Water temperature and timing of capelin spawning determine seabird diets

Gail K. Davoren[1]*, Paulette Penton[1], Chantelle Burke[2], and William A. Montevecchi[2]

[1]Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada R3T 2N2
[2]Cognitive and Behavioural Ecology Programme, Memorial University of Newfoundland, St John's, NL, Canada A1B 3X9

*Corresponding author: tel: +1 204 4747497; fax: +1 204 4747588; e-mail: davoreng@cc.umanitoba.ca.

The capelin (*Mallotus villosus*) is the focal forage fish in many northern marine ecosystems. Its capacity to respond to changes in ocean climate is explored and the usefulness of seabird diets as indicators evaluated by integrating the timing of capelin spawning and temperature (0–150 m) during gonadal development (February–June) with colony-based measures of prey deliveries to chicks of common murres (*Uria aalge*) and northern gannets (*Morus bassanus*) on the east coast of Newfoundland during the years 1991–1993 and 2003–2010. Great variation was observed in the timing of spawning, with similar annual trends in different regions of coastal Newfoundland. Spawning was later in years of colder-than-average temperature, although the importance of other variables (e.g. fish size) could not be ruled out. The relationship between temperature during gonadal development and timing of spawning was weak at demersal spawning sites, suggesting that timing may be regulated by other factors (e.g. temperature at spawning sites). When spawning was early in warmer years relative to chick-rearing, common murres delivered a lower percentage of energy-rich gravid capelin to their chicks and northern gannets delivered a lower percentage of capelin. Integrating multiple data sources will be important to monitor marine ecosystem health as ocean climate changes.

Keywords: capelin, climate change, diet, Newfoundland, seabird, temperature, timing of spawning.

Introduction

Climate change has consequences for marine fish, because metabolic rates of ectothermic animals are fundamentally contingent on the temperature conditions of their environment (Wright and Trippel, 2009). Climate change is predicted to result in shifts in distributional range, primarily northwards during climate warming (Rose, 2005); however, some species may remain in areas despite lower quality conditions (Wright and Trippel, 2009). In such cases, temperature will likely have a strong influence on phenology, such as the timing of spawning (Rijnsdorp *et al.*, 2009). Temperature may influence the timing of spawning through direct alterations of rates or the onset of gametogenesis (Hutchings and Myers, 1994; Slotte *et al.*, 2000; Kjesbu *et al.*, 2009), or indirect changes to adult size and condition (Wright and Trippel, 2009), or both (Ware and Tanasichuk, 1989; Carscadden *et al.*, 1997). Timing of spawning directly influences the conditions experienced by offspring, including thermal, prey, and predator regimes, so has strong links to the reproductive success of marine fish (Hjort, 1914; Cushing, 1990).

Understanding the nature and strength of the relationship between water temperature and species-specific timing of spawning is critical to assess the capacity of marine fish populations to respond to and tolerate predicted changes in ocean climate.

The capelin (*Mallotus villosus*) is the dominant forage fish species in many northern marine ecosystems and is the primary prey of the large vertebrate food web in the Northwest Atlantic, including groundfish, seals, whales, and birds (Lavigne, 1996). Capelin winter offshore and undergo extensive migrations to coastal areas during spring to spawn (Carscadden and Nakashima, 1997). Timing of the inshore arrival and spawning of capelin in coastal Newfoundland is highly variable, with temperature being an important factor explaining variability (Shackell *et al.*, 1994; Carscadden *et al.*, 1997, 2001; Regular *et al.*, 2008). When cold temperatures prevail, spawning is delayed.

Dramatic changes in capelin biology and behaviour were noted during 1991, including delayed and protracted spawning (Carscadden and Nakashima, 1997), in association with the coldest water event during the past 50–100 years (Drinkwater,

1996). Delays in the timing of spawning and, therefore, the inshore arrival of capelin have resulted in altered interactions with endothermic predators, which are particularly well-documented for seabirds (Carscadden *et al.*, 2002). Delayed spawning in the early 1990s led to dietary shifts (Davoren and Montevecchi, 2003; Montevecchi, 2007), delayed seabird breeding chronology (Davoren and Montevecchi, 2003; Regular *et al.*, 2008), lower breeding success and reproductive output (Regehr and Montevecchi, 1997), and increased predation on eggs, chicks, and adults by predatory gulls attributable to food stress early in the breeding cycle before capelin arrived inshore (Regehr and Montevecchi, 1997; Stenhouse and Montevecchi, 1999). Similarly, the phenology of primary prey species has been linked to variability in the breeding success of seabirds elsewhere (e.g. Bertram *et al.*, 2001; Hipfner, 2008).

The purpose of this study is twofold. First, data on the timing of capelin spawning and an integrated water temperature measure during gonadal development are used to test the strength and nature of the relationship between temperature and the timing of spawning in coastal Newfoundland. Second, we explore whether seabird diets indicate the timing of spawning. Common murres (*Uria aalge*) are excellent samplers of capelin biology, because in the Northwest Atlantic they specialize in preying on capelin, delivering >94% capelin to their chicks (Davoren and Montevecchi, 2003). In contrast, northern gannets (*Morus bassanus*) prefer larger pelagic fish, and their dietary composition reflects the presence or the absence of these fish within foraging ranges (Montevecchi and Myers, 1995; Montevecchi, 2007), with capelin comprising the bulk of the diet when large pelagic fish are absent (Montevecchi *et al.*, 2005).

Methods

Timing of spawning

Capelin spawn both intertidally at the beach and in deep water (demersal) in the study area (Davoren *et al.*, 2008; Penton *et al.*, 2012). This study was centred on 5 spawning beaches and 11 demersal spawning sites of capelin, located at varying depths (18–33 m) and distances from shore (2.5–17.7 km; Davoren *et al.*, 2008) on the exposed northeast Newfoundland coast, southwest of the Funk Island Seabird Ecological Reserve (Figure 1). Demersal spawning begins 1–2 weeks after the initiation of beach spawning (Penton *et al.*, 2012), and it is associated with the arrival of the main migration (i.e. peak biomass) of capelin in the study area (GKD, unpublished data).

As capelin produce eggs that adhere to sediment, the presence of eggs is easily determined by monitoring sediment at known spawning sites. To determine the first date of spawning, gravel at known beach and demersal spawning sites was examined for the presence of eggs starting in early July of 2003–2010. Egg development is temperature-dependent (Frank and Leggett, 1981) and proceeds through a number of well-described developmental stages (Fridgeirsson, 1976). Therefore, if initial egg deposition was missed when sites were not monitored daily, the first day of spawning was estimated by combining spawning site-specific temperature with the egg developmental stages present (see below). Data on the timing of spawning at one beach site in the study area (site E in Figure 1) during the period 1991–1993 were provided by Fisheries and Oceans Canada, extending our study period to 1991–2010, with data available during two periods: 1991–1993 and 2003–2010. To examine whether the timing of spawning in our study
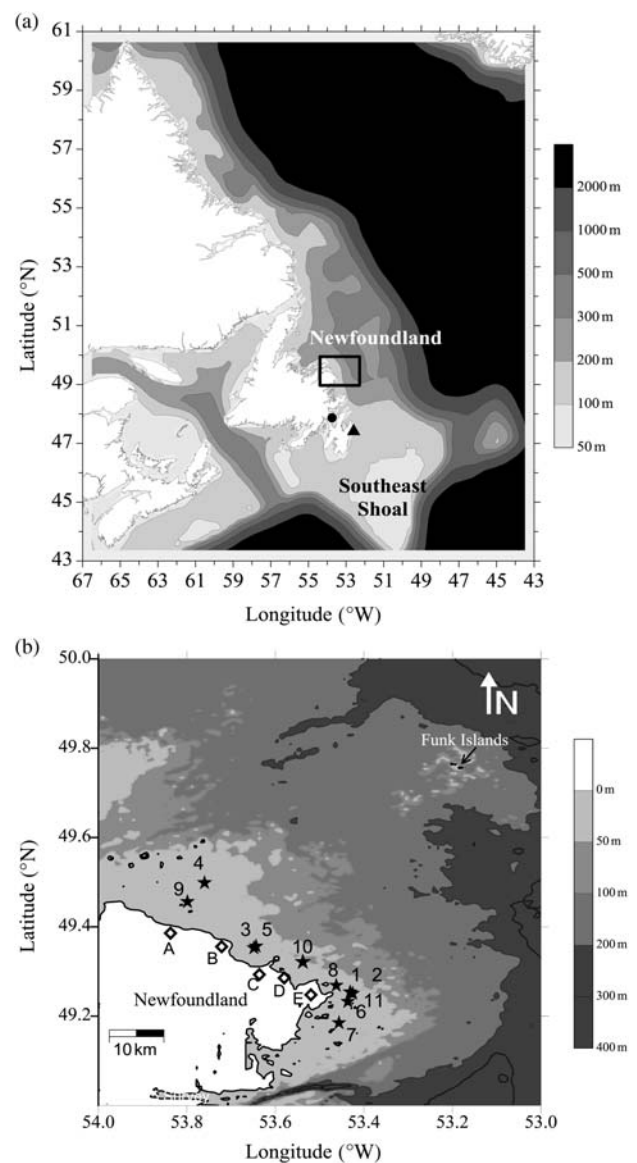
Figure 1. Map of Newfoundland, indicating (a) the location of the study area (Notre Dame Bay; box), the Southeast Shoal, oceanographic station 27 (triangle) and Bellevue Beach, Trinity Bay (black dot), within eastern Canada, and (b) the location of all beach sites (diamonds) and demersal sites (stars) of capelin, the Funk Island Seabird Ecological Reserve, and depth contours.

area was coherent with other regions of Newfoundland, the first days of peak capelin spawning at Bellevue Beach, Trinity Bay (Figure 1), a long-term site monitored by Fisheries and Oceans Canada, were obtained for the years 1990–1999 (Nakashima and Slaney, 2000) and estimated for 2000–2010 (Anon., 2011).

Spawning site-specific temperature was measured from 2003 to 2010 primarily by *in situ* temperature loggers (2004–2006: Vemco; 2007–2010: 42 K Hobo Water Temperature Pro V2 Loggers) moored near the seabed at all known demersal sites and at one beach spawning site (site D) at the high, mid-, and low tidal zones before spawning. Temperature was recorded every hour during prespawning and spawning. In 2003, a Sea Bird SBE-19 was used to characterize temperature near the seabed at demersal sites before and during spawning. At all other beach sites and at

site D in 2003, water temperature at waist height was used to characterize temperature before and during spawning.

Egg developmental stages were quantified by collecting a sample of egg-bearing gravel once egg presence was noted. A 0.3-m^2 Van Veen Benthic Grab System was used to collect sediment from demersal sites, and sediment was examined at the mid-tidal zone on beaches. A 20-ml sample of eggs/sediment was preserved in Stockard's solution (% volume: 4 glacial acetic acid, 5 formaldehyde, 6 glycerine, 85 water). This solution clears the yolk sac, allowing the determination of egg developmental stages (Frank and Leggett, 1981). In the laboratory, a random sample of 50 eggs from each sample was examined to quantify the number of eggs at each developmental stage (Fridgeirsson, 1976). If some eggs were already in later stages (>stage 3), the date of first spawning was estimated from the oldest developmental stage present in the sample, using mean daily incubation temperatures at each site and assuming that eggs spend an equal amount of time at each developmental stage. The data are summarized as the ordinal date of first spawning, with day 1 being 1 January of each year, over all beach and demersal sites.

Temperature during gonadal development

Carscadden et al. (1997) showed that an integrated measure of temperature (TEMPSUM) at 0–20 m during the period of gonadal development for capelin (February–June) was important in determining the timing of spawning. Those authors used temperature data from oceanographic station 27 (47°32′N 52°35′W; Figure 1), because several researchers have shown that oceanographic conditions at that station represent those on the Newfoundland shelf (Petrie et al., 1988; Drinkwater, 1996). TEMPSUM, however, could not be calculated owing to missing data in some months in more recent years. Instead, a temperature anomaly was calculated using the mean monthly (February–June) temperatures at 0, 50, 100, and 150 m at station 27 over the years 1946–2010, following Óskarsson and Taggart (2009). The depth range was extended beyond surface waters, owing to recently observed deeper vertical distribution of capelin during gonadal development (Mowbray, 2002). Mean temperature at depth per month was calculated over all years, and the difference between this mean and the annual mean monthly temperatures at each depth provided a residual, which was then averaged for each year ("temperature anomaly"). A negative anomaly refers to a cooler-than-average year, whereas a positive anomaly refers to a warmer-than-average year. This method accounts for missing data at depths in certain months, with equal weighting of all measurements despite differences in measurement effort (Óskarsson and Taggart, 2009). Using all archived temperature data (1946–2010) to calculate temperature anomalies during the study period (1991–2010) places the anomalies in a historical context.

Seabird diets

Parental deliveries of prey to chicks of common murres and northern gannets were sampled at the Funk Island Seabird Ecological Reserve (49°45′N 53°11′W; Figure 1) during a temporally fixed 2-week trip every year in late July or early August (Montevecchi, 2007). Funk Island supports North America's largest colony of common murres (412 524 breeding pairs; Chardine et al., 2003) and 9837 breeding pairs of northern gannets (Chardine, 2000). Prey samples were obtained from gannets by approaching roosting birds that regurgitate as they move away from researchers (Montevecchi and Myers, 1995). Samples were also obtained at

times from birds captured for datalogger attachments and removals and from discarded regurgitations and scraps in the colony. Regurgitated prey items were identified to species and counted. Chick diets are summarized as the percentage total mass of capelin over all regurgitations in each year. This was calculated by dividing the number of regurgitations with capelin by the total number of regurgitations, multiplying this percentage by the mean mass of capelin in that year, and dividing by the total mass of all regurgitations sampled in that year.

Prey samples were obtained from murres by capturing fish-carrying adults with polenets. The species, sex, and maturity (gravid, spent, immature) of each fish were recorded. Spent and immature capelin could not always be distinguished, so were pooled in a single category. As gravid capelin are likely preferred prey owing to their higher energy densities relative to post-spawning (spent), immature, and male capelin (Montevecchi and Piatt, 1984), researchers have hypothesized that the proportion of gravid capelin delivered to murre chicks likely depends on the timing of capelin spawning relative to the chick-rearing period (Davoren and Montevecchi, 2003; Burke and Montevecchi, 2008). Therefore, prey deliveries to murre chicks are summarized as the percentage (by number) of capelin as well as the percentage of gravid capelin.

Data analysis

Least-squares regression were used to fit linear and non-linear models to describe the nature and strength of the relationship between the ordinal date of first spawning at beach and demersal sites (dependent variables) and temperature anomaly (independent variable). Additionally, the relationships between the date of first spawning at beach and demersal sites (independent variables) and the percentage of gravid capelin in diets of murre chicks (dependent variable) and the percentage of capelin in diets of gannet chicks (dependent variable) were described.

An estimate of the strength of each modelled relationship and its statistical significance were evaluated using r^2 and p-values, with $\alpha = 0.05$. Data were fitted to null (i.e. no relationship or a slope of zero), linear, polynomial (second order or quadratic), and exponential models, because the relationship between the independent and dependent variables was unknown a priori. To determine the model of best fit among those examined, we used AIC values, corrected for small sample sizes (AIC$_c$; Burnham and Anderson, 2002). The model with the lowest AIC$_c$ value was assumed to be the best fit. As a rule of thumb, other models with a difference of <2 in AIC$_c$ from the lowest were considered to be plausible, or alternate, models (Burnham and Anderson, 2002). The AIC$_c$ weight (ω) was also calculated to represent the relative probability that each model was the best-fitting model among those considered, whereby the weights of all models considered in an analysis sum to 1 (Burnham and Anderson, 2002).

Results
Timing of spawning and temperature during gonadal development

The temperature anomaly varied over the study period (1991–2010; Figure 2). Water temperatures were primarily colder than average during the period February–June from 1991 to 1997, except 1996, then shifted to primarily warmer than average after 1997 (Figure 2). In this context, the period over which timing of spawning was determined at demersal spawning sites in the
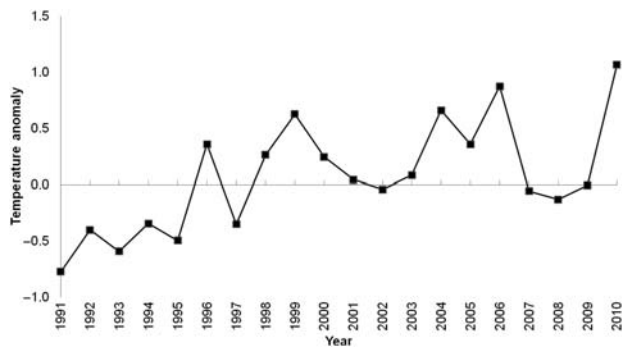
Figure 2. Temperature anomaly (annual deviation of mean monthly (February–June) temperature anomaly at 0, 50, 100, and 150 m from the overall average for the same months, 1946–2010) at oceanographic station 27 during the period of gondal development of capelin. The oceanography at station 27 (47°32.8′N 52°35.2′W) represents conditions on the Newfoundland shelf.
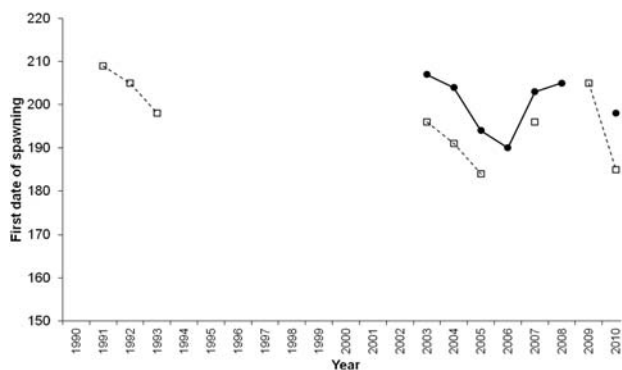
Figure 3. The date of first spawning (ordinal date) over all demersal (dot, solid line) and beach (open square, dashed line) sites on the northeast Newfoundland coast (Notre Dame Bay), 1991–1993 and 2003–2010.

study area (2003–2010) overlapped with warmer-than-average temperatures, except slightly below average temperatures during the years 2007–2009. Including data provided by Fisheries and Oceans Canada on the timing of spawning from a beach site in the study area (site E; Figure 1) from 1991 to 1993 allowed the extension of the beach-spawning dataset into the colder period.

The timing of capelin spawning varied among years in the study area (Figure 3). There was no spawning at demersal sites in 2009 or at beach sites in 2006 and 2008 in the study area. The dates of first spawning at Bellevue Beach were significantly correlated with those at beach sites in the study area ($r = 0.686$, $n = 9$, $p = 0.006$), but not at demersal sites ($r = 0.513$, $n = 7$, $p = 0.070$).

When temperature was colder than average during the months of gonadal development, capelin generally spawned later. Although the date of first spawning at demersal sites was generally later in colder-than-average years, this relationship was weak and not significant (Table 1, Figure 4). In contrast, this negative relationship was strong and significant for beach sites, being described well by both negative linear and exponential models (Table 1, Figure 4).

Seabird diets and timing of spawning

From 1991 to 2010, diets of murre chicks at Funk Island generally were 95–100% capelin, although 56.5% of the diet was capelin in

2009. In all years, the majority of capelin delivered was female (73.6–99.0%), and the remainder was immature or male capelin. Murres had a lower percentage of gravid capelin during diet sampling at Funk Island in years when the first date of demersal spawning was early (2005, 2006). During those years of early spawning, gravid capelin were replaced by spent and immature capelin. Of the models examined, the exponential model had the highest explained variance, was statistically significant, and was similarly plausible as the best fit model (Table 1, Figure 5). The relationship between the date of first spawning at beach sites and the percentage of gravid capelin in the diet was best described by a polynomial curve, which also explained the highest variance and was statistically significant (Table 1, Figure 5). When the timing of beach spawning was intermediate (i.e. not early or late in relation to chick-rearing; days 191–198), the percentage of gravid capelin varied during diet sampling at Funk Island.

Diets of gannet chicks at Funk Island varied from 1.8 to 94.3% capelin from 1991 to 2010, with larger pelagic fish comprising the remaining fish (Montevecchi, 2007). Of the models examined, the relationship between the date of first spawning at beach and demersal sites and the percentage of capelin in gannet chick diets was best described by polynomial curves, but only the relationship with the date of first demersal spawning was significant (Table 1, Figure 5). Therefore, when the date of first spawning was early at spawning sites in the study area, capelin had a lower representation in gannet diets sampled at Funk Island.

Discussion

Overall, when temperature was colder than average during the months of gonadal development (February–June), capelin spawned later. Although the best models were non-linear, linear models were also plausible given the low ΔAIC_c values. The relationship between water temperature and timing of spawning was weak at demersal relative to beach sites. The timing of beach spawning is associated with the initial arrival of capelin inshore, whereas demersal spawning is associated with the arrival of the main migration, or peak biomass, of capelin inshore (GKD, unpublished data). Upon arrival in the study area, capelin remain in particular areas (staging areas), where they may complete gonadal development, before moving to spawning sites (Davoren *et al.*, 2006). Therefore, the timing of demersal spawning also may be mediated by temperature in these staging areas before spawning, as well as at spawning sites. In support, demersal spawning in Newfoundland is initiated at suitable sites only when water temperature reaches $>2°C$ (Carscadden *et al.*, 1989; Nakashima and Wheeler, 2002). This weak relationship also may be due to the demersal spawning dataseries being restricted to a warmer and near-average period (2003–2010) compared with the beach dataseries, which included data from the colder period during the early 1990s.

The negative relationship between timing of spawning and temperature is consistent with previous research on capelin (Shackell *et al.*, 1994; Carscadden *et al.*, 1997; Regular *et al.*, 2008). The mechanism underlying this relationship is thought to be related to spring temperatures that directly influence rates of gametogenesis (i.e. maturation) and indirectly impact growth by influencing the abundance and distribution of prey. In support, when spring temperature (0–75 m) was warmer, the percentage of mature capelin was higher during a temporally fixed survey in May (Shackell *et al.*, 1994). Capelin feed extensively (Gerasimova, 1994) and gonad development is rapid (Winters, 1970) during spring (March–June). Therefore, temperature regulation of the timing of spring

Table 1. Models describing the highest explained variance, AIC_c best fit (i.e. the lowest ΔAIC_c value) along with the AIC_c weight (ω) for the relationships between each of the pairs of independent and dependent variables.

Independent variable	Dependent variable	Model	Form	r^2	p	ΔAIC_c	ω
Temperature anomaly	Demersal DFS	Highest variance	Polynomial*	0.404	n.s.	0	0.30
		AIC_c best fit	Polynomial	–	–	–	–
		Alternate	Exponential	0.381	n.s.	0.1	0.29
			Linear	0.383	n.s.	0.1	0.29
	Beach DFS	Highest variance	Exponential*	0.657	0.008	0	0.49
		AIC_c best fit	Exponential	–	–	–	–
		Alternate	Linear	0.655	0.008	0.1	0.46
Common murre diet							
Demersal DFS	% gravid capelin	Highest variance	Exponential*	0.635	0.032	0.7	0.24
		AIC_c best fit	Polynomial	0.453	n.s.	0	0.37
		Alternate	Linear	0.443	n.s.	0.1	0.33
Beach DFS	% gravid capelin	Highest variance	Polynomial*	0.782	0.002	0	0.87
		AIC_c best fit	Polynomial	–	–	–	–
		Alternate	n/a	–	–	–	–
Northern gannet diet							
Demersal DFS	% capelin	Highest variance	Polynomial*	0.672	0.024	0	0.38
		AIC_c best fit	Polynomial	–	–	–	–
		Competing	Linear	0.579	0.047	0.8	0.34
Beach DFS	% capelin	Highest variance	Polynomial*	0.412	n.s.	0	0.45
		AIC_c best fit	Polynomial	–	–	–	–
		Alternate	n/a	–	–	–	–

Alternate models (i.e. $\Delta AIC_c < 2$) are shown. The asterisks denote the trend lines shown in Figures 4 and 5. Note that all null models (i.e. no relationship between independent and dependent variables) had $\Delta AIC_c > 2$, so did not provide substantial support and hence the results are not reported further. DFS refers to the ordinal date of first spawning of capelin over all beach or demersal sites in the study area on the exposed northeast Newfoundland coast (Notre Dame Bay). n.s., not significant; n/a, not applicable.
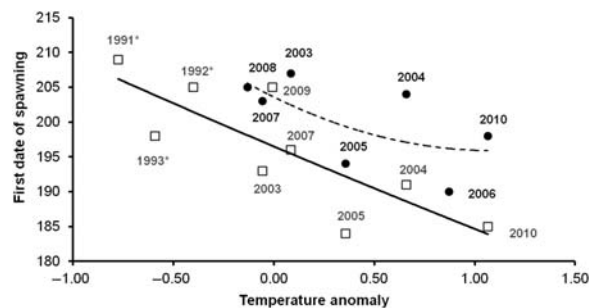
Figure 4. First day of spawning (ordinal date) at beach (open square, solid black line) and deep-water (dot, dashed line) spawning sites of capelin on the northeast Newfoundland coast (Notre Dame Bay), and the temperature anomaly during gonadal development of capelin. The dashed line indicates a trend that is not statistically significant. Asterisks marked against years indicate data on the timing of spawning obtained for beach site E from Fisheries and Ocean Canada.

zooplankton production results in the delayed onset of spring feeding, and, hence, growth and maturation, ultimately leading to later spawning (Shackell *et al.*, 1994; Carscadden *et al.*, 1997).

Temperature during gonadal development, however, may not be the most important explanatory variable for timing of spawning. For instance, Carscadden *et al.* (1997) found that fish length explained a similar amount of variation in the timing of peak spawning of capelin as surface temperature during gonadal development. Regular *et al.* (2008) reported that the timing of inshore arrival of capelin was explained to a greater extent by the date of capelin arrival in the previous year than by ocean temperature (0–150 m) in the current year. The latter is also possibly evidence of the importance of population-level fish size and condition.

Fish size is related to the timing of spawning, with the typical pattern in marine teleosts being that older, larger fish arrive and spawn first relative to smaller, younger fish (e.g. Pacific herring, *Clupea harengus pallasi*; Ware and Tanasichuk, 1989; capelin, Templeman, 1948; Vandeperre and Methven, 2007). The mechanism underlying this pattern is unclear, but it may be related to size-dependent onset (Slotte *et al.*, 2000) or rate of maturation (Flynn and Burton, 2003), condition-dependent maturation (Slotte *et al.*, 2000), and/or size-dependent migration speeds (Vandeperre and Methven, 2007). For instance, Flynn and Burton (2003) found that longer male and female capelin had more advanced gametogenesis than shorter fish at a given sampling date, indicating that larger fish may be capable of spawning earlier. Historically (pre-1991), capelin showed a distinct pattern of larger females and males arriving inshore earlier than smaller fish (Vandeperre and Methven, 2007). Since the cold-water event in 1991, however, spawning waves appear to be a mixture of large and small fish (Nakashima, 1996).

Seabird diets reflected the timing of capelin spawning at demersal sites, but to a lesser extent at beach sites. The percentage of gravid capelin delivered to common murre chicks increased as spawning was later and overlapped more with the sampling period (i.e. chick-rearing; ∼21 d), as hypothesized previously (Davoren and Montevecchi, 2003; Burke and Montevecchi, 2008). At beach sites, when the timing of spawning was intermediate (i.e. not early or late in relation to chick-rearing), the percentage of gravid capelin in the diets of murre chicks was highly variable. Similarly, the percentage of capelin delivered to chicks of northern gannets increased as demersal spawning was later, but showed no statistically significant relationship with the timing of beach spawning.

A greater dietary response to variation in timing of demersal spawning may reflect the importance of demersal sites as seabird
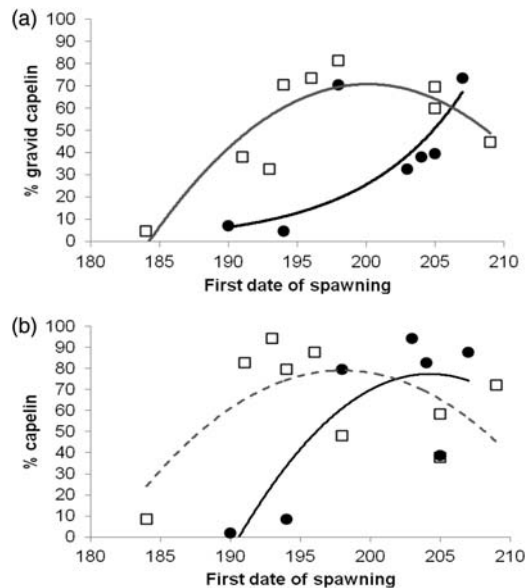
Figure 5. Relationships between the date of first spawning (ordinal date) over all beach (open squares) and demersal (dots) sites on the northeast Newfoundland coast (Notre Dame Bay), and (a) the percentage of gravid capelin in the diets of common murre chicks, and (b) the percentage of capelin in diets of northern gannet chicks at the Funk Island Seabird Ecological Reserve. The dashed line indicates a trend that is not statistically significant. Note that the diets of seabird chicks were sampled annually between days 208 and 218.

foraging areas during chick-rearing. Demersal spawning provides spatially predictable and highly abundant food sources for seabirds and whales (Davoren, 2007). Murres and gannets minimize energetically expensive search activities for prey by using memory and local enhancement to return to forage within these sites (e.g. Davoren *et al.*, 2003; Montevecchi *et al.*, 2009). In contrast, a lesser abundance of capelin spawn at beach sites and, therefore, seabirds are rarely observed associated with capelin at those sites, except large, ephemeral flocks of gannets on occasion. Overall, concentrating foraging effort at abundant and predictable capelin shoals within demersal sites will result in diets reflecting the fish available at these sites rather than the entire study area.

The diets of northern gannets showed a less clear response to the timing of spawning than those of common murres. Gannets tend to prefer larger pelagic fish, and their dietary composition reflects the presence or the absence of these fish within foraging ranges (Montevecchi and Myers, 1995; Montevecchi, 2007), with capelin comprising the bulk of the diet when large pelagic fish are absent (Montevecchi *et al.*, 2005). To illustrate this, the dietary composition of northern gannets shifted between large migratory pelagic species (e.g. Atlantic mackerel, *Scomber scombrus*; Atlantic saury, *Scomberesox saurus*; short-finned squid, *Illex illecebrosus*) during warmer water temperatures (1970s and 1980s) and primarily capelin and other cold-water pelagic fish (Atlantic herring, *Clupea harengus*; Atlantic salmon, *Salmo salar*) during colder water temperatures in the 1990s (Montevecchi and Myers, 1997). As earlier spawning and migratory movements into the region were more likely in warmer-than-average years, the availability of warm-water large pelagic fish was greater, as indicated

by fisheries catches (Montevecchi, 2007). Therefore, even if capelin were highly available during those years, it is likely that gannets would have incorporated less capelin in their diets and more of their preferred, larger prey.

Conclusions

Similar to other researchers, we found great variation in the timing of spawning of capelin, with similar annual trends in different regions of coastal Newfoundland, which was linked to ocean temperature. As suggested by Carscadden *et al.* (1997), this relationship suggests that ocean temperature can be used as an important predictor of the timing of capelin spawning, along with other related variables (e.g. sea-ice extent). Collecting a longer time-series to elucidate the influence of these climatic variables on the timing of spawning will be critical to determining the capacity of this important forage species to respond to and tolerate predicted changes in ocean climate. Linking these data with long-term datasets on the dietary composition of seabirds will provide opportunities to use seabirds as sentinels of changing ocean climate conditions (Bertram *et al.*, 2009). Studying seabirds offers many advantages, because they are highly visible at sea and often aggregate in large, multispecies breeding colonies during summer. Overall, integrating multiple datasets from different sources to monitor marine ecosystem health is critical, especially in light of the rising awareness of marine conservation issues and predicted climate change.

References

Anon. 2011. Assessment of capelin in Subarea 2 + Divisions 3KL in 2010. Department of Fisheries and Oceans Canadian Science Advisory Report, 2010/090. 16 pp.

Bertram, D. F., Harfenist, A., and Hedd, A. 2009. Seabird nestling diets reflect latitudinal temperature-dependent variation in availability of key zooplankton prey populations. Marine Ecology Progress Series, 393: 199–211.

Bertram, D. F., Mackas, D. L., and McKinnell, S. M. 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. Progress in Oceanography, 49: 283–307.

Burke, C. M., and Montevecchi, W. A. 2008. Fish and chicks: forage fish and chick success in co-existing auks. Waterbirds, 31: 372–384.

Burnham, K. P., and Anderson, D. R. 2002. Model Selection and Multimodel Inference: a Practical Information—Theoretic Approach. Springer, New York.

Carscadden, J., and Nakashima, B. S. 1997. Abundance and changes in distribution, biology, and behavior of capelin in response to cooler waters of the 1990s. *In* Forage Fishes in Marine Ecosystems, pp. 457–468. Proceedings of the International Symposium Forage Fishes in Alaska, Sea Grant Program Report, 97-01.

Carscadden, J., Nakashima, B. S., and Frank, K. T. 1997. Effects of fish length and temperature on the timing of peak spawning in capelin

(*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences, 54: 781–787.

Carscadden, J. E., Frank, K. T., and Leggett, W. C. 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Canadian Journal of Fisheries and Aquatic Sciences, 58: 73–85.

Carscadden, J. E., Frank, K. T., and Miller, D. S. 1989. Capelin (*Mallotus villosus*) spawning on the southeast shoal: influence of physical factors past and present. Canadian Journal of Fisheries and Aquatic Sciences, 46: 1743–1754.

Carscadden, J. E., Montevecchi, W. A., Davoren, G. K., and Nakashima, B. S. 2002. Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. ICES Journal of Marine Science, 59: 1027–1033.

Chardine, J. W. 2000. Census of northern gannet in the Atlantic region in 1999. Canadian Wildlife Service Technical Report Series, 361. 16 pp.

Chardine, J. W., Robertson, G. J., Ryan, P. C., and Turner, B. 2003. Abundance and distribution of common murres breeding at Funk Island, Newfoundland, 1972 and 2000. Canadian Wildlife Service Technical Report Series, 404. 26 pp.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations—an update of the match mismatch hypothesis. Advances in Marine Biology, 26: 249–293.

Davoren, G. K. 2007. Effects of gill-net fishing on marine birds in a biological hotspot in the Northwest Atlantic. Conservation Biology, 21: 1032–1045.

Davoren, G. K., Anderson, J. T., and Montevecchi, W. A. 2006. Shoal behaviour and maturity relations of spawning capelin (*Mallotus villosus*) off Newfoundland: demersal spawning and diel vertical movement patterns. Canadian Journal of Fisheries and Aquatic Sciences, 63: 268–284.

Davoren, G. K., May, C., Penton, P., Reinfort, B., Buren, A., Burke, C., Andrews, D., *et al.* 2008. An ecosystem-based research program for capelin (*Mallotus villosus*) in the Northwest Atlantic: overview and results. Journal of Northwest Atlantic Fishery Science, 39: 35–48.

Davoren, G. K., and Montevecchi, W. A. 2003. Signals from seabirds indicate changing biology of capelin stocks. Marine Ecology Progress Series, 258: 253–261.

Davoren, G. K., Montevecchi, W. A., and Anderson, J. T. 2003. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecological Monographs, 73: 463–481.

Drinkwater, K. F. 1996. Atmospheric and oceanic variability in the Northwest Atlantic during the 1980's and early 1990's. Journal of Northwest Atlantic Fishery Science, 18: 77–97.

Flynn, S. R., and Burton, M. P. M. 2003. Gametogenesis in capelin, *Mallotus villosus* (Muller), in the Northwest Atlantic Ocean. Canadian Journal of Zoology, 81: 1511–1523.

Frank, K. T., and Leggett, W. C. 1981. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic, and biological factors. Canadian Journal of Fisheries and Aquatic Sciences, 38: 1327–1338.

Fridgeirsson, E. 1976. Observations on spawning behaviour and embryonic development of the Icelandic capelin. Rit Fiskideildar, 5: 3–40.

Gerasimova, O. V. 1994. Peculiarities of spring feeding by capelin (*Mallotus villosus*) on the Grand Bank in 1987–90. Journal of Northwest Atlantic Fisheries Science, 17: 59–67.

Hipfner, J. M. 2008. Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. Marine Ecology Progress Series, 368: 295–304.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer, 20: 1–228.

Hutchings, J. A., and Myers, R. A. 1994. Timing of cod reproduction: internannual variability and the influence of temperature. Marine Ecology Progress Series, 108: 21–31.

Kjesbu, O. S., Righton, D., Kruger-Johnsen, M., Thorsen, A., Michalsen, K., Fonn, M., and Witthames, P. R. 2009. Thermal dynamics of ovarian maturation in Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 67: 605–625.

Lavigne, D. M. 1996. Ecological interactions between marine mammals, commercial fisheries and their prey: unraveling the tangled web. *In* Studies of High-Latitude Seabirds. 4. Trophic Relationships and Energetics of Endotherms in Cold Ocean Systems, pp. 59–71. Ed. by W. A. Montevecchi. Canadian Wildlife Service Occasional Paper, 91.

Montevecchi, W., Garthe, S., and Davoren, G. 2005. Biophysical influences on seabird trophic assessments. *In* Top Predators in Marine Ecosystems, pp. 118–130. Ed. by I. L. Boyd, S. Wanless, and C. J. Camphuysen. Cambridge University Press, Cambridge, UK.

Montevecchi, W. A. 2007. Binary dietary responses of Northern Gannets *Sula bassana* indicate changing food web and oceanographic conditions. Marine Ecology Progress Series, 352: 213–220.

Montevecchi, W. A., Benvenuti, S., Garthe, S., Davoren, G. K., and Fifield, D. 2009. Flexible foraging tactics by a large opportunistic seabird preying on forage- and large pelagic fishes. Marine Ecology Progress Series, 385: 295–306.

Montevecchi, W. A., and Myers, R. A. 1995. Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. Marine Ecology Progress Series, 117: 1–9.

Montevecchi, W. A., and Myers, R. A. 1997. Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-west Atlantic: implications for climate change. ICES Journal of Marine Science, 54: 608–614.

Montevecchi, W. A., and Piatt, J. 1984. Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*)—implications for seabird predators. Comparative Biochemistry and Physiology, Part A: Physiology, 78: 15–20.

Mowbray, F. K. 2002. Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland. ICES Journal of Marine Science, 59: 942–949.

Nakashima, B., and Slaney, B. W. 2000. Spawning and early development of capelin (*Mallotus villosus*) at Bellevue Beach, Trinity Bay in 1999. DFO Atlantic Fisheries Research Document, 2001/161.

Nakashima, B., and Wheeler, J. P. 2002. Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters—the interaction between beach and demersal spawning. ICES Journal of Marine Science, 59: 909–916.

Nakashima, B. S. 1996. The relationship between oceanographic conditions in the 1990s and changes in spawning behaviour, growth and early life history of capelin (*Mallotus villosus*). NAFO Science Council Studies, 24: 55–68.

Óskarsson, G. J., and Taggart, C. T. 2009. Spawning time variation in Icelandic summer-spawning herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences, 66: 1666–1681.

Penton, P., Davoren, G., Andrews, D., and Montevecchi, W. A. 2012. A comparison of egg developmental and survival rates in capelin (*Mallotus villosus*) on beach and demersal spawning sites in Newfoundland. Canadian Journal of Zoology, 90: 248–256.

Petrie, B., Akenhead, S. A., Lazier, S. A., and Loder, J. 1988. The cold intermediate layer on the Labrador and Northeast Newfoundland shelves, 1978–86. NAFO Science Council Studies, 12: 57–69.

Regehr, H. M., and Montevecchi, W. A. 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. Marine Ecology Progress Series, 155: 249–260.

Regular, P. M., Shuhood, F., Power, T., Montevecchi, W. A., Robertson, G. J., Ballam, D., and Piatt, J. F. 2008. Murres, capelin and ocean

climate: inter-annual associations across a decadal shift. Environmental Monitoring and Assessment, 156: 293–302.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Mollmann, C., and Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. ICES Journal of Marine Science, 66: 1570–1583.

Rose, G. A. 2005. On distributional responses of North Atlantic fish to climate change. ICES Journal of Marine Science, 62: 1360–1374.

Shackell, N. L., Carscadden, J. E., and Miller, D. S. 1994. Migration of pre-spawning capelin (*Mallotus villosus*) as related to temperature on the northern Grand Bank, Newfoundland. ICES Journal of Marine Science, 51: 107–114.

Slotte, A., Johannessen, A., and Kjesbu, O. S. 2000. Effects of fish size on spawning time in Norwegian spring-spawning herring. Journal of Fish Biology, 56: 295–310.

Stenhouse, I. J., and Montevecchi, W. 1999. Indirect effects of the availability of capelin and fishery discards: gull predation on breeding storm-petrels. Marine Ecology Progress Series, 184: 303–307.

Templeman, W. 1948. The life history of the caplin (*Mallotus villosus* O. F. Muller) in Newfoundland waters. Bulletin of the Newfoundland Government Laboratory, 17: 1–151.

Vandeperre, F., and Methven, D. 2007. Do bigger fish arrive and spawn at the spawning grounds before smaller fish: cod (*Gadus morhua*) predation on beach spawning capelin (*Mallotus villosus*) from coastal Newfoundland. Estuarine, Coastal and Shelf Science, 71: 391–400.

Ware, D. M., and Tanasichuk, R. W. 1989. Biological basis of maturation and spawning waves in Pacific herring *Clupea-harengus-pallasi*. Canadian Journal of Fisheries and Aquatic Sciences, 46: 1776–1784.

Winters, G. H. 1970. Biological changes in coastal capelin from the over-wintering to the spawning condition. Journal of the Fisheries Research Board of Canada, 27: 2215–2224.

Wright, P. J., and Trippel, E. A. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish and Fisheries, 10: 283–304.

Handling editor: Audrey Geffen