

# Annual survival of North American Razorbills (*Alca torda*) varies with ocean climate indices

J.L. Lavers, I.L. Jones, A.W. Diamond, and G.J. Robertson

**Abstract:** According to life-history theory, survival in long-lived animals is not expected to vary greatly with environmental conditions. However, recent studies of a number of seabirds have shown that ocean climate indices such as the Pacific Decadal Oscillation index and sea surface temperature are correlated with adult survival. Here we evaluated whether annual adult survival of Razorbills (*Alca torda* L., 1758) at two breeding colonies covaried with oceanographic conditions in the North Atlantic during 1995–2006. We also examined pre-breeder survival (from fledging to age 2). The relationship between local adult survival and the North Atlantic Oscillation and two oceanographic variables (Labrador Current temperature profile and Bay of Fundy sea surface temperature) were evaluated using the program MARK. Capture–mark–recapture data fit the assumptions of the program MARK reasonably well with  $\hat{c}$  values ranging from 1.390 to 2.404. Pre-breeder survival rates were high for Machias Seal Island ( $\Phi = 0.778 \pm 0.041$ ) and low for the Gannet Islands ( $\Phi = 0.482 \pm 0.033$ ), likely the result of hunting pressure. On Machias Seal Island, constant adult survival ( $\Phi = 0.967 \pm 0.028$ ) was the best model; however, time-dependent models that included a climate covariate performed nearly as well. On the Gannet Islands, adult survival ( $\Phi = 0.890 \pm 0.053$ ) was negatively correlated with Labrador Current temperature. Overall, our results show significant differences in survival rates across sites over the same time period and highlight the importance of multisite studies and smaller scale climate indices for local populations. In addition, our study contributes to the growing body of evidence that survival in long-lived animals may vary with environmental conditions more than previously expected.

**Résumé :** D'après la théorie démographique, la survie des animaux à forte longévité ne devrait pas varier beaucoup en fonction des conditions du milieu. Cependant, des études récentes de plusieurs oiseaux marins indiquent que des indices du climat océanique, comme l'indice d'oscillation décennale pacifique et la température de surface de la mer, sont en corrélation avec la survie des adultes. Nous vérifions ici si la survie annuelle des adultes du petit pingouin (*Alca torda* L., 1758) dans deux colonies de reproduction de l'Atlantique Nord en 1995–2006 varie en fonction des conditions océaniques. Nous évaluons aussi la survie pré-reproductive (de l'envol à l'âge 2). Le logiciel MARK nous permet de déterminer la relation entre la survie locale des adultes et l'oscillation nord-atlantique et deux variables océaniques (profil de température du courant du Labrador et température de surface de la mer dans la baie de Fundy). Les données de marquage et de recapture s'accordent raisonnablement bien aux présuppositions du logiciel MARK avec des valeurs allant de 1,390 à 2,404. Les taux de survie avant la reproduction sont élevés à Machias Seal Island ( $\Phi = 0,778 \pm 0,041$ ) et faibles aux îles Gannet ( $\Phi = 0,482 \pm 0,033$ ), sans doute à cause de la pression de chasse. À Machias Seal Island, une survie constante des adultes ( $\Phi = 0,967 \pm 0,028$ ) représente le meilleur modèle, bien que des modèles dépendant du temps qui incluent une covariable climatique fonctionnent presque aussi bien. Aux îles Gannet, la survie des adultes ( $\Phi = 0,890 \pm 0,053$ ) est en corrélation négative avec la température du courant du Labrador. Globalement, nos résultats montrent des différences significatives des taux de survie entre les sites durant une même période de temps et ils mettent en évidence l'importance pour l'étude des populations locales des recherches faites à des sites multiples et des indices climatiques à plus petite échelle. De plus, notre travail ajoute à la masse croissante de données qui indiquent que la survie des animaux à forte longévité peut varier avec les conditions du milieu plus qu'on ne le croyait antérieurement.

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## Introduction

According to life-history theory, adult survival in most long-lived seabirds has the highest elasticity, meaning that this parameter explains the most variation in lifetime reproductive success (Croxall and Rothery 1991; Sandvik et al.

2005). Adult survival has therefore been assumed to be the life-history trait that would be least affected by climate variability (Cairns 1987; Gaillard and Yoccoz 2003). A number of studies reported that seabird productivity and diet were the most sensitive to changing environmental conditions (Nettleship and Birkhead 1985; Montevecchi 1993). How-

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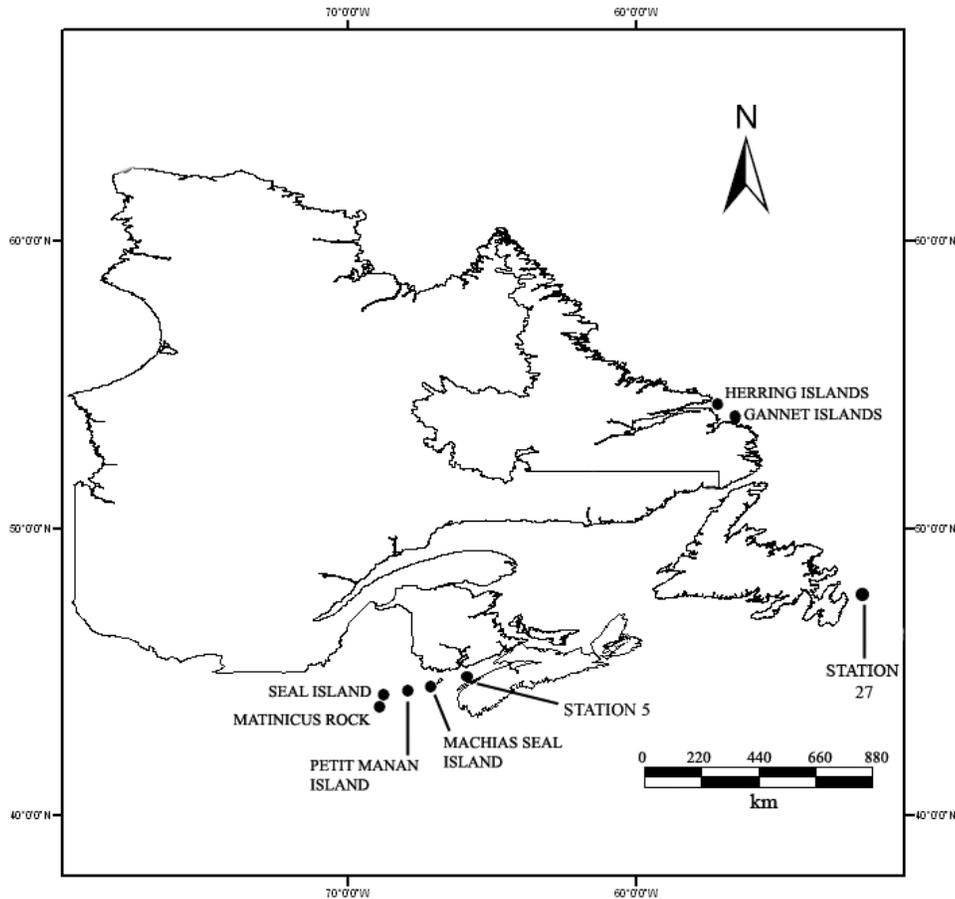
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**Fig. 1.** Map of Atlantic Canada showing the main study sites, the Gannet Islands and Machias Seal Island, as well as secondary sites in relation to Fisheries and Oceans Canada climate stations 5 and 27.



ever, extreme weather conditions such as El Niño – Southern Oscillation events (ENSO; Barber and Chavez 1983), storms (Underwood and Stowe 1984; Harris and Wanless 1996), and hurricanes (Morris and Chardine 1995) have been linked to direct and indirect adult mortality. Growing evidence now link seabird annual adult survival and continuous variation in climate (Thompson and Ollason 2001; Weimerskirch et al. 2001; Jones et al. 2002; Durant et al. 2004; Grosbois and Thompson 2005; Jones et al. 2007) with similar broad trends for many aspects of marine ecosystems (i.e., prey availability; Aebischer et al. 1990; Nakashima 1996; Alheit and Hagen 1997; Hjermmann et al. 2004). The urgent questions are now how widespread are these reported tendencies across seabird species and populations, and what are the mechanisms that explain patterns of covariation between survival and environmental conditions?

Ocean climate varies considerably between years and has been characterized by indices such as the North Pacific index, Pacific Decadal Oscillation index, and ENSO index (Trenberth and Hurrell 1994; Zhang et al. 1997). In the North Atlantic, the most important index is the North Atlantic Oscillation (NAO), which is derived as the pressure differential between the subtropic high-pressure zone centered over the Azores and the atmospheric low-pressure zone over Iceland (Wallace 2000; Ottersen et al. 2001; Hurrell et al. 2003). The NAO exerts a dominant influence on winter sea surface temperature (SST). When the NAO index is positive, strong northerly winds over Greenland and Canada

carry cold wind southward, resulting in decreased SST over the northwest Atlantic (Hurrell and Dickson 2004). Since the 1980s, the NAO has been in a mostly positive phase, resulting in colder and stormier winters (Hurrell and Dickson 2004). Such changes in surface temperature (and related changes in rainfall and storm frequency) can have significant impacts on marine organisms, including seabirds. Here we examine the relationship between climate covariates such as the NAO and adult survival in a long-lived seabird, the Razorbill (*Alca torda* L., 1758), over a 12-year period at two breeding colonies, which extend over almost their entire North American breeding range. The aims of our study were (i) to quantify annual adult and pre-breeder (from fledging to age 2) survival of Razorbills at two representative colony sites in the western Atlantic during 1996–2006, (ii) to examine whether adult survival covaried with climate indices, and (iii) discuss possible mechanisms for any patterns observed.

## Materials and methods

### Study sites

Fieldwork was conducted at the Gannet Islands, Labrador, Canada (53°56'N, 56°30'W), and Machias Seal Island, New Brunswick, Canada (MSI; 44°3'N, 67°06'W; Fig. 1). The Gannet Islands cluster includes six islands (GC1–GC6), which support the largest colony of Razorbills in North

America (~9800 breeding pairs; Chapdelaine et al. 2001). The Gannet Islands represent one of the most northerly major Razorbill breeding colonies in North America. In contrast, MSI is located at the southern extent of the Razorbill's breeding range and supports 592 pairs (Grecian 2005).

### Capture – mark – recapture or resight

Razorbill adults and chicks were banded with size 5 US Fish and Wildlife Service triangular stainless steel leg bands. Banding of Razorbills on MSI and the Gannet Islands began in 1995 and 1996, respectively, and continued until 2006. Since 1995, 7039 birds (mostly chicks) have been banded. Banding effort varied between years on MSI, ranging from 20 to 270 individuals per year; however, effort on the Gannet Islands was relatively constant. Nine bands were replaced on MSI and two on the Gannet Islands during this study owing to wear and erosion of the bands caused by the birds walking over rough terrain (Lyngs 2006). Adult Razorbills were captured on MSI and GC2 and GC4 from May to early August using noose carpets or barrel traps on prominent display rocks (adjacent to the breeding sites) where birds gathered daily to socialize. Razorbill chicks were captured on MSI and GC2 by hand or with a small net when they were about 10 days old. This was the preferred age for banding because the chicks were able to thermoregulate, but had limited mobility and could be captured on steep cliffs with minimal disturbance.

Razorbill resighting was conducted from blinds and cliff ledges on the Gannet Islands and MSI from 1998 to 2006 using a spotting scope. In July 2005, we also visited the Herring Islands (54°20'N, 57°7'W), located 70 km northwest of the Gannet Islands, to look for Razorbills originally banded on the Gannet Islands that were breeding on the Herring Islands. We also sought evidence for Razorbill dispersal from MSI. Resighting data for Razorbills on Petit Manan Island (44°23'N, 67°49'W), Seal Island, and Matinicus Rock (approximately 44°23'N, 67°49'W) in the Gulf of Maine were provided by US Fish and Wildlife Service and National Audubon Society personnel. An individual bird was not considered confirmed or entered into the database until it had been resighted at least twice from 1998 to 2006. This would likely reduce the chance of band reading errors (Lavers 2007), but unavoidably cause the omission of individuals that were correctly resighted only once. On the Gannet Islands, 101 birds banded as chicks and 13 adults were seen only once during the study period. On MSI, 34 birds banded as chicks and 22 adults were also only seen one time. These birds were excluded from the data set.

Protocols specifying the minimum amount of daily resighting effort were not implemented until 2000; therefore data collected during the early years of the study, specifically from 1995 to 1998, were sparse. For example, on MSI, only 15 adults were banded and 4 resightings recorded from 1995 to 1998. The removal of this small amount of data (resightings made during 1995–1998) resulted in improved fit of the models and more accurate parameter estimates. On the Gannet Islands, adult resighting was initiated on one plot only in 1998 and was included in the analyses. However, no birds banded as chicks were observed that year; therefore the pre-breeder survival data set began in 1999.

**Table 1.** Mean values of environmental covariates used in the analyses from March of the previous year to February of the current year.

Year	North Atlantic Oscillation (NAO)	Station 27 (Labrador Current, °C)	Station 5 (Bay of Fundy, °C)
1995	0.67	0.80	7.36
1996	-0.27	0.85	6.56
1997	0.02	1.51	6.67
1998	-0.15	0.94	6.67
1999	-0.37	1.03	6.85
2000	0.52	1.35	7.43
2001	-0.03	1.17	7.44
2002	-0.05	1.27	6.97
2003	0.00	1.08	7.28
2004	0.08	1.43	6.39
2005	0.23	1.62	5.89

### Environmental covariates

To test the hypothesis that Razorbill annual survival varied with oceanographic variability we looked for a correlation between survival and three North Atlantic climatic indices (Table 1): (1) NAO, (2) the Labrador Current as indicated by the ocean temperature profile (to a depth of 175 m) from Fisheries and Oceans Canada (DFO) station 27 (Fig. 1), and (3) sea surface temperature (to a depth of 1 m) for the Bay of Fundy provided by DFO station 5 (Fig. 1). We used mean values from March of the previous year to February of the current year (i.e., the 12 months leading up to the start of the current breeding season;  $M-F_{t-1}$ ), as well as the mean of the previous November to March (i.e., the 5 winter months leading up to the start of the current breeding season;  $winter_{t-1}$ ), mean of the current year (i.e., January to December of the current year), and the mean of November to March of the current year (i.e., the winter months immediately following the current breeding season;  $winter_t$ ).

### Model selection

Apparent survival ( $\Phi$ ) and recapture probabilities ( $p$ ) were estimated using capture – mark – recapture or resight (CMR) models (Lebreton et al. 1992) with the program MARK (White and Burnham 1999). For birds banded as chicks, there was significant variation in recapture rate for all cohorts in all years at both study locations. Variability in resighting rate is known to create problems in estimating survival (Martin et al. 1995; Prévot-Juilliard et al. 1998), so we evaluated models with a different recapture rate parameter for each year and cohort until birds reach adulthood at age 3 (i.e., complete time dependence;  $p(\text{cohort})$ ) and with recapture rate parameters that were pooled across similar years (i.e.,  $p(\text{pooled})$ ).

Since our marking technique was known to catch both nonbreeding and breeding adult birds, we expected that some individuals (“prospectors”) might show lower site fidelity, and hence lower local survival rates, after their first capture (Pradel et al. 1997; Prévot-Juilliard et al. 1998; Bertram et al. 2000). We allowed survival rates in the year after the initial capture to be modeled independently of survival in subsequent years. Structurally, this is similar to age mod-

els (Lebreton et al. 1992). In these models, apparent survival after the 1st year of capture is a combined estimate of true survival and permanent emigration rates (because the sample of marked individuals includes transient birds), while survival in subsequent years (of resident individuals) is a better approximation of true survival (Pradel et al. 1997). In summary, for our global model for adults, we used a two age class survival model with time dependence in all years after initial capture and time dependence in recapture probability.

Since most juvenile Razorbills do not return to the colony to prospect or breed until at least 2 years of age (Lloyd and Perrins 1977) and are therefore not available to be resighted, it was not possible to estimate annual survival during their 1st year of life. Instead, we estimated survival from fledging to age 2 ( $y_0$ – $y_2$ ), referred to as pre-breeder survival. These models were similar to models for adults in that apparent survival from first capture until age 2 was a combined estimate of true survival and permanent emigration.

The goodness of fit of the global model to the data was determined using the parametric bootstrap approach described in Cooch and White (2001). From these bootstraps, we extracted a mean of the model deviance and a mean  $\hat{c}$ . The parameter  $\hat{c}$  is a measure of overdispersion, or extra-binomial variation, in the data. It arises when some model assumptions are not met, such as variation in survival or recapture rates among individual animals (Burnham and Anderson 1998). The observed deviance and  $\hat{c}$  were divided by the mean of bootstrapped values, and the higher of the two values was taken as an estimate of  $\hat{c}$  (Cooch and White 2001). We restricted our candidate models to the global model, plus a series of reduced parameter models, to assess whether age structure was appropriate. We did not construct every reduced parameter model, as this would have led to a large number of models, many of which had poor fit. Instead, we used the approach described in Lebreton et al. (1992) by first modeling recapture rates to determine the best structure and then modeling survival rates.

We modeled the climate covariate with survival only after the initial capture period, as we were not interested in the influence of oceanographic conditions on birds not resident in the study area.

Model selection was based on comparison of the QAIC<sub>c</sub> (quasi Akaike's information criterion corrected for small sample sizes), where the models with lowest QAIC<sub>c</sub> values suggest the best compromise between good fitting models and models with relatively fewer explanatory variables (Burnham and Anderson 1998). QAIC<sub>c</sub>, instead of AIC<sub>c</sub>, was used to rank models to acknowledge the extra-binomial variation in the data set, which is represented by  $\hat{c}$  (Burnham and Anderson 1998). QAIC<sub>c</sub> weights were also calculated, as they provide a relative measure of how well a model supports the data compared with other models (Burnham and Anderson 1998). For all models we used notation similar to Lebreton et al. (1992), where the parameterization of each class was explicitly described ( $y_1$ , 1st year class;  $y_2$ , 2nd year class;  $y_3+$ , all subsequent year classes) using  $t$  for time (year) effects. We used year classes instead of age classes, since the age of birds banded as adults is not known.

## Results

### Dispersal of Razorbills

Survival rates were inferred from resightings of marked individuals. Because fidelity of adult Razorbills to breeding sites is high (Gaston and Jones 1998), we expected little permanent emigration and assumed our approach provides a close approximation to true survival. However, philopatry (birds banded as chicks) on the Gannet Islands was relatively low (Lavers et al. 2007) and dispersal of individuals outside the study area was a concern. We attempted to account for this by including resightings of birds that had dispersed to other islands (i.e., these birds were marked as alive). Resighting was conducted on three islands in the Gulf of Maine and on the Herring Islands to look for birds that dispersed from the island where they were banded. We found a total of 5 birds that had dispersed from the Gannet Islands to the Herring Islands and 12 from MSI that had dispersed to another island in the Gulf of Maine (all banded as chicks; Lavers et al. 2007). In addition, three birds banded on the Gannet Islands (one as an adult) were later resighted on MSI and one bird banded as an adult on MSI was resighted on the Gannet Islands. Only 4 of the dispersal birds were known to be breeding on their new island; it is possible that the remaining 17 birds are vagrants and may be attending both colonies (3 birds were seen on both the Gannet Islands and MSI and 1 bird was seen on Matinicus Rock and Seal Island). These birds were included in the CMR data set even though they had moved outside of the main sampling area.

### Gannet Islands: adult survival

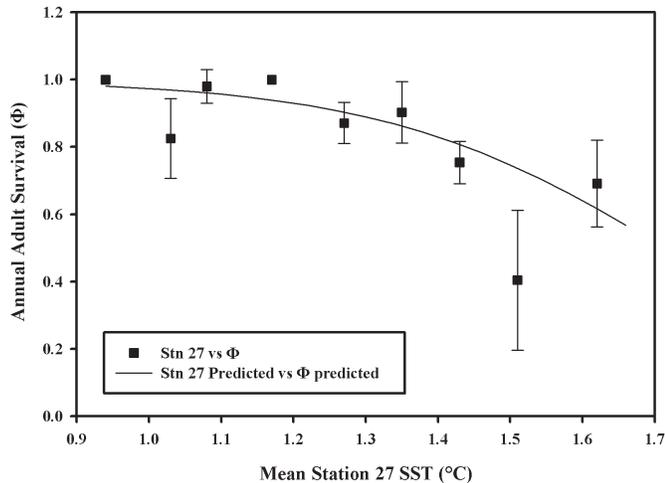
A total of 311 Razorbill adults were captured on GC2 and GC4, of which 191 were resighted at least twice. The data provided a good fit to our global model with two age classes. After constructing reduced parameter models, it was clear that the recapture rate was best modeled without complete time dependence, but instead with seven time parameters that included three groups of years with similar recapture rates (very low: 1998; moderate: 2000; high: 2002 and 2004). Therefore only this parameterization (pooled) was used in building subsequent models. From the parametric bootstrap,  $\hat{c}$  was calculated to be 1.390, suggesting the presence of some but not major amounts of extra-binomial variation. This value of  $\hat{c}$  was used to adjust all QAIC<sub>c</sub> values. Models with two age structure were well supported by the data (Table 2a), and models with time-dependent survival rates 2 years after initial capture (denoted as  $y_1$ ,  $y_2+ \times t$ ) were ranked higher than models with constant survival. Therefore, we used survival rate after the first interval and recapture in three groups of years to model climatic covariates.

The most parsimonious model for birds banded as adults at the Gannet Islands in the candidate model set was a two age class model in which survival covaried with the Labrador Current (station 27) climate index during the preceding March to February ( $\Phi(y_1, y_2+ \times \text{Stn27 M-F}_{t-1}) p(\text{pooled})$ ; Table 2a, Fig. 2). The relationship between survival and the Labrador Current was negative ( $\beta = -5.04 \pm 0.85$  (mean  $\pm$  SE); 95% CI = -7.03 to -3.06; note that the 95% confidence limits do not bound zero). This model was four times better

**Table 2.** Summary of the top five models for Razorbills (*Alca torda*) banded from 1996 to 2006 as (a) adults on Gannet Islands GC2 and GC4, and (b) chicks on Gannet Island GC2.

Model	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	QAIC <sub>c</sub> weight	Likelihood	#Par	QDev
<b>(a) Adults from GC2 and GC4 (<math>\hat{c} = 1.390</math>)</b>						
$\Phi(y1, y2+ \times \text{Stn27 } M-F_{t-1}) p(\text{pooled})$	955.26	0.00	0.621	1.000	10	250.55
$\Phi(y1, y2+ \times \text{Stn27 } \text{winter}_{t-1}) p(\text{pooled})$	958.22	2.96	0.141	0.228	10	253.51
$\Phi(y1, y2+ \times \text{Stn5 } M-F_{t-1}) p(\text{pooled})$	959.23	3.97	0.085	0.137	10	254.52
$\Phi(y1, y2+ \times \text{Stn5 } \text{winter}_{t-1}) p(\text{pooled})$	959.23	4.27	0.073	0.118	10	254.82
$\Phi(y1, y2+ \times \text{Stn27}_t) p(\text{pooled})$	960.93	5.67	0.036	0.059	10	256.22
<b>(b) Chicks from GC2 (<math>\hat{c} = 2.404</math>)</b>						
$\Phi(y0-y2, y3+) p(y1, y2, y3+ \times t)$	736.44	0.00	0.567	1.000	14	106.52
$\Phi(y0-y2, y3, y4+) p(y0-y2 \times t, y3+ \times t)$	738.17	1.72	0.240	0.423	15	106.19
$\Phi(y0-y2, y3+) p(y1-y3 \times t, y4+ \times t)$	738.60	2.16	0.192	0.340	15	106.63
$\Phi(y0-y2, y3, y4+) p(y1-y3 \times t, y4+ \times t)$	748.86	12.41	0.001	0.002	16	114.82
$\Phi(y0-y2, y3+) p(y0-y2 \times t, y3+ \times t)$	764.99	28.55	0.000	0.000	29	103.92

**Note:** Models are sorted by increasing QAIC<sub>c</sub> (quasi Akaike's information criterion corrected for small sample sizes) value, with the most parsimonious model at the top. Factors in the model are as follows:  $\Phi$ , survival parameter;  $y$ , year class (i.e.,  $y1$ , 1st year since banding);  $p$ , resighting probability; "pooled", years with similar recapture probability are pooled;  $t$ , time; M, March; F, February; and "winter", November to March. #Par is the number of estimable parameters.

**Fig. 2.** Adult Razorbill survival ( $\Phi$ ) on the Gannet Islands, Labrador, in relation to station 27 Labrador Current sea surface temperature (SST; °C) during 1998–2005.

supported than the next best model ( $0.621/0.141 = 4.404$ ). It is possible to provide a mean survival rate after first capture for this model; however, the estimate would be constrained by the covariate. Instead, we used the variance components method to take into account annual variance and sampling variance in survival rate (based on the model  $\Phi(y1, y2+ \times t) p(\text{pooled})$ ). Our mean estimate of Razorbill adult survival at the Gannet Islands during 1996–2006 was  $0.890 \pm 0.053$  and recapture probability was  $0.514 \pm 0.129$ .

### Gannet Islands: pre-breeder survival

No birds banded as chicks in 1996–1998 were resighted until 2001. To ensure that the pre-breeder data set did not include any birds that would have already achieved adult status (age 3+) when first sighted in 2001, we excluded birds banded in 1996–1998. A total of 885 chicks were banded on the Gannet Islands (island GC2 only) from 1999 to 2006, of which 157 were resighted at least twice. The data provided a reasonably good fit to our global model

with two age classes and time dependence in survival rate and time variance in recapture rate. From the parametric bootstrap,  $\hat{c}$  was calculated to be 2.404. This value of  $\hat{c}$  was used to adjust all QAIC<sub>c</sub> values.

After constructing reduced parameter models, it was clear that recapture rate was best modeled with years with similar probabilities pooled together. This parameterization was used in building subsequent models. The most parsimonious model for birds banded as chicks in the candidate model set was one with constant survival for ages 0–2 and 3+, and constant, pooled recapture probabilities for the 1st and 2nd age classes followed by time dependence for the age 3+ class ( $\Phi(y0-y2, y3+) p(y1, y2, y3+ \times t)$ ; Table 3b). This model was more than twice as well supported as the next best model ( $0.567/0.240 = 2.362$ ). The mean estimate of Razorbill pre-breeder survival on the Gannet Islands from 1996 to 2006 was  $0.482 \pm 0.033$  and was  $0.970 \pm 0.030$  once the birds were 3 years of age and older. Mean recapture probability was  $0.113 \pm 0.039$ .

### Machias Seal Island: adult survival

A total of 274 adult Razorbills were banded on Machias Seal Island from 1999 to 2006, of which 193 were resighted at least twice. The data provided a reasonably good fit to our global model with two age classes and time dependence in survival rate and time dependence in recapture rate. From the parametric bootstrap,  $\hat{c}$  was calculated to be 1.671.

The most parsimonious model for birds banded as adults was a two age class model with constant survival in the intervals following first capture and time dependence in recapture rate ( $\Phi(y1, y2+) p(t)$ ; Table 3a). This model was only slightly better supported than the next nine best models, all of which included a climate covariate (Table 3a). Models incorporating station 5 SST did not rank in the top five best models. Local adult Razorbill survival on MSI in the year of banding is estimated at  $0.752 \pm 0.054$  and all subsequent years is  $0.967 \pm 0.028$  and recapture probability was  $0.395 \pm 0.063$ .

### Machias Seal Island: pre-breeder survival

The pre-breeder survival data set (601 birds were banded

**Table 3.** Summary of the top five models for Razorbills banded and resighted as (a) adults and (b) chicks on Machias Seal Island from 1999 to 2006.

Model	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	QAIC <sub>c</sub> weight	Likelihood	# Par	QDev
<b>(a) Adults (<math>\hat{c} = 1.671</math>)</b>						
$\Phi(y1, y2+) p(t)$	738.65	0.00	0.145	1.000	9	110.75
$\Phi(y1, y2+ \times \text{Stn27 winter}_{t-1}) p(t)$	739.49	0.84	0.095	0.657	10	109.50
$\Phi(y1, y2+ \times \text{NAO winter}_t) p(t)$	739.50	0.85	0.095	0.654	10	109.51
$\Phi(y1, y2+ \times \text{Stn27 M-F}_{t-1}) p(t)$	739.70	1.06	0.086	0.589	10	109.72
$\Phi(y1, y2+ \times \text{Stn27 winter}_t) p(t)$	739.79	1.14	0.082	0.566	10	109.80
<b>(b) Chicks (<math>\hat{c} = 1.492</math>)</b>						
$\Phi(y0-y2, y3+) p(y1, y2, y3+ \times t)$	1085.94	0.00	0.296	1.000	20	72.52
$\Phi(y0-y2, y3+) p(\text{cohort})$	1087.17	1.23	0.160	0.541	30	52.37
$\Phi(y1, y2+) p(\text{cohort})$	1087.55	1.61	0.132	0.447	30	52.75
$\Phi(y1, y2, y3+) p(y1, y2, y3+ \times t)$	1087.57	1.62	0.131	0.444	21	72.03
$\Phi(y0-y2, y3, y4+) p(y1, y2, y3+ \times t)$	1088.05	2.10	0.103	0.349	21	72.51

**Note:** Models are sorted by increasing QAIC<sub>c</sub> (quasi Akaike's information criterion corrected for small sample sizes) value, with the most parsimonious model at the top. Factors in the model are as follows:  $\Phi$ , survival parameter;  $y$ , year class (i.e.,  $y1$ , 1st year since banding);  $p$ , resighting probability;  $t$ , time; M, March; F, February; "winter", November to March; and "cohort", complete time and age dependence in recapture probability. #Par is the number of estimable parameters.

as chicks, 225 of which were later resighted at least twice) provided a reasonably good fit to the global model with two age classes and time dependence in survival rate and time dependence in recapture rates. From the parametric bootstrap,  $\hat{c}$  was calculated to be 1.492.

Machias Seal Islands pre-breeder model structure was very similar to that of the Gannet Islands with the most parsimonious model having two age classes and time independence for survival during the first 2 years following capture and pooled recapture probabilities for similar years ( $\Phi(y0-y2, y3+) p(y1 \times t, y2 \times t, y3+ \times t)$ ; Table 3b). However, several models performed nearly as well (Table 3a), their QAIC<sub>c</sub> weighting deviating by less than two from the optimal model. The survival estimates for the top model were  $0.778 \pm 0.041$  for age class 0–2 years and  $0.912 \pm 0.052$  for all subsequent years (3 years of age and older). Mean recapture probability was  $0.176 \pm 0.056$ .

## Discussion

Our best fitting models for local survival and recapture rate indicated that after initial capture some individuals (transients) permanently left the trapping area, and that adult survival at the Gannet Islands varied with the Labrador Current index. Local adult survival during the first interval after marking was  $0.634 \pm 0.038$  for the Gannet Islands and  $0.752 \pm 0.054$  for MSI, while survival thereafter was  $0.890 \pm 0.053$  and  $0.967 \pm 0.028$ , respectively. These estimates suggest that 21%–25% of newly marked adults were transients. Given the propensity for Razorbills to visit arena-like gathering areas (Wagner 1992), the capture of nonresident birds was not surprising. The survival estimates for birds age 3+ years from the known-age (i.e., banded as chicks) data set were higher on the Gannet Islands ( $0.970 \pm 0.030$ ) than the estimates generated using birds banded as adults, but were lower for MSI ( $0.912 \pm 0.052$ ; Table 4; Fig. 3). We speculate that the slightly lower adult survival rate from birds banded as chicks on MSI may be due to the classification of possibly pre-breeding or inexperienced birds as adults. For example, birds age 3–5 are considered to be

adults but may not be breeding (Harris and Wanless 1989). If these young birds show slightly lower survival or site fidelity compared with the rest of the adult population, then lower survival rates are expected. Since the majority of chicks banded on MSI were banded between 1999 and 2006, most of the birds making up the known-age adult sample were 3–6 year olds. Band wear was detected on both study areas, with an indication that this was more prevalent at MSI, but this was not considered to be frequent enough to significantly modify the survival estimates.

Our adult survival estimates for Razorbills from the Gannet Islands fall within the range reported for Europe and Quebec (Lloyd 1974; Harris and Wanless 1989; Chapdelaine 1997; Poole et al. 1998; Sandvik et al. 2005; Table 4). However, among all studies, we found MSI to have the highest reported adult and pre-breeder survival rates (Table 4, Fig. 2). This suggests there were differences in environmental conditions, mortality (e.g., hunting), or disturbance pressures such that the Gannet Islands population experienced lower true survival rates and (or) higher rates of permanent immigration than the MSI population. However, there is little reason to suspect that the Gannet Islands would experience a higher rate of permanent emigration. Because breeding habitat is not limiting on the Gannet Islands (Lavers 2007), there would appear to be no pressure for individuals to leave the area. At MSI, habitat may be limiting owing to the small size of this single, isolated island, so permanent emigration might be expected to be higher. Disturbance by researchers is controlled at both sites; however, MSI likely experiences higher disturbance overall because of the 30 tourists permitted on the island per day during June and July (C. MacKinnon, personal communication (2007)). Taken together, these points suggest that it would have been higher at MSI (opposite to what is suggested by our local survival estimates) if there was a difference in permanent emigration.

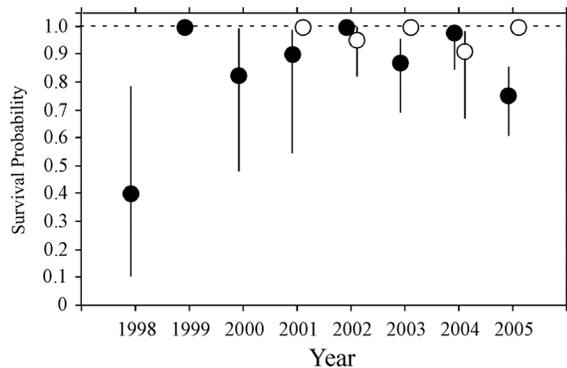
Mortality would appear to be a better explanation for the difference in local survival rates between the Gannet Islands and MSI. Razorbills from the Gannet Islands are shot illegally during the annual Newfoundland Murre (genus *Uria*

**Table 4.** Mean Razorbill survival estimates ( $\Phi$ ) and their variability for the Gannet Islands and Machias Seal Island and other colonies across their breeding range.

Colony	Method	Age class	$\Phi$ (mean $\pm$ SE)	Years	Source
<b>Western Atlantic</b>					
Gannet Islands	Resight (metal bands) <sup>a</sup>	Pre-breeder (0–2 years)	0.482 $\pm$ 0.033	1996–2006	Present study
		Age 3–11 years	0.970 $\pm$ 0.030		
		Banded as adult (3+ years)	0.890 $\pm$ 0.053		
Machias Seal Island	Resight (metal bands) <sup>a</sup>	Pre-breeder (0–2 years)	0.778 $\pm$ 0.041	1999–2006	Present study
		Age 3–8 years	0.912 $\pm$ 0.052		
		Banded as adult (3+ years)	0.967 $\pm$ 0.028		
		Pre-breeder (0–5 years)	0.380 $\pm$ 0.04		
Quebec, Canada	Band recoveries and resightings (metal and color bands) <sup>a,b</sup>	Adult	0.895 $\pm$ 0.03	1925–1995	Chapdelaine 1997
<b>Eastern Atlantic</b>					
Shiant Islands, Scotland	Resight <sup>a,c,d</sup>	Adult	0.921 <sup>e</sup>	1971–1977	Steventon 1979
		Adult	0.919 $\pm$ 2.5 <sup>f</sup>	1995–2003	Sandvik et al. 2005
		Pre-breeder (0–4 years)	0.570 $\pm$ 4.8 <sup>g</sup>	1923–1971	Lloyd 1974
		Adult	0.890 $\pm$ 1.0 <sup>g</sup>	1982–1987	Harris and Wanless 1989
Isle of May, Scotland	Resight (color bands) <sup>a</sup>	Adult	0.888 $\pm$ 0.05	1963–1973	Lloyd and Perrins 1977
		Pre-breeder (0–4 years)	0.180 <sup>e</sup>		
Skokholm, Wales	Resight (metal and color bands) <sup>a</sup>	Adult	0.890 $\pm$ 6.1 <sup>f</sup>		

<sup>a</sup>Survival probabilities estimated using CMR analysis.<sup>b</sup>Pre-breeder survival estimated indirectly using adult survival rate, age at first breeding, and breeding success.<sup>c</sup>Band type (metal or color) not reported.<sup>d</sup>Survival rates estimated using return rates (i.e., by dividing the number of marked individuals encountered in year  $i + 1$  by the number marked in year  $i$ ).<sup>e</sup>Variation not reported.<sup>f</sup>Value is mean  $\pm$  SD.<sup>g</sup>Value is a percentage (mean  $\pm$  SD).

**Fig. 3.** Adult Razorbill survival rates ( $\Phi$ ) on the Gannet Islands (●;  $\Phi(y1, y2+ \times t) p(\text{pooled})$ ) and Machias Seal Island (○) during 1998–2005, with 95% confidence limits. The best model for Machias Seal Island was one with constant survival ( $\Phi = 0.967 \pm 0.028$ ). Here we present the time-dependent survival estimates from the global model ( $\Phi(y1, y2+ \times t) p(t)$ ) for comparative purposes. Factors in the model are as follows:  $\Phi$ , survival parameter;  $y$ , year class (i.e.,  $y1$ , 1st year since banding);  $p$ , resighting probability; “pooled”, years with similar recapture probability are pooled; and  $t$ , time).



Brisson, 1760) hunt (Elliot 1991; Chapdelaine 1997), with 28 banded birds (4 shot as adults) occurring as recoveries since 1996 (Lavers 2007), suggesting that hunting alone could account for the lower survival rate. Ship, offshore oil and gas, and gill nets off Newfoundland are other sources of mortality that could affect the Gannet Islands population (Piatt and Nettleship 1987; Wiese 2002). Regardless of the cause, the survival difference has important population implications, especially for the Gannet Islands.

The best adult survival model for the Gannet Islands incorporated a climate covariate (Table 2a), but MSI did not. This may be due partly to the shorter term data set for MSI (1999–2006, six occasions excluding the beta estimate for 2005–2006 year) compared with the data set for the Gannet Islands (1996–2006, nine occasions). Lack of correlation between climate and survival on MSI may also have been due to the high adult survival estimate ( $\Phi = 0.967$ ), which exhibited little interyear variation. However, models incorporating climate covariates performed nearly as well as the top model, suggesting that it may be possible with more years of data to detect a correlation between annual survival and climate at MSI.

In the northeastern Atlantic, warm water currents such as the Slope and Norwegian Coastal Currents draw warm waters up from the south (McCartney and Talley 1982; Sherwin et al. 1999). Warm water is normally associated with reduced ocean productivity and poor feeding conditions for seabirds (e.g., Hatch 1987; Bertram et al. 2001; Gjerdrum et al. 2003), so it was not surprising that adult survival in Norway in three alcid species, including Razorbills, was found to be negatively correlated with Norwegian Sea SST and positively correlated with prey abundance (Sandvik et al. 2005). Our results suggest that adult Razorbill survival at the Gannet Islands was negatively correlated with Labrador Current temperatures, a dominant cold system in the northwest Atlantic, during the year leading up to the current breeding season (i.e.,  $M-F_{t-1}$ ). This suggests that conditions

throughout the year (not just during the harsh winter months) influence survival. We speculate that adult Razorbills wintering in Newfoundland waters (like those from the Gannet Islands) have higher survival when the Labrador Current is cold because of increased primary productivity and recruitment of their prey resulting from cooler conditions (Sundby 2000; Hirst and Kioboe 2002). However, there likely exists a limit beyond which cold temperatures lead to reduced survival, because it is anomalous cold years for the Labrador Current that cause poor growth and recruitment of marine organisms which seabirds prey on (Nakashima 1996; Dutil et al. 1999). None of these anomalous cold years occurred during the time span of our study, but this phenomenon could have been important in the late 1980s and early 1990s immediately preceding our study (Montevicchi and Myers 1997).

Pre-breeder survival on the Gannet Islands ( $\Phi = 0.482$ ) was significantly lower than on MSI ( $\Phi = 0.778$ ). This could have resulted either from higher rates of permanent emigration from the Gannet Islands by pre-breeders, or from a greater mortality rate. Band recoveries of juvenile birds shot illegally are consistent with the latter process (88% of Razorbills from the Gannet Islands shot in the hunt are pre-breeders; Lavers 2007). Unlike Razorbills from MSI, which winter primarily in the Bay of Fundy (Chapdelaine et al. 2001; Huettmann et al. 2005), Razorbills that bred on the Gannet Islands must migrate south through ice-free waters south of Newfoundland (Brown 1985; Huettmann et al. 2005). The timing and migration route of Razorbills from Labrador overlap significantly with the timing and zones set out for the annual Newfoundland and Labrador Murre hunt (Elliot 1991; Chapdelaine 1997). It is illegal to shoot Razorbills (except for Labrador Inuit, who are permitted to legally hunt Razorbills under the Migratory Birds Convention Act; Chardine et al. 1999), but many Razorbills are shot accidentally during the hunt because of their close physical resemblance to Murres (Elliot 1991; Chapdelaine 1997; Chardine et al. 1999). The number of Razorbills shot is not known, but recoveries of banded birds suggest that many hundreds to thousands may be shot each year (Elliot 1991; Chapdelaine 1997). Mortality from the hunt likely accounts for some (perhaps most) of the 27.8% difference in Razorbill pre-breeder mortality between the Gannet Islands population (which is affected by the hunt) and the MSI population (which is not).

By including observations of Razorbills on the Herring Islands and Gulf of Maine islands in the CMR data set, we attempted to partly account for the negative bias in the pre-breeder survival estimates that result from dispersal of birds outside the sampling area. However, resighting effort on the Gulf of Maine islands from 2004 to 2006 was significantly greater than at the Herring Islands. Dispersal thus from the Gannet Islands was likely underestimated.

A number of seabird studies have shown that the NAO explains a larger portion of the variability in adult survival than smaller scale indices such as local SST (Grosbois and Thompson 2005; Votier et al. 2005). Our data on survival and climate suggest that in some cases SST values provide a better predictor of adult Razorbill survival than large-scale climate indices like NAO. This may be due in part to the Razorbill's relatively limited and coastal range compared

with other seabirds like the Northern Fulmar (*Fulmarus glacialis* (L., 1761)), which are wide ranging and would be more likely to be influenced by climate at a larger scale (Frederiksen et al. 2004). However, station 27 does represent temperature from the relatively large Labrador Current while station 5 did not rank in the top five models for MSI despite its close proximity to the study site and received little support from the Gannet Islands ( $\Delta QAIC > 2$ ). The lack of a relationship with station 5 temperatures was unexpected given that both populations are thought to winter in the Bay of Fundy (Huetmann et al. 2005); however, it does suggest that climate at a larger scale (Atlantic Canada) has more of a role in influencing Razorbill survival. Overall, these results underline the need for further long-term detailed investigations into seabird demography and the influence of climate.

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## References

- Aebischer, N.J., Coulson, J.C., and Colebrook, J.M. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* (London), **347**: 753–755. doi:10.1038/347753a0.
- Alheit, J., and Hagen, E. 1997. Long-term climate forcing of European herring and sardine populations. *Fish. Oceanogr.* **6**: 130–139. doi:10.1046/j.1365-2419.1997.00035.x.
- Barber, R.T., and Chavez, F.P. 1983. Biological consequences of El Niño. *Science* (Washington, D.C.), **222**: 1203–1210. doi:10.1126/science.222.4629.1203. PMID:17806711.
- Bertram, D.F., Jones, I.L., Cooch, E.G., Knechtel, H.A., and Cooke, F. 2000. Survival rates of Cassin's and Rhinoceros Auklets at Triangle Island, British Columbia. *Condor*, **102**: 155–162. doi:10.1650/0010-5422(2000)102[0155:SROCSA]2.0.CO;2.
- Bertram, D.F., Mackas, D.L., and McKinnell, S.M. 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. *Prog. Oceanogr.* **49**: 283–307. doi:10.1016/S0079-6611(01)00027-1.
- Brown, R.G.B. 1985. The Atlantic Alcidae at sea. In *The Atlantic Alcidae*. Edited by D.N. Nettleship and T.R. Birkhead. Academic Press, London. pp. 383–426.
- Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference — a practical information-theoretic approach. Springer-Verlag, Berlin.
- Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. *Biol. Oceanogr.* **5**: 261–271.
- Chapdelaine, G. 1997. Pattern of recoveries of banded Razorbills (*Alca torda*) in the western Atlantic and survival rates of adults and immatures. *Colon. Waterbirds*, **20**: 47–54. doi:10.2307/1521763.
- Chapdelaine, G., Diamond, A.W., Elliot, R.D., and Robertson, G.J. 2001. Status and population trends of the Razorbill in eastern North America. *Can. Wildl. Serv. Occas. Pap. No.* 105.
- Chardine, J.W., Collins, B.T., Elliot, R.D., Levesque, H., and Ryan, P.C. 1999. Trends in the annual harvest of murre in Newfoundland and Labrador. *Bird Trends Newsl.* **7**: 11–14. Available from [http://www.cws-scf.ec.gc.ca/publications/btnews/bt99/ins9\\_e.cfm](http://www.cws-scf.ec.gc.ca/publications/btnews/bt99/ins9_e.cfm).
- Cooch, E.G., and White, G.W. 2001. Program MARK: a gentle introduction. 5th ed. Available from <http://www.phidot.org/software/mark/docs/book/> [accessed 15 February 2007].
- Croxall, J.P., and Rothery, P. 1991. Population regulation of seabirds: implications of their demography for conservation. In *Bird population studies: their relevance to conservation and management*. Edited by C.M. Perrins, J.-D. Lebreton, and G.J.M. Hirons. Oxford University Press, London. pp. 272–296.
- Durant, J.M., Stenseth, N.C., Anker-Nilssen, T., Harris, M.P., Thompson, P.M., and Wanless, S. 2004. Marine birds and climate fluctuation in the North Atlantic. In *Marine ecosystems and climate variation — the North Atlantic*. Edited by N.C. Stenseth, G. Ottersen, J.W. Hurrell, and A. Belgrano. Oxford University Press, Oxford. pp. 95–213.
- Dutil, J.-D., Castonguay, M., Gilbert, D., and Gascon, D. 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **56**: 1818–1831. doi:10.1139/cjfas-56-10-1818.
- Elliot, R.D. 1991. The management of the Newfoundland turr hunt. In *Studies of high latitude seabirds*. Vol. 2. Conservation biology of the thick-billed Murre in the Northwest Atlantic. Edited by A.J. Gaston and R.D. Elliot. Canadian Wildlife Service, Ottawa, Ont. pp. 29–35.
- Frederiksen, M., Harris, M.P., Daunt, F., Rothery, P., and Wanless, S. 2004. Scale-dependent climate signals drive breeding phenology of three seabird species. *Glob. Change Biol.* **10**: 1214–1221. doi:10.1111/j.1529-8817.2003.00794.x.
- Gaillard, J.-M., and Yoccoz, N.G. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**: 3294–3306. doi:10.1890/02-0409.
- Gaston, A.J., and Jones, I.L. 1998. The auks. In *Bird families of the World*. Edited by C.M. Perrins, W.J. Bock, and J. Kikkawa. Oxford University Press, New York.
- Gjerdrum, C., Vallée, A.M., St. Clair, C.C., Bertram, D.F., Ryder, J.L., and Blackburn, G.S. 2003. Tufted Puffin reproduction reveals ocean climate variability. *Proc. Natl. Acad. Sci. U.S.A.* **100**: 9377–9382. doi:10.1073/pnas.1133383100. PMID:12871995.
- Grecian, V.D. 2005. The effect of physical and biological parameters on the breeding success of Razorbills (*Alca torda* L. 1758) on Machias Seal Island, N.B., in 2000 and 2001. M.Sc. thesis, Department of Biology, University of New Brunswick, Fredericton.
- Grosbois, V., and Thompson, P.M. 2005. North Atlantic climate variation influences survival in adult Fulmars. *Oikos*, **109**: 273–290. doi:10.1111/j.0030-1299.2005.13774.x.
- Harris, M.P., and Wanless, S. 1989. The breeding biology of Razorbills *Alca torda* on the Isle of May. *Bird Study*, **36**: 105–114.
- Harris, M.P., and Wanless, S. 1996. Differential responses of Guillemot *Uria aalge* and Shag *Phalacrocorax aristotelis* to a late winter wreck. *Bird Study*, **43**: 220–230.
- Hatch, S.A. 1987. Did the 1982–1983 El-Niño – Southern Oscillation affect seabirds in Alaska? *Wilson Bull.* **99**: 468–474.

- Hirst, A.G., and Kioboe, T. 2002. Mortality of marine planktonic copepods: global rates and patterns. *Mar. Ecol. Prog. Ser.* **230**: 195–209. doi:10.3354/meps230195.
- Hjermann, D.O., Stenseth, N.C., and Ottersen, G. 2004. Indirect climate forcing of the Barents Sea capelin: a cohort effect. *Mar. Ecol. Prog. Ser.* **273**: 229–238. doi:10.3354/meps273229.
- Huettmann, F., Diamond, A.W., Dalzell, B., and MacIntosh, K. 2005. Winter distribution, ecology and movements of Razorbills *Alca torda* and other auks in the outer Bay of Fundy, Atlantic Canada. *Mar. Ornithol.* **33**: 161–171.
- Hurrell, J.W., and Dickson, R.R. 2004. Climate variability over the North Atlantic. In *Marine ecosystems and climate variation*. Edited by N.C. Stenseth, G. Ottersen, J.W. Hurrell, and A. Belgrano. Oxford University Press, Oxford. pp. 15–31.
- Hurrell, J.W., Kushnir, Y., Ottersen, G., and Visbeck, M. 2003. An overview of the North Atlantic Oscillation. In *The North Atlantic Oscillation: climate significance and environmental impact*. Edited by J.W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck. *Geophys. Monogr.* **134**: 1–37.
- Jones, I.L., Hunter, F.M., and Robertson, G.J. 2002. Annual adult survival of Least Auklets (*Aves, Alcidae*) varies with large-scale climatic conditions of the North Pacific Ocean. *Oecologia (Berl.)*, **133**: 38–44. doi:10.1007/s00442-002-0991-8.
- Jones, I.L., Hunter, F.M., Robertson, G.J., Williams, J.C., and Byrd, G.V. 2007. Covariation among demographic and climate parameters in Whiskered Auklets (*Aethia pygmaea*). *J. Avian Biol.* **38**: 450–461.
- Lavers, J.L. 2007. Cumulative mortality and population parameters for a vulnerable seabird, the Razorbill *Alca torda*, in Atlantic Canada. Ph.D. thesis, Department of Biology, Memorial University of Newfoundland, St. John's.
- Lavers, J.L., Jones, I.L., and Diamond, A.W. 2007. Natal and breeding dispersal of Razorbills (*Alca torda*) in eastern North America. *Waterbirds*, **30**: 593–599.
- Lebreton, J.-D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**: 67–118. doi:10.2307/2937171.
- Lloyd, C.S. 1974. Movement and survival of British Razorbills. *Bird Study*, **21**: 102–115.
- Lloyd, C.S., and Perrins, C.M. 1977. Survival and age of first breeding in the Razorbill *Alca torda*. *Bird-Banding*, **48**: 239–252.
- Lyngs, P. 2006. Wear and loss of rings used on Razorbills *Alca torda* – further caution in the estimation of large auk survival. *Ring and Migration*, **23**: 39–44. Available from [http://blx1.bto.org/pdf/ringmigration/23\\_1/lyngs.pdf](http://blx1.bto.org/pdf/ringmigration/23_1/lyngs.pdf).
- Martin, T.E., Clobert, J., and Anderson, D.A. 1995. Return rates in studies of life history evolution: are biases large? *J. Appl. Stat.* **22**: 863–875. doi:10.1080/02664769524676.
- McCartney, M.S., and Talley, L.S. 1982. The subpolar mode water of the North Atlantic Ocean. *J. Phys. Oceanogr.* **12**: 1169–1188. doi:10.1175/1520-0485(1982)012<1169:TSMWOT>2.0.CO;2.
- Montevecchi, W.A. 1993. Birds as indicators of change in marine prey stocks. In *Birds as indicators of environmental change*. Edited by R.W. Furness and J.J.D. Greenwood. Chapman and Hall, London. pp. 217–266.
- 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 J. Mar. Sci.* **54**: 608–614. doi:10.1006/jmsc.1997.0265.
- Morris, R.D., and Chardine, J.W. 1995. Brown Noddies on Cayo Noroeste, Culebra, Puerto Rico: what happened in 1990? *Auk*, **112**: 326–334.
- Nakashima, B.S. 1996. The relationship between oceanographic conditions in the 1990s and changes in the spawning, behavior, growth, and early life-history of capelin (*Mallotus villosus*). *NAFO (Northwest Atl. Fish. Organ.) Sci. Coun. Stud.* **24**: 55–68.
- Nettleship, D.N., and Birkhead, T.R. 1985. *The Atlantic Alcidae*. Academic Press, London.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C., and Stenseth, N.C. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia (Berl.)*, **128**: 1–14. doi:10.1007/s004420100655.
- Piatt, J.F., and Nettleship, D.N. 1987. Incidental catch of marine birds and mammals in fishing nets off Newfoundland, Canada. *Mar. Pollut. Bull.* **18**: 344–349. doi:10.1016/S0025-326X(87)80023-1.
- Poole, J., Smith, S., Perrins, C.M., Birkhead, T.R., and Thompson, K.R. 1998. Seabird monitoring on Skomer Island in 1996. Rep. No. 277, Joint Nature Conservation Committee, Peterborough, UK.
- Pradel, R., Rioux, N., Tamisier, A., and Lebreton, J.-D. 1997. Individual turnover among wintering teal in Camargue: a mark-recapture study. *J. Wildl. Manag.* **61**: 816–821. doi:10.2307/3802189.
- Prévot-Juilliard, A.C., Lebreton, J.-D., and Pradel, R. 1998. Re-evaluation of adult survival of Black-headed Gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *Auk*, **115**: 85–95.
- Sandvik, H., Erikstad, K.E., Barrett, R.T., and Yoccoz, N.G. 2005. The effect of climate on adult survival in five species of North Atlantic seabirds. *J. Anim. Ecol.* **74**: 817–831. doi:10.1111/j.1365-2656.2005.00981.x.
- Sherwin, T.J., Turrell, W.R., Jeans, D.R.G., and Dye, S. 1999. Eddies and a mesoscale deflection of the slope current in the Faroe-Shetland Channel. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* **46**: 415–438. doi:10.1016/S0967-0637(98)00077-6.
- Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, **85**: 277–298.
- Thompson, P.M., and Ollason, J.C. 2001. Lagged effects of ocean climate on fulmar population dynamics. *Nature (London)*, **413**: 417–420. doi:10.1038/35096558. PMID:11574887.
- Trenberth, K.E., and Hurrell, J.W. 1994. Decadal atmosphere-ocean variations in the Pacific. *Clim. Dyn.* **9**: 303–319. doi:10.1007/BF00204745.
- Underwood, L.A., and Stowe, T.J. 1984. Massive wreck of seabirds in eastern Britain, 1983. *Bird Study*, **31**: 77–88.
- Votier, S.C., Hatchwell, B.J., Beckerman, A., McCleery, R.H., Hunter, F.M., Pellatt, J., Trinder, M., and Birkhead, T.R. 2005. Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecol. Lett.* **8**: 1157–1164. doi:10.1111/j.1461-0248.2005.00818.x.
- Wagner, R.E. 1992. Extra-pair copulations in a lek: the secondary mating system of monogamous Razorbills. *Behav. Ecol. Sociobiol.* **31**: 63–71. doi:10.1007/BF00167817.
- Wallace, J.M. 2000. North Atlantic Oscillation / annular mode: two paradigms – one phenomenon. *Q. J. R. Meteorol. Soc.* **126**: 791–805. doi:10.1256/smsqj.56401.
- Weimerskirch, H., Zimmermann, L., and Prince, P.A. 2001. Influence of environmental variability on breeding effort in the long-lived seabird, the Yellow-nosed Albatross. *Behav. Ecol.* **12**: 22–30.
- White, G.C., and Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study*, **46**: 120–139.
- Wiese, F.K. 2002. Estimation and impacts of seabird mortality

from chronic marine oil pollution off the coast of Newfoundland. Ph.D. dissertation, Department of Biology, Memorial University of Newfoundland, St. John's.

Zhang, Y., Wallace, J.M., and Battisiti, D.S. 1997. ENSO-like interdecadal variability: 1900–93. *J. Climatol.* **10**: 1004–1020. doi:10.1175/1520-0442(1997)010<1004:ELIV>2.0.CO;2.