were examined in a light microscope (LM) mounted with a video camera. The video image was digitalized and analyzed using the software package Image Pro®. Otolith area, perimeter, minimum/maximum radii from core to hatch check (HC) and first feeding check (FFC)[2] (only Gr. halibut) was measured on both the left and right otolith (Fig. 2). All measurements were averaged per individual fish that fulfilled the following criteria; coefficient of variation (CV) between left and right otolith was less than 20% for otolith area and less than 10% for all other measurements. If these criteria were not met, the individual was excluded from further analysis. The number of increments was counted and increment widths measured along the axis where they appeared most distinct. Increment widths were measured semi-automatic using the tool CALIPER in Image Pro. Increment widths were standardized to the maximum otolith radius. Data on increment width was randomly chosen from one of the sagittae otoliths. In most otoliths there were sectors along the selected axis where increments could not be identified. In these sectors the number of increments was interpolated by linear regression calculated from the surrounding 10 to 20 increments using a lower threshold on 0.6 µm per increment. Larval age was estimated by the number of increments from the first complete increment formation at the otolith edge to the FFC mark (Gr. halibut otoliths) or to the egg HC mark (sandeel otoliths) (Fig. 2). Increments were assumed to be formed daily. Larval age was estimated by calculating the average number of increments from the two sagittae for each individual larvae.

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[2] To check marks were visible in Gr. halibut otoliths. In order to distinguish between HC and FFC a number aquaculture Atlantic halibut (*Hippoglossus hippoglossus* L.) larvae otoliths were examined from larvae in different stages from yolk- to feeding larvae. The first check in Gr. halibut otoliths was positioned in the same distance from the core as the validated HC in Atlantic halibut.

It was difficult to interpret otolith microstructures from both Gr. halibut and sandeel from the May and June cruises. Narrow zones (0.5 to 1 μm) were visible at the outer edge of the otoliths but it was difficult or impossible to identify increments closer to the hatch mark. Thus a selection of otoliths from May, June and July were examined in a scanning electron microscope (SEM) following the procedures described in Fox et al. (2003). SEM analysis of increments showed agreement between zone formations interpreted in LM and SEM along the outer part of the axis analysed, but not at the inner section close to the hatch mark (10 to 20 μm from the hatch mark). The width of increments not discernable in LM, but visible in SEM, were measured to less than 1 μm. Because increment width in otoliths from May and June were generally 1 μm or less, age analysis using LM in larvae from these sampling periods was considered unreliable and otolith microstructure analysis was only carried out on larvae from the July cruise.

Growth was examined by analysing otoliths and not somatic growth thus statistical problems associated with back-calculation to larval length were avoided (Simpson 1981, Weisberg 1986, Francis 1990). This was possible because there was a linear relationship between otolith radius and larval standard length (SL) for both Gr. halibut (Gr. halibut SL=3.25 x radius – 22.34, N=144, r^2=0.80, p>0.0001 and sandeel (sandeel SL=3.32 x radius – 17.06, N=656, r^2=0.87, p>0.0001) The standardized increment widths were used to define individual otolith radius. The change in radii over time was used to determine otolith growth. This was done in 5 day periods to obtain a "long term" growth history, G_{long}, going back 30 days, and on a daily basis to obtain a "short term" growth history, G_{short}, going back 10 days.

Larvae distributions and growth of Gr. halibut and sandeel

Differences in spatial distribution and growth were assessed against the biological and physical environment the larvae were living in at the time of capture. Initial analysis on G_{long} showed similar patterns in all larvae caught at the same station in the last 10-15 days (see results). This was interpreted as larvae sharing or coexisting in the same environment during this period. Consequently the biological and physical

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environment measured at each station was assumed to be representative within at least a 10 day period. Based on these assumptions the relationships between G_{short} and the biological and physical parameters between stations were analysed. The following geographical classifications of the sampling stations and biological/physical factors used in the analyses are as follows (UPPERCASE):

AREA defines the location of the station as; FJORD: all stations in the fjord; COAST: all stations close to the coast and with depths less than 100 m; SLOPE: all stations east or west of the Banks on the bank slope at depths between 100 to 300 m; BANK: all stations on the Bank itself, depth below 100 m; OFFSHORE: all stations West of the Banks with a depth of more than 300 m.

PREY abundance by size of the copepod that was available as prey for Gr. halibut and sandeel was estimated per station as available prey biomass (APB) in mg C m^{-2} using methods outlined in Simonsen et al. (2006). Copepods constituted more than 88% of the stomach contents by weight on all 3 cruises (Simonsen et al. 2006).

TEMPERATURE and SALINITY were obtained by CTD sampling following the procedures outlined in Pedersen et al. (2002). Mean temperature and salinity was calculated per station in the depth intervals 4 to 40 m deep (or station depth if shallower).

STABILITY of the water column to 40 m depth was found by the potential energy anomaly Φ (PEA) in J m^{-3} which is indicative of the energy input required to cause complete vertical mixing of the water column and is therefore directly proportional to the strength of stratification (Simpson 1981):

(equation 1) $PEA = \dfrac{1}{h} \int_{-h}^{0} (\overline{\rho} - \rho)\, gz \; dz; \quad \overline{\rho} = \dfrac{1}{h} \int_{-h}^{0} \rho\, dz$

where h is water depth, ρ is water density, g is gravity, z is depth and dz is width of depth stratum.

FRONT activity was identified by the relative change in PEA over distance, ΔPEA. Frontal activity on a station was expressed as the ΔPEA on the two surrounding transect stations:

(equation 2) $\Delta PEA_b = \left| \dfrac{\Phi a - \Phi c}{D_{AC}} \right|$

where D_{ac} is distance between station A and C in m. For transect boundary stations the distance to the nearest station was used instead.

Statistical analysis

Larval abundance and its dependence of geographical and environmental parameters AREA, APB, t S, PEA and ΔPEA were analysed by non-parametric Kruskal-Wallis tests, where AREA is the classification of stations to FJORD, BANK, OFFSHORE, SLOPE; APB is the available prey biomass in 0.25 intervals of $\log_{10}$ transformed dry weight in mg C m^{-2}; t is 0.5 intervals of mean temperature in C°; s is 0.25 intervals of mean salinity; PEA is 0.2 intervals of $\log_{10}$ transformed potential energy anomaly in J m^{-3}; ΔPEA is 0.5 intervals of the $\log_{10}$ change in PEA over distance in J m^{-3} m^{-1}.

Due to their longitudinal nature individual larval growth trajectories were analysed by a multivariate repeated-measurement analysis (RMA) following the guidelines in Singer & Willett (2003) and Anon. (2005) using the procedure PROC MIXED in SAS/STAT software. Initial analyses showed that a compound symmetry for the variance-covariance structure fitted data best.

G_{long} was analysed by the RMA linear model;

(equation 3) $S = G_{long}\ ST \times G_{long}\ SL$

where S is otolith radius; G_{long} is the repeated measurements of $\log_{10}$ transformed otolith radius in μm at 0, 5, 10.… to 30 days from capture; ST is station SL is standard larval length in mm.

G_{short} was analysed in RMA analyses with a stepwise reduction of the model:

(equation 4) $S = G_{short} \ (AREA \ APB \ t \ S \ PEA \ \Delta PEA) \ SL$

where S is otolith radius; G_{short} is the repeated measurements of $\log_{10}$ transformed otolith radius in μm at 0, 1, 2.… to 10 days prior to capture; the other dependent variables follow the nomenclature defined earlier. APB, PEA and ΔPEA were $\log_{10}$ transformed.

Cross shelf variability in G_{short} was estimated by equation 4 and evaluated against observed standardized G_{short} (lsmeans in SAS/STAT).

All statistical analyses were performed in the SAS/STAT software Version 9 of the SAS System for PC, SAS Institute Inc. Copyright © 2002-2003 SAS Institute Inc. (SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA).

Results

Larvae development

All Gr. halibut larvae caught during the cruises were well developed with a functional mouth and digestive system. However, small remains of yolk sac was visible on some larvae on the May cruise. Larvae length progressively increased in the three periods studied (Fig. 3). In May Gr. halibut mean SL was 18.0 mm, in June 24.1 mm and in July 31.5 mm. All sandeel caught were also well developed and SL progressively increased from a mean SL of 9.6 mm in May to 17.8 mm in June and 26.1 mm in July (Fig. 3). The range in larval sizes on the June and July cruises were relatively large for sandeel compared to Gr. halibut (Fig. 3). If it is assumed that the cruises were

conducted in sequence and ignore that the length-at-age data violate the assumption for simple linear regression (Francis 1990), the retrospective-growth for Gr. halibut was around 0.21 mm day^{-1} and for sandeel around 0.26 mm day^{-1}.

Larval distribution and biological / abiotic factors

The concentrations of sandeel larvae were generally 10 to 100 higher than for Gr. halibut. The highest larval concentration for both species was found in May (Fig. 4) where the abundance of Gr. halibut was up to 0.8 individuals per m^2 and the abundance of sandeel was up to 36 individuals per m^2. The abundance of sandeel was generally lowest in the June survey while Gr. halibut abundance steadily declined from surveys in May, June and July. Correlation analysis between larval concentration of the two species at different stations showed no relationship in May (r=-0.27, p>0.17); a moderate and significant correlation in June (r=0.53, p<0.001) and only a weak or no correlation in July which was only significant when excluding a station with very high sandeel but low Gr. halibut abundances (r=0.36, p<0.03). Thus there was there was no correlation (r=0.21, p>0.22) when all data for July was included.

The spatial distribution pattern of the two species was analyzed against their biological and physical environment for each survey:

In May the analysis of larval distribution patterns to <u>AREA</u> showed notable differences between the different area categories and species (for Gr. halibut p<0.002; sandeel p<0.03). Gr. halibut was almost exclusively distributed in Davis Strait and had the highest scores for the area OFFSHORE while sandeel was closely associated to the central parts of Fylla and Sukkertop Bank with the highest scores for the area BANK (Fig. 4). Gr. halibut distribution also showed a clear affiliation to the class <u>PREY</u> with the highest scores at the greatest prey concentration $\geq$ 2.25 mg C m^{-2} (p<0.024), and to the class <u>SALINITY</u> with the highest scores for water masses with a salinity $\geq$ 33.75 (p<0.006). High levels of the classes <u>PREY</u> and <u>SALINITY</u> were found in the offshore area in Davis Strait.

In June the larval distribution analysis showed a significant difference between AREA for both species (for Gr. halibut p<0.01; sandeel <0.04). Gr. halibut had highest scores for the areas BANK and SLOPE while sandeel had the highest scores in BANK. A closer examination of their distribution showed that Gr. halibut occurred on most of the transect stations on the bank area, but not on the ones furthest offshore or coastal, whereas sandeel were much more associated to stations on the central bank area (Fig. 4). Furthermore, the distribution for Gr. halibut was significant for the class TEMPERATURE with high scores for the 2°C and > 2.5°C intervals of warm water (p<0.011), while sandeel showed a significance association for both the class SALINITY (p<0.05) and the class FRONT activity expressed by ΔPEA (p<0.021). The highest scores were however seen at intermediate values of both salinity and ΔPEA which made interpretation difficult.

In July the analysis of larval distribution patterns showed that only sandeel was distributed differently in the class AREA and had the highest scores for the SLOPE (p<0.01). The same trend was seen for Gr. halibut however, this was not significant (p>0.15). Distribution patterns showed that both species were almost absent from the southern transect 1, but frequently observed at the two northern transects 4 and 5 (Fig. 4). For both species the class SALINITY was significant and the highest scores were observed at stations with the highest salinity (p<0.0001). The distribution of Gr. halibut was further effected by the class STABILITY where the highest scores were seen in less stratified water masses (p<0.0027). The same tendency was also observed for sandeel although this was not significant (p<0.09).

Larval vertical distribution

The two oblique hauls per station down to 35m (shallow) and 200m (deep) were used to compare the relative larvae concentration per volume. In May, larval concentration was highest in the shallow haul for Gr. halibut (t-test, p<0.05) while for sandeel the number of hauls in their main distribution area (at the shallow part of the bank) was too few to support statistical analyse (four comparable hauls to shallow/deep). In

June, Gr. halibut and sandeel larval concentrations were highest in the shallow haul (t-test, p<0.001) while in July it was only evident for sandeel in July (t-test, p<0.04).

In the specific depth stratified hauls in May and July, larval concentrations varied considerably between tows in the same depth intervals and thus no significant difference between the depth strata was found (Kruskal-Wallis, p>0.20). However, in May in the offshore area targeting only Gr. halibut high concentrations were only observed in the 0-50m and 0-100m depth intervals (Fig. 5a). Very few Gr. halibut (5 specimens) were caught in the 400-800m depth interval while none were caught in the other depth intervals (100-200m; 200-400m or 800-1000m). These results strongly suggest that the main vertical distribution of Gr. halibut was in the upper part of the water column (<100m). In this area water masses were well mixed with a temperature around 0.2 °C and salinity at 33.7 (Fig. 5b). In comparison, the depth stratified sampling in July targeting both Gr. halibut and sandeel showed sandeel larvae had a more shallow distribution (mainly the 13-25m strata) compared to Gr. halibut (mainly the 25-40m strata) (Fig. 6 a+b). Temperature and salinity profiles showed stratified water masses with a salinity below 33 and a temperature around 6°C in the surface. At 15m salinity increased sharply to above 33.6 while temperature decreased more gradually to 2 °C at 40m (Fig. 6c).

Larval growth

In general there was a good agreement between increment counts (IC) from the two sagittae on the same individual. The CV for IC was less or equal to 10% in 78% and 81% of the cases for Gr. halibut and sandeel, respectively. Larval length as a function of IC was found to be linear (Linear regression, p<0.0001). The 95% confidence interval on the slope was between 0.14 and 0.22 mm IC^{-1} for Gr. halibut and between 0.22 to 0.28 mm IC^{-1} for sandeel. This change in larval length per IC was similar to the overall daily growth rate of 0.21 mm day^{-1} for Gr. halibut and 0.26 mm day^{-1} for sandeel as described earlier.

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The analysis of G_{long} found large differences in the growth pattern between stations (RMA, p<0.0001). The relative change in standardized G_{long} per station is illustrated by the three stations having the highest, and the three stations having the lowest growth rate in the last period prior to catch in Fig. 7. Growth rate within the high growth and low growth groups was similar in the time intervals 0-5 days and 5-10 days, except for a single station. Hereafter the difference between stations became less evident either as a result of a more homogenous growth at the different stations or because of the higher variation in growth among larvae at the same station. An analysis of the standard error to the mean otolith radius showed that it was most likely due to a higher variation in growth as the standard error increased with time (Linear regression, p<0.002).

The G_{short} growth trajectory analysis in the RMA showed that front activity (DPEA) significantly affected Gr. halibut growth (Table 2). For sandeel the level of DPEA, mean salinity (S) and available prey biomass (APB) influenced growth trajectories significantly (Table 2). The significant effects on otolith growth trajectories were used in the model (equation 4) to evaluate their effect on growth in a 10 day period. The influence on growth from the observed range of DPEA, S and APB was evaluated separately by holding the other variables constant. With change in DPEA opposite growth responses were found for Gr. halibut and sandeel such that an increase in DPEA resulted in an increase in growth for Gr. halibut but a decrease in growth for sandeel and vice-versa. Growth in sandeel was also significantly associated with trends in salinity (S) and available prey biomass (APB) as the highest larval growth was estimated at the lowest S and the highest levels of APB (Fig. 8, Table 2).

Cross shelf variation in the modelled G_{short} indicated that Gr. halibut had lowest growth at the shallow bank and highest offshore or towards the coast in July (Fig. 9a). The modelled G_{short} fitted the observed G_{short} well at transect 5 but performed poorly at transect 4 where large discrepancies were observed at the stations at the bank slope area. Here the observed G_{short} was high but modelled low. The observed G_{short} was

significantly higher (no overlap in 95% confidence intervals) at stations at the bank slope compared to all other stations. For sandeel the modelled G_{short} showed greatest growth around the shelf break area and toward the coast (Fig. 9b). As for Gr. halibut there was good agreement between estimated and observed G_{short} at transect 5 but also inconsistencies in the same areas of transect 4. Modelled growth at transect 1 indicated very high cross shelf variability for both species, but as very few larvae were present there was no observed G_{short} to confirm the results. There seemed to be no strong relationship with either observed or modelled G_{short} and larval abundance (Fig. 9b). Enhanced growth was observed at some of the stations with a high abundance of G. halibut, but high growth did not seem to be prerequisite for high larval abundance.

Discussion

Larvae distribution

The May distributions of Gr. halibut in Davis Strait and sandeel at the BANK were clearly distinct. The OFFSHORE distribution of Gr. halibut in Davis Strait was in accordance with earlier studies by Jensen (1935) and Smidt (1969). Jensen describes the larvae caught in Davis Strait in May as "quite tiny larvae, 10-18 mm long, with many still having the yolk-sac attached". He hypothesized that the offshore distribution pattern was connected to spawning in the deeper southern part of Davis Strait. Later studies have confirmed that the Davis Strait is the most important spawning site for Greenland halibut in West Greenland waters (Gundersen et al. 2004, Simonsen & Gundersen 2005). Jensen (1935) also studied Gr. halibut larval vertical depth distribution during his May survey and concluded that they were located between 600 and 1000 m of depth. Jensen hypothesised that the yolk sac larvae are bathypelagic and gradually rise towards the surface as they utilize the yolk. Even though the same areas in Davis Strait as Jensen were examined, only a few specimens were found at the 400-800 depth strata with the highest concentrations being in the surface layers (<100 m). Jensen's hypothesis, however, cannot be

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rejected as larvae caught in the present study were actively feeding (Simonsen et al. 2006) indicating that they was in a more progressed ontogenetic stage than the larvae Jensen reported and would therefore, according to Jensens hypothesis, also be distributed in shallower depths. Furthermore, all the Gr. halibut larvae examined in the oblique hauls had a distinct mark at the outer edge of the otolith (Fig. 2). In larval otoliths from May this mark was positioned only 0.7 to 2.7 µm from the otolith edge and thus were formed recently. Check marks in otoliths are known to form when larvae hatch, begin first feeding or are exposed to temperature changes (Campana & Jones 1992, Geffen 1995, Folkvord et al. 1997). The mark was therefore interpreted as a first feeding mark or a temperature induced mark from when the larvae goes from bathypelagic water masses with low prey concentrations and 2-4°C warm water (>100 m) to high prey concentrations and ~0.2 °C cold water near the surface (0-100 m) (Simonsen et al. 2006). The available information thus supports the theory that larvae do not enter surface layers before yolk is utilized and are forced to seek their own food. The first feeding period is by many believed to be a critical period in larval ecology as larvae have to find food within a relatively short time window in order to avoid starvation (Hjort 1914, Cushing 1990). In a study by Simonsen et al (2006) it was shown that offshore Davis Strait had the highest prey concentrations and that Gr. halibut larvae in this area also had the highest stomach/gut fullness. The spatial match between distribution of Gr. halibut larvae, prey and higher ingestions rates in Davis Strait thus seems central in understanding recruitment dynamics for this species. Drift models of Gr. halibut egg and yolk-sac larvae have shown that spawning at three sites in Davis Strait along the 63°30 N parallel all resulted in a larval dispersal in offshore Davis Strait (Stenberg et al. in prep). Physical oceanographic features restricted dispersal of eggs and early stage larvae to this food rich area. Vagrant larvae were dispersed to less food rich areas which likely resulted in higher mortality rates. Consequently, match in time and space of the emergence of first feeding Gr. halibut may have the potential to affect recruitment success and potentially control year class strength.

The distribution of sandeel on the shallow parts of Fylla and Sukkertop Banks in May has not been described before from Greenland waters. However, from other areas it has been shown that larvae in early stages in spring are mainly distributed in shallower areas on banks and in bight areas (Wright & Bailey 1996, Munk et al. 2002). The spawning area for sandeel in Greenland waters is unknown, but from other areas it has been described that sandeel (*A. marinus* and *A. hepaxpterus*) spawns on coarse sand sediment near shore or on offshore shallow banks at depths down to 100 m (Wright & Bailey 1996, Proctor et al. 1998, Robards et al. 1999, Wright et al. 2000). Consequently, it is likely that sandeel in West Greenland spawns on the shallow banks off the coast. Sandeel hatch size reported from other areas is between 4.5 to 5.5 mm (Wright & Bailey 1996, Robards et al. 1999). With an average larval size of 9.6 mm in the May survey, and an assumed growth rate of 0.23 mm day^{-1}, larvae were estimated to have hatched around 20 days earlier. Deployed drift buoys on the May survey showed that hydrographical mechanisms on Sukkertop Bank retained the drifters here for several weeks (Pedersen et al. 2002). The observed larval affiliation to the parameter BANK could therefore be explained by retention of eggs and larvae in the bank area. Furthermore, a study on the sandeels feeding ecology showed that their stomach/gut fullness was significantly higher in May on the shallow part of the banks (Simonsen et al. 2006). Consequently, as for Gr. halibut, the early sandeel larval distribution seems to be further explained by enhanced feeding opportunity.

The June and July distribution of Gr. halibut and sandeel showed that they were mostly abundant on BANK and SLOPE, however more specific spatial patterns indicated adaptation to different cross shelf habitats by both species. From June to July there was a gradual shift in distribution of Gr. halibut and sandeel larvae from occurring together mostly on BANK and SLOPE to a greater tendency for sandeel to be distributed in the more shallow part of the slope in comparison to Gr. halibut that were more abundant on the deeper parts of the slope near the shelf break. This was confirmed by the analysis of vertical distribution were Gr. halibut were distributed

deeper than sandeel in July. These cross shelf distribution patterns corresponded to a previous study of the West Greenland shelf area (Munk et al. 2003). Furthermore, Munk et al (2003) found that sandeel abundance was particularly high in areas with frontal activity between the Polar and West Greenland Current. Even though front zones between cold Polar water and mixed shelf water over the banks were observed in the June and July surveys, they were much less pronounced (Pedersen et al. 2002). The lack of clear and well-defined frontal zones in this study could explain why no significant effect of front activity was found for either Gr. halibut or sandeel assemblages. The greater tendency for both Gr. halibut in June and sandeel in July to be in these mixed water masses and the higher occurrence of Gr. halibut in weak stratified water masses in July did, however, indicate that the hydrodynamic situation still played an important role in their distribution patterns. Mixing between water masses took place particularly on the shelf slope due to the along-shelf flowing currents, which might have been strengthened by upwelling which model simulations predicted to occur more frequently in these areas (Pedersen et al. 2005). Pedersen and Rice (2002) analysed a time series of plankton and hydrographic samples off West Greenland from 1950 to 1984 and also found that the occurrence of fish larvae was related to both plankton and copepod abundance as well as the hydrographic characteristics salinity and temperature. However, they found that Gr. halibut abundances were higher in locations with stratified water masses whereas sandeel abundances, as the present study, were highest in weak stratified water masses. The reason for this discrepancy could be the use of different stratification indices. In this study the Simpson stratification index was used, which is based on the energy input required to cause complete vertical mixing of the water column, whereas Pedersen and Rice used a simple temperature difference at two different depths. Even though a reanalysis of the data found that the relationship between the two types of indices was statistically significant ($p<0.001$), their R square was only 0.59. Using the Pedersen and Rice stratification index an effect was only found for sandeel, which occurred more frequently at stations with weak stratification ($p<0.05$). The relationship between Gr. halibut and sandeel occurrence and their prey was not straightforward.

Even though a study on the feeding ecology of both Gr. halibut and sandeel larvae showed that Gr. halibut and sandeel in June and July had higher gut fullness on the slope (Simonsen et al. 2006), there was no association between both fish larvae and the occurrence of their prey. Distribution of size relevant prey was also addressed in the study by Munk et al (2003), but they too found no clear relationship between copepod prey and fish larvae abundance. Munk et al (2003) suggested that one problem is the dilemma between sampling and scaling. Sampling methods in this study are intergrated on a larger scale than the scale of the patchy plankton distribution. Any important small-scale variations are therefore unclear. Furthermore, fish larval feeding is complex and is not only a simple question involving the occurrence of prey items. Superior feeding habitats are characterized by enhanced larvae - prey encounter rates as well as attack success which again is influenced by small scale hydrodynamics (Kiørboe & MacKenzie 1995, MacKenzie & Kiørboe 2000) and light (Blaxter 1966). The spatial distribution of Gr. halibut and sandeel larvae showed that the two species partly coexisted, especially in June, but also had preference for different cross shelf habitats. The weak hydrographical fronts made it difficult to evaluate their significance for larval distribution patterns, however Gr. halibut in particular showed preference for stratified water masses. In general, there was no direct coupling of larval occurrence and their prey, but feeding conditions were enhanced on the slope

Larvae growth

The different response in G_{short} to the biotic and abiotic factors confirmed that the two species was adapted to different cross shelf environments. In particular, their different and opposite response to frontogenesis was interpreted as a reaction to this. Within the range of the observed front activity (0-160 J $m^{-3}m^{-1}$) there was a difference in growth of approximately +10% for Gr. halibut and -5% for sandeel. In studies of frontal systems in the North Sea fish larvae had growth rate differences in and outside fronts of up to 20-40 % (percentage calculations from growth rate in mm day^{-1}) (Munk 1991, Munk & Nielsen 1994). However, frontal residence may not always

result in enhanced larval growth as it is not the fronts themselves that influence larval growth, but rather the environments they provide for the fish larvae. The biotic environment is often characterised by enhanced primary and secondary production (Kiørboe et al. 1988, Heilmann et al. 1994), and abiotic retention mechanisms which may also help accumulate plankton in these areas (Franks 1992, Lochmann et al. 1997). Turbulence in these areas also enhance the contact rate between larvae and their prey (MacKenzie 2000). According to the different spatial distribution of larval gadoid species in relation to frontal structures it is assumed that they have a preference for different levels of these biotic and abiotic factors (Munk et al. 1999). Similarly, these same mechanisms may explain why Gr. halibut and sandeel growth responded differently to the observed levels of frontal activity.

The positive effect of prey biomass and sandeel G_{short} only suggested that food resources were limited for sandeel but not for Gr. halibut as a growth response is only expected if larval growth was suboptimal and limited by food availability. Indirect evidence that prey resources were insufficient was seen in Gr. halibut and sandel's prey size preference (Simonsen et al. 2006). Sandeel in July preferred much larger prey items compared to Gr. halibut which was hypothesized to have evolved as a result of prey competition on a limited resource. Evidence for development of size specific prey preference under competing conditions has been seen among other fish larvae (Kane 1984) (Fortier & Harris 1989). It is, however, uncertain whether larval growth, particularly that of sandeel, was effected by food limitations due to intra- or inter specific prey competition. This could be further studied by including measurements on the total predation pressure and its impact on shared food resources.

The cross shelf variation in G_{short} showing the highest growth for Gr. halibut offshore and toward the coast and the highest growth for sandeel at the shelf break and toward the coast was not unconditionally supported by the observed G_{short}. For example, the model did not expose the enhanced growth of Gr. halibut observed at the slope of transect 4. This emphasizes the difficulties in trying to model complex processes with larval growth in a highly dynamic environment. Regardless, the results from this

study do suggest a variety of cross shelf environments that can sustain enhanced growth for either Gr. halibut or sandeel or both species.

Whether enhanced growth resulted in higher larval survival is a key question. Enhanced growth was observed at some of the stations where Gr. halibut was most abundant. However enhanced growth did not seem to be a prerequisite for high larval abundance. In general and overall, there was no clear association between larval growth and larval abundances in this study. Such a relationship was, however, expected as mortality rates in fish larvae generally decrease with increasing growth and larvae size (Miller et al. 1988). The observed patchiness in the spatial distribution of larvae could have either been a result of hydrographic processes that retained and accumulated organisms (Franks 1992) or due to other biological processes other than growth controlled survival. Mortality of fish larvae from predation from larger individuals or other species have been shown to have a substantial impact on larval concentrations (Folkvord & Hunter 1986, Folkvord 1997, Houde 2002). Thus larvae mortality due to predation could also be important in controlling larval distribution patterns. During the July survey a study on the predatory impact by juvenile wolffish (*Anarhichas* spp) was also undertaken (Munk 1992). This study showed that juvenile wolfish selectively targeted the smaller sandeel larvae in the population and that predation mortality could be as high as 5% per day. Even though Gr. halibut larvae were also present in the plankton they were not eaten by the wolffish. Thus predation mortality was both species and size specific which enhance the complexity of analysing and interpreting spatial distribution patterns.

Conclusion

In May small first feeding Greenland halibut were almost exclusively found offshore in Davis Strait. Their distribution coincided with their prey resources while vagrant larvae were dispersed to less food rich areas, which likely resulted in higher mortality rates. Consequently, the emergence of first feeding Gr. halibut larvae matched in time

and space with their prey is believed to be crucial for survival success at this critical stage in their development. In May sandeel was closely associated to the central parts of the banks where feeding opportunity apparently was enhanced compared to other areas. Consequently, the early sandeel larval distribution also appears to be associated with a greater abundance of prey and enhanced feeding opportunities. In June Gr. halibut and sandeel coexisted, mostly on the banks or slopes, whereafter from June to July there was a gradual shift in their distribution as especially Gr. halibut in particular moved to the deeper parts of the slope near the shelf break area. The lack of clear and well-defined frontal zones made it difficult to evaluate the significance of hydrographical processes for larval distribution patterns. However Gr. halibut in particular did show a preference for stratified water masses.

Growth analysis of larvae from July showed that the growth of Gr. halibut and sandeel responded differently to their biological and hydrographic environmental conditions. This suggested that the two species were adapted to different cross shelf environments. Gr. halibut had better growth while sandeel had poorer growth at high levels of frontal activity. Furthermore, sandeel growth increased with increasing prey biomass suggesting that sandeel growth was suboptimal and limited by food availability. Cross shelf variation in growth showed that enhanced growth was observed at some stations where Gr. halibut was most abundant. However, overall, there was no clear association between larval growth and larval abundances. The observed patchiness in larval distribution could therefore also be a result of retention mechanisms and / or mortality due to predation.

Acknowledgements

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Tabels and figures

Table 1. Kruskal Wallis test statistics for the effect of the classes AREA, PREY (prey biomass in $\log_{10}$ scale intervals of mg C m^{-2}), TEMPERATURE (C°), SALINITY, PEA (Potential Energy Anomaly in $\log_{10}$ scale intervals of J m^{-3}) and ΔPEA (change in PEA per km in $\log_{10}$ scale intervals) on Greenland halibut and sandeel larval abundance (N m^{-2}). Intervals for the different class variables are shown by midpoint values. N is the number of observations, Score is the mean Wilcoxon Scores for larval abundance, P is the probability of no differences among classes.

Category			N	Greenland halibut Score	P	Sandeel Score	P
AREA	May	COAST	2	10.5	P< **0.002**	15.0	P< **0.034**
		SLOPE	7	12.0		16.0	
		BANK	5	10.5		20.8	
		OFFSHORE	6	21.8		9.0	
		FJORD	6	10.5		8.5	
	June	COAST	2	5.0	P< **0.011**	5.5	P< **0.043**
		SLOPE	8	14.1		9.0	
		BANK	7	15.0		17.0	
		OFFSHORE	5	5.0		10.2	
	July	COAST	3	6.3	P> 0.154	12.2	P< **0.012**
		SLOPE	17	19.1		21.4	
		BANK	6	16.3		12.8	
		OFFSHORE	6	14.3		8.4	
PREY	May	≤1.25	4	10.5	P< **0.024**	11.0	P> 0.199
		1.5	3	10.5		19.0	
		1.75	5	12.6		17.7	
		2	6	10.5		13.0	
		≥2.25	8	18.9		8.8	
	June	≤0.75	3	15.7	P> 0.249	17.0	P> 0.231
		1	3	15.7		7.7	
		1.25	5	13.0		12.3	
		1.5	5	8.8		7.6	
		≥1.75	6	8.3		13.8	
	July	≤1	5	17.1	P> 0.959	17.1	P> 0.412
		1.25	9	17.1		19.5	
		1.5	17	16.3		13.1	
		1.75	1	12.0		17.5	
TEMPERATURE	May	≤0	16	13.8	P> 0.721	13.2	P> 0.788
		≥0.5	10	13.0		14.0	
	June	≤1.5	6	5.0	P< **0.011**	9.3	P> 0.148
		2	11	14.3		10.5	
		≥2.5	5	13.2		16.4	
	July	≤3	5	12.0	P> 0.199	7.9	P> 0.126
		3.5	11	14.7		16.9	
		4	10	21.6		20.0	
		4.5	6	15.1		17.2	
SALINITY	May	≤33.25	8	10.5	P< **0.006**	11.4	P> 0.058
		33.5	12	12.3		17.2	
		≥33.75	6	19.8		9.0	
	June	≤33	5	13.2	P> 0.529	16.4	P< **0.050**
		33.25	4	7.5		14.0	
		33.5	8	11.6		6.8	
		33.75	5	12.8		12.2	
	July	≤33	8	7.1	P< **0.000**	9.0	P< **0.000**
		33.25	11	14.9		12.8	
		33.5	13	23.6		24.2	
PEA	May	≤0.6	6	13.1	P> 0.974	16.2	P> 0.164
		0.8	15	13.7		14.3	
		≥1	5	13.4		8.0	
	June	≤0.8	9	13.0	P> 0.083	11.4	P> 0.972
		1	8	13.3		11.9	
		≥1.2	5	6.0		11.0	
	July	0.8	6	18.0	P< **0.027**	22.8	P> 0.094
		1	7	21.1		20.6	
		1.2	7	21.6		15.6	
		1.4	5	6.5		10.1	
		1.6	7	12.6		12.4	
ΔPEA	May	≤0	7	14.1	P> 0.953	12.7	P> 0.053
		0.5	2	10.5		20.5	
		1	4	13.6		19.8	
		1.5	4	13.1		16.5	
		≥2	9	13.8		8.4	
	June	≤0	4	16.5	P> 0.348	17.3	P< **0.021**
		0.5	6	9.7		6.2	
		1	5	10.2		8.8	
		≥1.5	7	11.1		14.7	
	July	≤0.5	7	15.2	P> 0.393	19.6	P> 0.062
		1	7	21.9		23.1	
		1.5	6	14.5		12.0	
		≥2	12	15.1		13.1	

Table 2. Significant effects in RM ANOVA during short term growth trajectories in otolith radius for Greenland halibut and sandeel. Where ΔPEA is front activity (J m^{-3}/m^2), S is salinity, APB is available prey biomass (mg C m^{-2}) and SL is larval total length in mm.

Species	Effect	Estimate	Error	DF	t-value	P
Gr. halibut	ΔPEA	2.461E-07	0.007471	76	3.29	0.0015
	SL	0.009708	0.002431	76	3.99	0.0001
Sandeel	ΔPEA	-2.324E-07	0.009148	376	-2.54	0.0115
	S	-0.1359	0.02994	376	-4.54	<.0001
	APB	0.0521	0.02046	376	2.55	0.0113
	SL	0.02417	0.000893	376	27.07	<.0001
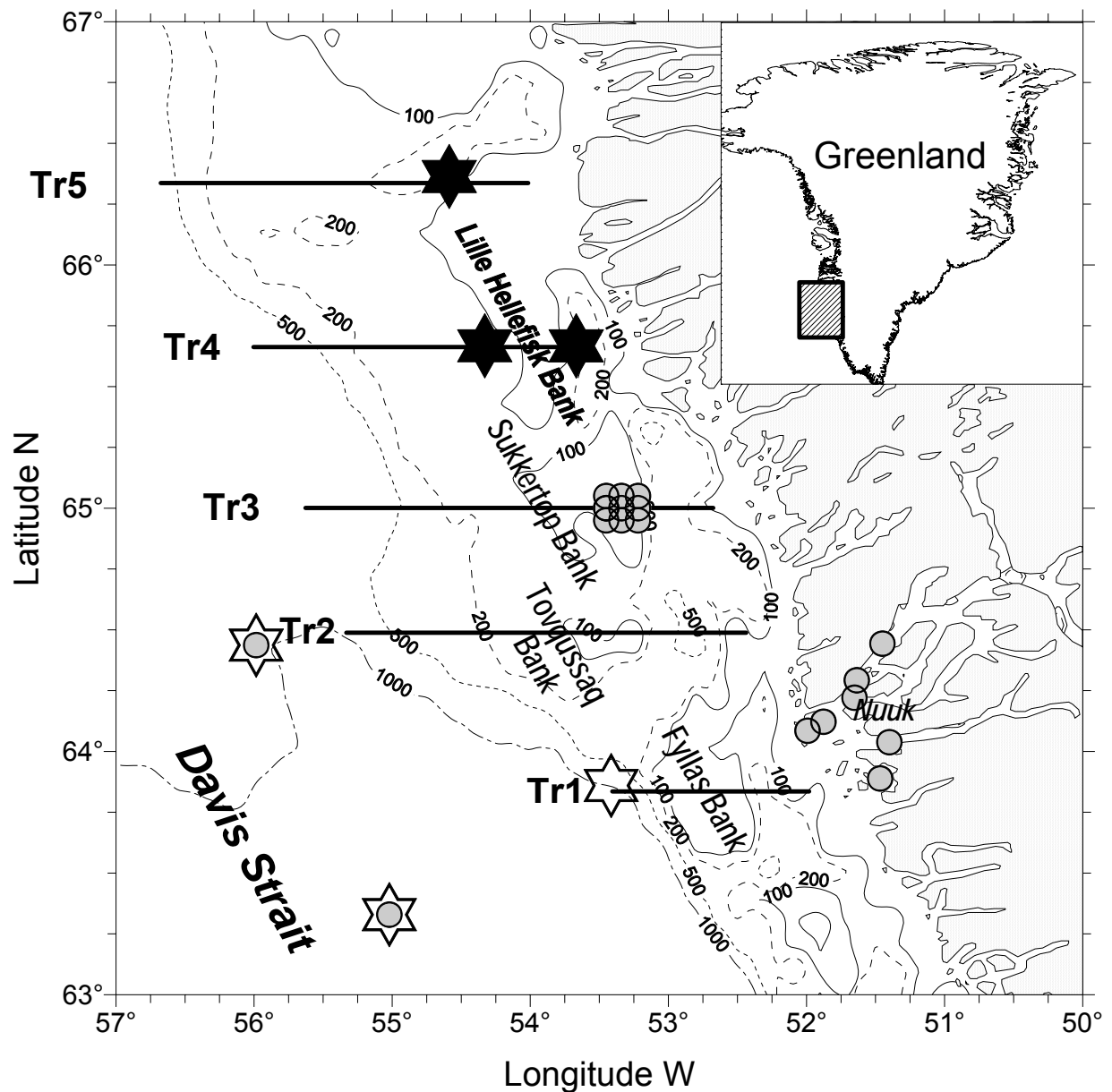
Fig. 1. Map of investigated area off West Greenland. Bathymetry is shown by contour lines for 100, 200, 500 and 1000 m depths. Stations in transect (Tr) 1 to 5 were positioned 4, 8 and 15 km apart. Tr1 was visited on the cruises May and July; Tr2 on the June cruise; Tr3 on the cruises May and June; Tr4 and Tr5 on the July cruise. In addition 7 stations were sampled in the fjords near Nuuk and 2 stations in Davis Strait (grey filled circles) on the May cruise. On the June cruise sampling was done in a grid of 9 stations spaced 4 km apart in Tr 3 (grey filled circles). Depth stratified sampling was carried out at 3 stations in May (white star) and July (black star).
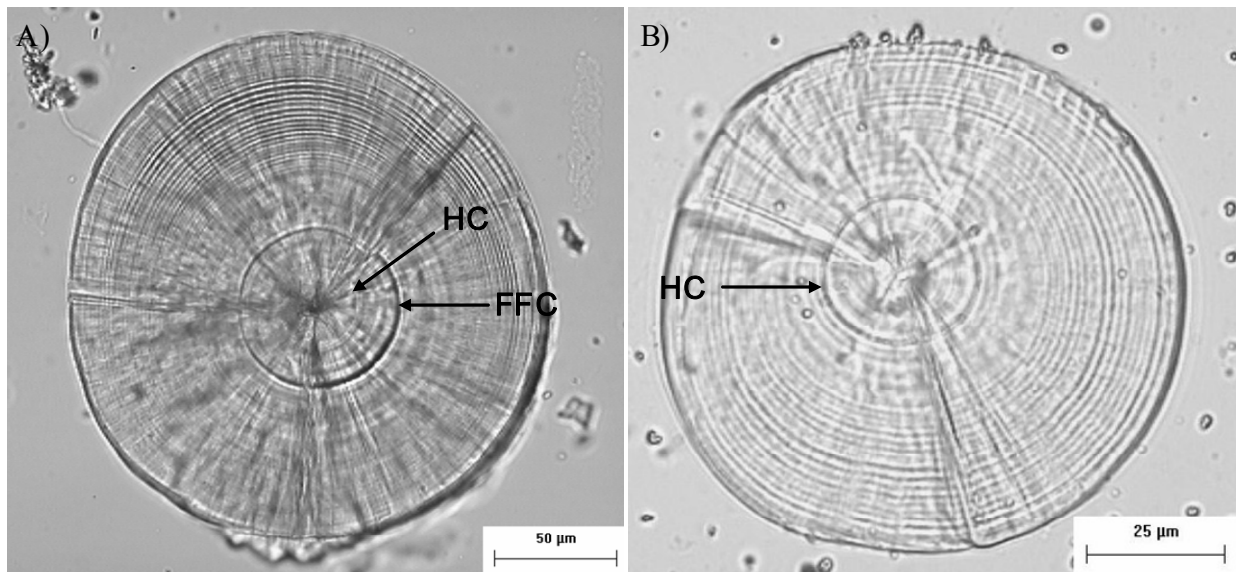
Fig. 2. Sagittae otoliths from A) Gr. halibut and B) from sandeel. Arrows indicate hatch check mark (HC) and first feeding check mark (FFC). FFC was only identifiable on Gr. halibut otoliths.
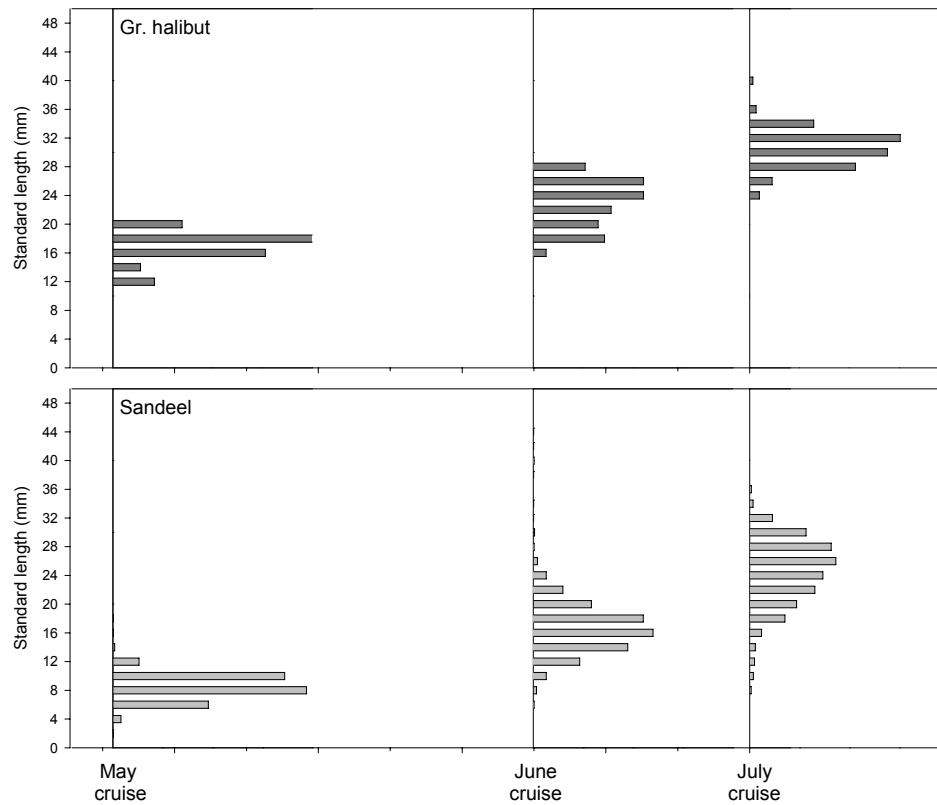
Fig. 3. Gr. halibut and sandeel length distribution on the May, June and July cruises. Frequency distributions on each cruise shown by histograms X-axis scaled to number of days between cruises.
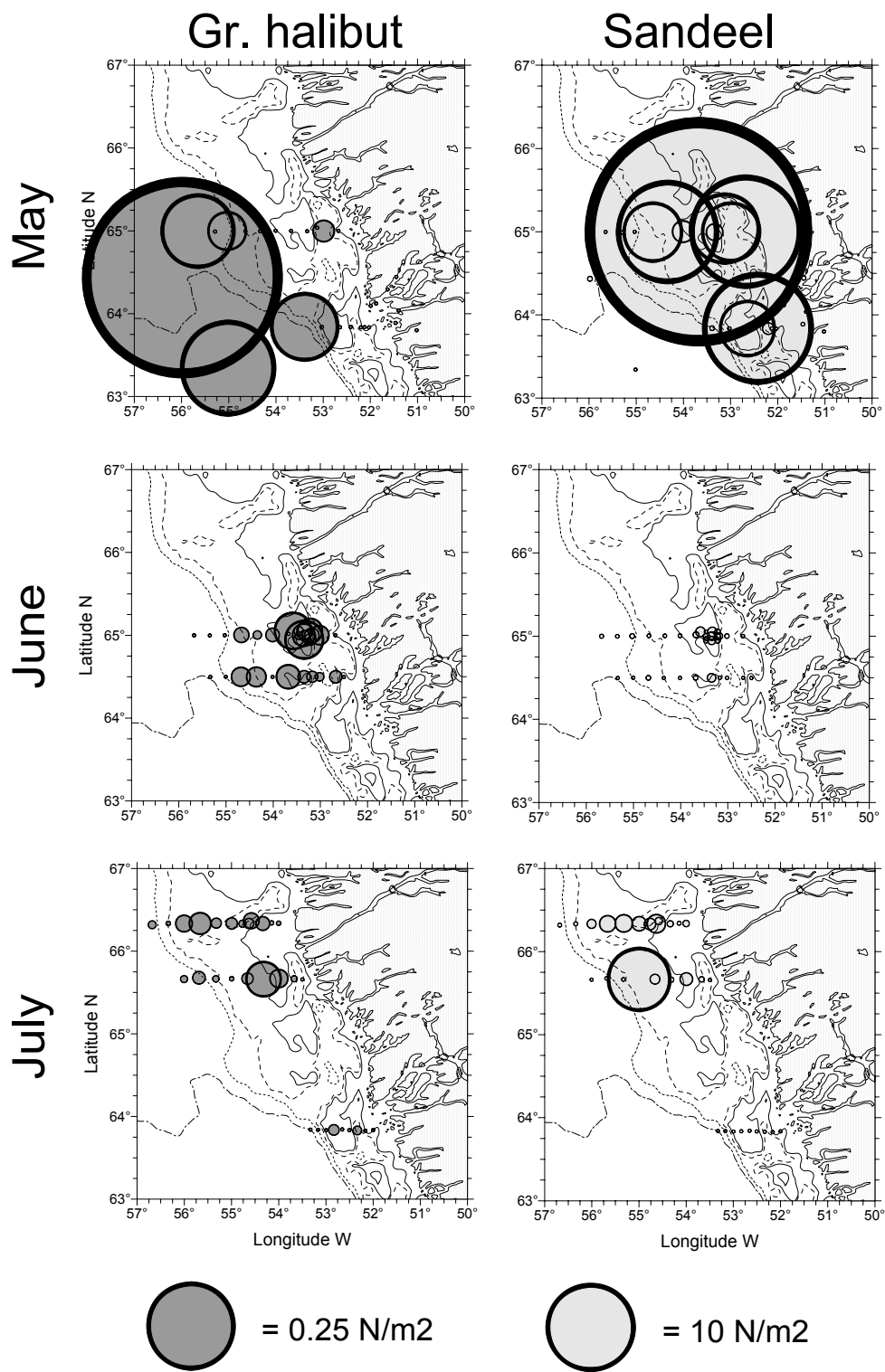
Fig. 4. Abundance (number m^{-2}) of Greenland halibut and sandeel larvae during the cruises in May, June and July.

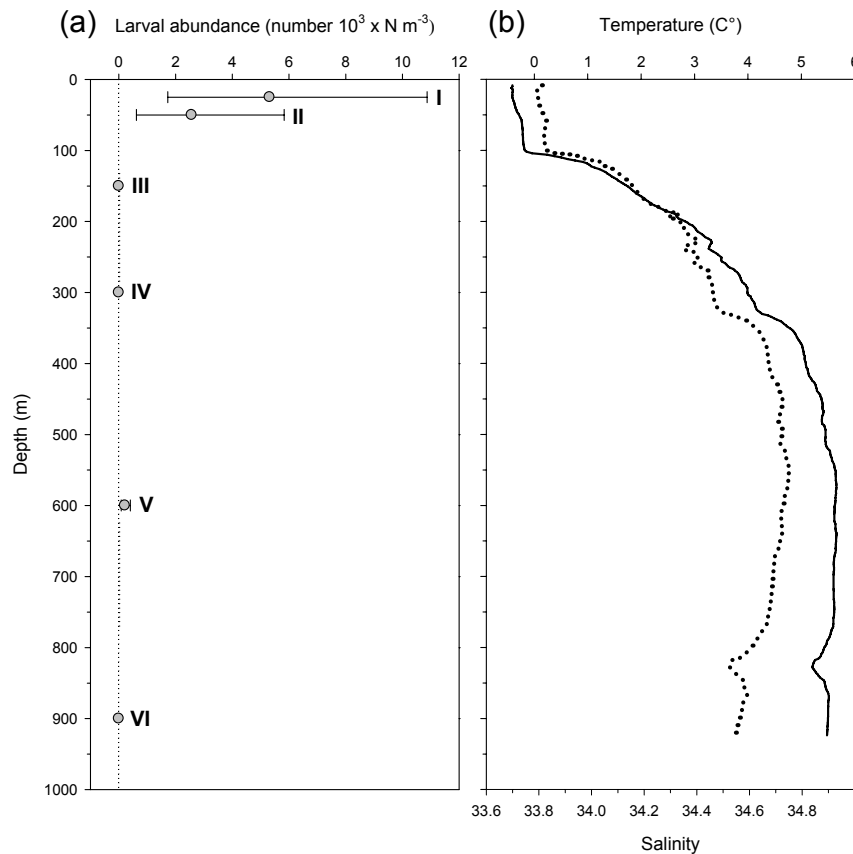**Fig 5.** Vertical distribution (mean n m^{-3} $\pm$ SE) of Greenland halibut (a) in May at station in Davis Strait (56°00W; 64°26N) from depth stratified tows (marked as tow I to VII on graph); Tow I 0-50m; II 0-100m; III 100-200m; IV 200-400m; VI 400-800m; VII 800-1000m and the associated vertical profiles of temperature (C°, dotted line) and salinity (solid line) (b). No larvae were caught in tows III, IV and VII.
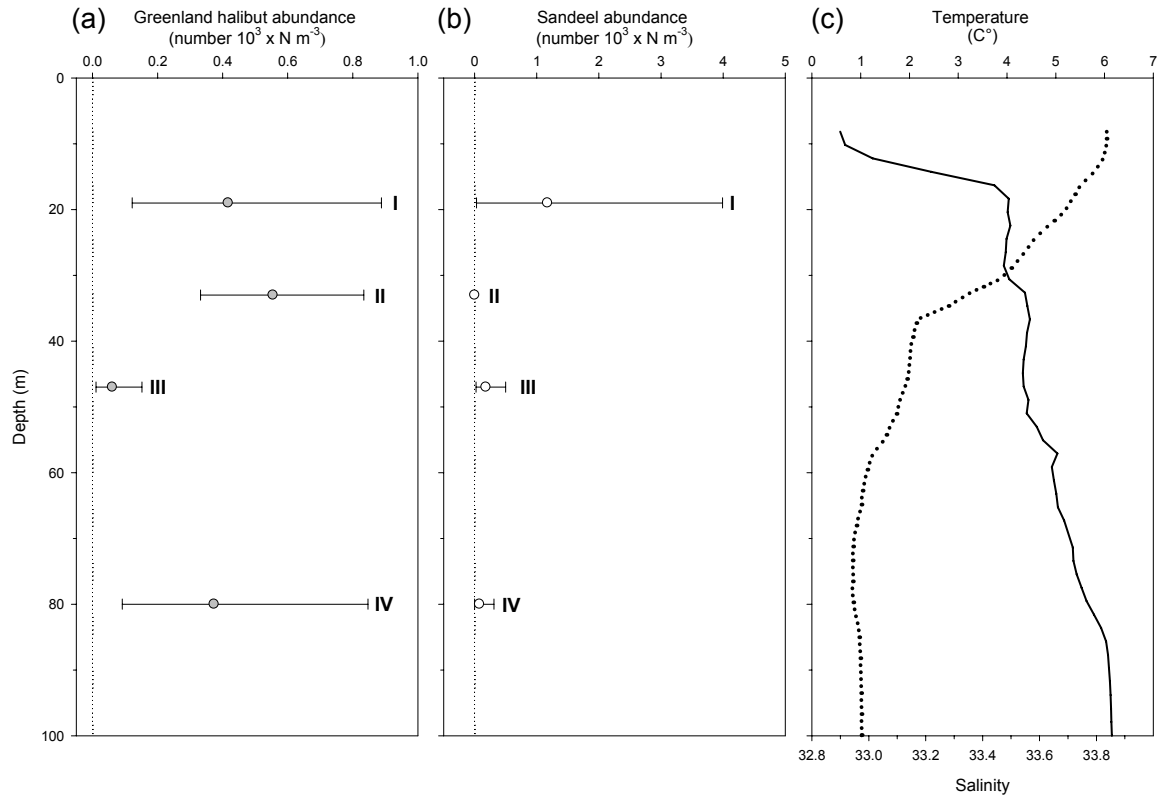
Fig. 6. Vertical distribution (mean n m^{-3} $\pm$ SE) of Greenland halibut (a) and sandeel (b) at station on Hellefisk Bank (54°20W; 65°40N) in July from depth stratified tows (marked as tow I to IV on graph); Tow I 13-25m; II 25-40m; III 40-55m; IV 55-100m and the associated vertical profiles of temperature (C°, dotted line) and salinity (solid line) (c).
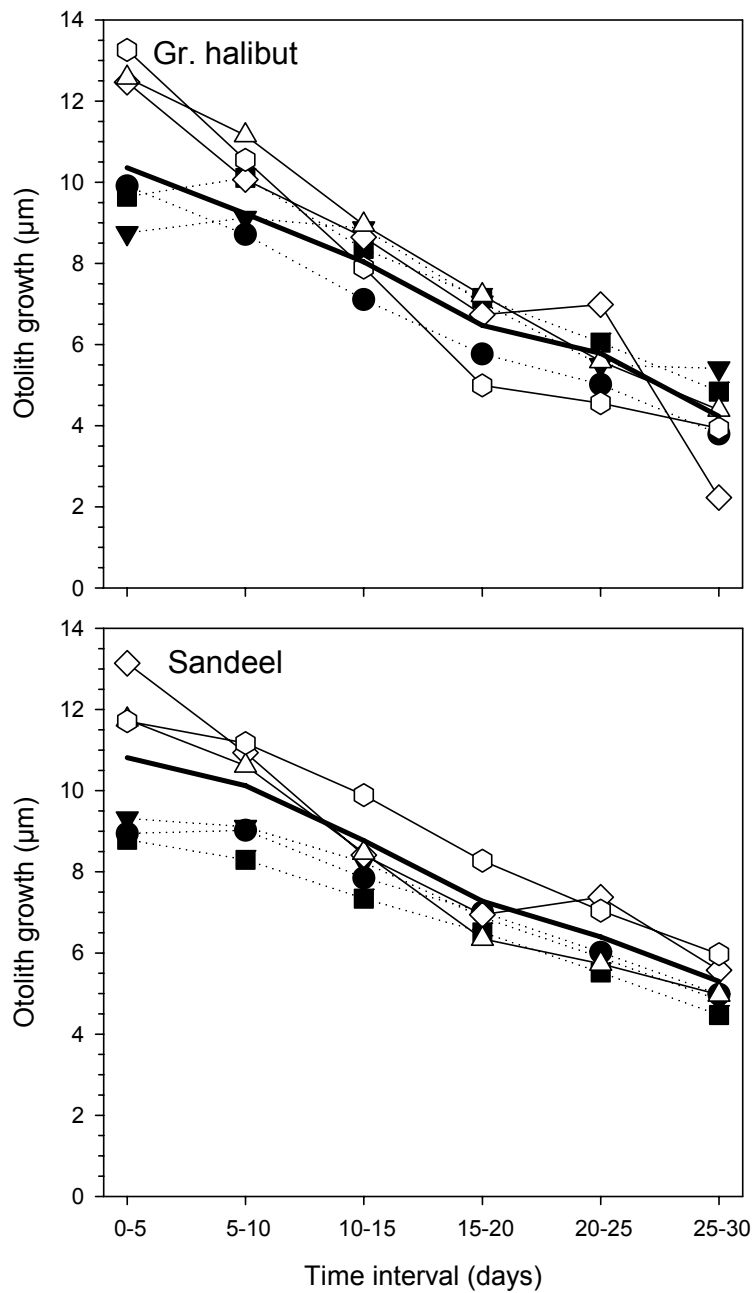
Fig. 7. Otolith growth rates (μm 5 day^{-1}) from capture and 30 days previous to capture at the three stations with the highest (white symbols), lowest (black symbols) growth rates. The mean growth rate is represented by the thick solid line.
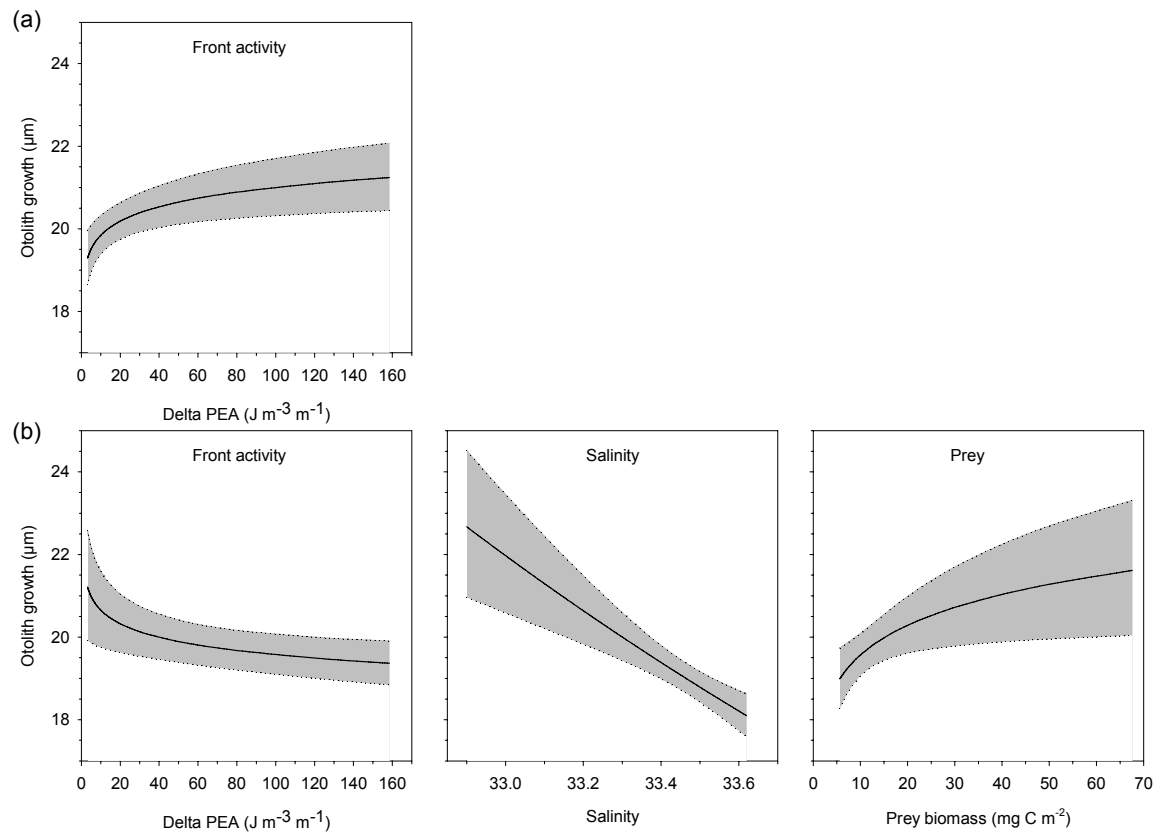
Fig. 8. Graphs illustrating the effect FRONT activity that had an significant effect on short term otolith growth G_{short} (Δ µm 10 day^{-1}) in Greenland halibut (a) and the parameters FRONT activity, SALINITY and PREY biomass that had a significant effect on otolith growth in sandeel (b). 2 SE is indicated by shaded area.
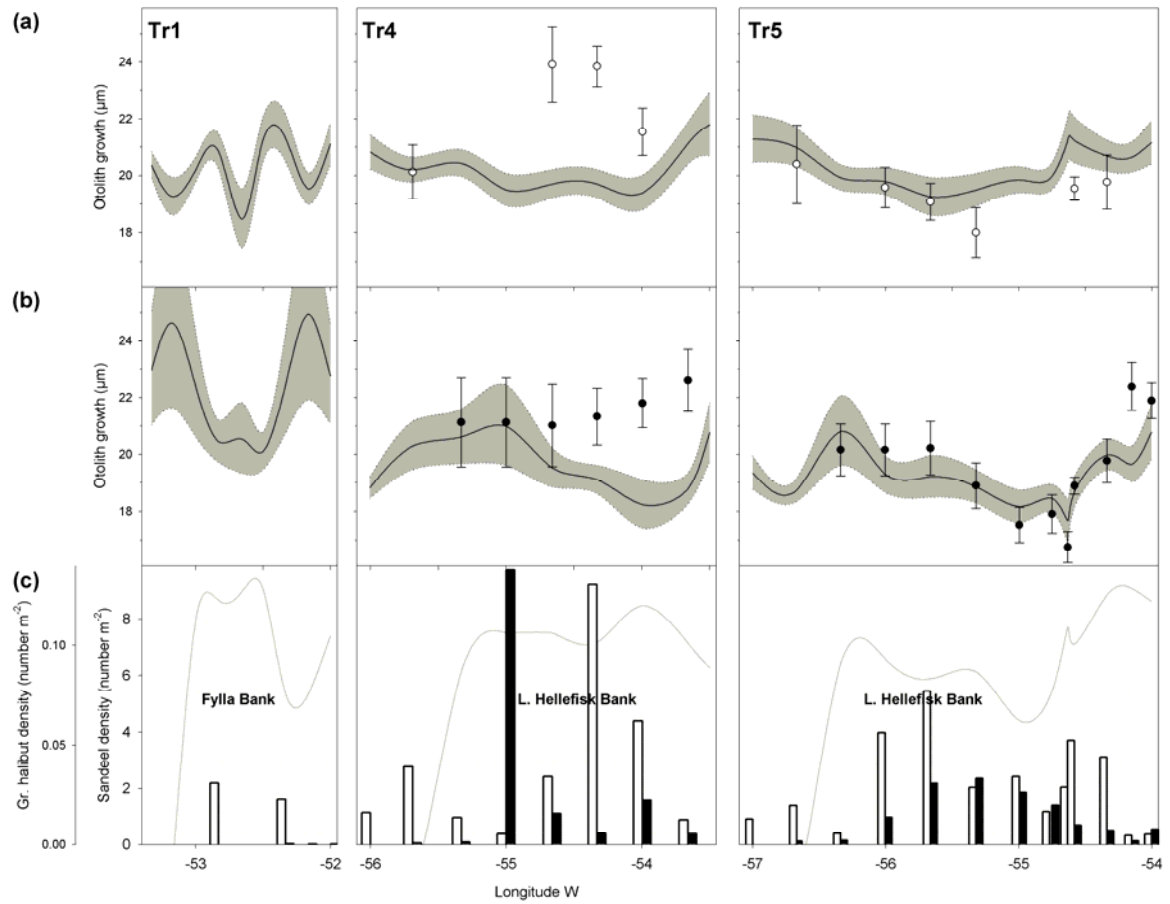
Fig. 9. Cross shelf otolith growth G_{short} for Gr. halibut (a) and sandeel (b) at transect 1, 4 and 5 in July. Observed G_{short} expressed as standardized station mean shown by white circles (a) with 2 SE indicated by error bars. Model estimated G_{short} (Δ µm 10 day^{-1}) (shown in Table 2) shown here by solid line (b) with 2 SE indicated by shaded area. Cross shelf larvae density (numbers m^{-2}) for Gr. halibut (white histograms) and sandeel (black histograms) (c). Cross shelf bottom topography shown by light grey shaded area (0-500 m) (c).

Paper III

RESEARCH ARTICLE

C. S. Simonsen · P. Munk · A. Folkvord
S. A. Pedersen

Feeding ecology of Greenland halibut and sandeel larvae off West Greenland

Abstract Feeding ecology of Greenland halibut (Gr. halibut) (*Reinhardtius hippoglossoides*) and sandeel (*Ammodytes* sp.) larvae on the West Greenland shelf was studied during the main part of the productive season (May, June and July). Copepods were the main prey item for larval Gr. halibut and sandeel, constituting between 88 and 99% of the ingested prey biomass. For both species, absolute size of preferred prey increased during ontogeny. However, preferred copepod size in relation to larval length differed markedly. In Gr. halibut, the relative size of the prey declined during growth of the larvae, while it remained constant for sandeel at a level of 2.7% of larval length. This led to a reduction in prey niche overlap between the two species. The available prey copepod biomass differed distinctly across the shelf area. In May, the prey density of Gr. halibut was the highest in the off-shelf area in Davis Strait. In June and July, the prey-rich areas for both species were mainly located at the slopes of the banks and at the shelf break area. Gut fullness was higher in these areas than in neighbouring areas, suggesting that the larval food resource could be scarce. The feeding ecology of Gr. halibut and sandeel could explain why larval abundance indices of the two species have historically shown opposite responses to yearly environmental conditions and total zooplankton occurrence.

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Introduction

Off West Greenland, larvae of both the Greenland halibut (*Reinhardtius hippoglossoides* Walbum), in the following named as Gr. halibut, and sandeels (*Ammodytes* sp.) are sympatric and occur during the same period of the year (Pedersen and Rice 2002; Munk et al. 2003). The historic time series of larval abundance of these two species show opposite responses to yearly environmental conditions and zooplankton densities (Pedersen and Rice 2002). The reason for this inverse correlation remains unresolved but nonetheless seems to be important for an understanding of the population dynamics of both species. Since the maintenance of viable stocks depends on survival and growth of the larvae, detailed knowledge about the feeding ecology of the sympatric larval stages of Gr. halibut and sandeel is important for a better understanding of parent stock recruitment processes. It is evident that larvae can only ingest organisms smaller than their mouth size, but in addition the larvae must throughout its ontogenetic development be able to detect and catch the prey (Munk 1992; Hart and Gill 1993). The progressive changes in prey size and type during larval ontogeny have been studied in sandeel (e.g. Monteleone and Peterson 1986; Pearre 1986; McGurk et al. 1992) but never in Gr. halibut. A single study on the diet of Gr. halibut has been carried out in the eastern Norwegian and Barents Seas but this did not report on the size of the prey items (Haug et al. 1989). There is therefore a need for improved knowledge of the larval feeding biology of these two species in West Greenland waters and information on the potential prey competition between them.

The waters off West Greenland show marked variability in hydrographical and biological conditions. The area includes both polar and temperate regimes, which is reflected in the species composition and community structures (Møller and Nielsen 2000; Pedersen and Rice 2002; Munk et al. 2003; Pedersen et al. 2005). In the cross-shelf variability of zooplankton abundance, high abundances are often found over the slopes of the banks, and plankton distribution is apparently related to hydrographic fronts between along-shelf flowing current structures (Pedersen et al. 2005). Likewise, the distribution of fish larvae seems to show patterns related to shelf topography and water mass characteristics (Pedersen and Rice 2002; Munk et al. 2003).

The objective of this study is to analyse and compare the feeding ecology of co-occurring Gr. halibut and sandeel larvae in West Greenland waters. Diet analysis and prey preference considerations will be used to assess spatial variation in prey availability and feeding. Potential niche overlap and competition for prey will be evaluated from prey availability and larval gut contents. Our primary goal is to analyse seasonal and cross-shelf variability in prey availability of Gr. halibut and sandeel in the area, hypothesizing that feeding conditions are optimal in central areas of fish larval distribution, and that timing of larval emergence is synchronised with prey availability.

Materials and methods

Fish larvae

Samples of larval Gr. halibut, sandeel and zooplankton were obtained during three surveys in May (2000), June (1999) and July (2000) covering the sea off West Greenland between 63°20′N and 66°20′N (Fig. 1). Except for three stations positioned in Davis Strait during the survey in May, stations were located along East–West transects crossing the shelf banks. Transect 3 was sampled both in June 1999 and May 2000 while transects 4 and 5 were sampled in July 2000 only. Sampling on all surveys took place within the period sunrise to sunset. Gr. halibut and sandeel larvae were collected with two types of ring nets. In May we used a Bongo net with a diameter of 0.6 m and a mesh size of 500 μm, while in June and July a ring net (MIK) with 2 m diameter and 1,000 μm mesh size was used. The nets were changed because the Bongo net (500 μm) is more efficient for catching smaller larvae common in May while the MIK net (1,000 μm) is more efficient in sampling larger larvae more prevalent later in the season (P. Munk, unpublished results). Oblique hauls with the Bongo or MIK net from the surface to 200 m of depth or 5 m above the seafloor were carried out while the ship's speed was three knots. A flow meter in the net opening recorded the filtered water volume.

Larvae were immediately sorted from the other plankton in the samples and transferred to 96% ethanol, or frozen after net retrieval. The remaining plankton sample was preserved in 4–8% formaldehyde solution and later checked for missed larvae. Larval standard length (SL) was measured to 1 mm below and the length of the lower jaw was measured from the joint with the maxilla bone to the tip of the mouth were measured with the aid of a microscope. Samples containing more than 80 larvae per station were sub-sampled for SL while jaw length was measured on a representative size range of all the sampled larvae. Jaw length is proportional to gape size (Shirota 1970). Larval shrinkage was adjusted by shrinkage corrections given by Fey (1999) and Hjörleifsson and Klein-MacPhee (1992).

Prey environment

Micro- and mesozooplankton were sampled in May and June with a WP-2 net (diameter 0.58 m, mesh size 50 μm) and in July by a submersible zooplankton pump (900 l min^{-1}, equipped with a 50 μm conical net). WP-2 net and pump sampling of zooplankton affords comparable density estimates (Pillar 1984). Vertical haul taken was from bottom (or max 200 m) to surface at regular intervals along the transect lines in order to give depth-integrated information on regional zooplankton distribution. In addition, zooplankton was sampled at discrete depth intervals on selected stations during the May and July surveys. During the May survey, the depth intervals were 0–100 m; 100–200 m; 200–400 and 400–800 m; and in July, 0–13 m; 13–25 m; 25–40 m and 40–100 m. Detailed descriptions of the sampling and processing protocols for zooplankton are given by Pedersen et al. (2002).

A total of 202 Gr. halibut and 348 sandeel larvae covering the entire larval size spectrum were selected for prey analysis. For Gr. halibut, larvae from May, June and July surveys were included in order to cover the size spectrum while for sandeel it was only necessary to include larvae from the May and July surveys. The guts were extracted and prey items identified and counted. For copepods, we measured the length and width of the prosome, while in other prey items only the maximum length-width distance. Measurements were made with the aid of a microscope and a video analysing system. When more than 40 prey items of the same type were present in one larva, measurements were performed only on a sub-sample. Information on taxa, abundance and length of the prey items were used for estimation of carbon biomass content using the live length-weight keys given by Pedersen et al. (2002).

Carbon weight of fish larvae was estimated from length to dry weight (DW) relationships assuming a carbon to dry weight factor of 0.45 (Kiørboe et al. 1987). Dry weights were obtained by regressing individual length against individual dry weight (60°C for 72 h) after removal of the gut, otoliths and extraction of lipids in chloroform methanol for 48 h. The otolith and lipid extraction was carried out for a study not reported here. The larval length to DW relationships were:

Fig. 1 The area of investigation off western Greenland. Bathymetry is shown by *shaded contour lines* for 100, 250, 500, 1,000 and 2,000 m depths. Stations for this study were placed along three transects. Transect 3 in June 1999 and May 2000, transects 4 and 5 in July 2000 (same nomenclature for transect as in Pedersen et al. (2002). The *star symbol* shows additional stations were depth-stratified zooplankton sampling was performed—*white stars* stations in May 2000; *black stars* stations in July 2000
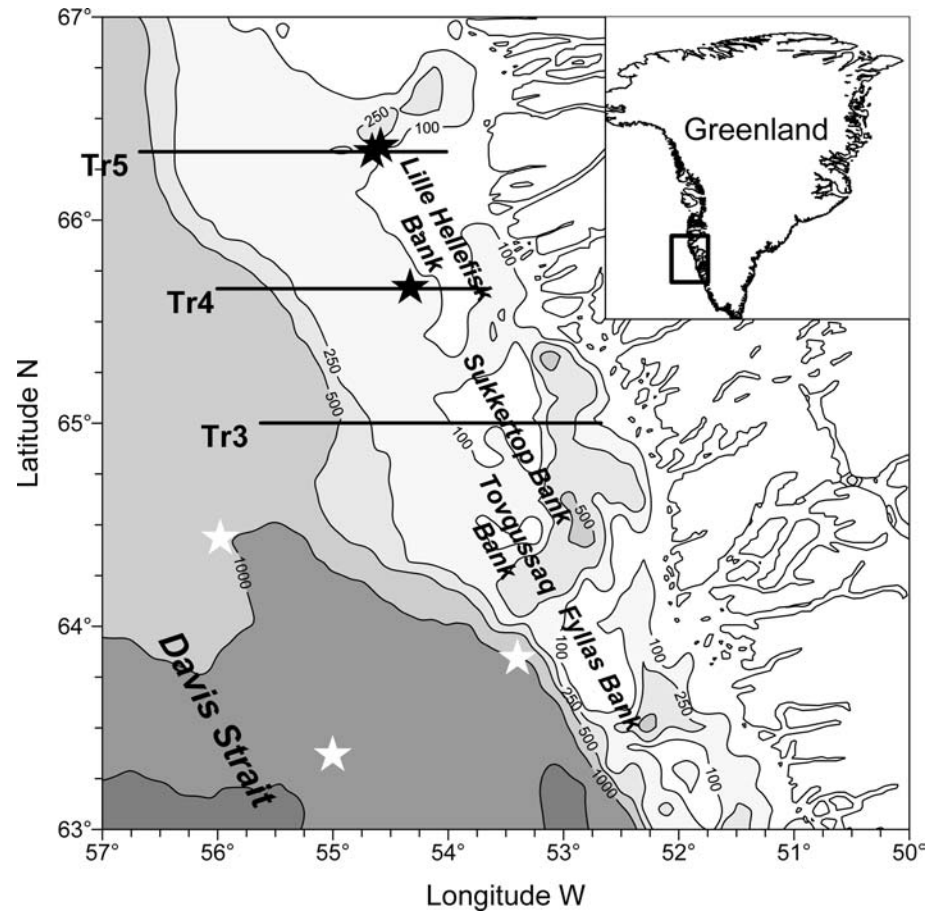
$$\text{Gr. halibut DW (SL)} = 6.12 \times 10^{-2} \times \text{SL}^{3.47},$$

$$r^2 = 0.90,$$

$$N = 53, \text{ SL interval } 12.9\text{--}36.2\,\text{mm}$$

$$\text{Sandeel DW (SL)} = 7.61 \times 10^{-2} \times \text{SL}^{2.61}, \ r^2 = 0.90,$$

$$N = 147, \text{ SL interval } 9.5\text{--}36.8\,\text{mm}$$

where SL was in mm and DW in μg. The relative gut fullness was calculated as carbon content of ingested prey divided by larval carbon weight.

Prey size preference of Gr. halibut and sandeel was ascertained from the relative frequency of prey size in their diet in relation to the relative frequencies in the environment. The zooplankton and prey items were grouped into $\log_{10}$ spaced intervals in order to ensure that an adequate number of observations were present also for the larger-sized items. The $\log_{10}$ interval step was 0.1 from −1 ($\log_{10}$ to 0.1 mm). The size prey preference was calculated by the Chesson prey preference index α (Chesson 1978):

$$\alpha_i = (a_i/n_i)\left(\sum a_j/n_j\right)^{-1} \ (j = 1....m),$$

where a_i and n_i are the abundance of prey items of the ith size interval in the gut and the environment,

respectively, and m is the number of intervals considered. The α value was calculated for each larval size interval on each station. Gr. halibut and sandeel were grouped in 4 mm length intervals for larvae up to 16 and 2 mm intervals for larger larvae (in order to ensure a reasonable number of prey items in each interval). The frequency distribution of α is assumed to be normally distributed and the mean of this frequency distribution thus indicates the prey size of maximal preference. Prey niche breadth was described by the standard deviation of the maximum prey size preference (equal to the SLH index presented by Pearre 1986). The obtained estimates of prey niche breadth and maximum preference for the average size Gr. halibut and sandeel larvae during each survey were used to estimate the relative preference (p) for the ith size interval from the normal distribution of p:

$$p(i) = q(i)/\sum_{j=1}^{m} q(i) \qquad (j = 1,....,m),$$

$$where \quad q(i) = (\exp(\log(i) - \log(\text{prey}_{\max}))^2)/(-2/\sigma^2),$$

where i is the size interval, $\text{prey}_{\max}$ is the prey size of maximal preference for a given fish larvae length, σ is the standard deviation of the maximum prey size preference. The available prey ($\text{prey}_{\text{available}}$) for a given fish larvae

size was estimated from the relative preference on size intervals of zooplankton biomass:

$$\text{prey}_{\text{avaliable}} = \sum_{j=1}^{m} p(i) \times a_i \quad (j = 1....m),$$

where p(i) is the relative preference for the ith size interval.

All statistical analyses were performed in the SAS/STAT software Version 9 of the SAS System for PC, SAS Institute Inc., Cary, NC, USA. The following abbreviations were used for statistical tests: analysis of variance (ANOVA); analysis of covariance (ANCOVA); general linear model (GLM).

Results

Fish larvae

The average standard length (SL) of both Gr. halibut and sandeel larvae increased between the surveys in May (mean SL Gr. halibut 17.6 mm; sandeel 9.0 mm) and July 2000 (mean SL Gr. halibut 31.0 mm; sandeel 25.5 mm), while larvae sampled in June 1999 were of an intermediate size (mean SL Gr. halibut 23.5 mm; sandeel 17.3 mm) (Fig. 2). Gape size increased significantly with larval length both in absolute terms and relative to larval length in both species (GLM, $P < 0.001$). The slopes of the relative jaw length to larval length were similar for Gr. halibut and sandeel (homogeneity of slopes test, $P = 0.73$), but since Gr. halibut generally had a larger relative gape size, the curves are significantly displaced (ANCOVA, $P = 0.002$) (Fig. 3).

Fish larval prey

Overall, 97% of the Gr. halibut and 85% of the sandeel larvae contained prey items. These prey items were from more than 13 different taxonomic groups. In biomass, the copepods were the dominant prey for both Gr. halibut and sandeel in all sampling periods (Table 1). The copepods constituted between 88 and 99% of total gut content in all sampled periods. In July, relatively more of the prey items were bivalves and gastropod larvae, eggs and appendicularians. This was especially noticeable for sandeel in the size intervals 25–30 and 30–35 mm. In terms of biomass, however, they comprised less than 13% of the total gut content.

Prey environment

The small plankton (< 200 μm) were dominated by copepod eggs or eggsacks and bivalvia larvae while larger-sized plankton were mainly nauplii and copepodite stages of copepods (Fig. 4). The most abundant copepods were *Pseudocalanus* sp. nauplii in May and *Oithona* sp. copepodites in June and July. They were
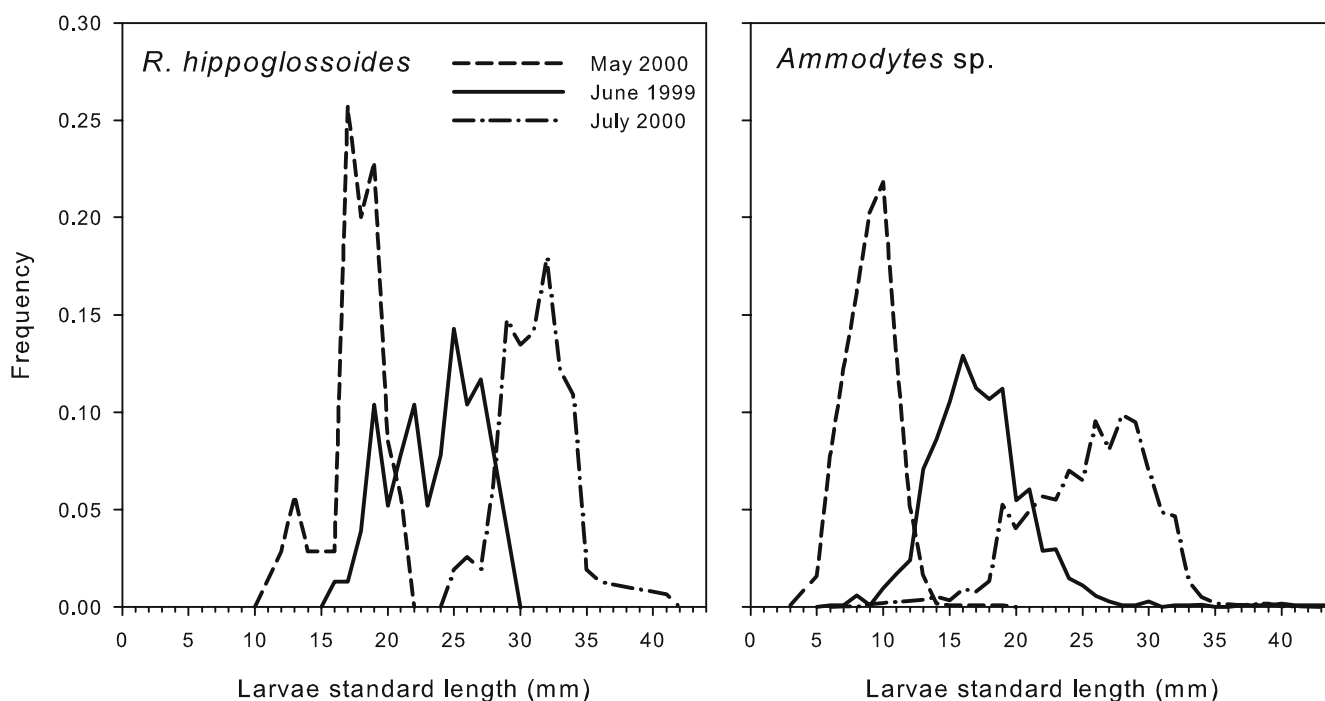
Fig. 2 Length distribution (standard length, corrected for shrinkage) for Greenland halibut (*R. hippoglossoides*) and sandeel (*Ammodytes* sp.) larvae on the surveys in May 12–21 2000, June 21–30 1999 and July 11–23 2000. Mean size for halibut: May 17.6 mm; June 23.5 mm; July 31 mm. Sandeel: May 9.0 mm; June 17.3 mm; July 25.5 mm
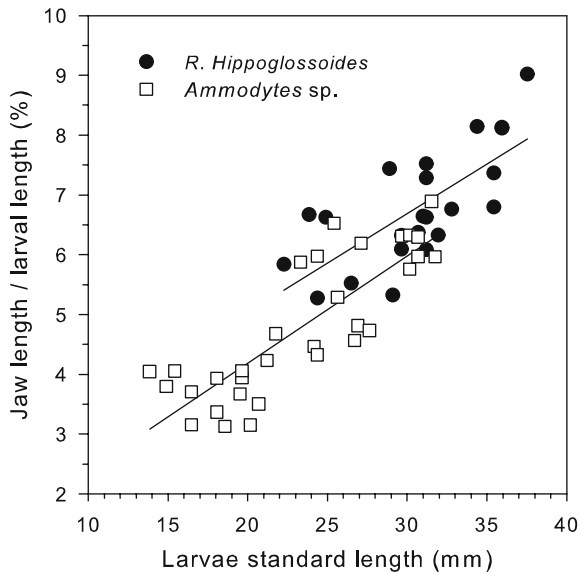
Fig. 3 Relative gape size in percent of larvae length for halibut (*R. hippoglossoides*) and sandeel (*Ammodytes* sp.). Linear regression: sandeel $f(x) = 0.18x + 0.61$; halibut $f(x) = 0.17x + 1.73$

especially abundant in the length intervals from 200 to 634 µm. *Calanus* sp. copepodites were also observed in high numbers, especially in June and July. *Calanus* sp. were most abundant in intervals from 800 µm. In terms of weight, *Pseudocalanus* sp. made up 25% of the total copepod biomass in May, while in June and July *Calanus* sp. constituted more than 50% of the total biomass.

Vertical distribution

In May, the vertical distribution of plankton was similar at the three stations examined (ANOVA, $P > 0.3$). For most groups, the density was highest in the 0–100 m depth interval and gradually decreased with depth (Fig. 5). Except for *Oithona* sp. copepodites and euphausiid eggs, most of their respective biomass was distributed here. *Oithona* sp. copepodites and euphausid eggs were mainly found in the 100–200 m depth interval. In the deeper 200–400 and 400–800 m intervals, abundance and biomass was low for all groups. There was no significant difference in size distribution within the plankton groups at the different vertical depth strata (ANOVA, $P > 0.3$) or for all plankton groups together (ANOVA, $P = 0.68$).

In July, depth-stratified sampling at three stations on the shelf (Fig. 1) showed similar vertical distribution patterns (ANOVA, $P > 0.12$). The highest density was found in the depth intervals 0–13 and 13–25 m for nauplii and copepodites from the groups *Oithona* sp. and "other copepoda species", while *Calanus* sp. and *Pseudocalanus* sp. were mainly in the 25–40 and 40–100 m depth intervals (Fig. 6). Eggs from both euphausiids and copepods had the highest occurrence in the 25–40 m interval, but their distribution pattern differed.

While euphausiid eggs also were distributed in relatively high numbers in the shallower 13–25 m interval, the distribution pattern of copepod eggs included the deeper 40–100 m interval. The size distribution within the different plankton groups did not change significantly with depth (ANOVA, $P > 0.19$) or for all plankton groups together (ANOVA, $P = 0.18$) even though there was a tendency to an increase in biomass for the larger size intervals at the deeper depth strata (Fig. 6).

Prey size

The log-scaled size of the main prey items (cf. Table 1) found in sandeel guts generally increased significantly with larval length (GLM, $P < 0.05$) (Fig. 7a–d) except in the cases of gastropod larvae (GLM, $P = 0.64$) and appendicularians (GLM, $P = 0.41$). In contrast, only a very slight increase in width and length of prey items was observed with increasing size of Gr. halibut larvae. Only for eggs (GLM, $P = 0.05$) and copepod width (GLM, $P = 0.02$) (Fig. 7a) did prey size increase significantly. Comparisons of prey size within prey item groups indicate that Gr. halibut and sandeel fed on the same size of appendicularians (ANCOVA $P = 0.70$) and bivalvia (ANCOVA, $P = 0.13$) but on different sizes of eggs and copepods (ANCOVA, $P < 0.0001$). In sandeel, eaten eggs were generally smaller compared to those found in Gr. halibut (Fig. 7b). Smaller Gr. halibut larvae (< 20 mm) generally ate larger copepods than sandeel of similar length, while the pattern was reversed for larger larvae (Fig. 7a).

Prey size preference

Prey size preferences in Gr. halibut and sandeel were significantly different (ANCOVA, $P = 0.003$) (Fig. 8). The relative size of preferred prey (RSPP) declined significantly for Gr. halibut by a rate of -4.49×10^4 SL (GLM, $P < 0.001$) while RSPP was constant for sandeel at approximately 2.7% of larval length (GLM, $P = 0.43$). The prey size niche breadth was constant for both Gr. halibut and sandeel throughout larval ontogeny (GLM, $P > 0.20$) but significantly different among them (ANCOVA, $P < 0.001$). The Gr. halibut preferred prey within a narrower size range (prey size niche breadth 0.10) than sandeel (prey size niche breadth 0.13).

The prey size preference in the three periods studied showed that in May, Gr. halibut preferred almost twice as large a prey as sandeel (highest preference for 420 versus 240 µm) (Fig. 9). In June, Gr. halibut and sandeel preferred almost identical sizes of prey (highest preference for, respectively, 498 and 462 µm). Their preferred size ranges were between 200 and 700 µm, which in terms of copepodites were the most abundant size classes (Fig. 9). In July, Gr. halibut larvae preferred almost the same prey size as in June (highest preference for 554 µm), while sandeel had increased its preference towards larger prey

Table 1 Individual average stomach/gut content per 5 mm length interval in number and estimated corresponding weight in µg carbon

| Period	Species	Length (mm)	Obs (N)		*Copepoda*	Bivalvia	*Gastropoda*	Eggs	*Appendicularia*	Other	Total
May 2000	Sandeel	5	19	N	1.7	–	–	0.2	–	0.1	2
				µg C	1.27	–	–	0.01	–	0.0	1
		10	58	N	2.0	–	–	0.4	–	–	2
				µg C	0.31	–	–	0.01	–	–	0
		20	1	N	–	–	–	3.0	–	–	3
				µg C	–	–	–	0.07	–	–	0
	Halibut	10	4	N	23.0	–	–		–	–	23
				µg C	47.32	–	–		–	–	47
		15	20	N	1.5	–	–	0.2	–	–	2
				µg C	1.98	–	–	0.06	–	–	2
June 1999	Halibut	15	1	N	9.0	–	–	–	–	–	9
				µg C	15.03	–	–	–	–	–	15
		20	20	N	7.6	0.1	–	–	–	–	8
				µg C	28.22	0.02	–	–	–	–	28
		25	19	N	13.9	–	–	–	–	0.1	14
				µg C	21.47	–	–	–	–	0.38	22
		40	1	N	13.0	–	–	–	–	–	13
				µg C	251.06	–	–	–	–	–	251
July 2000	Sandeel	10	1	N	2.0	1.0	–	3.0	4.0	–	10
				µg C	0.53	0.08	–	0.09	0.19	–	1
		15	18	N	1.6	0.7	0.1	3.4	0.4	0.8	7
				µg C	1.00	0.09	0.01	0.26	0.02	0.07	1
		20	38	N	3.7	2.0	0.6	3.5	2.0	0.3	12
				µg C	29.33	0.25	0.07	0.28	0.17	0.10	30
		25	80	N	9.9	7.2	1.2	37.7	7.2	0.8	64
				µg C	29.90	0.89	0.11	2.06	0.46	0.80	34
		30	123	N	15.3	9.3	1.2	35.7	6.1	1.0	69
				µg C	106.09	1.29	0.11	7.57	0.38	1.61	117
		35	9	N	41.2	20.3	0.8	1.3	3.0	0.1	67
				µg C	278.68	3.25	0.11	0.11	0.20	0.06	282
		40	1	N	38.0	–	–	1.0	–	4.0	43
				µg C	162.56	–	–	0.04	–	1.69	164
	Halibut	20	1	N	3.0	–	–	–	–	–	3
				µg C	0.03	–	–	–	–	–	0
		25	79	N	34.2	–	–	0.6	–	0.3	35
				µg C	62.19	–	–	0.33	–	0.02	63
		30	55	N	41.3	0.5	–	4.1	0.3	0.7	47
				µg C	61.99	0.06	–	13.62	0.01	0.08	76
		35	2	N	39.0	–	–	51.5	–	0.5	91
				µg C	46.71	–	–	188.31	–	0.66	236

The category *Copepoda* includes nauplii and copepodite stages, *Bivalvia* and *Gastropoda* include larval stages only, *Eggs* includes copepod and euphausiid eggs. *Appendicularia* includes various pelagic tunicates, *Other* includes annelids, egg sacs, different malacostraca larvae, different species in the Ostracoda group, phytoplankton (mostly diatoms) and protozoa. All constituting less than 1% in either number or weight of the average stomach content are excluded

sizes (highest preference for 682 µm) (Fig. 9). The size preference for Gr. halibut was thus on or close to size intervals with highest copepod abundance while that for sandeels was on size intervals larger in terms of biomass. A consequence of the different prey size preference for Gr. halibut and sandeel was that the available copepod prey biomass differed in May and July. In May, Gr. halibut on average had access to a three-fold larger prey biomass than sandeel (163 mg C m^{-2} for Gr. halibut versus 50 mg C m^{-2} for sandeel) while in July, the available prey biomass for sandeel was about 1.5 times larger than for Gr. halibut (43 mg C m^{-2} for sandeel, 30 mg C m^{-2} for Gr. halibut).

The vertical distribution of available prey biomass in May showed that almost all prey biomass for both Gr. halibut (81%) and sandeel (87%) was located in the 0–100 m depth interval with only little biomass at greater depth intervals (Fig. 10a). In July, prey densities were highest for Gr. halibut in depth intervals 13–25 m (41%) and 25–40 m (39%), while for sandeel, prey density was highest at the 25–40 m interval (41%) (Fig. 10b).

The variation in available copepod biomass and the relative larval gut fullness across transects was large (Fig. 11). In May, the available prey biomass for Gr. halibut was higher at the stations offshore in Davis Strait and West of the bank than at other stations. Relative gut fullness was also generally higher on the offshore stations in Davis Strait. The difference in available copepod biomass for sandeel was less marked but gut fullness peaked on the shallow part of the bank. In June, the largest prey biomass for Gr. halibut was in the shelf break area, which coincided with highest relative gut fullness. On the
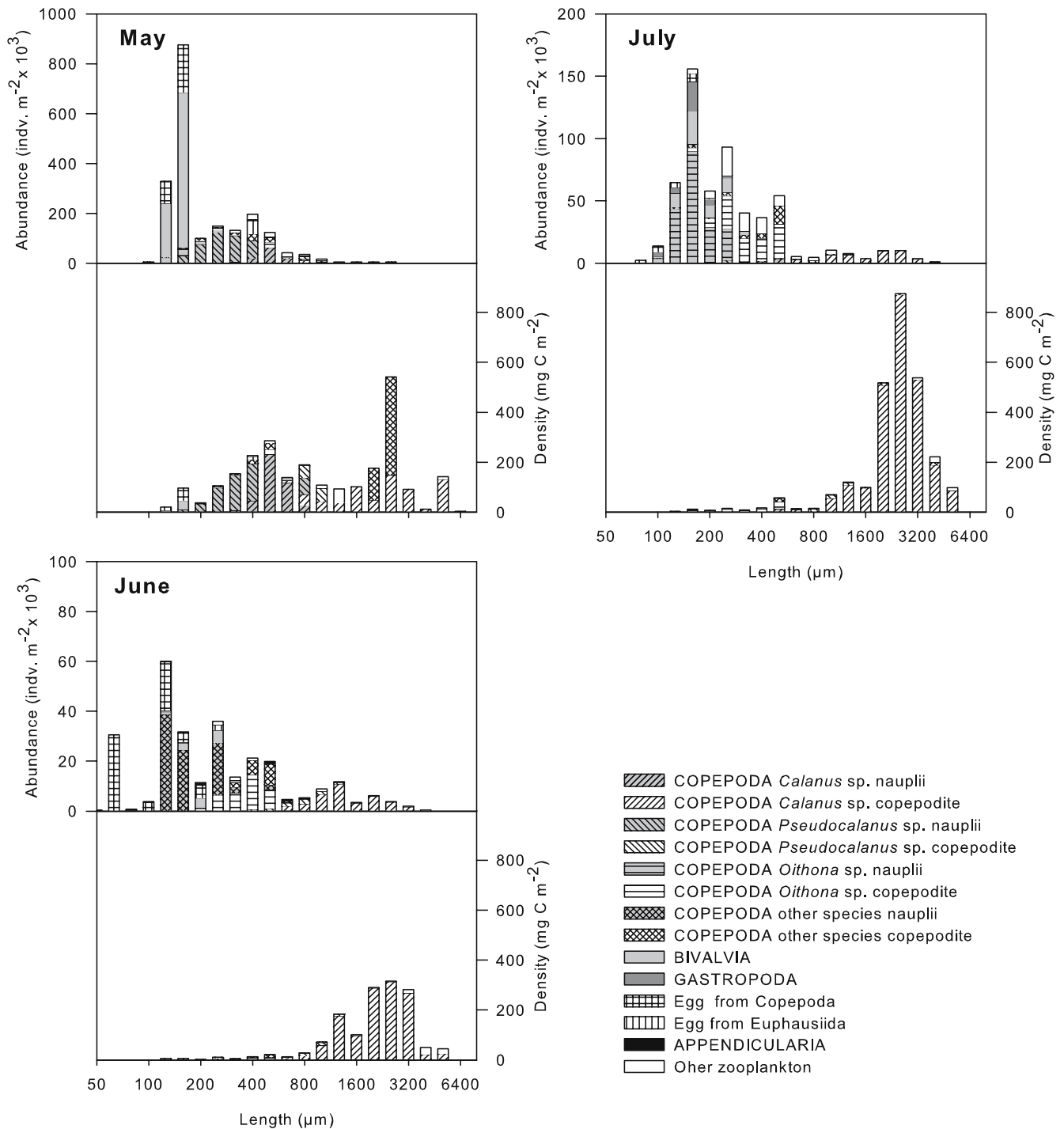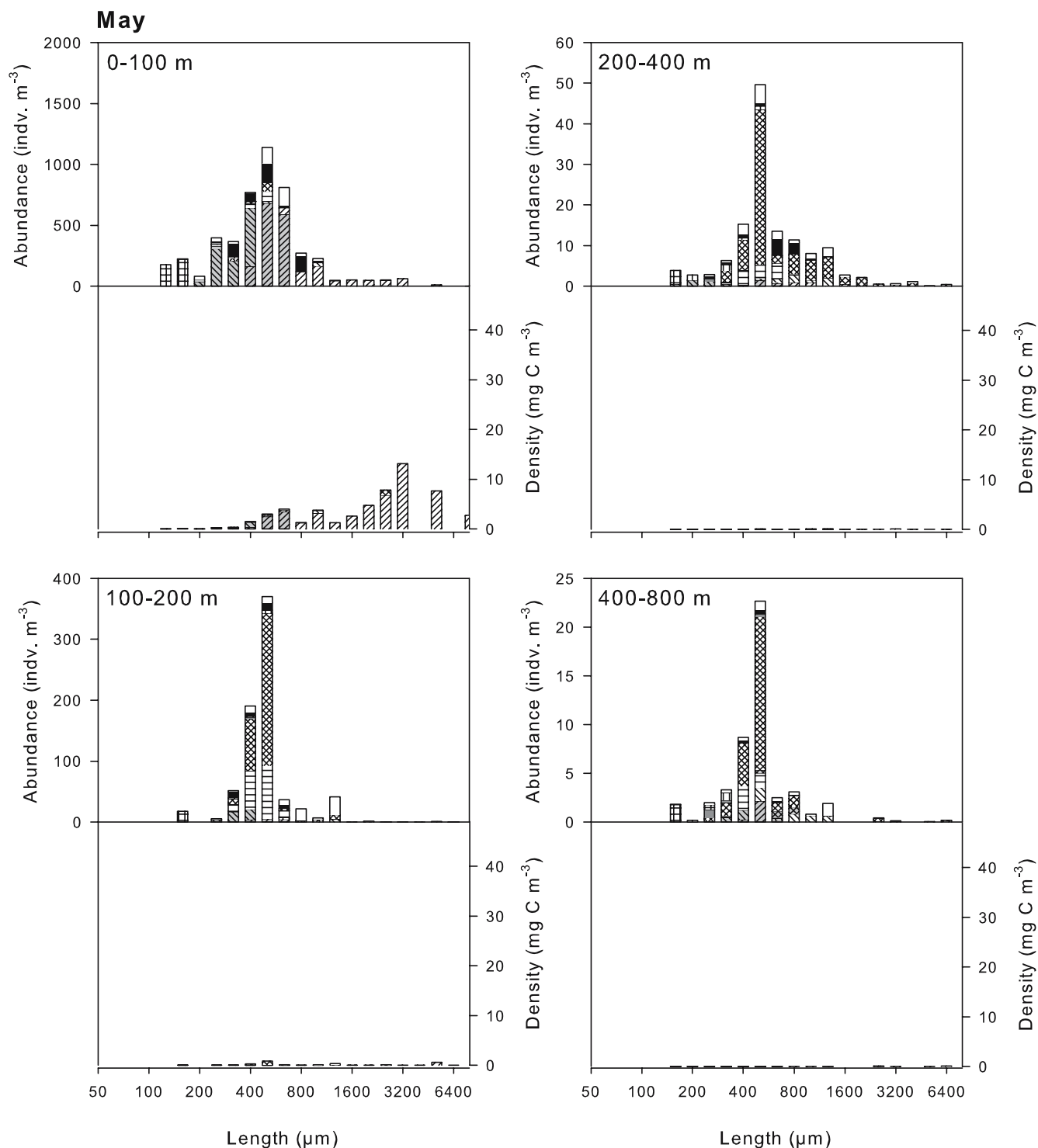
Fig. 4 Mean abundance (*upper panel*, individuals m^{-2}×10^3) and density (*lower panel*, mg C m^{-2}) of zooplankton in 0.1 log$_{10}$ spaced intervals (μm) in May, June and July surveys. Midpoints of intervals were 50, 63, 79, 100, 126, 159, 200, 252, 317, 400, 503, 634, 799, 1,007, 1,268, 1,598, 2,013, 2,536, 3,194, 4,024, 5,070, and 6,387 μm. Copepod species in the category "COPEPODA other species" were of the genera *Acartia, Bradyidius, Candacia, Centropages, Coryceus, Cyclopoida, Euchaeta, Harpacticoida, Metridia, Microcalanus, Microsetella, Monacilla, Oncaea, Paraeuchaeta, Scolecithricella Spinocalanus* and *Temora*

shallower part of the banks, the available biomass was less than half the amount available at the shelf break. In July, the general tendency was higher copepod biomass for both Gr. halibut and sandeel at the shelf break area or at neighbouring stations which also were the areas where

highest relative gut fullness for both species was found. However, the pattern was not unambiguous. Even though high gut fullness only was observed at stations with high prey availability, there were cases of low gut fullness in areas of high prey availability.

Fig. 5 Vertical distribution of zooplankton in mean abundance (*upper panel*, individuals m^{-3}) and density (*lower panel*, mg C m^{-3}) in the May survey (for location of stations see Fig. 1) in log$_{10}$ spaced intervals (μm). Midpoints of intervals, zooplankton categories and legends are as in Fig. 4. *Depth intervals* are indicated on each plot
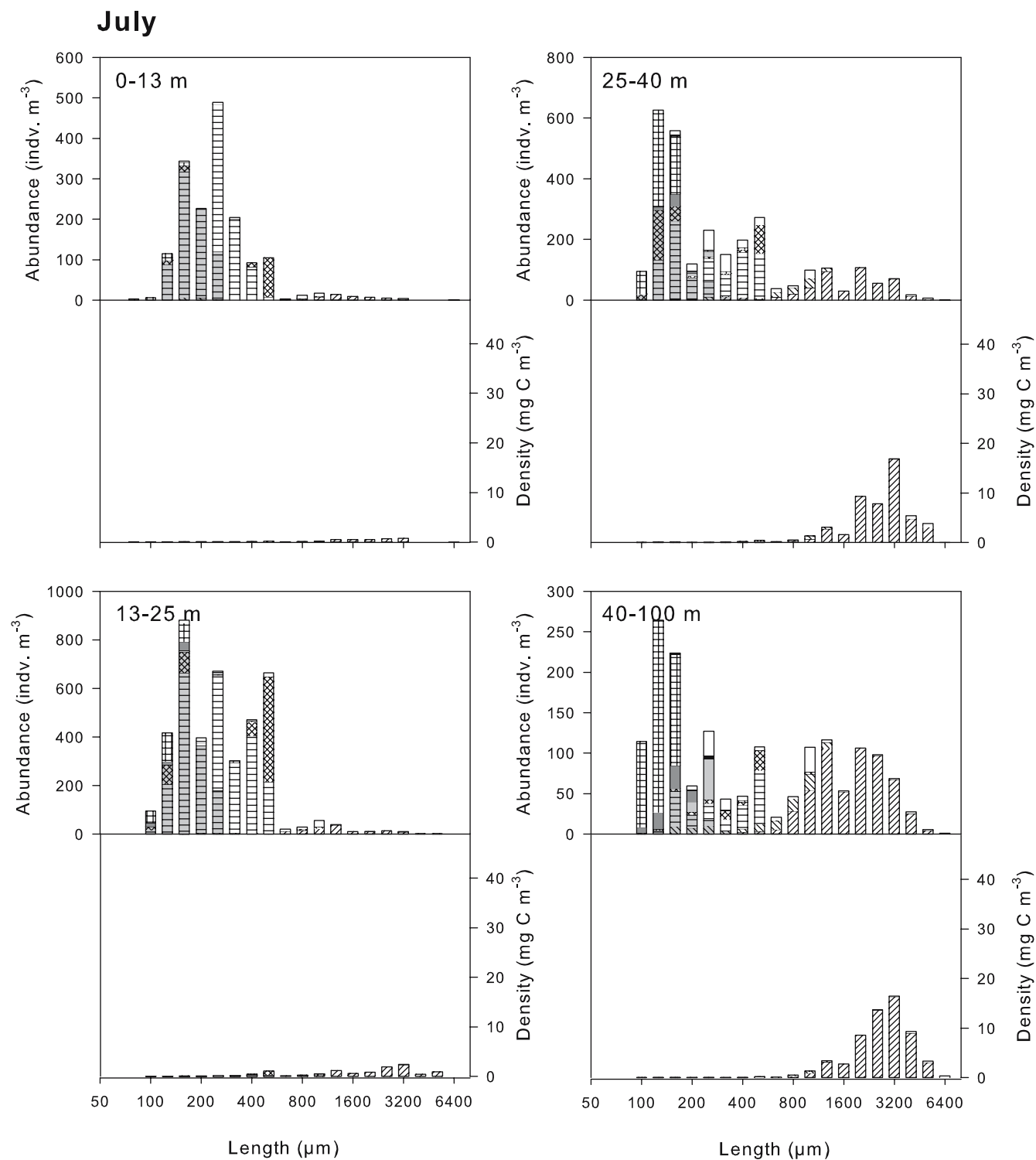
July

Fig. 6 Vertical distribution of zooplankton in mean abundance (*upper panel*, individuals m^{-3}) and density (*lower panel*, mg C m^{-3}) in July (see Fig. 1) in log$_{10}$ spaced intervals (μm). Midpoints of intervals, zooplankton categories and legends are as in Fig. 4. *Depth intervals* are indicated on each plot

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Fig. 7 Size (μm, axis $\log_{10}$ scaled) of the main prey items listed in Table 1 (except the groups *Appendicularia* and other) versus sandeel (*Ammodytes sp.*) and halibut (*R. hippoglossoides*) standard length (mm). **a** *Copepoda* (nauplii and copepodite stages), sandeel (ANOVA, $P < 0.0001$), halibut ($P = 0.09$). **b** *Eggs*, sandeel $P < 0.0001$, halibut $P = 0.05$ **c** *Bivalvia larvae*, sandeel $P = 0.04$, halibut $P = 0.62$. **d** *Gastropod larvae*, sandeel $P = 0.62$, halibut no observations
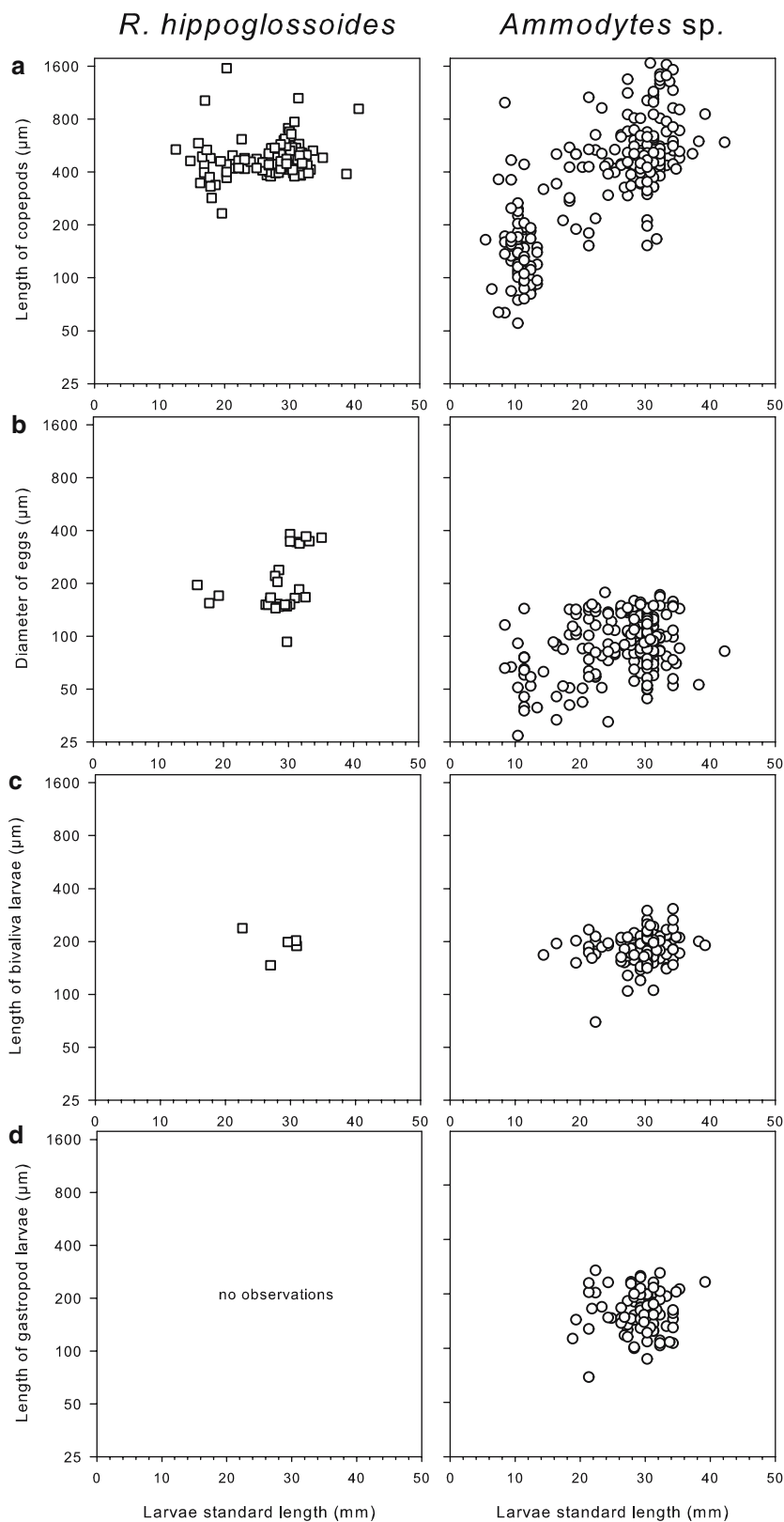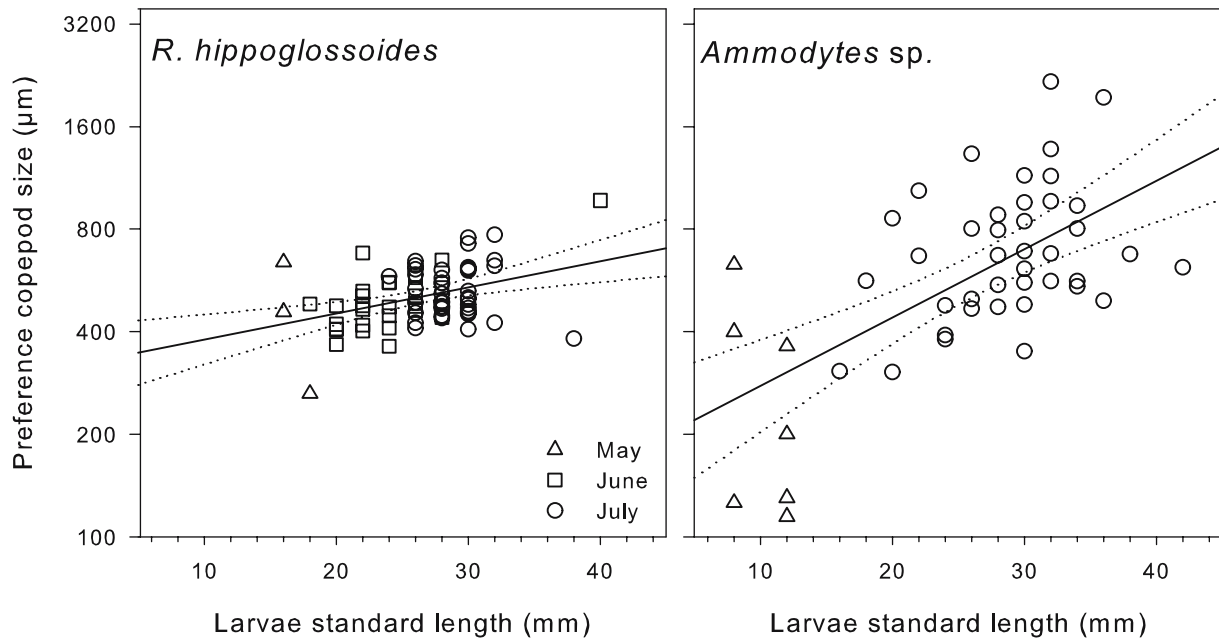
Fig. 8 Copepod size (µm, axis $\log_{10}$ scaled) preference versus length (mm) of halibut (*R. hippoglossoides*) and sandeel (*Ammodytes* sp.). Regression lines including 95% confidence limits are shown for each species (halibut $P = 0.0007$, $r^2 = 0.15$; sandeel $P = < 0.0001$, $r^2 = 0.37$)

Discussion and conclusion

General feeding ecology

The study shows marked differences in the feeding ecology of Gr. halibut and sandeel larvae in the sea off West Greenland. While sandeel increased its preferred prey size during ontogeny, Gr. halibut had an almost constant prey size preference throughout the investigated size range. Consequently, the RSPP was constant for sandeel while declining for Gr. halibut. The RSPP of 2.7% for sandeel was identical to estimates on sandeel (*Ammodytes hexapterus*) from the study by Pearre (1986; Fig. 2). Often the preferred prey size for fish larvae is within the range of 2–8% of larval length (Pearre 1986; Munk 1997; Østergaard et al. 2005). The steady RSPP have been suggested to reflect that predator and prey improve their attack and escape abilities with the same rate through ontogeny (Folkvord and Hunter 1986; Munk 1992). One hypothesis to explain the difference in size preference could thus be a hunting capabilities hypothesis; Gr. halibut do not improve their hunting capabilities at a rate that allows them to keep up the prey's avoidance skills. We will return to this and alternative hypotheses later in the discussion.

Larval diet

Greenland halibut and sandeel differ not only in preferred prey size, but also in preferred prey type. For large sandeels, eggs, bivalvia and gastropod larvae were more important in the diet than for Gr. halibut. Hence,

sandeel appear as more opportunistic predators than Gr. halibut. However, it should be noted that nauplii and copepodites still constituted between 88 and 99% of the gut content biomass for all sizes of both sandeel and Gr. halibut. The prevalence of copepods in the diet of the sandeel diet is in agreement with earlier reports on their feeding. For example, data from Monteleone and Peterson (1986) show that >97% of the food items in sandeel (*A. americanus*, 8–24 mm) were nauplii or copepodites. The diet of Gr. halibut larvae have only been described in a study from the eastern Norwegian and Barents Seas (Haug et al. 1989). In this study, calanoid copepods were the main prey.

Based on the size of the prey items and the size and abundance of sympatric plankton, it was likely that the relatively small eggs (>200 µm) in sandeel stomachs were copepod eggs while the larger eggs found in Gr. halibut were euphausiid eggs. As for the copepod prey items, it was likely that for sandeel it was nauplii of *Pseudocalanus* sp. in May and the early copepodite stages of *Calanus* sp. in July. Copepods of the genus *Pseudocalanus* were reported to be preferred by sandeel (*A. tobianus*) at a length of about 24 mm while larger larvae preferred copepodites of the genera *Temora* and *Calanus* (O'Connell and Fives 1995). The size composition in the diet of Gr. halibut indicated that the prey were nauplii of *Pseudocalanus* sp. and *Calanus* sp. in May and copepodites of *Oithona* sp. in June and July. Many other fish larvae (cod, haddock, herring, walleye, pollock and redfish) seem to avoid *Oithona* copepods (Cohen and Lough 1983; Kane 1984; Anderson 1994; Napp et al. 2000). Apparently, fish larvae have problems catching *Oithona* copepods due to their high evasion speed and, if captured, their large and
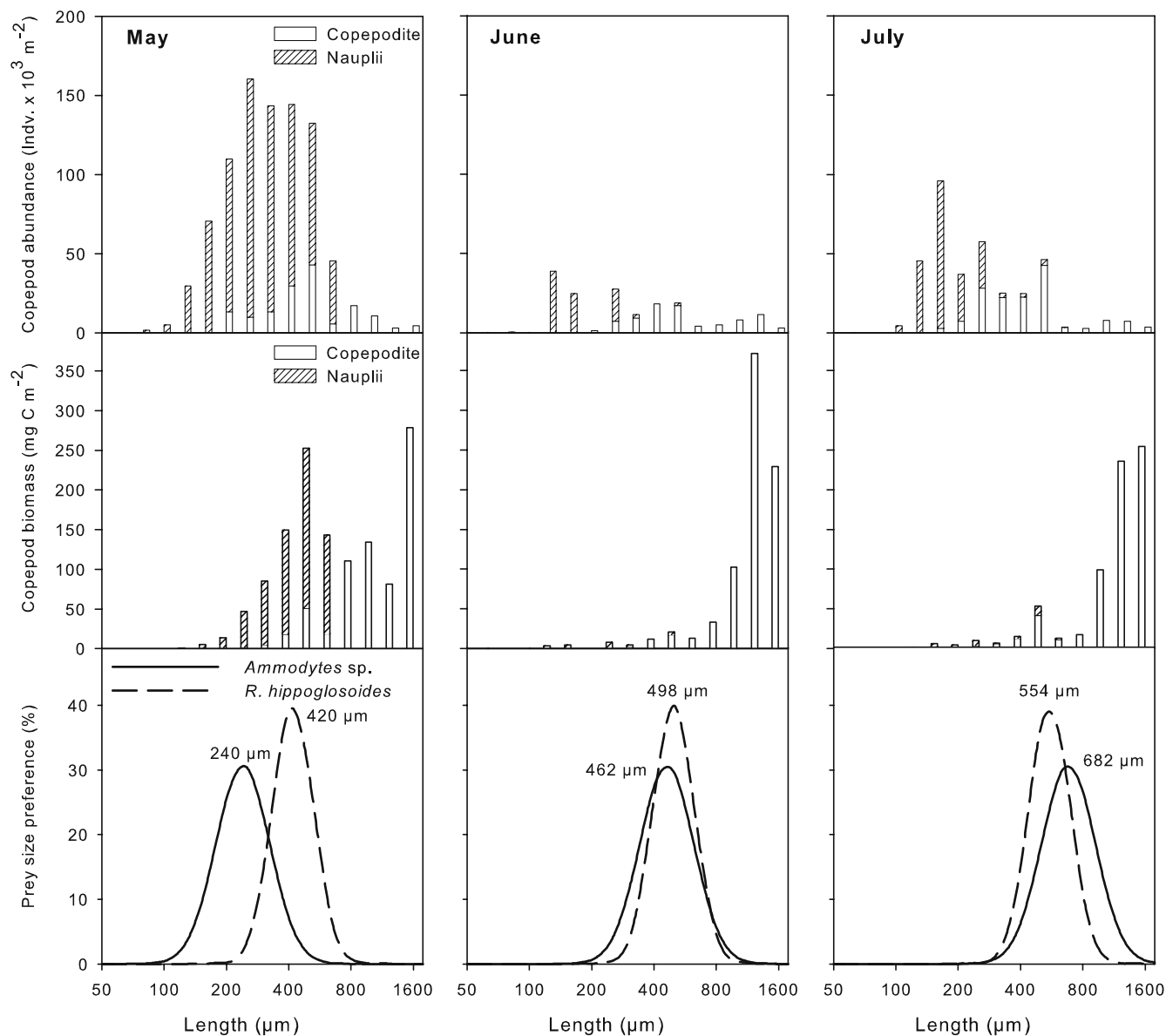
Fig. 9 Total available copepodite and nauplii stages of copepods in numbers (*upper panel*, individuals m^{-2}×10^3), biomass (*middle panel*, mg C m^{-2}) and larval prey size preference (*lower panel*, prey size preference in percent) for mean size halibut and sandeel larvae (see Fig. 2) in May, June and July surveys. The maximum preferred size indicated next to size preference *curves*

extended antenna makes them difficult to handle (Kane 1984). If Gr. halibut has a species preference for *Oithona*, then the earlier mentioned hunting capabilities hypothesis has to be rejected. An alternative hypothesis we put forward is the reduction in prey niche overlap hypothesis; in an environment where other abundant sympatric fish larvae exploit gradually increasing prey sizes during ontogeny, it can be advantageous for Gr. halibut to continue to exploit a constant prey size thereby reducing the prey niche overlap and thus competition for food. Evidence for such a hypothesis has been found in other studies (Kane 1984; Pepin and Penney 2000). For example, Kane (1984) found that for co-existing cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae, haddock larvae during certain periods utilized a different prey size than cod in order to minimize interspecific food competition. It could be the same mechanism observed in the present study for Gr. halibut and sandeel in July. The preference for sandeel in July was, as mentioned earlier, probably the genus *Calanus. Calanus* sp. is one of the key food items for fish larvae in general (Skjoldal et al. 1992; Anderson 1994; Sundby 2000) and the cumulated predation pressure on this genus could thus be high. The size preference by Gr. halibut could therefore be an avoidance of niche overlap thereby lessening interspecific food competition. A prerequisite for the reduction in prey niche overlap hypothesis to be valid is that a competition among predators for the same prey sizes has taken place. Before this is studied, the hypothesis can neither be confirmed nor rejected.

Fig. 10 The relative vertical distribution of available prey biomass in May (**a**) and July (**b**) surveys for halibut (*R. hippoglossoides*) and sandeel (*Ammodytes* sp.)
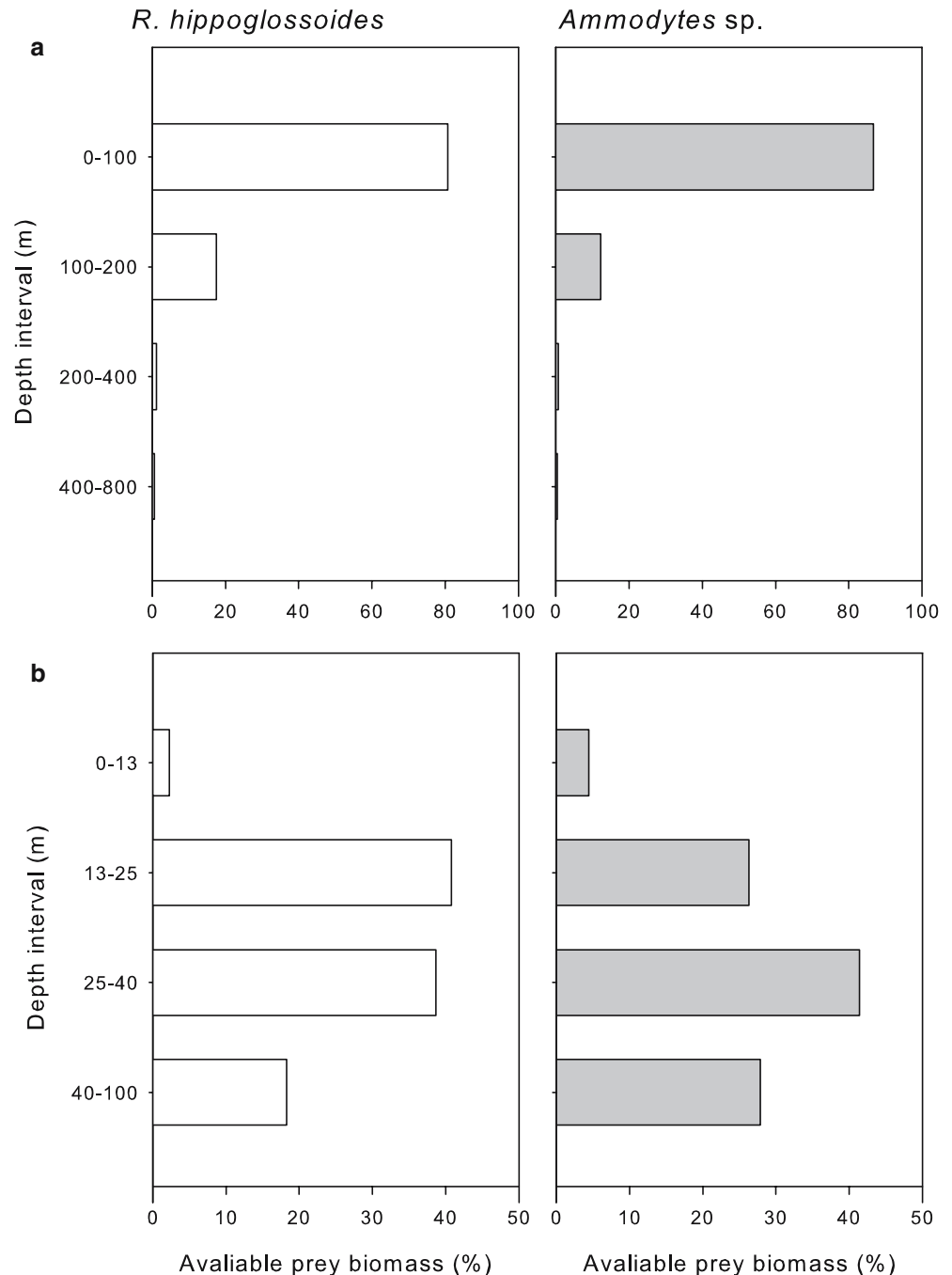
Vertical distribution

Sampling resolution was very coarse in May but generally food for Gr. halibut and sandeel was distributed only in the upper 100 m of the water column. As the larvae were active-feeding, they were expected to be distributed together with their food resources. This was confirmed for Gr. halibut from data on vertical distribution in the May cruise presented by Simonsen (unpublished data). Vertical distribution of Gr. halibut was also studied by Jensen (1935). Jensen stated that 10–18 mm long Gr. halibut larvae were distributed between 600 and 1,000 m depth. He furthermore reported that many of the larvae still had yolk sac attached which was interpreted as that they were not active-feeding. This is not in agreement with the present study were prey was found in the gut of larvae as small as 12.5 mm and most larvae between 12 and 16 mm were feeding. Remains of the yolk sac were observed in some larvae, but all larvae had apparently functional mouth and digestive apparatus. In the study by Jensen (1935), the Gr. halibut could have been in an earlier ontogenetic stage than in the present study, but judged from larval length this was not

Fig. 11 Distribution of mean relative gut fullness $+1\times$SE (*left axis*, in %) and size-preferred copepod biomass (*right axis*, in mg C m^{-2}) per station for halibut (*left panel*) and sandeel (*right panel*) at survey transects (see Fig. 1). *Shaded areas* indicate bottom topography along transects (down to 500 m)
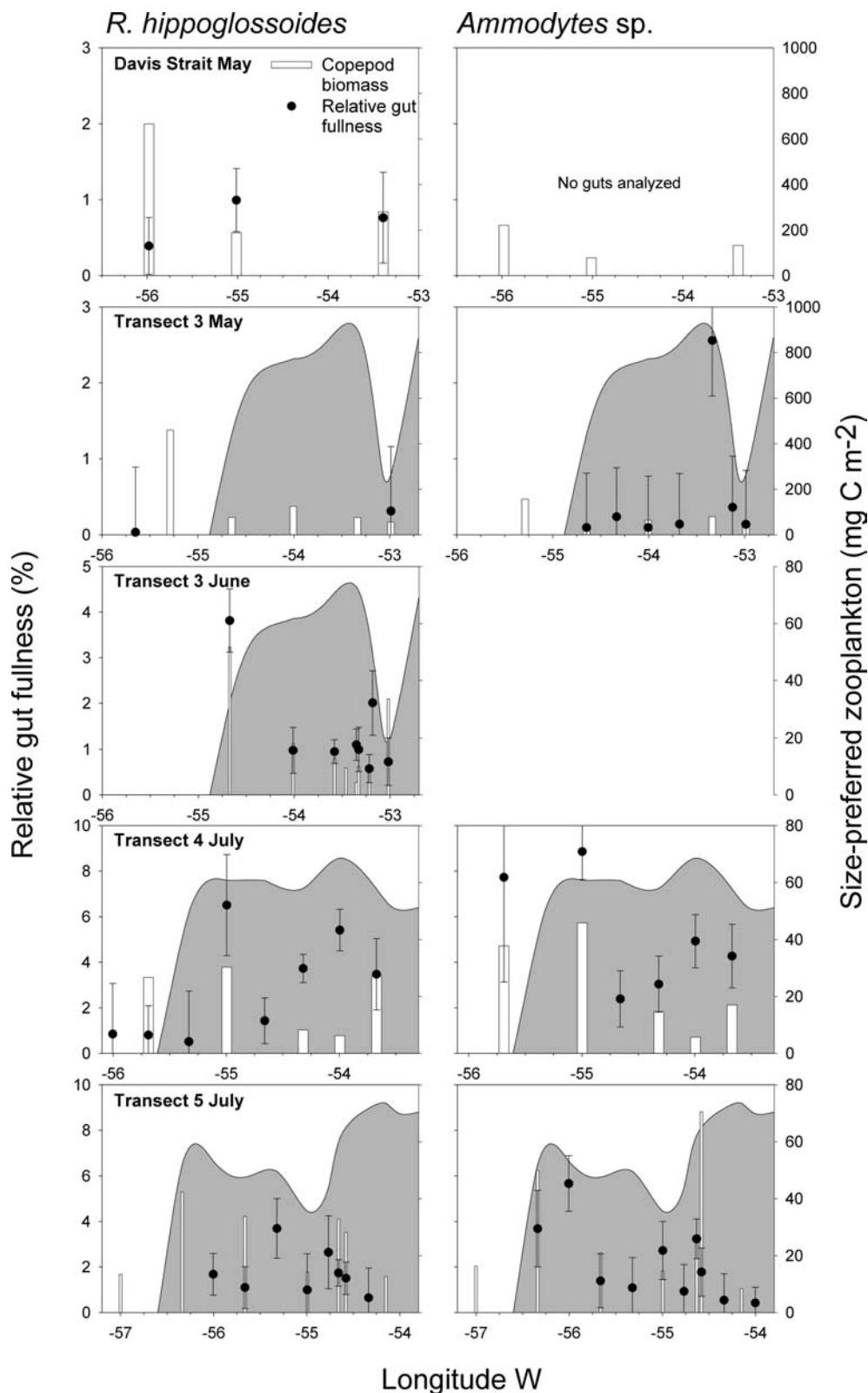
the case. Jensen probably misinterpreted the depth larvae were caught in due to the gear methodology used.

In July, the prey distribution both with regard to prey size and prey groups for Gr. halibut and sandeel was overlapping vertically between 13 and 100 m.

A difference in the vertical distribution of Gr. halibut and sandeel would therefore not result in exposure to different prey size niches. This could be a third hypothesis to explain the different size preference among the two species in July. However, even though Gr. halibut and sandeel prey were vertically overlapping, there was a tendency for both the Gr. halibut prey (available copepod biomass and euphausiid eggs which were found only in Gr. halibut stomachs) to be partly displaced to the upper water column compared that of sandeel prey (available copepod biomass and copepod eggs which were mainly found in sandeel stomachs). This could indicate a shallower distribution for Gr. halibut compared to sandeel, but further studies using a higher vertical resolution of both prey and fish larvae are needed to firmly establish this. Studies on vertical distribution of Gr. halibut and sandeel larvae from the July cruise showed large variation in Gr. halibut and sandeel larval abundance within the specific depth strata, and no significant difference in vertical distribution pattern was found Simonsen (unpublished data).

Transect distribution

Specific sections of the cross-shelf transects showed enhanced prey abundance to Gr. halibut and sandeel in parallel with increase in gut content of the larvae. Apparently, the offshore area west of the bank was an important feeding area for Gr. halibut in May. For sandeel, the important feeding area was the central part of the bank. In June and July, the feeding area for both Gr. halibut and sandeel had apparently shifted to the shelf break area. Prey abundance and gut content were generally higher here compared to other areas due to an increased biological production and/or an aggregation of the plankton. It is likely that production was enhanced since the phytoplankton community in June was in a post-bloom situation with general nutrient depletion in the upper water column (Poulsen and Reuss 2002). A recent study from West Greenland showed that the shelf break area was characterized by frequent upwelling events (Pedersen et al. 2005). Upwelling would provide such a mechanism for nutrient transport that would lead to increased biological production. Also, accumulation of plankton might take place while retention of particles in this area has been evidenced by drift simulations and deployment of drift buoys (Pedersen et al. 2005). These findings of higher abundance of zooplankton prey on the shelf break area agreed with studies on cross-shelf biological variability from other marine ecosystems where abundances of plankton to fish larvae generally were higher at the break (e.g. Richardson 1985; Lochmann et al. 1997; Munk et al. 2004). Highest mean gut content of the larvae was in all cases but one observed on stations with high prey availability. This indicates that prey abundance at other stations were sub-optimal. The observed cross-shelf variability in prey therefore probably lead to differentiated survival chances for Gr.

halibut and sandeel. In May, the feeding conditions were most favourable for Gr. halibut in the offshore area. This coincided with the area where newly hatched larvae emerge in April–May (Jensen 1935; Smidt 1969). In June and July, the most favourable area for both Gr. halibut and sandeel was the slopes of the banks and at the shelf break area. These were the same areas where Munk et al. (2003) and Simonsen (unpublished data) found higher larval abundance.

In conclusion, the relative prey size declined during Gr. halibut larval growth, while it remained constant for sandeel. Of the three hypotheses suggested to explain this difference, "the hunting capabilities hypothesis" was rejected while "the reduction in prey niche overlap hypothesis" and "the vertical distribution hypothesis" both needed further studies to be confirmed or rejected. Irrespective of the background, different prey size preference for Gr. halibut and sandeels resulted in differentiation in the available copepod prey biomass both in absolute terms and in spatial availability. In May, Gr. halibut prey density was highest in the off-shelf area in Davis Strait. In June and July, the prey-rich areas for both species were mainly located at the slopes of the banks and at the shelf break area. In these areas, gut fullness was higher than in neighbouring areas, suggesting that the larval food resource may be scarce in other areas.

The different prey size niches of Gr. halibut and sandeels in May and July make it plausible that their diet in these months were based on different copepod species. Unless their prey size niches were a result of interspecific competition for prey, their feeding foundation thus depends on population dynamics of different copepod species. Absence or low occurrence of these respective copepod species in the plankton environment could therefore reduce the feeding foundation and have severe complication for the recruitment success of Gr. halibut or sandeel. This mutual independence could explain why abundance indices of Gr. halibut and sandeel larvae in West Greenland waters historically have shown opposite responses to yearly environmental conditions and total zooplankton occurrence.

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Paper IV

Drift of Greenland halibut (*Reinhardtius hippoglossoides*) egg and larvae and the settling process

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Abstract

Drift and growth of Greenland halibut from egg throughout the pelagic larval stage was tracked from sub-populations spawning areas in Davis Strait, Baffin Bay, East Greenland and West Iceland by combing drift- and individual-based egg and larval temperature dependent growth models. Three surveys were carried out off West Greenland in July, August and September 2002 in order to validate the models and to examine time and spatial distribution in two sub-areas of Hellefisk Bank in West Greenland. The drift model showed that the exchange of individuals among the geographically-separated sub-populations could be important for metapopulation dynamics. Larvae from the spawning area in Davis Strait were primarily (>60%) transported to Canadian waters. Only larvae from the eastern part of the spawning area in Davis Strait remained in W Greenland. All larvae from the East Greenland spawning area were transported south of Cape Farewell and to W Greenlandic (82%) or Canadian (18%) waters. From the W Icelandic spawning areas larvae either, depending on the spatial location on the emergence first feeding larvae, drifted to E Greenland (45-53%), W Greenland (19−34%) or N Iceland (21−28%) or almost all

larvae (>98%) remained in Iceland waters. In Baffin Bay low water temperature resulted in very slow development rates and egg probably never hatched. The temperature dependent larval model showed fastest growth for the larvae spawned in W Iceland and estimated peak settling as early as July. For the other areas peak settling was in September to December, latest for larvae in Canada. The surveys showed that in W Greenland settling started in August and continued in September but the settling peak period could not be determined. The study in the two areas of Hellefisk Bank showed that juveniles at age 1 and 2+ almost exclusively occurred in one area while the 0-group was equally distributed in both areas. In the area of high abundance of juveniles age 1 and 2+, condition and stomach fullness was significantly higher. Nursery ground processes within the first year clearly restricted the successful nursery area to a more specific bottom habitat types. The concentrating of juveniles to more specific nursery areas implies that juvenile densities may approach the carrying capacity of their habitats in years when settlement is high which would dampens the annual variability in year class strength of Gr. halibut

Keywords: Greenland halibut, drift, modeling, settling, acoustic seabed classification, nursery ground, recruitment, connectivity

Introduction

Eggs and larvae of Greenland halibut (Gr. halibut) (*Reinhardtius hippoglossoides*, Walbaum) are transported by currents in the bathypelagic and upper pelagic water masses for more than half a year before they settle to the bottom (Jensen 1935, Smidt 1969). The drift of early life stages and the subsequent settling process in Greenlandic and adjacent waters is the target of this study.

The drift route of the eggs and larvae, and the position of their final destination where they settle to the bottom and become more stationary, are determined by: 1) the location of spawning site including the depth, 2) the specific gravity of the eggs and the resulting depth where they find their neutral buoyancy, 3) the buoyancy of the larvae and their behaviour with respect to depth selection. In addition, the ambient temperature along the

drift path determines how long they are subjected to free drift with the currents. Each of these stages can be summarized as:

Spawning in the NW Atlantic is not exactly localized. Observations of ripe female Gr. halibut and drifting eggs suggest that spawning areas exist in four main areas: In the Davis Strait off the Greenland /Canadian shelf (Jensen 1935, Smidt 1969, Templeman 1973, Gundersen et al. 2004, Simonsen & Gundersen 2005); W of Iceland along the shelf to the Irminger Sea (Magnusson 1977, Sigurdsson 1977); in E Greenland close to Kap Bille (Gundersen et al. 2001) and in Baffin Bay (Gundersen et al. 2004). In other areas of the North Atlantic the spawning is known to be demersal and occur at depths of 800 to 1200 m (Bowering & Nedreaas 2000, Albert 2003, Morgan et al. 2003).

Vertical depth distribution of Gr. halibut eggs will, like other bathypelagic eggs (e.g. eggs from Atlantic halibut in Norwegian fjords) be embedded around the halocline, and have a neutral buoyancy with reference to a specific salinity. This is because fish eggs have the temperature of the ambient water, but keep specific water content by osmoregulation. There are observations on Gr. halibut eggs in Davis Strait by Smidt (1969) but the depth distribution is somewhat uncertain as only wire lengths from 600 to 1600 m have been reported. The ratio between wire length and fishing depth was probably around 0.4 (Stenberg unpublished results). This suggest that Gr. halibut eggs are at 240 to 640 m depths which corresponds to the lower part of the halocline (salinity 34.8) that is located at 200 to 500 m depth (Buch 1990). After hatching, the larvae become lighter because of the loss of the chorion which is the heavy material of the egg. Hence, the larvae get additional hydraulic lift and rise further up in the water column. After the yolk sac has been consumed the larvae must be distributed in the same depth range as their prey, and as they continue feeding and become more mobile they will be able to control their depth distribution independent of buoyancy. In W Greenland this is at 13−40m depth (Simonsen et al. 2006, Stenberg et al. *in prep.*).

The time from egg fertilization to hatching can be determined by a simple degree-day calculation (defined as days multiplied by degrees in Celsius) (Pittman et al. 1990,

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Neuheimer & Taggart 2007). In a study in the Barents Sea the developing time for Gr. halibut egg from fertilization to hatching was 53 days or around 115 degree-days (5 days at 4°C and subsequent 48 days at 2°C) (Stene et al. 1998). At hatching Gr. halibut larvae are not in an advanced state of development, but are equipped with a large yolk sac (Jensen 1935, Stene et al. 1998). The duration of the yolk sac stage is unknown. In Atlantic halibut (*Hippoglossus hippoglossus*) the yolk sac is fully resorbed in 305 to 395 degree days after hatching (Pittman et al. 1990). First feeding in Atlantic halibut starts about half way through the yolk sac stage (Kjørsvik & Reiersen 1992). As Atlantic halibut resemble Gr. halibut, e.g. in egg size (3 mm (Pittman 1996)), hatching time (~80 degree days (Pittman 1996)) and its primitive development at hatching (Pittman 1996) it seems plausible that Gr. halibut have an similar absorption and first feeding time. Temperature is one of the parameters that most significantly affects growth rate of the larval stage (Houde 1989, Otterlei et al. 1999, Neuheimer & Taggart 2007). In a review by Houde (1989) on the effect of temperature on fish larval growth weight-specific daily growth rate increased significantly by 0.01 for every 1°C increase.

The change from pelagic larvae to dermersal juveniles, the settling process, has been suggested to take place in autumn at a size of 65−70 mm (Jensen 1935, Smidt 1969) but has otherwise never been studied in detail. Abundance of juvenile Gr. halibut in W Greenland waters is high on Hellefisk and Disko Bank (Jensen 1935, Smidt 1969) and in Canadian waters in Ungava Bay and on Hammilton Bank (Lear 1970, Templeman 1973) (see Fig. 1). In E Greenland and Iceland waters there are apparently no grounds with juveniles abundance similar to the those observed in W Greenland (Boje & Hjörleifsson 2000).

The aim of this study is to reconstruct and analyze the overall drift pattern and growth of Gr. halibut eggs and larvae from geographically-separated sub-populations (metapopulations) around Greenland by combining drift modelling and individual based egg and larval temperature-dependent growth models. The focus will be the spatio-temporal distribution of small first feeding and large settling larvae, and the connectivity between metapopulations. Model results of drift distributions of eggs

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and larvae in W Greenland waters are compared to results from a July trawl survey. Small-scale spatio-temporal distribution and the settling process will be examined in August and September at areas at Store Hellefisk Bank at two surveys. Seafloor sediment characteristics and information on Gr. halibut juvenile feeding and condition are analyzed for geographical differences.

Materials and Methods

The ocean circulation model

The ocean circulation model used is the Hybrid Coordinate Ocean Model (HYCOM). The model is described in detail by Bleck (2002), and online information is found at http://hycom.rsmas.miami.edu. It is a primitive equation ocean general circulation model which solves the three-dimensional prognostic equations for horizontal velocity, continuity (giving elevation and layer thickness), salt and temperature. The vertical coordinate is generalized. In the hybrid configuration the vertical coordinate is isopycnal in the open, stratified ocean, but smoothly reverts to a terrain-following coordinate in shallow coastal regions, and to z-level coordinates in the mixed layer and/or unstratified seas. This makes the model suitable for simulations of the open ocean as well as shallow coastal seas and unstratified parts of the world ocean.

Tidal forcing is included as a body tidal potential, meaning that the tidal wave is generated within the model domain. The routines for tide generation have been developed at NCEP/NOAA. The model includes a thermodynamic representation of sea ice, but sea ice dynamics (ice drift) is lacking.

The model covers the Atlantic Ocean from about 20°S and the entire Arctic Ocean with an approximately 50 km horizontal resolution and 29 vertical levels. For the drift simulations we used a one-way nesting of about 10 km resolution and 26 vertical levels covering the Greenland Waters. The atmospheric forcing was taken from the DMI numerical weather prediction model DMI-HIRLAM-T (Yang et al. 2005) covering a large part of the northern hemisphere with a 0.15 degree resolution.

River runoff data was applied as mean monthly climatological discharges from the 115 largest river discharge stations of the Global Runoff Data Centre (GRDC, http://grdc.bafg.de) and scaled as in Dai & Trenberth (2002). No data on river discharge climatology exists for the large Greenlandic fjords. Therefore, pseudo monthly climatologies was made for 5 fjords using discharges taken from an ice-cap model (Box et al. 2004). The surface temperature and salinity was relaxed towards (1/4°) climatological temperature and salinity fields by Boyer et al. (2005). A detailed description of the ocean model setup is found in Ribergaard et al. (2006) including a preliminary validation of the model performance.

The particle tracking model

The modelling of particle transport is driven by the input current field. The quality of the particle trajectories is therefore limited by the quality of this field. We use the drift model used by Ribergaard et al (2004). The drift model solve the advection-diffusion equation for a passive tracer C given by

$$\frac{\partial C}{\partial t} + \vec{\nabla} \bullet (\vec{u}C) - \vec{\nabla} \bullet (k\vec{\nabla}C) = 0 \tag{1}$$

where t denotes time, k horizontal diffusion and $\vec{u} = (u, v)$ is the horizontal advection velocity.

For the turbulent diffusion a random walk model is used. The basic idea is that the ensemble mean of the square of the particle displacement $\vec{x} = (x, y)$ satisfies

$$\frac{d < \vec{x}^2 >}{dt} = 2k \tag{2}$$

For each particle the solution of equation 2 at time step n+1 is of the form

$$\vec{x}_{n+1} = \vec{x}_n + R_n \sqrt{\frac{2k\Delta t}{r}} \tag{3}$$

where R_n is a random number with mean $< R >= 0$ and standard deviation $< R^2 >= r$. We choose R as uniformly distributed between -1 and +1, in which case r=1/3.

Following Visser (1997) and Spagnol et al (2002), the solution of equation 1 is

$$\vec{x}_{n+1} = \vec{x}_n + \vec{u}\Delta t + \nabla k_{\bar{x}_n}\Delta t + R_n\sqrt{\frac{2k_{\left(\bar{x}_n + \frac{1}{2}\nabla k_{\bar{x}_n}\Delta t\right)}\Delta t}{r}} \qquad (4)$$

where the diffusion, k, is allowed to vary in space. The two first terms on the right hand are the solution for pure advection with no diffusion. The fourth term is the random walk diffusion similar to equation 3 but as the diffusion varies in space, the diffusion is estimated at a distance $\frac{1}{2}\nabla k_{\bar{x}_n}\Delta t$ offset $\vec{x}_n$. The third term is an additional advective term that tends to transport particles towards regions of increasing diffusivity. Without this term, the particles will concentrate at regions of low diffusion which is obviously incorrect (e.g. Visser, 1997).

The drift model was run with a time step of 300 seconds and the horizontal diffusion was taken to be constant 60 m^2/s as in Ribergaard et al. (2004)

The drift simulations

The drift simulation of Gr. halibut egg and yolk sac stages were made for "potential spawning" areas for metapopulations in Greenland and adjacent waters areas. Potential spawning areas are defined as areas where numerous Gr. halibut eggs or sexual ripe females have been observed. These were Davis Strait, Iceland, E Greenland at Kap Bille Bank and in Baffin Bay (cf. introduction). A total of 8 spawning sites were chosen within these 4 areas (Table 1). Egg spawning was simulated by release of 1000 particles at each site. The release was in time assumed to following a normal distribution (f=a*exp(-.5*((x-x0)/b)^2)) starting in mid-February and with a duration of 40 days (Gundersen et al. 2004). The normal distribution coefficients was found by a Gaussian, 3 parameter fitting of the Gr. halibut larval size distribution in May (Simonsen et al. 2006). The coefficient were determined to; a= 0.4; b=8.1; x0=31. The bathypelagic eggs and yolk sac larvae were assumed to be embedded just below the halocline, which in W Greenland waters is found as the upper part of the Irminger water component, and in SE Greenland waters in upper ~200 m. In the isopycnal hydrodynamic ocean model these depths correspond to the density (Sigma-theta) 27.63 kg m^{-3}. The use of a constant gravity of the eggs and yolk sac larvae for

the entire period may have introduced some error, however its magnitude is believed to be minimal: In the first few days the specific gravity of the fertilized eggs increases during the gastrulation until closing of the blastopore (Stene et al. 1998). This will result in an initial rise of the eggs from the spawning depths and a subsequent decent due to the increase in specific gravity. Because of the short temporal nature of this up and down vertical motion it will be of small consequence for the resulting horizontal transport. The drift of the eggs and subsequently the drift of yolk sac larvae were estimated until the larvae reached the first feeding stage (FF larvae) which was assumed to have a duration of 300 degree-days (from Atlantic halibut: Pittman et al. 1990). Where degree-days was defined as the time [days] integrated temperature [ºC]. In order to ensure a minimum growth also at temperatures around zero degrees a minimum increase in degrees-days was set to 0.1 per day.

The drift simulation in the pelagic larval phase was carried out from the stages FF larvae to settling larvae (SE larvae). In order to evaluate the effect of depth a 20 m and a 40 m depth drifting scenario were carried out. A thousand particles were released in the area of highest density of FF larvae obtained from the egg and yolk sac larvae drift simulation (Fig. 2). Starting date was set to the average calendar day for the completion of egg and yolk sac larvae drift simulation. The vertical distribution was assumed constant during the pelagic larval phase at 20 or 40 m. Temperature has a high influence on larval growth rates and thereby on the duration of the larval drift phase. The ambient daily temperature of the drifting particles was therefore used to estimate daily larval growth. Gr. halibut larval size distribution and water temperature (in the depth interval 5-40 m) in their distribution area in W Greenland waters was available from May, June and July (Simonsen et al. 2006) and size of newly settled fish was available from survey in September. The increase in fish weight from these 4 periods (see table 2) was used to estimate the weight-specific growth rates (G) as

$$G = (\ln W_2 - \ln W_1)/(d_2 - d_1) \tag{5}$$

where W_2 and W_1 are dry weights in mg at the calendar days d_2 and d_1, respectively.

G for the different larval sizes/periods was estimated to be 0.024 to 0.054 at temperatures between 0.13°C to 3.75°C (table 2). This corresponded to a increase in G with 0.014 for each degree which is very similar to Houde's temperature factor on 0.1 (Houde 1989). We searched for a relationship between the growth rates as a function of weight, but found it to be insignificant. The daily temperature-dependent growth increase is calculated as:

$$W_i = W_{i-1} * \exp(G + (0.014 *(T_{mod}-T_{mid}))) \tag{6}$$

where W_i is dry weight in mg of the specific day; W_{i-1} is dry weight in mg the day before; T_{mid} is in situ midpoint temperature; T_{mod} is temperature for the drift particle in the model; G is weight-specific growth rate (table 2). The larvae were followed from an initial length of 12 mm length or a weight of 0.34 mg (smallest pelagic larval size observed in the upper water masses (Jensen 1935)) , to a terminal length of 65 mm or a weight of 210 mg (approx. the largest pelagic larvae and smallest newly settled observed (Jensen 1935; this study).

The surveys

Three surveys were conducted off W Greenland. The first survey was carried out from 3 July-7 August 2002 (July survey) and covered an area from NAFO 1F at 60°N to NAFO 1A at 71°N. Sampling was undertaken at 186 stations as part of the annual shrimp and fish trawl survey conducted by the Greenland Institute of Natural Resources. The survey covers depths from 70-600 m. The second and third surveys were carried out in two areas of the Hellefisk Bank in NAFO 1B from 25−27 August 2002 (August survey) and 27−29 September 2002 (September survey). AREA 1 was at N 68°15−68°54 to W 56°−57° and AREA 2 at N 67°30−67°54 to W 57°−58°. Six stations in each area were revisited in the August and September survey.

On all survey stations a trawl haul with a Skjervøy 3000/20 trawl with bobbin gear and double bag was carried out. The mesh size in the codend was 20 mm. The 20 mm mesh size will give a full selectivity on Greenland halibut from sizes of about 9 cm assuming a selection factor of 3.1 as found by Huse et al. (1999). The trawl doors were Greenland Perfect size 370*270 cm and wing spread was set as 19.0 m. The tow

speed was 2.5 knots and duration was 15 or 30 minutes. All trawl hauls were carried out during daytime. After each haul, the Greenland halibut catch was length measured (total length to the cm below), counted and the total weighs recorded (to 0.1 kg). In larger catches only sub-samples of fish was measured. All catches were standardized to one hour trawling. In order to homogenize variance abundance was transformed by the natural logarithm to n+1 prior to statistical analysis. From each haul in the two sub-areas up to about 50 fish smaller than 25 cm were preserved in 4−6 % formaldehyde for later processing in the laboratory.

In the laboratory each fish was weighed and liver and stomach (stomach plus intestine) were removed and weighed separately. Liver weight indicates the amount of energy reserves the fish has built up and was used as a proxy for fish condition. Difference in liver weight ($\log_e$ transformed to obtain linearity and homogenous variances) between the two areas was examined by analysis of variance using fish length as a covariate. Stomach weight was used as a proxy for stomach fullness. Difference in stomach weights ($\log_e$ transformed) between areas was analyzed as for liver weight.

Gr. halibut were separated on ages 0, 1 and 2+ by their length distribution. This approach have been used in Gr. halibut to validate ages up to four years (Lear & Pitt 1975, Bowering & Nedreaas 2001). We performed a modal progression analysis using the "Bhattacharya" method (Bhattacharya 1967) in the FiSAT II version 1.2 (Gayanilo et al. 2005). The separation resulted in different cohorts with a mean length and standard derivation to the mean. Mean length +/- 1.96 *standard derivation was used to define 95% confidence intervals for the age cohorts (Sokal & Rohlf 1995).

On the September survey the seabed was classified into 6 different classes based on acoustic data obtained from a Furuno FCV-161 dual frequency echo sounder operating at 28 KHz, a 3.0 ms pulse length and using a transducer beam width of 22 degrees. The acoustic data were sampled by the QTC-V acquisition system (Quester Tangent Co) and processed in the QTC IMPACTTM software from Quester Tangent. This processing approach has proven to be an effective technique for bottom mapping

(Hamilton et al. 1999). Prior to input to the classification algorithms, the envelope of the echo return was calculated, and time-varying gain applied. The onset of the bottom return was then automatically picked, the echoes aligned with respect to the bottom pick, and the echoes coherently stacked to reduce noise. To compensate for variations in depth, the standard echo length of data (the expected length of echo return from a flat seabed given the pulse length, sounder frequency and beam width) beyond the depth pick was fitted onto a fixed number of points (100 points). A window of 256 samples of each stacked echo was selected, with the first point a small fixed number of samples prior to the bottom return pick. These windowed echoes, which depend on both the specular and scattered energy returned from the seafloor, were inputted to a suite of algorithms to extract echo features based on the shape and spectral content of the echoes. The features are stored as a vector, and further reduced to three values (Q-values) using principle component analysis. These three values were then used to cluster the echoes into six classes based on acoustic diversity which represent different bottom types. To ground truth the classification results, 13 sediment box cores were collected during the survey.

All statistical analyses were performed in the SAS/STAT software Version 9 of the SAS System for PC, SAS Institute Inc., Cary, NC, USA. The following abbreviations were used for statistical tests; ANOVA: analyse of variance; ANCOVA: analysis of covariance; GLM: general linear models. ANOVA, ANCOVA and GLM analyses were carried out by the GLM procedure which accommodate unequal balance designs.

Results

Model simulations

Egg and yolk sac larvae stages

In the Davis Strait releases I to III there was a marked difference in distribution pattern after 300 degree-days of drift. For release I and II simulated first feeding larvae (FF-larvae) were distributed parallel to the shelf break both N and S of the release point with the majority in areas NAFO 1C (49%) and 1D (29%) (Fig. 2a,

Table 3). FF larvae from release III were distributed more W with the far majority in NAFO 0B (91%) (Fig. 2b, Table 3). Vertically, they were embedded in water masses about 300 to 700 m, deepest for the particles closest to Greenland. The development time from egg to FF larvae in the Davis Strait releases varied between 80 to 110 days. There was a tendency to longer development time for larvae distributed toward W. The drift simulations from release I-III suggested that the 300 degree-days ontogenesis was reached at May 23, 24 and 27 respectively.

In the Baffin Bay release IV the development time was very prolonged in the cold water masses. In August the mean degree-days was only about 60 and the maximum observed was 128 degree-days. The simulated egg and yolk sac larvae were thus not even half way through their 300 degree-days ontogenesis to FF larvae. Due to the cumulative mortality effect the long time span must result in few, if any, hatched FF larvae (Pepin 1991). Furthermore, even if larvae succeeded they would be off phase with the plankton bloom resulting in starvation of the first feeding larvae (Bagenal 1971, Smidt 1979). Larvae in Baffin Bay were therefore not included in the further analyses.

In the E Greenland release V the FF larvae were distributed offshore around Cape Farewell into Labrador Sea in NAFO 1E (24%), 1F (60%) and 2G (1%) but some remained in the Irminger Sea in ICES IRMGRL (15%) (Fig. 2c, Table 3). Vertically the model showed a deeper distribution in Labrador Sea, 600–700 m, compared to 400–500 m in the Irminger Sea. Development time varied between 80 and 140 days, longest in the Labrador Sea. On average the 300 degree-days was reached at June 20.

In the Iceland releases VI to VIII the drift resulted in very different distribution of FF larvae. From release VIII FF larvae were mainly distributed along the Icelandic shelf from SW Iceland (SICE 86%) and across the Danmarks Strait to N Iceland (ICES NICE 10%). Releases VI and VII FF larvae remained at the SW Iceland shelf (SICE 58 and 70%) and into the Irminger Sea (IRMICE 70 and 30%) (Fig. 2d, Table 3). Vertically there was also considerable difference in distribution. In SW Iceland the simulated larvae were distributed around 600–700 m but only at 100–200 m in NW Iceland.

Development time for the Icelandic releases was only 50 to 90 days. Fastest growth was seen for the particles distributed SW. On average the 300 degree-days was reached at May 3, 4 and 15 for release VI, VII and VIII respectively.

Pelagic larvae to settling stages

Drift simulations of the FF larvae to settling larvae (SE larvae) from Davis Strait showed that more than half (58% for the 20 m; 72% for 40 m) of the SE larvae from release I were distributed in Canadian waters (in NAFO OB, 2G-H-J) while for release II and III it was almost all (>89%) (Table 4). The Canadian distribution covered an extended area from NAFO 0B to 2J and the 40 m drift simulation resulted in a more southerly distribution compared to the 20 m simulations (Fig. 3). Some SE larvae were observed to hit the models southern boundary. High SE larval concentrations were especially seen over deep waters in NAFO 0B and at more shallow depths over the shelf and Hamilton bank in NAFO 2 J (Fig. 3). In W Greenland SE larvae were, especially for the 20 m drift simulation, distributed over northern part of Hellefisk Bank, Disko Bank and inside Disko Bay in NAFO 1A (Fig. 3, Table 4).

In E Greenland, larvae from release V was mostly transported to W Greenland waters, but some drifted to Canadian waters as well (Table 4). In W Greenland SE larvae from the 20 m simulation had a more northern distribution which included the bank areas in NAFO 1B-C but highest concentrations were seen in NAFO 1E-D over deep waters. For the 40 m simulation highest SE larval concentration was seen in the southern part of NAFO 1F over deep waters. The larvae that was transported to Canadian waters were mainly seen in the deep waters in NAFO 2G.

In Iceland, larval drift was simulated from three positions in SW, W and NW Icelandic shelf as they were well represented by the general distribution pattern from the three Icelandic spawning releases. This approach was taken because there was no well-defined centre of mass for the FF larvae distribution and because initial simulations showed a great variability in drift route for the FF larvae depending on choice of release position within only 20-30 km distance. The SW position was the

area with high FF larvae density from spawning release VII, while the W and NW positions were from the spawning release VIII (referred to as VIIIA VIIIB). Larvae from SW almost all (>98%) remained in Icelandic waters (Table 4) and were transported from S Iceland to the shelf area (Fig. 5a). From W larvae were retained in the same area until they reached settling size (Fig. 5b). However, a continuation of the drift model hereafter showed that they began to drift to E Greenland a few weeks later (mid August) and one month later almost all had drifted to the E Greenland shelf and followed the same drift route as many of the NW larvae. Most NW larvae drifted toward E Greenland and were, similar with SE larvae, distributed with about 50% in E Greenland waters, mainly at the shelf from 60 to 65°N (in GRLIMR 45% to 53%), 20% to 30% around Cape Farewell to W Greenland waters (in NAFO 1F-E-D-E and 1B 19 to 34%) and a smaller number, about 15% of the larvae that did not drift toward E Greenland, were transported to the shelf N of Iceland (in NICE 15 to 16%) (Fig. 5c, Table 4).

Larval growth simulations for the different releases showed differences between the settling date for the 20 and 40 m drift depth scenarios within the same area. In Canadian waters simulated larvae in 40 m settled about 1½ to 2 months later compared to the 20 m scenario (Table 5). In the ICES areas, the difference between the 20 and 40 m simulation was less than 1 week. The earliest settling period was seen for the Icelandic spawning releases. Here settling was estimated to have its peak as early July for larvae S of Iceland (Table 5) while larvae that drifted to E Greenland (in ICES IRMGRL) had its maximum settling period around September. The latest settling period was seen in Davis Strait spawning releases (I-III) that drifted to Canadian waters (in NAFO 0B and 2HGJ). Here settling had its maximum in October–January, latest for the 40 m drift scenario. In W Greenland waters the Davis Strait (I) releases that drifted to NAFO 1AB settled over a relative long time span starting in August and ending in January with a peak around November for the 20 m and around December for the 40 m simulation. The E Greenland spawning release (V) had its maximum settling in NAFO 1CDEF in October (Table 5).

Survey

Fish size and age classes in W Greenland

The Gr. halibut size distribution showed distinct cohorts (Fig. 6). The separation on age classes by the Bhattacharya method separated the age 0 and 1 with good precision and no overlap in size distribution while it was more difficult to identify older age class cohorts precisely (Table 6). Hence, they were pooled into a 2+ age group. All fish above the minimum length for age 2 was thus classified into this group (see Table 6). Age 0 was not observed before the August survey and had highest concentrations on the September survey (Fig. 6). For age 1 there was a progressive increase in mean length between the three surveys from 14.8 cm in July to 17.2 cm in September.

Spatial distribution of settled Gr. halibut in W Greenland

The July survey covered the W Greenland shelf area from 60 to 71°N but was conducted too early to catch the 0-group. Age 1 Gr. halibut was observed in the entire survey area, but they were clearly more abundant at 68° to 70°N at the slopes of Hellefisk Bank and Disko Bank and inside Disko Bay at 200 to 400 m depth (Fig. 7). Average concentration for stations north of 68°N was 93 specimens per hour (SD=160 n=92) while south of 68°N concentration was 5 specimen per hour (SD=13 n=77). Age 2+ were also most abundant between 68° to 70°N but the centre of distribution were in the central parts of Disko Bay at 300 to 500 m depth (Fig 7). Average concentration for stations north of 68° N was 17 specimen per hour (SD=32 n=92) while south of 68°N 1 specimen per hour (SD=2 n=77). A significant correlation between fish size and depth (GLM, P<0.0001) indicated a general migration toward greater depths as the fish grew.

The surveys in August and September at the slope of Store Hellefisk Bank in the two sub areas AREA 1 and AREA 2 showed considerable difference in the spatial distribution pattern of the 0-group and the older Gr. halibut (Fig. 8). For the 0-group there was no difference in concentration between sub areas on both surveys (ANOVA, August P>0.7; September P>0.3) (Fig. 8), but for both age 1 and 2+ there was a highly significant difference in concentration between areas in both August and

September (ANOVA, P<0.0001). The age 1 and 2+ fish was clearly associated to area AREA 1 (Fig. 8).

As for the July survey, the August and September survey also show significant increase in Gr. halibut size (length) with fishing depth (GLM, P<0.0005).

Stomach fullness and condition of settled Gr. halibut

Stomach weight increased significantly with fish size for all ages (GLM, p<0.001) and there were no interaction effects of area (homogenity of slopes, p>0.15) Almost all age 1 and 2+ fish in AREA 2 had stomach weight, below average (Fig. 9) and the difference between the areas was highly significant (ANCOVA, P<0.0001). The difference in standardized mean (LSMEANS) stomach weight was for age 1 fish 38% and for age 2+ fish 44%. For age 0 there was no difference between areas. (ANCOVA, P=0.50).

Liver weight also increased with fish size for all ages (GLM, P<0.001) and there were no interaction effects of area for age 0 and 2+ (homogenity of slopes, P>0.12) but an effect for age 1 (homogenity of slopes, P<0.04) (Fig. 10). We observed the same pattern as for stomach weight with a relatively larger liver weight for most individuals in AREA 1. The difference between the two areas was significant for age 1 with a length $\geq$ 16 cm (separate slope model, P<0.002) and for all age 2+ fish (ANCOVA, P<0.03) while not different for the 0 group (ANCOVA, P<0.66). The difference in standardized mean liver weight was 20 to 30% for age 1 length $\geq$ 16 cm and 24% for the age 2+ group.

Sediment

Classification of the echo sounder data resulted in six acoustic classes as descriptors of seabed type; three types predominated in the studied areas at the slope of Hellefisk Bank (Fig 14). In AREA 1 the predominated classes where 1 and 2 while class 4 predominated in AREA 2 (Fig. 11). Box cores showed that the class 1 and 2 was clay and silt w. shell or little organic material while class 4 was silty sand w. gravel, less clay and some shells (Fig 14).

Discussion

Drift and population structure

The present study is the first that quantitatively models drift of Gr. halibut early life stages and show, that 0-group Gr. halibut at Hellefisk Bank, mainly are recruited from a spawning in Davis Strait. The drift modelling also shows that the 0-group Gr. halibut spawned in Davis Strait reach the banks off Baffin and Labrador. 0-group in SW Greenland are recruited from spawning areas in E Greenland or W Iceland while those in E Greenland and N Iceland are recruited from a spawning area off W Iceland. However, it was evident that drift from a given spawning site did not result in a uniform flow direction. Some egg and larvae drifted to other areas and mixed with larvae from other spawning sites and probably later recruited to local populations: For example some larvae from spawning in Iceland drifted to W Greenland and from E Greenland to the Banks off Labrador. The exchange of individuals is apparently great enough to sustain a genetic homogeneous structure of Gr. halibut in the NV Atlantic (Vis et al. 1997). This suggests that connectivity plays an important role in the local and metapopulation dynamics, community structure and genetic diversity across Gr. halibut populations in the NW Atlantic.

Drift from spawning to first feeding larvae

Drift simulations of the spawned egg until the end of the yolk sac stage suggested an offshore distribution of the first feeding larvae for all releases. This distribution pattern corresponded well with observations from the Davis Strait made by Jensen (1935), Smidt (1969) and Simonsen et al (2006). They found that small larvae (~10-22 mm length) primarily were distributed offshore in April−May. There are no reports on captures of yolk sac or small Gr. halibut larvae from the other areas. However, research surveys from theses areas are in early spring carried out outside of the small larvae's believed distribution area.

Drift of pelagic larvae and the settling areas

Drift simulations of the pelagic larvae from FF stage to the SE stage showed that spawning in Davis Strait would recruit to both Canadian and W Greenlandic waters.

The more westerly a spawning was conducted; the larger was the proportion of larvae that drifted to Canadian waters. From the 3 spawning sites chosen in Davis Strait, the ratio of eggs/larvae transported to Canada / W Greenland is from 60/40 to 100/0. Larval drift from Davis Strait to Labrador and/or to W Greenland has long been hypothesized. Templeman (1973) suggested that larvae from the spawning complex in Davis Strait are caught in the current off Baffin Island and drift south in the Labrador Current and settle on the banks off Labrador and eastern Newfoundland. Lear (1970) and Templeman (1973) found large numbers of 8–16 cm Gr. halibut in trawl hauls and in cod stomachs in this area, especially at Hamilton bank off Labrador and at Ungava Bay. Model results presented here confirmed that especially larvae from central or western part of the spawning area in Davis Strait would follow such a drift route toward the bank areas off Labrador. The high concentration of SE-larvae off Baffin Island in NAFO 0B corresponded at shallower depths (<400 m) with high abundance of juveniles , length mode at 12 cm, from trawl survey in September / October in NAFO 0B (Bowering 1978). This modal size of fish was virtually absent in hauls from depths beyond 500 m. It is well known that juveniles mainly inhabit shallow waters i.e. continental shelves at depths lesser than approx. 300 m (e.g. Riget & Boje 1988, Bowering & Chumakov 1989, Jørgensen 1997a). This raise questions about the fate of larvae that metamorphose and start a settling process over great depths. During metamorphosis larvae lose traits that were advantageous for the pelagic life while gaining traits that adapt them to a dermesal habitat. Even though there probably is some plasticity in the settling time window, and thus the period to reach a good settling area by drift or active swimming, higher mortality must be expected among those larvae. Following this argumentation, SE larva seen in deep waters and far offshore in NAFO 0B and 2G will probably be lost from the population.

A significant part of the particles released in the eastern part of the spawning area in Davis Strait drifted to W Greenland. Results on the 1908-09 "Tjalfe" expeditions and the 1963 "Norwestlant" investigations are summarized in Smidt (1969). He noted an increase in Gr. halibut larval length from 64 to 68°N and hypothesized that larvae were caught in the W Greenland Current and transported northward. Our drift model

verified a northwards larvae drift, but also stressed that only larvae from the eastern part of the spawning area would follow a drift route northward along W Greenland. Satellite tracked drifting buoys with drogues at 15 m depth confirmed this pattern and demonstrate that the advection towards Canada was especially high for drifters between 61 to 64 °N (Jakobsen et al. 2003). Satellite tracked drifting buoys with drogues at 30 m were deployed in May 2000 at and off Fylla Bank (64°N) (Pedersen et al. 2002). From May to September they drifted northward along W Greenland following the bathymetry and in September to November, the period we estimated to be the main settling period (Table 5), they drifted along the slopes of Hellefisk Bank and from northern part of Hellefisk Bank to and across Disko Bank (Fig. 7. Pedersen et al. 2002). The position in September to November corresponded very well to our distribution pattern of juvenile Gr. halibut from the July survey. High abundance of juvenile Gr. halibut at Hellefisk Bank, Disko Bank and in Disko Bay has been confirmed by several other studies (eg. Jensen 1935, Smidt 1969, Templeman 1973, Riget & Boje 1988). Most studies have been conducted prior to the settling of 0-group Gr. halibut, but a study by Jørgensen (1997a) included surveys in November and showed high densities of newly settled 0-group settled in the same areas, i.e. the slopes of banks west of Disko and northern and western slopes of Hellefisk Bank.

Larval drift from spawning in E Greenland and/or Iceland to W Greenland has also been hypothesized (Riget & Boje 1988). Ådlandsvik (2000) simulated drift of Gr. halibut egg from Kap Bille in E Greenland. Ådlandsvik used a different model setup, but showed that after 120 days of drift most larvae were transported to W Greenland and were distributed up to NAFO 1 D. Our drift simulations also estimated that most larvae (up to 82%) would drift to W Greenland but we simulated a distribution as northerly as NAFO 1A. The more northern distribution could be explained by a much longer drift phase in the present study. This distribution of larvae in NAFO 1 A and B implied that some larvae would settle in the same area as those from a Davis Strait spawning origin. Many of the larvae from our and Ådlandsviks drift simulations were distributed in the offshore area in Labrador Sea. As discussed above these SE larva will probably be lost from the population.

Riget and Boje (1988) suggested that larvae from an Icelandic spawning could be transported by the E Greenland Current from Denmark Strait to the E and SW Greenland areas. The present study confirmed that most of the pelagic larvae with a start position NW of Iceland would drift to Greenland waters. However, the relative amount of larvae that drifted to Greenland seems to be extremely sensitive to their position in Denmark Strait. The area is characterized by sharp frontal activity between Polar and Irminger Water, and only a small spatial displacement results in a shift from one water mass to the other. Wind directions and the resulting Ekman transport must therefore be expected to be important for which water mass the larvae enter and thereby the drift direction to either E Greenland or N Iceland shelf (Ribergaard 2004).

The present drift simulations showed that SE larvae were abundant on most of the shelf of E Greenland from 62 to 65°N and in SW Greenland to 60°45N (in 1F). The distribution off E Greenland was concurrent with the general higher densities of Gr. halibut larvae at 61 to 65°N observed from 0-group surveys in 1970–97 by Iceland (Albert et al. 2002). The presence of Gr. halibut larvae in E Greenland was also noted by Smidt (1969) but he emphasized that larval abundance here was much lower compared to the W Greenland area from 62°30 to 66°15N. The same conclusion was made by Boje and Hjörleifsson (2000) on juvenile Gr. halibut (<28 cm). They analysed the spatial distribution of the juveniles in Greenlandic and Icelandic waters and found that in E Greenland they were more abundant in the same area as Smidt identified, but that juvenile concentrations were considerably lower, about an order of magnitude, compared to Hellefisk Bank, Disko Bank and Disko Bay in W Greenland. The SW Greenland area where the present simulation model showed high abundance of SE larvae, was not supported by significantly higher catch rates of 1 or 2+ year old on the July survey, but earlier investigations by Jensen (1935) and Smidt (1969) have shown that these year classes can be abundant in the area. The view by Riget and Boje (1988) that Gr. halibut in SW Greenland was transported to the area as larvae in the E Greenland Current from an Icelandic spawning area thus find support in the present study.

The positions W and SW of Iceland from where we modelled the drift of the pelagic larvae, did on, the other hand, show no signs of drift out of Icelandic waters. They drifted to the W and S Iceland shelf. We found no support in the literature on Gr. halibut nursery areas here. In spite of considerable survey effort Gr. halibut larvae and juveniles less than 45 cm have only rarely, and always in very limited numbers, been reported from Icelandic waters (Sigurdsson 1980, Boje & Hjörleifsson 2000, Albert et al. 2002). We compared the simulated larval distribution patterns with the ones from Ådlandsvik (2000) and noted that he also had a considerable amount of particles distributed W and SW of Iceland. Deployed drifters have shown that a westward or southward transport is possible (Ribergaard 2004). The drift scenario for the simulated Gr. halibut larvae to W or S Iceland thus seems plausible. Drift simulations showed that even small spatial displacements of the spawning area or the distribution of FF larvae would result in different SE larvae distributions. The background for the definition of the spawning area is however sparse. It is based on distribution of mature females from one scientific bottom trawl cruise and a few observations of bathypelagic eggs (Magnusson 1977, Sigurdsson 1977). This emphasize a need for further investigations on where Gr. halibut spawn in the area before firm conclusions can be made on the drift and settling areas of larvae from this spawning area.

Development time and effect of temperature

Egg and larvae drifted in water masses with different temperatures, and according to the temperature-dependent growth models, different egg development time and larval growth rates between areas were expected. For the development of the egg and yolk sac to FF larvae the difference was up to up to one month, earliest for W Iceland, latest for SW Greenland. In Davis Strait the FF-larvae was estimated to occur in the upper pelagic around 23−27. May. This corresponded well with survey information from Davis Strait offshore by Simonsen et al. (2006) who found small feeding larvae in mid May and from Jensen (1935) and Smidt (1969) who observed small larvae with remains of yolk in the end of April and beginning of May. For the pelagic larvae it was somewhat surprising that contrasting growth resulted in as much as a four month difference in development to SE larvae. However, comparison of larval sizes

from the different areas supports the existence of such large differences. For example in E Greenland the Icelandic 0 group surveys carried out in August reports a mean length on 65 mm (Albert et al. 2002) compared with 47 mm in W Greenland August ichthyoplankton survey (Smidt 1969). The estimated settling period in W Greenland in NAFO 1A in late October and November was partly confirmed by our survey results: The missing observations from July and increased abundance from August to September fitted the trends in the model. However, as surveys were not conducted later we were not able to validate a possible peak settling in late October. Other studies from the banks and Disko Bay in NAFO 1A have suggested a settling in autumn: Jensen (1935) and Smidt (1969) concluded that with a larval size of ~47 mm in August settling was likely to occur in September/October. Jørgensen (1997) observed many newly settled fish with a mode length around 7.5 cm in November. In Canada in NAFO 2GHJ there was no survey information to confirm the estimated settling period in November and December. However, there are reports of 0-group Gr. halibut 5.7-7.7 cm long in cod stomachs at Hamilton Bank caught on October 21, 1967 (Lear & Pitt 1975). Direct information is also missing from E Greenland, the Icelandic pelagic 0-group survey find modal larval length of 65 mm and a size distribution was skewed to the left which suggest that settling was ongoing. This correlates well with our estimate that larvae would be around 65 mm and ready to settle in the beginning of September. Clearly, the large difference in the duration of the early pelagic life stages, up to twice as high for egg and larvae in Canadian waters that drifted to NAFO 2 GHJ compared to those from E Greenland, can have a significant impact on cumulated larval survival. The trade-off is between growth and starvation risk: higher growth result in shorter larval phase duration, and as mortality is highest in the egg and larval phase, a higher survival rate (Walsh 1994, Hare & Cowen 1997). However, high temperature not only influence growth rate but also increases the metabolic costs and thus the demand for food (Buckley et al. 2000). Periods of prey shortage will therefore be faster critical for larvae living at higher temperatures compared cold temperatures (McGurk 1984). We therefore hypothesize that year class variability in larval survival may be higher for larvae drifting in the

warm Irminger Current component from Iceland to E Greenland compared to larvae drifting in the cold Baffin Island Current along from Davis Strait to Canada.

Hellefisk Bank – a settling and nursery area

It was notable that the age 1 and 2+ fish almost exclusively only occurred in AREA 1 while age 0 was equally distributed in AREA 1 and AREA 2 of Hellefisk Bank. The major environmental difference between the areas was the sediment structure. Many flatfish species show a preference for a fine grain sediment at settling and thereafter a progressively coarser sediment as they grow larger (e.g. Moles & Norcross 1995: Platichthys stellatus, Stoner & Abrokire 2002: Hippoglosssus stenolepis). The distribution of the newly settled 0-group Gr. halibut on both types of sediment did not indicate such size structured preference until they reached age 1 and 2+. For flatfish the key role of the sediment is to provide burial to avoid predators and for benthivorous flatfish a habitat that holds fauna as prey (Gibson et al. 1998). Feeding ecology studies on Gr. halibut have shown that small juveniles mainly feed on pelagic crustaceans such as *Parathemisto* sp., while larger juveniles mainly feed on pandalid shrimps and small fish (Godø & Haug 1987, Jørgensen 1997b). Their feeding ecology was reflected in their diurnal migration pattern as all juvenile Gr. halibut during daylight were found at or near bottom but during night most juveniles < 15 cm migrated up in the water column (Jørgensen 1997b). This partly pelagic life for the smallest Gr. halibut could explain why sediment preference first was seen for age 1 and 2+ when they became more associated to the dermersal habitat.

Biologically, the key difference between areas was the higher abundance, better condition and higher stomach fullness for age 1 and 2+ fish, but not the age 0, in AREA 1 compared to AREA 2. The positive relationships between abundance and area suggest that there was an active density dependent habitat selection for the older juveniles but not for the newly settled. However, according to the "ideal free distribution" (IFD) individuals will distribute themselves evenly among habitat according to the available resources (Fortier & Harris 1989). In such a scenario individuals will have the same fitness across habitats, but habitats will support different abundance densities. The distribution of age 1 and 2+ Gr. halibut did

therefore not follow the IFD as condition was better in the area with higher abundance. According to the IFD predictions Gr. halibut age 1 and 2+ then under-utilized the best habitat in AREA 1 and over-utilized the poorer habitat in AREA 2 (Kennedy & Gray 1993). The same distribution pattern and individual conditions response have been seen in haddock (*Melanogrammus aeglefinus*) (Hiddink et al. 2005). On the other hand the patchy distribution of Gr. halibut age 1 and 2+ and the correlation between abundance and conditions showed that habitat mattered. Fish in bad condition have a higher mortality (Dutil & Lambert 2000). Consequently, it seems that Gr. halibut, just as it has been shown for Atlantic cod (*Gadus morhua*) and cunner (*Tautogolabrus adspersus*) (Juanes 2007), settle over different bottom habitats types, but that post-settlement mortality is habitat specific and determine the habitats juvenile density the following year. The nursery areas are therefore not determined at settling but within the first year. The concentrating of juveniles to more specific nursery areas implies that juvenile densities may approach the carrying capacity of their habitats in years when settlement is high which would dampens the annual variability in year class strength of Gr. halibut. Such density dependent mortality effects is well described for flatfish (Gibson 1994, Iles & Beverton 2000, Nash & Geffen 2000). This stresses that even though both our drift model and surveys showed that Gr. halibut settle took place over a wide range of areas and habitats, it is post-settlement processes within the first year that determine the actual nursery areas. Knowledge on these processes will therefore be important for understanding of overall recruitment dynamics for Gr. halibut.

In conclusion, the drift simulations showed that egg and larvae can drift for long distances and that there was exchange of individuals between metapopulations. However, the main drift directions were generally opposite the migration direction of adults within Davis Strait (Khan et al. 1982, Bowering 1984, Bowering 1988, Boje et al. 1997, Boje 2002) and from W Greenland to Iceland (Boje et al. 1997, Boje 2002). Therefore, the self recruitment within populations seems to be substantial. An improved understanding of the connectivity and its role for the metapopulation structure seems a prerequisite for successful development of management strategies for this species. The study off W Greenland showed that even though settling appears

to take place over a wider area and at different bottom type habitats, processes within the first year restricted the successful nursery area to more specific bottom habitat types. This suggests that habitat related processes on nursery grounds will dampen rather than generate recruitment variability in Gr. halibut.

Acknowledgement

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Tables & figures

Table 1. Release point of particles in egg and yolk sac larvae simulations. 1000 particles were released on each release position (I, II….VIII) following a normal distribution curve with peak spawning in mid February and a spawning window of 40 days. Reference refers to publications that have defined the spawning area.

Area	N		W		release	reference
Davis Strait	63 °	30	53 °	30	I	Gundersen et al. 2004;
	63 °	30	55 °	48	II	Simonsen and
	63 °	30	57 °	42	III	Gundersen 2005
Baffin Bay	72 °	30	61 °	48	IV	Gundersen et al. 2004;
East Greenland	62 °	09	40 °	24	V	Gundersen et al. 2001
Iceland	63 °	00	26 °	00	VI	Magnusson 1977;
	64 °	01	27 °	24	VII	Sigurdsson 1977
	65 °	02	28 °	15	VIII	

Table 2. Mean temperature and Gr. halibut larvae length and dry weight from surveys in May, June and July (from Simonsen et al 2006). September observations were from present study for 65 mm fish just metamorphosed. Weight specific growth rate G is from equation 5

Cruise date	Temperature (°C) 5-40m	midpoint T	Larval length (mm)	Dry weight (mg)	G (exp mg / day)
15-May	0.13		17.6	1.28	
25-Jun	2.76	1.45	23.5	3.50	0.024
15-Jul	3.75	3.26	31.0	9.16	0.048
11-Sep	3.43	3.59	65.0	210.50	0.054

Table 3. Relative distribution (in %) between areas of simulated egg and bathypelagic larvae from spawning releases I to VIII after 300 degree-days. N is the number out of the 1000 successful simulated egg bathypelagic larvae that did not hit land and reached 300 degree-days before August 1.

Spawning release	NAFO											ICES				N
	0A	0B	1A	1B	1C	1D	1E	1F	2G	2H	2J	NICE	SICE	IRMICE	IRMGRL	
I	-	-	-	-	49.0	28.7	18.4	3.8	0.2	-	-	-	-	-	-	506
II	-	1.9	-	-	51.7	46.3	-	-	-	-	-	-	-	-	-	976
III	-	91.0	-	0.4	2.8	5.8	-	-	-	-	-	-	-	-	-	999
IV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
V	-	-	-	-	-	-	24.1	60.4	0.5	-	-	-	-	-	14.9	970
VI	-	-	-	-	-	-	-	-	-	-	-	-	58.3	41.7	-	1000
VII	-	-	-	-	-	-	-	-	-	-	-	-	70.4	29.6	-	1000
VIII	-	-	-	-	-	-	-	-	-	-	-	10.2	85.9	0.8	3.2	905

Table 4. Relative distribution (in %) between areas of simulated Gr. halibut larvae from spawning releases I, II, III, V, VII and VIII at settling size (210 mg). N is the number out of the 1000 successful simulated larvae that did not hit land and reached settling size before December 31.

Spawning release	depth	NAFO											ICES				N
		0A	0B	1A	1B	1C	1D	1E	1F	2G	2H	2J	NICE	SICE	IRMICE	IRMGRL	
I	20 m	3.9	33.7	27.4	7.1	1.2	0.7	-	-	22.3	3.6	0.2	-	-	-	-	588
II		0.2	41.4	2.2	0.1	1.5	8.3	-	-	36.9	8.0	1.3	-	-	-	-	851
III		-	52.4	-	-	0.6	2.2	-	-	12.8	8.7	23.3	-	-	-	-	996
V		0.2	5.1	3.1	7.0	13.3	18.9	28.3	12.1	11.9	-	-	-	-	-	-	972
VII		-	-	-	-	-	-	-	-	-	-	-	-	98.5	1.5	-	997
VIII A		-	-	-	-	-	-	-	-	-	-	-	0.7	98.4	0.2	0.7	999
VIII B		-	-	-	-	0.2	2.3	5.0	11.5	-	-	-	15.2	12.3	0.4	53.0	479
I	40 m	1.0	30.8	13.3	2.6	5.4	6.4	-	-	15.8	15.0	9.6	-	-	-	-	607
II		-	16.6	0.2	-	9.4	2.2	-	-	19.2	17.4	35.0	-	-	-	-	500
III		-	3.1	-	-	0.3	-	-	-	7.1	15.8	73.7	-	-	-	-	650
V		-	2.9	-	-	1.4	4.0	14.3	62.5	14.6	-	-	-	-	-	0.3	1000
VII		-	-	-	-	-	-	-	-	-	-	-	-	99.4	0.6	-	1000
VIII A		-	-	-	-	-	-	-	-	-	-	-	1.4	98.3	-	0.3	1000
VIII B		-	-	-	0.1	1.7	8.3	9.7	13.9	-	-	-	16.4	4.8	0.3	44.7	689

Table 5. Mean estimated settling date for the different spawning releases in the different NAFO and ICES areas.

Spawning release	depth	NAFO											ICES			
		0A	0B	1A	1B	1C	1D	1E	1F	2G	2H	2J	NICE	SICE	IRMICE	IRMGRL
I	20 m	Nov 13.	Nov 07.	Oct 28.	Oct 28.	Oct 09.	Oct 14.	-	-	Nov 24.	Dec 21.	Dec 23.	-	-	-	-
II	20 m	Nov 13.	Oct 27.	Nov 12.	Nov 30.	Oct 20.	Oct 20.	-	-	Nov 12.	Dec 07.	Dec 09.	-	-	-	-
III	20 m	-	Oct 07.	-	-	Oct 15.	Oct 11.	-	-	Oct 11.	Oct 16.	Oct 13.	-	-	-	-
V	20 m	Nov 01.	Oct 21.	Oct 27.	Oct 19.	Oct 06.	Sep 30.	Sep 27.	Sep 23.	Sep 26.	-	-	-	-	-	-
VII	20 m	-	-	-	-	-	-	-	-	-	-	-	-	Jul 08.	Jul 12.	-
VIII A	20 m	-	-	-	-	Oct 02.	Sep 20.	Sep 11.	Sep 05.	-	-	-	Aug 02.	Jul 24.	Jul 22.	Aug 04.
VIII B	20 m	-	-	-	-	-	-	-	-	-	-	-	Aug 22.	Jul 31.	Aug 01.	Sep 07.
I	40 m	Nov 19.	Nov 28.	Nov 26.	Nov 12.	Nov 05.	Nov 07.	-	-	Dec 19.	Dec 21.	Dec 27.	-	-	-	-
II	40 m	-	Dec 22.	Nov 30.	-	Dec 13.	Dec 17.	-	-	Dec 23.	Dec 23.	Dec 19.	-	-	-	-
III	40 m	-	Dec 04.	-	-	Dec 06.	-	-	-	Nov 24.	Dec 07.	Dec 02.	-	-	-	-
V	40 m	-	Oct 15.	-	-	Oct 10.	Oct 07.	Oct 06.	Oct 01.	Oct 07.	-	-	-	-	-	-
VII	40 m	-	-	-	-	-	-	-	-	-	-	-	-	Jul 11.	Jul 09.	Sep 13.
VIII A	40 m	-	-	-	-	-	-	-	-	-	-	-	Aug 09.	Jul 29.	-	Aug 09.
VIII B	40 m	-	-	-	Nov 20.	Oct 08.	Oct 04.	Sep 26.	Sep 16.	-	-	-	Aug 30.	Aug 03.	Aug 05.	Sep 12.

Table 6. Decomposition of composite Gr. halibut length distributions using Bhattacharya method (Bhattacharya 1967). Size interval for age class defined as mean TL +/- 1.96 S.D.

Survey	age class	TL		TL size interval for age class	
		mean (mm)	S.D.	min (mm)	max (mm)
July	1	14.82	1.25	12.37	17.27
	2	21.89	1.74	18.48	25.30
	3	25.33	0.54	24.27	26.39
August	1	16.01	1.29	13.48	18.54
	2	21.91	1.71	18.56	25.26
	3	25.79	0.94	23.95	27.63
September	0	7.09	0.7	5.72	8.46
	1	17.22	1.22	14.83	19.61
	2	23.07	1.41	20.31	25.83
	3	27.58	0.84	25.93	29.23
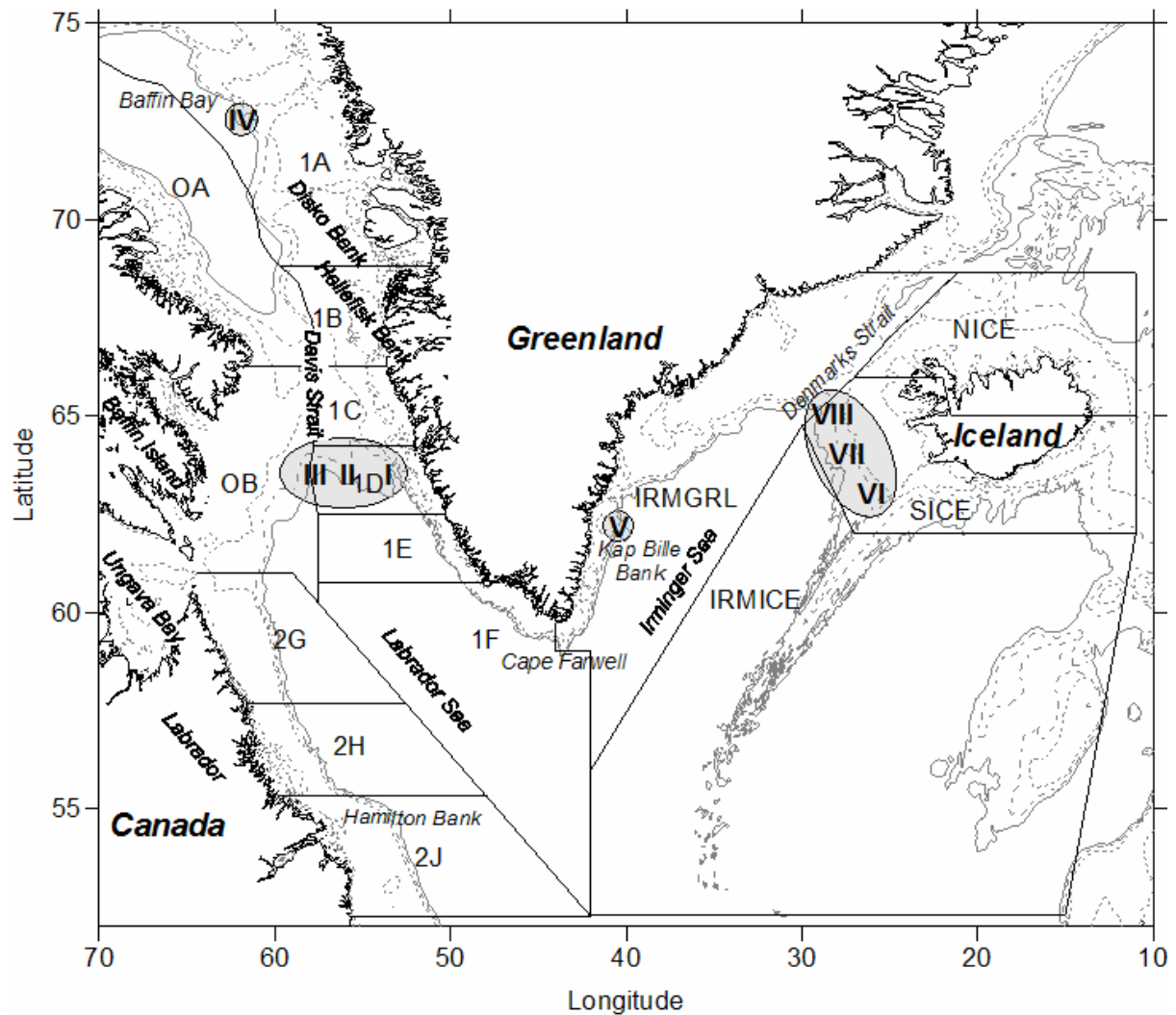
Fig 1. Map of study area. "Spawning areas" where mature ripe female and/or eggs have been reported is shown by shaded grey areas. Numbers I to VIII refers to release points listed in table 1. Depth contours shown for 100, 500, 1000 and 1500 m.
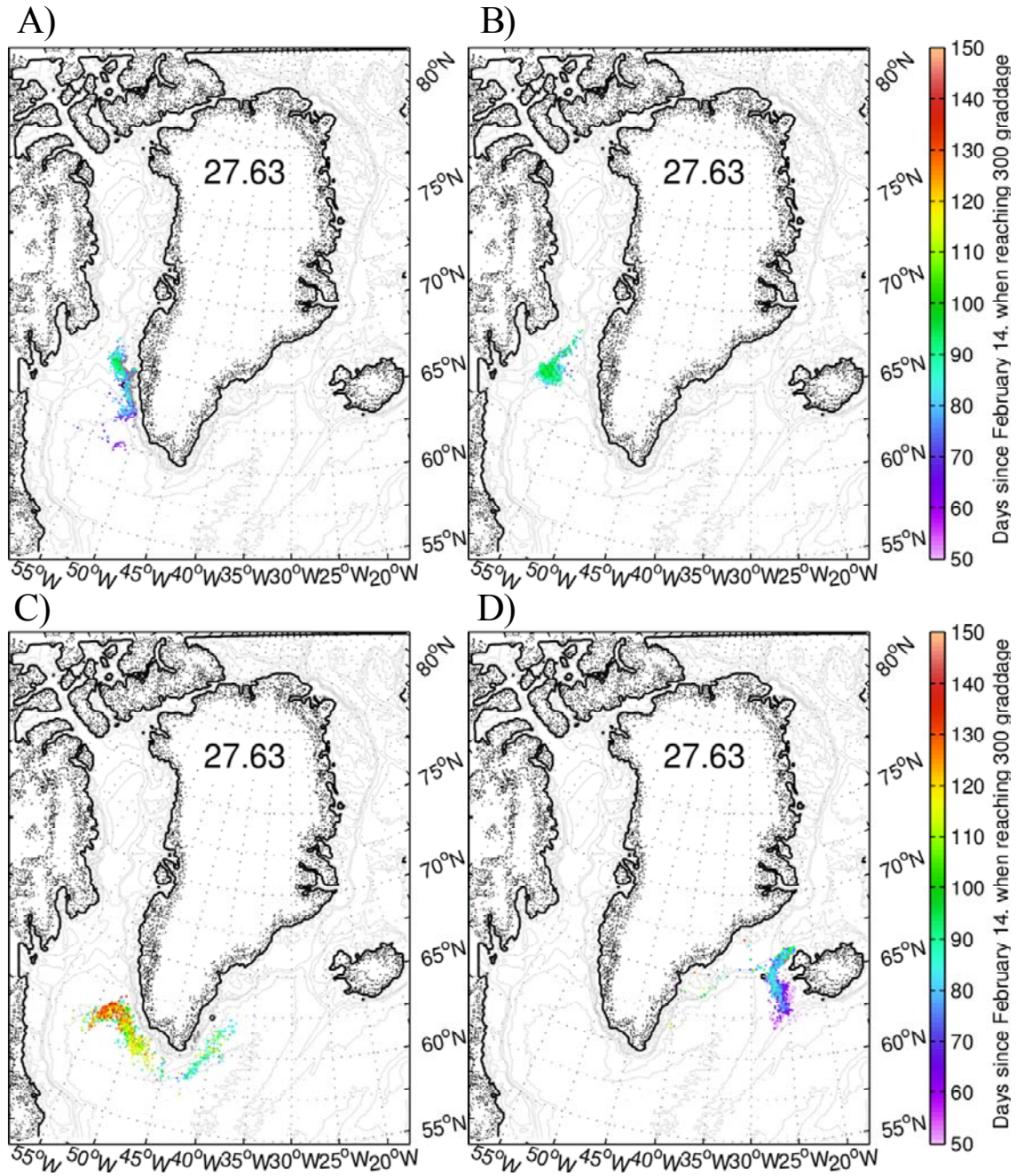
Fig. 2. Drift simulation of egg and yolk-sac stages of Gr. halibut from mid February and for 300 degree-days at density interval σ_θ =27.63. A) release I, B) release III, C) release V, D) release VIII (table 1). Release point shown by black circle.
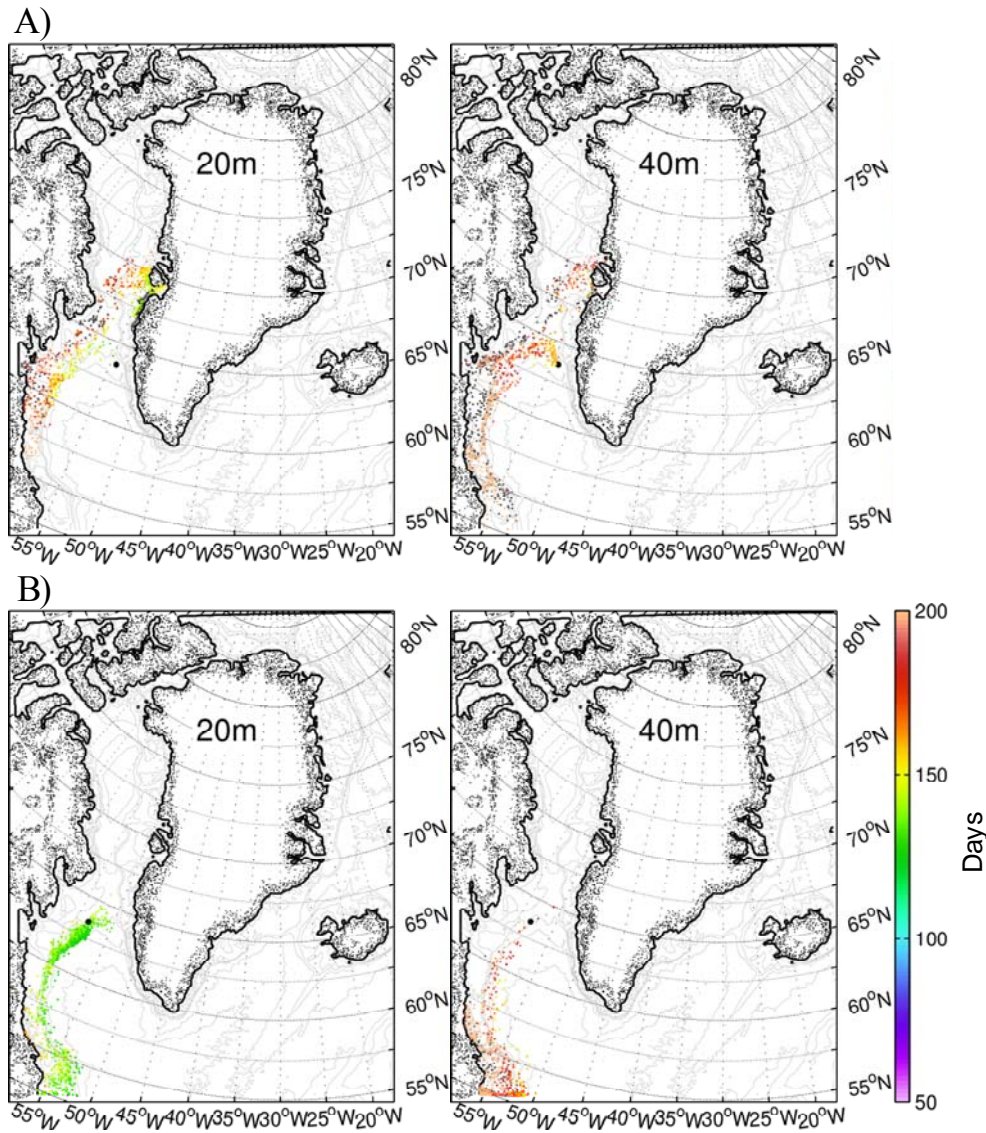
Fig. 3. Drift simulation of Gr. halibut pelagic larvae from Davis Strait release I A) and III B) in 20 and 40 m depth from first feeding (DW 0.3 mg) to settling size (DW 210 mg). Start position of drift simulation is A) 63°40N, 54°12W B) 63°29N, 58°21W. Release point shown by black circle.
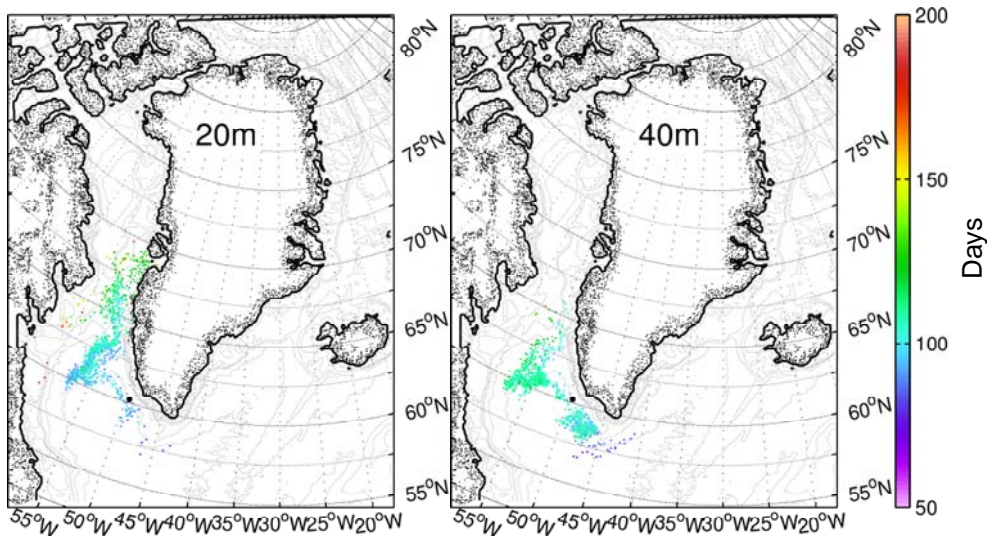
Fig. 4. Drift simulation of Gr. halibut pelagic larvae from East Greenland release V in 20 and 40 m depth from first feeding (DW 0.3 mg) to settling size (DW 210 mg). Start position of drift simulation is 60°13 N, 49°29W. Release point shown by black circle.
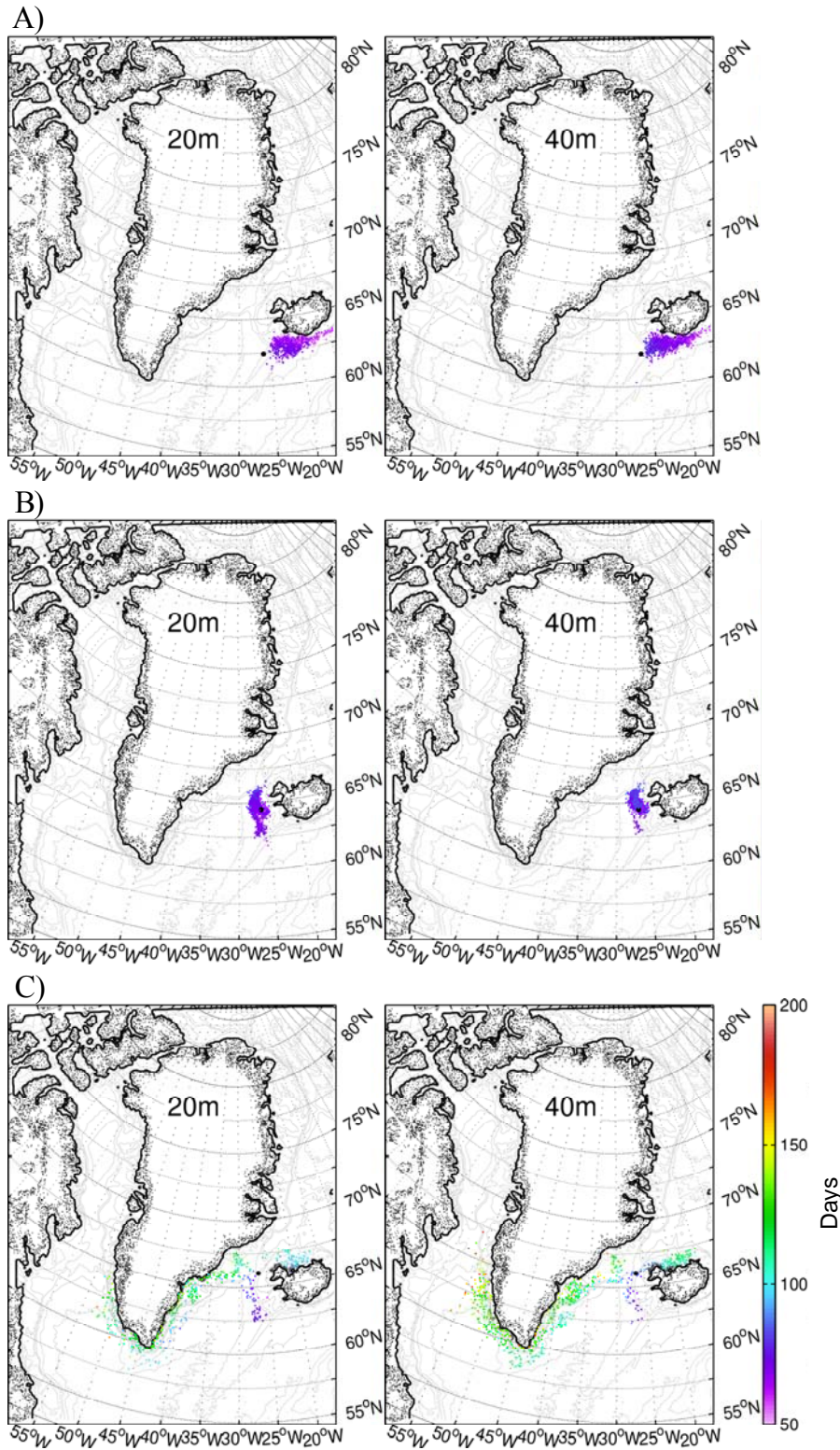
Fig. 5. Drift simulation of Gr. halibut pelagic larvae from Iceland release VII (A), and VIII (B and C) in 20 and 40 m depth from first feeding (DW 0.3 mg) to settling size (DW 210 mg). Start position of drift simulation is A) 62°26N, 26°08 W B) 64°29N, 26°13 W C) 66°00N, 26°30W. Release point shown by black circle.
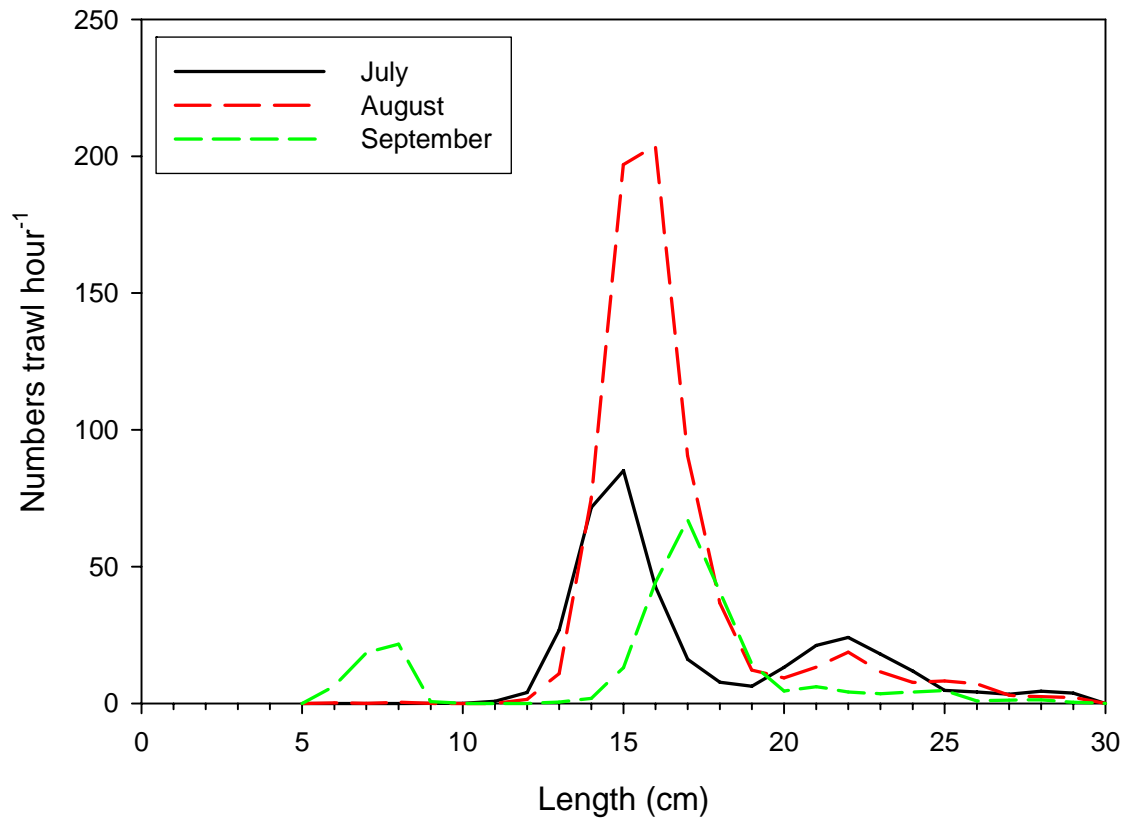
Fig 6. Number of Gr. halibut (standardized to one trawl hour) in each 1 cm length group on the July (black solid line), August (red dashed line) and September survey (green dashed line).
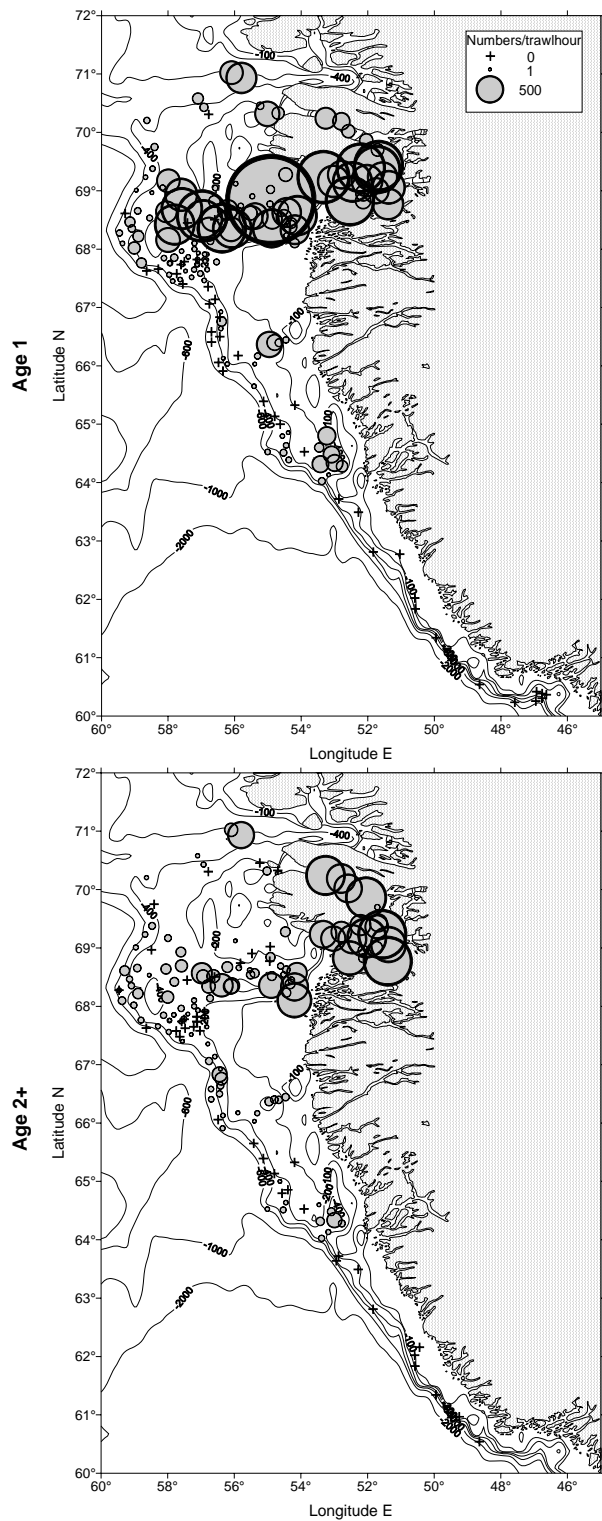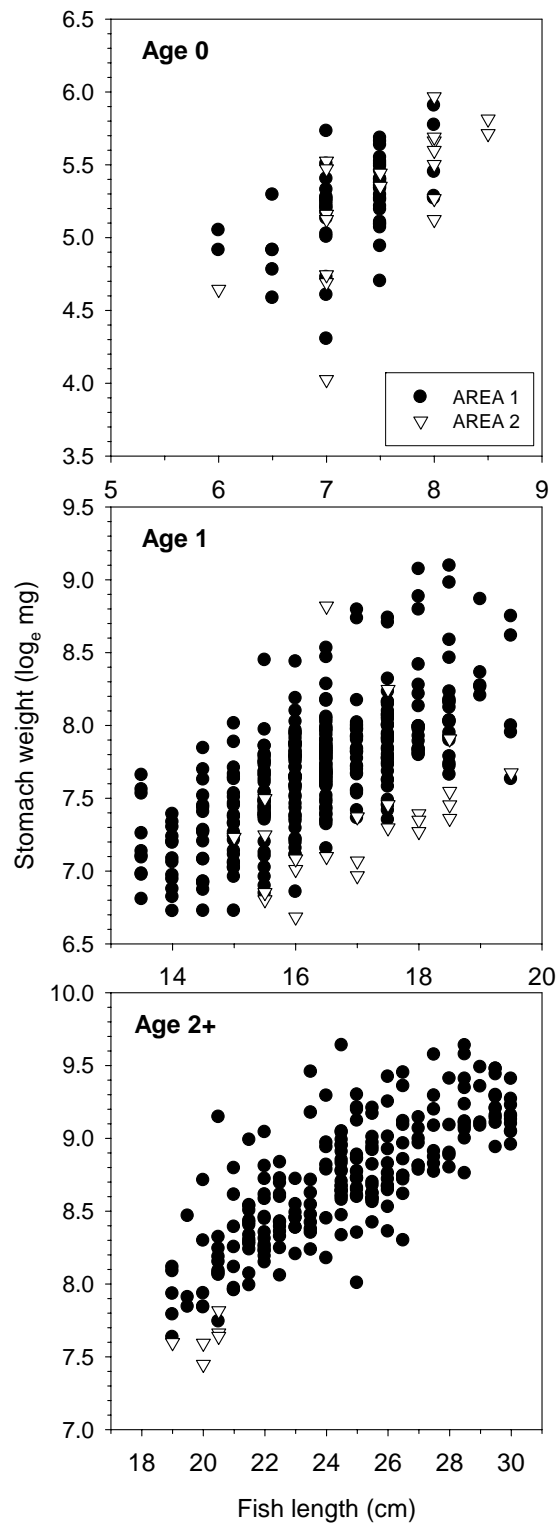
Fig. 7. Abundance of 1 year old Greenland halibut on July survey. Area of circle is showing abundance as numbers per trawl hour.
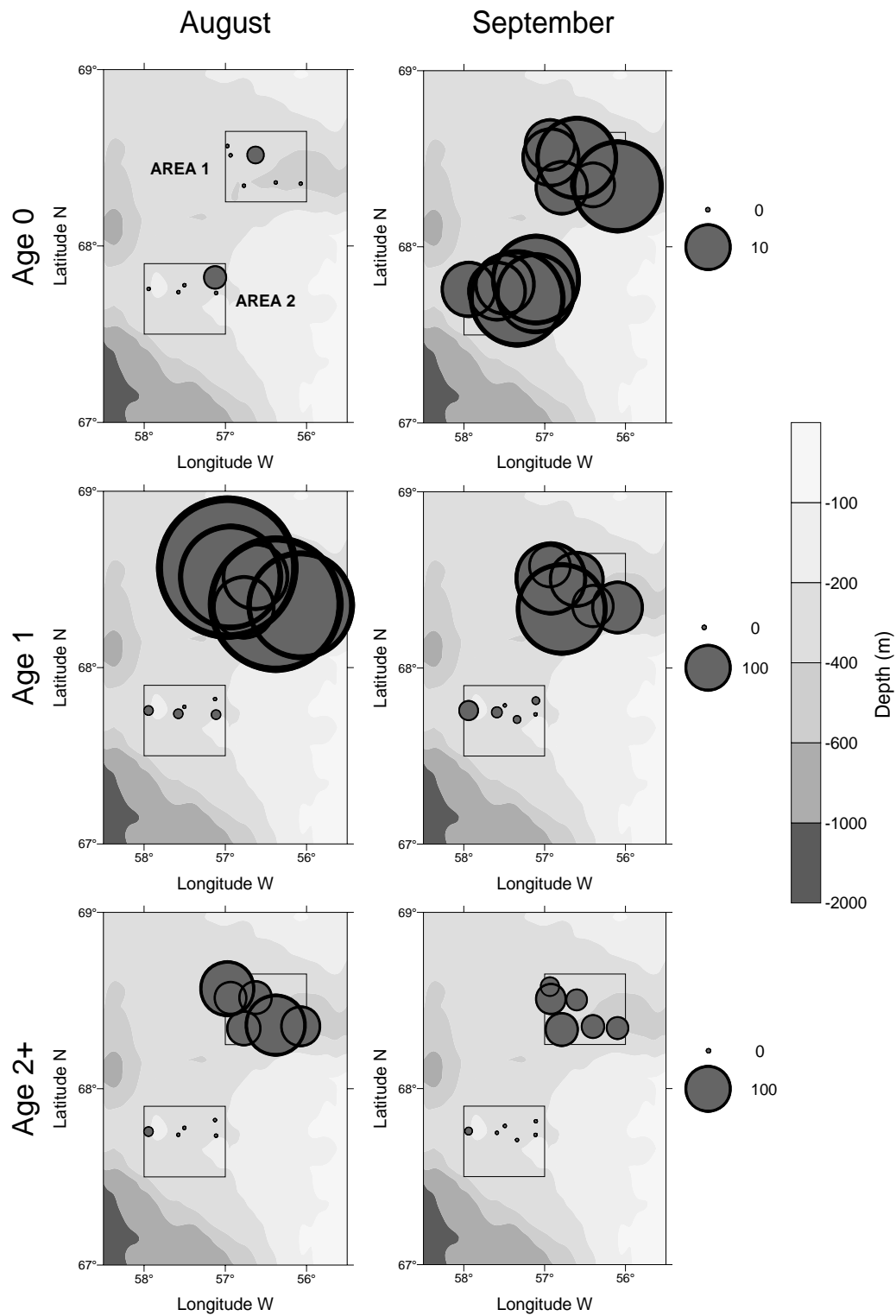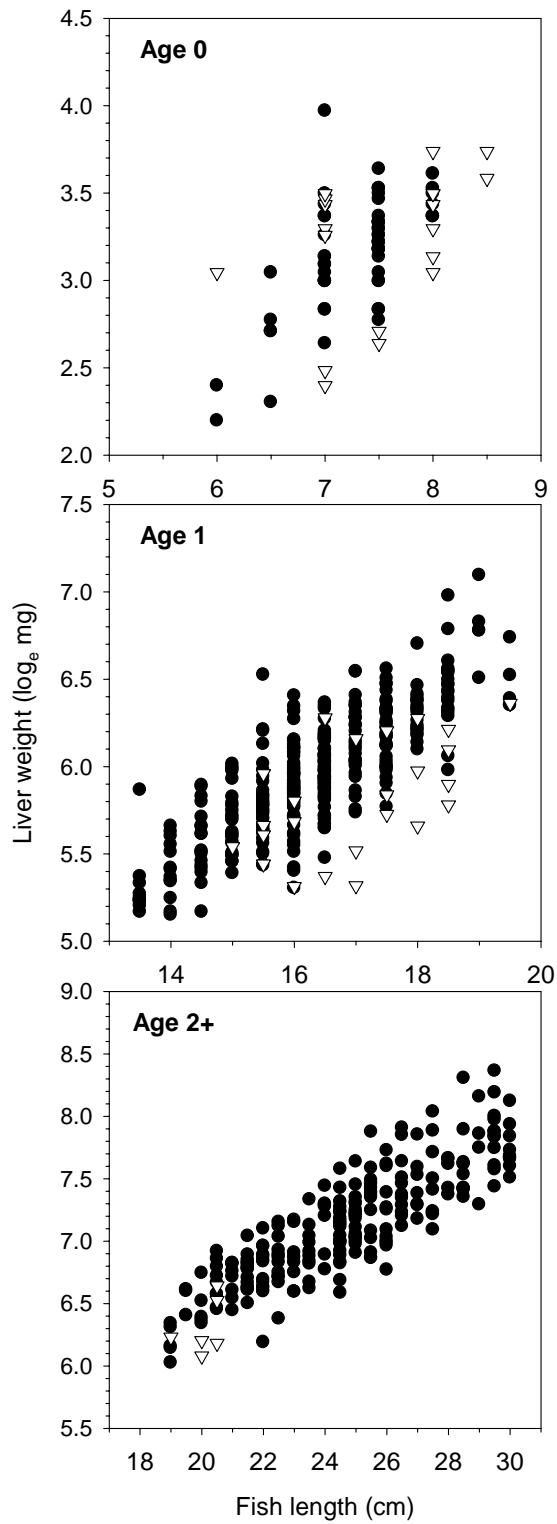
Fig. 8. Abundance of 0, 1 and 2+ year old Greenland halibut on August and September survey (number trawl hour^{-1}) in AREA 1 and AREA 2. Depth contours shown by grey scale.
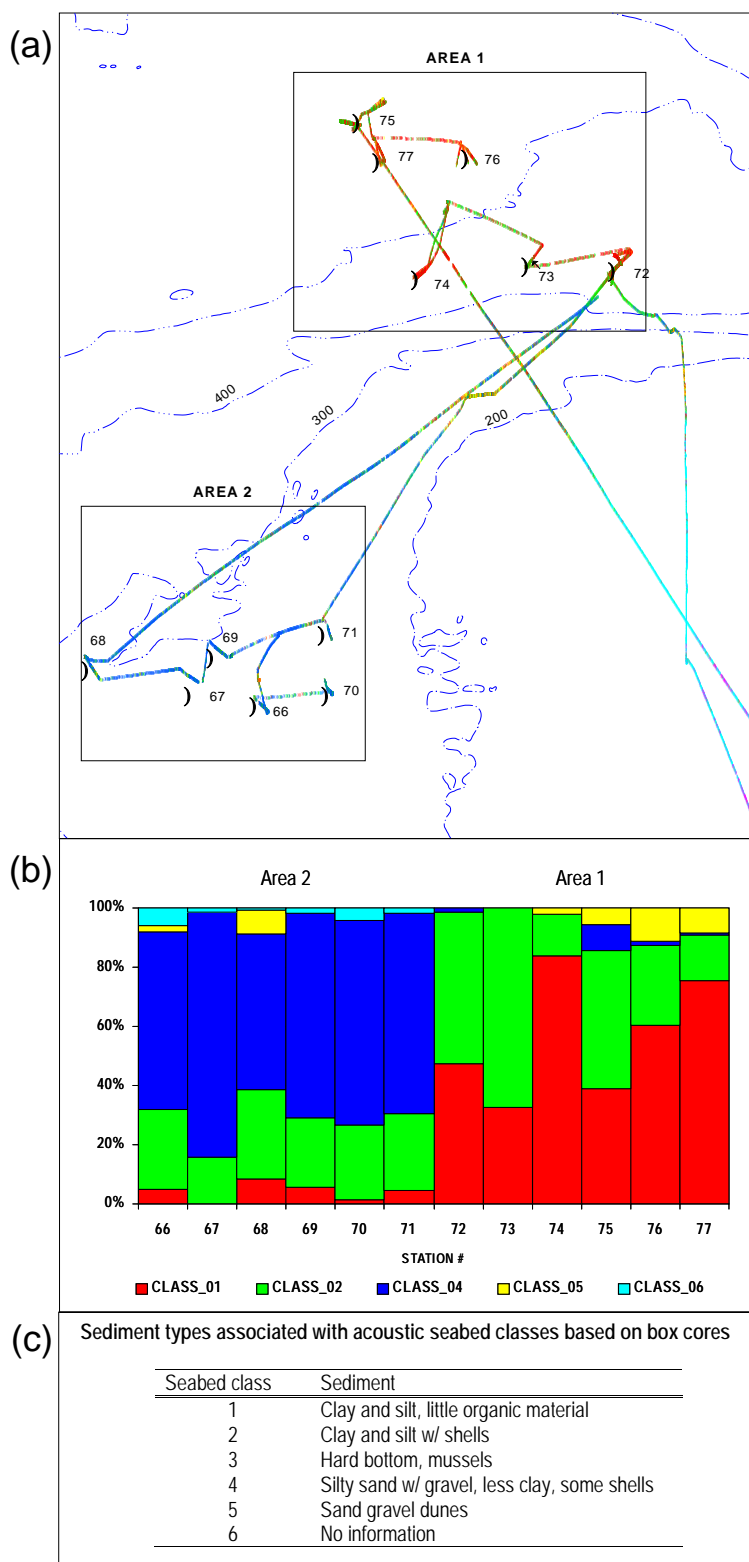
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Fig. 9. Stomach weight ($\log_e$ mg) versus fish length (cm) for age 0, 1 and 2+ for AREA 1 (black circles) and AREA 2 (white triangle)

Fig. 10. Liver weight ($\log_e$ mg) versus fish length (cm) for age 0, 1 and 2+. Legends as in Fig. 9.

Fig. 11. (a) Sediment classification on Hellfisk Bank with the two sub-areas "Area 1" and "Area 2". (b) Relative cluster distribution in the sub-areas using 6 clusters of which 5 were present. (c) Box core sediment samples and the associated acoustic classification.