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Effects of zooplankton density and diel period on surface-swimming duration of basking sharks

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The surface-swimming duration of basking sharks (*Cetorhinus maximus*) was determined in the western English Channel from May to July over a five-year period. Surface duration showed marked variation from 0.17 to 1.45 h over the short time period from late May to mid-June. Stepwise multiple regression was used to identify any relationships between surface-swimming duration and time of day, daily sea surface temperature (SST), and zooplankton density. There was no support for any effects of SST or two measures of zooplankton density (median and maximum densities). However, there were significant relationships for surface duration with time of day and minimum zooplankton density (r^2=0.50) indicating basking sharks respond to the abundance of prey and its temporal availability. This suggests that the probability of sighting sharks at the surface will vary depending on the diel period and the surface abundance of zooplankton.

INTRODUCTION

The behaviour patterns shown by marine fish in response to variations in external factors such as water temperature and prey abundance are important to understand because they influence fish distribution, availability and, therefore, catch rates (Fréon & Misund, 1999). Despite a large amount of literature describing numerous aspects of fish behavioural ecology (e.g. Godin, 1998), surprisingly little is known about the feeding strategies utilized by wild fish, and in particular, how they respond to changes in prey abundance (Josse et al., 1998; Sims & Quayle, 1998). This is because fish movements, and behaviour in relation to prey densities, are rarely monitored simultaneously. The plankton-feeding basking shark (*Cetorhinus maximus*) is an appropriate model species with which to examine foraging strategy in a wild fish because it can be tracked at the surface where simultaneous measurements of prey density and other characteristics are possible (Sims & Quayle, 1998).

One potential use of behavioural data on the foraging and migratory strategies of basking sharks is in survey design. During summer months in the north-east Atlantic basking sharks surface-feed on zooplankton in inshore areas, however their occurrence is often unpredictable (Sims et al., 1997). For large marine vertebrates such as basking sharks and cetaceans, population sizes are usually estimated by ship and aerial line-transect surveys where the probability of encountering animals along the trackline is not equal to one (Kenney et al., 1985; Barlow, 1995; Barlow et al., 2001; Stockin et al., 2001). Many factors can affect the probability of sighting animals at the surface (for overview see Barlow et al., 2001). These include perception bias factors such as sea state, swell height and observer visual range (Barlow, 1995), and availability bias factors such as animal activity and diving behaviour (Stockin et al., 2001). Therefore, determining the influence of external factors on behaviour is vital for assessing availability bias.

The amount of time basking sharks spend at the surface will have a direct effect on the probability of sightings made by ship and aerial surveys. Hence, the aim of the present study was to evaluate the influence of five factors (time of day, sea surface temperature, and minimum, median and maximum zooplankton density) on the surface-swimming duration of basking sharks that were tracked in the English Channel by research vessels.

MATERIALS AND METHODS

Shark tracking

Basking sharks (*Cetorhinus maximus*) were located by ship survey in the English Channel off Plymouth (area: 50°20′–50°10′N, 003°57′–004°20′W). Daytime surveys were conducted from 0800 to 1700 h from 3 May to 16 August 1996 (390 h), from 1 May to 31 July in 1997 (155 h), 1999 (111 h) and 2000 (151 h), and from 1 May to 8 August in 2001 (246 h). Tracking of solitary and grouped sharks was achieved using a 10-m research vessel which stayed within 10–50 m of sharks at all times, mostly with the engine disengaged, the vessel drifting in the same direction as the resultant movements of feeding sharks (for example, see figure 3 in Sims & Quayle, 1998). Vessel position was plotted every 5–10 min using a Global Positioning System (Garmin 120S, Kansas, USA; Valsat 03, MLR Electronique, France). The time spent by sharks at the surface (surface duration) was taken to be the time from when they were first encountered to the time when they were last seen, the latter of which was verified by checking that no sharks surfaced at that location for at least 1 h after the last shark was sighted. The total number of sharks observed during each tracking bout was counted by identifying individuals based upon a body length estimate (Sims et al., 1997) combined with details on unique fin morphology and body

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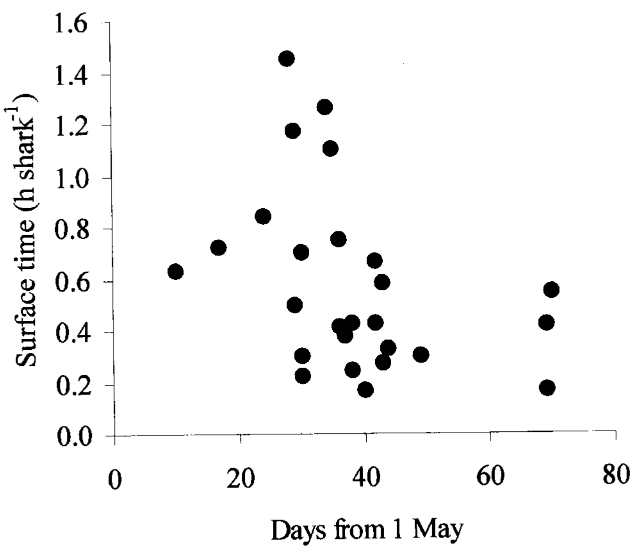

Figure 1. The surface-swimming duration of basking sharks tracked in the western English Channel during summer (May–July) over a five-year period. Day 1=May 1.

markings (Sims et al., 2000). The time of day when surface swimming occurred was recorded as the time when a shark or group was first sighted. For the analysis, this variable was expressed as the number of hours from 0800 h, the time when surveys commenced.

Zooplankton and temperature sampling

Zooplankton samples were taken during trackings of solitary and grouped basking sharks. A zooplankton sample consisted of a vertical haul from 10 m depth of a weighted simple plankton net (net diameter=30 cm, mesh diameter=0.25 mm). Zooplankton was removed by sea-water washing after each haul and fixed immediately in 4% formaldehyde. Samples were taken within 50 m of sharks but when sharks passed close to the vessel (<3 m), a zooplankton sample was taken in front of, or to the side of, an oncoming shark. Total zooplankton catch in each sample was filtered and weighed wet, then carefully resuspended in 70% ethanol. There were 127 zooplankton samples taken during 28 trackings (1–19 samples per track). Only one sample per track was obtained for seven tracks of solitary sharks due to the short time these individuals spent at the surface.

Sea surface temperature was measured on each day that sharks were tracked at sampling station Sl (50°18′N, 004°09′W), located in a zone of shallow, vertically mixed water. Measurements were taken at 1–5 m depth between 0800 and 1000 h using either a YSI Model 58 meter (Yellow Springs Instruments, Ohio, USA), or a Vemco Minilog TDR (Vemco Ltd, Nova Scotia, Canada). Each instrument was calibrated against a standard mercury thermometer.

Statistical analysis

Stepwise multiple regression (Minitab Release 13, Minitab Inc., PA, USA) was used to determine which factors influenced the observed variation in basking shark surface-swimming duration over the summer period. The initial factors included in the model were: (1) time of day; (2) sea surface temperature at Sl; (3) minimum zooplankton density; (4) median zooplankton density; and (5) maximum zooplankton density. For the seven trackings for which only one zooplankton sample was taken per track, the single prey-density measurement was used for minimum, median and maximum values in the regression analysis. An alpha (α) level of 0.05 was used as the significance level for entry or removal of the six predictors in the stepwise regression model.

RESULTS

Over the five-year study period 28 trackings were completed where a known end point for surface-swimming duration was reached, that is, no re-surfacing occurred for at least 1 h after the last shark was sighted. Of the 28 trackings satisfying this criteria, nine were of solitary sharks, and for the 19 groups tracked the median group size was five sharks (mean SD, 5.2 ±2.8; range, 2–12). The number of sharks observed was positively correlated with the total duration of surface swimming by solitary or grouped sharks (r=0.68, t=4.72, $t_{0.05,2,26}$=2.06, P<0.001) indicating that larger aggregations facilitated concomitantly longer observation times. This effect of group size on observation time was bias-reduced by expressing surface-swimming duration as a function of the number of sharks counted during each tracking. There was no correlation between the surface-swimming duration expressed in hours per shark (h shark^{-1}) and the number of sharks counted in each tracking (r=0.04, t=0.19, $t_{0.05,2,26}$=2.06, P>0.50), suggesting that this individual-based measure of surface-swimming duration was independent of the total number of sharks observed. For the purpose of this study it was assumed that this measure was a reasonable estimate of an individual shark's surfacing time irrespective of the group size in which it was observed.

There was marked variation in the surface-swimming duration of basking sharks during early summer (May to

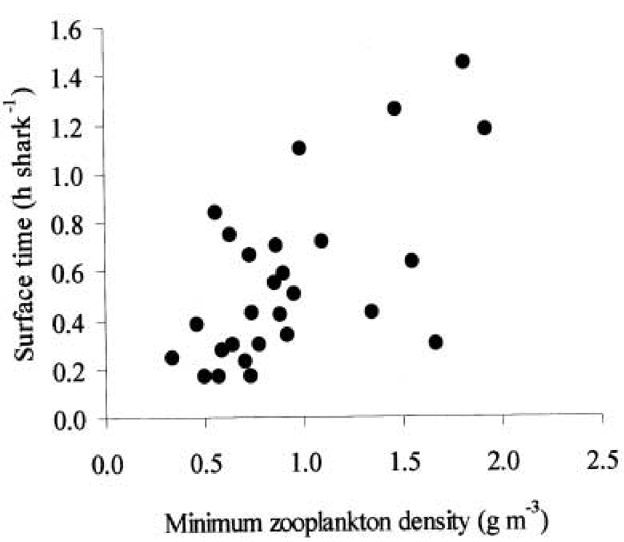

Figure 2. Surface-swimming duration of basking sharks in relation to minimum zooplankton densities measured during trackings. See text for regression model.

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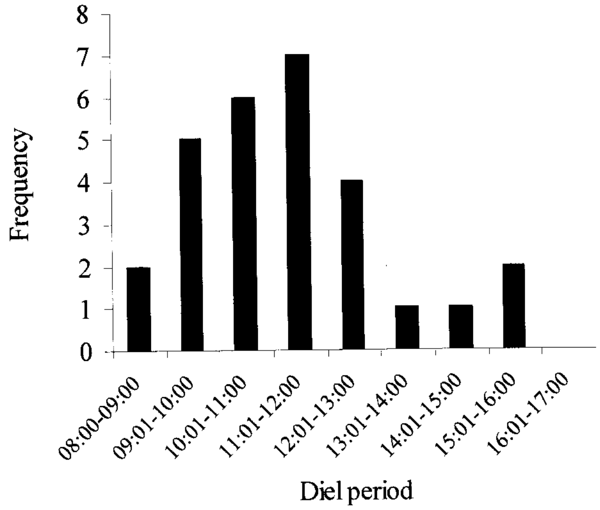

Figure 3. Frequency distribution of the time of first sightings of tracked sharks over the diel period from 0800 to 1700 h.

July) (Figure 1). For example, between day 30 and 40 (late May to mid-June) surface-swimming duration per shark ranged from 0.17 to 1.45 h. Stepwise multiple regression was used to determine which of five factors was, or combination of factors were the most important in accounting for the observed variation in surface-swimming duration of basking sharks. There was no support for any effects of SST, median or maximum zooplankton densities. However, there were significant relationships for surface-swimming duration with time of day (t=2.38, $t_{0.05,2,26}$=2.06, $P<0.05$) and minimum zooplankton density (t=4.71, $t_{0.05,2,26}$=2.06, $P<0.001$), summarized by the regression equation:

$$T_s = 0.242 + 0.560d_{min} - 0.063t_d \quad (1)$$

where T_s is basking shark surface-swimming duration in h per shark, d_{min} is the minimum zooplankton density measured per track in wet weight g per cubic metre, and t_d is time of day in h since 0800 h. In separate analyses, there was no significant correlation between time of day (TOD) and minimum, median or maximum zooplankton density (ZD) measurements (TOD vs minimum ZD, r=0.15, t=0.78, $t_{0.05,2,26}$=2.06, $P>0.20$; TOD vs median ZD, $r=-0.01$, $t=-0.06$, $t_{0.05,2,26}$=2.06, $P>0.50$; TOD vs maximum ZD, $r=-0.05$, $t=-0.25$, $t_{0.05,2,26}$=2.06, $P>0.50$), indicating that they were independent factors in the dataset used. The two factors in the model accounted for 50% (r^2=0.50) of the observed variation in surface-swimming duration of basking sharks, although about 39% of the variation could be explained by the effect of minimum zooplankton density on surface duration alone (Figure 2). There was a significant effect of time of day in the model, with a weak negative relationship between surface-swimming duration and time of day (represented by increasing time from 0800 h). A higher frequency of trackings commenced between 0800 and 1200 h (N=20) compared to after 1300 h (N=8) (Figure 3).

DISCUSSION

The results indicate that the time spent at the surface by basking sharks depends largely on the minimum abundance of prey in the surface layer and the time of day. This suggests that the foraging strategy of basking sharks is linked to both prey abundance and its temporal availability. In this study the surface-swimming duration increased significantly with increasing minimum zooplankton density rather than with median or maximum densities, suggesting that lower, near-threshold levels of zooplankton abundance may be more important in determining surfacing duration than higher levels. This finding is distinct from, but consistent with a previous behavioural study that showed basking sharks spend progressively more time in areas with higher zooplankton densities (Sims & Quayle, 1998). The latter study dealt with the behaviour of sharks in a two-dimensional plane (e.g. discrete surface patches of prey), whereas the current investigation introduces the depth dimension by using the measurement of surfacing times rather than horizontal trajectory, and relating these to factors such as zooplankton density and time of day. In addition, a related study showed that basking sharks increased their swimming speed as zooplankton density declined towards threshold levels (Sims, 1999). Taken together with previous results, the present study indicates that the behavioural responses of basking sharks to low levels of food supply near the surface probably acts to reduce surface-swimming duration directly, leading to sharks selecting to forage at depth. However, one likely source of error in the model produced here was the estimation of surface-swimming duration by sharks, because for most trackings the actual time of first surfacing, rather than the time when sharks were first encountered, was not known. Clearly, future studies need to focus on determining the actual surfacing time of sharks in relation to zooplankton abundance. This could be achieved by combining archival tracking of depth preferences of sharks with simultaneous measurements of zooplankton abundance.

In addition to the influence of zooplankton density on duration, there was also an effect of time of day. Even though minimum zooplankton density was independent of time of day in the dataset used, the observation that duration declined as day progressed may be a consequence of the diel movements of zooplankton that were not detected by surface-to-10 m depth sampling employed in the present study. We showed that 2.5 times as many trackings commenced before 1200 h than after that time, which combined with a negative relationship between surface-swimming duration and time of day, suggest that a decrease in the abundance of zooplankton at the surface could account for our observations. The phenomenon of diel vertical migration in a diverse range of zooplankton species has long been recognized by researchers (e.g. Hardy & Bainbridge, 1951). The predominant zooplanktonts in samples collected near basking sharks were calanoid copepods, principally *Calanus helgolandicus* (Sims & Merrett, 1997). In the Celtic Sea, adults of this species are known to undertake diel vertical migration such that higher densities are present in the surface layer (0–20 m) at night than during the day, when the highest proportion can be found at depths between 60 and 80 m (Williams & Conway, 1984). In a study in the western English Channel off Plymouth, *C. helgolandicus* was shown to exhibit diel vertical migration, but significant numbers still remained in the top 10 m of water before 1200 h, whereas few remained

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there after 1200 h (Southward & Barrett, 1983). Therefore, in this study, we speculate that the effect of time of day on surfacing time and duration in basking sharks may have been related to deeper depths selected by zooplankton prey after 1200 h, behaviour which acted to reduce directly the likelihood of sharks occurring in the surface layer as the day progressed. Even though an effect of time of day on minimum zooplankton density was not evident in this study, samples taken over a greater depth range than the top 10 m in future studies may help to determine precisely why the surface-swimming duration of basking sharks decreased as day progressed.

The results of the present study describe some aspects of foraging behaviour in basking sharks, but perhaps more importantly, it draws attention to survey design criteria for estimating basking shark populations. Our results indicate that about 50% of the variation in surface-swimming duration of basking sharks can be accounted for by zooplankton density in the surface layer and time of day. Hence, surveys in areas with low abundance of near-surface zooplankton prey preferred by basking sharks (predominantly calanoid copepods; Sims & Merrett, 1997) will have a lower probability of sighting sharks than those conducted in more productive areas, e.g. tidal fronts (Sims & Quayle, 1998). Moreover, the probability of sightings may decrease in the afternoon due to downwards migration of important zooplankton species.

Even though basking shark population size in any region of the world has yet to be estimated using robust scientific techniques (e.g. Barlow, 1995; Barlow et al., 2001), this species is listed as endangered in the north-east Atlantic (Hilton-Taylor, 2000), presumably as a result of at least two centuries of exploitation (Pawson & Vince, 1999). Therefore, shipborne or aerial surveys aimed at determining population sizes of basking sharks are urgently required. Such surveys would benefit from bias-reduction and thus more accurate population density estimates if search effort is stratified according to time of day and observed differences in prey abundance.

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