



Annual survival of adult Atlantic Puffins *Fratercula arctica* is positively correlated with Herring *Clupea harengus* availability

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Atlantic Herring is a keystone species in several marine ecosystems, supporting intensive fisheries as well as many predators including seabirds. Biomass of this stock in eastern North America has declined considerably in recent years, potentially putting at risk populations of its predators. Although adult survival in seabirds is considered robust to moderate changes in food availability, it is also the life-history component most critical to sustaining populations of long-lived birds. To investigate the possibility that Atlantic Puffin survival has been affected by reduced abundance of its main prey, we analysed the encounter histories of 2999 Atlantic Puffins ringed on Machias Seal Island to estimate annual adult survival for the years 1999–2011 and assess trends in survival and the effects of several biological and environmental covariates. Features of Puffin biology and resighting procedures likely to introduce heterogeneity into our resighting probabilities were accounted for and models of survival were assessed using standard methods. We used the variance components procedure in Program MARK and survival estimates from a time-varying model to estimate the process variance (biological variation in survival) accounted for by suspected covariates of survival. Two proxies of food availability each explained more than half of the variation in annual survival: fishery landings of Atlantic Herring (52%) and per cent (by mass) of 1-group Herring in the diet of Puffin chicks (51%). In addition to these proxies, May sea-surface temperature accounted for 37% of variance in survival, but winter values of North Atlantic Oscillation showed no effect. Of those parameters of Puffin biology examined, chick growth rate explained 19% of the process variance in annual survival; laying date, fledging condition and fledging date all explained no variance. A decline in fishery landings of Herring since the early 1990s, and a concurrent decline in adult Puffin survival, reinforces concern for the health of the population of Herring, a keystone forage fish in this region, and of the community of marine predators in the Gulf of Maine that rely on Herring for their survival and reproduction.

Keywords: Bay of Fundy, Gulf of Maine, threshold, variance partitioning.

Changes in food-web relationships are found with increasing frequency in marine ecosystems (Worm *et al.* 2006, Halpern *et al.* 2008). As apex predators in such systems, marine birds (seabirds) have the potential to reflect such shifts in several aspects of their demographics (Cairns 1987, 1992, Weimerskirch 2001), and their sensitivity to changes in both quality and quantity of prey is

well known (Monaghan 1996, Diamond & Devlin 2003, Wanless *et al.* 2005, Breton *et al.* 2008). A recent global review of the impacts on seabird communities of reduced food supply found that depletion of keystone prey species consistently depressed breeding success in a variety of seabird species when stock abundance fell below one-third of the maximum abundance on record (Cury *et al.* 2011). Such keystone prey species are often immature schooling pelagic fish, such as Atlantic Herring (hereafter Herring) *Clupea harengus*.

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Cairns (1987) proposed that breeding success (the demographic response examined by Cury *et al.* 2011) ‘increases rapidly when food availability increases from poor to moderate, but only gradually when food supply is good’. Adult survivorship, on the other hand, declines only when food is ‘extremely scarce’, and varies little at higher levels of food supply. The meta-analysis by Cury *et al.* (2011) advanced the general relationship proposed by Cairns (1987) and others, by establishing a threshold of food supply (~33% of the maximum) below which breeding success is significantly affected. Here we add to the comparatively small number of studies (Harris & Bailey 1992, Grosbois *et al.* 2009) that examine changes in adult survival of a seabird in relation to availability of its main prey in an ecosystem notable for the changes in its food-web in recent years.

In particular, we address the potential impact of a marked change in apparent availability of yearling (1-group) Herring on adult survival of Atlantic Puffins *Fratercula arctica* breeding in the Bay of Fundy/Gulf of Maine ecosystem. Note that 1-group Herring are young fish hatched the previous autumn; they are termed 0-group until 1 January in fishery nomenclature and 1-group thereafter. The commercial fishery harvests Herring between 2 and 11 years old; it is fish in this age bracket that produce the immature fish on which Puffins feed. Our data come from the Machias Seal Island (MSI) Puffin colony, which although small by global standards (6000–7000 pairs; A.W. Diamond unpubl. data) is the largest in the Gulf of Maine and the most important source of recruits to other colonies in the region (Breton *et al.* 2006a). Between 1995 and 2000, 1-group Herring was the predominant prey item fed to chicks by four seabird species breeding on MSI: Puffins, Razorbills *Alca torda*, Common Terns *Sterna hirundo* and Arctic Terns *Sterna paradisaea* (Diamond & Devlin 2003, Gaston *et al.* 2009). This period was followed by a steady reduction of 1-group Herring in the diets of seabird chicks raised on MSI. Since 2000, and particularly since 2004 when fishery landings also declined (Fig. 1), Herring have been partly replaced in seabird diets by a mixture of prey taxa including euphausiid shrimp (mainly *Meganyctiphanes norvegicus*), pre-metamorphosis (larval) fish and juvenile schooling fish generally of lower nutritional value than Herring (Diamond & Devlin 2003). Following the reduction in Herring, about

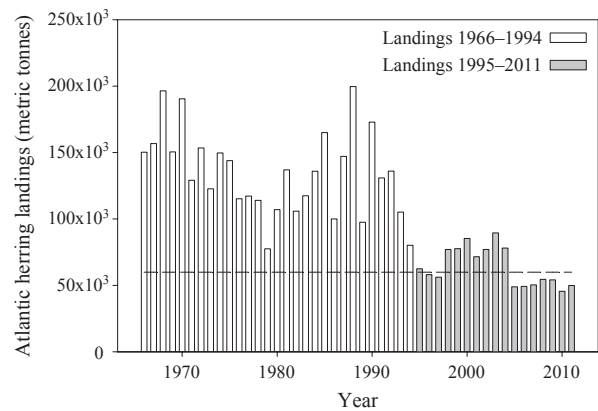


Figure 1. Landings of Atlantic Herring from the Canadian fishery in the Gulf of Maine including the Bay of Fundy (Department of Inland Fisheries 2011 and R. Singh, DFO, *in litt.*). Landings from 1995 to 2011, the period overlapping with our Atlantic Puffin chick diet study, are highlighted with grey bars. The dashed line identifies landings at 33% of the maximum (199 600 tonnes) over the 1966–2011 time series.

1000 breeding pairs of Common Tern and 2000 pairs of Arctic Tern deserted the island in 2006, and those that returned have experienced complete breeding failure every year since (Gaston *et al.* 2009). This is particularly noteworthy given that the tern colony on MSI has been active for at least 150 years, during which time terns abandoned the island for only one summer (MacKinnon & Smith 1985). Effects on Puffins and Razorbills have been less clear-cut; breeding success and chick growth have varied considerably, but most of the years in which breeding success was low, or chick growth was slow, have occurred after the diet shift (A.W. Diamond unpubl. data).

Breeding success and chick growth are sensitive to short-term changes in food supply relative to adult survival (Cury *et al.* 2011) but adult survival has a far greater impact on population dynamics than the former in long-lived species (Stahl & Ohli 2006). Survival in seabird demography studies is generally measured between the end of one breeding season and the start of the next, i.e. over the autumn, winter and early spring. Because most adult mortality of Puffins occurs in winter (Hudson 1985) and for convenience, we summarize this period as ‘winter’. Our primary objective in this paper was to assess whether over the period of available mark-recapture data (1999–2011), over-winter survival of adult Puffins breeding on MSI was depressed in winters with poor recruitment of their most important prey, 1-group Atlantic

Herring, and to explore other factors with potential direct and indirect effects on survival. As part of our mark–recapture survival analysis, we used a variance components method that allowed us to estimate survival process variance that was explained by our time-varying (one value per year) environmental and biological covariates (White *et al.* 2001, Burnham & White 2002). In addition, we assessed the individual covariate (one value per bird) maximum detection frequency as a covariate of our detection probabilities, an effect that may prove useful to other mark–recapture studies.

METHODS

Study area

The Gulf of Maine is a marine ecosystem with a long history that has demonstrated decadal (or shorter) bottom-up changes driven by climatic or oceanographic variation (Peterson *et al.* 2006, Friedland & Hare 2007, Ji *et al.* 2008, Balch *et al.* 2012) and multi-decadal top-down impacts of overfishing (Steneck 1997, Jackson *et al.* 2001, Daskalov *et al.* 2007). This marine food-web is characteristically ‘wasp-waisted’, funnelling energy between diverse producers and consumers through one or a few species of secondary consumers, often planktivorous fish (Cury *et al.* 2000, Bakun *et al.* 2009). Herring is widely recognized as a keystone species in the Gulf of Maine, of high importance in the diets of many marine mammals, birds and predatory fish that raise their young there and in the Bay of Fundy (Budge *et al.* 2002, Bakun *et al.* 2009, Pikitch *et al.* 2012). The importance of this energy-rich food source (Lawson *et al.* 1998, Budge *et al.* 2002) is likely to extend to those species that migrate seasonally to the Gulf from as far away as the southern oceans (Overholtz & Link 2007, Diamond 2012). Some combination of impacts led to prominent declines in fishery landings of Herring in the Canadian portion of the Gulf of Maine (Fig. 1) adjacent to our study site, Machias Seal Island (MSI). The most recent decline, after 2004, was reflected in a reduction in catch quotas of Herring. During the period of our study, Herring landings have closely matched the quota, or total allowable catch (TAC), which in turn is set according to estimates of the spawning stock biomass derived from fishery statistics, research surveys and acoustic surveys (Department

of Fisheries & Oceans 2011). Fishery landings data refer to fish 2 years old and older, most of which are too large to be eaten by Puffins. However, during our study period, fish size has declined considerably (Department of Fisheries & Oceans 2011), probably putting some 2-year-old fish within the size range of adult Puffins. In the absence of data on the abundance of fish of a size eaten by Puffins, we have assumed that large landings reflect an influx of recruits by large numbers of young.

MSI is a small (9.5-ha) treeless island equidistant (19 km) from Grand Manan Island, Canada, and the coast of Maine, USA, at the edge of the Bay of Fundy where it opens up into the Gulf of Maine. The granite bedrock is exposed as wide expanses of bare rock on the south and west coasts, separated from the vegetated interior by a berm of large storm-tossed boulders; smaller boulders along the sheltered northern and eastern shores separate a cobble beach from the vegetated interior. Terns previously nested throughout the island, Razorbills and Common Guillemots *Uria aalge* nest among large boulders in the south and west, and Puffins breed sparsely among the boulders but also excavate burrows in the shallow peaty soil. Researchers were present from early May to mid-August each year.

Chick diet

Prey fed to Puffin chicks was identified during intensive watches from observation hides; observers recorded the species (or higher taxon), number and length (relative to the adult’s bill) of prey brought in bill-loads to a defined area close to the hide. Dropped items were collected opportunistically in the colony and weighed and measured to allow determination of each taxon’s contribution to the biomass of chick diet. No allowance could be made for dehydration between capture of an item and its collection at the colony, as suggested by Montevecchi and Piatt (1987).

Ringling and resighting

Puffins were caught mainly using a box trap fitted with a swivelling lid; a much smaller number of birds were captured in burrows. We resighted birds from hides using binoculars and spotting scopes. Three field-readable ring designs were deployed: incoloy, non-ridged, twice or thrice engraved and stainless steel, ridged, thrice

engraved; character engravings were identical. These rings were deployed on MSI from 1999 to 2007 (incoloy twice engraved), 2007 to 2011 (incoloy thrice engraved) and 2005 to 2006 (stainless steel). Wear rates due to abrasion on these ring types appeared to be identical, and extremely slow (see wear rates for incoloy rings in Breton *et al.* 2006b); few rings showed any wear at all.

Subsample and heterogeneity

A subsample of 2999 birds and their annual encounter histories was extracted from a larger capture–mark–recapture/resight (CMR) dataset using criteria (more below) aimed at minimizing within-group differences, or heterogeneity, in detection probabilities. Heterogeneity is a common source of bias in survival estimates (Anderson *et al.* 1994, Williams *et al.* 2002). Birds were aged on all encounters based on number of bill grooves and presence of a brood patch (Friars & Diamond 2011, Harris & Wanless 2011). We subsequently used these age data to determine the initial release year for each bird: we added birds into the sample when aged 4 years and older in order to include only breeding-aged, non-transient adults. For example, a bird marked in 2000 in their 2nd year and seen again in 2002, 2004 and 2005 would have encounter history 0001011000000 rather than 0101011000000. Here, each character in the encounter histories represents a season or year starting with 1999 and ending in 2011.

Resighting and trapping effort were not distributed randomly or evenly across the island, nor was the activity of individual birds. For Puffins nesting very close to research hides, we expected resighting probabilities to be relatively high, and that these birds would be resighted many times within a season. At the other extreme were individuals that were rarely seen. Most birds are likely to be resighted at frequencies between these extremes. We attempted to account for these two sources of heterogeneity (research intensity and behaviour of individual birds) in the structure of our models by grouping Puffins by their maximum number of detections within a breeding season: detected one to two times (group 1), three to four times (group 2) and more than four times (group 3). We used this group structure when performing goodness-of-fit tests in U-CARE and initially in Program MARK.

Capture–mark–recapture analysis

Goodness-of-fit testing was done in the program U-CARE (Burnham *et al.* 1987, Choquet *et al.* 2005). We deployed standard tests 3.SR and 2.CT to test for transience (3.SR) and trap-dependence (2.CT). Following this goodness-of-fit assessment, the overdispersion parameter \hat{c} (Anderson *et al.* 1994) was estimated by dividing the sum of the χ^2 values from tests 3.SM, 3.SR, 2.CT and 2.CL over all groups by the sum of the degrees of freedom (Choquet *et al.* 2005). Modelling was performed in Program MARK (White & Burnham 1999) using parameterization and assumptions of the Cormack–Jolly–Seber (CJS) model (Williams *et al.* 2002). Parameters in the CJS model are apparent survival, ϕ (survival confounded by permanent emigration), and detection probability, P . We used Akaike's information criterion adjusted for small sample size (AIC_c), AIC_c weights and AIC_c differences (ΔAIC_c) to quantify support between competing models (Burnham & Anderson 2002), and we used odds ratios to quantify model effect sizes (Neter *et al.* 1996). Covariate effect sizes and their 95% confidence intervals are provided on the logit scale, and statistical significance was determined using analysis of deviance tests (Grosbois *et al.* 2008, Lebreton *et al.* 2012).

Modelling stages

We first assessed all possible combinations of year, group and trap-dependence (groups 1–3) fitted to detection probabilities, and year and transience (group 1 only) effects fitted to survival probabilities. We next considered two variations of trap-dependence in our top model(s): trap-dependence in only groups 1–2, and in only group 1. Next, we replaced the group effect in the top model(s) with the individual covariate maximum detection frequency (the covariate used to specify our three groups). Finally, we attempted to account for any remaining heterogeneity in detection probabilities by adding two additional covariates, engraving pattern and ring type, to our top models.

We used the top model from the previous stage including categorical year effects fitted to survival and the variance component option in Program MARK to estimate the process variance ($\hat{\sigma}^2$), standard deviation ($\hat{\sigma}$) and mean ($\hat{\mu}$) of the distribution from which our estimates of survival (12 in total) were drawn (intercept only; White *et al.* 2001,

Burnham & White 2002). To remove variance that is a function of sampling error ($\hat{\sigma}_s^2$), the method shrinks the maximum likelihood estimates (MLEs) from the time-varying model towards the mean, resulting in a set of shrinkage estimates which are used to estimate $\hat{\sigma}^2$, $\hat{\sigma}$ and $\hat{\mu}$ (details in White *et al.* 2001 and Loison *et al.* 2002). We subsequently constrained the fully time-dependent model by (one at a time) a suite of suspected covariates of survival and again estimated the process variance. By subtracting the difference in variance (var) between the base model (bm; no covariate) and the constrained model (cm), and then dividing by the base model variance, we estimated the variance explained by each covariate as $(\text{var}_{\text{bm}} - \text{var}_{\text{cm}})/\text{var}_{\text{bm}}$.

Finally, to quantify the effect size, direction and statistical significance for each of our covariates, we replaced the categorical year effects in our time-varying model with each covariate. To facilitate effect size comparisons across covariates, we standardized each covariate prior to fitting them to the data using the z transformation $(x - \bar{x})/\text{sd}(x)$ where x is the value of the covariate being transformed and \bar{x} and $\text{sd}(x)$ are the estimated mean and standard deviation of the distribution. Under this common transformation, the mean is zero and the range is roughly -3 to $+3$. To determine the relative support for these models compared with the unconstrained time-varying survival model, we report AIC_c weights. We assumed the functional form of the relationship between annual survival and each covariate was linear in all cases. Combinations of covariates were not assessed because of the high probability that all of these were confounded to some extent.

Environmental effects and predictions

Although subject to annual variation in energy content (Diamond & Devlin 2003, Lane *et al.* 2011), Herring is typically the most energy-rich component of food-webs in the Bay of Fundy (Lawson *et al.* 1998, Budge *et al.* 2002), as well as elsewhere in the Gulf of Maine (Hall *et al.* 2000). To assess the relationship between 1-group Herring abundance and overwinter survival of adult Puffins, we used two annual indices of Herring abundance as time-varying covariates: per cent by mass (% of the biomass of each food load) of 1-group Herring from our chick diet studies in the previous summer (see below); and landings of

adult (2–11 years old) Herring (metric tonnes) in the following summer and autumn in the Canadian portion of the Gulf of Maine recorded by the Department of Fisheries and Oceans (2011). During this study, landings have closely followed a quota that reflects estimated spawning stock biomass (SSB) as derived from virtual population analysis (VPA) and acoustic surveys (Araújo & Bundy 2011); it may be argued that these data therefore reflect management decisions more than actual biomass, but we assume only that the two (quota and biomass) have a constant relation to each other over this time period. We predicted that greater total landings in the summer would reflect a greater abundance of 1-group Herring the previous winter and a higher survival probability for adult Puffins during that period.

The proportion of Herring in chick diet reflects prey availability in summer, which is likely to affect the condition of adults going into the following winter, especially in times of food shortage such as MSI seabirds have been subject to since 2001 (Diamond & Devlin 2003, Gaston *et al.* 2009). We assessed per cent by mass of Herring, combined Herring and Sandlance (*Ammodytes* sp.), and Sandlance in Puffin chick diet measured in summer as time-varying covariates of survival over the following winter period. Sandlance was common in chick diets in some years, especially when Herring was scarce, and has a calorific value second only to Herring (Budge *et al.* 2002, Diamond & Devlin 2003) in Puffin chick diet.

Several studies have found correlations between Puffin survival and large-scale climate proxies such as the North Atlantic Oscillation (NAO; Sandvik *et al.* 2008) and sea-surface temperature (SST; Harris *et al.* 2005, Grosbois *et al.* 2009). We therefore included the mean January–March value of the North Atlantic Oscillation ('extended' winter NAO), and average May SST ($^{\circ}\text{C}$) measured at MSI, as time-varying covariates of survival in our models. We predicted that May SST, as a proxy of winter severity, would co-vary with survival from the previous winter period. Since the effect(s) of NAO would affect adult survival only indirectly, and the strength of the NAO signal is known to vary geographically (Sandvik *et al.* 2008) and temporally (Harris & Wanless 2011), we did not predict an effect direction or strength.

Other indirect factors that might be expected to influence adult survival include the timing of the breeding season (Durant *et al.* 2005). For

example, a relatively long, presumably food-poor, breeding season might not give adults time to recoup condition before the onset of winter. We used median hatch dates to reflect the timing, and median fledge date of chicks to indicate the end of the season (fledge date); these dates varied by similar amounts over the years (21–22 days). Our predictions were that late fledging would be correlated with low survival (poor food year) and an early lay date with high survival in the subsequent winter. We also included as covariates of adult survival, the productivity, fledge condition and mean rate of mass growth of chicks over the linear growth period (10–30 days; Harris & Wanless 2011). We predicted a positive correlation between survival and all of these time-varying covariates. Productivity was estimated as the proportion of occupied Puffin nests monitored annually on MSI that fledged a chick. Fledge condition was estimated as the mean mass (g) divided by the mean wing chord length (mm) (to correct for body size) of fledging chicks caught at night below an active light tower on MSI.

RESULTS

The global goodness-of-fit tests summed across groups was significant: quadratic $\chi^2 = 228.92$, $df = 169$, $P < 0.05$. The global one- and two-sided tests for transience were not significant: $P = 0.32$ and $P = 0.16$, respectively. The global two-sided test for trap-dependence was significant ($P < 0.05$). The group-specific results for test 3.SR (transience) was significant for group 1 only ($P < 0.05$). Group-specific 2.CT tests provided evidence of trap-dependence in group 1 ($P < 0.05$) and possibly group 2 ($P = 0.06$); P -values associated with all other subtests within test 2.CT were > 0.18 . The signs of the trap-dependence statistics were negative, suggesting trap-happiness. To assess whether the trap-dependence effect occurred on just the first occasion after release we used the 'suppress first encounter' and 'clean data' options in U-CARE (Choquet *et al.* 2005). After making these changes, the global goodness-of-fit test (quadratic $\chi^2 = 127.36$, $df = 129$, $P = 0.53$, $\hat{c} = 0.99$), tests for transients ($P = 0.17$, $P = 0.92$) and trap-dependence ($P = 0.16$) were not significant. Based on these results, we included a transience effect for group 1 and trap-dependence effects (initially) for all groups in models specified in Program MARK.

Of all possible combinations of year, group and trap-dependence (groups 1–3) fitted to detection probabilities and year and transience (group 1 only) effects fitted to survival probabilities, only two models acquired support, the ΔAIC_c values of all other models being > 46 . These top models were the full model (all effects just described) and the full model without time-variation in survival. We next considered two variations of our top models: models with trap-dependence in only groups 1–2 and only group 1. Neither model acquired support; ΔAIC_c values were > 16 . We then replaced the group effect in the top models with the individual covariate maximum detection frequency (the same covariate used to specify our three groups). The covariate models acquired exclusive support (ΔAIC_c values were > 32 for all group models). We attempted to account for any remaining heterogeneity in detection probabilities by adding two additional covariates: ring type and engraving pattern. Models that did not include these individual covariates acquired no support ($\Delta AIC_c > 10$). At this stage we assessed an apparent slight negative trend in survival demonstrated by estimates from the top time-varying survival model. This *post-hoc* test was accomplished by replacing the categorical year effects with a trend effect. Despite receiving an AIC_c weight of 0.58, the trend effect size confidence interval widely bounded zero: $\beta = -0.0470$ (-0.0995 , 0.0055 ; logit scale). Estimates of the trap-dependence, transience and individual covariate effect sizes from these models were virtually identical, and differences in year effect sizes fitted to detection probabilities were also very similar. We report effect sizes from the time-varying survival model below.

Based on odds ratios, transients were 5.4 times less likely to survive or stay in the study area (confounded processes) than non-transients. The acute effect of trap-dependence was positive: initial detection was 1.6 times more likely than all subsequent detections. For the individual covariate maximum detection frequency ($\beta = 0.3876$ (0.3422, 0.4329)), birds were 1.5 times more likely to be detected, in any year, for each unit increase in maximum frequency. Thus, a bird seen at most 10 times was 50 times more likely to be detected in any year than a bird seen at most once. As expected, birds wearing thrice-engraved rings were 1.9 times more likely to be identified compared with birds wearing twice-engraved rings ($\beta = 0.6514$ (0.4377, 0.8651)); and unexpectedly,

birds wearing non-rigged rings were 1.7 times more likely to be seen than those wearing rigged rings ($\beta = -0.5116$ ($-0.2137, -0.8095$)).

The process variance, standard deviation and mean of the shrunk time-varying survival estimates were 0.0004 (0, 0.0024 95%CI), 0.0198 (0, 0.0491) and 0.9239 (0.0089 se), respectively. The shrunk estimates of survival, which are favoured over the MLEs from the time-varying model as they include (estimate) only process variation, are provided in Table 1. Process variance explained by each covariate is provided in parentheses: per cent Herring in chick diet (51%); fishery landings of adult Herring (52%); mean May SST (37%); chick growth rate (19%); per cent Herring and Sand-lance (9%); productivity (0%); fledge condition (0%); lay date (0%); fledge date (0%); and NAO winter index (0%). Patterns of survival, fishery landings, per cent Herring in diet and May SST are shown in Figure 2.

When we added the time-varying covariate models to the previous model set, the model containing fisheries landings acquired 34% of the AIC_c weight. May SST, productivity, per cent Herring in the diet, trend and chick growth each acquired 9% of the weight. Remaining models acquired between 0 and 5% of the AIC_c weight (Table 2). Effect sizes (Table 3) and per cent variance explained provided near identical support for

Table 1. Shrunk estimates of apparent survival probabilities for adult Atlantic Puffins breeding on Machias Seal Island, 1999–2000 to 2010–2011. Estimates from the top time-varying survival model were shrunk to remove sampling error using the variance components procedure provided in Program MARK (White *et al.* 2001, Burnham & White 2002).

Winter period	Apparent survival	RMSE ^a	Lower 95% CI	Upper 95% CI
1999–2000	0.954	0.033	0.888	1
2000–01	0.908	0.036	0.838	0.979
2001–02	0.909	0.027	0.855	0.962
2002–03	0.956	0.024	0.909	1.000
2003–04	0.947	0.012	0.923	0.970
2004–05	0.909	0.015	0.880	0.939
2005–06	0.923	0.012	0.899	0.948
2006–07	0.917	0.014	0.890	0.944
2007–08	0.894	0.020	0.856	0.932
2008–09	0.913	0.017	0.880	0.945
2009–10	0.926	0.016	0.894	0.957
2010–11	0.915	0.022	0.872	0.959

^aRoot mean square error, an estimator of the unconditional sampling error.

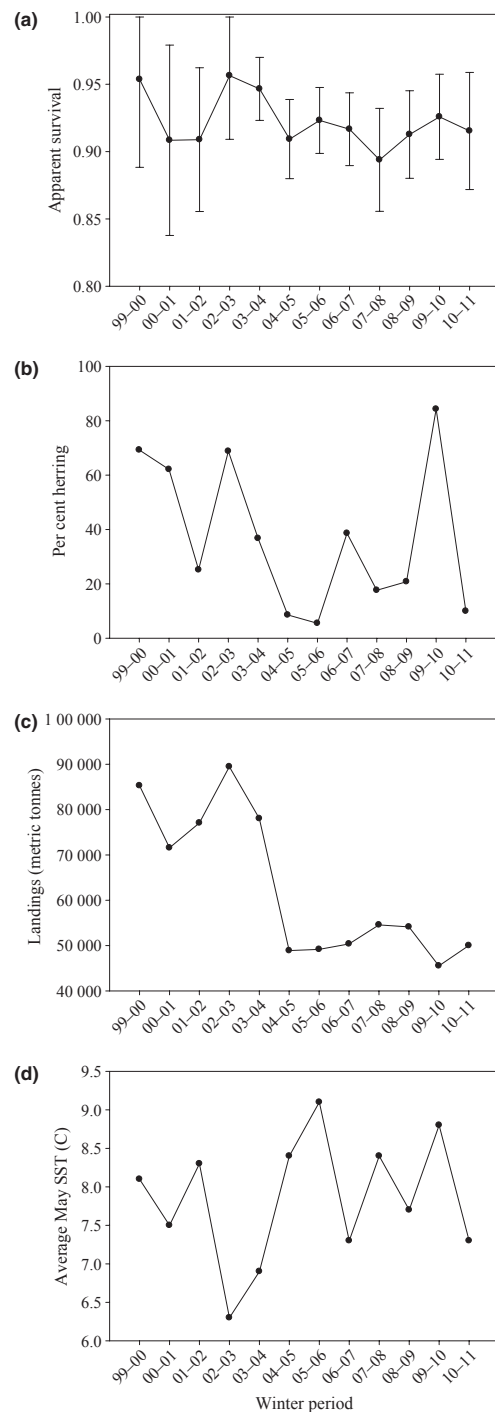


Figure 2. (a) Shrunk estimates of apparent survival probabilities (95% CI) for adult Atlantic Puffins over the winter period (Table 1); (b) per cent Atlantic Herring in the diet of Atlantic Puffin chicks from Machias Seal Island in the previous summer; (c) total adult Atlantic Herring landings (metric tonnes) reported by the Department of Fisheries and Oceans, Canada; and (d) average May sea-surface temperature (SST, °C) measured adjacent to Machias Seal Island.

Table 2. Models with AIC_c weights > 0.0005 after adding time-varying covariates of survival to our model set.

Model effects ^a	AIC_c	ΔAIC_c	AIC_c weights	Num. Par	Deviance
Herring landings	9120.87	0	0.34	19	9082.68
Mean May SST	9123.35	2.48	0.10	19	9085.16
Productivity	9123.43	2.56	0.10	19	9085.24
Per cent Herring in diet	9123.48	2.61	0.09	19	9085.29
Trend	9123.49	2.62	0.09	19	9085.30
Chick growth	9123.54	2.66	0.09	19	9085.35
No covariates	9124.49	3.61	0.06	18	9088.31
Per cent H + S ^b	9125.82	4.95	0.03	19	9087.63
Fledge date	9126.28	5.40	0.02	19	9088.08
Winter NAO	9126.39	5.51	0.02	19	9088.19
Fledge condition	9126.42	5.54	0.02	19	9088.22
Lay date	9126.43	5.55	0.02	19	9088.24
Year	9128.37	7.49	0.01	29	9069.93

Num. Par, Number of Parameters.

^aAll models include an effect of transience on survival and effects of trap-dependence, maximum detection frequency, engraving pattern and ring type on detection probability; 'No covariates' refers only to time-varying covariates of survival.

^bPer cent Herring and Sandlance in Atlantic Puffin chick diet.

fisheries landings and per cent Herring in chick diet, the strongest survival effects we detected in our analysis. Consistent with our predictions, fisheries landings and per cent Herring in the diet effect sizes were positive, and the fisheries landing effect size was very close to significance at the 0.05 α level (Table 3). Despite marginally bounding zero, the per cent Herring in chick diet effect size was strongly positive, implying, together with per cent variance explained for this effect, a biologically significant result. Weak odds ratios and wide confidence intervals preclude reliable inference for all other covariate effects included in our survival analysis.

DISCUSSION

Adult survival in our study population of Puffins has varied in recent years in conjunction with a significant reduction in the availability of young Herring in the region as indicated by two separate proxies (chick diet and fishery landings).

After removing sampling variation, the variance components procedure that we used (White *et al.* 2001, Burnham & White 2002) allowed us to estimate the shape of the distribution and associated parameters (mean, sd, variance) from which our 12 estimates of annual survival were drawn. The shape of the distribution is consistent with adult

Table 3. Time-varying, covariate, effect sizes on the logit scale; all effects listed were fitted to survival probabilities. The odds ratio applies to a change of 1 standard deviation (sd) in the time-varying covariate. Statistical significance (P) of covariate effect sizes from analysis of deviance tests is also provided (Lebreton *et al.* 2012).

Time-varying covariate	Mean	sd	Effect size	se	Lower	Upper	Odds ratio	Rank	P
Herring landings	61 839.3	15 148.46	0.2028	0.0889	0.0286	0.377	1.2248	1	0.06
Per cent Herring in diet	35.89	26.01	0.1617	0.0972	-0.0288	0.3522	1.1755	2	0.19
Chick growth	6.15	2.12	0.1423	0.085	-0.0244	0.309	1.153	3	0.2
Mean May SST	7.83	0.8	-0.1395	0.0792	-0.2947	0.0157	0.8698	4	0.18
Productivity	0.62	0.15	0.1096	0.062	-0.0119	0.2311	1.1158	5	0.19
Per cent H + S ^a	46.66	27.84	0.0616	0.0755	-0.0863	0.2096	1.0636	6	0.55
Winter NAO	0.12	0.55	-0.0317	0.0932	-0.2143	0.1509	0.9688	7	0.8
Fledge date	7.57	4.6	-0.0317	0.0663	-0.1617	0.0983	0.9688	8	0.73
Fledge condition	1.99	0.12	-0.0231	0.0777	-0.1754	0.1292	0.9772	9	0.83
Lay date	14.78	5.54	-0.0178	0.0644	-0.1441	0.1085	0.9824	10	0.84

^aPer cent Herring and Sandlance in Atlantic Puffin chick diet.

survival estimates for Puffins in other studies and regions (see summary in Breton *et al.* 2005), for long-lived birds in general and associated life-history theory (Sæther *et al.* 1996, Ricklefs 2000, Sæther & Bakke 2000). Variance explained, historically a common and insightful parameter in regression analysis, has typically not been estimated with mark–recapture data. Our analysis and others (Loison *et al.* 2002, Frederiksen *et al.* 2008, Sandvik *et al.* 2008) demonstrate that this need not be the case.

Despite wide and often overlapping 95% confidence intervals (Fig. 2a), point estimates of survival co-varied with two proxies of food availability (Fig. 2b,c), and per cent variance explained was above 50% in both cases. Per cent of 1-group Herring in chick diet the previous summer explained 51% of the variation among our 12 annual survival estimates; this covariate represents summer food availability and (we suggest) is a proxy for the condition of birds going into the winter period. Landings by the Herring fishery in the summer, a proxy of food availability over the previous winter period, explained 52% of the variation in annual survival. These results carry significant implications for the conservation of Puffins in the Gulf of Maine/Bay of Fundy ecosystem, in particular in relation to management of Herring fisheries in the region. They also illustrate the value of effectively modelling heterogeneity in detection probabilities, and the utility of the variance components procedure (White *et al.* 2001, Burnham & White 2002) and analysis of deviance for assessing covariates (Lebreton *et al.* 2012).

We are not aware of another mark–recapture analysis that has used the maximum detection frequency of an animal as a covariate of detection probability. This covariate accounted for two confounded sources of heterogeneity: research intensity in an area and the behaviour of individual Puffins. The utility of this covariate motivates us to suggest recording all observations of a marked animal whenever possible. The variables ring type and engraving pattern also proved valuable for absorbing problematic heterogeneity (Anderson *et al.* 1994) in our recapture probabilities. For example, birds wearing thrice-engraved rings were almost twice as likely to be detected as birds wearing twice-engraved rings. This result also provides significant quantitative support for deploying thrice- rather than twice-engraved rings despite any increased cost that may be incurred.

The appropriate theoretical framework for considering seabirds' demographic responses to changing food abundance was established by Cairns (1987) who envisaged each parameter (chick growth, breeding success and adult survivorship) being affected by successively lower thresholds of food availability. Thus, chick growth would respond to the smallest change in food abundance, breeding success to greater change, and adult survival would decline only 'when food is extremely scarce'. The threshold of food availability affecting adult survival is therefore expected to be much lower than the threshold at which breeding success or chick growth rates would begin to decline.

Quantification of such thresholds is challenging but Cury *et al.* (2011) proposed a threshold of about 33% of the maximum stock size recorded below which further reductions in stock size had significant negative effects on breeding success in seabird populations sampled at 14 locations around the world. In our region, the minimum Herring landing over the period of Puffin survival data (1999–2011; 45 534 tonnes; Fig. 1) was 51% of the maximum (89 461 tonnes) over the same period, well above the 33% threshold of Cury *et al.* (2011). However, this minimum was just 23% of the maximum during the entire time series of available Herring landings data 1966–2011 (199 600 tonnes; Department of Fisheries & Oceans 2011 and R. Singh, DFO, *in litt.*) reflecting substantial declines in fisheries landings since the early 1990s (Fig. 1). Of greater significance, even the average of Herring landings from 1999 to 2011 was just 32% of the 1966–2011 time series maximum. Despite overlapping 95% confidence intervals (Fig. 2a), consistently low adult survival point estimates since 2003–2004 also suggest that Herring availability may have declined in our region to such an extent that it is currently below the threshold when 'food is extremely scarce' (Cairns 1987). Based on our results, we suggest the prey threshold at which adult survival was initially affected was between 23 and 32%, closer than expected to the 33% threshold for breeding success proposed by Cury *et al.* (2011).

In our study, overwinter survival increased as a function of the following year's catch of 'adult' Herring (Table 3). Fishery landings of adult Herring encompass fish 2 years old and older (mostly 2–7 years). Although a rough proxy, since fishery landings include Herring from multiple cohorts, our use of summer landings was an attempt to

capture changes in an important food resource for Puffins in the previous winter period. Since 1994, landings have been restricted by a quota system, which in turn is set by a combination of virtual population analysis and acoustic surveys, used to estimate the spawning stock biomass (Araújo & Bundy 2011). Thus, our assumption in using this proxy is that landings data show a more or less constant relation to the abundance of Herring, and hence to the availability of 1-group Herring to Puffins in winter. Co-variation among our annual survival estimates and Herring landings (Fig. 2a,c) provides considerable validation of this assumption.

Our use of proxies for Herring availability to adult Puffins in winter rests on at least two additional assumptions: (1) that adults, like chicks, eat mainly 1-group Herring in summer, and (2) that adult diet does not switch in winter, e.g. to krill as inferred by Hedd *et al.* (2010). Little is known about the winter distribution or diet of the Gulf of Maine Puffin population, but stable-isotope ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) analysis of MSI chick and winter-grown adult Puffin feathers shows neither the seasonal difference in diet described by Hedd *et al.* (2010) in Newfoundland birds nor a significant difference between chick and adult diet in summer (Bond 2007, A.L. Bond unpubl. data). In addition, as in any correlational study, the correlations we have found, although strong, may not be causative; Herring landings, Herring in chick diet and Puffin survival might all be responding to another, unmeasured factor. We recognize this possibility but argue that the biological case for Puffin survival being driven at least in part by food availability, and especially 1-group Herring in our region (Budge *et al.* 2002, Bakun *et al.* 2009, Pikitch *et al.* 2012), is fundamentally sound.

As our other proxy for food, per cent Herring in chick diet, increased, its (indirect) effect on adult Puffin survival in the following winter also tended to be positive (Fig. 2a,b). Given that the foraging range of adult MSI Puffins in winter is likely to be much more extensive than their summer range, as it is in most seabirds including Puffin populations in Europe (Anker-Nilssen & Aarvak 2009, Harris *et al.* 2010, Guilford *et al.* 2011), it is hard to see how availability of high-quality food for Puffins foraging from MSI in summer could reliably predict availability of food over an assumedly much wider area of the western Atlantic in winter. For this reason, we favour the

interpretation that chick diet predicted parental body condition, and hence survival in the following winter.

The interpretation that summer diet affects the condition of breeders going into winter contradicts life-history theory in the sense that adults of long-lived species should not put their own survival at risk in favour of raising young. However, the investment trade-off between adult survival and breeding success in Puffins appears somewhat complex. Erikstad *et al.* (2009) described Puffins' parental investment strategy as 'highly flexible' and adjusted 'according to their own individual quality and the survival prospects of the chick'. Most relevant to our results is perhaps their finding that subsequent survival in adults that raised a foster chick was positively related to the adult's body mass, suggesting that adult condition in the breeding season may indeed have a carry-over effect on subsequent survival.

Results of our analyses of two proxies of 1-group Herring abundance suggest that Herring, already known to be extremely important to seabirds, marine mammals (especially cetaceans – Kenney *et al.* 1997) and other apex predators such as Bluefin Tuna *Thunnus thynnus* (Golet *et al.* 2007), is also important for the conservation of Puffins on MSI and probably elsewhere in the Gulf of Maine (Breton *et al.* 2006a). Recent reductions in the fishery quota for this species as well as restrictions on mid-water trawling for Herring suggest that regional regulators are increasingly aware of the importance of this keystone species not only to the economy of the region, but also to the diversity of predators that it supports (Kenney *et al.* 1997, Diamond 2012). The biomass of Herring in the Bay of Fundy has declined by 32% between the time periods 2001–2004 and 2005–2010, in spite of reduced quotas, and is cause for concern among regulators (Department of Fisheries & Oceans 2011, Guénette & Stephenson 2012). The uncertainty among fishery scientists about the status of the Herring stock, reflected in large discrepancies between different methods of assessment (Araújo & Bundy 2011, p.83), gives rise to further concern for the future of Puffins and other marine predators in the Gulf of Maine.

Co-variation between May SST and our shrunk estimates of annual survival was also considerable, at 37% (Fig. 2). In the eastern Atlantic, Grosbois *et al.* (2009) found a strong relationship between January-and-May SST and adult Puffin survival at

four colonies across a wide geographical scale, and concluded that SST acts at both global and local scales, with other unidentified environmental factors accounting for the variance not explained by SST. Thus, our study further demonstrates the use of SST for predicting marine predator responses to their environment. Nonetheless, the effect size associated with May SST overlapped zero in our models. This result implies a potential spurious effect (Anderson *et al.* 2001). We also note that the functional form (linear) that we assessed between May SST and survival may have been inappropriate. Under a competing hypothesis, such as a 2nd-order polynomial, explained variation might have increased.

We have shown that annual survival of adult Puffins in this system has varied over a 12-year period and is correlated with proxies of abundance of their main prey, Herring, as reflected in both Puffin chick diet (an index of adult body condition going into the winter period) and fishery landings (an index of 1-group Herring abundance in the previous winter). Overlapping conclusions from AIC_c model weights, effect sizes and per cent variance add weight to the concern for the sustainability of the Atlantic Puffin population in the Gulf of Maine, as do recent ocean-warming trends (Melvin *et al.* 2009). These concerns are compounded by other indicators of declines in the Herring stock and negative changes to the marine food-web in general (Steneck 1997, Golet *et al.* 2007, Bakun *et al.* 2009, Balch *et al.* 2012). We caution that the Bay of Fundy Gulf of Maine ecosystem may be approaching a state in which it is unable to support populations of cold-water seabirds such as Puffins.

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