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Effects of recent decreases in arctic sea ice on an ice-associated marine bird

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ABSTRACT

Recent major reductions in summer arctic sea ice extent could be expected to be affecting the distributions and life histories of arctic marine biota adapted to living adjacent to sea ice. Of major concern are the effects of ice reductions, and associated increasing SST, on the most abundant forage fish in the Arctic, Arctic cod (*Boreogadus saida*), the primary prey for the region's upper trophic level marine predators. The black guillemot (*Cepphus grylle mandtii*) is an ice-obligate diving seabird specializing in feeding on Arctic cod and has been studied annually since 1975 at a breeding colony in the western Beaufort Sea. The data set is one of the few allowing assessment of the response of an upper trophic marine predator to recent decadal changes in the region's cryosphere. Analysis of oceanographic conditions north of the colony from 1975 to 2012 for the annual period when parents provision young (mid-July to early September), found no major regime shifts in ice extent or SST until the late 1990s with major decreases in ice and increases in SST in the first decade of the 21st Century. We examined decadal variation in late summer oceanographic conditions, nestling diet and success, and overwinter adult survival, comparing a historical period (1975–1984) with a recent (2003–2012) one. In the historical period sea ice retreated an average of 1.8 km per day from 15 July to 1 September to an average distance of 95.8 km from the colony, while in the recent period ice retreat averaged 9.8 km per day to an average distance of 506.9 km for the same time period. SST adjacent to the island increased an average of 2.9 °C between the two periods.

While Arctic cod comprised over 95% of the prey provided to nestlings in the historical period, in the recent period 80% of the years had seasonal decreases, with Arctic cod decreasing to <5% of the nestling diet, and nearshore demersals, primarily sculpin (Cottidae), comprising the majority of the diet. A five-fold increase in the rate of nestling starvation and reductions in nestling growth and fledging mass were associated with the shift from Arctic cod. Annual adult survival during the nonbreeding season (September–May), showed no significant difference between the two periods, indicating no major change in availability of Arctic cod or other prey in the wintering area in the Bering Sea. Our findings of a substantial decrease in Arctic cod availability in late summer in response to decreased ice extent and increasing SST have implications for the entire Arctic given the ongoing and predicted basin-wide reductions in sea ice.

1. Introduction

Arctic sea ice has undergone major reductions in recent decades with September ice extent (the area covered by ⩾15% sea ice) declining more than 11% per decade since 1979 while decreases in multiyear ice and ice thickness resulted in an 80% reduction in volume (Comiso, 2012; Laxon et al., 2013). In Alaskan waters these changes have been most pronounced in seas that historically had perennial ice, the Chukchi and Beaufort seas, and less pronounced in the seasonal ice present in the Bering Sea in winter, which has demonstrated high annual variation but no decreasing trend in ice extent (Stabeno et al., 2012; Wendler et al., 2013). Until recently, the Chukchi and Beaufort seas retained extensive ice cover even during the period of melt in summer and fall, but now both seas experience extensive and rapid ice loss in July–September, resulting in increases in sea surface temperature (SST) in areas of open water. Continuing reductions in summer sea ice are anticipated with the disappearance of summer ice from the Arctic Basin predicted to occur in coming decades (Livina and Lenton, 2013; Maslowski et al., 2012; Overland and Wang, 2013; Singh et al., 2013). While the loss of ice has been well documented with satellites, the effects of ice loss on ice-associated biota is

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poorly known. The fish and zooplankton components of the sympagic (or cryopelagic) under-ice marine ecosystem are an important energy source for arctic marine predators (Bradstreet and Cross, 1982; Melnikov et al., 2002), and the recent and predicted decreases in sea ice and increases in SST could be expected to alter the abundance and availability of prey for marine upper trophic level predators (Moline et al., 2008; Wassmann, 2011) such as seabirds and seals, throughout the Arctic.

Arctic cod (*Boreogadus saida*), also known as polar cod, is the primary forage fish in the sympagic ecosystem and the major link in the transfer of energy from lower to upper trophic levels for ice-associated and cold water (<4 °C) pelagic food webs in the Arctic (Welch et al., 1992). It is an important prey item for many marine birds and mammals in the Alaskan Chukchi and Beaufort seas (Divoky, 1984; Frost and Lowry, 1984; Watson and Divoky, 1972) and elsewhere in the Arctic Basin (Bradstreet and Cross, 1982; Hop and Gjosaeter, 2013; Moline et al., 2008). Arctic cod feed on sympagic zooplankton (Lonne and Gulliksen, 1989) which are also important prey for birds and mammals associated with sea ice (Craig et al., 1982; Divoky, 1976; Frost and Lowry, 1984; Lowry and Frost, 1981). Although Arctic cod are also found at depth and in waters without sea ice (Craig et al., 1982; Matley et al., 2013; Walkusz et al., 2013), they are thought to be either more abundant or more available to marine birds and mammals in surface waters with sea ice cover (Crawford and Jorgenson, 1990; Hop and Gjøsæter, 2013). In the late 20th Century an estimated 29,000 metric tons of Arctic cod were consumed annually by predators on the Alaskan Beaufort Sea shelf (Frost and Lowry, 1984). Assessing the effects of reductions in sea ice on arctic marine predators and their sympagic prey is important as continuing reductions in arctic sea ice are predicted (Wang and Overland, in press), as is the disappearance of summer ice within decades (Overland and Wang, 2013). Previously published evidence of the effect of recent sea ice retreat on Arctic cod availability to seabirds was obtained at a subarctic thick-billed murre (*Uria lomvia*) colony in Hudson Bay where the proportion of Arctic cod decreased beginning in the late 1990s coincident with decreasing summer ice (Gaston et al., 2012, 2003).

Guillemots (*Cepphus* spp.) are diving marine birds that can reach depths as great as 40 m (Masden et al., 2013) but in northern Alaska typically feed at <25 m (Divoky pers comm.). While provisioning young, guillemots differ from most seabirds in that, rather than foraging over a large expanse of offshore waters and exploiting patchy prey sources, they utilize nearshore fish (Ainley et al., 1990a). The limited foraging range of the genus during breeding, typically within a few km of the colony (Ainley et al., 1990b; Cairns, 1987; Ewins, 1990) and the ability to exploit a diversity of schooling and demersal fish, makes guillemots effective monitors of prey availability in nearshore ecosystems (Litzow et al., 2000). The black guillemot (*Cepphus grylle mandtii*) is a high arctic seabird that is a pack-ice obligate, breeding in colonies adjacent to summer sea ice and wintering throughout the pack ice as far south as ice extends into the Bering Sea (Kessel and Gibson, 1978). Arctic cod and sympagic invertebrates are the primary prey for the species throughout the Arctic Basin (Bradstreet and Cross, 1982; Divoky, 1984; Lonne and Gabrielsen, 1992). While adult black guillemots prey on both fish and invertebrates, parent guillemots provision nestlings mainly fish (Bradstreet and Brown, 1985). Unlike most alcids, guillemots lay two eggs with pairs frequently able to successfully fledge two young, reflecting their relatively close proximity to foraging areas, typically within 10 km of the nest site (Bradstreet and Brown, 1985). Provisioning guillemot parents return with a single prey item per successful foraging trip. In northern Alaska black guillemots provision nestlings from mid-July to early September during the period of summer sea ice retreat. After nesting, most black guillemots breeding in northern Alaska first move north to the ice edge in the Beaufort and Chukchi seas and then south through the Bering Strait with advancing sea ice. After wintering (December–April) near the southern extent of sea ice in the eastern Bering Sea (Divoky pers.comm.) they return to the area of Pt. Barrow in late April and early May (J.C. George pers. comm.).

A Black Guillemot colony on Cooper Island, Alaska (Fig. 1) has been monitored annually from 1975 to the present, a period that includes the entire satellite record of ice extent (1979 to present). Here we first examine long-term variation in the physical oceanography of the areas utilized by guillemots during provisioning of chicks and then present data on nestling diet and condition for historical and recent periods to determine the effects of the physical oceanographic changes on prey availability. We also examined annual survival of adult guillemots to assess if decadal variation in the availability of Arctic cod or other ice-associated prey was affecting guillemot survival on the wintering area (Fig. 2) or during migration.

2. Methods

2.1. Study site and study periods

Black guillemots have been studied annually from 1975 to present (2014) at Cooper Island (71° 20′N, 155° 41′W), a sand and gravel bar 35 km SE of Point Barrow, Alaska (Fig. 1). Guillemots are cavity-nesting alcids, typically breeding in cavities in scree and talus on rocky shorelines (Cairns, 1980; Harris and Birkhead, 1985) but all nests used on Cooper Island are in manmade cavities, giving investigators access to all nest contents. Creation of nest sites by investigators from 1975–1986 allowed the colony to grow from 10 breeding pairs in 1972 to 220 in 1988 (Divoky, 1998; Divoky et al., 1974); declining to 116 pairs in 2012 (Divoky pers. comm.).

We compare black guillemot nestling diet, breeding success (nestling growth, weight and mortality) and adult survival at Cooper Island for two decades, a historical period (1975–1984) that predates the onset of rapid basin-wide declines in summer sea ice extent in the early 1990s (Maslanik et al., 1996; Serreze et al., 1995) and a recent period (2003–2012) that includes years when summer ice extent and year-round volume were at historic lows (Cavalieri and Parkinson, 2012; Stroeve et al., 2007) (Fig. 3). We examined changes in SST and ice conditions between the

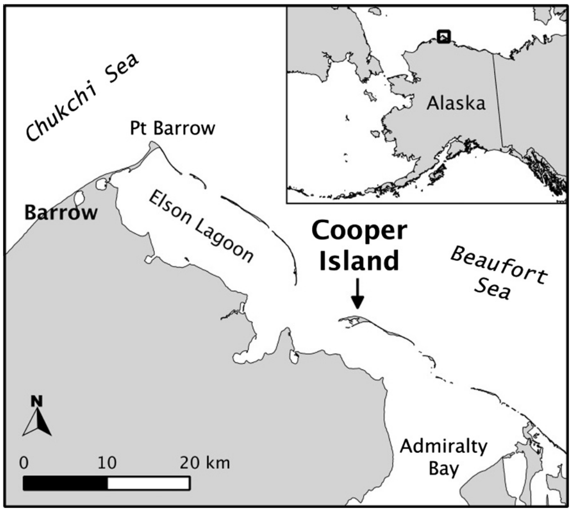

Fig. 1. Location of Cooper Island, Alaska where fieldwork was conducted.

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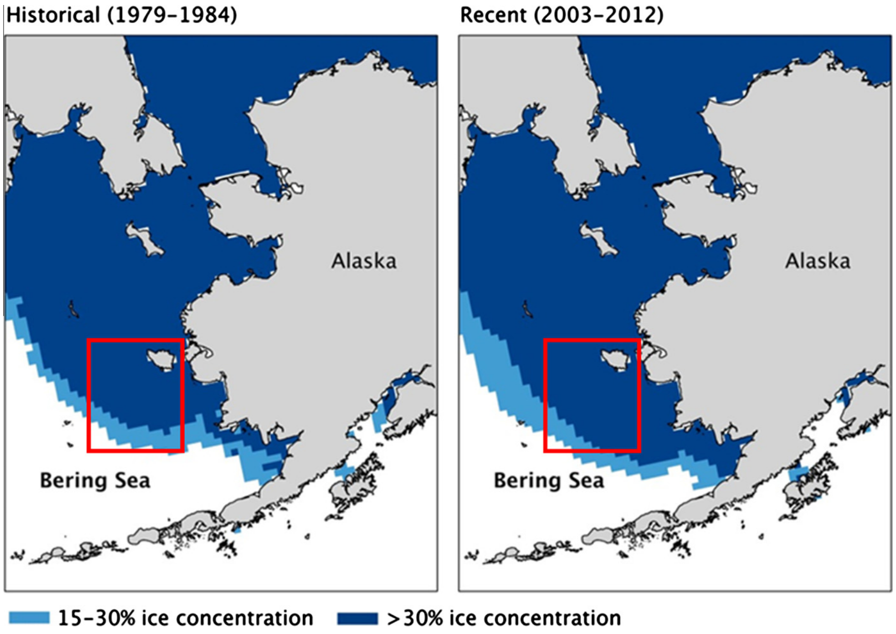

Fig. 2. Average ice concentration in the Bering Sea on March 9—the average date of the sea ice maximum—for a historical (1979–1984; left) and recent (2003–2012; right) time period. Red box shows approximate wintering location of Black Guillemots breeding on Cooper Island (Divoky unpublished data). Source: Daily SMMR, SSM/I, and SSMIS passive microwave data accessed from the National Snow and Ice Data Center.

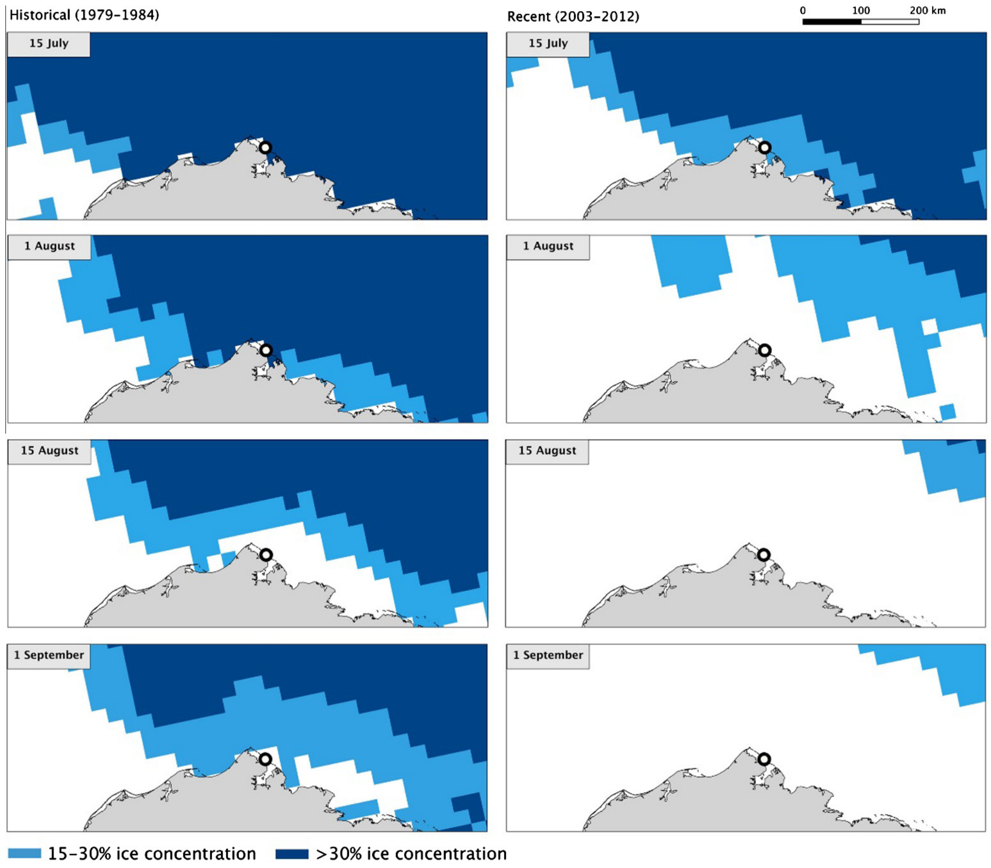

Fig. 3. Average ice concentration in the Chukchi and Beaufort seas on four specific dates during the period when black guillemots are provisioning young ice treat for a historical (1979–1984; left column) and recent (2003–2012; right column) time period. Source: Daily SMMR, SSM/I, and SSMIS passive microwave data accessed from the National Snow and Ice Data Center.

historical and recent periods in and adjacent to the waters used by guillemots provisioning young on Cooper Island. We also examined the available satellite record (1979–2012 for ice and 1981–2012 for SST) for regime shifts to determine the timing of any changes in SST and ice conditions occurring between the historical and recent periods.

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2.2. Physical oceanography north of Cooper Island

We examined annual variation in seasonal physical oceanographic variables (SST and distance to ⩾30% ice) in the guillemots' foraging range during the period of chick rearing. The mean SST for four periods when guillemots provision chicks (20–31 July, 1–15 August, 16–31 August and 1–10 September) was obtained from daily SST values for the quadrant 71°15′ – 71°30′N, 155°30 – 155°45W, with its southern border 2 km from Cooper Island and its north 30 km. SST was obtained from Advanced Very High Resolution Radiometer (AVHRR) Pathfinder data (1981–2005) and operational AVHRR data (2006–2012), provided by NOAA's National Climate Data Center (NCDC). Satellite-derived SST is not available before 1982 and sea ice not before 1979 but based on shipboard SST (Aagaard, 1984) and historical ice concentrations (Planning, 2014) (seaiceatlas.snap.uaf.edu) it appears that values from 1982 to 1984 are representative of the period.

Distance to sea ice cover ⩾30% was obtained from NIMBUS-7 SMMR (Scanning Multichannel Microwave Radiometer) and DMSP SSM/I (Special Sensor Microwave Imager/Sounder Passive Microwave Data), which was available every other day 1979–1986 and daily 1987–2012. The distance from Cooper Island to the center of the nearest 25 × 25 km grid cell (pixel) with sea ice concentration ⩾30%, if in a pixel cluster of greater than 1 pixel, was measured using the measuring tool in the QGIS software package. Distance was measured on four dates: 15 July, 1 and 15 August, and 1 September) for years 1979–1984 and 2003–2012. We mapped ice conditions for the area of ⩾15% and ⩾30% ice cover for those four dates (Fig. 3) from data obtained from the daily SMMR SSM/I and Special Sensor Microwave Imager/Sounder (SSMIS) passive microwave data accessed from the National Snow and Ice Data Center.

In addition to comparing SST and sea ice between the two ten-year periods, we also examined the long-term time series for SST (1981–2012) and distance to ⩾30% sea ice coverage (1979–2012) on 15 July, 1 and 15 August, and 1 September to determine the timing of regime shifts in those variables. We used a parametric sequential *t*-test analysis of regime shift (STARS) developed by Rodionov (2004) and modified by Rodionov and Overland (2005), that provides a probability level when identifying the year of a regime shift, based on the Student's *t*-test. The method calculates a Regime Shift Index (RSI), representing a cumulative sum of normalized anomalies relative to a critical value. A decision is made at each time step (year) to accept or reject the null hypothesis (no regime change occurred), or to keep testing. In STARS the time scale to be detected is controlled primarily by the cut-off length, which is similar to the cut-off point in low-pass filtering, and determines the minimum length of the regimes for which the magnitude of the shifts remains intact. A longer cut-off length hence identifies the strongest signal (as opposed to many smaller events). We used a cut-off length of 10 years with a probability level detector of 0.1.

2.3. Prey provided to chicks by guillemot parents

We assessed annual variation in nestling diet in two ways: (1) daily observations of prey carried by provisioning parents to determine when there was a prey shift from Arctic cod; and (2) daily recording of all fish found in nests during the weighing and measuring of nestlings, allowing assessment of increases in alternate prey. Black guillemots provision young by carrying a single fish crosswise in the bill to the chicks in the nest cavity, allowing identification of prey items. Observations of parents carrying prey were made during the course of daily nest checks, in dedicated feeding watches and with motion sensitive cameras. We estimated the daily percentage of Arctic cod in the nestling diet based on observations of prey being carried by provisioning parents. A year was considered to have undergone a prey shift from Arctic cod, which the chicks were fed exclusively at the start of the nestling period, when the percentage of the daily diet became <25% Arctic cod. In no year when cod were reduced to <25% of the daily diet was there a subsequent day when cod increased above that amount.

All prey items found in nests with nestlings were identified to genus or species and counted and measured. While Arctic cod are consumed by chicks upon delivery, sculpin are frequently either rejected completely or not consumed immediately, and are found in nest cavities. The rejection of sculpin may be due to their large spiny heads that result in chicks having difficulty swallowing larger sculpin (>100 mm) with instances of guillemot chick mortality from sculpin lodged in the throat uncommon but regular on Cooper Island. We used the number of active nests containing sculpin and the mean number of sculpin in nests that contained sculpin as an annual indicator of the extent of decrease in the availability of the preferred prey, Arctic cod.

2.4. Chick condition and success

Guillemot chicks were weighed at least every other day between hatching and fledging (range 28–37 days of age), except in 1975, when chicks were not weighed, and in 1982 and 1983 when chicks were weighed only during the last two weeks of the nestling period and linear growth was not obtained.

Four annual measures of chick condition were obtained: (1) mean daily change in mass (g/day) during the linear growth phase from age day 8 to day 18 (Emms and Verbeek, 1991); (2) peak mass; (3) fledgling mass; and (4) nestling mortality from starvation. Peak mass is the highest recorded weight and fledgling mass is the last recorded weight before fledging, usually the day of fledging but sometimes the day before. Annual means of chick growth and mass metrics were computed for each year and then averaged to obtain a mean for the period.

Nestling mortality from starvation is the percentage of all chicks that hatched that died from apparent starvation. Chicks assumed to have died from starvation include (1) chicks that died after a sustained decrease in mass or sustained lack of growth, (2) beta chicks (the younger of the two chicks in a brood) that died after showing signs of sibling aggression and concurrent decreases in mass or lack of growth: and (3) chicks that died in the nest whose deaths could not be attributed to other causes such as nest disturbance or predation. While the latter category can include death not related to prey quantity or quality all observed annual and seasonal increases in nestling mortality have been associated with decreases in growth.

2.5. Adult annual survival

Survival of black guillemot adults was obtained through banding of adults during the breeding season. From 1976 to 2012, breeding guillemots were captured at nest-sites, either while on the nest or through the use of a noose carpet at the nest entrance. Birds were banded with a metal USGS band and each received a unique combination of three plastic (Darvic) color bands allowing identification of individuals with binoculars. Individuals which lost color bands were recaptured and rebanded. Birds banded with a USGS band as nestlings were given color bands when recaptured as adults. Annual apparent survival was computed for the years following the breeding seasons discussed in this paper and totaled 734 breeding adults observed from 1976 to 1984 and 801 observed from 2003 to 2012. A total of 67 breeding adults was observed in both the historical and recent periods. The percentage of breeding

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birds that were banded was high, averaging 65% for the historical period and 87% for the recent.

We estimated survival using a multi-state mark-recapture model including live resightings and dead recoveries (Lebreton and Pradel, 2002). We included all observations of guillemots from 1976 to 2012 in the analysis because there is information about survival in the years of this study contained in the observations of birds in other years (2085 unique birds, 1468 of which were observed during the early or late periods). The model was fit in Program Mark (White and Burnham, 1999). We considered breeding and non-breeding as separate states for the model because breeding guillemots are much easier to detect and likely exhibit a different survival probability than non-breeding birds. Birds were considered breeders if they were using a nest box that contained at least one egg. We fit a single multi-state mark-recapture model that allowed survival to vary by year and breeding state. Recapture probability (resighting) was constant across years, but varied by state. Transition probability between states varied by current state. We used a variance components analysis to estimate mean survival during the early and late periods along with the process standard deviation of survival (Burnham and White, 2002).

3. Results

3.1. Physical oceanography of foraging area

Regime shifts in SST and sea ice conditions 1975–2012—During the annual period black guillemots provision young on Cooper Island, oceanographic conditions within and directly adjacent to the foraging area were relatively stable from the late 1970s to the late 1990s, with no regime shifts in SST or distance to ⩾30% ice before 1998 (Table 1). Between 1998 and 2009, however, statistically significant regime shifts occurred in SST for all four time periods and for distance to ⩾30% ice for three of the four sampling dates (Table 1).

SST north of the island remained low (<1.7 °C) and without a regime shift from 1981 to 2002. Beginning in 2003 regime shifts occurred in all four time periods with the largest SST increases occurring after mid-August. Late June and early August had increases of 1.1 °C in 2004 and 1.9 °C in 2003, respectively. Larger increases occurred in late August (2.8 °C in 2007) and early September (2.7 °C in 2009) raising the mean SST for both the late August and early September periods to 4.3 °C.

Distance from the colony to ⩾30% sea ice had no regime shift from 1979 to 1997 but beginning in 1998 large and statistically significant shifts occurred for three of the four dates on which distance was measured, the exception being 15 July which had a statistically insignificant shift in 2007. All of the remaining dates had two regime shifts occur with substantial increases in distance to ⩾30% ice. In 1998 there were shifts of 160 km and 207 km for 15 August and 1 September respectively. These same two dates had regime shifts in 2008 of 113 km and 345 km respectively. These shifts resulted in increases in distance to ⩾30% ice of 273 km for 15 August and 553 km for 1 September.

Decadal variation in SST and sea ice conditions—Both SST and distance to ⩾30% ice cover during the nestling period increased significantly between the historical and recent periods (Table 2 and Fig. 3). In the historical period, SST averaged <1 °C for all four annual sampling periods and no year had a maximum SST >1.5 °C. The decadal increases in average SST ranged from 1.79 to 3.27 °C for the four annual sampling periods with maximum SST in the recent decade ranging from 4.5 °C in late July to >7.0 °C for early September.

The distance to ⩾30% sea ice and the rate of ice retreat from Cooper Island underwent substantial changes between the historical and recent periods with significant differences in distance to ice for all four sample dates (Table 2 and Fig. 5). In the historical period on 15 July ice was present directly adjacent to the island in all years, with the 12.5 km distance reflecting the distance to the center of a 25 km × 25 km cell directly north of Cooper Island. In the recent period distance to ⩾30% ice on 15 July averaged 47.4 km with a range of 12.5–157.0 km. The rate of retreat for the 48 days after 15 July had a major increase between the two periods with sea ice retreating 1.7 km/d in the historical period and 9.6 km/d in the recent. On 1 September, as the nestling period was ending, distance to ⩾30% ice during the recent period was over >400 km more than it was in the historical period.

3.2. Prey provided to chicks

We observed a prey shift between the two sampling periods with nestling diet in the historical period being almost exclusively Arctic cod while in the recent period there was frequently an abrupt seasonal decline and disappearance of Arctic cod with a shift to nearshore demersals, primarily four-horned sculpin (*Myoxocephalus quadricornis*) comprising the majority of the diet (Table 3). While none of the years in the historical period had

Table 1
Regime shifts for (1) sea surface temperature north of Cooper Island (1982–2012) and (2) distance to ⩾30% sea ice concentration from Cooper Island (1979–2012).

1 – Sea surface temperature

	Year of shift	Pre-shift mean[a] (°C)	Post-shift mean[a] (°C)	Shift (°C)	Regime Shift Index[b]	*p*-Value [c]
Late July	2004	1.2	2.3	+1.1	0.18	0.03
Early August	2003	1.4	3.3	+1.9	0.25	0.01
Late August	2007	1.5	4.3	+2.8	0.88	<0.01
Early September	2009	1.7	4.3	+2.7	0.54	0.05

2 – Distance to ⩾30% ice concentration

	Year of shift	Pre-shift mean distance.[a] (km)	Post- shift distance.[a] (km)	Shift distance (km)	Regime Shift Index[b]	*p*-Value [c]
15 July	2007	20.4	70.8	50.4	<0.01	0.25
1 August	2003	40.2	131.6	97.4	0.87	0.07
	2009	131.6	250.1	118.5	0.12	0.03
15 August	1998	96.2	256.2	160.0	0.46	<0.01
	2008	256.2	369.4	113.2	1.23	0.05
1 September	1998	139.7	347.1	207.4	0.39	<0.01
	2008	347.1	692.4	345.3	3.14	0.04

[a] Weighted mean of the regime using Huber's weight function with the parameter = 1.

[b] Cumulative sum of normalized anomalies relative to a critical value.

[c] Confidence level of the difference between the mean values of the neighboring regimes based on the Student's two-tailed *t*-test with unequal variance.

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Table 2
Sea surface temperature (SST °C) north of Cooper Island, Alaska and distance (km) to ⩾30% sea ice concentration from Cooper Island for historical (1975–1984) and recent (2003–2012) periods. SST for the historical period is from 1982 to 1984.

		Historical		Recent				
		$\bar{x}$	Range	$\bar{x}$	Range	Increase	*t*	*p*-Value
Sea surface temperature (°C)	20–31 July	0.39	−0.3 to 1.0	2.18	0.2–4.5	1.79	−2.44	0.03
	1–15 August	0.54	0.5 to −0.7	2.93	0.4–5.3	2.38	−2.33	0.04
	16–31 August	0.13	−0.2 to 0.6	3.40	0.9–7.0	3.27	−3.09	0.01
	1–15 September	0.29	−0.4 to 1.5	3.20	1.0–7.1	2.91	−2.72	0.02
Distance to ⩾30% ice (km)	15 July	12.5	12.5	47.4	13–157	34.9	−2.21	0.05
	1 August	33.3	13–65	178.1	13–295	144.8	−4.43	<0.01
	15 August	81.2	13–173	317.4	106–460	236.2	−5.55	<0.01
	1 September	95.8	13–225	506.9	92–1083	411.1	−4.21	<0.01

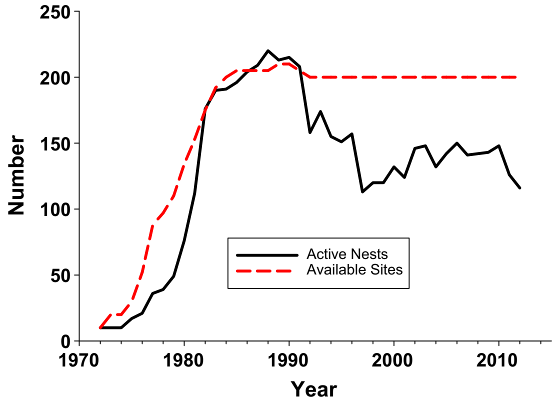

Fig. 4. Number of available nest sites and breeding pairs of black guillemots on Cooper Island, 1975–2012. Multiple pairs breeding in a single site allows the number of breeding pairs to exceed available nest sites.

Arctic cod reduced to <25% of the chick diet, a prey shift occurred in 8 of 10 years in the recent period. Sculpin were found in 10% of the nests during the historical period (the majority of which occurred in a single year, 1982) compared to 29% of the nests in the recent period. The number of sculpin in nests increased between the two periods, with the historical period averaging 0.22 per nest (again mainly in 1982) while the recent period averaged 1.36 sculpin per nest ($t = -2.6$, $p = 0.03$).

3.3. Chick condition and mortality

Guillemot nestling condition and survival decreased between the historical and recent periods. Chicks in the linear growth phase grew an average of 2.2 g more per day during the historical period than the recent (Table 3). While there was no significant difference in peak weight, average weight at fledging declined 25 g between the historical and recent period.

3.4. Adult annual survival

Adult annual survival of breeding guillemots was not measurably different between periods (historical period = 0.896, SE = 0.018; recent period = 0.866, SE = 0.018). In addition, the estimated process variation in survival was equal (SD = 0.05) for both periods.

4. Discussion

4.1. Variation in nestling diet and quality

The marine waters adjacent to Cooper Island underwent a series of shifts in the late 20th and early 21st Century going from being oceanographically “arctic” with perennial ice cover and SSTs <1 °C to being “subarctic”, with an extended annual period with no ice cover and SSTs >4 °C (Table 1). The *mandtii* subspecies of black guillemot breeding on Cooper Island is a true arctic seabird

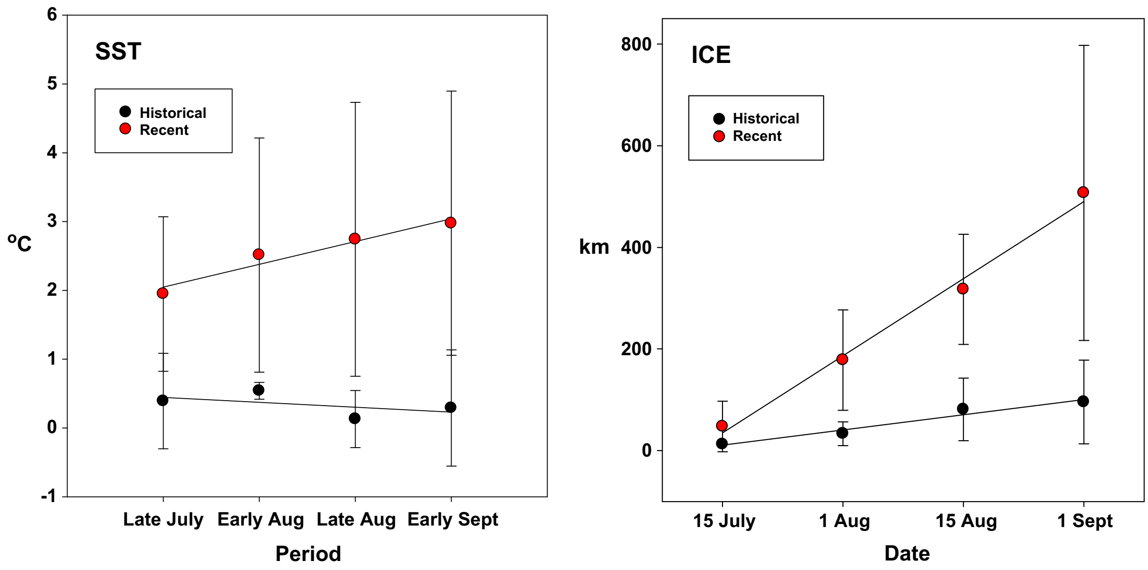

Fig. 5. Sea surface temperature (SST °C) north of Cooper Island, Alaska and distance (km) to ⩾30% sea ice concentration from Cooper Island for historical (1975–1984) and recent (2003–2012) periods. For the historical period SST is from 1982–1984 and distance to ice 1979–1984.

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Table 3
Annual chick condition and prey for historical (1976–1984 for chick growth and weight and 1975–1984 for percent starved, prey shift and sculpin present) and recent (2003–2012) decades. n = years data obtained.

		Historical			Recent			
	n	$\bar{x}$	s.d	n	$\bar{x}$	s.d.	t	p-Value
Chick condition								
Linear growth[a] (g/d)	6	15.0	1.2	9	12.8	2.1	2.6	0.02
Peak weight (g)	5	348	9.8	8	347	13.1	0.1	0.9
Fledge weight (g)	7	320	12.1	8	296	21.3	2.6	0.02
Percent starved[b]	10	5%	0.1	10	24%	0.2	−3.3	0.01
Prey								
Sculpins in nest[c]	10	0.2	0.2		1.4	1.4	−2.6	0.03
		Percent			Percent			
Nests with chicks where sculpin present	9	10%		10	29%			
Years with prey switch[d]	10	0%		10	80%			

[a] Growth (g/d) for age 8–18 d.
[b] Percent of hatched chicks presumed to die from starvation.
[c] Number of sculpin in nests where sculpin found.
[d] Percent of years when Arctic cod decreased to <25% of daily nestling diet.

having been restricted to an ice-covered portion of the Arctic Basin during the Last Glacial Maximum (Kidd and Friesen, 1998) where prey was apparently limited to sympagic fish and invertebrates associated with sea ice, causing it to become one of the few marine birds reliant on the arctic sea ice ecosystem for the entire year. The breeding distribution and wintering area of the subspecies in the western Arctic indicates it has maintained a dependence on ice-associated prey. Guillemots began breeding at Cooper Island sometime after the U.S. Navy left wooden boxes on the island in the mid-1950s and before the discovery of the colony in 1972 (Divoky et al., 1974). The rapid growth of the colony, from 10 to 210 pairs, in response to the provision of nest cavities by investigators in the 1970s and 1980s (Fig. 4) occurred during a period when summer ice retreat from the coast was minimal and SST <2 °C. The increasing number of foraging parents had no apparent effect on the amount of Arctic cod available to individual parents, as nestling growth and fledging rates of nestlings were high. Breeding productivity at other colonies in the region was also apparently high, given the large number of immigrants recruiting at Cooper Island during the period of colony growth. The rapid retreat of summer sea ice and concurrent increases in August SST in the 21st Century have reduced Arctic cod availability at the time of greatest caloric needs for the colony (mid-July to early September) as guillemot nestlings are undergoing a ten-fold increase in mass to near adult weight and parents provisioning chicks have their highest energy demand of the breeding season (Mehlum et al., 1993).

The clearest evidence of how the change in Arctic cod availability has influenced black guillemot breeding success is the almost fivefold increase in nestlings dying from starvation from the historical to recent period, increasing from 5% to 24%. Nestling mortality due to starvation is a more sensitive metric of prey quality and availability than nestling growth and mass for guillemots, as the latter two metrics can be misleading for species with two-chick broods and facultative sibling aggression and brood reduction. The asymmetric growth of the alpha and beta chicks due to facultative aggression by the alpha chick, (Cook et al., 2000) serves to mask the effects of decreases in prey quality or availability and facultative brood reduction frequently results in an increase in the mass of the surviving nestling.

The observed increase in nestling starvation in the recent period would have been larger had not many of the chicks losing weight and likely to die of starvation been killed by horned puffins (*Fratercula corniculata*) prospecting for nest sites or eaten by polar bears (*Ursus maritimus*). Nestling mortality due to horned puffins and polar bears increased from 2% in the historical period to 18% in the recent. The increase in both species on Cooper Island is related to the same oceanographic changes that have reduced the availability of Arctic cod. Horned puffins are a subarctic species that prospected nest sites on Cooper Island during the historical period (Divoky, 1982) and first bred on Cooper Island in 1986 (Divoky pers. comm.). Polar bears were rare on Cooper Island until 2002, but since have been regular visitors after late July (Divoky unpublished data), as summer sea ice loss forces polar bears to land throughout the Arctic Basin (Stirling and Derocher, 2012).

While we compare here a recent period beginning in 2003, with one two decades earlier that ended in 1984, our examination of regime shifts (Table 1) indicates that oceanographic shifts did not occur until the late 20th Century, with increases in distance to $\geqslant$30% ice, and early 21st Century, with increases in SST at the start of our recent period. The timing of these oceanographic changes near Cooper Island coincided with changes occurring in the Arctic Basin where SST increases were particularly pronounced since 1995, and especially since 2000 (Steele et al., 2008). While in two years before 2003, 1982 and 1988, increased numbers of sculpin in nest sites indicated some parents had shifted from Arctic cod to demersals, a colony-wide shift to sculpin did not occur until 2003. Oceanographic variables associated with the 2003 prey shift included a regime shift in the early August SST from 1.4 °C to 3.3 °C with a concurrent regime shift in distance to $\geqslant$30% sea ice on 1 August, from 40.2 km to 131.6 km. In the recent period only two years failed to have sculpin become the primary prey in the colony, 2006 and 2009.

Guillemot colonies elsewhere frequently have seasonal and annual shifts in prey species provided to chicks, as we observed (Ainley et al., 1990b; Barrett and Anker-Nilssen, 1997; Golet et al., 2000). Our observations of decreased nestling quality and survival associated with seasonal and annual dependence on demersal prey is similar to findings for pigeon guillemots (*C. columba*) in the Gulf of Alaska where breeding quality varied in response to geographic and annual variation in the availability of nearshore schooling fish, with chick growth and survival decreasing as the proportion of high-lipid schooling fish, Pacific sand lance (*Ammodytes hexapterus*), decreased and low-lipid demersal fish increased (Litzow et al., 2002).

While the decreases in black guillemot chick condition and survival in the recent period are correlated with a seasonal shift from Arctic cod to sculpin and other nearshore demersals, the causes for the decrease in chick condition associated with the prey shift are unclear but could include: (1) lower caloric value or decreased digestibility and assimilation of demersal prey, (2) the spines and

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girth of sculpin causing avoidance by parents and rejection by chicks, (3) lower abundance of demersals decreasing rates of chick provisioning.

The prey shift from Arctic cod to sculpin does result in a decrease in the energy density of prey provided to chicks. Analysis of fish collected at and near Cooper Island in 2013 found that Arctic cod had a slight but statistically significant higher caloric value than four-horned sculpin (6.04 ± 0.83 kJ/g wet mass, $n = 8$ vs 4.11 ± 0.39 kJ/g dry mass, $n = 7$, $t = 2.23$, $p < 0.01$) (R. Heintz, pers. comm.). Perhaps equally important is the decreased desirability of sculpin, compared to Arctic cod, to both guillemot adults and chicks. The large bony head, long sharp pectoral fins and opercular spines make sculpin hard to hold, manipulate and swallow for both adult guillemots and chicks. Although sculpin are present in the nearshore throughout the nestling period and in years when there is no prey shift (Johnson et al., 2010), adult guillemots do not provide them to young until Arctic cod have decreased in availability. This avoidance by adults may be due to the regular rejection of sculpin by nestlings which can occur even with chicks experiencing decreased growth rates. Small numbers, approximately 1% per year, of guillemot nestlings choke to death on sculpin and young regularly reject sculpin of any size and especially when >90 mm. One chick took three minutes to swallow a sculpin of 130 mm and another rejected a similar size sculpin after trying to swallow it for two minutes. In contrast Arctic cod up to 160 mm are readily consumed by guillemot nestlings as soon as they are brought to the nest.

While we lack information on the digestibility and assimilation efficiency of Arctic cod and sculpin, it is likely that the large bony head and spines of sculpin would increase residency time in the stomach, over that of Arctic cod, and reduce the rate at which nestlings could consume fish. Decreases in breeding success in seabirds in Great Britain was attributed, in part, to increased reliance on snake pipefish (*Entelurus aequoreus*) which had both nutritional and structural deficiencies as an alternative prey (Harris et al., 2008). Additionally, prey shifting is known to have an effect on digestive efficiency (Hilton et al., 2000) and assimilation efficiency is less for lower fat content fish.(Brekke and Gabrielsen, 1994).

The switch from Arctic cod to the lower quality sculpin is apparently necessitated by the low diversity of the nearshore ichthyofauna near Cooper Island. While a number of studies have found *Cepphus* spp. to regularly shift from schooling fish to less abundant demersal prey (Ainley et al., 1990b; Golet et al., 2000; Litzow et al., 2000, 2002), those studies and others (Barrett and Anker-Nilssen, 1997; Cairns, 1987; Ewins, 1990) have found guillemots to provide their young a diverse diet of nearshore demersals. Our findings differ from those studies in that we found guillemots switching from one primarily single-species diet of Arctic cod to another of the lower quality sculpin.

Our observations of a prey shift away from Arctic cod differ from that observed for thick-billed murres (*U. lomvia*) at colonies in the Canadian Arctic, where, as Arctic cod decreased in the chick diet, subarctic species, such as capelin (*Mallotus villosus*), increased, and might have been increasing in abundance as arctic waters warmed (Provencher et al., 2012). While subarctic species are expanding into the Beaufort Sea (Rand and Logerwell, 2011) and Pacific sand lance and capelin are present in the Point Barrow area and most abundant in years with higher SST and less sea ice (Johnson et al., 2010), subarctic prey are not increasing in the Cooper Island chick diet, as the demersal prey being consumed there are indigenous to arctic waters. The rarity of sand lance in the nestling diet at Cooper Island (<5%) as an alternative to Arctic cod is surprising given that it is a preferred prey of pigeon guillemots in subarctic Alaska (Golet et al., 2000) as is the scarcity of other suitable prey species, such as capelin, that are common to abundant near Cooper Island (Johnson et al., 2010; Rand and Logerwell, 2011).

There is evidence that other black guillemot colonies in the Western Arctic have undergone changes in population size and breeding success similar to what we observed on Cooper Island. At a colony on Herschel Island, Canada, in the eastern Beaufort Sea, the number of adults present at the colony has dropped by half from the 1980s and breeding success has been low since 2003, with the low success in 2014 associated with a shift to demersal prey, primarily sculpin (*Myoxocephalus* sp.) in the nestling diet (Eckert, 2014). There is indirect evidence of decreases in the productivity of other colonies in the region correlated with decreases in summer sea ice. The number of breeding birds (Fig. 4) and rates of immigration at the Cooper Island colony began decreasing in the early 1990s following a record ice minimum in 1990 and the onset of the rapid basin-wide decrease in summer sea ice (Maslanik et al., 1996; Serreze et al., 1995), including the waters adjacent to the large, >1000 birds, colonies in the western Chukchi and East Siberian seas (Golovkin, 1984) that are the likely source colonies for immigrants to Cooper Island.

4.2. Variation in adult survival

Adult seabirds are characterized by having high annual survival with the majority of mortality occurring during the nonbreeding season (Reynolds et al., 2011). Variation in annual survival of seabirds is sensitive to physical oceanographic conditions on the wintering area (Jones et al., 2002; Morrison et al., 2011) that affect prey availability. Sea ice extent and location in winter have been shown to affect seabird survival in Arctic regions (Ballerini et al., 2009; Smith and Gaston, 2012). Adult survival is a more elastic life history metric (Lebreton and Clobert, 1991) than breeding parameters since in the nonbreeding season adults can select areas of high prey density. During the breeding season seabirds are central-place foragers and breeding success is sensitive to seasonal and annual variation in prey availability within a relatively small foraging range.

Our findings of no significant difference in adult survival between the historical and recent periods suggests there have been no major changes in prey availability in the marginal ice zone of the Chukchi Sea in fall and spring or the Bering Sea in winter. Black guillemot movements during the nonbreeding period appear to be dictated by the formation and presence of ice with most birds remaining in the marginal ice zone in the Chukchi Sea in fall and in the winter primarily in the southeast Bering Sea (Divoky pers. comm.) or occupying leads in the ice in the Chukchi (Bailey, 1948). The lack of decadal change in adult survival between the historical and recent periods indicates that recent major decreases in multi-year ice in the Arctic Basin have not affected Arctic cod availability in the marginal ice zone in the Chukchi where they are known to be an important prey species. The importance of Arctic cod or any sympagic prey to black guillemots wintering in the Bering Sea is unknown. Arctic cod do occupy the Bering Sea shelf in winter, (Wyllie-Echeverria and Wooster, 1998) but given the diversity and abundance of forage fish in the Bering Sea, guillemots could rely on a number of subarctic species in winter should Arctic cod not be available.

Our finding of no decadal trend in adult survival is reflective of the relative long-term stability of the extent of sea ice occupied by Black Guillemots in the Bering Sea from December–April (Wendler et al., 2013). In the Canadian Arctic variation in sea ice concentration and SST in the wintering area affected survival of Thick-billed Murres with survival increasing slightly in years with more ice and lower SST (Smith and Gaston, 2012).

The lack of decadal change in adult survival of guillemot's breeding on Cooper Island also indicates that the presumed

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increased costs of reproduction associated with the switch from schooling mid-water prey to more dispersed benthic prey have not resulted in increased overwinter mortality. Pigeon guillemots provisioning young on dispersed demersal prey had significantly reduced resting time compared to birds exploiting schooling prey (Litzow and Piatt, 2003).

4.3. The importance of Arctic cod to seabirds and other upper trophic marine predators

Seabirds as upper trophic level marine predators are increasingly seen as reliable indicators of temporal variation in marine ecosystems (Anderson et al., 2014), and can be especially useful in remote areas, like the Arctic, which lack a commercial fishery and where traditional marine biological sampling methods are logistically and environmentally limited. While the importance of Arctic cod to marine birds is well known, our findings are the first to reveal that the recent decadal decreases in sea ice and increases in SST in the Alaskan Arctic are affecting Arctic cod availability and add to the observations elsewhere on the decreased availability of Arctic cod to upper trophic level predators (Gaston et al., 2003; Harwood et al., in press; Provencher et al., 2012). Given the importance of Arctic cod to Arctic marine predators, their decreasing availability has implications for much of the Arctic Basin as ongoing and predicted pan-arctic loss of ice and increases in SST are expected to greatly decrease Arctic cod distribution (Cheung et al., 2015).

Guillemots, as generalist nearshore feeders, typically exploit relatively reliable prey resources, utilizing nearshore schooling fish when available but reverting to lower quality but less ephemeral nearshore demersals as discussed above. Most studies of the genus have been conducted at subarctic or temperate colonies where guillemots can exploit a diverse demersal ichthyofauna when higher quality schooling prey are unavailable. Black guillemots breeding on Cooper Island, and elsewhere in the Arctic, have more limited prey options, as shown by our results, with parent birds going from a diet dominated by Arctic cod to one dominated by sculpin. This reliance on a single-species for the majority of a diet is characteristic of both marine and terrestrial ecosystems in the Arctic (Usher et al., 2005) where a trophic level may consist almost entirely of a single species, whose temporal or spatial variation in abundance can have major effects on the reproduction and survival of higher trophic level predators.

For guillemots and other nearshore marine predators in the Arctic, the paucity of alternative prey species is compounded by the low productivity and diversity of nearshore waters due to the effect of sea ice on nearshore benthic habitats (Barnes, 1999; Conlan et al., 1998). The regular disturbance of nearshore sediments and biota by anchor ice and scouring by ice keels can occur to depths up to 30 m (Conlan et al., 1998) and prevents the development of a temporally stable nearshore community (Barnes, 1999). Sessile benthic species, such as kelp (*Laminaria* spp. and *Macrocystis*) that can be an important feeding habitat for guillemots and other predators in the subarctic (Ewins, 1988; Follett and Ainley, 1976) are unable to develop in the Arctic except when isolated from ice scour (Wilce and Dunton, 2014). The consequences to guillemot reproduction on the reliance on a low diversity nearshore prey base is demonstrated by a black guillemot colony in Finland where a nearshore demersal, eelpout (*Zoarces viviparus*), composed over 95% of the prey delivered to chicks (Bergman, 1971). In two of the 16 years the colony was studied, eelpout availability decreased due to elevated SST leading to starvation of all chicks in both of those years (Bergman, 1978).

Our findings of annual and seasonal decreases in the presence of Arctic cod in guillemot nestling diets associated with decreasing ice and increasing SST have implications for many of the numerically important seabirds of the Beaufort and Chukchi seas that depend on Arctic cod while breeding or during migration. The seabird colonies at Capes Thompson and Lisburne in the Alaskan Chukchi, where recent changes in ice retreat have been similar to the western Beaufort, support >700,000 murres (*Uria* spp.) and >50,000 Black-legged Kittiwakes (*Rissa tridactyla*), both of which depend on Arctic cod during breeding (Springer et al., 1984). In addition many tundra-breeding migrants that utilize the Chukchi and Beaufort seas for summer staging and fall migration prey on Arctic cod (Divoky, 1976, 1984; Watson and Divoky, 1972).

The lack of decadal variation in black guillemot overwinter survival suggests that the abundance of Arctic cod and other prey at the ice edge in the Beaufort, Chukchi and Bering Seas has not undergone any major changes in the last four decades. While the abundance of Arctic cod and other sympagic organisms was believed to be closely related to the age and history of the ice (Lonne and Gabrielsen, 1992; Lonne and Gulliksen, 1991), the recent decline of multiyear ice in the Arctic (Comiso, 2012) is not affecting guillemot overwinter survival.

5. Conclusions

Our findings demonstrate how recent loss of sea ice and increase in SST have decreased the availability of Arctic cod, the primary forage fish in the Arctic Basin, and how that decrease has affected an arctic seabird adapted to utilizing prey associated with sea ice and Arctic waters. We observed significant changes in black guillemot nestling diet and decreases in nestling condition and survival between historical and recent periods but no change in adult annual survival. The difference in the two life history stages, nestlings and adults, appears to be related to the contrast in decadal trends in the two regions with extreme changes occurring in the oceanography of the western Beaufort Sea, while the wintering area in the Bering Sea has experienced no similar change, with ice extent and winter SST having high variability but no decadal trend (Wendler et al., 2013). Adult survival in seabirds is known to be sensitive to conditions on the wintering area (Jones et al., 2002; Smith and Gaston, 2012). This contrast in the response of the two life history stages demonstrates the utility of the black guillemot as a monitor of the sea ice ecosystem sensitive to both seasonal and geographic variations in marine conditions affecting prey availability.

Our findings provide evidence of the effects of recent loss of sea ice on the primary forage fish of the arctic marine ecosystem. The area of arctic marine waters affected by loss of summer ice, and where Arctic cod could now be expected to be less available to upper trophic level predators, is large with summer ice extent in 2007–2012 averaging 2,000,000 sq. km less than the 1979–2000 average. This loss of ice and associated increase in SST could be assumed to be limiting Arctic cod availability to other marine predators and could be expected to have a range of effects on the trophics, distribution and abundance of artic marine birds.

Within a few decades, arctic seabirds will be occupying marine ecosystems similar to those now found in the subarctic should summer ice disappear as predicted (Livina and Lenton, 2013; Maslowski et al., 2012; Wang and Overland, 2009), with higher temperatures and less scouring of benthos as ice thickness decreases. Unlike marine birds at lower latitudes that can shift their distribution poleward as the distribution of their prey responds to increasing ocean temperatures, arctic species dependent on prey associated with sea ice will have to adapt to a marine environment with an ever increasing annual ice-free period and concurrent loss of sympagic prey. The changes occurring in the Arctic may be too rapid to allow natural selection and the success of individuals will depend on phenotypic plasticity (Gilg et al., 2012), as is being seen at the Cooper Island black guillemot colony, where successful pairs are those best able to adapt to increasing variation in annual and seasonal foraging conditions.

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