

Annual social behaviour of basking sharks associated with coastal front areas

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Comparatively little is known about reproductive behaviour in wild sharks as it has proved extremely difficult to study, especially in large pelagic sharks. Here we describe annual courtship-like behaviour in the second-largest fish species, the basking shark (*Cetorhinus maximus*), from 25 separate episodes observed and tracked during a five-year study period (1995–1999) off south-west England. Social behaviours observed between paired, or three or four, sharks were consistent with courtship behaviours seen in other shark species, namely nose-to-tail following, close following, close flank approach, parallel and echelon swimming. Mature individuals between 5 and 8 m total body length (L_T) exhibited these behaviours whereas smaller sharks (3–4 m L_T) did not. Lead individuals were identified as female on a number of occasions and interactions were prolonged; the longest continuous observation of socializing was 1.8 h, although intermittent track data indicates bouts may last for up to 5–6 h. Locations of courtship-like behaviour events were not distributed randomly and were significantly associated with thermal fronts. Our results indicate that putative courtship behaviour occurs between May and July along oceanographic fronts, probably as a consequence of individuals aggregating to forage in rich prey patches before initiating courtship. Thus, locating the richest prey patches along fronts may be important for basking sharks to find mates as well as food in the pelagic ecosystem. As courtship-like behaviours occur annually off south-west England we speculate that this region may represent an annual breeding area for this protected species, but mating itself probably takes place at depth as it was not seen at the surface.

Keywords: courtship; breaching; reproduction; sea surface temperature; tidal fronts

1. INTRODUCTION

Courtship behaviours are used by animals to attract potential mates and as a prelude to mating. The significance of courtship between sexes is primarily associated with species identification and assessment of potential mates (McFarland 1993). Very little is known about the courtship and mating behaviour of sharks, especially pelagic sharks (Tricas & Le Feuvre 1985). Actual reproductive behaviours such as courtship, pairing, copulation or post-copulatory activities have been described in only nine out of the 380 or so species of sharks and most of these have been for captive animals (Carrier *et al.* 1994). The reproductive strategy of sharks is characterized by slow growth to sexual maturity and low fecundity, which, together with the predominance among pelagic species of live bearing and maternal input (Dulvy & Reynolds 1997), puts these fishes at particular risk from fisheries exploitation (Pratt & Casey 1990). Therefore, identifying courtship and mating locations of pelagic sharks and the spatio-temporal distribution of reproductive events will provide important data on the extent and frequency of breeding areas for particular species globally.

Reproduction in the basking shark (*Cetorhinus maximus*), the world's second-largest fish, has been studied only from anatomical examinations of fishery-caught individuals (Matthews 1950). These studies suggest breeding occurs during early summer but apart from anecdotal behavioural observations of interactions between sharks

before capture, there have been no detailed studies of social or courtship behaviour on an interannual basis. One reason for the lack of basic information on reproductive behaviour in this large, active shark species is that accurate observations of behaviour over long time-periods in remote sea areas are necessary to identify specific activities.

Elements of courtship and putative mating behaviours among a group of 13 basking sharks at the surface were recently recorded for a 5-min period off the coast of Nova Scotia, Canada (Harvey-Clark *et al.* 1999). During this short observation period of a single group, interactions consistent with general elasmobranch reproductive behaviours were identified (e.g. following, flank approach). But although these observations are timely in view of our lack of knowledge on reproduction in this species, it was not possible for the authors to verify the sex of individuals exhibiting these behaviours, to characterize the behaviours over longer time-periods for quantitative comparison with those seen in other shark species or to determine courtship duration and its spatio-temporal occurrence. In this paper we describe 25 separate observations and trackings of courtship-like behaviour in basking sharks made during a five-year study of their behaviour. These results represent the first detailed investigation of annual social and putative courtship behaviour in this species and the only detailed natural observations for a shark in the order Lamniformes. Our findings identify ecologically important thermal-front regions off south-west England as key aggregative features for social behaviour in this protected shark species.

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2. STUDY ANIMAL AND METHODS

The basking shark feeds on zooplankton and is distributed in warm-temperate to boreal waters circumglobally (Compagno 1984), but apart from this much of its life history and whereabouts throughout the year remain unknown (Kunzlik 1988; Sims 1999). Recent studies have shown that this species forages selectively on specific zooplankton assemblages along thermal-front systems in shallow coastal regions of the north-east Atlantic from May to August (Sims *et al.* 1997; Sims & Merrett 1997; Sims & Quayle 1998). Annually, numerous groups of two to 12 basking sharks, ranging in size from 3 to 8 m total body length (L_T) feed in rich zooplankton patches along seasonally persistent fronts off the south-west coast of England (Sims *et al.* 1997; Sims & Quayle 1998) providing an unparalleled opportunity for their close study.

(a) Surveys and behaviour observations

Daytime surveys for surface-feeding *C. maximus* were conducted from a 10 m research vessel within a 350 km² study area off Plymouth, UK, in the western basin of the English Channel (50°16'N, 4°09'W), between March and October in 1995, May and August in 1996, and May and July in 1997 and 1999. During these periods day surveys were conducted when weather permitted, generally when wind speeds were Beaufort Scale force 4 or less, as calm seas increase the probability of sighting surfacing sharks. Further surveys of shorter duration were undertaken at two other locations off the south-west coast of England: from the eastern shore of the Lizard peninsula, south Cornwall (50°16'N, 5°08'W), in May 1998, and from the shore and a 10 m vessel off Padstow, north Cornwall (50°35'N, 4°59'W), in July 1999.

When basking sharks were encountered during surveys, body lengths were estimated using the method given in Sims *et al.* (1997) and individual- and group-feeding sharks were tracked visually, and measurements of zooplankton density and sea surface temperature (SST) taken at intervals. Apart from normal surface-feeding behaviours exhibited by solitary basking sharks, individuals of between 5 and 8 m L_T that aggregated in dense zooplankton patches were seen to interact socially by exhibiting close-following behaviour. Separate episodes of close-following behaviour between basking sharks were recorded during the study period ($n = 25$), and from these 12 tracks of routes taken by sharks during interactions were recorded in 1996–1997, of which five were fine-scale trackings of swimming paths. Broad- and fine-scale tracks were recorded and reconstructed according to the methods given in Sims & Quayle (1998). Briefly, we stayed within 10–50 m of sharks during broad-scale tracking, plotting our location using a global positioning system (GPS) (Garmin 120S or Valstat 03; MLR Electronics, France). Fine-scale foraging routes were determined by vectors (when the vessel was within 10 m of individual sharks) using the time each shark spent on successive course headings (obtained from a hand-held digital compass, with headings recorded in real time on audiotape) multiplied by the mean swimming speed, to calculate estimated distance travelled between course deviations. Feeding cruising speeds were measured for six sharks (not engaged in close following) using on-board differential GPS (Valstat 03) and a digital flow-meter (Solomat 520c) attached to a towed propeller (General Oceanics 2030R, Miami, FL, USA) (Sims & Quayle 1998). From these measurements, a mean swimming speed of $0.97 \pm 0.03 \text{ m s}^{-1}$ ($n = 59$ determinations, mean $L_T = 4.7 \pm 1.1 \text{ m}$)

was used to estimate distances travelled from time spent on successive course headings. Tracks of close-following sharks were reconstructed graphically using the compass headings and data on distance travelled. In addition, when the weather conditions were perfectly calm, the sex of basking sharks involved in following behaviour was determined by recording presence or absence of male claspers in the ventral pelvic region.

(b) Shark positioning analysis

Photographs and videotape recordings of following behaviours were taken at regular intervals during the longest of the 12 tracks obtained. From these, the relative distance between sharks showing following behaviour was calculated. Relative distances between individuals could be determined because their first dorsal and caudal fins (and snouts also on occasion) showed above the water allowing direct comparisons of body length to be made between animals. When the snout (rostrum) tip was not visible above the surface the distance from rostrum tip to first dorsal fin tip was calculated by multiplying the first dorsal fin tip to caudal fin tip distance by a scaling factor of 0.84 (Compagno 1984). The relative distance between the caudal fin tip of the lead shark and the rostrum tip of the following shark was calculated for all photographed interactions, and individual distances were assigned to 0.5 body-length (BL) classes (relative to the lead shark's caudal fin tip). Hence, following-behaviour type was described numerically according to the different BL increment classes: body position of the rearward shark between -1 and -0.5 BL of the lead shark denoted parallel swimming; between -0.5 and 0 BL was close flank approach; between 0 and 0.5 BL was nose-to-tail following; and 0.5 – 1 , 1 – 1.5 and 1.5 – 2 BL classes denoted the rearward shark following at increasing distances. Horizontal positions of following sharks (left, centre or right) in relation to the lead shark were also determined from the same photographs. Differences in frequency of observed body positions of interacting basking sharks compared with those expected assuming equal frequency ratios between different positions were analysed statistically using χ^2 goodness-of-fit tests.

(c) Spatio-temporal distribution of behaviours

Positions of individual incidences of close-following behaviour between sharks, determined using GPS, were mapped onto false-colour images of SST taken by the Advanced Very High Resolution Radiometer aboard National Oceanic and Atmospheric Administration satellite 14. Images of SST used for mapping were those taken at times broadly coincident with times when close-following behaviours were observed but during night-time so as to avoid surface warming anomalies associated with daytime images that can obscure the location of the frontal boundary. In 1997, however, extensive cloud cover during much of May and June (when close-following behaviour events were seen) meant that an SST satellite image taken on 8 July 1997 was used.

A thermal front is a region characterized by a larger-than-average horizontal gradient in water temperature, which forms a boundary between warm, stratified and cold, mixed waters (Le Fèvre 1986). The heterogeneity of water-mass type present in the study areas in each year between 1996 and 1999 at the times when shark social behaviours were observed was determined by defining on the SST maps the areas covered by stratified, mixed and frontal regions, and counting the number of square kilometres attributable to each of these thermal categories. Locations of fronts on maps were characterized as the

Table 1. Summary of thermal-front characteristics and temporal distribution of close-following behaviour events

year	date and time of sea surface temperature satellite image	frontal temperature gradient (°C)	front mean width (km, \pm 1 s.d.) ^a	dates between which social interactions were observed	number of days when social interactions were observed	number of different pairs or three or four sharks	mean water temperature (°C, \pm 1 s.d.)
1996	13 June, 03.02	3.0	3.1 \pm 1.3 (18)	10 May–17 July	6	6	14.2 \pm 1.1
1997	8 July, 02.29	1.5	5.3 \pm 2.7 (28)	29 May–13 June	3	6	14.3 \pm 0.6
1998	17 May, 03.47	3.0	4.6 \pm 1.9 (30)	16 May	1	2	12.5
1999	18 July, 04.52	1.5	5.0 \pm 3.0 (21)	17–21 July	3	11	14.2 \pm 0.3

^a Number of determinations in parentheses.

regions between stratified and mixed water masses over which the steepest gradient in SST occurred. Front widths were quantified on maps by measuring the shortest distance over which this largest change in SST occurred at 1 km intervals along the horizontal axis of the front (table 1). Between 18 and 30 width determinations were made for fronts on each SST map. A χ^2 -test was used to examine the frequency of individual close-following behaviour events associated with each water-mass type.

Randomness in spatial distribution of individual close-following behaviour episodes was also tested by dividing the study-area maps for all years into 58 equal-area squares (each of 30 km²). First, the expected number of behaviour events per square was calculated using the Poisson probability distribution (Zar 1999). The expected number of squares containing no close-following behaviour events was calculated to be 38, whilst a single record of social behaviour was expected in each of 16 squares, two events in each of only three squares, and only one square containing three or more events was predicted. The differences between observed frequencies of behaviour events in map grid squares and those expected from Poisson probabilities were compared using a χ^2 -test.

3. RESULTS

Surveys for basking sharks were conducted on 203 days over the five summer seasons with a total search time of 1372 h. Single and/or groups of sharks were seen on 45 survey days between 1995 and 1999. Close-following behaviours between sharks were seen on 13 of these days; none were observed in 1995. Over these 13 days we recorded 25 separate bouts of close-following behaviour between different pairs, or between three or four sharks (table 1). These behaviours were not seen within a discrete time-period common to all 13 days but occurred throughout the daytime-period of observation (08.00–18.00). The first time in any year that social behaviours between basking sharks were observed was on 10 May, and the latest was 21 July (table 1).

The close-following (social) behaviours were classified as nose-to-tail following (0–0.5 BL behind), following at > 0.5 BL behind, close flank approach, parallel swimming, and echelon swimming (when two or more sharks followed an individual to form an echelon formation). Close-following behaviours were observed between pairs of sharks and between three or four individuals but closely interacting groups of more than four sharks at the surface were not seen. The sizes of basking sharks exhibiting following behaviour were 5–8 m L_T , with the majority of individuals being 6–7 m L_T . On three occasions (10 May 1996, 5 June 1996, 7 June 1996) when

nose-to-tail following was seen between a pair of sharks, the leading shark was identified as female. Smaller sharks (3–4 m L_T) were often also present in zooplankton patches but were not seen to engage in following behaviours at any time during the study.

Out of the 25 following-behaviour events recorded, 12 trackings were made, five of which were fine-scale tracks (table 2). Lead sharks undertook convoluted swimming paths similar to those seen in solitary, feeding basking sharks (see tracks in Sims & Quayle 1998). Rearward sharks made identical adjustments in their swimming trajectories indicating they were following precisely the movements of the shark in front. On a broader scale, however, sharks were sometimes seen to swim on large circular courses consisting of 180°, 360° or figure-of-eight turns (mean = 0.25 turns min⁻¹, $n = 4$ tracks analysed). In contrast with the almost continuous filter feeding seen in solitary individuals, sharks engaged in following behaviour spent significant periods with their mouths closed, indicating feeding was secondary during this particular activity. Analysis of shark body position interrelationships taken from photographs and video sequences ($n = 42$) demonstrated that sharks following others at the surface were most frequently seen swimming nose-to-tail within 0.5 BL of the leading shark (χ^2 -test, $\chi^2_{0.05,5} = 11.07$, $\chi^2 = 27.99$, $p < 0.001$; figure 1a). Nose-to-tail following within 0.5 BL of the lead shark was nearly twice as frequent as close flank approach to the lead shark by the rearward shark (figure 1a). Nose-to-tail following was three times more common than following behaviour at distances greater than 0.5 BL from the lead shark, whilst parallel swimming occurred only twice in photographed interactions (figure 1a). Rearward sharks were observed to swim on the left and right sides of the lead shark more frequently than directly behind but this difference was not significant (χ^2 -test, $\chi^2_{0.05,2} = 5.99$, $\chi^2 = 2.71$, $p > 0.25$; figure 1b).

Out of the time basking sharks conducted following behaviour at the surface where direct observation was possible, the median observable (track) time was 72.5 min (mean = 59.4 min, range = 5–107 min, $n = 12$; table 2). The limit in observation time was due to sharks diving beneath the water's surface and being lost to sight, rather than being observed to cease social following activity. During the study we did not see basking sharks break off following behaviour at the surface. Nevertheless, two discontinuous observations in addition to the continuous trackings suggested a possible time-frame for duration of close-following behaviour. On 10 May 1996, two 5 m L_T sharks showed following behaviour and the lead shark was identified as female. The pair exhibited nose-to-tail

Table 2. Duration of observable close-following behaviour between basking sharks and the occurrence of breaching during trackings

(Numbers in parentheses each represent the duration between first observation of close-following between basking sharks and the subsequent re-sighting of one or both of the individuals originally engaged in close following.)

date	observable close-following time (h)	number of sharks interacting	number of breaches during and or after close following
10 May 1996	1.3 (5.8)	2	0
28 May 1996	1.7 (< 23.2)	2	0
3 June 1996	0.1	2	1
5 June 1996	1.6	3	2
7 June 1996	1.8	3	2
17 July 1996	0.2	2	0
29 May 1997	0.5	2	0
12 June 1997	0.4	3	0
12 June 1997	1.2	3	1
13 June 1997	0.3	2	1
16 May 1998	1.6	2	0
18 July 1999	1.3	3	2

following lasting 70 min, whereupon the pair dived at 11.45 and were lost from sight. At 16.30 these two sharks (identifiable from dorsal-fin and body markings) were re-sighted close to their original position and still engaged in nose-to-tail following behaviour. If these sharks were in constant association between our surface sightings it indicates that close following between this pair lasted for a minimum of 5.8 h. On 28 May 1996, at 12.15, two sharks exhibiting following behaviour were tracked for 1.7 h before they dived. The next day, *ca.* 21.5 h later, the larger of the two sharks was sighted at the surface and further close observation confirmed that this shark was solitary and feeding almost continuously.

During six of the 12 trackings of sharks engaged in following behaviour, single or multiple full breaches occurred near to the individuals being tracked (table 2). A full breach consisted of a basking shark leaping clear of the water and falling on its side or back against the water's surface. One shark that breached parallel with, and *ca.* 7 m from, the research vessel with its ventral surface facing toward one of us (D.W.S.) was female and *ca.* 6–7 m L_T .

Close-following behaviours were observed between 0.5 and 20 km offshore in three main locations around the south-west coast of England (figure 2) in water depths between 20 and 55 m. Following behaviours were only seen when sharks were aggregated in rich zooplankton patches along thermal fronts (e.g. patch density in 1997: median, 1.80 g m⁻³; total number of zooplanktons, 2324.6 m⁻³; $n = 67$ samples). Front and non-frontal regions were surveyed equally during our study but the locations of basking sharks exhibiting social following behaviour were not distributed randomly (Poisson probability test, $\chi^2_{0.05,2} = 5.99$, $\chi^2 = 15.80$, $p < 0.001$) and were significantly associated with thermal-front boundaries rather than areas of mixed or stratified water (χ^2 -test, $\chi^2_{0.05,2} = 5.99$, $\chi^2 = 22.65$, $p < 0.001$; figure 2). Close-following interactions between sharks were observed in

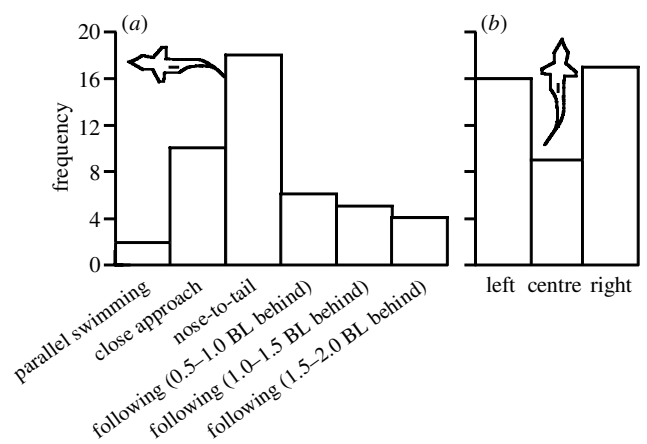


Figure 1. Frequency distributions of (a) behaviour type observed between lead and following sharks, and (b) the horizontal position of rearward sharks relative to the lead individual.

mean water temperatures of 12.5–14.3 °C (table 1) and were seen 3.2 times as frequently on frontal boundaries than on the mixed side of the front, but were not seen in stratified water. SST-map analysis of shark locations was not biased spatially towards frontal regions as these areas made up a mean of $29.7 \pm 2.9\%$ ($n = 4$) of the area analysed each year, with mixed and stratified regions making up the remaining 39.5% and 30.8%, respectively.

4. DISCUSSION

Basking sharks surface feed in coastal waters during the summer and are entirely solitary in this behaviour. They do form loose aggregations at times, however, because individuals often feed in the same discrete patches of zooplankton, sometimes within relatively small areas (Sims & Quayle 1998; Sims 1999). Individual sharks actively avoid each other when foraging in patches by swimming away from conspecifics that come too close. In contrast, social behaviour between basking sharks, consisting of organized or synchronized swimming movements, has not often been observed and has not been studied quantitatively (Matthews 1950; Maxwell 1952; Harvey-Clark *et al.* 1999). The present study describes interannual observations of social (close-following) behaviours between basking sharks at the surface in three main locations around the south-west peninsula of England over five summer seasons, which represents the first, to our knowledge, sustained scientific investigation of social behaviour in this species.

The results show that sharks between 5 and 8 m L_T engage in close-following behaviour, often for an hour or more, along thermal fronts in coastal waters off south-west England from May to July. Whilst our observations have not determined the precise function of close-following behaviour in basking sharks, our results point to the possibility that close following is a courtship-related activity in this species. Anatomical evidence from a previous study supports the hypothesis that basking sharks undertake mating during the summer months off the British Isles (Matthews 1950). Adult basking sharks caught off west Scotland during the summer of 1946 were in breeding condition and showed signs of having recently

copulated (Matthews 1950). Females bore recent or unhealed cloacal wounds inflicted by the claw on the clasper of the male during copulation. A female examined closely contained many spermatophores (packets of sperm), while both males and females carried abrasions near the pelvic area possibly due to contact of the roughly denticulated skin in this region made during pairing (Matthews 1950). On the basis of these data, Matthews (1950) concluded that the breeding season was in 'full swing' during the second half of May off west Scotland. However, he was not able to determine breeding-season length as poor weather prevented further catches and dissections being made in July and August. Our observations of annual close-following behaviour in basking sharks off south-west England are temporally coincident with the period when Matthews thought courtship and mating occurred in this species off Scotland.

In the present study, close following between basking sharks was not associated primarily with food capture but presumably occurred for other reasons as individuals spent considerable periods of time not feeding during interactions. In contrast, during foraging they are solitary and feed almost continuously. Our observations were similar to following behaviours seen over a 5-min period in a group of basking sharks at the surface of deep water (*ca.* 130 m) off Nova Scotia, Canada (Harvey-Clark *et al.* 1999). In the latter study, nose-to-tail following, flank approach, close approach including rostrum-body contact, parallel and echelon swimming and possible pectoral biting were observed and interpreted to be consistent with courtship and mating behaviours. Similar behaviours have also been seen in other shark species. There are descriptions and observations of close-following behaviour in a number of shark species, including blacktip (*Carcharhinus melanopterus*) and whitetip (*Triaenodon obesus*) reef sharks in the wild (Johnson & Nelson 1978), captive bonnethead sharks (*Sphyrna tiburo*) (Myrberg & Gruber 1974) and captive (Klimley 1980) and free-ranging nurse sharks (*Ginglymostoma cirratum*) (Carrier *et al.* 1994).

In wild nurse sharks four distinct stages of mating were identified: pre-coupling, coupling (female fin grasping by male), positioning and alignment, and insertion and copulation (Carrier *et al.* 1994). The most frequent behaviour typifying pre-coupling or courtship in nurse sharks was males following females by less than a BL. The duration of following behaviour was frequently longer than the 15 min seen in captive *G. cirratum* (Klimley 1980; Carrier *et al.* 1994) but always less than 90 min, before pectoral-fin grasping (coupling) occurred prior to alignment and copulation (Carrier *et al.* 1994). Parallel swimming was also seen to occur between nurse sharks engaged in courtship (Carrier *et al.* 1994). Interestingly, in the present study nose-to-tail following (0–0.5 BL behind) was the most frequently observed behaviour between interacting basking sharks, together with close flank approach, although parallel swimming was less common. The duration of close-following behaviour between *C. maximus* in this study lasted at least 1.8 h (our longest continuous track) but may last for up to 5.8 h (our longest intermittent observation). The median duration of close-following behaviour in basking sharks was similar to the longest observed in nurse sharks. Therefore by

comparison with other shark species, our observations of prolonged close-following behaviour between basking sharks suggest this activity may form part of courtship behaviour.

In support of this suggestion it was apparent that this activity was only seen in individuals between 5 and 8 m L_T . Despite smaller sharks being present in food patches, they did not engage in close-following behaviour. Male basking sharks have been estimated to become sexually mature at lengths of 4.6–6.1 m (Matthews 1950; Compagno 1984; Kunzlik 1988). The length at which females mature is not known (Kunzlik 1988) although lengths of 7 m L_T (Matthews 1950; Parker & Stott 1965) and between 8.1 and 9.8 m L_T (Compagno 1984) have been suggested. Clearly, the observed lengths for basking sharks engaged in courtship-like behaviour off south-west England in this study do not contradict previous estimates for the expected lengths of sexually active individuals of this species.

We also verified during three different interactions that lead sharks were female. It proved impossible to identify the sex of the rearward shark during close-following events because when slowly approached they would descend deeper in the water column, but all the time still pursuing the female. On several occasions, however, clasper-like structures were seen trailing from the pelvic fins of rearward sharks, although we cannot discount the possibility that these structures were not claspers but parasitic sea lampreys (*Petromyzon marinus*), which sometimes attach to the pelvic fins of basking sharks. We believe, however, that rearward sharks in this study were likely to be male because Maxwell (1952), fishing for basking sharks off Scotland, harpooned two rearward sharks in a group of five 'that followed each other almost nose to tail' and found them both to be male. One of these males also emitted a large quantity of spermatophores (Maxwell 1952). This anecdote, taken together with our formal observations of prolonged close-following behaviour with females as lead sharks and the lengths of sharks involved being consistent with the expected lengths of sexually mature individuals, does not suggest against the proposal that the social behaviour we observed in *C. maximus* was courtship.

Breaching by basking sharks also occurred during observed social interactions in the present study. Breaching is thought to function as social communication between predatory white sharks when entering their seasonal reproductive mode (Pyle *et al.* 1996) and between filter-feeding whales, where it may also be used as a courtship display (Whitehead 1985). Indeed, most breaches by humpback whales and right whales are seen when males engage in intraspecific competition for a particular female (Whitehead 1985). Interestingly, in the current study only large basking sharks breached, and only when three sharks interacted were multiple breaches observed in close succession. These may have been the result of courtship displays during male-male competition. On one occasion we identified a breaching shark to be female and of sexually mature size implying breaching behaviour in the summer months could also function in females to announce receptivity to mating. Similarly, in basking sharks Matthews & Parker (1951) obtained detailed information on frequencies of breaching, which

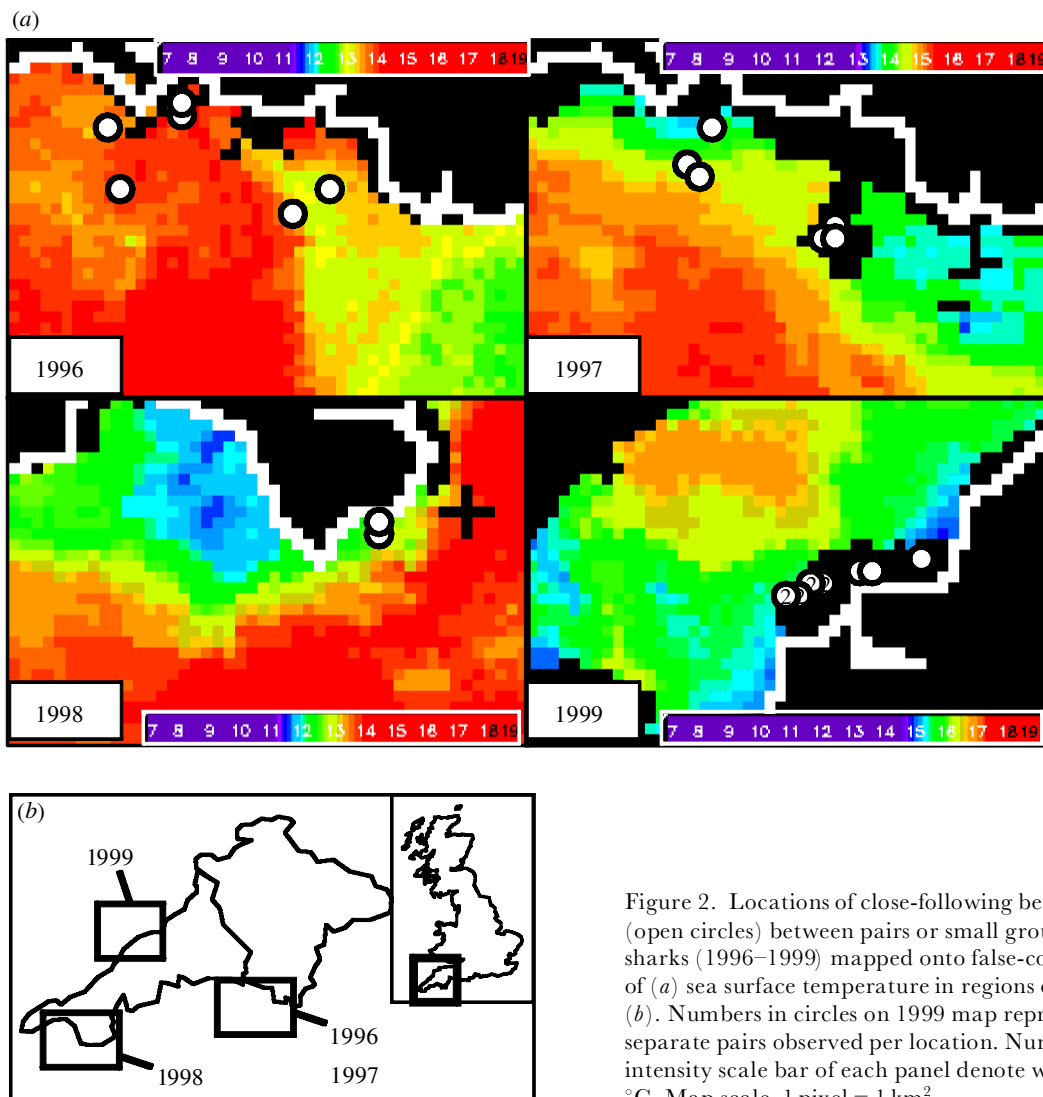


Figure 2. Locations of close-following behaviour events (open circles) between pairs or small groups of basking sharks (1996–1999) mapped onto false-colour satellite images of (a) sea surface temperature in regions off south-west England (b). Numbers in circles on 1999 map represent the number of separate pairs observed per location. Numbers on the colour-intensity scale bar of each panel denote water temperature in °C. Map scale, 1 pixel = 1 km².

stated that it was most prevalent at the mating time between May and June. Clearly our results are consistent with this finding, which further supports the idea that basking sharks undertake courtship during the summer months off south-west England.

Basking shark following behaviours observed by us were significantly associated with seasonally persistent fronts rather than mixed or stratified water. This is similar to the spatial distribution recorded previously for surface foraging locations chosen by members of this species (Sims & Quayle 1998). We observed close-following behaviours only when large sharks were aggregated in relatively high numbers in rich zooplankton patches, which suggests patch aggregation and the resultant close proximity of mature individuals was a controlling factor in whether putative courtship was sighted by us. In addition, although basking sharks were seen at the surface on 45 days over five summer seasons, close-following behaviour between different pairs or small groups of sharks occurred on only 13 days. Furthermore, between 1 and 3.7 separate pair or small-group social interactions were seen on each of these days (mean = 2.2, s.d. = 1.1, $n = 4$ years) implying courtship-like interactions were temporally clustered. Spatial analysis using Poisson

probabilities for randomness in social-behaviour location showed close-following events were not randomly distributed but were also clustered. In the analysis this was predominantly due to a much lower number of grid squares containing a single social interaction compared to that predicted, while three or more observed interactions per square occurred more frequently than predicted. Taken together these results indicate that when social interactions between basking sharks do occur, they occur more frequently when particular aggregations form in zooplankton patches along fronts. Thus, the occurrence of close-following activity could be related to the density of sexually mature individuals present in these areas, as might be expected if the behaviour we observed was indeed courtship.

Mammalian species' mating systems are thought largely to be determined by the spatial and temporal distribution of resources controlling the distribution of receptive females (Clutton-Brock 1989). Factors such as predation pressure and the behaviour of conspecifics may modify the system but in general the more that a resource is defensible (usually by males), the more likely it is that a polygamous mating system of some type will develop (Clapham 1996) leading to the clustering together of

many receptive females. On the basis of this general rule it is predicted that humpback whale (*Megaptera novaeangliae*) females should not cluster, as zooplankton are in low supply or absent and so males cannot monopolize more than one female at a time. This prediction is supported by observations that humpback whales exhibit no territoriality on the breeding grounds (Tyack 1981); females are not clustered but unpredictably distributed, and hence males compete for single rather than multiple females (Clapham 1996). Like humpback whales, basking sharks feed on patchily distributed zooplankton and so courtship and mating in this species may also be influenced by the spatial and temporal distribution of prey resources. However, although breeding in the absence of prey resources may lead to wide and unpredictable distributions of females (as it does in *M. novaeangliae*), our results show basking sharks exhibit putative courtship only when among surface-feeding groups. One individual we tracked that was engaged in following behaviour was re-sighted 21.5 h later and was solitary and feeding continuously, so courtship may be an activity undertaken within foraging bouts. Assuming close-following behaviour constitutes a part of courtship we suggest that solitary *C. maximus* aggregate in front-located prey patches to feed, possibly by using fronts as foraging 'corridors' (Sims & Quayle 1998), and that these groupings increase the likelihood of mature individuals meeting to initiate courtship. Therefore, finding the richest zooplankton patches in coastal front areas during the summer may be important to basking sharks for finding mates as well as food in the large expanse of the pelagic environment.

Actual mating behaviour was not seen between basking sharks in our study but this should not be taken to indicate that annual close-following behaviour is not part of pre-copulatory behaviour in this species. In comparison, despite thousands of hours of observations of humpback whales on their breeding grounds, actual copulation has yet to be observed, even though courtship behaviours have been identified for humpbacks by analogy with behaviours seen prior to mating in other whale species (e.g. right whale, *Eubalaena australis*) (Clapham 1996). Clapham suggested the reason for the lack of direct observation of mating in humpback whales was because they copulate exclusively underwater. We suggest that basking sharks probably also mate predominantly at depth.

The results of our five-year study demonstrate for the first time, to our knowledge, that basking sharks engage in annual social behaviour in addition to foraging when aggregated in prey patches along fronts off the south-west coast of England. We propose that the behaviours during the prolonged interactions we observed (e.g. nose-to-tail following, flank approach) are, by analogy with other shark species, consistent with courtship behaviour. This suggests that fronts are oceanographic features of importance not only as feeding areas for south-west coast basking sharks, but may also be areas where annual courtship and breeding takes place. Because basking sharks are listed as vulnerable on the IUCN–World Conservation Union *Red list of threatened animals* (1996) and no breeding areas have yet been identified for this species anywhere in the world, further research effort should be aimed at determining whether mating itself occurs during the summer off south-west England. The fact that the duration of

summer stratification in sea coastal areas is likely to be altered by climate warming (Wood & McDonald 1997) raises the question of how predicted changes in the persistence of thermal fronts will affect the timing and location of social and foraging behaviour in this species. Furthermore, because, as seems likely from our findings, basking sharks engage in courtship at or near the surface close to shore annually between May and July, there is concern that these important behaviours may be at future risk of increased disturbance from anthropogenic sources, such as commercial shipping, leisure and ecotourism vessels.

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