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A temporal shift in trophic diversity among a predator assemblage in a warming Arctic

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Climate change is leading to northward shifts in species distributions that is altering interspecific interactions at low- and mid-trophic levels. However, little attention has been focused on the effects of redistributions of species on the trophic ecology of a high trophic-level predator assemblage. Here, during a 22-year period (1990–2012) of increasing sea temperature (1.0°C) and decreasing sea ice extent (12%) in Cumberland Sound, Nunavut, Canada, we examined the trophic structure of a near-apex predator assemblage before (1990–2002) and after (2005–2012) an increase in the availability of capelin—generally an indicator species in colder marine environments for a warming climate. Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were used in a Bayesian framework to assess shifts in diet, niche size and community-wide metrics for beluga whales (*Delphinapterus leucas*), ringed seals (*Pusa hispida*), Greenland halibut (*Reinhardtius hippoglossoides*) and anadromous Arctic char (*Salvelinus alpinus*). After 2005, consumption of forage fish increased for all predator species, suggesting diet flexibility with changing abiotic and biotic conditions. An associated temporal shift from a trophically diverse to a trophically redundant predator assemblage occurred where predators now play similar trophic roles by consuming prey primarily from the pelagic energy pathway. Overall, these long-term ecological changes signify that trophic shifts of a high trophic-level predator assemblage associated with climate change have occurred in the Arctic food web.

1. Introduction

Biodiversity within marine ecosystems varies across environmental gradients, of which temperature is one of the most important and can regulate functioning of marine ecosystems [1]. With lower productivity at the poles when compared to lower latitudes, polar ecosystems are more consumer- than resource-controlled [2]. This consumer control leads to lower food web complexity and decreased connectance [3]. However, a warming climate is currently altering global ecosystem structure and driving species distributions to higher latitudes, thereby leading to altered interspecific interactions with unspecified consequences [4,5]. Climate-driven ecosystem shifts are pronounced in the Arctic—the fastest warming region on the planet [6]. Changes to Arctic sea temperature and sea ice phenology have facilitated a punctuated poleward shift in the distribution of more temperate species including apex predators (e.g. killer whales *Orcinus orca* [7]), near-apex predators (e.g. harp seals *Pagophilus groenlandicus* [8]), forage fish (e.g. capelin *Mallotus villosus* [9]) and invertebrates (e.g. blue mussels *Mytilus edulis* [10]). This has led to observed and ongoing changes to Arctic ecosystem productivity, species abundances, population mixing and disease/pathogen transmission for its fauna [11,12].

Forage fish are small pelagic species that provide the most important conduit of energy transfer from phytoplankton and zooplankton to predators in global marine ecosystems [13]. In the Arctic, endemic Arctic cod *Boreogadus saida* facilitate the majority of energy transfer (up to approx. 90%) to seabirds and marine mammals [14] but are probably undergoing an associated decline in abundance and shifts in distribution across several regions with a warming climate [3,15–17]. Arctic cod are typically associated with colder water temperatures (less than 5°C) [18], therefore declining sea ice and a warming ocean, especially at lower latitudes, will continue to alter the timing of Arctic cod reproduction and larval development and lead to a northward retraction in its range [16]. This retraction in range is exacerbated by the northward expansion of competitors, such as more temperate capelin that is also one of the most-used forage fish by marine mammals and sea birds in the Barents Sea and waters near Newfoundland [19,20]. Capelin are considered a sea ‘canary’ for a warming climate in colder marine ecosystems as their presence and abundance generally increase with temperature [9]. Furthermore, capelin can spawn over a large range of latitudes (42–72° N), temperatures (1–14°C) and habitats (e.g. beach and deep-water spawning), signifying their high plasticity to environmental variability and change [21,22].

Opportunistic upper trophic-level predators act as sentinels to trophodynamic and species assemblage changes lower in the food web through their diet [23]. For example, thick-billed murre (*Uria lomvia*) of Hudson Bay and polar bears (*Ursus maritimus*) of East Greenland have shifted their diet from Arctic cod to capelin, and from ringed seals (*Pusa hispida*) to subarctic seal species (e.g. hooded seals *Cystophora cristata*), respectively [24,25]. However, the effects of climate-driven dietary shifts on the overall community structure of concurrent near-apex predators are generally unknown. Here, we examine the diet and isotopic niche of beluga whales (*Delphinapterus leucas*), ringed seals, Greenland halibut (*Reinhardtius hippoglossoides*) and anadromous Arctic char (*Salvelinus alpinus*) across a temporal scale that captures a rapid warming period and where capelin have become increasingly abundant since the mid-2000s [19] (A Fisk 2006, personal observation and R Kilabuk from Pangnirtung, Nunavut, 2011, personal communication).

Beluga whales, ringed seals, Greenland halibut and Arctic char all inhabit Cumberland Sound (Nunavut, Canada) a large inlet where summer sea temperatures have increased by 1.0°C since 1990 (see Results). Beluga whales consume forage fish (Arctic cod [26] and increasingly capelin [27,28]), Greenland halibut [29], squid and benthic invertebrates (decapods and amphipods [26,30]). Ringed seal and Greenland halibut diet consists of a wide variety of pelagic invertebrates including *Goniatid* squid [31,32] and forage fish (e.g. Arctic cod, capelin and sand lance [33–35]), while Arctic char consume invertebrates (e.g. amphipods and shrimp) and forage fish (e.g. herring and capelin [36]).

Stable isotope analysis of animal tissues provides time-integrated information on habitat use and diet and has become one of the principal tools to elucidate prey contributions to predator diet and spatio-temporal variation of trophic interactions among species [37]. Specifically, combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data have been used to quantify inter-annual variation and long-term changes in trophic structure of aquatic systems [38–40]. Stable isotopes consequently provide a proven tool to assess the impact of human-driven climate shifts on the structure and dynamics of predator communities in polar aquatic environments [37,41].

Here, we determine prey contributions to the diet of beluga whales, ringed seals, Greenland halibut and Arctic char, quantify predator niche sizes and apply six community-wide metrics to characterize the trophic structure of this near apex predator assemblage in Cumberland Sound, Nunavut, Canada

Table 1. Summary of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm s.d.), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges and median Bayesian standard ellipse area (SEA_B) by time period for predator species from Cumberland Sound, Nunavut, Canada.

common name	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ range (‰)	$\delta^{15}\text{N}$ range (‰)	SEA_B (‰ ²)
1990–2002						
beluga	47	-18.1 ± 0.3	17.2 ± 1.1	1.5	5.2	1.0
ringed seal	175	-18.7 ± 0.6	15.2 ± 0.9	3.3	4.8	1.7
Greenland halibut	14	-19.6 ± 0.7	16.6 ± 0.4	2.3	1.4	0.8
Arctic char	72	-20.0 ± 0.5	15.0 ± 0.7	2.2	2.7	0.9
2005–2012						
beluga	25	-18.3 ± 0.4	15.9 ± 0.8	1.3	3.0	1.0
ringed seal	53	-19.1 ± 0.5	15.0 ± 0.8	2.2	3.2	1.3
Greenland halibut	21	-19.4 ± 0.4	16.4 ± 0.7	1.7	2.5	0.7
Arctic char	122	-19.1 ± 0.6	15.0 ± 0.7	3.3	3.6	1.3

(65°13'0" N, 65°45'0" W). We provide the first empirical evidence of long-term (1990–2012) alteration to the trophic structure of a near-apex predator assemblage associated with changes in the composition of forage fish species availability coincident with a rapidly warming climate.

2. Material and methods

2.1. Environmental data

Mean summer sea surface temperatures in Cumberland Sound for the study period 1990–2012 (June–October) were obtained from National Oceanographic and Atmospheric Administration, Earth System Research Laboratory (<http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html>, accessed September 2016) at 1° latitude \times 1° longitude spatial resolution. Sea ice concentration for the Davis Strait was also estimated for the same period for the month of June—a month which mainly encompasses sea ice breakup in the area—using Canadian Ice Service's IceGraph 2.0 Tool (<http://iceweb1.cis.ec.gc.ca/IceGraph>, accessed September 2016).

2.2. Sample collections

To allow examination of a potential shift in predator diet, we separated all predator and prey sample collections into two time periods (1990–2002 and 2005–2012) to coincide with increased availability of capelin in Cumberland Sound (mid-2000s [19]). Inuit hunters inhabiting Southeast Baffin Island have not reported the occurrence of capelin in beluga whale stomachs in the 1990s despite their opportunistic feeding strategy [29], thereby supporting a recent shift in capelin availability. Division of the sampling period into these two time periods was further defined by a significant decrease in beluga whale $\delta^{15}\text{N}$ and sympagic carbon source use for both beluga whales and ringed seals after the early 2000s in Cumberland Sound [42,43]. Beluga whale and ringed seal muscle samples were collected during May–October by Inuit hunters in Cumberland Sound as part of their subsistence harvests during 1992–2009 and 1990–2011, respectively (table 1; see electronic supplementary material, table S1 for sample size by year per species). The beluga whale population inhabits Cumberland Sound year-round [44] and Cumberland Sound ringed seal movements are generally restricted during the summer (D Yurkowski 2011, unpublished data). Greenland halibut were captured from bottom longlines in western Davis Strait near the entrance to Cumberland Sound in September 1996 and again during August 2012 in the central region of Cumberland Sound. Arctic char were collected from gill nets set from shore at tidal flats in 2002, 2008 and 2011 in northern Cumberland Sound near Lake Kipisa and Isuituq, and stable isotope values were obtained from [45]. Year-round movements of Greenland halibut occur in Cumberland Sound [46] and at-sea movements of anadromous Arctic char are generally restricted [47]. Muscle samples from all predator species

represent long-term dietary integration of prey due to its slower turnover rate compared to more metabolically active tissues [48]. Stable isotope values of shrimp (*Pandalus borealis*) and Arctic cod were obtained from [49] which were caught from fishing vessel trawls in western Davis Strait near the entrance to Cumberland Sound in October 2000, 2001 and 2004. Arctic cod collected in 2004 were categorized in the 2005–2012 time period. Shrimp (*Lebbeus polaris*) and capelin samples were collected from Cumberland Sound in August 2007–2009. Owing to the unavailability of *Themisto* sp., a pelagic omnivorous invertebrate and common prey item for Arctic marine predators, *Goniatid* squid stable isotope values (caught September–October in 2001 and 2011) were used instead to represent this functional group (e.g. omnivorous invertebrate [50]). All predator and prey sample tissues were stored at -20°C prior to analysis.

2.3. Stable isotope analysis

Owing to the presence of lipids affecting fish and mammal tissue $\delta^{13}\text{C}$ values [51,52], frozen predator and prey samples were lyophilized for 48 h, homogenized using a mortar and pestle and lipid-extracted using 2:1 chloroform:methanol following the methods of [53]. Subsequently, 400–600 μg of predator and prey tissue were weighed into tin capsules and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured by a Thermo Finnigan DeltaPlus mass spectrometer (Thermo Finnigan, San Jose, CA, USA) coupled with an elemental analyser (Costech, Valencia, CA, USA) at the Chemical Tracers Laboratory, Great Lakes Institute for Environmental Research, University of Windsor. Stable isotope ratios are expressed in per mil (‰) in delta (δ) notation using the following equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where X is ^{13}C or ^{15}N and R equals $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The standard reference material was Pee Dee Belemnite carbonate for CO_2 and atmospheric nitrogen N_2 . A triplicate was run for every 10th sample, and a measurement precision for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was 0.1‰ and 0.1‰, respectively. The instrumentation accuracy was determined based on NIST standards 8573, 8547 and 8548 for $\delta^{15}\text{N}$ values and 8542, 8573, 8574 for $\delta^{13}\text{C}$ values ($n = 75$ for all). The mean differences from the certified values were $\leq 0.1\text{‰}$ for $\delta^{15}\text{N}$ values and $\leq 0.1\text{‰}$ for $\delta^{13}\text{C}$ values.

2.4. Data analysis

To examine shifts in environmental parameters over the study period, linear regression of sea surface temperatures and logit-transformed sea ice concentration versus year (1990–2012) were performed. Alpha was set to 0.05. To quantify prey contributions to focal predators (beluga whale, ringed seal, Greenland halibut and Arctic char) over the two defined study periods, we used Bayesian mixing model analysis in SIAR v. 4.2.2 [54] in R v. 3.3.2 [55] with uninformative priors. These mixing models were run at 500 000 iterations, a burn-in of 300 000 and thinned by 100 (see table 2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each prey and electronic supplementary material, figures S1 and S2 for stable isotope bi-plots). Prior to analysis, we assessed normality of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using a χ^2 quantile–quantile plot for each predator species. As capelin and Arctic cod are a part of the same functional group (i.e. forage fish) and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the two species were similar (capelin: mean \pm s.d.; $-19.5\text{‰} \pm 0.3$ and $13.8\text{‰} \pm 0.5$; Arctic cod: $-20.4\text{‰} \pm 0.5$ and $13.7\text{‰} \pm 1.1$, respectively), these prey items were combined to reduce the total number of prey sources to four and allow a more constrained, diffuse solution [56]. For ringed seals and beluga whales, we used known diet tissue discrimination factors (DTDF) for phocid muscle ($\Delta^{13}\text{C}$: 1.3‰, $\Delta^{15}\text{N}$: 2.4‰ [57]) and cetacean muscle ($\Delta^{13}\text{C}$: 1.3‰, $\Delta^{15}\text{N}$: 1.2‰ [58]), respectively. We estimated DTDFs for Greenland halibut and Arctic char muscle using linear models from meta-analysis of fish muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relative to diet isotope values; 1.2‰ for $\Delta^{13}\text{C}$ and 2.1‰ for $\Delta^{15}\text{N}$ [59,60]. Following the recommendation of [54], we incorporated variability in DTDFs (standard deviation = 0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for each species (see the electronic supplementary material for other practical assumptions). As well, few individuals who did not fall within simulated mixing polygons (i.e. statistical outliers) were removed prior to mixing model analysis (see [61]; electronic supplementary material, figures S3 and S4). We estimated the probability that contributions of forage fish to each predator diet were higher in 2005–2012 than 1990–2002 by calculating the percentage of estimates from the posterior probability distribution that were higher in 2005–2012 than 1990–2002 relative to the total number of estimates from the posterior probability distribution (2000).

To examine variation in isotopic niche sizes and relative niche position for each predator species over the two study time periods, standard ellipses were estimated using the SIBER package v. 2.0.3 [62] in R which also uses Bayesian inference. Each ellipse represents the variance and covariance of x and y

Table 2. Mean \pm s.d. of $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values for potential prey items and their median contribution (95% Bayesian credible interval) to predator diet by time period from Cumberland Sound, Nunavut, Canada.

common name	species name	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	contribution to beluga diet (%)	contribution to ringed seal diet (%)	contribution to Greenland halibut diet (%)	contribution to Arctic char diet (%)
1990–2002								
squid	<i>Gonatilid</i> sp.	7	-20.3 ± 0.9	11.4 ± 0.9	1 (0–4)	64 (60–68)	6 (0–18)	59 (47–71)
shrimp ^b	<i>Pandalus borealis</i>	10	-18.7 ± 0.5	13.3 ± 1.0	19 (3–33)	6 (0–14)	13 (0–38)	11 (0–33)
Arctic cod ^b	<i>Boreogadus saida</i>	8	-19.2 ± 0.5	14.1 ± 1.2	15 (1–36)	12 (1–23)	79 (55–97)	29 (10–44)
Greenland halibut	<i>Reinhardtius hippoglossoides</i>	14	-19.6 ± 0.7	16.6 ± 0.4	63 (51–74)	19 (13–24)	—	—
2005–2012								
squid	<i>Gonatilid</i> sp.	5	-19.8 ± 0.6	11.2 ± 1.3	14 (0–31)	48 (39–58)	2 (0–8)	34 (29–39)
shrimp ^a	<i>Lebbeus polaris</i>	7	-18.2 ± 0.2	13.9 ± 0.4	8 (0–18)	1 (0–4)	2 (0–10)	1 (0–2)
Arctic cod/capelin ^a	<i>Boreogadus saida</i> / <i>Mallotus villosus</i>	22	-20.0 ± 0.4	13.7 ± 0.8	35 (3–56)	49 (34–60)	95 (87–100)	66 (61–71)
Greenland halibut	<i>Reinhardtius hippoglossoides</i>	21	-19.4 ± 0.4	16.4 ± 0.7	42 (27–63)	2 (0–9)	—	—

^aSource [30].

^bSource [49].

thereby containing approximately 40% of the total data [62]. The niche ranges measured by the highest and lowest individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were calculated for each species separately. This allowed the ability to discern which predator species contributed more to the temporal changes in isotope values of the predator assemblage. We estimated the Bayesian standard ellipse area (SEA_B ; iterations = 2 000 000, burn-in = 100 000, thin by = 10) for statistical comparisons among predators. To examine differences in SEA_B between both time periods, we calculated percentage of estimates from the posterior probability distribution for SEA_B that were lower in 2005–2012 versus 1990–2002 relative to the total number of estimates from the posterior probability distribution (10 000).

Six community-wide metrics representative of the interactions among the realized niches of the four-predator species assemblage were also estimated using SIBER with Bayesian inference. These metrics include total extent of spacing within $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space and the relative trophic position of the predator assemblage to provide a measure of trophic diversity and redundancy. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges measure the distance between the two individuals with highest and lowest values, and thus represent the variability in basal carbon source and relative trophic position of the predator assemblage. Mean distance to centroid is the mean Euclidean distance of each species' niche to the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ centroid of the predator assemblage and represents the overall degree of trophic diversity. Mean nearest neighbour distance is the mean Euclidean distance to each species' nearest neighbour in isotopic space, thereby representing density of species packing where species with similar trophic ecologies (i.e. trophic redundancy) exhibit smaller mean nearest neighbour distances. Standard deviation of the nearest neighbour distance is the standard deviation of Euclidean distance of each species to its nearest neighbour and thus represents packing of species in isotopic space and trophic redundancy. Total community area was modified by calculating the total isotopic area among the means of each species' niche and thus is less biased to convex hull extremities [63]. Total community area is used as a proxy for the total extent of trophic diversity within the predator assemblage. All six metrics were derived from 2 000 000 iterations, a burn-in of 100 000 and thinned by 10 leaving 10 000 posterior estimates from the posterior probability distribution. To determine differences in community-wide metrics between both time periods, we quantified the percentage of estimates from the posterior probability distribution that were lower in 2005–2012 versus 1990–2002 relative to the total number of estimates from the posterior probability distribution (10 000). The ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of selected prey sources between both time periods were similar allowing a comparison of the community-wide metrics between both time periods (table 2). To eliminate bias associated with DTDF variability by taxa, body size and diet [59], all focal predator isotope values were corrected with designated DTDFs prior to trophic structure analysis. In regard to the division of sampling periods (1990–2002 and 2005–2012) and increased capelin availability in the mid-2000s, similar results of analyses described above from 2007–2012 are provided in the electronic supplementary material.

3. Results

Over the entire study period (1990–2012), there were marked shifts in sea ice concentrations in the Davis Strait and summer sea surface temperatures within Cumberland Sound; a 12% decline in sea ice extent (slope = -0.025 , intercept = 49.30, $r^2 = 0.23$, $p = 0.02$) occurred and an increase in temperature of 1°C was found (slope = 0.043, intercept = -85.50 , $r^2 = 0.24$, $p < 0.001$).

A comparison of the posterior distributions of prey items from stable isotope mixing models revealed that Cumberland Sound beluga whale diet consisted predominantly of Greenland halibut during both focal time periods, but there was a 94% probability that its contribution to diet decreased between 1990–2002 and 2005–2012 (table 2 and figure 1). Concomitantly, the probability of increased forage fish in the diet of beluga whales between 1990–2002 and 2005–2012 was 81% (table 2 and figure 1). Ringed seal diet consisted of both squid and forage fish, but similar to beluga whales, a probability of increased consumption of forage fish was greater than 99% from 1990–2002 to 2005–2012. In turn, the probability of a decreased squid contribution to ringed seal diet between the two time periods was greater than 99% (table 2 and figure 1). The probability of an increased forage fish contribution to Greenland halibut diet between 1990–2002 and 2005–2012 was 97% where their diet principally consisted of forage fish (95%; Bayesian credible intervals: 87–100; table 2 and figure 1). For Arctic char, the probability of increased consumption of forage fish in their diet from 1990–2002 to 2005–2012 was greater than 99% (table 2 and figure 1).

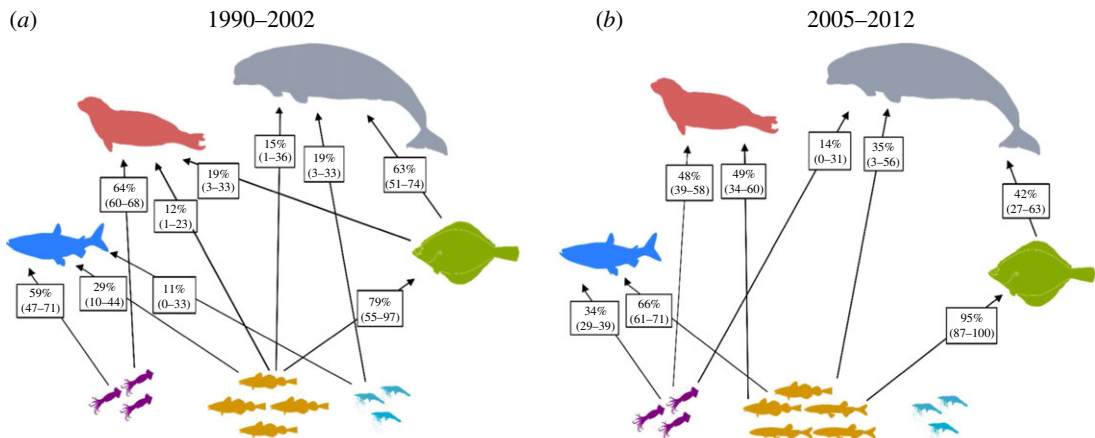


Figure 1. Stable isotope mixing model results depicting the median contributions (95% Bayesian credible intervals) of prey $\geq 10\%$ to beluga, ringed seal, Greenland halibut and Arctic char diet from 1990–2002 to 2005–2012 from Cumberland Sound, Nunavut, Canada. Species symbols represent beluga (grey), ringed seals (pink), Greenland halibut (green), Arctic char (blue) squid (purple), shrimp (blue) and forage fish (Arctic cod during 1990–2002 and Arctic cod/capelin during 2005–2012; yellow).

The probability that SEA_B size for ringed seals became smaller between the two time periods was 95%, whereas the probability that SEA_B size for Arctic char increased over time was 99%. By species, isotopic niche shifts occurred along the $\delta^{13}C$ -axis for Greenland halibut and Arctic char and along the $\delta^{15}N$ -axis for beluga whales (figure 2). Furthermore, the $\delta^{13}C$ range of Greenland halibut and ringed seals decreased by 0.6 and 1.1‰, respectively, between 1990–2002 and 2005–2012, while the $\delta^{15}N$ range increased by 1.1‰ for Greenland halibut, and decreased by 1.6 and 1.1‰ for ringed seals and beluga whales, respectively (table 1). For Arctic char, the $\delta^{13}C$ and $\delta^{15}N$ ranges increased by 1.1 and 0.9‰, respectively, between 1990–2002 and 2005–2012 (table 1).

3.1. Temporal changes in community structure of an Arctic predator assemblage

All six community-wide metrics of trophic structure were lower in the most recent sampling period (2005–2012) than the 1990–2002 time period (figure 3). By analysing the posterior distribution, the probability of lower $\delta^{13}C$ (i.e. variability in basal carbon source use) and $\delta^{15}N$ (i.e. relative trophic position) ranges for the predator assemblage in 2005–2012 was greater than 98% (figures 2 and 3). The probability of mean distance to centroid, mean nearest neighbour distance and total area being lower in 2005–2012 compared to 1990–2002 were all greater than 99%, identifying a decrease in trophic diversity and higher trophic redundancy among the predator assemblage over time (figures 2 and 3). The probability of a decrease in the standard deviation of nearest neighbour distance in 2005–2012 was 50% (figures 2 and 3).

4. Discussion

With a warming ocean and continuing reduction in sea ice extent, Arctic marine ecosystems continue to face multiple abiotic and biotic stressors that are impacting species interactions and overall ecosystem structure and function [11,64]. While temporal shifts in diet related to climate have been documented for several endemic upper trophic-level predators in the Arctic [24,25], our study provides evidence for a simultaneous isotopic niche shift of several sympatric higher trophic position predators over the past two decades. The observed predator assemblage shifts are associated with interactions among abiotic and biotic variables including decreased sea ice concentration, increased summer sea surface temperature and changes to forage fish species composition in Cumberland Sound over the 22-year period. Our stable isotope mixing model estimates, which represent the proportional contributions of prey to predator diets, demonstrate that the predator assemblage now consumes more pelagic forage fish during 2005–2012 than 1990–2002 probably through increased capelin availability, an expanding species from the south. These temporal shifts in diet of the predator assemblage indicate flexibility in foraging tactics of Arctic marine predators in response to abiotic and biotic change. Moreover, these data provide strong support of a temporal shift from a trophically diverse to a more trophically redundant predator assemblage associated with climate change.

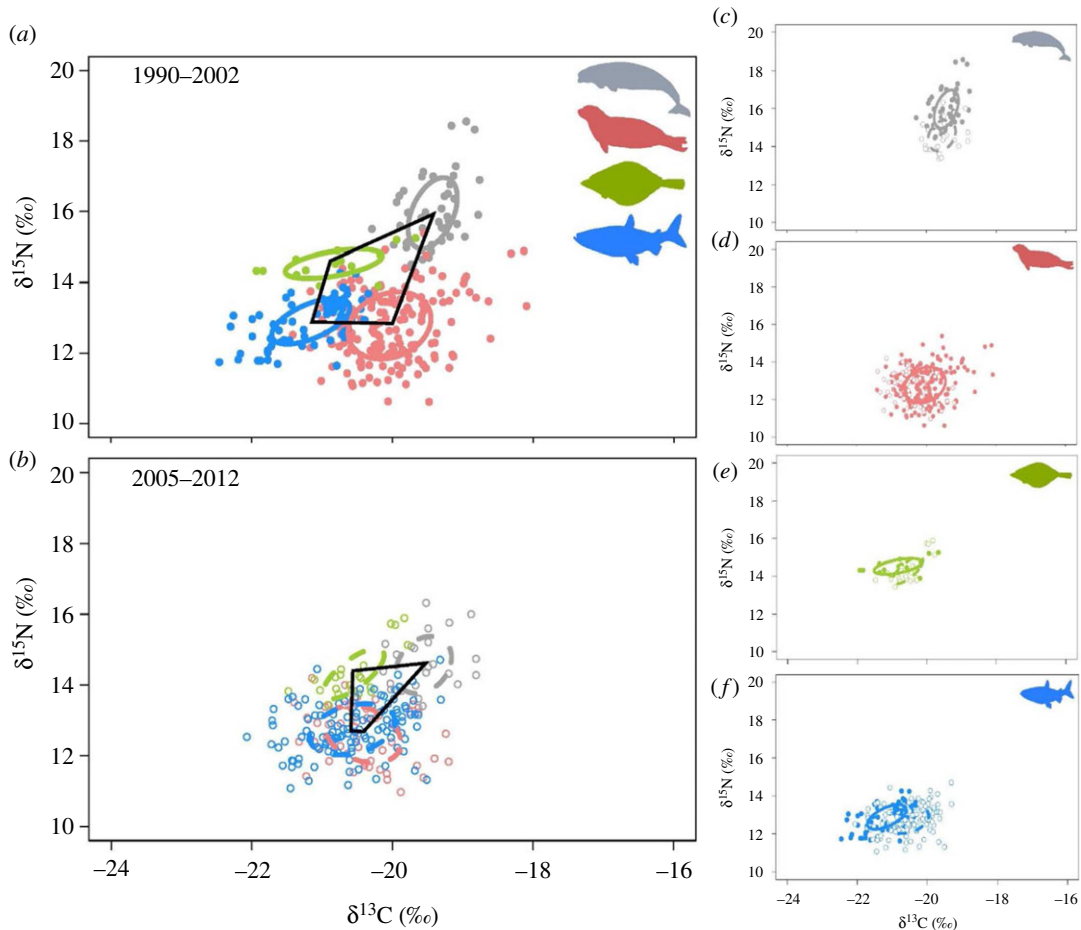


Figure 2. Stable isotope bi-plot representing the 40% isotopic niche sizes of beluga, ringed seals, Greenland halibut and Arctic char during 1990–2002 (solid lines; *a*) and 2005–2012 (dashed lines; *b*) with solid black lines characterizing the community metric of total area. (*c*–*f*) Isotopic niche shifts for each predator species between both time periods. Symbols and ellipses are colour-coded by species similar to figure 1.

Beluga whales, ringed seals, Greenland halibut and Arctic char exhibited flexible foraging behaviour over the study period with consumption of higher proportions of forage fish in the 2005–2012 time period. Flexible foraging behaviour is pervasive in nature and allows opportunistic predators to exploit shifting prey diversity and abundance in response to seasonal and inter-annual variations in environment [65]. For example, a substantial increase in the consumption of capelin associated with a decline in sea ice and decreased consumption of sympagic Arctic cod in diets of thick-billed murrens over time was, at least in part, due to increased availability of capelin modulating a switch to this prey species [24].

The most probable explanation for the increase of forage fish consumption among the four near-apex predator species is the increased availability of capelin since the mid-2000s. Cumberland Sound beluga whales have been previously documented to consume both Arctic cod and capelin, though with an increasing reliance on capelin over time [27,30]. In addition, Cumberland Sound beluga whales dive to shallower depths (0–100 m) in the summer compared to the late-autumn and winter where dives are greater than 400 m, suggesting a seasonal switch from foraging on forage fish in shallower waters to deep-water fishes such as Greenland halibut [27,66]. Ringed seals have been shown to respond to varying prey availability and distribution by exhibiting high flexibility in their movement ecology and diet with increasing latitude [35,67]. With decreasing sea ice extent, Cumberland Sound ringed seals have also been shown to be less dependent on sympagic carbon and more dependent on pelagic carbon [42], further supporting our results of a substantial increase in consumption of forage fish over time. Greenland halibut have been reported to consume Arctic cod during the open water period at higher latitudes [68] and capelin in Cumberland Sound [69] which is also consistent with our mixing model results. For Arctic char, stomach content analysis of individuals in Cumberland Sound found a diet switch from invertebrates to a capelin-dominated diet in the late 2000s [45], comparable to our

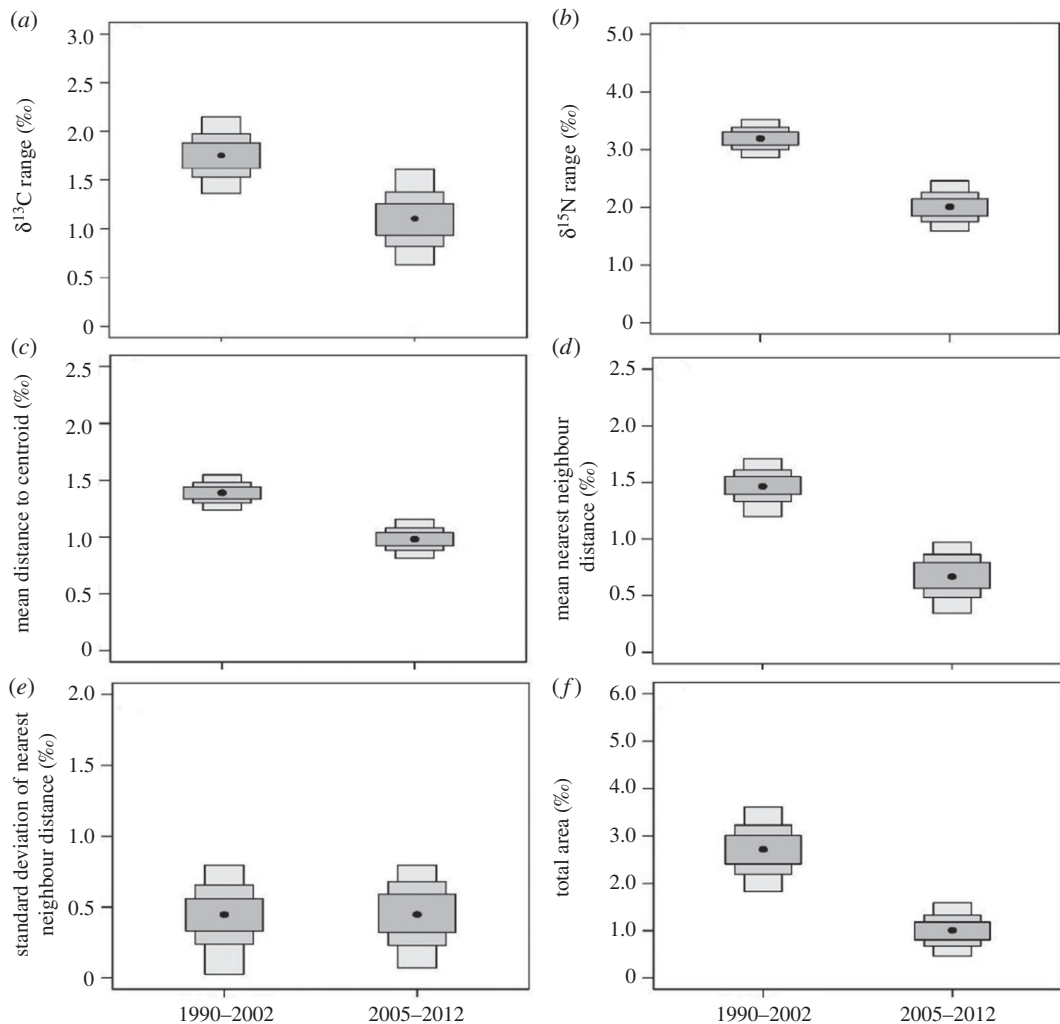


Figure 3. Boxplots representing Bayesian mode estimates for each community-wide metric including $\delta^{13}\text{C}$ range (a), $\delta^{15}\text{N}$ range (b), mean distance to centroid (c), mean nearest neighbour distance (d), standard deviation of nearest neighbour distance (e) and total area (f) from 1990–2002 to 2005–2012. Boxes indicate Bayesian credible intervals at 50% (dark grey), 75% (medium grey) and 95% (light grey).

mixing model results. Arctic char adopts an opportunistic foraging strategy where their diet typically reflects prey availability, especially when exploiting high density prey patches [70], such as large aggregations of beach-spawning capelin. Therefore, increased capelin availability allows greater accessibility for Arctic char to consume a high-lipid prey item which, in turn, positively affects growth rates [45] and body condition [71].

Given that capelin are highly adapted to survive across a broad range of temperatures (2°C to 12°C), and their northward expansion in distribution is linked with increasing sea temperatures [9], Cumberland Sound provides ideal colonizing potential for this highly plastic species. Beach spawning of capelin is now prevalent in Cumberland Sound during the summer and there are indications of capelin overwintering (see electronic supplementary material, figure S5), thereby increasing its overall availability to predators throughout the year. Scant details are known about capelin's overall occurrence and distribution across the Arctic, as most current information comes from either Inuit observation or studies on temporal changes in seabird diet [19,24]. However, distributional shifts of the northwest and northeast-central Atlantic capelin related to temperature have occurred recently in waters around Newfoundland, Labrador and Iceland, and a northeastward shift has been reported in the Barents Sea [19]. With high capacity to track suitable climatic conditions, these northward distributional shifts of more-temperate fish species such as capelin to warming Arctic waters are predicted to accelerate [72].

Comparison of the metrics measuring the trophic structure of the predator assemblage between 1990–2002 and 2005–2012 in Cumberland Sound revealed the latter having less variability in basal

carbon source use and trophic position, such that the community exhibited less trophic diversity and more trophic redundancy. Warming waters and phenological changes to sea ice over time strongly influence the seasonal pulse of algal productivity during the summer allowing more prolonged availability of this energy pathway to consumers [64]. In turn, the sympagic and detrital energy pathways probably become dampened leading to predators and prey capitalizing on resources from the pelagic energy pathway, thereby decreasing overall variability in basal carbon source use among the predator assemblage. Furthermore, lower variability in the relative trophic position of the predator community in 2005–2012 was predominantly driven by a niche shift in beluga whale diet from consuming less Greenland halibut to a higher proportion of forage fish. Cumberland Sound trophic diversity (i.e. mean distance to centroid and total area) decreased, while trophic redundancy (i.e. mean nearest neighbour distance) increased over time. This suggests that the individual species of the predator assemblage now play similar trophic roles within the food web by primarily consuming resources from the pelagic energy pathway and occupying a more-similar trophic position.

Climate-driven community shifts in the Arctic will probably accelerate with warming temperatures and decreasing sea ice leading to more subarctic and temperate species, from phytoplankton to predators, invading Arctic waters [8]. This northward shift will probably have detrimental consequences on Arctic community composition by causing a decline in the abundance of endemic Arctic species with associated consequences on the functional biogeography and spatial coupling between pelagic and benthic energy compartments of the ecosystem [19,73]. For example, functional traits typical of boreal marine fish communities (e.g. larger body sizes, increased piscivory and utilization of pelagic resources and high generalism) are becoming more prevalent in the Barents Sea and impacting its trophic structure and dynamics [3,73]. Over a 22-year period, our study in Cumberland Sound found dietary shifts among a sympatric predator assemblage resulting in decreased trophic diversity and increased trophic redundancy with potential implications on spatial coupling between benthic and pelagic energy compartments. Given the scale of defaunation in the current Anthropocene [74] and marine taxa tracking climate velocities by expanding or retracting their ranges [75], the reconfiguration of ecological interactions in the Arctic will persist and probably intensify in the future leading to continued change in the structure, function and resilience of Arctic food webs.

Ethics. All tissue samples were acquired through Fisheries and Oceans Canada Licences to Fish for Scientific Purposes. Data accessibility. Data supporting our results are provided in the electronic supplementary material.

Authors' contributions. D.J.Y., N.E.H., A.T.F. and S.H.F. conceived and designed the study. D.J.Y. analysed, interpreted the data and wrote the manuscript with all authors providing input and approving the final version.

Competing interests. We have no competing interests.

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