



Spatial ecology and conservation of seabirds facing global climate change: a review

David Grémillet*, Thierry Boulinier

Centre National de la Recherche Scientifique, Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175,
1919 Route de Mende, 34 293 Montpellier cedex 5, France

ABSTRACT: In this review we detail the impact of climate change on marine productivity, on marine environmental stochasticity and cyclicity, and on the spatio-temporal match–mismatch of seabirds and their prey. We thereby show that global warming has a profound bottom-up impact upon marine top-predators, but that such effects have to be studied in conjunction with the (top-down) impact of human fisheries upon seabird food resources. Further, we propose seabird ecological features, such as memory effects and social constraints, that make them particularly sensitive to rapid environmental change. We provide examples of how seabirds may nonetheless adapt when facing the consequences of climate change. We conclude that our understanding of the spatial ecology of seabirds facing environmental change is still rudimentary, despite its relevance for the conservation of these vulnerable organisms and for the management of marine ecosystems. We define the following research priorities. (1) Determine the factors affecting seabird distribution and movements at sea using biotelemetry, as well as colony dynamics on land. (2) Link seabird distribution patterns to those of their prey. (3) Determine further the role of historical and metapopulation processes in contributing to the dynamics of the spatial distribution of seabirds. (4) Assess phenotypic plasticity and the potential for microevolution within seabird spatial responses to climate change, since both will greatly affect the quality of modelling studies. (5) Adapt existing models to define and predict the impact of climate change onto seabird spatial dynamics. (6) Synthesize all gathered information to define marine protected areas and further conservation schemes, such as capacity reduction of fisheries. This research effort will require maintaining existing long-term monitoring programmes for seabirds, as well as developing new approaches to permit the integration of processes occurring at various scales, in order to be able to fully track the population responses of these long-lived vertebrates to environmental changes.

KEY WORDS: Fisheries · Marine protected areas · Match–mismatch · Metapopulation dynamics · Phenotypic plasticity · Regime shift · Top-down/bottom-up control

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INTRODUCTION

The oceans have long been considered an unlimited resource and have been used as such for transportation, resource extraction and waste disposal. There are now clear signs that human activities and resulting global changes are exerting considerable stress on marine ecosystems (Halpern et al. 2008). These disturbances affect all components of aquatic food webs, including top-predators such as seabirds. Seabirds are

exposed to a variety of anthropogenic threats (reviews in Schreiber & Burger 2002). (1) Harvest of eggs, juveniles and adults, as well as guano scraping, severely disturbed/depleted seabird populations in historic times, but have ceased more or less completely following efficient protection of breeding sites. Involuntary seabird harvest by fishing vessels (bycatch) nonetheless still occurs and severely threatens numerous populations of petrels and all albatrosses. (2) Substantial efforts have been made to eradicate alien plant and

*Email: david.gremillet@cefe.cnrs.fr

animal species from oceanic islands, but such species still have dramatic effects on the breeding performance and survival of some seabirds. (3) Marine pollution via heavy metals, organochlorides, oil products and plastics is a recurrent threat to seabirds on a worldwide scale; the global consequences for this community are difficult to assess. (4) Most seabirds are piscivorous, and two-thirds of the world's fish stocks are overexploited by industrial fisheries, potentially starving numerous seabird populations. (5) Anthropogenic climate change can have direct (review in Schreiber 2002), or indirect impacts on seabirds. In the latter case, climate change affects oceanic processes, and the spatio-temporal availability of seabird prey. This effect is exacerbated by the simplification of upper trophic levels by fisheries (see Österblom et al. 2007, Watermeyer et al. 2008). (6) Finally, global warming and human presence at seabird breeding sites are likely to increase the occurrence and virulence of avian pathogens, as well as their impact on seabird populations (Ricciardi 2008).

All threats listed above cause substantial disturbance to seabird populations, several of which are of major global relevance to the conservation and the management of marine ecosystems. This is particularly the case for ongoing and rapid climatic changes (Ducklow et al. 2007, Hinke et al. 2007). Responses of seabirds to climate changes in historic times, up until the end of the 20th century, have been reviewed by Ainley & Divoky (2001). These authors distinguished between direct and indirect responses to climate change, whereby the former was linked to the thermal preferences of each species and the latter used characteristics of the thermal environment (e.g. sea surface temperature, SST) as a proxy for climate-induced changes in the distribution and abundance of seabird prey. They listed a number of case studies supporting these trends, with a major emphasis on polar and upwelling ecosystems. We take this matter further, with an emphasis on the spatial ecology of seabirds facing climate change. Spatial ecology is concerned with understanding and, ultimately, predicting the processes affecting the spatial distribution of organisms in the environment. It largely relies on the identification of spatial patterns, but it also requires integrating complementary approaches at various spatial scales. Predicting the spatial responses of species facing climate change is one of the great scientific challenges of the 21st century (Clark et al. 2001), above all because it requires an interdisciplinary, metapopulation framework.

In the present review, we first identify the impact of climate change on atmospheric and oceanic circulation and the productivity of marine waters. We then show how climatic changes affect the spatio-temporal distribution of this productivity and its predictability to

seabirds. We also discuss the combined effects of climate change and overfishing on seabird foraging performance, and stress the fact that these disturbances should not be considered in isolation. Further, we show how seabird demographic, social and behavioural traits condition their marked sensitivity to high levels of environmental stochasticity. We then provide examples of seabird species/communities that show behavioural adaptation to the consequences of climate change. We conclude that the study of the impact of climatic changes on seabird spatial ecology and populations has only just begun. We then define key research targets in order to optimise future investigations of the interplay between seabird spatial ecology and climatic changes (see Fig. 4).

GLOBAL WARMING AND MARINE PRODUCTIVITY

Due to human activities, CO₂ levels in the atmosphere have been rapidly rising since the middle of the 19th century, with noted acceleration in the last 50 yr. The related greenhouse effect is strongly suspected to induce increased air temperatures. These changes have profound effects on marine climate. The main known direct impacts of global warming on marine productivity can be summarized as follows. (1) Rising air temperatures tend to warm up surface waters, thereby reducing their density and causing them to expand. Not only does the sea level rise, but such warm surface water does not mix well with deep, cool, oceanic water. This reduces the upward transfer of deep, nutrient-rich water into the euphotic zone, thereby reducing phytoplankton growth and the overall productivity of surface waters, especially in the tropics (Fig. 1; Behrenfeld et al. 2006). (2) Rising air temperatures also induce melt of Arctic and Antarctic coastal and inland ice and Arctic permafrost melt, which, in turn, cause increased freshwater inflow into some regions of the polar oceans and their so-called 'freshening' (Jacobs et al. 2002, Greene & Pershing 2007). Such low-salinity water masses have the same effect as warmer water masses: they build a low-density surface layer, which drastically reduces vertical mixing, nutrient inflow into the euphotic zone and the productivity of surface waters during the summer period. (3) However, rising air/water temperatures also contribute to a reduction of the Arctic and Antarctic sea ice cover and a related increase in spring primary productivity (Greene & Pershing 2007). Warmer water temperatures also directly favour phytoplankton growth at high latitudes (Behrenfeld & Falkowski 1997). However, decreasing ice cover changes the seasonality and extent of the marginal ice zone and its phytoplankton bloom, which, in turn, can have significant effects on

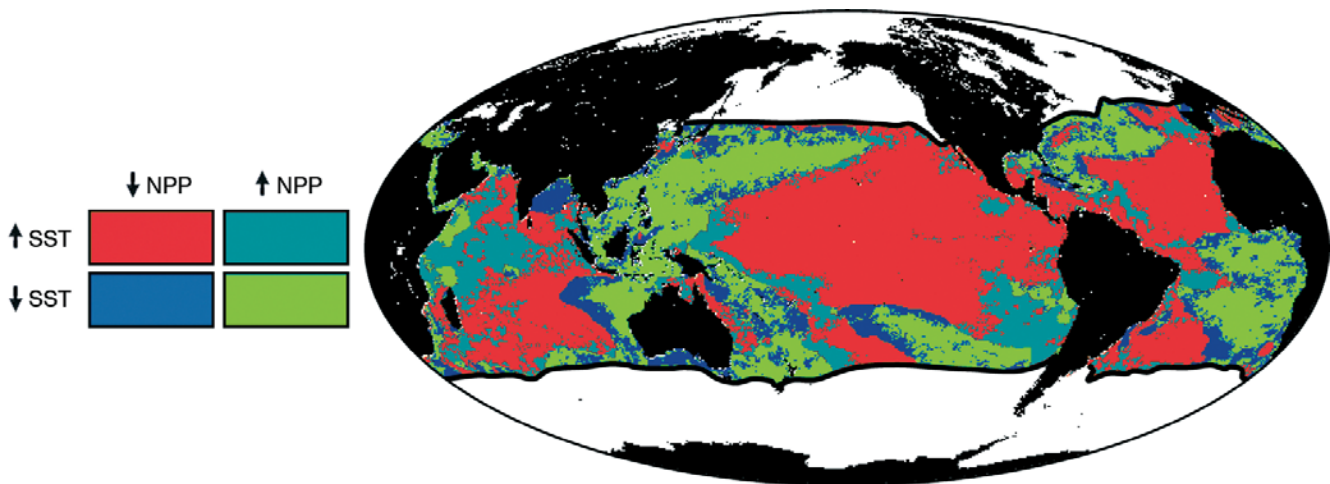


Fig. 1. Over the 1999 to 2004 time period, major changes in sea-surface temperature (SST) and net primary productivity (NPP) occurred worldwide. Overall, SST increased and NPP decreased for 74% of the permanently stratified ocean (red). Green: decrease in SST and increase in NPP. Blue: decrease in SST and NPP. Turquoise: increase in SST and NPP. Adapted from Behrenfeld et al. (2006)

regional productivity/carbon budgets and food web structure (Stabeno et al. 2005, Montes-Hugo et al. 2009). (4) Rising air temperatures generate large atmospheric pressure differentials, which result in stronger winds, frequent storms and hurricanes. Higher wind stress on the surface of the oceans favours the vertical circulation of water masses, the upward transfer of nutrients into the euphotic zone, and enhances primary productivity (Toggweiler & Russell 2008). (5) Most CO₂ released into the atmosphere dissolves in oceanic waters. However, the buffering capacity of the ocean is not endless, and the current massive increase in dissolved CO₂ is resulting in the acidification of marine water. Changes in seawater pH, combined with the temperature increase mentioned above, favour some phyto- and zooplankton species, while putting additional environmental stress upon others (Orr et al. 2005). The actual impact of acidification upon overall marine productivity is still being evaluated, but it is clear that it will lead to major changes in the composition of marine plankton communities (Hays et al. 2005).

The overall impact of these different, antagonistic environmental constraints is difficult to judge and is bound to vary strongly on a regional scale. Nevertheless, global ocean primary productivity, as assessed by remote-sensing, has been shown to have declined significantly since 1999 (Fig. 1; Behrenfeld et al. 2006). This drop in marine primary productivity is highly correlated with large-scale climatic indices, strongly suggesting that global warming has a negative impact on overall marine primary productivity and, hence, on the energy flow in the food web supporting top-predators, such as seabirds (e.g. Le Bohec et al. 2008).

CYCLIC AND EXTREME CLIMATIC EVENTS

Atmospheric and ocean circulation stand in a delicate balance, and so does the earth's climate. Cyclic and extreme climatic events are inherent to these systems, and have taken place long before man-induced global warming. Seabirds evolved in this fluctuating environment, but there is some evidence that environmental stochasticity is increasing rapidly as a consequence of global warming (Alley 2003).

Pressure fields and the resulting atmospheric circulation establish well-defined patterns (e.g. Walker cells, prevailing wind systems), which are nonetheless subject to variability at different spatial (regional and global) and temporal (daily, seasonal, multi-annual, decadal) scales. An array of climate indices has been tailored to characterize atmospheric variability and integrate measurements reflecting several environmental variables. The most famous are the El Niño–Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO) and, in the Southern Hemisphere, the Southern Annular Mode, but every single region of the globe has its own, or several, climate indices that are widely used in studies to decipher the impact of climate patterns on the biosphere (review in Stenseth et al. 2003).

Spectral analyses indicate a certain level of cyclicity within these oscillations. For instance, El Niño events currently have a 5 yr period (Collins 2005). Whether these cycles occur and rotate on a predictable basis is being debated (Park et al. 2004). Their existence is probably linked to the strength of ocean–atmospheric coupling. A strong coupling enables efficient feedback

and predictable cycles, whereas a weak coupling leads to a dilution of these cycles into environmental stochasticity. None of the general circulation models developed so far has been able to entirely grasp the complexity of these phenomena and predict their occurrence (Philander & Fedorov 2003). Maybe this is due to the fact that these events are neither entirely cyclic, nor totally random. In this context Philander & Fedorov (2003) adequately describe the ENSO as 'a damped pendulum subject to modest blows at random times'. Since these cyclic oscillations are weak, environmental stochasticity may trigger phase shifts. For instance, the ENSO tended to swing with a period of 3 yr in the 1960s and 1970s versus a period of 5 yr in the 1980s and 1990s. This phase shift was also linked to different operating modes during past El Niño/La Niña events (Philander & Fedorov 2003).

To summarize, large-scale oceanic-climatic oscillations are subject to substantial spatial and temporal variability, and this variability is extremely difficult to forecast. Recent climate change may have 2 major impacts on these oscillations. (1) It has been suggested that global warming may induce more frequent El Niño events (Timmermann et al. 1999), or may even lead to permanent El Niño conditions. This scenario is still being debated (Collins 2005), but if El Niño conditions become more frequent this will trim the productivity of upwelling ecosystems in the eastern Pacific by reducing nutrient influx to surface waters, or even world-wide (see 'Global warming and marine productivity'), thereby significantly diminishing the availability of pelagic fish to numerous seabird species. (2) Abrupt climatic changes are also more frequent in a warming world (Alley 2003). As seen above, climate oscillations are generally weak and may be prone to disturbance by random events, even of limited magnitude. More frequent and violent winter storms at high latitudes and hurricanes in tropical seas (Alley 2003) are typical examples of extreme events that can disrupt ongoing oscillations and drastically modify the operating modes of these oscillations, with cascading consequences for marine productivity and food availability to avian predators (Frederiksen et al. 2008).

REGIME SHIFTS, BOTTOM-UP AND TOP-DOWN CONTROLS

Marine food webs are unstable constructions and remain prone to sporadic and cyclic reorganisation, as are the oceanic and atmospheric circulations described in the previous section. Such reorganisations are termed 'regime shifts', which are defined as 'a persistent radical shift in typical levels of abundance or productivity of multiple important components of the

marine biological community structure, occurring at multiple trophic levels and on a geographical scale that is at least regional in extent' (Bakun 2004, p. 973). Using multi-disciplinary data sets, regime shifts have been identified in the northeastern Pacific for the years 1925, 1947, 1976 and 1998 (Peterson & Schwing 2003) and in the northern Atlantic in the 1920s and 1930s (Drinkwater 2006), and again in the mid-1980s (Beaugrand 2004). As a trendy concept in biological oceanography, regime shifts and their consequences are now being studied in all regions of the world's oceans (e.g. Oguz & Gilbert 2007). To take just one example of this type of event into consideration, the North Sea regime shift (1982 to 1988) was most probably caused by large-scale changes in wind intensity and direction, and an increase in SSTs. These alterations were coupled with an inflow of warm, nutrient-poor oceanic water into the North Sea and stronger stratification of surface water. These events favoured a northward expansion of warm-water copepod species and a decline in cold-water zooplankton (Beaugrand 2004). During this shift, warm-water conditions were established in the North Sea, thereby modifying primary and secondary productivity and reducing the availability of small pelagic fish to seabirds, which, in turn, influenced the reproductive performance of seabirds (Frederiksen et al. 2006).

This suite of events typifies a bottom-up control of marine food webs: climatic variability influences ocean circulation, which impacts primary productivity (phytoplankton), secondary productivity (zooplankton), fish and, finally, marine top-predators such as seabirds. This line of thought has been promoted by researchers wishing to link some of the climate indices listed in the previous section with population characteristics of marine top-predators. In particular, the ENSO and the NAO have been used extensively (e.g. Jenouvrier et al. 2003, Thompson & Ollason 2001). But 'it cannot all be climate' (Ainley et al. 2007), and a vision of bottom-up controlled marine food webs might be all too simplistic. Equally, there is ample evidence that marine food webs can be controlled via top-down effects (Österblom et al. 2007, Coll et al. 2008). For instance, Ainley and colleagues (2006) showed that enhanced predatory pressure by penguins and whales may have generated a trophic cascade in the western Ross Sea, and Worm & Myers (2003) also demonstrated top-down control by predatory fish (cod, *Gadus morhua*) on North Atlantic food webs.

As so often in ecological science, the actual event has multiple causes, and it seems unwise to focus on single mechanisms. Taking the southeastern Bering Sea as an example, Hunt et al. (2002) proposed the oscillating control hypothesis, which suggests that both top-down and bottom-up forcing may rule marine food webs

alternatively, whereby the latter occurs during 'warm' phases and the former during 'cold' phases. Similarly, Frank et al. (2007) performed a meta-analysis of trophic structure in 9 areas of the western North Atlantic and showed that top-down control tended to rule in northern (colder) areas, whereas bottom-up control occurred more often in southern (warmer) areas, potentially due to lower species diversity at higher latitudes (Fig. 2). Finally, Cury et al. (2000) suggested that upwelling ecosystems have a 'wasp-waist' structure, whereby intermediate trophic levels (small pelagic fish) exert both bottom-up and top-down control, thereby playing a crucial role in the response of these food webs subjected to climate-driven El Niño events.

COMBINED IMPACT OF CLIMATE CHANGE AND FISHERIES

Studies cited in the previous section show that the operating modes of trophic control can vary strongly in space and time within marine food webs (see also Lit-zow & Ciannelli 2007) and that bottom-up control by climate change is not necessarily the overriding force. The visionary statement of Parsons and colleagues (1984, p. 277) 'no form of marine pollution is in any way comparable to the ecological impact which occurs with the removal of ca. 70 million tons per year of predatory fish from the ocean ecosystem' has, sadly, been confirmed by numerous recent studies, and there is now ample evidence that humans are 'fishing down marine food webs' (Pauly et al. 1998). Intense fishery pressure on predatory fish drastically modifies the top-down control of these ecosystems. For instance, the removal of large baleen whales from Antarctic ecosystems by fisheries is strongly suspected to have caused a release of predatory pressure on Antarctic krill, with cascading consequences for regional marine food webs (Ainley et al. 2007). Modelling studies also have shown that harvesting and fisheries, more than climate change, have had a profound impact on the marine ecosystem of the Baltic Sea (Österblom et al. 2007), or the Benguela current (Watermeyer et al. 2008), and it is particularly difficult to envisage what the 'natural' state of North Atlantic ecosystems might have been prior to centuries of exploitation by humans (Pauly & MacLean 2003).

The most recent information indicates that the greatest threat to fish stocks upon which seabirds prey is the combined effect of climate change and overfishing (Brander 2007). Indeed, a number of studies now strongly suggest that rapid climate change and uncontrolled removal of fish resources have drastic consequences for seabird breeding success and survival

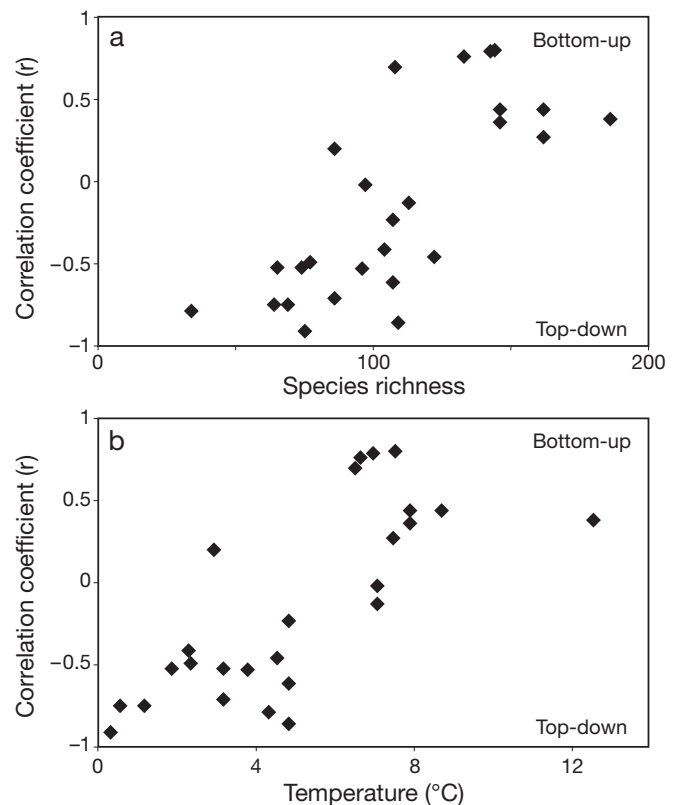


Fig. 2. In the North Atlantic, marine ecosystems are controlled by bottom-up and top-down trophic forces, depending on (a) species richness and (b) temperature, whereby the type of trophic forcing is expressed by the sign of the correlation between predator and prey abundance. The species richness–trophic forcing relationship is significant ($r = 0.75$, $n = 26$, $p < 0.001$), as is the temperature–trophic forcing relationship ($r = 0.74$, $p < 0.001$). Adapted from Frank et al. (2007)

and, ultimately, for population stability (Frederiksen et al. 2004, Ainley & Blight 2009). Therefore, although this review primarily focuses on the impact of climate change on seabird spatial ecology, we wish to stress that such impacts should not be considered in isolation, and we strongly recommend multi-factorial analyses assessing the consequences of the diverse forms of global change (i.e. climate change, overfishing, pollution, infectious disease spread) on seabird spatial ecology.

GLOBAL WARMING AND RANGE SHIFTS IN SEABIRD PREY

The climatic changes alluded to in previous sections have direct and indirect effects on the distribution and abundance of marine fish, the primary resource upon which seabirds forage (Shealer 2002, Cheung et al. 2008). As ectothermic organisms, fish have a well-defined thermal niche of $\pm 2^\circ\text{C}$ (Magnuson & Destasio

1997). Climate-induced warming of surface oceanic waters beyond the boundaries of a fish species' thermal niche can, therefore, have a direct effect on its distribution. Moreover, within this thermal niche, even subtle ($<0.5^{\circ}\text{C}$) temperature changes can have profound effects on growth, survival and reproduction. Such impacts operate via ecological forcing (food availability to fish) and physiological processes (e.g. enzyme kinetics). Examples abound (Perry et al. 2005, Hiddink & Hofstede 2008), but one of the most recent events with consequences for seabirds is the sharp numerical increase of snake pipefish *Entelurus aequoreus* in the northeastern Atlantic (Kirby et al. 2006). This population rise is due to the positive influence of warmer (up to $+0.5^{\circ}\text{C}$) waters on the reproductive performance of snake pipefish, and this numerical increase coincides with a northward range expansion to at least 79°N (Svalbard; Fleischer et al. 2007). Synoptically, lesser sandeels *Ammodytes marinus*, which used to be the food-base of a vast seabird community around the British Isles, have been depleted by the combined effects of overfishing and climate change (Poloczanska et al. 2004), and also show diminished calorific value (Wanless et al. 2005). Seabirds, in particular kittiwakes *Rissa tridactyla*, now feed increasingly on snake pipefish, which have low calorific value (Harris et al. 2007a), and are particularly difficult to swallow for seabird chicks, causing regular suffocation (Harris et al. 2007b). Therefore, there is little chance that numerous snake pipefish will be a valid alternative to the absent/meagre natural prey of many UK seabirds.

MATCH–MISMATCH OF FORAGING SEABIRDS AND FOOD RESOURCES

We have seen that climate change has a profound effect on global primary productivity of the world's oceans. Beyond potentially diminishing the total volume of marine resources upon which seabirds rely, climatic changes also perturb global oceanic circulation and the structure of marine food webs. Regime shifts and associated range shifts of marine species occur naturally, but there is some evidence that recent climate change increases the frequency of abrupt changes, with an overall trend towards chaotic ecosystem dynamics (Alley 2003). Such a trend is most probably facilitated by the combined effects of overfishing and climate change.

Overall, there is therefore a higher probability that food resources will not occur where and when seabirds expect them to be. This would typify a mismatch of predators and resources, and reflects the concept of match–mismatch introduced by Hjort (1914) and

championed by Cushing (1969, 1990). The match–mismatch hypothesis (MMH) was primarily formulated to describe the temporal mismatch of juvenile pelagic fish and of the plankton resources necessary to their growth (Cushing 1969). Nevertheless, it has been demonstrated that this concept can easily be expanded into the spatial dimension, and that it can generally refer to the spatio-temporal match–mismatch of predators and their resources (Fig. 3; Grémillet et al. 2008a). The impact of climate on match–mismatch events has been thoroughly reviewed by Durant et al. (2007, see also Suryan et al. 2006, Cury et al. 2008). In essence, the authors confirm that climate change is very likely to profoundly affect trophic web structure because (1) even (apparently) minor environmental changes can strongly modify the spatio-temporal availability of food resources necessary to predators (via non-linear responses) and (2) different food-web components are unlikely to respond to environmental change in the same manner, causing different degrees of spatio-temporal match–mismatch between these components, with resulting deconstruction of the food web in question. This has been demonstrated in the southern Benguela upwelling zone, where primary productivity is still one of the highest of the world's oceans, but where the combined effects of climate change and overfishing have altered the spatial occurrence of pelagic fish (anchovies and sardines) upon which a vast community of seabirds feed. In this situation, seabird foraging ranges still match with areas of high primary productivity, but mismatch with the current distribution zone of pelagic fish (Fig. 3; Grémillet et al. 2008a), thereby greatly diminishing seabird foraging profitability (Pichegru et al. 2007).

SEABIRD LIFE-HISTORY TRAITS, SOCIAL STRUCTURE AND ECOLOGICAL TRAPS

Rapid advances in biotelemetry techniques (Wilson et al. 2002) and systematic observations of seabirds at sea (Tasker et al. 1984) revolutionised our perception of the foraging and migratory behaviour of seabirds. It now appears that the marine environment is reasonably predictable to them (Hunt et al. 1999, Weimerskirch 2007), both at high latitudes and in the tropics (Ballance et al. 1997). Seabirds are long-lived organisms, with delayed sexual maturity. A prolonged bachelor period and extended life-span provide seabirds with ample time to explore marine habitats and to gather crucial information about prey patches and spatio-temporal variability in their availability (Daunt et al. 2007). There is increasing evidence that memory effects help individual seabirds to optimise their foraging strategies, most probably in conjunction with local

enhancement via feeding flocks (Camphuysen & van der Meer 2005), but not necessarily (Irons 1998). It has also been speculated that seabird colonies function as information centres and that individuals within breeding assemblages tend to share specific foraging patterns and foraging distributions, which remain stable through time (foraging site fidelity). In this context Grémillet et al. (2004a) indicated that neighbouring seabird colonies foraging in a similar marine environment may develop different behavioural types due to strong local 'cultural identities' tailored by group and memory effects.

Cultural identities of seabird colonies are also linked to their social structure and to the paucity of convenient insular breeding sites. It takes a long time (years to decades) to establish a viable seabird colony, and birds born at 1 specific site typically show high levels of philopatry (>80%). Similarly, adult seabirds are reluctant to change breeding sites, and sometimes prefer to forage and breed under unfavourable environmental conditions than to emigrate. In some species, such as the kittiwake, it is now clear that differential recruitment and dispersal at small spatial scales can be driven by adaptive strategies for the selection of breeding habitat, based on the performance of conspecifics (Danchin et al. 1998, Boulinier et al. 2008a). Nevertheless, dispersal at large scales, and factors susceptible to affect this process, are notoriously difficult to study (Cam et al. 2004).

In conclusion, current knowledge of seabird foraging and breeding biology strongly suggest that these top-predators gain detailed knowledge of the marine environment, thereby optimising their use of resources

subject to environmental stochasticity (Grémillet et al. 1999). However, their life-history characteristics and their social structure also result in high behavioural resilience, which makes them particularly vulnerable to the abrupt environmental changes detailed in previous sections. In that sense, they are likely victims of ecological traps, which are defined as habitats 'low in quality for reproduction and survival [that] cannot sustain a population, yet...[are] preferred over other available, high-quality habitats' (Donovan & Thompson 2001, p. 872). Such an ecological trap has recently been identified for Cape gannets *Morus capensis* feeding on fishery wastes in the Benguela upwelling (Grémillet et al. 2008b).

HOW SEABIRDS COPE (OR NOT) WITH CURRENT ENVIRONMENTAL CHANGE

Climatic changes, overfishing and the associated rapid modifications of marine food webs described above might cause single seabird populations/species to: (1) modify their trophic status and their foraging ecology to survive and reproduce within the same distribution zone, (2) modify their distribution zone, or (3) go extinct. These 3 options are not mutually exclusive since a bird population/species can attempt to modify its feeding habits as a response to environmental change, while changing its breeding range (or subsequently), and finally go extinct (Ducklow et al. 2007).

(1) Seabirds are capable of adapting their foraging effort to buffer the consequences of environmental change, in particular lower availability of their preferred prey (Arcos & Oro 1996, Litzow et al. 2002), and of evolving life-history traits that allow them to respond to environmental change (Erikstad et al. 1998). There are nonetheless clear eco-physiological limits to this plasticity, and, below a certain threshold of prey availability, foraging is unprofitable (Enstipp et al. 2007), jeopardising reproduction (Harding et al. 2007) and potentially adult survival. Moreover, seabirds generally have a specialised diet, consisting of a limited number of taxa (fish, squid and crustaceans; Shealer 2002). At the species level, this specialisation is even more pronounced (Barrett 2007), with major exceptions, such as in herring gulls *Larus argentatus* (Pierotti & Annett 1991). Nevertheless, numerous seabirds do seem capable of modifying their diet when confronted with scarcity of their natural prey. Seabird diet shifts following climate and fishery-

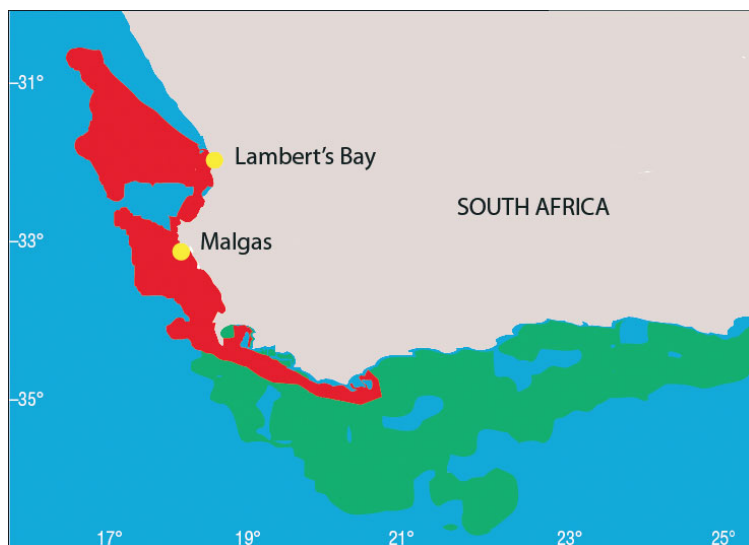


Fig. 3. Combined effects of climate change and overfishing can result in spatial match-mismatch of seabirds and their prey. This is shown here by overlaying Cape gannet *Morus capensis* home ranges (red) from the Malgas and Lambert's Bay breeding colonies with charts of anchovy *Engraulis capensis* distribution (green). Adapted from Grémillet et al. (2008a)

induced environmental change have been demonstrated in many regions of the world's oceans, such as in the Southern Ocean (Hilton et al. 2006, Ainley & Blight 2009), the south-eastern Pacific (Jaksic 2004), the southern California current (Sydeman et al. 2001), the Bering Sea (Springer et al. 2007), the Greenland Sea (Karnovsky et al. 2003), the Norwegian Sea (Durant et al. 2003), the Barents Sea (Barrett & Krasnov 1996), the North Sea (Wanless et al. 2007) and the Benguela upwelling zone (Crawford & Dyer 1995). Whenever assessed, all these shifts had a negative impact on seabird breeding performance, strongly suggesting the importance of dietary specialisation in these marine predators and their difficulties to adapt to rapid environmental change.

(2) Range shifts following climatic changes have been recorded in a variety of seabird species during different phases of their life cycle (breeding and non-breeding). Such patterns are well known within upwelling ecosystems. They were first noticed following El Niño events off the Pacific coast of South America (Ainley & Divoky 2001), and were subsequently extensively studied off California. Veit et al. (1996) showed that non-breeding sooty shearwater *Puffinus griseus* populations that mainly breed in New Zealand, spending the austral winter off the coast of California, declined by 90% in this latter zone between 1987 and 1994, most probably because global warming caused a 90% decrease in zooplankton biomass in the California upwelling system (Roemmich & McGowan 1995, Veit et al. 1997). The distribution of wintering shearwaters then probably shifted towards the central, equatorial Pacific, where climate change had favoured enhanced primary productivity (Ainley & Divoky 2001). A northward distributional shift of further non-breeding species, such as brown pelicans *Pelecanus occidentalis*, Heerman's gulls *Larus heermani* and black *Oceanodroma melania* and least storm petrels *O. microsoma* occurred during the same time period (Ainley et al. 2005), and a warming climate is also the likely cause of a sharp decline of the local Cassins auklet *Ptychoramphus aleuticus* population (Lee et al. 2007). Further examples of seabird range modifications probably caused by climate change (sometimes in interaction with other constraints such as fisheries) were recorded in polar areas (Ainley & Divoky 2001), and in the temperate zone of the North Atlantic (Thompson 2006, Wynn et al. 2007, but see Votier et al. 2008).

(3) Nevertheless, not all seabird species show such geographic plasticity. Some endemics are trapped in restricted areas and face likely extinction due to the impact of climate change. This is most probably the case for the Galápagos penguin *Spheniscus mendiculus* (Vargas et al. 2007) and the marbled murrelet *Brachyramphus marmoratus* (Becker et al. 2007).

MAJOR OBJECTIVES OF SEABIRD SPATIAL ECOLOGY

Determining the factors affecting seabird distribution and movements at sea and on land

Despite the few case studies detailed in the previous sections, it appears that our knowledge of the spatial ecology of seabirds facing the consequences of climate change is rather anecdotal and that such investigations are still at the pioneering stage (Fig. 4). One of the major targets of seabird ecology is, therefore, to make use of the most recent tools to investigate the short- and long-term movements of individual seabirds at sea, as well as distributional shifts in their breeding populations.

Exploration of seabird movements at sea is booming at the moment (Ropert-Coudert & Wilson 2005). This is because the miniaturisation of tracking systems such as Global Location Sensors (GLS, see Wilson et

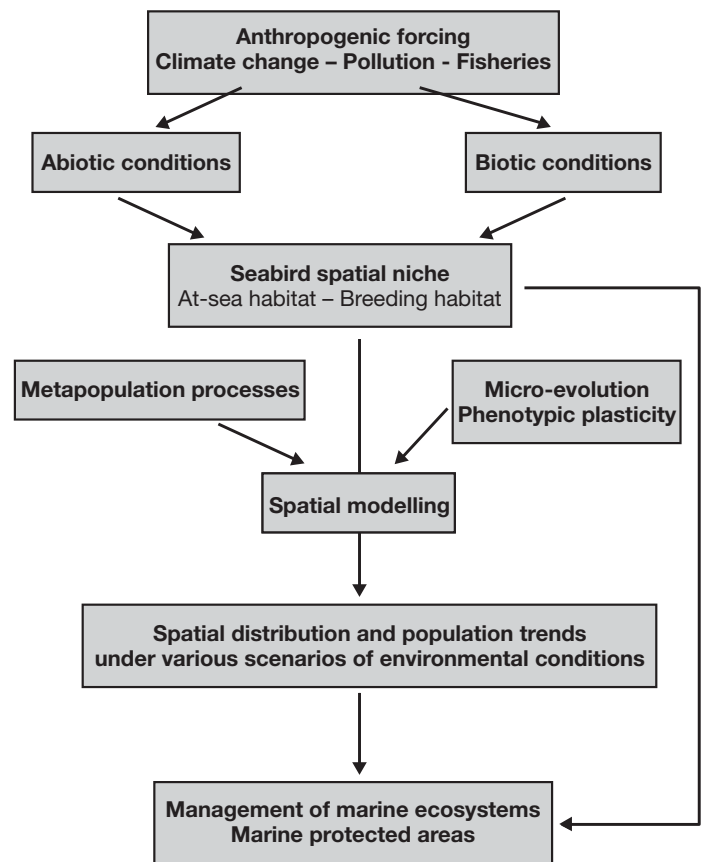


Fig. 4. Factors influencing the spatial niche of seabirds, and key topics for future research. Note that exploration of current spatial niches of seabirds (at sea and on land) and modelling of their future spatial niches both provide major contributions to the design of marine protected areas and management schemes for marine ecosystems

al. 1992) and Global Positioning Systems (GPS) has enabled deployment of <10 g tags on a wide range of seabird species. Information gathered using these techniques, in combination with direct at-sea observations, will fill huge gaps in our knowledge of the home ranges of breeding and non-breeding seabirds, especially for small species that are poorly detected during at-sea surveys (Croxall et al. 2005). Beyond the gathering of crucial spatial information, the range of analytical tools used to define seabird distribution and movements is expanding rapidly. For instance, foraging tracks can be analysed using simple sinuosity indexes, whereby the most tortuous sections are associated with prey consumption and more linear sections with commuting between feeding sites (Grémillet et al. 2004a). First passage time analysis (*sensu* Fauchald et al. 2000) is a refinement of this technique, and enables the identification of oceanic zones within which birds display area-restricted searches, which is also thought to be tightly related to prey consumption (Pinaud 2008). Application of this method to seabird spatial ecology has attracted much attention (Weimerskirch et al. 2007), but has recently been criticised (Barraquand & Benhamou 2008). The adequacy of this technique and of further analytical methods, e.g. the fractal dimension approach (Tremblay et al. 2007), remains a key objective of investigation in the near future. Furthermore, the pertinence of kernel analyses, which have also been routinely used to map the distribution of seabirds at sea, has been criticized (Hemson et al. 2005), and should likewise be reassessed and potentially replaced by more refined mapping techniques.

In parallel to at-sea investigations, further efforts have to be made to understand factors affecting changes in numbers of breeders in the colonies. This is because integrated land-based and at-sea seabird ecology would provide a more complete appraisal of factors affecting seabird distribution. Global warming may, for example, cause breeding habitat loss via sea-level rise and potential shifts in the geographic ranges of predators and parasites, which could, in turn, affect the dynamics of breeding colonies. As seabird populations are subdivided at different spatial scales and are made of breeding groups that can exchange individuals and become extinct, they may function as metapopulations. A key process requiring specific efforts is thus to understand which factors affect the dispersal of individuals and their consequences.

We urge that at-sea and land-based research of seabird spatial ecology be considered in combination. Both areas of research are involved in the same ecological processes, which ultimately determine breeding output and survival and, thereby, shape population dynamics (Fig. 5). Beyond this integrative approach, it is essential that such investigations become part of

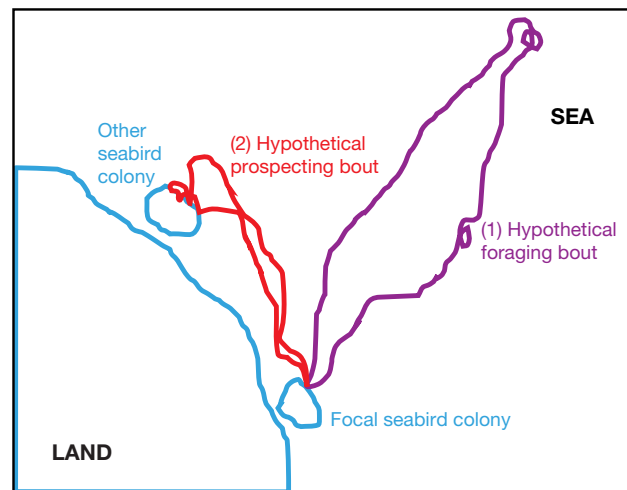


Fig. 5. Hypothetical tracks of the movements of a breeding seabird, illustrating the significance of combining at-sea and land-based studies using modern tools to investigate the responses of seabird populations to environmental changes: (1) foraging bout, showing the spatial scale at which foraging occurs, and (2) 'prospecting bout', showing the spatial scale at which breeding dispersal may occur. Biotelemetry tools have been extensively used for at-sea studies, but they could also be used to explore behavioural processes involved in population dynamics (e.g. prospecting for a potential future breeding site; Boulinier et al. 1996)

long-term monitoring projects (considering seabird longevity, these have to last several decades) developed in a spatial context. In addition to the identification of specific questions that need to be addressed (see the 2 following subsections), the design of such monitoring programmes requires the consideration of spatial variability in the estimated parameters (Yoccoz et al. 2001). Longitudinal data sets collected at multiple study sites should, thus, be very valuable in assessing and modelling the impact of global change in seabird spatial ecology.

Linking seabird distribution patterns to those of their prey

As demonstrated by Aebischer et al. (1990) in a spectacular manner, seabirds cannot be studied in isolation, and spatial information alluded to in the previous section has to be put into a wider ecological context if we are to understand observed trends. Modern seabird ecologists are therefore also oceanographers, capable of analysing seabird distribution, movements, diet and trophic status in combination with biotic and abiotic environmental conditions, in particular prey availability/quality. Indeed, remote-sensed values of chlorophyll *a* concentration, SST and sea-surface

height have been, and are still being, widely used as surrogates for the relative productivity of oceanic waters and their potential profitability to foraging seabirds (Pinaud & Weimerskirch 2007). However, these variables are proxies for primary productivity, while seabirds are top-predators, which usually feed 2 to 3 trophic levels higher up the food chain. Correlations between seabird distribution and indices of primary productivity can consequently be quite misleading (Grémillet et al. 2008a), and we urge investigators to favour spatial analyses linking seabird at-sea ecology with direct assessments of prey availability (the key resource required by seabirds) conducted from research vessels (e.g. pelagic fish population assessments via echo-sounding). The remote-sensing data mentioned earlier may nonetheless feature co-variables useful in complementing statistical models to predict the distribution and movements of seabirds facing climate change.

Impact of historical and metapopulation processes on seabird spatial distribution

Factors affecting dispersal, the dynamics of colonization and the extinction of local populations are keys to understanding the spatial dynamics of seabird (meta-) populations. Constraints on dispersal and historical events may explain some broad patterns of seabird spatial distribution, such as the absence of auks in the southern hemisphere or the absence of albatrosses in the North Atlantic. At the scale of seabird metapopulations (i.e. populations linked by dispersal events), these aspects are particularly important to consider. Estimating dispersal rates and quantifying factors affecting dispersal are difficult tasks, despite strong ecological and evolutionary implications (Clobert et al. 2001), notably in the context of global change (Kokko & López-Sepulcre 2006). This is because the probability of detecting dispersal events is strongly affected by re-sighting probabilities at potential breeding locations, which are difficult to account for (such probabilities are often low, heterogeneous, or not estimated). Comparisons of estimated local population growth rates with those that can be obtained from estimated demographic parameters can provide information on potential source sink dynamics (Pulliam 1988, Oro 2003). Such an approach has, for instance, been used to show that emigration and immigration can be very significant to the dynamics of local breeding populations of gulls (Danchin & Monnat 1992, Danchin et al. 1998, Suryan & Irons 2001). A more formal metapopulation framework and capture–recapture modelling (Spendelov et al. 1995, Cam et al. 2004) allow stronger inference concerning the factors potentially affecting

dispersal rates. Studies inferring dispersal and movements of individuals using indirect methods, such as population genetics and biogeochemical analyses (Riffaut et al. 2005, McCoy et al. 2005, Gómez-Díaz & González-Solís 2007) can provide important information in this context (e.g. on population structure, gene flow and the geographic origin of individuals).

If natal dispersal is now generally considered to be important in many species, relatively little is known about recruitment processes and breeding habitat selection behaviour because of the large temporal scale involved (Boulinier et al. 2008b). Population genetic approaches have nevertheless shown that dispersal can occur at various scales (Riffaut et al. 2005, Shepherd et al. 2005). Further, detailed work on breeding habitat selection (Danchin et al. 1998, Boulinier et al. 2008b) and the role of prospecting individuals in kittiwakes (Boulinier et al. 1996) has stressed that the local breeding success of colonies or sub-colonies could amplify population change via the dispersal of individuals and their differential recruitment as a function of the relative attraction towards successful areas prospected the year before. Such studies have nevertheless been conducted at relatively small spatial scales. Prospecting by individuals not born locally has been recorded to occur over wide spatial scales (Reed et al. 1999). Up until now, most habitat selection studies have nevertheless been conducted at relatively small spatial scales and it is not clear how those processes may translate at broader scales, scales at which effects of climate change may occur. Moreover, competition for sites, density dependence effects on breeding success and the mere attraction conspecifics are other key processes involving individual behaviour that need to be considered and that can complicate observed patterns (Kokko et al. 2004, Oro et al. 2006). One benefit of considering dispersal and breeding habitat selection strategies in an adaptive framework is that it underlines the importance of looking at the spatio-temporal patterns of variation of breeding habitat quality in which a considered species has evolved (Boulinier & Lemel 1996, Doligez et al. 2003), which can be affected by climate change. For instance, if predictable changes in food availability and expected reproductive success become more unpredictable because of global warming and fish depletion, then one could expect some species to be caught in ecological traps. The problem becomes even more complex if we consider that habitat quality will also affect the survival of adult and immature individuals and that variability at various hierarchical scales has to be considered. Breeding habitat selection behaviours, as well as dispersive behaviours at sea, thus have the potential to strongly mediate the effect of climate change on the distribution and abundance of seabirds.

Assessing phenotypic plasticity and the potential for microevolution

Current field investigations and models seldom take into account the capacity of seabirds to display phenotypic plasticity and microevolution of spatial traits (*sensu* Visser 2008). Most models alluded to in the next section are built around sets of empirical/theoretical relationships between seabird spatial variables and further environmental components. Model predictions typically assume that these relationships do not evolve through time, although this is highly unlikely to be the case. Indeed, the shape of existing functional relationships can shift widely due to the phenotypic plasticity of individuals, i.e. their capacity to display behavioural and physiological short-term adaptation to given environmental conditions. In seabirds this becomes most apparent when studying functional relationships between seabird predatory performance and local prey abundance, which are essential to understand and predict seabird spatial patterns. In cormorants for instance, trials under controlled conditions generated significant, positive functional relationships between fish abundance and seabird predatory performance (Enstipp *et al.* 2007). However, similar investigations in the wild indicated that cormorants are capable of maintaining very high predatory performance, even when exploiting fish resources at low density (Grémillet *et al.* 2004b). This strongly suggests substantial phenotypic plasticity in the form of behavioural adaptability, which considerably reduces our capacity to predict the spatial response of predators such as cormorants to the consequences of global warming (White *et al.* 2008).

Beyond phenotypic plasticity, recent investigations in land birds clearly showed the importance of considering the impact of the microevolution of functional traits on the spatial response of individuals and populations to climate change (Visser 2008). True, seabirds are particularly long-lived species and it is unlikely that microevolution will influence their overall spatial response as much as phenotypic plasticity, but it remains a fascinating, and yet largely unexplored, research avenue (Reed *et al.* 2006).

Exploring phenotypic plasticity and microevolution of functional relationships is not possible via office-based theoretical modelling. This requires detailed, longitudinal field investigations of seabird spatial ecology and population dynamics using the modern tools mentioned earlier, from biotelemetry to quantitative genetics. This, once more, calls for the continuation of the development of long-term monitoring programmes of seabird populations integrating multidisciplinary approaches.

Modelling present and future seabird habitats and populations

A vast panel of algorithms has been computed in recent years to assess future range and abundance of species exposed to global warming. To name just a few, we may use climate envelope models (CEMs), generalized additive models (GAMs), mechanistic models (MMs), discriminant analysis, artificial neural networks, maximum entropy, or hierarchical Bayesian models (see, for instance, Pearman *et al.* 2008). To take a more general perspective, the evolution of seabird spatial niches might also be considered within the framework of marine ecosystem-based models (Cury *et al.* 2008). This approach has the major advantage of considering entire predator communities, thereby including interspecific competition, an aspect which may be neglected using other species-centred modelling techniques.

The techniques mentioned here follow different approaches. For instance, widely used CEMs explore and characterise functional relationships between seabird spatial variables (home range size and position, foraging path characteristics) and the abiotic and biotic variables mentioned in the subsection 'Linking seabird distribution patterns to those of their prey'. They then extrapolate these statistical relationships to predict future spatial distributions and abundances of seabirds (Hijmans & Graham 2006). CEMs have 2 major weaknesses: (1) identified functional relationships are correlative and usually cannot be tested and (2) there is no way to test that these relationships will be sustained in the future. Seabird reaction norms may vary due to phenotypic plasticity and microevolution, which, as we have seen in the previous subsection, can be a problem. Beyond CEMs, the use of MMs to evaluate future seabird distribution and abundance is currently being explored. In contrast to CEMs, MMs are not based upon observed statistical correlations, but rebuild the thermal and ecological niche of organisms using first principles of thermodynamics (Hijmans & Graham 2006). In such cases functional relationships between the spatial characteristics of given species and environmental parameters are not fitted, but calculated. MMs provide exciting perspectives, but their pertinence also remains to be tested.

The use of such methods is extremely recent in seabird ecology (e.g. Österblom *et al.* 2007, Ainley *et al.* 2008), but is bound to increase dramatically in coming years. Nevertheless, current land-based investigations show that predicting species distribution and abundance in a rapidly changing world is a daunting task, to say the least (Pearman *et al.* 2008). Knowing that marine ecosystems and marine biodiversity are traditionally much harder to study than their terrestrial

equivalents, it remains unclear whether such modelling approaches will yield significant advances in our understanding of seabird spatial ecology. They will nevertheless be useful to generate broad predictions that can provide useful material to combine with data from population studies. As we have seen in the previous subsection 'Impact of historical and metapopulation processes on seabird spatial distribution', the integration of metapopulation processes is also required in modelling, notably when predictions are to be made at regional spatial scales.

Helping define marine protected areas (MPAs) and refining further conservation schemes

Marine habitats are the last frontier of conservation. Seabird ecologists have the exciting, yet daunting, task to participate in defining marine conservation plans, in particular the design of MPAs and capacity reduction areas for sea fisheries. Seabird breeding colonies have been efficiently protected for about a

century, and have greatly benefited from these measures; for instance, dozens of colonies have been designated Antarctic Specially Protected Areas, which are recognized internationally under the Antarctic Treaty. As another example, around the British Isles, seabird numbers were low at the beginning of the 20th century, due to centuries of hunting. However, as a result of protection of most of their breeding habitats, they increased throughout the second half of the 20th century, and the seabird community of Britain and Ireland on the whole prospered during this latter period (Grandgeorge et al. 2008). In contrast, the early 21st century has witnessed major breeding failures along the North Sea coast of the UK, clearly demonstrating that land-based seabird conservation is not sufficient (Wanless et al. 2007). Indeed, seabird population dynamics are conditioned by food availability at sea just as much as by the availability of suitable breeding habitat on land.

Seabirds are now threatened on a world-wide scale (Butchart et al. 2004), and general agreement exists that they will greatly benefit from MPAs, as will all fur-

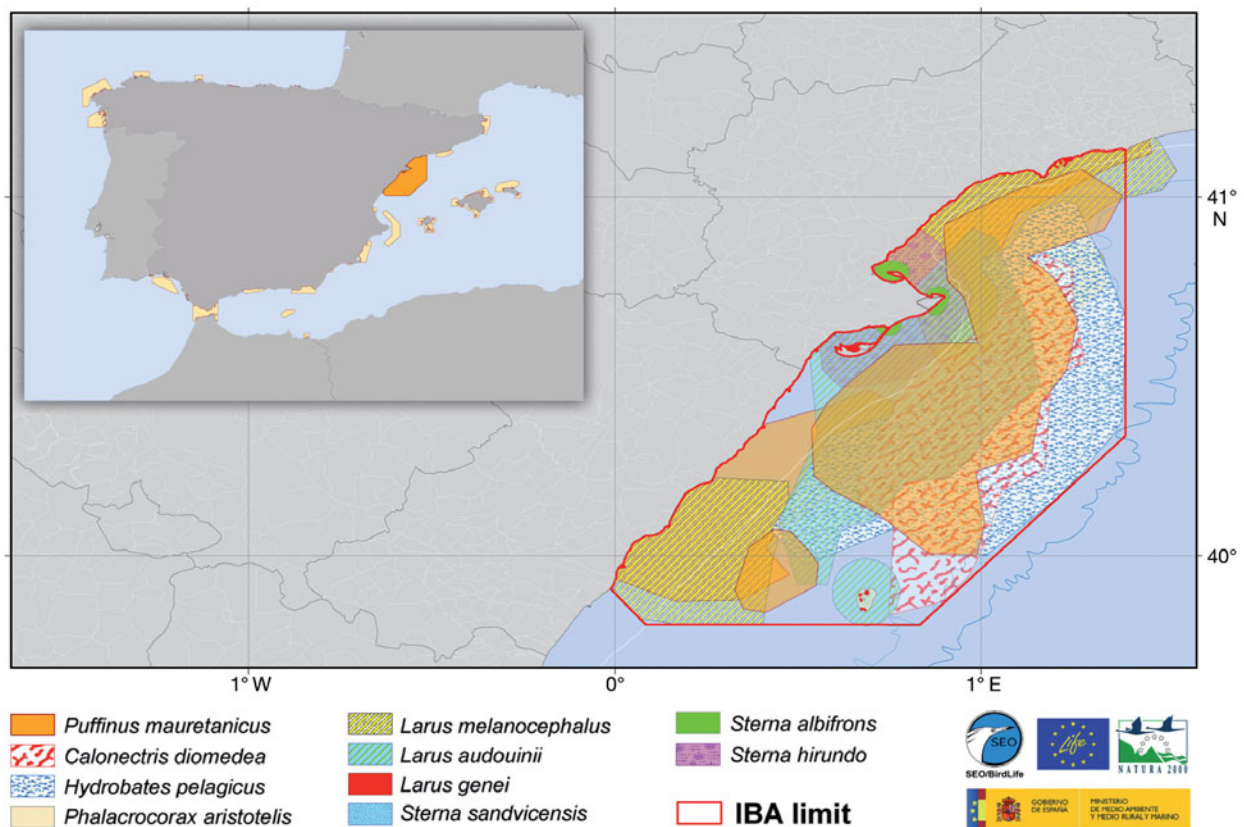


Fig. 6. Seabird spatial studies can help identify marine Important Bird Areas (IBAs). In a study performed by SEO/BirdLife covering the whole of Spanish waters, the assessment of breeding colony distribution, biotelemetry studies (PTT [platform transmitter terminal] and GPS), aerial-surveys, at-sea observations, and land-based observations were used for a series of vulnerable seabird species to identify marine IBAs. The situation map shows proposed marine IBAs around the Spanish section of the Iberian Peninsula, and the detailed map shows the IBA proposed for the Ebro Delta (orange zone on the situation map). Provided by SEO/BirdLife, adapted from Arcos et al. (2009)

ther components of marine ecosystems critically challenged by anthropogenic global change. Australia and the USA have been pioneers in the establishment of MPAs, while European nations have committed themselves to establishing a network of marine IBAs (Important Bird Areas) over their territorial waters by 2012 (Arcos et al. 2009). BirdLife International is in the process of identifying a network of marine IBAs worldwide, with the aim of providing guidance, with respect to seabirds, for the creation of MPAs. Spain and Portugal have led this initiative, with marine IBA inventories published in 2009 that are expected to become Special Protection Areas in the near future (Arcos et al. 2009).

Most unfortunately, as we have seen in previous subsection, marine ecosystem structure is highly labile, both spatially and temporally, and defining marine reserves is immensely more complicated than defining terrestrial reserves (Hyrenbach et al. 2000, Hooker & Gerber 2004). With respect to seabirds, and to marine top-predators in general, one of the major, and most urgent, tasks is to compile algorithms allowing researchers and managers to define the spatial and temporal cover of MPAs, while balancing the contrasting requirements of marine megafauna and human activities (Fig. 6; Harris J et al. 2007, Pichegru et al. 2009, this Theme Section). A range of such statistical methods is already available for the management of terrestrial habitats, and some of these methods are currently being adapted to marine habitats (Fig. 6; Arcos et al. 2009).

Beyond establishing MPAs, and because their efficiency is still being evaluated, it becomes increasingly clear that further conservation measures have to be employed, especially capacity reductions of industrial fisheries (Okes et al. 2009).

Further exploration of the spatial ecology of seabirds using the diverse approaches mentioned in the previous subsections, in particular biotelemetry, will play an essential role in defining these conservation strategies. Present seabird ecologists are living in a challenging, yet highly exciting period.

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