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RESEARCH ARTICLE

Increased parental effort fails to buffer the cascading effects of warmer seas on common guillemot demographic rates

Sarah Wanless[1] | **Steve D. Albon**[2] | **Francis Daunt**[1] | **Blanca Sarzo**[3,4] | **Mark A. Newell**[1] | **Carrie Gunn**[1] | **John R. Speakman**[5,6] | **Michael P. Harris**[1]

[1]UK Centre for Ecology & Hydrology, Penicuik, UK; [2]The James Hutton Institute, Aberdeen, UK; [3]Institut Cavanilles de Biodiversitat i Biologia Evolutiva, University of Valencia, Valencia, Spain; [4]School of Mathematics and Maxwell Institute for Mathematical Sciences, University of Edinburgh, Edinburgh, UK; [5]School of Biological Sciences, University of Aberdeen, Aberdeen, UK and [6]Shenzhen Key Laboratory of Metabolic Health, Center for Energy Metabolism and Reproduction, Shenzhen Institute of Advanced Technology, Chinese Academy of Sciences, Shenzhen, China

Correspondence
Sarah Wanless
Email: swanl@ceh.ac.uk

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Abstract

1. Climate warming can reduce food resources for animal populations. In species exhibiting parental care, parental effort is a 'barometer' of changes in environmental conditions. A key issue is the extent to which variation in parental effort can buffer demographic rates against environmental change.
2. Seabirds breed in large, dense colonies and globally are major predators of small fish that are often sensitive to ocean warming. We explored the causes and consequences of annual variation in parental effort as indicated by standardised checks of the proportions of chicks attended by both, one or neither parent, in a population of common guillemots *Uria aalge* over four decades during which there was marked variation in marine climate and chick diet. We predicted that, for parental effort to be an effective buffer, there would be a link between environmental conditions and parental effort, but not between parental effort and demographic rates.
3. Environmental conditions influenced multiple aspects of the prey delivered by parents to their chicks with prey species, length and energy density all influenced by spring sea surface temperature (sSST) in the current and/or previous year. Overall, the mean annual daily energy intake of chicks declined significantly when sSST in the current year was higher.
4. In accordance with our first prediction, we found that parental effort increased with sSST in the current and previous year. However, the increase was insufficient to maintain chick daily energy intake. In contrast to our second prediction, we found that increased parental effort had major demographic consequences such that growth rate and fledging success of chicks, and body mass and overwinter survival of breeding adults all decreased significantly.

5. Common guillemot parents were unable to compensate effectively for temperature-mediated variation in feeding conditions through behavioural flexibility, resulting in immediate consequences for breeding population size because of lower adult survival and potentially longer-term impacts on recruitment because of lower productivity. These findings highlight that a critical issue for species' responses to future climate change will be the extent to which behavioural buffering can offer resilience to deteriorating environmental conditions.

KEYWORDS

Ammodytes, behavioural plasticity, climate change, marine predators, population resilience, sandeel, sprat, *Uria aalge*

1 | INTRODUCTION

Seabirds play a key role as ecosystem sentinels of global climate change with some of the strongest signals apparent as changes in the demography of fish-eating species in the northern hemisphere (Sydeman et al., 2021). Climate-driven impacts on seabird performance appear to be mainly indirect, acting through changes in food webs, marine productivity, and food availability (Durant et al., 2003; Grémillet & Boulinier, 2009; Jenouvrier, 2013; Macdonald et al., 2015). Accordingly, many studies have focussed on relationships between measures of marine climate and seabirds' demographic rates. However, seabirds may buffer the effects of environmental conditions on demographic rates by adjusting key behaviours, such as parental care or diet choice. A recent global review of climate-change impacts on marine predators found that only 6% of studies of seabirds included diet as a mediating response variable and even fewer considered behavioural responses (Orgeret et al., 2021). This lack of explicit incorporation of behavioural plasticity in studies of climate effects on demography currently limits our understanding of key mechanistic pathways, and ultimately, our ability to predict the effects of future climate change on seabird populations.

Theoretical studies, supported by extensive empirical data from diverse seabird species and regions, have demonstrated a consistent hierarchy of responses to varying environmental conditions during the breeding season with parental effort identified as one of the most sensitive indicators, particularly in species that lay a clutch of one egg and thus which do not have the option of adjusting clutch or brood size (Ashbrook et al., 2008; Burger & Piatt, 1990; Cairns, 1988; Lewis et al., 2006). Flexible time budgets reflecting variation in parental effort offer the potential for individuals to buffer demography against variation in availability of resources. This behavioural mechanism may be particularly critical for species feeding on pelagic prey, where the foraging environment often varies greatly in space and time, and effects are intensified in central-place foragers where foraging ranges are restricted and energetic demands on parents are high (Elliott et al., 2013; Ricklefs, 1984; Thaxter et al., 2013). For parental effort to be an effective buffer, we would predict a close link with environmental conditions but no relationship with demographic rates. In contrast, linked relationships between environmental conditions, diet, parental effort and demographic rates would indicate that behavioural plasticity was unable to successfully buffer the cascading effects of climate change on demography.

Here, we use behavioural, demographic and dietary data from common guillemots (*Uria aalge* hereafter guillemot) collected over four decades of intensive study at the Isle of May, a major breeding colony in the western North Sea, UK, to explore the behavioural, dietary and demographic effects of warmer seas. While previous studies of guillemots on the Isle of May have documented marked temporal variation in many aspects of their demography, parental activity and chick diet, in some cases, correlated with climate and/or availability of prey (e.g. Ashbrook et al., 2010; Frederiksen et al., 2006; Lahoz-Montfort et al., 2014; Rindorf et al., 2000; Wanless et al., 2018), none have comprehensively explored the extent to which parental behaviour can buffer demographic rates against variation in sea temperature.

Since the mid-1980s, there has been a general warming of surface waters in the Northern North Sea where the Isle of May is located (Dye et al., 2013; Tinker & Howes, 2020). These changes have been associated with major shifts in abundance and distribution of many marine organisms including the copepods *Calanus finmarchicus* and *C. helgolandicus* (Reid et al., 2003; Wilson et al., 2016). These species are key prey for small, pelagic, lipid-rich fish, notably lesser sandeel (*Ammodytes marinus* hereafter sandeel) in the North Sea, which in turn form the diet of many predatory fish, marine mammals and seabirds including guillemots (Anderson et al., 2014; Engelhard et al., 2014; Furness & Tasker, 2000; Wanless et al., 2018; Wilson & Hammond, 2019). In contrast to many other fish species, sandeels cannot move into deeper, cooler water to avoid warming sea temperatures because they are tightly associated with sandy sediments of a specific grain size (Holland et al., 2005; Langton et al., 2021; Wright et al., 2000). As a result, sandeel populations are spatially structured with discrete populations exhibiting markedly different trends in abundance and/or growth rate (Boulcott & Wright, 2011). Changes in sandeel growth rate, and hence body length and energy density at a given age, are of relevance to guillemot/sandeel trophodynamics because guillemots are obligate single-prey loaders so a parent can only deliver one prey item to the chick per feeding trip. Given that one of the parents must remain with the chick in order to protect it from attack from predators or neighbouring guillemots

(Ashbrook et al., 2008), guillemots do not normally choose the option of increasing prey delivery rates by both parents foraging simultaneously. However, they can increase delivery rates by increasing the time the non-brooding individual spends foraging at the expense of other activities such as resting and socialising at the colony (Ashbrook et al., 2010). Furthermore, the quality (energy value) of individual prey items is critical for successful breeding (Frederiksen et al., 2006; Kadin et al., 2012; Wanless et al., 2005). Over the last four decades mean annual length of 1+ group sandeel (fish at least 1 year old) in the population around the Isle of May, and in the diet of seabird chicks, has decreased by *c.* 0.4 mm per year (Rindorf et al., 2016; Wanless et al., 2018). Availability of this age class may also have become temporally mismatched with the guillemot chick rearing period (Harris et al., 2022). Concurrently, sprat *Sprattus sprattus*, another lipid-rich, small, shoaling pelagic forage fish has become increasingly important in guillemot chick diet (Anderson et al., 2014; Wanless et al., 2018). Although less abundant than sandeel, sprat have increased in the North Sea since 2000 (Heath et al., 2012; Lenoir et al., 2011).

In this study, we explored the extent to which parental behaviour can buffer demographic rates against environmental variation by first quantifying the effects of warmer sea temperatures on chick diet and then assessing the effects of increased parental effort on chick growth and fledging success, and adult mass and overwinter survival. We predicted that, for parental effort to be an effective buffer, there would be a link between environmental conditions and effort but no relationship between parental effort and demographic rates. Our findings are discussed in terms of their likely consequences for common guillemots, one of the most abundant avian predators in the North Atlantic pelagic ecosystem, given the current projections for future climate warming in this region.

2 | MATERIALS AND METHODS

2.1 | Study site and population trends

The Isle of May National Nature Reserve (56°11′N, 02°33′W) lies 8 km offshore in the Firth of Forth, Scotland, and is the site of one of the major concentrations of nesting seabirds in the North Sea—*c.*70,000 pairs of 11 species (Outram & Steel, 2018). Between 1982 and 2019 standardised data were collected on the numbers of pairs of breeding guillemots, their feeding ecology, parental behaviour, chick and adult condition, breeding success and adult survival (Ashbrook et al., 2008; Harris & Wanless, 1988; Outram & Steel, 2018; Wanless et al., 2018). During this period, guillemot numbers fluctuated from less than 12,000 breeding pairs in the late 1980s/early 1990s to more than 20,000 in the early 2000s, before declining until 2013, since when they have increased again (see Supporting Information: Figure S1a). Mean spring (February–March) sea surface temperature (sSST) has previously been used as a proxy for local conditions affecting prey availability of Isle of May seabirds (Burthe et al., 2012; Frederiksen, Harris, et al., 2004; Howells et al., 2017). During our study period, sSST in the area surrounding the Isle of May bounded by 56°–57°N and 1°–3°W and encompassing the foraging areas used by guillemots during the breeding season (Thaxter et al., 2010), varied between 4.7°C and 7.1°C but showed no overall temporal change or significant correlation between sSST in consecutive years ($r = 0.145$, $p > 0.3$; (Supporting Information: Figure S1b; Bundesamt für Seeschifffahrt und Hydrographie www.bsh.de/en/Marine_data).

2.2 | Breeding phenology, fledging success and chick growth index

Information on chick rearing of between 536 and 1014 pairs (mean 832 ± 114 standard deviation [SD]) of guillemots breeding in a range of cliff types and bird densities, dispersed along about 250 m of cliff on the west side of the island, was collected each year (details in Harris & Wanless, 1988). Visual checks 3–5 times a day allowed the determination of dates of hatching and fledging. Annual median hatching date varied between 30 May and 18 June and median fledging date varied between 20 June and 10 July. The guillemot has an intermediate breeding strategy with the chick being taken to sea by the male parent when only 20%–35% grown and unable to fly (Varoujean et al., 1979). Even so, the chick's departure from the breeding site is conventionally described as ‘fledging’. A chick was considered to have fledged successfully if it reached an age of at least 15 days and there was no subsequent evidence to the contrary (Harris et al., 2020). Fledging success was taken to be the proportion of hatched chicks that fledged. Young guillemots normally fledge at night and fledging age was taken as the period (in days) between the date of hatching and the morning that the chick was first recorded as being absent from the breeding site, when both hatching and fledging dates were known to within 1 day. Mean fledging age varied between years from 19.5 to 24.0 days.

Although chicks cannot fly when they fledge, the ratio of body mass/wing area is critical for successful fledging. In our study population once a guillemot chick has a wing length ≥60 mm there is relatively little increase in mass with increasing wing length before fledging (Harris et al., 1992). Weights of such chicks (annual mean sample size = 59 chicks; range 6–140) were used as an index of fledging mass, and an annual index of chick growth rate was obtained by dividing mean fledging mass of chicks with wings ≥60 mm by mean age at fledging in days (index range 8–13). Mean annual fledging mass and age at fledging were strongly negatively correlated ($r = -0.677$, $p < 0.001$) indicating that when chicks grew slowly, on average, they fledged at older ages and at lower masses. Our growth rate index was validated by comparing it with growth rates (g/mm increase in wing length) of chicks during the period of linear growth for the 29 years (1982–2010) for which both measures were available: the asymptotic relationship between these measures was highly significant ($F_{2,26} = 23.06$, $p < 0.001$: see Supporting Information, Figure S2).

2.3 | Parental effort

Both parents participate in chick-rearing with the chick normally brooded by one parent while the other is away foraging (Thaxter et al., 2009). When feeding conditions are good, parents can spend more than 30% of daylight hours together at the breeding site. However, when conditions are poor parents may leave their chick unattended which brings with it a risk of predation from gulls (*Larus* spp.) or attack by other guillemots (Ashbrook et al., 2008). Hence, measures of parental attendance can provide an index of parental effort, which increases across a gradient from both parents being present with the chick to neither being in attendance.

In 33 of the 38 years (excluding 1982, 1983, 1987–1989), a sample of chicks (annual mean number at the peak of the chick period = 287; range 99–449) was checked around mid-day when attendance by birds at the colony is least variable and the proportion of chicks with both parents is highest (Lloyd, 1975; Richardson et al., 1981; Wanless & Harris, 1986). To allow for any seasonal and/or daily variation, checks were made throughout the chick-rearing period (annual mean number of days = 27; range 7–37) to determine the proportion of chicks with both parents, one parent or neither parent in attendance (Ashbrook et al., 2008).These daily attendance values were then used to calculate an annual index of parental effort as a weighted sum (WS), which could range from zero, when all chicks were attended by both parents, to 2.0 when all chicks were unattended:

$$\mathrm{WS} = \sum_{i=0}^{2} X_i W_i,$$

where i denotes the three possible states: chicks attended by both parents ($i = 0$), one parent ($i = 1$), and chick unattended ($i = 2$); X_i represents the value at each state: $X_0 = 0$, $X_1 = 1$, and $X_2 = 2$; and W_i indicates the weights by state, that is, the proportion of chicks in each of the states (by year).

For a subset of 32 days over 22 years for which we had detailed behavioural observations of the time that members of a pair spent together with the chick between foraging trips, as well as our daily index of parental effort, the two measures were significantly and positively related ($F_{2,29} = 24.2$, $p < 0.001$; see Supporting Information, Figure S3). Further support for our assumption that increased time away from the breeding site reflected increased parental foraging effort was provided by data from time activity loggers that showed a positive and highly significant correlation between trip duration and time spent foraging (Thaxter et al., 2013).

2.4 | Guillemot chick diet

Chick diet was quantified by recording the species and qualitative length class (very small, small, medium, large or very large relative to the size of the parent's bill) of fish fed to chicks in observations made throughout the day during the whole chick-rearing period. These descriptive length classes were converted to actual lengths by measuring fish found in the colony when chicks were being ringed each year (Harris & Hislop, 1978). The diet was made up of two main fish families: Ammodytidae (sandeels mainly lesser sandeel) and Clupeidae (sprat and herring *Clupea harengus*). Other fish (mainly Gadidae) made up an average of only 1.70 ± 0.06% SE of the diet by number over the 38 years. Sprat and small herring are impossible to separate in the field but 139 out of 151 (92%) Clupeidae dropped by guillemots were sprat so, for convenience, all Clupeidae are referred to as sprats. In 19 years (1985–1988, 1995, 1996, 1999, 2004–2015) samples of fish were collected to determine species-specific length-calorific value relationships (see Supporting Information: Appendix S1 for details). Systematic all-day watches in two plots in the study area where chick diet data were collected, were carried out to record the frequency of feeds to chicks (annual mean number of chicks = 57, range 19–158) during daylight on two to 8 days (mode = 2) each year.

The data on prey species and prey length were used to provide annual estimates of the proportion (by number) of each prey species in chick diet and the mean species-specific prey length. Data on calorific value and prey length were used to estimate species-specific length-calorific value relationships (Supporting Information: Figure S4). To elucidate annual differences in the energy value of prey that integrated variation in calorific value and prey length, relative calorific values were estimated from the mean annual deviation from the species-specific exponential curve (Figure S4), expressed as a proportion of the calorific-length predictions. Thus, for the subset of years for which we had information on every aspect of chick diet, we estimated the mean annual daily energy intake using the annual proportion of each fish species in the diet, the annual mean length for each species, the annual mean energy content of each species, and the annual mean number of fish delivered per day.

2.5 | Adult survival and body mass

Adult survival was determined over a 38-year period from 1982 to 2019 by following a total of 1025 adults each marked with a unique combination of colour-rings and breeding in the same areas where fledging success was followed. In each year intensive searches were made to find these birds, both where they had been ringed (fidelity of experienced breeders to the previous year's breeding area is 98%; Harris et al., 1996) and elsewhere on the island, and new birds were ringed to replace those that had disappeared. The mean number of marked birds seen in any year was 326 (range 101–418).

Data on adult body mass during chick rearing were collected in areas close to those where data on breeding and chick growth were recorded in all years except 1996 and 1997. Samples of adults with chicks (annual mean = 41; range 1–130) were caught using a 7 m extendable noose pole and weighed to the nearest 5 g, to provide annual estimates of the mean mass of chick-rearing adults.

The majority of data used in this analysis did not require ethical approval since they were collected using observations from permanent hides 10–30 m from the study plots without disturbing the birds. Captures of adults (to record body mass and for colour-ringing to estimate adult survival), and chicks (to record body mass and wing length) were carried out under licence from the British Trust for Ornithology (personal licence numbers A400, A2332 and A4607 for MPH, SW and MAN, respectively).

2.6 | Statistical analysis

Statistical analyses were performed using Genstat v.20 (VSN International, 2020). Relationships between dependent variables and potential explanatory independent variables were initially explored using spline regressions with two degrees of freedom. We used these to guide the likely choice of non-linear curve (e.g. exponential, rectangular hyperbola, logistic), selecting the best model using the sums of squares explained given the increase in terms fitted from a simple linear model. For non-linear curves, we checked for significant correlations between the residuals and other candidate explanatory variables. For multiple linear regressions with two or more explanatory variables, we show the relationship of the dependent variable adjusted for the other variables in the model. Since sample sizes of adult mass and chick mass were particularly variable among years (two orders of magnitude – 1–130 and 6–140, respectively), we used weighted least-squares regressions, where the 'weights' were the square root of the sample size in that year.

Given that the influence of parental effort on both fledging success and adult survival could be both direct and indirect via chick growth and adult body mass, respectively, we explored the significance of alternative pathways using partial correlation analysis (Grace, 2006). This approach corrects any pairwise correlation for the correlation each might have with other variables in the pathway. Since some of the relationships between pairs of variables were non-linear, before undertaking partial correlation analysis, we used the logit transformation of proportions to meet the assumption of linearity.

Many of the variables showed significant trends over the course of the 38-year study: adult body mass during chick rearing, the three measures of chick development (chick fledging mass, age at fledging and growth rate index; see Supporting Information, Figure S5), the parental effort index, and both fledging success and adult survival all showed significant temporal trends. Accordingly, to reduce the risk of spurious correlations between any two variables with strong temporal trends, we detrended covariates by fitting the regression curve that best captured each temporal trend and then explored the relationships between the sets of residuals (see Supporting Information: Figures S7 and S9).

The estimated lengths of both sandeel and sprat indicated that guillemots fed their chicks almost exclusively on 1+ group fish (those that are at least 1-year old, Heessen et al., 2015; Rindorf et al., 2000). Thus, climate-mediated effects on prey could potentially be influenced by conditions in both the current ($t0$) and previous year ($t-1$). Therefore, when using spring sea surface temperature, we tested for effects in both the current (sSST_{t0}) and the previous year (sSST_{t-1}).

Density-dependent effects on breeding performance are important in this population (Ashbrook et al., 2010; Bennett et al., 2022). Accordingly, we tested for the effects of population size (breeding pairs) in the current year. We considered that the effects of density could also carry-over into subsequent seasons, and thereby affect the condition of birds in the following breeding season, so we also fitted breeding pairs in the previous year.

Adult overwinter survival was estimated using a Bayesian Cormack-Jolly-Seber model (Cormack, 1964; Jolly, 1965; Seber, 1965) implemented via the JAGS software (Plummer, 2003) within the R program (R Core Team, 2021). We assumed full time dependence on model parameters. As no prior knowledge about the parameters was available, non-informative prior distributions (Uniform (0,1)) were elicited for survival and recapture probabilities. Three independent chains were run, each for 9000 iterations, discarding the first 900 as burn-in (to ensure that the Markov chain has reached the stationary distribution) and thinning every 10 of the iterations for memory storage purposes and to reduce auto-correlation.

3 | RESULTS

3.1 | Trends in adult attendance and parental effort

The proportion of chicks attended by both parents declined markedly from between 0.2 and 0.3 in the 1980s to less than 0.05 in most years after 2000 (Figure 1a). Unattended chicks were recorded from 1998 onwards and the proportion was markedly higher between 2004 and 2008 (0.04–0.14). As a result of these changes in attendance behaviour, our parental effort index increased significantly over the course of the study (best described by a logistic regression: $F_{3,29}=9.35$, $p<0.001$; Figure 1b).

3.2 | Changes in chick diet species composition, fish length and energy content

In the first 11 years of the study, sandeel was always the numerically dominant species in chick diet (mean proportion 0.77 compared with 0.22 for sprat) (Figure S6). Sprat was numerically dominant every year from 2001 onwards (mean proportion 0.82 vs. 0.14 for sandeel). Gadids represented less than 0.005 of the prey in most years and rarely accounted for more than 0.05 of the prey (Figure S6). However, the proportion of gadids increased over the course of the study ($F_{1,36}=4.71$, $p=0.037$), notably after 2004 when sandeels became scarcer. Superimposed on this shift in chick diet species composition were temporal declines in mean body length of both sandeel and sprat (Figure 2a). Overall sandeel length declined by 0.627 ± 0.219 SE mm year^{-1} ($p=0.007$) and sprat length declined by 0.391 ± 0.155 SE mm year^{-1} ($p=0.016$). Mean annual lengths of the two fish species were significantly correlated ($r=0.417$, $p=0.009$). There was no significant change in gadid length over the course of the study ($b=0.172\pm0.271$ SE, $p>0.5$).

Energy content increased exponentially with increasing fish length in both species (Figure S4). Length-for-length energy content of a sandeel was always less than that of a sprat ($F_{1,362}=232.3$, $p<0.001$), so although the overall mean sandeel length (114 ± 24.9 SD mm) was greater than that of a sprat (102 ± 17.2 SD mm), the mean energy content was only 22.1 kJ compared with 37.0 kJ for sprat. Gadids were markedly smaller than either sandeel or sprat (mean length $=49.6\pm13.9$ SD mm) with a mean energy content of only 3.0 kJ.

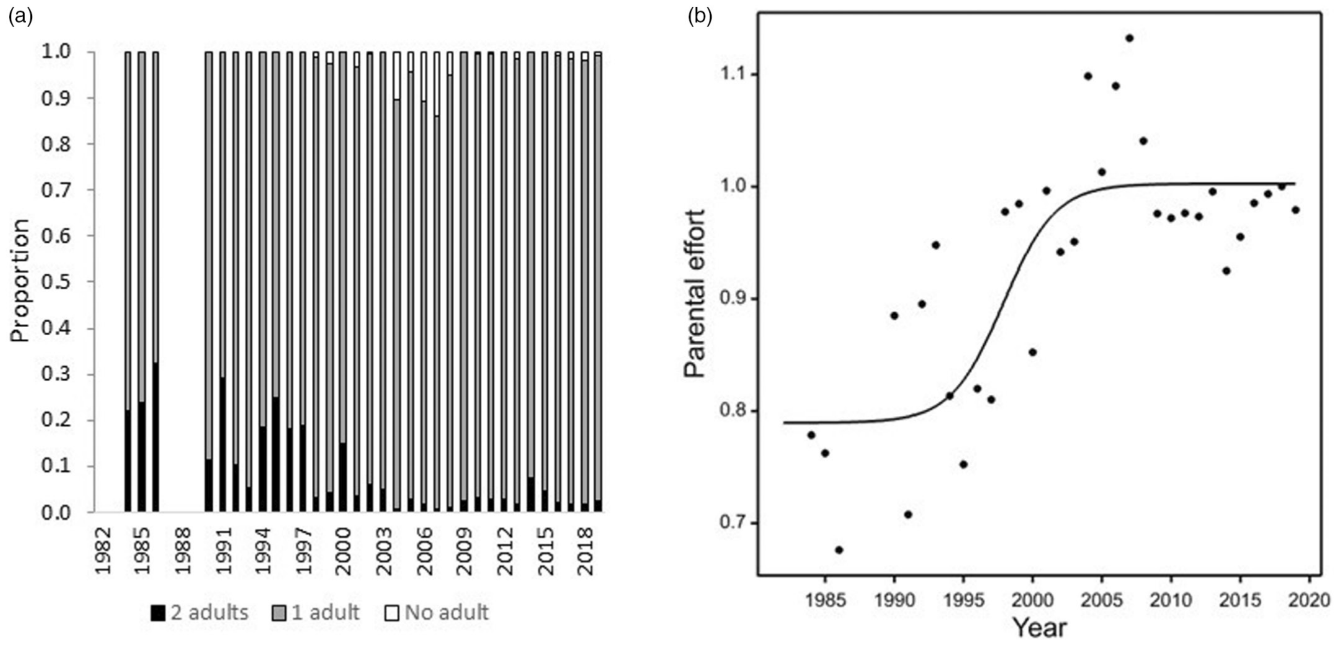

FIGURE 1 (a) The proportion of chicks attended by two adults, one adult and no adult each year between 1984 and 1986 and 1990 and 2019 and (b) the change in parental effort index over the course of the study.

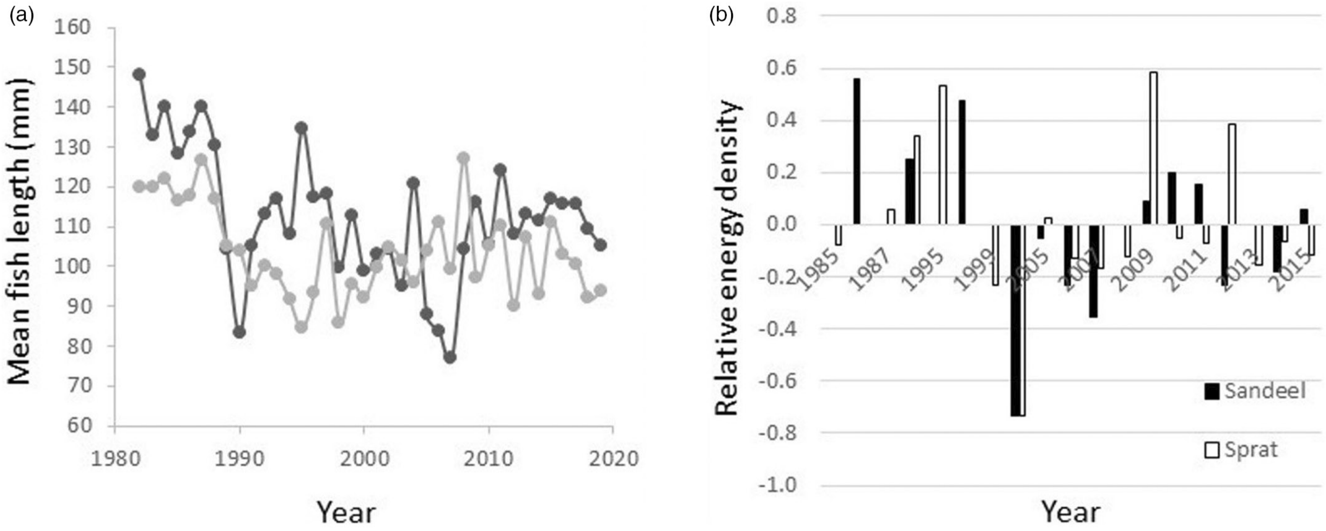

FIGURE 2 Temporal changes in (a) mean annual length of sandeel (black circles) and sprat (grey circles) fed to guillemot chicks and (b) the relative annual energy density standardised to the species-specific exponential curve of calorific value on fish length (see Figure S4).

Length-corrected energy content of both sandeel and sprat differed significantly between years (sandeel: intercepts, $F_{11,160}=5.48$, $p<0.001$; exponential shape parameters, $F_{11,149}=4.1$, $p<0.001$; sprat: intercepts, $F_{16,160}=3.22$, $p<0.001$; exponential shape parameters, $F_{16,144}=1.91$, $p=0.024$). In years when we had samples for both sandeel and sprat there was a significant positive correlation ($r=0.777$, $N=11$, $p<0.01$) between the relative calorific values (mean annual deviation from the species-specific exponential curve in Figure S4, expressed as a proportion of the calorific-length predictions: Figure 2b). In contrast, gadids showed no significant between-year differences in length-corrected energy content after excluding 2007, when only four fish were sampled ($p>0.9$).

3.3 | Chick diet and sea surface temperature

When sea surface temperature was high in both the current (Figure 3a) and previous years (Figure 3b), the proportion of sandeel in chick diet declined ($F_{2,35}=3.70$, $p=0.035$). As sprat was the main alternative prey to sandeel, the proportion of sprat in chick diet consequently

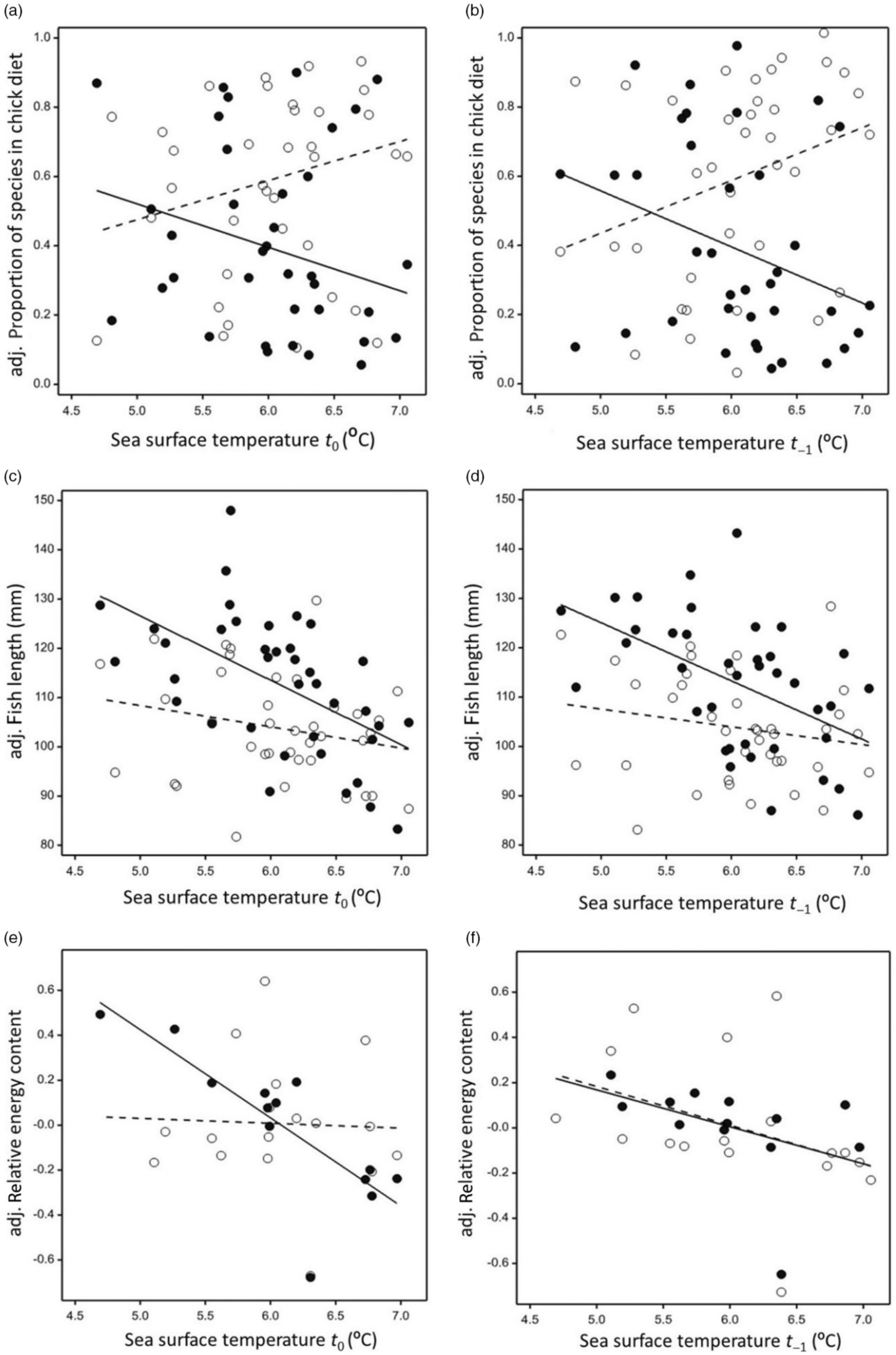

FIGURE 3 Variation in the proportion of sandeel (filled circles, solid lines) and sprat (open circles, dashed lines) in guillemot chick diet (a and b), mean annual length of each fish species (c and d), and mean annual relative energy content of each fish species (e and f) in relation to sea surface temperature in the current year (a, c, e) and the previous year (b, d, f). In each case, the annual values of the response variable are adjusted (adj.) for the other independent variables in the full model.

increased when temperature in both the current and previous years was high ($F_{2,35} = 3.37$, $p = 0.046$).

Higher sSST was also associated with a significant decline in sandeel length but not sprat length. The reduction in sandeel length was associated with higher sSST in both the current (Figure 3c) and the previous year (Figure 3d). Sandeel length decreased by 13.1 mm ±3.24 SE ($p < 0.001$) for a 1°C increase in sSST_{t0}, and decreased by a further 11.8 mm ±3.26 SE ($p < 0.001$) for a 1°C increase in sSST_{t-1}. Sprat length decreased by only 4.31 mm ±4.58 SE ($p > 0.5$) for a 1°C increase in sSST_{t0}, and by only 3.59 mm ±4.61 SE ($p > 0.5$) for a 1°C increase in sSST_{t-1}.

Furthermore, in the years for which we had estimates for length-adjusted energy content, relative energy content declined when sSST_{t0}, was higher (Figure 3e) in sandeel (slope $= -0.391 \pm 0.119$ SE, $p = 0.003$), but not sprat (slope $= -0.022$, ± 0.171 SE, $p > 0.8$). There was also an independent negative effect of sea surface temperature in the previous year (sSST_{t-1}) on length-adjusted energy content, of similar magnitude in both sandeel and sprat (Figure 3f: both slopes $= -0.169 \pm 0.079$ SE, $p = 0.043$).

3.4 | Parental effort, environmental variation and chick daily energy intake

In accordance with our first prediction, parental effort increased when sSST was higher in both the current (sSST_{t0}: Figure 4a: slope $= 0.0635 \pm 0.0266$ SE, $p = 0.024$) and previous year (sSST_{t-1}: Figure 4b: slope $= 0.08 \pm 0.0276$ SE, $p = 0.007$). In addition, parental effort increased in years when the number of breeding pairs in the current year was higher (Figure 4c: slope $= 0.00001715 \pm 0.0000068$ SE, $p = 0.017$). Together these three variables accounted for 40.2% of the variation in parental effort, and 45.2% if breeding pairs in the previous year was used instead of breeding pairs in the current year.

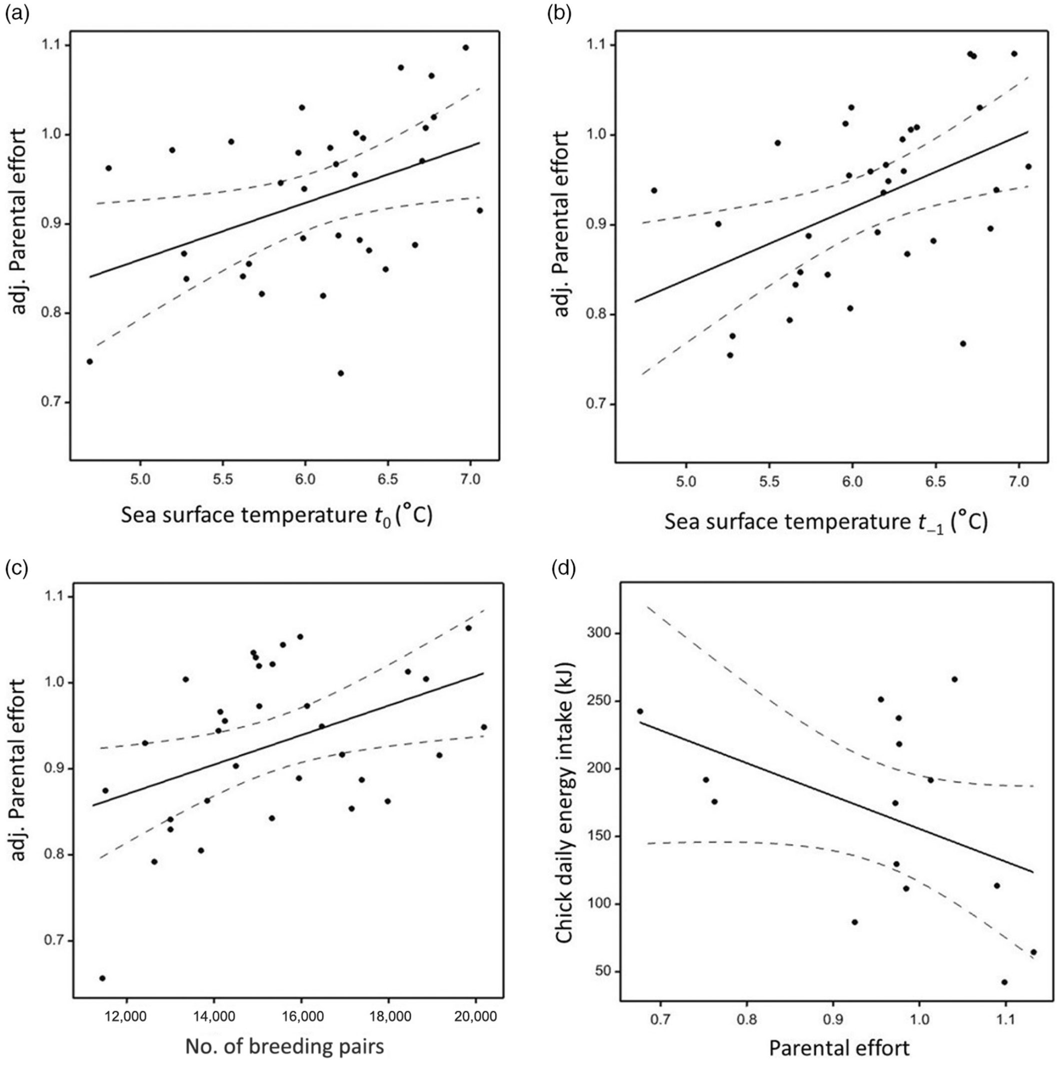

FIGURE 4 Parental effort plotted against (a) spring sea surface temperature in the current year (t_0) and (b) spring sea surface temperature in the previous year ($_{t-1}$) and (c) the number of breeding pairs that summer. The solid lines show the fitted regression line and the dashed lines the 95% confidence intervals. In each case, the annual values of parental effort are adjusted (adj.) for the other independent variables in the full model. Panel (d) shows the regression and 95% confidence intervals for the relationship between estimated chick daily energy intake and parental effort.

However, increased parental effort in years when sSSTs were higher was insufficient to fully compensate for the fact that chick daily energy intake declined when sea surface temperatures were higher, and there was a negative relationship between daily energy intake of chicks and parental effort (Figure 4d: slope = −243 ± 135 SE, $p = 0.096$).

3.5 | Effects of increased parental effort on fledging success and chick growth

Fledging success of guillemot chicks varied markedly between years (Figure 5a) with a series of particularly low years from 2004 to 2008, before recovering to around 0.9 after 2009. Nonetheless, even after excluding these five poor years, there was a significant decline suggesting fledging success in the last decade was lower than in the early decades (slope = −0.002183 ± 0.00054, $p < 0.001$).

Fledging success across all 38 years was strongly related to the annual chick growth rate index with the fitted rectangular hyperbola accounting for 78% of the variation in fledging success (Figure 5b: $F_{2,35} = 66.77$, $p < 0.001$). The strong association between fledging success and chick growth remained even after removing the five poor years, with a simple linear model still accounting for 50% of the variation in fledging success ($F_{1,31} = 32.88$, $p < 0.001$). The annual variation in chick growth over the entire study was strongly related to between-year differences in parental effort (Figure 5c), with the fitted logistic regression explaining 82% of the annual variation in the chick growth index ($F_{3,29} = 49.08$, $p < 0.001$).

The detrended relationships (Supporting Information Figure S7) suggest that, independent of other temporal correlations, parental effort contributes to variation in chick growth, and, in turn, fledging success. Indeed, in the raw data, parental effort alone, fitted as a logistic regression, explained 89% of the variation in fledging success (Figure 5d: $F_{3,29} = 85.9$, $p < 0.001$). The logistic relationship was not a function of the coincidence of the extremely low fledging success and high parental effort between 2004 and 2008, since there was no significant difference in the fitted regression parameters (asymptotes and slopes) comparing the years prior to 2004 with those afterwards (see Supporting Information: Figure S8). There was no independent effect of either breeding pairs in the current year or breeding pairs in the previous year, on fledging success after having fitted parental effort ($F_{1,30} = 1.07$, $p = 0.31$; $F_{1,30} = 0.09$, $p = 0.77$, respectively).

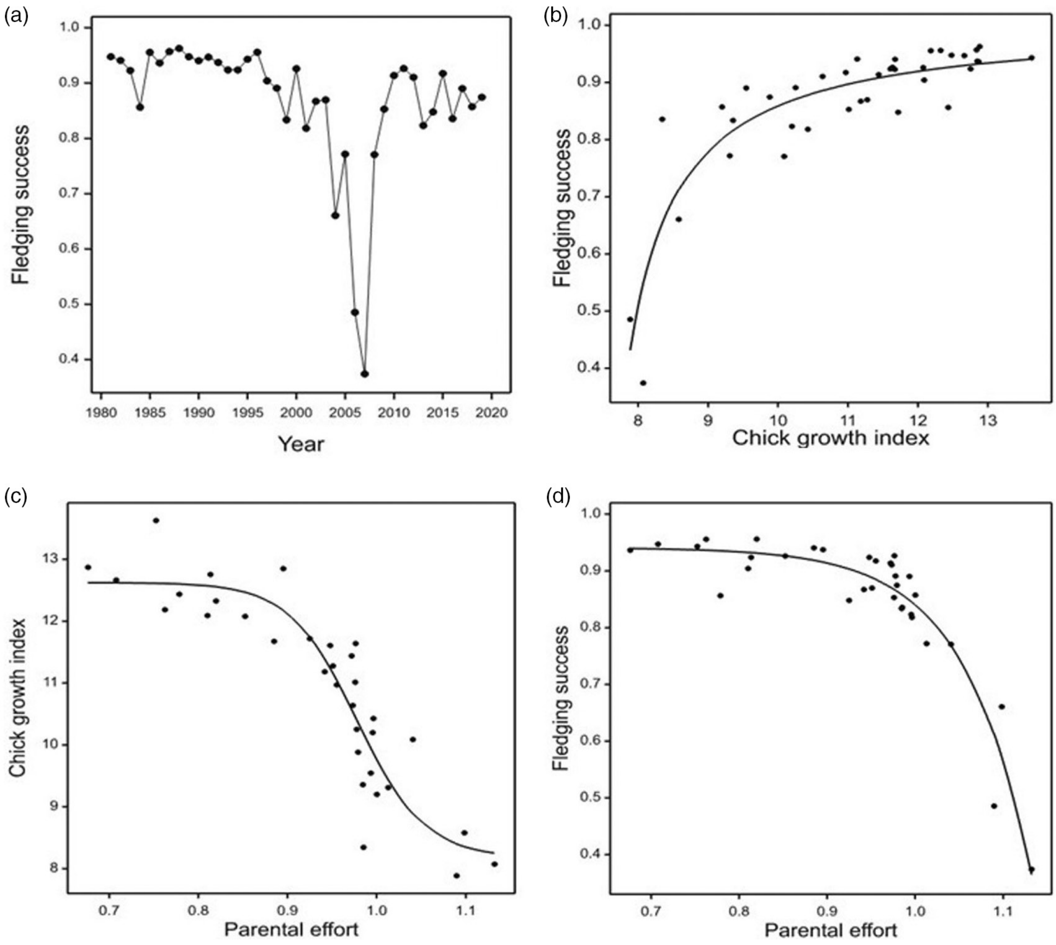

FIGURE 5 (a) Annual variation in fledging success, (b) fledging success plotted against chick growth index for the same years, (c) chick growth index plotted against parental effort and (d) fledging success plotted against parental effort.

3.6 | Effects of increased parental effort on adult survival and adult mass

Adult survival to the next breeding season varied markedly between years (Figure 6a) and, like fledging success, was particularly low between 2004 and 2008. Nonetheless, when these 5 years were excluded, there was still a significant decline in survival (slope $= -0.000938 \pm 0.000339$ SE, $p = 0.009$). Adult survival decreased significantly when adults were lighter ($F_{2,32} = 6.19$, $p = 0.005$: Figure 6b), with body mass explaining 23% of the variance in survival. Adult mass declined as parental effort increased (slope $= -108.6 \pm 32.9$, $p = 0.003$: Figure 6c), with parental effort explaining 26% of the variation in adult mass. The detrended relationships (Supporting Information Figure S9) suggest that, independent of other temporal correlations, both adult mass and parental effort contribute to variation in adult survival. However, in the raw data parental effort alone (fitted as a logistic regression Figure 6d) explained 71% of the variation in adult survival over the next winter ($F_{3,28} = 26.6$, $p < 0.001$). There was no independent effect of either breeding pairs in the current year or breeding pairs in the previous year on adult survival having fitted parental effort ($F_{1,30} = 0.08$, $p = 0.77$; $F_{1,30} = 1.37$, $p = 0.25$, respectively).

3.7 | The direct and indirect pathways affecting fledging success and adult survival

Given that we had both a direct relationship between parental effort and fledging success and an indirect relationship via chick growth rate, we compared the partial correlation coefficients of the different paths (Figure 7). This showed that both elements of the indirect pathway via chick growth were significant ($p < 0.01$) and that the effect on fledging success (the product of the two partial correlations −0.326) was greater than the direct pathway between parental effort and fledging success, which was not significant (−0.186). Thus, the data did not support our second prediction that increased parental effort, because of weather-mediated variation in sea surface temperature, would be sufficient to maintain fledging success with the negative response operating via the growth rate of the chicks.

When we compared the partial correlation coefficients for adult survival, both elements of the indirect pathway via adult mass were non-significant ($p > 0.2$), and the effect on adult survival (the product of the two partial correlations −0.052) was considerably smaller than the significant ($r = -0.588$, $p < 0.001$) direct effect of parental effort on adult survival (Figure 7). Thus, as for fledging success, the data indicated that increased parental effort, associated with variation in marine climate, had negative demographic consequences. However, in this case, the response appeared to operate directly on overwinter survival, rather than via adult body condition.

4 | DISCUSSION

Our findings provide important new insights into the mechanistic linkages underpinning the population dynamics of common guillemots, one of the most abundant avian predators in the North Atlantic (Figure 7). In particular, they demonstrate that although parental effort (as indicated by the time parents spend away foraging) increased in response to temperature-driven variation in prey species and energy value fed to chicks, the increased effort was insufficient to maintain the daily energy intake of chicks. Moreover, elevated levels of parental effort had negative effects on both immediate reproductive performance and subsequent overwinter survival of adults. Taken together our results highlight the limitations of behavioural plasticity in safeguarding demographic rates from environmental variation, suggesting that future climate warming could have major consequences for population viability.

4.1 | Behavioural plasticity and population viability

Behavioural plasticity is an important adaptive response to changing conditions, particularly rapid responses to changes in the external environment (Sol & Lefebvre, 2000; Wong & Candolin, 2015; Wright et al., 2010). It is geographically and taxonomically widespread (e.g. great tits *Parus major* Charmantier et al., 2008; black bears *Ursus americanus* Johnson et al., 2020; poison frogs (Dendrobatoidea) Justicia et al., 2022). Responses mediated via parental effort have been best documented in birds, particularly colonially breeding species with restricted foraging ranges and energetically expensive foraging methods, and parental effort is widely used as a 'barometer' of changes in environmental conditions (Burger & Piatt, 1990; Fayet et al., 2021; Harding et al., 2007). Yet few studies have quantified whether buffering is effective across the full range of conditions experienced and whether any fitness costs are immediate or delayed. In our study, parental effort varied markedly but crucially was insufficient to compensate fully for unfavourable conditions associated with higher sea surface temperatures in both the current and previous year. There was also evidence of intra-specific competition as reflected by increased parental effort when the breeding population in the current year was higher, indicating that prey might have been directly depleted, or possibly that conspecific interference made prey temporarily less available (Ashmole, 1963; Lewis et al., 2001). However, we found no support for an independent effect of breeding population size on fledging success after having fitted parental effort. Taken together our findings indicate that despite increased parental effort, the daily energy intake of the chicks was depressed, and both the quality (reduced growth rate) and quantity (reduced fledging success) of chicks were adversely affected. Our analyses indicated that the effects on fledging success probably operated via chick growth rate, consistent with the observed reduction in daily energy intake. However, under the most extreme conditions, guillemot parents left their chicks unattended. Although this strategy potentially increases the rate at which chicks are fed, it also increases the risk of unattended chicks being attacked and killed by neighbouring guillemots or being taken by avian predators (Ashbrook et al., 2010). Reduced growth rate is also associated with a longer fledging period thereby increasing the time the chick is at risk in the colony, and the mean age at which chicks are lost is older in years when parental non-attendance is high and breeding success is

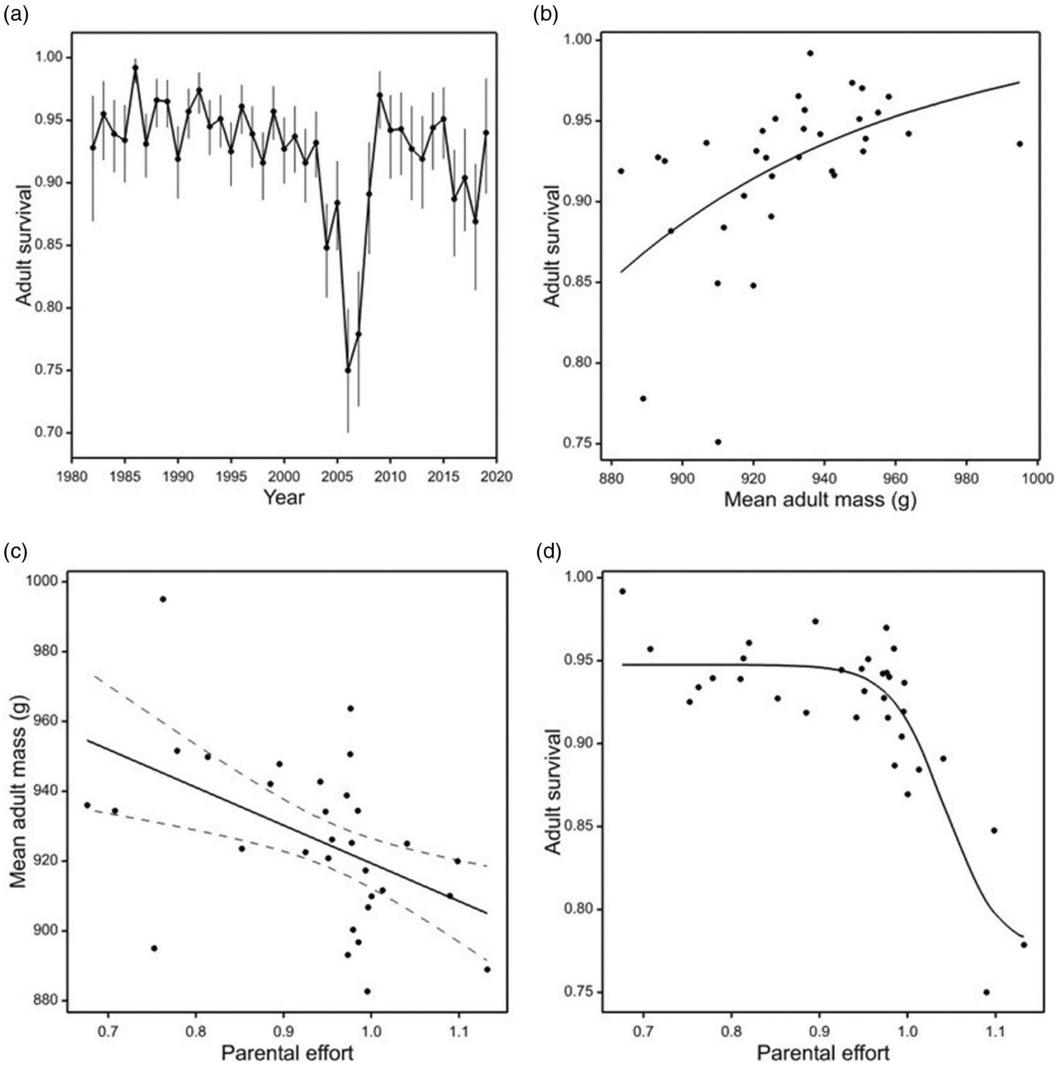

FIGURE 6 (a) Annual variation in estimated adult survival (see methods), (b) annual adult survival plotted against mean adult mass, (c) mean adult mass plotted against parental effort showing the fitted regression line and 95% confidence intervals and (d) adult survival plotted against parental effort.

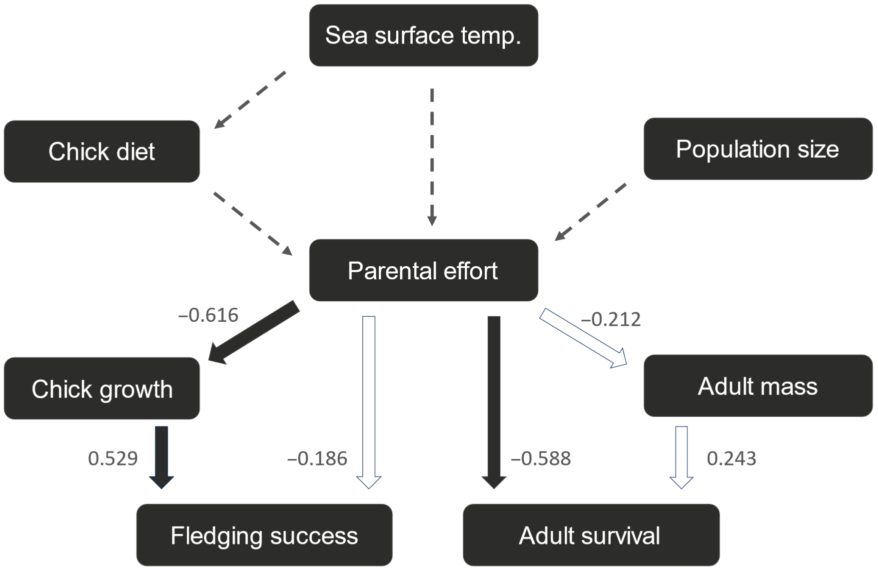

FIGURE 7 Schematic showing the linkages between major components of the Isle of May guillemot system. Dashed lines show bottom-up effects on parental effort. The black solid arrows indicate significant partial correlations and their coefficients, and the open arrows show non-significant partial correlation coefficients associated with the direct and indirect pathways of influence of parental effort on fledging success and adult survival.

low (Ashbrook et al., 2010). Thus, increased parental effort impacts not only the energy intake of chicks but also the likelihood of conspecific and predator attacks. A previous study of guillemots in the Baltic found a similar negative relationship between feeding rate (a proxy for parental effort) and prey length (a proxy for energy value). However, in that population the compensating mechanism was effective and in contrast to the Isle of May, no negative effects on productivity or parental condition were apparent (Kadin et al., 2016). The Baltic study also considered the direct effects of elevated air temperature on parental attendance behaviour during chick rearing and found that parents spent less time together as temperature on the breeding ledge increased, and even temporarily abandoned their chicks at the highest temperatures (Olin et al., 2023). However, there was no evidence that reduced parental attendance, as a result of higher air temperatures, significantly increased the risk of failure during chick rearing. We did not record microclimate on the breeding ledges on the Isle of May so could not test for this effect but incorporating air temperature into future analyses would be informative.

In long-lived species, parents are predicted to optimise breeding effort not to jeopardise future survival and breeding prospects (Stearns, 1989). A previous study suggested this life history strategy was apparent in guillemots, such that breeding adults prioritise self-maintenance at the expense of the chick (Hentati-Sundberg et al., 2021). However, we found that increased parental effort was associated with an immediate negative effect on parental condition (reduced body mass during chick rearing) and downstream effects (lower survival over the following winter). In contrast to fledging success where the response operated via chick condition, the effect of increased parental effort on adult survival appeared to be direct rather than via adult condition as indicated by reduced parental body mass during the chick period. Auks notably common guillemots, have exceptionally high wing loading (wing area relative to body mass) and hence energy costs of flight are high (Elliott et al., 2013). Parents can therefore, potentially reduce the energetic cost of provisioning the brood by losing body mass, and thus reduced mass of chick-rearing guillemots can be viewed as an adaptive response to poorer feeding conditions during the breeding season, rather than the stress of breeding. This mechanism may explain the apparent lack of an indirect effect of parental effort on adult survival via body condition. Although the precise pathway underpinning the direct link between parental effort and survival remains unclear, the inability to prioritise self-maintenance may arise because of cross-seasonal correlations in environmental conditions, leading to positive relationships between breeding performance and subsequent survival probability. Overall, it seems likely that guillemots will increasingly experience poor conditions both at sea and at the colony, and further data are needed to elucidate the negative effects of these multiple stressors on adult survival.

4.2 | Effects of climate on diet, parental effort and demography

Frederiksen et al. (2013) previously found a negative effect of late winter SST on the breeding success of guillemots on the Isle of May and proposed a mechanistic link via a negative association of the copepod *Calanus finmarchicus*, a key prey item of sandeel (van Deurs et al., 2009), with SST. Here we extend these results to show that parental effort during chick rearing is strongly and negatively related to sSST (in both the current and previous year) with negative consequences not only for current breeding performance but also for subsequent adult survival. Furthermore, our findings that the contribution, body length and length-adjusted energy content of 1+ group sandeel in guillemot chick diet are negatively correlated with current and previous sSST provide support for a more direct link between this key prey species and predator demography.

Most studies of trophic interactions involving North Sea seabirds have focussed explicitly or implicitly on sandeel (Carroll et al., 2015; Frederiksen et al., 2006; Frederiksen, Wanless, et al., 2004); thus, a novel feature of our study was the consideration of climate effects on sprat that are now a major prey item in chick diet at many guillemot colonies in the North Sea (Anderson et al., 2014) and are also the dominant prey at colonies in the Baltic (Kadin et al., 2012). The contribution of sprat in chick diet was a mirror image of that of sandeel, such that sprat was more important when sSST was higher. Although sprat body length declined with increasing sSST, the relationship was not statistically significant, but length-adjusted energy content was negatively related to sSST in the previous year. The quality of sandeel was, therefore, poorest when there were two successive warm years affecting both body length and length-adjusted energy content, whereas the quality of sprat was poorest when the previous year was warm and driven mainly by reduced length-adjusted energy content. The recent dominance of sprat in guillemot chick diet on the Isle of May suggests that parental effort and demographic rates are currently mainly determined by conditions operating in the previous year. Our findings accord well with independent data on changes in sandeel and sprat abundance which indicate that declines in sandeel largely appear to be related to climate, particularly in the northwest North Sea (Lindegren et al., 2018; Régnier et al., 2017), while sprat abundance has increased since 2000, including the population associated with the Firth of Forth (Jennings et al., 2012; Lenoir et al., 2011). More generally, our analysis highlights how temperature constraints on marine ectotherms, such as forage fish, which are resulting in decreases in mean body size (Wright et al., 2020), are being propagated up the food chain to impact endothermic predators such as seabirds.

Negative effects of higher SST on breeding success, adult survival and/or chick diet have previously been demonstrated in other members of the North Sea seabird community: black-legged kittiwake *Rissa tridactyla* (Carroll et al., 2015; Frederiksen et al., 2013; Frederiksen, Wanless, et al., 2004), Atlantic puffin *Fratercula arctica* (Frederiksen et al., 2013) and European shag *Gulosus aristotelis* (Howells et al., 2017). Again, the mechanisms were thought to operate primarily via bottom-up effects acting on 1 group and 0 group sandeel, although in these cases primarily on abundance rather than quality (Frederiksen et al., 2006, 2013; Frederiksen, Wanless, et al., 2004). Because of their morphological and behavioural characteristics, guillemots are relatively insensitive to changes in sandeel availability (Furness & Tasker, 2000). However, their sensitivity is likely to increase as forage fish get smaller in length and calorific value declines in response to increased sea temperature. Although temperature-related effects of prey quality on guillemot performance were apparent across the four decades of the study, the year when length-adjusted energy content of sandeel and sprat was lowest (2004), was an outlier with values dramatically lower than those predicted from sSST in either the current or previous year in our study area (Figure 3e,f). By contrast, the other 4 years (2005–2008) when parental effort was particularly high and fledging success and adult survival were depressed, were associated with a succession of warmer years with no intervening cooler years, conditions that impacted the quality of both sandeel and sprat. This period also coincided with a higher incidence of gadids in the diet (Figure S6) which are even lower in calorific value than sandeel or sprat. Given that (1) temperatures in the North Sea are predicted to increase over the next 80 years (Tinker et al., 2015, 2016), (2) sprat are now a major component of guillemot chick diet at many colonies in the region (Anderson et al., 2014) and (3) cross-colony breeding abundance throughout the area varies in a consistent fashion (Cook et al., 2011), the climate-mediated demographic responses that we found may well apply over a much wider area.

4.3 | Wider implications

Our study exemplifies how top predators integrate climatic, environmental, and food-web variation to provide signals of changes in whole ecosystems that can in turn provide important insights for monitoring and management. In our analysis, we focussed on climate-mediated bottom-up effects, and in some ecotypes such as marine and polar ecosystems, it can be challenging to manipulate these processes through conservation measures. In such systems, management measures typically focus on top-down impacts such as harvesting, species control or habitat alteration. In the marine environment, fisheries are the dominant top-down pressure exerted by humans and can have an important impact on protected species, particularly in the Northern Hemisphere where the proliferation of industrial fisheries has increased direct competition with seabirds (Grémillet & Boulinier, 2009; Sydeman et al., 2017). Sydeman et al. (2021) concluded that the prognosis for sustained breeding productivity of Northern Hemisphere seabirds was poor unless the availability of their food resources could be improved and suggested that managing fisheries targeting forage fish, especially those operating near seabird colonies during the breeding season, should be a high priority. The North Sea is one of the most intensively fished regions in the world (Worm et al., 2009), and sandeels and sprats are both commercially important target species. Concerns about the effects of the sandeel fishery off the east coast of Britain on populations of marine predators (Monaghan, 1992), resulted in a moratorium on sandeel fishing in waters adjacent to seabird colonies, including the Isle of May, in 2000 which remains in place up to the present (2023). While the closure appeared to benefit some seabird species, notably improvements in black-legged kittiwake breeding success and survival (Frederiksen, Wanless, et al., 2004), it had no detectable effect on guillemot breeding success (Frederiksen et al., 2008; Searle et al., 2023) nor did it reverse the decline in importance of sandeel in guillemot chick diet (Wanless et al., 2018). During our study the local sprat stock gradually recovered after its collapse due to over-fishing in the 1970s and 1980s, and there is pressure for the fishery to reopen (Jennings et al., 2012). However, given the current reliance of guillemots on sprat during chick rearing, the apparent lack of suitable alternative prey and the previous history of over-fishing of this stock, re-opening the fishery would run counter to the precautionary recommendations of Sydeman et al. (2021) for increasing the resilience of seabird populations in the face of rapid environmental change and increasing human activities in coastal waters. Crucially, our results suggest that it is not appropriate to assume that breeding individuals can adjust their work rate to buffer against human-induced reduction in key prey resources. This buffering capacity will depend on the strength of human perturbation and sensitivity of the species in question and is also likely to vary over time, as seen in this study where there have been marked changes in predator diet over the last four decades.

Increasing pressures on ecosystems from multiple anthropogenic sources, for example, climate change, habitat loss, invasive species, harvesting, pollution and renewable developments are intensifying the need for comprehensive information about these systems, including knowledge of cascading impacts on non-target species (Casini et al., 2009; Henle et al., 2008; Macdonald et al., 2015; Niemelä et al., 2005; Őserblom et al., 2006; Pinnegar et al., 2000). The likelihood of identifying the impacts of climate change on top predators increases with study duration and varies among species, biological responses and geographic regions (Orgeret et al., 2021; Thackeray et al., 2010). However, long-term, data-rich studies such as the Isle of May guillemot study are rare, hindering our ability to assess species vulnerabilities at the breeding distribution scale. This is a serious issue for many top predators that are globally threatened, including seabirds (Dias et al., 2019; Paleczny et al., 2015). Therefore, there is an urgent need to either make better use of existing data or develop new methods of data collection. Our results suggest that parental effort based on a simple measure, such as offspring attendance, might be a sensitive index of the 'health' of a population in terms of both its productivity and adult survival. Compared with monitoring these demographic rates directly, collecting data on parental effort could, in many situations, be relatively straightforward and could lend itself to technological approaches such as the use of cameras. Therefore, monitoring parental efforts might provide a cost-effective way of increasing geographic coverage and thereby provide an early warning system identifying populations and regions at high risk from environmental change.

AUTHOR CONTRIBUTIONS

Conceptualisation: Sarah Wanless, Steve D. Albon, Michael P. Harris and Francis Daunt. Data acquisition: Michael P. Harris, Sarah Wanless, Mark A. Newell and Carrie Gunn. Methodology: Michael P. Harris, Steve D. Albon, Francis Daunt, Blanca Sarzo, John R. Speakman and Sarah Wanless. Investigation: Steve D. Albon, Francis Daunt, Blanca Sarzo and Sarah Wanless. Visualisation: Steve D. Albon and Francis Daunt. Writing—original draft: Sarah Wanless,

Steve D. Albon, Michael P. Harris and Francis Daunt. *All authors contributed critically to the drafts and gave final approval for publication.*

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no competing interests.

DATA AVAILABILITY STATEMENT

Data are available from the Environmental Information Data Centre https://doi.org/10.5285/f7676346-a67e-4fdf-9d30-e79ad2585195 (Wanless et al., 2023).

ORCID

Sarah Wanless https://orcid.org/0000-0002-2788-4606

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Annual variation in (a) counts of breeding pairs of common guillemots on the Isle of May, (b) spring (February–March) sea surface temperature.

Figure S2. Validation of our chick growth rate index (mean weight of chicks with wings ≥60 mm/mean age at fledging in days) by comparison with mean annual values of chick growth rate estimated as the increase in mass during the linear period of wing growth (g per mm for chicks with wing lengths of 25–59 mm) for 29 years (1982–2010). For the latter measure chicks (annual mean sample size = 230 chicks; range 38–478) were weighed once. The asymptotic relationship predicts chick growth = 12.98-(47.7*(0.289*EXP(chick growth rate (g/mm wing length)))).

Figure S3. Validation of our measure of parental effort as shown by plotting daily values of parental effort against the mean daily time (minutes) both parents were present at the breeding site with their chick during 32 all-day watches made in 22 years. The mean number of pairs followed during all-day watches was 28 (range 14–36). The rectangular hyperbola predicts parental effort = 0.915-(0.231/(1–0.1461*mean time both parents present)).

Figure S4. The exponential relationship between calorific value and fish length in sandeel (solid black circles) and sprat (open circles). The overall fitted curves, ignoring year differences, (sandeel: 0.9123*(EXP(0.0282*(length))); sprat: 0.8158*(EXP(0.0374*(length))).

Figure S5. Temporal changes between 1982 and 2019 in (a) mean adult mass during chick rearing (slope = −1.15 ±0.255SE g day^{-1}, $p < 0.001$); (b) mean chick fledging mass (slope = −1.06 ± 0.288SE g day^{-1}, $p < 0.001$); (c) mean age at fledging (slope = 0.065 ±0.0122SE day year^{-1}, $p < 0.001$); and (d) mean chick growth index (slope = −0.084 ±0.0164SE, $p < 0.001$).

Figure S6. Annual variation in the proportion (by number) of prey species in guillemot chick diet.

Figure S7. Plots of the relationships between detrended annual measures of (a) fledging success, (b) chick growth, and (c) parental effort. All pairs of relationships between residuals from the original temporal trends were significant ($p < 0.001$). Thus, over and above the decadal covariation, the annual variation about the temporal trends were generally highly correlated, suggesting similar annual driving forces, although it does not follow that the relationship is necessarily causal.

Figure S8. The logistic relationship between fledging success and parental effort distinguishing the years before 2004 (1984–86 and 1990–2003: filled triangles) and years 2004–2019 (open triangles). There is no significant difference in either the asymptotes ($F_{1,29} = 0.29$, $p = 0.59$) or slopes ($F_{1,28} = 0.28$, $p = 0.60$).

Figure S9. Plots of the detrended annual measures of adult survival on (a) detrended adult mass, and (b) detrended parental effort. In both cases relationships between residuals from the original temporal trends were significant ($p < 0.001$). However, there was no significant relationship between the residuals from adult mass and residuals from parental effort ($p > 0.25$). Thus, over and above the decadal covariation, the annual variation about the temporal trends were generally highly correlated, suggesting similar annual driving forces, although it does not follow that the relationship is necessarily causal.

Appendix S1. Fish energy determinations.

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