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Original Article

Historical climate drivers and species' ecological niche in the Beaufort Sea food web

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Abstract

Climate change impacts have been particularly acute and rapid in the Arctic, raising concerns about the conservation of key ecologically and culturally significant species (e.g. beluga whales, Arctic cod), with consequences for the Indigenous community groups in the region. Here, we build on an Ecopath with Ecosim model for the Canadian Beaufort Sea Shelf and Slope to examine historical (1970–2021) changes in the ecological dynamics of the food web and key species under climate change. We compare the individual and cumulative effects of (i) increased sea surface temperature; (ii) reduced sea ice extent; (iii) ocean deoxygenation; and (iv) changing ocean salinity in the ecosystem models. We found that including salinity time series in our ecosystem models reduced the diversity found within the ecosystem, and altered the trophic levels, biomass, and consumption rates of some marine mammal and fish functional groups, including the key species: beluga whales, as well as Arctic and polar cods. Inclusion of the dissolved oxygen time series showed no difference to ecosystem indicators. The model findings reveal valuable insights into the attribution of temperature and salinity on Arctic ecosystems and highlight important factors to be considered to ensure that existing conservation measures can support climate adaptation.

Keywords: arctic; climate change impacts; ecosystem modeling; environmental niche; multistressors; adaptation; MPAs

Introduction

The cumulative impacts of multiple stressors onto sensitive ecosystems due to climate change can be profound (Noone et al. 2013). In the Arctic, the impacts of climate change are more severe relative to the global average (Arctic Council 2013, Pörtner et al. 2014), raising concerns about the future of ecologically and culturally significant species such as beluga whales (*Delphinapterus leucas*) and Arctic cod (*Boreogadus saida*) (Laidre et al. 2015, Geoffroy et al. 2023). Climate impacts can interact synergistically (larger impacts than the sum of the individual stressors), antagonistically (lower impacts than the individual sum), or additively (sum of each stressor) (Crain et al. 2008). For example, longer open water seasons due to increased sea surface temperature (SST) and reduced sea ice extent allow for more atmospheric mixing (Francis and Vavrus 2012), enhanced cross-shelf exchanges (O'Brien et al. 2011, Janout et al. 2013), and upwelling of nutrient-rich water (Carmack and Chapman 2003, Anderson et al. 2010, Forest et al. 2014). However, increased temperatures and freshwater input also enhance vertical density gradients and stratification, limiting the rate of ventilation of the thermocline, resulting in reduced nutrient supply and mixing (Wassmann and Reigstad 2011, Tremblay et al. 2015, Hoppe et al. 2018).

Temperature, dissolved oxygen (DO) concentration, and salinity are key environmental drivers of fish community structure and function in estuaries, such as the Mackenzie River Estuary (Whitfield and Elliot 2002). The Mackenzie Shelf (herein the "Beaufort Sea Shelf"), estuarine characteristics extend over the entire shelf, with strong seasonal processes (Carmack et al. 1989). Temperature and salinity in the region are driven by river inflow and turbidity, sea ice melt and freezing, solar insolation, air-sea exchange processes, and wind patterns (Cameron 1953, Carmack et al. 1989). Salinity and temperature have been identified as the main factors determining the distribution, and habitat suitability of estuarine fish (Whitfield 1999, Jaureguizar et al. 2004, Eick and Thiel 2014). Environmental tolerance ranges for fish species can be calculated to understand predator-prey interactions, production and consumption rates, distribution, and key life processes. Changes in environmental parameters increase the physiological demands of fish species, alter feeding opportunities, recruitment, growth, and migrations, and modify species

community structure (Roessig et al. 2004, Reist et al. 2006, Gillson 2011, Morrongiello et al. 2014).

Ecosystem modeling tools, such as Ecopath with Ecosim (EwE), have been useful to understand climate effects on marine species, as the models can simulate potential change over time. EwE is a widely used ecosystem modeling software suite applied to describe ecosystem structure including food-web linkages, and energy cycling, and to simulate ecological dynamics under the influence of human and environmental pressures (Christensen et al. 2005). A species environmental tolerance range and ecosystem modeling tools can be used together to assess the impacts of climate change on the biodiversity and food web interactions (based on the foraging arena size) (Walters and Christensen 2007) of the Beaufort Sea Shelf and Slope (BSS) and the Tarium Niryutait Marine Protected Area (TN MPA) (see The BSS EwE models subsection). Climate variations, both short- and long-term, can threaten the success and conservation objectives of the TN MPA (DFO 2010). Species physiological limits to temperature, DO, and salinity are not well defined in the Arctic (Werner et al. 2007, Allen and Polimene 2011, Steiner et al. 2016), and the lack of comprehensive data contributes to food web model uncertainty (AMAP 2017). Temperature is considered a primary driver of fish species distribution (Pörtner 2001, Hochachka and Somero 2002), where other variables such as DO and salinity may be of importance depending on the species life stage or habitat requirements (Steiner et al. 2018). To date, the majority of studies employing the EwE platform have focused on one climate impact or pathway, or covered a limited set of climate stressors (Stock et al. 2023). However, the analysis of relative and cumulative impacts of climate stressors is necessary to understand how species interactions are changing as a result of climate change, and to discern which climate effects are driving changes in the ecosystem.

Here, we update an existing BSS ecosystem model (Hoover, et al. 2021; Sora et al. 2022) with updated functional group data and investigate historical (1970–2021) changes in the ecological dynamics of this Arctic marine ecosystem. The analysis examined the effects of single and multiple climate-induced stressors, including increases in SST, sea ice loss, ocean deoxygenation, and changing ocean salinity. We focused on the environmental response of fish communities of the BSS and TN MPA in relation to the changing water properties and species' preferred environmental tolerance range or niche. To inform the effectiveness of the TN MPA, broad monitoring indicators that extend into the surrounding Beaufort Sea were used to determine the connections between large-scale ecosystem relationships, sensitivity to climate change, and processes to support future goals of the protected area. The models developed in this study provide a useful baseline for projections of the BSS ecosystem under future climate change, and offer valuable insights on impacts of changing environmental conditions on Arctic ecosystems, and how existing and planned conservation measures such as protected areas, might need to be adaptive to ensure their goals under a changing climate.

Methods

The BSS EwE models

Seven BSS EwE models were developed for this study (see Experimental model comparisons subsection). All models cover an area between −141.08°W and −128.20°W, and from the shoreline to the 500 m isobath, including the TN MPA. The TN MPA is composed of three sub-areas: Niaqunnaq, Okeevik, and Kittigaryuit, (DFO 2010, Loseto et al. 2010) (Fig. 1). The management objectives of the TN MPA include the conservation of beluga whales, anadromous fishes, and birds, along with their habitat, ecosystem, and traditional harvest (DFO 2010). Six Indigenous communities reside within the Inuvialuit Settlement Region (ISR), and three communities (Aklavik, Inuvik, and Tuktoyaktuk) have harvesting locations for whales, seals, birds/fowl, and fishes within the model area, including the TN MPA (DFO 2010).

Ecopath with ecosim framework

The EwE framework includes: (i) Ecopath, a snapshot of the mass-balance trophic model for any given time (Polovina 1984, Christensen and Pauly 1992, 1993), and (ii) Ecosim, a time-dynamic model that hindcasts or forecasts simulations built upon the initial Ecopath model (Walters et al. 1997, Walters 2000, Christensen and Walters 2004).

Functional groups

The BSS EwE models represents 31 living functional and species groups, 2 detritus functional groups, and 7 subsistence harvest groups. The living groups include trophic levels from primary producers to polar bears (*Ursus maritimus*), including important harvest species [e.g. beluga whales, bowhead whales (*Balaena mysticetus*), and seals]. For detailed descriptions of each functional group, including complete species lists, diet composition, vulnerabilities, biomass (B), production/biomass (P/B), consumption/biomass (Q/B), and ecotrophic efficiency (EE) calculations or estimates see Hoover, et al. (2021) (Tables S1–S3, SI).

Fish functional groups in the BSS EwE models include diadromous, estuarine, and marine fishes. Functional groups were created based on life history, diets and ecological characteristics, (Table S4, SI) (Hoover, et al. 2021). Functional groups of single or few species were created for common species or key food web species (e.g. functional groups: Arctic Char & Dolly Varden (*Salvelinus alpinus*, *Salvelinus malma*), Arctic & Polar Cods (*B. saida*, *Arctogadus glacialis*), Capelin (*Mallotus villosus*).

Data from the Beaufort Regional Environmental Assessment Marine Fishes Project (BREA-MFP, 2012–2014) were used to provide the list of fish species from the BSS for the fish functional groups in the EwE models for this study and Hoover, et al., (2021) (Table S5, SI). BREA-MFP was the first comprehensive sampling of fish, habitats, and food web of the shelf, slope, and deep waters of the Beaufort Sea, establishing a baseline of fish biodiversity in the region. BREA-MFP conducted sampling transects in the BSS with stations at 20–45, 75, 200, 350, and 500 m depths, along four transects [Transboundary (TBS), Garry (GRY), Kugmallit (KUG), and Dalhousie (DAL)] (Fig. 1). Two additional sampling stations at 30 m depths along the KUG transects during the 2014 sampling year were conducted in the Amauligak Lease Area. Sampling was undertaken using a modified Atlantic Western IIa otter trawl, lined with 1.27 cm stretched mesh (Niemi et al. 2020). Fish catches were sorted to the lowest taxonomic level possible onboard the vessel prior to freezing. Each specimen was later identified to the lowest taxonomic level possible. Taxonomic identification from the families Zoarcidae,

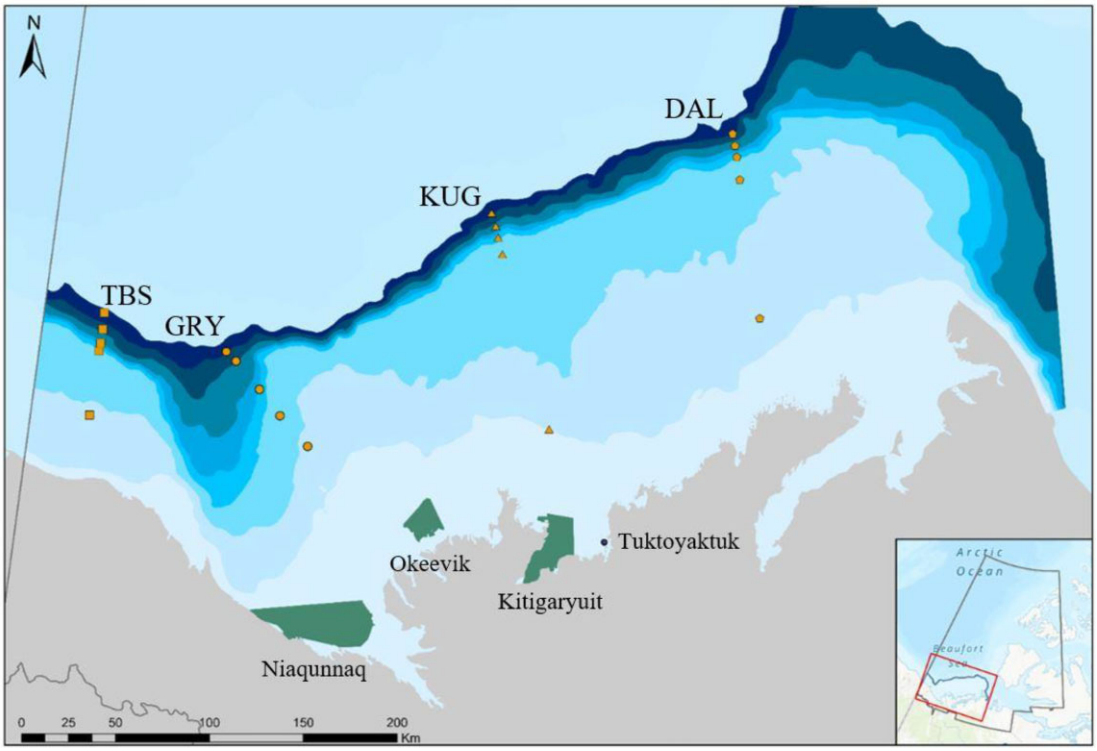

Figure 1. Beaufort sea shelf and slope (BSS) ecosystem model area extending from shore to 500 m. Contour areas include 20, 50, 100, 150, 200, 300, 400, and 500 m depths. The three sub-areas of the TN MPA are identified in green: Niaqunnaq, Okeevik, and Kittigaryuit within the ISR (black line) of the Canadian Arctic (shown in insert). Model data comes from stations (orange) sampled during the Beaufort Regional Environmental Assessment Marine Fishes Project (BREA-MFP, 2011–2014). BREA-MFP conducted sampling along four transects [Transboundary (TBS), Garry (GRY), Kugmallit (KUG), and Dalhousie (DAL)]. For this map, the base map: World Topographic Map, projected coordinate system: NAD 1983 CSRS Yukon Albers, geographic coordinate system: NAD 1983 (CSRS). Data kindly provided by Claire Hornby, DFO.

Liparidae, and Stichaedae, and genus *Artediellus* were verified using DNA barcoding (Niemi et al. 2020).

BSS mass-balance ecopath models

Ecopath provides an overview of food web structure and energy flows, where mass-balance indicates there is enough production (P_i) of each group i to support consumption, harvest, and other mortalities, as expressed in Equation 1 (Christensen et al. 2005):

$$P_i = Y_i + B_i{*}M2_i + E_i + BA_i + P_i{*}(1 - EE_i)\,. \qquad (1)$$

Where the total production (P_i) of group i equals the fishery catch rate for group i (Y_i) + biomass of i (B_i) $*$ predation mortality on prey group i from predator group j ($M2_i$) + net migration (emigration-immigration) rate (E_i) + biomass accumulation (BA_i) + other mortality ($P_i * (1\text{-}EE_i)$). Equation 1 can be re-expressed as Equation 2 (Christensen et al. 2005):

$$B_i{*}\left(\frac{P}{B}\right)_i * EE_i - \sum_{j=i}^{n} B_j{*}\left(\frac{Q}{B}\right)_j {*}DC_{ji} - Y_i - E_i - BA_i = 0. \qquad (2)$$

Where in addition to values in Equation 1, the production/biomass ratio is P/B_i, the consumption/biomass ratio is Q/B_j, and the diet of predator j of prey i is DC_{ji}. The basic parameter values for the BSS Ecopath models were based on Hoover, et al. (2021), where details of the parameter values and estimates can also be found (Tables S1–S3, SI).

Marine mammal harvest time series

We extended the harvest time series used in Hoover et al. (2021) for polar bears, bearded seals (*Erignathus barbatus*) and ringed seals (*Pusa hispida*), as well as bowhead whale abundance from 2012 to 2021, applying similar assumptions to those described in Hoover, et al., (2021) (Fig. S1, SI). Data from the Eastern Beaufort Sea Beluga Stock Assessment were used to update the beluga whale harvest time series (Harwood et al. 2020), applying similar assumptions to those described in Hoover, et al., (2021) (Fig. S1, SI).

Ecosim temporal simulations

Ecosim was used to evaluate selected climate drivers, including SST, sea ice, DO, and salinity over 51 years of simulation (1970–2021). Ecosim is a time-dynamic response to the initial Ecopath model (Christensen and Walters 2004), as expressed in Equation 3 (Christensen et al. 2005):

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)\,B_i. \qquad (3)$$

Where the growth rate for group i over time t is dB_i/dt for biomass B_i and growth efficiency (g_i, production/consumption ratio), the other natural mortality is M_i, fishing mortality is F_i, and emigration and immigration rates represented as e_i and I_i, respectively. $\sum Q_{ji}$ is the consumption rate of all prey groups i, and $\sum Q_{ij}$ is the consumption rate of all predators j onto groups i.

Environmental forcing and mediation functions

The impact of climate drivers is simulated in EwE through three different mechanisms: forcing functions (FFs), mediation functions, and environmental response functions. FFs directly force a functional group biomass, or can be used with environmental response functions. Environmental response functions represent each functional groups' environmental tolerance range or niche (see New environmental response functions subsection). When FF and environmental response functions are combined, they alter the foraging arena size via the search rate parameter (Walters and Christensen 2007). While mediation functions are used when the interactions of two functional groups are impacted by a third group (Christensen and Walters 2004). The delta SST (average °C for the model area, see Climate bias correction using the delta method subsection) FF was applied using the Apply FF (primary producer) form (i.e. Time dynamic (Ecosim) > Input > FF > Apply FF (primary producer)) (Christensen et al. 2005) following the methodology described in Hoover, et al. (2021) to directly drive modeled primary production (*P/B* ratio). Additional impacts were determined by extending the SST time series from 2012 to 2021 (British Atmospheric Data Centre 2010) (Fig. S2, SI).

New to this study, we also included an upper quartile FF for the SST (Fig. S2, SI) as a secondary temperature FF to represent temperatures at ~350–500 m depths. Within the BSS, suitable fish habitat is structured by depth, characterized by water temperature, nutrients, and salinity (McLaughlin et al. 2004, Majewski et al. 2016). The Pacific Ocean water mass is situated at ~200–350 m depths, and the warmer and more saline Atlantic water mass extends from ~400–800 m depths (Majewski et al. 2016, Stasko et al. 2017). Benthic fish (Functional groups: Flounder & Benthic Cods, Small Benthic Marine Fish) associate with these distinct habitats in the vertical structure of the BSS; where temperatures are greater than 0°C (and as high as 1°C) for depths and water masses at ~350 m (lower Pacific Ocean layer) and ~500 m (upper Atlantic Ocean layer) (Majewski et al. 2016) (Fig. S3, SI).

The mediation functions were applied in EwE using the Apply mediation (consumer) form [i.e. Time dynamic (Ecosim) > Input > Mediation > Apply mediation (consumer)] (Christensen et al. 2005) to consumer search rates. Following Hoover, et al. (2021), the sea ice (% cover for model area) time series was extended from 2012 to 2021, and used to drive the ice algae functional group via sigmoid mediation shapes (Fig. S4 and S5, SI). The sea ice mediation functions were used to model the relationship between sea ice and (i) polar bears, and (ii) Arctic cod and polar cod functional groups. In the models, reductions of sea ice cover and extent (represented by ice algae in the models) decreased hunting grounds for polar bears (Stirling et al. 1999, Hunter et al. 2007, Schliebe et al. 2008, Stirling et al. 2008), and increased vulnerability of cods to predators (Gradinger and Blumm 2004, Wieckowski et al. 2009). For the sea ice and polar bears relationship, the sigmoid shape was chosen where the starting year near the y-value maximum, as the beginning of the historical time series had higher sea ice cover and polar bears had access to ringed and bearded seals (Stirling 2002) (Fig. S5A, SI). Sigmoid shape and placement starting point was tested during the Hoover, et al. (2021) model fitting. For the Arctic & Polar Cods functional group, the sigmoid shape was chosen to represent vulnerability to predators, where the higher sea ice cover increases protection up to a threshold at the mid-point (Fig. S5B, SI).

New environmental response functions

Global temperature (°C), salinity (no units), and DO (μmol/kg) data were extracted from the World Ocean Atlas 2018 (WOA) for the environmental niche of fish species identified from BREA-MFP (Garcia et al. 2019a). Average decadal climate normal data (1981–2010), as defined by the World Meteorological Organization (WMO 2017), were extracted for temperature and salinity (Garcia et al. 2019a). DO data were available as "all years" from the WOA, which is defined as the annual mean for data collected, regardless of month or year from 1960 to 2017 (Garcia et al. 2019b). The environmental data from WOA was combined with the species data to calculate the environmental response function based on the species' preferred environmental tolerance range or niche.

FishBase and SeaLifeBase (Froese and Pauly 2023) databases provided the ecological and biological information for the temperature, salinity, and DO preferences for the modeled fish species. The Ocean Biodiversity Information System (OBIS), Global Biodiversity Information Facility (GBIF), and Nippon Foundation Nereus Program databases provided fish species occurrence record data. The R packages rworrms (Chamberlain and Vanhoorne 2023), rfishbase (Boettiger et al. 2023), robis (Provoost et al. 2022), and rgbif (Chamberlain et al. 2023) were used to determine the occurrence data of described fish species from the literature and BREA-MFP (2011–2015). The ecological, biological, and occurrence data were combined with environmental data from WOA in R Statistical Software (v2022.02.3 + 494; R Core Team 2022) to determine the species' histograms as the minimum (1st percentile), preferred minimum (10th percentile), preferred maximum (90th percentile), and maximum (99th percentile) temperature, DO, and salinity ranges of each species (Table S5 SI). The optimum values were estimated by averaging the 10th and 90th preferred percentiles. For functional groups with multiple species, the weighted averages by biomass were used for the environmental response functions.

FFs of DO (μmol/kg) and salinity (no units) were added to the BSS EwE models. Surface, bottom, and average (of surface and bottom values) DO and salinity values were extracted from two Earth System Models (ESMs): Geophysical Fluid Dynamics Laboratory-ESM4 (GFDL) and Institut Pierre-Simon Laplace-CM6A-LR (IPSL), for historical (1970–2015) values and the scenario (2016–2021) of Shared Socioeconomic Pathway (SSP) 8.5 (SSP5-8.5). SST, DO, and salinity FFs were used with environmental response functions to drive changes in fish functional group biomasses. Fish functional groups' environmental response functions for temperature (Fig. S2, SI), DO (Fig. 2), and salinity (Fig. 3) were applied to the foraging rates through the FF values (foraging arena theory). The FF used to drive the fish response was dependent on the species ecology (e.g. surface FF values for pelagic species, bottom FF values for benthic species, average FF values for mixed species groups). To avoid over-constraining the models, forcing, mediation, and environmental response functions were not applied together for any functional group. For example, as the Arctic & Polar Cods functional group was altered using the mediation function for sea ice, the environmental response for SST was not applied.

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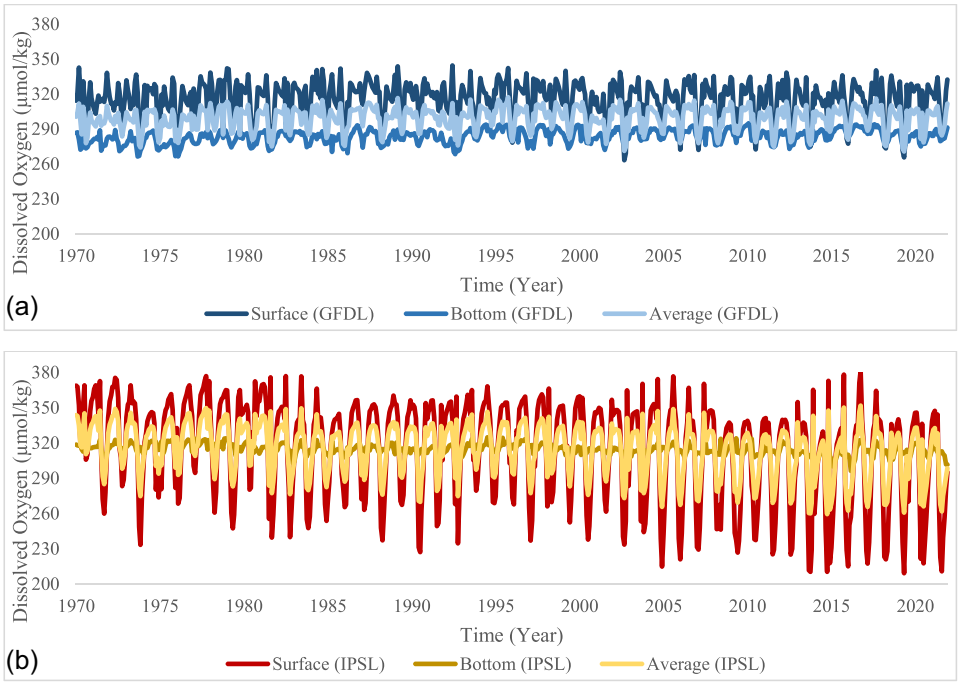

Figure 2. Earth System Model (ESM) depth-integrated values for DO (μmol/kg) extracted from (A) GFDL, and (B) IPSL. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. ESM data was used as FFs and fish functional group environmental responses in the BSS models.

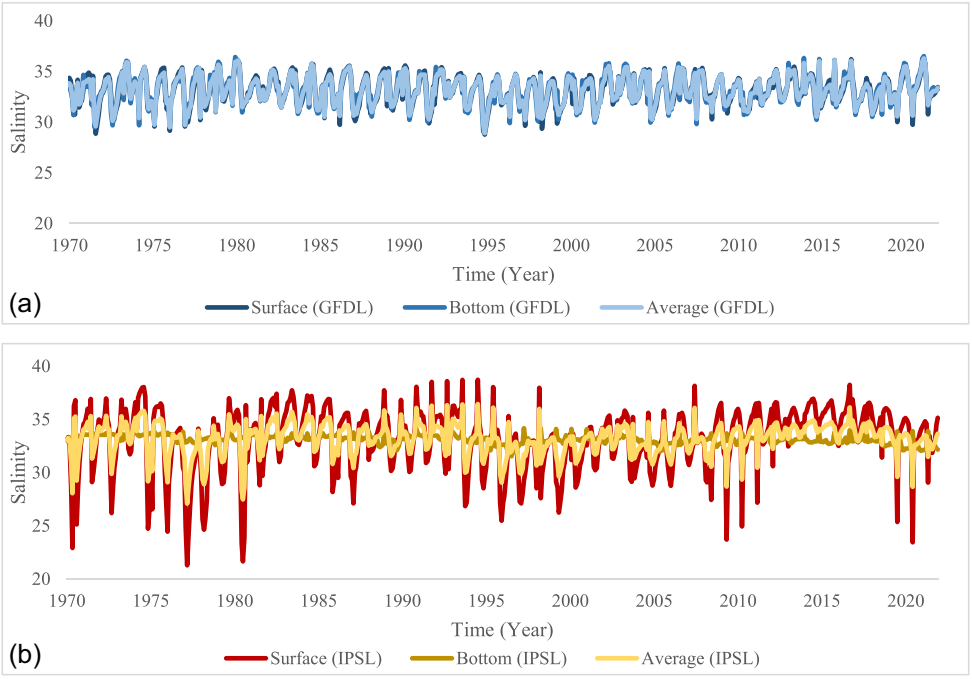

Figure 3. Earth System Model (ESM) depth-integrated values for salinity (no units) extracted from (A) GFDL, and (B) IPSL. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. ESM data was used as FFs and fish functional group environmental responses of the BSS models.

Climate bias correction using the delta method

Biases in modeled climate data can be addressed with bias correction, such as the delta method (Middelkoop et al. 2001, Räty et al. 2014, Miralha et al. 2021). From global climate models, data was corrected using the delta method, along with observational data as a reference. The delta method used in this study maintains the distribution of the climate data (SST, DO, and salinity) by calculating the mean differences between historical data (p), the scenario data (s), and observational data (o), as described by Equation 4 (Wilby and Wigley 2000, Arnell et al. 2003, Diaz-Nieto and Wilby 2005):

$$Delta = mean\,(o) + (s - mean\,(p))\,. \tag{4}$$

Table 1. Forcing functions, mediation functions, and environmental response functions applied to the 1970–2021 BSS EwE experimental food web models.

Functional group	Baseline SST, sea ice	GFDL			IPSL		
		All parameters	O_2 added	Salinity added	All parameters	O_2 added	Salinity added
Marine mammals (mediation function)							
Polar bears	ICE	ICE	ICE	ICE	ICE	ICE	ICE
Fish [environmental response functions, and mediation function (ICE only)]							
Char & dolly varden	SST	SST, SSS, SO2	SST, SO2	SST, SSS	SST, SSS, SO2	SST, SO2	SST, SSS
Ciscos & whitefish	SST	SST, SSS, SO2	SST, SO2	SST, SSS	SST, SSS, SO2	SST, SO2	SST, SSS
Salmonids	SST	SST, SSS, SO2	SST, SO2	SST, SSS	SST, SSS, SO2	SST, SO2	SST, SSS
Herring & smelt	SST	SST, SSS, SO2	SST, SO2	SST, SSS	SST, SSS, SO2	SST, SO2	SST, SSS
Arctic & polar cods	ICE	ICE, SSS, SO2	ICE, SO2	ICE, SSS	ICE, SSS, SO2	ICE, SO2	ICE, SSS
Capelin	SST	SST, SSS, SO2	SST, SO2	SST, SSS	SST, SSS, SO2	SST, SO2	SST, SSS
Flounder & benthic cods	SSTQ	SSTQ, SBS, BO2	SSTQ, BO2	SSTQ, SBS	SSTQ, SBS, BO2	SSTQ, BO2	SSTQ, SBS
Small benthic marine fish	SSTQ	SSTQ, SBS, BO2	SSTQ, BO2	SSTQ, SBS	SSTQ, SBS, BO2	SSTQ, BO2	SSTQ, SBS
Other fish	SST	SST, AS, AO2	SST, AO2	SST, AS	SST, AS, AO2	SST, AO2	SST, AS
Primary producers (direct FF)							
Producers > 5 μm	SST	SST	SST	SST	SST	SST	SST
Producers < 5 μm	SST	SST	SST	SST	SST	SST	SST
Ice agae	ICE	ICE	ICE	ICE	ICE	ICE	ICE

Data were extracted from the British Atmospheric Data Centre (2010) for SST (°C, SST), SST upper quartile (°C, SSTQ), and sea ice extent (% cover, ICE). Data were extracted from ESMs (GFDL and IPSL) for sea surface salinity (no units, SSS), sea bottom salinity (no units, SBS), average salinity (no units, AS), surface DO (μmol/kg, SO2), bottom DO (μmol/kg, BO2), and average DO (μmol/kg, AO2). Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity)

Table 2. Monte Carlo simulations and EcoSampler samples from the 1970–2021 BSS EwE "Baseline" (SST, sea ice) and experimental food web models (ESMs, GFDL, and IPSL), historical and scenario values of SSP5-8.5. Experimental models are named "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

	Baseline SST, sea ice	GFDL			IPSL		
		All parameters	O_2 added	Salinity added	All parameters	O_2 added	Salinity added
No. of samples	1000	1000	1000	1000	1000	1000	1000
No. of samples after review	939	738	938	846	861	912	873
Original sum of squares	9.081	8.866	9.081	8.768	8.697	9.106	8.730
Best sum of squares	5.690	5.030	3.935	5.384	5.026	4.955	4.644

Experimental models are named "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

Where for each climate variable (SST, DO, and salinity), the average from the ESM over 1970–2021 (p) were subtracted from each monthly climate data value (s), and added to the average observational WOA data (o). Average WOA spans 1981–2010 for SST and salinity, and 1960–2017 for DO.

Experimental model comparisons

Six experimental BSS EwE models were compared to the baseline model (includes SST and sea ice extent, herein "Baseline") in this analysis (Table 1). Models using SST, sea ice extent, DO, and salinity as forcing and mediation functions, as well as fish functional group responses, were created to determine individual and combined impacts of these environmental drivers on the BSS ecosystem. Experimental models were named "all parameters" (includes SST, sea ice, DO, salinity), "O_2 added" (includes SST, sea ice, DO,), and "salinity added" (includes SST, sea ice, salinity). SST and sea ice extent were included in all model variations as they were identified by the Special Report on the Ocean and Cryosphere in a Changing Climate (SROCC) (Meredith et al. 2019) as consistent climate-related stressors in polar regions, altering Arctic marine and terrestrial habitat, ecosystem structure and function, including species abundance, distribution, and composition, and impacted human communities.

Model uncertainties

Assessment of the temporal uncertainty of EwE modeled outputs was performed using the Monte Carlo and EcoSampler routines, following steps detailed in Steenbeek et al. (2018). Monte Carlo alters, in a stepwise fashion, the EwE input parameters in accordance with the data pedigree coefficient (i.e. coefficient of variation) (see Sora et al. 2022) to determine the best fit temporal models (Steenbeek et al. 2018). Ecosampler was used to assess parameter uncertainty for the Baseline model and experimental models of the BSS modeled time series. Ecosampler contains three modes: (i) record, which saves the alternate mass-balanced models from Monte Carlo; (ii) review, where the saved alternate models are loaded and reviewed for realistic ecosystem values; and (iii) run, where saved alternate models are loaded one at a time and run through Ecopath, and Ecosim (Steenbeek et al. 2018). One thousand Monte Carlo simulations were run for the Baseline model and experimental BSS EwE models (Table 2). The alternate models were recorded, reviewed, and run through

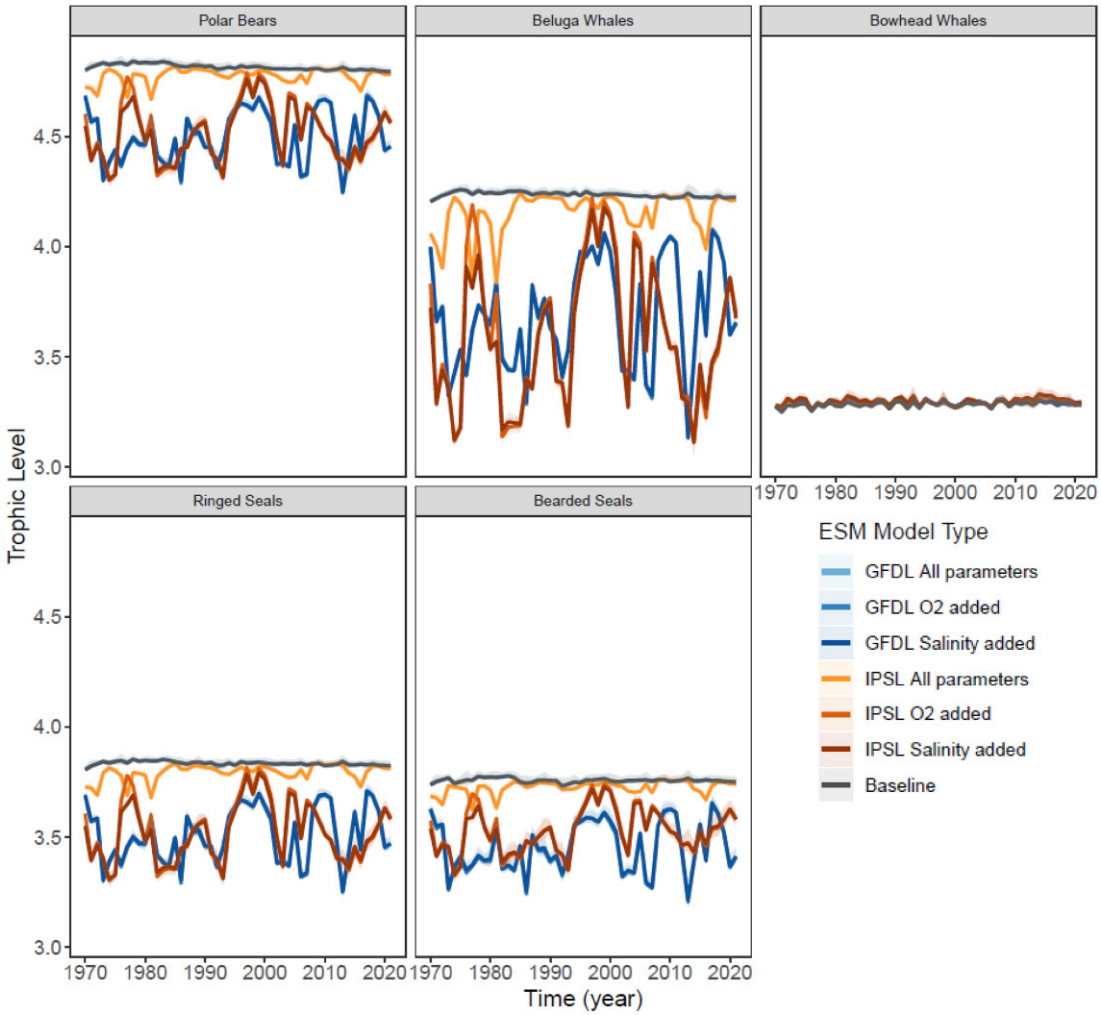

Figure 4. Historical marine mammal functional group trophic levels for the BSS. Lines indicate the mean of model predictions from EcoSampler perturbed model outputs for Baseline model, GFDL and IPSL experimental ESMs. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. Shaded areas represent the range between 5% and 95% percentiles. Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

Ecosampler to determine the uncertainty in parameters. Indicators for biomass, consumption, trophic level, Shannon diversity index (SDI), and Kempton's Q were then plotted with the 5th to 95th percentile ranges.

Biomass, consumption, trophic level, SDI, and Kempton's Q indicators were used in this study to understand the structure of the modeled BSS ecosystem (e.g. energy flow, food availability, stability of the trophic structure). SDI and Kempton's Q diversity indicators evaluated the complexity of the BSS food web. SDI compares the energy flows within a community (MacArthur 1955, Brown et al. 2006), in terms of an expected maximum diversity and richness for the ecosystem (Berrios et al. 2018). Kempton's Q controls for sample size changes by using quartile slopes to evaluate the effects of changing environmental variables onto biodiversity (Ainsworth and Pitcher 2006).

Sensitivity of ecosystem biomass to earth system modeled projections

The sensitivity of functional group biomasses to changes in ecosystem variables (SST, sea ice, DO, salinity) were tested using a sensitivity score. For the Baseline model and the six experimental BSS EwE models described in this analysis, we calculated the ΔB as the change in the experimental model biomass per year relative to the Baseline model biomass per year, Equation 5:

$$\Delta B = \frac{B_{experimental} - B_{baseline}}{B_{baseline}}, \quad (5)$$

where $B_{experimental}$ is the functional group annual biomass for each experimental BSS EwE model, and $B_{baseline}$ is the annual biomass for the corresponding Baseline model biomass of the functional group.

We calculated the ΔESM as the change in each monthly climate variable by the 1970–2021 average. To standardize ΔESM, we divided obtained values by the standard deviation of each climate variable from 1970–2021, Equation 6:

$$\Delta ESM = \frac{X_i - \bar{x}}{sd}, \quad (6)$$

where X_i is the climate variable for month i, x is the climate variable average from 1970–2021, and sd is the standard deviation of the climate variable.

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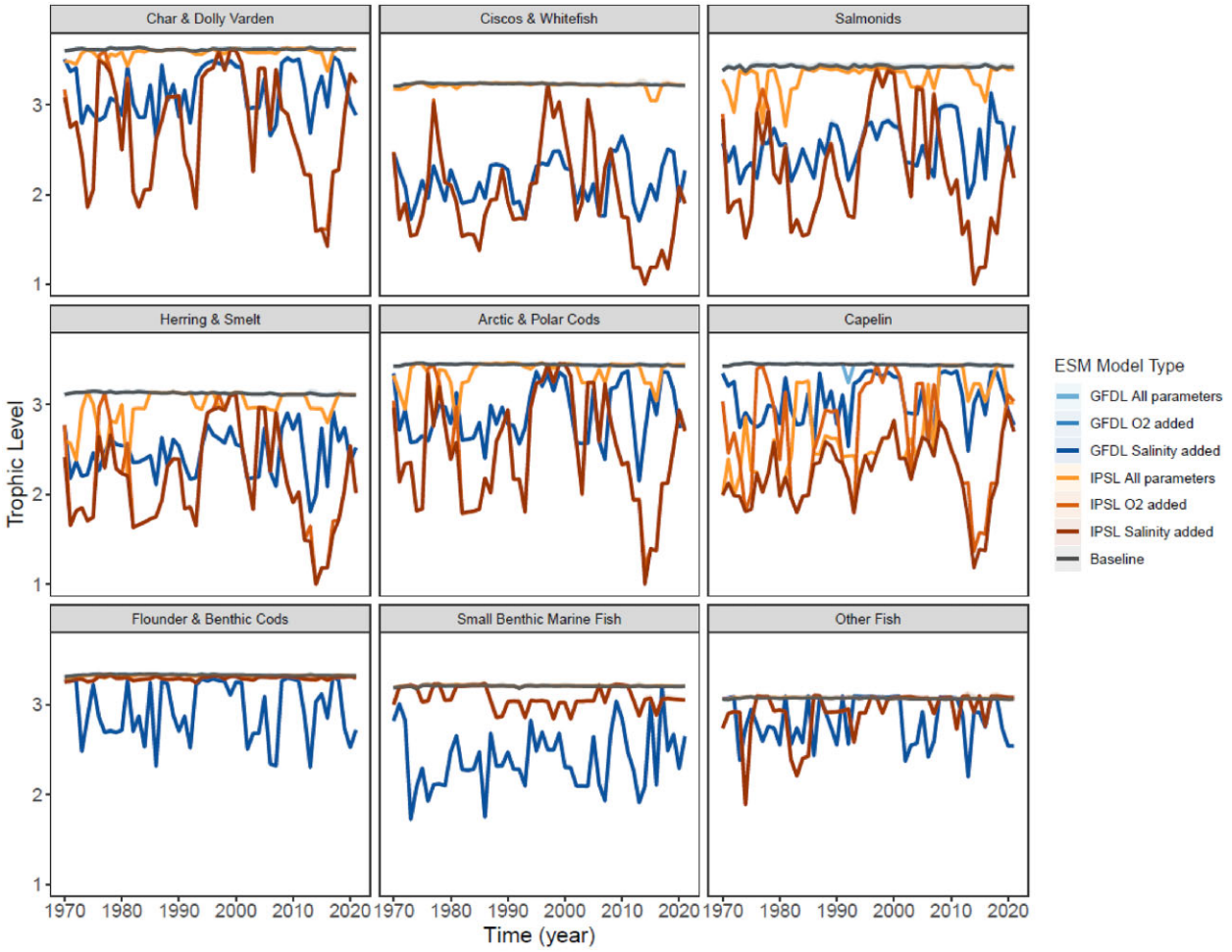

Figure 5. Historical fish functional group trophic levels for the BSS. Lines indicate the mean of model predictions from EcoSampler perturbed model outputs for Baseline model, GFDL and IPSL ESMs. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. Shaded areas represent the range between 5% and 95% percentiles. Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

The sensitivity score for each functional group is equal to the ratio between the ΔB and ΔESM of each climate variable. The farther the deviation away from 0, the higher the sensitivity of the functional group biomass to the climate variable.

Canonical correspondence analysis

The multivariate direct ordination method of canonical correspondence analysis (CCA) was used to understand the impacts of the environmental variables (SST, sea ice, DO, salinity) on the biomass of fish species in the BSS EwE experimental and Baseline models. CCA identifies joint modes or mutual information between the datasets of environmental variables and fish biomass, where a singular value decomposition (SVD) is applied to the covariance matrix (Zhang et al. 2020). The maximum covariance between the multidimensional variables is calculated via CCA (Zhang et al. 2020). CCA assumes species-environment associations that are linear, ranking the importance of the environmental variables to each species (ter Braak 1986, ter Braak and Cajo 1994, ter Braak and Verdonschot 1995). All CCA statistical tests were performed using the vegan library in R (Oksanen et al. 2022).

In CCA, the maximum covariance between the variables (W and V) is calculated to determine the correlation coefficient ($C_1 = cor(W_1 \cdot V_1)$), (Kotsias et al. 2020). The CCA outputs include "predictor" and "predictand" variables, canonical scores for each variable, and canonical correlations (Kotsias et al. 2020). Biological and environmental data from the six experimental models and one Baseline model were included as continuous predictor variables in the CCA. Ordination biplots for each experimental model were generated, indicating the correlation between the species and environmental variables (Quinn and Keough 2002).

Results

Trophic levels for marine mammals and fish functional groups

Most marine mammals and fish functional groups had high variability in mean trophic levels when an experimental model included salinity (GFDL and IPSL "all parameters" and "salinity added"). Decreases in mean trophic levels were simulated in the historical time series in 1974, 1982, 1993, 2014 (Figs. 4 and 5). Low variability was simulated when oxygen was included in the IPSL models compared to the Baseline model. Bowhead whales, Flounder & Benthic Cods, and Other Fish functional groups showed no major changes in trophic

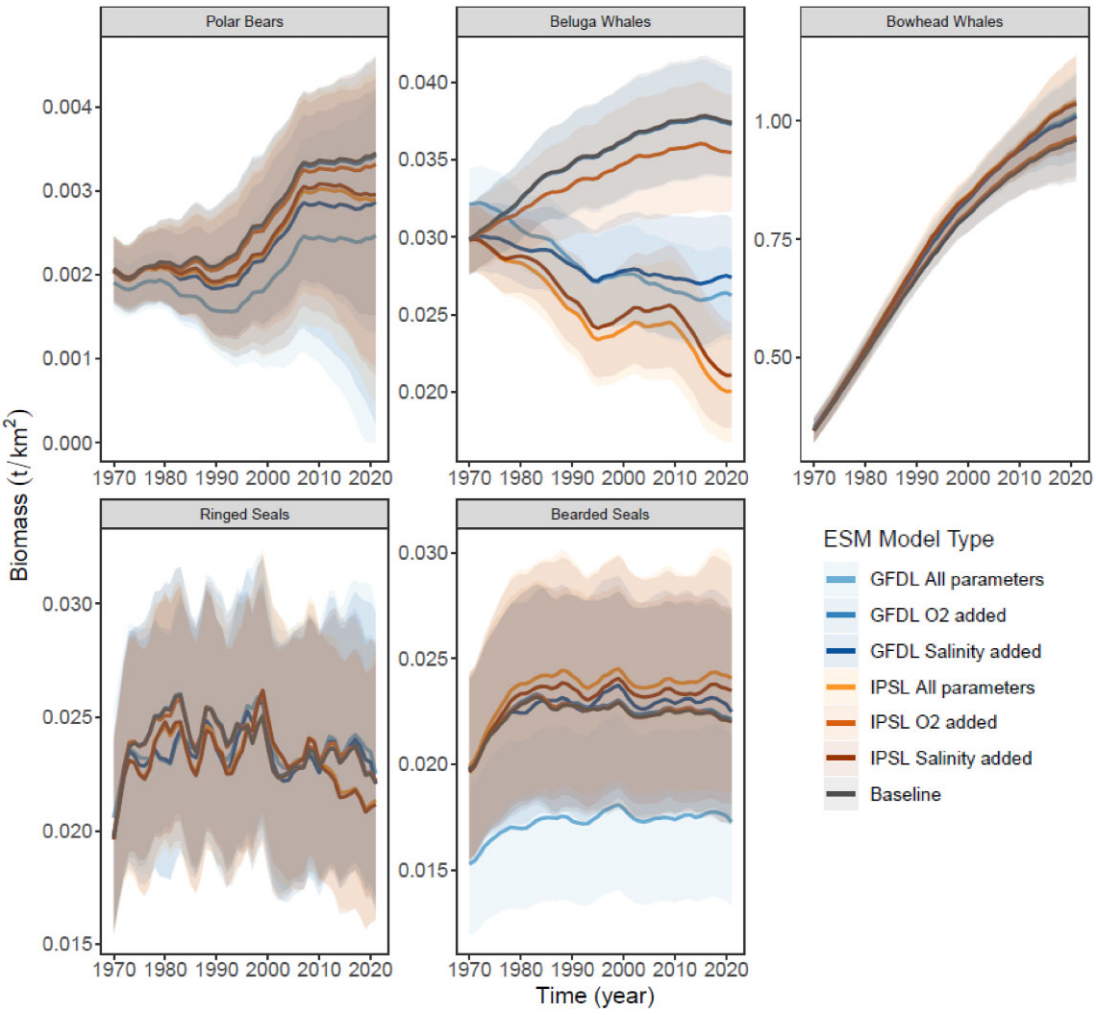

Figure 6. Historical marine mammal functional group biomass (t/km^2) for the BSS. Lines indicate the mean of model predictions from EcoSampler perturbed model outputs for Baseline model, GFDL and IPSL ESMs. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. Shaded areas represent the range between 5% and 95% percentiles. Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

levels with the addition of salinity or oxygen over the time series.

Biomass for marine mammals and fish functional groups

The mean biomass of most marine mammal functional groups increased or remained stable over the historical time series, with all experimental ESM model types per functional group following a similar trendline (Fig. 6). Polar bears biomass increased until 2005, then stabilized for the remainder of the simulated time series. Bowhead whales biomass continued to increase throughout the time series. Ringed and Bearded Seals biomass increased for the first few years of the historical time series (~1974), then stabilized for the remainder of the time series. Beluga Whales was the only functional group with modeled differences in historical trends between experimental ESMs (i) IPSL "all parameters" and "salinity added" models (low biomass), and (ii) baseline model, GFDL and IPSL "O_2 added" models (high biomass).

As simulated with changes in trophic levels and consumption (see Consumption/biomass for marine mammal and fish functional groups subsection) Ciscos & Whitefish, Herring & Smelt, and Arctic & Polar Cods functional group biomass decreased during the years 1974, 1982, 1993, 2014 when the experimental models included salinity (GFDL and IPSL "all parameters" and "salinity added") (Fig. 7). Char & Dolly Varden, Salmonids, Capelin, and Other Fish were the only functional groups to have biomass stability over the historical time series. The IPSL models had larger variability over the historical time series than the GFDL models. When comparing the GFDL and IPSL experimental models, an opposite trend was simulated for the Small Benthic Marine Fish functional group, where GFDL ESMs decreased the biomass, and IPSL ESMs increased the biomass.

Consumption/biomass for marine mammal and fish functional groups

Similar historical trendlines for marine mammal consumption rates were observed across all experimental ESMs (Fig. 8). The majority of marine mammal functional groups did not have a simulated difference in consumption rates between the Baseline model or experimental models. In general, the

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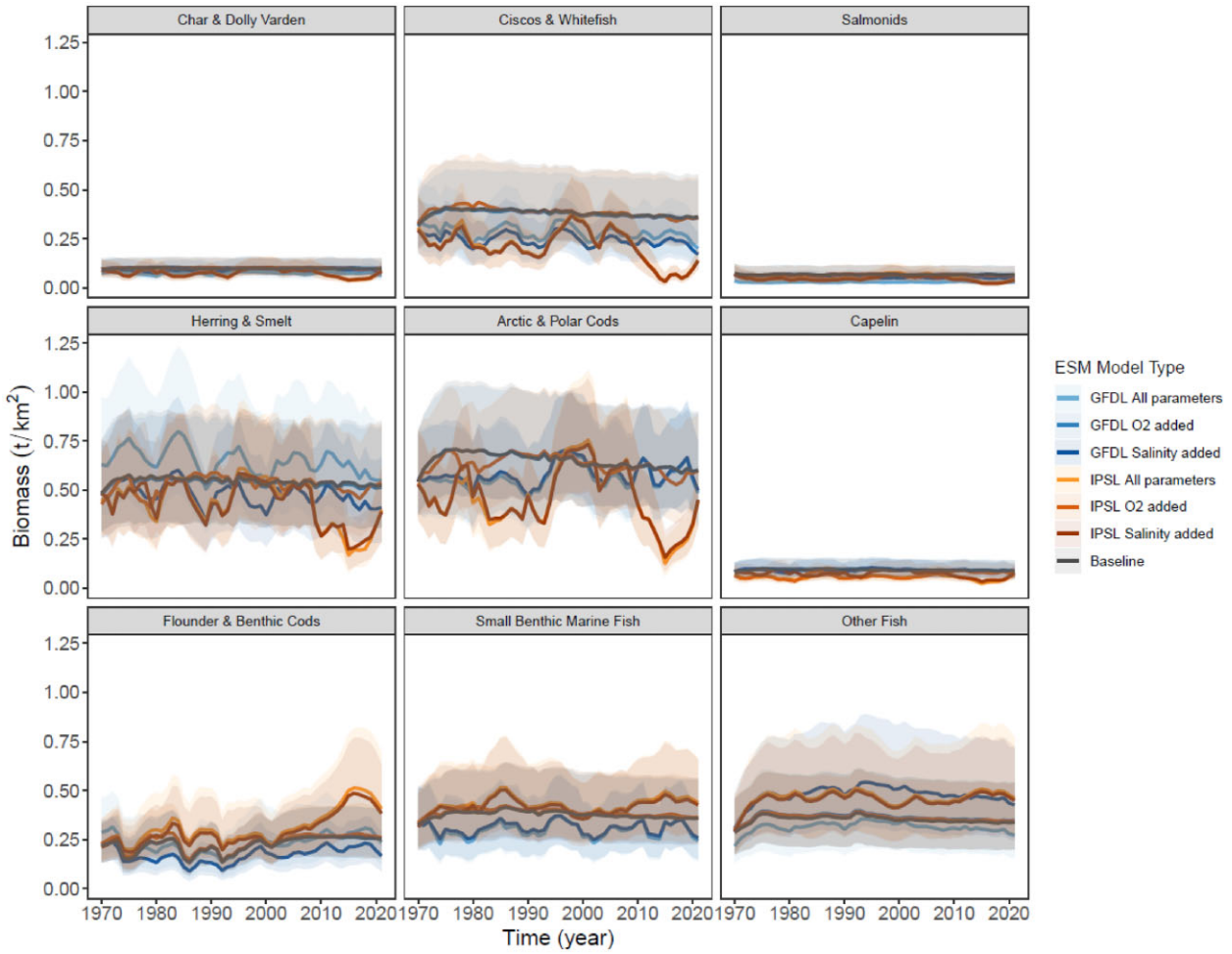

Figure 7. Historical fish functional group biomass (t/km^2) for the BSS. Lines indicate the mean of model predictions from EcoSampler perturbed model outputs for Baseline model, GFDL and IPSL ESMs. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. Shaded areas represent the range between 5% and 95% percentiles. Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

IPSL "salinity added" model provided the lowest consumption rates, while the GFDL "all parameters" model provided the highest consumption rates.

Most fish functional groups had large variations throughout the simulated time series. Ciscos & Whitefish, Salmonids, Herring & Smelt, and Arctic & Polar Cods functional groups approached low consumption rates in 2014 for the simulated IPSL time series, followed by a quick recovery in subsequent years (Fig. 9). Any variation observed in fish consumption rates was highest in the GFDL and IPSL "all parameters" and "salinity added" models, and coincided with the similar years of fish biomass increases or decreases. No difference was observed between the Baseline model or GFDL and IPSL "O_2 added" models.

Shannon diversity index (SDI) and Kempton's Q

No simulated differences in SDI values was observed between the Baseline model or experimental ESMs (Fig. 10A). The Kempton's Q index (Fig. 10B) had similar trendlines for (i) GFDL "O_2 added" and Baseline models (little variation), (ii) GFDL "all parameters" and "salinity added" models (high variation), and (iii) IPSL "all parameters" and "salinity added" models (high variation). IPSL "O_2 added" model differed slightly from the GFDL "O_2 added" and Baseline models with a lower Kempton's Q index.

The GFDL and IPSL "all parameters" and "salinity added" experimental models had the highest variation over the historical time series. For these ESMs, the lowest Kempton Q index was in the years: 1979, 1990, 1996, and 2000. The highest index values were recorded in the years: 1974, 1983, 1993, 2003, 2013.

Sensitivity analysis of ecosystem biomass to ESMs

Results from the sensitivity analysis show that ΔB are most sensitive to changes in salinity, followed by temperature (SST, Baseline), and DO across all fish groups and ESMs (Fig. 11). Overall, increasing salinity led to decrease in biomass across the fish functional groups.

Char & Dolly Varden, Ciscos & Whitefish, Herring & Smelt, and Arctic & Polar Cods registered decreases in biomass with both GFDL and IPSL "salinity added" experimental models. Capelin functional group biomass was only negatively impacted by the IPSL "O_2 added" and "salinity added" ESMs Flounder & Benthic Cods, and Small Benthic

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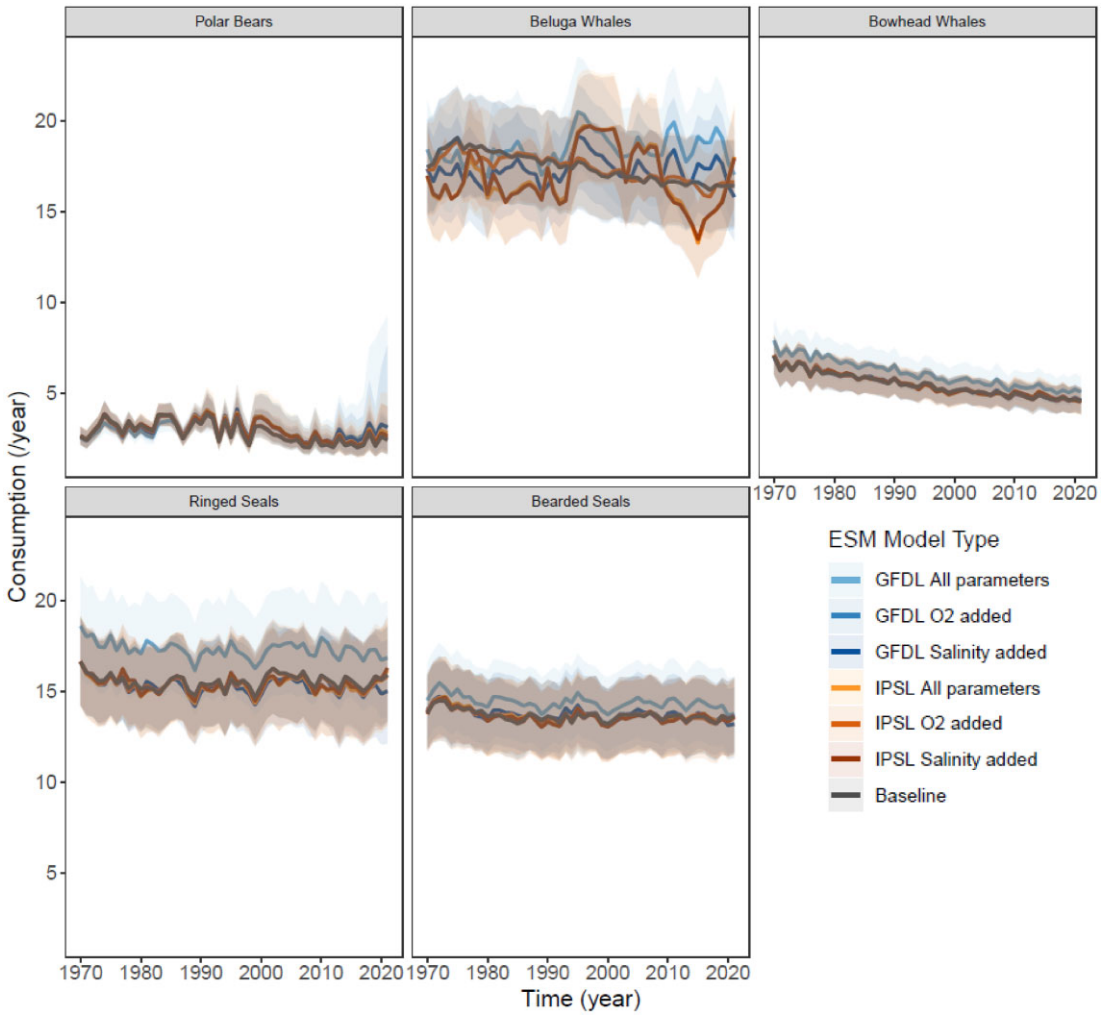

Figure 8. Historical marine mammal functional group consumption rates (/year) for the BSS. Lines indicate the mean of model predictions from EcoSampler perturbed model outputs for Baseline model, GFDL and IPSL ESMs. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. Shaded areas represent the range between 5% and 95% percentiles. Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

Marine Fish had decreases in biomass only in the GFDL "O_2 added" and "salinity added" ESMs Flounder & Benthic Cods, Small Benthic Marine Fish, and Other Fish functional groups had increases in biomass when salinity was included in the experimental ESMs Fish functional group sensitivity to changes in DO concentrations showed little deviation away from 0 in ΔB. This sensitivity score suggests that the fish biomass in the historical experimental time series are not sensitive to changes in DO.

Species-environment associations through CCA

In the six experimental BSS EwE models, the CCA1 and CCA2 axes correlations differed between the GFDL and IPSL models (Table 3). For the GFDL models, the CCA1 axis was most correlated with SST, and the CCA2 axis was most correlated with sea surface salinity, followed by DO. For the IPSL models, the CCA1 axis was most correlated with sea surface salinity (SSS), and the CCA2 axis in was most correlated with SST, followed by sea ice. The % correlation in the GFDL and IPSL experimental models ranged from 24% to 45%, and 40% to 60%, respectively (Table 4). The IPSL models had a higher % correlation than the GFDL models for the "all parameters" and "salinity added" models. Similar % correlations for the "O_2 added" GFDL and IPSL models were simulated, with a slightly higher correlation than the Baseline model.

The amount of influence each environmental variable possesses onto the functional groups (arrow proximity and direction) can be seen when comparing across experimental models. In the plots for both ESMs, temperature and salinity arrows were longer than DO. This is reinforced in Table 4, where SST and SSS had a strong correlation for CCA1 and CCA2 axes, respectively. Furthermore, the lower influence of DO compared to salinity can be seen when comparing environmental variable arrows in the "all parameters" and "salinity added" models. Arrow directions remained the same in the Figs. 12A and C for GFDL ESMs, and Figs. 13A and C for IPSL ESMs The influence of DO is masked when salinity is included in the models. The addition of DO to the ESMs exhibited a small influence to arrow directions as shown in the "O_2 added" models (Figs. 12B and 13B) compared to the Baseline model (Fig. 14). Therefore, the influence on arrow proximity and direction varied through the addition of each environmental variable.

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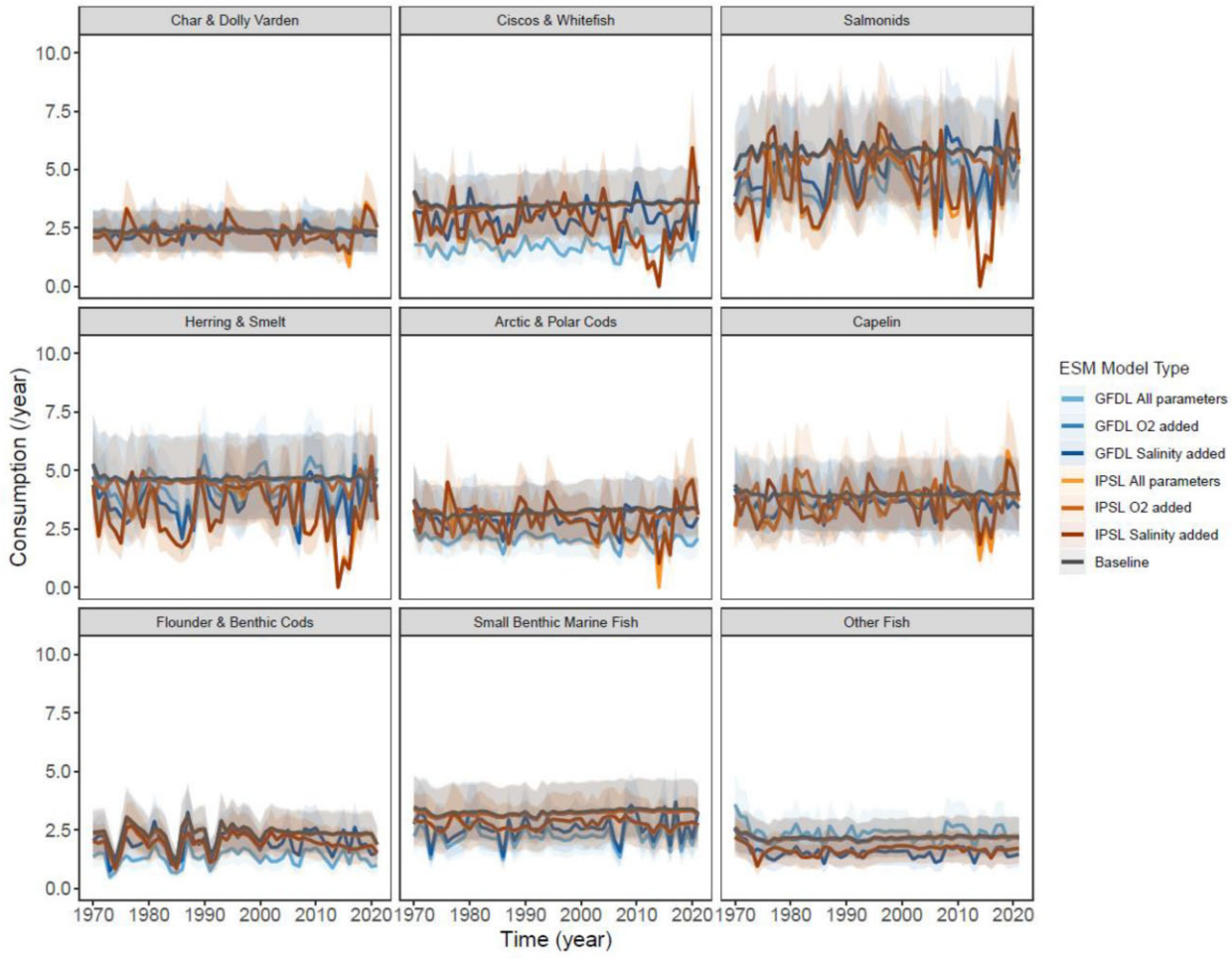

Figure 9. Historical fish functional group consumption rates (/year) for the BSS. Lines indicate the mean and of model predictions from EcoSampler perturbed model outputs for Baseline model, GFDL and IPSL ESMs. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. Shaded areas represent the range between 5% and 95% percentiles. Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

Within each CCA for the experimental models and the Baseline model, fish functional groups were similarly clustered. In the Baseline model, Char & Dolly Varden, Salmonids, and Flounder & Benthic Cods were positively correlated with SST and sea ice, while all other fish functional groups had a slight negative correlation. In the GFDL models, the strong correlations were as follows: (i) Salmonids, and Flounder & Benthic Cods positively associated with SST, (ii) Char & Dolly Varden, Arctic & Polar Cods, and Small Benthic Marine Fish were positively associated with DO and negatively associated with salinity, and (iii) Ciscos & Whitefish, Herring & Smelt, Capelin, and Other Fish were positively associated with DO and negatively associated with temperature. No strong positive or negative correlations with sea ice were observed in the GFDL models. In the IPSL models, the strong correlations were as follows: (i) Flounder & Benthic Cods were positively associated with temperature, (ii) Herring & Smelt, Capelin, Small Benthic Marine Fish, and Other Fish were negatively associated with temperature and positively associated with salinity and DO, (iii) Char & Dolly Varden, Ciscos & Whitefish, Salmonids, and Arctic & Polar Cods were positively associated with sea ice and negatively associated with salinity.

Discussion

Sea surface temperature and salinity time series

Climate-driven models can explain how changes in environmental variables are affecting ecosystem dynamics and production (Brander 2015). Within ecosystem modeling, predator consumption rates can be altered to incorporate temperature-dependent physiological and bioenergetic costs (Johansen et al. 2015). In this study, the experimental models with increased SST and salinity time series decreased marine mammal and fish trophic levels, biomass, consumption rates, and the diversity indicator Kempton's Q. Sensitivity of the experimental models to temperature was indicated with the ΔB analysis and negative correlations in the CCA. Ciscos & Whitefish, Arctic & Polar Cods, Capelin, and Herring & Smelt functional groups had negative correlations with temperature, indicating they are not tolerant to ocean warming. Environmental variables such as water temperature impact the physiological rates and bioenergetics (e.g. metabolic processes, life history traits) of fish, as they are ectotherms (Jobling 1994, Humphries and McCann 2014, Chabot et al. 2016). Fish have a higher metabolic demand with increased SST, where high temperatures can trigger a stress response and reduced con-

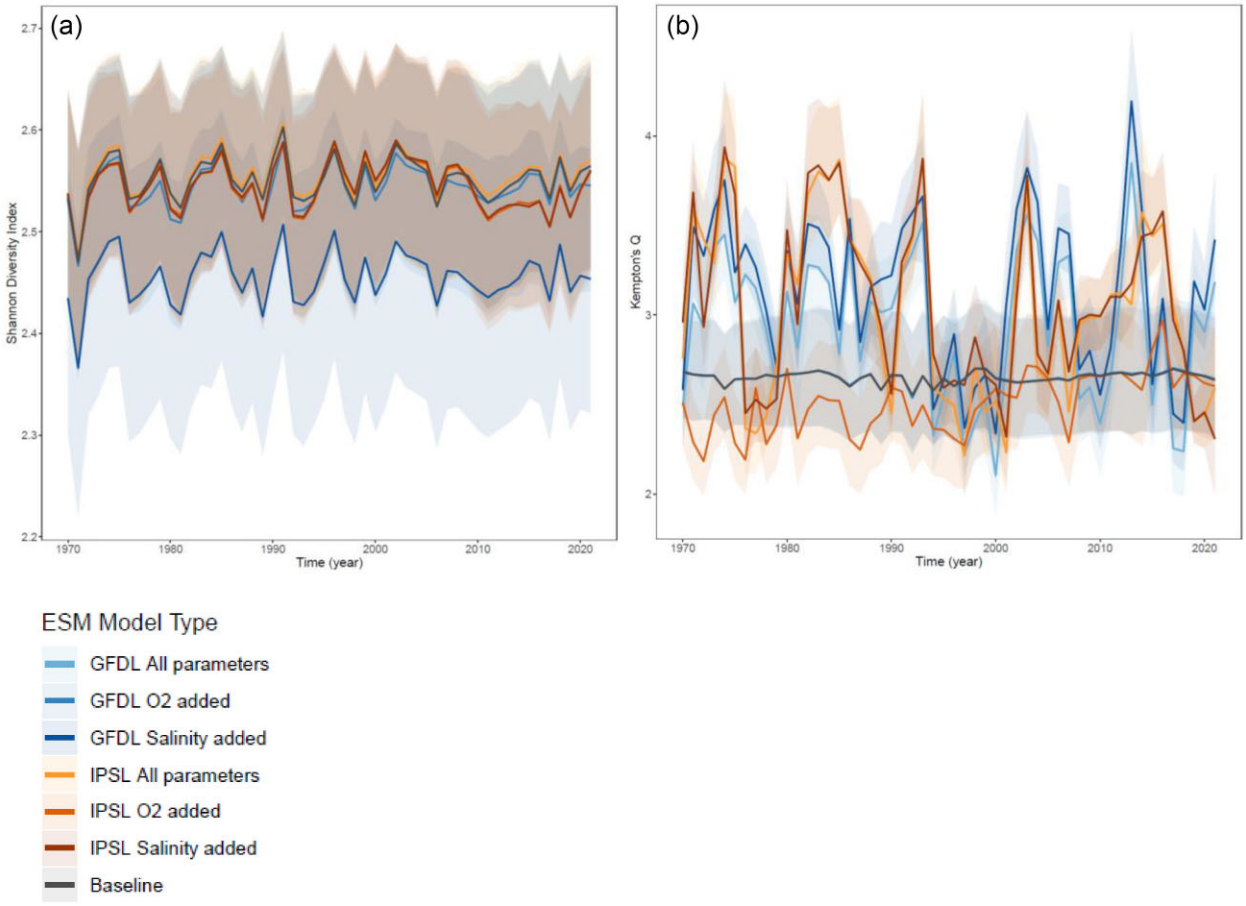

Figure 10. Diversity Indicators of (A) SDI, and (B) Kempton's Q index for the BSS. Lines indicate the mean of model predictions from EcoSampler perturbed model outputs for Baseline model, GFDL and IPSL ESMs. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. Shaded areas represent the range between 5% and 95% percentiles. Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

sumption rates when approaching their maximum temperature range (Brett 1971, Jobling 1997, Nowicki et al. 2012, Johansen et al. 2014). In this study, fish consumption rates (*Q/B* ratio) were simulated to decline during extreme high temperature and salinity years, but recovered quickly once modeled temperature and salinity time series returned to normal values. Metabolic simulations by Jobling (1994) and Fogarty and Collie (2020), also show consumption rates increasing in warming waters to an optimum, then decreasing quickly once temperatures reach the maximum of the temperature range, or when temperatures returned to cooler values. Furthermore, the higher metabolic demands at higher water temperature can limit the energy available for growth and reproduction (*P/B* ratio) (Jobling 1994, Neubauer and Andersen 2019). Sustained unfavorable environmental conditions has previously led to stock collapse, e.g. Bering Sea snow crab (*Chionoecetes opilio*) (Szuwalski et al. 2023) or Gulf of Alaska Pacific cod (*Gadus macrocephalus*) (Barbeaux et al. 2020). These specific populations declined dramatically after years of marine heat waves due to water temperatures raising metabolic demands beyond foraging and consumption rates, reduced prey availability, and recruitment.

Climate-induced changes in the BSS and TN MPA have important implications for fish distributions, particularly for species currently at the limit of their latitudinal distribution (Hollowed et al. 2013, Fossheim et al. 2015). Altered habitat suitability may lead to changes in species life cycles or other physiological adaptations (Logan et al. 2014). The Aquatic Species Physiological Limits Database compiled a list of 90 Arctic species, with physiological tolerances of temperature and pH for 12 fish species from laboratory studies (Table S6, SI) (Steiner et al. 2018). Temperature niches/limits for some Arctic fish species were calculated to be narrower in this study than in Steiner at al. et al. (2018): Arctic Char (0°C–23°C) vs this study's Char & Dolly Varden (-1.2°C–11.9°C), Arctic Cod (-1.4°C–10.8°C) vs this study's Arctic & Polar Cods (-1.2°C–4.1°C), Capelin (-1.5°C–14°C) vs this study's Capelin (-0.5°C–7.4°C), and Pacific Herring (4.7°C–13.3°C), vs this study's Herring & Smelt (-0.5°C–9.8°C). Differences between our study and Steiner et al. (2018), may be due to the database using laboratory studies, where this study utilized presence/absence species distributions. Furthermore, the inclusion of additional fish species in the functional groups with lower temperature ranges (e.g. Dolly varden temperature range: -1.2–9.5°C, Polar cod temperature range: -1.3–3°C) decreased the overall weighted average of the calculated environmental niche. The fish temperature ranges were based on global species distributions, which does not account for local acclimation (Johnson and Kelsch 1998). Moreover, this study did not include multi-stanza functional groups for species' life history stages, where egg or larvae stages are more sensitive to environmental changes (Pörtner and Peck 2010). We do not

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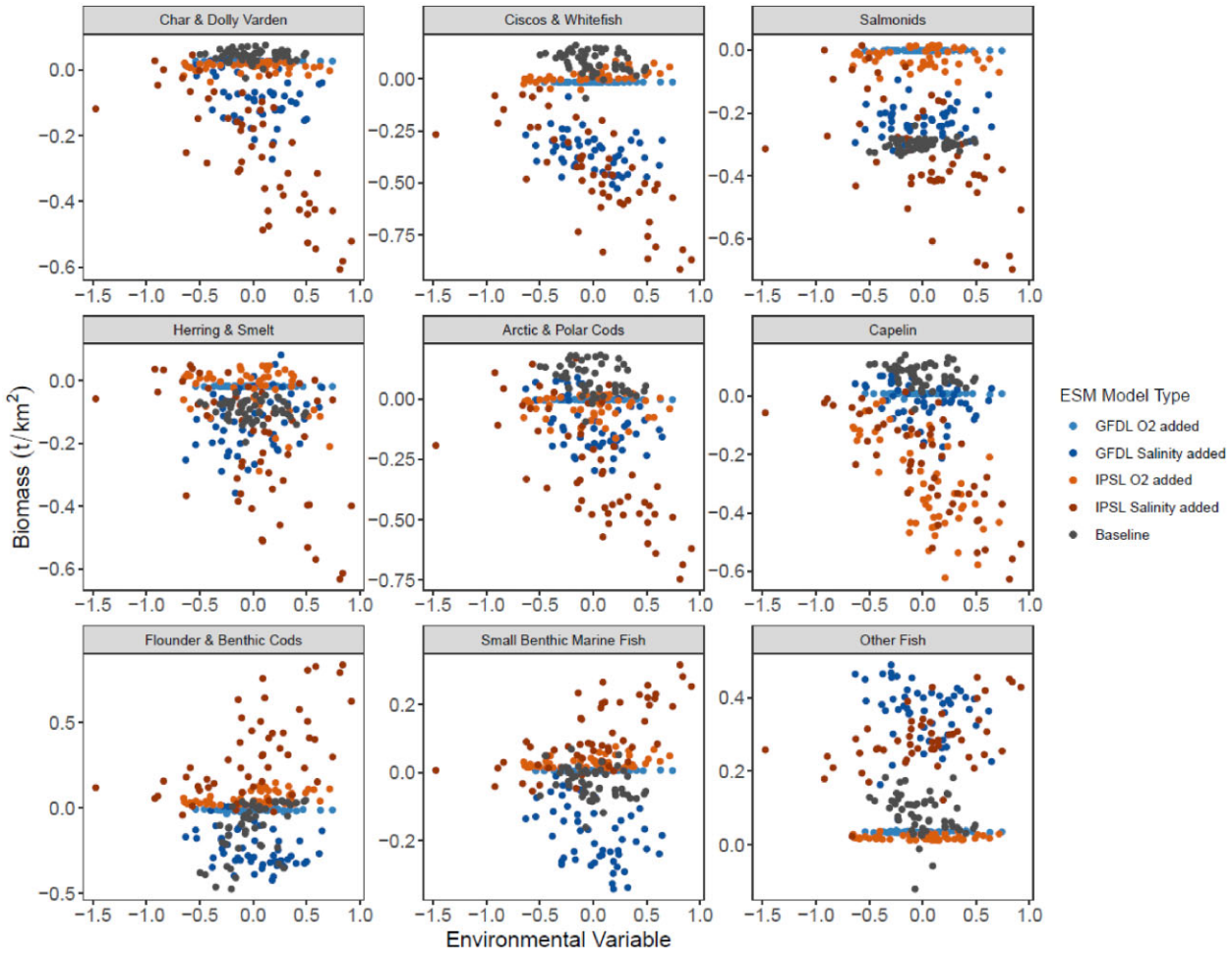

Figure 11. Sensitivity of fish biomass to changes in experimental Earth System Modeled historical projections of salinity, oxygen, and temperature, in the BSS. Data includes historical (1970–2015) and scenario (2016–2021) values of SSP5-8.5. Experimental models are named "Baseline" (SST, sea ice), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity).

expect the use of narrower temperature ranges calculated in this study to have an impact on the robustness of the indicators or the analysis.

The variability of salinity and temperature due to freshwater inputs are important drivers of the BSS, including estuarine habitat created by the Mackenzie River (2nd largest river outflow of the entire Arctic). The Mackenzie River plume extent is directed by ice and atmospheric forcing, where freshwater discharge can flow beyond the study area to the east into the Canadian Arctic Archipelago, or north to the Canada Basin (McLaughlin et al. 2011, Doxaran et al. 2015). Output from Arctic rivers like the Mackenzie River have increased recently, and may continue to do so in the future (Doxaran et al. 2015). Salinity is indicated as the main factor restricting the abundance, distribution, habitat suitability, and key life processes (e.g. feeding, growth, migration) of marine and anadromous fish (Roessig et al. 2004, Reist et al. 2006, Gillson 2011, Morrongiello et al. 2014, Roux et al. 2016) hence supporting the results presented here. In this study, the experimental models with salinity time series decreased the trophic levels of the functional groups of marine mammals (Beluga Whales) and fish (Char & Dolly Varden, Ciscos & Whitefish, Salmonids, Herring & Smelt, Arctic & Polar Cods, Capelin), marine mammals' biomass and consumption (Beluga Whales, Ringed Seals), fish biomass and consumption (Ciscos & Whitefish, Herring & Smelt, Arctic & Polar Cods), and the ecosystem diversity indicator Kempton's Q. These declines were simulated after high salinity events in the experimental ESMs time series (ranging from 34.1–35.4). Abundance and distribution changes in small pelagic forage fishes such as capelin (*M. villosus*) and Pacific herring (*Clupea pallasii*) have been observed in other high latitude ecosystems after unfavorable conditions (e.g. Anderson and Piatt 1999, Hay et al. 2001, Carscadden et al. 2013, Ingvaldsen and Gjøsæter 2013, McGowan et al. 2020, Yasumiishi et al. 2020, Baker and Siddon 2021). Fish species with limited ecological niches have a higher sensitivity to climate change (Roessig et al. 2004, Reist et al. 2006, Pörtner and Peck 2010). The preferred salinity ranges for fish functional groups in this study encompassed lower salinity or more estuarine values (e.g. Ciscos & Whitefish preferred salinity range: 24.61–33.25). ΔB analysis and the axes of the CCA correlated strongest with salinity, temperature, and sea ice, indicating that these environmental factors significantly influenced the fish functional groups in the BSS. Negative correlations with salinity for the fish functional groups Char & Dolly Varden, Ciscos & Whitefish, Salmonids, Herring & Smelt, and Small Benthic Marine Fish indicated they are tolerant of freshening in the BSS likely reflecting their natural life history.

Table 3. Correlation of the environmental variables: SST (°C, SST), sea ice extent (% cover, ICE), sea surface salinity (no units, SSS), sea bottom salinity (no units, SBS), surface DO (μmol/kg, SO2), bottom DO (μmol/kg, BO2) per experimental ESM (GFDL, IPSL), with the first two axes of the CCA (CCA1 and CCA2) on the biomass of fish species in the BSS.

	Baseline		GFDL		IPSL	
Environmental variable	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2
"All parameters" models						
SST	**−0.87**	0.49	**0.67**	−0.10	0.51	**−0.57**
ICE	−0.27	**−0.96**	−0.02	−0.11	−0.17	−0.10
SSS	–	–	−0.48	**−0.79**	**0.85**	0.44
SBS	–	–	−0.31	−0.65	−0.23	0.49
SO2	–	–	−0.40	0.63	−0.75	0.48
BO2	–	–	0.28	0.29	−0.72	0.31
"O_2 added" models						
SST	–	–	**0.77**	0.22	−0.69	0.19
ICE	–	–	0.24	0.09	−0.21	**0.64**
SO2	–	–	−0.40	0.04	**0.86**	0.47
BO2	–	–	0.48	**−0.59**	0.72	0.37
"Salinity added" models						
SST	–	–	**0.76**	−0.54	0.50	**−0.73**
ICE	–	–	−0.07	−0.26	−0.20	−0.12
SSS	–	–	−0.69	**−0.57**	**0.85**	0.45
SBS	–	–	−0.45	−0.37	−0.23	0.64

Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity). Highest correlated values are in bold.

Table 4. Overall correlation of the environmental variables (temperature, sea ice, DO, salinity), with the first two axes of the CCA (CCA1 and CCA2) on the biomass of fish species in the BSS per experimental ESM (GFDL, IPSL).

ESM model type	CCA1 (%)	CCA2 (%)	Total (%)
Baseline	34.20	0.02	34.22
GFDL "All parameters"	29.87	8.64	38.51
GFDL "O_2 added"	43.43	1.37	44.80
GFDL "Salinity added"	19.17	4.60	23.77
IPSL "All parameters"	53.80	6.18	59.98
IPSL "O_2 added"	33.45	6.83	40.28
IPSL "Salinity added"	55.88	4.26	60.14

Experimental models are named "Baseline" (SST, sea ice), "All parameters" (SST, sea ice, DO, salinity), "O_2 added" (SST, sea ice, DO), and "Salinity added" (SST, sea ice, salinity)

Dissolved oxygen time series

We found that including DO time series did not have an apparent impact on fish functional groups in the experimental models of this study. However, there were no simulated changes in historical time series for DO concentrations, and no thresholds were surpassed in the BSS, so this result is expected. Future projections of ocean deoxygenation time series may change this result. Furthermore, while oxygen solubility increases with colder water temperatures (leading to greater DO concentrations), and oxygen demands of fish decreases (Roessig et al. 2004); other polar estuarine studies found that the gradient of DO did not impact the distribution or abundance of fish species (Carmack and Macdonald 2008). Therefore, the experimental model response including DO time series are not unexpected.

Model uncertainties

Uncertainty in the model input data reveals knowledge gaps that persist in the BSS ecosystem. Fish biomass was estimated by the EwE models due to limited abundance data of fish populations in the BSS. Similarly, as marine mammal abundance and harvest estimates are limited, data time series followed similar assumptions as Hoover, et al., (2021). Additionally, biases from the sampling or harvest studies used for input data may not provide the full spectrum of species interactions or regional uncertainty due to sampling occurring in summer months. Environmental time series of temperature, sea ice, DO, and salinity were additional sources of uncertainty in this study. Assumptions made in the generation of the time series may mask seasonality, extreme events, or other limiting factors for primary and secondary producers, and fish functional groups. EwE models are complex and there can be tradeoffs between increased realism and the uncertainty (Collie et al. 2016), where the scope of modeled ecosystem processes may be beyond the data currently available (Beckage et al. 2011, Ruiz and Kuikka 2012, Planque 2016).

As data are limited and models represent an abstract version of reality, the complexity and interactions of the input data are subject to uncertainty (Loucks et al. 2005). Six experimental models were created to explore individual and synergistic climate drivers, allowing for the exploration of each driver's influence on the system and individual species groups. However, input parameter uncertainties and model uncertainties can interact, where uncertainties are then associated with modeled output (Loucks et al. 2005). For example, diet composition inherently has bias due to limited data available or regional and/or seasonal uncertainty due to summer sampling. Within EwE, the uncertainty analysis was based around the precision, associated with individual parameters, as inputted via the pedigree in Ecopath (Christensen and Walters 2004). EcoSampler and Monte Carlo routines were used to investigate model robustness and uncertainty (Christensen and Walters 2004), and explore other plausible models from the input parameters (Steenbeek et al. 2018). The model uncertainty suggests that as the process of mass-balance is subjective,

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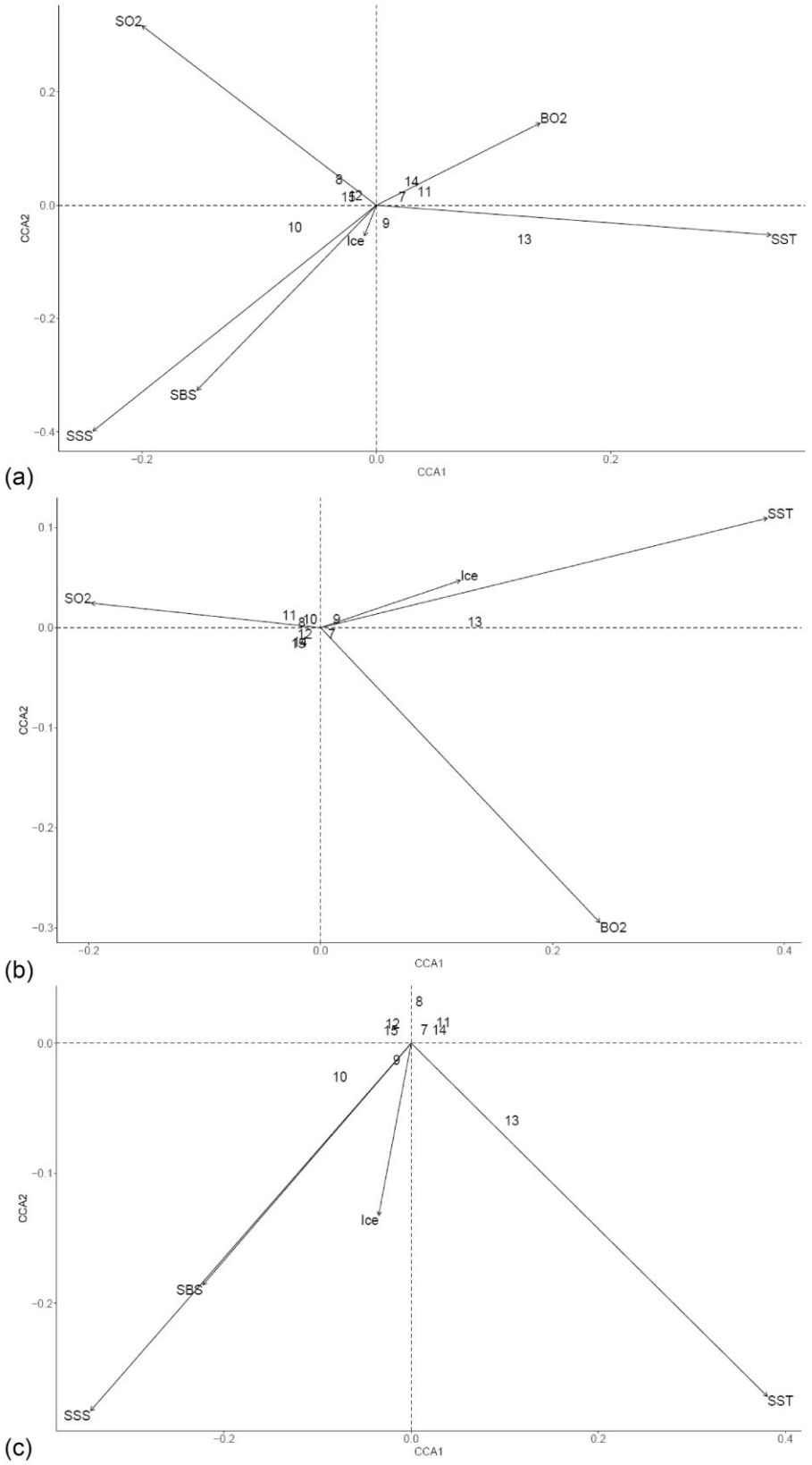

Figure 12. Canonical correspondence analysis (CCA) to understand fish biomass distributions under the effects of the described environmental variables (temperature, sea ice, DO, salinity), in GFDL experimental BSS EwE models. CCA for the experimental models as follows: (A) GFDL "All parameters" (SST, sea ice, DO, salinity), (B) GFDL "O_2 added" (SST, sea ice, DO), (C) GFDL "Salinity added" (SST, sea ice, salinity). Number values of fish functional groups are as follows: 7 = Char & Dolly Varden, 8 = Ciscos & Whitefish, 9 = Salmonids, 10 = Herring & Smelt, 11 = Arctic & Polar Cods, 12 = Capelin, 13 = Flounder & Benthic Cods, 14 = Small Benthic Marine Fish, 15 = Other Fish.

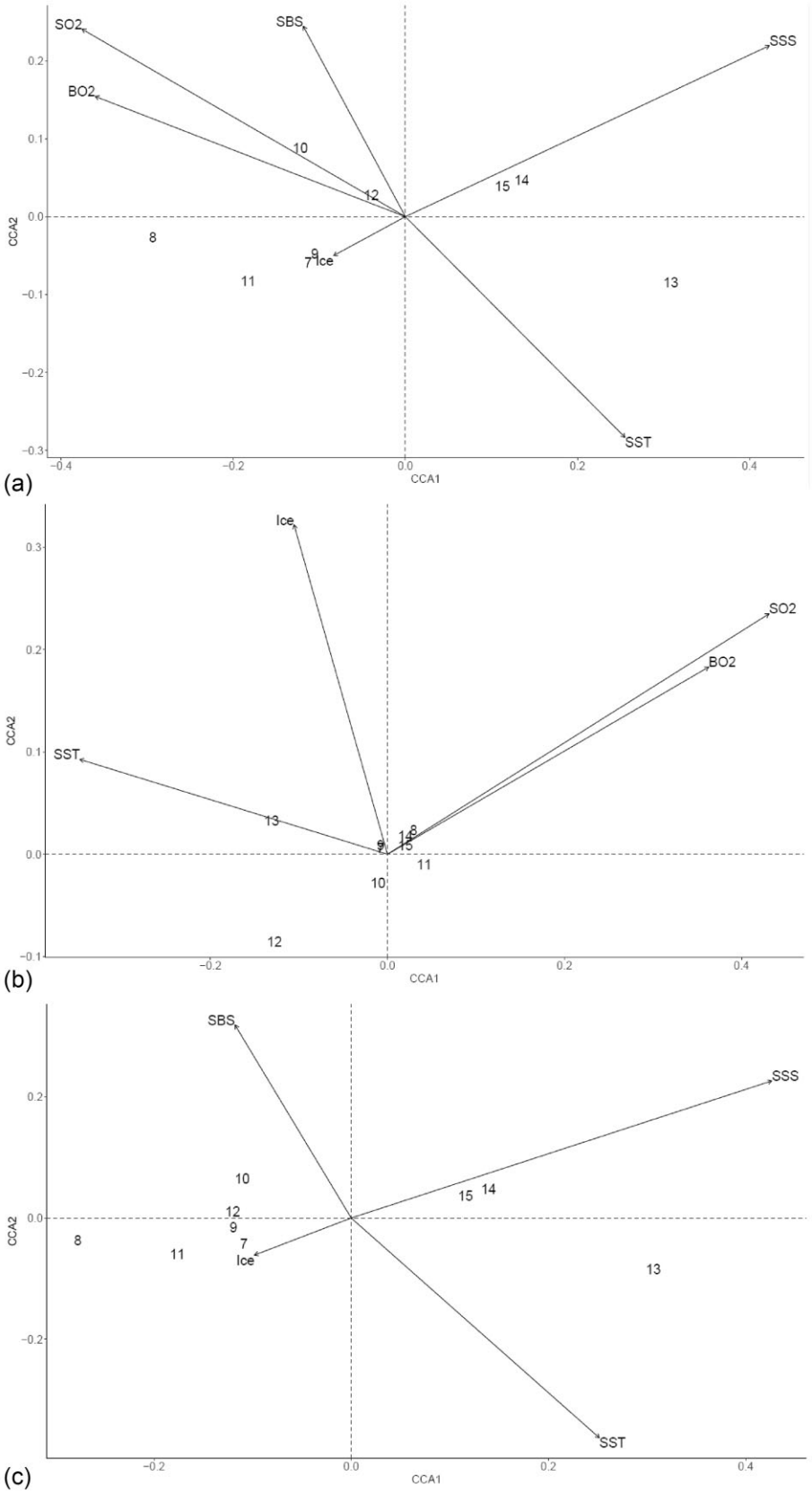

Figure 13. Canonical correspondence analysis (CCA) to understand fish biomass distributions under the effects of the described environmental variables (temperature, sea ice, DO, salinity), in IPSL experimental BSS EwE models. CCA for the experimental models as follows: (A) IPSL "All parameters" (SST, sea ice, DO, salinity), (B) IPSL "O_2 added" (SST, sea ice, DO), (C) IPSL "Salinity added" (SST, sea ice, salinity). Number values of fish functional groups are as follows: 7 = Char & Dolly Varden, 8 = Ciscos & Whitefish, 9 = Salmonids, 10 = Herring & Smelt, 11 = Arctic & Polar Cods, 12 = Capelin, 13 = Flounder & Benthic Cods, 14 = Small Benthic Marine Fish, 15 = Other Fish.

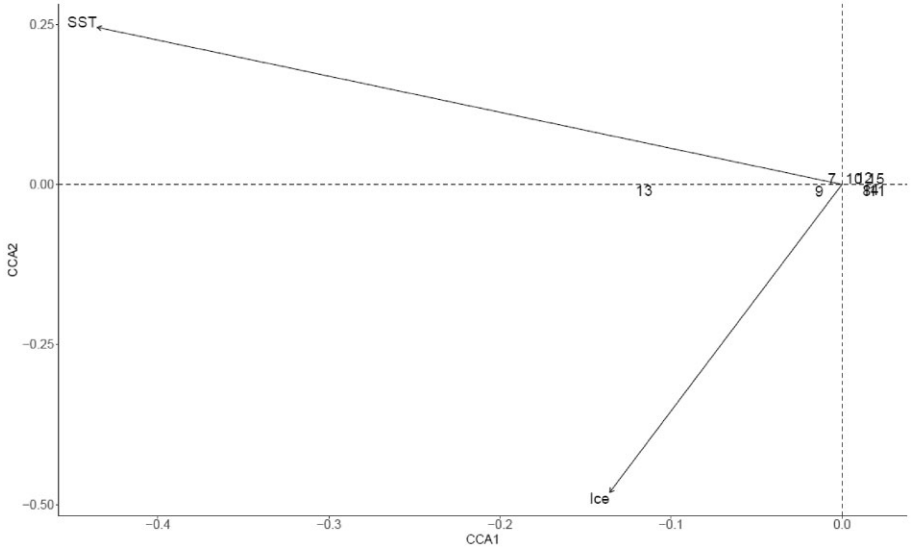

Figure 14. Canonical correspondence analysis (CCA) to understand fish biomass distributions under the effects of the described environmental variables (SST, ice), in Baseline BSS EwE model. Number values of fish functional groups are as follows: 7 = Char & Dolly Varden, 8 = Ciscos & Whitefish, 9 = Salmonids, 10 = Herring & Smelt, 11 = Arctic & Polar Cods, 12 = Capelin, 13 = Flounder & Benthic Cods, 14 = Small Benthic Marine Fish, 15 = Other Fish.

the Monte Carlo routine generated notably different outputs across simulations, where some values diverged from expected values (Susini and Todd 2021). Sensitivity analyses clarified these uncertainties around model outputs (Saltelli 2002) by quantifying the contributions and uncertainties of the parameter data and model performance (Zheng et al. 2014). Sensitivity analysis were used to assess the impact of the uncertainties on the range of the model outputs and the degree to which the uncertainty range impacts the functional groups or indicators (Susini and Todd 2021). The uncertainty ranges from Monte Carlo and sensitivity analyses highlight the wide range of input values and parameters; however, this did not impact the main indicator trends for the functional groups. Sensitivity analyses and multiple climate scenarios allow us to explore potential sources of uncertainty and identify how they may impact the model.

Conclusions

The models developed in this study provide a useful ecological baseline for future projections and species distribution models of the BSS ecosystem to understand the climate risks and vulnerabilities for priority species by the end of the century. Broadly, in this study, the experimental models with increased salinity and temperature time series as an environmental driver had negative impacts on modeled fish biomass, as metabolic demand increased when approaching the maximum of the species' tolerance range. Building upon an existing BSS EwE food web model, this analysis aimed to examine the effects of single and multiple climate-induced stressors on the environmental response of modeled fish communities of the BSS and TN MPA. The findings from this study provides insights into other studies aiming to attribute projected climate change effects on Arctic ecosystems to 2100, and how existing conservation measures (e.g. TN MPA) can help adapt to climate change impacts. Projections of environmental suitability of the BSS and TN MPA can expand upon the groundwork from this study to help understand potential climate-driven species distribution shifts and identify future hotspots of diversity and refugia in the region under contrasting climate scenarios.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manusrcipt.

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Data availability

The data underlying this article are available in the article and in its online supplementary material.

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