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Ágrip

Nýliðun er lykilþáttur varðandi viðgang fiskistofna. Upplýsingar um nýliðun eru mikilvægar í stofnmati enda segja þær til um fjölda einstaklinga sem bætast munu við stofna og veiðar á komandi árum. Hrygningarstofn þorsks við Ísland hefur farið stækkandi á síðustu árum en á sama tíma hafa fáir sterkir árgangar þorsks komið inn í stofninn. Í þessari skýrslu er tekin saman núverandi þekking á lífsögu þorsks frá hrygningu þar til hann er 4 ára. Notast er við efni úr birtum greinum en einnig eru tekin saman gögn úr gagnagrunni Hafrannsóknastofnunar.

Abstract

Recruitment is one of the major events in the life history of aquatic species and information on recruitment is of great importance for stock assessment. The spawning stock biomass of Icelandic cod has increased in the past years, but despite increasing spawning stock biomass recruitment has remained at relatively constant levels. In this report information on early life stages of Icelandic cod, from spawning until the age of four, are summarized by using information from published papers as well as available data from the Marine and Freshwater Research Institute.

Lykilorð: *cod, recruitment, Gadus morhua, distribution, juveniles*

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Contents

Page

List of tables

List of figures

Appendices

Introduction

Recruitment is one of the major events in the life history of aquatic species. For demersal fish this is often marked by a transition from a planktonic larval stage to a juvenile stage as individuals settle and join the population. In studies on population dynamics, recruitment is often defined as the number of young-of-the-year measured at a certain time of year. Recruitment is a complex process driven by the biological and physical variability of the environment (Cushing, 1996; Chambers and Trippel, 1997). Information on recruitment is therefore of great importance for stock assessment as provides the means for predicting the number of individuals available for fishing in stock predictions. However, despite numerous research performed in recent decades, the specific mechanisms determining the strength of year classes of marine species are still poorly known.

Atlantic cod (*Gadus morhua* L.) is a commercially important groundfish species widely distributed in the North Atlantic and has been a major fishery resource in Icelandic waters for over a century (Jónsson, 1990). The spawning stock biomass declined from about 1 million tonnes in the early 1950s to less than 200 thousand tonnes in the early 1980s (ICES, 2018). Since 1993, the spawning stock biomass has grown steadily and in 2018 it exceeded 600 thousand tonnes (MFRI, 2018a). At the same time, recruitment has remained at relatively constant levels but has not followed the increase in the spawning stock biomass. Therefore, the total biomass increase is likely to be a result of a lower harvest rate rather than higher recruitment (MFRI, 2018a). However, this pattern has raised some questions why recruitment has not increased in the past years despite growing spawning stock biomass.

The main objective of this report is to summarise information on early life stages of the commercially important Icelandic cod to gain a broader overview on recruitment patterns. This overview is necessary to facilitate more detailed data analyses and further research in recruitment processes of Icelandic cod in the future. Icelandic cod is considered to recruit to the fishery at age 4, so analyses focus on fish younger than age 4 as well as spawning activity. We compile available information from published reports and papers on early life stages including spawning, fecundity, drift of larvae and growth. Furthermore, we draw distribution maps, indices and diet of juvenile cod around Iceland. For that we use available data from surveys conducted by the Marine and Freshwater Research Institute (MFRI) in Icelandic waters.

Spawning

Areas of spawning

Atlantic cod spawn in a variety of habitats and congregate annually at specific locations to spawn (Robichaud and Rose, 2001). The main spawning grounds of Icelandic cod are located off south and southwest Iceland (Jónsson, 1996; Jónsson and Pálsson, 2013) i.e. from the south coast (near Vestmannaeyjar) to Breiðafjörður (Sæmundsson, 1926; Jónsson, 1982, 1996; Jónsson and Pálsson, 2013). Spawning on the main grounds in the southwest usually lasts from the middle of March until the middle of May (Jónsson, 1982) with older individuals spawning earlier and over a longer period (Marteinsdottir and Björnsson, 1999).

Apart from these main spawning grounds, numerous smaller regional spawning aggregations along the coast from the northwest to the southeast (Figure 1) are also considered. These make a significant contributions to the productivity of the stock in certain years, depending on environmental and biological factors that determine dispersal and survival (Begg and Marteinsdottir, 2000, 2002a, 2002b; Marteinsdottir *et al.*, 2000a; Brickman *et al.*, 2007a; Thorsteinsson *et al.*, 2012). Furthermore, evidence of finer spatial structure and depth segregation in spawning aggregations, particularly in the main spawning area in the southwest region, has been accumulating.

Numerous studies have focused on biological variation in spawning components based on tagging studies (Pálsson and Thorsteinsson, 2003; Grabowski *et al.*, 2011; Sólmundsson *et al.*, 2015), size structure (Marteinsdottir *et al.*, 2000a), otolith characteristics (Jónsdóttir *et al.*, 2006a; Petursdottir *et al.*, 2006), genetic variation (Pampoulie *et al.*, 2006), and morphology (McAdam *et al.*, 2012; Bardarson *et al.*, 2017) showing spatial variation within the spawning grounds. In general, larger, older, faster growing and more fecund spawning cod were present in shallower water closest to coast (Jónsdóttir *et al.*, 2002, 2006a; Petursdottir *et al.*, 2006).

It has been argued that cod has many characteristics of a lekking mating system (Nordeide and Folstad, 2000; Rowe and Hutchings, 2003; Windle and Rose, 2007). A lek is an aggregation of members of one sex (usually males) which is visited by the opposite sex solely for the purpose of mating (Höglund Alatalo, R.V., 1995). This exhibits a strong sex ratio bias toward males while aggregated during spawning periods in certain areas. Studies have shown that the sex ratio of Icelandic cod was skewed towards males in nearly all spawning regions around Iceland (Taaning, 1931; Fridriksson, 1933; Jónsson, 1982; Bogason *et al.*, 2019) indicating a lek mating system in Icelandic waters.

Results from data storage tags show evidence of two behavioural ecotypes; a coastal cod which follows the seasonal trend in temperature and is found in shallow waters, and frontal cod that migrates to deeper and cooler waters in the feeding season (Pálsson and Thorsteinsson, 2003; Thorsteinsson *et al.*, 2012). These two behavioural types appear to spawn sympatrically. However, studies have shown that they are, at least to some extent, reproductively isolated by fine-scale differences in spawning habitat selection, primarily depth (Grabowski *et al.*, 2011). Additionally, the different groups occupy distinct seasonal thermal and bathymetric niches that generally demonstrate low levels of overlap throughout the year (Pálsson and Thorsteinsson, 2003; Grabowski *et al.*, 2011; Thorsteinsson *et al.*, 2012; Sólmundsson *et al.*, 2018).

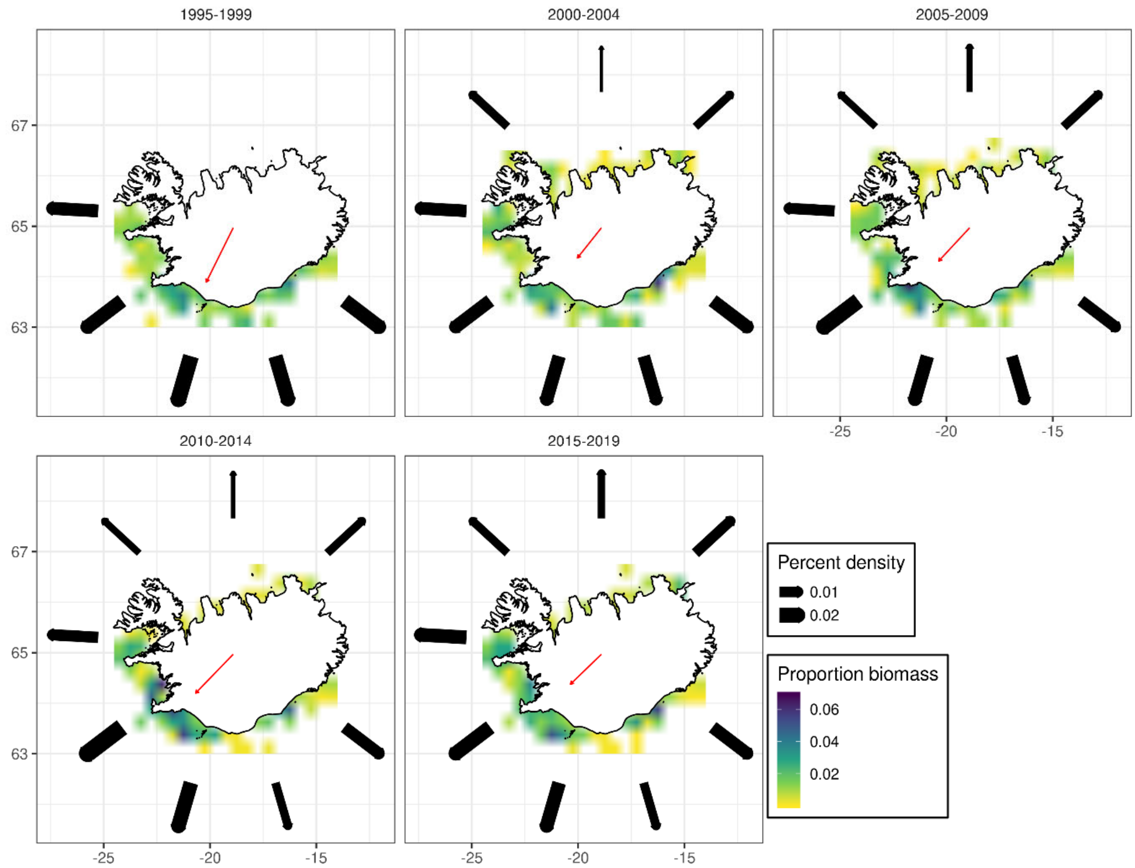

Figure 1. Spawning areas of cod in April based on cod biomass in SMN. No survey was conducted north of Iceland in 1995-1999, off the Westfjords in 1995-1999 and after 2009, and the areas east of Iceland, from Bakkaflói to Eystrahorn, have never been surveyed. Colour of each tile reflects density of total cod biomass over the period that can be attributed to gillnet sets within that tile area. The black arrows were calculated the same way. First, a midpoint of Iceland was defined and then nine points (far tips of the plotted arrows) were chosen as 400 km out from the centre, at degrees 0-320 in steps of 40 degrees. All tows were assigned to the closest point, and their mean biomass density calculated. Then these were summed, and the proportion of the total used to control the thickness of the arrow. The red arrows were calculated by taking mean densities at the nine points and calculating the weighted mean latitudes and weighted mean longitudes.

Spawning migrations

The Icelandic cod behaviour ranges from mainly sedentary to exhibiting long-distance (several thousand kilometres annually) migration. After spawning in spring/summer at various locations, cod migrates to feeding areas (feeding migrations) and back to spawning areas in early spring (spawning migrations) and in general, this behaviour is repeated annually (Thorsteinsson *et al.*, 2012). However, the extent of these migrations varies highly between areas and/or populations of cod. The oldest description of spawning migrations of cod in Icelandic waters is by Skúli Magnússon (1785, see (Jónsson, 1996)). He described two main routes: westwards along the southeast and south coast and a route southward along the west coast. Spawning and postspawning migrations within Icelandic waters have been demonstrated by extensive tagging experiments. The main spawning grounds at the southwest coast are at the centre of those migrations, where tagging experiments have demonstrated return migrations of repeating spawners (Jónsson, 1996).

Early tagging studies revealed spatial structure in Icelandic cod such as extensive migrations of mature cod from West Greenland to Iceland, first recorded in the 1930s (Hansen *et al.*, 1935; Hansen, 1941) indicating long-distance natal homing of Icelandic cod (Bonanomi *et al.*, 2016). An extensive analysis of a large data set of both conventional tag recaptures and data storage tags (DSTs) revealed low spatial overlap among a number of spawning components and high fidelity to spawning grounds. These results underpin a high degree of spatial structure within the Icelandic cod population (Sólmundsson *et al.*, 2015). Furthermore, tagging studies have also revealed regional differences in migration behaviour, i.e. postspawning cod from the southwest region undertakes long-distance migrations to the main feeding grounds located northwest and southeast of Iceland, taking route either west or east of the country while postspawning cod from the northeast regions stays more local (Jónsson, 1996; Pálsson and Thorsteinsson, 2003; Sólmundsson *et al.*, 2018).

Fecundity

Cod is highly fecund such that hundreds of thousands or millions of eggs in multiple batches are released over a prolonged period in each spawning season (Kjesbu *et al.*, 1996, 1998). While fecundity does not give information on offspring viability, it does provide the maximum number of potential offspring that can be produced and is therefore one of the essential components for estimating an individual's reproductive potential. Females are batch spawners, releasing several batches of eggs over the course of a spawning season. The time elapsed between the release of a batch of eggs and ovulation of the next is variable and ranges about 2-6 days (Kjesbu, 1989; Kjesbu *et al.*, 1996).

Like for most other fish, female cod fecundity is positively correlated with body length and weight. Larger and older females produce more batches, spawn over longer periods of time and have increased egg size and fecundity as well as increased quality and survival of larvae (Kjesbu, 1989; Kjesbu *et al.*, 1996, 1998; Marteinsdottir and Steinarsson, 1998; Marteinsdottir *et al.*, 2000a; Marteinsdottir and Begg, 2002; Imsland and Jonsdottir, 2003; Rowe and Hutchings, 2003). Batch sizes (i.e. number of eggs in each batch) are also positively related to female total length. Thus, the smallest females (50-80 cm) usually do not produce batches greater than 500 thousand eggs but females >100 cm normally produce batches exceeding one million eggs (Marteinsdottir and Begg, 2002). Condition has also a significant positive effect on both maturation and fecundity. A fish in better condition can invest more and earlier into reproduction than fish in poor condition (Kjesbu *et al.*, 1998; Marteinsdottir and Begg, 2002). Poor condition may lead to skipped spawning (Skjaeraasen *et al.*, 2009; Skjæraasen *et al.*, 2012) as cod in poor condition does not have the extra energy to develop mature gonads (Wootton, 1998).

Larvae and juveniles

Drift

Following spawning, eggs and larvae drift with currents towards nursery grounds and in the absence of parental care, face high rates of mortality during the first year of life. Incubation time from egg to larvae has been estimated to be 9-10 days in Icelandic waters at 7.3°C (Friðgeirsson, 1978). Most of the information about larval and juvenile drift come from two surveys. An extensive pelagic survey of 0-group juvenile cod carried out in August-September in 1970-2003, focused on a juvenile period during which cod is schooling and not yet settled demersally (Sveinbjörnsson and Hjörleifsson, 2003) and sporadic egg and larval surveys southwest and west of Iceland, carried out earlier in the season (Jonasson *et al.*, 2009). The focus of many studies has been to look at the drift from the main spawning grounds located off the southwest coast (Marteinsdottir and Björnsson, 1999), towards nursery areas in the northwest and north of Iceland. During the drift period, larval cod goes through metamorphosis to become a juvenile cod. In general, metamorphosis is thought to happen at 12-15 mm length (Brander, 2005), although some aspects of metamorphosis, like stomach development, happens at later time when the juveniles are between 20-40 mm (Pedersen and Falk-Petersen, 1992).

Begg and Marteinsdottir (2002a) analysed the spatial and temporal pattern of cod from the 0-group pelagic surveys, where the mean survey date was August 20th. In waters off the south coast, the mean length of juvenile cod was 58±10 mm but off the Westfjords and the north coast, 46±5 mm. Cod found offshore were slightly larger (48±5 mm) than inshore (46±6 mm). Higher proportions of juveniles were caught north of Iceland, compared to the south and in some years, a high proportion of juveniles were found in East Greenlandic waters. Begg and Marteinsdottir (2002a) concluded based on their findings and the age estimation by Marteinsdottir et al. (2000b) that in any given year, more than half of the juveniles found in the northern region likely originated from the main spawning areas southwest of Iceland. The mean length of 0-group cod in the 0-group surveys was positively related to sea surface temperature and the strength of the coastal current. The observed clockwise size gradient, smaller juveniles in the northern part compared to the western part, was age-related and due to cod spawning later in the colder northerly areas (Marteinsdottir *et al.*, 2000a).

Based on hatch date distribution, drift of larvae and juveniles from the main southwest spawning grounds was more pronounced in 1997 compared to 1995 and 1996, which was also reflected in higher 0-group abundance index (Marteinsdottir *et al.*, 2000a). In 1997, there was also an increased influx of Atlantic water onto the northern shelf, providing good conditions for growth and drift of larvae from the main spawning area to the nursery grounds in the north (Jónsson and Valdimarsson, 2005). In years of high 0-group abundance (1973, 1976, 1984 and 1985), large aggregation of pelagic juveniles was found in East Greenlandic waters. The juveniles have most likely originated from the main spawning grounds in southwest Iceland, based on prevailing currents as well as the length and hatch date distribution (Begg and Marteinsdottir, 2000).

Surveys were carried out during 1998-2001, in late June/early July on the proposed drift route of larvae and juveniles in the western part of the Icelandic shelf (Jonasson *et al*., 2009). Information were provided on approximately 2-8-week-old individuals (6-35 mm). Great variation was observed in abundance and hatch-date distribution between years, which varied from early April to middle of June. The highest relative abundance was found at temperatures above 7.5°C and in low-salinity waters, characteristic of the coastal current. That pattern is in agreement with previous studies that have demonstrated a potential link between the freshwater discharge or the strength of the coastal current and recruitment of cod (Begg and Marteinsdottir, 2002a).

The proportion of larvae that are thought to have originated from the main spawning grounds differed greatly between years, and only in 1999 a high proportion of larvae north of 66°N presumably originated from the main southern spawning grounds. The lower ratio of larvae thought to have originated from the main spawning sites contradicts with what Begg and

Marteinsdottir (2002a) proposed, but as discussed in an earlier paper (Begg and Marteinsdottir, 2000) their estimate was conservative towards the presumed main spawning ground and may be regarded as a minimum value. For the years 1998-2000, the larval drift resulted in medium sized year classes (MFRI, 2018a). During 2001, few larvae were estimated to have originated from the main spawning grounds in the south and west and the 2001 year-class size was estimated poor at the age of three (MFRI, 2018a).

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.*, 2000a). Further, Brickman et al. (2007a) discussed a problem with the drift model overestimating the abundance of cod juvenile in the southern part of Iceland. The possible explanation was that demersal settlement could have already taken place there at the time of the 0-group surveys (mean date 20th of August) but information on settlement is presented on page 10.

Growth

Growth analysis of pelagic juvenile cod in Icelandic waters has only been carried out sporadically. In a study from 1995 to 1997, cod growth was relatively higher in 1996 compared to the adjacent years. Growth rates ranged between 0.36-0.77 mm/day but varied between years and areas (Marteinsdottir *et al.*, 2000a). Further, growth rate of the years 1998-2001 was modelled and showed that the highest growth rate was in 1998 and the lowest in the small 2001 year class (Jonasson *et al.*, 2009). Observed size gradient in juvenile length from southwest to northeast in the 0-group survey has been predicted to arise from different temperature exposed to the individuals on the drift route from the main spawning ground in southwest Iceland (Astthorsson *et al.*, 1994). It was pointed out that the spatial variation in size was age related, and in some instances, juveniles caught in northern Iceland experienced faster growth than those caught in western Iceland (Marteinsdottir *et al.*, 2000a).

Feeding

Thorisson (1989) presented the most thorough analysis of food composition of cod larvae and juveniles to date. He conducted monthly sampling from May to August, on the proposed drift route from the spawning areas in the southwestern part clockwise towards the northwestern grounds. In May, the main prey items of the larvae were nauplii and copepodites. The smallest larvae (4-5 mm SL) predominately feeding on nauplii but the larger on copepods and copepodites (mostly *Calanus finmarchicus*). In June, the cod juveniles were 10-20 mm (most had gone through metamorphosis) and the most numerous prey items were the copepods

Temora and *Acartia*, but *C. finmarchicus* was most abundant by weight. Few juvenile stomachs were analysed in July (size range between 10 and 28 mm), but copepods (*Pseudocalanus*) were the most dominant prey items. In August, the cod juveniles (40-65 mm SL) were split into shallow and deep water stations, with smaller juveniles observed at the shallow station. The juveniles at the shallow station fed mainly on fish larvae and euphausiids while copepods were more important at the deeper station (41% compared to 12% at the shallow station). Thorisson (1989) highlighted the importance of copepod eggs as the first feeding item of Icelandic cod larvae.

Food items change when cod juveniles shift from pelagic to benthic habitats (Ólafsdóttir *et al.*, 2015). Food items of newly settled cod and saithe (*Pollachius virens*) in Ísafjarðardjúp, caught close to the shore with a seine, were analysed from July to November of 2015 (Nickel, 2016). The first cod samples were from late August (size range 33-39 mm). Benthic copepods (Harpacticoida) were the most common prey items in August, followed by Cyclopoida copepods. In general, for both cod and saithe, the proportion of benthic prey gradually decreased over the study period to more pelagic organisms.

The interesting contrast in dependence on pelagic versus benthic prey between those two studies (Thorisson, 1989; Nickel, 2016) can possibly be explained by different methods of sampling. Nickel (2016) already found the juveniles to be benthic at sizes well below the average size found on the pelagic "shallow" station (~100 m depth, sampling depth of 5-80 m), during the same month. The greater importance of harpacticoid near the shore compared to *C. finmarchicus* in the outer pelagic station is most likely a result of differences in depth and distance offshore.

Other studies have looked indirectly at the effect of food on abundance of juveniles. A positive correlation between the abundance of 0-group cod in the pelagic surveys and the biomass of zooplankton has been described (Astthorsson *et al.*, 1994).

Settlement

The ontogenetic shift or settlement of juvenile cod from the pelagic to the benthic stage has been reported to happen at variable length intervals across cod stocks; 60-80 mm at Georges Bank (Bolz and Lough, 1988), 30-60 mm in Nova Scotia (Tupper and Boutilier, 1995), 45-53 mm in the Baltic Sea (Hüssy *et al.*, 1997) and 50-60 mm in the North Sea (Robb and Hislop, 1980). Juveniles may settle in different habitats; reefs, rocks, sand, gravel, seagrass beds, and macrophytic algal stands. It appears to be an advantage to settle early and at a large size (Tupper and Boutilier, 1995).

Many of the routine surveys in Iceland are most likely conducted too late in the year to capture the settling period of cod. However, it has been discussed that the settlement period could be either a gradual transition period (Bowman, 1981) or rather abrupt, based on the shift in diet of individuals (Hüssy *et al.*, 1997). The various sources regarding settlement of cod in Icelandic waters indicate that the 0-group cod start to settle around 30-50 mm and most likely a high percentage of cod at sizes 50-60 mm has already settled to the bottom.

In Iceland, Bjarni Sæmundsson observed in 1908 that juveniles of cod and saithe had started to settle in Ísafjarðardjúp in the middle of July and average length of 0-group cod settlers was 30-40 mm (range 20-60 mm) (Pálsson, 1976). An extensive study was carried out on 0-group cod in Ísafjarðardjúp in 1973, where cod was analysed from shrimp trawl samples (Pálsson, 1976). 0-group and 1-year old cod increased in number in the inner part of Ísafjarðardjúp from September to November (Pálsson, 1976), but the average size of 0-group cod was 97 mm in the first survey in late September, indicating that settlement had occurred at least a month earlier. During 2015, the feeding pattern of newly settled cod and saithe was studied again in Ísafjarðardjúp with a beach seine at a shallow depth (Nickel, 2016). The first cod was caught on August 17^{th}. The length distribution of cod ranged from 33-39 mm until middle of September, with smallest individual of 30 mm. The length distribution was, however, 41-50 mm from middle of September to November (Nickel, 2016), indicating that most settlement was likely over by mid-September, after which lengths increased due to growth by settled individuals. The fact that average size doesn't exceed 50 mm in November at the coast compared to the average length of 97 mm in the annual shrimp survey in late September, could indicate that only a small fraction of the 0-group cod or small individuals stay in the very shallow waters (less than 1.5 m). Depth distributions of commercial catches also indicate that recently settled cod juveniles are found in slightly deeper waters (Figure 2). For example, extensive fishing trials on cod juveniles for aquaculture rearing, took place in August and September, during 2001 to 2006 in Ísafjarðardjúp. There, 50-90 mm cod juveniles were caught at the depth interval 15-37 m. During that period close to 3 million cod juveniles were caught (Guðfinnsson, 2006).

Figure 2. A photograph of juvenile (0-group) cod in Ísafjarðardjúp taken with an underwater camera in October 2018. Photo: MFRI.

Materials and methods

Surveys/data

The analysis in this report is based on data collected from several annual surveys conducted by the Marine and Freshwater Research Institute (Table 1).

Table 1. Overview of surveys used in this report.

Survey	Area	Period	Season
0-group pelagic survey	All around Iceland	1970-2003	August
Bottom trawl survey in spring (SMB)	All around Iceland	1985-2019	March
Bottom trawl survey in autumn (SMH)	All around Iceland	1996-2018	October
Gillnet survey (SMN)	All around Iceland, except east Iceland and Westfjords	1996-2019	April
Icelandic beam trawl survey (GRU)	All around Iceland	2016-2019	July-September
Shrimp survey (SMR)			
Snæfellsnes	Snæfellsnes	1990-2018	April
Offshore	North of Iceland	1988/90-2018	July
Inshore	NW and N of Iceland	1988-2018	September-October

The Icelandic 0-group survey was conducted annually in August (occasionally extended from July or to September) 1970-2003 and provides information on the distribution and abundance of pelagic cod juveniles around Iceland (Sveinbjörnsson and Hjörleifsson, 2003). The purpose was to monitor the distribution and abundance of 0-group fish to obtain a first index of the year class strength. Acoustic records of 0-group fish were obtained and samples were collected in the scattering layer using a pelagic trawl (Vilhjálmsson and Friðgeirsson, 1976).

The bottom trawl survey in spring (SMB) was initiated in 1985 and has been conducted annually in March. The bottom trawl survey in autumn (SMH) started in 1996 and has been conducted annually since, except in 2011. The purpose of these surveys is to monitor the distribution and abundance of demersal species. Bottom trawls with 40 mm cod end are used to collect samples (Kristinsson *et al.*, 2017; Sólmundsson *et al.*, 2019).

The gillnet survey (SMN) started in 1996 and is conducted during the spawning season in April. Until 2001, it was only conducted south and west of Iceland but since 2002 it has also covered the areas north of Iceland. The purpose of the gillnet survey is to monitor timing and general condition of spawning cod in various spawning areas around Iceland (Jónsdóttir *et al.*, 2010; Bogason *et al.*, 2019).

The shrimp surveys (SMR) have been conducted since 1988-1990 depending on the area. The purpose of these surveys is to monitor the distribution and abundance of the northern shrimp (*Pandalus borealis*). No sorting grid is used, and all by-catch species are accounted for. A shrimp trawl with 40 mm cod end was used in all shrimp surveys (Jónsdóttir, 2018).

The Icelandic beam trawl survey (GRU) was initiated in 2016 when samples were collected west of Iceland, but the sampling area increased in the following years and now covers shallow waters (<50 m) all around Iceland. A 4-m beam trawl was used for sampling with 40 mm cod end (Sigurðsson and Pálsson, 2018).

Data analysis

Because ageing methods for 0-group cod varied through the time series, cod less than 14 cm in length from the groundfish or shrimp surveys were assumed to be age 0 and included for analysis. For ages 1-3, year-specific age-length keys were created as described by Björnsson et al. (2007) to convert length distributions to age distributions per tow in 2 cm intervals. In cases where age data were lacking to form age-length keys, the next closest seasonally similar data set were used instead. Age data from SMB, SMH, SMR-inshore from years 2001 to present, and from SMR-offshore during the years 2001, 2006, 2007, and 2010-present, were used to form age-length keys for length data from the same samples. As all other cases had insufficient age data, SMB age-length keys were used to convert lengths to ages from the GRU survey, and SMH age-length keys from the same year were used when needed to convert length data from both SMR surveys from 1996 onwards. SMR-inshore length data were also available earlier than the beginning of the SMH time series; therefore, the age-length key for 1996 SMH were used to convert these data.

In distribution maps of age 0-3 cod from groundfish or shrimp surveys (SMB, SMH, and SMR), the colour of each tile reflects mean density of cod biomass over all tows within that tile area. In distribution maps of 0-group pelagic surveys, raw catches of age 0 cod are indicated by circle size at each tow site, with lines between tows indicating the survey route. All cod caught in this survey were assumed to be age 0. Black arrows were created the same way in all distribution plots: by first defining a midpoint of Iceland, then the nine arrow points (outer tips) were chosen as 400 km out from the centre, at degrees 0-320 in steps of 40 degrees. All tows were assigned to the closest point, and the mean biomass density (groundfish or shrimp surveys) or mean abundance density (0-group pelagic survey) were calculated per arrow, calculated across assigned tows. The proportion of the totals summed over all arrows is reflected by thickness of the arrow. Red arrow tips reflect the mean latitudes and longitudes of the tows, weighted by the values per tow (mean densities or total catches, not proportions). Mean bearing and strength of distributions are calculated as the bearing (degrees from north) and length of red arrows in distribution plots.

A potential relationship between spawning stock biomass (SSB) and recruitment (R) in the period 1955-2016 was analysed by plotting SSB against number of cod at age of 3, three years later. For visual clarity, the period was divided into three 16-years and one 14-years long parts. A Ricker model (Ricker, 1954) was fitted to the SSB-R data. The Ricker curve rises to a maximum where recruitment is highest but then falls and heads towards zero. The Ricker model is written as:

$$R = \alpha S e^{-S/K}$$

where *R* is recruitment, *S* is SSB, and α and *K* are constants. Residuals from the Ricker model fit were plotted to observe if there were time trends in the SSB-R relationship. A two-tailed Fisher's exact test was used to test if the number of years with above vs. below average recruitment differed statistically between years with above vs. below spawning stock biomass.

Diet analysis

When available, up to 5, 10 and 25 cod were randomly sampled at each station for detailed diet analysis onboard for SMR, SMB and SMH, respectively. Total length of each cod was measured to the nearest centimetre, whole and gutted weight recorded, and otoliths removed for age determination. The stomachs were cut open, and the contents were macroscopically identified with all prey items classified to the lowest taxonomic level possible. To avoid possible bias from fish swallowing food items in the trawl, any prey items not displaying signs of digestive action were discounted. The number of individuals of each prey type was counted, and its wet weight was recorded. Data were assigned to seven prey categories or groups, including the most prominent prey species, capelin (*Mallotus villosus*) and northern shrimp. Other prey types were pooled into five main groups: annelids, crustaceans, euphausiids, fish, and other prey types including e.g. echinoderms, molluscs and unidentified items.

0-group cod

Abundance index

The Icelandic 0-group surveys indicate a higher abundance of 0-group cod in Icelandic waters in 1976-1980 as compared to most years in 1981-1996 (Figure 3). In 1998-2002, abundance indices were high. There were two periods of relatively high abundance of 0-group cod in SMH; 1998-2000 and 2014-2017 (Figure 3). Most autumn surveys in 2001-2013 had relatively low abundance of 0-group, even the years 2001-2002, which contrasts with high values found in the 0-group survey.

Distribution

In August, 0-group cod were usually found in highest abundance in areas from the northwest clockwise to southeast of Iceland (Figure 4). In most years, densities were higher in nearshore than offshore areas, but abundance and distribution in offshore areas was highly variable. In the 0-group survey, there was a shift towards higher abundance and a more widespread distribution of cod pelagic juveniles after 1996. After 1990, there was a shift towards more easterly distribution, especially in the high-abundance years of 1999-2002 (Figure 4).

The coverage of the 0-group survey in August in the waters between Iceland and Greenland varied between years. Drift of larvae towards Greenland was variable between years (Figure 5). In some years, few or no larvae were found, whereas in some years (e.g. 1979 and 1985) there was substantial drift of larvae towards Greenland. This area was last surveyed in 1995.

0-group cod in SMH were mainly found north of Iceland from shallow waters to the edges of the continental shelf (Figure 6). In 1999, 2001 and 2015, a significant proportion was found in the east, as indicated by a north-easterly mean bearing.

Distribution of 0-group cod in SMR was highly variable (Appendix 1). This may reflect annual biological/environmental variability but may partly be due to “match/mismatch” in timing of the survey with bottom settlement of larvae. Moreover, not all areas were sampled annually.

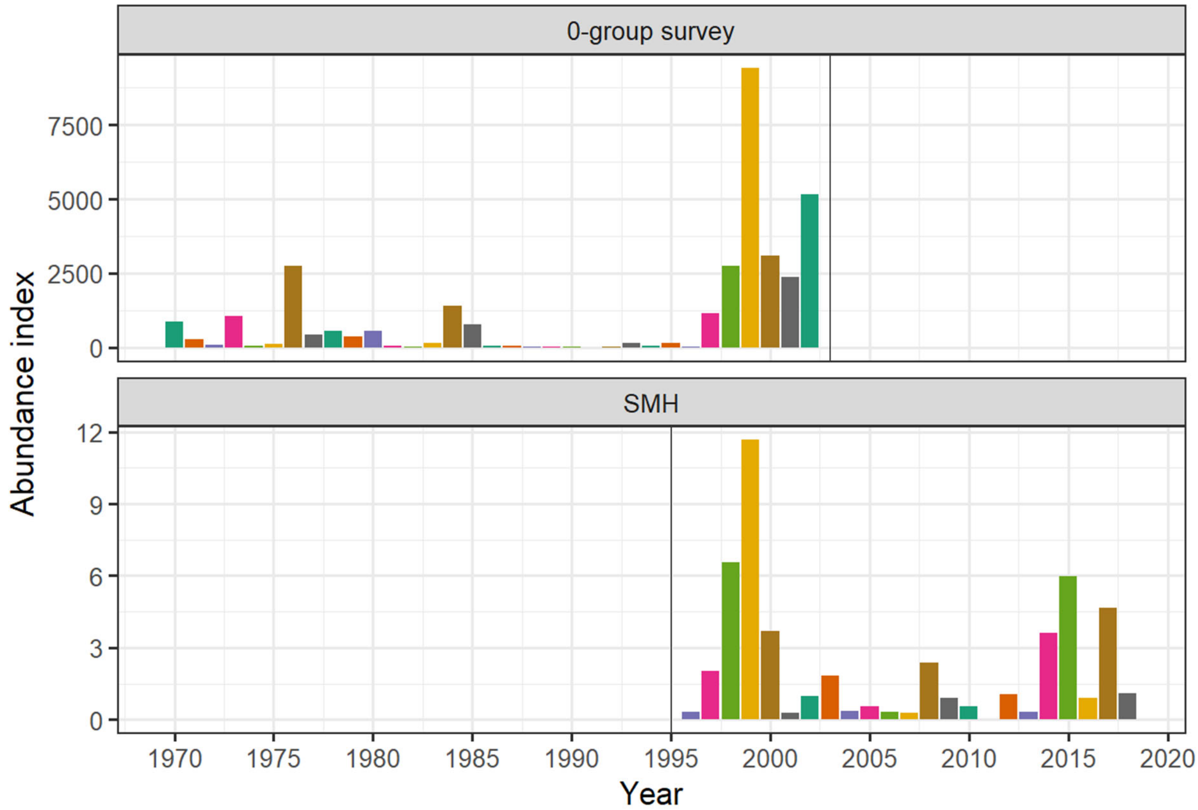

Figure 3. Abundance indices for 0-group cod in the Icelandic 0-group surveys 1971-2002 and in SMH in 1996-2018. Vertical black bars indicate boundaries of the survey time series.

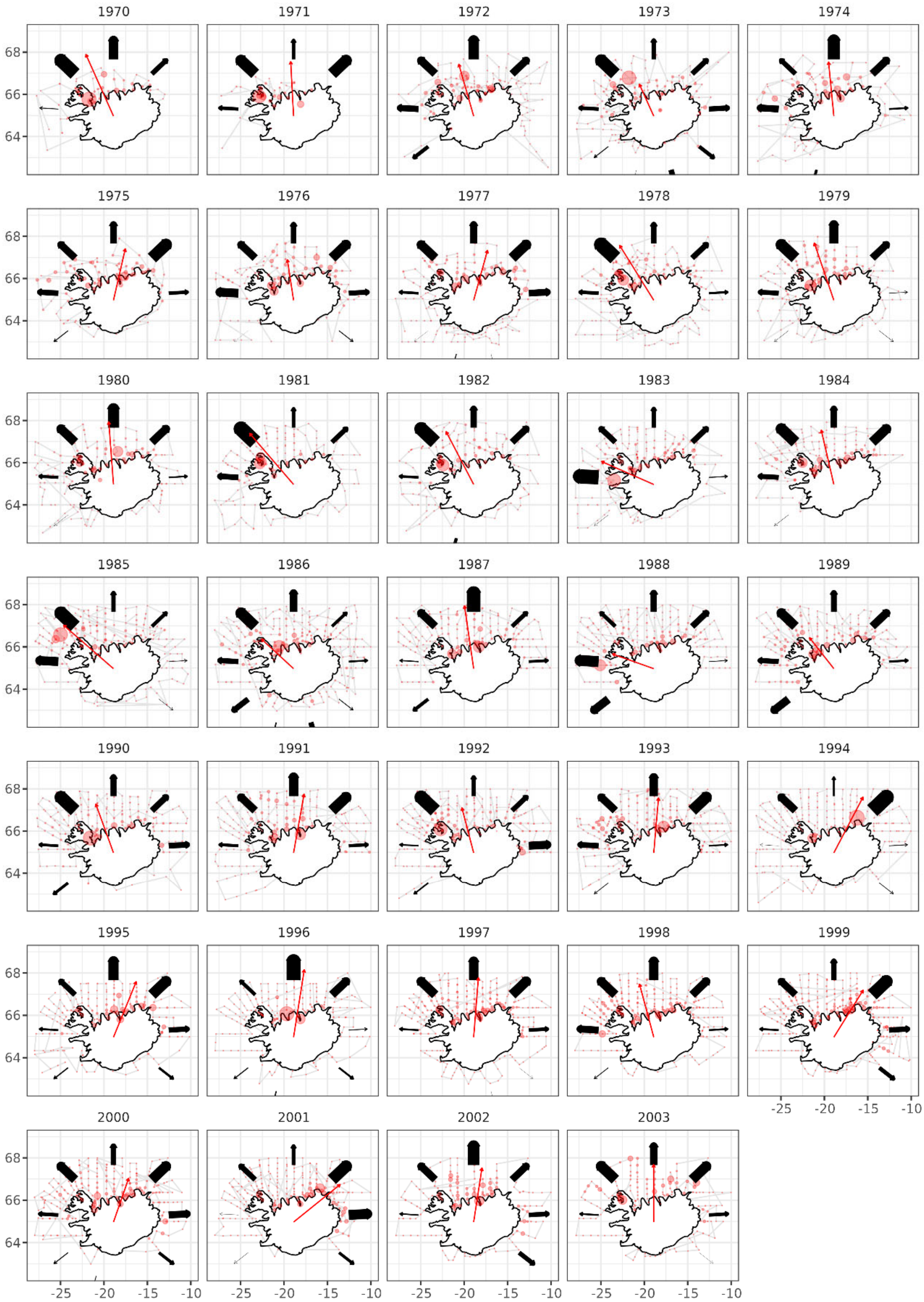

Figure 4. Distribution of 0-group cod in pelagic surveys in Icelandic waters. Raw catches of 0-group cod are indicated by circle size at each tow site, with lines between tows indicating the survey route. Black arrow thickness indicates the tendency of cod to be found in the indicated direction from the center of Iceland. The red arrow indicates the weighted mean tendency. See the main text for arrow calculation details.

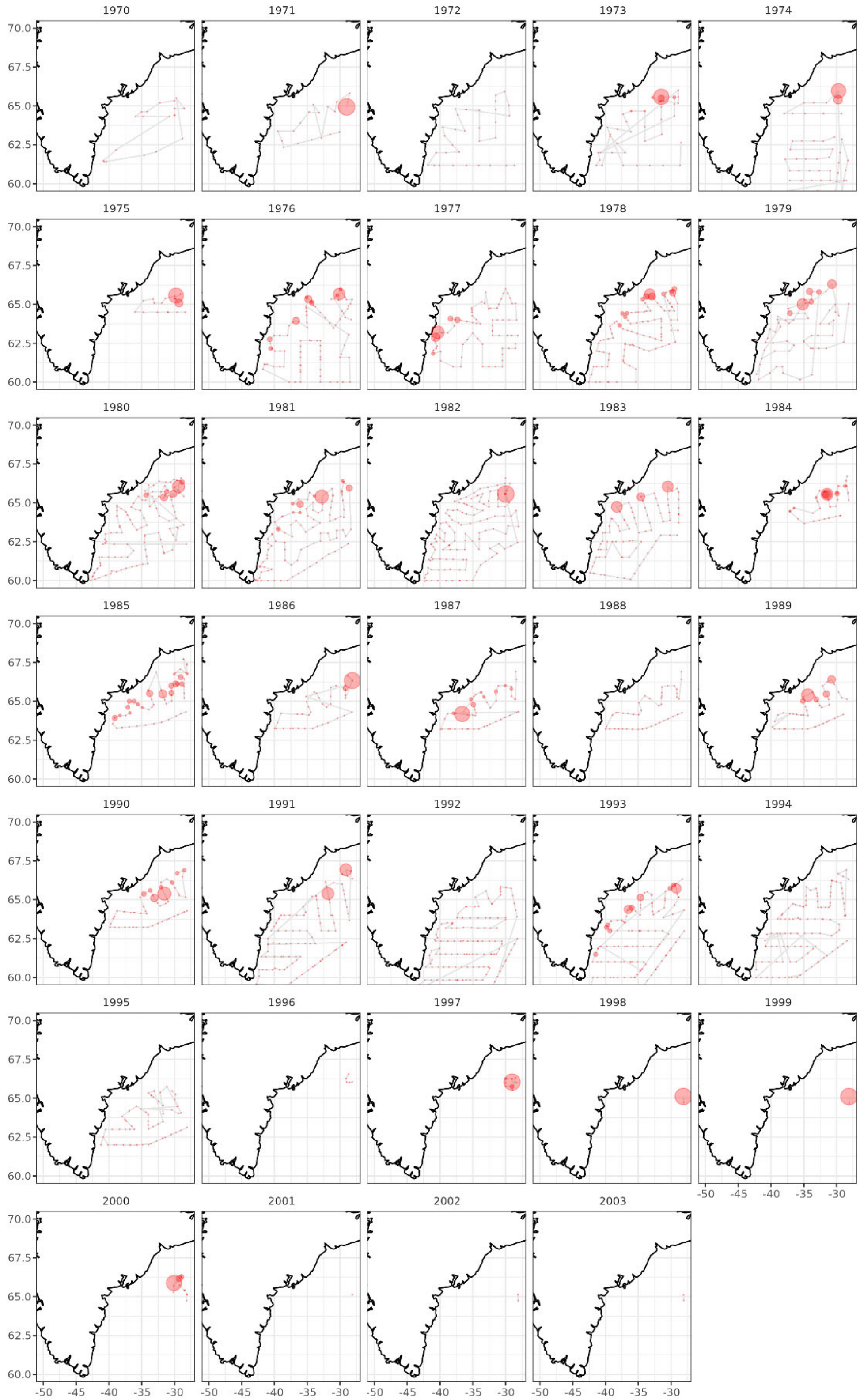

Figure 5. Distribution of 0-group cod in pelagic surveys in East-Greenland waters. Raw catches of 0-group cod are indicated by circle size at each tow site, with lines between tows indicating the survey route.

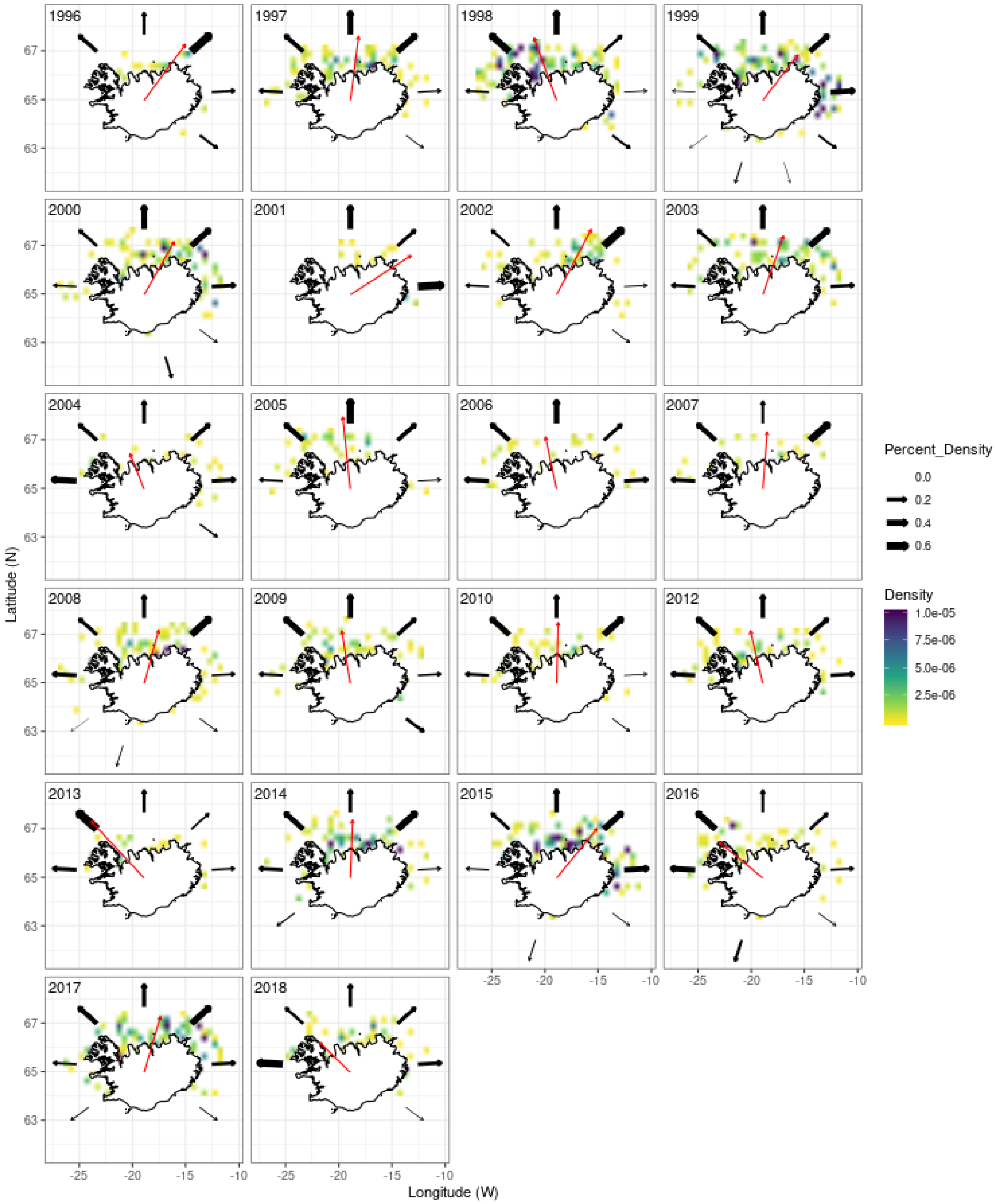

Figure 6. Distribution of 0-group cod in SMH. Black arrow thickness indicates the tendency of cod to be found in the indicated direction from the center of Iceland. The red arrow indicates the weighted mean tendency. See the main text for arrow calculation details.

Length distribution

Length data of 0-group cod are available from SMH, GRU and SMR. Mean length of 0-group cod in these surveys usually ranges from 7-10 cm (Figure 7). There was no clear temporal trend, although values tended to be lower in 1992-2001 than in 2004-2014.

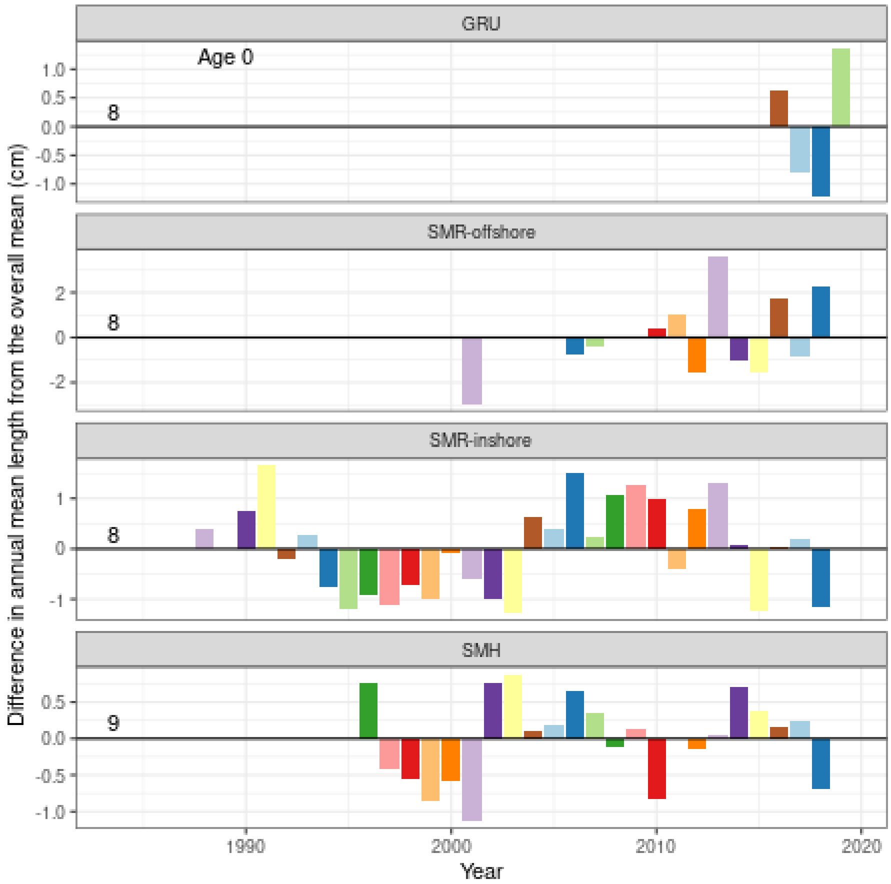

Figure 7. Annual mean length of 0-group cod shown for each survey as the difference from the overall survey mean. Colours correspond with year classes across Figures 7, 12, 17 and 22.

0-group cod were commonly caught in SMR in September and October. The average 0-group cod within each fjord and year, was usually between 7-10 cm, generally larger in Ísafjörður and Arnarfjörður, which are warmer compared to the fjords off the north coast (Figure 8). The smallest individuals (the 5% quantiles) usually ranged between 6-8 cm, but on few occasions, they were smaller or 4 and 5 cm.

The beam-trawl survey (GRU) in shallow areas has been conducted since 2016. In 2016, the survey was conducted from 12-20 September, in 2017 between 24 August and 4 September, in 2018 from 22 August to 3 September and in 2019 from 15-24 of July. The mean length of 0-group cod (< 14 cm) was 7.20 cm (the 5% quantiles were 5 cm and minimum length 4 cm). In Faxaflói and Breiðafjörður, the mean length was 9.65, 7.15, 7.86 and 6.26 cm (the 5% quantiles were 7, 6, 6 and 5.2 cm) in 2016-2019, respectively. In Westfjords and north of Iceland, corresponding mean lengths were 7.95, 7.15, 5.98 and 5.25 (the 5% quantiles were 6, 5, 5 and 4.5 cm). This difference between years is likely caused by different sampling times.

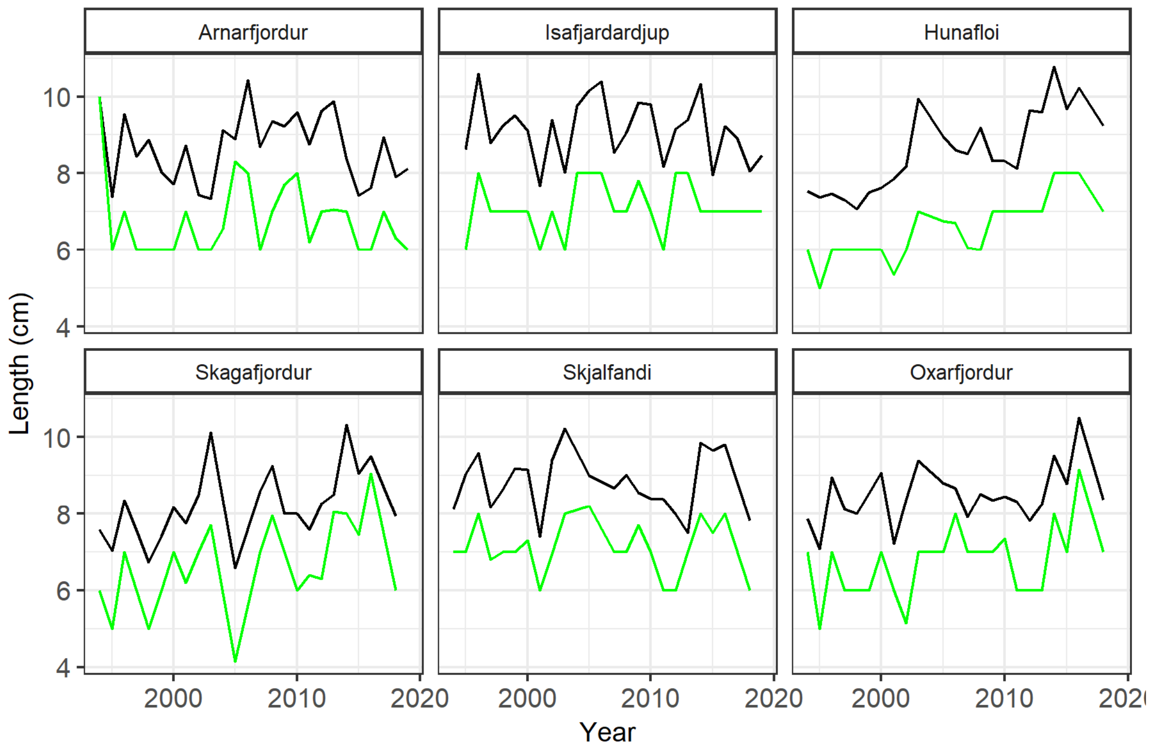

Figure 8. Average length of 0-group cod caught in inshore shrimp surveys from 1994-2019 (black line) and 5% quantiles (green line).

1-year-old cod

Abundance index

The abundance of 1-year-old cod in SMB was relatively high in 1985-1986, followed by a period of low abundance in 1987-1997 (except 1994) (Figure 9). In SMB 1997-2001, 1-year-old cod abundance was medium or relatively high, followed by a historically unprecedented low abundance in 2002. Since 2003, the abundance indices of 1-year-old cod fluctuated from low (2005, 2011, 2014, 2017) to high (2009, 2010, 2012, 2015, 2016) values but extremely low values have not been observed. Abundance indices of 1-year-old cod in SMH show a pattern similar to SMB, with years 1997 and 2002 showing extremely low values but 2010, 2012, 2015, 2016 showing high values (Figure 9).

Distribution

In SMB, 1-year-old cod were mainly found northwest, north and east of Iceland but only in low numbers in the south and southwest (Figure 10). In years with high abundances of 1-year-old cod, distributions tended to be easterly (1985, 2000, 2001, 2009, 2012), but in some high-abundance years 1-year-old cod were more evenly distributed clockwise from northwest to southeast (1986, 2010, 2013, 2015, 2016). In years with low abundance, the relative

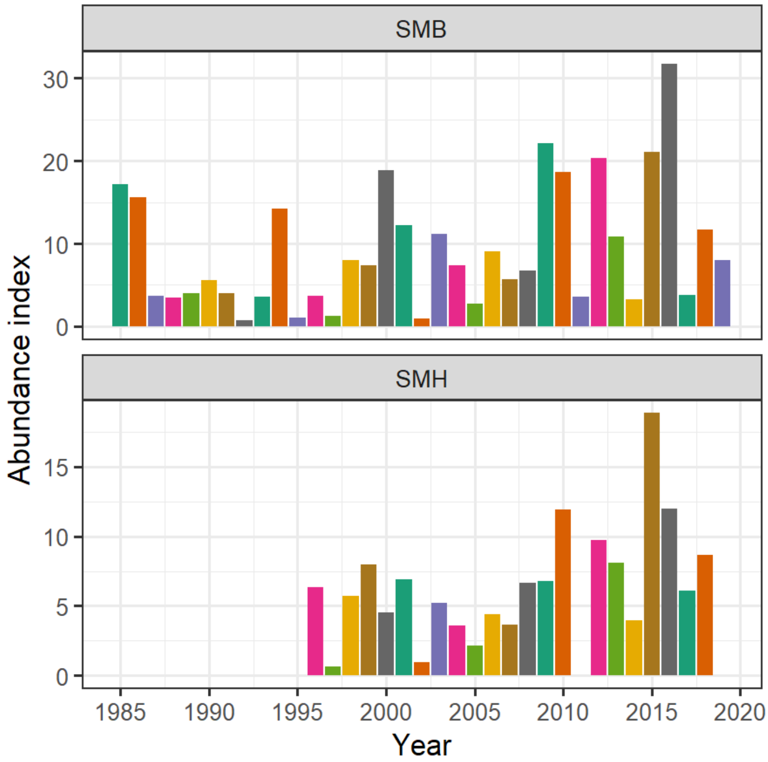

Figure 9. Abundance indices for 1-year-old cod in SMB and SMH.

abundance of 1-year-old cod was usually low off the east coast (most years in 1987-1997). This is reflected in the mean bearing of 1-year-old cod distribution plotted against time, indicating a shift towards more easterly distribution after 1999 (Figure 11).

In SMH, similar to SMB, the highest abundance of 1-year-old cod was found in areas clockwise from the northwest to the southeast (Appendix 2). Mean bearing tended to be 0-25°, similar to SMB in 1996-2018 (Figure 11).

In SMR, a higher abundance of 1-year-old cod was usually found inshore than offshore (Appendix 3). High abundance inside Arnarfjörður and Ísafjarðardjúp was the main reason for a more westerly distribution as compared to SMB and SMH. Inconsistent sampling (not all areas sampled throughout the study period) make comparisons between years/periods difficult.

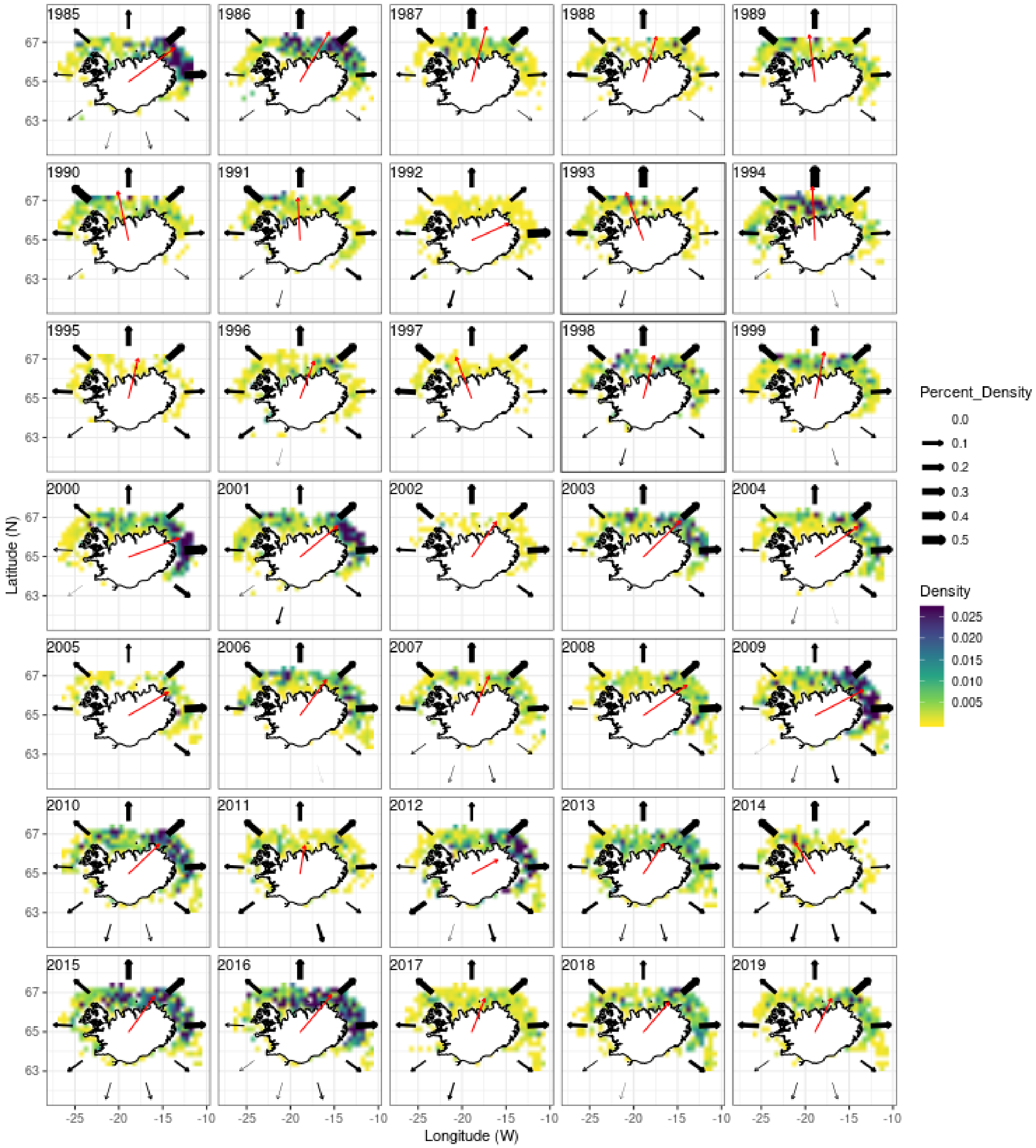

Figure 10. Distribution of 1-year-old cod in SMB. See legend for Figure 6.

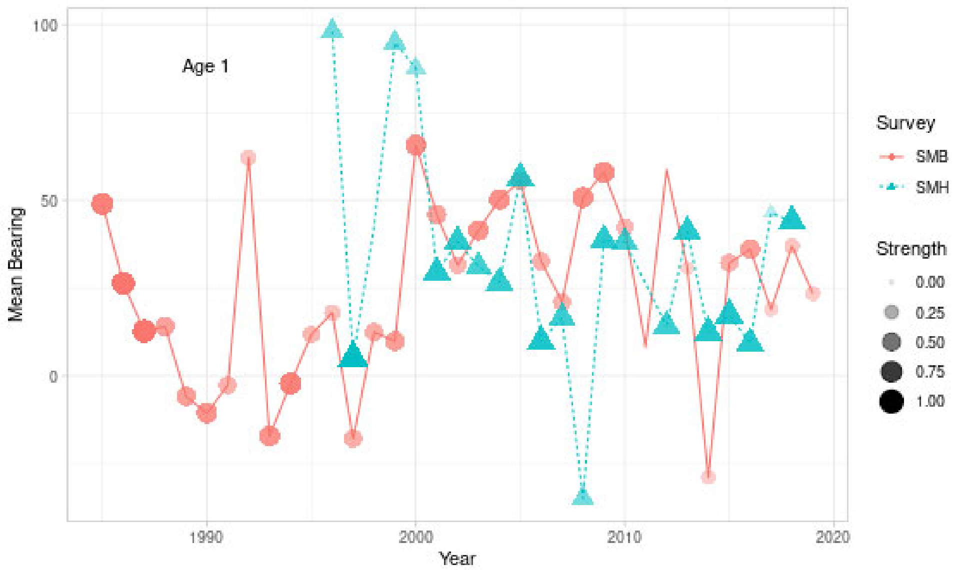

Figure 11. Mean bearing of 1-year-old cod abundance in SMB and SMH. A mean bearing of 0 indicates north, positive values indicate degrees east of north and negative values degrees west of north. Size and opacity of dots/triangles indicates how strongly directional the mean bearing is. Mean bearing and strength are the direction and length of red arrows in distribution plots.

Length distribution

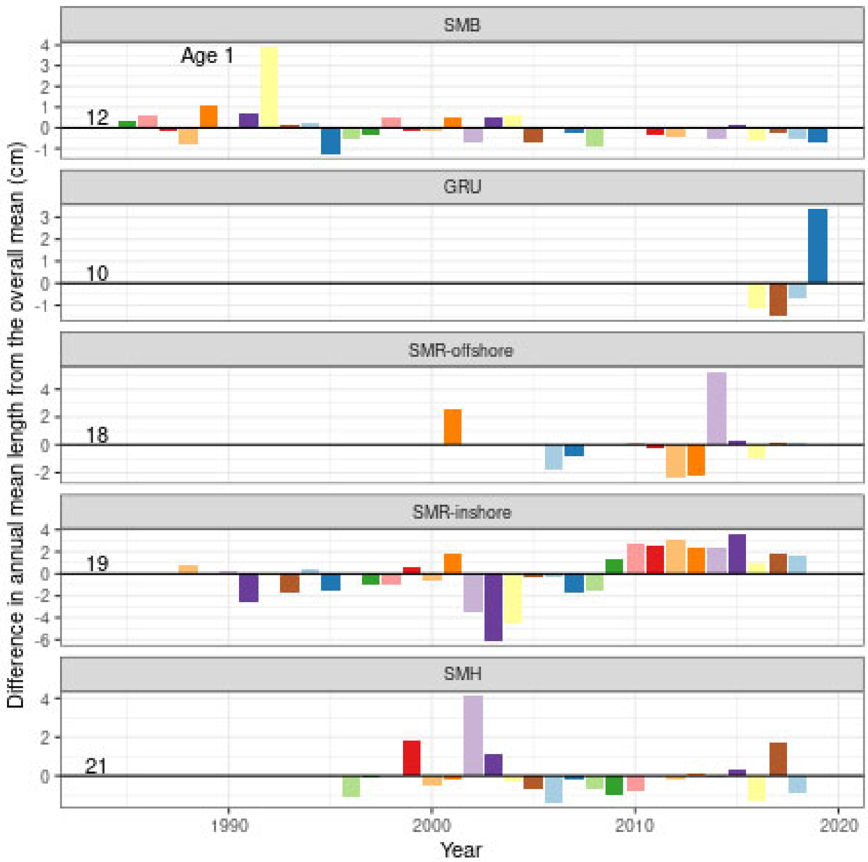

Figure 12. Annual mean length of 1-year-old cod shown for each survey as the difference from the overall survey mean. Colours correspond with cohorts across Figures 7, 12, 17 and 22.

In SMB, the mean length of 1-year-old cod ranged annually from 11 to 13 cm with few exceptions and little year-to-year variability (Figure 12). In SMH, sampling takes place about seven months later after the main growth period, so that the mean length of 1-year-old cod ranged from 19 to 23 cm, similar to the length range from the SMR-inshore (15-25 cm) that takes place at similar time of year.

Diet

From 1996-2017, a total of 0-23, 0-196 and 20-390 stomachs of 1-year-old cod were examined in SMB, SMR-inshore and SMH, respectively (Appendix 4). The mean proportion of 1-year-old cod with empty stomachs was usually in the range of 30-60% (Appendix 5).

The diet of 1-year-old cod in SMB was variable (Figure 13) but note the low sample size. Within fjords in autumn, shrimp was usually the most important prey of 1-year-old cod, but at the same time of year in a more extended area (SMH), shrimp is partly replaced by various fish and crustaceans.

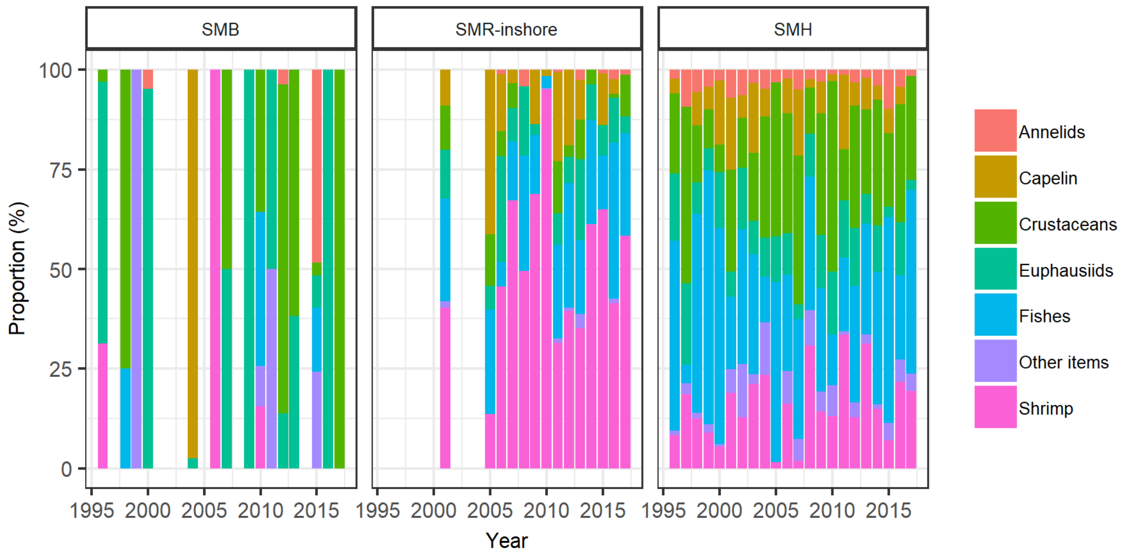

Figure 13. Proportion (% of total stomach content by weight) of the 7 main prey groups of 1-year-old cod in SMB, SMR-inshore and SMH.

2-year-old cod

Abundance index

For 2-year-old cod in SMB, the highest abundance indices were observed in the first two years (1985 and 1986) (Figure 14). As for 1-year-old cod, year classes 1997-2000 had relatively high abundances as 2-year-old. The four lowest values of 2-year-old cod abundance were those of year classes 1991, 1994, 1996 and 2001, just as observed for 1-year-old cod. Temporal changes in 2-year-old cod abundances in SMH were similar to SMB, but SMH showed relatively higher values in 2010-2018 compared to earlier years (Figure 14).

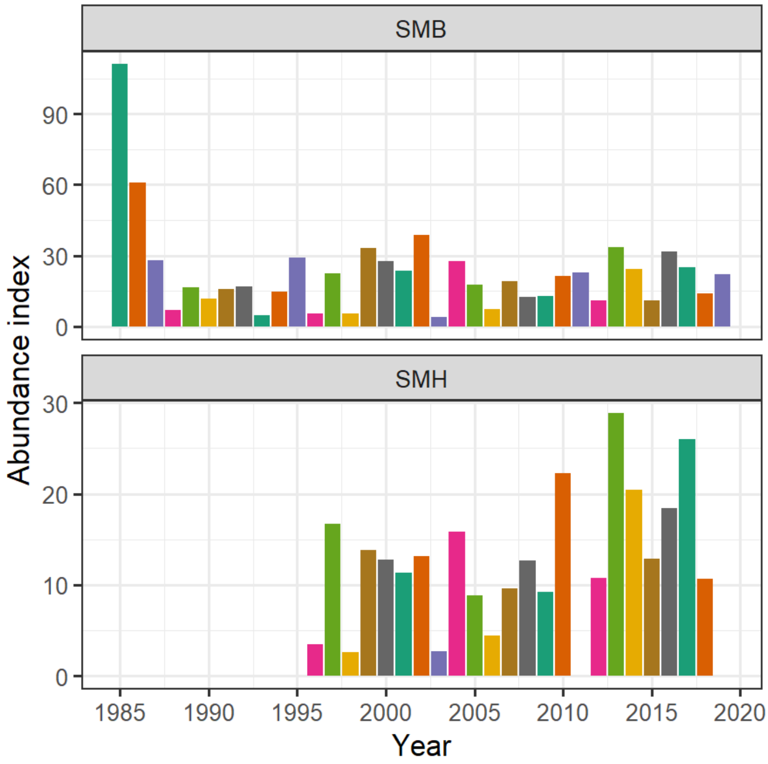

Figure 14. Abundance indices for 2-year-old in SMB and SMH.

Distribution

The distribution of 2-year-old cod in the three trawl surveys (Figure 15, Appendix 6, 7) resembled that of 1-year-old cod. The shift towards a more easterly distribution in mean bearing at the turn of the century can be seen for both SMB and SMH (Figure 16). The strong year class of 1983 had a relatively westerly distribution as 2-year-old fish in SMB 1985, and the same was apparent for 2-year-old (and 1-year old, Figure 11) in 1989-1991.

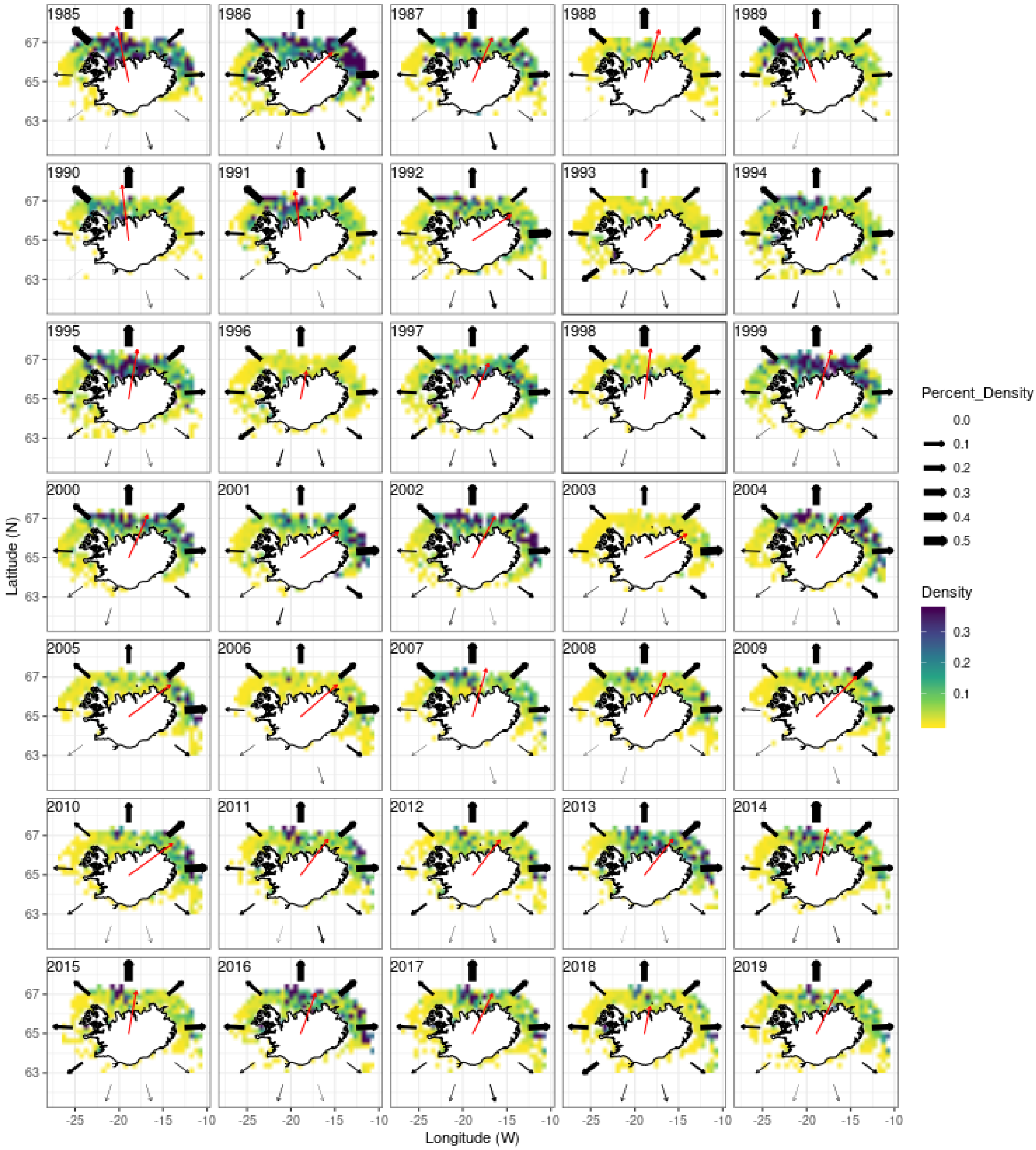

Figure 15. Distribution of 2-year-old cod in SMB. See legend for Figure 6.

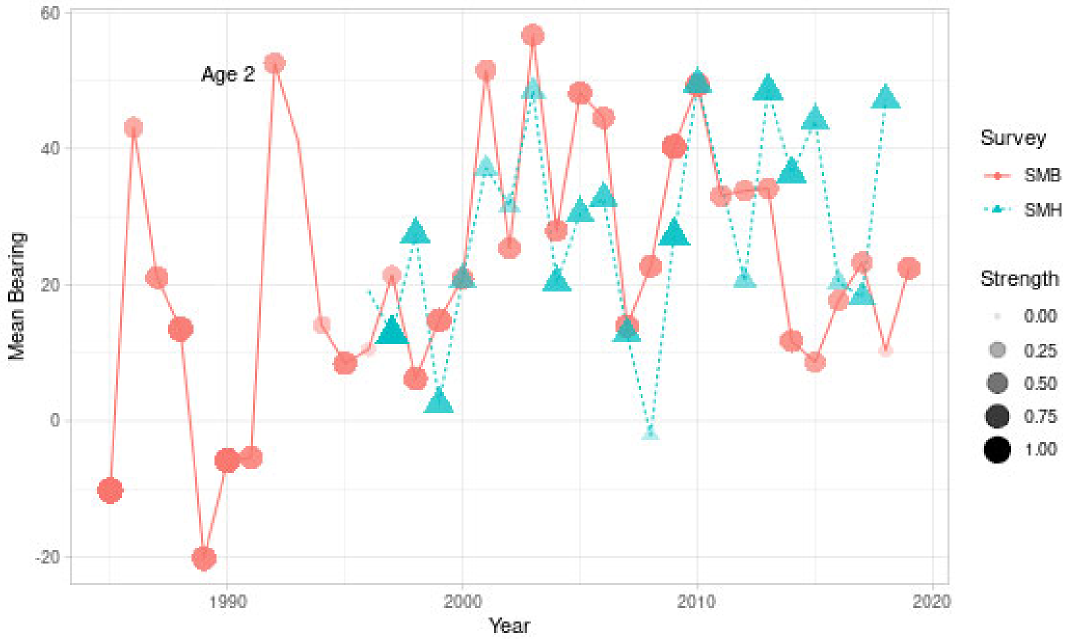

Figure 16. Mean bearing of 2-year-old cod abundance in SMB and SMH. See legend for Figure 11.

Length distribution

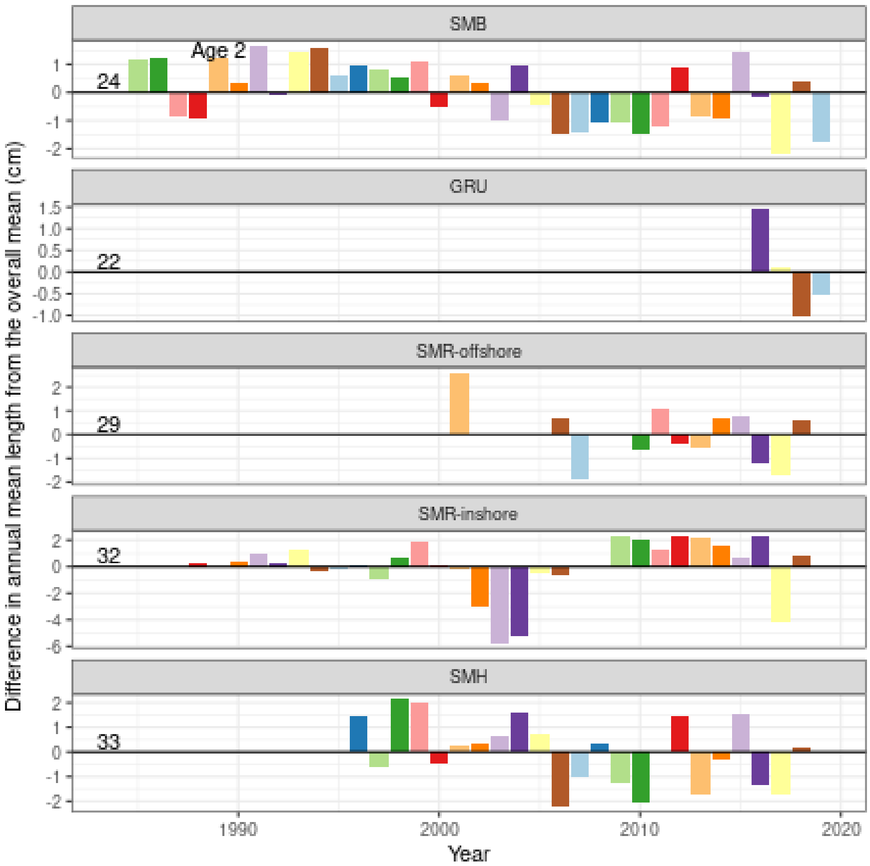

Figure 17. Annual mean length of 2-year-old cod shown for each survey as the difference from the overall survey mean. Colours correspond with cohorts across Figures 7, 12, 17 and 22.

In SMB, mean length of 2-year-old cod ranged from 22-26 cm, in SMR-offshore 27-31 cm, and in SMR-inshore and SMH 26-35 cm. In SMB, the mean length was usually above average before 2000, but below average after 2004. A similar trend can be seen in SMH (Figure 17).

Diet

From 1996-2017, a total of 64-930, 0-287 and 58-1591 stomachs of 2-year-old cod were examined in SMB, SMR and SMH, respectively (Appendix 4). For all surveys, the mean proportion of cod with empty stomachs was around 45% (Appendix 5).

Capelin was the most important prey item of 2-year-old cod in SMB, usually ranging from 25-60% of the diet (Figure 18). The proportion of capelin as prey was lower in SMH, when 2-year-old cod fed more on shrimp and different species of fish and crustaceans. Within the fjords in October (SMR-inshore), shrimp was the main prey composing about 25-75% of the diet.

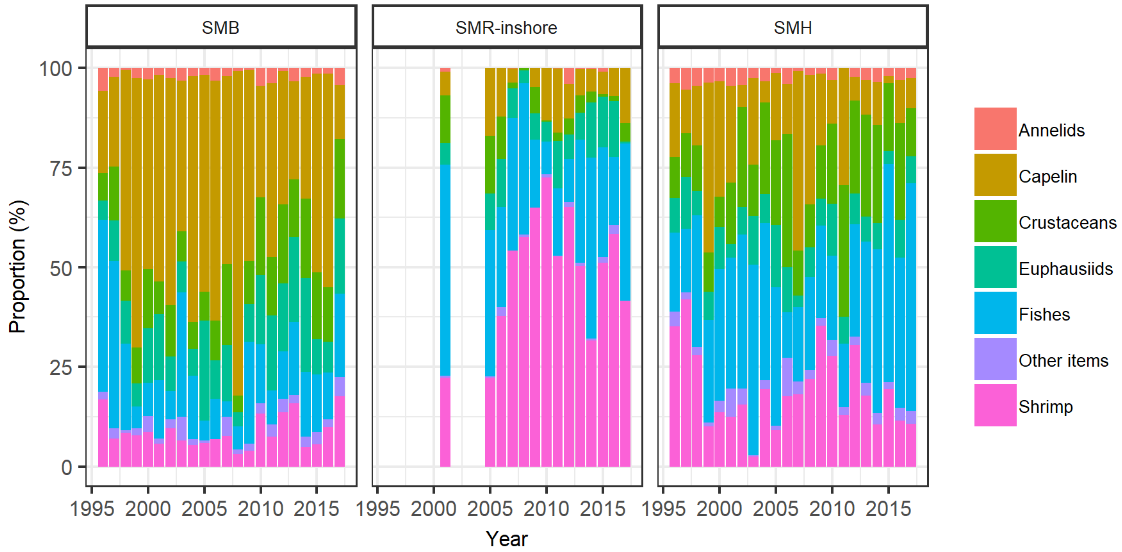

Figure 18. Proportion (% of total stomach content by weight) of the 7 main prey groups of 2-year-old cod in SMB, SMR-inshore and SMH.

3-year-old cod

Abundance index

The abundance index of 3-year-old cod was high in 1986-1988 (Figure 19). The fluctuations in the index were similar in SMB and SMH. However, in 2014, 2015 and 2017 the index was higher in SMH compared to adjacent years, which was not noticeably observed in SMB.

Distribution

The 3-year-old cod were mainly found in the northwest, north and east of Iceland (Figure 20). From 1985-1998, the distribution was more to the north and northwest, changed to more north-eastern direction after that time but since 2014 has moved again towards the north (Figure 21). However, a higher abundance of 3-year-old cod was found southwest and southeast of Iceland compared to younger cod (Figure 20 and Appendix 8). In July 1988-1995, 3-year-old cod was not abundant north of Iceland, but in 1996 the abundance increased (Appendix 9). In SMR, the abundance was higher northwest of Iceland in almost all years (exceptions in 1989, 1991, 2017 and 2018).

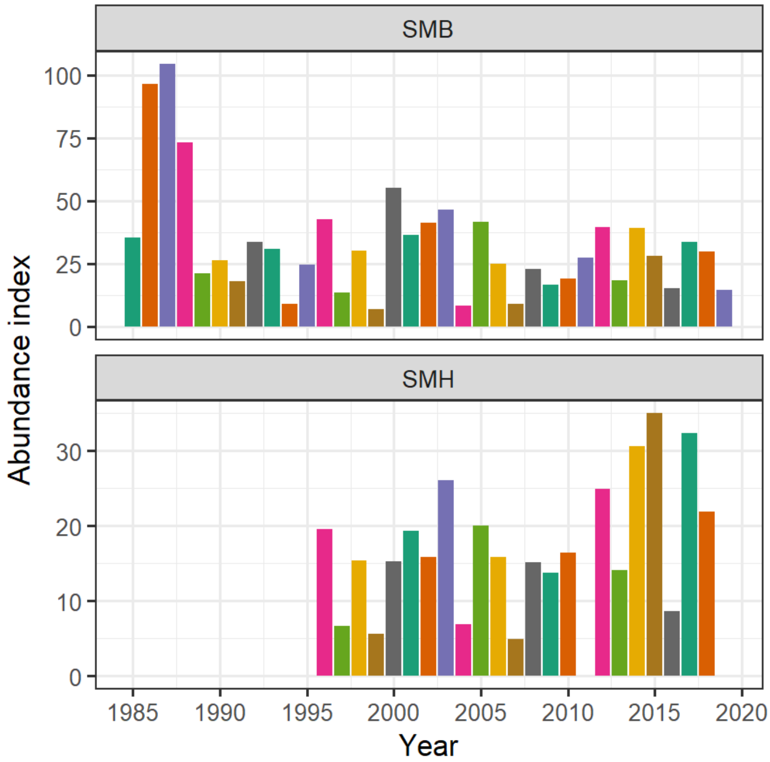

Figure 19. Abundance indices for 3-year-old cod in SMB and SMH.

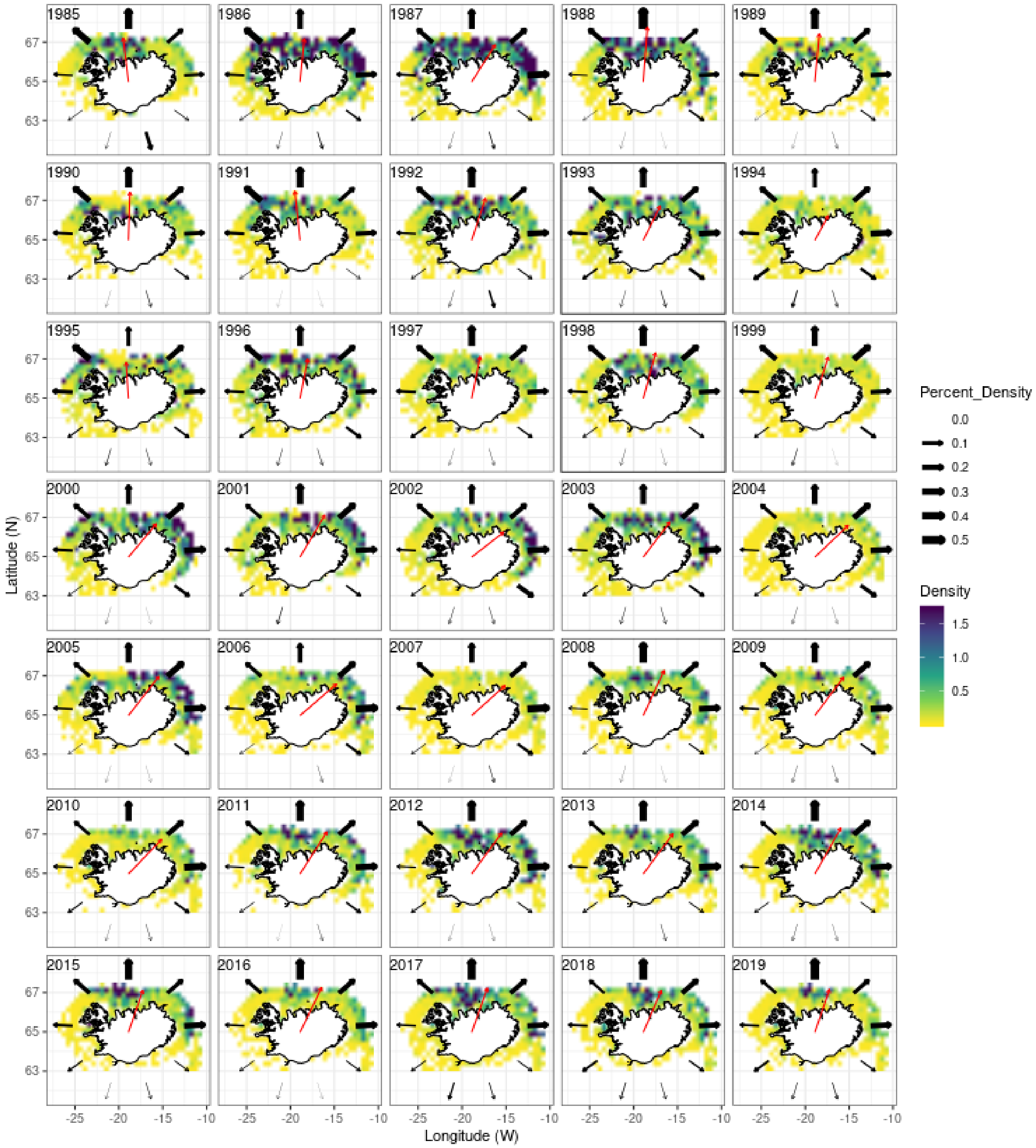

Figure 20. Distribution of 3-year-old cod in SMB. See legend for Figure 6.

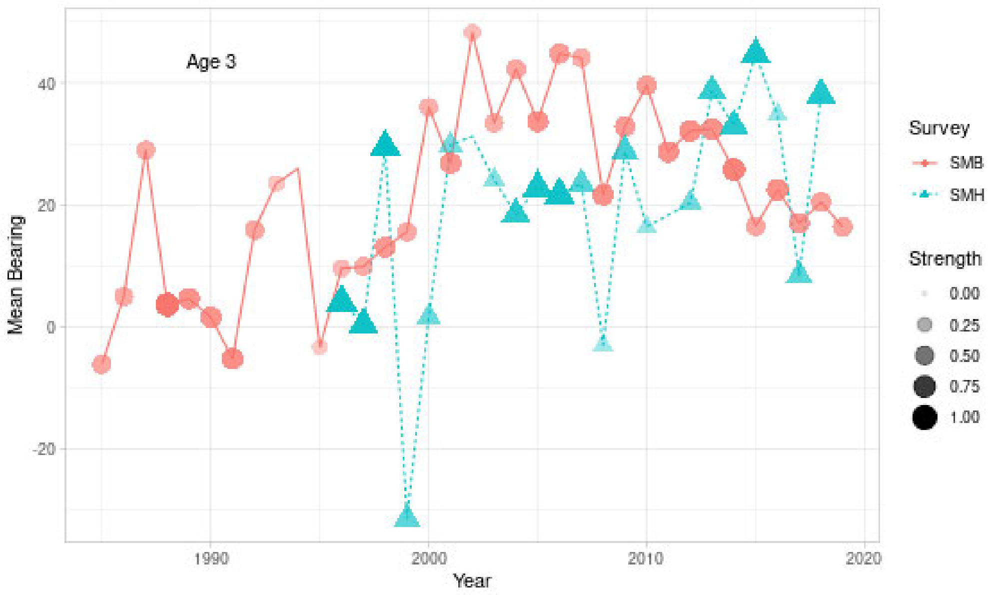

Figure 21. Mean bearing of 3-year-old cod abundance in SMB and SMH. See legend for Figure 11.

Length distribution

The mean length of 3-year-old cod ranged f33-40 cm in SMB and 35-43 cm north of Iceland in July (SMR-offshore). In SMR-inshore, the mean length of 3-year-old cod was 37-47 cm, but 41-47 cm in SMH. In general, 3-year-old cod was larger before 2006 but have been smaller after that time (Figure 22).

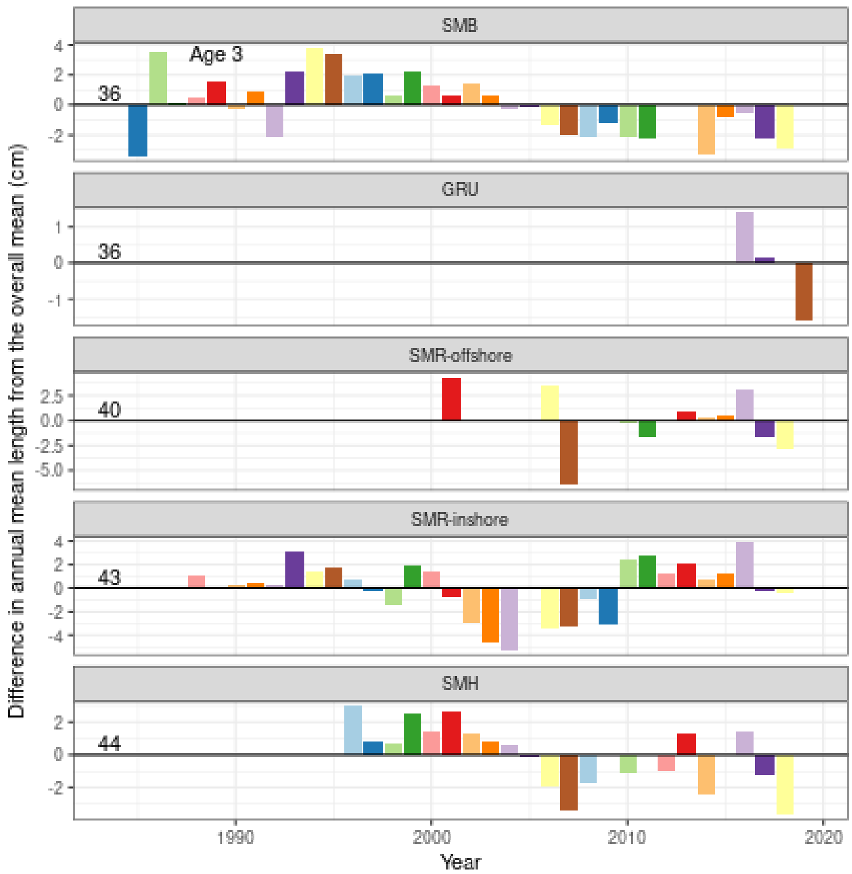

Figure 22. Annual mean length of 3-year-old cod shown for each survey as the difference from the overall survey mean. Colours correspond with cohorts across Figures 7, 12, 17 and 22.

Diet

From 1996 to 2017, 202-2391, 18-330 and 58-1591 stomachs from 3-year-old cod were examined in SMB, SMR-inshore and SMH, respectively (Appendix 4). The mean proportion of cod with empty stomachs was lowest in March (42.8%) compared with later in the year when the mean proportion was 57.9% and 53.9% in SMR-inshore and SMH, respectively (Appendix 5).

Capelin was the most important prey item in SMB, when it composed 50-75% of the diet of 3-year-old cod (Figure 23). Capelin was also an important prey in SMH, but the proportion of capelin found in the diet in SMH has been decreasing steadily over the past decade. Capelin is not an important prey in SMR-inshore areas where shrimp and various fish species were the main food items.

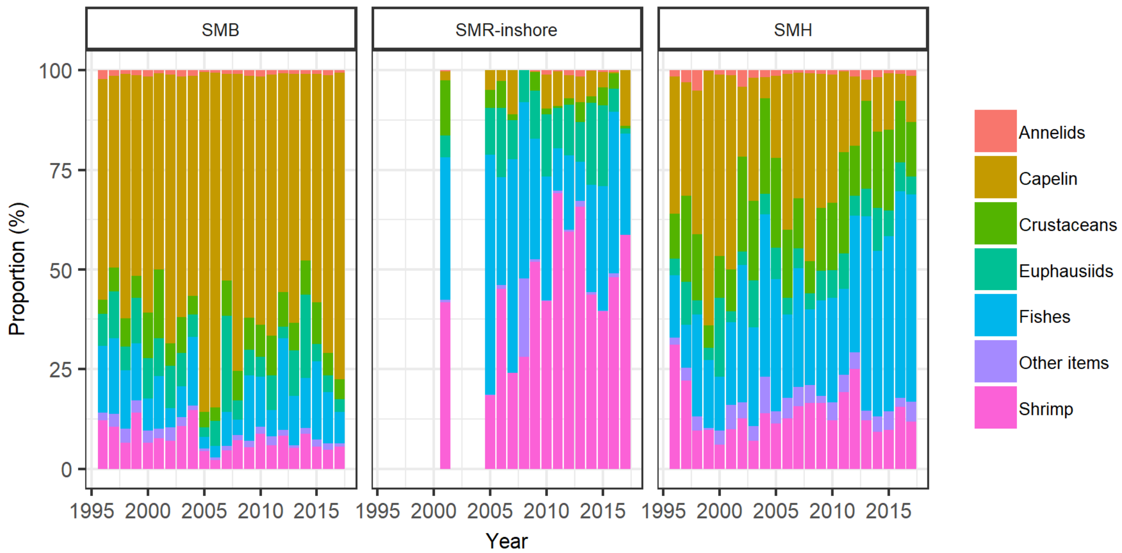

Figure 23. Proportion (% of total stomach content by weight) of the 7 main prey groups of 3-year-old cod in SMB, SMR-inshore and SMH.

Correlation of year-class abundances

A significant correlation was found between cod abundance (base-10 log scale) at a specific age and cod one year older in the same survey (Figure 24, 25, 26). Lower degree of correlation was between 0-year-old cod and 1-year-old cod in SMH (Figure 25) but improved with increasing age.

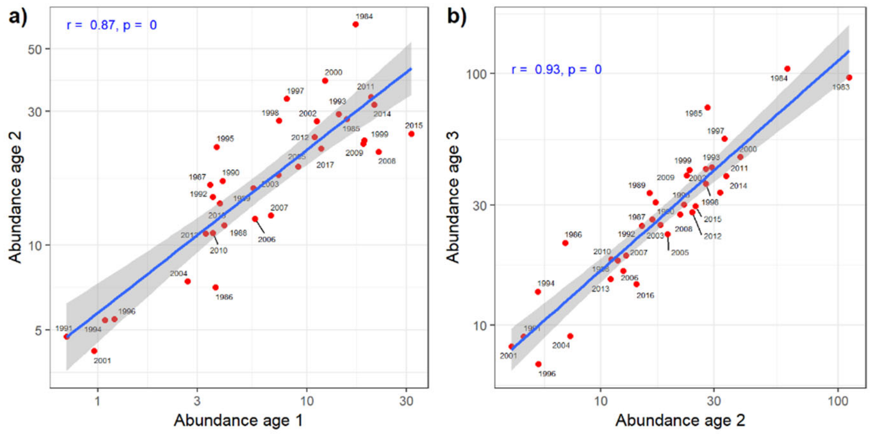

Figure 24. Pearson correlation between abundance indices (in millions of fish) of cod at age x (x-axis) and cod at age x+1 (y-axis) in SMB. Labels indicate year classes. Axes are base-10 log scale. Grey bands show 95% confidence intervals for predictions from linear models.

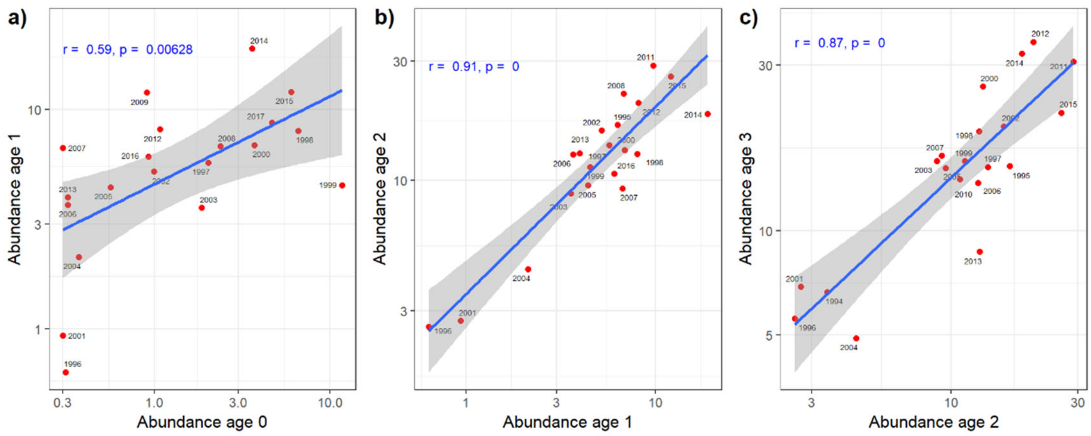

Figure 25. Pearson correlation between abundance indices (in millions of fish) of cod at age x (x-axis) and cod at age x+1 (y-axis) in SMH. Labels indicate year classes. Axes are base-10 log scale. Grey bands show 95% confidence intervals for predictions from linear models.

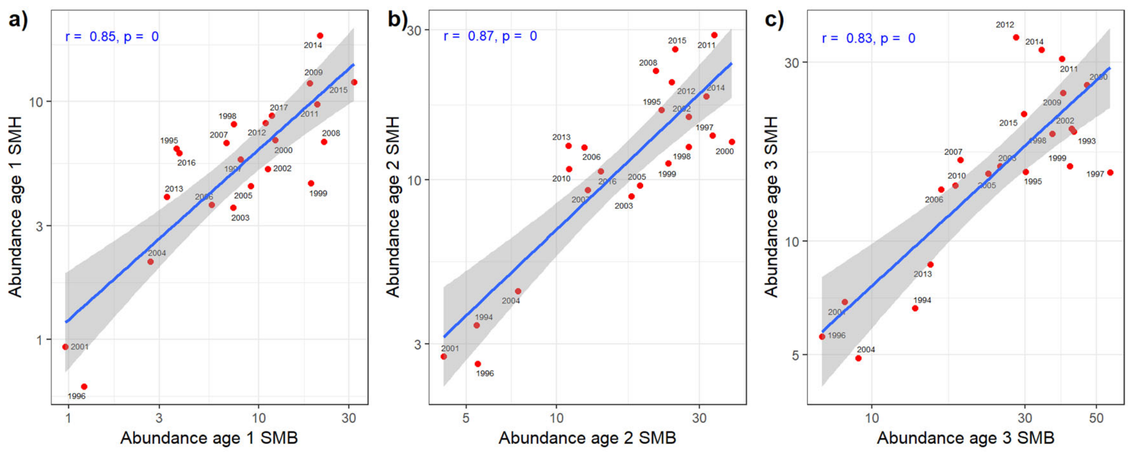

Figure 26. Pearson correlation between abundance indices (in millions of fish) of cod at age x in SMB (x-axis) and cod at the same age in SMH the same year (y-axis). Labels indicate year classes. Axes are base-10 log scale. Grey bands show 95% confidence intervals for predictions from linear models.

Spawning stock – recruitment relationship

Over the past 65 years, the spawning stock biomass (SSB) of Icelandic cod has ranged between 122 and 942 thousand tonnes, and at the same time recruitment at age 3 (R) has been estimated between 71 and 368 million fish (Figure 27a). The spawning stock biomass was high from 1955-1960 and rapidly declined until 1976. Since then it has fluctuated at low levels until it started to increase again in 2008 (Figure 27a). Recruitment fluctuated greatly from 1955 to 1986 (corresponding to year classes 1952 to 1983) (Figure 27b), including a number of very high recruitment events (>200 million individuals). From 1987 to 2007, a handful of very small year classes (<100 million individuals) were estimated. No year class above 200 million individuals has occurred after 1986.

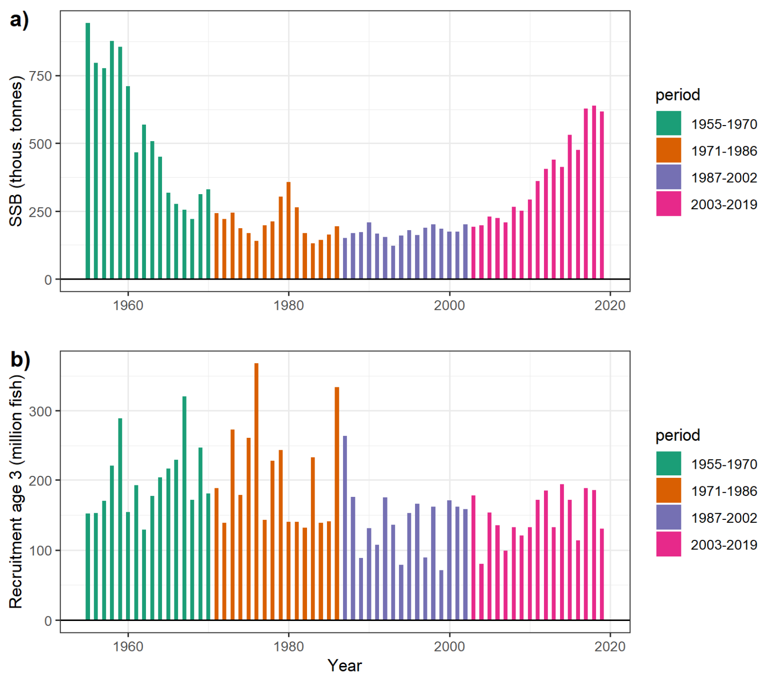

Figure 27. a) Spawning stock biomass (thousand tonnes) and b) recruitment (millions of 3-year old) of cod in Icelandic waters.

There are clear differences in SSB-R relationships between periods. In 1955-1970, large but highly variable SSBs produced variable, but usually above-average, recruitment (Figure 28). In contrast, in the period 1987-2002 both SSB and recruitment were consistently low. In 1971-1986, small SSBs produced either strong or poor year classes, the 1973 and 1983 year classes being the two largest in the time series. In the latest period, 2003-2016, recruitment has usually been below average despite increasing SSB (Figure 28).

Overall, below average spawning stocks appear less likely to produce above average recruitment (only 14 out of 42 years). On the other hand, large spawning stocks appear more likely to produce strong than poor recruitment (13 out of 20 years; Figure 28). Using a two-tailed Fisher's exact test, the null hypothesis that the probability of getting strong recruitment is the same whether SSB is above or below average, was rejected (P = 0.02825).

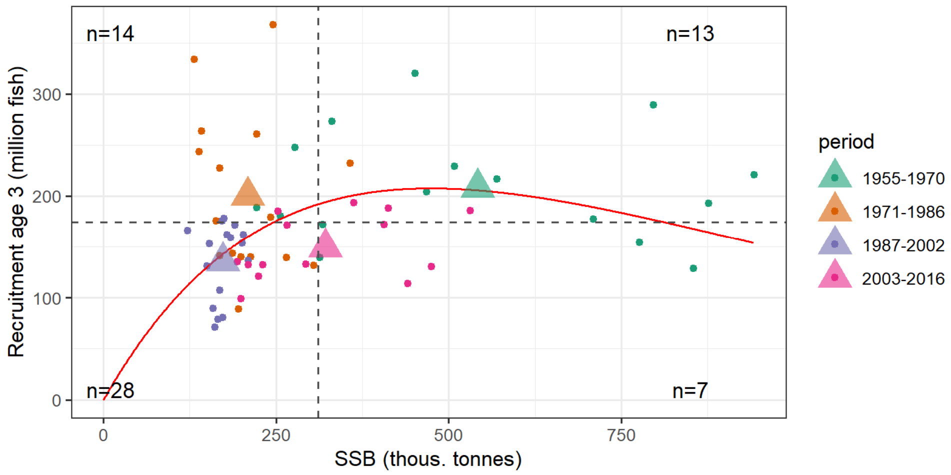

Figure 28. Spawning stock biomass (SSB in thousand tonnes) and recruitment at age 3 (millions of fish) three years later based on stock assessment of Icelandic cod. The red curve is fitted based on the Ricker function (see Methods). Dots indicate individual years and colours represent four equally long 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.

When analysing the SSB-R relationships for Icelandic cod, differences between periods need to be kept in mind with higher values in the beginning of the period but lower values more apparent in later years. Residuals from the Ricker function show a temporal trend, from being mostly positive for year classes 1955-1985 to mostly negative thereafter (Figure 29). This means that for a given spawning stock biomass, recruitment is poorer in recent years as compared to 1955-1985.

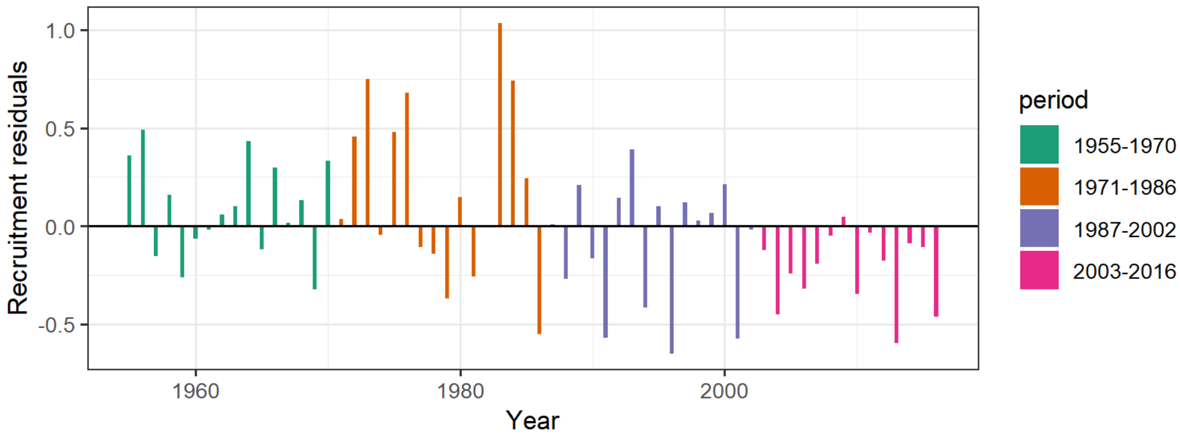

Figure 29. Residuals from the Ricker curve (see Figure 28) as a function of time.

Discussion

In this report we have summarized available information on the first life stages of cod in Icelandic waters as well as compiled data from the MFRI database. In the past 25 years, various aspects of cod have been studied. An effort was made to study the early life of Icelandic cod and several papers were published between 1998-2003 (e.g Begg and Marteinsdottir, 2002a; Marteinsdottir et al., 2000b, 2000a; Marteinsdottir and Begg, 2002; Marteinsdottir and Steinarsson, 1998). Soon after, emphasis was on stock structure (Jónsdóttir *et al.*, 2006a, 2006b; Pampoulie *et al.*, 2006; Petursdottir *et al.*, 2006) and drift of larvae (Brickman *et al.*, 2007a; Jonasson *et al.*, 2009). In the past years, tagging data have been used to study the life history of Icelandic cod (Grabowski *et al.*, 2011, 2014, 2015; Thorsteinsson *et al.*, 2012; Jónsdóttir *et al.*, 2014; Sólmundsson *et al.*, 2015, 2018). Hence, we have a good overview of some of the basic factors in the life history of Icelandic cod. However, knowledge is still lacking on what controls recruitment variability, which is not surprising as the answer to this question has remained a mystery to fisheries scientists studying a variety of marine species for centuries. It may be that we will never fully understand this due to the various mechanisms interacting to influence dynamics throughout the life of an individual as they are either poorly known or only hold for a specific time period (Myers, 1998). Further, a good example of the complexity of this matter was discussed in Brander and Mohn (2004), as the contrasting effect of temperature on recruitment of the Icelandic cod stock. As such, temperature has been documented to both have positive (Planque and Frédou, 1999) and negative (Brander, 2000) effects on recruitment, most likely arriving from different spatial data source of temperature. In the same meta-analysis, it was documented that the NAO index had positive effect on recruitment of the Icelandic stock but negative effect on the North-, Baltic- and the Irish Sea cod stocks (Brander and Mohn, 2004).

One of the factors that have been noted to affect recruitment is biocomplexity of the stock (Hilborn *et al.*, 2003). Both larger and smaller scale segregation of spawning aggregations around the country have been noted. The contribution of each component varies with their productivity. Despite several spawning aggregations and prolonged spawning time of each one, only a few days' egg production may result in successful recruitment due to variable survival conditions. This may be studied by estimating hatch date and spawning area within a given year. The observed diversity in spawning components has been proposed as an explanation for the relatively stable recruitment around Iceland, compared to other stocks in the North Atlantic (Marteinsdottir *et al.*, 2000a). With greater distributional coverage, juveniles have a greater chance of survival. Contribution from the southwest spawning area is variable and when low, may have negative effect on overall recruitment. In 1995 and 1996, relatively few 0-group cod were estimated to have originated from the southwest spawning area and the recruitment indices of those year classes were exceptionally low (Marteinsdottir *et al.*, 2000a). Spawning in the southwest area has decreased in the past years (Bogason *et al.*, 2019), which may negatively affect the overall recruitment of the Icelandic cod stock, but this still needs to be tested. Less productive populations may be more vulnerable to heavy fishing pressure than more productive ones (Jennings *et al.*, 1998). Therefore, a major concern is to distinguish the different components and try to prevent overexploitation.

Commercial fishing generally removes large and old individuals from fish stocks, thereby reducing age diversity among spawners. Age diversity is an important component in stock-recruitment models and two of the largest year classes in Icelandic waters after 1950 (the 1983 and 1984 year classes) were generated during period of high age diversity (Marteinsdottir and Thorarinsson, 1998). Decreased age diversity may reduce ranges in spawning period and spawning areas, which may lead to reduced spatial distribution of fish eggs and larvae and more homogeneous ambient environment within each year class. This may lead to reduced buffering against negative environmental influences and lower recruitment. Furthermore, total egg production is higher in years with older and larger females (Stige *et al.*, 2017), which produce more viable eggs and larvae (Marteinsdottir and Steinarsson, 1998). Hence, in the past years, emphasis was on increasing the proportion of older females in the Icelandic cod spawning stock, a strategy that has succeeded (MFRI, 2018b), but its impacts on recruitment have not been comprehensively studied.

From 1985, recruitment has been poorer given the same spawning stock biomass as compared with year classes before that time. Even though spawning stock biomass and recruitment are functionally related (Ricker, 1954; Beverton and Holt, 1957), this relationship is often poorly defined (Marteinsdottir and Thorarinsson, 1998), as it is heavily dependent on early mortality rates of recruits, the causes of which are not always clear. Recruitment is a complicated process in which many factors can have an effect, so that the relationship between spawning stock and recruits does not fully explain all the variability in recruitment (King, 1995). Like with many marine species, the year-class strength of Atlantic cod is mainly determined during the first weeks, months and/or year of life (Campana *et al.*, 1989). During this time, recruits begin life as pelagic eggs and larvae that drift from spawning areas to nursery areas, where they shift from pelagic to benthic habitats. Studying the dynamics of marine populations at this life stage remains a great challenge, as currents, temperature, food availability and predation are among the many factors that may influence the survival in the first year. Cod produce millions of eggs, even at low spawning biomass, but the larval mortality is very high. Consequently, small changes in survival of larvae can result in highly variable year class sizes (Hjort, 1914).

Density of juveniles (per square meter) is higher in inshore areas compared to offshore. The inshore areas therefore play an important role as nursery areas for juvenile cod. Cod and haddock (*Melanogrammus aeglefinus*), are closely related demersal species that co-occur in many regions in the North Atlantic. The nursery areas of these species vary but they seem to settle in relatively shallow waters but haddock quickly move to deeper waters (Bastrikin *et al.*, 2018). Juvenile cod settling in shallow waters also moves to deeper waters with increasing age (Dalley and Anderson, 2011). The haddock biomass increased greatly in Icelandic waters after the appearance of the large 2003 year class. Furthermore, distributional changes were observed for haddock, which distribution became more northerly (Solmundsson *et al.*, 2010; Valtysson and Jonsson, 2018). It is possible that the increased abundance of haddock north of Iceland also has led to slower growth and higher mortality of cod and haddock juveniles, through density-dependent effects of increased competition for food and space.

Conclusion

Population dynamics during the first years are often poorly known and may be extremely hard to study in the marine environment. No single survey in Icelandic waters is dedicated to study recruitment of cod and haddock. Monitoring of the distribution of early life history stages has been done in several ecosystems, including Icelandic waters (the 0-group pelagic survey from 1970 to 2003 and sporadic larval surveys). However, connecting information from such surveys to the recruitment of the target species have proven difficult. The first months are characterised by very high mortality and less than 1% of spawned eggs survive the first year. Furthermore, a proportion of eggs and larvae may drift away from Iceland to nursery areas off Greenland. Therefore, it may be more reliable to try to estimate the year-class size after settlement of the juveniles. However, relating 0-group cod abundances to the abundances of older ages is also difficult, both from SMH (Figure 25) and SMR, which may not be suitably designed to represent these age classes due to the limited sampling area (Skúladóttir *et al.*, 2003).

Some information can be obtained from other surveys conducted by the MFRI that focus on older life stages and/or other species, as the combined information from data sampled in these surveys provide overviews of distributions, lengths and abundances of cod after settlement. Information on the pelagic stages are, however, lacking, that is from the time of spawning until settlement of the cod juveniles. There are several topics that should be addressed in the future:

- Variability in recruitment. Can variability in recruitment be related to factors like temperature, freshwater discharge, inflow of Atlantic water to the northern area, and primary production (chlorophyll)? Why have no large year classes appeared despite increasing spawning stock biomass in the past years?
- Spawning time and drift. More information is needed on variability in drift of eggs and larvae to nursery areas and its relationship to hatch dates and origin.
- Nursery areas. Knowledge on depth distribution and seasonal migrations of juveniles in nursery areas is limited.
- Diet and condition. Knowledge of feeding ecology, growth and condition of larvae and juveniles in Icelandic waters is limited.
- Spawning stock biomass has increased in the past years. How does this influence L_{50}, A_{50}, and age distribution in the stock?

Some of the questions of interest have already been looked at but it would be worthwhile to revisit them as we have more data and longer time series. Some of the research questions are possible to study without additional sampling but others would require additional data, some of which can be collected within ongoing annual surveys. Those include more detailed sampling of juvenile cod in autumn, such as collecting weight data, stomach samples and otolith samples to estimate age (daily increments), hatching date and likely spawning site. However, a specific sampling effort is required for studying cod larvae in June/July requiring additional days at sea.

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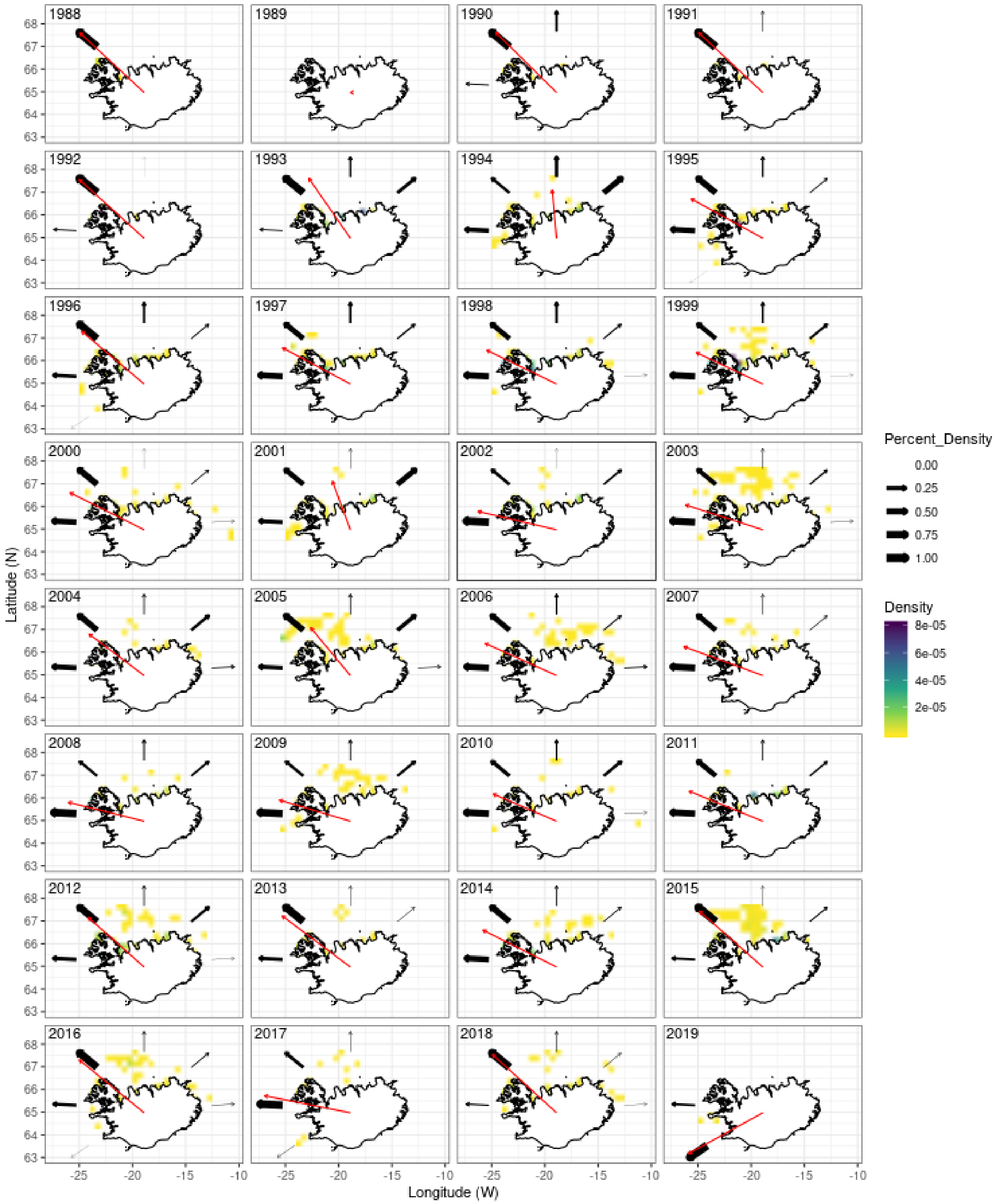
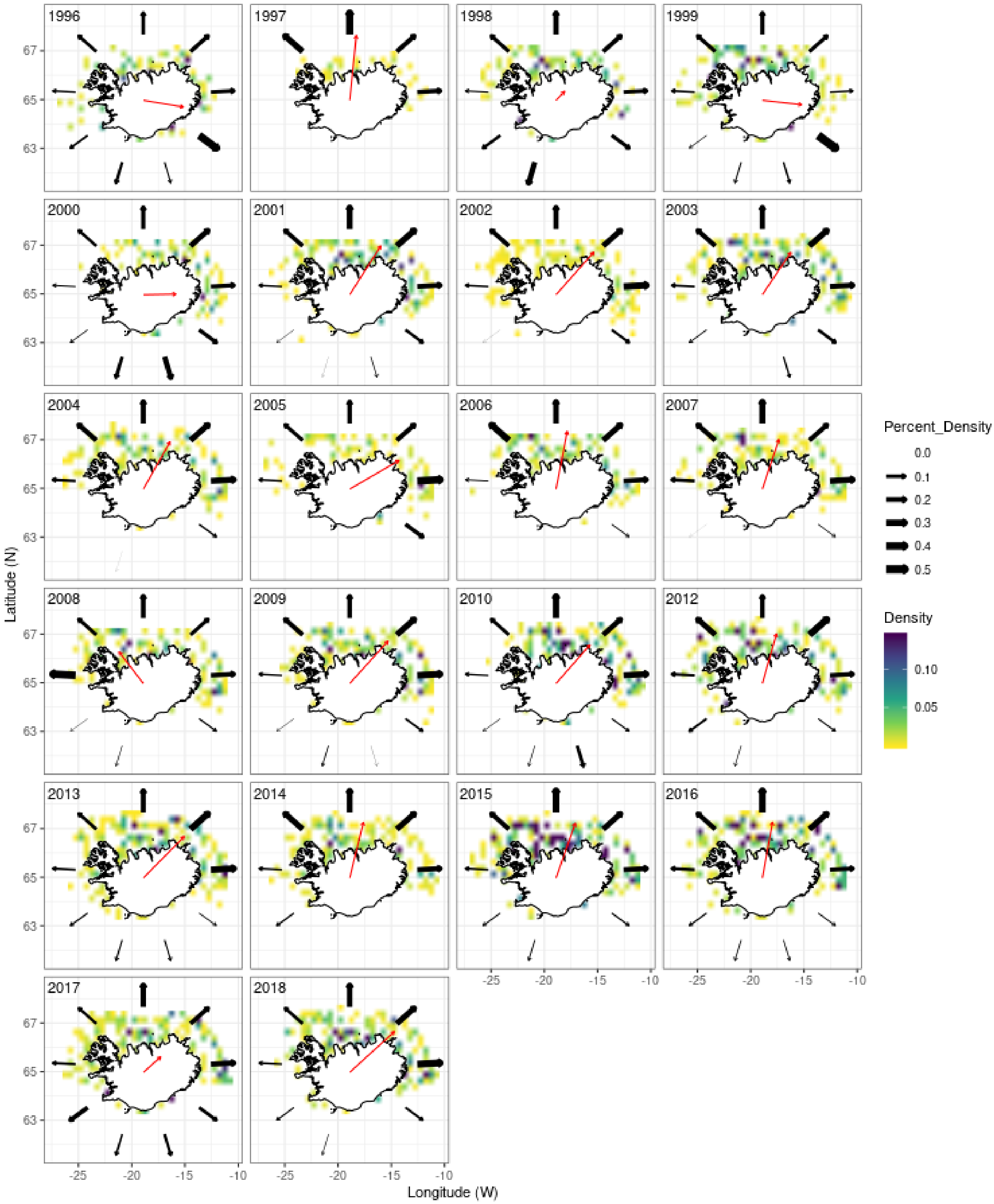
Appendix

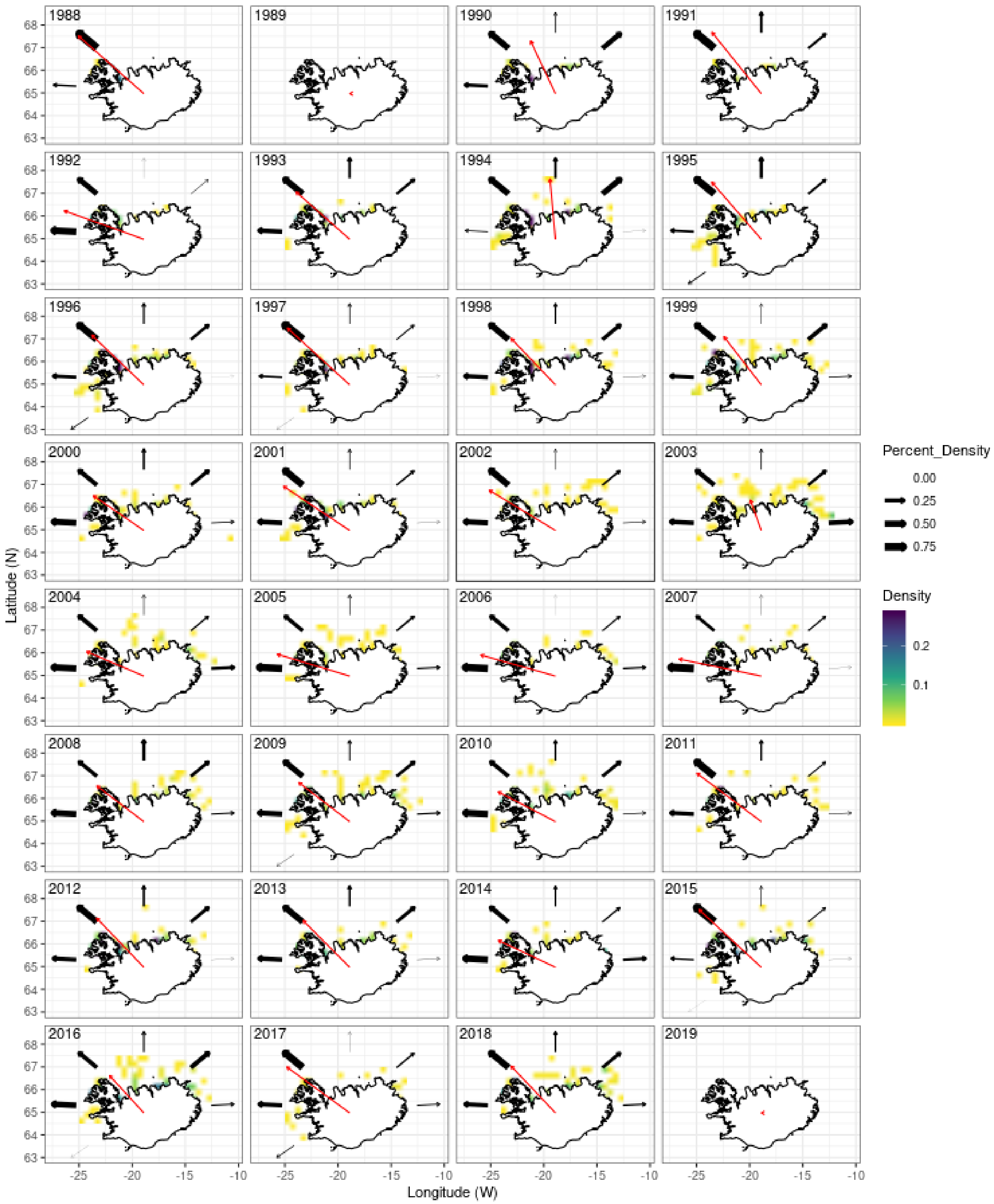
***Appendix 1**. Distribution of 0-group cod in SMR inshore and offshore. See legend for Figure 6.*



Appendix 2. *Distribution of 1-year-old cod in SMH. See legend for Figure 6.*



Appendix 3. *Distribution of 1-year-old cod in SMR inshore and offshore. See legend for Figure 6.*



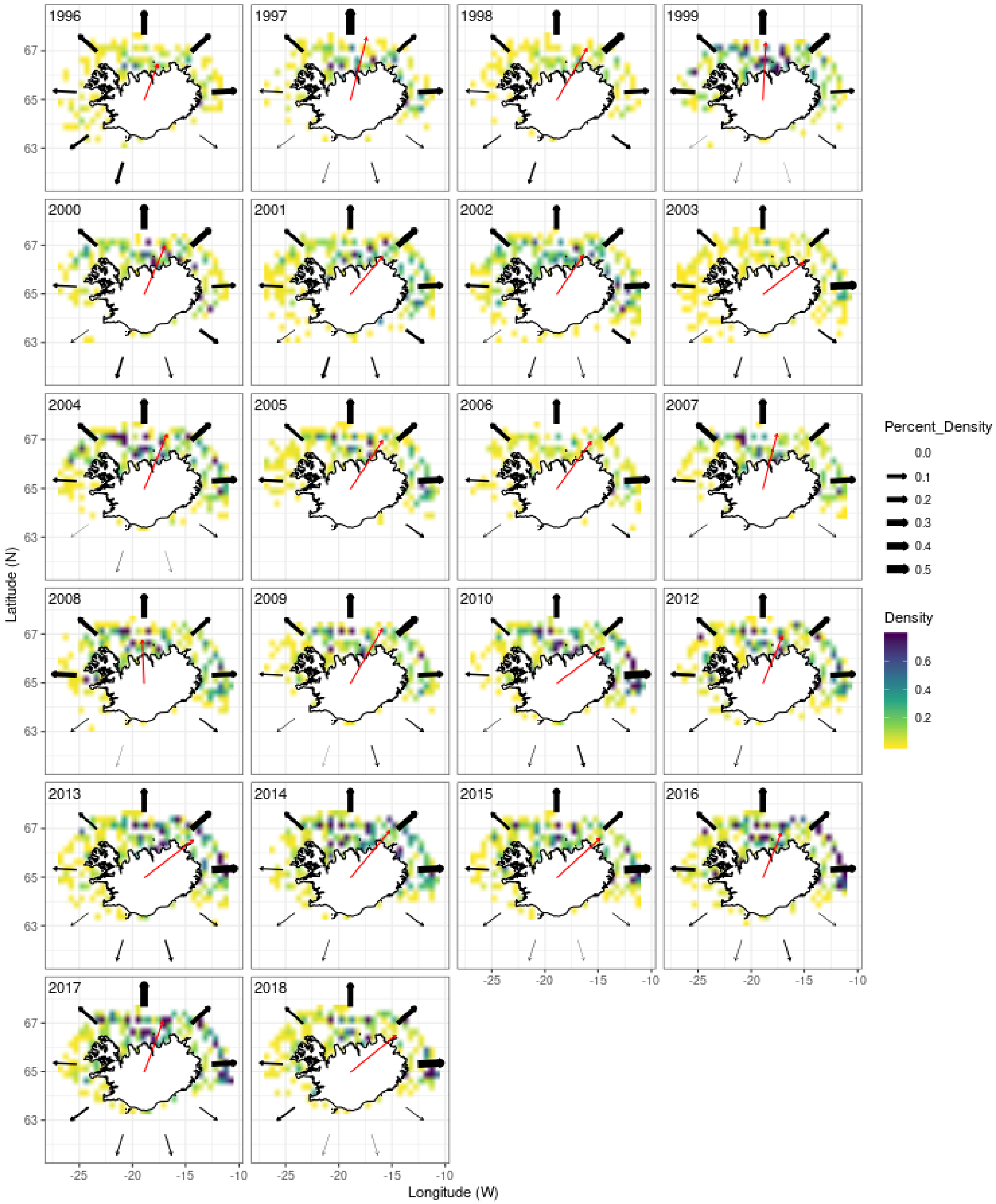
Appendix 4. *Number of cod stomachs collected each year at ages 1, 2 and 3 in SMB, SMR-inshore and SMH.*

	SMB			SMR-inshore			SMH		
	Age			Age			Age		
Year	1	2	3	1	2	3	1	2	3
1996	21	124	718	-	-	-	222	275	1591
1997	2	543	471	-	-	-	20	606	406
1998	3	67	788	-	-	-	194	190	1124
1999	1	850	252	-	-	-	279	886	298
2000	2	930	2391	-	-	-	134	712	1332
2001	0	333	756	153	118	141	197	666	1394
2002	0	734	1159	-	-	-	52	883	1051
2003	2	64	1190	-	-	-	262	128	1527
2004	7	519	202	-	-	-	147	759	393
2005	0	316	1052	32	287	330	83	500	1236
2006	3	88	592	196	165	196	145	229	847
2007	8	410	270	73	122	94	131	619	331
2008	0	266	778	13	29	28	163	592	857
2009	15	243	520	-	-	-	175	438	672
2010	13	327	487	34	157	108	262	786	873
2011	7	384	782	75	169	179	57	61	58
2012	23	225	850	139	173	229	355	502	1103
2013	15	449	413	51	181	167	235	914	670
2014	1	303	786	25	113	151	129	654	1049
2015	10	189	601	98	53	35	390	392	1111
2016	2	364	273	60	176	82	328	933	538
2017	3	241	666	-	-	-	-	-	-

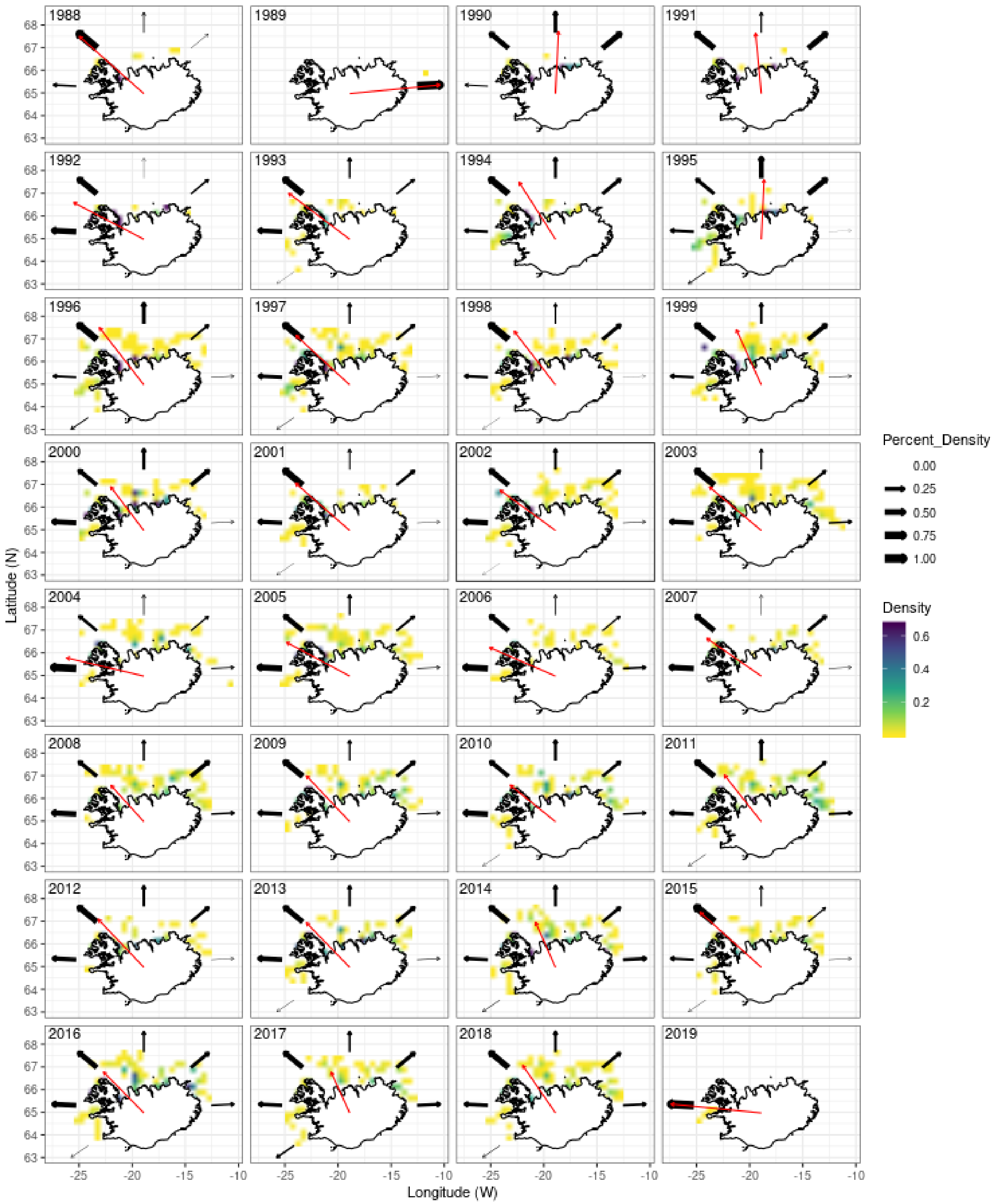
Appendix 5. *Proportion of empty stomachs each year at ages 1, 2 and 3 in SMB, SMR-inshore and SMH.*

	SMB			SMR - inshore			SMH		
	Age			Age			Age		
Year	1	2	3	1	2	3	1	2	3
1996	76.2	37.1	42.8	-	-	-	42.3	51.6	57.9
1997	100	41.8	51.0	-	-	-	50.0	53.0	58.9
1998	33.3	44.8	50	-	-	-	44.3	48.9	57.9
1999	0	39.5	47.6	-	-	-	39.4	54.2	57.4
2000	50	40.6	49.9	-	-	-	44.8	52.9	60.2
2001	-	40.5	50.5	35.3	48.3	53.9	42.6	50.3	58.5
2002	-	37.5	45.1	-	-	-	51.9	50.7	57.8
2003	100	46.9	48.7	-	-	-	45.8	39.8	57.4
2004	71.4	42.6	43.6	-	-	-	54.4	48.9	58.0
2005	-	53.2	50.8	56.3	59.6	58.8	47.0	53.2	54.6
2006	66.7	51.1	42.4	45.9	49.7	51.0	37.9	45.4	49.6
2007	87.5	39.0	45.2	31.5	34.4	52.1	42.7	40.1	43.8
2008	-	36.1	42.5	7.7	34.5	35.7	47.9	44.9	51.0
2009	93.3	46.1	43.3	-	-	-	44.6	44.1	50.9
2010	38.5	44.6	46.2	55.9	40.1	45.4	46.2	42.9	52.3
2011	71.4	43.5	45.4	38.7	38.5	41.3	29.8	44.3	56.9
2012	52.2	44.9	47.3	31.7	42.8	45.4	47.0	45.6	49.8
2013	33.3	42.8	43.6	51.0	49.7	52.1	54.0	56.2	52.5
2014	100	39.3	44.3	44.0	48.7	41.1	48.8	50.3	51.1
2015	30	40.2	43.8	44.9	39.6	48.6	47.7	44.6	50.6
2016	50	42.9	39.6	38.3	46.0	51.2	59.4	52.4	55.2
2017	66.7	42.7	40.7	-	-	-	-	-	-

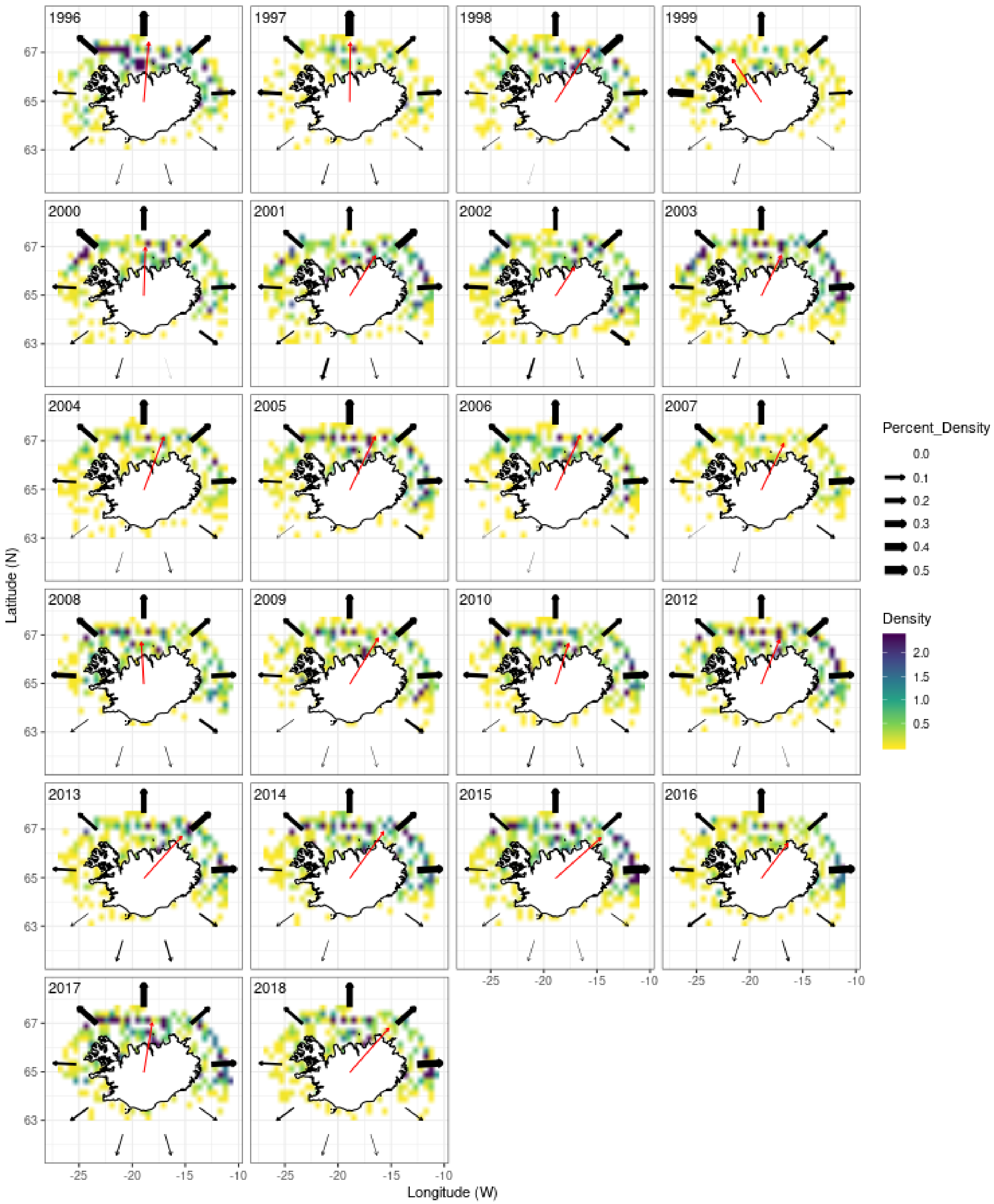
***Appendix 6**. Distribution of 2-year-old cod in SMH. See legend for Figure 6.*



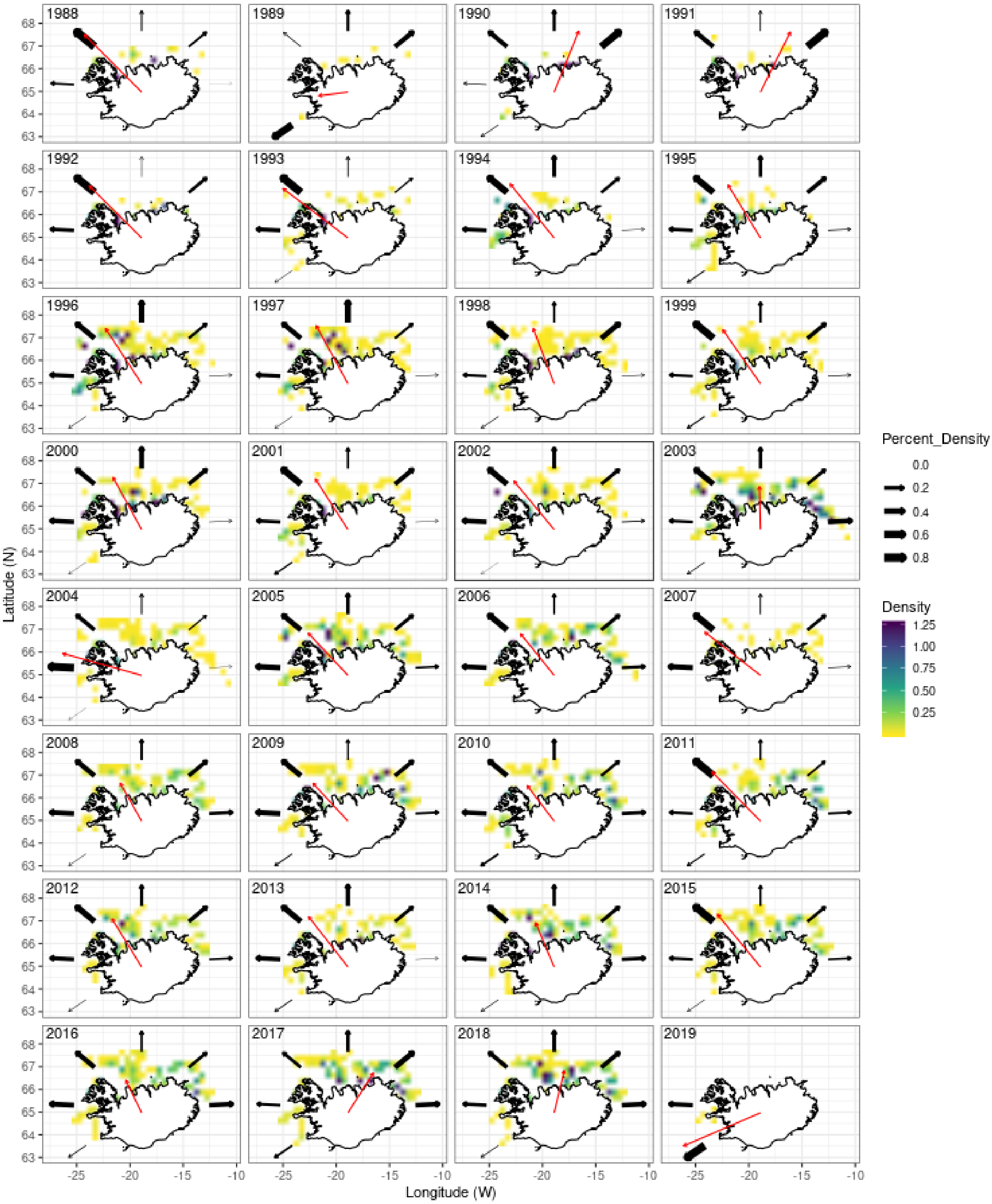
***Appendix 7**. Distribution of 2-year-old cod in SMR inshore and offshore. See legend for Figure 6.*



Appendix 8. *Distribution of 3-year-old cod in SMH. See legend for Figure 6.*



***Appendix 9**. Distribution of 3-year-old cod in SMR inshore and offshore. See legend for Figure 6.*



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