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Contribution to the Theme Section 'Spatiotemporal dynamics of seabirds in the marine environment'

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Introduction and synthesis: spatial ecology of seabirds at sea

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ABSTRACT: The spatial ecology of seabirds has greater precedence today than ever before because of impacts on the marine environment from human exploitation, pollution, and climate change. Specific life history traits make seabirds particularly sensitive to these impacts, currently driving many species to unsustainable population declines. To evaluate the risk posed by human activities, we need integrative studies on seabird abundance, distributions, and movements in relation to the biophysical marine environment. Also interpreting the limits of these relationships is fundamental to understanding historical constraints and behavioural adaptations of seabirds that are shaped by evolutionary processes. In this Theme Section, we assembled 4 review papers and 10 case studies that highlight some of the latest techniques to study seabird spatial ecology. This includes the application of tracking tags, ship-based surveys, and remotely sensed environmental data, to characterize seabird movement patterns, fine scale behaviour, and overall distribution combined with measures of the oceanic habitats to enhance our understanding of the functional role that seabirds play. Overall, this knowledge is crucial for understanding and predicting the impacts that fisheries, climate change and pollution are exerting on marine ecosystems and will provide opportunities for developing marine protected areas, conservation action plans and species management.

KEY WORDS: Ecosystems · Impacts · Marine · Seabirds · Spatiotemporal dynamics · Tracking

IMPACTS ON MARINE ENVIRONMENT

Human pressure on marine ecosystems has increased enormously over the last several decades (Halpern et al. 2008). This pressure takes many forms, such as massive fishery activities, incidental entanglement in fishing gear by non-target species, episodic and chronic contamination, and ingestion of harmful plastics. Climate change is also beginning to show measurable effects on marine ecosystems, particularly at high latitudes.

As a result, human activities on the marine environment are directly responsible for the deaths of hundreds of thousands of marine predators worldwide each year. Apical species are particularly sensitive to these impacts and may show non-linear responses in the form of sharp unexpected collapses in their populations. Among marine vertebrates, seabirds (comprised of nearly 400 species) are particularly vulnerable because most species are top marine predators that exhibit high adult survival, but low annual fecundity and slow population growth overall (Ricklefs 1990). Since many impacts increase adult mortality, seabirds, particularly pelagic species, have become threatened at a faster rate globally than all other groups of birds (BirdLife International; www.birdlife.org/worldwide/index.html). Currently about 30% of pelagic species are threatened with unsustainable population declines, e.g. the extinction of the Balearic shearwater is modelled to take place in 40 yr if the impact of longlining on adult mortality is not minimized (Oro et al. 2004).

Understanding spatiotemporal dynamics in seabirds at sea is critical to identify and manage seabird responses to human-induced or climate-related changes on marine ecosystems. Moreover, it is not just a matter of identifying and describing seabird and biophysical patterns, but also there is an urgent need to understand the specific physical and biological processes that contribute to the dynamic nature of these patterns. This task is particularly difficult to elucidate because seabirds have impressive mobility, unparal-

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leled among marine predators. They can easily move hundreds, thousands, or tens of thousands of kilometres in a matter of hours, days or weeks, respectively. Therefore, integrating a spatial component to the study of interactions between seabirds and the marine ecosystem is particularly relevant and greatly needed.

Technological advances have greatly improved our ability to concurrently examine the movements of free-ranging seabirds and the marine environment at relevant spatial and temporal scales, in ways never dreamed possible even a few years ago. These advances are typified by (1) an incessant miniaturization of electronic tags to monitor seabird movements, distributions, and activity; (2) improvements and standardization of methods to survey seabirds and their prey at sea; and (3) global coverage of remotely-sensed oceanographic features to characterize marine habitat. Integrative approaches are also facilitated by greater computational resources for modelling interactions between seabirds and oceanographic traits, fishing activity, and contamination in a geospatial environment. Consequently, we assembled this Theme Section by bringing together 4 reviews and 10 case studies that clearly integrate these advances to enhance our understanding of the different patterns and processes related to the dynamics in seabirds at sea.

SYNOPSIS OF THEME SECTION

Across broad scales, biological and physical characteristics of the ocean define the potential habitats of seabirds. Since these traits can change over seasons or years, understanding the spatial dynamics in seabirds requires detailed ecologically-based studies on seabird abundances, distributions, and movements in relation to the biophysical marine environment (Catry et al. 2009, Garthe et al. 2009, González-Solís et al. 2009, Kubetzki et al. 2009, Louzao et al. 2009, Phillips et al. 2009, Shaffer et al. 2009, Weimerskirch et al. 2009, all this Theme Section). However, this knowledge is also essential for understanding the effects that climate change is exerting on the spatial ecology of seabirds. Climate is a major driver of biophysical coupling in the ocean and has significant impacts on marine productivity, environmental stochasticity and cyclicity. Physical forcing and bottom-up processes ultimately change prey availability and distribution and can, therefore, induce spatial changes in marine predators. However, rapid modifications may lead to ecosystem instability because not all food-web components respond in the same manner to environmental change, resulting in a spatiotemporal match-mismatch of predators (i.e. seabirds) and their prey (reviewed in Grémillet & Boulinier 2009, this Theme Section).

Beyond the biophysical environment, historical constraints and behavioural adaptations remind us of the evolutionary processes that underlie all aspects of spatial ecology. One major process producing complex spatial patterns is the interaction between seabirds and their prey. Despite its superficial homogeneity, the sea is a heterogeneous environment where prey is patchily distributed in a hierarchical organization. We would expect seabirds to track their prey by closely matching the spatial and temporal dynamics in prey. However, spatial constraints between predators and their prey and behavioural responses of the predatory interactions make these relationships more elusive than expected (reviewed in Fauchald 2009, this Theme Section). Seabirds can be spatially constrained by past and present competition promoting resource partitioning among species. In some circumstances this process can even shape the spatial segregation between males and females at intraspecific levels (Weimerskirch et al. 2009). The fundamental spatial constraint for all seabirds, however, arises from the need to breed on land but also in areas more or less inaccessible to terrestrial predators. This double condition has confined many pelagic seabirds to breed on remote oceanic islands often far from the best feeding grounds, thus promoting the emergence of specific morphological adaptations as well as behavioural strategies that enhance energetic efficiency while breeding. For example, many pelagic seabirds alternate short foraging trips to maximize energy delivery to the chick with long foraging trips to restore their own reserves (Weimerskirch et al. 1994). However, strategies can vary among species and populations, and this needs to be studied in depth before making any generalities about a particular strategy (Phillips et al. 2009).

Currently, the greatest source of competiton for seabirds is human fishing activity. Seabirds and fisheries often exploit similar resources at similar spatiotemporal scales, overlapping particularly on most continental shelves worldwide (Karpouzi et al. 2007). Although seabirds are sometimes dismissed as a component of the marine ecosystem, at least 15 species have more than 10 million individuals, which equates to a huge biomass that consumes about 100 Mt of marine prey annually (Brooke 2004). This value represents about 10% of global marine productivity and is close to the overall fishery extraction. However, seabirds exploit marine prey in a sustainable way, whereas fisheries have already overexploited two-thirds of the world's fish stocks (Worm et al. 2009). Overexploitation of marine resources can collapse stocks of seabird prey and drive seabird populations to starvation, exacerbating the effects of climate change, which also purportedly will affect the distribution and abundance of forage fish (reviewed in Grémillet &

Boulinier 2009). Furthermore, some fishery types, such as longlining, are responsible for the direct death of more than a hundred thousand seabirds each year (BirdLife International). Therefore, assessing the spatial overlap between seabirds and fisheries is a critical step for understanding their potential interactions (Pichegru et al. 2009, this Theme Section).

Despite the enormous potential of tracking technology, some limitations and biases make biogeochemically intrinsic markers an excellent complement to study the feeding ecology and spatial dynamics in seabirds (Weimerskirch et al. 2009). Stable isotope or elemental analyses of seabird tissues have emerged as a powerful and sometimes unique alternative, in particular to study species that cannot be tracked because of size limitations or accessibility. It is now possible to use geographic gradients or water mass-specific signatures as tools for determining foraging habitats in the marine environment (Ramos et al. 2009). However, the lack of a detailed spatial knowledge of baseline isotope variations hampers our understanding of the isotopic dynamics. In this context, compound-specific isotopic analyses (CSIA) of trophic versus source amino acids provide a new tool to track isotopic baseline levels, which is also critical for a better understanding of the feeding ecology of seabirds (Lorrain et al. 2009, this Theme Section).

Describing and quantifying the association between seabirds and the marine habitat is also essential to model spatial patterns and predict responses of seabirds to the environment. However, this is not an easy task because new scientific approaches and methodological tools to collect and analyse spatial data are evolving rapidly (reviewed by Tremblay et al. 2009, this Theme Section). For example, oceanic features can now be inferred from the remotely-sensed biophysical traits of the water masses, allowing for more process-based, rather than descriptive, approaches. Moreover, collection of particle-like data (Lagrangian) such as that obtained from tracking devices is increasing compared to the more traditional grid-like data (Eulerian) based on ship surveys. Without question, tracking studies provide opportunities to study individual behaviour from birds of known origin and status. Most importantly, the detection of specific foraging behaviours (e.g. travel speeds, turn angles, etc.) associated with particular environmental traits or feeding events, open new opportunities for understanding seabird spatial ecology as well as identifying key foraging grounds. Although non-independence of tracking data is challenging, new statistical methods are now capable of dealing with these problems (reviewed in Wakefield et al. 2009, this Theme Section). Seabird surveys from vessels, however, provide a more integrative multispecies approach from a large scale perspective. Clearly, the 2 approaches can yield complementary perspectives on habitat use and suitability, calling for more integrative studies to identify key marine areas for management and conservation purposes (e.g. Louzao et al. 2009). Obviously, a major goal of studying the spatial ecology of seabirds is the contribution made toward identifying important bird areas and to help designate marine protected areas (Garthe et al. 2009, Grémillet & Boulinier 2009, Louzao et al. 2009). However, this process is far more complicated at sea than in terrestrial environments because both risk exposure and key areas are more variable in distribution, time, and extent with changing human activities and biophysical traits of the marine ecosystem.

SUMMARY AND CONCLUSIONS

In summary, the assemblage of contributions provided in this Theme Section demonstrate that it is now possible to integrate spatial and temporal aspects into the study of seabirds at sea more rigorously than ever before. While this integration is not always straightforward, it has substantially enhanced our understanding of complex ecological relationships in general as well as of the risks posed to seabirds at sea. Overall, this knowledge will be crucial for predicting the impacts that fisheries, climate change and pollution are exerting on marine ecosystems, since we now have the first clear signs that spatial dynamics in seabirds at sea are being affected. Therefore, incorporating this knowledge into the management of marine ecosystems will facilitate effective conservation of seabird populations and help preserve their marine habitat and its biodiversity.

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