

# Are Cape gannets dependent upon fishery waste? A multi-scale analysis using seabird GPS-tracking, hydro-acoustic surveys of pelagic fish and vessel monitoring systems

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## Summary

1. Climate change and fishing impact marine ecosystems, potentially modifying the availability of small pelagic fish to marine top predators. Some seabirds that primarily rely upon these resources have switched to feeding on fishery waste. It has therefore been argued that seabirds might become dependent upon this artificial resource.

2. To test this hypothesis, we studied the foraging behaviour of Cape gannets *Morus capensis* breeding off the coast of South Africa using high-resolution Global Positioning System-tracking in relation to the availability of pelagic fish assessed by acoustic at-sea surveys, and fishing effort by the two main south African fisheries (purse seiners that compete with seabirds for pelagic fish, and demersal trawlers that process fish at sea and discharge fish waste) tracked with vessel monitoring systems. Conjoint seabird, fish and fisheries information were analysed at mesoscale (*c.* 100 km) and sub-mesoscale (*c.* 10 km) in years of high (2002), medium (2009) and low (2005) pelagic fish biomass within gannets' foraging range.

3. We found substantial inter-annual variability in spatial use by breeding gannets, which was driven primarily by pelagic fish availability. At the mesoscale, birds and purse seiners exploited similar marine areas, but no fine-scale dependence of birds on purse seiners was detected. Crucially, fine-scale dependence of gannets upon trawlers producing fishery waste was only detected in 2005, when pelagic fish biomass was lowest, indicating a direct effect of trawlers on gannet foraging behaviour in the absence of natural prey.

4. Further overlap analyses of gannet and trawler foraging areas during 2002–2010 confirmed that breeding birds only seek trawlers when pelagic fish availability is low, strongly suggesting reversible seabird dependency upon fishery waste.

5. *Synthesis and applications.* Our study demonstrates that seabirds such as Cape gannets depend on fishery waste when their natural prey is scarce, but revert to feeding on natural resources whenever available, showing highly flexible foraging behaviour. These results have important implications in the context of the anticipated legislation banning at-sea disposal of fishery waste in different regions, including European seas, highlighting the necessity to concomitantly promote sustainable fishing allowing the restoration of pelagic fish stocks.

**Key-words:** fisheries management, junk food hypothesis, pelagic fish, purse seiner, southern Benguela upwelling zone, sub-mesoscale, trawler

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## Introduction

Fisheries have the potential to strongly modify marine ecosystems by removing fish, destroying habitats and non-target organisms and dumping an estimated 7.3 million tonnes of fishery waste annually into the world's oceans (Jennings *et al.* 2001; Kelleher 2005; Bellido *et al.* 2011). The impact of fishery waste on marine trophic networks has long been underestimated, but there is now strong evidence that this practice is an incentive to overfishing and significantly perturbs trophic flows across benthic and pelagic ecosystems (Bellido *et al.* 2011). As a result, several countries including Canada, Iceland, New Zealand and Norway have implemented total or partial bans on at-sea dumping of fishery waste. The European Union is also planning similar action and is currently debating such a proposal (Anon 2011; Diamond & Beukers-Stewart 2011). From a conservation point of view, there are concerns that an enforced abrupt stop to the at-sea dumping of fishery waste might threaten populations of vulnerable marine species which have become dependent upon this artificial food resource. This is particularly true for seabirds, many species of which follow trawlers in anticipation of an easy meal (Garthe & Huppopp 1994). Audouin's gulls *Larus audouinii* (Near-Threatened) for instance depend on fishery waste generated off Spain's Ebro Delta (Oro, Jover & Ruiz 1996). Cape gannets *Morus capensis* (Vulnerable) in the Benguela upwelling zone might be lured into an ecological trap (*sensu* Dwernychuk & Boag 1972; Gates & Gysel 1978; Robertson & Hutto 2006) by the fishery waste of demersal trawlers. This resource is predictable and abundant, and results in high survival rates of adults feeding upon it, yet its calorific value is 50% lower than that of pelagic fish which are the Cape gannet's (hereafter referred to as gannet) natural prey, resulting in malnourished chicks and low breeding success (Grémillet *et al.* 2008a). Key issues in this context are the long-term dependency of seabirds upon fishery waste, whether this dependency is reversible, and the prerequisites to this reversibility (Granadeiro *et al.* 2011).

Seabird dependency on fishery waste can be tracked via dietary analyses, through either stomach contents or stable isotope studies (Votier *et al.* 2004). However, the sub-mesoscale ecological mechanisms linking seabirds, their natural prey and fisheries in the marine environment require parallel investigations of the spatio-temporal occurrence of these different players. This has only recently become possible through the advent of seabird Global Positioning System (GPS)-tracking (Weimerskirch *et al.* 2002) and of Vessel Monitoring Systems (VMS) which allow continuous tracking of fishing vessels fitted with Argos-GPS devices (Witt & Godley 2007; Votier *et al.* 2010).

The southern Benguela ecosystem normally supports a large biomass of small pelagic forage fish (sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*) that interact with both lower and higher trophic levels (i.e. zooplankton and top predators). These fish are

targeted by purse seiners and support South Africa's largest fishery, with average annual catches of around 400 000 tons that are taken predominantly off the west coast (van der Lingen, Coetzee & Hutchings 2011). Both species exhibit strong inter-annual variability in biomass, in particular during the last decade (van der Lingen *et al.* 2006; Coetzee *et al.* 2008; Hutchings *et al.* 2009). Following a steady eastward shift in the relative distribution of sardine during the late 1990s and early 2000s and subsequent successive years of very poor recruitment of juvenile fish (Coetzee *et al.* 2008; van der Lingen, Coetzee & Hutchings 2011), sardines were absent from much of the South African west coast for several years in the mid-2000s. Anchovy spawners also showed a south-eastward shift in spatial distribution (Roy *et al.* 2007). The local disappearance of sardine may have been due to localized overfishing, environmental variability or a combination of both drivers with natural stochasticity, and these hypotheses are currently being tested (Roy *et al.* 2007; Coetzee *et al.* 2008; Crawford *et al.* 2008). In the southern Benguela upwelling zone, breeding gannets normally feed exclusively on small pelagic fish. In the absence of their natural prey, gannets switched to feeding predominantly on the abundant fishery waste discarded by trawlers targeting hake *Merluccius* sp. (Pichegru *et al.* 2007, 2010a; Grémillet *et al.* 2008a).

In considering this system, our specific objectives were therefore (i) to test the spatio-temporal co-occurrence of foraging seabirds, purse seiners targeting sardine and anchovy, and demersal trawlers producing fishery waste and (ii) to study how these associations may vary depending on the biomass of small pelagic fish. Our analyses were performed on data gathered during 2002–2010, with a particular focus on 2002, 2005 and 2009, years that were characterized by high, low and intermediate combined biomasses of anchovy and sardine, respectively. Joint analyses of seabird foraging behaviour and fisheries have been the focus of high-profile research in recent years (Bartumeus *et al.* 2010; Votier *et al.* 2010; Granadeiro *et al.* 2011; Torres *et al.* 2011) yet, to the best of our knowledge, and in contrast to former work conducted in the Benguela, our analysis is the first to consider all four players in this system (pelagic fish, seabirds, trawlers and purse seiners) at very fine spatio-temporal scales and across years of contrasting pelagic fish abundance. It is also the first analysis of VMS data for the Benguela upwelling ecosystem.

## Materials and methods

### DATA SETS

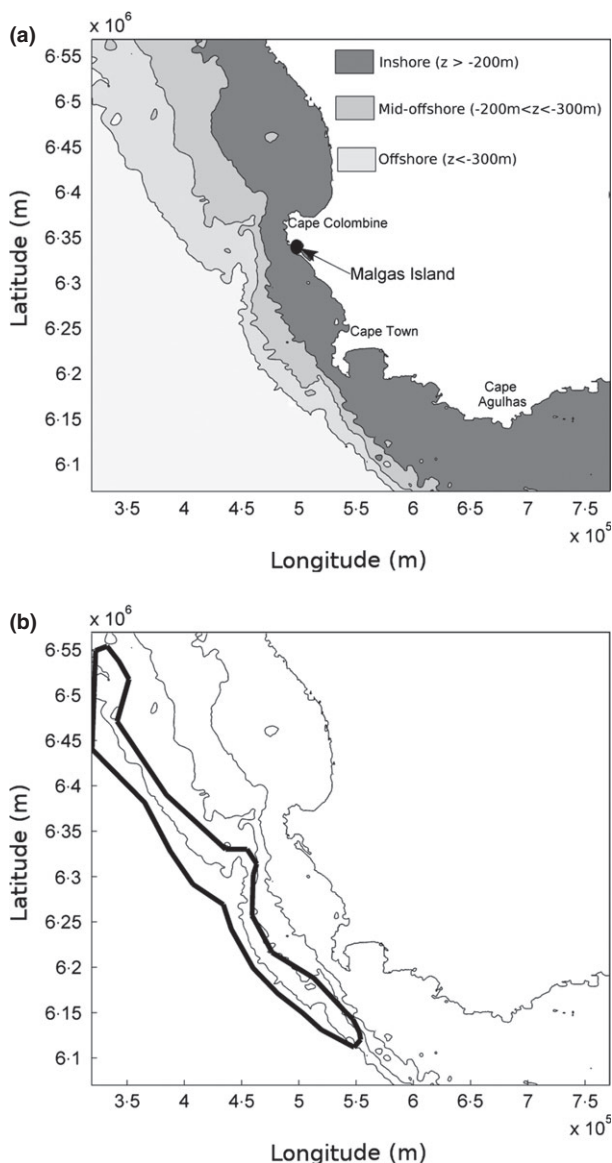
#### *Marine domains*

The study area (latitude 31°S–35.5°S, longitude 16°E–21°E) is situated in the southern Benguela current off the west coast of South Africa, where both demersal trawl fisheries and small pelagic purse seine fisheries operate. The demersal trawl fishery exploits deep areas (depth > 300 m) along the continental shelf,

whereas the purse seine fishery mainly targets inshore (depth < 200 m) to mid-offshore areas (200–300 m depth). We therefore considered three marine domains: inshore waters (depth < 200 m), mid-offshore waters (200–300 m depth) and offshore waters (depth > 300 m) (Fig. 1a). We used bathymetry from the GINA Grid with a spatial resolution of 2.6 km (Lindquist *et al.* 2004).

### Small pelagic fish abundance and distribution

We investigated spatio-temporal variability in the biomass of sardine and anchovy, the main prey of gannets, using data from hydro-acoustic surveys of shelf waters in the southern Benguela



**Fig. 1.** (a) Map of the study area in the southern Benguela upwelling ecosystem. Bathymetric domains are shown as inshore waters, mid-offshore waters and offshore waters. (b) Polygon area defined by demersal trawler spatial distribution along the continental slope. Coordinates are in Universal Transverse Mercator 33–34 South (UTM).

conducted annually in November since 1984 (Coetzee *et al.* 2008) (see Appendix S1, Supporting information).

### Fisheries: purse seiners and demersal trawlers

Vessel monitoring system (VMS) data for purse seine vessels and demersal trawlers were obtained from Chief Directorate: Monitoring Control and Surveillance of the Branch, Fisheries Management, South African Department of Agriculture, Forestry and Fisheries. Access to VMS data sets was restricted due to administrative and legal issues. We focussed on three periods for which we had access to the data. These corresponded to three gannet-breeding seasons (October–January 2002–2003, 2005–2006 and 2009–2010) in years with marked differences in the abundance of sardine and anchovy (the most common prey for both gannets and purse seiners), biomass being high in 2002, medium in 2009 and low in 2005 (van der Lingen *et al.* 2006; Coetzee *et al.* 2008; Hutchings *et al.* 2009). All VMS data were anonymous as vessels were identified using arbitrary numbers. Global Positioning System (GPS) locations included in the VMS data were registered daily every 10–15 min for purse seiners and every 2–6 h for trawlers. Because VMS data contain erroneous entries, we performed a cleaning of the data base (Appendix S2, Supporting information). Overall, between 36.4–75.4% of available purse seiner data and 52.8–83.3% of available trawler data were considered for the analyses, depending on year (Table S1, Supporting information).

### Seabird tracking data

The at-sea behaviour of gannets breeding on Malgas Island (33°03'S, 17°55'E) was studied across 2002–2010 (see Grémillet *et al.* 2004 for protocol details). As mentioned above, we focused on three breeding seasons (2002–2003, 2005–2006 and 2009–2010) for which we had access to VMS data. Miniaturized GPS loggers weighing <2% of the birds' body mass were attached with waterproof tape to the lower back of breeding adults provisioning small chicks. The loggers were programmed to record a location every 10 s. Each individual was only tracked once to avoid pseudo-replication. A total of 26 tracks were recorded in 2002, 36 in 2005 and 20 in 2009 (Table S2, Supporting information). All locations within 2 km of the centre of the gannet-breeding colony were removed from the analysis as most of these locations corresponded to terrestrial locations, and none of them were associated with a vessel location.

### ANALYSES

#### *Spatial distribution of sardine and anchovy off the west coast of South Africa*

The acoustic data informed us about the overall abundance of sardine and anchovy within the study area in any one year and hence provided a context within which our results could be interpreted. However, data on the spatial distribution and abundance of pelagic fish observed during hydro-acoustic surveys were not directly compared with gannet foraging activities at the mesoscale (corresponding to oceanic structures and ecological processes which span temporal scales from days to weeks, and spatial scales from 10 to 100s of kilometres) and sub-mesoscale (spatial scale

<10 km and temporal scale from hours to days) because surveys of fish and seabirds occurred over different periods (pelagic fish survey in November of each year, and gannet GPS-tracking between October and January).

### Movement analyses

As gannets rest on water at night (Votier *et al.* 2010), we only considered daylight locations. We then segmented each seabird foraging trip to determine the sequence of homogenous bouts corresponding to specific behaviours (resting, fishing and transiting). Resting phases were identified based on a speed less than a  $10 \text{ km h}^{-1}$  threshold (Louzao *et al.* 2009; Hintzen *et al.* 2012). To identify foraging locations, we used the residence time method (Barraquand & Benhamou 2008), which is an extension of the first passage duration method (Fauchald & Tveraa 2003) and clearly improves the assessment of the exploitation intensity of areas where animals perform area-restricted search (ARS) through alterations of path structure (Appendix S3, Supporting information). Based on residence time frequency distributions, we rated path sections with low residence times (<2 min) as transit periods and path sections with higher residence times as area-restricted search (potential foraging) sections.

Similarly, concerning purse seiners, a distinction was made between three activities: drifting, fishing and steaming (Hintzen *et al.* 2012). Coupling multimodal distributions of residence time and speed, locations characterized by high residence time and speeds <1  $\text{km h}^{-1}$  were considered as involving immobility. Based on residence time frequency distributions, we considered that purse seiners were fishing when residence times were larger than 7 min, and steaming otherwise.

We had no access to instantaneous vessel speeds of either purse seiners or demersal trawlers and so estimated these using the distance and the time interval between consecutive VMS locations, under the assumption that vessels travelled in a straight line at a constant speed (Mills *et al.* 2007). As the time between two vessel locations was 2–6 h for demersal trawlers, which only towed their gear for 1–3 h (FAO 2010), it was not possible to estimate fishing areas. Indeed, in the absence of instantaneous speed records, calculated trawler speeds would be underestimated, with subsequent effects on the detection of nontrawling and trawling locations (Mills *et al.* 2007; Gerritsen & Lordan 2011). In this context, demersal trawler VMS data were not used to relate fishing or discard locations with seabird locations, but to test whether birds followed vessels.

### Degree of overlap between gannets and fisheries at the mesoscale

To test whether gannets modified their activity patterns in the vicinity of fisheries at the mesoscale, we performed hierarchical cluster analysis on the bathymetry associated with every ARS, using a Mahalanobis measure of distance and group average sorting. The spatial distribution of ARS of the birds belonging to a given cluster was then estimated using the kernel density method (AdeHabitatHR R package) with smoothing parameters computed using the least-square cross-validation method. We estimated the spatial distribution of the fishing areas of purse seiners and trawlers in the same way. For this step, we considered all the data collected during the bird-tracking period. We evaluated the overlap between gannet and fishery spatial distribution using the volume of intersection (VI) statistic (Fieberg & Kochanny 2005, see Appendix S4, Supporting information).

### Sub-mesoscale relationships between gannets and fisheries

To evaluate whether foraging birds tend to follow vessels, we focused on the behaviour of gannets approaching vessels during a foraging trip. Considering simultaneous movements from vessels and seabirds, we thereby investigated whether the bird was more likely to remain in the vicinity (within radius of 500, 1500 or 4000 m) of the vessel than expected under the null hypothesis of a random movement using a binomial test (see Appendix S5, Supporting information).

### Longer-term foraging behaviour of gannets

A preliminary analysis of the spatial variability associated with trawler distributions showed similar spatial distribution patterns along the continental shelf edge in all 3 years (VI >0.5 for the spatial distribution of trawlers in the year couples 2002–2005, 2005–2009 and 2002–2009). On this basis, we defined an at-sea polygon corresponding to the trawling area (Fig. 1b). For each year and each bird, we computed the ratio of the number of potential foraging locations within the trawling area over the total number of potential foraging locations. The mean ratio for each year was considered a proxy for the attractiveness of trawlers to gannets. We initially performed this analysis on the three focus breeding seasons (2002, 2005 and 2009). However, as trawling activities focussed on the same, restricted zone across years, we extended our analysis to the full range of years for which we had GPS-tracked gannets (i.e. 2002–2010).

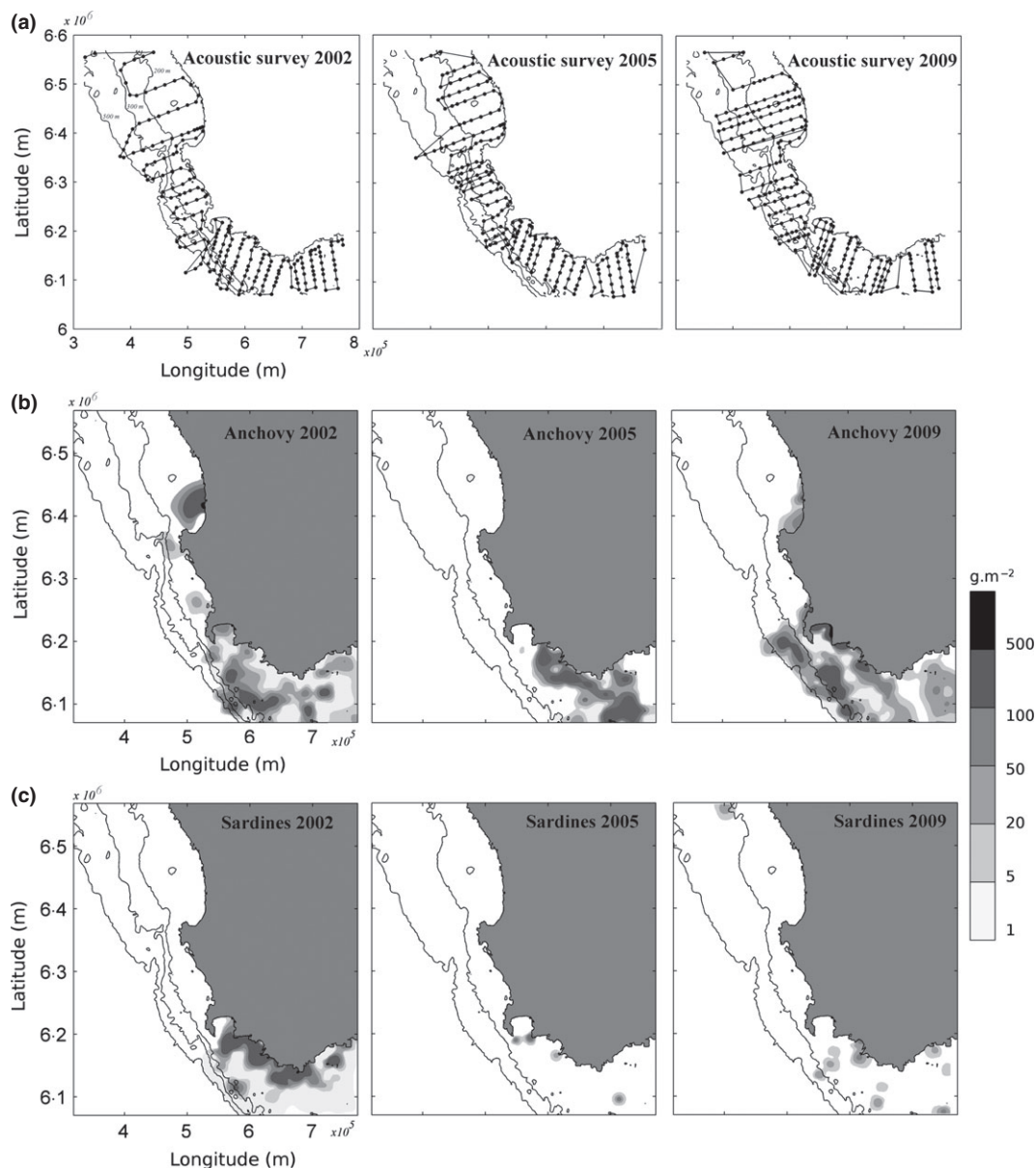
## Results

### SPATIAL DISTRIBUTION OF SARDINE AND ANCHOVY OFF THE WEST COAST OF SOUTH AFRICA

The spatial distribution of anchovy differed markedly between years. In 2002, anchovy occurred in high density ( $>100 \text{ g m}^{-2}$ ) in two main inshore areas: one north of Cape Columbine and one south-east of Cape Town (Fig. 2b). Similar zoning was observed in 2009, yet with lower densities in the area north of Cape Columbine ( $20\text{--}50 \text{ g m}^{-2}$ ) and high densities ( $>100 \text{ g m}^{-2}$ ) of anchovy spreading farther northwards in the south. In 2005, anchovy occurred only south of Cape Town, with a more south-eastward location and a lower density ( $50\text{--}100 \text{ g m}^{-2}$ ) than in 2002 and 2009. Sardine was mainly located south of Cape Town in all 3 years. The density of sardine in the study area clearly decreased between 2002 and 2005–2009, from  $50\text{--}100 \text{ g m}^{-2}$  in 2002 to  $5\text{--}20 \text{ g m}^{-2}$  in 2005 and 2009 (Fig. 2c).

### MESOSCALE DEPENDENCE OF GANNETS ON FISHERIES

In 2002, classification analyses revealed two groups of gannet foraging trips relative to water depth (Kruskal–Wallis test,  $P < 0.001$ ): one occurred in inshore waters (G1<sub>2002</sub>, 9 tracks, bathymetry: mean  $\pm$  SD =  $-158 \pm 37 \text{ m}$ ) and the other in mid-offshore waters (G2<sub>2002</sub>, 17 tracks,  $-281 \pm 37 \text{ m}$ ). The potential foraging locations corresponding to

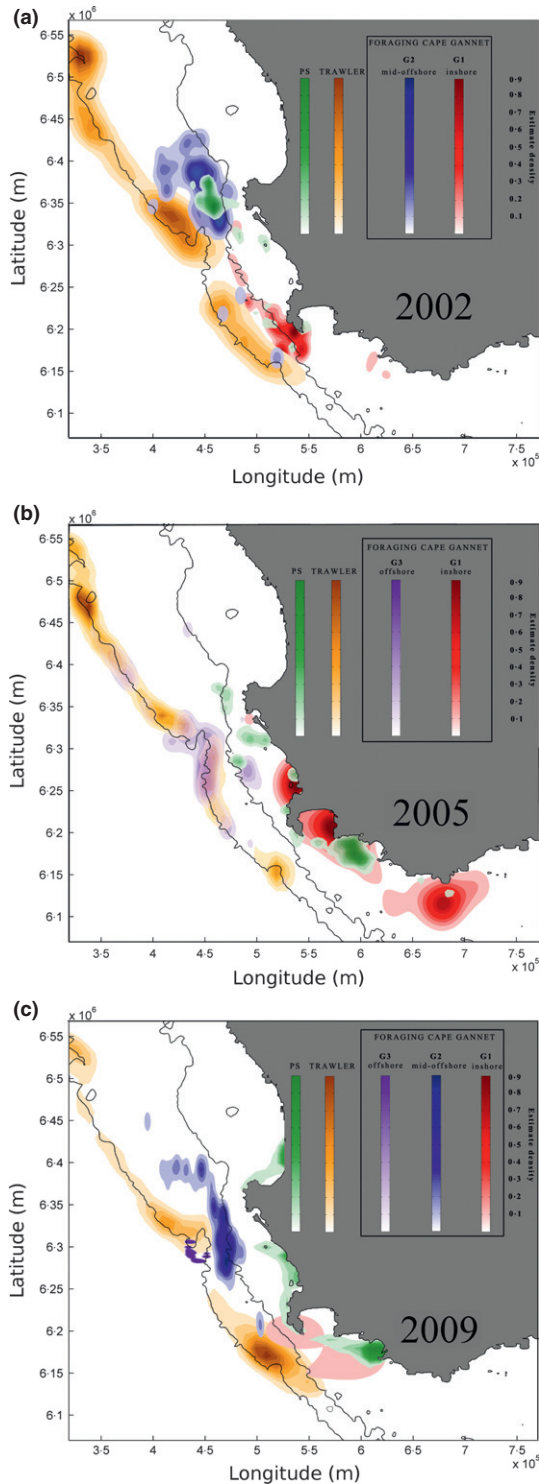


**Fig. 2.** Spatial distribution of acoustic survey transects (a), anchovies density (b) and sardines density (c) in 2002, 2005 and 2009. Biomasses are expressed in  $\text{g m}^{-2}$ .

these two groups were determined using a kernel density estimator (Fig. 3a). For 2005, we also identified two groups, one inshore ( $G1_{2005}$ , 11 birds,  $-41 \pm 40$  m) and one offshore ( $G3_{2005}$ , 25 birds,  $-428 \pm 126$  m), along the continental shelf edge (Fig. 3b). In 2009, three categories of trips were detected: one inshore ( $G1_{2009}$ , 2 birds,  $-99 \pm 51$  m), one mid-offshore west of Cape Columbine (17 birds,  $-258 \pm 77$  m) and one offshore (1 bird,  $-565 \pm 126$  m) (Fig. 3c). Analysis of bathymetry distributions for all seabird foraging locations confirmed different annual spatial patterns (Kruskal–Wallis, d.f. = 2,  $P < 0.001$ ).

Spatial kernel density estimators of estimated purse seine fishing over the period of observations of gannets' foraging were compared with seabird potential foraging locations. In December 2002, only birds foraging in

mid-offshore waters ( $G2_{2002}$ ) overlapped with purse seiner activity, with high ( $>0.5$ ) VI (Fig. 4), whereas birds from the  $G1_{2002}$  category foraged farther south (Fig. 3a), showing little overlap with purse seiner activity (nonsignificant). In October–November 2005, birds from the coastal  $G1_{2005}$  category foraged mainly in the same area as purse seiners south-east of False Bay, whereas birds from the offshore category  $G3_{2005}$  co-occurred with demersal trawlers (Fig. 3b), resulting in high VI for these two categories (Fig. 4). In 2009, purse seine fishing activity north of Cape Point was concentrated inshore (water  $<100$  m deep) along the coast, and spatial overlap was detected with inshore-feeding seabirds ( $G1_{2009}$ ) south of False Bay. However, most seabirds foraging activity that year occurred in mid-offshore waters (85% of birds in  $G2_{2009}$

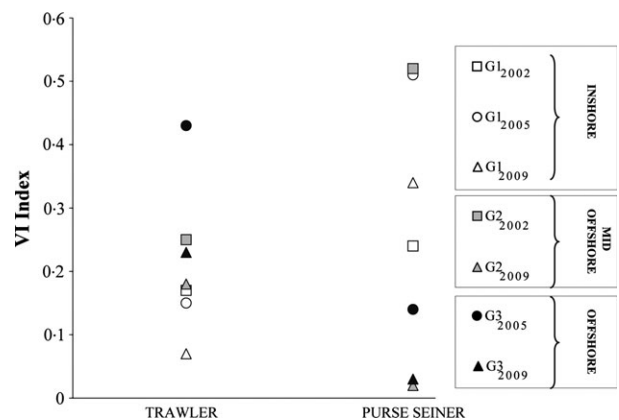


**Fig. 3.** Kernel density estimates of trawler activity areas (orange), purse seiner fishing areas (green) and categories of foraging Cape gannets as discriminated by classification analysis (red, blue and violet). Purse seiner and trawler data are synoptic with Cape gannet monitoring: (a) Two groups of birds G1 (red) and G2 (blue) for December 2002; (b) Two groups of birds G1 (red) and G3 (violet) for October–November 2005 and three groups for October–November 2009 (G1: red; G2: blue; G3: violet). Scales of estimated kernel densities were centred on the maximum to allow comparison across groups.

category, Table 1), along the 250 m isobaths, indicating an absence of spatial association between birds and purse seiners (Fig. 3c).

**SUB-MESOSCALE DEPENDENCE OF GANNETS ON FISHERIES**

Although we observed broad spatial overlaps between birds and purse seiners in 2002 and 2005, no significant relationships were found between gannets and purse seiners at a sub-mesoscale in any of the three study years (Table 2). We also tested for dependence of gannets on trawlers in 2002 and 2009, and gannets and purse seiners in 2009, although those were very unlikely to be detected given the quasi-absence of overlap at the mesoscale between seabird and vessel distributions. We found no significant dependence of gannets on demersal trawlers during periods of high (2002) and medium (2009) abundance of natural prey (Table 2). Strong sub-mesoscale dependence of seabirds on trawlers was, however, observed in 2005 (Table S3, Supporting information). Within 4000 m of a fishing vessel, 88% (72%, and 50% for  $r = 1500$  and  $r = 500$  m, respectively) of birds of the category G3<sub>2005</sub> crossed the track of a demersal trawler at least once, corresponding to 61.1% of all gannets studied in 2005. Additionally, of the birds that crossed the track of a demersal trawler within this radius, 67.5% of them followed it (resp. 67.7 and 70% for  $r = 1500$  and  $r = 500$  m) (Table S3, Supporting information). Binomial tests for dependence of gannets on trawlers were highly significant in 2005 for all radii considered, indicating that seabird path direction was not random after encountering a trawler (Table 2). This clearly shows dependence of gannets on trawlers in 2005. Daily patterns of long- and short-term dependence of gannets in 2005 are shown (Fig. 5a,b), where gannet movements zig-zag along



**Fig. 4.** Variability of the Volume of Intersection (VI) index for groups of Cape gannets that showed spatio-temporal overlap with trawler home range (right) and purse seiner potential fishing area (left), for proportions of conditional 95% utilization distributions (percentage).

**Table 1.** Characteristics of Cape gannets foraging trips in relation to three categories of oceanic domains: inshore (G1, <200 m water depth), mid-offshore (G2, 200–300 m deep) and offshore (G3 > 300 m deep), during years of high (2002), low (2005) and medium (2009) abundance of natural prey. Values are mean  $\pm$  SD

	2002			2005			2009			Total
	G1	G2	Total	G1	G2	Total	G1	G2	G3	
Sample sizes and Proportions of birds (%)	9 (34.6)	17 (65.4)	26 (100)	11 (30.5)	17 (69.5)	28 (100)	2 (10)	17 (85)	1 (5)	20 (100)
Mean maximum distance to the colony (km)	165 $\pm$ 36.6	95 $\pm$ 31.5	106 $\pm$ 60	191.2 $\pm$ 85.2	115 $\pm$ 46.6	132.6 $\pm$ 60.4	184.9 $\pm$ 49.2	87.6 $\pm$ 32.8	80.3	97 $\pm$ 44
Mean bathymetry (m)	-157.7 $\pm$ 37	-280.5 $\pm$ 37.15	-226.6 $\pm$ 9	-41 $\pm$ 40	-428.9 $\pm$ 126.2	-299.3 $\pm$ 225.2	-98.8 $\pm$ 50.7	-257.5 $\pm$ 77	-564.5 $\pm$ 126	-259.6 $\pm$ 96.2
Foraging trip duration (h)	30.4 $\pm$ 10	19.4 $\pm$ 6.4	22.8 $\pm$ 9.8	33.6 $\pm$ 14.06	27.75 $\pm$ 13.9	29.6 $\pm$ 14	34.4 $\pm$ 16.4	20.9 $\pm$ 5.6	21.7	22.2 $\pm$ 7.6

the linear track of the trawlers in movements typical of feeding.

#### ESTIMATING IMPACTS OF FISHERY WASTE ON GANNETS OVER THE LAST DECADE

The time series of gannet natural prey abundance and foraging behaviour show strong inter-annual variability (Fig. 6). The breeding season 2002–2003 was characterized by a high sardine and anchovy combined biomass, followed by a period of reduced combined biomass (owing mainly to a sharp decline in the biomass of sardine) between 2004 and 2007 and again in 2010 (mainly due to a drastic decline in the biomass of anchovy). By comparison, the proportion of seabird foraging locations within the trawler area shows the inverse pattern, with high proportions of gannets in the trawler area when natural prey biomass is low (2004–2007, 2010) and low proportions when the biomass of natural prey is high (2002–2003, 2008–2009; Fig. 6a). A strong negative correlation was found between the biomass of sardine and the proportion of gannets foraging in the trawler zone ( $R^2 = 0.5$ ,  $P = 0.03$ ) (Fig. 6b) and a weaker, yet still significant negative correlation was found for anchovy ( $R^2 = 0.44$ ,  $P = 0.05$ ) (Fig. 6c). The combined biomass of anchovy and sardine biomass also was negatively correlated to the proportion of gannets in the trawler area ( $R^2 = 0.67$ ,  $P = 0.007$ ) (Fig. 6d).

#### Discussion

Our analysis was based on the expectation that the two main South African fisheries (for pelagic fish by purse seiners and for hake by demersal trawlers) impact gannet foraging strategies. To test this hypothesis, we evaluated spatio-temporal overlaps between purse seiners and trawlers and foraging gannets, at meso (*c.* 100 km)- and sub-meso (*c.* 10 km)-spatial scales across years of contrasting pelagic fish biomass. This is the first study to specifically test the interplay of seabirds and fisheries in the Benguela current using VMS data and has important, general implications for the management of fishery waste across marine ecosystems.

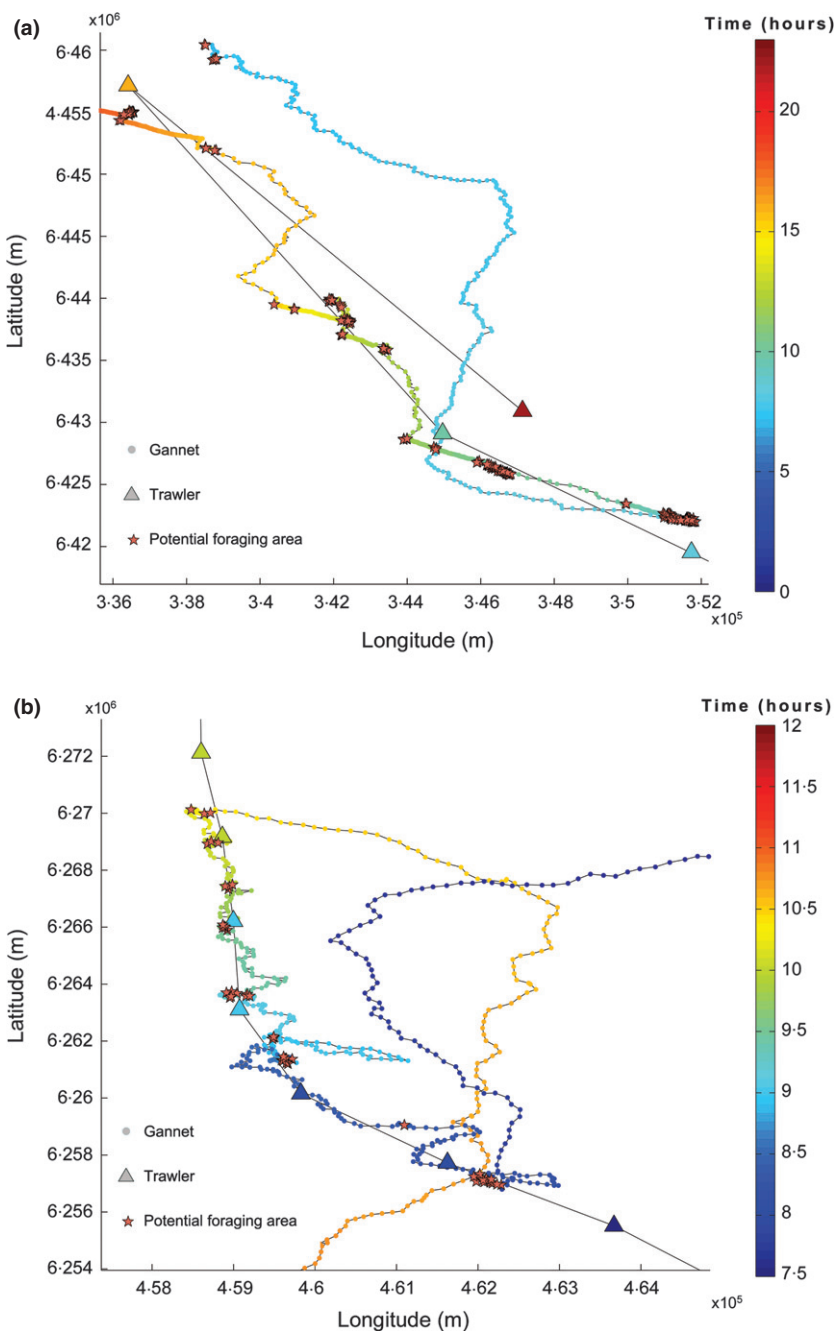
#### METHODOLOGICAL LIMITATIONS

Our calculated speeds for purse seiners may underestimate actual speeds (Mills *et al.* 2007), yet this potential error was limited by small time intervals between VMS records (*c.* 11 min in purse seiners). Further work is required to refine ARS detection in gannets (following Hamer *et al.* 2009), for instance using time-depth-recorders and stomach temperature loggers in parallel to GPS-recorders so as to detect feeding dives and prey ingestion in seabirds (Wilson, Cooper & Plotz 1992) and by combining VMS tracks with seabird data collected by observers on-board fishing vessels. It would also be

**Table 2.** Dependence of seabirds on vessels in 2002, 2005 and 2009 at small scale. *P*-value: result of the binomial tests for dependence of gannets on fishery (H0: seabird path direction is random, after encountering a vessel)

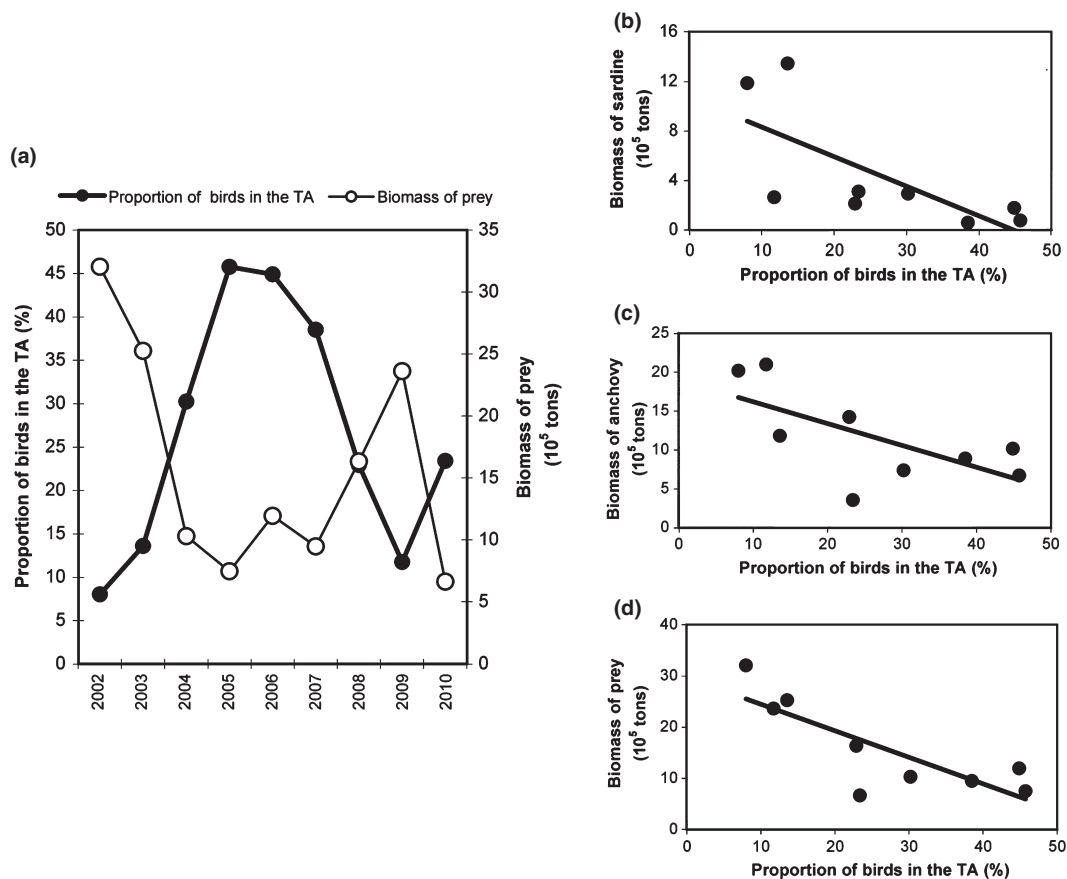
	2002			2005			2009											
	Dependence on purse seiner	Dependence on Trawler		Dependence on purse seiner	Dependence on Trawler		Dependence on purse seiner	Dependence on Trawler										
Radius (m)	500	1500	4000	500	1500	4000	500	1500	4000	500	1500	4000	500	1500	4000			
<i>P</i> -value	–	NS	NS	–	–	NS	–	–	–	***	***	***	–	–	NS	–	–	NS

NS, not significant.  
 \*\*\**P* < 0.0001.



**Fig. 5.** Example of (a) long-term (9 October 2005) and (b) short-term dependence (15 October 2005) of Cape gannets (paths) on trawlers (triangles). The blue-to-red colour scale gives the time line of observations. Red stars represent potential seabird foraging locations estimated using the residence time method.





**Fig. 6.** (a, left panel) Time series of biomass of combined biomass (solid line and white circle) and relative proportion of foraging locations within trawled areas (TA), from 2002 to 2009 (solid line and black circle). Relationships between anchovy (b), sardines (c) and total prey (d) biomass and % of Cape gannet foraging locations in TA.

important to refine fishing areas using observers' data (Walker & Bez 2010), logbooks and acoustic survey and to improve estimations of the fishing effort (Witt & Godley 2007). Nevertheless, we think that our analyses were the best we could perform within the limitations imposed by the data currently available.

#### SPATIO-TEMPORAL VARIABILITY IN SMALL PELAGIC FISH BIOMASS

During the study period (2002–2010), there was strong variation in the availability of small pelagic fish to fisheries and seabirds in the southern Benguela upwelling area, as a consequence of an increase in the biomass in the east such that more fish were eventually found in the east than in the west and higher fishing pressure on sardine in the west together with lower sardine recruitment from east coast spawning and hence later lower sardine biomass in the west (van der Lingen *et al.* 2006; van der Lingen, Coetzee & Hutchings 2011). This shift has caused a spatial mismatch between top predators and their prey (Grémillet *et al.* 2008b). Sardine stocks in particular have diminished in this region, yet anchovy showed strongly improved recruitment

in 2008 and 2009 compared to previous years (Coetzee *et al.* 2008; J.C. Coetzee and C.D. van der Lingen, pers. obs.). Probable causes of this spatio-temporal shift in sardine distribution, such as higher fishing pressure in the west and/or low recruitment due to environmental changes, are still being debated (Roy *et al.* 2007; Coetzee *et al.* 2008).

#### GANNETS VS. PURSE SEINERS

Sardine and anchovy are exploited by both seabirds and purse seiners. At the mesoscale, our analyses revealed co-occurrence of both predators attending this resource (Fig. 2) and confirm results found by Okes *et al.* (2009). However, interestingly, finer, sub-mesoscale analysis shows that birds and purses-seiners harvested patches of pelagic fish within broadly similar zones, yet at different times, and did not actually overlap at sea (Fig. 2). This confirms direct observations that gannets do not actively follow purses-seiner at sea (N. Okes, pers. comm.) and that seabirds are generally capable of discriminating between vessels potentially generating waste and those such as purse seiners which keep all harvested fish on board (Louzao *et al.* 2006).

## GANNETS VS. TRAWLERS

Our detailed analysis shows that gannets mainly feed in the coastal and mid-coastal zones that correspond to the core areas of sardine and anchovy. However, during periods of reduced abundance of these natural prey items, a significant number of birds switched to feeding extensively on fishery waste (group G3<sub>2005</sub> in our study; see also Pichegru *et al.* 2007). Crucially, we revealed significant overlap between gannet and trawler movements at the mesoscale, confirmed with the detection of sub-mesoscale dependence of gannets on trawlers in 2005. This clearly illustrates how these seabirds seek and attend trawlers in search of fishery waste. This analysis is the first to specifically demonstrate the spatio-temporal co-occurrence of seabirds and fisheries in the Benguela upwelling area using GPS-tracking and VMS data. It complements former analyses by Votier *et al.* (2010), Granadeiro *et al.* (2011) and Torres *et al.* (2011) conducted in other marine systems, notably by performing a retrospective analysis over a period of contrasting pelagic fish availability (Fig. 6).

## GANNETS DID NOT BECOME DEPENDENT UPON FISHERY WASTE

Large volumes of fishery waste are available to Benguela seabirds on a year-round basis. Within our study area, they are generated by 45–90 trawls each day (Grémillet *et al.* 2008a). From a management point of view, it is essential to determine whether the constant presence of such large volumes of fisheries waste modifies gannet foraging behaviour in the longer-term. Indeed, previous work demonstrated that adult gannets survive well on a diet mainly composed of fishery waste, but fail to reproduce (Grémillet *et al.* 2008a). A permanent dependence upon fishery waste is therefore predicted to further diminish the population of gannets already classified as vulnerable on the IUCN red list.

Using our multi-year analysis, we clearly show that gannets revert to feeding on their natural prey as soon as it is available in sufficient quantities, and that their association with trawlers only lasts as long as pelagic fish biomass remains too low to be energetically profitable. Gannets therefore do not become dependent upon human waste, unlike some populations of larids (Oro, Bosch & Ruiz 1995; Oro, Jover & Ruiz 1996) and various mammals such as foxes (Meadows 2010). However, we are aware that some of the methods that we developed to test multi-year dependence of seabirds on trawlers require further refinements. For instance, the spatial persistence of the polygon corresponding to the trawling area should be confirmed using the full VMS data set. Nevertheless, since demersal trawlers specifically target hake along the edge of the continental shelf, the assumption that trawling always occurs in the same zone within our study area seems reasonable.

## MANAGEMENT IMPLICATIONS

Using our combined, multi-scale analysis, we reject the hypothesis of a permanent behavioural change, brought about by the discard of fishery waste, for gannets in the Benguela upwelling area.

This finding is essential within the context of the current debate pertaining to the management of fishery waste. Indeed, it shows that seabirds that have become accustomed to feeding on fishery waste may revert to feeding on their preferred natural prey if sufficiently abundant. Of course, this does not solve the issue of providing sufficient biomass of natural prey to sustain current seabird numbers. For instance, there are reasons to believe that the North Sea is currently so heavily overfished and its fish community so impoverished in terms of biomass that, in the absence of waste generated by fisheries, several seabird species including northern gannets *Morus bassanus* and northern fulmar *Fulmarus glacialis* will rapidly decline (Garthe, Camphuysen & Furness 1996; Votier *et al.* 2004; Wagner & Boersma 2011). Similarly, a reduction in the volume of fishery waste produced in the Ebro Delta off Spain in the Mediterranean has been shown to trigger a population decline in Andouins' gulls *Larus andouinii* which had been feeding from this artificial resource due to the depletion of their natural prey (small pelagic fish) by overfishing (Oro, Bosch & Ruiz 1995; Oro *et al.* 2004; Palomera *et al.* 2007).

Seabird functional traits and behavioural plasticity generate varied responses to the combined effects of food shortage and fishery waste abundance. For instance, alcid and penguin populations, which consume an estimated 50% of all seabird food (Brooke 2004), do not prey at all on fishery waste and are therefore insensitive to its availability. Nevertheless, in areas where large populations of birds do respond to the presence of fishery waste, such as in the North Sea and the Mediterranean, precautions should be taken to concomitantly promote an increase in the abundance of natural seabird prey (Cury *et al.* 2011) if a moratorium on dumping fishing waste at sea is to be declared. These examples show the complexity of taking fisheries waste into consideration within an ecosystem approach to fisheries management, particularly since their nutritional input to some marine populations is not negligible.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Acoustic survey.

**Appendix S2.** VMS data handling.

**Appendix S3.** Residence time.

**Appendix S4.** Overlaps between fisheries and Cape gannets.

**Appendix S5.** Estimate the probability that a bird follows a vessel.

**Table S1.** Characteristics of Vessel Monitoring Systems (VMS) data in 2002, 2005 and 2009 for purse-seine fishing vessels and trawlers.

**Table S2.** *Morus Capensis*. Summary of the GPS tracking effort, including information on the tracking period, number of complete trips.

**Table S3.** Characteristics of interactions between Cape gannets and trawlers for each choice of radius in 2005.