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Seabirds and climate: knowledge, pitfalls, and opportunities

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As a physical driver of ecosystem functioning, it is not surprising that climate influences seabird demography and population dynamics, generally by affecting food availability. However, if we zoom in ecologically, seabirds are in fact very heterogeneous, ranging in size from very small to very large species (with a difference of more than two orders of magnitude in body weight), from planktivorous forms to predators of large fish and squid, from benthic to pelagic, from species with small foraging ranges to species feeding throughout the whole circumpolar region, and from resident species (at a spatial mesoscale) to trans-equatorial migrating seabirds that travel large distances across several oceanographic systems. Due to this high variability and the difficulty in obtaining direct reliable estimates of long-term food availability, global climatic indices have been extensively used in studying seabird demography and population dynamics. However, the use made by researchers of these indices has certain conceptual and methodological pitfalls, which I shall address in this review. Other factors, such as anthropogenic impacts (including oil-spills and interaction with fisheries), may further alter or confound the association between climate and seabird demography. These pitfalls and environmental noise, together with the inability to incorporate resilience, may bias our predictions regarding the future impact of global warming on seabirds, many of which have vulnerable populations.

Keywords: predictive models, resilience, methodological bias, evolution, global change, climate, seabirds

HISTORICAL BACKGROUND

A search performed in June 2014 using the words "climate & seabird" in the ISI Web of Science resulted in 946 items. Even though some of those items dealt with other marine organisms or were focused on some related issues (such as oceanographic processes), that result represents a large number of scientific contributions on the topic of how climate may influence seabird ecology. The influence of climate on marine organisms has been extensively studied in seabirds because, compared to most other species (except some marine mammals such as seals and sea-lions), their demography and population dynamics can be easily monitored in breeding colonies.

Up to the 90s, the changes in demographic parameters and population size in seabirds were explored mostly in relation to intrinsic features of the colonies such as their size or the presence of predators (Hunt et al., 1986). The effects of climate (mostly in the form of oceanographic indices) on seabird ecology were seldom analyzed in those years (Myres, 1979), and research efforts were addressed mostly to determining the distribution of seabirds at sea (Abrams, 1985). The influence of oceanographic features was outlined especially when extreme and anomalous events occurred (such as cyclones or El Niño-Southern Oscillation (ENSO) years (e.g., Blomqvist and Peterz, 1984; Graybill and Hodder, 1985), whereas some pioneering studies dealt with the relationship between climatic events and seabird mortalities (La Cock, 1986). In the 90s some papers started to highlight the potential impact of climate warming on seabirds (Burger, 1990; Brown, 1991; Duffy, 1993) and the role played by climate on bottom-up control mechanisms, food availability and its effects on seabird population dynamics (Crawford, 1991; Ainley et al., 1994). Nevertheless, it was not until the end of the 90s that the literature on climate and seabirds exponentially increased (Montevecchi and Myers, 1997; Guinet et al., 1998; Lyver et al., 1999) (see **Figure 1**) and that the first paper relating climate and adult survival of a seabird appeared using reliable and robust quantitative methods (Barbraud et al., 2000). That exponential phase was likely the result of the increasing interest of the scientific community about climate change in the ecological literature during those years, together with the appearance of new statistical tools and the improvement of computational power (**Figure 1**) (Green et al., 2005).

Given that previous papers have recently reviewed thoroughly the state-of-the-art knowledge on seabirds and climate (Schreiber, 2002; Barbraud et al., 2012; Sydeman et al., 2012; Jenouvrier, 2013; Quillfeldt and Masello, 2013), here I shall concentrate on more conceptual issues, knowledge gaps and pitfalls typical of the studies dealing with how climate influences the ecology of seabirds.

CLIMATE AND ITS INFLUENCE ON SEABIRDS

It is no surprise that bottom-up control in marine ecosystems exerted by oceanographic drivers, which is mostly controlled by

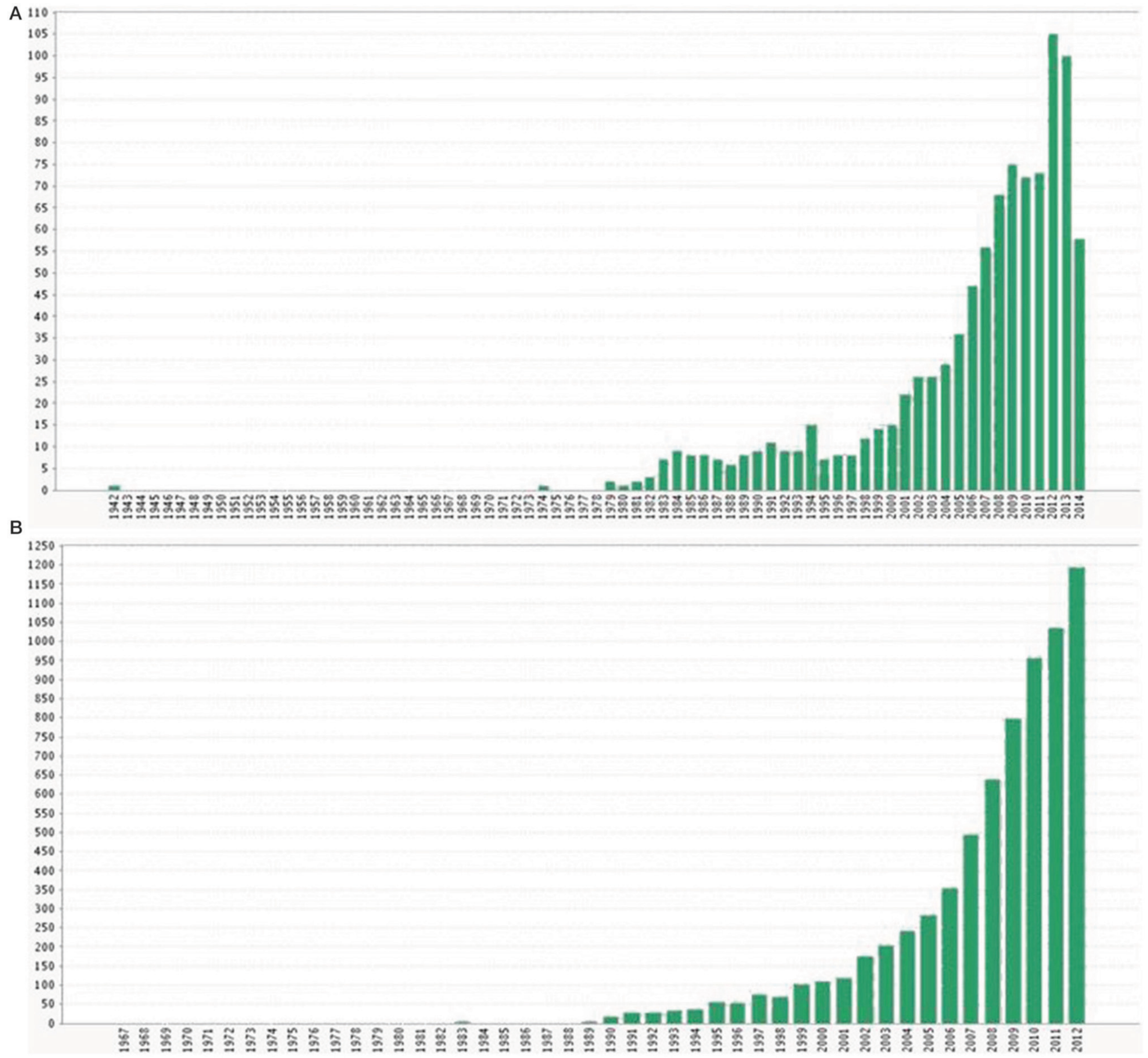

FIGURE 1 | Number of publications (including papers, reports, books, meetings and any scientific document available) using the ISI web of knowledge about a) climate and seabirds since 1942 to 2014 and (B) climate change and ecological studies since 1967 to 2012. Note that the 2014 value in panel **(A)** may represent half of the publications because the search was performed in June.

climate variables (e.g., wind, temperatures, air pressure) influence the ecology of marine top-predators such as seabirds. As it should be expected, seabirds respond to the variability in climate change and warming (e.g., Schreiber, 2002; Jenouvrier, 2013), and responses occur at both proximal (ecological) and ultimate (evolutionary) levels (Parmesan, 2006; Weimerskirch et al., 2012). The scientific literature has been sensitive to the warning message involving climate warming and papers dealing with seabirds have not been an exception (Votier et al., 2008a). Massive breeding failures following climate perturbations have attracted the attention of researchers, and records on El Niño events and its ecological consequences are a good example (e.g., Glantz, 2001; Velarde et al., 2004; Devney et al., 2009). In general, the literature shows that climate variability influences most ecological parameters analyzed, including range shifts (in breeding but mostly in foraging areas) and changes in both phenology and demographic parameters (including survival, dispersal, recruitment and breeding propensity). Back in the 80s, some papers already recorded events of adult seabird mortality overlapping with extreme climate years (La Cock, 1986). But more unexpected has been the range of papers that have found linear relationships between adult survival and climate variables, because adult survival should be a highly conservative parameter due to evolutionary canalization, typical of long-lived organisms including seabirds (Stearns et al., 1995; Gaillard and Yoccoz, 2004). One possible reason is that more powerful statistical tools, such as capture-recapture models, have allowed researchers to take advantage of the large number of long-term data bases collected in the last 40–50 years on seabird ecology (mainly population trends and individually marked monitoring). With these long time series researchers can detect more subtle associations between climate factors and demographic parameters like survival, that exhibit relatively low amounts of temporal variation. In fact, the amount of available long-term data on several species and populations of seabirds is amazing, compared to other marine or even terrestrial organisms (Grosbois et al., 2008; Sydeman et al., 2012). I found up to 49 papers (some of them corresponding to several species, morphs or colonies) assessing the potential impact of climate on adult survival using methods accounting for recapture probability (**Table 1**). Those papers included 36 different species (most of them Procellariiformes) and seldom considered time lags between the climate index and adult survival (24% of the cases). More than 77% of the 75 species*colonies studies found a relationship (linear in most cases) between climate and adult survival. Nevertheless, Grosbois et al. (2008) warned about several potential biases that could occur when assessing the effects of climate on survival, including the test of multiple covariates without correcting α-values of statistical significance (in cases where classical null hypothesis statistical testing is employed for inference purposes), collinearity between those covariates and survival, or the inclusion or not of lag times when testing for those effects (see below).

Charles Darwin was fascinated by the size of seabird colonies, formed by millions of individuals. After centuries of direct harvesting, introduced mammalian predators and destruction of suitable breeding habitat, most of those colonies have been decimated, and environmental stochasticity, including climate variation, has a greater impact on population changes than it did in the past, because population sizes are smaller and closer to the quasi-extinction thresholds than ever before. Nevertheless, ecological responses of seabirds facing climate variability suggest that they can have highly resilience responses, and this should be viewed as a buffer against decline or extinction (see below) (Forcada et al., 2008; Gremillet et al., 2012). Changes in seabird populations or demographic parameters associated with climate are often described as "alterations" and "reductions," with an implied warning message or value-judgment (Martínez-Abraín and Oro, 2013). Only when researchers can show that changes in seabird ecology associated with climate variability fall outside the range of inherent variability in biological parameters (at the level of both individuals and populations) should we be concerned about the fate of a population or a species due to climatic change. In fact, much less has been published on the influence of climate on population dynamics of seabirds (e.g., Frederiksen et al., 2004b; Jahncke et al., 2004; Forcada and Trathan, 2009; Burthe et al., 2014; Woehler et al., 2014) but even in those cases it is difficult to know which percentage of the variance in population size or density is explained by climate forcing compared to other factors such as competition, density-dependence, predation or dispersal (Bustnes et al., 2013).

PITFALLS AND GAPS OF THE CLIMATE-SEABIRD RESEARCH

Scientific generalizations are helpful because the message of the concept is clearer: climate warming is a scientific fact, and the resulting changes in the biosphere follow the same fast trend. I am not going to discuss here the particularities involving climate change (e.g., spatial heterogeneity in warming, consequences for other components such as precipitation, humidity, or atmospheric pressure); however, given that I use the general term "seabirds," it is difficult to avoid dealing with the variability across taxa. Seabird body sizes range from very small to very large forms (with a difference of more than two orders of magnitude in body weight); their diets range from planktivorous to predators of large fish and squid; their foraging habitats range from neritic to pelagic areas, there are species with small foraging ranges while others feed throughout the whole circumpolar regions; some are divers and some forage at the sea surface; some seabirds are resident species (at a spatial mesoscale) whereas others are trans-equatorial migrators, which travel large distances across several oceanographic systems. With this variability in life history strategies and ecology, we should expect that the impacts of climate on seabird ecology to vary across ecological parameters and species that are impacted by climate variation. For instance, Kitaysky and Golubova (2000) showed that climate change differentially influenced reproductive performance of sympatric alcid species depending on their foraging strategy (e.g., planktivorous vs. piscivorous). Other studies have also addressed the influence of environmental variation in some seabird communities and the specific effects on each species relative to their particular ecology (Sydeman et al., 2001; Sabarros et al., 2012). Even for the same species in different studies, results are not always similar (see **Table 1**), suggesting differences among populations (Tavecchia et al., 2008) or raising doubts about the suitability of selected climate indexes, the temporal window analyzed or the power of each data set to detect associations between climate and the seabird parameter of interest, especially when these associations are not statistically significant (Jenouvrier, 2013). For instance, some studies found that the influence of increased SST on adult survival was positive or negative depending on the study colony or the genetic morph (Harris et al., 2005; Reiertsen et al., 2012), and these are good examples of how little we still know about the mechanisms linking climate and vital rates (Forero et al., 2001). Finally, non-linear relationships between demographic parameters and climate indices can also result in differences between studies on the same species when different temporal windows are considered. For example, if adult survival is associated non-linearly with a climate covariate that changes through time, then performing the same analysis during two different time windows may yield different results.

It would be interesting (though very challenging) to have a global review available to understand what species and populations are more sensitive to climate variability, how important extreme climate events can be, how important a role intrinsic individual and state attributes (such as age, sex, breeding state, and physical condition) are playing, what temporal and

Table 1 | Studies assessing the effects of climate on seabird adult survival.

Species	Index	Effects on adult survival	Time lag	References
CHARADRIFORMES				
Least auklet	North Pacific Index	Yes	No	Jones et al., 2002
Cassin's auklet	SOI	Yes	No	Lee et al., 2007
Cassin's auklet	ENSO	Yes at four study colonies	No	Bertram et al., 2005
Cassin's Auklet, Rhinoceros Auklet and Tufted Puffin	Two extreme climate events: a strong El Nino event in 1997–1998 and an atmospheric blocking event	No for the two first species; yes only for females of the third species	No	Morrison et al., 2011
Atlantic puffin	NAO, SST	Yes in four out of five study populations	Both lagged and not-lagged indexes	Harris et al., 2005
Little auk	NAO, SST	Yes	Both lagged and not-lagged indexes	Hovinen et al., 2014
Audouin's gull	NAO	No	No	Tavecchia et al., 2007
Razorbill	Labrador Current temperature	Yes at one colony but not clear in the other	Both lagged and not-lagged indexes	Lavers et al., 2008
Brünnich's guillemot	Arctic Oscillation, SST	Very slight	Both lagged and not-lagged indexes	Smith and Gaston, 2012
Common guillemot	SST	Yes	Both lagged and not-lagged indexes	Reiertsen et al., 2012
Common guillemot, Brunnich's guillemot, razorbill, Atlantic puffin and black-legged kittiwake	NAO, SST	Yes except for razorbill	Both lagged and not-lagged indexes	Sandvik et al., 2005
Black-legged kittiwake	NAO, SST	Slight	Both lagged and not-lagged indexes	Frederiksen et al., 2004b
PROCELLARIIFORMES				
Cory's shearwater	SOI	Yes at all six study populations	No	Jenouvrier et al., 2009
Cory's shearwater	SOI, NAO, SST	Yes	No	Boano et al., 2010
Cory's shearwater	SST	Yes	No	Ramos et al., 2012
Cory's shearwater	SOI	Yes at two colonies	Variable depending on the covariate	Genovart et al., 2013
Indian yellow-nosed Albatross	SOI	No	No	Rolland et al., 2009a
Amsterdam albatross	DMI, SOID, SST	No	No	Rivalan et al., 2010
Amsterdam albatross, black-browed albatross, snow petrel	SST for albatrosses, sea- ice concentration for petrel	Only for black-browed Albatross	No	Barbraud et al., 2011
Wandering, sooty, yellow-nosed and black-browed albatross	SOI, SST	Only for black-browed Albatross	No	Rolland et al., 2010
Black-browed albatross	SST	Yes	No	Rolland et al., 2008
Black-browed albatross	SST	Yes	No	Pardo et al., 2013
Black-browed albatross	SOI, SST	Yes for inexperienced breeders, no for experienced	No	Nevoux et al., 2007
Black-browed albatross	SOI, SST	Yes for inexperienced breeders at the two study colonies	No	Nevoux et al., 2010a
Black-browed albatross	SOI, SST	Only for immatures, no for adults	No	Nevoux et al., 2010b
Black-browed albatross	SOI, SST	Yes for inexperienced and experienced breeders	No	Rolland et al., 2009b
White-chinned petrel	SOI	Yes	Both lagged and not-lagged indexes	Barbraud et al., 2008
Snow petrel	Extent of sea-ice, SST	Yes	No	Barbraud et al., 2000

(Continued)

Table 1 | Continued

Species	Index	Effects on adult survival	Time lag	References
Snow petrel	Air temperature, sea- ice concentration	No	No	Jenouvrier et al., 2005b[a]
Blue petrel	ENSO	Yes	Both lagged and not-lagged indexes	Barbraud and Weimerskirch, 2003
Blue petrel	Sea surface height	Only for inexperienced individuals	No	Barbraud and Weimerskirch, 2005
Mediterranean Storm Petrel	14 covariates	Yes	No	Soldatini et al., 2014
Monteiro's storm petrel	Chl-a, SST	Yes	No	Robert et al., 2012
Thin-billed prion	Winter sea ice concentration	Yes	No	Nevoux and Barbraud, 2006
Southern fulmar	SST, sea- ice concentration	Yes	No	Jenouvrier et al., 2003
Northern fulmar	NAO	Yes for females, not clear for males	No	Grosbois and Thompson, 2005
SPHENISCIFORMES				
Adélie penguin	SOI	Yes	No	Jenouvrier et al., 2006
Adélie penguin	Winter sea ice extent	Yes	No	Ballerini et al., 2009
Adélie penguin	Sea-ice concentration during breeding	No	No	Lescroël et al., 2009
Adélie penguin	7 sea-ice variables, SOI, SAM	Yes	No	Emmerson and Southwell, 2011
Yellow-eyed penguin	SOI	Yes	No	Peacock et al., 2000
King penguin	SOI, SST	Yes	Both lagged and not-lagged indexes	Le Bohec et al., 2008
Rockhopper penguin	SST	Yes	No	Dehnhard et al., 2013
Macaroni penguin	SST, ENSO, SAM	Yes	Both lagged and not-lagged indexes	Horswill et al., 2014
Emperor penguin	Air temperature-sea ice concentration	Yes	No	Barbraud and Weimerskirch, 2001
Emperor penguin	Air temperature-sea ice concentration	Yes	No	Jenouvrier et al., 2005b[a]
Emperor penguin	Sea ice concentration anomalies	Yes	No	Jenouvrier et al., 2012
SULIFORMES				
European shag	Winter gales	Yes	No	Frederiksen et al., 2008
Blue-footed Booby	SOI, SST	Yes	No	Oro et al., 2010

SOI, Southern oscillation index; NAO, North Atlantic oscillation index; DMI, dipole mode index; SAM, southern annular mode; SOID, Southern Indian Ocean dipole; SST, sea surface temperature.

[a] *This study is duplicated because included two species of different orders.*

spatial scales are most important, and how other biological processes (such as density-dependence, interference competition or predation) interact with climate (see also below). For instance, Ezard et al. (2007) suggested that to avoid drawing incorrect conclusions regarding variability in demographic or ecological parameters (such as breeding phenology) and/or the factors responsible for these perceived changes, researchers need to be sure and control for strong inherent sources of variation, such as age. These authors had a very detailed demographic data-set that is not always available in conventional studies, but these types of confounding biotic factors (i.e., age, sex) that should be taken into account when studying the effect of climate on seabird populations. An increasing number of studies showed that the effects of climate factors or pollutants on demographic parameters are state dependent (Nevoux et al., 2010a; Goutte et al., 2014). This also matches with life history theory since energetic costs and metabolism differ between breeding and non-breeding individuals, which may in turn affect their demographic performance.

Another open question on climate-seabird research might be: is survival of larger seabirds (such as albatrosses) less sensitive to climate variability than survival of smaller species such as storm petrels? Larger species tend to have higher survival than smaller species (Weimerskirch, 2002), so environmental canalization (Gaillard and Yoccoz, 2004), i.e., the process of buffering environmental stochasticity should be stronger in the former than in the later. However, a qualitative look at available results is not so clear (see **Table 1**), maybe because biological reasons (e.g., life-history pressures, type of foraging habitat, noise from other processes such as intra-guild predation, competition, anthropogenic impacts) or because of methodological biases (increase of survival estimates through time due to appearance of more reliable statistical tools, Weimerskirch, 2002) or differential criteria to select climate indexes. It seems that there is no association between adult survival and body mass in Procellariiformes when phylogeny is taken into account in a capture-recapture modeling framework (Abadi et al., 2014); this may also explain the discrepancies found in several studies (**Table 1**), although this remains to be investigated in other seabird families.

When assessing the global impact of climate on seabirds, it should also be important to include the potential effects of breeding habitat loss or gain (typical of Arctic and Antarctic seabirds, but also among ground coastal nesting seabirds due to sea level rise), and the additive effects of anthropogenic impacts (mainly fisheries and direct harvesting, but also invasive species and pollutants) (Barbraud et al., 2012; Lewison et al., 2012; Goutte et al., 2013). To have some universal and comparable measure of the impact of climate on different species and populations, Jenouvrier (2013) proposed the use of a thorough new index, the "population robustness to climate change," together with retrospective and prospective analysis of population models.

Another gap of the association between seabirds and climate is the low number of studies on tropical seabird species. Most of seabird-climate studies have been conducted in temperate or polar marine ecosystems, whose functioning is different from tropical regions, where many seabirds occur with often poor conservation status. Future studies should thus attempt understanding tropical seabird ecology and demography and the effects of climate if we want to have better understanding of seabird climate relationships.

THE IMPORTANCE OF SUITABLE TEMPORAL AND SPATIAL SCALES

The use of oceanographic indexes to test the influence of climate on seabird ecology has been quite common (Sydeman et al., 2012), and mainly covered three spatial scales: some of them were more local (mainly climate around the breeding sites such as sea surface temperature, wind speed, air temperature, sea level pressure), some other were more regional (e.g., the Western Mediterranean Oscillation index WeMOi), whereas other indexes were more global such as El Niño-Southern Oscillation index (ENSO), Southern Oscillation index (SOI), the Southern Annular Mode (SAM), or the North Atlantic Oscillation index (NAO). The use of different spatial scales is not clearly justified in all studies (e.g., Soldatini et al., 2014) and an understanding of the spatial use of marine habitat made by each species in each period of the life cycle is essential to test appropriate hypotheses on the effect of climate on seabird ecology (Frederiksen et al., 2004a; Scott et al., 2006). To that end, the improvement of technology in recent decades (e.g., Burger and Shaffer, 2008; Wakefield et al., 2009) has allowed researchers to increase their knowledge about migration routes (e.g., Guilford et al., 2009; Egevang et al., 2010), wintering areas (González-Solís et al., 2007; Frederiksen et al., 2012) and foraging areas also during reproduction (Gremillet et al., 2004; Guilford et al., 2008) and apply oceanographic indices at more appropriate temporal and spatial scales (Duffy, 1993; Weimerskirch et al., 2012).

Regarding the temporal window of the climate indexes used in each study, even though it has also been explained in most cases, it is not always coincident among studies either. This does not nullify the results of each individual study, but makes it harder to develop any common pattern from retrospective studies that encompass completely different snapshots in time. This is particularly worrying when analyzing survival, because this is the most sensitive parameter for seabird population dynamics, and it is crucial to understand what period of the whole year is more critically affecting this parameter. Some studies used only the temporal window of the breeding season (implying that conditions during breeding are more important for survival than conditions during winter, maybe through the costs of reproduction, what is against the expectations of life-history theory in long-lived organisms capable of reducing breeding effort in a given season if survival is threatened), whereas others used only climate conditions during winter (assuming that most mortality occurs in this period, Harris et al., 2005; Genovart et al., 2013), during the two periods separately (e.g., Barbraud and Weimerskirch, 2003) or even during the whole year as an integration of all year-round variability (Gordo et al., 2011). The temporal scale also defines the difference between weather and climate: the former consists of short-term (minutes to months) changes in the atmosphere, whereas the later is the average of weather over time and space. Some weather events (such as strong storms and tsunamis, Viera et al., 2006; Sherley et al., 2012) are not necessarily correlated with climate indexes and can introduce some noise when analysing their potential association with some ecological parameters, particularly short-term processes such as reproduction and hence breeding success (Schreiber, 2002).

In general, researchers need to be very careful to present results and conclusions, particularly from retrospective observational studies, because the study design and analytical approach used must be appropriate to properly answer research questions of interest. This is true for any spatial and temporal scales used, and positive results do not necessarily ensure that the index tested is the one explaining the most variance or alternatively that there is no effect on the parameter analyzed when negative results are reported. Little is known about the frequency of negative results that do not ever get published but the potential bias against these studies by journal reviewers and editors might bias a meta-analysis or any general review of the global effects of climate on seabirds (Sydeman et al., 2012). A general recommendation to properly select the most suitable indices at both temporal and spatial scales would be first partitioning the life cycle into breeding and non-breeding seasons, and then researchers should identify the foraging ranges used by the study species in each of those seasons and test for climate effects over the corresponding spatial scales.

THE MECHANISMS LINKING CLIMATE VARIATION TO SEABIRD POPULATION CHANGE

Since most climate studies are based upon correlational evidence, the mechanistic processes linking climate variation to seabird ecology remain in most cases unclear, especially when global indexes are used (e.g., Breton et al., 2008; Sydeman et al., 2009). Typically, the first parameters to be affected when environmental conditions change are reproductive success because climate influence oceanographic conditions and food available for breeding, which is the main driver of fertility in the absence of predation (Oro et al., 1999; Schreiber and Burger, 2002; Frederiksen et al., 2006). Even though population change in seabirds is in theory less sensitive to changes in breeding success, this parameter, which influence recruitment rates, is often the vital rate that exhibits the most variation and it certainly constitutes an important factor that can affect population fluctuations. Sometimes the association between climate and breeding success is either direct in the form of heat strokes and catastrophic events such as volcanic eruptions, gales or tsunamis (Viera et al., 2006; Finkelstein et al., 2010; Sherley et al., 2012), or indirect, i.e., mediated by parasitism or diseases (Gaston et al., 2002; Cooper et al., 2009; Rolland et al., 2009a). That association should be strong in seabirds, because they are long-lived organisms and selection pressures have shaped conservatism in the energy devoted to reproduction: when environment is harsh, individuals invest less or may refrain from breeding and very low breeding success or even failures are commonly recorded for a number of species (La Cock, 1986; Frederiksen et al., 2006). However, there are other drivers that influence breeding success such as predation, food subsidies obtained from anthropogenic activities (mainly fisheries) and stochasticity in the links between climate and food-webs (Oro et al., 1996; Regehr and Montevecchi, 1997; Frederiksen et al., 2006).

The same correlation nature of studies linking climate variability with adult survival hinders the mechanisms involved, which are far from being well understood. This is particularly true when the process invoked is food availability through bottom-up control in food webs, because at the population level, adults should not jeopardize their own survival (i.e., the most conservative parameter in long-lived organism) when environmental conditions are bad and trade-offs such as survival *in lieu of* reproduction should be observed (but see Olsson and van der Jeugd, 2002; Oro and Furness, 2002). Studies suggesting direct mortality caused by harsh marine conditions during winter (e.g., gales, hurricanes) (Frederiksen et al., 2008; Boano et al., 2010; Genovart et al., 2013) are clearer examples of the potential mechanisms linking climate and survival. Population fluctuations should be more sensitive to changes in adult survival in accordance with the theory of life-histories and the evolutionary canalization of adult survival, but this association is not always clear (Harris et al., 2005).

In general, the mechanisms involved in the association between climate and vital rates (e.g., breeding success, survival, recruitment, dispersal) can be associated directly with climate (extreme values of temperature, precipitation, winds) or indirectly, through climate effects on a critical resource (e.g., food, nest sites, wintering grounds) or an interacting biological component of the ecosystem (e.g., parasites, predators). Indirect effects are often harder to distinguish in that association because the complex nature of biological interaction in food webs.

In addition, time lags in climate indexes relative to survival and population change, for example, appear reasonable when climate effects on adult survival are mediated by the food-web, because seabirds are top-predators, and some delay between climate, physical forcing and a large part of the food chain is to be expected (Thompson and Ollason, 2001; Arnott and Ruxton, 2002; Lloret et al., 2004; Martín et al., 2012). Furthermore, this delay may depend on the species, with some taxa feeding on relatively low trophic levels (e.g., fish larvae), whereas some species feed on higher food web prey (e.g., squid). However, the range of time-lags recorded between climate and adult survival has been variable among studies or not tested at all (**Table 1**, see also Jenouvrier, 2013) and the confounding effects of time, cohort and age on survival and recruitment sometimes make it difficult to assess the reliability of results. Correlations between climate covariates and population fluctuations are also analyzed either with time lags or without lagged associations. In the former case, researchers assume that those covariates influence mainly fertility and the effects on population numbers are reflected some years later, owing that seabirds do not reach sexual maturity for several years until recruitment (Cook et al., 2014). In some other cases, climate covariates of the previous year were tested, and researchers assume that conditions prior to breeding were more important by influencing adult survival, breeding propensity and immigration (Jenouvrier et al., 2003; Frederiksen et al., 2008; Irons et al., 2008; Devney et al., 2009; Lauria et al., 2012). The absence of time lag in the response of seabirds to climate variability may be reasonable in some situations, even when the process invoked is food availability, because availability of food depends on its abundance, accessibility, and distribution, which can be directly influenced by climate. Jenouvrier et al. (2005a) found that climate may have a direct or a lagged effect on population dynamics depending on environmental stochastic conditions. Some studies showed that climate have a simultaneous effects both direct and lagged because each demographic parameter are affected differently by climate (Erikstad et al., 2013; Sandvik et al., 2014). Finally, the existence of non-linear relationships between climate and seabird ecological parameters has seldom been explored (e.g., Durant et al., 2004; Jenouvrier et al., 2005a; Ballerini et al., 2009; Regular et al., 2009), despite the importance of identifying tipping points and thresholds when buffering capacity (i.e., both behavioral and demographic) is overcome.

PREDICTING THE FUTURE IMPACTS OF CLIMATE ON SEABIRDS

What is our capacity to forecast the effects of climate change on seabird abundance, distribution and viability? Several now relatively old papers anticipated the importance of predicting how climate would affect marine food webs and top-marine predators (Crawford, 1991). However, climate is just one driver among environmental-change agents and our ability to modify climate, compared to some other components of environmental change (e.g., pollutants, habitat fragmentation, fisheries interactions), is very limited. In addition, climate has a strong inertia, so it is difficult to apply conservation and management actions even if we are able to build reliable predictions for some extreme cases with detailed demographic information (e.g., some penguin, petrel and albatross species typical of Polar regions). Predictions are challenging because they rely on models built using retrospective data (i.e., "past" relationships) and thus include considerable uncertainty regarding future trajectories (Hulme, 2005; Sutherland, 2006). In addition, the best predictive models rely on large amounts of high quality demographic data, and sophisticated quantitative approaches. Yet, generating general predictions is difficult because of the inherent ecological variability amongst species, ecosystems (Chambers et al., 2011) and even among individuals (Lescroël et al., 2009, 2010; Lescroel et al., 2014) and populations (Tavecchia et al., 2008; Dias et al., 2010). These predictions, if they are local, can also be biased by dispersal processes (e.g., Woehler et al., 2014), because seabirds are very vagile, even species considered as highly philopatric (Genovart et al., 2007). Despite those constraints, population models together with tools for time-series analysis have yielded very promising results when long-term data sets and detailed estimations of demographic parameters were available (Jenouvrier et al., 2009, 2012, 2005a). Thus, research on the effects of climate on seabirds (or on any other organism and ecosystem) should be focused to building solid scientific evidence on predicted rates of population change, meta-population dynamics, and changes in species distribution given the present rates of warming (Sydeman et al., 2012). Testing hypotheses about the effects of climate on seabird ecology (e.g., diet, behavior, and phenology) is a first step toward making predictions regarding climate effects on population trajectories and to understanding the mechanisms linking patterns and processes, but this is just the first step. In general, we should move to a research devoted more toward forecasting the effects of global change (not only climate, but considering the synergetic effects of several agents of global change (e.g., Votier et al., 2008b; Finkelstein et al., 2010; Rolland et al., 2010; Lebreton, 2011), and to offer evidence that can help managers develop a roadmap of conservation actions (Jenouvrier, 2013). However, we need to collect the foundational information regarding links between demographics and climate, and the mechanisms that link them as we must have robust estimates of vital rates to build predictive models, and this constitutes a big challenge. In general, there is more potential to manage the impacts of other global change agents such as overharvesting (Jahncke et al., 2004; Becker and Beissinger, 2006), bycatch in fisheries (Bunce et al., 2002; Barbraud et al., 2008; Rolland et al., 2008; Ramos et al., 2012), habitat deterioration (Lindenmayer and Fischer, 2013), pollution (Croxall et al., 2012) or invasive species (Nogales et al., 2004; Ruffino et al., 2009; Major et al., 2013) than there is for managing climate (Rogelj et al., 2013), so this can be an indirect way of battling the impacts of climate warming.

Finally, population predictions must take into account the resilience of species to environmental change including extreme events, which are predicted to increase in frequency. For example, Hass et al. (2012) forecasts the impact of increasing hurricanes on the viability of the already endangered black-capped petrel *Pterodroma hasitata*, and predicted that this increase in hurricane frequency could nearly double the expected number of wrecked petrels over the next century, placing the species at greater risk of extinction by acting upon already much reduced populations due to human action (e.g., harvesting, bycatch, loss of breeding habitat). In addition Gremillet et al. (2012) showed that foraging behavior plasticity in little auks *Alle alle* maintained fitness levels across a wide range of sea surface temperatures, which may buffer them against at least the initial impacts of climate change. Several ecological parameters (e.g., vital rates, distribution, and foraging ranges) have been observed to shift as a result of changes in climate in several seabird species, but relatively little is known about the potential for changes in other demographic mechanisms to buffer these shifts. I can hypothesize that changes in recruitment rates, breeding propensity and increased fertility, as well as the role of immigration in source-sink systems at local population level, all have the potential to offset potential declines in survival for example, in relation to climate change. Some of these compensatory mechanisms have been already found in harvested populations of fish and ungulates (Lebreton, 2005; Servanty et al., 2011).

At the scale of geological times, seabirds have a long evolutionary history. Bone remains of a *Phaeton* tropicbird have been recently found in Morocco preserved from the Ypresian Age, in the lower Eocene, ca. 48×10^6 years ago (Bourdon et al., 2008). In geological- time scales, seabirds have experienced changes in climate, including warming and cooling periods, and extreme events. The previous interglacial period ($1.2–1.3*10^5$ years BP) was substantially warmer than the present one; about 2°C in the North Temperate Zone and 5°C in the Arctic, and it may have been the warmest period since the onset of the Pliocene (Fedorov et al., 2013). Some species have likely shown more plasticity to adapt to such changes and to anthropogenic factors acting in synergy with climate change, and we have to identify what species would be more sensitive to the current rate of climate change. A major difference between the so-called Anthropocene with previous geological periods is major habitat alteration due to the growth of human population (breeding habitat destruction, introduced predators, pollutants) with these factors acting in synergy with climate. Therefore, plasticity may be not enough to adapt to climate change given these additional factors for which many seabird species were not previously exposed and selected for. For instance, Igual et al. (2007) showed that Cory's shearwaters, due to their limited behavioral plasticity and heavy evolutionary loads, did not perceive the presence of invasive predators signaling differences in predation risk and in turn of breeding success.

Climate has in itself the features of a paradigmatic complex system: emergent properties that cannot be explained by the sum of its components. So the study of its influence on seabird ecology is far from being straightforward because climate has many emergent properties that cannot be explained solely by the sum if its own components, to a large extent because of its random structure, and additionally because many other factors can be involved, including extrinsic (e.g., predators in the case of small and medium-sized species, prey density, competition) and intrinsic (e.g., density-dependence, age-structure, sex) factors.

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