Report to the Hawaii Department of Land and Natural Resources

SPATIAL DYNAMICS OF TIGER SHARKS (*GALEOCERDO CUVIER*) AROUND MAUI AND OAHU

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EXECUTIVE SUMMARY

Maui has experienced more shark bites than any other Hawaiian island. In an attempt to explain this phenomenon, we used a combination of acoustic and satellite tagging to quantify movements of tiger sharks captured near high-use ocean recreation sites around Maui and Oahu, and compared shark spatial behavior in Maui and Oahu waters with behavior observed elsewhere in Hawaii.

Between October 2013 and December 2014, we captured and electronically-tagged 26 tiger sharks at sites around Maui, and an additional 15 tiger sharks around Oahu. Individual sharks were tracked for periods of up to 613 days. We compared our results with previous data obtained from 55 tiger sharks captured between 2003 and 2013 at French Frigate Shoals atoll, Oahu and Hawaii Island, and tracked for periods of up to 6 years.

The movements of tiger sharks captured around Maui and Oahu during the current study were broadly similar to those documented by previous research conducted in Hawaii. Individual tiger sharks tended to utilize a particular ‘core’ island, but also swam between islands and sometimes ranged far offshore (up to 1,400 km – 840 miles). However, the current study also revealed new details of tiger shark habitat use, showing that tiger shark movements were primarily oriented to insular shelf habitat (0-200 m depth) in coastal waters, and that individual sharks utilized well-defined core areas within this habitat. The core areas of multiple individuals overlapped at locations such as Kihei, Maui, and Kahuku Point off Oahu. Overall, core use areas for large tiger sharks were closer to high-use ocean recreation sites around Maui than Oahu.

Generally, individual tiger sharks made infrequent (average of 1 visit every 13.3 days) and short (average of 11.8 minutes in duration) visits to shallow ocean recreation sites monitored around Oahu and Maui. However, overall frequency of tiger shark detections (proportion of monitored days on which any electronically-tagged tiger shark was detected) was higher at monitored ocean recreation sites around Maui (62-80%) than Oahu (<6%). This disparity held true even when accounting for the fact that in this study fewer sharks were tagged around Oahu (15) than Maui (26). Although routinely detected in shallow areas, our tracking data suggest tiger sharks primarily occupy deeper waters (50-100 m depth) when they are over the insular shelf. They are vertically dynamic and make “yo-yo” dives between the seabed and the surface.

We found evidence of seasonal migration to Maui by tiger sharks originally captured around Oahu, but no evidence of seasonal inter-island, or offshore, migrations by tiger sharks captured around Maui, most of which were highly site-attached to the Maui Nui insular shelf for the 21 month duration of monitoring. Overall, tiger sharks tagged around Maui typically exhibited greater residency and smaller home ranges than those tagged around other Hawaiian islands. The high residency shown by tiger sharks captured around Maui suggests they are able to obtain

all necessary resources (food, mates, pupping habitats) on the extensive Maui Nui insular shelf, which is larger in area than the equivalent shelf habitat of all other Main Hawaiian Islands combined. Seasonal influxes of tiger sharks to Maui waters suggest the extensive shelf habitat surrounding Maui Nui is also attractive to tiger sharks from elsewhere in Hawaii.

Overall, our results suggest the insular shelf surrounding Maui Nui is an important natural habitat for Hawaii tiger sharks, and consequently large tiger sharks are routinely and frequently present in the waters off ocean recreation sites around Maui. This may explain why Maui has had more shark bites than other Main Hawaiian Islands, although we cannot exclude differences in the numbers of ocean recreation activities between Maui and other islands as the primary cause of inter-island differences in shark bite rates. Despite the natural presence of large sharks in waters around Maui, the risk of shark bite remains relatively low and variable between years. Notably, 2015 saw only 1 unprovoked shark bite in Maui waters whereas there were 5-8 bites in 2013-2014. This variability exists even though our tracking data unequivocally show the same large, tagged tiger sharks were present in Maui waters, and visiting Maui ocean recreation sites, throughout the entire 2013-2015 period. Oahu-tagged sharks were also visiting these sites during that period. Thus, even though more unprovoked shark bites occurred around Maui in 2012, 2013 and 2014 than in any previous year since records began, the reasons for these “spikes” remain unclear.

Based on historical precedent in Hawaii, culling sharks neither eliminates nor demonstrably reduces shark bite incidents. Our current results further clarify why historical shark culling was ineffective. Tiger sharks found around Maui exhibit a broad spectrum of movement patterns ranging from resident to highly transient. This mixture ensures a constant turnover of sharks at coastal locations. Sharks removed by culling are soon replaced by new individuals from both local and distant sources.

The most pragmatic approach to mitigating shark bite risk is probably to pro-actively raise public awareness of tiger shark presence in Hawaii waters (equivalent to informing people of predator presence in terrestrial wilderness habitats such as North American forests), and explain what people can do to reduce bite risk. For example, making our tiger shark satellite tracks publicly-available on the Pacific Islands Ocean Observing System (PacIOOS) shark tracking website, showed people in 72 countries that large tiger sharks are routinely present in coastal waters of Maui and Oahu. Efforts are currently underway to inform and educate people about the risks of ocean-drownings in Hawaii, a natural hazard that is an order of magnitude more frequent than shark bites. These efforts could be expanded to include shark bite facts. A well-informed public can make their own fact-based decisions on ocean use.

INTRODUCTION

Over the past 20 years, Maui County has had more than twice the total number of unprovoked[1] shark bites, and a higher overall *per capita* shark bite rate, than any other Hawaii county (Figure 1), and Maui Island experienced more shark bites in 2012, 2013 and 2014 than in any previous year since records began (Figure 2). These statistics have driven speculation about changes in the abundance and behavior of large tiger sharks around Maui, and concern that Maui has an ongoing, elevated shark bite risk. However, we lack comprehensive data on the type and volume of in-water recreational activities occurring around each island that would allow us to evaluate the potential contribution of inter-island differences in ocean recreation practices to these patterns. We also lack baseline data quantifying shark behavior or abundance around Maui, so it is not currently possible to determine whether the number of tiger sharks around Maui has increased, or whether their behavior has altered in recent years. There is also no reliable way of measuring tiger shark abundance around Maui, because individuals move routinely (but unpredictably) between islands and far out into open ocean, which violates key assumptions (that immigration and emigration are known) underlying the 'mark-recapture' methods used by biologists to estimate wild animal population sizes.

Although it is not possible to accurately assess the number of sharks around Maui, nor determine whether they are becoming less wary of humans, electronic tagging techniques can be used to quantify their movements and determine whether tiger sharks around Maui are exhibiting patterns of spatial behavior substantively different to those observed around other Hawaiian islands where fewer shark bites have occurred. Specifically, electronic tagging can tell us whether large tiger sharks captured at sites of concern around Maui show any evidence of being more resident ("site-attached"), visiting coastal recreation sites more often, or spending more time in these areas, than tiger sharks captured around other Hawaiian islands. Electronic tagging can also determine how far tiger sharks captured around Maui range into surrounding waters, and can identify seasonal, or episodic, influxes of tiger sharks into Maui waters, by monitoring for immigration of previously-tagged tiger sharks captured around other Hawaiian Islands. Understanding tiger shark movement patterns around Maui can help managers to identify the most appropriate shark bite mitigation and response strategies.

Although tiger shark movements around Maui have not been previously well-studied, their movements have already been extensively studied around several other Hawaiian islands (e.g. Oahu, Hawaii Island, French Frigate Shoals; Holland et al. 1999, Meyer et al. 2009, 2010, Papastamatiou et al. 2013). These previous studies provide baseline behavior patterns for comparison with Maui sharks. Moreover, these studies have demonstrated that the simultaneous

[1] Unprovoked as defined by the International Shark Attack File: "Incidents where an attack on a live human by a shark occurs in its natural habitat without human provocation of the shark. Incidents involving shark-inflicted scavenge damage to already dead humans (most often drowning victims), attacks on boats, and provoked incidents occurring in or out of the water are not considered unprovoked attacks".

use of satellite and acoustic telemetry (i.e. equipping individual sharks with two different types of transmitter) provides the best overall insight into tiger shark movements, and collectively have revealed complex dispersal patterns potentially linked to both foraging and breeding. Individual tiger sharks tend to utilize a particular ‘core’ island, but also swim between islands and range far offshore (Holland et al. 1999, Meyer et al. 2009, 2010, Papastamatiou et al. 2013). State-space models predict that 25% of mature females swim from French Frigate Shoals atoll to the Main Hawaiian islands (MHI) during late summer/early fall, potentially to give birth (individual females give birth every third year; Whitney & Crow 2007). Females with core home ranges within the MHI remain within this region, where movements between islands are better explained by sea temperature and chlorophyll *a* concentration, suggesting they may be driven by foraging (Papastamatiou et al. 2013).

In this study, we used a combination of satellite and acoustic tagging to quantify movements of tiger sharks captured off high use ocean recreation sites around Maui and Oahu, and compared shark spatial behavior in Maui waters with behavior observed around Oahu, Hawaii Island and French Frigate Shoals to identify any major differences in site-attachment and habitat use between islands that might help to explain the higher number of shark bites occurring around Maui.

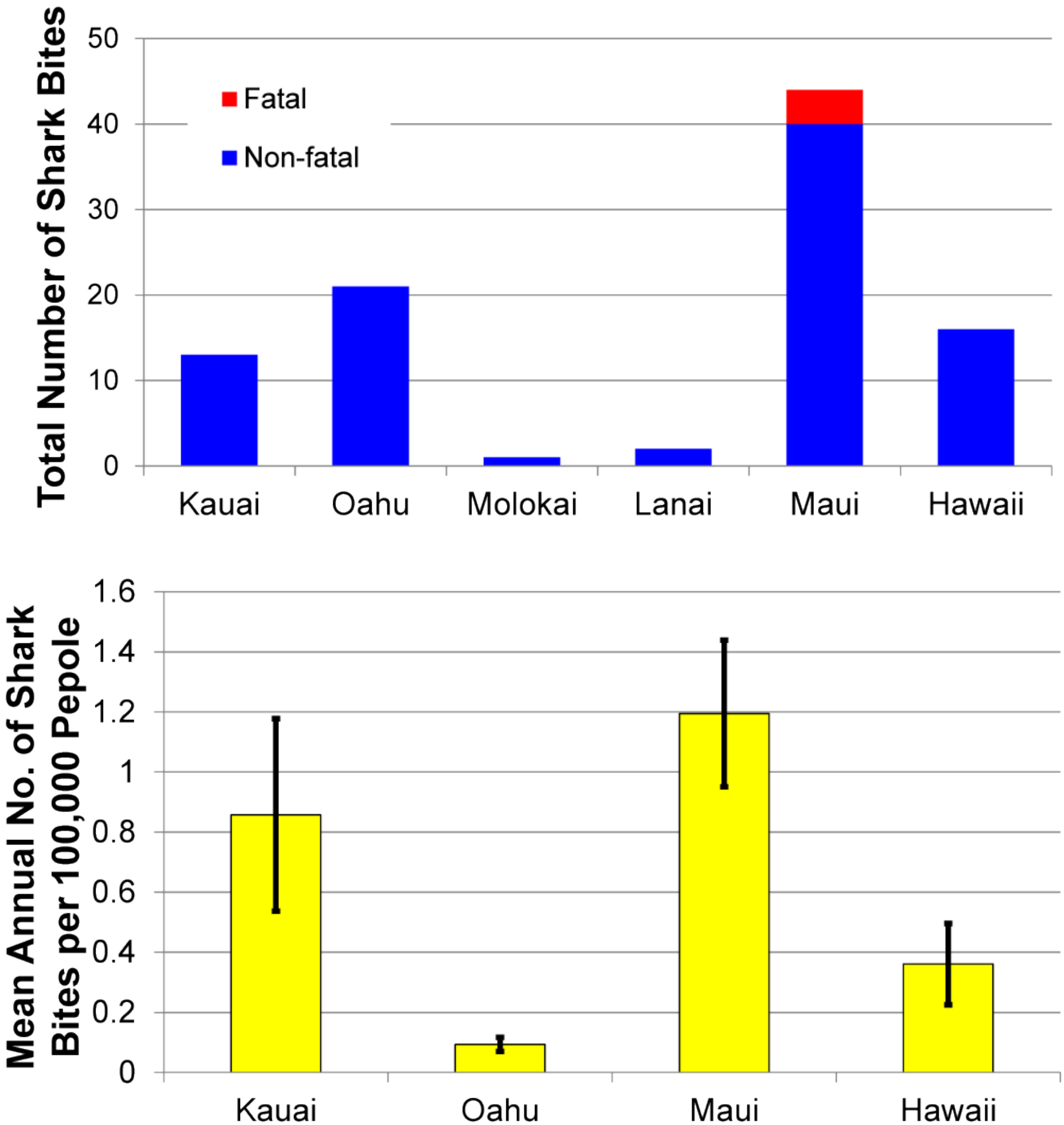


Figure 1. Top: Total numbers of unprovoked shark bites recorded on each Main Hawaiian Island 1995-2015. Bottom: Twenty year (1995-2014) average *per capita* shark bite rate (no. of unprovoked shark bites per 100,000 people) in Kauai, Honolulu, Maui and Hawaii counties. Error bars are Standard Error. Note: the *per capita* estimates are based on *de facto* population size estimates which combine Hawaii residents and visitors. Sources, DLNR-DAR and Hawaii Department of Business, Economic Development and Tourism (DBEDT).

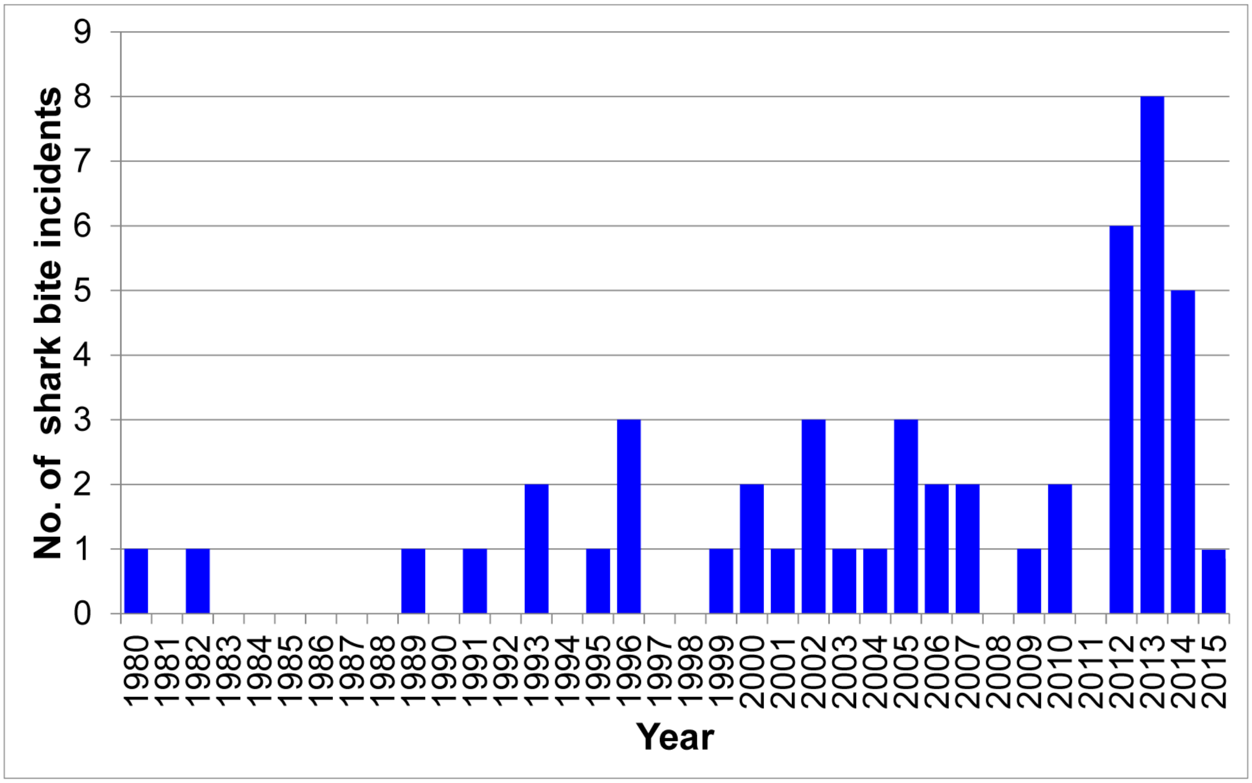


Figure 2. Annual numbers of shark bite incidents around Maui island, 1980-2015. Source Hawaii Department of Land and Natural Resources - Division of Aquatic Resources.

GOALS & OBJECTIVES

Our overarching goal was to obtain empirical shark movement data from around Maui to enable Hawaii's resource managers to identify the best strategies for managing shark incidents around that island. We subsequently increased the scope of the project to include contemporaneous tagging of tiger sharks around Oahu, with the aim of comparing shark behavior between these two populous islands during the same time frame. Specific objectives included:

(1) Capturing large tiger sharks at sites of concern (popular ocean recreation sites, including locations of previous shark bite incidents) and instrumenting them with both satellite and acoustic transmitters.

(2) Installing an array of underwater receivers at key sites around Maui, and maintaining an existing array around Oahu.

(3) Using both acoustic and satellite systems to determine how frequently large tiger sharks visit sites of concern, how much time they spend in these areas, and how extensively they range beyond these locations.

(4) Monitoring for immigration of electronically-tagged tiger sharks captured around other Hawaiian islands under the auspices of other projects.

(5) Comparing shark behavior around Maui with that observed simultaneously around Oahu, and previously observed around Hawaii Island and French Frigate Shoals atoll.

(6) Evaluating management implications of tiger shark movement and habitat use data.

METHODS

Study area

The Hawaiian archipelago stretches 2,580 km along a SE-NW axis in the central north Pacific (Figure 3). The upper (NW) 1,955 km of the chain is a series of uninhabited atolls, submerged banks and seamounts, with extensive areas of photic and mesophotic (0-100 m) reef habitats. We have previously quantified tiger shark movements at these remote, uninhabited locations, and unpublished acoustic monitoring data from French Frigate Shoals atoll are included for comparative purposes in the current analyses. French Frigate Shoals (N23^{o} 45' W166^{o} 10') is located in the middle of the Hawaiian archipelago (Figure 3). The atoll consists of a 34 km long oval platform bounded on the east side by a 50 km long crescent-shaped barrier reef (Figure 4). Habitat outside the barrier reef consists of classical spur and groove formations running from the reef crest down to depths of 20-30 m. The western half of the atoll is open to the ocean and shelves gradually from depths of 20 to 100 m over a distance of 18 km, before descending more steeply to >1000 m depth. The eastern half of the atoll consists of a shallow (<1 to 10 m deep) lagoon enclosed between the outer barrier and an inner crescent shaped reef, and is 12 km wide at its midpoint. Lagoonal habitats include reticulate and patch reefs, submerged sand and coral rubble, and small sandy islets. Total coral reef area of the shoals is >940 km^2 and total land area of the sandy islets is 0.25 km^2.

The lower (SE) 625 km of the Hawaiian archipelago consists of a series of 8 oceanic, high islands (Main Hawaiian Islands, MHI), of which Oahu and Maui were the focus of shark capture and tagging during this study (Figures 3 & 4). Both Oahu and Hawaii Island have been sites of previous tiger shark research (Holland et al. 1999, Meyer et al. 2009, Papastamatiou et al. 2010) and acoustic monitoring data from these previous research efforts are incorporated in the current analyses. The MHI are surrounded by insular shelf sloping gradually from the shore out to a shelf break beginning at depths of between 100 and 200 m. The width of insular shelf varies among islands, with the Maui Nui complex (the islands of Maui, Kahoolawe, Lanai and Molokai) having a more extensive insular shelf than the islands of Niihau, Kauai, Oahu and Hawaii (Figure 4, Table 1). The insular shelf contains a variety of photic and mesophotic coral reef and sandy habitats.

Maui County (the islands of Maui, Lanai, Molokai and Kahoolawe) is the second most populous in the State of Hawaii, with a similar population to Hawaii County, and double the population of Kauai County (Table 1). All of the major MHI have well-developed public beach park infrastructure and public shoreline access, allowing easy access to the ocean for recreational activities including swimming, snorkeling, spearfishing, surfing, paddleboarding and kite surfing. These activities occur year-round and are participated in by both residents and visitors. The coastlines of each MHI include both highly-developed, heavily-used areas, and rugged, inaccessible areas where ocean recreation is much less common. The gross spatial distribution of shark bites around each island largely reflects overall spatial patterns of human recreational ocean activities (i.e. most shark bites occur at locations frequently used for ocean recreation). For example, the eastern coastline of Maui is remote, rugged and wind-exposed. Few ocean recreation activities occur along this stretch of coastline, and consequently shark bite incidents are extremely rare in this area (see Figure 5). Similarly the north-eastern coast of Oahu has relatively-low recreational ocean use and a low number of shark bite incidents (Figure 6). However, some of the most heavily-used beaches (e.g. Waikiki, Oahu) also have a low rate of shark bite incidents suggesting the number of people present in the water is not the only determinant of where shark bites occur.

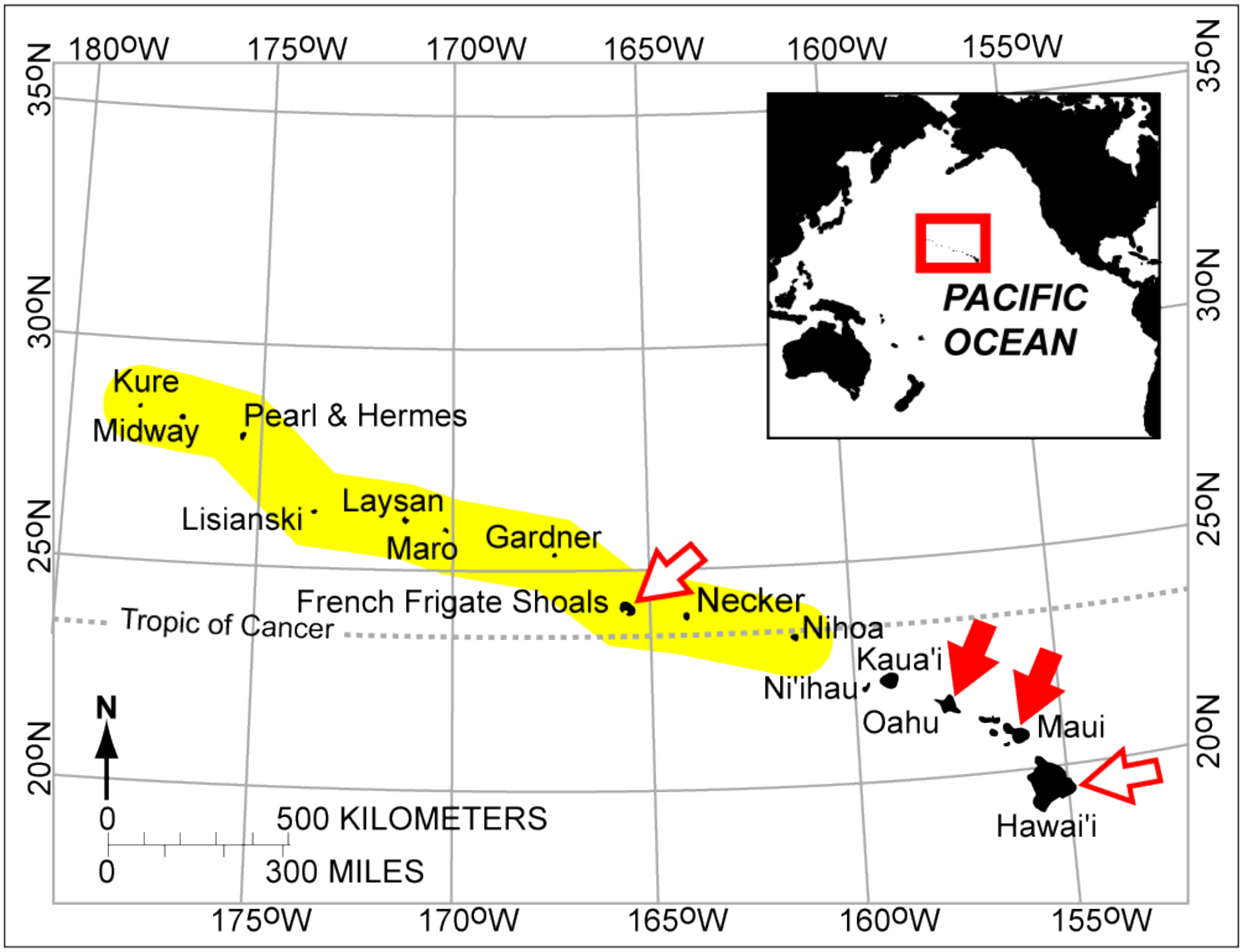


Figure 3. Hawaiian Archipelago showing locations of islands around which tiger shark tracking was conducted during the current (closed arrows) and previous (open arrows) studies. Yellow shaded area indicates the Papahānaumokuākea Marine National Monument. Inset: Location of the Hawaiian Archipelago (red box) in the north Pacific.

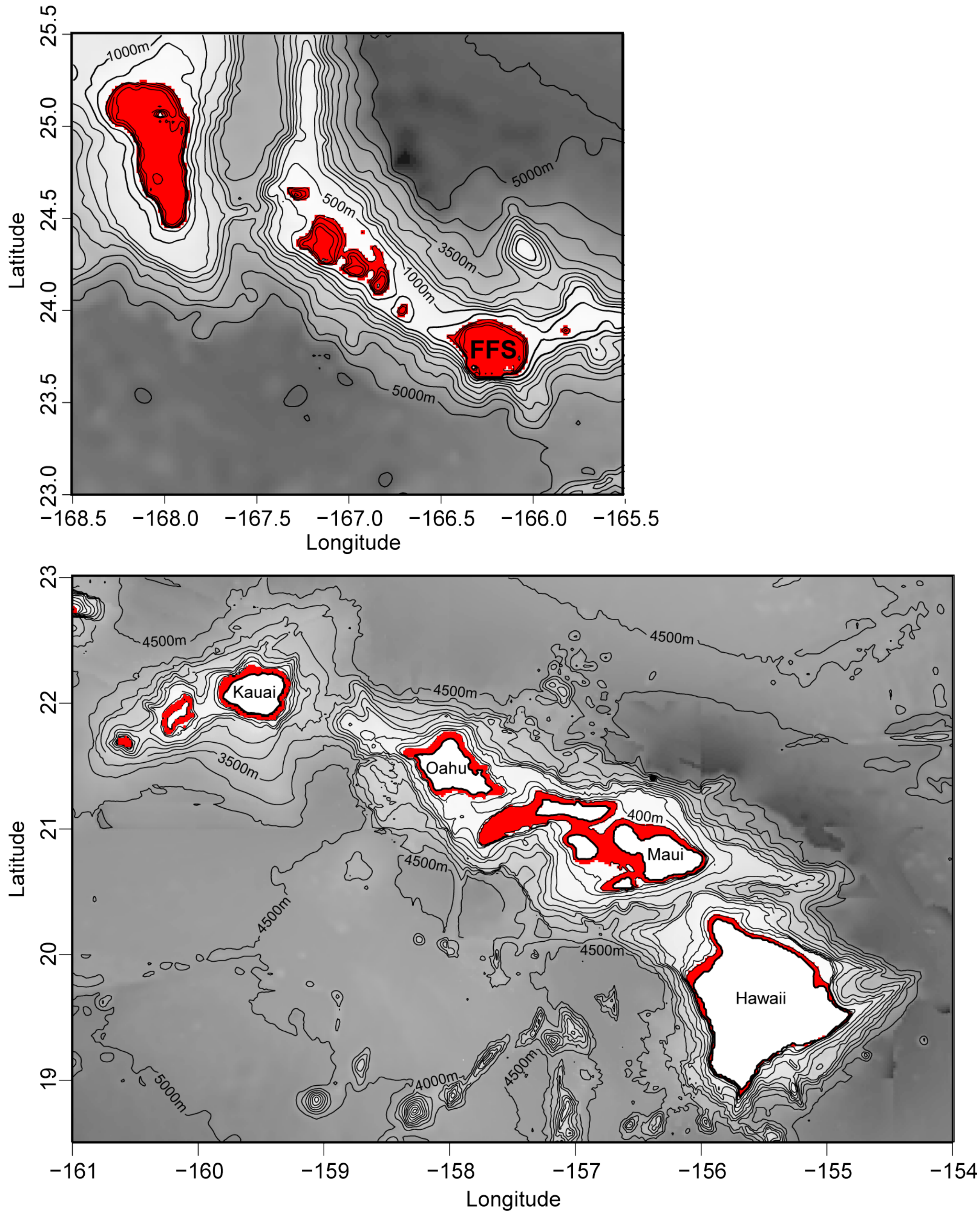


Figure 4. Bathymetry of French Frigate Shoals and adjacent submerged banks (top), and (bottom) the Main Hawaiian Islands highlighting the insular shelf between depths of zero and 200 m (red shaded area).

Table 1. Human population sizes, shark bite numbers and area of insular shelf within the 200m isobath for each county within the State of Hawaii. Honolulu County encompasses the island of Oahu. Maui County includes the populated islands of Maui, Lanai and Molokai.

County	2014 human population*	Total shark bites (1995-2015)[+]	Grand mean annual (1995-2015) shark bites per 100,000 people	Insular shelf area (km^2)
Kauai	88,186	13	0.86	923
Honolulu	937,026	21	0.10	927
Maui	169,573	47	1.63	3,641
Hawaii	164,942	16	0.50	1,056

*Source: Hawaii Department of Business, Economic Development & Tourism (DEBDT).

[+]Source: Hawaii Department of Land and Natural Resources-Division of Aquatic Resources.

Shark capture and tagging

At all four islands (Hawaii, Maui, Oahu and French Frigate Shoals), we used bottom-set lines equipped with 10-15 large (20-0 gauge) circle hooks to capture tiger sharks. Hooks were baited with large tuna heads and other large fish scraps, and typically set around dawn at depths of 30-100 m and soaked for 3-5 hours before hauling from a 6-8 m skiff. Overnight sets were used for tiger shark research work off west Hawaii Island (see Meyer et al. 2009). Captured tiger sharks were brought alongside the skiff and a soft rope noose was placed around the caudal peduncle, allowing the sharks to be secured at both head (via the leader) and tail, before being inverted to induce tonic immobility. While inverted, sharks were measured (Precaudal Length, Fork Length and Total Length, and inner and outer clasper lengths for males) to the nearest centimeter, and an acoustic transmitter (V16-6H, Vemco, Bedford, Nova Scotia, Canada) was implanted into the peritoneal cavity through a small incision in the abdomen. The incision was closed using interrupted sutures.

Following acoustic transmitter implantation, sharks were rolled upright to allow for attachment of dorsal fin-mounted satellite transmitters. We used a drilling template to align four small (3 mm diameter) holes through the dorsal fin (close to the thick leading edge), pushed short, stainless steel bolts extending from the transmitter through these holes, and then secured the device on the opposite side of the fin with washers and lock nuts.

To provide a 'sharks-eye' view of habitat use, two individuals were also equipped with a small video camera package attached to the left pectoral fin. The camera (DVL400L, Motion JPEG, VGA [640 x 480, max. 30 fps], Little Leonardo Inc., Tokyo, Japan), embedded within a small syntactic foam float, was held in place via a fusible steel band, passed around the package and through two small holes drilled through the pectoral fin. The entire package had a forward view when deployed on the shark, and was released after 72h by an electronic timer. The camera was programmed to begin filming around sunrise on day 3 of the deployment, and continue to film all day before detaching from the shark. Once at the surface, the camera package was located and recovered using satellite and VHF transmitters attached to the float.

Finally, sharks were fitted with ID tags (wire-through Hallprint™ shark tags, unique identification number printed at head and tail of tag, reward message and phone number printed on the tag shaft) using titanium-steel darts inserted through the shark's skin at the base of the dorsal fin and locked in place through the dorsal ceratotrichia. Tagged sharks were released by removing the hook and tail rope.

The entire handling process took between 30 and 45 minutes. Shark handling and tagging activities were carried out in accordance with the animal use protocols of the University of Hawaii (protocol #05-053).

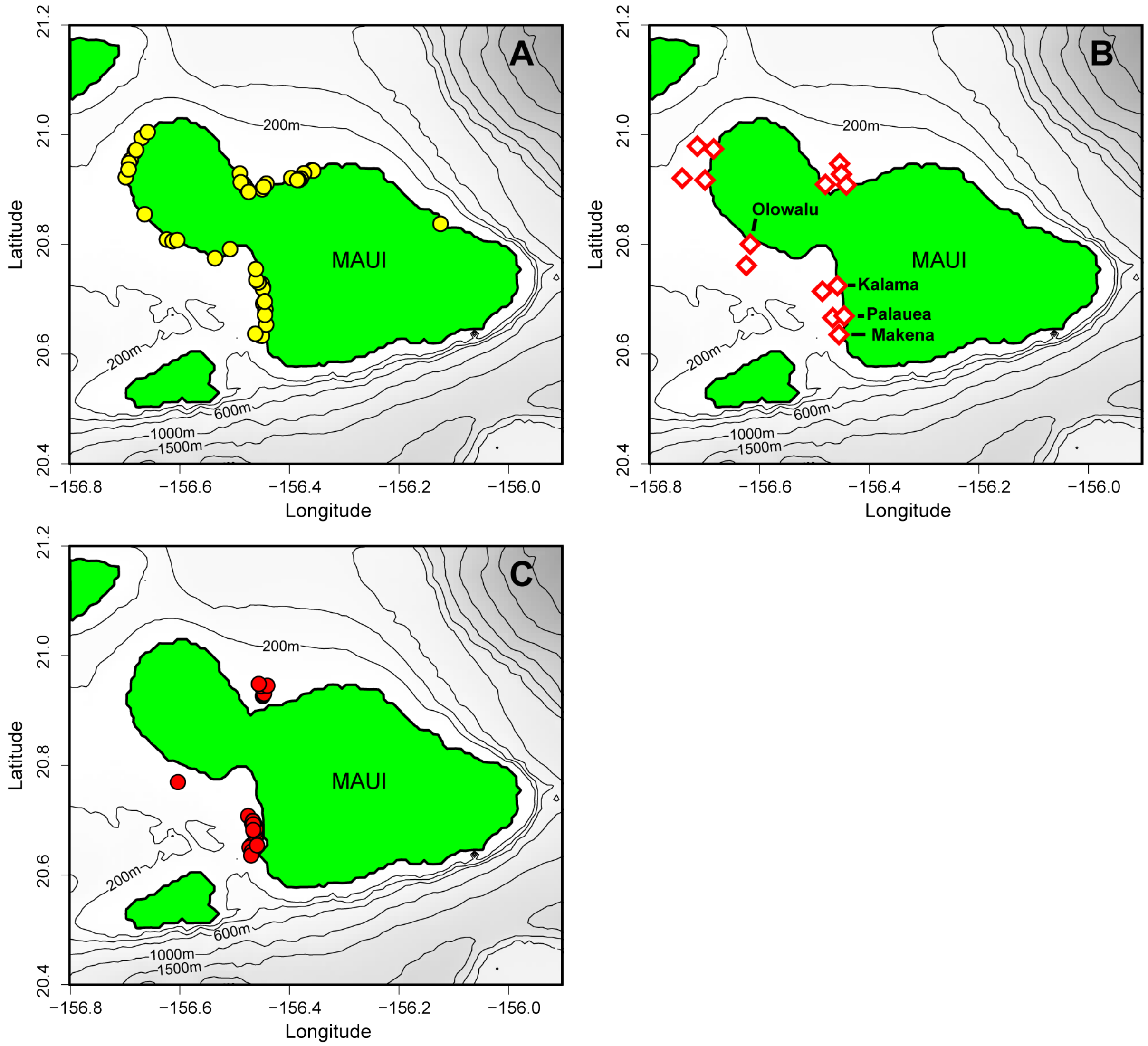


Figure 5. Maui island showing locations of (A) shark bite incidents from 1980 to 2015, (B) acoustic receiver monitoring locations, and (C) tiger shark tagging locations in 2013 and 2014.

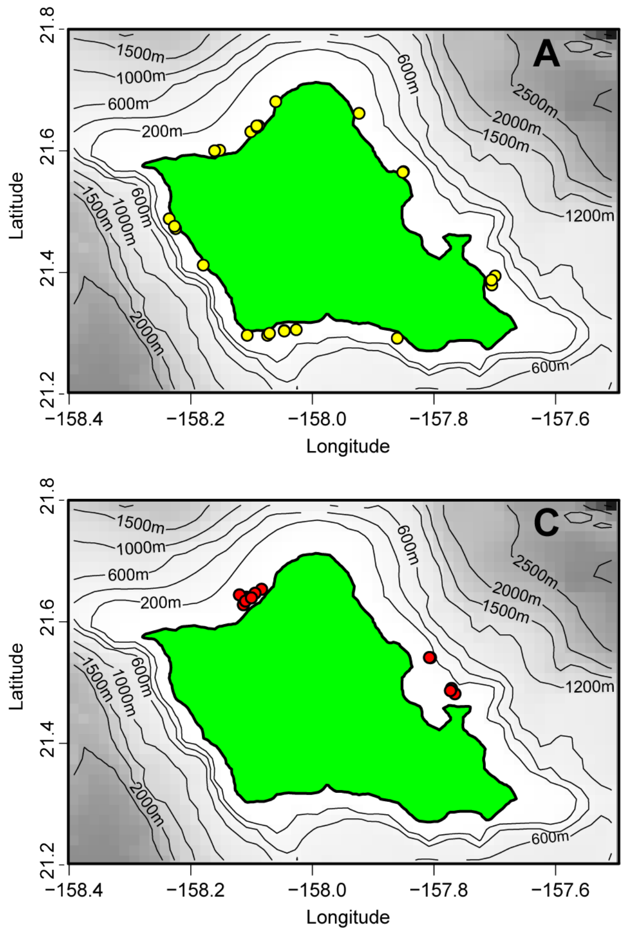


Figure 6. Oahu island showing (A) locations of shark bite incidents from 1980 to 2015, (B) acoustic receiver monitoring locations, and (C) tiger shark tagging locations in 2013 and 2014.

Electronic tags overview

We used two types of electronic telemetry tag to quantify different aspects of tiger shark spatial dynamics; (1) Dorsal fin-mounted satellite transmitters to provide a broad overview of shark horizontal movements and habitat use patterns, and (2) Surgically-implanted, coded acoustic transmitters to provide long-term presence-absence data at specific locations monitored by underwater acoustic receivers. Some of the satellite transmitters were equipped with depth and/or temperature sensors to provide additional insight into shark vertical behavior and thermal environment.

Dorsal fin-mounted Satellite Transmitters

Three different types of dorsal-fin mounted satellite transmitters were used to quantify tiger shark horizontal and vertical movements; (1) SPOT tags (SPOT-258A, 106 mm x 45 mm x 19 mm, 53 g, Wildlife Computers, Redmond, WA, USA), which only yield Argos quality location estimates for tagged sharks, (2) SPLASH tags (SPLASH10-312A, 133 mm x 44 mm x 19 mm, 85 g, Wildlife Computers, Redmond, WA, USA) which provide an Argos-quality location together with a packet of sensor data from onboard depth, temperature and other sensors, and (3) Fastloc-GPS tags (SPOT-F-338A, 109 mm x 53 mm x 21mm, 81g) which capture Global Positioning System (GPS) quality positions that are then transmitted to the Argos satellite array. Fin-mounted tags transmit a signal to the Argos satellite array whenever the dorsal fin breaks the surface of the water. These transmissions yield geolocation estimates with location accuracy classes ranging from 3 to 1 (best to worst). The following root mean squares errors are provided by the Argos tracking and environmental monitoring system (www.argos-system.org), Class 3 < = 150 m, Class 2 = 150-300 m, and Class 1 = 350-1000 m. Location qualities of 0, A, B, and Z (in order of decreasing quality) are also obtained, but no estimates of error size are given for these classes. However, accurate fixes are possible with all location qualities except Z, and previous studies have shown that, with appropriate filtering, Argos location classes (LC) 0, A and B can provide useful information for tracking marine mammals (Vincent et al. 2002). Fastloc-GPS tags provide both Argos quality and GPS quality (<4 m) positions.

Argos satellite coverage averages only 6-12 minutes per hour in Hawaii, with only a subset of this coverage composed of high-quality satellite passes. To increase data recovery from SPLASH and Fastloc-GPS tags, two prototype land-based satellite receivers (Mote-system™, Wildlife Computers, Redmond, WA, USA) were deployed at high elevations on Maui. These land-based receivers increased data recovery from individual satellite tags by up to 700%.

Prior to deployment, satellite tags were coated with two types of antifouling compound to prolong their functional lives. Non-conducting surfaces were coated with Propspeed™ (Oceanmax Manufacturing Ltd., Auckland, New Zealand), and the wet-dry electrodes were coated with electrically conductive C-Spray antifouling compound (YSI Inc., Yellow Springs, OH, USA).

Analysis of satellite tag data

Satellite data reduction and filtering

Argos locations from satellite tag-equipped sharks were filtered prior to analysis. We first manually removed obviously spurious distant locations, and then used a land-avoiding swim-speed filter to eliminate remaining low-probability class A, B and 0 locations. Our chosen swim speed threshold (4.2 km/h) was based on empirical tiger shark swimming speed data derived from previous active tracking (Holland et al. 1999) and shark-mounted accelerometers containing speed sensors (Nakamura et al. 2011), together with GPS quality locations and multi-day, highly-directional swimming events from the present study. Higher-quality locations (i.e. LC 1, 2 and 3) were used to anchor the swim speed filter. Thus LC A, B and 0 locations that lay within a 4.2 km/h buffer of a previous higher-quality location were retained, whereas those beyond the buffer were eliminated from the data set.

Coastal Home Range Analyses of Satellite Tracking Data

We used the T-LoCoH (Time Local Convex Hull) package (Lyons et al. 2013) in R (R Core Team 2014) to construct home range utilization distributions from tiger shark Argos and GPS locations. To avoid oversampling bias, speed-filtered data were first inspected for detection bursts, and then transformed from Latitude-Longitude to Universal Transverse Mercator (UTM Zone 4) coordinates.

We then evaluated 3 alternative methods (k-based, r-based and adaptive) for creating hulls and density isopleths (i.e., utilization distributions). The k-based method constructs kernels from k-1 nearest neighbors of root points, the r-based method constructs kernels from all points within a fixed radius ‘r’ of each reference point, and the adaptive method constructs kernels from all points within a radius ‘a’ such that the distances of all points within the radius to the reference point sum to a value less than or equal to ‘a’.

We found that the k-based method was prone to Type I errors (including unused area outside the home range) and the r-based method prone to Type II errors (omitting area the animal used). The adaptive method provided the most robust estimates of home range utilization distribution (see also Lyons et al. 2013), and we selected this method for constructing tiger shark home range utilization distributions. We removed offshore migrations (i.e. those points forming obvious offshore loops extending beyond the 4000 meter coastal isobath) from the analyses of coastal habitat use, as including these resulted in extensive Type I errors within coastal areas. All other locations were included in the analyses, with no time-based weighting (i.e. S=0). The location and size of core (25%) isopleths for each shark were stable across a wide range of ‘a’ values, whereas the outer (95%) isopleths expanded with increasing ‘a’ values until they overlapped terrestrial habitat. We selected ‘a’ values that eliminated gaps within the 95% isopleth surfaces while avoiding overlap with terrestrial habitat.

Bathymetry profiles from ARGOS locations

We used the Marmap package (Pante & Simon-Bouhet 2013) in R to extract underlying bathymetry values for each of the speed-filtered Argos locations. These values do not reflect swimming depth (sharks must be at the surface for Argos detections to occur), but rather indicate the depth of the ocean floor over which the shark was detected. Habitat depth estimates were obtained from a 3 arc-second (approx. 93 m) resolution bathymetry matrix around the MHI and a 30 arc-second (approx. 926 m) resolution matrix for offshore locations.

Swimming depth data from SPLASH tags

To obtain insights into tiger shark vertical movements, we equipped several individuals with dorsal-fin mounted SPLASH tags that collect information on swimming depth and ambient temperature at 10 second intervals. These data are summarized (75 s and 10 min intervals) onboard the tag, and transmitted in a sequence of data packets when the dorsal fin emerges above the surface. Transmitted data were recovered via both the ARGOS satellite array and land-based Mote system of receivers. SPLASH tags also yield ARGOS locations and we used harvested bathymetry profiles (see section above) to provide a bottom depth reference for tiger shark vertical movements.

Acoustic monitoring system

We used the Vemco VR2W acoustic monitoring system to quantify tiger shark presence at specific locations around the coastlines of Maui and Oahu. This system consists of small (340 mm long x 60 mm diameter, weight in water 300 g), self-contained, single channel (69 kHz) underwater receivers which listen continually for the presence of coded-pulse acoustic transmitters. Sharks captured around Maui and Oahu between October 2013 and February 2015 were equipped with Vemco V16-6H transmitters (16 x 94 mm, weight in water 14 g) which periodically emit a 'pulse train' of closely spaced 69 kHz 'pings', uniquely identifying each shark. These pulse trains average 3 to 5 s in duration, and transmitters were silent for a randomized period of 20 to 230 s between each pulse train (Table 2). Each successfully decoded pulse train is recorded as a single detection by a VR2W receiver, and is stored in the receiver memory as the unique transmitter number, date and time of detection.

The nominal transmitter battery lives ranged from 2 to 10 years, depending on transmission duty cycle (i.e. how often the identification code is sent). Most transmitters deployed in tiger sharks captured around Maui during the present study had 10-year nominal battery lives, and are expected to continue to transmit until 2023 and 2024 (Table 2). Transmitters deployed in tiger sharks captured around Oahu during the Maui study, had nominal battery lives ranging from 2-10 years, with all expected to continue transmitting beyond the 2-year time frame of the Maui study (Table 2).

Table 2. Summary detection data for tiger sharks captured around Maui (N=26) and Oahu (N=15) between October 2013 and February 2015. Underlined Total Length (TL) indicates sharks above the size of sexual maturity based on reproductive data from Whitney and Crow (2007).

Tagging Island	Sex	Total Length (cm)	Date Tagged	Acoustic Xmitter #	Acoustic Detection Span (Days)	Total Acoustic Detection Days	Total Acoustic Detections	Satellite Xmitter #	Satellite Detection Span (Days)	Total Satellite Detections
Maui	M	408	1/16/14	26895[2]	449	32	102	81182	484	512
Maui	F	448	7/25/14	26903[2]	334	125	877	122984	196	817
Maui	F	377	7/26/14	26891[2]	306	69	308	132062	64	5602
Maui	M	283	10/19/13	26878[2]	604	358	1695	133361	418	298
Maui	F	413	10/20/13	13411[1]	600	185	712	133362	97	177
Maui	F	381	1/13/14	26888[2]	517	264	1628	133363	82	80
Maui	F	388	1/13/14	26897[2]	516	167	666	133364	-	-
Maui	M	323	1/13/14	26887[2]	427	39	124	133365	431	1055
Maui	F	332	1/13/14	26892[2]	-	-	-	133366	443	662
Maui	F	388	1/13/14	26896[2]	503	182	767	133367	7	14
Maui	F	409	10/18/13	26876[2]	609	272	1223	133368	79	17
Maui	F	375	10/17/13	26875[2]	605	301	1631	133369	293	1537
Maui	F	432	10/18/13	26885[2]	-	-	-	133370	55	48
Maui	F	373	10/18/13	26882[2]	565	245	1097	133371	430	405
Maui	F	375	10/19/13	26879[2]	-	-	-	133372	161	528
Maui	F	392	10/20/13	13407[1]	613	347	1986	133373	595	485
Maui	F	310	10/19/13	13405[1]	582	301	1244	144554	162	518
Maui	F	273	10/17/13	26884[2]	610	294	1238	144555	93	277
Maui	F	401	12/9/14	30092[3]	193	90	1821	145988	163	93

Table 2 ctd.

Tagging Island	Sex	Total Length (cm)	Date Tagged	Acoustic Xmitter #	Acoustic Detection Span (Days)	Total Acoustic Detection Days	Total Acoustic Detections	Satellite Xmitter #	Satellite Detection Span (Days)	Total Satellite Detections
Maui	F	347	10/20/13	26881[2]	613	365	2235	145989	143	159
Maui	F	307	10/19/13	26877[2]	604	189	763			
Maui	F	246	10/18/13	26883[2]	507	354	2065			
Maui	F	282	1/14/14	26893[2]	479	185	1102			
Maui	F	379	12/9/14	26900[2]	39	25	123			
Maui	F	385	12/8/14	26901[2]	117	86	425			
Maui	F	365	10/20/13	13409[1]	604	217	864			
Oahu	F	329	9/19/14	30098[3]	-	-	-	132063	-	-
Oahu	M	368	10/16/14	26898[2]	152	25	71	137070	165	378
Oahu	F	445	10/16/14	26890[2]	-	-	-	137072	-	-
Oahu	F	383	10/16/14	26880[2]	236	37	166	137073	164	813
Oahu	F	324	9/19/14	30099[3]	238	72	2318	137074	329	99
Oahu	M	363	10/8/14	7915[4]	216	21	195	137077	280	199
Oahu	F	414	3/5/14	26902[2]	8	5	40	137078	180	78
Oahu	F	379	9/29/14	30095[3]	234	59	1979	137079	107	202
Oahu	F	255	2/17/15	18802[5]	24	5	11			
Oahu	M	203	2/17/15	38673[5]	-	-	-			
Oahu	F	373	9/17/14	30093[3]	122	48	911			
Oahu	F	334	8/23/14	30097[3]	268	77	2320			
Oahu	M	278	3/5/14	26889[2]	399	32	130			
Oahu	M	300	2/18/15	7910[4]	99	26	674			
Oahu	F	217	10/1/14	7913[4]	245	33	529			

Table 2 ctd.

[1]Estimated transmitter life = 3493 days, random off time (min-max) = 130-230 seconds, temperature sensor tag

[2]Estimated transmitter life = 3498 days, random off time (min-max) = 130-230 seconds

[3]Estimated transmitter life = 885 days, random off time (min-max) = 20-40 seconds

[4]Estimated transmitter life = 707 days, random off time (min-max) = 20-40 seconds

[5]Estimated transmitter life = 622 days, random off time (min-max) = 30-90 seconds

In addition to tiger sharks captured and tagged for the present Maui-Oahu focused study, the Maui and Oahu acoustic arrays also listened for transmissions from 20 'legacy' tiger sharks that were captured and acoustically-tagged around Oahu (N=17), French Frigate Shoals (N=1), Lisianski Island (N=1) and Pearl & Hermes Reef (N=1) during earlier research projects (2009-2013). These transmitters had nominal battery lives ranging from 2-10 years resulting in both full and partial overlap of transmitter lives with the 2-year monitoring period around Maui (Table 3).

Acoustic detection ranges were empirically determined by deploying transmitters on a weighted line from a skiff equipped with an onboard GPS-equipped Vemco VR100 receiver and hydrophone. The transmitter was first deployed directly over each receiver, and allowed to transmit 10 times before recovery. This same process was repeated at 100 m intervals beyond the receiver to a maximum distance of 1.5 km. The VR100 receiver recorded the time and position of each transmission. The originating positions of transmissions logged by the underwater VR2W receivers during range tests were subsequently determined by cross-referencing VR2W and VR100 logs. Detection range was up to 900 m.

We deployed 27 receivers around the coasts of Maui (15 receivers, of which 14 were recovered) and Oahu (12 receivers) (Figures 5 & 6). Our array spanned the depth range of the insular shelf, with shallow (5-20 m depth), inshore units deployed at high recreational use (i.e. swimming, snorkeling and surfing) sites, including locations of recent shark bite incidents, and offshore units deployed in deeper (100 – 200 m depth) waters up to several km offshore (Figures 5 & 6). This array design allowed us to compare tiger shark presence between deep and shallow areas, between different coasts of the same island, and between Maui and Oahu. The geographic spread of receivers also allowed for cross-validation of acoustic and satellite data obtained from individual tiger sharks equipped with both kinds of transmitter.

Receivers were deployed on subsurface moorings consisting of an end weight, or sand screw, 2-3 m of polypropylene rope and a hard float. Receivers were attached to the mooring rope using a combination of heavy duty nylon cable ties and stainless steel hose clamps. Shallow receivers were recovered by either SCUBA divers or snorkelers. Deep receivers incorporated an acoustic release (AR-60-E, Sub Sea Sonics LLC, El Cajon, CA, USA) between the end weight and the polypropylene rope. To recover deep receivers, a surface control box, equipped with a hydrophone, activated burn wires attaching the acoustic release to the end weight, freeing the mooring from the seabed and allowing it to float to the surface.

Table 3. Summary metadata for “legacy” tiger sharks captured and acoustically-tagged around Oahu (N=17), French Frigate Shoals (N=1), Lisianski Island (N=1) and Pearl & Hermes Reef (N=1) during earlier research projects (2009-2013). These sharks were all equipped with transmitters that were still active during all or part of the current Maui-focused project. Underlined Total Length (TL) indicates sharks above the size of sexual maturity at tagging based on reproductive data from Whitney and Crow (2007). Age and size estimates are based on the Hawaii tiger shark growth curve from Meyer et al. (2014).

Tagging Island	Xmitter	Total Length (cm) at Tagging	Estimated Age at Tagging (y)	Sex	Tagging Date	Xmitter Death Date	Total Maui Detection Days	Estimated Age (y) at First Maui Detection	Estimated Total Length (cm) at First Maui Detection
FFS	5659[1]	<u>380</u>	8.5	F	6/7/08	6/5/18	0		
Lisianski	660[2]	<u>410</u>		F	7/14/07	10/30/13	0		
Oahu	371[3]	<u>333</u>	4.9	M	2/19/08	12/24/14	0		
Oahu	374[3]	323	4.4	F	9/10/08	7/16/15	0		
Oahu	375[3]	276	3.0	F	2/2/07	12/7/13	0		
Oahu	376[3]	<u>335</u>	5.0	F	9/27/07	8/1/14	0		
Oahu	377[3]	<u>430</u>		F	9/27/07	8/1/14	0		
Oahu	379[3]	201	1.5	F	2/4/08	12/9/14	0		
Oahu	381[3]	312	4.0	F	9/27/07	8/1/14	0		
Oahu	54782[4]	295	3.5	M	5/27/09	11/12/13	0		
Oahu	54786[4]	<u>327</u>	4.6	M	10/6/09	3/24/14	2	8.8	<u>382</u>
Oahu	54790[5]	183	1.2	F	5/19/09	5/17/19	26	5.9	<u>352</u>
Oahu	54791[5]	256	2.5	F	2/6/09	2/4/19	2	8.5	<u>380</u>
Oahu	54792[5]	256	2.5	F	1/28/09	1/26/19	0		
Oahu	54793[5]	287	3.3	F	2/6/09	2/4/19	53	8.1	<u>377</u>
Oahu	54795[5]	268	2.8	F	9/17/09	9/15/19	0		
Oahu	54796[5]	291	3.4	F	11/17/09	11/15/19	0		
Oahu	61971[6]	254	2.4	F	4/10/13	3/11/15	0		
Oahu	30100[7]	319	4.3	F	4/22/13	9/24/15	22	5.8	<u>350</u>
PHR	661[8]	<u>395</u>	11.9	F	8/31/07	12/17/13	0		

[1]Estimated transmitter life = 3650 days, random off time (min-max) = 150-300 seconds

Table 2 ctd.

[2]Estimated transmitter life = 2300 days, random off time (min-max) = 150-300 seconds
[3]Estimated transmitter life = 2500 days, random off time (min-max) = 150-300 seconds
[4]Estimated transmitter life = 1630 days, random off time (min-max) = 30-90 seconds
[5]Estimated transmitter life = 3650 days, random off time (min-max) = 30-90 seconds, low power (V16-6L)
[6]Estimated transmitter life = 700 days, random off time (min-max) = 10-35 seconds
[7]Estimated transmitter life = 885 days, random off time (min-max) = 20-40 seconds
[8]Estimated transmitter life = 2300 days, random off time (min-max) = 150-300 seconds

Historical acoustic data sets for comparison with current results

To provide a frame of reference for current acoustic monitoring results from receiver stations around Maui and Oahu, we include two previous data sets in our analyses. These data were collected during tiger shark acoustic tagging studies conducted around Hawaii Island (2003-2005; Table 4) and French Frigate Shoals atoll (2009-2011; Table 5). Both of these previous studies utilized the Vemco acoustic monitoring system and equipped tiger sharks with surgically-implanted V16-6H transmitters. The duty cycles of transmitters used at FFS and around Hawaii island were faster (i.e. a higher number of transmissions per unit time) than those used in the current study, and consequently the transmitter lives were shorter (~2 years; Tables 4 & 5).

The use of different transmitter duty cycles at different islands is a potential source of detection bias. In this case, the bias is for less frequent detection of sharks tagged around Maui compared to the other three islands, due to a combination of slower Maui transmitter duty cycles, and very low risk of signal collision reducing detection rates of faster duty cycle tags deployed around other islands, because tiger sharks rarely overlap in time and space. We mitigate (but cannot completely eliminate) any potential bias by using comparative metrics with relatively large time footprints (i.e. the longer you listen, the higher the probability you have of detecting a tag, regardless of its duty cycle). For example, we are using calendar days as the basis of our Site Fidelity Index.

The Hawaii Island monitoring array consisted of 33 receivers deployed at depths between 5-30 m on fringing reef along 115 km of the western coastline (Figure 7). The FFS array was comprised of 24 receivers deployed primarily across the extensive atoll lagoon, but also at several sites outside the barrier reef (Figure 7). Both Hawaii Island and FFS receiver arrays had narrower, shallow-skewed depth ranges compared to those deployed around Oahu and Maui (Table 6).

Table 4. Summary acoustic detection data for tiger sharks captured off Hawaii Island 2003-2004. All sharks were equipped with acoustic transmitters with anticipated battery lives of 732 days, and random off time (min-max) = 10-35 seconds. Underlined Total Length (TL) indicates sharks above the size of sexual maturity at tagging based on reproductive data from Whitney and Crow (2007).

Sex	Total Length (cm)	Date Tagged	Acoustic Xmitter #	Acoustic Detection Span (Days)	Total Acoustic Detection Days	Total Acoustic Detections
F	219	12/3/03	304	72	19	51
F	<u>355</u>	12/4/03	305	497	19	53
F	<u>375</u>	12/3/04	313	792	46	648
F	<u>383</u>	12/1/04	317	924	140	1364
F	<u>413</u>	12/1/04	306	495	47	560
F	<u>439</u>	6/26/04	316	820	70	856
F	<u>449</u>	12/3/03	303	768	66	208
F	<u>460</u>	12/4/03	301	101	49	421
M	181	6/27/04	309	779	72	780
M	218	6/27/04	311	0	1	2
M	279	6/27/04	315	42	15	186

Table 5. Summary acoustic detection data for tiger sharks captured at French Frigate Shoals atoll in 2009. All sharks were equipped with acoustic transmitters with anticipated battery lives of 700 days, and random off time (min-max) = 10-35 seconds. Underlined Total Length (TL) indicates sharks above the size of sexual maturity at tagging based on reproductive data from Whitney and Crow (2007).

Sex	**Total Length (cm)**	**Date Tagged**	**Acoustic Xmitter #**	**Acoustic Detection Span (Days)**	**Total Acoustic Detection Days**	**Total Acoustic Detections**
F	450	5/27/09	55222	559	17	131
F	444	6/30/09	55887	220	33	275
F	443	6/7/09	55193	703	138	1825
F	440	6/14/09	55220	700	88	1076
F	437	5/23/09	55901	501	7	10
F	434	5/11/09	55924	674	91	909
F	432	7/21/09	55872	2	2	27
F	431	6/11/09	55898	666	28	154
F	431	7/30/09	59502	0	1	2
F	425	7/5/09	59515	321	15	120
F	420	7/17/09	59508	771	346	4697
F	418	5/24/09	55914	897	103	1192
F	418	7/4/09	59516	361	18	134
F	416	6/29/09	55886	569	44	180
F	410	7/16/09	55870	60	12	90
F	409	6/7/09	55191	492	15	140
F	408	5/10/09	55921	423	19	129
F	406	7/6/09	55869	267	18	114
F	405	6/15/09	55236	659	13	70
F	395	7/4/09	59519	690	172	1877
F	395	7/2/09	59523	711	45	462
F	393	6/29/09	55228	661	51	595
F	372	6/7/09	55192	272	55	809
F	371	7/6/09	59513	700	78	1919
F	370	7/27/09	55876	383	57	617
F	360	5/20/09	55893	702	15	237
F	350	6/12/09	59535	769	32	241
F	320	5/21/09	55895	594	330	4203
F	302	5/26/09	55221	688	284	3237
F	272	6/15/09	55227	949	164	2359
F	261	7/1/09	55889	193	10	37

/ctd.

Table 5 ctd.

Sex	Total Length (cm)	Date Tagged	Acoustic Xmitter #	Acoustic Detection Span (Days)	Total Acoustic Detection Days	Total Acoustic Detections
M	406	6/4/09	55223	684	46	579
M	403	7/6/09	59525	733	30	274
M	363	7/2/09	55207	622	25	141
M	347	5/24/09	55907	792	101	1123
M	337	6/4/09	55218	696	157	1178
M	328	6/15/09	55229	693	92	2009
M	291	5/23/09	55912	691	74	842
M	284	6/14/09	59533	20	2	23

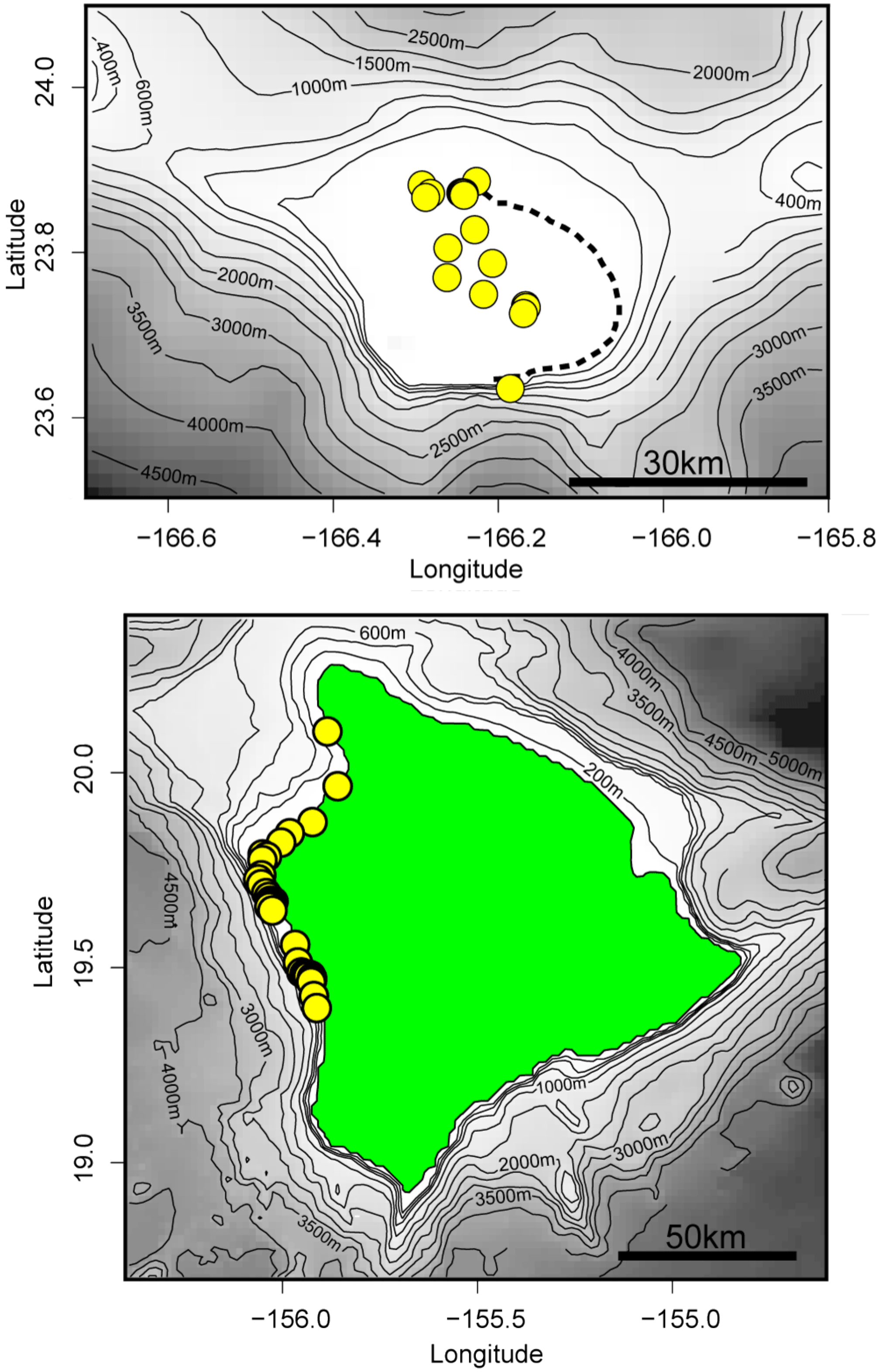


Figure 7. Receiver deployments (yellow points) at French Frigate Shoals (Top, dashed line indicates emergent barrier reef) and Hawaii Island (Bottom).

Table 6. Number and depth of receivers deployed around French Frigate Shoals (FFS), Oahu, Maui and Hawaii Island.

Island	**No. of Receivers**	**Receiver Depth (m)**		
		Minimum	**Maximum**	**Mean**
FFS	24	0.9	45.7	8.9
Oahu	12	11.9	195.7	87.2
Maui	15	7.9	78.6	37.8
Hawaii	36	3.0	37.5	18.6

Analysis of acoustic data

Site fidelity and duration of visits to receiver locations

To determine whether tiger sharks captured at sites of concern around Maui show any evidence of being more resident, visiting coastal recreation sites more often, or spending more time in these areas than tiger sharks captured around other Hawaiian islands, we compared Site Fidelity Indices and visit characteristics (duration and frequency of visits to receiver locations) of tiger sharks captured around Maui, with those captured around Oahu, Hawaii Island, and French Frigate Shoals atoll.

Site Fidelity Index (SFI) was calculated by dividing the number of days a shark was detected at each receiver, by the monitoring period for that site (e.g. Papastamatiou *et al.* 2010), and then expressed as a percentage by multiplying by 100. The SFI assumes zero tag battery failure, and the monitoring period for each receiver-transmitter combination was adjusted to account for receivers that were deployed after sharks were tagged (i.e. monitoring period commenced with receiver deployment) and vice versa, and also to account for the anticipated battery lives of each transmitter.

The duration of tiger shark visits to each receiver location was quantified by calculating the time elapsed between the first and last transmitter detections during each visit. A visit started and ended when either the location changed, or the transmitter was not detected for 30 minutes (e.g. Meyer et al. 2009). Visits consisting of single transmitter detections were considered to last 7.7 minutes (equivalent to the longest transmitter pulse train duration of 3.6 sec, preceded and followed by listening periods equivalent to the maximum random off time of 230 sec). These buffer criteria were based on the slowest transmitter duty cycles and were applied to all transmitters included in our analyses to avoid bias resulting from faster transmitter duty cycles yielding inherently shorter visits. The time elapsed between consecutive visits was used to determine how long each shark was absent from its most frequently visited location.

For each shark, we calculated the mean (excluding zeros) and maximum SFI values, the mean and maximum visit duration (min), and the mean (excluding zeros) and maximum number of visits per day, and then used one-way ANOVAs to compare tiger shark overall average site fidelity and visit characteristics among tagging islands (preliminary analysis indicated shark sex and the interaction between sex and tagging island had no significant influence on mean site fidelity or visit characteristics). Averaging the response variables by individual shark was necessary to meet the assumption that observations are independent of one another. Box-Cox transformations were used to normalize each dataset prior to testing, but failed to produce normally-distributed residuals for maximum number of visits per day, therefore a nonparametric alternative (Kruskal-Wallis test with Wilcoxon rank-sum test) was used to compare means of this variable among tagging islands. Following Box-Cox transformation, data were tested for equality of variance using Levene's test and Bartlett's test. All variables except maximum SFI were heteroscedastic, thus a conventional one-way ANOVA (with Tukey's HSD) was used to compare average maximum SFI values among islands, and Welch's ANOVA (with Games-Howell test), which accounts for unequal variance when comparing means, was used to compare the tagging-island averages of the remaining site fidelity and visit characteristic variables.

We used Generalized Linear Mixed-effects Models (GLMM) to examine the influence of shark sex, size and tagging island, and receiver depth and distance from tagging site on tiger shark site fidelity and visit characteristics. GLMM analyses were conducted in R, using packages ‘glmmADMB’ (Skaug et al. 2012) and ‘lme4’ (Bates et al. 2014). For our analyses of site fidelity, we selected the total number of days detected at each receiver station as the response variable, and used the total number of days that each receiver was actively listening for each tagged shark as an offset term in the models. This approach was taken because non-integer Site Fidelity Index values could not be included directly in models (hence the use of total detection days), and the number of monitored days at each receiver station varied among individual sharks (due to different shark tagging dates etc.) requiring the inclusion of the unique number of days that each receiver was actively listening for each tagged shark as an offset.

We used mean visit duration as our response variable in analyses of factors influencing visit characteristics at receiver sites. To make the visit data suitable for use in GLMM analyses, we first rounded the mean visit duration values to the nearest integer, and used a Kolmogorov-Smirnov two-sample test to compare the original and rounded values to ensure that integer smoothing did not significantly alter the distributional properties of the visit duration data.

For both analyses of site fidelity and visit characteristics, our fixed effects included the distance between shark tagging site and receiver location, receiver station depth, shark sex, total length and tagging island, and the interactions between sex and depth and between tagging site-receiver distance and depth. The justification for selecting these interaction terms were *a priori* evidence of sex segregation among mature tiger sharks (males further offshore than females), and core-structured home ranges (receivers at preferred depths but at the periphery of the home range will have low SFI values). Interactions were only considered in models containing both main effects (rule of marginality). Transmitter (i.e. the individual shark) and receiver station were included as random effects in models to account for the repeated measures associated with multiple detections of the same individuals on the same receivers.

Prior to fitting models, we conducted exploratory data analyses to visualize possible relationships between dependent and predictor variables, and check for outliers in both the dependent and predictor variables, zero-inflation in the dependent variables, and collinearity and possible interactions in the predictor variables (Zuur et al. 2010). We generated scatterplots and co-plots of raw data to identify obvious trends and interactions, and used boxplots and Cleveland dotplots to visually identify potential outliers (Zuur et al. 2010). To check for collinearity among predictor variables, we calculated Pearson Correlation coefficients and Variance Inflation

Factors (VIF; R package ‘car; Fox and Weisberg 2011). Thresholds for collinearity were absolute Pearson correlation coefficients >0.8, and VIF values >3 (Zuur et al. 2010).

Exploratory data analyses revealed no evidence of collinearity (all VIF values were <2), but indicated our raw SFI detection data were extremely (>70%) zero-inflated and highly-skewed. The zero-inflation was a by-product of a receiver array that extended beyond the home ranges of individual sharks. This meant that receivers stationed in frequently-visited locations for some tiger sharks, did not detect other individuals tagged much further away, even though those particular habitats were apparently attractive to tiger sharks (i.e. some potentially good habitats are located outside the home ranges of individual sharks). For the purpose of model building, we assumed that these were structural rather than sampling zeros (i.e. home range boundaries were a virtual ‘fence’, beyond which even very highly-desirable habitats would not be visited simply because sharks were unaware of resources located outside of their familiar areas). Zero-inflation was not a concern for analyses of visit duration, because ‘visits’ of zero minutes are absences, and thus were not included in our analyses.

For our analyses of SFI, we used a hurdle model approach (Min and Agresti 2005, Zuur et al. 2009) where the binary (presence/absence) and proportional (i.e. non-zero) components of the data are analyzed separately. This technique essentially poses two questions; (1) What factors determine whether or not a shark is ever detected, and (2) When a shark is detected, what factors influence how often it is detected? Our analyses of visit characteristics focused exclusively on factors influencing visit duration (i.e. the proportional component).

We used a binomial error distribution with a logit link for the binary component of the hurdle model, and a negative binomial error distribution with a log link for the proportional component of the hurdle models. For the binary analyses, site fidelity data were converted to zeros (never detected on a receiver) and ones (detected on a receiver). Continuous fixed effects were mean centered and scaled prior to analyses (Schielzeth 2010). After fitting models, we plotted residuals against fitted values to evaluate homogeneity of variance, and used Q-Q plots and histograms to assess normality of distribution in residuals (Zuur et al. 2010). We used a goodness of fit test based on the deviance and Pearson residuals to calculate whether data were under, or over-dispersed (Zuur et al. 2010).

Multimodel inference was used to explicitly account for model selection uncertainty (Burnham et al. 2011). We used the dredge function from R package ‘MuMin’ (Barton 2014) to average predictions and coefficient estimates across models, based on corrected Aikake Information Criteria (AIC_c) scores and Akaike weights, which approximate the probability that each model is the best model. We set a delta-AIC_c threshold of 2 to select well-fitting nested models for averaging. Best nested models were compared against the null model using maximum likelihood ratio tests.

The general framework described above was initially applied to two-island models (Maui and Oahu data only), and then subsequently to four island models (Maui, Oahu, FFS and Hawaii Island). We subdivided analyses in this way because tagging and monitoring on Maui and Oahu were contemporaneous (i.e. all sharks tagged around Maui and Oahu were in theory detectable by all receivers deployed around both islands), whereas FFS and Hawaii Island data were historical and non-overlapping (i.e. sharks tagged at these islands could only be detected on the arrays at the tagging islands due to the timing of the studies and transmitter battery life constraints), and these islands also had receivers arrays deployed across a narrower depth range (1-46 m) than Maui and Oahu (8-195 m)(Table 6).

Temporal Patterns

We used graphical techniques to identify temporal (diel and seasonal) patterns in the total number of tiger sharks visiting receiver sites. Detection data were pooled across the 21 month monitoring period and aggregated into hourly and monthly bins to determine how the number of individuals detected varied at both diel and seasonal scales. Seasonal patterns were evaluated at island level (Maui versus Oahu) and diel patterns were examined at each of the shallow ocean recreation sites around Maui. We assumed a null pattern (i.e. no diel or seasonal effect on frequency of detection) would be represented by an equal (the mean) number of individuals detected in all diel or seasonal bins, and used Kolmogorov-Smirnov two-sample tests to compare the null frequency against the observed frequency of detection.

Public Outreach

Outreach activities conducted during this project included public lectures (detailing project goals and findings) on Maui and Oahu in 2014 and 2016, presentations at international scientific conferences in 2015, interviews with local, national and international media, and posting of near-real time tiger shark satellite tracks on a website constructed and supported by the Pacific Islands Ocean Observing System (PACIOOS).

RESULTS

Overview

During the current Maui and Oahu-focused study (2013-2015), a total of 41 tiger sharks (217 to 448 cm Total Length [TL]) were captured around Maui (26 sharks) and Oahu (15 sharks), and equipped with electronic tags (Table 2). Of these, 28 individuals were equipped with both surgically-implanted acoustic tags and dorsal fin mounted satellite transmitters, and the remaining 13 with acoustic tags only (Table 2). Thirty-eight (93%) of these sharks were subsequently detected via either satellite or acoustic transmissions over periods ranging from 7-613 days (Table 2). Two sharks were also equipped with video cameras, with useable footage recovered from one individual (the camera detached prematurely from the other shark).

In addition, 20 "legacy" tiger sharks acoustically-tagged at 4 Hawaiian islands (but primarily around Oahu) before the current Maui and Oahu-focused study started, were theoretically still detectable during the time frame of the current study (because their transmitters were still active during all or part of the current Maui-Oahu focused project -Table 3). Five (25 %) of these sharks were detected around Maui during the current project window of October 2013 to June 2015. All 5 of these legacy sharks were originally captured and tagged around Oahu, with the earliest tagging event for a detected legacy shark occurring in February 2009 (Table 3).

For comparative purposes, we also included historical data from tiger sharks acoustically-tagged around Hawaii Island (Table 4) and at French Frigate Shoals atoll (Table 5) in our analyses of tiger shark spatial dynamics. Hawaii Island tiger shark data were obtained from 11 individuals ranging in size from 181 to 460 cm TL, and detected over periods ranging from <1-924 days (Table 4). French Frigate Shoals data were derived from 39 tiger sharks ranging in size from 261 to 450 cm TL, and detected over periods ranging from <1 to 949 days (Table 5).

A non-parametric Kruskal-Wallis test revealed no significant differences in mean tiger shark size among tagging islands ($H = 7.722$, $df = 3$, $p = 0.0521$).

Dorsal fin-mounted satellite tags

Twenty-five (89%) satellite-tagged tiger sharks yielded Argos location estimates over periods ranging from 7 to 595 days (median 164 days)(Table 2), and were detectable for up to 756 days. In the latter case, the unique satellite-tag identification codes continued to be registered by both satellite and land-based receivers, but data were insufficient for calculating Argos location estimates, although detection via the land-based receivers indicated these sharks were still present in waters around Maui.

Satellite tracking data revealed extensive (>100 km up to 1,460 km) offshore movements by seven tiger sharks, with some individuals spending months in open-ocean with only brief visits to coastal waters, but the majority (78.7%) of satellite detections occurred in coastal (<500 m depth) waters around Oahu, Maui Nui and Hawaii Island (Figures 8 & 9). Most individuals were detected most frequently in waters around their tagging island, but sharks tagged around Maui also visited waters around Molokai, Lanai, Kahoolawe and Hawaii Island. Tiger sharks tagged around Oahu also visited waters around Kauai, Molokai, Maui and Lanai.

Coastal Home Range Analyses of Satellite Tracking Data

Satellite tracking revealed that each shark had unique home range characteristics but there were several common themes of space and habitat use among individuals. For example, tiger shark home ranges typically included waters around several adjacent islands, and sharks were most frequently detected over insular shelf habitat within the 200 m isobath (Figure 8). Nineteen satellite-tagged sharks yielded sufficient positions for home range isopleth analyses (Figures 10 & 11). Most of these individuals utilized clearly-defined core areas (the area where satellite fixes were most strongly clustered) associated with relatively wide areas of insular shelf (Figures 10 & 11). Tiger shark home range core use areas around Maui were often adjacent to ocean recreation beaches, with overlapping core areas of 7 individuals identified in waters off SW Maui (Figure 11). Around Oahu, overlapping tiger shark home range cores were documented in waters off the North coast, and some Oahu-tagged tiger sharks also utilized core use areas on Penguin Banks (a westward extension of the insular shelf surrounding Maui Nui - Figure 11).

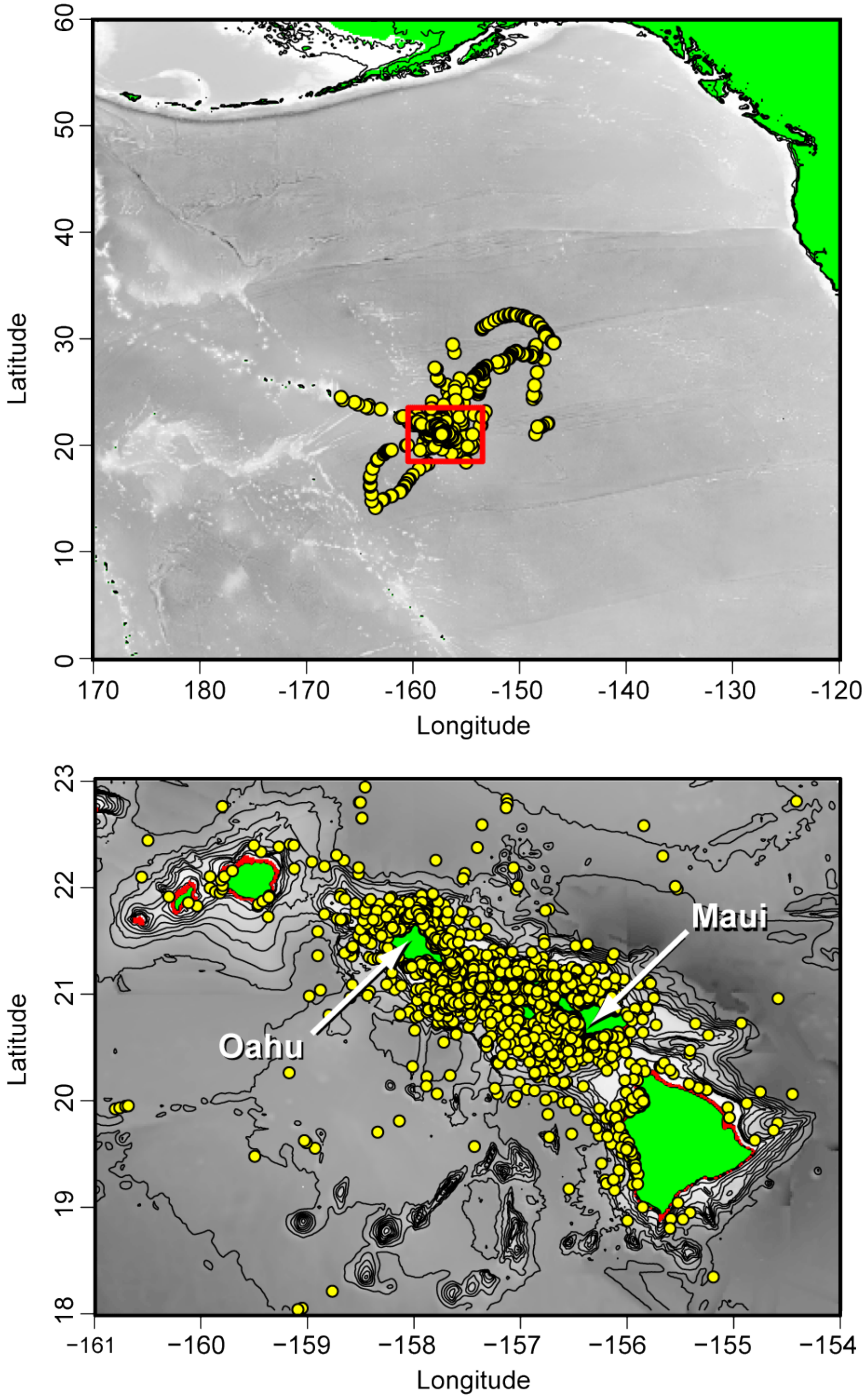


Figure 8. Top panel: Overview of ARGOS locations (yellow points) from 32 tiger sharks captured off Maui and Oahu, and equipped with dorsal fin-mounted satellite transmitters (SPOT tags). Red box indicates area shown in detail in bottom panel. Bottom panel: Tiger shark ARGOS locations (yellow points) within coastal habitats of the Main Hawaiian Islands.

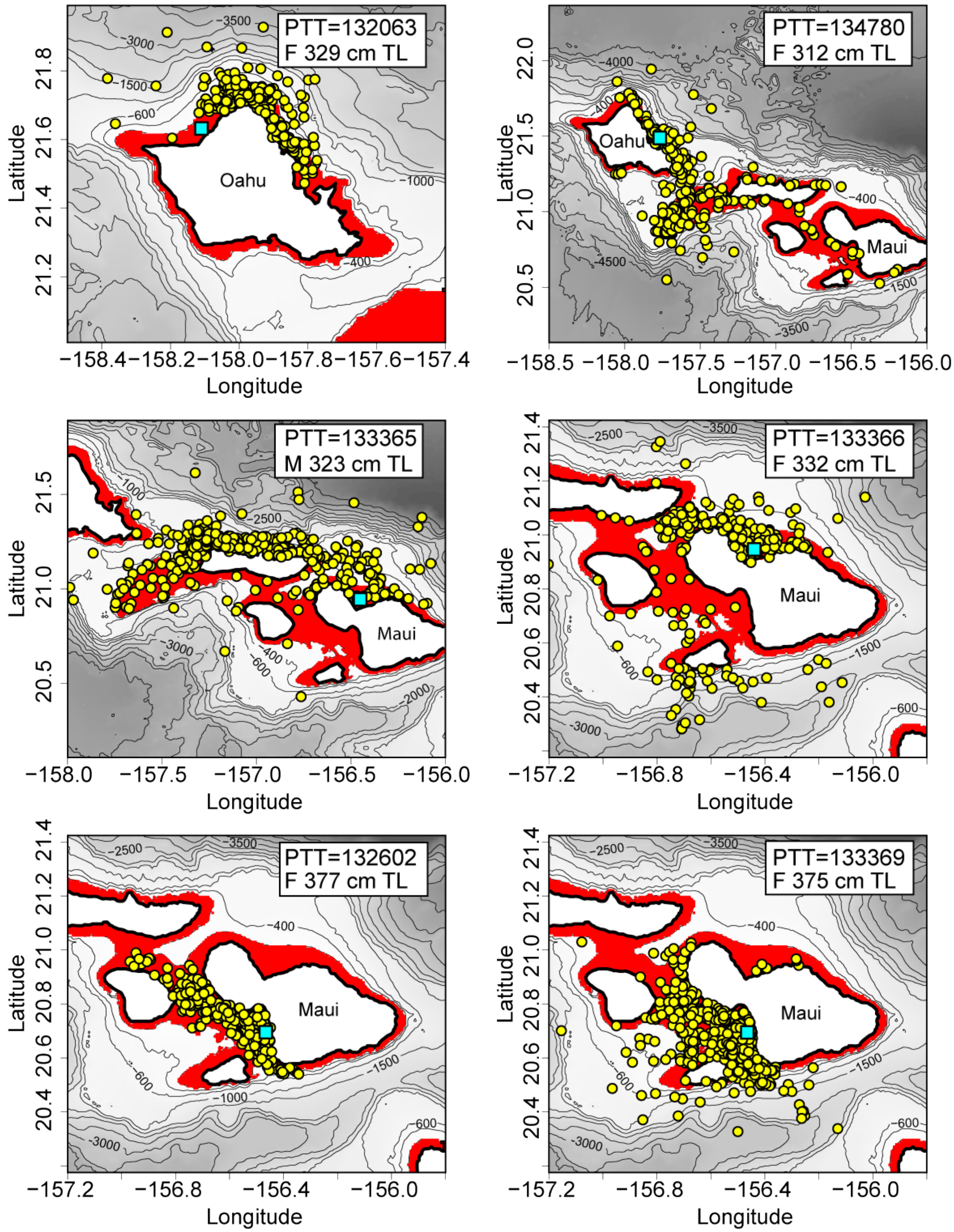


Figure 9. Satellite detections locations (yellow points) of six individual tiger sharks (M/F =sex, TL = Total Length in cm) showing concentration over insular shelf habitat (0-200 m depth, red shading). Light blue squares indicate tagging locations of each shark.

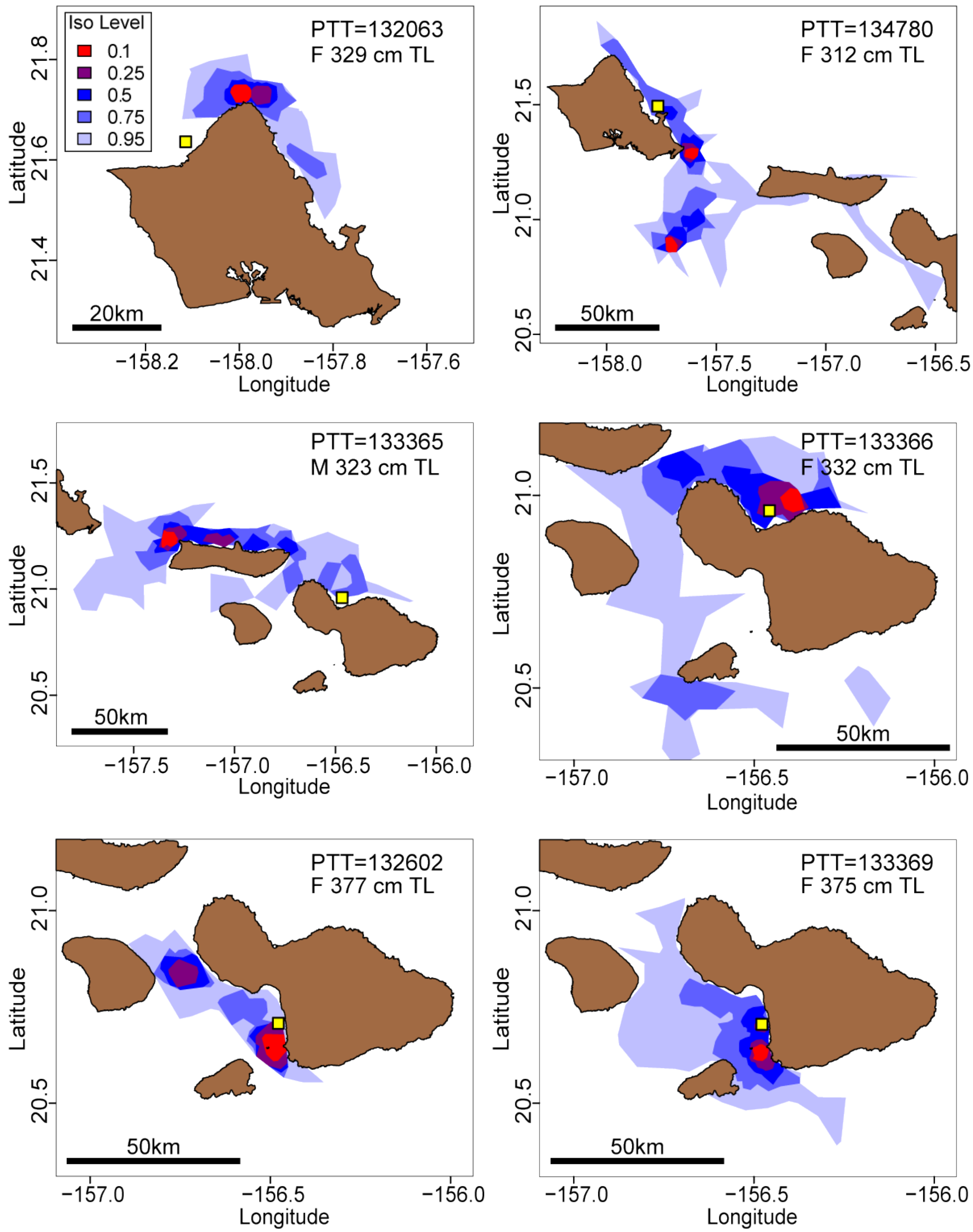


Figure 10. Home range isopleths for tiger sharks captured around Maui and Oahu. Yellow square indicates original tagging location. Isopleth levels indicate the proportion of total satellite locations enclosed by the polygon (e.g. area in red = 10%, dark blue = 50%, light blue = 95%).

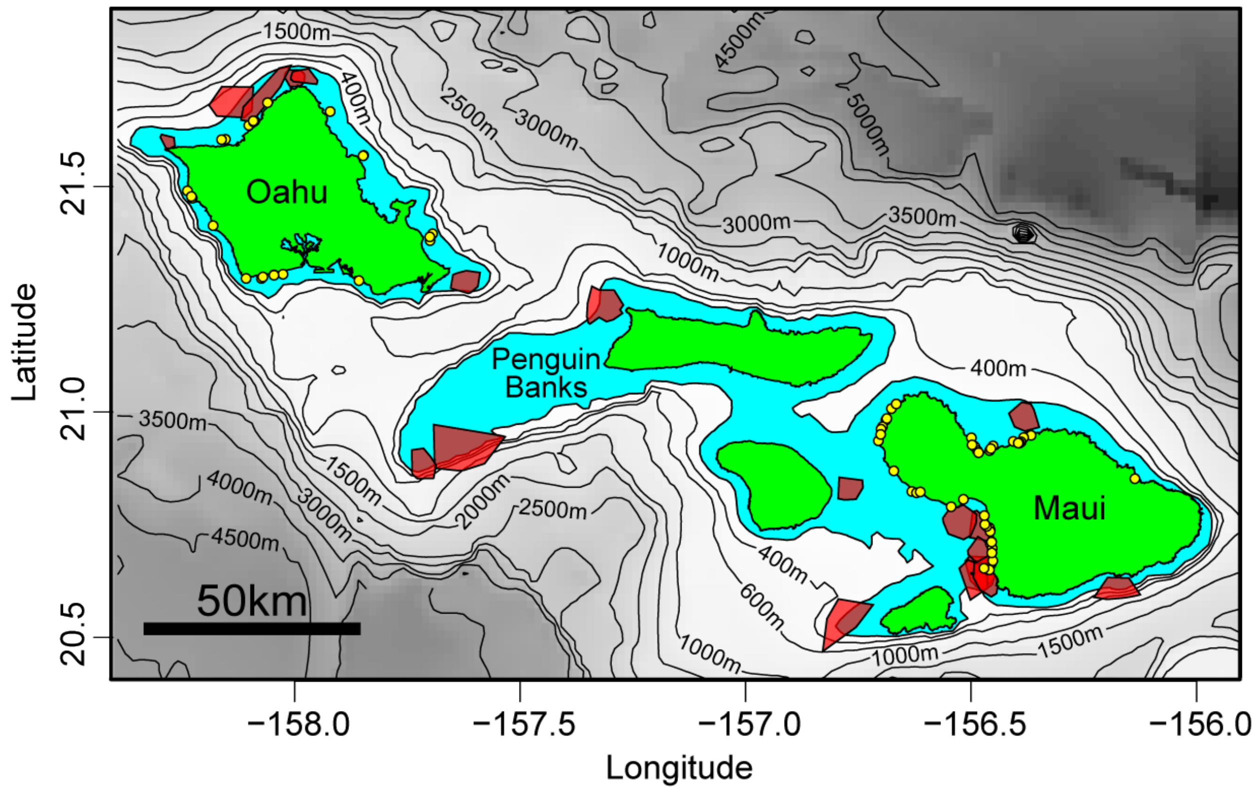


Figure 11. Home range core use areas (translucent red polygons) of 19 satellite-tagged tiger sharks captured around Maui (N=13) and Oahu (N=6). Note the cluster of core areas in waters off SW Maui (overlapping core areas of 7 individuals were identified in waters between Mā‘alaea and Makena). Blue shaded area indicates insular shelf (depth 0-200m). Yellow points indicate locations of documented shark bite incidents.

Bathymetry profiles from ARGOS locations

Bathymetry profiles harvested from satellite fixes (Figure 12) show that although tiger sharks utilize the full depth range of the insular shelf, including shallow habitats close to shore, the modal bathymetry depth, and likely center of tiger shark activity, is between 50 and 100 m. Male average bathymetry profiles suggest they favor habitats further offshore than females (Figure 12). For example, on average 50% of female satellite locations occurred within the 100 m depth contour, whereas on average only 28% of male satellite locations occurred across the same depth range. Note that these bathymetry depths do not represent the swimming depths of satellite-tagged sharks (see section below), but the depth of water below the shark while it was at the surface.

Swimming depth and temperature data from SPLASH tags

Two female individuals equipped with depth and temperature-logging dorsal fin satellite transmitters (SPLASH tags) exhibited yo-yo vertical swimming profiles, bouncing repeatedly between the surface and depths of around 100m, with occasional deeper dives to depths of 250m and temperatures below 15 ^{o}C (Figures 13 & 14). Swimming depth frequency histograms indicate these two tiger sharks respectively spent 10% and 20% of their time within 2m of the surface (Figure 14), and satellite location-harvested bathymetry depths from the same individuals suggest that both sharks were typically ranging between the surface and the sea floor (i.e. their bounce dives terminated at or close to the sea floor - Figure 13).

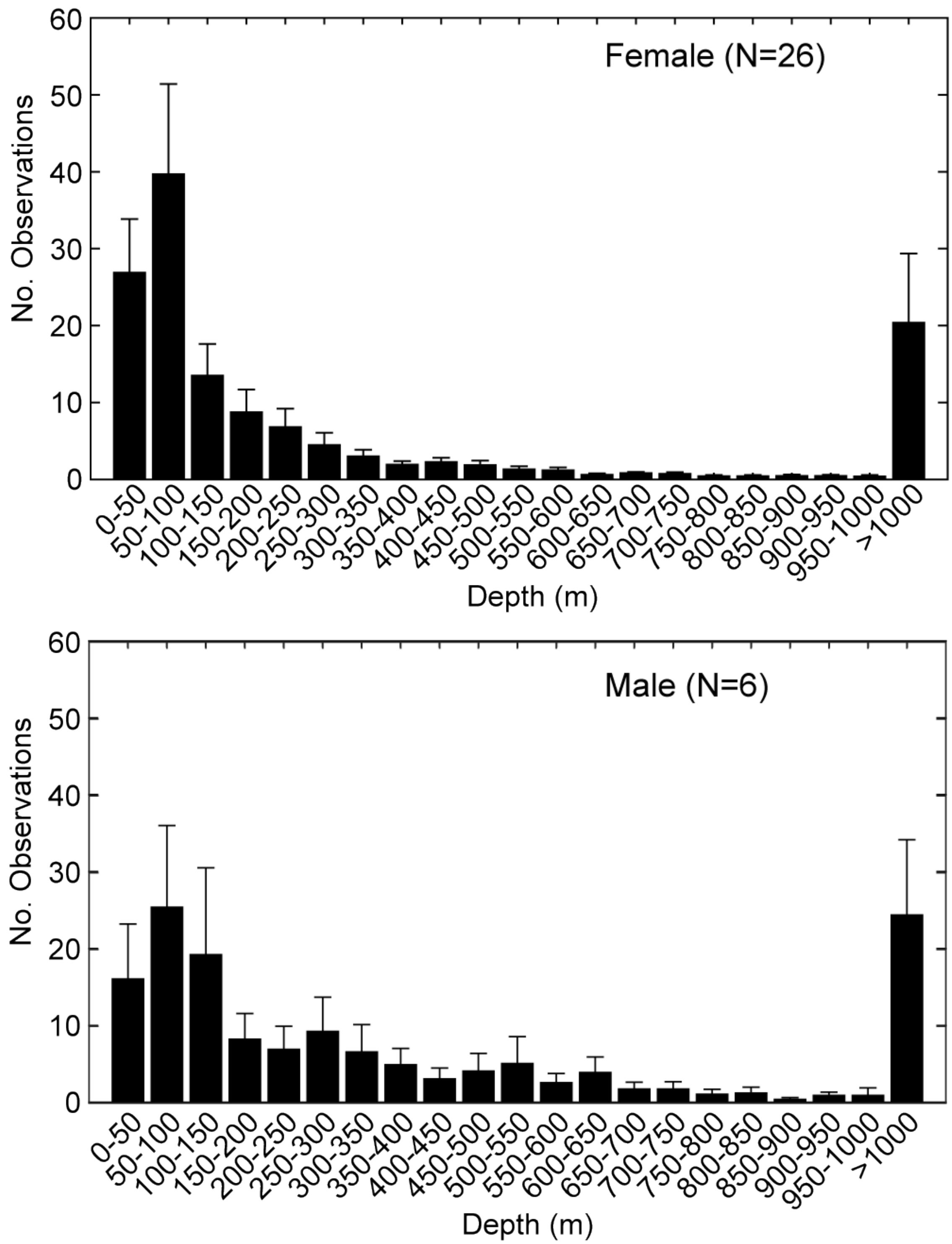
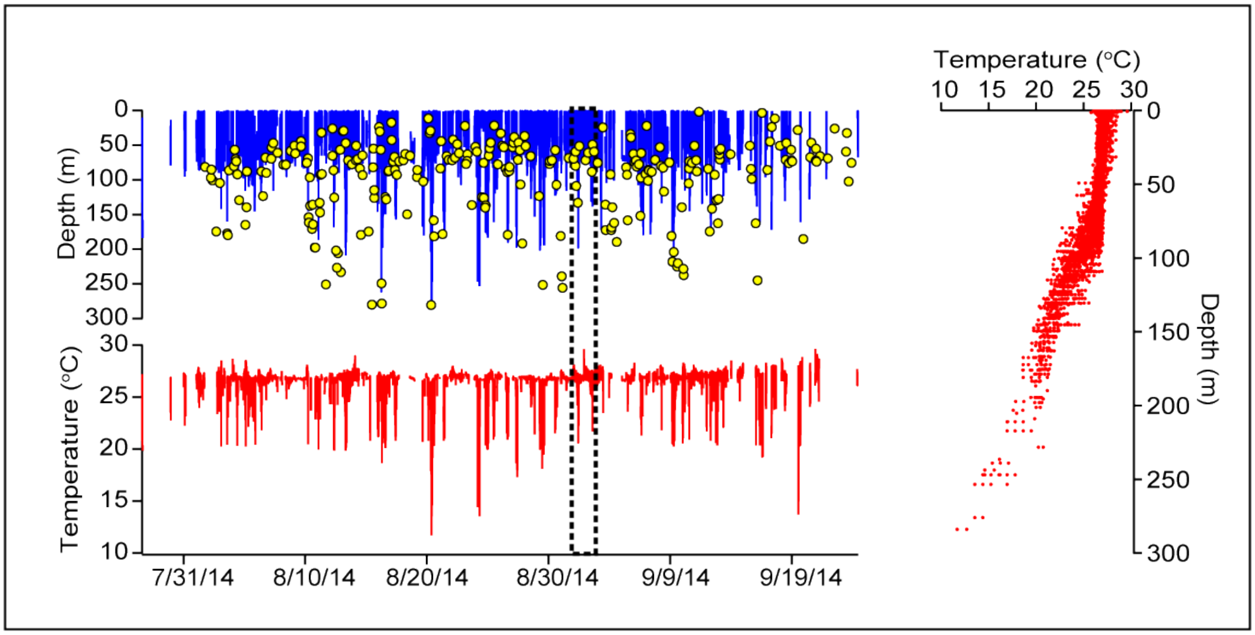


Figure 12. Depth frequency distribution (mean +- SE) of bathymetry underlying Argos locations of female (top panel) and male (bottom panel) tiger sharks equipped with dorsal fin-mounted satellite transmitters. Note that these depths do not represent the swimming depths of satellite-tagged sharks (see Figures 13 & 14), but the depth of water below the shark when the satellite location was obtained while the animal was at the surface.



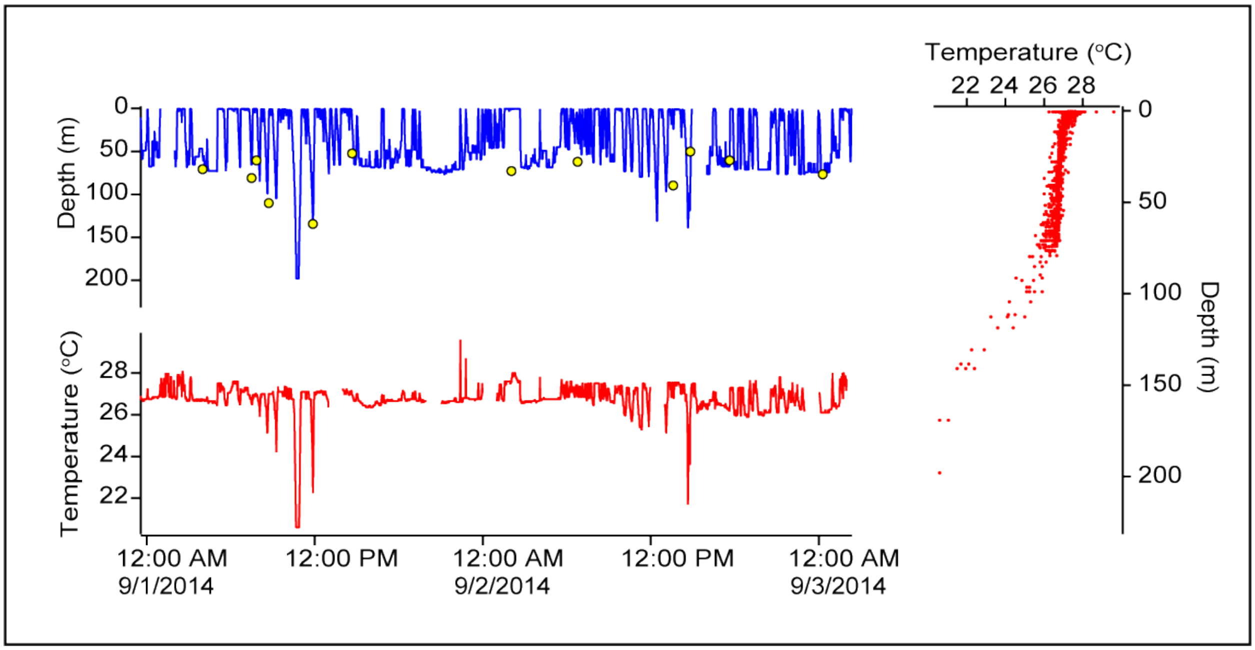


Figure 13. Depth and temperature time series data from SPLASH-tag equipped tiger shark 132062. Top panel: Overview of entire time series. Bottom panel: Detail of 48 hour sample of larger time series. Yellow points are harvested bathymetry values (water depth below shark estimated from surface positions).

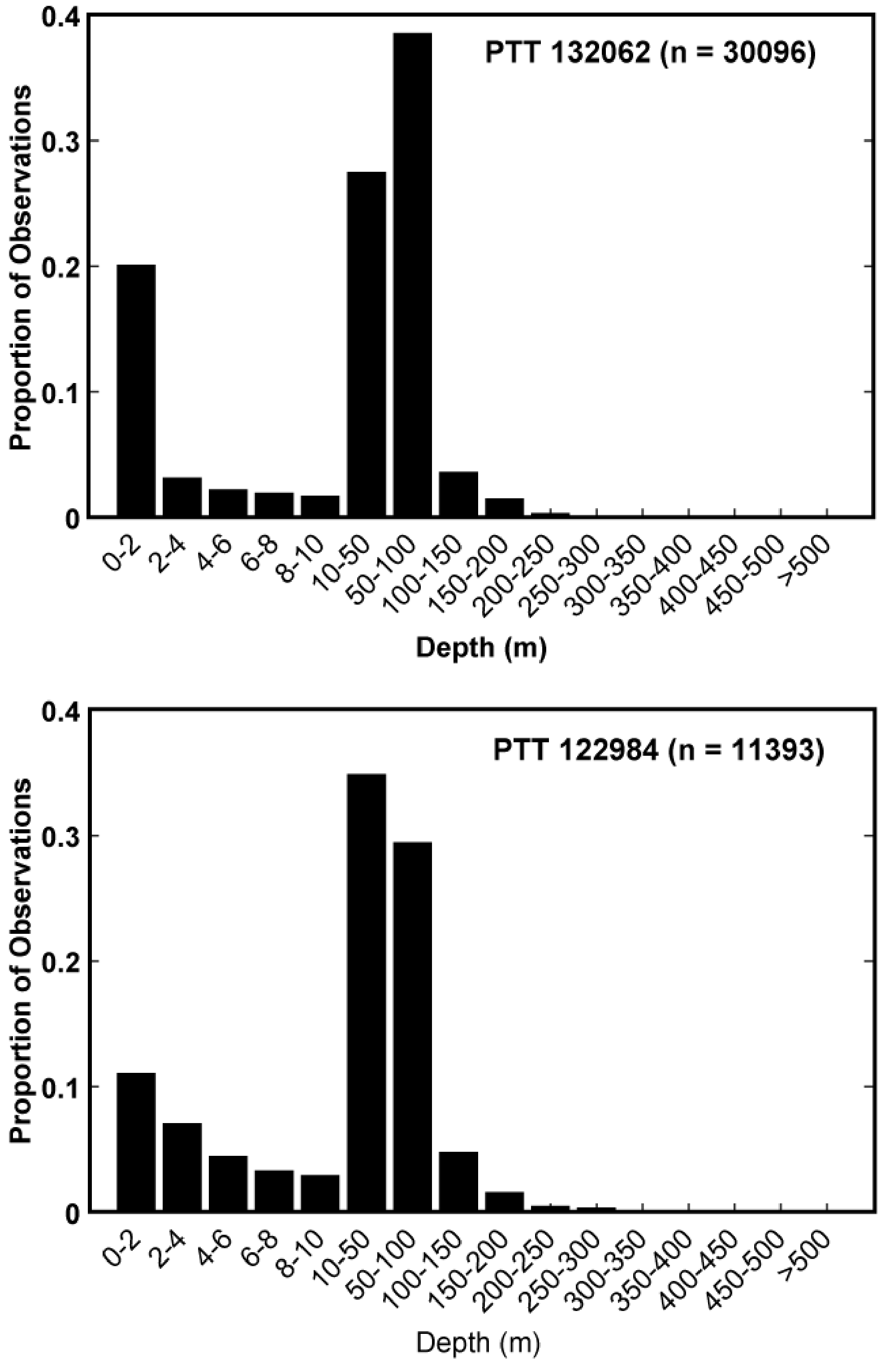


Figure 14. Swimming depth frequency distribution from tiger shark vertical profiles collected by SPLASH tags. Sample sizes (n) indicate the number of depth measurements taken by each tag. N.B. Different bin sizes are used on the horizontal axis to provide a higher resolution view of tiger shark use of surface (0-10m) waters.

Acoustic Monitoring Results

2013-2015 Maui-Oahu acoustically-tagged sharks

During the current study, 25 (100% of successfully recovered) receivers deployed around Maui and Oahu detected 35 (85%) of 41 acoustically-tagged tiger sharks over periods ranging from 8 to 613 days (Table 2). The total number of detection days ranged among individuals from 5 - 365, and total detections ranged from 11-2,320 (Table 2). Six (40%) of 15 Oahu-tagged sharks were detected on Maui receivers, but none of the 26 Maui-tagged sharks were detected on Oahu receivers. This is particularly noteworthy because capture dates for Maui-tagged sharks were earlier on average (mean capture date 1/19/2014) than Oahu-tagged sharks (9/29/14), whereas acoustic monitoring around Oahu began slightly earlier overall (mean start date 5/20/2014) than around Maui (mean start date 5/24/2014). This resulted in a total number of potential detection days (the sum of total monitoring days for each transmitter at each receiver station) for Maui-tagged sharks on Oahu receivers (149,308 d) that was actually higher than the total number of potential detection days for Maui-tagged sharks on Maui receivers (132,761 d), and more than double the total number of potential detection days for Oahu-tagged tiger sharks around Maui (57,638 d).

The raw detection frequencies of tiger sharks around Maui and Oahu are likely skewed by the higher number of individuals tagged around Maui (26 versus 15 around Oahu), even though Maui and Oahu-tagged sharks were free to swim to other islands (and in the case of Oahu-tagged sharks, 40% did swim to Maui, and increased detection metrics for that island). Despite these limitations, raw detection frequencies provide a basic sense of the relative "sharkiness" of each island. For example, Around Maui, at least one acoustically-tagged tiger shark was detected on more than 50% of monitored days at 8 (57%) of 14 receiver sites, whereas around Oahu this 50% detection day threshold was only exceeded at 1 (9%) of 11 receiver sites. Individual Maui sites also had higher detection day frequencies than Oahu sites. For example, at least one tagged tiger shark was detected at Maui deep sites off Kalama and Palauea on >90% of days monitored, >80% of monitored days at Makena, 79% and 62% of monitored days at the Kalama shallow and Palauea shallow sites respectively. Around Oahu, the highest detection day frequency was 55% and occurred at a deepwater site off the north coast. Oahu shallow water sites all had detection day frequencies <6%. If we assume that these detection frequencies are approximately proportional to the number of sharks tagged around each island, doubling the frequencies observed around Oahu (equivalent to 30 tagged tiger sharks around Oahu) would still result in shallow site detection day frequencies well below those observed around Maui.

A similar pattern was evident in daily detections of multiple tiger sharks at receiver sites around Maui and Oahu. Multiple tiger sharks were detected on the same day on all Maui receivers on between 1 and 66 % of days monitored, with the highest incidences of daily detections of multiple individuals at shallow water locations occurring at Makena (51%), Kalama (47%), Palauea (29%) and Olowalu (25%). The highest number of tagged tiger sharks detected on a single day at any Maui site was 8 at the shallow Olowalu receiver on January 2, 2015 (Figure 15). Detections of multiple tagged tiger sharks only occurred on 4 Oahu receivers on between <1 and 20 % of monitored days, and highest number of tiger sharks detected on one day was 3.

There were no detections of multiple tiger sharks on the same day at any Oahu shallow ocean recreation sites.

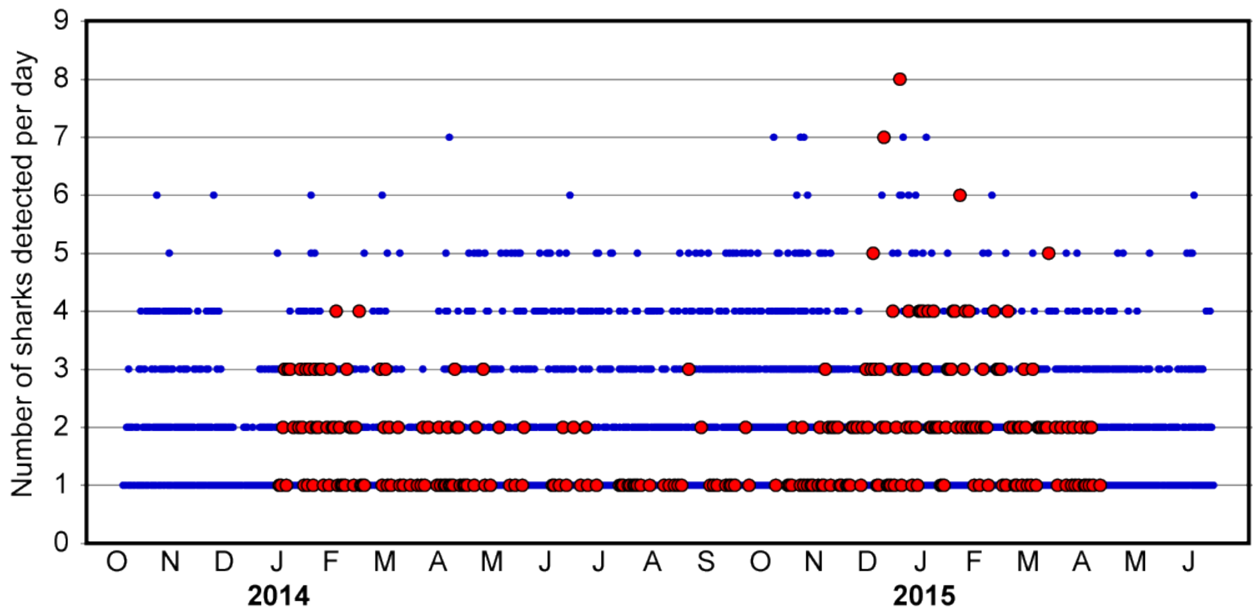


Figure 15. Scatter plot illustrating detections of multiple sharks on the same day at Maui receiver sites. Blue points: number of sharks detected per day (y axis) at all Maui receiver sites except Olowalu. Red points: number of sharks detected per day (y axis) at Olowalu. Note how detections of multiple individuals peak during tiger shark mating season (Jan-Mar) at Olowalu.

Legacy sharks – (individuals tagged before current Maui-Oahu project, with transmitters with lifespans overlapping the current project)

Five (25%) of 20 legacy tiger sharks were detected on our Maui receivers during the course of the current 2013-2015 study (Figure 16). All 5 sharks were originally captured and tagged off Oahu, with 4 individuals tagged in 2009, and one in early 2013 (Table 3). During the current study, three of the legacy sharks were detected around both Maui and Oahu, and the remaining two were only detected around Maui (Figure 16). Legacy sharks were detected on 11 (79%) of 14 Maui receivers over periods ranging from 2 to 53 days (Table 3). One male was already large enough to be sexually mature at tagging in 2009, but the remaining 4 females were subadults at tagging (Table 3). A previous NOAA-sponsored project maintained an array of acoustic monitors in Maui waters from August 2008 to July 2010 (F. Parrish, unpublished data). During this earlier window of monitoring, one of the 5 legacy sharks (a subadult female) was detected around Maui, whereas the remaining 3 individuals (one shark was not tagged until early 2013) were only detected around Oahu (Figure 16). We used a Hawaii tiger shark age and growth curve (Meyer et al. 2014) to estimate the age of each of the legacy sharks at tagging, and then to estimate their age and size at the date of their first detection around Maui during the current (2013-2015) project. Although we cannot determine whether any of these sharks visited Maui during the July 2008-October 2013 period when no acoustic monitoring occurred around that island, all 5 legacy sharks were estimated to be sexually mature when first detected around Maui during the current 2013-2015 project (Table 3).

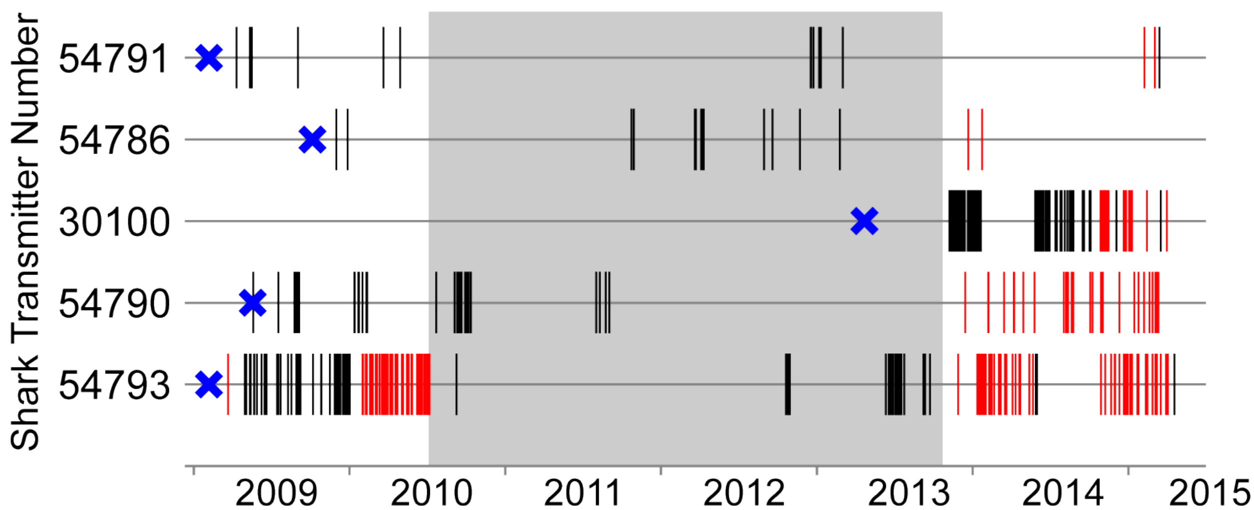


Figure 16. Abacus plot showing multi-year detections of five 'legacy' tiger sharks tagged on Oahu (2009-2013) and subsequently detected around Oahu (black vertical lines) and Maui (red vertical lines). Shaded section indicates period of no acoustic monitoring around Maui. Blue crosses indicate capture and tagging dates.

Site fidelity to receiver locations

SFI values ranged among individuals and receiver sites from 0 to 37.9%, and the highest SFI values for each individual were typically spatially-clustered among adjacent receivers (consistent with tiger shark use of home ranges with well-defined core areas – Figure 17). Some receiver sites (e.g. Palauea Deep, Figure 17) had relatively high SFI values for multiple sharks (suggesting core use areas of multiple individuals were overlapping). Tagging-island had a significant influence on both mean and maximum SFI values, and post hoc testing revealed significant differences in site fidelity between all islands except FFS versus Hawaii, and Maui versus Oahu (Table 7), suggesting a broad dichotomy in tiger shark site fidelity among islands, with relatively high mean SFI values observed around Maui and Oahu, and relatively low mean

SFI values observed around Hawaii Island and at FFS. For example, sixteen (84%) of 19 observed SFI values exceeding 20% (equivalent to a shark visiting at least once every 5 days) were at sites around Maui, with the remaining three at sites around Oahu (Figure 17). By island, the highest SFI values observed for any shark at any receiver site were 37.9% (Maui) , 26.6% (Oahu) , 17.4% (FFS) and 6.1% (Hawaii Island). The highest SFI value observed (37.9% at Makena Pt., Maui) is equivalent to this shark (a 246 cm TL female) visiting Makena every 2-3 days. Sixteen (64%) of 25 Maui-tagged sharks had SFI values >10% (equivalent to at least one visit every 10 days) at multiple receiver sites, including inshore sites at Makena, Palauea and Kalama (Figure 17), whereas SFI values >10% were only documented in 33% of Oahu-tagged sharks, 11% of FFS-tagged sharks and none of the Hawaii Island-tagged sharks.

Table 7. Results of one-way Analysis of Variance examining the influence of shark tagging island on overall average Site Fidelity Index (SFI) and average maximum SFI values. Note that mean SFI data exhibited unequal variance among islands. This was accounted for by using a Welch's ANOVA (with post-hoc Games-Howell test). Maximum SFI was evaluated using a normal one-way ANOVA (with post hoc Tukey's HSD).

		N	**Mean**	**SE**
Mean SFI	FFS	38	1.31[a]	0.22
	Oahu	12	3.72[b]	0.91
	Maui	23	6.34[b]	0.74
	Hawaii	11	0.80[a]	0.09
Max SFI	FFS	38	3.70[a]	0.68
	Oahu	12	11.68[b]	2.67
	Maui	23	19.13[b]	2.05
	Hawaii	11	2.78[a]	0.49

Islands without a shared letter were significantly different (Games-Howell test and Tukey's HSD, df = 3, P < 0.05).

	$\mathbf{df}_{among}$	$\mathbf{df}_{within}$	$\boldsymbol{F}$	$\boldsymbol{p}$
Mean SFI*	3	33.4	42.4	< 0.0001
Max SFI	3	80	27.6	< 0.0001

*Welch's ANOVA

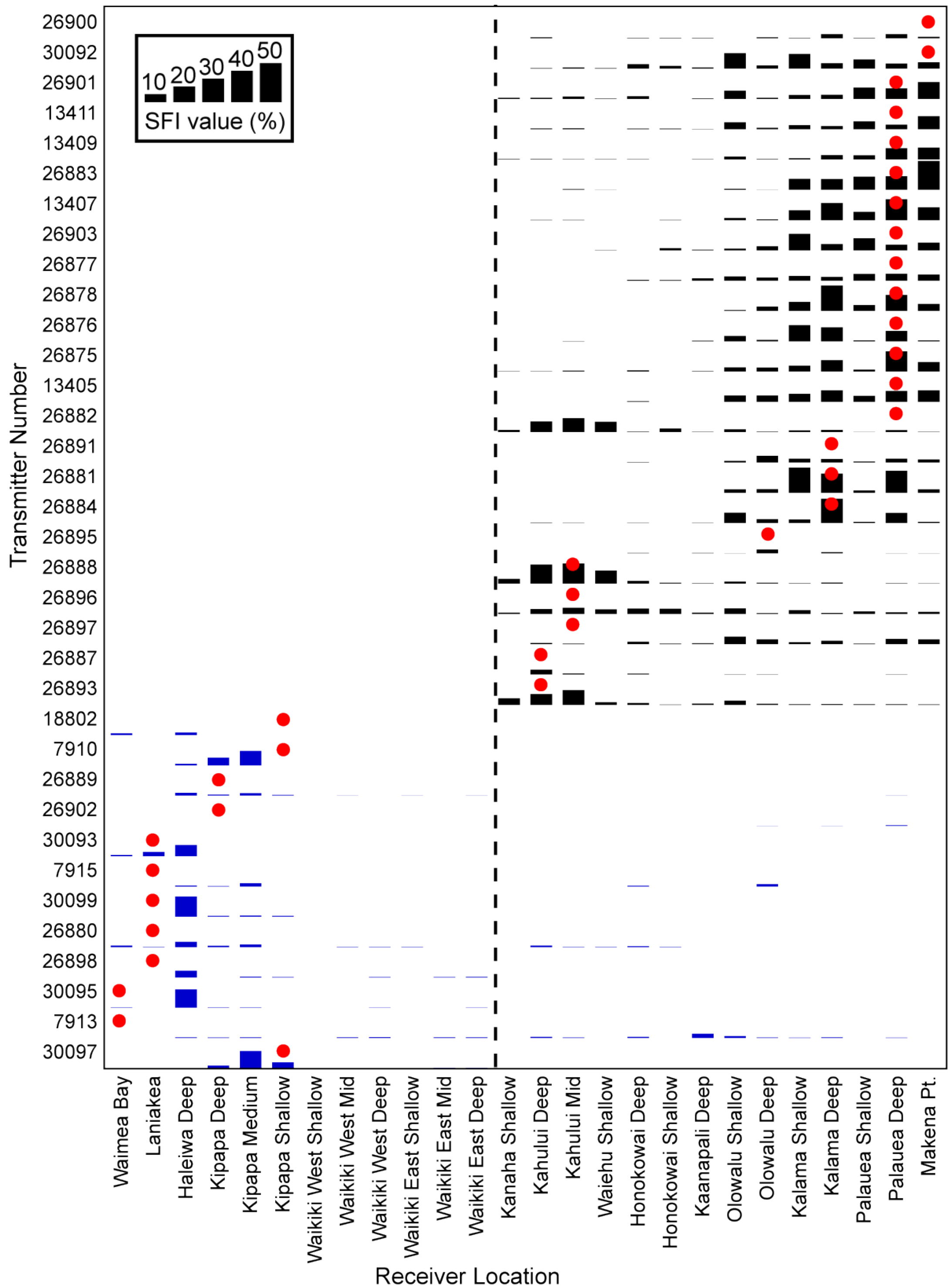


Figure 17. Matrix plot illustrating Site Fidelity Index (SFI) values for all Maui and Oahu-tagged sharks on all Maui & Oahu receivers. The blue bars indicate sharks tagged around Oahu, black bars are sharks tagged around Maui. Red points indicate the receiver station closest to the capture/tagging location of each shark. The dashed line bisecting the plot indicates the boundary between islands (Oahu receivers to the left, Maui receivers to the right).

GLMM analyses of the proportional component of SFI data (i.e. when a shark is detected, what factors influence how often it is detected?) produced models which were very weakly predictive (percent deviance explained was only 2.6% and -0.5% for the best averaged two and four-island models respectively). However, models exploring the binary (presence/absence) component of SFI data (i.e. what factors determine whether or not a shark is ever detected?) were more robust, explaining 53.5% and 31.5% of deviance for two and four-island models respectively. All models were significantly better than the null model, and model averaging was conducted on 7 two-island models and 3 four-island models that best fitted the data ($\Delta AIC_c < 2$).

(A) Two-island models - Binary (presence/absence) component

Whether or not a tiger shark was detected at a receiver site was significantly influenced by the distance between the shark tagging location and receiver site (probability of presence declined with increasing distance from tagging site)(Table 8, Figure 18).

(B) Four-island models

In contrast, the four-island models revealed that tagging island and the interaction of distance between the shark tagging location and receiver site significantly influenced whether or not a tiger shark was detected at a receiver site (Table 9). Sharks tagged around Oahu and Maui had a significantly higher probability of detection than FFS (Table 9, Figure 19). Model averaging also indicated that the interaction between receiver depth and distance between tagging location and receiver site had a significant effect on the probability of detection with a higher probability of detection at deeper sites near tagging location (Table 9, Figure 20). However, effects of receiver depth on detection probability in the four-island models need to be interpreted with caution because of the narrower, shallow-skewed depth range of receiver deployments at FFS and Hawaii Island compared to Maui and Oahu (Table 6).

Frequency and duration of visits to receiver locations

Individual tiger sharks made generally infrequent (overall average of 1 visit every 24 days) and short (overall average of 13.6 minutes in duration) visits to receiver sites. Visits ranged in duration from the nominal minimum of 7.7 minutes to 264.2 minutes, with the longest visits (>90 mins, n = 17) to MHI locations occurring primarily at deep receivers around Oahu (n = 4) and Maui (n = 8), but also at several shallow sites including Kalama (n = 2) and Makena Point (n = 2), Maui, and Honokohau Channel (n = 1), Hawaii Island. Visits to shallow ocean recreation sites around Oahu and Maui ranged in duration from 7.7 minutes to 139.2 minutes, with an overall average visit duration of 11.8 minutes, and each individual visiting on average every 13.3 days. It should be noted that these are average individual patterns, and total shark presence at any location is the sum of visits by multiple individuals (i.e. raw detection frequencies – see description above in '*2013-2015 Maui-Oahu acoustically-tagged sharks*').

Table 8. Spatial and biological (shark size and sex) effects on tiger shark probability of presence from averaged, best-fitting, two-island models. Predictor variables were mean centered and scaled for comparison. Asterisks indicate a significant effect (P < 0.05) on probability of tiger shark presence at acoustically-monitored sites around the islands of Maui and Oahu.

	Estimate Std. ±SE	**Z value**	**P value**	**Relative importance**
(Intercept)	0.000 ± 0.000	NA	NA	-
Depth	-0.069 ± 0.315	0.220	0.826	0.54
DistTagRec	-3.049 ± 0.257	11.874	<2e-16 ***	1.00
IslandOahu	1.224 ± 1.168	1.048	0.295	0.70
SexMale	-0.669 ± 1.087	0.615	0.539	0.65
Depth:SexMale	0.409 ± 0.449	0.911	0.362	0.54
Depth:DistTagRec	-0.011 ± 0.080	0.144	0.886	0.09
Total Length	-0.008 ± 0.140	0.056	0.955	0.08

Table 9. Spatial and biological (shark size and sex) effects on tiger shark probability of presence from averaged, best-fitting, four-island models. Predictor variables were mean centered and scaled for comparison. Asterisks indicate a significant effect (P < 0.05) on probability of tiger shark presence at acoustically-monitored sites around the islands of Maui, Oahu, Hawaii Island and French Frigate Shoals atoll.

	Estimate Std. ±SE	***Z* value**	***P* value**	**Relative importance**
(Intercept)	0.000 ± 0.000	NA	NA	-
Depth	1.014 ± 0.290	3.500	<0.001***	1.00
DistTagRec	-2.665 ± 0.219	12.175	<2e-16***	1.00
IslandHawaii	1.917 ± 1.030	1.861	0.063	1.00
IslandMaui	3.144 ± 0.886	3.546	<0.001***	1.00
IslandOahu	4.071± 1.042	3.903	9.49e-05***	1.00
Depth:DistTagRec	-0.379 ± 0.191	1.984	0.047 *	1.00
SexMale	-0.128 ± 0.407	0.315	0.753	0.26
Total Length	-0.017 ± 0.137	0.126	0.900	0.20

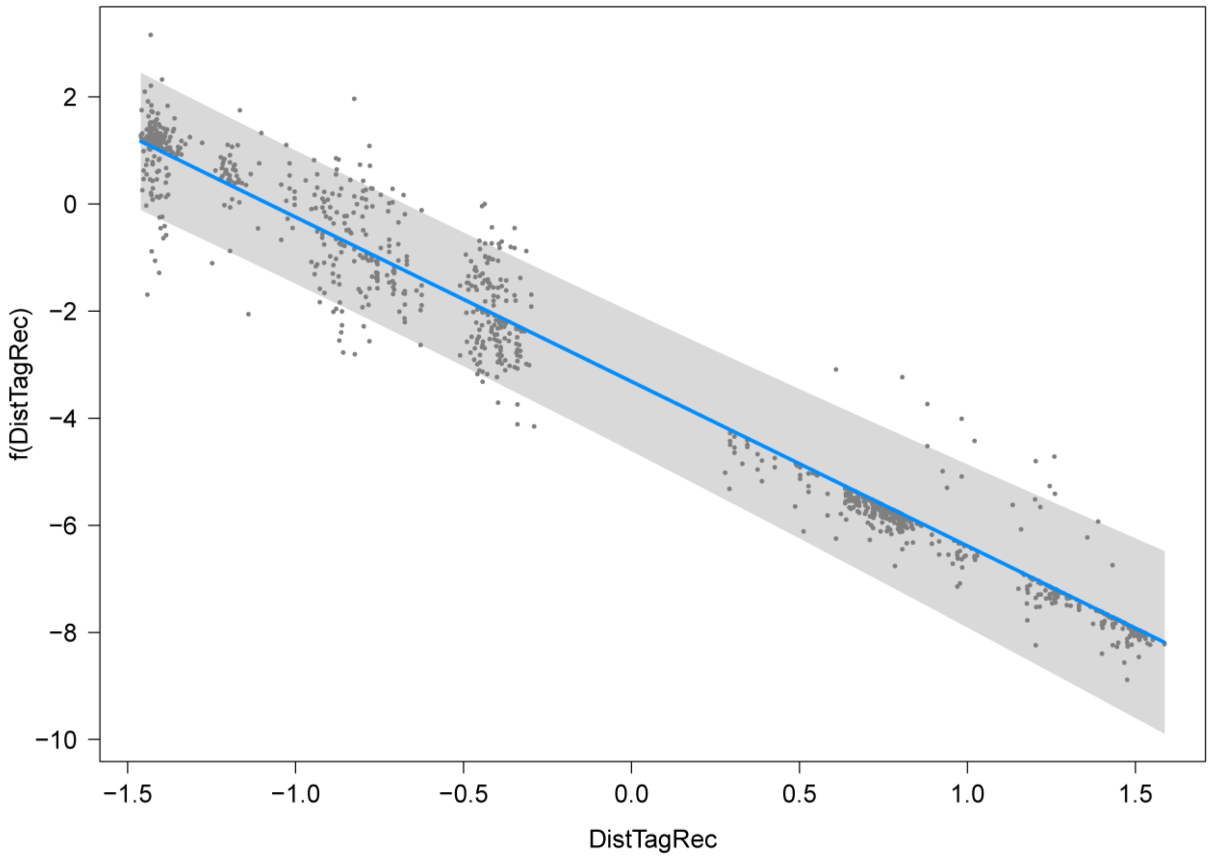


Figure 18. Modelled influence of distance between tagging site and receiver location on the probability of presence of tiger sharks at receiver locations around Maui and Oahu from October 2013 to June 2015. The slope line represent mean presence, shading indicates 95% confidence intervals and points are partial residuals. Distance values on axes have been mean-centered and scaled.

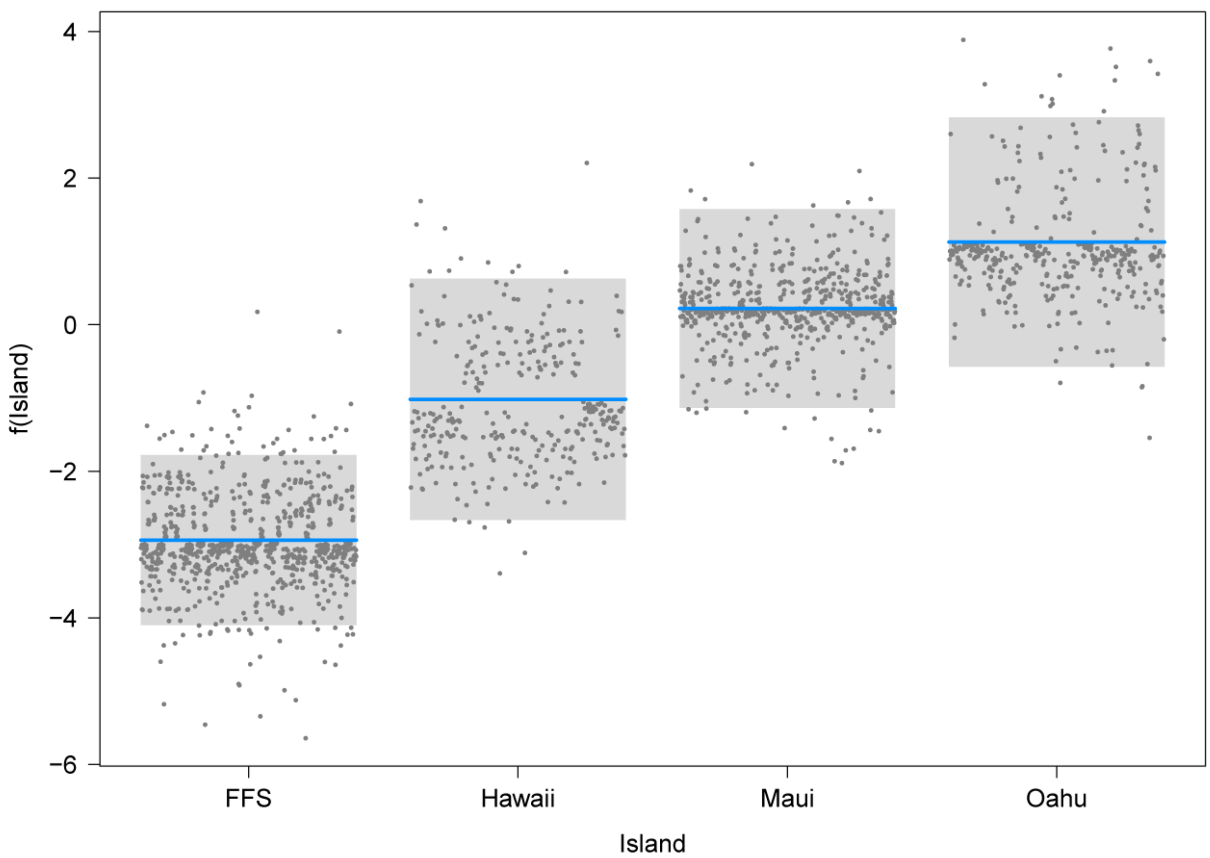


Figure 19. Modelled influence of island on the probability of presence of tiger sharks at receiver locations around Maui, Oahu, Hawaii Island and French Frigate Shoals atoll. Lines represent mean presence, shading indicates 95% confidence intervals and points are partial residuals.

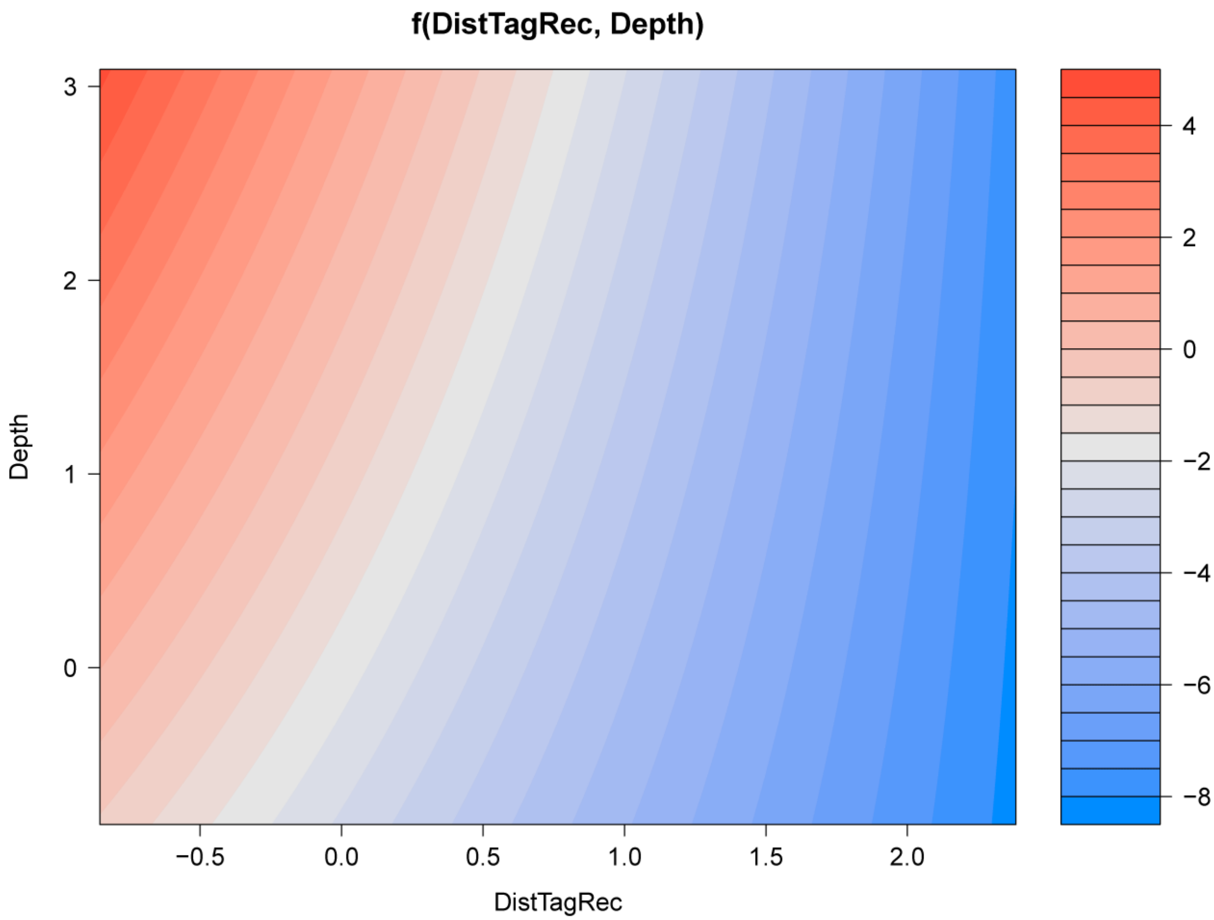


Figure 20. Bivariate plot of modelled influence of the interaction between receiver depth and the distance between shark tagging location and receiver site on the probability of presence of tiger sharks at receiver locations around Maui, Oahu, Hawaii Island and French Frigate Shoals atoll. Axis distance and depth values are centered and scaled.

Tagging island had a significant influence on both frequency and duration of tiger shark visits to receiver sites (Tables 10 & 11). Both the overall mean and average maximum number of daily visits were higher for sharks tagged off Maui (overall mean = 1 visit every 12.8 days, average max = 4.6 visits per day) than any other island (Table 10), but only significantly higher than for sharks tagged around Hawaii Island and FFS. Mean frequency of daily visits was significantly higher for sharks tagged around Oahu than sharks tagged either at FFS or off Hawaii Island, but there were no significant differences in the average maximum number of daily visits to receiver sites between sharks tagged at FFS, Oahu or Hawaii Island (Table 10). Average duration of visits to receiver sites was in the 10-20 minute range for all 4 islands, and average maximum visit duration ranged from 35 minutes (Hawaii Island) to 84 minutes (Maui)(Table 11). Post hoc testing revealed significant differences in mean visit duration between all islands except Maui and Oahu, whereas significant differences in average maximum visit duration only occurred between Maui and Hawaii, and Maui and FFS (Table 11). GLMM analysis of mean visit duration produced models that were very weakly predictive, with best fitting averaged models explaining only 0.8% and 0.3 % of deviance from the null model for two and four-island models respectively.

Time series results

Diel patterns

Tiger sharks were detected at shallow ocean recreation sites around Maui at all times of the day and night, whereas shark bites only occurred during daylight hours, with 71% of bites occurring between 0900 and 1600 (Figure 21). Kolmogorov-Smirnov two sample tests indicated that the diel frequency of sharks detected was not significantly different from the null frequency (an equal number of sharks detected across all hour bins) at any of the Maui ocean recreation sites, indicating no diel influence on the overall numbers of sharks visiting these locations.

Seasonal patterns

Kolmogorov-Smirnov two-sample tests indicated no significant influence of season on the number of Maui-tagged tiger sharks detected around Maui, whereas there was a significant (D = 0.8333, P <0.001) difference between the observed monthly frequency of Oahu-tagged tiger sharks detected around Maui and the null frequency (an even number of sharks detected each month). The number of Oahu-tagged tiger sharks detected around Maui had a distinct winter peak coinciding with tiger shark mating season (Figure 22). The number of Oahu-tagged sharks detected around Oahu exhibited a slight dip corresponding to the January peak seen around Maui (Figure 22), suggesting winter movements of Oahu sharks to Maui .

Table 10. Results of tests comparing overall mean and average maximum visit frequency (visits per day) to receiver sites among islands. An unequal variance F-test (Welch's ANOVA with post-hoc Games-Howell test) was used to compare overall mean visit frequency to receiver sites among islands. Due to non-normality of transformed residuals, a non-parametric Kruskal-Wallis test (with Wilcoxon rank-sum test) was used to compare average maximum visit frequency among tagging islands.

		N	**Mean**	**SE**
Mean Visits per Day	FFS	38	0.016[a]	0.003
	Oahu	12	0.049[b]	0.012
	Maui	23	0.078[b]	0.010
	Hawaii	11	0.011[a]	0.001
Max Visits per Day	FFS	38	3.87[a]	0.70
	Oahu	12	3.58[ab]	0.63
	Maui	23	4.57[b]	0.38
	Hawaii	11	3.18[a]	0.62

Islands without a shared letter were significantly different (Games-Howell test and Wilcoxon rank-sum test, df = 3, $P < 0.05$).

	$\mathbf{df}_{\boldsymbol{among}}$	$\mathbf{df}_{\boldsymbol{within}}$	$\boldsymbol{F}$	$\boldsymbol{p}$
Mean Daily Visit Frequency	3	32.8	37.7	< 0.0001

	df		$\boldsymbol{H}$	$\boldsymbol{p}$
Max Daily Visit Frequency*	3		8.54	0.0361

***** Kruskal-Wallis test

Table 11. - Results of one-way Welch's ANOVA (with post-hoc Games-Howell test) examining the influence of shark tagging island on overall mean and average maximum visit duration (min) to receiver sites.

		N	**Mean**	**SE**
Mean Visit Duration (min)	FFS	38	13.1[a]	0.4
	Oahu	12	19.1[b]	1.7
	Maui	23	14.3[b]	0.3
	Hawaii	11	9.5[c]	0.3
Max Visit Duration (min)	FFS	38	67.7[a]	10.3
	Oahu	12	68.1[ab]	11.8
	Maui	23	84.4[b]	7.1
	Hawaii	11	35.0[a]	9.0

Islands without a shared letter were significantly different (Games-Howell test, df = 3, P < 0.05).

	$\mathbf{df}_{\boldsymbol{among}}$	$\mathbf{df}_{\boldsymbol{within}}$	$\boldsymbol{F}$	$\boldsymbol{p}$
Mean Visit Duration (min)	3	27.4	34.6	< 0.0001
Max Visit Duration (min)	3	28.6	8.4	0.0004

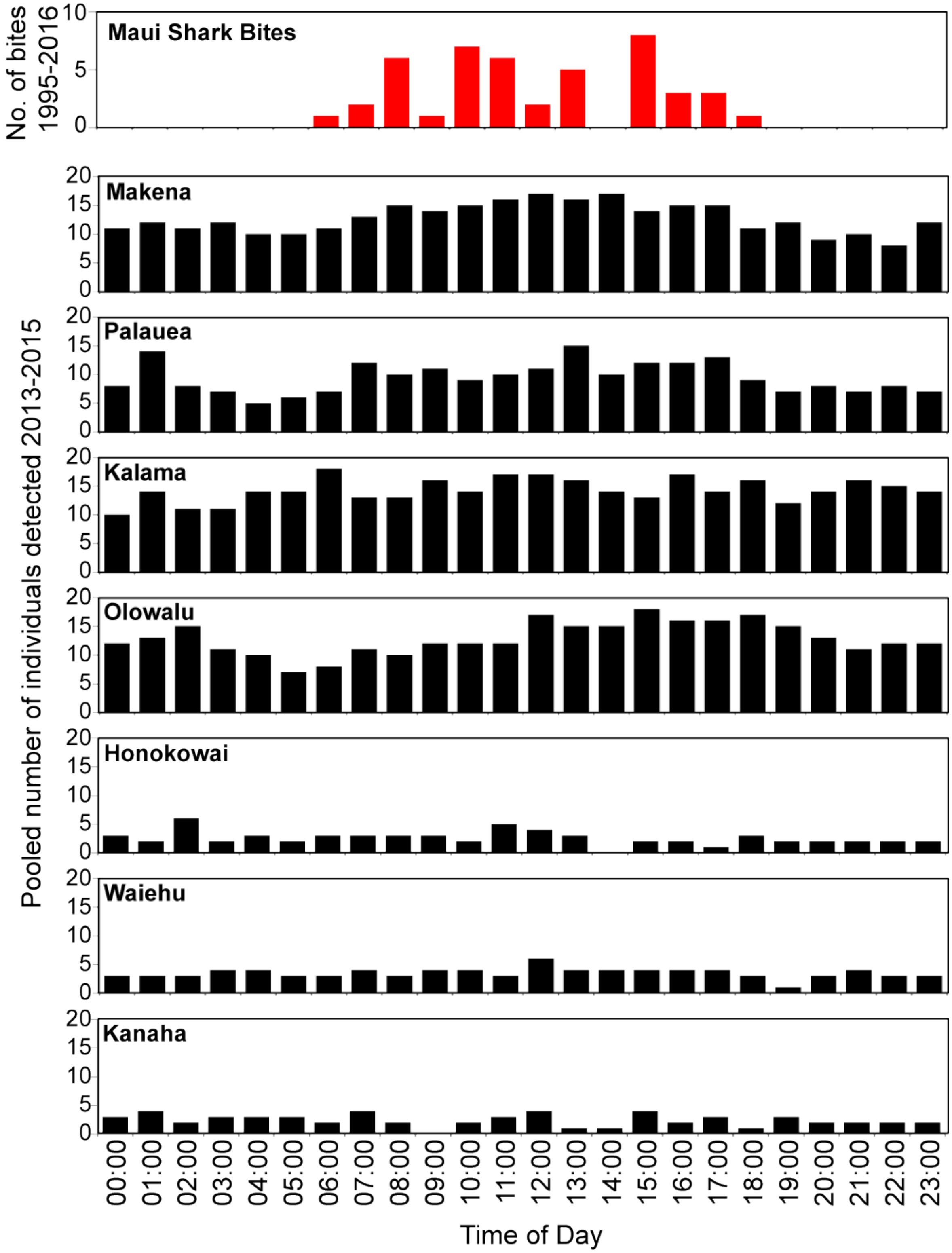


Figure 21. Diel patterns of shark bite incidents around Maui 1995-2016 (top in red) and pooled numbers of tagged tiger sharks detected at ocean recreation sites around Maui 2013-2015 (black).

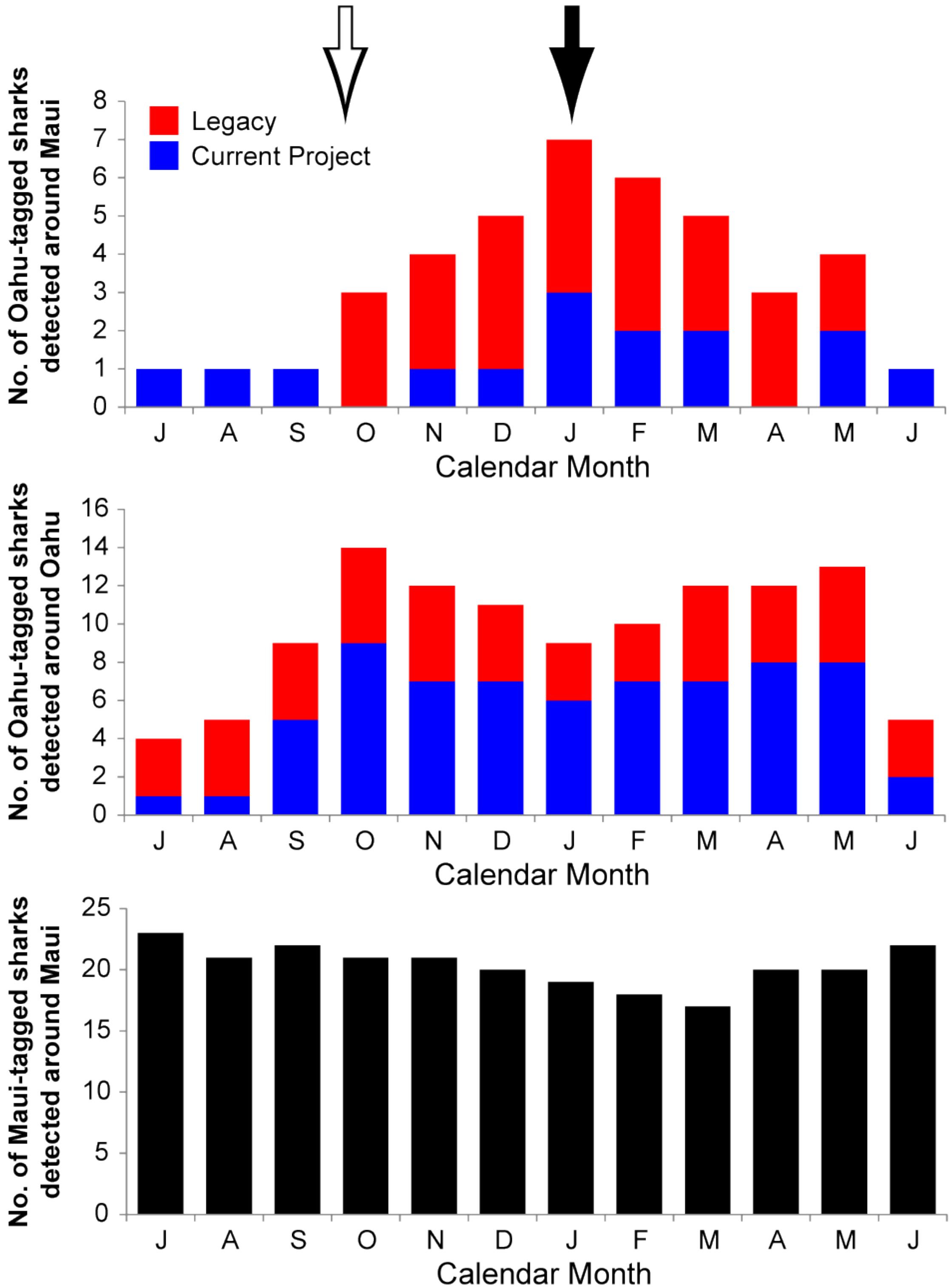


Figure 22. Monthly number of Oahu-tagged tiger sharks detected around Maui. Blue: sharks tagged during current 2013-2015 project. Red: 'legacy' sharks tagged around Oahu 2009-2013. Open arrow: peak tiger shark pupping season (Whitney and Crow 2007). Closed arrow: peak tiger shark mating season (Whitney and Crow 2007).

The number of Oahu-tagged sharks detected around both Maui and Oahu was lowest during the months of July to September (Figure 22). This may be due in part to the timing of shark tagging and receiver downloads during the current project (we primarily tagged sharks around Oahu in September and October 2014, and then did our last receiver downloads in June 2015, so we had no opportunity to detect these sharks in July or August). However this does not apply to 'legacy' tiger sharks tagged around Oahu before the current project started, and would only drive down numbers for July and August (the missing months for the current batch of Oahu-tagged tiger sharks), thus should have no influence on the January Maui peak/ Oahu dip in detections of Oahu-tagged sharks around Maui.

Camera results

The shark-mounted video camera was deployed on two tiger sharks during the course of the study. The first deployment (on a 323 cm TL female captured off Makena, Maui) resulted in a premature detachment and no useable footage. The second deployment was on a large (436 cm TL) male tiger shark captured off Kaneohe Bay (Oahu) in January 2015, during mating season for tiger sharks in Hawaii. The shark had fresh abrasions on one clasper suggesting that it been actively mating shortly before capture. The camera successfully filmed for 11h (0710 – 1810) on day 3 (Jan 11, 2015) of the deployment, before detaching from the shark, and surfacing off Kahuku Point, Oahu at approximately 2325 (time of first satellite fix on the floating package) in an area that satellite tracking results identified as a core home range area for several Oahu-tagged tiger sharks (see example in top-left panel Figure 10). Most of the camera footage showed the shark swimming slowly and steadily, ranging vertically between the surface and benthic habitats in which a wide variety of coral reef fishes were visible. The shark made no attempt to chase any of these fishes, nor did the fishes show any obvious flight behavior. At 1243 the shark suddenly accelerated along the bottom in a straight-line, burst-swimming event lasting 22 seconds, and culminating in tight circling close to the bottom for 22 seconds. At the end of this spiral swimming behavior, an apparently- mature (based on size relative to other natural features in the video) female tiger shark came into camera view at close proximity to the male shark (Figure 23). The male tiger shark swam briefly up over the dorsal surface of the female, with the camera revealing apparent mating scars behind her dorsal fin (Figure 23). The female shark appeared to avoid contact with the male, and displayed a nictitating membrane response during the brief (8 sec), close-proximity encounter (Figure 23). The male then continued to follow the female for a further 5.85 minutes, during which the camera recorded brief additional glances of her in the distance. The total encounter (start of burst swimming to final image of female) lasted 6.75 minutes.

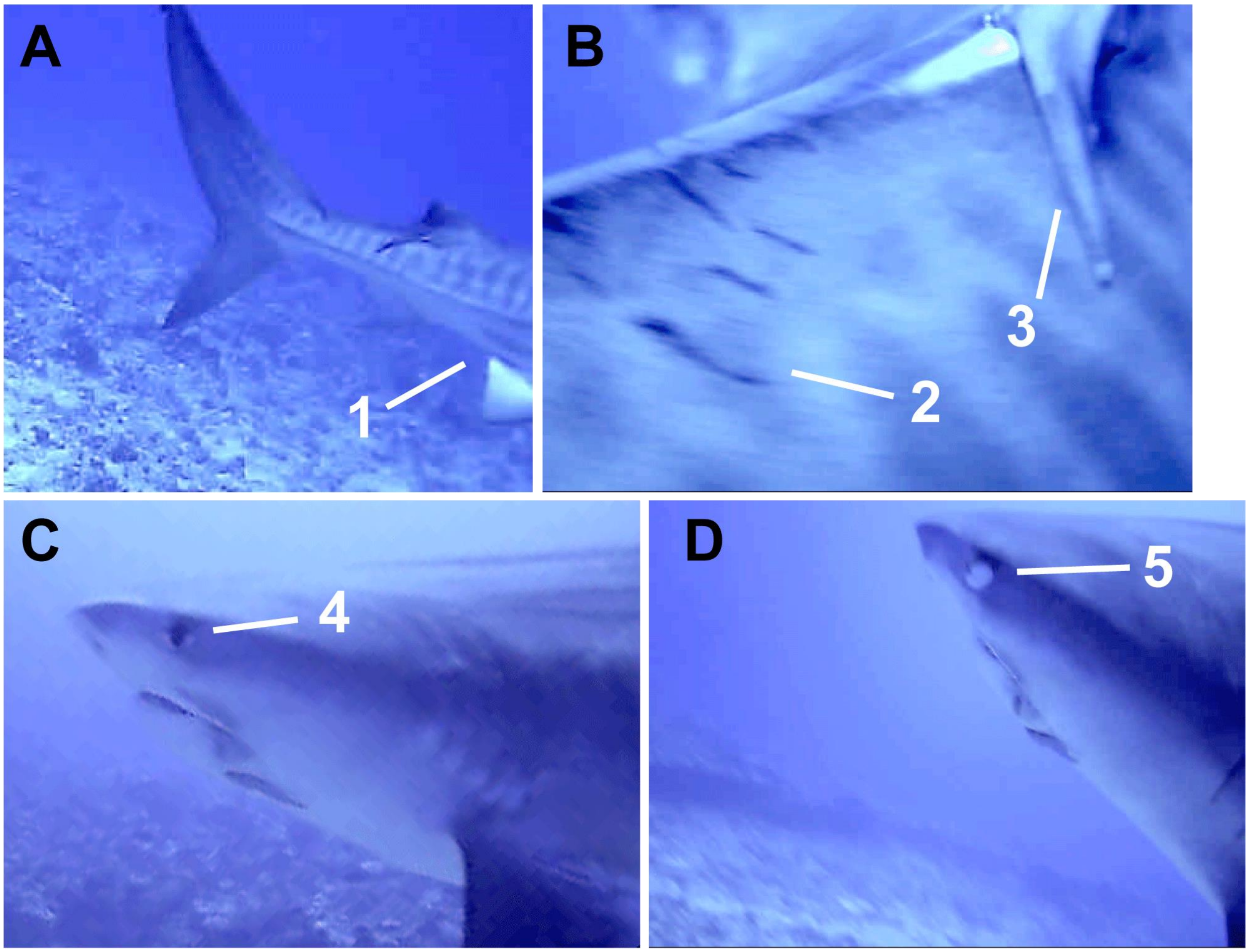


Figure 23. Frame grabs from video recovered from shark-mounted camera deployed on 436 cm TL male tiger shark captured off Kahuku in January 2015. A. Rear of tiger shark approached by camera shark showing no evidence of claspers on the pelvic fins (1), indicating this shark is female. B. View of dorsal surface showing evidence of mating scars (2) behind the trailing edge of the dorsal fin (3). C. Profile view of female tiger shark as camera shark approaches, showing nictitating membrane is retracted (4). D. As camera shark makes closer approach to female tiger shark, nictitating membrane can be seen entirely-covering the eye (5).

Public Outreach

Project goals and results were detailed in public lectures at Maui Ocean Center (July 2014), Myiami Theater (November 2014) and at the Waikiki Swim Club (March 2016). In addition, project results were presented and discussed at international scientific conferences held in Britain (Shark Symposium of the Fisheries Society of the British Isles) and Canada (International Fish Telemetry Conference) in July 2014.

Interviews describing the project were also given to a broad array of local, national and international media, including Maui News Now, West Hawaii Today, Star Advertiser, Honolulu Magazine, Hawaii News Now, KITV, KHON, Los Angeles Times, CBS news, Geo Magazine, New Scientist Magazine, National Geographic Magazine, German public radio (ARD) and Voice of America among others.

Between the initial launch in November 2013 and April 2016, people in 72 countries visited the PacIOOS tiger shark tracking web page, generating 431,178 total unique page views of the main Tiger Shark Tracking page and over 1,363,000 engagement clicks associated with exploring individual shark tracks. These numbers actually underestimate total use of the site because visits direct to the tracking data pages, without passing through the main page, are not tallied. The average number of daily visits to main page was 337 and the maximum (on November 15, 2013) was 9,222 (30,821 including all engagement clicks). The majority (93.7%) of visits were from the USA (83.4%) and Canada (10.3%), with Hawaii accounting for 36.4% of all visits. The regional distribution of visits was closely connected to the media coverage featuring a link to the tracking page. For example, a Los Angeles Times article on Jan 15, 2014 drove California visitors to the page, generating a spike in visits, and contributing to California visitors accounting for 14.4% of visits overall. Media coverage surrounding shark bite incidents also produced spikes in the number of page visits (Figure 24).

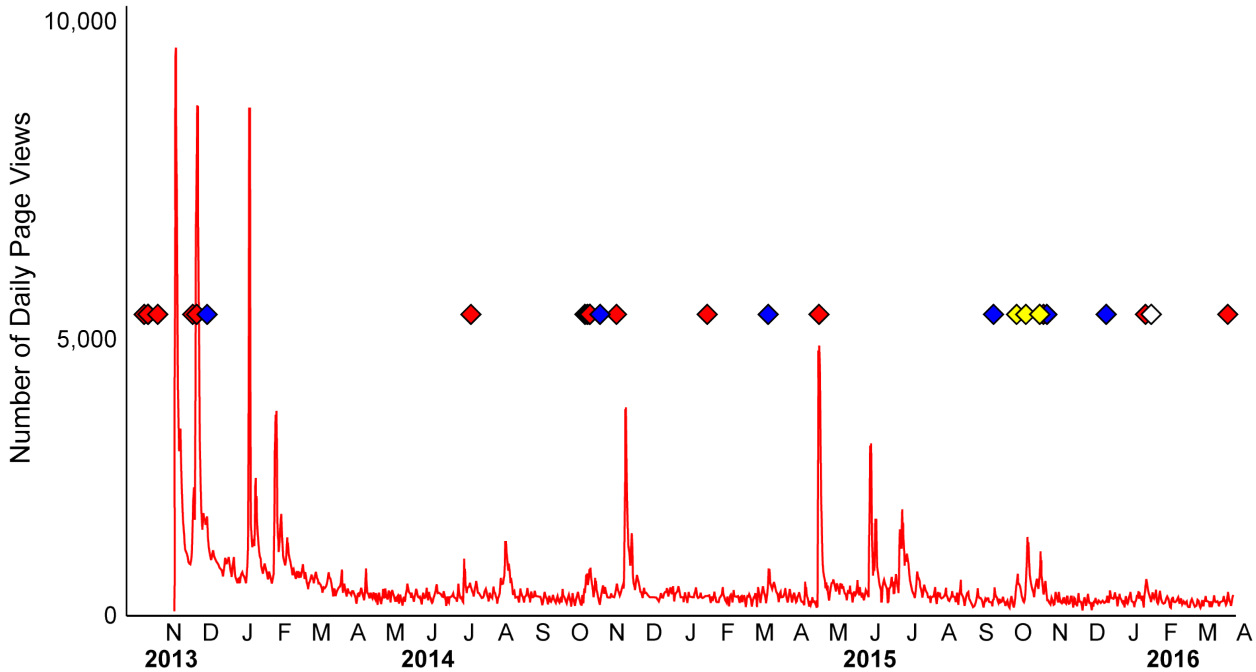


Figure 24. Number of daily visits to the PacIOOS tiger shark tracking page November 2013-April 2016. Colored diamonds indicate dates of shark bite incidents around Hawaii Island (blue), Maui (red), Oahu (yellow) and Kauai (white).

DISCUSSION

Tiger shark movement patterns observed during the current study broadly match those seen during previous studies conducted in Hawaii and elsewhere throughout the species geographic range. Tiger sharks captured around Maui and Oahu exhibited a combination of wide-ranging movements (including movements between islands and extensive open-ocean excursions) and high site-fidelity to coastal habitats around 'home' islands. Wide-ranging movements, including open-ocean crossings of thousands of km, have been previously documented in tiger sharks captured in Hawaii (Meyer et al. 2010, 2014) and elsewhere in the Indo-Pacific (Heithaus et al. 2007, Holmes et al. 2014, Werry et al. 2014) and Atlantic regions (Kohler et al. 1998, Hammerschlag et al. 2012, Vaudo et al. 2014, Lea et al. 2015). We observed long (multi-month), open-ocean residence times for some Maui and Oahu-tagged individuals, and similar duration use of open-ocean habitats has also been previously documented in tiger sharks tagged at FFS, Hawaii (Meyer et al. 2010), and at Bimini (Bahamas) and Challenger Bank (Bermuda) in the Atlantic Ocean (Hammerschlag et al. 2012, Lea et al. 2015). Tiger sharks are also captured in high-seas longline fisheries in both North Pacific (Polovina and Lau 1993), and Atlantic Oceans (Kohler et al. 1998, Beerkircher et al. 2002, Domingo et al. 2016) providing further evidence of the species widespread use of open-ocean habitats.

Although tiger sharks routinely utilize open-ocean habitats in both Atlantic and Pacific oceans, the majority (78.7%) of satellite detections of tiger sharks captured around Maui and Oahu during the present study were in coastal waters over insular shelf habitat. Tiger shark affinity for coastal waters and shelf habitats has been documented in previous studies in Hawaii (Meyer et al. 2009, 2010), Australia (Holmes et al. 2014), the Bahamas and Florida (Hammerschlag et al. 2012), although movements are generally much wider-ranging over the extensive continental shelf areas off Australia and Florida, than over the smaller insular shelf habitats in Hawaii. Conversely, most tiger sharks tagged at Challenger Bank (Bermuda, Atlantic Ocean) predominantly used open-ocean habitat (Lea et al. 2015). These apparently conflicting patterns of open-ocean versus coastal habitat use by tiger sharks may partly stem from the demographic characteristics of sharks tagged in these different studies. For example, eighteen (95%) of 19 highly-migratory tiger sharks tagged by Lea et al. (2015) were mature males, whereas tiger sharks tagged during the current and previous Hawaii studies (Meyer et al. 2009, 2010, Papastamatiou et al. 2013) were mainly (59- 80%) mature females which predominantly utilized coastal habitats. These differences in habitat use between mature males and females are consistent with sex segregation of adult tiger sharks, with females occupying coastal areas, and males occupying offshore habitats (Papastamatiou et al. 2013, Meyer et al. 2014).

During the current study, we documented seasonal patterns of tiger shark movement, with sexually-mature individuals originally captured around Oahu visiting Maui most frequently in winter during peak mating season (Whitney and Crow 2007). A previous analysis of tiger shark movements in Hawaii also found inter-island movements between MHI locations (Oahu, Maui and Hawaii Island) peaked during winter, and additionally identified migrations from the NWHI to the MHI coinciding with tiger shark pupping season during fall (Papastamatiou et al. 2013). We found no evidence of a fall migration from the NWHI to Maui or Oahu, but this was probably due to the very low number of remaining NWHI legacy sharks (3 individuals, Table 3) with active transmitters during the current study (i.e. fall migrations could have occurred undetected by our receivers). Seasonal migrations by tiger sharks have also been documented in the Atlantic (Lea et al. 2015), Indian Ocean (Wirsing et al. 2006) and Pacific (Holmes et al. 2014), and appear to be linked to sea surface temperature, especially in more temperate regions toward the latitudinal limits of tiger shark distribution (Holmes et al. 2014, Lea et al. 2015).

Although we found evidence of seasonal migration to Maui by tiger sharks originally captured around Oahu, we saw no evidence of seasonal migrations by tiger sharks captured around Maui, most of which were highly site-attached to the insular shelf surrounding Maui Nui for the 21 month duration of monitoring. In fact, tiger sharks tagged around Maui typically exhibited greater residency and smaller home ranges than those tagged around other Hawaiian islands, and Hawaii tiger sharks display overall greater residency and smaller coastal home ranges than tiger sharks in most other locations. Site-fidelity to core islands (typically the island of capture) has been previously described for tiger sharks captured at several Hawaiian islands (Meyer et al. 2010 and Papastamatiou et al. 2013), but detailed data were not previously available for tiger sharks captured around Maui. Our current analyses suggest the home ranges of Maui-tagged tiger sharks tend to be largely contained within the extensive insular shelf habitat surrounding Maui Nui, and these home-ranges are generally smaller, with more frequently-utilized core areas, than those of tiger sharks captured around other Hawaiian Islands. Tiger shark home range core areas around Maui are closer to high-use ocean recreation sites than equivalent core areas documented around Oahu. More broadly, there is some evidence of higher tiger shark residency at isolated oceanic islands compared with locations on, or close to, extensive continental shelves. For example, Werry et al. (2014) observed high residency in tiger sharks captured at the remote Chesterfield Islands (Coral Sea), whereas the same study found transient behavior by tiger sharks captured in coastal habitats of New Caledonia and the Australian Great Barrier Reef. Similarly, tiger sharks captured on wide continental shelf habitats in Australia (Holmes et al. 2014) and Florida (Hammerschlag et al. 2012), or at islands close to continent shelf habitats (e.g. Bahamas, Hammerschlag et al. 2012) roam far more extensively than most individuals captured in Hawaii waters (Meyer et al. 2009, 2010, Papastamatiou et al. 2013, this study).

Inter-island and regional differences in tiger shark residency and home range characteristics likely reflect different patterns of resource distribution among locations. Primary resources for tiger sharks include food, conspecifics (for mating) and suitable pupping habitats, and the high residency of tiger sharks observed around Maui suggest all of these resources are available on the extensive insular shelf surrounding the islands of Maui Nui. Reef-associated organisms form the bulk of tiger shark diet in Hawaii (Lowe et al. 1996) and elsewhere (e.g. Simpfendorfer et al. 2001). In Hawaii, coral reef habitats are found to depths of at least 130 m (Kahng et al. 2014), and their horizontal distribution likely broadly mirrors that of the insular shelf (Rooney et al.

2010). As a consequence, the extensive Maui Nui insular shelf (56% of all MHI shelf habitat – Table 1), which is known to support high densities of coral reef fishes (Rooney et al. 2010), may be able to support a larger number of tiger sharks than the smaller areas of shelf habitat surrounding the other MHI. In terrestrial systems, predator home range size is inversely-related to prey density (i.e. home ranges are smaller when prey density is high) in a variety of animals including African lions (Loveridge et al. 2009), Eurasian lynx (Herfindal et al. 2005), and northern spotted owls (Zabel et al. 1995). The generally-smaller tiger shark home ranges and overlapping core areas observed around Maui may indicate higher habitat quality (i.e. prey density) on the extensive Maui Nui shelf than around the other MHI.

Seasonal influxes of tiger sharks from adjacent islands and as far away as the NWHI suggest the extensive Maui Nui shelf habitat is also attractive to tiger sharks from elsewhere in Hawaii, and may be an important 'hub' for tiger sharks within the Hawaiian chain. These migrations peak during both the fall pupping season (Papastamatiou et al. 2013) and the winter mating season (Papastamatiou et al. 2013, this study) for tiger sharks in Hawaii (Whitney and Crow 2007), suggesting reproduction may be driving these seasonal movements. If the Maui Nui shelf does in fact support more tiger sharks than other Hawaiian Islands, this could enhance the probability of encountering conspecifics during mating season, especially where home range cores overlap. Footage from our shark-mounted camera suggests mating may occur in these home range core areas.

Generally, individual tiger sharks made infrequent (average of 1 visit every 13.3 days) and short (average of 11.8 minutes in duration) visits to shallow ocean recreation sites that we monitored around Oahu and Maui. However, overall frequency of tiger shark detections (proportion of monitored days on which any electronically-tagged tiger shark was detected) was higher at monitored ocean recreation sites around Maui (62-80%) than Oahu (<6%). This disparity held true even when accounting for the fact that in this study fewer sharks were tagged around Oahu (15) than Maui (26). Assuming our tagged sharks are only a subset of all tiger sharks in Hawaii coastal waters, our detection frequencies suggest a daily, or near-daily, presence of large tiger sharks in waters adjacent to ocean recreation sites in Maui (especially SW Maui).

Although routinely detected in shallow areas, our tracking data suggest tiger sharks primarily occupy deeper waters (50-100 m depth) when they are over the insular shelf. They are vertically dynamic and make "yo-yo" dives between the seabed and the surface, behavior that has been extensively documented in previous studies in Hawaii (Holland et al. 1999, Nakamura et al. 2011), Australia (Holmes et al. 2014) and the Atlantic Ocean (Vaudo et al. 2014). In all cases, tiger sharks are highly surface-oriented, spending 10-20% of their time within 2m of the surface around Maui during the current study, the majority of their time at depths of <20m in waters off Australia (Holmes et al. 2014) and up to 51% of their time within the upper 5 m of the water column in the Atlantic Ocean (Vaudo et al. 2014).

Overall, our results suggest the extensive Maui Nui insular shelf is an important natural habitat for Hawaii tiger sharks, and consequently large tiger sharks are routinely and frequently present in the waters off ocean recreation sites around Maui. This may explain why Maui has had more shark bites than other Main Hawaiian Islands (Figure 25), although we cannot exclude differences in the numbers of ocean recreation activities between Maui and other islands as the primary cause of inter-island differences in shark bite rates. Despite the natural presence of large sharks in waters around Maui, the risk of shark bite remains relatively low and variable between years. Notably, 2015 saw 2 unprovoked shark bites in Maui waters (compared to 5-8 bites in 2013-2014) even though our tracking data unequivocally show the same large, tagged tiger sharks were present in Maui waters, and visiting Maui ocean recreation sites, from 2013-2015, and sharks from Oahu were also visiting these sites during that period. The fact that relatively few bites occur despite near-daily visits by large tiger sharks to high use recreation sites, suggests that tiger sharks are mostly disinterested in, or actively avoiding, people.

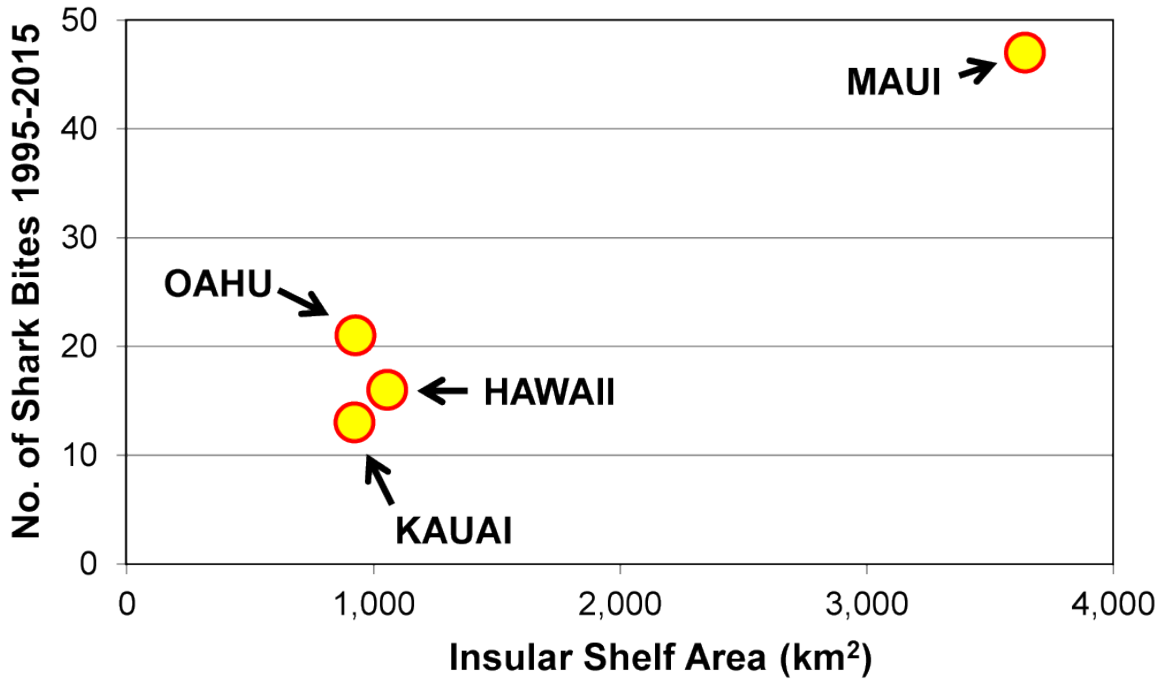


Figure 25. Total number of shark bites 1995-2015 versus the insular shelf area (km^2) of Hawaii, Maui, Oahu and Kauai counties.

Based on historical precedent in Hawaii, culling sharks will neither eliminate nor demonstrably reduce shark bite incidents. For example, the largest historic culling effort in Hawaii (1967-69 Hawaii Co-operative Shark Control and Research Program) removed 280 tiger sharks, including 114 individuals from waters around Oahu (Wetherbee et al. 1994), yet 2 out of 3 documented shark bite incidents in the 1960's occurred off Oahu in 1969, 3 months before, and 5 months after, the conclusion of culling. Our current results further clarify why historical shark culling was ineffective. Tiger sharks found around Maui exhibit a broad spectrum of movement patterns ranging from resident to highly transient. This mixture ensures a constant turnover of sharks at coastal locations. Sharks removed by culling are soon replaced by new individuals from both local and distant sources.

The most pragmatic approach to mitigating shark bite risk is probably to pro-actively raise public awareness of tiger shark presence in Hawaii waters (equivalent to informing people of predator presence in terrestrial wilderness habitats such as North American forests; Lackey and Ham 2004, Dunn et al. 2008), and explain what people can do to reduce bite risk. For example, making our tiger shark satellite tracks publicly-available on the Pacific Islands Ocean Observing System (PacIOOS) shark tracking website, showed people in 72 countries that large tiger sharks are routinely present in coastal waters of Maui and Oahu. Efforts are currently underway to inform and educate people about the risks of ocean-drownings in Hawaii, a natural hazard that is an order of magnitude more frequent than shark bites. These efforts could be expanded to include shark bite facts. A well-informed public can make their own fact-based decisions on ocean use.

Recommendations for future research

Some of the legacy sharks included in this study were tagged in 2009 and, although relatively few in number, gave us important insights into longer-term (up to 6 years) patterns of tiger shark movements around Maui and Oahu. Tiger sharks tagged around Maui during the current project have acoustic tags that should last until 2023-2024, and continued monitoring of their movements will determine whether the high residency documented during the 21 month monitoring period of the current project persists for up to a decade. This is an important question because female tiger sharks in Hawaii are believed to have a 3 year reproductive cycle (i.e. each mature female pups every third year, Whitney and Crow 2007), and movements linked to reproduction could be occurring at longer timescales than the current project. Similarly, to help refine our understanding of the scale of the fall migration of female tiger sharks to Maui and Oahu from elsewhere in Hawaii, additional mature females should be tagged with long-life (e.g. 10 year) transmitters at multiple locations along the length of the Hawaiian Archipelago.

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