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A regime shift in the Southeast Greenland marine ecosystem

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Abstract

Two major oceanographic changes have recently propagated through several trophic levels in coastal areas of Southeast Greenland (SEG). Firstly, the amount of drift-ice exported from the Fram Strait and transported with the East Greenland Current (EGC) has decreased significantly over the past two decades, and a main tipping element (summer sea ice) has virtually disappeared since 2003 leading to a regime shift in oceanographic and ecological conditions in the region. The following 20-year period with low or no coastal sea ice is unique in the 200-year history of ice observations in the region, and the regime shift is also obvious in the volume of ice export through the Fram Strait after 2013. In the same period, the temperature of the EGC south of 73.5 N has increased significantly (>2°C) since 1980. Secondly, the warm Irminger Current, which advects warm, saline Atlantic Water into the region, has become warmer since 1990. The lack of pack ice in summer together with a warming ocean generated cascading effects on the ecosystem in SEG that are manifested in a changed fish fauna with an influx of boreal species in the south and the subarctic capelin further north. At higher trophic levels there has been an increase in the abundance of several boreal cetaceans (humpback, fin, killer, and pilot whales and dolphins) that are either new to this area or occur in historically large numbers. It is estimated that the new cetacean species in SEG are responsible for an annual predation level of 700,000 tons of fish. In addition, predation on krill species is estimated at >1,500,000 tons mainly consumed by fin whales. Simultaneously, there has been a reduction in the abundance and catches of narwhals and walruses in SEG and it is suggested that these species have been impacted by the habitat changes.

KEYWORDS

biodiversity, habitat changes, ice volume export, marine mammals, ocean warming, predation estimates, teleconnection, tipping element, tipping point

Gísli Víkingsson-deceased.

1 | INTRODUCTION

Climate change is affecting the distributions and productivities of species, the interactions among species, and the flows of energy through food webs (IPCC, 2019). Many of these effects have been occurring gradually and/or in proportion to the velocity of climate change. For example, changes in distributions of fish species around North American coasts are strongly linearly correlated with a thermal climate velocity index (Pinsky et al., 2013), and commercial fish catches in regional seas also follow linear changes with local temperatures (Cheung et al., 2013). However, changes in species distributions, biodiversity, food web dynamics, and ecosystem functioning can also occur more abruptly in a nonlinear manner. When characteristics of a system (i.e., tipping elements; Lenton et al., 2008) pass beyond critical thresholds (i.e., tipping points; Wassmann & Lenton, 2012), the system transitions into a new regime. In the Arctic, tipping elements that are driving changes in marine ecosystems are typically sea ice, sea temperatures and currents (IPCC, 2019). Tipping points are reached when tipping elements exhibit changes that cause abrupt nonlinear changes in the ecosystem leading to "substantial widespread Earth system impacts" (Armstrong McKay et al., 2022). Ecological regime shifts are sudden, and sometimes irreversible, changes in ecosystems that are clearly detectable. They are sometimes driven by underlying environmental conditions, for example, changes in climate systems (Grebmeier et al., 2006) but may also result from anthropogenic perturbations, such as fishing/hunting, eutrophication, or introduction of species (e.g., Biggs et al., 2009). The new regime will, therefore, have new ecosystem and biodiversity properties substantially different from the pre-tipping point regime.

Examples of the nonlinear systems, or tipping point elements, vulnerable to climate change-related tipping point dynamics include the deep-water formation and the Atlantic Meridional Ocean Circulation, coral reefs whose survival, structure and functioning are subject to the effects of acidification and temperature changes, and Arctic sea ice melt and ecosystem functioning (IPCC, 2022). Crossing of the tipping point of these tipping elements represents major changes in biodiversity, ecosystem functioning and the provision of ecosystem goods and services to humanity and such changes would occur at rates faster than those in the linear dynamic systems associated with recent climate change velocity estimates.

Here we hypothesize that the large-scale marine ecosystem adjacent to southeast Greenland (hereafter referred to as SEG, see Figure S1) has already crossed such a tipping point in the past 1–2 decades and has entered a new regime. We investigated changes in the climate, physical oceanography, megafauna community (marine mammals and some key fish species in the food web) and some trophic interactions in the southeast Greenland coastal and shelf ecosystem since the early 2000s and compared them with historical data. Hydrographically, the coastal and shelf area of SEG has usually been covered by dense masses of multi-year drifting pack ice originating from the Arctic Ocean and transported southward by the East Greenland Current (EGC) through the Fram Strait along the coast of East Greenland (Figure 1; Schmith & Hansen, 2003). Because of the regular and seasonally extensive ice cover in the region, the marine mammal community includes several ice-dependent species tolerant of cold temperatures; these include narwhals (*Monodon monoceros*), walruses (*Odobenus rosmarus*), hooded (*Cystophora cristata*) and ringed seals (*Pusa hispida*). The fish community has been mainly composed of demersal, bathypelagic, mesopelagic and ice-adapted species (e.g., Greenland halibut (*Reinhardtius hippoglossoides*), redfish (*Sebastes* sp.), polar cod (*Boreogadus saida*); Astthorsson, 2016; Møller et al., 2010) typical of boreal-polar ecosystems (van Denderen et al., 2018).

The massive barrier of drift-ice has for centuries precluded exploration of the East Greenland coast and contact with the small and scattered groups of Inuit that inhabited the coast. The east coast of Greenland was rarely or never visited by whalers that were pursuing bowhead whales (*Balaena mysticetus*) in off-shelf waters of East Greenland, with the exception of Scoresby (1823), because drifting coastal pack-ice prevented the entry of whalers to the shore. Exploitation has been low also because the region was, and still is, sparsely populated by humans. In the 19th century, the only inhabited area of East Greenland was the Tasiilaq area (latitude ca. 65.50 N) that had 413 inhabitants in 1884–1885 (Holm & Petersen, 1921). Regular contact of the local society with non-indigenous humans (e.g., from Denmark) was only established in 1894, before which there is little written quantitative information about marine life in the area.

In general, the combination of low temperatures and extensive sea ice has provided habitat for a cold- and ice-adapted community of megafauna in the region. These climate-ocean conditions are changing, generating cascading effects on distribution and abundance of several top predator and megafauna species. We further estimate some of the trophic consequences and implications of these changes for prey species in the ecosystem. Our findings demonstrate that the tipping element has shown increasingly rare or disappearance of coastal drift-ice since the early 2000s. The disappearance of the drift-ice may represent a regime transition across a tipping point (sensu IPCC, 2022) with cascading consequences for the local ecosystem including a shift in biodiversity and ecosystem functioning. The changes seen in SEG could, therefore, be a forerunner of ecological events expected if another, and larger, tipping element, summer Arctic Ocean ice (IPCC, 2019, 2022) disappears in future decades.

2 | MATERIALS AND METHODS

2.1 | General oceanographic context in Southeast Greenland coastal and shelf-seas

Oceanographic conditions in SEG are dominated by the cold (<0°C) and low salinity (<34.2 psu) EGC (Figure 1a) that transports water masses from the polar basin, together with drifting multiyear sea ice and runoff from glaciers, south along the East Greenland coast

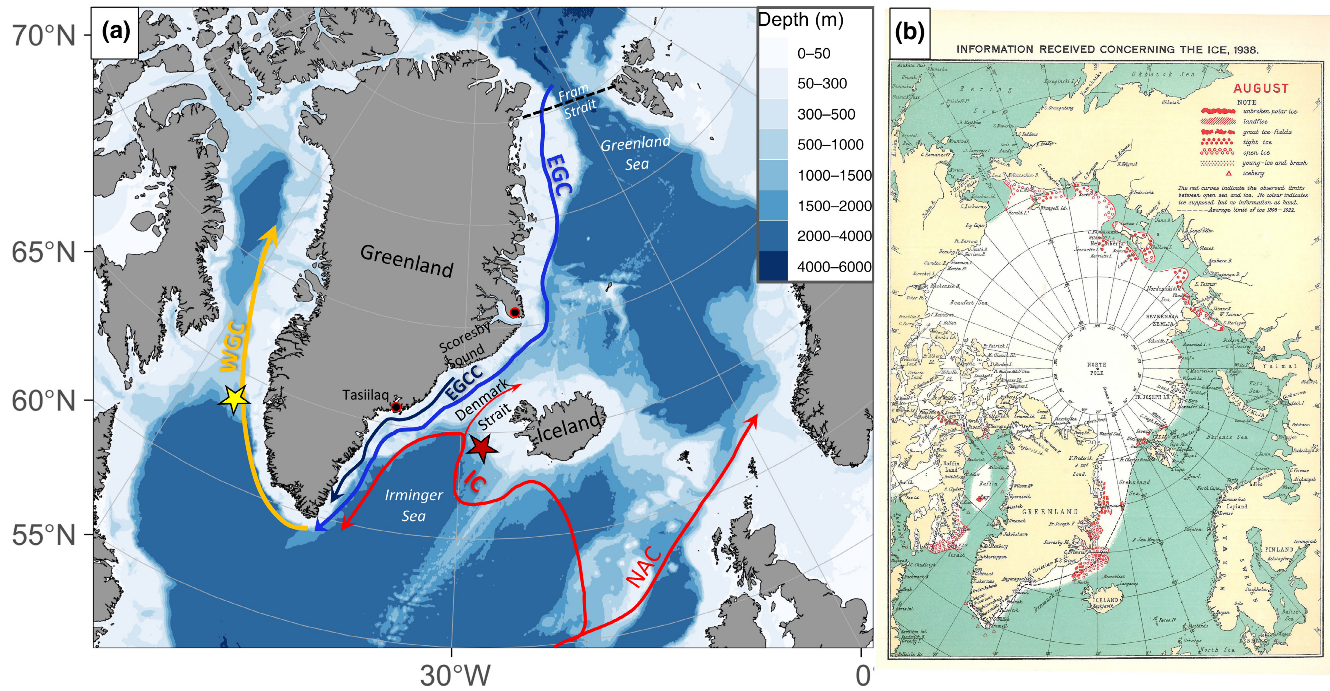

FIGURE 1 (a) Map of the study area with major currents indicated. EGC = East Greenland Current, EGCC = East Greenland Coastal Current, IC = Irminger Current, NAC = North Atlantic Current, WGC = West Greenland Current. The red star indicates the position of the Faxaflói 9 station, and the yellow star indicates the position of the Fylla Bank station. (b) Extent of sea ice in the North Atlantic in August 1938 during a warm period (DMI, 1939). Note the continuous belt of ice along East Greenland that reaches up along the southern coast of West Greenland (the so-called "Storis").

(Håvik, Pickart, et al., 2017; Håvik, Våge, et al., 2017; Koch, 1945; Sutherland & Pickart, 2008). The water masses in SEG are mixed at depths with warmer and saltier water from the Irminger Current (IC), a side branch of the warm North Atlantic current. A colder and even less saline East Greenland Coastal Current flows southward from ~68°N close to the coast (<15 km from land).

The width of the SEG shelf varies from 50 to 100 km and it has deep troughs that intersect the banks (depth 100–200 m). The overall hydrographic conditions on the shelf include a layer with warm water (3.5–4°C) from the IC at depths below 200 m and a layer of cold water of polar origin above. In summer and fall, the sea surface temperatures (SSTs) of the IC just outside Sermilik can reach 8–11°C (Sutherland et al., 2013).

2.2 | Sea ice data

"Storis" is the Danish expression for the dense concentration of drift-ice older than 1 year, that is transported from the Arctic Ocean around Cape Farewell to Southwest Greenland by the EGC. The seasonal strength of the Storis concentration was indexed by Valeur (1976) and defined as the northernmost position on the southwest coast of Greenland that the Storis, reaches in a given month. A time series covering 1820–1994 was described in Fabricius et al. (1995) and Schmith and Hansen (2003), and updated through 2021 by Andresen et al. (2012) and Rosing-Asvid (2006), and Greenland Institute of Natural Resources. Following Schmith and Hansen (2005) a Storis Index (SI) was developed by standardization:

$$SI_j = \text{mean}\left[\frac{(M_{\text{June},i} - \bar{x}_j)}{SD_j}; \frac{(M_{\text{July},i} - \bar{x}_j)}{SD_j}; \frac{(M_{\text{August},i} - \bar{x}_j)}{SD_j}\right]$$

where M is the observation in each of 3 months (June, July, and August) for each year (i), $\bar{x}$ is the monthly (j) mean for the entire period 1900–2021 and SD is the monthly standard deviation for the period 1900–2021.

Monthly data during 1979 to 2019 of ice area (km^2) and volume export (km^3) along the cross-section (78.875 N, 20.125 W–13.625 E, Figure 1) of the Fram Strait were obtained as model output from the MITgcm-ECCO2 with the JRA-25 atmospheric data reanalysis as the model forcing (see Wei et al., 2019). Annual standardized means of ice and volume across all months were calculated as specified above.

2.3 | Oceanographic data

To predict the combined influence from warm Atlantic water and cold water of polar origin on the SEG continental shelf, a Shelf Index has been derived. This index weighs the two water masses equally and uses SST measurements from the south of Iceland as a proxy for Atlantic Water variability, and the Storis Index as a proxy for polar water variability (see Andresen et al., 2012, Appendix S1).

No time series of in situ records of oceanographic conditions exist from SEG. Instead, we use proxies from neighboring stations for evaluating trends. In the Irminger Sea, a time series of temperature and salinity averaged over 0–200 m was derived from the hydrographic observations of MFRI-Iceland from stations in Faxaflói for the period 1971–2021. The observations are from the station FX9 (64.2° N 27.95° W, Figure 1) for the period 1983–2021, but the earlier data are from station RE8 (64.0° N 27.25° W) 29 miles to the southeast of FX9, also within the core of the Irminger Current (Ólafsdóttir et al., 2020). Data consist of interpolated bottle data before 1990, but full-resolution CTD profiles thereafter. Annual and seasonal (winter from January to March, summer from July to September) mean temperatures and salinities were estimated. In West Greenland, sea temperatures at depths between 0 and 40 m taken at a standard station (Fylla Bank 2: 63.97 N–52.73 W) in June/July were updated for the period 1950–2020 (updated from Ribergaard (2014) using annual NAFO SCR reports by J. Mortensen). The measurements for Fylla Bank, corrected for annual variation to get the mid-June temperature, were used as a time series in the analysis.

Between 1993 and 2020, average of SST, sea ice concentration (SIC), and mixed layer depth (MLD) in the coastal area of SEG (see Figure S1) were extracted monthly in August from the products *Global Ocean Physics Reanalysis Glorys12v1* (1993–2016) and *Global Ocean and Physics Analysis Forecast* (2016–2021) at a 1/12° spatial resolution (https://marine.copernicus.eu/). Between 1980 and 2020, surface and at-depth averaged temperatures were extracted from the ORAS5 global ocean reanalysis constrained by observational data (https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-oras5?tab=overview) for the period 1990–2020 for the following:

(a) Two sections (10–100 km offshore) along Northeast Greenland between 69 and 73.5 N and between 73.4 and 81 N averaged over 0-20 m water depth in August.

(b) Five sections of SST values along East Greenland in August (see Figure S1).

(c) Depth averaged (0–200 m) values at the location of the Flaxaflói station 9 in July–September.

The index of the North Atlantic Oscillation (NAO) after 1900 was obtained from the Climate Analysis Section, NCAR (Hurrell et al., 2003).

2.4 | Marine mammal data

Abundance estimates of cetaceans from the coastal area of SEG are only available from 2015 (Hansen et al., 2018). A previous survey in 1988 failed due to ice and inclement weather conditions. The survey in 2015 represents the recent situation. To extend the time series of marine mammal presence back in time catch histories were used to infer the presence in earlier years. Officially reported catches of marine mammals were obtained from the Greenland Institute of Natural Resources and the North Atlantic Marine Mammal Commission for the period after 1970. Catch data provide a representative view of the availability of exploited animals, if the hunting or fishing effort has not changed substantially over time. There is no evidence that hunting effort has declined or become more focused on small cetaceans in the last 30–40 years. Marine mammal hunting in SEG is conducted opportunistically by local people in search of species for local consumption (Flora et al., 2019). Species were, therefore, caught as they became available to hunters. Except for minke whales, walrus and narwhal, there has been no catch regulations and catches were unrestricted by management actions, or catches were below the quotas, suggesting that catches were limited by ecological and population-related processes, rather than hunting effort. We consider, therefore, that the catches are a valid indicator of major (i.e., biogeographic) changes occurring in the ecosystem and its biodiversity.

2.5 | Fish data

We evaluated changes in distribution and abundance of three pelagic species whose life histories make them particularly sensitive to ecosystem changes and which have key roles as predators and prey in regional food webs. Two of these are primarily zooplanktivores, that is, mackerel (*Scomber scombrus*) and capelin (*Mallotus villosus*), and one species is mainly piscivore (bluefin tuna, *Thunnus thynnus*). All three species migrate long distances for feeding and spawning during their lifetimes. Mackerel and capelin, as intermediate-sized species in food webs, are considered major prey species for higher trophic levels, including many of the marine mammals considered here (Carscadden et al., 2013; ICES, 2021). They can be very abundant and drive population dynamics and distributions of their predators. Bluefin tuna is a direct predator of mackerel in the northern parts of its range, including the North Sea and Norwegian Sea and is believed to have evolved its highly migratory foraging behavior to northern areas to feed on this and other similarly sized, lipid-rich fish species such as herring (*Clupea harengus*) (Cury et al., 1998).

We compiled abundance indices for these species from surveys (mackerel, capelin) conducted by the Greenland Institute of Natural Resources and the Icelandic Marine and Freshwater Research Institute and from commercial catch (mackerel, capelin) and bycatch data (bluefin tuna) reported to national authorities.

2.6 | Predation estimate

Predation was estimated for the seven marine mammals that occur in the coastal areas of SEG. Abundance estimates with confidence limits were obtained from Hansen et al. (2018), mean mass of the predators and their prey preference was obtained from Sigurjónsson and Víkingsson (1997), the daily food ingestion rate was assumed to vary between 2 and 4% of the mean body mass (Skern-Mauritzen et al., 2022; Trites & Spitz, 2018), and the residence time in SEG was assumed to be 180 days except for the two migratory seal species (harp seal *Pagophilus groenlandicus* and hooded seal) where the residence time was assumed to be 90 days (Andersen et al., 2009; Stenson et al., 2020). SEG is a feeding area for marine mammals during summer and it was assumed that they were feeding constantly during their residence on the East Greenland shelf. Total predation level by each species was estimated by resampling (1000x) the lognormal distribution of the abundance estimates and multiplying this with the average mass of the animals and the predation rate resampled from a uniform distribution of 2%–4% of body mass.

Loess (local estimated scatterplot) plots were used for smoothing the time series in *ggplot2* (R Core team, 2020). Linear regressions were used for the time series after 1989. A sequential regime test analysis (Rodionov & Overland, 2005) was applied to detect differences in regimes for the time series of the Storis Index and for both ice volume and ice area ice export through the Fram Strait. We checked for the presence of regimes having different means in the time series. Regime test analyses were performed using cutoff length of 8 years, Hubert tuning parameter of 2 and probability level of .05.

3 | RESULTS

3.1 | Physical changes

Ice charts compiled from vessels navigating the North Atlantic in the 1930s have documented a sea ice extent along East Greenland different from modern conditions (Figure 1b). During a warm period in the 1930s, multiyear polar ice exported from the Fram Strait dominated the coastal waters all along East Greenland. The latitudinal dispersal of drift-ice along West Greenland is used in the Storis index as a measure of the strength of the transport of drift-ice along East Greenland (Figure 2a).

A regime shift of Storis index was detected at a high statistical significance level ($p<.0001$), showing a transition to a new regime with low-ice years after 2003. The decline was initially accompanied with occasional high-ice years during the 1980s–90s, but the frequency of these high-ice events has become rarer in later decades. After 2000 sea ice has virtually disappeared from the SEG shelf area (Figure 2b,c). Accordingly, the probability of occurrence of a relatively high Storis index year (i.e., corresponding to one in the upper 25th percentile of the frequency distribution of all Storis index observations from 1900 to 2021, equivalent to a Storis index ≥0.8) significantly decreased from 40% during the previous regime (1900–2002) to 0% during the new regime (2003–2021; Chi-square = 7.6, $p<.01$, df = 1). In contrast, the probability of occurrence of a relatively low Storis index year (i.e., one in the lower 25th percentile of the frequency distribution of all Storis index observations from 1900 to 2021, corresponding to a Storis index <−0.6) significantly increased from 12% during the first regime to 63% during the second regime (Chi-square = 43, $p<.005$, df = 1). In combination, these changes in the frequencies of extremely high and low Storis index years have led to a significant overall decline in *variability* of sea ice coverage (Figure 2a) between the two regimes (σ^2 declined from 0.79 to 0.25; Bartlett's test of homogeneity of variance of regime-specific anomalies for the two regimes: $p=.004$). We observed similar results using the entire 200-year history of Storis index data: a significant regime shift was detected in 2003, and the new regime shows the lowest mean Storis index values during the entire period from 1820 (see Figure S2). In addition, the frequencies of extremely high- and low-ice years have significantly decreased and increased, respectively, between the two regimes in the ways similar to those shown by the analysis using the data from 1900 (i.e., from 29% to 0% and 18% to 95%, respectively; Chi-square test: $p<.025$ and $<.005$). Coastal and shelf ice coverage has consistently been low during the recent regime, with high-ice years now being extremely rare for both the post-1900 and post-1820-timescales.

The sea ice export through the Fram Strait since 1980 showed a consistent decline after 2012/2013 and reached its lowest levels in 30 years in 2019 (Figure 2d,e). The decline was obvious for the sea ice area (Anova, $F=4.08$, df = 27, $p=.053$) and was even more pronounced for the sea ice volume ($F=24.43$, df = 27, $p<.01$), reflecting a thinning of the exported ice and further reduction in multi-year ice in its polar origin. A statistically significant regime shift of the Fram Strait sea ice volume export was detected ($p<.0001$), suggesting a transition to a new regime with low-ice export after 2012. Note that the regime shift detection does not show significance for the Fram Strait sea ice area export ($.05<p<.10$). However, sea ice volume is an accurate measure of sea ice mass balance, integrating both sea ice area and thickness. The detected regime shift in sea ice volume export is likely associated with the changes in atmospheric circulation forcing and corresponding ocean circulation (Zhang et al., 2008).

Simultaneously with the disappearance of drift-ice in summer along SEG, the depth integrated (0–20 m) temperature in Northeast Greenland between 69 and 73.5 N increased significantly ($F=11.84$, df = 29, $p<.01$) in August between 1980 and 2020, but this trend was less obvious ($F=1.65$, df = 29, $p=.21$) north of 73.5 N (Figure 3a,b). The mean SST in August observed in the coastal area of SEG showed a significantly ($F=12.68$, df = 27, $p=.001$) increasing trend from about 4°C in 1993 to >6°C in 2019 (Figure 3c,d). This coincides with a similar decline in August of the Storis index and the reduction of SIC from an average of ~7% in the 1990s to <1% in the 2010s (Figure 2b,c). Most of the years after 2007 had no sea ice on the coastal area of SEG although the peak of SIC and the Storis index in 2020 probably reflects a pulse of ice export from the Fram Strait. The significant increase in MLD in the coastal area of SEG was not correlated to SST or SIC (Figure 3d).

Within the coastal area of SEG, there was a bimodal distribution of the warm water contrasting with the areas north of 66.50 N, which had similar temperature trends and were colder than the East Greenland Coastal Current areas south of 66.50 N (Figure S3).

Different from the Storis index, the Shelf Index mainly shows a decadal-scale variation, indicating a peak during the 1940s with warmer Atlantic water on the shelf and a decline through 1980 before it increased again (Figure 3). On Fylla Bank, the temperature reached a maximum (index = 0.2 or ~ 2°C) around 1940 but decreased until 1980 (Figure 3f). Thereafter it increased again and

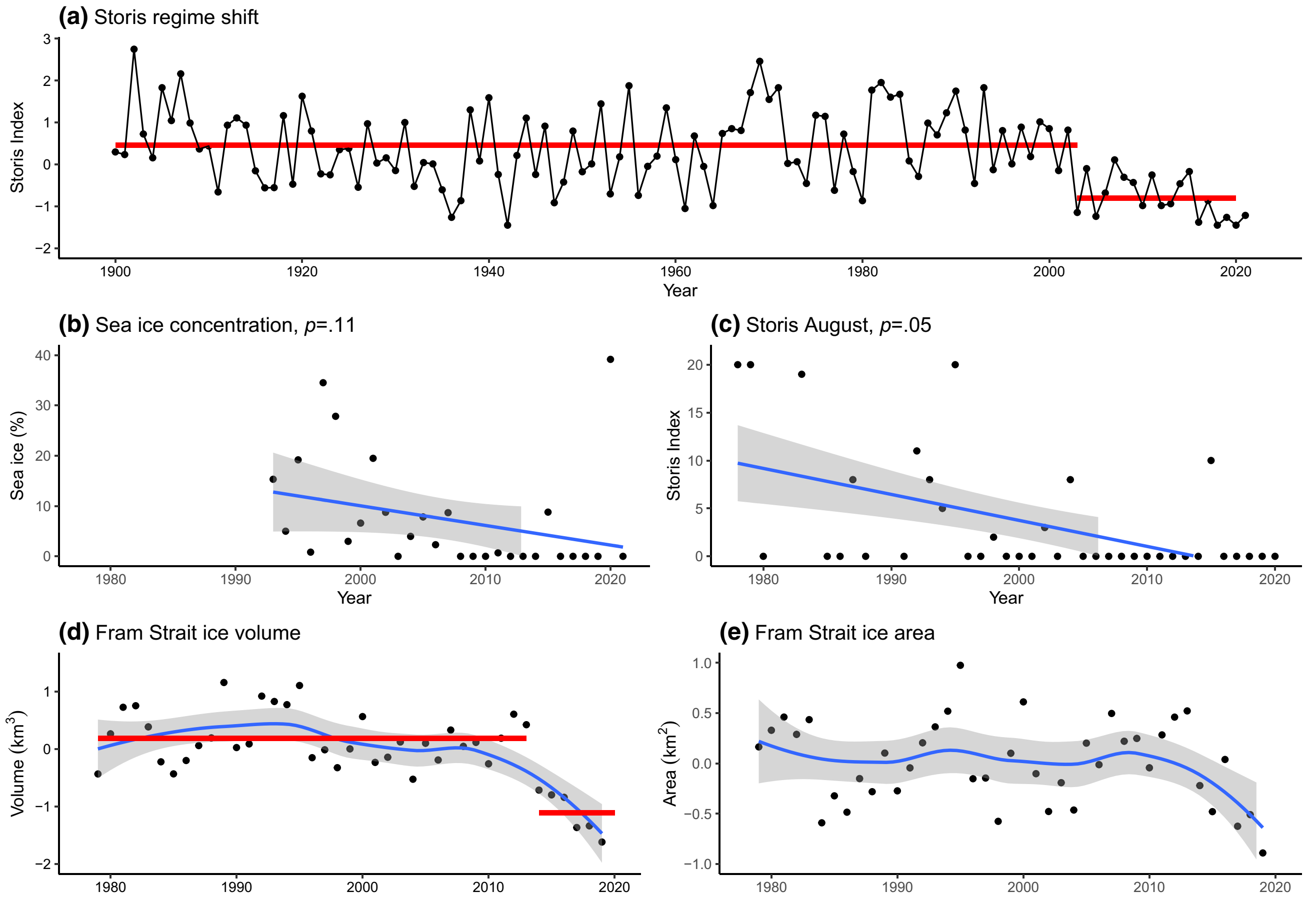

FIGURE 2 Changes in sea ice conditions in East Greenland. Upper panel: Temporal variability in the summer averaged Storis Index (June–July–August) since 1900 together with regime-specific means identified by a sequential regime shift detection algorithm (Rodionov, 2016; Rodionov & Overland, 2005). The indices for the series starting in 1900 are standardized indices derived using averages for the period 1900–2021. Black line with dots: standardized Storis Index for June–August; red line: regime-specific means. See Methods for details. Middle panel: Linear trends in sea ice concentration in SEG (see Figure S1 for delineation of SEG) and the occurrence of Storis after 1979. If the outlier in sea ice concentration from 2020 is excluded the *p*-value drops to .01. Lower panel: Loess plots of the trends in the annual export of sea ice (area and volume) from the Fram Strait during 1979–2019. The regime shift is shown in red for the ice volume plot.

reached its highest values in 2010s. The NAO reached its lowest period in the 1960s that corresponds to low temperatures and high ice indices (Figure S4).

The hydrographic station in the Irminger Sea (FX9) provides an offshore time series of the trends in salinity and temperature (Figure 4). The mean temperature (and salinity) of all months increased between 1990 and 2010 from 6.8°C (range 6.3–7.5°C) to 7.6°C (7.1–8.0) and has remained high (mean = 7.4°C, 7.0–7.6°C) but declining since then. The summer temperature reached its maximum in 2007 (8.8°C) and has remained high (mean = 8.2°C) but declining thereafter (7.4–8.8°C). The summer salinity increased significantly from 1971 through 2009 ($p = .01$), but declined significantly after 2009 ($p = .001$) indicating a major freshening of the Irminger Sea. The observations at Faxaflói stations also align with ORAS5 reanalysis data between 1990 and 2020, showing significant warming until 2010 (Figure S5). SST at different locations along SEG also shows consistent warming, particularly from 1990 until ca. 2010 (Figure S3).

3.2 | Trends in abundance and distribution of selected fish species

Mackerel suddenly appeared in the Irminger Sea after 2010 and its biomass peaked in 2016, but then it declined and apparently disappeared after 2019 (Figure 5). Bluefin tuna were first reported in the area in 2012 as bycatch in the mackerel fisheries and subsequently nearly every year since then until 2019 when mackerel fishing effort declined and then ceased in 2020 and 2021. Capelin abundance in the Irminger Sea and the Denmark Strait peaked in the mid-1990s and has been on a steady decline since then. The spatial distribution of juveniles shifted from the north of Iceland and east of the SEG shelf break before 2000 to the SEG shelf and closer to the Greenland coast after the early 2000s. In addition, the spatial distribution of young juvenile capelin expanded farther south on the shelf into the Denmark Strait, where previously these age classes were absent, and in general, 2003 was observed to be a year of abrupt changes in

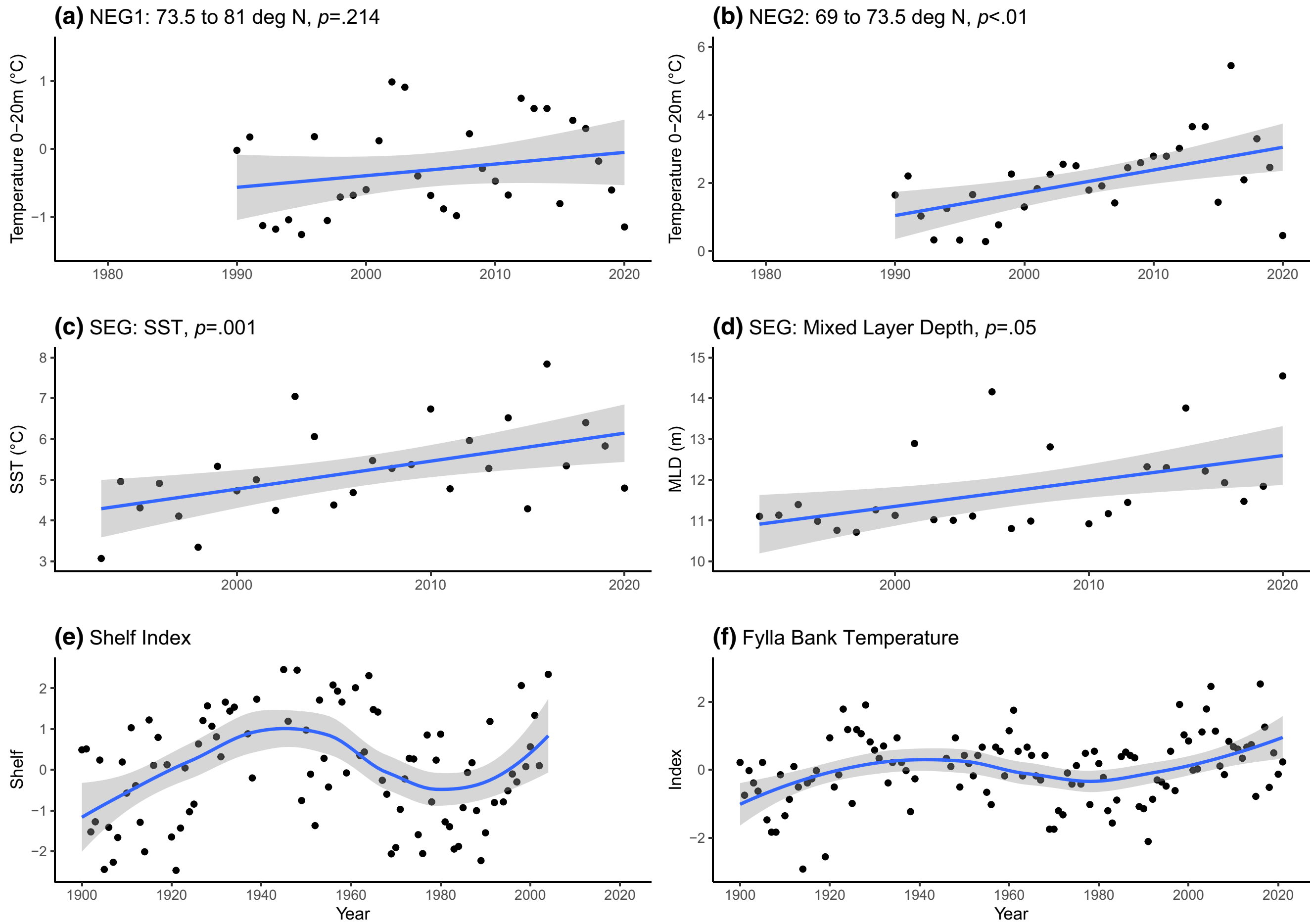

FIGURE 3 Linear trends in depth integrated water temperatures (0–20 m) at two sections (10–100 km from shore) along Northeast Greenland after 1979 (a, b), and in sea surface temperature (c) and mixed layer depth in SEG (d) after 1992, and Loess plots of the trends in sea temperature in the Shelf Index (an index of the inflow of Atlantic water to the SEG shelf, and e) the index of temperature changes from in situ measurements on Fylla Banke in West Greenland after 1899 in June integrated over 0–40 m depth (f). For definition of SEG and position on Fylla Banke, see Figure S1.

capelin distribution (Jansen et al., 2021, Figure S6; original data from Carscadden et al., 2013).

3.3 | Response of marine mammals

The village of Tasiilaq, with its five hamlets with a total of 2000 inhabitants (2020), is the only community in SEG where marine mammal hunts are still regularly performed. Catches of ringed seals declined significantly since the late 1990s (Anova, $p < .001$) and catches of hooded seal declined precipitously after 1995 and was much reduced in the 2000s ($p < .001$, Figure 5). Harp seal catches have on the other hand increased since the late 1990s ($p = .07$) and a gradual reduction of bearded seal (*Erignathus barbatus*) catches occurred after 2007.

Catches of narwhals in Tasiilaq increased significantly between 1955 and 2004 (not shown, Anova df = 43, $F = 14.9$) and reached their maximum in 1981. The catches remained high with an annual average catch of 50 whales until 2004 but declined significantly after 2004 (Figure 6, df = 13, $F = 11.8$). Quotas were first installed in 2009, and catches exceeded the quota twice but remained below the quota for 11 of the years after 2009.

Catches of walrus in SEG has declined since the 1990s in parallel to the reduced transportation of drift-ice along the East Greenland coast, and the quotas installed in 2009 were never reached (Figure 6).

There were no documented catches of killer whales (*Orcinus orca*), long-finned pilot whales (*Globicephala melas*) and white-beaked dolphins (*Lagenorhynchus albirostris*) in the 1990s in Tasiilaq (Figure 6). The first catches of pilot whales were taken in 2001 but the catch level remained low (<50 per year) until 2017, after which the catches increased rapidly and reached a maximum of 178 in in 2019. A similar trend through 2019 is evident in catches of killer whales and dolphins.

The only baleen whale currently hunted in East Greenland is the common minke whale (*Balaenoptera acutorostrata*) and the low number of catches fluctuates a lot but have increased significantly in recent years (Anova, $p < .001$). Fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) are not hunted

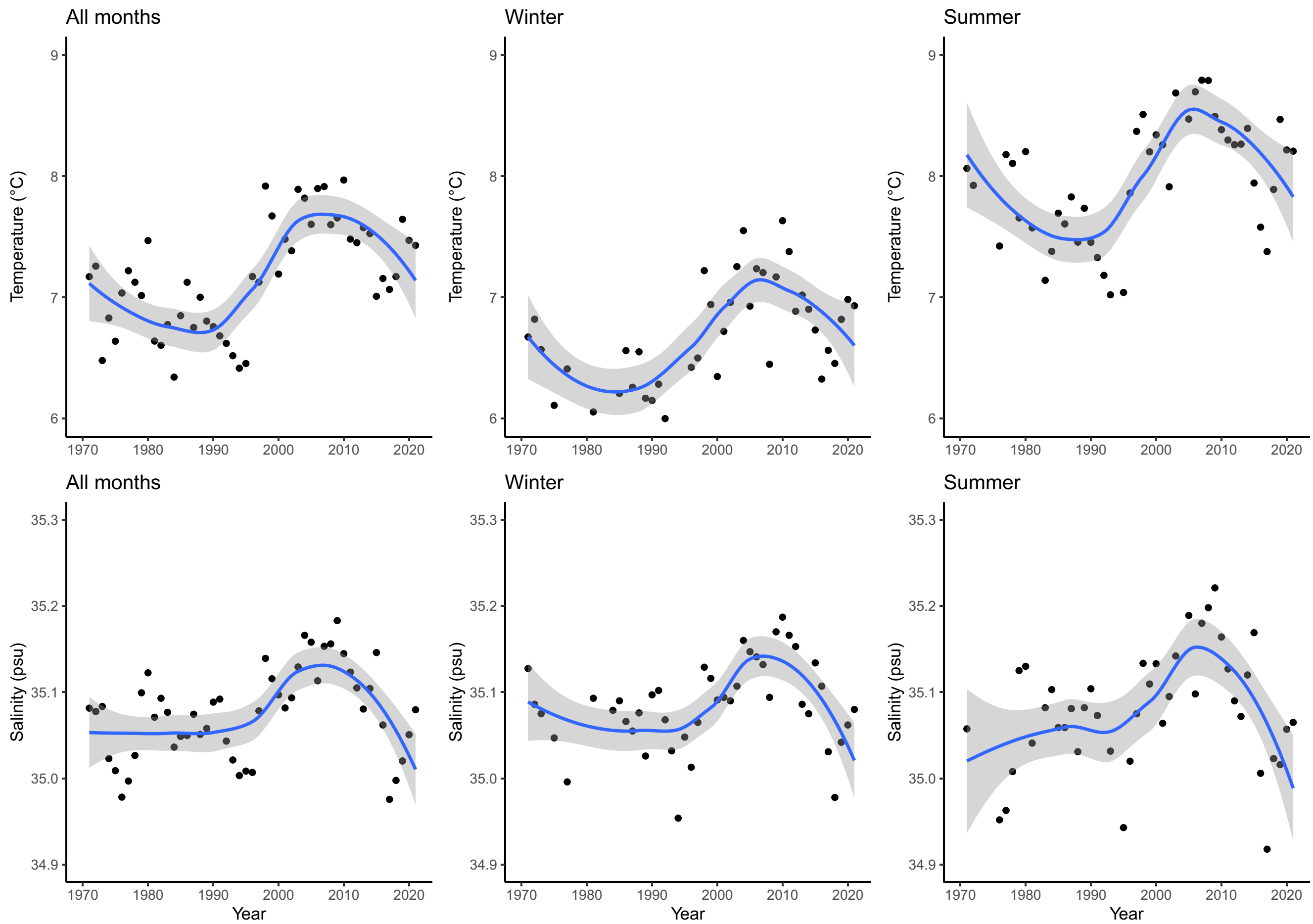

FIGURE 4 Observed temperature and salinity in the northern Irminger Sea averaged over 0–200 m depth, from the Icelandic FX9 and RE8 stations (see Figure 1 for position). Winter refers to January–February–March, summer to July–August–September data.

in East Greenland but the large abundances estimated from the aerial survey in 2015 are in striking contrast to the few historical observations in coastal areas. Harbour porpoises (*Phocoena phocoena*) were also encountered in low numbers during the survey in 2015.

3.4 | Predation levels by marine mammals

The total consumption by the three baleen whales, the toothed whales and harp and hooded seals on the East Greenland shelf represent >2 mill tons of biomass (Figure 7). Consumption levels by other species are either considered to be low (narwhals and walrus) or impossible to estimate due to lack of abundance estimates (ringed seal and killer whale). Species composition of prey items is assumed to be similar to prey selection identified in studies of stomach contents of marine mammals in Iceland and West Greenland (Kapel, 1979; Sigurjónsson & Víkingsson, 1997). Most of the biomass is consumed by fin whales that primarily target euphausiids. The total consumption of fish species is around 750,000 tons per year on the East Greenland shelf. Humpback whales are clearly the biggest consumer of fish species and recent satellite tracking of whales to the cold water of the East Greenland shelf (Figure S7), as well as visual observations during aerial surveys (Pike et al., 2019), support the notion that humpback whales are targeting the capelin that have migrated on to the shelf area. Another important predator on capelin is the harp seal that is frequently found in large groups in the same inshore areas of East Greenland where humpback whales occur.

4 | DISCUSSION

There is an increasing need for understanding of how large-scale climate forcing, through teleconnection and changes in oceanographic conditions, impact ecosystem functioning and what the consequences are for fisheries and ecosystem services. Observations from sub-arctic shelf areas are good indicators of decadal shifts in climate, as they are transition zones between cold-fresh Arctic water masses to the north, and warm-saline water masses to the south. The boundary between the transition zones can be identified by the extent of sea-ice, but data on ecosystem functioning are often sparse, especially at lower trophic levels, and often marine mammals and sea birds are the best indicators of trends in

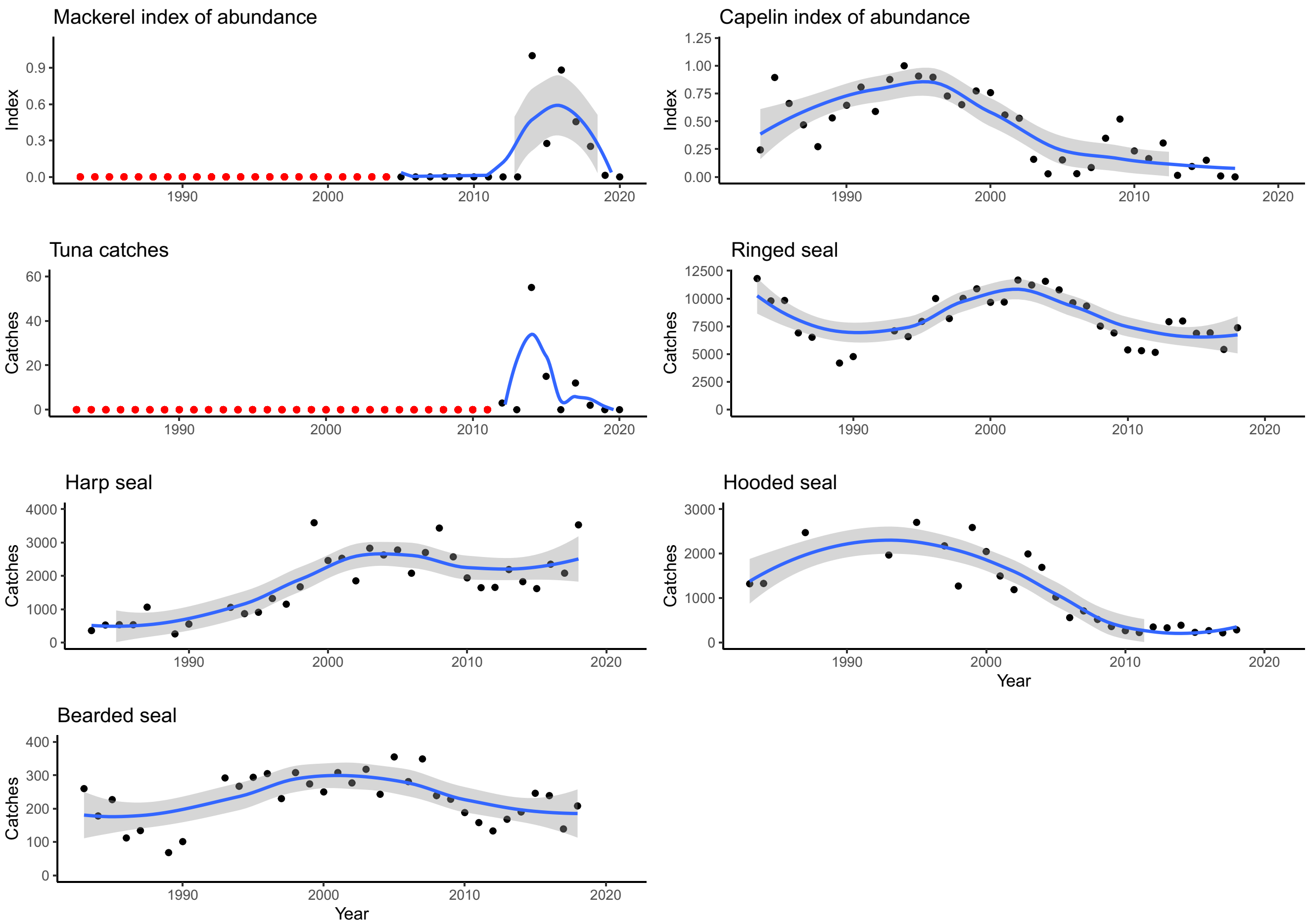

FIGURE 5 Upper panel: Loess plots of the time series of the index of abundance of two pelagic fish species, mackerel and capelin in the Irminger Sea. Data from Post et al. (2021). Lower panels: Catches of Atlantic bluefin tuna in the Irminger Sea (data from Jansen, Nielsen, et al. (2021)) and catches of four seal species at Tasiilaq (data from Anon, 1983–1992 and the Greenland Directorate for Fisheries, Hunting and Agriculture). Red dots indicate that there is no information on the presence or catches.

subarctic ecosystems (Sigler et al., 2012). In the following we discuss how large-scale changes in circulation patterns in the Arctic Ocean, including the Beaufort gyre and transpolar ice drift, that affects the Fram Strait ice export (Timmermans & Marshall, 2020), have had cascading effects on the ecological conditions several thousand kilometers away in SEG.

The main tipping element driving the regime shift in SEG is the virtual disappearance of summer sea ice in SEG (as evidenced by the SI). The Fram Strait ice export is the main supplier of sea ice in SEG, but the record of ice export is shorter than the SI (41 compared with 201 years), and the ice observations from the Fram Strait are located ~2500 km north of where we have documented ecological changes. When it comes to determining the timing of the initiation of the transition to the new regime the locally derived SI is a more accurate tipping point element than sea temperature. The latter is correlated with sea ice, but it is also affected by the large-scale current systems and its variations are, therefore, more difficult to interpret and monitor consistently with current methods. As a tipping element, sea temperature may, therefore, be a more complex indicator of regime shifts and transitions across tipping points. Independent of this, the SST along East Greenland shows an increasing trend over the last ~25 years and which support the ecological changes observed in SEG.

4.1 | Physical forcing

The SEG shelf area has undergone radical oceanographic changes over the past century. One of the most prominent is the virtual disappearance of multiyear drift-ice advected from the polar basin during the last 20–25 years. There is no corresponding 20-year period with similarly low levels of summer ice in the last 120 years for which data are most reliable, nor in the entire 200-year record of available data. Furthermore, paleoclimate information suggests that heavy ice export through the Fram Strait commenced in the 1300 and continued for centuries (Miles et al., 2020). In addition, the most recent low-ice period is unique throughout the full period because of its consistently low level of ice without intermittent high-ice years. The period since 2003 differs from a previous low Storis period in the 1920s–40s because the post-2003 regime not only has *average* low-ice conditions but lacks the occasional

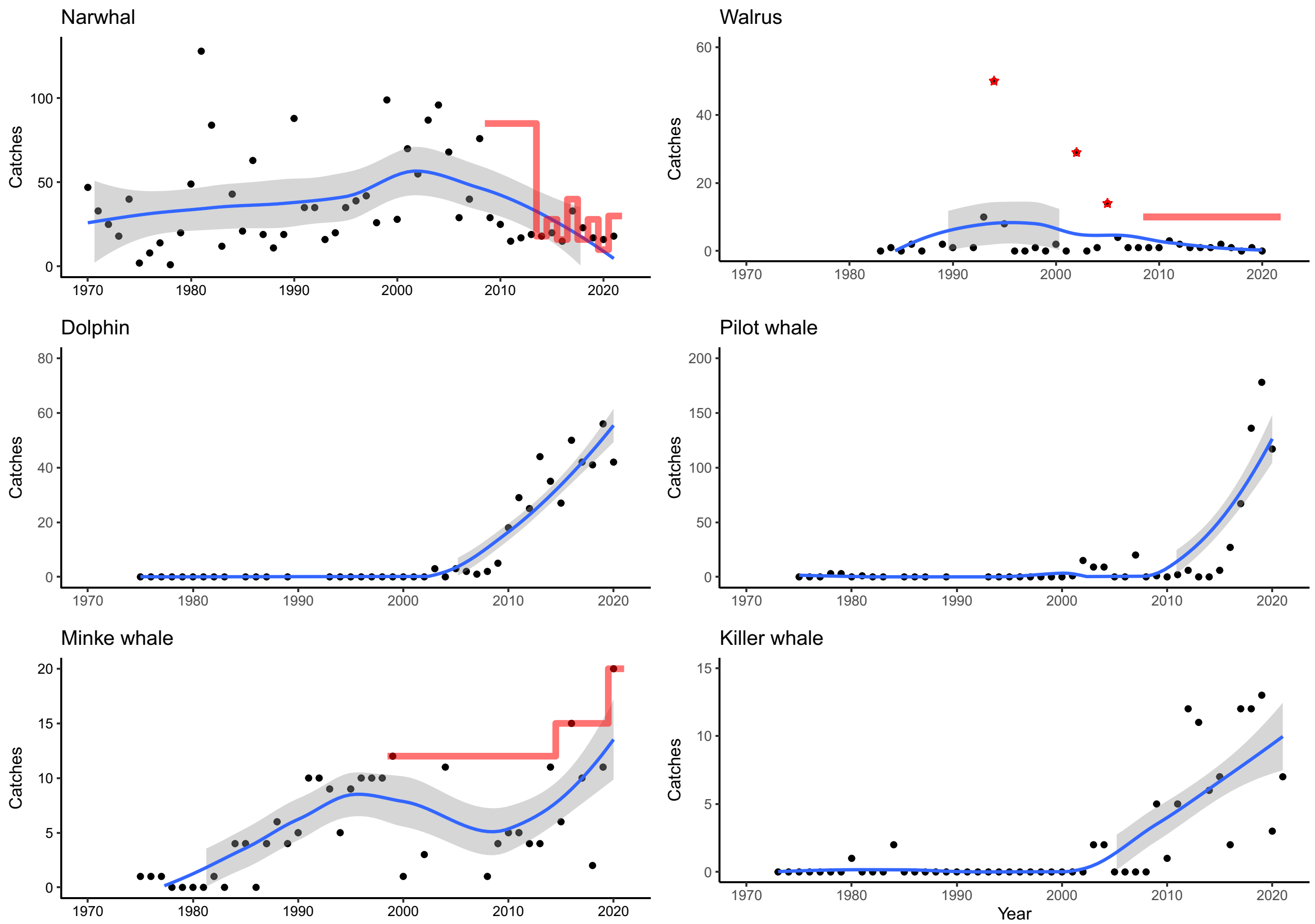

FIGURE 6 Loess plots of catches of marine mammals in Tasiilaq 1970–2020 (data from the Greenland Directorate for Fisheries, Hunting and Agriculture, (Anon, 1983–1992; Garde et al., 2019, and IWC Secretariat). Red lines indicate quotas, and red stars for walrus catches indicate uncertain levels of catch reporting.

high-volume ice years, which occurred frequently during the earlier event.

The general reduction of the East Greenland ice occurs between 1992 and 1999 and 2000–2008, which show a decrease by 10%–20% during winter and 30%–55% during summer (Kern et al., 2010) with a 2-month longer ice-free season in the Irminger Sea (from August to October) after 2000. A major contributor to the East Greenland coastal sea ice is the export of multi-year polar drift-ice through the Fram Strait. The export increased from 1979 to the mid-1990s (Smedsrud et al., 2017), largely due to the positive polarity of NAO (e.g., Zhang et al., 2003). Nevertheless, the continuing warming, decrease in ice volume export, and the decline in the annual local production of sea ice in the Greenland Sea has contributed to the reduction in sea ice in the EGC (Lavset et al., 2018; Lindsay & Schweiger, 2015; Moore et al., 2015; Wei et al., 2019; Zhang et al., 2008).

Offshore in the Irminger Sea, hydrographic observations indicate nonlinear changes in temperature and salinity between 1971 and 2021. These variations in the oceanographic conditions in the Irminger Sea reflect activity in the sub-polar gyre (Post et al., 2021; Reverfdin, 2010; Våge et al., 2011), and the recent warming reflected in the SST appears to have promoted the northward expansion of boreal species as conditions on the SEG shelf region became suitable (Post et al., 2021).

4.2 | Ecosystem biological changes

4.2.1 | Marine mammals

No studies have yet directly addressed the biological effects of the reduction in sea ice transport along East Greenland. This ongoing 20-year event represents a major change in habitat in the coastal and shelf area because it previously directly provided living space (e.g., resting and breeding areas; refuge from potential predators) for megafaunal species and indirectly via cooling affected local temperatures of the surrounding water. Extensive ice cover also inhibited use of such areas by other species, including several identified here. The general absence of multiyear summer drift-ice and increasing temperatures during most of the last two decades has opened the coastal and shelf area for a number of boreal marine mammals and temperate-boreal fishes. The simultaneous increase in sea temperatures has accelerated this process by a faster ice melt and presumably increased productivity.

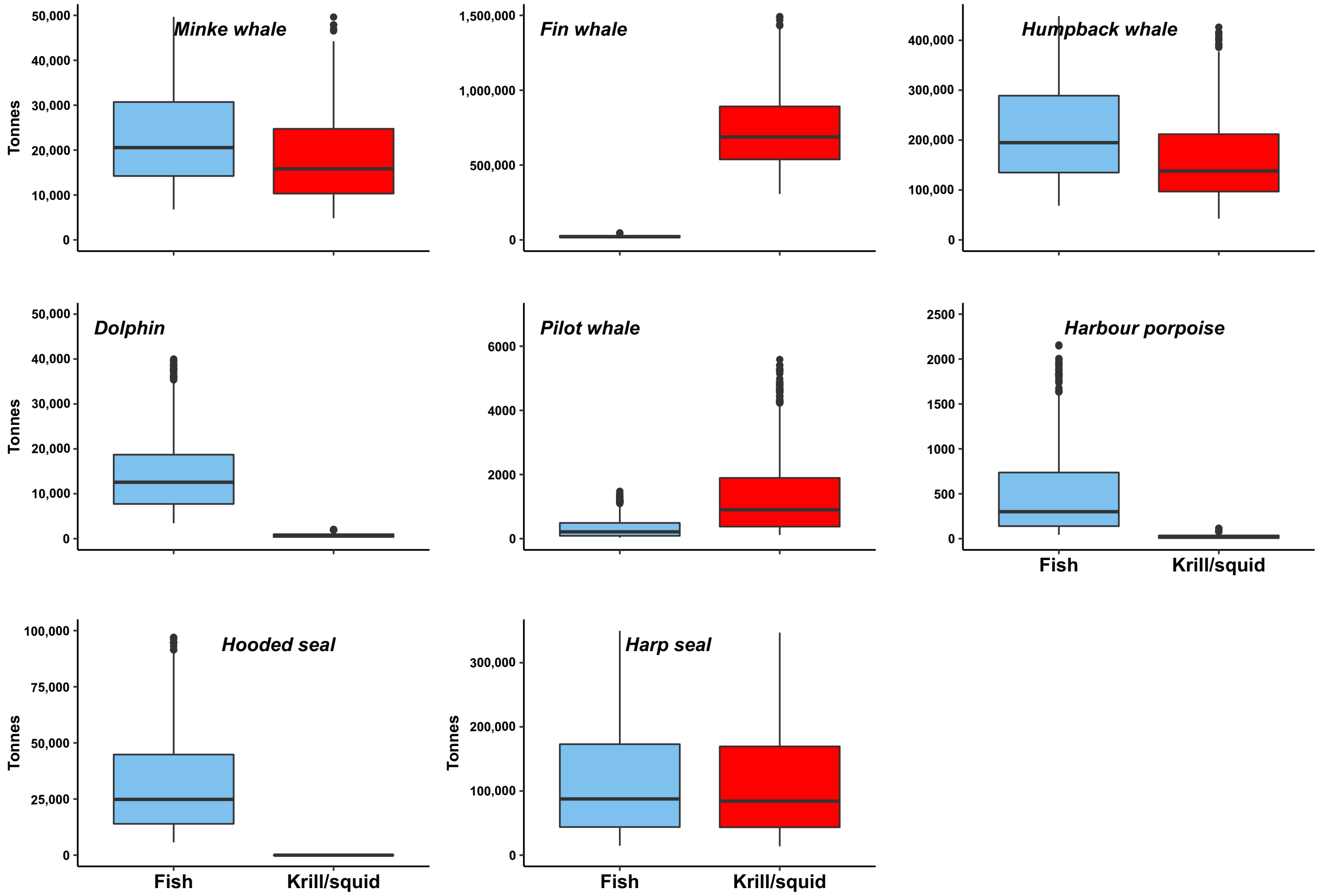

FIGURE 7 Box-plot presentation of the consumption by eight species of marine mammals that are present in large numbers in the East Greenland shelf area for an estimated 90 to 180 days with abundances ranging from 50 to 2,000,000 individuals.

Because of its threshold-like nature, associated with a particular combination of temperatures and ocean currents that affect melting and transport of ice, this process can be considered a tipping element which has surpassed a tipping point and led to a major habitat change, which is not likely reversible in the foreseeable future, given expected greenhouse gas emissions, associated climate change scenarios and the projection of increasing sea temperatures in the North Atlantic (Alexander et al., 2018; IPCC, 2019).

Many of the ecological changes we report are associated with migrations to entirely new habitats where the species have rarely, if ever, been observed before in recorded history. Most boreal whale species are not well adapted to dense multi-year sea ice and they would not venture into coastal areas of SEG under past ice conditions. For example, there were only eight recorded observations of killer whales in Tasiilaq during 1942–1984 and three recorded catches between 1950 and 1986 (Heide-Jørgensen, 1988). This is in sharp contrast to the period 2003–2018 where at least 77 killer whales were caught and presumably many more observed. There is little evidence for regular presence of pilot whales and dolphins in Tasiilaq before 2000 when the first catches were recorded (Holm & Petersen, 1921; Winge, 1902). The high catch levels reached after 2010 are unprecedented for this area. No abundance estimates are available for killer whales on the shelf area of East Greenland but the abundance of dolphins was estimated at 11,889 (95% CI: 4710–30,008) in 2015 and the pilot whales were estimated at <300 individuals in 2015 before the major rise in catch numbers occurred (Hansen et al., 2018).

Narwhals are year-round residents in the Arctic and they migrate between winter offshore areas of the Denmark Strait and the Greenland Sea and fjords in SEG in summer. Narwhal catches in SEG peaked in 1992, during a period when the ice transport with EGC was in a decline and when the SST was rising. The fjord systems where narwhals are found in summer, are however also affected by the increase in sea temperature from inflow of warm Atlantic water (Andresen et al., 2012; Dietz et al., 1994). When leaving the fjord systems and travelling to their wintering grounds, the narwhals will be affected by increasing sea temperatures and reduced transport of sea ice along East Greenland. There is evidence that narwhals have a narrow temperature niche of 0.3–1.3°C where most of their diving and feeding activities takes place (Heide-Jørgensen et al., 2020). Only areas dominated by the EGC seem to be suitable habitat for narwhals and areas with influx of dense and warm Atlantic water masses seem unsuitable, which will likely lead to a substantial habitat loss for such populations due to climate change (Chambault et al., 2022). The recent collapse of narwhal stocks in SEG could be a combination of excessive hunting pressure and habitat changes due to increasing sea temperatures (Chambault et al., 2020; NAMMCO, 2022).

There is no resident population of walrus in SEG, but individuals from the population in Northeast Greenland are occasionally seen in Southeast Greenland (Born et al., 1998). These stragglers are usually hauling out on drifting ice and are passively transported southward. The volume of sea ice exported through the Fram Strait is estimated to have declined by 27 ± 2% per decade between 1992 and 2014 (Spreen et al., 2020), which is definitely affecting the availability of walrus in SEG.

Migratory baleen whales use the absence of ice along SEG to enter coastal areas and one example is the humpback whale. Humpback whales make annual migrations between winter mating grounds in the Caribbean and summer feeding grounds in the North Atlantic but no summer feeding ground has so far been identified in East Greenland (Hansen et al., 2018; Stevick et al., 2003, 2006). Based on the examination of expedition reports, local informants and official accounts from the Royal Greenland Trade Department, Winge (1902) concluded that there are no confirmed sightings of humpback whales in East Greenland. Later, Holm and Petersen (1921) mentioned that humpback whales visit coastal areas of Tasiilaq infrequently and only in years when no coastal ice is present in summer. However, a fifth and new North Atlantic summer feeding ground off the East Greenland coast was recently documented by Hansen et al. (2018). An aerial line transect survey conducted in August 2015 covered the area from the coast up to 50 km offshore crossing the shelf break in East Greenland. The fully corrected abundance estimate was 4223 (95% CI: 1845-9666) humpback whales or about one-fifth of the current total estimate for the North Atlantic. Despite the lack of previous surveys in the area, the abundance estimate detected in 2015 was remarkably high and probably due to an influx from neighboring areas driven by a combination of an ice-free coastal zone and a substantial availability of prey.

A key prey species for predation by some of the migratory marine mammals is the capelin that in the past two decades has shifted its distribution from the Iceland Sea north of Iceland toward the East Greenland coast and shelf region (Bárðarson et al., 2021; Pálsson et al., 2012). The capelin is a cold-water species known to be an important prey of humpback whales in West Greenland and Iceland (Clapham, 2009; Laidre et al., 2010). A redistribution of capelin could alone explain the increase in humpback whales in coastal areas of East Greenland, especially in the area north of Tasiilaq, detected in the surveys in 2015. In the same year, cetacean surveys around Iceland and in West Greenland detected substantial declines in abundance of humpback whales (Hansen et al., 2018; Pike et al., 2019). Satellite tracking experiments of humpback whales in East Greenland in 2019 and 2021 confirm the presence of this capelin predator in the new capelin habitat on the East Greenland shelf (Figure S6).

It is well known that there is a large concentration of fin whales in the Irminger Sea west and southwest of Iceland (Pike et al., 2019; Víkingsson et al., 2009, 2015). Fin whales in the Irminger Sea primarily target euphausiids (Sigurjónsson & Víkingsson, 1997). The general warming of the Irminger Sea in recent decades (Víkingsson et al., 2015) has likely improved conditions for several zooplankton species, making the area attractive for foraging fin whales. However, a large number of fin whales were unexpectedly found in the coastal waters of East Greenland (<50 km from shore) in August 2015; a fully corrected abundance estimate showed that there were 6440 fin whales (95% CI: 3901-10,632, Hansen et al., 2018) in the region, even though there is little or no historical evidence of fin whales in coastal waters of East Greenland (Holm & Petersen, 1921; Jensen, 1928; Winge, 1902). It is furthermore unlikely that the influx of fin whales to SEG is due to deteriorating conditions in the offshore area of the Irminger Sea because abundance has also increased there (Víkingsson et al., 2009) and the estimate from 2015 (36,000 fin whales) was the highest in the NASS series 1987–2015 (Pike et al., 2019).

Habitat conditions for whales in SEG may, aside from new ice-free access to the coast, have improved due to higher ocean productivity in the coastal areas. The SEG shelf areas probably experienced climate driven changes in pelagic productivity that have supported feeding by large changes in abundance of zooplanktivorous fish and marine mammal species. New investigations are needed to confirm how lower trophic levels have been affected by the change in sea ice and temperature.

4.2.2 | Fish community

Additional changes in the biodiversity and food web of the SEG marine ecosystem have occurred during the same period as the changes in the marine mammal community. The rapid increase of mackerel in the Irminger Sea and on the East Greenland shelf during 2010–2019 was probably driven by a combination of factors, including (1) an increase in summer SST, (2) increasing mackerel productivity and abundance in its main distributional area along and on the northwest European continental shelf, and (3) habitat distributional changes (zooplankton prey availability) due to production dynamics and competition with large biomasses of two other zooplanktivorous species in the northeast Atlantic (herring, and blue whiting, *Micromesistius poutassou*) (ICES, 2021; Jansen et al., 2016; Olafsdottir et al., 2019). However, in 2020 and 2021, no mackerel were observed in East Greenland/Irminger Sea waters and the commercial mackerel fishery did practically not operate in this area (ICES, 2021). Reasons for the commercial disappearance of mackerel from the region have not yet been identified (ICES, 2021), but it has been suggested that it could be due to the recent overall decline by ca. 25% of mackerel spawning biomass in the northeast Atlantic, in combination with changes in other ecosystem factors (temperatures, zooplankton abundances of zooplankton and mackerel competitors) elsewhere in the northeast Atlantic.

Bluefin tuna were first reported in East Greenland waters in 2012 and have been observed nearly every year until 2018 as bycatch in mackerel fisheries (Jansen, Nielsen, et al., 2021; MacKenzie et al., 2014). The absence of bycatches since 2019 is due to low or no fishing effort for mackerel so it is unknown whether bluefin tuna has been present or not since 2019. The presence of bluefin tuna in this area is likely due to a combination of increasing surface temperatures in the Irminger Sea/Denmark Strait region, the presence of mackerel which is a key prey for bluefin tuna in northern foraging areas (Jansen, Nielsen, et al., 2021; Varela et al., 2022), and an overall increasing biomass of bluefin tuna in the northeast Atlantic and Mediterranean Sea since ca. 2008–2010 (ICCAT, 2020). The role of temperature on the presence of both bluefin tuna and mackerel in East Greenland waters is important: until the early 2010s, sufficiently warm summer temperatures were typically found in smaller areas and in shorter seasons for these species. Consequently, the observed increases in temperature expanded the thermal habitats and made them available for these species in the years where the other dynamics favored northwestward migration. East Greenland waters are still likely marginal for regular seasonal occurrence of bluefin tuna and mackerel.

However, if recent warming trends continue, then the size and duration of the thermal habitats will increase, potentially creating a more permanent summer habitat for these species. We also hypothesize that, provided that thermal conditions in this region become suitable, bluefin tuna could become present, even if mackerel are rare or absent (for example, if mackerel abundance becomes lower than at present). This hypothesis is supported by the summer presence of bluefin tuna in commercially exploitable quantities in the shelf break area south of Iceland and in the Iceland Basin (i.e., east of the Reykjanes Ridge) during the late 1990s–early 2000s (Olafsdottir & Ingimundardottir, 2003). At that time, mackerel were still rare in Icelandic waters (Astthorsson, 2016) and bluefin tuna fed primarily on other prey such as mesopelagic fishes and squids (Olafsdottir et al., 2016).

The spatial distribution and productivity of capelin has also changed since the early 2000s and 2003 was observed as a year of abrupt change for the capelin (Carscadden et al., 2013; Jansen, Hansen, & Bardason, 2021). Capelin are most often found in temperature and salinity regimes between −1 and 6°C and salinities between 33 and 35 psu, and they are known to prefer the border zones between cold Arctic and warmer Atlantic water (Rose, 2005). Large-scale shifts in occurrence of capelin have been documented since the early 2000s and hypothesized to be a result of changing sea temperatures (Figure S6). Juvenile capelin now occupies shelf waters closer to the East Greenland coast than before ca. 2000 (a shift of several 100 km westward), and the distribution of feeding areas of adult capelin have shifted farther to the west and north (Bárðarson et al., 2021). The increase in sea temperatures in the coastal and shelf area off SEG and north of Iceland is likely driving the observed range shift of capelin toward the East Greenland coast and also of declining recruitment to the stock (Jansen, Hansen, & Bardason, 2021). The latter may also be a consequence of the increase in predatory megafauna, such as humpback whales and harp seals.

The changes in these three pelagic fish species are being accompanied by changes in distributions of many other species in Greenlandic waters. These include species in other functional groups and depth layers than considered here (Post et al., 2021), including demersal and bathypelagic species such as greater argentine (*Argentina silus*). In addition to expansions of ranges of local species, new species previously absent from Greenlandic waters are arriving from warmer areas (Møller et al., 2010); these authors documented five new species of warmer water origin in Greenlandic waters since 1992. These biodiversity changes reflect what occurred during a previous warming event in the early decades of the 20th century (Jensen, 1939), and which are ongoing in other parts of the Arctic/sub-Arctic region (IPCC, 2019, 2022).

The current warming event is however expected to continue, suggesting that the distributional changes may be more permanent. In this context, we hypothesize that another pelagic species, herring, which is currently native to Greenland (Møller et al., 2010), could also expand its distribution and abundance. This species, which is a key zooplanktivore and prey for top predators in other north Atlantic shelf ecosystems, is presently sparsely distributed in Greenlandic coastal areas. However, as temperatures rise, it could potentially also increase its abundance and become an important part of local food webs, including as prey for seasonal migrants such as those discussed here. Local populations currently exist in fjords (Møller et al., 2010; Nielsen, 1960) and could expand in abundance and distribution if oceanographic conditions continue to become more favorable for this species.

In contrast, other species that are ice-dependent and cold-tolerant are declining. For example, polar cod abundance in the East Greenland–Iceland area has been declining as temperatures have increased (Astthorsson, 2016). The southern range limit of this species in SEG will likely, therefore, shift farther north as summer ice disappears.

The duration of this ongoing event is now longer than the generation times of many of the megafauna species considered here (see Table S1 for data on age at maturity for species affected by the regime shift). This means that generations of individuals alive in 2003 at the start of the transition to the current regime have likely produced offspring which have never experienced the shelf pack ice conditions in this area typical of their parents' lives and earlier generations, and that offspring generations are being exposed to novel oceanographic and habitat conditions to which they must adapt. Such adaptations would include changes in spatial distributions and migratory behavior and phenologies. Furthermore, the low frequency of summer drift-ice in these areas is likely allowing exploratory and stray seasonal migrants to the area to learn locations of new foraging habitats (De Luca et al., 2014; Mariani et al., 2016; Petitgas et al., 2010). Given the long period of years with low levels of summer drift-ice, this situation will also enable offspring of seasonal migrants to learn new migration routes and foraging sites from their parents. Mechanisms such as these are probably leading to the respective declines and increases in ice-adapted and more boreal or sub-Arctic species reported in our study.

4.2.3 | Changes in trophic interactions in the food web

The changes in both the marine mammal and fish communities of the SEG have consequences for species interactions, including prey abundances and distributions, and the food web. Predators affect prey populations both by direct consumption (and mortality) of individuals and indirectly by creating fear and subsequently causing prey to change their behavior, including their spatial distributions, to reduce encounters with predators (Matthews et al., 2020; Wirsing et al., 2008).

We made an initial exploration of the direct consumptive effects of the presence of some of the new predators in the SEG marine ecosystem. These calculations indicated that the newly arrived predators are consuming ca. 2 million tons of biomass/year, though seasonally compressed into a few months. Since the predator biomass we report represents an increase in local predator biomass over historical levels, this consumption represents an increase in natural mortality of prey species. Presently, the species composition of fish and zooplankton in the predator diets is partly unknown, as are the abundances and productivities of the prey species, so it is speculative to conclude whether this new consumption will affect biomasses of prey populations. However, we believe that the magnitude of this consumption justifies new studies of the predation impacts on prey and the food web, including cascading effects, using advanced modeling approaches (e.g., size-based and bioenergetic methods; Coll et al., 2020; Mariani et al., 2017). Outputs of such models could provide updated input to existing stock assessments for species such as capelin where predation by marine mammals are an integral but not recently updated element that propagates into fisheries quota advice (ICES, 2022). Or to new integrated ecosystem-based management approaches for sustainable human activities in this region (Bossier et al., 2020), including identifying the levels of exploitation of prey species that would ensure sufficient prey remains available for predator consumption (Cury et al., 2011).

The changes in distributions and abundances of the marine mammal and fish species reported here may to some extent be coupled to each other via trophic interactions. For example, in other regions, killer whales are known predators of both mackerel (Nøttestad et al., 2014) and bluefin tuna (Guinet et al., 2007) and bluefin tuna are predators of mackerel. Movements of a prey species into the region could, therefore, attract exploratory searching predators and encourage their return in subsequent years. Given the predator–prey interactions among such species elsewhere (e.g., Norwegian Sea; ICES, 2021), it is likely that new trophic interactions and cascades are emerging in the SEG shelf and shelfbreak ecosystem involving these and other combinations of predators and prey. The appearance of new predators in the system could, therefore, be altering abundances of prey species via consumption and fear-induced behavioral (and spatial distributional) changes of prey (Matthews et al., 2020; Wirsing et al., 2008).

5 | CONCLUSION

The SEG coastal and shelf ecosystems have entered a new regime, which has probably not been observed in this region for at least the past 200 years. Conditions that were previously dominant (extensive summer drift-ice and low temperatures) are now rare, suggesting a tipping point involving summer ice coverage has been crossed and a new state with open water in summer has been reached. As a result, several large mobile predator species are expanding their ranges into new habitats. The presence of these species is likely having direct and indirect effects on other species in the community and on biodiversity–function relationships of the food web. Many of these species occupy high levels in the food web and their consumption will probably impact prey and have cascading effects to lower trophic levels in food webs. Other ice-dependent and cold-tolerant species are declining. Given a continued increase in sea temperature in SEG (Alexander et al., 2018; IPCC, 2019) and reduced sea ice export through the Fram Strait (Spreen et al., 2020), it is likely that the abundance of boreal cetaceans and fishes will increase, whereas Arctic species such as narwhals will disappear from SEG. The observed changes in SEG demonstrate that a regime shift has occurred and are likely to be the first signal of what will become an increasingly common scenario in the Arctic.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The environmental variables and catch statistics and quota levels data that support the findings of this study are publicly available on Zenodo at https://zenodo.org/record/7151530#.Y1BM6XbMJD8 and hydrographic observations are available on SeaDataNet under the search point Faxaflói (https://cdi.seadatanet.org/search).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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