

RESEARCH ARTICLE

Structure and function of the western Baffin Bay coastal and shelf ecosystem

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Arctic marine species, from benthos to fish and mammals, are essential for food security and sovereignty of Inuit people. Inuit food security is dependent on the availability, accessibility, quality, and sustainability of country food resources. However, climate change effects are threatening Inuit food systems through changes in abundance and nutritional quality of locally harvested species, while foundational knowledge of Arctic food webs remains elusive. Here, we summarized scientific knowledge available for the western Baffin Bay coastal and shelf ecosystem by building a food web model using the Ecopath with Ecosim modeling framework. Based on this model, we calculated ecological network analysis indices to describe structure and function of the system. We used Linear Inverse Modeling and Monte Carlo analysis to assess parameter uncertainty, generating plausible parameterizations of this ecosystem from which a probability density distribution for each index was generated. Our findings suggest that the system is controlled by intermediate trophic levels, highlighting the key role of Arctic cod (*Boreogadus saida*) as prey fish, as well as the importance of other less studied groups like cephalopods in controlling energy flows. Most of the ecosystem biomass is retained in the system, with very little lost to subsistence harvest and commercial fisheries, indicating that these activities were within a sustainable range during the modeling period. Our model also highlights the scientific knowledge gaps that still exist (e.g., species abundances), including valued harvest species like Arctic char (*Salvelinus alpinus*), walrus (*Odobenus rosmarus*), and seals, and importantly our poor understanding of the system in winter. Moving forward, we will collaborate with Inuit partners in Qikiqtarjuaq, NU, Canada, to improve this modeling tool by including Inuit knowledge. This tool thus serves as a starting point for collaborative discussions with Inuit partners and how its use can better inform local and regional decision-making regarding food security.

Keywords: Marine environment, Food security, Food web, Climate change, Network analysis, Subsistence harvest

Introduction

From 2013 to 2020, the Arctic registered a seven-year-long streak of the warmest temperatures ever recorded,

with October 2015 to September 2016 as the warmest period, showing temperatures 2°C above the 1981–2010 average (Ballinger et al., 2020). The extent of summer sea

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ice over the Arctic Ocean has been decreasing, meaning increased open water area and season, along with a decline in ice thickness, with first-year ice largely replacing multiyear ice (Arrigo and van Dijken, 2011; Ardyna and Arrigo, 2020). These changes deeply affect the phenology (timing) and extent of primary production in Arctic marine ecosystems (Tedesco et al., 2019; Ardyna and Arrigo, 2020). Although less ice coverage and longer open water seasons can sustain higher primary production, concurrent increases in water column stratification resulting from freshening and warming of the surface layer could also trigger nutrient depletion, eventually leading to decreased primary production (Ardyna and Arrigo, 2020). Both scenarios are probable and could easily prevail depending on region and circumstances. In addition, there is mounting evidence of Arctic borealization, i.e. the advection of sub-Arctic, Atlantic and Pacific waters and marine biota into the Arctic Ocean, with consequences for the whole food web (Wassmann et al., 2011; Fossheim et al., 2015; Polyakov et al., 2020). For example, a northward expansion or increasing abundance of North Atlantic/sub-Arctic fishes, including capelin (*Mallotus villosus*) and sand lance (*Ammodytes* spp.), has been observed in the Canadian Arctic (Gaston et al., 2012; Provencher et al., 2012; Falardeau et al., 2017; Ulrich and Tallman, 2021). Killer whales (*Orcinus orca*) have also been observed more consistently in the eastern Canadian Arctic during the open water season (Higdon and Ferguson, 2009). Changes in the distribution and body condition of Arctic marine species have already been detected in association with climate change (Wassmann et al., 2011; Divoky et al., 2015; Harwood et al., 2015; Laidre et al., 2020; Matthews et al., 2020). However, despite growing concern regarding the future of Arctic marine ecosystems, their structure and function remain poorly understood.

For centuries, Inuit have harvested local marine species such as whales, seals, fish, and mollusks to survive in the extreme Arctic environment. These species are rich in important micronutrients (e.g., omega-3 fatty acids and selenium), protein, and vitamins (e.g., vitamin D), providing the base of Inuit food security (Rosol et al., 2016; Kenny et al., 2018a), i.e. the availability and access to sufficient, safe, and nutritious food to meet their dietary needs and preferences in a sustainable manner (Food and Agriculture Organization of the United Nations, 2008). Yet, Inuit in Canada face food security challenges, including economic challenges like the high cost of harvest activities and market foods (Hoover et al., 2013a; Hoover et al., 2016) and climate-related challenges such as unreliable sea ice conditions for travelling and hunting, along with changes in the availability of their main harvest species. These factors contribute to food insecurity, with Inuit being ten times more food insecure than the Canadian average (Egeland, 2011; Health Canada, 2012; Kenny et al., 2018b). At the same time, new opportunities may arise from local Inuit-led fisheries, with the exploration of new food and economic resources (Government of Nunavut and Nunavut Tunngavik Inc., 2005; DFO, 2019). Improving our knowledge of the structure and function of Arctic marine ecosystems is thus a priority, so that we can better

project and mitigate the effects of climate change on these ecosystems, and on Inuit food security, health, and well-being.

Ecosystem models are useful tools to describe complex ecological interactions or processes such as predator-prey interactions, competition, and migration, involving ecosystem components such as species or functional groups (group of species sharing similar feeding habitats and taxonomic characteristics; Geary et al., 2020). These models can be visualized as complex networks, where the components are nodes linked by their feeding relationships. The effects of climate change and other stressors, such as fisheries and invasive species, can be incorporated as interacting players in these models, making them useful to understand complex interactions in the context of a changing Arctic. Among the available modeling techniques, the Ecopath with Ecosim (EwE) approach has been widely used for ecosystem-based fisheries management (e.g., Coll and Libralato, 2012; Cisneros-Montemayor et al., 2020) to assess the impact and placement of protected areas throughout the world (e.g., Coll  ter et al., 2012), with some applications in understanding the structure, function, and changes of Arctic marine ecosystems (Hoover et al., 2013b; Hoover et al., 2013c). This modeling approach describes the flows of energy in aquatic food webs, consisting mainly of a mass-balance snapshot of the food web (Ecopath), from which temporal (Ecosim) and spatial (Ecospace) simulations can be implemented (Christensen et al., 2005).

Ecological Network Analysis (ENA) can be applied to the EwE model outputs to analyze all fluxes within a food web, producing indices that define holistic properties of a system (Ulanowicz, 1986). ENA is a powerful tool to assess functioning, stability, health, and maturity of the system, allowing for comparison of different states of an ecosystem over time (Heymans et al., 2014; Saint-B  at et al., 2015; Safi et al., 2019). Therefore, some of the ENA indices have been proposed for use in ecosystem-based management to assess, for example, the state of an ecosystem before and after different policies have been applied or after environmental pressures (Safi et al., 2019). Studying marine ecosystems poses challenges to data collection and quantification of interactions, which is aggravated in the Arctic due to its remoteness and seasonal ice coverage. These challenges highlight the need to be transparent about data and model limitations, and model uncertainty, especially in an Arctic context (Safi et al., 2019; Geary et al., 2020). Uncertainty in ecosystem modeling can arise from uncertainty in input parameters, when estimates of abundance and diet composition, for example, are scarce, and from structural uncertainty, with regard to the inclusion of all relevant processes and food web components (Geary et al., 2020). Such uncertainties are then propagated in all further network analysis. Considering uncertainty in input parameters thus improves interpretation of ENA results and allows for statistical comparisons with other models. This approach was recently demonstrated in a model of the Irish Sea where generating ranges for ENA indices based on uncertainty in

dietary data provided more trustworthy results (Bentley et al., 2019a).

In this study, we present an updated Ecopath model (Janjua et al., 2015) of the western Baffin Bay coastal and shelf ecosystem that describes ecosystem structure and function using ENA-derived indices and respective uncertainty distributions. We present eight indices that describe the size, growth and development of the system, the cycling and retention of biomass within the system, and the role of the different system components. This model and accompanying analytical framework provide a foundational tool to serve as a summary of scientific knowledge of the ecosystem.

Material and methods

The development of this model is a joint interdisciplinary and collaborative effort, including: datasets from the Green Edge Project (<http://www.greenedgeproject.info>), a multidisciplinary oceanographic research project conducted in Baffin Bay in 2016 to understand the dynamics of the phytoplankton bloom in the Arctic Ocean and how it affects lower compartments of the food web, as well as human populations; data on benthos and Arctic cod (*Boreogadus saida*) from Amundsen Science CCGS *Amundsen* icebreaker expeditions (<https://amundsenscience.com>); and updates from a preliminary Ecopath model developed for this region (Janjua et al., 2015). In establishing the input parameters for the western Baffin Bay (WBB) ecosystem model, consultations with experts on the ecology of several marine mammal, seabird, and fish species that occur in the area were used to supplement published literature and improve understanding of the ecosystem. Model development was originally planned as a collaborative effort including Inuit partners throughout the whole process, but due to COVID-19 travel restrictions, the current study is a purely scientific endeavor.

Western Baffin Bay coastal and shelf ecosystem

Baffin Bay is a semi-enclosed sea delimited by Greenland to the east and Baffin Island to the west, located at the southern margin of the Arctic Ocean while still hosting North Atlantic waters. In the south, it opens to the North Atlantic through the Davis Strait, whereas in the north it connects to the greater Arctic Ocean through narrow passages across the Canadian Archipelago. The study area comprises the western coast and shelf of Baffin Bay along the Canadian side, spanning approximately 200 km offshore, with a total area of 81,448 km². Almost 73% of the area is deeper than 500 m, and the maximum depth is 1,256 m (Figure 1). Here, the water masses of Arctic origin moving southward are colder and fresher (Baffin Island Current: 0 to 5°C at the surface and salinities of 30 to 32) compared to the eastern side of the bay where northward currents bring in water masses from Atlantic origin (West Greenland Current) (Wang et al., 1994; Tang et al., 2004). Sea ice melt begins as early as April, and the whole bay is completely ice-free in September. Freeze-up starts in October, from north to south, reaching its maximum in March (Wang et al., 1994; Tang et al., 2004).

The study area comprises the ecologically and biologically significant areas (EBSA) Baffin Bay Coastline and Baffin Bay Shelf Break defined by Fisheries and Oceans Canada (DFO, 2011). These areas were identified based on the importance of the extensive fjord habitat of the Baffin Island coastline for marine species and productivity (e.g., nursery grounds for the bowhead whale, *Balaena mysticetus*, seabird colonies, denning/foraging areas for the polar bear, *Ursus maritimus*), which extends offshore to the floe edge, as well as a migratory pathway for marine mammals. This area encompasses important hunting grounds supporting subsistence harvest for the communities of Qikiqtarjuaq and Clyde River (Government of Nunavut, 2010; 2014), who harvest mainly Arctic char (*Salvelinus alpinus*), ringed seal (*Pusa hispida*), narwhal (*Monodon monoceros*), harp seal (*Pagophilus groenlandicus*), bearded seal (*Erignathus barbatus*), and polar bear (Priest and Usher, 2004). Although not often consumed by Inuit, the Greenland halibut (*Reinhardtius hippoglossoides*) supports the only offshore commercial fishery in the area, falling under the Northwest Atlantic Fisheries Organization (NAFO) Division 0A (Jørgensen and Treble, 2016). The offshore portion has been given commercial status since 2007, while the inshore portion falls within the Nunavut Settlement Area. The halibut fishery uses single and twin bottom otter trawls, as well as longline and gillnets, taking place from June to November (Janjua et al., 2015; Hurtubise, 2016; Nanang, 2020). There is also a small-scale commercial Arctic char fishery in Qikiqtarjuaq and Clyde River (Priest and Usher, 2004). Subsistence harvesting includes the hunting or fishing activities taking place in Inuit communities to meet local food, clothing, and livelihood needs (see Nunavut Agreement Article 5), while a commercial fishery is the harvesting of fish and seafoods from the wild for profit. Both types of harvesting are critical for food security and food sovereignty in the region, food sovereignty being the right of people to define their own food systems and policies, as well as what is culturally and ecologically appropriate for them (ICC-Alaska, 2020).

Ecopath with Ecosim modeling framework

Ecopath with Ecosim (EwE) is a modeling software widely used for marine ecosystem modeling, especially in fisheries management (Christensen et al., 2005). Ecopath creates a static mass-balanced snapshot of the trophic network formed by species (or functional groups) from a given ecosystem according to their feeding interactions, represented by linked biomass “pools.” Functional groups are aggregations of species with similar roles in the ecosystem. Ecopath is mainly based on two master equations. The first equation describes how the production term for each functional group i can be split into components representing essential biological and ecological processes:

$$P_i = \sum B_j \cdot M_{2ij} + Y_i + E_i + BA_i + P_i \cdot (1 - EE_i) \quad (1)$$

where P_i is the total production rate of i , B_j is the biomass of the predator group j with predation mortality on i , M_{2ij} , Y_i is the total fishery catch rate of i , E_i is the net migration

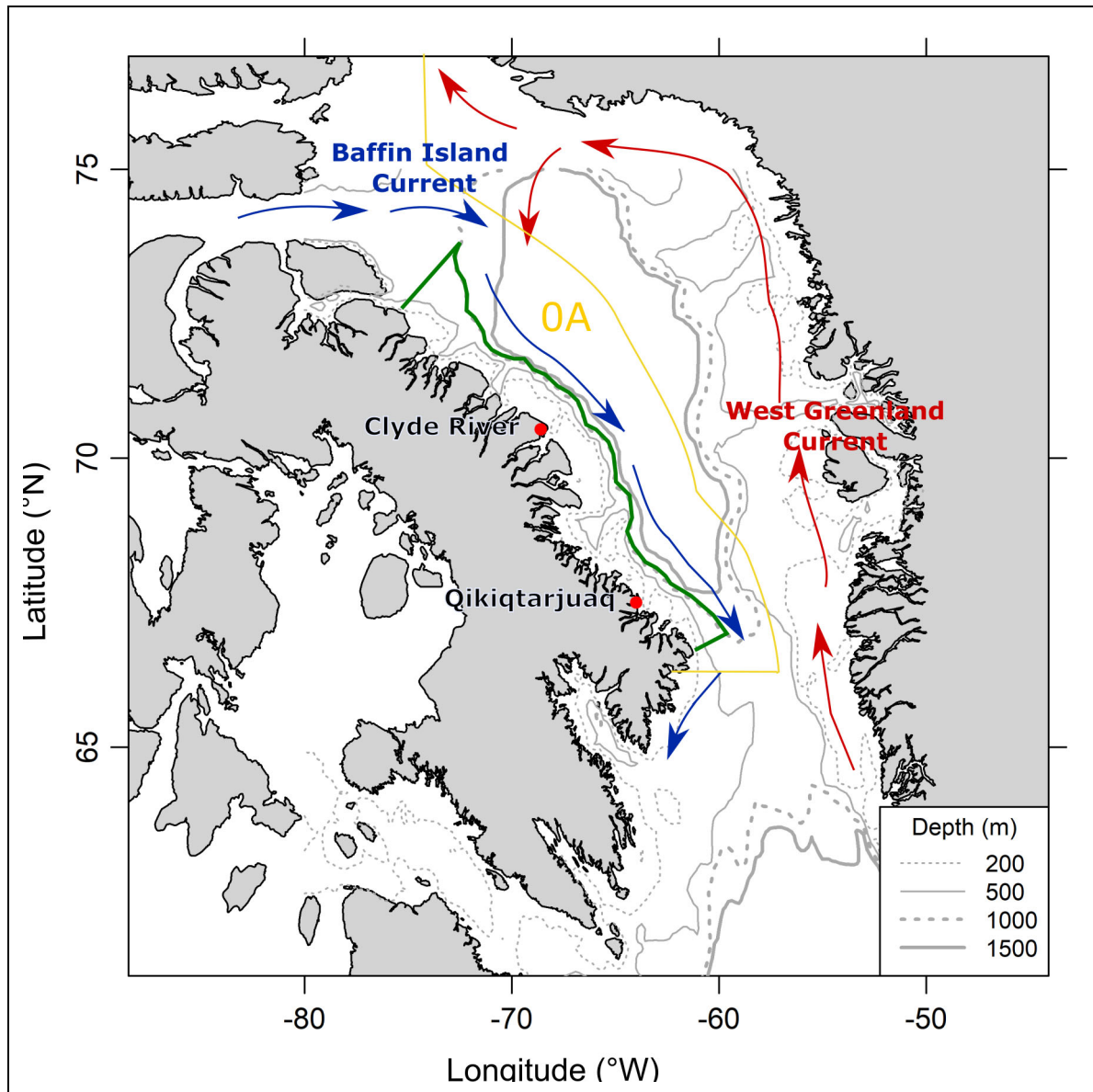


Figure 1. Model area of the western Baffin Bay coast and shelf ecosystem. The model area is delineated in green and the Northwest Atlantic Fisheries Organization division 0A is delineated in yellow. The Baffin Island Current is represented by the blue arrows (colder water) and the West Greenland Current by the red arrows (warmer water).

rate (emigration – immigration), BA_i is the biomass accumulation rate for i , while $P_i \cdot (1 - EE_i)$ is the “other mortality” rate for i . In other words, EE_i is the ecotrophic efficiency or proportion of production that is consumed within the system by predators or exported out of the system through fishing or migration (Christensen et al., 2005). The algorithm used to solve the set of linear equations that balance Ecopath models uses the following equation, which is another way to express Equation 1 that facilitates parameterization of ecological data:

$$B_i \cdot \left(\frac{P}{B}\right)_i = \sum B_j \cdot \left(\frac{Q}{B}\right)_j DC_{ji} + Y_i + E_i + BA_i + \left(\frac{P}{B}\right)_i \cdot (1 - EE_i) \quad (2)$$

where $(P/B)_i$ is the production to biomass ratio, $(Q/B)_j$ is the consumption by predator j per unit biomass, and DC_{ji} is the

proportion of prey i in the average diet of predator j . P/B is generally equal to total mortality Z (sum of natural and fishing mortalities) in a mass-balance system (Allen, 1971).

Equation 1 estimates the parameters to ensure mass balance between groups, but only considers the production flow within each group, therefore being insufficient to balance the energy flows within groups. The second master equation considers the other flows needed to ensure energy balance within each group by describing the consumption of each group as follows:

$$B_i \cdot \left(\frac{Q}{B}\right)_i = \left(\frac{P}{B}\right)_i \cdot B_i + UN + R_i \quad (3)$$

where UN is the portion of food that is not assimilated (e.g., excreted) and R_i is respiration, i.e. the portion of consumed food that is not used for production or excreted (or metabolic costs).

To balance an Ecopath model, these linear equations are solved for each functional group in the system using an algorithm, whereby at least three of the four basic parameters (P/B, Q/B, B and EE), as well as diet composition and fisheries catches (and migration if known) must be input. Ideally, the B, P/B and Q/B are entered for all groups and only the EE is estimated, given that no procedure exists for its field estimation. The model is considered balanced when the EE for each group is between 0 and 1. In cases where B, P/B or Q/B are unknown, EE can be assumed, forcing the model to estimate the other key parameters (Christensen et al., 2005; Heymans et al., 2016).

Ecopath input parameters and uncertainty levels

Species included in each functional group, parameter calculations, as well as the literature sources are described in more detail in Tables S1–S4. When parameterizing the model, we prioritized data available for the 2010s (the period studied), sampled locally and with high precision to maximize confidence in input parameters. In general, when meeting this priority was not possible, we used data for the same species in another Arctic ecosystem, or a similar species in another ecosystem. If no data were available for a parameter, Ecopath is able to calculate one missing parameter per functional group as a function of the mass-balance Ecopath model, whereby an algorithm solves for the missing parameters to satisfy the mass-balance assumption (Christensen et al., 2005). Parameters with the highest confidence (i.e., pedigree) were used if possible, depending on data availability. This approach follows the way uncertainty in input parameters is “classified” within EwE; i.e. uncertainty is simplified into a qualitative grading of data, called the pedigree. The data pedigree consists of six to eight qualitative levels of uncertainty around each input parameter based on the data source, which translates into different predefined coefficients of variation. For example, for biomass the grading has six levels, from “sampling/locally high precision” (lowest uncertainty) corresponding to a coefficient of variation of 10%, to “estimated by Ecopath” (highest uncertainty) with a coefficient of variation of 40% (Tables S5 and S6, more details in the supplementary material and in Aydin et al., 2007). The pedigree can be used to assess overall uncertainty in input parameters of an ecosystem model, or conversely how much we know about the ecosystem.

Functional groups

The local food web was simplified into 30 single and multi-species functional groups and set to years of 2011–2016 (Table S1). The years represented were chosen based on data availability, especially for zooplankton and primary producers that provide the base of the trophic network. Detailed data for these lower trophic levels were obtained during the Green Edge expedition, where local abundance, production and consumption rates of zooplankton, phytoplankton, and bacteria were determined (Massicotte et al., 2020; Saint-Béat et al., 2020). Due to their importance for Inuit subsistence harvest we included the following species as single-species groups: polar bear

(Baffin Bay subpopulation), ringed seal, narwhal (Eastern Baffin Bay stock), bowhead whale (Eastern Canada-West Greenland population), walrus (*Odobenus rosmarus rosmarus*) (Hudson Bay-Davis Strait stock), and Arctic char. Killer whales and Greenland shark (*Somniosus microcephalus*) were also included as single-species groups due to their role as top predators in Arctic ecosystems, while Greenland halibut was included due to its importance for commercial fisheries in the region.

When aggregating species into functional groups, we prioritized their role in the food web; that is, we grouped the species based on their size and feeding habitat/preferences as well as taxonomic characteristics. For consistency, we also considered the structure of other Ecopath models developed for Arctic ecosystems when data were available and food web structure corresponded (Pedersen and Zeller, 2001; Hoover et al., 2013b; Janjua et al., 2015). Within each group, the species for which more data were available was selected as representative of the group. Aggregating species into functional groups, especially when the data available for such species are scarce, decreases complexity in the model, which tends to also decrease the uncertainty in model predictions (Geary et al., 2020). Seals (other than ringed seals) and seabirds that frequent the area in the summer were included in two multi-species groups. We aggregated fish and large invertebrates in seven functional groups (Arctic/polar cods, with polar cod being *Arctogadus glacialis*, small pelagic fish, sculpins/eelpouts, small demersal fish, large demersal fish, large crustaceans, and cephalopods), and benthic organisms into four functional groups (polychaetes, echinoderms, bivalves, and other benthos). Zooplankton species were also grouped based on their sizes and feeding preferences following Saint-Béat et al. (2020), resulting in four functional groups (carnivorous zooplankton, omnivorous zooplankton, *Calanus* copepods, and microzooplankton). We included pelagic phytoplankton and sea ice algae as primary producers in the model, one microbial group (bacteria) and one organic detritus group.

Dealing with seasonality in the WBB ecosystem

The seasonality in sea ice cover in the WBB ecosystem leads to a strong seasonality in primary production blooms, along with seasonal migration of many marine mammal and seabird species. Sea ice algae live beneath the ice and within brine channels and are a critical food source in the Arctic in late winter and early spring (Grossi and Sullivan, 1985; Aumack et al., 2014), while the pelagic phytoplankton bloom occurs in the spring/summer (Ardaya et al., 2020). All marine mammal species (except for polar bear and ringed seal), as well as seabirds, occur in the WBB area only during the ice-free season to feed, to breed or to pass through as part of their migratory routes (Mallory et al., 2019; Yurkowski et al., 2019).

To deal with seasonality within Ecopath, we used an “average” model of the whole year by adjusting the biomasses of all seasonal functional groups, as well as primary production. That is, if a species or functional group occurs in the model area only in summer (1/4 of the year), we divided their biomass estimate for the summer season

by four, spreading this biomass over the whole year. Year-averaging is a common approach in modeling of Arctic ecosystems (Pedersen and Zeller, 2001; Hoover et al., 2013b; Whitehouse et al., 2014; Hoover et al., 2021) where our poor understanding of the polar night does not allow for a solid representation of winter months. Even though we recognize that this approach represents an important caveat in this modeling exercise, we decided to take it instead of modeling just the summer season due to the occurrence of subsistence harvest year-round for species like polar bear and ringed seal (Priest and Usher, 2004; SWG, 2016a). This approach preserved mass-balance and will allow for multi-year simulations with Ecosim in future work.

Ecopath biomasses—B

Except for polar bear and ringed seal, the biomass of marine mammal species and seabirds was divided by four to account for seasonal migration. Biomasses were calculated based on abundance estimates from survey reports and peer-reviewed research (Text S1, Table S2).

As fish biomasses in this region are largely unknown, we let the model estimate their biomasses by setting the EE to 0.95 (Christensen et al., 2005; Heymans et al., 2016), assuming that within the model most fish production is consumed or harvested (except for Greenland shark, where we assumed an EE of 0.5, as it is a top predator; Table S3). An EE value of 0.95 assumes that very little of the population dies of old age (Christensen et al., 2005).

Zooplankton species were separated according to their size and feeding habits (Saint-Béat et al., 2020), and abundances were estimated during the Green Edge expedition in 2015 and 2016 (Massicotte et al., 2019; Massicotte et al., 2020; Saint-Béat et al., 2020) and converted to biomass using allometric formulas (Text S1, Tables S7 and S8). Abundances of phytoplankton and sea ice algae, bacteria and detritus were also measured during the Green Edge expedition in open water of Baffin Bay, and under the ice in an ice-camp off the west coast of Baffin Island (Massicotte et al., 2019; Massicotte et al., 2020; Saint-Béat et al., 2020).

Biomass data for benthos was included when available; when not available, we set the EE to 0.95 and let Ecopath estimate it. All biomasses were included as biomass per area (ton km^{-2}).

Ecopath production to biomass ratios—P/B

Values for P/B (or for Z, total mortality) for marine mammals were calculated as the sum of natural mortality and harvest mortality (Text S1, Table S2). Natural mortality rates for marine mammals were calculated based on values from life history tables and estimates of longevity based on equations from Barlow and Boveng (1991). Harvest mortality was calculated as catch over biomass, based on reported subsistence and commercial catches (depending on the species). For seabirds, we used reported values for natural mortality and harvest, weighed by the species included in the functional group.

For fish, natural mortality was estimated from the empirical relationship linking mortality, the parameters

of the von Bertalanffy Growth Function, and mean environmental temperature from Pauly (1980; Text S1, Table S3). We used the life-history tool in FishBase (www.fishbase.org) to make these calculations for the different fish species within the model (Froese and Pauley, 2008). Fishing mortality was included for Arctic char from the subsistence harvest, and for Greenland halibut from the commercial fishery.

For benthos and other invertebrates, P/B rates are poorly described. Due to lack of data, the P/B ratios for all benthic groups, as well as cephalopods and large crustaceans (shrimps and crabs), were based on Ecopath models representing other high latitude marine regions (Pedersen and Zeller, 2001; Guénette et al., 2005; Aydin et al., 2007; Hoover et al., 2013b). In these models, P/B ratios were calculated either based on local growth/production studies available for some species or based on Brey's database on microbenthic productivity (Jarre-Teichmann and Guénette, 1996).

Production and consumption rates of zooplankton groups and bacteria, as well as diet composition, were calculated in Saint-Béat et al. (2020), while production for phytoplankton and sea ice algae was measured during the Green Edge expedition (Text S1). All P/Bs were calculated as a yearly rate (year^{-1}).

Ecopath consumption to biomass ratios—Q/B

The Q/Bs for marine mammals and seabirds were calculated from field metabolic rates or similar energetic equations (e.g., Williams et al., 2020) and converted to a yearly rate based on the average energy density of prey items previously reported (Hunt et al., 2000; Guénette et al., 2005; Harter et al., 2013) and diet composition of marine mammals or seabirds (Text S1, Table S2). For fish, we used the empirical formula from Palomares and Pauly (1998) implemented in the life-history routine of FishBase (Text S1, Table S3).

Similar to P/B, Q/B ratios for all benthic groups, cephalopods, and large crustaceans (shrimps and crabs) were taken from other Ecopath models (Pedersen and Zeller, 2001; Guénette et al., 2005; Aydin et al., 2007; Hoover et al., 2013b). These ratios were based on a range of mean gross efficiencies, from 9% for herbivores/detritivores to 30% for carnivores (Jarre-Teichmann and Guénette, 1996). Q/Bs were also calculated as a yearly rate (year^{-1}).

Ecopath diet matrix

The diet matrix was constructed based on data from published diet studies of stomach contents, stable isotopes (SI), or fatty acid (FA) composition studies in the region (Table S4). SI and FA composition studies quantify these food web markers in marine species and can provide useful insights regarding their trophic position, foraging habitat and food source when comparing SI and FA composition of predator with their potential prey (Kelly, 2000; Budge et al., 2006). We prioritized stomach content studies reporting prey contribution on a weight basis when available because, contrary to reported values on a frequency basis or SI and FA methods, values on a weight basis are more representative of dietary mass flows. When

not available in the region, we considered diet studies from other Arctic regions. For some groups, such as benthos, diet studies were not available, so we used generalized diets based on life history traits for these groups considered in other Ecopath models. For some marine mammals, we considered that a proportion of their diet was imported into the model, to account for feeding on prey not considered in the model area (e.g., polar bears feeding more offshore on belugas).

For species groups that are known to have high cannibalism, such as fish (e.g., Nielsen et al., 2019), diets had to be adjusted in the model. Large values of cannibalism in the diet of a species or functional group can cause numerical instability when balancing the Ecopath model (Heymans et al., 2016). Although this instability can be remediated by splitting the species into multiple stanzas (or life history stages), we did not have enough information regarding the life cycle of species with noted cannibalism (e.g., Greenland halibut and Greenland shark) to reduce uncertainty in the model. Rather, we limited cannibalism to <2% of the diet to reduce the instability in the Ecopath (and Ecosim) models (Heymans et al., 2016).

Ecopath model balancing

When all the parameters were inputted in Ecopath, the model did not achieve mass balance. This imbalance is expected, as there are many sources of uncertainty and unknown parameters when building a model of a whole ecosystem, especially in an understudied system like the WBB (Table S7). The EE of several groups was above 1, meaning that these groups were being consumed at a higher level than they were reproducing, thus failing the mass-balance assumption required for Ecopath. These groups included mainly marine mammals, Greenland shark, Arctic/polar cod, Greenland halibut and zooplankton groups. Ecopath does not currently have an automated way of achieving mass balance. Common practice is to balance the model manually by adjusting the parameters incrementally through an iterative process during which small changes (e.g., $\pm 10\%$) are made to the parameters and the results on EE for the groups with high EEs are checked (Christensen et al., 2005; Heymans et al., 2016). We started the balancing process by prioritizing the parameters with the highest uncertainty (i.e., the lowest pedigree); hence, we started by adjusting diet composition, followed by Q/Bs or P/Bs, and then biomasses. We also started with top predators and went down the food web until mass-balance was achieved, adjusting parameters within a functional group with the lowest pedigrees that allowed the model to balance. Diet composition studies in the Arctic only represent summer diets and may therefore be quite uncertain relative to the prey items and respective percentage of mass. Useful outputs of Ecopath are the mortalities and predator mortality rates that allow to identify the sources of mortality for each group and the ones causing high EE. If the mortality was too high from predation pressure, we adjusted diet composition of the predator; then, if it was not sufficient to lower the EE of the prey, we altered the Q/B of the predator, the P/B of the prey, the biomass of the predator or the prey, or a mix

of all. The most noticeable imbalance was the high predation of Greenland shark on its main prey, such as seals, which was a consequence of the ecologically unrealistic Q/B and P/B calculated for Greenland shark. For some marine mammal groups, the biomasses and P/Bs were changed to accommodate predation levels because adjusting diet composition alone did not balance the model. For zooplankton and sea ice algae, the biomasses were adjusted within the calculated maximum and minimum values from the Green Edge expedition.

A few further adjustments were made on P/Bs or Q/Bs after evaluating a set of pre-balance diagnostics, or PREBAL (Link, 2010; Heymans et al., 2016). PREBAL diagnostics are based on general ecological and fishery principles in aquatic ecosystems, including checking if biomasses across taxa and trophic levels make ecological sense (e.g., lower biomass of top predators compared to intermediate trophic levels). These diagnostics consist of a set of guidelines and rules of thumb and were developed with the intent of adding rigor in terms of quality control and assurance when using large ecosystem models in fisheries management (Link, 2010; Heymans et al., 2016). Mass balance was achieved when the EE of all groups was below one, after passing the PREBAL diagnostics.

Ecological Network Analysis —ENA

Ecopath calculates a set of ENA indices, but these are single values derived from a unique flow matrix with no associated uncertainty. In order to account for uncertainty in input parameters, we performed an ENA of the WBB ecosystem using the enaR package (version 3.0.0), which takes into account uncertainty in input parameters when deriving ENA indices (Borrett and Lau, 2014). To do so, the Ecopath model was converted to the SCOR format (Ulanowicz and Kay, 1991), consisting of node storage (corresponding to the biomasses in Ecopath), network inputs in the system (gross primary production and diet imports), network exports out of the system (fisheries and harvest), respiration for each living group (calculated in EwE outputs), and a flow matrix (corresponding to Ecopath consumption matrix), all in $\text{tons km}^{-2} \text{year}^{-1}$. Because neither gross primary production nor respiration of primary producers are calculated within Ecopath, we calculated these terms for phytoplankton and sea ice algae using values in western Baffin Bay calculated by Saint-Béat et al. (2020) and following the equations in Aoki (2006) and the procedure by Bentley et al. (2019):

- a) Gross primary production = respiration + production + flow to detritus;
- b) Respiration = $\sigma \times$ gross primary production

where σ is the ratio of annual respiration to gross production. Both production and flow to detritus can be obtained from Ecopath. Before computing the ENA indicators, the model was balanced within enaR using the AVG2 method (Allesina and Bondavalli, 2003).

The uncertainty analysis allows us to quantify how the combined error in all model input parameters propagates through model calculations to generate uncertainty in

ENA indicators (Hines et al., 2018). For this analysis, we used the `enaUncertainty` function in the R software package `enaR` (Lau, 2017; Hines et al., 2018), which combines linear inverse modeling with Monte Carlo sampling to generate a set of 10,000 balanced network parameterizations based on the original WBB model and uncertainty data for each parameter (Hines et al., 2018). Linear inverse modeling is an empirical technique for estimating the best linear stochastic model consistent with a set of multivariate data (Penland, 1989). In this case, it combines the uncertainty data for each parameter with the original model to generate a set of plausible models. The Monte Carlo sampling technique randomly samples from the distribution of possible values within the defined uncertainty ranges.

This set of models was then used to calculate distributions of ENA indicators. We used symmetric uncertainty for each parameter (**Table 1**): for respirations, which are not inputs but rather outputs in Ecopath, we used coefficients of variation estimated from meta-analysis studies on physiological rates (Elgar and Harvey, 1987; Steffensen, 2005; Dunn et al., 2018) or based on values from the Green Edge expedition for zooplankton (based on Saint-Béat et al., 2020). When such studies were not available, we used the coefficients of variation corresponding to the most uncertain pedigree classification in Ecopath (40%). We considered the same coefficients of variation for the flow matrix and diet imports. For the export flows, we used coefficients of variation derived from temporal data on harvest for the last five years for which harvest data were available (Priest and Usher, 2004; SWG, 2016a; NAMMCO, 2018).

We analyzed a set of eight essential ENA indices to describe the structure and functioning of the WBB coast and shelf ecosystem derived from the `enaR` package with associated uncertainty (Heymans et al., 2014; Saint-Béat et al., 2015). These indicators describe the size (total system throughout, TST), growth and development of the system (average mutual information, AMI; ascendancy, A; relative ascendancy, A/C; and robustness), the cycling and retention of biomass flows within the system (indirect flow intensity, IFI; average path length, APL) and recycling of organic matter (Finn's cycling index, FCI), and the influence of the different system components on the whole system and on each other (control difference and system control; **Table 2**).

ENA indices can be used to assess resistance and resilience or, in other words, the sustainability of an ecosystem. Resistance is the ability of an ecosystem to maintain its original state after external perturbations, while resilience is the speed at which a system returns to the equilibrium state after a perturbation (Saint-Béat et al., 2015). Stability is reached when the ecosystem presents a balance between resistance and resilience (Ulanowicz et al., 2009; Saint-Béat et al., 2015; Saint-Béat et al., 2018). In general, to achieve stability, the tendency of an ecosystem is that of increasing activity and complexity, that is, the number of flows (TST), the storage of energy (biomasses), the efficiency of biomass flows (ascendancy), and the biomass cycling (FCI; Finn, 1976; Ulanowicz, 1986; Heymans et

al., 2007; Saint-Béat et al., 2015). An increase in ascendancy can thus indicate an increase in maturity and resistance of the system to internal perturbations, as it becomes more organized, but a decrease in resilience, as a high level of organization means less flexibility to bounce back (Fath, 2015; Saint-Béat et al., 2015). In this context, we can use A/C and robustness to assess the sustainability of the ecosystem (**Table 2**; Ulanowicz et al., 2009; Fath, 2015). When plotting robustness against A/C, all values fall on a theoretical curve of sustainability described by Ulanowicz et al. (2009) and Fath (2015), with the maximum occurring when A/C is approximately 0.37 (see Figure S1). The peak of this curve represents the region where the trade-offs between redundancy and resiliency are optimally balanced. Control is defined based on the premise that energy (or biomass) cycles in ecosystems and, for that reason, every ecosystem component affects and is affected by every other directly or indirectly (Dame and Patten, 1981). Then, one component will control another if it affects the other to a larger extent than the other affects it, in terms of biomass flow. This effect can be expanded to the whole ecosystem if one or more components are more often “controllers” in pairwise relationships than “controlled” (Schramski et al., 2006).

To identify species that play a key role as prey in the WBB, we calculated the SURF index (SUpportive Role to Fishery ecosystems), as defined by Plagányi and Essington (2014), which considers the degree of dependency of predators on their prey and corrects for total number of links in the food web. If this index is higher than 0.001, then the species is considered a key prey in the ecosystem.

Additionally, we report trophic levels and network statistics related to fisheries and harvest taken from Ecopath outputs (not including uncertainty). These are: 1) mean trophic level of catch (TLC), which reflects the main structural component of the food web that fisheries are targeting and is calculated by Ecopath as the weighted average of TL of the harvested species; 2) catch/TST, which indicates how much of the total energy flows are channeled to catches (fisheries and harvest are the only types of export considered in this model); and 3) percent primary production required for the catch (%PPR), which represents the energy required from the ecosystem to support catches (Pauly and Christensen, 1995; Tudela et al., 2005). The %PPR in combination with TLC can be used as a quantitative index to understand the effect of fisheries on a given ecosystem (Tudela et al., 2005). That is, for the same %PPR, a fishery targeting a higher trophic level would be less disruptive than one targeting a lower trophic level.

Results

Ecopath mass-balanced model and data pedigree

The adjustments made to the diet matrix, biomasses of polar bear, zooplankton groups and phytoplankton, as well as P/Bs and Q/Bs of other groups, varied from 0.1 to 614% from the initial input values (see Tables S9 and S10 for more details). The parameters with the largest adjustments were the P/Bs of Greenland shark (614%) and Greenland halibut (264%), which were initially too small to accommodate predation and fishing mortality rates. We

Table 1. Coefficients of variation used as inequalities in the enaUncertainty function for each flow^a

Group Number and Name	Flow	Respiration	Import	Export
1 Killer whale	0.25	0.25	0.25	– ^b
2 Polar bear	0.25	0.25	0.25	0.07
3 Narwhal	0.25	0.25	0.25	0.06
4 Bowhead whale	0.25	0.25	0.25	0.19
5 Ringed seal	0.25	0.25	–	0.27
6 Other seals	0.25	0.25	0.25	0.74
7 Walrus	0.25	0.25	–	0.94
8 Seabirds	0.61	0.61	0.61	0.40
9 Greenland shark	0.53	0.53	–	0.65
10 Greenland halibut	0.53	0.53	–	0.09
11 Arctic char	0.53	0.53	–	0.38
12 Arctic/Polar cod	0.53	0.53	–	–
13 Small pelagic fish	0.53	0.53	–	–
14 Sculpins/Eelpouts	0.53	0.53	–	–
15 Small demersal fish	0.53	0.53	–	0.35
16 Large demersal fish	0.53	0.53	–	0.47
17 Large crustaceans	0.40	0.40	–	–
18 Cephalopods	0.40	0.40	–	–
19 Carnivorous zooplankton	0.84	1.28	–	–
20 Omnivorous zooplankton	0.84	3.01	–	–
21 Calanus	0.84	1.14	–	–
22 Microzooplankton	0.84	1.88	–	–
23 Polychaetes	0.40	0.40	–	–
24 Echinoderms	0.40	0.40	–	1.41
25 Bivalves	0.40	0.40	–	0.77
26 Other benthos	0.40	0.40	–	–
27 Bacteria	0.40	0.40	–	–
28 Ice algae	–	0.40	0.40	–
29 Phytoplankton	–	0.40	0.40	–
30 Detritus	0.40	0.40	–	–

^aBolded values indicate those cases where the highest value of pedigree uncertainty from Ecopath was used (when no meta-analysis studies on physiological rates were available).

^bIndicates no corresponding coefficients of variation (flows were not available or were zero).

consider the adjusted values ecologically sound, as they were also within those previously reported in Ecopath models of Arctic ecosystems (Pedersen and Zeller, 2001; Hoover et al., 2013b; Janjua et al., 2015), noting specifically that the P/B calculations used from FishBase often underestimate higher latitude species (Pauly, 1980). After all adjustments, the Ecopath model was balanced (Tables 3 and S4b): ecotrophic efficiencies were close to 1 for fish and invertebrate groups, which tend to be consumed within the food web; EEs were closer to zero for top predators that are not consumed or harvested, such as

killer whales; and the EE for primary producers was closer to 0.5, which is expected, as a large portion of primary production biomass sinks as detritus (Christensen et al., 2005; Heymans et al., 2016).

The trophic levels ranged from 1 to 5 (Table 3, Figure 2), with killer whale and polar bear occupying the highest trophic positions, followed by narwhal, Greenland shark, Greenland halibut, “other” seals, and ringed seal. Seabirds, bowhead whale and walrus occupy a trophic level of 3, along with Arctic/polar cods and the other fish groups, cephalopods, and carnivorous zooplankton. Large

Table 2. Ecological network indicators calculated for the western Baffin Bay ecosystem

Indicator	Description	Formula	Units	Source
Size, growth, and development				
Total system throughput, TST	Sum of input, output, and internal biomass flows in the food web. It measures the size and activity of the system, indicating the amount of biomass production in the food web. TST here differs from total system throughflow (TST _{flow}), which is the sum of either all the inputs or all the outputs.	$\sum(\text{internal flows} + \text{inputs} + \text{outputs})$	tons km ⁻² year ⁻¹	Ulanowicz, 1986
Average mutual information, AMI	Pathways of biomass flows among functional groups. It is calculated based on the joint probability of a certain biomass flow occurring, the marginal probability of a biomass flow entering functional group <i>j</i> , and the conditional probability that this flow leaves functional group <i>i</i> . It thus indicates the specialization and constriction of biomass flows within the food web.	$k \cdot \sum_{ij} \frac{\text{flow}_{ij}}{\text{TST}} \cdot \log \frac{\text{flow}_{ij} \cdot \text{TST}}{\text{flow}_i \cdot \text{flow}_j}$	bits	Ulanowicz, 1986; Fath et al., 2019
Ascendency, A	Measures both the growth (TST) and development (AMI) of the system. It can indicate the level of activity and organization within the system, representing the efficient part of the food web.	$\text{TST} * \text{AMI}$	bits	Ulanowicz, 1986
Relative ascendency, A/C	Ratio between ascendency (A) and development capacity (C). It is the maximal value of ascendency (or organization) that the food web can reach.	$\frac{A}{-\sum_{ij} \text{flow}_{ij} \cdot \log \frac{\text{flow}_{ij}}{\text{TST}}}$	no units	Ulanowicz, 1986; Fath et al., 2019
Robustness	Combines organization and efficiency of a system (ascendency), rendering it resistant, with redundant options in case of disturbance (redundancy), rendering it resilient. It varies between 0 and 1, with optimal results falling in the middle.	$-\frac{A}{C} \cdot \log \frac{A}{C}$	no units	Fath, 2015
Cycling				
Finn's cycling index, FCI	Indicates the fraction of the TST _{flow} that is recycled in the system, that is, how much of the biomass flow revisits the same functional group multiple times before exiting the system. High FCI indicates that the biomass stays in the system longer.	$\frac{\sum \text{TST}_{\text{flow}_{cycled}}}{\text{TST}_{\text{flow}}}$	no units	Finn, 1976; Fath et al., 2019
Indirect flow intensity, IFI	Proportion of TST _{flow} derived from indirect pathways of biomass flows.	$\frac{\sum \text{indirect flows}}{\text{TST}_{\text{flow}}}$	no units	Borrett et al., 2006
Average path length, APL	Average number of functional groups biomass inputs or outputs pass through before exiting the food web. It measures the retention of biomass within a system. A high APL is generally associated with a longer food chain.	$\frac{\text{TST}_{\text{flow}}}{\sum \text{inputs}}$	no units	Finn, 1976

(continued)

Table 2. (continued)

Indicator	Description	Formula	Units	Source
Control				
Control difference, cd	Quantifies pair-wise dependencies between each pair of functional groups, i.e. functional group <i>i</i> controls functional group <i>j</i> if the direct and indirect biomass flow from <i>i</i> to <i>j</i> exceeds that from <i>j</i> to <i>i</i> , within the flow environments of <i>i</i> and <i>j</i> . For component <i>i</i> to be controlling <i>j</i> , it must be more important in the input environment E_j' than in the output environment E_j , and vice-versa. In terms of TST_{flow} , the control can be defined based on the difference between the fractional transfer values between <i>i</i> and <i>j</i> . The magnitude of cd indicates the level of control while the direction of control is quantified as positive or negative.	$cd_{ij} = \frac{E_{ij}}{TST_{flow_i}^{out}} - \frac{E_j'}{TST_{flow_j}^{in}}$	no units	Dame and Patten, 1981; Schramski et al., 2006
System control	Relative influence of each functional group towards the movement of biomass through the entire food web. If positive, the group controls the system, and if negative the group is controlled by the system. It corresponds to the sum of cd_{ij} .	$\sum cd_{ij}$	no units	Schramski et al., 2006; 2007

crustaceans, benthic groups, the other zooplankton groups, and bacteria are at trophic level 2, while primary producers and detritus are in the bottom of the food web at trophic level 1. In general, these trophic levels were along the range of those reported in the literature in similar Arctic ecosystems (Tables S11–S13). For killer whales, the lower trophic level reported in the literature was likely calculated based on a generalized diet of killer whales around the globe (Trites et al., 1995). A higher trophic level would be expected for killer whales in Baffin Bay feeding to a larger extent on marine mammals. For some groups such as large crustaceans, polychaetes and other benthos, our model estimated trophic levels lower than those found for some species in the literature. Yet, these groups include several species within the respective taxa, potentially increasing the variability in trophic level of the functional groups.

The overall data pedigree index was 5 (of the 6–8 levels: Tables S5 and S6), meaning that the input data are from local studies or at least for similar species in similar systems, but overall were sampled with low precision. More uncertainty was associated with benthos and fish groups, and the least uncertainty was associated with zooplankton and primary producers.

Ecopath summary statistics related to harvest and fisheries

In the WBB ecosystem, the primary production required to sustain the whole harvest was 23.15% of the total primary production. The catch to total system throughput ratio

(catch/TST) was 0.11, indicating that only a small fraction of the total flows in the WBB system goes to fisheries and harvest. The mean trophic level of the catch was 4.4, which is relatively high within an ecosystem with 5 trophic levels.

Ecological network analysis and SURF index

The results for the ENA indices on the original enaR model (and uncertainty ranges) are reported in **Table 4** and **Figure 3**. The results based on the original model were generally lower than the average of the distribution for size and development indices (0.4–6.3%) and higher for cycling indices (1.9–5.4%). ENA indices reported here were generally similar to those in other polar ecosystems (**Table 4**). The exceptions were a higher FCI and relative ascendancy in the WBB compared to other Arctic ecosystems, and a lower relative ascendancy and IFI compared to Antarctic ecosystems.

Killer whales and polar bears had negative system control, indicating that these groups are controlled by others in the system (**Figure 4**). The same was observed for seabirds and, to a lesser extent, Greenland shark, as there is large uncertainty to the direction of system control in these sharks. Cephalopods, ringed seal, bowhead whale, narwhal, and walrus had the highest control over other groups, followed by Arctic/polar cods, small pelagic and small demersal fish, and other mid-trophic level groups. The direction of system control for Greenland halibut and other seals was not defined.

Table 3. Ecopath parameters^{a,b} used in the balanced model representing the western Baffin Bay shelf and coastal ecosystem in the 2010s, and their value to Inuit communities^c

Group Number and Name	TL	B	P/B	Q/B	EE	P/Q	Landings	Value to Inuit
1 Killer whale	5.23 ^b	0.0001	0.03	9.11	0.00	0.00	0.000	na ^c
2 Polar bear	5.13	0.0013^b	0.15	6.00	0.52	0.03	0.0001	SH ^c
3 Narwhal	4.55	0.0470	0.04	19.80	0.76	0.00	0.0010	SH
4 Bowhead whale	3.71	0.0460	0.01	14.23	0.32	0.00	5.7 × 10 ⁻⁵	SH
5 Ringed seal	4.10	0.1070	0.15	15.32	0.76	0.01	0.0086	SH
6 Other seals	4.25	0.0610	0.09	39.60	0.80	0.00	0.00088	SH
7 Walrus	3.20	0.0024	0.09	30.40	0.44	0.00	2.6 × 10 ⁻⁵	SH
8 Seabirds	3.88	0.0010	0.24	254.4	0.35	0.00	2.3 × 10 ⁻⁵	SH
9 Greenland shark	4.50	0.100	0.05	0.40	0.50	0.11	0.0018	na
10 Greenland halibut	4.42	0.934	0.51	2.30	0.97	0.22	0.108	CF ^c
11 Arctic char	3.54	0.095	0.19	2.30	0.95	0.08	0.005	SH, CF
12 Arctic/Polar cod	3.14	5.74	0.65	3.25	0.95	0.20	0.000	na
13 Small pelagic fish	3.35	1.23	0.63	4.85	0.95	0.13	0.000	na
14 Sculpins/Eelpouts	3.68	2.15	0.35	2.89	0.95	0.12	0.000	SH
15 Small demersal fish	3.54	2.78	0.53	3.13	0.95	0.17	1.9 × 10 ⁻⁵	na
16 Large demersal fish	3.60	3.45	0.14	1.58	0.95	0.09	0.00097	na
17 Large crustaceans	2.69	3.16	0.86	6.00	0.95	0.14	0.000	na
18 Cephalopods	3.98	0.36	2.55	6.90	0.95	0.37	0.000	na
19 Carnivorous zooplankton	3.02	7.80	3.10	17.70	0.93	0.18	0.000	na
20 Omnivorous zooplankton	2.03	12.1	6.30	20.10	0.85	0.31	0.000	na
21 <i>Calanus</i> spp.	2.02	24.3	4.90	12.60	0.84	0.39	0.000	na
22 Microzooplankton	2.02	1.10	32.60	100.4	0.77	0.33	0.000	na
23 Polychaetes	2.28	18.1	1.00	4.00	0.51	0.25	0.000	na
24 Echinoderms	2.59	10.3	0.55	2.20	0.82	0.25	3.6 × 10 ⁻⁵	na
25 Bivalves	2.18	8.58	0.57	6.33	0.95	0.09	0	SH
26 Other benthos	2.09	13.4	2.50	12.50	0.44	0.20	2.4 × 10 ⁻⁵	na
27 Bacteria	2.00	1.72	11.10	170.2	0.20	0.07	–	–
28 Ice algae	1.00	2.30	149.5	–	0.84	–	–	–
29 Phytoplankton	1.00	3.71	172.4	–	0.41	–	–	–
30 Detritus	1.00	14.8	–	–	0.61	–	–	–

^aTrophic level (TL), biomass in the model area (B in t·km⁻²), production/biomass (P/B in year⁻¹), consumption/biomass (Q/B in year⁻¹), ecotrophic efficiency (EE), production/consumption (P/Q), and landings (t·km⁻²).

^bValues estimated by Ecopath are in italics; values adjusted during model balancing are in bold. Some parameters were not possible to calculate (–).

^cNot available or not known (na); subsistence harvest (SH); commercial fishery (CF). Subsistence harvest includes use as meat, but also skin, fur, bone, and other body parts depending on the species.

The control difference matrix allows us to compare the strength of pairwise relationships from the perspective of the donor or recipient group (Figure 5). The highest magnitudes of control were exerted by narwhal, bowhead whale and Greenland shark as prey for killer whales, and ringed seal as prey for polar bears. Cephalopods also exerted control over Greenland shark. Greenland halibut,

the only commercial fishery species in the area, seems to be controlled to a certain extent by its main predator, narwhal, but overall does not strongly influence the system.

Considering only consumers, the SURF index was above the threshold distinguishing key from non-key forage species for carnivorous zooplankton, bivalves, *Calanus*

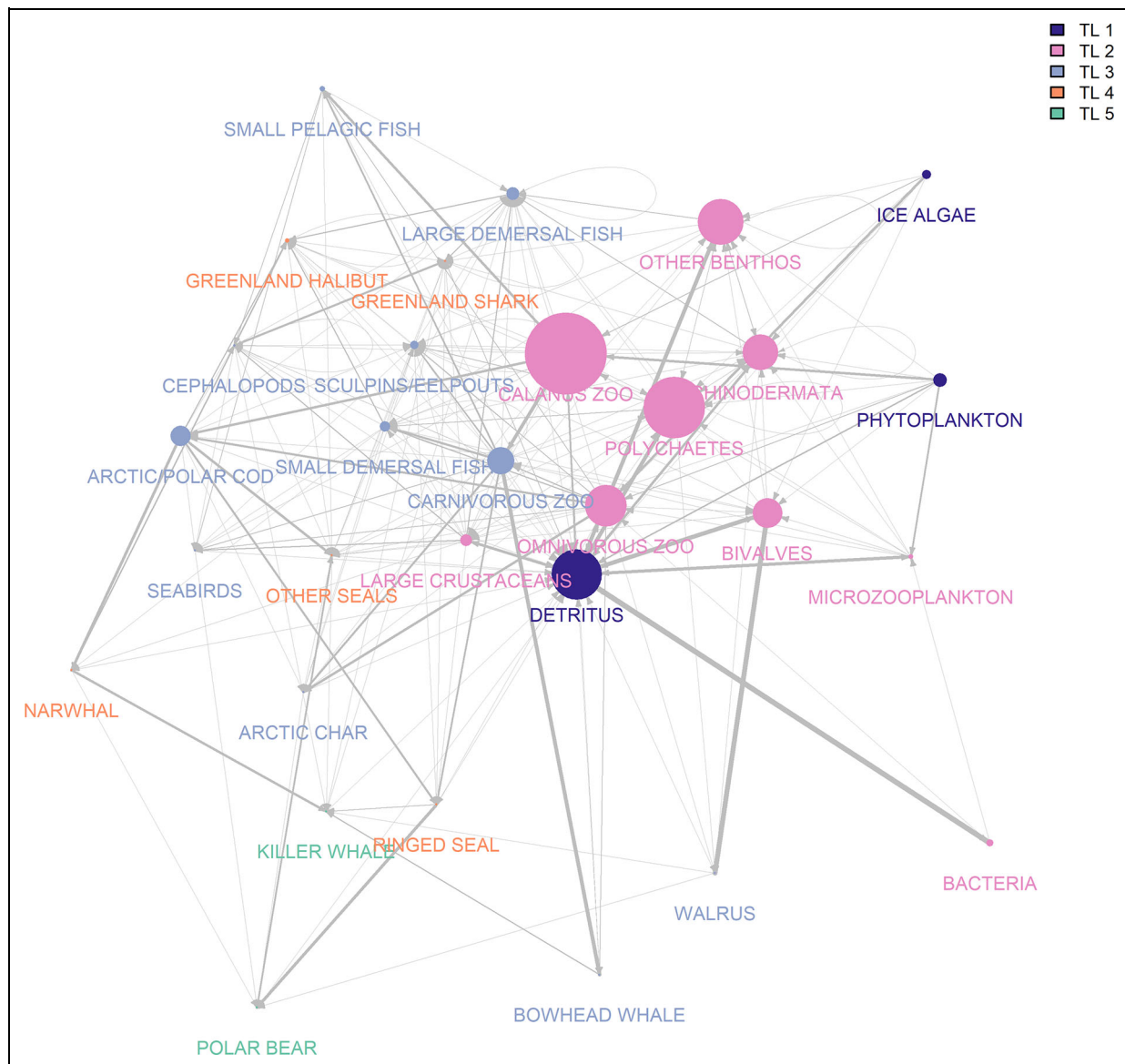


Figure 2. Representation of the western Baffin Bay shelf and coastal food web interactions. The area of the nodes represents relative biomass, while different colors indicate trophic level. The thickness of the links represents the percent contribution to predator diet, indicated by arrows.

copepods, omnivorous zooplankton, Arctic/polar cod, and cephalopods (Figure S2), from highest to lowest. Among fish functional groups, the SURF index calculated for Arctic/polar cod was one order of magnitude above any other.

Discussion

The present model revealed that forage fishes (especially Arctic/polar cod, small pelagic and small demersal fishes), cephalopods, and mammals (except for top predators) have a key role in the western Baffin Bay coastal and shelf food web, confirming the importance of a few intermediate trophic level species channeling energy in Arctic ecosystems (Whitehouse et al., 2014; Murphy et al., 2016). Intermediate trophic levels are prey for culturally important species in the region, and therefore climate and other environmental changes threatening the fitness of these species may affect the whole food web, including subsistence harvest species. The ENA index

robustness suggests that the WBB ecosystem presents a balance between its capacity for resilience and resistance to perturbations, with exploitation from subsistence harvest and commercial fisheries within a sustainable range, rendering the dynamics of this ecosystem overall sustainable. Yet, many gaps in scientific knowledge persist regarding the ecology and seasonality of key components of the WBB food web.

The WBB food web

Understanding the structure of the ecosystem and how the functional groups interact from a holistic perspective provides useful information regarding local food resources for Inuit (Steiner et al., 2019). The control analysis of our model indicated that small fish and other intermediate trophic levels, like cephalopods and many marine mammals, play a central role in controlling the movement of energy through the food web. Arctic ecosystems are

Table 4. Ecological network analysis (ENA) indices and uncertainty range calculated for the western Baffin Bay coastal and shelf ecosystem, including range of values reported for Arctic and Antarctic ecosystems

ENA Index	Average for the WBB Model (Minimum–Maximum)	Arctic Ecosystems ^a	Antarctic Ecosystems ^b
TST (t km ⁻² year ⁻¹)	4,255 (2,796–4,955)	1,719–19,845	na ^c
AMI	1.54 (1.45–1.67)	na	1.11–1.44
Ascendency	8,378 (5,831–10,061)	na	na
Relative ascendency (A/C)	0.310 (0.290–0.349)	0.24–0.27	0.414–0.472
Robustness	0.363 (0.359–0.367)	na	na
APL	3.59 (3.22–4.16)	3.17–4.73	3.08–4.82
FCI	0.160 (0.118–0.220)	0.034–0.136	0.081–0.292
IFI	0.504 (0.445–0.576)	na	0.60–0.77
Number of functional groups	30	33–140	24–38
Model area (1,000 k ²)	81.4	109–1400	45–637

^aBased on models from the Beaufort Sea, Chukchi Sea, Barents Sea, Eastern Bering Sea, and Gulf of Alaska (Sora et al., 2022).

^bBased on models from South Georgia, West Antarctic Peninsula, Ross Sea, and Prince Edward Islands (based on original models in Hill et al., 2021).

^cNot available (na).

characterized by low metazoan diversity and the dominance of a small number of fish species, connecting low trophic levels to predatory fish, marine mammals, and seabirds (Whitehouse et al., 2014; Murphy et al., 2016). The importance of intermediate trophic level groups in the WBB food web suggests that it could be a wasp-waist controlled system, where not only fish but mostly marine mammals and cephalopods control the abundance of predators through a bottom-up interaction, and the abundance of prey through a top-down interaction (Cury et al., 2000; Fauchald et al., 2011; Griffiths et al., 2013).

Among fish, Arctic and polar cods are the most important in the WBB, being key prey in this ecosystem (Plagányi and Essington, 2014). Arctic cod is one of the most abundant fish in the Arctic, with thousands preyed upon by predatory fish like Greenland halibut, seabirds, and marine mammals (Welch et al., 1993; Hop and Gjøsaeter, 2013; Steiner et al., 2019), some of which are part of the Qikiqtarjuaqqi subsistence harvest (Priest and Usher, 2004). Due to this role in energy flow from lipid-rich copepods to upper trophic levels, Arctic cod has been characterized as a key prey or keystone species in other Arctic ecosystems (Hop and Gjøsaeter, 2013; Whitehouse et al., 2014; Steiner et al., 2019; Sora et al., 2022). Disruptions in the Arctic cod life cycle caused by ongoing changes in sea ice conditions have already led to shifts in diet for predators like beluga, ringed seal, and seabird species, with concurrent declines in predator body condition in some cases in the Hudson Bay, the Beaufort Sea and the European Arctic (Gaston et al., 2003; Provencher et al., 2012; Divoky et al., 2015; Harwood et al., 2015; Vihtakari et al., 2018; Choy et al., 2020), making important an understanding of how climate change may affect this species.

Our results not only support the known role of Arctic cod as prey in Arctic ecosystems, but more importantly, we highlight the role of other functional groups like zooplankton, cephalopods, and bivalves as prey (or ecosystem controllers) in the WBB food web. Abundant herbivorous zooplankton, such as *Calanus* copepods, promptly convert carbon from primary production into high-energy lipid compounds, which are stored in their bodies and then channeled up the food chain, being the major source of energy for many fish, marine mammals and seabirds (Falk-Petersen et al., 2000; Berge et al., 2012). Yet, the role of mollusks like cephalopods and bivalves are generally less understood. In the WBB their importance as prey may be related to the dependency of Greenland shark on cephalopods (45% of their diet), and walrus on bivalves (94% of their diet) as prey. The uncertainty related to the diet of predators in the region, aggravated by poor understanding of seasonal variation and poor knowledge on the ecology of cephalopods and bivalves, underlines the need for more research on the role of these key groups in Arctic ecosystems.

Top predators (killer whales and polar bears) seem to be controlled by their prey in the system. Sightings of killer whales in the eastern Canadian Arctic have been increasing, indicating a more constant or greater presence in local ecosystems, likely as a consequence of a longer ice-free season and abundance of marine mammal prey (Higdon et al., 2014). Killer whales can cause cascading pressures in other ecosystems (e.g., Subramaniam et al., 2020), and may already be affecting the migration patterns of narwhal and bowhead whale populations in the eastern Canadian Arctic (Lefort et al., 2020a; Matthews et al., 2020). In our model, we considered a low biomass of killer whales because sightings have been less frequent in the

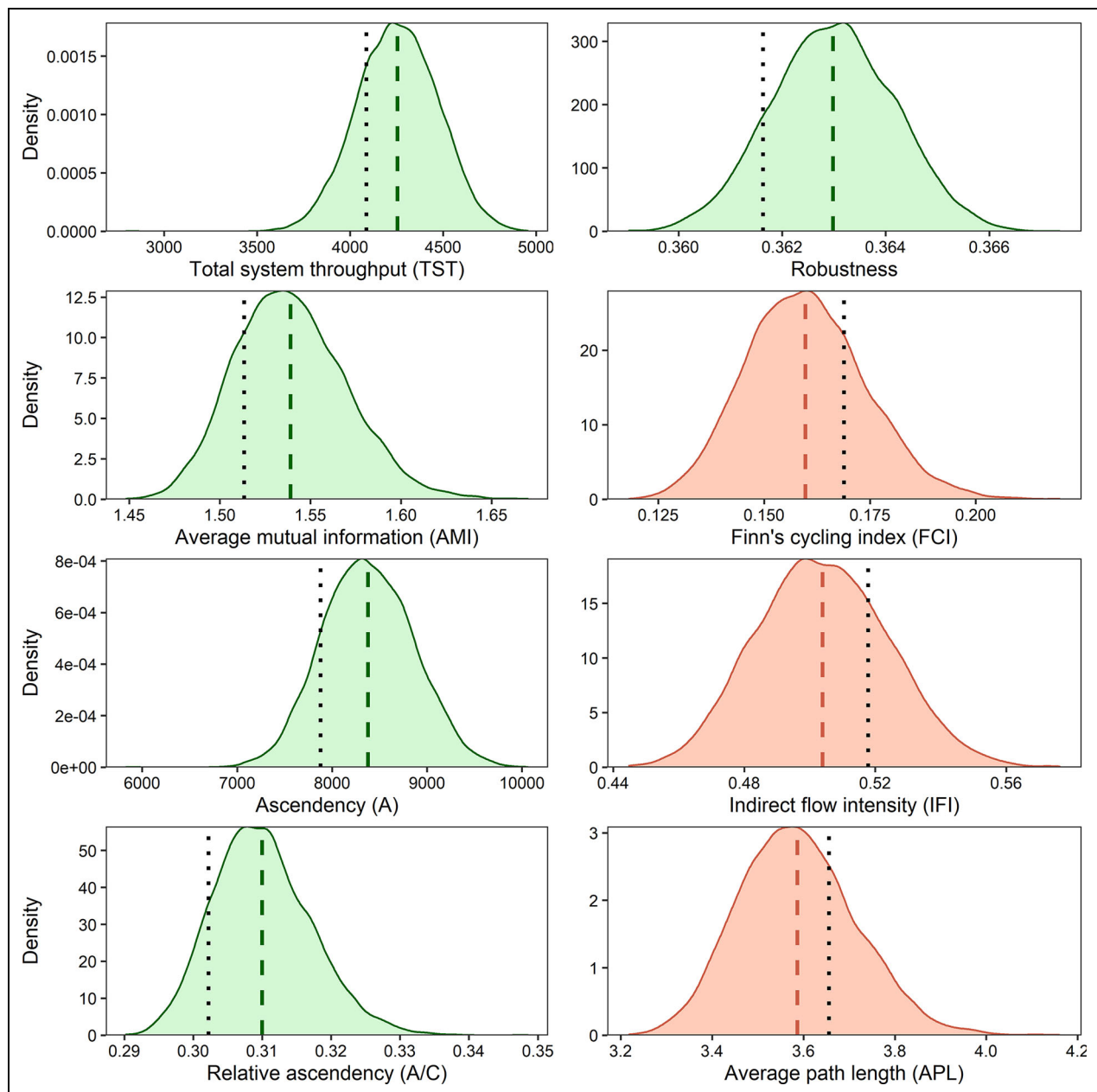


Figure 3. Distributions of ecological network analysis indices in the western Baffin Bay food web. In these probability density plots, using data-guided uncertainty, the dotted black lines correspond to the ecological network analysis (ENA) indices from the original model of the western Baffin Bay shelf and coastal food web, while the dashed colored lines show the average value from ENA results based on the uncertainty distributions. Green represents size, growth, and development indices, while orange represents cycling indices.

WBB compared to other Arctic regions (Lefort et al., 2020b), which could also explain the bottom-up control on killer whales in this ecosystem. As for polar bears, the control relationship between polar bear and ringed seal in the WBB food web supports current understanding regarding the tight predator-prey relationship between these species (Galicia et al., 2021). This tight link, and the increasing difficulty of catching seals, has led to consequences to the body condition of Baffin Bay polar bears (Laidre et al., 2020). More specifically, as the ice-free season becomes longer, bears spend more time on land, a period in which ice-associated seals are not accessible and polar bears are reliant on stored energy reserves

(SWG, 2016b; Laidre et al., 2020). Continued sea ice loss could eventually lead to demographic consequences for polar bears, including reduced adult survival (Molnár et al., 2010).

In terms of the overall impact of fisheries, our results showed that the subsistence harvest and commercial fisheries, which tend to target higher trophic levels, may be within sustainable levels. Primary production required to sustain fisheries has been conceived as an ecological footprint. Percent PPR, as a part of total primary production, in combination with trophic level of the catch, provides a quantitative ecosystem index to capture the sensitivity of an ecosystem to fisheries (Tudela et al., 2005). In the

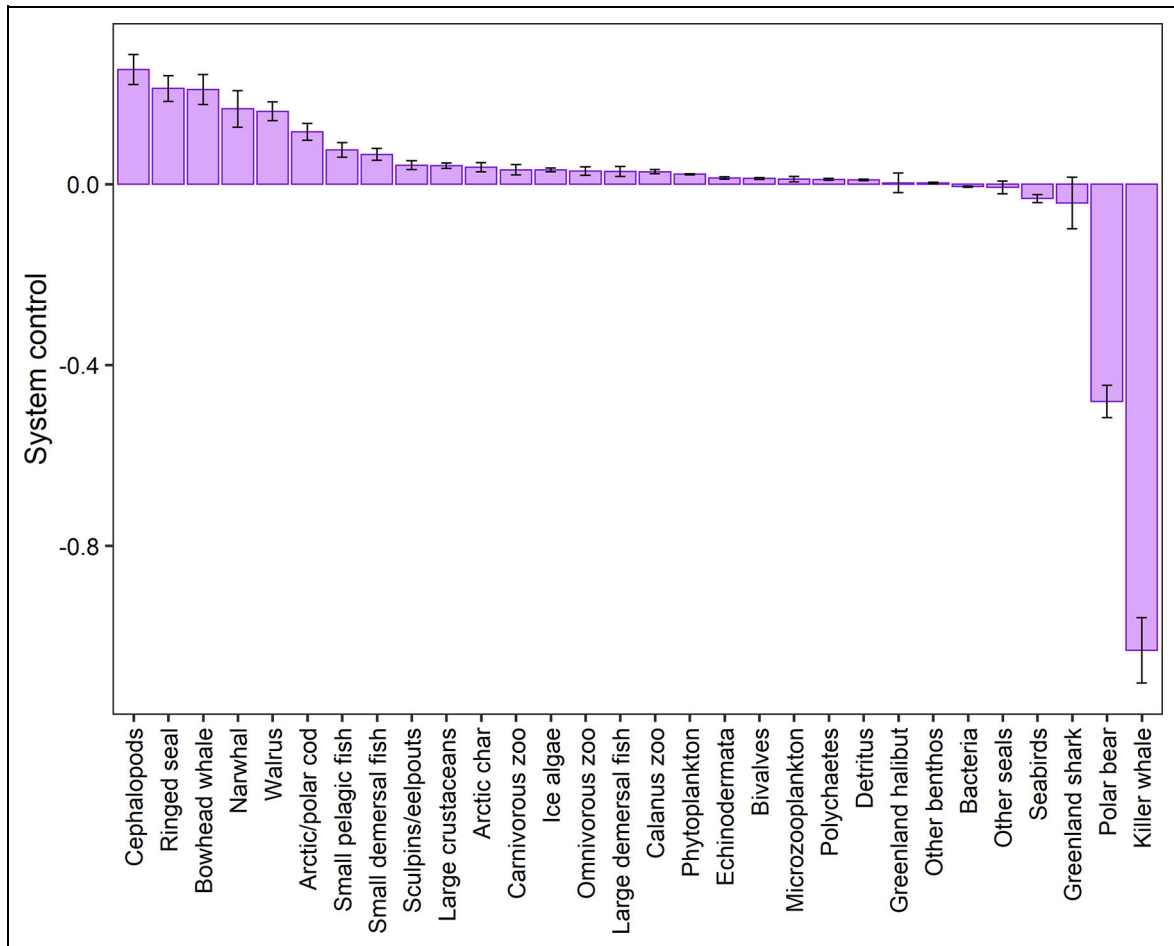


Figure 4. System control vectors for the western Baffin Bay shelf and coastal food web. Error bars represent the standard deviation based on the distributions from the 10,000 plausible models based on the uncertainty analysis. Positive values indicate that the groups control the system, while negative values indicate the groups are controlled by the system.

WBB, the low catch/TST, high trophic level of the catch and moderate %PPR to export indicate that the fishery and harvest during the modeling period were within a sustainable range (comparatively, a low TLC with the same %PPR or higher may result in ecosystem overfishing; Tudela et al., 2005).

Ecosystem holistic properties

Polar food webs are described as systems with restricted energy flows to higher trophic levels through one or two mid-trophic level species, suggesting low functional redundancy and high organization (Murphy et al., 2016). The amount of biomass production in the WBB, indicated by the TST, was comparable to that of other shelf Arctic ecosystems, and within values found for coastal, shelf and slope ecosystems globally (which are on the lower side compared to more productive reefs, for example; Heymans et al., 2014; Sora et al., 2022). In the WBB, relative ascendancy was close to, but below the optimal value of approximately 0.37 suggested in ecological network theory. Compared to other ecosystems, the WBB had relative ascendancy just slightly higher than other Arctic ecosystems, but lower than in the Antarctic, and lower than neighboring oceans such as the East Atlantic and North

and Baltic seas (Heymans et al., 2014; Hill et al., 2021; Sora et al., 2022). These results suggested that efficiency in energy transfer between species can still improve in this and other Arctic food webs. In other words, the transfer of biomass through species feeding relationships can be more efficient (with less energy loss) and avoid functional redundancy when, for instance, several species have the same role as prey in the food web as opposed to a predator being dependent on one or just a few species for food. But lower efficiency also suggests that predators tend to have more flexible diets, as biomass flows are not concentrated in a few organized paths; this scenario is consistent with the limited number of strong relationships observed in our control analysis (Figure 5). Therefore, our results suggest that there may be more flexibility in the WBB food web flow paths than is assumed for Arctic ecosystems in a global context, without completely dismissing the central role of mid-trophic level species channeling energy, such as cephalopods, marine mammals, and Arctic cod. In any case, values of robustness and relative ascendancy of the WBB food web suggest that this system is sustainable, with the trade-offs between resistance (efficiency) and resilience (redundancy) being within what is considered optimal balance (Figure S1).

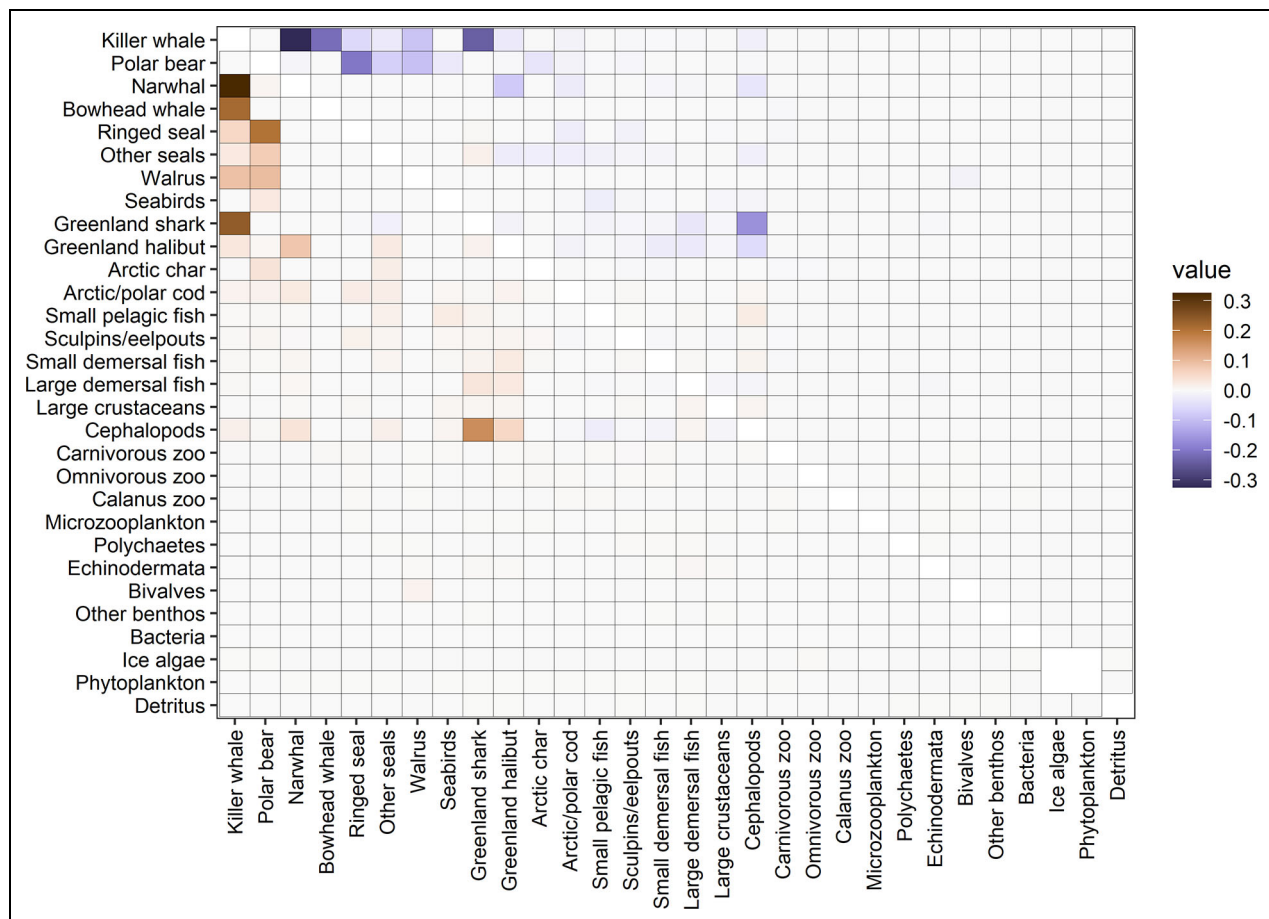


Figure 5. Control difference matrix for the western Baffin Bay coastal and shelf food web. Darker values indicate stronger pairwise relationships. The values are negative (purple) when the group on the y-axis is being controlled by the group on the x-axis, and positive (orange) when the group on the y-axis controls the group on the x-axis.

Cycling allows the use of biomass stored in detritus by living organisms, thus allowing biomass to circulate in the system again, which renders the system more efficient. In the WBB, the FCI was relatively high compared to the Beaufort Sea ecosystem, and more comparable to the Barents Sea and Antarctic ecosystems (Hill et al., 2021; Sora et al., 2022). Higher FCIs have been found in smaller compared to larger ecosystems (Heymans et al., 2014). Yet, this index was above the range found for ecosystems of its size throughout the globe, being more comparable to that of ecosystems of 10–1,000 km². Both bacteria and detritivory by zooplankton play important roles in biomass cycling processes in food webs, affecting the FCI (Saint-Béat et al., 2018; Saint-Béat et al., 2020). Higher values found in WBB compared to similar ecosystems could be related to the way that these processes were considered in other Ecopath models, which did not always include the microbial loop. Here, we built on pelagic planktonic models developed for the region (Saint-Béat et al., 2020) that considered these processes in more detail. High recycling tends to be associated with high retention of biomass in the system (APL), but high retention was not the case for the WBB food web which had a higher FCI but APL within values found for other polar ecosystems. This difference had already been observed by Saint-Béat et al. (2020) who,

comparing the planktonic food web of the WBB with eastern Baffin Bay, suggested that in the WBB recycled biomass goes through shorter cycles, with a small amount of recycled biomass reaching high trophic levels.

The IFI indicates the importance of indirect effects in an ecosystem, or the ability of one functional group to influence another without directly interacting with it (direct effects being, for example, polar bear eating ringed seal; Borrett et al., 2006; Chen et al., 2011). In the WBB, indirect flows represent around half of the TST, indicating that indirect effects are important in this food web. As no indirect effects were observed clearly in the control analysis, such effects may be more associated with recycling or other processes (Borrett et al., 2006). While a high IFI can increase the resistance of an ecosystem to change, it also increases its complexity, making it harder to predict in what way an ecosystem will react to perturbations.

Knowledge gaps and uncertainty in a data-poor system

Uncertainty in input parameters in this model reveals the knowledge gaps that persist for many groups of organisms, especially fish and benthos. The ENA indices calculated without considering uncertainty in input parameters tended to consistently underestimate size and development

indices, and overestimate cycling indices, relative to the mean of the uncertainty distributions. Although the values without uncertainty fell within the uncertainty-based distributions, these results highlight the importance of considering uncertainty when deriving ENA indices and when using the model for scenario testing.

The biomass of most fish groups was estimated by Ecopath due to the lack of readily available data on the abundance of fish populations in WBB. As for diet composition, there are virtually no local dietary studies for fish and benthos in WBB; as a result, we adapted fish diets in the model based on stomach contents for several fish species in other Arctic regions and used qualitative diet reported for benthic species. Additionally, estimates of P/B and Q/B for benthic invertebrates were taken from other Arctic ecosystem models in the absence of system-specific estimates, contributing to the overall low pedigree score.

Despite the importance of ringed seal, Arctic char, and some mollusks like clams for Inuit subsistence harvest (Priest and Usher, 2004), the ecology of these species in the greater WBB is not well documented. For example, we did not include clams in a separate functional group due to the lack of data on the harvested species (large-scale abundance, diet composition, etc.), while for ringed seal, the only large-scale abundance estimates existent in the area are extrapolated from polar bear abundance and predation rates (Kingsley, 1998). For other groups, like seabirds, abundance estimates exist, but date from the 1970s and do not comprise all seabird species that frequent the area (Mallory et al., 2019). Another source of uncertainty common to other Arctic ecosystems is related to the sea ice seasonality, especially with regards to primary production, marine mammal, and seabird migratory species. Assuming a year-average primary production could be masking how limiting may be the availability of primary producers, and consequently zooplankton, for the whole ecosystem in winter months. Further, our results could be biased by diet studies that have only sampled species in the summer or the breeding season, potentially masking species interactions that may occur only in the winter. For example, the importance of cephalopods and bivalves as controllers and/or key prey in this ecosystem could be a result of this bias, as there is seasonal and regional uncertainty on the diets of Greenland shark and walrus (their main predators, respectively). Species like narwhal and bowhead whale feed intensely in some areas of their migratory routes, while in other areas they just pass through or feed sporadically (Laidre and Heide-Jørgensen, 2005; Fortune et al., 2020). Yet, for migratory species, weighting the biomass by time spent in the area corrects for this uncertainty to some extent.

Towards knowledge co-production in modeling the WBB ecosystem

Traditional ecological knowledge (TEK; also called Inuit Qaujimaqatuaqangit in Inuktitut, or IQ) has been defined as a cumulative body of knowledge, practice, and values regarding the relationships between living organisms, and between organisms and their environment, acquired and

transferred through experience and observation, from generation to generation (Pearce et al., 2015). The few projects that have engaged local communities in ecosystem modeling have proved the efficiency of co-design in improving model structure (Bentley et al., 2019b) and the accuracy of model predictions (Bentley et al., 2019c; Sánchez-Jiménez et al., 2019), filling gaps in science knowledge, especially in data-poor systems (Bevilacqua et al., 2016; Bentley et al., 2019c; Cisneros-Montemayor et al., 2020), and identifying key players at the ecosystem level, such as stressors unknown to scientists (Rosa et al., 2014). Thus, despite the qualitative nature of TEK, it can provide complementary information to scientific evidence on the relative importance of food web relationships and temporal trends in species abundances and fisheries catches that can be used to improve model parameterization and fill in gaps in temporal trends.

To improve our understanding of the WBB ecosystem, we intend to gather TEK through interviews with Qikiqtarjumiut hunters and fishers, which will focus on filling gaps on, e.g. the relative abundance of species in the region, their migration patterns, and temporal trends, if there are any new species in the area, how environmental changes are affecting the species, and which species are most important for local harvest and commercial fisheries. Next, we will conduct workshops with different Qikiqtarjumiut representatives using the information from this Ecopath model of the WBB as input for discussions on changes in the system over time, and scenario development in Ecosim guided by Inuit perspectives and concerns. Distributions of ENA-derived indices for each scenario can be used to compare different states of the WBB ecosystem as a whole in a more accurate way. Among the indices reported here, we believe that control indices, the SURF index, mean trophic level of catch, and robustness may be of particular interest in future discussions. The mean trophic level of the catch can be useful to understand the impacts of the fishery at high trophic levels, such as important marine mammals for Inuit, because fishing pressure tends to deplete top predators more severely than lower trophic level species. In some instances, a decrease of this index indicates increased fishing pressure (Fath et al., 2019). The control analysis and the SURF index highlight important relationships between species, and the relevance of harvest species, as well as their prey, for the whole ecosystem. Robustness can be used to provide a holistic perspective on the impact of different scenarios on the overall ecosystem resiliency. For example, how will the role of key species change under different climate change scenarios? If key species are affected by climate change, what will happen to harvest species? How will marine mammals be affected if commercial fisheries intensify? Will the ecosystem be resilient to different climate conditions and fishing scenarios?

Conclusion

Ecosystem flow models and ENA indices are powerful tools to assess the status of marine ecosystems, and they are recommended increasingly in fisheries management and conservation (Safi et al., 2019). Given the holistic

approach of these models, they were recently proposed as a key tool to address the objectives of the United Nations Decade of Ocean Science and sustainable development (Heymans et al., 2020). This initiative calls for more inclusive and participatory approaches in designing and executing ocean science, bringing multiple sectors and disciplines to a dialogue, and developing innovative and accessible ways to communicate ocean science to achieve a sustainable and healthy ocean (United Nations, 2020). To achieve sustainable development and serve a societal purpose like that of supporting food security, ecosystem models should span physical and human drivers of change and be more transparent in terms of model limitations and uncertainties in predictions, highlighting the knowns and the unknowns. Further, co-design and engagement with a broader set of knowledge holders and model users should be ensured to increase the effectiveness of models in management and decision-making from community to regional scales (Safi et al., 2019; Heymans et al., 2020; Saltelli et al., 2020).

Here we have provided a preliminary ecosystem model of the WBB food web, summarizing the scientific knowledge of the region and thus taking a first step towards understanding this ecosystem. The overall uncertainty in model development propagating to ENA results indicates that many unknowns persist for fish and marine mammal species, groups that are key for the energy flow of this food web. Once refined with community partners in Qikiqtarjuaq, this model and ENA results will provide a foundation for discussions with community members to test scenarios of climate change and food security in the community and the region. In this way, we also hope to contribute to more transparent, inclusive, and participatory ocean science, and provide a framework that can be applied in other regions.

Data accessibility statement

The Ecopath model is available at the Ecopath consortium database for Ecopath with Ecosim models [<http://ecobase.ecopath.org/>]. A technical report with more detailed description of the parameters used in this model is also available at Université Laval's repository CorpusUL [<https://corpus.ulaval.ca/jspui/>].

Supplemental files

The supplemental files for this article can be found as follows:

Text S1. Tables S1–S13. Figures S1 and S2. Docx

Acknowledgments

We acknowledge our partners in Qikiqtarjuaq, the hamlet of Qikiqtarjuaq and hunters and trappers' association, who are active participants in this project. We also thank the valuable contribution of experts consulted during model development: Nigel Hussey, Steven Ferguson, Caroline Bouchard, Cory Matthews, Kyle Elliot, Marcus Dyck, Marianne Marcoux, Courtney Watt-Wheeler, Mark Mallory, and Margaret Treble. We thank the data contribution from the research programs Green Edge (M. Babin), ArcticNet and Amundsen Science (M. Geoffroy).

Funding

Funding for this project came from MEOPAR (2019–2022, to M. Lemire), CIHR (2019–2022, to L. Chan and M. Lemire), Sentinel North (2017–2022, to J-E. Tremblay and M. Lemire), ArcticNet (to M. Little and T-F. Kenny) and a Sentinel North postdoctoral fellowship (2020–2022, to S. Pedro). M. Lemire is the titular of the Littoral Research Chair, which is funded mainly by Sentinel North and the Northern Contaminant Programme (NCP) of the Crown-Indigenous Relations and Northern Affairs Canada (CIR-NAC). M. Lemire also received a salary grant from the Fonds de recherche du Québec – Santé (FRQS): Junior 1 (2015–2019), and Junior 2 (2019–2023). M. Lemire, F. Maps, S. Pedro, T-A. Kenny, G. Yunda-Guarin, J-E. Tremblay, M. Babin are members of Québec Océan.

Competing interests

J-E. Tremblay is an associate editor for Elementa. He played no role in the review process for this manuscript. The authors declare that there are no competing interests.

Author contributions

Contributed to the conception and design of the study: MeL, FM, T-AK, MaL, LC, SP.

Contributed to data acquisition and data cleaning: SP, M-AM, JB, CH, MB, J-ET, JH, MG, GY-G, BS-B.

Assembled the data and developed the ecosystem model: SP.

Contributed to data interpretation: SP, CH, BS-B, MYJ.

Led the drafting of the manuscript: SP.

Contributed to the discussion of the results and preparation of the manuscript and approved the submitted version for publication: All authors.

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How to cite this article: Pedro, S, Lemire, M, Hoover, C, Saint-Béat, B, Janjua, MY, Herbig, J, Geoffroy, M, Yunda-Guarin, G, Moisan, M-A, Boissinot, J, Tremblay, J-E, Little, M, Chan, L, Babin, M, Kenny, T-A, Maps, F. 2023. Structure and function of the western Baffin Bay coastal and shelf ecosystem. *Elementa: Science of the Anthropocene* 11(1). DOI: <https://doi.org/10.1525/elementa.2022.00015>

Domain Editor-in-Chief: Jody W. Deming, University of Washington, Seattle, WA, USA

Associate Editor: Julie E. Keister, School of Oceanography, University of Washington, Seattle, WA, USA

Knowledge Domain: Ocean Science

Published: February 16, 2023 **Accepted:** January 5, 2023 **Submitted:** January 26, 2022

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