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Sub-Arctic no more: Short- and long-term global-scale prospects for snow crab (*Chionoecetes opilio*) under global warming

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Abstract

Snow crab is a sea-ice associated species that supports several economically important fisheries in northern latitudes. During the past decade considerable stock range changes have occurred, characterized by a general shift from sub-Arctic ecosystems into the Arctic. We developed predictive models for short-term biomass trajectories and long-term habitat potential under a changing climate. Sea ice extent and the Arctic Oscillation were important variables in the short-term models. Future sea ice extent was used as an analog for long-term habitat potential and was predicted as a function of projected atmospheric carbon dioxide concentrations and the Arctic Oscillation. Our results show that global scale snow crab habitat and biomass are currently at or near historically measured highs. Similar overall habitat potential to historic and current levels is expected to continue out to 2100 under best case CO_2 scenarios but declines below historic levels are projected to begin after about 2050 under worst cast CO_2 scenarios. In the short-term, most historical stock ranges are expected to maintain productive fisheries while new habitats open. In the long-term, under all CO_2 scenarios, we project a shift in habitats from historic ranges into new frontiers as sea ice recedes. Future population trajectories depend upon the ability of snow crab to track habitat shifts and we discuss possible forthcoming changes in context of potential socioeconomic outcomes.

Introduction

Expanding stock ranges & fisheries

The cold-water stenothermic snow crab (*Chionoecetes opilio*) has historically been classified as a sub-Arctic species (i.e., [1]), with largest stocks all lying below the Arctic Circle. Over the past half century, dominant stocks and fisheries have occurred in northern portions of both the Pacific (i.e., Bering Sea, Sea of Okhotsk, and Sea of Japan) and Atlantic (i.e., Eastern Canada and West Greenland) Oceans (Fig 1).

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The global exploitation of snow crab over time, including mapping of recent range expansions into Arctic waters is detailed in [7]. At-present, distributions in the Pacific are widespread and continuous, ranging from South Korea in the west and British Columbia in the east and extending north through the eastern and western Bering Seas into the Beaufort and East Siberian Seas inside the Arctic Circle. In the Atlantic, discrete distributions occur in Atlantic Canada and off West Greenland, while the Barents and Kara Seas within the Arctic Circle also have a discrete distribution of snow crab. The two historically dominant stocks in Atlantic Canada, Newfoundland & Labrador (NL) and the southern Gulf of St. Lawrence (sGSL), are both assessed as being healthy [8, 9] while the historically dominant stock in the Pacific, in the Eastern Bering Sea of Alaska (AK), recently and abruptly collapsed, for which definitive reasons are unknown [10].

Although reliable fishery statistics are not available from all global regions, [7] detail a long-term increase in global biomass harvested, from a few thousand tonnes in the 1950s to around 200 thousand tonnes currently [11]. Alaska dominated landings over the 1990–2000 period, reaching levels of about 150 kt per year in the early 1990s, but Atlantic Canada emerged as the dominant supplier

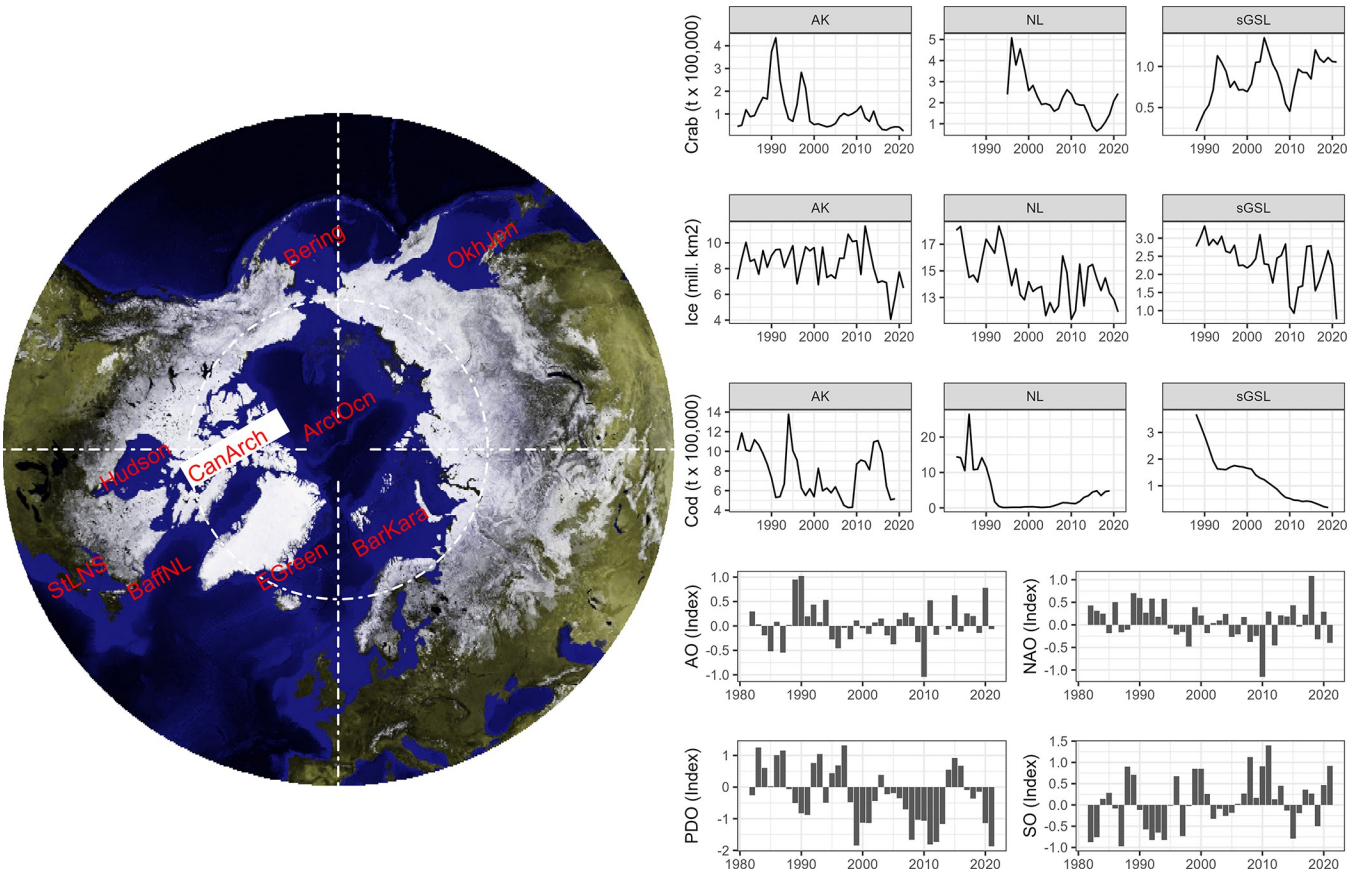

Fig 1. Left. Artic Circle view of the northern hemisphere showing the nine sea Ice Regions considered in analysis. Dashed circle shows Arctic Circle delineation. Right. Top Row: Snow crab total exploitable biomass index by Stock Region (AK = Alaska, NL = Newfoundland & Labrador, sGSL = Southern Gulf of St. Lawrence). Second Row: Maximum sea ice extent index by snow crab Stock Region. Third Row: Cod biomass index by snow crab Stock Region. Fourth Row: Annual Arctic Oscillation and North Atlantic Oscillation Indices. Bottom Row: Annual Pacific Decadal and Southern Oscillation Indices. Map source file "The Blue Marble" modified from and credited to NASA Earth Observations (https://neo.gsfc.nasa.gov/view.php?datasetId=BlueMarbleNG-TB). Snow crab distribution is related to seasonal ice cover. Globally, areas either perpetually or ephemerally covered in sea ice do not support large stock biomasses. In cases where exceptions occur, such as in the southernmost (ice-free) extent of the Atlantic Canadian stock range (Nova Scotia), direct cold water inputs from adjacent ice-covered ecosystems occur (Petrie and Drinkwater, 1993). In recent decades, increased ice free periods in Arctic Regions have enabled habitat shifts for snow crab. Numerous recent observations of increasing abundances or first occurrences in Arctic waters (i.e. north of 66.56˚N) such as the Chukchi [2], Beaufort [3], Barents [4]), Kara [5], and East Siberian and Laptev Seas [6] collectively confirm that the distribution of snow crab is now near-circumpolar and that the species should no longer be characterized as sub-Arctic.

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at the end of the 20th century, with NL now being the largest fishery in most years (2022 and 2023 quotas of >50 kt. This largely reflects a shift from a focus on cod to snow crab as the focal fishery in NL following groundfish collapses in the early 1990s [12]. New fisheries associated with shifting habitats into the Arctic Circle still remain a small fraction of total recorded harvests [7].

Habitat variables

The relationship between sea ice and snow crab habitat reflects large volumes of dense and near-freezing water masses that develop from melting sea ice and remain in the subsurface water column through the ice-free season [13–17]. The cold bottom area created where these water masses interact with the seafloor has been related to snow crab habitat [8, 18–20]. The extent of cold bottom water during early-mid ontogeny is the most consistent factor known to correlate with productivity across major global stocks [21–23].

Snow crab habitat is affected by both short-term and long-term climate phenomena. The relationship between sea ice dynamics, cold bottom water conditions, and snow crab habitat enables a quantitative exploration of potential predictive tools for snow crab habitat and by extension potential biomass, both inter-annually and in context of anthropogenic climate change. On interannual time scales, several important teleconnection patterns are known to affect ocean climate in the northern hemisphere and in-turn potentially influence population dynamics of snow crab, including the North Atlantic Oscillation (NAO, [20]) and the Pacific Decadal Oscillation (PDO, [24]). Of note, quantitative linkages of these systems and early life stages of snow crab have been established or inferred [20, 24]. Most recently, an inference was made that the Arctic Oscillation (AO) had an association with productivity in the Eastern Bering Sea snow crab stock [25]. On longer time scales, global-scale sub/Arctic (referring to both sub-Arctic and Arctic regions) sea ice has been in steady decline for four decades as a result of greenhouse effect global warming [26, 27], opening potential new frontiers for the species as evidenced by recent rapid changes in range distributions (i.e. [4, 5]).

Study objectives

This analysis is part of a larger multi-disciplinary collaboration among a group of physical, biological, social, and economic scientists. The lucrative snow crab is a harbinger of global warming and an ideal study candidate to investigate biological and by extension socioeconomic impacts of climate change [7]. Two main objectives are pursued. The first objective is to predict short-term (<10 years) outcomes of snow crab biomasses in major global stocks, specifically by evaluating biomass responses to historic climate variables for stocks featuring sufficient time series of available data. The second objective is to infer plausible long-term (up to year 2100) outcomes of global-scale snow crab habitat potential. For the long-term analysis, scenario-based levels of atmospheric carbon dioxide (CO_2) concentration are modelled alongside randomized inputs of the AO to predict sea ice extent outcomes for major geographic regions of the sub/Arctic, which are in-turn used to infer future snow crab habitat potential.

Because snow crab is a prized commodity resource, with its commercial fisheries consistently featuring among the world's most lucrative fisheries [28–30], we elaborate on how physical oceanic changes could affect potential future supplies over the long-term.

Background and methods

Snow crab stock biomasses

Three survey time series of exploitable biomass (large males available to the commercial fishery) from major global snow crab stocks were compiled for comparative correlation analysis

with climate system indices. These include portions of the North American west and east coasts, with one from the Pacific [10] and two from the Atlantic (sGSL, [8, 9, 31]) (Fig 1). Note that in the AK stock the exploitable biomass is defined as males >101mm carapace width (CW) while in the NL and sGSL stocks it is defined as males >94mm CW.

The AK stock represents the dominant component of snow crab contained in the Bering Sea ("Bering") Ice Region while the NL stock is the dominant contributor to snow crab within the Baffin Bay / NL ("BaffNL") Ice Region. The sGSL stock occurs within the St. Lawrence / Nova Scotia ("StLNS") Ice Region, comprising the majority of snow crab biomass within it. The NL and sGSL populations occur within one genetic unit [32, 33] but are herein treated as discrete stocks due to geographical separation by a network of deep ocean trenches [34] and long-term asynchrony in biomass trajectories. Other smaller populations of snow crab in the northern Gulf of St. Lawrence (StLNS Ice Region) and West Greenland (BaffNL Ice Region) do not have biomass estimates available.

The three focal stocks have accounted for most of the world supply of known snow crab catches for three decades. The Sea of Okhotsk in Eastern Russia has also been a major contributor to overall global supplies but reliable data on landings and biomass from that stock are unavailable. The annual exploitable biomass index from each focal stock was combined with reported fishery landings to derive indices of total exploitable biomass within each stock unit.

Atmospheric teleconnections

Several teleconnection patterns have been related to snow crab productivity either in short-, mid-, or long-term scales, including the Pacific Decadal Oscillation [PDO, 24], the Arctic Oscillation [25], the Southern Oscillation [SO], and the North Atlantic Oscillation [20]. These teleconnections affect snow crab at different life stages via regulation of ocean climate conditions over large spatial scales.

Although a correlation analysis is performed with all teleconnections cited as important in the literature, the analysis ultimately focuses on the AO, which geographically bridges the north Pacific and north Atlantic stocks. The AO is a proxy for the strength of the polar jet stream and measures the first mode of variability of atmospheric pressure over the Arctic (20–90˚N). Monthly values (anomalies from the mean) of the AO since 1951 were obtained from the National Oeanographic and Atmospheric Administration (NOAA) Climate Prediction Center (https://psl.noaa.gov/data/climateindices/list/, accessed on Nov. 30, 2022).

Changes in the AO will impact geographical areas within and adjacent to the Arctic differently [35]. For example, under postive AO the eastern Arctic and northwest Atlantic typically experience prevailing westerly Arctic-origin winds and overall cold conditions. Conversely, under negative AO the influence of westerly Arctic winds is lower and the areas experience warmer conditions. Similar to the eastern Arctic and northwest Atlantic, the Eastern Bering Sea of Alaska typically experiences cold and warm conditions under positive and negative phases of the AO respectively. The Barents Sea would typically operate in converse, with warm conditions prevailing during positive AO, as would much of continental North America and Europe/Asia. Given differences in spatiotemporal climate outcomes under different phases of the AO, a single directional relationship with snow crab stock productivity would not hold for all sub/Arctic regions.

Other influential factors

Beyond teleconnection systems, sea ice extent has been shown to be related to recruitment strength in snow crab [25]. Accordingly, an index of ice extent was explored as an explanatory variable in modelling future exploitable biomass in each focal Stock Region. The data for

monthly sea ice extent for nine sub/Arctic Ice Regions (Fig 1), along with an overall Arctic level index, extending back to 1978 were available from the National Sea and Ice Data Center (NSIDC - https://nsidc.org/data/NSIDC-0192/versions/3/print; 36]). The Bering Sea Ice Region data were applied to the AK snow crab stock, the Baffin Bay/NL Ice Region data were applied to the NL crab stock, and the St. Lawrence / Nova Scotia Ice Region data were applied to the sGSL crab stock. These continuously monitored satellite data on ice extent are captured on a pixel grid system with the presence of sea ice defined as a grid having a concentration exceeding 15% ice cover [36].

Finally, predation was explored as a regulatory mechanism affecting snow crab productivity in the historically dominant global snow crab stocks. For this, we focused on cod (*Gadus morhua* [Atlantic], *Gadus macrocephalus* [Pacific]) because they are known predators of small to mid-sized crab (i.e., $<$ 50 mm CW) [37] in all focal snow crab stocks and published indices of cod biomasses were available in each Stock Region. Tabulated model estimates for total biomasses (all ages) of cod were taken from DFO [38] for NL, [39] for the sGSL, and [40] for AK. These were deemed sufficient proxies for predation potential as large cod (large enough to consume snow crab) dominate overall stock biomasses in each case.

Correlative explorations

Total biomasses of exploitable crab in each Stock Region were initially cross-correlated with the four teleconnection patterns, sea ice extent, and cod biomasses at lags of 0–13 years to identify focal variables for a preditive model. Snow crab life history was segregated into three periods of long-, mid-, and short-term stages, with annual lag correlation periods corresponding to ages of crab, because certain factors are known to influence specific life stages. For example, the short-term (within a few years) influence of cod predation would not be expected to be meaningful in regulating snow crab biomass as large crab are virtually immune from predation. Similarly, the AO has been described as improving fits in stock-recruitment models, suggesting potentially important influences on early ontogeny (long-term outcome). To further complicate the matter on differential life stages of influential drivers, opposite directions of relationships of responses to any given driver may occur at different life stages [24].

Long-term life stage correlations were partitioned at lags of 10–13 years to focus on drivers important during early ontogeny, either at larval or early benthic settlement stages. This invoked an assumption that most crab in the exploitable biomass in any given stock were 10–13 years of age. This assumption was based on including additional years above the mimimum 9 years identified by [41, 42] to reach 95mm CW to account for skip-molting in these populations [43–45] and is supported by recent work on age determination in male snow crab in the NL stock which showed them to average 10–12 years of age when first recruiting to exploitable size [46]. A proportion of the exploitable biomass in each Stock Region would normally consist of residual crab, present in the population for a year or more, but different fisheries exploitation rates across Stock Regions would affect temporal signals in lag periods for relationships in this long-term outcome stage. Specifically, shorter lags could occur in the sGSL where there has been lower presence of residual (old-shell) crab in the exploitable population compared to NL and AK for most of the times series [8–10]. This reflects generally highest exploitation rates in that region. Moreover, the larger size definition of exploitable crab in AK would align with a longer lag in AK relative to the other two focal stocks.

Mid-term life stage correlations were partitoned at lags of 2–9 years and were intended to focus on drivers affecting growth transitions within populations. The snow crab has a complex multinomial molting (growth) process whereby during any given molting period an animal can: 1) molt/grow and subsequently be able to molt again; 2) skip-molt, whereby it delays a

molt but can still molt/grow again; or, 3) terminally molt, whereby molting and growth cease for the remainder of life [47].

Finally, short-term life stage correlations were defined as lags of 0–1 years and were intended to identify factors that could have an impact on near-immediate survival of crab in the exploitable biomass from one year to the next. In this regard, the recent unanticipated collapse of the AK snow crab stock [10] was thought to be particularly relevent.

For cross-correlation explorations, annual monthly means of each of the four teleconnections were used. Examination of annual indices for each teleconnection were deemed to coarsely capture impacts during all seasons including spring and autumn plankton blooms, which affect pelagic-stage feeding conditions for crab(i.e. [48, 49]).

Measurements of sea ice extent were limited to February-April observations to capture the period when sea ice would be at its maximum extent in any given Ice Region and year. To include a temporal element of ice expanse as well, the three months of ice cover in each Ice Region and year were summed. Finally, the cod biomass index from each Stock Region was an annual survey index.

The exploratory correlation analysis was limited to the 1995–2019 period for snow crab biomasses to ensure a consistent comparative window across all three stocks, with no surveys prior to 1995 in the NL Region, and also in consideration of survey problems in all three Stock Regions since 2019. Specifically, AK and NL have missed annual surveys since that time [8, 10] and the sGSL has concerns of a potentially inflated biomass index due to increased catcbability of a new survey vessel and other on-going changes in survey performance [9]. Correlation coefficients (r) were based on simple Pearson associations.

Short-Term Prediction Model (STPM)

A predictive model of total exploitable stock biomass (tBIO) was developed based on identification of consistent correlations among drivers at each life-stage across Stock Regions. Sea ice extent was chosen as the explanatory variable for the long-term life stage because it showed consistency in directional relationships with biomass across all three areas. For NL and AK, where it was anticipated this lag would be longer due to lower exploitation rates, 12–13 year lags were chosen, while for the sGSL 11–12 year lags were chosen. AK fitting in the longer time frame is also consistent with the larger CW definition of exploitable size in that stock. For the mid-term life stage, the AO at 7–8 year lags were chosen due to consistent high correlation across stocks. Finally, the AO at lags of 0 and 1 years were chosen to model short-term stock drivers due to relatively strong correlations in all three Stock Regions.

The short-term prediction model (STPM) was fit as a generalized additive model (GAM) in the mgcv package [50] in R version 4.0.2. [51], assuming a Gaussian family distribution and identity link. Tensor product interaction smooths (te) were used on thin-plate splines for explanatory variables for each life stage. Each interaction term was set to a low number of basis knots ($k = 3$) to allow the model to converge. An autoregressive (AR1) rho parameter on the residuals was included in each model due to the autoregressive process of stock biomass measurements (i.e., the entire biomass does not renew each year), with the preceding level of exploitable biomass affecting the subsequent years measurement. A rho parameter was calculated from the autocorrelation function for each independent model run.

The STPM was run separately for each of the three Stock Regions due to *a priori* observations of different directions of AO effects. Moreover, a build-up approach was invoked in examining effects of the explanatory variables at each life stage. For example, for the AK & NL Stock Regions the base (long-term) model was defined as [1], which was consecutively built on to construct runs featuring both long- and mid-term explanatory terms [2], and additionally

to include terms for all life stages [3], which we termed the full model.

$$tBIO_t \sim te(Ice12, Ice13) + rho\_y_{(t-1)} + \varepsilon_t \quad [1]$$

$$tBIO_t \sim te(Ice12, Ice13) + te(AO7, A08) + rho\_y_{(t-1)} + \varepsilon_t \quad [2]$$

$$tBIO_t \sim te(Ice12, Ice13) + te(AO7, AO8) + te(AO0, AO1) + rho\_y_{(t-1)} + \varepsilon_t \quad [3]$$

where, t refers to year, Ice refers to cumulative February-April ice extent, AO refers to annual Arctic Oscillation Index, numerics with each explanatory term refer to lag years (0,1,7,8,12,13), *rho (t-1)* refers to autoregressive AR1 parameter, and ε represents white noise error. Note the long-term ice interaction term was (*Ice11*, *Ice12)* for the sGSL model runs.

Contour plots of interaction smooths for each explanatory term in the STPM were plotted by life-stage to assess the influence and relative strength of each effect. Subsequently, biomass projections for forthcoming years were constructed by fitting models [2, 3] with lagged input data of sea ice extent and the AO. Model [2] projections extended out to 2025 and model [3] projections extending out to 2021 in accordance with the available time series of data measurements. The model projections out to 2021 enabled comparison with subsequently measured stock biomass estimates in 2020 and 2021 for each Stock Region, albeit with aforementioned potential problems in each. Both annual point estimates and two (1.96) standard errors of the means were presented in biomass projections. Model fits were based on visual assessment of residual patterns and adjusted r^2 statistics.

Along with formulating a basis for short-term biomass expectations, the STPM was ultimately intended to establish a basis for focus on sea ice and the AO as important processes to examine in subsequently attempting to predict long-term snow crab habitat outcomes.

Future Habitat Model (FHM)

Habitats were grouped into "Historic Ranges" and "New Frontiers", reflecting historic presence or absense of large stock biomasses. The Baffin Bay / Newfoundland and Labrador, St. Lawrence / Nova Scotia, Bering Sea, and Seas of Okhotsk and Japan Ice Regions were treated as historic ranges, encompassing the NL, sGSL, AK, and Sea of Okhotsk stock units respectively, while all other Ice Regions were treated as new frontiers. Predictive sea ice models were developed to fit to the nine sub/Arctic Ice Regions (Fig 1) contained in the NSIDC dataset. Additionally, data for a tenth Region defined as the Total Arctic and reflecting the sum of Region-specific monthly ice extents were provided and fit with the same model. Atmospheric concentrations of carbon dioxide (CO_2) were used alongside monthly AO values to model ice extent for each Ice Region. CO_2 was deemed an appropriate focal proxy for atmospheric greenhouse gas effects because of its dominant role in affecting global warming rates [52].

Monthly CO_2 data were available dating back to 1960, measured in parts per million concentration by air flask sampling at the Mauna Loa Observatory in Hawaii [53]. The data were downloaded from Scripps Institution of Oceanography at the University of California (http://scrippsco2.ucsd.edu, accessed on June 25, 2021). The raw data were used for analysis (seasonal cycles inherent in the data). The CO_2 data were merged by year and month to the AO and ice extent data, forming a complete monthly dataset for the time series from January, 1979 to December, 2020.

A future habitat model (FHM) to explain ice extent in each Ice Region was constructed using a GAM. Given large differences in the size of each Ice Region and associated ice extent measurements, the ice data were converted to proportional area covered, with the maximum possible extent (proportion of 1) based on maximum historic levels recorded in any given Ice

Region. The model family was quasibinomial to accommodate frequent observations of either 0 and 1 in any given Ice Region and the default logit link function was used.

The FHM was fit by Ice Region and is defined as [4]:

$$pIce \sim s(Month) + te(AO, CO_2) + \varepsilon_t \quad [4]$$

where, *pIce* represents proportional ice extent, *s* represents a smoother, *te* represents a full interaction smoother, *AO* represents the Arctic Oscillation index, CO_2 represents carbon dioxide (ppm), and εt is error. Thin-plate splines were used on the AO*CO_2 interactions, with the number of basis knots set to 5 to safeguard against excessive degrees of freedom. The month term was fit as a cubic cyclic spline with 12 basis knots to account for each calendar month. The model was fit using restricted maximum likelihood and assessed as a good fit based on visual analysis of residuals and adjusted r^2 statistics. Two (1.96) standard errors of monthly point estimates were used to estimate confidence intervals for upper and lower limits. Areal extents of predicted sea ice cover were calculated by multiplying predicted proportions of ice cover against maximum historic ice extent observed in each Ice Region. Contour plots of interaction marginal effect smooths for explanatory terms in the FHM were plotted by Ice Region alongside marginal effect smooths for month. An intent of the FHM was to establish tight fits to the historic monthly data in the training model for each Ice Region toward developing a sound quantitative basis for projecting future sea ice extent.

Future monthly sea ice extent was simulated for each Ice Region using randomized inputs of the AO along with CO_2 emission scenarios produced by the International Panel on Climate Change (IPCC). For this exercise, future years were blocked into decadal units (2030, 2040, . . . 2100) to conform with the structure of the CO_2 projections data. Each month within those years was populated with the CO_2 projection estimate for that calendar year provided by the IPCC (all months in a calendar year had the same CO_2 value) alongside 5,000 random draws of the AO index constrained within a -3.0 to 3.0 range to conform with historic norms of monthly minima and maxima values. Two separate model runs of the training model were completed: the "Best Case" scenario from the IPCC projections data (scenario B1) and the "Worst Case" scenario (scenario A1FI) for the CO_2 emission scenarios. The snow crab habitat potential index was calculated from each run as the difference between annual predictions for maximum and minimum sea ice extent for each Ice Region to correspond with the definition of habitat as being areas both covered and uncovered by ice each year. Bootstrapped prediction intervals (5th and 95th percentiles) for monthly sea ice extents were developed from producing error estimates based on 5000 random draws (with replacement) from residual value distributions for each Ice Region and adding them to the one-step standard errors produced from the model fits. For presentation, annual upper and lower predicted values were plotted based on maximum and minimum values among the monthly estimates produced for each year.

FHM validation

Following the development of numerous global climate models in recent decades, standards have been developed to assess the reliability of fits to baseline data and associated future predictions. The Coupled Model Intercomparison Project (CMIP) has progressed to its sixth stage of model intercomparisons (CMIP6). In this context, [54] recently evaluated 36 sea ice models and detailed methods for making comparisons, which focused on fits to monthly sea ice extent observations during the 1979–2014 period. We required and developed sea ice projections at regional scales but additionally produced a model at the total Arctic scale. As a first validation for our model, we compared monthly medians of model fits to the 1979–2014 period to results detailed in [54]. As a second validation, we presented our prediction time to

an "essentially ice-free Arctic", defined as predicted ice extent of 1 million km^2 during September, for comparison to the suite of models reviewed in [55]. The 2020 calendar year also allowed direct comparisons of monthly predictions to observed ice extents for each Ice Region.

Results

Snow crab stock biomasses

The AK Stock Region had the longest time series of stock size measurments, with peak biomass in that stock occurring at >400 kt in 1990–1991 (Fig 1). The NL stock has been the largest in size throughout most of the post-1995 time series. Overall, with the exception of an increase to exceed >700 kt in 1996–1998, when the NL stock was at its largest, the total production of the three stocks has been relativley stable at 200–400 kt per year for the past two decades.

All combinations of biomass comparisons among the three focal stocks had significant relationships ($p<0.05$). A positive relationship was found between NL and AK ($r = 0.66$) and negative relationships were found between sGSL and both NL ($r = -0.54$) and AK ($r = -0.47$).

Biomasses predictor variables

Maximum ice extent in the AK Stock Region (Bering Sea Ice Region) varied between 7 to 10 million km^2 over most of the 1980–2007 period (Fig 1). However, it increased to measured highs exceeding 10 million km^2 in several years over the 2008–2011 period, with a record high measurement of 11.3 million km^2 in 2012. Maximum ice extent precipitously declined in the 2013–2018 period, to just 4 million km^2 in 2018. Sea ice coverage has since increased, but the approximately 7 million km^2 extent in recent years remains low relative to historical levels.

Counter to the erratic pattern of maximum ice coverage observed in the AK Region, the NL (BaffNL Ice Region) and sGSL (StLNS Ice Region) Stock Regions have both featured oscillating decline patterns over the time series. In the NL Stock Region (BaffNL Ice Region) maximum annual ice coverage occurred in the mid-1980s and early 1990s, when >18 million km^2 were covered. Low periods occurred in the mid-2000s and in 2021, when <12 million km^2 maximum coverage occurred. In the sGSL Stock Region (StLNS Ice Region), maximum ice coverage occurred at the start of the measured time series, with about 3 million km^2 maximum annual extent in most years of the late 1980s and early 1990s. Lows during the trough periods of the oscillating decline pattern in maximum ice coverage have become progressively lower throughout the time series, with <0.5 million km^2 covered in 2021.

The cod stocks in the three focal Stock Regions have undergone different biomass trajectories since the early 1980s. In AK, the cod stock has fluctuated over the time series with the most recent peak of about 1.4 million tonnes in 2015 (Fig 1). In NL, the stock declined precipitously from a peak estimate of 2.6 million tonnes in 1986 to just 9,800 t in 1994. It remained under 100,000 t until 2006 and has since gradually increased to 480,000 t in 2019. Meanwhile, the sGSL cod stock has undergone continuous declines throughout the time series, with the peak estimate of 368,000 t occurring in 1998 and a historic low of 18,000 t in 2019.

The AO index has experienced short-term phase oscillations throughout the time series with a notable prolonged strong positive phase persisting from 1989–1994 and a pattern of increasing variability in the most recent decade featuring a strong negative phase (index <-1.0) in 2010 and a strong positive phase (index = 0.78) in 2020 (Fig 1). Trends in the NAO were similar to those of the AO, featuring strong persitent positive phase during 1989–1994, and a historic high negative index in 2010. However, in recent years, the historic high positive index in 2018 (1.08) did not match the AO. The PDO has shown more systematic conformity to prolonged directional phases than either the AO or NAO, but since the mid-1990s it has

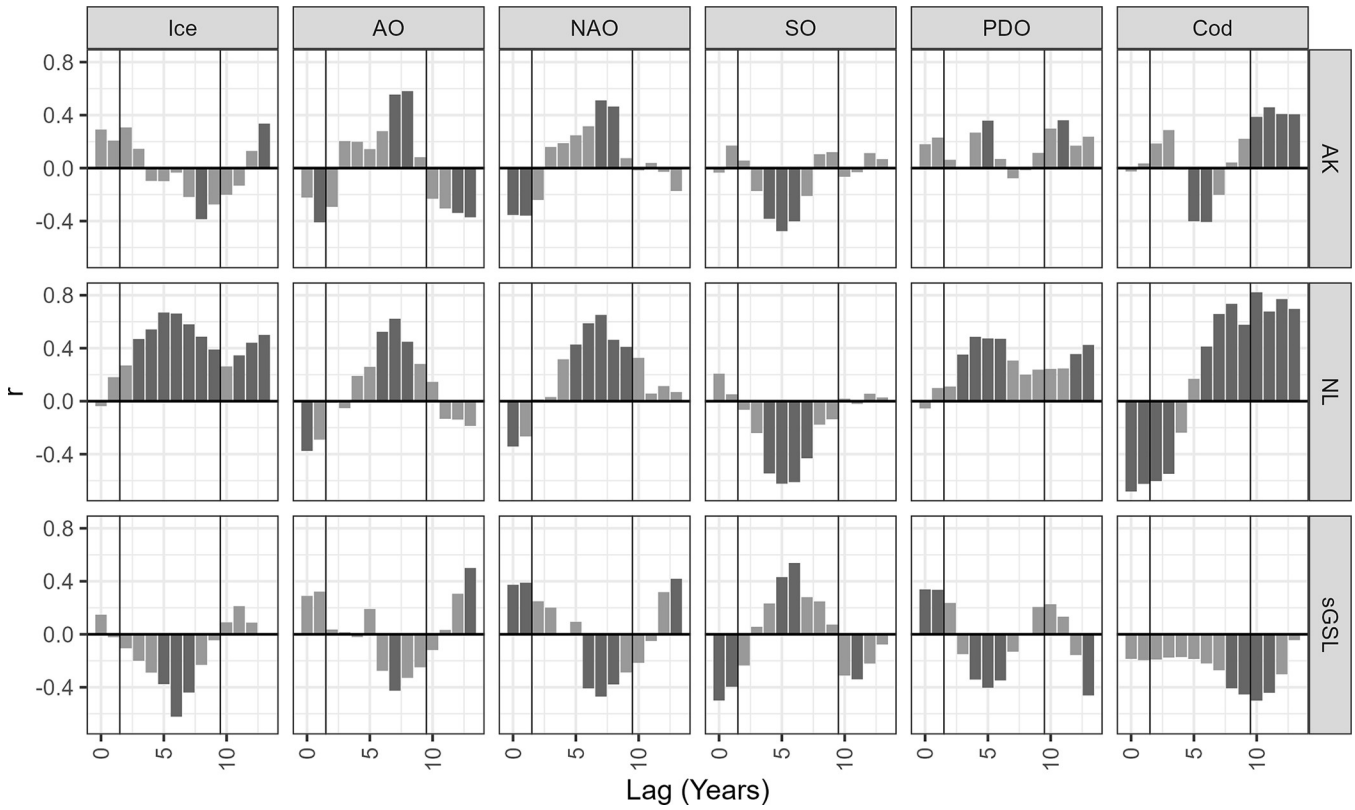

Fig 2. Pearson cross-correlations with total exploitable biomass (tonnes) versus sea ice and climate system indices (North Atlantic Oscillation, NAO; Southern Oscillation, SO; Pacific Decadal Oscillaion, PDO) as well as cod biomass indices (tonnes) by Stock Region (Alaska, AK; Newfoundland and Labrador, NL; southern Gulf of St. Lawrence, sGSL). Dark bars show correlations significant at $p<0.1$.

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been overall dominated by negative phase with three strong signals occurring during that period, including during the past two years (Fig 1). Conversely, the SO has shown brief periods of negative phase dominance since the mid-1990s but has overall been dominated by positive phase during the most recent two decades, including during 2020–2021 (Fig 1).

Sea ice extent showed postive correlations with snow crab exploitable biomass at lags longer than 10 years in all stocks but the relationships were both strongest (i.e. $r > 0.3$) and most consistent in NL (Fig 2). In AK, like NL, the strongest relationship occurred ($r = 0.34$) at 13 years lag while in the sGSL the strongest relationship occurred at 11 years. The AO showed some negative long-term relationships (lags of 12–13 years) with stock biomass in AK and positive relationships in the sGSL, while the weaker relationships in NL were consistently negative. Similarly, relationships between the PDO and long-term biomass were directionally consistent in AK and NL (positive) while opposite in the sGSL (negative). Cod biomass showed a positve long-term relationship with crab biomass in both AK and NL. The negative pattern of lagged relationships between cod biomass and lagged biomass of snow crab at all annual increments in the sGSL reflects the cod stock decline over the entire time series in that Region.

For mid-life stage correlations, the AO and NAO both showed correlations with snow crab biomass at lags of 7–8 years, with that pattern opposite in the sGSL stock (Fig 2). Similarly, the negative relationships between stock biomass and the SO in AK and NL during the mid-term analysis were opposed by postive relationships in the sGSL. Finally, the postive PDO relationships with mid-term biomass in AK and NL were opposed by negative relationships in the sGSL.

With respect to short-term relationships between crab exploitable biomass and climate variables, sea ice showed relatively weak but positive relationships in all areas, while AO and NAO showed relatively strong negative relationships in AK and NL (positive in sGSL) (Fig 2). The relationships between SO and PDO and stock biomass in the short-term analysis in the sGSL were not as evident in either AK or NL.

Short-term outlook: Short-term Prediction Model (STPM)

The STPM conditioned with only long-term predictor (ice) variables was the least explanatory in all three Stock Regions (Table 1). In all cases model fits were significantly improved with the addition of the mid-term predictor variables (adj. r^2 range 0.43–0.67). In terms of explained deviance, the addition of the short-term predictor terms modestly improved model fits in each Stock Region (range 4–12% increase among regions). The AO7*AO8 interaction term was the overall most consistently influential predictor term in all Stock Regions ($p<0.3$ in all model runs).

The model interaction smooths showed consistency in directional effects of sea ice in all Stock Regions, with heavy ice extent in both years in the interactions combining to promote strong long-term stock biomass (Fig 3). Conversely, light ice conditions in both years interacted to promote low long-term stock biomasses.

In terms of both mid-term and short-term interactions, the AO was associated with different directional effects in stock biomass in the sGSL versus both AK and NL (Fig 3). In AK and NL, strong positive AO positively related to mid-term latent stock biomass while positive AO negatively related to mid-term latent biomass in the sGSL. Similarly, the negative effects of positive phase AO on short-term stock biomass outcomes in AK and NL were opposed by positive stock responses to positive AO in the sGSL in the short-term.

Table 1. Short-term Prediction Model (STPM) outputs by snow crab Stock Region (AK refers to Alaska, NL refers to Newfoundland & Labrador, and sGSL refers to Southern Gulf of St. Lawrence). Long term predictor terms are for effects on stock biomasses at lag periods of 10–13 years, mid-term predictor terms are for lag periods of 2–9 years, and short-term predictor terms are for lag periods of 0–1 years. Ice refers to ice extent and AO refers to Arctic Oscillation. Numerics next to Ice and AO refer to lag years. edf refers to effective degrees of freedom, Ref.df refers to reference degrees of freedom, and dev.expl. refers to deviance explained.

Region	Predictor Terms	Interactions	edf	Ref.df	F	p	adj. R^2	dev. expl. (%)
AK	Long	Ice12 * Ice13	5.7	6.5	0.78	0.6	0.02	24.4
AK	Long, Mid	Ice12 * Ice13	5.4	6.21	1.1	0.40	0.67	80.3
AK		AO7, AO8	4.32	4.76	9.32	<0.00		
AK	Long, Mid, Short	Ice12 * Ice13	4.46	5.06	0.76	0.61	0.64	85.3
AK		AO7, AO8	5.41	5.96	5.67	0.01		
AK		AO0, AO1	4.35	4.78	0.56	0.71		
NL	Long	Ice12 * Ice13	5.49	6.23	2.2	0.09	0.18	36.4
NL	Long, Mid	Ice12 * Ice13	4.83	5.49	1.46	0.23	0.67	80.6
NL		AO7, AO8	5.27	5.94	3.64	0.02		
NL	Long, Mid, Short	Ice12 * Ice13	5.38	5.79	3.45	0.06	0.81	92.4
NL		AO7, AO8	4.83	5.47	4.58	0.02		
NL		AO0, AO1	4.34	4.79	1.64	0.25		
sGSL	Long	Ice11 * Ice12	4.70	5.56	0.56	0.83	-0.08	13.1
sGSL	Long, Mid	Ice11 * Ice12	3.30	3.56	1.90	0.16	0.43	62.7
sGSL		AO7, AO8	4.89	5.29	3.5	0.03		
sGSL	Long, Mid, Short	Ice11 * Ice12	3.63	4.03	1.73	0.2	0.41	68.3
sGSL		AO7, AO8	4.28	4.78	1.38	0.27		
sGSL		AO0, AO1	3.29	3.49	0.73	0.57		

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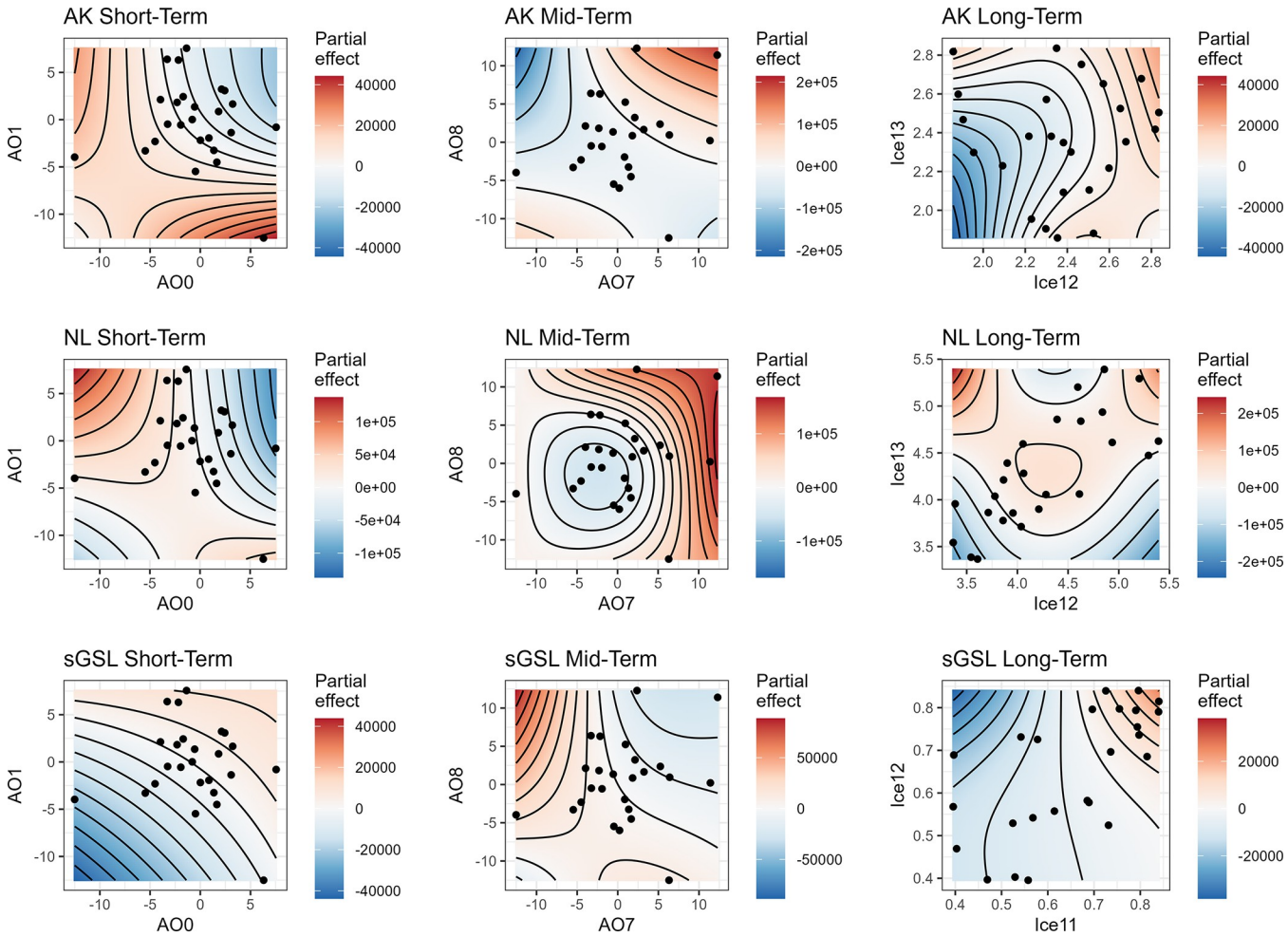

Fig 3. Contour plots of smoothed interaction effects on stock biomasses for short, mid, long-term effects for each stock region (Alaska, AK; Newfoundland and Labrador, NL; southern Gulf of St. Lawrence, sGSL) in the Short-Term Prediction model (STPM). Short-term effects are Arctic Oscillation at 0 and 1 year lags, Mid-term effects are Arctic Oscillation at 7 and 8 year lags, and long-term effects are sea ice extent at lags of 11, 12, and 13 years. Black dots depict observed data values.

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The STPM was able to re-create the time series of observed biomasses relatively well in all Regions, both with and without the short-term predictor variables applied (Fig 4). However, notable exceptions did occur, such as a negative residual pattern in AK during 1999–2004 whereby the biomass estimates remained high relative to survey estimates, and a positive residual pattern during 2005–2010 in AK, as well as in the SGSL during 2014–2019. The full model incorporating short-term predictors improved model fit in the NL Region over the 2003–2015 period.

The future confidence intervals of the STPM were broad in most cases. However, the patterns of both model runs overall suggest an increase is expected in both AK and NL over the 2020–2022 period before declines begin again, with both increases and decreases remaining within ranges of typical stock biomasses observed over the past three decades.

In the sGSL, the STPM predicts biomass may decline to low levels over the 2020–2022 period before recovery occurs. However, the persistence of the positive residual pattern in observed versus predicted biomass in 2021 and 2022 suggest some other unaccounted-for factor may be influencing the sGSL biomass trajectory.

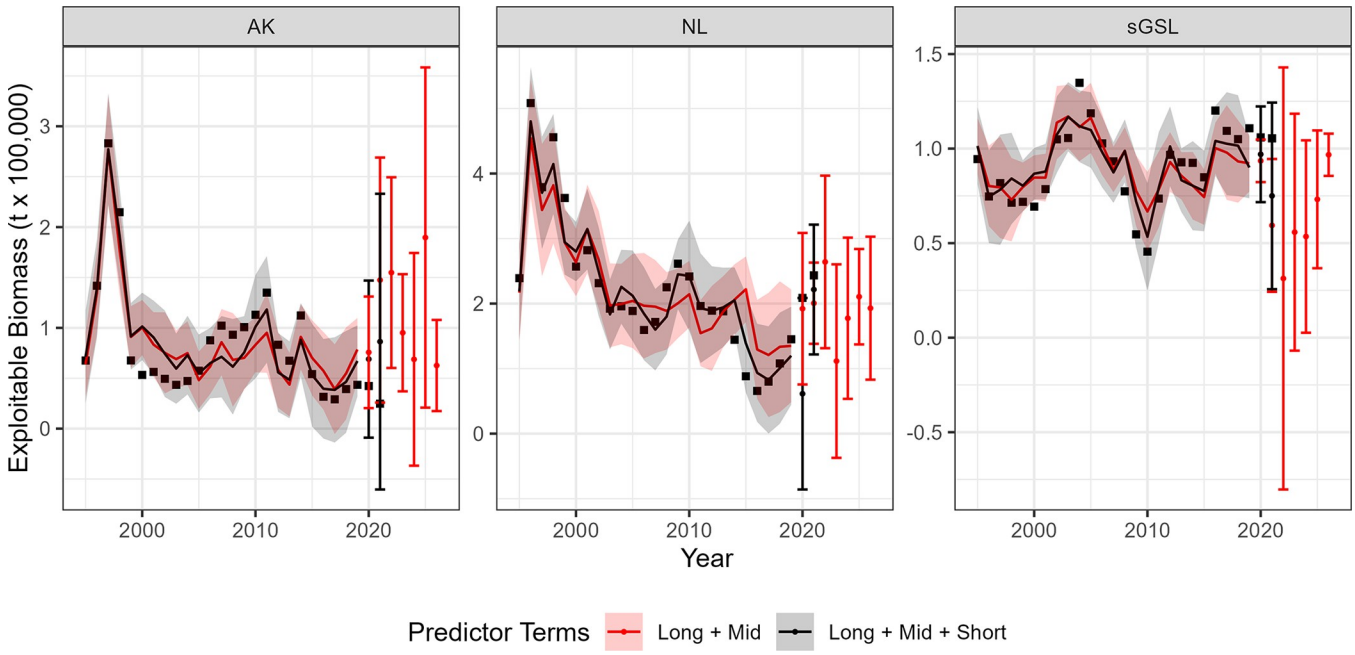

Fig 4. Short-term prediction model of biomasses for Alaska (AK), Newfoundland & Labrador (NL), and southern Gulf of St. Lawrence (sGSL) stock units. Black squares are survey indices (2020 in Alaska is model estimate). Black lines and dots and associated error bars are full model fits (short-, mid-, long-term effects) and red lines and dots and error bars are model run with no short-term effects. Shaded areas are 95% confidene intervals of model fits.

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Overall, despite recognition that the STPM provides incomplete resolution of all factors occurring to affect snow crab stock biomasses in these three stocks, the STPM sufficiently confirms that AO and sea ice are important influential factors and therefore appropriate to focus on in predicting future habitat potential.

Long-term outlook: Future habitat model

Snow crab potential habitat was defined as the difference between maximum and minimum ice cover. Compared to historic ranges, there is about three times as much total area in new frontiers that could potentially support snow crab habitat moving forward (maximum ice cover of about 15 million km^2; Fig 5). These new frontiers include the Hudson Bay, Canadian Archipelago, Arctic Ocean, East Greenland, and Barents & Kara Seas Ice Regions (Fig 1). Minimum ice levels have been occurring in each Ice Region in recent years (or long-been zero in Hudson Bay throughout the time series), and particularly within the dominant Arctic Ocean Region since about the year 2000. Overall, potential habitat area in new frontiers is increasing and has been at about 7.5 million km^2 in recent years.

Within historic ranges, maximum annual ice coverage levels have been in overall decline for four decades, decreasing from about 4.5 to 3.25 million km^2 over the time series. This overall decline is however less pronounced in the Seas of Okhotsk & Japan Ice Region, where the approximately 1.25 million km^2 maximum coverage levels observed since 2016 are similar to the long-term average. Overall, potential habitat area for snow crab within the sub/Arctic portion of the northern hemisphere has been gradually increasing since 1980, with a particularly notable increase to a level of about 10–11 million km^2 occurring in most years since 2008.

Three broad Ice ecosytem types were evident in the analysis, those that have consistently been 100% full of ice during peak periods of the annual cycle (Arctice Ocean, Canadian Archipelago, Hudson Bay; termed "Maximum Ice Regions"), those that have not consistently

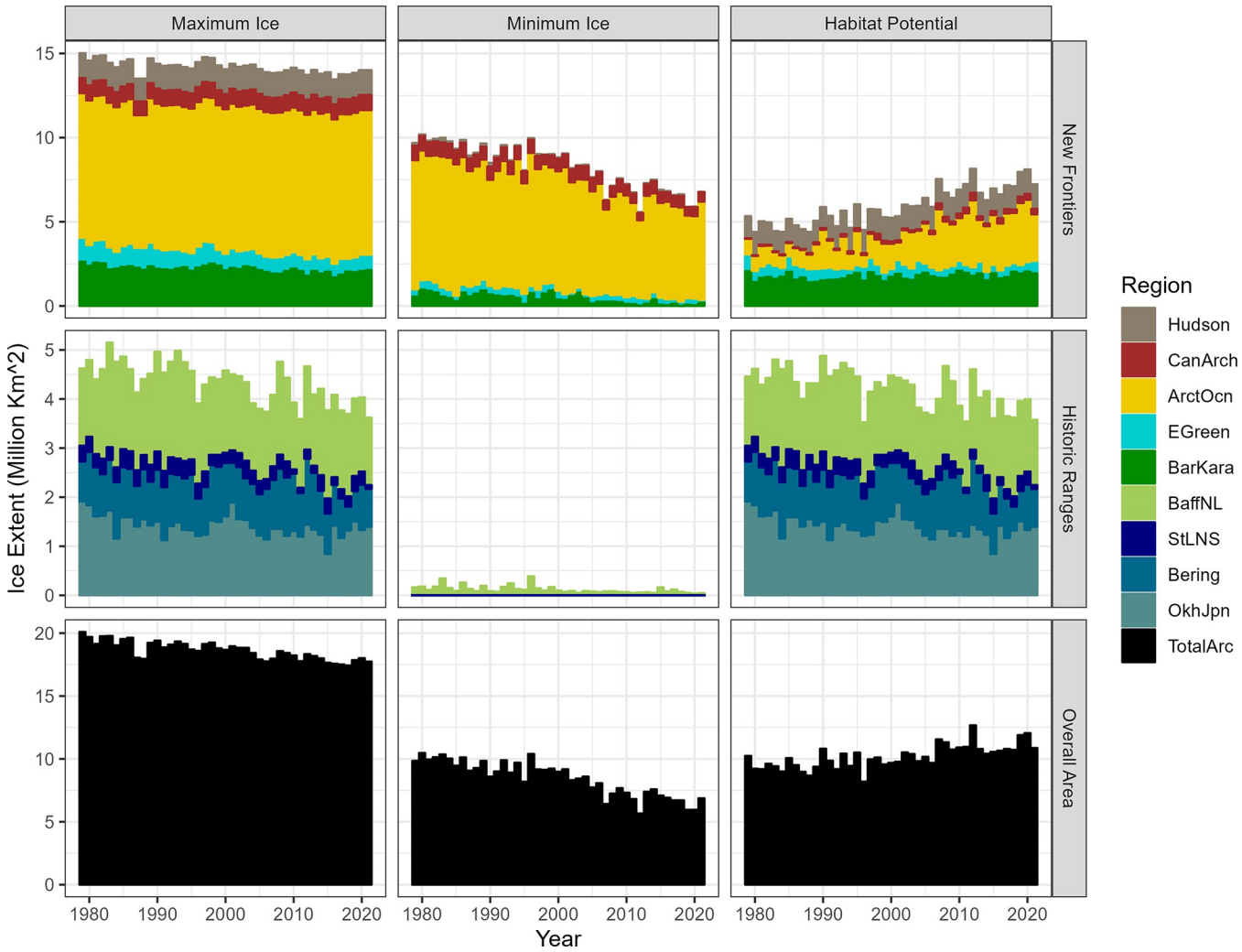

Fig 5. Ice extent indices by Ice Region grouped as new frontiers, historic ranges, and overall area. Maximum and minimum based on annual observations and Habitat Potential based on difference of maximum-minimum values. Data from NOAA satellite observations.

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reached either maximum or minimum possible (i.e. zero) ice extent within the annual cycle (Total Arctic, East Greenland, Barents & Kara Seas, Baffin Bay and Newfoundland & Labrador; termed "Variable Ice Regions"), and those that are always ice-free at some point in the year (Gulf of St. Lawrence & Nova Scotia, Bering Sea, Seas of Okhotsk & Japan; termed "Minimum Ice Regions") (Fig 6).

The interactions of CO_2 with month were overall stronger in terms of effect sizes (Chi.Sq. range 24.14 to 116.61) than the interactions of AO and month (Chi.Sq. range 2.70 to 19.98) in predicting sea ice extent in any given Ice Region (Table 2). The model produced tight fits to the data in all Ice Regions (adj. r^2 range 0.80 to 0.97).

All Ice Regions underwent a gradual decline in average ice cover over the time series (Fig 6). Overall reductions in Maximum Ice Regions reflect lower levels of annual minima ice coverage, with each continuing to reach maximum potential coverage levels during spring months in any given year. The progressive declines in average ice extent in Variable Ice Regions reflect reductions in both maximum and minimum sea ice extent over the time series. Levels of zero ice extent during the calendar year have been more commonly approached or reached in both

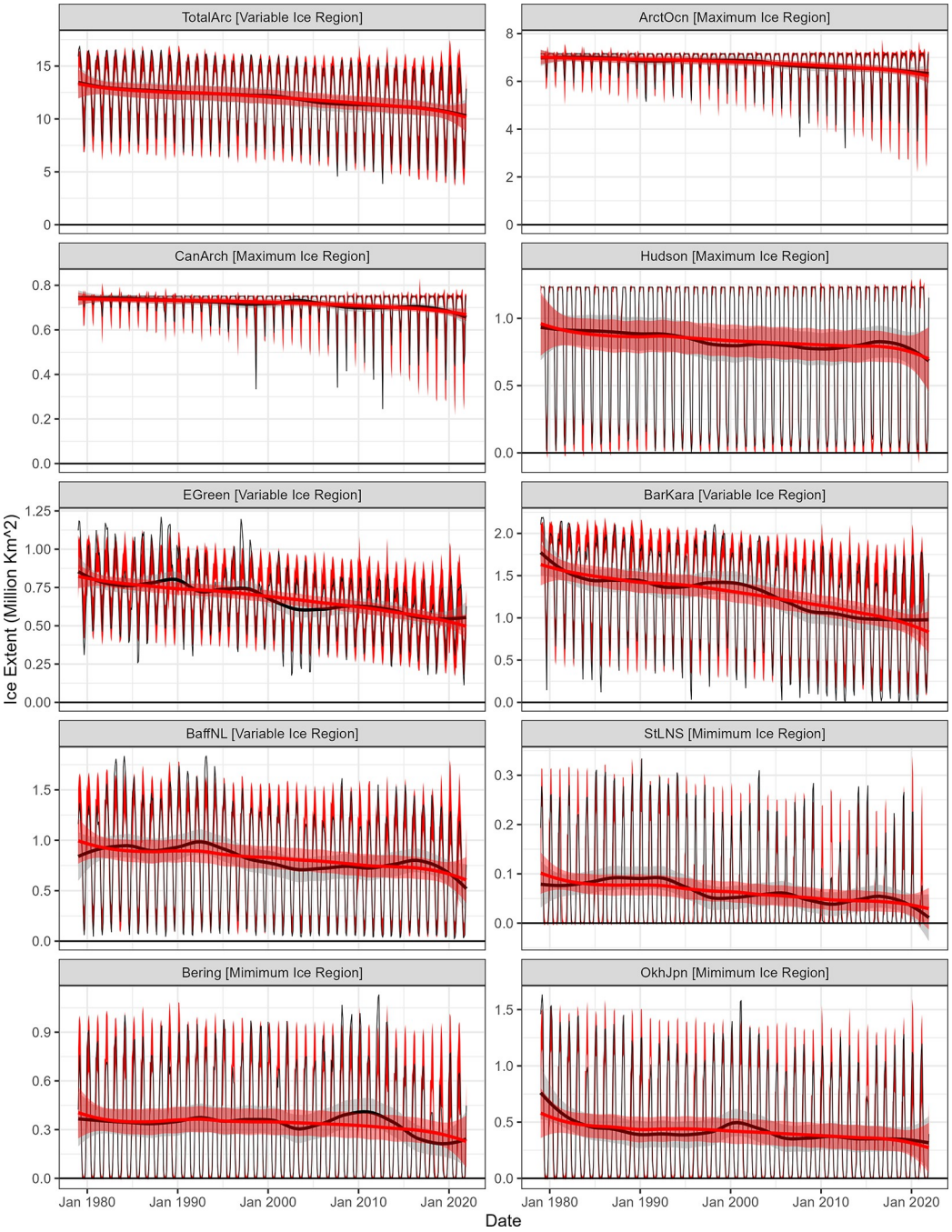

Fig 6. Observed (black) versus predicted (red) ice extent (million km^2) by month from 1980 to 2020 by Ice Region. Observed data are from NOAA satellite observations and predicted ata are from the Future Habitat Model. Horizontal lines and associated 95% confidence intervals are loess regression curves fit to the data for visual assessment of mean trends. Maximum Ice Regions refer to those consistently full of ice during the calendar year, Minimum Ice Regions refer to those consistently fully deplete of ice during the calendar year, and Variable Ice Regions refer to those neither consistently full nor deplete of ice during the calendar year.

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the Barents & Kara Seas and Baffin Bay and Newfoundland & Labrador Regions over about the last decade than prior, while East Greenland has not yet become fully devoid of ice at any point in the time series. The Minimum Ice Region declines in average ice cover reflect overall

Table 2. Future Habitat Model (FHM) outputs by Ice Region (Total Arctic [TotArc], Arctic Ocean [ArcOcn], Canadian Archipelago [CanArch], Huddon Bay [Hudson], East Greenland [EGreen], Barents and Kara Seas [BarKara], Baffin Bay and Newfoundland & Labrador [BaffNL], Southern Gulf of St. Lawrence [sGSL], Bering Sea [Bering], and Seas of Okhotsk and Japan [OkhJpn]). Predictor terms are calendar month, Arctic Oscillation (AO) and carbon dioxide (CO_2). edf refers to effective degrees of freedom, Ref.df refers to reference degrees of freedom, and dev.expl. refers to deviance explained.

Region	Predictor Terms	edf	Ref.df	Chi.Sq.	p	adj. R2	dev. expl. (%)
TotArc	Month	2.9	10	66.6	<0.0001	0.96	94.6
TotArc	AO*CO_2	3.0	3.0	4.7	0.19		
ArctOcn	Month	2.9	10	31.3	<0.0001	0.91	92.7
ArctOcn	AO*CO2	3.0	3.0	6.97	0.07		
CanArch	Month	2.96	10	24.14	<0.0001	0.81	87.2
CanArch	AO*CO2	3.0	3.0	6.53	0.09		
Hudson	Month	4.15	10	116.61	<0.0001	0.97	95.5
Hudson	AO*CO2	3.0	3.0	8.00	0.07		
EGreen	Month	2.75	10	41.93	<0.0001	0.80	75.7
EGreen	AO*CO2	3.0	3.0	10.00	0.02		
BarKara	Month	3.83	10	104.01	<0.0001	0.90	86.8
BarKara	AO*CO2	3.0	3.0	19.98	0.0002		
BaffNL	Month	3.93	10	109.82	<0.0001	0.92	89.4
BaffNL	AO*CO2	3.0	3.0	5.70	0.13		
StLNS	Month	3.7	10	74.50	<0.0001	0.82	82.9
StLNS	AO*CO2	3.0	3.0	12.61	0.006		
Bering	Month	4.42	10	93.22	<0.0001	0.89	89.5
Bering	AO*CO2	3.5	3.8	2.70	0.54		
OkhJpn	Month	3.89	10	94.65	<0.0001	0.91	91.0
OkhJpn	AO*CO2	3.0	3.0	3.99	0.26		

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reductions in maximum ice extent (among annual varibility in the process). The rate of decline in maximum ice extent in the Bering Sea Ice Region since 2012 has been particularly abrupt. At the total Arctic scale, there has a been a gradual decline in both maximum in minimum annual ice coverage extents over the time series.

The scatterplots of predicted versus observed values showed the FHM fit the monthly ice extent data well throughout the time series in all Ice Regions (Fig 7). Few exceptions included the emergence of lower observed than predicted values in the Canadian Archipelago and Arctic Ocean Regions in recent years, reflecting poor fits during minimum ice extent periods within the annual cycle (Fig 6), and a period or relatively poor fit in the Gulf of St. Lawrence & Nova Scotia Ice Region during the 1980s-1990s, where maximum ice levels were lower than predicted in many years (Fig 6). Nonetheless, these minimal exceptions had little effect on the overall performance of the FHM in being able to fit to past ice extent data at both the Regional and Total Arctic scales.

Marginal effect smooths of month in the FHM showed a consistent cyclic pattern of heaviest ice coverage occurring in about February to April and lowest ice coveage occurring in about August to September in any given Ice Region (Fig 8). Despite the overall consistent pattern there was variability both within and across Ice Regions. For example, the Gulf of St. Lawrence & Nova Scotia Region showed most variability when low ice periods occurred, with higher potential to have extended low ice periods in spring and fall relative to other areas. Conversely, areas such as Hudson Bay, the Canadian Archipelago, and the Arctic Ocean showed higher potential to be heavily covered in ice during about December to May than most other Ice Regions. In terms of magnitude of seasonal ice extent differences, East Greenland, the Barents & Kara Seas, and Baffin Bay and Newfoundland & Labrador, and the Total Arctic

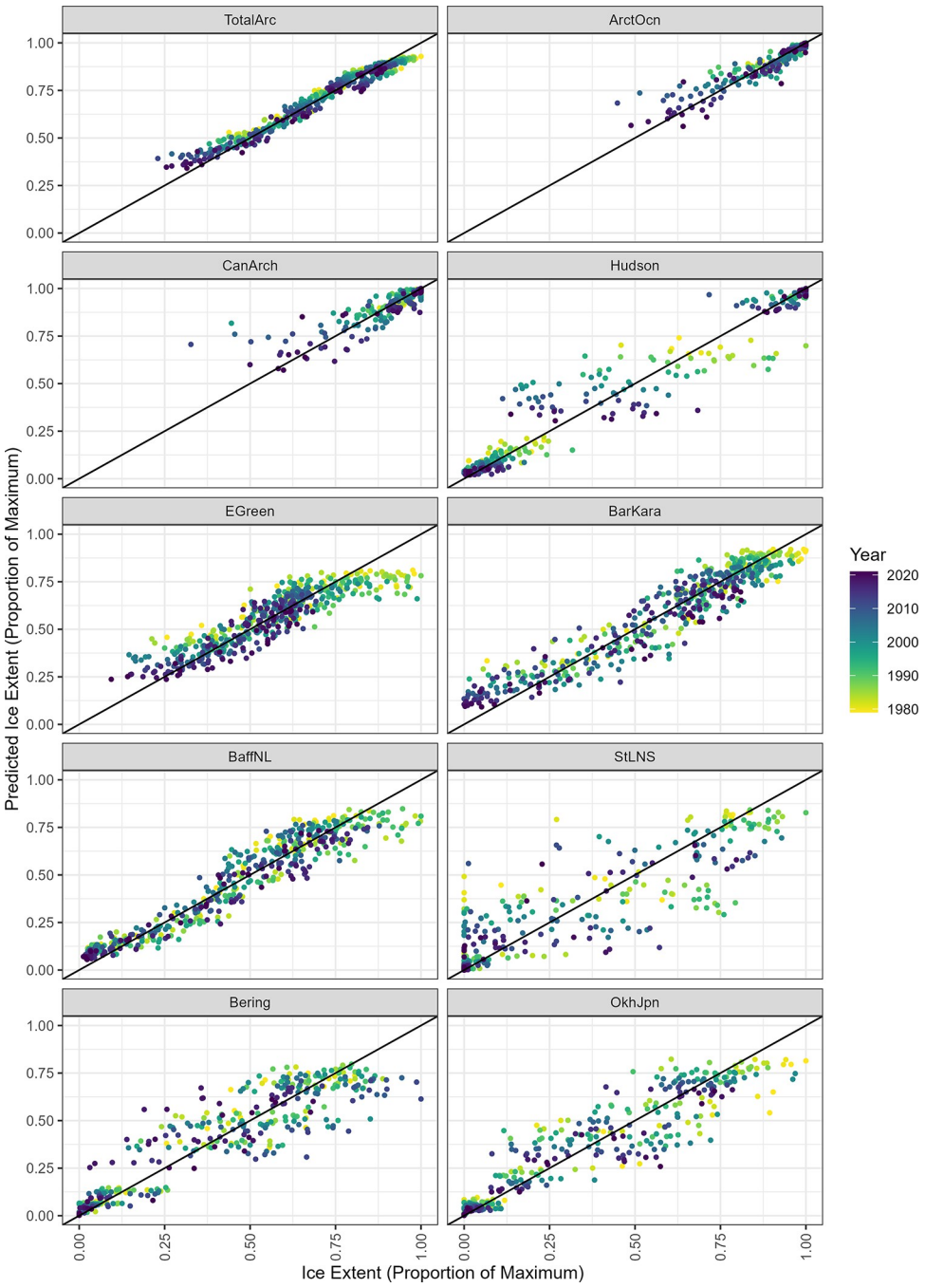

Fig 7. Future habitat model (FHM) of predicted versus observed values of ice extent by Ice Region and year. Points represent monthly values.

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as a whole, showed relatively dampened oscillations compared to Hudson Bay, the the Gulf of St. Lawrence & Nova Scotia, the Bering Sea, and the Seas of Okhotsk & Japan.

The contour plots of interactions of CO_2 and AO revealed how opposite phases of the AO differentially affect Ice Regions in regulating sea ice, but also showed an over-arching pattern of elevated CO_2 being assoicated with low ice extent in all areas (Fig 8). Under low levels of CO_2 (i.e. below about 375 or 400ppm in any given Ice Region), positive AO is associated with

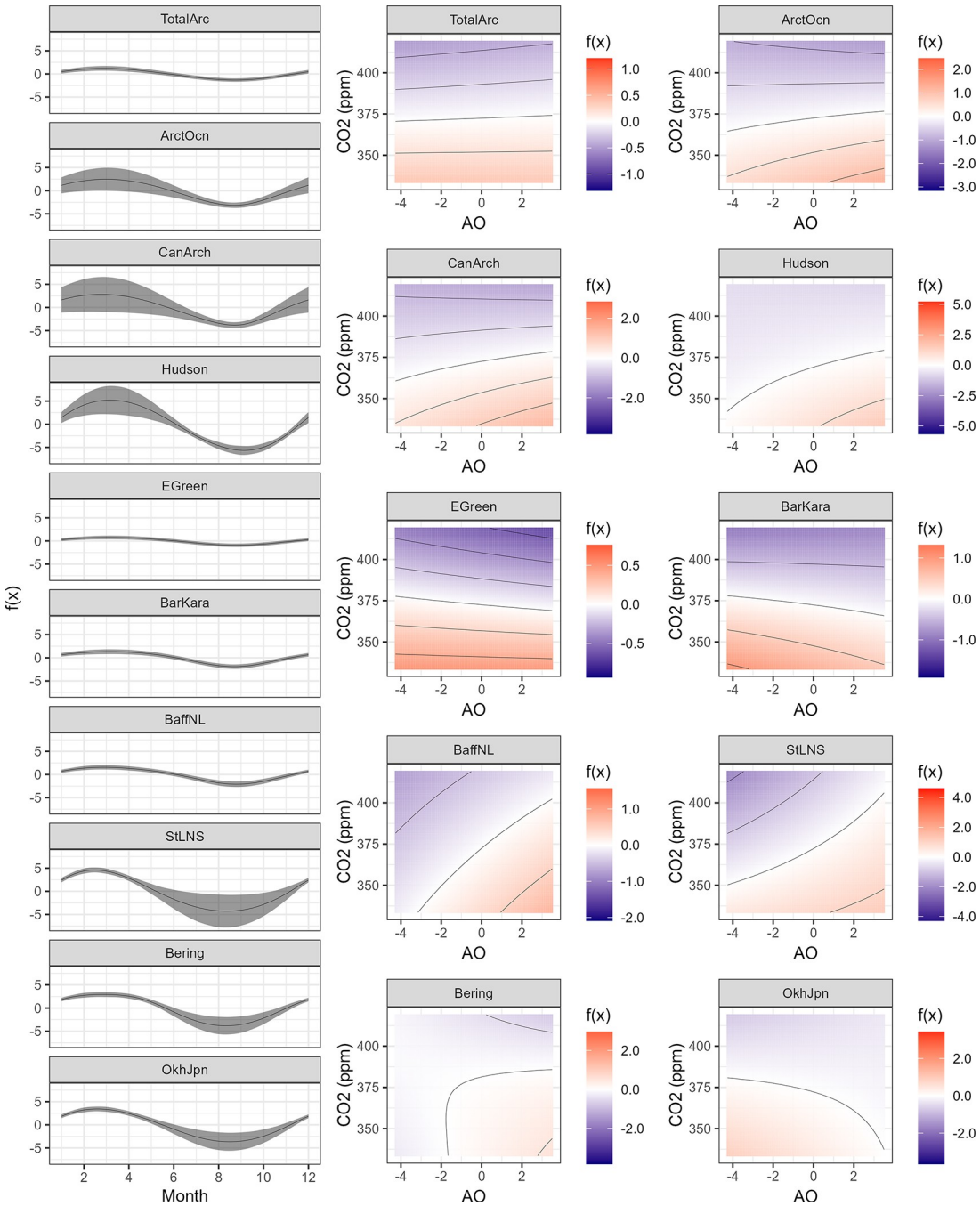

Fig 8. Left. Marginal effect smooths of monthly ice extent patterns by Ice Region. Right. Contour plots of smoothed interaction effects of atmospheric CO_2 concentration and the Arctic Oscillation on ice extent in the Future Habitat Model (FHM).

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heavy ice coverage in Baffin Bay and Newfoundland & Labrador, Gulf of St. Lawrence & Nova Scotia, Bering Sea, Hudson Bay, and Canadian Archipelago, while the opposite effect occurs in the Barents & Kara Seas and Seas of Okhotsk & Japan, with negative AO associated with heavy ice. On the whole, the AO showed a neutral pattern in its relationship with ice extent for the Total Arctic Region. Despite spatial differentiation in regional relationships between ice extent and AO, in all Ice Regions, ice extent is low under elevated CO_2. Overall, the patterns suggest

that if CO_2 continues to increase it will be domiant compared to AO in regulating sea ice extent in all Ice Regions moving forward.

The FHM showed sea ice loss can be expected in all Ice Regions under both best and worst-case CO_2 loading scenarios in the coming decades (Fig 9). In the most optimistic case, the Arctic Ocean, Canadian Archipelago, and Hudson Bay Ice Regions are predicted to maintian full ice extents during peak periods of the seasonal cycle extending out to 2100 under the best case CO_2 scenario. However, even these areas are expected to experience progressive declines in minimum ice extent and be virtually ice-free during summer months by 2100 under the best-case CO_2 scenario. Sea ice loss is predicted to be most abrupt in the Gulf of St. Lawrence & Nova Scotia Ice Region, which is predicted to be virtually ice-free during all parts of the year by 2050 under either CO_2 scenario.

The FHM compared well to existing sea ice models. The monthly medians [and one standard deviation] of model predictions over the 1979–2014 period for the Total Arctic ranged from a maximum of 15.37 [0.26] million km^2 in March to a minimum of 7.87 [0.74] in September (not shown). These estimates are well aligned with the suite of CMIP6 models reviewed by Shen et al. (2021). The benchmark of a nearly ice free Arctic defined as 1 million km^2ice extent during September was reached in 2060 (1.02 million km^2) under the worst-case CO_2 scenario, while under the best-case CO_2 scenario the lowest level of ice predicted in September was 2.40 million km^2 in 2100. Both predictions are very similar to the suite of models reviewed by [55] under low and high CO_2 loading scenarios.

When translated in terms of potential habitat area for snow crab, the overall sea ice-based total sub/Arctic estimate shows little change extending out to 2100 from the present level of about 10 million km^2 under the best case CO_2 scenario, with a point estimate of about 9 million km^2 in 2100 (Fig 10). However, after 2050 notable declines in overall habitat potential are expected under the worst case CO_2 scenario, with an approximate 50% reduction to 5 million km^2 by 2065. All historic ranges are expected to progressively lose habitat in the coming decades under both CO_2 scenarios, with virtually no habitat predicted to be available in the Gulf of St. Lawrence & Nova Scotia Ice Region by 2050 under the worst case scenario. The Arctic Ocean, Canadian Archipelago, and Hudson Bay Ice Regions are projected to increase to or maintain near maximum habitat potential extending all the way out to 2100 under the best case CO_2 scenario but under the worst case scenario each is expected to begin to lose potential habitat from peak or maximum levels over the 2050–2075 timeframe.

Discussion

Key findings

Recent studies consistently highlight dramatic and abrupt changes occurring with snow crab stocks throughout the northern hemisphere including increased presence in the Arctic and a collapse of the Eastern Bering Sea stock. This analysis addressed two central objectives of predicting short-term outcomes for recent major snow crab stocks and inferring plausible long-term outcomes for global scale habitat potential with continued global warming. The analysis finds a consistent directional effect of sea ice in affecting snow crab stock productivities, with low levels of sea ice associated with dampened productivity in association with reduced cold water habitat in areas that experience seasonal coverage of sea ice. The Arctic Oscillation is shown to exert similar temporal impacts on stocks but to act in different directions across spatial regions. Overall, recent global-scale habitat potential and stock biomasses are at or near historical highs. Despite uncertainties associated with recent surveys in focal study stocks, overall global-scale biomass is not expected to change appreciably over extending out to 2026 largely due to high productivity from Atlantic Canadian stocks as new frontiers continue to

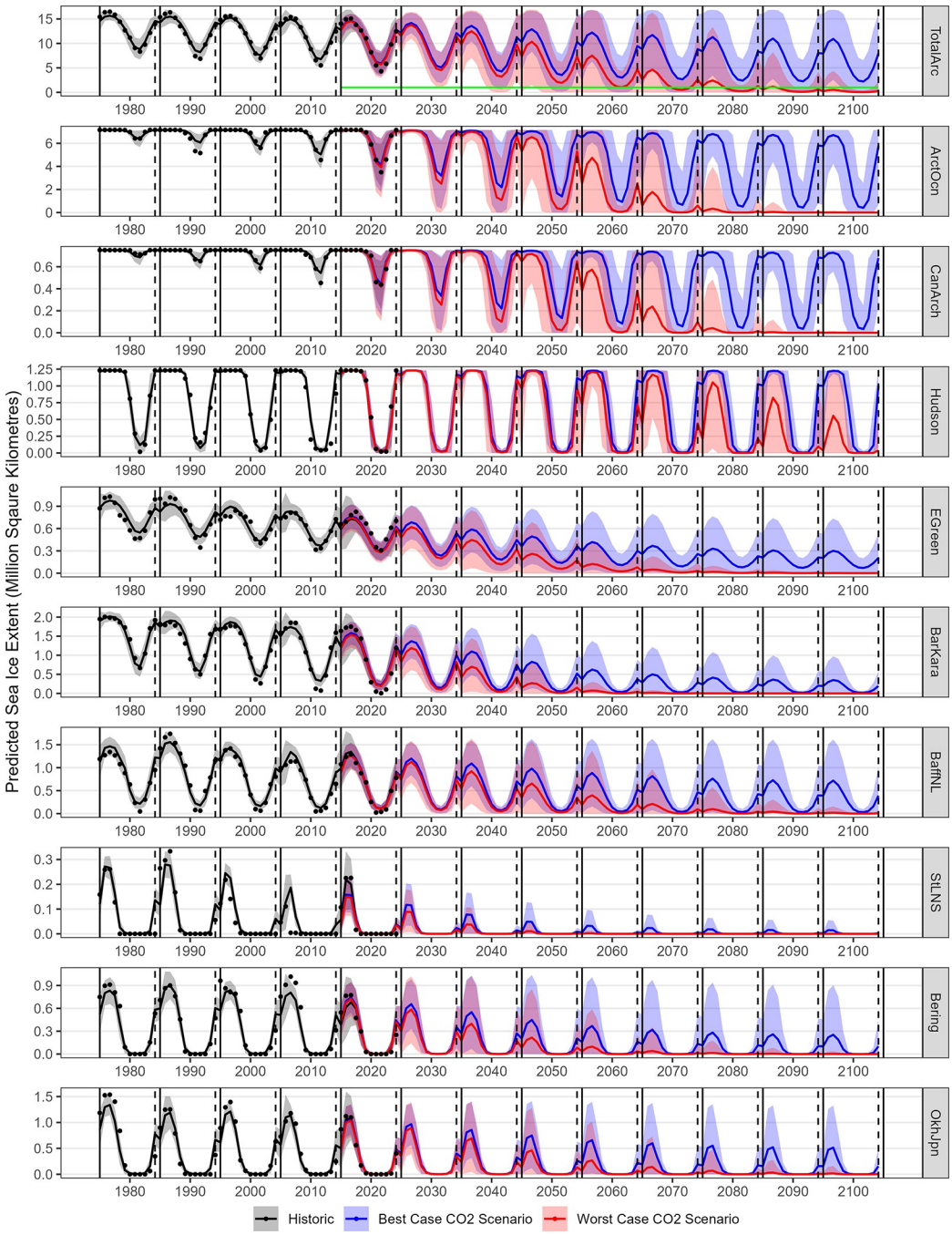

Fig 9. Historic data on monthly ice extent values from NOAA satellite observations by Ice Region (black dots) with Future Habitat Model fits (black lines) and 95% confidence intervals (gray shades). Blue and red lines show projections under best and worst case CO_2 emissions scenarios respectively. Red and blue shaded areas represent bootstrapped 95% prediction intervals. Data are fit by month with calendar years restricted to those indicated on the x-axis. Vertical solid black lines show January and vertial dashed black lines show December. Horizontal green line on Total Arctic panel (top panel) shows 1 million square kilometres ice coverage level.

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open. An examination of factors affecting sea ice extent and by extension snow crab habitat potential shows atmospheric CO_2 concentrations to be becoming increasingly dominant over the Arctic Oscillation in regulating sea ice dynamics in all northern hemisphere ecosystems.

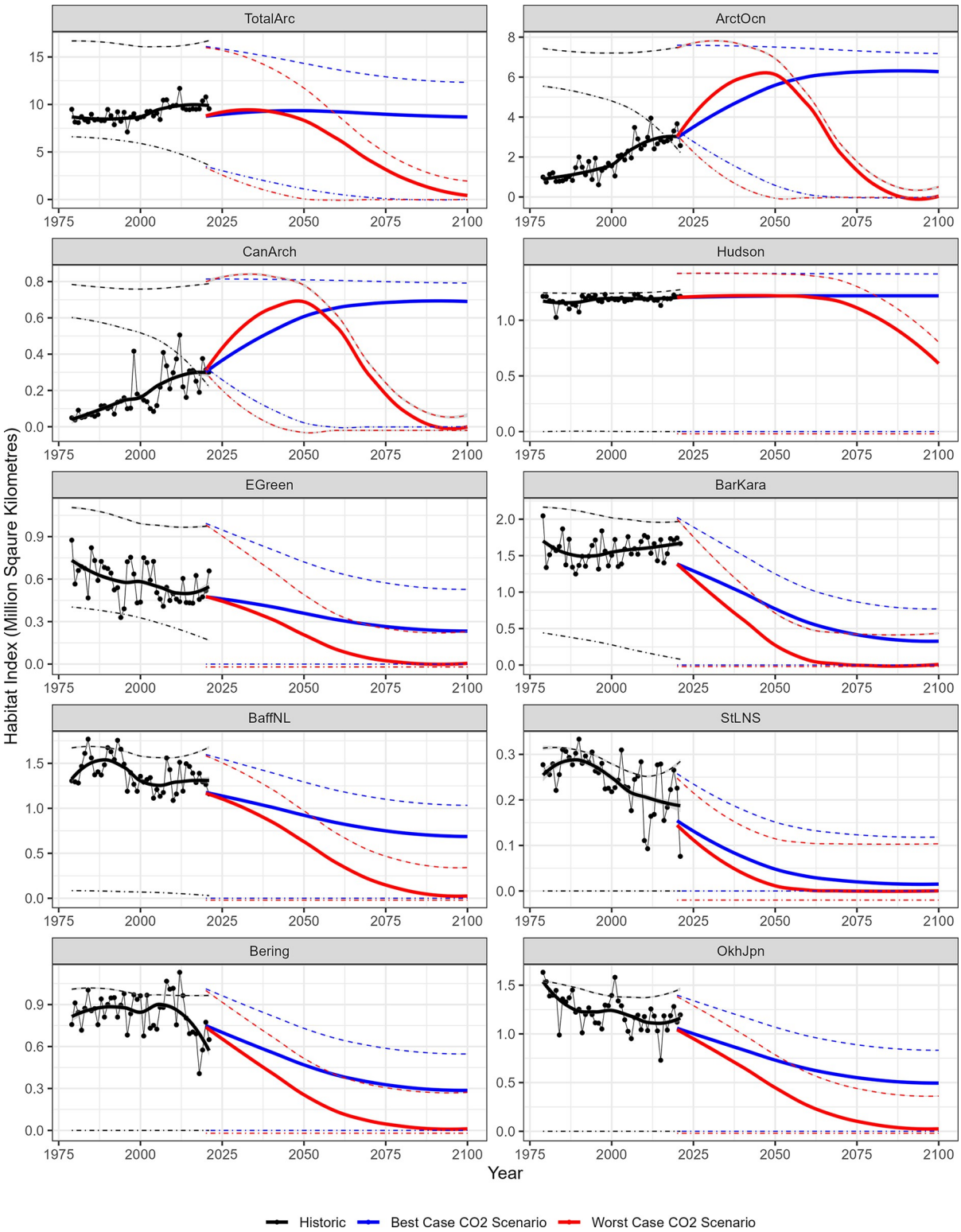

Fig 10. Snow crab potential habitat index by Ice Region. Black points show ice extent areas based on historic NOAA satellite observations of maximum minus minimum ice extent in a calendar year. Black lines are loess regression curves. Blue and red solid lines are best- and worst-case CO_2 emission scenarios projections, with the index calculated from model point estimates of maximum and minimum monthly ice extent values. Thin-dashed black lines show upper and lower 95% confidence interval bounds for model fits. Corresponding thin-dashed blue and red lines show upper (95th percentile) and lower (5th percentile) levels of predicted ice extent for a given calendar year. Lowest levels of ice predictions equal to zero in the worst-case scenario model run are plotted below zero for presentation.

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This phenomenon will likely lead to continued shifts of snow crab stock ranges from historic ranges and into new frontiers due to increased ice free periods in all areas. Ice-free periods differentially affect sub-Arctic versus Arctic areas, with prolonged ice free periods limiting habitat potential in most sub-Arctic areas and increased incidence of periodic ice recedence increasing habitat potential in most Arctic areas. Despite anticipated habitat shifts, characterized by an overall northward creep in locations of dominant stocks, overall potentially habitual area for snow crab is not expected to appreciably decline if atmospheric CO_2 loading is held to the best-case emissions scenario. However, overall rapid declines in habitual area are anticipated to occur after about 2050 under the worst case CO_2 loading scenario.

Snow crab, sea ice, AO, and CO_2 dynamics

Our analyses both support general existing knowledge on the importance of climate processes in regulating snow crab productivity and advance knowledge on the linkage of snow crab productivity with sea ice. It is not surprising that sea ice emerged as an important predictor for snow crab biomasses across historic stock ranges as its very presence is an obvious indicator of a cold marine ecosystem. This study also highlights the association between snow crab habitat and areas seasonally covered by sea ice, which enables future projections of potential snow crab habitat.

The specific mechanisms by which sea ice may regulate snow crab productivity are unknown, though multiple hypotheses exist. For example, given established relationships between areal extent of cold bottom water and early-life stages, a first possibility is that cold water could provide beneficial habitat, such as refugia to safeguard small crab from predation (i.e. [56]). A second possibility is that sea ice processes could operate through ecosystem production and associated match-mismatch phenology of early-life feeding (i.e. [57]), as suggested by [58, 59]. Although specific mechanisms of environmental regulation of stock productivity resulting from both sea ice and AO require further research, our research indicates that sea ice has a consistent directional effect on stock productivity while AO has a regionally specific directional role in regulating stocks.

Our results show that CO_2 has been a consistent unidirectional driver of ice extent across all sub/Arctic Regions over the past four decades, while AO was more inconsistent both in terms of direction and strength in regulating ice across regions. Effectively, the analysis determines that CO_2 explains most of the underlying declining trends in sea ice while AO has historically contributed to variability in time and space. However, our work also reveals that CO_2 has become increasingly dominant in the interaction of the two variables in regulating ice in all sub/Arctic areas. Assuming the pattern of reduced AO control over ice dynamics beyond about 375–400 ppm atmospheric CO_2 concentration holds, like most sea ice models (i.e. [54, 60–63]), the FHM indicates ice loss is inevitable in all sub/Arctic marine ecosystems during the coming century. Therefore, by extension, snow crab habitat shifts are also likely inevitable. Despite spatial habitat shifts, overall, the area of potential snow crab habitat is not expected to appreciably decline if atmospheric CO_2 loading is held to the best-case CO_2 emissions scenario.

Limitations and unexplained processes and events

Our two focal models were parsimonious in structure. Despite recognition that not all important explanatory processes were captured in either model, we highlight that both the FHM and STPM performed reasonably well where information to measure their accuracy was possible. For the FHM we were able to accurately reflect 1979–2014 monthly ice extent predictions with the suite of models contained in the CMIP6 project, develop an estimate to time to an

"essentially ice-free Arctic" consistent with other models, and accurately predict 2020 monthly ice extents consistent with observed measurements in all ten Ice Regions. In the case of the STPM, predictive performance is harder to judge due to recent survey issues in all three Stock Regions but the overall forecasts for short-term increases in the Alaska and NL stocks are consistent with recent stock assessments [10, 20].

From a qualitative perspective, the association between teleconnections, sea ice, and stock biomass, has limitations. For example, we examined ice extent but in reality other measures of sea ice dynamics such as retreat timing could be important determinants of stock success. Nonetheless, such alternative measures of sea ice dynamics and more broadly other ocean climate phenomenon are typically correlated with one another (i.e. [64]), thus the approach sufficiently establishes sea ice as an important focal variable to associate with snow crab habitat and productivity. Beyond selection of inclusion for specific climate variables to attempt to model snow crab biomass, intrinsic population processes could affect predictive performance of the STPM. For example, within portions of the Gulf of St. Lawrence it has been suggested that pulses of larval abundance are partially moderated through a cohort resonance phenomenon resulting from cannibalism by females and operating on a 7–9 year repeated cycle [58, 59].

From a quantitative perspective, long-term environment-recruitment relationships in fisheries resources often erode over time [65]. This can be due to exogenous factors beyond those being examined in the quantitative relationships themselves. Two recent events detailed in this analysis require consideration in context of on-going or inevitable erosion of demonstrated climate-snow crab relationships. Specifically, the sudden and unexpected collapse of Alaska snow crab and the prolonged continual increase in the sGSL stock. Regarding the Alaskan stock collapse, our work indicates that whatever occurred was not due to poor long or mid-term ecosystem conditions. We therefore infer that a recent and spatially broad-based ocean climate event likely promoted the collapse. This inference is based on a key observation that all stock components including both sexes and all instar and maturity stages were adversely affected at once, with habitat partitioning known to exist among these different population components over large spatial scales in the Eastern Bering Sea [19, 44]. In specific reference to the recent unexplained trajectory of the sGSL stock, beyond the possibility that recent upward biases in stock size measurements could be occurring [9], we suggest that release from cod predation [66] could be a factor progressively enabling continued high productivity in the stock, with extremely low levels of cod biomass for over a decade and a possible extinction of cod from that ecosystem within decades [39].

Although more research is needed to understand both the Alaska snow crab collapse and the unexpected prolonged high productivity of the sGSL stock, it is worth considering if the two events could have underlying linkages. For example, we showed inverse correlations with the AO and biomasses between the two stocks. It is known that the AO has been in an overall positive phase since 2010 and was exceptionally positive in 2020. From a statistical perspective, this would be expected to promote negative responses in the Alaskan stock and positive responses in the sGSL stock. Interestingly, [67] described the high positive winter 2019 and spring 2020 AO event as being unusual in comparison to the previous twelve positive AO events by being split into two dominant spatiotemporal domains. Accordingly, further investigations of regionalized AO effects could be warranted in trying to explain both events.

The inverse relationship between stock biomasses in the sGSL versus AK and more particularly NL is intriguing given that NL and sGSL ecosystems are adjacent to one another and considering all three ecosystems showed consistent direction of AO association with sea ice extent. We suggest intricacies of how AO affects water masses in Atlantic Canada likely promote the inverse stock trajectories. To elaborate, the sGSL ecosystem occurs downstream of the NL marine shelves along the path of the cold Labrador Current. Positive phases of the

NAO (and by inference AO) are related to a strengthening of Labrador Current transport flow along the Labrador slope and a weakening of the cold shelf break current on the Scotian shelf, and vice-versa [68]. During positive NAO periods, a stronger transport in the North Atlantic subpolar gyre builds up as a response to stronger wind curl above the North Atlantic, and greater amounts of Labrador Current water are diverted offshore toward the Northeast Atlantic, rather than to the regions west of the Grand Banks including the Scotian Shelf and the Gulf of St. Lawrence [69]. This easterly displacement of Labrador Current water under positive NAO reduces the influence of fresh cold arctic water to the western extremities of the Gulf of St. Lawrence ecosystem [70–72]. Opposite west/east Labrador Current transport flows occur under negative NAO/AO.

Applying sea ice recedence to potential snow crab habitat in new frontiers invokes an assumption that the crab can successfully inhabit new areas. Although zoological evidence from recent decades confirms that the species is able to quickly adapt to new areas, it is not realistic to assume this can occur everywhere. Even within existing stock areas there is evidence to suggest this assumption may not hold. For example, within the Baffin Bay and Newfoundland & Labrador Ice Region snow crab currently only exist in the southern portion of it, along the NL shelves. It may not be possible for snow crab to occupy the more northern extremities of the Region in presence of the strong southerly flowing Labrador Current. This suggestion is raised in context of recent observations of a contraction of the snow crab stock range from its northernmost extent off the Labrador Coast [20]. However, conversely, given that the species distribution is now near circumpolar, the extent to which physical movements or larval drift can limit future invasions could become reduced, and increased shipping activity in progressively ice-free waters would also likely help foster more future invasions.

Sea ice was used as a predictable proxy for potential habitat, extending upon operationalized definitions of cold bottom water extent as representing snow crab habitat. However, surface ice extent would not be expected to directly correspond to available habitat on the seafloor. In most cases, the surface index would likely overestimate actual habitat area. For example, snow crab does not typically occupy either shallowest or greatest depths of the continental shelf in any given area. Thus, it is understood that our projections are coarse grain, and that shoreline or deep areas of new frontiers may not be inhabitable at all, even if surface ice dynamics are suitable.

Despite limitations and uncertainties, our work importantly highlights that beyond the next decade geographic shifts in snow crab stock abundances should be expected, with an overall predicted pattern of a northward creep in locations of dominant stocks. This is ecologically important, but it is also important from socioeconomic perspectives.

Application of results–Future fisheries ecosystem

Sea ice extent predictions were used to project potential future habitat for snow crab at the northern hemisphere scale, constituting an important exploration of global warming outcomes into future "fisheries ecosystems". The fisheries ecosystem embodies a range of ecological and anthropogenic disciplines. At present, we determined recent global-scale habitat potential to be at or near historically measured highs of about 10–11 million km^2. Coincidentally, known indicators from the burgeoning Barents Sea snow crab stock suggest the biomass (personal communication, Sergey Bakanev, PNIRO) and fishery [33, 73] continue to expand. Accordingly, in conjunction with the two Atlantic Canada stocks being moderate-high at once, overall global snow crab supplies are also expected to be at or near historical highs.

The available information suggests global-scale biomass and fisheries yields have conformed relatively well to our habitat index to-date. We suggest this recent success of the species

at the global scale reflects a transition period in global warming processes whereby the majority of examined sub/Arctic ecosystems are now experiencing periods of both ice cover and recedence in a given year, with neither or few ecosystems overly limited by either perpetual or ephemeral ice cover at-present.

Our work shows there will be both winner and loser regions in terms of how global warming affects future snow crab habitat and by extension possibilities for fisheries. New frontiers are anticipated to benefit from sea ice loss due to reductions in annual ice extent minima while historic ranges are likely to suffer from sea ice loss due to reductions in annual ice extent maxima. At-present, coincidental productive fisheries in NL and sGSL in Canada would be expected to maintain global supplies at a high level no matter what is occurring in other regions, with the two Regions combining for a catch of about 82,000 t in 2022 [74]. However, both at-present and in coming decade, the offsetting impacts of the collapse of the Alaskan snow crab fishery versus the growth of the Barents & Kara Seas crab fisheries are likely to have significant impacts on the extent to which overall global-scale fishery yields change. Recently, the two Regions would appear to roughly balance one another. For example, [75] reported 13,615 t of removals from the Barents Sea in 2019, which was similar to the 15,400 t of removals from Alaska in the 2019/2020 management year [10]. Although recovery in the Alaskan stock may occur, our predictions are for continued deterioration of habitat prospects in Alaska as well as reduced habitat potential in the Barents & Kara Seas moving forward. The increasing trend in habitat potential in the Barents & Kara Seas for the past three decades could now be near maximized because there is little new area for ice recedence to occur. For example, to-date, habitat and associated stock growth there has been most apparent in the western portion of the Region, in the Barents Sea, where pronounced seasonal ice recedence has long occurred. However, stock growth has recently also been occurring in the eastern portion of the Region, the Kara Sea, where appreciable levels of seasonal ice recedence have now become more commonplace. Indeed, recent seasonal melting of ice in the Kara Sea has been documented as enabling self-reproducing populations of snow crab to persist [76] and in 2022 Russia opened new commercial fisheries of snow crab in this sea. Even if our definition of habitat potential in the Region is now near maximized, it is not likely ecosystem carrying capacities have yet been realized in the still burgeoning populations of snow crab, thus it should not be assumed stock or fisheries productivity from the Barents & Kara Seas Region are yet maximized even if habitat potential is.

Spatially, the future fisheries ecosystems for snow crab will undoubtedly look much different than at-present, but notwithstanding likely re-distributions of dominant habitats, we project that overall potential habitual area could remain similar to present levels if CO_2 emissions are curtailed to best-case scenario levels. In extension of this, if the relationship between potential habitat area and global-scale yields were to continue to hold, it would be inferred that global supplies could remain similar to current levels extending out to 2100. However, if CO_2 emissions continue to increase and follow the worst-case scenario, global-scale prospects for snow crab supplies would appear poor relative to current levels after about 2050.

Moving forward, it is expected that states whose northern peripheries border the Arctic Ocean will be potential beneficiaries of new snow crab fisheries. In this regard, Russia appears positioned to continue as a dominant source of global supplies in the long-term. Much of the continental shelf in what we describe as promising habitat prospects for the spatially dominant Artic Ocean Ice Region occurs in Russian waters ranging from the Chukchi to Laptev Seas. Moreover, the snow crab is already there [6, 77]. Canada may also benefit from the opening of new frontier areas moving forward, particularly if areas of the Canadian Archipelago and Hudson Bay become inhabited. Snow crab do not yet knowingly exist in these areas but populations to the west, in the Beaufort Sea, are thought to be expanding [77].

Many factors will affect the dynamics of potential snow crab occupation of new frontiers moving forward. First, regarding pace, it cannot be overlooked that in some Maximum Ice Regions (Arctic Ocean, Canadian Archipelago) melting is occurring faster than our model could predict. Accordingly, the time necessary for invasions to occur may not be distant. This is important to consider alongside the potential for pre-existing but unknown presences of snow crab. For example, [33] recently found that Barents Sea snow crab populations are genetically distinct from those in both Atlantic Canada and Alaska, raising the possibility of other seed populations beyond those receiving most presumptive focus to-date. Dahle et al. [33] importantly highlighted that the Arctic has been ice-free several times in the past few hundred thousands of years, thus marine taxa have been exchanged across oceanic basins in the past. The possibility of established but unknown populations of snow crab within the Arctic Basin exists. Potential future occupation of new frontiers, or conversely resilience to reduced habitat in historic ranges, could also be affected by advection patterns of water from melting ice. For example, southerly flowing Arctic Currents deliver water to continental shelves of both the NL and Seas of Okhotsk and Japan, thus these areas may be able to maintain healthy stocks even in the absence of seasonal sea ice cover. Another possibility that could affect population dynamics in both new frontiers and historic ranges is climate-related catastrophic events. For example, the unforeseen collapse of the Alaskan stock could be indicative of a rapid response to climatic factors. Furthermore, fleet dynamics of where, when, how, or if to harvest, would undoubtedly affect the success of stocks in both new frontiers and historic ranges moving forward. Fisheries can exert strong top-down control on snow crab populations [45], thus it will be important to understand how industries and regulatory agencies respond to shifting habitat potentials.

Finally, in extension of how fisheries will respond to shifting habitats for snow crab moving forward, it is important to consider political responses to climate change. For example, for non-sedentary species, developed nations including Canada, China, Denmark, Iceland, Japan, Norway, Russia, Korea, the United States, and the European Union have jointly agreed not to initiate commercial fishing in the central Arctic Ocean until there is more knowledge about fish stocks within it [78]. Although the agreement does not pertain to the sedentary snow crab [79–81], it highlights how socio-political factors and actions of sovereign nations are interconnected with ecological change in affecting outcomes for natural resources with climate change. Beyond unknowns about where and when the snow crab may show up, it is not clear whether nations will choose to exploit them. The reality is that the lucrative snow crab is sub-Arctic no more and that further expansions of this species into Arctic areas could be indicative of how we as people respond to outcomes of the climate we helped change.

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