

Murres, capelin and ocean climate: inter-annual associations across a decadal shift

P. M. Regular · F. Shuhood · T. Power ·
W. A. Montevecchi · G. J. Robertson ·
D. Ballam · J. F. Piatt · B. Nakashima

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Abstract To ensure energy demands for reproduction are met, it is essential that marine birds breed during periods of peak food availability. We

examined associations of the breeding chronology of common murres (*Uria aalge*) with the timing of the inshore arrival of their primary prey, capelin (*Mallotus villosus*) from 1980 to 2006 across a period of pervasive change in the Northwest Atlantic ecosystem. We also assessed the influence of ocean temperature and the North Atlantic Oscillation (NAO; an index of winter climate and oceanography) on these interactions. We found a lagged linear relationship between variations in murre breeding chronology and the timing of capelin arrival in the previous year. On a decadal level, we found a non-linear threshold relationship between ocean temperature and the timing of capelin arrival and murre breeding. Centennially anomalous cold water temperatures in 1991 generated a marked shift in the timing of capelin spawning inshore and murre breeding, delaying both by more than 2 weeks. By the mid-1990s, ocean temperatures returned to pre-perturbation levels, whereas the temporal breeding responses of capelin and murres were delayed for a decade or more. Oceanographic conditions (temperature, NAO) were poor predictors of the timing of capelin arrival inshore in the current year compared to the previous one. Our findings suggest that knowledge of the timing of capelin availability in the previous year provides a robust cue for the long-lived murres, allowing them to achieve temporal overlap between breeding and peak capelin availability.

P. M. Regular (✉) · W. A. Montevecchi
Cognitive and Behavioural Ecology Program,
Memorial University of Newfoundland,
St. John's, NL A1B 3X9, Canada
e-mail: paul.regular@mun.ca

F. Shuhood · T. Power
Parks and Natural Areas Division,
Department of Environment and Conservation,
Government of Newfoundland and Labrador,
33 Reid's Lane, Deer Lake, NL A8A 2A3, Canada

G. J. Robertson
Wildlife Research Division, Environment Canada,
6 Bruce Street, Mount Pearl, NL A1N 4T3, Canada

D. Ballam
Nature Conservancy of Canada,
49-55 Elizabeth Avenue, Suite 208, P.O. Box 11,
St. John's, NL A1A 1W8, Canada

J. F. Piatt
USGS Alaska Science Center, 1011 E Tudor Road,
Anchorage, AK 99503, USA

B. Nakashima
Fisheries and Oceans Canada,
Canada Northwest Atlantic Fisheries Centre,
80 East White Hills Road, St. John's,
NL A1C 5X1, Canada

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Introduction

Energy costs are high during breeding, and animals tend to reproduce when food is most abundant (e.g., Lack 1954). In marine systems, phytoplankton production is driven by physical oceanography, leading to seasonal increases in the availability of zooplankton and forage fishes (Aebischer et al. 1990; Bertram et al. 2001). Seabirds may rely on environmental cues to adjust their timing of breeding (Frederiksen et al. 2004). Local conditions, such as ocean temperature, could provide reliable cues about when to initiate breeding, yet species that disperse widely outside the breeding season may have to rely on environmental cues outside the breeding area (Both and Visser 2001). Owing to spatial variation in ocean climate, these cues are potentially less reliable (Deser and Blackmon 1993).

Pervasive changes in Northwest Atlantic food webs and ecosystems occurred in the early 1990s. The coldest surface water event during the past 50 to 100 years occurred in 1991 (Drinkwater 1996). The commercial extinction of northern cod (*Gadus morhua*) led to the closure of the eastern Canadian ground-fishery in 1992 (Hutchings and Myers 1994; Hutchings 2000). Through their influences on the timing, movement patterns and abundance of pelagic fishes and invertebrates, these events caused unexpected changes in food webs and trophic interactions. Capelin (*Mallotus villosus*), primary forage fish in the Northwest Atlantic (Lavigne 1996) and the major prey of cod (Bundy et al. 2000) exhibited delayed spawning and smaller sizes following the 1991 cold-water perturbation (Carscadden and Nakashima 1997; Carscadden et al. 2002). Capelin spawned 4 to 6 weeks later throughout the 1990s and into the early 2000s.

In the context of these ecosystem changes, we examined the timing of breeding common murres (*Uria aalge*), the primary avian predator of capelin in the Northwest Atlantic (Montevecchi

2000). These seabirds provision their chicks primarily with capelin in Newfoundland colonies (e.g., Piatt 1987; Davoren and Montevecchi 2003; Burke and Montevecchi 2008). Consequently, successful chick-provisioning and reproduction depends on the timing and inshore availability of capelin (Burger and Piatt 1990; Davoren and Montevecchi 2003; see also Vader et al. 1990). Thus, to help ensure energy demands for reproduction are met, murres should coincide breeding with the inshore movements of capelin schools (Cairns et al. 1987; Piatt 1987, 1990).

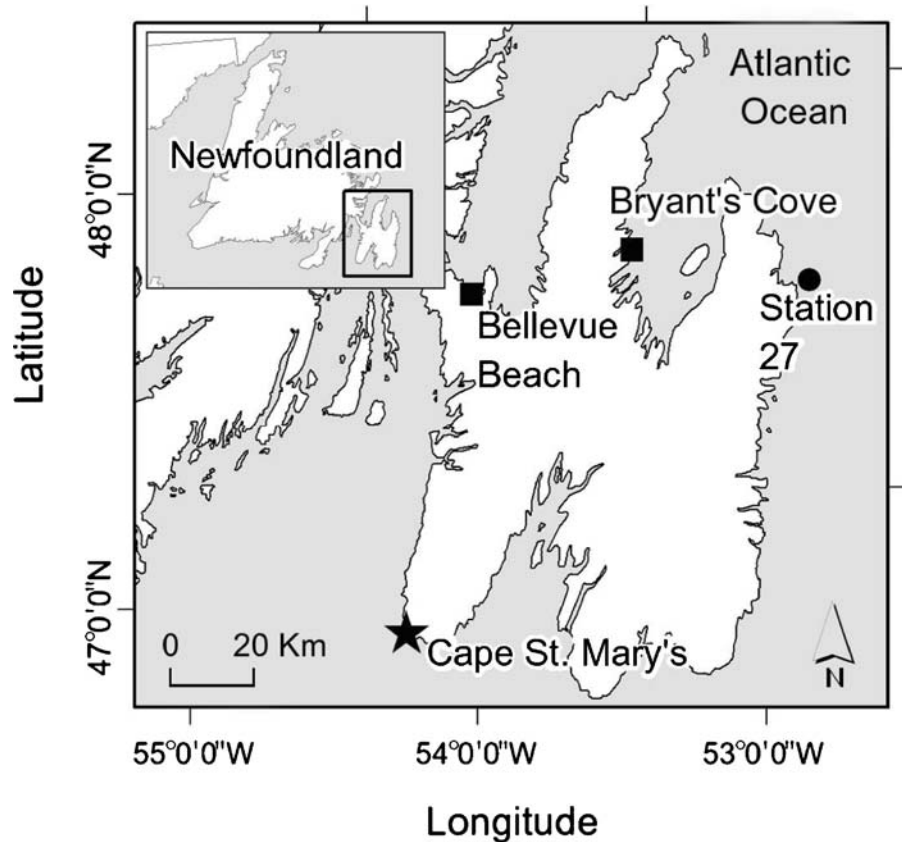
In this paper, we analyze the breeding times of common murres at Cape St. Mary's Ecological Reserve, Newfoundland from 1980 to 2006. With this relatively long-time series available, we examine the hypotheses that the timing of murre breeding chronology is associated with the timing of the inshore migration of capelin, and variations in ocean temperatures and oceanography, as indexed by the North Atlantic Oscillation (NAO).

Methods

The study was carried out at the Cape St. Mary's Ecological Reserve (CSM; 46°50'N, 54°12'W), Newfoundland, Canada (Fig. 1). Near-vertical cliffs composed of stratified sedimentary rock rise 100–150 m above sea-level and are lined with numerous broad and narrow horizontal ledges suitable for breeding by both common and thick-billed (*Uria lomvia*) murres. The total breeding population of murres was estimated at 10,000 and 1,000 pairs of common and thick-billed murres, respectively (Nettleship 1980).

From 1980 to 2006, common murres were monitored using the Type II method described by Birkhead and Nettleship (1980). Observations were made from late-May to early-August on six study plots (containing ~1,000 common murres), throughout the breeding cycle from laying through to fledging. Observations were usually conducted every 1–7 days in fair weather, with wider intervals between observations when weather was poor (heavy rain, strong wind and/or dense fog), from 11:00 to 16:00 Newfoundland Daylight Savings Time. Observers counted the number of murres within plots and watched for

Fig. 1 Location of Cape St. Mary's Ecological Reserve (filled star), capelin spawning beaches (filled square), and hydrographic station 27 (filled circle); inset shows location of Avalon Peninsula on insular Newfoundland



the presence/absence of eggs and/or chicks, allowing annual patterns in attendance to be observed (e.g., Piatt and McLagan 1987) and the timing of various aspects of murre breeding biology to be estimated. Although data on the timing of egg laying ($n = 12$ years) and fledging ($n = 18$ years) were collected in several years, the analyses in this paper are based on first hatching date because these were recorded every year from 1980 to 2006, except for 2003 ($n = 26$). The timing of hatching was taken as the date of the first sighting of a chick under a brooding parent.

Capelin arrival was recorded at local beaches (<50 km from CSM) and at Bryant's Cove and Bellevue Beach about 100 km north of CSM (Fig. 1). Throughout the study period, dates of the first spawning activity of capelin at local beaches were obtained from capelin spawning records kept by T. Power and local fishers ($n = 11$ years). Peak capelin spawning dates (day with the highest new fertilized egg deposition) from Bryant's Cove and Bellevue Beach were available from 1980 to

1990 and 1991 to 2006, respectively. The dates of first spawning activity on local beaches were significantly correlated with the combined series of peak spawning dates from Bryant's Cove and Bellevue Beach ($r = 0.667$, $n = 11$, $P = 0.025$). Given the combined spawning data from Bryant's Cove and Bellevue Beach is a complete dataset, and the patterns corroborate with local spawning dates, we used the combined peak spawning dates from Bryant's Cove and Bellevue Beach as an index of capelin chronology. Capelin timing and availability are used synonymously throughout this paper, because we assume that capelin are available to breeding murres when they arrive in inshore waters.

Ocean temperatures (0–150 m) for February–June, 1980–2006, were obtained from hydrographic station 27 (47°31'50"N, 52°35'10"W) situated 17 km east of St. John's, Newfoundland in the Avalon Channel branch of the Labrador Current, approximately 140 km northeast of CSM (Fig. 1). The hydrographic measurements

obtained from station 27 provide robust indices for oceanographic conditions of the Labrador Current which dominates the entire Newfoundland and Labrador Shelf (Petrie et al. 1988; Drinkwater 1996). Values for winter (December to March) NAO indices were obtained from the US National Centre for Atmospheric Research (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>) as indices of overall physical variability spanning breeding and migratory locations. NAO models the pressure differential between the Icelandic low and the high pressure system near the Azores. In the Northwest Atlantic, negative (positive) NAO indices generally indicate warmer (colder) conditions in northern regions. The opposite response is seen in the southern regions of the Northwest Atlantic (Petrie 2007).

We used simple and multiple linear regressions (without interactions) to test associations between variables. All possible models were constructed starting with the global model (the model including all variables of interest) and proceeding to simpler models. Predictors to explain the timing of murre hatching included: the time of murre hatching in the previous year, the timing of capelin in the current and previous years, ocean temperature and the winter NAO index. For capelin timing, timing of capelin in the previous year, ocean temperature and the NAO index were considered. This resulted in 25 models with the date of first chick sighting as the response variable, and seven models with the date of capelin arrival as the response variable. For oceanographic conditions, we also considered logical comparisons of positive to negative states and time lags of 1, 2, 3, 4, and 5 years. The most appropriate model was selected using Akaike's Information Criterion adjusted for small sample size (AIC_c). This value selects the model with the best balance between bias and precision, irrespective of sample size (Burnham and Anderson 2002). AIC_c rewards goodness of fit (log-likelihood, $\log(L)$) and also includes a penalty that is an increasing function of the number of estimated parameters (K). The model with the smallest AIC_c is the best in the sense that it explains the most variation in the data without using an excessive number of parameters. The relative importance of models is compared according

to Anderson et al. (2001) using ΔAIC_c and AIC_c weights (w), where ΔAIC_c is the absolute differences to the smallest AIC_c value in a set of models and w is the relative likelihood of a model given the data.

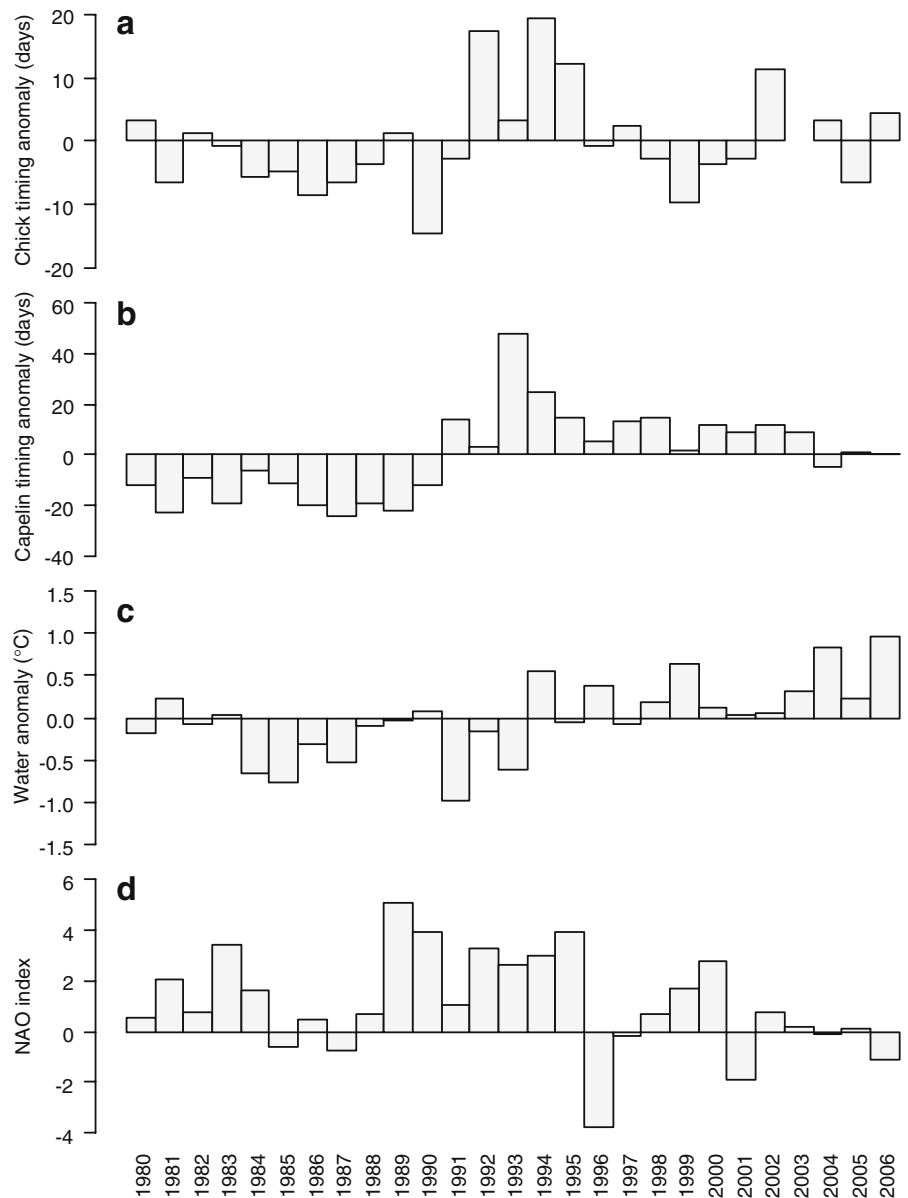
Results

The date of first chick sighting was relatively stable throughout the 1980s and were delayed substantially by approximately 3 weeks beginning in 1992 (Fig. 2a). Chick timing ranged from 8 June in 1990 to 12 July in 1994 (mean = 21 June, SD = 8.1 days, CV = 4.7). The date of capelin arrival was delayed by ~1–5 weeks during the early 1990s (Fig. 2b). Capelin arrival ranged from 12 June in 1987 to August 23 in 1993 (mean = 6 July, SD = 17.0 days, CV = 9.0). Ocean temperatures (0–150 m) from February to June also varied greatly across the study period: minimum = -1.14°C (1991), maximum = 0.79°C (2006), mean = -0.16°C , SD = 0.46°C , CV = -292.27 (Fig. 2c). NAO index was positive for 20 of the 26 years in this study (Fig. 2d). The maximum NAO index was 5.1 in 1989, and the minimum was -3.8 in 1996 (mean = 1.1, SD = 2.0, CV = 175).

Of the models fitted against the date of the first chick sighting, the model which included the date of first chick sighting in the previous year and the date of capelin arrival in the previous year best fit the data ($w = 0.44$, $\Delta AIC_c > 2$ for competing models; Table 1). The next best model which received about 3.7 (0.44/0.12) times less support, only included the date of capelin arrival in the previous year (Table 1; Fig. 3). Models including timing of capelin in the current year, NAO and ocean temperatures were not strongly supported (Table 1). The date of capelin arrival in the previous years was clearly the most important predictor, appearing in all models with ΔAIC_c values < 4 , and not appearing in models with ΔAIC_c values > 10 (Table 1).

The model that best explained the date of capelin arrival included the variables date of capelin arrival in previous year and ocean temperature in the current years ($w = 0.65$, $\Delta AIC_c > 2$ for competing models; Table 1). Alone, the date of capelin arrival in the previous year explained

Fig. 2 Mean annual anomalies for (a) the date of the first Common Murre chick sighting at Cape St. Mary's Ecological Reserve, (b) the date of peak capelin spawning at Bryant's Cove and Bellevue Beach and (c) mean February–June ocean temperature at 0–150 m from hydrographic station 27, Newfoundland, and (d) December–March North Atlantic Oscillation (NAO) index, 1980–2006



a substantial amount of variation in the date of capelin arrival in the current year ($w = 0.17$, $\Delta AIC_c = 2.75$; Table 1) and other models that included the date of capelin arrival in previous year performed well. The NAO index was not a good predictor of capelin timing (Table 1).

Logical comparisons of the timing of murre and capelin to water temperature and NAO states did not yield any compelling results. Similarly, comparisons of lagged oceanographic conditions to murre and capelin timing did not generate any

biologically meaningful results. Although there are no clear logical, linear, or lagged-linear associations between the date of the first chick sighting and between peak capelin spawning and oceanographic conditions, there are clear non-linear relationships. The cold-water event in 1991 had striking consequences for both murre and capelin timing (Fig. 2). Mean ocean temperature before 1991 was -0.37°C ($SD = 0.32^\circ\text{C}$). In 1991, ocean temperatures declined substantially (reaching -1.14°C), but returned to pre-perturbation

Table 1 Fitted regression models with ΔAIC_c values >10 to the variation in the date of first chick sighting at Cape St. Mary's (chick timing), and all possible models for the date of peak capelin spawning at Bryant's Cove and Bellevue Beach (capelin timing), Newfoundland, 1980–2006

Model	log(L)	K	n	AIC _c	ΔAIC_c	w
Chick timing						
Chick _{t-1} + capelin _{t-1}	-77.8	4	22	165.7	0.0	0.44
Capelin _{t-1}	-80.5	3	24	168.2	2.6	0.12
Chick _{t-1} + capelin _t + capelin _{t-1}	-77.7	5	21	168.7	3.0	0.1
Capelin _{t-1} + NAO _t	-79.4	4	23	168.8	3.2	0.09
Chick _{t-1} + capelin _t + capelin _{t-1} + NAO _t	-76.4	6	20	169.8	4.1	0.06
Capelin _{t-1} + temp _t	-80.2	4	23	170.5	4.8	0.04
Capelin _t + capelin _{t-1}	-80.4	4	23	171.0	5.3	0.03
Capelin _{t-1} + temp _t + NAO _t	-79.1	5	22	171.5	5.9	0.02
Chick _{t-1} + capelin _t + capelin _{t-1} + temp _t	-77.4	6	20	171.6	6.0	0.02
Capelin _t + capelin _{t-1} + NAO _t	-79.3	5	22	172.0	6.3	0.02
Chick _{t-1} + capelin _t	-81.2	4	22	172.5	6.9	0.01
Chick _{t-1} + capelin _t + capelin _{t-1} + temp _t + NAO _t ^a	-76.1	7	19	173.3	7.6	0.01
Capelin _t + capelin _{t-1} + temp _t	-80.2	5	22	173.7	8.0	0.01
Chick _{t-1} + capelin _t + NAO _t	-80.6	5	21	174.4	8.8	0.01
Chick _{t-1}	-83.6	3	23	174.4	8.8	0.01
Chick _{t-1} + capelin _t + temp _t	-80.9	5	21	175.1	9.5	0
Capelin _t + capelin _{t-1} + temp _t + NAO _t	-79.1	6	21	175.1	9.5	0
Capelin timing						
Capelin _{t-1} + temp _t	-99.9	4	23	209.7	0.0	0.65
Capelin _{t-1}	-102.7	3	25	212.5	2.7	0.17
Capelin _{t-1} + temp _t + NAO _t ^a	-99.9	5	23	212.8	3.1	0.14
Capelin _{t-1} + NAO _t	-102.7	4	24	215.2	5.5	0.04
Temp _t	-114.3	3	26	235.6	25.9	0
NAO _t	-114.3	3	26	235.6	25.9	0
Temp _t + NAO _t	-114.3	4	25	238.4	28.7	0

Models ranked according to ΔAIC_c and w values

^aGlobal models

levels in the following year (1992 [-0.32°C]). With the exception of 1993 (-0.77°C), ocean temperatures have not fallen below pre-perturbation temperatures since, remaining warmer than average from 1994 to 2006 (Fig. 2c). The mean date of the first chick sighting before 1991 (pre-perturbation) was 17 June (SD = 5.2 days) compared to 25 June (SD = 8.6 days) after 1990. The response of murre breeding chronology lagged behind the amelioration of the physical environment, taking about 7 to 8 years for the date of first chick sighting to return to pre-perturbation levels in 1998 (June 19) and 1999 (12 June). Even more evident is the delayed response of capelin timing, whereby the date of peak capelin spawning is yet to be recorded at or earlier than the pre-perturbation mean of 19 June (SD = 6.2 days). In the most recent years, capelin

spawning times appear similar to those recorded more than 15 years ago (Fig. 2b).

Discussion

The breeding chronology of common murres and the inshore availability of capelin (primary prey of breeding murres) ranged by about 1 month from 1980 to 2006. Capelin spawned later than average throughout the 1990s and 2000s (Carscadden et al. 2002), and in response, common murres delayed breeding. Murres likely delay breeding to maximize the temporal match between hatching and capelin availability within foraging ranges (Cairns et al. 1987; Piatt 1987, 1990; Bertram et al. 2001; Davoren and Montevecchi 2003). Similar to our

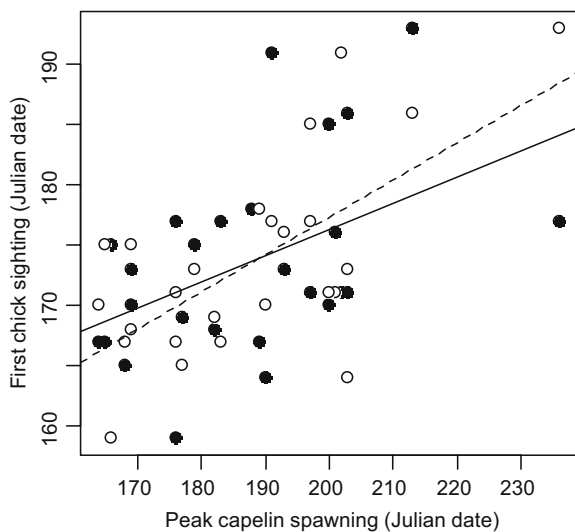


Fig. 3 Relationship between the date of first chick sighting at Cape St. Mary's Ecological Reserve to date of peak capelin spawning in the same year (*solid dots, solid line* is the linear regression) and in the previous year (*open dots, broken line*), Newfoundland, 1980–2006

results, Durant et al. (2004) found that food availability in the previous year was a robust predictor of the hatching date of Atlantic puffins (*Fratercula arctica*). The delayed response to the changing timing of capelin suggests that murres do not have a mechanism through which they can forecast the timing of capelin arrival to inshore waters in a given year. Likewise, Davoren and Montevecchi (2003) found that common murres at the species' largest colony on Funk Island did not delay breeding in the cold-water years of 1991 and 1992; it was not until 1993 that a delay in the murres' breeding was evident. Thus, the murres may go through an adjustment period once prey conditions change (Davoren and Montevecchi 2003). This lagged response in murre breeding chronology could be due to a carry-over effect of adult condition as a consequence of capelin timing and availability in the previous year. Alternatively, murres could be adjusting their seasonal cycle based on information of the timing of capelin arrival in the previous year. Though this would undoubtedly result in an imperfect relationship in a dynamic marine ecosystem, it could create a successful stable strategy for

long-lived murres (up to 20–25 years) since they can “afford” timing mismatches during their 10–15 years of reproductive efforts (cf. Sandvik and Erikstad 2008). As adult survival is the life-history trait under the strongest selection for long-lived seabirds (Stearns 1992), variable breeding success could help ensure future breeding attempts (Drent and Daan 1980).

Several studies have shown that the inshore migration of capelin is delayed in cold years (Shackell et al. 1994; Carscadden et al. 1997, 2002). This effect was especially apparent during the cold-water perturbation of 1991 (Carscadden and Nakashima 1997). Ocean temperatures returned to pre-perturbation conditions by the mid-1990s, nevertheless, capelin continued to spawn later for about another decade (Carscadden et al. 2002). The 1991 cold-water perturbation acted as a physical forcer, delaying the inshore arrival of capelin. Both murres and capelin exhibited a lagged response to this oceanographic event, taking more than 7 and 15 years, respectively, to return to pre-perturbation levels. Since 1991, capelin have also shifted their vertical distribution into deeper colder waters, likely as a result of changes in prey availability (Mowbray 2002). These circumstances could contribute to the prolonged response of capelin (and consequently murres) to the 1991 perturbation. There is no obvious ‘bottom-up’ relationship between murre breeding chronology or capelin timing and changing ocean temperatures. The 1991 cold-water event also inhibited the migration of warm-water pelagic species (mackerel, saury, squid) into the region, resulting in a regime shift in the pelagic food web (Montevecchi and Myers 1995, 1996). Though ocean temperatures returned relatively quickly to pre-perturbation levels, the shift in the pelagic food web was prolonged by more than 15 years, and therefore exhibited no linear relationship between the prey landed by northern gannets (*Sula bassana*) and ocean temperatures (Montevecchi 2007).

Ocean temperatures would seem to serve as the most reliable cue to predict the timing of the inshore movements of capelin, because their movements ultimately depend on thermal conditions (Shackell et al. 1994; Carscadden et al.

1997). Yet apparently the relationship between capelin spawning and ocean temperature is weak with a low and degraded signal-to-noise ratio. Only in addition to capelin timing in the previous year does ocean temperature in the current explain some residual variation in capelin timing in current year. Accordingly, there was no strong relationship between murre breeding chronology and ocean temperature. This finding indicates that murre do not use or solely rely on local environmental conditions to adjust breeding times but may use conditions in non-breeding areas (Frederiksen et al. 2004). Relationships between breeding chronology and NAO have been found for common murre (Frederiksen et al. 2004) and other widely dispersing alcids, such as Atlantic puffins (Durant et al. 2004) and rhinoceros auklets (*Cerorhinca monocerata*; Bertram et al. 2001). Yet, we found little support for relationships between murre breeding chronology or the timing of capelin arrival with NAO; local ocean temperature in the previous year was a better predictor of capelin availability. In the system we examined, oceanographic conditions outside the seabirds' breeding range appear to be potentially less reliable than local cues to help ensure matching the timing of breeding with food availability (see also Both and Visser 2001). More generally, long-lived seabirds, such as the common murre, with low fecundity and a large foraging range, are less responsive to climate variability, apparently because they live long enough to integrate such environmental stochasticity into their reproductive activities across multiple years (Sandvik and Erikstad 2008).

Murres could be using multiple cues to predict capelin arrival. Mechanisms for shifts in avian breeding ecology are unknown but are assumed to be driven by bottom-up food web processes (e.g., Aebischer et al. 1990). Although bottom-up oceanographic drivers of timing are unclear in our study, variations in pre-breeding conditions likely shape murre breeding chronology. Further research into the diet and physiology of pre-breeding common murre is needed to elucidate the trophic interactions that shape breeding chronology. Notwithstanding this, murre timed breeding according to the timing of the inshore movements of capelin in the previous year which

is a better predictor of the date of capelin arrival in a given year than ocean temperatures or NAO indices.

Most comparisons of murre breeding chronology to the inshore arrival of capelin in the Northwest Atlantic have been limited by a lack of comparable long-term data. Associated with the delayed inshore movements of capelin in the early 1990s, Davoren and Montevecchi (2003) found that the common murre at Funk Island delayed breeding by 2–3 weeks. Common murre at Witless Bay also delayed breeding in 1992 and 1993 (Carscadden et al. 2002). The present long-term study confirms the lagged association between murre and capelin and illustrates the complexity of relationships between predator, prey and the physical environment. Shifts in capelin biology were reflected in the murre's breeding biology, indicating significant effects at higher trophic levels. And although non-linearly related, anomalously cold ocean temperatures in 1991 had clear prolonged effects on the timing of capelin and murre breeding chronologies.

Owing to the murre's longevity and life history, variations in prey availability and ocean climate indirectly influence murre population dynamics over the long-term. During our three decade study, ocean temperature has varied much more than either the timing of capelin migration or murre breeding. Ocean conditions in 2005 through 2007 suggest that the Northwest Atlantic is shifting to warm water conditions (Colbourne et al. 2006; Montevecchi 2007). It is important for assessments of changing ocean conditions and their influences on upper trophic levels that the long-term monitoring of the interactions between predators, prey and the marine environment be continued.

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