ECOLOGY

Major heat wave in the North Atlantic had widespread and lasting impacts on marine life

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Marine heat waves (MHWs) are increasing in frequency and intensity, but wider effects are unexamined in the North Atlantic, and there are uncertainties regarding the spatial scale, magnitude, and persistence of MHWs' impacts on ecosystems. We show that a sudden and strong increase in the frequency of MHWs in and after 2003 was linked to widespread and abrupt ecological changes. This upheaval spanned multiple trophic levels, from unicellular protists to whales. Every examined region showed a reorganization from species adapted to colder, ice-prone environments to those favoring warmer waters and the event's impacts altered socioecological dynamics. This review provides evidence for large-scale connectivity across ocean basins. However, it reveals that the magnitude of ecological impacts seems to vary among events highlighting key knowledge gaps for predicting ecosystem responses to MHWs. Understanding the importance of the subpolar gyre and air-sea heat exchange will be crucial for forecasting MHWs and their cascading effects.

INTRODUCTION

Ecosystems around the world are undergoing significant transformations driven by climate change and other anthropogenic stressors (*1*, *2*). These ecological changes can be persistent and may entail regime shifts that abruptly and profoundly alter the organization and function of ecosystems (*3*–*6*). Identifying ecological regime shifts poses a substantial challenge due to the logistical and methodological constraints involved in the detection of widespread, synchronized changes across ecological parameters. Marine heat wave (MHW) is a term used to describe a period of anomalously warm water relative to historical temperatures (*7*–*9*). MHWs are drivers of ecological alteration, regime shifts, and changes in regional fisheries management strategies, and their increasing frequency and intensity are linked to anthropogenic warming and are predicted to intensify in the future (*7*, *10*–*18*). However, there is no clear understanding about whether MHWs of similar extent produce comparable ecological impacts. The available evidence paints a diverse picture, indicating that not every temperature anomaly characterized as MHW has equivalent consequences for marine ecosystems (*19*, *20*). These oceanic extreme events have a complex physical causation, which involves atmospheric and oceanographic variables including shifts in the distribution of major water masses, ocean advection events, changes in local ocean-atmosphere heat fluxes, and teleconnections (*7*, *14*, *21*, *22*).

A key characteristic of the North Atlantic's environmental influence is the intricate network of ocean currents that traverses its expanse and plays a vital role in shaping local and global environmental conditions (Fig. 1) (*21*, *23*–*26*). Notably, the circulation of water masses facilitates the movement of cold Arctic waters southward along Greenland's east coast and warm, saline, subtropical Atlantic waters northward, extending the Gulf Stream's reach through the Iceland-Scotland ridge toward the Arctic. The origin of these oceanic currents is primarily linked to a complex interplay of thermal and saline gradients and to the movement of winds, giving rise to phenomena, such as oceanic gyres, a term to describe a large-scale vortex in the sea. There is agreement in the scientific community that the circulation intensities of the subpolar gyre and the Norwegian Sea gyre play a vital role in the mixing of subarctic and Atlantic currents in the North Atlantic, thereby regulating the contributions of Arctic water and Atlantic water feeding into the Norwegian Sea, the Barents Sea, and the Arctic (*21*, *27*–*29*). A strong subpolar gyre should lead to a dispersal of cold, fresh, nutrient-rich waters toward the Northeast Atlantic, while a weak subpolar gyre should allow for expansion of subtropical waters northward and westward leading to a diffusion of warm, saline conditions (*21*, *29*–*32*). In 2003, a weak subpolar gyre was linked to a sudden, increased volume of subtropical water entering the Norwegian Sea via the Atlantic inflow (*30*, *33*). Concurrently, there was an unusually low inflow of Arctic waters into regions east of Iceland and into the Norwegian Sea (*30*, *34*). The warm waters extending into the North Atlantic advance westward toward Greenlandic ecosystems and northward toward the Fram Strait, ultimately reaching the Arctic Ocean within 1 to 3 years (*21*, *25*, *35*, *36*).

It is uncertain whether the shift in water masses was the main or the sole driver of a sudden rise in sea temperatures or whether elevated air temperatures also played a role as oceanic temperature records coincided with an atmospheric heat wave across central Europe and the North Atlantic with summer air temperatures of 1° to 4°C higher than usual (*37*–*39*). This overlap raises questions about the sequence of events in ocean-atmosphere heat fluxes and whether high air temperatures helped to sustain elevated ocean temperatures or vice versa. The consequences were stark with a marked decline in summer sea ice concentration around Southeast Greenland (*40*–*42*), a significant reduction in sea ice import to the Barents Sea following a record high in the winter of 2002/2003 (*42*, *43*), and reduced sea ice extent in West Greenland and the Canadian Arctic (*42*, *44*, *45*). The year 2003 saw substantial increases in sea surface temperature in Southeast Greenland, south of Iceland, the Faroe area, the Faroe-Shetland channel, the Irminger Sea, West Greenland, and Newfound-Labrador (*25*, *34*, *38*, *40*, *41*, *46*–*52*) and, notably, in the Norwegian Sea, where

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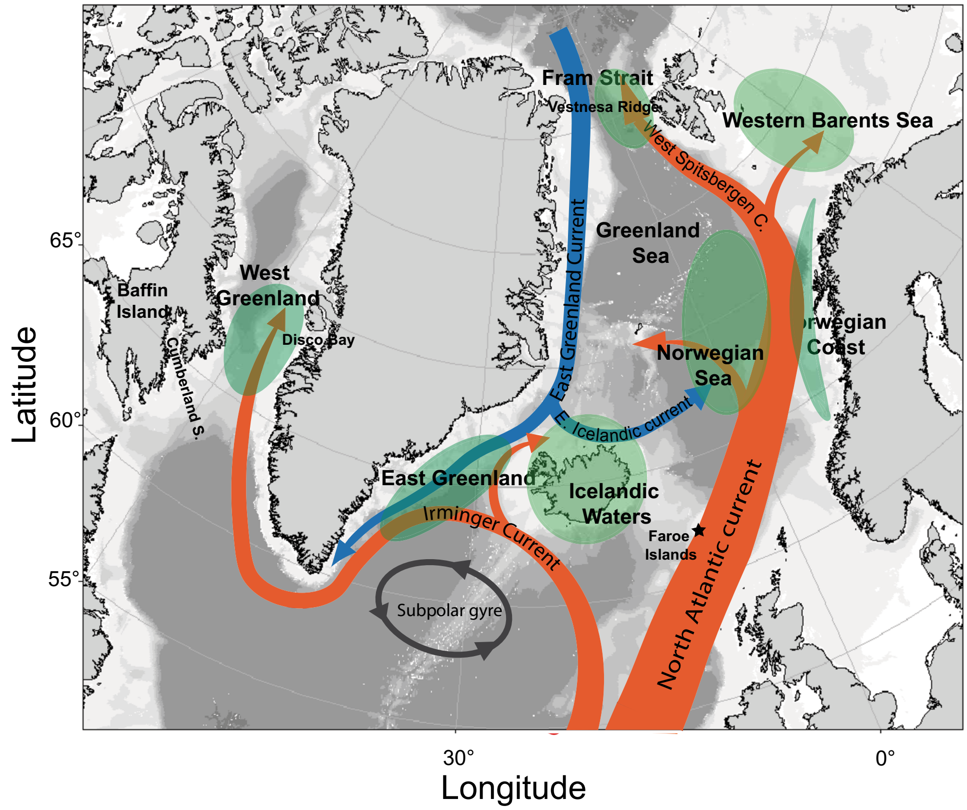

Fig. 1. Major currents in the North Atlantic. Case study areas highlighted in green.

rising temperatures could be observed from the sea surface down to depths of 700 m (*25*, *33*, *34*). Hence, 2003 stood out as the warmest year registered since the late 1950s and early 1960s in areas with available long observational records (*46*, *48*, *51*, *52*).

It is the first objective of this study to test whether this sudden and stark rise in oceanic temperatures classifies as an MHW. We collated 88 temperature time series with a minimum record length of 30 years (*7*), which, to our knowledge, are all freely available time series of this length (Fig. 2). These 88 time series represent a combination of point-based, annual, in situ observational records given roughly at 100-m water depth [https://ocean.ices.dk/core/iroc#; accessed October 2023 and (*48*)] and gridded sea surface temperatures using the HadISST database [downloaded from www.metoffice.gov.uk/hadobs/hadisst/data/download.html; accessed December 2023 (*53*)], averaged using the arithmetic mean in five time periods (January to March, April to June, July to September, October to December, and the complete year). HadISST is a monthly global field of sea surface temperature gridded on a 5° latitude by 5° longitude, starting in 1850 and extending to the present day. The data are adjusted for effects of changes in instrumentation throughout the years. Any of these records is longer than 60 years, with the ICES Report on Ocean Climate (IROC) Greenland-Fylla time series (blue point in "L" in Fig. 2) being the shortest one starting in 1963 (i.e., 61 years) and the two longest time series starting in 1947. The choice of the time series matched the areas, which were later reviewed for ecological changes. We used these time series to count the number of MHWs each year over all years. To identify heat waves in the obtained temperature records, we used a high-percentile threshold method (*7*). For this purpose, we defined a

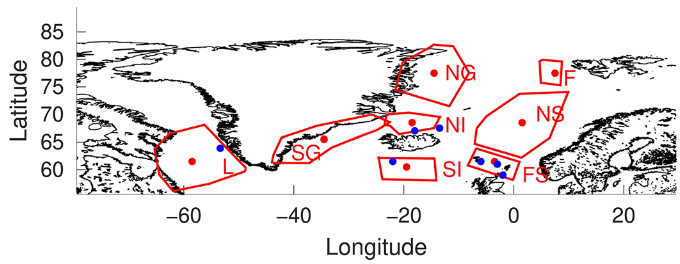

Fig. 2. Overview over subregions used to extract temperature time series and calculate heat wave frequency. Red polygons denote regions for calculating area averages, red dots show points used for punctual data extractions, and blue dots denote locations of observational records. L, Labrador Sea; SG, Southeast Greenland; NG, Northern Greenland Sea; F, Fram Strait; NI, North Iceland; SI, South Iceland; NS, Norwegian Sea; FS, Faroe-Shetland Ridge.

reference period of normal temperatures from 1870 to 1969, from which we calculated the 99th percentile. For the subsequent years, we associated a temperature value with a heat wave, if it exceeded this 99th percentile.

Whereas previous studies from the subpolar North Atlantic reported spatially and taxonomically isolated effects linked to environmental changes following the exceptional physical alterations in 2003, it is the second and main objective of this study to synthesize the ecological upheaval triggered by these environmental changes in its entire geographic and functional breadth. We aim to enhance our understanding of the mechanisms and consequences of physical disturbances by examining these changes, which is essential for predicting and mitigating future threats to marine biodiversity and ecosystem services. We compiled and reviewed information from peer-reviewed journal publications and fishery species stock assessment reports used as scientific advice for fishery managers and policy makers for this purpose (table S1). Data used for these scientific advice reports offer detailed numbers on age-specific abundance over time for a wide range of commercially exploited species. These were, in turn, used as data source for several of the peer-reviewed journal publications examined. Complementing information from peer-reviewed scientific publications with selected age- and life stage–dependent information for commercially exploited fishes and crustaceans allowed a more comprehensive overview of changes in ecosystems of the North Atlantic.

RESULTS

The events of 2003, which followed a preceding warm year 2002, signaled the beginning of a prolonged heating phase across numerous North Atlantic locations unlike any observed before (Fig. 3). Sudden rises in temperatures were classified as MHWs with an appearance of locally and regionally extreme temperatures. Although the year 2003 stands out as maximum, where most MHWs were counted, several years in the following period showed similarly high numbers. As it is reviewed in the following sections, the resulting ecological reorganization across these regions underscores the profound impact of extreme events on marine ecosystems.

Impacts of heat waves on regional marine ecosystems

The availability of data for different taxa and functional groups varied across regions, leading to disparities in the comprehensiveness of the ecological records. Certain areas are characterized by a wealth of information on low-trophic and noncommercial species, offering insights into foundational changes of the ecosystem (Fig. 4). Conversely, other regions have data predominantly focused on high-trophic, commercially exploited fish species, as well as charismatic megafauna, such as whales.

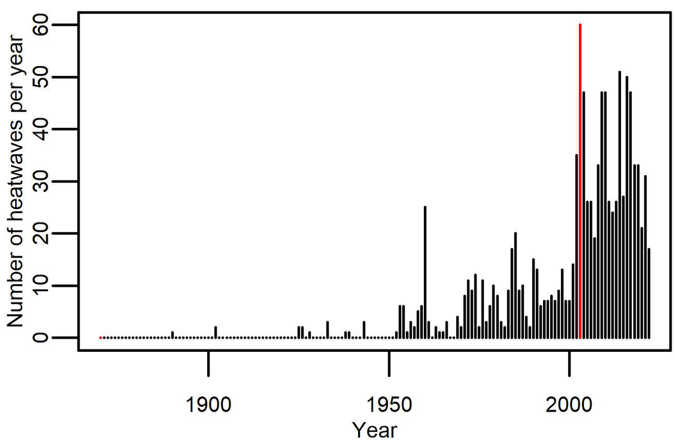

Fig. 3. Number of MHWs counted in each year. Number based on time series with a reference period from 1870 to 1969 for the time period 1870 to 2022 (*7*, *44*, *51*). A total of 88 time series were searched for heat waves in total. Year 2003 highlighted in red.

Low-trophic changes around Iceland and in the Norwegian Sea

The marine ecosystems surrounding Iceland and the Norwegian Sea are dynamic and represent important fishing grounds for many nations. Following the 2003 MHW, these areas have experienced notable shifts in low-trophic organisms, which comprise the foundation of marine food web and play crucial roles in nutrient cycling and energy transfer, thereby sustaining higher trophic levels. Three species of calanoid copepods are found in the Arctic and the subpolar North Atlantic: *Calanus finmarchicus*, associated with Atlantic waters, and *Calanus glacialis* and *Calanus hyperboreus*, both Arctic species (*54*). Arctic waters flow southward with the East Greenland Current until they blend with Atlantic waters north of the Iceland-Faroe Ridge and in the Norwegian Sea after further flowing with the East Icelandic Current (Fig. 1). As result, a continuous transport of *C. hyperboreus* and *C. finmarchicus* takes place southeastward from the Greenland Sea into the Norwegian Sea, where it becomes widely dispersed within the current systems (*55*–*57*). The reduced inflow of nutrient rich Arctic waters caused an abrupt "cutoff" in the flow of *C. hyperboreus* and *C. finmarchicus* in 2003 (*30*, *33*). Information from diet studies of Atlantic salmon (*Salmo salar*) suggest that the availability of other, energy-rich zooplankton, such as fish larvae and amphipods, also declined (*58*, *59*). These two factors might explain the sudden drop in overall zooplankton biomass observed in the Norwegian Sea after 2003 (*34*). Ultimately, the reduction of Arctic waters suggests that local ecological processes were curbed by changes in productivity (*31*, *32*). High temperatures and low zooplankton biomass led to an immediate decline in body growth and feeding conditions for Atlantic mackerel (*Scomber scombrus*), Scando-Atlantic herring (*Clupea harengus*), and Atlantic salmon (*34*, *58*–*61*). Because Atlantic salmon is an anadromous migrating fish, such a change in individual growth might affect estuarine and river ecosystems later. Scando-Atlantic herring expanded its feeding migration southwestward to Faroese and Icelandic waters and lower availability of zooplankton along drift routes of their larvae contributed to suppressed juvenile survival rates (*61*–*64*). The 2003 MHW was likely one of the initiating drivers of the sudden rise in abundance and expansion of Atlantic mackerel northward and westward in the first two decades of the 20th century and triggered the start of a borealization of groundfish communities along the Norwegian coast (*65*–*67*). The extent of this event, in both geographic and trophic range, made Hátún *et al.* (*68*) and Vollset *et al.* (*34*) hypothesize a regime shift in the Norwegian Sea.

Ecological cascades and changes in benthic-pelagic connectivity in the Fram Strait

After subtropical water enters the southern Norwegian Sea, it is transported northward with the North Atlantic Current, reaching the Barents Sea opening and the Fram Strait with a delay of ~1 to 3 years (*25*, *35*, *69*). Such an inflow of warm water occurred between 2004 and 2006 and led to an increase in chlorophyll a concentrations both in the Eastern and the Western Fram Strait (*70*, *71*). Initially dominated by large diatoms, the Eastern Fram Strait gradually transitioned to being predominantly populated by smaller flagellates and the haptophyte *Phaeocystis pouchetii*. This development became more pronounced following the warm-water anomaly, marking a notable ecological transformation in the region (*71*, *72*). Diet composition of zooplankton, which preyed upon all sizes of phytoplankton before the anomaly and mainly small phytoplankton during and after the anomaly, reflected this shift (*72*). Export of biogenic matter

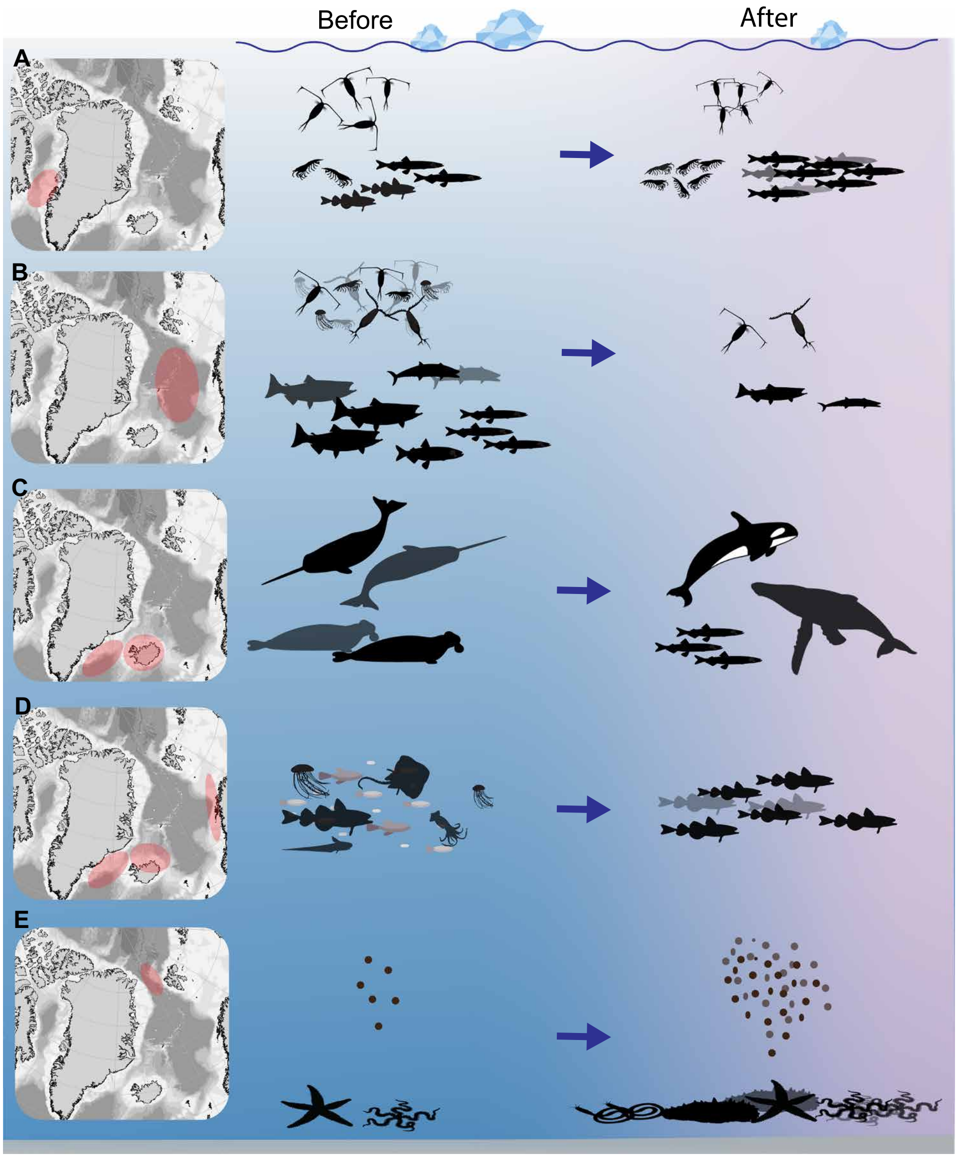

Fig. 4. Conceptual diagram of regional ecological reorganizations following the 2003 MHW. (**A**) Borealization of zooplankton, decline of polar cod, and increased densities of capelin and shrimp. (**B**) Drop in zooplankton densities, reduced growth, and redistribution of pelagic fish species. (**C**) Changes in the distribution of capelin and marine mammals. (**D**) Borealization of demersal fish communities and diversity loss. (**E**) Borealization of plankton, higher productivity, and increased benthic densities.

changed accordingly with a higher export of small zooplankton fecal pellets (*73*). The composition of pteropods, i.e., pelagic snails, changed from a dominance of the polar and subpolar species *Limacina helicina* to the boreal, warmer-water, Atlantic-adapted species *Limacina retroversa* (*74*, *75*). Increasing temperatures led to an increase in abundance of the copepod *C. finmarchicus* in the West Spitsbergen Current, while the cold-water, boreal-arctic copepod species *Triconia borealis* decreased (*76*, *77*). *Themisto compressa*, a pelagic amphipod, which has its center of distribution more toward the temperate Atlantic than the Arctic, appeared in the Fram Strait during the warm-water anomaly and has been a stable part of the local zooplankton diversity ever since (*75*, *78*).

Changes in the upper water column affected food availability and benthic density, biomass, and diversity at the seafloor from shelf regions to abyssal depths (*75*, *79*–*82*). Time-series data from the Long-Term Ecological Research Observatory HAUSGARTEN in the Fram Strait showed increasing concentrations in sediment-bound chloroplastic pigments, implying strongly increasing amounts of phytodetrital matter at the deep seafloor during the warm-water anomaly (*75*). However, there is evidence that the nutritional value of the organic matter reaching the seafloor and representing the major food source for benthic organisms is constantly decreasing over the period after the anomaly. This is confirmed by higher exoenzymatic activities of sediment-dwelling bacteria before the anomaly and overall decreasing densities of sediment-dwelling meiofauna organisms (*81*, *83*). Density and diversity of sediment-inhabiting nematodes, which represent the main meiofauna taxa in deep-sea sediments, peaked during and shortly after the warm-water anomaly, likely due to a quantitative increase in organic matter reaching the seafloor, which implies close benthic-pelagic coupling (*81*). A closer inspection of the nematode community revealed a change in dominant feeding type from epistrate and selective deposit feeders before the temperature anomaly to nonselective feeders following the warm-water inflow (*84*, *85*), which could be an ecological consequence of the changes higher up in the water column. The increase in primary production and benthic food availability also led to an increase in macrofauna density, species richness, and functional diversity along a bathymetric transect from 203- to 5561-m water depth off the Svalbard archipelago (*79*). Benthic megafauna on the Vestnesa Ridge (1280-m water depth) showed a similar trend with a strong increase in densities of the most common species, i.e., the brittle star *Ophiocten gracilis* and an unspecified sabellid polychaete. Different communities were found for deeper sites in the eastern Fram Strait (2500-m water depth) before and after the warm-water anomaly. For example, initially absent from a site in the northeastern Fram Strait, densities of the larger holothurian *Kolga hyalina* peaked in 2007 and subsequently declined until 2015 (*82*). Overall, these observations revealed a faster reaction in the smaller compared to the larger benthic organisms to changes under environmental conditions and food availability and confirmed a time lag of 0.5 to 1 year, as previously proposed for macro- and megafauna (*86*, *87*).

Impacts on intermediate and high trophic level species around Iceland and in Southeast Greenland

Information about low-trophic species is considerably scarcer for the Irminger Sea and East Greenland waters than for the Fram Strait, while data availability for fishes is richer, especially for commercial species. Chlorophyll a production exhibited a prominent peak in Southeast Greenland and the northwestern Irminger Sea in 2003, followed by another peak southwest of Iceland in 2004 (*48*). Notably, this peak was not observed in southern Icelandic shelf areas potentially explaining record-low krill abundance in 2003 (*48*, *49*). One of the ecologically most important shifts pertained to the sudden change in the distribution and abundance of capelin (*Mallotus villosus*), a vital forage fish for species such as Atlantic cod (*Gadus morhua*), humpback whale (*Megaptera novaeangliae*), and common minke whale (*Balaenoptera acutorostrata*) (*41*, *49*, *88*–*91*). Capelin larvae suddenly started drifting several 100 km further westward to South-East Greenland shelf waters in 2003, coinciding with a sudden decline of capelin fishery catches beginning with the year class of 2003 (*41*, *91*, *92*). One hypothesized driver of this shift is the warming-driven northward shift in spawning locations along the south and west coasts of Iceland, which altered larval drift patterns causing unfavorable conditions for early life stages (*91*, *93*). During the same time, adult capelin started migrating further northward and westward toward the East Greenland coast for feeding (*41*, *91*, *92*).

Commercial fishing fleets in Iceland adjusted their operations to follow the shift in spawning location, which emphasizes how MHWs might extend their impact beyond a purely biological one (*93*, *94*). Observations from the Pacific previously demonstrated how these redistributions as response to MHW can pose unexpected management challenges and increase bycatches of endangered species (*95*, *96*). The shift in distribution of capelin toward East Greenland shelf waters has not reversed (*41*, *97*, *98*). Large numbers of baleen whale species, such as fin whales (*Balaenoptera physalus*) and Humpback whales (*M. novaeangliae*), recorded seldomly over the past 150 years and only during summer ice-free coastal waters, were detected in 2015 in East Greenland waters as likely response to the sudden reduction in sea ice, rise in water temperature, and the shift in capelin distribution (*41*, *99*). Killer whale (*Orcinus orca*) sightings rose steadily beginning in 2003 after being nearly absent for more than 50 years (*41*). Conversely, catches of ice-dependent, cold water–adapted narwhals (*Monodon monoceros*) and hooded seals (*Cystophora cristata*) southeast of Greenland either significantly declined after 2004 or experienced a considerable decrease in the mid-2000s (*41*).

The year 2003 also marked the turning point in composition of fish and invertebrate communities in northern Icelandic fjord areas (*100*). Here, demersal fish communities dominated by boreal, predatory fish species, such as Atlantic cod and haddock (*Melanogrammus aeglefinus*), increased in abundance, while bottom dwelling species such as small eelpouts, blennies, and flatfish decreased in abundance, indicating that environmentally driven changes in distribution interacted with top-down regulated changes in the food web (*100*). Juvenile survival of haddock reached the highest value recorded across a 45-year span in 2003, suggesting unusually favorable conditions for early life stages, which caused commercial fishery catches to increase subsequently (*101*, *102*). High haddock densities following the 2003 cohort likely caused a reduction under body condition (*102*). Although data are not as detailed for all fish species as for haddock, biomass estimates indicate a rise of other boreal species, such as ling (*Molva molva*) or tusk (*Brosme brosme*) following the 2003 temperature anomaly in Icelandic waters (*103*, *104*). This development might have also been enhanced by a reduction in commercial fishery catches of these species in the early 2000s (*103*).

These borealization trends coincided with a sudden disappearance of sandeel (*Ammodytes* sp.) as crucial prey item for haddock in 2003 and a subsequent decline in minke whale stomachs starting in 2004 (*49*, *105*). Compared to a sampling period in the late 1970s and 1980s, there was an increase in minke whales' consumption of boreal species, such as Atlantic herring and Atlantic cod, coupled with a reduced dependence on cold-water species, such as capelin or krill after 2003 (*105*). These observations match patterns from eastern Greenland waters, where haddock as typical boreal species responds positively to rising temperatures and a weak subpolar gyre (*106*). Here, high abundance of juvenile haddock following the 2003 cohort mirrored trends seen in other boreal species, such as blue whiting (*Micromesistius poutassou*), tusk, or greater argentine (*Argentina silus*), which rose in abundance after 2003 and remained persistent parts of the ecosystem thereafter (*104*, *106*–*108*). Atlantic cod is a boreal species known to thrive in Greenland waters when temperatures rise (*109*–*111*). The species also demonstrated a remarkable surge for the 2003 cohort in East Greenland potentially related to higher abundances of zooplankton during warm periods, which led to a reestablishment of the commercial cod fishery in subsequent years (*109*, *112*–*115*). Cod exhibited also elevated recruitment in Icelandic waters in 2003, although not reaching historically peak values due to reduced recruitment following a sudden regime shift in the late 1980s (*116*). At the community level, fishes experienced a significant shift in composition moving from a blend of Arctic and Boreal-Arctic species to predominantly boreal species between 2000 and 2016 (*40*, *106*). The influence of Atlantic waters and the expansion of warmer waters onto slope and shelf areas prompted a swift redistribution of fish species, extending down to water depths of 900 m in 2003 (*40*, *106*).

Implications for West Greenland and the Canadian Arctic

Located at the edge of the subpolar gyre and the far reach of the North Atlantic current, western Greenland waters and the Canadian

Arctic showed less pronounced physical impacts from the 2003 MHW. Ecological information from these areas is limited. Still, there are indications of a range expansion of boreal and boreal-arctic species northward along with a retreat of Arctic species following the 2003 event. The zooplankton community in Disko Bay transitioned from a dominance of *C. glacialis* and *C. hyperboreus* to *C. finmarchicus* as response to a retreat of sea ice and a stronger inflow of Atlantic water between 2001 and 2005 (*117*). The composition of krill changed from a dominance of *Thyssanoessa inermis* to *Meganyctiphanes norvegica* between the 1990s and 2010 based on the diet of Thick-billed Murres (*Uria lomvia*), a bird wintering in shelf regions off southwest Greenland (*118*). Although available data do not allow for a direct connection to the extreme 2003 event, the information fits the trends of a borealization of West Greenland ecosystems (*117*, *118*). Biomass of Northern shrimp (*Pandalus borealis*), which serves as important prey species for higher trophic level species, such as Atlantic cod, redfish (*Sebastes* spp.), and Greenland halibut (*Reinhardtius hippoglossoides*), displayed a sudden, steep increase in west Greenland waters in 2003 with levels remaining higher in the years after compared to before 2003 (*119*–*121*). However, rising shrimp biomass in 2003 also benefitted from strong recruitment in the preceding years (*122*). The concentration of harvestable shrimp biomass and primary fishing grounds for Northern shrimp shifted northward after 2003, suggesting adaptation to newly favorable habitats toward higher latitudes aligning with observations that a moderate increase in temperature within the lower end of the tolerance range supported stock growth (*119*, *122*).

The distribution and abundance of forage fish species has not been systematically studied in western Greenland waters and the Canadian Arctic. However, anecdotal information from local residents, commercial fishery bycatches, and diet information from higher-trophic species indicate that capelin abundance around eastern Baffin Island and Cumberland Sound increased in the early 2000s, especially around 2003 and 2004 (*44*, *92*, *123*). This implies a northward range expansion induced by water warming in this colder environment. Strong signals, such as from dietary fatty acids in beluga whales (*Delphinapterus leucas*), exist, indicating that the abundance of the Arctic, ice-associated, and historically important forage fish species in the region, polar cod (*Boreogadus saida*), decreased during the same period (*44*, *92*, *123*). These ecological changes led to ecological restructuring toward a more trophically redundant predator assemblage, which is characterized by a change in the diet spectrum toward a more pelagic energy pathway in beluga whales, Greenland halibut, Arctic char (*Salvelinus alpinus*), and ringed seals (*Pusa hispida*) between 2001 and 2005 (*44*, *123*). In offshore areas of West Greenland and the Canadian Arctic, survival of juvenile Greenland halibut abruptly rose in 2003 and remained at higher levels (*124*).

DISCUSSION

This work documents widespread ecological reorganization across multiple trophic levels following a strong increase in the frequency of MHWs in 2003. The evidence reviewed suggests that many of the observed ecosystem changes are consistent with the characteristics of regime shifts, yet it also raises the question, why the ecological implications of the anomalously warm year 2003 seem to differ markedly from those observed during later periods with similarly frequent MHWs.

The complete picture behind the physical drivers of the 2003 MHW is complex and not yet fully understood. Although the weakened subpolar gyre might have altered the distribution and volume of Atlantic and Arctic waters in the Nordic Seas, a recent study raised the question of whether the strength of the subpolar gyre is a consequence of these changes, through alterations in ocean heat content, rather than their cause, as previously hypothesized (*125*). The appearance of an atmospheric heat wave combined with a weak subpolar gyre and a retraction of Arctic water masses northward hints at a complex interaction of mechanisms. This complex causation mirrors previous findings, indicating that large-scale MHWs can develop through a combination of multiple, interacting mechanisms (*7*). While the subpolar gyre was weak in 2003, it became even weaker in subsequent years (*125*, *126*). These are conditions, which, in theory, should have allowed for an even larger amount of warm, subtropical waters to enter the North Atlantic, but the number of MHWs did not increase. Our results contribute to this discussion because they indicate that the subpolar gyre is not alone responsible for the frequency of MHWs, while heat exchange between ocean and atmosphere might play a more important role.

Our study examines both the immediate and delayed effects of the extreme event in 2003. Nevertheless, it cannot be ruled out that the prolonged period of locally and regionally elevated temperatures helped sustain and reinforce the ecological reorganization following the 2003 MHW. This interpretation aligns with previous investigations, showing that repeated extreme events can limit ecosystem recoveries leading to persistently altered states compared to single disturbances (*11*, *127*). Although the ecological impacts of the 2003 event are well documented, there is less clear evidence for comparable impacts in subsequent years with similarly high MHW frequency. This supports the notion that MHWs of similar intensity can differ markedly in their ecological consequences (*19*). Similar patterns were observed in the Barents Sea, where successive strong MHWs had different effects on the same ecological parameters (*19*). This suggests that ecosystem responses may change in both magnitude and direction after an initial, strong heat wave, consistent with observations that MHWs of similar strengths can have highly divergent ecological effects (*20*). This variability may help explain their limited predictability and detectability during subsequent events.

Evidence from other oceanic regions reinforces this interpretation and has shown that repeated or successive MHWs can produce cumulative, variable, and context-dependent effects on marine organisms (*128*–*130*). In a rocky intertidal community in southeastern Hokkaido, Japan, repeated heat waves caused cumulative carryover effects in resident organisms (*128*). Similarly, initial thermal stress and successive warming events affected hard and soft corals differently in coral reef ecosystems of the central Indian ocean (*130*), whereas reef fish around the Canary Islands displayed variable distributional shifts in response to several successive MHWs over a 5-year time period (*129*). Collectively, these observations highlight that recurrent MHWs can generate complex, multidirectional, and, sometimes, obscured ecological responses, suggesting that the repeated heat waves following 2003 may have produced additional yet undetected ecological implications potentially interacting with other stressors.

Our findings indicate that MHWs affect life stages in distinct ways: They can trigger immediate impacts, such as one-time changes in the survival of early life stages, or lead to broader shifts, such as regime shift–like changes or redistribution of adults to more favorable habitats. The appearance of changes in adult populations following changes in mortality rates in the early life stages is contingent upon species-specific factors such as growth rates, maturation, and other life-cycle characteristics, as detailed in (*104*). This might help explain why MHWs do not always lead to immediate and comprehensive changes in metrics such as the biomass of groundfish communities (*20*), as the effects may only become apparent years later, once affected cohorts reach maturity. However, most of the published age-specific information about distribution and abundance pertains to commercially exploited fish species. Thus, it remains unclear whether these observations can be transferred to other organisms. Our study underscores the necessity for both a species-specific approach and community approach to accurately discerning the ramifications of physical extreme events on marine biodiversity, echoing the insights of Smith *et al.* (*11*) and Welch *et al.* (*10*) regarding the unequal susceptibility of species to these events.

We found that the impacts of the MHW are pronounced in the core regions, but discerning its impact becomes more challenging in peripheral areas of the subpolar gyre, such as the Canadian Arctic and the Barents Sea and the Faroe Islands, where impacts of the MHW have also not gone unnoticed (*27*, *68*, *131*). This challenge arises from limited data and the complexity of existing information. Decadal shifts in sea ice concentration, primary production, and dynamics in the Barents Sea stock of Atlantic cod have been correlated with fluctuations in the subpolar gyre (*27*, *132*, *133*). However, the mechanisms linking trends in the subpolar gyre with the volume of Atlantic water are not yet fully understood, despite well-documented impacts of rising water temperatures and ecosystem borealization (*131*).

Despite the varying degrees of data availability across trophic levels and regions, insights from well-studied lower trophic organisms, such as in the Fram Strait, suggest that similar transformations may have gone unnoticed in less monitored areas. These overlooked changes are likely connected to alterations observed at higher levels of the food chain in those regions. For example, observations linking changes in deep benthic biodiversity to changes in upper parts of the water column offer only a vague notion of what may have occurred in regions lacking systematic monitoring of both pelagic, low-trophic processes and benthic communities. The current lack of ecological understanding in much of the subpolar North Atlantic is largely the consequence of limitations in monitoring of species abundances and trophic relationships. Strengthening ecological monitoring is essential not only for understanding and predicting the impacts of MHW and climate change (*11*) but also for enabling informed human responses. As societies seek to adapt to a warming ocean, sustained and expanded monitoring is critical for the sustainable management of natural resources and the protection of vulnerable ecosystems.

Our results further emphasize the critical role of connectivity and advection between regions that are often administratively separated by national borders (*134*). Regional changes in biodiversity may be driven by advection and site-specific processes and frequently result from a combination of both. Such an interplay highlights the necessity for focused studies at the juncture of spatial ecology, trophic ecology, and ecophysiology to unravel the complexities of climate-driven ecological transformations.

Understanding and quantifying the relative contributions of shifts in the distributions of water masses, the strength of the subpolar gyre and air-sea heat exchange to local and regional abiotic conditions is necessary to understand the impacts of MHWs on marine ecosystems in the North Atlantic. While this review documents widespread ecological effects of a large-scale MHW, it remains unclear why MHWs of comparable strength did not produce similar abrupt changes. Our findings suggest not only that even larger temperature anomalies may be required to trigger further ecosystem restructuring but also that changes following successive warming events after 2003 might have not been noticed yet. These observations emphasize the potential for tipping points in marine systems and highlight the need to characterize ecosystems before and after these changes take place.

Supplementary Materials

This PDF file includes:

Table S1

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