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Subsurface observations of white shark *Carcharodon carcharias* predatory behaviour using an autonomous underwater vehicle

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In this study, an autonomous underwater vehicle (AUV) was used to test this technology as a viable tool for directly observing the behaviour of marine animals and to investigate the behaviour, habitat use and feeding ecology of white sharks *Carcharodon carcharias* near Guadalupe Island off the coast of Mexico. During the period 31 October to 7 November 2013, six AUV missions were conducted to track one male and three female *C. carcharias*, ranging in estimated total length (L_T) from 3·9 to 5·7 m, off the north-east coast of Guadalupe Island. In doing so, the AUV generated over 13 h of behavioural data for *C. carcharias* at depths down to 90 m. The sharks remained in the area for the duration of each mission and moved through broad depth and temperature ranges from the surface to 163·8 m depth (mean ± s.d. = 112·5 ± 40·3 m) and 7·9–27·1° C (mean ± s.d. = 12·7 ± 2·9° C), respectively. Video footage and AUV sensor data revealed that two of the *C. carcharias* being tracked and eight other *C. carcharias* in the area approached ($n = 17$), bumped ($n = 4$) and bit ($n = 9$) the AUV during these tracks. This study demonstrated that an AUV can be used to effectively track and observe the behaviour of a large pelagic animal, *C. carcharias*. In doing so, the first observations of subsurface predatory behaviour were generated for this species. At its current state of development, this technology clearly offers a new and innovative tool for tracking the fine-scale behaviour of marine animals.

Key words: AUV; feeding ecology; Guadalupe Island; REMUS; tracking.

INTRODUCTION

Investigations of animal habitat use and behaviour are important for understanding the ecology of animals and are vital for making informed conservation decisions. In the marine environment, it is very difficult to directly observe the behaviour of large animals that range widely, such as marine mammals and large pelagic fishes, including sharks (Nelson, 1977). This is particularly true for feeding behaviour because predation events are rarely witnessed. Indeed, much of what is known about the foraging behaviour of sharks is derived from a limited number of direct observations in shallow water (Tricas, 1985), from submersibles (Nelson *et al.*, 1986) and from animal-borne imaging (Marshall, 1998). Given the paucity of such observations, the feeding ecology

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of large oceanic animals has been inferred from tagging and tracking data (Skomal & Benz, 2004), stomach contents (Cortés, 1997) and fatty-acid and stable-isotope analyses (Iverson *et al.*, 2004; Estrada *et al.*, 2006; Hussey *et al.*, 2012). While such information can be useful for designating critical habitat and trophic relationships, these studies reveal little about animal behaviour.

The foraging behaviour of the white shark *Carcharodon carcharias* (L. 1758) is well studied because this is one of the few pelagic sharks that is predictably drawn to aggregation sites to feed. Numerous studies have documented surface attacks by this species on pinnipeds off California, South Africa and South Australia, firmly quantifying the ethology, environmental conditions and prey species associated with these feeding events (Ainley *et al.*, 1981, 1985; Tricas & McCosker, 1984; Klimley, 1985, 1994; McCosker, 1985; Tricas, 1985; Klimley *et al.*, 1992, 1996*a*; Anderson *et al.*, 1996*a*, *b*; Pyle *et al.*, 1996; Strong *et al.*, 1996; Martin *et al.*, 2005, 2009; Hammerschlag *et al.*, 2006, 2012; Laroche *et al.*, 2008; Fallows *et al.*, 2012).

It is also well established that *C. carcharias* exhibit deep-diving behaviour associated with coastal as well as ocean-basin-scale movements (Boustany *et al.*, 2002; Bonfil *et al.*, 2005; Bruce *et al.*, 2006; Weng *et al.*, 2007; Domeier & Nasby-Lucas, 2008, 2012; Nasby-Lucas *et al.*, 2009; Jorgensen *et al.*, 2010; Duffy *et al.*, 2012; Francis *et al.*, 2012). The extent to which this behaviour is associated with feeding (Domeier & Nasby-Lucas, 2008; Nasby-Lucas *et al.*, 2009) or reproduction (Jorgensen *et al.*, 2012) remains a topic of scientific debate simply because there are no observations of *C. carcharias* behaviour at depth.

In addition to the aggregation sites noted above, Guadalupe Island off the coast of Mexico is a seasonal host to *C. carcharias* and three species of pinnipeds, including Guadalupe fur seals *Arctocephalus townsendi*, northern elephant seals *Mirounga angustirostris* and California sea lions *Zalophus californianus* (Domeier *et al.*, 2012). Presumably, *C. carcharias* are drawn to the island to feed upon these animals, yet predation on these pinnipeds has rarely been observed (Domeier & Nasby-Lucas, 2007; Domeier, 2009; E. M. Hoyos-Padilla, pers. obs.). It has been hypothesized that *C. carcharias* prey upon pinnipeds at greater depths at Guadalupe, and acoustic telemetry data from several adult *C. carcharias* have revealed deep-diving behaviour (Hoyos-Padilla, 2009). These data suggest that *C. carcharias* take advantage of great underwater visibility to search for seals in deep water adjacent to seal colonies so as to ambush and disable pinnipeds (by removing the hind flippers), and following the carcass to the surface (Hoyos-Padilla, 2009). Although 10 seal predation events of this nature have been recorded at the surface (shark feeding on the carcass) in the past 6 years, they have yet to be observed underwater (E. M. Hoyos-Padilla, pers. obs.).

Over the course of the last two decades, new technologies have been developed to track the movements of marine animals over multiple spatial and temporal scales. Although these technologies have shown remarkable movements (Skomal *et al.*, 2009), they do little to reveal what these animals are actually doing. The use of autonomous underwater vehicles (AUV) has led to the discovery of unique geological, geochemical and biological phenomena, and to furthering understanding of many important natural processes. Acting as underwater drones, these vehicles can provide data that are virtually impossible to collect with conventional techniques. Conceivably, an AUV may provide the optimal, economical platform to track and image the behaviour of marine animals at depths beyond standard applications. The first efforts to use an AUV to track a marine animal were conducted by Clark *et al.* (2013) when they successfully followed a leopard shark *Triakis semifasciata* Girard 1855 off the coast of California. In doing so, these authors demonstrated that an AUV could be used to track the coarse movements of a marine animal.

The remote environmental monitoring unit (REMUS) AUV was initially developed by the Woods Hole Oceanographic Institution (WHOI) for coastal mapping and monitoring. These vehicles are now used as platforms for a wide variety of oceanographic instrumentation operating at depths ranging from 0 to 6000 m. They are fitted with a GPS, wireless communication, iridium capabilities and an inertial navigation system, which use ring-laser gyroscopes to orient the vehicle spatially and accelerometers to sense changes in speed and velocity. As a result, REMUS AUVs are now being deployed on missions ranging from complex underwater mapping (Shcherbina *et al.*, 2008) to undersea search and survey. In this study, a REMUS AUV was modified to locate, follow and record the behaviour of *C. carcharias* off Guadalupe Island. The objectives were not only to advance and test this technology as a viable tool for directly observing the behaviour of marine animals but also to investigate the behaviour, habitat use and feeding ecology of *C. carcharias* when they move vertically out of sight.

MATERIALS AND METHODS

STUDY AREA

Guadalupe Island is a volcanic island located 241 km off the west coast of Mexico's Baja California peninsula (29° 7′ N; 118° 21′ W; Fig. 1). This study was conducted off the north-east coast of the island, which is characterized by an extremely narrow continental shelf with depths of 3600 m found close to shore (Pierson, 1987) and series of deep canyons (Gallo-Reynoso & Figueroa-Carranza, 2005) (Fig. 1).

This work was conducted from 29 October to 10 November 2013 onboard the M.V. *Horizon*, one of the commercial *C. carcharias* diving operations working seasonally off the north-east coast of Guadalupe Island. During this time, four *C. carcharias* were tagged with an acoustic transponder while free-swimming in close proximity to the vessel and tracked with a REMUS AUV.

AUV TRACKING

In this study, a REMUS-100 AUV (custom built at the WHOI) was modified to locate, follow and videotape a tagged shark as described by Packard *et al.* (2013). In short, the tracking system consists of a 25 kHz transponder, which is attached to the shark, and the REMUS-100 vehicle, which is rated to a maximum depth of 100 m and equipped with an omnidirectional ultra-short baseline (USBL) array and navigation algorithms to perform three-dimensional autonomous tracking, following and filming of a randomly moving target (*i.e.* the shark).

Each shark was tagged at the base of the dorsal fin with the transponder, which was 7·6 cm in diameter, 38 cm long, slightly positively buoyant (Fig. 2) and tethered to an intramuscular dart; the transponder was equipped with a depth sensor rated to 100 m. For two missions, a neutrally buoyant WHOI-built camera was affixed to the transponder to record behavioural observations from the perspective of each tracked shark. After tagging, the REMUS was launched immediately and given an initial position based on the assumed shark position. The vehicle was programmed to dive, immediately orient itself in the direction of the shark and interrogate (ping) the transponder every 3 s while listening for replies. The transponder would then respond with two replies. From the first reply, the vehicle estimated range and bearing to the shark and the second reply provided depth of the shark (Kukulya *et al.*, 2015). The AUV was programmed to match the depth of the shark so as to maximize the probability of capturing behavioural footage on one of its six high definition video cameras. The vehicle combined

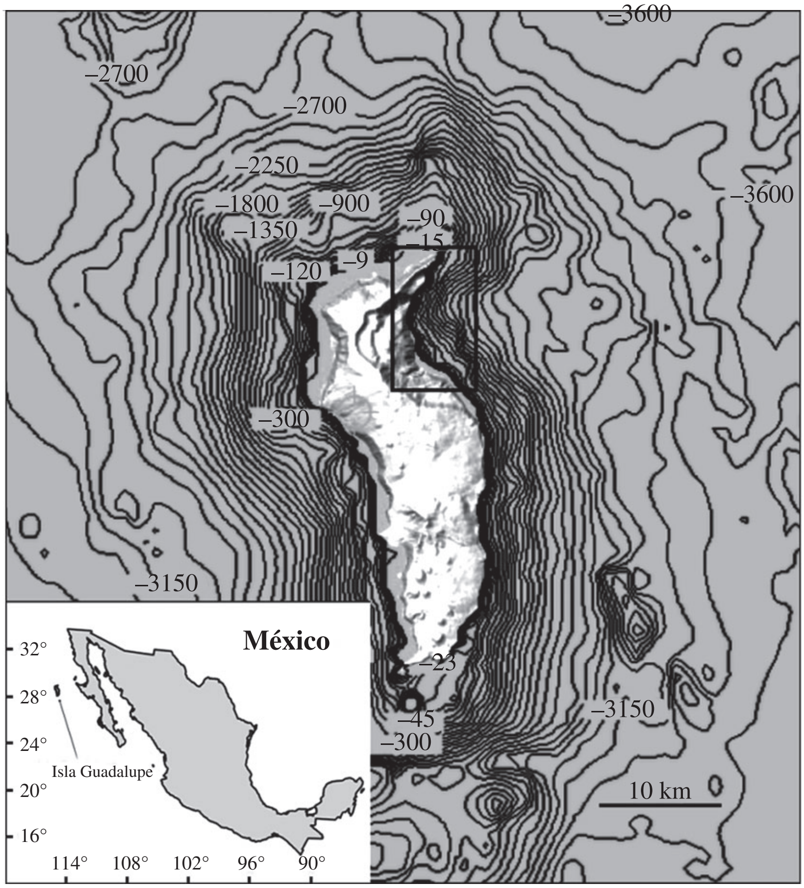

FIG. 1. Location of Guadalupe Island showing bathymetry (soundings in m) and study area (☐).

the relative position of the target with the known position of the vehicle to provide accurate latitude, longitude, depth and time data for the shark over the duration of each mission. Once the vehicle localized the shark's position, it estimated the animal's track, course and speed. Using continual updates, the vehicle autonomously re-planned the mission path to approach the tagged shark from behind, and eventually pass the animal in a pre-planned, user-defined orientation. The AUV was programmed to follow the transponder, increase its speed to catch the shark when the range was long, and slow to match the speed of the animal when it was nearby. Once the vehicle had passed the shark, it would circle back and re-approach for another pass. This navigational protocol turned out to be a successful way of imaging different perspectives of the animal swimming in its natural environment.

During each mission, the vehicle telemetered information back to the shipboard tracking station *via* its WHOI micromodem and digital ranger, thereby allowing operators to monitor the positions of both the shark and AUV. Real-time transmissions of depth and position data allowed the operators to offset the vehicle depth above or below the depth of the shark while the mission was still underway. When the shark was working near the bottom, the vehicle's on-board altimeter was used to maintain a minimum range of 2 m above the sea floor. Real-time data packets also provided vital status updates on the vehicle's performance. This included vehicle altitude, attitude (pitch, roll and heading rate), range to ship and shark, vehicle and shark depth, velocity, voltage levels and other system diagnostics. The age of each USBL fix also provided a baseline for how well the vehicle was tracking the shark.

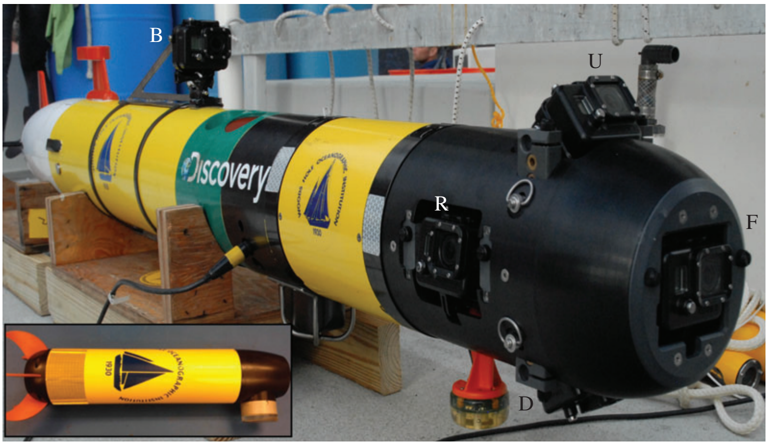

FIG. 2. Autonomous underwater vehicle and transponder (inset) used to track *Carcharodon carcharias* off the coast of Guadalupe Island, Mexico. Video cameras mounted in nose were oriented directly forward (F), upward (U), downward (D), right (R) and left (L, not shown). The backward facing camera (B) was mounted topside for tracks WS01, WS02 and WS03, and on the underside for the three tracks of WS04.

To collect environmental information and imagery, the AUV also carried a variety of sensors and cameras including a 1200 kHz up–down looking acoustic Doppler current profiler (ADCP) (Teledyne RDI; www.rdinstruments.com) for current data and speed over ground measurements, a conductivity–temperature (CT) probe (YSI; www.ysi.com), magnetic heading sensor, pressure sensor and six high-definition video cameras (Model Hero3+; GoPro, Inc.; https://gropro.com/). Five cameras were mounted in a custom camera nose section: one facing directly forward, one forward and upward 45°, one forward and downward 45°, one port and one starboard (Fig. 2). An additional camera was mounted topside or on the bottom of the main AUV pressure housing, dependent on the mission, facing aft (Fig. 2).

Upon completion of each mission, the transponder was sent an acoustic command to mechanically release from the animal and float to the surface for retrieval. The digital ranger was used to locate the transponder for recovery. The transponder was also outfitted with a three-tiered release system in the event that acoustic communication was lost. In addition, the tag would release itself if the fish were to swim below 350 m. In the event that battery power was lost in the transponder, a corrodible link was put in place to release the tag from the animal after *c*. 8 h.

To independently track the shark from a small vessel, an acoustic transmitter [Model V16TP (depth range 0–136 m, 0·6 m resolution; temperature range −5 to 35° C, resolution 0·15° C) or V16T (temperature range 10–40° C, resolution 0·12° C, Vemco Inc.; www.vemco.com)] was affixed to the transponder and detected with a directional hydrophone (Model VH110, Vemco Inc.) connected to an acoustic receiver (Model VR100, Vemco Inc.). Depth and ambient temperature data were telemetered to the receiver and recorded for the duration of each track.

RESULTS

During the period 31 October to 7 November 2013, six AUV missions were conducted to track one male and three female *C. carcharias*, ranging in estimated (derived by comparing the size of the shark to the known length of the tagging vessel) total length (L_T) from 3·9 to 5·7 m, off the north-east coast of Guadalupe Island (Table I). Although these sharks were tracked for up to 6 h using the smaller vessel, AUV mission durations ranged from 1·43 to 2·93 h resulting in a total of 13·62 h of tracking data. Mission depth

TABLE I. *Carcharodon carcharias* tracked by the autonomous underwater vehicle

Shark	Sex	L_T (m)	Date	Time (hours) Start	Time (hours) End	Duration (h:min)	Distance (km)
WS01	Male	3·9	30 October 2013	1434	1706	2:32	18·3
WS02	Female	4·8	31 October 2013	1142	1403	2:21	15·5
WS03	Female	4·5	2 November 2013	1045	1240	1:55	9·3
WS04a	Female	5·7	6 November 2013	1711	1837	1:26	6·1
WS04b			7 November 2013	1245	1512	2:27	15·5
WS04c			7 November 2013	1536	1832	2:56	17·6
Total						13:37	82·3

L_T, total length.

was constrained to 50 m as an initial setting for the first track (WS01), but increased to 90 m for the remaining missions because the tracked sharks were moving deeper. Due to the 100 m limit of the transponder depth sensor, the telemetered acoustic data were used to characterize the depth and ambient water temperature of each tracked shark during missions WS01, WS02, WS03 and WS04a. Because only temperature transmitters were used during missions WS04b and WS04c, the depth of the shark was calculated using the depth (D) and temperature (T) linear relationship resulting from the previous four tracks: $D = 269{\cdot}57 - 12{\cdot}414\,T$, ($r^2 = 0{\cdot}82$, $n = 9400$).

In general, the sharks remained in the area for the duration of each mission (Fig. 3) and moved through broad depth and temperature ranges from the surface to 163·8 m (mean ± S.D. = 112·5 ± 40·3 m) and 7·9–27·1° C (mean ± S.D. = 12·7 ± 2·9° C). The most significant observations can be characterized as interactions between the AUV and *C. carcharias* at depths in excess of 50 m. Upon review of video footage and AUV sensor data, it was found that two of the *C. carcharias* being tracked by the AUV in addition to eight other *C. carcharias* in the area exhibited the following behaviours: approach, bump and bite. During an approach, a *C. carcharias* actively moved towards the AUV and followed in close proximity. A bump was defined as brief physical contact with the AUV, typically with its snout. As implied, a bite was defined as forceful grasping of the AUV by the jaws of an approaching *C. carcharias*. During the six tracks, a total of 30 interactions were observed between 10 individual *C. carcharias* and the AUV comprising 17 approaches, four bumps and nine bites (Table II). With the exception of the track of WS03, all of the interactions occurred at or near the maximum AUV depth of each mission (53–90 m; Table II). Specific information for each AUV mission is as follows.

WS01: 3·9 M L_T MALE, 30 OCTOBER 2013, DURATION 2 H 32 MIN, DISTANCE 18·3 KM

During this track, the AUV was constrained to a maximum depth of 53 m. After tagging, WS01 moved north parallel to the shoreline for *c.* 30 min [Fig. 3(a)]. During this time, the shark remained largely associated with the surface and swam directly past a vessel belonging to another commercial *C. carcharias* dive operator. WS01 then moved offshore and dived to the maximum depth of the acoustic transmitter [154 m; Fig. 4(a)]. For the balance of the track (*c.* 2 h), the shark remained below the depth

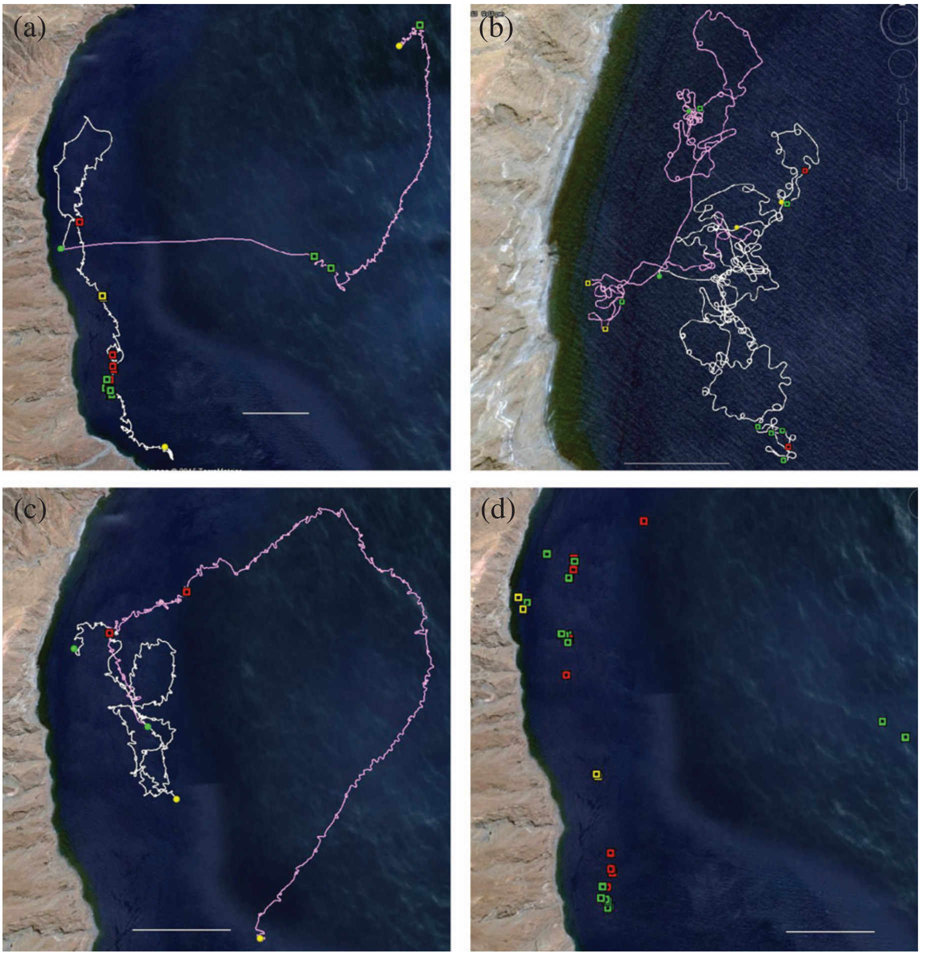

Fig. 3. Tracks of *Carcharodon carcharias* off the coast of Guadalupe Island as determined by an autonomous underwater vehicle (AUV): (a) WS01 (white line) and WS02 (—), (b) WS03 (white line) and WS04a (—), (c) WS04b (white line) and WS04c (—) and (d) locations of all interactions between *C. carcharias* and AUV; start (●) and end (●)indicated. Scale = 1 km except (b) = 0·3 km. Squares in each panel indicates locations of interactions between *C. carcharias* and AUV: approaches (□), bumps (□) and bites (□).

of the AUV, although it made periodic excursions to depths as shallow as 86 m. The extent to which these were vertical movements or simply following the bottom was unknown. While WS01 remained deep and the AUV was, on average, 0·54 km offshore at a depth of 52 m, 13 behavioural interactions between other *C. carcharias* and the AUV were recorded by the video cameras [Table II and Figs 3(a) and 4(a)] and the on-board instrumentation [Fig. 4(b)]. During the approaches and bumps, the sharks were recorded by cameras facing down, aft and left. In cases when the AUV was bitten, all of the sharks were recorded on the camera facing down. Based on the video, it was determined that these interactions involved no less than four individual sharks, including one female and three males (one was later identified as a locally known shark named Bubba).

TABLE II. Behavioural interactions recorded by the autonomous underwater vehicle (AUV) during *Carcharodon carcharias* tracks

Track	Approach	Bump	Bite	Total	Number of sharks	AUV depth (m)		Distance (km)
						Mean ± S.D.	Maximum	Mean ± S.D.
WS01	6	2	5	13	4	52·8 ± 0·5	55·3	0·54 ± 0·06
WS02	3	0	0	3	1	90·0 ± 0·2	91·3	5·35 ± 0·55
WS03	5	0	2	7	2	89·6 ± 0·5	92·6	0·57 ± 0·05
WS04a	2	2	0	4	1	36·4 ± 16·7	91·6	0·19 ± 0·08
WS04b	0	0	0	0	0		91·4	
WS04c	1	0	2	3	2	90·1 ± 0·3	91·4	0·89 ± 0·42
Total	17	4	9	30	10	71·8 ± 25·5		1·50 ± 2·20

Distance, straight-line distance from shore.

Direct physical contact by the attacking shark caused the attitude and depth of the AUV to change dramatically. For example, the first bite resulted in disruptions in pitch, roll and heading rate to the extent that these sensors hit their maximum values and the vehicle was driven 2·5 m upward in the water column [Fig. 4(b)]; bite durations spanned 2–7 s.

WS02: 4·8 M L_T FEMALE, 31 OCTOBER 2013, DURATION 2 H 21 MIN, DISTANCE 15·5 KM

After tagging, WS02 moved directly offshore to the east for the duration of the track [Fig. 3(b)]. The shark swam at the surface for the initial 25 min and then dived to ≥154 m where it remained for most of the track; the AUV was constrained to a depth of 90 m [Fig. 5(a)]. WS02 ascended four times, three of which involved rapid approaches towards the AUV (Fig. 5). During each ascent (maximum rate = 0·92 m s^{-1}), the shark approached from below and was vertically oriented [Fig. 5(b)]; the camera mounted on the transponder recorded the shark moving vertically towards the AUV silhouetted against the surface [Fig. 5(c)]. After each approach, the shark was recorded following the AUV by the aft-facing camera [Fig. 5(d)] before actively descending rapidly (maximum rate = 2·6 m s^{-1}) in a vertical orientation [Fig. 5(e)]. The approaches occurred 4·8–5·9 km from shore (mean ± S.D. = 5·3 ± 0·6 km).

WS03: 4·5 M L_T FEMALE, 2 NOVEMBER 2013, DURATION 1 H 55 MIN, DISTANCE 9·3 KM

Over the duration of the track, WS03 moved over a very small area south and north along the coastline at a distance ranging from 0·35 to 0·68 km from shore [Fig. 3(b)]. The shark moved repeatedly through a depth range of 68–155 m [Fig. 6(a)]. The AUV, which was constrained to a depth of 90 m, was able to track the shark closely when it moved within its depth range, and the shark was observed frequently swimming along the bottom [Fig. 6(b)]. One hour into the track, WS03 was at a depth of 147 m and the AUV was at 90 m when a male shark bit the AUV, striking it from below; the bite was recorded by the aft-facing video camera [Fig. 6(c)]. The duration of the bite was 11 s, after which the shark, later identified as a previously locally known shark (ID#153), followed and approached the AUV four times over the next 8 min. The AUV was bitten

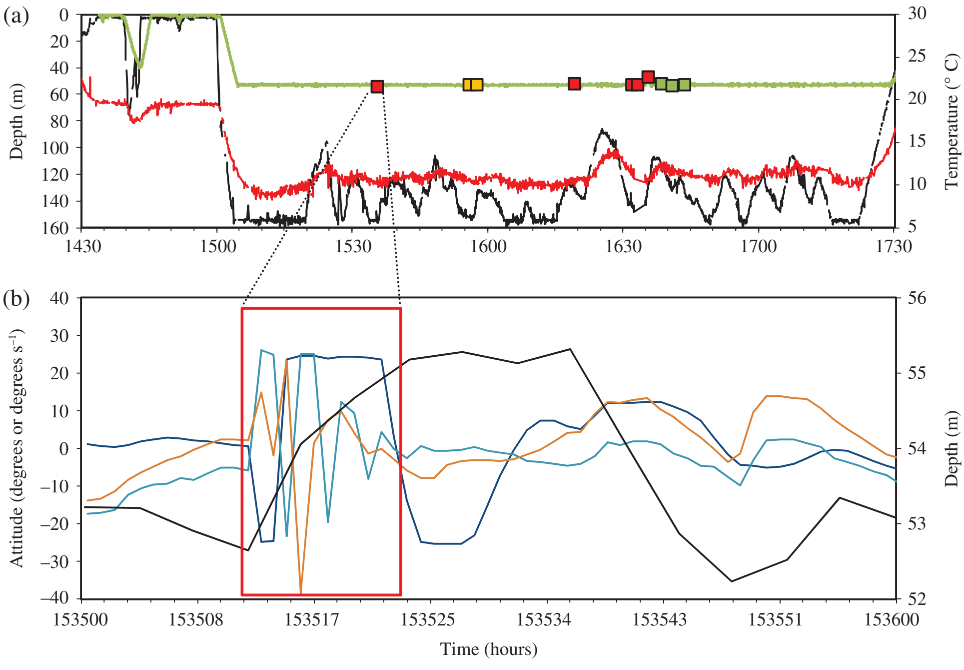

FIG. 4. (a) Depth and water temperature of WS01, depth of autonomous underwater vehicle (AUV) and behavioural interactions between *Carcharodon carcharias* and AUV: approach (□), bump (□) and bite (□). (b) Detail showing attitude and depth of the AUV before, during (□) and after an interaction with a *C. carcharias* during the track of WS01. Note disruption of pitch, roll and heading rate during the attack (□) as shark pushes the AUV upward 2·5 m. (a) —, shark; —, AUV; —, temperature. (b) —, pitch; —, roll; —, heading rate; —, AUV.

a second time 30 min later by a female shark at the same depth (90 m). This bite lasted 15 s, during which the shark struck the aft section of the AUV from below and moved progressively forward, adjusting its bite and rolling its eyes backward [Fig. 6(d)]. The shark approached the AUV after releasing it and exhibited mouth gaping. This bite caused water intrusion into the hull of the REMUS and the mission was aborted. The two bites observed during the track of WS03 occurred at a mean $\pm$ S.D. distance of $0{\cdot}57 \pm 0{\cdot}05$ km from shore [Table II and Fig. 3(b)].

WS04A: 5·7 M L_T FEMALE, 6 NOVEMBER 2013, DURATION 1 H 26 MIN, DISTANCE 6·1 KM

This large female was tracked three times over the course of 2 days. During this first mission, the shark moved *c.* 1 km north, but gradually returned to the general vicinity of where it was tagged [Fig. 3(b)]. With the exception of the last 10 min of the track, WS04 remained within the depth range of the AUV [<90 m; Fig. 7(a)] and the AUV was able to follow within several metres of the shark as it moved along the bottom [Fig. 7(b)]. In doing so, the AUV was able to confirm the sex of the shark while video documenting the colouration, scarring patterns and fin shapes [Fig. 7(b)]. During the track, WS04 reacted to the presence of the AUV by approaching it twice and bumping it twice [Fig. 7(c)]. The shark was accompanied by several yellowtail amberjack *Seriola*

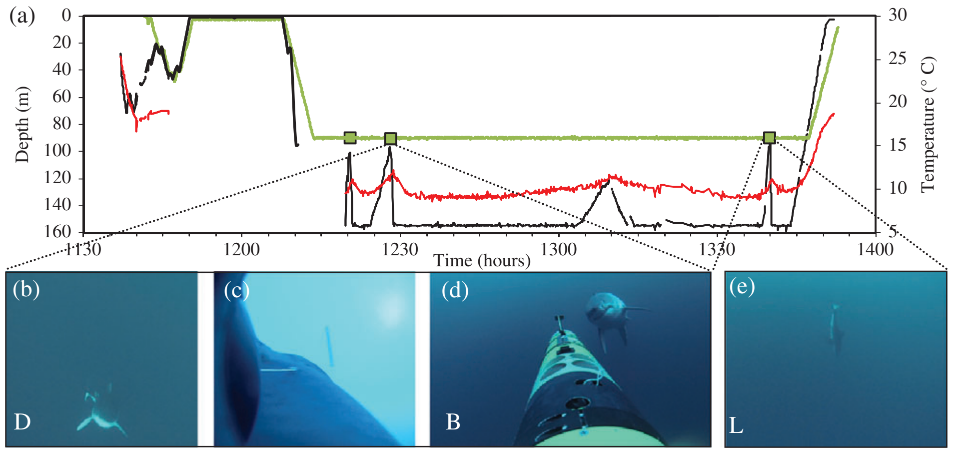

FIG. 5. (a) Depth and water temperature of WS02, depth of autonomous underwater vehicle (AUV) and behavioural interactions between *Carcharodon carcharias* and AUV: approach (□). (b–e) Images captured from (b, d, e) AUV video cameras and (c) transponder camera of WS02 approaching the AUV by (b, c) ascending vertically in the water column, (d) following AUV and (e) rapidly descending vertically; upper-case letters refer to camera positions noted in Fig. 2. ——, shark; ——, AUV; ——, temperature.

lalandi Valenciennes 1833 [Fig. 7(d)] during this period. The interactions with the AUV occurred at a mean ± S.D. depth of 36·4 ± 16·7 m and distance of 0·19 ± 0·08 km from the shoreline.

WS04B, C: 5·7 M L_T FEMALE, 7 NOVEMBER 2013, TOTAL DURATION 5 H 23 MIN, TOTAL DISTANCE 33·1 KM

WS04 was re-tagged and tracked again the following day. Although the smaller tracking vessel remained with the shark for the entire duration of the track, the AUV was retrieved midway through the track to offload and recharge video cameras. During the first half of the track, WS04 remained in the general vicinity of the vessel, moving south and then north at a distance of 0·3–1·4 km from the shoreline [Fig. 3(c)]. During the second half of the track, the shark moved offshore to the east reaching a maximum distance of *c*. 5 km from the shoreline; the shark then looped south and inshore [Fig. 3(c)]. Shortly after tagging, the shark descended to and remained at a depth of ≥145 m for the total duration of the track [Fig. 8(a)]. Due to depth of the shark relative to the AUV (90 m), WS04 was not observed by the AUV during most of the track. Three interactions with other *C. carcharias* were recorded comprising a single approach and two bites [Fig. 8(a)]. During the first two interactions, which lasted for 16 s, a male *C. carcharias* later identified as a locally known shark (Tairua; *c*. 4·7 m L_T) approached and passed under the AUV, circled around to the rear, approached again and bit the AUV at the location of the aft-facing camera. About 30 min later, a female *C. carcharias*, later identified as Lucy, approached from behind and below the AUV and bit its aft section [Fig. 8(b), (c)]. The shark released the AUV, circled to the right side, bumped the nose [Fig. 8(d)], circled around to the rear and followed the AUV for another 30 s before diving out of sight. These interactions with the AUV occurred at a mean depth of 90 m

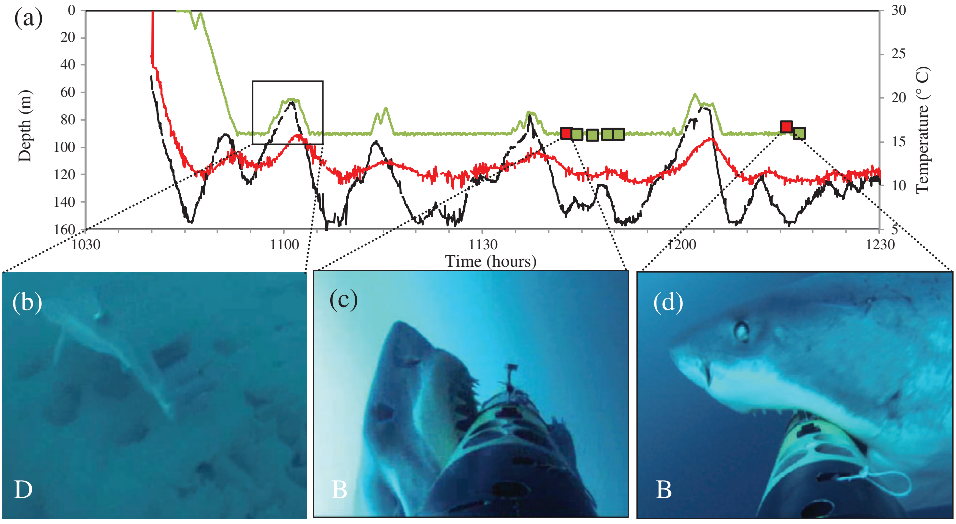

FIG. 6. (a) Depth and water temperature of WS03, depth of autonomous underwater vehicle (AUV) and behavioural interactions between *Carcharodon carcharias* and AUV: approach (■) and bite (■). (b–d) Images captured from AUV video cameras of WS03 (b) swimming along bottom, (c) the AUV being bitten by different male and (d) female sharks; (d) note eye of shark rolling back during the bite. Upper-case letters refer to camera positions noted in Fig. 2. ___, shark; ___, AUV; ___, temperature.

and mean ± S.D. distance of 0·89 ± 0·42 km from shore; bite durations were 6 s (Tairua) and 15 s (Lucy).

DISCUSSION

AUV TECHNOLOGY

In this study, an AUV was used to generate over 13 h of observations of *C. carcharias* at depths up to 90 m off the coast of Guadalupe Island. This ground-breaking work represents the first successful efforts to autonomously track and image any animal in the marine environment. While the imaging of subsurface animal behaviour has been achieved with animal-borne imaging systems (*e.g.* 'Crittercam', Heithaus *et al.*, 2001), this technology has many limitations. First and foremost, these systems are not currently capable of horizontal tracking and the animal must be followed simultaneously using traditional vessel-based tracking methods. Second, these systems typically comprise a single camera that is fixed to the animal facing forward, thereby limiting the extent to which the animal can be observed. Moreover, sharks and other animals must be captured and handled for camera attachment, which can result in acute and chronic stress and aberrations in post-release behaviour (Skomal *et al.*, 2007). Lastly, animal-borne systems cannot accommodate a vast array of scientific instrumentation. In contrast, the REMUS-100 AUV provided high-resolution three-dimensional position information of the animal under observation, approached the tagged animal to provide visual data about its behaviour and

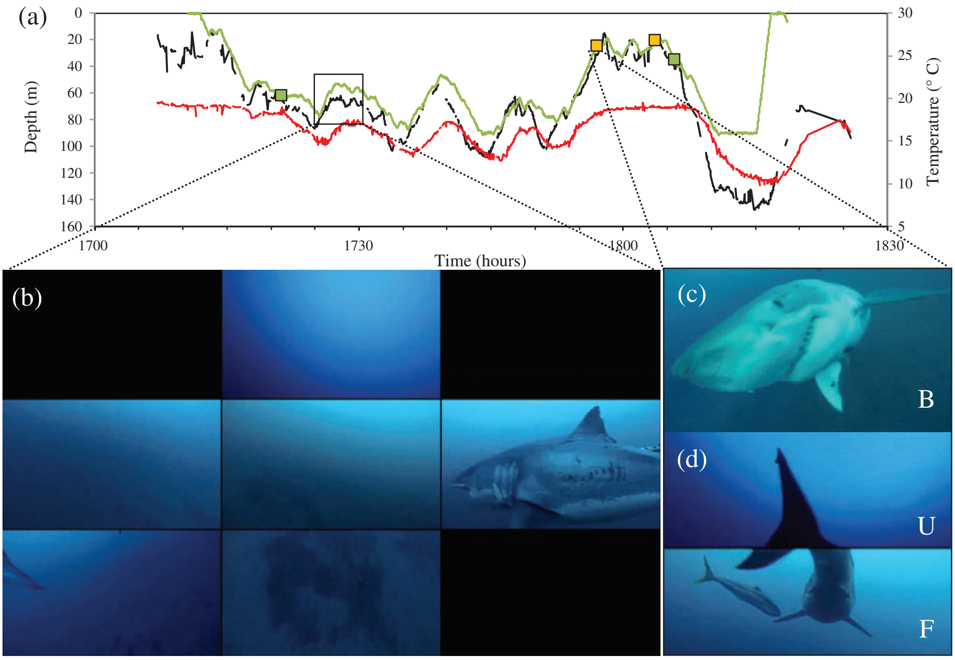

FIG. 7. (a) Depth and water temperature of WS04a, depth of autonomous underwater vehicle (AUV) and behavioural interactions between *Carcharodon carcharias* and AUV: approach (■) and bump (■). (b) Image showing WS04 swimming along bottom as observed by all video cameras. (c) Image from video camera showing WS04 bumping AUV from below and behind and (d) accompanied by a *Seriola lalandi*. Upper-case letters refer to camera positions noted in Fig. 2. ——, shark; ——, AUV; ——, temperature.

habitat from multiple angles and perspectives, does not require that the shark be captured and handled and can be modified to carry a vast array of instrumentation. Hence, this approach resulted in the direct measurement of the shark's location and depth yielding far greater positional accuracy than traditional vessel-based tracking methods (Sundström *et al.*, 2001) and thereby allowing for the moving shark to be filmed at close range.

The idea of tracking an animal with an AUV is not unique. Clark *et al.* (2013) used an AUV to follow a *T. semifasciata* off the coast of California for up to 1·67 h. In that approach, they used a particle filter to produce a state estimate of the tag location. During those efforts, the AUV was constrained to the surface, lacked the capacity to monitor animal depth, and resulted in a coarse estimate of the shark's horizontal movements. In contrast, the REMUS AUV has the capability to track the three-dimensional movements of marine animals with great geopositional accuracy while collecting video imagery and ambient environmental data. This information not only allows researchers to track the horizontal and vertical movements of marine animals but also collect direct observations of animal behaviour and environmental data sufficient for fine-scale habitat modelling.

Although the unit (REMUS-100) was depth-limited, other REMUS units are rated to depths well in excess of 1000 m, which allows for tighter, close-range tracking at greater depths. In addition, the limitation of the transponder depth sensor (100 m) did

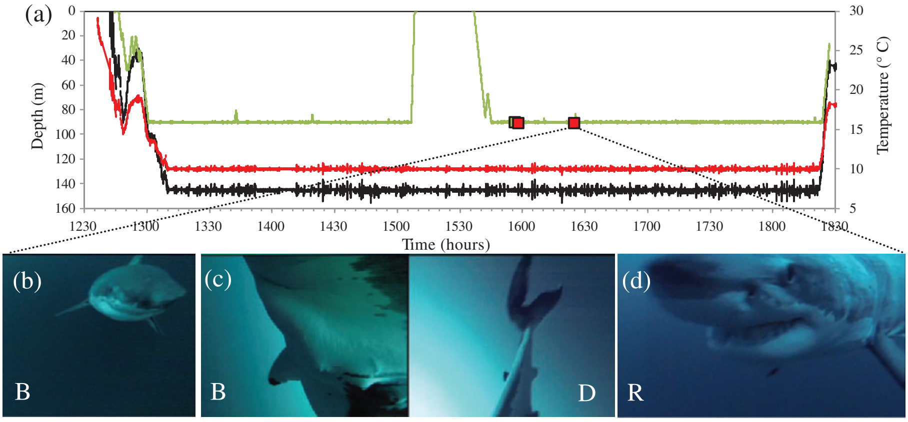

FIG. 8. (a) Depth and water temperature during the tracks of WS04b and WS04c, depth of autonomous underwater vehicle (AUV) and behavioural interactions between *Carcharodon carcharias* and AUV: approach (■) and bite (■). (b, c) Images showing *C. carcharias* Lucy (b) approaching from below immediately prior to biting, (c) biting and (d) bumping the AUV; note deformed caudal fin used to later identify Lucy. Upper-case letters refer to camera positions noted in Fig. 2. ___, shark; ___, AUV; ___, temperature.

not allow the AUV to record the exact depth of the shark, but this can be easily corrected for future work. In this study, the AUV was programmed to approach the shark and maintain close-range tracking to within 1 m. The unit, however, can be programmed to maintain any distance from the animal, the bottom and the surface. Hence, each mission can be readily customized to meet study objectives.

The greatest limitation of the autonomous tracking technique hinges on deployment duration. The AUV has the capacity to operate for periods up to 12 h, which may be adequate for some studies but insufficient for broad-scale tracking. In addition, the portable video cameras deployed during the current study severely curtailed the track durations to <3 h due to battery and storage capacity. Future work will centre on increasing track durations and behavioural observations by deploying larger batteries and directly coupling camera systems with the AUV electronics.

CARCHARODON CARCHARIAS PREDATORY BEHAVIOUR

It is well established that *C. carcharias* are top predators of marine mammals and fishes (Compagno, 2001), but virtually all of the published observations of *C. carcharias* predatory behaviour are based on surface interactions with pinnipeds at well-studied *C. carcharias* aggregation areas, including the south-east Farallon Islands (Ainley *et al.*, 1981, 1985; McCosker, 1985; Bruce, 1992; Klimley *et al.*, 1992, 1996*a*, 2001; Anderson *et al.*, 1996*a*, *b*, 2008; Pyle *et al.*, 1996), Seal Island, South Africa (Martin *et al.*, 2005, 2009; Hammerschlag *et al.*, 2006, 2012; Laroche *et al.*, 2008; Fallows *et al.*, 2012) and South Australia (Tricas & McCosker, 1984; Strong *et al.*, 1996). In this study, *C. carcharias* were observed to approach, bump and bite the AUV at depths of 36–90 m, constituting the first observations of such behaviour well below the surface.

Admittedly, when the AUV was deployed to track and image the behaviour of *C. carcharias* off the coast of Guadalupe, the observed interactions were not

FIG. 9. Autonomous underwater vehicle with tooth rakes resulting from nine bites from *Carcharodon carcharias*; note that all of the marks are located on the lower aft section of the vehicle.

anticipated. During the 13·5 h of tracking, 30 interactions were documented by no less than 10 individual *C. carcharias* (five males and five females), most (80%) of which were not the shark being tracked. These observations collectively provide novel evidence of subsurface predatory behaviour by *C. carcharias* in general and, specifically, at the island of Guadalupe.

It has been suggested that *C. carcharias* are drawn to Guadalupe Island to prey upon the seasonal presence of pinnipeds, but this behaviour has rarely been observed (Domeier & Nasby-Lucas, 2007; Domeier, 2009; Hoyos-Padilla, 2009). Although seal carcasses have been observed floating at the surface, the predation event has not been witnessed (E. M. Hoyos-Padilla, pers. obs.). In addition, satellite (Domeier *et al.*, 2012) and acoustic tracking (E. M. Hoyos-Padilla, unpubl. data) data indicate that *C. carcharias* routinely make daily dives to depths in excess of 100 m when around Guadalupe. The four *C. carcharias* tracked during this study spent, on average, 80% of the time at depths >100 m and only 5% of their time at depths <25 m. Collectively, these observations suggest that predation events occur below the surface. In other areas, it has been established that *C. carcharias* avoid the surface and remain at depths down to 50 m while near pinniped rookeries in autumn and winter; this is consistent with a silhouette-based hunting strategy (Weng *et al.*, 2007). In this study, *C. carcharias* were observed approaching, bumping and biting the AUV at depths ranging from 53 to 90 m, thereby providing direct evidence of *C. carcharias* predatory behaviour at depth. These data suggest that *C. carcharias* take advantage of great underwater visibility to search for seals in deep water adjacent to seal colonies so as to ambush and disable pinnipeds and, perhaps, follow the carcass to the surface (Hoyos-Padilla, 2009). Of course, the AUV spent the bulk of the tracking periods at these depths and there is a possibility that attacks also occur at shallower depths, but there is no evidence of this to date.

Surface observations provide substantial evidence that *C. carcharias* are highly visual predators that typically ambush their prey vertically from below and behind (Tricas & McCosker, 1984; Anderson *et al.*, 1996*b*; Strong, 1996; Goldman & Anderson, 1999; Martin *et al.*, 2005, 2009; Hammerschlag *et al.*, 2012). Similar behaviour was observed in this study as almost all of the interactions between *C. carcharias* and the AUV were recorded by the backward–downward-facing cameras, indicating that *C. carcharias* initiate predation from below. When the sharks physically attacked and bit the AUV, the force was so great so as to displace the AUV as much as 2·5 m vertically in the water column, leave tooth rake marks on the aft section of the AUV (Fig. 9) and, in one case, compromise the hull of the AUV. The vertical approach was rapid and from depths well below the AUV. For example, during the track of WS02, this shark moved vertically from a minimum depth of 154 m to approach the AUV at a maximum rate of 0·92 m s^{-1}. The camera mounted on the transponder (*i.e.* the shark) clearly shows the shark moving vertically towards the back-lit silhouette of the AUV [Fig. 5(c)]. After a brief period of following the AUV, the shark actively swam downward at a maximum rate of 2·6 m s^{-1}. This rapid dive may be indicative of an effort to remain concealed at depth. These observations constitute the initial stages of the predation cycle during which a predator detects, identifies and approaches a prey item (Endler, 1986).

Numerous studies indicate that *C. carcharias* strike a fine balance between visibility and detectability when feeding on pinnipeds (Strong, 1996; Goldman & Anderson, 1999; Hammerschlag *et al.*, 2006; Laroche *et al.*, 2008; Martin *et al.*, 2009; Martin & Hammerschlag, 2012; Huveneers *et al.*, 2015). Strong (1996) described *C. carcharias* as speculative hunters relying heavily on visual cues to initiate a predation event, approach the potential prey and ultimately bite, bump or abort. As a result, the predatory behaviour of *C. carcharias* is tightly linked to site-specific environmental conditions (Pyle *et al.*, 1996; Fallows *et al.*, 2012), such as water clarity, which is thought to play a critical role (Strong, 1996; Martin *et al.*, 2009; Martin & Hammerschlag, 2012). Hence, it has been suggested that *C. carcharias* utilize the optimal depth so as remain undetected while maximizing the probability of prey detection and capture (Strong, 1996; Goldman & Anderson, 1999). Off the coast of Guadalupe Island, water clarity is often 25–30 m (Gallo-Reynoso *et al.*, 2005), thereby increasing the detectability of a *C. carcharias* by its prey in shallow water. Water depth, however, increases dramatically to >1000 m within 5 km of the shoreline at Guadalupe Island (Fig. 1; Domeier *et al.*, 2012), and *C. carcharias* may be utilizing these greater depths to remain undetected while stalking prey.

Based on the satellite-tagging data, Domeier *et al.* (2012) found that the seasonal distribution of *C. carcharias* around Guadalupe coincides with the seasonal presence of pinnipeds. During this study, which occurred in early November, all of the *C. carcharias* were tagged and remained off the north-east coast of Guadalupe Island (Fig. 3), which provides important habitat for three pinnipeds species (Domeier *et al.*, 2012). During this time of year, northern elephant seals are returning to this region of the island to breed, and it is possible that *C. carcharias* are patrolling the shoreline to intercept the movements of these animals. With the exception of three approaches exhibited about 5 km from shore by WS02 [Fig. 3(a)], all of the observed interactions occurred at a distance of 0·1–1·2 km from the shoreline. This distance could represent a feeding zone for *C. carcharias* off Guadalupe [Fig. 3(d)]. At the Farallon Islands and Seal Island, where *C. carcharias* are frequently observed preying upon pinnipeds, researchers have described similar high-risk zones in which the frequency of predation events is the highest, <450 m from shore (Klimley *et al.*, 1992; Goldman *et al.*, 1996; Martin *et al.*, 2005, 2009; Fallows *et al.*, 2012).

It is well documented that *C. carcharias* approach and bite inanimate objects and decoys (Anderson *et al.*, 1996*a*, *b*; Collier *et al.*, 1996; Strong, 1996; Martin *et al.*, 2005; Hammerschlag *et al.*, 2012). In these studies, it has been presumed that these predatory events are indicative of predatory tactics used to prey upon pinnipeds. Similarly, the present observations of subsurface interactions between *C. carcharias* and the AUV probably constitute predatory behaviour and not social (Klimley *et al.*, 1996*b*) or reproductive behaviours (Domeier *et al.*, 2012). Although the participation of both males and females in these interactions rules out the latter, some of these interactions may be indicative of agonistic behaviour. *Carcharodon carcharias* are thought to exhibit a variety of agonistic behaviours, including jaw gaping, bumping and biting (Martin, 2007), which were observed in this study. For example, during the track of WS04a, this shark approached and bumped the AUV twice when the vehicle approached [Fig. 7(c)]. Agonistic bites are typically less forceful than predatory bites, are of short duration and tend to be concentrated on the forward section of the body, head and fins. In contrast, the bites observed in this study were rendered with great force from behind and below (typical of a predatory attack), lasted up to 15 s and were largely to the aft section of the AUV (Fig. 9). Therefore, it is more likely that the biting behaviour observed in this study was associated with predation attempts and not agonistic behaviour.

In this study, it was not possible to identify the intended prey species. Based on the aforementioned information, pinnipeds are a likely prey of *C. carcharias* in Guadalupe, but numerous species of fishes, including *S. lalandi* and yellowfin tuna *Thunnus albacares* (Bonnaterre 1788), are also present. Based on simple feeding experiments in Guadalupe, Domeier (2009) concluded that *C. carcharias* show a preference for *T. albacares* when compared with California sea lions. In this study, *S. lalandi* were observed following the shark during the track of WS04 [Fig. 7(d)], but it is not unusual for prey species to be in close proximity to the predator. Clearly, additional studies are needed to identify the prey species targeted by *C. carcharias* at depth in Guadalupe.

In conclusion, the REMUS-100 tracking vehicle demonstrated a remarkable ability to autonomously monitor, follow, approach and image a randomly moving tagged target. The vehicle, which can easily be deployed in waters inaccessible to or unsafe for divers, is capable of producing high-precision tracks while collecting environmental data and behavioural imagery over periods of several hours. Moreover, the vehicle is versatile and can take on different payloads to meet science goals. In this study, it was demonstrated that an AUV can be used to effectively track and observe the behaviour of a large pelagic animal, *C. carcharias*. In doing so, the first observations of subsurface predatory behaviour were observed in this species. At its current state of development, this technology clearly offers a new and innovative tool for tracking the fine-scale behaviour of marine animals. It is anticipated that new advances in this field will ultimately be used to collect observations over broader temporal and spatial scales.

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