



Reduced seasonal sea ice and increased sea surface temperature change prey and foraging behaviour in an ice-obligate Arctic seabird, Mandt's black guillemot (*Cephus grylle mandtii*)

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Abstract

While decreases in Arctic sea ice affect all marine communities in the Arctic Basin, the effects are greatest on the cryopelagic ecosystem and species with critical life history stages dependent on the presence of sea ice. During the recent and ongoing period of rapid sea ice loss these species have been subject to spatial and temporal disruptions requiring behavioural plasticity. Mandt's Black Guillemots (*Cephus grylle mandtii*) is one of the few ice-obligate Arctic seabirds. Polar cod (*Boreogadus saida*) is their preferred prey. We monitored their prey selection and diving behaviour during the annual period of chick provisioning from 2011 to 2017, to assess their ability to respond to the now common seasonal loss of sea ice and increased water temperature in their nearshore foraging area. The percentage of polar cod fed to nestlings decreased with increasing SST, with fourhorn sculpin (*Myoxocephalus quadricornis*), a nearshore demersal, becoming common (20% of deliveries) with SST > 2.0 °C and comprising more than half of the prey when SST > 3.4 °C. This prey-switch coincided with a marked increase in dives and time underwater per day and a decrease in dive duration as birds switched to nearshore, benthic habitats. Sea ice is declining and SST increasing throughout the Arctic Basin and other upper-trophic level predators dependent on polar cod could be expected to be exhibiting similar prey-switching and modifications in foraging effort.

Keywords Black guillemot · Polar cod · *Boreogadus saida* · *Myoxocephalus quadricornis* · Arctic · Foraging · Seabird

Introduction

Several Arctic species are dependent on sea ice and adjacent near-freezing waters for critical parts of their life history (Harwood et al. 2015; Prop et al. 2015). As the Arctic continues to warm twice as fast as global averages, September Arctic sea ice extent is decreasing at a rate of 13% per decade, with an "ice-free" Arctic summer anticipated by mid-century (Overland and Wang 2013; Stroeve et al. 2014; Wang et al. 2018). In the past half-century, the three Alaska

seas supporting perennial or seasonal sea ice cover have experienced major physical changes associated with drastic reductions in sea ice extent and volume (Stroeve and Notz 2018), leading to major modifications in the extent and seasonality of the cryopelagic (or sympagic) ecosystem. Upper-trophic level ice-associated species are being increasingly impacted through top-down effects, such as increased predation (Prop et al. 2015), and bottom-up effects as changes in physical oceanography affect lower trophic levels, reducing energy available to higher trophic levels; (Divoky et al. 2015; Harwood et al. 2015; Wilson et al. 2017; Steiner et al. 2019). Lower trophic levels often respond more quickly to warming seas than higher trophic levels, creating a mismatch between the timing of a predator's peak food requirements and the period when their prey is most available (Evans and Moustakas 2018).

The primary forage fish in the Arctic Basin, polar cod (*Boreogadus saida*), is frequently associated with sea ice and feeds on zooplankton typically occupying waters < 4 °C (Drost et al. 2014). Occurring in shelf and slope habitats throughout the Arctic Basin (Steiner et al. 2019), polar cod is lipid-rich

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and supplies approximately 90% of the energy transfer to seabirds and marine mammals in High Arctic marine food webs (Welch et al. 1993). Low ice cover and high water temperature reduce the survival of early life stages, with a recruitment collapse predicted given anticipated ice-reductions and heating in the Arctic Ocean (Huserbraten et al. 2019).

The rapid loss of Arctic sea ice and concurrent increases in SST in recent decades have resulted in major 'bottom-up' shifts in the abundance and availability of prey, including polar cod (Moline et al. 2004). In response, species reliant on polar cod, whether year-round or seasonally dependent, need to adapt to the decreased availability of their preferred prey through behavioural plasticity or natural selection. In the long-term, adjustments could include modifications in distribution and/or annual phenology to accommodate spatial and temporal changes to polar cod availability, but in the short-term individuals will need to modify foraging behaviour and/or switch to alternative prey. Seabirds, as a group, are reliant on marine prey resources that frequently have high temporal (annual and seasonal) and spatial variation in abundance with plasticity in foraging behaviour common (Monaghan et al. 1994; Kowalczyk et al. 2015; Gaglio et al. 2018). During the non-breeding period, seabirds can shift distribution in response to variation in prey. In contrast, breeding seabirds are central-place foragers, dependent on prey resources within the foraging range of the species, and require plasticity in foraging behaviour to respond to variation in prey type, abundance and location. For example, thick-billed murre (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*), both formerly dependent on polar cod in the Canadian and Atlantic Arctic, switched to capelin (*Mallotus villosus*) (Gaston and Elliott 2014; Vihtakari et al. 2018). Little auks (*Alle alle*) have demonstrated plasticity in prey selection of zooplankton and diving behaviour in response to decreases of sea ice and increased SST off Greenland (Grémillet et al. 2012).

Seabird species that carry only one prey at a time (single-prey loaders) with short foraging ranges when provisioning young are more sensitive to variation in prey supply than other seabird species (Monaghan et al. 1992; McLeay et al. 2009; Gaglio et al. 2018). The limited foraging range of *Cephus* guillemots provisioning young, up to 13 km, makes them excellent monitors of local prey type and availability in nearshore waters (Bradstreet and Brown 1985; Cairns 1987; Shoji et al. 2015). *Cephus* guillemots are usually shallow, benthic divers which also facilitates their use as samplers of nearshore prey (Masden et al. 2013; Shoji et al. 2015). The 30–45 day period of chick provisioning (Petersen 1981) is long for an alcid and provides a large sampling window. Identification of prey type is facilitated by parents returning with a single prey per provisioning trip and carried cross-wise in the bill (Petersen 1981; Cairns 1987; Mehlum and Gabrielsen 1993).

Mandt's black guillemot, one of the few ice-associated Arctic seabirds, has been studied annually on Cooper Island, Alaska since 1975. The subspecies is reliant on sea ice throughout the year (Divoky et al. 2016) and the Cooper Island population is more dependent on food webs based on sea ice algae than other upper-trophic level predators in the region (Budge et al. 2008). Hatching of Mandt's Black Guillemots nestlings begins in mid-July with parents provisioning nestlings until early September. During this period the energy costs of provisioning parents rises by 40% (Mehlum et al. 1993), increasing the need for a reliable and satisfactory food supply. This period of high energy demand for a critical life history stage occurs during the annual period of sea ice retreat from the Beaufort Sea coast (Frey et al. 2015) causing the nearshore waters to undergo major changes in physical and biological oceanography.

During the period of study on Cooper Island, SST in the waters north of Cooper Island averaged under 2 °C during the entire nestling period from 1975 to 2002. Beginning in 2003, SST from early August through mid-September frequently averaged > 3 °C. The early 21st Century also saw a rapid advance in the timing of annual sea ice retreat during chick provisioning, with ice concentration of > 30% within 100 km of the colony before 2003 and increasing to > 200 km after 2003 (Divoky et al. 2015). While parents provisioned their young almost exclusively on polar cod from 1975 to 2002, beginning in 2003 there have been seasonal shifts to fourhorn sculpin, a nearshore demersal fish not associated with sea ice. The prey shift has resulted in decreased growth and survival of guillemot nestlings apparently due to the decreased energy density, palatability, digestibility, and availability of sculpin, especially as the large bony head and spines would be difficult to digest (Divoky et al. 2015). Additionally, prey shifting is known to reduce digestive efficiency (Hilton et al. 2000) and assimilation efficiency is less for lower fat content fish (Brekke and Gabrielsen 1994). Polar cod has the highest percent lipid of any marine fish in Alaska, 2–3 times higher than fourhorn sculpin, leading to higher overall energy density (Rizzolo 2017; Vollenweider et al. 2018). Models of diet choice suggest that whether a predator includes a secondary prey into its diet depends on the availability of the primary prey and not on characteristics of the secondary prey (Evans and Moustakas 2018). Thus, the switch from polar cod to sculpin is likely driven primarily by a decline in the former rather than an increase in the latter. Nonetheless, the trophic plasticity of a predator will allow the population to persist in a particular location longer than it would otherwise.

While distributional and phenological shifts of populations in response to climate change have been well documented, changes in feeding behaviour in response to climate-induced changes in prey by upper-trophic level predators has been less studied (Evans and Moustakas 2018). We

investigated the diving behaviour of Mandt's Black Guillemot parents provisioning nestlings from 2011–2017 to assess the influence of annual and seasonal oceanographic variation on prey selection and diving behaviour. We conducted observations of prey type and used leg-mounted time-depth-temperature recorders (TDRs). We hypothesized that decreases in sea ice and SST would cause a seasonal decrease in the occurrence of polar cod in the diet and, like other auks, Mandt's Black Guillemots would display considerable behavioural plasticity in response to temporal and spatial variation in prey type and availability (Elliott et al. 2008). We expected changes in dive frequency, daily time under water, dive depth, and foraging habitats and locations as birds switched from polar cod, a schooling cryopelagic fish found throughout the water column to fourhorn sculpin, a non-schooling nearshore demersal.

Materials and methods

Field methods

All observations and recordings were conducted on Cooper Island, Alaska ($71^{\circ} 15'N$, $155^{\circ} 41'W$) (Fig. 1) in the western Beaufort Sea where, since 1975, Mandt's black guillemots have been monitored for adult survivorship, breeding chronology and success, chick growth, prey selection and colony attendance (Divoky 1998; Divoky et al. 2015; Sauve et al. 2019). All nests at the colony are in artificial nest sites, providing unique investigator access to breeding birds. While nests were originally in wooden nest sites (Divoky et al. 1974), modified plastic Nanuk Cases (Plasticase, Montreal) replaced all nests in 2011 to prevent nest predation by polar

bears (*Ursus maritimus*) which have become regular summer visitors to the island since 2002 (Cox et al. 2017).

From 2011 to 2017, between late June and early September, we deployed time-depth-temperature recorders (TDRs; Lotek, St John's, Canada; LTD_1500, 3.2 g; pressure and temperature recorded at 1 Hz [2011] or 0.5 Hz [2012–2017] when wet and pressure > 0.5 dbar) to the plastic colour bands of 71 individuals using duct tape. TDRs were typically attached to birds during incubation. Individuals were selected based on stage of breeding and proximity to camp and other nest sites where TDRs were deployed. We avoided deploying units on first-time breeders to prevent disrupting breeding activities. Initial capture and deployment typically occurred while birds were in the nest-cavity incubating eggs or brooding chicks. Handling time was usually < 5 min. Birds were recaptured on the nest if still incubating or with a monofilament noose mat at the nest entrance if provisioning nestlings. Downloading of data and release of the birds typically took < 5 min. When units were removed from the bird, handling was < 1 min. Six adults could not be recaptured prior to fledging and the TDRs were removed the following year. Guillemot parents brood their chicks for approximately 6 days after hatching and only data from birds with chicks > 6 days of age were included in the analysis to avoid inclusion of data from the period of brooding. Data obtained after parental provisioning ended were not included in this analysis.

Prey type carried by provisioning parents was obtained through daily direct observations and motion-activated cameras (Reconyx, Holmen WI, USA) to acquire a daily estimate of the percentage of prey type for the entire colony. For this analysis, we used the proportion of polar cod per day as a metric of polar cod availability. Fourhorn sculpin

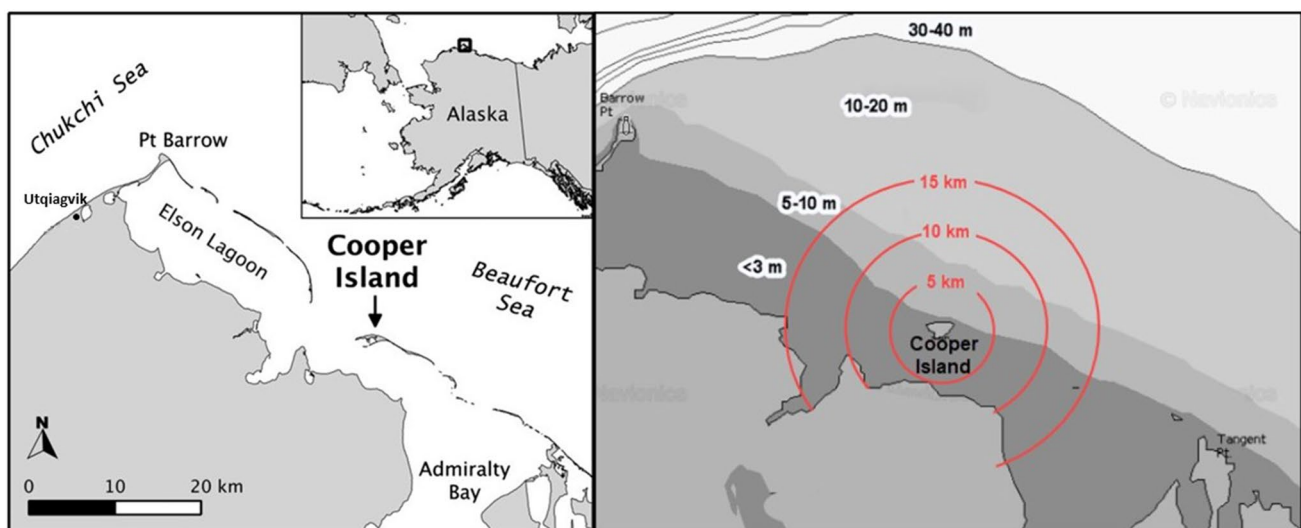


Fig. 1 Location of Cooper Island and depth profile for potential foraging range

constituted 95% of the alternative prey with smaller numbers of other demersals (primarily eel blenny *Lumpenus fabricii*). Additionally, we used cameras to obtain fish observations at nests with individuals outfitted with a TDR to obtain trip-specific data for known prey type. Cameras were placed 0.5–1 m from the nest entrance. Only images with a definite prey identification were included, with time of image used to identify the dive activity associated with the observed prey item. Of the 37 images where TDR birds were carrying identifiable fish, there were 14 polar cod, 20 fourhorn sculpin, 2 Pacific sand lance (*Ammodytes hexapterus*) and 1 capelin (*Mallotus villosus*). The last dive recorded before a prey observation allowed us to calculate: (1) time between feed and nest site arrival, (2) time underwater since last at colony and (3) number of dives in the dive bout.

Statistical analysis

The following parameters were extracted using a program written in Visual Basic: dive duration, maximum depth, benthic index (time allocation at depth providing depth providing an index of dive shape, sensu Mori et al. 2001), Mori's index of patch quality (Mori and Boyd 2004), sea surface temperature (SST) and post-dive surface interval. Time underwater per day was computed by summing dive duration. Given the bathymetry of the foraging area, dive depth can be used as a proxy for distance from the colony.

Mori's index of patch quality (Patch Quality) assumes that individuals maximize energy gained per time spent in the entire dive cycle, and has been shown to correlate with energy gain rates in larger auks and seals (Mori and Boyd 2004; Elliott et al. 2008). Patch Quality should reflect prey density encountered by birds during a dive. The benthic index (or time allocation at depth, TAD) is an indicator of dive shape. V-shaped or bounce dives indicate pelagic feeding; U-shaped or square flat/bottom dives indicate prospecting; or foraging on benthic prey (Elliott et al. 2008). While V-shaped dives may be associated with searching in other species, V-shaped dives are usually associated with pelagic feeding in auks, which can use flight, partially, for searching (Kuroki et al. 2003; Elliott et al. 2008, 2010). Dives where the bird spends a high proportion (index ~ 1.0) of time below average depth are square or "U-shaped" (benthic) dives while dives where the bird spends only half of its time (index ~ 0.5) below average depth are "V-shaped" (pelagic) dives. We used the sequential differences method to classify separate dive bouts (necessary for estimating average surface interval duration) as occurring when the sequential differences in surface intervals was greater than 25 s, given the breakpoint in the log surface interval-log frequency graph at that point (Mori et al. 2001). We also considered all dives separated by a surface interval of greater than 75 s to be separate bouts, and we only used surface intervals

occurring within bouts for analyses. We also recorded SST as the average temperature (corrected for device time lag) within one minute before and after each dive. We removed from SST analysis any dive bouts with an SST above 9 °C as they likely represented measurements of body surface temperature rather than SST due to leg-tucking (less than 0.1% of dives). SST recorded by the TDRs correlated with SST obtained by satellite ($r=0.32$, $p<0.0001$), and consequently for the dive analysis we used SST from the TDR (representing fine-scale SST) as the only measure of SST for the remaining analyses. The relatively low correlation ($r=0.32$) is likely because dives near the lagoon would have a higher SST than that determined by satellite for waters north of the island. We determined the lowest temperature recorded during each dive after using the formula in Daunt et al. (2003) to account for the time-delay in the thermistor within the TDR.

We obtained daily SST estimates for 2011–2017 from NOAA's Optimum Interpolation (Reynolds et al. 2002) 0.25-degree-resolution global OISST Version 2 grids, disseminated by a NOAA ERDDAP Server at <https://coastwatch.pfeg.noaa.gov/> [accessed September–October, 2020] for the quadrant 71°15'–71°30' N and 155°30'–155°45' W with its southern border 2 km from Cooper Island and its northern 30 km from Cooper Island. Daily sea ice concentration for 2011–2017 was obtained using 25-km-resolution grids distributed by the National Snow and Ice Data Center (Fetterer et al. 2017). SST and ice conditions prior to the satellite record (before 1982 for SST and before 1979 for sea ice) were estimated based on shipboard SST (Aagaard 1984) and historical ice concentrations on Scenarios Network for Alaska and Arctic Planning (2020)

We analysed 466,554 dives covering 143 days. Statistical analysis occurred in RStudio (Version 1.1.383). We calculated the average values per day for duration, maximum depth, benthic index, IPQ and surface interval. We correlated maximum depth against dive duration and surface interval duration. We then conducted a principal components analysis of number of dives per day, daily average SST, minimum temperature per dive, duration, maximum depth, benthic index, IPQ and surface interval. Organizing the data by day allowed us to correlate dive data with daily prey observations, daily sea surface temperature (SST), daily ice concentrations. Finally, we examined relationships between those variables that varied significantly and SST measured by the TDR (which correlated with SST and ice coverage from satellites). We then examined how dive behaviour varied as guillemots switched from polar cod to sculpin.

Three major trophic phases: Polar cod, Transition and Sculpin were identified based on the daily percentage of polar cod carried by provisioning parents: Polar cod phase, > 75% polar cod; Transition phase, beginning when polar cod ≤ 75% for two consecutive days; Sculpin phase

beginning when polar cod $\leq 40\%$ or lower for two consecutive days. Sampling did not occur in all three phases for the seven years preventing us from making annual comparisons in this analysis. Additionally, in 2017 there was no polar cod or Transition phase. We used Akaike's Information Criterion (AIC) to determine whether dive depth or dive duration was a better fit with surface intervals and whether ice coverage or SST was a better fit with percent cod.

Our analysis includes only dive behaviour assumed to be at sea, seaward (north) of the colony. Since 2003, provisioning parents regularly seasonally forage in Elson Lagoon, the shallow (< 3 m) lagoon immediately south of the island (Fig. 1), where sculpin are the primary prey (Divoky et al. 2015). We removed 'lagoon' dives (dive bouts < 3 m in water > 5 °C, occurring after periods of at-sea diving with lower water temperature and deeper dives), and reanalysed daily variation metrics. Brood size (one or two nestlings) was not significant in any of the dive analyses, and was excluded from the final analyses. Clearly, more prey is needed to raise two nestlings, but none of the measured dive parameters reflected this difference; other studies have shown a similar lack of relationship between dive parameters and brood size in seabirds, perhaps because those individuals that are capable of raising more nestlings are more efficient foragers (e.g. Stothart et al. 2016).

To put the findings from the seven years of our study in context, after determination of the conditions responsible for the shifts in prey type and foraging behaviour, we examined seasonal variation in oceanographic conditions obtained from the NOAA satellite data described above for sea ice concentration 1979–2019 and SST 1982–2019, to assess when prey availability could be assumed to be modifying foraging behaviour in years before our dive study period. All data are presented in Online Resource # 1.

Results

Prey type

The percentage of polar cod in the nestling diet decreased, while the amount of fourhorn sculpin and other demersals, increased with seasonal reductions in sea ice concentration and higher SST in the foraging area. SST explained 50% of the variation in percent cod, while ice cover explained 44% of the variation in percent cod ($\Delta\text{AIC} = 3.02$ between the two best-fit logistic models), partly because ice cover was often zero and thus variation in ice cover could not explain variation in polar cod proportions once ice cover ceased. Polar cod frequently constituted 100% of the prey observed for days when SST was < 2 °C (Fig. 2). The proportion of polar cod declined most steeply at SST of ~ 3.4 °C and reached an average of 20% of deliveries at 5 °C.

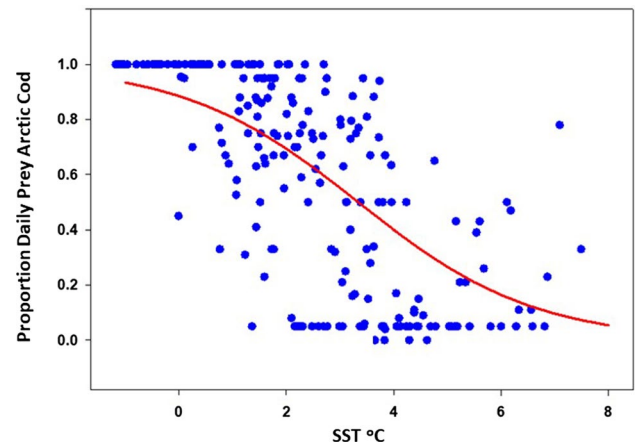


Fig. 2 Proportion of daily prey observations consisting of polar cod delivered to black guillemot chicks relative to sea surface temperature, 2011–2017. Regression line is best-fit logistic regression, with inflection point at 3.4 °C and a coefficient of $-0.61\text{ }^{\circ}\text{C}^{-1}$

Dive behaviour

For all dives for all trophic phases average dive depth was 4.9 ± 3.9 m (maximum 29.6 m), average dive duration 31.9 ± 14.7 s (maximum 99.7 s), surface interval 18.5 ± 12.7 s, dives per day 398 ± 206 , and time underwater per day 3.53 ± 2.44 h. Both dive duration and surface interval increased with dive depth (Fig. 3). Surface interval correlated with both dive depth and duration, but the correlation was stronger with dive depth implying that dive costs (and time at the surface needed to obtain oxygen to power those costs) were primarily associated with overcoming buoyancy to dive to depth ($\Delta\text{AIC} > 2.0$). Surface interval correlated better with subsequent dive depth than preceding dive depth implying birds were using time at the surface to prepare for subsequent dives rather than recover from previous dives ($\Delta\text{AIC} > 2.0$). However, dives per day was largely independent of dive depth ($R^2 = 0.01$). Days with greater dive depth and duration had higher benthic indices and Patch Quality, and higher temperatures. SST from TDRs was strongly correlated with minimum temperature of a dive (Fig. 4), and so we did not analyse minimum temperature in more detail. Similarly, dive duration and dive depth, Patch Quality and benthic index were strongly correlated (Fig. 4). Thus, we did not analyse dive depth, Patch Quality or benthic index in more detail. Dive duration ($p < 0.0001$) and dives per day ($p < 0.0001$) increased with SST: excluding dates in late 2014 with exceptional environmental conditions. Dive duration and dives per day were significantly correlated with SST. A seasonal shift in diving location occurred as 6.9% of July dives were lagoonal (shallow depth and high SST) compared to 29.4% of dives in August.

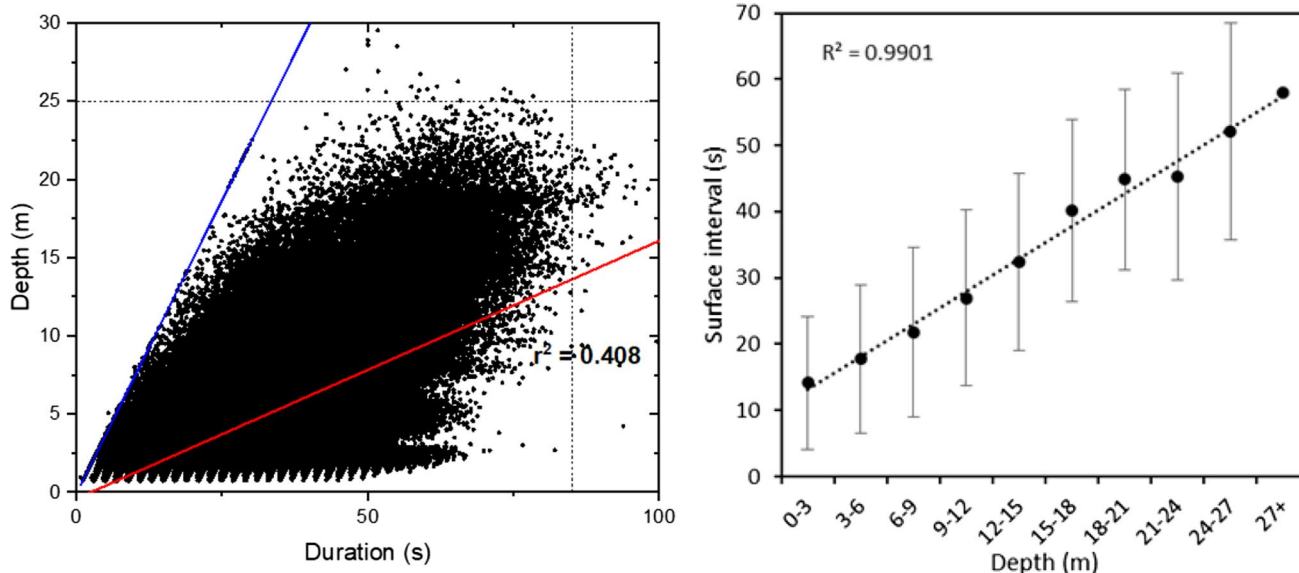


Fig. 3 Black guillemot dive depth during 2011–2017 increased with both duration (left) and surface interval (right). For (a) minimum duration (blue line) set by a max dive speed of 1.5 m/s. Maximum

depth set by bathymetry at 25 m and maximum duration set by an aerobic dive limit of 85 s

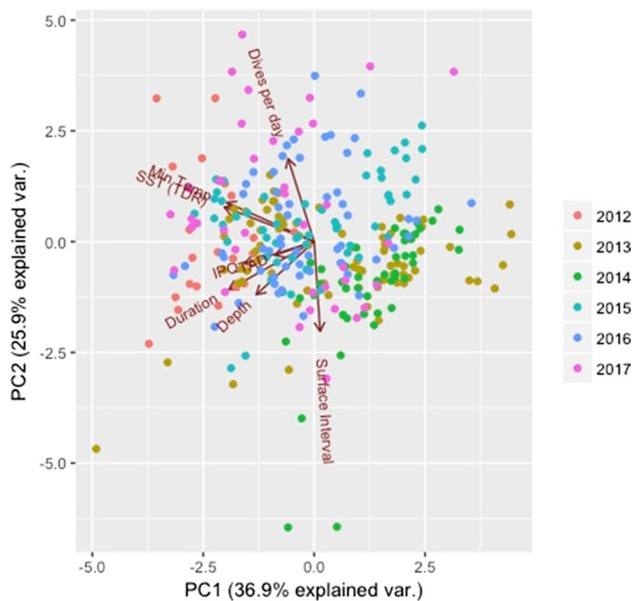


Fig. 4 Principal component analysis of mean daily dive behaviour (dives per day, index of patch quality [IPQ], dive shape [TAD], duration, depth, surface interval) and environmental variables (SST, minimum temperature per dive) from 2011 to 2017

Changes in dive behaviour with prey type

Dives per day and time underwater per day were low during the Polar cod phase and high during the Sculpin phase, with the Transition phase being intermediate, and showed high variation within a phase (Table 1 and Fig. 5). Not

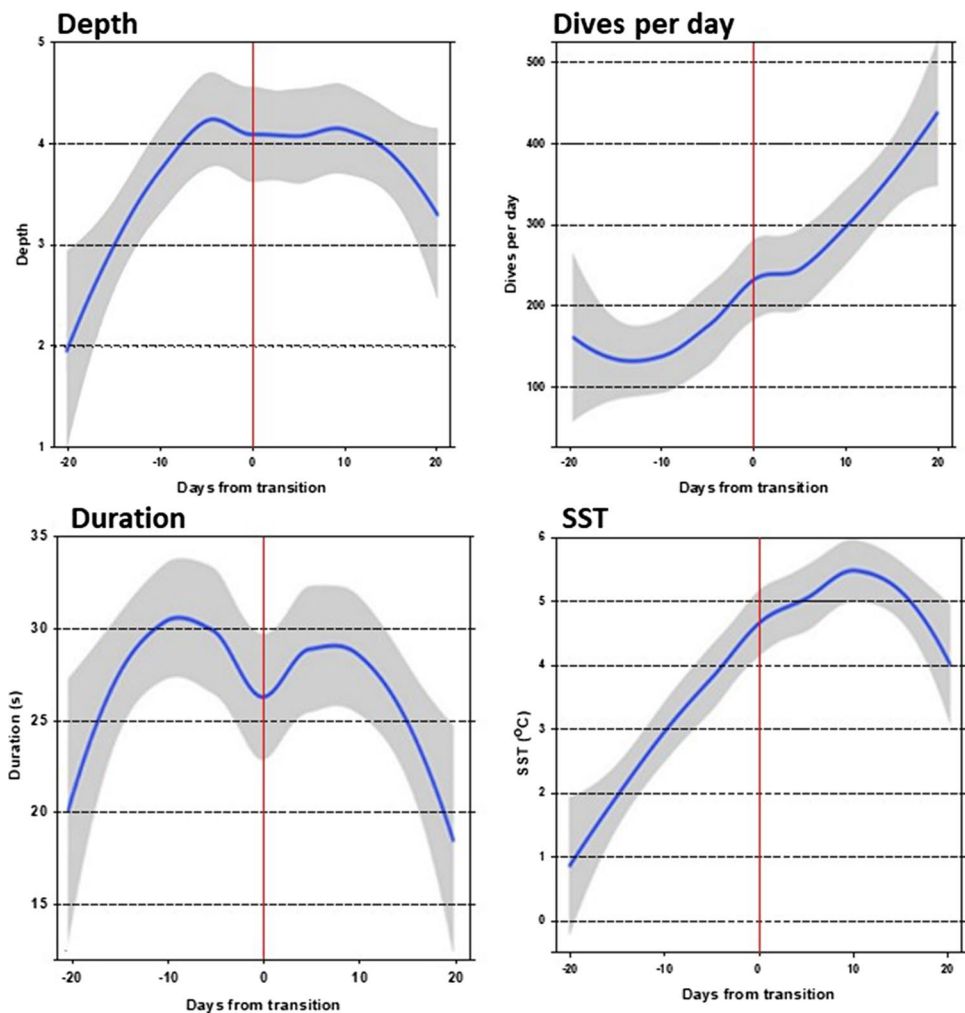
surprisingly, SST was low during the Polar cod phase, and was similar between the Transition and Sculpin phase (all Kruskal–Wallis $p < 0.0001$). In contrast, dive duration was slightly higher in the Transition phase than Polar cod phase, but then decreased substantially during the Sculpin phase (Kruskal–Wallis $p < 0.0001$; Fig. 5). Dive frequency had a major increase with the seasonal increase in SST, especially after the Transition phase. Dive parameters varied within a prey phase reflecting temporal variation in prey availability with some displaying considerable variation. The short-term variability in dive behaviour is shown in the dive profile for one bird in early August 2013 (Fig. 6). This bird samples a range of depths and distances from the colony over a two-week period in which SST was near 3.5 °C. Within-day variation was high on 12 August as foraging occurred at increasing depth in waters of 2.5–3.0 °C, indicating that the bird likely foraged progressively farther offshore due to decreased prey near the colony. On 13 August, after a period of no diving activity in the morning, this bird is assumed to be feeding in nearshore lagoon waters of > 5 °C. The profile clearly shows switching from offshore to lagoon feeding that was common for many birds in our dataset.

For dives associated with specific prey observations (Table 2), sculpin were obtained at shallower depths (2.55 m) than polar cod (5.08 m). SST was higher prior to sculpin deliveries and it is important to note the observed polar cod were taken at an atypically high SST for that species. The relatively small size of polar cod, which are age 1 individuals, contrasts with earlier work when SST was low and polar cod mass was typically above 120 mm (Harter

Table 1 Black guillemot dive parameters by trophic phase 2011–2017. See text for definition of trophic phases

	Polar cod Mean ± SD	Transition Mean ± SD	Sculpin Mean ± SD	Kruskal test <i>p</i> value	Significant
Sample size (d)	122	47	107		
Dates sampled	19 Jul–18 Aug	25 Jul–27 Aug	5 Aug–3 Sep		
Dives per day	124 ± 67	279 ± 121	387 ± 242	< 0.00001	Yes, between all factors
Dive duration (s)	24.2 ± 7.0	26.5 ± 5.5	19.5 ± 7.5	< 0.00001	Yes, between all factors
Time underwater per day (h) (range)	3.30 ± 0.39	3.49 ± 0.31	4.69 ± 0.41	< 0.00001	Yes, between all factors
Dive depth (m)	3.53 ± 1.4	4.25 ± 1.6	3.63 ± 1.4	0.00027	Yes, but not between cod and sculpin (Wilcoxon test, <i>p</i> = 0.63)
Surface pause (s)	19.0 ± 4.1	16.4 ± 5.7	16.1 ± 2.5	< 0.00001	Yes, between all factors
Time at depth	0.82 ± 0.07	0.81 ± 0.09	0.83 ± 0.11	0.52	No
Patch Quality	0.58 ± 0.08	0.66 ± 0.23	0.60 ± 0.08	0.004	Yes, but not between cod and sculpin
SST (TDR) (°C)	2.13 ± 1.9	4.27 ± 1.5	4.10 ± 3.31	< 0.00001	Yes, between all factors

Fig. 5 Change in depth, dives per day, duration and SST relative to the transition in prey type provided to nestlings from polar cod to sculpin. Day zero is the first day < 40% polar cod for two consecutive days



et al. 2013). Both polar cod and sculpin were delivered following benthic and pelagic dives, as was true for our analysis of daily dive types by trophic phase. Dive duration, time underwater and time in transit did not vary with prey

type and dive depth and SST are the main discriminants of polar cod versus sculpin feeds. The length of time in transit indicates birds were spending some time on the water after capturing a fish. Parent birds with prey are frequently seen

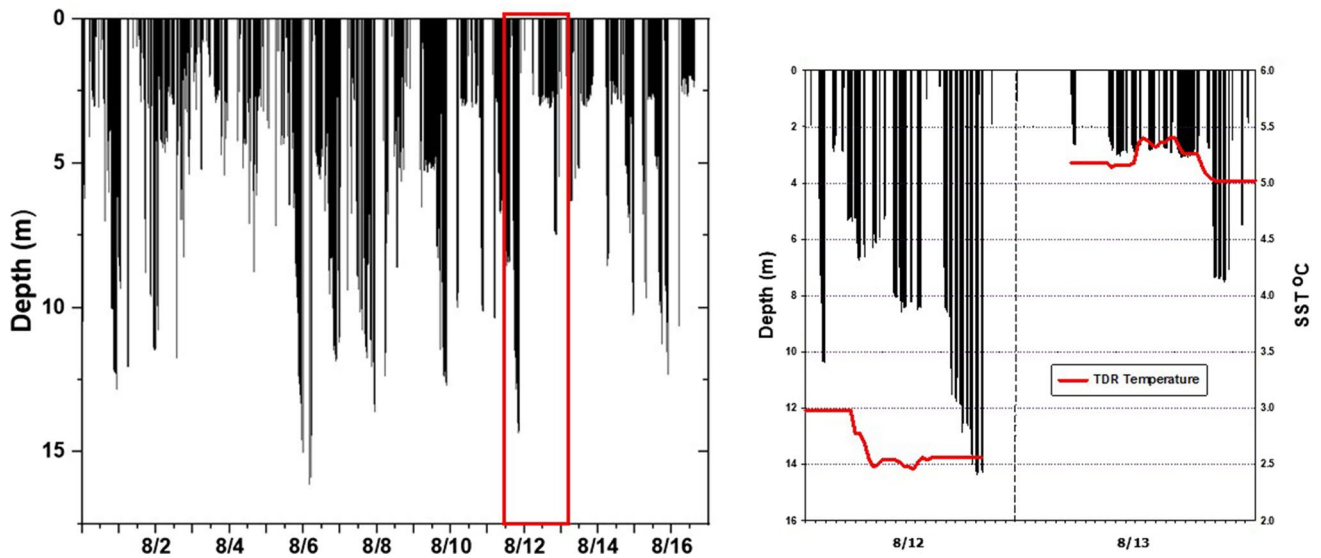


Fig. 6 Dive depth and sea surface temperature (SST) for a single bird in early August 2013 (left) and for 12–13 August 2013 (right). Left panel shows high variation in depths sampled between and within days. The two days on the right panel show increasing dive depths in

cold ($<3.5\text{ }^{\circ}\text{C}$) offshore waters on 12 August and more uniform dives in shallow warm ($>4\text{ }^{\circ}\text{C}$) waters on 13 August, assumed to be in the lagoon

Table 2 Dive parameters prior to delivery of cod or sculpin by black guillemots

	polar cod	Sculpin	Sand lance	Capelin	Wilcoxon <i>p</i> value
Sample size	14	20	2	1	
Fish length (mm)	84 ± 24	84 ± 30	60	75	
Dive depth (m)	5.1 ± 3.2	2.6 ± 1.0	6.3 ± 6.8	3.9	0.025
Dive duration (s)	29.1 ± 14.1	23.2 ± 10.3	21.4 ± 8.8	11.8	0.42
SST (TDR) ($^{\circ}\text{C}$)	5.0 ± 1.4	6.9 ± 1.3	6.8 ± 0.6	4.8	0.00073
Time underwater (min)	6.2 ± 7.2	8.6 ± 7.7	5.8 ± 7.0	23.0	0.17
Time in transit (min)	27.3 ± 48.7	13.9 ± 14.6	7.0 ± 5.7	32.3	0.87
Benthic dives (number)	7	12	0	0	
Pelagic dives (number)	7	8	2	1	

Parameters were: average length of fish delivered during these observations, maximum dive depth, dive duration, sea surface temperature (SST), time underwater since previous trip to colony, time in transit during return trip to colony following diving (time between last dive and photograph at the colony) and number of times the final dive prior to return to the colony was benthic or pelagic. Mean values \pm SD are shown except for benthic and pelagic dives where total number are shown. Average length of fish delivered during these observations is shown. Due to small sample sizes for sand lance and capelin, Wilcoxon *p* value refers to difference between polar cod and sculpin

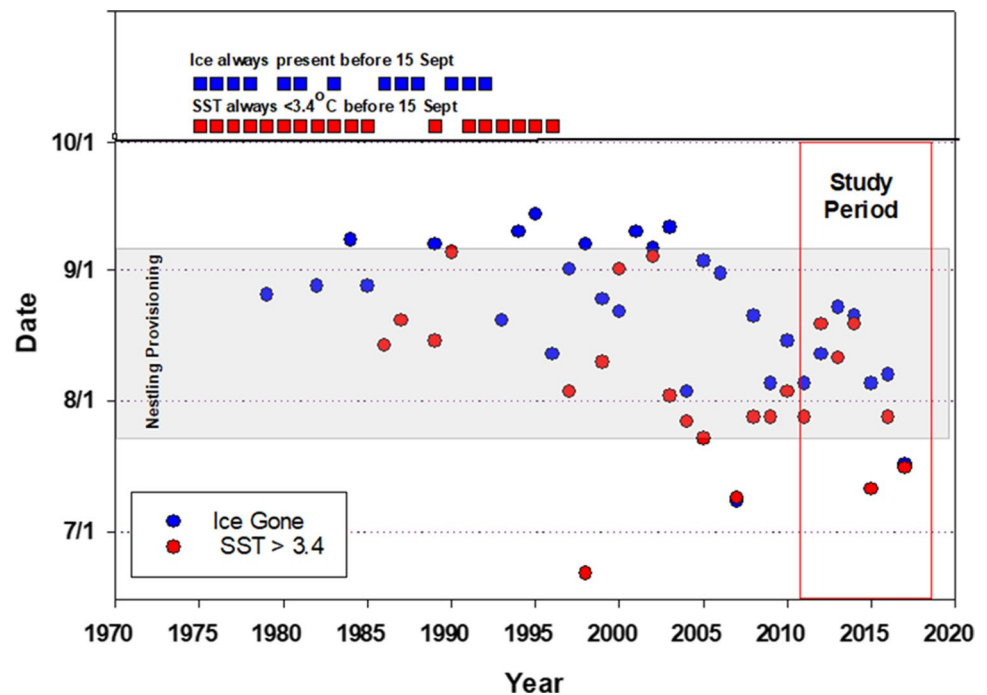
sitting on the water adjacent to the colony, apparently assessing predation or kleptoparasitism risks.

Decadal changes

The occurrence and timing of annual oceanographic thresholds associated with the prey shift and modifications in dive behaviour (loss of sea ice and $\text{SST} > 3.4\text{ }^{\circ}\text{C}$) displayed major variation during the last four decades, with the frequency of years when that threshold was crossed increasing and timing of the threshold advancing during the 21st Century

(Fig. 7). From 1979 to 1999, in August, when the majority of chick growth occurs, sea ice was reduced to zero in 57% of the years, averaging 30 August, while in the 21st Century (2000–2019) sea ice was lost during or before August in all years with an average date of loss of 12 August. The SST threshold of $> 3.4\text{ }^{\circ}\text{C}$ was reached in August in 39% of years from 1979 to 1999, averaging 4 September, while in the 21st Century that thermal threshold was reached in all years, averaging 1 August.

Fig. 7 Date of sea ice disappearance (1979–2019) and SST > 3.4 °C (1982–2019) in the quadrant 71°15′–71°30′ N, 155°30′–155°45′ W, extending from 2 to 30 km north of Cooper Island



Discussion

Our research provides information on (1) how climate-induced changes in nearshore physical oceanography are reducing the availability of polar cod, the primary forage fish in the Arctic Basin, to upper-trophic level predators and (2) the behavioural response of an ice-associated upper-trophic level predator to the reduction of its preferred prey.

Comparison with other *C. grylle*

Mandt's Black Guillemot is genetically distinct from other members of the species, restricted to an unglaciated portion of the Arctic Basin during the Last Glacial Maximum (Kidd and Friesen 1998; Harkness 2017). Mandt's Black Guillemots could be suspected of having diving behaviour different from sub-Arctic subspecies of the genus, but we found no evidence of that. While Mandt's Black Guillemots provisioning young have shallower dives (mean = 4.9 m; max = 29.6 m) and of shorter duration (mean = 32 s; max = 100 s) than for sub-Arctic *Cepphus* (9–32 m and 54–95 s; Shoji et al. 2015), both of these differences can be explained by the shallower nearshore bathymetry adjacent to Cooper Island (Fig. 1). Post-breeding offshore dives of birds from Cooper Island regularly exceed 20 m. Although black guillemots typically have shallower but longer dives than expected from body mass alone (Shoji et al. 2015), and the Cooper Island guillemots fit with that trend, maximum dive depth and duration likely represents bathymetric rather than physiological constraints.

The number of dives per day showed high seasonal variation, as discussed below, but the average of 398 dives per day, was higher than 186 dives per day found by Shoji et al. (2015). Mean surface interval of about 18.5 s was less than 27.5 s reported by Cairns (1992) and expected given the short dive duration. Time underwater per day showed high seasonal variation and was more than the 2.13 h found by (Shoji et al. 2015) for all trophic phases.

Seasonal variation in prey availability

Mandt's Black Guillemots breeding on Cooper Island provide their nestlings a low-diversity diet, consisting of > 90% polar cod before transitioning to a diet of > 90% fourhorn sculpin (Fig. 2). A nestling diet composed primarily of one or two prey species is not uncommon for the species as some sub-Arctic populations show a similar lack of diversity with a single species frequently making up 60 percent, and occasionally > 90 percent of the diet, even in sub-Arctic areas with high nearshore fish diversity (Butler 2020).

This study and other long-term observations from Cooper Island colony show that when SST is below 2 °C, provisioning parents are able to find sufficient amounts of their preferred prey to provision their young without turning to demersals, with the percentage of sculpin increasing with SST and with few polar cod taken on days with SST > 4 °C (Fig. 2). As polar cod is a cold-water fish, the decline in proportion fed to nestlings with increasing SST is not surprising, but the mechanism causing the decrease is not clear as the species is frequently found at higher SST.

Decreases in sea ice extent, volume and age would be expected to have a number of effects that would decrease cod availability and age composition. In nearshore Canada, polar cod are widely dispersed under sea ice but aggregate in dense schools and move to deeper water in the absence of ice, apparently for predator avoidance (Crawford and Jorgenson 1993; Kessel 2015). Reductions in sea ice and its age could also reduce the size of polar cod available to parents with a resulting reduction in prey quality as energy density is dependent on fish length (Harter et al. 2013). Older individuals (ages 1 and 2), of the size parent guillemots feed their young (typically 8–15 cm), are found under thicker and multi-year ice where they use cracks or crevices as refuges from predation (Lonne and Gulliksen 1989; David et al. 2016), while young-of-the-year are usually associated with first-year ice or open water (Baranenkova 1966). When present, sea ice could assist foraging parents in locating prey, as it would provide a visual cue of productive foraging areas, while also providing roosting sites (Owen et al. 2019).

The decline of polar cod in the diet began at SST of 2 °C and declined rapidly past that point. Nonetheless, polar cod regularly inhabit waters with higher temperatures elsewhere. Studies of the physiological limits of the species found a range of optimum temperatures from 1.0 to 5.4 °C, with metabolic performance declining at 10.0–12.3 °C (Steiner et al. 2019). In the central Beaufort Sea, polar cod were most common in the nearshore central Beaufort at 6–7 °C (Craig et al. 1982), while offshore, polar cod were found in small schools in the upper 20 m, in waters 2–5 °C (Crawford et al. 2012).

It appears the decreased availability of polar cod at 2 °C is due to factors other than thermally induced physiological stress and could be due to changes occurring in the supporting food web. The species is considered a zooplankton generalist (Cusa et al. 2019) and their disappearance from the guillemot's diet may be due to changes in the zooplankton community of the foraging area. The copepod, *Calanus glacialis*, is the primary zooplankton in Arctic Basin food webs and is a major component of the polar cod diet in the Beaufort Sea (Bouchard and Fortier 2020; Vollenweider et al. 2018). Increasing SST and decreasing ice in the foraging area could both be expected to have decreased *Calanus* numbers as they are dependent on ice algae and more abundant in colder years with later ice retreat (Spear et al. 2019). Studies in the Eastern Arctic show the species to be dependent on an early spring ice algae bloom from April to June and then on pelagic phytoplankton for the remainder of the summer (Soreide et al. 2010). The loss of sea ice from the foraging area could be expected to affect the abundance and physiological condition of polar cod by decreasing the density of their preferred prey and leading to water temperatures above the species thermal tolerance (Vollenweider et al. 2018; Bouchard and Fortier 2020). Polar cod also occupy

lagoonal habitats in the Beaufort, but primarily as juveniles, where they are independent of under-ice food, feeding on mysids and other benthos and reliant on a benthic food web supported by both phytoplankton and terrestrial carbon, peat (Craig et al. 1984).

Whatever the reasons for the decrease in polar cod, its disappearance leaves provisioning parents with few options other than turning to the other dominant fish in the Beaufort Sea nearshore, fourhorn sculpin (Craig et al. 1985; Vollenweider et al. 2018). Fourhorn sculpin are a nearshore demersal found occupying shallow waters with sand and gravel bottoms in water from –2 to 15 °C where they feed on amphipods and isopods (Thorsteinson and Love 2016). They occupy the guillemot's summer foraging area throughout the year and their appearance and then dominance in the diet of nestlings is due to their being an alternative prey in the absence of the preferred prey and not an increase in their availability. They differ from polar cod by being more abundant in Elson Lagoon than the ocean side of the island (Logerwell et al. 2015; Vollenweider et al. 2018) and also by not being a schooling fish. Two other potential alternate prey taken by *Cephus* in the sub-Arctic are sand lance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*) (Golet et al. 2000; Litzow et al. 2002). These are higher quality prey than sculpin and common in the waters adjacent to Cooper Island (Johnson et al. 2010; Vollenweider et al. 2018) but primarily as juveniles. The scarcity of sand lance and capelin in the diet of Cooper Island guillemots suggests they are either too uncommon or small to be a regular alternative prey.

In the eastern Arctic, loss of sea ice and increasing SST are allowing high quality sub-Arctic fish to expand their ranges northward and are being consumed by seabirds formerly reliant on polar cod, as part of the “Atlantification” of the Eastern Arctic (Gaston and Elliott 2014; Vihtakari et al. 2018). While similar northward expansions are occurring in the Pacific Arctic, primarily the Chukchi Sea (Huntington et al. 2020), sub-Arctic forage fish of sufficient abundance and suitable size have apparently not entered the Beaufort Sea nearshore. Continued warming of nearshore waters could increase the abundance of sand lance and capelin, which are most abundant in the Beaufort Sea nearshore in warm years (Jarvela and Thorsteinson 1999) and could provide alternative prey when the seasonal loss of polar cod occurs.

Dive behaviour in response to the increasing SST and the prey shift

Dive frequency increased linearly with calendar date, with a concurrent nearly linear increase in SST, indicating a prey base that was declining throughout the nestling period (Table 1 and Fig. 5) and also increases in nestling energy

requirements with age (Sotillo et al. 2019) (Table 1 and Fig. 5). The increase in dive depth when polar cod were the primary prey, and resulting increase in dive duration, indicates a decreased availability in the shallow waters close to the colony. The increase in dive depth and duration during the Transition phase to the highest observed values is indicative of birds expanding their foraging range as polar cod became less available near the colony, before returning to shallower depths for sculpin, as is shown for a single bird in Fig. 6.

A lack of a significant difference in time at depth and patch quality between the Polar cod and Sculpin phases (Table 2) is surprising, given that the former is a schooling fish present throughout the water column, while the latter is a non-schooling demersal. Indeed, thick-billed murres repeatedly returning with polar cod have short dives but more time spent flying compared with those returning with sculpin, implying that cod are easy to find and capture underwater once a school is encountered but that finding schools can be challenging in the absence of ice (Elliott et al. 2009a, b). Perhaps in the relatively homogenous, shallow nearshore environment near Cooper Island, variation in time at depth and patch quality is difficult to detect even between these two preys with relatively different lifestyles. Interestingly, the dive profiles of thick-billed murres preying on sculpin and polar cod also overlapped considerably, which was believed to reflect polar cod being caught primarily during benthic dives after the ice has left (Elliott et al. 2008).

Decadal overview and prospects

Seasonal reductions in sea ice and increase in water temperature in the foraging area, similar but smaller in scale to the ones we found affecting prey type and behaviour, have occurred since the late 1990s (Fig. 7). Based on our observed increase in dive effort in response to increasing SST, it is reasonable to assume that prey reductions and a behavioural response to them have been occurring since the late 1990s. The extent of multi-year ice in the Beaufort declined in the late 1990s with a corresponding decrease in ice thickness (Kwok 2018; Li and Yin 2020). Since sympagic (under-ice) fauna, including polar cod, are most abundant under multi-year ice (Lonne and Gulliksen 1991a, 1991b), the decrease of multi-year ice could be expected to affect the regional availability of sympagic prey. Thinner ice would also result in earlier melting of sea ice, advancing its disappearance from the foraging areas and the timing of the seasonal increase in SST, as evidenced by Fig. 7.

While changes in diving behaviour were likely to occur from the oceanographic changes occurring since the late 1990s, it was not until 2003 that a colony-wide prey shift occurred with early August SST increasing from a long-term mean of 1.4 °C for earlier years to 3.3 °C and distance to

sea ice of > 30% increasing from 40.2 to 131.6 km (Divoky et al. 2015). Our current observations provide further evidence that a prey shift from polar cod occurs at SST of \approx 3.5 °C, but as that threshold occurred in earlier years with no prey shift, the 100 km increase in distance to the pack ice in 2003, appears to have been a major factor affecting polar cod availability, demonstrating the importance of oceanographic conditions adjacent to the foraging area.

The major advancement, approximately two weeks, in the timing of annual sea ice loss during the last two decades (Fig. 7) has decreased the period during which parents can provision their young with lipid-rich preferred prey. This trophic mismatch is offset somewhat by an advancement of breeding phenology (egg laying), as earlier snowmelt has allowed earlier access to nest cavities with date of egg laying advancing approximately 8 days since 1975 (Cox et al. 2017; Sauve et al. 2019). Even in years when polar cod are not present during the nestling period, as in 2017 and 2019, earlier breeding would still benefit parents as our dive data indicates sculpin availability declines throughout the period they are the primary prey, perhaps in part from predation by guillemots.

Ecosystem effects

Sea ice loss and increasing SST are affecting other species that utilize the foraging area of the Cooper Island guillemots and other areas of the nearshore Beaufort and similar effects could be expected elsewhere in the Arctic. Fauna linked to under-ice food webs provided a major food source for both breeding birds and migratory flocks of a number of surface-feeding seabirds in the extreme Western Beaufort in the late 1970s. The breeding success of a colony of 75 Arctic Terns studied on Cooper Island in the late 1970s, was sensitive to annual variation in the availability of prey associated with multi-year sea ice (Boekelheide 1979). With little multi-year ice present for over a decade that colony is now reduced to less than ten pairs with regular colony-wide breeding failure. In the 1970s in July and August the waters around Cooper Island supported large numbers of migratory flocks of surface-feeding seabirds, primarily Glaucous Gull (*Larus hyperboreus*), Sabine's Gull (*Xema sabini*), Black-legged Kittiwake and Arctic Tern (*Sterna paradisaea*) feeding on polar cod and the ice-associated amphipod, *Apherusa glacialis* whose annual and seasonal abundance was dependent on the presence of decomposing multi-year ice (Boekelheide 1979; Connors 1984). In the last two decades feeding flocks of migrants are less regular and decreased in number and, when present, primarily feed on euphausiids, *Thysannoessa* sp.

Decreased availability of polar cod is also affecting marine predators in the Eastern Beaufort Sea. Ringed Seals

(*Pusa hispida*) in the eastern Beaufort have had a two-decade decline in body condition attributed to decreased availability of polar cod (Harwood et al. 2015). A colony of Mandt's Black Guillemots on Herschel Island, NWT, monitored for the last five decades, has, like the Cooper Island colony, experienced a major population decline since the 1990s and a shift from polar cod to nearshore demersals in the last decade (Eckert 2014).

Conclusions

These and earlier observations indicate that a nearshore marine environment, capable of maintaining successful breeding and a stable population at the Cooper Island Mandt's Black Guillemot colony, existed only when seawater temperatures and ice conditions in the foraging area facilitated the presence of polar cod (Fig. 7). In response to the reduction and absence of polar cod, Mandt's Black Guillemot demonstrated plasticity in foraging behaviour by both prey-switching and modifying diving behaviour and location. Nonetheless, the response is unlikely to ensure the maintenance of the Cooper Island colony. To forage on the alternative prey, fourhorn sculpin, adults increase their dive frequency and time underwater, potentially increasing the cost of reproduction and decreasing adult survival. Additionally, the condition and survival of nestlings decreases with the switch to the alternative prey (Divoky et al. 2015) with current fledging success unable to sustain the colony. While the loss of polar cod has contributed to decreases in breeding success, the decline of the colony, from over 200 pairs in 1989 to <50 pairs in 2020, began before a prey-switch was observed in 2003 (Divoky et al. 2015). The initiation of the decline was correlated with a shift in the Arctic Oscillation in 1989/90 causing increased atmospheric temperatures and decreased sea ice extent throughout the Western Arctic (Maslanik et al. 1996; Rigor et al. 2002) and a decrease in the rate of immigration to the Cooper Island colony. The response of parent birds to the loss of polar cod, switching to a low-quality prey, greatly increasing dive effort, and switching from ocean to lagoonal foraging, all indicate the low quality of the foraging area in the absence of the cryopelagic ecosystem. The low species diversity of the Arctic results in few suitable alternative prey, while the extremely shallow foraging areas, prone to ice scour that limits nearshore sessile benthos that provide foraging habitats at more southern latitudes, presents a limited seascape for the guillemots in northern latitudes to exploit. Our observations likely foreshadow broader effects that may lead to the disappearance of a cryopelagic nearshore predator from the Beaufort Sea ecosystem. The timing of the annual loss of the cryopelagic system from the nearshore will almost certainly advance

in coming years, reducing even further the availability of polar cod during the provisioning of nestlings and increasing dependence on nearshore benthic prey. The colony of Mandt's Black Guillemots on Herschel Island, after a number of years of breeding failure and decline, in 2018 and 2019 had birds occupying the colony but failing to lay eggs (Eckert 2018 pers. comm.) indicating a lack of prey at the start of the breeding season.

A reliance on sea ice-associated prey, primarily polar cod, is likely why High Arctic Black Guillemot colonies can attain numbers well above *Cephus* colonies at lower latitudes. Few *Cephus* colonies outside of the Arctic exceed one thousand birds, while three Arctic islands adjacent to summer sea ice have populations estimated at 10 thousand birds or more: Herald (60–70 thousand), Wrangel, De Long and Devon Islands (10 thousand each) (Golovkin 1984; Stishov 2004; Artukhin 2016; Birdlife International 2021). While nest-cavity availability can limit colony size for the genus (Preston 1968; Petersen 1981; Ainley et al. 1990), lower latitude colonies, including Arctic colonies not associated with sea ice, never reach the numbers found in other cavity-nesting alcids, indicating both the limitations of reliance on ichthyofauna present in a spatially-restricted shallow foraging area and the potential for density-dependent reductions in benthic prey with increasing colony size (Storer 1952; Elliott et al. 2009a, b). That some Arctic colonies, able to exploit the cryopelagic ecosystem and its primary forage fish, polar cod, support numbers an order of magnitude larger than elsewhere, indicates sea ice provides a prey base of schooling fish that alleviates constraints imposed by the dependence on nearshore benthic prey. Our findings presented here, and the reduction of the Cooper Island colony from > 200 pairs in the late 1980s to < 50 in 2020, during a period of rapid ice loss and increasing SST in the region, indicate the Cooper Island colony is becoming similar to lower latitude *Cephus* colonies, with a smaller number of pairs dependent on nearshore demersal prey.

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Author contributions EB collected the 2017 data, compiled the dive dataset, Figs. 3, 4 and 5 and the Tables. She wrote the original draft as part of her Honours thesis. GJD collected, or oversaw collection of,

data for all remaining years. He produced Figs. 1, 2, 6 and 7 and rewrote much of the paper. KHE produced the remaining figures, supervised EB and edited subsequent drafts of the paper.

Compliance with ethical standards

Ethical approval All activities were approved by federal and state permits, and under the guidelines of the Canadian Council for Animal Care (Permit: 2015–7599). The authors declare no competing interests.

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