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

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Running headline: Tracking white sharks with an AUV

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Abstract

Investigations of animal habitat use and behaviour are important for understanding the ecology of animals and are vital for making informed conservation decisions. Most of what is known about shark behaviour comes from direct observations at shallow depths, captive studies, baited and chance encounters, and inferences from tracking and tagging data. 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, but they do little to reveal what these animals are actually doing. It is well established that the white shark, *Carcharodon carcharias*, is a top predator of marine mammals and fishes, but virtually all published observations of white shark predatory behaviour are based on surface interactions with pinnipeds at well-studied white shark aggregation areas. Guadalupe Island off the coast of Mexico is a seasonal aggregation site for white sharks, which are presumably drawn to the island to feed upon pinnipeds, yet predation has rarely been observed. 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 off Guadalupe Island. During the period 31 October – 7 November 2013, six AUV missions were conducted to track one male and three female white sharks, ranging in estimated total length (TL) from 3.9-5.7 m, off the northeast coast of Guadalupe Island. In doing so, the AUV generated over 13 hours of behavioral data for white sharks at depths up to 90 m. The white 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 (mean ± SD = 112.5 ± 40.3 m) and 7.9-27.1 °C (mean ± SD = 12.7 ± 2.9 °C), respectively. Video footage and AUV sensor data revealed that two of the white sharks being tracked and eight other white sharks in the area approached (n=17), bumped (n=4), and bit (n=9) the AUV during these tracks. In this study, it was demonstrated that an AUV can be used to effectively track and observe the behaviour of a large pelagic animal, the white shark. 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: *Carcharodon carcharias*, behaviour, AUV, Guadalupe Island, REMUS

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 (e.g. Tricas, 1985), from submersibles (e.g., Nelson et al., 1986), and from animal-borne imaging (e.g., Marshall, 1998). Given the paucity of such observations, the feeding ecology of large oceanic animals has been inferred from tagging and tracking data (e.g., Skomal and 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*, 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; Klimley, 1984; Tricas and McCosker, 1984; Klimley, 1985; Ainley et al, 1985; Tricas, 1985; McCosker, 1985; Klimley et al., 1992; Klimley et al., 1996; Anderson et al, 1996a; Anderson et al, 1996b; Pyle et al., 1996;

Strong et al., 1996; Martin et al., 2005; Martin et al., 2009; Hammerschlag et al., 2006; Laroche et al., 2008; Fallows et al., 2012; Hammerschlag et al., 2012).

It is also been well-established that white sharks 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 and Nasby-Lucas, 2008; 2013; Nasby-Lucas et al, 2009; Jorgenson et al, 2010; Duffy et al., 2012; Francis et al., 2012). The extent to which this behaviour is associated with feeding (Domeier and Nasby-Lucas, 2008; Nasby-Lucas et al, 2009) or reproduction (Jorgenson et al, 2012) remains a topic of scientific debate simply because there are no observations of white shark behaviour at depth.

In addition to the aggregation sites noted above, Guadalupe Island off the coast of Mexico is a seasonal host to white sharks 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, the white sharks are drawn to the island to feed upon these animals, yet predation on these pinnipeds has rarely been observed (Domeier and Nasby-Lucas, 2007; Domeier, 2009; Hoyos-Padilla, personal communication). It has been hypothesized that white sharks prey upon pinnipeds at greater depths at Guadalupe and acoustic telemetry data from several adult white sharks has revealed deep diving behaviour (Hoyos-Padilla, 2009). These data suggest that white sharks 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 six years, they have yet to be observed underwater (Hoyos-Padilla, personal communication).

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 (e.g., 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 our 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 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 REMUS (Remote Environmental Monitoring UnitS) AUV was initially developed by the Woods Hole Oceanographic Institution for coastal mapping and monitoring. These vehicles are now used as platforms for a wide variety of oceanographic instrumentation operating at depths ranging from 0-6000 meters. They are outfitted with a Global Positioning System (GPS), wireless communication, iridium capabilities, and an inertial navigation system, which uses ring laser gyroscopes to orient the vehicle spatially and accelerometers to sense changes in speed and velocity. As a result, REMUS AUV’s 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 white sharks off Guadalupe Island. Our objectives were not only to advance and test this technology as a viable tool for directly observing the behaviour of marine animals, but to also investigate the behaviour, habitat use, and feeding ecology of white sharks 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 at 29º 7´ N, 118º 21´ W (Fig. 1). This study was conducted off the northeast coast of the island, which is characterized by an extremely narrow continental shelf with depths of 3,600 m found close to shore (Pierson, 1987) and series of deep canyons (Gallo-Reynoso and Figueroa-Carranza 2005) (Fig. 1).

This work was conducted from October 29-November 10, 2013 onboard the M/V Horizon, one of the commercial white shark diving operations working seasonally off the northeast coast of Guadalupe Island. During this time, four white sharks were tagged with an acoustic transponder (see below) 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 Woods Hole Oceanographic Institution (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 omni-directional Ultra-Short BaseLine (USBL) array and navigation algorithms to perform three-dimensional autonomous tracking, following, and filming of a randomly moving target (i.e., 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 behavioral 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 three seconds 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 behavioral footage on one of its six high definition video cameras (see below). The vehicle combined 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, 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.

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, Poway, CA) for current data and speed over ground measurements, a conductivity-temperature (CT) probe (YSI. Yellow Springs, OH) , magnetic heading sensor, pressure sensor, and six high definition video cameras (Model Hero3+, GoPro, Inc., San Mateo, CA). 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. Additionally, the tag would release itself if the fish were to swim below 350 meters. In the event that battery power was lost in the transponder, a corrosible link was put in place to release the tag from the animal after approximately 8 hours.

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 -5-35°C, resolution 0.15 °C) or V16T (temperature range 10-40°C, resolution 0.12 °C, Vemco, Inc., Nova Scotia) was affixed to the transponder and detected with a directional hydrophone (Model VH110, Vemco, Inc., Nova Scotia) connected to an acoustic receiver (Model VR100, Vemco, Inc., Nova Scotia). Depth and ambient temperature data were telemetered to the receiver and recorded for the duration of each track.

Results

During the period 31 October – 7 November, 2013, six AUV missions were conducted to track one male and three female white sharks, ranging in estimated (derived by comparing the size of the shark to the known length of the tagging vessel) total length (TL) from 3.9-5.7 m, off the northeast coast of Guadalupe Island (Table I). Although these sharks were tracked for up to 6 hrs using the smaller vessel, AUV mission durations ranged from 1.43-2.93 hours resulting in a total of 13.62 hrs of tracking data. Mission depth 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 was used to characterize the depth and ambient water temperature of each tracked shark during missions WS01, WS02, WS03, and WS04a. Since only temperature transmitters were used during missions WS04b and WS04c, the depth of the shark was calculated using the depth/temperature linear relationship resulting from the previous four tracks where:

Shark Depth = 269.57 - 12.414(temperature), $R^2 = 0.82$, n= 9,400.

In general, the sharks remained in the area for the duration of each mission (Figure 3) and moved through broad depth and temperature ranges from the surface to 163.8 m (mean ± SD = 112.5 ± 40.3 m) and 7.9-27.1 °C (mean ± SD = 12.7 ± 2.9 °C), respectively. Our most significant observations can be characterized as interactions between the AUV and white sharks at depths in excess of 50 m. Upon review of video footage and AUV sensor data, it was found that two of the white sharks being tracked by the AUV in addition to eight other white sharks in the area exhibited the following behaviors: approach, bump, and bite. During an approach, a white shark actively moved toward 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 white shark. During the six tracks, a total of 30 interactions were observed between 10 individual white sharks and the AUV comprising 17 approaches, 4 bumps, and 9 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 TL male, 30 October 2013, duration: 2:32, 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 ~30 mins [Fig. 3(a)]. During this time, the shark remained largely associated with the surface and swam directly past a vessel belonging to another commercial white shark dive operator. WS01 then moved offshore and dove to the maximum depth of the acoustic transmitter [154 m; Fig. 4(a)]. For the balance of the track (~2 hrs), the shark remained below the depth 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 behavioral interactions between other white sharks and the AUV were recorded by the video cameras [Table II, Fig. 3(a), 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).

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 secs.

WS02: 4.8 m TL female, 31 October 2013, duration: 2:21, 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 mins, and then dove to ≥154 m where it remained for most of the track; the AUV was constrained to a depth of 90m [Fig. 5(a)]. WS02 ascended four times, three of which involved rapid approaches toward the AUV (Fig. 5). During each ascent (maximum rate = 0.92 ms^{-1}), the shark approached from below and was vertically oriented [Fig. 5(b)]; the camera mounted on the transponder recorded the shark moving vertically toward 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 ms^{-1}) in a vertical orientation [Fig. 5(e)]. The approaches occurred 4.8-5.9 km from shore (mean = 5.3 ± 0.6 km).

WS03: 4.5 m TL female, 2 November 2013, duration: 1:55, 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 0.35-0.68 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 147m 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 secs, 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 mins. The AUV was bitten a second time 30 minutes later by a female shark at the same depth (90 m). This bite lasted 15 secs, 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 an average distance of 0.57 (±0.05 SD) km from shore [Table II and Fig. 3(b)].

WS04a: 5.7 m TL female, 6 November 2013, duration: 1:26, distance: 6.1 km.

This large female was tracked three times over the course of two days. During this first mission, the shark moved about 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 mins 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 meters 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 coloration, 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 lalandi*) [Fig. 7(d)] during this period. The interactions with the AUV occurred at a mean depth of 36.4 ± 16.7 m and mean distance of 0.19 ± 0.08 km from the shoreline.

WS04b, c: 5.7 m TL female, 7 November 2013, total duration: 5:23, 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, 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 about 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 (90m), WS04 was not observed by the AUV during most of the track. However, three interactions with other white sharks were recorded comprising a single approach and two bites [Fig. 8(a)]. During the first two interactions, which lasted 16 secs, a male white shark later identified as a locally known shark (Tairua; ~4.7 m TL) 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 mins later, a female white shark, 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 secs before diving out of sight. These interactions with the AUV occurred at a mean depth of 90 m and mean distance of 0.89 (± 0.42) km from shore; bite durations were 6 secs (Tairua) and 15 secs (Lucy).

Discussion

AUV technology

In this study, an AUV was used to generate over 13 hours of observations of white sharks 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 habitat from multiple angles and perspectives, does not require that 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 (reviewed by Sundstrom 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 leopard shark off the coast of California for up to 1.67 hours. 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 modeling.

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 our transponder depth sensor (100 m) did 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 one meter. However, the unit 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 our autonomous tracking technique hinges on deployment duration. The AUV has the capacity to operate for periods up to 12 hours, 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 our track durations to less than three hours due to battery and storage capacity. Future work will center on increasing track durations and behavioral observations by deploying larger batteries and/or directly coupling camera systems with the AUV electronics.

White Shark Predatory Behaviour

It is well established that white sharks are top predators of marine mammals and fishes (reviewed by Campagno, 2001), but virtually all of the published observations of white shark predatory behaviour are based on surface interactions with pinnipeds at well-studied white shark aggregation areas, including the Southeast Farallon Islands (Ainley et al., 1981; Ainley et al, 1985; Bruce, 1992; McCosker, 1985; Klimley et al., 1992; Klimley et al., 1996; Anderson et al, 1996a; Anderson et al, 1996b; Pyle et al., 1996; Klimley et al, 2001; Anderson et al, 2008), Seal Island, South Africa (Martin et al., 2005; Martin et al., 2009; Hammerschlag et al., 2006; Laroche et al., 2008; Fallows et al., 2012; Hammerschlag et al., 2012), and South Australia (Tricas and McCosker, 1984; Strong et al., 1996). In this study, white sharks 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 white sharks off the coast of Guadalupe, the observed interactions were not anticipated. During the 13.5 hours of tracking, 30 interactions were documented by no less than 10 individual white sharks (5 males, 5 females), most (80%) of which were not the shark being tracked. These observations collectively provide novel evidence of subsurface predatory behaviour by white sharks in general and, specifically, at the island of Guadalupe.

It has been suggested that white sharks are drawn to Guadalupe Island to prey upon the seasonal presence of pinnipeds, but this behaviour has rarely been observed (Domeier and 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 (Hoyos-Padilla, personal communication). In addition, satellite (Domeier et al. 2012) and acoustic tracking (Hoyos-Padilla, unpublished data) data indicate that white sharks routinely make daily dives to depths in excess of 100 m when around Guadalupe. The four white sharks tracked during the current study spent, on average, 80% of the time at depths > 100 m and only 5% of their time at depths

<25m. Collectively, these observations suggest that predation events occur below the surface. In other areas, it has been established white sharks avoid the surface and remain at depths up to 50 m depth while near pinniped rookeries in autumn and winter; this is consistent with a silhouette-based hunting strategy (Weng et al., 2007). In this study, white sharks were observed approaching, bumping, and biting the AUV at depths ranging from 53-90m, thereby providing direct evidence of white shark predatory behaviour at depth. These data suggest that white sharks 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 white sharks are highly visual predators that typically ambush their prey vertically from below and behind (Tricas and McCosker, 1984; Anderson et al, 1996b; Strong 1996; Goldman and Anderson, 1999; Martin et al., 2005; Martin et al., 2009; Hammerschlag et al., 2012). Similar behaviour was observed in this study as almost all of the interactions between white sharks and the AUV were recorded by the backward and/or downward facing cameras, indicating that white sharks 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 ms^{-1}. The camera mounted on the transponder (i.e., shark) clearly shows the shark moving vertically toward 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 ms^{-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 white sharks strike a fine balance between visibility and detectability when feeding on pinnipeds (Strong, 1996; Goldman and Anderson, 1999; Martin et al., 2009; Hammerschlag et al., 2006; Laroche et al., 2008; Martin and Hammerschlag, 2012; Huveneers et al., 2015). Strong (1996) described white sharks 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 white sharks 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, 1996b; Martin et al., 2009; Martin and Hammerschlag, 2012). Hence, it has been suggested that white sharks utilize the optimal depth so as remain undetected while maximizing the probability of prey detection and capture (Strong 1996, Goldman and Anderson, 1999). Off the coast of Guadalupe Island, water clarity is often 25-30 m (Gallo-Reynoso et al., 2005b), thereby increasing the detectability of a white shark by its prey in shallow water. However, water depth drops dramatically to >1000 m within 5 km of the shoreline at Guadalupe island (Fig. 1; Domeier et al., 2012) and white sharks may be utilizing these greater depths to remain undetected while stalking prey.

Based on satellite-tagging data, Domeier et al. (2012) found that the seasonal distribution of white sharks around Guadalupe coincides with the seasonal presence of pinnipeds. During this study, which occurred in early November, all of the white sharks were tagged and remained off the northeast 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 white sharks 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 white sharks off Guadalupe [Fig. 39d)]. At the Farallon Islands and Seal Island, where white sharks are frequently observed preying upon pinnipeds, researchers have described similar 'high risk' zones in which the frequency of predation events is highest <450m from shore (Klimley et al., 1992; Goldman et al., 1996; Martin et al., 2005; Martin et al., 2009; Fallows et al., 2012).

It is well documented that white sharks approach and bite inanimate objects and decoys (Anderson et al., 1996; 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, our observations of subsurface interactions between white sharks and the AUV likely constitute predatory behaviour and not social (Klimley et al., 1996) 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. White sharks are thought to exhibit a variety of agonistic behaviours, including jaw gaping, bumping, and biting (reviewed by Martin, 2007), which were observed in the current 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 secs, and were largely to the aft section of the AUV (Fig. 9). Therefore, it is more likely that the biting behavior observed in this study was associated with predation attempts and not agonistic behaviour.

In this study, we were not able to identify the intended prey species. Based on the aforementioned information, pinnipeds are a likely prey of the white shark in Guadalupe, but numerous species of fishes, including yellowtail amberjack (*Seriola lalandi*) and yellowfin tuna (*Thunnus albacares*), are also present. Based on simple feeding experiments in Guadalupe, Domeier (2009) concluded that white sharks show a preference for yellowfin tuna when compared to California sea lions. In the current study, yellowtail amberjack 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 white sharks 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 behavioral imagery over periods of several hours. Moreover, the vehicle is versatile and can take on different payloads to meet science goals. In the current study, it was demonstrated that an AUV can be used to effectively track and observe the behaviour of a large pelagic animal, the white shark. In doing so, the first observations of subsurface predatory behaviour were observed of 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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Table I. White sharks tracked by the AUV.

Shark	Sex	TL (m)	Date	Time		Duration	Distance
				Start	End	(H:M)	(km)
WS01	Male	3.9	30-Oct-13	14:34	17:06	2:32	18.3
WS02	Female	4.8	31-Oct-13	11:42	14:03	2:21	15.5
WS03	Female	4.5	2-Nov-13	10:45	12:40	1:55	9.3
WS04a	Female	5.7	6-Nov-13	17:11	18:37	1:26	6.1
WS04b			7-Nov-13	12:45	15:12	2:27	15.5
WS04c			7-Nov-13	15:36	18:32	2:56	17.6
Total						13:37	82.3

Table II. Behavioral interactions recorded by the AUV during white shark tracks; Distance = straight-line distance from shore.

Track	Approach	Bump	Bite	Total	No.	AUV Depth (m)		Distance (km)
					Sharks	Mean (SD)	Max	Mean (SD)
WS01	6	2	5	13	4	52.8 (0.50)	55.3	0.54 (0.06)
WS02	3	0	0	3	1	90.0 (0.24)	91.3	5.35 (0.55)
WS03	5	0	2	7	2	89.6 (0.46)	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 (0.34)	91.4	0.89 (0.42)
Total	17	4	9	30	10	71.8 (25.5)		1.50 (2.20)

Figure Captions

Figure 1. Location of Guadalupe Island showing bathymetry (soundings in meters) and study area (box).

Figure 2. Autonomous Underwater Vehicle and transponder (inset) used to track white sharks 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.

Figure 3. Tracks of white sharks off the coast of Guadalupe Island as determined by an AUV: (a) WS01 (white) and WS02 (pink); (b) WS03 (white) and WS04a (pink); (c) WS04b (white) and WS04c (pink); and (d) locations of all interactions between white sharks and AUV. Circles represent start (green) and end (yellow); scale = 1 km except B = 0.3 km. Squares in each panel indicate locations of interactions between white sharks and AUV: approaches (green), bumps (yellow), and bites (red).

Figure 4. (a) Depth and water temperature of WS01, depth of AUV, and behavioral interactions between white sharks and AUV: approach (green box), bump (yellow box), and bite (red box). (b) Detail showing attitude and depth of the AUV before, during (red box), and after an interaction with a white shark during the track of WS01. Note disruption of pitch, roll, and heading rate during the attack (red box) as shark pushes the AUV upward 2.5 m.

Figure 5. (a) Depth and water temperature of WS02, depth of AUV, and behavioral interactions between white sharks and AUV: approach (green box), bump (yellow box), and bite (red box). (b-e) Images captured from AUV video cameras (b, d, e) and transponder camera (c) of WS02 approaching the AUV by ascending vertically in the water column (b, c), following AUV (d), and rapidly descending vertically (e); upper case letters refer to camera positions noted in Fig. 2.

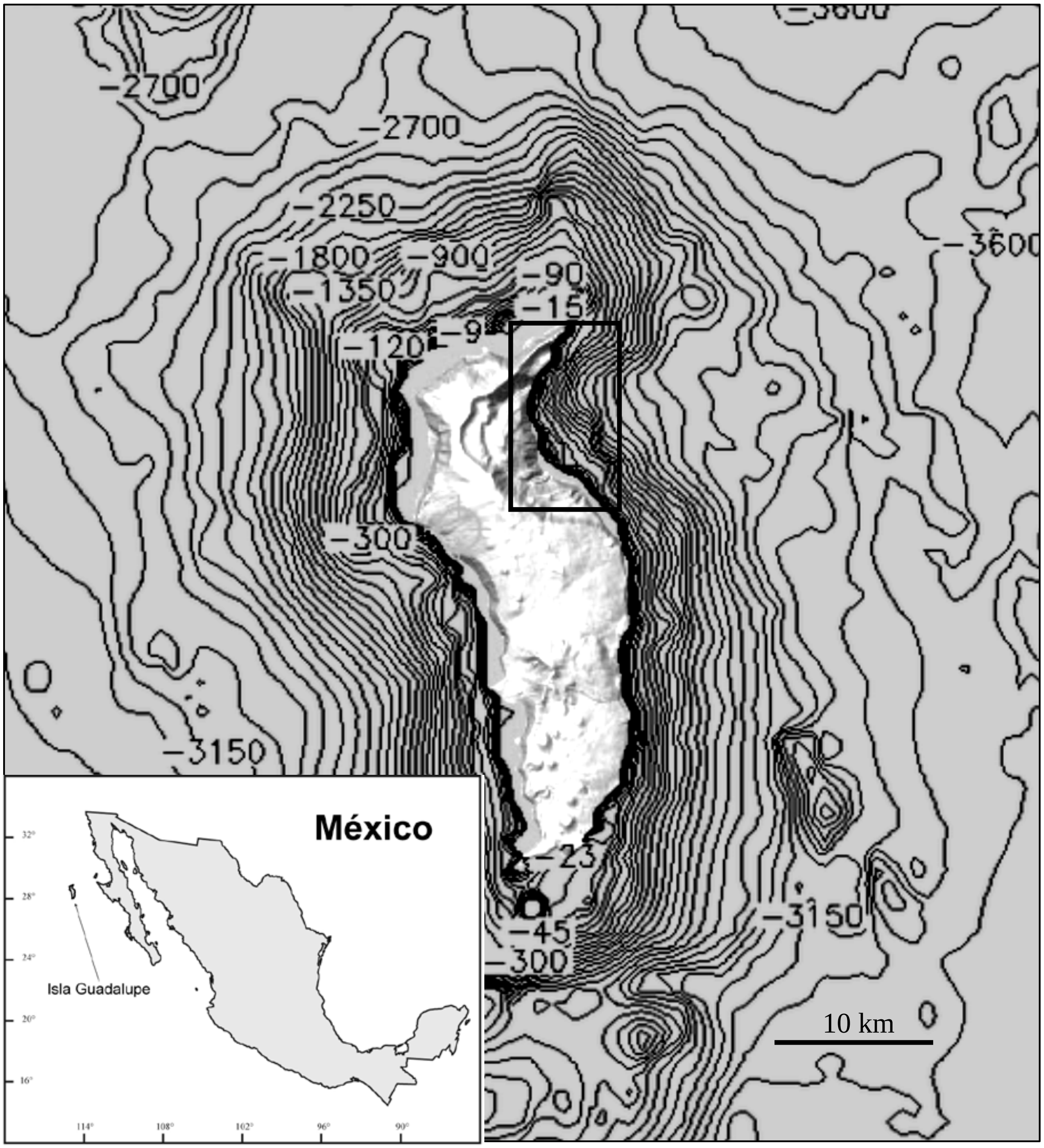
Figure 6. (a) Depth and water temperature of WS03, depth of AUV, and behavioral interactions between white sharks and AUV: approach (green box) and bite (red box). (b-d) Images captured from AUV video cameras of WS03 swimming along bottom (b), the AUV being bitten by different male (c) and female (d) sharks; note eye of shark rolling back during the bite (d). Upper case letters refer to camera positions noted in Fig. 2.

Figure 7. (a) Depth and water temperature of WS04a, depth of AUV, and behavioral interactions between white sharks and AUV: approach (green box) and bump (yellow box). (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 accompanied by a yellowtail amberjack (*Seriola lalandi*). Upper case letters refer to camera positions noted in Fig. 2.

Figure 8. (a) Depth and water temperature during the tracks of WS04b and WS04c, depth of AUV, and behavioral interactions between white sharks and AUV: approach (green box) and bite (red box). (b, c) Images showing white shark Lucy approaching from below

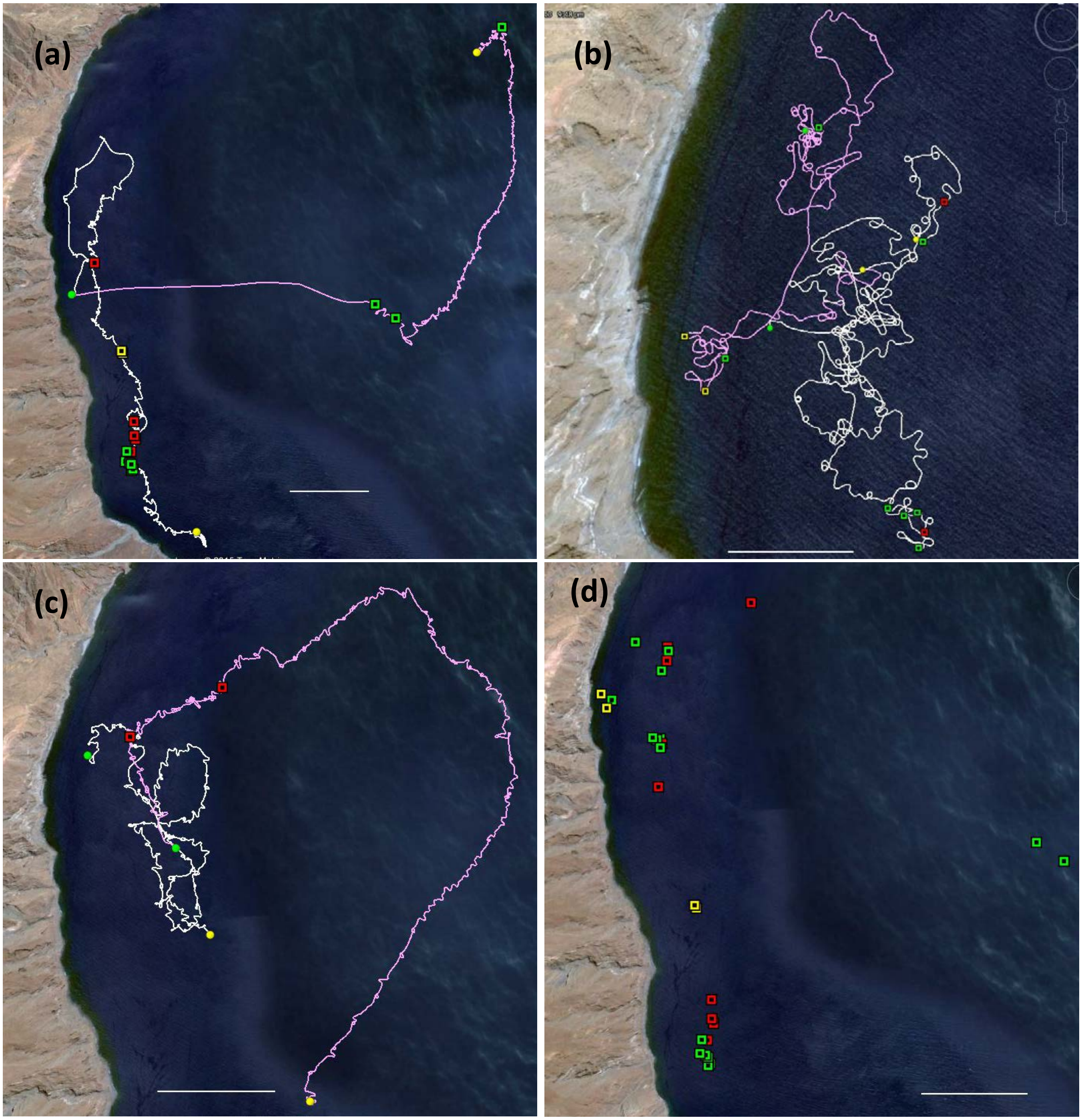
immediately prior to biting (b), biting (c), and bumping (d) the AUV; note deformed caudal fin used to later identify Lucy. Upper case letters refer to camera positions noted in Fig. 2.

Figure 9. AUV with tooth rakes resulting from nine bites from white sharks; note that all of the marks are located on the lower aft section of the vehicle.

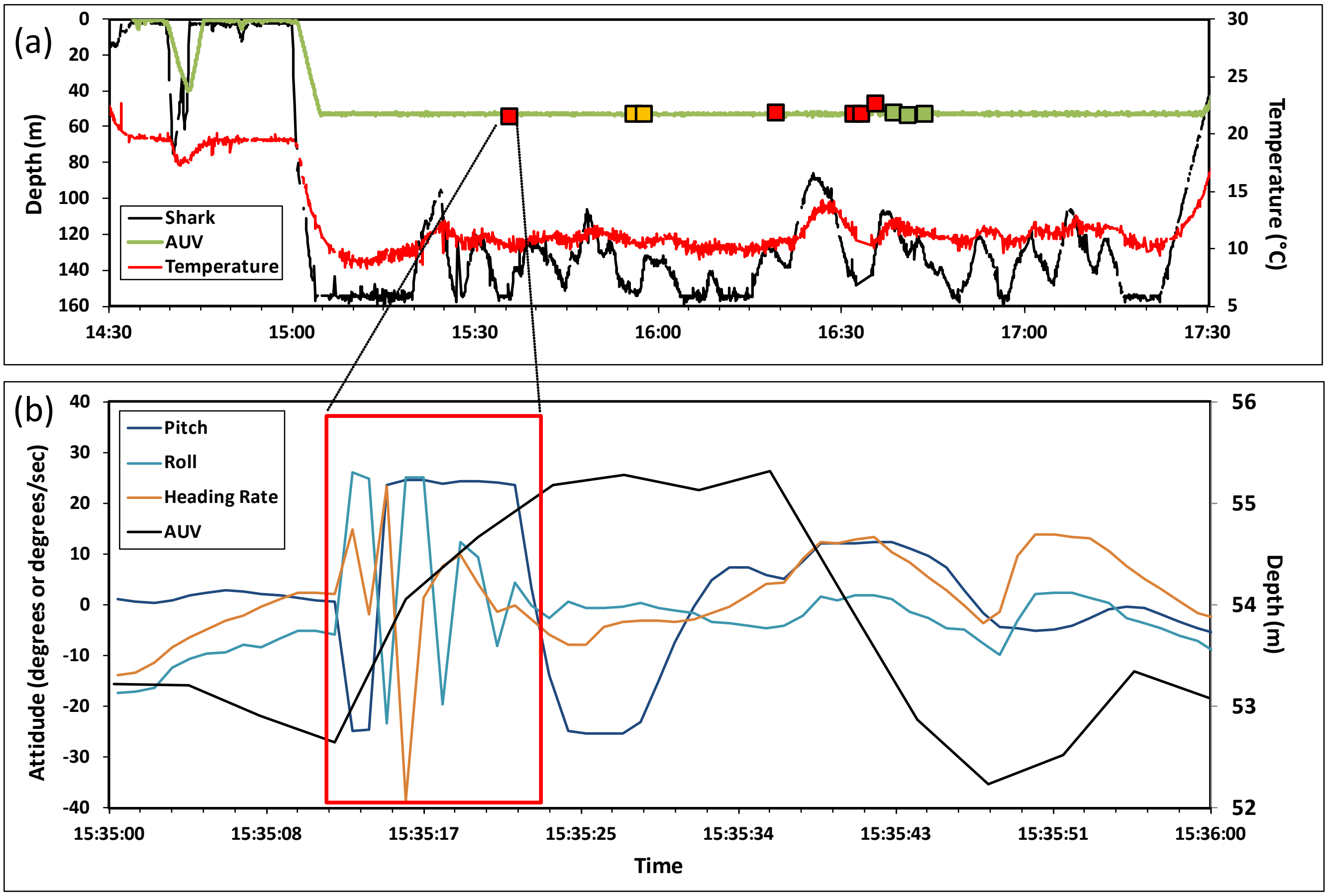


−2700
−2700
−3600
−2250
−1800
−900
−90
−3600
−1350
−15
−9
−120
−300
−3150
−23
−45
−3150
−300
10 km
México
Isla Guadalupe
32°
28°
24°
20°
16°
114°
108°
102°
96°
90°

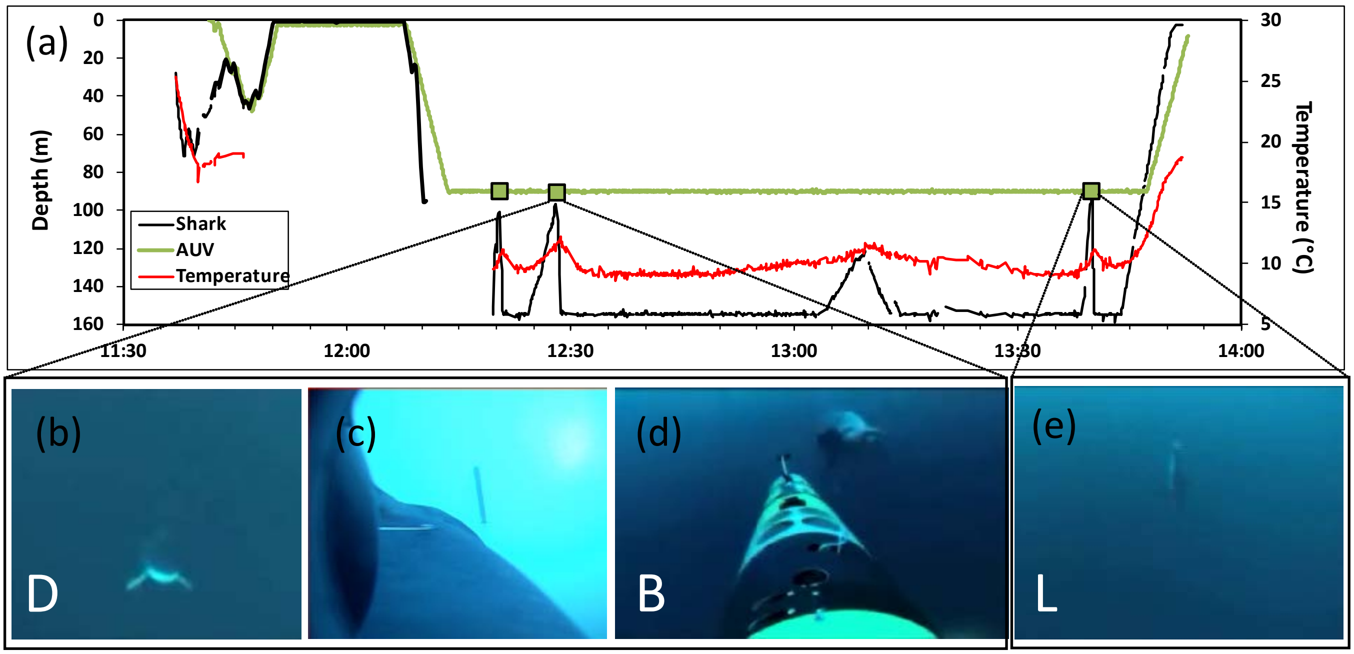

B
U
R
F
D
Discovery

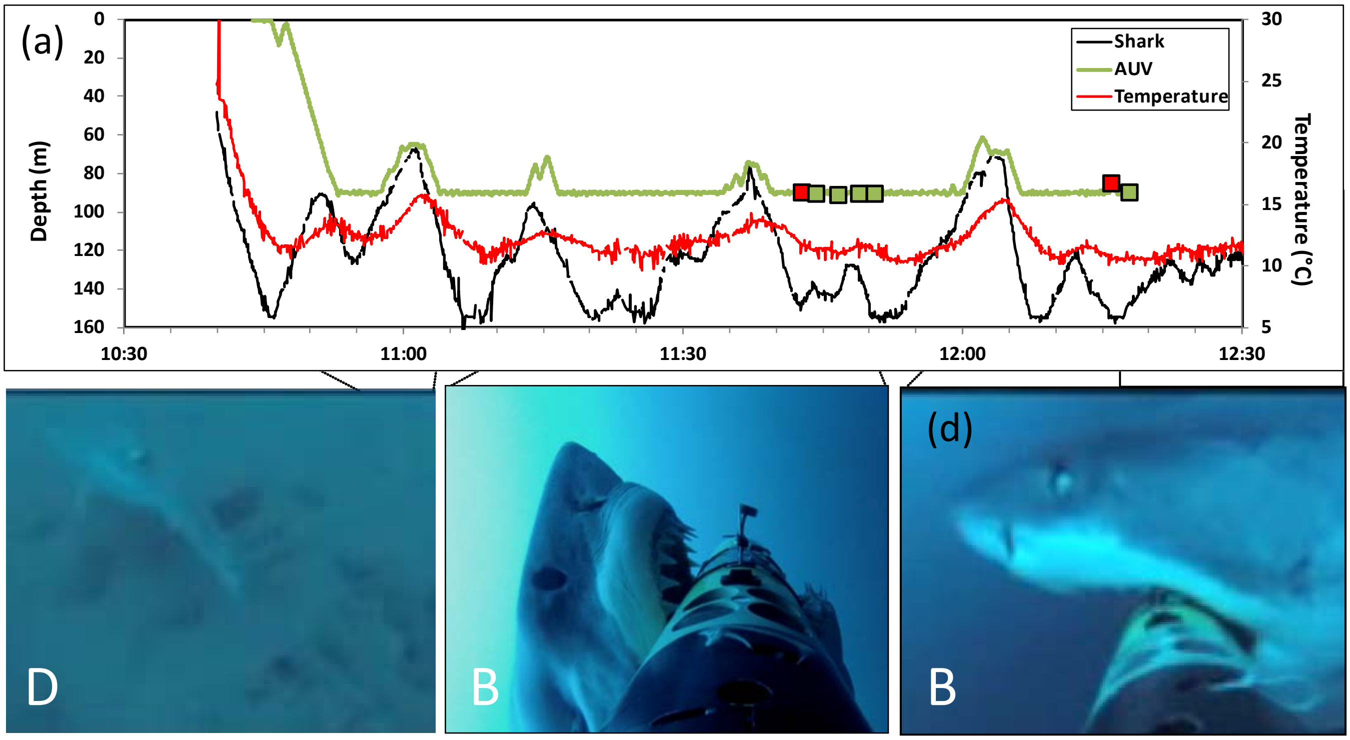

(a)
(b)
(c)
(d)

.

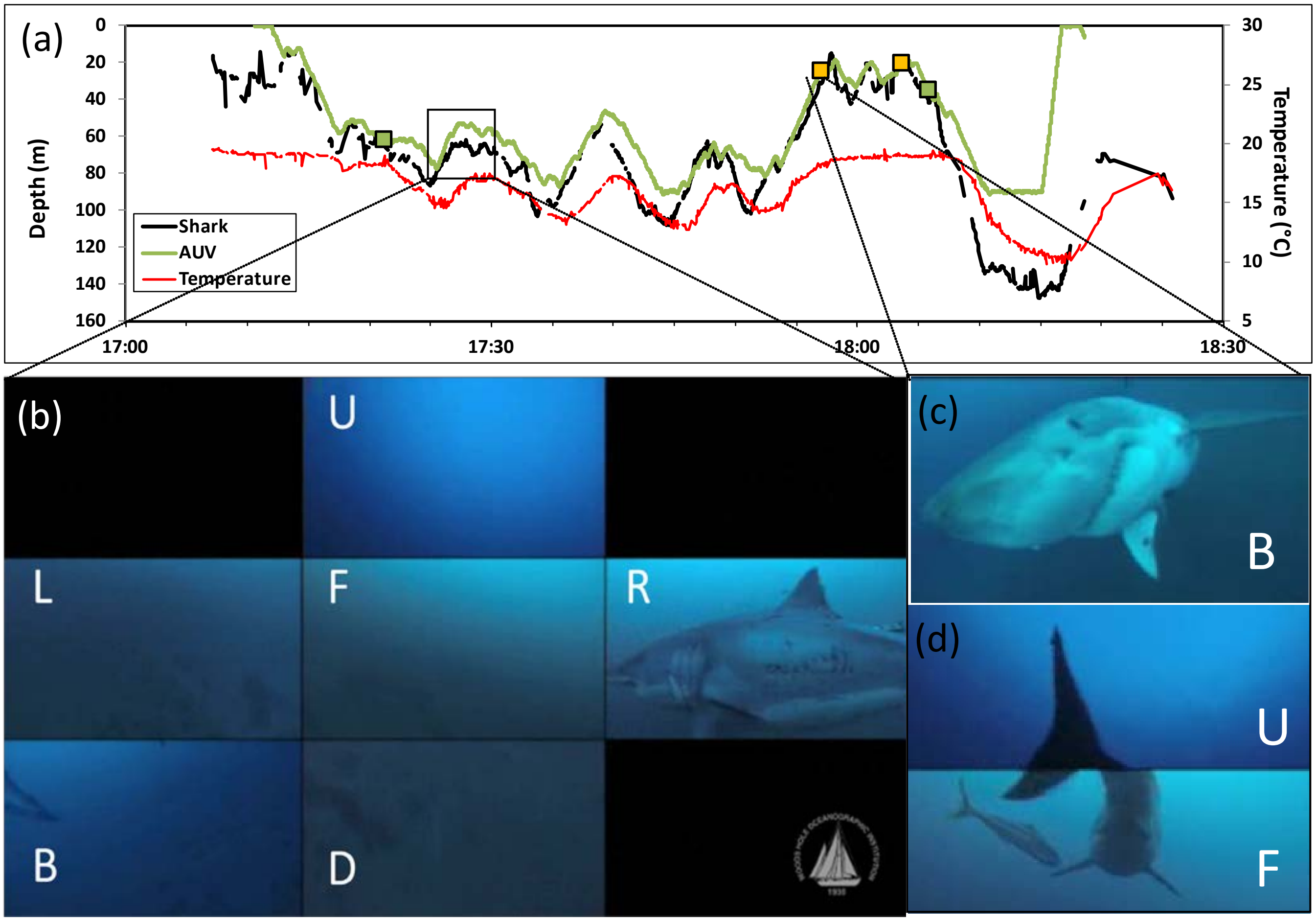


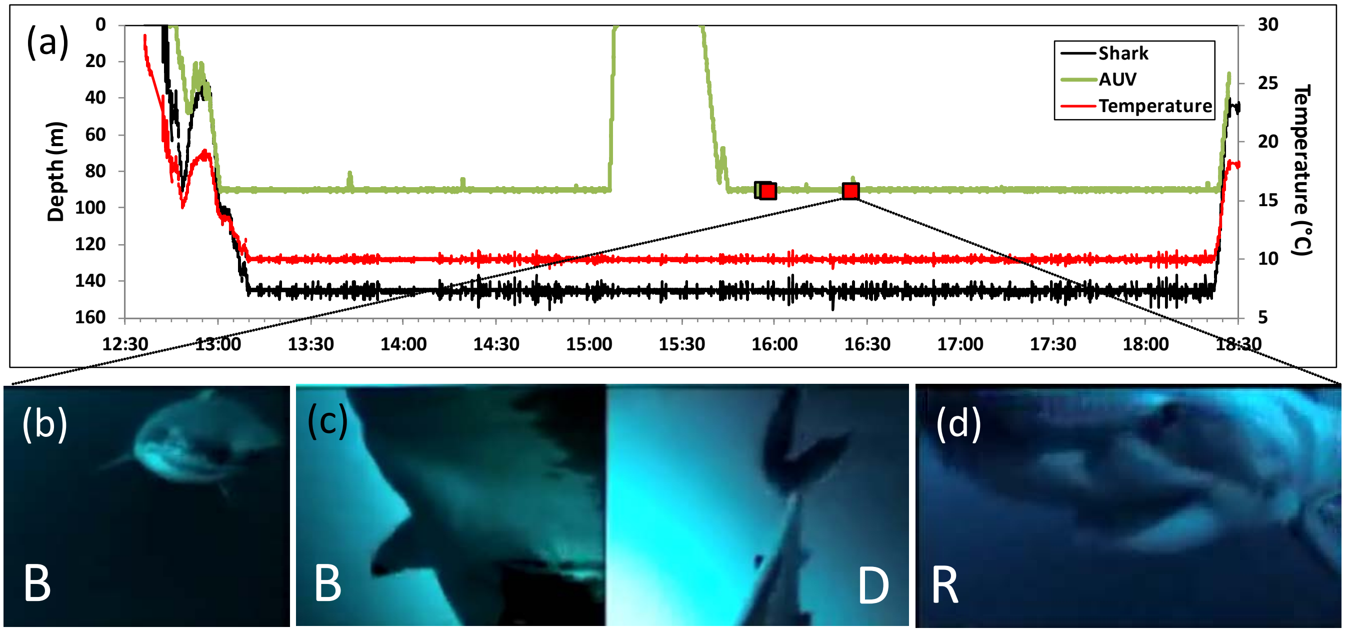
(a)
Depth (m)
Temperature (°C)
Shark
AUV
Temperature
14:30
15:00
15:30
16:00
16:30
17:00
17:30
(b)
Attidude (degrees or degrees/sec)
Depth (m)
Pitch
Roll
Heading Rate
AUV
15:35:00
15:35:08
15:35:17
15:35:25
15:35:34
15:35:43
15:35:51
15:36:00
Time


(a)
Depth (m)
Temperature (°C)
Shark
AUV
Temperature
0
20
40
60
80
100
120
140
160
30
25
20
15
10
5
11:30
12:00
12:30
13:00
13:30
14:00
(b)
D
(c)
(d)
B
(e)
L



(a)
Depth (m)
Temperature (°C)
Shark
AUV
Temperature
0
20
40
60
80
100
120
140
160
30
25
20
15
10
5
10:30
11:00
11:30
12:00
12:30
D
B
(d)
B


(a)
Depth (m)
Temperature (°C)
Shark
AUV
Temperature
0
20
40
60
80
100
120
140
160
30
25
20
15
10
5
17:00
17:30
18:00
18:30
(b)
U
L
F
R
B
D
(c)
B
(d)
U
F



(a)
Depth (m)
Temperature (°C)
Shark
AUV
Temperature
0
20
40
60
80
100
120
140
160
30
25
20
15
10
5
12:30
13:00
13:30
14:00
14:30
15:00
15:30
16:00
16:30
17:00
17:30
18:00
18:30
(b)
B
(c)
B
D
(d)
R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