Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation

David W. Sims[1,*], Emily J. Southall[1], Anthony J. Richardson[2], Philip C. Reid[2], Julian D. Metcalfe[3]

[1]Marine Biological Association, and [2]Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, United Kingdom

[3]Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 0HT, United Kingdom

ABSTRACT: Habitat selection processes in highly migratory animals such as sharks and whales are important to understand because they influence patterns of distribution, availability and therefore catch rates. However, spatial strategies remain poorly understood over seasonal scales in most species, including, most notably, the plankton-feeding basking shark *Cetorhinus maximus*. It was proposed nearly 50 yr ago that this globally distributed species migrates from coastal summer-feeding areas of the northeast Atlantic to hibernate during winter in deep water on the bottom of continental-shelf slopes. This view has perpetuated in the literature even though the 'hibernation theory' has not been tested directly. We have now tracked basking sharks for the first time over seasonal scales (1.7 to 6.5 mo) using 'pop-up' satellite archival transmitters. We show that they do not hibernate during winter but instead undertake extensive horizontal (up to 3400 km) and vertical (>750 m depth) movements to utilise productive continental-shelf and shelf-edge habitats during summer, autumn and winter. They travel long distances (390 to 460 km) to locate temporally discrete productivity 'hotspots' at shelf-break fronts, but at no time were prolonged movements into open-ocean regions away from shelf waters observed. Basking sharks have a very broad vertical diving range and can dive beyond the known range of planktivorous whales. Our study suggests this species can exploit shelf and slope-associated zooplankton communities in mesopelagic (200 to 1000 m) as well as epipelagic habitat (0 to 200 m).

KEY WORDS: Shark · Strategy · Satellite archival telemetry · Oceanographic fronts

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INTRODUCTION

Only 3 of the approximately 500 species of shark obtain food by filtering zooplankton, but these are among the largest sharks, and of all marine vertebrates only whales are larger. In contrast to baleen whales, however, the habitat of planktivorous sharks is largely unknown because tracking their movements and behaviour is comparatively difficult (Nelson et al. 1997, Eckert & Stewart 2001). This is despite an urgent need for more information because, for example, the second largest fish species, the basking shark *Cetorhinus*

maximus, is classified as endangered in the northeast Atlantic as a result of at least 2 centuries of exploitation (Hilton-Taylor 2000). Although basking sharks apparently grow slowly (Parker & Stott 1965), have a late age at maturity (Matthews 1950), and a low reproductive rate (Sund 1943), a lack of knowledge about movements and habitat requirements continues to hinder appropriate conservation assessment of this species. Until now, only 1 short-term tracking of an individual has been possible (Priede 1984).

During summer months in boreal to warm-temperate waters of the Atlantic Ocean, basking sharks filter-

feed on near-shore zooplankton (Sims & Quayle 1998), but beyond these brief glimpses their whereabouts for much of the year remains a mystery. It has long been thought that basking sharks migrate from summer feeding grounds to deep-water for winter hibernation because they are absent from surface waters at this time, and apparently shed their gill-raker filtering apparatus (Parker & Boeseman 1954). To counter this potential energy loss from swimming without the possibility of gainful feeding, it was proposed they hibernate on the seabed until spring when zooplankton densities increase (Parker & Boeseman 1954, Matthews 1962). However, a recent study showed basking sharks feed profitably at much lower threshold densities of zooplankton than previously thought, suggesting hibernation to be unnecessary (Sims 1999).

To test these ideas directly, and to determine for the first time the seasonal movements and habitat of basking sharks, we attached 'pop-up' satellite archival transmitters to individuals as they foraged during summer off the UK coast. In addition to providing the first information on the movements and behaviour of basking sharks over seasonal scales, we combine satellite-archival telemetry with remote sensing of ocean colour and continuous plankton recorder survey data to investigate whether movements are related to areas of enhanced secondary productivity.

MATERIALS AND METHODS

Study areas. Basking sharks were located in 2 study areas. An area in the English Channel off Plymouth (50° 20′–50° 10′ N, 003° 57′–004° 20′ W) was investigated during May 2001, and an area comprising Lower Loch Fyne and the northern Clyde Sea, Scotland (56° 00′–55° 35′ N, 004° 57′–005° 28′ W) was investigated in July 2001.

Fish tagging. To track basking sharks we used 'pop-up' archival transmitting (PAT) tags (length: 175 mm; mass in air: 76 g). These tags combine a data-logger that records swimming depth, water temperature and light level with an Argos-certified transmitter with 0.5 W power output (Wildlife Computers). Depth is measured to 1000 m (min. resolution: 0.5 m), temperature from –40 to 60°C (min. resolution, 0.05°C), and light level is measured as irradiance (W cm^{-2}) at 550 nm wavelength. These parameters are sampled each minute and stored as summary data over set intervals of 4 or 6 h (time-at-depth and time-at-temperature histograms; temperature-depth profiles; maximal change in light intensity over time). PAT tags were fitted with a 1.8-m long monofilament tether connected to a 40-mm long stainless steel T-bar arrowhead via wire tracer. Using a 10 m research vessel, we

approached surface-feeding sharks slowly from behind at a lateral distance of about 1 m. When the vessel's bow drew level with the shark's first dorsal fin, the arrowhead was fastened rapidly (<1 s) through the middle of the fin using a rubber-band speargun pulled at approximately 40 kg pressure. Attached PAT tags trailed behind sharks close to the body, and the known distance from tag to the first dorsal fin (1.8 m) was used to obtain an estimate of total body length. After attachment, and at a preprogrammed time, each tag released itself from its host shark and floated to the surface where it was geolocated by Argos satellites (the 'pop-up' location) and data summaries transmitted.

Track reconstruction. The estimated accuracy of 'pop-up' locations of PAT tags determined by Argos receivers was between 350 and 1000 m. Satellite-retrieved data of daily maximal rate of change in light intensity were used to estimate the local time of midnight or midday for longitude calculations (Hill 1994). The accuracy of these estimates is between ±0.15 and 1.20° of longitude (1° longitude = 71.7 km) (Welch & Eveson 1999, Block et al. 2001). Only consecutive longitude estimates <3° apart were used for geolocation. Longitude estimates were discarded for days when the maximal light-intensity change was dive-induced, i.e. measured at times inconsistent with the regionally expected times of dawn or dusk. Latitude was fixed using summary data. Daily temperature-depth (TD) profiles from sharks, or histogram summaries of swimming depth and water temperature, were used to determine minimum and maximum sea surface temperature (SST) on each day for which longitude was estimated. We then used nighttime advanced very high resolution radiometer (AVHRR) remote-sensing images of SST to fix latitude along the longitude. A java applet viewer (JAV) was used to determine SST values for individual pixels on each false-colour image. Colour intensity in each pixel (representing a 1 × 1 km area) was coded by a number from 0 to 256. By scanning each image using the JAV's cursor, the latitude representing the best fit of temperature-scaled colour criteria to measured SST values was made along each longitude estimate. Colour-criteria number values were converted to °C using a calibrated scale on each image. If cloud cover was high on a particular day, remote sensing SST images on the next closest day (before or after) were used to fix latitude. Only images to a maximum of 5 d before or after were used. The latitude estimate, fixed using SST, was then filtered for water-mass type, depth and swim-speed anomalies. TD profiles were used to determine water-mass type (stratified, frontal, mixed). If the water mass at the shark's location from SST images was inconsistent with that determined from TD profiles, then further JAV scans on the next available image were conducted.

Similarly, if the maximum daily depth attained by each shark was greater than the known depth at the estimated location shown on oceanographic charts, and/or the distance between consecutive geolocations was greater than 100 km d^{-1} straight-line travel speed (1.4° longitude; Sims 2000), then the geolocation was considered anomalous and further JAV scans were initiated. If a shark's position could not be resolved using other daily SST images, then the longitude estimate was discarded from the dataset.

The accuracy of latitude-position estimates varied over the range of standard deviation per location of 0.01 to 1.56° latitude (1.11 to 173.52 km; n = 31 locations examined), which were similar error fields to those associated with longitude estimation (Welch & Eveson 1999, Block et al. 2001).

Plankton analysis. The surface chl a pigment concentration at each geolocation of Shark 1 was determined for a 6 mo period (1 April to 30 September 2001) using daily SeaWiFS (nasa_chlor_a) remote sensing images. As with SST determinations, a JAV was used to obtain precise number values corresponding to map-colour criteria, which were converted to chl a concentrations using the formula:

$$C = 10^{[(n \times 0.015) + \log_{10}(0.01)]}$$

where C is chl a concentration in mg m^{-3} and n is pixel colour-criteria number. At each geolocation, 13 determinations were made: 1 at the estimated location of the shark and 3 others at 0.2° intervals in each of 4 compass directions (north, east, south, west) originating at the shark's estimated location.

To estimate the long-term monthly chlorophyll and copepod abundance for the Goban Spur region (48.0–50.0° N, 10.5–12.5° W) we used data from the continuous plankton recorder (CPR) survey. This plankton sampler, which is towed behind merchant ships on their normal routes at about 7 m depth, filters plankton from the water on a constantly moving band of silk of 270 µm mesh. Samples equivalent to 10 nautical miles (18.5 km) of tow and approximately 3 m^3 of water filtered are analysed under a microscope using a standard procedure (Warner & Hays 1994). To estimate

chlorophyll, we used phytoplankton colour, a visual index of the intensity of greenness observed on the silk, and for total copepod abundance, we summed all the counts for all species found (developmental stages: copepodites, CI to CV; adults, CVI). Data were from 1955 to 2000 and comprised 1094 samples.

RESULTS

'Pop-up' locations and behavioural data were obtained for 5 basking sharks, totalling 686 d tracking time between May 2001 and January 2002 (Table 1). These data provide unique insights into their summer movements and over-wintering behaviour.

Summer movements

Shark 1, a 4.5 m long female, travelled a minimum distance of 1878 km in 77 d (24 May to 8 August) (Table 1). From the tagging area off Plymouth it moved west and then northward before the PAT tag released and was geolocated by satellites, just south of the Hebrides in Scotland (Fig. 1A). The track reconstruction for this individual showed that in early June, within 7 to 10 d of being tagged, Shark 1 was near the productive Ushant tidal front off Brittany (B), France (Fig. 1A). Daily vertical temperature profiles confirmed the frontal habitat. This shark spent between 49 (night) and 71 % (day) of the time in the uppermost 10 m of water, although short-term dives to between 90 and 120 m depth did occur, though mainly at night (Fig. 2A). Some 11 d later, this shark was geolocated 460 km west, on the shelf edge (Goban Spur region), where it remained for at least 8 d (Fig. 1A,C). Near the shelf edge, Shark 1 spent progressively less time in the uppermost 10 m during the day (39 decreasing to 12 %), whilst more time was spent at depths below 90 m (Fig. 2B,C). The temporal change in maximum daily dive depth shows that Shark 1 undertook frequent dives through the water column from shallow 20 m depths to 100 m depths, dives which then in-

Table 1. *Cetorhinus maximus.* Summary of tracking data for basking sharks

| Shark	Estimated total body length (m)	Sex	Date tagged (dd/mm/yy)	Latitude tagged (°N)	Longitude tagged (°W)	'Pop-up' date	Latitude 'pop-up' (°N)	Longitude 'pop-up' (°W)	No. of track days	No. of locations	Min. distance moved between locations (km)
1	4.5	F	24/05/01	50.39	4.11	07/08/01	56.42	7.26	77	10	1878
2	6.0	–	25/05/01	50.32	4.13	07/12/01	49.87	2.42	197	8	1616
3	6.5	–	31/07/01	55.87	5.39	20/09/01	55.59	5.12	52	2	39
4	7.0	F	28/07/01	55.87	5.39	05/01/02	50.79	5.35	162	26	3421
5	5.5	F	24/05/01	50.29	4.11	07/12/01	52.28	1.81°E	198	3	581
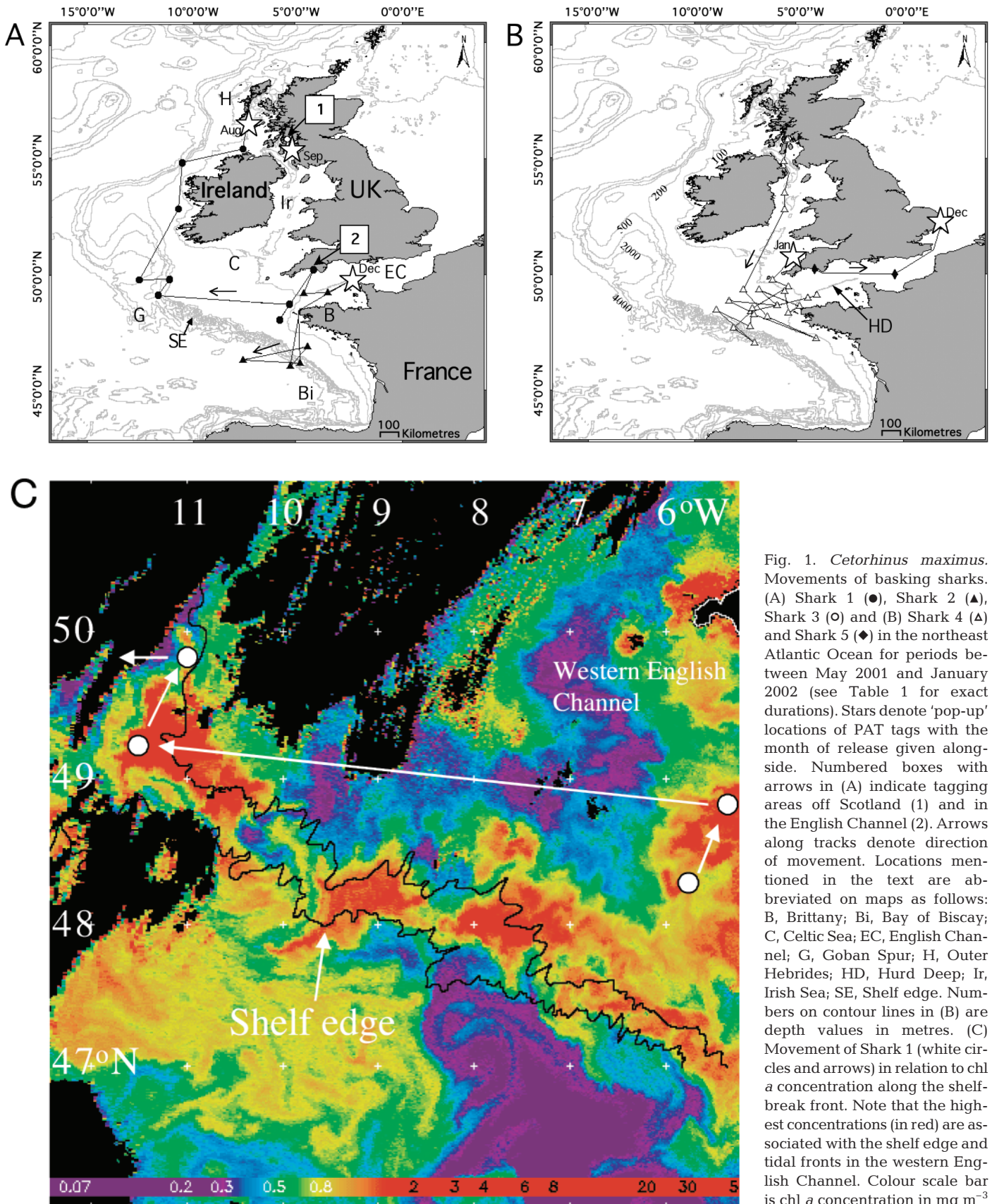
Fig. 1. *Cetorhinus maximus.* Movements of basking sharks. (A) Shark 1 (●), Shark 2 (▲), Shark 3 (○) and (B) Shark 4 (△) and Shark 5 (◆) in the northeast Atlantic Ocean for periods between May 2001 and January 2002 (see Table 1 for exact durations). Stars denote 'pop-up' locations of PAT tags with the month of release given alongside. Numbered boxes with arrows in (A) indicate tagging areas off Scotland (1) and in the English Channel (2). Arrows along tracks denote direction of movement. Locations mentioned in the text are abbreviated on maps as follows: B, Brittany; Bi, Bay of Biscay; C, Celtic Sea; EC, English Channel; G, Goban Spur; H, Outer Hebrides; HD, Hurd Deep; Ir, Irish Sea; SE, Shelf edge. Numbers on contour lines in (B) are depth values in metres. (C) Movement of Shark 1 (white circles and arrows) in relation to chl *a* concentration along the shelf-break front. Note that the highest concentrations (in red) are associated with the shelf edge and tidal fronts in the western English Channel. Colour scale bar is chl *a* concentration in mg m^{-3}
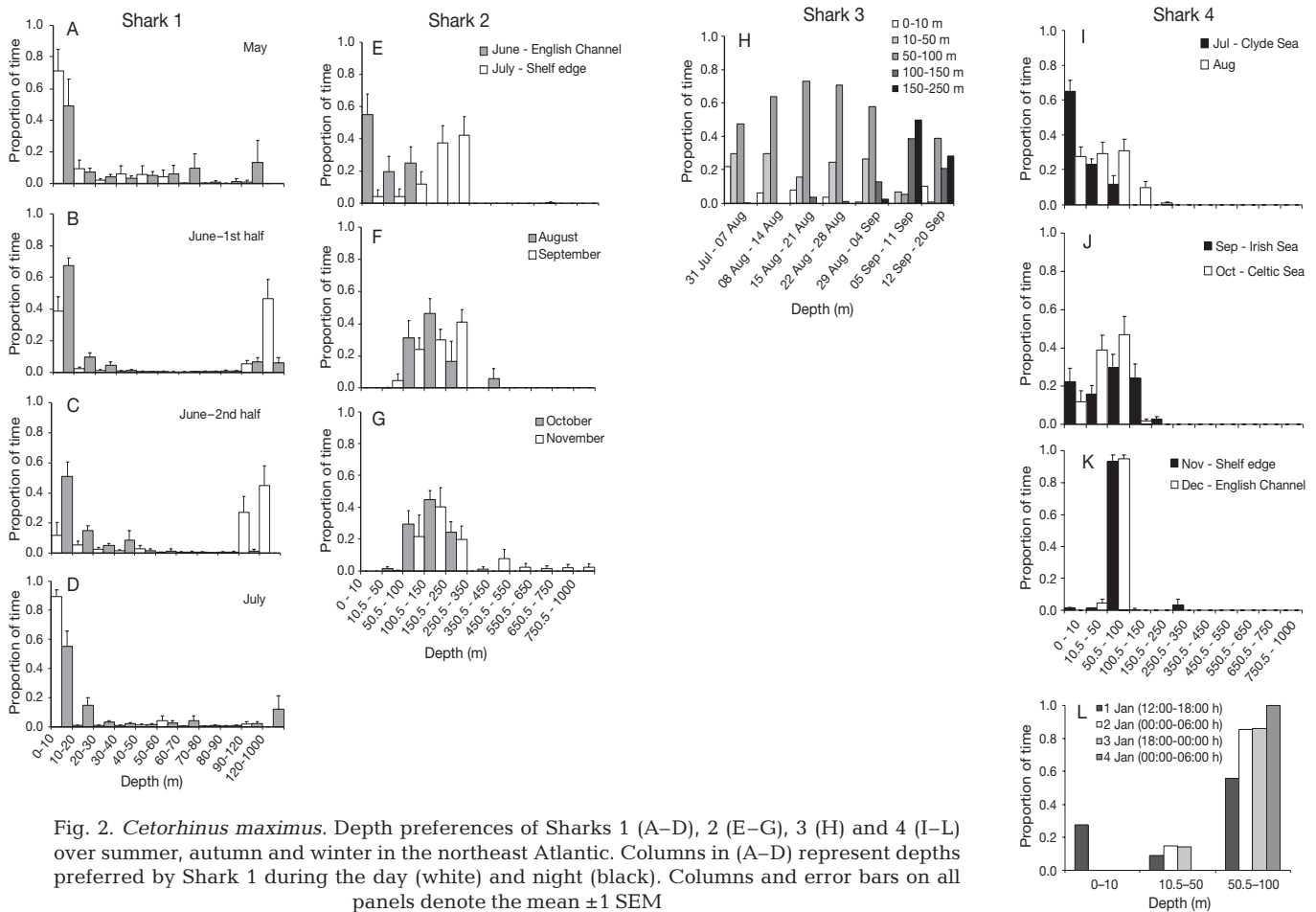
Fig. 2. *Cetorhinus maximus.* Depth preferences of Sharks 1 (A–D), 2 (E–G), 3 (H) and 4 (I–L) over summer, autumn and winter in the northeast Atlantic. Columns in (A–D) represent depths preferred by Shark 1 during the day (white) and night (black). Columns and error bars on all panels denote the mean ±1 SEM

creased in maximum depth from 120 to 180 m when near the shelf edge (Fig. 3A). The temperature–depth profile indicates that this shark dived offshore in strongly stratified water masses with a vertical temperature range of approximately 9 to 15°C (Fig. 3A). When this shark moved into shallower shelf waters off western Scotland in July (Fig. 2D), a daytime shallow-diving pattern, similar to that seen in the English Channel in May and June, resumed.

In 197 d Shark 2 moved a minimum distance of 1616 km (Table 1). A similar summer behaviour pattern was shown by this 6 m long individual as seen for Shark 1, in that during May and June it spent time in the western English Channel near tidal fronts, before moving offshore in July to the shelf edge (Fig. 2B). This change in summer habitat from shelf to shelf edge-frontal regions also reflected a shift from surface feeding in June (75% of time spent in 0 to 50 m depth), to deeper vertical habitat selection during July and August on the shelf edge (modal time-at-depth: 100 to 150 and 150 to 250 m). There were also occasional dives to between 350 and 650 m depth (Fig. 2E,F). This shark occupied shelf-edge habitat in the Bay of Biscay

(Fig. 1A) which was further south than areas selected by Shark 1. The Biscay region was characterised by warmer surface waters (16 to 17°C), although the shark continued to undertake frequent deep dives into cooler water (10 to 13°C) (Fig. 3D).

This general pattern of deep diving when vertical-habitat extent increased was supported by Sharks 3 and 4. Although they remained in the deep, fjord-like Clyde Sea for 1 to 2 mo during summer, they made very frequent, sometimes daily dives from the surface to 80 to 160 m and back again (Figs. 2H,I,J & 3B,C). These sharks occupied stratified and frontal water masses in summer, and during dives experienced a temperature change of between 8 and 16°C (Fig. 3B,C). In mid-September, Shark 3 dived to between 160 and 185 m, where it remained for 6 d before surfacing (Figs. 2H & 3B).

Shelf-edge movements

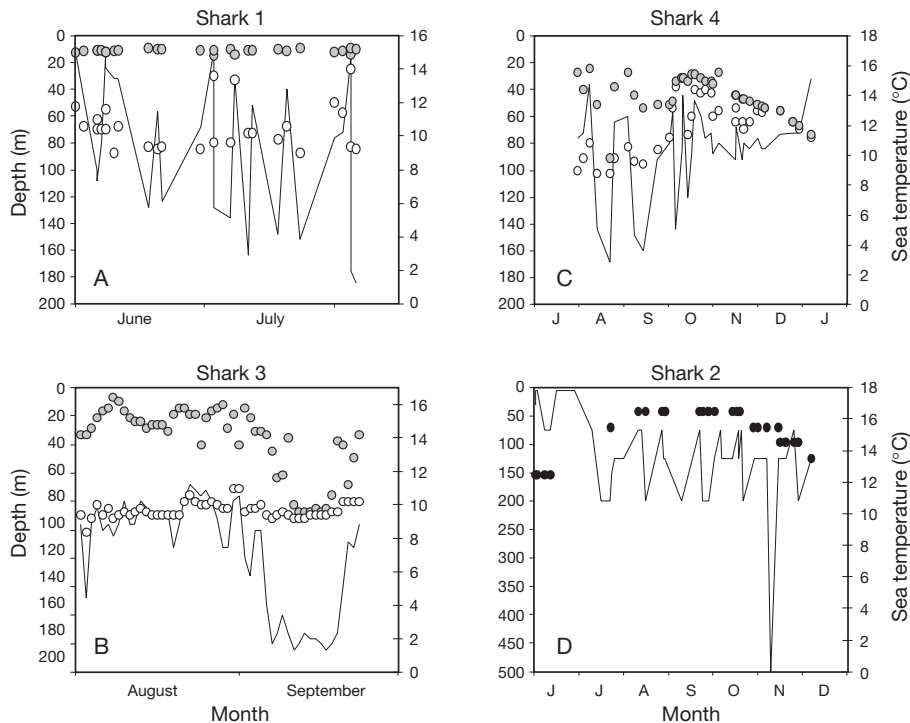Basking sharks utilised not only inshore tidal fronts for summer foraging, but also shelf-edge areas (loca-

Fig. 3. *Cetorhinus maximus.* Temperature and depth profiles of basking sharks tracked in the northeast Atlantic. (A–C) Maximum daily dive depth (black line) and minimum (open circle) and maximum (shaded circle) daily temperature; (D) midpoint depth in each daily modal-depth class (black line) and the midpoint temperature in each daily modal-temperature class (filled circle)

tions >200 m deep). To determine, for the first time, the relationship between broad-scale plankton abundance and foraging movements of basking sharks, we investigated trends in surface primary production (chl *a* pigment concentration) at each position of Shark 1 over a 6 mo period (1 April to 30 September 2001) using Sea-WiFS remote-sensing images (e.g. Fig. 1C). The shelf-edge positions occupied by Shark 1 on 14 and 17 June coincided with the highest levels of surface primary production seen at these locations for 6 mo (between 2 and 67 mg m^{-3} compared to a background level of <1 mg m^{-3}), and higher than those encountered previously off France (Fig. 4A). A SeaWiFS chl *a* image from 19 June 2001 indicates that in mid-June Shark 1 was associated with a discrete productivity 'hotspot' over the shelf edge (Fig. 1C). By contrast, prior to this shark moving north on or after 22 June, the level of primary production around its position had declined to about 0.5 mg m^{-3} (Fig. 4A).

Patterns of phytoplankton and total copepod abundances measured by the CPR survey over the same area show high congruence (Fig. 4B), indicating that peaks in primary and secondary production in this region are tightly coupled temporally. Basking Shark 1 arrived in the Goban Spur region at a time when total copepod abundance peaked (Fig. 4B). Decreased numbers of copepods in July at the Goban Spur coincided with the relatively fast northward movement of Shark 1 into areas where copepod abundance peaked in August (CPR data not shown).

Autumn-winter behaviour

In addition to summer foraging movements, 3 basking sharks were tracked across seasonal scales (May to December and July to January) (Sharks 2, 4, 5; Table 1). In December and January these individuals were located by satellites in shelf waters off southern England (Fig. 1A,B). Basking sharks in the Clyde Sea showed limited horizontal movements during summer foraging, but Shark 4 moved south during September, indicating residence in the Clyde Sea was a transitory behaviour. This shark, a 7 m long female, left the Clyde Sea in mid-September (temperature range: 11.0 to 14.0°C) and moved south through the Irish Sea over the next month before arriving in the southern Celtic Sea near the shelf edge in mid-October (temperature range: 14.0 to 16.0°C). From mid-October 2001 to early January 2002 this shark remained off south-west England, undertaking ranging movements to the shelf edge and into the western English Channel near a deep, narrow trench known as the Hurd Deep (Fig. 1B). In November and December this female spent 80 to 90% of its time between 50 and 100 m depth, although it occasionally went shallower and dived from the surface to between 250 and 350 m depth (Fig. 2K). Large-amplitude vertical movements in winter were less frequent than during summer because the maximum dive depth became progressively shallower (~90 to 50 m), concomitant with movements into inshore areas with a fairly constant temperature of approximately 11°C (Fig. 3C).
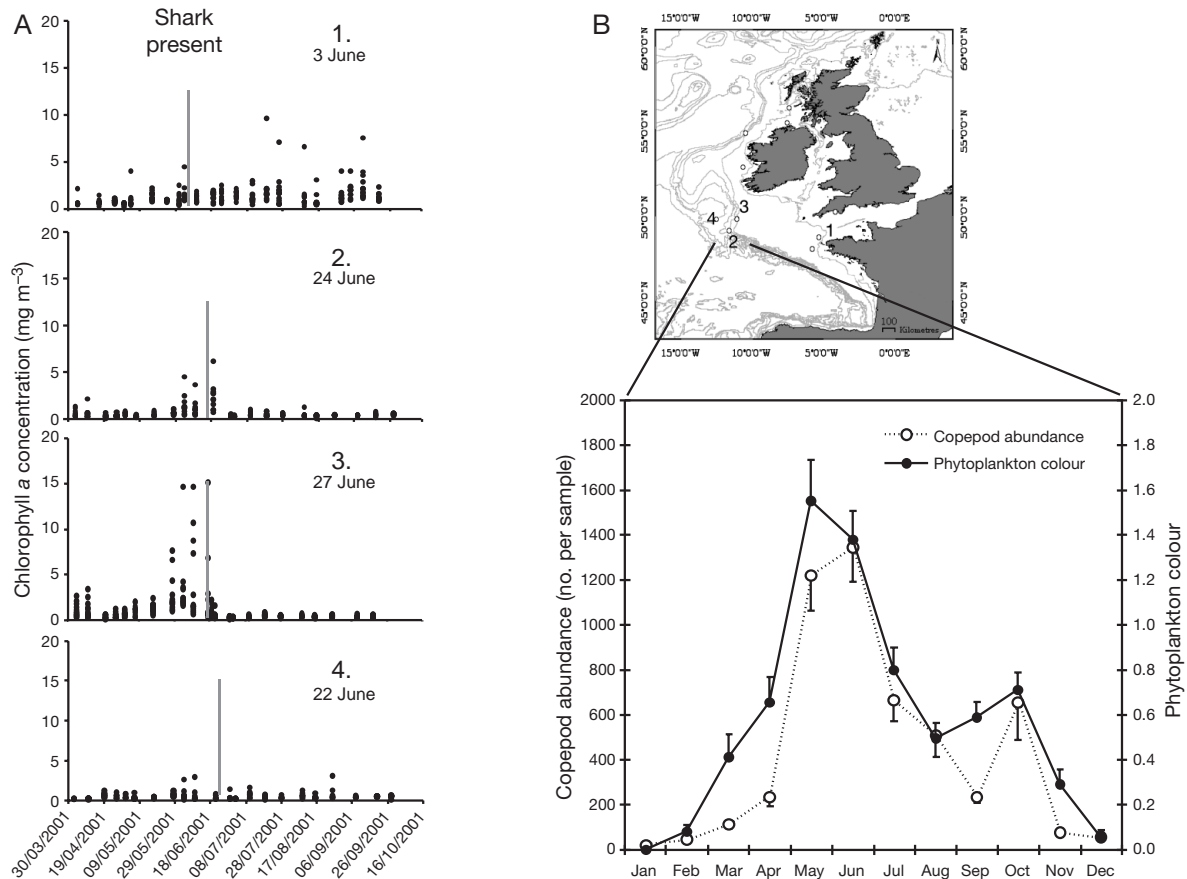
Fig. 4. *Cetorhinus maximus.* Trends in chl *a* pigment concentration at (A) 4 positions occupied by Shark 1 between 3 and 22 June (Panels 1–4) determined from SeaWiFS satellite images. The 6 mo period in each panel extends from 1 April to 30 September 2001. Grey vertical lines denote the time when Shark 1 was present at each location during the 6 mo period. Two high chl *a* values (41 and 67 mg m^{-3}) that occurred immediately prior to the shark's presence at that location were omitted from Panel 3 for clarity. (B) Mean monthly phytoplankton colour and total copepods measured by the CPR survey in the Goban Spur region (shown on inset map) between 1955 and 2000. Numbered locations on inset map (1–4) refer to positions examined for phytoplankton concentrations in Panels 1–4 in (A). Error bars on mean monthly values denote 1 SEM. Arrow denotes time when Shark 1 was present in the Goban Spur region

Movements of Sharks 2 and 5 were similarly broad during winter. Shark 5, a 5.5 m long immature female, remained within the English Channel from summer to winter occupying water of about 17.0°C in October, before moving into the southern North Sea (Fig. 1B). By contrast, from mid-October to mid-November Shark 2 was geolocated on the shelf edge in the Bay of Biscay where it had possibly remained since the summer. It moved through the water column between 10 and 250 m on a regular basis, with some dives to between 350 and 450 m (Fig. 2F). One dive in November extended from the surface to between 750 and 1000 m depth at the mesopelagic–bathypelagic boundary, where the shark stayed for nearly an hour (Fig. 2G). Between 17 November and 7 December this shark moved back into the western English Channel and conducted similar deep-diving behaviour in the Hurd Deep (maximum dive depth: 176 m). At fine time-

scales we also found this shark was active during 6 h time periods on consecutive days in early December, ranging between 50 and 250 m depth. Similarly, in early January 2002, Shark 4 also showed vertical movements on consecutive days ranging from between 0–10 and 50–100 m (Fig. 2L). However, even though basking sharks were active during winter, they generally spent less time near the surface compared to depths preferred in summer months (Fig. 2G,K,L).

DISCUSSION

Over fine- to meso-horizontal scales (m to 10s km) in the western English Channel, basking sharks exhibit selective foraging behaviour in the richest zooplankton patches, and move between patches along tidal fronts over periods of 1 to 2 d (Sims & Quayle 1998). How-

ever, nothing is known of broad-scale seasonal movements in response to production associated with large-scale oceanographic features.

The seasonal movements of basking sharks in this study were generally over long distances, but routes were exclusively associated with the continental shelf. Extended movements into open-ocean regions away from north-east Atlantic shelf and shelf-edge waters were not observed. A unifying feature of the movements, however, was that they resulted in the occupation of habitats with enhanced productivity in both inshore (English Channel and Clyde Sea) and offshore shelf-edge areas (Pingree et al. 1975, Adams 1986, Le Fevre 1986). The continental shelf-edge area where Sharks 1 and 2 spent between 1 and 4 mo respectively, is a frontal region of high relative phyto- and zooplankton abundance (Le Fevre 1986). We found that Shark 1 travelled west for about 500 km to the shelf-edge, and located and remained within a productivity 'hotspot' for about 1 wk. Whilst we do not know whether this individual was actively feeding, it seems likely this movement was related to foraging given that basking sharks are known to feed from at least May until August (Sims & Merrett 1997, Sims et al. 1997). Our study suggests that as well as foraging within and between prey patches over fine- to meso-scales (Sims & Quayle 1998), basking sharks probably locate and remain within temporally discrete productivity 'hotspots' occurring seasonally along large-scale frontal features at much greater spatial scales (100s to 1000s of km). The physiological and behavioural mechanisms used by this species to orientate to distant locations is unknown, but could involve active orientation to geophysical directional clues, such as the earth's magnetic field (Metcalfe et al. 1993), or thermoreception (Sand 1938, Crawshaw & Hammel 1973) of sharp changes in water temperature that is characteristic of frontal systems.

The consistent pattern of vertical movements of basking sharks through the water column in both shelf and shelf-edge habitat probably represents prey-searching behaviour. Short-term trackings of whale sharks *Rhincodon typus* showed frequent dives from the surface to near bottom (50 to 80 m) and back again when foraging along a reef edge (Gunn et al. 1999). Hence, dives by this plankton-feeding shark as well as in basking sharks may function in the location of discrete layers of prey (Josse et al. 1998) and possibly olfactory trails (Carey & Scharold 1990). Olfactory and gustatory stimuli useful for locating food or identifying particular water masses will be distributed more extensively in the horizontal plane than vertically, due to current shear between horizontal water layers of differing density (Carey & Scharold 1990, Klimley et al. 2002). Thus, deep diving probably facilitates sampling

of a large number of water-mass layers for chemical clues over a short time period. Frequent deep dives have also been documented for pelagic predatory sharks (e.g. blue and great white sharks) (Carey & Scharold 1990, Boustany et al. 2002), and teleosts such as blue marlin and bluefin tuna (Block et al. 1992, 2001), indicating this behaviour is probably a ubiquitous search strategy for both epipelagic planktivores and macropredators.

However, basking sharks in the Clyde Sea and in shelf-edge habitat also spent more time during the day at deep depths compared to nighttime when they were generally within 10 to 50 m of the surface. This diel change in preferred depth of basking sharks is consistent with a response to diel vertically migrating zooplankton, which also occupy deeper depth strata during the day before rising to near the surface at night (e.g. Hays et al. 1995). Basking sharks, therefore, probably prospect for zooplankton by utilising deep dives irregularly, but also show predictable vertical movements presumably when feeding in thick swarms of diel migrating zooplankton.

The basking sharks tracked in this study utilised a very broad vertical habitat (0 to 750–1000 m depth), extending from the surface across both epipelagic and mesopelagic zones over a time scale of hours. Together with their long-distance movements, this indicates that survival on patchily distributed zooplankton by large-bodied animals requires both extensive horizontal and vertical movements. Broad-scale movements of baleen whales also reflect this apparent necessity, but maximum dive depths recorded for these species range from 170 to 470 m (Schreer & Kovacs 1997, Panigada et al. 1999). Therefore, by diving deeper and without the need to surface for air, basking sharks may gain a significant advantage over mammalian competitors (notably mysticete whales) by exploiting deep-water zooplankton communities beyond their range. This suggests a revised niche for basking sharks, and perhaps other plankton-feeding elasmobranchs (e.g. whale sharks, mobulid rays), as fish capable of exploiting resources throughout the epipelagic and mesopelagic realms.

It was hypothesised about 50 yr ago that basking sharks hibernate during winter in deep water off the continental slope (Parker & Boeseman 1954, Matthews 1962). We showed from PAT tag release locations in December and January that basking sharks were located in continental shelf areas, often close to the coast. Their horizontal habitat selection in summer, autumn and winter was broadly similar. Furthermore, they exhibited diving activity and long-range movements during winter indicating they do not remain motionless on the seabed to conserve energy when seasonal zooplankton levels decline, as suggested in previous studies (Parker & Boeseman 1954, Matthews

1962). Taken together, our data show that basking sharks do not hibernate. Instead, we show that the continental shelf and shelf edges are winter habitats for this species in the northeast Atlantic. Basking sharks have also been caught in trawls during winter off shelf edges in New Zealand (Francis & Duffy 2002), indicating that this habitat type may be globally important for this species. Although we can now reject the long-standing 'hibernation' theory as an explanation of the seasonal disappearance of basking sharks, we did find that they spent less time near the surface during winter than in summer. This seasonal decrease in basking behaviour means they are much less likely to be observed, which probably explains why for so long this species was thought to disappear into the depths during cold months.

The basking sharks in this study did not undertake prolonged movements into open-ocean regions away from productive shelf areas, which, coupled with evidence that approximately half the number of winter-caught specimens do not shed gill rakers (Parker & Boeseman 1954), suggests some individuals probably feed in winter. The winter diving activity, as during summer, may serve to locate discrete layers of zooplankton prey. Energy-rich calanoid copepods such as *Calanus finmarchicus* and *C. helgolandicus*, the predominant prey of basking sharks, over-winter in shelf and shelf-edge deep water (100 to 2200 m) (Hirche 1983, Williams & Conway 1984, Heath et al. 2000) and so may be the targets of the very deep dives we measured. Non-migrating, deep-water copepods such as *Euchaeta* spp. (Mauchline 1995) could also be utilised by basking sharks at these depths.

Furthermore, it seems unlikely that basking sharks form local populations as was previously thought (Parker & Stott 1965), because we found that sharks from the English Channel move to Scottish waters and vice versa over relatively short time periods (1 to 2 mo). Nevertheless, that fact that 1 basking shark tagged off Plymouth returned to the English Channel in winter, after spending most of the intervening time at the Bay of Biscay shelf edge, suggests some individuals may exhibit philopatry. This emphasises the importance of tidal and shelf-break frontal zones as foraging and over-wintering habitat for individual *Cetorhinus maximus* over annual cycles. In the northeast Atlantic this species is listed as endangered in the IUCN Red List of Threatened Species (Hilton-Taylor 2000). Current concerns about its conservation status as a result of suspected over-exploitation has led to statutory protection within UK territorial waters (up to 19 km from shore). Basking sharks in this study spent the majority of time outside the UK protected area, implying that if directed fisheries intensify in the future, this statutory measure will be ineffective.

A 5.5 m long female shark in this study, which was probably sexually immature (Matthews 1950), moved into the southern North Sea during winter. Basking sharks are known from this area in winter, although mature individuals have not been recorded (Van Diense & Adriani 1953, Parker & Boeseman 1954). Further tagging studies should focus on the movements of juveniles and sub-adults, because they may occupy areas where fishing activity is intense, increasing the likelihood of incidental capture in gear.

Finally, in free-ranging marine-animal behaviour studies, the abundance and availability of prey is rarely, if ever, assessed over the same spatial scales as predator movements (e.g. Weimerskirch et al. 1994). Hence, virtually nothing is known about search strategies and prey selection in relation to prey availability for highly mobile marine animals in the wild. In this study we related archival tracking of a basking shark to both remote-sensing images of ocean colour and CPR data. Although requiring further development, the initial results presented here identify the basking shark as a potential model species for testing hypotheses on free-ranging foraging strategies of a planktivorous fish over various spatio-temporal scales.

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