1

2   Running head: MURRES, CAPELIN AND OCEAN CLIMATE

3

4   **Murres, Capelin and Ocean Climate: Inter-annual Associations across a**

5   **Decadal Shift**

6

7   **P. M. Regular • F. Shuhood • T. Power • W. A. Montevecchi • G. J. Robertson • D.**

8   **Ballam • J. F. Piatt • B. Nakashima**

9

10   _____

11   P. M. Regular (✉) • W. A. Montevecchi

12   Cognitive and Behavioural Ecology Program

13   Memorial University of Newfoundland

14   St. John's, NL A1B 3X9, Canada

15   tel: 1-709-737-7668, e-mail: paul.regular@mun.ca

16

17   F. Shuhood • T. Power

18   Parks and Natural Areas Division

19   Department of Environment and Conservation

20   Government of Newfoundland and Labrador

21   33 Reid's Lane

22   Deer Lake, NL A8A 2A3, Canada

23

1   G. J. Robertson

2   Wildlife Research Division

3   Environment Canada

4   6 Bruce Street

5   Mount Pearl, NL A1N 4T3, Canada

6

7   D. Ballam

8   Nature Conservancy of Canada

9   49-55 Elizabeth Ave., Suite 208, P.O. Box 11

10   St. John's, NL A1A 1W8, Canada

11

12   J. F. Piatt

13   USGS Alaska Science Center

14   1011 E Tudor Rd

15   Anchorage, Alaska 99503, USA

16

17   B. Nakashima

18   Fisheries and Oceans Canada

19   Canada Northwest Atlantic Fisheries Centre

20   80 East White Hills Road

21   St. John's, NL A1C 5X1, Canada

22

23

1   **Abstract** To ensure energy demands for reproduction are met, it is essential that marine

2   birds breed during periods of peak food availability. We examined associations of the

3   breeding chronology of common murres (*Uria aalge*) with the timing of the inshore

4   arrival of their primary prey, capelin (*Mallotus villosus*) from 1980-2006 across a period

5   of pervasive change in the Northwest Atlantic ecosystem. We also assessed the influence

6   of ocean temperature and the North Atlantic Oscillation (NAO; an index of winter

7   climate and oceanography) on these interactions. We found a lagged linear relationship

8   between variations in murre breeding chronology and the timing of capelin arrival in the

9   previous year. On a decadal level, we found a non-linear threshold relationship between

10   ocean temperature and the timing of capelin arrival and murre breeding. Centennially

11   anomalous cold water temperatures in 1991 generated a marked shift in the timing of

12   capelin spawning inshore and murre breeding, delaying both by more than 2 weeks. By

13   the mid-1990s, ocean temperatures returned to pre-perturbation levels, whereas the

14   temporal breeding responses of capelin and murres were delayed for a decade or more.

15   Oceanographic conditions (temperature, NAO) were poor predictors of the timing of

16   capelin arrival inshore in the current year compared to the previous one. Our findings

17   suggest that knowledge of the timing of capelin availability in the previous year provides

18   a robust cue for the long-lived murres, allowing them to achieve temporal overlap

19   between breeding and peak capelin availability.

20

21   **Keywords** capelin, life history, murres (*Uria aalge*), NAO, Northwest Atlantic, ocean

22   climate, oceanography, reproductive timing

23

1   **1. Introduction**

2

3   Energy costs are high during breeding, and animals tend to reproduce when food

4   is most abundant (e.g., Lack, 1954). In marine systems, phytoplankton production is

5   driven by physical oceanography, leading to seasonal increases in the availability of

6   zooplankton and forage fishes (Aebischer et al., 1990; Bertram et al., 2001). Seabirds

7   may rely on environmental cues to adjust their timing of breeding (Frederiksen et al.,

8   2004). Local conditions, such as ocean temperature, could provide reliable cues about

9   when to initiate breeding, yet species that disperse widely outside the breeding season

10 may have to rely on environmental cues outside the breeding area (Both and Visser,

11 2001). Owing to spatial variation in ocean climate, these cues are potentially less reliable

12 (Deser and Blackmon, 1993).

13   Pervasive changes in Northwest Atlantic food webs and ecosystems occurred in

14 the early 1990s. The coldest surface water event during the past 50 to 100 years occurred

15 in 1991 (Drinkwater, 1996). The commercial extinction of northern cod (*Gadus morhua*)

16 led to the closure of the eastern Canadian ground-fishery in 1992 (Hutchings and Myers,

17 1994; Hutchings, 2000). Through their influences on the timing, movement patterns and

18 abundance of pelagic fishes and invertebrates, these events caused unexpected changes in

19 food webs and trophic interactions. Capelin (*Mallotus villosus*), primary forage fish in

20 the Northwest Atlantic (Lavigne, 1996) and the major prey of cod (Bundy et al., 2000)

21 exhibited delayed spawning and smaller sizes following the 1991 cold-water perturbation

22 (Carscadden and Nakashima, 1997; Carscadden et al., 2002). Capelin spawned 4 to 6

23 weeks later throughout the 1990s and into the early 2000s.

1   In the context of these ecosystem changes, we examined the timing of breeding

2   common murres (*Uria aalge*), the primary avian predator of capelin in the Northwest

3   Atlantic (Montevecchi, 2000).   These seabirds provision their chicks primarily with

4   capelin in Newfoundland colonies (e.g., Piatt, 1987; Davoren and Montevecchi, 2003;

5   Burke and Montevecchi, 2008).   Consequently, successful chick-provisioning and

6   reproduction depends on the timing and inshore availability of capelin (Burger and Piatt,

7   1990; Davoren and Montevecchi, 2003; see also Vader et al., 1990).   Thus, to help ensure

8   energy demands for reproduction are met, murres should coincide breeding with the

9   inshore movements of capelin schools (Cairns et al., 1987; Piatt, 1987, 1990).

10   In this paper, we analyze the breeding times of common murres at Cape St.

11   Mary's Ecological Reserve, Newfoundland from 1980–2006.   With this relatively long-

12   time series available, we examine the hypotheses that the timing of murre breeding

13   chronology is associated with the timing of the inshore migration of capelin, and

14   variations in ocean temperatures and oceanography, as indexed by the North Atlantic

15   Oscillation (NAO).

16

17

18   **2. Methods**

19

20   The study was carried out at the Cape St. Mary's Ecological Reserve (CSM;

21   46°50´N, 54°12´W), Newfoundland, Canada (Fig. 1).   Near-vertical cliffs composed of

22   stratified sedimentary rock rise 100–150 m above sea-level and are lined with numerous

23   broad and narrow horizontal ledges suitable for breeding by both common and thick-

1   billed (*Uria lomvia*) murres. The total breeding population of murres was estimated at

2   10,000 and 1,000 pairs of common and thick-billed murres, respectively (Nettleship,

3   1980).

4   From 1980–2006, common murres were monitored using the Type II method

5   described by Birkhead and Nettleship (1980). Observations were made from late-May to

6   early-August on 6 study plots (containing ~1,000 common murres), throughout the

7   breeding cycle from laying through to fledging. Observations were usually conducted

8   every 1-7 days in fair weather, with wider intervals between observations when weather

9   was poor (heavy rain, strong wind and/or dense fog), from 11:00-16:00 Newfoundland

10 Daylight Savings Time. Observers counted the number of murres within plots and

11 watched for the presence/absence of eggs and/or chicks, allowing annual patterns in

12 attendance to be observed (e.g., Piatt and McLagan, 1987) and the timing of various

13 aspects of murre breeding biology to be estimated. Although data on the timing of egg

14 laying (n = 12 years) and fledging (n = 18 years) were collected in several years, the

15 analyses in this paper are based on first hatching date because these were recorded every

16 year from 1980-2006, except for 2003 (n = 26). The timing of hatching was taken as the

17 date of the first sighting of a chick under a brooding parent.

18   Capelin arrival was recorded at local beaches (<50 km from CSM) and at

19 Bryant's Cove and Bellevue Beach about 100 km north of CSM (Fig. 1). Throughout the

20 study period, dates of the first spawning activity of capelin at local beaches were obtained

21 from capelin spawning records kept by T. Power and local fishers (n = 11 years). Peak

22 capelin spawning dates (day with the highest new fertilized egg deposition) from

23 Bryant's Cove and Bellevue Beach were available from 1980-1990 and 1991-2006,

1   respectively. The dates of first spawning activity on local beaches were significantly

2   correlated with the combined series of peak spawning dates from Bryant's Cove and

3   Bellevue Beach ($r = 0.667$, n = 11, P = 0.025). Given the combined spawning data from

4   Bryant's Cove and Bellevue Beach is a complete dataset, and the patterns corroborate

5   with local spawning dates, we used the combined peak spawning dates form Bryant's

6   Cove and Bellevue Beach as an index of capelin chronology. Capelin timing and

7   availability are used synonymously throughout this paper, because we assume that

8   capelin are available to breeding murres when they arrive in inshore waters.

9   Ocean temperatures (0–150 m) for February-June, 1980-2006, were obtained

10   from hydrographic station 27 (47°31´50˝ N, 52°35´10˝ W) situated 17 km east of St.

11   John's, Newfoundland in the Avalon Channel branch of the Labrador Current,

12   approximately 140 km northeast of CSM (Fig. 1). The hydrographic measurements

13   obtained from station 27 provide robust indices for oceanographic conditions of the

14   Labrador Current which dominates the entire Newfoundland and Labrador Shelf (Petrie

15   et al., 1988; Drinkwater 1996). Values for winter (December to March) NAO indices

16   were   obtained   from   the   US   National   Centre   for   Atmospheric   Research

17   (http://www.cgd.ucar.edu/cas/jhurrell/indices.html)   as   indices   of   overall   physical

18   variability spanning breeding and migratory locations. NAO models the pressure

19   differential between the Icelandic low and the high pressure system near the Azores. In

20   the Northwest Atlantic, negative (positive) NAO indices generally indicate warmer

21   (colder) conditions in northern regions. The opposite response is seen in the southern

22   regions of the Northwest Atlantic (Petrie 2007).

1   We used simple and multiple linear regressions (without interactions) to test

2   associations between variables. All possible models were constructed starting with the

3   global model (the model including all variables of interest) and proceeding to simpler

4   models. Predictors to explain the timing of murre hatching included: the time of murre

5   hatching in the previous year, the timing of capelin in the current and previous years,

6   ocean temperature and the winter NAO index. For capelin timing, timing of capelin in

7   the previous year, ocean temperature and the NAO index were considered. This resulted

8   in 25 models with the date of first chick sighting as the response variable, and 7 models

9   with the date of capelin arrival as the response variable. For oceanographic conditions,

10   we also considered logical comparisons of positive to negative states and time lags of 1,

11   2, 3, 4, and 5 years. The most appropriate model was selected using Akaike's

12   Information Criterion adjusted for small sample size (AIC_c). This value selects the model

13   with the best balance between bias and precision, irrespective of sample size (Burnham

14   and Anderson, 2002). AIC_c rewards goodness of fit (log-likelihood, $\log(\mathcal{L})$) and also

15   includes a penalty that is an increasing function of the number of estimated parameters

16   (K). The model with the smallest AIC_c is the best in the sense that it explains the most

17   variation in the data without using an excessive number of parameters. The relative

18   importance of models is compared according to Anderson et al. (2001) using ΔAIC_c and

19   AIC_c weights (w), where ΔAIC_c is the absolute differences to the smallest AIC_c value in a

20   set of models and w is the relative likelihood of a model given the data.

21

22

23   **3. Results**

1

2   The date of first chick sighting was relatively stable throughout the 1980s and

3   were delayed substantially by approximately 3 weeks beginning in 1992 (Fig. 2a). Chick

4   timing ranged from 8 June in 1990 to 12 July in 1994 (mean = 21 June, SD = 8.1 days,

5   CV = 4.7). The date of capelin arrival was delayed by ~1-5 weeks during the early 1990s

6   (Fig. 2b). Capelin arrival ranged from 12 June in 1987 to August 23 in 1993 (mean = 6

7   July, SD = 17.0 days, CV = 9.0). Ocean temperatures (0-150 m) from February to June

8   also varied greatly across the study period: minimum = -1.14 °C (1991), maximum = 0.79

9   °C (2006), mean = -0.16 °C, SD = 0.46 °C, CV = -292.27 (Fig. 2c). NAO index was

10   positive for 20 of the 26 years in this study (Fig. 2d). The maximum NAO index was 5.1

11   in 1989, and the minimum was -3.8 in 1996 (mean = 1.1, SD = 2.0, CV = 175).

12   Of the models fitted against the date of the first chick sighting, the model which

13   included the date of first chick sighting in the previous year and the date of capelin arrival

14   in the previous year best fit the data (w = 0.44, ΔAIC_c > 2 for competing models; Table

15   1). The next best model which received about 3.7 (0.44/0.12) times less support, only

16   included the date of capelin arrival in the previous year (Table 1). Models including

17   timing of capelin in the current year, NAO and ocean temperatures were not strongly

18   supported (Table 1). The date of capelin arrival in the previous years was clearly the most

19   important predictor, appearing in all models with ΔAIC_c values < 4, and not appearing in

20   models with ΔAIC_c values > 10 (Table 1).

21   The model that best explained the date of capelin arrival included the variables

22   date of capelin arrival in previous year and ocean temperature in the current years (w =

23   0.65, ΔAIC_c > 2 for competing models; Table 1). Alone, the date of capelin arrival in the

1   previous year explained a substantial amount of variation in the date of capelin arrival in

2   the current year (w = 0.17, ΔAIC_c = 2.75; Table 1) and other models that included the

3   date of capelin arrival in previous year performed well. The NAO index was not a good

4   predictor of capelin timing (Table 1).

5   Comparing the timing of murres and capelin to water temperature and NAO states

6   did not yield any compelling results. Similarly, comparisons of lagged oceanographic

7   conditions to murre and capelin timing did not generate any biologically meaningful

8   results. Although there are no clear logical, linear, or lagged-linear associations between

9   the date of the first chick sighting and between peak capelin spawning and oceanographic

10   conditions, there are clear non-linear relationships. The cold-water event in 1991 had

11   striking consequences for both murre and capelin timing (Fig. 2).   Mean ocean

12   temperature before 1991 was -0.37 °C (SD = 0.32 °C). In 1991, ocean temperatures

13   declined substantially (reaching -0.84 °C), but returned to pre-perturbation levels in the

14   following year (1992 [-0.32 °C]).   With the exception of 1993 (-0.77 °C), ocean

15   temperatures have not fallen below pre-perturbation temperatures since, remaining

16   warmer than average from 1994-2006 (Fig. 2c). The mean date of the first chick sighting

17   before 1991 (pre-perturbation) was 17 June (SD = 5.2 days) compared to 25 June (SD =

18   8.6 days) after 1990. The response of murre breeding chronology lagged behind the

19   amelioration of the physical environment, taking about 7 to 8 years for the date of first

20   chick sighting to return to pre-perturbation levels in 1998 (June 19) and 1999 (12 June).

21   Even more evident is the delayed response of capelin timing, whereby the date of peak

22   capelin spawning is yet to be recorded at or earlier than the pre-perturbation mean of 19

1   June (SD = 6.2 days). In the most recent years, capelin spawning times appear similar to

2   those recorded more than 15 years ago (Fig. 2b).

3

4

5   **4. Discussion**

6

7   The breeding chronology of common murres and the inshore availability of

8   capelin (primary prey of breeding murres) ranged by about 1 month from 1980–2006.

9   Capelin spawned later than average throughout the 1990s and 2000s (Carscadden et al.,

10   2002), and in response, common murres delayed breeding. Murres likely delay breeding

11   to maximize the temporal match between hatching and capelin availability within

12   foraging ranges (Cairns et al., 1987; Piatt, 1987, 1990; Bertram et al., 2001; Davoren and

13   Montevecchi, 2003). Similar to our results, Durant et al. (2004) found that food

14   availability in the previous year was a robust predictor of the hatching date of Atlantic

15   puffins (*Fratercula arctica*). The delayed response to the changing timing of capelin

16   suggests that murres do not have a mechanism through which they can forecast the timing

17   of capelin arrival to inshore waters in a given year. Likewise, Davoren and Montevecchi

18   (2003) found that common murres at the species' largest colony on Funk Island did not

19   delay breeding in the cold-water years of 1991 and 1992; it was not until 1993 that a

20   delay in the murres' breeding was evident. Thus, the murres may go through an

21   adjustment period once prey conditions change (Davoren and Montevecchi, 2003). This

22   lagged response in murre breeding chronology could be due to a carryover effect of adult

23   condition as a consequence of capelin timing and availability in the previous year.

1   Alternatively, murres could be adjusting their seasonal cycle based on information of the

2   timing of capelin arrival in the previous year. Though this would undoubtedly result in

3   an imperfect relationship in a dynamic marine ecosystem, it could create a successful

4   stable strategy for long-lived murres (up to 20-25 years) since they can "afford" timing

5   mismatches during their 10-15 years of reproductive efforts (cf. Sanvik and Erikstad

6   2008). As adult survival is the life-history trait under the strongest selection for long-

7   lived seabirds (Stearns, 1992), variable breeding success could help ensure future

8   breeding attempts (Drent and Daan 1980).

9   Several studies have shown that the inshore migration of capelin is delayed in

10   cold years (Shackell et al., 1994; Carscadden et al., 1997, 2002). This effect was

11   especially apparent during the cold-water perturbation of 1991 (Carscadden and

12   Nakashima, 1997). Ocean temperatures returned to pre-perturbation conditions by the

13   mid-1990s, nevertheless, capelin continued to spawn later for about another decade

14   (Carscadden et al., 2002). The 1991 cold-water perturbation acted as a physical forcer,

15   delaying the inshore arrival of capelin. Both murres and capelin exhibited a lagged

16   response to this oceanographic event, taking more than 7 and 15 years, respectively, to

17   return to pre-perturbation levels. Since 1991, capelin have also shifted their vertical

18   distribution into deeper colder waters, likely as a result of changes in prey availability

19   (Mowbray 2002). These circumstances could contribute to the prolonged response of

20   capelin (and consequently murres) to the 1991 perturbation. There is no obvious

21   'bottom-up' relationship between murre breeding chronology or capelin timing and

22   changing ocean temperatures. The 1991 cold-water event also inhibited the migration of

23   warm-water pelagic species (mackerel, saury, squid) into the region, resulting in a regime

1   shift in the pelagic food web (Montevecchi and Myers, 1995, 1996). Though ocean

2   temperatures returned relatively quickly to pre-perturbation levels, the shift in the pelagic

3   food web was prolonged by more than 15 years, and therefore exhibited no linear

4   relationship between the prey landed by northern gannets (*Sula bassana*) and ocean

5   temperatures (Montevecchi, 2008).

6   Ocean temperatures would seem to serve as the most reliable cue to predict the

7   timing of the inshore movements of capelin, because their movements ultimately depend

8   on thermal conditions (Shackell et al., 1994; Carscadden et al., 1997). Yet apparently the

9   relationship between capelin spawning and ocean temperature is weak with a low and

10   degraded signal-to-noise ratio. Only in addition to capelin timing in the previous year

11   does ocean temperature in the current explain some residual variation in capelin timing in

12   current year. Accordingly, there was no strong relationship between murre breeding

13   chronology and ocean temperature. This finding indicates that murres do not use or

14   solely rely on local environmental conditions to adjust breeding times but may use

15   conditions in non-breeding areas (Frederiksen et al., 2004). Relationships between

16   breeding chronology and NAO have been found for common murres (Frederiksen et al.,

17   2004) and other widely dispersing alcids, such as Atlantic puffins (Durant et al., 2004)

18   and rhinoceros auklets (*Cerorhinca monocerata*; Bertram et al., 2001). Yet, we found

19   little support for relationships between murre breeding chronology or the timing of

20   capelin arrival with NAO; local ocean temperature in the previous year was a better

21   predictor of capelin availability. In the system we examined, oceanographic conditions

22   outside the seabirds' breeding range appear to be potentially less reliable than local cues

23   to help ensure matching the timing of breeding with food availability (see also Both and

1   Visser, 2001). More generally, long-lived seabirds, such as the common murre, with low

2   fecundity and a large foraging range, are less responsive to climate variability, apparently

3   because they live long enough to integrate such environmental stocasticity into their

4   reproductive activities across multiple years (Sandvik and Erikstad 2008).

5   Murres could be using multiple cues to predict capelin arrival. Mechanisms for

6   shifts in avian breeding ecology are unknown but are assumed to driven by bottom-up

7   food web processes (e.g., Aebischer et al., 1990). Although bottom-up oceanographic

8   drivers of timing are unclear in our study, variations in pre-breeding conditions likely

9   shape murre breeding chronology. Further research into the diet and physiology of pre-

10   breeding common murres is needed to elucidate the trophic interactions that shape

11   breeding chronology. Notwithstanding this, murres timed breeding according to the

12   timing of the inshore movements of capelin in the previous year which is a better

13   predictor of the date of capelin arrival in a given year than ocean temperatures or NAO

14   indices.

15   Most comparisons of murre breeding chronology to the inshore arrival of capelin

16   in the Northwest Atlantic have been limited by a lack of comparable long-term data.

17   Associated with the delayed inshore movements of capelin in the early 1990s, Davoren

18   and Montevecchi (2003) found that the common murres at Funk Island delayed breeding

19   by 2–3 weeks. Common murres at Witless Bay also delayed breeding in 1992 and 1993

20   (Carscadden et al., 2002). The present long-term study confirms the lagged association

21   between murres and capelin and illustrates the complexity of relationships between

22   predator, prey and the physical environment. Shifts in capelin biology were reflected in

23   the murres' breeding biology, indicating significant effects at higher trophic levels. And

1   although non-linearly related, anomalously cold ocean temperatures in 1991 had clear

2   prolonged effects on the timing of capelin and murre breeding chronologies.

3   Owing to the murres' longevity and life history, variations in prey availability and

4   ocean climate indirectly influence murre population dynamics over the long-term.

5   During our three decade study, ocean temperature has varied much more than either the

6   timing of capelin migration or murre breeding. Ocean conditions in 2005 through 2007

7   suggest that the Northwest Atlantic is shifting to warm water conditions (Colbourne et

8   al., 2006; Montevecchi, 2008). It is important for assessments of changing ocean

9   conditions and their influences on upper trophic levels that the long-term monitoring of

10   the interactions between predators, prey and the marine environment be continued.

11

12

References

Aebischer, N. J., Coulson, J. C. & Colebrook, J. M. (1990). Parallel long-term trends across four marine trophic levels and weather. *Nature,* 347, 753-755.

Anderson, D. R., Link, W. A., Johnson, D. H. & Burnham, K.P. (2001). Suggestions for presenting the results of data analyses. *Journal of Wildlife Management*, 65, 373-378.

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

1   Birkhead, T. R. & Nettleship, D. N. (1980). Census methods for murres, *Uria* spp.: a

2   unified approach. *Canadian Wildlife Service Occasional Papers*, No. 43.

3

4   Both, C. & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival

5   date in a long-distance migrant bird. *Nature*, 411, 296–298.

6

7   Bundy, A., Lilly G. R. & P. A. Shelton (Eds.) (2000). *A mass balance model of the*

8   *Newfoundland-Labrador Shelf.* (Canadian Technical Report of Fisheries and

9   Aquatic Sciences 2310).

10

11 Burke, C. M. & Montevecchi, W. A. (2008). Fish and chicks: Forage fish and chick

12   success in two co-existing auks. *Waterbirds* (in press)

13

14 Burger, A. E. & Piatt, J. F. (1990). Flexible time budgets in breeding common murres:

15   buffers against variable prey abundance. *Studies in Avian Biology,* 14, 71-83.

16

17 Burnham, K. P. & D. R. Anderson. (2002). *Model selection and multimodel inference: a*

18   *practical information-theoretic approach*. (Springer-Verlag, New York).

19

20 Cairns, D. K., Bredin, K. A. & Montevecchi, W. A. (1987). Activity budgets and

21   foraging ranges of breeding Common Murres. *Auk*, 104, 218-224.

22

1   Carscadden, J. E. & Nakashima, B. S. (1997). Abundance and changes in distribution,

2   biology and behaviour of capelin in response to cooler waters of the 1900s. (In

3   *Forage fishes in marine ecosystems*. (pp. 457-468). Proceedings of the

4   International Symposium Forage Fishes in Alaska, Sea Grant Program Report No.

5   97-01).

6

7   Carscadden, J. E., Nakashima, B. S. & Frank, K. T. (1997). Effects of fish length and

8   temperature on the timing of peak spawning in capelin (*Mallotus villosus*).

9   *Canadian Journal of Fisheries and Aquatic Science*, 54, 781-787.

10

11 Carscadden, J. E., Montevecchi, W. A., Davoren, G. K. & Nakashima, B. S. (2002).

12   Trophic relationships among capelin (*Mallotus villosus*) and marine birds in a

13   changing ecosystem. *ICES Journal of Marine Science*, 59, 1027-1033.

14

15 Colbourne, E. B., Loengt, H., Drinkwater, K. F. & Ozhigin, V. (2006). *Ocean climate*

16   *variability – comparisons of the Northwest Atlantic to the Barents and Nordic*

17   *Seas*. (NAFO Symposium. Nova Scotia, Canada).

18

19 Davoren, G. K. & Montevecchi, W. A. (2003). Signals from seabirds indicate changing

20   biology of capelin stocks. *Marine Ecology Progress Series*, 258, 253-261.

21

22 Deser, C. & Blackmon, M. L. (1993). Surface climate variations over the North Atlantic

23   Ocean during winter: 1990-1989. *Journal of Climate*, 6, 1743-1753.

1

2 Drent, R. H. & Daan, S. (1980). The prudent parent: energetic adjustments in avian

3   breeding. *Ardea* 68, 225-252.

4

5 Drinkwater, K. F. (1996). Atmospheric and oceanic variability in the northwest Atlantic

6   during the 1980's and early 1990's. *Journal of Northwest Atlantic Fisheries*

7   *Science*, 18, 77-97.

8

9 Durant, J. M., Anker-Nilssen, T., Hjerman, D. Ø. & Stenseth, N. C. (2004). Regime shifts

10   in the breeding of an Atlantic puffin population. *Ecology Letters*, 7, 388-394.

11

12 Frederiksen, M., Harris, M. P., Daunt, F., Rothery, P. & Wanless, S. (2004). Scale-

13   dependent climate signals drive breeding phenology of three seabird species.

14   *Global Change Biology*, 10, 1214-1221.

15

16 Hunt, G. L. Jr. & Schneider, D. C. (1987). Scale dependent processes in the physical and

17   biological environment. (In J. P. Croxall (Ed.), *Seabirds: feeding ecology and*

18   *roles in marine ecosystem* (pp. 7-41). Cambridge University Press, Cambridge).

19

20 Hutchings, J. A. (2000). Collapse and recovery of marine fishes. *Nature*, 406, 882-885.

21

1   Hutchings, J. A. & Myers, R. A. (1994). What can be learned from the collapse of a

2   renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and

3   Labrador. *Canadian Journal of Fisheries and Aquatic Science*, 51, 2126-2146.

4

5   Lack, D. (1954). *The natural regulation of animal numbers*. (Oxford University Press,

6   Oxford).

7

8   Lavigne, D. M. (1996). Ecological interactions between marine mammals, commercial

9   fisheries and their prey: unraveling the tangled web. (In W. A. Montevecchi (Ed),

10   *High-latitude seabirds. 4. Trophic relationships and energetics of endotherms in*

11   *cold ocean systems* (pp. 59-71). Canadian Wildlife Service Occasional Paper 91).

12

13   Montevecchi, W. A. (2000). Seabirds. (In A. Bundy, G. R. Lilly & P.A. Shelton (Eds.),

14   *Bulk biomass model of the Newfoundland Shelf* (pp. 15-18). Canadian Technical

15   Report of Fisheries and Aquatic Sciences 2310).

16

17   Montevecchi, W. A. (2007). Binary responses of northern gannets (*Sula bassana*) to

18   changing food web and oceanographic conditions. *Marine Ecology Progress*

19   *Series* 352: 213-220.

20

21   Montevecchi, W. A. & Myers, R. A. (1995). Prey harvest of seabirds reflect pelagic fish

22   and squid abundance on multiple spatial and temporal scales. *Marine Ecology*

23   *Progress Series*, 117, 1-9.

1

2 Montevecchi, W. A. & Myers, R. A. (1996). Dietary changes of seabirds indicate shifts in

3   pelagic food webs. *Sarsia*, 80, 313-322.

4

5 Mowbray, F. (2002). Changes in the vertical distribution of capelin (*Mallotus villosus*)

6   off Newfoundland. *ICES Journal of Marine Science*, 59, 942–949.

7

8 Nettleship, D. N. (1980). A guide to the major seabird colonies of eastern Canada:

9   identity, distribution and abundance. *Canadian Wildlife Service Manuscript*

10   *Report* 97.

11

12 Petrie, B. (2007). Does the North Atlantic Oscillation affect hydrographic properties on

13   the Canadian Atlantic continental shelf? *ATMOSPHERE-OCEAN*, 45, 141-151.

14

15 Petrie, B., Akenhead, S. A., Lazier, S. A. & Loder, J. (1988). The cold intermediate layer

16   on the Labrador and Northeast Newfoundland Shelves, 1978-86. *NAFO Science*

17   *Council Studies*, 12, 57-69.

18

19 Piatt, J. F. (1987). Behavioural ecology of common murre and Atlantic puffin predation

20   on capelin: implications for population biology. Ph.D. dissertation, Memorial

21   University of Newfoundland.

22

1   Piatt, J. F. (1990). The aggregative response of common murres and Atlantic puffins to

2   schools of capelin. *Studies in Avian Biology*, 14, 36-51.

3

4   Piatt, J. F. & McLagan, R. L. (1987). Common murre (*Uria aalge*) attendance patterns at

5   Cape St. Mary's, Newfoundland. *Canadian Journal of Zoology*, 65, 1530-1534.

6

7   Shackell, N. L., Carscadden, J. E. & Miller, D. S. (1994). Migration of pre-spawning

8   capelin (*Mallotus villosus*) as related to temperatures on the northern Grand Bank,

9   Newfoundland. *ICES Journal of Marine Science*, 51, 107-114.

10

11   Sandvik, H., & Erikstad, K. E. (2008). Seabird life histories and climatic fluctuations: a

12   phylogenetic-comparative time series analysis of North Atlantic seabirds.

13   *Ecography*, 31, 73-83.

14

15   Stearns, S. C. (1992). *The evolution of life histories*. (Oxford University Press, Oxford).

16

17   Vader, W., Barrett, R. T., Erikstad, K. E. & Strann, K. B. (1990). Differential responses

18   of Common and Thick-billed Murres to a crash in the capelin stock in the

19   southern Barents Sea. *Studies in Avian Biology*, 14, 175-180.

20

1   **Table 1** Fitted regression models with ΔAIC_c values > 10 to the variation in the date of

2   first chick sighting at Cape St. Mary's (chick timing), and all possible models for the date

3   of peak capelin spawning at Bryant's Cove and Bellevue Beach (capelin timing),

4   Newfoundland, 1980-2006. Models ranked according to ΔAIC_c and w values.

| Model	$\log(\mathcal{L})$	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*	-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*	-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

5   * global models
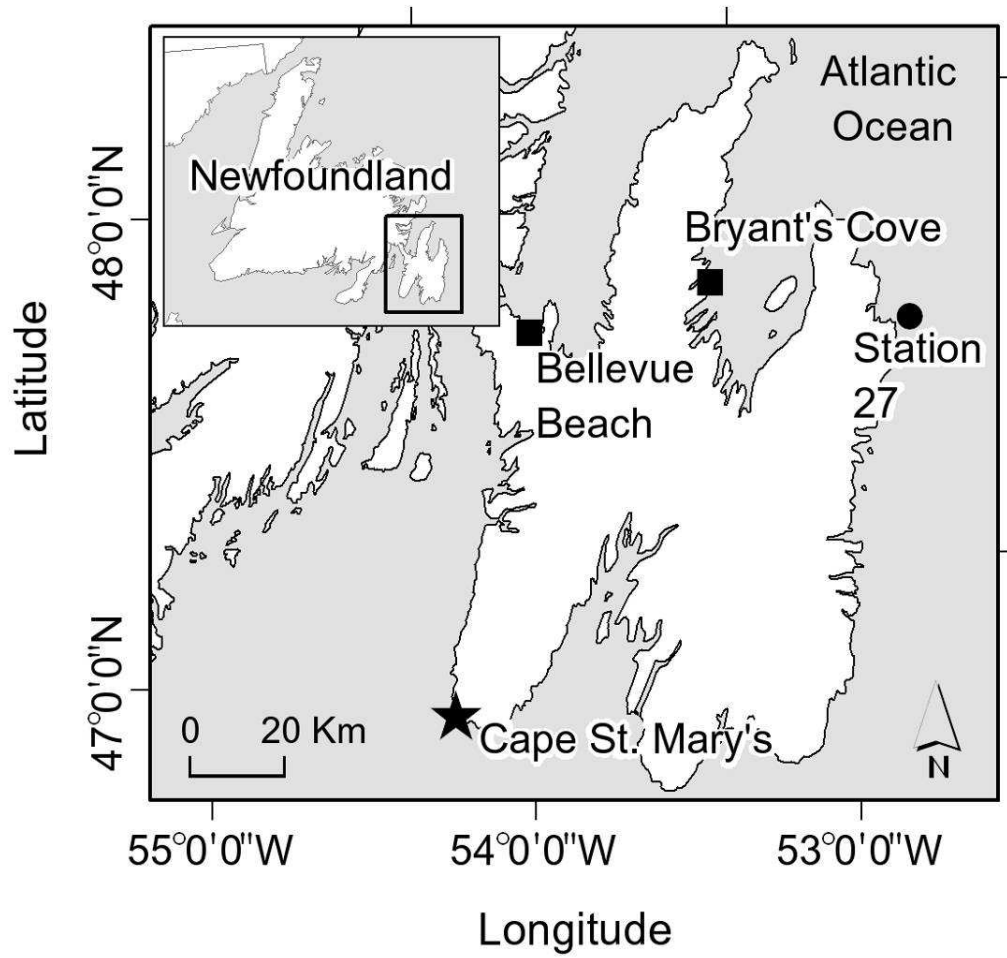
1

2 **Fig. 1** Location of Cape St. Mary's Ecological Reserve (★), capelin spawning beaches

3 (■), and hydrographic station 27 (●); inset shows location of Avalon Peninsula on insular

4 Newfoundland.

5

6

7

8
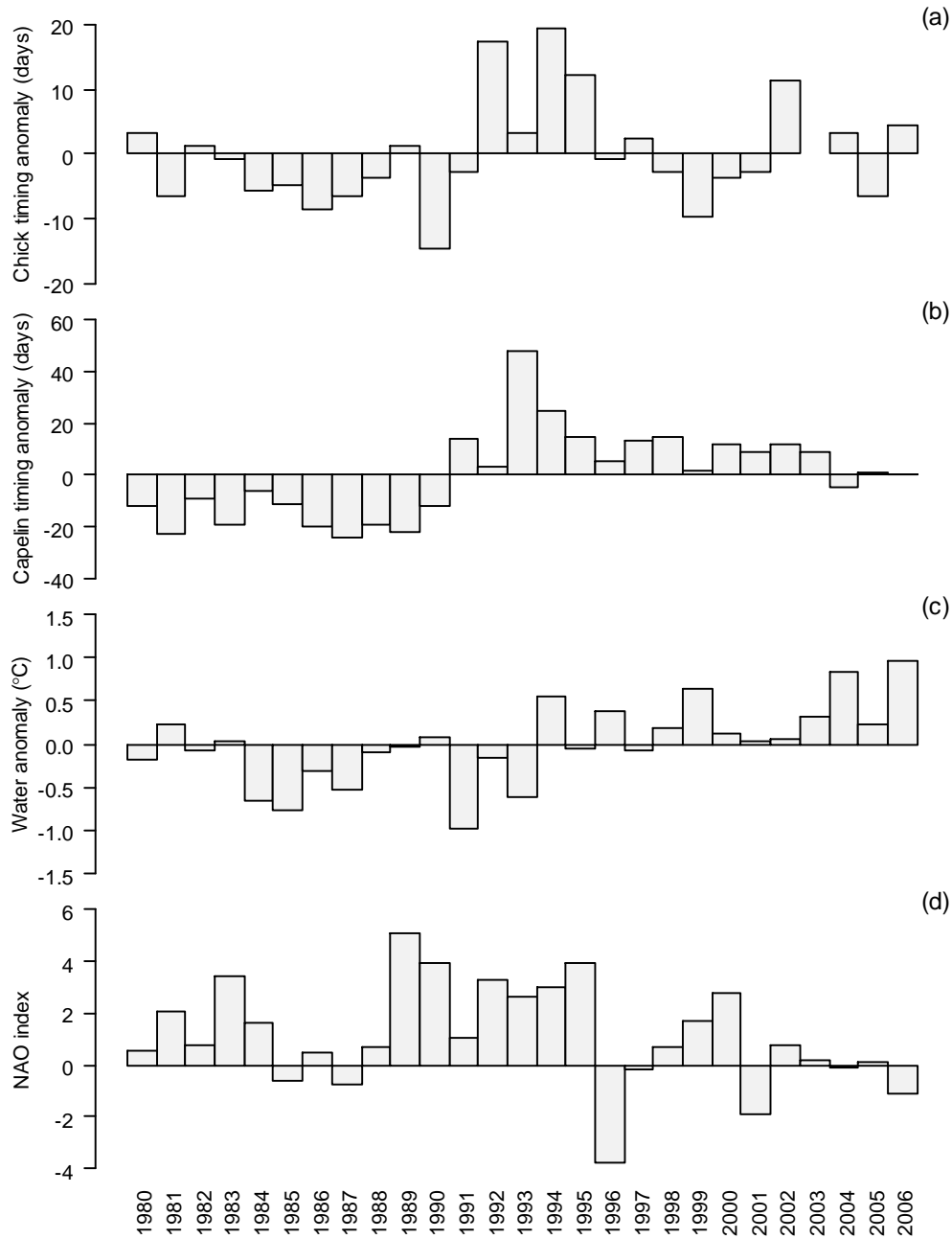
Fig. 2 Mean annual anomalies for (a) the date of the first Common Murre chick sighting at Cape St. Mary's Ecological Reserve (b) the date of peak capelin spawning at Bryant's Cove and Bellevue Beach and (c) mean February-June ocean temperature at 0–150 m from hydrographic station 27, Newfoundland, and (d) December-March North Atlantic Oscillation (NAO) index, 1980–2006.

1
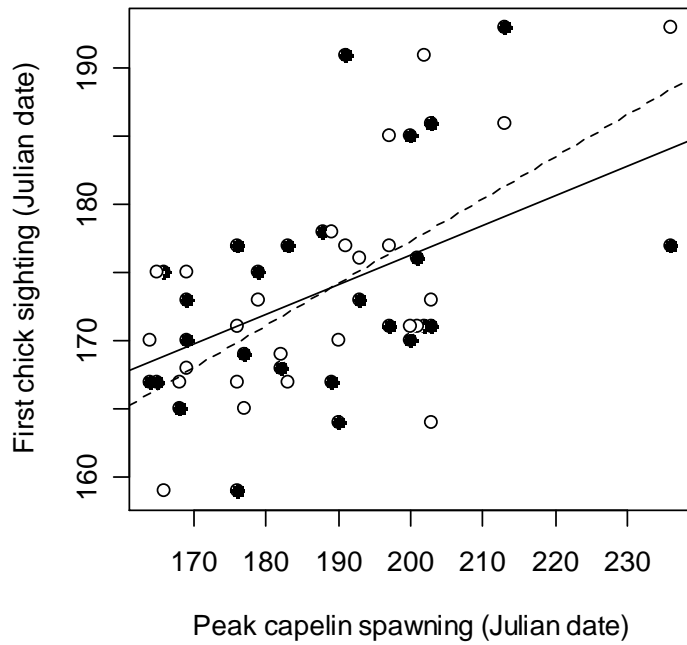
2

3   **Fig. 3** Relationship between the date of first chick sighting

4   at Cape St. Mary's Ecological Reserve to date of peak

5   capelin spawning in the same year (solid dots, solid line is

6   the linear regression) and in the previous year (open dots,

7   broken line), Newfoundland, 1980–2006.

8