Article title: **“**Effects of climate and spawning stock structure on the spatial distribution of Northeast Arctic cod larvae”

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Abstract

The spatial distribution of fish early life stages can impact recruitment at later stages and affect population size and resilience. Northeast Arctic (NEA) cod spawning occurs along the Norwegian coast. Eggs, larvae and pelagic juveniles drift near-surface towards the Barents Sea nursery area. In this study, a 35-years long time series of NEA cod larvae data was analysed in combination with factors that potentially may affect the distribution of eggs and larvae. These factors included biological aspects of the spawning stock, and environmental variables, such as water temperature, wind, ocean current, and prey abundance. Our aim was to shed light on how these factors influence larval abundance and distribution, and how larval abundance and distribution influenced recruitment at age 3. We found that biomass and mean weight of the spawners were positively associated with larval abundance, and that a high liver condition index of the spawners was associated with a north-easterly distribution of the larvae. The environmental variables showed generally weak or no correlations with abundance or distribution of larvae. Lastly, we found significant association between larval abundance and year-class abundance at age 3, while the spatial distribution metrics of the larvae, i.e., distribution extent, mean longitude and mean latitude, showed no significant association with future year-class abundance.

Key words

Gadus morhua
Barents Sea cod
Larvae distribution
Environmental effects
Demographic structure

Introduction

Recruitment variability is regarded as one of the main causes for the observed fluctuations of fish stock abundance over time. According to Hjort (1914), the fluctuations observed in the stocks cannot only be attributed to a constant and regular factor, such as fisheries, but are likely also dependent on variable natural conditions. To explain the variability in year class success, Hjort (1914) proposed that the dispersal of fish to unfavourable areas during the early life stages would impair recruitment of fish to fisheries. This means that the spatial distribution of the early life stages have an impact on the survival to later stages, also known as the “aberrant drift” hypothesis (Houde, 2008). Understanding the factors that explain recruitment variability still remains as one of the biggest challenges in fisheries research (Ottersen *et al.*, 2014)

The Northeast Arctic (NEA) stock of Atlantic cod (*Gadus morhua*) is among the largest and most studied cod stocks (Yaragina *et al.*, 2011). Atlantic cod is a long-lived species, with high fecundity and large fluctuation in year class strength. NEA cod is known to perform long reproductive migrations from its feeding grounds in the Barents Sea towards the spawning banks along the Norwegian coast, between Finnmark (71 °N) and Møre (63 °N) with highest spawning activity around the Lofoten region (69 °N)(Opdal *et al.*, 2008). After the spawning period, the eggs and larvae drift north and east towards the Barents Sea. The pelagic drift follows the Norwegian Coastal current on the shelf and the Norwegian Atlantic current at the shelf-break and more offshore areas (Vikebø *et al.*, 2005).

The individual drift routes of early life stages of fish result in highly variable biotic and abiotic exposure, and corresponding survival probabilities (Vikebø *et al.*, 2007; Putman *et al.*, 2016). The potential influence of environmental conditions is especially large for fish that are spawned far away from the nursery areas as they drift for longer distances and experience variable environments over longer periods of time, as is the case for the NEA cod. The early life stages of NEA cod drift between 600 and 1200 km during their pelagic phase from spawning between early March and late April until bottom settlement from September to October in the Barents Sea (Vikebø *et al.*, 2005; Ottersen *et al.*, 2014). During their pelagic phase eggs and larvae of NEA cod drift in the upper mixed layer, being susceptible to temporally and spatially varying climatic conditions that might affect the strength and duration of the flow (Vikebø *et al.*, 2007), and varying temperature, turbulence, prey availability and predation (Ottersen *et al.*, 2014).

The biological condition of the spawners and the demographic structure of the spawning stock also have impacts on the distribution and survival of the early life stages of fish. Demography of the spawning stock, through variable age or size structure, is reported to influence spawning location, time and duration (Kjesbu, 1994; Jørgensen *et al.*, 2008; Opdal and Jørgensen, 2015; Langangen *et al.*, 2019). It has previously been shown that high average age and size of the spawning stock of NEA cod result in high egg abundance and widespread egg distribution (Stige *et al.*, 2017). A wide egg distribution increases the diversity in conditions experienced by early life stages of a fish cohort, increasing the probability that a significant fraction of the cohort reaches the recruitment stage (Brunel, 2010). Moreover, the spawning locations are influenced by other processes, e.g. climate variability (Sundby and Nakken, 2008).

Here, we use a combination of time-series and spatiotemporal statistical analysis, to elucidate how demographic factors and environmental conditions influence recruitment dynamics through effects on the spatial distribution and abundance of NEA cod larvae. We have two main questions: (1) What are the effects of the demography of the adult population and of the environment on NEA cod larvae abundance and distribution? (2) What are the effects of larval abundance and distribution on recruitment at age three?

Materials and Methods

A spatio-temporal dataset of Northeast Arctic cod larvae for the period from 1959 to 1993 was used to construct seasonal indexes of abundance and distribution of cod larvae for the Barents Sea. The indexes were calculated separately for spring (before day 150, *i.e.* 30th of May) and summer (after day 150) encompassing every year in the dataset (further details on the construction of the indexes can be found in the section *Plankton data*). These indexes were used as response variables in a temporal analysis of the interannual variation in cod larval abundance and distribution. We considered both the abundance and distribution of all cod larvae and the abundance and distribution of only those larvae that were larger than 16 mm (hereafter termed “large larvae”). Large larvae analysis was carried out only for the summer, since there are very few NEA cod larvae larger than 16 mm in spring. Previous analyses suggest that recruitment at age 3 is more strongly associated with the abundance of large larvae than the abundance of all larvae three years previously (Stige *et al.*, 2015). Predictor variables were biological characteristics of the adult spawning stock and biotic and abiotic environmental conditions that the early life stages might have experienced until they settle to the bottom in the Barents Sea (Table 1). Subsequently, we investigated in more detail how the selected variables are associated with cod larval distribution using spatiotemporal statistical analysis. Finally, the annual NEA cod larval indexes were regressed against recruitment at age 3, the age when fish are considered to be recruited to the fisheries stock, to evaluate how larvae distribution and abundance affect recruitment to the adult stock.

Plankton data

Ichthyoplankton (Northeast Arctic cod larvae) and copepod (*Calanus* sp. nauplii and *Calanus finmarchicus* copepodites) data were collected by Russian dedicated ichthyoplankton surveys by the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO, currently the Polar Branch of the Russian Federal Research Institute of Fisheries and Oceanography, VNIRO) from 1959 to 1993 (Nesterova, 1990; Mukhina *et al.*, 2003). The surveys were conducted twice a year; one survey in the spring (April/May) - except for the spring of 1967 due to technical problems - and one in the summer (June/July). The surveys covered the main drift areas of NEA cod early life stages, covering an area from ~7 to 500 km off the coast in the area from 67° 30'N to 74° 30' N and from 4°E to 33° 30' E (Figure 1 – orange dots). Note that the more coastal and southern parts of the distribution of the early life stages of NEA cod were not sampled by the surveys (Ottersen *et al.*, 2014).

An egg net (IKS-80) with mesh size of 0.505 mm, a diameter of 80 cm and 1.5 m height was used for the spring surveys sampling of ichthyoplankton. The sampling at each station consisted of one vertical haul, from the bottom or from a maximum depth of 500 m; and of 10 minutes horizontal tows from 0 and 25 m depths. In the summer surveys two types of net were used: an IKS-80 net with the same configuration as for the spring surveys and a ring-trawl net with mesh size of 3 mm, a diameter of 1.5 m and 3.0 m height. At each station vertical hauls with both nets were taken; and 10 minutes horizontal tows were taken at 0 and 25 m depth with the IKS-80 net and at 50 m depth with the ring-trawl. The zooplankton were sampled using Juday plankton nets (37 cm diameter, 180 µm mesh). For further information on the Russian ichthyoplankton data we refer to Mukhina *et al.* (2003) and for the zooplankton data to Nesterova (1990) and Kvile *et al.* (2014).

The larvae samples were identified to species, counted, measured to the nearest millimetre and grouped into five different size intervals: 1 – 5 mm, 6 – 10 mm, 11 – 15 mm, 16 – 20 mm and 21 mm or larger. For the purpose of the analysis performed in this study, we have grouped larvae in two groups, one composed of all larvae sizes and the other of larvae larger than 16 mm, henceforth referred to as all cod larvae and large cod larvae, respectively. For 17 % of the stations with non-zero cod larvae data, only a subsample of the total larvae sampled were length-measured. The size-fractioned abundance data at these stations were rescaled by multiplying with a correction factor defined as the total number of larvae at the station divided by the total number of size-measured larvae.

Zooplankton abundance indexes were included among the environmental variables (Table 1), since zooplankton are main prey items for cod larvae (Sundby, 2000). Zooplankton indexes were calculated separately for spring and summer. Zooplankton data was divided into *Calanus* sp. nauplii (*naup*) and *Calanus finmarchicus* copepodites (*cop*). For spring, only the nauplii data was considered, while in summer, only the copepodite data were used, based on findings that copepod nauplii are main prey of first-feeding NEA cod larvae while larger cod larvae rely on larger zooplankton prey (reviewed by Ottersen *et al.*, 2014). The nauplii and copepodite abundance indexes were calculated following the same procedure as for the cod larvae abundance data, described in the section *Pre-processing of the data.*

The surveys sampling coverage varied in number, time and extent among the years, but usually followed regular transects (Mukhina *et al.*, 2003). Spring survey sampling dates varied between day of the year 83 (24th of March) and day 150 (30th of May), with mean date 128 (8th of May). The summer surveys occurred between day 151 (31st of May) and 216 (4th of August), with mean day 176 (25th of June).

Adult cod data

Spawning stock biomass (*SSB*, tonnes) and recruitment (number of individuals at age 3) data were obtained from the International Council for the Exploration of the Sea stock assessment report (ICES, 2018). *SSB* is calculated based on the state-space assessment model using both fisheries and research survey data. It is a sum across ages of age-specific products of stock number, weight and proportion mature (ICES, 2018), equation 1 and 2. The biomass-weighted mean weight (MW) of the spawning stock was calculated from the same data using equation 3 (Stige *et al.*, 2017).

$$SSB_{aj} = N_{aj}W_{aj}M_{aj} \qquad (1)$$

$$SSB_j = \sum_a SSB_{aj} \qquad (2)$$

$$MW_j = \frac{\sum_{a=3}^{a=15+}(W_{aj}SSB_{aj})}{\sum_{a=3}^{a=15+}SSB_{aj}} \qquad (3)$$

where *a* is age, *j* is year, *N* is number, *W* is weight, and *M* is the proportion mature. By weighting by biomass and not abundance of each age class, the MW index represents the sizes that dominate the spawning stock in terms of potential egg production.

The liver condition index (*LCI* - %) used was calculated for cod measuring 41-70 cm sampled in January-December by PINRO in the year previous to spawning estimated according to equation 4 (Yaragina and Marshall, 2000).

$$LCI_j\,(\%) = \frac{\sum_{m=1}^{m=12}\frac{\sum_n liver\ wet\ weight}{\sum_n total\ wet\ weight}*100}{12} \qquad (4)$$

where *n* is the total number of observations for a given year (*j*), month (*m*) and size class. This index has a positive correlation to recruitment in the NEA cod stock (Marshall *et al.*, 1999) and to cod egg distribution and abundance (Stige *et al.*, 2017).

Temperature and ocean current data

The Regional Ocean Modeling System (ROMS) model is a three dimensional baroclinic ocean circulation model with terrain following s-coordinates in the vertical (Shchepetkin and McWilliams, 2005). The Nordic Seas 4 km numerical ocean model hindcast (SVIM) archive is available as daily and monthly averaged outputs from an application of ROMS for the Norwegian and the Barents Sea with a resolution of 4 km and 32 sigma levels (Lien *et al.*, 2013). Temperature ($TEMP$ - °C) and ocean current speed (OC - m s^{-1}) were extracted from the monthly averaged SVIM archive for the period 1960 – 1993. For each variable, annual indexes for spring (SPR) and summer (SUM) were calculated, resulting in the variables $TEMP_{SPR}$, $TEMP_{SUM}$, OC_{SPR} and OC_{SUM}. Note that spring was considered as the average from March through May and summer was the average from June through July. The temperature was averaged for the upper 50 m of the water column for the same region as the PINRO survey samples (Figure 1– area outlined by the black dot-dashed line). Average ocean current speeds were extracted in the Lofoten region (68.2° N – 69.2° N latitude and 12.2° E – 14.9° E longitude, Figure 1 – purple solid line) following the bathymetry of the continental shelf break between the 300 and the 500 m isobaths for the upper 50 m in the water column, corresponding to a key area for larval dispersal *en* route from the spawning grounds towards the nursery areas (Strand *et al.*, 2017).

Wind data

The wind data were obtained from the MET Norway Reanalysis (NORA 10) downscaled from the European Reanalysis project (ERA-40) to a 10 km grid covering the Norwegian Sea, the North Sea, and the Barents Sea (Reistad *et al.*, 2011). Winds were extracted at a point location (69° N - 12° E; Figure 1 – brown star) at the shelf edge off the Lofoten archipelago. This is a particular narrow part of the shelf where larval dispersal is highly dependent on wind direction and strength, potentially also resulting in off-shelf transport (Strand *et al.*, 2017). Annual indexes for northeasterly (NE) and southwesterly (SW) winds for the period from 1959-1993 were calculated for spring (March-May) and summer (June-July). We only considered winds stronger than 5 m s^{-1} and with a duration of at least 3 days to cause significant variation in the predominant flow and egg and larval dispersal (Skarðhamar and Svendsen, 2005; Skagseth *et al.*, 2015; Strand *et al.*, 2017). The wind indexes (NE_{SPR}, NE_{SUM}, SW_{SPR}, SW_{SUM}) were defined as the fractions of time with winds above these thresholds (scaled from 0 to 1).

Pre-processing of the data

We quantified larval indexes of abundance and distribution (abundance-weighted mean latitude, longitude and distribution extent) for all cod larvae and for large cod larvae. Separate larval indexes for spring and summer of each response and predictor variable were calculated. Note that in the spring analysis of cod larval abundance and distribution, only environmental predictor variables for spring were considered. Whereas in the analysis of cod larval abundance and distribution in summer, environmental predictor variables for both spring and summer were considered, except for spring nauplii abundance, which would reduce the number of analysed years, leaving only 15 years, because of different missing years for spring and summer.

As the number of samples (egg net and ring trawl hauls) varied between stations, we used station-aggregated data on mean larval abundance per sample in the analyses. The data (cod larvae, *Calanus* spp. *nauplii* and *C. finmarchicus* copepodites separately) were resampled to mean abundance per grid cell of 1° latitude × 3° longitude in order to account for spatial variability in the sampling. For each year and season (spring or summer), the natural logarithm of the average abundance (N) of NEA cod larvae (or nauplii or copepodites) across all grid cells was then calculated for all cod larvae and for the large larvae. We only used grid cells with consistent sampling across years (Supplementary Figure A1- grid cells marked with an X) in subsequent calculations and only included years with data from all these grid cells, resulting in time-series of 21 years in spring and 22 years in summer with good spatial coverage (Supplementary Figure A2).

For nauplii and copepodites the indexes were calculated for the same years as used for the cod larvae indexes. Note that mean abundance values of 0 (3 years, in spring only) were replaced by the minimum abundance to avoid logarithm of 0. Mean annual latitude and longitude of occurrence in spring and summer were weighted by NEA cod larvae abundance for each grid cell. A distribution extent index (D, scaled from 0 to 1) was calculated annually for spring and summer, by ranking the grid cells from high to low abundance and counting how many cells represented a cumulative proportion of cod larvae above a threshold of 0.9. We tested how sensitive results were to the choice of threshold by also conducting the analyses with alternative thresholds of 0.8 and 0.95 (results in Table A1). The index was scaled to maximum 1 by dividing on the total number of grid cells.

Time-series analyses of predictor effects on larval abundance and distribution indexes

The first objective of our analyses was to identify which factors explain year-to-year variability in indexes of cod larvae abundance and distribution. We considered 12 cod larval abundance and distribution indexes (i.e., abundance, mean latitude, mean longitude and distribution extent for all cod larvae in spring, and in summer for both all cod larvae and large cod larvae). For each larval index (Supplementary Figure A2) we conducted a multiple linear regression analysis with the adult cod data (Supplementary

Figure A3) and the environmental variables as potential predictors (Supplementary Figure A4). Linear models were chosen based on a lack of significant nonlinear associations. The generic formula for the model was:

$$Y_t = \beta_0 + \beta_1 X_{1,t} + \beta_2 X_{2,t} + \ldots + \beta_n X_{n,t} + \varepsilon_t \qquad (5)$$

where Y_t refers to a given larval index for year t; $X_1 \ldots X_n$ are the potential predictor variables as given by Table 2; β_0 is the intercept; $\beta_1 \ldots \beta_n$ are coefficients for the effects of these predictor variables; and ε is the error term.

The predictor variables (Table 1 and Table 2) were selected by forward stepwise selection based on Akaike's Information Criterion corrected for small sample size (AICc; Hurvich and Tsai, 1989).Terms were added if leading to a reduction in the model's AICc. If the difference in the AICc between two models was smaller than 2, we considered the two models to have similar statistical support and report the results of both models. Residuals were checked for outliers, deviations from normality and autocorrelation through normal quantile-quantile plots and plots of the autocorrelation function (not shown). While several of the potential predictor variables were correlated (Table A3), the correlations among the predictor variables in the selected models were not so high (variance inflation factors ≤ 1.79).

Spatiotemporal statistical analysis of larval abundance and distribution

In a second step of the analysis we investigated the spatiotemporal variation in cod larval abundance in more detail. Varying-coefficient Generalized Additive Models (GAMs) (Hastie and Tibshirani, 1993) were used to evaluate the effects of selected predictor variables on the spatial distribution of NEA cod larvae. In this analysis, we used as response variable all the spatiotemporal data for cod larvae abundance for all years (1959-1993, aggregated to average values for each grid cell, season and year). GAMs estimate potentially nonlinear effects as smooth functions; seasonal and spatial patterns can for example be estimated as smooth functions of day of year, longitude and latitude. Spatial varying-coefficient GAMs estimate complex interaction effects, in which the spatial pattern depends on one or more continuous variables that represent factors that influence distribution. Specifically, the model assumes the effect of each of these variables to be linear at any given location, but the coefficient for this linear effect to vary as a smooth function of longitude and latitude. The model may also include predictor effects that are spatially homogeneous, i.e., having the same coefficient value at all locations. The predictor variables in our varying-coefficient GAMs were chosen according to the best fitted models in the time-series analyses. Specifically, predictor variables that significantly affected cod larval distribution variables were assumed to have spatially-varying coefficients, whereas predictor variables that significantly affected larval abundance but not distribution were assumed to have spatially-homogenous effects. The generic model formula is described by equation 6.

$$\ln(N_{it}) = \alpha + f_1(x_{1,t}) + f_2(x_{2,t}) + \ldots + g(day_i) + h_0(lon_i, lat_i) + h_1(lon_i, lat_i)\cdot y_{1,t} + h_2(lon_i, lat_i)\cdot y_{2,t} + \ldots + \varepsilon_{it} \qquad (6)$$

Here, N_{it} is mean larval abundance in grid cell i and time t; α is an intercept; f_1, f_2,..., g are smooth functions (i.e., natural cubic splines) of predictor variables with spatially-homogeneous effects (here referred to by the generic variables x_1, x_2,..., and *day-of-year*); h_0 gives the mean spatial pattern and h_1, h_2,... are two-dimensional smooth functions (i.e., tensor products of natural cubic spline basis functions) that give spatially-varying coefficients for predictor variables y_1, y_2,...; and ε_{it} is a normal distributed error term. Zero data were added the minimum abundance value and grid cells where there was no sampling were not used in the analysis.

Time-series analyses of associations between larval abundance and distribution indexes and recruitment

In a third step of the analysis we investigated the associations between the larval indexes and recruitment. The relationship between recruitment of 3-year-old cod and the abundance and distribution of the same year-class as larvae three years earlier was evaluated by fitting a multi-linear regression model, where the predictor variables were the larval indexes calculated from the PINRO samples. The general formulation for this model was:

$$R_t = \gamma_0 + \gamma_1 X_{1,t-3} + \gamma_2 X_{2,t-3} + \gamma_3 X_{3,t-3} + \gamma_4 X_{4,t-3} + \varepsilon_t \quad (7)$$

where R_t is the recruitment at age 3 in year t, X_1, X_2, X_3, X_4 are cod larvae abundance, mean latitude, mean longitude and distribution extent indexes for either all larvae spring, all larvae summer or large larvae summer; and ε is the error term.

Temperature, ocean current and wind data were processed in Matlab version R2019a. All statistical analyses were performed in R version 3.5.1, and the R-package mgcv version 1.8-28 (Wood, 2017) was used to perform GAM analysis.

Results

Time-series analyses of predictor effects on larval abundance and distribution indexes

According to our analysis of the abundance of all cod larvae, the variability in abundance in spring is best explained as a positive function of spawning stock biomass (Figure 2 A). An alternative model with similar statistical support in terms of AICc suggests that the variation in cod larval abundance in spring can also be explained as a function of nauplii abundance (Supplementary Table A2). Note that spawning stock biomass and nauplii abundance are positively correlated in the investigated period (Supplementary Table A3). In summer, the abundance of all cod larvae is explained as a function of the spawning stock biomass, the mean weight of the spawners and, non-significantly (P>0.05), by the spring ocean current speed (Figure 3 A). Large larvae abundance is best explained as a function of the spawning stock biomass and the mean weight of the spawners (Figure 4 A). Alternative models for summer abundance of cod larvae includes SW_{SUM} and OC_{SUM} instead of OC_{SPR} for all larvae, and OC_{SPR} for large larvae, however these are non-significant (Supplementary Table A2).

The spatial distribution of larvae was divided into three indexes indicating their north-south (latitudinal) distribution, east-west (longitudinal) distribution and an index indicating the general occupation across the sampling area (distribution extent) (Supplementary Figure A2). We found no significant explanatory variables for mean latitudinal variation in distribution of all cod larvae in spring. In summer, mean latitude of all cod larvae and of large larvae are positively associated with the liver condition index of the spawners and negatively associated (though non-significantly (P>0.05) for all cod larvae) with the ocean current speed in summer (Figure 3 B and Figure 4 B, respectively). Alternative models suggest that temperature and spawning stock biomass can replace ocean current speed as predictor for latitudinal distribution for, respectively, all cod larvae and large larvae in summer (Supplementary Table A2). Note that in summer, temperature in summer and ocean current speed in summer are positively correlated during the time period analysed (Supplementary Table A3).

The mean longitude of all cod larvae in spring was found to be best explained as a positive function of spring temperature (Figure 2 C), with also indication of a non-significant association with spawning stock biomass (Supplementary Table A2). Mean longitude of all larvae in summer was best explained as a positive function of the liver condition index of the spawners and a non-significant negative function of the abundance of copepodites (Figure 3 C); or, in an alternative model with nearly identical statistical support, as a positive function of spawning stock biomass and a negative function of abundance of copepodites (Supplementary Table A2). Mean longitude of large larvae was best explained as a positive function of the liver condition index of the spawners and a negative function of the southwesterly winds in spring (Figure 4 C).

The NEA cod larvae distribution extent in spring was best explained by the abundance of nauplii (Figure 2 C); and in summer, as functions of the liver condition index of the spawners, ocean current speed and, non-significantly, summer temperature (Figure 3 D). There was also indication of a non-significant association of summer distribution extent with the mean weight of the spawners (Supplementary Table A2). Large cod larvae distribution extent was associated positively with the spawning stock biomass and non-significantly with the mean weight of the spawners (Figure 4 D). Liver condition index and ocean current speed were selected as predictors of distribution extent of large larvae in summer, if the distribution index represented the distribution of 80 % rather than 90 % of the larvae; otherwise the choice of threshold for the distribution index had only minor effects on results (Supplementary Table A1).

Spatiotemporal statistical analysis of larval abundance and distribution

From the previous analysis we found that spawning stock biomass and nauplii abundance were the predictor variables that showed strongest association with cod larvae abundance in spring. In the summer for both all larvae and for large larvae, the most consistent predictor variables for abundance and distribution were mean weight of spawners, spawning stock biomass and the liver condition index of the spawners. The selected predictor variables were used in the varying coefficient GAM analysis, which showed in more detail how the distribution of cod larvae changed in response to the selected variables.

For the spring, our model shows that abundance tends to increase with increasing spawning stock biomass (Figure 5A). We further observe that in years with low nauplii abundance, the cod larvae in spring tend to be few in all parts of the study area (Figure 5B). When there is higher abundance of nauplii the cod larvae distribution is expanded to offshore areas, mostly in the Norwegian Sea (Figure 5C), where the Norwegian Atlantic current splits in two branches. Day of the year for survey sampling was not included in the final spring model, because it suggested initially (data not shown) a decrease in cod larvae abundance until mid-spring, which is unlikely to be real; and we believe this is due to sampling effect. Survey cruises normally started farther south along the Norwegian coast and moved towards the northeast into the Barents Sea (Supplementary Figure A1), which may influence the effect of day of the year in the abundance sampling.

The results for the distribution of large larvae in summer resembled the results for all larvae in summer (Figure 6 and Figure 7). Larvae abundance increases to a maximum around days 180-190 (29th June – 9th July) and then it starts to decrease. When there is a low spawning stock biomass (Figure 6B and Figure 7B) there is also a low abundance of cod larvae and large larvae in the study area. With high spawning stock biomass (Figure 6C and Figure 7C), larvae tend to spread in most directions, especially closer to the coastal areas. A similar pattern can be observed with low and high mean weight of the spawning stock (Figure 6D, E and Figure 7D, E). The overall abundance of larvae varies little between years with low and high liver condition index, but we see that in years with low liver condition index (Figure 6F and Figure 7F), the larvae are concentrated a little farther south in the coastal regions around 68-70 °N compared to years with high liver condition index (Figure 6G and Figure 7G).

Time-series analyses of associations between larval abundance and distribution indexes and recruitment

The AICc selection for recruitment to the adult stock selected abundance of cod larvae as the main variable (Table 3). For summer, all larvae distribution extent index was also selected, but it was not significant.

Discussion

The results in this study contribute to the knowledge on the effects of demographic structure and environmental variables on the spatial distribution and abundance of cod larvae, and on the implications of larval distribution and abundance for recruitment. We show that the demographic characteristics of the spawners were significantly associated with cod larvae abundance and distribution while the environmental variables considered showed weaker associations. We also show that abundance of cod larvae, but not spatial distribution metrics of the larvae, correlated significantly with the recruitment to the fisheries at age 3.

The role of stock demography and the environment for NEA cod larval abundance and distribution

Cod larvae abundance in spring and summer was higher when there was higher spawning stock biomass, as expected from the higher egg production potential these years. Our results showed that spawning stock biomass was similarly strongly correlated with the abundance of large larvae as with the abundance of all larvae indirectly suggesting that mean size of the larvae was independent of spawning stock biomass. Also other factors showed similar associations with the abundance of all larvae as with the abundance of large larvae, which are the larvae that seem to contribute most to recruitment (Stige *et al.*, 2015). Large body size appears important for survival of Northeast Arctic cod juveniles through the first winter of life (Stige *et al.*, 2019), possibly because large individuals have survival advantages compared to smaller individuals through reduced predation risk and increased tolerance of starvation and physical extremes (Miller *et al.*, 1988; Bailey and Houde, 1989).

The abundance of both total and large larvae in summer was positively associated with the mean weight of the spawners. Likewise, egg abundance from the same surveys was found to be higher when there was older and larger individuals in the spawning stock (Stige *et al.*, 2017). Interestingly, the mean weight of the spawners was estimated to have a much stronger effect on larval than egg abundance. For a change in mean weight of the spawners from 3.75 kg to 7.16 kg, which represent 5% and 95% of mean weight respectively, we estimated a 12-fold increase in larval abundance, compared to a 4-fold increase in egg abundance (Stige *et al.*, 2017). This result supports that survival of eggs to larvae is higher when the mean weight of the spawners is high, consistent with large female cod producing larger and more viable eggs (Marteinsdottir and Begg, 2002).

Note, however, that spawning of the NEA cod is a complex multilevel process prolonged in space and time. NEA cod are batch spawners with varying egg size per batch. According to lab investigations, egg size decreased from first to last batch and the egg dry weight decreased by about 20–30%; then, the number of eggs liberated in each batch followed a dome-shaped curve with time (Kjesbu, 1989). NEA cod are also multiple spawners that participate in spawning for several years. There are indications that younger fish spawn later (Jørgensen *et al.*, 2008) and stay at spawning grounds during shorter periods than older ones (Kjesbu *et al.*, 1996). Both mentioned biotic reasons could impact egg size, number of eggs released in different areas, and consequently larvae abundance and mortality.

Cod larvae distribution and extent (mean latitude, mean longitude and distribution extent) in summer, and in particular for large larvae, are more strongly correlated with the liver condition index of the spawners than with any other variable considered. The higher the liver condition index the more northeasterly the larvae are distributed. For the Atlantic cod, liver is the primary reserve for lipids, being a good indicator of recent adult feeding opportunity and fecundity (Lambert and Dutil, 1997; Marshall *et al.*, 1999; Yaragina and Marshall, 2000). The liver energy reserve also supports the spawning migration from the Barents Sea. For NEA cod it has been found that the Kola section temperature was not consistently correlated with the annual mean liver condition index, but the annual mean liver index was non-linearly related to capelin stock biomass. Also, liver condition index and the frequency of occurrence of capelin in cod stomachs were positively associated (Yaragina and Marshall, 2000). We hypothesize that years with favourable feeding opportunities and hence good liver condition index are likely promoted by higher temperatures, that has been proposed to shift feeding distribution to the northeast in the Barents Sea and spawning distribution to the northeast along the Norwegian coast (Sundby and Nakken, 2008).

Abundance of cod larvae presented few significant associations with the environmental variables. Abundance of cod larvae in spring was, however, associated with the abundance of nauplii. High copepod nauplii abundance and high temperatures in spring have also been found to be positively associated with higher abundance of cod larvae in summer (Stige *et al.*, 2015). Temperature may have an impact on food availability, growth rates and development of cod larvae (Sundby, 2000), although not detected in our analysis. Temperature was not found to have significant correlation with the abundance of cod larvae, following the same patterns as found for the NEA cod eggs (Stige *et al.*, 2017).

Of the environmental variables, ocean current speed and the wind events were found to be associated with distribution of NEA cod larvae. Cod eggs and larvae drift near-surface north- and eastwards towards the feeding habitat in the Barents Sea, following the main ocean currents, i.e., the Norwegian Coastal Current and part of the Norwegian Atlantic Current. Some larvae may be transported off-shelf by episodic events which may vary in frequency and timing from year to year, mostly depending on the occurrence of north-easterly winds and consequent advection of individuals off the shelf (Strand *et al.*, 2017). Eggs and larvae positioning in the water column is also important (not available from the used survey data) since the correlation between winds and the near-surface ocean current weakens with depth up to 40 m (Strand *et al.*, 2017). Ocean current speed had a negative association with the distribution extent and the mean latitude of the larvae. Though this relation is counter intuitive since both the Norwegian coastal current and the Norwegian Atlantic Current flow northwards, it is possible that strengthened shelf flow is associated with south-westerly winds resulting in downwelling along the coast and Ekman-transport of larvae towards the shore. In fact, the Norwegian Atlantic current is reported to be stronger and confined closer to the Norwegian coast in years with strong south-westerly winds, which occurs during positive phases of the North Atlantic Oscillation (Blindheim, 2004).

NEA cod larvae abundance and distribution and their relation to recruitment

Similar to previous studies (e.g., Helle *et al.*, 2000; Mukhina *et al.*, 2003; Stige *et al.*, 2015), we found that larval abundance was significantly correlated with recruitment. Recruitment correlated similarly strongly with the abundance of large larvae as with the total abundance of larvae, which is slightly different from previous results showing the highest correlation for large larvae (Stige *et al.*, 2015). Our analysis differs from the previous, Stige *et al.* (2015), by only including years with good data coverage, which reduces the risk of sampling bias but also reduces the length of the time series and potentially the statistical power.

As we found strong associations between mean weight in the spawning stock and larval abundance and between larval abundance and recruitment at age 3, our results suggest that high mean weight (larger individuals) in the spawning stock has positive effect on recruitment. Recruitment of Northeast Arctic cod at age 3 is not generally higher in years with older and larger individuals in the spawning stock (Ottersen, 2008), suggesting that effects of spawning stock structure on egg and larval abundances are often overruled by other factors that influence recruitment. Part of the reason may be changes in which factors drive recruitment variability, as indicated by the finding that correlations between recruitment and environmental indexes and between recruitment and juvenile-abundance indexes change over time (Ottersen *et al.*, 2013). For example, large egg size may hypothetically mainly increase survival under adverse environmental conditions, when a large yolk-sac may enable the newly hatched larvae to survive longer without feeding (Nissling *et al.*, 1998). Another hypothetical reason for the lack of association with recruitment is that many of the eggs and larvae in years with older and larger individuals in the spawning stock are located in areas where survival chances are low. Specifically, we found indications that the distribution extent of the larvae was higher in these years, as was also the case for the eggs (Stige *et al.*, 2017); if survival prospects in marginal areas are lower than in central areas, the increased abundance of larvae will be partly offset by reduced survival of the larvae. Although mortality is higher during the first months of life, year-class strength and recruitment can also be affected considerably by processes taking place later, before age 3, e.g. cannibalism and predation by other inhabitants of the Barents Sea (Bogstad *et al.*, 2016).

Recruitment to the fisheries at age 3 was not significantly associated with any spatial distribution metrics of the cod larvae, that is, distribution extent, mean longitude and mean latitude. The lack of association with distribution extent is similar to what has been found for Northeast Arctic cod eggs and questions the biological significance of a wide offspring distribution for increasing offspring survival (Stige *et al.*, 2017). In contrast, for all larvae in summer there was indication of a negative rather than positive association between distribution extent of larvae and recruitment, after controlling for the effect of larval abundance (Table 3). While we should be cautious not to over-interpret this non-significant negative association, it could have a biological explanation by the marginal areas of the distribution being sub-optimal for survival of larvae to recruitment.

The lack of significant association of recruitment at age 3 with mean longitude and mean latitude fails to support a significant role of the “aberrant drift hypothesis” (Hjort, 1914; Houde, 2008) in explaining Northeast Arctic cod recruitment. The “aberrant drift hypothesis” proposes that eggs and larvae that were transported to unfavourable areas would not be recruited to the fisheries stock, i.e., that recruitment variability of NEA cod can be mostly explained by how large fraction of the larvae reach the Barents Sea nursery grounds to the north and east of the larval distribution (Ottersen *et al.*, 2014). There may be several explanations to the non-significant associations, including inadequate statistical power, across-shelf transport of fish larvae from the offshore areas back onto the continental shelf (Strand *et al.*, 2017), and trade-offs between favourable locations for larval and juvenile survival up until recruitment (Langangen *et al.*, 2014).

Caveats

The lack of significant relations between the response variables and the predictors can also be a case of insufficient or inadequate data; similarly, some of the statistical associations may have arisen just by chance. Although care has been taken to correct for temporal and spatial sampling variability in the data, it is possible that the statistical power of the analysis performed is not sufficient to detect signals through noise, which is unavoidable when analysing survey data, mainly due to patchiness in marine population distribution (time and space). Moreover, it is possible that if other indexes had been used for distribution or environmental variables, different associations would be captured. The statistical findings of this study should therefore be considered hypotheses for future research; the possible mechanisms behind the associations can, for example, be tested through using a coupled biophysical model.

Conclusions

Factors regulating recruitment of fish stocks have been discussed for more than a hundred years and there are still many unanswered questions (Ottersen *et al.*, 2014). Recruitment and survival of cod larvae is a result of a combination of processes and mechanisms, ranging from the spawning stock characteristics to climate variables. Through statistical analysis of long-term scientific monitoring data, our results contribute to disentangle the quantitative importance of some of these processes. Our results suggest that spawning stock structure, as measured by the mean weight of the spawners, has strong effects on larval abundance and distribution; and that larval abundance but not distribution correlates significantly with recruitment at age 3. Also spawning stock biomass and liver condition index correlated significantly with larval abundance and/or distribution, while the investigated biotic and abiotic environmental factors showed weaker effect. These results underline the importance of ecological processes prior to spawning for offspring production, such as the availability of suitable prey for the spawners to build up their energy reserves. While the links from spawning stock structure to recruitment remains incompletely understood, the results presented here further motivate fisheries management strategies that support desirable age- and size-structures and thereby high reproductive potential of harvested fish populations. In sum, our study underlines that sustainable exploitation of the NEA cod stock requires that managers consider not only the biomass of the spawning stock, but also the demographic structure and the biomass of prey species. In turn, this increases the chances of sustainability in the exploitation of the fish stocks under a varying and changing climate.

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Tables

Table 1. Predictor variables considered for NEA cod larvae abundance and distribution. Environmental predictor variables and prey predictor variables were calculated for spring (SPR) and/or summer (SUM).

Variable	Description
SSB	Spawning stock biomass (ln[tonnes]) - yearly index
MW	Mean weight of the spawners (kg) - yearly index
LCI	Liver condition index (%) – liver wet weight as percentage of total wet weight of cod between 41-70cm in length for January and December on the year before spawning (Yaragina and Marshall, 2000) - yearly index
Naup	*Calanus* spp. *nauplii* abundance (ln[N]) yearly index in spring only
Cop	*Calanus finmarchicus* copepodites abundance (ln[N]) yearly index in summer only
T_{SPR}, T_{SUM}	Mean temperature (°C) averaged over the upper 50 m of the water column for the area sampled in the PINRO stations for spring and summer
OC_{SPR}, OC_{SUM}	Mean surface ocean current magnitude (m/s) for the upper 50 m in the water column in between the isobaths of 300 – 500 m depth for spring and summer
NE_{SPR}, NE_{SUM}	North-easterly wind events (fraction of time, scaled from 0 to 1) stronger than 5m/s and with wind events with duration of more than 3 days in the Lofoten region (69° N – 12° E) for spring and summer
SW_{SPR}, SW_{SUM}	South-westerly wind events (fraction of time, scaled from 0 to 1) stronger than 5m/s and with wind events with duration of more than 3 days in the Lofoten region (69° N - 12° E) for spring and summer

Table 2. Predictor variables (columns) and response variables (rows) considered in analyses of predictor effects (marked with an X) on annual larval abundance and distribution (Eq. 5). Each response variable was analysed separately. Acronyms are explained in Table 1.

	SSB	*MW*	*LCI*	*Naup*	*Cop*	T_{SPR}	T_{SUM}	OC_{SPR}	OC_{SUM}	NE_{SPR}	NE_{SUM}	SW_{SPR}	SW_{SUM}
Larval indexes spring*	X	X	X	X		X		X		X		X	
Larval indexes summer**	X	X	X		X		X	X	X	X	X	X	X

* Abundance (ln[N]), mean latitude, mean longitude, and distribution extent of all cod larvae

** Abundance (ln[N]), mean latitude, mean longitude, and distribution extent of all cod larvae, and of large cod larvae

Table 3. Effect of the NEA cod larvae abundance (N) and distribution (*D*) on the recruitment at age 3. Model parameter estimates and standard errors (in parentheses), proportion of variance explained (R^2) of the best model for recruitment and the selected NEA cod larvae abundance and distribution predictors. Note spring and summer were analysed separately due to different year coverage in the time series. Significance levels: * p<0.05, **p<0.01 and ***p<0.001

	Parameter estimates (SE)		
ln(Recruitment)	Intercept	Parameters	R^2
All larvae spring	13.97 (0.36)	+ 0.28 (0.10) * ln(N)	0.287
All larvae summer	14.68 (0.65)	+ 0.43 (0.12) ** ln(N) - 6.07 (3.63) *D*	0.428
All larvae summer	13.66 (0.23)	+ 0.28 (0.08) ** ln(N)	0.377
Large larvae summer	13.75 (0.24)	+ 0.22 (0.06) ** ln(N)	0.387

Figures

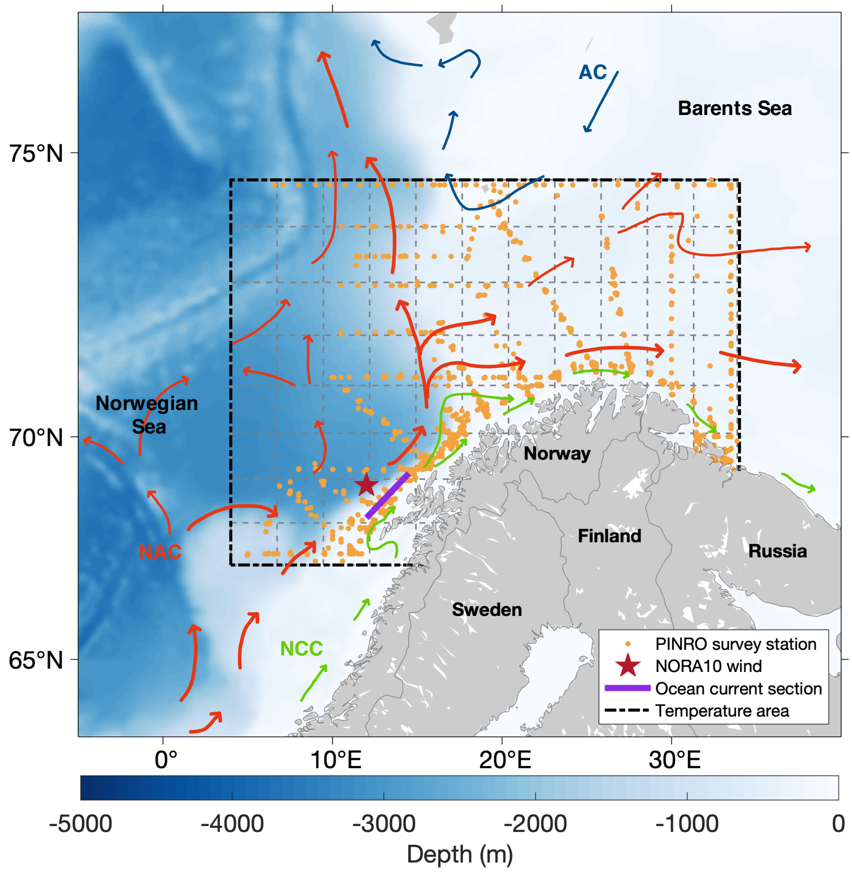


Figure 1. Study area. Polar Research Institute of Marine Fisheries and Oceanography (PINRO) research cruise stations (orange dots); wind point location (brown star); ocean surface current section (purple line) and surface temperature area (black dashed line). Grid used in the spatiotemporal statistical analysis (dashed grey lines). Main ocean surface circulation pattern in the Barents Sea and Norwegian Sea: Norwegian Coastal Current (NCC – green arrows), Norwegian Atlantic Current (NAC – red arrows) and Arctic Current (AC – blue arrows).

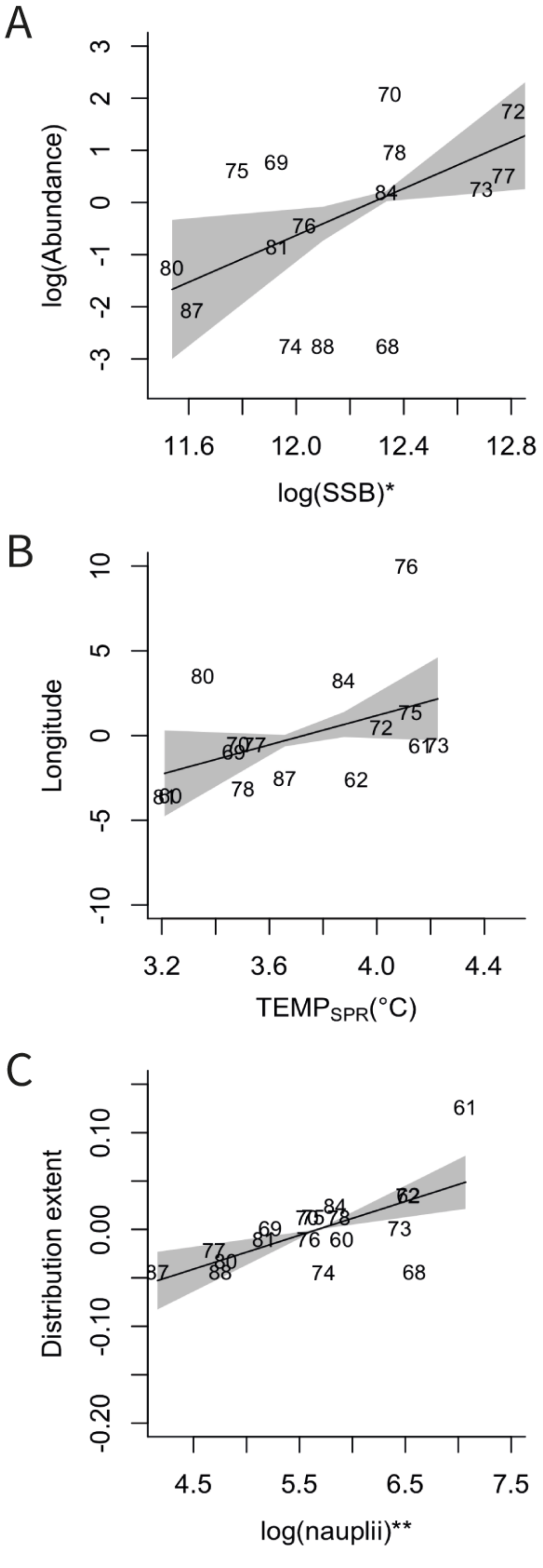


Figure 2. Linear effects of the AICc-selected predictor variables (acronyms are stated in Table 1) on the abundance and distribution of total Northeast Arctic cod larvae in spring. Equations for each model (A - C) can be found in *italics* in table A2 – Total NEA

cod larvae - Spring. Each row shows the selected model for one larval index, abundance (A), mean longitude (B), or distribution extent (C). Each panel shows the partial effect of one variable, with partial residuals per year shown by the plotted numbers (= year – 1900). Asterisks after the x-axis variable indicate statistical significance: * p<0.05, ** p<0.01, *** p<0.001.

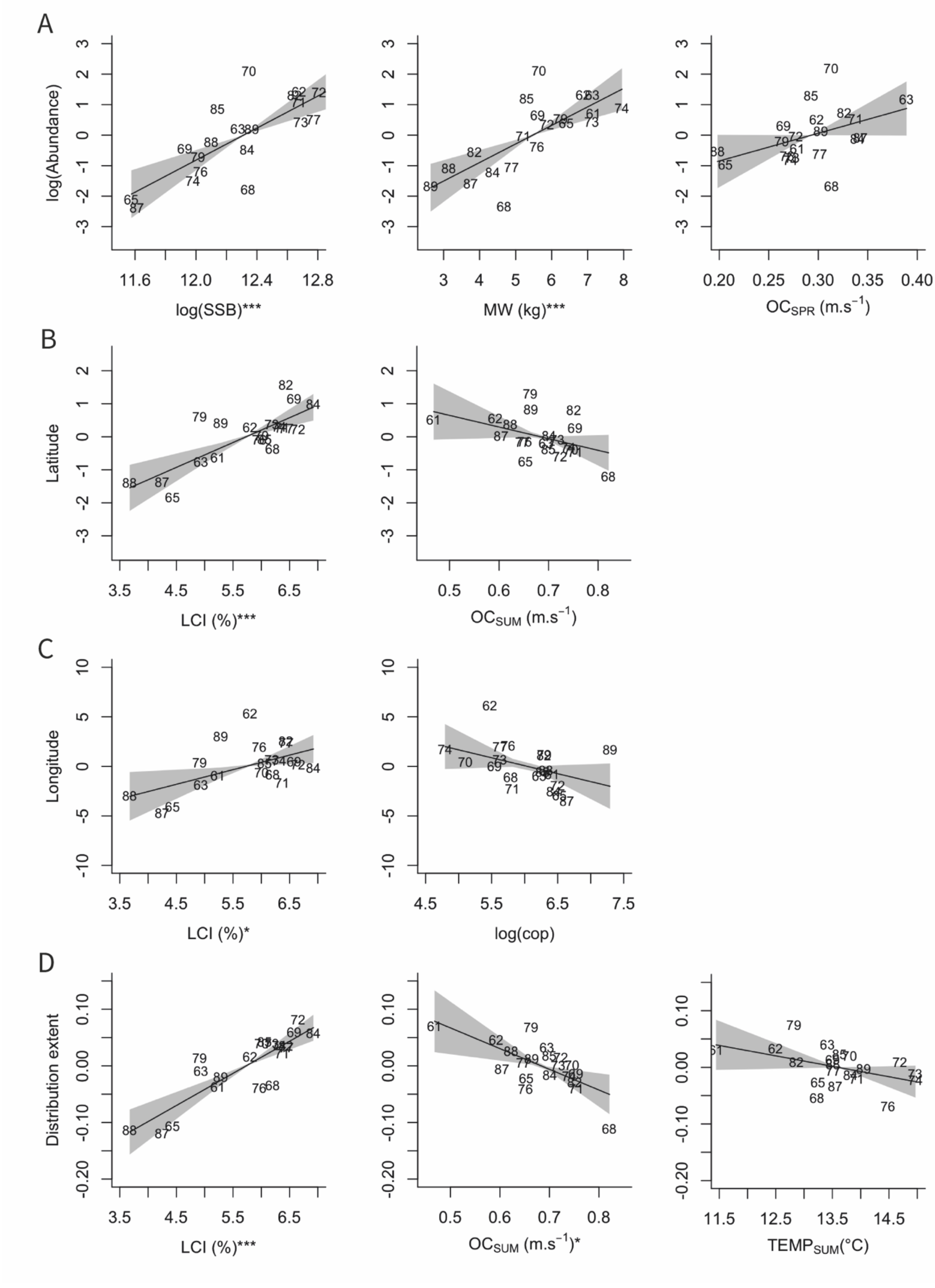


Figure 3. Linear effects of the AICc-selected predictor variables (acronyms are stated in Table 1) on the abundance and distribution of total Northeast Arctic cod larvae in

summer. Equations for each model (A - D) can be found in italics in table A2 – Total NEA cod larvae - Summer. Each row shows the selected model for one larval index, abundance (A), mean latitude (B), mean longitude (C), or distribution extent (D). Each panel show the partial effect of one variable, with partial residuals per year shown by the plotted numbers (= year – 1900). Asterisks after the x-axis variable indicate statistical significance: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

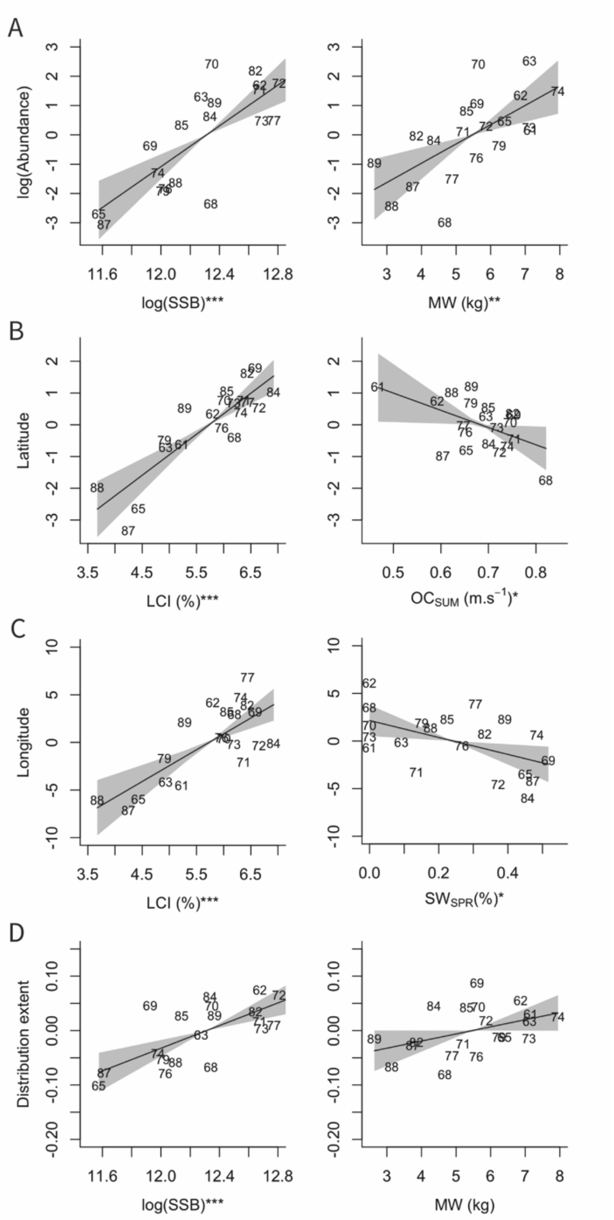


Figure 4. Linear effects of the AICc-selected predictor variables (acronyms are stated in Table 1) on the abundance and distribution of large Northeast Arctic cod larvae in summer. Equations for each model (A - D) can be found in italics in table A2 – Large NEA cod larvae - Summer. Each row shows the selected model for one larval index, abundance (A), mean latitude (B), mean longitude (C), or distribution extent (D). Each panel show the partial effect of one variable, with partial residuals per year shown by

the plotted numbers (= year – 1900). Asterisks after the x-axis variable indicate statistical significance: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

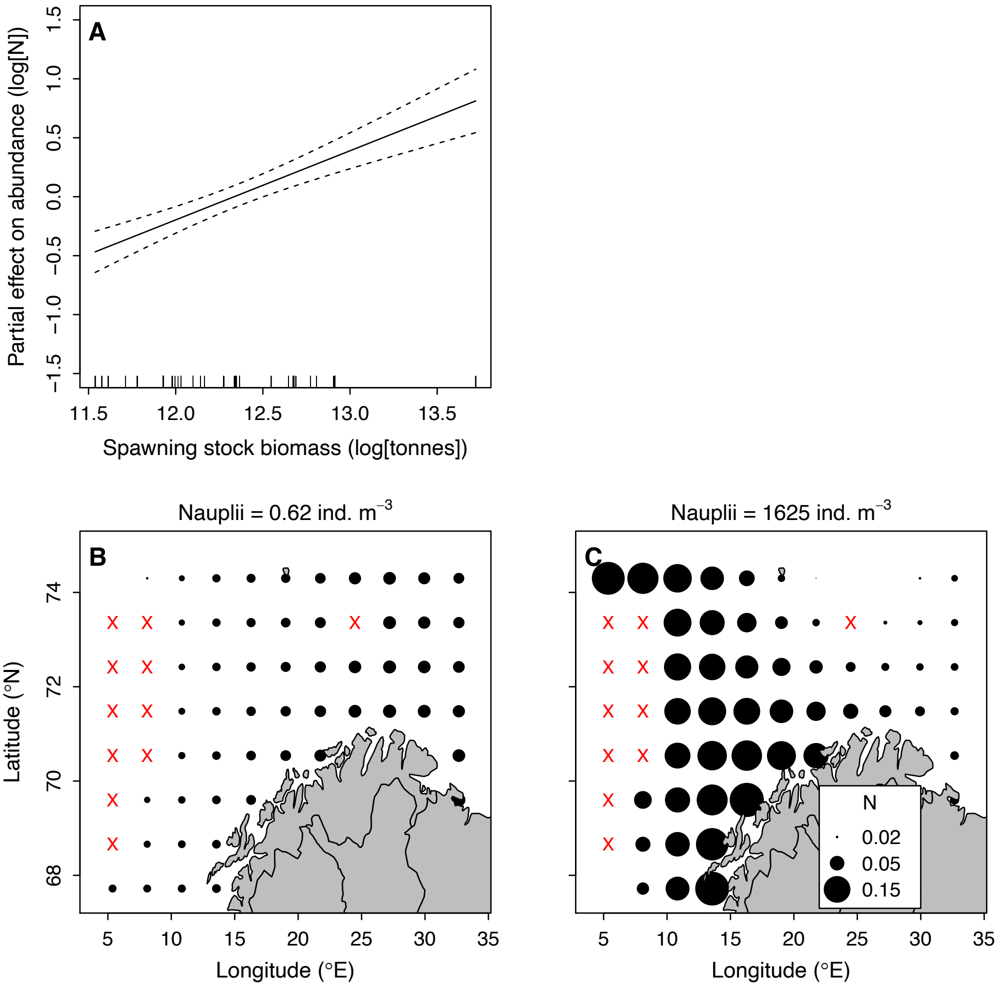


Figure 5. Spatial patterns of all cod larvae abundance in spring estimated by a varying coefficient generalized additive model. The broken lines show 95 % nominal confidence bands (not accounting for possible residual spatial autocorrelation). (A) Effect of the spawning stock biomass on all cod larvae abundance in spring. (B-C) Spatial association between *Calanus* spp. nauplii abundance and all cod larvae abundance in spring. The maps show predicted abundance of cod larvae in periods of low (5th percentile - B) and high (95th – C) abundance of nauplii. Note that red X represent no sampling in the grid cell.

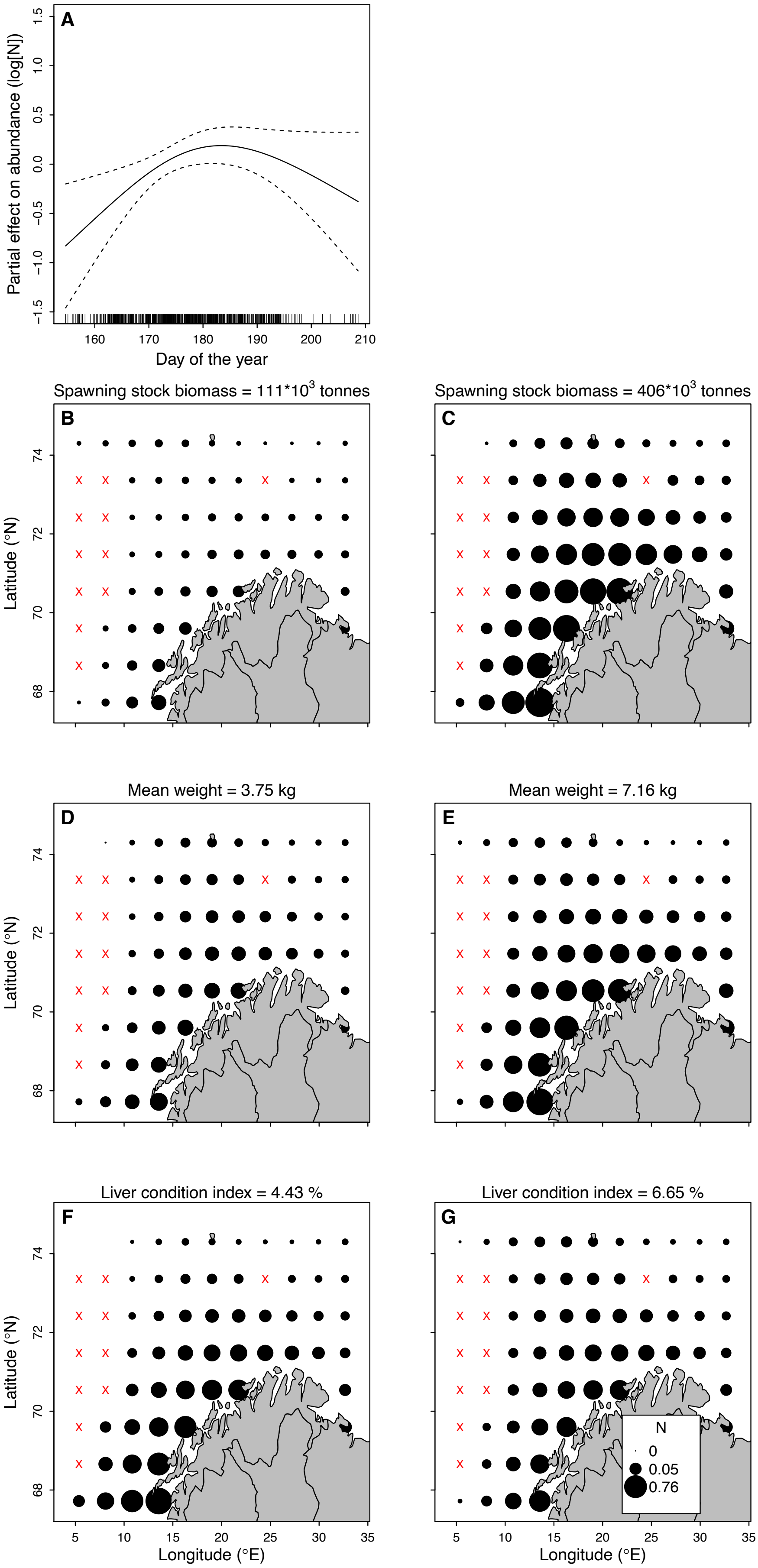

A
Partial effect on abundance (log[N])
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
160
170
180
190
200
210
Day of the year
Spawning stock biomass = 111*10^3 tonnes
B
Spawning stock biomass = 406*10^3 tonnes
C
Mean weight = 3.75 kg
D
Mean weight = 7.16 kg
E
Liver condition index = 4.43 %
F
Liver condition index = 6.65 %
G
Latitude (°N)
74
72
70
68
Longitude (°E)
5
10
15
20
25
30
35
N
0
0.05
0.76

Figure 6. Spatial patterns of all cod larvae abundance in summer estimated by a varying coefficient generalized additive model. The broken lines show 95 % nominal confidence bands (not accounting for possible residual spatial autocorrelation). (A) Effect of the day of the year on all cod larvae abundance in summer. (B-C) Spatial association between the spawning stock biomass and all cod larvae abundance. (D-E) Spatial association between mean weight of the spawners and all cod larvae abundance. (F-G) Spatial association between the liver condition index of the spawners and the all cod larvae abundance. The maps show predicted abundance of all cod larvae in the summer for periods of low (5th percentile – B,D,E) and high (95th – C,E,G) spawning stock biomass or mean weight or liver condition index. Note that red X represent no sampling in the grid cell.

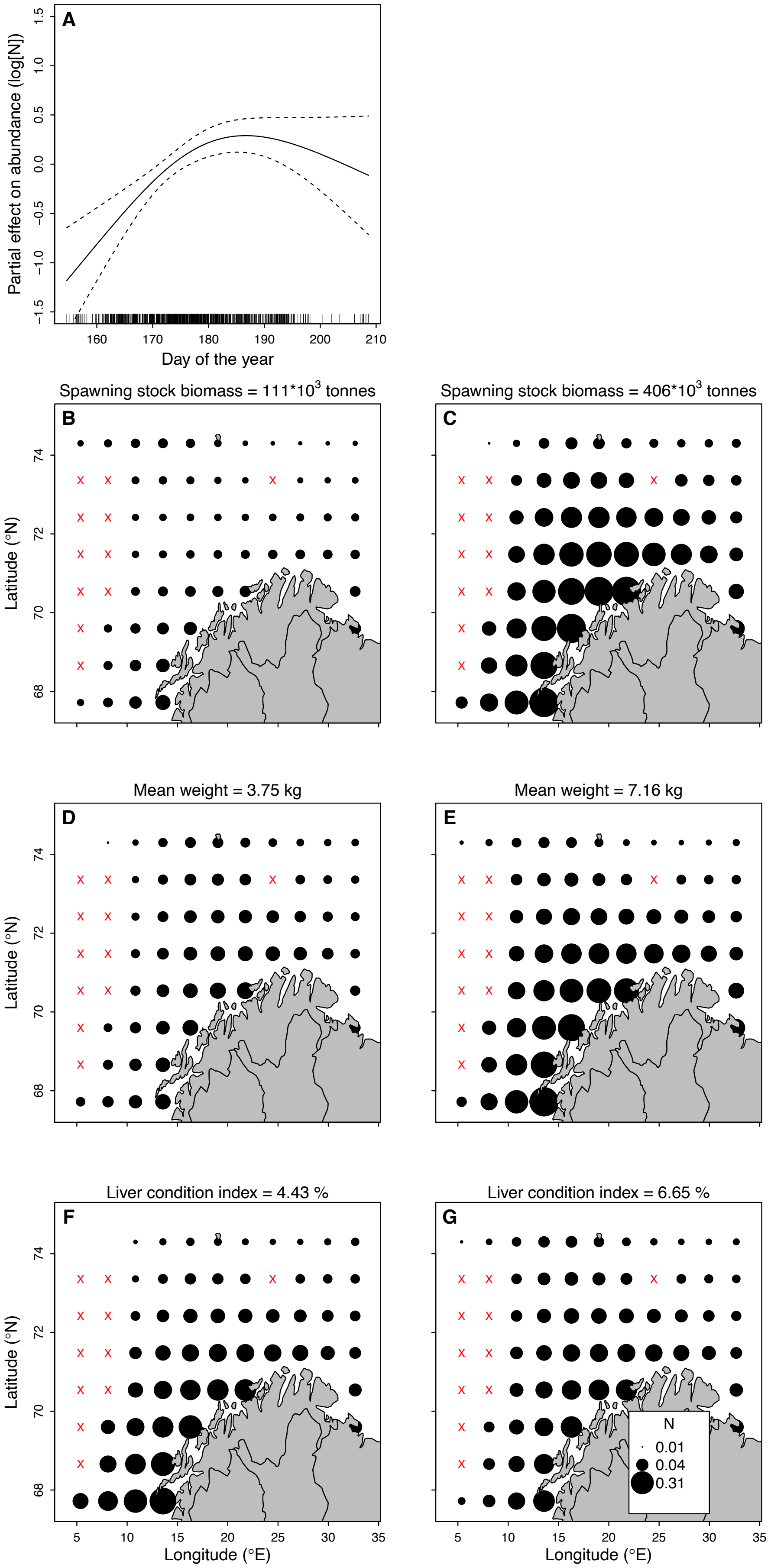

A
Partial effect on abundance (log[N])
−1.5
−1.0
−0.5
0.0
0.5
1.0
1.5
160
170
180
190
200
210
Day of the year
Spawning stock biomass = 111*10^3 tonnes
B
Spawning stock biomass = 406*10^3 tonnes
C
Mean weight = 3.75 kg
D
Mean weight = 7.16 kg
E
Liver condition index = 4.43 %
F
Liver condition index = 6.65 %
G
Latitude (°N)
68
70
72
74
Longitude (°E)
5
10
15
20
25
30
35
N
0.01
0.04
0.31

Figure 7 - Spatial patterns of large cod larvae abundance in summer estimated by a varying coefficient generalized additive model. The broken lines show 95 % nominal confidence bands (not accounting for possible residual spatial autocorrelation). (A) Effect of the day of the year on large cod larvae abundance in summer. (B-C) Spatial association between the spawning stock biomass and large cod larvae abundance. (D-E) Spatial association between mean weight of the spawners and all cod larvae abundance. (F-G) Spatial association between the liver condition index of the spawners and large cod larvae abundance. The maps show predicted abundance of large cod larvae in the summer for periods of low (5th percentile – B,D,E) and high (95th – C,E,G) spawning stock biomass, mean weight, liver condition index respectively. Note that red X represent no sampling in the grid cell.

Supporting information

Tables

Table A1. Sensitivity analysis for threshold selection used to calculate the distribution extent index. Selected models for each threshold are in _italics_. The model selected in this study is in **bold**. Model equations are shown as coefficients estimates and standard errors (in parentheses), proportion of variance explained (R^2) and AICc difference (ΔAICc) compared to the best model (in bold). Significance levels: * p<0.05, **p<0.01 and ***p<0.001.

Threshold	Equation	R^2	ΔAICc
	Total NEA cod larvae – Spring		
_0.8_	_Distribution extent = -0.11 (0.04) + 0.03 (0.01) ** ln(nauplii)_	_0.369_	-
___0.9___	___Distribution extent = -0.154 (0.06) + 0.04 (0.01) ** ln(nauplii)___	___0.395___	__-__
_0.95_	_Distribution extent = -0.197 (0.07) + 0.04 (0.01) ** ln(nauplii)_	_0.423_	-
	Total NEA cod larvae – Summer		
_0.8_	_Distribution extent = 0.08 (0.05) + 0.04 (0.007) *** LCI – 0.35 (0.08) *** OC_{SUM}_	_0.646_	-
0.8	_Distribution extent = 0.18 (0.09) + 0.04 (0.007) *** LCI – 0.29 (0.09) ** OC_{SUM} - 0.011 (0.008) $TEMP_{SUM}$_	0.668	0.68
0.8	Distribution extent = - 0.74 (0.22) + 0.063 (0.02) ** ln(SSB) + 0.007 (0.005) MW	0.407	10.33
_0.9_	Distribution extent = 0.11 (0.07) + 0.056 (0.010) *** LCI - 0.47 (0.12) ** OC_{SUM}	0.596	0.36
___0.9___	___Distribution extent = 0.29 (0.12) + 0.06 (0.01) *** LCI – 0.37 (0.13) * OC_{SUM} – 0.02 (0.01) $TEMP_{SUM}$___	___0.640___	__-__
0.9	Distribution extent = - 0.99 (0.29) + 0.085 (0.02) ** ln(SSB) + 0.011 (0.0065) MW	0.434	7.1
_0.95_	_Distribution extent = 0.15 (0.09) + 0.07 (0.014) *** LCI – 0.59 (0.16) ** OC_{SUM}_	_0.570_	_6.64_
0.95	Distribution extent = 0.34 (0.16) + 0.07 (0.013) *** LCI – 0.47 (0.17) * OC_{SUM} - 0.020 (0.014) $TEMP_{SUM}$	0.596	8.66

0.95	Distribution extent = -1.281 (0.35) + 0.108 (0.028) ** ln(SSB) + 0.017 (0.008) * MW	0.501	-
	Large NEA cod larvae – Summer		
0.8	*Distribution extent = 0.042 (0.06) + 0.042 (0.009) *** LCI - 0.31 (0.11)* * OC_{SUM}	*0.499*	-
0.8	Distribution extent = -0.79 (0.24) + 0.07 (0.02) ** ln(SSB) + 0.009 (0.005) * MW	0.402	3.55
0.9	Distribution extent = 0.059 (0.09) + 0.059 (0.013) *** LCI - 0.43 (0.16) * OC_{SUM}	0.478	2.05
0.9	***Distribution extent = -1.25 (0.30) + 0.10 (0.03) *** ln(SSB) + 0.01 (0.007) MW***	***0.529***	**-**
0.95	Distribution extent = 0.009 (0.12) + 0.067 (0.018) ** LCI - 0.52 (0.21) * OC_{SUM}	0.403	6.64
0.95	*Distribution extent = -1.59 (0.36) + 0.13 (0.030) ** ln(SSB) + 0.019 (0.008) * MW*	0.572	-

Table A2. Alternative models for abundance (N) and distribution (latitude, longitude and distribution extent) of Northeast Arctic cod larvae. Model equations are shown as coefficients estimates and standard errors (in parentheses), proportion of variance explained (R^2) and AICc difference (ΔAICc) compared to the best model (in italic), but with similar statistical support (ΔAICc < 2.0). Significance levels: * p<0.05, **p<0.01 and ***p<0.001

Equation	R^2	ΔAICc
Total NEA cod larvae – Spring		
ln(N) = -31.42 (11.26) + 2.24 (0.92) * ln(SSB)	_0.227_	-
ln(N) = -10.44 (3.08) + 1.16 (0.54) * ln(naup)	0.175	1.17
longitude = 2.53 (9.36) + 4.32 (2.50) $TEMP_{SPR}$	_0.124_	-
longitude = 35.73 (21.65) + 5.33 (2.42) _$TEMP_{SPR}$_ - 3.00 (1.79) ln(SSB)	0.232	0.02
Distribution extent = -0.154 (0.06) + 0.04 (0.01) ** ln(nauplii)	_0.395_	-
Total NEA cod larvae – Summer		
ln(N) = -40.72 (6.38) + 2.63 (0.54) *** ln(SSB) + 0.61 (0.14) *** MW + 9.10 (4.70) OC_{SPR}	_0.743_	-
ln(N) = -40.82 (6.17)+ 2.65 (0.53) *** ln(SSB) + 0.60 (0.14) ** MW - 1.86 (1.27) SW_{SUM}+ 9.36 (4.55) OC_{SUM}	0.760	0.97
ln(N) = -41.61 (6.86) + 2.93 (0.56) *** ln(SSB) + 0.58 (0.15) ** MW	0.702	1.04
latitude = 68.86 (1.19) + 0.75 (0.17) *** LCI - 3.53 (2.01) OC_{SUM}	0.479	-
latitude = 70.41 (2.15) + 0.67 (0.16) *** LCI - 0.26 (0.17) _$TEMP_{SUM}$_	0.460	0.74
longitude = 20.33 (7.79) + 1.47 (0.61) * LCI - 1.60 (0.93) ln(cop)	_0.412_	-
longitude = - 3.97 (16.77) + 3.06 (1.27) * ln(SSB) -2.42 (0.84) * ln(cop)	0.411	0.04
longitude = 8.58 (3.30) +1.98 (0.57) ** LCI - 3.55 (2.7) SW_{SPR}	0.373	1.30
Distribution extent = 0.29 (0.12) + 0.06 (0.01) *** LCI – 0.37 (0.13) * OC_{SUM} – 0.02 (0.01) $TEMP_{SUM}$	_0.640_	-
Distribution extent = 0.23 (0.12) +0.054 (0.010) LCI *** -0.33 (0.13) * _OC_{SUM}_ - 0.018 (0.010) _$TEMP_{SUM}$_+ 0.006 (0.005) MW	0.648	1.89

Large NEA cod larvae – Summer (sum)		
*ln(N) = -49.67 (8.49) + 3.48 (0.69) *** ln(SSB) + 0.66 (0.19) ** MW*	*0.676*	-
ln(N) = -48.75 (8.18) +3.17 (0.70) *** ln(SSB) +0.69 (0.18) ** MW + 9.34 (6.03) OC_{SPR}	0.701	0.37
*latitude = 66.98 (1.50) + 1.29 (0.22) *** LCI – 5.43 (2.54) ** OC_{SUM}	*0.647*	-
latitude = 56.49 (53.49) +0.83 (0.21) ** LCI + 1.01 (0.49) ln(SSB)	0.643	0.24
*longitude = 2.82 (4.19) + 3.34 (0.72) *** LCI - 8.90 (3.44) ** SW_{SPR}	*0.562*	-
*Distribution extent = -1.25 (0.30) + 0.10 (0.03) *** ln(SSB) + 0.01 (0.007) MW*	*0.529*	-
Distribution extent = -1.08 (5.51) + 0.07 (0.49) *** ln(SSB) + 0.02 (0.013) LCI	0.499	1.21

Table A3. Pearson’s correlation among variables

Variables	MW	ln(SSB)	LCI	ln(naup)	ln(cop)	TEMP$_{SPR}$	TEMP$_{SUM}$	OC$_{SPR}$	OC$_{SUM}$	NE$_{SPR}$	NE$_{SUM}$	SW$_{SPR}$	SW$_{SUM}$
MW	1												
ln(SSB)	0.66	1											
LCI	0.10	0.35	1										
ln(naup)	0.84	0.72	0.24	1									
ln(cop)	-0.34	-0.07	-0.29	0.03	1								
TEMP$_{SPR}$	0.58	0.44	-0.04	0.73	0.34	1							
TEMP$_{SUM}$	-0.24	-0.21	0.41	-0.22	-0.10	0.06	1						
OC$_{SPR}$	-0.70	-0.32	-0.30	-0.47	0.31	-0.37	-0.10	1					
OC$_{SUM}$	-0.24	-0.24	0.64	-0.24	-0.39	-0.38	0.79	-0.06	1				
NE$_{SPR}$	-0.40	-0.47	-0.50	-0.70	0.03	-0.51	0.03	0.03	-0.03	1			
NE$_{SUM}$	-0.35	-0.30	-0.36	-0.48	0.35	-0.39	-0.21	-0.01	-0.20	0.84	1		
SW$_{SPR}$	-0.78	-0.59	0.17	-0.61	0.46	-0.41	0.28	0.24	0.33	0.38	0.56	1	
SW$_{SUM}$	0.08	-0.06	0.45	0.12	-0.06	0.15	0.37	-0.07	0.47	-0.48	-0.38	0.14	1

Figures

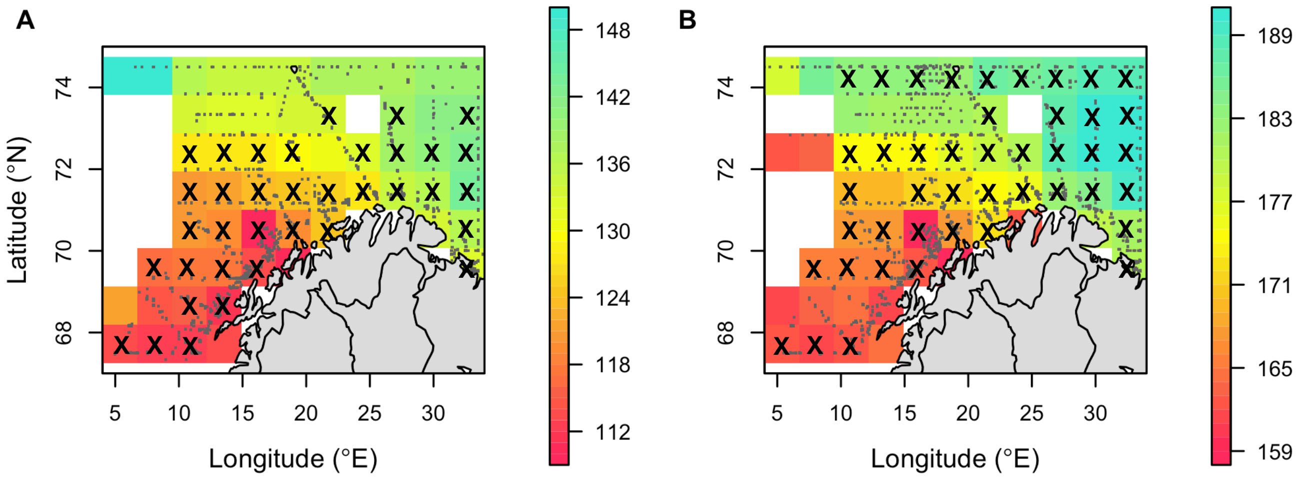
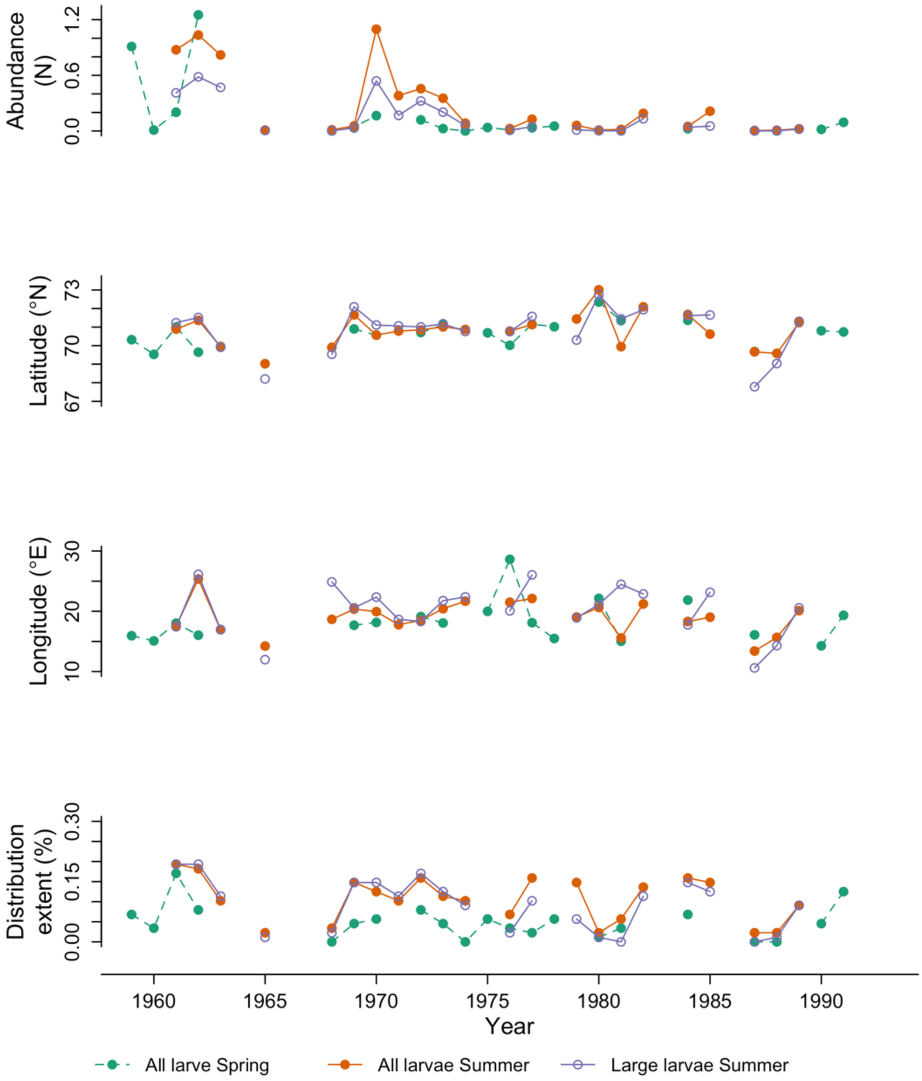


Figure A1. Mean sampling day of the year for each grid cell in spring (A) and summer (B). The selected cells to calculate the annual indexes for cod larvae are marked with an X. Note that day of the year in the colour bar are in different scales for spring and summer.



861

862 Figure A2. Annual indexes of the analysed years for the mean abundance, latitude, longitude and distribution extent of Northeast Artic (NEA) cod larvae. All size fractions of NEA cod larvae is represented by filled circles, in spring in green and dashed lines; and in summer in orange and solid lines. Large NEA cod larvae are represented by open circles in purple and solid lines for summer only.

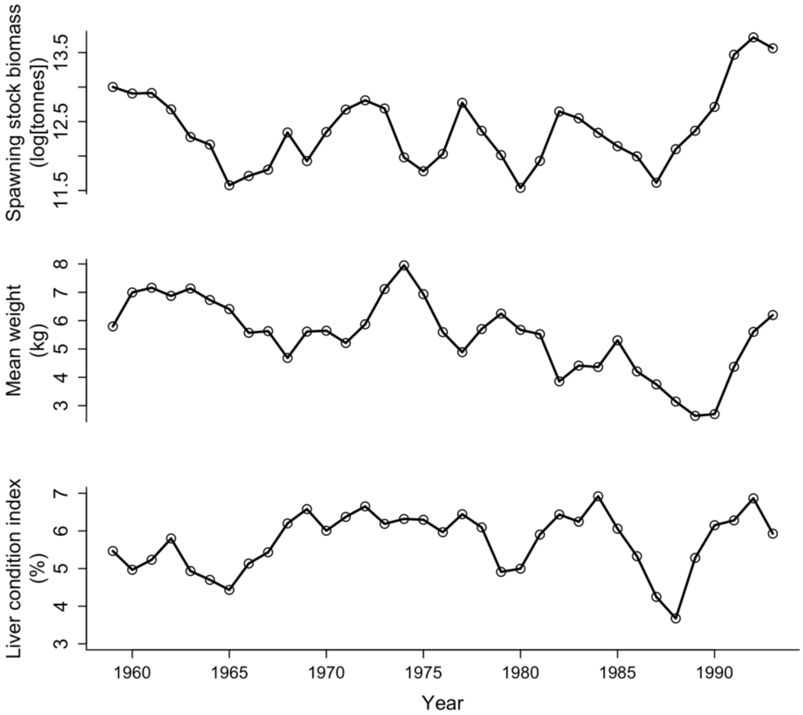


Figure A3. Annual indexes (1959 - 1993) of the spawning stock biomass, the mean weight of the spawners and the liver condition index of the spawners.

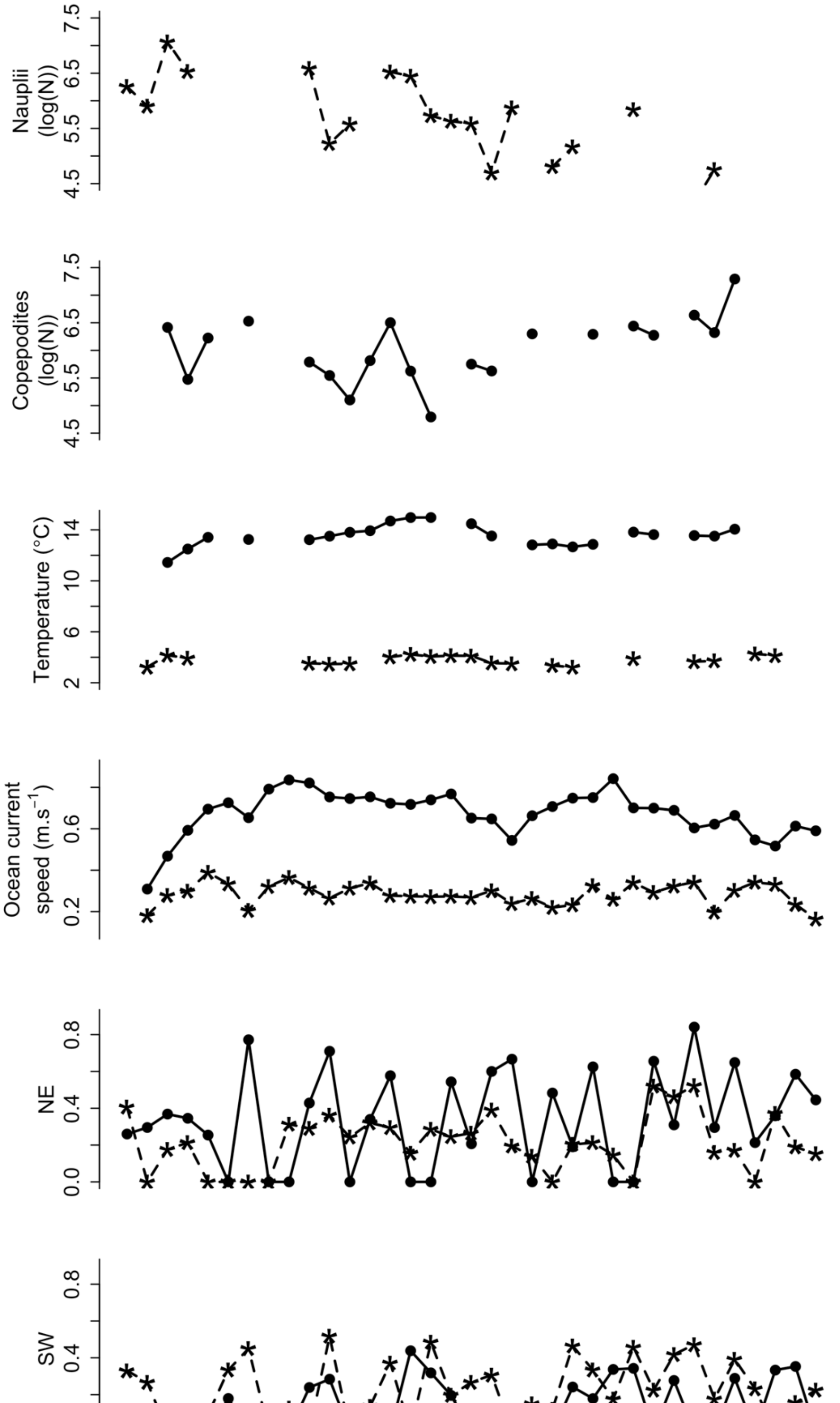


Figure A4. Annual indexes of the predictor variables for spring (asterisks with dashed lines) and summer (full circles with full lines).