Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions?

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Summary

1. Remote-sensing measurements of marine primary productivity are widely used to predict the distribution and movements of marine top predators, despite the fact that predators do not feed directly on phytoplankton but several trophic levels higher up the food chain.

2. To test for potential links between primary productivity and top-predator feeding hotspots, we assessed spatial match–mismatch across four trophic levels of the Benguela upwelling zone (south-east Atlantic). The food chain studied consisted of phytoplankton, zooplankton (copepods), pelagic fish (anchovies and sardines) and two top predators (Cape gannets *Morus capensis* and human fisheries).

3. Remote-sensing data of sea-surface temperature (SST) and chlorophyll_a concentration were used as indices of phytoplankton abundance throughout the study area. Copepod biomass and pelagic fish density were determined during at-sea surveys in the South African section of the Benguela using net tows and hydro-acoustics, respectively. Seabird (Cape gannet) home ranges and foraging zones were assessed from two Namibian breeding colonies (Mercury and Ichaboe) and two South African colonies (Lambert's Bay and Malgas) using global positioning system (GPS) tracking. Industrial fishing for anchovies and sardines was investigated using South African landing statistics and logbooks.

4. Our spatial analyses revealed a strong match of seabird at-sea habitat and zones of high primary productivity throughout the southern Benguela. Conversely, there was a marked spatial mismatch between copepods and pelagic fish, as well as between pelagic fish, seabirds and human fisheries: copepods were present in the southern Benguela but pelagic fish usually feeding upon them were located further east (Indian Ocean), outside of the Benguela *sensu stricto*. Consequently, the majority of these pelagic fish were out of reach for seabirds and fisheries confined to the southern Benguela.

5. *Synthesis and applications.* Our study demonstrates the impact of an ecosystem shift across one of the world's most productive marine ecosystems and highlights the limitations of using remote-sensed patterns of primary productivity to interpret the foraging behaviour of marine top predators. These findings underline the importance of a better knowledge of food web spatial dynamics to support ecosystem-based fisheries management and the conservation of marine top predators.

Key-words: biotelemetry, ecosystem shift, industrial fisheries, match–mismatch hypothesis, remote-sensing

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Introduction

The cohesion and resilience of food webs are ensured by the spatio-temporal match of consumers and their resources. Environmental stochasticity and human disturbance can cause a mismatch of predators and prey, with profound impacts on energy flow, population dynamics and ecosystem structure. The match–mismatch hypothesis (MMH), formulated by Cushing (1974), underlines the importance of this equilibrium for the recruitment of pelagic fish feeding on zooplankton. Several studies have confirmed the pertinence of the MMH for our understanding of trophic functioning (Sinclair & Tremblay 1984; Conover *et al.* 1995). Cushing's concept primarily referred to temporal match–mismatch occurring at lower trophic levels, such as within a plankton–fish system. Nevertheless, recent investigations indicate that this framework can be expanded to a spatial context, i.e. that it can be applied to the spatial match–mismatch of predators relative to prey fields (Chick & van den Avyle 1999). Further studies suggest that the MMH is equally valid for a wide range of terrestrial and marine predator–prey systems, including predators operating at the highest trophic levels (Stenseth & Mysterud 2002; Durant *et al.* 2005). However, tests of the MMH have typically considered only two trophic levels and have not specifically assessed the spatial match–mismatch of predator and prey distributions, but rather focused on temporal features, often using proxies of predator occurrence, such as reproductive success. No studies have included human fisheries as predators of natural resources. From a management perspective, an assessment of spatial match–mismatch from primary producers to top predators, including humans, is essential for two reasons.

First, studies assessing the impact of environmental change (natural or anthropogenic) on ecosystems should ideally consider all food web components. However, this approach is too time consuming and costly to be implemented routinely. Researchers and managers have therefore been on the lookout for ecological indicators, i.e. species or trophic guilds that can be used to inform us about the ecological status of entire ecosystems (Dale & Beyeler 2001). In the marine environment, satellite data of sea-surface temperature (SST) and surface concentrations of chlorophyll_a are used extensively to map patterns of primary productivity. As an increasing number of studies indicate that marine ecosystems are controlled via bottom-up processes (Frank, Petrie & Shackell 2007), it is tempting to use these remote-sensed estimates of primary productivity to interpret and predict the occurrence of marine top predators, such as predatory fish, turtles, seabirds and marine mammals (Polovina *et al.* 2004; Bailleul *et al.* 2005; Zainuddin *et al.* 2006; Pinaud & Weimerskirch 2007). However, we tend to forget that marine top predators do not feed on SST or on phytoplankton. In fact, there are one to four intermediate trophic levels between primary production assessed via remote-sensing and marine top predators (Barnes & Hughes 1988). If there is no close spatio-temporal match between the different trophic components of these food webs, it is questionable whether satellite charts of primary productivity can be used to assess the spatial ecology of marine top predators.

Secondly, in the current context of marked environmental changes and their impact on species' distributions, natural resources and biodiversity (Parmesan & Yohe 2003), there is an urgent need to understand the spatial links across marine food webs and how environmental perturbations might affect them. Modifications in the distributional ranges of species facing global change can be gradual or catastrophic. The latter may be associated with ecosystem shifts (also termed regime shifts), which feature rapid changes in ecosystem structure and ecological functioning (de Young *et al.* 2004). Such catastrophic events are natural and/or driven by anthropogenic perturbations such as climate change, overexploitation and habitat destruction (de Young *et al.* 2004).

In this study we assessed spatial match–mismatch across four trophic levels of a marine food web. Our study was performed in the Benguela ecosystem, one of the four major upwelling zones of the world's oceans, located along the Atlantic coasts of Namibia and South Africa. The ecological functioning of the Benguela is classically described as follows (Shannon 1985). Nutrient-rich upwelled water boosts growth of large-celled phytoplankton, which is beneficial for the zooplankton (principally copepods) community feeding upon it. Both phyto- and zooplankton are consumed by pelagic fish such as anchovies *Engraulis encrasicolus* L. and sardines *Sardinops sagax* Jenyns, which in turn nourish a vast community of predatory fish, seabirds and marine mammals. Anchovies and sardines are also targeted by human fisheries (Griffiths *et al.* 2004).

Despite the bounty provided by upwelling of intermediate water masses, some of the predators endemic to the Benguela declined markedly in the 20th century, including three major seabird species: Cape cormorant *Phalacrocorax capensis* Sparrman, Cape gannet *Morus capensis* Lichtenstein and African penguin *Spheniscus demersus* L. These declines have been attributed to *inter alia* (i) direct harvesting of seabirds and their eggs, (ii) destruction of their breeding habitat via guano scraping, (iii) oil pollution and (iv) overexploitation of pelagic fish by industrial fisheries (Hockey, Dean & Ryan 2005).

Benguela seabird populations are also exposed to environmental stochasticity. The relative abundance of their main prey (sardines and anchovies), for instance, varies widely both in time and space. This is probably because of population cycles inherent to the anchovy–sardine duet, with alternating dominance of each species observed in all eastern boundary current systems, including the Benguela (van der Lingen *et al.* 2006). However, ecosystem shifts can also affect the entire structure of regional food webs, as for the pelagic ecosystem of the northern Benguela (off Namibia) in the 1980s (Roux & Shannon 2004). The links between (over)fishing, population cycles of pelagic fish, ecosystem shifts and El Niño events are still unclear (Cury & Shannon 2004) but it is generally agreed that seabirds of the Benguela live in a potentially rich yet labile environment, where they are exposed to the combined effects of natural stochasticity and anthropogenic forcing.

We used a bottom-up approach, synoptically gathering data concerning the spatial structure of the abiotic environment (bathymetry and SST), the abundance and distribution of primary producers (chlorophyll_a levels), primary consumers (copepods), secondary consumers (pelagic fish) and tertiary consumers (seabirds and fisheries). With respect to seabirds, we focused on the Cape gannet, a large seabird that feeds by plunge-diving on pelagic fish (Hockey, Dean & Ryan 2005). With approximately 500 000 breeding individuals, Cape gannets are the second most abundant avian predators in this area (after the Cape cormorant). They are also the species with the largest foraging range while breeding, theoretically allowing them the greatest flexibility to respond to spatial changes in the distribution of prey species. Using this extensive data set, we provide the first assessment of spatial match–mismatch across all major trophic levels of a marine food web.

Methods

All data collection occurred between 20 October 2003 and 6 January 2004. At this time of the year, upwelling activity is strong in the Benguela, primary productivity is marked, pelagic fish are engaged in spawning and most seabirds are breeding. We focused on the areas used by Cape gannets foraging off four breeding sites, two located in Namibia and two in South Africa (Fig. 1; Lewis *et al.* 2006). Data concerning zooplankton, pelagic fish and fisheries, which were provided by Marine and Coastal Management, South African Department of Environmental Affairs and Tourism, were only available for the South African sector of our study zone.

DATA COLLECTION

Bathymetry was derived from GTOPO30, a global digital elevation model (DEM) with a horizontal grid spacing of 30 arc seconds (approximately 1 km) derived from several raster and vector sources

of topographic information and available from http://edc.usgs.gov/products/elevation/gtopo30/dem_img.html, accessed June 2004 (Smith & Sandwell 1997).

SST (°C) was obtained from the moderate-resolution imaging spectroradiometer (MODIS) Aqua satellite. We extracted MODIS level 1 daily satellite images on the SeaWiFS data server (http://oceancolor.gsfc.nasa.gov/SeaWiFS.html, accessed May 2005). The level 1 data set is part of the 33 data sets that comprise the ECS (Earth (Observation System Data and Information System) Core System) data collection (http://modis.gsfc.nasa.gov/, accessed May 2005). Daily maps were compiled at a 1-km grid scale on a cylindrical equidistant map projection. Data sets are available in hierarchical data format (HDF) from the Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Center (JPL PO.DAAC, Pasadena, Califoria, USA).

Primary productivity was assessed using chlorophyll_a measurements derived from MODIS/Aqua Ocean Color (NASA, Washington, USA). Daily maps of level 3 data (mg m^{-3}) were compiled on a 1-km grid scale. Data sets are available in HDF from the NASA Goddard Space Flight Center Distributed Active Archive Center (GSFC DAAC, Washington, USA).

Zooplankton samples were collected from 161 stations positioned at 10 nautical mile (nm) intervals along selected transects within the 200-m isobath (Fig. 2). Zooplankton was sampled quantitatively using a paired Bongo net system (0·57 m diameter, 200-μm mesh, Marine & Coastal Management, Rogge Bay, South Africa) equipped with a calibrated electronic flow meter and hauled vertically from 200 m (or 5 m off the bottom if shallower) to the surface to avoid potential biases as a result of zooplankton vertical migration. Samples were preserved in 5% buffered formalin. In the laboratory, they were allowed to settle in a graduated measuring cylinder for 24 h and then diluted to 10 times the zooplankton settled volume. Two 2-mL subsamples were removed using a 6-mm bore glass tube attached to a graduate polyethylene syringe, and all copepods were counted and identified to species where possible, and to copepodite stage for *Calanus agulhensis* De Decker, Kaczmaruk & Marska and *Calanoides carinatus* Krøyer. Abundance (number m^{-2}) of all copepod species
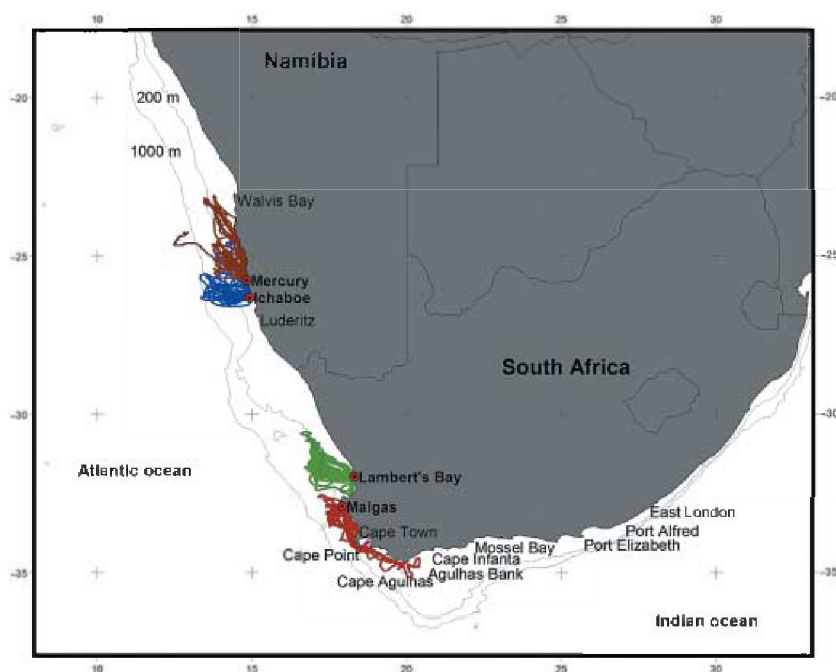

Fig. 1. Map of the study area showing GPS tracks recorded for 93 Cape gannets foraging off four breeding colonies in Namibia and South Africa, along with the 200-m and 1000-m isobaths and main geographical features.
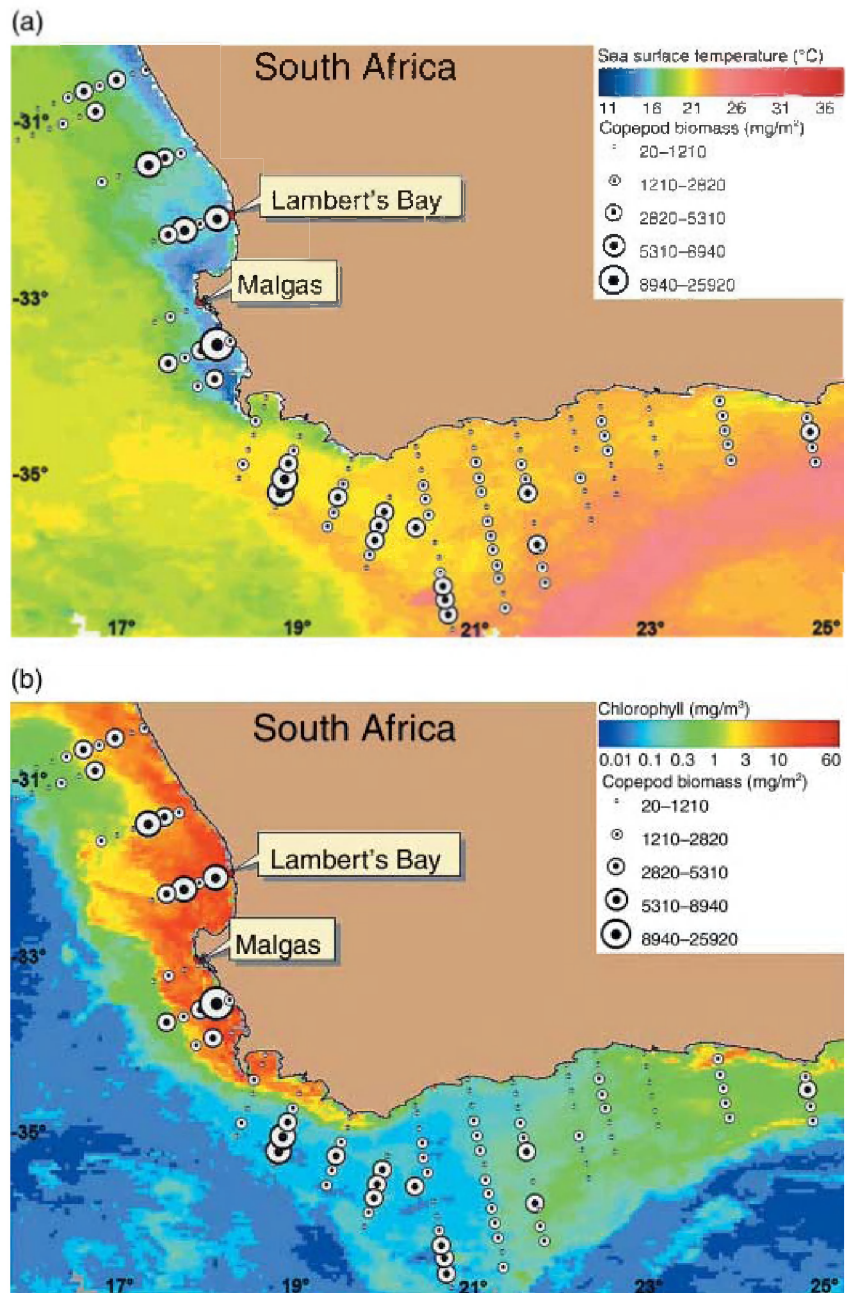
Fig. 2. Overlay of copepod biomass at 161 sampling stations on (a) SST charts from remote-sensing and (b) chlorophyll_a charts from remote-sensing.

(39 categories) was converted to biomass (mg dry mass m^{-2}) using known or estimated dry weights (Peterson, Painting & Hutchings 1990; Richardson *et al.* 2001), and these were summed to obtain total copepod biomass at each station.

Densities of small pelagic fish (primarily anchovy and sardine) were estimated using echo-sounding for 545 intervals along 62 stratified random transects orientated perpendicularly to the coast and extending across the continental shelf from close inshore to around the 200-m depth contour. Echo-integration techniques were used to estimate fish density (g m^{-2}) along survey transects, and midwater trawling was used to determine the species composition and size frequency distributions of pelagic fish. Each transect was divided into 10-nm segments and the density of anchovy and sardine was estimated for each segment and assigned to the segment midpoint. A full description of the methods used during these surveys is given by Hampton (1992). These fish produce several batches of eggs and do not cease feeding during the spawning season (Melo 1994).

Seabird feeding behaviour was studied for 20 adult Cape gannets breeding on Malgas Island (33°03′ S, 17°55′ E) and 29 on Bird Island, Lambert's Bay (32°5′ S, 18°18′ E) in South Africa's Western Cape Province, and 26 on Ichaboe Island (26°17′ S, 14°56′ E), and 18 on Mercury Island (25°43′ S, 14°50′ E) in Namibia (Fig. 1). These four colonies support 99·6% of gannets breeding along the Atlantic coast of southern Africa (Lewis *et al.* 2006). Each bird was fitted with a miniaturized global positioning system (GPS) before foraging at sea to provision its chick (for methods see Grémillet *et al.* 2004; Lewis *et al.* 2006). GPS positions and travelling speeds recorded at 10-s intervals were filtered to categorize sections of the tracks into three activities: (i) resting at the water surface (speed < 6 km h^{-1}); (ii) commuting between the colony and a feeding site or between feeding sites (speed > 6 km h^{-1} and low path sinuosity); (iii) actively exploiting a food patch (speed > 6 km h^{-1} and high path sinuosity). For details about the filtering procedures and validation of this method see Grémillet *et al.* (2004, 2006).

Spatial patterning in South Africa's commercial fishery for pelagic fish was assessed in terms of catch weight (t) and species composition of each purse seine haul located on a $10 \times 10'$ Minutes (1/60 degrees) cell grid (approximately 18.5×16 km). Two sources of data were used to allocate pelagic catches to a grid cell: (i) logbooks, where estimations from vessel skippers of the weight per species per set are recorded, and (ii) the total landings per species and per trip for each boat as reported by inspectors working at harbours. When catches from one trip came from different grid cells, the skipper estimates per cell were corrected by the ratio of total volume landed to total volume estimated by the skipper, and the catch composition by cell was either estimated from single set trips by another boat(s) or, more often, considered equal in each cell visited by the boat (most of the time these cells were adjacent).

DATA ANALYSES

All analyses were conducted using ArcGis 9·0 (ESRI Inc.), Access (Microsoft), Matlab 6·5 (The MathWorks Inc.) and Genstat Release 8·1 (VSN International Ltd). Calculations ran in four phases.

First, average SST, chlorophyll_a levels and anchovy and sardine densities were calculated for a 1-nm zone around each zooplankton sampling station on the day of sampling. This analysis was restricted to the South African sector of the study zone.

Secondly, home range data of Cape gannets (i.e. all recorded GPS positions) from the four study colonies were overlaid on SST, chlorophyll_a and bathymetry maps to determine the general environmental conditions experienced by birds at sea. This analysis was conducted at a 1-km spatial scale and for daily temporal resolution. Summary statistics were compiled using each foraging trip (per bird, as one trip was recorded per bird) and breeding colony as the sampling units.

Thirdly, Cape gannet foraging positions (third activity definition as given above) from the four different colonies (South Africa and Namibia) were overlaid on SST, chlorophyll_a and bathymetry maps to determine the general environmental conditions experienced by birds actively foraging at sea. Averaged values for SST, chlorophyll_a and bathymetry were computed as in the second phase.

Kernel analyses (Wood *et al.* 2000) were used to map and measure the areas corresponding to the total zone utilized by Cape gannets at sea (all GPS positions, hereafter termed home range) and their preferred foraging areas (third activity category, hereafter termed foraging zone), as well as the distribution patterns of anchovy, sardines and catches made by commercial pelagic vessels in South African waters. We then calculated the percentage of overlap between bird distributions, distributions of prey and human fisheries, as well as the respective fish densities and commercial catches within the different zones utilized by the birds during the study period. This analysis was restricted to South African waters and therefore only concerned data for gannets from the Lambert's Bay and Malgas Island colonies.

Results

ABIOTIC ENVIRONMENTAL CONDITIONS AND PRIMARY PRODUCTION

Low SST and high chlorophyll_a levels revealed typical strong upwelling along the Atlantic coast of South Africa and Namibia (Figs 2 and 4). This pattern faded towards Cape Agulhas, with higher temperatures and lower chlorophyll_a

levels on the Agulhas Bank and in the Indian Ocean sector of our study area (Fig. 2). During the study period there was a marked negative relationship between SST and phytoplankton abundance ($F_{1,152} = 127.1$, $P < 0.001$, $r^2 = 0.45$), assessed via remote-sensing.

PHYTOPLANKTON VS. ZOOPLANKTON

Copepod biomass during the study was relatively low compared with mean biomass levels measured between 1988 and 2000 (generally > 5 g dry mass m^{-2} north of Malgas and < 5 g dry mass m^{-2} elsewhere; Huggett *et al.* 2006). The mean copepod biomass was 2.3 ± 4.0 g dry mass m^{-2} along the Atlantic coast north of Cape Point and 1.6 ± 1.4 g dry mass m^{-2} east of this landmark (Fig. 2). For the entire study zone, there was a weak negative correlation between SST and copepod biomass ($F_{1,152} = 4.9$, $P = 0.03$, $r^2 = 0.05$) and a positive, although non-significant, relationship between chlorophyll_a levels and copepod biomass ($F_{1,152} = 3.0$, $P = 0.08$, $r^2 = 0.02$).

ZOOPLANKTON VS. PELAGIC FISH

Crucially, pelagic fish (sardines and anchovies) that feed on zooplankton and, to a lesser extent, phytoplankton, were virtually absent from the highly productive waters of the southern Benguela along the Atlantic coast during our study period. Fish schools were almost entirely located east of Cape Point, along the south coast of South Africa (Fig. 3). Consequently there was no significant relationship between zooplankton abundance and the abundance of sardines and anchovies ($F_{1,152} = 0.9$, $P = 0.36$, and $F_{1,152} = 0.1$, $P = 0.94$, respectively).

SEABIRDS VS. PHYTOPLANKTON

During our study period, GPS-tracked Cape gannets foraged within 200 km from the coast and mainly exploited the highly productive (low temperatures, high chlorophyll_a concentrations) shallow waters of the Benguela upwelling zone (Figs 1 and 4 and Table 1). For three out of four colonies there were no significant differences between the SST, chlorophyll_a levels and bathymetry within home ranges (compiled using all recorded GPS positions) and foraging zones (compiled using the positions of the third category of bird activity). However, birds from Lambert's Bay foraged in areas that were significantly warmer, poorer in chlorophyll_a and deeper than their overall home range, resulting from a higher degree of offshore foraging by birds from this colony compared with others (Table 1 and Fig. 4). Namibian gannets had larger home ranges (Ichaboe 23 800 km² and Mercury 25 300 km²) than birds from South African colonies (Malgas 16 500 km² and Lambert's Bay 12 800 km²), despite supporting smaller breeding populations. Foraging zones were of similar sizes for birds from the different colonies (Malgas 5000 km², Lambert's Bay 6400 km², Ichaboe 4900 km² and Mercury 5400 km²) but Namibian birds showed more fragmented/dispersed foraging zones (Fig. 4).
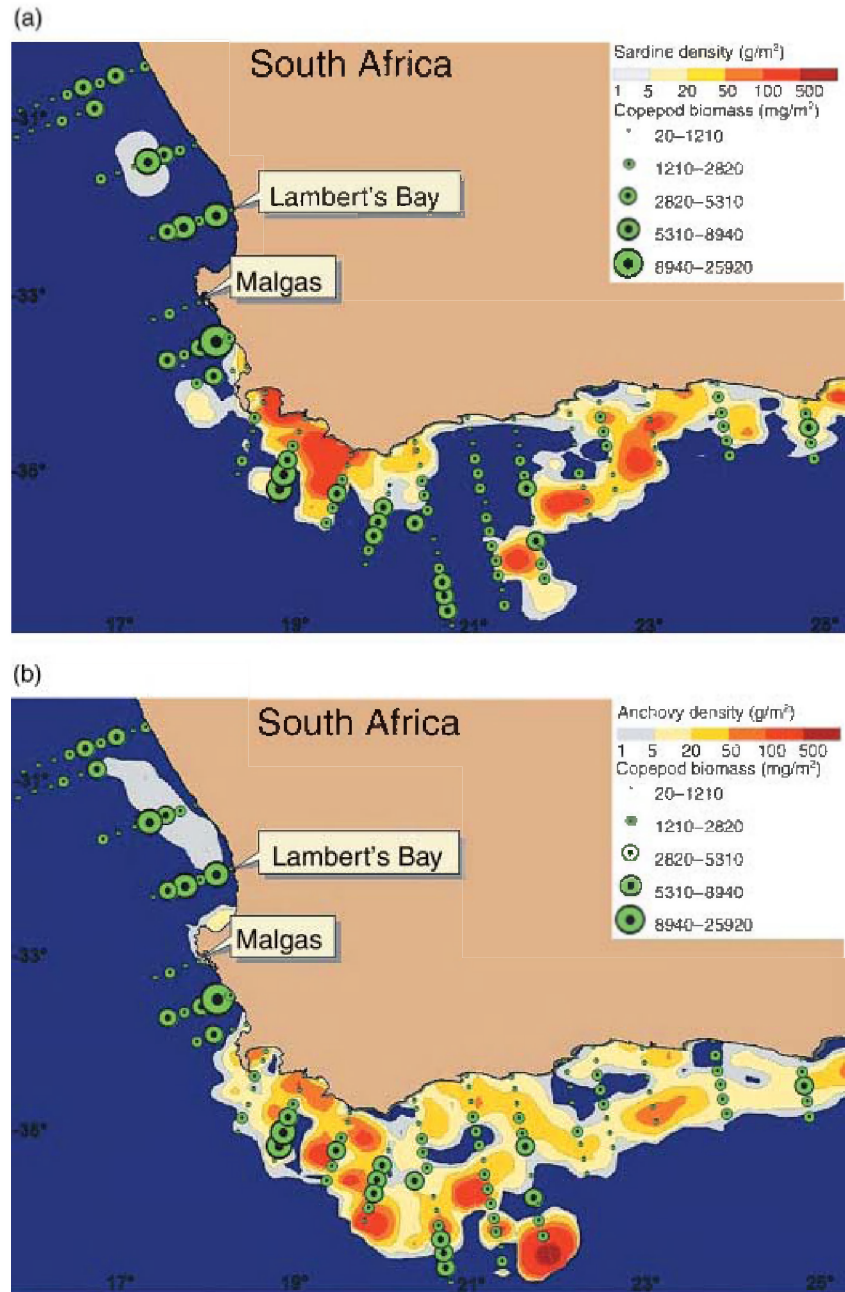
Fig. 3. Overlay of copepod biomass at 161 sampling stations on (a) charts of sardine density from echo-sounding and (b) charts of anchovy density from echo-sounding.

Table 1. Environmental conditions within the home ranges (HR) and foraging zones (FZ) of Cape gannets from South African (Malgas and Lambert's Bay) and Namibian (Ichaboe and Mercury) breeding colonies. Average values are given ± SD. Significant statistical tests are in bold

|	SST (°C)			Chlorophyll_a (mg m⁻³)			Bathymetry (m)		
	HR	FZ	Test	HR	FZ	Test	HR	FZ	Test
Malgas	16·46 ± 0·87	16·78 ± 1·23	$F_{1,39} = 0·93$ $P = 0·342$	9·8 ± 3·0	9·0 ± 4·5	$F_{1,39} = 0·45$ $P = 0·508$	133 ± 90	141 ± 120	$F_{1,39} = 0·05$ $P = 0·823$
Lambert's Bay	16·49 ± 0·47	16·96 ± 0·71	$\boldsymbol{F_{1,57} = 8·76}$ $\boldsymbol{P = 0·005}$	8·7 ± 3·1	6·0 ± 5·4	$\boldsymbol{F_{1,57} = 5·16}$ $\boldsymbol{P = 0·027}$	164 ± 44	207 ± 65	$\boldsymbol{F_{1,57} = 8·71}$ $\boldsymbol{P = 0·005}$
Ichaboe	15·60 ± 1·54	15·70 ± 2·28	$F_{1,51} = 0·03$ $P = 0·856$	8·7 ± 6·2	7·5 ± 7·0	$F_{1,51} = 0·39$ $P = 0·536$	263 ± 151	281 ± 173	$F_{1,51} = 0·15$ $P = 0·697$
Mercury	16·58 ± 0·65	16·63 ± 0·69	$F_{1,35} = 0·04$ $P = 0·838$	8·6 ± 4·2	8·4 ± 4·3	$F_{1,35} = 0·03$ $P = 0·862$	226 ± 258	244 ± 345	$F_{1,35} = 0·03$ $P = 0·865$
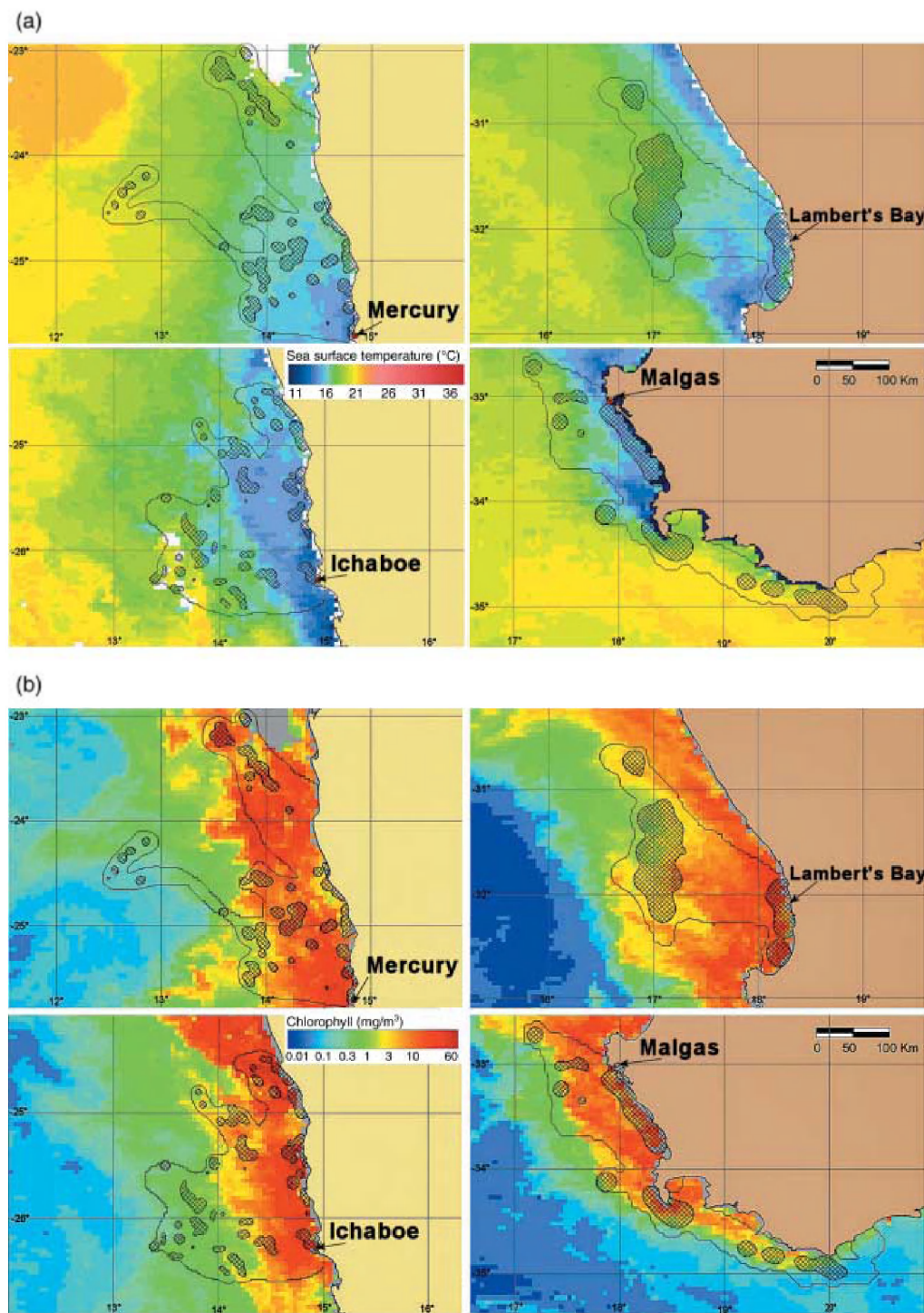
Fig. 4. Overlay of Cape gannet home ranges (line-delimited areas) and foraging zones (hatched zones within the home ranges) from four breeding colonies on (a) SST charts from remote-sensing (see the Methods for technical details and definitions) and (b) chlorophyll_a charts from remote-sensing.

PELAGIC FISH VS. SEABIRDS AND FISHERIES

During our study, anchovies and sardines were mainly found east of Cape Point, on the Agulhas Bank, and along the south coast of South Africa. Acoustic surveys revealed that sardines spread over an area of *c.* 84 000 km² and anchovies over *c.* 113 000 km² (Fig. 5). For birds from Malgas Island, home range and foraging areas overlapped by 42% and 49%, respec-

tively, with the distribution of anchovies, and by 42% and 60%, respectively, with the distribution of sardines. For birds from Lambert's Bay, home range and foraging areas overlapped by 33% and 10%, respectively, with anchovies, and by 14% and 21%, respectively, with sardines. Sardine densities averaged 2·8 g m⁻² and 4·2 g m⁻² within the home range and foraging zone of birds from Lambert's Bay, and 50·9 g m⁻² and 47·0 g m⁻² within the home range and foraging zone of birds
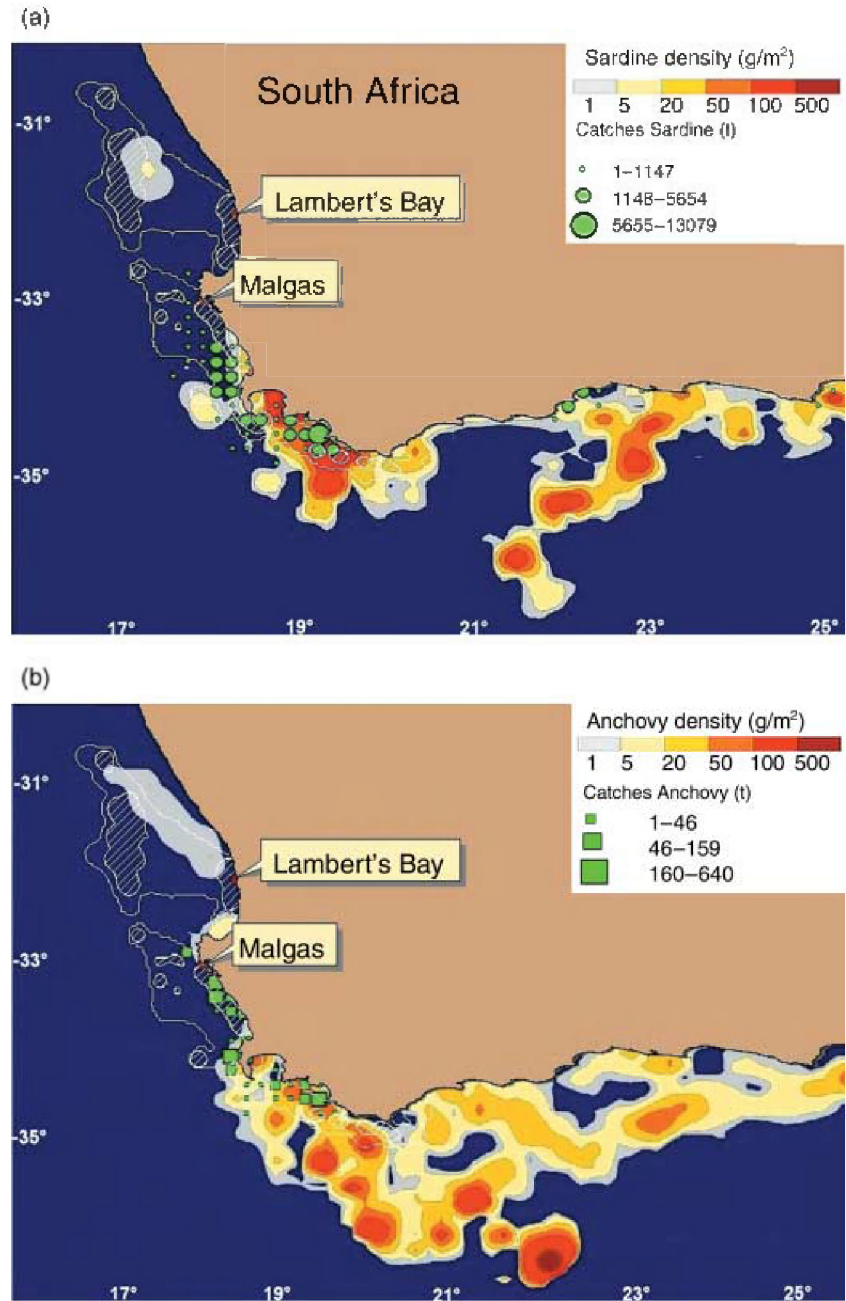
Fig. 5. Overlay of Cape gannet home ranges (areas delimited by white line) and foraging zones (hatched zones within home ranges) from the Malgas and Lambert's Bay colonies on charts of (a) sardine density (colour scale) and catches of sardine made by commercial fishing vessels (green dots) and (b) anchovy density and catches of anchovy made by commercial fishing vessels (green squares).

from Malgas. Anchovy densities averaged 2·6 g m^{-2} and 1·2 g m^{-2} within the home range and foraging zone of birds from Lambert's Bay, and 16·1 g m^{-2} and 11·6 g m^{-2} within the home range and foraging zone of birds from Malgas.

Human fishing activity was mainly concentrated within the western-most section of the distributional ranges of sardines and anchovies during our study period (Fig. 5). No fish were caught within the foraging zones and the home range of gannets from Lambert's Bay. In contrast, fisheries caught 42 204 t sardines and 2250 t anchovies within the home range of birds from Malgas Island. Comparative figures for their foraging area were 11 644 t sardines and 888 t anchovies. Within the commercially exploited zone, average sardine abundance (estimated via hydro-acoustics) was 48·9 g m^{-2}, compared with 63·1 g m^{-2} for the rest of the zone utilized by sardines.

Similarly within the commercially exploited zone, average anchovy abundance (estimated via hydro-acoustics) was 20·5 g m^{-2}, whereas it was 107·2 g m^{-2} for the rest of the zone utilized by sardines.

Discussion

MATCH OF MARINE TOP PREDATORS AND PRIMARY PRODUCERS

Our study confirms that all Cape gannets breeding along the Atlantic coast of southern Africa forage within areas of extremely high primary productivity (Grémillet *et al.* 2004). This area corresponds to a 100–200-km wide band along the Atlantic coast, in water < 500 m deep (Fig. 1 and Table 1).

Summer upwelling is intense within this zone and drives domes of cooler, nutrient-rich intermediate water from several hundred metres depth to the surface. The strength and the spread of the upwelling can be seen clearly on satellite maps of SST and chlorophyll_a (Figs 2 and 4). Most gannets foraged within the core of the upwelling, but some cruised its western edge, with individuals occasionally venturing into warmer oceanic waters (Fig. 4). Levels of SST recorded within the home ranges and foraging zones of Cape gannets (15·6–17·0 °C; Table 1) were typical of Benguela surface waters at that time of the year (Demarcq, Barlow & Schillington 2003). Chlorophyll_a levels associated with the home ranges and foraging zones of the birds were surprisingly high (6·0–9·8 mg m^{-3}; Table 1) and corresponded to the upper range of chlorophyll concentrations recorded by previous investigators for the Benguela (Demarcq, Barlow & Schillington 2003). These concentrations are also among the highest values recorded world-wide for oceanic waters (Parsons, Takahashi & Hargrave 1988). Consequently, an investigation restricted to overlays of Cape gannet foraging distributions, satellite images of SST and chlorophyll_a leads us to the conclusion that these marine top predators exploit zones of intense primary productivity that are expected to be extremely profitable foraging grounds characterized by high fish availability. However, this conclusion is not supported by the investigation of intermediate trophic levels.

APPARENT MISMATCH OF PHYTOPLANKTON AND ZOOPLANKTON

The greatest zooplankton biomasses were recorded in the southern Benguela, north of Cape Point, along with the highest chlorophyll_a concentrations (Fig. 2b). However, the zooplankton biomass recorded on the Agulhas Bank was only marginally lower, although chlorophyll_a levels were markedly lower within this zone. Our analysis therefore suggests a spatial mismatch between phytoplankton distributions, as assessed via remote-sensing, and zooplankton distributions, determined *in situ* (Fig. 2b). In this context, it is important to note that satellite-based sensors only assess primary production within the top few metres of the water column. Deep chlorophyll maxima, which can occur at depths > 50 m, are often overlooked (Barlow *et al.* 2002). Such subsurface chlorophyll maxima are known to occur on the Agulhas Bank during summer (Probyn *et al.* 1994), resulting in poor agreement between surface and deeper chlorophyll concentrations (Shannon, Schlittenhardt & Mostert 1984). These phytoplankton populations are far less abundant than those occurring in the southern Benguela but they provide sufficient food for some copepods to grow (Verheye *et al.* 1994). Consequently, the limited overlap of primary producers and primary consumers indicated by our analysis might only be an apparent mismatch.

MISMATCH OF ZOOPLANKTON AND PELAGIC FISH

During our study period, substantial copepod biomass was found along the Atlantic coast of South Africa, north of Cape Point, but intriguingly hardly any anchovies or sardines were recorded in this area. Indeed pelagic fish were virtually absent from the southern Benguela, instead occurring mainly on the Agulhas Bank and along the south coast (Fig. 5). The abundance and distribution of pelagic fish such as sardines and anchovy can vary widely from one year to the next (Lluch-Belda *et al.* 1989). The reasons for such fluctuations remain obscure, but potential candidates include: (i) the age and genetic structure of the spawning stock; (ii) the availability of planktonic food as well as water temperatures at the spawning sites, which both influence fish body condition and egg production; (iii) the proportion of eggs remaining in highly productive coastal waters vs. those lost to less productive oceanic waters; and (iv) the proportion of juvenile fish reaching nursery areas and recruiting into age classes accessible to seabirds and fisheries (van der Lingen & Huggett 2003). At present, some eggs and larvae are still advected to the west coast by a northward shelf-edge jet current off Cape Point, and ultimately reach the nursery area in St Helena Bay, north of the Malgas gannet colony (Huggett *et al.* 2003). However, over the last few years, adult pelagic fish previously associated with the southern Benguela have undergone an eastward shift into the Indian Ocean (van der Lingen *et al.* 2005). Sardine distribution has shown a progressive eastward shift since the mid-1990s (van der Lingen *et al.* 2005; Coetzee *et al.* 2006), and the distribution of anchovy spawners on the Agulhas Bank has also shown an eastward shift, initiated in 1996, with the bulk of anchovy spawners now being found to the east of Cape Agulhas, whereas before 1996 it was farther west (van der Lingen, Coetzee & Hutchings 2002). Linkages between the sardine eastward shift and changes in the environment are not obvious (van der Lingen *et al.* 2005) but it has been hypothesized that there may be a genetic basis for the shift: intense fishing pressure on west coast sardines may have critically depleted this stock, thereby enabling the dominance of individuals genetically tuned to live along the south coast of South Africa and on the Agulhas Bank (Coetzee *et al.* 2006). This sudden redistribution of an important food web component (pelagic fish) is an indication of an ecosystem shift in the southern Benguela as the absence of these species from the region is likely to have significant impacts on the structure and functioning of the local marine ecosystem.

We do not have detailed information on the distribution of sardines and anchovies off Namibia, where birds from Ichaboe and Mercury forage. However, monitoring of these fish species showed that their stocks collapsed because of over-fishing in the 1960–70s, resulting in an ecosystem shift that restructured the northern Benguela (i.e. off Namibia) in the 1980s (Roux 2003). During this ecosystem shift, pelagic goby *Sufflogobius bibarbatus* von Bonde and gelatinous plankton (i.e. jellyfish and salps) took over the ecological niche previously occupied by sardines and anchovies, probably preventing the recovery of pelagic fish stocks via predation of fish eggs and larvae (Lynam *et al.* 2006). What used to be the largest pelagic fish stocks in the Benguela, and among the largest fisheries in the world, have not yet recovered and are unlikely to do so (Roux 2003). At the time of our investigations, the

total biomass of sardines and anchovies in the northern Benguela was estimated to be < 0·5 million t, 5–10% of the biomass present before the ecosystem shift (van der Lingen *et al.* 2006).

MISMATCH OF PELAGIC FISH, SEABIRDS AND FISHERIES

Our study highlights an interesting paradox: although Cape gannets breeding along the Atlantic coast forage within zones of intense primary productivity that might be expected to be associated with abundant pelagic fish populations, such species are currently largely absent. This contrasts with the situation pre-1950, when this area provided abundant resources for both marine top predators and human fisheries (Cury & Shannon 2004). Substantial stocks of sardines and anchovies remain off southern Africa, but they are hardly present within the Benguela *stricto sensu* (i.e. the Atlantic coast north of Cape Point). Therefore there were very few sardines and anchovies within the home range and foraging zones of Cape gannets breeding at Lambert's Bay (Fig. 5). Conditions were markedly better for birds at Malgas Island, but they had to travel round trips of > 400 km to exploit dense schools of pelagic fish between Cape Point and Cape Agulhas. Such a spatial mismatch of top predators and their preferred prey species has a marked impact upon the former: all Namibian Cape Gannet colonies have been declining since the 1960s (Lewis *et al.* 2006) and recent investigations indicated that the attendance rates of Cape gannets at colonies along the Atlantic coast of South Africa might have been decreasing for the past 10 years (Crawford *et al.* 2007). Further data suggest that the birds that do attend these colonies have a very low breeding success (Marine and Coastal Management, unpublished data). Under these circumstances, coastal breeding seabirds are disadvantaged compared with other top predators, such as marine mammals and sea turtles, that are not linked to a specific site. The latter forage over wider areas and can better track large-scale movements of their prey (Luschi *et al.* 2006).

In the longer term birds might none the less move towards the south coast of South Africa, where recent investigations indicate significantly better feeding conditions for gannets breeding off Port Elizabeth (Pichegru *et al.* 2007). However, there is only a limited number of potential island breeding sites along the south coast, and seabirds such as Cape gannets show high levels of philopatry that place social limitations on intercolony movements (Hockey, Dean & Ryan 2005). The outcome of the conflict between seabird cultural resilience and their capacity to move on to exploit spatially modified food resources is likely to condition the fate of this vulnerable bird species.

MANAGEMENT IMPLICATIONS

This study confirms the relevance of Cushing's MMH for a better understanding of trophic interactions in a changing environment. As we have demonstrated, the MMH can be expanded successfully to several trophic levels and to a spatial context. Crucially, our analysis has revealed that the lowest trophic level (phytoplankton) of a marine food web can match with the highest (top predators) while mismatching with intermediate trophic levels (pelagic fish).

The recorded match–mismatch pattern highlights the potential misuse of remote-sensed patterns of primary productivity to interpret the foraging behaviour of marine top predators (Ainley *et al.* 2005; Hays *et al.* 2006). Spatial overlap between these two components should be interpreted with caution because it can overlook mismatches across intervening trophic levels. In the Benguela this approach is currently particularly biased because of the strong mismatch of zooplankton and pelagic fish populations. Even if all trophic levels were to match spatially, other factors could prevent a straightforward link between indices of primary production and seabird foraging areas. For instance, the complete cycle of phytoplankton bloom development and decline occurs within 6–8 days in the southern Benguela (Brown & Hutchings 1987) while copepods typically require 14–40 days to grow to adulthood (Hutchings *et al.* 1995). Such spatio-temporal lag effects potentially occur between each trophic level, thereby substantially blurring the functional link between upwelling activity and top predator foraging profitability.

Our findings have far-ranging implications in the context of the ecosystem-based management of fisheries (EBMF) and the management of marine top predators challenged by environmental change. There is growing evidence that single-stock fishery management has failed and that managing fishing impacts should be focused at the ecosystem level (Shannon *et al.* 2006). Our study demonstrates that it is essential to gain an understanding of spatial dynamics across all major trophic levels prior to implementing such EBMF. This is particularly true in the Benguela upwelling zone, which is one of the first marine regions within which EBMF will be established (Shannon *et al.* 2006). Furthermore, recent studies have highlighted the importance of top predators as buffers against environmental change (Sala 2006). In the marine environment predatory fish, mammals, turtles and seabirds potentially play such a tempering role and management plans should ensure that their conservation is given highest priority. According to our results this is very much the case in the Benguela upwelling zone, where seabird populations feeding on pelagic fish are being critically perturbed by recent ecosystem shifts.

Acknowledgements

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