

Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation

Nuno Queiroz^{1,2}, Nicolas E. Humphries^{1,4}, Leslie R. Noble³, António M. Santos², David W. Sims^{1,5,6*}

1 Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, United Kingdom, **2** CIBIO – U.P., Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, Rua Padre Armando Quintas, Vairão, Portugal, **3** School of Biological Sciences, University of Aberdeen, Aberdeen, United Kingdom, **4** School of Marine Science and Engineering, Marine Institute, University of Plymouth, Plymouth, United Kingdom, **5** Ocean and Earth Science, National Oceanography Centre, University of Southampton, Waterfront Campus, Southampton, United Kingdom, **6** Centre for Biological Sciences, University of Southampton, Highfield Campus, Southampton, United Kingdom

Abstract

Dramatic population declines among species of pelagic shark as a result of overfishing have been reported, with some species now at a fraction of their historical biomass. Advanced telemetry techniques enable tracking of spatial dynamics and behaviour, providing fundamental information on habitat preferences of threatened species to aid conservation. We tracked movements of the highest pelagic fisheries by-catch species, the blue shark *Prionace glauca*, in the North-east Atlantic using pop-off satellite-linked archival tags to determine the degree of space use linked to habitat and to examine vertical niche. Overall, blue sharks moved south-west of tagging sites (English Channel; southern Portugal), exhibiting pronounced site fidelity correlated with localized productive frontal areas, with estimated space-use patterns being significantly different from that of random walks. Tracked female sharks displayed behavioural variability in diel depth preferences, both within and between individuals. Diel depth use ranged from normal DVM (nDVM; dawn descent, dusk ascent), to reverse DVM (rDVM; dawn ascent, dusk descent), to behavioural patterns where no diel differences were apparent. Results showed that blue sharks occupy some of the most productive marine zones for extended periods and structure diel activity patterns across multiple spatio-temporal scales in response to particular habitat types. In so doing, sharks occupied an extraordinarily broad vertical depth range for their size (1.0–2.0 m fork length), from the surface into the bathypelagic realm (max. dive depth, 1160 m). The space-use patterns of blue sharks indicated they spend much of the time in areas where pelagic longlining activities are often highest, and in depth zones where these fisheries particularly target other species, which could account for the rapid declines recently reported for blue sharks in many parts of the world's oceans. Our results provide habitat targets for blue shark conservation that may also be relevant to other pelagic species.

Citation: Queiroz N, Humphries NE, Noble LR, Santos AM, Sims DW (2012) Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation. PLoS ONE 7(2): e32374. doi:10.1371/journal.pone.0032374

Editor: Yan Robert-Coudert, Institut Pluridisciplinaire Hubert Curien, France

Received: August 31, 2011; **Accepted:** January 28, 2012; **Published:** February 29, 2012

Copyright: © 2012 Queiroz et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: Funding was received from the Save Our Seas Foundation (www.saveourseas.org), Fundação para a Ciência e a Tecnologia (FCT) Grant PTDC/MAR/100345/2008 and Scholarship SFRH/BPD/70070/2010 (www.fct.pt), and the UK Natural Environment Research Council (NERC) Oceans 2025 Strategic Research Programme (Theme 6, Science for Sustainable Marine Resources) (www.oceans2025.org) through grant awards to DWS and NQ. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: dws@mba.ac.uk

Introduction

Information on movements and behaviour is an often overlooked, but nevertheless crucial part of assessing population trends of mobile animals since at specific locations movement greatly influences temporal changes in population density [1]. However, for many exploited marine animals such as large fishes, accurate fisheries-independent population assessments of space use are still lacking, hampering effective conservation and management efforts. Understanding patterns of habitat use, both horizontal and vertical, in marine predators with regards to physical features of the environment is important because they influence predators' movements and distribution to a large degree [2], and aid our prediction of animal behaviour in the face of changing environmental conditions [3]. Moreover, such information is valuable for management purposes, especially in species

that are at risk from expanding fisheries [4,5]. In the North Atlantic alone, many pelagic species which undergo long-distance movements or migrations are vulnerable to large-scale fishing pressure, either from directed or incidental captures [5,6,7]. In particular, the estimated abundance of oceanic sharks has declined by between 21 and 99% in recent years when compared with estimates preceding extensive exploitation [8,9]. Commonly reported as the most frequently caught shark species [e.g. 10,11], the blue shark *Prionace glauca* is no exception, with estimated declines in some regions of 60–80% since the 1980s and 1990s [6,12].

Longline surveys and mark-recapture studies in the Atlantic have provided considerable information on the distribution and extensive movements of pelagic sharks, and for blue sharks in particular [13]. These studies naturally fail, however, to provide a detailed understanding of how pelagic sharks respond to

dynamic changes in ocean habitat type. Previous studies on plankton-feeding pelagic sharks have quantified the importance of productive areas such as oceanographic fronts (boundaries between different water mass types) for foraging opportunities [14,15,16] or by highlighting the behavioural tactics such species use when faced with habitat changes [17]. A similar understanding for horizontal movements of predatory pelagic sharks, that are often highly migratory and that can move long distances over relatively short time periods, is not so well established. In the Pacific Ocean there is quantitative evidence for area-restricted movements by predatory sharks [18,19] characteristic of foraging occurring in productive regions, and it is reasonably well documented in tunas [3,20]. However, no comparable studies on predatory pelagic sharks have been undertaken in the Atlantic Ocean, where longline fishing pressure is up to eight-fold higher (Fig. S1). In this context, it is important to determine association rates of Atlantic sharks with strong environmental gradients (e.g. sea surface temperature, SST) that are often targets for intensive fishing activities [21,22].

Understanding the patterns of vertical movement in relation to environmental variations will identify the locations and depths occupied by sharks, underpinning much-needed assessments of overlap with depth ranges targeted by longline fisheries in the region. Vertical movements, in particular diel depth changes, have been recorded in diverse marine species, from zooplankton to large vertebrates [e.g. 17,23,24]. Diel vertical migration (DVM) in a wide range of zooplankton species is thought to be a trade-off between reduced predation risk with increasing depth, and improved feeding opportunities in prey-rich surface waters [23,25,26]. It is generally accepted that relative changes in light intensity are also a principal driver of diel migrations [27]. Hence, so-called normal DVM is often characterised by an ascent into shallow water at sunset followed by a descent at sunrise to greater depths (dusk – ascent; dawn – descent). In addition, diel migration patterns may be regulated by physical oceanographic structures (stratification, eddies) and by the depth of the chlorophyll maximum layer [28]. Similar changes in the timing of vertical migration have been observed in larger invertebrates [e.g. jellyfish, squid; 29,30] and also small fish [31]. Therefore, it is not surprising that large predators, such as sharks and tunas, modify their diving behaviour in response to diel migrating prey. As a result, diel patterns of activity in apex predators have frequently been linked to foraging or search behaviour [32,33]. In these studies pelagic fish displayed consistent diel patterns of vertical movement at different temporal scales, geographic regions and across life-history stages (i.e. juveniles, adults), frequently with increased diving activity rhythms at specific periods of the day. Additional theories to explain diel changes in behaviour have also been proposed. For example, diel depth changes in a demersal shark have been linked to increased bioenergetic efficiency, whereby sharks hunt in warm surface waters at night and rest in cooler waters during the day [34]. It has also been shown that fish may alter diving behaviour in an attempt to minimise predation risk [35].

In this study, pop-off satellite-linked archival transmitter (PSAT) tags were deployed on blue sharks at two different latitudes with varying oceanographic features, including frontal zones, to determine patterns of space use and their linkage with physical characteristics of the environment. We also examined diel vertical behaviour in relation to oceanographic features to investigate whether behavioural patterns were related to temperature (thermal structure) or probable prey movements.

Methods

Study species

The blue shark is a wide-ranging shark occurring in all tropical and temperate seas. Distribution of the Atlantic population is complex with spatial and temporal segregation by sex and age, in addition to short and longer range seasonal and annual migrations, including trans-Atlantic and trans-equatorial movements [36]. In the eastern Atlantic adult females are found around the Canary Islands and North Africa in winter, many of which are pregnant [36]. Adult males are found further north, mainly off Portugal, along with juveniles and sub-adult females, the latter group undertaking a summer migration into the western English Channel and Irish waters [37,38]. Adult males and juveniles are also found in offshore regions, particularly off the Azores [39]. Mark-recapture studies have, however, also shown apparent long-term site fidelity to specific, relatively localised regions by some components of the population [40], although such studies are largely influenced by the spatial and temporal distribution of fishing effort, and likely reflect the movement of the fishing vessels rather than describing actual movement or residence patterns of blue sharks [41].

Shark tagging

Blue sharks were captured using rod and line and brought onboard for body-length measurement and tagging. Fishing took place between July 2006 and June 2008 in two areas: the English Channel off south-west England and off southern Portugal (Fig. 1A). A total of 16 blue sharks were tagged with PSAT tags in these two sites. Shark 1 was tagged with a Mark 4 PSAT tag (PAT4, Wildlife Computers, WA, USA), which records depth (maximum: 1000 m; accuracy: 0.5 m), water temperature (range: -40 to 60°C ; accuracy: 0.05°C) and light level (at 550 nm wavelength) and relays data via an Argos-certified satellite transmitter. The tag was programmed to sample each parameter every 10 s and detach after 30 days. The remaining sharks (#2–16) were tagged with Mk10 PSAT tags (Wildlife Computers). Parameters were sampled throughout the deployment at varying intervals (from 1 to 10 s) and stored as summary data over set intervals of 4 or 6 h. For each integration interval, PSAT tags relayed information on the minimum and maximum depth obtained and selected temperatures across this range so that temperature/depth profiles could be generated. Tags were programmed to detach after 60, 90, 120 or 180 days after tagging. In 2006/2007, PSATs were attached via a 20-cm long monofilament tether (250 lb test) connected to a 5 cm long stainless steel T-bar arrowhead; in 2008 tags were rigged with a 15-cm monofilament tether and an 'umbrella' type nylon dart. All tags were inserted into the dorsal musculature at a 45° angle to a maximum depth of 10 cm.

Horizontal movements and space-use

The movement of each shark was estimated using either satellite relayed data from each tag or from archival data after the tags were physically recovered. Positions of each shark between attachment and tag pop-up were reconstructed using software provided by the manufacturer (WC-GPE, global position estimator program suite), where daily maximal rate-of-change in light intensity is used to estimate local time of midnight or midday for longitude calculations, and day-length estimation for determining latitude. Anomalous longitude estimates resulting from dive-induced shifts in the estimated timings of dawn and dusk from light curves were discarded from the dataset. Geolocations $>3^{\circ}$ of longitude from the previous longitude estimate were also removed

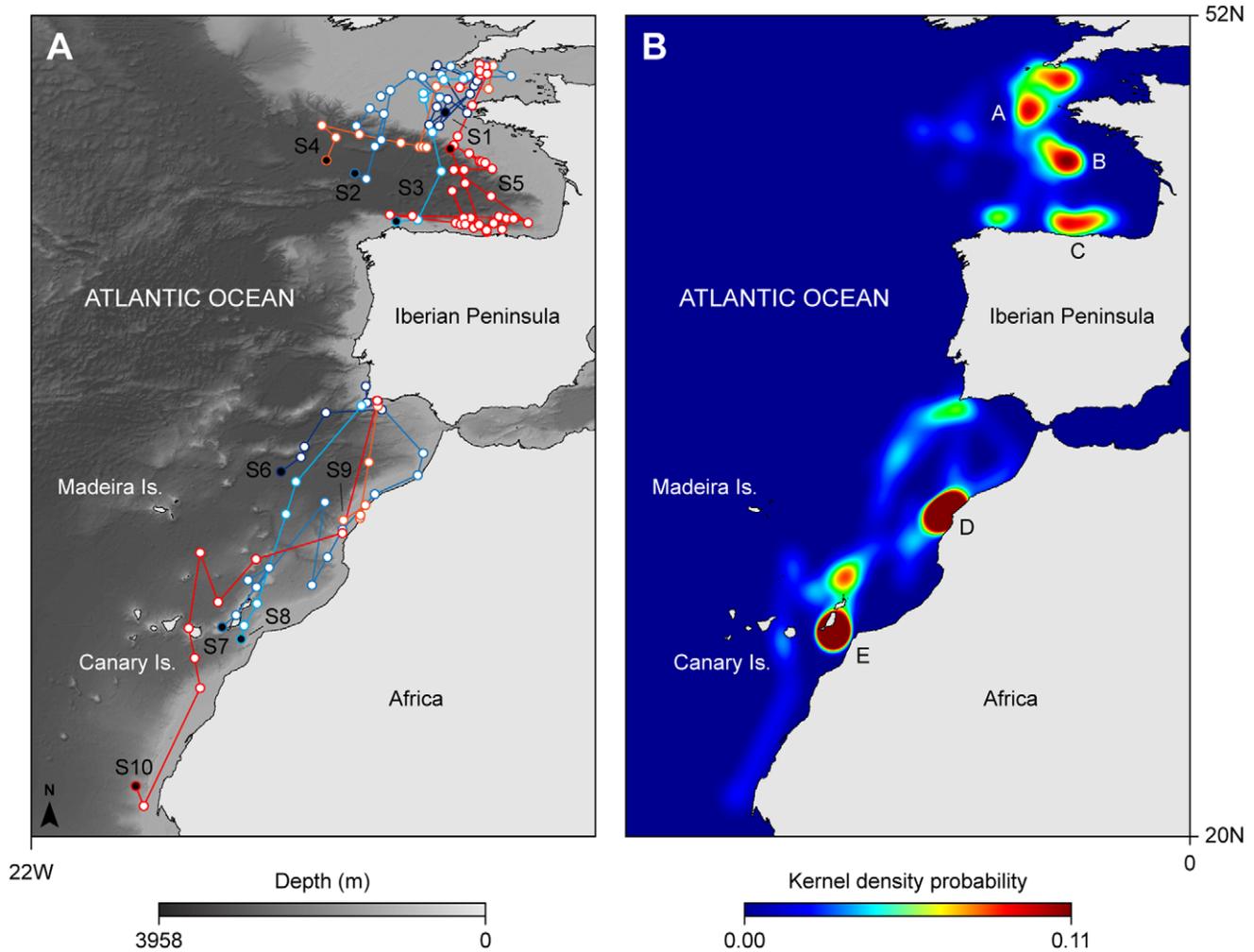


Figure 1. Movement and high space use areas occupied by PSAT-tagged blue sharks. (A) General movement patterns overlaid on bathymetry; black circles denote pop-up locations and white circles the geolocated positions. (B) Kernel density plot showing five major areas of prolonged residency labelled A–E.
doi:10.1371/journal.pone.0032374.g001

[16]. Latitude along the longitude was then corrected by matching minimum and maximum tag-recorded water temperatures from the shallowest bin recorded in each period to sea surface temperature (SST) values on night-time, 8-day composite, moderate-resolution, imaging spectroradiometer (MODIS) remote-sensing images. The most parsimonious location was derived by matching individual pixel SSTs within a variable-sized circular area (radius 100–500 km) around the previous tag position. If no matches were obtained within the smaller area, the radius was increased until matches occurred. Variable-sized areas were used because geolocations at constant intervals were not always determined due to gaps in the data. A geographic mean position was calculated from all possible pixel locations within this area to derive each shark position. Maximum dive depth was compared with seabed depths from a digital bathymetry map (general bathymetric chart of the oceans GEBCO 30" dataset) within each area to filter anomalous positions where the dive depth was greater than seabed depth. Using the ArcGIS geographical information system (ESRI Inc., CA, USA), intermediate waypoints were applied to track steps where trajectories between located positions crossed land. The final estimated positions were then analysed point-to-point with a 1 m s^{-1} swim speed filter, which is the

maximum over-the-ground swimming speed measured for blue sharks [42] and is consistent with swimming speeds of other pelagic sharks. A position separated from an adjacent position by a distance too great to achieve in the speed-filter-imposed time between those points was shifted to a location along the track where the forced speed limit provided an acceptable distance. Previous studies using this general method estimated the mean error distance of light/SST geolocation compared to tagging or pop-up locations to be $75.5 \text{ km} \pm 54.5 \text{ S.D.}$ (range: 36.9–183.9 km) [16] and $78.0 \text{ km} \pm 21.4 \text{ S.D.}$ (range: 54.7–100.0 km) [43].

Shark tracks were initially partitioned into 1 h data points; the interpolated points were then plotted against a $0.5 \times 0.5^\circ$ grid in ArcGIS. Total time spent in each grid cell was calculated by summing the number of hourly points located within them (Fig. S2A). To test if the observed movement patterns (and in particular the aggregations at some cells) were different from simple random movement, a Brownian normal diffusion random-walk model was used. For each simulation, 10 particles (model sharks) were started from points corresponding to the actual tagging positions of blue sharks (five were released off southwest England and five off southern Portugal). The movement path of each particle comprised a sequence of discrete steps and turning angles, with

the former limited by the actual number of individual steps recorded for each tracked shark. In each iteration, step length was drawn from a normal distribution with an average and standard deviation estimated from tracked sharks and limited by the minimum and maximum step lengths observed. Angles were derived from a uniform distribution between -180° and $+180^\circ$. After computing a new position, a check was made to ensure that it did not fall within land masses. If so, the position was rejected and a new angle and step length were drawn. At the end of each simulation, a final map with a $0.5 \times 0.5^\circ$ grid was constructed with the total number of hours computed for each grid cell (for examples see Fig. S2B–D). A total of 5000 simulation runs of 10 model sharks were completed. To test whether the observed pattern differed significantly from the random-walk generated patterns, the distribution of the mean/variance ratio of the number of hours per cell was computed using the simulations. The mean/variance proportion was also computed for the observed data and was compared with the distribution computed previously to estimate its p value [44].

Interpolated data points were also used to calculate shark space use by performing a kernel density estimate in ArcGIS [spatial analyst/kernel density]. Since data was not normally distributed (Shapiro-Wilk; $W=0.733$, $p<0.001$), a Spearman Rank correlation was carried out to test whether there was a significant relationship between the estimated space use and enhanced primary production (using mean chlorophyll a concentration as a proxy). Similarly, hourly interpolated vessel monitoring system (VMS) data from surface longliners (tracked between 2006 and 2008 in the summer/autumn period) were used to estimate kernel point density; a Spearman Rank correlation was subsequently performed between the estimated longliner space use patterns (data not normally distributed; Shapiro-Wilk; $W=0.863$, $p<0.001$) and mean chlorophyll a levels.

Vertical movement analysis

A modified version of the split-moving window (SMW) method was employed to detect significant shifts in time-at-depth (TAD) data and, thus, define behavioural phases [3,45]. Briefly, a variable-sized split window ranging from 4 or 6 h to a maximum of 5 days was used to compute dissimilarities between the two halves of the window along the time steps of the vertical track. A multivariate measure of dissimilarity (Euclidean) was computed between every possible pair of samples from different halves and the values of all comparisons were then averaged. The value obtained was assigned to the centre of the window, which then moved one step forward, repeating this process until the window reached the end of the data series. Statistical significance of dissimilarities for each window's midpoint was computed using a randomisation procedure. The result from each window size was then plotted by piling them vertically, resulting in an inverted triangle with the lower vertex pointing to the boundary location whenever a significant shift was detected [3,45]. This modified method has the advantage of not requiring evenly distributed data, which is suitable for satellite-transmitted summary data, given that it often has data gaps due to the limited bandwidth of the Argos satellite relay system. This limits data recovery rates during the data upload period when the tag is at the sea surface and prior to its batteries becoming exhausted (~ 14 days). Data for each behavioural phase was pooled and summarized as diel frequencies of time spent at depth, to distinguish between different patterns of behaviour that could be similar among sharks. T-tests were used to determine whether there were significant day/night differences in maximum depth and were performed at the $p=0.05$ level of significance. To test if the vertical movements of blue sharks were

linked to behavioural thermoregulation, a time-weighted average of the temperature experienced by sharks was calculated for each integration period, and a non-parametric Mann-Whitney U test was performed to determine whether there were significant diel differences in temperature.

Results

A total of six females, with body-lengths varying from 1.30 to 1.99 m (fork length, FL) were tagged off south-west England. An additional 10 sharks, eight females (0.95 to 2.00 m FL) and two males (1.40 and 2.00 m FL), were tagged off southern Portugal. Hence, juvenile, sub-adult and adult sharks were tagged in both locations (Table 1, 2). Overall, three tags failed to uplink to Argos satellites. With one exception (tag deployed on shark 1, S1), all reporting tags detached prematurely between 13 and 105 days. Of these, three reported very little archived data and no geolocations, and as a result, no further analyses were performed. Three tags were physically recovered and full archival datasets were downloaded. All analyses were restricted to data recorded prior to premature release dates. Overall, blue shark movements and behaviour were tracked for a total of 401 days, covering an estimated average distance of 1429.40 ± 807.74 km.

Horizontal movements and space-use

Blue sharks generally moved south-west of the tagging sites, both in the English Channel and off southern Portugal (Fig. 1A). Off south-west England, only S1 remained in a restricted area of the continental shelf for the whole duration of the deployment. The general area occupied by S1 was dominated by seasonally persistent tidal fronts, principally the Ushant front (Fig. 2). Shark 2 (S2) moved west into the Celtic Sea shelf area, before moving south into deeper water. Sharks 3 and 4 (S3, S4) moved south-west along the edges of the highly productive Ushant front into the Bay of Biscay region of the continental shelf edge, prior to moving into deeper water; S3 was geolocated in northern Spanish waters in late August. S5 initially moved south, crossing the frontal region, and arrived at the shelf edge in late August, approximately 10 d after tagging. This shark continued to move southeast along the continental shelf edge for ~ 18 d, and in late September was geolocated off the northern Spanish coast, where it remained until late October. By early November the shark had moved north and was captured by a longline fishing vessel near the shelf edge. Off southern Portugal, shark 6 (S6) made an initial northward movement into the western coast shelf area before moving south-west into deeper water. Shark 8 (S8) also moved in a south-westerly direction into oligotrophic waters (Fig. 2b) and was geolocated near the Canary Islands in late June, remaining in the area for approximately 50 d. Shark 7 (S7) moved southwest along the African coast, also being geolocated near the Canary Islands by mid-November. Sharks 9 and 10 (S9, S10) were tagged on the same day 1 h apart; both sharks displayed an initial southward movement towards the African coast, with S9 remaining in this upwelling region for ~ 40 d, until the tag popped-up in early August. S10 continued to move south, past the Canary Islands, reaching the Western Sahara upwelling system in mid-July (Fig. 1A, Fig. 2).

The estimated space use pattern was statistically different from spatial distributions calculated from random walks ($p<0.05$). The observed high persistence of sharks in some grid cells caused the variance to increase in relation to the average time spent per cell. Shark space use was also correlated with chlorophyll a concentration (Spearman Rank correlation; $r_s=0.24$, $p<0.05$). Hence, excluding tagging areas (where high space use results from tagging

Table 1. Summary data of the 16 blue sharks tagged with pop-off satellite-linked archival transmitters. F – female; M – male; * no geolocation data received; DNR – did not report.

ID	Fork length (cm)	Sex	Location tagged	Tagging date	Programmed release days	Pop-up location	Pop-up date	Days-at-liberty	Minimum distance (Km)	Minimum distance/day (Km)
Shark 1	199	F	England	06 Jul. 06	30	48.24N 05.99W	05 Aug. 06	30	1058	35.27
Shark 2	153	F	England	21 Jul. 06	60	45.86N 09.52W	10 Aug. 06	20	1403	70.15
Shark 3	130	F	England	08 Aug. 06	60	44.00N 07.91W	29 Aug. 06	21	848	40.38
Shark 4	130	F	England	01 Aug. 07	60	46.38N 10.63W	14 Aug. 07	13	907	69.77
Shark 5	150	F	England	21 Aug. 07	90	46.83N 05.80W	02 Nov. 07	70	2789	39.84
Shark 6	95	F	Portugal	10 Oct. 06	60	34.23N 12.40W	30 Oct. 06	20	614	30.70
Shark 7	115	F	Portugal	04 Oct. 07	60	28.18N 14.70W	15 Nov. 07	42	2029	48.31
Shark 8	200	F	Portugal	03 Jun. 08	120	27.71N 13.96W	15 Aug. 08	73	1232	16.88
Shark 9	180	F	Portugal	04 Jun. 08	120	32.35N 09.67W	04 Aug. 08	61	693	11.36
Shark 10	180	F	Portugal	04 Jun. 08	180	21.99N 27.60W	25 Jul. 08	51	2721	53.34
Shark 11*	110	F	Portugal	12 Oct. 06	120	34.64N 07.42W	28 Oct. 06	16	-	-
Shark 12*	200	F	Portugal	06 Jun. 08	180	47.20N 13.38W	03 Dec. 08	±105	-	-
Shark 13*	200	M	Portugal	11 Jun. 08	180	28.80N 21.16W	22 Jan. 08	±12	-	-
Shark 14	162	F	England	08 Aug. 06	120	DNR				
Shark 15	120	F	Portugal	02 Jun. 08	90	DNR				
Shark 16	140	M	Portugal	09 Jun. 08	120	DNR				

doi:10.1371/journal.pone.0032374.t001

Table 2. Summary data for behaviour and environment of tracked female blue sharks.

ID	Fork length (cm)	Life stage	Days-at-liberty	Diel behaviour	Time performed		Water column
					Nr. days	%	
Shark 1	199	Adult	30	Surface oriented	30	100.0	Stratified
Shark 2	153	Sub-adult	20	Surface oriented	20	100.0	Stratified
Shark 3	130	Juvenile	21	Surface oriented	5	23.8	Stratified
				nDVM	16	76.2	Stratified
Shark 4	130	Juvenile	13	rDVM	8	61.5	Isothermal
				nDVM at-depth	3	23.1	Stratified
				nDVM	2	15.4	Stratified
Shark 5	150	Sub-adult	70	rDVM	8	11.4	Isothermal
				nDVM at-depth	22	31.5	Stratified
				nDVM	8	11.4	Frontal
				nDVM at-depth	8	11.4	Stratified
				nDVM	24	34.3	Stratified
Shark 6	95	Juvenile	20	Surface oriented	20	100.0	Stratified
Shark 7	115	Juvenile	42	Irregular	11	26.2	Isothermal
				Surface oriented	31	73.8	Stratified
Shark 8	200	Adult	73	Irregular	73	100.0	Isothermal
Shark 9	180	Adult	61	Surface oriented	20	32.8	Isothermal
				nDVM at-depth	41	67.2	Stratified
Shark 10	180	Adult	51	Irregular	8	15.7	Isothermal
				nDVM	5	9.8	Isothermal
				Irregular	38	74.5	Isothermal

For sharks that shifted between different behaviour types, these are sorted chronologically (top: first; bottom: last).

doi:10.1371/journal.pone.0032374.t002

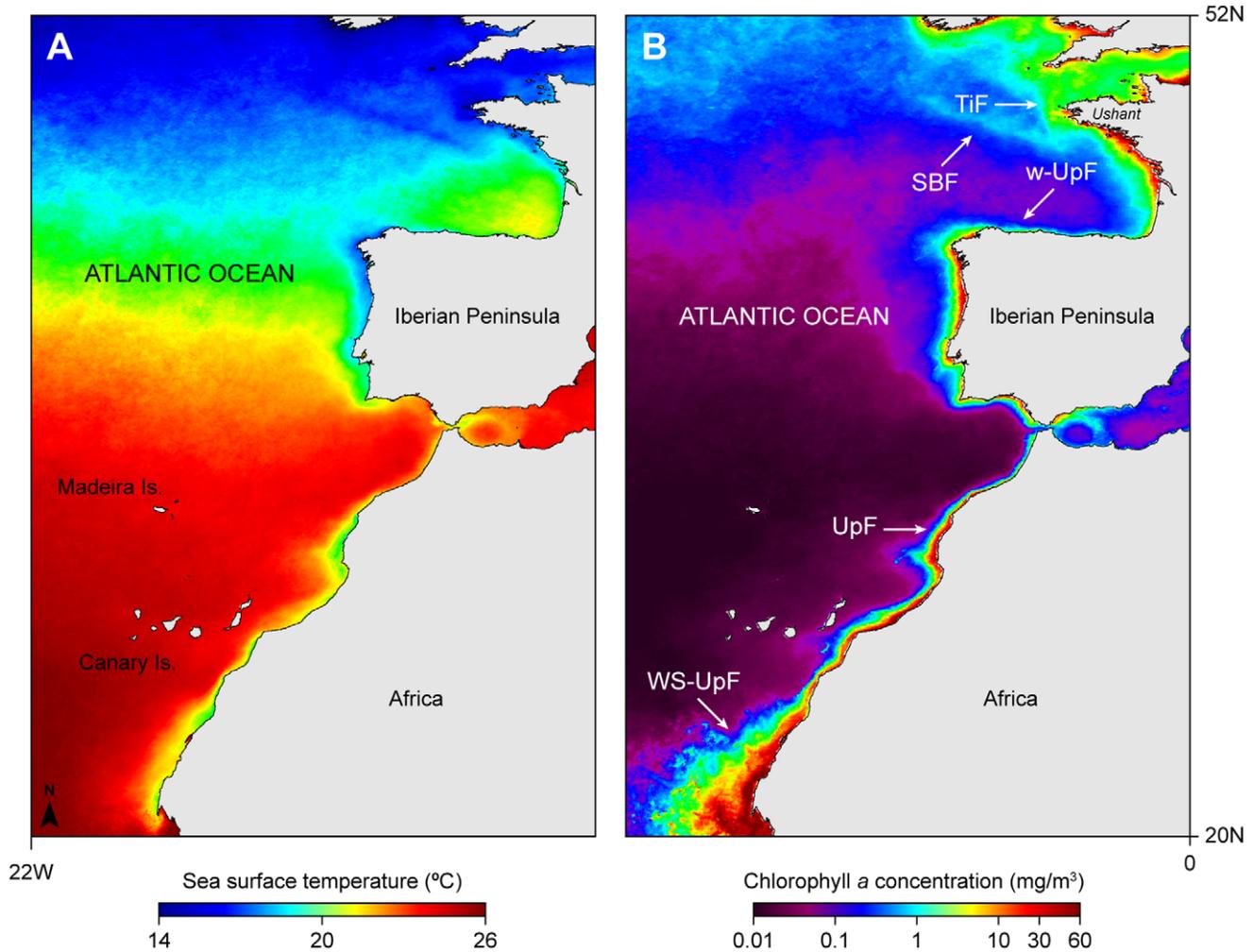


Figure 2. Map of the study area in the North-east Atlantic. Three-year (2006–2008) summer/autumn seasonal average of (A) sea surface temperature and (B) chlorophyll a concentration; TIF, tidal induced front; SBF, shelf-break front; w-UpF, weak upwelling front; UpF, upwelling front; WS-UpF, Western Sahara upwelling front.
doi:10.1371/journal.pone.0032374.g002

activity itself), spatial activity of tracked female blue sharks concentrated in five major areas (A–E; Fig. 1B). These regions are characterised by the presence of thermal front boundaries and associated enhanced primary production (Fig. 2) [46].

Diel vertical movements

Blue sharks demonstrated a wide vertical distribution, inhabiting depths from the surface to a maximum of 1160 m (S10), to our knowledge the deepest dive depth recorded for this species, and spanning water temperatures from 7.2 to 27.2°C. Moreover, all sharks displayed significant variations in diving behaviour, phases of which were detected by the split-moving window procedure [3,45]. Overall, five general behaviour types could be identified, ranging from normal DVM (nDVM) to reverse DVM (rDVM), and including behavioural patterns where no diel differences were apparent.

The first nDVM pattern was characterised by a continued residence at depth during daylight hours, with sharks spending between 70 and 100% of time below the thermocline (~100 m). Night time time-at-depth (TAD) occupation was irregular, but ~50% of the time was spent diving in the mixed layer (Fig. 3A). This behaviour was only observed in stratified, productive

shelf-edge waters of the Bay of Biscay and off western Africa (Table 2). In the second identified nDVM pattern sharks usually spent ~80% of the day near the surface, but consistently performed deeper dives during the day than during the night ($p < 0.05$, $n = 346$). Daytime maximum dive depths averaged 247 ± 14 m (mean \pm SE, $n = 177$), whereas night time maximum dive depths averaged 180 ± 9 m ($n = 169$). Hence, a second favoured depth range below the thermocline was noticeable, where 10–20% of time was spent. This behaviour was often associated with stratified water (Fig. 3B; Table 2) and the night time depth-range was largely restricted to the mixed layer above the thermocline.

When in shallow shelf waters off England, blue sharks tagged in 2007 displayed a reverse diel vertical migration (rDVM) pattern, spending about 60% of time at depth during the night, and over 60% of time in the top 20 m during the day (Fig. 4). Depth-temperature profiles of the water column indicated sharks were diving through generally isothermal, well-mixed water (Fig. 4, right panel).

Surface-oriented behaviour was only observed in stratified water with both day and night time TAD occupation generally restricted to thermocline depths (Fig. 5A). Sharks showed no differences

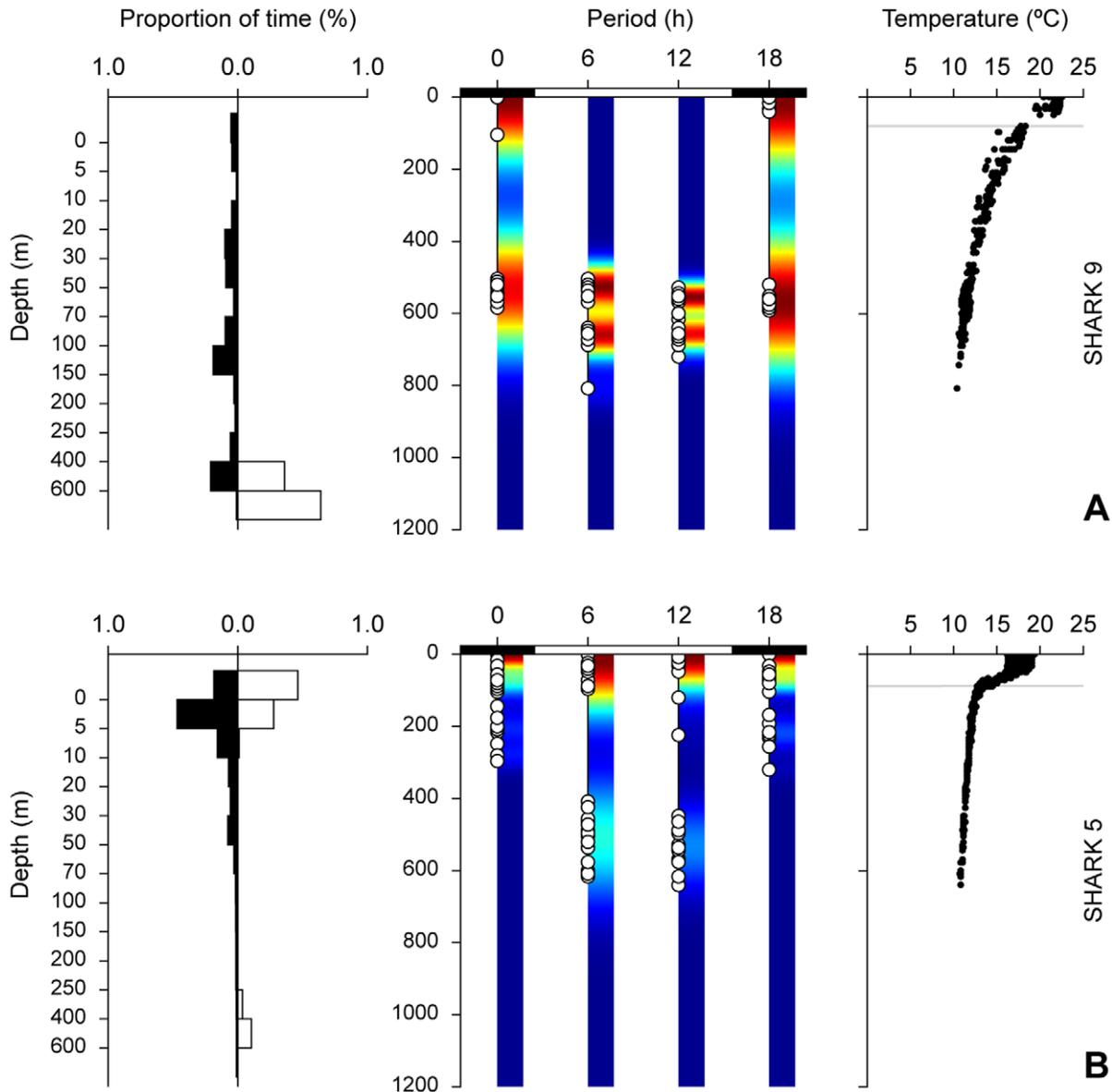


Figure 3. Normal DVM with permanence at depth (A) and normal DVM (B) behaviour plots, from sharks 9 (pooled over 41 days) and 5 (pooled over 24 days), respectively. Left: frequency distributions showing amount of time spent at different depths; black bar denotes essentially night (00:00 and 18:00) and white bar day (06:00 and 12:00). Centre: minimum-maximum depth within each integration interval; white circles represent actual observations; colour represents kernel density estimates for minimum-maximum depth. Right: temperature-at-depth profiles (depth scale is similar to central panel); horizontal grey line represents thermocline depth. Note continued permanence at depth in A. doi:10.1371/journal.pone.0032374.g003

between night and daytime behaviour in either TAD or maximum depth ($p=0.76$, $n=253$), with individual sharks performing occasional deep, fast dives below the thermocline. Finally, blue sharks in oceanic areas also showed apparently irregular diving behaviour with no obvious differences between light-dark cycles in either TAD or diving depth ($p=0.44$, $n=78$), which typically ranged from the surface to ~200–1160 m (Fig. 5B). Irregular diel behaviour was only displayed in isothermal water (Table 2).

Discussion

The results of tagging blue sharks with satellite-linked archival transmitters indicate that female sharks display fidelity to localised high-productivity regions characterised by the presence of thermal

fronts, at least for the time periods over which they were tracked. Blue shark diel behaviour showed extensive variability, both within and between individuals: diving behaviour ranged from patterns where differences in diel vertical migration were observed, to patterns where no day-night differences were apparent. The study also demonstrated that blue sharks are capable of bathypelagic dives to at least 1160 m.

Horizontal movements and space-use

Number-tagged blue sharks in south-western English waters and off Ireland have previously been recaptured in the Bay of Biscay in summer and autumn months [37,38]. Wide-ranging migrations to temperate and warm-water zones have also been described. Although there is no clear seasonal trend in recaptures off West

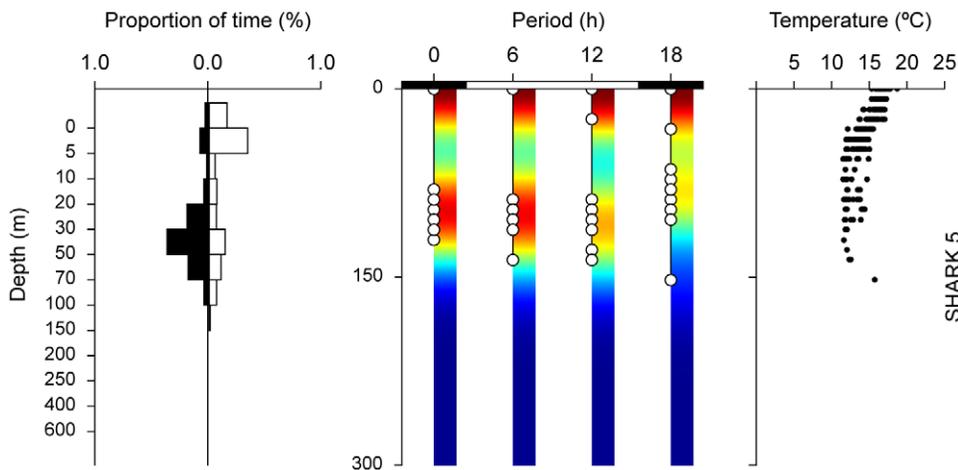


Figure 4. Reverse DVM behaviour plot, from shark 5 (pooled over eight days). Left: frequency distributions showing amount of time spent at different depths; black bar denotes night (00:00 and 18:00) and white bar day (06:00 and 12:00). Centre: minimum-maximum depth within each integration interval; white circles represent actual observations; colour represents kernel density estimates for minimum-maximum depth. Right: temperature-at-depth profiles (depth scale is similar to central panel). doi:10.1371/journal.pone.0032374.g004

Africa, female blue sharks have been recaptured off the Canary Islands (and further south) in winter and spring months [36,37,40]. In this study, blue sharks displayed broad-scale horizontal movements away from the tagging sites, moving across different habitat types, from shelf, shelf-edge and into deep oceanic water. However, movements remaining within spatially restricted areas of the Celtic Shelf, Bay of Biscay and western Africa were significantly different from distributions of model sharks moving according to simple random walks. Blue shark movements were statistically correlated, albeit weakly, with frontal regions. A low correlation between space use and chlorophyll *a* concentration was not unexpected, as there is a spatial and temporal mismatch between shark location and remotely sensed data. The former arises from the limited spatial accuracy of light level geolocation of pop-up satellite tags, whereas the latter derives from the unevenness of remote sensed data (e.g. lack of data as a consequence of cloud cover) which forces pooling at wider temporal scales. Despite these limitations, a general correlation between space use and enhanced productivity areas was present in our tracking data. Our type of study will benefit from the recent development of tags with greater spatial accuracy (e.g. GPS) [47], as well as from advances in remote sensing instrumentation and improvements in interpolation algorithms which have resulted in spatially complete, ultra-high temporal and spatial resolution products.

Frontal zones are typically characterised by high primary and secondary production, where physical processes passively aggregate plankton and therefore generally concentrate higher abundances of prey species [48,49]. Hence, frontal zones represent regions of forage accumulation [50] and higher *in situ* primary growth [51], and are known to influence the movement and distribution of marine predators [52,53]. Prolonged residence in productive 'hotspots' has been described for several species, from birds [54,55], fish [17,20], turtles [56,57] to marine mammals [58]. In a parallel study in the North-eastern Atlantic, blue sharks tagged with near real-time Argos transmitters, also spent more time in rich frontal zones off the Iberian Peninsula, Bay of Biscay and Celtic Shelf (Fig. S3). Likewise, basking (*Cetorhinus maximus*) and porbeagle sharks (*Lamna nasus*) satellite tracked in the same general area, displayed restricted movements and high space-use

of fine to large-scale frontal features [14,15,43]. These findings coupled with our results, suggest predators may orientate to high-productivity frontal areas to find food in more predictable habitat than in other areas. Once abundant prey patches are located, predators may remain in these discrete regions for extended periods of time, as seen for tracked blue sharks in this study, which ultimately leads to their spatial aggregation [14]. As well as spending extended periods of time in one area, tracked blue sharks also moved into oligotrophic waters. Although the reasons for these large-scale movements are unknown, they might be linked with dispersing food resources or associated with search for widely distributed prey [58,59].

Diel vertical movements

Several hypotheses could be proposed to account for differences in the diel behaviour of pelagic sharks, such as foraging, thermoregulation, predator avoidance and/or orientation. However, as there is no empirical evidence for deep dives (generally performed during daytime) playing a role in the navigational abilities or processes of sharks, diel behavioural orientation seems less likely as an explanation. Of the remaining hypotheses, predator avoidance seems equally unlikely, since we would then expect diel patterns to differ between sharks of different sizes, from juveniles to adults [35]: however, such differences were not observed in satellite tracked sharks in this study (Table 2). If behavioural thermoregulation was responsible for the observed diel patterns the vertical movements of tracked sharks should be regularly linked to thermocline depths, with blue sharks occupying on a daily basis water masses with different temperatures [34]. Again, this hypothesis was not supported by our tracking data ($U = 63042.5$, $t = 138395.5$, $P = 0.08$). Moreover, a recent study of blue sharks in the western Atlantic also demonstrated that diving patterns were not consistent with movements associated with behavioural thermoregulation [60]. Instead, our results indicate that blue sharks belonging to varying age groups exhibited similar diel behavioural strategies at different geographical areas, thus supporting the hypothesis that differences in diel behaviour were likely linked to foraging.

In well-stratified off-shelf regions, zooplankton organisms predominantly undertake regular vertical movements, generally

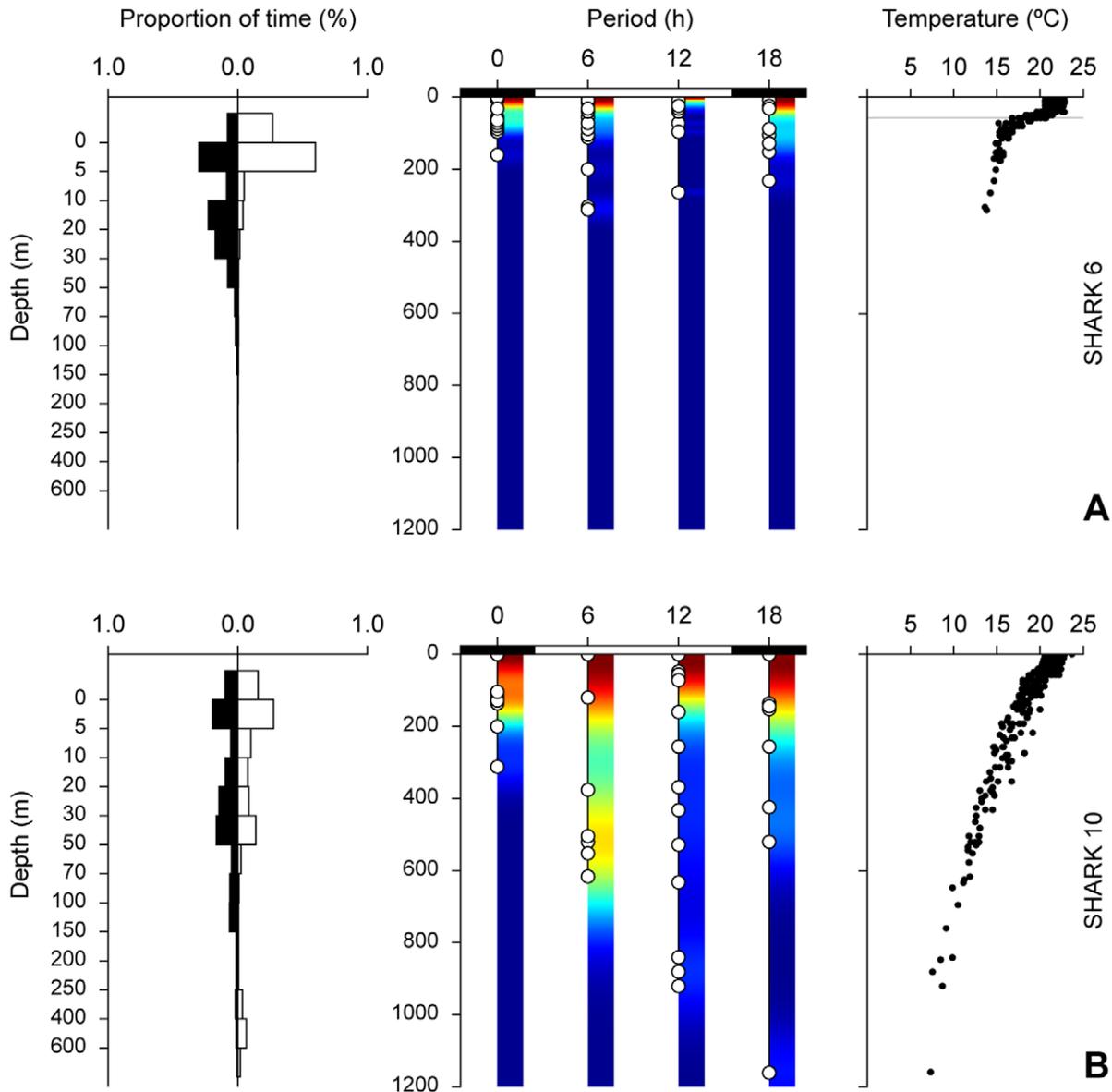


Figure 5. Surface-oriented (A) and irregular (B) diel behaviour plots, from sharks 6 (pooled over 20 days) and 10 (pooled over 38 days), respectively. Left: frequency distributions showing amount of time spent at different depths; black bar denotes essentially night (00:00 and 18:00) and white bar essentially day (06:00 and 12:00) phases. Centre: minimum-maximum depth within each integration interval; white circles represent actual observations; colour represents kernel density estimates for minimum-maximum depth. Right: temperature-at-depth profiles (depth scale is similar to central panel); horizontal grey line represents thermocline depth.
doi:10.1371/journal.pone.0032374.g005

occurring at depth during the day and approaching the surface during the night. Downward migrations of zooplankton occur at sunrise and upwards at sunset and are thought to be an adaptive response to reduce predation risk [23]. Normal DVM diving patterns were commonly observed in blue sharks tracked by us, but there were significant differences in diel diving behaviour. In shelf-break regions blue sharks displayed a continuous residence at depth during the day, while swimming near the surface at night. This pronounced diel migratory pattern is consistent with tracking vertically migrating prey, such as squid, suggesting sharks maximised the time spent within a prey patch (see below). This behaviour has recently been observed for blue sharks in the northwest Atlantic [60], suggesting that residence at depth may be a more common occurrence than previously thought in frontal

systems, such as the Gulf Stream or the Biscay shelf edge. Thus far, such marked nDVM behaviour has only been observed in relatively few large predatory fish, such as bigeye tuna (*Thunnus obesus*) [33], swordfish (*Xiphias gladius*) [61] and bigeye thresher shark (*Alopias superciliosus*) [62].

In this study, blue sharks displaying the second nDVM pattern spent more time near the surface during the day and night, but displayed a distinct normal diel component in maximum depth, repeatedly diving deeper during the day, while night time excursions were frequently limited to thermocline depths. Deep descents below the mixed layer during daylight hours most likely represent foraging dives. Furthermore, the uniformity of dive depth (between 200–400 m) implies prey patches remained in a confined depth layer. The stomach content of blue sharks also

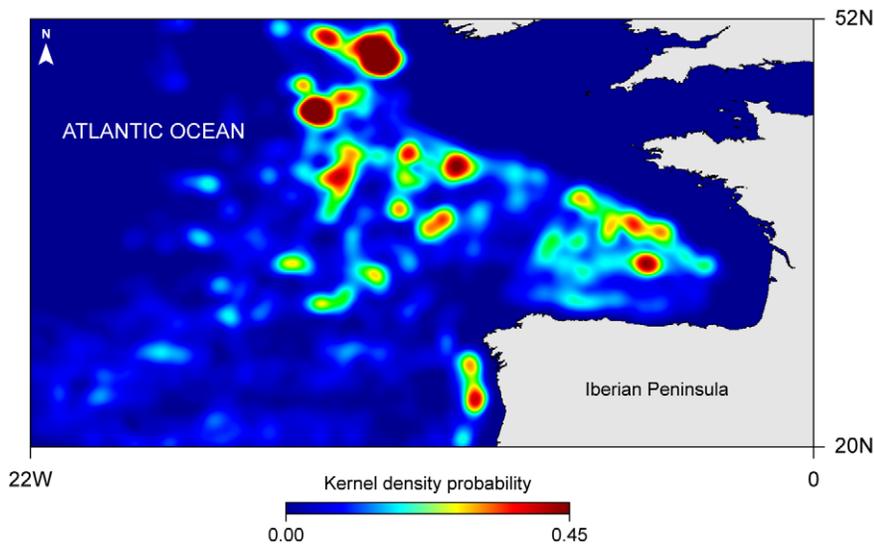


Figure 6. Kernel density estimation plot of 3-year (2006–2008) summer/autumn longline space-use in the northeast Atlantic derived using vessel monitoring system (VMS) data.
doi:10.1371/journal.pone.0032374.g006

suggests foraging at depth, with deep-water squid known to be an important item in the diet of this species in the region where we tracked them [63]. An ongoing study in the North-eastern Atlantic reveals a clear dominance of cephalopod prey items in the stomach contents of longline-caught blue sharks (index of relative importance, IRI, of 94%); deep-water squid species such as *Vampyroteuthis infernalis* and *Mastigoteuthis* sp. were commonly identified (N. Queiroz, unpublished data). This indicates blue sharks may forage on cephalopods at considerable depths.

Over the European continental shelf, blue sharks in well-mixed or weakly stratified water showed a pattern consistent with reverse diel vertical migration (rDVM) behaviour. A similar behavioural pattern has been described for basking and porbeagle sharks tracked over the continental shelf [17,43]. Interestingly, rDVM behaviour was observed in basking sharks foraging in inner-shelf regions characterised by tidal fronts [17]. In the former study, reverse DVM of tracked sharks was linked to zooplankton behaviour and distribution, which aggregated in surface waters during daytime, possibly influencing schooling fish distribution. Hence, a possible reason for the rDVM seen in tagged blue sharks here was tracking of pelagic fish (e.g. mackerel, *Scomber scombrus*), or of the predators of small pelagic fish such as squid.

Billfish and tuna species generally exhibit a marked preference for the mixed layer, rarely crossing the thermocline, e.g. [64,65]. Likewise, blue sharks tracked in this study displayed a similar surface-oriented behavioural pattern in stratified oceanic regions, where no apparent diel differences in diving were observed. Surface-oriented behaviour could indicate near-surface prey patches are dense enough for high encounter rates [2]. Finally, irregular diving seen in tracked blue sharks was probably related, directly or indirectly, to changes in the thermal structure of the water column [45]. Strikingly, this behavioural pattern was observed in S8 and S10 while the sharks were associated with well-mixed waters, typical of the Western Sahara upwelling region [66]. Overall, shifts in the diel behaviour of blue sharks may be related to changes in prey type or density, e.g. low prey levels near the surface may induce foraging at depth [2], although in some circumstances, these behavioural changes may have also been direct responses to the thermal profile of the water column, which can influence the availability of prey resources [17].

Future research in this area would benefit from studies focusing on resolving the movements of predatory sharks, and other large pelagic vertebrates, in relation to the distribution and abundance of their prey species. This would enable more process-based investigations aimed at identifying how and under what conditions sharks search for prey. Furthermore, there is a need for more information about the movements of male sharks, and for both sexes in the winter and spring period so as to build a more complete picture of blue shark population structuring in the eastern north Atlantic [67], which will be important for their conservation and management in the face of high fishing pressure.

Fisheries and behaviour

Blue sharks are commonly caught as bycatch in longlines targeting swordfish and tuna species, e.g. [10]. Pelagic longlines comprise a mainline, which can extend up to 100 km in length, suspended in the water column, with baited hooks on branch-lines attached at evenly spaced intervals. Longlines are generally deployed overnight and hooks set at depths typically ranging from ~100 to 300 m [22,68]. Given that the observed blue sharks night-time habitat was generally restricted to near-surface depths (i.e. surface to ~100 m), there is therefore a spatial and temporal overlap between the longline fishing effort and the vertical niche of blue sharks. Hence, analysis of the recorded tracks suggest the vertical overlap between blue shark night-time occupation in open ocean areas and hook depth, ranges from ~76% to as high as 100%. Strikingly, VMS data of pelagic longliners operating in the northeast Atlantic shows longlining activities significantly concentrate in high productivity areas ($r_s = 0.56$, $p < 0.05$; Fig. 6). Space-use patterns of satellite-linked sharks suggest they spend much of the time in the same type of areas where longline fisheries target commercially important marine fish, which could account for the high levels of by-catch of blue sharks and the rapid declines reported for this species [6,12]. Consequently, high productivity regions may be ideal habitat targets for the implementation of high seas marine protected areas (MPAs), not only for blue sharks, but also for other large pelagic predators.

Supporting Information

Figure S1 Longline yearly averaged effort data by 5×5 degree squares for the North Atlantic (1972–2003) and Pacific (1950–2004); class breaks were determined statistically by finding adjacent feature pairs between which there was a relatively large difference in data value – natural breaks.

(TIF)

Figure S2 Density grid of number of hours spent per 0.5×0.5° unit area for observed (A) and three different simulated particles (B–D).

(TIF)

Figure S3 Movement and high space use areas occupied by smart position-only transmitting (SPOT) tagged blue

sharks. (A) General movement patterns overlaid on bathymetry; black circles denote last transmission locations and white circles geolocated positions. (B) Kernel density plot of 3-year (2006–2008) summer/autumn seasonal average of (C) sea surface temperature and (D) chlorophyll *a* concentration. Note prolonged residence off the Iberian Peninsula wind-driven upwelling region, shelf-break and tidal induced fronts in the Bay of Biscay and Celtic Sea, respectively (Spearman Rank correlation; $r_s = 0.45$, $p < 0.05$).

(TIF)

Author Contributions

Conceived and designed the experiments: DWS NQ. Performed the experiments: NQ DWS. Analyzed the data: NQ NEH DWS. Contributed reagents/materials/analysis tools: LRN AMS. Wrote the paper: NQ DWS.

References

- Turchin P (1998) Quantitative analysis of movement: Measuring and modeling population redistribution in animals and plants. Sunderland, USA: Sinauer Associates.
- Sims DW, Southall EJ, Merrett DA, Sanders J (2003) Effects of zooplankton density and diel period on surface-swimming duration of basking sharks. *Journal of the Marine Biological Association of the United Kingdom* 83: 643–646.
- Humphries NE, Queiroz N, Dyer JRM, Pade NG, Musyl MK, et al. (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature* 465: 1066–1069.
- Lutcavage ME, Brill RW, Skomal GB, Chase BC, Goldstein JL, et al. (2000) Tracking adult North Atlantic bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic using ultrasonic telemetry. *Marine Biology* 137: 347–358.
- Block BA, Teo SLH, Walli A, Boustany AM, Stokesbury MJW, et al. (2005) Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434: 1121–1127.
- Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, et al. (2003) Collapse and conservation of shark populations in the northwest Atlantic. *Science* 299: 389–392.
- Hays GC, Houghton JDR, Myers AE (2004) Pan-Atlantic leatherback turtle movements. *Nature* 429: 522.
- Baum JK, Myers RA (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters* 7: 135–145.
- Ward P, Myers RA (2005) Inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1130–1142.
- Buencuerpo V, Ríos S, Morón J (1998) Pelagic sharks associated with the swordfish, *Xiphias gladius*, fishery in the eastern North Atlantic Ocean and the Strait of Gibraltar. *Fishery Bulletin* 96: 667–685.
- Rogan E, Mackey M (2007) Megafauna bycatch in drift nets for albacore tuna (*Thunnus alalunga*) in the NE Atlantic. *Fisheries Research* 86: 6–14.
- Simpfendorfer CA, Hueter RE, Bergman U, Connett SMH (2002) Results of a fishery-independent survey for pelagic sharks in the western Atlantic, 1977–1994. *Fisheries Research* 55: 175–192.
- Kohler NE, Turner PA (2001) Shark tagging: a review of conventional methods and studies. *Environmental Biology of Fishes* 60: 191–223.
- Sims DW, Quayle VA (1998) Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* 393: 460–464.
- Sims DW, Southall EJ, Richardson AJ, Reid PC, Metcalfe JD (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Mar Ecol Prog Ser* 248: 187–196.
- Sims DW, Witt MJ, Richardson AJ, Southall EJ, Metcalfe JD (2006) Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proceedings of the Royal Society B: Biological Sciences* 273: 1195–1201.
- Sims DW, Southall EJ, Tarling GA, Metcalfe JD (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology* 74: 755–761.
- Weng KC, Castilho PC, Morrissette JM, Landeira-Fernandez AM, Holts DB, et al. (2005) Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* 310: 104–106.
- Weng KC, Foley DG, Ganong JE, Perle C, Shillinger GL, et al. (2008) Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Marine Ecology Progress Series* 372: 253–264.
- Walli A, Teo SLH, Boustany A, Farwell CJ, Williams T, et al. (2009) Seasonal movements, aggregations and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. *PLoS One* 4: e6151.
- Podestá G, Browder JA, Hoey JJ (1993) Exploring the association between swordfish catch rates and thermal fronts on U.S. longline grounds in the western North Atlantic. *Continental Shelf Research* 13: 253–277.
- Ward P, Myers RA (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology* 86: 835–847.
- Hays GC (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503: 163–170.
- Baird RW, Webster DL, Schorr GS, McSweeney DJ, Barlow J (2008) Diel variation in beaked whale diving behaviour. *Marine Mammal Science* 24: 630–642.
- De Robertis A (2002) Size-dependent visual predation risk and the timing of vertical migration: an optimization model. *Limnology and Oceanography* 47: 925–933.
- Dupont N, Klevjer TA, Kaartvedt S, Aksnes DL (2009) Diel vertical migration of the deep-water jellyfish *Periphylla periphylla* simulated as individual responses to absolute light intensity. *Limnology and Oceanography* 54: 1765–1775.
- Ringelberg J (1995) Changes in light intensity and diel vertical migration: a comparison of marine and freshwater environments. *Journal of the Marine Biological Association of the United Kingdom* 75: 15–25.
- Labat J-P, Gasparini S, Mousseau L, Prieur L, Boutoué M, et al. (2009) Mesoscale distribution of zooplankton biomass in the northeast Atlantic Ocean determined with an optical plankton counter: relationships with environmental structures. *Deep-Sea Research I* 56: 1742–1756.
- Markaida U, Rosenthal JJC, Gilly WF (2005) Tagging studies on the jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico. *Fishery Bulletin* 103: 219–226.
- Kaartvedt S, Klevjer TA (2007) Diel vertical migration of individual jellyfish (*Periphylla periphylla*). *Limnology and Oceanography* 52: 975–983.
- Neat FC, Wright PJ, Zuur AF, Gibb IM, Gibb FM, et al. (2005) Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). *Marine Biology* 148: 643–654.
- West GJ, Stevens JD (2001) Archival tagging of school shark, *Galeorhinus galeus*, in Australia: initial results. *Environmental Biology of Fishes* 60: 283–298.
- Schaefer KM, Fuller DW, Block BA (2009) Vertical movements and habitat utilization of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), and bigeye (*Thunnus obesus*) tunas in the equatorial eastern Pacific Ocean, ascertained through archival tag data. *Tagging and Tracking of Marine Animals with Electronic Devices* 9: 121–144.
- Sims DW, Wearmouth VJ, Southall EJ, Hill JM, Moore P, et al. (2006) Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology* 75: 176–190.
- Scheuerell MD, Schindler DE (2003) Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. *Ecology* 84: 1713–1720.
- Stevens JD (1990) Further results from a tagging study of pelagic sharks in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 70: 707–720.
- Stevens JD (1976) First results of shark tagging in the north-east Atlantic, 1972–1975. *Journal of the Marine Biological Association of the United Kingdom* 56: 929–937.
- Fitzmaurice P, Green P, Keirse G, Kenny M, Clarke M (2005) Stock discrimination of the blue shark, based on Irish tagging data. *Collective Volume of Scientific Papers, International Commission for the Conservation of Atlantic Tuna* 58: 1171–1178.
- Litvinov FF (2006) On the role of dense aggregations of males and juveniles in the functional structure of the range of the blue shark *Prionace glauca*. *Journal of Ichthyology* 46: 613–624.
- Queiroz N, Lima FP, Maia A, Ribeiro PA, Correia JPS, et al. (2005) Movements of blue shark, *Prionace glauca*, in the north-east Atlantic based on mark-recapture data. *Journal of the Marine Biological Association of the United Kingdom* 85: 1107–1112.

41. Bolle L, Hunter E, Rijnsdorp A, Pastoors M, Metcalfe J, et al. (2005) Do tagging experiments tell the truth? Using electronic tags to evaluate conventional tagging data. *ICES Journal of Marine Science* 62: 236–246.
42. Carey FG, Scharold JV (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology* 106: 329–342.
43. Pade NG, Queiroz N, Humphries NE, Witt MJ, Jones CS, et al. (2009) First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: Area fidelity, wider-scale movements and plasticity in diel depth changes. *Journal of Experimental Marine Biology and Ecology* 370: 64–74.
44. Manly BFJ (1997) Randomization, bootstrap and Monte Carlo methods in biology. Boca RatonFL: Chapman & Hall/CRC. pp 455.
45. Queiroz N, Humphries NE, Noble LR, Santos AM, Sims DW (2010) Short-term movements and diving behaviour of satellite-tracked blue sharks *Prionace glauca* in the northeastern Atlantic Ocean. *Marine Ecology Progress Series* 406: 265–279.
46. McGregor HV, Dima M, Fischer HW, Mulitza S (2007) Rapid 20th-Century Increase in Coastal Upwelling off Northwest Africa. *Science* 315: 637–639.
47. Sims DW, Queiroz N, Humphries NE, Lima FP, Hays GC (2009) Long-term GPS tracking of ocean sunfish *Mola mola* offers a new direction in fish monitoring. *PLoS One* 4: e7351.
48. Wolanski E, Hamner WM (1998) Topographically controlled fronts in the ocean and their biological influences. *Science* 241: 177–181.
49. Genin A (2004) Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems* 50: 3–20.
50. Olson DB, Hitchcock GL, Mariano AJ, Ashjian CJ, Peng G, et al. (1994) Life on the edge: marine life and fronts. *Oceanography* 7: 52–60.
51. Le Fevre J (1986) Aspects of the biology of frontal systems. *Advances in Marine Biology* 23: 163–299.
52. Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, et al. (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences USA* 103: 12799–12802.
53. Zainuddin M, Kiyofuji H, Saitoh K, Saitoh S-I (2006) Using multi-sensor satellite remote sensing and catch data to detect ocean hot spots for albacore (*Thunnus alalunga*) in the northwestern North Pacific. *Deep-Sea Research II* 53: 419–431.
54. Weimerskirch H, Le Corre M, Bost CA (2008) Foraging strategy of masked boobies from the largest colony in the world: relationship to environmental conditions and fisheries. *Marine Ecology Progress Series* 362: 291–302.
55. Shaffer SA, Weimerskirch H, Scott D, Pinaud D, Thompson DR, et al. (2009) Spatiotemporal habitat use by breeding sooty shearwaters *Puffinus griseus*. *Marine Ecology Progress Series* 391: 209–220.
56. Hays GC, Farquhar MR, Luschi P, Teo SLH, Thys TM (2009) Vertical niche overlap by two ocean giants with similar diets: Ocean sunfish and leatherback turtles. *Journal of Experimental Marine Biology and Ecology* 370: 134–143.
57. López-Mendilaharsu M, Rocha CFD, Miller P, Domingo A, Prodocimi L (2009) Insights on leatherback turtle movements and high use areas in the Southwest Atlantic Ocean. *Journal of Experimental Marine Biology and Ecology* 378: 31–39.
58. Field I, Hindell M, Slip D, Michael K (2001) Foraging strategies of southern elephant seals (*Mirounga leonina*) in relation to frontal zones and water masses. *Antarctic Science* 13: 371–379.
59. Bruce BD, Stevens JD, Malcolm H (2006) Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. *Marine Biology* 150: 161–172.
60. Campana SE, Dorey A, Fowler M, Joyce W, Wang Z, et al. (2011) Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the northwest Atlantic. *PLoS One* 6: e16854.
61. Sedberry GR, Loefer (2001) Satellite telemetry tracking of swordfish, *Xiphias gladius*, off the eastern United States. *Marine Biology* 139: 355–360.
62. Weng KC, Block BA (2004) Diel vertical migration of the bigeye thresher shark (*Alopias superciliosus*), a species possessing orbital retia mirabilia. *Fishery Bulletin* 102: 221–229.
63. Stevens JD (1973) Stomach contents of the blue shark (*Prionace glauca* L.) off south-west England. *Journal of the Marine Biological Association of the United Kingdom* 53: 357–361.
64. Weng KC, Stokesbury MJW, Boustany AM, Seitz AC, Teo SLH, et al. (2009) Habitat and behaviour of yellowfin tuna *Thunnus albacares* in the Gulf of Mexico determined using pop-up satellite archival tags. *Journal of Fish Biology* 74: 1434–1449.
65. Horodysky AZ, Kerstetter DW, Latour RJ, Graves JE (2007) Habitat utilization and vertical movements of white marlin (*Tetrapturus albidus*) released from commercial and recreational fishing gears in the western North Atlantic Ocean: inferences from short duration pop-up archival satellite tags. *Fisheries Oceanography* 16: 240–256.
66. Marchesiello P, Estrade P (2009) Eddy activity and mixing in upwelling systems: a comparative study of Northwest Africa and California regions. *International Journal of Earth Sciences* 98: 299–308.
67. Mucientes GR, Queiroz N, Sousa L, Tarroso P, Sims DW (2009) Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biology Letters* 5: 156–159.
68. Bigelow K, Musyl M, Poisson F, Kleiber P (2006) Pelagic longline gear depth and shoaling. *Fisheries Research* 77: 173–183.