

PATTERNS AND MECHANISMS OF
SEABIRD-ENVIRONMENT INTERACTIONS
IN SOUTHERN AFRICA
POPULATION AND INDIVIDUAL STUDIES

PHILIPPE SUNIL SABARROS

SUPERVISORS

NILS C. STENSETH (CEES NORWAY)

ERIC MACHU (CEES NORWAY, IRD FRANCE)

MAIN COLLABORATORS

DAVID GRÉMILLET (CEFE FRANCE, UCT SOUTH AFRICA)

ROBERT J. M. CRAWFORD (MCM SOUTH AFRICA)

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KEYWORDS

African penguin • Anchovy • Area-restricted search • Behaviour ecology •
Bio-physical interactions • Breeding ecology • Cape cormorant •
Cape gannet • Climate change • GPS tracking • Eddies • Fisheries • Forage
fish • Foraging ecology • Fronts • **Mechanisms** • Mesoscale •
Micronekton • Mozambique Channel • **Scale** • Oceanographic structures •
Organization level of processes • Overfishing • Population ecology •
Predator-prey relationships • Processes • Sardine • **Seabirds** •
South Africa • Southern Benguela upwelling • **Spatial interactions**
• Swift tern

SUMMARY

The interactions between seabirds and their environment, notably their prey, include complex spatial patterns and mechanisms that span over different scales of processes (e.g. physiology, behaviour, population). To understand large-scale patterns in seabird populations it is necessary to develop insight in the respective fields of study of physiology, behaviour and population ecology, and to reconcile these levels. Working along this line of research, I propose in this thesis to appreciate seabird-environment relationships from different perspectives: at the level of the population and of the individual. The first part of the thesis investigates whether regional trends of South African seabird populations (African penguin, Cape gannet, Cape cormorant and swift tern) follow a major shift in the distribution of their prey [Paper 1]. I demonstrate that for these seabirds the breeding populations respond at the level of the colony to the spatio-temporal variability of their prey, and I propose potential mechanisms for such responses [Paper 2]. The second part is dedicated to the analysis of patterns in prey distribution and individual seabird movements in relation to oceanographic mesoscale features such as fronts. I evidence that frontal structures are predictable areas where to find prey [Paper 3] and that seabirds like Cape gannets adjust their foraging strategies to such structures in order to optimize their foraging success [Papers 4 and 5]. This thesis underlines the importance of the spatial dimension in the relationships between seabirds and their prey, and highlights the importance of oceanographic features as catalysts of seabird-prey interactions.

INTRODUCTION

SEABIRDS AND THEIR ENVIRONMENT

Seabirds are birds that are adapted to and that depend on the marine environment. They are generally long-lived species that gather in colonies several months per year to breed. The breeding season is a critical period because marine birds face important constraints that are related to nesting and rearing their chicks (e.g. energetic constraint, vulnerability of chicks at nest). Their principal activity during the reproductive season is dedicated to finding food – foraging – for themselves and for their chicks. Foraging is a key process that involves energy expenditure [Mullers *et al.* 2009], food intake [Barraquand *et al.* 2009] and nest attendance [Regehr & Montevecchi 1997], and is thereby determinant to various demographic parameters linked to physiology and behaviour (e.g. breeding success, survival) [e.g. Le Bohec *et al.* 2008]. Seabird foraging movements and success are directly or indirectly susceptible to be affected by many factors, including: prey availability [e.g. Barraquand *et al.* 2009], environmental conditions (wind for instance), as well as inter- and intraspecific competition and facilitation [e.g. Evans 1982, Daroven *et al.* 2003]. Prey are the proximate cause for foraging, so prey availability is therefore a prime factor in seabird foraging ecology and population ecology [Durant *et al.* 2009, Tremblay *et al.* 2009].

Historically, studies of marine birds and related fields of study have developed hand in hand with the technological and methodological improvements for their observation. The earliest marine bird studies consisted in monitoring breeding colonies on land (e.g. numbers, diets). Then, researchers were able to improve their knowledge of seabird at-sea distribution and eventual species assemblages by observing birds from ships. Later, technological and methodological advances made it possible to study associations between seabird distribution (e.g. with GPS transmitter) and activity (e.g. by inferring feeding, area-restricted search) with their environment (e.g. satellite remote-sensing, hydroacoustic sea surveys). This field has grown exponentially since the 1970s and the leading research now uses process-based approaches in order to investigate oceanographic features that enhance the availability of seabirds prey at specific scales [Bost *et al.* 2009, Tremblay *et al.* 2009].

STUDY SYSTEM: THE SOUTHERN BENGUELA UPWELLING SYSTEM

Eastern boundary upwelling systems (EBUS) are referred to as subtropical coastal oceanic regions (e.g. Benguela, Humboldt, California, Canary) where the local atmospheric circulation drives an offshore transport of surface waters (i.e. Eckman transport) that are replaced by nutrient-rich subsurface waters [Hutchings *et al.* 2009]. These enriched waters support intense primary and secondary productions that sustain large fish biomass and the world's largest fisheries [FAO 2001, Pauly & Christensen 1995]. EBUS present a particular food chain structure termed 'wasp-waist'. It is characterized by a few species in the intermediate level of the food chain (usually forage fish like clupeids) that are present in large numbers and that channel most of the energy flow of the food chain – key species. These key species control the lower trophic level (i.e. plankton) as well as the upper level (i.e. top-predators) [Cury *et al.* 2000] and when these are affected by climate change or other perturbations (e.g. overfishing), the whole food chain is impacted [Cury *et al.* 2003].

The Benguela upwelling ecosystem is located on the Atlantic coasts of Angola, Namibia and South Africa, between 16°S to 37°S and 0-26°E [Shillington *et al.* 2006]. The southern Benguela refers to the South African part, located south of Orange River (28.6°S). The sardine (*Sardinops sagax*) and the anchovy (*Engraulis encrasicolus*) are abundant pelagic fish heavily targeted by the purse-seine fishery as well as many top-predators (e.g. seabirds) in the region [Crawford 1980]. The African penguin (*Spheniscus demersus*), the Cape gannet (*Morus capensis*) and the Cape cormorant (*Phalacrocorax capensis*) are three endemic and emblematic seabirds of South Africa [Plate 1] that rely upon sardines and anchovies [Hockey *et al.* 2005]. These seabirds are representative of the many species threatened by climate change and overfishing worldwide [Tasker *et al.* 2000, Furness 2003] and for which conservation efforts are under way [BirdLife International 2004, Pichegru *et al.* 2009].



Plate 1. Seabird species

AIMS OF THE THESIS

My ultimate goal – which extends beyond the scope of this thesis – is to develop the understanding of the mechanisms involved in the response of predators to perturbations (natural or induced by human activities) affecting their biotic and abiotic environments.

The interaction of an animal with its environment, and by extension the response of the predator to perturbations in its environment, spans over different and embedded scales of processes (e.g. physiology, behaviour, population) [Fig. 1]. Processes at the physiological level (e.g. energy intake and expenditure) drive behaviours (e.g. decisions related to foraging and breeding) that in turn drive population processes (e.g. breeding success, survival). These different levels of

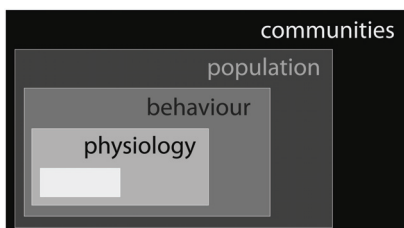


Figure 1. Embedded scales of observation and levels of processes

processes usually correspond to different and separate scales of observation and study. To go further, there is a need to bridge the gap between the population, behaviour and physiological levels by elucidating the mechanisms that link them.

Following this direction of research in my thesis, I propose to appreciate here seabird-environment interactions from different perspectives, i.e. different scales of observations, which are reflected in the two parts of the thesis. In the first part, I describe population studies of several seabird species (i.e. African penguin, Cape gannet, Cape cormorant and swift tern) that investigate whether regional seabird population trends follow the spatial shift of their prey [Paper 1] and, in particular, how their breeding numbers respond at the colony level to the spatio-temporal variability of the prey [Paper 2]. In the second part, I focus on individuals and investigate the interaction between seabirds and their prey by using diverse sources of data (e.g. satellite remote-sensing for oceanographic structures, acoustic survey data for fish, GPS tracking for seabirds). First, I examine the link between aggregations of fish and frontal structures in the Mozambique Channel [Paper 3]. Then, I review different methods to study area-restricted search (ARS) in seabird movements [Paper 4] and finally, by investigating the relationships between activities such as feeding and ARS with the presence of fronts, I evaluate whether Cape gannets track and use oceanographic structures like fronts in the southern Benguela region [Paper 5].

PART I. REGIONAL AND LOCAL RESPONSE OF SEABIRD POPULATIONS TO SPATIO-TEMPORAL FLUCTUATIONS OF THE RESOURCE

Marine ecosystems are threatened by human activities. Humans have polluted and degraded marine habitats where seabirds feed and live. Fisheries compete unevenly with top-predators for resources, leading to the depletion of marine resource [Cury *et al.* 2008]. Furthermore, climate change, caused by human development, also critically affects the marine environment [Harley *et al.* 2006]. Combined, these different factors (i.e. overfishing, climate change, pollution, habitat degradation and loss) may impact the food chain structure and stability from the lower trophic levels to the upper trophic levels i.e. top-predators such as seabirds. In upwelling systems, climate change and other perturbations induced by human activity (e.g. overfishing) may affect the whole food chain via the intermediate level [Cury *et al.* 2000, 2003] and ultimately induce a critical ecosystem shift such as it occurred in Namibia [Hutchings *et al.* 2009].

In southern Benguela, the distribution of small pelagic fish (mostly sardine, but also anchovy) previously associated with the western coast of South Africa have progressively shifted towards the east in the late 1990s [van der Lingen *et al.* 2005, Fairweather *et al.* 2006]. No sardines were caught west of Cape Point since 2004 [van der Lingen *et al.* 2005]. It may be environmental fluctuations linked to climate change [Roy *et al.* 2007] and/or overfishing on the west coast [Coetzee *et al.* 2008] that have caused the fish distributional shift. Over the period of the spatial shift the biomass of sardines and anchovies also fluctuated [van der Lingen *et al.* 2005, Fairweather *et al.* 2006]. Knowing that colonies of African penguins, Cape gannets, Cape cormorants and swift terns are spread along the South African coast and that these species rely extensively on those pelagic fish, we wonder if they have eventually been affected by this spatial shift and prey fluctuations.

In this first part of the thesis, I present studies on the breeding populations of African penguins, Cape gannets, Cape cormorants and swift terns, which have been monitored yearly and several times a year at their respective colonies since 1987 [Underhill *et al.* 2006, Crawford *et al.* 2007a, 2007b]. As in most population studies

[e.g. Lewis *et al.* 2006] we observe the number of breeding birds at the peak of the breeding season. Using census data from 20 years (1987-2007), including the critical moment of the eastward shift in prey (late 1990s), we investigated the regional trends (west vs. east coast) of these four seabirds [Paper 1] relative to the distributional shift of the sardine, and their local response (i.e. at the level of the colonies for three of those seabirds) to the spatio-temporal variability of their sardine and anchovy prey [Paper 2]. In this part, I address the following questions:

- *Do seabird regional trends 'follow' the eastward shift in prey?* [Paper 1]
- *Is the number of breeding birds at a given colony controlled by prey abundance and distance?* [Paper 2]
- *What are the potential processes involved in such a relationship?* [Paper 2]
- *Are the responses of different seabird species to spatio-temporal fluctuations of their shared prey comparable?* [Paper 2]
- *How do sympatric seabird species share the resource?* [Paper 2]

PAPER 1. IMPLICATIONS FOR SEABIRD POPULATIONS OF A LONG-TERM CHANGE IN PREY DISTRIBUTION

By studying regional trends (west coast vs. east coast) of four seabird species: African penguin, Cape gannet, Cape cormorant and swift terns (*Sterna bergii*), we evaluated the impact of the eastward shift in sardines, which exhibited the most dramatic shift among the small pelagic fish. Sardines shifted 400 km to the south and east so they became less available to the colonies located west and north, and more available to the colonies located further south and east. Such fluctuations in prey distribution may induce additional foraging costs for birds located in the western province and reduced costs for those that breed in the eastern province. In fact, breeding populations decreased in the depleted area (north and west coast) and built up in the fish enriched area (south and east coast), with slight differences in response among seabird species. While sardines became progressively less available in the Western Cape Province, the survival of adult African penguins decreased and the number of breeding individuals decreased by 45% between 2004 and 2006. In the Western Cape, the number of breeding Cape gannets decreased by 38% between

2001/02 and 2005/06 and the contribution of sardines to their diet fell from an average of 40% during 1987–2003 to 5-7% in 2005 and 2006. The proportions of Cape cormorants and swift terns breeding in the south of the province increased as sardines moved south and east. In the Eastern Cape Province, the number of breeding penguins halved between 2001 and 2003, and they also established a new eastern colony in 2003 (De Hoop). After 2002 there was an increase in the number of breeding Cape gannets as well as in the contribution of sardines to their diet. It is likely that in this province sardines became increasingly available to gannets but remained beyond the shorter foraging range of penguins. These birds (like many colonial species) are faithful to their partner and hence to their colony, and so would not relocate to another colony where conditions are more favourable. If they existed, population movements would have occurred through the recruitment of first time breeders to colonies with favourable conditions [Crawford *et al.* 1999].

This study – among others – has provided valuable knowledge for making management decisions to mitigate the impacts on seabirds of changes in the distribution of the prey (which are partly due to fisheries). Since 2009, Marine and Coastal Management (Cape Town, South Africa) – a governmental structure of the Department of Environmental Affairs and Tourism of South Africa – has managed to set up protected areas where fishing is not allowed around some breeding colonies to allow threatened birds to recover [see Pichegru *et al.* 2009].

PAPER 2. DIFFERENTIAL POPULATION RESPONSES OF THREE SEABIRDS TO SPATIO-TEMPORAL VARIABILITY OF SHARED RESOURCE

To better understand the regional trends of seabird populations [cf. Paper 1] we figured we needed to investigate the detailed response of these seabirds at the level of the colonies. In this paper, we investigated the local response of populations (at the colony level) to the spatio-temporal variability of prey, including anchovies, which were not taken into account in Paper 1 and that may have sustained African penguins on the west coast. From corrected fishing data (that were validated by hydroacoustic survey data) we derived an index of prey distribution along the South African. Here the distance and abundance of prey are explicitly investigated because we assumed that foraging on scarce prey located far from the colony would increase

the energetic cost and reduce the amount of time spent with the chick, and thereby may impact the reproductive success of birds, and subsequently the number of breeders present at each colony.

Each year, the number of breeders at the respective colonies can be related to the abundance and the distance of the peak of prey abundance. As expected, African penguins and Cape gannets breed in greater numbers when food is abundant and nearby. It was not the case with Cape cormorants that appear to be favoured over other species when prey abundance decreases [see Fig. 2 in Paper 2]. To understand these patterns, we looked at the species-specific characteristic of these birds (e.g. breeding periods, foraging range, diet plasticity, hunting technique). Gannets and cormorants breed at the same time of the year and therefore compete for resources. We hypothesized that in conditions of high prey abundance, gannets would benefit from sub-surface predators, which would push prey towards the surface, while this underwater competition would be detrimental to cormorants, which would rather rely on other prey items such as benthic prey [see Fig. 3 in Paper 2]. In contrast, when fish are scarce, fewer sub-surface predators would be present to make prey available to gannets, and cormorants would benefit from their ability to forage efficiently on scarce prey. Considering that penguins and gannets breed at different moment of the year, we actually understand that this temporal separation allows both species to have access to the shared prey resource when it is most needed during their respective breeding periods while minimizing competition. In conclusion, species-specific traits related to the use of prey enable sympatric species to share resources.

PART II. FACTORS AND MECHANISMS DRIVING FORAGING BEHAVIOUR AND PATTERNS IN INDIVIDUAL SEABIRD MOVEMENTS

Prey distribution is patchy and unpredictable in marine systems [Weimerskirch 2007]. The distribution and aggregation patterns of schooling fish depend on self-organization mechanisms (social behaviour) and environmental forcing (dynamic structures). Typical aggregation units (e.g. school, cluster, stock) are associated with typical scales of physical forcing. For instance, fish clusters (groups of schools) are different associated with submeso- to mesoscale features (100s m to 100s km) [Bertrand *et al.* 2008]. Top-predators such as seabirds are likely to have adapted their foraging strategies and associated movements to the distribution of their prey across scales [Fauchald & Tveraa 2006, Fauchald 2009]. The study of the link between seabird distribution, activity, and the environment, especially large oceanic structures (e.g. polar front) and finer scale structures (e.g. mesoscale eddies, fronts and filaments) is leading the research on foraging ecology today thanks to new means for observing birds in their environment and for measuring the environment itself. Movements of seabirds can be accurately recorded with positioning systems (e.g. GPS) along with diverse parameters (e.g. pressure, stomach temperature and pH, heart beat rate) that allow us to deduce the bird's activity (e.g. dives, feeding) [Durant *et al.* 2009].

Oceanographic structures shape the distribution of plankton organisms and, thereby, drive indirectly the distribution and aggregation patterns of intermediate (forage fish) and upper trophic levels (top-predators). In this second part of the thesis, I principally consider mesoscale features (kms to 100s km) such as fronts, eddies and filaments [see Fig. 1 in Hofmann & Powell 1999]. I investigate the link between the distribution and aggregation patterns of the prey of seabirds and mesoscale eddies in the Mozambique Channel [Paper 3]. Then, I use individual foraging movements of Cape gannets recorded in the southern Benguela with GPS devices from 2002 onwards to investigate the relationships between the searching and the feeding activity [Paper 4], and finally the relationships between these activities and oceanographic structures such as fine mesoscale fronts [Papers 5]. More specifically, I

address the following questions:

- *Are small fish associated to oceanic mesoscale frontal structures?* [Paper 3]
- *Is feeding activity inherent to area-restricted search?* [Paper 4]
- *Are area-restricted search and feeding linked to oceanic fronts?* [Paper 5]
- *How may Cape gannets detect and use fronts?* [Paper 5]

PAPER 3. INFLUENCE OF MESOSCALE STRUCTURES ON THE DISTRIBUTION AND AGGREGATION PATTERNS OF PREY

Compared to the rich and productive waters of the southern Benguela upwelling, the Mozambique Channel, located in the southwest Indian Ocean between Mozambique and Madagascar, is an oligotrophic system. Previous studies have shown that great frigate birds preferentially forage at the periphery of mesoscale eddies [Weimerskirch *et al.* 2004]. Despite a profusion of studies investigating the influence of oceanic mesoscale features (10s km to 100s km; eddies, fronts, filaments) on the distribution of lower and upper trophic levels (primary/secondary producers and top-predators respectively), the association between such structures and the intermediate level of the food chain (i.e. prey of seabirds) have so far been poorly documented [e.g. Bakun 2006, Bertrand *et al.* 2008].

Satellite measures of sea level anomalies (AVISO) allowed us to track mesoscale eddies. Since, eddy peripheries are generally characterized by strong gradients (i.e. fronts), we investigated the influence of mesoscale eddy fronts on the distribution and aggregation pattern of seabird prey (i.e. micronekton: fish, crustaceans, squids), which were monitored with hydroacoustic surveys. We found that these prey tend to aggregate in large structures in frontal zones between eddies. In fact, this demonstrates that fronts between mesoscale eddies actually favour foraging activity of seabirds (e.g. great frigate birds) [Weimerkirch *et al.* 2004] by attracting and concentrating their prey.

PAPER 4. A CRITICAL ASSESSMENT OF METHODS TO STUDY AREA-RESTRICTED SEARCH IN SEABIRDS

Area-restricted search (ARS) is thought to be an intensified foraging mode (i.e. lower speed, increased turn rate) realized in response to locally enhanced prey availability [Kareiva & Odell 1987]. This ARS pattern was first described in insects [Banks 1957]. Several methods have been used to identify ARS behaviour in seabird foraging movements [e.g. sinuosity SIN: e.g. Benhamou 2004, first-passage time FPT: Fauchald & Tveraa 2003, fractal landscape FL: Tremblay *et al.* 2007], occasionally for the purpose of extrapolating feeding activity [Grémillet *et al.* 2008].

This study investigates whether feeding activity can be derived from ARS behaviour as usually assumed, especially in the case of seabirds like the Cape gannet [Grémillet *et al.* 2008]. We used GPS tracks of Cape gannets recorded in 2002 to evaluate three commonly used track-based ARS plus one method we specifically developed that is not impeded by the non-flying phases in seabird foraging movements (first-passage distance FPD). By using feeding opportunities (dives monitored by time-depth recorders) to optimize ARS identification in each method, we evaluated the ability of these methods to identify putative feeding areas.

We found that FPT analysis was unable to identify ARS, whereas SIN, FL and FPD analyses did identify clear ARS activity (with nested patterns in FPD). However, the ARS regions determined with the three methods largely differed from each other, which underlines the general lack of coherence among ARS methods. Except FPD, we found that neither SIN nor FL would readily associate ARS to enhanced feeding activity. FPD analysis is able to do so when all operational scales are included since more dives are embedded in ARS as the scale increases. Otherwise, a substantial amount of dives occur outside ARS. We conclude that in the Cape gannet an intensified search mode (ARS) is primarily linked to areas where birds expect to find prey, but not necessarily where feeding activity actually takes place.

In order to better understand the searching and feeding behaviour of seabirds in ocean systems, it is needed to investigate the bird's spatial-memory of feeding areas and interactions with congeners or other species at sea, as well as the recognition of mesoscale oceanographic features such as fronts.

PAPER 5. FINE-SCALE RECOGNITION AND USE OF MESOSCALE FRONTS BY CAPE GANNETS

Physical processes associated with oceanographic features can concentrate and enhance primary and secondary production and thereby attract fish. Oceanographic features such as fronts have been suggested to be predictable areas where to find prey [Weimerkirch 2007, Bost *et al.* 2009]. It was for example the case in the Mozambique Channel with fronts located between interacting mesoscale eddies [Paper 3] that provided valuable foraging grounds to great frigate birds [Weimerskirch *et al.* 2004]. It is easily understandable that in oligotrophic regions (e.g. Mozambique Channel) oceanographic features locally enrich surface waters and likely represent foraging grounds for seabirds, but we wonder if fronts can also favour foraging in rich areas, such as the Benguela upwelling.

Here we analyzed high-frequency foraging tracks (GPS, 1 s sampling) in relation to daily high-resolution chlorophyll maps (MODIS, 1 km) on which mesoscale fronts were identified. Knowing that searching activity (i.e. area-restricted search, ARS) and the actual feeding occurrences are only partially linked in Cape gannets [Paper 4], we investigated if (i) the ARS activity and (ii) the diving activity are linked to mesoscale fronts in the southern Benguela.

Both the searching activity and the feeding activity are linked to frontal structures (although to a different extent). Cape gannets actually shift from a transiting mode to an ARS mode at around 6.7 km (2-11 km) from fronts. This result suggests that they might be able to sense fronts (smell or vision) and that this process could trigger enhanced investigation of their surroundings (i.e. ARS). Phytoplankton releases an odour compound (dimethyl sulfide) that can be smelled by a range of seabird species [Nevitt 2000]. We hypothesized that Cape gannets, similar to procellariiforms, can sense the odor landscape and use it to orient themselves. This remains to be further tested in the field similar to Nevitt [2008]. Another crucial finding is that diving probability increases near fronts in 55% of the tracks investigated, suggesting that Cape gannets prefer fronts for feeding; in the remaining cases birds may use other cues, including the occurrence of fishing vessels. Fishermen commonly use seabirds to locate fish schools and seabirds may do the same. Any person who has been on a fishing boat can relate how seabirds are highly attracted to boats when they pull up nets full of fish or release fish material such as the by-catch

(unwanted species) or the fish parts they have no use for (heads and guts for instance). Cape gannets of the west coast of South Africa are known to scavenge on fish discarded by trawlers [Grémillet *et al.* 2008] and our results suggest that this explains the lack of association of these birds with environmental structures, mostly when comparing the west coast where fishing vessels are abundant with the east coast where the fleet is not as developed. Recent studies have been able to concomitantly analyse trajectories of boats (e.g. vessel monitoring system VMS) and seabirds (e.g. GPS) to show association between seabirds and boats [e.g. Votier *et al.* 2010]. Spotting congeners or other predators (including fishing vessels) that have successfully located a prey patch might help seabirds to find prey [e.g. Evans 1982, Daroven *et al.* 2003]. For that reason, mono- and multispecies assemblages at sea deserve further investigations.

GENERAL DISCUSSION

UNDERSTANDING POPULATION RESPONSES OF COLONIAL SEABIRDS TO MAJOR ENVIRONMENTAL CHANGES THROUGH THE OBSERVATION OF BREEDING POPULATIONS

By investigating the impact of a climate- or overfishing-induced shift in the distribution of the main resource of several South African seabirds [van der Lingen *et al.* 2005, Fairweather *et al.* 2006], we showed that the populations of African penguin, Cape gannet, Cape cormorant and swift tern also shifted since their breeding numbers decreased at the westernmost colonies (except African penguins) and increased at their easternmost colonies [Paper 1]. One may think that birds emigrated from the western colonies to relocate at eastern colonies. However, it is unlikely that breeders from the western colonies relocated eastwards when the local conditions became more favourable (except for a few individuals) because these seabirds – like most colonial seabirds – are faithful to their partners and hence their colony of reproduction [Hockey *et al.* 2005]. Eastern colonies may actually have increased by recruiting young birds that do not yet belong to any colony and that seek a colony to join and mate for the first time [Crawford 1998, Paper 2]. A more detailed investigation of the actual relationship between the local breeding numbers (i.e. at the level of the colonies) and prey availability (abundance and distance) suggested that the decrease of breeding populations in the western colonies may be attributed to the fact that African penguins and Cape gannets breed in lesser numbers when prey availability is altered [Paper 2] as adult birds may skip reproduction in this situation [Crawford *et al.* 1999]. However, it was not the case with Cape cormorants, which actually breed in greater numbers when prey is scarce because the competition with Cape gannets (that breed at the same time of the year) might be reduced [Paper 2].

In order to better understand and predict the fate of South African seabird populations, or colonial seabirds in general, to major environmental changes, it is necessary to be able to model the actual yet complex dynamic structure of these populations (composed of several colonies), for which most processes are controlled by prey availability (as an extrinsic and prevalent factor) [Fig. 2]. First, there are birds that have not bred yet (immatures) and are not reliably associated to their natal colony

and therefore constitute a common pool (to all colonies) from which they may be recruited to a colony where conditions are favourable [e.g. Boulinier & Lemel 1996, Crawford 1998, Becker & Bradley 2007, see Fig. 2]. Then, each colony is associated with a pool of adult birds that have already established and from which a fraction will annually breed, depending on their body condition and the local availability of prey near the colony at the beginning of the reproductive period [e.g. Danchin & Cam 2002, Vleck & Vleck 2002]. The decision to breed and their success are crucial processes for comprehending the variations in breeding numbers since these processes drive the instantaneous response of populations to resource availability [Paper 2, see Fig. 2]. The breeding population actually corresponds to the ‘observable’ fraction of the total population. It is important to acknowledge that this fraction is not proportionally constant to the total population, since the number of breeders is controlled each year by external factors such as prey availability [Paper 2]. Finally, the most investigated demographic parameters that are often related to prey availability and that are most necessary to model the dynamics of the population are the survival of immature and adult birds [e.g. Paper 1, Le Bohec *et al.* 2008] and the reproductive output of breeders [e.g. Barrett & Krasnov 1996, Crawford *et al.* 2006, Lewis *et al.* 2006].

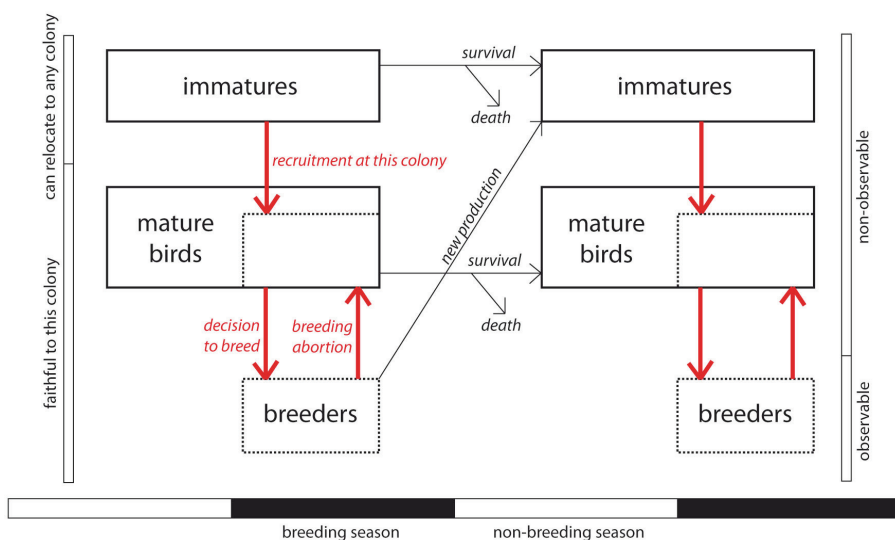


Figure 3. Schematic representation of the dynamical processes at a seabird colony. Breeders are the observable variable. Arrows represent processes that are likely to be controlled by resource availability. Red arrows represent processes that directly control the number of breeding birds.

IMPORTANCE OF PHYSICAL PROCESSES TO SEABIRD-PREY INTERACTIONS

It has been well documented worldwide that, at various scales, oceanographic features (e.g. fronts, eddies) associated with physical processes concentrate and enhance plankton production and attract top-predators like seabirds [e.g. Ainley *et al.* 2009, Bost *et al.* 2009]. Such oceanographic features are assumed to be predictable grounds where to find prey for top-predators [Weimerskirch 2007] although this was only demonstrated in a limited number of studies [e.g. Bertrand *et al.* 2008]. In the second part of this thesis, I investigated how oceanographic structures, particularly mesoscale features, influence seabird-prey interactions. I demonstrated that shear fronts between mesoscale eddies attract large aggregations of prey (micronekton) [Paper 3] and are thereby predictable feeding grounds for seabirds like great frigate birds in the Mozambique Channel [Weimerskirch *et al.* 2004, Tew-Kai *et al.* 2009]. In the southern Benguela, I assumed that mesoscale fronts may also attract prey aggregations and that seabirds like Cape gannets may use these structures as environmental cues. By analysing the searching patterns and feeding activity of Cape gannets, I evidenced that these birds do track and use fine mesoscale fronts in the Benguela upwelling system [Papers 4 and 5]. In the southern Benguela, the Mozambique Channel and most marine systems worldwide [e.g. Ainley *et al.* 2009, Bost *et al.* 2009], flow elements and oceanographic features associated with physical processes shape the distribution of plankton organisms and thereby the distribution of plankton-eating species (e.g. fish) and the foraging patterns of top-predators (e.g. seabirds) [Fig. 3a]. In fact, physical processes catalyse seabird-prey interactions.

The Mozambique Channel (MC) and the southern Benguela upwelling (BU) largely differ in terms of productivity and also in regards to the nature and structure of the frontal structures that can be found. The MC is oligotrophic (i.e. poor 'blue' waters) whereas the BU is a productive upwelling (i.e. 'green' waters). The circulation in the MC is ruled by cyclonic and anticyclonic eddies [Schouten *et al.* 2003]. They run along the coasts advecting at their periphery rich coastal waters they inject into the channel [Tew-Kai & Marsac 2008]. By displacing rich waters from the coasts to the middle of the MC, eddies participate to enhance the biological production in the usually non-productive waters of the MC. The advected coastal waters are concentrated in shearing fronts between interacting eddies (that rotate in opposite directions) where these nutrient-rich waters enable local biological

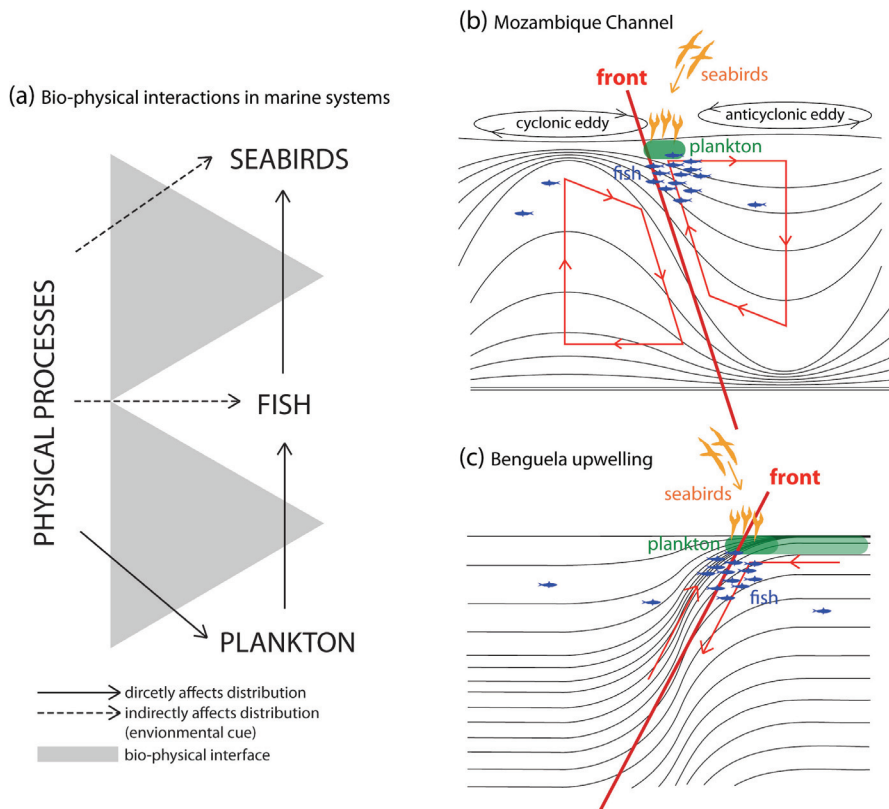


Figure 3. Structure of bio-physical interactions (a) in marine systems and schematic representation of a biological hot-spots in (b) the Mozambique Channel and in (c) the southern Benguela upwelling.

production [Tew-Kai & Marsac 2008]. The vertical structure of interacting eddies and the associated vertical flows support biological production near the surface at the front, which attracts the fish [Paper 3] and ultimately the seabirds [Weimerskirch *et al.* 2004, Tew-Kai *et al.* 2009] [Fig. 3b]. In an upwelling system like the BU where waters may appear as a ‘soup’ of plankton, one may think that mesoscale features are of lesser importance to fish and top-predators relative to an oligotrophic system like the MC where any local biological enrichment is very critical. In fact, I found that in the BU seabirds do use mesoscale fronts over the continental shelf of South Africa to find prey [Paper 5]. At this stage it would be valuable to confirm the actual association between fish patches and fronts in the BU. These fronts can vary in nature and structure, although there are no fronts like those of the MC. They may be either typical upwelling fronts that have a strong vertical structure and flow dynamic that generates a local enrichment near the surface [Fig. 3c], they may also be convergence

phenomena between two waters masses due to the current patterns or the result of the elongation of a local production cell (e.g. filament). However, it is hardly possible to discriminate the different types of fronts from satellite snapshots of sea surface temperature or chlorophyll [e.g. Paper 5]. New methods to discriminate these fronts would be welcomed to the field. Also, further investigations on how these different types of fronts influence plankton, fish, and top-predators are needed to fully understand the dynamics of biological hot-spots at fronts [e.g. Fig 2c].

From the point of view of a seabird, the actual nature of the front (e.g. shearing front, upwelling front, surface convergence) might not be relevant as long as the front is associated with prey patches and the front can be somehow detected by the bird. The perception of such structures has been related to the senses of smell and vision in a range of seabirds [Nevitt 2008], and I hypothesized that it could also be the case in Cape gannets [Paper 5]. In upwelling systems, the production landscape (chlorophyll distribution) is tightly linked to the sea surface temperature (more production in the cold upwelled waters) [Capet *et al.* in press]. In fact, fronts delimit water masses that differ in temperature and chlorophyll concentration [see Fig. 1 in Paper 5]. Vertical atmospheric currents are generally stronger above warm waters than cold waters. Because of that, an alternative to relying on olfactory and visual cues to navigate could be that seabirds like Cape gannets might be able to sense changes in temperature and air lift (vertical air flow) when flying across fronts and so use air temperature and gradients to navigate and eventually adapt their searching effort [e.g. Paper 5].

I argued in this thesis that oceanographic features are important to seabird-prey interactions since predictability of prey increases near these structures [Papers 3 and 5]. This statement does not exclude the fact that the prey patches may not be associated with oceanographic features. Indeed, opportunistic encounters of prey patches may also occur away from fronts even when birds are not actively searching [e.g. Cape gannet Papers 4 and 5, wandering albatross Weimerskirch *et al.* 2007]. The detection of such patches could either be direct or managed via spotting multi-species feeding assemblages that may include large predatory fish, marine mammals, or other seabirds [Evans 1982, Daroven *et al.* 2003].

TOWARDS UPSCALING: INDIVIDUAL INFORMATION MAY BE USEFUL TO POPULATION

The foraging activity and success of a seabird involve energy expenditure and gain (physiological level) and as well as strategies and decisions (behaviour). Physiological and behavioural processes are embedded within population processes that they actually drive [Fig. 1]. Thanks to increasingly powerful technologies and methodologies, studies investigating the physiological (e.g. energy expenditure) and behavioural levels (e.g. area-restricted search, decision to breed) are growing [e.g. Mullers *et al.* 2009, Tremblay *et al.* 2009]. More importantly, it is now necessary to investigate the mechanisms that link different levels of processes (e.g. physiology and behaviour); the causality of a decision may be related to the physiological state of a bird for instance. Elucidating the physiological and behavioural processes and the connection between them would certainly be helpful to understand the patterns at the level of the population [Beckerman *et al.* 2010]. This is called ‘upscaling’; it represents the idea of making use of the knowledge acquired at small-scales (e.g. physiology and behaviour) for comprehending larger scale processes (e.g. population). ‘Upscaling’ would particularly be helpful to study the impact of large-scale perturbations on seabird populations, especially when considering several species with species-specific characteristics that may eventually respond differentially to a same perturbation [e.g. Papers 1 and 2]. The studies described in the second part of this thesis [Papers 3, 4 and 5] followed this line of research since they aim at understanding the mechanisms behind individual seabird foraging movements, mostly on the behavioural level. In practical terms, it would be necessary to address the population as a sum of individual agents (individual-based modelling IBM) [Grimm & Railsback 2005] to model and predict population patterns. These models could include the formulation of the dynamic energy budget theory (DEB) proposed by Kooijman [2010] to manage the physiological aspects, and the formulation of space-state models to manage movements and behaviour of individuals [Patterson *et al.* 2008].

LITERATURE CITED

- Ainley D.G., Dugger K.D., Ford R.G., Pierce S.D., Reese D.C., Brodeur R.D., Tynan C.T. & Barth J.A. (2009) Association of predators and prey at frontal features in the California Current: competition, facilitation and co-occurrence. *Marine Ecology Progress Series*, 389:271-294.
- Bakun A. (2006) Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Scientia Marina*, 70:105-122.
- Banks C.J. (1957) The behaviour of individual coccinellid larvae on plants. *British Journal of Animal Behaviour*, 5:12-24.
- Barraquand F., Inchausti P. & Bretagnolle V. (2009) Cognitive abilities of a central place forager interact with prey spatial aggregation in their effect on intake rate. *Animal Behaviour*, 78:505-214.
- Barrett R.T. & Krasnov Y.V. (1996) Recent responses to changes in stocks of prey species by seabirds breeding in the southern Barents Sea. *ICES Journal of Marine Science*, 53:713-722.
- Becker P.H. & Bradley J.S. (2007) The role of intrinsic factors for the recruitment process in long-lived birds. *Journal of Ornithology*, 148 (Suppl. 2):S377-S384.
- Beckerman A., Petchey O.L. & Morin P.J. (2010) Adaptive foragers and community ecology: linking individuals to communities and ecosystems. *Functional Ecology*, 24:1-6.
- Benhamou S. (2004) How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology*, 229(2):209-220.
- Bertrand A., Gerlotto F., Bertrand S., Gutiérrez M., Alza L., Chipollini A., Díaz E., Espinoza P., Ledesma J., Quesquén R., Peraltilla S. & Chavez F. (2008) Schooling behaviour and environmental forcing in relation to anchoveta distribution: An analysis across multiple spatial scales. *Progress in Oceanography*, 79:164-277.
- BirdLife International (2004) *State of the World's birds: indicators for our changing world*. Cambridge, UK.

- Bost C.A., Cotté C., Bailleul F., Cherel Y., Charassin J.-B., Guinet C., Ainley D.G. & Weimerskirch H. (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, 78:363-376.
- Boulinier T. & Lemel J.-Y. (1996) Spatial and temporal variations of factors affecting breeding habitat quality in colonial birds: some consequences for dispersal and habitat selection. *Acta Oecologica*, 17(6):531-552.
- Capet X., Colas F., Penven P., Marchesiello P. & McWilliams J. (in press) Eastern boundary subtropical upwelling systems. *Geophysical Monograph Series*.
- Coetzee J.C., van der Lingen C.D., Hutchings L. & Fairweather T.P. (2008) Has the fishery contributed to a major in the distribution of South African sardine? *ICES Journal of Marine Science*, 65(B:11):1676-1688.
- Crawford R.J.M. (1998) Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. *South African journal of Marine Science*, 19:355-364.
- Crawford R.J.M. (1980) Seasonal patterns in South Africa's Western Cape purse-seine fishery. *Journal of Fish Biology*, 16:649-664.
- Crawford R.J.M., Barham P.J., Underhill L.G., Shannon L.J., Coetzee J.C., Dyer B.M., Leshoro T.M. & Upfold L. (2006) The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation*, 132:119-125.
- Crawford R.J.M., Dundee B.L., Dyer B.M., Klages N.T.W., Meyer M.A. & Upfold L. (2007a) Trends in numbers of Cape gannets (*Morus capensis*), 1956/1957 - 2005/2006, with a consideration of the influence of food and other factors. *ICES Journal of Marine Science*, 64:169-177.
- Crawford R.J.M., Dyer B.M., Kemper J., Simmons R.E. & Upfold L. (2007b) Trends in numbers of Cape cormorants (*Phalacrocorax capensis*) over a 50-year period, 1956-57 to 2006-07. *Emu*, 107:1-9.
- Crawford R.J.M., Shannon L.J. & Whittington P.A. (1999) Population dynamics of the African penguin *Spheniscus demersus* at Robben Island, South Africa. *Marine Ornithology*:139-147.
- Cury P., Bakun A., Crawford R.J.M., Jarre A., Quinones R.A., Shannon L.J. & Verheye H.M. (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science*, 57:603-618.

- Cury P., Shannon L. & Shin Y.-J. (2003) 7. The Functioning of Marine Ecosystems: a Fisheries Perspective. In Sinclair M. & Valdimarsson G. (eds.) *Responsible Fisheries in the Marine Ecosystem*, pp. 103-123. .
- Danchin E. & Cam E. (2002) Can non-breeding be a cost of breeding dispersal? *Behavioral Ecology and Sociobiology*, 51:153-163.
- Daroven G.K., Montecechi W.A. & Anderson J.T. (2003) Distribution patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. *Marine Ecology Progress Series*, 256:229-242.
- Durant J.M., Hjermann D.Ø., Frederiksen M., Charassin J.B., Le Maho Y., Sabarros P.S., Crawford R.J.M. & Stenseth N.C. (2009) Pros and cons of using seabirds as ecological indicators. *Climate Research*, 39:115-129.
- Evans P.G.H. (1982) Associations between seabirds and cetaceans: a review. *Mammal Review*, 12(4):187-206.
- Fairweather T.P., van der Lingen C.D., Booth A.J., Drapeau L. & van der Westhuizen J.J. (2006) Indicators of sustainable fishing for South African sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*. *African Journal of Marine Science*, 28:661-680.
- FAO (2001) www.fao.org.
- Fauchald P. (2009) Spatial interaction between seabirds and prey: review and synthesis. *Marine Ecology Progress Series*, 391:139-151.
- Fauchald P. & Tveraa T. (2006) Hierarchical patch dynamics and animal movement pattern. *Oecologia*, 149(3):383-395.
- Fauchald P. & Tveraa T. (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, 84(2):282-288.
- Grimm, V. & Railsback, S. F. (2005) *Individual-based modeling and ecology*. Princeton University Press.
- Grémillet D., Lewis S., Drapeau L., van der Lingen C., Huggett J.A., Coetzee J., Verheye H.M., Daunt F., Wanless S. & Ryan P.G. (2008a) Spatial mismatch in the Benguela upwelling zone: could we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology*, 45:610-621.
- Harley C.D.G., Randall Hughes A., Hultgren K.M., Miner B.G., Sorte C.J.B., Thornber C.S., Rodriguez L.F., Tomanek L. & Williams S.L. (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, 9:228-241.

- Hockey, P., Dean, W. R. J. & Ryan, P. G. (2005) *Roberts Birds of Southern Africa*. John Voelker Bird Book Fund.
- Hofmann E.E. & Powell T.M. (1998) Environmental variability effects of marine fisheries: four case histories. *Ecological Applications*, 8(1) Suppl.:S23-S32.
- Hutchings L., van der Lingen C.D., Shannon L.J., Crawford R.J.M., Verheye H.M.S., Bartholomae C.H., van der Plas A.K., Louw D., Kreiner A., Ostrowski M., Fidel Q., Barlow R.G., Lamont T., Coetzee J., Shillington F., Veitch J., Currie J.C. & Monteiro P.M.S. (2009) The Benguela Current: An ecosystem of four components. *Progress in Oceanography*, 83:15-32.
- Kareiva P. & Odell G. (1987) Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. *The American Naturalist*, 130(2):233-270.
- Kooijman, S. A. L. M (2010) *Dynamic energy budget theory for metabolic organisation*. Cambridge University Press.
- Le Bohec C., Durant J.M., Gauthier-Clerc M., Stenseth N.C., Park Y.-H., Pradell R., Gremillet D., Gendner J.-P. & Le Maho Y. (2008) King penguin population threatened by Southern Ocean warming. *Proceedings of the National Academy of Sciences USA*, 105(7):2493-2497.
- Lewis S., Gremillet D., Daunt F., Ryan P.G., Crawford R.J.M. & Wanless S. (2006) Using behavioural and state variables to identify proximate causes of population change in a seabird. *Oecologia*, 147:606-614.
- van der Lingen C.D., Coetzee J.C., Demarcq H., Drapeau L., Fairweather T.P. & Hutchings L. (2005) An eastward shift in the distribution of southern Benguela sardine. *Globec International Newsletter*, 11(2):17-22.
- Mullers R.H.E., Navarro R.A., Daan S., Tinbergen J.M. & Meijer H.A.J. (2009) Energetic costs of foraging in breeding Cape gannets *Morus capensis*. *Marine Ecology Progress Series*, 393:131-171.
- Nevitt G.A. (2008) Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *Journal of Experimental Biology*, 211:1706-1713.
- Nevitt G.A. (2000) Olfactory foraging by Antarctic procellariiform seabirds: Life at high Reynolds numbers. *Biology Bulletin*, 198:245-253.
- Patterson T.A., Thomas L., Wilcox C., Ovaskainen O. & Matthiopoulos J. (2008) Space-state models of individual animal movement. *Trends in Ecology and Evolution*, 23(2):87-94.
- Pauly D. & Christensen V. (1995) Primary production required to sustain global

- fisheries. *Nature*, 374:255-257.
- Pichegru L., Ryan P.G., Le Bohec C., van der Lingen C.D., Navarro R., Petersen S., Lewis S., van der Westhuizen J. & Grémillet D. (2009) Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas. *Marine Ecology Progress Series*, 391:199-208.
- Regehr H.M. & Montecechi W.A. (1997) Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effect of fisheries activities and implications for indicator species. *Marine Ecology Progress Series*, 155:249-260.
- Roy C., van der Lingen C.D., Coetzee J.C. & Lutjeharms J.R.E. (2007) Abrupt environmental shift associated with changes in the distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela. *African Journal of Marine Science*, 29(3):309-319.
- Schouten M.W., de Ruijter W.P.M., van Leeuwen P.J. & Ridderinkhof H. (2003) Eddies and variability in the Mozambique Channel. *Deep-Sea Research, II* 50:1987-2003.
- Shillington F.S., Reason C.J.C., Rae C.M.D., Florenchie P. & Penven P. (2006) Large scale physical variability of the Benguela Current Large Marine Ecosystem (BCLME). In Shannon L., Hempel V., Moloney C. & Malanotte-Rizzoli P. (eds.) *Benguela: Predicting a large marine ecosystem*, pp. 49-70. Elsevier.
- Tasker M.T., Camphuysen C.J., Cooper J., Garthe S., Montevecchi W.A. & Blaber S.J.M. (2000) The impacts of fishing on marine birds. *ICES Journal of Marine Science*, 57:531-547.
- Tew-Kai E. & Marsac F. (2008) Patterns of variability of sea surface chlorophyll in the Mozambique Channel: A quantitative approach. *Journal of Marine Systems*, 77:77-88.
- Tew-Kai E., Rossi V., Sudre J., Weimerskirch H., Lopez C., Hernandez-Garcia E., Marsac F. & Garçon V. (2009) Top marine predators track Lagrangian coherent structures. *Proceedings of the National Academy of Sciences USA*, 106(20):8245-8250.
- Tremblay Y., Bertrand S., Henry R.W., Kappes M.A., Costa D.P. & Schaffer S.A. (2009) A review of analytical approaches to investigate seabird-environment interactions. *Marine Ecology Progress Series*, 391:153-163.

- Tremblay Y., Roberts A.J. & Costa D.P. (2007) Fractal landscape method: an alternative approach to measuring area-restricted searching behavior. *Journal of Experimental Biology*, 210:935-945.
- Underhill L.G., Crawford R.J.M., Wolfaardt A.C., Whittington P.A., Dyer B.M., Leshoro T.M. & Ruthenberg M. (2006) Regionally coherent trends in colonies of African penguins *Spheniscus demersus* in the Western Cape, South Africa, 1987-2005. *African Journal of Marine Science*, 28:697-704.
- Vleck C.M. & Vleck D. (2002) Physiological condition and reproductive consequences in Adelie penguins. *Integrative and Comparative Biology*, 42:76-83.
- Votier S.C., Bearhop S., Witt M.J., Inger R., Thompson D. & Newton J. (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology*, 47:487-497.
- Weimerskirch H. (2007) Are seabirds foraging for unpredictable resources? *Deep-Sea Research II*, 54:211-223.
- Weimerskirch H., Chastel O., Cherel Y., Henden J.-A. & Tveraa T. (2001) Nest attendance and foraging movements of northern fulmars rearing chicks at Bjørnøya Barents Sea. *Polar Biology*, 24:83-88.
- Weimerskirch H., Le Corre M., Jaquemet S., Potier M. & Marsac F. (2004) Foraging strategy of a top predator in tropical waters: great frigatebirds in the Mozambique Channel. *Marine Ecology Progress Series*, 275:297-308.
- Weimerskirch H., Pinaud D., Pawlowski F. & Bost C.-A. (2007) Does Prey Capture Induce Area-Restricted Search? A Fine-Scale Study Using GPS in a Marine Predator, the Wandering Albatross. *The American Naturalist*, 170(5):734-743.

LIST OF THE PAPERS

PAPER 1

Crawford R.J.M., Sabarros P.S., Fairweather T., Underhill L.G. & Wolfaardt A.C. (2008) Implications for seabirds off South Africa of a long-term change in the distribution of sardine. *African Journal of Marine Science*, 30(1):177-184

PAPER 2

Sabarros P.S., Durant J.M., Grémillet D., Crawford R.J.M. & Stenseth N.C. (in revision) Differential responses of three marine top-predators to spatio-temporal variability of shared resource. *Marine Ecology Progress Series*

PAPER 3

Sabarros P.S., Ménard F., Lévénéz J.-J., Tew-Kai E. & Ternon J.-F. (2009) Mesoscale eddies influence distribution and aggregation patterns of micronekton in the Mozambique Channel. *Marine Ecology Progress Series*, 395:101-107

PAPER 4

Sabarros P.S., Grémillet D., Stenseth N.C., Ryan P.G. & Machu E. (in revision) A critical assessment of methods to study area-restricted search in seabirds using Cape gannets. *Methods in Ecology and Evolution*

PAPER 5

Sabarros P.S., Grémillet D., Demarcq H., Moseley C., Mullers R.H.E., Pichegru L., Stenseth N.C. & Machu E. (submitted) Fine-scale recognition and use of submesoscale fronts by Cape gannets in the southern Benguela region. *Marine Ecology Progress Series*