Circumpolar dynamics of a marine top-predator track ocean warming rates

Running head: Predator dynamics and ocean warming rates

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ABSTRACT

Global warming is a non-linear process and temperature may increase in a stepwise manner. Periods of abrupt warming can trigger persistent changes in the state of ecosystems, also called regime shifts. The responses of organisms to abrupt warming and associated regime shifts can be unlike responses to periods of slow or moderate change. Understanding of non-linearity in the biological responses to climate warming is needed to assess the consequences of ongoing climate change. Here we demonstrate that the population dynamics of a long-lived, wide-ranging marine predator are associated with changes in the rate of ocean warming. Data from 556 colonies of black-legged kittiwakes *Rissa tridactyla* distributed throughout its breeding range revealed that an abrupt warming of sea-surface temperature in the 1990s coincided with steep kittiwake population decline. Periods of moderate warming in sea temperatures did not seem to affect kittiwake dynamics. The rapid warming observed in the 1990s may have driven large-scale, circumpolar marine ecosystem shifts that strongly affected kittiwakes through bottom-up effects. Our study sheds light on the non-linear response of a circumpolar seabird to large-scale changes in oceanographic conditions and indicates that marine top predators may be more sensitive to the rate of ocean warming rather than to warming itself.

INTRODUCTION

Global warming is a non-linear process characterized by varying rates of temperature change (Franzke, 2014, Ji *et al.*, 2014). In the last five decades, ocean temperatures have increased in a stepwise manner with an intensification of warming during several periods (Lo & Hsu, 2010, Reid & Beaugrand, 2012). Responses of organisms may be different during periods of rapid warming than during periods of slow or moderate warming as rapid environmental warming could drive large-scale regime shifts, i.e. abrupt and persistent changes in the state of the environment (Grebmeier *et al.*, 2006, Doney *et al.*, 2012, Kortsch *et al.*, 2012, Rocha *et al.*, 2015). Hence, changes in the environment that organisms have to cope with may not be linearly related to changes in temperature and may be exacerbated in periods of rapid change. Understanding this non-linearity and associated variation in the rate of warming is therefore needed to assess biotic responses to ongoing climate change.

While considerable evidence indicates that climate warming affects free-living populations (e.g. Parmesan, 2006, Hoegh-Guldberg & Bruno, 2010, Jenouvrier, 2013, Descamps *et al.*, 2016, Scheffers *et al.*, 2016), these studies typically address a single population or group of individuals (e.g. a seabird colony). Results from single-site studies can contribute to a detailed understanding of local mechanisms linking climate changes to population dynamics, but may not apply to other locations. Indeed, as warming rates vary spatially (Belkin, 2009) and as wildlife responses to changing environmental conditions vary both in time and space (Jenouvrier, 2013, Lauria *et al.*, 2013) the response of a particular population cannot necessarily be extrapolated to others. Consequently, predicting how a broad-ranging species will respond to climate warming requires range-wide, spatio-temporal information, and thus for most species, remains an open question.

Here, we addressed non-linearity in the effects of rising ocean temperatures on a long-lived marine predator, the black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake). Using data from 556 breeding colonies distributed throughout the northern hemisphere, we assessed the relationships between rates of ocean warming and kittiwake population dynamics. More specifically, we tested the prediction that faster rates of warming were associated with faster rates of decline. Then, we quantified the proportion of declining colonies throughout the kittiwake breeding range and the synchrony in kittiwake colony size fluctuations. Assuming that periods of rapid warming were associated with stronger environmental forcing, we predicted a higher proportion of declining colonies, associated with a higher synchrony among kittiwake populations, in periods of rapid warming. Finally, we assessed the effect of ocean temperature *per se* (as opposed to ocean warming trends) on kittiwake population size and tested the prediction that this effect varied through time and was more pronounced in periods of rapid warming.

METHODS

Study organism

The kittiwake, the most numerous gull in the world (Coulson, 2011), has a circumpolar distribution and breeds throughout the arctic and boreal zones across much of the Northern Hemisphere (Coulson, 2011). The species is migratory and disperses after breeding from coastal areas to the open ocean where it spends the entire non-breeding season (McKnight *et al.*, 2011, Frederiksen *et al.*, 2012). Birds return to their breeding areas in spring and egg-laying usually begins between early May and mid-June. Peak hatching occurs in June-July depending on the colony and is usually later at higher latitudes (Burr *et al.*, 2016). Kittiwakes breed on coastal cliffs in single- or mixed-species colonies ranging in size from tens to tens of thousands of breeding pairs and forage in coastal and pelagic habitats up to several hundred kilometers from the colony (Irons, 1998, Goutte *et al.*, 2014, Paredes *et al.*, 2014). Their diet consists predominantly of fish and marine invertebrates located in the upper 1-2 m of the water column (Coulson, 2011).

Study sites and time-series

Data from 556 colonies were collected during 1975-2010, resulting in a total of 3909 colony size estimates (see *Supplementary Material 1* for details). Colony size time-series length varied from 1 to 34 years, with 274 colonies (49%) represented by ≥ 5 years of data. In some colonies, these data corresponded to the whole colony while in others, only a portion of the colony was counted annually. In such cases, counts were based on several plots spread throughout the colony to ensure that changes in the colony would be reflected in the plot counts. At each colony, counts were done every year at the same period making counts comparable among years. Field procedures to define plots and count active nests were similar at each colony and followed international guidelines for seabird monitoring (Walsh *et al.*, 1995). Monitored colonies were distributed throughout the Northern Hemisphere (between 46°N and 80°N) covering the species' entire breeding range (Fig. 1).

Environment predictor

We calculated the spring sea-surface temperature or SST (average of mean SST in May and June) in 2x2° latitude/longitude cells adjacent to each colony (Fig. 1). Such large areas should encompass most of the kittiwake foraging grounds in spring and summer (see Daunt *et al.*, 2002, Goutte *et al.*, 2014, Paredes *et al.*, 2014 for some examples of tracking studies describing the foraging range of kittiwakes in different parts of its breeding range). Data on reconstructed SST were obtained from the climate data library from the International Research Institute for Climate and Society http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.ERSST/.version3b/.sst/ (Xue *et* *al.*, 2003, Smith *et al.*, 2008). The area of these 2°x2º cells vary by latitude (up to a three-fold difference from 47 to 79ºN). As our results were not based on any latitudinal gradient, such latitudinal differences in areas did not affect our conclusions.

We focused on the spring SST as this environmental parameter is a good proxy of prey availability during the breeding or pre-breeding season and affects kittiwake reproduction, hence population size, through bottom-up effects (Murphy *et al.*, 1991, Moe *et al.*, 2009, Carroll *et al.*, 2015). Colder spring SST may indeed be associated with higher fish abundance in spring and summer, earlier kittiwake breeding and higher kittiwake productivity (Shultz *et al.*, 2009).

Statistical analyses

Our statistical analyses and the different approaches and models used are summarized in Table 1.

We first described, using additive models, the general shape of the sea surface temperature and kittiwake colony size as a function of the year. Then, we performed three complementary analyses (steps 2 to 4 in Table 1) to test our first prediction that the decline in kittiwake colony size was steeper when ocean warming was faster. As periods of rapid warming were not known prior to our analyses, we could not predict exactly when kittiwake responses should be more pronounced. Instead, we quantified the gradual changes in ocean warming and colony size through time using a sliding window approach (details below). The second analysis aimed at testing whether or not the observed changes in kittiwake trends through time were statistically significant. This analysis was a post-hoc test based on time periods identified by the previous sliding window method. The third analysis regarding our first prediction aimed at testing whether the apparent association between trends in ocean temperature and trends in kittiwake colony size was statistically significant.

To test our second prediction that the proportion of declining colonies were higher and the synchrony in colony size fluctuations stronger in periods of rapid ocean warming, we performed first sliding window analyses to describe the gradual changes in both the proportion of declining colonies and synchrony in colony size fluctuations through time (steps 5 and 6 in Table 1). These analyses were followed by a post-hoc comparison to determine whether the observed changes in the proportion of declining colonies and in the population synchrony varied significantly among different time periods.

Finally, to test our third prediction that the effect of ocean temperature *per se* (as opposed to ocean warming trends) on kittiwake population size varied through time and was more pronounced in periods of rapid warming, we performed a similar procedure based on a sliding window approach (step 7 in Table 1) followed by a post-hoc test. The latter aimed at testing whether or not the observed changes in the SST effect through time were statistically significant (step 8 in Table 1).

In all subsequent analyses, colony count data were ln-transformed and both colony count and SST data were centered on their mean (within-colony centering). Analyses were performed in R 3.1.1 (R Development Core Team, 2014). Linear and additive models were based on a Gaussian error distribution. For all models, the distribution of residuals (residuals plotted as a function of predicted values) indicated no violation of the normality or homoscedasticity assumptions.

Temporal dynamics of sea-surface temperature and kittiwake colony size.

We first described the trajectories of spring SST and kittiwake population size using additive mixed models. We built models with the colony counts and spring SST (separately) as the response variables and the year as the smoothing term. Colony identity was included in these models as a random factor to take into account the non-independence in the data (Bolker *et al.*, 2009, Regular *et al.*, 2010, Descamps *et al.*, 2013). We used the functions *gamm* (*mgcv* package, Wood, 2006) in R 3.1.1 (R Development Core Team, 2014) with the default setting of the *gamm* function to fit penalized regression splines. To assess how well the *gamm* fitted the yearly variation, we estimated yearly values by fitting a model (with the *lmer* function in package *lme4*, Bates *et al.*, 2015) with year as a fixed categorical factor and colony as a random factor.

Then, to quantify the temporal changes in kittiwake and spring SST trends, we used a sliding window approach to estimate the (linear) trend of the kittiwake population(s) or spring SST over 10-year periods from 1981 to 2010 (see Jenouvrier *et al.*, 2005 for an other application of such sliding window approach). We ran consecutive models with colony size and spring SST as the response variable and year as the predictor for periods 1975-1984, 1976-1985, …, until 2001-2010, and considered the trend (i.e. slope of the year effect) for every decadal interval. The 10-year window was chosen to ensure that each period would have enough data to allow model convergence but also be short enough to assume trends in SST or colony size to be linear within each period. Using a shorter time-window (e.g. 5 years) led to similar results and conclusions (results not shown). Models were run using the function *lmer* in *lme4* package (Bates *et al.,* 2015). To estimate the uncertainty (95% confidence interval) around the trends, we used a bootstrapping approach (detailed in *Supplementary Material 2*). Then, to test that the trends in kittiwake colony size varied significantly through time, we performed a post-hoc test based on periods identified by the previous sliding window. We considered three different time periods (1975-1990, 1991-2000 and 2001-2010) and tested for an interaction between the linear trend and this time period variable on kittiwake colony size. We performed linear mixed models with colony identity defined as random factor using the function *lmer* in *package lme4* (Bates *et al.*, 2015) We compared different models with and without the interaction using the Akaike's Information Criterion to determine which processes best explained changes in kittiwake populations (Burnham & Anderson, 2002).

Using such a sliding window approach, trend estimates were not independent as each trend was based on data also used to calculate the nine previous ones. Even if such dependency does not affect the value of the trend estimates, it could affect the outcome of statistical analyses testing for an association between trends in kittiwake colony size and trends in spring SST. To deal with this dependency and test for such association, we built a generalized least square (*gls*) model with trend in colony size as the response, trends in spring SST as the predictor, and with a moving average correlation structure. The order of the moving average process was determined with the *auto-arima* function of the *forecast* package (Hyndman & Khandakar, 2008). This order was then used to build the *gls* model with an appropriate correlation structure using the *gls* function of package *nlme* (Pinheiro et al., 2016). Auto-correlation of residuals were not significantly different from zero indicating no issue of dependency among residuals (*Supplementary Material 3*).

Synchrony among colonies

We quantified the synchrony of SST and kittiwake population fluctuations by using cross-correlation functions with annual spring SST and then annual kittiwake colony size data. We calculated the mean cross-correlation and associated bootstrap confidence intervals using the *mSynch* function (*ncf* package), as described in Bjørnstad *et al.* (1999). The cross-correlations represent the region-wide synchrony for all kittiwake colonies (or for all areas where spring SST has been extracted from). Again, we applied a 10-year sliding window approach explained above to describe the temporal changes in synchrony during 1975-2010. We then performed a post-hoc comparison based on time periods identified in the previous step. We compared the synchrony in colony size (and its 95% associated confidence interval) in three independent periods 1975-1990, 1991-2000 and 2001-2010.

Changes in the number of declining colonies

We calculated the proportion of declining colonies among our sample of 556 kittiwake colonies and assessed the changes in this proportion through time using the same 10-year sliding window approach. For each time window, we calculated the trend in the size of every colony using linear models (function *lm* applied to each colony time-series). Then, we calculated the proportion of declining colonies (i.e. colonies characterized by a negative slope over the 10-year period considered). To calculate the trend within each period, we included colonies counted more than once in the period considered. Standard errors around each proportion p were calculated as $\sqrt{\frac{p\times(1-p)}{n}}$ where n equals the number of colonies counted more than once in the 10-year time window considered. We then performed a post-hoc comparison based on time periods identified in the previous step. We compared the proportion of declining colonies (and its 95% associated confidence interval) in three independent periods 1975-1990, 1991-2000 and 2001-2010.

Temporal changes of spring SST effects on kittiwake colony size

Finally, we used the same 10-year sliding window approach to assess the temporal changes in spring SST effects on kittiwake colony size with the prediction that spring SST should have a more pronounced effect in periods of rapid warming. For each 10-year window, we calculated the slope of the linear regression with colony size as the response variable and spring SST as the predictor. We also included the colony identity as a random factor to take into account the non-independence among count data.

Next, to test statistically that the spring SST effect on kittiwake colony size varied through time, we performed a post-hoc test based on the results from the sliding window approach that identified periods where the spring SST seemed to vary. We considered three different time periods (1975-1990, 1991-2000 and 2001-2010) and tested for an interaction between the spring SST and this time period variable on kittiwake colony size. We performed linear mixed models with colony identity defined as random factor using the function *lmer* in *package lme4* (Bates *et al.*, 2015). We compared different models with and without the interaction using the Akaike's Information Criterion to determine which processes best explained changes in kittiwake populations (Burnham & Anderson, 2002).

RESULTS

Temporal dynamics and synchrony of sea-surface temperature and kittiwake colony size

After a short period of population increase, kittiwakes declined from the early/mid-1990s onwards (Fig. 1). This decline paralleled a rapid warming of the sea adjacent to the breeding colonies (Fig. 1). The dynamics of kittiwake colonies were non-linear throughout our study period and declines alternated with periods of relative stability or even increase (Fig. 2). The average trend was mostly constant until the end of the 1980s (constant and positive in period 1975-1980, and then constant but negative in 1981-1990), and declines started to accelerate in the early 1990s (Fig. 2). This acceleration continued until the late 1990s when the decline slowed (i.e. trends remained negative but less so until the 2000s; Fig. 2). These changes in the rate of decline were significant (i.e. a model including an interaction between the trend and the time period was preferred over a model with constant rate of decline; Table 2). Decline was faster in 1991-2000 than in 1975-1990 and 2001-2010 (rate of decline in 1975-1990, 1991-2000 and 2001-2010 respectively: -0.004±0.007 SE, -0.06±0.01 SE and -0.02±0.01 SE).

Kittiwake population trends tracked changes in spring sea-surface temperature (SST) around the colonies whose warming accelerated from the early to late 1990s then slowed (Fig. 2; correlation between average trends in spring SST and average trends in colony size: r=-0.80). This association was statistically significant (t=-3.56, p=0.002 from a *gls* model with a residual correlation structure defined as a moving average process of order 2).

Moreover, the faster kittiwake decline in the 1990s was associated with an increase in population synchrony (Fig. 3). This increase in synchrony in the 1990s was also apparent in spring SST fluctuations (Fig. 3). Synchrony in period 1991-2000 (mean synchrony: 0.13, 95% confidence interval: 0.074-0.21) was higher than in 1975-1990 (mean synchrony: 0.052, 95% confidence interval: 0.015-0.98) and 2001-2010 (mean synchrony: 0.034, 95% confidence interval: -0.001-0.077) but confidence intervals overlapped slightly between periods 1975-1990 and 1991-2000.

Changes in the proportion of declining kittiwake colonies were concordant with observed changes in population trends and synchrony. Indeed, the number of declining colonies peaked in the late 1990s when more than 70% of all monitored colonies were declining (Fig. 4-top panel). The proportion of declining colonies was higher in period 1991-2000 (average : 66%, 95% CI: 60-73%) than in 1975-1990 (average : 44%, 95% CI: 38-50%) and 2001-2010 (average : 58%, 95% CI: 52-64%) but confidence intervals overlapped between periods 1991-2000 and 2001-2010.

Temporal changes in the spring SST effects on kittiwake colony size

Previous results indicated that kittiwake decline was more pronounced when spring SST was rapidly warming. Outside the periods of rapid ocean warming, the association between ocean warming and kittiwake dynamics was weaker (Figs. 2 and 4). This suggests that spring SST had different effects on kittiwake colony size depending on the period considered (i.e. period of rapid vs. slow warming). The temporal changes in the slope of the spring SST effect on colony size confirmed the non-linear relationship between spring SST and kittiwake colony size (Fig. 4, bottom panel). A model with a variable SST effect depending on the period considered was preferred (i.e. lower AIC and higher pseudo-r^2) over a model with a constant SST effect (Table 3). Indeed, the slope of the spring SST effect on colony size was not significantly different from zero during 1975-1990 (-0.16 ± 0.08 SE) when warming was moderate but was significantly different from zero afterwards when warming was faster. The slope of the spring SST effect was the highest in 1991-2000 (-0.30 ± 0.08 SE), which was the period of fastest warming, but was similar to the slope in 2001-2010 (-0.26 ± 0.08 SE; Table 3).

DISCUSSION

Temporal changes in the dynamics of kittiwake populations and sea-surface temperature. Kittiwake populations declined rapidly in the 1990s throughout most of the species' breeding range, corroborating results of previous studies at local scales (Frederiksen *et al.*, 2004, Labansen *et al.*, 2010, Sandvik *et al.*, 2014). Changes in kittiwake population trends tracked changes in trends of spring SST around the colonies and when the ocean warming was faster, the decline in kittiwake colony size was steeper. In a period of fast warming and rapid kittiwake decline, synchrony in the fluctuations of ocean warming and synchrony in the fluctuations of kittiwake colony size were higher. The increased synchrony observed in the 1990s was likely the consequence of a more similar trend in ocean warming and in kittiwake decline throughout our study area (i.e. the kittiwake breeding range). In other words, this was the consequence of a generalized ocean warming throughout the species' breeding range associated with a higher proportion of declining colonies compared to other periods. These patterns in ocean warming and kittiwake decline were observed throughout the Northern Hemisphere and were not driven by a specific region or ocean basin. On the contrary, results from each region, the Pacific, West Atlantic, East Atlantic, and the Arctic showed a similar pattern and kittiwake decline was steeper from the early/mid-1990s and beyond when ocean warming was faster in these different regions (*Supplementary Material 4*). These results support the hypothesis of a strong and large-scale (circumpolar) environmental forcing during the 1990s that affected kittiwake population dynamics throughout its breeding range.

Rapid ocean warming associated with large-scale regime shifts

The large-scale changes in kittiwake dynamics and SST observed in the early 1990s fit the occurrence of marine pelagic regime shifts (i.e. persistent reorganizations of the structure and function of marine ecosystems) in the Northern Hemisphere (Beaugrand *et al.*, 2015). Indeed, there is evidence for quasi-synchronicity of marine pelagic regime shifts in the late 1980s both within and between ocean basins including the North Atlantic, North Pacific and North Sea (Beaugrand *et al.*, 2015). These regime shifts have been generally inferred from changes in plankton assemblages (Beaugrand *et al.*, 2015). Large-scale changes in plankton communities could explain the changes in the kittiwake population dynamics through changes in the availability of specific plankton species (such as the copepod *Calanus finmarchicus* in the Atlantic, Planque & Batten, 2000) that are important prey for small pelagic fish favored by seabirds like kittiwakes (Frederiksen *et al.*, 2013, Buren *et al.*, 2014). These shifts in plankton assemblages also coincided with reported shifts in some fish stocks, like capelin (*Mallotus villosus)* and Atlantic cod (*Gadus morhua)* off the Newfoundland and Labrador Shelf around 1990 (Buren *et al.*, 2014). Such declines in fish stocks could have affected kittiwakes directly through reduced food availability but also indirectly through increased predation by larger gulls (Regehr & Montevecchi, 1997, Massaro *et al.*, 2000). The drivers of these regime shifts and of their quasi-synchrony in the late 1980s/early 1990s are still uncertain (Beaugrand *et al.*, 2015), but the abrupt warming seen in the Northern Hemisphere climate (Lo & Hsu, 2010) combined with a strongly positive phase of the Arctic Oscillation stand as robust potential candidates (Beaugrand *et al.*, 2015).

This large scale shift in the marine environment and associated changes in kittiwake prey availability could have affected kittiwake population trajectories through several, non-mutually exclusive, demographic mechanisms (e.g. through an effect on reproductive and/or survival parameters). Our study emphasized the potential effect of changes in spring SST close to the breeding grounds, but changes in other periods of kittiwake annual cycle may also have played a significant role (e.g., Reiertsen *et al.*, 2014). Spring SST is associated with prey availability in the pre-breeding and breeding periods (e.g. Shultz *et al.*, 2009) which could affect kittiwake breeding propensity and/or breeding success. The population growth rate of long-lived species such as the kittiwake is generally more sensitive to changes in adult survival than to changes in reproductive parameters (Sæther & Bakke, 2000), but substantial changes in reproductive parameters can also drive population growth rate, even in long-lived species (Gaillard *et al.*, 2000). Our study does not allow us to address the respective roles of reproductive versus survival parameters as drivers of kittiwake population dynamics, and further detailed demographic studies would be needed.

Can industrial fisheries explain kittiwake population dynamics?

An alternative hypothesis to explain the rapid large-scale changes in kittiwake colony size in the 1990s could be that human fisheries led to a depletion in stocks of forage fish (i.e. stocks of small pelagic fish that represent the main prey for kittiwakes). This depletion could have occurred in the foraging areas used by kittiwakes during the pre-breeding or breeding seasons and then affected their reproduction. It could also have occurred in their winter foraging grounds and thus affected, for example, their over-winter survival with carry-over effects into the breeding season (e.g., Sedinger *et al.*, 2011, Crossin *et al.*, 2012). In the North East Atlantic, intense sandeel (*Ammodytes spp.*) fisheries in the 1990s were related to low kittiwake breeding success (Frederiksen *et al.*, 2004). In the East Atlantic, fisheries and potential associated depletion of kittiwake prey could thus explain part of the observed decline in some kittiwake colonies. However, even if fisheries have played a role locally in affecting some kittiwake populations in the East Atlantic, fisheries for forage fish were very limited in Alaska and Greenland, and in Canada were over-ridden by a bottom-up population collapse (Buren *et al.*, 2014, Fisheries and Oceans Canada, 2015). Fisheries were therefore negligible in waters used by most kittiwakes for foraging during both the breeding and non-breeding seasons (see Frederiksen *et al.*, 2012 for a description of the winter distribution of kittiwakes breeding throughout the Atlantic range). Consequently, as the acceleration in kittiwake decline was also observed in these regions (*Supplementary Material 4*), industrial fisheries appeared unlikely to be the main driver behind the circumpolar changes we observed in kittiwake dynamics.

What matters: a warmer sea or a rapidly warming sea?

When ocean warming was faster, kittiwake populations declined more rapidly. This coherent fingerprint of the ocean warming rate on kittiwake dynamics across its entire breeding range suggests that what matters in terms of top predator responses to environmental changes is not the changes *per se* but the speed of these changes (see also Irons *et al.*, 2008, Pinsky *et al.*, 2013 for coherent findings).

Kittiwake life history and population dynamics may be impacted to a much smaller degree by slow changes in sea temperatures. This would explain the temporally variable relationships between SST and kittiwake colony size as well as the apparent contradiction between some previously reported SST effects on kittiwake life history. For instance, there is evidence of positive effects of increasing SST on Atlantic seabird reproduction including the kittiwake (Sandvik *et al.*, 2008, Moe *et al.*, 2009) but also of negative effects on kittiwake reproduction (Frederiksen *et al.*, 2007) and on kittiwake population growth rate (Sandvik *et al.*, 2014).

Changes in the rate of warming (but not the warming itself) could be the key parameter to consider when assessing wildlife response to climate change. In our case, a warmer sea did not have necessarily negative consequences for kittiwake abundance whereas a sea warming rapidly did. Abrupt changes in SST can be associated with ocean-scale regime shifts that disrupt underlying food webs with cascading consequences for apex predators (Buren *et al.*, 2014). This does not mean that the magnitude of the changes in sea temperature is never an important factor to consider. Large, but slow, changes may in theory lead to abrupt community shifts. This depends ultimately on the thermal niche of the species and on where in this niche the species lies (Beaugrand 2015). Rapid changes in ocean temperatures have often been assumed to be at the origin of regime shifts in pelagic ecosystems, but the exact mechanisms by which changes in the environment trigger abrupt community shifts are still not fully understood (Beaugrand 2015).

Whatever the environmental changes triggering regime shifts, such abrupt changes in the environment may have led to a lower availability of forage fish (i.e. kittiwake main prey) which then affected kittiwake populations. These fish species may have been unable to adapt (through micro-evolution or phenotypic plasticity) to rapidly changing conditions, leading to a lower prey availability for kittiwakes. Alternatively, these prey species may have been replaced by other fish species that kittiwakes were unable to forage efficiently upon.

After some years, these altered food webs may potentially reach another equilibrium that apex predators and/or forage fish eventually adapt to through flexible foraging and dietary plasticity (e.g. Pettex *et al.*, 2012). Such behavioral adaptation could however vary regionally depending on the food web structure and changes (Lauria *et al.*, 2013). Local variation in kittiwake behavior combined with small spatial scale variations in food web responses to rapid ocean warming could explain our observations of colonies that were increasing while the overall kittiwake population was generally declining at a larger scale (Fig. 4). Despite such variation at small spatial scales, the acceleration in ocean warming during the 1990s was associated with a coherent acceleration in kittiwake population decline throughout its entire range. Our findings emphasize the importance of investigating, in more detail, why marine food webs are so vulnerable to abrupt changes in ocean temperature, and how this can best be accounted for in the future management of species at high trophic levels.

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Supporting information

Supplementary Material 1. Detailed information on the black-legged kittiwake colonies included in the study and colony count data.

Supplementary Material 2. Bootstrap procedure to estimate confidence intervals around trends in spring SST and kittiwake colony size.

Supplementary Material 3. Auto-correlation of residuals from the gls model.

Supplementary Material 4. Regional variation in the temporal trends in spring SST and black-legged kittiwake colony size.

Table 1. Summary of the different models and analytical steps. Steps 1 to 6 aimed to describe the dynamics and synchrony of both the spring SST (spring sea surface temperature around the colonies) and kittiwake colony size in period 1975-2010 and focused on how these dynamics changed through time. Steps 7 and 8 focused on the varying effect (in terms of magnitude and sign) of the spring SST on kittiwake colony size. Count data were ln-transformed and both count and SST data were centered on their mean (within-colony centering). All analyses assumed a Gaussian distribution of errors.

Step	Approach	Data used	Response variable(s)	Explanatory variables	Objective
1	Mixed additive models	Annual data at the colony level	Spring SST Colony size	Year	General description of the spring SST or colony size trajectories
2	Mixed linear models / sliding window	Annual data at the colony level	Spring SST Colony size	Year	Assess gradual temporal changes in the trends in spring SST or colony size
3	Mixed linear models	Annual data at the colony level	Colony size	Linear trend and its interaction with a three modality variable corresponding to three different time-periods	Post-hoc test to confirm that the trend in kittiwake colony size differed between the periods considered.
4	GLS model	10-year trend estimates	Colony size	Spring SST	Test of the association between changes in SST trends and in colony size trends

5	Cross-correlations / sliding window	Annual data at the colony level	Spring SST Colony size		Assess temporal changes of synchrony in spring SST and synchrony in colony size
6	Linear models / sliding window	Annual data (each colony analyzed separately first)	Colony size	Year	Assess gradual temporal changes in the proportion of declining colonies
7	Mixed linear models / sliding window	Annual data at the colony level	Colony size	Spring SST	Assess gradual temporal changes in magnitude and size of the spring SST effect on colony size
8	Mixed linear models	Annual data at the colony level	Colony size	Spring SST and its interaction with a three modality variable corresponding to three different time-periods	Post-hoc test to confirm that the spring SST effect on kittiwake colony size differed between the periods considered.

Table 2. Linear trend of kittiwake colony size. Results are from linear mixed models with the colony identity included as a random factor. The response variable was the annual colony size. We considered two different explanatory variables (a linear trend and the time period) and their interaction. The time period variable had three modalities corresponding to years 1975-1990, 1991-2000 and 2001-2010. "np" refers to the number of parameters, "AIC" to the Akaike's Information Criterion, ΔAIC to the difference in AIC between the model of lowest AIC and the model considered and "Pseudo-r^2" is the squared-correlation between the annual average colony size estimates from a given model and the observed average annual colony sizes.

Model	Deviance	np	AIC	ΔAIC	Pseudo-r^2
Intercept only	11754.26	3	11760.26	437.32	
Trend	11350.27	4	11358.27	35.33	0.41
Trend x Time period	11306.94	8	11322.94	0.00	0.56

Table 3. Effect of the spring sea surface temperature (SST) on kittiwake colony size. Results are from linear mixed models with the colony identity included as a random factor. The response variable was the annual colony size. We considered two different explanatory variables (the spring SST and the time period) and their interaction. The time period variable had three modalities corresponding to years 1975-1990, 1991-2000 and 2001-2010. "np" refers to the number of parameters, "AIC" to the Akaike's Information Criterion, ΔAIC to the difference in AIC between the model of lowest AIC and the model considered and "Pseudo-$r^2$is the squared-correlation between the annual average colony size estimates from a given model and the observed average annual colony sizes.

Model	Deviance	np	AIC	ΔAIC	Pseudo-r^2
Intercept only	11666.76	3	11672.76	463.33	
Spring SST	11459.39	4	11467.39	257.33	0.35
Spring SST x Time period	11193.43	8	11209.43	0.00	0.51

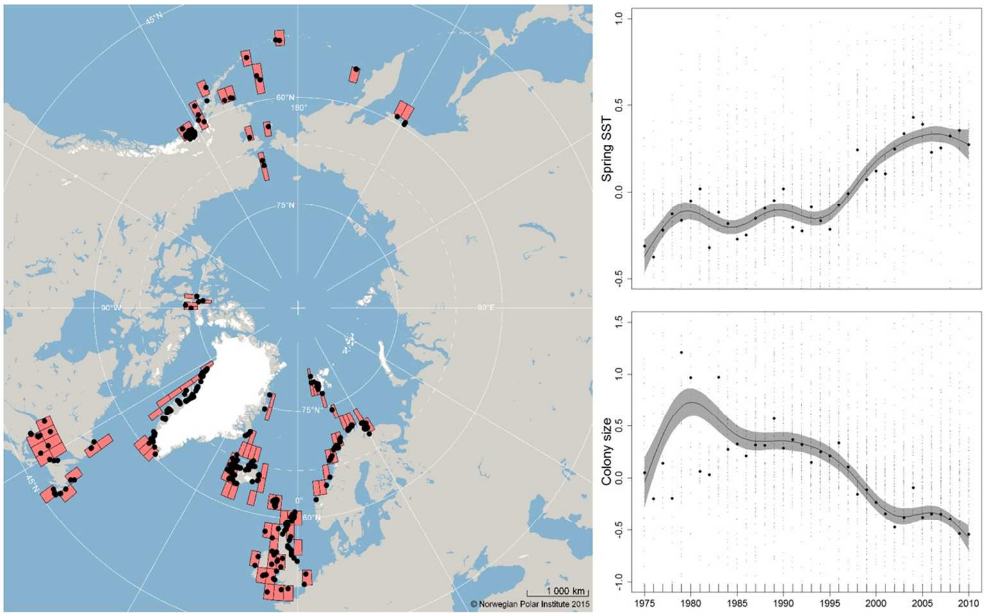
Figure legends

Figure 1. Breeding colony distribution and population trends of black-legged kittiwakes. The left panel shows the location of kittiwake colonies included in our study (black dots) and of the 2x2° grids where spring sea surface temperatures (SST) were extracted (rectangles). The right panels represent the SST (top) and ln-transformed colony counts (bottom), and their associated long-term trends (±95% CI) from additive models (values centered on the mean). Points represent the yearly values from models with year as a fixed categorical factor and colony as random factor.

Figure 2. Temporal changes in spring sea-surface temperature and black-legged kittiwake population dynamics. The panels show the trends in spring SST at colony sites (top) and in kittiwake colony size (bottom). Each point represents the average (± 95% CI) trend in the parameter considered over a 10-year period centered on its x-coordinate (i.e. the first point represents the average trend for period 1975-1984, the second one for 1976-1985, etc.; details in Methods). The shaded area is for illustrative purpose only to stress the period of greatest changes.

Figure 3. Temporal changes in the synchrony in spring sea-surface temperature and black-legged kittiwake populations. The panels show the synchrony in spring SST at colony sites (top) and the synchrony in kittiwake colony size (bottom). Each point represents the average (±95% CI) synchrony in the parameter considered for a 10-year period centered on its x-coordinate (i.e. the first point represents the average synchrony for period 1975-1984, the second for 1976-1985, etc.; details in Methods). The shaded area is for illustrative purpose only to stress the period of greatest changes.

Figure 4. Proportion of declining colonies of black-legged kittiwakes (top panel) and effects of SST on kittiwake colony size (bottom panel). Symbols in the top panel represent the proportion (±SE) of kittiwake colonies that were declining (i.e. negative slope) during a 10-year period centered on its x-coordinate (i.e. the first point represents the % for period 1975-1984, the second one for 1976-1985, etc.; details in Methods). Symbols in the bottom panel represent the average (±95% CI) slope of the spring SST effect on ln-transformed colony counts for the 10-year period considered (centered on the x-coordinate). The shaded area is for illustrative purpose only to stress the period of greatest changes.



Breeding colony distribution and population trends of black-legged kittiwakes.

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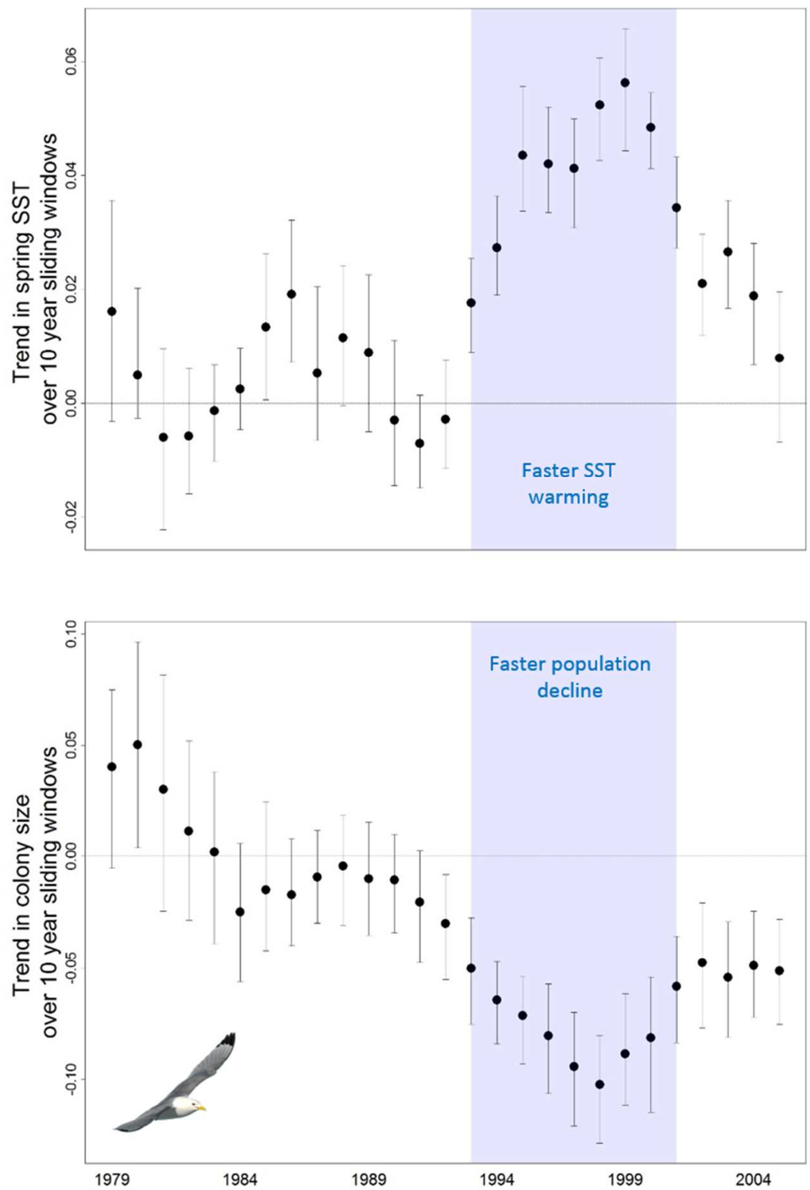

Temporal changes in spring sea-surface temperature and black-legged kittiwake population dynamics.

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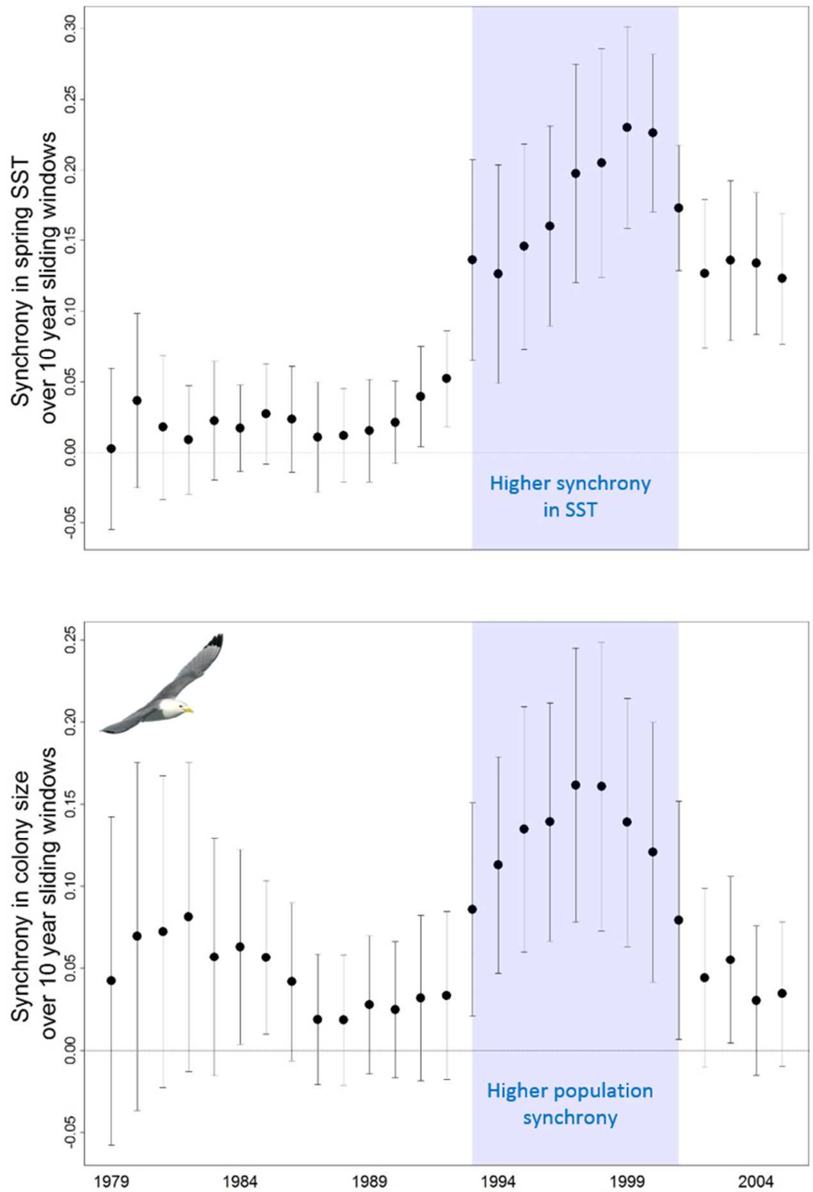

Temporal changes in the synchrony in spring sea-surface temperature and black-legged kittiwake populations.

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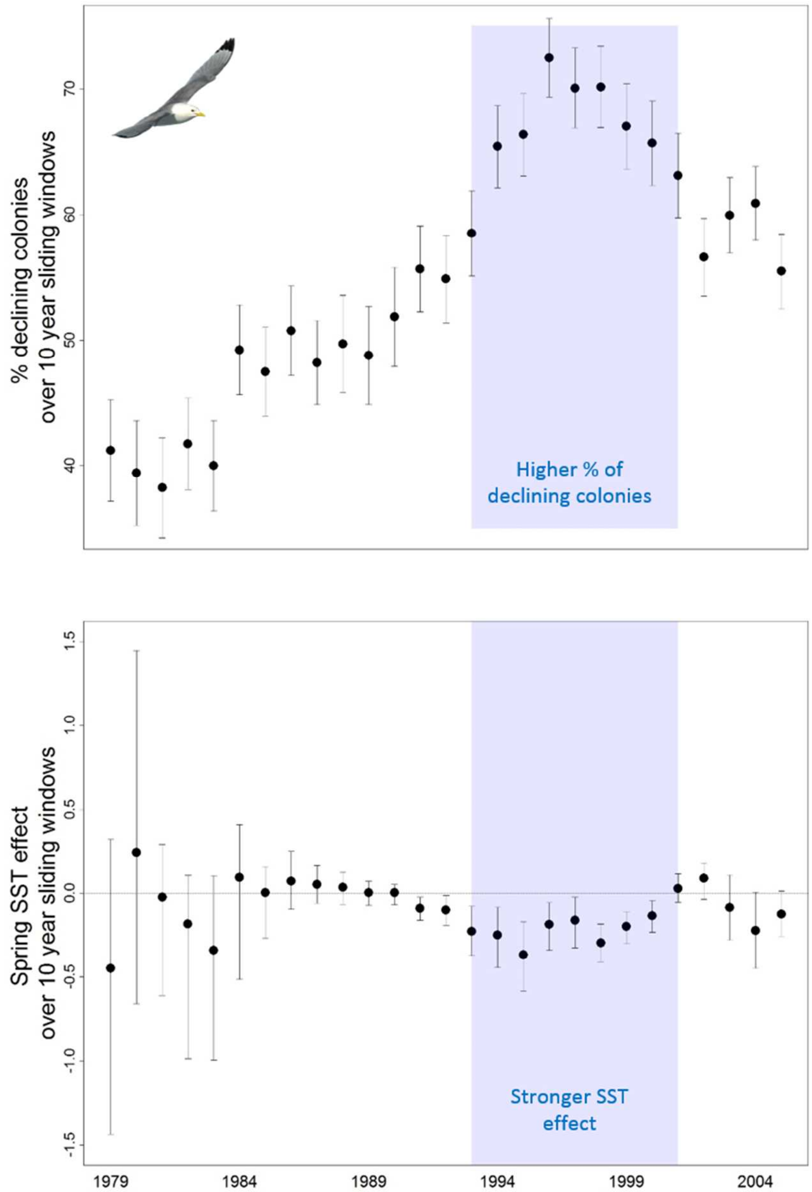

Proportion of declining colonies of black-legged kittiwakes (top panel) and effects of SST on kittiwake colony size (bottom panel).

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