Article

Environmental control on the productivity of a heavily fished ecosystem

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Sustainable fisheries management requires an understanding of the links between environmental conditions and fish populations, especially in the context of climate change. From this perspective, identifying the phases in which ocean climate fluctuations and changes in ecosystem productivity coincide could provide a powerful tool to help inform fisheries management. Using more than 70 years of climate and fisheries data, we show that cyclical changes in the Newfoundland and Labrador (NL) ecosystems productivity, from primary producers to piscivorous fish, coincide with changes in the regional ocean climate and the atmospheric settings of the northern hemisphere. This broad correspondence between climate and lower and higher trophic levels advances ideas for incorporating environmental knowledge into fisheries management on the NL shelves or in other regions facing similar dynamics.

Fisheries productivity is known to be affected by broad-scale environmental processes such as those captured by the North Atlantic Oscillation (NAO)[1], the Pacific Decadal Oscillation[2] or the El Niño Southern Oscillation (ENSO)[3]. However, separating the effects of changes in recruitment or fishing mortality and varying ecosystem productivity due to variations in environmental conditions remains a major challenge in the evaluation of fish stocks around the world[4]. These considerations are even more pressing in the face of anthropogenic climate change[5]. Integrating environmental knowledge into stock assessment processes is a key step, along with moving beyond single-species approaches[6], to achieving ecosystem-based fisheries management (EBFM)[7,8]. One practical limitation often put forward for not including environmental information in fisheries management is the fact that their quantitative impact on resources is often poorly understood[9,10].

The Newfoundland and Labrador (NL) shelves are a broad region of the northwest (NW) Atlantic ocean that includes the Labrador shelf, the Newfoundland shelf, and the Grand Banks of Newfoundland (Fig. 1). Following centuries of exploitation, the NL Northern Cod (*Gadus morhua*) stock, together with other groundfish stocks, collapsed in the early 1990s[11]. More than 30 years later, most of these stocks have yet to recover to their pre-collapse levels, and the region's ecosystems have shown important changes in their community structure (shifting from groundfish-dominated to shellfish-dominated, and are now returning to a groundfish-dominated structure)[12-15]. Although the exact causes of these changes continue to be investigated, it appears that both overfishing and environmental changes contributed to the collapse of many populations[16-18]. More specifically, the collapse of groundfish stocks occurred during one of the coldest periods of the last century in the NW Atlantic[19] and coincided with the collapse of capelin (*Mallotus villosus*), a key pelagic forage fish species for the NL ecosystems, and several groundfish species that were not subjected to directed commercial fishing[13,20].

Several studies have investigated the role of environmental changes in the collapse of fish stocks on the NL shelves[12,21-25]. Less work has been directed towards the period prior to the collapse, when a recently mechanized fleet achieved record-high catches during the warmest and potentially most productive period of the last century in the NW Atlantic[26,27]. Could the collapse of NL fish stocks have been prevented if the changes in environmental conditions and related

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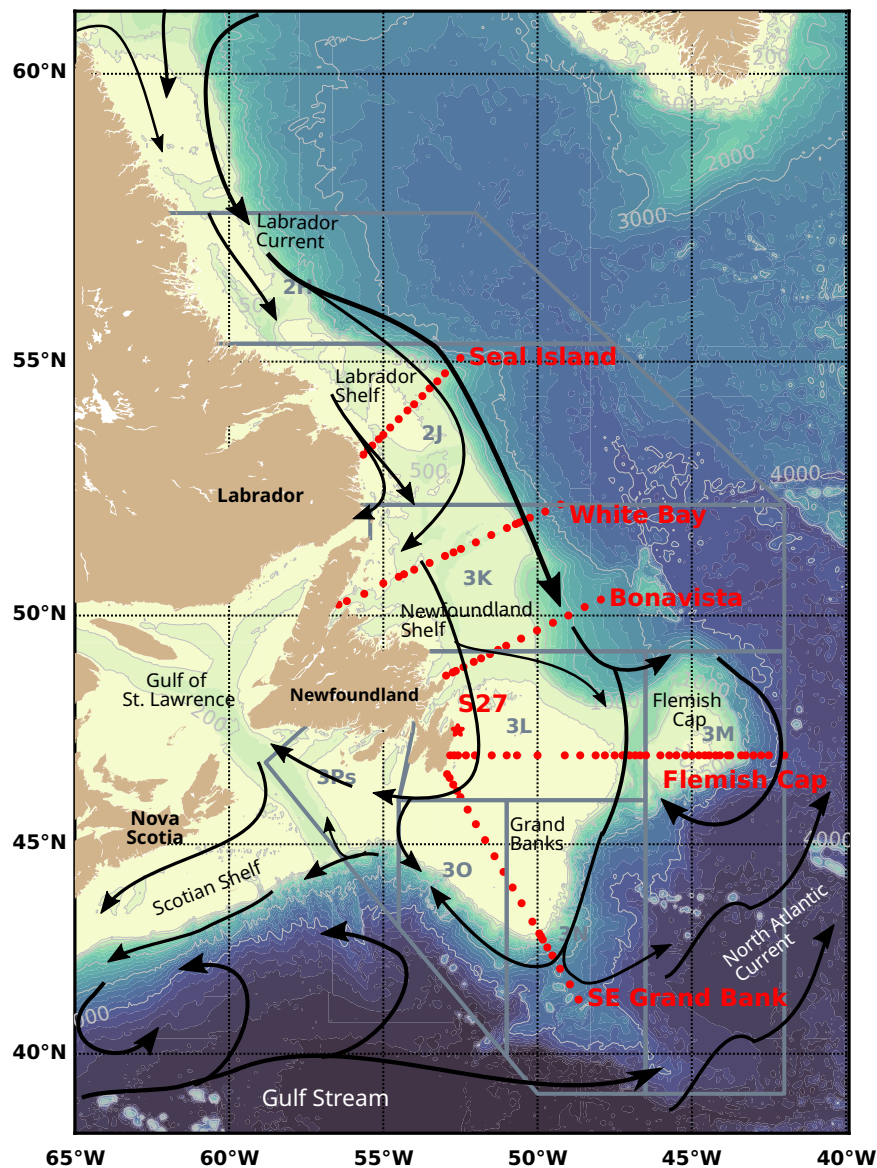
Fig. 1 | Map of the study region in the northwest Atlantic Ocean. The color map shows the bathymetric features obtained from the General Bathymetric Chart of the Oceans[92]. A sketch of the main surface currents is shown in black. NAFO Divisions 2H, 2J, 3K and 3L, 3N, 3O, 3M and 3Ps are shown in slate gray for reference. The red dots aligned in sections (also identified) represent the hydrographic stations where zooplankton samples used in this study were collected. Hydrographic Station 27 is shown with a red star.

productivity regimes of the ecosystem (e.g., the recognition of anomalously warm and productive 1960s and anomalously cold and less productive 1980s/90s) been factored into fisheries stock assessments at the time? Although we cannot definitively answer this question, as it involves both science and policy or political considerations, we propose an approach to identify when an ecosystem is characterized by particular productivity regimes and argue that it offers a mechanism for adjusting fisheries management given changes in climatic conditions going forward.

In this work, we argue that the lack of precise quantitative knowledge on the effect of the environment on fish stocks does not preclude its integration into stock assessments and its consideration in fisheries management decisions. Using more than 70 years of data from the NL shelves, we show that the ecosystem goes through productivity phases on decadal time scales. We also show that these phases can be identified using proper environmental monitoring and be used to guide fisheries management. For example, more

conservative fisheries management policies (e.g., lower extraction rates, stronger emphasis on conservation when evaluating the trade-off between stock conservation and socio-economic objectives) could be used in phases of low productivity, and more relaxed fisheries management policies (e.g., higher extraction rates, increased emphasis on socio-economic objectives) could be used in phases of higher productivity.

Results
Northwest Atlantic Ocean Climate
Located in Atlantic Canada at the confluence of Arctic, sub-Arctic, and subtropical currents, the NL shelves (Fig. 1) are strongly influenced by changes in ocean circulation at the scale of the NW Atlantic. These changes impact not only the regional ocean climate but also the overall composition of water masses and the immediate habitat of numerous commercial and non-commercial fish and invertebrate species.
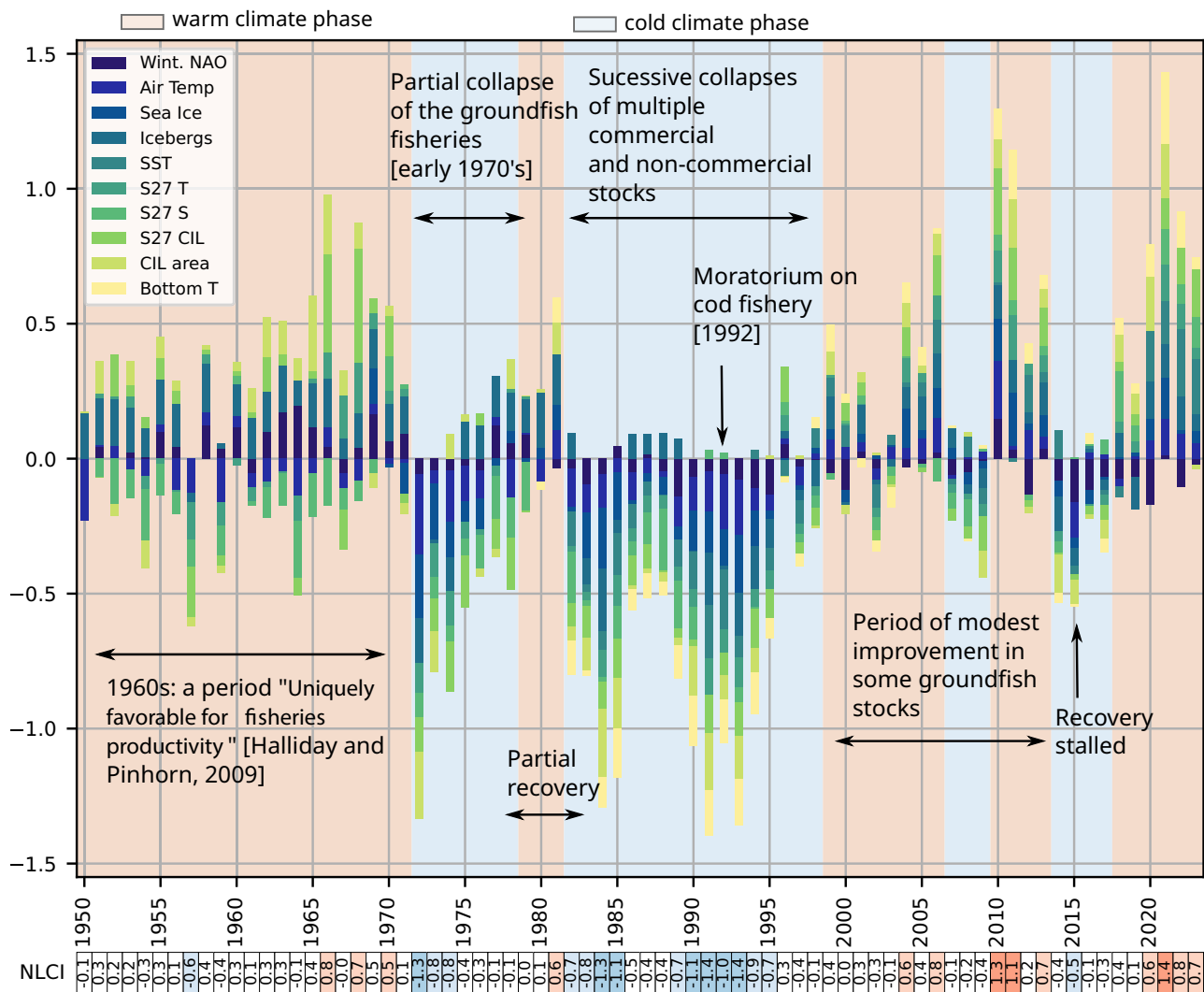
Fig. 2 | The Newfoundland and Labrador Climate Index (NLCI). The NLCI (unitless) is the average of 10 environmental time series: the Winter North Atlantic Oscillation (NAO) index, air temperature (Air Temp), sea ice season duration and maximum area, the number of icebergs drifting on the NL shelves, sea surface temperature (SST) of the NL shelves, vertically averaged temperature (T) and salinity (S) at Station 27 (S27), cold intermediate layer (CIL) core temperature at Station 27, summer CIL area on the hydrographic sections Seal Island, Bonavista Bay and Flemish Cap, and spring and fall bottom temperatures in NAFO Div. 3LNOPs and 2HJ3KLNO (See Cyr and Galbraith, 2021 for details[19]). The relative contribution of each sub-index to the NLCI is proportional to the length of each bar in the stacked bar plot, while the averaged value is reported in a scorecard at the bottom of the figure. Different climate phases are identified with orange and blue shades for warm and cold, respectively. A new phase is identified when the NLCI is positive or negative for at least three successive years. Qualitative information on the fisheries during the different climate phases has been added with black arrows.

The environmental conditions on the NL shelves and the NW Atlantic can be described using a climate index[19,28]. Presented as a composite graph showing the average and relative contributions of standardized anomalies from 10 environmental time series, the NL Climate Index (NLCI; https://doi.org/10.20383/101.0301 [consulted 5 May 2024]) shows annual changes in ocean climatic conditions for more than seven decades (Fig. 2). Different climate phases can be identified by looking at periods where the NLCI is mostly positive or mostly negative. These phases are delimited here using the simple rule that a new phase occurs when the mean value of the NLCI (scorecard at the bottom of Fig. 2) has a positive or negative run for at least three consecutive years (minimum number of years for which a linear regression can be fitted with uncertainty).

Eight climate phases, generally characterized by warmer or colder ocean conditions, were identified between 1951 and 2017 (orange and blue shades in Fig. 2). A ninth warm and potentially more productive climate phase has emerged since 2018. Although its effect on fish stocks has yet to be quantified, some signs of improvement in the finfish community have already been detected (see Discussion). These phases are driven by large-scale atmospheric conditions, shown here with mean sea level pressure (SLP) anomalies over the northern hemisphere (Fig. 3). Phases characterized by warmer climate (1951–1971, 1979–1981, 1999–2006, and 2010–2013) have mostly positive SLP anomalies above the pole and negative anomalies in the subtropics (except the 1999–2006 phase, where the patterns are unclear). In contrast, the phases characterized by a colder climate (1972–1978, 1982–1998, 2007–2009, and 2014–2017) all have negative SLP anomalies above the pole and positive anomalies in the subtropics.

Negative SLP anomalies above the pole are associated with positive phases of the NAO and are accompanied by a strengthening of the westerlies and the atmospheric jet stream above the NW Atlantic. This in turn leads to more frigid Arctic airflow above the NW Atlantic, particularly in winter, which promotes deeper convection in the Labrador Sea[29], larger volumes of cold water on the Labrador shelf[30], and changes in the pathways and strength of the Labrador current[31] and the subpolar gyre[32,33].
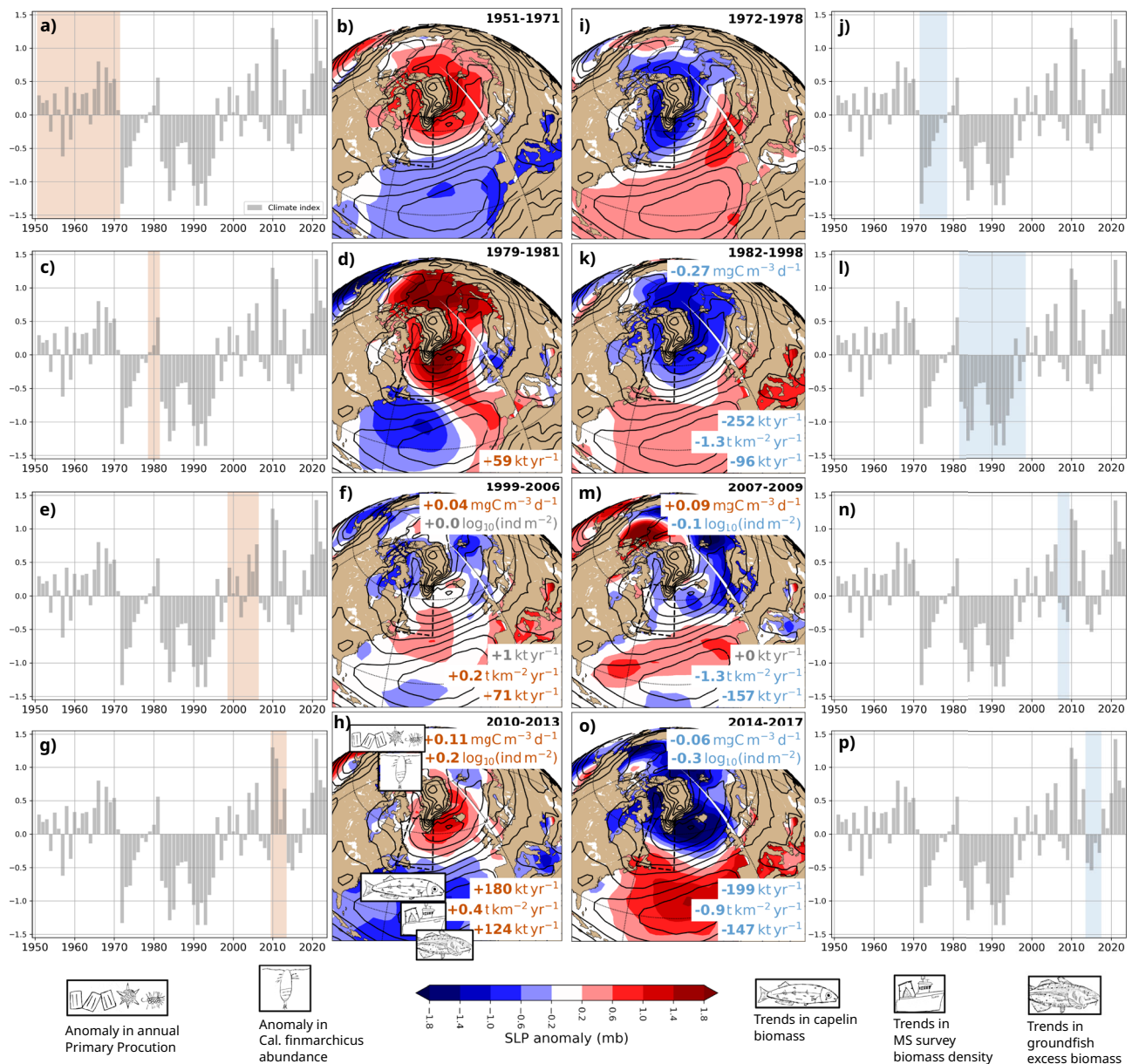
Fig. 3 | Maps of the sea level pressure (SLP) anomalies over the North Atlantic for 8 different periods. b 1951–1971, (**i**) 1972–1978, (**d**) 1979–1981, (**k**) 1982–1998, (**f**) 1999–2006, (**m**) 2007–2009, (**h**) 2010–2013 and (**o**) 2014–2017. Each of these periods correspond to the climate phases identified in Fig. 2, recalled in a side panel showing the NLCI (gray bars, unitless) with orange/blue shades showing the warm/cold phase of interest (subfigures **a**, **j**, **c**, **l**, **e**, **n**, **g** and **p**, respectively). Anomalies in the annual primary production above the NW Atlantic and *Calanus finmarchicus* density on the NL shelves are shown in the top of each SLP panel (where available). The trends in capelin biomass, multi-species bottom trawl survey biomass density, and groundfish biomass are indicated in the bottom of SLP subfigures (see legend). The anomalies and trends have been highlighted in orange, blue and gray for positive, negative and non-significant, respectively.

Seven Decades of Climate and Fisheries

Important milestones for the NL fisheries have been linked to the ocean climate (Fig. 2). Following centuries of relatively small-scale fisheries, the post-World War II period saw the introduction of large mechanized fishing vessels, including factory trawlers[34]. Historical reconstructions suggest that cod catches remained below 300,000 tonnes/year for hundreds of years before rapidly increasing in the 1950s and 1960s, reaching a peak of more than 800,000 tonnes in 1968[35] (see also Supplementary Fig. 6). Although the capabilities of this new fishing fleet were undeniable, it should be noted that record catches of the 1960s were achieved during one of the warmest period in (at least) seven decades on the NL shelves[19]. This period was characterized as uniquely favorable for groundfish productivity[26].

A first partial collapse of the groundfish fisheries occurred in the early 1970s[34] during a relatively cold phase that was in sharp contrast to the warm climate of the 1950s and 1960s (note that 1972 is the third coldest year recorded by the NLCI, tied with 1984). This collapse on the NL shelves coincided with general decreases in Atlantic Cod stocks across the NW Atlantic and was attributed to poor environmental conditions[36]. A partial recovery followed in the late 1970s, a period again characterized by warmer ocean conditions and positive SLP anomalies above the pole. This partial recovery of groundfish stocks was also aided by a reduction in fishing pressure in coastal waters following international agreements that led to the establishment of exclusive economic zones of 200 miles for maritime nations[36,37].

From the early 1980s to the late 1990s, the NW Atlantic entered its coldest phase in the last 70 years (a first cold pulse was recorded in the

mid-1980s and a second in the early 1990s). Multiple commercial and non-commercial fish populations successively collapsed during this period[13]. The biomass of the capelin stock in Northwest Atlantic Fisheries Organization (NAFO) Divisions (Div.) 2J3KL rapidly collapsed from 5800 kt in spring 1990 to 600 kt in fall 1990 − probably due to environmental drivers rather than fishing − before the collapse of the northern cod stock[20]. The collapse of cod led to the eventual establishment of a series of moratoria on groundfish fisheries beginning in 1992, while 1991 and 1993 were the coldest years recorded by the NLCI (Fig. 2). In the following decades, some cold water shellfish stocks became more productive[15], although their increases in biomass never fully compensated for losses in groundfish biomass[14,38]. Although some finfish stocks have shown signs of improvement in the following decades[39], the recovery of many groundfish and pelagic stocks appears to have stalled during the 2014–2017 phase[40–42]. This period again coincides with a shift in climate towards colder conditions, with the 2014–2017 phase sharing some similarities with that of the early 1990s[29], albeit of much shorter duration. Following a reanalysis of cod stocks using a longer time series[43], the Northern cod commercial fishing moratorium ended in 2024.

We also note that in addition to 2014–2017, another cold phase of lesser magnitude (2006–2009) interrupted the otherwise positive run of the NLCI that occurred between the late 1990s and the mid-2010s. Since the late 1990s, the NL climate has exhibited alternating colder and warmer conditions over relatively short phases, and the NLCI has not returned to a positive run similar to the one observed in the 1950s and 1960s. Provided that the ocean climate is influential on fish stocks, this means that the climatic conditions and the setup preceding the record catches of the 1960s have not been replicated over the past 50 years.

Ecosystem productivity changes

To better quantify and explain the changes observed in the ecosystems, we examined, for the different phases of the climate introduced above, the evolution in primary and secondary production, forage and groundfish biomass, and the biomass density of finfish and commercial shellfish collected during scientific surveys. We treated these five time series differently (see Methods section). For primary and secondary production, we look at the mean level for each climate phase compared to the average of the entire time series (that is anomalies, because biomass cannot generally accumulate from one year to the next). For fish and finfish biomass, we look at trends during the different climate phases because surplus production can accumulate over time.

Primary production levels in the NW Atlantic, as well as the density of *Calanus finmarchicus*, a key zooplankton species on the NL shelves, were generally above average during warmer climate phases and below average during colder climate phases (Supplementary Figs. 1 and 2).

Similarly, trends in the capelin biomass index derived from acoustic-trawl surveys, the finfish and shellfish biomass density index derived from scientific multi-species bottom trawl surveys, and the groundfish excess-biomass derived from a surplus production model accounting for density-dependent effects and fisheries catches generally increased during warm climate phases and decreased during cold phases. Here, trends refer to the slopes of linear regression fits to annual biomass, biomass index and density time series during climate phases (Supplementary Figs. 3–5).

For nearly all climate phases identified with the NLCI, there is a good correspondence between the atmospheric large-scale SLP patterns, the regional NL climate and, where data are available, the productivity of the ecosystems determined by the mean level of primary and secondary production, as well as the trends in surplus groundfish biomass and multispecies biomass density. For example, during warmer phases of the climate (Fig. 3a–h), primary and secondary

production levels were generally above average, and the three biomass metrics described above increased (mostly orange numbers). In contrast, during the colder phases of the climate (Fig. 3i–p), primary and secondary production levels were generally below average, and the three biomass metrics described above decreased (mostly blue numbers). Exceptions include above average primary production during the cold 2007–2009 phase (Fig. 3m) and near-average abundance of *Calanus finmarchicus* during the warm 1999–2006 phase (Fig. 3f). Furthermore, the evidence for the importance of climate phases in trends in capelin biomass is not as compelling as that of groundfish and multispecies biomasses. Specifically, although the capelin biomass is marked by a decline during the groundfish collapse phase (1982–1998; Fig. 3k), its biomass increased between 1982-1990 before collapsing in 1990-1991 (Supplementary Fig. 3). The reasons for this increase in capelin biomass in the 1980s are unclear. It may be associated with a reduction in predation pressure when groundfish stocks began to decrease in the mid to late 1980s[13]. Alternatively, capelin stocks may have had reduced spatial overlaps with their predators during the cold 1980s[44], but then the capelin also collapsed during the very cold anomaly of 1990-1993. Trends in capelin biomass were also not significantly different from zero during the 1999–2006 and 2007–2009 climate phases, unlike the trends in the groundfish and multi-species biomasses (Fig. 3f, m). However, the SLP patterns during these two phases did not exhibit clear positive or negative signals centered around the pole as seen in other phases, which corresponded to rapid fluctuations of the NLCI (especially during the 1999–2006 phase). This may suggest changes in predation dynamics upon capelin or that the species responds more rapidly to environmental changes.

Overall, the NLCI, the SLP patterns and the productivity of the different components of the NL ecosystems track each other well. Autocorrelation in the environmental time series provides a challenge in detecting changes in climate conditions, but it also highlights the consistency in the signal for extended periods of time, particularly when consistent across multiple trophic levels. Collectively, this suggests that not only does the ocean climate, driven by large-scale atmospheric forcing, change on decadal time scales, but also that the overall productivity of the ecosystems (from primary and secondary production to forage fish and higher trophic levels) changes in relative synchronicity with climate fluctuations. These results support the description of the fisheries made in Fig. 2 and suggest that productivity changes may have also occurred in periods where no fisheries-independent data were available (e.g., productive 1960s and less productive early 1970s)[16]. This is supported by historical Northern Cod catches reconstructed for the NW Atlantic[35] that shows periods of increase and decline aligned with the different climate phases, especially before the 1990s collapse (Supplementary Fig. 6). This study also supports the idea that the period preceding the late 1960s, when the highest extraction rates by fisheries occurred, was likely a period with an unusually large climatic anomaly for the NL shelves[26]; and that those sustained warm and productive conditions during the 1950s and 1960s have not been observed since.

Discussion

In ecology, bottom-up trophic control refers to ecosystems that are resource-driven and limited by biotic or abiotic factors (physical environment, primary and secondary production, etc.), while top-down trophic control refers to a consumer-driven cascade where the dominant control is exerted by predators such as fish, marine mammals and/or fisheries[45]. By demonstrating a consistent correspondence between the atmospheric setting on ocean climate and the influence of climate on primary and secondary production, forage fish, groundfish, and overall biomass density, this study provides evidence for strong bottom-up control of the NL shelves ecosystems.

With the NL shelf being located in the coldest part of the range for many groundfish species, it is not surprising to find a positive

relationship between recruitment and temperature for some stocks, such as Atlantic cod[46]. However, it is important to acknowledge that the effects of warmer and colder climate phases go far beyond the simple physiological response of organisms to temperature. Changes in climate phases involve changes in ocean circulation, water mass composition, plankton phenology, etc. Here, a series of hypotheses linking climate and ecosystem productivity and fish biomass are reviewed.

The NL shelves are characterized by the presence of near-freezing(< 0 °C) Arctic-origin waters in their subsurface for most of the year[47]. In colder climate phases, larger volumes of these cold waters are found on the NL shelves[19], potentially limiting the distribution of species that are less cold tolerant[48], or resulting in distributional changes of some stocks toward areas with more suitable conditions[21]. The different climate phases on the NL shelves also imply changes in the severity of winter and sea ice conditions, which alter the timing of post-winter ocean re-stratification and the phenology of spring phytoplankton blooms, with earlier blooms associated with warmer climate, and vice versa[49].

Warmer climate phases are also associated with higher densities of *Calanus finmarchicus*, a key copepod species in the NL ecosystems[49]. The increases in their density can be explained not only by increases in primary production, but also by a better match between the end of the *C. finmarchicus* winter diapause and the timing of the phytoplankton bloom[50,51]. In addition, there may be better retention of secondary production on the NL shelves during warm phases due to the weaker subpolar gyre associated with reduced wind curl over the North Atlantic[32,52]. The energy rich *C. finmarchicus* is a key prey for capelin, a keystone forage fish species that is responsible for the transfer of energy between secondary producers and higher trophic levels[53,54]. Thus, it is not unexpected to see capelin biomass trend upwards when *C. finmarchicus* abundances are high. Higher capelin biomass also has a direct effect on higher trophic levels, such as cod, a key predator of capelin[55], and other groundfish species. In general, this study supports the idea that the availability of energy at the base of the food web is an important limiting factor for overall ecosystem productivity, as indicated by concurrent increases in capelin, groundfish, and other fish species biomasses in periods when *C. finmarchicus* densities are high (and vice versa).

We have been able to identify climate phase as an underlying mechanism that explains prolonged periods of low and high productivity for multiple trophic levels in the NL ecosystems. Unlike previous studies that have typically focused on single characteristics of the climate system (e.g., the NAO[1]), our approach builds on the simple concept that no single indicator can fully encapsulate all relevant environmental processes that impact ecosystem productivity. We leverage environmental indicators provided by the NLCI to uncover the relationship between the ocean climate state and ecosystem function.

The NLCI used in this study includes the winter NAO as well as nine other subindices. The advantage of integrating these additional climate indices (both on a regional scale and on a broad scale) into a climate index is that we do not rely on the trend of one index alone to identify climate phases. While we have time series of variable lengths, especially for lower trophic levels, the relative concordance between productivity trends across trophic levels supports the use of the NLCI to identify periods of low and high productivity.

Previous studies on Atlantic cod stocks across the North Atlantic basin have noted a general coherence in stock collapses during the 1980s and 1990s, suggesting that environmental forcing was an important underlying factor in addition to fishing impacts[36,56,57]. In the northeast Atlantic, the prevalence of warmer ocean conditions since the 1980s, combined with the application of precautionary biological reference points in applied fisheries management, has contributed to the rebuilding of the Atlantic Cod stock to record levels[58]. Additional

work on some of these stocks has shown how changing environmental conditions affected cod through impacts in lower trophic levels[59], and how the availability of a forage species like capelin emerges as a common driver for two cod stocks with very different trajectories in the northwest and northeast Atlantic[55]. These observations from several North Atlantic ecosystems are consistent with our finding that ecosystem productivity appears to be generally associated with the prevailing phase of ocean climate, and suggest that identifying such phases could provide information on overall ecosystem functioning more generally.

It has been hypothesized that the lack of recovery of most commercial fisheries to pre-collapse biomass levels was due to a sustained low productivity regime since the early 1990s[57,60,61]. This study offers a perspective on this hypothesis. First, it confirms that the climatic setting that led to record high cod catches in the 1960s − e.g., sustained warmer than average ocean conditions with potentially earlier spring blooms and higher levels of primary and secondary production − have not been observed since. Second, warm phases since 1998 provide an explanation for the modest improvements experienced by capelin and some groundfish stocks since the collapses in the early 1990s[20,62,63], but the lack of further recovery to pre-collapse levels may be associated with what appears to be an increased variability in the periodicity of changes in climate phases such as the short-lived but intense cold and low productivity phases for groundfish between about 2006 and 2009, and 2014 and 2017[14,64] (Figs. 2 and 3). The warmer phase emerging since about 2018 may, however, signify a transition to a more productive phase in the coming years, consistent with a recent improvement of the capelin fall condition index[65].

Disentangling fishing mortality (e.g., overfishing) and natural fluctuations of fish populations is a challenge because they are intrinsically related[36,57]. Favorable environmental conditions can allow for fishing levels that may not be otherwise sustainable. That may have been the case, for example, on the NL shelves in the 1960s. In contrast, fishing mortality can exacerbate the impacts of poor environmental conditions on ecosystems and accelerate the decline of fish stocks[66]. A stock historically fished sustainably may become over-fished if its production declines below a certain level due to changes in environmental conditions.

Linking environmental fluctuations with fish stock dynamics is a key step in the implementation of EBFM[67,68]. Towards this goal, this study demonstrates how 70 years of fluctuations in NL ecosystems productivity and changes in fish biomass can be explained using a simple climate index. Recognizing the phases (or productivity regimes) that an ecosystem is subject to, such as the ones described in this study, provides a powerful tool to inform fisheries management. This environmental information can be taken into account either qualitatively or quantitatively.

Qualitatively, it allows setting more conservative extraction targets, or even ecosystem quotas, during periods when environmental conditions are deemed less favorable for productivity, or more permissive ones when these conditions appear favorable. Although conceptually a straightforward approach, real-life applications of these concepts would be expected to be more complex and likely involve the use of environmental conditions to inform risk assessments aimed at evaluating trade-offs between the conservation of the exploited stocks and socioeconomic pressures. A recent illustration of this idea is the decision of Peru to suspend the 2023 anchoveta fishery season as a trade-off for conservation[69]. This decision was motivated by the high number of juvenile fish in the exploratory fishery as a result of the developing El Niño phase of the ENSO in 2023, a situation known to impact the anchoveta fishery[70].

Quantitatively, environmental trend analyses could be used to adjust target levels of fishing mortality (*sensu* F_{eco})[6] or these trends could be explicitly included in the operating models used in management strategy evaluations (MSE) to fully integrate environmental

signals in the development of harvest control rules[71]. Another alternative would be to adjust ecosystem-level quotas based on a scaling factor determined by ocean climate. This is analogous to the idea of establishing ecosystem overfishing thresholds based on primary production metrics[72], except this time on the basis of a climate index. This type of approach would be well suited for current applications of ecosystem indicators for total sustainable catches, such as the one implemented by NAFO that scales estimates of fisheries production potential using total biomass density, and which our study has shown responds to identified climate phases[18,73,74]. However, in the context of fisheries management based on maximum sustainable yield (MSY), factoring in changes in ecosystem productivity may, in some circumstances, have the unintended consequence of increasing anthropogenic pressure on a stock by lowering its limit reference point[75]. Climate-adaptive fisheries management strategies in the context of MSY should therefore be carefully studied if the protection of marine resources is the priority.

Fisheries management actions in relation to a changing climate are plagued by many unknown unknowns[76] that should nevertheless be considered when setting management objectives, since these decisions can affect the future state of natural resources[77]. This work joins a growing body of literature that proposes pragmatic solutions to how to overcome these challenges.

Methods

Sea level pressure anomalies
Monthly SLP between 1948 and 2021 were retrieved from the National Centers for Environmental Prediction (NCEP) and the National Center for Atmospheric Research (NCAR) (NCEP-NCAR Reanalysis 1 data). These are provided by the National Oceanic and Atmospheric Administration Physical Science Laboratory in Boulder, Colorado, USA, and accessible on their website at https://psl.noaa.gov [consulted 4 May 2022][78]. The SLP anomalies for each of the climate phases discussed above were calculated as the difference between the average for each time window (all months considered) and the average of the 1950–2020 period (Fig. 3).

Annual primary production
The annual net primary production (in $mgC\,m^{-3}\,d^{-1}$) over the NW Atlantic was obtained from a Mercator-Ocean biogeochemistry hindcast for the global ocean at https://doi.org/10.48670/moi-00019 [consulted 4 October 2022]. The monthly resolution data were averaged in annual means and over a geographical region covering the NW Atlantic [47-65°N; 47-65°W] (dashed box in Fig. 3). The resulting time series runs from 1993 to 2020 (Supplementary Fig. 1). The average primary production for each climate phase were reported as horizontal dashed-green lines with shading representing the 80% confidence interval (Supplementary Table 1). The anomalies of primary production for each climate phase are calculated as the difference between the average of each climate phase and the average of the entire time series (1993–2020). These anomalies are reported in Fig. 3 in orange when positive and blue when negative.

Calanus finmarchicus density
Physical and biogeochemical data are regularly collected on the NL shelves at standard stations along oceanographic transects since 1999 as part of Fisheries and Oceans Canada's (DFO) Atlantic Zone Monitoring Program (AZMP)[79]. Up to three missions (spring, summer and fall) occur annually in the NL waters as part of the AZMP. During the spring and fall, Southeast Grand Bank, Flemish Cap and Bonavista Bay transects were occupied in most years while the Seal Island transect was only occupied from 2009 to 2015 during fall missions (Fig. 1). In the summer, the Flemish Cap and Seal Islands transects were occupied in most years while the White Bay transect was occupied every 1 to 3 years between 1999 and 2007.

In addition to those transects, zooplankton samples were also collected at Station 27 (47°32.8′N, 52°35.2′W) two to four times per month on average, from April through December. This Station is located just east of St. John's, NL and has a total depth of 176 m (Fig. 1). It is downstream from the incoming flow from the Labrador shelf, and its local oceanographic conditions are considered representative of the climate of the NL shelves and the NW Atlantic[19,80,81].

Zooplankton samples were collected at the stations described above by vertically towing a pair of conical ring nets (200 μm) that were mounted side by side (e.g., "bongo nets") from 10 m off the bottom to the surface at a speed of ~1 m s⁻¹. Material collected from each of the conical ring nets was preserved separately in a buffered 2% formaldehyde solution. The material from one net was sent to a taxonomy lab for species identification and counting. For each vertical tow, the copepod density per surface area (C in ind m⁻²) was estimated by dividing the number of individuals in the tow (N) by the area of the net opening (0.44 m²). Annual estimates of copepod *Calanus finmarchicus* ($\overline{C}$) were obtained by fitting a linear model of the form shown in equation (1):

$$\overline{C} = \alpha + \beta_{\text{year}} + \delta_{\text{station}} + \gamma_{\text{season}} + \epsilon. \tag{1}$$

Here $\overline{C}$ is the mean annual density of Calanus (in ind m⁻²), α is the intercept, ϵ is the error, and β, δ, γ are the categorical effects of the factors Year, Station and Season, respectively. $\overline{C}$ was log-transformed (ln) to normalize the skewed distribution of the observations. This model accounts for the fact that the number of stations and seasons sampled annually by the AZMP may slightly vary from year to year. To control for the order of the variables in the model, annual means were estimated using adjusted sums of squares[82]. The assumptions of the models were assessed, i.e., the residuals were examined for independence as well as for normality and homogeneity of variance.

Annual *C. finmarchicus* densities are reported in Supplementary Fig. 2. The horizontal dashed brown lines correspond to the average level for each climate phase identified in the study, with shading representing the 80% confidence interval (Supplementary Table 1). The anomalies in *C. finmarchicus* density for each climate phase are calculated as the difference between the average of each climate phase and the average of the entire time series (1999–2021). These anomalies are reported in Fig. 3 in orange text when positive and blue text when negative.

Capelin biomass index
The capelin biomass index (in kt) was estimated during the annual DFO spring capelin acoustic survey (Supplementary Fig. 3). The spring capelin acoustic survey has taken place annually in its current form since 1982, except for 1983-84 and 2021, and there were no acoustic surveys in 1993–1995, 1997-1998, 2006, 2016, and 2020[60].

The acoustic survey is typically conducted in May and covers the majority of NAFO Div. 3L, and since 1996, the southern NAFO Div. 3K. Div. 3L is an area of particular importance for juvenile and non-migratory age-1 + capelin, although all age classes acoustically surveyed are included in the annual capelin biomass index. A depth-delimited stratified survey design is conducted each year, although the transect design, stratum boundaries, and areas covered have changed over time[83,84]. Acoustic backscatter attributed to capelin was converted to capelin biomass using biological data from directed mid-water and bottom trawls.

Linear trends were calculated for each climate phase previously identified by a least squares regression with bootstrap (1000 repetitions). The mean trends, defined as the average of all repetitions, are reported in Fig. 3 in orange text when positive and in blue text when negative, while the 80% confidence intervals are reported in Supplementary Table 1. Slopes for which the confidence interval bounds have different signs are left gray.

Multi-species biomass density

The total biomass density index from DFO multi-species bottom-trawl scientific surveys (in kt km^{-2}) was calculated from DFO Fall and Spring surveys for NAFO Div. 2J3KLNOPs (Supplementary Fig. 4). The large marine ecosystem in the NL shelves is typically subdivided into Ecosystem Production Units (EPUs) which correspond to relatively well defined, but still interconnected, functional ecosystems[85–87]. DFO multi-species surveys have covered these EPUs differently over time. The Fall surveys have systematically surveyed the Newfoundland Shelves (NAFO Div. 2J3K) EPU since 1981, and the Grand Bank (NAFO Div. 3LNO) EPU since 1990. The Spring surveys have systematically covered the Grand Bank EPU since 1985, and the Southern Newfoundland (NAFO Div. 3Ps) EPU since 1982. The gear used in these surveys changed in 1995 for the Fall surveys and 1996 for the Spring surveys when the Campelen trawl replaced the Engel trawl. The introduction of the Campelen trawl permitted the beginning of the systematic recording of commercial shellfish species in DFO surveys. This was important given that shellfish species like Northern shrimp and snow crab had increased after the collapse of the groundfish community[14,38]. While these biomass increases were substantial, especially in the mid-late 1990s, they did not compensate for the losses of groundfish[14]. Northern shrimp was the dominant species among commercial shellfish, and available approximations of its biomass prior to the introduction of the Campelen gear indicate that it was only starting to increase in a significant way when the Campelen gear was introduced[88]. The available evidence[88,89] suggest that commercial shellfish biomass was a relatively modest fraction of the total biomass before the collapse. It follows that considering only finfish for the Engel period, when groundfish heavily dominated the total biomass, is a reasonable approximation to the total biomass signal.

For each EPU and season, total biomass density was calculated as the total biomass for all finfish and commercial shellfish, when shellfish data is available, species divided by the total area surveyed. Total biomass was obtained as the sum of individual species biomass estimates calculated as the standard areal expansion of survey biomass based on the random-stratified survey design. Scaling factors were applied to the Engel series to provide comparability in the order of magnitude between the Engel and Campelen data[14,38]. These scaling factors are not available for the Southern Newfoundland EPU, so only Campelen data (i.e., 1996 forward) was considered in this analysis for this EPU. Given that the Grand Bank EPU is typically surveyed twice a year (spring and fall surveys), the biomass density signal for this EPU was summarized as the average of the estimated biomass densities from these two surveys. The total biomass density signal at the scale of the NL shelf was estimated as the median of all available total biomass densities by EPU in a given year.

Linear trends were calculated for each climate phase previously identified by a least squares regression with bootstrap (1000 repetitions). The mean trends, defined as the average of all repetitions, are reported in Fig. 3 in orange text when positive and in blue text when negative, while the 80% confidence intervals are reported in Supplementary Table 1. Slopes for which the confidence interval bounds have different signs are left gray.

Change in groundfish biomass

Groundfish biomass was estimated using a state-space multi-species surplus production model for the NL shelves. Within each region (NAFO Div. 2J3K and 3LNO), the biomass of each species at the start of year y was given by equation (2):

$$B_{y,s} = \left(B_{y-1,s} + r_s B_{y-1,s} \left(1 - \frac{\sum_s B_{y-1,s}}{K} \right) - C_{y-1,s} \right) e^{\delta_{y,s}}, \quad (2)$$

where r_s is the maximum per-capita rate of change for species s, K is the carrying capacity, $C_{y-1,s}$ is the catch through year $y-1$ for species s, and

$\delta_{y,s}$ is process error. Process errors were modeled using a multivariate normal distribution, estimating temporal and species-to-species correlation. Relative biomass indices for species s in year y from survey i was given by equation (3):

$$I_{y,i,s} = q_{i,s} B_{y,s} e^{\varepsilon_{y,i,s}}. \quad (3)$$

where $q_{i,s}$ is the time-invariant catchability coefficient for the survey index i, and $\varepsilon_{y,i,s}$ is the observation error, which was assumed to be normally distributed. This model was implemented using template model builder (TMB)[90] within R[91].

The process errors of this model, $\delta_{y,s}$, correspond to the variance unexplained by density-dependent processes and fishing mortality (i.e., changes presumably caused by environmental variables). The changes in biomass imposed by these errors were calculated (in kt) and averaged for all species (Supplementary Fig. 5).

Linear trends were calculated for each climate phase previously identified by a least squares regression with bootstrap (1000 repetitions). The mean trends, defined as the average of all repetitions, are reported in Fig. 3 in orange text when positive and in blue text when negative, while the 80% confidence intervals are reported in Supplementary Table 1. Slopes for which the confidence interval bounds have different signs are left gray.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data needed to evaluate the conclusion are provided here at https://doi.org/10.5281/zenodo.15359627. In addition, updates of the Newfoundland and Labrador Climate Index (NLCI), sea level pressure and primary production data are available at 10.20383/101.0301 [consulted 5 May 2024], https://psl.noaa.gov [consulted 4 May 2022], and 10.48670/moi-00019 [consulted on 4 October 2022], respectively.

Code availability

All relevant code used to generate the figures are available at https://doi.org/10.5281/zenodo.15359627.

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Author contributions

F.C. conceptualized the study and led the data analysis, writing and editing. A.A. and H.M. curated capelin data and contributed to the writing and editing. D.B. and P.P. curated zooplankton data and contributed to the writing and editing. M.K.A. curated scientific survey biomass density data and contributed to the writing and editing. P.R. curated groundfish excess biomass data and contributed to the writing and editing. D.M. curated data that did not make the final version of this study and contributed to the writing and editing.

Competing interests

The authors declare no competing interests.