



OPEN Climate-induced shifts in cod spawning phenology across the North Atlantic

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Spawning underpins fish stock regeneration. Here, we investigate climate effects on spawning phenology in Atlantic cod (*Gadus morhua*), a severely exploited species whose stocks are now also affected by climate change. For the first time, we model daily cod egg occurrences as a spawning proxy across the North Atlantic. With a concordance of 84% between our model and basin-scale observations, our results predict different climate change outcomes for western (eastern Newfoundland) and eastern (North Sea) stocks. In eastern Newfoundland where cod is at the centre of its thermal niche, a phenological shift in spawning was observed. In the warmer North Sea, such a phenological adjustment did not occur, leading to a substantial reduction in spawning. Our model explains fluctuations in the North Sea cod stock better than those in the Eastern Newfoundland stock, where unaccounted anthropogenic (overfishing) and environmental (trophodynamics) factors may have influenced cod abundance over the considered time series. Our results provide an improved understanding of how future climate change and other drivers interact in driving stock dynamics.

Keywords Atlantic cod, Climate change, Phenology, Spawning, North Atlantic, Niche

Atlantic cod (*Gadus morhua*) is a commercially emblematic fish that has played a central role in major fisheries throughout the eastern and western North Atlantic¹. This species remains among the ten most landed species² in 2021, despite an overall decline due to the collapse of several stocks. Intensive fishing has been described as a primary driver of the decline³. However, alongside fishing, fluctuations in cod abundance are significantly influenced by environmental conditions^{4–6} leading to over a century of fishery research on the influence of environmental factors in cod recruitment^{7,8}.

The arrival of a new cohort in an exploitable stock is referred to as « recruitment »⁹, which has been one of the key focal points of fisheries science^{10,11}. Recruitment is affected by (i) the Spawning Stock Biomass (SSB) and factors that influence fecundity, *i.e.* the number of mature fish, their physiological conditions as well as size at age^{12,13} (Supplementary Fig. 1), all shaped by biotic and abiotic environment^{7,14} and, (ii) the survival of early life stages, influenced by prey availability and quality, metabolism and predation^{15,16}.

Spawning represents the first step of stock regeneration, and its success will directly influence recruitment. Atlantic cod generally spawns between February and June, with spawning starting earlier in the Northeast Atlantic than in the Northwest Atlantic¹⁷. Most stocks exhibit a single annual spawning event, except for the West Scotian Shelf and Georges bank which can display a second spawning event in autumn^{18,19}. During the spawning season, the pelagic eggs are found in shallow waters²⁰.

Spawning in cod is driven by the niche-environment interaction, resulting in timing adjustments to enhance reproductive success^{21,22}. For instance, Atlantic cod can adjust the spawning season as a function of light intensity²³, temperatures²⁴ and plankton production^{25–28}. Climate-induced Environmental Change (CEC), through its effect on the pelagic environment, may also deeply modify the structure and functioning of the ecosystems, thereby affecting both the spawning grounds²⁹ and the early life dynamics of cod. Rising temperatures may affect spawning by inhibiting egg release³⁰ and the fate of spawned eggs by affecting prey abundance and creating a mismatch between the emergence of larval cod and plankton prey¹⁵.

In the context of CEC, effective stock management requires the consideration of environmental influences³¹ and makes the modern concept of Ecosystem-Based Fisheries Management³² (EBFM) easy to appreciate and essential to adopt, though seldom implemented³³. Here, our main objective is to examine how CEC through its

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effects on temperature, Photosynthetically Active Radiation below the sea surface (PAR_0), surface chlorophyll-a, salinity and ice may have changed the phenology of Atlantic cod spawning between 1959 and 2020. Using observed egg occurrence as a proxy, we apply different approaches of a presence-only Ecological Niche Model (ENM) to assess the regeneration niche³⁴ at the scale of the North Atlantic. First, we present seasonal changes in the timing of spawning at the scale of the North Atlantic. We then focus on two stocks with contrasting environments: eastern Newfoundland (often referred to as the Northern cod stock) and the North Sea, for which substantial declines in biomass have been observed over the time series. Finally, we discuss how our ENM effectively explains stock fluctuations in the North Sea but does not fully capture the dynamics observed in eastern Newfoundland, suggesting an important role of other drivers.

Results

Validating the cod egg distribution model

Daily habitat suitability of cod eggs was determined based on a presence-only Ecological Niche Model (ENM) forced by Sea Surface Temperature (SST), Photosynthetically Active Radiation under the surface (PAR_0) as a proxy for light intensity³⁵ and surface Chlorophyll-a (Chl_{os}) as a proxy for larval prey availability⁴(Methods). This daily habitat suitability was finally modified locally by three filters: (i) a salinity, (ii) a Sea Ice Concentration (SIC), and (iii) an ontogenic filters. We tested two different approaches based on the presence-only ENM named NPEN³⁶. The first approach (hereafter called Model 1) is a method that consists of modeling the potential regeneration niche based on the whole spatial range of the species (*i.e.* all North Atlantic cod egg occurrences). The second approach (hereafter called Model 2) consists of merging two distinct potential regeneration niches (Methods); the northwest (NW) and the northeast (NE) Atlantic (separation line: 30°W), considering the transatlantic genomic divergence³⁷. In this study, we added Pseudo-Presences (PPs, Supplementary Fig. 2) (Methods) to complete the training set. A cross-comparison of Models 1 and 2 was subsequently carried out by testing them both with and without PPs. The addition of PPs in Model 2 was especially important to account for the bimodality resulting from the spatial separation between the two sides of the North Atlantic. We found strong justifications for Model 2 as the niche estimated from SST and PAR_0 was distinct on both sides of the Atlantic (Supplementary Fig. 3).

Although differences in terms of global performance were small, Model 2 with PPs performed better overall in reconstructing cod egg spatial distribution and phenology than Model 1 (Table 1; Fig. 1). While the Continuous Boyce Index (CBI) focuses on the predicted-to-expected ratio³⁸, the simple concordance index checks the percentage of match-ups between modeled habitat suitability of cod eggs and spawning observations based on 17 stocks originating from basin-scale observations¹⁷ in the North Atlantic (Fig. 1A). This review was subsequently revised based on more observations from complementary studies (Supplementary Table 1, Fig. 1A). We also used the Jaccard index, which is based on the same principle as the simple concordance index but excludes double zeros³⁹.

Both models exhibited high CBI values and good concordance with basin-scale observations. While Model 1 (without PPs) was characterised by the highest CBI, Model 2 (with PPs) showed better simple concordance and Jaccard indices (Table 1; Fig. 1). Model 2 had an 84% concordance between modeled and observed egg occurrence at a monthly scale (Fig. 1A, C) *versus* 79% recorded for Model 1 (Fig. 1A, B). Based on the sum of the three indicators, Model 2 with PPs had the highest score and was thereby subsequently retained for further analyses. The threshold to binary habitat suitability of cod eggs was selected by means of a sensitivity analysis based on many different combinations of habitat suitability and duration (Supplementary Table 2).

Investigating spatial changes in cod egg phenology

Model 2 (with PPs) was used to map annual changes in habitat suitability of cod eggs in the North Atlantic (Fig. 2). Our results revealed a gradual rise in suitability in the North Sea, Baltic Sea, Irish Sea and Celtic Sea in the NE Atlantic during January-March (Fig. 2A-C). Then, habitat suitability expanded in March-May at higher latitudes including Iceland and the Norwegian and Barents Seas (Fig. 2C-E). In the NW Atlantic, habitat suitability of cod eggs increased one month later in the year in the Gulf of Maine and on Georges Bank, at the southern limit of cod distribution (February-March, Fig. 2B-C). Then, habitat suitability extended northwards from March to July into the Gulf of St. Lawrence, St. Pierre Bank, Grand Banks, eastern Newfoundland and Greenland (Fig. 2C-G). The additional analysis of the decadal changes in the spatial distribution of mean anomalies also revealed that,

Model type	Mean CBI 1/10	Concordance index	Jaccard index	Sum
Model 1 (no PPs)	0.94	0.79	0.59	2.32
Model 1 (with PPs)	0.91	0.80	0.55	2.26
Model 2 (no PPs)	0.82	0.78	0.54	2.14
Model 2 (with PPs)	0.86	0.84	0.63	2.33

Table 1. Comparison of the performance of Models 1 and 2 (without and with PPs). Model performance was assessed by means of three indices: the Continuous Boyce Index (CBI) as well as the simple concordance and the Jaccard indices, which compared habitat suitability of cod eggs to cod spawning data reported in the literature review¹⁷. This review was subsequently revised based on more observations from complementary studies (Supplementary Table 1; Methods). The sum with the highest score is shown in bold. PPs: Pseudo-Presences; for information on PP generation, see the Methods section.

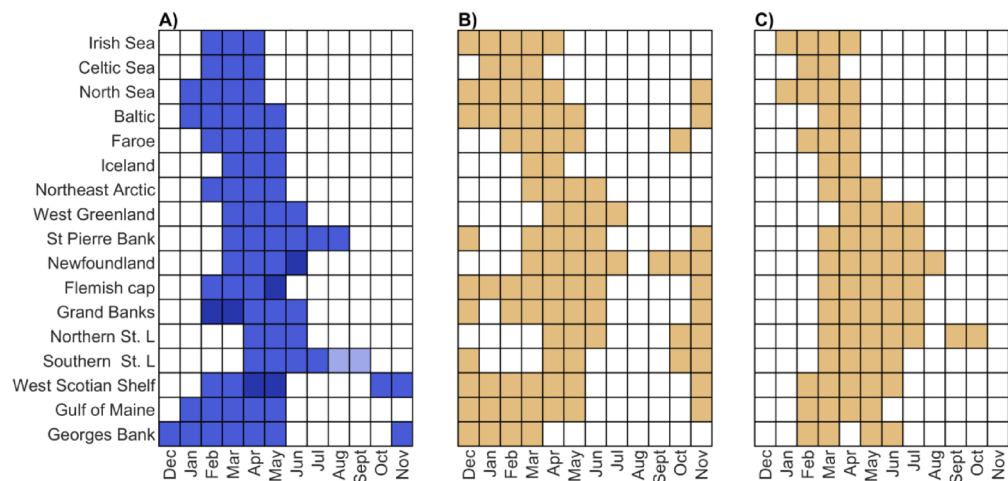


Fig. 1. Representation of the Atlantic cod spawning season for different stocks. **(A)** Reported spawning season in the literature review¹⁷ in blue. Monthly spawning for each stock was included (dark blue) or excluded (light blue) following complementary studies (Supplementary Table 1). **(B)** Output from Model 1 without PPs and **(C)** Output from Model 2 with PPs. For both **B** and **C**, a sensitivity analysis was performed to calibrate the optimal thresholds for identifying a spawning presence (*i.e.* habitat suitability and day thresholds). In **B**, spawning season corresponds to months when a habitat suitability value ≥ 0.15 persisted for at least 15 days. In **C**, our best model, spawning season corresponds to months when a habitat suitability value ≥ 0.4 persisted for at least 15 days (Supplementary Table 2). For practical reasons, the names of the 17 stocks were labelled, but this analysis focused on the habitat suitability of cod eggs in their main spawning ground (Supplementary Table 3). The concordance index between **A** and **C** is 84% (63% for the Jaccard index) versus 79% (59% for the Jaccard index) between **A** and **B**. The figure was created in MATLAB 24.2.0.2923080 (R2024b) (<https://fr.mathworks.com/>).

since the 1990s, positive and negative habitat suitability anomalies are found more frequently at the northern and southern boundaries of the species' spatial distribution, respectively (Supplementary Fig. 4).

Long-term changes in the phenology of cod egg habitat suitability

To investigate past changes in cod egg habitat suitability, we focused on eastern Newfoundland and the North Sea; two stocks with contrasting environments, which have been the focus of past intensive research^{4,15,40–42} (Fig. 3). The eastern Newfoundland stock is more central to the thermal niche whereas the North Sea stock is more peripherally located at the warmer edge. Changes in spawning phenology were assessed through ice and SST; SST changes were detrended to global warming signal (*i.e.* detrended Atlantic Multidecadal Oscillation, AMO⁴³). We chose to invert the AMO for clarity in Fig. 3C, D.

The habitat suitability of cod eggs was higher from March to July in eastern Newfoundland whereas it was concentrated between February and April in the North Sea (Fig. 3A–B). Since the 2000s, the period of high habitat suitability has decreased in both areas: it decreased at the end of the spawning season in eastern Newfoundland (Fig. 3A–C) and at the beginning of the spawning season in the North Sea (Fig. 3B–D). A shift in cod egg habitat suitability anomalies was observed after the mid-1990s when the Atlantic Multidecadal Oscillation (AMO) shifted from a negative (*i.e.* negative temperature anomalies) to a positive (*i.e.* positive temperature anomalies) state (Fig. 3C–D). In eastern Newfoundland, the shift in cod egg habitat suitability anomalies corresponded to a decrease in summer anomalies that paralleled an increase in spring anomalies (Fig. 3C). In the North Sea, where the spawning season is more restricted, the model only anticipated a reduction in suitability anomalies. Therefore, despite widespread negative cod egg suitability anomalies after the mid-1990s, a phenological compensation may still occur in eastern Newfoundland in contrast to the North Sea. The shift in suitability anomalies in eastern Newfoundland is strongly due to temperature and its likely influence on mean Sea Ice Concentration (SIC). After visually identifying a spring and a summer period in cod egg habitat suitability, we found that spring suitability anomalies were correlated significantly and negatively with Spring SIC (Fig. 3E).

Investigating stock and plankton influence

We also extended our analysis to explore potential relationships between mean annual cod egg habitat suitability, SSB, recruitment (R) and plankton abundance (Fig. 4). We integrated annual abundances of *Calanus finmarchicus* (CFIN) and *Para-Pseudocalanus* (Para-PseudoCAL) identified as key larval prey in the North Sea¹⁵ and eastern Newfoundland⁴⁴, respectively. We used the Continuous Plankton Recorder survey (labelled “CPR” in y axis) for the North Sea stock and reanalysed CPR abundance (labelled “Modeled” in y axis) in eastern Newfoundland to address a sampling gap in CPR. We also integrated the Plankton Index¹⁵ exclusively in the North Sea (Fig. 4F), as these data are unavailable for eastern Newfoundland.

In contrast to the North Sea where there were strong relationships between SSB, *C. finmarchicus* abundance, the Plankton Index and annual cod egg habitat suitability (Fig. 4B, D, F), we found no significant relationships in

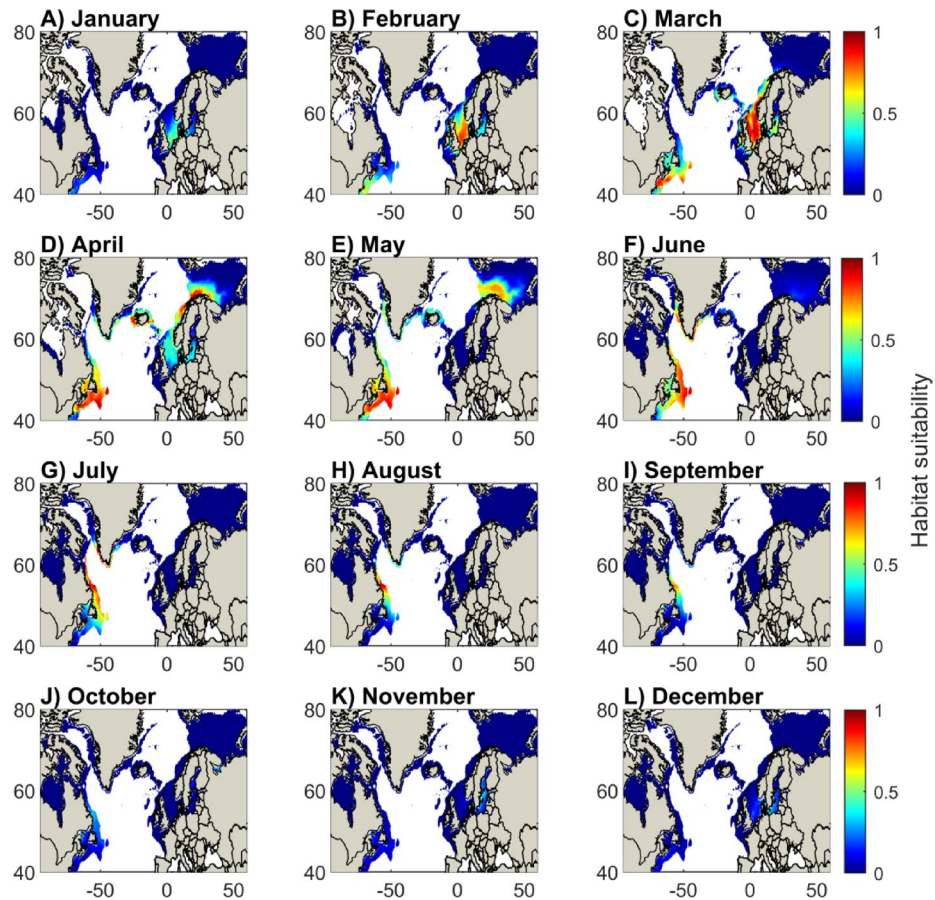


Fig. 2. Averaged monthly spatial distribution in the habitat suitability of cod eggs occurrence in the North Atlantic (1959–2020). The figure was created in MATLAB 24.2.0.2923080 (R2024b) (<https://fr.mathworks.com/>).

eastern Newfoundland (Fig. 4A, C,E). The absence of detectable relationships suggests that distinct mechanisms may be involved.

Therefore, we plotted the representation of annual SSB and annual cod egg habitat suitability for the North Sea and eastern Newfoundland, (Fig. 5A). This revealed a significant positive correlation, excluding the collapse period determined visually from Fig. 5A, (*i.e.* 1992–2013, in orange). These results, outlined by the residuals of the linear regression analysis, (Fig. 5B), suggest that other potential processes such as environmentally-driven trophodynamics^{45,46} and fishing pressure⁴² may have played a role in SSB fluctuations.

Discussion

Our approach successfully reconstructed the phenology of cod spawning throughout the North Atlantic and showed how Climate-induced Environmental Change (CEC) may influence the habitat suitability of eggs in space and time. We found better results when the NE and NW Atlantic niches of cod were considered separately, which was expected as it allowed for better consideration of the specific environments experienced by each stock. The decision to divide the Atlantic into two regions and to choose specific ecological variables (SST, PAR_{0-10} , Chl_a in the model and salinity, SIC, ontogenic indicator in post-processing) enabled us to achieve 84% concordance between modeled and observed egg occurrences at a monthly scale. Our model output also appeared to successfully describe habitat suitability in areas where no egg data was publicly available, for example in the Baltic Sea (Fig. 2; Supplementary Fig. 6). However, because of an absence of training data for this area, combined with its distinct physical regime (*i.e.* semi-enclosed sea), the resulting outputs in this region should be used with caution. The model also showed some limitations in capturing autumnal spawning dynamics (*e.g.* West Scotian Shelf and Georges Bank stocks, Fig. 1).

Our model revealed that the AMO (an indicator of the Atlantic Multidecadal Variability⁴⁷, or AMV) may have affected the phenology of cod spawning in the North Atlantic and its adjacent seas. Although a debate exists on whether or not the AMO is driven by internal hydro-climatic variability⁴⁸, the patterns of past AMO-like SST variations are real⁴⁹. Therefore, it is likely that the relationship between cod egg habitat suitability and AMO is driven by SST; note that SSTs are detrended prior to the calculation of the AMO index⁴³. Because the AMO is unlikely to be an internal source of hydro-climatic variability⁴⁸, a return to a negative phase cannot be expected in the context of anthropogenic global climate change⁴⁹.

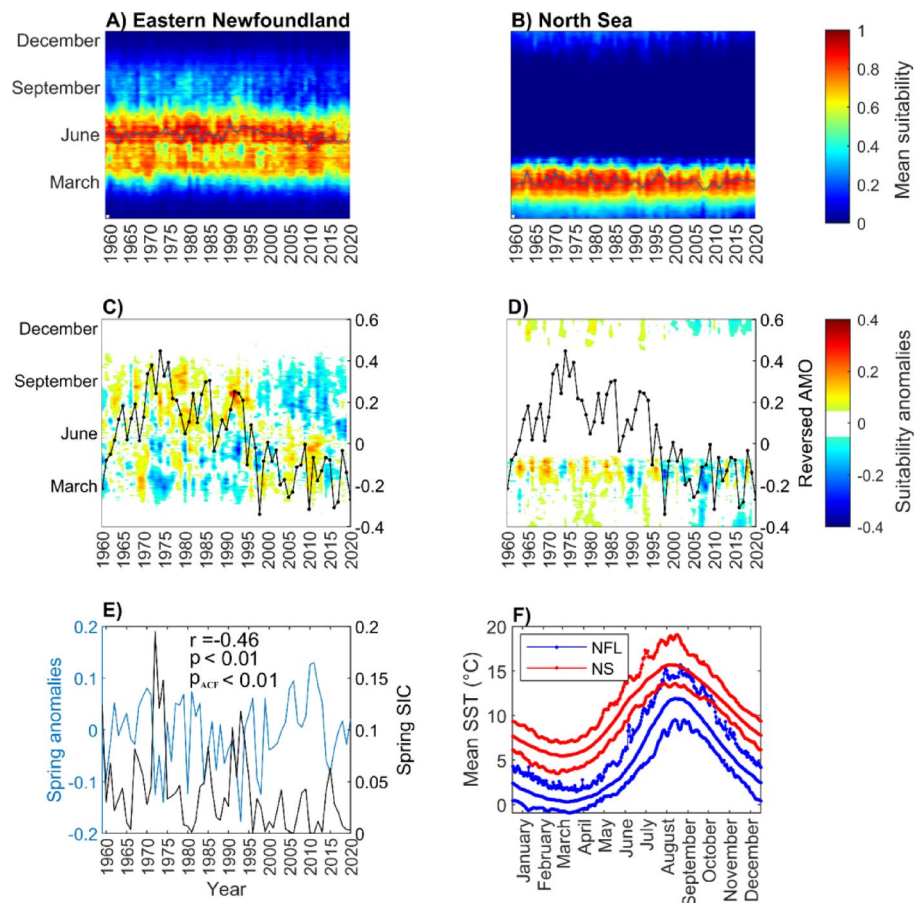


Fig. 3. Daily changes in cod egg habitat suitability (A–B), in suitability anomalies (C–D) and in spring suitability anomalies (E) for 1959–2020 in eastern Newfoundland (NFL; A,C, E) and the North Sea (NS; B,D). The minimum, mean and maximum SST observed during the study period is additionally included for both areas (F). In **panels A and B**, the blue line highlights the day with the highest cod egg habitat suitability. In **panels C and D**, suitability anomalies are represented with the state of the Atlantic Multidecadal Oscillation; the AMO was reversed here to emphasize the relationships with suitability anomalies. We assessed suitability anomalies by subtracting the average habitat suitability of the time series from the suitability. In **panel E**, the “spring” anomalies correspond to habitat suitability anomalies (panel C) from March to June. This period is visually identified from cod egg habitat suitability in panel A, which precedes the “summer” period (June, the persistent red in panel A). The spring anomalies are represented with the mean Sea Ice Concentration (SIC) during the same period. Pearson's linear correlation (r), p -value without (p) and with correction for temporal autocorrelation (p_{ACF}) are superimposed. The figure was created in MATLAB 24.2.0.2923080 (R2024b) (<https://fr.mathworks.com/>).

We also investigated more closely the phenology of spawning in two regions (eastern Newfoundland and North Sea), where drivers of stock fluctuations are likely to be different^{15,40,42}. Our focus on the two regions revealed the complexity of mechanisms and pathways through which environmental changes may influence recruitment. The North Sea is a temperate ecosystem close to the warm southern limit of the species' range. In this area, a strong relationship was observed between changes in the phenology of spawning, plankton composition (i.e. *C. finmarchicus*) and cod recruitment (Fig. 4). North Sea stock fluctuations have been frequently explained by CEC^{15,40}. Our results showed that spawning, restricted between February and April, is expected to decrease with further warming and that no phenological adjustment seems possible. However, not only has spawning decreased but the larval cod survival has considerably diminished due to the direct and indirect influence of warming¹⁵. Although the effect of fishing should not be underestimated⁴, the alteration in the planktonic environment induced by the warming of the North Sea has likely played a major role¹⁵. The increase in the abundance of *C. helgolandicus* may not counterbalance the reduction in *C. finmarchicus*, as this copepod is rarely preyed upon by larval cod⁴⁴ (see Heath & Lough, their Table 2). The rarity of *C. helgolandicus* in larval cod stomachs might be explained, however, by a temporal mismatch between its peak abundance and larval cod emergence¹⁵. All biological changes seem to be unfavorable for larval cod survival in the North Sea. Within this stock, climate and fishing can both influence abundance as was seen during the period 1963–2019 where the stock was almost equally influenced by climate and fishing (~55% fishing and ~45% climate), with fishing being more prominent before ~2000 and climate more dominant after ~2000⁴.

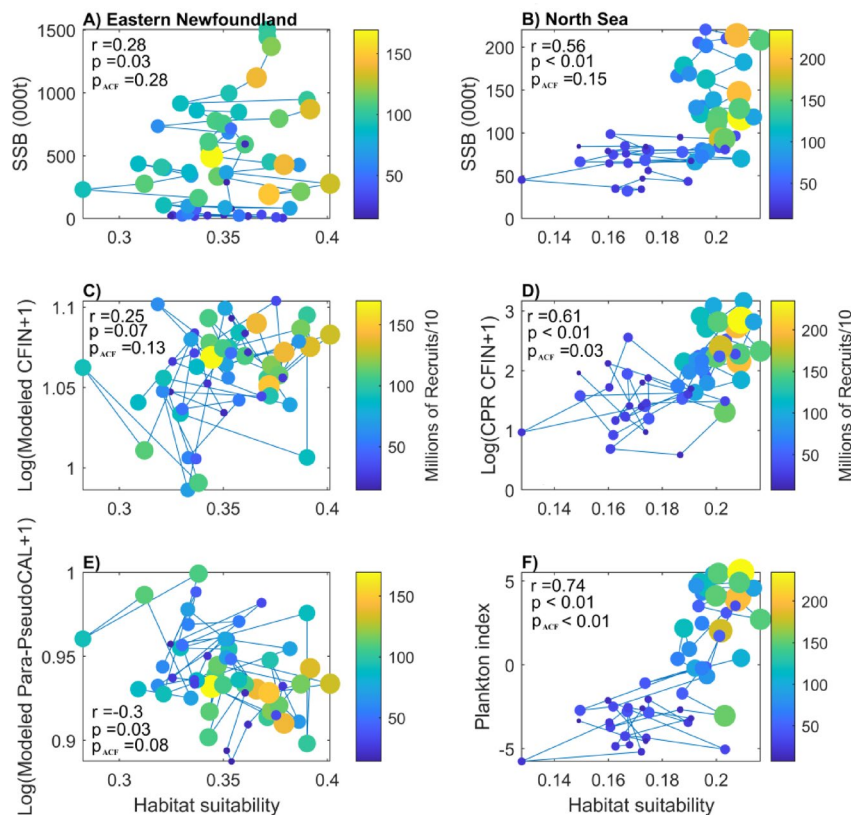


Fig. 4. Relationships between SSB and annual cod egg habitat suitability (A–B), *Calanus finmarchicus* (CFIN) abundance (C–D), *Para-Pseudocalanus* (Para-PseudoCAL) abundance (E) and the Plankton Index (F) in eastern Newfoundland (left side) and the North Sea (right side). Plankton abundances were not included in our ENM; they were used only in the analyses (log transformed using the function $\log_{10}(x+1)$). The period considered ranges from 1963 to 2017, with 1963 being the earliest date for which North Sea stock data is available and 2017 marking the final date of our CPR series. Pearson's linear correlation (r), p -value without (p) and with correction for temporal autocorrelation (p_{ACF}) are superimposed. To link recruitment to the environmental conditions at the time of spawning, we adjusted recruitment values back to the year of birth using the age at recruitment (at age 1 for North Sea and at age 3 for eastern Newfoundland). The figure was created in MATLAB 24.2.0.2923080 (R2024b) (<https://fr.mathworks.com/>).

Eastern Newfoundland is a sub-polar ecosystem with very different hydrodynamics compared to the North Sea (e.g. sea-ice occurrence) and cod is close to the center of its thermal niche. Consequently, in contrast to the North Sea where the habitat is already warm for cod, warming conditions in the eastern Newfoundland environment did not have a negative effect and recruitment is nearly optimal. Therefore, although the AMV influences the habitat suitability of cod eggs (Fig. 3C), our analyses revealed weak or nearly absent relationships between CEC-driven effects on the phenology of spawning, recruitment and *C. finmarchicus* or *Para-Pseudocalanus* abundance in eastern Newfoundland (Fig. 4A, C, E). We hypothesize that this lack of association might partially be due to the limited relevance of surface chlorophyll-*a* as a proxy for prey availability in this area. Although the spawning season is longer in eastern Newfoundland than the North Sea, earlier warming-driven ice retreat may paradoxically expose eggs and larvae to colder seasonal waters. Lower surface temperature may increase pelagic duration through reduced larval growth⁵⁰ and thus result in increased mortality rate due to longer exposure to predation⁵¹. Additionally, the observed rapid climatically-driven environmental changes reflected by the AMV are likely to have negatively affected SSB, which was already made vulnerable by the effects of fishing through the truncation of fish age and size composition⁵². This, in turn, could have reduced the capacity for this stock to adapt to environmental fluctuations^{53,54}, and impacted egg quantity and quality through a maternal effect¹².

In terms of stock dynamics, environmental conditions provided a strong explanation for changes in spawning patterns and their potential consequences on North Sea cod dynamics, in contrast to eastern Newfoundland where such relationships were less evident. In this latter region, although multiple cold temperature intervals were accounted for in our model (Supplementary Fig. 5A), they had no influence on spawning phenology (Supplementary Fig. 5B). Nevertheless, these cold intervals might have disrupted system trophodynamics by reducing the abundance of *C. finmarchicus*⁴⁶, and/or by impacting the productivity of capelin (*Mallotus villosus*), the main prey of adult Atlantic cod^{55,56}, (Supplementary Fig. 5C). Stock recovery can be considerably slower

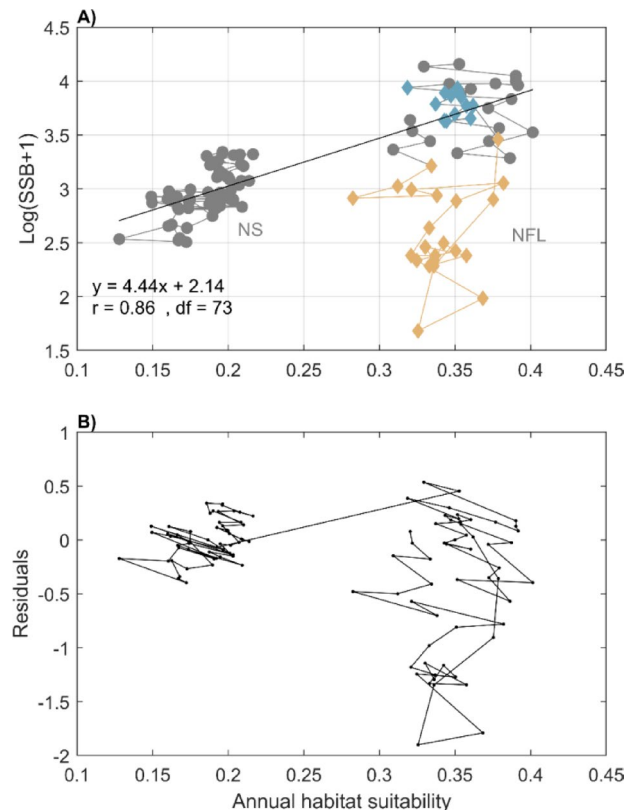


Fig. 5. Long-term changes (1963–2020) in the Spawning Stock Biomass (SSB) as a function of long-term changes in annual cod egg habitat suitability (**A**). The linear regression is superimposed in black; the regression fitted on North Sea (NS) and eastern Newfoundland (NFL) data but excluding the collapse and post-collapse period (1992–2013, orange). In Newfoundland, cold periods determined in Supplementary Fig. 5 are highlighted in blue (1970–1973, 1981–1986 and 1989–1991). (**B**) Residuals of the above regression including the NFL collapse period, the solid line connecting the data points illustrates the temporal evolution of the error term. To link the SSB to the environmental conditions at the time of spawning, we adjusted habitat suitability values back to the year of birth using the age at recruitment (at age 1 for NS and at age 3 for NFL). The figure was created in MATLAB 24.2.0.2923080 (R2024b) (<https://fr.mathworks.com/>).

when environmental conditions become unsuitable⁴ and the reversal in the state of the AMV may therefore prevent the stock from rebuilding rapidly.

We caution that the present study only investigated the influence of the environment on the phenology of spawning. Timing of spawning⁵⁷ as well as the number and quality of eggs also depends upon the size of spawners^{9,12}, which may be regulated by fishing through the truncation of the age structure of a stock⁵². Therefore, while our study shows how environmental fluctuations may have affected spatial patterns in the phenology of spawning in the North Atlantic, the characteristics of spawners may also explain changes in larval survival and recruitment^{12,53}. We are also aware that some environmental variables are strongly correlated globally: for example, SST and PAR_{0-} vary in phase without lag and surface chlorophyll-*a* is particularly associated with PAR_{0-} ⁵⁸. Finally, we also caution that we did not consider the effect of larval drift on the distribution of early stages. For instance, a larval drift was reported in the Gulf of Maine stock, from offshore to the coast⁵⁹. Drifts were also documented from the South of Greenland up to Davis Strait, and from Southwest Iceland to East Greenland⁶⁰. Finally, for the northeast Atlantic, a drift may also occur from the North Sea to the southern Norwegian coast⁶¹, and then northwards along this coast to the Barents Sea⁶². In some cod stocks, interannual variability in larval drift patterns may thus represent a source of bias when interpreting the meaning of local prey production on larval feeding conditions.

Although our study suggests that a modulation of the AMV influences the spatial distribution and phenology of spawning of Atlantic cod, we also acknowledge that other drivers such as environmentally-driven trophodynamics⁴⁶, overfishing⁴² as well as trophic cascade through the food web (e.g. the capelin prey of adult cod^{45,46}) have been hypothesized in the literature to have played a role in the collapse and the slow recovery of the eastern Newfoundland stock. Previously, the interplay between fishing and environment has been shown in the North Sea cod stock⁴. A spatial-temporal reorganisation of spawning has occurred, and this trend may reinforce in the future under anthropogenic global climate change. The careful management of cod stocks is crucial because they may otherwise become difficult to restore in ecosystems where the environment becomes adverse, especially for stocks distributed near the margins of the species' environmental niche. In fact, restoring stocks to levels observed before a collapse may be illusive when the environmental regime becomes unsuitable⁴.

Our results show why it is critical to consider both the position of the stock within its niche and the direction of environmental change to understand the interaction between fishing and climate.

Materials and methods

Environmental data

We first collected variables identified as ecologically significant for Atlantic cod spawning in the literature. Among them, temperature is a key driver of spawning^{63–65}; photosynthetically Active Radiation below the water surface (PAR_0) is a proxy for the photoperiod and light intensity³⁵, two parameters commonly used in aquaculture to induce spawning^{65–67} and surface chlorophyll-a is a proxy for larval prey availability⁴. Along with the primary variables, variables of local interest have been collected (bathymetry, salinity and ice). We summarise this information in Supplementary Table 4. Detailed information on these variables are presented below:

Bathymetry (m) originated from the 2022 GEneral Bathymetric Chart of the Oceans (GEBCO) website (<https://www.gebco.net/>). The resolution was 15 arc-second intervals.

Sea Surface Temperature (SST, K converted into °C) originated from the ERA5 hourly reanalysis data and were downloaded at the Copernicus Climate Data Store (CDS) website (<https://cds.climate.copernicus.eu/datasets>). The data (1940–2021) had a resolution of $0.25^\circ \times 0.25^\circ$.

Sea Ice Concentration (SIC, Dimensionless), referred to as Sea-Ice Cover, originated from the same ERA5 database as SST. They exhibited the same spatial resolution (*i.e.* $0.25^\circ \times 0.25^\circ$).

Sea Surface Salinity (SSS, PSU) originated from the ORAS5 global ocean reanalysis monthly data and were downloaded at the Copernicus Climate Data Store (CDS) website. They were characterised by a spatial resolution of $0.25^\circ \times 0.25^\circ$ (1958–2022).

Photosynthetically Active Radiation below the water surface (PAR_0 , $W.m^{-2}$). The data (1958–2022) had a spatial resolution of $0.25^\circ \times 0.25^\circ$. PAR_0 was used here as a proxy for light intensity. There was no missing data.

Surface chlorophyll-a (Chl_a, $kg.m^{-3}$ converted into $mg.m^{-3}$) originated from the Deutsches KlimaRechenZentrum (DKRZ) node at the Earth System Grid Federation (ESGF) website (<https://esgf-meta.grid.cloud.dkrz.de/search>). The $0.5^\circ \times 0.5^\circ$ resolution final matrix resulted from averaging four Earth System Models (ESMs; Supplementary Fig. 7), which correlated better with merged satellite data of GlobColour project (<https://hermes.acri.fr>; Supplementary Table 5). These CMIP6 data included historical records prior to 2014 and Shared Socioeconomic Pathways (SSP) middle of the road (SSP 2.45) after the subsequent period. The decision of averaging different Chl_a models, referred to as Multi-Model ensemble Averaging (MMA approach), allowed us to improve performance while mitigating bias and variability within individual models⁶⁸. Access information available prior to 1997 also guided our decision to choose a modeled product type.

Atlantic Multidecadal Oscillation (AMO) originated from the National Oceanic and Atmospheric Administration (NOAA) website (<http://www.psl.noaa.gov/data/timeseries/AMO/>). This annual hydro-climatic index was used as a proxy of Atlantic Multidecadal Variability (AMV).

The Newfoundland and Labrador shelf Climate index. This index is constructed from 10 subindices; each of the 10 subindices reflects normalised anomalies of distinct environmental parameters. Among the several variables, changes in SST and ice are considered.

In this study, we integrated the Newfoundland and Labrador shelf Climate index (Supplementary Fig. 5 A, B) and the AMO (Fig. 3C, D) to investigate the potential influence of climate-induced changes in the environmental regime on the phenology of spawning of the Atlantic cod.

Biological data

Atlantic cod egg occurrences (stages I to V pooled) were collected from three public databases: Ocean Biodiversity Information System (OBIS, <https://obis.org/>), Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/fr/>) and Eggs and larvae survey from the International Council For the Exploration of the Sea (ICES, <https://www.ices.dk/data/Pages/default.aspx>). The surveys that supplied the data are referenced in Supplementary Tables 6 and the egg occurrences are mapped in Supplementary Fig. 6. For regions lacking data, no open access datasets were available and/or our formal request to the relevant institutes were met with the response that these data were not publicly available.

Occurrences were collected between 1960 and 2009; therefore, beyond this point, results should be considered as projections. From a temporal perspective, 47% of egg data were collected before 2001 and 53% since the beginning of the century. However, occurrences were spatially more concentrated in the northeast (NE) Atlantic than in the northwest (NW) Atlantic (west-east boundary set at $30^\circ W$ longitude) with 68% and 32% respectively. After removing duplicates, 1473 egg occurrence data were considered, including 1007 occurrences in the NE Atlantic and 466 occurrences in the NW Atlantic. Some cod eggs linked to SST exceeding $10^\circ C$, conditions under which spawning is not expected due to warm temperatures^{64,69}; these occurrences were sampled outside their traditional spawning season (*i.e.* in summer) in the southern limit of cod distribution. Since our ENM is robust to inaccuracies³⁶ and as these occurrences represent a direct outcome of the survey, we included them in our dataset.

With 1473 occurrences, our dataset exceeded the minimum requirements for a robust ecological niche modeling, aligning with general literature recommendation^{70,71}, and meets an excellent resolution according to NPPEN literature³⁶ (*i.e.* probability resolution = $1/1473$).

Atlantic cod recruitment and SSB data were digitised from DFO assessment⁵⁵ for eastern Newfoundland. Regarding the North Sea, this stock is now managed as three sub-stocks. As most of our study period corresponded to a time when this stock was managed as a single unit, we used the most recent ICES advice providing a unique dataset for the whole North Sea⁷². Capelin landings in eastern Newfoundland were digitised from DFO⁵⁶ assessment.

Calanus finmarchicus and *Para-Pseudocalanus* yearly mean abundances were assessed from the original CPR dataset for the North Sea and from a reanalysed CPR dataset⁷³ for eastern Newfoundland. Finally, details on the calculation of the plankton index used in the North Sea can be found in the study presenting this index¹⁵.

Ecological Niche Model

Cod egg habitat suitability were derived by means of the Non-Parametric Probabilistic Ecological Niche model³⁶ (NPPEN), a presence-only model that uses a simplified version of the Multiple Response Permutation Procedures (MRPP) based on the generalised Mahalanobis distance. The MRPP was used to determine whether a given environment belongs to a group of environmental observations associated with egg occurrences data. Originally used with a Euclidean or a chord distance, MRPP is based on the generalised Mahalanobis distance in NPPEN to consider the general correlations among environmental dimensions. Full mathematical reference and description of the model are provided in the original paper³⁶.

The decision to adopt this model was influenced by the fact that (i) presence-only model had the simplest rules and assumptions⁷⁴ and (ii) did not imply the use of Pseudo-Absences (PAs), which requires decisions regarding their weight, quantity, and generation method^{74,75}. These choices hold considerable importance given that they directly affect the model. For example, the most common method for PA generation is a random sampling across the study area (“random” method^{74,75}) and there is no consensus on the performance of this method⁷⁵. Finally, (ii) NPPEN shows good performance when compared with other models⁷⁶.

Processing

The analyses were conducted in four steps (Supplementary Fig. 8). In this methodological section, we refer to the term “probability” which is a proxy for “habitat suitability”.

Step 1: Preprocessing

Preprocessing involved environmental and biological datasets. First, we interpolated spatially the environmental matrices to ensure they shared a common spatial resolution of $0.5^\circ \times 0.5^\circ$ ($30\text{--}90^\circ\text{N}$ and $100^\circ\text{W}\text{--}80^\circ\text{E}$): this was done by neighbor interpolation⁷⁷. The matrices were subsequently interpolated on a daily basis by selecting common dates (1959–2020). The monthly Chlos and SSS were interpolated daily by means of a Piecewise Cubic Hermite Interpolating Polynomial and a linear interpolation, respectively. Although differences among interpolation techniques were small, their choice was driven by the type of data and dimension (*i.e.* spatial – nearest – or temporal – linear or cubic –). We excluded cod egg data deeper than 600 m because eggs are mainly found in shallow waters²⁰.

Finally, each egg occurrence record was paired with environmental data using a nearest-neighbor interpolation⁷⁷, matching the spatial coordinates (latitude and longitude) and the exact date of the survey.

Step 2: Ecological niche modeling

Step 2.1. Variable selection

To achieve a parsimonious model (*i.e.* the most effective model using a minimum number of variables), we only included the SST, PAR_{0-} and Chlos variables in NPPEN. Other ecologically relevant variables were integrated during the preprocessing and postprocessing phase. As they do not have a direct effect on eggs, the influence of bathymetry (pre) and SIC (post) were considered before and after the application of NPPEN, respectively. Regarding salinity (post), the unavailability of egg data from the Baltic Sea (*i.e.* data not publicly available) prevented us from including the variable into NPPEN; the absence of low salinity training data would have had no direct influence on this region. Lastly, Chlos was integrated both into the model due to influence on the spawning season^{26,27,78}, but also after the application of NPPEN by implementing an ontological filter to consider the influence of food supply for the whole pelagic phase (see environmental filters section).

Step 2.2. Two different approaches

Based on NPPEN, we used two different approaches to model cod egg habitat suitability. A first approach considered the potential regeneration niche (because we only used part of the environmental parameters that would enable a full characterisation of the niche) based on all observations of the North Atlantic. A second approach considered separately the potential regeneration niche on the NE and NW sides of the North Atlantic (separation line: 30°W). Therefore, for this second approach, we developed two independent models and the two outputs were subsequently merged into a single global North Atlantic model (Supplementary Fig. 8). When the eastern Newfoundland and North Sea stocks were analysed, we directly extracted the habitat suitability values from the corresponding areas within the merged global model.

NPPEN was not directly applied on gridded observations but instead on the following hypercube, with each dimension being fixed by minimum and maximum values: (i) SST, from -5 to 40°C every 0.1°C ; (ii) PAR_{0-} , from 0 to 160 W.m^{-2} every 2.5 W.m^{-2} ; and (iii) Chlos, from 0 to 8 mg.m^{-3} , every 0.05 mg.m^{-3} . Then, NPPEN habitat suitability were subsequently interpolated by applying the nearest neighbor interpolation method to assess daily maps of habitat suitability of cod egg occurrence for 1959–2020.

Step 2.3. Generation of Pseudo-Presences

Like most models, NPPEN needs a substantial training set against which each environmental combination is tested. This is especially true when the number of environmental dimensions is high. When considering the regeneration niche separately in the NW and NE part of the Atlantic, the size of the two training sets diminished substantially (466 observations for NW and 1007 for NE). To overcome the reduction in the size of the training sets as well as its morcellation, we generated Pseudo-Presences (PPs), by performing an iterative NPPEN in association with a procedure based on the convex hull⁷⁹. We called this new method NPPEN-PP. (Note that

NPPEN-PP was also carried out for Model 1 for comparison purposes.) In this study, we coupled the two distinct modeling approaches (*i.e.* global potential regeneration niche, Model 1 and NE/NW split potential regeneration niche, Model 2) with and without inclusion of PPs. Although the global nature of Model 1 precludes the bimodality typically seen in NE/NW splits, PPs were also included in Model 1 for comparison.

Regarding Model 2, we first identified the convex hull of the niche for NW and NE Atlantic: the convex hull was the smallest convex set including all (cod egg) points of the training set⁷⁹. This step was a pre-requisite to maximise the mean probabilities within the convex hull. Four NPPENs were carried out: we began by running two initial NPPEN models - one for the NE Atlantic, one for the NW Atlantic - excluding PPs. The last two NPPENs introduced PPs (*i.e.* combination of observations included in the convex hull) from 10% to 200% of every 10%, step by step, in the NE and the NW Atlantic. The reported percentage of PPs refers to the proportion of the initial size of the training set. Therefore, 20 (percentage of PPs) $\times$ 5 (random simulations) = 100 iterations were carried out for both NW and NE Atlantic (Supplementary Fig. 9). After each generation of PPs, we recalculated NPPEN with the PP-added training sets.

After each iteration of PPs, we calculate an index (ψ) which quantifies the gain (or loss) in probabilities induced by added PPs inside the convex hull, compared with the initial cod egg dataset without PPs (blue line in the Supplementary Fig. 9). Our index was calculated as follows:

$$\psi = \frac{1}{b} \sum_{i=1}^b (p_i - p_i^{ref}) \quad (1)$$

With b the total number of observations for a given original (*i.e.* uncompleted) training set; p_i as the probability of a given combination of variables of the original training set when NPPEN was performed using as a reference the filled training set and p_i^{ref} the probability of the same combination of variables when NPPEN was performed using as a reference the original training set. The index can be negative or positive. It was negative when completing the training set reduced the mean probability of the original training set and it was positive when the probability of the completed training set improved the results.

We also assessed the first (*i.e.* all cells adjacent to the outside of the convex hull) and second crown (*i.e.* all cells adjacent to the outside of the first crown) of the initial convex hull to check an unwanted increase in the probability of cod egg occurrence outside the regeneration niche: a numerical contagion of the probability outside the convex hull would extend the spatial range of the species and its phenology, which would artificially diminish the sensitivity of the species to environmental changes.

At the end, using the first crown, we select the iteration containing the pool of PPs that maximises probabilities within the convex hull (*i.e.* here, the smallest envelope that contains all points of occurrence) at the same time as controlling an extension of the probability outside the niche (Supplementary Fig. 2).

Step 3: Environmental filters

Because their impacts were only regional or concerned high-latitude regions, three other parameters were considered after the calculation of the habitat suitability by the ENM: (i) Sea Surface Salinity (SSS, *i.e.* decrease in probability of cod egg occurrence below 10 PSU⁸⁰) (*e.g.* northern Baltic Sea), (ii) Sea ice Concentration (SIC, *i.e.* no probabilities in area where ice concentration exceeding 6 months per year⁶²) and (iii) a ontogenic filter considering that survival is compromised when food is insufficient for more than 30 days¹¹ (Methods). The influence of these three filters is shown in Supplementary Fig. 10. A sensitivity analysis was conducted on parameters of the salinity (r) and the ontogenic (t) filters to determine the threshold optimizing results while decreasing habitat suitability (Supplementary Table 7).

The salinity filter reduced the habitat suitability of cod eggs obtained by the model in areas where salinity was too low for cod egg development. We used a sigmoidal logistic function as it represents the species' gradual adaptation to varying salinity levels. Suitability decreases as follows:

$$\sigma(x) = \frac{L}{1 + e^{-r(x-x_0)}} \text{ with } 0 < \sigma(x) < 1 \quad (2)$$

Where L was the maximum habitat suitability (*i.e.* $L=1$) and r the controlling curve steepness ($r=0.8$; Supplementary Table 7). Finally, x_0 represented the point of inflection. It was calibrated to center the function between two salinity thresholds, 10 and 5 PSU, where massive cod egg mortality occurs⁸⁰ (*i.e.* $x_0=5$).

The ice filter was intended to reduce the habitat suitability generated by NPPEN in areas where ice occurs for more than half the year. For this purpose, daily SIC between 0 and 1 were transformed into binary data with a threshold of 0.15, above which areas are generally considered ice-covered in remote sensing studies⁸¹. Next, these daily binary data were transformed into monthly data averaged over the entire period (*i.e.* 12-month binary data) and finally, the average monthly data were divided by the 12 months of the year to obtain an ice quantity indicator where 0 represents an ice-free zone throughout the year and 1 represents an area covered permanently by ice. In this case, the requirement to remain ice-free for 6 months motivated the use of a rectangular function. Based on the ice indicator, a threshold of 0.5 was used as an adjustment factor to reduce the habitat suitability of cod eggs. Below this threshold, the habitat suitability remained unchanged. Above this threshold, the habitat suitability of eggs were set to 0 because the presence of ice over half a year was incompatible with the life cycle of Atlantic cod, which needs about 6 months to complete its pelagic phase⁶².

Finally, as our niche-environment approach indicates only whether the environment is immediately suitable for cod spawning, we added an ontogenic filter to consider that the environment should also remain suitable for larvae post hatching. Here, we use the same surface chlorophyll-*a* data as in the model, but consider environmental conditions six months later to account for the full pelagic phase of Atlantic cod⁶². Therefore, this

filter consists of a sliding window of 180 days to assess the number of consecutive days below a food threshold ($t = 0.1 \text{ mg.m}^{-3}$; Supplementary Table 7). Then, we apply a linear function to represent the direct relationship between the duration of food deprivation and mortality. Our adjustment factor Δ was calculated as follows:

$$\Delta(x) = 0 \quad \text{When} \quad m > 30 \quad (3)$$

$$\Delta(x) = \frac{d_2 - m}{d_2 - d_1} \quad \text{When} \quad d_1 \leq m \leq d_2 \quad (4)$$

$$\Delta(x) = 1 \quad \text{When} \quad < d_1 \quad (5)$$

Where k was the number of consecutive days below the food threshold ($0 \leq k \leq 180$). If more than one period fell below the food threshold, only the longest k was retained. The parameters d_1 and d_2 were the number of threshold days between which the habitat suitability of eggs decreased linearly (Eq. 4). In this study, parameters d_1 and d_2 were fixed to 15 and 30 days, respectively (digitised from Houde¹¹; his Fig. 1). Over d_2 days, $\Delta(x) = 0$ (Eq. 3) and therefore habitat suitability of cod eggs becomes 0. Below d_1 days under the food threshold, $\Delta(x) = 1$ (Eq. 5) and thereby habitat suitability remained unchanged.

Step 4: Model performance

A random k-fold ($k = 5$) cross-validation approach was carried out⁷⁴; four folds were used for training and one for model evaluation. For each of the k simulations, the generated PPs were exclusively included in the four training folds, however. These training folds with PPs were used to assess the habitat suitability of cod from the environmental matrix (*i.e.* hypercube). Finally, at the end of the modeling process, the five runs for NW and the five runs for NE were averaged and the two final models were combined to reconstruct habitat suitability of cod eggs across the North Atlantic.

To evaluate our models, three indices were used. First, the Continuous Boyce Index³⁸ (CBI) is a non-parametric indicator, ranging from -1 to 1 , used to measure performance of presence-only models^{38,76}. As a threshold-free version of the Boyce index, the CBI consists of a sliding window along the habitat suitability (*i.e.* between 0 and 1). The first parameter W (window width) creates intervals over which the window slides according to the second parameter called step (*i.e.* sliding window increment). For each interval (i), this index calculates the ratio between the frequency of the habitat suitability predicted by the model (Predicted, P_i) and the frequency of habitat suitability associated with occurrence points in test data obtained by cross validation (Expected, E_i). Finally, the Spearman correlation is performed between the predicted-to-expected (P_i/E_i) ratios and the corresponding predicted habitat suitability (P_i) of each interval to get the index between -1 and 1 . In this study, the model evaluation was carried out with $W = 1/10$ for a step = 0.01 . The CBI was calculated after the application of each environmental filter (Supplementary Table 8).

We also used the simple concordance and Jaccard indices³⁹. The two indices were calculated to assess the percentage of match-ups between modeled and observed data based on the empirical work of Brander¹⁷ which compiled spawning information for 17 cod stocks in the North Atlantic. To create the same type of grid for our model and thus calculate the best match-ups between literature and results, it was necessary to determine (i) a threshold above which habitat suitability data were transformed into binary data and (ii) the number of consecutive days required to declare the presence of a spawning season. Both parameters were determined by means of a sensitivity analysis (Supplementary Table 2). Once the grid of the model was built, the simple concordance (*i.e.* common cells between the two grids) and the Jaccard indices (*i.e.* similar to the concordance index but penalises cells not in common) were calculated.

Statistical analyses

Modeling, data analyses and figure generation were performed in MATLAB 24.2.0.2923080 (R2024b) (<https://fr.mathworks.com/>).

Mean comparisons

To determine statistical differences among groups, we applied a one-sample Kolmogorov-Smirnov test to check for normality and a Bartlett's test to assess the homogeneity of variances to perform an ANOVA or a Kruskal-Wallis test⁸².

Mean comparisons are primarily conducted within the context of threshold selection for environmental filters (Supplementary Tables 7 and 8). In this case, we rely on the Continuum Boyce Index (CBI) data. Given that we use a k-fold cross-validation (with $k = 5$), five separate runs were carried out, producing five CBI (tables display the average CBI). For every threshold considered, we compare how the five CBIs differ (*e.g.* 3 threshold = 3 groups of 5 values). As our ENM provides daily probabilities, a CBI is consequently calculated on a daily basis.

Biplot representation

Habitat suitability of eggs and occurrences in Supplementary Fig. 3 were represented by categories: days, 1 to 366 every 1 day; SST, from -5 or -2 to 40°C every 0.1 – 0.5°C ; $\text{PAR}_{0.1}$, from 0 to 140 or 160 W.m^{-2} every 2.5 W.m^{-2} and Chlos, from 0 to 3 mg.m^{-3} , every 0.1 mg.m^{-3} .

Simple concordance and Jaccard indices

We extracted habitat suitability in the spawning ground of each of the 17 stocks. For each stock, we extracted the maximum habitat suitability of the whole period ($366 \text{ days} \times 62 \text{ years}$). Then, maximum habitat suitability was averaged and transformed into binary data (mean $366 \text{ days binary} \times 1$) based on habitat suitability thresholds

(0.05, 0.1, 0.15, 0.2, 0.25, 0.4, 0.5, 0.6, 0.75). Along this 366-day vector, the single ones (e.g. 1s surrounded by 0s become 0s) are corrected to 0. Finally, for each month, we assessed the number of consecutive days at 1 and if this number was above the current day threshold tested (15, 20, 25 and 30 consecutive days), the month was designated as a spawning month of the current area.

Seasonal maps

Spatial distribution in the habitat suitability of cod eggs was explored by generating twelve maps, corresponding to each calendar month. Each map represents the mean monthly distribution for 1959–2020.

Decadal maps

We also calculated the average monthly habitat suitability during the period 1959–2020. Then, for each year of the six decades, anomalies were assessed by subtracting the mean monthly habitat suitability of the year from the mean monthly habitat suitability over the period. Finally, a map that depicts the average anomalies for the past 10 years was built for each decade. In the case of the eastern part of the Barents Sea, our index of habitat suitability remains low (Fig. 2), reflecting the absence of cod eggs in this area; as a result, an anomaly of less than 0.1 represents about 10% of an already negligible signal.

Daily change and habitat suitability anomalies

We chose two key areas to investigate closely long-term changes in the phenology of spawning. The areas examined were the North Sea, 27.4.a.b.c FAO area (latitudes 51°N and 60°N and longitudes 3°W and 10°E) and Newfoundland, 21.3KL FAO area (latitudes 46°N and 52°N and longitudes 54°W and 46.5°W). For the second stock, we focused on the NAFO 3KL area only as the majority of cod fishing activity takes place in these divisions⁵⁵.

To assess daily changes in cod egg habitat suitability, we calculated the average suitability of the area for each day of the year over 62 years. For the daily changes in cod eggs anomalies, as in the case of the decadal maps, we calculated anomalies by subtracting the daily habitat suitability from the 366 days average habitat suitability of the time series.

Relationships between habitat suitability and SSB, R, *Calanus finmarchicus* and *Para-Pseudocalanus*

To represent the relationships between habitat suitability and variables, daily data (i.e. habitat suitability and *Calanus finmarchicus*, CFIN and *Para-Pseudocalanus*, Para-PseudoCAL abundance) were merged to obtain annual data. Plankton abundance and recruitment were log-transformed using $\log_{10}(x + 1)$.

Regression and correlation analyses

To better understand observed changes in annual cod egg habitat suitability, we performed a simple regression analysis between the SSB and habitat suitability, reflecting environmental influence. Cold periods highlighted in Supplementary Fig. 5; 1970–1973, 1981–1986 and 1989–1991, were added to the analysis in blue. For this regression years from 1992 to 2013 were not considered in the analysis because they corresponded to the period when cod stock was anomalously low (e.g. collapse of Atlantic cod). Residuals were assessed as the difference between the observed and predicted SSBs, including this time the 1992–2013 period. For all correlations, the significance of the linear coefficient was adjusted to correct for temporal autocorrelation⁸³ (p_{ACF}).

Data availability

All data and code required to repeat the analyses of the results are available online and assigned a DOI: <https://doi.org/10.6084/m9.figshare.29610224.v1>.

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References

- Holm, P., Nicholls, J., Hayes, P. W., Ivinson, J. & Allaire, B. Accelerated extractions of North Atlantic cod and herring, 1520–1790. *Fish Fish.* **23**, 54–72 (2022).
- FAO. *The State of World Fisheries and Aquaculture 2024 – Blue Transformation in action* (FAO, 2024). <https://doi.org/10.4060/cd0683en>.
- Myers, R., Hutchings, J. A. & Barrowman, N. Hypotheses for the decline of cod in the North Atlantic. *Mar. Ecol. Prog. Ser.* **138**, 293–308 (1996).
- Beaugrand, G., Balembois, A., Kléparski, L. & Kirby, R. R. Addressing the dichotomy of fishing and climate in fishery management with the FishClim model. *Commun. Biol.* **5**, 1146 (2022).
- Planque, B. & Frédou, T. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **56**, 2069–2077 (1999).
- Drinkwater, K. F. The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES J. Mar. Sci.* **62**, 1327–1337 (2005).
- Houde, E. D. Recruitment variability. In *Fish Reprod. Biol. Implic. Assess. Manag.* 98–187 (2016). <https://doi.org/10.1002/9781118752739.ch3>.
- Kjesbu, O. S., Tiedemann, I., Alix, M., Thorsen, A. & Sundby, S. Half a century of high-latitude fisheries oceanography research on the “recruitment problem” in Northeast Arctic cod (*Gadus morhua*). *ICES J. Mar. Sci.* **80**, 1179–1201 (2023).
- Ricker, W. E. Stock and recruitment. *J. Fish. Res. Board Can.* **11**, 559–623 (1954).
- Leggett, K. T. & Frank, W. C. Paradigms in fisheries oceanography. In *Oceanography and Marine Biology: An Annual Review* 331–363 (CRC Press, 2008).
- Houde, E. D. Emerging from Hjort’s shadow. *J. Northwest Atl. Fish. Sci.* <https://doi.org/10.2960/J.v41.m634> (2008).
- Barneche, D. R., Robertson, D. R., White, C. R. & Marshall, D. J. Fish reproductive-energy output increases disproportionately with body size. *Science* **360**, 642–645 (2018).

13. Kjesbu, O. S., Solemdal, P., Bratland, P. & Fonn, M. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **53**, 610–620 (1996).
14. Stiasny, M. H. et al. Divergent responses of Atlantic cod to ocean acidification and food limitation. *Glob. Change Biol.* **25**, 839–849 (2019).
15. Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S. & Reid, P. C. Plankton effect on cod recruitment in the North Sea. *Nature* **426**, 661–664 (2003).
16. Moyano, M., Illing, B., Christiansen, L. & Peck, M. A. Linking rates of metabolism and growth in marine fish larvae. *Mar. Biol.* **165**, 5 (2018).
17. ICES. *Spawning and Life History Information for North Atlantic Cod Stocks* Vol. 274 (ICES Cooperative Research Report, 2005).
18. Miller, T. J., Herra, T. & Leggett, W. C. An individual-based analysis of the variability of eggs and their newly hatched larvae of Atlantic cod (*Gadus morhua*) on the Scotian Shelf. *Can. J. Fish. Aquat. Sci.* **52**, 1083–1093 (1995).
19. Weiss, E., Sanderson, M. & Gerlach, G. Population structure and essential fish habitat mapping of western georges bank cod. *Coop. Res. Partners' Program. Northeast Reg. Off Natl. Mar. Fish. Serv.* 32 pp (2005).
20. Stenevik, E. K., Sundby, S. & Agnalt, A. L. Buoyancy and vertical distribution of Norwegian coastal cod (*Gadus morhua*) eggs from different areas along the coast. *ICES J. Mar. Sci.* **65**, 1198–1202 (2008).
21. Opdal, A. F. et al. Spawning fish maintains trophic synchrony across time and space beyond thermal drivers. *Ecology* **105**, e4304 (2024).
22. Al-Emran, M., Zahangir, M. M., Badruzzaman, M. & Shahjahan, M. Influences of photoperiod on growth and reproduction of farmed fishes - Prospects in aquaculture. *Aquac. Rep.* **35**, 101978 (2024).
23. Hansen, T. et al. Growth, gonadal development and spawning time of Atlantic cod (*Gadus morhua*) reared under different photoperiods. *Aquaculture* **203**, 51–67 (2001).
24. McQueen, K. & Marshall, C. T. Shifts in spawning phenology of cod linked to rising sea temperatures. *ICES J. Mar. Sci.* **74**, 1561–1573 (2017).
25. Kristiansen, T., Drinkwater, K. F., Lough, R. G. & Sundby, S. Recruitment variability in North Atlantic cod and match-mismatch dynamics. *PLoS One* **6**, e17456 (2011).
26. Brander, K. The location and timing of cod spawning around the British Isles. *ICES J. Mar. Sci.* **51**, 71–89 (1994).
27. Gaard, E. & Steingrund, P. Reproduction of Faroe Plateau cod: Spawning grounds, egg advection and larval feeding. *Fróðskaparrit - Faroese Sci. J.* **48**, 87–103 (2001).
28. Myers, R. A., Mertz, G. & Bishop, C. A. Cod spawning in relation to physical and biological cycles of the northern North-west Atlantic. *Fish. Oceanogr.* **2**, 154–165 (1993).
29. Dahlke, F. T. et al. Northern cod species face spawning habitat losses if global warming exceeds 1.5°C. *Sci. Adv.* **4**, eaas8821 (2018).
30. Alix, M., Kjesbu, O. S. & Anderson, K. C. From gametogenesis to spawning: How climate-driven warming affects teleost reproductive biology. *J. Fish. Biol.* **97**, 607–632 (2020).
31. Bastardie, F. et al. A review characterizing 25 ecosystem challenges to be addressed by an ecosystem approach to fisheries management in Europe. *Front. Mar. Sci.* **7**, 629186 (2021).
32. Pikitch, E. K. et al. Ecosystem-based fishery management. *Science* **305**, 346–347 (2004).
33. Skern-Mauritzen, M. et al. Ecosystem processes are rarely included in tactical fisheries management. *Fish. Fish.* **17**, 165–175 (2016).
34. Grubb, P. J. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol. Rev.* **52**, 107–145 (1977).
35. Castant, J., Vantrepotte, V., Frouin, R. & Beaugrand, G. Comprehensive gridded dataset of photosynthetically active radiation in the upper ocean from 1958 to 2022. *Remote Sens. Environ.* **311**, 114305 (2024).
36. Beaugrand, G., Lenoir, S., Ibanez, F. & Manté, C. A new model to assess the probability of occurrence of a species, based on presence-only data. *Mar. Ecol. Prog. Ser.* **424**, 175–190 (2011).
37. Berg, P. R. et al. Trans-oceanic genomic divergence of Atlantic cod ecotypes is associated with large inversions. *Heredity* **119**, 418–428 (2017).
38. Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Model.* **199**, 142–152 (2006).
39. Legendre, P. & Legendre, L. *Numerical Ecology* (Elsevier Science Ltd, 2012).
40. Blöcker, A. M., Sguotti, C. & Möllmann, C. Discontinuous dynamics in North Sea cod *Gadus morhua* caused by ecosystem change. *Mar. Ecol. Prog. Ser.* **713**, 133–149 (2023).
41. Dawe, E., Koen-Alonso, M., Chabot, D., Stansbury, D. & Mullowney, D. Trophic interactions between key predatory fishes and crustaceans: Comparison of two Northwest Atlantic systems during a period of ecosystem change. *Mar. Ecol. Prog. Ser.* **469**, 233–248 (2012).
42. Hutchings, J. A. & Myers, R. A. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* **51**, 2126–2146 (1994).
43. Enfield, D. B., Mestas-Núñez, A. M. & Trimble, P. J. The Atlantic Multidecadal Oscillation and its relation to rainfall and river flows in the continental U.S. *Geophys. Res. Lett.* **28**, 2077–2080 (2001).
44. Heath, M. & Lough, R. A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). *Fish. Oceanogr.* **16**, 169–185 (2007).
45. Cyr, F. & Galbraith, P. S. A climate index for the Newfoundland and Labrador shelf. *Earth Syst. Sci. Data Discuss.* **2020**, 1–23 (2020).
46. Cyr, F. et al. Environmental control on the productivity of a heavily fished ecosystem. *Nat. Commun.* **16**, 5277 (2025).
47. Lapointe, F. et al. Annually resolved Atlantic sea surface temperature variability over the past 2,900 y. *Proc. Natl. Acad. Sci. U. S. A.* **117**, 27171–27178 (2020).
48. Mann, M. E., Steinman, B. A., Brouillette, D. J. & Miller, S. K. Multidecadal climate oscillations during the past millennium driven by volcanic forcing. *Science* **371**, 1014–1019 (2021).
49. Gray, S. T., Graumlich, L. J., Betancourt, J. L. & Pederson, G. T. A tree-ring based reconstruction of the Atlantic Multidecadal Oscillation since 1567 A.D. *Geophys. Res. Lett.* <https://doi.org/10.1029/2004GL019932> (2004).
50. Pepin, P. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Can. J. Fish. Aquat. Sci.* **48**, 503–518 (1991).
51. Robert, D. et al. Life in the fast lane: Revisiting the fast growth—High survival paradigm during the early life stages of fishes. *Fish. Fish.* **24**, 863–888 (2023).
52. Barnett, L. A. K., Branch, T. A., Ranasinghe, R. A. & Essington, T. E. Old-growth fishes become scarce under fishing. *Curr. Biol.* **27**, 2843–2848.e2 (2017).
53. Hsieh, C., Yamauchi, A., Nakazawa, T. & Wang, W. F. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquat. Sci.* **72**, 165–178 (2010).
54. Morrongiello, J. R., Sweetman, P. C. & Thresher, R. E. Fishing constrains phenotypic responses of marine fish to climate variability. *J. Anim. Ecol.* **88**, 1645–1656 (2019).
55. DFO. NAFO divisions 2J3KL Northern cod (*Gadus morhua*) stock assessment to 2024. *DFO Can. Sci. Advis Sec Sci. Advis Rep* **2024049** (2024). https://publications.gc.ca/collections/collection_2025/mpo-dfo/fs70-6/Fs70-6-2024-049-eng.pdf
56. DFO. Assessment of divisions 2J+3KL capelin to 2023. *DFO Can. Sci. Advis Sec Sci. Advis. Rep.* 2024050 (2024). https://publications.gc.ca/collections/collection_2025/mpo-dfo/fs70-6/Fs70-6-2024-050-eng.pdf

57. Kjesbu, O. S. et al. Thermal dynamics of ovarian maturation in Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **67**, 605–625 (2010).
58. Froin, R., McPherson, J., Ueyoshi, K. & Franz, B. A. A time series of photosynthetically available radiation at the ocean surface from SeaWiFS and MODIS data. in *Remote Sensing of the Marine Environment II* vol. 8525 234–245SPIE, (2012).
59. Huret, M. et al. Dispersal modeling of fish early life stages: Sensitivity with application to Atlantic cod in the Western Gulf of Maine. *Mar. Ecol. Prog. Ser.* **347**, 261–274 (2007).
60. Wieland, K. & Hovgård, H. Distribution and drift of Atlantic cod (*Gadus morhua*) eggs and larvae in Greenland offshore waters. *J. Northwest. Atl. Fish. Sci.* **30**, 61–76 (2002).
61. Huserbråten, M. B. O., Moland, E. & Albretsen, J. Cod at drift in the North Sea. *Prog. Oceanogr.* **167**, 116–124 (2018).
62. Ottersen, G. et al. A review of early life history dynamics of Barents Sea cod (*Gadus morhua*). *ICES J. Mar. Sci.* **71**, 2064–2087 (2014).
63. Hansen, Ø. J., Puvanendran, V. & Mortensen, A. Importance of broodstock holding temperature on fecundity and egg quality in three groups of photo-manipulated Atlantic cod broodstock. *Aquac. Res.* **44**, 140–150 (2012).
64. Van Der Meer, T. & Ivannikov, V. P. Seasonal shift in spawning of Atlantic cod (*Gadus morhua* L.) by photoperiod manipulation: egg quality in relation to temperature and intensive larval rearing. *Aquac. Res.* **37**, 898–913 (2006).
65. Puvanendran, V. & Brown, J. A. Foraging, growth and survival of Atlantic cod larvae reared in different light intensities and photoperiods. *Aquaculture* **214**, 131–151 (2002).
66. Hansen, T. et al. Growth, gonadal development and spawning time of Atlantic cod (*Gadus morhua*) reared under different photoperiods. *Aquaculture* **203**, 51–67 (2001).
67. Hoover, E. E. & Hubbard, H. E. Modification of the sexual cycle in trout by control of light. *Copeia* **1937**, 206–210 (1937).
68. Teegne, G., Melesse, A. M. & Worqlul, A. W. Development of multi-model ensemble approach for enhanced assessment of impacts of climate change on climate extremes. *Sci. Total Environ.* **704**, 135357 (2020).
69. Alix, M., Kjesbu, O. S. & Anderson, K. C. From gametogenesis to spawning: How climate-driven warming affects teleost reproductive biology. *J. Fish. Biol.* **97**, 607–632 (2020).
70. Wisz, M. S. et al. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* **14**, 763–773 (2008).
71. Van Proosdij, A. S. J., Sosef, M. S. M., Wieringa, J. J. & Raes, N. Minimum required number of specimen records to develop accurate species distribution models. *Ecography* **39**, 542–552 (2016).
72. ICES. Cod (*Gadus morhua* L.) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). *Rep. ICES Advis. Comm.* ICES Advice cod.27.47d20, (2022). (2022).
73. Castant, J., Vantrepotte, V., Thibault, H. & Beaugrand, G. Long-term changes in depth distribution and phenology of four North Atlantic plankton species. *Mar. Ecol. Prog. Ser.* **771**, 33–53 (2025).
74. Guisan, A., Thuiller, W. & Zimmermann, N. E. *Habitat Suitability and Distribution Models: With Applications in R* (Cambridge University Press, 2017).
75. Barbet-Massin, M., Jiguet, F., Albert, C. H. & Thuiller, W. Selecting pseudo-absences for species distribution models: How, where and how many?. *Methods Ecol. Evol.* **3**, 327–338 (2012).
76. Schickele, A. et al. Modelling European small pelagic fish distribution: Methodological insights. *Ecol. Model.* **416**, 108902 (2020).
77. Wackernagel, H. *Multivariate Geostatistics* (Springer, 2003). <https://doi.org/10.1007/978-3-662-05294-5>.
78. Opdal, A. F. et al. Spawning fish maintains trophic synchrony across time and space beyond thermal drivers. *Ecology* **105**, e4304 (2024).
79. Cornwell, W. K., Schwilk, D. W. & Ackerly, D. D. A trait-based test for habitat filtering: Convex hull volume. *Ecology* **87**, 1465–1471 (2006).
80. Nissling, A. & Westin, L. Egg mortality and hatching rate of Baltic cod (*Gadus morhua*) in different salinities. *Mar. Biol.* **111**, 29–32 (1991).
81. Parkinson, C. L., Cavalieri, D. J., Gloersen, P., Zwally, H. J. & Comiso, J. C. Arctic sea ice extents, areas, and trends, 1978–1996. *J. Geophys. Res. Oceans* **104**, 20837–20856 (1999).
82. Sokal, R. R. & Rohlf, F. J. *Biometry: The Principles and Practice of Statistics in Biological Research* (WH Freeman and company, 1995).
83. Pyper, B. J. & Peterman, R. M. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* **55**, 2127–2140 (1998).

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Author contributions

C.P.-C., G.B. and D.R. conceived the study. C.P.-C., G.B., M.L. performed the analysis. J.C. contributed modelised data (e.g. PAR₀ and plankton datasets). C.P.-C., G.B., M.L. developed the new methodology. C.P.-C., G.B., D.R., R.K., J.C. and M.L. wrote the manuscript.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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