

# Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems

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## Summary

1. The large amount of discards produced by commercial fisheries can have major impacts on marine predator populations: this abundant food may increase populations of some scavengers or decrease others via accidental bycatch. Yet, despite the conservation implications of discard practices, the ecology of individual scavengers is poorly understood.

2. Here, we assess the influence of commercial fisheries' activity on the foraging behaviour of individual breeding northern gannets *Morus bassanus*. Using recent developments in stable isotope mixing models (Stable Isotope Analysis in R or SIAR) we estimate individual discard consumption. Using GPS tracking and the Vessel Monitoring System (VMS), we investigate behavioural responses to trawlers.

3. Analysis of conventional diet samples, as well as stable isotope ratios of carbon and nitrogen in blood (plasma and cells), highlight marked individual differences in the proportion of fishery discards in the diet. Individual differences in foraging behaviour revealed by stable isotopes show evidence of both short-term consistency and behavioural flexibility.

4. At-sea path tortuosity of 25 gannets (tracked using GPS loggers) revealed scale-dependent adjustments in response to VMS-derived fishing vessel locations, as well as to sea surface temperature, chlorophyll *a* concentration and copepod abundance. The results also indicate individual variability in behavioural response to trawlers.

5. Individual differences in the amount of discards estimated from SIAR were negatively correlated with differences in foraging trip length and body condition, indicating potential fitness consequences.

6. *Synthesis and applications.* The management of commercial fisheries and apex predators is a daunting task. Ultimately, reducing bycatch and removing dependency on discards remain key conservation priorities, but managers should also ensure that scavenging species have sufficient alternative food to meet their energetic needs, to ameliorate potential unforeseen knock-on consequences. The results of Stable Isotope Analysis (SIAR) reveal intra-population differences in discard consumption by gannets; differences that have impacts on foraging effort and body condition. The use of GPS tracking and Vessel Monitoring Systems (VMS) reveal that gannet at-sea behaviour is influenced by fishing vessels, although this also varies among individuals. A combination of SIAR, GPS tracking and VMS can be used to study fishery/scavenger interactions in detail at the individual level, to answer fundamental questions about scavenging behaviour.

**Key-words:** bycatch, fisheries, foraging, GPS tracking, prey choice, scavenging, stable isotopes, VMS

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## Introduction

Commercial fisheries have fundamentally altered marine ecosystems. Their industrialization and expansion has had global impacts on sustainability (Pauly *et al.* 2002), has transformed the structure and function of marine food webs (Pauly *et al.* 1998) and has depleted stocks of some fish to near extinction (Casey & Myers 1998). By providing huge quantities of food in the form of bait, undersized catch and offal, the demographics of large marine predator populations has also been profoundly altered (Furness 2003; Lewison *et al.* 2004).

Understanding the way in which discarding impacts upon marine systems is a key question in applied ecology, for a number of different reasons. Firstly, for species that can compete effectively for discards, this food may be beneficial – it is novel (much of the waste is from demersal fish beyond the normal diving range of most species), plentiful, and can be obtained without the costs of diving. Fishery waste may therefore be advantageous for some species (Furness 2003). Also, however, it may have knock-on eco-system level effects on other prey such as smaller seabirds (Votier *et al.* 2004c), or represent an ecological trap (Gremillet *et al.* 2008b). Conversely, the same scavengers attracted to fishing vessels for food are also at risk from becoming accidentally hooked or entangled and then drowned in fishing gear and this ‘bycatch’ has emerged as a major conservation issue of global concern (Lewison *et al.* 2004). Yet despite the evidence that both bycatch and fishery waste can alter the population dynamics and community structure of large marine predators (Lewison *et al.* 2004; Votier *et al.* 2004b; c), surprisingly little is known about the ecology of scavenging. This is in part due to a focus on population-level studies, which reveal nothing about individual tactics in relation to discard use. Given the importance of intra-population variation in foraging behaviour for population-level responses (Bolnick *et al.* 2003; Inger *et al.* 2006; Woo *et al.* 2008), a better understanding of individual scavenging tactics is highly desirable.

In the past, a problem inherent in studying individual marine predators and their interaction with capture fisheries has been the inability to study at-sea foraging behaviour in detail, while simultaneously recording feeding behaviour and fishing vessel activity. However, three key developments now make this a possibility. Firstly, miniaturised GPS logging devices now enables the study of free-living animal movement, at costs compatible with obtaining appropriate sample sizes for rigorous statistical analysis (Ropert-Coudert & Wilson 2005). Secondly, although conventional dietary studies provide information on prey consumption, they may be biased towards certain foods and only reflect short-term intake (Votier *et al.* 2003). The analysis of stable isotope ratios in consumer tissues and potential prey is now widely used to study individual feeding ecology (Rubenstein & Hobson 2004; Inger & Bearhop 2008). For example, in marine ecosystems the ratio of naturally occurring isotopes of carbon ( $^{13}\text{C}$  and  $^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}$  and  $^{14}\text{N}$ ) vary as a function of depth, and as a function of trophic status. Therefore, because demersal fish form the bulk of discards, they are isotopically distinct from naturally caught

pelagic prey (Navarro *et al.* 2009). Used in combination with recent developments in Bayesian isotope mixing models (Stable Isotope Analysis in R or SIAR, Jackson *et al.* 2009), it is now possible to robustly estimate discard use over periods of different tissue growth. Thirdly, Vessel Monitoring Systems (VMS) have been adopted by many fishing nations and provide high resolution data on the spatial and temporal distribution of fishing effort (Mills *et al.* 2007; Witt & Godley 2007). In Europe, the European Commission has introduced legislation to monitor fishing activity so that all vessels > 15 m long are required to transmit their locations, estimated by GPS, at intervals of 2 h or less, so that data are comparable with data provided by remote animal sensing. Used in combination, these developments, as well as access to remotely sensed environmental data, form a robust suite of techniques to study in detail individual foraging behaviours of large marine predators in relation to fisheries, and form the basis of this study.

Here we assess the relative influence of commercial fishery activity on the foraging behaviour of individual breeding northern gannets *Morus bassanus* Linnaeus, (hereafter gannet), while constrained to return to the nest. Using a combination of conventional dietary sampling, analysis of stable isotope ratios in tissues, GPS data loggers, fine-scale data on the distribution of fishing vessels (using VMS) and environmental covariates, we address a number of key questions: (1) do breeding gannets consume fishery waste, (2) is there intra-specific variation in the use of fishery discards, (3) are individual foraging differences consistent in the short-term, (4) what cues influence at-sea path tortuosity and derived flight speed, in particular do gannets adjust their behaviour in response to fishing vessels, and (5) what are the consequences (in terms of foraging trip length and adult body condition) of utilising fishery waste? We then use the answers from these questions to assess the conservation implications for individual scavenging strategies and consider the utility of using a combination of SIAR, GPS tracking data and VMS to better manage scavenger/fishery interactions.

## Materials and methods

Work was conducted on Grassholm, Wales, UK (51°43'N, 05°28'W), a small offshore island with approximately 30,000 pairs of gannets, during late incubation and chick-rearing, June–July 2006.

### DIET AND STABLE ISOTOPE ANALYSIS

We opportunistically obtained spontaneous regurgitates from adult gannets during handling, which provide broadly similar results to other dietary sampling techniques (Votier *et al.* 2003). Although gannets also regurgitated on approach, these samples are rapidly scavenged by gulls. The majority of regurgitates came from breeding individuals. Prey items were identified to the lowest possible taxon until stored frozen prior to stable isotope analysis.

Thirty-seven breeding gannets (with an egg or chick) were caught on the nest at changeover, using a brass noose on the end of a carbon fibre pole. Birds were selected at random, away from the edge of the colony. On capture and recapture we sampled approximately 0.2 mL blood from the tarsal vein using 23 gauge needles under licence from the UK Home Office. Within 2–3 h, blood samples were separated

into plasma and red blood cells (RBC), using a centrifuge, and then stored frozen until preparation for stable isotope analysis. Prior to analysis samples were freeze-dried, homogenised and ~0.7 mg was weighed into a tin cup. Analyses were conducted at the East Kilbride Node of the Natural Environment Research Council Life Sciences Mass Spectrometry Facility via continuous flow isotope ratio mass spectrometry using a Costech (Milan, Italy) ECS 4010 elemental analyser interfaced with a Thermo Electron (Bremen, Germany) Delta XP mass spectrometer. Isotope ratios are reported as  $\delta$ -values and expressed as ‰ according to the equation  $\delta X = [R_{\text{sample}}/R_{\text{standard}}] - 1 \times 1000$ , where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$  and  $R$  is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  and  $R_{\text{standard}}$  is the ratio of the international references PDB for carbon and AIR for nitrogen. Precision was 0.1‰ and 0.2‰ for carbon and nitrogen isotope measurements, respectively.

To estimate the contribution of different prey we adopted a Bayesian multi-source stable isotope mixing model, SIAR (Jackson *et al.* 2009). SIAR offers a number of advantages over earlier mixing models as it can incorporate known variability in sources, uncertainty in Trophic Enrichment Factors (TEFs), and other unquantified variation within the model. SIAR can also incorporate multiple measurements from an individual, here we used four isotopic values for each bird – plasma and RBC (reflecting assimilated diet over the previous 2–5 days and weeks, respectively; (Hobson 2005), for both initial capture and recapture. Results therefore represent truly robust estimates of diet over the previous days and weeks. SIAR also differs from earlier mixing models in that the outputs represent true probability density functions, rather than a range of feasible solutions as is the case with IsoSource (Phillips & Gregg 2003), so that results can be readily incorporated into subsequent analysis.

High uric acid and lipid concentrations in blood plasma can lead to particularly depleted  $\delta^{13}\text{C}$  values (Bearhop *et al.* 2000). Conventionally, lipid extraction can reduce these problems but given the small quantities of blood plasma this was not possible, therefore we included a + 0.5‰ correction to  $\delta^{13}\text{C}$  plasma to account for this (Cherel, Hobson & Hassani 2005). We included the mean and standard deviation of isotope signatures of the four main prey sources regurgitated by gannets on Grassholm following lipid extraction: mackerel *Scorpaenopsis scorpaenoides* (L.); garfish *Belone belone* (Grignion); sprat *Sprattus sprattus* (L.) and demersal whitefish (haddock *Melanogrammus aeglefinus* (Gill) and unidentified Gadid spp.) in the SIAR analysis. Previously published TEFs were taken from work on great skuas *Stercorarius skua* (Brunnich); 2.8 for Nitrogen and 1.1 for Carbon (Bearhop *et al.* 2002) and a standard deviation of  $\pm 1\%$  added to account for potential differences in fractionation factors between great skuas and gannets. As well as estimating the relative contribution of different fish types over previous days and weeks, we used our SIAR model estimates to determine discard use in relation to trip duration and body condition.

#### GPS TRACKING

65 g GPSlog loggers (earth & OCEAN Technologies, Kiel, Germany) were deployed on 37 birds attached to feathers at the base of the tail using Tesa® tape. All birds flew off strongly and although a period of intense washing often followed release, there was no indication of ill effects. No problems were detected when the same devices were attached to gannets in Canada (Garthe *et al.* 2007a). The loggers were programmed to acquire a fix every three minutes and in this 'intermittent' mode, 90% of the fixes were within 19 m of the 'true' location (earth & Ocean Technologies, Kiel, Germany). We made 32 recaptures from 37 deployments –

three birds had removed the devices and we were unable to catch the remaining two.

We quantified the at-sea behaviour of gannets by calculating tortuosity and derived ground speed. We preferred this approach to First Passage Time (FPT) (Pinaud & Weimerskirch 2005) because FPT cannot differentiate between changes in tortuosity and speed. This is relevant because fishing vessels are visible at range (unlike subsurface prey) and trawl in straight lines, therefore gannets might adjust their foraging behaviour in different ways to typical hierarchical search behaviour shown by other marine predators (Fauchald & Tveraa 2006). We calculated path tortuosity as the total distance travelled between entry and exit locations of a circle along the flight path, divided by the straight line distance within the same circle. Because movement patterns tend to be scale dependent (Pinaud & Weimerskirch 2005), we determined path tortuosity and speed at circles of radius 5 km, 10 km and 30 km (which correspond to the spatial scale of our covariates). Gannets typically rest on the water at night (Hamer *et al.* 2000), so only daylight tracks were used.

#### ENVIRONMENTAL EXPLANATORY VARIABLES

We do not have information on the location of forage fish. Instead we used sea surface temperature (SST), chlorophyll *a* concentration and copepod abundance as proxies of suitable foraging locations independent of fisheries. These environmental variables were collected at the same spatial scale as the tracking data, but temporal matches were not always possible.

Sea surface temperature (SST, °C) and chlorophyll *a* were obtained from the MODIS instrument on the Aqua satellite (<http://modis.gsfc.nasa.gov/>), both on an 8-day temporal frequency and using a 5 by 5 km pixel size. Monthly mapped copepod abundance ( $\text{m}^{-3}$ ) was derived from data collected by the Continuous Plankton Recorder (CPR) survey. The CPR is an upper layer plankton sampler towed behind vessels of opportunity along regular shipping routes, and we constructed copepod abundance maps using counts of copepods (115 calanoid species) from 1953 to 2002 following the procedure of Sims *et al.* (2006). These maps were generated at a spatial scale of 30 by 30 km.

#### FISHERY ACTIVITIES FROM VMS

High resolution data on the location of commercial fishing boats was provided by VMS (Mills *et al.* 2007; Witt & Godley 2007), and was modelled in two ways. Firstly, we modelled the effect of contemporaneous fishing vessels on the movement of tracked gannets during June/July 2006. We modelled the presence/absence of fishing vessels within 2 h and 5 km for each bird GPS location. This 'window' was included because the temporal scale of the gannet fixes (every three minutes) did not match exactly with the temporal scale of the VMS fixes (every 2 h). Secondly we investigated gannet foraging behaviour in relation to mean annualised VMS data 2000–2004 at 5 by 5 km pixel resolution travelling between 1.5 and 5.5 knots. The speed filter excludes the majority of vessels that were steaming. Although these data do not match temporally with the gannet tracking data, the location of fishing vessels show a high degree of spatial consistency across months and years (Witt & Godley 2007).

#### ADULT BODY CONDITION

The pelagic and epipelagic fish that predominate in the diet of gannets have a much higher calorific value than the demersal whitefish that form the bulk of discards (Gremillet *et al.* 2008b), so adopting a

scavenging lifestyle may influence body condition. Therefore we estimated the body mass index (BMI) of all captured birds. We measured the maximum flattened wing chord, bill length (to feathering) and maximum tarsus (Redfern & Clark 2001) and recorded body mass (to the nearest 50 g) as the bird was about to change-over at the nest – therefore the stomach was empty, ensuring reliable BMI estimates. We extracted the first principal component of a Principal Components Analysis (PCA) using wing, bill and tarsus – which explained 67.83% of the variance – as a measure of body size. The residuals of body mass (at initial capture) plotted over the body size PCA and expressed as a percentage of the predicted component mass represents BMI (Bolton, Monaghan & Houston 1991). BMI was compared with the SIAR estimates for discarded demersal fish.

#### STATISTICAL ANALYSIS

We estimated consistency in foraging tactics by regressing stable isotope ratios in blood plasma on stable isotope ratios in RBCs (Podlesak, McWilliams & Hatch 2005). Although there is overlap in the timing of synthesis in these tissues, blood plasma typically has a half-life of around 2–5 days (representing an average of all meals consumed in the previous few days) whereas blood cells turnover more slowly with half-lives of several weeks (representing an average of all meals consumed in the previous few weeks) and therefore they represent quite different timescales (Podlesak *et al.* 2005). Moreover, we took RBC from initial capture and plasma from recapture (between 1 and 23 days difference) reducing the amount of overlap between the samples. Because these two values represent repeat measurements of the same individual, we calculated repeatability, the intra-class coefficient (Lessells & Boag 1987 as a measure of consistency).

To determine factors influencing at-sea path tortuosity and speed, we used Generalized Linear Mixed Models (GLMM). Tortuosity is bounded by zero and one, and models showed evidence of over dispersion, therefore we used a quasibinomial error structure with a logit link function. Gaussian models were used to model derived flight speed. Tortuosity or speed were the response variables and individual included as a random factor because of repeat observations. We modelled SST, chlorophyll *a* concentration, copepod abundance and average VMS density over 2000–2004 as continuous fixed factors and contemporaneous presence/absence of fishing vessels as a two-level factor. For all analysis the environmental variables were at the same spatial scale as the behavioural data. Copepod abundance was  $\log_{10}$  transformed to conform to assumptions of normality. We fitted a full model and then investigated the significance of terms sequentially deleted last from this initial model (Crawley 2007). We considered a range of two-way interactions but because there were no *a priori*

predictions about such terms, and because of the large number of explanatory variables, they were not fitted.

We used the median proportion of whitefish (arcsine square-root transformed), obtained from SIAR outputs, to determine whether this was related to foraging trip length by calculating the Pearson product-moment correlation coefficient. Only birds with complete trips were used and where there was more than one complete trip, we took the average of these. The relationship between BMI and (arcsine square-root transformed) median proportion of whitefish was investigated, also using Pearson correlation.

## Results

#### DIET AND STABLE ISOTOPE ANALYSIS

We obtained fish regurgitates from 19 birds; 6 mackerel, 6 garfish, 6 demersal whitefish and 1 sprat. The whitefish samples were either haddock, or could not be identified to species. They were typically large fish (>20 cm) and several had cleanly removed heads (possibly due to high grading by fishermen). The size and evidence of processing strongly suggest these were demersal whitefish obtained from fishing vessels.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, as well as C/N mass ratios, for these four prey types and blood samples from 32 individual gannets are shown in Table 1. The same isotope values were used in stable isotope mixing models (Fig. 1).

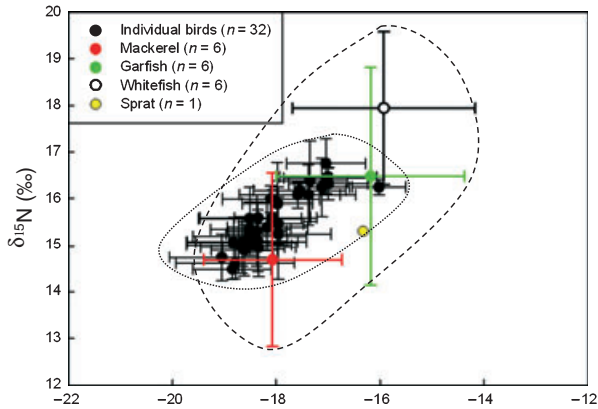
SIAR mixing model outputs revealed a high degree of individual variability in contribution of the four main prey types (Fig. 2). Although much overlap in credibility intervals exist, the results indicate that a number of individual gannets obtain a proportion of their diet from demersal whitefish and these species are most likely to have been obtained as discards. Garfish and sprat are not fished commercially in the region, but it is not clear whether mackerel were caught naturally or scavenged.

Because  $\delta^{13}\text{C}$  has a trophic component, we used the studentized residuals of the relationship with  $\delta^{15}\text{N}$  (RBC:  $F_{1,30} = 185.217$ ,  $P < 0.001$ ,  $r^2 = 0.861$ ; Plasma:  $F_{1,30} = 25.112$ ,  $P < 0.001$ ,  $r^2 = 0.456$ ) to determine the degree of repeatability in  $\delta^{13}\text{C}$ , independent from trophic effects. Residual  $\delta^{13}\text{C}$  values showed some repeatability between RBC on initial capture and plasma on recapture (intra-class coefficient:  $r = 0.455$ ,  $F_{31,32} = 2.666$ ,  $P = 0.004$ ) (Fig. 3a).  $\delta^{15}\text{N}$  values also showed some repeatability between RBC on initial

	<i>n</i>	$\delta^{13}\text{C}$ (per mil)	$\delta^{15}\text{N}$ (per mil)	C/N mass ratio
<b>Northern gannet</b>				
RBC (initial capture)	32	$-17.33 \pm 0.68$	$15.18 \pm 0.69$	$3.28 \pm 0.04$
Plasma (initial capture)	32	$-18.79 \pm 0.82$	$15.98 \pm 0.73$	$4.73 \pm 0.22$
RBC (recapture)	32	$-17.37 \pm 0.64$	$15.18 \pm 0.68$	$3.34 \pm 0.32$
Plasma (recapture)	32	$-18.61 \pm 0.94$	$15.91 \pm 0.61$	$4.66 \pm 0.37$
<b>Prey items</b>				
Mackerel	6	$-19.17 \pm 0.34$	$11.89 \pm 0.86$	$3.37 \pm 0.08$
Garfish	6	$-17.28 \pm 0.81$	$13.68 \pm 1.34$	$3.33 \pm 0.05$
Whitefish	6	$-17.03 \pm 0.76$	$15.14 \pm 0.64$	$3.32 \pm 0.09$
Sprat	1	$-17.43$	$12.52$	$3.19$

**Table 1.** Stable isotope ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) and C/N ratios of northern gannet blood plasma and red blood cells, as well as prey items

Values are means  $\pm$  1 SD.



**Fig. 1.**  $\delta^{13}\text{C}$  (‰) and  $\delta^{15}\text{N}$  (‰) values in the blood of 32 individual gannets and four key prey types. Symbols represent mean values and error bars  $\pm$  1SD of four measurements: blood plasma and red blood cells on initial capture and on subsequent recapture. Values for fish prey are derived from lipid extracted whole regurgitated samples adjusted for fractionation and error. Dashed ellipses (drawn by eye) represent range of source and tissue values.

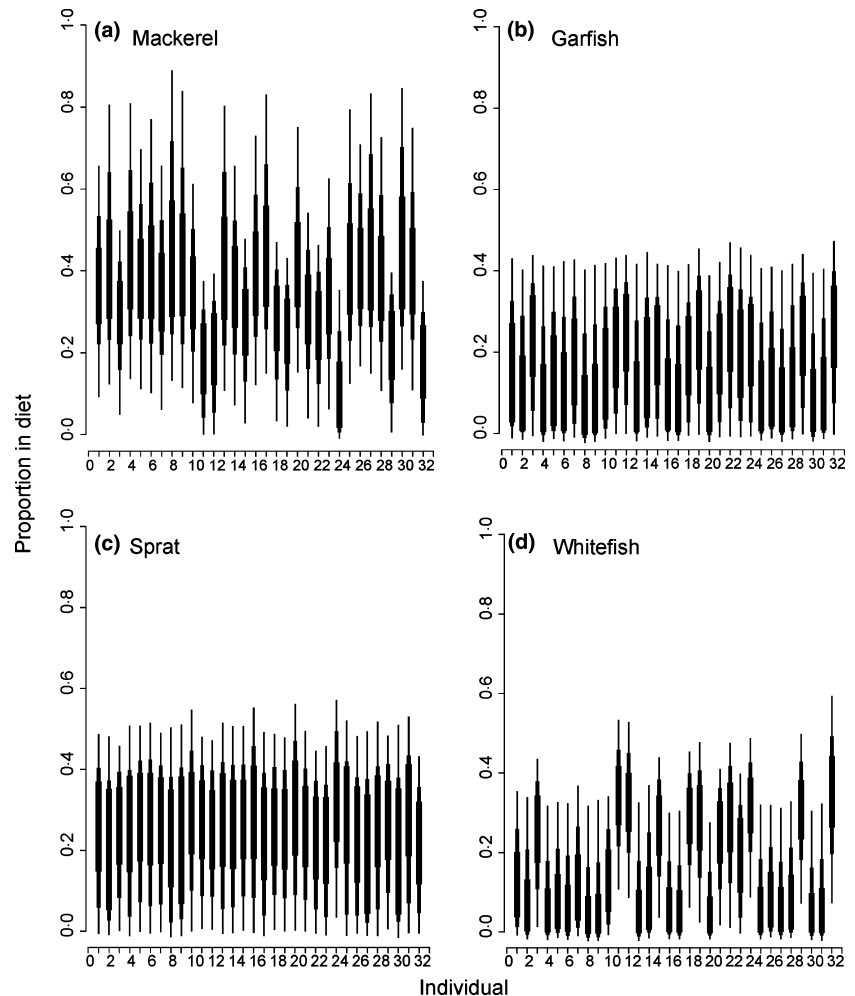
capture and plasma on recapture (intra-class coefficient:  $r = 0.5483$ ,  $F_{31,32} = 1.811$ ,  $P = 0.050$ ) (Fig. 3b). These results suggest greater variation among individuals than within individuals, indicating foraging consistency.

#### FORAGING BEHAVIOUR

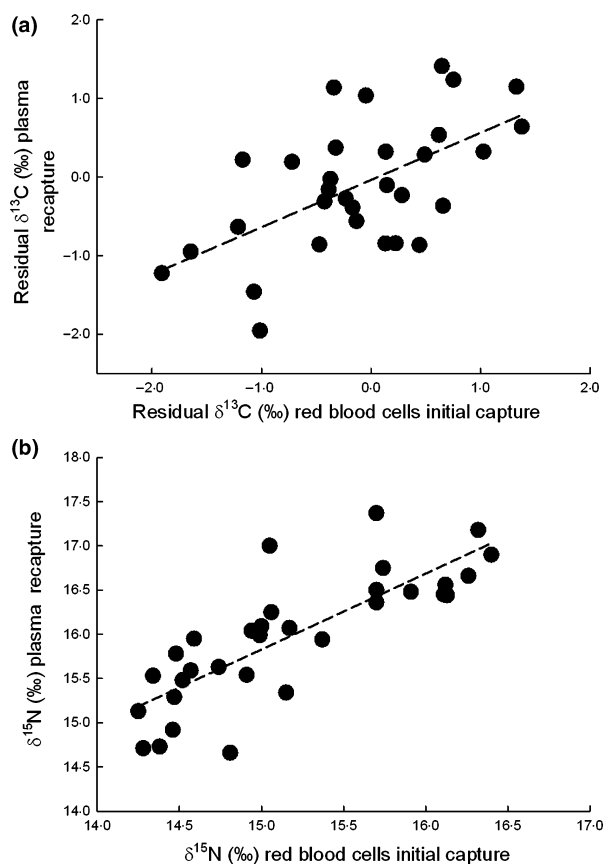
We obtained foraging trips from 25 birds, of which 23 were complete. For the 23 individuals with at least one trip, the average duration was  $25.14 \pm 17.04$  h (minimum = 3.70, maximum = 73.90) and distance travelled  $370.47 \pm 251.34$  km (minimum = 70.45, maximum = 1121.13). Distance travelled and trip duration were positively correlated (Pearson product-moment correlation:  $r_{23} = 0.820$ ,  $P < 0.001$ ).

#### PATH TORTUOSITY

Individual gannets showed complex, scale-dependent, changes in path tortuosity in relation to environmental cues (Fig. 4). In general, gannets showed significantly straighter flight paths in relation to the long-term average of VMS density at 30 km and the contemporaneous presence/absence of fishing vessels at 10 km and 30 km (Table S1 Supporting Information, Fig. 5a). At all scales, gannets showed significantly straighter flight paths in relation to chlorophyll *a* concentration. Gannets showed scale-dependent adjustments to SST – path tortuosity was negatively correlated at 5 km, not correlated at 10 km and positively correlated at 30 km (Table S1 Supporting Information, Fig. 5a). Copepod abundance was only available at the



**Fig. 2.** Range of possible contributions of (a) mackerel, (b) garfish, (c) sprat and (d) whitefish in the diet of individual gannets. Decreasing bar widths represent 50%, 75% and 95% credibility intervals estimated from Bayesian mixing models (SIAR).



**Fig. 3.** Repeatability in (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$ . Points indicate the stable isotope values of RBC from individual gannets on initial capture and then plasma upon recapture.  $\delta^{15}\text{N}$  values largely reflect trophic status of prey whereas  $\delta^{13}\text{C}$  reflect differences between inshore/off-shore and benthic/pelagic, as well as a small trophic component. To control for this trophic effect in  $\delta^{13}\text{C}$  we used the residuals of  $\delta^{13}\text{C}$  plotted against  $\delta^{15}\text{N}$  values in our analysis.

scale 30 km, where it was strongly positively correlated with path tortuosity (Table S1 Supporting Information, Fig. 5a).

#### FLIGHT SPEED

Differences in the derived ground speed of foraging gannets were also influenced by explanatory covariates. There was no relationship between ground-speed and the long-term average of VMS density, but at all scales gannets increased flight speed in relation to the presence of contemporaneous fishing vessels (Table S2 Supporting Information, Fig. 5b). At all spatial scales measured, SST was negatively correlated with flight speed, chlorophyll *a* was positively correlated with flight speed, and copepod abundance negatively correlated with flight speed (Table S2 Supporting Information, Fig. 5b).

#### INDIVIDUAL TRACKS

Scrutiny of the 23 complete trips also revealed individual differences in foraging tactics (Fig. 6, Fig. S1 Supporting Information). Six birds exhibited area-restricted search behaviours in areas where fishing vessels were present, 5 of these being at the

distal part of the foraging track. 11 birds encountered fishing vessels along the foraging route, but they were not associated with area-restricted search behaviours. Eight birds did not encounter contemporaneous fishing vessels as recorded by VMS.

#### LINKING STABLE ISOTOPE VALUES WITH FORAGING TRIP CHARACTERISTICS

The (arcsine square-root transformed) median proportion of whitefish in the blood of individual gannets (estimated from SIAR mixing models) was negatively correlated with total foraging trip length ( $r_{22} = -0.489$ ,  $P = 0.021$ , Fig. 7a).

#### LINKING STABLE ISOTOPES VALUES WITH BMI

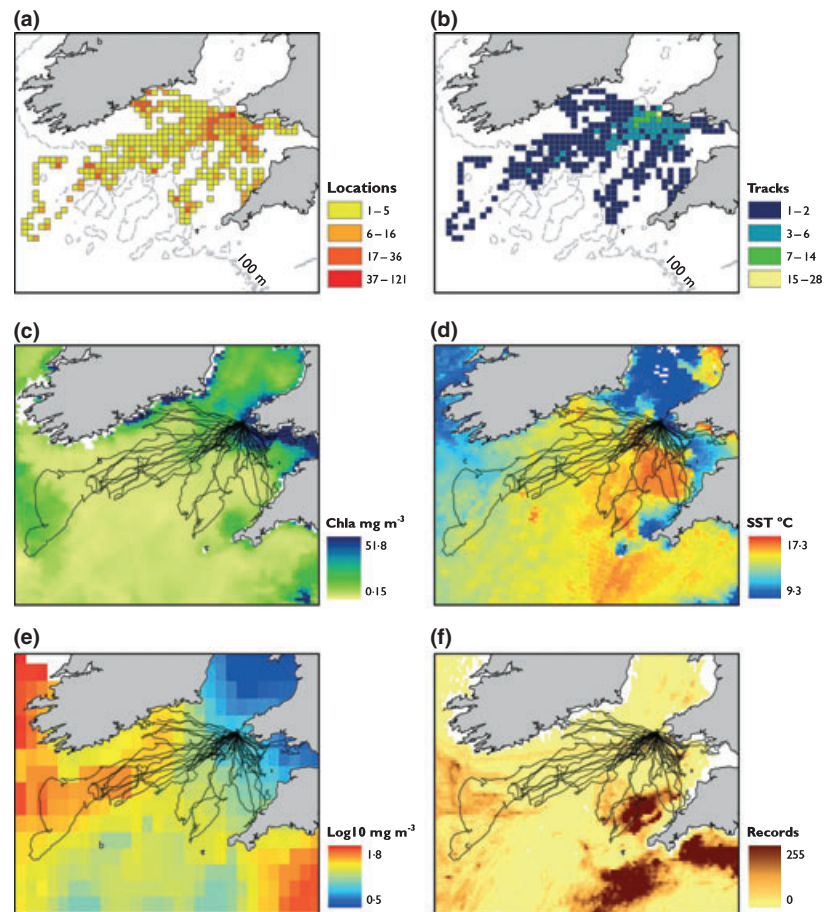
BMI was weakly negatively correlated with the (arcsine square-root transformed) median proportion of whitefish in the diet of individual gannets (obtained from SIAR mixing models) ( $r_{24} = -0.411$ ,  $P = 0.046$ , Fig. 7b).

#### Discussion

We address a number of questions about the foraging tactics of individual central place marine predators in relation to commercial fisheries: (1) do breeding gannets scavenge from fishing boats, (2) is there individual variation in the use of discards, (3) are foraging differences consistent, (4) how do the distribution of fishing vessels and environmental conditions influence at-sea behaviour, and (5) what are the consequences (in terms of foraging trip duration and adult body condition) of scavenging for fisheries waste? We discuss our findings in light of these questions, consider their implications for assessing the impact of commercial fisheries on marine predators in general and seabirds in particular, and also consider the application of SIAR and VMS to study scavenger/fishery interactions.

Adult gannets consume a range of fish species, with breeders regurgitating demersal whitefish which could only have come from commercial fisheries. This, together with evidence from GPS tracking data (Figs 4 and 6), indicates that centrally placed breeding adult gannets scavenge from fishing boats. Although seabirds are conspicuous scavengers at fishing vessels (e.g. Hudson & Furness 1989), it is not normally possible to determine the origins or reproductive status of these birds and therefore whether breeders are involved.

Analysis of spontaneous regurgitates revealed individual differences in consumption of fishery waste – only 32% of prey samples were discarded whitefish. Nevertheless, this represents a very small number of prey items sampled over a narrow time period. A more robust estimate of assimilated prey was obtained by analysing stable isotope ratios in blood plasma and RBC (Fig. 1). SIAR estimated that the relative contribution from fisheries waste varied considerably among individuals; from 8% to 34% (Fig. 2). Therefore our results indicate that although fisheries waste does not form the majority of prey for breeding gannets, it forms a significant component of the diet for certain individuals. It is also possible that gannets



**Fig. 4.** Plots of gannet GPS locations and environmental covariates used in the analysis: (a) gannet GPS fixes 2006, (b) gannet foraging tracks 2006, (c) chlorophyll *a* concentration ( $\text{mg m}^{-3}$ ) 2006, (d) SST ( $^{\circ}\text{C}$ ) 2006, (e) average copepod abundance ( $\log_{10} \text{mg m}^{-3}$ ) 1953 to 2002, and (f) average fishing vessel locations from VMS 2000–2004.

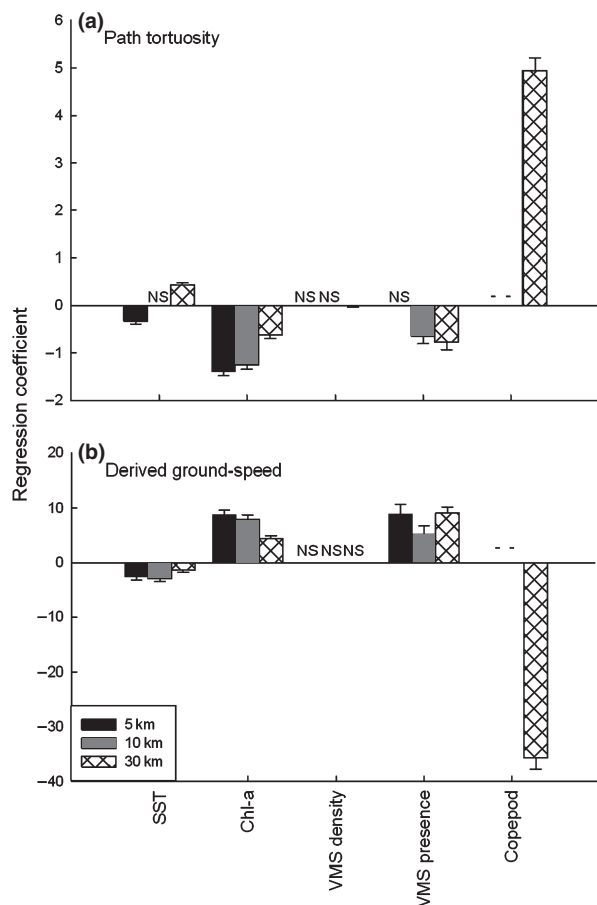
obtain mackerel from fishing boats, so the relative contribution of discards may be an underestimate. Although gannets are flexible foragers (Montevecchi & Myers 1997; Montevecchi *et al.* 2009), changes in discard availability could impact certain individuals more than others.

A comparison of  $\delta^{13}\text{C}$  values (corrected for trophic fractionation) in RBC upon initial capture and blood plasma upon recapture indicate that, in the short-term, individual gannets foraged in isotopically similar locations (Fig. 3a).  $\delta^{15}\text{N}$  values were also weakly repeatable among tissue types, suggesting short-term consistency in trophic status of prey (Fig. 3b). While there is some overlap in the synthesis of these tissues, they represent different time scales and any prey switching should be reflected in isotopic differences (Podlesak *et al.* 2005). These data indicate that although individual gannets show individual flexibility in foraging tactics (the relationships between temporally segregated isotope values were not 1:1), they show a degree of foraging site fidelity and prey type consistency. Earlier work has shown similar consistencies in foraging behaviour in both this species (Garthe, Montevecchi & Davoren 2007b; Kakela *et al.* 2007) and in other species of centrally placed marine predators (Bradshaw *et al.* 2004; Votier *et al.* 2004a; Bearhop *et al.* 2006).

Our results show that gannets adjust at-sea path tortuosity and flight speed in relation to fishing vessel positions (Tables S1 and S2 Supporting Information, Fig. 5). We found

a weakly significant effect of average fishing vessel density 2000–2004 and a strong effect of contemporaneous presence/absence on path tortuosity, with gannets exhibiting more direct flight paths at scales of 10 km and 30 km (Table S1 Supporting Information, Fig. 5a). Moreover, gannets showed no difference in flight speed in relation to the long-term average of vessel density, but significantly faster flight speeds associated with the current presence of fishing vessels (Table S2 Supporting Information, Fig. 5b). Long-term average vessel density appears to have a weak impact on foraging behaviour, despite the fact that fishing hotspots are consistent over months and years (Witt & Godley 2007), highlighting the importance of achieving temporal concordance between tracking data and fishing vessel location.

It is unclear whether gannets exhibit straighter flight paths because they are following towing vessels or because they are flying directly towards them, but the increase in speed indicates the latter. It is also unclear whether gannets adjust their behaviour in response to fishing boats or whether fishermen use gannets to decide where to fish, although it seems unlikely that fishermen rely heavily on foraging seabirds instead of sonar to locate fish. Moreover, we cannot be certain that trawlers and gannets are not simply targeting the same shoals of fish, but the fact that gannets regurgitate discards suggests that this behaviour represents scavenging. Although scavenging from fishing boats is a common strategy for many seabirds (Furness



**Fig. 5.** Effect of explanatory variables on path tortuosity (a) and derived ground speed (b), measured at three spatial scales (5 km, 10 km, and 30 km), of breeding northern gannets foraging at sea. Bars indicate regression coefficients ( $\pm$  1 SE). SST = Sea surface temperature; Chl-*a* = chlorophyll *a* concentration; Copepods = mean copepod abundance 1956–2002; VMS density = fishing vessel density from the vessel monitoring system averaged 2000–2004; VMS present = presence/absence of contemporaneous fishing vessels; NS = not statistically significant; ‘-’ = data not available at this spatial scale.

2003) and there is also evidence of spatial and temporal links between fisheries and scavengers (Votier *et al.* 2008), this is the first demonstration (to our knowledge) of a centrally placed predator adjusting search behaviour in relation to the activity of fishing vessels.

The response of gannets to contemporaneous fishing vessels varied among individuals – some birds showed decreasing speeds and increasing turn rates, while others showed no clear change in foraging behaviour (Fig. 6). These differences provide further evidence that not all individuals interact with fisheries in the same manner.

Similar to studies of other marine predators (Pinaud & Weimerskirch 2005), we have shown that gannets exhibit scale-dependent movement in relation to environmental cues. Higher copepod abundance was associated with increased path tortuosity (Table S1 Supporting Information, Fig. 5a), and reduced flight speed (Table S2 Supporting Information,

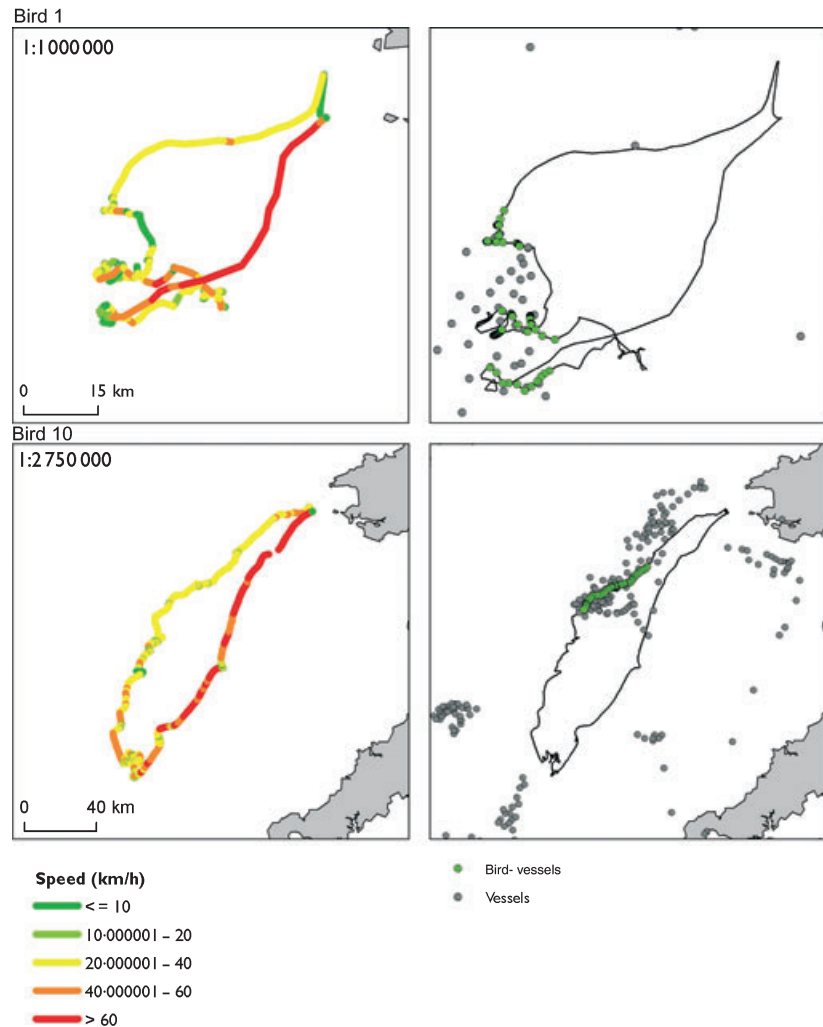
Fig. 5b), which is strongly linked with increased foraging effort (Hamer *et al.* 2009). Since gannets are not known to feed on zooplankton, it is most likely that copepod abundance is correlated with the availability of forage fish (Gremillet *et al.* 2008a). Copepod abundance emerged as a significant predictor of path tortuosity, despite representing data averaged over the period 1953 to 2002 – indicating that productive patches are predictable over time (Weimerskirch 2007). Gannets exhibited a complex change in path tortuosity in relation to water temperature (Table S1 Supporting Information, Fig. 5a) but travelled at consistently higher speeds in cooler water (Table S2 Supporting Information, Fig. 5b). Areas of high chlorophyll *a* concentration were associated with straighter flight paths (Table S1 Supporting Information, Fig. 5) and increased flight speed (Table S2 Supporting Information, Fig. 5b). Although previous work showed that some seabirds increased search activity in relation to chlorophyll abundance (Pinaud & Weimerskirch 2005), our results indicate that gannets quickly transit through areas of high primary productivity. This may reflect the fact that current chlorophyll abundance does not necessarily equate to current food abundance. Instead, high chlorophyll concentration may represent a standing stock not yet exploited by zooplankton, or species of phytoplankton unpalatable to grazing zooplankton. Despite finding significant relationships between at-sea behaviour of gannets and environmental covariates, we urge caution in interpreting these results because of a temporal mismatch in the data.

We found that the proportion of fishery waste in the diet of individual gannets was weakly negatively correlated with trip duration (Fig. 7a). Therefore, because gannets have an energetically costly mode of flight (Birt-Friesen *et al.* 1989), birds scavenging for discards may have reduced foraging costs compared with those feeding on pelagic fish.

The negative correlation between the median proportion of whitefish in the diet and BMI (Fig. 7b), an index primarily reflecting body lipid reserves (Zwarts *et al.* 1996), suggests that either discards are poor quality food or that poor quality individuals consume discards. While whitefish may negatively affect chick survival and growth (Wanless *et al.* 2005), evidence from other studies indicates that fishery waste is beneficial for adults of both generalist predators (Hüppop & Wurm 2000) and specialist piscivores like gannets (Gremillet *et al.* 2008b). Therefore the evidence hints that poor quality birds feed more on discards, although this requires further investigation.

#### MANAGEMENT IMPLICATIONS

Linking GPS tracking data with VMS data indicates that fishing boats shape the at-sea foraging behaviour of seabirds. Therefore VMS, when in tandem with animal tracking data, has the potential to draw links between scavengers and specific fisheries or even specific vessels, providing a potentially powerful monitoring tool. Future research should focus on more complete VMS coverage (we did not have access to data on non-UK vessels) and gear-specific data, as well as studying links at different times of the year – discards may be more important in winter (Garthe, Camphuysen & Furness 1996),



**Fig. 6.** Tracks of 2 gannets (Bird 1 and Bird 10) showing derived ground-speed and spatial and temporal relationship with current fishing vessel activity. In the right hand figure grey symbols indicate location of contemporaneous fishing vessels and green symbols indicate when the bird is within 2 h and 5 km of a vessel (denoted 'bird-vessels'). The left hand figure indicates derived ground speeds.

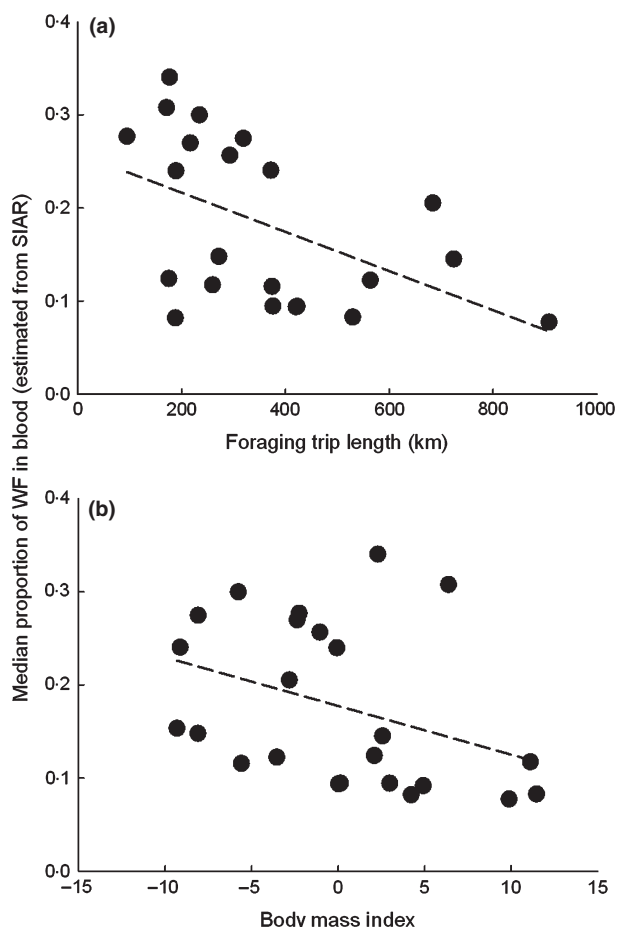
or for different age classes – immature seabirds may be more reliant on discards than adults (Gremillet *et al.* 2008b). Unfortunately, it is not clear how vessels less than 15 m can be effectively monitored. Nevertheless our analysis highlights the value of combining tracking and VMS, and represents an important advancement in our level of understanding of scavenger/fishery interactions.

SIAR proved a robust approach to estimate individual level discard consumption. This technique could be used elsewhere but relies on isotopic differences between fishery waste and natural prey. Therefore in areas where discards comprise many pelagic fish this same approach would be less effective – here SIAR would not be able to differentiate between scavenged and naturally caught prey, emphasizing the importance of gathering conventional dietary data such as regurgitates.

Individual gannets showed clear differences in discard consumption and foraging adjustments to trawlers, which has a number of management implications. The risks of becoming entangled in fishing gear and the effects of changes in discarding policy are not the same for all breeding birds. Variation in scavenging behaviour may be advantageous because only a small proportion of the population is at risk of bycatch or from the potential ecological trap caused by discards. Conversely, this

difference makes it more difficult to predict the population-level effects of changes in fisheries management. Also, individual differences in discard use were related to differences in BMI and foraging effort, which may in turn have fitness consequences. Therefore individual-based modelling might be an appropriate way to study the impacts of fisheries on scavengers.

To conclude, a combination of SIAR, GPS tracking and VMS provide a powerful suite of techniques to study in detail the nature of interactions between individual marine top predators and commercial fisheries. These techniques could be used to identify those age classes or genders most at risk of entanglement, or most reliant on discards for food, to improve predictive demographic or bio-energetic modelling. Moreover, in theory, VMS could be used to identify fisheries or specific vessels with particularly high rates of scavenger co-occurrence and therefore high entanglement risk, should the data be made available. Ultimately, reducing bycatch and removing dependency on discards remain key conservation priorities, but managers should also ensure that scavenging species have sufficient food to meet their energetic requirements in the absence of fishery waste, to reduce possible indirect eco-system effects (Votier *et al.* 2004c). This level of eco-system management remains daunting – even without the small matter of global climate change.



**Fig. 7.** The proportion of whitefish in the blood of individual gannets (estimated from SIAR) is: (a) negatively correlated with foraging trip length ( $r_{22} = -0.489$ ,  $P = 0.021$ ) and (b) negatively correlated with Body Mass Index ( $r_{24} = -0.411$ ,  $P = 0.046$ ).

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## Supporting Information

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

**Table S1.** Relationship between at-sea path tortuosity of gannets and environmental variables

**Table S2.** Relationship between derived ground speed of foraging gannets and environmental variables

**Fig. S1.** Foraging tracks of 25 individual northern gannets. Green dots indicate when birds are within 5 km and 2 h of a contemporaneous fishing vessel.

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