Population dynamics of fish juveniles and invertebrates in Icelandic waters

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Dissertation submitted in partial fulfillment of a
Philosophiae Doctor degree in Biology

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Abstract

The marine ecosystem around Iceland is shaped by its position in one of the most hydrographically complicated regions of the North Atlantic. The response of marine populations to those diverse conditions is expected to be different across taxonomically distinct species but by comparing and analysing the differences we can better understand the system as a whole. In the present study, population dynamics of juvenile cod (*Gadus morhua*), juvenile plaice (*Pleuronectes platessa*), brown shrimp (*Crangon crangon*) and Iceland scallop (*Chlamys islandica*) were analysed with respect to recruitment patterns and fluctuations. The studies were carried out during a period of increased influx of Atlantic waters around Iceland and consequently higher temperatures. The studied species either have their core distributional areas in Iceland, like the cod, or are at their southern borders, like the Iceland scallop. We also analysed population trends at sheltered sandy beaches, which is an essential habitat for the juvenile plaice and also the brown shrimp, a newly found invasive species and important predator of juvenile plaice.

Findings revealed the highest abundance of cod larvae within low-salinity waters, characteristic of the Icelandic coastal current (ICC). That is in line with previous studies that have demonstrated a potential link between the freshwater discharge or the strength of the ICC and recruitment of cod. The distribution of the cod juveniles within the boundaries of the ICC highlights the role of the freshwater driven coastal current in successfully transporting larvae from the spawning areas into the northern nursery grounds. The fluctuation in recruitment is relatively small in the Icelandic cod stock and likely dampened by the smaller northerly grounds.

In an effort to establish the natal origins of juveniles of plaice around Iceland, settlement and growth patterns of juvenile plaice were estimated. There were differences in the size and age distribution around Iceland, which led to the conclusion that juvenile plaice originated from multiple spawning events and locations. Further, the observed spatial variation in size of the juveniles was explained by age difference, not by different temperature-induced growth rates. The study provides evidence of the existence of a local population structure within the Icelandic plaice stock and supports recent findings on adult plaice, which could have implications for the management of the stock, that currently is managed as a single unit. The study also identified extremely high density peaks of juvenile plaice at the nursery grounds. We further studied two years with variable population density by ageing juveniles and comparing growth of individuals on particular dates during the settlement period and later in the summer. There was indication of density-dependent growth patterns. Recruitment of the plaice has been stable for the past 25 years. Density dependent processes at the nursery grounds are a likely contribution to that fact, but also the possible complex population structure within the Icelandic plaice stock.

The brown shrimp which was recently found in Icelandic waters (2003), has been described as a potentially invasive species. It has rapidly adapted and became established in its newly colonized area. There was an indication of bi-annual spawning with the number of juveniles increasing in July/August and again in February. The number of recruiting juveniles from previous years significantly affected the adult abundance as well as a positive effect of the sea surface temperature. Different population trends were observed in the Iceland scallop, where surveys with available environmental- and biological data from 1993 to 2003 were analysed. The period was also marked by an increase in summer sea surface temperature on the studied southern border of the sub-arctic species' distributional range. The stock was heavily fished but also suffered high natural mortality that was later related to an apicomplexan parasite or gray meat. Further, low recruitment levels towards the end of the 1990s made the stock vulnerable to increased fishing pressure and consequently, the stock appeared unable to withstand the fishing pressure and declined to historically low levels, leading to a halt to fishing in 2003.

The relative stable cod and plaice stocks in Icelandic waters can most likely be attributed to the their stock subcomponents as well as density dependent processes occurring at the plaice nursery ground. The collapse of the Iceland scallop stock in Breiðafjörður, among the decline or collapse of the northern inshore shrimp stocks, were maybe the first species influenced by the current warm regime which started around 1996. During this period there have also been several records of invasive species, such as the brown shrimp, with the new regime favouring the establishment of the new species. The causes and drivers of recruitment variation are common over a wide range of species and the way forward to understand the key processes influencing recruitment, must be greater emphasis on research on a broader scale.

Útdráttur

Við Ísland er að finna eitt flóknasta hafstraumakerfi í Norður Atlantshafi. Hér má búast við mismunandi áhrifum umhverfisbreytinga á ólíka stofna sjávarlífvera, en með því að skoða nokkrar tegundir má draga víðtækari ályktanir af eðli áhrifanna. Meginviðfangsefni þessa verkefnis var rannsókn á ungviði og stofnsveiflum með tilliti til nýliðunar hjá þorski (*Gadus morhua*), skarkola (*Pleuronectes platessa*), sandrækju (*Crangon crangon*) og hörpudiski (*Chlamys islandica*). Rannsóknin tók yfir tímabil þegar innstreymi hlýs Atlantssjávar jókst með tilsvarandi hækkun sjávarhita. Fjallað var bæði um tegundir líkt og þorskinn þar sem Ísland er við miðju útbreiðslunnar og hörpudisk sem finnst hér á suðurmörkum útbreiðslu sinnar. Einnig voru skoðaðar skjólsælar sandfjörur, en þær eru mikilvægasta búsvæði kolaseiða og sandrækju, sem er ný ágeng tegund og mikilvægur afræningi á seiðum skarkolans.

Niðurstöðuð rannsóknanna á þorskungviði sýndu fram á háan þéttleika í seltuminni sjó nærri landi, einkennandi fyrir strandstrauminn (ICC). Það rennur stoðum undir eldri rannsóknir sem hafa bent á mögulegar tengingar hans við árangursríkari nýliðun í þorski og mikilvægi ferskvatnsknúna strandstraumsins í flutningi á lirfum frá hrygningarsvæðum yfir á norðlægari uppeldissvæði. Almennt séð eru sveiflur í nýliðun þorsks litlar við Ísland en líklegt er að hrygning frá smærri norðlægari hrygningarsvæðum jafni frávikin.

Botntaka og vöxtur skarkolaseiða allt í kringum Ísland var metinn til að varpa ljósi á uppruna seiðanna. Munur var á stærð og aldursdreifingu seiðanna og benti hann til mismunandi hrygningartíma og svæða. Mun á stærð milli svæða mátti einkum rekja til aldurs en ekki hitastigsháðs vaxtar. Niðurstöðurnar benda til að um staðbundnar stofneiningar geti verið að ræða hjá skarkolastofninum, sem er stutt af rannsóknum á eldri kola, en núverandi ráðgjöf gerir ráð fyrir einni stofneiningu. Mjög háan þéttleika af kolaseiðum var að finna í nokkrum fjörum. Skoðuð voru frekar áhrif þéttleika á vöxt og borin saman ár með lágum og háum þéttleika við botntöku og síðar um sumarið. Merki sáust um þéttleikaháð áhrif á vöxtinn. Nýliðun skarkola hefur verið stöðug undanfarin 25 ár, en líklegt er að þéttleika háð áhrif spili þar inní sem og dreifðar og aðskildar hrygningaeiningar.

Sandrækjan hefur aðlagast hratt að nýjum heimkynnum. Skýr merki voru um tvær aðskildar hrygningar innan ársins, en ungviði sást í júlí/ágúst og aftur í febrúar. Fjöldi nýliða fyrra árs hafði jákvæð áhrif á magn eldri rækju ári síðar sem og jákvæð áhrif hitastigs. Hið gagnstæða má segja um stofn hörpudisks í Breiðafirði, en skoðuð voru gögn úr leiðöngrum auk ýmissa umhverfis og líffræðilegra þátta fyrir árin 1993 til 2003. Það tímabil markaðist af aukningu í yfirborðshita á þessum suðurmörkum útbreiðslusvæðis tegundarinnar. Hátt veiðiálag var á rannsókartímabilinu, en einnig hár náttúrulegur dauði, sem síðar var tengdur við frumdýrasýkingu (Apicomplexa) sem nefnd hefur verið "grár vöðvi". Nokkru fyrr eða í lok tíunda áratugar síðustu aldar var nýliðun í stofninn metin mjög léleg en með náttúrulegum afföllum og auknu veiðiálagi lækkaði stofnvísitalan hratt. Það leiddi svo til þess að lagt var til veiðibann árið 2003.

Stofnstærðarsveiflur hjá þorski og skarkola við Ísland eru almennt litlar og má að einhverju leyti rekja ástæður þess til flókinnar stofngerðar tegundanna og að auki hemjandi þéttleikaháðum áhrifum á uppeldisslóð skarkolans. Hörpudisksstofninn í Breiðafiði var ásamt innfjarðarrækjustofnum, fyrsta tegundin við Ísland sem hrundi í kjölfar núverandi hlýindaskeiðs sem hófst í kringum árið 1996. Á þessu tímabili greindust einnig nokkrar ágengar

lífverur í sjó, meðal annars sandrækja sem naut góðs af hlýindunum í hafinu. Almennt má segja að drifkraftur nýliðunarsveiflnanna sé sameiginlegur milli ólíkra tegunda og þarft er að skoða sveiflurnar á víðum grunni.

“Þegar öllu er á botninn hvolft
þá er lífið þó umfram allt saltfiskur en ekki draumaríng”

Halldór Kiljan Laxness (Salka Valka)

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Paper II: Björn Gunnarsson, Jónas Páll Jónason and Bruce J. McAdam. 2010. Variation in hatch date distribution, settlement and growth of juvenile plaice (*Pleuronectes platessa* L.) in Icelandic waters. Journal of Sea Research **64:** 61–67.

Paper III: Elzbieta Baranowska, Björn Gunnarsson, Sigurður Snorrason, Guðrún Marteinsdóttir and Jónas Páll Jónasson. Density dependant growth dynamics of juvenile European plaice (*Pleuronectes platessa* L.). Unpublished manuscript.

Paper IV: Ingibjörg G. Jónsdóttir, Jónas Páll Jónasson, Svavar Ö. Guðmundsson, Helena Puro, Guðrún Marteinsdóttir and Björn Gunnarsson. 2016. Establishment of brown shrimp (*Crangon crangon*) in a newly colonized area. Crustaceana **89(8):** 901–914.

Paper V: Jónas Páll Jónasson, Guðrún Þórarinsdóttir, Hrafnkell Eiríksson, Jón Sólmundsson and Guðrún Marteinsdóttir. 2007. Collapse of the fishery for Iceland scallop (*Chlamys islandica*) in Breidafjordur, West Iceland. ICES Journal of Marine Science. **64:** 298–308.

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1 General introduction

1.1 Introduction and aims of the thesis

> Akri ársánum
> trúi engi maðr
> né til snemma syni,
> - veðr ræður akri.
> en vit syni;
> hætt er þeira hvárt.
>
> Let none put faith in the first sown fruit
> nor yet in his son too soon;
> whim rules the child, and weather the field,
> each is open to chance.
>
> (Hávamál)

Recruitment success is subject to numerous variables, some are whims or a matter of chance, as quoted in a verse of Hávamál, the ancient Old Norse poem. From the perspective of a fisheries' scientist studying recruitment variability, the drivers of fluctuations as stated in Fogarty et al. (1991) are the "high population fecundity and random variation in mortality rates during the early life stages".

The main objective of the present study is to examine the early life history and stock fluctuations of ecologically and commercially important species in Icelandic waters. The studies were carried out during a period where we have witnessed increased influx of Atlantic waters around Iceland and consequently higher temperatures. I will bring together research on distinct species in Icelandic waters; Atlantic cod (*Gadus morhua*; Linnaeus, 1758), European plaice (*Pleuronectes platessa*; Linnaeus, 1758), brown shrimp (*Crangon crangon*; Linnaeus, 1758) and Iceland scallop (*Chlamys islandica*; Müller, 1776) to analyse how their populations fluctuate and to understand and predict future scenarios. This consequently requires general understanding of the dynamics of the early life stages. By studying diverse species, that all live in a common environment we hope to be able to address question weather the causes of recruitment variation act across a range of taxa, or whether the issues are species specific.

In the following papers we both studied species that have their core distributional area in Iceland, like the cod; and other species at their southern borders like the Iceland scallop. As well as surveying at sea we analysed population trends at sheltered sandy beaches, which is an essential habitat for juvenile plaice. At the beach an important predator of juvenile plaice has recently been found, the invasive brown shrimp (Gunnarsson et al., 2007).

Paper I evaluated the annual distribution, abundance and growth patterns of cod larvae and juveniles on the drift route west of Iceland, extending from the southerly located spawning grounds towards the northern nursery area, in relation to recruitment and variable environmental conditions.

Paper II made the first attempt to analyse the origin of juvenile plaice in Icelandic waters by estimating the hatch date distributions by means of otolith microstructure. Spatial variations in age–length relationships are then analysed to determine whether geographical size differences are growth-related.

Paper III investigated the effect of density on growth of juvenile plaice. Two years with variable population density were chosen and growth compared during the settlement period and later in the summer. Furthermore, the width of otolith increments at settlement were measured to investigate recent growth.

Paper IV investigated whether brown shrimp has established in Icelandic waters. Specifically, this comprises estimation and description of annual and seasonal changes in population abundance of brown shrimp southwest of Iceland based on samples collected over a 10 year period.

Paper V looked for possible causes for the dramatic decline in the stock of Iceland scallop in Breiðafjörður between 1999 and 2003. Data from stock surveys, specific sampling, and fishery logbooks were explored in order to analyse stock biomass, natural and fishing mortality, muscle condition and recruitment.

In this introductory chapter I will introduce briefly, general stock fluctuations (chapter 1.2), the Icelandic marine ecosystem (chapter 1.3), including the variation in oceanographic condition and research on recruitment. Followed by a biological background of each species with emphasis on Iceland and surrounding waters (chapter 1.4), before I discuss recent findings and their relevance to the Icelandic marine ecosystem, recruitment in general and the effect of climate change (chapter 2).

1.2 Stock fluctuations

Population fluctuations are recognized as common phenomena of both marine and terrestrial animals (Elton, 1924). For diverse species, such as the wide range of fish and shellfish exploited in Iceland it is necessary to distinguish between different sorts of fluctuation and the drivers behind them. With warming climate it is vital for a fishing nation like Iceland that depends heavily on its marine resources to get as clear a picture as possible of those processes. Good examples are the collapse of the herring stocks (*Clupea harengus*) in the late sixties to early seventies (Jakobsson and Stefansson, 1999), and the recent decline in the key ecological and commercially important capelin (*Mallotus villosus*) (Pálsson et al., 2012), which has spurted economical troubles in coastal communities. Even in heavily monitored species like those the underlying causes or drivers of the fluctuations are usually not clear.

Caddy and Gulland (1983) classified fish (including shellfish) stocks into four categories according to their pattern of fluctuation: steady stocks, cyclical stocks, irregular stocks and spasmodic stocks. Jennings et al. (2001) catagorized the drivers of those fluctuations for marine species by the physical and biological processes that affect the survival of eggs and larvae, the growth and mortality during juvenile and adult stages, and by behavioural processes. Further, Shelton and Mangel (2011) classified the sources of fluctuations into three main hypotheses: (*i*) species interactions (predator - prey interaction or diseases); (*ii*) nonlinearity in single species dynamics ; and (*iii*) environmental variability that affects vital rate (survival and growth). They stressed that the causes of fluctuations have important implications both for the management and conservation of given stocks.

Global records prior to the industrialized fishing age have shown clear long term trends and fluctuation in stocks. Perhaps the best example comes from the the Pacific sardine and northern anchovy fluctuations, were records from fish scales in the sediment cores showed large periodic fluctuations (Baumgartner et al., 1992). On average those cycles were around sixty years. The Pacific Decadal Oscillation (PDO), has been linked with the historical fluctuation in catches and biomass of the sardines (Zwolinski and Demer, 2012). However, when much longer time series of paleo-sardine and paleo-PDO indices were analysed the correlation was no longer found (McClatchie, 2012). It was also stressed that mechanistically slow multidecadal index like the PDO is most likely of less importance then the El Niño-Southern Oscillation (ENSO) index which operates on a scale of a few years and has shown to affect the environment and consequently the spawning success of the sardines (Song et al., 2012).

Klyashtorin and Lyubushin (2007) showed several examples of changes in fish productivity related to climate fluctuations, which were based on smoothed time series, to address the question about the effect of climate on large scale fisheries. But usually the available timeseries are rather short given the long period of the large scale fluctuations. It might be better to talk about 'regime shifts' that have been documented in many regions (Szuwalski et al., 2015). As such, Conners et al. (2002) described 'regime shift' in the Bering sea, but they also discussed the lack of response in recruitment of walleye pollock (*Gadus chalcogrammus*) to either isolated 'cold' or 'warm' years, addressing that the change in the climate forcing may need to be sustained to generate a change in fish abundance. Regime shift has been found to cause fundamental changes in energy pathways, through a 'bottom up' mechanism that was clear in increased biomass of non-commercial benthic invertebrates and skates (Conners et al., 2002). As mentioned in Szuwalski et al. (2015), expected forecast of future recruitment should be based on the current regime, as has been used in the case of the the walleye pollock (Ianelli et al., 2016).

But what are the effects of fishing on fluctuations in stocks? Shelton and Mangel (2011) predicted that, based on simulation at exploitation level close to maximum sustained yield, populations will increase in temporal variability or experience increased coefficients of variation. But they also stressed their findings that recruitment variability will contribute substantially to population variability compared to relatively little contribution from variation in both natural and fishing mortality. Hsieh et al. (2006) also presented evidence that exploited species exhibit higher temporal variability in abundance than unexploited species, based on long term studies of both non and exploited species larvae abundance. They argued that the fishery induced truncation of the age structure would cause increased variability of recruitment. The effects of reduced adult abundance can also be delayed. Walters and Kitchell (2001) describe the depensatory effect that population faces when it reach a certain size, due to fishing. Then the juvenile survival is inhibited by lack of predation pressure on important pelagic species. At that stage the stock could be inhibited to bounce back. They proposed that delayed depensation may occur in 10 - 20% of severely overfished stocks and to insure against it, spawning stock abundance should generally be not less than 50% of virgin stock.

In general it can be said that both defining and understanding the fluctuations in the fish and shellfish stock has proven to to be difficult. Shepherd (1990) discussed stock fluctuations in one of of his paper and concluded maybe the obvious: "They certainly aren't due to anything very obvious, or someone would have figured it out long ago. There are still a lot of people trying to find out what causes these fluctuations, but don't hold your breath while you're waiting for the answer".

1.2.1 Recruitment patterns

The Norwegian fishery scientist Hjort (1914) was the first to propose that year class success was most likely determined during early life in marine fishes as he documented strong year classes in various fish stocks. He suggested that variation in food availability either during a critical stage or inter-annual variation in the transport of eggs and larvae from spawning to nursery areas were likely causes of the observed difference in survival. Since then a lot of work and hypotheses have been put forward to our understanding of the recruitment processes. One of the more important steps was the extension of Cushing's 1990 work on Hjort's. Cushing merged his two hypotheses into a single Match/Mismatch Hypothesis which suggested that larval survival was the results of a fixed time of spawning coupled with a variable time of plankton blooms. Cushing also introduced the importance of the Sverdrups critical depth, which is the depth were phytoplankton growth is matched by loss of phytoplankton biomass. The critical depth must be deeper than the mixed layer or the seabed in tidal areas.

It has also been pointed out that a certain feeding paradox exists regarding the larval stage (*e.g.,* Cowan and Shaw, 2002). It seems that fish larvae are able to feed close to saturation independent of measured prey density in the field. It is however difficult to measure the ongoing production of new zooplankton that would serve as food items, but it follows somewhat Cushing's diagram on the importance of secondary production. Rothschild and Osborn (1988) suggested that turbulence at a small scale improves the feeding success of a given predator "because the predator can rely upon turbulent rather than the metabolic energy to capture a particular prey". Their theory was named the plankton contact hypothesis. On the other hand, Lasker's (1981) "Stable ocean hypothesis" was formulated after he observed extremely poor recruitment during stormy years when wind turbulence was high (called Lasker events). That was mostly based on experience from coastal upwelling regions of the eastern Pacific. In those regions patches of suitable food for the larvae are established when the upwelling recedes. Further, other near shore oceanographic features like the magnitude of river discharge plumes have been shown to affect fish recruitment (Grimes and Kingsford, 1996). That could happen through several pathways like increased production and hence growth of the juveniles within the plumes, but also retention mechanisms of both adults and larvae within areas. Freshwater runoff in Iceland, particularly from the large glacial rivers in south, are highly important for the near shore ecosystem (see chapters 1.3.1 and 1.3.3).

While the importance of optimal environment for the growth of the larvae has been highlighted by the theories described above, the importance of successful retention of larvae and juveniles into preferred nursery grounds has been highlighted by the "member - vagrant" hypothesis of Iles and Sinclair, formulated in Sinclair (1988). The mean year class size or the absolute abundance of each population is a function of the size of larval retention area. The integrity of the area might vary from year to year based on variation in regional physical oceanography, and thus explain the variation in population abundance (Iles and Sinclair, 1982). Sinclair and Power (2015) revisited the argument for the member/vagrant hypothesis that was originally put forward on Atlantic herring data. They showed, based on surveys, that spawning locations of herring were persistent over decades and there was a limited downstream drift of larvae for their first 2-3 months. Their interpretation was that the system behaves more in accordance to the member/vagrant hypotheses than to hypotheses of active transport away from the spawning sites, such as the migration triangle hypotheses of Harden Jones (1968) and the adopted migrant hypotheses (McQuinn, 1997). Regarding the Icelandic cod stock, the knowledge about the transport, is that it is active away form the spawning sites, clockwise around the country and in some years large concentrations of pelagic juveniles are found as far away as in Greenlandic waters (Begg and Marteinsdottir, 2000).

As discussed above the fate of the larvae is shaped by the survival or mortality during the early life phases, as Houde (2002) points out the common truth that the "average fish larva is a dead fish larva". As survival is only a small fraction of a percent, it is necessary to think carefully about the rate or the unit at which these events take place, which is usually measured in days or months. The interaction between growth and predation can play a crucial role due to size specific mortality, as predation mortality decreases rapidly with size during larval and juvenile stages (Bailey and Houde, 1989). The argument was that relatively small changes in growth and predation rate could cause more than two orders of magnitude difference in survival of each cohort (Houde, 1987), this was later called the Stage Duration Hypothesis (Cowan and Shaw, 2002). Longer stage duration due to slow growth will increase the changes of being eaten during an early life stage. Direct evidence of that is however difficult to find, but papers like Meekan and Fortier (1996) have shown that survivors within given cohorts grew faster, but that difference varied between years. Recruitment can also be buffered through density dependent processes, as mortality could increase proportionally with abundance (Houde, 2002). Predation can be density dependant through cannibalism of older or faster growing conspecifics but buffering of recruitment can also occur where there is space limitation in the settlement habitat. In the marine realm, maybe the best example of density dependant regulation is found in flatfish species (*e.g.* plaice (*Pleuronectes platessa*)), where individual cohorts can reach the carrying capacity of the shallow waters nursery grounds (Iles and Beverton, 2000; Nash et al., 2007).

The underlying correlation between recruitment and stock parameters has to be clarified so the environmental variables can be truly disentangled and identified (Cardinale and Hjelm, 2006). Plausible environmental factors have often been difficult to find as re-examination of published environmental-recruitment correlations usually do not hold, with the exception of populations at the limit of the species' geographical range (Myers, 1998). This is manifested in the large amount of noise around the best fit stock-recruitment relation used in most fisheries' assessments with many of little predictive value. That is the case with the relative long

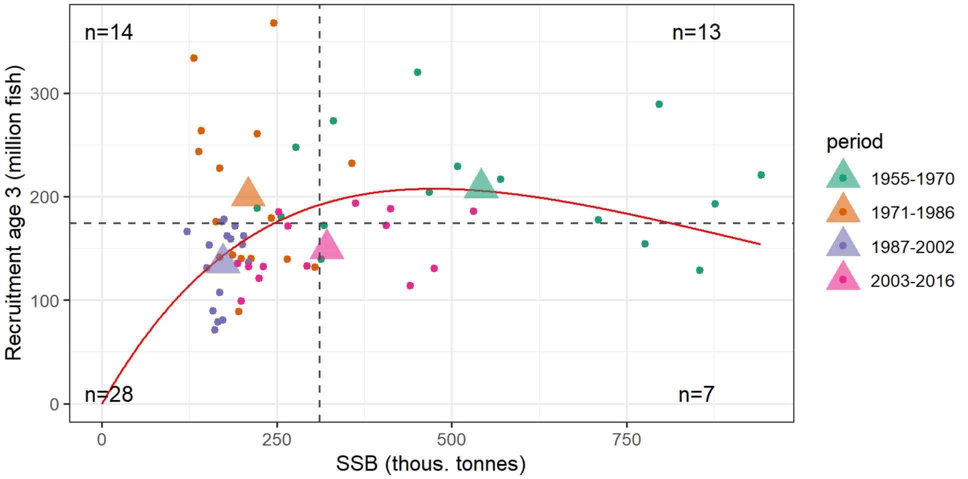

Figure 1.1. Spawning stock biomass (SSB in thousand tonnes) and recruitment at age 3 (millions of fish), based on stock assessment of Icelandic cod. The red curve is fitted based on the Ricker function. Dots indicate individual years and colours represent four equally long periods. Triangles show average SSB and recruitment for each period. Broken vertical and horizontal lines show average SSB and recruitment, respectively, and values represent the number of years within each of the four boxes. Figure from (Jónsdóttir et al., 2019).

timeseries of Icelandic cod stock as is illustrated in Figure 1.1. However, when the spawning stock of the Icelandic cod stock is below average it is less likely to produce above average year-classes (Jónsdóttir et al., 2019). Studies on a single species, like the Icelandic cod, highlight questions on the causes of variation, and whether the same factors are likely to affect the diverse species studied in this thesis; species that have the same strategy of broadcast spawning, common in marine vertebrates and invertebrates, but rare in terrestrial systems. As adressed in Myers (2001), when the spawning stock is small, mortality of eggs and larvae is more likely to result from stochastic density independent conditions of the physical and biological environment. Further, Hilborn and Walters (1992) stated : "While recruitment may be largely independent of stock size as a fishery develops, experience has shown that most fisheries will reach the point where recruitment begins to drop due to overfishing".

1.3 The Icelandic marine ecosystem

1.3.1 Topography and currents

The volcanic island of Iceland is located at the intersection of the Mid-Atlantic Ridge and the Greenland-Iceland-Scotland Ridge where the warm waters of the North Atlantic Current (NAC, a continuation of the Gulf Stream) meets the cold Arctic waters from the north. The continental shelf surrounding Iceland has an average depth between 50 and 200 m and covers around 212 thousand km^2 (Astthorsson and Vilhjalmsson, 2002). Iceland is connected to Greenland, the Faroe Islands and eventually to Scotland by a system of ridges (Figure 1.2). The locations of the ridges shapes the pattern of currents and separates the cold Arctic deepwater of Iceland and Norwegian sea from the relatively warm waters of the North-east Atlantic (Stefánsson, 1962). To the southwest of Iceland lies the Reykjanes Ridge which is the part of the mid Atlantic Ridge that reaches Iceland.

The waters around Iceland form one of the hydrographically most complicated regions of the North Atlantic (Logemann et al., 2013). The NAC brings warm (6-11°C) and saline (35.0 - 35.2) Atlantic waters to the southern and western areas of Iceland (Stefánsson, 1962). The main flow is rather slow moving east of the Reykjanes Ridge (Figure 1.3). West of the ridge is the more energetic Irminger Current (IC, a Gulf Steam continuation) (Logemann et al., 2013). The IC mostly recirculates in the Irmenger Sea, but a small fraction of it, a branch called the North Icelandic Irminger Current (NIIC), carries warm water north and then eastward to the

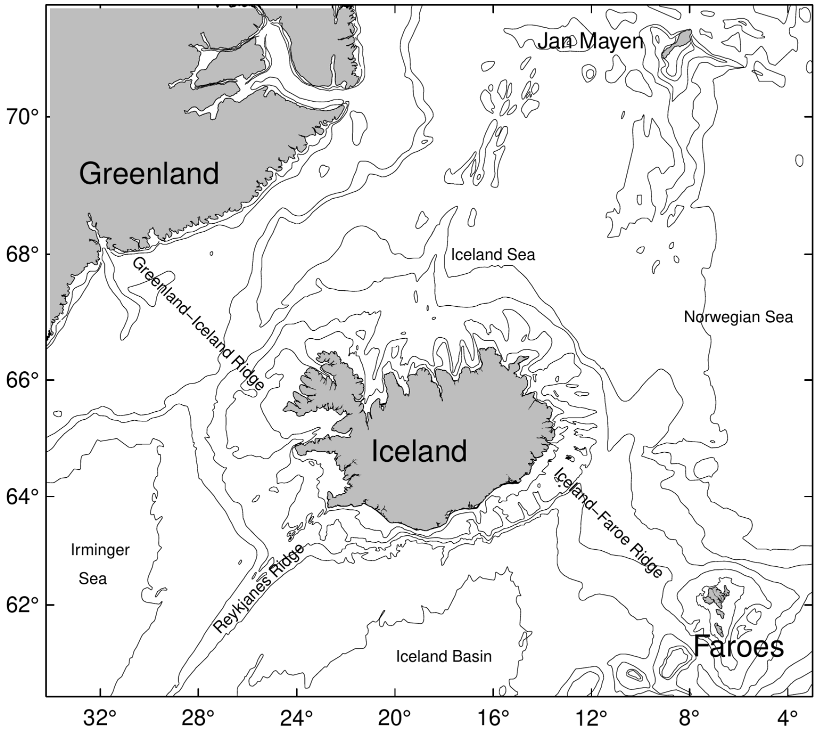

Figure 1.2. Bottom topography of Iceland and surrounding waters. The thin lines represent 100, 200, 500, 1000 and 2000 m depht contours.

North Icelandic continental shelf area (Kristmannsson, 1998). The NIIC is responsible for the relatively mild climate north of Iceland and fluctuations in the current strongly shapes the marine ecosystem north of Iceland (Astthorsson and Vilhjalmsson, 2002). On their eastward path north of Iceland the NIIC waters are mixed with the Arctic waters of the East Iceland Current (EIC) which also flows eastward along the continental slope. The EIC water is mainly formed of old Atlantic waters that had been carried over the Iceland-Faroe Ridge, cooled down in Iceland- and Greenland Seas and mixed with freshwater. Also there is an admixture of Polar Water in the EIC. It has a temperature of -1 to 4°C and salinity of 34.6 to 34.9 (Swift, 1986). The EIC runs along the eastern flank of the Kolbeinsey Ridge onto the north-eastern shelf area of Iceland continuing to the northern flank of the Iceland- Faroe Ridge where it meets the NAC (Logemann et al., 2013).

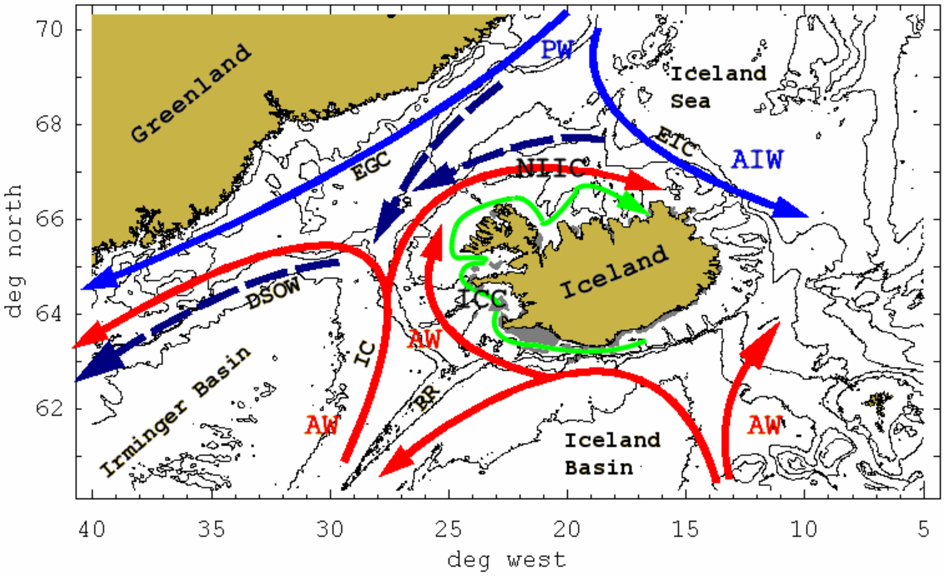

Figure 1.3. The main oceanic currents around Iceland. The isobaths are: 200, 500, 1000, 2000 and 3000 meters. Green arrows: coastal waters, red arrows: Atlantic Water (AW), blue arrows: Polar Water (PW) and Arctic Intermediate Water (AIW), dashed blue arrows: Denmark Strait Overflow Water (DSOW). Other abbreviations are as follows: EGC—East Greenland Current, EIC—East Icelandic Current, IC—Irminger Current, ICC—Icelandic Coastal Current, NIIC—North Icelandic Irminger Current, RR—Reykjanes Ridge (from Jonasson et al. (2009) but modified after Logemann and Harms (2006)).

Closer to the east coast of Greenland is the East Greenland Current (EGC) that transports Polar water originated in the surface layers of the Arctic Ocean, formed from the atmospheric cooling and the large rivers of Siberia and Canada. It is very cold and fresh with a temperature between -1.7 and 0°C and a salinity between 30 and 34 (Hopkins, 1991). It forms a Polar Front where it meets the Arctic and Atlantic water masses (Logemann et al., 2013). Most of the EGC passes Iceland through the western part of the Denmark Strait (Figure 1.3). A small fraction of the EGC mixes with the NIIC (Logemann and Harms, 2006). Near to the coast another current exists: the Icelandic Coastal Current (ICC, Figure 1.3) which flows clockwise around Iceland (Astthorsson and Vilhjalmsson, 2002). The current is driven by the barotropic pressure field which is related to the cross-shore density gradient induced by riverine freshwater (largely driven by the output of the large glacial river on the south coast) (Logemann et al., 2013). It is enriched by the riverborne silicate but has a lower amount of nitrates and phosphate than the Icelandic shelf water (Olafsson et al., 2008). In the south-western part of Iceland, formation of density layers as well as high amount of silicates within the ICC facilitates the early spring algal bloom in late March (Thordardóttir, 1986). Generally, spring bloom starts later or in middle of May on the off-shelf areas, after a thermocline has been formed (Thordardóttir, 1986).

1.3.2 Variation in oceanographic condition

Abrupt fluctuations are common in the ecosystem around Iceland. That is specially true for the northern part of the Icelandic waters. The Polar Water was in fact observed to dominate the North Icelandic shelf during the period between 1965 and 1971 (Malmberg and Kristmannsson, 1992). Prior to that there was a generally warm period in the waters north of Iceland from 1920 to 1964 (Astthorsson et al., 2007). The temperature difference between the two periods was up to 4°C (Malmberg and Jonsson, 1997). During the period between 1971 and 1995 there was an alternate of 1-4 years of either cold (1975, 1977, 1979, 1981-1983, 1989-1990 and 1995) or warm periods (1972-1974, 1980, 1984-1987 and 1991-1994) (Astthorsson et al., 2007). Around 1997 the flow of Atlantic waters into the northern shelf had intensified by 50 % from 1994 and 1995 values (Jónsson and Valdimarsson, 2005). As such, for all years between 1996 until 2016, temperatures in upper layers have been relatively high on the northern shelf, apart from the spring of 2002 (Olafsdóttir et al., 2018).

The oceanographic condition south and southwest of Iceland is more constant than on the northern shelf. Regular hydrographic sections are available for that region from 1970 and onwards (Olafsdóttir et al., 2018). As such, the salinity was below average for the periods, 1974-1974, 1985-1988 and 1992 - 1995, whereas all of those have been related to "Great Salinity Anomalies" in the northern North Atlantic (Astthorsson et al., 2007; Belkin, 2004). Since 1996, both salinity and temperature has been high, with highest salinity values of past 30 years measured in 2005 (Olafsdóttir et al., 2018). Salinity was high in south and south-western Iceland until 2010, but since 2011 until 2016 it has been declining as it reached values of past 1996 (Olafsdóttir et al., 2018).

Astthorsson et al. (2007), discuss the effect of atmospheric influences on the ocean circulation around Iceland, and points out that variation in the ocean climate north of Iceland seems to be of local origin. As such, the frequency of local northerly/southerly wind and the and the influx of Atlantic water onto the northern shelf has been demonstrated (e.g. Jónsson and Valdimarsson, 2005). In similar manner Olafsson (1999), found correlation between northern/southern wind and the hydrographic condition in northern Iceland, but could not relate that to the large scale North Atlantic Oscillation (NAO) atmospheric index. However, the observed temperature increase south of Iceland since 1996 and the subsequently recent cooling has been linked with larger scale processes in the North Atlantic (Olafsdóttir et al., 2018), such as the Atlantic multidecadal Oscilliaton (AMO) which is an index of decadal variability based on sea surface temperature (SST). There was a cool anomaly in the 1980s and 90s in the AMO, and warm period from late 90s to 2014. However since 2014 - 2016 the AMO has declined, mainly due to cooling within in the subpolar gyre region (Frajka-Williams and Beaulieu, 2017). The dynamics of the subpolar gyre (SPG) has recently been linked, through a gyre index (based on the difference of sea surface height (SSH) between subpolar and subtropical gyres), to various climatic and ecological aspects in the North Atlantic Ocean (e.g. Hátún and Chafik, 2018). The gyre index dates back to 1993, it increased rapidly after 1996 and remained high with some fluctuation until 2012 (Hátún and Chafik, 2018), that coincides well with marked increase in temperature both south and north of Iceland.

New insights on the circulation around Iceland are presented in Logemann et al. (2013), where they use a combination of a numerical ocean model and hydrographic measurements. They show that the main driving mechanism of the NIIC is the barotropic pressure gradient between the Arctic and Atlantic waters with local windstress influencing only the NIIC variability, i.e not forming its main forcing as has been suggested in older papers. They also propose a designation of a current of Atlantic water (7.0 - 7.6°C) over the southern and south eastern Icelandic shelf, the South Icelandic Current (SIC). It flows towards the east and north east and is driven in similar manner as the NIIC. The ICC is also discussed in the model excercise of Logemann et al. (2013), as they have coupled a hydrological model with a hydrodynamical model. The ICC is well detectable in south and western part of Iceland, and also within some fjords like Húnaflói in the north. In the south-eastern part of Iceland it is barely seen and it contradicts that the ICC flows clockwise all around Iceland (Stefánsson and Ólafsson, 1991).

1.3.3 Recruitment patterns of Icelandic stocks

The location of Iceland at the boundaries between the warm Atlantic and the cold water from the north with the hydrological fluctuations observed (see chapter 1.3.2) is reflected in stock trends of most of the commercial and non-commercial species around Iceland. Most emphasis and research has been on the recruitment patterns of cod, but in this section I will discuss in general the available literature on recruitment of Icelandic fish and invertebrate stocks.

Cod and demersal species

During the last century, almost all cod and other gadoid stocks in the North Atlantic, experienced dramatic declines in number (Marteinsdottir and Pardoe, 2008). As a consequence recruitment levels generally decreased and in some stocks such as the Icelandic cod stock, recruitment has been below average over an extended period of time (Jónsdóttir et al., 2019). Furthermore, a meta analysis demonstrated that Gadiformes were the most common order where strictly spawning biomass driven dynamics were found (Szuwalski et al., 2015), meaning that recruitment decreases with biomass (applicable when the biomass is less that half of the maximum). There have been differences in the spawning stock biomass recruitment relationship between periods in Iceland, but when the spawning stock biomass is below average it is less likely to produce above average recruitment (Jónsdóttir et al., 2019). Older analyses have also highlighted the importance of greater age diversity in the stock which has shown to influence recruitment success (Marteinsdottir and Thorarinsson, 1998).

In a comparative analysis on recruitment of cod and haddock (*Melanogrammus aeglefinus*) from eight regions in the North Atlantic, recruitment variability was generally higher for haddock than cod, which was also true for Iceland (Fogarty et al., 2001). The recruitment fluctuations of both species in Iceland were comparatively low and there was a positive correlation between the recruitment indices of both species in Icelandic waters, indicating a rather stable environment and that the species are experiencing similar hydrographic conditions. A correlation between 0-group cod abundance from pelagic surveys and the biomass of zooplankton was desrcibed in Astthorsson et al. (1994). Further they also demonstrated a link between the 0-group cod abundance and the number of cod recruits derived from assessment, However, after 1996, coinciding with increased inflow of Atlantic waters onto the northern shelf, there was great increase in the abundance of juveniles caught in the pelagic survey (Jónsdóttir et al., 2019). That increase was not reflected in larger year-classes, although some of them were around average. Recruitment of both cod and haddock has been suggested to be influenced by the the strength of the coastal current (Figure 1.3), measured as a thickness of the freshwater layer along the larval drift route from main spawning grounds to the nursery areas (Olafsson, 1985). Later studies have also demonstrated the positive influence of the coastal current on the recruitment of cod (Olafsson et al., 1993; Begg and Marteinsdottir, 2002). Brickman et al. (2007b) investigated larval drift of cod using a high-resolution circulation model. Based on climatological 0-group data, they predicted that the contribution from the main spawning grounds decreases with clockwise distance, in agreement with what had been proposed by hatch date distribution and information on spawning periods (Marteinsdottir et al., 2000b). Further, Brickman et al. (2007a) discussed a problem with the drift model overestimating the abundance of cod juvenile in the southern part of Iceland during experiment for the years 2002-2003. A possible explanation was that demersal settlement could already have taken place there at the time of the 0-group surveys (mean date 20th of August).

Cod from Icelandic waters has been included in several meta-analyses where recruitment parameters were analysed in regards to environmental parameters. The result has been a bit confusing as addressed in Brander and Mohn (2004), with contrasting effects of temperature on recruitment of the Icelandic cod stock. Temperature was documented to have positive (Planque and Frédou, 1999) and also negative (Brander, 2000) effects on the recruitment index of the Icelandic stock, this difference could stem from different spatial data sources of temperature measurements or estimates. In the study of Brander and Mohn (2004) the NAO index was found to positively influence recruitment of the Icelandic cod stock.

Perhaps the greatest positive influence on cod recruitment has been during years when there has been an extensive drift of larvae all the way west to Greenland (Jakobsson and Stefansson, 1998). Recruits at age three usually never exceed 300 millions (Schopka, 1994) and haven't been higher than 200 millions since 1986 (Jónsdóttir et al., 2019). However, during the period 1920 to 1964 the entire Iceland - Greenland Sea, were what was phrased as cod "paradise" (Jakobsson and Stefansson, 1998). There was a sudden warming in the early 1920's in Greenlandic waters after a relatively cold period that extended the possible distributional area along the west coast of Greenland north to 69° (Schopka, 1994), with generally warm conditions as well in Iceland during the same period (Astthorsson et al., 2007). Recruits originated in Greenlandic waters have been estimated to be more than 500 million on three occasions, in 1922, 1924 and 1945 (Schopka, 1994). This great shift in potential habitat can be categorized as a regime-shift in the stock (Szuwalski et al., 2015) or a space-limited environment when cod is only confined to Icelandic nursery areas (Cowan and Shaw, 2002).

Coinciding with the recent increased inflow of Atlantic waters onto the Icelandic shelf (Hátún et al., 2005), after 1996 there was extended distribution of many common 'southern or warm water species' in SW part of Iceland (Stefansdottir et al., 2010). In one of them the monkfish *Lophius piscatorius*, there was an increase in recruitment following the inflow (Solmundsson et al., 2010). The authors stated that changed environmental conditions had increased the suitable area and likely increased larval transport or larval survival. However, a substantial reduction in recruitment started in 2008 which has prevailed to 2020 (MFRI, 2020b), albeit really warm conditions throughout most of that period (Olafsdóttir et al., 2020). This recent lack of recruitment has been witnessed as well for most of the 'southern' commercial species in Icelandic waters (MFRI, 2020e). As such, recruitment indices of blue ling (*Molva dypterygia*) were exremely low between 2010 and 2016 (MFRI, 2020c), ling (*Molva molva*) indices in 2013 - 2020 (MFRI, 2020h), tusk (*Brosme brosme*) indices in 2010 - 2018 (MFRI, 2020l), witch (*Glyptocephalus cynoglossus*) indices in 2011 - 2018 (MFRI, 2020m) and megrim (*Lepidorhombus whiffiagonis*) indices in 2012 - 2020 (MFRI, 2020i).

Greenland halibut (*Reinhardtius hippoglossoides*) in Icelandic waters is currently assessed as the West Nordic stock (WN) with components in East-Greenland and the Faroe Islands (MFRI, 2020f). The stock is bordering the Northeast Atlantic stock component (NEA), but so far no studies have shown genetic difference between those two stocks. Recently it was demonstrated that a significant number of juveniles from the Svaldbard region in the NEA stock component migrate to both management areas (Albert and Vollen, 2015). These results suggest that recruitment indices from Svalbard should be used to predict future biomass of both stocks and that is questionable if NW and NAC components should be assessed together. Further, it highlights the importance of research on the early life stages and connectivity of stocks in general.

The most common sandeel species in Iceland is the *Ammodytes marinus*, but they are not commercially harvested. Consistent monitoring of them started in 2006, or a year after a great breeding failure in most of the seabirds stocks all around Iceland (Lilliendahl et al., 2013). From 2005 to 2012 only one year-class, the 2007, was really evident in the surveys around the Vestmannaeyjar archipelago, the stronghold of puffins (*Fratercula arctica*) in Iceland (Lilliendahl et al., 2013). From 2013 to 2019, really few sandeels where caught around Vestmannaeyjar, but there was a marked increase in the 2020 survey (MFRI, unpublished data).

Pelagic species

Historically three herring (*Clupea harengus*) stocks have been fished in Icelandic waters. The Atlanto-Scandian herring which have been utilized during warm periods on it's feeding ground, north and east of Iceland (Jakobsson and Stefansson, 1998). Additionally two local stocks, the Icelandic summer spawning herring which has been targeted for more than a century now and a spring spawning herring that went extinct in the 1970's (Marteinsdottir and Pardoe, 2008). Oskarsson and Taggart (2010) analysed the recruitment time series of Icelandic summer spawning herring from 1963-1999. They examined the recruitment variation in relation to spawning stock biomass, egg production in regards to spawning experience and condition. They further tested the influence of NAO, temperature and zooplankton indices at various lags on recruitment. They found that a fair amount of recruitment variability could be explained by the total egg production of recruited spawners, positively by the NAO index (lagged by one year) and with increasing temperature at the Siglunes section of northern Iceland. During recent years (2014-2019) recruitment has been poor MFRI (2020a).

Capelin is perhaps the key fish species in the Icelandic ecosystem and the most important foraging fish for cod and many other important demersal species (Jakobsson and Stefansson, 1998). It has been an important commercial species since the early 1970's (Astthorsson and Vilhjalmsson, 2002). In a short lived species like the capelin, where the fishable biomass is built mainly up of two year-classes, rather large fluctuations are expected. There was a sharp decline in the stock in the beginning of the 1980s and again ten years later in the 1990s. Those fluctuations were thought to be caused by environmental condtions rater than overfishing (Jakobsson and Stefansson, 1998). Carscadden et al. (2013) attempted to fit a stock recruitment relationship for this stock, but it was insignificant. Further there has also been inability to establish correlations between the recruitment and environmental parameters (temperature, salinity, plankton abundance) (Carscadden et al., 2013). To establish any meaningful correlations the authors proposed extensive monitoring of the fate of the larvae in the complex drift route along the coastal current towards their juvenile areas in the north and east of Iceland. Great decline in recruitment of capelin was observed from the mid 2000s (Pálsson et al., 2012), but the juvenile index (1-2 year old) has been low since then with the exception of the years 2010, 2012-2013 and 2019 (MFRI, 2019). The capelin shifted its distribution northward after the increased inflow of Atlantic water that started in late 1997 (Vilhjalmsson, 2002). A large project on the ecology of the capelin was carried out between 2006 to 2008 (Pálsson et al., 2012). One of the outcomes, based on larval distribution, was increasing spawning activity of capelin in the northern part of Iceland. That was considerably greater than was previously assumed in recent time, but comparable to what was reported during the warm period that started in 1920 and lasted until 1964 (Sæmundsson, 1934; Astthorsson et al., 2007).

Mackerel *Scomber scomber*, was observed occasionally, mainly during warmer periods in Icelandic waters, but since 2007 extensive summer feeding migration and fisheries have occurred (Astthorsson et al., 2012). Gunnarsson et al. (2019) described for the first time overwintering of juveniles within Icelandic near shore areas during the winters of 2010/11 and 2014/15. They proposed that most likely the juveniles had originated from spawning within the south-eastern EEZ of Iceland. Olafsdottir et al. (2019) concluded based on extensive surveys and models that the expansion of mackerel summer feeding into Nordic seas was primarily driven by increased stocksize.

Invertebrates

Historically, the northern shrimp (*Pandalus borealis*) is the commercially most important invertebrate species that is harvested in Icelandic waters. The recruitment of the offshore component of the northern shrimp, which is located in waters north and northeast of Iceland, was analysed in Jónsdóttir et al. (2012). Recruitment had decreased and been at record low levels since 2005. They found no significant relationship between recruitment and spawning stock biomass, but a strong negative effect of SST and cod biomass. It was discussed that SST was likely to influence the planktonic stage and cod biomass the demersal one. For the inshore northern shrimp component (located inside fjords of western and northern part of Iceland) relationship between stock and recruitment was also generally poor (Jónsdóttir, 2018). That applied also to the weak correlation between total egg production and recruitment.

Norway lobster (*Nephrops norvegicus*), a commercially important invertebrate in Icelandic waters, on the other hand is at its northern distributional limits at the southern shore of Iceland (Eiríksson and Jónasson, 2018). A positive influence of bottom temperature on CPUE, fishable stock and recruitment has been demonstrated (Eiríksson, 2009). However, since 2005 recruitment has been lacking and the stock has declined to a level that has led to monitoring fishery (Eiríksson and Jónasson, 2018; MFRI, 2020j). In contrast to older results, a maximum salinity and temperature of the past 30 years was reached in 2005, a condition that prevailed to 2010 (Olafsdóttir et al., 2020) and should have had a positive influence according to Eiríksson (2009).

Conclusions of recruitment patterns in Iceland

Overall, rather few meaningful relationships have been proposed regarding the effects of the environment on the recruitment of the main commercial stocks in Icelandic waters. The importance of the coastal current has been put forward as a mechanism that facilitates good year-classes for cod and haddock. Positive anomalies of the NAO index have been linked with recruitment success of both cod and the summer spawning herring. There is a need to revisit those and other environmental factors that have been put forward with longer timeseries as it has been shown that those often only hold for a specific time period (Myers, 1998).

It is an intriguing fact that after less than a decade of warm period in the waters around Iceland, something happens around 2005. At least that seems to be true both for species that have their core distribution at the southern part of Iceland and those who have their southern distributional limits at Iceland. Southern species include; sandeel and *Nephrops* and northern; capelin and northern shrimp. Further, around and shortly after 2010 a recruitment failure is evident in many southern species or species that spawn at the southern part of Iceland like; monkfish, blue ling, ling, tusk, witch, megrim and herring. Those taxonomically distinct species have all evolved similar ecological properties as broadcast spawners. It would seem that the drivers of fluctuations in recruitment are common across those taxa, i.e. that there are general ecological laws governing recruitment in marine systems. The underlying mechanism is not clear but a logical explanation is changed environmental factors of the last 10-20 years (MFRI, 2020e). A plausible large scale mechanism that could contribute to the main drivers of this decline is described in Hátún et al. (2017). They describe a great decline in pre-bloom silicate concentration in areas south of Iceland within or under the influence of the SPG dynamics (see chapter 1.3.2) that would eventually have great impacts on higher trophic levels as theoretically the pre-bloom silicate controls the maximum potential production of the spring bloom. As such, the observed pre-silicate values from the Irminger sea decreased from 2000 to 2010 and remained low to the last value presented in 2015. The effect of the SPG system on other biological processes has been demonstrated before (Hátún et al., 2009, 2016).

1.4 Biology of the study species

1.4.1 Atlantic cod, *Gadus morhua*

Distribution

Atlantic cod, *Gadus morhua* (Order Gadiformes; Family Gadidae, Figure 1.4) has a wide distribution and is found in a variety of habitats, from shallow waters close to the shore to deeper waters off the continental shelf (Jónsson, 1992). Cod is distributed from Cape Hatteras in the western Atlantic, off Labrador and the western coast of Greenland, north to southern Svalbard and Novaya Zemlya in the Barents Sea and south to the North Sea and in the Baltic Sea, with 26 recognised stocks or management units (Marteinsdottir and Rose, 2019). Cod is an eurythermal fish, which occupies areas with a range of annual temperatures from 2 - 11°C (Brander, 1994), but cod has been exposed to average daily temperature of -1.5 to 19°C (Righton et al., 2010). Cod is also classified as an eyryhaline species and tolerates salinities down to 7 but egg development requires salinity of at least 11 (Provencher et al., 1993; Westin and Nissling, 1991). The Icelandic cod stock lies close to the mean temperature and distributional area (Sundby, 2000). In Icelandic waters it is most common at depths between 100 - 400 m and is seldomly caught deeper than 550 m (Jónsson and Pálsson, 2006). Cod is a demersal species but can frequently be found feeding midwater (Jónsson and Pálsson, 2006).

Age and growth

Cod commonly reaches lengths of 110 - 120 cm in Icelandic waters and an age of 13 - 14 (MFRI, 2018). The largest cods in Icelandic waters have been between 167 - 186 cm, and 18 - 19 years of age, but elsewhere cod is thought to have reached 200 cm and with maximum recorded age of 24 years (Jónsson and Pálsson, 2006). In Icelandic waters in March, the average size of one year old juveniles is usually between 11-13 cm, two year old between 22 - 26 cm and three year old 33 - 40 cm (Jónsdóttir et al., 2019). Growth rate differs between regions and is considerably faster in the warmer Atlantic waters in the southern and south-western part of Iceland (Jónsson and Pálsson, 2006).

Maturity and spawning

Cod in Iceland reaches maturity (L_{50}) at 71.4 cm and age of 6.2 (A_{50}) (Marteinsdottir and Begg, 2002). Males reach maturity slightly smaller at 67.2 cm and age of 5.8 and females at 75.6 cm and age of 6.6. There is a difference between the northern and southern part of Iceland as L_{50} is higher in the north compared to the south, or 77.0 cm and 65.9 cm for both sexes, respectively. Correspondingly, cod in the northern part reaches maturity at age of 7.0 and in the southern part at age of 5.4 (Marteinsdottir and Begg, 2002).

In Iceland the main spawning grounds for cod are along the south and southwest coast, from the Vestmannaeyjar archipelago to the fjord Breiðafjörður (Jónsson, 1992). Spawning usually takes place from mid March until middle of May (Jonsson, 1982). In addition to the main spawning grounds, cod is known to spawn in different areas all around the country, with spatial and temporal variation in the contribution of the various spawning grounds to each cohort (Marteinsdottir et al., 2000a; Begg and Marteinsdottir, 2000; Jónsdóttir et al., 2007). Cod generally spawns at depth of 40 - 100 (150) m in Icelandic water, close to the seabed or midwater (Jónsson and Pálsson, 2006). Larger females start to spawn earlier and also over a longer period (Marteinsdottir and Björnsson, 1999). The females spawn in batches, young females may spawn all their eggs in a single batch while larger and older females may spawn several batches, but the time elapsed between batches ranges from 2 - 6 days (Kjesbu et al., 1996).

In Iceland there is evidence of segregated spawning of different ecotypes of cod, based on behaviour and genetic differences (Pampoulie et al., 2008; Thorsteinsson et al., 2012). The frontal cod which spawns in frontal waters and the coastal cod which spawns in shallow near shore areas. There seems to be a fine-scale difference in spawning habitat selection, mainly depth, at a fine scale within individual spawning grounds (Grabowski et al., 2011). Those ecotypes have further been analysed in regards to marked differences in otolith shape (Bardarson et al., 2017) and morphometry (McAdam et al., 2012).

*Figure 1.4. Juvenile cod (*Gadus morhua*) and northern shrimps (*Pandalus borealis*) in Ísafjarðardjúp, NW - Iceland. Photo from the inshore shrimp survey of MFRI.*

Early life history

Egg and larvae are known to drift with currents from the main spawning grounds to the west, north and east of Iceland. In some years embryos and larvae may drift to the east coast of Greenland (Astthorsson et al., 1994; Jónsson and Valdimarsson, 2005; Brickman et al., 2007b). The extent of embryo and larval drift depends on the strength of the inflow of Atlantic Water onto the North Icelandic Shelf (Jónsson and Valdimarsson, 2005). Thus, in different locations around Iceland each cohort may be of mixed origin, to a variable extent (e.g. Jónsdóttir et al., 2007; Thorisson et al., 2011), depending on the strength of the inflow along with spatial and temporal variation in spawning success.

Reconstructed hatch day distribution from larval and juvenile surveys in Icelandic waters have revealed that, the hatch starts around calender day 105 south of 66°N and day 116 north of 66°N, with average hatch around days 133 and 139, respectively (Jonasson et al., 2009). The incubation time in Iceland waters at 7.3°C, has been estimated to be 9 - 10 days (Friðgeirsson, 1978). According to that, spawning starts in late March early April with the peak spawning time in early May and spawning activity stretching into the latter part of May.

A comprehensive study on larval and juvenile cod feeding in Icelandic waters, unveiled that the main prey item of larvae in May, were nauplii and copepodites (Thorisson, 1989). In June, at the size of 10 - 20 mm (and most already past metamorphosis) the main prey was copepods, *Calanus finmarchicus* most important by weight, but *Acartia sp.* and *Temora sp.* by numbers.

Few studies have been carried out on settlement of Icelandic cod. It has been suggested that it starts as early as July. The first Icelandic fisheries' scientist Bjarni Sæmundsson, observed in 1908 that juvenile cod and saithe had settled in mid July with the average length between 30 - 40 mm (Pálsson, 1976; Jónsdóttir et al., 2019). An extensive pelagic 0-group survey all around Iceland was conducted in August from 1970 - 2003. A high number of pelagic cod juveniles were caught in it. Age distribution of the juveniles matched poorly with observed spawning in March and April, but highlighted the importance of local spawning in north and the east, as the expected size distribution (larger juveniles in the south compared to the norhtern part) was not caused by temperature induced growth difference but rather originated from local spawning components (Marteinsdottir et al., 2000b). The authors suggested that unequal survival or that older larvae had drifted off the bank at the time of the survey. On similar notes, Begg and Marteinsdottir (2002) showed, based on the 0-group survey length frequency distribution and estimated growth patterns, that peak spawning was estimated in early May in the south and southwestern regions. They also demonstrated that in some years the production from local spawning components can be substantial. A plausible explanation of the lack of juveniles originated from spawning in March and April in those studies, could simply be that the juvenile had just already settled (Brickman et al., 2007a).

Fluctuations in stock size

Atlantic cod is among the most valuable commercial fish species in the North Atlantic and has been very important for the fisheries around Iceland. The maximum landings were reached in 1968 when over 3.9 million tonnes of cod were landed (FAO, 2020b). Landings decreased from that peak down to 770 thousand tonnes in 2008 but increased again to 1.3 million tonnes in 2016. The status of almost all cod stocks in the North Atlantic at the start of this century was that most of them had declined by some 20 - 90%, both due to effects of intensive fishing but also because of environmental effects (Hutchings and Baum, 2005; Marteinsdottir et al., 2005). However, there has been a positive reversal of the Icelandic cod stock in recent years, as the spawning stock biomass is now estimated to be over 600 thousands tonnes, the same size it was during the late fifties (ICES, 2018). Recruitment has been rather stable for the past decade, without particularly large year-classes entering the fisheries, but since 1976 only two strong year-classes (1983 and 1984) have entered (Jónsdóttir et al., 2019).

1.4.2 European plaice, *Pleuronectes platessa*

Distribution

European plaice, *Pleuronectes platessa* (Order Pleuronectiformes; Family Pleuronectidae, Figure 1.5), is a demersal flatfish, who's distribution stretches from the western Mediterranean, along the European coast, around the Faroe Island's and Iceland and all the way to the White sea (FAO, 2020c). It has also been documented at times at the southwest coast of Greenland (Jónsson and Pálsson, 2006). It is found at mixed bottom substrate, from only a few meters to about 100 m, juveniles are commonly found at beaches and older individuals are found deeper (FAO, 2020c). Around Iceland, adult plaice is found on the continental shelf and slope with usually the highest abundance in the south-west and west of the island, but it can also be found in high densities in the south-east and northern Iceland (Sólmundsson et al., 2020). It is found on a sandy or muddy substrate, occurring at depths ranging from the coast down to 200 m (Jónsson and Pálsson, 2006). Small and juvenile individuals, habitat intertidal areas down to approximately 10 m, while older and larger individuals are found in deeper waters (Gunnarson et al., 1998).

Age and growth

Plaice generally reach 30 to 50 cm length in Icelandic waters, but 25 to 40 cm is more common in Europe (Jónsson and Pálsson, 2006). In Iceland the oldest plaice was a 22 year old female and the largest was 85 cm (Jónsson and Pálsson, 2006), but it can reach a meter in length (FAO, 2020c). There is sexual dimorphism in growth and maturation and mortality as females grow slower to larger size and reach maturity later (van Walraven et al., 2010). In Icelandic waters, only a small portion of the males grow larger than 45 cm, but for females that limit is 55 cm (MFRI, 2020k).

Maturity and spawning

Males reach average size of maturity at 33 cm but females at 38 cm in Icelandic waters (MFRI, 2020k). The main spawning takes places on several distinct grounds in south and west of Iceland (Solmundsson et al., 2005). The spawning period there starts in late February and lasts into early June, with peak spawning in April (Solmundsson et al., 2003; Gunnarsson et al., 2010). Spawning also takes place in colder waters in northern and eastern part of Iceland in April to June, with peak in May (Gunnarsson et al., 2010). Solmundsson et al. (2005) demonstrated a high fidelity to both spawning and feeding areas in south and west of Iceland, but less is known about other spawning populations, although most of the recaptures from the previous tagging experiments of Sigurðsson (1989) in north-east Iceland came within the same location. Female plaice in the North Sea are in spawning condition for approximately 3 - 6 weeks with increasing duration with age. Males arrive at spawning site before the females and are in spawning condition for up to 11 weeks (Rijnsdorp and Witthames, 2005). Males arrive as well earlier in Iceland at spawning grounds and stay longer (Sigurðsson, 1989). Spawning behaviour is also different as males are more active on spawning grounds, likely searching for mates that makes them more susceptible for being caught (Solmundsson et al., 2003).

*Figure 1.5. Newly settled and few weeks old European plaice (*Pleuronectes platessa*) caught during monitoring in Álftanes, SW - Iceland.*

Plaice spawns in batches, where eggs are released into final maturation every two to five days over the spawning period (Rijnsdorp, 1989). Most of the spawning takes place at 50 - 100 m depth in Icelandic waters (Jónsson and Pálsson, 2006). From the main spawning grounds in Iceland the pelagic egg drift in a clockwise fashion with the Atlantic water currents from the south and the coastal current which divides from the warm Atlantic current (Gunnarsson et al., 2010). The developmental time is temperature dependent and the egg hatches after 10 days at 14°C and after 35 days at 2.8°C (Gibson, 1999). The vertical distribution of the eggs is generally wide with occasional clusters near the surface (Gibson, 1999).

Early life history

The larvae are between 5 - 7.5 mm and symmetrical when they hatch (Russell, 1976). They get nourishment from the yolk sac for roughly two weeks (Gibson, 1999). The length of the larval period is inversely related to experienced temperature and varies between 31 - 100 days (Fox et al., 2007; Karakiri and Westernhagen, 1989). Average larval period in different regions around Iceland has been estimated to be 53 - 61 days (Gunnarsson et al., 2010). Metamorphosis, when the symmetrical larvae go through radical morpho- and physiological changes into benthic flatfish, starts off-shore in the pelagic phase when the larvae are around 10 - 12 mm (Geffen et al., 2007; Brooks and Johnston, 1993). Settlement and metamorphosis are not fixed events as the juvenile can still stay in the water column, but the denser juvenile spends increased time on the bottom (Gibson, 1999; Geffen et al., 2011). Geffen et al. (2011) connected the settlement to lunar rhythms, if the end of metamorphosis happens during a neap tide, the movement to the beach may be delayed until next spring tide. The settlement in Icelandic waters has been noted to start in middle of to the end of May (Hjörleifsson and Pálsson, 2001). The nursery areas during the first summer are well defined, but juvenile plaice aggregates on relatively sheltered soft bottom beaches (Gibson, 1994; Able et al., 2005).

Fluctuations in stock size

Plaice is a commercially important species, the maximum total landings were in 1985 with 205 thousand tonnes being caught (FAO, 2020c). In Iceland, maximum landings were also reached in 1985 with 14.5 thousand tonnes (Jónsson and Pálsson, 2006). The juvenile survey index (<20 cm) in Iceland has been low since 1998 with irregular peaks, but the estimated number of 3 year old recruits from analytical assessment, has remained stable between 12 - 20 millions during 1995 - 2020 (MFRI, 2020k).

It has been proposed that the long-term dynamics of species like plaice, that concentrates into nursery ground during early life history (concentration hypothesis), may be controlled by density-dependent processes (Beverton, 1995). That however, relies on the nursery ground carrying capacity, a process that has been explained by self thinning lines, which indicate how the total biomass is reflected in density and mean weight (Nash and Geffen, 2012).

1.4.3 Brown shrimp, *Crangon crangon*

Distribution

Brown shrimp, *Crangon crangon* (Order Decapoda: Family Crangonidae, Figure 1.6) is widely distributed in the coastal areas of the eastern Atlantic. It is found from the coast of Morocco to the White Sea in the north, including the Mediterranean, Black Sea and Baltic waters (Tiews, 1970; Campos and van der Veer, 2008). *C. crangon* is usually found in the eulittoral and sublittoral soft-bottom habitats of temperate waters, usually in large numbers (Henderson and Holmes, 1987). *C. crangon* is euryhaline and can withstand a wide range of temperatures but has lower salinity tolerance at low temperature (Lloyd and Yonge, 1947; Boddeke, 1976).

It was first recorded in 2003 in southwest Iceland and it is though that the colonization occurred between 2001 and 2003, but it was suggested that the shrimp was introduced by ballast water (Gunnarsson et al., 2007). Brown shrimp has been classified as a potentially invasive species in Icelandic waters (Thorarinsdottir et al., 2014).

Age and Growth

For the first year, growth rate is similar for both sexes but after that females grow more rapidly (Lloyd and Yonge, 1947). Females also live longer and reach larger sizes than males (Lloyd and Yonge, 1947; Siegel et al., 2008). Females can reach 80 mm and five years of age, but only few females survive the fourth winter as the average shrimp tends to live for three year (Lloyd and Yonge, 1947; Norte-Campos and Temming, 1998). Growth rate is mainly driven by temperature and is at hight during summer months (Norte-Campos and Temming, 1998).

*Figure 1.6. Specimen of brown shrimp (*Crangon crangon*) caught during plaice monitoring in Álftanes, SW - Iceland.*

Maturity and Spawning

C. crangon has been reported to be a facultative protandric hermaphrodite, *i.e.* that it can sometimes change sex, although result seem to be conflicting, with some investigations that documented sex change while other did not (Schatte and R., 2006). Females reach sexual maturity during their second year when they moult into egg carrying condition and normally carry eggs in the spring and summer at length about 50 mm (Lloyd and Yonge, 1947). In the spring shorter egg carrying females can be found (Siegel et al., 2008). In Iceland L_{50} for egg carrying females was estimated 48.1 mm (Jónsdóttir et al., 2016). Males reach maturity at smaller size or around 30 mm length (Lloyd and Yonge, 1947), but they are predominating in smaller size classes (Siegel et al., 2008). Breeding extends over much of the year (January to June), with two distinct spawning peaks and broods, the main brood in winter (January - June) and summer (July - September) (Oh and Hartnoll, 2004). Latitudinal variation may be seen in the breeding season of brown shrimp (Oh and Hartnoll, 2004; Campos et al., 2009). The eggs are carried until they hatch for about four weeks during mid summer and thirteen weeks during winter (Lloyd and Yonge, 1947).

Early life history

C. crangon has a planktonic larval stage which last around five weeks depending on temperature (Lloyd and Yonge, 1947). Abundance of juveniles can also be affected by weather conditions and a juvenile peak may be delayed by weeks after cold winters (Temming & Damm, 2002). Juvenile peaks in Iceland are one to two months later than observed in the North Sea (Jónsdóttir et al., 2016; Temming and Damm, 2002).

Fluctuations in stock size

Fluctuations in *C. crangon* population size have been reported, where predation and water temperature are believed to be the main causes (Oh et al., 1999). As such Oh et al. (1999) reported significant decrease in one year out of four in a time-series, which coincided with a record cold temperature that year.

Brown shrimp is an important food source for several species such as cod and whiting (*Merlangius merlangus*) of commercial value and variations in the shrimp stock size can have immediate affect on those stocks (Siegel et al., 2005). The brown shrimp is of commercial interest and sustains a very important traditional fishery in the North Sea (Temming and Damm, 2002). Mean annual catches in Europe from 1950 to 1994 were around 40 thousand tonnes (Oh and Hartnoll, 2004). Maximum catches were reached in 1963, 72 thousand tonnes and minimum in 1990, or roughly 16 thousand tonnes (FAO, 2020a).

1.4.4 Iceland scallop, *Chlamys islandica*

Distribution

Iceland scallop, *Chlamys islandica* (Order Pectinida: Family Pectinidae, Figure 1.7) is a commercially important scallop species distributed in the North Atlantic. Its southern distributional limits lies at sea surface temperature of 12 - 15 °C (Sundet, 1988; Hovgaard et al., 2001) and is usually found at depth less than 100 m (Caddy and Gulland, 1983; Wiborg, 1963).

Garcia (2006) describes the distribution of Iceland scallop, in the North-East Atlantic it is found from the southwest Kara Sea in the east, Barents Sea, around Svalbard, south to the west coast of Norway. It is common around Bear Island, Svalbard and around Iceland, apart from the southern shore. In Eastern Greenland it is found mainly at the King Frederick VI coast in the SE-part as the cold East Greenland Current prevents it from thrive in more northern locations. In the North-West Atlantic, Iceland scallop is found all along the west coast of Greenland from 77°N south to 60°N. Along the east coast of Canada from Cumberland Peninsula, Hudson Bay and Foxe Basin down south to Cape cod in the United States.

Iceland scallop prefers a rough seabed, with a mixture of sand, shell debris or gravel. It is seldomly found in muddy or really hard bottom substrates (Wiborg, 1963). Like many filter feeders it prefers strong currents and is often attached to substrate by byssus threads (empty shell and stones), especially juveniles (Wiborg, 1963; Arsenault and Himmelman, 1996a,b).

Age and Growth

Size of scallop is generally measured as the height of the animal, from the umbo to the ventral valve margin. Growth rate and maximum size is highly variable after areas and is driven by temperature and food availability (Vahl, 1981). In Breiðafjörður, West Iceland, it reaches 60 mm shell height (SH) around 6 years of age and is then part of the fishable stock (Jonasson et al., 2007). In Greenland, it takes 9 years to reach 60 mm SH (Pedersen, 1994), in Newfoundland they are also thought to be 9 years (DFO, 2010) and in Northern Norway 7

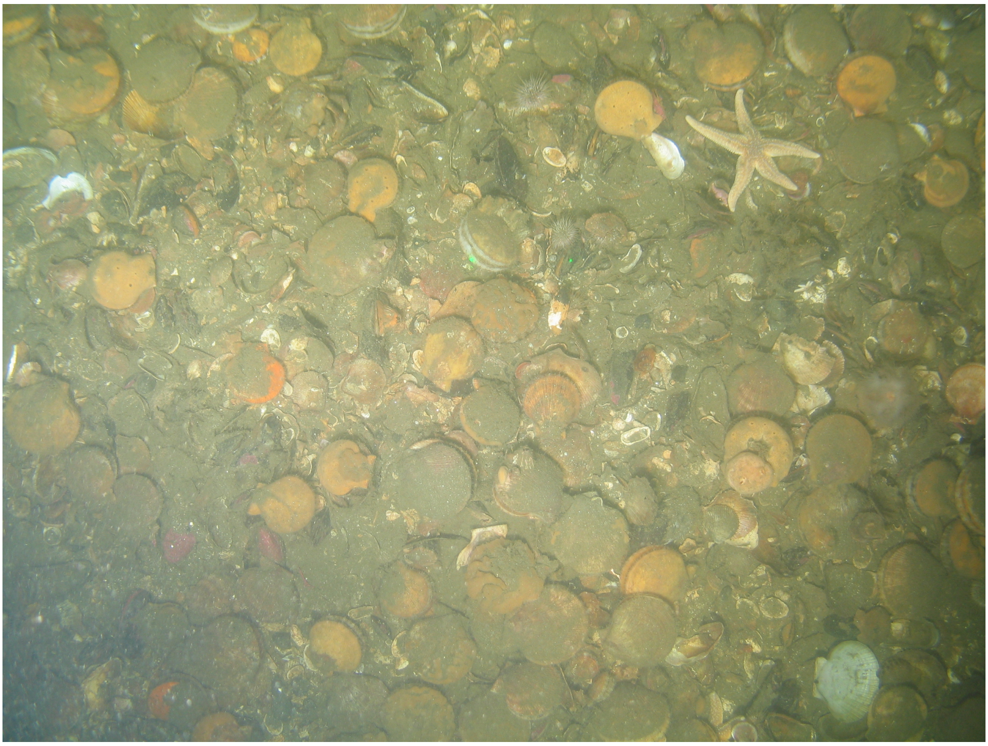

*Figure 1.7. Healthy bed of Iceland scallop (*Chlamys islandica*) in the fjord Hvammsfjörður of Breiðifjörður bay in August of 2017. Photo from the drop-frame scallop survey of MFRI.*

years of age (Vahl, 1980). In Iceland, it is common for Iceland scallop to reach 80 - 100 mm SH, but the maximum sized animal in Iceland are from Jökuldjúp in northwest Iceland, where scallop can reach around 140 mm SH (Hrafnkell Eiríksson pers. comm.). Iceland scallop is a long lived species. In Norway, Vahl (1981) reported maximum age of 23. In Greenland, animal older than 35 have been reported and in some beds it was estimated that more than 40% of the population was older than 21 years (Pedersen, 1989).

Maturity and Spawning

Around Iceland, Iceland scallop reaches maturity around 40 - 50 mm SH, or at four or five years of age (Eiriksson, 1986). It is a hermaphrodite with an equal number of sexes (Eiriksson, 1986). The development of the gonads is temperature and food dependent (Skreslet and Brun, 1969; Thorarinsdóttir, 1993). It spawns usually once a year during the middle of the summer. The main spawning in Breiðafjörður is in the end of June and reaches high peak in the beginning of July when temperature and food availability are at peak (Eiriksson, 1970, 1986; Thorarinsdóttir, 1993). In Balsfjord, Northern Norway, a peak in spawning was related to a quick increase in SST (Skreslet, 1973). In Newfoundland spawning begins earlier or in April – May and is also thought to be initiated by short-term variation in temperature (DFO, 2010).

Early life history

In Norway, Iceland scallop larvae are pelagic for around 6 weeks (Skreslet and Brun, 1969; Sundet, 1988). In Iceland, the larva settle as spat in September after around 6 - 8 weeks at planktonic stage (Thorarinsdóttir, 1991; Garcia et al., 2003). In Newfoundland they are planktonic up to 10 weeks (DFO, 2010). Scallop spat (post-larvae) has been found to prefer to settle on filamentous substrata, dead hydroids and red algee (*Rhodophytes*) (Harvey et al., 1993). Small scallops are generally found in crevices, under dead shells and rocks attached with byssal thread, but the usage of refugium decreases with size (Arsenault and Himmelman, 1996a). There is gradual swimming of juvenile scallop into greater depth, possibly due to longer swimming periods when scallop swim downslope, that can cause spatial size partitioning with depth (Arsenault et al., 2000).

Fluctuations in stock size

Large fluctuations in stock size have been described for several Iceland scallops stocks. Those changes have been linked with abrupt changes in salinity and temperature (Wiborg, 1963), predation by starfishes (Brun, 1968) and due to overfishing (Hovgaard et al., 2001). Recruitment pattern is highly variable between different stock. After a couple of years of intense fishing during 1986 -1987 on Iceland scallop beds in Jan Mayen and in the Svalbard region that caused collapse of the stock (Anon., 1988), recruitment was not witnessed until 1996 (Anon., 2002). That implies that strong recruitment is infrequent, although depletion of the spawning stock could also be of importance. It has been discussed that a negative relationship could occur between spawning stock size and recruitment (Vahl, 1981). On the west coast of Greenland most of the beds are built up of old individuals and recruitment is generally low, that makes them fragile for fishing pressure (Pedersen, 1994). On fishing beds around St. Pierre and Miquelon near Newfoundland recruitment patterns where rather stable (Naidu and Anderson, 1984). Later surveys in the same region revealed that significant mortality and biomass decrease could be related to starfish predation (DFO, 2010). The main scallop population in Icelandic water, Breiðafjörður, collapsed in 2000–2004 (Jonasson et al., 2007). No fishery for Iceland scallop has been conducted there since 2003 with the exception of an experimental fishery during 2014 - 2019 (MFRI, 2020g).

2 Population dynamics of juvenile fish and invertebrates

The general view of spawning and recruitment pattern of many of the most important demersal fishes in Iceland, including, cod and plaice is that the main and most important spawning happens at the southern part of Iceland in the "Selvogsbanki" region. This general pattern is derived from the earliest studies of both cod and plaice juveniles in Icelandic waters (*e.g.* Tåning, 1929), which assumed that difference in larval and juvenile size between southern and northern region of Iceland was mainly due to different growth rates in the colder waters of the northerly areas. The most extensive fish juvenile research carried out in Icelandic waters were 0-group surveys. They were carried out in August, between 1970 until 2002 and covered in most years the full extent of the Icelandic shelf (Sveinbjornsson and Hjorleifsson, 2002). However, the 0-group cod abundance was not correlated to the abundance of 1 year old caught in the following groundfish survey (Sæmundsson, 2005), and due to that fact and also because of cost they were abandoned. Less attention has been given to cod larvae and early juveniles in Icelandic waters, but that is one of the topics covered here. Further, for species like the plaice, little is known about their nursery areas, which are becoming more dynamic with the recent addition of its main juvenile predator the brown shrimp. Likewise nothing had been written about the population dynamics of the Iceland scallop, a sub-arctic species that suffered population collapse and fishing moratorium only a few years after the warming of the coastal waters.

2.1 Abundance and growth of larval and early juvenile cod *Gadus morhua* in relation to variable environmental conditions west of Iceland

In **Paper I** abundance and growth of larval and juvenile cod was examined (approximately 2-8 week-old individuals). A series of cruises were conducted in June/July of 1998–2001 along the expected drift route of cod and other important benthic stocks southwest and west of Iceland. The surveys were carried out in a period of intensified flow of Atlantic waters (The NIIC) into the northern shelf and increasing strength of the sub-polar gyre (Stein, 2005), but since 1998 the Atlantic waters have been detected along a grid line on the north Icelandic shelf (Olafsdóttir et al., 2018).

We found great variation in both abundance and hatch dates distribution between years, which varied from early April to the middle of June. Highest relative abundance was found in temperatures above 7.5 °C and in low-salinity waters, characteristic for the coastal current (ICC). That is in line with previous studies that have demonstrated a potential link between the freshwater discharge or the strength of the ICC and recruitment of cod (Jonsson and

Fridgeirsson, 1986; Olafsson et al., 1993; Begg and Marteinsdottir, 2002). The proportion of larvae that are thought to have originated from the main spawning grounds differed greatly between years, and only during 1999 a high proportion of larvae north of 66° presumably originated from the main southern spawning grounds. For the years 1998 - 2000 the larval drift resulted in medium sized year-classes (ICES, 2018). During 2001, few larvae were estimated to have originated from the main spawning ground in the south and also western spawning ground. The 2001 year-class was estimated poor at the age of three (the 3rd smallest (ICES, 2018)). It is worth mentioning that fluctuation in recruitment is relatively small in the Icelandic cod stock. Here the importance of smaller northerly spawning grounds (Begg and Marteinsdottir, 2002), is likely to play a role in dampening the recruitment fluctuations. The distribution of the cod juveniles within the boundaries of the ICC highlights the role of the freshwater driven coastal current in successfully transporting larvae from the spawning areas into the northern nursery grounds. The facilitation of early spring algal bloom within the ICC (Thordardóttir, 1986) also highlight its possible importance on larval growth and survival. The ICC could be one of the main mechanisms influencing recruitment variability in the Icelandic cod stock.

2.2 Variation in hatch date distribution, settlement and growth of juvenile plaice (*Pleuronectes platessa* L.) in Icelandic waters

In **Paper II** settlement and growth pattern of juvenile plaice around Iceland was estimated. In spite of high fishing mortality and decreasing catches prior to this research (MFRI, 2020k), few studies have been carried out on juvenile population structure, dynamics and natal origin. Here we estimated hatch date distributions by means of otolith microstructure in an effort to establish the natal origins of juveniles. The samples came from beam trawl surveys which were carried out on 31 beaches all around Iceland in July of 2006.

We found significant differences in the size and age distribution around Iceland and concluded that juvenile plaice in 2006 originated from spawning events at different time and locations. The observed spatial variation in size of the juveniles was explained by age difference, not by different temperature-induced growth rates (Tåning, 1929). The juveniles at the south coast hatched earlier than juveniles on the north and east coasts and had a shorter larval period, a similar pattern as was seen in the earlier study on juvenile cod which follow similar larval drift route (**Paper I,** Jonasson et al., 2009). Further, the estimated time for eggs and larvae to drift from the main spawning areas in the south did not fit with the expected time needed to reach the northern nursery area. The study provides evidence for the existence of a local population structure within the Icelandic plaice stock and supports the findings of Solmundsson et al. (2005) on highly structured population. That could have implication for the management of the stock, but currently it is managed as a one unit (MFRI, 2020k).

2.3 Density dependant growth dynamics of juvenile European plaice (*Pleuronectes platessa* L.)

In **Paper III** the influence of density-dependent processes on growth of juvenile plaice was evaluated at a highly productive plaice beach in SW Iceland. Previous studies (**Paper II,** Gunnarsson et al., 2010) had measured extremely high density peaks of juvenile plaice at Icelandic nursery grounds. Here we analysed two years with variable population density by ageing juveniles and compared growth of individuals on particular dates during the settlement period and later in the summer. Furthermore, width of otolith increments was measured during settlement period (June-July) to investigate recent growth.

We observed indication of density-dependent growth patterns. No difference was detected between growth rates at settlement. However, the growth rate was slower at the high density year during the recent 10 days, and also at the onset of emigration. Variation within-year growth has been addressed in a number of studies (e.g. van der Veer et al. (2010)), and generally it was concluded that no relationship was between densities and intra-annual growth variations. Variation in growth is however well documented at inter-annual basis, due to factors like a positive influence of temperature (Teal et al., 2008) and negative of densities (Geffen et al., 2011) on growth. The temperature was colder in this study during the low density year. Few other fish species are found at beaches in Icelandic waters but the non-native, brown shrimp was also at higher densities during the high density plaice year (**Paper IV,** Jónsdóttir et al., 2016).

Recruitment of the plaice stock has been stable for the past 25 years (MFRI, 2020k). Density dependent processes at the beach are likely contributing to that fact, but also the possible complex population structure within the Icelandic plaice stock (**Paper II,** Gunnarsson et al., 2010).

2.4 Establishment of brown shrimp (*Crangon crangon*) in a newly colonized area

In **Paper IV** annual and seasonal changes in population of brown shrimp were analysed. The brown shrimp is only recently detected in Icelandic waters (Gunnarsson et al., 2007) and has been described as an potentially invasive species in Icelandic waters (Thorarinsdottir et al., 2014). Here we looked at annual and seasonal changes in the population abundance from 2005 to 2014 at the same beach surveyed in the previous two plaice studies, at a highly productive sandy beach in southwest of Iceland.

The population of brown shrimp grew at the beginning period of the study and seems to have somewhat stabilized at the end of it. The average density of shrimps rarely exceeded 200 individuals per 100 m^2. There was an indication of bi-annual spawning with the number of juveniles increasing in July/August and again in February. The number of recruiting juveniles from the previous year significantly affected the adult abundance as well as the positive effect of the sea surface temperature.

Brown shrimp seems to have rapidly adapted to Icelandic waters, has become established and is highly successful in the newly colonized area. It has already dispersed with the prevailing ICC and NIIC currents and reached the Westfjord region (Koberstein, 2013). The brown shrimp has yet to been found in the northern part of Iceland, but chances are that they might establish there if the SST will continue to be high in that region, but the newest salinity measurement south of Iceland predict that the warm period has at least come to a temporary pause (Olafsdóttir et al., 2018). Lowering of temperatures could benefit subarctic species like the Iceland scallop that seem to have suffered during the recent warm period (**Paper V,** Jonasson et al., 2007).

2.5 Collapse of the fishery for Iceland scallop (*Chlamys islandica*) in Breidafjordur, West Iceland

In **Paper V** stock collapse of the most import fishing ground of Iceland scallop in Breiðafjörður Iceland was analysed. During the scallop fishery, initiated in this region in 1970, until the moratorium in 2004, 254 thousand tonnes were landed from this region (Jonasson, 2007). Information from scallop dredge surveys from 1993 to 2003 were analysed in this paper, with information on the landing statistics and available environmental and biological data. This period was also marked by an increase in summer sea surface temperature but studies had shown that the temperature had not yet reached critical level (Jonasson et al., 2004).

The scallop stock suffered very high total fishing mortality throughout the study period. High natural mortality based on the ratio of "cluckers" (Jonasson, 2004) was observed in the southern part of the fjord that was later related to an apicomplexan parasite or gray meat (Kristmundsson et al., 2015), although mortality did also rise in other areas, just not as abruptly. In the southern area the stock index had already been declining since 1994. Further, low recruitment levels towards the end of the 1990s made the stock vulnerable to increased fishing pressure, and a strong relationship was found between the recruitment and delayed harvestable biomass. Consequently, the stock appeared unable to withstand the fishing pressure and declined to historically low levels, leading to a halt in fishing in 2003.

2.6 Conclusions and future perspectives

Recruitment of cod, haddock and plaice in Icelandic waters has shown to be relatively stable (Fogarty et al., 2001; MFRI, 2020k). For Icelandic cod, this has been attributed to the stock subcomponents or subpopulations (Begg and Marteinsdottir, 2002, 2000; Jónsdóttir et al., 2007), and was further supported with the findings from **Paper I**. The plaice stock in Iceland likely also comprises several subpopulations (**Paper II**), that could facilitate the reduction of recruitment fluctuations, with further dampening by density dependant processes occurring at the nursery grounds (**Paper III**). The cod and plaice stocks in Iceland could be categorized as steady stocks (Caddy and Gulland, 1983), and although the catches have fluctuated more than 20-30% for the past 40 years, they have been stable during the current warm regime in Iceland (see chapter 1.3.2). In a similar manner the Iceland scallop stock in Breiðafjörður (**Paper V**) could be classified as a spasmodic stock (Caddy and Gulland, 1983), where the drivers of the observed fluctuation are species interaction (disease) and most likely environmental variability (Shelton and Mangel, 2011). The implications for management are different for those two cases as the steady stocks tend to behave as predicted by models, but the management of spasmodic stocks is more complicated. Fishing does often play a crucial role in the timing and the extent of the collapse of spasmodic stocks, as is evident in the instance of the Iceland scallop (Caddy and Gulland, 1983).

During the past two decades there has been emphasis on research of the stock structure of the Icelandic cod. As such, the two ecotypes that have been described, the frontal and the coastal, seem to be reproductively isolated, mainly by depth, even on the same spawning ground (Grabowski et al., 2011). However, so far the subpopulations have not been accounted for in the management of the stock. The estimated size of the cod stock has increased steadily in the recent decade, following a reduction in the harvest rate during 2010 (MFRI, 2020d). Nevertheless, when looking at the biomass indices of individual areas, from the annual gill net survey, they have all increased, apart from the Kantur (Edge) area in the south (Bogason et al., 2018). That area has predominantly frontal cod, *Pan* I^{BB} genotypes (Pampoulie et al., 2008). A long term study showed, during a period of high fishing pressure or from the middle of the last century until present time, that the ratio of frontal cod decreased severely (Jakobsdóttir et al., 2011). These examples highlight the importance of monitoring and possibly mitigating the reduction in certain stock components. Otolith shape analysis has been proposed as the easiest and a cost effective marker to account routinely for ecotype discrimination (Bardarson et al., 2017). The way forward could be to manage them as separate units (Goethel et al., 2011) or use temporal and spatial closures if appropriate. However, the mixing of cod subpopulations on feeding grounds, makes spatial management difficult to implement (Jónsdóttir et al., 2007). Spawning closure is a good tool for protecting semidiscrete spawning aggregations, in synergy with other management approaches (Frank and Brickman, 2001; Zemeckis et al., 2014). Temporal spawning closures are currently implemented in Iceland ("Easter stop"), but could possibly be expanded for the entire spawning season of vulnerable subpopulations. Less is known about the population structure of the Icelandic plaice stock. Extensive tagging experiments have shown a high degree of fidelity in the adult populations (Sigurðsson, 1989) and more recent tagging experiments in the south western part have demonstrated high degrees of homing to spawning grounds (Solmundsson et al., 2005). Due to that fact, spatial management could be more relevant for the plaice stock, but further research is needed on the stock structure of plaice in Iceland.

The importance of the coastal current has been put forward as a mechanism that facilitates good year-classes for cod and haddock in older studies. This is discussed in **Paper I** in regards to distribution of cod offspring. The coastal current which is driven by the output of the large glacial river at the south coast, acts both as a retention mechanism (Iles and Sinclair, 1982), as well as facilitating faster growth (Houde, 1987) through the early spring algal bloom that starts in the low saline silicate enriched water layers (see chapter 1.2.1). Although Iceland is sparsely populated, a direct anthropogenic impact could possibly affect the dynamics of that current, through hydrological damming of the major glacial rivers of southern Iceland (Marteinsdóttir et al., 2009). As such, in Þjórsá, one of the two largest river in the south, the winter runoff was higher and less variable after the constructions of dams in the early seventies. On a completely different scale, the productive sandy beaches that where studied in **Papers II - IV** can be considered to be essential fish habitats (Wennhage et al., 2007). Numerous fjords and the coasts in Iceland have been crossed by roads and bridges to shorten driving distances as the highly convoluted coast is often lined with narrow strips of lowlands (Ingólfsson, 2007). The plaice has more constricted nursery areas than most flatfishes (Gibson, 1994) and may be 'saturating' the carrying capacity of those habitats (Beverton, 1995). Therefore it is important to account for all those habitats and preserve them as best as possible. The expected loss of juvenile plaice habitat, has in some instances, been given a direct monetary value (Stål et al., 2008).

The waters around Iceland are dynamic and bound to large fluctuations in oceanographic conditions. Campana et al. (2020) demonstrated around 40 km average re-distribution of demersal fishes per °C, during the current warm period. They argued that new spawning and recruitment sites could be established, but not as rapidly as active migration. Recruitment failure of many species, with their core distribution in the south of Iceland or species at their southern distributional limits in Iceland, during almost the same period as the aforementioned study was discussed in chapter 1.2.3. This scenario could perhaps be categorized as a regime shift in the ecosystem around Iceland (Conners et al., 2002). The collapse of the scallop fishery (**Paper V**), among the decline or collapse of the northern inshore shrimp stocks (Jónsdóttir et al., 2017), were maybe the first species influenced by the current warm regime. During this period there also been several records of invasive species in Icelandic waters (Thorarinsdottir et al., 2014). The chance of new invasive species becoming established is influenced by climate change by eliminating cold temperatures (Rahel and Olden, 2008). The Atlantic rock crab (*Cancer irroratus*), is a good example of that. It was first found in 2006 in Icelandic waters and has become established on more than 70% of the coastline, but its environmental and ecological effects are not fully known, although there is a strong indication that it is outcompeting its rival native species (Gíslason et al., 2020). Less is known about the effects that the new invaisive *C. crangon* has had (**Paper IV**). Under the warm conditions it is thriving well in Icelandic waters. It is of great interest to monitor the shrimp population and increase research into its roles as the major predator of juvenile plaice, as it is has been shown to regulate year-class strength (Pihl, 1990). The Atlantic rock crab is also a potential predator of both plaice and shrimp, but that aspect of its ecology has not yet been studied. Recently, or in 1999 the first European flounder (*Platichthys flesus*) was documented in Icelandic waters (Jónsson et al., 2001). The flounder shares nursery grounds with the plaice and it has been demonstrated that there is a niche overlap between them in regards to prey items (Henke et al., 2020). Although, 0-group flounder was not found in SW Iceland in 2012 (MFRI, unpublished), in the study of Henke et al. (2020) the ratio of juvenile flounder and plaice were similar on two sites and the flounder was in the majority on one site in western Iceland. In 2017 the flounder was documented to have spread all around Iceland and the arrival of the flounder is likely to negatively affect the productivity of the nursery grounds in regards to plaice.

The question of what drives or controls recruitment variability has remained a mystery to fisheries' science now for more than a century for most species. Relatively little emphasis has been put into research on the early stages of fish and invertebrates at the main marine research body in Iceland, the Marine and Freshwater Research Institute, for now close to two decades, or since systematic juvenile surveys were abolished. In general it can be stated, given both their economical and ecological role, that the larval and juvenile stages of most of the Icelandic commercial shell- and finfish stocks are poorly studied. The lessons learned from this thesis demonstrate that many of the causes and drivers of recruitment variation are common over a wide range of taxa. The way forward to understand the key processes influencing recruitment, must be greater emphasis on research in that field on a wide spectrum of species. To achieve this, a combination of field, laboratory and modelling studies is required (Hufnagl et al., 2015). Rijnsdorp et al. (2009) asserted that the most effective approach is an integrated life-cycle approach, that inspects and identifies the importance of all, and pins out the most important developmental stages and mechanisms for life cycle closure and recruitment. This way of thinking somewhat resembles the Paulik diagram approach (Paulik, 1973), presented in the seventies. A useful, adapted version of the diagram has been presented in recent work on plaice (Nash and Geffen, 2012). It is clear that abiotic changes and biological responses to future climate change will be complex (Harley et al., 2006), but we must advance and try our very best to determine the consequences of future challenges to our resources and ecosystem.

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Paper I

Abundance and growth of larval and early juvenile cod *Gadus morhua* in relation to variable environmental conditions west of Iceland

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Abundance and growth of larval and early juvenile cod (*Gadus morhua*) in relation to variable environmental conditions west of Iceland

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ABSTRACT

Around Iceland, the west- and north-flowing coastal current, induced by freshwater runoff, provides a transport mechanism for pelagic eggs and larvae derived from the main spawning grounds off the southwest coast to the main nursery grounds off the north coast. In the present study, abundance and growth of larval and juvenile cod were recorded during a series of cruises conducted in June/July of 1998–2001 along the drift route southwest and west of Iceland. The cruises provided information on approximately 2–8-week-old individuals. Hatch dates and abundance varied greatly between years. Hatch dates ranged from Julian Day 92 to 167. Growth rate differed also between the years studied. Relative abundance was generally greatest in temperatures above 7.5 °C and in low-salinity waters, characteristic for the coastal current. The study demonstrates the link between the coastal current and larval/juvenile distribution, thus providing evidence for its importance in promoting successful recruitment of the Icelandic cod stock.

1. Introduction

Ocean physics plays an important role in the retention or dispersal of progeny to favorable nursery grounds and habitats, thus directly influencing year-class strength and subsequent recruitment success of fish stocks (Iles and Sinclair, 1982; Werner et al., 1996; Vikebø et al., 2005). During dispersal the timing of the coupled physical and biological processes including the onset of the spring bloom must also match development and first feeding of larvae for maximum recruitment success (Cushing, 1990). The match–mismatch theory has been difficult to test but progresses in remote-sensing techniques have demonstrated direct links between primary production and recruitment (Platt et al., 2003).

In Atlantic cod, recruitment has been linked with variable growth during the larval and juvenile stages (Campana, 1996). These observations have been supported by observations of faster growth among surviving individuals (Meekan and Fortier, 1996). Myers (2001) demonstrated that at low spawning stock abundance, mortality of eggs and larvae is likely to result from stochastically density-independent conditions of the physical and biological environment. Conversely, at higher spawning stock abundance, variability of survival is likely to also be density dependent, thus reducing the variation in year-class strength.

Due to their location in the transitional zone between the cold arctic and warm Atlantic waters, eggs and larvae of the Icelandic cod stock are exposed to intense environmental variation. The effects of such intense environmental variation on offspring survival may be difficult to forecast (Malmberg and Kristmannsson, 1992). However, recruitment variability, both for cod and for haddock (*Melanogrammus aeglefinus*) in Icelandic waters, has proved to be relatively low compared to other areas (Jakobsson, 1992; Marteinsdottir et al., 2000b; Fogarty et al., 2001). Several factors could contribute to this stability. The main spawning area of both cod and haddock in Iceland are located on the continental shelf of the southwest coast (Palsson, 1984; Marteinsdottir et al., 2000a) in areas dominated by the warm saline Atlantic water of the Irminger Current, and less-saline coastal water closer to shore (Malmberg and Valdimarsson, 2003). The area's annual temperature variation is small (seasonal variation ~1.5 °C) compared to those of the north coast, with mean temperature around 5.5 °C (Logemann and Harms, 2006) close to the average annual temperature experienced by cod stocks (2–11 °C, Brander, 1995). The hydrography of the main spawning area on the southwest shelf is strongly influenced by freshwater runoff (Fig. 1). The freshwater runoff facilitates stratification through formation of density layers, as well as providing essential nutrients for the high primary production, which characterises this area in early spring (Thordardottir, 1986). Furthermore, the presence of several smaller cod spawning aggregations around Iceland

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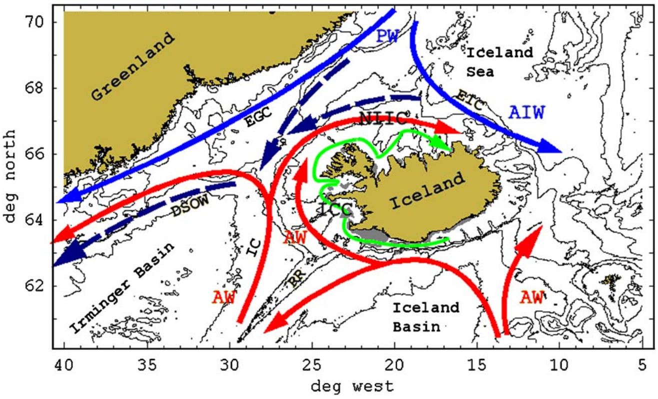

Fig. 1. Bathymetry around Iceland showing depth isoclines at 200, 500, 1000, 2000 and 3000 m. Cod spawning sites are displayed in grey (Marteinsdottir et al., 2000b). Green arrows: coastal waters, red arrows: Atlantic Water (AW), blue arrows: Polar Water (PW) and Arctic Intermediate Water (AIW), dashed blue arrows: Denmark Strait Overflow Water (DSOW). Other abbreviations are as follows: EGC—East Greenland Current, EIC—East Icelandic Current, IC—Irminger Current, ICC—Icelandic Coastal Current, NIIC—North Icelandic Irminger Current, RR—Reykjanes Ridge (modified after Logemann and Harms, 2006). For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

(Marteinsdottir et al., 2000a; Begg and Marteinsdottir, 2000) is likely to contribute to the relatively low recruitment fluctuation. In the Icelandic cod stock, recruitment is based on numbers at age 3. In some years, the smaller spawning grounds along the West, North and East coasts have been shown to contribute significantly to the total abundance of 0-group cod (Marteinsdottir et al., 2000a; Brickmann et al., 2007). So far mixed stock analyses have not successfully estimated the proportional contribution of the different spawning areas to the surviving population of juveniles (Anon., 2007a). Therefore, all recruitment estimates are based on a single stock model. Large fluctuations within individual units are therefore likely to be, at least partially, concealed by successful production of the other spawning areas (Marteinsdottir et al., 2000a).

The production of the main spawning area of cod near the south coast is dependent on currents that transport eggs and larvae towards the main nursery grounds of the northern shore (Begg and Marteinsdottir, 2000, 2002, 2003; Marteinsdottir et al., 2000a; Brickmann et al., 2007). The northward-flowing Irminger current (NIIC) and freshwater-driven coastal current (driven by the output of the large glacial river on the south coast) provide a transport mechanism for the pelagic eggs and larvae (Fig. 1). A relationship has been demonstrated between the coastal current and the abundance of juveniles presumably derived from the main southern spawning areas as well as the number of 3-year-old recruits (Begg and Marteinsdottir, 2002). In addition, the flow of the NIIC current has been linked with increasing abundance and better condition of juvenile cod (Jonsson and Valdimarsson, 2005).

The purpose of this paper was to evaluate the annual distribution, abundance and growth patterns of cod larvae and juveniles on the drift route west of Iceland, extending from the southerly located spawning grounds towards the northern nursery area, in relation to recruitment and variable environmental conditions.

2. Material and methods

Abundance, length, weight and age of larvae and juvenile cod were recorded during a series of cruises conducted along the drift route southwest and west of Iceland during 1998–2001 (Table 1). The survey in 1998 covered the coastal area all around Iceland, but for comparison only data west of 22°W were analysed in this study.

Table 1
Summary of pelagic larval and juvenile fish surveys analyzed in this paper; number of stations and individuals length measured on board (Nr.), the survey abundance index and the number of 3-year-old recruits in millions from VPA analysis (Anon., 2007b).

Year	Dates (Julian)	Stations	Nr.	Index	Recr.
1998	25 June–1 July (175–181)	54	1902	2.95	160
1999	10–16 June (160–166)	71	2329	2.50	161
2000	14–21 June (164–171)	64	2228	3.06	185
2001	13–16 June (163–166)	49	630	0.77	64

At each station a conductivity, temperature and depth instrument (CTD) was lowered to the sea floor. Salinity and temperature measurements at 10 m depth were used throughout the study. Fish larvae were sampled with a 4-m^2 Tucker trawl (2×2 m mouth opening, 1000 μm mesh); see Suthers and Frank (1989) for a complete description of this net. The Tucker trawl was lowered to a 40 m depth and hauled slowly up to the surface while the vessel cruised at 1.08 m s^{-1}. This meant that the trawl spanned depths representative of the peak concentrations of larvae and juveniles (Wiborg, 1960; Lough and Potter, 1993; Grønkjær et al., 1997). All cod larvae and juveniles were counted, and a random sample of 50–100 individuals were length measured onboard under a microscope attached to a computer equipped with an image analysing system (Leica Q 500). Sub-samples were frozen for otolith aging and weight measurements. Age readings were based on the number of increments from the hatch check of the lapillar otoliths (see methods in Marteinsdottir et al., 2000b).

Growth of larval and juvenile cod was estimated using a non-linear fit to the Laird–Gompertz growth equation (1), which has been shown to fit the larval period well (Laird et al., 1965;

Jones, 2002):

$$L_t = L_0 e^{(g_0/a)(1-e-at)} \quad (1)$$

where L_t is length at time t, L_0 is the length at hatching ($t = 0$), g_0 is the specific growth rate (SGR) at hatching and a is the exponential decay of the specific rate.

Larval and juvenile dry weight (DW) was fitted to standard length (SL) with data for individual years by the following equation:

$$DW = aSL^{\beta} \quad (2)$$

where a and β are constants from a linear regression model of dry weight on standard length using natural log-transformed data.

Estimated temperature-dependent growth patterns were analysed with the size and temperature-dependent third-degree polynomial growth model given by Folkvord (2005) for the Norwegian coastal cod. The model describes daily specific growth rate (SGR) in regard to dry weight ($\log DW$):

$$SGR = 1.2 + 1.8t - 0.078t(\log DW) - 0.0946t(\log DW)^2 + 0.0105t(\log DW)^3 \quad (3)$$

where t is the estimated individual temperature recording. Daily temperature was estimated based on daily temperature reading at two fixed stations at the sea surface (Fig. 2). Larvae caught at latitudes higher than 66°N were allocated a temperature corresponding to the station in Æðey (66°05′N and 22°39′W). Larvae caught at latitudes below 66°N were allocated a temperature based on data from the Flatey station (65°23′N and 22°55′W, Fig. 3). Individual larval dry weight was then back-calculated with the aid of a recursive algorithm, based on their original dry weight and their daily estimated temperature, to the time of hatching. As a result, the estimated dry weight at hatching provides valuable information on how well the model and the estimated experienced temperature fit the data.

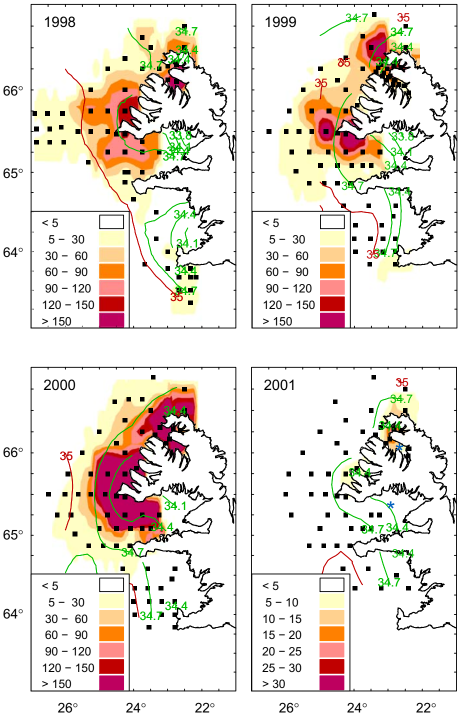

Fig. 2. Geographical distribution of the standardized abundance of 10 mm larvae (numbers/1000 m^3), during 1998–2001. Survey stations are marked with dots. Salinity isoclines of 10 m depth are plotted with values (red color indicates Atlantic water and green coastal water). Note different scale in 2001. Temperature stations used for the STDG back-calculated growth estimates are marked with blue stars in the graph for the year 2001. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

Hatch date distributions and abundance of larvae and juveniles were corrected for mortality using the following procedure: abundance values of individually length measured larvae/juvenile (number caught in the trawl per 1000 m^3 divided by the number of length measured larvae per station) were standardized to the individual's estimated value at 10 mm length. The standard length was first transformed into weight with the year-specific dry weight–standard length relationship (Eq. (2), Table 2). The specific daily mortality Z_t (or survival rate if the individual was above 10 mm) was calculated as a power function of larval dry weight W using the relationship given by McGurk (1986):

$$Z_t = 2.2 \times 10^{-4}\, W^{-0.85} \quad (4)$$

The mortality or survival was summarized for each day it took the larvae to attain 10 mm length, based on the year-specific Laird–Gompertz age–length relationships (Table 3, Fig. 4). The new estimated abundance values for each larvae/juvenile were summarized for each station. Standard length measurements

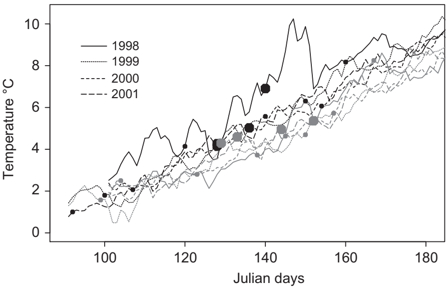

Fig. 3. Sea-surface temperature recordings during 1998–2001 from Flatey (65°23′N and 22°55′W) black lines and Æðey (66°05′ N and 22°39′ W) grey lines. The mean hatch day distributions (see Fig. 8) from each area are marked with large circles and the 99% quantiles are marked with small circles.

Table 2
Linear regression of log-standard length (mm), on log-dry weight (mg), of larval and juvenile cod during 1998–2001.

Year	Dry weight–standard length relationships	n	R^2
1998	$Dry\ weight = 0.000627 \times SL^{3.078}$	389	0.790*
1999	$Dry\ weight = 0.00180 \times SL^{2.752}$	356	0.719*
2000	$Dry\ weight = 0.000667 \times SL^{3.223}$	371	0.823*
2001	$Dry\ weight = 0.00616 \times SL^{2.161}$	156	0.284*

* $p < 0.001$.

were missing for 13 out of a total 54 stations in 1998 and from 9 out of a total 71 stations in 1999. A linear relationship between abundance and standardized abundance ($R^2 = 0.87$ in 1998 and $R^2 = 0.81$ in 1999) was used to predict a standardized value for stations with missing values. Most of these stations were characterized by low abundance.

Annual abundance indices of pelagic larvae and juvenile were calculated for each year following procedure similar to that used by Astthorsson et al. (1994). The abundance data were log transformed to normalize the distribution and reduce the influence of a few large catches. The abundance index (A) was then calculated for each year with the following equations:

$$X = 1/N \sum \log(X_i) \tag{5}$$

$$P = N/N_t \tag{6}$$

$$A = XP \tag{7}$$

where X is the logarithmic mean standardized abundance of larvae and juveniles, N the number of stations where catch was >0, X_i the number of cod captured per 1000 m^3 at station i where catch was >0, P the proportion of non-zero tows and N_t the total number of stations.

We used generalized additive models (GAMs) to examine the patterns of cod larvae/juvenile density and abundance. GAMs are nonparametric generalizations of multiple linear regression that are not restricted to specific functional relationships (i.e., linearity) or underlying statistical distributions (i.e., normality) of the data (Hastie and Tibshirani, 1990; Swartzman et al., 1992). In this study, the GAMs were constructed using version 1.3-12 of the mgcv library in the statistical package R (Wood and Augustin, 2002). The construction of the GAM model followed the guidelines of Wood and Augustin (2002), using penalized regression splines with integrated backward model selection via generalized cross-validation scores, where GCV or UBRE optimization selects the degrees of freedom for each term automatically.

The data were analysed in two steps. First, the effects of environmental parameters (salinity and temperature) and spatial location were investigated for the presence or absence of cod. To do this, we fitted a logistic model to the probability to catch a cod at station i with following terms in the starting model:

$$\log_e(\mathrm{pi}/(1-\mathrm{pi})) = \beta_0 + year + s(T_i) + s(S_i) + s(lat_i, lon_i) \tag{8}$$

where β_0 is the intercept, *year* is a factor, T_i is the temperature at 10 m depth, S_i is the salinity at 10 m depth, lat_i, lon_i is the spatial location as an isotropic bivariate function of longitude and latitude and s is the cubic B-spline smoother.

Afterwards we removed stations with zero abundance from the analysis and the remaining data were log transformed to normalize the distribution and reduce heteroscedasticity (see discussion in Brynjarsdottir and Stefansson, 2004). The starting model for this step was constructed in a similar manner as model (8), except that here we estimate the relative abundance A_i of larval/juvenile cod at station i:

$$\log_e(A_i) = \beta_0 + year + s(T_i) + s(S_i) + s(lat_i, lon_i) \tag{9}$$

where β_0 is the intercept, *year* is a factor, T_i is the temperature at 10 m depth, S_i is the salinity at 10 m depth, lat_i, lon_i are the spatial locations as an isotropic bivariate function of longitude and latitude and s is the cubic B-spline smoother.

The analyses presented here were performed partly in R (http://www.r-project.org) and partly using version 6.0 S-PLUS software (Venables and Ripley, 2002).

Table 3
Estimated coefficients with standard errors from the Laird–Gompertz equation of log(standard length) at age (Laird et al., 1965; Jones, 2002), for the years 1998–2001.

Year	L_0		g_0		a		n
	Value	s.e.	Value	s.e.	Value	s.e.	
1998	1.582	0.0716	0.0181	0.00311	0.0123	0.00496	408
1999	1.500	0.0738	0.0178	0.00304	0.0140	0.00432	367
2000	1.525	0.0597	0.0164	0.00280	0.0127	0.00501	397
2001	1.395	0.1195	0.0166	0.00735	0.0139	0.01642	224

L_0 is the length at hatching ($t = 0$), g_0 is the specific growth rate at hatching and a is the exponential decay of the specific growth rate, n is the sample size.

3. Results

During the survey period (1998–2001), annual variations were observed in abundance and hatch dates of cod larvae and juvenile collected along the drift route west of Iceland. The horizontal distribution was mainly influenced by the low-saline coastal waters.

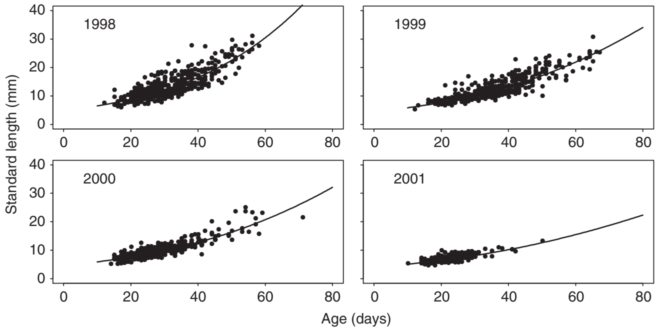

Fig. 4. Relationships between larvae and juvenile standard length and age in days, in June 1998–2001. Lines represent the fit of the Laird–Gompertz growth equation for each year (Table 3).

3.1. *Growth*

The estimated growth rate of larvae and juveniles varied between years (Table 3, Fig. 4). The model that included dummy variables for individual years was preferred over one which ignored yearly differences in growth ($F_{2,1396} = 235.3$, $p < 0.001$), indicating significantly different growth rates between years (Roff, 2006). The 1998 year class displayed the highest growth rate with the highest growth rate at hatching (g_0) and lowest rate of exponential decay of specific growth rate (a). Comparison of growth models for individual years revealed that a model including year as a parameter was consistently significantly better, except between the years 1999 and 2000. As a result, the larvae caught in 2001 experienced the slowest growth.

The sea-surface temperatures were higher in the southern area as expected (Fig. 3). However, the temperature estimates of the mean hatch day were similar between years and areas during 1999–2001, except for the southern area in 1998 when the mean temperature was higher compared to other years.

The estimated dry weight at hatching varied between years (Fig. 5). Back calculation with the STDG model of Folkvord (2005) predicted low hatch weight in 1998 (median = 0.0356 mg) and 2001 (0.0401 mg). In contrast, the model results gave a good fit to the 2000 (0.0513 mg) data, while growth was underestimated in 1999 (0.0612 mg) resulting in unexpectedly high hatch weight that year. Outliers characterized by underestimated growth were detected in all years.

3.2. *Abundance and distributions*

Abundance of adjusted 10 mm cod larvae varied extensively between years, but less between areas. In 1998–2000, relatively high abundance of larvae and juveniles were detected in low-salinity waters at and outside the Westfjord area northwest of Iceland (Fig. 2). The abundance index was slightly higher in 2000 than for 1998–1999 (Table 1). In contrast, the larvae were scarce in 2001 compared to the previous three years (Table 1). During the year 2001, distribution of larvae was mainly limited to the fjord Isafjarðardjup, northwest of Iceland (Fig. 2). These interannual differences in larval and juvenile abundance appeared to be reflected by a similar fluctuation exhibited by the number of 3-year-old recruits from the same cohorts (VPA results Anon., 2007b, Table 1, linear regression; $p = 0.018$, $n = 4$).

The final term found to have a significant effect on cod presence or absence was spatial location, which differed between years. The main distributions were north of 65°N and east of 25°30′W (Fig. 6). The distribution of cod was much less pronounced in 2001 compared to other years. Overall the model explained 42.7% of the total deviance (Table 4).

All of the model terms were found to have a significant effect on the relative abundance of cod (Table 5). Salinity had a negative linear effect on the relative abundance. Relative abundance increased with increasing temperature, but the effects stabilized at stations with temperature higher than 7.5 °C (Fig. 7).

The highest abundance of cod was generally in waters around the Westfjord area northwest of Iceland (Fig. 7), with the lowest abundance predicted in 2001. The final GAM model for the relative abundance of larval and juvenile cod explained 75.1% of the total deviance (Table 5).

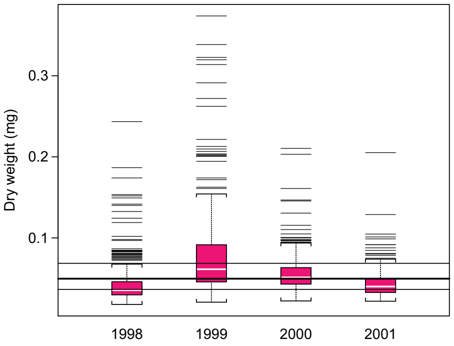

Fig. 5. Back-calculated larval dry weight at time of hatching for the years 1998–2001. The STDG model given by Folkvord (2005) was used for this procedure with temperatures from two fixed coastal stations (Fig. 2). The horizontal lines represent the range (0.0364–0.0686 mg) and the mean (0.0497 mg) of the hatch dry weight for Icelandic cod given by Marteinsdottir and Steinarsson (1998) with the approximations of Solberg and Tilseth (1987) for embryonic weight.

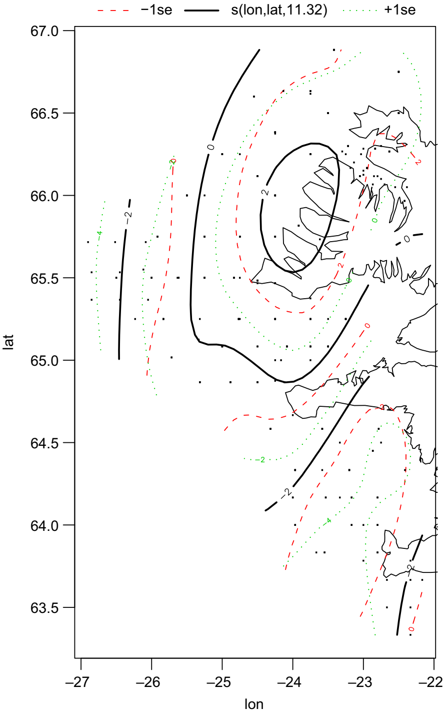

Fig. 6. The bivariate smooth of the spatial effect on the presence/absence of larval and juvenile cod shown as a contour plot over the survey area with the Icelandic coastline superimposed for orientation, and sampling locations marked with dots.

Table 4
Results of the GAM model for the presence/absence of cod including the final terms spatial location (s(lon,lat)) and years as factor after dropping non-significant terms ($n = 238$)..

Linear terms	Estimate	s.e.	p-Value	Overall deviance explained
(Intercept)	4.0418	0.77224	<0.001	
Factor(1999)	−1.6259	0.8067	0.043	
Factor(2000)	−0.3647	0.8309	0.661	
Factor(2001)	−3.7730	0.9046	<0.001	
Smoother term	*edf*	χ^2	p-Value	
s(lon,lat)	11.32	67.43	<0.001	42.7%

Table 5
Results of the GAM model for the relative abundance of cod larvae and juveniles including the final terms; salinity, temperature, spatial location (s(lon,lat)) and years as factor ($n = 185$)..

Linear terms	Estimate	s.e.	p-Value	Overall deviance explained
(Intercept)	26.0986	11.5308	0.0249	
Salinity	−0.6552	0.3313	0.0497	
Factor (1999)	−0.4862	0.2190	0.0278	
Factor (2000)	0.1106	0.2119	0.6024	
Factor (2001)	−2.6403	0.2483	<0.001	
Smoother terms	*edf*	F-Value	p-Value	
s(temperature)	2.698	2.622	0.0188	
s(lon,lat)	16.442	6.607	<0.001	75.1%

3.3. *Hatch day distributions*

Standardized hatch day distributions varied between years (Fig. 8). In 1998, cod larvae and juveniles originated from a relatively late hatch period. The average hatch day south of 66°N in 1998 was May 21 (DOY = 140, 99% percentiles = 120, 160) and June 2 (152, 138, 167) north of 66°N. In contrast, larvae collected in 1999 originated from an earlier hatch with an average hatch day south of 66°N of May 10 (129, 99, 150), with two distinctive peaks. Interestingly, the hatch day distribution north of 66°N was nearly identical as the distribution in the south, with an average hatch day of May 9 (128, 100, 150). The hatch day distributions of the year 2000 overlapped somewhat between regions with average hatch day on May 17 (136, 107, 154) south of 66°N and May 25 (144, 123, 157) north of 66°N. In 2001, the core hatch day distributions were rather narrow and similar between north and south of 66°N. The average hatch days south and north of 66°N in 2001 were May 4 (128, 92, 140) and May 9 (133, 104, 145), respectively.

4. Discussion

Dispersal of juveniles and survival mediated through growth of early life-stages are thought to be key factors responsible for recruitment variability of marine fishes (Heath, 1992). In this study, growth and abundance of larval/juvenile cod varied interannually and their distribution appeared to be affected by the coastal current. High abundance of larvae and juveniles within these low-salinity near shore waters highlights the importance of the coastal current as a mechanism for transport and retention of larvae from the main spawning grounds off the south and SW coast of Iceland. One of the main characteristics of this current is its relatively wide temperature range (Malmberg and Valdimarsson, 2003). The current can be distinguished from Atlantic water,

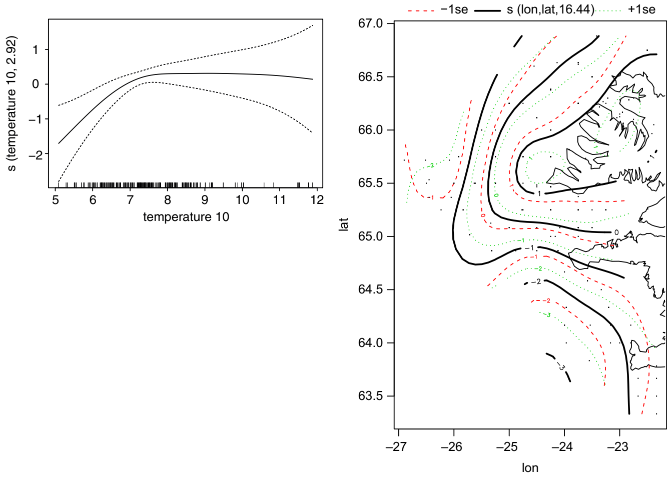

Fig. 7. (Left) GAM smoothing curve of the conditional effects of temperature at 10 m depth on the relative abundance of larval and juvenile cod. The y-axis is scaled to zero and reflects the relative importance of the covariate. The rugplot on the x-axis represents the number of observations. Dashed lines represent the 95% confidence intervals. (Right) The bivariate smooth of the spatial effect on the relative abundance of larval and juvenile cod as a contour plot over the survey area with the Icelandic coastline superimposed for orientation and sample locations marked with dots.

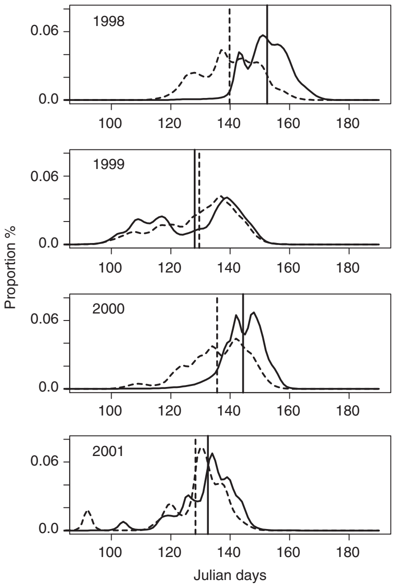

Fig. 8. Hatch day distribution of standardized 10 mm cod larvae collected at locations <66°N (solid lines) and > 66°N (dotted lines) during 1998–2001. The horizontal lines indicate the mean hatch day for each area. The data of individual year were transformed with a GAM smoother ($df = 15$).

which has been defined as being > 35.0 in salinity (Jonsson and Valdimarsson, 2005). Previous studies have demonstrated a potential link between freshwater discharge, strength of the coastal current and recruitment (Jonsson and Fridgeirsson, 1986; Olafsson et al., 1993; Begg and Marteinsdottir, 2002). However, this is the first study to describe the temporal variation in abundance of larvae and juvenile within the coastal current. In this study, larvae from the main spawning component at the SW coast, as well as from other local spawning components along the West coast of Iceland, were found within the boundaries of the coastal current. In other areas, numerous field studies have demonstrated an association between larval assemblages and coastal fronts (Heath, 1992; Munk et al., 2002). Spawning sites and larval drift routes of some cod stocks have been linked with haline fronts, e.g., the Browns Bank (Campana et al., 1989) and/or a formation of density layers that can be either freshwater driven as in Iceland (Thordardottir, 1986), or due to melting of sea ice as in Hudson Bay for the Arctic cod, *Boregadus saida* (Drolet et al., 1991). In the Norwegian cod stocks, it has also been suggested that dispersal is strongly linked to vertical gradients of horizontal currents (Vikebø et al., 2005). Such vertical gradient may also play a role along the coastline of Iceland; however, this has not yet been studied. Other non-haline frontal mechanisms are also widespread, e.g., the tidal front retention at the Georges Banks (Lough and Manning, 2001) and advection from the Norwegian Coastal Current to the warm and saline Norwegian Atlantic Current; transporting larvae from the Arcto-Norwegian cod stock into the Barents Sea (Vikebø et al., 2007).

Observed differences in the hatch day distribution of larvae and juveniles are most likely due to disproportional output from different spawning components situated around Iceland (Marteinsdottir et al., 2000b). The same study showed that in 1995 individuals from the main spawning ground had originated from hatch days 90–150 (Marteinsdottir et al., 2000b). This hatch date period was also confirmed by the collection of young and newly hatched larvae at the SW coast in 1998 (Anon., 2007a). Larvae with later hatch days are therefore likely to have originated from more northern located spawning grounds characterized by a later spawning season at lower temperatures. Furthermore, particle tracking runs using average climatological flow fields have shown that it takes at least 30 days for the larvae to drift from the main spawning grounds to north of 66°N (Brickmann et al., 2007); therefore the individuals found north of 66°N that hatched later than day 120–130 are unlikely to have originated from the south. The year 1999 stands out among the four surveyed years with a high proportion of individuals found both north and south of 66°N, which had presumably originated from the main southern spawning grounds. During 1998 and 2000, a high proportion of the individuals south of 66°N were also likely to have originated from the main spawning areas. In contrast, only a small number of larvae captured in 2001 are likely to have originated from southern spawning areas. The individual found south of 66°N that had hatched early came from a sample that was an order of magnitude smaller than those in previous years. For example, the hatch day proportion around day 90 south of 66°N in 2001 is due to capture of a single individual.

In most years, the estimated back-calculated dry weight at hatching seems to fit well to background values of dry weight for the Icelandic cod stock (based on values collected by Marteinsdottir and Steinarsson, 1998). The large discrepancies observed in 1999 possibly can be explained by the high proportion of individuals that may have originated from the more southerly located spawning areas. The larvae and juveniles that drift from the south experience higher temperature along their drift route than larvae that originate from spawning grounds in the west or north. The outliers found in other years are also likely to have originated from more southern locations. The use of temperature readings from fixed stations rather than a model output from particle tracking exercises enabled the identification of individuals that need a higher temperature in order to fit to their growth regime. The STDG growth model has been shown to fit well to growth estimates from most field studies of various cod stocks (Folkvord, 2005). However, in the study of Folkvord (2005) there were two examples of underestimated growth by the STDG model from cold regions, in which one came from northern Iceland (Begg and Marteinsdottir, 2000). Folkvord (2005) speculated that the underestimation of growth in the model resulted from underestimation of age due to the presence of very narrow increments in the otolith formed at low temperatures (Otterlei et al., 2002). However, this apparent fast growth also could be caused by mixing of individuals from warmer southern spawning areas, which was likely the case for the 1999 cohort in the present study.

Intensive 0-group surveys were conducted in Icelandic waters during 1970–2003 (see Sveinbjörnsson and Hjörleifsson, 2003; Astthorsson et al., 1994 and revisions in Begg and Marteinsdottir, 2002). The surveys stretched far-out into the Irminger current and in some years large aggregations of juveniles were found in Greenland waters, although the highest abundance was usually closer to shore (Astthorsson et al., 1994). The fact that low number of larvae/juvenile were found in this study in the high-saline NIIC current (in contrast to the low-saline waters of the coastal current) is in an agreement with the findings of Astthorsson et al. (1994). They found no relationship between the flow of NIIC water onto the northern shelf and the abundance of 0-group cod sampled in nursery areas north of Iceland. Jonsson and Valdimarsson (2005) found a connection between the inflow of Atlantic waters and abundance of pelagic cod, but they did not distinguish the coastal current from the NIIC current, as they justifiably pointed out that fresher water closer to shore is mainly NIIC water that has been diluted with freshwater runoff. Begg and Marteinsdottir (2002) separated coastal ($>$ 100 m) and offshore waters in their analysis and demonstrated that abundance of 0-group was generally higher in the offshore waters. This is in contrast to the observed larval/juvenile distribution in the present study. However, the large offshore abundance indices also could have resulted from the relatively large size of these areas compared to the inshore areas, thus potentially resulting in overestimation of the offshore component.

The results of this study indicate a possible relationship between the abundance of larvae/juvenile collected on the drift route west of Iceland and the number of cod at recruitment (age 3). Other studies have demonstrated correlations between 0-group and recruitment ($R^2 = 0.50$, Begg and Marteinsdottir, 2002). This relationship broke down in recent years (since 1997), during which unusually large year classes of 0-group were observed (Sveinbjörnsson and Hjörleifsson, 2003). These cohorts (1997–2003) did, however, not return in high abundance at age 3 years and recruitment has been equal or below average throughout this period (Anon., 2007b). This recent increase in 0-group abundance coincides with increasing strength of the sub-polar gyre (Stein, 2005), which has resulted in intensified flow of Atlantic water onto the shelf north of Iceland. The increase in 0-group abundance at the northern nursery areas could also be related to greater spawning activity or survival of larvae from local spawning sites inside the northern fjords (Begg and Marteinsdottir, 2000). However, most of these juvenile cod apparently did not survive the first winter as they were not detected in any significant abundance in the following spring surveys (Saemundsson, 2005). Interestingly, in comparison to the 0-group index, the data on larval and juvenile abundance in the present study appear to correlate better with abundance at age 3. For example, in 2001 the 0-group index was measured as the seventh highest ever on record. This year class did not excel others at the time of recruitment; indeed at age 3, it was the weakest cohort ever recorded (Anon., 2007b). Furthermore, based on the result from this study, the abundance of larvae/juvenile along the drift route was also the lowest in 2001, out of the 4 years sampled. As the spawning stock biomass was quite similar during this period (Anon., 2007b), it is tempting to conclude that low recruitment of the 2001 year class reflected the limited number of larvae derived from the main spawning grounds at the south, SW and west coasts of Iceland.

The findings of the present study have strengthened previous knowledge on factors influencing the early larval and juvenile abundance and distribution in Icelandic waters. The role of the coastal current in successfully transporting larvae from the spawning areas into the northern nursery grounds is likely to be one of the main mechanisms influencing recruitment variability in the Icelandic cod stock. Future work should focus on the relative contribution of the different spawning sites and attempt to explain why the fate of weak year classes such as 2001 is determined during the first few weeks of their life. The results of the present study also indicate that mid-summer surveys, which collect information on larval condition, feeding levels and abundance during their northward transport, may be a valuable tool in understanding and predicting recruitment variation in this cod stock.

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Paper II

Variation in hatch date distribution, settlement and growth of juvenile plaice (*Pleuronectes platessa* L.) in Icelandic waters

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Variation in hatch date distributions, settlement and growth of juvenile plaice (*Pleuronectes platessa* L.) in Icelandic waters

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ABSTRACT

Hatch date distribution, larval phase and subsequent growth of juvenile plaice (*Pleuronectes platessa* L.) in different regions around Iceland were determined by otolith microstructure analysis. Length, age and hatch date frequency distributions were obtained from juveniles captured in a 1 m beam trawl on 31 stations at 0.5–1 m depth all around Iceland in July 2006. The main spawning has previously been assumed to take place on the south and south-west coasts with eggs and larvae then distributed by currents along the west and north coasts. Contrary to this expected dispersal pattern, both size and age of juvenile plaice decreased from south to north. The results indicate that the observed spatial variation in size of the juveniles is not explained by different growth rates but by age. The juveniles at the south coast hatched earlier than juveniles on the north and east coasts and had a shorter larval period. Growth differed between regions and was partially explained by temperature. The study provides evidence that the juvenile plaice population may in fact originate from multiple spawning sites located not only along the south and south-west coasts, but along the entire coast of Iceland. The findings are discussed in relation to currents and temperature in Icelandic waters.

1. Introduction

The origin and dispersal of juvenile fish and their subsequent distribution are vital processes underlying population structure (Hanson, 1996). Failure to account for stock diversity can lead to erosion of spawning components, detrimental local effects and loss of biological diversity (Bailey, 1997). Furthermore, the insight of how growth and survival of early life stages affect stock structure will facilitate understanding of recruitment variability and lead to better estimates of the stock–recruitment relationship (Begg and Marteinsdottir, 2002).

Populations of the European plaice (*Pleuronectes platessa* L.) are found on the continental shelf around Iceland, most abundantly in the warmer waters to the south and west of the country (Solmundsson et al., 2005). The main spawning grounds are located along the south and the west coasts with spawning beginning in late February, peaking in March and April and mostly finished by the middle of May (Sæmundsson, 1926; Sigurðsson, 1989; Solmundsson et al., 2003). Pelagic eggs and larvae are believed to drift from spawning areas clockwise around the country with the coastal current and the warm saline Atlantic water (Tåning, 1929; Gunnarsson et al., 1998). The Atlantic water of the Irminger Current flows towards the south coast of Iceland. South of Iceland the Irmingar Current splits and one branch flows along the south-east coast eastwards to Faroese waters (Valdimarsson and Malmberg, 1999; Logemann and Harms, 2006; Fig. 1). The larger branch follows the bottom contours along the west coast, and splits into two branches west of Iceland's Westfjord peninsula (Stefánsson, 1962). The largest part of the Irminger Current flows west towards Greenland, but a smaller branch continues north onto the shelf north of Iceland. This northward flow is often interrupted by the East Greenland Current, which originates in the Arctic Ocean and transports cold water south along the east coast of Greenland. The collision of warm and cold water masses causes considerable variability in hydrographic conditions of the north Icelandic waters and influences the local biological productivity (Malmberg et al., 1996; Gudmundsson, 1998; Jónsson and Valdimarsson, 2005). Although not well documented, spawning of plaice has been reported at locations all around the country. Sæmundsson (1926) and Tåning (1929) reported that spawning of plaice occurred on the north-west, north and east coasts but concluded that it was limited compared to the main spawning grounds. More recently, Solmundsson et al. (2005) found spawning plaice all around the island (Fig. 1).

Plaice has spatially restricted nursery grounds located in shallow soft bottom areas, where the nursery areas only make up a small fraction of the species distribution range (Gibson, 1999). Little is known about the general biology of the juvenile stages of plaice in Icelandic waters. Tåning (1929) summarized investigations from the first three decades of the 20th century on settled 0-group plaice. He showed that plaice settled on sandy beaches on the west, north and

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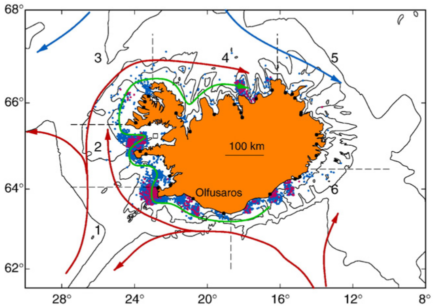

Fig. 1. Bathymetry around Iceland showing depth isoclines at 100, 200, and 1000 m. Green arrows: coastal waters, red arrows: Atlantic Water (AW), blue arrows: Polar Water (PW; modified after Logemann and Harms, 2006). Plaice spawning grounds indicated by the distribution of actively spawning (running) female (in violet) and male (blue) plaice registered in the fish database of the Marine Research Institute from 1987 to 2004 (modified from Solmundsson et al., 2005). Location of the six regions and the 31 stations sampled for juvenile plaice in July 2006 (black circles). Temperatures were obtained at locations shown by the open boxes.

east coasts, starting at the end of June on the western coast and continuing for up to two months along the northern and eastern coastlines. He also noticed a decline in size of the juveniles clockwise around the country, from west to east, and proposed that this was mainly due to temperature-induced growth differences and only partly due to difference in spawning time. The larval and juvenile growth rates may have been enhanced by the warmer water on the west coast and retarded by the cooler waters off the north and east coasts.

In recent years, the Icelandic plaice stock has been severely depleted (Anon., 2007). Despite the economic and ecological importance of the species, studies on the population structure, dynamics and natal origin are few. Consequently, further information on the life history of the juvenile plaice is clearly needed in order to improve our understanding on the spatial stock structure and recruitment.

In this study, we make the first attempt to analyse the origin of juvenile plaice in Icelandic waters by estimating the hatch date distributions by means of otolith microstructure. Spatial variations in age–length relationships are then analysed to determine whether geographical size differences are growth-related. The present analysis provides information on the larval phase duration.

2. Material and methods

2.1. Sampling

The coastline of Iceland is estimated to be roughly 6500 km in length, excluding tidal flats. The greatest portion of the coastline consists of moderately steep rocky shores (approximately 4900 km), while very steep shores, including vertical cliffs, are estimated to be about 600 km in length. Exposed apparently barren, sandy shores are estimated to be about 560 km in length (Ingólfsson, 2006). The sampling sites (stations) were selected based on shore type (unvegetated sandy substrates) and accessibility by a 4-wheel drive vehicle. A total of 31 stations were sampled between the 16th and the 28th of July 2006 covering almost all the main coastal areas of Iceland (Fig. 1). Sampling was done with a 1 m beam trawl during 2 h around neap tide. The 5.5 m long trawl was equipped with a tickler-chain and 8 mm mesh size in the main body and 7 mm in the cod end. The gear was pulled parallel to the beach by two people for approximately 3 min. The towing speed was kept as constant as possible during sampling, at an average of 35 m min^{-1}. GPS equipment was used to record the distance covered and the surface area sampled. It was aimed to cover 100 m^2 in every tow, but due to local difference the tow length varied between 30 to 100 m^2 (Table 1). The average depth at each station ranged from 0.5 to 1 m. On each occasion, two to three replicate hauls were made. Samples were stored in plastic buckets and sorted within a few hours in the laboratory. The juvenile flatfish were identified to species level, counted, and the total length was measured to the nearest 0.1 mm. Samples were then preserved in 96% ethanol until extraction of otoliths. When converting the catch to numbers per 100 m^2, no correction was made for gear efficiency. The length of individuals was first converted into age by region specific age–length keys (see growth section). Density was then estimated as number of individuals that settled (12 mm) at that location, using the specific daily survival of 0.018 d^{-1} (Beverton and Iles, 1992) to estimate this.

2.2. Temperature measurements

Temperatures were obtained from continuously recording thermometers positioned in surface waters at locations within regions 1–5 (Fig. 1). In region 1 the thermometer was located by the island of Heimaey. The temperature observed there is generally considered to represent the temperature conditions in regions 1 and 6 (Malmberg et al., 1996), and since no temperature readings were available from region 6 the measurement from region 1 was used for both regions. Temperatures were recorded every 2 h and daily temperatures were obtained by averaging all measurements between 0000 h and 2400 h. In general, temperatures in March to May were 2–4 °C higher on the south coast compared to local temperatures within the fjords on the west, north and east coasts (Fig. 2). On the south coast, temperatures rose gradually from approximately 6 °C in the beginning of April to 8 °C in end of May, exceeding 10 °C at the end of July. Temperatures on the west, north and east coasts were at or below 2 °C in March and approached 6 °C in the beginning of June. At the end of July, temperatures on the west and north coasts had reached the same temperatures as on the south coast while the temperatures on the east coast were about 1 °C lower.

2.3. Data analysis

Otolith microstructure analysis was used to determine growth rates, larval phase duration and age in days of plaice juveniles from around Iceland. To assess the spatial variation, the survey area was divided into six regions (Fig. 1). Juveniles from stations within every region were pooled together and preserved samples were randomly drawn for analysis. The sagittal otoliths were removed, cleaned and mounted on microscopical slides, sulcus up, with cyanoacrylate glue. The otoliths were polished on both sides with metallurgical lapping film until the accessory primordia and the increments were visible. The final polishing was done with aluminia powder (0.3 µm). Approximately 100 otoliths were analysed from each region. Counts of growth increments were repeated three to five times by the first author until a consistent age was obtained. If any of the counts differed more than ±10%, often due to poor sample preparation, the otolith was discarded (approximately 7% overall). The innermost accessory primordia was determined as the settlement mark (Alhossaini et al., 1989; Modin et al., 1996) which provides an estimate of the timing of settlement to benthic habitat. Total increment counts between the hatch ring and capture provided an estimate of the total age in days on the assumption that the increments had been deposited daily (Karakiri et al., 1989).

Growth rates (daily instantaneous) after metamorphosis were determined by fitting an exponential model:

$$L_t = L_0 e^{gt}$$

Table 1
31 beaches and their plaice populations sampled all around Iceland in 2006.

Region	Beach no.	Latitude	Longitude	Sampling date in July	Number of tows	Average tow length (m)	Density of plaice (ind. 100 m^{-2}) ± SE	Estimated settlement density (ind. 100 m^{-2})	Median length (mm)
1	1	64.0244	−22.7076	16	3	50	241.3 ± 9.3	484	28.8
2	2	64.0978	−22.0335	17	3	100	235 ± 14.6	390	22.1
2	3	64.3140	−22.0552	19	3	100	27.3 ± 0.7	52	27.1
2	4	64.8236	−23.3722	18	2	100	0	–	–
2	5	64.8920	−23.6840	18	3	100	38.7 ± 4.6	76	28.9
2	6	65.5160	−23.1759	20	3	100	55.3 ± 3.3	108	27.7
3	7	65.5513	−23.9397	20	3	100	213.7 ± 11.6	318	19.2
3	8	65.8987	−23.4940	21	2	100	1022 ± 66	1493	19.5
3	9	66.0275	−23.4334	21	2	100	105 ± 10	179	22.7
3	10	66.1503	−23.2329	21	2	100	220.5 ± 6.5	362	22.7
4	11	65.7696	−21.7133	22	3	30	127.8 ± 4.8	204	21.9
4	12	65.3471	−20.9518	22	2	100	136.5 ± 8.5	194	18.5
4	13	65.7444	−19.6163	22	2	100	25.5 ± 2.5	34	17.6
4	14	65.9678	−18.5162	23	2	100	27.5 ± 1.5	42	20.4
4	15	65.7823	−18.1526	23	2	50	26 ± 2	39	18.9
4	16	65.6708	−18.0791	23	2	100	60 ± 4	100	22.3
4	17	66.0944	−17.3166	24	3	100	30.3 ± 2.2	50	22.5
4	18	66.2862	−16.4391	24	2	75	56.3 ± 15	77	17.8
4	19	66.2286	−15.7045	24	2	100	7.5 ± 1.5	11	19.6
5	20	66.1966	−15.3339	25	2	50	106 ± 18	166	21.6
5	21	66.1069	−15.1861	25	3	100	0	–	–
5	22	65.7826	−14.8313	25	3	100	0	–	–
5	23	65.7367	−14.8553	25	3	100	2.7 ± 0.3	4	21.2
5	24	65.2796	−13.9942	25	3	36.7	339.7 ± 45.4	453	18.3
5	25	65.0597	−13.9946	25	3	100	5.3 ± 0.9	6	13.1
5	26	64.7898	−14.0089	26	3	100	125.3 ± 5.8	177	18.7
6	27	64.2947	−14.9158	27	2	100	201.5 ± 6.5	391	27.7
6	28	64.2435	−15.1732	27	2	100	1034.5 ± 90.5	2117	29.0
6	29	63.8765	−16.5551	27	2	100	52.5 ± 10.5	124	37.0
1	30	63.4090	−19.1019	28	2	100	7.5 ± 1.5	18	38.2
1	31	63.7675	−20.7802	28	2	40	322.5 ± 52.5	772	36.7

Geographical location in region, sampling date in July, number of tows, average tow length, density of 0-group plaice with SE, estimated settlement density (at 12 mm) and median length of plaice.

where L_t is length (mm total length) at time t, L_0 is estimated length at settlement, g is instantaneous growth coefficient, and t is estimated age (days after settlement).

Analysis of covariance was used to investigate the effects of region on growth and the additional effects of both the estimated mean observed temperature of the juveniles and the estimated settlement density.

Hatch date frequency distributions were derived from back calculated age class distributions, based on number of increments from the hatch check until time of capture. Hatch date, and larval phase frequency distributions among regions were then compared with a Kolmogorov–Smirnov (KS) test.

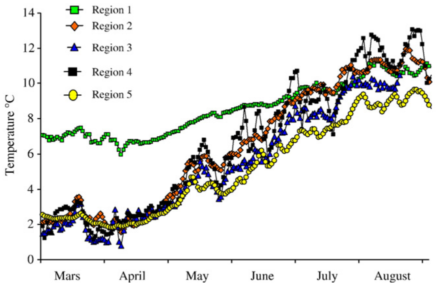

Fig. 2. Average daily temperature in regions 1–5 during late winter to summer of 2006.

3. Results

3.1. Spatial and size distributions

Juvenile plaice were caught at 28 out of 31 sampled beaches (Fig. 3). The estimated density of plaice ranged from 0 to 2117 settled ind. 100 m^{-2} among the investigated stations, with an overall average density in the study area of 272 settled individuals per 100 m^{-2}. The two stations with the highest densities were found in regions 3 and 6 with estimated 1493 and 2117 settled ind. 100 m^{-2}, respectively (Table 1). These regions also included several other stations with high numbers of juveniles while stations with the lowest densities were

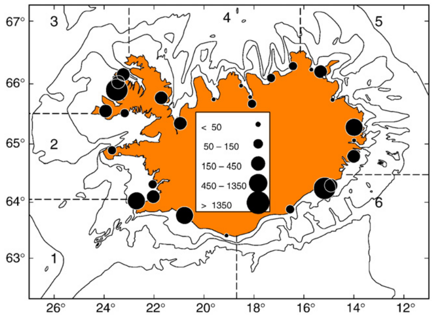

Fig. 3. Expanding symbol plot of juvenile plaice estimated settled density (abundance 100 m^{-2}) during sampling in July 2006. Stations with zero catch are marked with an open circle.

found in region 4, on the north coast. At only two stations were other fish species (gadoids) caught with the beam trawl and their numbers were low.

A general decline in size of the juveniles was noticed from the southern shore clockwise around the country. Within each area distributions were generally skewed towards smaller individuals. The median total length decreased from region 1 (31.5 mm; Table 2) on the south-west coast, clockwise around the country to region 5 on the east coast who had the smallest median length (18.8 mm). In region 6, on the south-east coast, the median length increased again to (30.1 mm).

3.2. Growth

The growth of plaice as described by the exponential model differed between the regions (Fig. 4; Table 3a). Visual inspection of the length data clearly shows an exponential growth curve and therefore it was not appropriate to calculate and compare average daily growth increments as the sampled age distribution was variable between regions. The estimated growth was highest in region 6 (2.3% per day) and lowest in region 3 (1.88%) and estimated intercept of 12.55 was close to stated 12 mm total length at metamorphosis (Ryland, 1966; Modin et al., 1996).

We considered temperature as an additional explanatory variable for the variation in growth rate between regions. The estimated mean temperature varied between regions. Highest estimated temperatures were registered in regions 1 and 6 (Fig. 5). Slightly but significantly lower temperatures were in regions 2 and 4 while juveniles in region 3 and 5 experienced the lowest temperatures. Estimated mean temperature had a positive effect on juvenile growth (Table 3b), but there were some discrepancies from this pattern. In particular, juveniles from region 5 experienced low temperatures but the growth rate was higher than expected. AIC model comparison favoured the model including both regional and temperature effects on growth, over region alone (Table 3). Density effects were not significant on the juvenile growth rate.

3.3. Hatch date distribution and larval period

A distinct gradual delay in average time of hatching was detected from west to east (Fig. 6; Table 2). Most of the juvenile plaice caught in regions 1, 2 and 3 hatched in mid- to late April. In regions 4 and 5 the juveniles hatched on average two to three weeks later. Some of the individuals in region 5 hatched as late as mid-June. In region 6, on the south-east coast, the mean hatch date was 24th April and range from late March to early June. The hatch date distributions all differed significantly from each other except in regions 1 and 2, 2 and 3 and 3 and 6 (Table 4).

The juvenile plaice in regions 1 and 6 had an average larval phase of 52 days, ranging from 46 days to 64 days (no significant difference between regions 1 and 6; Table 4). The plaice in regions 2 to 5 settled later and had significantly ($p<0.001$) longer larval period than in region 1 and 6, or about 60 days on average, ranging from 52 to 79 days, and were not significantly different from each other.

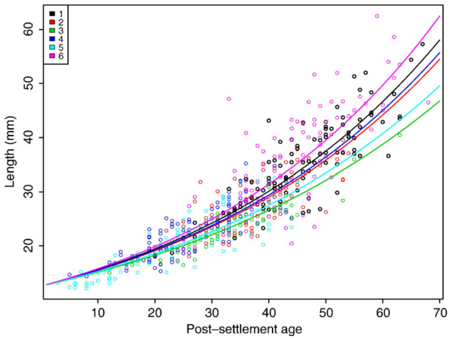

Fig. 4. Relationships between juvenile length and post-settlement age in days among regions. Lines represent the fitted exponential growth equation for each region (parameters in Table 3a).

4. Discussion

Our geographic comparison revealed significant differences in the size and age distribution around Iceland. The clockwise decreasing length gradient of juvenile plaice from the south to the east coasts, has previously been found to result mainly from temperature-induced growth (Tåning, 1929). Dispersal pattern had been thought to be facilitated by the coastal and Irminger currents, with larvae originating from main spawning grounds in the south and west of Iceland. We conclude, however, that juvenile plaice in 2006 originated from different spawning events and locations. In order to establish the natal origins of juveniles we compare known times for development of plaice eggs and larval period (measured from otoliths) with estimates of the time it would take eggs and larvae to drift from known spawning sites to juvenile sites. We also compare the subsequent growth of juveniles in different regions.

4.1. Spawning locations and origins of juvenile plaice

The first piece of evidence for separate spawning grounds is differences in the duration of the pelagic egg and larval phases between northern and southern juveniles. Differences in incubation temperatures prevail between plaice spawned in cooler waters off the north and east coasts and the warmer south. The duration of development of plaice eggs is between 13 and 26 days depending on the temperature (Apstein, 1909), and thus temperature could cause up to two weeks difference in development times. Furthermore, the development time of larvae is temperature-dependent with increasing sea temperature generally decreasing the pelagic stage duration (Hyder and Nash, 1998). The present study reveals that juvenile plaice from the warmer southern regions, 1 and 6, had significantly shorter larval periods (44 to 63 days) than plaice in

Table 2
Summary of the six regions: sample sizes, length, hatch date and length of larval period (± SD) from the July 2006 survey.

Region number	1	2	3	4	5	6
Number of stations	3	5	4	8	7	3
Number of plaice collected	437	1063	3336	818	484	1725
Number of plaice aged	91	74	76	108	87	98
Median length — survey (mm)[a]	31.5 ± 7.8	27.6 ± 4.5	21.0 ± 4.3	19.7 ± 4.8	18.8 ± 4.8	30.1 ± 6.3
Median length — aged (mm)[a]	33.2 ± 7.9	28.1 ± 4.5	23.4 ± 4.9	21.6 ± 8.3	19.9 ± 5.2	32.0 ± 7.5
Mean hatch date (day of year)	105 ± 11	108 ± 9	112 ± 11	122 ± 9	130 ± 12	114 ± 11
Mean larval period (days)	53 ± 6	58 ± 5	61 ± 6	58 ± 7	59 ± 7	52 ± 5

[a] Length not adjusted to mean cruise date.

Table 3

Parameters	Estimate	SE	*p*-value
a) Exponential growth model of juvenile plaice length against age among regions			
Intercept	2.530	0.0197	<0.001
Age	0.0219	0.000450	<0.001
Age: region 2	−0.000904	0.000484	0.062
Age: region 3	−0.003089	0.000524	<0.001
Age: region 4	−0.000591	0.000580	0.309
Age: region 5	−0.000226	0.000695	0.001
Age: region 6	0.001052	0.000402	0.009
$R^2 = 0.835$; AIC = −691.2			
b) Exponential growth model of juvenile plaice length against age including the effects of temperature and regions			
Intercept	2.466	0.0256	<0.001
Age	−0.00418	0.000676	0.536
Age: temperature	0.00295	0.000764	<0.001
Age: region 2	0.000978	0.000682	0.152
Age: region 3	0.00156	0.00131	0.235
Age: region 4	0.00114	0.000727	0.118
Age: region 5	0.00454	0.00189	<0.016
Age: region 6	0.000702	0.000407	0.0853
$R^2 = 0.839$; AIC = −704.1			

northern regions, 2 to 5 (52 to 78 days), and most likely shorter egg duration. The results from the warmer regions were close to the values for Irish Sea plaice who experienced temperatures >6 °C: 31 to 51 days (Fox et al., 2007), or 42 to 59 days (Alhossaini et al., 1989). The larval phase in regions 2 to 5 coincides with results from the colder North Sea: 50 to 82 days (Karakiri et al., 1991). The differences indicate that these plaice originated from different spawning grounds with different temperature leading to different larval durations.

The second piece of evidence for distinct spawning grounds comes from drift modelling of the pelagic life phases. Logemann and Harms (2006) developed a high resolution 3-D hydrodynamic model of Icelandic waters. Preliminary drift modelling using this model suggests that drift speeds are not high enough to transport plaice eggs and larvae from the south of Iceland into the shelf north of Iceland. According to the model, a drift at 10 m depth from a region 1, 1.5 km south of Olfusaros (see locations in Fig. 1), to north of 66°N would take at least 90 days in 2006. Since plaice larvae are known to not be able to delay metamorphosis for this length of time (Gibson and Batty, 1990), they would have switched from the pelagic phase and settled before entering the northern shelf. The observed spatial gradient in age is, therefore, most likely due to differences in the spawning location of juvenile plaice, with older individuals originating from spawning grounds in the south and younger juveniles from farther north and east. It is likely that the contribution from the spawning grounds in the south and south-west decreases with clockwise distance from the source region and is probably non-existent on the northern and the eastern shelf of Iceland.

A third piece of evidence for separate spawning areas comes from examining the hatch dates of the different regions. Only small periods of the hatch date distributions of juveniles in the north overlapped with the distributions from the main spawning grounds in region 1. According to the otolith microstructure analysis, hatching occurred mostly from early April to mid May in regions 1 and 2 (south-west)

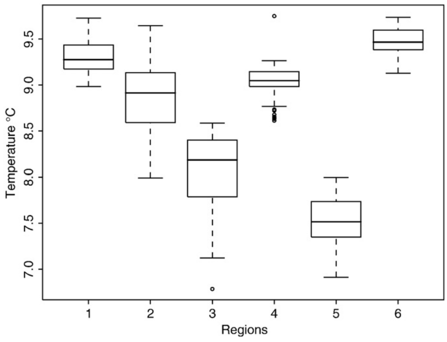

Fig. 5. Estimated mean ambient temperature experienced by post-settled juvenile plaice from each region. Each box shows the median (bold horizontal line) value and the 25 and 75 percentiles (upper and lower limit of the box respectively). The dashed vertical line indicates 1.5 times the interquartile range of the data, with points representing outliers.

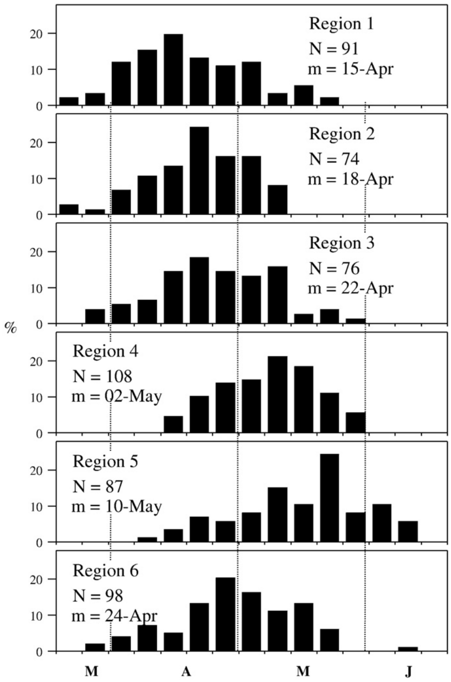

Fig. 6. Hatch date frequency distribution of juvenile plaice sampled around Iceland in July 2006. N: number of individuals; m: mean hatch date.

Table 4
Results of Kolmogorov–Smirnov two sample test probability levels.

	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6
Region 1	–	<0.001	<0.001	<0.001	<0.001	>0.10
Region 2	>0.10	–	>0.10	>0.10	>0.10	<0.001
Region 3	<0.05	>0.10	–	>0.10	>0.10	<0.001
Region 4	<0.001	<0.001	<0.001	–	>0.10	<0.001
Region 5	<0.001	<0.001	<0.001	<0.001	–	<0.001
Region 6	<0.001	<0.001	>0.10	<0.001	<0.001	–

Above the diagonal is the comparison of length of the larval plaice phase between regions, and below the diagonal is the comparison of hatch date between regions.

and from mid April to early June in regions 4 and 5 (north-east). It has been shown that plaice larva settle in water deeper than 5 m and move into shallow water following metamorphosis (Lockwood, 1974). When the fish grows to more than 40–50 mm they tend then to gradually migrate again into deeper water (Lockwood, 1974; Gibson et al., 2002). In regions 4 and 5, it is likely that newly settled juveniles were still entering the shallow coastal zones from deeper waters. At the same time it is possible that older juveniles, at least in region 1 and 6, had started to move out again into deeper waters. This would lead to even more pronounced differences in size and consequently age between the juveniles on the south coast and the north and east coasts respectively.

We therefore reject the hypothesis formerly proposed by Tåning (1929) that juveniles in the north of Iceland mainly originate from spawning grounds in the south and west. Furthermore, we find that the main cause of variations in size is the difference in age of juveniles in different areas, although the exponential growth model shows that there is also variation in growth rate.

4.2. Density in different regions

The quantity and the quality of the available nursery grounds have a regulating function for the strength of the year-class and are therefore important in the recruitment process of juveniles to the adult stock (Van der Veer, 1986; Beverton, 1995). These factors are then related to the regional pattern in the density of 0-group plaice (Wennhage et al., 2007). The present study shows that juvenile plaice is found on sandy beaches on the west, north and east coasts of Iceland, confirming Tåning's (1929) findings from the first decades of the 20th century. Additionally, we found that juvenile plaice are also present along the south coast. Sampling with 1 m beam trawl on the west coast of Iceland in 1999 (Hjörleifsson and Pálsson, 2001) indicated peak densities up to 10 ind. 100 m^{-2} while this study measured an order of magnitude higher density on the west coast. The magnitude of the highest estimates in this study are comparable to the densities on the Swedish west coast (Pihl et al., 2000) and considerably higher than those obtained in the nursery areas of the Scottish coasts (Poxton and Nasir, 1985) and the Wadden Sea (Berghahn, 1986). However, more detailed observations are required for further comparison of the abundance.

The major source of mortality in juvenile plaice is thought to be predation (Gibson, 1999). Predation by *C. crangon* and European shore crab (*C. maenas*) is an important factor regulating 0-group plaice densities shortly after settling on nursery grounds (Pihl, 1990; Van der Veer, 1986). For example, in Swedish bays, year-class strength of 0-group plaice is inversely related to the abundance of *C. crangon* and *C. maenas* in the nursery areas (Pihl, 1990). Prior to 2001, it had been speculated that few known predators on juvenile plaice existed in Icelandic waters (Hjörleifsson and Pálsson, 2001). Gunnarsson et al. (2007), however, suggest that the brown shrimp, *C. crangon* has colonized the intertidal areas of Iceland sometime between the year 2001 and 2003. In 2006, *C. crangon* was found along the coast in regions 1, 2, and 6. As Gunnarsson et al. (2007), discussed the *C. crangon* was still spreading and colonizing the beaches in 2006. Therefore, to evaluate the effects of C. crangon on juvenile plaice abundance would be difficult at this stage.

4.3. Causes of variation in growth of juveniles

Several studies have shown that growth rates can vary substantially over relatively short distances (Sogard, 1992; Duffy-Anderson and Able, 1999; Phelan et al., 2000). We found that observed differences in growth between regions in our study were partially explained by temperature. Numerous studies on juvenile plaice have demonstrated temperature dependent growth. For example, juvenile plaice consistently exhibit faster growth rates in the relatively warmer Wadden Sea and Swedish west coast than in estuaries around United Kingdom, apparently as a consequence of persistent differences in water temperature between the two regions (Van der Veer et al., 1990; Nash et al., 1994). Density had no effect on the growth rate in our study but some kinds of density regulation cannot be excluded through food limitation. Studies on dynamic thinning line of plaice however, suggest that plaice populations rarely reach the carrying capacity of their nursery grounds (Nash et al., 2007).

Many previous studies on growth of flatfishes (Karakiri et al., 1991; Sogard and Able, 1992; Glass et al., 2008) have compared daily growth increments. A confounding factor in growth rate comparisons is the size of the fish being compared. As our data shows a clear increase of growth rate with size and age, and our sampled juveniles are of different ages at different sizes, it was not appropriate to use that measure of growth in this study. Instead we fitted an exponential growth model that defines a percentage growth per day to each region, starting at a settlement size of approximately 12 mm. This method may still be biased towards higher growth rates for older fish if mortality is highly size dependant, with small fish experiencing higher mortality (Tian et al., 2007). Growth in region 5 in our study was faster than predicted by temperature alone. *C. crangon* was absent from this region in 2006 (Gunnarsson et al., 2007) and the littoral fish fauna of Iceland is poor compared to European continental shelf (Jónsson, 1992). That was also highlighted by the fact that only two gadoid species where caught as bycatch. Therefore, size dependent mortality is not likely to explain the faster growth in this cold region. A number of other factors could generate consistent spatial differences in growth, such as nutrient availability, primary production and genetic differences in growth capacity among local populations. Sogard et al. (2001) suggested that densities and growth rates of juvenile winter flounder (*Pleuronectes americanus*) at different regions along the coast of New Jersey were independent because of local environmental factors or genetic differences among local populations. Primary production on the northern and eastern shores is expected to be lower than on the southern and western shores (Gudmundsson, 1998) and should not favour faster growth in this region. This could suggest that juveniles in region 5 are adapted for faster growth in colder waters. Additionally, it has been suggested with the Icelandic cod stock that measured differences in thermal physiology of the northern and southern populations of cod would suggest optimization for growth and survival under different environmental conditions (Grabowski et al., 2009). Common garden growth experiments could further clarify the possible extent of local adaptation in different sub-stock of plaice in Iceland.

4.4. Implications for sustainable fishing

An important element in moving toward sustainable fisheries is the identification and conservation of essential fish habitats (Wennhage et al., 2007). For these purposes, information is needed to identify and evaluate how habitat quality and quantity may influence habitat use and recruitment success of plaice in Iceland. Such information is valuable for describing essential fish habitats and to determine the importance of different coastal areas for fish. The effects of the recently discovered predator *C. crangon* on the carrying capacity and production at the beaches in Iceland are also unknown.

Solmundsson et al. (2005) suggest the occurrence of geographically distinct spawning locations maintained by site fidelity and connected by straying, indicating a complex structure in Icelandic plaice. Further, the low effective population size that Hoarau et al. (2005) calculate for Icelandic plaice was suggested to be due to spawning site fidelity leading to elevated inbreeding. Genetic work has also revealed a relatively complex structure in plaice populations. With microsatellites difference was found between plaice in Iceland and on the European continental shelf (Hoarau et al., 2002) and by analyzing mitochondrial DNA, a local population structure within the continental shelf (Hoarau et al., 2004). The present study supports the findings of Solmundsson et al. (2005)

and provides evidence for the existence of a local population structure within the Icelandic plaice stock. This may have important implications for improving the management of the Icelandic plaice stock in the future. Future studies should collect evidence of spawning times, locations and genetic research around the country in order to identify local spawning and nursery grounds. Application of a high-resolution 3-D hydrodynamic model developed for Icelandic waters (Logemann and Harms, 2006; Brickman et al., 2006) would facilitate understanding of the observed abundance and the age distributions of the juveniles, contributions from the various spawning grounds and the extent of mixing in nursery areas.

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Paper III

Density dependant growth dynamics of juvenile European plaice (*Pleuronectes platessa* L.)

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Density-dependent growth dynamics of juvenile European plaice (*Pleuronectes platessa* L.).

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Abstract

Growth patterns of 0-group juvenile European plaice (*Pleuronectes platessa*) were examined during high and low settlement years on nursery grounds in SW-Iceland. During the high settlement year the density was approximately 10 ind./m^2 at highest peak, but around 2 ind./m^2 in a low settlement year. Otolith microstructure analysis was used to compare the growth during settlement and emigration periods and a recent growth analysis was applied as well during the settlement period. Inter- and intra-variability in growth on annual basis was confirmed. Juvenile growth patterns were similar to other European plaice nurseries, however higher intra-annual growth was observed during the second half of the the nursery ground period. Indication of density-dependent processes was detected during the recent growth analysis, demonstrated by faster growth of plaice juveniles from a low density year, ten-days prior to capture. Growth was also higher at emigration period during the low density year, albeit at a lower temperature, a further indication of possible density-dependent processes.

Keywords: Growth, age, juvenile, density-dependence, *Pleuroneces platessa.*

Introduction

Growth of early life-stages is often considered as one of the most influential factors in terms of survival and subsequent recruitment of fish populations (Anderson, 1988; Houde, 1987). Numerous fish species have a structural bipartite life cycle, where each specific developmental period is dependent on habitat types and availability (Gibson, 1994). For example, multiple flatfish species are attached to shallow inshore habitats during their first summer, where they accumulate and thrive in a limited geographical environment (Pihl & van der Veer, 1992). Although nursery grounds represent areas that provide conditions where the survival and the growth of juveniles are supposed to be maximized, they rarely provide an ideal setting throughout a whole summer season (Nash & Geffen, 2014).

Variability in juvenile plaice growth rate on temporal and inter-annual bases has been observed on many occasions in various nursery grounds in European shallow sandy areas (reviewed in Ciotti et al., 2014). Primarily, the influence of ambient water temperature was considered the main determinant for maximum growth (Gibson, 1994; van der Veer et al., 1990; van der Veer, 1986) as the "maximum growth - optimal food" hypothesis (van der Veer & Witte, 1993) assumed optimal food conditions in nursery areas and therefore no competition for food. However, intra-annual variability in juvenile plaice growth has been widely reported, especially the decline in growth rate during the second half of the nursery period which deviates from experimentally established maximum growth models with a large thermal range (Freitas et al., 2010; Jager et al., 1995; Nash et al., 2007; Nash et al., 1994; Teal et al., 2008; van der Veer et al., 1990; van der Veer & Witte, 1993). Some studies have observed a steady decline in growth rate during the whole nursery ground period (Freitas, Kooijman, & van der Veer, 2012; van der Veer et al., 2010). Others have shown a decline late in the summer (Amara, 2004; Ciotti, et al., 2013b; Freitas et al., 2010; Hjörleifsson & Palsson, 2001; Nash et al., 2007; van der Veer et al., 1990; van der Veer & Witte, 1993) and yet others did not identify any decline in growth pattern (van der Veer et al., 1990). Many influencing factors for the intra-annual growth variation have been identified. These include factors such as size-selective migration, food limitation or intake (Amara & Paul, 2003; Freitas et al., 2010) and inter-specific competition (Freitas et al., 2010). All of these have been proposed as potential influencing factors. Intra-specific competition has not been identified as an influencing factor for intra-annual growth variations (Ciotti et al., 2013b; van der Veer et al., 2010). However, mortality on the nursery ground is predominantly density dependent (Nash & Geffen, 2012).

Inter-annual growth variation has also received much attention and has been widely reported in nursery areas (Fox et al., 2007; Haynes et al., 2012; Modin & Pihl, 1994b; Teal et al., 2008; van der Veer et al., 2010). The keen interest of ecologists in this variability has been driven by a deeper understanding of inter-annual recruitment variability in adult populations. Factors mentioned earlier that influence the intra-annual variabilities have also been contributed to inter-annual variations along with annual changes in temperature (Teal et al., 2008; van der Veer et al., 1990; van der Veer, 1986) . It is often very difficult to untangle thermal variations from other environmental factors that may also be influenced by changes in temperature (Nash et al., 2007). Other causes include variations in prey abundance and condition (Karakiri et al., 1989). However intra-specific competition is probably the most intriguing factor. Effects of plaice density on inter-annual growth variation has been explored, however conclusions have been ambiguous. Some studies found negative (Teal et al., 2008) or no (Haynes et al., 2012) connections between plaice density and growth rate, but others observed slower growth rates in years of high juvenile density (Ciotti et al., 2013a; Geffen et al., 2011; Modin & Pihl, 1994; Nash et al., 2007).

The objectives of the current study were to investigate the effect of density on growth of juvenile plaice in Icelandic inshore waters. Two years representing variable population density were chosen from an 11-year-long data series of juvenile plaice. Individual growth was compared for selected dates during settlement as well as later in the summer. Furthermore, to identify recent growth patterns, the width of otolith increments in those two years, was measured during the settlement period (June/July).

Material and methods

The study area was located in Faxaflói bay in the south-west of Iceland, more specifically in Helguvík cove (64°05'54.5"N 22°01'55.9"W). It has a non-vegetated sandy substrate, is readily accessible and considered exposed with moderate sloping shore. The sampling period in Helguvík started in the end of May of 2005 and was ongoing biweekly through the summer months (May - September) annually until 2014. The sampling instrument was a beam trawl, 1-m wide and 5.5-m long, equipped with one tickler chain, it had 8 mm mesh size in its main body and 7 mm mesh size at the cod end. The trawl was pulled by two people, parallel to the beach, 3 - 6 times at low tide (-0.32 - 1.05 m). Sampling was undertaken during daytime and around the neap tide, since the newly settled plaice juveniles are concentrated near the surf-line at these times (Gibson et al., 2002). No corrections were made for gear efficiency. Sampled individuals were counted, and length measured (TL) to the nearest mm. Samples were preserved in 96% ethanol until extraction of otoliths. Sea surface temperature (SST) were recorded in the nearby (~13 km) Reykjavík harbor (64°09'10.3"N 21°55'55.5"W).

Otolith microstructure examination and analysis

Two years were picked out as an indicators of low - (2005) and high juvenile plaice density (2012) (Table 1). Sagittal otoliths (right and left) were extracted from randomly picked juveniles, around day 60 from first settlement (27 June 2005 and 4 July 2012) and again around day 85 (17 August 2005 and 20 August 2012). Total length (TL) of the juveniles, which the otoliths were extracted from, was measured to the nearest mm and correction was made for shrinkage due to dehydration caused by ethanol preservation.

Otoliths were cleaned, dried and mounted with convex side up on a standard microscopic slide and covered with quick-dry glue (containing: etyl-2-cyanoacrylate). As soon as the glue had fully dried (after approximately 24 hours) the otoliths were handground to the core with lapping film. The number of daily increments was counted using 1000x magnification (Campana & Neilson, 1985).

Each otolith was counted three to six times and if a consistent age was not obtained due to poor otolith preparation (counts differed by more than 10%), the otolith was discarded (Table 1). The secondary growth centres were used as indicator of the end of metamorphosis (Al-Hossaini & Pitcher, 1988; Karakiri & Westernhagen, 1989; Modin et al., 1996). Even though the juveniles can stay in the water column for a period of time after the secondary growth centres form (Geffen et al., 2011), we assumed that settlement and metamorphosis go together for settlement date calculations. For the recent growth analysis from the settlement period (June/July), 37 otoliths were extracted from juveniles who ranged between 15.96 - 21.66 mm TL (Table 2). Right sagittal otolith was chosen for diameter and recent growth analysis because of the anterior-dorsal/posterior-ventral axis, which produces the maximum growth axis caused by nucleus off-centering (Gilliers et al., 2004). A picture of a usable right sagitta was captured using a Microscope Camera (Leica DFC320), with 200x or 400x magnification and afterwards the daily increments were enhanced with a software (Adobe Photoshop). Image analysis system (ImageJ) was used to measure the longest diameter along the core rostrum axis and the width of the 10 most recently deposited daily increments where they are the widest for more accurate comparison (Modin & Pihl, 1994). The diameter in micrometres (µm) was recorded as otolith size at catch. The relationship between the sagittal size and size of the juveniles was identified as linear with strong correlation between the variables (R^2=0.8965) (Jones, 2002). Therefore, the mean daily increment width over the last 10 days before capture was calculated as an index of recent growth (Campana & Jones, 1992). Total length at 10 d before capture (TL10) was back–calculated from the otolith using the biological intercept method (Campana & Jones, 1992; Campana, 1990; seen in Suthers & Sundby, 1996):

$$TL10 = TL_C - [\text{“}10d\ width\text{”} * (TL_C - 6.5) / radius] \qquad \text{(Eq. 1)}$$

Where the $TL10$ is total length 10 days before capture, TL_C is total length at capture, *10d* width is the width of the latest 10 increments in micrometres (µm) and 6.5 mm was the chosen standard length of plaice larvae at hatch in Icelandic waters (Blaxter & Staines, 1971).

Analysis of individual instantaneous growth was done with two comparison years 2005 and 2012, at peak of settlement period (June/July) and start of emigration (August), was back-calculated from the otoliths as instantaneous growth rate (*G,* d^{-1}), where length at settlement was assumed to be 12 mm according to (Modin et al., 1996).

Growth rates (daily instantaneous) after metamorphosis were determined by fitting an exponential model during settlement period (June/July), emigration period (late August) and whole nursery ground period:

$$L_t = L_0 e^{gt} \qquad \text{(Eq. 2)}$$

where Lt is length (mm total length) at time t, L_0 is estimated length at settlement, g is instantaneous growth coefficient, and t is estimated age (days after settlement).

Sub-cohort analysis for each sampling date in years 2005 and 2012 was done using modal analysis, by fitting finite mixture distribution models to the length frequency histograms (Macdonald & Du, 2018). The length-frequency data in all sampling dates was compressed into bins of 3 mm. The number of sub-cohorts or means (μ), mixing proportions (π) and standard deviation (σ), at each separate sampling date was estimated visually before fitting the distribution. Constant coefficient of variation (CCV) constrain was set on standard deviation, as this constrain assumes that standard deviation (σ) increases with means (μ). The curves were fitted by the least squares and iterations, and chi-squared value gave the goodness of fit.

Results

Juvenile density and sea surface temperature

Settlement at the Helguvík nursery area started at the end of May in both years and reached a peak in density during mid-summer. In 2005, the densities were 2.3 ind. m^{-2} in late June and 1.2 ind. m^{-2} in mid-August. However, in 2012 the densities were higher, or 9.3 ind. m^{-2} in early July and 4.8 ind. m^{-2} in mid-August.

The mean SST two weeks prior to the sampling dates period was 10.3°C in 2005 (late June) and 12.5°C in 2012 (early July). The mean SST prior to the sampling date in August was 11.7°C in 2005 and 13.0°C in 2012.

Somatic and otolith growth

Otolith diameter from juveniles in settlement period (June/July) during both years, increased linearly with fish length ($F = 190.2$, $p < 0.01$) (Fig. 1), confirming that otolith growth reflects somatic growth. There was a significant difference in otolith diameter between the two comparison years ($F = 48.641$, $p < 0.01$), with larger otoliths during the high-density year of 2012.

Individual instantaneous growth

The comparisons of individual instantaneous growth rate ($G\ day^{-1}$) showed a significant difference between years during the settlement period (Table 2, Student´s t-Test, $p < 0.01$). Juveniles from the high density year (2012) grew a little faster than juveniles from the low density year (2005) (Fig. 2). There was also a significant difference between the means of total length in aged individuals during the settlement period (Student´s t-Test, $p < 0.01$). The range of the total length in settlement period individuals was 15.61-28.94 mm in 2005 and 15.82-42.08 mm in 2012. However, when fish from the same size interval were compared there was no significant difference between the years in growth during the settlement period (Student´s t-Test, $p = 0.9$). Juveniles in 2005, grew faster during the emigration period than juveniles in 2012 (Student´s t-Test, $p < 0.001$, Fig. 2). The difference in means of total length of individuals did not vary significantly between the years (Student´s t-Test, $p < 0.7$), however, juveniles from 2012 displayed a larger size range. The range of total length during emigration period in 2005 was 37.09-54.93 and 27.99-60.01 mm in 2012. Growth was also estimated by fitting exponential growth curves to the length-at-age plot (see parameters in Table 3). There was significant difference between the years when settlement and emigration periods were investigated separately, faster growth during settlement in 2012 and faster growth during emigration in 2005 (Fig. 3, Table 3). However, exponential growth curves for the whole period show no significant difference between the years ($p = 0.4$).

Back-calculation of the settlement date (Fig. 4) revealed that the aged individuals during the settlement period and at the end of it came from different sub-cohorts as there was no overlap in settlement dates in 2005 and only a partial overlap in 2012. Further estimation of the sub-cohorts for two sampling years was made by fitting a mixture model to the length frequency data (Fig. 5). During settlement period in 2005, a clear, single large “pulse” with a mean length of around 18 mm was identified and two older, smaller ones. There was also a small peak around 13 mm, signifying newly settled individuals. In 2012 there were four “pulses” more equal in size and with a less clear pattern. The largest one had the mean length around 22 mm. At the start of the emigration period, there were no small settling individuals identified and in both years the newest visible sub-cohort had a mean length of around 33 mm. In August 2005, there was a slightly older sub-cohort which was similar in size with a mean length of around 44 mm. Two older small sub-cohorts where also identified. During emigration in August 2012, the identified sub-cohorts were four, the largest one had a mean length around 33 mm and three older, smaller ones with mean lengths of 42, 53 and 66 mm.

Recent growth analysis

There was no significant difference in mean peripheral increment width between the two years in the June/July settlement period, which ranged between 7.26-10.25 µm in 2005 and 7.31 – 11.4 µm in 2012 (Student´s t-Test, $p = 0.452$). However, there was a significant difference in the post-metamorphic age and size (Student´s t-Test, $p < 0.0001$), which confirms that the 2012 juveniles had spent more time at the nursery grounds compared to the 2005 juveniles (8 days difference between the samples).

Biological intercept equation was used to back-calculate total lengths of juveniles 10 days before capture during settlement period in both years. The individual absolute growth rate in those ten days was between 0.42-0.62 (mm d^{-1}) in 2005 and 0.36-0.57 (mm d^{-1}) in 2012. There was a significant difference both in absolute and instantaneous growth rate between the two years (Student´s t-test and ANOVA, $p<0.001$), as individuals during settlement period in 2005 grew faster than individuals in 2012 (Table 4, Fig. 6).

Discussion

Using otolith microstructure analysis to compare the growth of juvenile plaice during two years of distinct density, revealed that recent growth (10 days before capture) at peak settlement was higher during the low density year. Also, at the start of emigration in late August, growth rates were higher during the low density year. These results are an indication that a density-dependent growth pattern of juvenile plaice was observed at Helguvík cove, where the density was among the highest reported.

The influence of variations in plaice density on inter-annual growth have been described on numerous occasions and when more thorough methods, such as otolith microstructure analysis or RNA-based index, were used, growth rate was lower at higher densities (Geffen et al., 2011; Modin & Pihl, 1994; Nash et al., 2007; Ciotti et al., 2013a). A densely populated juvenile settlement as witnessed in 2012 could influence the food availability experienced by individuals towards the end of the season. Food limitation (Pihl et al., 2000; Wennhage et al., 2007), intra-specific competition (Geffen et al., 2011; Modin & Pihl, 1994; Nash et al., 2007) or simply the disturbance in capturing and handling the prey (Heath, 1992) have all been suggested to influence growth. Predation and the effects of inter-specific competition on growth in those two years was not investigated, but as described in Jónsdóttir et al. (2016), densities of adult brown shrimp (*Crangon crangon*), an effective predator on juvenile flatfish (Van der Veer et al., 1990), were around two times higher during the high settlement year of 2012. Inter-specific competition has seldomly been investigated, but density of brown shrimp was not found to reduce growth in two studies from the west coast of Scotland (Ciotti, et al., 2013a; Ciotti, et al., 2013b). The European flounder (*Platichtys flesus*) is a new species in Icelandic waters, first found in 1999. A niche overlap has been described between juvenile European flounder and plaice in Iceland on nursery grounds (Henke et al., 2020). No 0-group flounder was found in 2012 in Helguvík (MFRI, unpublished data), but the recent colonization and high proportion in a recent study is likely to have competitive effects on juvenile plaice in Icelandic waters (Henke et al., 2020).

Growth rates were similar to those observed in other nurseries (Al-Hossaini et al., 1989; Amara & Paul, 2003; Berghahn et al., 1995; Geffen et al., 2011; Modin & Pihl, 1994; van der Veer et al., 2010) and slightly higher than from previous growth estimates from Iceland (Gunnarsson, et.al, 2010). Post-settlement habitat quality is thought to be an important factor in controlling growth in plaice during the nursery ground period (Fox et al., 2014). Temperature is also important and may influence both food quality and quantity. For example, temperature has been shown to have a positive effect on the biomass of brown shrimp in Helguvík (Jónsdóttir et al. 2016). The influence of variability in prey conditions (Karakiri et al., 1989) and nutrient condition (Teal et al., 2008) has been linked to inter-annual variability in growth rate, thus this could also be the case in Helguvík. In our study the temperature was considerably higher during the high-density year prior to both sampling periods which could have facilitated faster growth (Geffen, et al., 2011; Gunnarsson, et al., 2010), but was currently not observed. In general, growth variations have been frequently detected between different sub-cohorts (Al-Hossaini et al., 1989; Geffen et al., 2011; Modin & Pihl, 1994). In this study we were not able to follow the same sub-cohort between sampling dates, but 3 -

4 sub-cohorts were detectable from the catch distribution during both years of this study. It has been shown that growth rates are higher in later arriving sub-cohorts and that was positively related to temperature (Geffen et al., 2011), which is the same trend as seen in this study. Considering that the maximum growth period is shorter at higher latitudes (Freitas et al., 2010) and the ambient water temperature experienced by the juveniles in August was higher than during the settlement period (June/July), our sampling could have been performed too early to observe growth decline in aged individuals which have been tied with end of the nursery ground period in other studies.

The general increment widths in our study appear to be relatively wide compared to previous studies (Karakiri et al., 1991, 1989; Modin & Pihl, 1994; Raedemaecker, 2011; Selleslagh & Amara, 2012). However they were well within range of studies performed during high growth periods such as the one by Al-Hossaini et al., (1989) executed in July-August in Red Wharf Bay in North Wales. The short growth period at higher latitudes starts later in comparison to European nurseries (Freitas et al., 2010; Hjörleifsson & Palsson, 2001). Therefore, our wide increments could correspond to a high growth period starting relatively late in the season. Also, the increment widths in juvenile plaice have not been measured before in Icelandic waters or in higher latitude nurseries. During summer the day is longer at these northern locations, thus providing more visibility and an increased feeding period which could lead to wider increment widths (Al-Hossaini & Pitcher, 1988; Karakiri & Westernhagen, 1989; Suthers & Sundby, 1996).

There was no significant difference in increment width between the years, however the otolith diameters in juveniles from 2012 were larger, which could indicate a slower growth in 2012, as the increment widths can increase with otolith size, even under constant (or decreasing) growth rates (Campana & Jones, 1992). Selleslagh & Amara, (2012) showed a clear response in biological factors (recent otolith growth, the Fulton´s condition index and RNA/DNA ratio) in regard to starvation of juvenile plaice. In Helguvík´s juveniles the otoliths recent increment widths were similar in both years, and much larger than the reference point of 3.99 micrometres which indicates that the fish was not starving during the settlement period (Selleslagh & Amara, 2012). Size-selective mortality can also have an indirect influence on individual growth, especially in high density years. This is linked to observational bias, where if the individuals have been affected by size-selective mortality due to food-limitations, the remaining survivors are those which growth is close to optimal and therefore had higher chances of survival (reviewed in Le Pape & Bonhommeau, 2015). This could mean that the individuals that are compared from the high-density year are the “lucky” ones, in comparison to those from the low density year (Le Pape & Bonhommeau, 2015).

The influence of intra-specific competition on within-year growth variabilities in European nurseries have been addressed in a number of studies (Amara, 2003; Ciotti et al., 2013b; Freitas et al., 2010; Nash et al., 2007; van der Veer et al., 2010). In all those various nurseries the overall conclusion was that there was no relationship between the plaice densities and intra-annual growth variations. However, none of those nurseries had experienced the high densities observed in Helguvík. The lower growth rate at the start of the emigration period during the high density year, in a combination with the lower recent 10 day growth during the settlement period are an indication of a intra-specific competition processes occurring at this beach. To clarify the observed trend, these results warrant studying more years, in a similar manner and preferably to follow individuals from the same sub-cohort (e.g. Geffen et al., 2012). Combining further work with RNA-based growth indices would also reveal the recent short-term growth (Ciotti, et al., 2013b). Incorporating more sites would further highlight and strengthen the understanding of the overall dynamics of juvenile plaice in Icelandic waters, as the population structure has been shown to be complex (Gunnarsson, et al., 2010).

It has been proposed that the long-term dynamics of species like plaice, that concentrates into nursery ground during early life history, may be controlled by density-dependent processes (Beverton, 1995). Mortality is primarily density-dependent, and it occurs predominately during settlement and shortly after density peak (Nash & Geffen, 2012). For the past 25 years, there has been little variability in the recruitment of the Icelandic plaice stock (MFRI, 2020). Pihl et al.,

(2000) noted that density-dependent processes reduced growth at high juvenile densities (> 5 ind. m^2). Therefore, at the observed high densities in Helguvík in this study and on few other occasions (MFRI, unpublished data) density-dependent processes on juvenile plaice, could be considered as an influencing factor for recruitment variability in Icelandic waters.

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Figure legends

Figure 1. Relationship between otolith size and juvenile plaice lengths. Regression lines are plotted for both years.

Figure 2. Instantaneous growth rate (G day^{-1}) in aged juveniles from June/July and August samples from the years 2005 and 2012. Median values are showed for each box (bold horizontal line) and the 25 and 75 percentiles upper and lower limit of the box, respectively.

Figure 3. Fitted exponential growth curves for the aged June/July and August juveniles. Exponential growth lines; June/July line (····), August line (---) and whole season line (—).

Figure 4. Back-calculations of settlement dates, during settlement period June/July (grey) and emigration period mid-August (stripes / red stripes).

Figure 5. Plaice length histogram with estimated parameters and fitted curves, for sampling dates before density peak (a and c) and during emigration in August (b and d).

Figure 6. Relationship between recent growth (mm d^{-1}) and total length (mm) in comparison years 2005 and 2012. Regression lines are plotted for both years.

Tables

Table 1. Sampling years and dates, numbers of extracted and used otoliths for aging and width measurements, size range and the density of juvenile plaice at each sampling date.

Year	**Date**	**Otoliths extracted**	**Aged otoliths**	**Readable otoliths**	**Somatic/otolith growth**	**Size range (mm)**	**Width measure**	**Density ($100m^2$)**
2005	27.6	68	64	54	41	15.61 - 28.94	18	227.0 ±-7.5
2005	17.8	50	46	40	-	15.82 - 42.08	-	117.2 ± 46.4
2012	4.7	84	69	59	43	37.09 - 54.93	19	930.7 ± 100
2012	20.8	50	44	38	-	27.99 - 60.01	-	481±40.2

Table 2. Summary of growth rates for both settlement and emigration period from aged individuals in years 2005 and 2012.

Date	***n***	**Growth rate (mmd^{-1})**	**Instantaneous growth rate (G, m^{-1})**
27.6.2005	54	0.1-0.41	0.00735-0.024
4.7.2012	59	0.13-0.69	0.0095-0.033
17.8.2005	40	0.47-0.85	0.02-0.31
20.8.2012	38	0.35-0.74	0.018-0.028

Table 3. Resutls from exponential growth models of juvenile plaice lengths against age for a) whole season, b) settlement period and c) emigration period between the years 2005 and 2012.

Parameters	**Estimate**	**SE**	***p*-value**
a)			
Intercept	2.16	0.051	< 0.0001
Age	0.028	0.0013	< 0.0001
Age:2012	-0.0005	0.0007	0.441
AIC: 1188.3			
b)			
Intercept	2.59	0.081	< 0.0001
Age	0.012	0.0024	< 0.0001
Age:2012	0.0043	0.001	< 0.0001
AIC: 634.42			
c)			
Intercept	2.72	0.104	< 0.0001
Age	0.021	0.002	< 0.0001
Age:2012	-0.0016	0.0006	< 0.01
AIC: 445.53			

Table 4. Summary of growth rates for settlement period (June/July) in comparison years.

Date	***n***	**SST 10d before capture**	**Growth 10 days before capture, mmd^{-1} (G, m^{-1})**	**Mean growth 10 days b capture mmd^{-1} (G, m^{-1})**	**Length-at-age growth, mmd^{-1} (G, m^{-1})**	**Mean growth length-at-age mmd^{-1} (G, m^{-1})**
27.6.2005	18	11.21	0.42-0.62 (0.026-0.037)	0.52 (0.0312)	0.1-0.41 (0.00735-0.024)	0.24 (0.015)
4.7.2012	19	12.86	0.36-0.57 (0.02-0.03)	0.48 (0.0256)	0.13-0.69 (0.0095-0.033)	0.32 (0.018)

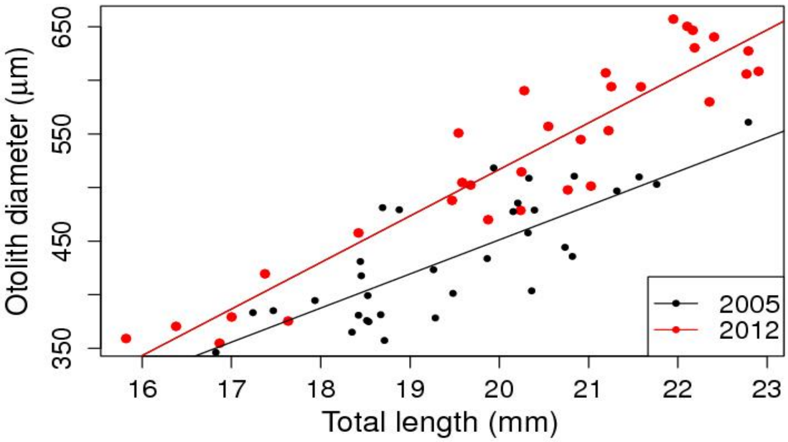

Otolith diameter (µm)
350
450
550
650
16
17
18
19
20
21
22
23
Total length (mm)
2005
2012

Figure 1

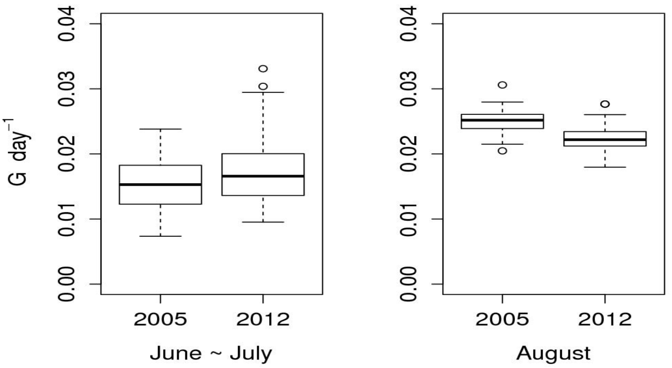

G day^{-1}
0.00
0.01
0.02
0.03
0.04
2005
2012
June ~ July
0.00
0.01
0.02
0.03
0.04
2005
2012
August

Figure 2

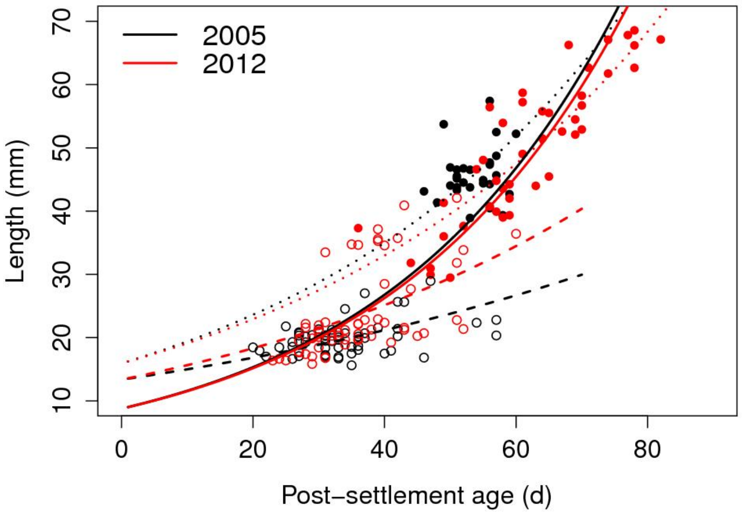
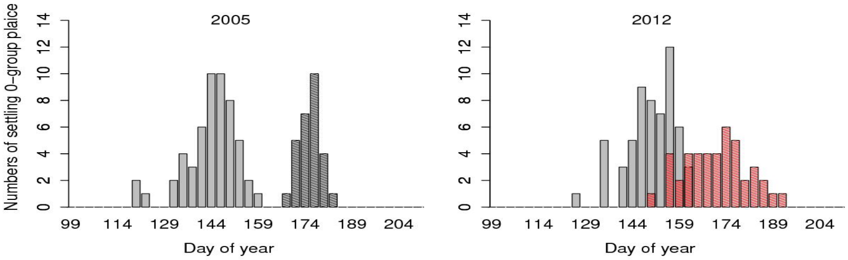

2005
2012
Length (mm)
10
20
30
40
50
60
70
0
20
40
60
80
Post−settlement age (d)

Figure 3


2005
2012
Numbers of settling 0−group plaice
0
2
4
6
8
10
12
14
99
114
129
144
159
174
189
204
Day of year

585

Figure 4

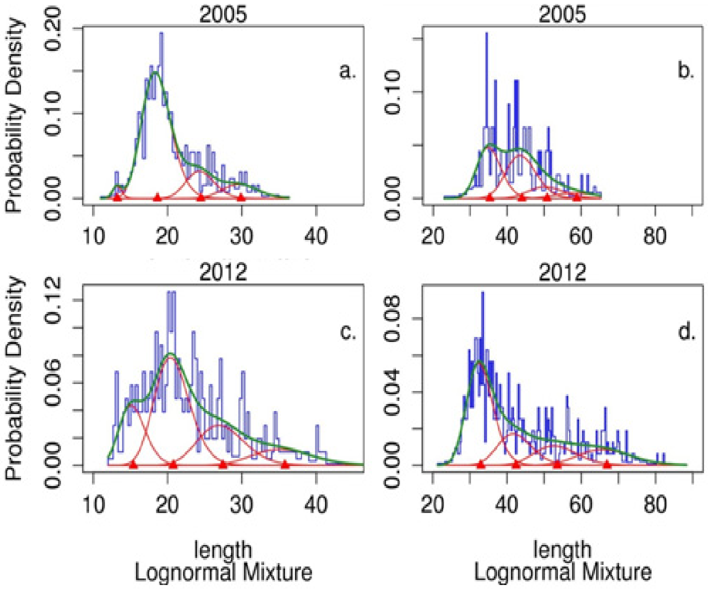

2005
a.
Probability Density
0.00
0.10
0.20
10
20
30
40
2005
b.
0.00
0.10
20
40
60
80
2012
c.
Probability Density
0.00
0.06
0.12
10
20
30
40
length
Lognormal Mixture
2012
d.
0.00
0.04
0.08
20
40
60
80
length
Lognormal Mixture

Figure 5

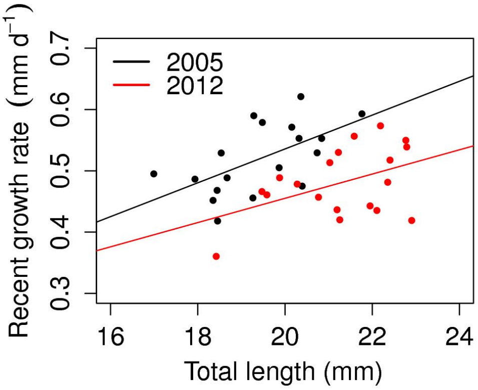

Recent growth rate (mm d^{-1})
0.3
0.4
0.5
0.6
0.7
2005
2012
16
18
20
22
24
Total length (mm)

Figure 6

Paper IV

Establishment of brown shrimp (*Crangon crangon*) in a newly colonized area

Ingibjörg G. Jónsdóttir, Jónas Páll Jónasson, Svavar Ö. Guðmundsson, Helena Puro, Guðrún Marteinsdóttir and Björn Gunnarsson

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BRILL

Crustaceana 89 (8) 901-914

CRUSTACEANA

ESTABLISHMENT OF BROWN SHRIMP (*CRANGON CRANGON*) IN A NEWLY COLONIZED AREA

BY

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ABSTRACT

The brown shrimp (*Crangon crangon*) is widely distributed in the coastal areas of the eastern Atlantic, but was only recently found in Icelandic waters. In this study, annual and seasonal changes in population abundance of brown shrimp southwest of Iceland were recorded from 2005 to 2014 in order to see whether the species has established itself in Icelandic waters. In general, the population grew in the beginning of the study period and seems to have somewhat stabilized in the past few years. The average density of shrimps each month rarely exceeded 200 individuals per 100 m^2. The number of juveniles increased in July/August and again in February, indicating bi-annual spawning. The relative abundance of adults was significantly affected by both the number of juveniles of the previous summer and the sea surface temperature. Brown shrimp seem to have rapidly adapted to Icelandic waters and have become established and are highly successful in the newly colonized area.

RÉSUMÉ

La crevette grise (*Crangon crangon*) est largement distribuée dans les zones côtières de l'Atlantique Est, mais a été seulement récemment trouvée dans les eaux islandaises. Dans cette étude, les changements annuels et saisonniers de l'abondance des populations de la crevette grise dans le sud-ouest de l'Islande ont été recensés de 2005 à 2014 afin de voir si l'espèce s'est établie dans les eaux islandaises. De façon générale, la population a augmenté au début de la période étudiée et semble s'être stabilisée ces dernières années. La densité moyenne de crevettes chaque mois excède rarement 200 individus pour 100 m^2. Le nombre de juvéniles a augmenté en juillet/aout ainsi qu'en février, indiquant une ponte bisannuelle. L'abondance relative des adultes a été significativement affectée par, à la fois, le nombre de juvéniles de l'été précédent et la température de surface de la mer. La crevette grise semble s'être rapidement adaptée aux eaux islandaises, elle s'est établie et a colonisé avec succès cette nouvelle zone.

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INTRODUCTION

Biological invasions frequently follow human induced introduction of new species (Carlton, 1989; Carlton & Geller, 1993; Streftaris et al., 2005). Currently, increasing numbers of marine species are transported between global regions with increased marine traffic (Carlton & Geller, 1993; Bax et al., 2003). Due to lack of suitable habitats, new colonizing species are not always successful in the new areas and hence, only a small fraction of the species is able to survive and successfully reproduce (Mack et al., 2000). However, introductions of new species that establish a population in the new regions have increased considerably in recent decades (Streftaris et al., 2005). Regarding their harmful impacts, the study of the establishment of invasive species are especially significant and devotion to the issue has increased in the past decades (Davis, 2009).

The brown shrimp, *Crangon crangon* (L., 1758) is widely distributed in the coastal areas of the eastern Atlantic (Oh & Hartnoll, 2004); the distribution extends from the White Sea and northern Norway, the Baltic Sea in the north to the Atlantic coast of Morocco, including the Mediterranean and the Black Sea in the south (Tiews, 1970; Campos & van der Veer, 2008). This is one of the most widely distributed species along the European coast with high abundance (Henderson & Holmes, 1987; Beukema, 1992; Del Norte-Campos & Temming, 1998; Temming & Damm, 2002). It inhabits eulittoral and sublittoral soft-bottom habitats of temperate waters, commonly in large numbers (Henderson & Holmes, 1987). In these habitats, the brown shrimp is of great importance as prey for fish and invertebrate species (Tiews, 1975), and as significant predator (Pihl & Rosenberg, 1984; Oh et al., 2001). It sustains a very important traditional fishery in the North Sea (Temming & Damm, 2002).

Brown shrimp was first detected in Icelandic waters in 2003 and has rapidly spread out to the northwest. It was thought to originate from colonization that occurred between 2001 and 2003 (Gunnarsson et al., 2007). Most likely, it was accidentally introduced by ballast water since the planktonic larvae is too short lived to reach Iceland with currents (Gunnarsson et al., 2007). In 2006, it was found at various locations from the southeast to the northwest of Iceland (Gunnarsson et al., 2007), but it has continued its invasion and is now found in more northern areas than ever before (Koberstein, 2013). Its establishment has, however, not yet been confirmed by long term monitoring.

The recent settlement of brown shrimp in Icelandic waters generated an unique opportunity to study the evolution of population dynamics of a newly established species. In this area no commercial fishing exists on brown shrimp and as a result, all changes in the population are by natural causes. The main objective of this study was to investigate whether brown shrimp has established in Icelandic waters.

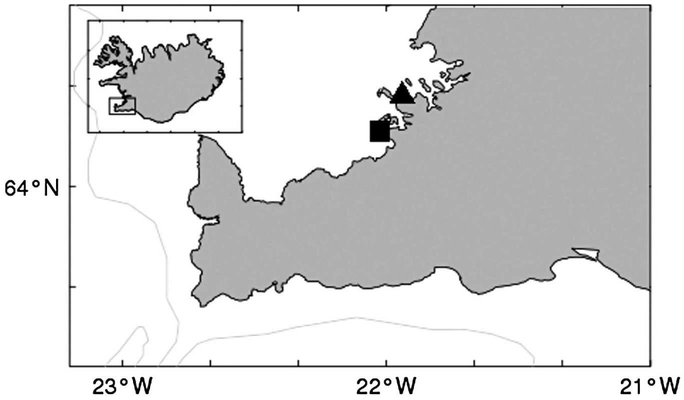

Fig. 1. Sampling location of brown shrimp, *Crangon crangon* (L., 1758), at Helguvík Bay (■) and temperature in Reykjavik harbour (▲). Depth contours at 100 and 200 m.

Specifically, this comprises estimation and description of annual and seasonal changes in population abundance of brown shrimp southwest of Iceland based on samples collected over a period of 10 years, from 2005 to 2014.

MATERIAL AND METHODS

Sampling site

Brown shrimp, *Crangon crangon*, were sampled at the beach in Helguvík Bay (64°09′78″N 22°03′35″W), southwest of Iceland, from May to September in 2005 to 2014 and during the winter months in 2009/2010 (fig. 1). Samples were taken twice a month in summer months May-September and once a month during winter months (October-April) with a 1 m wide, 0.2 m height, and 5.5 m long beam trawl. Mesh size was 5.5 mm in the cod end and 8 mm in the main body. Three tows parallel to the beach were taken during the low tide at 0.5-1 m depth by towing the trawl by two persons in south-north direction in first and third tow and north-south in second tow. Average towing speed was 35 m/min and it was aimed to be kept as constant as possible.

Shrimp measurements

All samples were stored in plastic buckets and sorted within few hours in the laboratory. From every tow all brown shrimps were counted and measured to nearest 0.01 mm (TL) between the anterior tip of the carapace (rostum) and tip of the telson using a sliding calliper. If catch numbers were greater than 120, the first

100 individuals were measured. Thereafter, the samples were fixed in formalin for at least 48 h, after which they were transferred to ethanol for storage. Sexes were determined for samples collected in summer 2008 and from August 2009 to July 2010. The sex was determined under a stereo microscope by looking at external sexual characteristics, i.e., the two first pairs of pleopods and their endopodites, according to descriptions by Lloyd & Yonge (1947) and Schatte & Saborowski (2006). Shrimps < 20.00 mm were treated as juveniles and sex was not defined because endopodites in the first pair of pleopods are equal-sized and difficult to separate (Lloyd & Yonge, 1947).

Temperature

Data on sea surface temperature (SST) were obtained from continuous thermometer located in the nearby Reykjavík harbour (64°07′40″N 21°57′04″W), which is less than 7 km away from Helguvík Bay. Monthly values of SST where constructed from the average daily SST for the years 2005-2014.

Data analysis

Density (individuals per 100 m^2, D) was calculated per each individual tow, and mean density for every month according to

$$D = \frac{C/T}{W} \times 100$$

where C is the total catch of shrimp, T is the tow length and W is the width of the trawl (1 m). No corrections where made for gear efficiency.

For each year, the length frequency was weighted with the total number of brown shrimp, estimated as

$$N = \frac{\bar{x}}{(W \times l)}$$

where N is the total number of brown shrimp, $\bar{x}$ is the average number per station, W the trawl width (m) and l the tow length. The data were smoothed with a generalized additive model (GAM) using a cubic B-line smoother with 10 degrees of freedom (Venables & Ripley, 1997). The GAM model was used as implemented in the *gam* package in R (Hastie & Tibshirani, 1990).

The sex ratio was estimated as the quotient between the number of females and the total number of females and males, excluding the juveniles. Thus, sex ratio values higher or lower than 0.5 indicate skews toward females or males, respectively.

Females were classified as mature or not based on the presence of attached eggs. Logistic regression was used to estimate the ogive of female maturity. Model fitting was carried out using the *glm* function in R (RCoreTeam, 2014) with the logit link function to the equation

$$p = \frac{1}{1 + \mathrm{e}^{-k(\mathrm{TL}-L_{50})}}$$

where p is the estimated proportion of shrimps in ovigerous stage, TL is the total length in mm, k is the coefficient and L_{50} is the length at which 50% of the female shrimp stock has attained sexual maturity.

Multiple regression was used to analyse the effects of SST in spring (May-June) and abundance of juvenile shrimp in the previous summer on the maximum average number of adult shrimp in early summer (Day of Year < 185). The dependent variable and abundance of juvenile shrimp were log-transformed to attain normality. The model was expressed as

$$A = \beta_0 + \beta_1 \times J + \beta_2 \times T + e$$

where A is the abundance of adults, J is the abundance of juveniles in the previous year and T the average temperature.

RESULTS

Population density

In total 14 943 individuals of *Crangon crangon* were measured or counted (table I). In general, the brown shrimp population fluctuated over the study period. In 2005 and 2006, the average density was less than 100 shrimps per 100 m^2 (fig. 2). Since 2008 the density often varied between 110 and 260 shrimps per

TABLE I
Information on sampling of brown shrimp, *Crangon crangon* (L., 1758), from 2005 to 2014

Year	Months	Number of tows	Total number of individuals
2005	May-September	18	870
2006	May-September	24	767
2007	May-October	26	1278
2008	May-September	24	3009
2009	May-December	33	2572
2010	January-October	41	2849
2011	June-August	21	1124
2012	June-September	21	1237
2013	June-September	18	393
2014	June-August	15	845

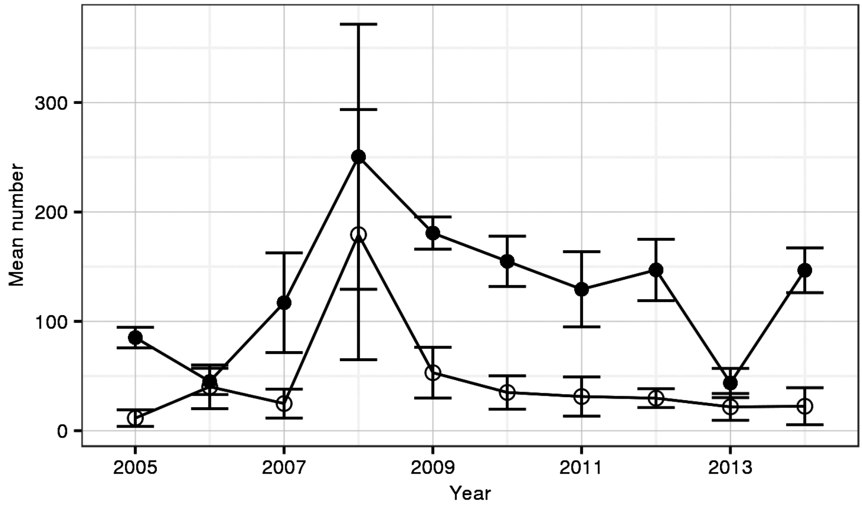

Fig. 2. Annual mean population density (±SE) of brown shrimp, *Crangon crangon* (L., 1758), from 2005 to 2014. Filled symbols indicate adults (TL > 19.99 mm) and open symbols refer to juveniles (TL < 20.00 mm).

100 m^2, except in 2013 when the density was 45 shrimps per 100 m^2. In August 2008, the density was very high (fig. 3), when a high number of young brown shrimp entered into the stock.

The density of juveniles was always low during the spring and early summer (fig. 3). However, every year in July the number of juvenile brown shrimp increased, indicating the income of juveniles at that time of the year (fig. 3). In the only year when samples were taken during winter time (2010), the number of juvenile brown shrimp was also slightly higher in February, indicating bi-annual spawning.

As indicated by the intra-annual fluctuations in densities (fig. 3), the proportion of juveniles showed two peaks, indicating that brown shrimp spawned twice a year (fig. 4). Juveniles originating from the winter brood entered the population in July 2008 and were found in high abundance in August 2009 (fig. 3). In January 2010, the proportion of juveniles increased again, with a peak in February, when the juveniles from the summer brood entered the population (fig. 3). The proportion of males decreased during the time of juvenile peaks.

The total length of brown shrimp ranged between 7.9 and 62.8 mm. The first samples each year were collected in mid-May and at that time juvenile brown shrimps were seldom found. However, in mid-September, when the last samples were usually collected, the majority of the brown shrimp were juveniles.

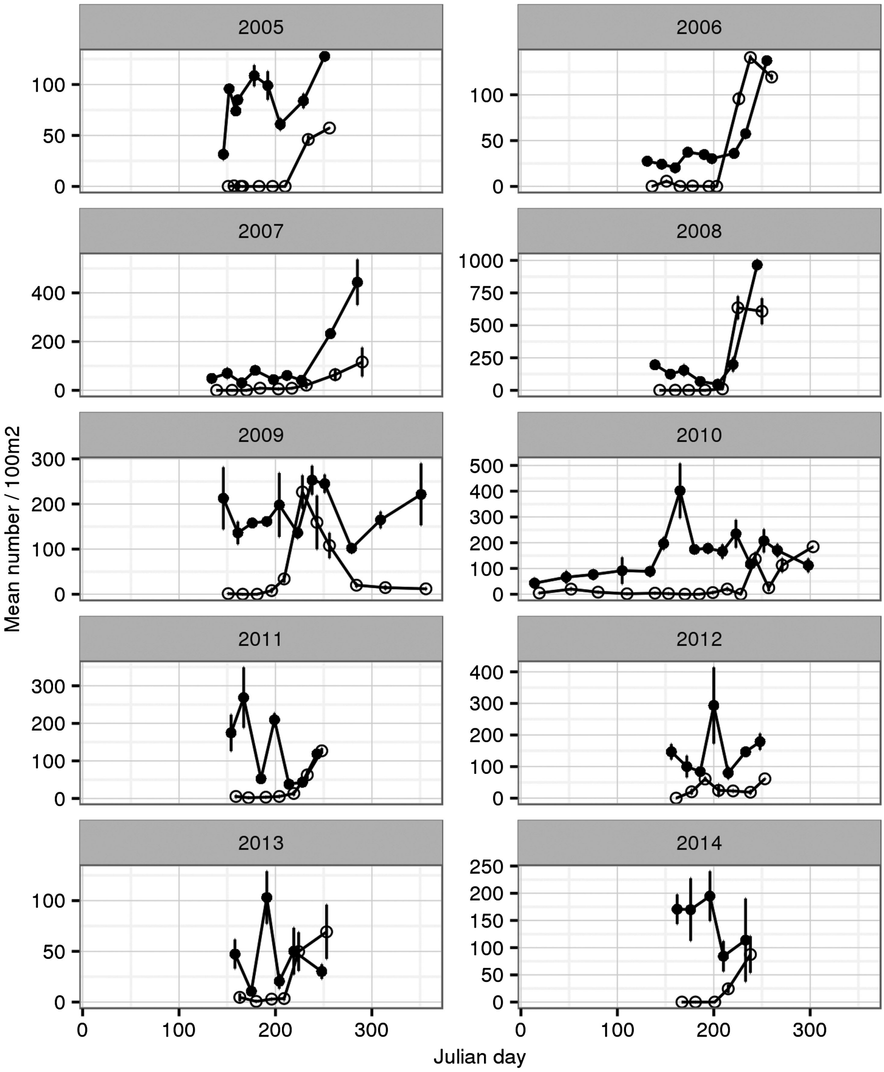

Fig. 3. Population density (mean number per 100 m^2 ± SE) of brown shrimp, *Crangon crangon* (L., 1758), from 2005 to 2014. Filled symbols indicate adults (TL > 19.99 mm) and open symbols refer to juveniles (TL < 20.00 mm).

Temperature

The average SST showed clear seasonal trend, with fluctuations from 1.5 to 13°C. The temperature was lowest in January-March, when it ranged between 1.4 and 3.9°C (fig. 5). In April, the average sea temperature started to increase until

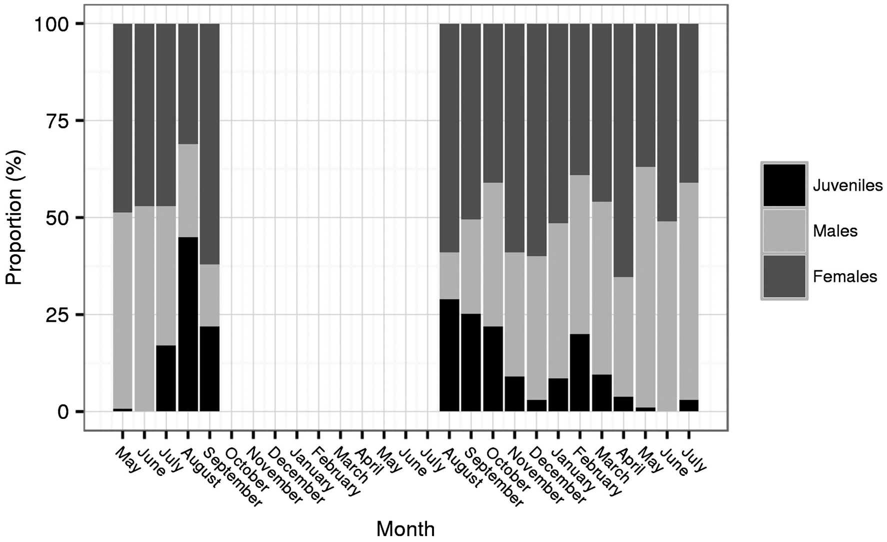

Fig. 4. The proportion of juveniles, males and females of the brown shimp, *Crangon crangon* (L., 1758), from May 2008 to July 2010. No sample was collected from October 2008 to July 2009.

it reached its highest levels in July and August, when it ranged between 10.4 and 13.2°C (fig. 5). Slight inter-annual temperature variation was also observed, where the difference between the highest and lowest average temperatures were 1.4-3.1°C. The temperature in December 2007 was the highest temperature observed in that month during the study period.

The relative abundance of adult brown shrimp was significantly affected by the number of juvenile brown shrimp of previous summer and the SST (table II). Both factors had a positive effect on the numbers of adults caught. The temperature contributed greater than juvenile abundance to the regression sums of squares (table II). Overall, the multiple regression explained 61% of the variation in adult abundance. However, due to low sample size in terms of years, the results need to be interpreted with caution.

Sex ratio

In total, sex was determined for 1060 individuals sampled in 2009 and 2010. The size-specific sex ratio was calculated for all individuals combined, regarding the year. The sex ratio was not linearly related with length. Higher proportions of small brown shrimps were females (fig. 6). The proportion of females decreased from 20 to 35 mm total length, where the proportion of females was lowest at 0.32. From 36 to 51 mm, the proportion of females increased again and individuals larger than 50 mm were exclusively females (fig. 6).

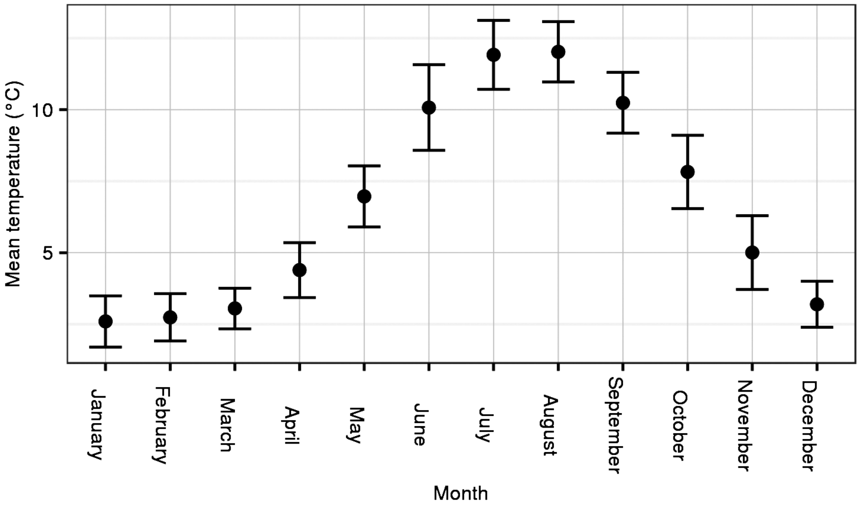

Fig. 5. Average monthly mean temperature (±SE) from 2005 to 2014 in Reykjavík harbour.

Length at female sexual maturity

The length at 50% female sexual maturity (L_{50}) was estimated using 811 egg-bearing females from 2008 to 2010. The data points were scarce for the larger individuals and combined for all years there were less than 10 individuals per mm bin for females of 34 mm and larger. With the exception of one individual at 29 mm, the onset of female maturity occurred at 36 mm (fig. 7). Thereafter, the proportion of mature females increased with female length. The overall estimated length at 50% sexual maturity (L_{50}) ± SE was 48.16 ± 0.779 mm (fig. 7). There was some annual variability in L_{50} but due to few data points for the larger individuals, the model fit was poor.

TABLE II
Analysis of variance of relative abundance, ln of maximum number of adult brown shrimp, *Crangon crangon* (L., 1758) (before Day of Year 185), 2006-2014, examining the main effects

	df	Sum of squares	Mean square	*F*	*P*-value
Juvenile shrimp	1	1.741	1.741	6.827	0.040
Sea surface temperature in spring	1	1.972	1.972	7.735	0.032
Residual error	6	1.53	0.225		

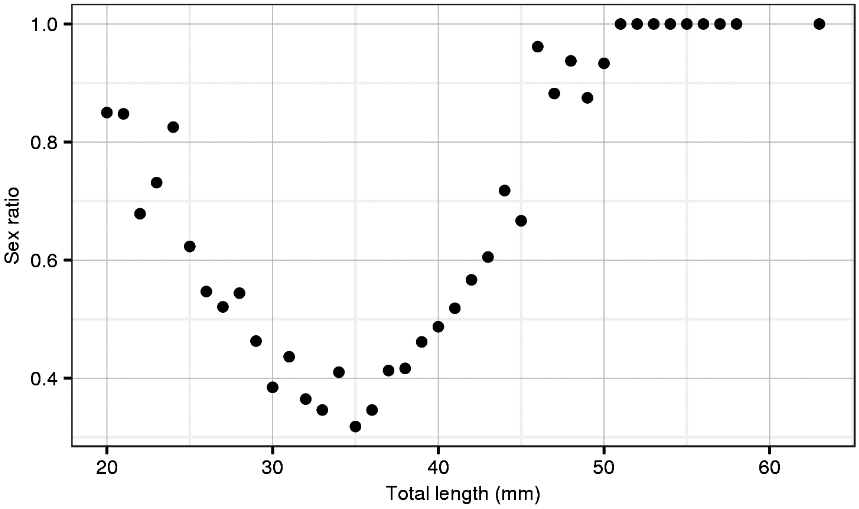

Fig. 6. The proportion of females of brown shrimp, *Crangon crangon* (L., 1758), at different lengths.

DISCUSSION

Only a small fraction of species that are transported over the globe, either by accident or intentionally, are able to successfully reproduce and form a new population in the newly colonized area (Mack et al., 2000). The conditions for the newly established population of brown shrimp, *Crangon crangon*, in Icelandic

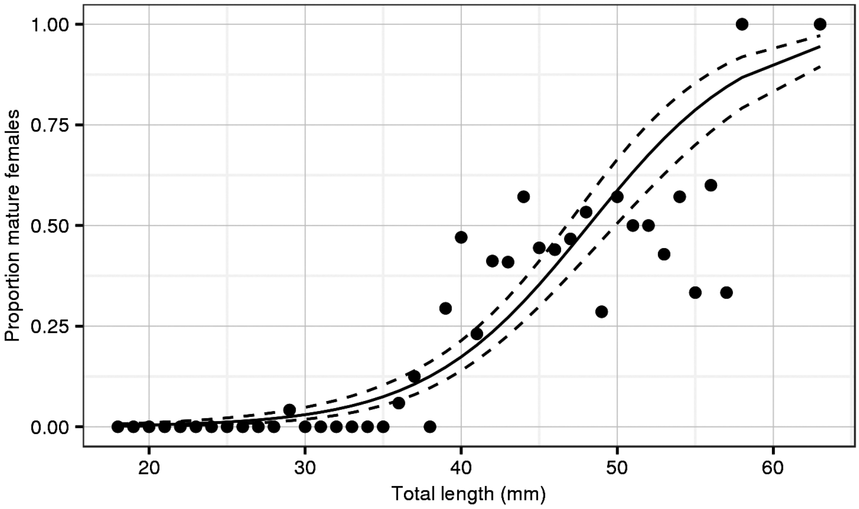

Fig. 7. The sex ratio of brown shrimp, *Crangon crangon* (L., 1758), in relation to total length (mm).

waters seem to be fairly good, as the results of this study showed that the population in this specific location reproduced successfully and the population grew in the beginning and during the 10 years studied, the population seems to have somewhat stabilized. It is therefore confirmed that brown shrimp has established in Icelandic waters.

Only a few years after settlement, there were indications of two discrete peaks of brown shrimp in August and February. Some latitudinal variation may be seen in the breeding season of brown shrimp (Oh & Hartnoll, 2004; Campos et al., 2009) and the juvenile peaks in the present study were one to two months later than observed in the North Sea (Temming & Damm, 2002). The number of juveniles was higher for the winter brood, which is generally considered to be the main brood with higher reproductive output values and bigger eggs (Boddeke, 1982; Oh & Hartnoll, 2004). The results of the present study indicate that the abundance of juveniles had a positive effect on the population size in the following year. Abundance of brown shrimp was also influenced by temperature. Temperature during the winter may be too low to sustain large summer broods, but low winter temperatures may potentially cause a retarded egg development (Siegel et al., 2005). In the present study, the timing of the juvenile peak from the winter brood varied slightly between years. As such, juvenile abundance in late summer varied by approximately one month and the peaks were observed in July or August. Abundance of juveniles can also be affected by weather conditions and a juvenile peak may be delayed by weeks after cold winters (Temming & Damm, 2002).

In light of the occurrence of brown shrimp in east Atlantic Arctic waters, it is interesting that successful colonization has not occurred before in Icelandic waters. In fact, the brown shrimp was first mentioned to have occurred in Icelandic waters in 1895 (Doflein, 1900), which was the first and only record until 2003. During the first decades of the twentieth century samples were collected by the ichthyologist and natural scientist biologist Bjarni Sæmundsson. After a re-examination of some of those samples, no brown shrimp was found (co-author B. Gunnarsson). However, a number of the closely related species *Crangon allmanni* Kinahan, 1860 was found. Furthermore, in routine sampling in shallow waters on tidal flats 15 km northeast of our sampling site from 1971 to 2006, another biologist never came across a specimen of *C. crangon* until spring 2004 while he, as well, found *C. allmanni* (cf. Gunnarsson et al., 2007). Therefore, rather than disappearing from Icelandic waters as suggested by Campos & van der Veer (2008), it is highly likely that the observation from 1895 was misidentified as *C. crangon*, as it may be hard to distinguish between these two species. Increasing sea temperature in the past years (Jonsson & Valdimarsson, 2012) is an unlikely reason for the invasion as the temperature in southern Iceland was within the temperature range observed in other geographical areas where brown shrimp is abundant (Campos & van der

Veer, 2008). More likely, the brown shrimp was accidentally introduced to Iceland by ballast water since the planktonic larvae is too short lived to reach Iceland with currents (Gunnarsson et al., 2007).

The observed size at sexual maturity of females in the present study was lower than in the brown shrimp populations in the North and Irish Seas but higher than observed in Norway (Lloyd & Yonge, 1947). Size at maturity is a highly plastic parameter that is influenced by many factors including temperature, population abundance, locality and seasons (Lloyd & Yonge, 1947; Wootton, 1998; Siegel et al., 2008). As brown shrimp is not under any fishing pressure in our study area, only natural fluctuations can be responsible for changes in size at maturity. However, only females that are clearly mature, like egg-carrying females or females with attached eggs in setae, were used. This may have biased the determination of the length at maturity as eggs are not laid immediately after copulation among larger shrimps and they are mature before eggs are visible. Gonadal examination would give more detailed information about sexual maturity.

The ecological impact of the colonization of brown shrimp in Iceland has not been estimated. However, invasive species are often characteristically more able to rapidly and efficiently utilise resources than native species (Dick et al., 2013; Alexander et al., 2014), and invasion of new species into an area usually affects the native species (Bax et al., 2003). The brown shrimp seems to have rapidly adapted to the Icelandic waters and has become established and highly successful in the new colonized area. The diet of a predator such as brown shrimp is determined by the composition of the benthic community and the abundance of available prey, both of which are strongly correlated with substrate type (Ansell et al., 1999). Due to its abundance, predation pressure by brown shrimp may have a significant impact on prey population dynamics. This may be of particular concern in the case of young plaice (*Pleuronectes platessa* Linnaeus, 1758) (cf. Oh et al., 1999). However, brown shrimp plays a trophic key role in the coastal marine food web, facilitating the transfer of energy between the benthic and the pelagic habitat (Pihl & Rosenberg, 1982, 1984; Evans, 1984), and may, therefore, in the long term, have an overall positive effect on the growth of different fish species.

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Paper V

Collapse of the fishery for Iceland scallop (*Chlamys islandica*) in Breidafjordur, West Iceland

Jónas Páll Jónasson, Guðrún Þórarinsdóttir, Hrafnkell Eiríksson, Jón Sólmundsson and Guðrún Marteinsdóttir, 2007

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Author contribution: Conceived and designed the experiments: JPJ, GÞ & GM. Performed the experiments: HE & JS. Analysed the data: JPJ. Wrote the paper: JPJ, GÞ, HE, JS & GM.

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Jonasson, J. P., Thorarinsdottir, G., Eiriksson, H., Solmundsson, J., and Marteinsdottir, G. 2007. Collapse of the fishery for Iceland scallop (*Chlamys islandica*) in Breidafjordur, West Iceland. – ICES Journal of Marine Science, 64: 298–308.

The stock index of the Iceland scallop (*Chlamys islandica*) in Breidafjordur on the west coast of Iceland has declined drastically in recent years. Total fishing mortality was very high throughout the study period from 1993 to 2003, a period characterized by a steady increase in summer sea surface temperature, in 2003 reaching the highest estimated level of the previous century. Between 1998 and 2005, estimates of chlorophyll *a* (food availability) fluctuated with periods of low chlorophyll followed by a reduction in muscle weight and high natural mortality. High levels of natural mortality were observed in the main fishing area in the southern part of Breidafjordur. There the stock index had been declining since 1994. Recruitment to the fishable stock was highly variable during the study period, with low recruitment towards the end of the 1990s. Subsequently the fishery has been on relatively few year classes, and the stock has been fragile because of several years of poor recruitment and high natural mortality. Consequently, the stock appeared unable to withstand the fishing pressure and declined to historically low levels, leading to a halt to fishing in 2004.

Keywords: *Chlamys islandica*, fishery collapse, Iceland scallop, mortality, recruitment, temperature.

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Introduction

Population fluctuations have long been recognized as common phenomena of both marine and terrestrial animals (Elton, 1924). In scallop stocks, population size can be influenced by numerous factors, including variability in recruitment and catastrophic mortality from various sources (Orensanz *et al.*, 1991). Fish and shellfish stocks have been classified into steady, cyclical, irregular, and spasmodic stocks according to their pattern of fluctuation (Caddy and Gulland, 1983).

The Iceland scallop (*Chlamys islandica*) is distributed within the Subarctic transitional zone at maximum sea temperatures of 12–15°C (Sundet, 1988; Hovgaard *et al.*, 2001) and at depths <100 m (Wiborg, 1963). It is relatively long-lived with a maximum observed age of at least 23 y (Vahl, 1981). Long-lived Arctic and boreal scallops, such as the Iceland scallop, may fall into the steady stock group (Orensanz *et al.*, 1991), but fluctuations in populations of Iceland scallop caused by changes in temperature and/or salinity (Wiborg, 1963), predation (Brun, 1968), and heavy fishing have been observed at several locations in the North Atlantic (Hovgaard *et al.*, 2001).

In Iceland, the Iceland scallop has been fished since 1969 (Eiriksson, 1997). Population size decreased in all major subpopulations in Icelandic waters towards the end of the 1990s. Stock biomass indices for small scallop stocks in the northwest decreased by 45–80%, and the greatest decline was in the area where fishing was minimal (Marine Research Institute, MRI, Reykjavík, unpublished data). The stock size index of the largest scallop population in Iceland, in Breidafjordur, declined by 70% during the period 2000–2003. Landings (total weight) there peaked at 12 700 t in 1986, decreased slightly in the following years, then remained relatively stable at 8000–9000 t during most of the 1990s. Then, between 2000 and 2003, the stock collapsed and annual landings decreased from 8600 to 800 t. As a result, fishing was stopped in 2004 (Anon., 2005).

The objective of the current study was to look for possible causes for the dramatic decline in the stock of Breidafjordur Iceland scallop between 1999 and 2003. Data from stock surveys, specific sampling, and fishery logbooks were explored in order to analyse stock biomass, natural and fishing mortality, recruitment, and muscle condition. Available environmental data (chlorophyll and temperature) were also analysed and are discussed in relation to the observed changes in the stock.

Material and methods

Survey data

Data were collected during the annual scallop surveys conducted by the MRI in the inner part of Breidafjordur, West Iceland, in March/April of the years 1993–2003 (Figure 1). On each survey, some 120 fixed standardized tows were taken. From 1993 to 1997, a 470 kg sledge dredge 1.5 m wide was used. In 1998, this was substituted with a 835 kg roller dredge 1.2 m wide (Garcia *et al.*, 2006). Both dredges were equipped with 60 mm steel rings. Earlier experiments on the sledge dredge had revealed that its efficiency was 20% (i.e. $e = 0.2$).

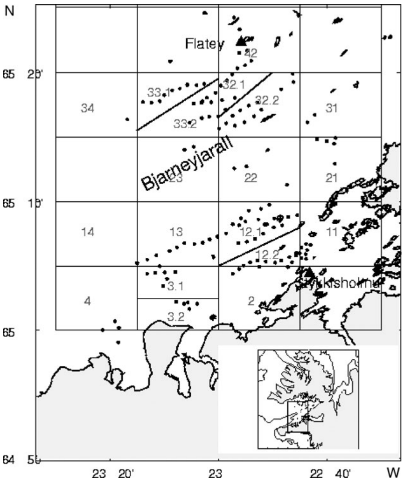

Figure 1. The study area in Breidafjordur, West Iceland. Each square containing a subarea is labelled. Squares on the main scallop grounds are divided into two subareas. Survey stations are marked with dots. Stations used for temperature recordings (Flatey and Stykkisholmur) are marked with triangles.

Comparative experiments between the roller and sledge dredge showed that the catch of scallops in roller dredge tows was on average 30% higher than in sledge tows, so e for the roller dredge was set at 0.26 ($n = 46$, MRI, unpublished data). Here, instead of using the average difference between the dredges, a single parameter regression was forced through the origin ($r = 0.94$). The regression had a slope of 0.70, corresponding to a fresh estimate for e of 0.285.

Each survey tow covered approximately 0.4 nautical miles and the tow speed was 4 knots. For the analysis, all tow lengths were standardized to 0.4 nautical miles. For each tow the total catch was weighed and a random subsample of approximately 25 kg taken. In each subsample, all live scallops were weighed and the height of about 100 was recorded. The remaining scallops were counted and the numbers of cluckers (dead scallops attached on their hinges, both damaged and whole shells) were noted.

The survey area was divided into subareas, based on a grid of squares of equal size. Squares positioned on the main scallop grounds were split into two subareas (Figure 1). The total region fished was divided into a northern area (subareas 31–42), north of Bjarneyjarall (a trench bisecting the fjord from west to east), and a southern area (subareas 2–14), south of the trench. The size of the scallop beds in each subarea was based on estimates conducted at the beginning of the surveys in the early 1970s, where the total area was estimated to be 72 km^2.

Stock biomass indices were estimated from

$$B_y = \sum_{i=1}^{n} \frac{(\bar{x}_s * \alpha_s/(\mathrm{dw} * \mathrm{tl} * 1.852))}{e}, \qquad (1)$$

where B_y is the total biomass (t), n the number of subareas, $\bar{x}_s$ the average biomass per subarea, α_s the size of the scallop beds per subarea (km^2), dw the width of the dredge (m), tl the tow length (nautical miles), and e the dredge efficiency.

Fishery data

Catch per unit effort (cpue) (landings per hour fishing) within each subarea was based on logbook catch reports, which are mandatory in the fishery. The cpue data go back to 1972, but with precise information from around 1985.

Fishing mortality and natural mortality

Fishing mortality was calculated by two non-model methods for the four major subareas in the fishery (12.1 and 12.2 in the south, and 42 and 32.2 in the north):

(i) A Beverton and Holt length-based fishing mortality ($^{\mathrm{BH}}F$) (Quinn and Deriso, 1999) was calculated from

$$^{\mathrm{BH}}F_s = K\frac{L_\infty - \bar{L}_s}{\bar{L}_s - l_c} - M_s, \qquad (2)$$

where in each subarea s, K is a growth constant from the von Bertalanffy growth function (VBGF) (Ricker, 1975) [Equation (6)], L_∞ the asymptotic shell height (SH) from the VBGF, $\bar{L}_s$ the mean SH beyond l_c (here 60 mm), and M_s is the calculated natural mortality [Equation (4)].

(ii) Equilibrium fishing mortality (^{Y}F) (Quinn and Deriso, 1999) was calculated from

$$^{Y}F_s = \frac{Y\tau_s}{B_s}, \qquad (3)$$

where in each subarea s, Y is the landings of scallops (t) for a 1-y period ($\tau = 1$) and B is the estimated biomass [Equation (1)] in tonnes at the beginning of the period. The method does not consider indirect fishing mortality (non-yield) from fishing gear.

Natural mortality was based on the occurrence of cluckers in survey tows (Dickie, 1955):

$$a = 1 - \mathrm{e}^{-(C/t)(1/L)365}, \qquad (4)$$

where a is the yearly ratio of natural death, C the number of cluckers, t the average time in days required for the shells of the cluckers to separate (211 d) (Jonasson, 2005), and L is the number of live scallops in the sample. The exponent is equal to the instantaneous mortality rate. The number of cluckers was adjusted for the numbers of scallop that disarticulate during the tow, by multiplying the number of cluckers in the sample by 1.211 (Naidu, 1988).

The geographical distribution of abundance and natural mortality of scallops from the surveys was plotted for the years 1994 and 2001–2003. In the plots of natural mortality, stations with <5 kg of scallops or where fewer than five scallops were measured were excluded. Data were interpolated spatially using a kriging method (Kaluzny *et al.*, 1998).

Environmental and biological data

Owing to the lack of a complete sea surface temperature (SST) data series for Breidafjordur, SST was estimated on the basis of the relationship of SST at Flatey (an island in the middle of Breidafjordur) and the air temperature at Stykkisholmur (Figure 1). All available monthly mean SST data from Flatey (May–August of 1990–2001; $n = 35$) were used (Jonasson *et al.*, 2004; $r^2 = 0.942$, $p < 0.001$).

Estimates of chlorophyll *a* (Chl *a*) in Breidafjordur were derived from the NASA SeaWiFS project. The information consisted of Level 3 data, which are statistical data products derived by mapping Level 2 GAC data to a fixed global grid whose resolution elements are approximately 9 × 9 km (Campbell *et al.*, 1995). In all, 50 monthly mean values were obtained from the region bounded by 65°02′–65°29′N and 22°41′–23°38′W. Mean values from March to September were calculated for each year of the period 1998–2005.

Measurements of adductor muscle wet weight were initiated in autumn 2000 when processing plants first experienced low meat yields. For those measurements, scallops were sampled from 65°17′5 N 22°52′5W in subarea 32.2 and from 65°05′3 N 22°42′7W in subarea 11 (Figure 1). Sampling was during the months September–December of 2000–2005. Muscle wet weight (W) of scallop was fitted to shell height (SH) by the equation

$$W = a\mathrm{SH}^{\beta}, \tag{5}$$

where a and β are constants from a linear regression model of wet weight on SH after log-transformations of the variables.

Age determination and recruitment

Age was determined from shell height using Bhattacharya's method (Sparre and Venema, 1998). Graphs were used for visual identification of frequencies perceived to belong to one age group. General additive model (GAM)-smoothed data from 1993 to 2003 in subarea 12.1 (south) were used for this procedure. The VBGF (Ricker, 1975) was fitted to the mean shell height at age by linear regression (Crawley, 2002), also using data from subarea 12.1. The VBGF was formulated as

$$\mathrm{SH}_t = \mathrm{SH}_\infty[1 - \exp(-K(t - t_0))], \tag{6}$$

where SH_t is the shell height (mm) at age t (y), SH_∞ the asymptotic shell height (108.1), K the growth constant (0.139), and t_0 the intercept of the growth curve on the age axis. The VBGF fitted well the estimated mean age of the scallops (Figure 2).

For analysis of year-class strength, the divergences from the mean shell height frequency indices of 1993–2003 were calculated for subarea 12.1 (south), during the same period, based upon a common method (Sund, 1930). For each year, the height frequency was weighted with the total numbers of scallops, estimated as

$$N = \frac{\bar{x} * a/(\mathrm{dw} * \mathrm{tl} * 1.852)}{e}, \tag{7}$$

where N is the total number of scallops (in thousands), $\bar{x}$ the average number per station, a the size of the subarea (km^2), dw the dredge width (m), tl the tow length (nautical miles), and e the dredge efficiency. The data were smoothed with a GAM model using a cubic B-line smoother with 20 degrees of freedom (Venables and Ripley, 1997).

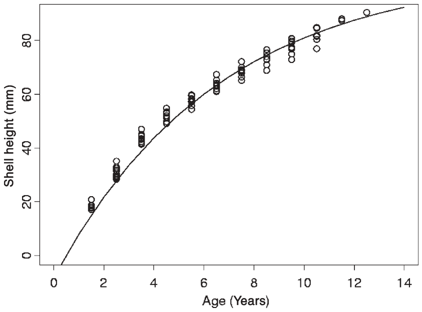

Figure 2. Shell height at age based on survey data from subarea 12.1 (south), 1993–2003, calculated using Bhattacharya's method, fitted with the VBGF.

Stock fluctuations in relation to biotic and abiotic factors

Multiple regression was used to analyse the effects of several biotic and abiotic factors on the number of harvestable scallops (≥60 mm) in all subareas for which data were available. The dependent variable was log-transformed to attain normality (Shapiro–Wilk normality test, $p = 0.7238$). The starting model included the log-transformed numbers of 45–60 mm scallop recruits 2 years earlier, the natural mortality determined from the surveys, the mean summer temperature of the previous year, the ${}^{Y}F$ for the preceding year, the ${}^{BH}F$ for the same year, and the effort of the previous year standardized by the number of harvestable scallops. Independent variables that did not contribute were removed by subtracting the least significant term in each step (Crawley, 2002).

All statistical analyses were performed using Version 6.0 S–PLUS software (MathSoft, 2001), except for Bhattacharya's method, which was performed with the Version 1.0 FISAT II statistical program (Gayanilo *et al.*, 2002).

Results

Stock size and the fishery

The stock index of Iceland scallop in Breidafjordur was relatively stable from 1993 to 1999, but it declined sharply from 2000 to 2003 (Figure 3). In 2003 (22 000 t), it was at a historically low level of some 30% of the average stock size during the 1990s.

The main trends in stock size differed between subareas (Figure 4). In subarea 12.1, the major fishing area in southern Breidafjordur, the stock index declined gradually from 1994. In subarea 32.2, the major fishing area in the northern part of Breidafjordur, the stock index fluctuated during the period 1993–2000, peaked in 1997, then steadily declined to a historical low in 2003 (Figure 5). In other subareas, stock size generally only declined (or was observed to do so) after 2000, although there was a steady decline in subareas 13 and 3.1 from 1993 and 1994, respectively.

Cpue, pooled for all areas in Breidafjordur, was relatively stable during the period 1986–1990, but it increased considerably from

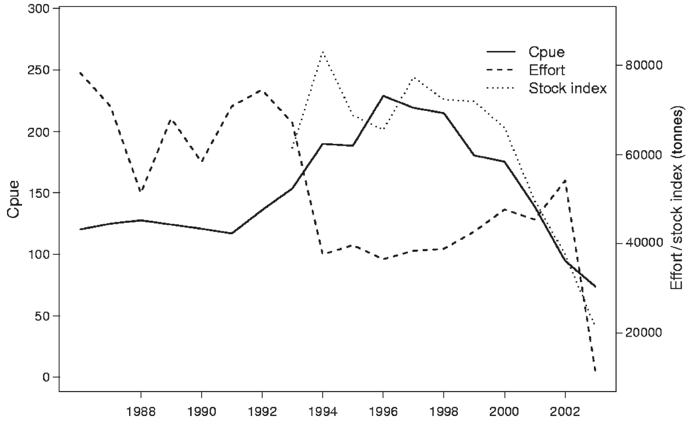

Figure 3. Cpue of Iceland scallop in Bredafjordur, 1986–2003 (kg of scallops per hour fishing/feet), effort (hours of fishing × dredge feet), and a stock index based on data from annual surveys conducted from 1993 to 2003.

1991 to 1996 (Figure 3). During the years 1996–1998, it was relatively high, but it then declined sharply from 1998 to 2003. The increase in cpue in the early 1990s coincided with changes in the scallop fishing gear, when the fleet changed from sledge dredges to the more efficient roller dredges.

Fishing effort was significantly higher during the period 1986–1993 than from 1994 to 1998, but it also increased again from 1999 to 2002, i.e. following an opposite trend to that in cpue (Figure 3). Throughout the period 1993–2000, the total allowable catch (TAC) was relatively stable at about 8000–8500 t (Anon., 2005). At that time, the recommended annual TAC was 10% of the total estimated biomass from stock surveys; since 1994, the national TAC and the landings have been in accord with the recommendations.

Fishing mortality and natural mortality

The estimates of the Beverton and Holt length-based fishing mortality (${}^{BH}F$) were relatively high in the main fishing areas between 1993 and 2003 (Figure 6). The estimates were stable in subarea 32.2 in the north, but in subarea 12.1 and 12.2 (south) and 42 (north), there was a slow but gradual decline in ${}^{BH}F$, followed by an increase in area 42 from 2001 and in area 12.1 from 2002. The equilibrium fishing mortality (${}^{Y}F$) was stable and substantially lower than ${}^{BH}F$ in all subareas (Figure 6).

The natural mortality observed on scallop grounds in Breidafjordur during the period 1993–2003 increased in most areas after 2000 (Figures 5 and 7). In general, natural mortality was high in subarea 12.1, increasing from 0.1 in 2001 to 0.4 in 2003. In other subareas in the south, the increase was not so clear, although there were years with natural mortality >0.15 in subareas 2 and 13. In the north, natural mortality was relatively low or approximately 0.05 from 1993 to 2000, then increased to 0.1 during the years 2001–2003.

Condition of Iceland scallop in relation to environmental parameters

The estimated mean SST at Flatey fluctuated periodically during the last century, with values above average in the years 1930–1950 and mainly below average from 1960 to 1990 (Figure 8). Mean SST then increased in 1990 and 1991, but declined again in 1992 and 1993. Since then, temperature has been gradually increasing towards a level similar to that of the 1930s; the maximum mean was >9°C in 2003 and 2004.

Estimates of mean summer Chl *a* data in Breidafjordur are available for 1998–2005 (Figure 9). The means fluctuated, with relatively low values in 1999 (1.73 mg m^{-3}) and 2005 (1.78 mg m^{-3}), and the highest measured value in summer 2003 (2.60 mg m^{-3}).

The fit of the relationship between scallop height and muscle wet weight was low, especially for the years 2001–2003, and muscle weight was not isometric with shell height in any year ($p < 0.001$). The number of scallops in poor condition increased from 2000 to 2002 on both northern and southern grounds, decreased in 2003, but increased again in 2004 and 2005 (Figure 9). Muscle weight during those years fluctuated in a manner similar to that of Chl *a*. Although not statistically significant, the correlation coefficients were 0.55 and 0.58 ($p = 0.26$ and 0.22, d.f. $= 4$) for northern and southern scallops, respectively.

Mean shell height and recruitment

In general, the average shell height of scallops in the surveys increased from 1993 to the end of the decade, but then declined (Figure 10). Maximum shell height in subareas 12.1 (71.2 mm) and 12.2 (69.8 mm) was in 1999. In subarea 32.2, shell height peaked in 2000 (69.5 mm), then declined slower than in other

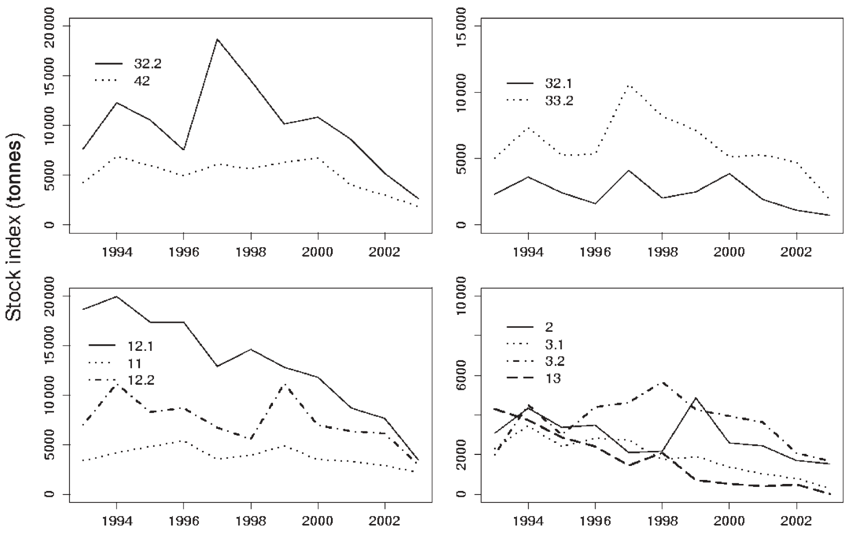

Figure 4. Stock indices in the major subareas of Breidafjordur based on data from the annual surveys conducted during the years 1993–2003. Northern areas are shown in the top two panels and southern areas in the bottom two panels. Note the different scale on the *y*-axis.

subareas. Maximum shell height in subarea 42 was in 2001 (69.1 mm).

Recruitment to the fishable stock (≥60 mm) was highly variable during the study period in subarea 12.1, with low recruitment towards the end of the 1990s (Figure 11). Similar fluctuations were observed in other subareas (Jonasson *et al.*, 2005). Relatively strong year classes entered the fishable stock between 1993 and 1996 (year classes 1987–1990), but then medium and weak year classes dominated until 2003. In 1993, the survey catch was dominated by shells of approximately 70 mm, i.e. mostly 7–9 years old, according to a length-based conversion (Figure 2), but 80 mm (10 years old) scallops were rare (Figure 11). The fishable stock then consisted, therefore, mainly of three year classes (1984–1986). During the period 1994–1996 the strong year classes of 1987–1990 grew and filled the gap observed around 80 mm in 1993. Medium or weak year classes from 1991 to 1992 appear to have entered the fishable stock in 1997 and 1998, and small year classes from 1994 and 1995 seem to have recruited to the fishable stock in 1999 and 2000. As a result, a gap in shell height from 60 to 70 mm was formed then. During 2001 and 2002, small year classes continued to enter the fishable stock, resulting in a scarcity of older age groups. In 2003, a year class from 1997 and a reasonably large year class from 1998 appear to have recruited.

Stock fluctuations in relation to biotic and abiotic factors

The relative abundance of harvestable scallops was significantly affected by the numbers of juvenile scallops (45–60 mm) 2 years earlier, ^{BH}F, standardized effort, and natural mortality (marginally). Juvenile abundance had a positive effect on the number of harvestable scallops, whereas other factors had negative effects. The number of juveniles contributed most to the regression sum of squares (Table 1). Overall, the multiple regression explained some 66% of the variation in stock size abundance, and a good fit of the model was demonstrated by the apparent lack of structure in the deviance residuals relative to predicted values. Temperature and ^{Y}F were not statistically significant.

Discussion

The Iceland scallop stock in Breidafjordur has declined considerably since 2000. The period has been characterized by a steady increase in SST, increasingly poor condition of the scallops, and limited recruitment to the fishable stock.

Fluctuations in the stock size of Iceland scallop have differed between subareas, perhaps because of spatially different patterns of recruitment and exploitation (Beukers-Stewart *et al.*, 2003), but possibly also through variable predation intensity or spread of disease. The effect of dredging on the seabed can also vary locally, but a new dredge introduced to the fishery around 1990 increased fishing efficiency substantially. The new dredge was heavier, could be towed faster, and was easier to operate than its predecessor. Consequently, cpue increased in all subareas for several years after the new dredge was introduced, but the total catch was stable, restricted by catch quotas. The survey data have the disadvantage of containing information from two different dredge types, because estimated comparisons are likely to include errors and thus bias stock estimates in one or the other direction.

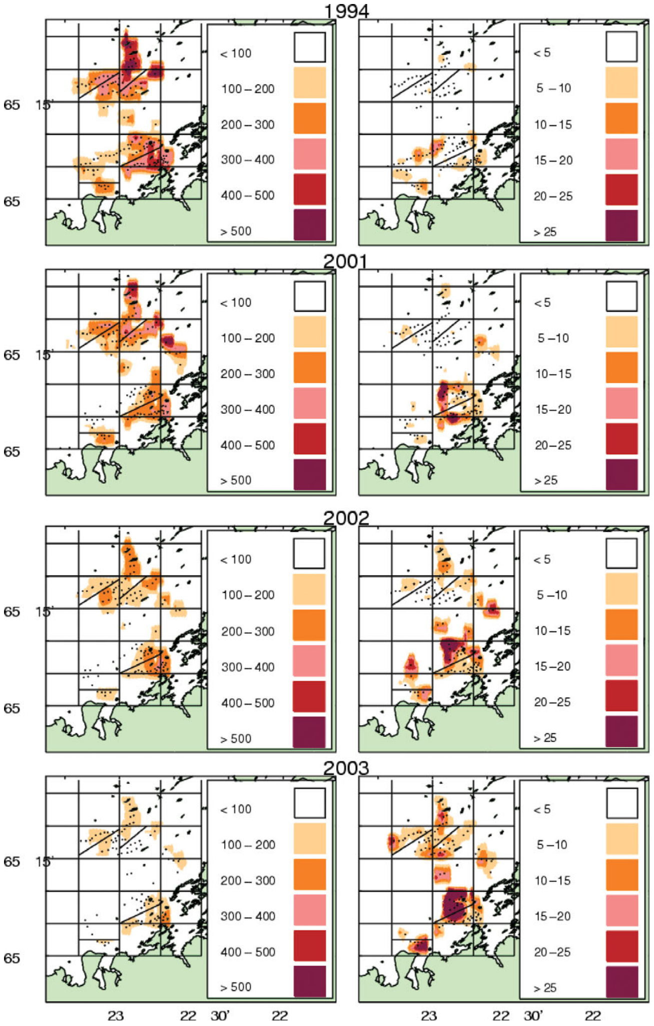

Figure 5. Geographic distribution of mean scallop weight (kg per survey tow, left column) and natural mortality of scallops (annual ratio, right column) in Breidafjordur, during the 1994 and the 2001 – 2003 surveys (stations are marked with dots).

Fishing mortality was relatively high throughout the study period. The equilibrium fishing mortality was low compared with the Beverton and Holt fishing mortality, but it only represents landings and is negatively biased in the presence of non-yield fishing mortality. The difference between the two estimates may indicate a substantial indirect fishing mortality, which can accompany scallop dredge fisheries (Caddy, 1989). Heavy gear may impose high levels of incidental damage to scallops, whether they

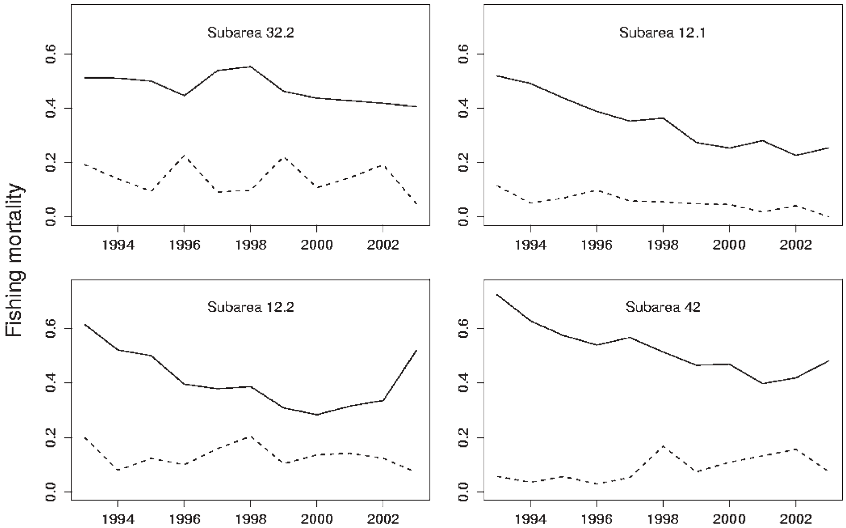

Figure 6. Fishing mortality estimates based on data from the four main subareas in Breidafjordur, 1993–2003. The Beverton and Holt length-based fishing mortality (solid line; $^{\text{BH}}F$) and equilibrium fishing mortality (broken line; ^{Y}F) are shown.

are retained, pass through the ring or inter-ring spaces, or are run over by the dredge (Caddy, 1989). In the present investigation, the mean difference between the Beverton and Holt F ($^{\text{BH}}F$) and equilibrium F (^{Y}F) was 0.284–0.439 over a period of 11 y (Figure 6). In an exploited scallop area in Canada, indirect fishing mortality was estimated to be as high as 0.364, based on cluckers and crushed scallops (Naidu, 1988). That area had been fished with a heavy dredge, similar to that used in Breidafjordur post-1990. In the presence of indirect fishing mortality, a rotational harvest strategy can provide equal or greater yield and maintain a higher spawning biomass (Myers *et al.*, 2000). As the dredge is only a "semiquantitative tool" (Caddy, 1989), rotational harvesting would benefit from more precise and accurate estimates of scallop density and size distribution, which can be monitored by a technique such as underwater photography (Stokesbury, 2002).

In the present study, natural mortality was generally higher in the southern than in the northern area, with an extremely high value (0.41) in subarea 12.1 in 2003. The rates of natural mortality in subarea 2 in 2001 and in subarea 13 in 2002 were also very high, 0.22 and 0.29, respectively. The same adjustment factor was used here for tow-induced disarticulation as described by Naidu (1988) for tows of 0.25 nautical miles. Naidu noted that on longer tows, more scallops would be expected to disarticulate. The values of natural mortality presented here could therefore be underestimated, because the average tow length was about 0.4 nautical miles. In contrast, part of the estimated natural mortality could be dredge-induced mortality. In heavily fished areas in Canada, natural mortality has been reported to be as high as 0.21 (Naidu and Cahill, 1984).

Along with the decline in the scallop population, the sea temperature in Breidafjordur increased, and in 2003 and 2004, the mean reached the highest estimated values in 100 years. However, nothing is known about the status of the scallop stock during the warm years of the 1930s. The Iceland scallop fishery in Breidafjordur started in 1970 (Eiriksson, 1997) and therefore has until comparatively recently been prosecuted during relatively cool periods. An experimental study by Jonasson *et al.* (2004) showed that scallops collected during late summer can tolerate temperatures up to 13°C, at least for up to 21 d, but there is considerable mortality at 14°C. The rising temperature in Breidafjordur during recent years has therefore brought the summer maximum temperature close to the apparent temperature tolerance of the stock, e.g. 12.2°C in August 2003 (Jonasson *et al.*, 2004). However, an increase in natural mortality had been observed already during the 2001 spring survey, so the direct effect of a high summer temperature is unlikely to have been the only factor inducing natural mortality of the stock. In contrast, Wiborg (1963) assumed that Iceland scallop located outside fjord sills in northern Norway were depleted at intervals owing to variations in temperature and/or salinity. Further, the drastic decline in the southernmost population of Iceland scallop in Hvalfjordur, Southwest Iceland, in 1983 was suggested to have been the result of elevated sea temperatures the previous year (Eiriksson, 1997). On several occasions, a high sea temperature has been associated with mass mortality of *Placopecten magellanicus* in Canada (Dickie and Medcof, 1963).

Chl *a* values provide an estimate of food availability to Iceland scallop. The highest mean value of Chl *a* in 2003 was 50% higher

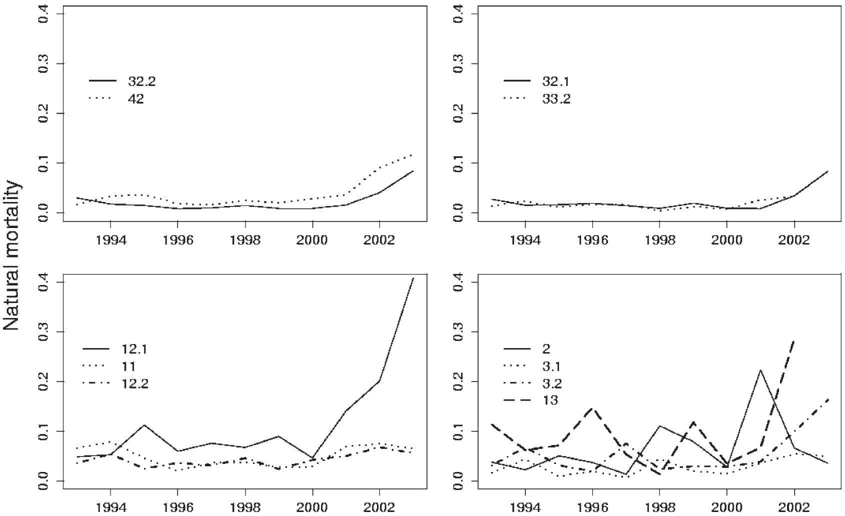

Figure 7. Annual ratio of mean natural mortality by subarea in Breidafjordur, 1993–2003. Northern areas are shown in the top two panels and southern areas in the bottom two panels.

than the lowest value in 1999, illustrating a considerable annual difference in food availability in Breidafjordur. Chl *a* data derived from the NASA SeaWiFS project fit well the *in situ* Chl *a* data in shallow waters (Tang *et al.*, 2003). Thorarinsdottir (1991) collected monthly Chl *a* samples 8 m deep in Breidafjordur and recorded mean values from March to September of 1990 and 1991 of 1.82 and 1.51 mg m^{-3}, respectively. Those values fall in the lower ranges of the values presented here (1.73–2.60 mg m^{-3}). The mean Chl *a* 2 m deep near a scallop ground in the mouth of Hvalfjordur from March to September 1997 was 2.63 mg m^{-3} (Eydal, 2003), close to the higher values observed during the current study.

The adductor muscles of scallops were in an abnormally poor condition at the time of the increase in scallop mortality (2000–2002). Muscle weight increased in 2003, coinciding with high values of Chl *a*, but decreased again with a low primary production in 2004 and 2005. At that time, two coccidia parasites were identified in Iceland scallop from Breidafjordur, one of which causes infection of muscle tissue (Kristmundsson *et al.*, 2004). The prevalence of infection was about 90%, with severe

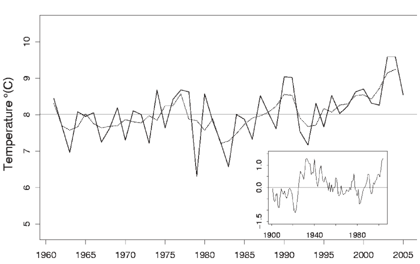

Figure 8. Estimated mean SST (May–August), 1960–2005 (solid line), and annual 3-y running mean of SST (dotted line) at Flatey, Breidafjordur. The horizontal line indicates the long-term mean. The subplot shows the annual 3-y running deviance from the mean (7.9°C) at the same location from 1900 to 2003 (May–August).

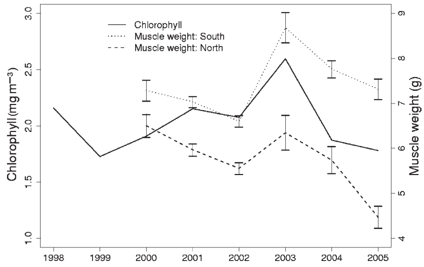

Figure 9. Average Chl *a* from March to September in Breidafjordur, 1998–2005 (data provided by the NASA SeaWIFS project) and calculated scallop muscle weight at 70 mm shell height, shown with 95% confidence intervals, from the southern (subarea 11) and northern part (subarea 32.1) of Breidafjordur, autumn 2000–2005.

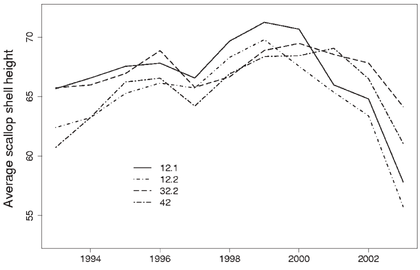

Figure 10. Average shell height (mm) of scallops from four different subareas in Breidafjordur, 1993–2003.

infections in large scallops. The poor condition of scallop muscles in 2001 and 2002 could be attributed to this infection, although a more complex interaction of infection, food availability, and temperature would seem a more plausible explanation. In other shellfish species, parasite prevalence has been related to elevated sea temperature (Cook *et al.*, 1998). Further, Yungkul and Powell (2004) proposed that malnourishment leading to death of surf clams (*Spisula solidissima*) was caused by an environmental shift that led to a mismatch between food supply and demand.

The increase in average shell height of Iceland scallop towards the end of the 1990s can misleadingly be interpreted as resulting from declines in exploitation rate (Caddy, 2004). The underlying cause was several years of weak and average recruitment to the fishable stock, which led to a relatively high proportion of older scallops in the total stock. The strong relationship between recruitment and harvestable biomass further supports the effect of variable recruitment in stock fluctuations, although fishing mortality and, consequently, effort also contribute to stock fluctuations. If other Iceland scallop beds in the Atlantic are compared, there is clear variability in recruitment between areas. In the Iceland scallop fishery off Jan Mayen and Svalbard, which collapsed through overfishing, the proportion of ≥65 mm scallops declined (Anon., 1988). A decline in older age groups would be expected in a selective overfishing scenario, but this trend was not observed in the present study. Better-than-average recruitment was rare in the Svalbard region after the depletion of the grounds during 1986 and 1987, good recruitment being first detected only in 1996 (Anon., 2002). In West Greenland, the Iceland scallop population is mainly old scallops. The area is characterized by low levels of recruitment, and scallop beds can be depleted quickly by fishing (Pedersen, 1994). In contrast, Naidu and Anderson (1984) suggested that the presence of several consecutive year classes of

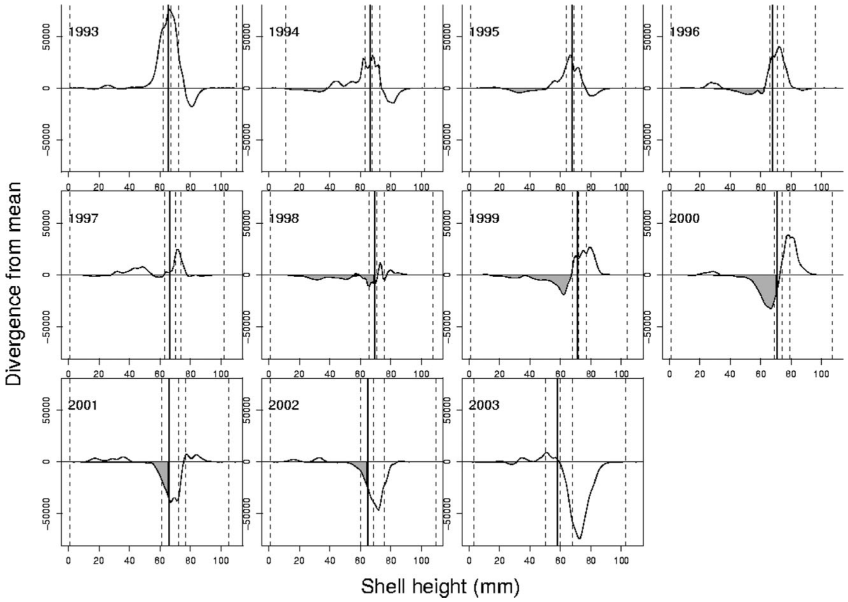

Figure 11. Divergence from the mean shell-height index in subarea 12.1, 1993–2001. The data were transformed with a GAM smoother. The vertical lines show the quantiles and the mean shell height for each year. The shaded area represents the negative divergence less the mean shell height, indicating low recruitment.

Table 1. Analysis of variance of relative abundance, ln (number per subarea) of harvestable scallops ($\geq$60 mm), 1995–2003, examining the main effects.

Source	d.f.	Sum of squares	Mean square	*F*	*p*-value
ln (juveniles 45–60 mm)	1	35.476	35.476	151.932	<0.0001
^{BH}F	1	4.945	4.945	21.179	<0.0001
Standardized effort	1	2.018	2.018	8.642	0.005
Natural mortality	1	0.903	0.903	3.866	0.052
Residual error	94	21.949	0.233	–	–

Iceland scallop on Canada's St Pierre Bank indicated relatively stable recruitment. Moreover, growth rates are considerably slower among Iceland scallop stocks off Svalbard and Greenland than off Norway, Iceland, and Canada (Pedersen, 1994), so making them less tolerant to fishing.

It is difficult to estimate the effects of size and age composition of the spawning stock on the variable year-class strength observed in the present study. Density-dependent responses of fish populations (particularly involving recruitment) are often obscured by variability, presumably because of fluctuating environmental (density-independent) factors (Sissenwine, 1984). Dickie (1955) demonstrated that fluctuations in catch and landings of *P. magellanicus* in the Bay of Fundy were caused largely by variable year-class strength and that recruitment to this stock was correlated with temperature, which influenced wind-driven transport during the pelagic larval period. Spatial and temporal patterns in settlement of benthic invertebrates can be strongly linked to transport by wind-driven currents (Bertness *et al.*, 1996).

Several factors may enhance the recruitment and survival of spat. Addition of dead scallop shells to scallop grounds could have a positive impact, supporting an increase in the number of juvenile scallops and other invertebrates in the area (Guay and Himmelman, 2004). Other things being equal, recent natural mortality could therefore be a positive influence on future recruitment. Marine protected areas (MPAs) have been shown to increase scallop biomass manifold and to increase recruitment outside the protected areas. This was evident for *P. magellanicus* on Georges Bank, where scallop biomass increased 14-fold in protected areas during the 4 y of closure, although with moderate or below-average recruitment during the same period (Murawski *et al.*, 2000). With increasing biomass in MPAs, there can be also a higher proportion of older animals (Bradshaw *et al.*, 2001; Beukers-Stewart *et al.*, 2005). Increased importance of gamete production with age has been shown for *P. magellanicus* by Langton *et al.* (1987) and for Iceland scallop by Vahl (1984). A high density of scallops may also increase fertilization rate (Claereboudt, 1999).

In summary, the fishable scallop stock in Breidafjordur in the late 1990s consisted of few year classes, and as the total (indirect and direct) fishing mortality was high, the stock was vulnerable to several years of poor recruitment. Moreover, there was high natural mortality, probably because of disease and unfavourable environmental conditions. Poor recruitment combined with intensified fishing and high natural mortality seems to have led to the collapse of the stock. In future and in order to predict future catch levels, the biomass of spat-fall and juvenile scallops should be estimated (Beukers-Stewart *et al.*, 2003), and the current results can be used to manage fishing effort better. Finally, there would seem to be a strong case for the establishment of MPAs in Breidafjordur as well as the development of a rotational harvesting strategy for the stock.

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