

Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark

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Summary

1. Megaplanktivores such as filter-feeding sharks and baleen whales are at the apex of a short food chain (phytoplankton–zooplankton–vertebrate) and are sensitive indicators of sea-surface plankton availability. Even though they spend the majority of their time below the surface it is still not known how most of these species utilize vertical habitat and adapt to short-term changes in food availability.

2. A key factor likely to control vertical habitat selection by planktivorous sharks is the diel vertical migration (DVM) of zooplankton; however, no study has determined whether specific ocean-habitat type influences their behavioural strategy. Based on the first high-resolution dive data collected for a plankton-feeding fish species we show that DVM patterns of the basking shark *Cetorhinus maximus* reflect habitat type and zooplankton behaviour.

3. In deep, well-stratified waters sharks exhibited normal DVM (dusk ascent–dawn descent) by tracking migrating sound-scattering layers characterized by *Calanus* and euphausiids. Sharks occupying shallow, inner-shelf areas near thermal fronts conducted reverse DVM (dusk descent–dawn ascent) possibly due to zooplankton predator–prey interactions that resulted in reverse DVM of *Calanus*.

4. These opposite DVM patterns resulted in the probability of daytime-surface sighting differing between these habitats by as much as two orders of magnitude. Ship-borne surveys undertaken at the same time as trackings reflected these behavioural differences.

5. The tendency of basking sharks to feed or rest for long periods at the surface has made them vulnerable to harpoon fisheries. Ship-borne and aerial surveys also use surface occurrence to assess distribution and abundance for conservation purposes. Our study indicates that without bias reduction for habitat-specific DVM patterns, current surveys could under- or overestimate shark abundance by at least 10-fold.

Key-words: archival telemetry, behaviour, conservation, shark, zooplankton.

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Introduction

The habitat selection strategies used by marine animals that feed on zooplankton are crucial to their survival. As zooplankton forms all or a major part of the diets of

diverse marine vertebrates, including sharks, seabirds and whales, it is vital they locate sufficient prey concentrations above threshold levels during foraging. However, the distribution and abundance of zooplankton in the oceans is highly heterogeneous over various time and space scales (Greene *et al.* 1998). Consequently, the problem facing planktivores is how best to track zooplankton. Despite the important role of foraging success in determining individual and, hence, population growth rates, the behavioural strategies used by

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marine vertebrates such as planktivorous sharks and whales to 'equalize' prey heterogeneity in the open ocean are poorly understood (Sims 2003). It has been demonstrated that oceanic and inner-shelf fronts are principal feeding areas for these species (Sims & Quayle 1998; Tynan 1998), but how they respond to vertical changes in zooplankton abundances is unknown.

The daily change in vertical abundance of zooplankton, termed diel vertical migration (DVM), is a widespread behavioural phenomenon among marine and freshwater species (Hays 2003) that influences foraging patterns of vertebrate predators (e.g. Wilson *et al.* 1993). Under a normal pattern of DVM, zooplankton populations remain in deeper water during the day, principally to avoid visually orientating predators such as fish (Bollens & Frost 1989), whereas at dusk, zooplankton rise to near the surface where they remain feeding before returning to depth at dawn. Despite a large body of literature on zooplankton DVM (e.g. Gliwicz 1986; Loose & Dawidowicz 1994), whether plankton-feeding marine vertebrates track these migrations directly is less well understood. It was shown recently that the planktivorous megamouth shark *Megachasma pelagios* exhibits normal DVM and it was proposed that this pattern was most likely maintained by selection for a constant level of ambient light (Nelson *et al.* 1997). Clearly, if planktivorous sharks use a DVM strategy based on light level, this may render them less able to respond to short- and long-term changes in the vertical distribution of zooplankton.

The basking shark *Cetorhinus maximus* is the world's second largest fish and feeds by obligate ram filtering on patches of large zooplankton such as *Calanus* spp. in temperate shelf waters circumglobally (Sims & Quayle 1998). In this study we used pop-off archival tags attached to basking sharks to investigate patterns of DVM in different oceanographic regimes, namely frontal and strongly stratified regions. From the most extensive dataset yet recorded on the vertical movements of a fish planktivore, together with measurements of zooplankton, we show that two DVM patterns exhibited by basking sharks are habitat specific.

Methods

ARCHIVAL TAGGING

Searches for basking sharks were undertaken in the English Channel off Plymouth, UK (50.33–50.17°N, 003.95–004.33°W) during May and June in 2001 and 2002, and an area comprising Lower Loch Fyne and the northern Clyde Sea, Scotland (56.00–55.58°N, 004.95–005.47°W) in July and August 2001 and 2002. Searches were conducted during daylight hours (06.00–22.00 h) when weather conditions were relatively calm (wind speed < 30 km h⁻¹, Beaufort wind force < 4, sea state < 3). A minimum of three crew members scanned the surrounding sea for the dorsal fins of basking sharks.

Shark movements and behaviour were tracked using 'pop-up' archival transmitting (PAT) tags (Wildlife Computers, Redmond, WA) (length: 175 mm; mass in air: 76 g). These tags combine a data-logger that records swimming depth to 1000 m (minimum resolution: 0.5 m), water temperature from -40 to 60 °C (minimum resolution: 0.05 °C), and light as irradiance (W cm⁻² at 550 nm wavelength), with an Argos-certified transmitter with 0.5 W power output. These parameters were sampled each minute for the duration of tag deployment. PAT tags were attached to sharks as described in a previous study (Sims *et al.* 2003). Briefly, tags were fitted to sharks via a 1.8-m long monofilament tether that was anchored into the base of the dorsal fin by a 40-mm long stainless steel T-bar arrowhead. PAT tags trailed behind the dorsal fin close to the body, and the known distance from tag to first dorsal fin was used to obtain an estimate of shark total body length. After the duration of deployment and at a pre-programmed time, each tag released itself from the host shark and floated to the surface where it was geolocated by Argos receivers aboard NOAA satellites (the 'pop-up' location). The estimated accuracy of 'pop-up' locations determined by Argos receivers was between 350 and 1000 m. The Argos system also received data from tags summarizing the amount of time each shark spent swimming in discrete depth 'bins' (time-at-depth data) in each 4- or 6-h period. However, the continuous minute-by-minute changes in swimming depth needed to identify precise patterns of DVM could only be accessed when tags were physically retrieved. Archived datasets of measurements of swimming depth, water temperature and light level recorded every minute were accessed in this study when tags washed ashore and were returned to us by members of the public. Using this long-term 'drifter' method we have so far recovered 33% of tags deployed.

To determine the patterns of vertical movement in specific areas visited by sharks, horizontal tracks were reconstructed using light-level data to estimate the local time of midnight or midday for longitude calculations (Wilson *et al.* 1992; Hill 1994) as described previously (Sims *et al.* 2003). To estimate latitude, tag-recorded water temperature for each day was matched with advanced very high resolution radiometer (AVHRR) remote-sensing images of sea surface temperature (SST) to fix latitude along the longitude (Sims *et al.* 2003). The latitude estimate, fixed using SST, was then filtered for water-mass type, depth and swim-speed anomalies. The accuracy of these estimates was between ± 0.15 and 1.20° of longitude (1° longitude = 71.7 km). Temperature–depth profiles constructed from tag data were used to determine water-mass type (stratified, frontal, mixed) at each shark's location.

ZOOPLANKTON DATA

DVM of zooplankton in the Clyde Sea area where basking sharks were tracked was recorded in August 1999 using a combination of acoustic and net sampling

methods. Acoustic data were collected using a 300 kHz Workhorse (broadband) acoustic Doppler current profiler (ADCP) moored on the seabed facing upward at 110 m (Inchmarnock Water, 55°80'N, 005°20'W). The ADCP recorded sound scattering layers (SSLs) between 16- and 104-m depth as described previously (Tarling *et al.* 2002). Briefly, the ADCP collected 15 depth 'bins' of 8-m depth and was set to ping at a frequency of 12 per 2 min averaging interval. The acoustic data were validated using conventional net sampling in August 1999 (Tarling *et al.* 2002). A 1-m² multiple open/closing net system (MOCNESS, BESS, Dartmouth, USA; Wiebe *et al.* 1985) fitted with up to nine nets with mesh sizes of either 330 or 2000 µm was used to sample six discrete depth strata (≤ 30 m) at all phases of the diel cycle in each of two 5-day periods. All samples were fixed in 10% formalin and subsequently preserved in alcohol. Counts were made using methodology given in Tarling *et al.* (2002).

Zooplankton samples from surface layers off Plymouth were taken between 18 and 25 June 2002 to coincide with deployment of a PAT tag on a basking shark on 18 June 2002 in the same location (50°18'N 004°26'W). Vertical hauls from 10-m depth of a weighted, WP2 plankton net (mesh size, 250 µm) were made in the area surrounding the tagging location between 10.30 and 13.40 h at intervals during the 7-day period following tagging. Species were counted according to the methodology given in Sims & Merrett (1997). Species numbers from these samples were compared with samples taken from basking-shark feeding paths in May and June 1997, using the same methods. Details on sampling from shark feeding paths is given in Sims & Quayle (1998). All samples were fixed in 4% formalin and subsequently preserved in alcohol.

DATA ANALYSIS

Swimming depth during the day and night was compared for each shark over a 3-day period using non-parametric two-sample tests with normal approximation (Zar 1999). Dive depths were separated into day and night groups by determining the local time of sunrise and sunset from each tag's light-level data, and checked against those given in nautical almanacs according to latitudinal position. Because the periods over which dive depths were analysed were between 5 June and 15 August for all sharks, the daylength was greater than the duration of night-time. Therefore, the total number of daytime dive depths were matched to the total number of night-time depths by random deletion of daytime depths. The total number of dive depths during each phase (day or night) that were compared ranged from 1440 to 1620. Similarly, zooplankton counts from samples between different years were compared using nonparametric two-sample tests. Where sample size differed significantly between the two sample groups, the larger number of observations in a group were reduced by random deletion to match that of the smaller set of observations in the other group.

Results

Surveys for basking sharks in the English Channel and Clyde Sea resulted in total search times of 193.2 and 215.9 h, respectively, undertaken on 30 days in each area. In the English Channel 73 sharks were sighted on 11 separate days, but in the Clyde Sea only nine sharks on 2 days were seen. Of the individuals tagged, archival data from returned PAT tags were obtained for four basking sharks (total length range, 4.5–6.0 m) representing a total of 333 tracking days between May 2001 and June 2002. Track reconstructions showed that specific patterns of DVM were associated with particular ocean habitat. Sharks *A* and *B* exhibited normal DVM (dusk ascent–dawn descent) when occupying deep water of the fjord-like Clyde Sea (maximum water depth, 200 m; Fig. 1) and when located on the European shelf edge (maximum depth, 1000 m; Fig. 1), respectively. The mean daytime depths selected by sharks *A* and *B* were significantly deeper than depths selected at night (Mann–Whitney *U*-tests with normal approximation: shark *A*, median daytime depth = 72.5 m, median night-time depth = 29.9 m, $Z = 29.1$, $P < 0.0001$; shark *B*, median daytime depth = 87.2 m, median night-time depth = 12.8 m, $Z = 62.41$, $P < 0.0001$). The deep-water habitats occupied by sharks *A* and *B* were strongly stratified thermally, with maximum vertical gradients of 5.4 °C (0–92 m depth) and 4.4 °C (0–128 m depth), respectively (Fig. 2). In contrast, sharks *C* and *D* showed reverse DVM (dusk descent–dawn ascent) in inner-shelf areas of the western English Channel (< 80 m depth) (Fig. 1). Mean night-time depths selected by sharks *C* and *D* were significantly deeper than depths selected during the day (Mann–Whitney *U*-tests with normal approximation: shark *C*, median daytime depth = 4.1 m, median night-time depth = 19.1 m, $Z = 28.0$, $P < 0.0001$; shark *D*, median daytime depth = 5.6 m, median night-time depth = 54.9 m, $Z = 25.6$, $P < 0.0001$). The inner-shelf habitats occupied by sharks *C* and *D* were characteristic of tidal fronts with shallow temperature gradients, with this change occurring mostly in the upper 20 m. Maximum gradients encountered by sharks were 2.6 °C (shark *C*) and 0.8 °C (shark *D*) between 0 and 64 m depth (Fig. 2).

Data on the vertical movements of zooplankton were compared with those for basking sharks in an attempt to explain the differences in the regional DVM patterns. The normal DVM pattern of shark *A* was sustained for a month in the Clyde Sea prior to tag release. Figure 3 shows the swimming depth of shark *A* superimposed on the absolute acoustic backscatter (dB) recorded with the ADCP. The backscatter spectrogram identifies an SSL at 50–80 m depth during the day, which ascends nocturnally into surface waters. Net sampling within the area used by shark *A* demonstrated *Calanus finmarchicus* comprised the major part of this nocturnally migrating SSL, with a peak concentration of 75 individuals m⁻³ (Tarling *et al.* 2002). The euphausiids *Meganctiphanes norvegica* and *Thysanoessa raschii*

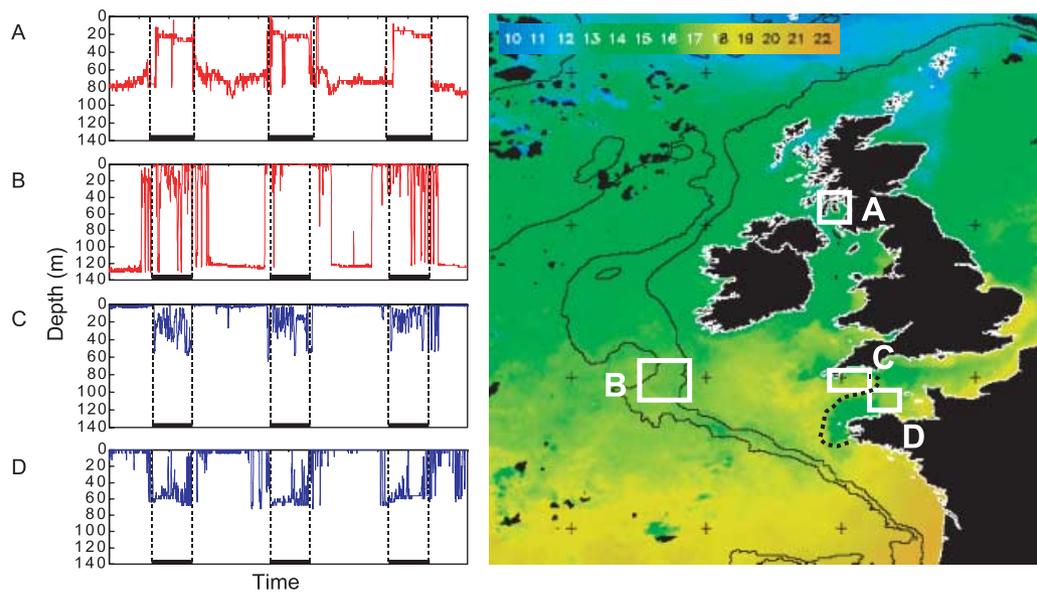


Fig. 1. Diel vertical changes in swimming depths of four basking sharks (A–D) in relation to thermal habitat occupied on the European continental shelf (areas A–D on the false-colour sea surface temperature (SST) remote sensing image; monthly night-time composite, August 2001). Sharks A and B followed a normal pattern (nocturnal ascent) in thermally stratified water masses, whereas sharks C and D showed a reverse pattern (nocturnal ascent) in frontal waters. Periods of diving behaviour shown: shark A (6 m L_T), 12–15 August 2001; shark B (4.5 m L_T), 12–15 June 2001; shark C (6 m L_T), 18–21 June 2002; shark D (6 m L_T), 5–8 June 2001. The black bars on panels A–D denote night-times between dawn and dusk. The colour scale bar on the SST map is surface water temperature in °C as derived from the advanced very high resolution radiometer aboard NOAA satellites. The dotted line on the SST map denotes the spring–summer position of the Ushant thermal front (Le Fèvre 1986). Continuous lines represent the 200 and 2000-m isobaths.

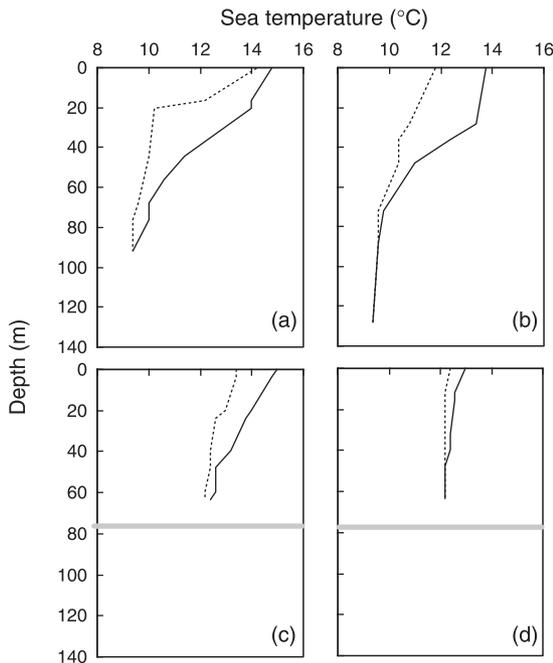


Fig. 2. Vertical sea-temperature profiles for sharks A and B in the Clyde Sea and Atlantic Ocean (Goban Spur), respectively, and sharks C and D in the western English Channel. Solid lines are maximum daily temperatures and dotted lines denote minimum daily temperatures. The grey lines on panels C and D denotes the seabed depth.

were recorded between 80 and 100 m depth during the day (peak concentration range, 0.5–3.0 individuals m^{-3}), and also migrated upward at dusk. The swimming depth of shark A during the day and night closely followed

Table 1. Comparison of *Calanus helgolandicus* and chaetognath numbers in samples taken from the feeding paths of basking sharks in 1997 (11–13 June, $n = 34$) and 2002 (18–25 June, $n = 25$)

		1997	2002
<i>C. helgolandicus</i> (individuals m^{-3})	mean	876.1	378.4
	median	708.4	263.2
Chaetognaths (individuals m^{-3})	mean	69.9	136.2
	median	59.4	82.1
Ratio*	mean	0.14	0.52
	median	0.09†	0.37†

The ratio of the number of chaetognaths to *C. helgolandicus* in each sample, with higher values representing increased potential risk of predation. †Denotes ratio in 2002 compared with 1997 was significantly higher, $P < 0.0001$.

the *C. finmarchicus* layer for much of the time; however, on occasions it switched to occupy the euphausiid layer. The shark mostly remained between 50 and 100 m during the day before dusk ascent into shallow depths between 0 and 20 m.

Shark C was surface feeding prior to being tagged and zooplankton samples taken at this time and at intervals over the next 7 days revealed high concentrations of *Calanus helgolandicus* in the uppermost 10-m layer (Table 1). We compared these samples with those taken from shark feeding paths in mid-June 1997, a year characterized by very high surface zooplankton abundance (Sims & Merrett 1997; Sims & Quayle 1998). Although the *C. helgolandicus* concentration was 57%

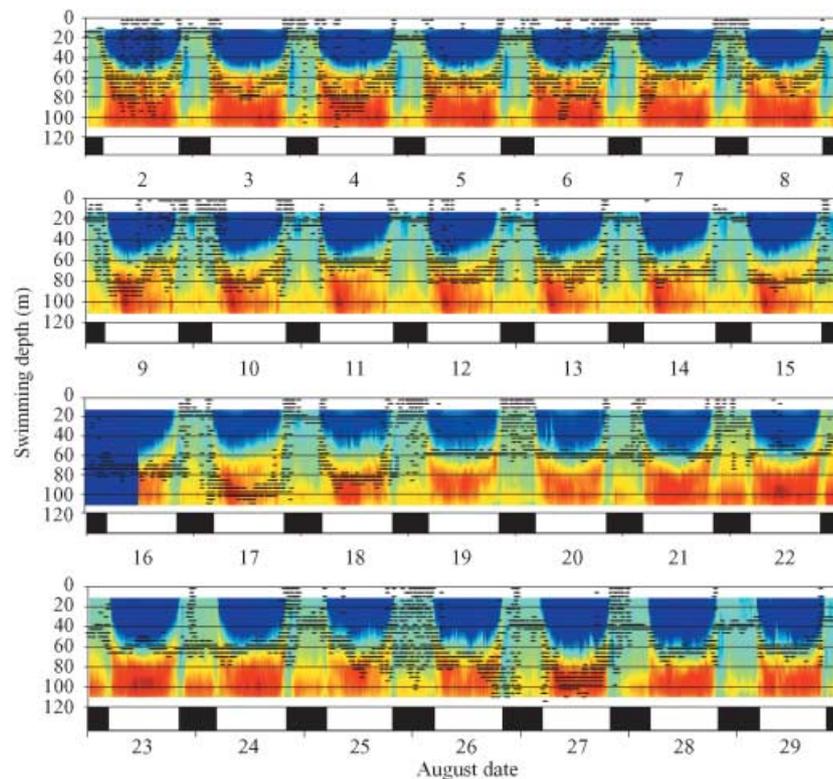


Fig. 3. The swimming depth of shark *A* (black dots) between 2 and 29 August 2001 overlaid on a false-colour image of absolute acoustic backscatter (dB) in the same area of the Clyde Sea between 2 and 29 August 1999. The yellow-coloured sound-scattering layer located at 50–80 m represents the *Calanus* layer depth.

lower in 2002 than for mid-June 1997, the daytime density of chaetognaths was 95% higher in the vicinity of the tagged shark (Table 1). Hence, the ratio of chaetognaths to *C. helgolandicus* numbers was significantly higher for surface waters in 2002 than for the same areas in 1997 (Mann–Whitney *U*-test with normal approximation: median ratio₁₉₉₇ = 0.09, median ratio₂₀₀₂ = 0.37, $Z = 11.6$, $P < 0.001$). There were no other predators of *C. helgolandicus* found in significant numbers in samples.

Discussion

High-resolution, long-term dive patterns of planktivorous sharks have not been obtained prior to this study because of the difficulties associated with retrieving data-logging (archival) tags. The method of retrieving ‘pop-up’ archival tags washed up on beaches has proved viable off the UK coast probably due to tags being pushed shoreward by prevailing south-westerly winds. Using these data this investigation provides the first evidence that DVM patterns are habitat specific in basking shark: both normal and reverse DVM patterns were observed, with each type being associated with a particular thermal habitat. Normal DVM predominated in deeper, thermally stratified waters of the Clyde Sea and European shelf edge, whereas reverse DVM occurred in inner-shelf areas of the western English Channel characterized by tidal fronts. The fact that reverse DVM is more likely to occur in a different

habitat type to that supporting normal DVM indicates as yet undocumented differences in basking shark behaviour that has implications for conservation.

The mechanisms underlying normal and reverse DVM patterns in basking sharks are not known precisely, but our results indicate they were related to variable zooplankton DVM. Previous studies have shown fine-scale surface foraging by basking sharks is selective for the densest patches of zooplankton characterized by high concentrations of large *Calanus*, together with smaller numbers of smaller species (Sims & Quayle 1998). Although it is intuitive that megaplanktivores such as basking sharks should track prey-concentration layers distributed throughout the water column and during population-level DVM, evidence for this behaviour has so far been lacking. Our data show that a shark in the Clyde Sea remained within the *Calanus finmarchicus* and euphausiid layers during the day, and tracked these populations during upward migration to the surface at dusk and followed them downward at dawn. Normal DVM was also shown by shark *B* west of the Celtic Sea on the shelf edge south-west of Ireland. Although zooplankton distribution and behaviour were not examined by us in this remote location, previous zooplankton studies in the Celtic Sea indicate *Calanus* spp. there undertake normal DVM (Williams & Conway 1984; Harris 1988).

By contrast, sharks *C* and *D* demonstrated reverse DVM which, to our knowledge, is the first observation

of this behaviour among planktivorous sharks. Analysis of zooplankton samples taken in the vicinity of a tagged shark indicated this pattern of behaviour may have been linked to reverse DVM of zooplankton prey, e.g. copepods. Reverse DVM has been observed in several species of zooplankton and these nocturnal descents serve as an escape response from normal vertically migrating invertebrate predators including chaetognaths (*Sagitta* spp.) (Ohman, Frost & Cohen 1983). There is clear evidence that DVM behaviour is selected for in zooplankton to evade predators (Gliwicz 1986; Cousyn *et al.* 2001). Crustacean zooplankton such as copepods can show rapid initiation (< 4 h) of vertical migration in response to invertebrate predators, indicating they are capable of flexible, predator-sensitive foraging (Neill 1990). In the current study, zooplankton close to shark *C* was not sampled at night; however, daytime sampling showed very high concentrations of predatory chaetognaths in the upper 10-m layer. This in turn resulted in a theoretical fourfold increase in 'predation risk' for *C. helgolandicus* from chaetognaths.

Studies in the Irish Sea have indicated that *Calanus* spp. actively avoid chaetognaths by adapting their DVM inversely to that of the chaetognaths (Irigoien, Conway & Harris 2004). Reverse DVM in *Calanus* spp. was initiated not by abundance of chaetognaths *per se*, but by their position in the water column during the day (Irigoien *et al.* 2004). Along tidal fronts off Plymouth *C. helgolandicus* are found in dense aggregations in the upper 10-m layer during the day (Sims & Quayle 1998), while chaetognaths in this region exhibit normal DVM over the depth range of 0–35 m (the upper 50% of the water column) (Russell 1931). The copepods are thought to be able to sense the position of the chaetognaths during the day and adapt the amplitude and direction of their DVM accordingly (Irigoien *et al.* 2004). Taken together, this suggests that the reverse DVM of sharks *C* and *D* may be attributable to reverse DVM of copepod prey as a consequence of chaetognaths being present in surface waters during the day. These observations point to an intriguing example of how a planktonic invertebrate predator indirectly affects the behaviour of a fish megaplanktivore.

The regional differences in DVM strategy we have identified have important implications for methods used to assess population size of fish megaplanktivores. There is concern that the world's two largest fish species, the whale shark *Rhincodon typus* and the basking shark, have low population levels as a result of human exploitation (Hilton-Taylor 2000). This remains difficult to resolve however, because data on population sizes for these species are lacking. Ship and aerial line-transect surveys are used widely for estimating the abundances and population sizes of various species of whales (Forney, Barlow & Carretta 1995), marine turtles (Coles & Musick 2000) and large fish (Kenney, Owen & Winn 1985). Diving behaviour is one factor contributing to errors associated with availability bias of surveys, which can influence the precision of population size estimates

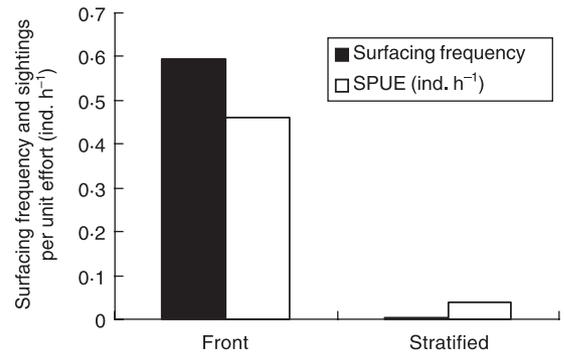


Fig. 4. The surfacing frequency (time spent at ≤ 1 m depth) (black bars) of sharks *A* (stratified) and *C* (front) during daylight hours compared with sightings of sharks per unit time (SPUE, individuals h^{-1}) (white bars) in each of these tracking locations.

(Barlow, Gerrodette & Forcada 2001). However, because fish do not breathe air and have no need to surface regularly, surveying fish populations in this way is more problematic than for whales and turtles.

In the current study we found that the existence of normal and reverse DVM patterns in individual sharks from the same population resulted in very different surfacing frequencies (time spent at ≤ 1 m depth). The daytime-surfacing frequency of a tracked individual feeding in an inner-shelf area near a front was over 100 times higher than another shark feeding in well-stratified water (Fig. 4). This large difference in 'basking' behaviour between regions was reflected in our survey data: 11.5 times more sharks per unit effort were observed in fronts than in stratified water (Fig. 4). This suggests sightings per unit effort may not reflect real differences in geographical (horizontal) abundance between areas because the probability of sighting a basking shark shifts from about 0.6 in fronts to < 0.01 in well-stratified zones. This difference will result in underestimating abundance in stratified areas by about 60-fold. Our data suggest bias reduction according to habitat type (and zooplankton behaviour) should be incorporated into surveys attempting to estimate abundance. It is possible that the variable patterns of DVM we show for basking sharks also occur commonly in essential habitats used by other megaplanktivores such as whales, which may affect encounter rates during surveys accordingly.

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