

Circles in the sea: annual courtship “torus” behaviour of basking sharks *Cetorhinus maximus* identified in the eastern North Atlantic Ocean

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Funding information

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Abstract

Groups of basking sharks engaged in circling behaviour are rarely observed, and their function remains enigmatic in the absence of detailed observations. Here, underwater and aerial video recordings of multiple circling groups of basking sharks during late summer (August and September 2016–2021) in the eastern North Atlantic Ocean showed groups numbering between 6 and 23 non-feeding individuals of both sexes. Sharks swam slowly in a rotating “torus” (diameter range: 17–39 m), with individuals layered vertically from the surface to a maximum depth of 16 m. Within a torus, sharks engaged in close-following, echelon, close-flank approach or parallel-swimming behaviours. Measured shark total body lengths were 5.4–9.5 m (mean L_T : 7.3 m \pm 0.9 s.d.; median: 7.2 m, $n = 27$), overlapping known lengths of sexually mature males and females. Males possessed large claspers with abrasions that were also observed on female pectoral fins. Female body colouration was paler than that of males, similar to colour changes observed during courtship and mating in other shark species. Individuals associated with most other members rapidly (within minutes), indicating toroidal behaviours facilitate multiple interactions. Sharks interacted through fin–fin and fin–body contacts, rolling to expose the ventral surfaces to following sharks, and breaching behaviour. Toruses formed in late summer when feeding aggregations in zooplankton-rich thermal fronts switched to non-feeding following and circling behaviours. Collectively, the observations explain a courtship function for toruses. This study highlights northeast Atlantic coastal waters as a critical habitat supporting courtship reproductive behaviour of endangered basking sharks, the first such habitat identified for this species globally.

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1 | INTRODUCTION

The process of courtship between animals includes behaviour that is a response of an individual to signals or individuals in its environment (West, 2009). Courtship behaviours between sexually mature individuals function to recognise species and sex, to attract potential mates, to increase sexual receptivity and to enable pre-copulatory choices of partner by both males and females and as a prelude to mating itself (McFarland, 1993). Courtship behaviour frequently involves conspicuous, repetitive, stereotyped movements between the sexes which, when prolonged, may result in groups of individuals forming to assess each other's reproductive potential and to compete for access to a potential mate or mates (McFarland, 1987). Group formation during courtship has been documented in large marine predators such as sharks (Carrier *et al.*, 1994; Jacoby *et al.*, 2012; Pratt & Carrier, 2001). Nonetheless, the courtship and mating behaviours of sharks are poorly known for the majority of species, having been described for only a few of over 500 species, with most observations being of captive individuals (e.g., Parsons *et al.*, 2008; Pratt & Carrier, 2001). Moreover, the courtship and mating behaviours of highly mobile pelagic sharks remain almost entirely unknown as the sustained observations needed for researchers to identify the function of specific behaviours are challenging to obtain in the open ocean (e.g., Salinas-de-Leon *et al.*, 2017). Consequently, there is limited information on the form and progression of reproductive behaviour of pelagic sharks, including which habitats support courtship and mating.

Bridging the knowledge gap of which behaviour patterns comprise courtship and thus where and when reproductive behaviour occurs is important for conservation and management of threatened sharks. Shark populations are particularly vulnerable to overfishing on account of slow growth rates, late age at sexual maturity and relatively low fecundity, which makes them more prone to extinction risk than most other marine fishes (Dulvy *et al.*, 2014). Large declines in global abundance of oceanic pelagic sharks driven by overfishing have occurred over the past half century (Pacoureau *et al.*, 2021) as a result of substantial overlap of preferred shark habitats co-occurring with industrialised fisheries, within which fishing-induced mortality is higher where spatial overlap is greater (Queiroz *et al.*, 2019, 2021). Intense fishing activities occurring in shark-breeding habitats without appropriate management to control catches can potentially lead to overexploitation of sexually mature sharks and more rapid population declines (Mucientes *et al.*, 2009). Therefore, understanding what constitutes courtship behaviour and where courtship and mating occur, particularly for endangered species, is essential for assessing potential targets for spatial conservation of breeding grounds.

The world's second-largest fish, the plankton-feeding basking shark, *Cetorhinus maximus*, is listed on the IUCN Red List as "endangered" in the northeast Atlantic Ocean (Sims *et al.*, 2015), as well as in other regions globally where it occurs (Rigby *et al.*, 2021). In the eastern North Atlantic, basking sharks have been the subject of targeted fisheries for over 200 years (Sims, 2008), with >100,000 individuals caught between 1946 and 1997 alone (Sims & Reid, 2002). Despite the large numbers encountered, captured and processed by fishing

operations over that time, key aspects of reproductive biology and ecology of the basking shark remain enigmatic. For example, courtship location and mating areas have not been confirmed for any region within its range (Sims, 2008), and in the northeast Atlantic only three pregnant females have ever been reported (Francis & Duffy, 2002). Pennant (1812) recorded a 30 cm long embryo in a basking shark; Sund (1943) reported a female harpooned in mid-western Norway being towed to shore that gave birth to six pups that were each 1.5–2.0 m long (five began swimming open mouthed at the surface; the sixth was stillborn); and Matthews (1950) noted a fisher's report in western Scotland of a pregnant basking shark they opened containing a 1.8 m long pup.

Anatomical investigations on fishery-caught basking sharks off western Scotland performed in 1946 indicated mating occurred during summer when sharks were in coastal areas in feeding aggregations (Matthews, 1950). Several large females examined were in breeding condition and showed signs of recent copulation, including recent or unhealed lacerations on the vaginal wall inflicted by the male's clasper claw during mating. Another female contained many spermatophores. Therefore, it was concluded that the basking shark breeding season was in "full swing" in the second half of May 1946 off the west coast of Scotland (Matthews, 1950). Although no confirmed basking shark courtship or mating events were reported by Matthews (1950), he noted in June 1947 in the Hebridean Sea, western Scotland, three or four basking sharks "following each other closely in a circular course of narrow radius," a behaviour that was widely different from the usual surface feeding. Matthews (1950) interpreted this to be preliminary behaviour to mate pairing before copulation. Although basking shark mating has not been observed or documented unequivocally in any region, courtship-like and putative mating behaviours have been proposed based on observations of shark groups engaged in close-following swimming behaviour and in echelon and circling formations (Sims, 2008).

Basking sharks in the western and eastern North Atlantic Ocean are most commonly observed when they surface filter-feed on dense patches of zooplankton associated with persistent fronts in coastal and shelf habitats between April and October (Braun *et al.*, 2018; Cotton *et al.*, 2005; Curtis *et al.*, 2014; Lieber *et al.*, 2020; Miller *et al.*, 2015; Priede, 1984; Siders *et al.*, 2013; Sims, 2008; Sims & Quayle, 1998; Sims *et al.*, 1997, 2003, 2005; Skomal *et al.*, 2009). There is usually a peak in surface sightings from May through September coinciding with the seasonal increase in zooplankton abundance (Berrow & Heardman, 1994; Kenney *et al.*, 1985; Sims, 2008; Sims *et al.*, 1997; Witt *et al.*, 2012). Basking sharks are primarily solitary; nonetheless, foraging responses to variations in prey density can lead to the formation of feeding aggregations because sharks exhibit increased area-restricted foraging (slower swimming speeds when filter-feeding; increased turning frequency) where patchily distributed zooplankton abundance is greater (Sims, 1999, 2000; Sims & Quayle, 1998). In the loose aggregations that result from solitary individuals feeding in the same discrete patches of zooplankton, basking sharks are also observed to engage in close-following behaviour, whereby a lead shark is closely followed by another feeding individual directly behind (nose-to-tail or to within one

body length) or in echelon formation, where a shark is rearward within one body length and to the side of a lead shark (Sims *et al.*, 2000). Most often the sharks in following groups continue filter-feeding although on occasion these also include non-feeding individuals (Sims *et al.*, 2000).

Circling behaviour by grouped basking sharks, where each shark within a group follows an individual in front of it to form a rotating circle, has been recorded in several studies since Matthews's (1950) early observation. All observations of large group-circling formations of basking sharks (to date) have been from the western North Atlantic, where following and circling sharks numbering between 13 and 1398 individuals have been recorded on seven occasions between 1980 and 2013 (Crowe *et al.*, 2018; Harvey-Clark *et al.*, 1999; Wilson, 2004). From these sightings, circling has been variably interpreted as courtship behaviour since nearly all sharks observed were not filter-feeding (Harvey-Clark *et al.*, 1999; Wilson, 2004), and as putative mating behaviour on account of fin touching and possible fin biting by sharks (Harvey-Clark *et al.*, 1999), but also as energetically beneficial group foraging behaviour because most following and circling sharks were filter-feeding (Crowe *et al.*, 2018). Although it was proposed over two decades ago that dense zooplankton patches aggregate basking sharks which may then result in social grouping (e.g., close-following behaviour involving males and females) potentially leading to courtship and mating behaviours (Sims *et al.*, 2000), the precise functions of close-following behaviour (Gore *et al.*, 2019) and the large circling groups remain elusive (Crowe *et al.*, 2018). Despite a courtship function being proposed for some large circling groups, the sexes of individual basking sharks within such groups were not determined on those occasions (Crowe *et al.*, 2018; Harvey-Clark *et al.*, 1999; Wilson, 2004), even though the presence of sexually mature females and males is necessary for courtship to be initiated before mate pairing. The sexes present in all previous large group-circling formations could not be identified because groups were observed in offshore locations by aircraft flying at altitudes of between 50 and 305 m (Crowe *et al.*, 2018; Harvey-Clark *et al.*, 1999; Wilson, 2004). Understandably, aerial observations do not allow for the sustained detailed investigations required to assess the function of circling groups. Another reason why detailed studies of basking shark circle formations have yet to be undertaken is that they appear to be rarely encountered in shallow (<100 m depth) coastal waters where sustained interannual studies are more feasible logistically.

Here, this study describes new observations of basking shark group-circling formations and behaviours that occurred in coastal waters off western Ireland and Scotland in the eastern North Atlantic Ocean in four summers over 6 years. Detailed aerial and underwater video recordings were coupled with direct observations of circling behaviours of basking sharks to investigate group function. In particular, recordings were used to (a) determine group size, formation and dimensions; (b) determine sex composition and body lengths of individuals within groups; (c) identify sharks individually to record interactions between them and associated behaviours (including feeding/non-feeding status); (d) quantify the shifts or persistence in interindividual and group dynamics; and (e) determine the seasonal timing and geographical distributions of groups in relation to the environment.

The study shows that close-following echelon formations of non-feeding basking sharks can lead to circle formations and *vice versa*, with the most common circle formation observed with higher numbers of sharks (≥ 6 individuals) being best approximated as a solid "torus" shape.

2 | MATERIALS AND METHODS

2.1 | Animal ethical statement

Behavioural observations and video recordings were made without disturbing the basking sharks encountered. Research adhered to the general advice of the Irish Basking Shark Group's basking shark Code of Conduct (Liamhán Gréine Cód Iompair) (www.baskingshark.ie) and the Shark Trust's Code of Conduct for basking shark encounters and specifically the guidance for swimmers, snorkellers, divers and watercraft handlers.

2.2 | Torus location and environmental data

In geometry a solid torus is a surface of revolution generated by revolving a disk about an axis that is coplanar with the disk in three-dimensional (3D) space, that is, a 3D shape resembling a bagel (Movie S1). The geographic location of each basking shark torus ($n = 19$ distinct groups encountered, numbered T1–T19; Table 1; Figure 1) was recorded from each vessel's Global Positioning System along with associated data on the environment when possible, such as water temperature, zooplankton observations or presence of other megafauna. For Figures 1 and 2 torus locations were overlaid (QGIS, v3.24) on gridded maps of derived sea-surface temperature (SST) gradient (sourced from Copernicus Marine Service Global Ocean OSTIA Sea Surface Temperature and Sea Ice Analysis product, www.copernicus.eu) depicting maximum temperature change per 500 m averaged for the month of August when about 80% of toruses were encountered (between the years toruses were observed and SST data were available, 2016–2020). SST maximum gradient maps were calculated for each pixel by determining the geodetic distance-corrected maximum thermal gradient ($^{\circ}\text{C}$ per 5 km). For Figures S3 and S4, fronts were detected for OSTIA SST rasters for the dates on which toruses were observed, and also for the previous 6 days, using an edge detection method (Cayula & Cornillon, 1995). Front frequency was calculated for the 7 day period for each pixel (number of detected fronts/total number of days).

2.3 | Recording group and individual behaviours

Off western Ireland, basking sharks were encountered from small vessels (6 or 10 m in length), and detailed observations of groups from both airborne drone and underwater videography were made simultaneously for two circling groups (T1 and T16) that were subjected to

TABLE 1 Summary of basking shark circling behaviour events studied off Co. Clare, Ireland, between 2016 and 2021

Torus number	Date	Observation time (hours)	Location	Latitude (°N)	Longitude (°W)	Airborne drone video	Underwater video	Surface video	Maximum number of individual sharks observed	Presence of females and males verified (Y/N)	Filter-feeding observed in circling sharks (Y/N)	Breaching observed (Y/N)
1	18 August 2016	13.00–15.00	5 km off Baltard, Co. Clare	52.734	9.710	✓ ^a	✓ ^b		16	Y	N	Y
2	27 August 2016	15.30–17.00	Southwest of Inishmaan, Aran Islands	52.998	9.694		✓ ^c		20	Y	N	N
3	15 August 2020	17.40–18.30	20.2 km off Baltard, Co. Clare	52.811	9.901	✓ ^d			11	N	N	N
4	15 August 2020	19.20–19.40	12.2 km off Baltard, Co. Clare	52.775	9.800			✓	6	N	N	N
5	16 August 2020	17.00	9.3 km off Baltard, Co. Clare	52.770	9.770			✓	6	N	N	Y
6	16 August 2020	17.40	9.2 km off Baltard, Co. Clare	52.768	9.756			✓	6	N	N	Y
7	16 August 2020	17.40	9.5 km off Baltard, Co. Clare	52.753	9.771	✓ ^d			9	N	N	Y
8	16 September 2020	11.00	West of Inishmore, Aran Islands	53.068	9.753			✓	4	N	N	N
9	28 August 2021	12.11	7 km off Kilkee, Co. Clare	52.717	9.748	✓ ^e		✓	6	N	N	N
10	28 August 2021	11.41	6 km off Kilkee, Co. Clare	52.691	9.744			✓	Two groups	N	N	N
11	28 August 2021	11.57	7.5 km off Kilkee, Co. Clare	52.733	9.726			✓	One group	N	N	N
12	28 August 2021	12.00	7.5 km off Kilkee, Co. Clare	52.699	9.769			✓	8	N	N	Y
13	28 August 2021	11.06	6.5 km off Loop Head, Co. Clare	52.681	9.829			✓	6	N	N	N
14	28 August 2021	12.18	7 km off Loop Head, Co. Clare	52.670	9.863	✓ ^e		✓	6	N	N	N
15	29 August 2021	12.00–15.40	3.5 km off Baltard, Co. Clare	52.736	9.683	✓ ^e	✓ ^f		9	Y	N	Y
16	30 August 2021	12.00–17.30	6.5 km off Kilkee, Co. Clare	52.715	9.729	✓ ^e	✓ ^f		14	Y	N	Y
17	1 September 2021	12.00–17.30	5 km off Kilkee, Co. Clare	52.714	9.706	✓ ^e	✓ ^f		23	Y	N	Y
18	3 September 2021	12.00–17.30	9 km off Kilkee, Co. Clare	52.717	9.772	✓ ^e	✓ ^f		21	Y	N	Y
19	3 September 2021	13.45 h	5 km off Kilkee, Co. Clare	52.692	9.729		✓ ^g		16	Y	N	Y

^aAirborne drone: DJI Phantom 4.^bUnderwater video: Red Epic Dragon 6 k camera, Canon 8–15 mm lens.^cUnderwater photo/video: Nikon D810 SLR/video, Nikon 17–35 mm lens.^dAirborne drone: DJI Phantom 4 Pro V2.0.^eAirborne drone: DJI Mavic 2 Pro.^fUnderwater video: GoPro Hero 3+.^gUnderwater photo/video: Panasonic GH5 4 k video, Olympus 14–28 mm lens.

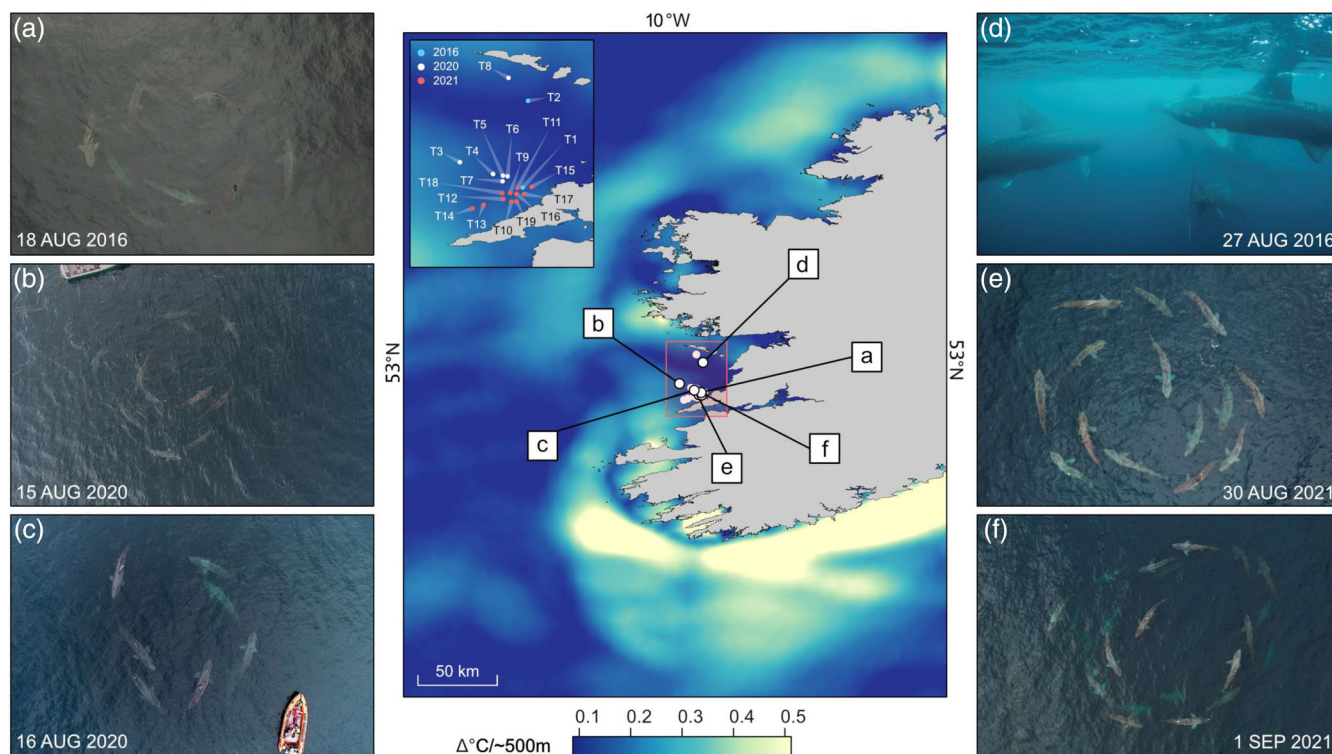


FIGURE 1 Locations of basking shark toruses off western Ireland. (a–f) Locations of all 19 toruses examined in this study, with the locations of the main toruses studied (main panel) between 18 August 2016 and 1 September 2021. Locations shown in relation to average gradients in sea-surface temperature (SST; average for August 2016–2020), denoted by the $\Delta^{\circ}\text{C}/500\text{ m}$ colour scale, that identify toruses close to coastal thermal fronts. Inset to main map panel shows locations of toruses by year. Images: (a) K. O'Sullivan, (d) N. Pfeiffer and (b, c, e, f) S. Berrow/Irish Basking Shark Group (IBSG)

detailed analysis (Table 1 provides date/time, location, equipment and recording methods used). Airborne drone, underwater video and/or surface video recordings were made for the other toruses as detailed in Table 1. For the Inner Hebrides, western Scotland, underwater video was recorded of a pair of circling sharks from a group of four, and both underwater and airborne drone videos were recorded for several groups (Table 2).

Some circling groups observed off western Ireland (T2, T3–8 and T17–19) and off western Scotland (2 August 2019 and 10 August 2020) were not subjected to detailed analysis (see later). Rather, *in situ* observations from these video recordings were used to determine the number of sharks in each torus and to identify any similarities with the composition and behaviour of the closely studied groups.

2.4 | Shark numbers

The numbers of sharks in circling groups were determined from frame-by-frame examination of drone and underwater video or photographic images and by surface observers' visual estimates. The maximum number of sharks in each torus counted by these methods was assumed to be the maximum number present.

2.5 | Torus diameter, rotation speed and inter-shark distances

The torus diameters (outer and inner) of T1 were measured from nine drone images using ImageJ software (National Institutes of Health, Bethesda, MD, USA) where the snorkeller's fin was clearly visible and used as a length scale (each fin was 0.925 m long when flat at the surface). The outer diameter spanned the circular torus and was estimated from three measurements across a circle placed around the outermost sharks visible in each drone still image. The inner diameter was the diameter of the space around which the sharks circled and was estimated by two length measurements. Torus rotation speed was determined from individual drone video images by focal tracking of four individual sharks at the sea surface as they completed each full rotation. Two full rotations were timed for three sharks (two positioned on the outer torus edge and one on the inner edge) and four rotations for a second shark on the inner edge. The over-the-ground swimming speed of one individual at the surface was estimated by measuring the straight-line distance moved (from snout tip to snout tip) between successive video images 4 s apart. Similarly, the number of sharks visible at or near the sea surface was determined from 43 successive drone images 4 s apart. Using the same images for which there was also the snorkeller's fin for length scale, the distances between surface-swimming sharks were estimated using ImageJ by

TABLE 2 Observations of circling behaviour between basking sharks off western Scotland

Date	Location	Airborne drone video	Underwater video	Behaviour type	Number of sharks	Presence of females and males verified (Y/N)	Filter-feeding observed in circling sharks (Y/N)
2 August 2019	56.580° N 6.714° W		✓	Circling	4	Y	N
10 August 2020	56.580° N 6.744° W	✓	✓	Circling	3	N	N

taking the shortest lateral distance between two sharks swimming parallel or in overlapping echelon formation and perpendicular to their direction of movement. In addition, the approximate diameters of T3, T15 and T17 were determined using ImageJ from single drone images of each torus near a 6 m vessel (T3 and T15) and a 10.5 m vessel (T17).

2.6 | Shark body length measurements

Total body length (L_T in m) measurements from close-up drone images were made for two sharks in T1 where the length scale was present, three sharks in T3, four sharks in T4, two sharks in T15 and seven sharks in T17 when they were close to a 6.0 or 10.5 m long vessel used by researchers. Video images were selected when the shark was least curved during swimming movements. Using ImageJ, three sub-lengths were measured per shark (snout to first dorsal fin, first dorsal to caudal-fin peduncle and caudal peduncle to upper caudal-fin tip) and summed up to give total length. A further 18 L_T measurements of nine sharks in T1 were made using the same method from length-scaled drone images at a higher altitude.

2.7 | Identification of individuals, sexes and body colour

For both T1 and T16, the number of sharks in the circling group and sex of the individuals were determined from frame-by-frame examination of underwater video images spanning a period of 10 min. In rotations of a torus past the stationary camera, individuals were identified by the presence of electronic or number tags, unique body markings singly or in combination (including the presence of dark pigmentation spots on the fins), white abrasion/scar marks on the dorsal and lateral surfaces and fins and/or the pattern of natural pigmentation along the side of a shark. Sex was assigned to individually identified sharks when it was possible to verify that claspers (paired male intromittent organs used for spermatophore transfer during internal fertilisation) were present or were not present in video images. Parasitic sea lampreys (*Petromyzon marinus*) were identified when present. It was not possible to mistake lampreys attached near pelvic fins for shark claspers because claspers are darker in pigmentation, thicker and stiffer than lampreys. For all video-recorded toruses the number of females and males was noted when it was certain that they were

different individuals based upon unique markings (rather than counting the same individual passing the video camera multiple times as the torus rotated). Any obvious differences in body colour between individuals in close proximity when circling in a torus were also noted.

2.8 | Female–male positioning and interactions

The positions of females relative to males and to individuals of unknown sex within torus T16 were studied from the analysis of simultaneous airborne drone and underwater video recordings (from 16.50 to 17.10 hours). Underwater video was used to identify each specific individual from a combination of body markings/features, presence of attached tags and presence/absence of claspers (see previous section). These individually identified sharks were then cross-referenced with the simultaneous drone video recording to locate individual shark positions within the torus over time. The positioning of each individual relative to the nearest other individuals within the torus when within a body width of each other (*i.e.*, during close-following, echelon, and close-flank approach or parallel swimming) was determined every 10 s in an 8 min continuous drone video sequence. The frequency with which each individual was thus associated by spatial proximity to any other individual(s) within a body-width distance was recorded in each of the 48 images. In addition, the direction of the association between any two interacting individuals was determined.

Finally, for all toruses, including T16, any incidences of close interactions or behaviours between two sharks such as body touching, biting or body rolling were also recorded when present. Breaching behaviour was recorded when it occurred in a torus or within a 600 m radius of the torus location.

3 | RESULTS

In three summers between August 2016 and September 2021, group-circling behaviours by basking sharks of large body size (Figure 1; Figure S1) were observed off County Clare and County Galway, western Ireland ($n = 19$ distinct groups encountered, numbered T1–19; Table 1) (Figure 1; Movie S1). The groups off Ireland were all located between 6 and 20 km from the coast in Galway Bay, between the Aran Islands in the north and the mouth of the Shannon Estuary in the south. Each circling group comprised a

maximum number of between 6 and 23 observed individuals. The circling by individual sharks was spread across different depths from the surface down to c. 16 m maximum depth, a shark group structure that resembled a rotating “torus” (Figure S1; Movie S1). A ubiquitous feature of all 19 groups was that none of the sharks encountered were observed to filter-feed, despite obvious zooplankton in the water where several groups were located (Figure S2; Table 1). For the large groups of circling, non-feeding basking sharks, the presence of both females and males was confirmed in each of seven toruses which were possible to study from the underwater video recordings.

3.1 | Distribution and seasonal timing

All circling groups were observed in August and early September in surface waters on the cooler margins of thermal fronts. The shark groups were associated with fronts that from SST data formed temperature gradients of c. 0.5°C per km (Figure 1; Figure S3 and S4). For example, T1 (Table 1) was observed c. 8 km west of Kilkee, Co. Clare, and a 2.0–3.0°C *in situ* temperature difference was recorded by observers across the area where T1 was located. The surface water where T1 was observed contained zooplankton, including gelatinous forms such as ctenophores and the cnidarian *Pelagia noctiluca*. Humpback (*Megaptera novaengliae*) and minke (*Balaenoptera acutorostrata*) whales, bluefin tuna (*Thunnus thynnus*), common dolphin (*Delphinus delphis*) and numerous seabird species were encountered and observed feeding upon sprat (*Sprattus sprattus*) and horse mackerel (*Trachurus trachurus*) in the area where T1 was observed during August and until the end of November 2016. In addition, T2 was observed c. 10 km southwest of Inishmaan Island, north of T1's location and 9 days later (Figure 1). The surface-water temperature recorded at the torus was 14.6°C and was on the cooler side of a thermal front that was also evident from mapped SST gradients (Figure 1; Figure S4). Humpback whales were observed several hours previously c. 10 km to the east in waters that were 1.0–1.5°C warmer.

The locations of toruses near fronts were consistent between years at the broad scale (Figure 1); nonetheless, at the local scale toruses in 2020 were generally located further offshore than in 2021 (Figure 1, inset). Within a year, toruses observed on consecutive days showed differing distances between one another. On some occasions, toruses located a day apart were several kilometres distant. For example, T15 comprising nine sharks observed on 29 August 2021 was located 11 km southwest of T14 comprising six sharks that was observed the day before. On other occasions, toruses encountered on consecutive days were closer in proximity. Torus T17 with 23 sharks on 1 September 2021 was located only c. 1.5 km east of where T16 (14 sharks) was found the day before.

Within each daily observation period, there was often more than one torus present in the local area, indicating multiple toruses formed separately (Table 1). Those observed on 15 and 16 August 2020 (T3–7) were notable in that five apparently separate torus groups

occurred within a relatively localised area. Furthermore, the vessel transect on 28 August 2021, which was undertaken c. 7 km offshore between Kilkee and Loop Head, recorded the surface distribution of six distinct circling groups (T9–14) as well as six solitary sharks and two pairs of sharks (Figure 2). The seven groups of non-feeding sharks were observed across a horizontal transect distance of c. 15 km, which confirms that multiple toruses co-occurred within the same area, with solitary and paired sharks seen moving in the areas between them. Breaching behaviour was also associated with two groups (Table 1; see Section 3.5).

3.2 | Characteristics of a torus

3.2.1 | Structure and rotation

For torus T1 in 2016, the airborne drone video recording showed that the circling group comprised an estimated 16 large basking sharks that were present throughout the 2 h observation period. During this time individuals continually swam relatively slowly in a counter-clockwise circling pattern that formed a 3D structure arranged vertically in approximately three discrete layers from the surface down to 5–10 m depth (Figure S2a). Underwater observations of all shark groups with six or more individuals confirmed the rotating torus structure. For example, sharks in T2 swam relatively slowly in a circle at the surface, which extended to some sharks at depth. The precise number of sharks was difficult to determine because some remained deeper during the observation period, slowly circling at 12–16 m depth and never moving shallower. At or near the surface (uppermost 5 m) there were 10–14 sharks (Figure 1b). The in-water observation of T19's structure was aided by clearer underwater visibility and confirmed a torus of basking sharks circling at discrete depths down to 12–13 m (Figure S1).

In T1, the maximum number of sharks visible in individual drone images (at 4 s intervals) at any one time ranged from 7 to 11 sharks (mean = 8.84 sharks \pm 1.08 s.d., n = 43). The average outer diameter of the torus determined from length-scaled drone images was 22.6 m (\pm 1.9 m s.d., n = 9), and the inner diameter of space around which the sharks circled was 7.9 m (\pm 1.6 m s.d., n = 9). Two sharks tracked at the surface while maintaining an outer position farthest from the centre of the torus completed a rotation in 73–79 s (mean = 75.75 s \pm 1.94 s.d., n = 4), whereas two sharks innermost to the spinning axis took 43–76 s to complete a full inner circle (mean = 50.17 s \pm 14.47 s.d., n = 6). From these rotation times, estimated movement speed around the outer edge was 0.94 m s⁻¹ and around the inner edge was 0.49 m s⁻¹, confirming sharks swam slower when closer to the centre of a torus. From consecutive drone images a mean over-the-ground swimming speed of 1.09 m s⁻¹ (\pm 0.28 s.e., n = 7) was calculated for one shark moving around the outer edge of the torus. The different speeds recorded indicate that parallel swimming between inner and outer sharks was maintained by adjusting the speed relative to their position from the torus centre.

7.15 m). For T1 the total body length of two sharks in low-altitude images was estimate to be 9.46 and 8.88 m L_T , the latter being an average of two determinations from images 7 s apart that were in good agreement (8.86 and 8.92 m L_T) (Figure 3). Higher-altitude drone images showed a range of total body lengths for nine sharks between 5.40 and 8.49 m. With the exception of the 5.40 m L_T individual (identified as male) which was clearly smaller than the other individuals, the L_T range was 7.20–8.49 m (mean = 7.93 m \pm 0.42 s.d., $n = 8$) (Figure 3). Intra-individual L_T determinations from higher-altitude drone images were more variable for the same individual than estimates from lower-altitude images, as expected. L_T was estimated multiple times from separate higher-altitude images for three sharks and maximum differences between three, four and five measurements per shark were 0.93, 0.65 and 0.76 m, respectively.

Total body lengths were estimated from drone images of four additional toruses where the vessel was used as a scale bar. Three sharks in T3 were estimated to be 6.04, 6.58 and 6.66 m L_T , and two sharks in T15 were estimated at 7.59 and 7.62 m L_T . The estimated mean L_T for four sharks in T7 was 6.74 m (\pm 0.22 s.d., median: 6.76 m), and that for seven sharks in T17 was 6.58 m (\pm 0.37 s.d., median: 6.49 m) (Figure 3).

3.2.3 | Sex composition

Detailed examination of the underwater video recording of T1 confirmed 16 individuals, with both females and males present (Figure S5). From individual body markings/features including presence/absence of male claspers, five females and eight males within T1 were identified; the sex of the remaining three individuals was unknown. In T1, all males identified had large claspers extending from the pelvic fin to beyond the anterior emargination of the ventral median (anal) fin (Figure S5a). This was consistent with males identified in other toruses; for example, the claspers on a large male in T19 extended beyond the posterior emargination of the anal fin (Figure S6). Furthermore, claspers were often observed as bearing apparent abrasions or bruises, in toruses T16 and T19 for instance, indicating recent mating activity (Figure S5b,c).

In T1, parasitic sea lampreys (*P. marinus*) were present on 5 of the 16 sharks (31%), both male and female, around the pelvic and/or second dorsal fins (Figure S5a,d), and white scars caused by rasp feeding of lampreys on shark skin were present in three others. Interestingly, four of the five female sharks identified were observed to have a paler body colouration than males (Figure S7, e.g., compare panels a and b). One of the female sharks observed was identified from a numbered tag that was attached by one of the authors (S.D.B.) in April 2016 a few kilometres south of the torus location, indicating this female had remained in, or returned to, the same area over the 4 month intervening period.

For T2, the estimated number of sharks comprising this torus was between 14 and 20 during the 2 h observation period. In contrast to the first torus, the sharks closer to the surface of this group comprised of mainly large female sharks, with fewer males evident. The

approximate ratio of females to males from *in situ* observations was 4:1. As before, many of the females appeared to have paler skin colouration compared to males in the group.

Torus 15 had a maximum of nine sharks, and of the six individuals visible during underwater video recording, three males and two females could be identified. One female swimming parallel to a male was noticeably paler (Figure 7d). Examination of T16 comprising 14 individuals resulted in 10 sharks for which sex was confirmed; four males and six females were present. The sex of the remaining four sharks could not be determined. For T18, comprising an estimated maximum of 21 sharks, it was possible to identify 6 males and 4 females. Overall, it was observed most often (four of five toruses) that there were only small differences in the numbers of males to females.

3.3 | Female–male movements within a torus

Analysis of T1 and T16 showed that there were no recorded associations between two or more basking sharks that persisted for the entire duration of observation (*i.e.*, minutes to hours). In general, associations between individuals within a torus were relatively short, with interactions lasting, for example, half a torus rotation (*c.* 30 s). Observations of T1 comprising 16 individuals showed that over short time periods individual sharks generally held position relative to the closest shark or sharks, with individuals closely following behind another or parallel swimming, in addition to swimming in an echelon relative to the shark in front. Shifts in position were evident over time as the torus rotated. There did not appear to be any strict or persistent sex-related positioning within the torus: females were present on the inner edge of the torus, males on the outer and *vice versa*. An exception was the smallest shark present (5.4 m male) (Figure 3), which was observed most often on the inner edge of the torus. The closest lateral distance between the body midlines of sharks in the same vertical plane at the surface was on average 2.41 m (\pm 0.25 s.e., $n = 15$). Given that the distance from the body midline to the pectoral-fin tip was *c.* 1 m for the large sharks in T1, the associating individuals' pectoral fins were therefore generally close to touching when parallel swimming.

A detailed study of 14 individually identified sharks in T16 (including 6 females and 4 males) over an 8 min sequence of torus rotations provided a more detailed picture of male and female interactions. Each shark was observed associating with most other sharks in the torus even within the short time frame. During this period, 13 of the 14 sharks were counted associating with between 10 and 13 other individuals (Figure 4a). Thus, there was no apparent sex difference in association of females and males with other individuals, and an individual of either sex was not observed to associate solely with a single individual of the opposite sex (Figure 4b–e). For example, F6 (female δ) associated with all 13 other individuals in the torus, whereas M9 associated with 8 of the 13 other sharks. There were repeat associations within the observation period; S4 (sex unknown) and F6 associated twice, and F6 and M10 associated three separate times within 8 min. These associations between sharks comprised several types: for example, all sharks (both males and females) were

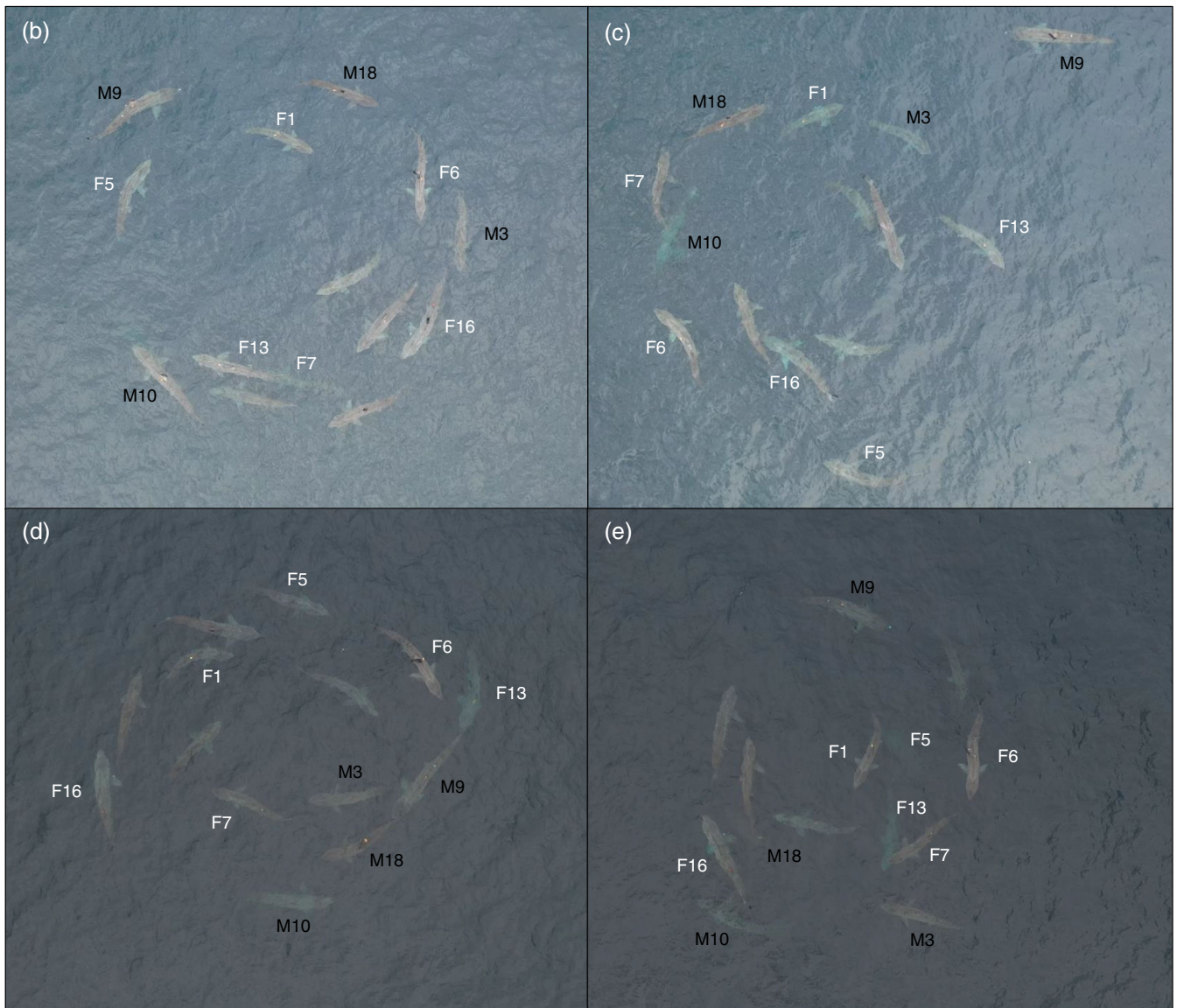
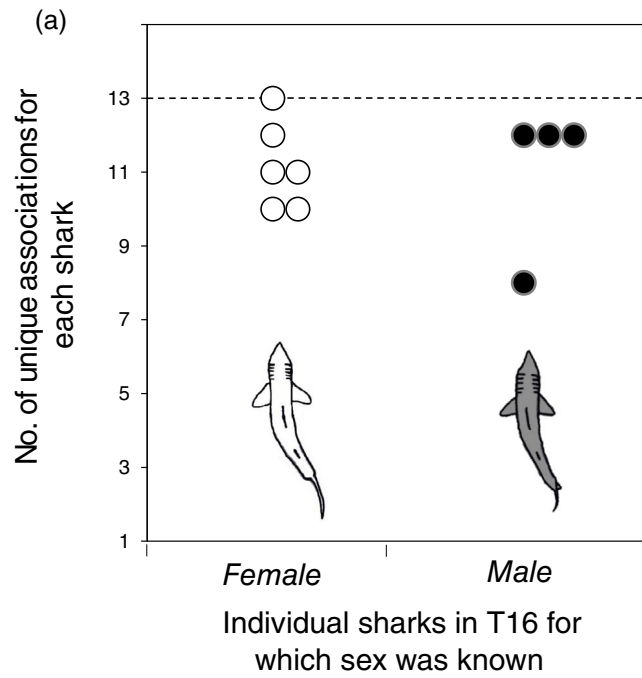


FIGURE 4 Legend on next page.

observed to (a) follow a surface-located shark either on or just below the surface, (b) actively engage in close (nose-to-tail) following and parallel swimming and (c) actively swim under another individual's body or cloacal or clasper area. Four males and one female swam under F16, the largest female in T16, whereas one of the largest males, M10, actively swam under every identified female but not under any of the males (Figure 4c,e). Similarly, M3 actively dived under three females (F6, F4 and F16) but also one male (M10). Diving under the body of another shark was sometimes associated with slower swimming speeds of the shark above together with slow, vertical undulations of the caudal fin. Additional movements included M9 and M10, the two largest males in the torus, spending 50% and 75% of the analysed time, respectively, swimming in the opposite direction (counter-clockwise) to the other individuals in the clockwise rotating torus (Figure 4b,c). Furthermore, F13, the second-largest female present, followed M9 on a straight-line swimming path out of and away from the torus. Both remained on the surface while F13 followed M9 and were several body lengths apart before they turned and returned to the torus 1 min later.

3.4 | Shark re-sightings within toruses

A female shark was re-sighted in two toruses on subsequent days in August 2021. Before the observations of T15 sharks were made on 29 August 2021, several individuals were marked with electronic tags by another research team. One of the tagged females (F6) from T15 was re-sighted the next day in T16 which was located 3.5 km away, indicating torus behaviour was persistent, either continuous or intermittent, over at least 24 h for this female. Furthermore, some sharks tagged on 29 August 2021 were still present in the same area 15 days later on 13 September 2021, indicating individuals previously active within toruses remained within a localised area for at least 2 weeks.

3.5 | Associated behaviours

Numerous behaviours by non-feeding sharks were observed in addition to group circling. A notable behaviour associated with 53% of toruses (10 of 19) was full body breaching of a shark above the water surface (Table 1). For example, in the 2 h observation of T1, two full body breaches by different basking sharks were observed. For T5, there were two breaches within 30 m of the research vessel by a male shark, where claspers were clearly visible.

Touching of the pectoral fins of one shark with another individual's fins or body was observed. For example, in T16 two females touched pectoral fins as they were parallel swimming. On one

occasion a female in T16 swam under a male shark and brushed the claspers with its dorsal fin. Nonetheless, sharks touching for any appreciable length of time was not observed, nor biting of the fins. Nonetheless, there was evidence of seemingly recent bite or scrape marks on the pectoral fins of numerous females, but even when present they were not the same type of marks as those apparent on the fins of males (Figure S8).

Underwater observation of T15 showed a female parallel swimming outside of a male that was exhibiting a whole body dorso-ventral flexion, resulting in head “nodding” and lifting of the caudal fin. Observation of T16 showed a female exhibiting the same type of body movement (Movie S2). In T19, nodding behaviour was also observed in a female that was parallel swimming alongside the right of a male. This example was notable because as the female displayed nodding behaviour the male rolled onto its left side with its ventral surface facing towards the female while undertaking a short vertical dive within its own body length before resuming normal swimming (Figure 5a-c; Movie S3). It was not apparent that the female followed the male in the new swimming direction. Body-rolling and diving behaviour by one shark alongside another was also observed in a torus from drone footage (T17; Figure 5d-f; Movie S3) and from surface observations (T18). Interestingly, the body-roll/dive behaviours occurred in toruses (T17–T19) that comprised 23, 21 or 16 individuals, respectively, and among the largest aggregations of basking sharks observed in the study.

Finally, in T16 several individuals were each observed at different times to beat their caudal fins powerfully to move faster than the torus rotation speed, resulting in their moving to another position further ahead. In addition, in T1 a shark exhibited a dorso-ventral undulating body movement that resulted in surface splashing of water. In T16, M3 (male 3) turned and swam towards a splash made by another shark in the torus. Except for breaching and surface splashing, the behaviours observed between individual sharks in a torus appeared subtle.

3.6 | Torus formation and progression

Several drone video sequences showed that a torus was formed from following behaviour between six or more sharks. For example, in T15 the non-feeding following behaviour between nine sharks swimming in echelon formation (Figure 6a) shifted within 2.3 min to group-circling behaviour between seven sharks (Figure 6b-d). Toruses were also observed to change rotation direction. In T16 comprising 14 sharks, it was evident that a single shark moving farther from the outermost edge of the torus elicited following behaviour in an adjacent shark (Figure S9a-c), which was followed by three other sharks

FIGURE 4 Individual basking shark associations in a torus. (a) Associations between identified individuals were counted over an 8 min period in T16. Dashed line denotes the maximum number of unique associations feasible between the 14 sharks present. Positions and movements of identified females and males in T16 after observation periods of (b) 2.33 min, (c) 5.17 min, (d) 8.0 min and (e) 10.0 min

FIGURE 5 Body-rolling behaviour of male and female basking sharks in toruses. (a - c) Video sequence of body rolling of a male that orientates the ventral surface towards a female swimming behind in echelon formation in T19 (3 September 2021). (d - f) Drone captured body rolling of a female that orientates the ventral surface towards a following shark (sex unknown) in T17 (1 September 2021). Images shown in each sequence were 2 s apart. Images: S. Berrow/IBSG

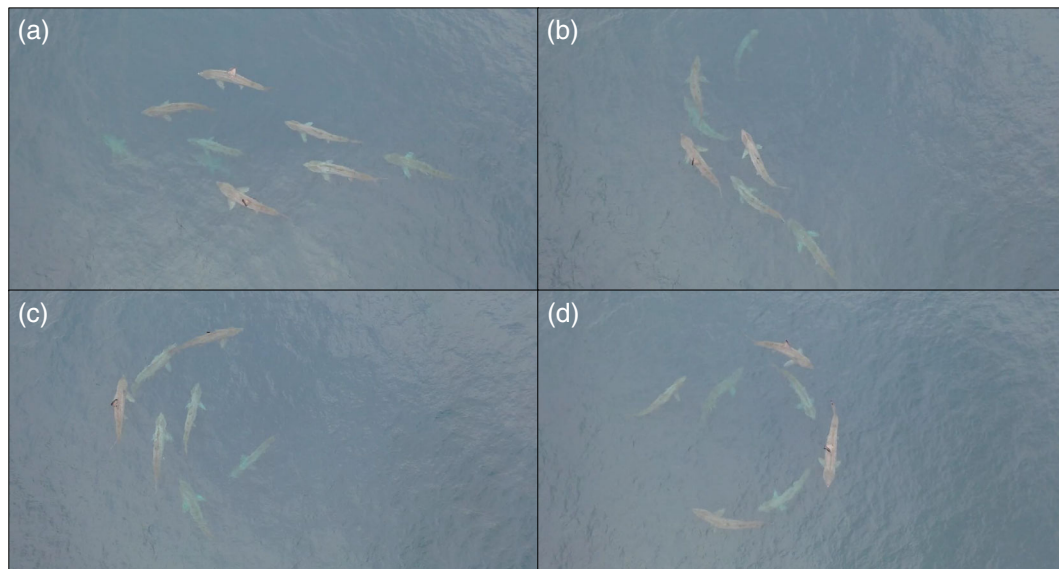
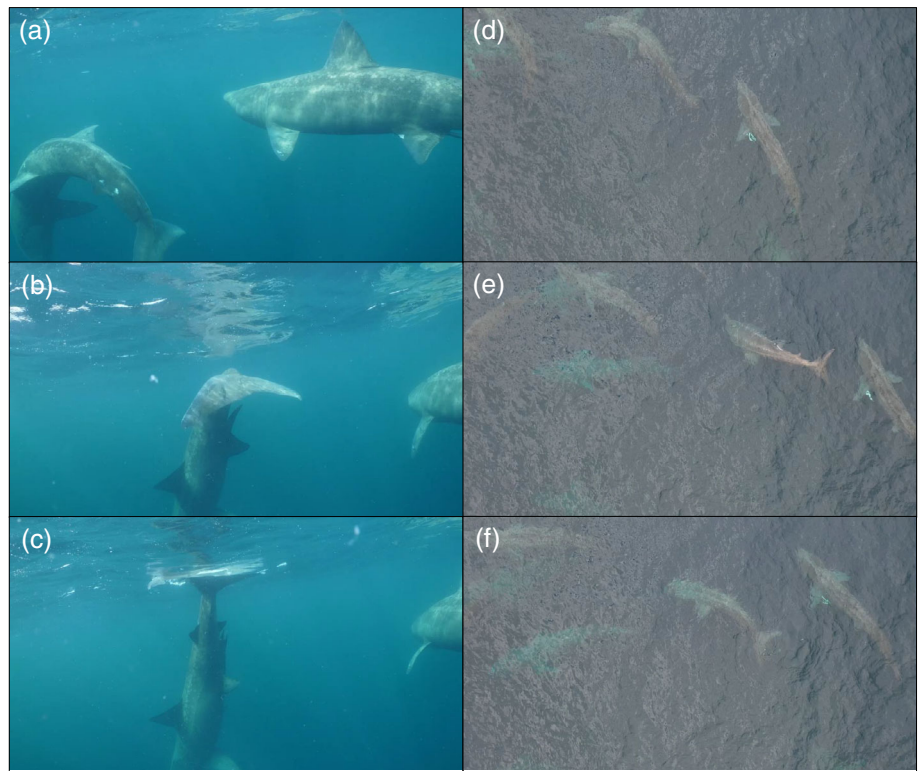


FIGURE 6 Basking shark torus formation from following behaviour. (a) Following behaviour and echelon swimming between at least nine non-feeding basking sharks in T15 on 29 August 2021 that forms into (b) clockwise turning and (c) the lead individual following the following group. (d) A clockwise rotating torus of seven sharks is formed 2.3 min after (a). Images: S. Berrow/IBSG

that were in turn followed by four others. The lead shark then rejoined the outermost edge of the torus but was now swimming in the opposite direction. The following behaviour shown by the seven sharks behind thereby led to a change from counter-clockwise to clockwise rotation in a little over 1 min (Figure 9d). Overall, there was a dynamic progression from non-feeding following behaviour to circling behaviour when a lead shark turned to follow the followers,

which with sharks at variable depths resulted in toroidal behaviour of the group.

The temporal persistence of the toruses observed was also notable. Toruses were relatively stable structures and could be observed for several hours, particularly when composed of large numbers of sharks. For instance, T1 and T2 that comprised 16 and 20 sharks, respectively, were observed for 2.0 and 1.5 h, respectively, and each

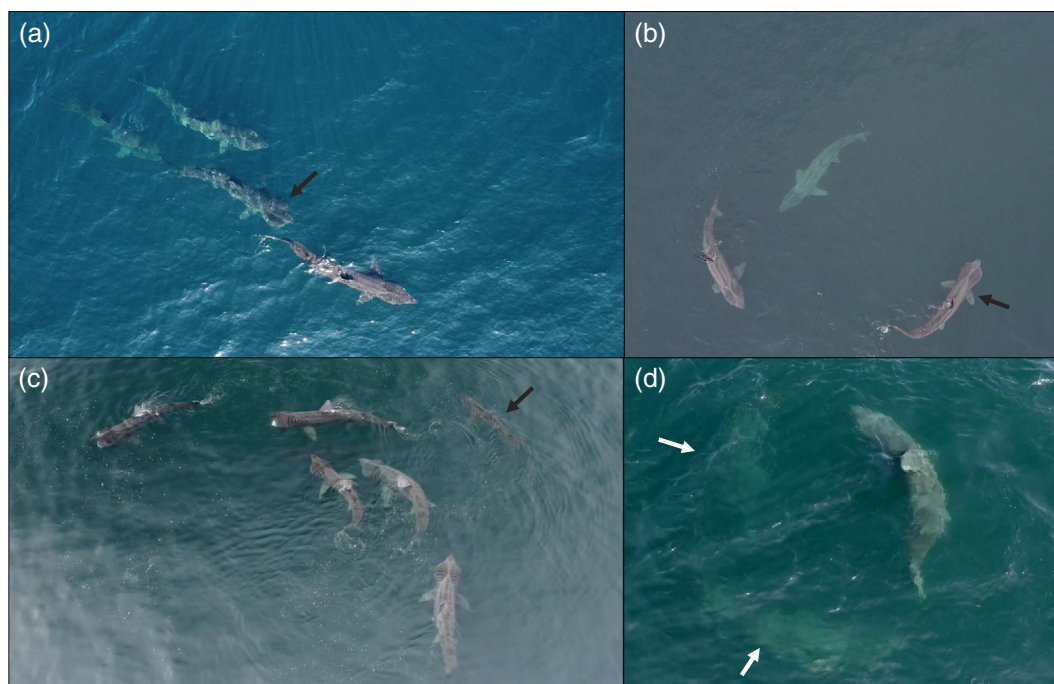


FIGURE 7 Diverse following and circling behaviours observed off western Scotland. Basking groups observed in August 2020 demonstrating (a) following behaviour between non-feeding and feeding (arrowed) sharks, (b) circling between non-feeding and feeding (arrowed) sharks, (c) feeding sharks following with a non-feeding individual (arrowed) and (d) tight circling between three non-feeding individuals. Deeper-swimming sharks (arrowed) signify the circle was descending. Images: B. Gregory

still remained when observers left the area. Similarly, toruses T16–18 each with between 14 and 23 sharks were observed for up to 5 h (Table 1).

3.7 | Additional observations from Ireland and Scotland

A torus of *c.* 30 sharks was also recorded by scuba divers further north in Co. Donegal, Ireland (off Arranmore Island), on 1 October 2020 (Table S1, see link to underwater video). These sharks were not visible at the surface as the torus was encountered near the seabed at *c.* 10–15 m depth. Furthermore, groups of feeding basking sharks in following and echelon formations were recorded in the Inner Hebrides, western Scotland, in August 2019 and 2020 (Figure 7a,c). Similar to female basking sharks observed in toruses off Ireland, females were observed with pectoral fin abrasions (e.g., Figure S10a). Following groups comprising non-feeding sharks were less frequently observed (e.g., Figure 7a), and short-lived circling between up to four sharks was observed (e.g., Figure 7b). However, sustained large group-circling behaviour similar to toruses in Ireland was not observed. Nonetheless, small group-circling formations occurred between four and between three individuals in August 2019 and 2020, respectively (Table 2). Circling behaviour between four basking sharks observed in August 2019 was video recorded 1–2 m below the surface. The sharks ceased feeding immediately before they started circling, and a non-feeding, circling pair of the

four comprising a male and female swam in a tight circle for *c.* 2 min before being lost from sight. As was the case for some females in toruses off Ireland, this female appeared to be paler in skin colouration than the male (Figure S10b). The circling group of three sharks in August 2020 was observed from a drone for *c.* 2 min (Table 2). Before circling, all three sharks were part of a feeding group engaged in following/echelon behaviour (Figure 7c). Circling behaviour appeared to be initiated when the three feeding sharks swam very close together and the two following sharks touched. They ceased feeding and the rearward shark then followed the two in front, and they formed a tight circle just below the surface that continued for *c.* 1.5 min until they swam deeper (Figure 7d).

4 | DISCUSSION

Group-circling behaviours by large numbers of basking sharks have been recorded a number of times over the past 40 years in the western North Atlantic, but similar formations have not been documented, to date, in the eastern North Atlantic Ocean. Moreover, none of the large circling groups observed to date have been investigated in detail to identify their function. From observations made off western Ireland and Scotland in four summers over 6 years, this investigation presents the first detailed study of groups of large basking sharks (average: 7.3 m L_T) swimming slowly in a rotating circle formation of narrow radius spanning different depths termed a “torus.”

4.1 | Occurrence, distribution and environmental characteristics

The circling groups of between 6 and 23 basking sharks were each found after first sighting one or more dorsal fins above the sea surface in the coastal waters off Co. Clare and Co. Galway. Surface sightings of basking sharks occur seasonally around the Irish coast, with peaks in numbers between May and September (Berrow & Heardman, 1994). However, a torus structure has not been recorded before. In the northwest Atlantic, surface formations resembling toruses have been observed infrequently (on only seven occasions) over the past four decades, indicating that they are rarely formed or that they occur frequently but are rarely observed on the surface. In contrast, the present study's observations of 19 toruses occurring in coastal waters off west Ireland in August/September of 3 years between 2016 and 2021 suggest that these group structures occur more commonly than presently realised and potentially on an annual basis. Why toruses have not been observed before in the northeast Atlantic, and apparently only rarely in the northwest Atlantic, might be explained by them usually occurring at depth. Contemporaneous with the present study's torus observations was the recording of a sub-surface group of 30 non-feeding basking sharks off Arranmore Island, Co. Donegal, in October 2020. In addition, a video-recording tag attached to a basking shark in western Scottish coastal waters in 2018 showed a group of nine non-feeding sharks near the seafloor engaged in close-follow and echelon swimming (Rudd *et al.*, 2021). Both incidences, along with the infrequent northwest Atlantic non-feeding circling formations, indicate that toruses may usually occur at depth. The toruses observed suggest that particular environmental conditions were necessary, combined with a high abundance of basking sharks, for these groups to form so frequently at the surface.

All the toruses studied were located in coastal areas of shelf seas near thermal fronts with horizontal gradients of $1.0\text{--}3.0^\circ\text{C km}^{-1}$ measured *in situ* and of *c.* $0.4\text{--}0.6^\circ\text{C km}^{-1}$ measured from averaged SST maps. Zooplankton and marine megafauna such as baleen whales, dolphins and tuna were also observed near toruses, and for several months thereafter, showing that a predator guild was present in productive waters used for foraging. In the northwest European shelf three types of fronts (tidal, shelf break and coastal) form boundaries between warm, stratified water and cold, mixed water (for detailed descriptions, see Holligan, 1981; Pingree & Mardell, 1981; Pingree *et al.*, 1975; Vlasenko & Stashchuk, 2008). Generally, fronts accumulate zooplankton at or near the surface through the action of complex upwelling and downwelling currents leading to surface convergence zones (Holligan, 1981; Le Fèvre, 1986; Pingree *et al.*, 1974; Pingree & Mardell, 1981). It is probable that these environmental conditions contributed to the surface occurrence of basking sharks aggregating to feed in spring and summer and subsequently for the formation of non-feeding torus behaviour observed later in the summer of multiple years in Irish coastal waters. Previous studies have demonstrated that basking shark presence is more likely to be associated with fronts with stronger gradients (*e.g.*, $>1.0^\circ\text{C}$) (Miller *et al.*, 2015) and that social close-following behaviour and large group-circling formations are

associated with thermal fronts and higher zooplankton abundance (Crowe *et al.*, 2018; Sims *et al.*, 2000; Wilson, 2004). Off southwest England, the locations of basking shark social following behaviour (including by non-feeding individuals) were not randomly distributed but were associated with persistent tidal thermal fronts (gradients of $0.3\text{--}1.0^\circ\text{C km}^{-1}$) (Sims *et al.*, 2000). Similar observations of close following between sharks in the southern Gulf of Maine, northwest Atlantic, were made in addition to large group-circling formations that were located along a persistent thermal front with an 8°C gradient from early September to mid-October (Wilson, 2004) and were recorded in autumn near to where there were high zooplankton concentrations (Crowe *et al.*, 2018).

The present study confirms that basking shark toruses in the northeast Atlantic were associated with productive thermal fronts during late summer and early autumn, presumably as a consequence of sharks aggregating to feed along zooplankton-rich fronts in the previous months. The detailed observations made are consistent with environments in the northwest Atlantic where surface-located circling groups of sharks were recorded. Furthermore, the toruses in August/September 2021 occurred closer to shore than in 2020, which could be explained by coastal fronts occurring closer to shore with a concomitant shift in front-located zooplankton in 2021, which may have acted to aggregate feeding sharks there earlier in the summer. A previous study off southwest England recorded spatial shifts in basking shark feeding locations along a thermal front due to shifts in frontal location associated with changes in offshore wind (Sims & Quayle, 1998). Overall, the observations suggest that toruses generally form in late summer to early autumn where higher numbers of sharks aggregate to feed in spring and summer in areas with strong thermal fronts and higher-associated zooplankton abundances. Although the fronts were most probably coastal fronts that are known to form in inshore waters of southwestern Ireland (Raine & McMahon, 1998), the precise physical characteristics, drivers and biological significance of the fronts forming off Co. Clare during 2016–2021 are yet to be determined. Nevertheless, the similarity in environmental context for large circling groups observed in the northwest Atlantic, and now in the northeast Atlantic, supports the hypothesis that surface front-located zooplankton patches bring usually solitary feeding basking sharks into closer proximity where loose aggregations of large numbers form for feeding and from which feeding and non-feeding social groups may develop (Sims *et al.*, 2000). Particularly notable was that toruses were observed in late summer and comprised non-feeding sharks, suggesting an annually occurring switch from spring/summer surface-feeding groups to late-summer, non-feeding toruses.

4.2 | Do toruses have a courtship function?

Many animals aggregate in specific resource-rich locations to engage in courtship as a prelude to mating (Clutton-Brock, 1989; McFarland, 1987). The distribution of resources is generally considered to determine the distribution of females, which consequently

determines the distribution of males (Sutherland, 1996). If the resources are patchily distributed (as found in zooplankton), then it might be expected that the distributions of females and males are also likely to be highly aggregated (Sutherland, 1996). The results of this study show that basking shark toruses were distributed near productive fronts but were also spatio-temporally aggregated (clustered). On four observation days (of nine in total) between two and six different toruses were observed in relatively small areas. The highly clustered distribution of groups and solitary/paired sharks observed suggests group formation is related to distributions of sharks and resources, both of which are dynamic and which reflect the highly aggregated groups that can occur spatially during sexually driven behaviours in many animals (Ruckstuhl & Neuhaus, 2005; Sutherland, 1996). This raises the question about the function of basking shark toruses and whether they are annually forming courtship groups.

The conditions necessary for successful mating include not only the aggregation of sexually mature females and males but also a reduction or cessation of other behaviours such as feeding. The present study found that none of the basking sharks in the toruses studied in detail across different years engaged in filter-feeding while grouped, confirming that the primary function of torus formation was unlikely to be related to feeding. Basking sharks that were not filter-feeding have been observed previously within close-following echelon and circle formations, which led to the conclusion that they were social and courtship-related behaviours (Harvey-Clark *et al.*, 1999; Sims *et al.*, 2000; Wilson, 2004). Similarly, mating activities of male sandtiger sharks (*Carcharias taurus*) have been observed to be accompanied by a reluctance to feed (Gordon, 1993), and adult nurse sharks (*Ginglymostoma cirratum*) on their mating grounds do not feed despite an abundance of potential prey (Pratt & Carrier, 2001). It is possible that non-feeding circling groups could form to reduce predation risk. However, group formation due to the presence of known predators of basking sharks (*e.g.*, orcas, sperm whales; Clark, 1956) could not account for the groups observed because no potential predators were observed in the areas with toruses, lending support to a courtship function for non-feeding circle formations.

The first detailed account of a large circling group of basking sharks comprised 13 individuals observed from the air (50 m altitude) off Nova Scotia, Canada (Harvey-Clark *et al.*, 1999). Based on the observation that the sharks at the surface (except one) were not visibly filter-feeding and were displaying behaviours such as parallel swimming and fin-fin and fin-body touching, it was concluded that this was a reproductive group of basking sharks engaged in courtship and putative mating behaviour (Harvey-Clark *et al.*, 1999). However, the presence of both sexes within this and other large circling groups observed in the northwest Atlantic was not possible to confirm (Crowe *et al.*, 2018; Harvey-Clark *et al.*, 1999; Wilson, 2004). In the present study, in addition to non-feeding behaviour occurring in studied toruses, they were formed of individuals of both sexes, which is expected if a torus represents a social structure where the sexes assort for recognition and assessment of potential mates before mate pairing and copulation. The present study's results show that the numbers of females and males identified within each torus were similar for

the majority of toruses and that there was no pattern across toruses for which one sex within a torus was predominant. A mathematical model developed by Sutherland (1996) to examine the dynamics of group courtship behaviour in animals indicates why approximately equal numbers of females and males may occur. The model assumed that the distribution of females was determined by the position of feeding locations, with the males able to distribute themselves freely in relation to a fixed distribution of females (Sutherland, 1996). The outcome of this simple model was that when competing for food in patches, consumers will aggregate in the patches of highest prey density. However, when males compete for females, the expectation is that males will be dispersed in direct proportion to the densities of females (Sutherland, 1996). This study's results are consistent with the predictions of this model: basking sharks formed toruses near front-located resources within which females and males were not in greatly different numbers.

The large sizes of basking sharks in toruses observed provide further evidence for a courtship function because individuals are expected to be sexually mature females and males if a primary function is courtship. It was estimated that the total body lengths of 27 different sharks across 5 toruses ranged from 5.4 to 9.5 m L_T with an average of 7.3 m, overlapping known lengths for sexually mature males and females in this species. In broad agreement with the present study, the torus observed by Harvey-Clark *et al.* (1999) comprised basking sharks estimated to be 6–8 m L_T , whereas Crowe *et al.* (2018) estimated that 90% of grouped sharks they measured were >5 m L_T . The size of the basking sharks at sexual maturity is not precisely known (Gore *et al.*, 2019; Sims, 2008), but mature males measure between 4.6 and 8.1 m (Bigelow & Schroeder, 1948; Matthews, 1950; Matthews & Parker, 1950), with a rapid increase in male clasper length between 6.0 and 7.5 m L_T with little change thereafter (Francis & Duffy, 2002). Although less certain (Kunzlik, 1988), females have been reported sexually mature between 6.9 and 9.8 m L_T (Matthews, 1950; Matthews & Parker, 1950; Compagno, 1984; Ali *et al.*, 2012). Therefore, at sexual maturity the minimum L_T that can be expected for males is 4.6 m and for females 6.9 m. All body lengths estimated from drone image measurements exceeded the lower length-at-maturity estimate for males and exceeded 17 of 26 length estimates that could have been females. In T1, the estimated L_T range was 7.2–8.5 m for 8 individuals of the remaining 15 sharks, of which 5 were female and 7 were male. Given the large size of all sharks in this torus, it is probable that the majority of males and females were sexually mature.

The length of claspers of male basking sharks is between 0.90 and 1.30 m for individuals between 7.5 and 9.0 m L_T (Francis & Duffy, 2002). The claspers of males in toruses in this study were also large in size and consistent with those measured for mature males. The claspers extended from the pelvic fin to beyond the anterior emargination (and for one male beyond the posterior emargination) of the ventral median fin, which was estimated from underwater images (*e.g.*, Figure S5) to be *c.* 1.0 m in the larger males observed. For many males present, claspers also carried apparent recent abrasions indicating sexual activity. Sexually active male sharks of other species during

seasonal courtship reproductive behaviours have been recorded with bruised claspers and possibly lesions and abrasions, including lemon sharks (*Negaprion brevirostris*), nurse sharks and blue sharks (*Prionace glauca*) (Clark & von Schmidt, 1965; Pratt, 1979; Pratt & Carrier, 2001).

Differences in body-surface colouration between male and female basking sharks within toruses were also evident. In three toruses, males that were engaged in parallel swimming or following behaviour were darker than females. The non-feeding, circling female basking shark observed off Scotland was also lighter in colour than the male. Interestingly, photographic sequences of mating events of nurse sharks in the wild examined by Klimley (1980) showed that males were always darker in body-surface colouration than the females. In contrast, observations of captive sandtiger sharks showed males became chromatically lighter during pre-copulatory behaviour (Gordon, 1993; Parsons *et al.*, 2008). This suggests that colour differences between male and female basking sharks were indicative of courtship behaviour.

4.3 | Courtship-like behaviours within a torus

Mating behaviour between basking sharks grouped in toruses was not observed in the current study. Without observing copulatory behaviour directly after courtship, it is not entirely certain that the behaviours observed within toruses were part of courtship. Nonetheless, the parallel-swimming and close-following behaviours observed in the different basking shark toruses studied have been documented during courtship between males and females of various shark species (for reviews see Pratt & Carrier, 2001 and Parsons *et al.*, 2008). Parallel swimming where a male and a female swim parallel and synchronously side by side occurs during pre-copulatory behaviour and courtship in lemon sharks (Pratt & Carrier, 2001) and nurse sharks (Klimley, 1980) and also in the pelagic scalloped hammerhead shark (*Sphyrna lewini*) immediately before mating (Salinas-de-Leon *et al.*, 2017). Close-following behaviour where a male swims parallel and behind a female close to its pelvic area (close-flank approach), or when a male swims directly behind a female (nose-to-tail close following), is known to occur during courtship of nurse sharks (Carrier *et al.*, 1994), blacktip reef sharks (*Carcharhinus melanopterus*) (Johnson & Nelson, 1978) and sandtiger sharks (Gordon, 1993). Furthermore, the associated behaviours observed between basking sharks in toruses, including touching of fins, rolling to expose the claspers or cloaca in front of a shark close-following in echelon formation and body undulation that acts to raise alternately the head and tail, are known to form part of courtship behaviours for shark species where courtship has been recorded before copulation (Parsons *et al.*, 2008; Pratt & Carrier, 2001). However, the torus behaviour observed differs from courtship of the planktivorous manta rays, *Mobula birostris* and *Mobula alfredi*, before mating attempts. In manta rays, multiple males can pursue a single female in a courtship “train” for long periods during which time the female evades the males until, when only one male remains, pre-copulation

positioning initiates, which includes male biting of the female's pectoral fin (Stevens *et al.*, 2018).

Male biting of the female's pectoral fin is another common behaviour in sharks before and during mating (Pratt & Carrier, 2001). Male grasping of the female's pectoral fin allows the pair to remain in a close parallel orientation while a clasper is inserted into the female's cloaca. It has been suggested that male biting may serve to maintain the pair bond during copulation in sharks (Tricas & Le Feuvre, 1985). Pectoral biting was not observed in the current study during the time that toruses were observed off Ireland. Nonetheless, it was found that many large female sharks bore abrasions on the pectoral fins, which suggests biting may have occurred. The absence of similar pectoral-fin marks on male basking sharks in toruses supports this possibility. While basking sharks often carry body-surface abrasions, most noticeably due to the skin feeding activities of parasitic sea lampreys, the abrasions on female pectoral fins were not due to the characteristic lamprey marks but were more similar to the raking marks caused by teeth scraping along the pectoral fins of females observed in other shark species during the mating season (Pratt & Carrier, 2001). That females and males were observed with abrasions on pectoral fins and claspers, respectively, suggests previous mating attempts by both sexes may have occurred before their presence in an observed torus. This raises interesting questions about reproductive strategies of male and female basking sharks. It is possible that toruses enable multiple mating opportunities for both sexes, an idea supported by re-sighting of an individually identified female occurring in two toruses on consecutive days.

Close physical associations within a torus occurred between females and males and also between the same sex, with interactions often occurring rapidly. It was evident that the torus structure combined with individual shark movements and behavioural interactions provides a mechanism for rapid mixing in this group. In T16, the majority of males and females tracked interacted with nearly all the other sharks present in the torus within just a few minutes. Harassment of females by males and male mate-guarding behaviour were not observed. Instead, it was notable that most large males associated with the largest female present, and one of the largest males swam under every identified female but none of the males, perhaps to assess mating receptivity from chemical signals secreted by females. Therefore, it appears that effective recognition and assessment of potential mates is facilitated through the dynamic structure of a torus. Rapid mixing of large numbers of males and females, such that most individuals have associated with most other individuals, may be an efficient mechanism that confers optimal information exchange on sharks' fitness potential.

Only in large toruses with >16 individuals was male or female body rolling to expose the ventral area to a following shark observed. It is possible that the larger toruses take longer to form, presumably by progressively aggregating or actively attracting greater numbers of receptive males and females. Sharks may be attracted to toruses and locate them *via* olfactory trails of sex pheromones released into the water by sharks already there. For example, male fish are known to upregulate the release of sex pheromones in response to pheromones

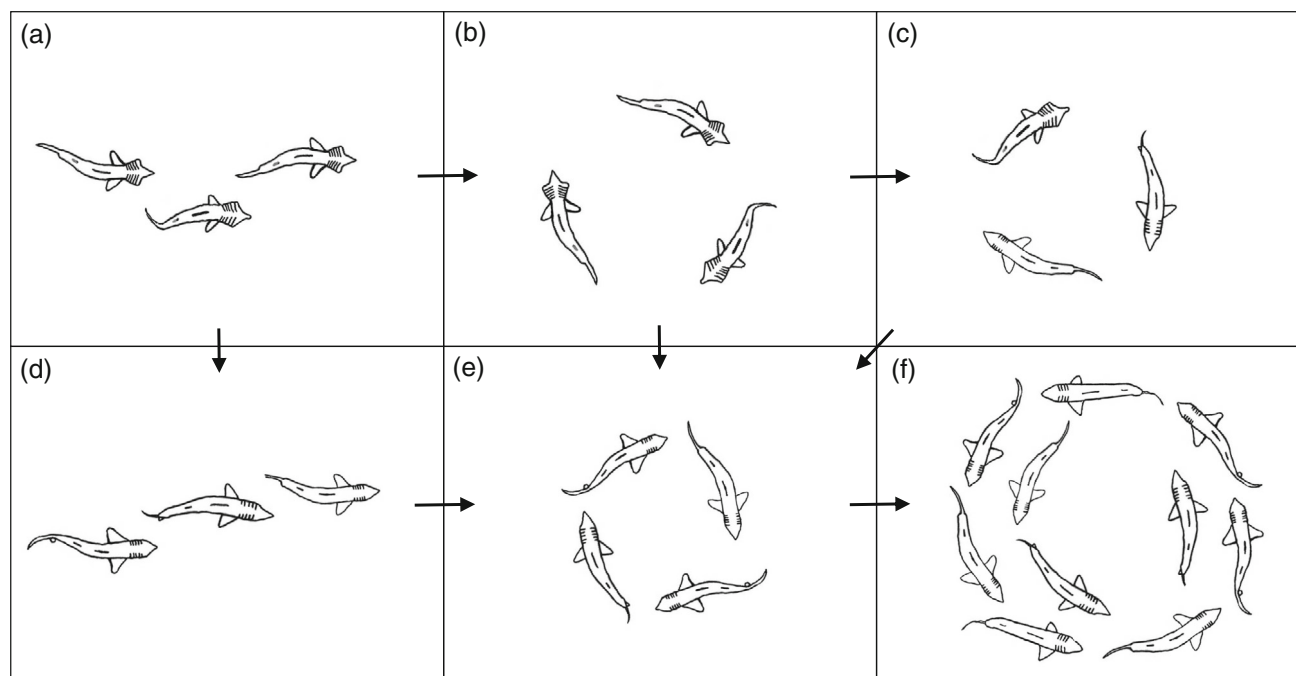


FIGURE 8 Conceptual model of social group behaviours. Observations from the present study indicate that (a) feeding sharks following one another can lead to (b) feeding circling behaviour and/or (c) circling between feeding and non-feeding sharks. Feeding following can also result in (d) non-feeding following which can lead to (e) non-feeding tight circling that may result in a torus if more sharks join the group such that multiple circling layers occur at different depths. Arrows between panels denote confirmed observations of which group type shifts to another type, where all transitions can be considered to be reversible. Note that not all shifts were recorded for the entire behavioural sequences (a)–(f)

released by competing males (Fisette *et al.*, 2020). If such sexual signalling occurs in basking sharks, it could also act to increase the chemical signals emanating from a torus that attracts other individuals. The combination of larger numbers of mature basking sharks together with the slower rotation speed of larger toruses may indicate a later stage of courtship before mate pairing and copulation.

Finally, the breaching behaviour of basking sharks within or near to over 50% of studied toruses does not argue against this behaviour having some role in courtship. Breaching by a basking shark involves an individual swimming upwards towards the surface at a steep angle (c. 75° from horizontal) at fast speeds of c. 5 m s^{-1} (Johnston *et al.*, 2018). The behaviour has been associated with various functions, including removal of external parasites (e.g., the sea lampreys observed), social communication and courtship display (Sims *et al.*, 2000), perhaps to indicate fitness. Breaching by filter-feeding humpback whales and right whales (*Eubalaena glacialis*) is most often observed when males engage in intraspecific competition for a particular female (Whitehead, 1985). Breaching was observed off southwest England between May and July and on 50% of occasions when social groups were observed on the surface (Sims *et al.*, 2000), leading to the hypothesis that if breaching is associated with courtship, it may function not only in male–male competition but also for females to announce receptivity to mating (Sims *et al.*, 2000). Similarly, in the present study breaching was not observed in all toruses, at least during the periods they were observed. It might be expected that if breaching was a regular component of courtship, then it may be more

frequent in larger toruses where competition for mates is likely to be more intense. There was marginal support for this: breaching was recorded in 5 of 7 toruses with >10 sharks and in 5 of 10 with <10 sharks, indicating a slightly greater tendency for breaching in larger toruses. Testing this idea more rigorously will require observations of more torus events and for longer time periods. Therefore, it appears that because breaching occurred only in half of toruses observed, it may not always occur as part of the courtship pattern and may indeed serve several behavioural functions other than courtship.

4.4 | Model of torus formation

Collectively, the results identify a courtship function for non-feeding basking shark torus groups, within which close-following, echelon and parallel-swimming behaviours occur. However, close-following, echelon and parallel-swimming behaviours are also observed between feeding basking sharks (Sims *et al.*, 2000), leading to suggestions that these apparent social behaviours may be unrelated to courtship itself (e.g., Gore *et al.*, 2019). The present study of basking shark torus formations, in addition to previous investigations of groups exhibiting following and circling behaviours by feeding or non-feeding individuals, presents the opportunity for a synthesis and conceptual model of how courtship toruses may form from following behaviour between feeding sharks (Figure 8).

Basking sharks filter-feeding at the surface on dense patches of zooplankton often result in large aggregations (Sims & Quayle, 1998) within which feeding individuals also commonly follow each other (e.g., close nose-to-tail following, parallel-swimming and echelon formations) (Sims *et al.*, 2000). These following formations were hypothesised to have a social function, including putative courtship behaviour (Harvey-Clark *et al.*, 1999; Jacoby *et al.*, 2012; Sims *et al.*, 2000; Wilson, 2004). Close-following and close-following echelon formations, of between two and four sharks during feeding, were hypothesised to be social behaviours associated with the early stages of courtship because non-feeding close-following groups were also documented off southwest England (Sims *et al.*, 2000), implying feeding may alternate with or co-occur with social following. Recently, there have been suggestions that following formations of feeding basking sharks are not related to courtship alone and may represent behaviours associated with efficient foraging (Crowe *et al.*, 2018; Gore *et al.*, 2019).

In this study following behaviour was observed between feeding sharks and between feeding and non-feeding sharks; circling by feeding and non-feeding sharks; and following, tight circling and torus groups formed between non-feeding sharks. This combination of shark feeding status within different group formations – with the exception of toruses that were always non-feeding – suggests that some social groupings may form under various conditions, with group behaviour gradually shifting from one type to another presumably as feeding conditions, levels of satiety and number of conspecifics present in the group change. For example, feeding sharks in following groups formed a circle when a lead shark turned and began following a rearward shark (Figure 8a,b). It was also evident that when a persistent circle forms, some individuals reduce or cease feeding (Figure 8c), presumably as feeding motivation declines in favour of courtship behaviour. Recent research on the behaviour of an invertebrate model species shows that feeding on protein-rich food can rapidly stimulate a gut-derived, nutrient-specific neuropeptide hormone that propels a switch from feeding to courtship behaviour (Lin *et al.*, 2022), suggesting feeding and courtship can be closely related under certain food conditions and in the presence of the opposite sex.

The current observations indicate that surface toruses form later in the summer after basking sharks have spent several months feeding in frontal regions. Basking sharks were observed at the surface feeding from April onwards in Irish waters – indeed a female tagged in April 2016 was re-sighted in a torus in August the same year; nonetheless, surface toruses were observed only from summer to early autumn. In the northwest Atlantic, Wilson (2004) recorded that smaller groups of basking sharks displayed following behaviour early in the feeding season, whereas larger groups were engaged in circling behaviour in late summer and early autumn. This suggests that surface feeding predominates when zooplankton abundance peaks in early summer (Sims *et al.*, 1997) but results in a greater likelihood of non-feeding social groups forming later in the season. This may explain how circling by feeding and non-feeding individuals switches to tight circling among non-feeding sharks and, ultimately, to torus formation as more sharks locate the torus (Figure 8e,f), perhaps by olfactory-mediated responses to pheromones exuded into

the water by females or males (Fisette *et al.*, 2020; Johnson & Nelson, 1978). Clearly, as both feeding and courtship behaviours are displayed in or near zooplankton patches, the change in proximity of other large sharks as well as changes in food quality and satiety could account for groups transitioning from feeding to non-feeding and perhaps back again as the season progresses and which could explain the different interpretations of group functions reported for basking sharks (Crowe *et al.*, 2018; Gore *et al.*, 2019; Harvey-Clark *et al.*, 1999; Sims *et al.*, 2000; Wilson, 2004).

Close following, echelon and parallel swimming was also observed between male basking sharks. This is expected within courting groups as all individuals are likely to assess all others to determine the sex and other characteristics of group members. This male–male behaviour is common among sharks. For instance, male nurse sharks will also follow other males during the breeding season, both during pursuit of females during courtship and as part of their normal daily ranging activities (Pratt & Carrier, 2001).

In summary, this study hypothesises that basking sharks transition from feeding to courtship when they are in close proximity in aggregations and when zooplankton density or quality changes temporally. This transition may be gradual in this species along a feeding-to-breeding continuum through time (spring to autumn) or may be more dynamic, with changes in group function occurring over shorter time scales. This does not exclude the possibility of hydrodynamic energetic advantages occurring for group formations of basking sharks (as for birds; Obst *et al.*, 1996; Weimerskirch *et al.*, 2001), but the concept of courtship group formation presented here does not argue against the inclusion of feeding formations because they have characteristics very similar to non-feeding groups and may be important precursors to courtship and mating itself. Research using long-term, shark-attached camera tags aimed at determining when and where individual basking sharks join and leave feeding and courtship groups, and what factors may elicit behavioural switches between feeding and courtship, will be necessary to disentangle this complex set of behaviours. Furthermore, accelerometer tags capable of recording fine-scale body movements at high temporal frequency (and with longer durations than video tags) may prove useful for detecting the signatures of mating events that are expected to be different to normal swimming movements.

5 | CONSERVATION IMPLICATIONS

Toruses off western Ireland in 2016, 2020 and 2021 were consistent in their timing, occurring in August and early September, and the apparent underwater torus in Co. Donegal occurred in early October 2020. This suggests an annual breeding season around summer/early autumn off Ireland. The additional observations made off western Scotland in August 2019 and 2020 shared similarities with the toruses off Ireland. It provides preliminary evidence that courtship toruses may form in Scottish waters at this time also.

In agreement with this study, the seasonal timings of group formations recorded by previous studies (late May: Matthews, 1950;

June: Harvey-Clark *et al.*, 1999; September–October: Wilson, 2004; June–November: Crowe *et al.*, 2018) indicate that basking shark courtship and mating likely occurs from May to November in both the northeast and northwest Atlantic regions. It also suggests that basking shark breeding grounds may extend throughout both the UK and Irish coastal and shelf seas where thermal fronts occur (Miller *et al.*, 2015; Scales *et al.*, 2014). These areas correspond to locations where basking shark “hotspots” have been identified off southwest England, the Celtic and Irish Seas and off western Ireland and Scotland (Berrow & Heardman, 1994; Southall *et al.*, 2005; Witt *et al.*, 2012).

The proposed annual breeding season for basking sharks overlaps spatially and temporally with known fisheries for this species that operated in the northeast Atlantic. There is a long history of hunting basking sharks by Irish coastal communities dating back to at least its first formal record in 1744 (McNally, 1976; Went & Súilleabháin, 1967) and more recently by industrialised harpoon fisheries in Scottish and Norwegian waters during the second half of the 20th century (Fairfax, 1998; Kunzlik, 1988; Sims & Reid, 2002). It is generally accepted that the large declines in numbers of basking sharks that occurred in various regions globally are attributable to fishing mortality, either targeted or incidental (McInturf *et al.*, 2022; Rigby *et al.*, 2021; Sims, 2008; Sims *et al.*, 2015). The results of this study indicate courtship areas (and by extension breeding grounds), where large, sexually mature individuals are most likely to aggregate, occur in the same coastal waters where fisheries were established and at the same time of year. The spatial and temporal persistence of surface-located courtship toruses in coastal and shelf seas also potentially exposes them to collisions with commercial shipping, marine leisure traffic and consequent effects of anthropogenic noise (Womersley *et al.*, 2022). Currently little is known about the extent to which important frontal habitat for feeding and courtship of basking sharks overlaps with major shipping routes (Womersley *et al.*, 2022). If overlap is relatively high, it is possible that fatal ship strikes may be more common than presently realised and is an area of research that requires greater attention.

The fact that courtship toruses are not observed every year in the same coastal locations could be due to shifting fronts or zooplankton; However, it may equally be due to toruses forming at depth in some years. Off Scotland, multiple surface breaches have been observed in the absence of larger groups visible at the surface (Hayes *et al.*, 2018). These observations could indicate the presence of courtship toruses occurring at depth. Breaching without surface presence of sharks also occurred in early November 2019 off west Ireland where several basking sharks were observed breaching repeatedly within 500 m of Loop Head when no sharks were visible on the surface (R. Collins, unpubl. obs.) but near to where toruses were observed the following year. There is the potential for this “hidden” sub-surface courtship behaviour to be exposed to anthropogenic threats such as incidental capture in midwater and bottom trawls and in set-nets.

To promote further the recovery of basking shark populations from historical overfishing and to protect them from contemporary threats such as incidental fishery capture, collisions with marine traffic and effects of noise on reproductive behaviour, habitats supporting basking shark courtship toruses will require additional

protection measures. The Irish and UK shelf sea fronts where courtship toruses and other groups have been observed, or where they may be reasonably predicted to occur based on frontal maps (Scales *et al.*, 2014), could be used to focus spatial management measures to mitigate risks to the population. In early 2022, basking sharks in Irish waters were given the status of a protected wild animal under Section 23 of the Wildlife Act 1976, making it illegal to hunt, injure, interfere with or destroy their breeding or resting places. Spatial management in the form of marine-protected areas (MPA) encompassing basking shark courtship torus habitats is one potential solution to protect breeding grounds. MPAs will need to be extensive enough to incorporate the dynamic aspect of torus locations, which shifted between years, and that may also shift distributions over longer time periods as hotspots of zooplankton abundance alter with environmental and oceanographic conditions (Sims & Quayle, 1998; Sims & Reid, 2002; Sims *et al.* 2006).

6 | CONCLUSIONS

The distinctive features across all circling groups of basking sharks that formed a torus were the presence of non-feeding female and male basking sharks of large body sizes that were generally consistent with the lengths expected at sexual maturity for males and for some females in this species. Females with paler skin colouration than males were observed in several toruses across years and in Irish and Scottish waters, observations consistent with sex differences in colour changes observed in other shark species during courtship and mating. Additional unifying characteristics were the presence of breaching behaviour, dynamic assorting of females and males within a torus and female–male interactions such as touching and rolling/diving behaviour. Collectively, the results strongly suggest a courtship function for the basking shark torus. The results also provide details of how a torus is formed from shark-following behaviour and how changes in direction are elicited, which together indicate that close-following behaviour is a precursor to courtship behaviour within a torus. Furthermore, productive thermal front habitats provide a key mechanism for feeding aggregations to form in spring and summer before basking sharks switching to non-feeding in late summer to form toruses. Specific spatial management measures will be required to safeguard basking shark-breeding areas.

AUTHOR CONTRIBUTIONS

D.W.S. conceived the research. S.D.B., K.M.O., N.J.P., R.C., K.L.S., B.M.P., P.C., S.W. and L.F. performed fieldwork and data collection. D.W.S. and E.J.S. analysed data. N.Q., N.E.H. and F.C.W. completed front analysis and mapping. D.W.S. prepared the manuscript. All authors contributed to subsequent drafts.

ACKNOWLEDGEMENTS

The authors thank B. Gregory and T. Warender for providing video footage. D.W.S. is supported by a Marine Biological Association Senior Research Fellowship.

REFERENCES

- Ali, M., Saad, A., Reynaud, C., & Capape, C. (2012). Occurrence of basking shark, *Cetorhinus maximus* (Elasmobranchii: Lamniformes: Cetorhinidae), off the Syrian coast (Eastern Mediterranean) with the first description of egg case. *Acta Ichthyologica et Piscatoria*, 42, 335–339.
- Berrow, S. D., & Heardman, C. (1994). The basking shark *Cetorhinus maximus* (Gunnerus) in Irish waters—Patterns of distribution and abundance. *Proceedings of the Royal Irish Academy B*, 94, 101–107.
- Bigelow, H. B., & Schroeder, W. C. (1948). Sharks. In J. Tee-Van, C. M. Breder, S. F. Hildebrand, A. E. Parr, & W. C. Schroeder (Eds.), *Fishes of the Western North Atlantic. Part 1. Lancelets, cyclostomes, sharks* (pp. 59–546). New Haven: Sears Foundation for Marine Research, Yale University.
- Braun, C. D., Skomal, G. B., & Thorrold, S. R. (2018). Integrating archival tag data and a high-resolution oceanographic model to estimate basking shark (*Cetorhinus maximus*) movements in the western Atlantic. *Frontiers in Marine Science*, 5, 25.
- Carrier, J. C., Pratt, H. L., & Martin, L. K. (1994). Group reproductive behaviours in free-living nurse sharks, *Ginglymostoma cirratum*. *Copeia*, 1994, 646–656.
- Cayula, J.-F., & Cornillon, P. (1995). Multi-image edge detection for SST images. *Journal of Atmospheric and Oceanic Technology*, 12, 821–829.
- Clark, E., & von Schmidt, K. (1965). Sharks of the central gulf coast of Florida. *Bulletin in Marine Science*, 15, 13–83.
- Clark, R. (1956). The biology of sperm whales in the Azores. *Discovery Reports*, 28, 1–200.
- Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proceedings of the Royal Society London B*, 236, 339–372.
- Compagno, L. J. V. (1984). *FAO species catalogue. IV. Sharks of the world. 1. Hexanchiformes to Laminiformes*. Rome: Food and Agriculture Organisation of the United Nations.
- Cotton, P. A., Sims, D. W., Fanshawe, S., & Chadwick, M. (2005). The effects of climate variability on zooplankton and basking shark relative abundance off southwest Britain. *Fisheries Oceanography*, 14, 151–155.
- Crowe, L. M., O'Brien, O., Curtis, T. H., Leiter, S. M., Kenney, R. D., Duley, P., & Kraus, S. D. (2018). Characterization of large basking shark *Cetorhinus maximus* aggregations in the western North Atlantic Ocean. *Journal of Fish Biology*, 92, 1371–1384.
- Curtis, T. H., Zeeman, S. I., Summers, E. L., Cadrin, S. X., & Skomal, G. B. (2014). Eyes in the sky: linking satellite oceanography and biotelemetry to explore habitat selection by basking sharks. *Animal Biotelemetry*, 2, 12.
- Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., et al. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife*, 3, e00590.
- Fairfax, D. (1998). *The Basking Shark in Scotland: Natural history, fishery and conservation*. East Linton: Tuckwell Press.
- Fisette, S. D., Bussy, U., Huerta, B., Buchinger, T. J., & Li, W. (2020). Evidence that male sea lamprey increase pheromone release after perceiving a competitor. *Journal of Experimental Biology*, 223, jeb226647.
- Francis, M. P., & Duffy, C. (2002). Distribution, seasonal abundance and bycatch of basking sharks (*Cetorhinus maximus*) in New Zealand, with observations on their winter habitat. *Marine Biology*, 140, 831–842.
- Gordon, I. (1993). Pre-copulatory behaviour of captive sandtiger sharks, *Carcharias taurus*. *Environmental Biology of Fishes*, 38, 159–164.
- Gore, M., Abels, L., Wasik, S., Saddler, L., & Ormond, R. (2019). Are close-following and breaching behaviours by basking sharks at aggregation sites related to courtship? *Journal of the Marine Biological Association of the United Kingdom*, 99, 681–693.
- Harvey-Clark, C. J., Stobo, W. T., Helle, E., & Mattson, M. (1999). Putative mating behavior in basking sharks off the Nova Scotia coast. *Copeia*, 1999, 780–782.
- Hayes, E., Godley, B. J., Nimak-Wood, M., & Witt, M. J. (2018). Basking shark breaching behaviour observations west of Scotland. *Marine Biodiversity Records*, 11, 17.
- Holligan, P. M. (1981). Biological implications of fronts on the northwest European continental shelf. *Philosophical Transactions of the Royal Society A*, 302, 547–562.
- Jacoby, D. M. P., Croft, D. P., & Sims, D. W. (2012). The social behaviour of sharks and rays: Patterns, implications and future research directions. *Fish and Fisheries*, 13, 399–417.
- Johnson, R. H., & Nelson, D. R. (1978). Copulation and possible olfaction-mediated pair formation in two species of carcharhinid shark. *Copeia*, 1978, 539–542.
- Johnston, E. M., Halsey, L. G., Payne, N. L., Kock, A. A., Iosilevskii, G., Whelan, B., & Houghton, J. D. R. (2018). Latent power of basking sharks revealed by exceptional breaching. *Biology Letters*, 14, 20180537.
- Kenney, R. D., Owen, R. E., & Winn, H. E. (1985). Shark distributions off Northeast United States from marine mammal surveys. *Copeia*, 1985, 220–223.
- Klimley, A. P. (1980). Observations of courtship and copulation in the nurse shark, *Ginglymostoma cirratum*. *Copeia*, 1980, 878–882.
- Kunzlik, P. A. (1988). *The basking shark*. Aberdeen: Department of Agriculture and Fisheries for Scotland.
- Le Fèvre, J. (1986). Aspects of the biology of frontal systems. *Advances in Marine Biology*, 23, 163–299.
- Lieber, L., Hall, G., Hall, J., Berrow, S. D., Johnston, E., Duffy, C., Francis, M. P., Wintner, S. P., Gubili, C., Sarginson, J., Witt, M. J., Hawkes, L. A., Doherty, P. D., Godley, B. J., Henderson, S., de Sabata, E., Shivji, M. S., Dawson, D. A., Sims, D. W., Jones, C. S., & Noble, L. R. (2020). Spatio-temporal genetic tagging of a cosmopolitan planktivorous shark provides insight to gene flow, temporal variation and site-specific re-encounters. *Scientific Reports*, 10, 1661.
- Lin, H.-H., Kuang, M. C., Hossain, I., Xuan, Y., Beebe, L., Shepherd, A. K., ... Wang, J. W. (2022). A nutrient-specific gut hormone arbitrates between courtship and feeding. *Nature*, 602, 632–638.
- Matthews, L. H. (1950). Reproduction in the basking shark *Cetorhinus maximus* (Gunner). *Philosophical Transactions of the Royal Society B*, 234, 247–316.
- Matthews, L. H., & Parker, H. W. (1950). Notes on the anatomy and biology of the basking shark *Cetorhinus maximus* (Gunner). *Proceedings of the Zoological Society of London*, 120, 535–576.
- McFarland, D. (1987). *The Oxford companion to animal behaviour*. Oxford: Oxford University Press.
- McFarland, D. (1993). *Animal behaviour*. Harlow: Longman.
- McInturf, A. G., Muhling, B., Bizzarro, J. J., Fanguie, N. A., Ebert, D. A., Caillard, D., & Dewar, H. (2022). Spatial distribution, temporal changes, and knowledge gaps in the basking shark (*Cetorhinus maximus*) sightings in the California Current Ecosystem. *Frontiers in Marine Science*, 9, 818670.
- McNally, K. (1976). *The sun-fish hunt*. Belfast: Blackstaff Press.
- Miller, P., Scales, K., Ingram, S. N., Southall, E. J., & Sims, D. W. (2015). Basking sharks and oceanographic fronts: Quantifying associations in the north-east Atlantic. *Functional Ecology*, 29, 1099–1109.
- Mucientes, G. R., Queiroz, N., Sousa, L., Tarraso, P., & Sims, D. W. (2009). Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biology Letters*, 5, 156–159.
- Obst, B., Hamner, W., Hamner, P., Wolanski, E., Rubega, M., & Littlehales, B. (1996). Kinematics of phalarope spinning. *Nature*, 384, 121.
- Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., ... Dulvy, N. K. (2021). Half a century of global decline in oceanic sharks and rays. *Nature*, 589, 567–571.
- Parsons, G. R., Hoffmayer, E. R., Hendon, J. M., & Bet-Sayad, W. V. (2008). A review of shark reproductive ecology: Life history and evolutionary

- implications. In M. J. Rocha, A. Aruke, & B. G. Kapoor (Eds.), *Fish reproduction* (pp. 435–469). London: Taylor and Francis.
- Pennant, T. (1812). *British zoology. IV. Fishes*. London: Wilkie and Robinson.
- Pingree, R. D., Forster, G. R., & Morrison, G. K. (1974). Turbulent convergent tidal fronts. *Journal of the Marine Biological Association of the United Kingdom*, 54, 469–479.
- Pingree, R. D., & Mardell, D. T. (1981). Slope turbulence, internal waves and phytoplankton growth at the Celtic Sea shelf break. *Philosophical Transactions of the Royal Society A*, 302, 663–682.
- Pingree, R. D., Pugh, P. R., Holligan, P. M., & Forster, G. R. (1975). Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature*, 265, 266–269.
- Pratt, H. L. (1979). Reproduction in the blue shark, *Prionace glauca*. *Fishery Bulletin*, 77, 445–470.
- Pratt, H. L., & Carrier, J. C. (2001). A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environmental Biology of Fishes*, 60, 157–188.
- Priede, I. G. (1984). A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote-sensing. *Fisheries Research*, 2, 201–216.
- Queiroz, N., Humphries, N. E., Couto, A., Vedor, M., da Costa, I., Sequeira, A. M. M., ... Sims, D. W. (2019). Global spatial risk assessment of sharks under the footprint of fisheries. *Nature*, 572, 461–466.
- Queiroz, N., Humphries, N. E., Couto, A., Vedor, M., da Costa, I., Sequeira, A. M. M., ... Sims, D. W. (2021). Reply to: Shark mortality cannot be assessed by fishery overlap alone. *Nature*, 595, E8–E16.
- Raine, R., & McMahon, T. (1998). Physical dynamics on the continental shelf off southwestern Ireland and their influence on coastal phytoplankton blooms. *Continental Shelf Research*, 18, 883–914.
- Rigby, C. L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., et al. (2021). *Cetorhinus maximus*. The IUCN red list of threatened species 2021: e.T4292A194720078.
- Ruckstuhl, K. E., & Neuhaus, P. (2005). *Sexual segregation in vertebrates: Ecology of the two sexes*. Cambridge: Cambridge University Press.
- Rudd, J. L., Bartolomeu, T., Dolton, H. R., Exeter, O. M., Kerry, C., Hawkes, L. I., ... Witt, M. J. (2021). Basking shark sub-surface behaviour revealed by animal-towed cameras. *PLoS One*, 16, e0253388.
- Salinas-de-Leon, P., Hoyos-Padilla, E. M., & Pochet, F. (2017). First observation on the mating behaviour of the endangered scalloped hammerhead shark *Sphyrna lewini* in the tropical eastern Pacific. *Environmental Biology of Fishes*, 100, 1603–1608.
- Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W., & Votier, S. C. (2014). On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, 51, 1575–1583.
- Siders, Z. A., Westgate, A. J., Johnston, D. W., Murison, L. D., & Koopman, H. N. (2013). Seasonal variation in the spatial distribution of basking sharks (*Cetorhinus maximus*) in the Lower Bay of Fundy, Canada. *PLoS One*, 8, e82074.
- Sims, D. W. (1999). Threshold foraging behaviour of basking sharks on zooplankton: Life on an energetic knife edge? *Proceedings of the Royal Society B*, 266, 1437–1443.
- Sims, D. W. (2000). Filter-feeding and cruising swimming speeds of basking sharks compared with optimal models: They filter-feed slower than predicted for their size. *Journal of Experimental Marine Biology and Ecology*, 249, 65–76.
- Sims, D. W. (2008). Sieving a living: A review of the biology, ecology and conservation status of the plankton-feeding basking shark *Cetorhinus maximus*. *Advances in Marine Biology*, 54, 171–220.
- Sims, D. W., Fowler, S. L., Clò, S., Jung, A., Soldo, A., & Bariche, M. (2015). *Cetorhinus maximus*. Europe Regional Assessment. The IUCN Red List of Threatened Species 2015. <http://www.iucnredlist.org/details/4292/1>
- Sims, D. W., Fox, A. M., & Merrett, D. A. (1997). Basking shark occurrence off south-west England in relation to zooplankton abundance. *Journal of Fish Biology*, 51, 436–440.
- Sims, D. W., & Quayle, V. A. (1998). Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature*, 393, 460–464.
- Sims, D. W., & Reid, P. C. (2002). Congruent trends in long-term zooplankton decline in the north-east Atlantic and basking shark (*Cetorhinus maximus*) fishery catches off west Ireland. *Fisheries Oceanography*, 11, 59–63.
- Sims, D. W., Southall, E. J., Quayle, V. A., & Fox, A. M. (2000). Annual social behaviour of basking sharks associated with coastal front areas. *Proceedings of the Royal Society B*, 267, 1897–1904.
- Sims, D. W., Southall, E. J., Richardson, A. J., Reid, P. C., & Metcalfe, J. D. (2003). Seasonal movements and behaviour of basking sharks from archival tagging: No evidence of winter hibernation. *Marine Ecology Progress Series*, 248, 187–196.
- Sims, D. W., Southall, E. J., Tarling, G. A., & Metcalfe, J. D. (2005). Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology*, 74, 755–761.
- Sims, D. W., Witt, M. J., Richardson, A. J., Southall, E. J., & Metcalfe, J. D. (2006). Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proceedings of the Royal Society B*, 273, 1195–1201.
- Skomal, G. B., Zeeman, S. I., Chisholm, J. H., Summers, E. L., Walsh, H. J., McMahon, K. W., & Thorrold, S. R. (2009). Transequatorial migrations by basking sharks in the western Atlantic Ocean. *Current Biology*, 19, 1019–1022.
- Southall, E. J., Sims, D. W., Metcalfe, J. D., Doyle, J. I., Fanshawe, S., Lacey, C., ... Speedie, C. D. (2005). Spatial distribution patterns of basking sharks on the European shelf: Preliminary comparison of satellite-tag geolocation, survey and public sightings data. *Journal of the Marine Biological Association of the United Kingdom*, 85, 1083–1088.
- Stevens, G. M. W., Hawkins, J. P., & Roberts, C. M. (2018). Courtship and mating behaviour of manta rays *Mobula alfredi* and *M. birostris* in the Maldives. *Journal of Fish Biology*, 93, 344–359.
- Sund, O. (1943). Et brugdebarsel. *Naturen*, 67, 285–286.
- Sutherland, W. J. (1996). *From individual behaviour to population ecology*. Oxford: Oxford University Press.
- Tricas, T. C., & Le Feuvre, E. M. (1985). Mating in the reef whitetip shark *Triaenodon obesus*. *Marine Biology*, 84, 233–237.
- Vlasenko, V., & Stashchuk, N. (2008). Three-dimensional shoaling of large-amplitude internal waves. *Journal of Geophysical Research*, 112, C11018.
- Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P., & Jiraskova, S. (2001). Energy saving in flight formation. *Nature*, 413, 697–698.
- Went, A. E. J., & Súilleabháin, S. O. (1967). Fishing for the sun-fish or basking shark in Irish waters. *Proceedings of the Royal Irish Academy*, 65, 91–115.
- West, K. (2009). *Animal courtship*. New York: Chelsea House Publishers.
- Whitehead, H. (1985). Why whales leap. *Scientific American*, 252, 70–75.
- Wilson, S. G. (2004). Basking sharks (*Cetorhinus maximus*) schooling in the southern Gulf of Maine. *Fisheries Oceanography*, 13, 283–286.
- Witt, M. J., Hardy, T., Johnson, L., McClellan, C. M., Pikesley, S. K., Ranger, S., ... Godley, B.J. (2012). Basking sharks in the northeast

Atlantic: Spatio-temporal trends from sightings in UK waters. *Marine Ecology Progress Series*, 459, 121–134.

Womersley, F. C., Humphries, N. E., Queiroz, N., Vedor, M., Sims, D.W. (2022). Global collision-risk hotspots of marine traffic and the world's largest fish, the whale shark. *Proceedings of the National Academy of Sciences of the United States of America*, 119, e2117440119.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sims, D. W., Berrow, S. D., O'Sullivan, K. M., Pfeiffer, N. J., Collins, R., Smith, K. L., Pfeiffer, B. M., Connery, P., Wasik, S., Flounders, L., Queiroz, N., Humphries, N. E., Womersley, F. C., & Southall, E. J. (2022). Circles in the sea: annual courtship “torus” behaviour of basking sharks *Cetorhinus maximus* identified in the eastern North Atlantic Ocean. *Journal of Fish Biology*, 101(5), 1160–1181. <https://doi.org/10.1111/jfb.15187>