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Fine-scale recognition and use of mesoscale fronts by foraging Cape gannets in the Benguela upwelling region

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ABSTRACT

Oceanic structures such as mesoscale fronts may become hotspots of biological activity through concentration and enrichment processes. These fronts generally attract fish and may therefore be targeted by marine top-predators. In the southern Benguela upwelling system, such fronts might be used as environmental cues by foraging seabirds. In this study we analyzed high-frequency foraging tracks (GPS, 1 s sampling) of Cape gannets *Morus capensis* from two colonies located on the west and east coast of South Africa in relation to mesoscale fronts detected on daily high-resolution chlorophyll-*a* maps (MODIS, 1 km). We tested the association of (i) searching behavior and (ii) diving activity of foraging birds with mesoscale fronts. We found that Cape gannets shift from transiting to area-restricted search mode (ARS) at a distance from fronts ranging between 2 and 11 km (median is 6.7 km). This suggests that Cape gannets may be able to sense fronts (smell or vision) or other predators, and that such detection triggers an intensified investigation of their surroundings (i.e. ARS). Also we found that diving probability increases near fronts in 11 out of 20 tracks investigated (55%), suggesting that Cape gannets substantially use fronts for feeding; in the remaining cases (45%), birds may have used other cues for feeding including fishing vessels, particularly for gannets breeding on the west coast. We demonstrated in this study that oceanographic structures such as mesoscale fronts are important environmental cues used by a foraging seabird within the rich waters of an upwelling system. There is now need for further investigations on how Cape gannets actually detect these fronts.

1. Introduction

Oceanic circulation and light availability play a key role in structuring ecosystems throughout the oceans. Oceanic circulation is crucial to supplying nutrients to the layer that light penetrates, and thereby sustaining and shaping primary productivity of marine food webs. Depending on the size, life span and diet of marine species, primary production may constrain the distribution of marine species across various spatiotemporal scales (Longhurst, 1998). Hydrodynamic features – from larger scales (several hundreds of kms) down to smaller scales (e.g. mesoscale, from 1–2 km to 100–200 km) – are known to drive the distribution and foraging patterns of top-predators because the predictability of prey is higher in and around these structures (Weimerskirch, 2007). It has been well documented that large convergence zones (e.g. polar front) correspond to foraging areas of marine birds and mammals (review by Bost et al. (2009)). At smaller scales, dynamic mesoscale structures such as eddies, vertically-structured fronts and filaments are essential to the enrichment, concentration and retention of nutrients and planktonic organisms in surface waters (*Bakun's triad*, cf. Bakun, 1996) which attract and shape the aggregation patterns of plankton-eaters such as small pelagic fish (Bakun, 2006; Bertrand et al., 2008; Sabarros et al., 2009). Mesoscale structures are considered as major attracting features for large predatory fish (Young et al., 2001; Seki et al., 2002), marine mammals (Campagna et al., 2006; Cotté et al., 2007) and seabirds (Nel et al., 2001; Weimerskirch et al., 2004, 2005; Ainley et al., 2005, 2009; Hyrenbach et al., 2006).

How top-predators find these structures – notably fronts – still remains poorly understood. Nevitt (2000, 2008) showed that a range of seabirds (procellariiforms) track and capitalize on fronts

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across different scales using olfactory and visual cues. Procellariiforms navigate at large scales by following odor compounds (e.g. dimethyl sulfide) that are released by plankton organisms that accumulate at fronts. Once in the visual range of fronts, procellariiforms may locate and dive onto fish patches. Only a limited number of studies investigated the association between particular foraging behavioral patterns in animal movements and environmental features. For example, Trathan et al. (2008) showed that king penguins at South Georgia concentrate their foraging effort to water masses with a particular temperature range, and Tew Kai et al. (2009) demonstrated that frigate birds feed at the edge of mesoscale eddies in the Mozambique channel. There is a crucial need for such insight to improve our understanding of the underlying mechanisms of seabird foraging behavior (Tremblay et al., 2009).

Eastern boundary upwelling systems (EBUS) are subtropical coastal oceanic regions where an important atmospheric forcing (i.e. winds) induces an offshore transport of surface waters that are replaced by nutrient-rich waters from subsurface layers (Capet et al., 2008). This newly upwelled water supports intense primary and secondary production that sustains the world's highest fish biomass and fisheries (Pauly and Christensen, 1995). In EBUS, mesoscale features such as eddies, vertically-structured fronts, and filaments, are generated by the instability of alongshore currents and the offshore Ekman transport of surface waters (Capet et al., 2008) especially close to the shore (Pedlosky, 1978; Durski and Allen, 2005). Local enrichment and concentration of nutrient in mesoscale features promotes plankton production (Bakun, 2006) and may thereby attract schools and clusters of planktivorous fish (e.g. Ainley et al., 2005; Sabarros et al., 2009). Surface mesoscale fronts associated to eddies, filaments and vertically-structured fronts are common in the southern Benguela upwelling – one of the major EBUS – located off the coast of South Africa. Such fronts may attract the most abundant planktivorous fish in that region that are the sardine *Sardinops sagax* and the anchovy *Engraulis encrasicolus* (van der Lingen et al., 2006). These pelagic fish constitute the main prey items of a medium-ranging seabird: the Cape gannet *Morus capensis* that breeds at two colonies located on the west and the east coasts of South Africa (Hockey et al., 2005). Cape gannets forage within the productive waters of the Benguela upwelling system on the continental shelf (Pichegru et al., 2007) and might therefore use fronts as environmental cues when foraging. Foraging mechanisms and cues used by Cape gannets are poorly known apart from the fact that Cape gannets sometimes scavenge fishing boat discards on the west coast of South Africa (Grémillet et al., 2008).

The influence of mesoscale oceanic structures of only a few kilometers wide on the distribution and foraging patterns of top predators has been little investigated due to the difficulty of observing properly these patterns by satellites (e.g. Tew Kai et al., 2009) or field measurements (e.g. van Franeker et al., 2002). Thanks to technological advances in both satellite remote sensing (e.g. high-resolution chlorophyll-*a* measurements) and seabird biotelemetry (e.g. high-frequency GPS) we are now able to study foraging patterns of marine predators in relation to their environment at the lower mesoscale (few kms). In the present study we use for the first time a combination of high-precision individual GPS tracks (1 s sampling) of Cape gannets and high-resolution daily maps of chlorophyll-*a* (1 km) provided by MODIS on which we have identified mesoscale fronts (with edge detection algorithm). We assume here that chlorophyll-*a* fronts are a proxy for the occurrence of seabirds' prey as shown in various studies (e.g. Ainley et al., 2005; Bakun, 2006; Sabarros et al., 2009). From GPS tracks we have extracted the bird's searching behavior (i.e. area-restricted search ARS) and feeding activity (i.e. dives). We use our datasets to test associations of (i) searching behavior and (ii) diving activity with the presence and location of mesoscale fronts in the Benguela upwelling system. We expect that the proximity of fronts will induce intensified search patterns by Cape gannets and that feeding activity will be concentrated around fronts.

2. Material and methods

2.1. Seabird tracks

Foraging movements of breeding Cape gannets were monitored at two South African colonies during the reproductive season of 2009

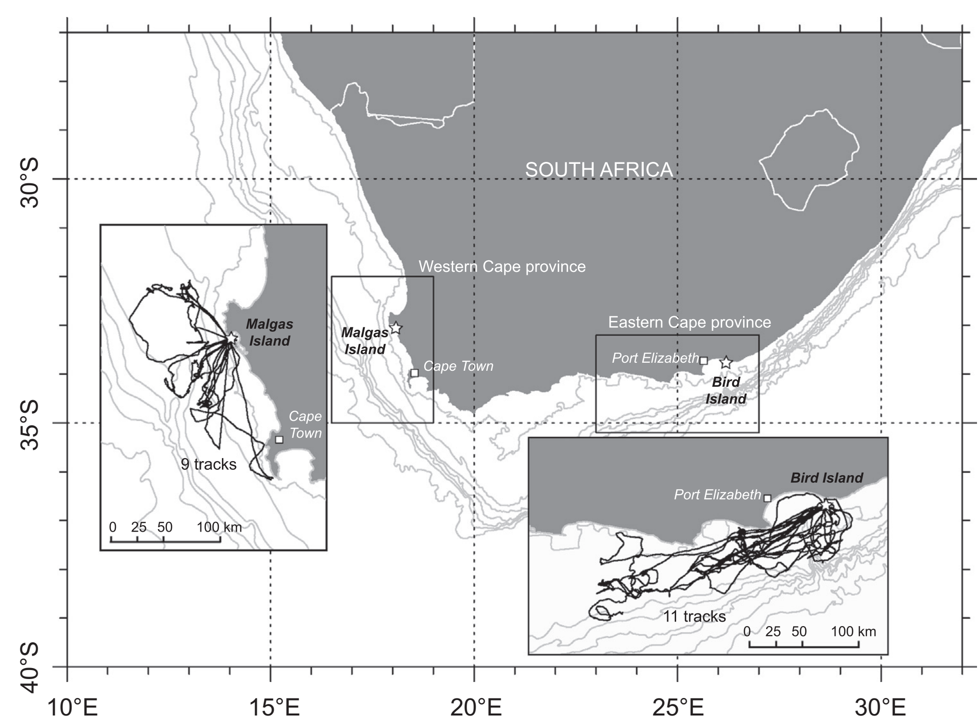

Fig. 1. Cape gannet tracks ($N=20$) recorded in October–November 2009 on the west and east coasts of South Africa.