



# Recruitment variability of fish stocks in the Barents Sea: Spatial and temporal variation in 0-group fish length of six commercial species during recent decades of warming (1980–2017)

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## ABSTRACT

Young-of-the-year (0-group) fish in the Barents Sea have been investigated in an annual joint Norwegian-Russian pelagic trawl survey in autumn, using a standardized procedure since 1980. We use a conceptual framework of ‘upstream’ spawning areas and ‘downstream’ nursery areas, recorded as 0-group distribution in the Barents Sea, to address spatial (geographical) and temporal (1980–2017) variation in 0-group length. Four boreal species (cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, herring *Clupea harengus*, and deepwater redfish *Sebastes mentella*) tended to have smaller 0-group individuals in the northern and eastern parts of the Barents Sea, with the largest individuals found in the central part where they were also most abundant. We interpret this to reflect slower growth as the ‘fore-runners’ of the seasonal cohort of juveniles are transported into colder waters (through lateral mixing). The Arctic species (capelin *Mallotus villosus* and polar cod *Boreogadus saida*) showed a different pattern with increasing 0-group length with increasing distance away from the spawning areas, seen most clearly for capelin. The longer juveniles in northern areas are probably older and stemming from early spawning.

There was temporal covariation in 0-group length between the six species over the 38-year time series, with highest correlation between cod and haddock. The covariation reflected similar fluctuations in four decadal ‘waves’, with maxima in 0-group length in the early/mid 1980s, 1990s, 2000s, and 2010s. There was a high degree of spatial consistency in the temporal patterns of variation in 0-group length, with synchronous variations in different geographical areas. There were also increasing linear trends over the time series for cod, haddock, and polar cod, which represented increase of about 20%, 40%, and 15% of the initial length for the three species, respectively. The fluctuations and trends in 0-group length were positively correlated with seawater temperature, which suggests a strong effect of climate variability and warming (by 1.5–2.0 °C since 1980) on 0-group length. The clear differences among the species, and the limited fraction of variance explained by temperature, suggest that other factors such as food play additional roles. Zooplankton biomass integrated over the water column had low explanatory power, but this may reflect intrinsic limitations in the data (e.g., depth-integrated, end of season) in providing an adequate representation of feeding conditions, rather than suggesting that food was not important.

## 1. Introduction

Recruitment variability of fish is an important but complex issue, which has an extensive history of research dating back >100 years to pioneering works such as Helland-Hansen and Nansen (1909) and Hjort (1914) who addressed recruitment of fish stocks in the Barents Sea. The ‘recruitment problem’ is basically what causes the large variations in

fish recruitment, and what consequences variable recruitment plays for the observed stock fluctuations; in short – why do fish stocks vary? (Rothschild 1986, Cushing 1996, Houde 2008, 2009, Skjoldal 2009, Huse 2016). The size of the juvenile fish reflects growth (in addition to variable spawning and hatching times) and is one aspect of the recruitment variability ‘puzzle’. Interaction between growth rate and mortality is implied in the ‘growth-mortality’ hypothesis (Beverton and

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Holt 1957, Cushing 1975, Anderson 1988, Houde 2009). Since the duration in a segment of larval development is inversely related to growth rate, the accumulated mortality from the impact of size-selective predators also varies inversely with growth rate. This mechanism is implied in the ‘bigger-is-better’ variant of this hypothesis, which predicts better survival for fast-growing larger larvae compared to smaller ones (Jørgensen et al. 2014).

Climate variability is a major factor for the large fluctuations in size of fish stocks, to a large extent mediated through the effects of climate on feeding conditions for spawners, location of spawning grounds, timing of spawning, drift of eggs and larvae, and feeding habitat for larvae and juveniles (Ottersen et al. 1998, Dragesund et al. 2008, Hysten et al. 2008, Skjoldal 2009, Boitsov et al. 2013). The Barents Sea has warmed by nearly 2 °C since 1980, as a linear trend superimposed on substantial interannual fluctuations (WGIBAR 2018, Skagseth et al. 2020). The warming has been associated with an expansion of Atlantic water, reduction in areal extents of Arctic water and sea-ice cover, and large changes in ecological conditions (Dalpadado et al. 2012, 2014, 2020, Johannessen et al. 2012, Fossheim et al. 2015, Lind et al. 2016, 2018, Eriksen et al. 2017, Lien et al. 2017, Ingvaldsen et al. 2021). Some of the strongest effects of global climate change are observed in the Arctic, where rates of warming are 2–3 times the global average (IPCC 2018, AMAP 2021). Within the Arctic region, the Barents Sea stands out as an area that experience strongest warming, reflected in the most pronounced decline in sea ice cover (Yang et al. 2016, Onarheim et al. 2018, Lind et al. 2018).

In the Barents Sea, pelagically distributed 0-group fish (age 0 – young of the year) has been monitored annually since 1965 in a joint Norwegian-Russian survey (Eriksen and Prozorkevich 2011). The 0-group investigations started as an acoustic survey and transformed into a standardized trawl survey in 1980, to become part of a joint Norwegian-Russian ecosystem survey (BESS) from 2004 (Dragesund et al. 2008, Eriksen and Prozorkevich 2011, Eriksen et al. 2018). The purpose of the 0-group survey was to obtain an early estimate of the year-class strength of commercial fish stocks in the Barents Sea. Sampling has been carried out with a pelagic trawl in a grid of stations, covering most of the open water area of the Barents Sea in autumn (Anon. 2004). Two parameters have been recorded for 0-group fish of different species in the trawl catches: number of individuals (numerical density and abundance) and length of individuals (individual size). In this study we address patterns of variability and change in individual size of six commercially and/or ecologically important species of fish: Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), Atlantic herring (*Clupea harengus*), Atlantic capelin (*Mallotus villosus*), polar cod (*Boreogadus saida*), and redfish of genus *Sebastes* (mainly deepwater redfish, *S. mentella*). We refer to these six taxonomic entities

as ‘species’.

The six species of fish conform to the classical model of life cycle closure by having larval drift with currents from ‘upstream’ spawning areas to ‘downstream’ nursery areas and then a compensatory spawning migration by adults back to the spawning areas (Harden-Jones 1968, Skjoldal 2009, Olsen et al. 2010). A common feature for the species is that they spawn at several spawning locations, or at elongated spawning grounds stretching along the shelf edge, that span large geographical distances (e.g., >1,000 km for cod and herring) (Fig. 1). Spawning and hatching of larvae take place over a considerable span of time, typically two months or longer. From the spawning grounds, pelagic eggs and larvae are transported by the currents towards the nursery grounds in the Barents Sea where they are surveyed as 0-group fish in the autumn (Fig. 2). The currents and ocean physics also disperse the larvae so that they occupy an expanding area as they are transported northwards and eastwards into the Barents Sea.

Four of the species (cod, haddock, herring, and redfish) are classified biogeographically as boreal, while the other two are classified as Arctic (polar cod) or Arctic-boreal (capelin) (Mecklenburg et al. 2018). A distinction between the two groups is that the boreal species spawn ‘upstream’, mostly outside the Barents Sea, while the Arctic species spawn inside the Barents Sea (Fig. 1). More background information on the six species and the transport system of ocean currents is provided in Supplementary material (part A).

Several studies have documented spatial and temporal variation in length of 0-group fish in the Barents Sea related to climate and temperature variation. Eriksen et al. (2012, 2015) observed lower 0-group length in colder waters in the eastern and northern Barents Sea. Stensholt and Nakken (2001) observed smaller 0-group individuals in the Svalbard area compared to the central and southern Barents Sea. Loeng et al. (1995) and Ottersen and Loeng (2000) found positive covariation in 0-group length as well as abundance for cod, haddock, and herring, with fluctuations in length related to similar fluctuations in temperature for the period from the late 1960s to the 1990s.

Conceptually, we expect that the spatial pattern in length of 0-group fish should reflect the location and time of spawning, as well as variable growth conditions which larvae and juveniles experience (Fig. 3). In general terms, we expect individuals from early spawning and individuals from northern spawning grounds to be further ahead in the transport direction than individuals from late spawning and from more southerly located spawning areas. This could lead to a spatial pattern of older and larger 0-group individuals farther along the transport routes north and east in the Barents Sea. However, this could be countered by slower growth of larvae that are hatched early or at northern spawning locations due to lower temperatures since they appear early relative to the seasonal warming and since temperature generally decreases in the

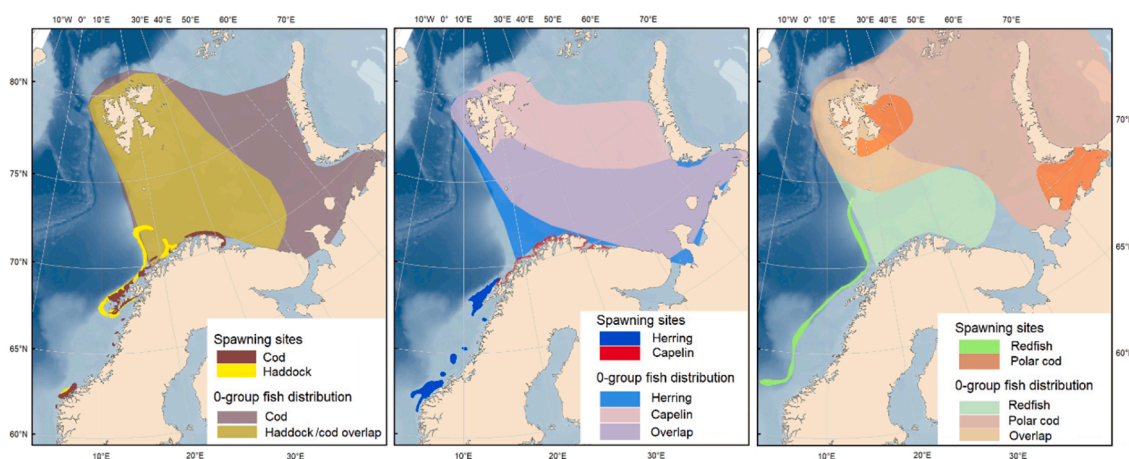
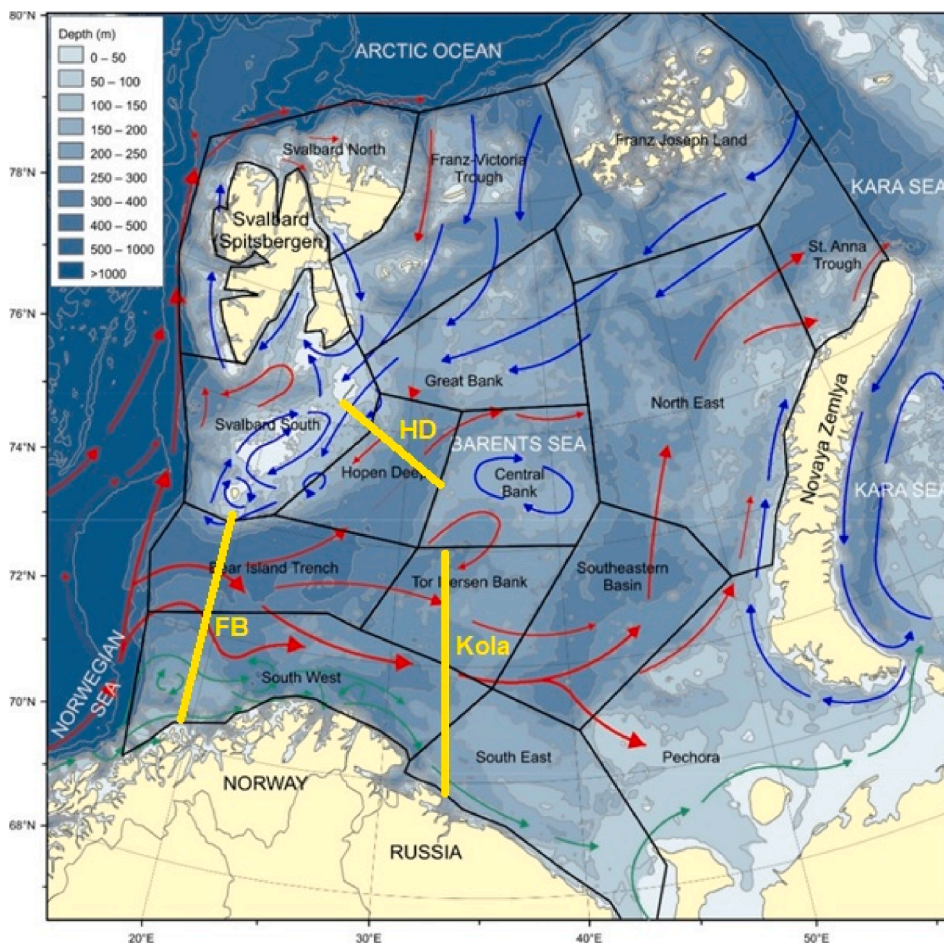


Fig. 1. Spawning area and distribution of 0-group of six species of fish - Atlantic cod and haddock (left panel), Atlantic herring and capelin (mid panel), and polar cod and beaked redfish (right panel).



**Fig. 2.** Map of the Barents Sea with bottom topography and ocean currents shown as arrows: green – coastal currents, red – Atlantic water currents, blue – Arctic water currents. Black lines show delineation of fifteen subareas or polygons (see Material and methods). Yellow lines show positions of the Fugløy-Bear Island (FB, or Barents Sea Opening BSO) and Kola oceanographic transects, and an E-W model transect across the Hopen Deep (HD). Abbreviations of polygon names: BIT – Bear Island Trench, CB – Central Bank, FJL – Franz Josef Land, FVT – Franz-Victoria Trough, GB – Great Bank, HD – Hopen Deep, NE – North-East, PE – Pechora, SAT – St. Anna Trough, SE – South-East, SEB – Southeastern Basin, SvN – Svalbard North, SvS – Svalbard South, SW – South-West. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

northward transport direction (Suthers and Sundby 1993, Vikebø et al. 2005). Moreover, the dispersal and mixing by ocean physics may act to erase or ‘cloud’ the impacts of spawning times and locations on the spatial distribution of the juveniles. Finally, the size distribution of 0-group fish can also be influenced by size-dependent predation.

With the conceptual framework illustrated in Fig. 3 as a basis, we are exploring spatial and temporal patterns in length of 0-group fish with a comparative view of similarities and differences among the six species. Specifically, we address the following questions:

1. Is there a difference in spatial patterns of variation in 0-group length between the groups of four boreal species (cod, haddock, herring, and redfish) which spawn ‘upstream’ outside the Barents Sea, and the two Arctic species (capelin and polar cod) which spawn inside the Barents Sea?
2. What degree of temporal covariation in 0-group length is there among the six species?
3. How has the length of 0-group fish responded to the general increase and decadal fluctuations in temperature?
4. Are there differences in spatial-temporal patterns between the groups of boreal and Arctic species, e.g., does the temporal pattern differ as function of geography?
5. To what degree does food (zooplankton biomass) explain the observed spatial and temporal patterns in 0-group fish length?

## 2. Material and methods

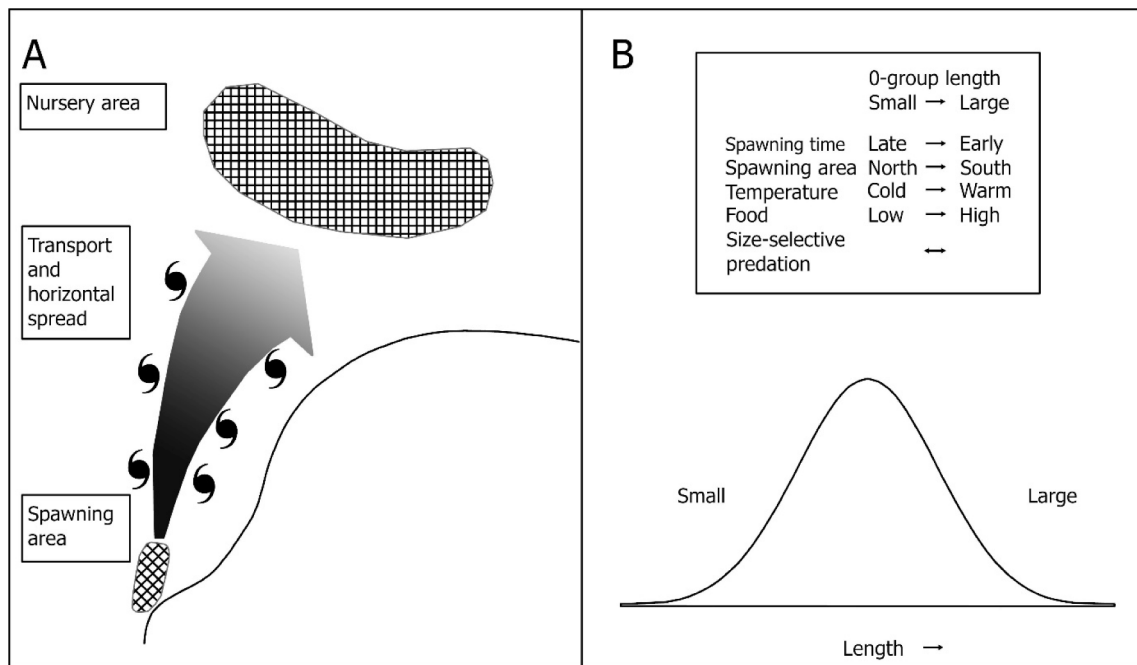
### 2.1. Survey, sampling and sample analyses

The 0-group surveys have been carried out in autumn with 3–5

research vessels each year to achieve semi-synopticity in coverage of the surveyed area which is of order 1 million km<sup>2</sup>. The survey period has typically spanned 4–6 weeks from mid-August to early October, and the survey design has generally been with sampling stations placed in a regular grid with approximately 30 nautical miles (nm) between stations (Eriksen and Prozorkevich 2011). On average, about 300 stations have been sampled each year (varying from 179 to 425; Table S-2). The survey originally covered the ice-free area of the southern and central Barents Sea and has generally included the full 0-group distributions of the four boreal species and capelin. With warming and less sea ice in the recent decades, the survey has expanded in the northern Barents Sea. This has probably led to a better coverage of the 0-group distribution of polar cod.

The survey has generally been carried out from south to north but with some variations regarding survey design (Fig. S-6). Since the coverage takes several weeks, the variation in sampling date has been taken into account when examining temporal changes in 0-group fish length over the time series (see section ‘Correction for effect of sampling date’).

A small-meshed pelagic trawl (“Harstad”) with 20 m\*20 m mouth opening has been used to sample 0-group fish from the upper 60 m. The Harstad trawl is constructed with seven panels, with mesh size decreasing from 200 mm in the first (front) panel to 60 mm in the last panel, and with 7 mm meshes in the cod-end (Godø et al. 1993). A procedure with stepwise hauls with the headline at 0 m, 20 m, and 40 m has been followed, where the trawl is towed for 10 min at a speed of 3 knots at each depth level (Anon. 2004, Eriksen et al. 2009). This corresponds to an integrated tow length of 0.5 nm or 0.93 km. The 0-group fish are usually found above the thermocline within the upper 60 m of the water column (Beltestad et al. 1975, Stensholt and Nakken 2001).



**Fig. 3.** Conceptual framework for variation in length of 0-group fish recorded in the autumn survey in the Barents Sea. **A** – Schematic representation of location of upstream spawning area and downstream nursery area for 0-group fish. The spawning area is shown elongated in the transport direction, reflecting S-N variation in spawning location (see Fig. 1) and the protracted time course of hatching and release of fish larvae over a ~ 2-month period. The nursery area is broadened from the general horizontal spread and splitting of current branches at the entrance to and inside the Barents Sea. **B** – Frequency distribution of individual size (length) of 0-group fish (lower part), and direction of influence of factors indicated by direction of arrows from small to large size (upper part). The schematic representation is most relevant for the four boreal species that spawn outside or at the entrance to the Barents Sea (cod, haddock, herring, and redfish), but the principles are applicable also to the two species which spawn inside the Barents Sea (capelin and polar cod).

On some occasions if dense concentrations of 0-group fish are recorded deeper than 60 m on the echo-sounder, additional steps are added in the tow with the headline at 60 and 80 m. Sampling was carried out during both day and night since there is limited diel vertical migration by the 0-group fish (Stensholt and Nakken 2001).

The catches (or a subsample, in case of large catches) of 0-group fish are sorted and identified to species level. 0-group individuals are distinguished by their size since there is little or no overlap with older individuals (1-group) of the same species.

From the sorted samples of 0-group fish, 100 individuals of each species are selected in a random manner and their body length is measured to nearest mm. All individuals are measured if the total number is < 100. From 2016, the procedure was changed based on statistical considerations (Pennington and Helle 2014) to measure 30 individuals instead of 100.

## 2.2. Data sets and data treatment

A total number of 11,408 stations were sampled in the 0-group surveys from 1980 to 2017. The number of stations with positive records for each of the six species ranged from 2,796 stations for polar cod to 7,086 stations for cod (Table S-2).

### 2.2.1. Correction for length-dependent catch efficiency

Small individuals of 0-group fish pass through the wide meshes in the front part of the trawl, and the capture efficiency of the trawl increases with fish length dependent on species (Godø et al. 1993, Hysten et al. 1995). Length-dependent correction factors based on empirical data for catchability (comparing trawl catches with acoustic estimates in one-species situations) have been established for cod, haddock, herring, capelin, and polar cod (Hysten et al. 1995, Mamylov 2004, Prozorkevich 2012). An equation for correction factor as function of 0-group length for each species is applied to the length frequency distribution of 0-

group individuals of the species at sampling stations to calculate corrected numbers of individuals and corrected length frequency distributions at each station as described by Dingsør (2005). The corrected data are in turn used to calculate annual abundance indices and mean 0-group fish lengths (Dingsør 2005, Eriksen et al. 2009). The effect of the correction was illustrated for cod and haddock by Dingsør (2005, see his Fig. 2; see also Fig. S-11 in the supplementary material). Capture efficiencies for 0-group redfish have not been determined, and the uncorrected fish length used here represent overestimates of 0-group redfish length since small individuals are under-sampled.

### 2.2.2. Division of the Barents Sea into subareas or 'polygons'

For the purpose of ecological synthesis, the Barents Sea has been divided into 15 areas or polygons based on topography and hydrography (Fig. 2; WGIBAR 2017). The polygons allow aggregation of information at a spatial scale between single sampling stations (or finer grid cells) and the whole Barents Sea. They have been used to examine and synthesize hydrography and heat exchange (Skagseth et al. 2020), primary production and zooplankton biomass (Dalpadado et al. 2020), and fish diet (Eriksen et al. 2020a, 2021). We have used them to calculate annual mean values for 0-group length for the stations within each polygon (see next section). Two of the polygons in the northeastern corner of the Barents Sea (FJL and SAT; see legend to Fig. 2 for abbreviations of polygon names) had few 0-group stations and were not included in analyses with polygon values. The FVT polygon lacked observations for many of the years in the early part of the time series and was also not included. We had therefore data for 12 polygons – all 12 for cod and capelin, 11 for haddock and herring (minus NE) and polar cod (minus SW), and 9 for redfish (minus GB, PE and NE).

### 2.2.3. Calculating mean length of 0-group fish

We calculate annual 0-group mean length in two different ways – unweighted and abundance-weighted. The annual unweighted mean

length is calculated across all stations for each species each year. This is the mean value across the geographical distribution area, with equal weight given to stations. We have also calculated an abundance-weighted annual mean length where the length at each station is weighted in proportion to the recorded density of 0-group fish of each species. The weighted mean is representative for the total population since it reflects the abundance across the distribution area. The unweighted mean is reflecting the geographical distribution regardless of whether the species occurs in high or low densities. Based on what they reflect, we denote these two series of annual means as ‘population’ mean (weighted) and ‘geographical’ mean (unweighted).

If we call the area with highest abundance the core area for 0-group of a species, and the surrounding areas with lower abundance as peripheral, then the difference between weighted mean (‘population’) and unweighted mean (‘geographical’) reflects the difference in length between core and periphery. If the difference is positive (‘population’ mean is largest), the length of individuals is larger in the core area than in the periphery. If the difference is negative (‘geographical’ mean is largest), the individuals are larger in the periphery than in the core area. We use this feature as a diagnostic tool when interpreting spatial patterns in 0-group length.

The mean length at the polygon level is calculated as an unweighted average (corresponding to what we call ‘geographical’ mean, in this case for the stations within a polygon).

#### 2.2.4. Correction for effect of sampling date

Sampling date affects length since the 0-group fish is growing during the period of survey. This effect is an artefact which influences geographical and temporal patterns in 0-group length. We have removed the effect of variable sampling date by using sampling date as a co-variate along with year and geographical position in a generalized additive model (GAM) analysis (described in a following section).

We used the near-linear effect on length between day-of-year number 220 and 260 predicted by GAM (see Fig. S-7) to calculate daily length increments for five of the species, assuming linear growth. For polar cod, we used days 230 and 270 suggested by the GAM results. The length increment between the two dates (corresponding to 8 August to 17 September for days 220 and 260) was around 2 cm (1.8–2.6 cm) for the larger species (cod, haddock, herring) and around 1 cm (0.5–1.5 cm) for the smaller species at the 0-group stage (capelin, polar cod, redfish) (Table S-4). The daily length increments (length increment/40 days) were used to correct the length at each sampling station to a fixed sampling date (the mean date for each species) by adding or subtracting the effect of daily length increment (corrected length = observed length + (mean date – sampling date) \* daily length increment). The mean date was nearly the same for all species – day-of-year 242–244, corresponding to 30 August–1 September.

#### 2.2.5. Environmental data – temperature, model transport, zooplankton biomass

We use water temperature, volume transport of water associated with the Atlantic inflow, and zooplankton biomass as explanatory variables for observed spatial and temporal patterns of 0-group fish length.

Temperature profiles were measured by CTD-casts at the same stations where 0-group trawl hauls were made (Skagseth et al. 2020). The hydrographical data from the autumn surveys have been used to calculate mean temperature for three depth layers (0–30, 30–100, and 100–200 m) in each of the geographical polygons (WGIBAR 2018). These values were used to calculate composite time series of temperature as empirical orthogonal functions (EOF-1) as an expression of the temperature conditions in the Barents Sea (Skagseth et al. 2020). We chose to use the EOF-1 for the deepest of the three layers (100–200 m), because this layer is most representative for the temperature of the Atlantic water and gave consistently the highest correlations with variation in 0-group length. Temperature anomalies in the Atlantic Water flowing from the Norwegian Sea to the Barents Sea generally

represent persistent and coherent anomalies when considering the Barents Sea shelf on timescales of less than one year (e.g., Furevik 2001, Skagseth et al. 2020). Using depth layers 0–30 m or 30–100 m yielded comparable results.

We use time series of modelled volume transport of water across three sections: the FB section (Barents Sea Opening) in south-west, the Kola section along 33.5°E, and an east–west section across Hopen Deep (Fig. 2). These three sections represent the main flow pattern of Atlantic water into the Barents Sea with a split into two main current branches. We use modelled net transport for the April–August period which span approximately the time between hatching in spring and 0-group survey in autumn. The transports were calculated from a model simulation utilizing the Regional Ocean Modeling System (ROMS; Shchepetkin and McWilliams 2005), forced with atmospheric reanalysis data. This model has been shown to realistically represent the variability of both climatic conditions and Atlantic water inflow to the Barents Sea (Lien et al. 2013, 2014, 2016).

Zooplankton is collected with vertical hauls with WP-2 net over the water column, and dry weight is determined following separation in three size fractions (Melle et al. 2004, Skjoldal et al. 2019). Screens with mesh size of 2 and 1 mm are used to split zooplankton into large (>2 mm), medium (1–2 mm), and small (<1 mm) size fractions. *Calanus* species dominate the biomass overall (making up 70–80 %, Aarflot et al. 2018b). Older copepodite stages of *Calanus* dominate in terms of biomass and are found in the medium fraction, while young copepodite stages of *Calanus* as well as other small copepods (*Pseudocalanus*, *Oithona* and others) dominate the small fraction (Skjoldal 2021). The small and medium fractions presumably contain the main prey items for larvae and 0-group juveniles of the investigated species (Pedersen and Fosheim 2008, Dalpadado et al. 2009).

Zooplankton biomass is generally determined at the same stations as 0-group fish are sampled during the 0-group surveys. However, we lack samples from the early part of the 0-group time series in the 1980s, and the standardized time series of zooplankton biomass is from 1989 onwards. The zooplankton data has been used to calculate mean biomass values for the geographical polygons. The data set and time series for polygons are described in Skjoldal et al. (2018).

In addition to the autumn survey, zooplankton biomass is collected (using the same net and method) at stations along the FB transect (Skjoldal et al. 2021). This sample set has seasonal resolution, and we are using data for the summer period (June and August) which correspond to the time when fish larvae and juveniles are transported with the currents into the Barents Sea (for the four species which spawn ‘upstream’ outside the Barents Sea).

### 2.3. Data exploration and statistical analyses

The data sets for 0-group fish length were used with full spatial resolution (station level) and aggregated (polygon) level in multivariate and statistical analyses to explore spatial and temporal patterns and to test their statistical significance.

**Generalized Additive Model (GAM) analysis** – We used GAM to examine effects of time (year), geographical position (latitude and longitude), and sampling date on 0-group fish length (at station level) according to the model (where  $s$  is smooth functions):

$$\text{Length} = s(\text{year}) + s(\text{latitude, longitude}) + s(\text{sampling date}) + e_i.$$

The analysis was done to isolate and test the effect of sampling date and to reveal the temporal (years) and spatial (geographical) patterns when the effect of sampling date was taken into account. GAM was performed with the R (version 2.12.2) package ‘mgcv’ (Wood and Augustin, 2002).

**Principal Component Analysis (PCA)** – PCA was performed with annual mean length for the six species to examine the general pattern of variation of 0-group length across the 6 species and over time (years). Two separate analyses were performed for the unweighted and weighted annual mean length respectively. PCA was also run with polygon data

for annual mean length for each species separately to examine spatial and temporal patterns and how they shifted over time. PCA was performed with the R package ‘vegan’ with data standardized to zero mean and unit variance.

**Correlation** – Pearson  $r$  (product-moment) correlation coefficient was used to indicate strength of relationships and to characterize fraction of variance explained by a co-variate ( $R^2$ ). Correlation coefficients were calculated for series of annual mean length (weighted and unweighted) of 0-group fish for pairwise comparisons across all six species. Correlation coefficients were also calculated for series of annual mean length versus temperature and zooplankton biomass as explanatory variables. Statistical significance of correlations was indicated by the  $t$ -statistic. The critical values of Pearson  $r$  at the 5 % and 1 % probability level are 0.32 and 0.42, respectively, for a sample size of 38 observations (38 years, 1980–2017; degrees of freedom are equal to  $n-2$ ). Effective degrees of freedom were calculated following Quenouille (1952) to account for autocorrelation in the time series.

The relation between 0-group length and time (years) was described with ordinary linear regression. Mann-Kendall trend test was used to identify whether a change in fish length with time was statistically significant. In this test, which is non-parametric, the trend can be linear or non-linear (Gilbert 1987).

### 3. Results

#### 3.1. Overall mean and statistical distribution of 0-group fish length

The mean fish length over all sampling stations varied from 3.65 cm for redfish as the smallest species to 8.6 cm for haddock as the largest (Fig. 4, Table S-3). The two Arctic species (polar cod and capelin) were smaller in comparison to three of the boreal species (cod, haddock, and herring) by an average difference of 2–3.5 cm. The relative variation, expressed as the coefficient of variation ( $CV = SD/mean$ ), was comparable among the six species, being around 20–25 % ( $CV$  0.19–0.27; Table S-3). Due to the high number of samples ( $n$  between 2796 and 7086), the standard error (SE) and confidence interval (CI) around the mean were low (CI 0.03–0.06).

#### 3.2. Effect of sampling date on 0-group length

Sampling date (as day of year) was included in the GAM analyses. There was a highly significant increase in length of 0-group individuals with increasing sampling date for each species (Table 1), with a similar curvilinear trend for all species except capelin (Fig. S-7). We used the near-linear portions of increase in length between day numbers 220 and

260 (230 and 270 for polar cod) from the GAM to estimate daily linear growth rates, which was lowest for capelin (0.2 % of body length per day) and varied between about 0.5 and 1 % per day for the other five species (Table S-4).

#### 3.3. Spatial patterns in 0-group fish length

The geographical patterns in length of 0-group fish are shown for polygons with box-whisker plots in Fig. 5. For cod and haddock, the largest individuals were generally found in the western and central polygons (BIT, TIB, HD, CB). Capelin showed the clearest overall pattern with an increase from southwest to northeast. The length of 0-group fish tended to be low in the polygons around Svalbard, most notably so for haddock, redfish, and cod, but also for herring and capelin. The length was relatively low in the SW polygon for cod, capelin, and redfish.

The GAM results show the geographical pattern of 0-group length in more detail (Fig. 6). All six species reveal a clear (and highly significant, Table 1) geographical pattern, with some similarities but also clear differences among the species.

The largest 0-group cod were found in a core area in the central Barents Sea between about 15 and 40°E and 72 and 76°N. Outside this area, the length of cod decreased towards west, north and east (Fig. 6A). The largest haddock were found in a similar zone but displaced somewhat further south (between about 70 and 74°N), and with a pronounced decrease in length towards the north (Fig. 6B). Haddock differed from cod in showing increasing length in the southwestern part of the surveyed area. The largest herring occurred in the southwestern part, with length decreasing towards north and east (Fig. 6C).

Capelin showed a clear pattern with the smallest individuals in southwest and with length increasing towards north and east (Fig. 6E). A somewhat similar pattern was shown by redfish with length increasing towards north and east, although the distribution for redfish was displaced farther to the west compared to capelin (Fig. 6D). Polar cod showed a bimodal pattern, with the longest fish in southeast and northwest and smaller fish in the central part and toward northeast (Fig. 6F).

#### 3.4. Temporal patterns in 0-group fish length

##### 3.4.1. Time series 1980–2017

The GAM results show highly significant changes in 0-group length over the time series consisting of both interannual fluctuations and trends over the nearly four decades of data (Fig. 7, Table 1). The GAM functions showed very similar patterns of fluctuations as the time series of annual unweighted means (where the effect of sampling date was removed), with the same local maxima and minima for each of the species. The variation in annual mean length across the time series from 1980 to 2017 was 0.08–0.13 when expressed as  $CV$  ( $SD/mean$ ) and 30–58 % when expressed as range (maximum–minimum) relative to the mean length for each of the six species. The largest (relative) variation in annual mean length was seen for herring (4.7–8.4 cm) and the smallest variation was for polar cod (3.4–4.6 cm). Cod and haddock varied in mean length over the years from 5.3 to 8.0 cm and from 6.2 to 10.6 cm, respectively.

The time series of annual abundance-weighted (population) mean length showed similar patterns to the GAM smooth functions and to the series of unweighted mean ( $R^2$  (Pearson  $r$ ) for the correlations between the weighted and unweighted series varying from 0.35 (capelin) to 0.89 (haddock)). For cod, haddock and redfish, the population means tended to be higher than the geographical means, reflecting that the individuals were larger where abundance was high (Fig. 8). Herring also tended to show larger population means, particularly in the early part of the time series (Fig. S-8). For polar cod, the opposite pattern was shown, with geographical mean being the largest (up to about 2005), reflecting larger individuals where abundance was low (Fig. 8). Capelin showed a variable pattern, with geographical mean tending to be the larger of the

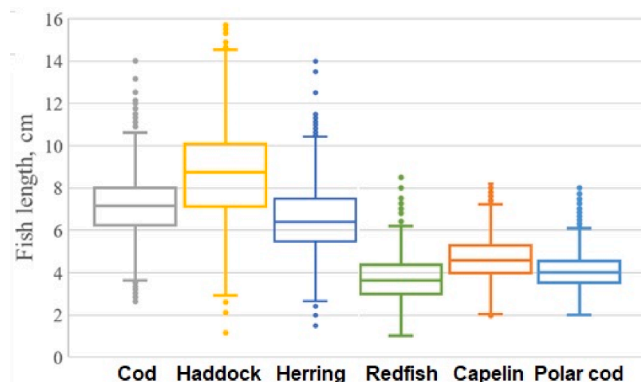


Fig. 4. Box-whisker plots of 0-group length for cod, haddock, herring, redfish, capelin, and polar cod with data for individual sampling stations at the 0-group surveys in 1980–2017. The figure shows median (horizontal line), 25 and 75 % quantiles (boxes), 5 and 95 % quantiles (vertical lines), and statistical outliers (dots).

**Table 1**

Summary of results for GAM analysis of 0-group fish length as response variable, and sampling date (day of year), year, and geographical position (latitude and longitude) as explanatory variables for six species of fish. edf – estimated degrees of freedom, F – F statistic, p – probability of significance. Intercept is the mean length over all sampling stations (n).

Species	Factor	edf	F	p	Deviance explained (%)	Intercept (cm)	n
Cod	s(Year)	28.34	66.56	<2e-16	40.1	7.1	7085
	s(lon,lat)	28.20	40.04	<2e-16			
	s(date)	5.44	92.86	<2e-16			
Haddock	s(Year)	28.51	61.52	<2e-16	53	8.61	4614
	s(lon,lat)	26.81	54.26	<2e-16			
	s(date)	8.53	117.72	<2e-16			
Herring	s(Year)	27.61	48.59	<2e-16	41.4	6.56	3159
	s(lon,lat)	24.79	21.98	<2e-16			
	s(date)	3.77	96.72	<2e-16			
Redfish	s(Year)	27.51	23.86	<2e-16	47.2	3.65	2982
	s(lon,lat)	27.54	26.00	<2e-16			
	s(date)	8.68	34.41	<2e-16			
Capelin	s(Year)	18.72	43.90	<2e-16	36.7	4.67	5364
	s(lon,lat)	24.70	64.70	<2e-16			
	s(date)	6.25	7.41	3.68e-09			
Polar cod	s(Year)	28.17	22.77	<2e-16	36.3	4.08	2796
	s(lon,lat)	25.92	17.95	<2e-16			
	s(date)	7.19	27.24	<2e-16			

two, except for the most recent years. As a pattern across the six species combined, the population means were generally larger than the geographical means, with two noticeable ‘dips’ to opposite pattern in the late 1980s and early 2000s (Fig. S-8).

### 3.4.2. Covariation among species

There are some commonalities as well as differences among the species in the temporal variation in 0-group length (Fig. 7). The ‘wavy’ character of the time series is common for all species with particularly large fluctuations in the first two decades (1980s and 1990s). There are three ‘waves’ with maxima in the early to mid- 1980s, 1990s, and 2000s. The covariation among the species was reflected in positive correlation coefficients that were generally statistically significant at the 95 or 99 % level in comparisons between cod, haddock, herring, and redfish (Table 2). The highest degree of covariation was seen for cod and haddock with  $R^2 = 0.67$ . The least degree of covariation was seen for capelin with low correlations with other species ( $r < 0.2$ ) except herring. Capelin and herring were moderately correlated ( $R^2 = 0.23$ ), reflecting that both species showed greatest length in the 1990s (Fig. 7). Polar cod and redfish were also positively correlated ( $R^2 = 0.32$  for the unweighted mean data) and showed a pattern of low length in the middle of the time series (1997–2003; Fig. 7). Non-parametric Spearman rank correlations (not shown) gave broadly the same results as the parametric Pearson product-moment correlations.

PCA on the two data sets for the six species (weighted and unweighted mean length) revealed a common pattern. All species ‘pointed’ in positive direction of PC1, reflecting that they are positively correlated (Fig. S-2). The species were separated along PC2, with capelin and herring on one hand and polar cod and redfish on the other, as the most dissimilar, and with cod and haddock in between. PC1 can be interpreted as a general measure of length of 0-group as a composite expression for the six species.

PC-2 reflects the difference in the temporal patterns of the six species, and it can be taken as a quantitative expression of the qualitative difference among species (Fig. S-3). Broadly speaking there was a shift around 2004, with capelin and herring tending to be large before this year and relatively small after (change in sign of PC-2; Fig. S-3). A noticeable exception was 1995 when capelin and herring tended to be small (relative to polar cod and redfish in particular) (Fig. 7).

### 3.4.3. Linear trend in 0-group length with time

The annual mean length trended positively with time for five of the species, and the trend was statistically significant for haddock and polar cod, and near-significant ( $p < 0.1$ ) for cod and redfish (Table 3). The

length increased by about 1.3 cm for cod and 3.0 cm for haddock over the 38-year time series, or by about 20% and 40% of the initial length for the two species. Redfish and polar cod increased by 0.4 and 0.8 cm over the period, or by about 10 and 20% of the initial length. The length trended negatively for capelin for the unweighted mean data (see Fig. 7E; near statistical significance at 95% level).

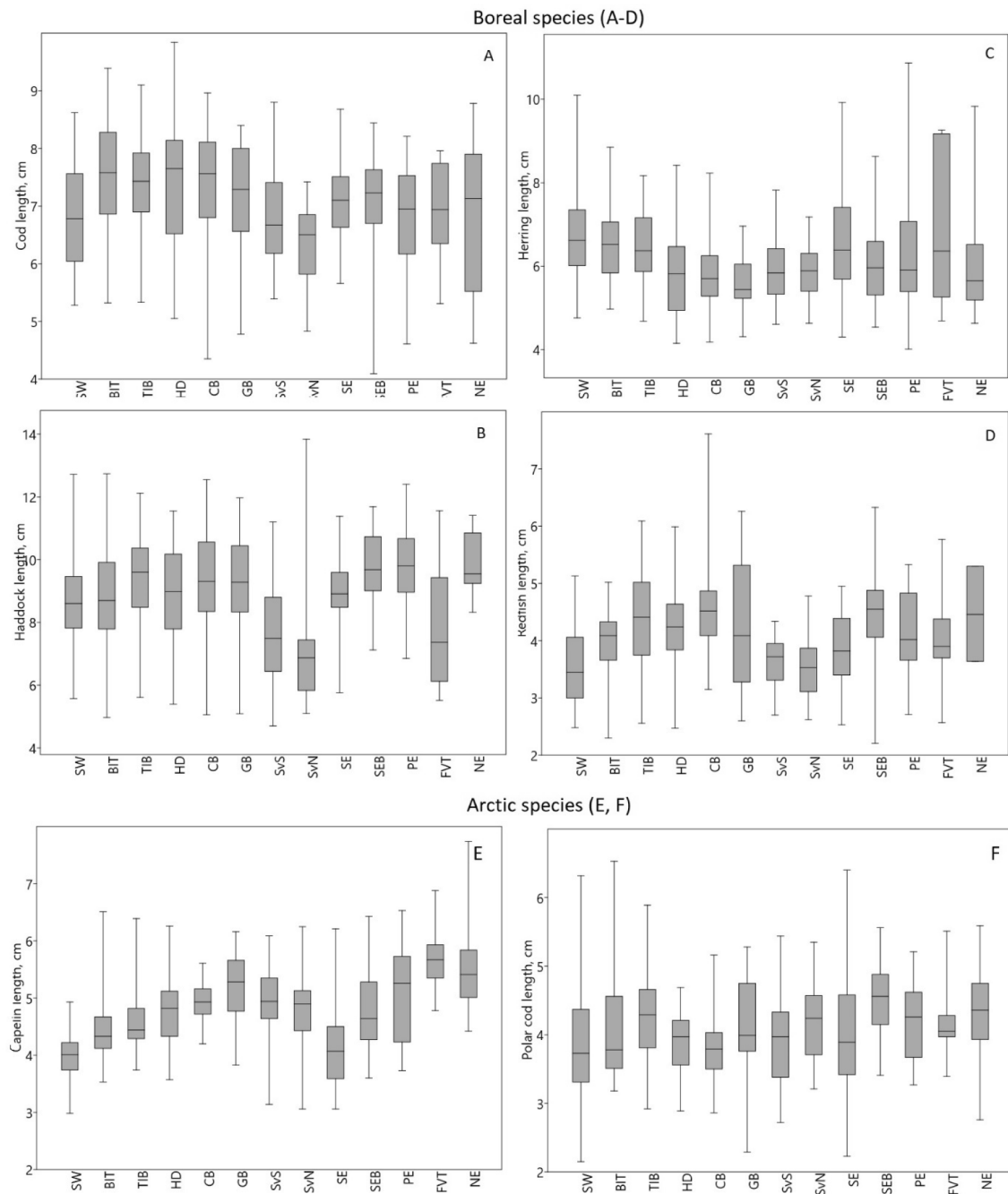
### 3.5. Interactions between time and space – Temporal patterns of polygon mean 0-group length

#### 3.5.1. Results from Principal Component Analysis

Using the data set of annual polygon means and Principal Component Analysis (PCA), we have examined if 0-group fish length showed different temporal patterns for different geographical areas (polygons) over the 1980–2017 time series. PCA showed a common pattern for the six species where all polygon variables were directed along the positive side of PC-1 (Fig. S-4). This reveals that the temporal variations for all polygons are positively correlated, and PC-1 is interpreted as a general expression of 0-group length. The polygons fanned out on the right-hand side of the PCA plots, with separation along PC-2 (Fig. S-4). The separation showed a clear geographical pattern for all species, broadly along a S-N or SW-NE gradient although with some differences in the arrangements of specific polygons. This reflected partly the differences in distribution of species (e.g., redfish mostly in the western and polar cod mostly in northern and eastern parts of the Barents Sea), and in the specific polygons that were included in the analysis of the species.

PC-1 explained from 36 % (capelin) to 65 % (haddock) of the total variance in 0-group length, while PC-2 explained from 10 % to 22 % (Table S-1). Together they explained from 55 % (capelin) to 81 % (redfish) of the variance. Since the polygon variables are standardized in the PCA, PC-2 reflects variability or differences in the temporal patterns of the polygons rather than consistent differences in length among the polygons (as shown in Fig. 5).

PC-2 conveys information on changes in the geographical pattern of 0-group length. The four boreal species – cod, haddock, herring, and redfish – showed some commonalities in the PC-2 time series, with lower values from around 1994 to about 2004, and higher and possibly increasing values after this time (Fig. S-5). PC-2, which explains a small fraction of the total variance (10–22 %), is characterized by considerable variability from year to year. Nevertheless, the time series showed significant correlations (at the 95 % level) for cod versus redfish, haddock versus herring, and herring versus redfish ( $r = 0.34$ – $0.44$ ).



**Fig. 5.** Box-whisker plots of length of 0-group fish of six species for 13 polygons (see legend to Fig. 2 for abbreviation of polygon names) showing median (horizontal line) and 25 and 75 % (boxes) and 5 and 95 % (vertical lines) quantiles for variation among all stations, 1980–2017. A – cod, B – haddock, C – herring, D – redfish, E – capelin, and F – polar cod.

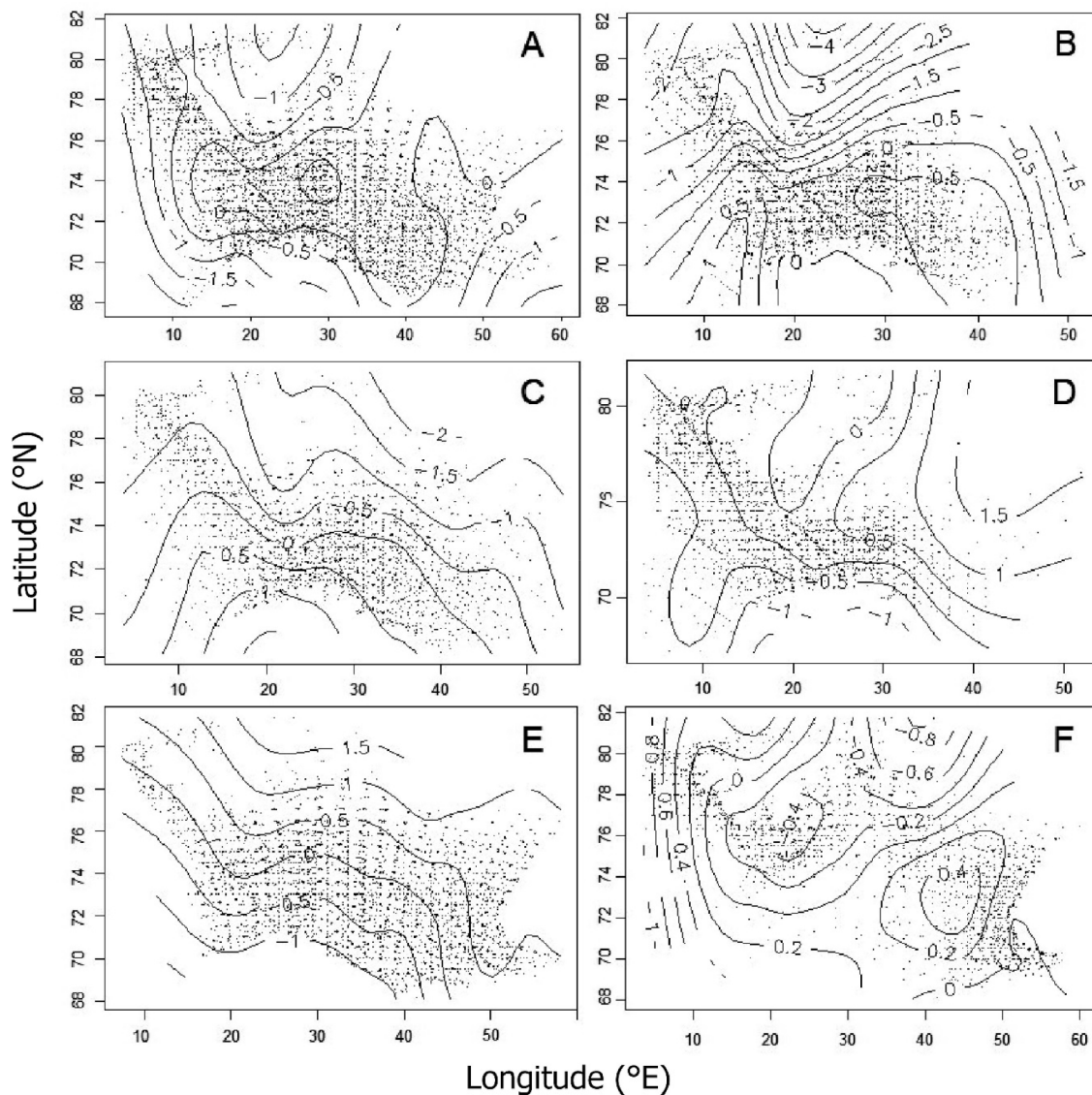
### 3.5.2. Temporal trends for geographical groups of polygons

Based on the results from the PCA for each of the six species, we have calculated mean length for groups of polygons separated along PC-2 for differences in temporal patterns. For cod and haddock, the groups of southern and central polygons showed similar increase over the time series, with the main effect of geography being shifts in the relative length between the polygons during the time series. For cod, this was reflected in (relatively) smaller 0-group individuals in the central polygons (CB, TIB, SEB) during the mid-part of the series (Fig. 9A). The 0-group individuals were smaller in the Svalbard polygons for both species (by 0.5–1 cm for cod and about 2 cm for haddock), with a similar increasing trend as for the southern and central polygons (Fig. 9A and S-9A).

0-group herring showed a complex pattern of variation with larger geographical difference in the period from the late 1990s to about 2004 when individuals were large in SW and relatively small in the eastern and northern polygons (Fig. 9B). The increasing trends with time were generally similar for the groups of polygons (increasing by about 1 cm) except for the northern polygons where there was no trend (Fig. 9B). Redfish showed considerable variation with time with no clear trends or differences in trends with time for groups of polygons (Fig. S-9B). The northern polygons (Svalbard) tended to have low length of 0-group redfish during the period from the late 1990s to about 2004, like the pattern for cod and herring.

Capelin differed from the other species by showing different temporal trends for groups of geographical polygons. 0-group length of





**Fig. 6.** Results from GAM analysis of 0-group fish length at sampling stations in the Barents Sea from 1980 to 2017 with model:  $\text{Length} = a + s(\text{Date}) + s(\text{Year}) + s(\text{Lat, Lon}) + e_i$ . Panels show smoother functions for effects of geographical position (latitude °N and longitude °E) for six species: A – cod, B – haddock, C – herring, D – redfish, E – capelin, and F – polar cod. The isolines in the map show the geographical pattern of positive and negative deviations (in cm) from the mean length (given as intercept values in Table 1). The grey dots are position of sampling stations. See Fig. 7 and Fig. S-7 for the effects from the GAM analyses of year and sampling date, respectively.

capelin decreased over the time series in eastern polygons (TIB, PE and NE, and SE and SEB), while it increased with time for the northern polygons (GB and Svalbard) (Fig. 10A). Thus, while individuals were largest in the central-eastern polygons (TIB, PE and NE) in the 1990s, this shifted to the largest individuals found in the northern polygons from 2004.

A similar difference in trends was shown by 0-group polar cod, where the length has been increasing more over the time series for the Svalbard polygons than for eastern and central polygons (Fig. 10B). The length decreased in the late 1990s to a minimum in 1997–99, followed by an increase to relatively high values for the eastern and northern polygons after 2004.

### 3.6. Relationship of 0-group length with warming and zooplankton prey

#### 3.6.1. Temperature

The Barents Sea has warmed corresponding to a linear trend of about 1.5–2 °C since 1980 (Skagseth et al. 2020). The warming has taken place

with fluctuations, most pronounced and with largest amplitudes for the northern and eastern polygons.

The two sets of time series for annual mean 0-group length (unweighted and weighted) showed positive and statistically significant correlations (at the 95 or 99 % level) with temperature for five of the six species (cod, haddock, herring, polar cod, and redfish; Table 4). Capelin showed weak correlations for the unweighted series ( $r < 0.2$ ), whereas the weighted mean series showed significant (95 % level) correlations. The relationships between 0-group length and temperature include two components: decadal fluctuations and linear trend over the time series. A common pattern shown by all six species was similar fluctuations in length as for temperature for the first two ‘waves’ in the 1980s and 1990s, although with some differences in timing (Figs. 7 and 11). Cod, haddock, and polar cod showed increasing trends in 0-group length (Table 3), as did the temperature climate series (Fig. 11). Removing the trends from the time series resulted in lower correlations for the three species, most markedly so for haddock where the detrended correlations became non-significant at the 95 % level (Table 4). For cod, herring,

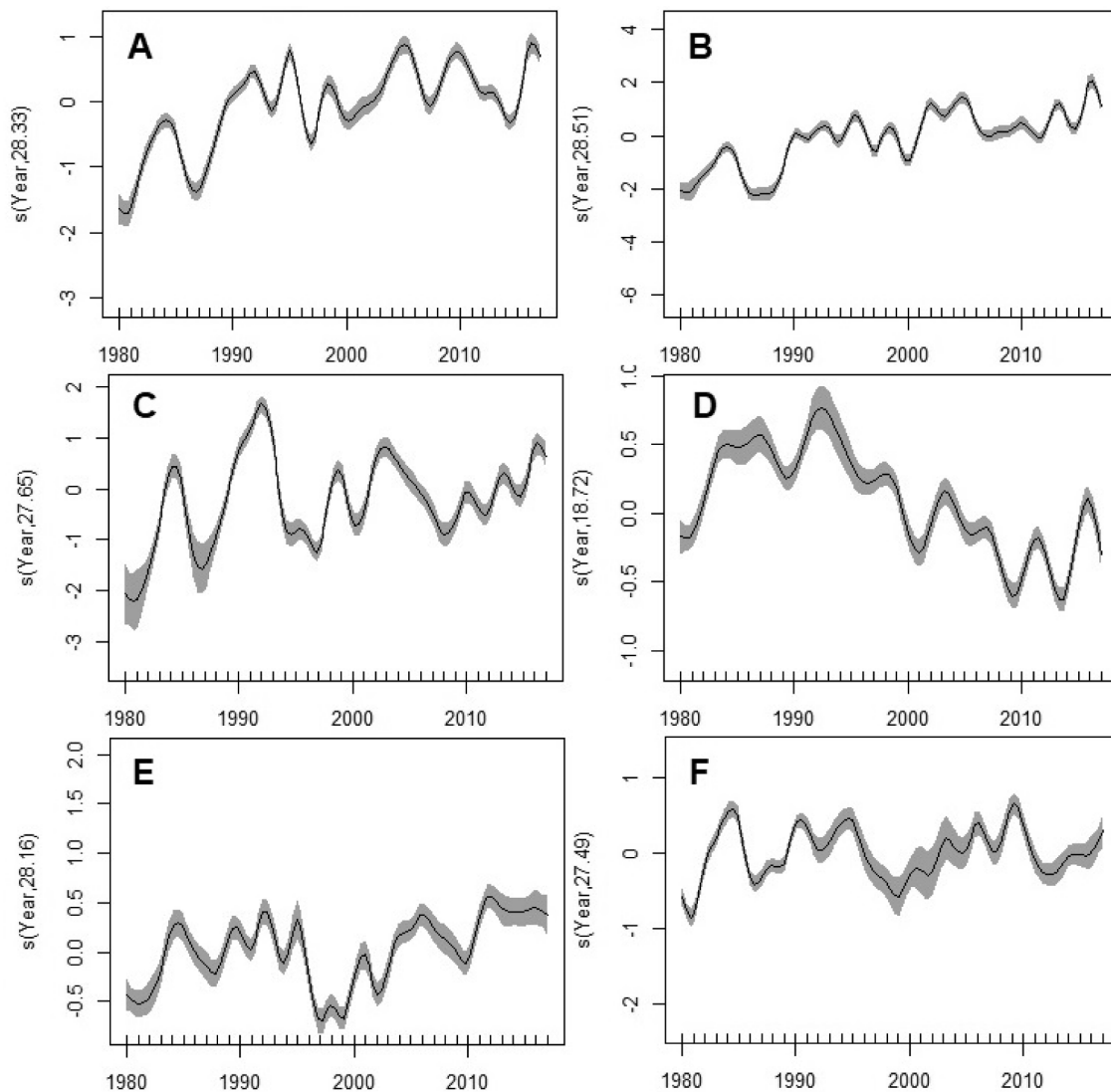


Fig. 7. Results from GAM analysis of 0-group fish length at sampling stations in the Barents Sea from 1980 to 2017 with model:  $\text{Length} = a + s(\text{Date}) + s(\text{Year}) + s(\text{Lat, Lon})$ . The lines are best-fit curves with 95% confidence interval shown as grey bands. The scales in these plots are deviation (in cm) from the overall mean length (intercept value in Table 1). A – cod, B – haddock, C – herring, D – capelin, E – polar cod, and F – redfish.

polar cod and redfish, the positive correlations with temperature remained statistically significant (at the 95 or 99 % level) after detrending, which demonstrate that the patterns of oscillation had a dominant influence on the correlations for these species. For capelin, detrending the data series improved the correlations to a statistically higher significance level (99 %) for the weighted mean series (Table 4).

Herring and capelin showed greatest length for the peak in the 1990s (Fig. 7). All species showed pronounced decrease in length associated with the cooling in the late 1990s, and all showed increasing trends with time and the warming after this cold event. Capelin was an exception in showing no significant relation with temperature for the unweighted mean length. In fact, the correlations were slightly negative, reflecting the declining trends for eastern polygons (Fig. 10A). By removing the trends, the correlations changed sign to positive, but the values were still low and insignificant for the unweighted as opposed to the weighted mean length series (Table 4).

The correlations with temperature for cod and haddock were between 0.5 and 0.7 (Table 4). This suggests that temperature explained somewhere between 25 and 50% of the variance in 0-group length of these two species.

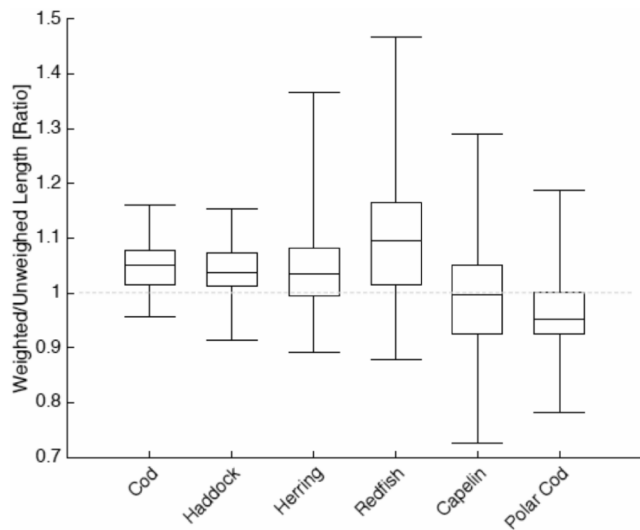
### 3.6.2. Model transport of water into the Barents Sea

The model transport of the two branches (Kola and Hopen) as annual averages for the April–August period showed considerable interannual variability, with the Kola branch being about twice as strong as the Hopen branch (around 1 Sv versus 0.5 Sv). Over the time series, there was an increase in the modelled transport in the Kola branch and a decrease in the Hopen branch (by about 0.2 Sv).

The model Kola transport showed weak to moderate positive correlations with 0-group length for several species ( $r$  up to 0.38), being statistically significant (at the 95 % level) for cod, haddock, and capelin. However, the model transport was moderately correlated with temperature ( $r = 0.35\text{--}0.40$ ), and the correlation with 0-group length could reflect this relationship with temperature.

### 3.6.3. Zooplankton biomass

Zooplankton biomass recorded during the 0-group cruises (from 1989) showed a common temporal pattern (but also some differences) for six selected polygons. All polygons had low biomass values around 1990 followed by a pronounced peak in 1994 or 1995, and a decline in the late 1990s (Fig. S-10A, B). Zooplankton biomass of the two series (polygon means and FB transect) showed no or weak linear correlations



**Fig. 8.** Box-whisker plot of the ratio between abundance-weighted and unweighted annual mean length of 0-group fish of six species. The horizontal lines (inside the boxes) are median values, the boxes span the 25–75 % quantiles, and the vertical lines show range of values (from minimum to maximum) for the time series 1980–2017.

**Table 2**

Correlation coefficients (Pearson *r*) for covariation in time series of weighted and unweighted annual mean length of 0-group fish of cod, haddock, herring, redfish, capelin, and polar cod, 1980–2017. Statistically significant correlations at 99 % and 95 % levels (adjusted for autocorrelation) are shown with bold type and italics, respectively. Acceptable degree of deviation from normality was indicated by skewness and kurtosis values < 1.1 (+/-).

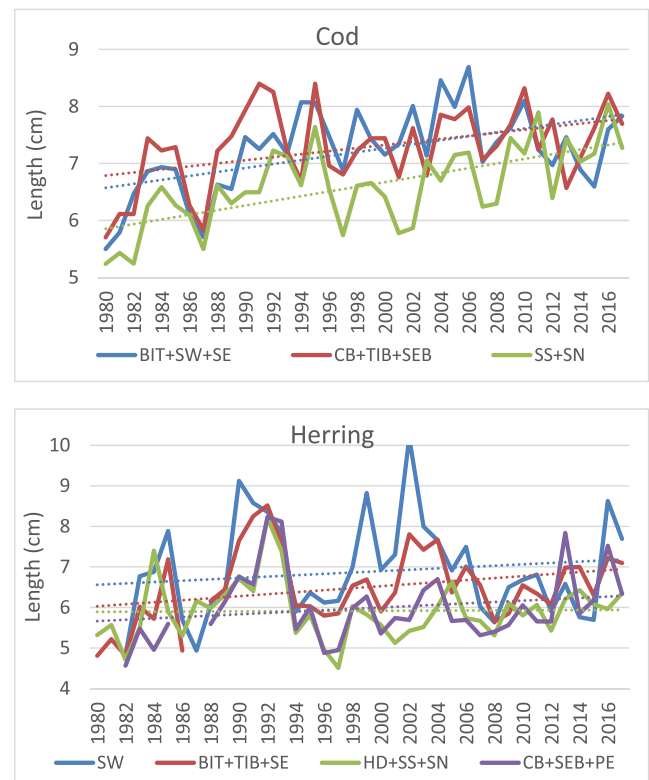
	Cod	Haddock	Herring	Redfish	Capelin
Weighted mean					
Haddock	<b>0.72</b>				
Herring	<b>0.55</b>	<i>0.37</i>			
Redfish	<i>0.37</i>	0.26	0.15		
Capelin	<i>0.39</i>	<b>0.43</b>	<b>0.49</b>	0.14	
Polar cod	0.22	0.35	-0.03	0.18	0.09
Unweighted mean					
Haddock	<b>0.82</b>				
Herring	<b>0.6</b>	<b>0.56</b>			
Redfish	<b>0.58</b>	<i>0.37</i>	0.37		
Capelin	0.15	0.15	<b>0.48</b>	0.19	
Polar cod	<b>0.47</b>	<i>0.42</i>	<i>0.34</i>	<b>0.57</b>	0.05

**Table 3**

Linear regression analysis of annual mean length (abundance-weighted) of 0-group fish of six species versus year over the time series 1980–2017. *a* is intercept corresponding to length in 1980, and *b* is regression slope (cm year<sup>-1</sup>). R<sup>2</sup> is the coefficient of determination (fraction of variance explained), and *p* is the statistical probability from Mann-Kendal test. The increase as a trendline from 1980 to 2017 is given in cm and as % of the initial length in 1980.

Species	a (L 1980)	b	R <sup>2</sup>	p	Increase 1980–2017	
					cm	%
Cod	6.74	0.033	0.19	0.074	1.26	19
Haddock	7.25	0.08	0.49	<0.001	3.06	42
Herring	6.66	-0.001	0	0.744	-0.03	0
Capelin	4.55	0.006	0.01	0.291	0.23	5
Polar cod	3.48	0.022	0.26	0.002	0.82	23
Redfish	3.74	0.011	0.07	0.056	0.42	11

with 0-group fish length, with a few exceptions (Table S-5). Thus, herring showed statistically significant (at the 99 or 95 % level) negative correlations for 0-group length versus the medium fraction and total

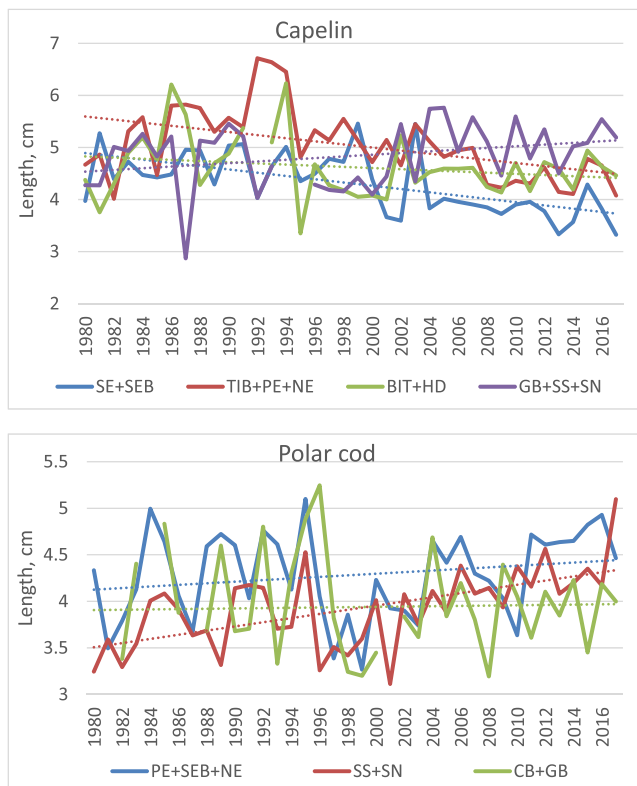


**Fig. 9.** Time series of annual means of 0-group length for groups of polygons for (A) cod and (B) herring, 1980–2017. For cod, time series are shown for southern polygons (BIT, SW and SE), central polygons (CB, TIB and SEB), and Svalbard polygons (SS and SN). For herring, time series are shown for the SW polygon and groups of southern-central (BIT, TIB, SE), central-eastern (CB, SEB, PE), and northern (HD plus Svalbard) polygons. See Fig. 2 for location and names of the polygons. Dotted lines are linear trendlines versus time.

zooplankton biomass for the polygon data set ( $r = -0.48-0.62$ ). These correlations, despite being statistically significant, may be coincidental rather than reflecting any causal relationships, particularly for the inverse relations between zooplankton and 0-group length of herring.

The zooplankton biomass tended to be highest for the BIT polygon, which showed relatively high values after 2004 (Fig. S-10A). In contrast, the biomass tended to be lowest for the CB polygon, and here biomass generally declined to a minimum in 2013. The zooplankton biomass values are the ‘end results’ at the time when 0-group fish are surveyed in autumn, and the six polygons span the main 0-group distribution area along the transport route into the eastern Barents Sea (BIT, TIB, SEB) and north into the Hopen Deep, Central Bank, and Svalbard (see Fig. 2). The peak in zooplankton biomass in 1994 was driven to a large extent by the small size fraction (small copepods and others), while the medium fraction (dominated by older copepodite stages of *Calanus* species; Skjoldal 2021) tended to dominate biomass in most years after 2001 (Fig. S-10B).

Average length of the six 0-group species (as anomalies) is plotted along with temperature (EOF-1) and zooplankton biomass (average for six polygons) in Fig. 11. The first two ‘waves’ of increase in 0-group length in the 1980s and early 1990s matched quite well the two up-swings in temperature. It is noteworthy that all six species showed an increase in 0-group length from minima in 1987 to relatively high values in 1990 (see Fig. 7), coinciding with warming, and despite the low zooplankton biomass at this time (Fig. 11). The subsequent increase in zooplankton to a pronounced peak in 1994 coincided with maintained high length of 0-group fish even as temperature was declining. 0-group length then declined along with zooplankton biomass to minima around year 2000. The third wave of increase in length of 0-group fish in the



**Fig. 10.** Time series of annual mean 0-group length for groups of polygons for (A) capelin and (B) polar cod. For capelin, time series are shown for groups of eastern (SE and SEB), central-eastern (TIB, PE and NE), western (BIT and HD), and northern (GB, SS and SN) polygons. For polar cod, time series are shown for groups of eastern (PE, SEB and NE), northern (Svalbard, SS and SN), and central (CB and GB) polygons. Dotted lines are linear trendlines versus time.

**Table 4**

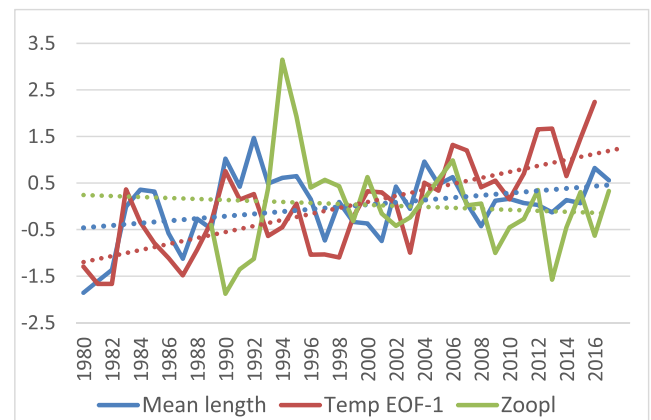
Correlations (Pearson  $r$ ) between 0-group length of six species of fish and temperature (expressed as the first Empirical Orthogonal Function (EOF) of a large data set of autumn temperature; Skagseth et al. 2020). Correlations are shown for the two sets of data for weighted and unweighted annual mean length, as the original data series and after removing trends with time. Statistically significant correlations at 95 % level (corrected for effect of autocorrelation but not accounting for multiple comparisons) are shown with bold type.

Species	Weighted		Unweighted	
	Original	Detrended	Original	Detrended
Cod	<b>0.50</b>	<b>0.41</b>	<b>0.66</b>	<b>0.40</b>
Haddock	<b>0.65</b>	0.26	<b>0.57</b>	0.19
Herring	<b>0.35</b>	<b>0.59</b>	<b>0.39</b>	<b>0.38</b>
Redfish	<b>0.36</b>	<b>0.35</b>	<b>0.46</b>	<b>0.50</b>
Capelin	<b>0.31</b>	<b>0.46</b>	-0.09	0.21
Polar cod	<b>0.44</b>	0.15	<b>0.63</b>	<b>0.58</b>

early 2000s coincided with a period of warming. The average 0-group length did not respond with an increase due to the temperature maximum in 2012, which coincided with relatively low zooplankton biomass (Fig. 11). We note that the six species showed different patterns in length in the last part of the time series (e.g., cod and haddock increasing, and capelin decreasing), when there was a difference in trends in zooplankton biomass between the western entrance and central areas further into the Barents Sea (Fig. S-10A).

### 3.7. 0-group fish length and abundance

The series of annual 0-group mean length are positively correlated

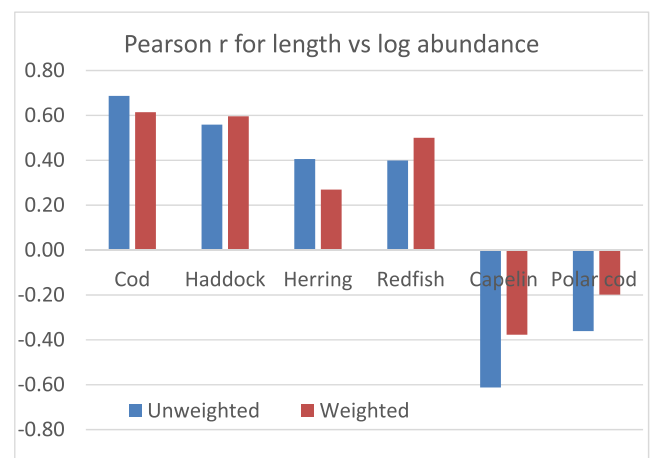


**Fig. 11.** Time series of standardized anomalies (zero mean, unit variance) of average 0-group length, temperature, and zooplankton biomass. Average 0-group length is the PC-1 from the PCA of annual unweighted (geographical) mean length of the six species (Fig. S-3). Temperature is the first EOF from analysis of polygon mean data from the 0-group survey (Skagseth et al. 2020). Zooplankton is the mean total biomass for the six polygons data set (Fig. S-10A). Dotted lines are linear trendlines.

with total abundance (log transformed, e.g., Hjermann et al. 2004) of the 0-group (year-class strength) for the four boreal species (cod, haddock, herring, and redfish) (Fig. 12). For the two Arctic species (capelin and polar cod), the correlations are negative (Fig. 12). The correlations are broadly similar for the two sets of annual means (weighted and unweighted).

## 4. Discussion

We have used a large dataset of individual length of six species of juvenile fish (cod, haddock, herring, beaked redfish, capelin, and polar cod) in the Barents Sea to investigate spatial and temporal patterns over the timespan 1980–2017. Our study differs from earlier studies of length of 0-group fish in that the data have been corrected for the effect of variable sampling date, and, in comparison with some of the earlier studies, for the influence of length-dependent capture efficiency (Eriksen et al. 2017). Overall, the observed length of 0-group fish is characterized by large variability.



**Fig. 12.** Correlation coefficients (Pearson  $r$ ) between length and abundance of 0-group of six fish species for annual mean values for 1980–2017. 0-group length is calculated as unweighted (geographical) and abundance-weighted (population) annual means. All but the two lowest correlations (herring and polar cod for the weighted mean length series) are statistically significant at the 95 or 99 % level (corrected for autocorrelation).

The 0-group survey each year lasts around 4–5 weeks, which is the time it takes to cover the large area of about 1 million km<sup>2</sup> with sampling by 4–5 ships. The correction for sampling date is based on estimated values of daily length increments from the GAM analyses (Table 1). These implied growth rates compare quite closely with estimates of daily growth based on length increments of juvenile cohorts between a summer cruise (June–July) and the 0-group cruise 1–2 months later (August–September), reported by Loeng et al. (1995) for the years 1977–1991. Our value for cod is somewhat lower than the estimate by Loeng et al. (0.45 vs 0.77 mm d<sup>-1</sup>), while the values are closer for haddock (0.9 vs 1.0 mm d<sup>-1</sup>) and the same for herring (0.6 mm d<sup>-1</sup> in both cases). Suthers and Sundby (1993) found a mean growth rate of 0.65 mm d<sup>-1</sup> for younger 0-group cod (around 3–4 cm in length) in July 1988 (based on otolith analysis).

We raised five questions in the Introduction. These questions are addressed in the following before we end the discussion with some consideration of recruitment variability and the final concluding section.

#### 4.1. Different spatial patterns between boreal and Arctic species

There is a difference in spatial patterns in 0-group length relative to abundance between the four boreal species (cod, haddock, herring, and redfish) and the two Arctic species (capelin and polar cod). The boreal species tended to be largest where juveniles were more abundant. One explanation for this could be that the conditions for growth and survival are better in the (dynamic) space of the ‘core area’ of 0-group distribution, resulting in higher densities and larger juveniles here than elsewhere. The ‘core area’ for boreal species is located in the inflow region of Atlantic water that provides a continuous supply of zooplankton which may give better feeding conditions for larvae and juveniles (Eriksen et al. 2015). The 0-group individuals of the four boreal species tended to be smaller in the Svalbard area than in the southern and central Barents Sea (see Figs. 5 and 6). This confirms the pattern found by Stensholt and Nakken (2001) of considerably smaller 0-group individuals of these species in the Svalbard area compared to the rest of the Barents Sea (for data from 1985 to 1998; see their Fig. 9). Lower growth rate due to lower temperature is a likely cause for the smaller 0-group individuals in the Svalbard area (Stensholt and Nakken 2001, Eriksen et al. 2012, 2015).

Cod, haddock, and herring also tended to be smaller in the ‘downstream’ direction in the eastern Barents Sea from the zones of positive length anomalies in the central core area (see Fig. 6). A likely cause for this pattern is reduced growth in the colder waters in the eastern region, which apparently has an overriding effect on that from age if the juveniles are older in the eastern ‘front end’ of distribution. A similar interpretation was given by Bjørke and Sundby (1987) for smaller juveniles of cod further into the Barents Sea compared to the Tromsøflaket region at the southwestern entrance in June–July. Suthers and Sundby (1993) used otolith microstructure to show that smaller individuals of juvenile cod (in July 1988) in the eastern compared to western areas reflected slower growth. A modelling study supported this pattern of smaller pelagic juveniles of cod in the eastern compared to the western Barents Sea (Vikebø et al. 2005). For herring, it has been shown that early spawned larvae may experience lower growth due to lower temperature while they are transported northward more rapidly by a narrower Norwegian Coastal Current (NCC) to the Barents Sea, compared to larvae from spawning later in the season (Vikebø et al. 2010, Slotte et al. 2019).

The two Arctic species (capelin and polar cod) showed an opposite pattern to that of the boreal species, with a tendency of being larger where they were less abundant. This could possibly be related to shorter distances and higher degree of dissipative spread of larvae and juveniles from the spawning areas within the Barents Sea. The general transport to the north for capelin, and for polar cod which spawn in the Pechora Sea, would give gradients of increasing age and size of juveniles away from

the spawning sites and at the same time decreasing numbers due to dissipative mixing and mortality of larvae and juveniles underway.

#### 4.2. Temporal patterns of 0-group length and covariation among species

The time series of 0-group length cover nearly four decades (38 years) and include interannual as well as decadal variations. The temporal variation in 0-group fish length consisted of a combination of fluctuations in wave-like patterns and an increasing trend during the period 1980–2017, with similarities but also clear differences among the six species (see Fig. 7). We recognize four ‘waves’ of increase in 0-group length, with roughly a decadal pattern. The first three ‘waves’ in the 1980s, 1990s, and 2000s are relatively distinct, whereas the last ‘wave’ in the 2010s is less clear.

The ‘waves’ reflect covariation and synchronicity in the temporal pattern of the species. Our results are similar to the covariation in length between cod, haddock, and herring reported by Loeng et al. (1995) and Ottersen and Loeng (2000) for the same 0-group data which included the first and second ‘waves’ in the 1980s and 1990s (up to 1996 in Ottersen and Loeng 2000). The amplitude of the fluctuations in 0-group length was larger than the effect of corrections for capture efficiency and variable sampling date, and the previously uncorrected and our corrected data show therefore qualitatively the same patterns of fluctuations (Fig. S-11). The two previous studies (Loeng et al. 1995, Ottersen and Loeng 2000) included data before 1980 (from 1965 and 1969 for cod and haddock, respectively) and showed synchronous variation in 0-group length also during the 1970s with high length in the first part of the 1970s dropping to low length in the late 1970s, before the increase in our first ‘wave’ in the 1980s.

The covariation was particularly strong between cod and haddock. These two species have main spawning areas just upstream of the entrance to the Barents Sea (Fig. 1). Larvae and pelagic juveniles are probably exposed to quite similar environmental conditions when they drift with the currents into the Barents Sea, even if cod and haddock initially are associated mostly with the NCC and the Norwegian Atlantic Current (NAC), respectively (Bjørke and Sundby 1984). Both are cod fishes (in family Gadidae) with similarities in the diet for larvae and 0-group individuals when they live pelagically in the southern Barents Sea (Dalpadado et al. 2009). The degree of covariation among the other species was less pronounced as reflected in positive Pearson *r* values < 0.6 (Table 2).

#### 4.3. Effects of temperature on 0-group length

Our results suggest a clear positive effect of temperature on 0-group length, both in terms of interannual variability (most pronounced on decadal timescales) and linear trends for some of the species, most notably cod and haddock. The temperature of the Atlantic water has increased corresponding to a positive trend of about 1.5 °C between 1980 and 2017, with an oscillatory variability superimposed onto the trend. The trends and oscillations seen in 0-group length resemble those in temperature (Figs. 7 and 11). Some earlier studies have found positive correlations between 0-group length and temperature that mainly reflected the short-term oscillatory fluctuations (Loeng et al. 1995, Ottersen and Loeng 2000, Helle et al. 2002). Our extended timeseries also indicate a temperature effect in the longer term manifested as an underlying long-term trend.

We can broadly recognize three different expressions of temperature: 1) temperature as a climate index, 2) ambient temperature for a population, and 3) temperature history of a cohort (or dynamic ambient temperature). The temperature history is probably the most appropriate expression, but it is difficult to estimate, both at individual and cohort or population levels. Core thermal habitat (CTH) has been described for the six species based on their distributions relative to ambient temperature, taken as the mean temperature in the upper 50 m at the sampling stations for the main part of the 0-group populations (80–90 %; Eriksen

et al. 2012, 2015). The CTH for the boreal species were about 5–9 °C, while the CTH for the two Arctic species were about 2–6 °C. While there is some spatial overlap, the CTH for the boreal species correspond to the temperatures of the southern and central polygons, while the CTH for the Arctic species correspond more to eastern and northern polygons.

We have used a temperature climate index to represent temperature. Previous studies of 0-group length have used temperature integrated over a section representing the Atlantic Water flow through the Barents Sea (e.g., the Russian Kola section – Ottersen and Loeng 2000, and the North Cape-Bear Island section – Loeng et al. 1995). In this study, we have used the first leading principal component of a PCA of annual mean polygon temperatures based on oceanographic data collected during the autumn 0-group surveys (WGIBAR 2018, Skagseth et al. 2020). The index is highly correlated with the Kola section temperature ( $R^2 = 0.90$ ) that has been used in earlier studies.

Linear regression for the relationship between length and temperature gives increases in length by about 1.0 and 1.5 cm per one °C for cod and haddock, respectively. For cod, this is comparable to a length increase of 0.7 cm for 5-month-old 0-group individuals predicted by a growth equation (Björnsson and Steinarsson, 2002) for a temperature increase from 5 to 6 °C. The predicted increase in length for a temperature trend of about 1.5 °C since 1980 (1.5 cm for cod and 2.3 cm for haddock) compares favorably with the observed increases by about 1.5 cm for cod and 2.5–3.0 cm for haddock. While the trend in temperature was apparently the most important component for haddock and partly also for cod, the fluctuations in temperature drove most of the correlations for the other species. The species apparently responded to the short-term temperature fluctuations with changes in 0-group length, while they showed various patterns over the time series in relation to the trend.

We interpret the reduced length of 0-group of the boreal species in northern and eastern parts of the Barents Sea as due to lower growth from lower temperature. Using station data for 0-group length, Eriksen et al. (2012, 2015) demonstrated clear effects of decreasing length with decreasing temperature below the zone of maximum length (at temperatures of 6–7 °C) for cod, haddock, herring, and redfish. Stensholt and Nakken (2001) reported a spatial effect of lower length at lower ambient temperature when annual mean values for stations in the Svalbard area were compared to mean values for the interior Barents Sea.

#### 4.4. Spatial-temporal patterns in 0-group length – Consistency and changes

The six species showed each a high degree of consistency in the spatial patterns over time, reflecting covariation and synchronicity in the variation of 0-group length for different geographical areas (polygons). The spatial consistency and synchronicity reflect similar fluctuations and trends superimposed on spatial differences in 0-group length, as illustrated in Figs. 9 and 10. These results suggest a large-scale climate influence, that has an overriding effect on 0-group length over the distribution area. This large-scale effect could be due to two main features. First, the larvae start out with a more limited distribution and possibly more homogenous conditions for larval growth than subsequently when the larval population have expanded geographically to become the 0-group distribution recorded in the Barents Sea in the autumn (see Fig. 1). Thus, the larval population may have a relatively uniform growth history in the first part of the cohort development, which is reflected in subsequent variation (Vikebø et al. 2005). Second, the variation in seawater temperature tends to be synchronous in different parts of the Barents Sea reflecting the large influence of the Atlantic water inflow (Skagseth et al. 2020).

The four boreal species (cod, haddock, herring, and redfish) and the two Arctic species (capelin and polar cod) showed different spatial-temporal patterns for 0-group length. The boreal species tended to show the same fluctuations and trends for different geographical areas

over the time series; that is, spatial patterns of differences in length tended to remain consistent over time. However, there was some spatial divergence, with larger spatial differences in part of the series from around the mid-1990s to mid-2000s (Fig. 9). The two Arctic species, in contrast, showed different temporal trends for different geographical areas. Thus, capelin showed a negative trend in 0-group length in the eastern Barents Sea, while polar cod showed a larger positive trend in length for the Svalbard area than for the southeastern Barents Sea (Fig. 10).

For capelin, the spatial difference in 0-group length widened from negative trend in east (e.g., SE and SEB polygons) and positive trend in northwest (see Fig. 10A). The decrease in length in the eastern areas took place mainly during the 2000s and 2010s, during a time of general warming. The reduced length may reflect poorer feeding conditions, later spawning and therefore younger individuals, or a combination of these factors. The growth of capelin tends to be slower and capelin individuals smaller in the eastern compared to the western parts of the distribution area in the Barents Sea (Gjøsæter 1998, Gjøsæter et al. 2011). This may lead to later spawning including summer spawning at eastern spawning locations along the Murman coast (Ushakov and Prozorkevich 2002, Hop and Gjøsæter 2013, Berg et al. 2021).

For polar cod, the trends in 0-group length reflected a complex pattern with an apparent shift to a lower level around year 2000 associated with a pronounced decrease in 0-group length at the onset of the cold event in the late 1990s (Fig. 10B). It is noteworthy that both stocks (Pechora and Svalbard) showed similar temporal patterns in 0-group length (significantly correlated with  $r = 0.48$  for PE + SEB + NE versus SS + SN in Fig. 10B), despite the different locations of the larval cohorts in the southeastern and northwestern parts of the Barents Sea. The Svalbard 0-group of polar cod have consistently been smaller than the Pechora 0-group in the eastern Barents Sea, but the difference has become less due to a stronger increase in length for the Svalbard component. The positive trends in 0-group length may reflect direct effects of increasing temperature on growth but possibly also earlier hatching of larvae due to less sea ice in the spawning areas (Bouchard and Fortier 2011, Bouchard et al. 2017, Huserbråten et al. 2019, Gjøsæter et al. 2020).

The spatial divergence in 0-group length for the boreal species in the late 1990s and early 2000s took place at a time of two cooling events following the warm event during the early 1990s. The spatial divergence was expressed as different relative geographical patterns with a tendency of smaller individuals in northern areas. While inflow (and throughflow) of Atlantic water has a dominant role for the oceanography and ecological conditions in the Barents Sea in general (Ottersen and Stenseth 2001, Lien et al. 2017, Skagseth et al. 2020), there is also an influence from variable conditions of sea ice and Arctic water in the northern Barents Sea (Kwok et al. 2005, Kwok 2009, Arthun et al. 2011, Lind et al. 2016, 2018, Onarheim et al. 2018). It appears that cold conditions influenced by events in the northern Barents Sea, caused or contributed to the observed spatial divergence in 0-group length for the boreal species in the late 1990s and early 2000s. The spatial divergence tended to be associated with low length in northern areas, which may reflect the cooling influence from north.

#### 4.5. Role of zooplankton for variations in 0-group length

Increased transport of *Calanus finmarchicus* into the Barents Sea has been considered a reason for better growth of fish larvae and juveniles (Helle and Pennington 1999, Helle et al. 2000, Ottersen and Loeng 2000, Sundby 2000). This copepod is a dominant prey for larvae and 0-group juveniles of cod, haddock, and herring among the boreal species (Ellertsen et al. 1989, Fossum 1996, Pedersen and Fosshem 2008). However, the variation in abundance of *C. finmarchicus* at the FB transect across the inflow region is large and with no clear relation to variable transport, although the development of the new spring generation was related to temperature (Skjoldal et al. 2021).

We used two series of zooplankton biomass, from the autumn (0-group) survey and at the FB transect in summer, respectively. None of them showed clear relationships with the variations in 0-group length. This may suggest that the availability of zooplankton has not been a limiting factor for juvenile fish growth. This would be in agreement with results from a model study that realistic concentrations of zooplankton nauplii are sufficient for optimal growth at the earlier larval life stages of cod in the Lofoten and Barents Sea area (Kristiansen et al. 2007). However, we note there are limitations in the available zooplankton data which prevent us from drawing a clear conclusion on this point. The zooplankton biomass data are integrated over the water column, while the 0-group fish are distributed in the upper 60 m, and often shallower above the seasonal thermocline (Stensholt and Nakken 2001). At the time of the 0-group survey, the zooplankton has started the descent from the upper layer to overwinter deeper in the water column, and most of the biomass is found deeper than the upper 60 m (Aarflot et al. 2018a, b). Furthermore, the zooplankton biomass measured in autumn at the 0-group survey is the end-result of the processes of growth, advection, and predation on the seasonally developing cohorts of *Calanus finmarchicus* and other zooplankton. The end point of seasonal trajectories may be poor reflections of the integrated feeding history of the drifting cohorts of larvae and juveniles.

The fourth ‘wave’ of increase in 0-group length in the 2010s is ill-defined and is characterized more by fluctuations and differences among the species, apart from high values for all species in 2016, which was a warm year (Eriksen et al. 2020b). Seen over the nearly four decades of fluctuations in 0-group length, the 2010s appear to be a time when the species separate to show different trends, with 0-group of herring and capelin being relatively small and those of the other species being relatively large. For herring, the relatively low length in the 2010s may have been caused by the situation upstream with low amount of zooplankton in the drift route of young larvae on the mid-Norwegian shelf as suggested by Toresen et al. (2019). For capelin, the low length especially in the eastern areas (see Fig. 10A) is possibly related to the decline in zooplankton biomass in the central Barents Sea (Dalpadado et al. 2020).

#### 4.6. 0-group length and recruitment variability

The year-class strength of fish stocks in the Barents Sea, notably cod and herring, are thought to be determined in the early life segment up to the 0-group stage (Sundby et al. 1989, Sætre et al. 2002). This is related to the very strong reduction in numbers from eggs to juveniles by many orders of magnitude (typically 3–5) due to sustained high rates of mortality, which inevitably result in large variation in the tiny, small fraction of survivors in this dramatic ‘reduction in numbers’ game (Skjoldal and Melle 1989, Skjoldal 2009). In theory, higher growth rates of the larval stages of fish should result in better survival since the time window of size-dependent predation becomes shorter for a given segment of larval development (Beverton and Holt 1957, Bailey and Houde 1989). While this is true as a general principle, the predator situation also plays a role which can change the ‘equation’. Thus, for herring it has been suggested that early spawning can be advantageous for year-class strength even if growth rate of the larvae is lower due to lower temperatures early in the season, because it is compensated for by lower overlap in time and space with major predators such as mackerel, blue whiting and saithe (Husebø et al. 2009, Slotte et al. 2019).

Previous studies have found positive correlations between 0-group length and 0-group abundance for the three boreal species cod, haddock, and herring in the Barents Sea (Ottersen and Loeng 2000, Helle et al. 2002). Our data confirm these results showing positive correlations between length and abundance (log transformed) of 0-group individuals for the four boreal species (cod, haddock, herring, and redfish) (Fig. 12). Our correlations for cod and haddock are similar to the values found by Ottersen and Loeng (2000) ( $r = 0.55$  for cod and  $0.60$  for haddock) but lower for herring ( $0.78$ ). We note that Ottersen and Loeng (2000) used a

different abundance index (‘logarithmic’) and different time periods (1965–1996 for cod and 1969–1996 for haddock).

## 5. Conclusions

There was a clear difference in the spatial patterns in 0-group length between the four boreal species (cod, haddock, herring, and redfish) and the two Arctic species (capelin and polar cod). The boreal species were generally larger in their core distribution areas where they were most abundant, while the Arctic species tended to be larger in the peripheral areas where they were less abundant. This geographic pattern possibly reflected differences in spawning times and location of spawning areas outside (‘upstream’) and inside the Barents Sea, leading to variation in both drift paths and drift times before sampling.

The fish lengths fluctuated in four more or less clear decadal ‘waves’, with maxima in the early/mid 1980s, 1990s, 2000s, and 2010s. In addition to these fluctuations, trends could be recognized, which differed somewhat among the species. Cod and haddock showed increasing trend over the whole period, herring and capelin showed largest length in the 1990s, while polar cod and redfish were relatively small in the early 2000s followed by an increase in the last decade.

The temporal variation in 0-group fish length showed positive correlation with seawater temperature, with highest correlations for cod and haddock and lowest for herring and capelin. Temperature has increased by 1.5–2.0 °C as a trend over the time series since 1980, with warming events matching broadly the ‘waves’ in 0-group length.

Each of the six species showed a high degree of consistency in the spatial patterns over time, reflecting similar variation of 0-group length for different geographical areas. These results suggest a large-scale climate influence that has an overriding effect on 0-group length over the distribution area, consistent with the observed effect of temperature. However, there was also some difference in the spatial-temporal patterns between the groups of boreal and Arctic species, with the latter (capelin and polar cod) showing different trends for some geographical areas.

Zooplankton biomass (in three size fractions), used as an expression of food for 0-group fish, had low explanatory power for the variation in 0-group fish length, which could be interpreted as if food has not been a limiting factor for growth of these 0-group species. However, there are methodological inadequacies of these plankton data (the biomass was integrated over the water column and data were mostly collected at the same time as the 0-group fishes were sampled), and they may therefore be a poor reflection of the feeding conditions of larvae and juveniles in the upper water layer through their growth period.

As a further step towards addressing recruitment variability of these six species of fish, we are currently examining spatial and temporal patterns in abundance. We plan to examine in more detail the influence of variable individual length of 0-group on year-class strength at the 0-group stage and subsequently at older age of the cohorts. The issue of density-dependence is central to the ‘recruitment problem’. In fact, the widely used asymptotic recruitment function of Beverton and Holt (1957) (number of recruits as function of adults) assumes density-dependent regulation of recruits, although this assumption is not well supported and may be erroneous (Skjoldal 2009).

We have witnessed four decades of unprecedented warming of the Barents Sea since 1980. As we have shown, temperature has a clear effect on length of 0-group fish, likely reflecting a direct effect on growth rate but possibly also on spawning time. The warming is likely to continue, and alteration of the length distribution of 0-group fish as one aspect of the ‘recruitment problem’ needs continued attention as we are trying to understand the on-going changes in this high-latitude ecosystem.

## Author contributions

EE prepared the data initially and performed statistical analyses.

HRS examined data and wrote the manuscript. All authors contributed to the preparation and reviewed and approved the manuscript.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data will be made available on request.

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### Appendix A. Supplementary data

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