PROCEEDINGS OF THE ROYAL SOCIETY B
FirstCite® e-publishing

Proc. R. Soc. B
doi:10.1098/rspb.2005.3444

Encounter success of free-ranging marine predator movements across a dynamic prey landscape

David W. Sims[1,*], Matthew J. Witt[1,†], Anthony J. Richardson[2,‡], Emily J. Southall[1] and Julian D. Metcalfe[3]

[1]*Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK*
[2]*Sir Alister Hardy Foundation for Ocean Science, Plymouth PL1 2PB, UK*
[3]*Centre for Environment, Fisheries and Aquaculture Sciences, Pakefield Road, Lowestoft NR33 0HT, UK*

Movements of wide-ranging top predators can now be studied effectively using satellite and archival telemetry. However, the motivations underlying movements remain difficult to determine because trajectories are seldom related to key biological gradients, such as changing prey distributions. Here, we use a dynamic prey landscape of zooplankton biomass in the north-east Atlantic Ocean to examine active habitat selection in the plankton-feeding basking shark *Cetorhinus maximus*. The relative success of shark searches across this landscape was examined by comparing prey biomass encountered by sharks with encounters by random-walk simulations of 'model' sharks. Movements of transmitter-tagged sharks monitored for 964 days (16 754 km estimated minimum distance) were concentrated on the European continental shelf in areas characterized by high seasonal productivity and complex prey distributions. We show movements by adult and sub-adult sharks yielded consistently higher prey encounter rates than 90% of random-walk simulations. Behavioural patterns were consistent with basking sharks using search tactics structured across multiple scales to exploit the richest prey areas available in preferred habitats. Simple behavioural rules based on learned responses to previously encountered prey distributions may explain the high performances. This study highlights how dynamic prey landscapes enable active habitat selection in large predators to be investigated from a trophic perspective, an approach that may inform conservation by identifying critical habitat of vulnerable species.

Keywords: satellite telemetry; foraging ecology; fish; strategy; tactics; cetacean

1. INTRODUCTION

A long-standing problem in behavioural biology is how free-ranging predators forage efficiently within complex, rapidly changing 'prey landscapes', where foraging decisions are often made with incomplete information about prey availability (Stephens & Krebs 1986). When resource distributions change such that no stable prior expectation of when and where to forage can be acquired (Giraldeau 1997), the selection of appropriate searching movements to track changes are important for successful foraging (Fauchald 1999). Finding new prey locations outside their immediate sensory detection range requires a predator to make adaptive decisions about which movement pattern to adopt to feed most profitably given a particular resource distribution. For a rate-maximizing behavioural strategy this pattern should minimize distance moved, and therefore energy expended, whilst maximizing prey capture. Recent advances in telemetry technology allow the free-ranging movements of terrestrial and marine predators in the natural environment to be spatially resolved, providing new insights into dispersal patterns and migration routes among diverse taxa (Metcalfe & Arnold 1997; Croxall *et al.* 2005), including what areas (habitats) predators select. However, movements generally convey little about why those habitats have been selected (Kramer *et al.* 1997). Because the distribution of prey is a key factor influencing predator movements, interpreting them within a prey landscape may provide a clearer picture of why certain habitats are selected over others by allowing estimation of relative foraging success of observed search patterns. Unfortunately, the lack of large-scale prey landscapes of sufficient resolution to summarize natural dynamics and complexity adequately, have so far precluded such analyses (Russell *et al.* 1992).

Previous investigations with marine predators have measured the prey captured or encountered along foraging paths (e.g. Weimerskirch *et al.* 1994; Sims & Quayle 1998), providing valuable information on habitat and prey selection behaviour. However, prey availability in areas outside of the movement path are yet to be considered. This is a central limitation because a non-biased analysis of active habitat selection should ideally also assess availability of appropriate habitat in areas not apparently chosen by the forager. This is because decisions underpinning patch-leaving behaviour may depend as much on expectations about prey availability in other, more distant patches, as on those currently experienced (Ollason 1983; Valone 1992; Sutherland 1996). Hence, because it is

---

* Author for correspondence (dws@mba.ac.uk).
[†] Present address: Centre for Ecology and Conservation, University of Exeter in Cornwall, Tremough TR10 9EZ, UK.
[‡] Present address: Department of Applied Mathematics, University of Queensland, St Lucia, Queensland 4072, Australia, and CSIRO Marine and Atmospheric Research, Cleveland, Queensland 4163, Australia.

The electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2005.3444 or via http://www.journals.royalsoc.ac.uk.

Received 24 October 2005
Accepted 6 December 2005

seldom clear what an individual predator is responding to when deciding to stay or leave an area, it is arguable that for better insights into the survival value of observed movement patterns, pathways should be related to changing prey landscapes. How a predator responds to prey fields outside of its immediate detection range is a key, but currently missing, component in studies of free-ranging predator behaviour.

The basking shark *Cetorhinus maximus* is an epipelagic shark distributed circumglobally in boreal to warm-temperate seas. It feeds preferentially on high densities of zooplankton assemblages dominated by calanoid copepods (Sims & Merrett 1997; Sims & Quayle 1998; Sims 1999). In the northeast Atlantic, they undertake extensive horizontal and vertical movements associated with the continental shelf and shelf edge throughout the year indicating this region is both a principal feeding, and overwintering area (Sims *et al.* 2003). However, whether large-scale movements reflect preferences for areas of high-zooplankton biomass has not been tested. Here, we assess the relative performance of basking shark movements compared to random-walk simulations through a dynamic zooplankton-biomass landscape assembled from samples collected throughout the northeast Atlantic. The purpose was to test the hypothesis that longer range movements over the continental shelf were principally aimed at locating high-density prey patches. Targeting these areas is important for efficient foraging, but may also serve to increase courtship and mating opportunities (Sims *et al.* 2000).

2. MATERIAL AND METHODS

(a) *Archival tracking*

Satellite-linked archival transmitters (pop-up archival transmitting (PAT) tags; Wildlife Computers, Redmond, USA) were attached to 20 basking sharks between May and August 2001 and 2002 as they foraged off southwest England and northwest Scotland. Sharks were located from a 10 m research vessel from which tags were deployed by attachment to the base of the first dorsal fin. Tagging was conducted under licences from the UK Home Office, English Nature and Scottish Natural Heritage. Geolocation accuracy of tagging positions was less than 5 m (DGPS, Valsat 03, MLR Electronics, France). Each tag remained attached to a shark for a pre-programmed time before detaching and floating to the surface where each was geolocated by Argos receivers on NOAA polar-orbiting satellites. Estimated accuracy of these ‘pop-up’ locations as determined by Argos was 150–250 and 350–1000 m (Argos location class 2 and 1, respectively). Positions of each shark between attachment and tag pop-up were reconstructed using satellite retrieved or archival data of daily maximal rate-of-change in light intensity to estimate local time of midnight or midday for longitude calculations. Light-level intensity measurements from tag data were used to calculate longitude by post-processing of data using the tag manufacturer’s software (WC-GPE, global position estimator program suite). Anomalous longitude estimates resulting from dive-induced shifts in the estimated timings of dawn and dusk from light curves were discarded from the data set. Geolocations greater than 3° of longitude from the previous longitude estimate were also removed. Latitude along the longitude was fixed by matching tag-recorded sea surface temperature (SST) to SST values on simultaneous night-time advanced very high-resolution radiometer (AVHRR) remote-sensing images (http://www.npm.ac.uk/rsdas/). The most parsimonious location was derived by matching SSTs within an area specified by swim-speed and depth filters. The maximum distance a basking shark swam at its measured cruising speed (Sims 2000) from the last geolocated position was used as a radial filter to limit the geographical area searched for matching SSTs between tag and remotely sensed measurements. Maximum dive depth was compared with seabed depths from a digital bathymetric map (GEBCO, British Oceanographic Data Centre) within each area to filter anomalous positions where the dive depth recorded was greater than seabed depth. The accuracy of the resulting geolocations of basking shark positions was tested by comparison of initial tagging and pop-up locations with light/SST geolocations determined immediately post-tagging and pre-pop-up. The mean error distance of light/SST geolocation compared with tagging or pop-up locations was 75.5 km ± 54.5 s.d. (median, 59.7 km; range 36.9–183.9 km). A discussion of geolocation methodology used here is given in the electronic supplementary material.

(b) *Prey field*

Although there is no real-time zooplankton data at the scale of the northeast Atlantic, we assembled the only zooplankton prey field feasible at this scale (2800×2200 km), which summarizes accurately the main spatio-temporal dynamics of prey abundance and distribution in the region. We used zooplankton samples from the continuous plankton recorder (CPR) survey (Richardson *et al.* 2006) to construct a near-surface, prey-biomass field with minimum spatial and temporal resolutions of 56×36 km and 14 days, respectively. The CPR has recorded the abundance of near-surface zooplankton in the northeast Atlantic and North Sea since 1931 along established shipping routes. We constructed prey fields based on the preferred zooplankton dietary items of basking sharks (copepods; Sims & Merrett 1997) from 50 years of CPR data from 1953–2002 ($n=145\,175$ samples). Each CPR sample comprised abundance counts for 115 species/genera of zooplankton. Mass (M, mg wet weight) for each species was estimated from the allometric relationship with total body length (L, mm) of $M=0.08\,L^{2.1}$ (Peters 1983). This was multiplied by the abundance of each species to attain total biomass per sample (Richardson *et al.* 2006). Samples each year were partitioned into 14-day bins. From these, inverse distance-squared interpolation (Beaugrand *et al.* 2003) with a node search radius of 2.7° was used to produce five prey fields for each 14-day bin, corresponding to the year classes 1953–1962, 1963–1972, 1973–1982, 1983–1992 and 1993–2002. The median of all five fields was used to obtain the final gridded product of prey biomass. These prey fields capture persistent areas of high zooplankton biomass for each two-week period over a 50-year dataset, and possess a similar minimum spatial resolution to the reconstructed shark tracks. The complexity of the prey field was also investigated (see electronic supplementary material).

Prey encounter rates estimated using the prey field are not directly comparable to prey densities measured from basking shark feeding paths (e.g. Sims & Quayle 1998) because the spatial resolution of the CPR does not resolve prey encountered in high-density localized patches. In addition, the CPR is known to underestimate absolute abundance, although it measures relative change in zooplankton

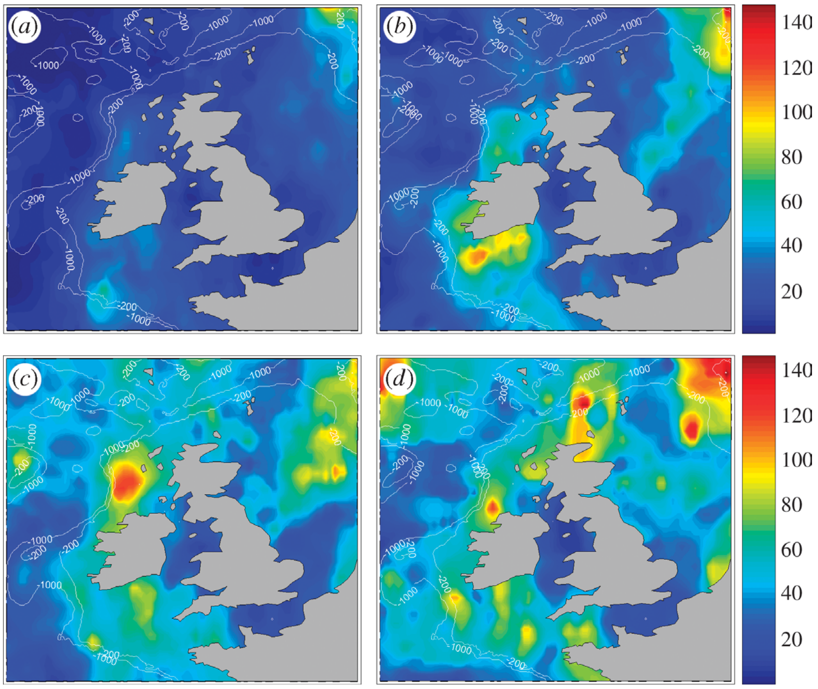

Figure 1. Examples of the zooplankton prey field showing the seasonal increase in biomass on the European continental shelf and shelf edge. Copepod biomass between (*a*) 16–28 April, (*b*) 29 April–11 May, (*c*) 12–24 May, and (*d*) 25 May–6 June. Scale bars denote biomass in mg m^{-3}.

abundance well (Richardson *et al*. 2006). Therefore, absolute masses of prey encountered by sharks in the model are not representative of actual capture rates, which are likely to be much higher than predicted here, but instead summarize likely individual (relative) differences in encounter success within and between areas visited.

To estimate prey-biomass encounter rates during shark movements, trajectories were related to spatio-temporal changes in zooplankton biomass within the dynamic prey field. Shark tracks were routed through the prey field such that along each successive step length, prey biomass encountered from each temporally matched prey field was ‘collected’ by each shark. At the end of a track, each shark accumulated a mass of zooplankton from all areas visited.

(c) *Model simulations*

To test the hypothesis that basking shark movements allow high encounter rates with prey, we compared prey biomass encountered by real sharks with masses encountered by randomly moving ‘model’ sharks. Random movements of model sharks were simulated (MATLAB, MathWorks Inc., MA), such that each model shark travelled the same estimated distance as each respective shark. Distances between successive positions (analogous to real shark geolocations), termed step lengths, were randomly chosen from the shark step-length frequency distribution and a random turn angle drawn from a uniform distribution was selected at the end of each step. Each model shark step length was validated against a high-resolution ($5'$) digital bathymetric map (TerrainBase, National Geophysical Data Centre) to preclude model sharks crossing land. The re-orientation angle and step length were replaced if the prior step was rejected. This routine allowed models to approach, but not cross, land.

Two sets of model-shark random-walk simulations were undertaken to control for the different starting locations of sharks, the different habitats occupied, and any fidelity of real sharks to the continental shelf. In the first set, random-walk model sharks were free to move into the open ocean away from the continental shelf (‘unconstrained’ movement). In the second set, simulations were constrained to the shelf (‘shelf-constrained’ movement). This was because output from unconstrained simulations could result in significant bias in the biomasses encountered if they were compared with shark tracks that stayed associated with the shelf and did not move into the open ocean. Thus, the first set of model shark movement simulations were unconstrained geographically ($n=1000$ per shark), while the second set of simulated movements were constrained to the continental shelf and shelf-edge (depths <1500 m; $n=1000$ per shark). Using the same procedure as for real sharks, prey biomass encountered during model shark movements was summed for each n simulation. In total, 14 000 simulations were completed.

3. RESULTS

Data were received for 7 of the 20 basking sharks (35%) fitted with electronic tags, comprising individuals ranging in total length from 2.5–7.0 m. These seven sharks were tracked for a total of 964 days (2.4–7.1 months per shark) between May 2001 and December 2002. During this time 186 geolocations were obtained at a rate of 0.20 geolocations d^{-1} (± 0.05 s.e.), and covering a total minimum distance of 16 754 km. Dive data transmitted via satellite showed all tracked sharks spent significant amounts of time within the uppermost layer of the ocean. Five individuals occupied the 0–10 m depth range for between 37 and 67% of the time, while two sharks spent 24–75% of time between 0 and 75 m. This confirmed that all sharks were associated significantly with near-surface prey fields during tag deployments.

The spatial distribution of copepod biomass summarized by the derived prey field was complex in both space and time (for examples see figure 1*a*–*d*). It was noticeable that copepod biomass exhibited patchiness over a range of

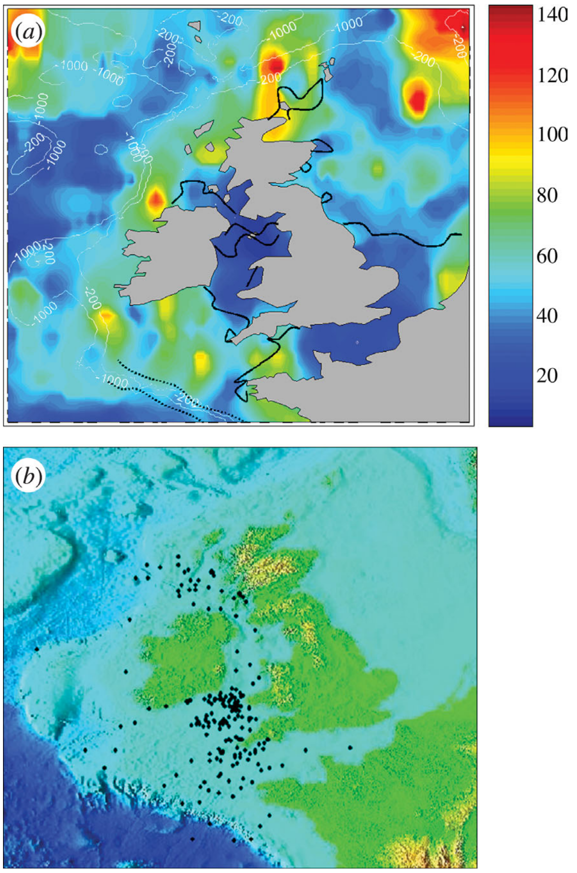

Figure 2. (*a*) Location of the main tidal fronts (solid black line) and the shelf-break front (dashed lines) in relation to copepod biomass between 24 May and 6 June. Front positions taken from Pingree (1978). (*b*) All geolocations of basking sharks between May 2001 and December 2002.

scales (figure 1*d*). Biomass distributions comprised two distinct maxima corresponding to clustered (negative binomial) and random (Poisson) distributions (see electronic supplementary material), indicating inherent complexity in prey distributions summarized within the landscape. Elevated biomass was often, but not exclusively, associated with physical features such as tidal fronts and the shelf edge (figures 1*c*,*d* and 2*a*). Particularly high biomass was present seasonally in the Celtic (figure 1*b*–*d*) and Hebridean Seas (figure 1*c*,*d*), with the increase in late April in the Celtic Sea and in early May further north (figure 1*b*,*c*). All tracked sharks remained on the continental shelf and shelf edge for the duration of tag deployments (figure 2*b*), primarily in areas characterized by the prey field as having elevated copepod biomass, although these were dynamic, with high densities sometimes relatively short-lived (14 d; figure 1*a*–*d*). In general, there was an absence of geolocations in areas with relatively low copepod biomass (figure 2*a*,*b*).

By mapping the reconstructed tracks onto the prey field we found that the average prey encountered was broadly similar for each shark, ranging from 17.9 to 53.7 mg m^{-3} per geolocation (mean, 40.2±4.2 s.e.m; median, 41.3). Relative differences in prey encountered by individuals were largely due to the different geographical regions visited by each shark. They moved over the entire western sector of the European continental shelf, from the Bay of Biscay off France in the south (46.5° N) to the Hebridean Sea off Scotland in the north (57.3° N; figure 3*a*–*g*).

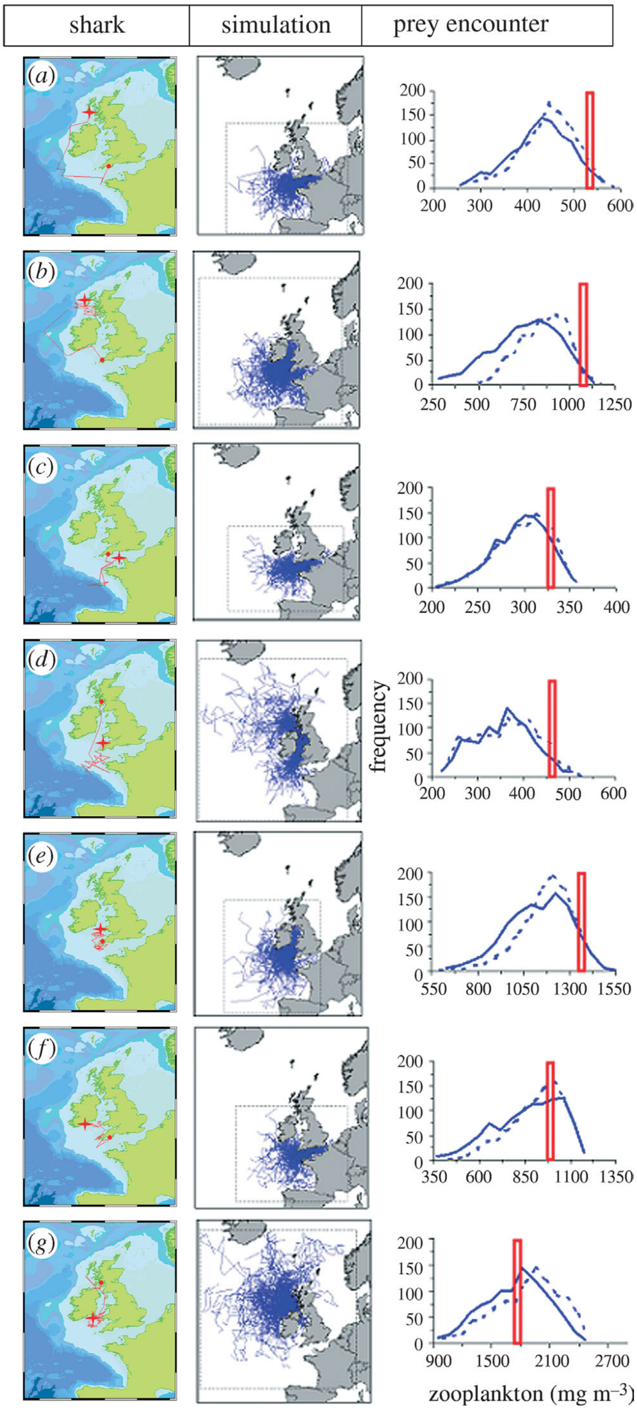

Figure 3. Success of large-scale foraging search patterns of (*a*–*f*) six adult and sub-adult basking sharks and (*g*) one juvenile. Movements of individual sharks given in the first column (shark) of panels show each track start (filled circle) and end point (cross). Blue shading indicates depth of water where lightest colour are depths <100 m and darkest are depths >4000 m. The second column of panels (simulation) shows the geographically unconstrained random walks generated for each respective shark from the step-length frequency distribution. Only 100 walks of the 1000 simulations for each shark are shown for clarity. The dashed black box in each panel denotes the absolute geographical extent of all simulation movements for each shark. The third column (prey encounter) indicates the success of search patterns of sharks within their foraging range in terms of prey encounter rate (open red bars) compared to the distribution of prey masses encountered by 1000 unconstrained random walks (solid blue line) and 1000 random walks constrained to the productive continental shelf (dashed blue line).

The individual successes of adult and sub-adult sharks adopting reconstructed movement patterns were strikingly high compared to both sets of model simulations (figure 3*a*–*f*). The total prey masses encountered by six sharks (4.5–7.0 m total length; >4 years old) were greater on average than 90.5% of prey masses encountered by unconstrained model sharks (mean $90.5\% \pm 11.2$ s.d., median 96.1%, range 69.8–98.8%). The performance of basking sharks was also greater than 87.6% of shelf-constrained models (mean $87.6\% \pm 12.7$ s.d., median 94.5%, range 66.0–97.3%). Four of the six sharks out-performed between 95.2 and 98.8% of model sharks (figure 3*a*,*b*,*d*,*e*). This shows that reconstructed trajectories of tagged sharks in the natural environment were estimated to be on average among the highest yielding ~10% of 12 000 simulated search patterns. Constraining random movements of model sharks to productive shelf regions improved model-shark foraging performance by $<3\%$. This indicates that even within their preferred, productive-shelf habitat, adult and sub-adult shark movements were highly successful for encountering higher prey biomass (figure 3). In contrast to high encounters by older sharks, we found a 2.5 m long, young-of-the-year basking shark exhibited the lowest relative prey encounter rate; 55.5% of 2000 simulations out-performed this juvenile, indicating it searched no better than average (figure 3*g*).

4. DISCUSSION

Prey distribution in the upper layers of the oceans is regulated by physical and biological processes that are highly stochastic, resulting in patchiness over a very broad range of scales (Steele 1976; Benfield *et al.* 1998). The complexity of our zooplankton near-surface prey field is consistent with the expected heterogeneity of ocean landscapes (Steele 1989; Gallager *et al.* 1996), where there are numerous types of prey distribution at different spatio-temporal scales (Ryer & Olla 1995). In addition to complex patchiness at smaller scales, our prey field resolves seasonally persistent zooplankton gradients associated with physical features of the European continental shelf and shelf edge. For example, elevated biomass appears seasonally in areas such as the Western Approaches to the English Channel, the Celtic Sea between southern Ireland and southwest England, and in the Hebridean Sea off northwest Scotland, where high productivity associated with tidal fronts is well known (Pingree *et al.* 1975; Pingree 1978; Le Fèvre 1986). It also summarizes accurately, both in timing and spatial extent, areas of enhanced copepod biomass near the continental shelf edge, especially southwest of Ireland (Le Fèvre 1986). These regions were those in which tagged basking shark movements were concentrated.

We hypothesized that broad-scale movements of basking sharks were aimed at locating areas of enhanced zooplankton biomass, which we tested by comparing shark trajectories with random search patterns. It was striking that adult and sub-adult basking sharks consistently encountered more zooplankton within prey fields than ~90% of random simulations. This suggests that the movement patterns they undertook enhanced encounter rates, which is noteworthy given that model sharks were programmed to 'forage' with the same step-length frequency distribution as real sharks. The relative success of tagged basking sharks within prey fields is probably due to selection of shorter displacement distances than would occur randomly, when high-density patches were encountered. Previous studies have shown that at small spatial scales (<10 km) basking sharks exhibit selective foraging behaviour by conducting area-restricted searching within zooplankton patches (Sims & Quayle 1998). This localized response to encountering a dense prey patch comprises an increased rate of turning and a reduction in speed from cruising (non-feeding) to filter-feeding (Sims & Quayle 1998; Sims 1999; Sims 2000). Together, these tactics dramatically increase the time spent in the richest prey areas, enhancing prey capture opportunities (Sims & Quayle 1998). Clearly, model sharks were not programmed with these simple behavioural rules. However, area-restricted searching behaviour cannot, in itself, account for the apparent selectivity of basking sharks for higher productivity zones over greater distances (50–500 km) observed in this study. This is because simple behavioural kineses of fish to prey are thought to be limited in the open sea to scales less than $\sim 10^3$ times the body length (Harden Jones 1968), about 2.5–7 km in the case of tagged basking sharks. Therefore, the successful foraging searches of basking sharks outside their sensory detection range suggests utilization of other behavioural tactics.

One possibility is that basking sharks possess knowledge of where the best locations to feed are geographically, perhaps based on responses to physical gradients such as geomagnetic fields (Meyer *et al.* 2005), theoretically enabling navigation to specific locations (Kalmijn 1984). However, although sharks may use these sensory systems during movements, they do not provide reliable information on the location of prey resources. This is because the location of zooplankton abundance changes. For example, distribution shifts in *C. maximus* have been documented when the location of centres of zooplankton abundance are different both within and between years (Sims & Quayle 1998; Sims & Reid 2002). Strict fidelity to geographic locations without reference to prey gradients will result in poor search performance as prey landscapes change. Our results indicate basking sharks are capable of tracking rich zooplankton patches across increasing spatio-temporal scales, although how they might achieve this is less clear.

Intensive searching at small spatial scales, exemplified by area-restricted searching, is an efficient tactic for locating prey within a patch. By contrast, extensive searching, characterized by straight movements will be effective for searching for widely dispersed prey (Hill *et al.* 2002). Studies on basking sharks demonstrate that when prey densities drop below a lower threshold density ($\sim 0.6\ \mathrm{g\ m^{-3}}$) within a patch, sharks leave on relatively straight paths (Sims & Quayle 1998; Sims 1999), suggesting they undertake extensive searching to locate new patches. In turn, this indicates basking sharks control movement patterns in response to encountered prey distributions. The results of the present study extend these observations by showing prey encounter success is maintained across increasing spatial scales, implying extensive search tactics may also possess intrinsic behavioural rules such as those observed during intensive searching.

Movement patterns across increasing scales (outside an animal's sensory detection range) could be structured so as to optimize encounter rates with highly dispersed prey. This may explain why basking shark encounter rates with prey were high in our study. Theoretical studies using movement data from a long-range foraging seabird, the wandering albatross *Diomedea exulans*, found search patterns conformed to a statistical distribution (a Lévy distribution) that was optimal for finding sparse prey (Viswanathan *et al.* 1996, 1999). Similarly, an empirical study with *D. exulans* showed that movements measured over a very broad range of spatial scales were adjusted to a particular search pattern during putative food-searching behaviour (Fritz *et al.* 2002). Although the distribution and availability of prey were unknown in the latter study, laboratory investigations demonstrate that the statistical distributions underlying the structuring of successive moves during searches by a predator change in response to variations in prey abundance (Bartumeus *et al.* 2003). It is possible that behavioural adjustment over wide scales (i.e. 10–1000 km) underpinned by different search statistics enables basking sharks to optimize prey encounter rates in the vast, but rapidly changing ocean environment.

Mostly, the prey searching strategies of free-ranging marine vertebrates that feed on zooplankton remain enigmatic (Hays *et al.* 2004). How they acquire knowledge about how to respond to prey in a variety of distributions across multiple spatio-temporal scales is unknown. However, differences in performance between the older sharks and the juvenile we tracked point towards learned behaviour in responses to different prey distributions encountered playing a role. One explanation for the difference in encounter success (~90% in adult/sub-adult, ~50% in juvenile) is that it reflects ontogenic differences in habitat selection, which may stem from the limited time juveniles have experienced their prey environment compared to sub-adults and adults. It is possible that individuals learn what movement pattern to adopt within particular prey distributions. Movement patterns of juvenile narwhal *Monodon monoceros* were significantly different from those of older individuals on summer foraging grounds off Baffin Island, Canada (Laidre *et al.* 2004). Differences were thought to be due to foraging inexperience or increased exploratory activities of younger individuals that were yet to have developed strict fidelity to particular routes (Laidre *et al.* 2004). Our result supports this finding, although more trackings of juvenile basking sharks will be needed to test this idea further.

In summary, understanding how animal movement relates to population spatial distribution and abundance requires that decisions, or 'rules', underpinning spatial behaviour in relation to environment be identified in free-living individuals. Knowledge about why predators select certain habitat rather than other types at particular times may afford better prediction of population-level dispersion. In this context, dynamic prey landscapes similar to the one we have developed could be a useful tool for probing behavioural processes of habitat selection for difficult-to-study predators at scales and in environments thought to be previously outside the realm of behavioural ecology.

Funding was provided by the UK Department for Environment, Food and Rural Affairs, the UK Natural Environment Research Council (NERC), The Royal Society, US National Geographic Society, Fisheries Society of the British Isles, and the Esmée Fairbairn Foundation. The CPR survey is funded by agencies from Canada, The Faroes, France, Iceland, Ireland, The Netherlands, Portugal, UK and USA. We thank P. Miller, the NERC Satellite Receiving Station and Remote Sensing and Data Analysis Service for image processing and advice, and P. Harris, G. Fraser, D. MacKenzie, S. Moszolics, D. Uren and the late A. Russell for assistance at sea. D.W.S. is supported by an NERC-funded MBA Research Fellowship. This research is part of the European Tracking of Predators in the Atlantic (EUTOPIA) programme in the European Census of Marine Life.

REFERENCES

Bartumeus, F., Peters, F., Pueyo, S., Marrasé, C. & Catalan, J. 2003 Helical Lévy walks: adjusting search statistics to resource availability in microzooplankton. *Proc. Natl Acad. Sci. USA* **100**, 12 771–12 775. (doi:10.1073/pnas.2137243100)

Beaugrand, G., Ibanez, F. & Lindley, J. A. 2003 An overview of statistical methods applied to CPR data. *Prog. Oceanogr.* **58**, 235–262. (doi:10.1016/j.pocean.2003.08.006)

Benfield, M. C., Wiebe, P. H., Stanton, T. K., Davis, C. S., Gallager, S. M. & Greene, C. H. 1998 Estimating the spatial distribution of zooplankton biomass by combining video plankton recorder and single-frequency acoustic data. *Deep-Sea Res. II* **45**, 1175–1199. (doi:10.1016/S0967-0645(98)00026-5)

Croxall, J. P., Silk, J. R. D., Phillips, R. A., Afanasyev, V. & Briggs, D. R. 2005 Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science* **307**, 249–250. (doi:10.1126/science.1106042)

Fauchald, P. 1999 Foraging in a hierarchical patch system. *Am. Nat.* **153**, 603–613. (doi:10.1086/303203)

Fritz, H., Said, S. & Weimerskirch, H. 2002 Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proc. R. Soc. B* **270**, 1143–1148. (doi:10.1098/rspb.2003.2350)

Gallager, S. M., Davis, C. S., Epstein, A. W., Solow, A. & Beardsley, R. C. 1996 High-resolution observations of plankton spatial distributions correlated with hydrography in the great south channel, Georges bank. *Deep-Sea Res. II* **43**, 1627–1663. (doi:10.1016/S0967-0645(96)00058-6)

Giraldeau, L.-A. 1997 The ecology of information use. In *Behavioural ecology: an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 42–68. Oxford, UK: Blackwell.

Harden-Jones, F. R. 1968 *Fish migration*. London, UK: Edward Arnold.

Hays, G. C., Houghton, J. D. R. & Myers, A. E. 2004 Endangered species: pan-Atlantic leatherback turtle movements. *Nature* **429**, 522. (doi:10.1038/429522a)

Hill, S., Burrows, M. T. & Hughes, R. N. 2002 Adaptive search in juvenile plaice foraging for aggregated and dispersed prey. *J. Fish. Biol.* **61**, 1255–1267. (doi:10.1111/j.1095-8649.2002.tb02469.x)

Kalmijn, A. J. 1984 Theory of electromagnetic orientation: a further analysis. In *Comparative physiology of sensory systems* (ed. A. Bolis, R. D. Keynes & S. H. P. Maddrell), pp. 525–560. Cambridge, UK: Cambridge University Press.

Kramer, D. L., Rangeley, R. W. & Chapman, L. J. 1997 Habitat selection: patterns of spatial distribution from behavioural decisions. In *Behavioural ecology of teleost fishes* (ed. J.-G. J. Godin), pp. 37–80. Oxford, UK: Oxford University Press.

Laidre, K. L., Heide-Jørgensen, M. P., Logsdon, M. L., Hobbs, R. C., Dietz, R. & VanBlaricom, G. R. 2004 Fractal analysis of narwhal space use patterns. *Zoology* **107**, 3–11. (doi:10.1016/j.zool.2003.09.001)

Le Fèvre, J. 1986 Aspects of the biology of frontal systems. *Adv. Mar. Biol.* **23**, 163–299.

Metcalfe, J. D. & Arnold, G. P. 1997 Tracking fish with electronic tags. *Nature* **387**, 665–666. (doi:10.1038/42622)

Meyer, C. G., Holland, K. N. & Papastamatiou, Y. P. 2005 Sharks can detect changes in the geomagnetic field. *J. R. Soc. Interface* **2**, 129–130. (doi:10.1098/rsif.2004.0021)

Ollason, J. G. 1983 Behavioural consequences of hunting by expectation: a simulation study of foraging tactics. *Theor. Popul. Biol.* **23**, 323–346. (doi:10.1016/0040-5809(83)90022-9)

Peters, R. H. 1983 *The ecological implications of body size*. Cambridge, UK: Cambridge University Press.

Pingree, R. D. 1978 Cyclonic eddies and cross-frontal mixing. *J. Mar. Biol. Assoc. UK* **58**, 955–963.

Pingree, R. D., Pugh, P. R., Holligan, P. M. & Forster, G. R. 1975 Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature* **258**, 672–677. (doi:10.1038/258672a0)

Richardson, A. J., Walne, A. W., John, A. W. G., Jonas, T. D., Lindley, J. A., Sims, D. W. & Witt, M. J. 2006 Using continuous plankton recorder data. *Prog. Oceanogr.* **68**, 27–74.

Russell, R. W., Hunt, G. L., Coyle, K. O. & Cooney, R. T. 1992 Foraging in a fractal environment: spatial patterns in a marine predator–prey system. *Landscape Ecol.* **7**, 195–209. (doi:10.1007/BF00133310)

Ryer, C. H. & Olla, B. L. 1995 Influence of food distribution on fish foraging behaviour. *Anim. Behav.* **49**, 411–418. (doi:10.1006/anbe.1995.0054)

Sims, D. W. 1999 Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife-edge? *Proc. R. Soc. B* **266**, 1437–1443. (doi:10.1098/rspb.1999.0798)

Sims, D. W. 2000 Filter-feeding and cruising swimming speeds of basking sharks compared with optimal models: they filter-feed slower than predicted for their size. *J. Exp. Mar. Biol. Ecol.* **249**, 65–76. (doi:10.1016/S0022-0981(00)00183-0)

Sims, D. W. & Merrett, D. A. 1997 Determination of zooplankton characteristics in the presence of surface feeding basking sharks (*Cetorhinus maximus*). *Mar. Ecol. Prog. Ser.* **158**, 297–302.

Sims, D. W. & Quayle, V. A. 1998 Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* **393**, 460–464. (doi:10.1038/30959)

Sims, D. W. & Reid, P. C. 2002 Congruent trends in long-term zooplankton decline in the north-east Atlantic and basking shark (*Cetorhinus maximus*) fishery catches off west Ireland. *Fish. Oceanogr.* **11**, 59–63. (doi:10.1046/j.1365-2419.2002.00189.x)

Sims, D. W., Southall, E. J., Quayle, V. A. & Fox, A. M. 2000 Annual social behaviour of basking sharks associated with coastal front areas. *Proc. R. Soc. B* **267**, 1897–1904. (doi:10.1098/rspb.2000.1227)

Sims, D. W., Southall, E. J., Richardson, A. J., Reid, P. C. & Metcalfe, J. D. 2003 Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Mar. Ecol. Prog. Ser.* **248**, 187–196.

Steele, J. H. 1976 Patchiness. In *The ecology of the seas* (ed. D. H. Cushing & J. J. Walsh), pp. 98–115. Oxford, UK: Blackwell.

Steele, J. H. 1989 The ocean ‘landscape’. *Landscape Ecol.* **3**, 185–192. (doi:10.1007/BF00131537)

Stephens, D. W. & Krebs, J. R. 1986 *Foraging theory*. Princeton, NJ: Princeton University Press.

Sutherland, W. J. 1996 *From individual behaviour to population ecology*. Oxford, UK: Oxford University Press.

Valone, T. J. 1992 Patch estimation via memory windows and the effect of travel time. *J. Theor. Biol.* **157**, 243–257.

Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Murphy, E. J., Prince, P. A. & Stanley, H. E. 1996 Lévy flight search patterns of wandering albatrosses. *Nature* **381**, 413–415. (doi:10.1038/381413a0)

Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P. & Stanley, H. E. 1999 Optimizing the success of random searches. *Nature* **401**, 911–914. (doi:10.1038/44831)

Weimerskirch, H., Doncaster, C. P. & Cuenot-Chaillet, F. 1994 Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proc. R. Soc. B* **255**, 91–97.