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Exploring novel North Water Polynya ecosystems under climate change

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Abstract

Climate change is rapidly reshaping species distributions in the Arctic, which could profoundly impact ecosystem structure and function. While considerable effort has focused on projecting future species distributions, assessing the impacts of range-shifting species on recipient communities and subsequent disruptions to food webs remains largely unstudied. Here, we address this gap by combining species distribution models and ecosystem models to explore the emergence of novel ecosystems in the North Water Polynya. The North Water Polynya is an open-water area between Greenland and Canada, surrounded by sea ice and one of the world's most productive ocean ecosystems. Using existing literature and projections from species distribution models of four marine species, we develop six plausible future ecosystem scenarios for the North Water Polynya. These scenarios include changing biomass of primary producers, changing biomass and size structure of copepods, shifting abundances of forage fish species, and the establishment of killer whales. We find that the biomass of higher trophic levels show pronounced decreases in response to the decrease in pelagic primary producers, with polar bear biomass halving compared to present conditions. Changes in the copepod size structure has the largest impact on the entire ecosystem compared to the other novel ecosystem scenarios, suggesting a strong reliance of higher trophic levels on large, lipid-rich copepods. We further show that increasing capelin with a simultaneous decrease in Arctic cod biomass causes large decreases in the biomass of marine mammals such as polar bear, beluga and ringed seal. Finally, we show the establishment of killer whales as a key novel predator could have cascading top-down effects on the North Water Polynya ecosystem. The framework presented here provides an approach for exploring the emergence of novel ecosystems and highlights how climate change could disrupt a high Arctic ecosystem.

1 Introduction

Climate change is rapidly altering Arctic marine ecosystems [1,2]. Sea ice is melting at an increasing rate [3], waters are warming, and species are shifting their distributions to keep

www.bio-oracle.org/). The North Water Polynya Ecopath model is publicly available through the EcoBase database of Ecopath with Ecosim models: http://ecobase.ecopath.org/#docs. Species distribution model results and output are fully available on Figshare (https://doi.org/10.6084/m9.figshare.c.7420774).

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pace with the changing climate [4]. As species shift their ranges, biotic interactions and ecological communities change [5], as local extinctions and invasions affect the respective food-web structure and functioning [6,7]. For example, the potential borealisation of the Arctic marine ecosystem could have profound implications on community structure and function [2,6–8]. In the Barents Sea, reduced sea ice and increasing water temperatures have led to colonization by boreal species, such as Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) [6,9]. These species are large generalists that increase food-web connectivity between the benthic and pelagic communities [6,7,9]. The movement of Atlantic cod into northern regions of the Barents Sea also implies increased predation pressure on native Arctic cod (*Boreogadus saida*) [2,10,11]. Such climate-driven range changes are likely to lead to formation of novel ecosystems, though the consequences of these new species interactions remain largely unknown [12,13]. Thus, a major challenge facing both biogeography and community ecology today is to understand how food webs may change with climate-induced range shifts, and the implications of these changes for ecosystem structure and function [14,15].

Climate change is presently impacting much of the Arctic, including the North Water (NOW) Polynya [16,17]. The NOW (Kalaallisut: *Pikialasorsuaq*; Inuktitut: *Sarvarjuaq*), a region in northern Baffin Bay, is the largest and most biologically productive polynya north of the Arctic circle. It has sustained, for millennia, the world's northernmost Inuit communities and several keystone Arctic species, including Arctic cod, beluga whales (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), Atlantic walrus *(Odobenus rosmarus*), and polar bears (*Ursus maritmus*) [17,18]. Due to climate change, the NOW Polynya formation has become less stable [16,19], threatening ecosystem structure and function, as well as Inuit communities on both sides of the polynya [16].

With climate-related changes in water temperatures and reduction in sea ice, the northward expansion of southern species into the NOW Polynya is expected [20]. For example, capelin (*Mallotus villosus*) has an unknown role in the current NOW ecosystem [20,21] but it may increase in the region in the future, competing with Arctic cod and zooplanktivorous birds for *calanoid* copepods [22]. Furthermore, increasing catches of Greenland halibut (*Reinhardtius hippoglossoides*) on the eastern side of the NOW Polynya suggest an abundance increase in the region, likely due to climate change [23]. However, the impacts of future climate-driven range shifts on the NOW Polynya ecosystem remains unknown.

Species distribution models (SDMs) are a popular method to understand and predict shifts in species' ranges in response to changing environmental factors [4,24–27]. These models use statistical relationships (correlations) between species occurrence data and environmental variables to infer the ecological niche of a species [28]. One limitation of SDMs is that they do not explicitly account for, or quantify, species interactions [29], hence the consequences of species distribution shifts cannot be quantified. The limitations of SDMs have been widely discussed in the literature [30–32] but, notwithstanding these limitations, they have the ability to improve our understanding of marine systems under climate change. Coupling SDMs with ecosystem models could result in a step-change in our understanding of the likely impact of climate change on marine systems [33].

In contrast to SDMs, marine ecosystem models offer a holistic approach to studying community ecology by integrating trophic interactions and energy flows among various species in an ecosystem [34]. These models can account for interactions such as competition and predator-prey relationships to simulate the complex dynamics of ecosystems [35]. Ecopath with Ecosim (EwE, http://www.ecopath.org) is one such modeling approach that has been widely applied to aquatic ecosystems since its development in the 1980s [36]. Ecopath represents static mass-balanced models of marine ecosystems, and Ecosim is an extension that simulates temporal dynamics [37,38]. EwE models can be used to examine the fundamental dynamics of ecosystems and assess their responses to environmental changes and fishing exploitation [39,40]. EwE models have been developed for several Arctic coastal and shelf ecosystems [11,41–44], including the NOW [45]. EwE models have been used to investigate the implications of different harvesting policies, identify data gaps, describe ecological dynamics for marine conservation purposes, and develop ecological indicators to evaluate the ecosystem-wide impacts of climate change [46–48]. In this context, EwE can be used to explore novel ecosystems, as species abundances increase or new species emerge and establish themselves in an ecosystem (e.g., [49]).

To understand the impacts of shifting species distributions on the structure and function of the NOW Polynya ecosystem, information on potential distribution shifts of both key novel and native species can be integrated into EwE models. Unlike SDMs, EwE models were not developed to predict novel colonists. As a result, the integration of SDMs into ecosystem models is a very active field [50]. Understanding the dynamics of species responses can aid in anticipating and mitigating the ecological consequences of climate change and facilitating informed conservation strategies.

Here, we combine SDMs with the EwE modeling framework to explore novel NOW Polynya ecosystems under two future climate change scenarios. Using the combined model approach, we address the following question: What are the ecosystem implications for the NOW Polynya due to climate change driven shifts in species distributions?

2 Materials and methods

2.1 The North Water Polynya ecosystem

The North Water (NOW) Polynya is situated in northern Baffin Bay, between Ellesmere Island (Canada) and northwest Greenland, and is linked to Lancaster Sound, Jones Sound, Kane Basin, Lincoln Sea, and central Baffin Bay (Fig 1). It has an average depth of 300 m, (range 170–600 m; [51,52]) and experiences strong seasonal variation through changing light availability, ice breakup, open water periods, and the timing of the spring phytoplankton bloom [20,53–55].

The NOW is one of the most productive Arctic ecosystems [53], attributed in part to early open water conditions that prolong the exposure of primary producers to light, resulting in an unusually early spring bloom [56,57]. The energy generated during the spring bloom predominantly accumulates in surface waters, and is subject to intense grazing by herbivorous zooplankton, such as *Calanus hyperboreus*. Tremblay et al. [56] estimated that only 27% of particulate primary production during a spring bloom exits the upper 50 m, with 1–7% reaching the benthos, contingent on water depth. Mid- and lower-trophic-level prey, including Arctic cod and meso-zooplankton, assume a crucial role in transferring energy to higher trophic level seabirds and marine mammals [58].

Delineating the precise boundaries of the NOW proves challenging due to sea-ice dynamics. Sea-ice melting commences in the spring in the southeast with the return of daylight, progressing northwest under the influence of the warmer West Greenland Current [19]. Extensive open water becomes prominent by May, reaching its maximum extent by late June or early July [16,59–61]. The polynya continues to expand until it merges with open water moving northward from Davis Strait, leading to the dissolution of the NOW Polynya as it joins the ocean by August [60,62]. The Ecopath model used in this study represents the period of polynya formation, full open water extent, and dissolution (from April to October). The model area boundaries are 76–78.5˚N and 80.5–65˚W [45]. This region represents the NOW Polynya, with an approximate size of 85,000 km^2, reflecting the observed peak extension in 2000 [63].

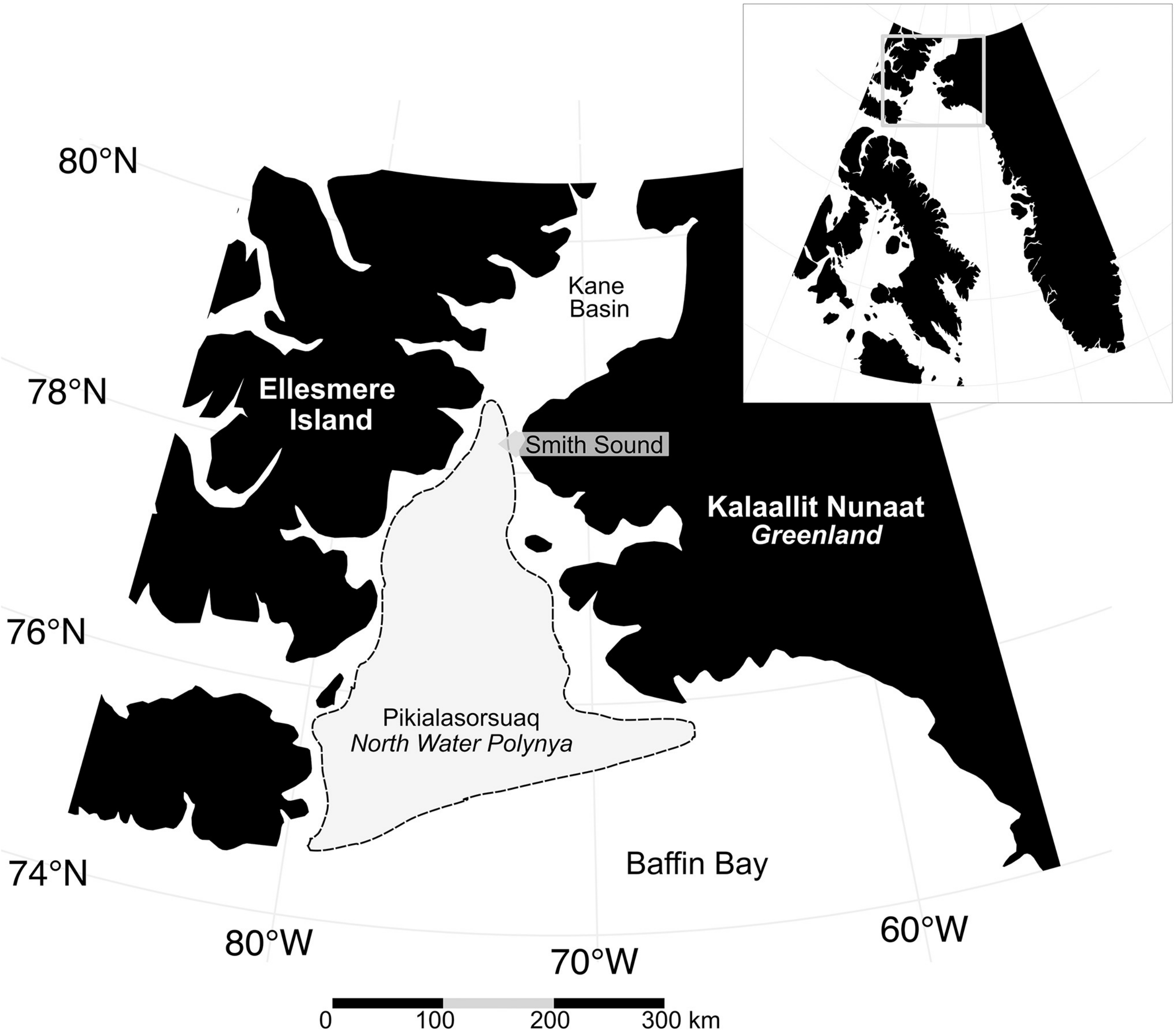

Fig 1. Overview of the study area, representing the maximum, open water extent of the North Water Polynya. From Bryndum-Buchholz et al. [45].

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2.2 Species distribution modeling

2.2.1 Selected species and occurrence data. Three fish and one marine mammal were selected for species distribution modeling, comprising: one important fish species already present in the NOW Polynya, Arctic cod (*B. saida*); one small pelagic fish expected to increasingly move into the polynya with warming, capelin (*M. villosus*); one commercially important demersal fish species, Greenland halibut (*R. hippoglossoides*); and one top marine predator, killer whale (*Orcinus orca*). We included capelin and Greenland halibut because previous studies suggest their distributions and abundances are already increasing in other Arctic regions [23,64,65]. Current information on killer whales in the NOW Polynya is limited [66] but they are considered occasional visitors to the western part of the polynya [67,68]. Sightings and reports suggest they are mainly observed south and southwest of the NOW [67,69]. Thus, we chose to model the potential habitat in the NOW Polynya of killer whales under climate change scenarios.

Occurrence data were gathered for the selected species from the Global Biodiversity Information Facility (GBIF; http://data.gbif.org) and the Ocean Biodiversity Information System (OBIS; http://www.iobis.org). GBIF data were downloaded on the 26th October 2022 using the 'rgbif' package [70] using the download link https://www.gbif.org/occurrence/download/0121994-220831081235567. OBIS data were downloaded on the 31st October 2022 using the 'robis' package [71]. The occurrence data were thoroughly cleaned and filtered to remove spurious records by (1) removing records from land, (2) removing fossil specimens, (3) removing records missing coordinates, (4) removing duplicate records, and (5) removing occurrences predating 2000 to match the temporal range of the environmental data to be used for elucidating species-environment relationships. Following this process, the GBIF and OBIS occurrences were combined and any duplicate records were removed. To account for the spatial clustering of occurrence records, species occurrences were rarefied by gridding them to a 0.5 x 0.5 degree grid. During the gridding process only one occurrence record per grid cell was retained. This is analogous to thinning occurrence records with a distance equal to that of the pixel size of the grid. As the grid was a relatively coarse size, the gridding process was adequate in thinning presence records whilst retaining as much data as possible.

2.2.2 Environmental data. Environmental data were downloaded from the publicly available dataset, Bio-ORACLE v2.1 (https://www.bio-oracle.org/; [72]), using the R package 'sdmpredictors' [73]. The following seven environmental variables were chosen as predictor variables in the SDMs: mean sea-surface salinity, mean sea-surface temperature, mean sea-bottom temperature, mean sea-surface chlorophyll concentration, mean sea-surface currents velocity, distance to shore and bathymetry. The first five variables are dynamic and liable to change over time, whilst the latter two remain static over our study period. All seven variables were downloaded for a current period (2000–2014). For the future time periods (2040–2050 and 2090–2100), the first five environmental variables were downloaded for all emissions scenarios (see below), available on Bio-ORACLE as averaged data from three atmosphere–ocean general circulation models (CCSM4, HadGEM2-ES and MIROC5) provided by the Coupled Model Intercomparison Project Phase 5 (CMIP5) [72]. The emissions scenarios, known as Representative Concentration Pathways (RCPs), comprised RCP 2.6 (a stringent mitigation scenario aiming to limit warming to below 2°C above pre-industrial levels), RCP 4.5 (a stabilization scenario where emissions peak around 2040 and then decline), RCP 6.0 (a stabilization scenario where emissions peak around 2080 and then decline), and RCP 8.5 (a high emissions scenario with increasing emissions over the century) [74]. For brevity, future time periods 2040–2050 and 2090–2100 are referred to as 2050 and 2100, respectively. The environmental variables were chosen based on the methods described in Titley et al. [75] and represent those used in most SDMs of marine species [76]. Stratification was not considered in our models as Bio-ORACLE does not provide environmental variables at multiple layers of the ocean. We do, however, include sea-bottom temperature as a variable in our models which was not collinear with sea-surface temperature and was found to be an important predictor in the SDMs. The environmental data were resampled to a coarser resolution to match the gridded occurrence data (0.5 x 0.5 degree grid).

2.2.3 Presence-only species distribution models. We modeled species-climate relationships following an approach adapted by Titley et al. [75] and others, which broadly follows the methods of Bagchi et al. [77], and further adapted for presence-only SDMs. We used occurrence data from species presence databases; locations where species are absent are unknown [78]. Presence-only SDMs are an appropriate and commonly used approach, requiring the generation of background data to be used as pseudo-absences [79]. Here, we used an ensemble of four model types to predict species distributions: Maximum Entropy (MaxEnt), Generalized Additive Models, Boosted Regression Trees, and Random Forests. These model types were chosen due to their effectiveness in handling presence-only data [79], and based on their prior performance in previous modeling studies [80,81]. To fit SDMs to presence-only data, 10,000 background pseudo-absences were randomly selected from the same realm(s) in which the target species currently occur. This minimized the selection of pseudo-absence points that are climatically suitable but unreachable. A brief summary of the four fitting methods is provided in the(S1 Text).

2.2.4 Model validation. A common issue that requires consideration in SDM techniques is the spatially dependent nature of the data. To reduce the effects of spatial autocorrelation, we followed a "blocking" method as per [77], whereby the gridded occurrence data were split into ten blocks (using 'blockTools' package in R [82]), based on marine realms and ecoregions using the Marine Ecoregions of the World [83] and Pelagic Provinces of the World [84]. We combined the latter two to get 16 final oceanic realms. For the ecoregions, we largely used the Marine Ecoregions of the World but as they do not cover the entire world's ocean, we used the Pelagic Provinces of the World to create an additional 37 ecoregions, so that there were no gaps of ocean that did not classify as a specific ecoregion. This resulted in a total 269 ecoregions covering the world's oceans. Each block comprises a subset of the 269 ecoregions, such that each block samples parameter space adequately. The blocking approach minimizes spatial autocorrelation of the data points used in the model fitting and testing.

Model performance was assessed using 10-fold cross-validation using the ten blocks. Each model was trained on nine of the ten blocks and then model performance was tested on the remaining tenth block. This was repeated ten times for each of the modeling approaches (resulting in 40 models per species, 10 blocks x four modeling approaches). Model performance was assessed using the Area Under the Curve (AUC) of the receiver-operating characteristic plot. AUC values provide a quantitative measure of a model's ability to correctly discriminate between presences and absences, with higher AUC scores indicating better model performance [85]. These models were then used to project future suitable niche-space for species in 2050 and 2100 (40 models per species for each emissions scenario), across the same realms that they currently occupy, as well as in adjacent realms. Projection results were weight-averaged across the 40 models (per emissions scenario), with individual model weightings based on the AUC scores of each model. In this sense, the best performing model in the ensemble lent the greatest weight to the final projected species distribution.

The current and future habitat suitabilities (probability of occurrence) were binarized based on species-specific thresholds that maximized sensitivity and specificity (Thresholds: *B. saida* = 0.07; *M. villosus* = 0.12; *R. hippoglossoides* = 0.23; and *O. orca* = 0.27) to summarize potential changes to species occupancy in the NOW Polynya. We also presented the results of the raw habitat suitabilities for each species when mapping changing habitat suitability under emissions scenarios, as thresholded suitabilities can overestimate occurrences.

2.3 Ecosystem model

We expanded a published Ecopath model for the NOW Polynya [45] by adding the following functional groups: Bowhead whale (*Balaena mysticetus*), Greenland halibut, and capelin (overview of all functional groups in Table 2). All of these species have been observed in the NOW Polynya [20]. Killer whale was added as a functional group as part of a novel ecosystem scenario in Ecosim to represent a novel establishment of this apex predator in the NOW Polynya (see below section 2.4 for more details on the justification of adding killer whales as a novel scenario). With these additions, the Ecopath model included 24 separately defined functional groups (see S1 Table) to characterize the NOW Polynya ecosystem. Parameter estimates were based on qualitative and quantitative studies from the NOW Polynya or other Arctic regions if local data were not available (S1 Table). Details on the Ecopath modeling framework are described in the (S1 Text).

2.3.1 Functional groups. For each functional group, biomass (*B*; tonnes per km^2) was estimated from abundance data found in survey reports and peer-reviewed research specific to the NOW Polynya (S1 Table). Production to biomass (*P/B*) was estimated by either computing values using total mortality rates (natural mortality rate (*M*) + fisheries mortality rate (*F*)) or from FishBase (www.fishbase.org). FishBase integrates mortality rates, parameters of the Bertalanffy growth function, and mean temperature to calculate *M* [86]. Estimates of *M* to calculate *P/B* were sourced from published literature for the NOW or other Arctic ecosystems. In cases where explicit information on *F* was unavailable in the literature, we computed *F* as total fish catch over the estimated biomass, based on reported subsistence catches from Canada and Greenland [87]. Consumption to biomass (*Q/B*) was primarily acquired for taxa in the NOW when available (S1 Table). In instances where information from the NOW was lacking, we used values from the literature or from other Ecopath models deemed most suitable for the NOW ecosystem or similar Arctic regions (S6 and S7 Tables). A diet matrix (S2 Table) was formulated using published diet studies for NOW taxa, when accessible. In the absence of diet studies specific to the NOW Polynya, we used diet composition estimates from the literature deemed most appropriate for the NOW region or from similar Arctic species (S1 Table). We categorized each data source using the Ecopath pedigree index that describes the origin of input data and assigns confidence intervals based on source to quantify uncertainty associated ([88,89]; S6 and S7 Tables).

Please refer to [45] for a detailed description of the initial functional groups. The North Water Polynya base model can be accessed in the Ecopath repository Ecobase (https://ecobase.ecopath.org/). Parameterizations for the additional functional groups of the expanded Ecopath model are given below. Data used for the parameterization were based on qualitative and quantitative studies from the North Water Polynya or other Arctic regions if local data were not available, as well as other Arctic Ecopath models (S1 Table).

Marine mammals–bowhead whales and killer whales—Data for the relevant populations or sub-populations were obtained from empirical studies and other Arctic Ecopath models, assuming that all marine mammals inhabited the NOW Polynya throughout the defined model timeframe. To estimate *B*, the number of individuals was multiplied by the average weight per individual (in tonnes), and then divided by the total model area (km^2). *B* estimates for bowhead whale were based on aerial observations in 2009 [90], 2010 [91], and tagging studies from 2014 [92], because direct observations for the NOW were not available for the base model timeframe. *P/B* and *Q/B* for bowhead whale considered *M* from the Western Baffin Bay Ecopath model [11] and *F* based on North Atlantic Marine Mammal Commission (NAMMCO) catch statistics [87]. Due to a lack of data for killer whales in the NOW, low initial values for *B* were defined for Scenario 4 (See next section), and *P/B* and *Q/B* values from the Western Baffin Bay Ecopath model were used.

Fish–Greenland halibut and capelin—*B* estimates for Greenland halibut were based on September trawl surveys for 2004, 2010, and 2012 for the Area A0 of the Northwest Atlantic Fisheries Organization [93,94], because direct observations for the NOW were not available for the set model timeframe. *P/B* was calculated accounting for *M* only (no commercial fisheries for Greenland halibut in the NOW Polynya), which was derived from the FishBase life-history tool. *Q/B* was also derived from the FishBase life-history tool. Due to a lack of data for capelin in the NOW Polynya, Ecopath estimated *B*, based on *P/B*, and Q/B estimates from the FishBase life-history tool.

2.3.2 Ecological indicators, network analysis, and SURF index. To evaluate the ecological roles of the defined functional groups in the NOW Polynya, we analyzed benthic-pelagic coupling. To evaluate the role of individual functional groups in benthic-pelagic coupling in the NOW Polynya ecosystem, we assigned domains based on feeding behavior—pelagic, bentho-pelagic, demersal, and benthic—to each functional group and let Ecopath calculate the consumption rate (t km^2 t^{-1}). The domains were used to determine the strength of direct interactions (i.e., amount of consumption) among functional groups across domains. Further, we conducted a Lindeman spine analysis of trophic flows, following Lindeman [95] and a Mixed Trophic Impact (MTI) analysis to gauge the direct and indirect impacts of changes in the biomass of one group on the biomass of other groups within the ecosystem [96]. Ecopath estimated omnivory and connectance indices, which quantify the width of the trophic spectrum for each functional group and provide a measure of food-web complexity and interconnection, respectively [88,96].

We derived ecosystem indicators for the NOW Polynya from the summary statistics and network analyses provided by Ecopath, including (i) Finn's Cycling Index, which indicates the fraction of total system biomass flow recycled in the system before leaving; (ii) Finn's Mean Path Length, which represents the average length of each cycle flowing through the food chain), and (iii) mean trophic transfer efficiency, representing the proportion of mean energy passed between trophic levels in ecosystems (refer to [88] for detailed explanations of individual Ecopath statistics and network indices). To identify important prey species, we computed the SUpportive Role to Fishery ecosystems index (SURF; [97]) for consumers (excluding polar bears). This index accounts for the level of reliance on prey by predators and adjusts for the overall number of connections in the food web. Species with values closer to zero are deemed non-key forage species, while larger values indicate key forage species. If the SURF index exceeds 0.001, the species is categorized as a central prey species within the ecosystem.

2.4 Novel ecosystem scenarios

SDMs were not coupled to the ecosystem models, as SDM results only provide information on the distribution of species rather than their local abundance. Instead, SDM results were used to infer plausible changes in species present to inform six novel ecosystem scenarios for the NOW Polynya (Table 1). The rationale, hypotheses, and key literature for each scenario are briefly described below and presented in S3 Table; the modified biomass values for each scenario are in Table 1. The values of the scenario-specific biomass changes in Table 1 were, when available, defined based on maximum future projected changes for the respective functional groups as found in published literature (S3 Table). When projections were unavailable, biomass values were defined to reflect the underlying assumptions of the respective scenario (S3 Table). The SDM model projections were used to inform the direction of biomass changes in the respective scenarios (Tables 1 and S3).

Scenario 1.1 and 1.2: *Changes in biomass of primary producers*—Climate change is likely to impact future primary production in the NOW Polynya [20]. Whether primary production will decrease or increase in the polynya is not yet determined. For the Arctic Ocean more generally, primary producer biomass is expected to increase due to a longer growing season caused by increases in both the extent and duration of the open water season and increasing storminess, enhancing average annual light availability for photosynthesis and mixing [98–100]. Congruently, projections by Earth System Models of primary production and phytoplankton biomass show increases for the NOW Polynya [101,102]. In contrast, if the Nares Strait ice-bridge disappears completely; primary producer biomass in the NOW Polynya is expected to decrease due to nutrient limitation caused by reduced mixing and/or upwelling, increased stratification, and reduced light penetration due to increased drifting of ice through the polynya [18,103]. Consequently, to consider these two possible future scenarios in our

Table 1. Overview of novel ecosystem Ecopath with Ecosim (EwE) scenarios for the North Water Polynya and associated biomass (*B* in t km^2) changes.

Scenario		Baseline *B*	Total biomass change	EwE *B*
1.1	Increase in pelagic primary producers	Lg pelagic producers (> = 5 μm): 25.00 Sm pelagic producers (0.7–5 μm): 13.00	+20%	Lg pelagic producers (> = 5 μm): 27.50 Sm pelagic producers (0.7–5 μm): 14.30
1.2	Decrease in pelagic primary producers		-30%	Lg pelagic producers (> = 5 μm): 21.5 Sm pelagic producers (0.7–5 μm): 11.05
2.1	Change in copepod community size-structure	Lg copepods: 23.42 Med copepods: 9.49 (ratio ~ 70 (lg copepods): 30(med copepods)	Change in ratio to 10 (lg copepods): 90 (med copepods).	Lg copepods: 3.35 Med copepods: 29.65
2.2	Decrease in copepod biomass	Lg copepods: 23.42 Med copepods: 9.49	-30%	Lg copepods: 21.08 Med copepods: 8.541
3	Shift in forage fish species abundances	Capelin: 0.026 Arctic cod (Age 1+): 5.50	+40% capelin -15% Arctic cod (Age 1+)	Capelin: 0.0364 Arctic cod (Age 1+): 4.675
4	Establishment of killer whales	———————	+ killer whale +40% capelin -15% Arctic cod (Age 1+)	Killer whale: 0.00014 Capelin: 0.0364 Arctic cod (Age 1+): 4.675

Lg = Large. Med = Medium. Sm = Small. Lg copepods include *Calanus hyperboreus*, *Calanus glacialis, and Metridia longa*; Med copedods include *Pseudocalanus spp*, *and Calanus finmarchicus*). The percent values for the respective biomass changes are based on published literature, presented in S4 Table.

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modeling, we devised two scenarios representing an increase (Scenario 1.1) and a decrease in the biomass of primary producers by the end of the 21st century (Scenario 1.2) (Table 1).

Scenario 2.1. and 2.2: *Changes in biomass and size structure of copepods*—Due to climate-change driven environmental alterations, such as increasing sea temperature, shifts in zooplankton distribution are expected to impact zooplankton biomass and species composition [20]. Shifts in the size composition within the NOW Polynya *Calanus* community are expected in the future due to increasing biomass of smaller, less fatty calanoid copepod species, such as *Calanus finmarchicus* [104,105]. This shift is suggested to decrease energy transfer in the NOW Polynya ecosystem, since larger copepods are richer in lipids, and so provide a higher energy intake per calorie spent searching and handling prey by consumers [106]. Overall, copepod biomass is expected to decrease in the NOW region, caused by an earlier onset of the phytoplankton spring bloom [107]. The earlier spring phytoplankton bloom escapes the copepod grazing due to a mismatch between onset of the spring bloom and the end of the copepod diapause [104], leading to reduced food availability for the copepod community in the spring [107]. Based on these two possible future changes in the copepod community, we devised two scenarios representing a change in the biomass ratio of large and medium copepods (Scenario 2.1) and a second representing a decrease in overall copepod biomass by the end of the 21st century (Scenario 2.2) (Table 1).

Scenario 3: *Shift in forage fish species abundances*—With the projected northward shift of capelin into the NOW Polynya, the Arctic cod population may be negatively impacted through direct competition for zooplankton prey [20,108]. Corroborated by our SDM projections for capelin and Arctic cod, and the existing literature (e.g., [109–112]), in Scenario 3 we assumed that Arctic cod will decrease in their biomass, and capelin biomass increase in the ecosystem.

Scenario 4: *Establishment of killer whales*—As the sea-ice free season lengthens with a warmer climate, better access results in abundance increases of marine top predators [20]. Killer whales were added as a functional group because SDMs projected suitable habitat for them currently (2000–2014) in the NOW. Currently, killer whales are only considered as 'occasional visitors' to the western part of the NOW [67,68,113], which corroborates our SDM projections. The NOW is at a considerably higher latitude than where sub-populations of killer whales currently inhabit in the Arctic—the largest population being in the Northwest Pacific. Populations in Nunavut and the NOW could largely be restricted by sea ice extent, and killer whales were never found in the past in Western Hudson Bay and in the High Arctic Islands. Their sightings have been steadily increasing in the high Arctic region since the 1950s [60,101]. Only recently have sightings suggested that killer whales have expanded their ranges into areas like Hudson Bay and northwest of Baffin Island [67,114], and has been linked to declining sea ice [114]. Additionally, more prey such as capelin could become available in the NOW with increasing climate change so the killer whale population may become more established and an ecosystem component. The increased frequency and possible establishment of a novel apex predator indicates a greater predation pressure on other large Arctic mammals, such as narwhals, belugas, and seals.

2.4.1. Ecopath with Ecosim simulations. To simulate the ecosystem response to *B* changes in the above described functional groups (Table 1), we used *B* values as the representation of future ecosystem scenarios. In other words, *B* values for the manipulated functional groups in each scenario were used as biomass forcing to simulated ecosystem wide responses due to these changes. We ran each simulation for 100 years for each novel ecosystem scenario and reported the mean *B* values for the last decade, for each functional group, after each simulation reached equilibrium. To avoid sudden ecosystem responses or collapse, the forcing commenced after 50 years, after a tune-up phase of steady biomass increase based on the estimated baseline model *B* from 2005–2007. Details on the Ecosim framework are described in the (S1 Text). Finally, for each scenario, we identified which functional groups differed by <20%, 20–40% and >40% in biomass compared to the baseline biomass estimates and calculated the proportion of functional groups impacted at each level (leaving out the impacting group).

2.4.2. Sensitivity analysis. We performed a sensitivity analysis for each novel ecosystem scenario. We ran two simulations to represent a range of parameter values (S4 Table). For *B*, where possible, the parameter range was based on the lowest, mid, and highest projected values found in the literature (S4 Table). When projections were unavailable, initial *B* estimates were increased and decreased by increments of 5% to determine the effect on the ecosystem. For each analysis, we identified which functional groups differed by <20%, 20–40% and >40% and calculated the proportion of functional groups impacted at each level (leaving out the impacting group).

3 Results

3.1. Projections from species distribution models

SDMs performed well, with the average Area Under the Curve (AUC) of ensemble models being 0.97 (± 0.03 SD), with values ranging from 0.88 and 1.0 (see S5 Table for all AUC results). Overall, the AUCs for Random Forests were slightly higher than the other models (average Random Forests AUC = 0.98 ± 0.02, c.f. averages of 0.97 ± 0.03, 0.97 ± 0.03 and 0.96 ± 0.03, for Boosted Regression Trees, MaxEnt and Generalized Additive Models respectively). Full model outputs from each SDM type are available on Figshare [115].

The NOW Polynya is projected to become climatically suitable for most of the modeled species. Suitable climate for capelin increased by 2050 and 2100 under both emissions scenarios, especially in northern and western areas of the polynya (Figs 2A, 2C, S5B and S5C). Median habitat suitability for capelin increased in the polynya by 13% by 2050 under RCP 4.5. In 2100, capelin range is projected to extend to occupy 80% of the polynya. Suitable habitat for Arctic cod in 2050 declined in the southwestern region of the polynya but increased slightly in central

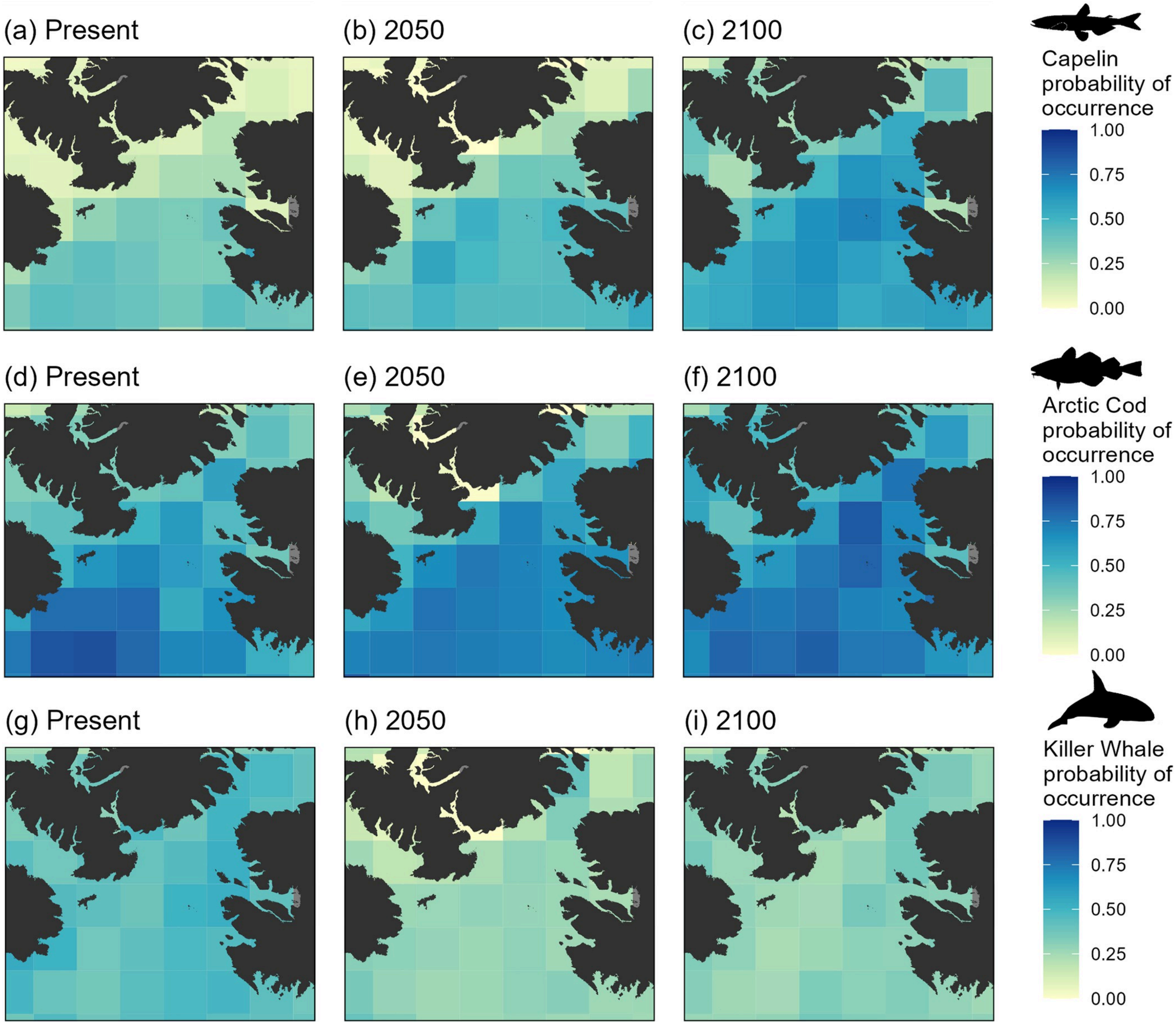

Fig 2. Ensemble projections of capelin (*Mallotus villosus*) (a-c), Arctic cod (*Boreogadus saida*) (d-f) and killer whales (*Orcinus orca*) (g-i) distribution in the North Water Polynya from present-day (2000–2014) to 2050 and 2100 under RCP4.5 emissions scenario. Projection results for the individual model types for each species are provided in the Supporting Information (S1–S4 Figs). Killer whale icon created by authors, other icons are public domain silhouette images by Milton Tan (*Gadus morhua*) and xgirouxb (*Thaleichthys pacificus*), via PhyloPic (www.phylopic.org).

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areas (Fig 2E), resulting in an average habitat suitability decrease of 5%. Suitable climate in 2100 generally shifts northward under a medium emissions scenario (Fig 2).

Under the high emissions scenario (RCP 8.5), by 2100, Arctic cod is projected to experience large declines in habitat suitability across the polynya (S5F Fig). Arctic cod is projected to occur in all grid cells at present (2000–2014) but to decline in range by 10% by 2050 and 2100 under RCP 8.5. Suitable climate for Greenland halibut was identified in the south-western region of the polynya (S6A Fig) and was projected to shift towards the northeast of the polynya and northwest below Ellesmere Island by 2100 (under RCP 4.5 and RCP 8.5). The SDM results suggest that at present (2000–2014), there may be suitable climate for killer whales in the

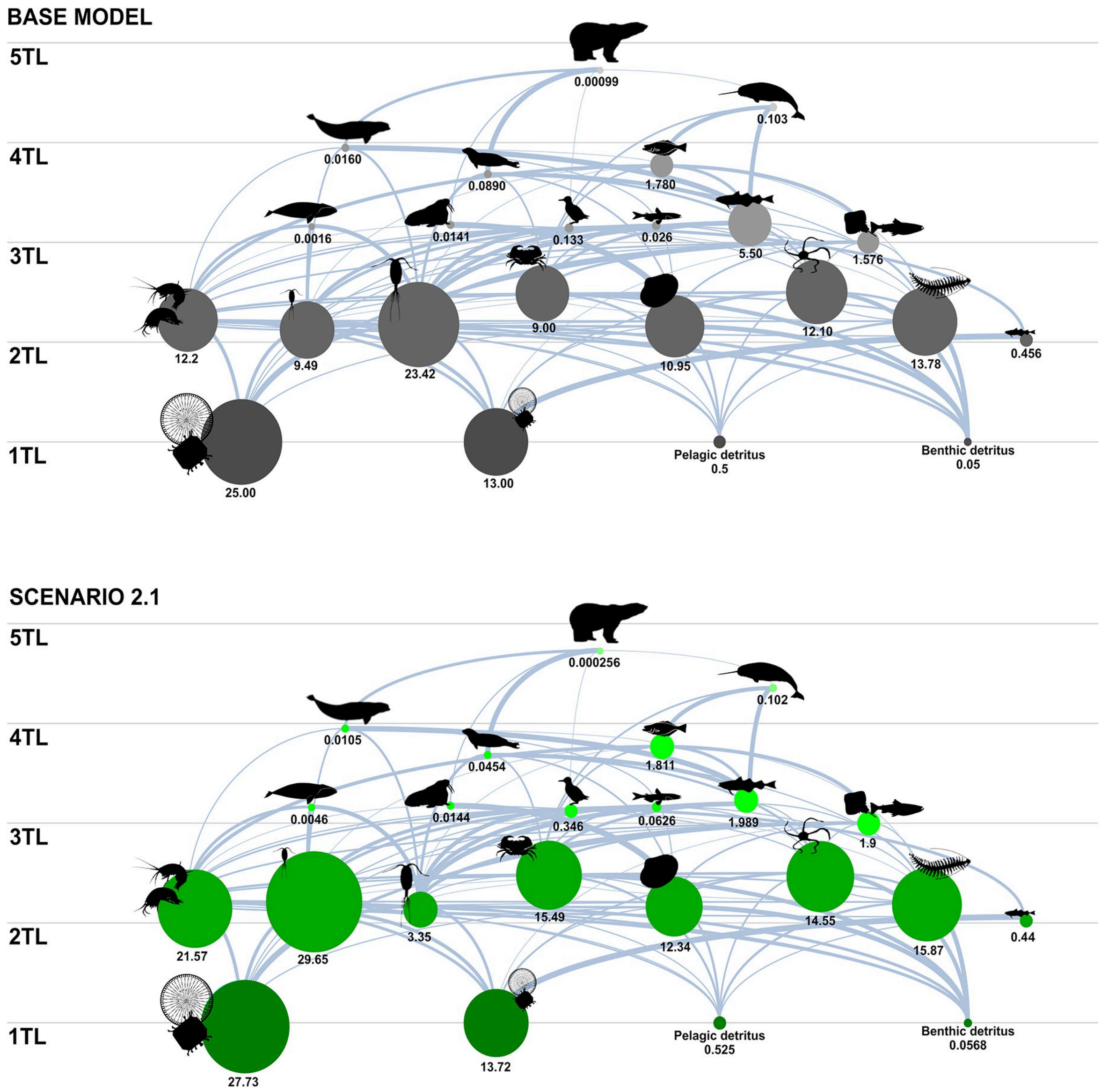

Fig 3. Ecopath base model flow diagram (upper panel), Ecosim flow diagram Scenario 2.1 (lower panel). The size of circles is proportional to the amount of biomass. Numbers below circles represent the biomass of the functional group in t km^2. TL = trophic level. Direction of energy flow is represented by position of line with relation to circle: Flows positioned on the top of a trophic group indicate biomass outgoing, while flows positioned on the side indicate entering biomass. The weight of the line indicates the amount of energy flowing between nodes. Narwhal (*Monodon monoceros*) icon created by authors, all other icons are public domain silhouette images by Tracy Heath (*Ursus maritimus*), Margot Michaud (*Odobenus rosmarus*) and others, via PhyloPic (www.phylopic.org).

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polynya. Habitat suitability for killer whales generally declined by 2050 under RCP 4.5 across the polynya (Fig 2H) by as much as 70% by 2100 (Fig 2I).

3.2. Ecopath base model

3.2.1. Model parameters. The pedigree index for biomass parameters was dominated by values between 4 and 6, meaning that the data relied heavily on local samples and indirect approximations (S6 and S7 Tables). For production and consumption to biomass ratios (*P/Q* and *Q/B*, respectively), the pedigree index was dominated by values between 3 and 4, indicating the input relied heavily on Ecopath models from other Arctic regions and empirical relationships (S6 and S7 Tables). Values for diet parameters were dominated by the index of 2, indicating the input relied heavily on Ecopath models from other Arctic regions (S6 and S7 Tables). The average pedigree score for the entire base model was 3.61.

3.2.2. Model balancing. This study used a balanced model [45]. To achieve mass-balance after adding new functional groups, parameter adjustments were made to the biomasses and *P/Q* of bowhead whale, Greenland halibut, and Arctic cod (Age 1+) (S8 Table). We considered the model balanced when Ecotrophic Efficiency (EE) $<$ 1 for all functional groups (Table 2).

3.2.3. Trophic levels and flows. In the base model, trophic levels (TLs) ranged from 1 to 4.73 (Table 2; Fig 3), with polar bear occupying the highest trophic position in the food web, followed by narwhal (TL 4.35), and beluga (TL 4.02). The groups of walrus, ringed seal, little auk, Greenland halibut, capelin, Arctic cod (Age 1+), and 'other fish' had estimated TLs between 3 (other fish) and 3.77 (Greenland halibut). Arthropods, bivalves, echinoderms, worms, the zooplankton groups, and Arctic cod (Age 0) had TLs between 2.06 (Arctic cod (Age 0)) and 2.50 (echinoderms). Primary producers and detritus were at the bottom of the food web with TL 1. In general, these estimated TLs agreed with the range of values reported in the literature for the NOW Polynya and other Arctic ecosystems (S9 Table). Trophic flows

Table 2. Parameters from the balanced Ecopath model for the North Water Polynya in 2005–2007.

Functional group		TL	Domain	*B*	*P/B*	*Q/B*	*EE*	*P/Q*
1	Killer whale	4.77	PEL	0.00014	0.03	9.11	*0.00*	*0.00*
2	Polar bear	4.73	PEL	0.001	0.40	6.00	*0.02*	*0.07*
3	Bowhead whale	3.16	PEL	**0.002**	0.07	9.50	*0.00*	*0.01*
4	Beluga	3.95	PEL	0.02	0.29	17.00	*0.27*	*0.02*
5	Narwhal	4.35	PEL	0.11	*0.001*	19.80	0.76	*0.00*
6	Walrus	3.16	PEL	0.02	0.07	30.4	*0.12*	*0.01*
7	Ringed seal	3.68	PEL	0.09	0.17	16.5	*0.27*	*0.01*
8	Little auk	3.14	PEL	0.13	0.15	64.61	*0.01*	*0.00*
9	Greenland halibut	3.77	DEM	**1.78**	0.51	1.30	*0.88*	*0.38*
10	Capelin	3.17	PEL	*0.026*	0.66	4.40	0.78	*0.15*
11	Arctic cod (Age 1+)	3.18	BP	**5.50**	**0.50**	2.63	*0.92*	*0.19*
12	Other fish	3.00	BP	*1.56*	0.51	2.40	0.95	*0.22*
13	Arthropods	2.47	DEM	9.00	0.75	6.00	*0.97*	*0.13*
14	Bivalves	2.16	BENT	10.95	0.62	6.33	*0.93*	*0.01*
15	Echinoderms	2.51	BENT	12.10	0.55	2.20	*0.97*	*0.25*
16	Worms	2.21	BENT	13.78	0.95	4.00	*0.85*	*0.24*
17	Lg copepods	2.16	PEL	23.42	5.50	20.00	*0.13*	*0.26*
18	Med copepods	2.12	PEL	9.49	18.00	45.00	*0.97*	*0.40*
19	Arctic cod (Age 0)	2.06	PEL	0.46	31.60	105.00	*0.11*	*0.31*
20	Other meso-zooplankton	2.21	PEL	12.20	22	80.00	*0.59*	*0.26*
21	Lg pel. producers	1.00	PEL	25.00	34.50	-	*0.71*	-
22	Sm pel. producers	1.00	PEL	13.00	64.87	-	*0.60*	-
23	Pelagic detritus	1.00	PEL	0.50	-	-	*0.27*	-
24	Benthic detritus	1.00	BENT	0.05	-	-	*0.87*	-

Values estimated by Ecopath are in italics; values adjusted during model balancing are in bold. TL = Trophic level; *B* = Biomass (t km^2); *P/B* = Production/biomass ratio (yr^{-1}); *Q/B* = Consumption/biomass ratio (yr^{-1}); *EE* = Ecotrophic efficiency (the fraction of total production of one functional group that is consumed by other groups; unitless); *P/Q* = Production/consumption (yr^{-1}). Lg = Large; Sm = Small; Med = Medium. PEL = Pelagic; BP = Bentho-pelagic; DEM = Demersal; BENT = Benthic. Gray shading: Functional group added to the base model for Scenario 4. Original parameter values were obtained from [42].

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estimated by the model indicated that pelagic and benthic communities were primarily connected by Arctic cod (Age 1+), bowhead whale, walrus, and ringed seal (Fig 3). The Lindeman spine analysis indicated that most energy flows occurred in the first two TLs, representing 53.3% of the total system throughput (TST; S8 Fig; TL1 = 23.56%, TL2 = 29.74%). TL2 largely contained large copepods (23.42 t km^2), other meso-zooplankton (12.2 t km^2), bivalves (10.95 t km^2), echinoderms (12.10 t km^2), and worms (13.78 t km^2) (Fig 3; Table 2), representing 44.64% of the total biomass excluding detritus. Average transfer efficiency (TE) for the NOW Polynya ecosystem was 9.17% (S10 Table), with the highest TE for TL2 (11.18%; S10 Table).

3.2.4. Ecological indicators, network analysis, and SURF index. The NOW Polynya ecosystem is characterized by many benthic-pelagic couplers, defined by the feeding domains of the specific functional group (i.e., pelagic, bentho-pelagic, demersal, and benthic). Consumption rates across feeding domains ranged from 9.11×10^{-7} t km^2 t^{-1} for killer whales to 59.95 t km^2 t^{-1} for Arctic cod (Age 0) in terms of total rates (S7 Fig). Notably, the pelagic and benthic-pelagic functional groups, such as walrus, narwhal, ringed seal, capelin, and Arctic cod (Age 1+) couple the pelagic and benthic domains by feeding on the entire range of domains. Arthropods, echinoderms, and worms, all of which are benthic invertebrates, couple the pelagic and benthic domain by scavenging on deposits of functional groups originating from the pelagic domain.

The MTI analysis (S9 Fig) revealed that, generally, most functional groups had a negative impact on themselves, reflecting intraspecific competition for resources, and a negative impact on their respective prey due to predation pressure. Bowhead whale, walrus, capelin, other fish, worms, and Arctic cod (Age 0) had very low to no impact on other groups, likely due to their relatively low *B* or *Q/B* ratios. Bivalves showed the largest positive impact on walrus, reflecting the diet of walrus in the NOW Polynya. Small pelagic producers had the largest positive impact on Arctic cod (Age 0), through their large role as prey for that age group. Arctic cod (Age 1+) largely consumes zooplankton and benthic invertebrates (as shown in the diet matrix in S2 Table) and has a negative impact on these functional groups. The largest negative impact was observed for little auk affecting Arctic cod (Age 0), as well as for beluga on capelin, through predation and, in the case for little auk, interspecific competition for resources, such as zooplankton. Interestingly, based on the MTI analysis, Arctic cod (Age 1+) had a relatively strong negative impact on capelin; however, capelin showed no impact on Arctic cod (Age 1+).

Key ecosystem properties (total system throughput, sum of consumption, exports, production, and total biomass) of the current iteration of the NOW model were largely comparable to values for the base model for the NOW Polynya (S11 Table). The system omnivory index for the NOW Polynya was low, indicating a relatively high diet specialization among the individual functional groups (S11 Table). Finn's Cycling Index was similar between the two models, signifying a relatively short cycling of biomass flow through the ecosystem [116]. Finn's mean path length was similar between the two models. Mean transfer efficiency increased from 8.18% in the first iteration of this model to 9.17% in this model (S11 Table), highlighting that the ecosystem with additional functional groups is more productive but with less energy being transferred to higher trophic levels. The SURF index identified large copepods, Arctic cod (Age 1+), other meso-zooplankton, medium copepods, bivalves, arthropods, ringed seal, worms, echinoderms, and Greenland halibut as key forage species (S10 Fig). Large copepods and Arctic cod (Age 1+) showed values at least an order of magnitude higher SURF index than the other functional groups (S10 Fig).

3.3 Novel ecosystem scenarios and sensitivity analysis

Scenarios 1.1 and 1.2: *Changes in biomass of primary producers*—with increasing biomass of pelagic primary producers (Scenario 1.1), higher trophic level functional groups showed a

Table 3. Direction of biomass change by functional groups for each North Water Polynya Ecosim scenario.

Functional group		TL	Direction of biomass change by scenario					
			1.1	***1.2***	***2.1***	***2.2***	***3***	***4***
1	Killer whale	4.77	/	/	/	/	/	↑↑↑
2	Polar bear	4.73	↑↑	↓↓↓	↓↓↓	↓↓	↓↓	↓↓
3	Bowhead whale	3.16	↑	↓↓	↑↑↑	↓↓	↑	↑↑↑
4	Beluga	3.95	↑↑	↓↓	↓↓	↓↓	↓↓	↓↓
5	Narwhal	4.35	↑	↓	↓	↓	↓	↓↓
6	Walrus	3.18	↑	↓↓	↑	↑	↓	↓
7	Ringed seal	3.68	↑↑	↓↓	↓↓↓	↓	↓	↓↓
8	Little auk	3.14	↑	↓↓	↑↑↑	↓↓	↑	↑
9	Greenland halibut	3.77	↑↑	↓↓	↑	↓	↓	↓
10	Capelin	3.17	↑	↓	↑↑↑	↓	↑↑	↑↑
11	Arctic cod (Age 1+)	3.20	↑	↓↓	↓↓↓	↓	↓	↓
12	Other fish	3.00	↓	↓	↑↑	↑	↑↑	↑
13	Arthropods	2.48	↑	↓	↑↑↑	↑	↑	↑
14	Bivalves	2.16	↑	↓	↑	↑	↓	↓
15	Echinoderms	2.50	↑	↓	↑↑	↑	↓	↓
16	Worms	2.21	↑	↓	↑	↑	↓	↓
17	Lg copepods	2.17	↑	↓	↓↓↓	↓	↑	↑
18	Med copepods	2.12	↑	↓	↑↑↑	↓	↓	↓
19	Arctic cod (Age 0)	2.06	↑	↓	↓	↑	↑	↑
20	Other meso-zooplankton	2.22	↑	↓	↑↑↑	↑	↓	↓
21	Lg pel. producers	1.00	↑	↓	↑	↑	↓	↓
22	Sm pel. producers	1.00	↑	↓	↑	↑	↑	↑
23	Pelagic detritus	1.00	↑	↓	↓	↑	↓	↓
24	Benthic detritus	1.00	↑	↓	↓	↑	↑	↑

Blue shading indicates biomass increases; red shading biomass decreases. Grey shading are functional groups that were modified as input for a given scenario. One arrow: $< 20\%$ change; two arrows: 20–40% change; three arrows: $> 40\%$ change; / = functional group is not part of the scenario. TL = Trophic level. Lg = Large; Sm = Small; Med = Medium.

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moderate increase in biomass, with the exception of "other fish", which showed a biomass decrease (Table 3; S11 Fig). Biomass across all functional groups responded to a decrease in pelagic primary producers (Scenario 1.2), with pronounced biomass decreases in higher trophic levels, especially for polar bear, Greenland halibut, beluga, walrus and ringed seal (Table 3; S12 Fig). Notably, for TLs > 4, biomass was halved compared to the base model (S12 Fig). For both scenarios, the sensitivity analysis showed less pronounced biomass responses in the ecosystem with lower changes in the biomass of pelagic primary producers (S12 Table).

Scenario 2.1. and 2.2: *Changes in biomass and size structure of copepods*—Changes in the copepod size structure (Scenario 2.1) had the largest impact on the entire ecosystem compared to the other novel ecosystem scenarios. For this reason, we chose to highlight this scenario in Fig 3 and have included diagrams of the other scenarios in the (S12–S15 Figs). Under this scenario, the relative biomass of the highest TLs (> 4) decreased substantially, to almost a third of the biomass of the baseline model (Fig 4A). Biomass of key prey species, such as ringed seal, and Arctic cod (Age 1+) declined while capelin biomass increased by > 40% (Table 3; Fig 3). Biomass of ringed seal–one of the main predators of Arctic cod (Age 1+)–declined drastically

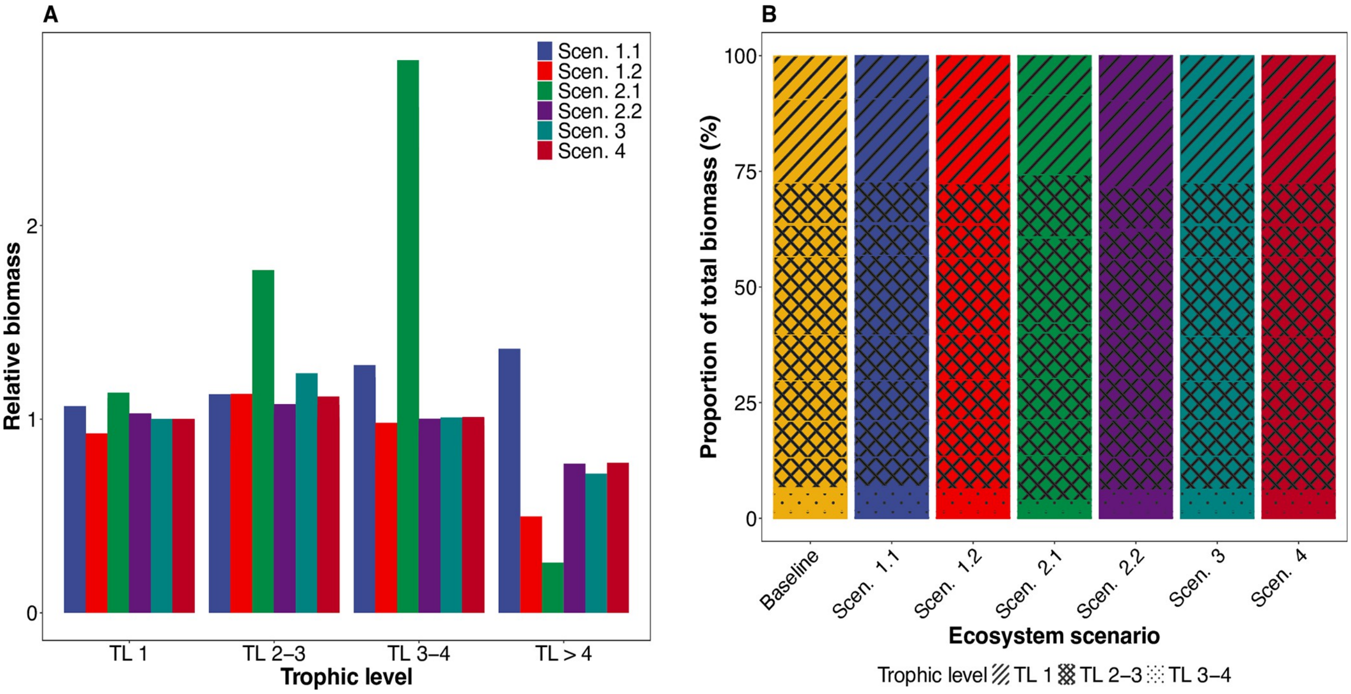

Fig 4. Biomass of trophic groups in the base ecosystem model and Ecosim scenarios by trophic level in the North Water Polynya ecosystem. (A) Biomass changes relative to the base ecosystem scenario. (B) Biomass proportion relative to the total biomass in the ecosystem. The different colors match the colors in (A); the shading represents the different trophic groups. Proportion of TL > 4 is < 0.005 in the base ecosystem and across Ecosim scenarios; hence not visible in panel (B). See biomass proportion relative to the total biomass for TL > 4 in S16 Fig.

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(>40%). Bowhead whale and little auk biomasses increased by > 40% (Table 3; Fig 3). In comparison, an overall decline in copepod biomass (Scenario 2.2) did not have as large an effect on the NOW Polynya ecosystem (Table 3; Figs 4 and S13). A copepod biomass decline of 20–30% produced the largest impacts on polar bear, bowhead whale, beluga, and little auk (Table 3; S13 Fig; S12 Table).

Scenario 3: *Shift in forage fish species abundances*—An increase in capelin with a simultaneous decrease in Arctic cod (Age 1+) biomass had the largest effect on marine mammals in the ecosystem (Table 3; Figs 4 and S14). Here, the largest declines were for polar bear, beluga, and ringed seal, in the scenario itself and the sensitivity analysis (Tables 3 and S12).

Establishment of killer whales—In response to increasing killer whale biomass, polar bear biomass decreased, as the biomass of their main prey, such as beluga, narwhal, and ringed seal decreased (Table 3; Figs 4A and S15). This pattern was also observed in the sensitivity analysis (S12 Table).

4 Discussion

Climate change is rapidly altering species distributions, which could have profound implications for the structure and function of ecosystems. Whilst the potential for future changes in species distributions has been extensively explored, largely using correlative models [25,26], we currently lack a framework to assess the impact of range shifting species on recipient communities and the subsequent disruptions to the ecosystem. Here, by combining two modeling frameworks, SDMs and ecosystem modeling, we explored the emergence of novel ecosystems in the NOW Polynya considering both climatic and ecosystem impacts.

4.1 Trophic flows

The NOW Polynya supports a high benthic biomass due to strong benthic-pelagic coupling [117]. One of the main underlying processes for this pattern is the high primary productivity despite the lower average transfer efficiency of 9.17% in the NOW polynya compared to other ecosystems in the region, such as Western Baffin and Western Greenland [45,53]. The spring bloom allows sufficient new production to reach the seabed and support the benthic community [117]. This pattern is also supported by our analysis, where the benthic invertebrate groups have relatively high consumption rates on prey from the pelagic domain.

Climate change is expected to increasingly affect benthic-pelagic coupling, for example, via (i) phenological shifts leading to trophic mismatches due to reduced sea ice as a result of increasing water temperatures, (ii) poleward shifts of pelagic and demersal species, (iii) and changing stratification patterns due to increasing storminess, vertical mixing, and changes in freshwater influx [8,99,100,118,119]. These mechanisms can manifest in changes in trophic interactions within an ecosystem. Scenario 2.2 explored the potential of such a trophic mismatch, whereby the phytoplankton blooms avoid substantial copepod grazing, reducing copepod biomass. The reduced grazing pressure by the copepod community benefits the benthic invertebrate community, as the phytoplankton carbon supply to the benthic zone from the surface increases.

The opposite can occur if the phytoplankton biomass decreases, as explored in Scenario 1.2, due to increasing stratification caused by increasing water temperatures and freshening [18,103], reducing biomass across functional groups in the ecosystem. These responses have already been observed in other Arctic regions such as the Chukchi Sea [120,121]. Moore et al. [121] showed that a decline in benthic prey, due to a reduction in phytoplankton carbon supply from surface waters, caused apex predators dependent on benthic prey (such as gray whales, *Eschrichtius robustus*) to shift their foraging ranges northward [121]. Years with reduced sea ice in the Chukchi Sea caused Pacific walrus (*Odobenus rosmarus*) to arrive earlier, stay longer and concentrate their foraging efforts in nearshore areas rather than offshore waters [120]. While our framework did not resolve movements due to changes in food supply specifically, we illustrated biomass change within a specific system, which could also reflect distribution shifts away from the study region.

4.2 Effects of changing copepod size-structure

The larger ecosystem impact of changing size-structure (Scenario 2.1) compared to changing overall biomass of copepods suggests a strong reliance of higher trophic levels on larger, lipid-rich copepods. Indeed, large, diapausing copepods are a crucial food source for fish and some Arctic whales [122], especially for bowhead whales [123]. They are larger targets for visual foragers and richer in lipids, and so provide a higher energy intake per calorie spent searching and handling prey by consumers [106]. Large copepods in the Arctic depend on sea-ice or deep sea habitats to survive, which reflects their dependence on local food availability, temperature refugia, and refugia from visual predators [124]. With climate change driving sea-ice melt and retreat, larger zooplankton species are already declining in some regions of the Arctic [104]. Our results support previous evidence that large copepods are an important trophic link in Arctic marine ecosystems [125,126], and implies climate change could strongly disrupt Arctic ecosystems by reducing trophic transfer efficiency, if smaller, less fat copepods replace their larger congenerics [104]. For example, in the Labrador Sea, capelin body size and condition have declined over 40 years [127] in response to a decline in large zooplankton [128], as capelin grow faster when feeding on larger *Calanus* species [129]. Similar effects have also been predicted for little auk [130]. Moreover, because of the variation in life histories and cycles (e.g., diapause timing, generation time, and breeding type) of large compared to smaller copepods, climate-driven shifts in the size structure can also affect the timing of energy transfer to higher trophic levels [104]. In Disko Bay, Greenland, longer open water periods resulted in *Calanus glacialis* changing from a biennial to an annual life cycle as a result of a change in available lipids. Sea-ice cover is expected to decline further with climate change in the NOW Polynya [18]. As a result, reduced reproductive success and condition of predators is likely due to changes in their copepod prey, with potential ecological consequences.

4.3 Effects of changing forage fish biomass

The projected increases in habitat suitability for capelin and the subsequent declines for Arctic cod replicate empirical data, indicating a shifting prey base in the Arctic [131,132]. However, the effect of changes in forage fish biomass (as a prey base) on higher trophic levels was not as strong as expected. The sensitivity analysis emphasized the role of Arctic cod (Age 1+) as a key prey species for predators such as ringed seals, beluga and narwhal. The decrease in beluga biomass could reflect reduced energy transfer and nutrition as a result of fewer Arctic cod (Age 1 +) in their diet [112]. This suggests the increasing abundance of a boreal species such as capelin may not substitute losses of Arctic cod in high-Arctic ecosystems. Indeed, the maximum lipid content of capelin is almost three times lower than Arctic cod [133]. Seabirds can shift their diet depending on local abundance of fish, but when, for example, Brunnich's guillemot switched to capelin, the growth rate of nestlings declined [134].

Generally, Arctic cod and capelin are significant consumers of zooplankton in marine ecosystems [133,135] (S2 Table), indicating a potential increase of resource competition between these two species in the future. However, the diet of Arctic cod differs with their size [136], hence prey competition may differ as well [112]. As seen in the diet matrix (S2 Table), immature and adult Arctic cod show a broader prey spectrum compared to more juvenile stages [112,133,135]; amphipods and copepods represent the largest fraction in their diet across age and sizes [112,136]. Notably, krill is preyed upon by both Arctic cod and capelin; however, the contribution to the prey field is larger for capelin compared to Arctic cod [133], suggesting that competition between capelin and Arctic cod may be limited. This species-specific differentiation across the prey field for capelin and Arctic cod was not captured in our model.

4.4 Cumulative impacts of changes in prey base and increasing biomass of apex predator

Our SDMs did not project any substantial increases in habitat suitability for killer whales in the NOW Polynya by 2050 or 2100. Killer whale movements in the Arctic are likely more dependent on the open-water season and so may not be distributed in the Arctic year-round [69]. As the SDMs did not distinguish summer vs. winter distributions of species, they may not have captured the full extent of killer whale occurrences and movements with climate change. Also, it is important to note that high or low climate suitability does not necessarily mean high or low abundance, especially for populations that change rapidly. SDM simulations suggested that all regions of the NOW are currently suitable for killer whale populations, which supported Scenario 4 of our analysis to explore the impacts of the addition of an apex predator to the NOW Polynya ecosystem.

The frequency of killer whale sightings in the NOW has increased since the 1950s [67,113], and the increasing ice-free, open waters in the Arctic have provided killer whales with better, more prolonged access to the high Arctic [114]. As such, we would expect the direct consumption of Arctic marine mammals to rise [68,137]. Our simulations supported this, showing biomass decreases in the main prey species of killer whales: narwhals, beluga and ringed seals, and also in its main competitor, the polar bear. Killer whales will not only directly affect prey abundances but could also disrupt prey behavior and ultimately their distributions [137,138]. These results suggest the addition of a key apex predator such as killer whales to the NOW Polynya ecosystem could have cascading ecosystem effects.

Further, in Scenario 4, bowhead whales responded with a large biomass increase, possibly due to a release of resource competition, as ringed seals and beluga decreased, which outweighed any increased predation by killer whales on bowhead whales. Killer whale predation was considered to be low in the model, reflecting the uncertainty of their predation effects on bowhead population sizes, distributions or habitat selection [137]. Predation of bowhead whales might increase due to longer ice-free periods which provide killer whales better access [137]. Despite this, other studies found killer whales did not have specialized diet preferences for bowhead whales (instead feeding mainly on narwhals and beluga) [139], and their feeding habits on bowhead whales can vary seasonally and regionally depending on population [140]. The specific feeding preferences of killer whale populations in the NOW Polynya remain unknown, and any potential changes to killer whale predation on bowhead whales are not reflected in the model but could be integrated by manipulating consumption rates of killer whales in separate scenarios, which goes beyond the present study.

4.5 Using SDMs to inform ecosystem scenarios

In this study, we present a new method using both SDMs and food-web models to explore potential future changes to an Arctic ecosystem with climate change. Since ecosystem models act as a ‘snapshot’ in time and space, we were able to use the results of SDMs to inform novel ecosystem scenarios for the NOW Polynya. Most attempts to date have used food-web models to improve outputs of SDMs which do not account for species interactions [14,141]. Previous studies have not used the output of SDMs to alter ecosystems created by Ecopath (but see [14]). Our modeling approach allows us to determine the implications of introducing or increasing southern species to Arctic ecosystems by analyzing the changing feeding links, biomass and energy transfer between species in an ecosystem. Further studies can build on this novel approach and answer questions about the consequences of climate-driven changes to species distributions for food-web structure and function. Our approach may also allow the testing of impacts of local species extinctions on ecosystems. A next step could be to integrate other human stressors such as fisheries which may spread and develop in the high Arctic as previously unreachable seas become available for human extraction.

The framework we developed is not limited to the NOW Polynya and could be applied across other ecosystems in both marine and terrestrial realms. Our approach applied climate change scenarios to a time static model with a defined change in biomass values. Another approach could use time dynamic projections with different climate change scenarios to run scenarios. These are not yet available, however time-series for functional groups are currently increasing due to increasing sampling efforts and collaborations with Indigenous Knowledge holders [142]. In addition, regional climate forcings for the NOW region have not yet been developed. Downscaling of global climate forcings is possible, but there are large uncertainties, especially in sea-ice systems [143,144]. One avenue for future work to overcome the lack of data for ecosystem models would be directly modeling species abundances in addition to species distributions. Then, information on projected species abundances could be used to infer biomass values for future scenarios of the NOW Polynya ecosystem.

The approach we developed here is not without its limitations. Marine SDMs are particularly hindered by a lack of full coverage of survey data, and still much is unknown with respect to the distributions of marine species. However, continuing survey efforts and increasing empirical data are expected to improve species distribution data over time. In addition, indirect effects of temperature changes, such as changes in biotic interactions and population dynamics, cannot be captured using SDMs [145]. Our approach also does not account for the timing of species distribution shifts and the model results are only a snapshot in time. As such, SDM results should always be treated with caution. Despite this, we argue they can be viewed as a complementary tool to explore the potential impacts of climate-driven range shifts on an Arctic marine ecosystem. Modeled species ranges can be refined and validated as more empirical data becomes available.

4.6 Conclusion

We present a novel framework for exploring the impacts of climate-driven range shifts on the NOW Polynya ecosystem, which could be applied across other ecosystems in both marine and terrestrial realms. We demonstrated the applicability of integrating SDM and ecosystem modeling methods in new and unexplored ways. We highlight key benthic-pelagic couplers in the ecosystem, with Arctic cod (Age 1+) and walrus standing out. Moreover, across all novel ecosystem scenarios, we demonstrated that changes in the copepod size structure had the largest impact on the entire ecosystem, suggesting a strong reliance of higher trophic levels on larger, lipid-rich copepods. Further, shifts in forage fish abundance had the largest effect on marine mammals in the food web. Finally, the addition of a key apex predator such as killer whales to the NOW Polynya ecosystem could have cascading effects on this Arctic ecosystem. Our method can be adopted and built on to explore the potential emergence of novel ecosystems with future climate change in the Arctic and beyond.

Supporting information

S1 Text. Supplementary methods. Detailed methods for species distribution models and Ecopath with Ecosim models.
(DOCX)

S1 Fig. Median projections (across 10 blocks) for each modeling approach for capelin (*Mallotus villosus*) for present-day, 2050 and 2100 (under RCP4.5 and RCP8.5 emissions scenarios). Public domain silhouette image is by xgirouxb, via PhyloPic (www.phylopic.org).
(TIF)

S2 Fig. Median projections (across 10 blocks) for each modeling approach for Arctic cod (*Boreogadus saida*) for present-day, 2050 and 2100 (under RCP4.5 and RCP8.5 emissions scenarios). Public domain silhouette image is by Milton Tan, via PhyloPic (www.phylopic.org).
(TIF)

S3 Fig. Median projections (across 10 blocks) for each modeling approach for Greenland halibut (*Reinhardtius hippoglossoides*) for present-day, 2050 and 2100 (under RCP4.5 and RCP8.5 emissions scenarios). Public domain silhouette image is by Tessa Rehill, via PhyloPic (www.phylopic.org).
(TIF)

S4 Fig. Median projections (across 10 blocks) for each modeling approach for killer whales (*Orcinus orca*) for present-day, 2050 and 2100 (under RCP4.5 and RCP8.5 emissions scenarios). Icon created by authors.
(TIF)

S5 Fig. Projected distribution of capelin (*Mallotus villosus*), Arctic cod (*Boreogadus saida)* and killer whales (*Orcinus orca*) in the North Water Polynya from present-day to 2100 under RCP8.5 emissions scenario. Capelin (a) present, (b) 2050 and (c) 2100. Arctic cod (d) present, (e) 2050 and (f) 2100. Killer whales (g) present, (h) 2050 and (i) 2100. Killer whale icon created by authors, other icons are public domain silhouette images by Milton Tan (*Gadus morhua*) and xgirouxb (*Thaleichthys pacificus*), via PhyloPic (www.phylopic.org).
(TIF)

S6 Fig. Projected current (2000–2014) and future (2100) distributions of Greenland halibut (*Reinhardtius hippoglossoides*) in the North Water Polynya under each emissions scenario. Public domain silhouette image by Tessa Rehill, via PhyloPic (www.phylopic.org).
(TIF)

S7 Fig. Benthic-Pelagic coupling represented by consumption rates of consumers on specific prey domains in the North Water Polynya ecosystem. PEL = Pelagic; BP = Benthopelagic; DEM = Demersal; BENT = Benthic. The consumption rate for killer whales is very low and not visible: Killer whales consume functional groups from the pelagic, bentho-pelagic and demersal domain (total rate is 9.11×10^{-7} t km^{-2} t^{-1}).
(TIF)

S8 Fig. Lindeman spline of trophic flows (t km2/yr) in the North Water Polynya ecosystem base model for 2005–2007. Flows to detritus are recycled through the detritus (D) and primary production (P) compartment at trophic level (TL) I. P: Primary producers; D: Detritus; TL: Trophic level; TE: Trophic efficiency; TST: Total system throughput.
(TIF)

S9 Fig. Mixed trophic impact analysis of the North Water Polynya ecosystem base model in 2005–2007. Diagram shows the positive (blue) and negative (red) impact of an increase in the biomass on the impacting group on the impacted group.
(TIF)

S10 Fig. SUpportive Role to Fishery ecosystems index (SURF; [97]) calculated for prey species in the North Water Polynya ecosystem. SURF index calculations include consumers only; top predators and primary producers were excluded. Dashed blue line represents the threshold (0.001) above which functional groups are considered key prey species in the ecosystem.
(TIF)

S11 Fig. Ecosim flow diagram for Scenario 1.1. The size of circles is proportional to the amount of biomass. Numbers below circles: Biomass of the functional group in t km^2. Numbers on the left indicate the trophic level. Direction of energy flow defined by position of line in relation to circles; flows positioned on the top of a trophic group indicate biomass outgoing, flows positioned on the side indicate entering biomass. Weight and color of the lines indicate the amount of energy flowing between nodes.
(TIF)

S12 Fig. Ecosim flow diagram for Scenario 1.2. See S11 Fig for detailed captions.
(TIF)

S13 Fig. Ecosim flow diagram for Scenario 2.2. See S11 Fig for detailed captions.
(TIF)

S14 Fig. Ecosim flow diagram for Scenario 3. See S11 Fig for detailed captions.
(TIF)

S15 Fig. Ecosim flow diagram for Scenario 4. See S11 Fig for detailed captions.
(TIF)

S16 Fig. Biomass proportion relative to the total biomass in the North Water Polynya food web for TL >4.
(TIF)

S1 Table. References for parameter estimates for the North Water Polynya Ecopath model. *B* = Biomass; *P/B* = Production/biomass ratio; *Q/B* = Consumption/biomass ratio. Modified from [45].
(DOCX)

S2 Table. Diet matrix for the North Water Polynya Ecopath models. Diets are expressed as a relative proportion (%) of the total diet. Diets in gray shading indicate cannibalizing trophic groups. Columns are predators; rows are prey.
(DOCX)

S3 Table. Novel ecosystem hypotheses and supporting literature underlying the Ecosim scenarios for the North Water Polynya.
(DOCX)

S4 Table. Ecosim sensitivity analysis parameter (B) changes compared to the initial scenarios.
(DOCX)

S5 Table. AUC results for the four species distribution modeling techniques (Generalized Additive Models (GAM), Boosted Regression Trees (BRT), Maximum Entropy (MaxEnt) and Random Forests (RF)) for the four species across each of the ten blocks.
(DOCX)

S6 Table. Data pedigree quality classification [96]. *B* = Biomass; *P/B* = Production/biomass ratio; *Q/B* = Consumption/biomass ratio.
(DOCX)

S7 Table. Data pedigree indices for the North Water Polynya ecosystem models with confidence intervals (+/-%). *B* = Biomass; *P/B* = Production/biomass ratio; *Q/B* = Consumption/biomass ratio. Orange shading indicates parameters with highest uncertainty. Sources were assigned an index based on the criteria in S2 Table.
(DOCX)

S8 Table. Magnitude of changes in parameter estimates (%) from initial unbalanced model to balanced model. *B* = Biomass; *P/B* = Production/biomass ratio; *Q/B* = Consumption/biomass ratio.
(DOCX)

S9 Table. Trophic levels reported for the functional groups in the North Water Polynya ecosystem and other high Arctic marine ecosystems. TL = trophic level; SE = standard error.
(DOCX)

S10 Table. Transfer efficiency in the North Water Polynya ecosystem.
(DOCX)

S11 Table. Comparison of the North Water Polynya with other Arctic ecosystem models. TL: Trophic level; TST: Total system throughput.
(DOCX)

S12 Table. Sensitivity analysis results for each scenario. Showing direction of change of biomass for each functional group.
(DOCX)

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