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Characterization of Shark Movements on a Mesophotic Caribbean Coral Reef and Temporal Association with Fish Spawning Aggregations

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CHARACTERIZATION OF SHARK MOVEMENTS ON A MESOPHOTIC CARIBBEAN CORAL REEF AND TEMPORAL ASSOCIATION WITH FISH SPAWNING AGGREGATIONS

By

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Abstract

Habitat use of mesophotic coral reefs by sharks is largely unknown. However, it is well established that mesophotic reefs are the site of spawning aggregations for many species of teleost fish. These aggregations represent seasonal concentrations of potential prey biomass that may influence the habitat use of predatory species such as large sharks. I employed acoustic monitoring to examine the movements of three shark species [lemon shark (*Negaprion brevirostris*), tiger shark (*Galeocerdo cuvier*), and Caribbean reef shark (*Carcharhinus perezi*)] to determine 1) the comparative spatiotemporal patterns of mesophotic reef habitat use by the three shark species and 2) the spatiotemporal relationship between these sharks and grouper spawning aggregations at a fish spawning aggregation (FSA) site (Hind Bank and Grammanik Bank) along the southern reef shelf edge off St. Thomas, United States Virgin Islands (USVI). Tiger and lemon sharks were detected across nearly the entire acoustic array, which spanned ~ 1060 km^2. When present, Caribbean reef sharks used a much smaller activity space, composed exclusively of mesophotic reef habitat located within FSA sites. Individuals from all three species were typically detected for stretches of several consecutive days, while periods without detections usually lasted less than one week. Lemon sharks were present at the FSA site more often during the grouper spawning season (Dec-May) than the non-spawning season (Jun-Nov), but showed no preference toward specific areas within the FSA site, which varied by location and grouper species composition. In contrast, there was no relationship between the presence of tiger and Caribbean reef sharks at the FSA site and the grouper spawning season. My results suggest that despite different habitat use

patterns and varying degrees of fidelity, this mesophotic reef serves as an important habitat to all three shark species.

Keywords: lemon shark, tiger shark, Caribbean reef shark, grouper, acoustic telemetry, habitat use, US Virgin Islands, Puerto Rico

Introduction

Mesophotic reefs, which have been loosely defined as ranging in depth from 30 m to depths where light levels are too low for coral phototrophic symbionts to sustain coral growth via photosynthesis [1], may make up a considerable amount of available reef habitat. Although mapping of mesophotic coral reef ecosystems is in its infancy, more than 186,000 km^2 of potential mesophotic coral habitat has been identified in U.S. waters alone [2]. However, because of technological limitations and safety issues associated with working near or below the depth limits of SCUBA diving, studies on mesophotic reef ecology have lagged greatly behind studies on shallow reefs [3-5].

Large sharks are upper level predators [6] and likely play an important structural role in marine ecosystems [7,8], including coral reef systems [9,10]. Because movement patterns determine the spatial and temporal extent of species interactions, understanding the movements and habitat use of these predators is a necessary step to determining their role in ecosystems. Although shark movements and habitat use have been studied in several shallow coral reef systems [11-14], little is known about how sharks use mesophotic reefs. Given the large amount of mesophotic reef habitat that exists and that worldwide many shark populations are declining [15,16], studies of shark movements on mesophotic reefs are of increased importance.

There are many factors that can affect movements and habitat use of mesophotic reefs by sharks. One such factor that can vary spatially and temporally is prey distribution. Fishes are an important component of the diets of many sharks [6], and mesophotic reefs are important habitats for many fishes, particularly during spawning. These spawning fishes seasonally form large fish spawning aggregations (FSAs) [17]. FSAs can be composed of hundreds to thousands of individuals and are highly predictable in both timing and location [17]. Such large and predictable prey aggregations have been known to attract shark species [11,18,19] and may similarly influence shark movements on mesophotic reefs.

The insular slope reefs of Puerto Rico and the United States Virgin Islands (USVI) are located predominantly at mesophotic depths (i.e., 30 – 100 m) [20] and are an ideal location to examine the movements of sharks, which occur in high densities in this area, on mesophotic reefs [21]. These reefs are also relatively undisturbed by anthropogenic influences because of the reef's considerable distance from land, runoff and other pollutants [20,22]. In addition, several well-studied FSAs are found on the mesophotic reefs south of St. Thomas, USVI, allowing for examination of the association of sharks and FSAs.

Here I describe the mesophotic reef use of three shark species along the Puerto Rico-Virgin Islands platform using passive acoustic monitoring. Specifically, my goals were to determine 1) the comparative spatiotemporal patterns of mesophotic reef habitat use by the three shark species and 2) the spatiotemporal relationship between sharks and grouper aggregations at fish spawning aggregation sites (Hind Bank and Grammanik Bank) along the southern reef shelf edge off St. Thomas, USVI.

Methods and materials

Study Site

This study was conducted along the mesophotic reef located on the southern insular shelf edge of the Puerto Rico-Virgin Islands platform, spanning ~100 km from St. John, USVI, to Vieques, Puerto Rico (Fig.1). This well developed linear reef is located at depths between 30 m and 45 m and is topographically complex, consisting of large (1–2 m) coral ridge colonies of *Montastraea spp.* [20,23].

The reef system includes two fishing closure areas 12 km south of St. Thomas: Hind Bank Marine Conservation District (MCD) and Grammanik Bank (Fig. 2). Hind Bank MCD (18°12N, 65°00W), established in December 1999, is permanently closed to fishing [17] and encompasses 22.5 km^2 of mesophotic reef, including two distinct spawning areas (referred to herein as MCD West and MCD East) for red hind grouper (*Epinephelus guttatus*) (Fig. 2). Grammanik Bank seasonal closure (18°11N, 64°57W), established in 2005, is closed to fishing between 1 February and 30 April, which coincides with the middle of the grouper and snapper spawning season [24]. Grammanik Bank's seasonal closure boundaries encompass 1.5 km^2 of mesophotic reef and include one multi-species spawning area for yellowmouth (*Mycteroperca interstitialis*), yellowfin (*M. venenosa*), Nassau (*E. striatus*), and tiger grouper (*M. tigris*) [17,25].

Sampling

A total of 30 sharks from three species: 17 tiger (*Galeocerdo cuvier*), seven lemon (*Negaprion brevirostris*), and six Caribbean reef (*Carcharhinus perezi*), were caught using bottom longlines (soak times: 3–4 hours) set adjacent to the Hind Bank MCD and Grammanik Bank FSA sites. Longlines were 366 m long with 25 360-cm long gangions (180 cm of 6-mm polypropylene rope and 180 cm of 3-mm stainless steel cable) terminating in a 16/0 recurved hook. Sharks were brought on board the fishing vessel using a customized slide that allowed easy retrieval and release of sharks and minimized handling. A seawater hose was placed in the mouth of sharks to irrigate the gills while sharks were measured (total length), sexed, and tagged with a conventional ID dart tag.

Acoustic transmitters (V16-3H (Vemco Ltd.) (16 x 64 mm) for sharks >150 cm total length and V13-1H (Vemco Ltd.) (13 x 36 mm) for smaller sharks), which had been coated with a 50:50 mixture of paraffin:beeswax to eliminate rough edges and to make the transmitters inert, were surgically implanted into the body cavity [26]. Transmitters emitted unique coded acoustic signals at 69 kHz with delays of 40–120 seconds and had an estimated battery life of 550–2350 days. The surgical incision was closed with 2–3 nylon sutures and the wound was doused with betadine. The entire procedure from bringing the shark on board to release was completed in approximately 10 minutes. All sharks appeared healthy and swam away upon release.

Acoustic monitoring

An array of VR2W acoustic receivers (Vemco Ltd. Halifax, Nova Scotia), comprising 127 different receiver locations, was deployed between 2007 and 2011 to monitor grouper movements around the FSA site and quantify shark habitat use around the mesophotic reef (Fig.1). Receivers were anchored to the substrate with a cement block and suspended ~1 m off the bottom using a float. Detection range of receivers was approximately 500–1000 m. When a transmitter's signal was detected, receivers recorded time, date, and transmitter ID. Receivers were periodically retrieved and archived data were downloaded. Because this array was initially deployed to monitor the fine-scale movement of grouper during the spawning season, receiver density was highest around the FSA sites. Some receivers were also moved during the non-spawning season to monitor the movement of grouper inshore.

Analysis

Mesophotic reef use

To examine area usage of the mesophotic reef by sharks, minimum convex polygons (MCP), modified to exclude land (Vieques Island, Puerto Rico) were drawn for each shark on the basis of the acoustic receivers on which they were detected using the ArcGIS 10.0 Spatial Analyst tool, Minimum Bounding Geometry (Convex Hull). A one-way analysis of variance (ANOVA) and Tukey's post-hoc test were used to compare the size of MCPs across species. In addition, for each species linear regressions were used to determine if a relationship existed between shark total length and MCP area, as well as length of detection history and MCP area. An MCP was also created using all the receiver detections from a given species to show the total area over which each species was detected across the entire acoustic array.

The detection history of each individual consists of discrete sets of days when a shark is either detected or not detected by acoustic receivers. Each individual alternates between periods when it is detected (i.e. a residence time) and when it is not detected (i.e. absence times). To examine temporal use of the mesophotic reef, I focused my analyses on residence times at and absence times from the entire acoustic array.

The mean residence times of individual sharks were used to compare residence times across species using a one-way ANOVA and Tukey's post-hoc test. Similarly, mean absence times for individual sharks were used to compare absence times across species using a one-way ANOVA and Tukey's post-hoc test. Additionally, to determine if the lengths of periods between days a shark was detected conformed to a random distribution, the number of days between successive days detected was calculated for each shark. By using the number of days between successive days detected, the number of times sharks were present on consecutive days (i.e., 0 days between successive days detected) can also be considered. For each shark, the frequencies of the number of days between successive days detected were compared to a Poisson distribution using a chi square test.

Association with the fish spawning aggregation site

Because of the proximity of spawning areas within the Hind Bank MCD and Grammanik Bank, and the frequency at which individual sharks were detected on receivers at multiple FSA areas on the same day, I combined data from the three spawning areas and considered them a single FSA site for analyses. I examined the temporal relationship between shark presence at the FSA site and the grouper spawning season, by comparing monthly shark presence between grouper spawning months (December - May) and non-spawning months (June - November) using a t-test. Shark presence was defined as the number of days during a month that a shark was detected at the FSA site standardized to a 30-day month to account for differences in month length. Monthly presence values for individual sharks were averaged by species over the five-year study period for use in the t-test.

Because increased presence at the FSA site could be the result of either lengthening the duration of each visit (residence time) to the FSA site or visiting the FSA site more frequently (shorter absence time), residence times were compared between the grouper spawning and non-spawning season for shark species exhibiting greater presence during the spawning season. For each shark, mean residence time was calculated for the grouper spawning and non-spawning season and these values were used in a paired t-test. Likewise, individual mean absence times from the FSA site were also calculated for the grouper spawning and non-spawning season for each individual and used in a paired t-test to determine if absence time decreased during the spawning season.

To determine if shark species that displayed an association with the FSA site during the spawning season exhibited preferential use of a particular spawning area, the percentage of days a given species was detected during the spawning season was calculated for each receiver in each of the three spawning areas (Hind Bank MCD West, Hind Bank MCD East and Grammanik Bank), by dividing the number of days sharks were detected at a receiver by the total number of days that receiver was listening during the spawning season. The percentages were arcsine transformed and compared between the three spawning areas using a one-way ANOVA to determine if a preference existed based on spawning area location. The arcsine transformed values were then compared between the entire Hind Bank MCD (both red hind spawning areas) and Grammanik Bank (one multi-species spawning area) using a t-test to determine if a preference existed based on potential prey species composition.

Results

Of the 30 sharks (17 tiger, seven lemon, six Caribbean reef) implanted with transmitters, analyses were conducted on 18 (10 tiger, six lemon, two Caribbean reef) (Table 1, Appendix 1). The remaining 12 sharks were excluded from analyses because they were detected on receivers for less than three months or not at all. Sharks used for analyses were detected over periods of 703 ± 450 days (mean ± SD) with a range of values from 91 – 1339 days (Appendix 1).

Mesophotic reef habitat use

Area usage of the mesophotic reef array varied considerably among both individuals and species. At the species level, both tiger and lemon sharks were detected over nearly the entire area of mesophotic reef monitored by the acoustic array (MCP areas of 887 km^2 and 863 km^2, respectively), while Caribbean reef sharks were detected over a much smaller area (8 km^2) (Fig. 1, Appendix 2a-g). At the individual level, the two Caribbean reef sharks shared common receivers and were detected within similar geographical areas (Appendix 2g). Individual MCP areas also varied in both size and location for lemon (5.64 – 341.17 km^2) and tiger sharks (20.32 – 387.49 km^2) (Appendix 2b & c, Appendix 2d-f). Mean MCP areas between the three species could not be statistically tested due to the small sample size of two for Caribbean reef sharks. However, mean MCP areas for lemon (152.69 ± 122.52 km^2) and tiger sharks (186.44 ± 129.78 km^2) did not differ (p = 0.877).

MCP areas for tiger sharks showed a positive relationship with the length of detection history (p = 0.034), but no such relationship existed for lemon sharks (p =

0.965). Neither tiger nor lemon shark MCP areas showed a relationship with shark length (p = 0.690 and p = 0.062, respectively). Caribbean reef shark data was excluded from the linear regression analyses due to small sample size (n = 2).

Variations in temporal patterns of mesophotic reef habitat use existed among the three shark species. Lemon sharks were typically detected at the mesophotic reef for one to two consecutive days, followed by short periods (1–10 days) of absence (Fig. 3, Appendix 3a-f). Three of the six lemon sharks monitored were detected at the mesophotic reef for at least three consecutive years, with one shark being detected a fourth consecutive year. The other three lemon sharks were detected at the mesophotic reef site for less than two years (Appendix 1).

The tiger sharks were detected monthly at the mesophotic reef, spending one to two days in the array before short (1–10 day) periods of absence (Fig. 3, Appendix 3g-o). However, five tiger sharks remained within the mesophotic reef array for periods of more than a week, with one shark detected within the array for 25 consecutive days. Of the ten tiger sharks studied, three were detected four consecutive years, two were detected three consecutive years, and one tiger shark was detected two consecutive years at the mesophotic reef array. The remaining four tiger sharks were detected at the mesophotic reef array for less than one year (Appendix 1). Three tiger sharks were detected every month of the year for at least one year.

Caribbean reef sharks monitored in this study spent long periods of time within the mesophotic reef array, interrupted by up to 20 months of absence (Fig. 3, Appendix 3p & q). Both of the sharks monitored were detected at the mesophotic reef array for at least 11 consecutive months.

For all species, sharks tended to be detected at the mesophotic reef for multiple consecutive days at a time. For 17 of the 18 sharks monitored the distribution of the number of days between successive days detected at the mesophotic reef array differed from a random distribution (Fig. 3) (all $p < 0.01$). For lemons, tigers, and Caribbean reef sharks, intervals of zero days between successive detections (i.e., consecutive days present) made up 52.77 ± 16.17%, 44.85 ± 17.66%, and 96.08 ± 0.40% of the total number of intervals between successive days detected, respectively. Intervals of 1–7 days between successive detections for lemons, tigers, and Caribbean reef sharks made up 30.86 ± 24.26%, 42.08 ± 26.72%, and 2.63 ± 2.46% of values, respectively (Fig. 3).

Residence time within the entire acoustic array varied between species, with the Caribbean reef shark mean residence time (25.26 ± 0.60 days) being longer than lemon (2.52 ± 0.62 days) and tiger shark (1.99 ± 0.23 days) mean residence times (Fig. 4) ($p < 0.0001$). There was no difference in mean residence time between lemon sharks and tiger sharks ($p = 0.669$). Absence time also varied between species, with the Caribbean reef shark mean absence time (35.28 ± 5.72 days) being longer than lemon (10.63 ± 2.17 days) and tiger shark (8.43 ± 2.39) mean absence times (Fig. 5) ($p = 0.001$). There was no difference in absence times between lemon sharks and tiger sharks ($p = 0.507$).

Association of sharks with the fish spawning aggregation site

Association with the FSA site during the grouper spawning season months (Dec – May) varied across shark species. Lemon sharks were detected at the FSA site more often each month (4.90 ± 2.26 days) during the grouper spawning season than during the non-spawning season (1.36 ± 0.43 days) (p = 0.011). This seasonal pattern was consistent each year of the five-year study period (Fig. 6, Appendix 4, 7a-c, 8a). There was no difference between the number of days tiger sharks were detected at the FSA site each month between the spawning and non-spawning seasons (p = 0.411, Appendix 5, 7d-i, 8b) and Caribbean reef sharks were not analyzed because of their small sample size (n = 2, Appendix 6, 7j & k, 8c).

Because lemon sharks were the only species to show a relationship to the spawning season, they were the only species examined further in regard to presence at the FSA site. Lemon shark mean residence time within the FSA site did not differ between the grouper spawning season (2.41 ± 0.49 days) and non-spawning season (1.82 ± 0.57 days) (p = 0.384). There was also no statistically significant difference found in the mean absence time from the FSA site during the grouper spawning season (7.96 ± 2.11 days) and non-spawning season (29.47 ± 11.55 days) (p = 0.148). However, five of the six lemon sharks had shorter mean absence times from the FSA site during the spawning season than during the non-spawning season. The increased presence of lemon sharks at the FSA site during the spawning season is therefore likely the result of more frequent visits to the FSA site during the spawning season, rather than longer residence times at the FSA site. Based on the comparison of presence across the three spawning areas, lemon sharks showed no preference between the three spawning areas (p = 0.247). In addition, a comparison of percent presence between Hind Bank MCD (9.2 ± 1.83%), which includes two red hind grouper spawning areas and Grammanik Bank (2.92 ± 0.87%), which includes one multi-species spawning area, revealed lemon sharks were detected more often at Hind Bank MCD ($p = 0.016$).

Discussion

Mesophotic reef habitat use

Lemon sharks used a large area of the mesophotic reef and spent a considerable amount of time within the acoustic array. The maximum number of consecutive days absent for lemon sharks (133 days) was shorter than that for tiger sharks (272 days) and Caribbean reef sharks (602 days). In addition, lemon shark absence periods typically lasted less than one week and they were often detected within the array for several consecutive days. On the basis of the short duration of gaps within the detection history of these sharks, many periods of absence are likely attributed to holes in acoustic array coverage; receiver density was much lower throughout the larger mesophotic reef array than within the FSA site. The infrequently observed longer absence times could be due to movements away from the acoustic array, as lemon sharks are capable of long distance movements [27].

Tiger sharks were detected over a slightly larger area of the mesophotic reef than lemon sharks. The large area used by tiger sharks is not surprising given that tiger sharks are known to cover large distances, including crossing ocean basins [26,28-30]. Even at shorter time scales (days to weeks), they may use large activity spaces (1000s of km^2) [31]. It is therefore likely that individual tiger sharks use a larger total area of mesophotic reef than what was monitored during this study. In fact, the area covered by monitored tiger sharks in this study was positively related to their time at liberty. They may simply rove over larger areas, only restricting movements to smaller scales where prey density is high. For example, tiger sharks in

Shark Bay, Australia select habitat patches (1000s of m) and microhabitats (100s of m) with high prey density [31,32].

Despite being known for using large areas, many of the tiger sharks in this study not only frequently used the area covered by the mesophotic reef array, but tended to return to the mesophotic reef on multiple occasions each month throughout the year, interrupted by short (<1 week) absence periods, indicating these sharks did not make large scale movements away from the area. Given that tiger shark habitat use has been linked to areas where prey is most abundant [29,32,33], the consistency in tiger shark detection within the mesophotic reef acoustic array (~900 km^2) suggests that this habitat may provide ample resources for these sharks.

In contrast to the lemon and tiger sharks, Caribbean reef sharks were detected across the smallest area of the mesophotic reef. Although small sample size precludes strong conclusions about use of the mesophotic reef by Caribbean reef sharks, both individuals behaved similarly, occupying small activity spaces roughly 5.5 km^2 in size, and demonstrating a high degree of site fidelity to the FSA site when present. This type of behavior is consistent with other species of coral reef-associated sharks, which generally inhabit small home ranges (<100 km^2) [13,34,35], including Caribbean reef sharks. Off New Providence, The Bahamas, Caribbean reef sharks were found to spend a high proportion of their time near a single acoustic receiver with a detection range of ~500 m [36]. While at Fernando de Noronha Archipelago and Atoll de Rocas, Brazil, which are small reef sites (26 km^2 and 5.5 km^2, respectively), juvenile Caribbean reef sharks were year-round residents of the reefs, with no seasonal variation of habitat use or emigration [37,38]. The small areas used at these locations, however, may be a result of habitat limitation because of the small size of these geographically isolated atolls.

Caribbean reef sharks showed high fidelity to the limited area of the mesophotic reef they used displaying long residence times punctuated by infrequent long absences. Interestingly, there was no seasonal pattern to the presence and absence of Caribbean reef sharks within the array. In the North-East Exuma Sound, The Bahamas, Caribbean reef sharks exhibited a seasonal peak in abundance during summer months, suggesting migratory behavior. Recapture of tagged individuals revealed sharks returned to this area after multiple years at liberty [39]. Residence patterns in this study were not indicative of yearly migrations, but may suggest some level of fidelity to specific areas of the mesophotic reef. Also, long periods without detections could be attributed to wide-ranging movements (~50 km), which have been occasionally observed in the Caribbean reef shark [14,40].

Association of sharks with the fish spawning aggregation site

The three species of sharks oriented to the FSA site differently, with only lemon sharks showing clear patterns of movement related to the FSA. Lemon sharks exhibited a marked increase in presence at the FSA site during the grouper spawning season, compared to the non-spawning season. This pattern was consistently observed each of the five years of the study with individual lemon sharks detected at the FSA site during the grouper spawning season for up to four consecutive years. The large concentration of fish at the FSA site may be attractive to lemon sharks because the fish represent a dense prey patch; teleost fish make up 74% of the diet of lemon sharks [41]. Increased presence of lemon sharks at the FSA site could arise by sharks arriving at the site opportunistically and remaining in the area because of the high abundance of potential prey, but the yearly periodicity of visits by individual sharks suggests that the lemon sharks do not arrive at the FSA site by chance but rather seek out this location because of the large, predicable influx of teleost biomass or aggregation of conspecifics. Repeated exposure to seasonal prey pulses could lead to the development of local knowledge, which can enhance foraging success and efficiency if an animal learns to return to a particular area where resources are spatially and temporally predictable, such as a FSA site [42-44].

While this study is the first documented observation of lemon sharks seasonally aggregating at a FSA site, the lemon shark's congener, the sicklefin lemon shark (*Negaprion acutidens*) has been documented to show increased fidelity to locations with predictable food pulses, albeit at much shorter time intervals. Sicklefin lemon sharks exposed to long-term daily provisioning in Moorea, French Polynesia, showed a significant increase in the number of times they were sighted during the provisioning period (44 months) compared to before provisioning was initiated [45].

Although Caribbean reef sharks are piscivorous like the lemon shark [46,47] and, therefore, might respond to aggregations of potential prey, they showed no difference in their presence at the FSA site between the grouper spawning and non-spawning seasons. Interestingly, similar indifference towards a predictable and more frequent prey source has been observed in Caribbean reef sharks at a popular dive site off New Providence, The Bahamas [36]. Despite long-term daily provisioning at the dive site, Caribbean reef sharks showed no changes in space use and movement, nor did they increase time spent at the feeding site. Sharks in the area, regardless of whether they frequented the provisioning site, exhibited similar degrees of residency at respective home receivers, and traveled similar daily distances [36].

Like the Caribbean reef sharks, tiger sharks also appeared to have no detectable association with the FSA site during the grouper spawning season. This may not be surprising given that tiger shark behavior is often characterized by wide-ranging movement, resulting in most animals remaining in a location for only short periods of time (days to weeks) [30,33,48]. However, wide-ranging, tiger sharks have been known to seasonally target areas where prey is abundant [11,49]. At French Frigate Shoals, Hawaii, tiger sharks congregate to prey on seasonally abundant fledgling albatross (*Phoebastria spp*.) [11]. Tiger sharks also exhibit seasonal cycles in abundance at well-established rock lobster fishing grounds in Western Australia where there is a substantial and regular input of bait [50]. Additionally, tiger shark abundance and spatial preference within Shark Bay, Australia correlate with the annual increased availability of dugongs, an energy-rich prey source [19,51,52].

The lack of association between tiger sharks and the FSAs may be influenced by tiger shark size. The tiger sharks monitored in this study were relatively large. Despite having a wide dietary breadth [49-51,53], reliance on teleosts decreases with tiger shark size, while the occurrence of crustaceans, elasmobranchs, and sea turtles in the diet increases [41,53,54]. In particular, in areas where sea turtles are abundant, they are one of the most frequently occurring prey items in the diets of large tiger sharks [50,53] and the Virgin Islands are home to green turtle (*Chelonia mydas*) [55] and hawksbill turtle (*Eretmochelys imbricata*) [56] nesting grounds, in addition to one of the largest nesting colonies of leatherback sea turtles (*Dermochelys coriacea*) [57]. Given the concurrent and year round abundance of turtles in this system, it is unlikely that tiger sharks will alter their behaviors to focus on aggregations of less preferred prey items.

Conclusions

The mesophotic reef tract of the Puerto Rico-Virgin Islands platform was used extensively, year round by all three species of sharks studied. However, each species exhibited different patterns of use of the mesophotic reef. Lemon sharks used nearly the entire mesophotic reef habitat monitored by the acoustic array and exhibited a strong association with the FSA site during the grouper spawning season. Tiger sharks also used the majority of the mesophotic reef habitat monitored. They were detected within the acoustic array over consecutive days throughout the year, interrupted by short periods of absence, indicating they did not travel far from the mesophotic reef array. Caribbean reef sharks were detected throughout the year within a small area exclusively within the FSA site. They exhibited long residence times but occasionally were absent from the array for over a year before returning. Both the frequency and duration of visits to the mesophotic reef by all three species suggest that it provides ample resources to support and attract multiple shark populations for prolonged periods of time, including species with otherwise highly mobile tendencies, like the tiger shark.

The association of lemon sharks with the FSA site demonstrates the influence of prey on movements of sharks. The lemon sharks' nearly continuous presence at the FSA site during the grouper spawning season illustrates the potential of sharks to interact with the spawning fish species, however, it is still unknown whether sharks target the spawning fish, or are targeting other species associated with the FSA. This is the first recorded seasonal association of a piscivorous shark with an FSA, and emphasizes the importance of FSAs within the system dynamics of mesophotic reefs.

Additionally, these interactions may influence populations of commercially important fishes, such as grouper, of which there is a great interest in protecting overfished stocks.

Species	Individuals	Male	Female	TL (cm)	Detections	Detection Time (days)
Tiger	10	4	6	260 - 347	15 – 4,842	91 – 1,186
Lemon	6	1	5	245 - 278	753 – 28,070	110 – 1,339
Caribbean reef	2	2	0	132 - 157	17,459 – 63,385	899 – 1,336

Table 1. Demographics and detection history for 18 sharks tagged with acoustic transmitters in this study. Detections = the total number of times a shark was detected by any acoustic array receiver. Detection time = the last date of detection at any receiver – the first date of detection at any receiver.

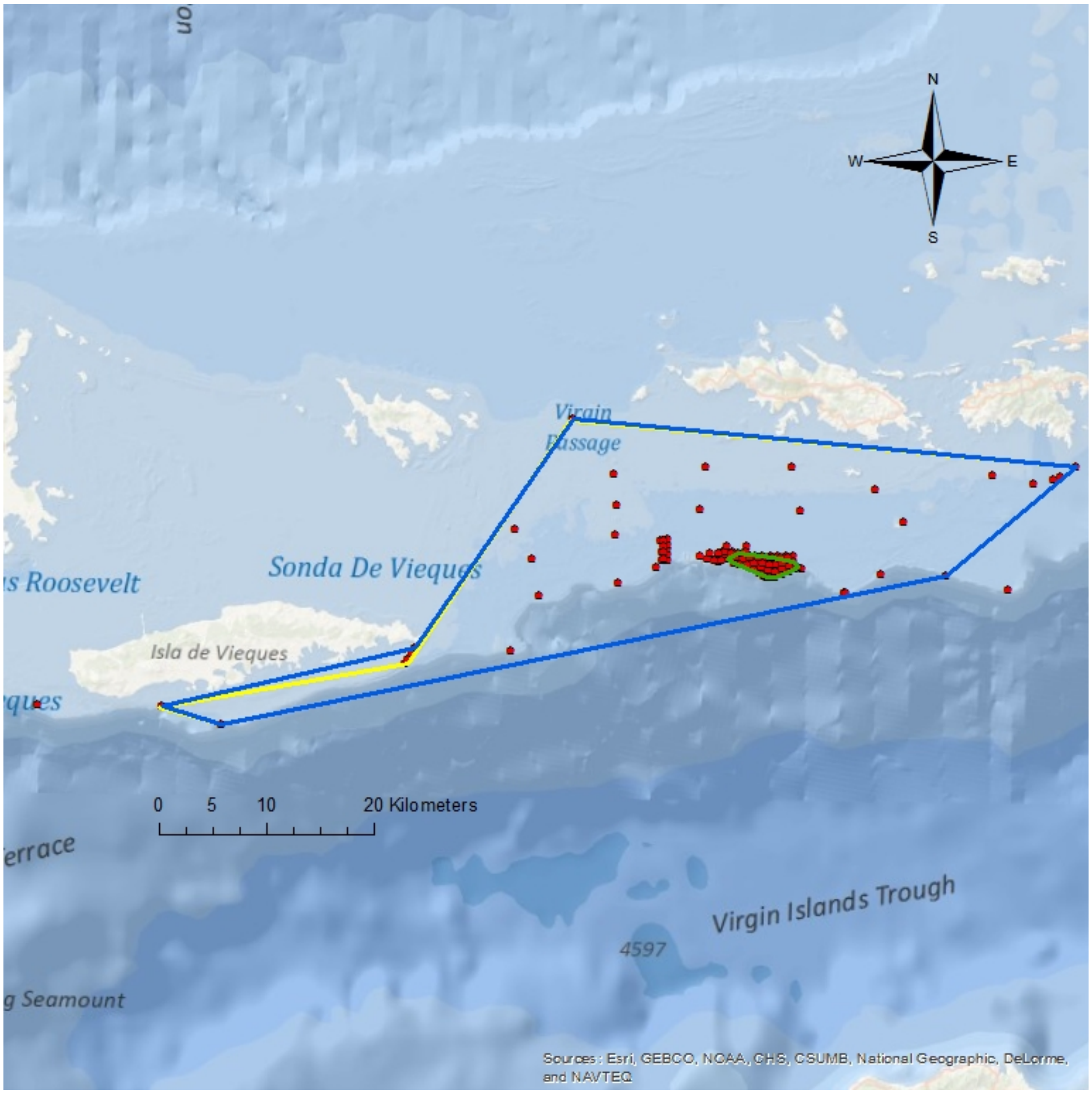


Figure 1. Red circles represent receivers and colored lines represent minimum convex polygons (MCPs) showing the total area over which each of the three species of sharks was detected across the entire acoustic array. Species total MCP areas were 887 km^2 for tiger sharks (blue), 863 km^2 for lemon sharks (yellow), and 8 km^2 for Caribbean reef sharks (green).

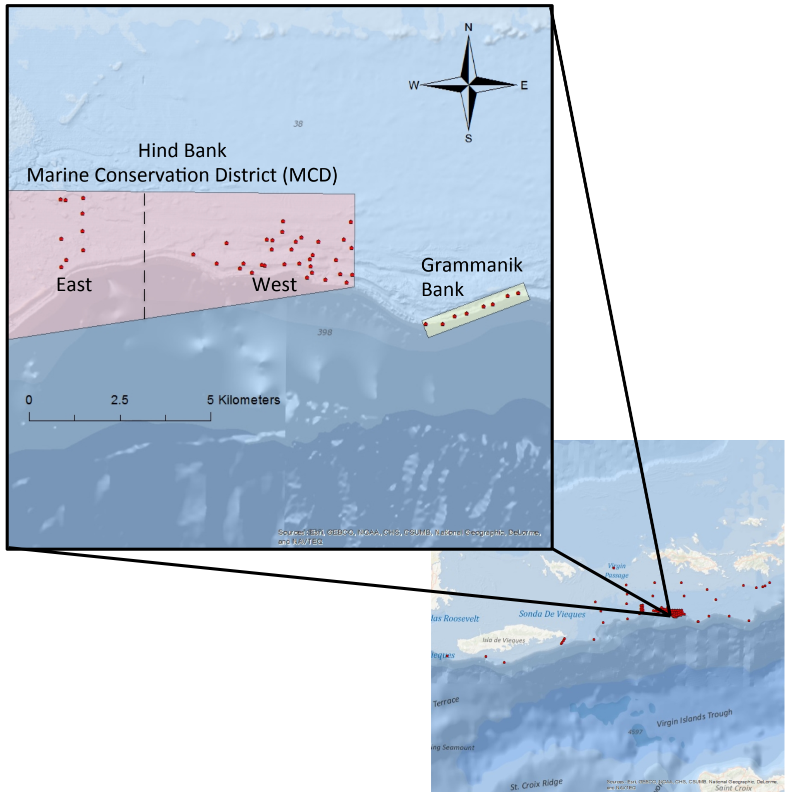


Figure 2. Three centers of spawning activity. Each center is monitored by the surrounding cluster of receivers. Two centers are located within the boundaries of Hind Bank Marine Conservation District (MCD); MCD East and MCD West. The third center is the Grammanik Bank seasonal fishing closure.

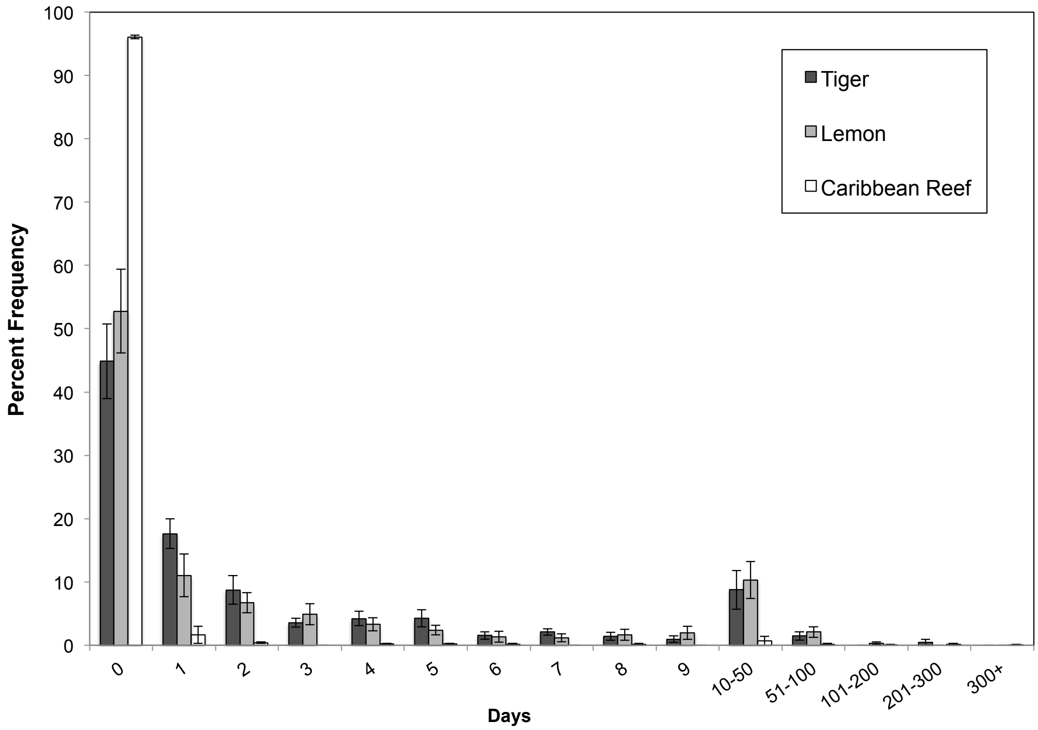


Figure 3. Average percent frequency of days between successive days detected at the acoustic array for all three species of sharks. A value of zero represents consecutive days detected at the acoustic array. Bars represent percent frequencies ± standard error.

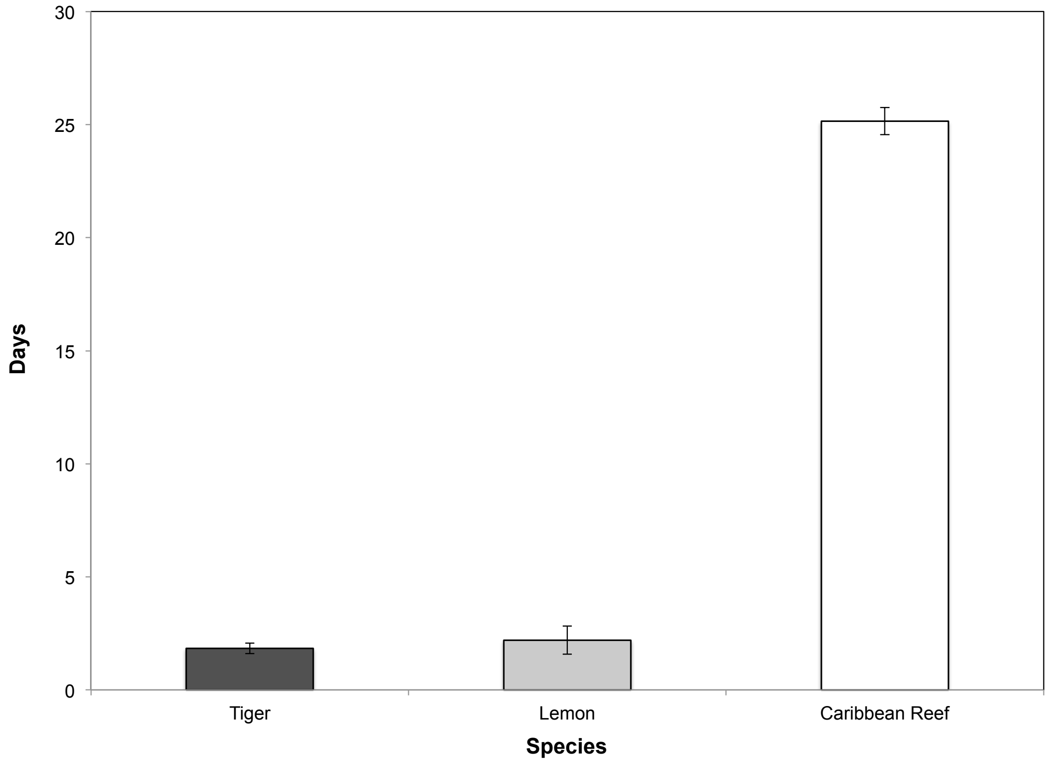


Figure 4. Average residence times within the acoustic array for tiger (1.84 days), lemon (2.20 days), and Caribbean reef sharks (25.16 days). Residence time = average number of single and consecutive days detected within the acoustic array. Bars represent means ± standard error.

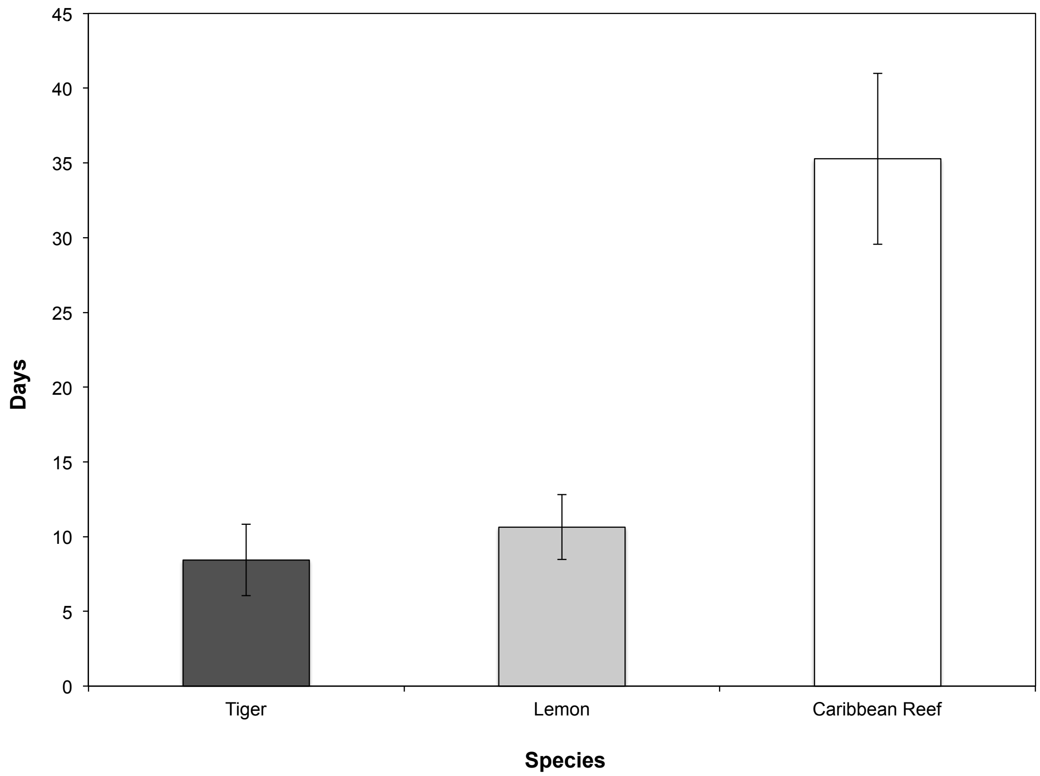


Figure 5. Average absence times within the acoustic array for tiger (8.43 days), lemon (10.63 days), and Caribbean reef sharks (35.28 days). Absence time = average number of single and consecutive days not detected within the acoustic array. Bars represent means ± standard error.

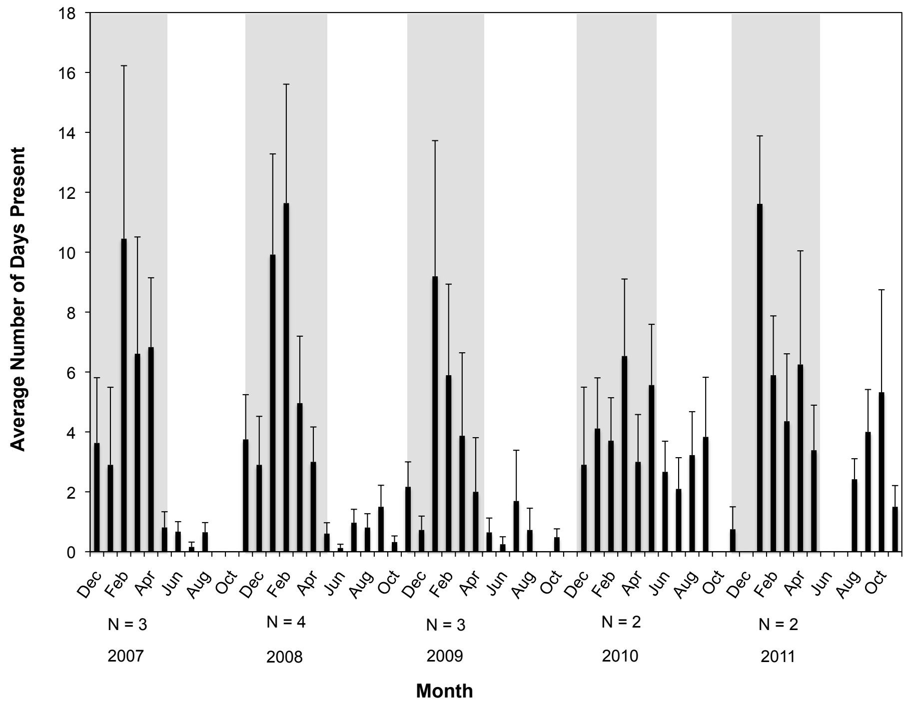
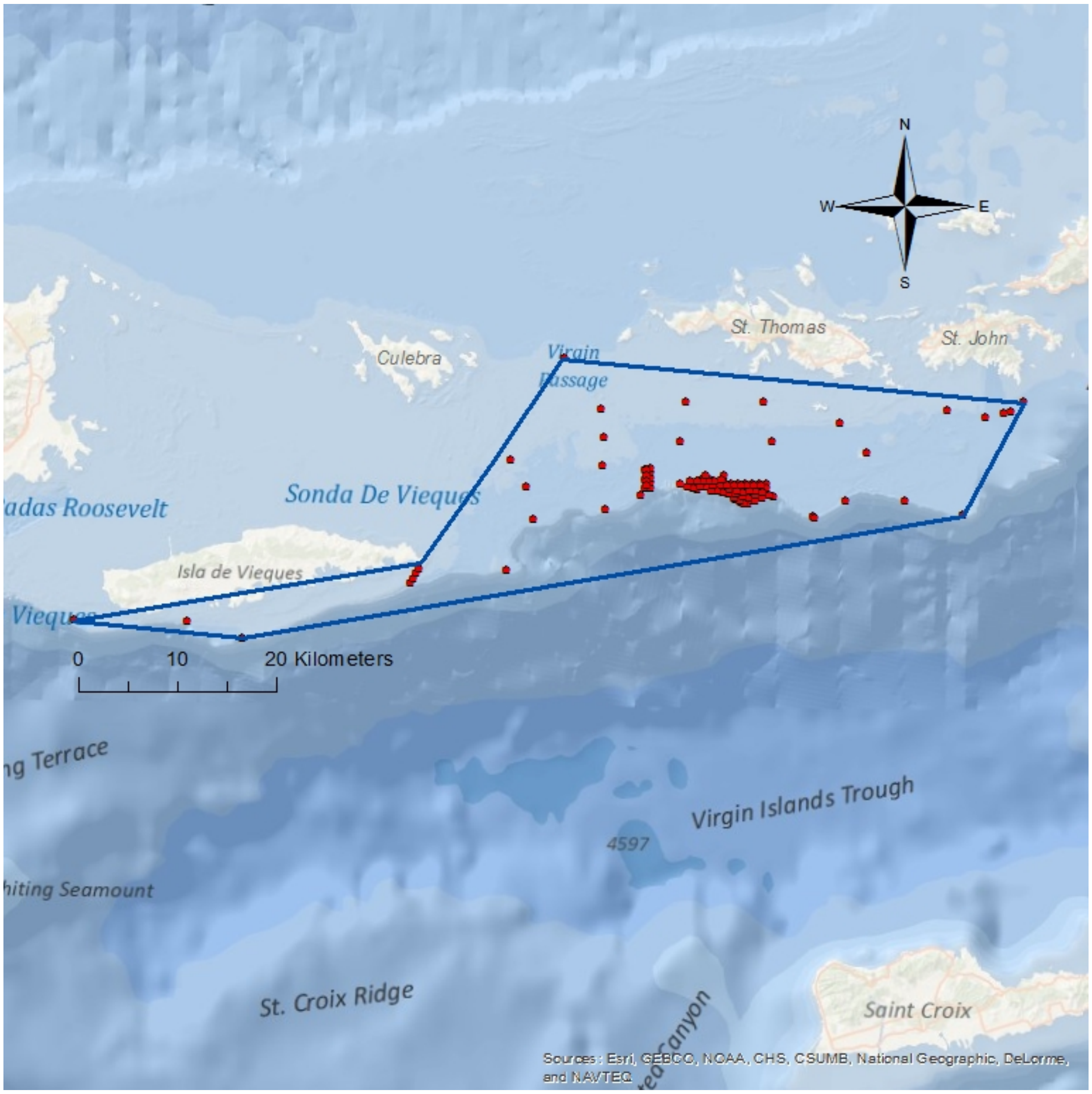


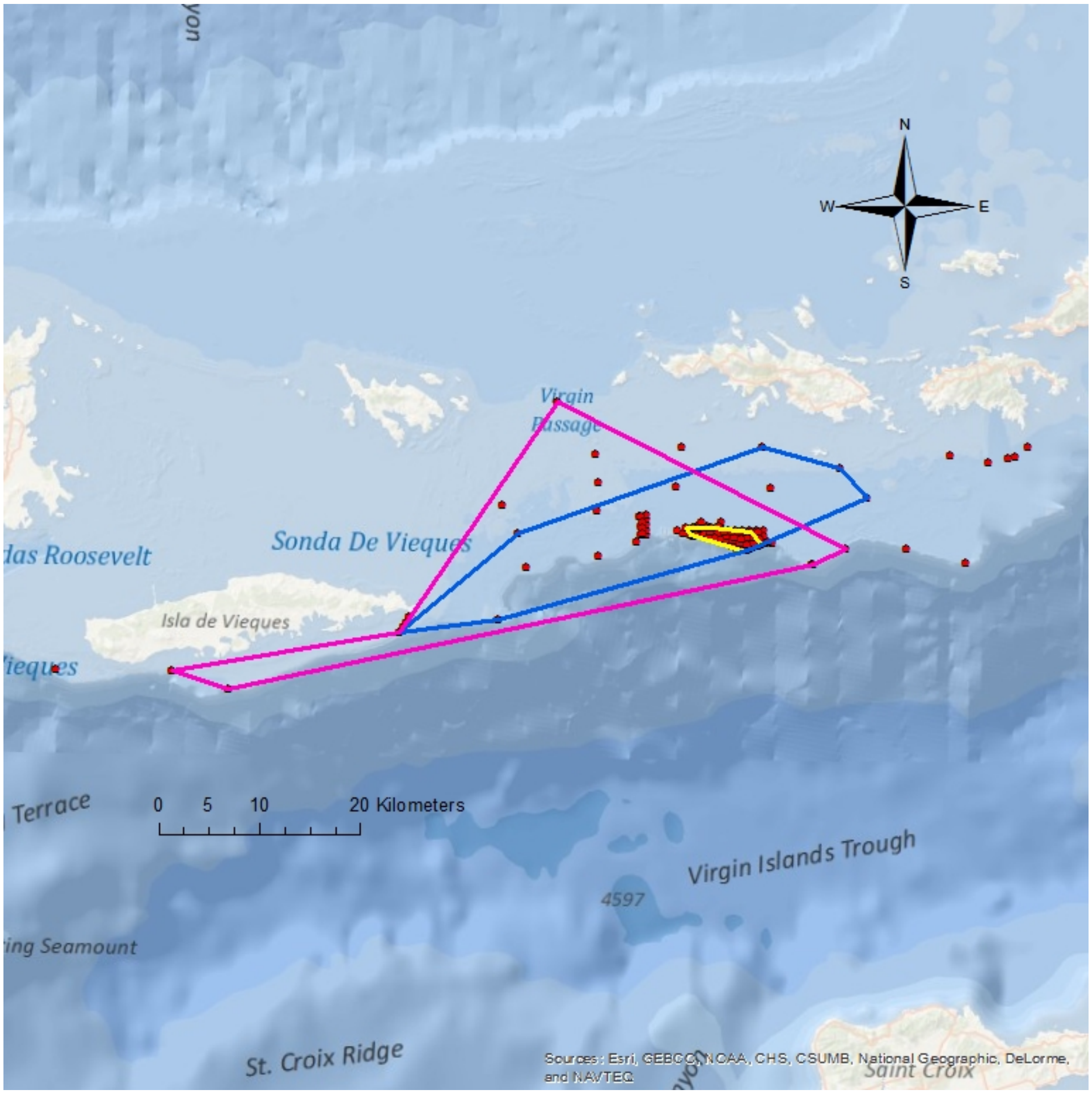
Figure 6. Average number of days each month lemon sharks were present at the FSA site during the grouper spawning season (gray) and the non-spawning season (white) from 2007 – 2011. Bars represent means ± standard error.

ID#	Species	TL (cm)	Sex	Stage	Detections	Detection Time (Days)
1475	Lemon	275	F	M	28,070	847
1479	Lemon	245	F	M	3,348	1,339
3743	Lemon	278	F	M	753	110
3747	Lemon	266	F	M	1,421	1,149
12384	Lemon	251	M	M	916	160
58129	Lemon	249	F	M	1,530	521
26	Tiger	316	F	M	1,792	264
1476	Tiger	298	F	M	4,330	850
1484	Tiger	315	F	M	965	878
1487	Tiger	275	F	M	151	551
3738	Tiger	270	M	M	4,842	1,070
3739	Tiger	330	M	M	431	1,068
3740	Tiger	260	F	M	407	179
3741	Tiger	347	M	M	4,056	1,186
12385	Tiger	278	F	M	124	166
49874	Tiger	341	M	M	15	91
1478	C. reef	157	M	IM	17,459	1,336
1486	C. reef	132	M	IM	63,385	899

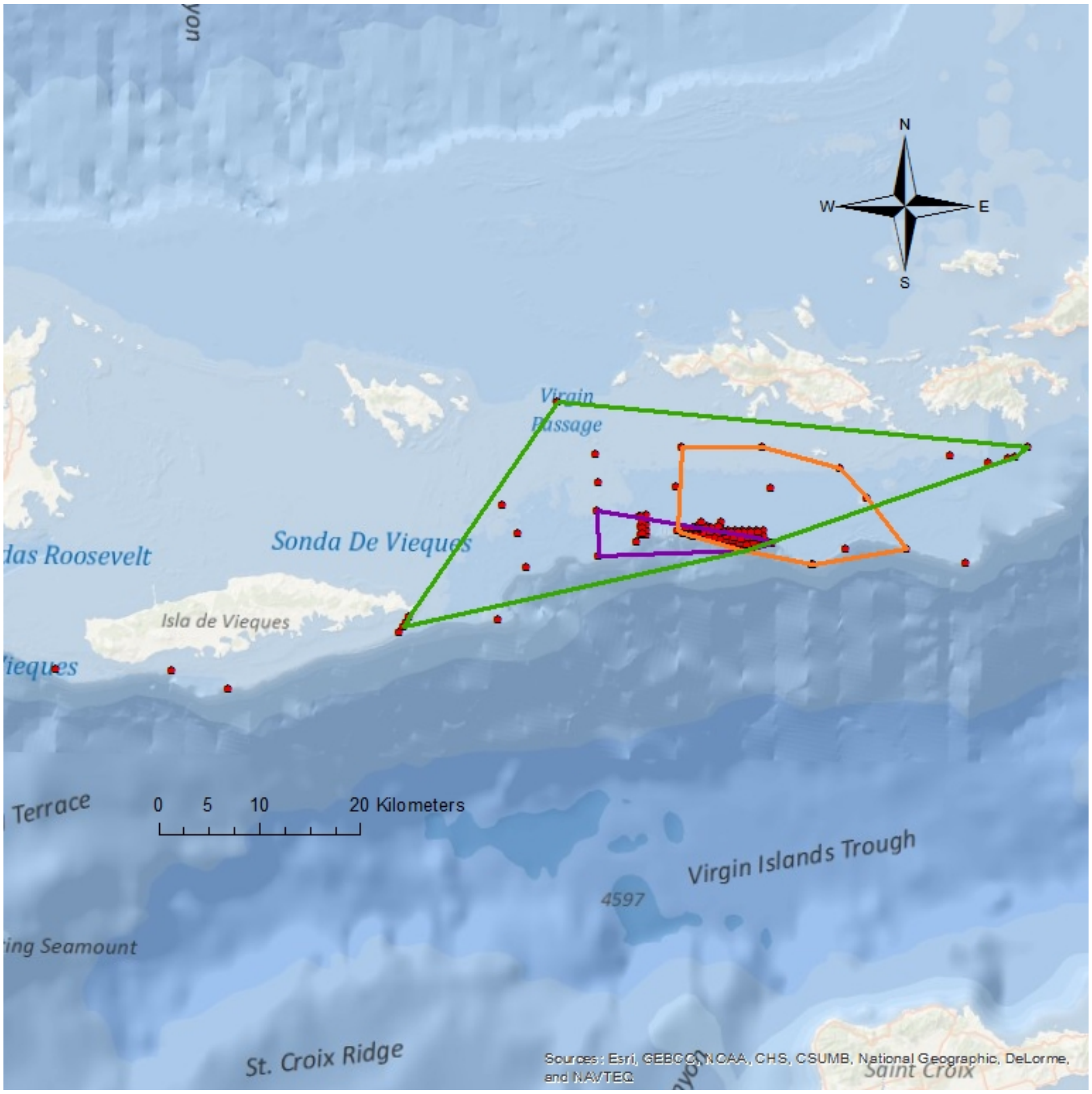
Appendix 1. Demographic and detection data for all 18 sharks analyzed.



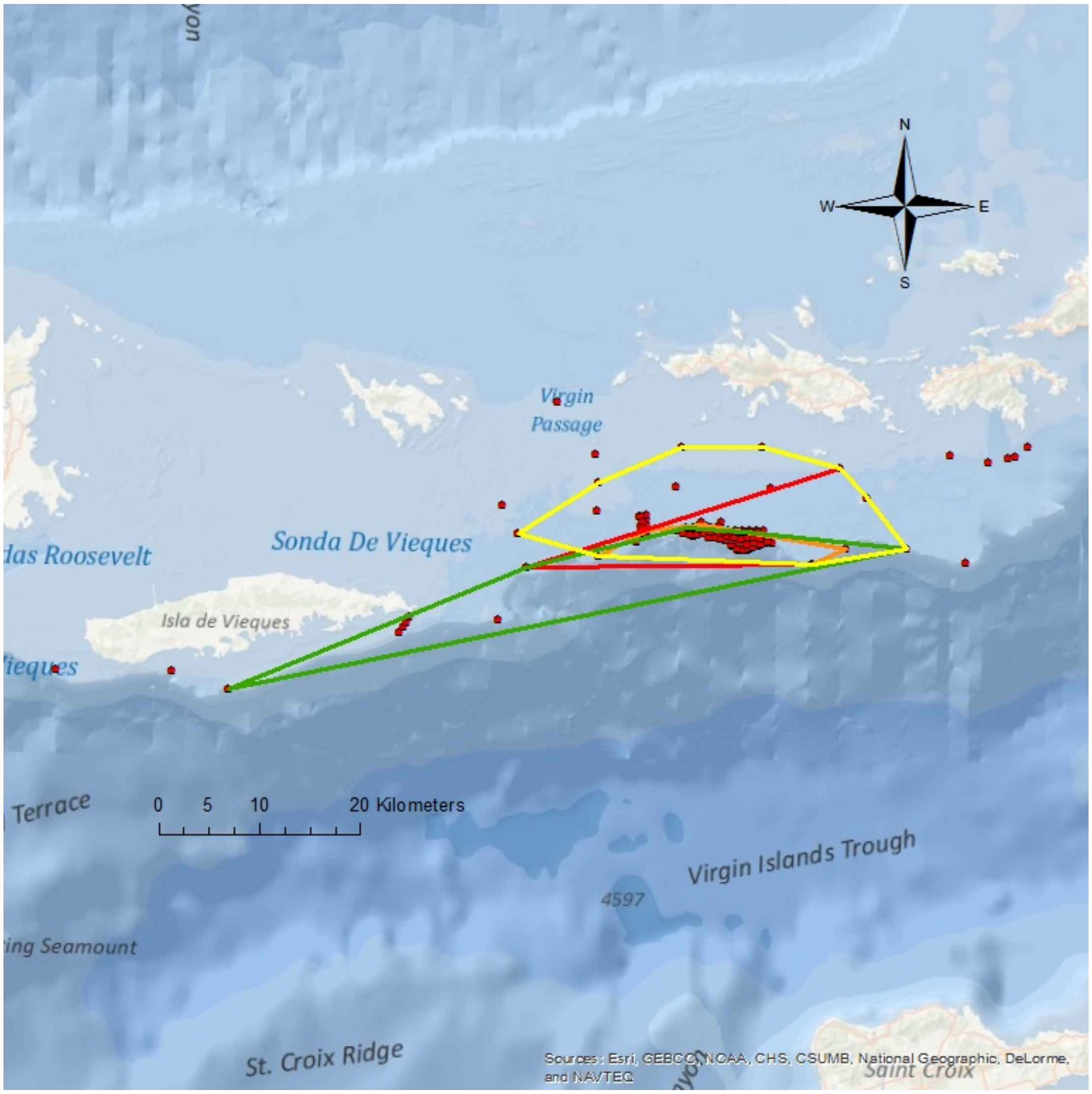
Appendix 2a. Minimum convex polygon (MCP) encompassing all acoustic array receivers (~1060 km^2).



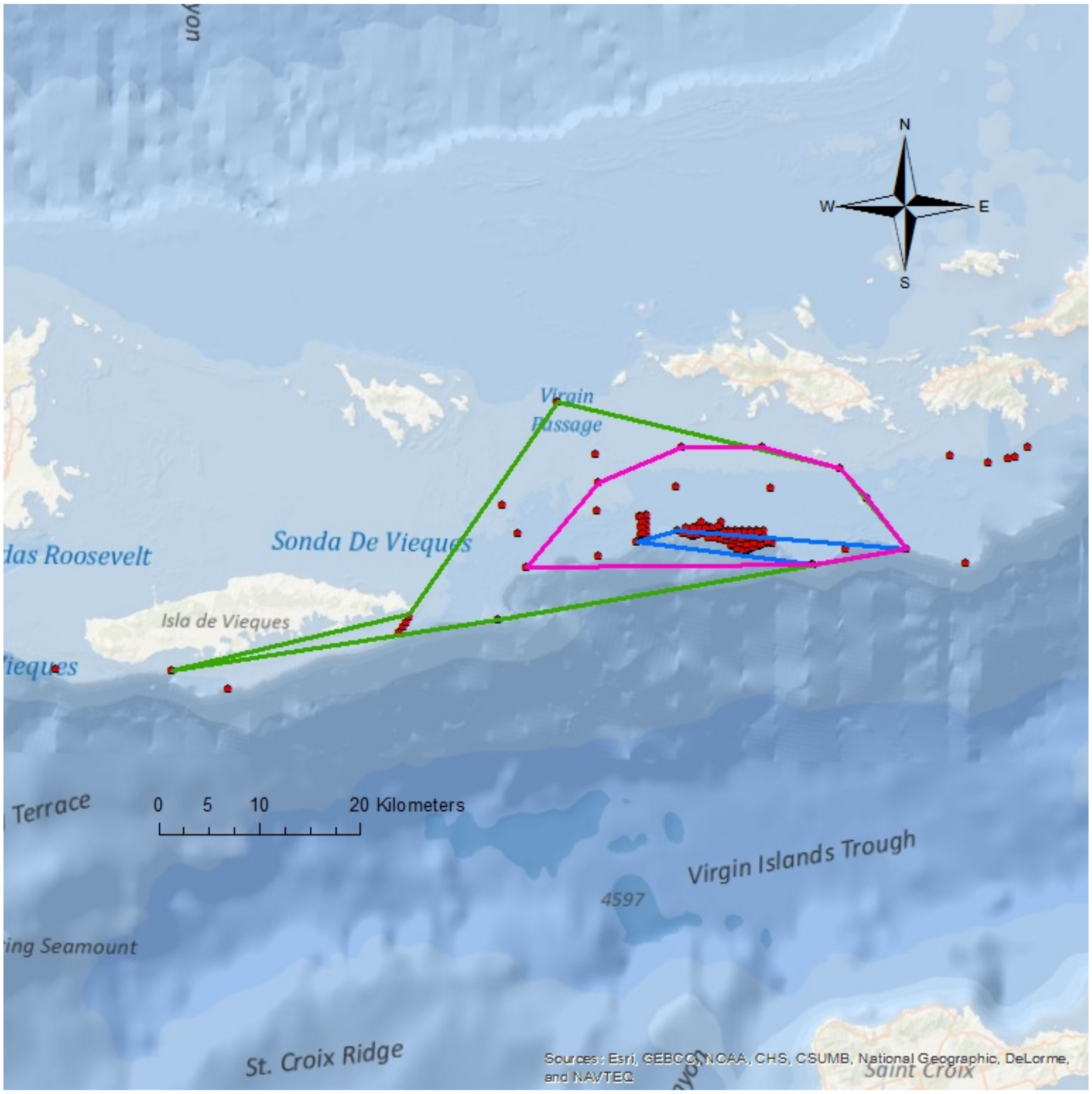
Appendix 2b. MCP's for lemon sharks 1475 (pink, 341 km^2), 1479 (blue, 163 km^2), and 58129 (yellow, 6 km^2).



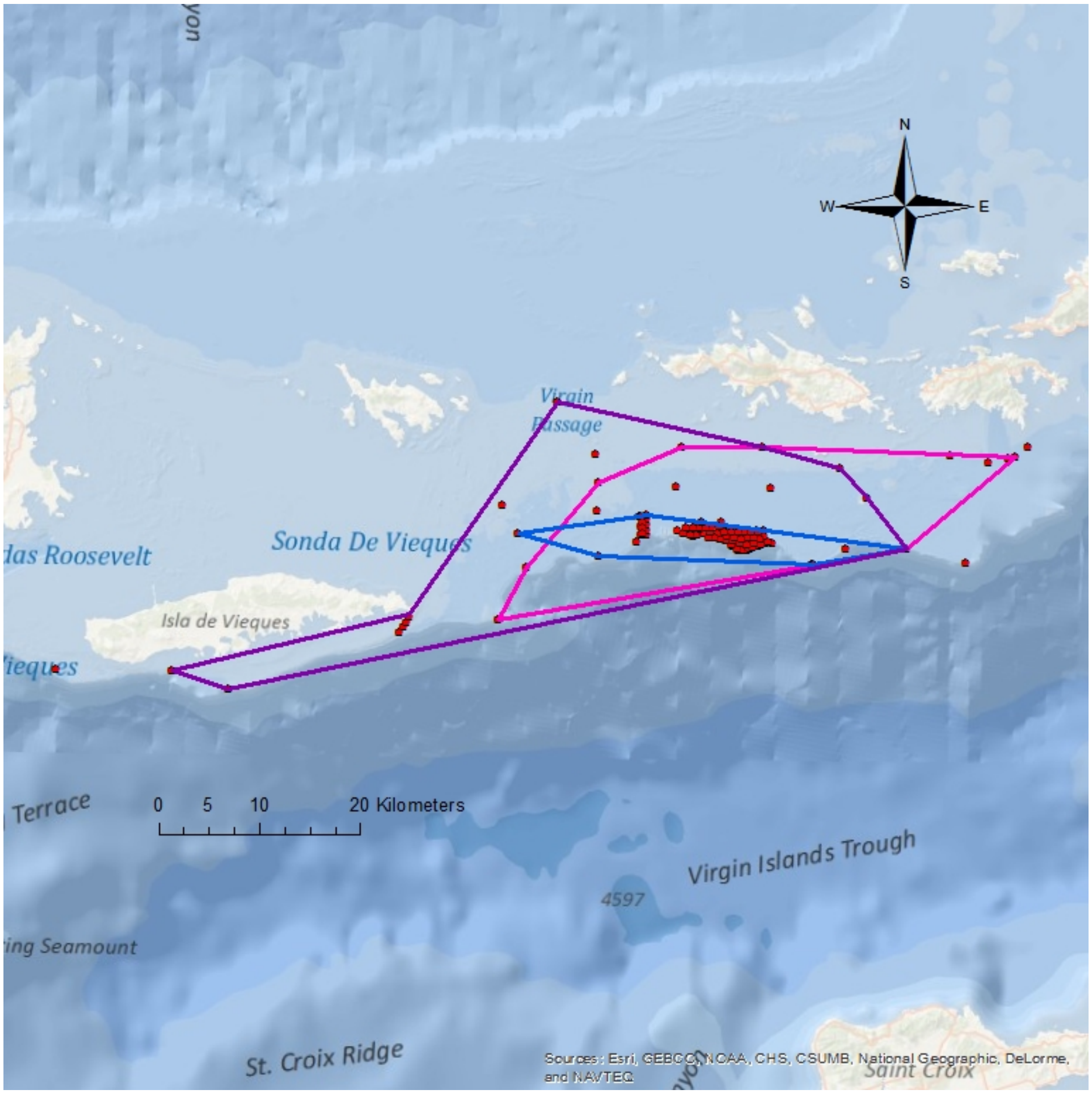
Appendix 2c. MCP's for lemon sharks 3743 (green, 219 km^2), 3747 (orange, 149 km^2), and 12384 (purple, 37 km^2).



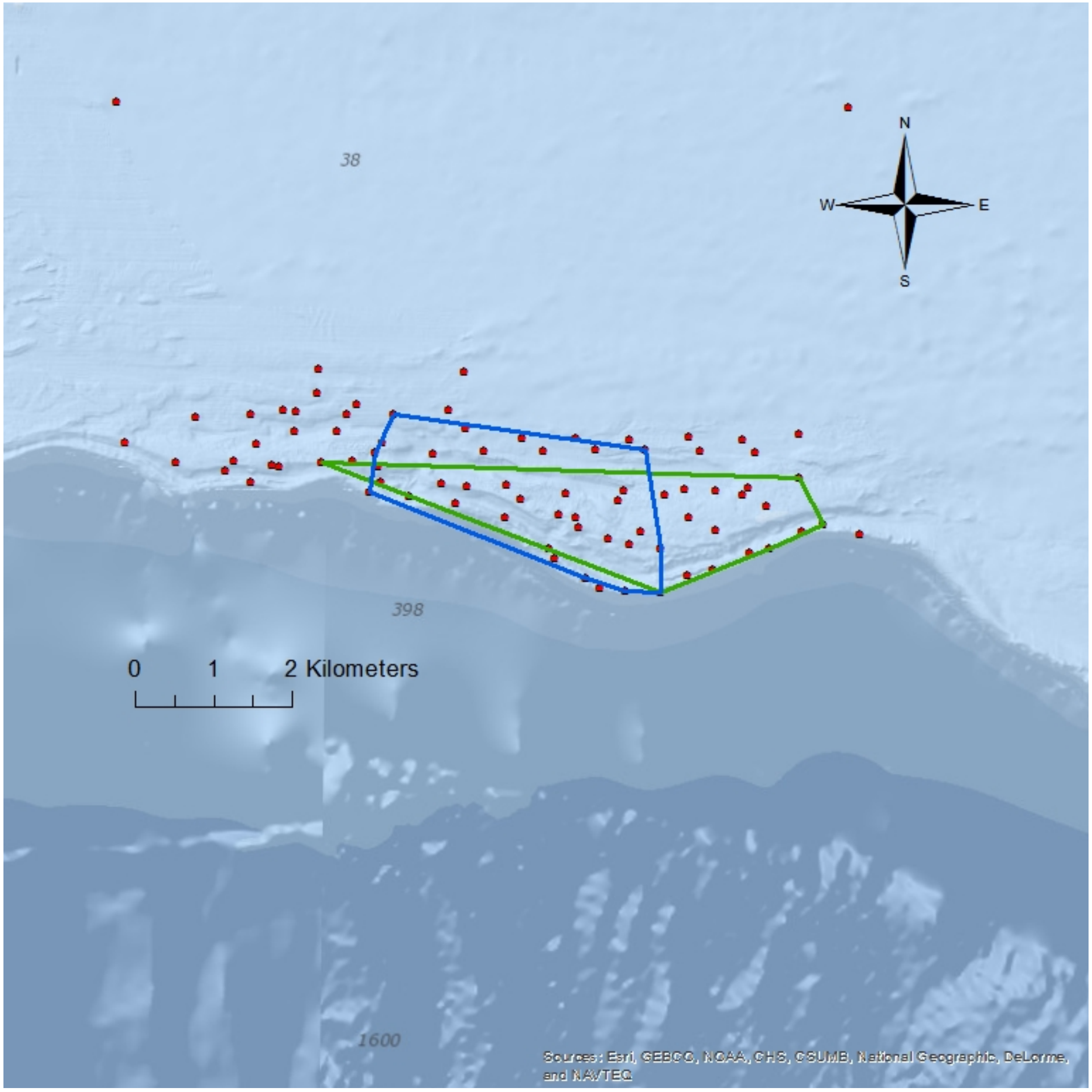
Appendix 2d. MCP's for tiger sharks 12385 (red, 97 km^2), 3739 (green, 250 km^2), 1484 (yellow, 185 km^2), and 26 (orange, 35 km^2).



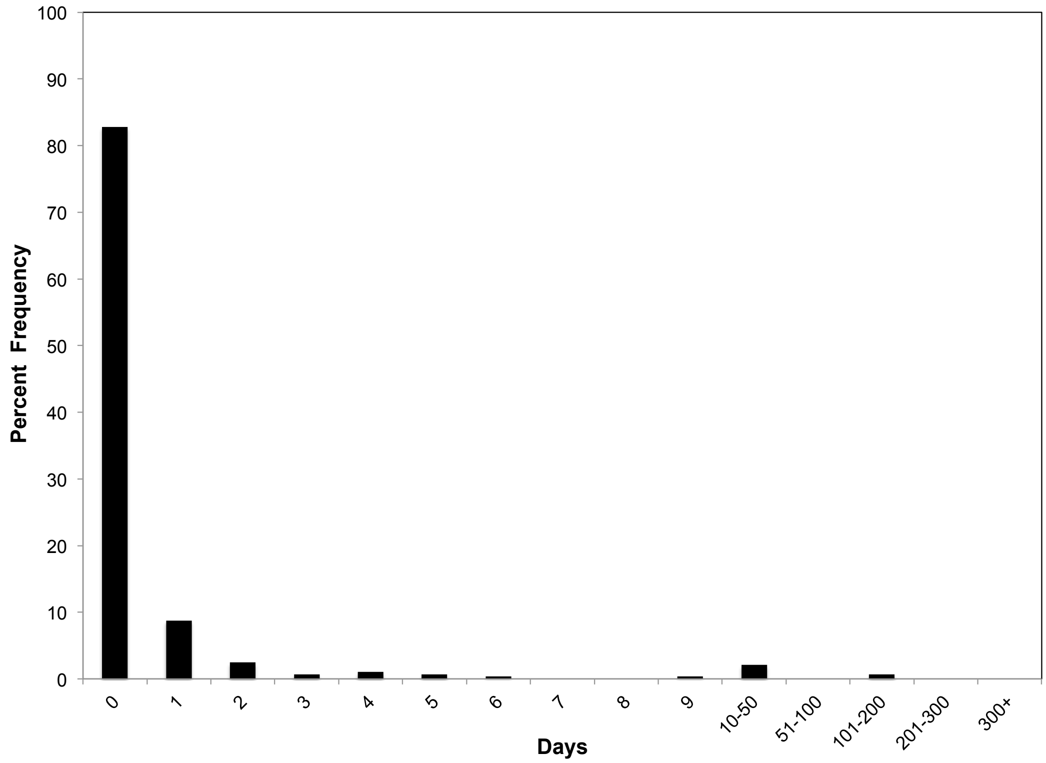
Appendix 2e. MCP's for tiger sharks 3740 (pink, 219 km^2), 3741 (green, 324 km^2), and 49874 (blue, 20 km^2).



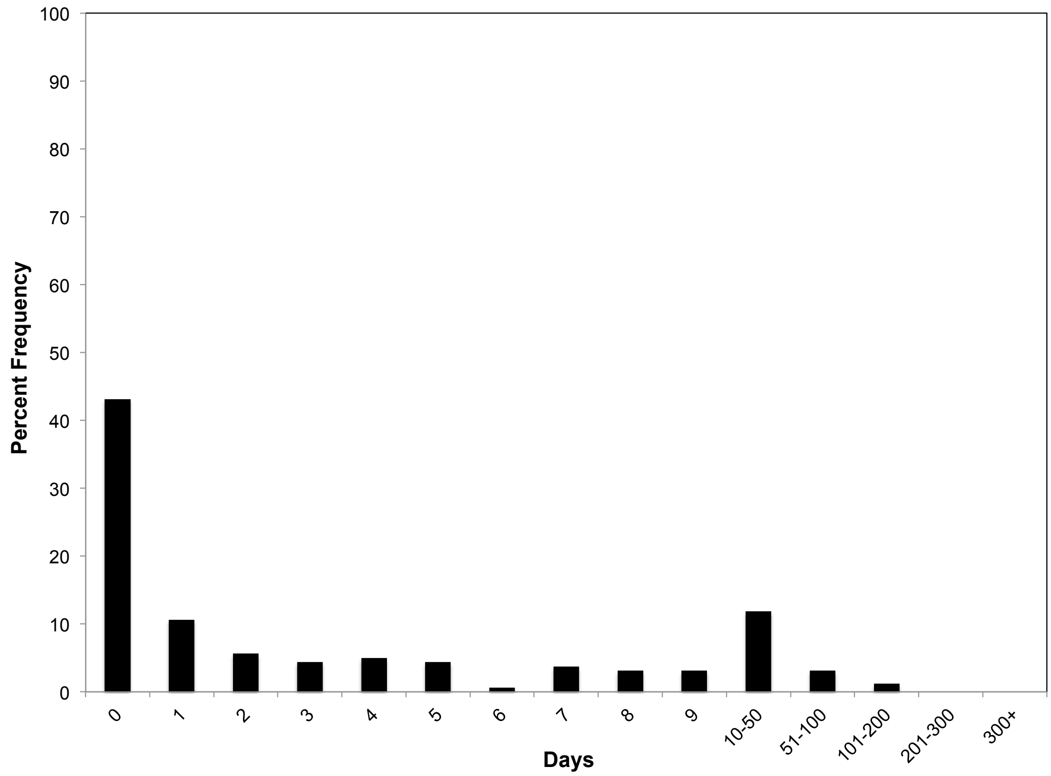
Appendix 2f. MCP's for tiger sharks 1476 (purple, 387 km^2), 1487 (blue, 97 km^2), 3738 (pink, 290 km^2).



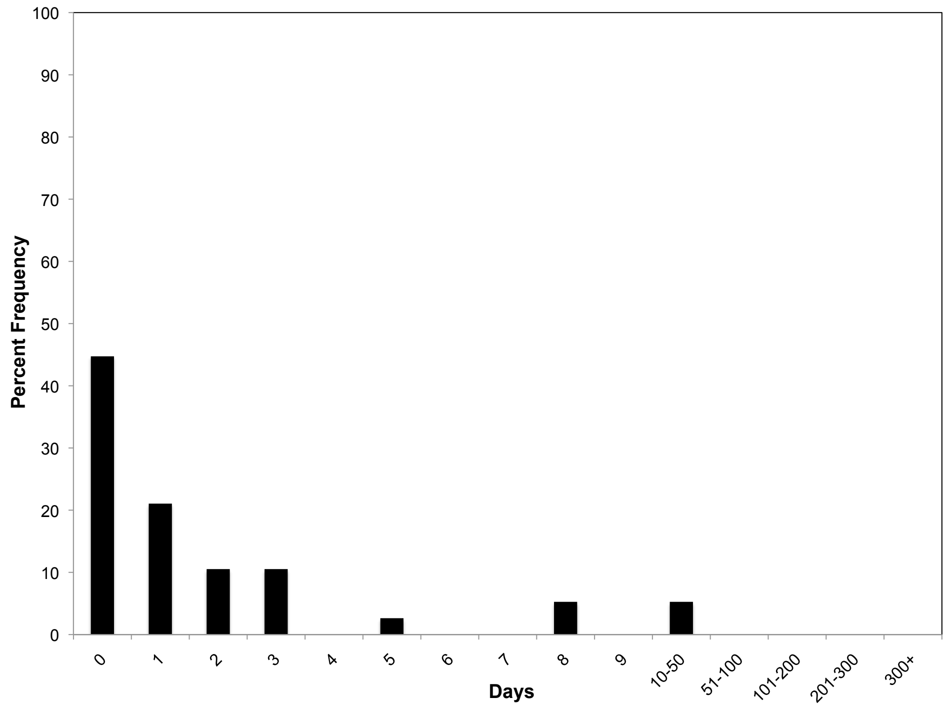
Appendix 2g. MCP's for Caribbean reef sharks 1478 (blue, 5 km^2) and 1486 (green, 5 km^2).



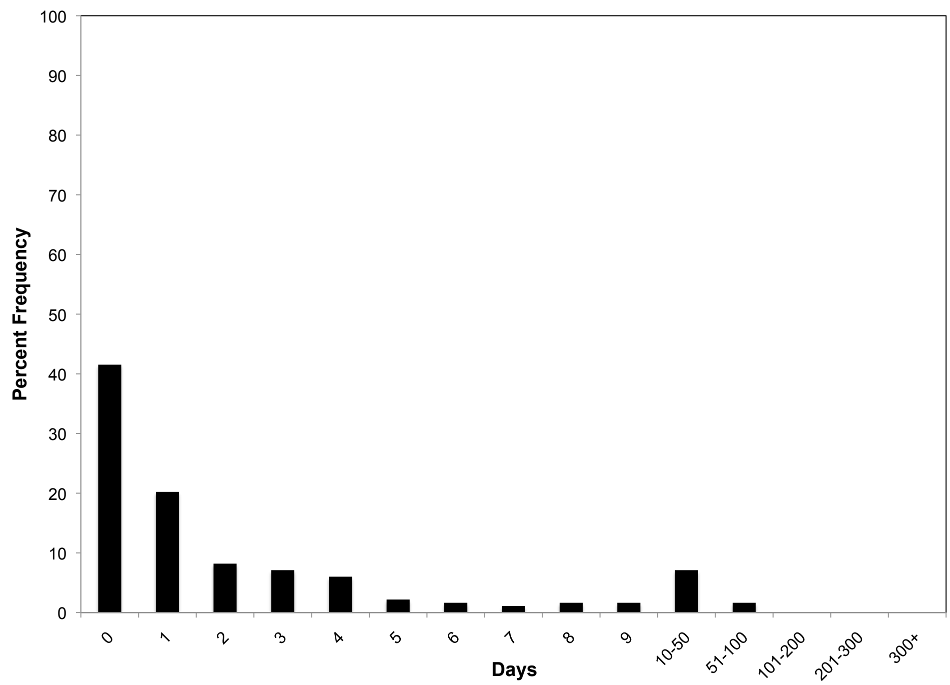
Appendix 3a. Lemon shark 1475 percent frequency of gap length from the mesophotic reef acoustic array.



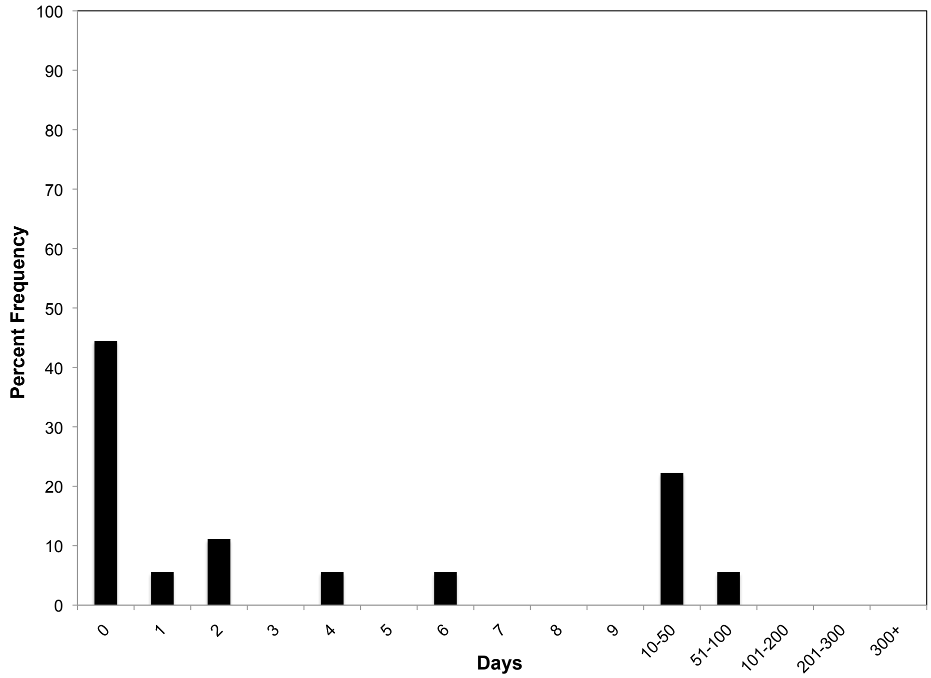
Appendix 3b. Lemon shark 1479 percent frequency of gap length from the mesophotic reef acoustic array.



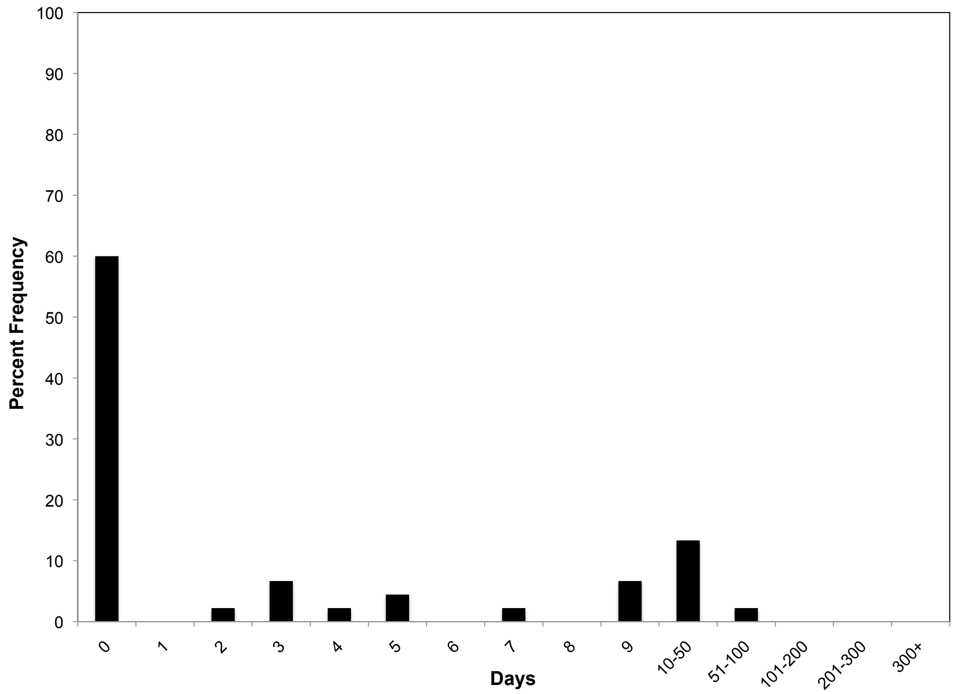
Appendix 3c. Lemon shark 3743 percent frequency of gap length from the mesophotic reef acoustic array.



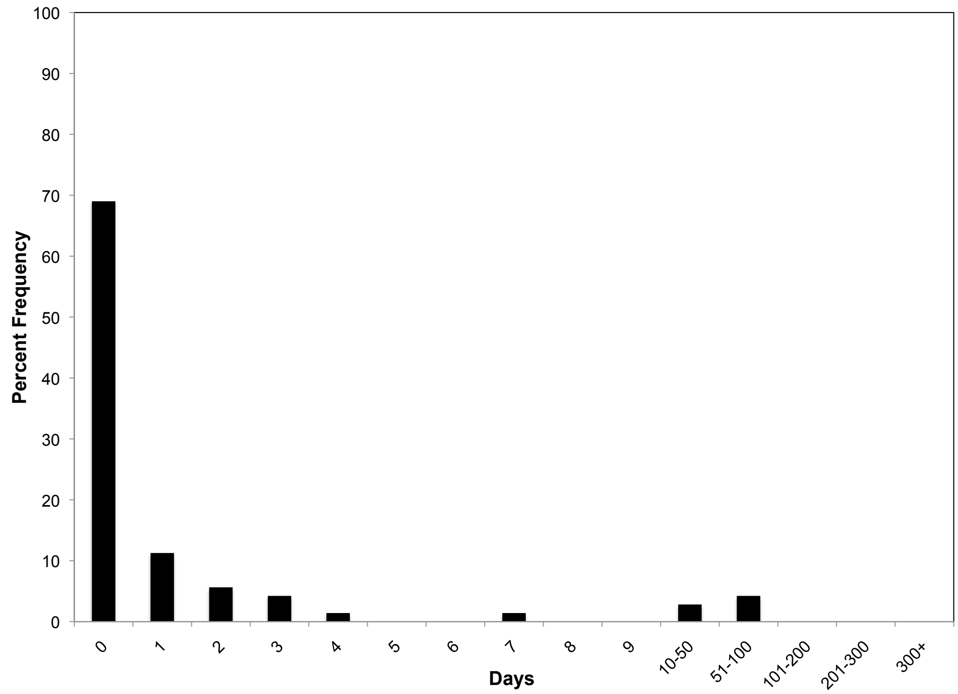
Appendix 3d. Lemon shark 3747 percent frequency of gap length from the mesophotic reef acoustic array.



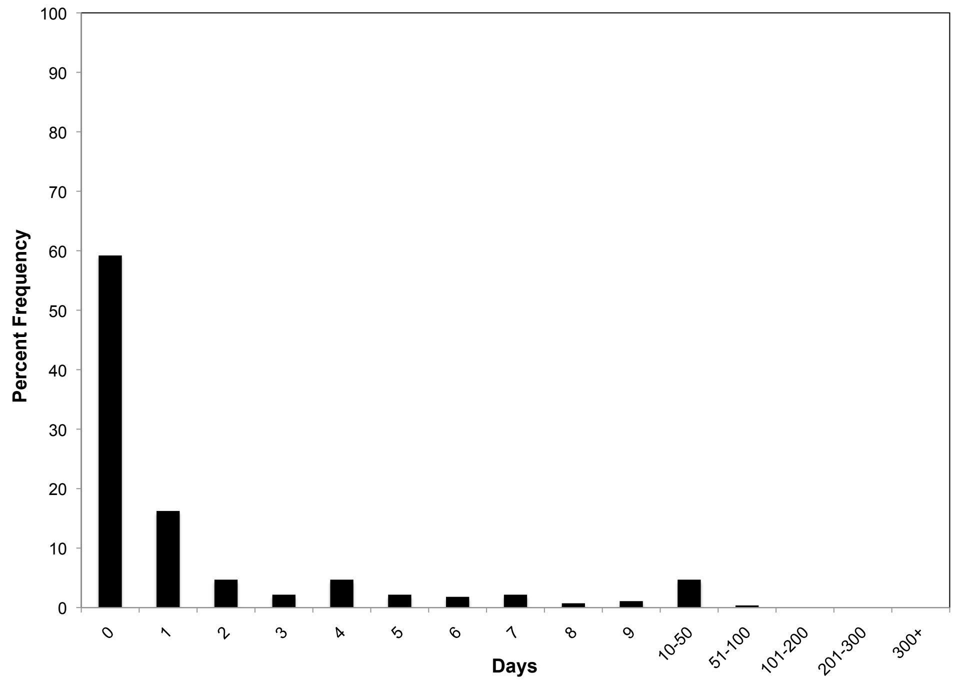
Appendix 3e. Lemon shark 12384 percent frequency of gap length from the mesophotic reef acoustic array.



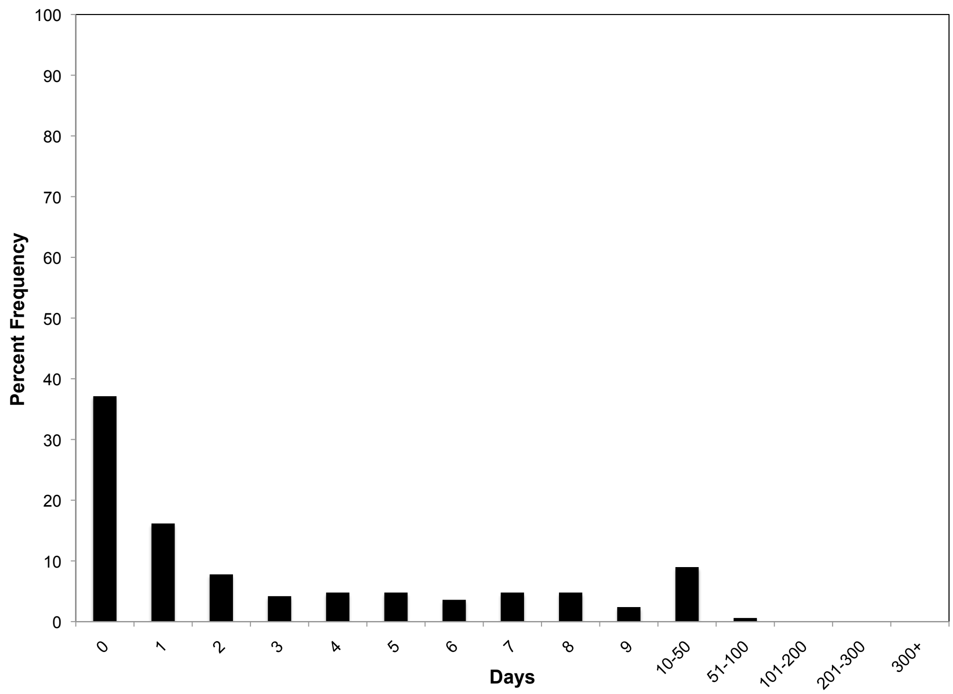
Appendix 3f. Lemon shark 58129 percent frequency of gap length from the mesophotic reef acoustic array.



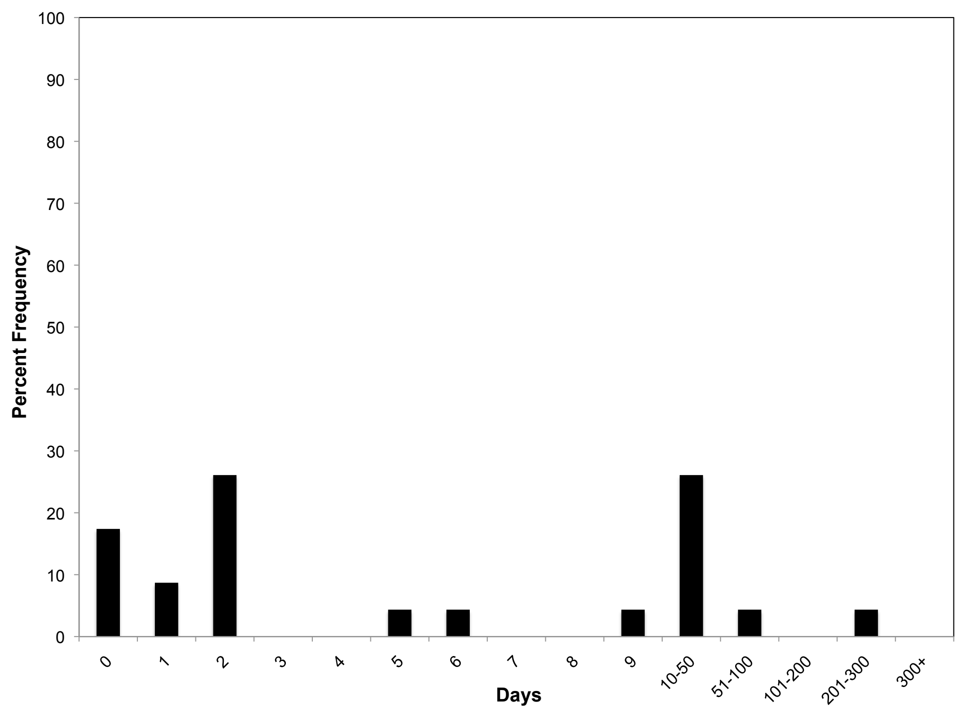
Appendix 3g. Tiger shark 26 percent frequency of gap length from the mesophotic reef acoustic array.



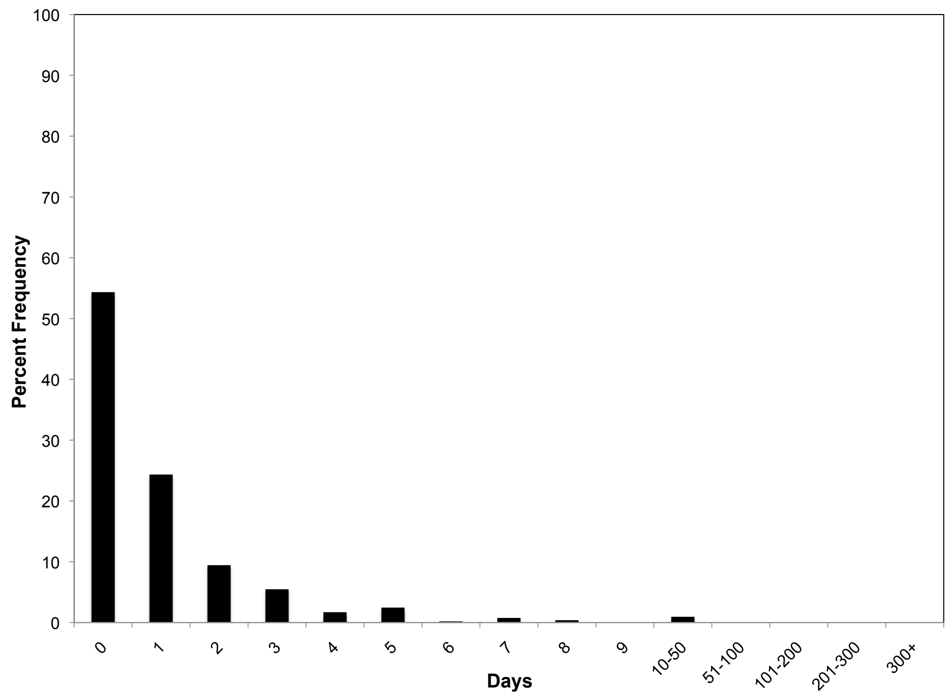
Appendix 3h. Tiger shark 1476 percent frequency of gap length from the mesophotic reef acoustic array.



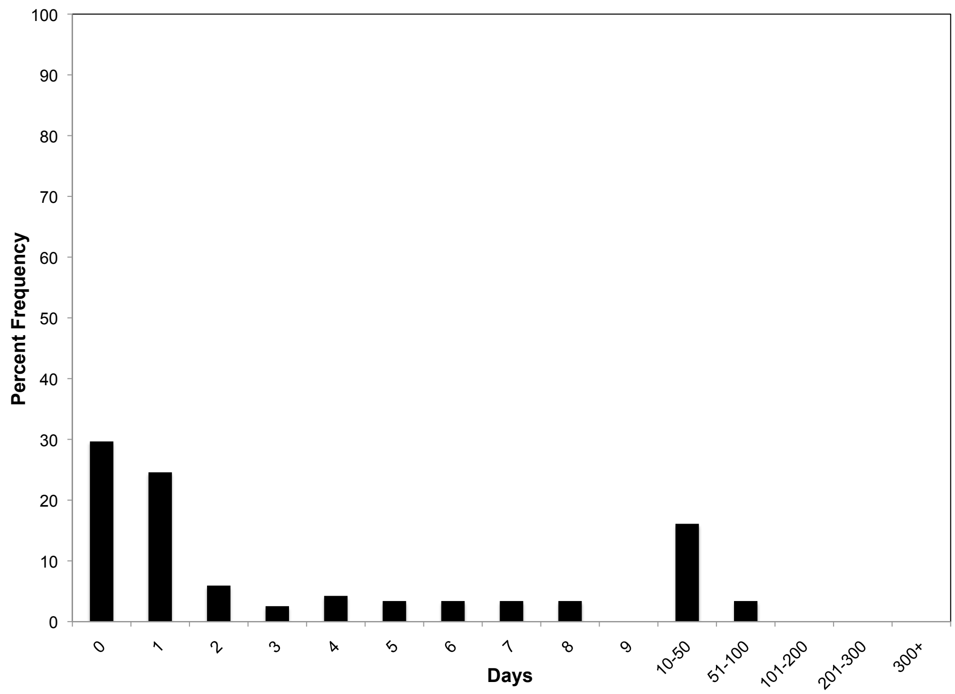
Appendix 3i. Tiger shark 1484 percent frequency of gap length from the mesophotic reef acoustic array.



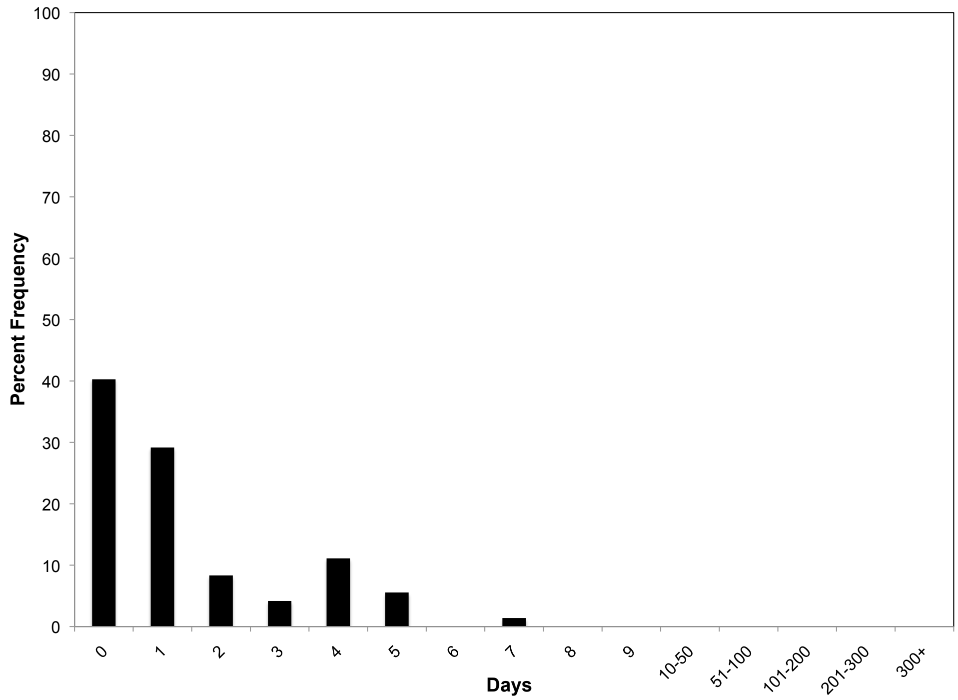
Appendix 3j. Tiger shark 1487 percent frequency of gap length from the mesophotic reef acoustic array.



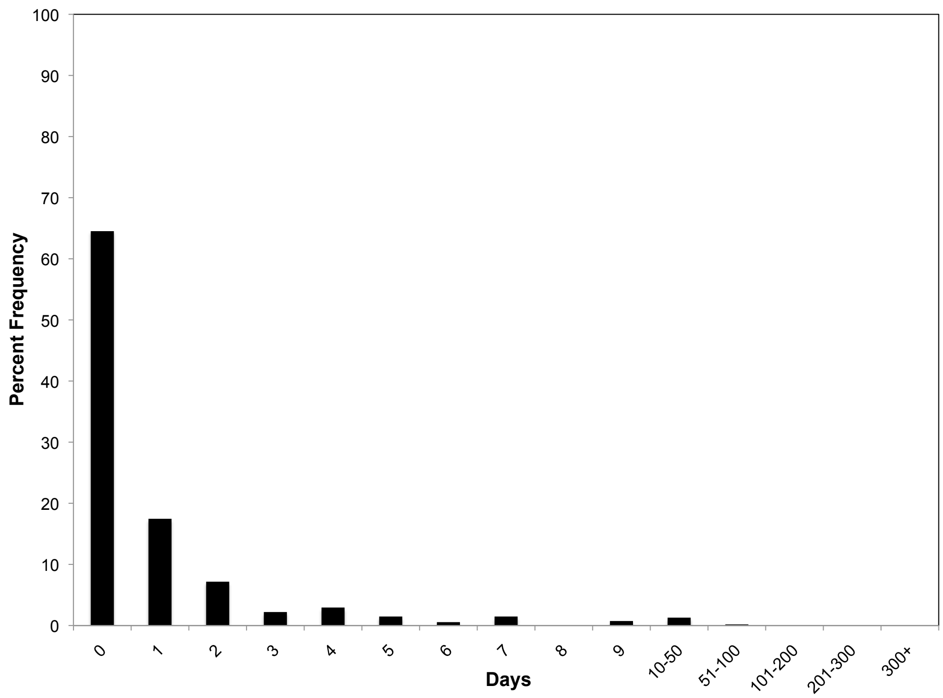
Appendix 3k. Tiger shark 3738 percent frequency of gap length from the mesophotic reef acoustic array.



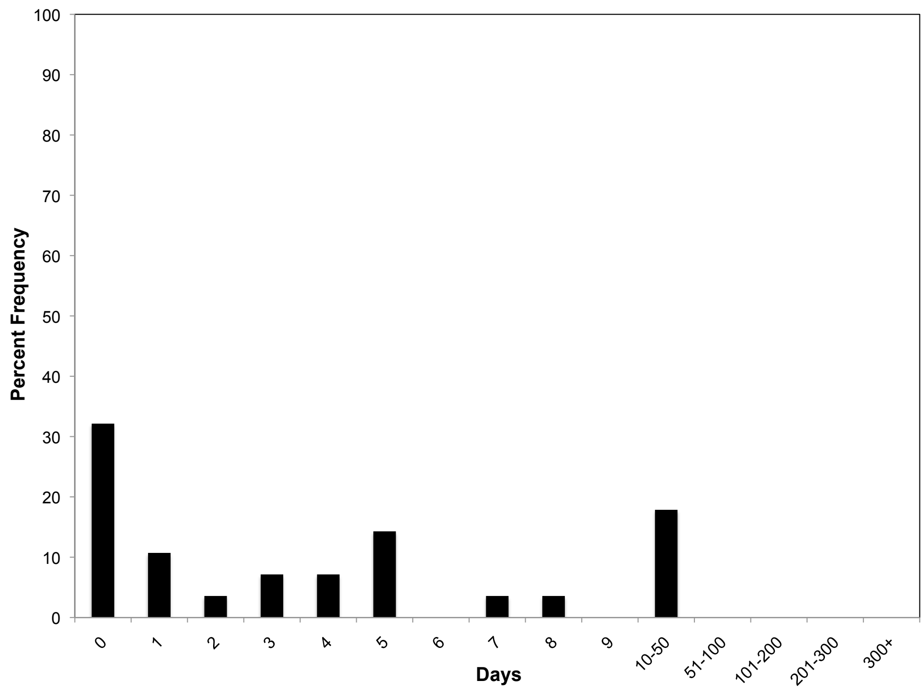
Appendix 3l. Tiger shark 3739 percent frequency of gap length from the mesophotic reef acoustic array.



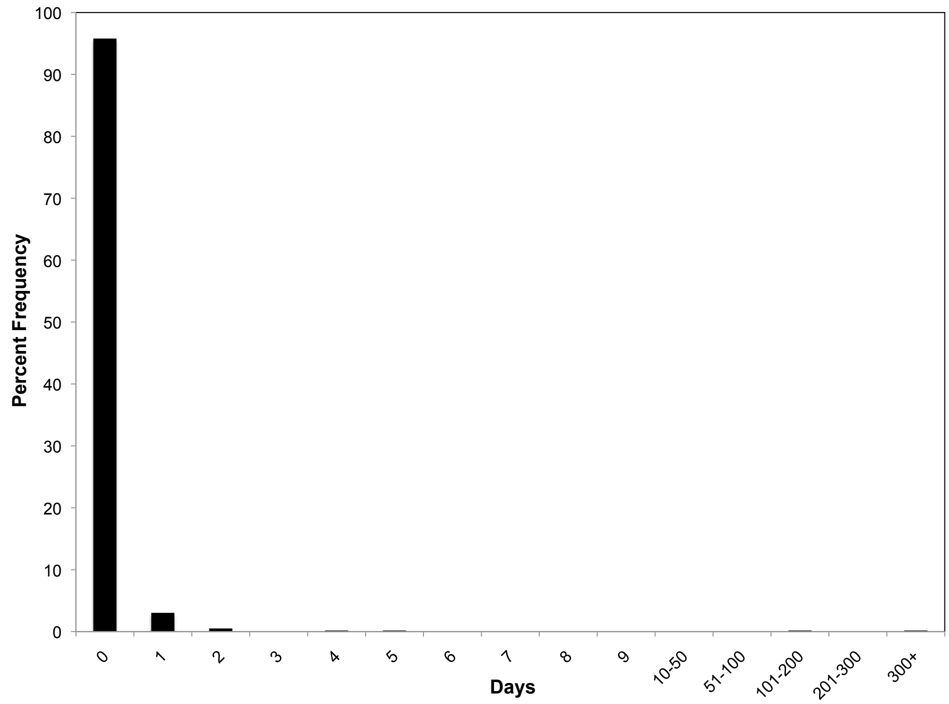
Appendix 3m. Tiger shark 3740 percent frequency of gap length from the mesophotic reef acoustic array.



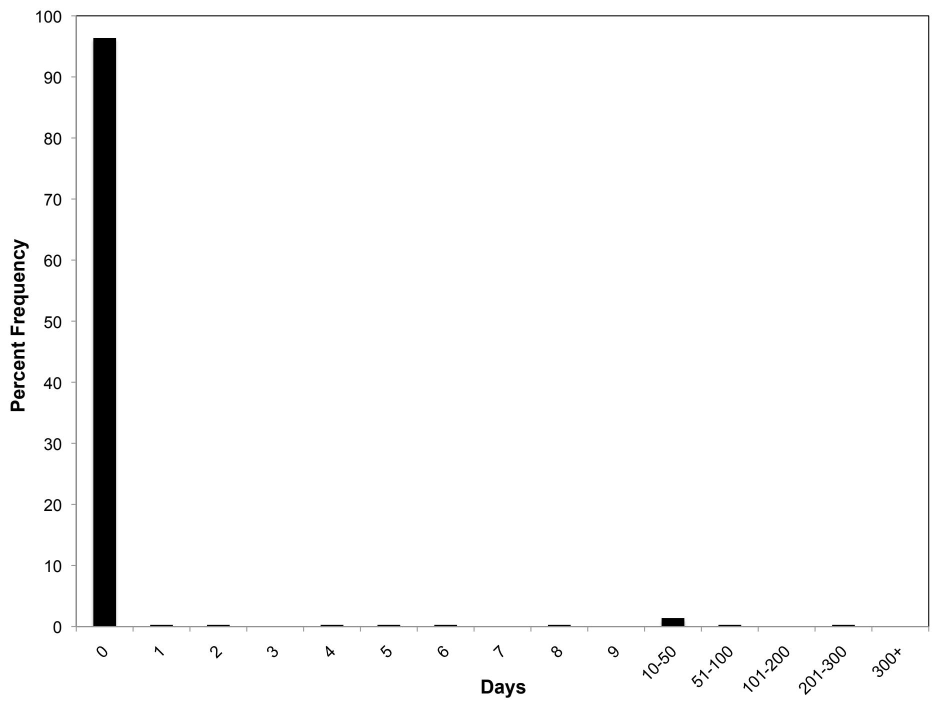
Appendix 3n. Tiger shark 3741 percent frequency of gap length from the mesophotic reef acoustic array.



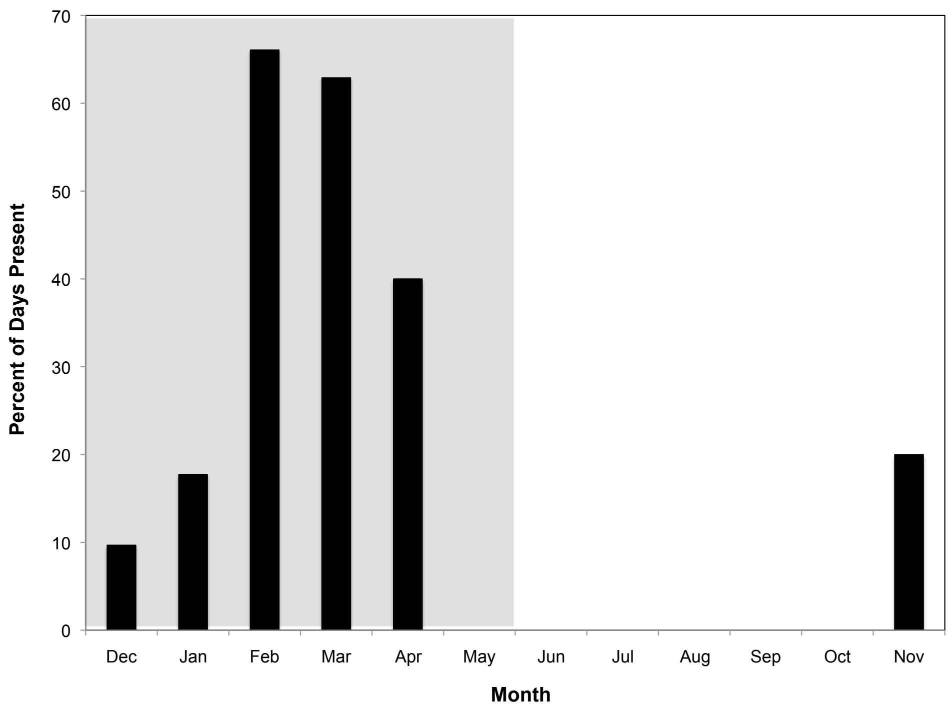
Appendix 3o. Tiger shark 12385 percent frequency of gap length from the mesophotic reef acoustic array.



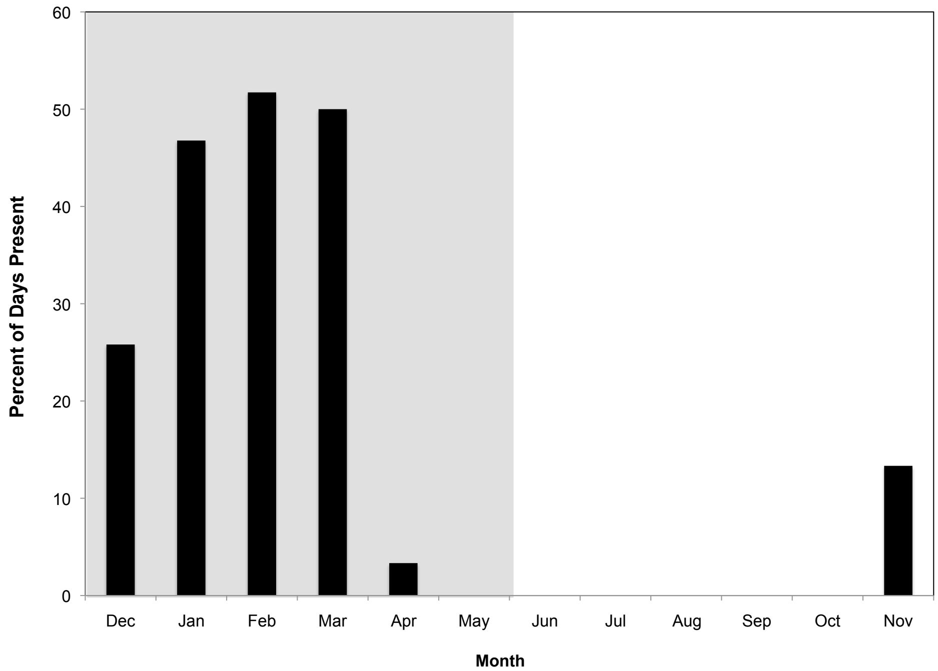
Appendix 3p. Caribbean reef shark 1478 percent frequency of gap length from the mesophotic reef acoustic array.



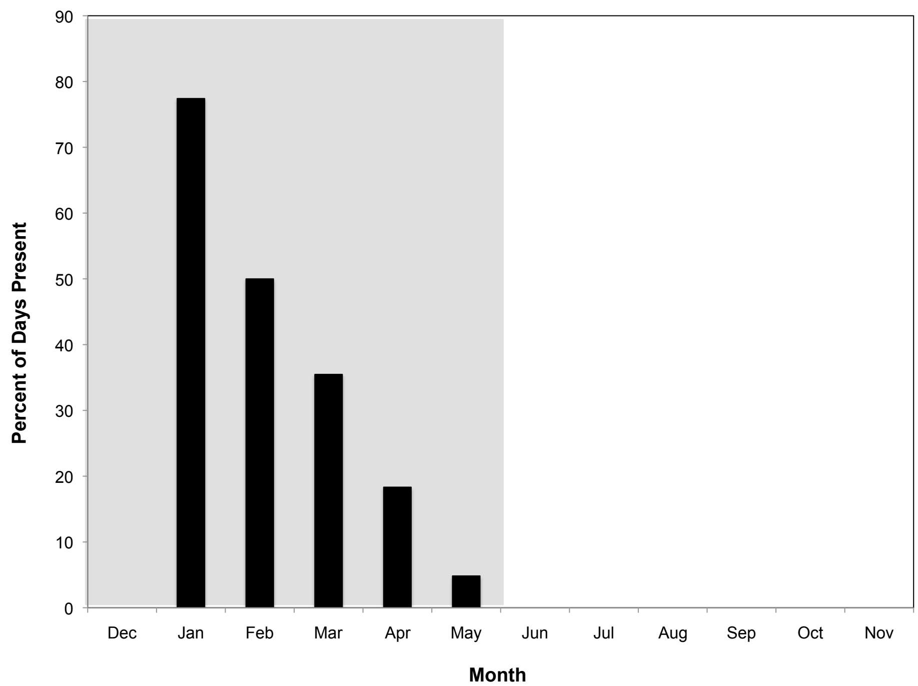
Appendix 3q. Caribbean reef shark 1486 percent frequency of gap length from the mesophotic reef acoustic array.



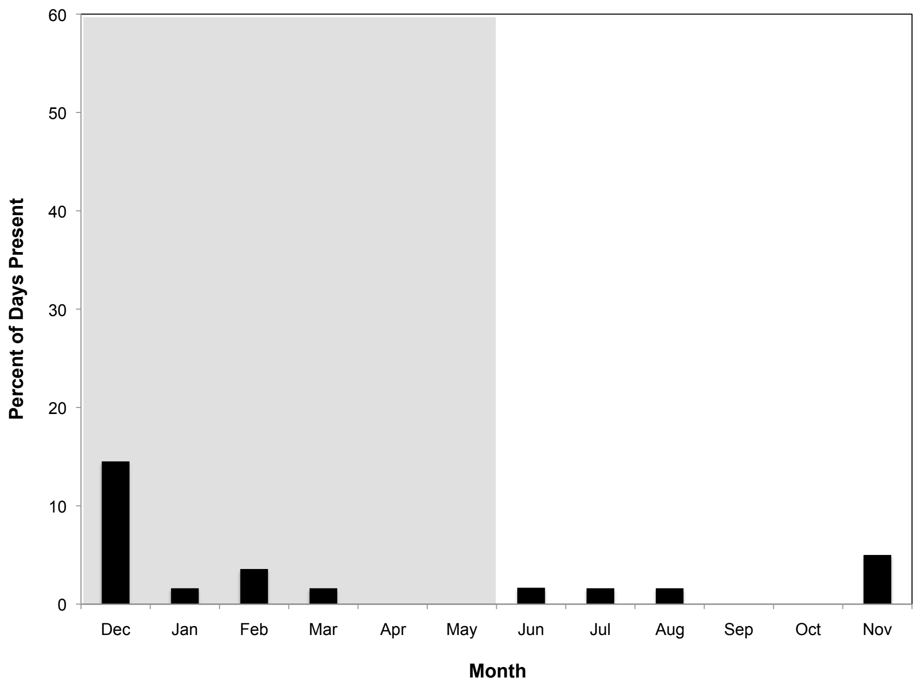
Appendix 4a. Lemon shark 1475 percent of days present at the FSA site each month during 2007. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



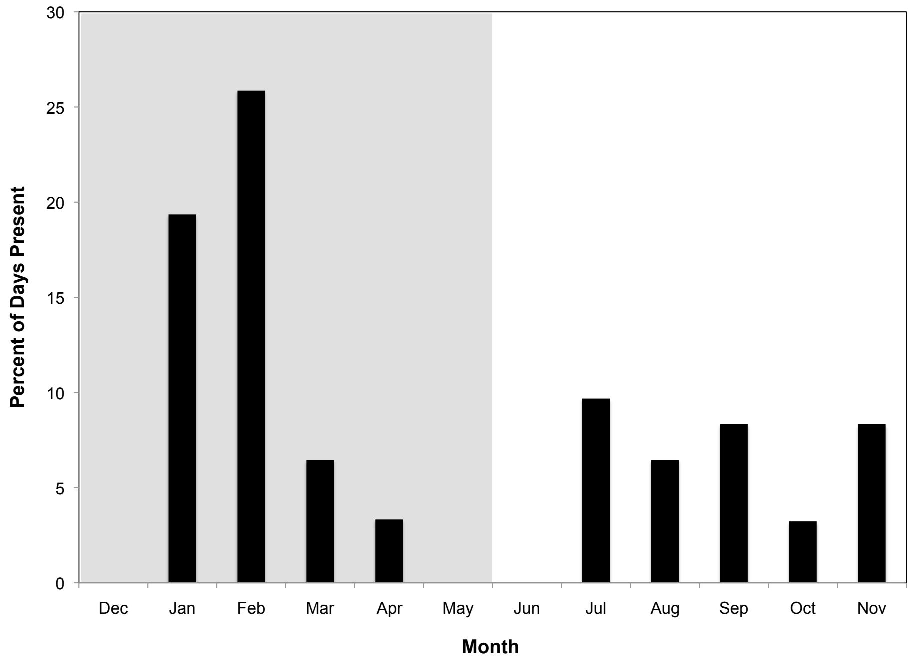
Appendix 4b. Lemon shark 1475 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



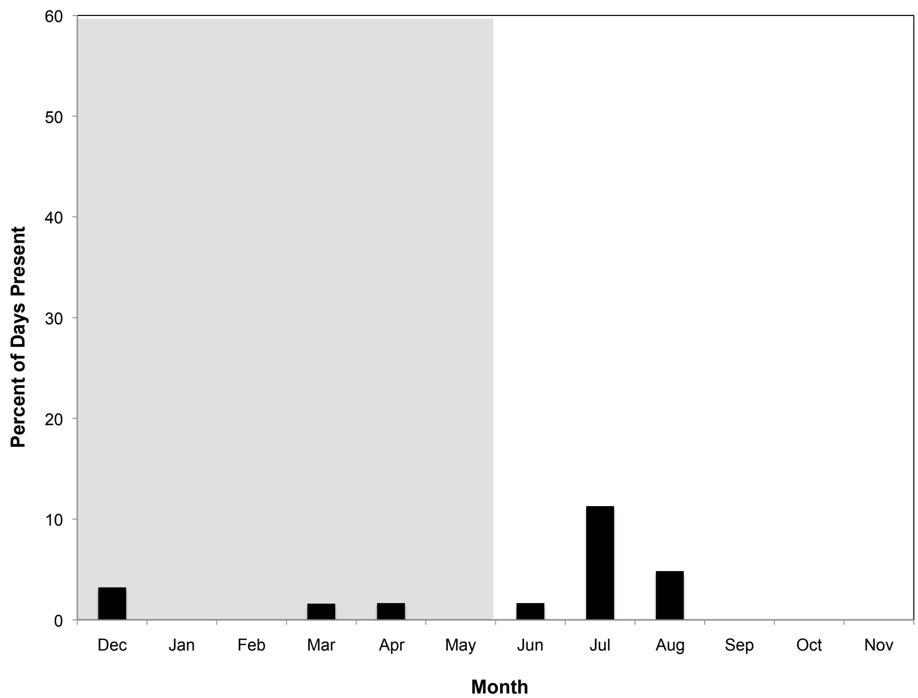
Appendix 4c. Lemon shark 1475 percent of days present at the FSA site each month during 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



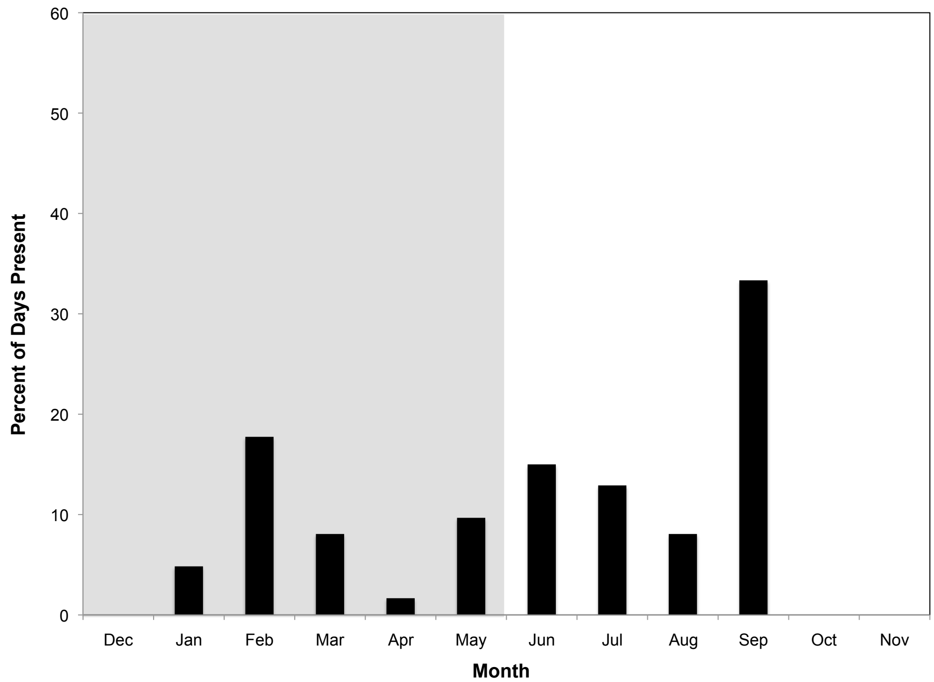
Appendix 4d. Lemon shark 1479 percent of days present at the FSA site each month during 2007. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



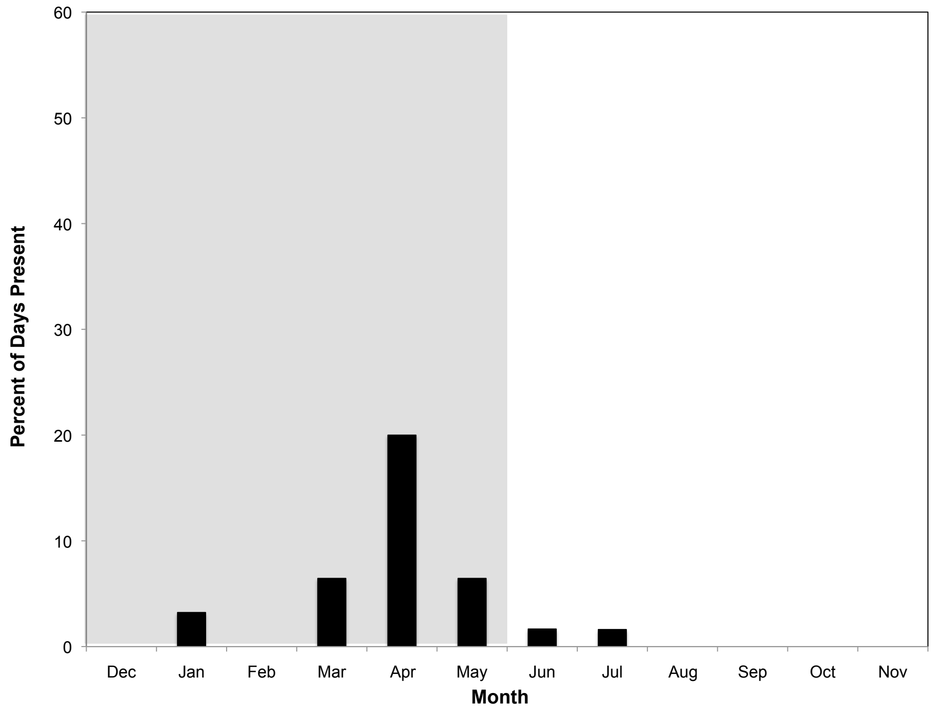
Appendix 4e. Lemon shark 1479 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



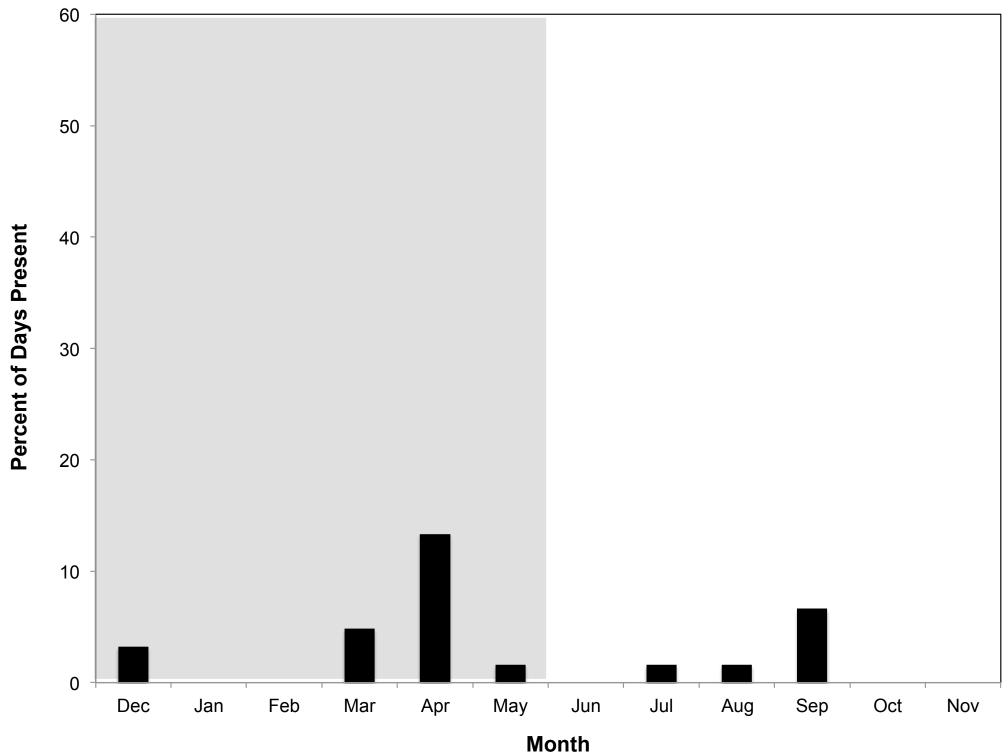
Appendix 4f. Lemon shark 1479 percent of days present at the FSA site each month during 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



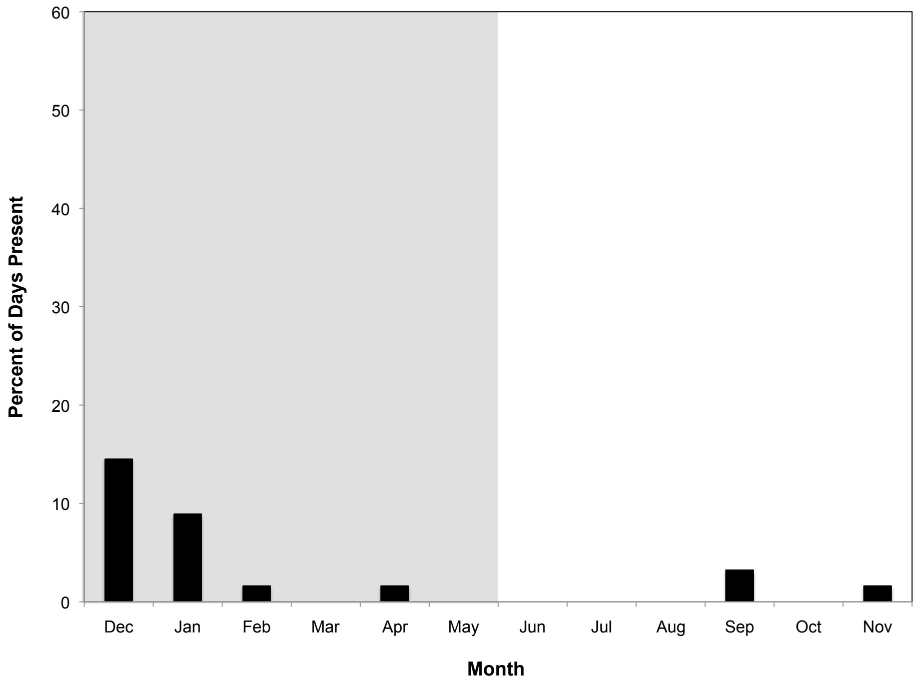
Appendix 4g. Lemon shark 1479 percent of days present at the FSA site each month during 2010. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



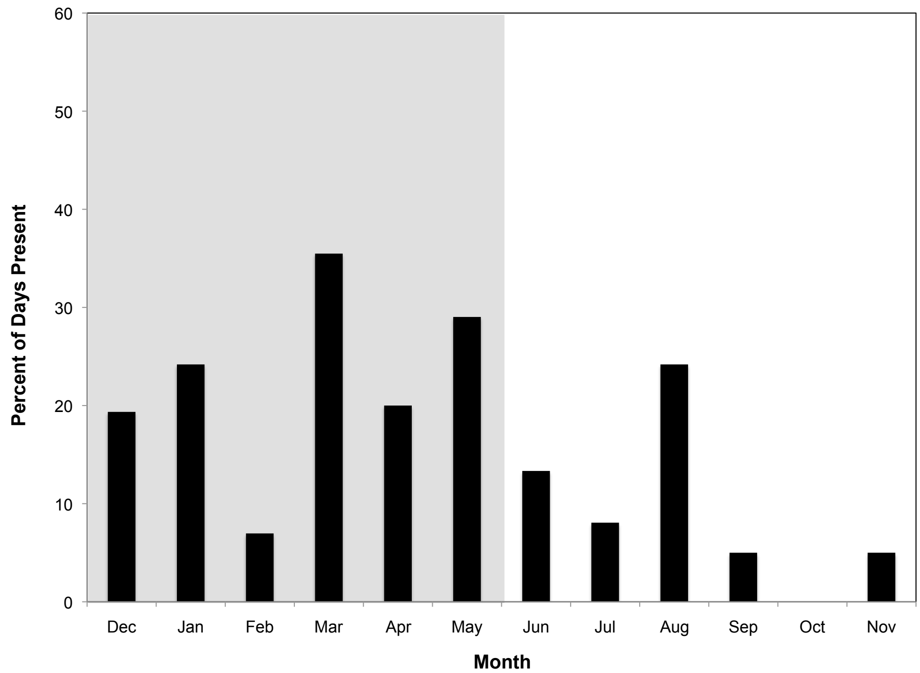
Appendix 4h. Lemon shark 3743 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



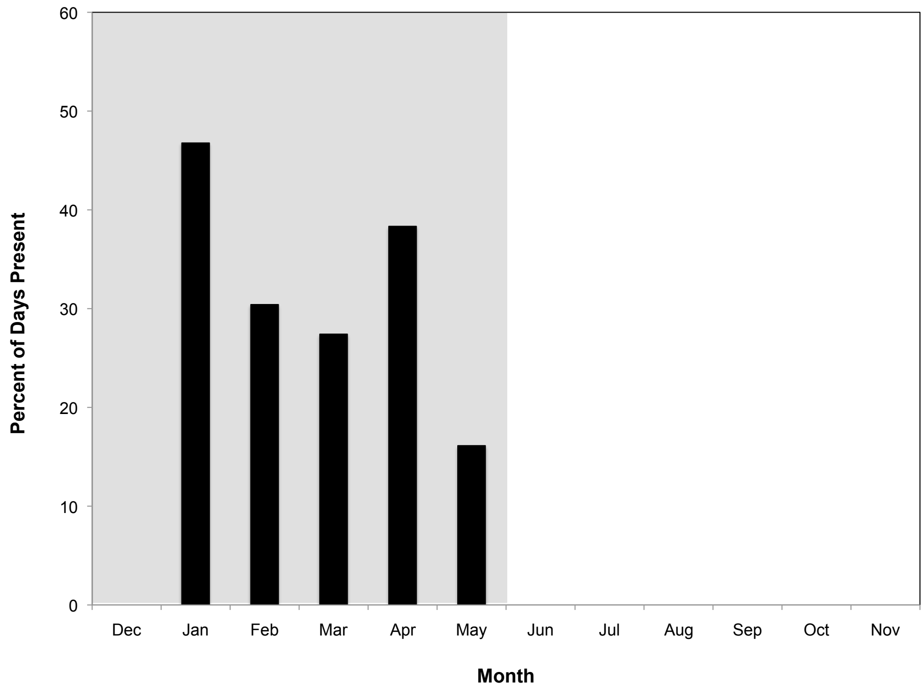
Appendix 4i. Lemon shark 3747 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



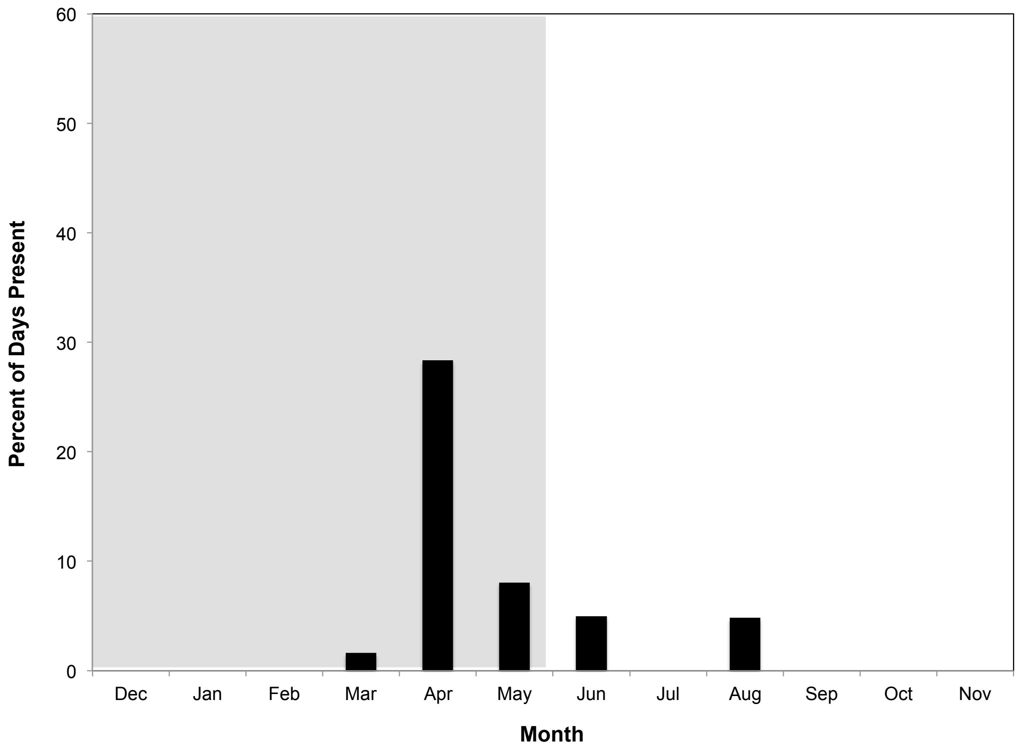
Appendix 4j. Lemon shark 3747 percent of days present at the FSA site each month during 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



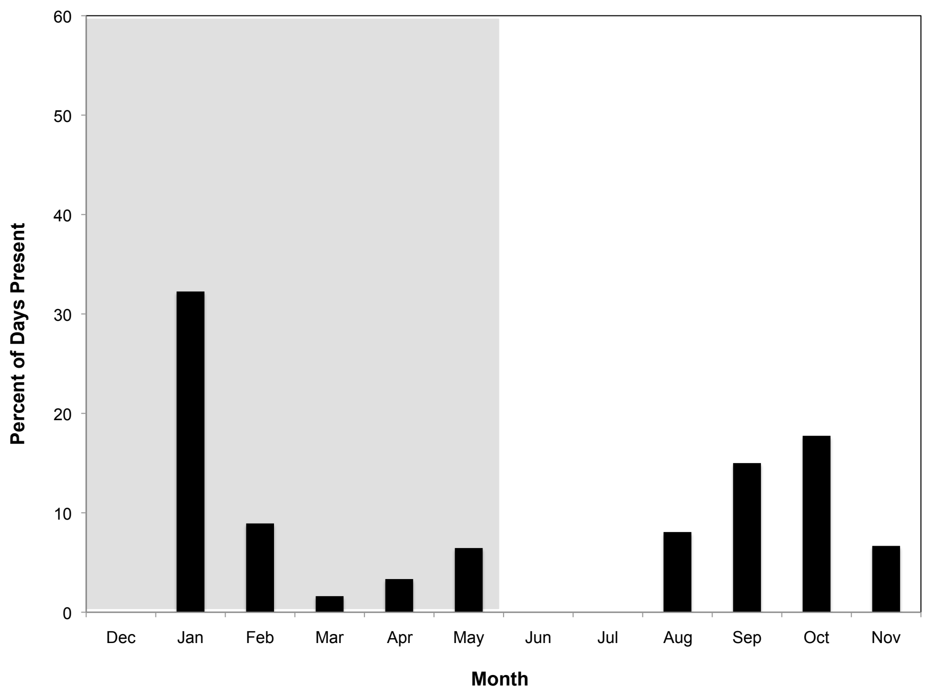
Appendix 4k. Lemon shark 3747 percent of days present at the FSA site each month during 2010. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



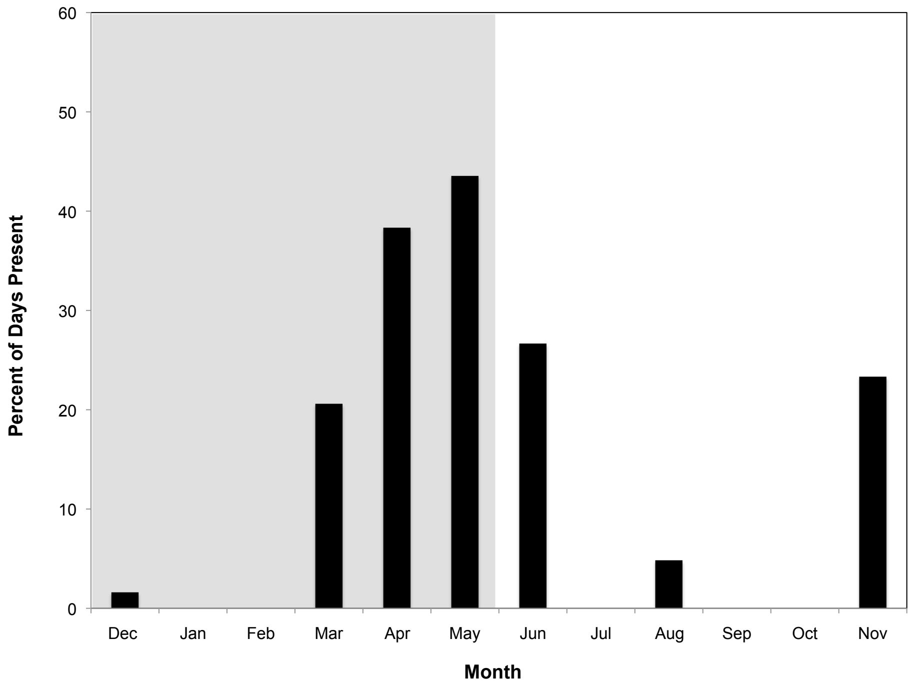
Appendix 4l. Lemon shark 3747 percent of days present at the FSA site each month during 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



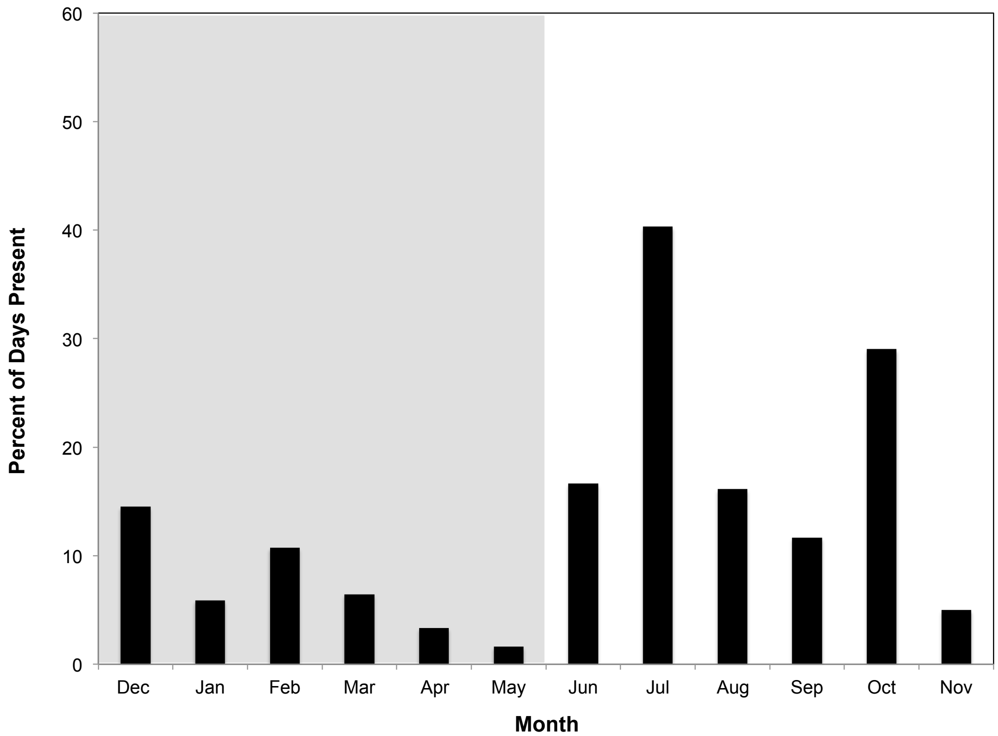
Appendix 4m. Lemon shark 12384 percent of days present at the FSA site each month during 2007. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



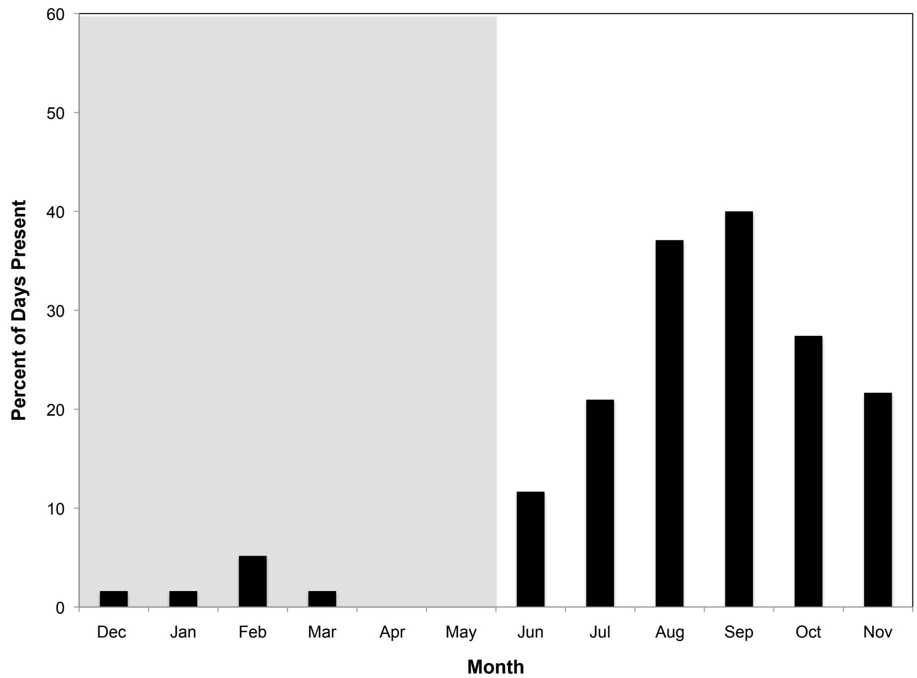
Appendix 4n. Lemon shark 58129 percent of days present at the FSA site each month during 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



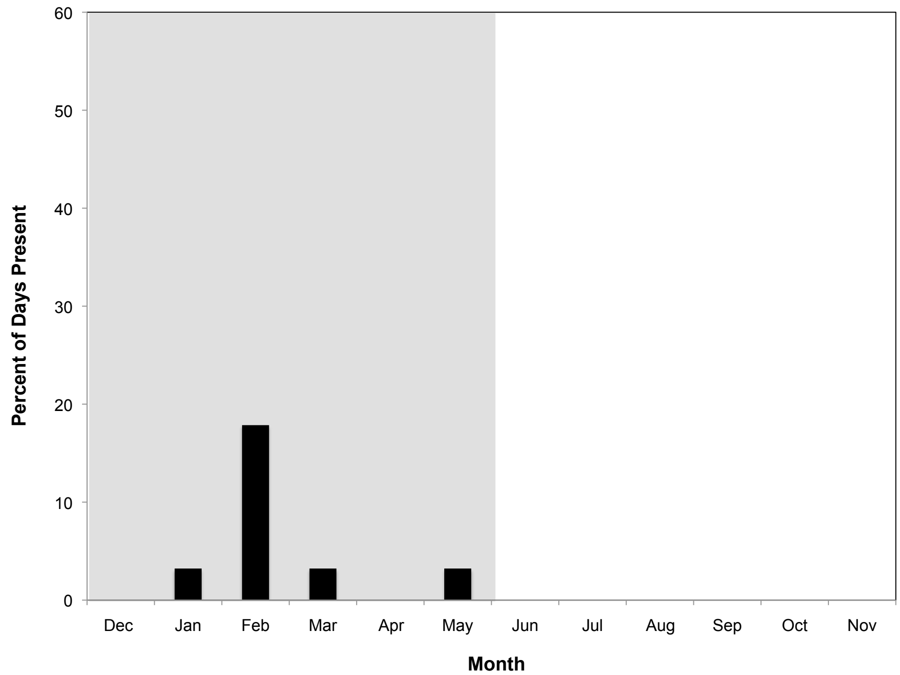
Appendix 5a. Tiger shark 26 percent of days present at the FSA site each month during 2007. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



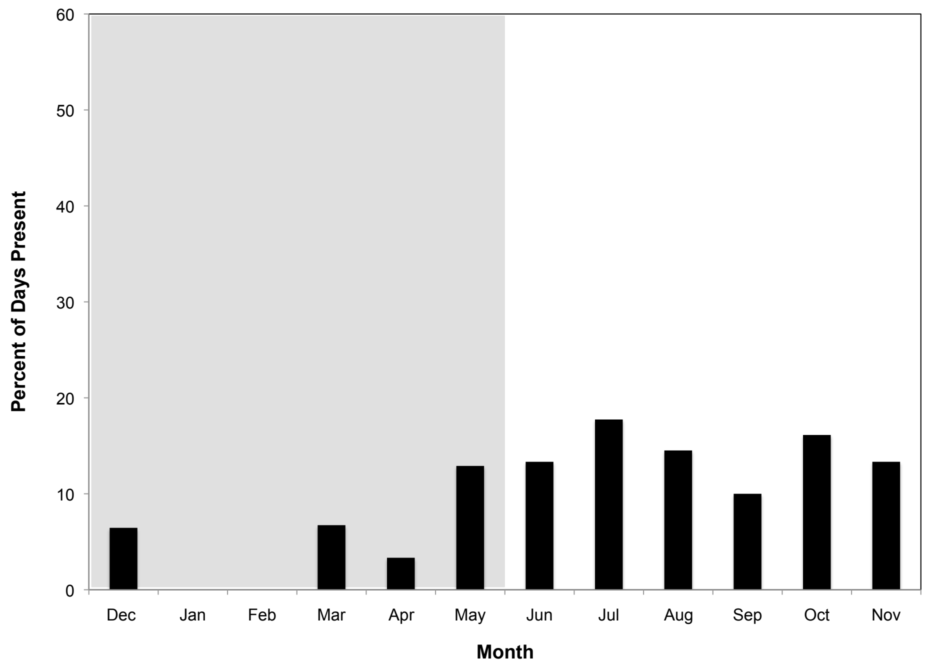
Appendix 5b. Tiger shark 1476 percent of days present at the FSA site each month during 2007. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



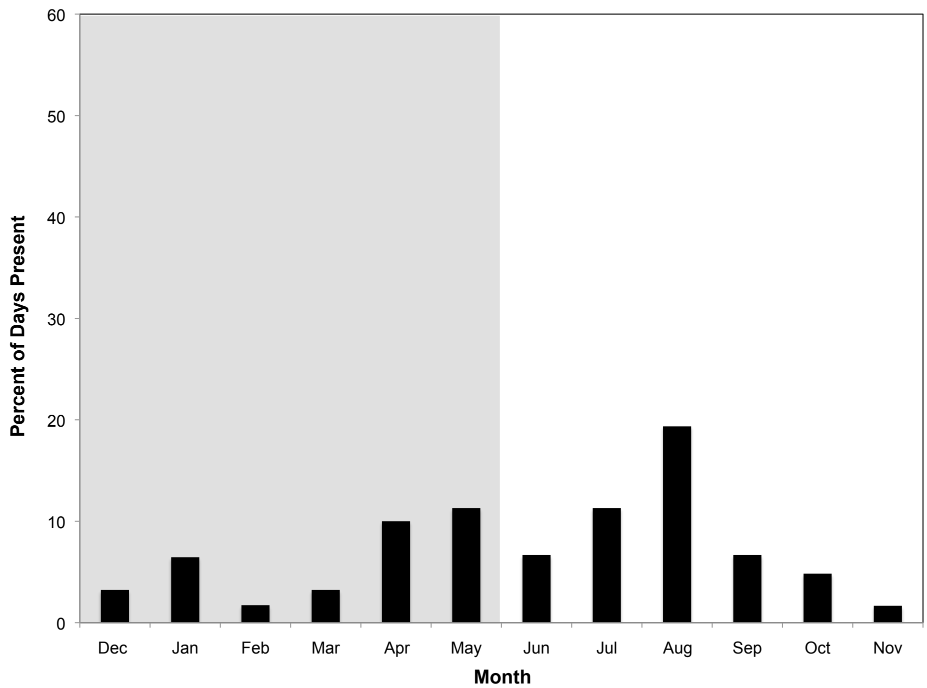
Appendix 5c. Tiger shark 1476 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



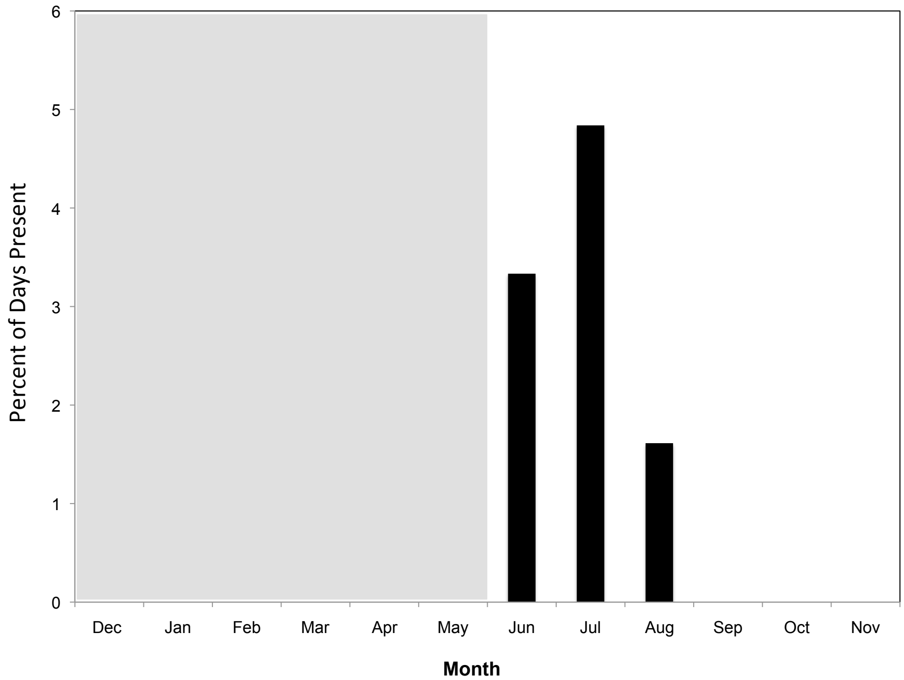
Appendix 5d. Tiger shark 1476 percent of days present at the FSA site each month during 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



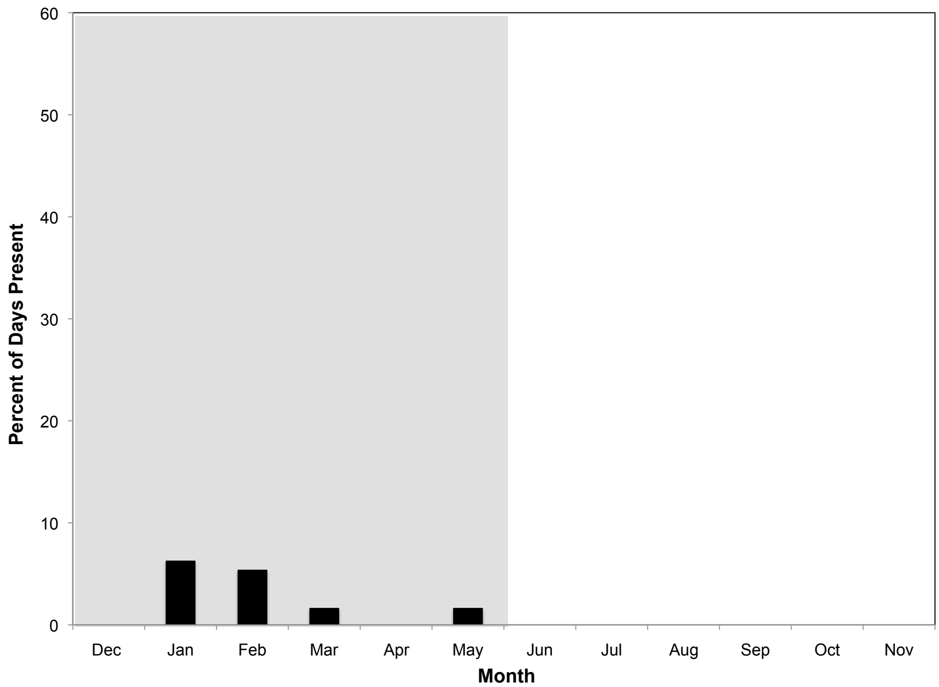
Appendix 5e. Tiger shark 1484 percent of days present at the FSA site each month during 2007. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



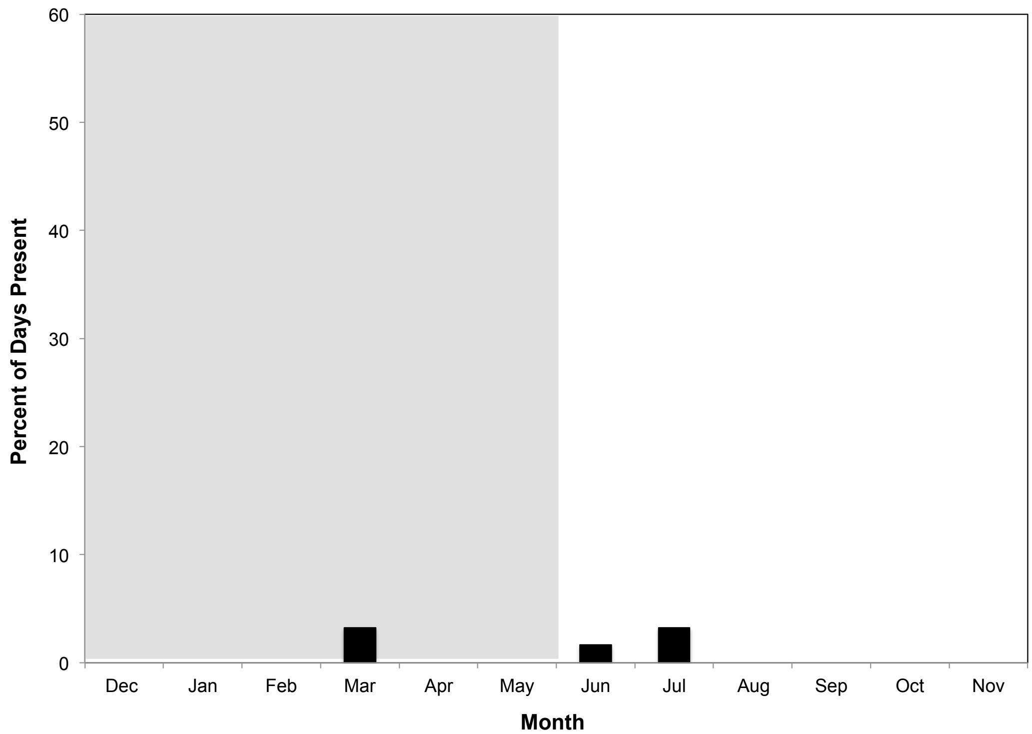
Appendix 5f. Tiger shark 1484 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



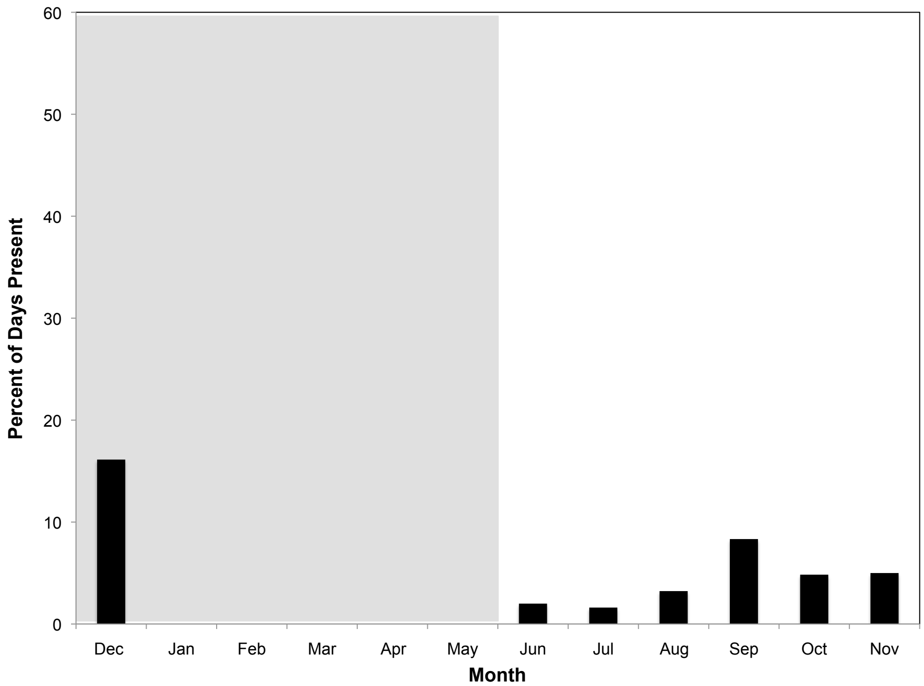
Appendix 5g. Tiger shark 1484 percent of days present at the FSA site each month during 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



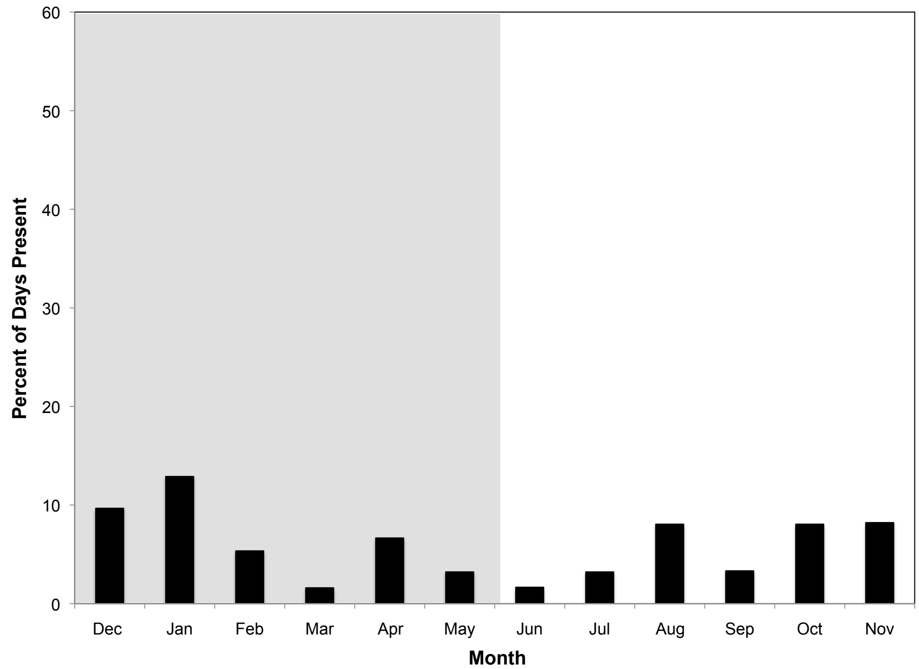
Appendix 5h. Tiger shark 1487 percent of days present at the FSA site each month during 2007. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



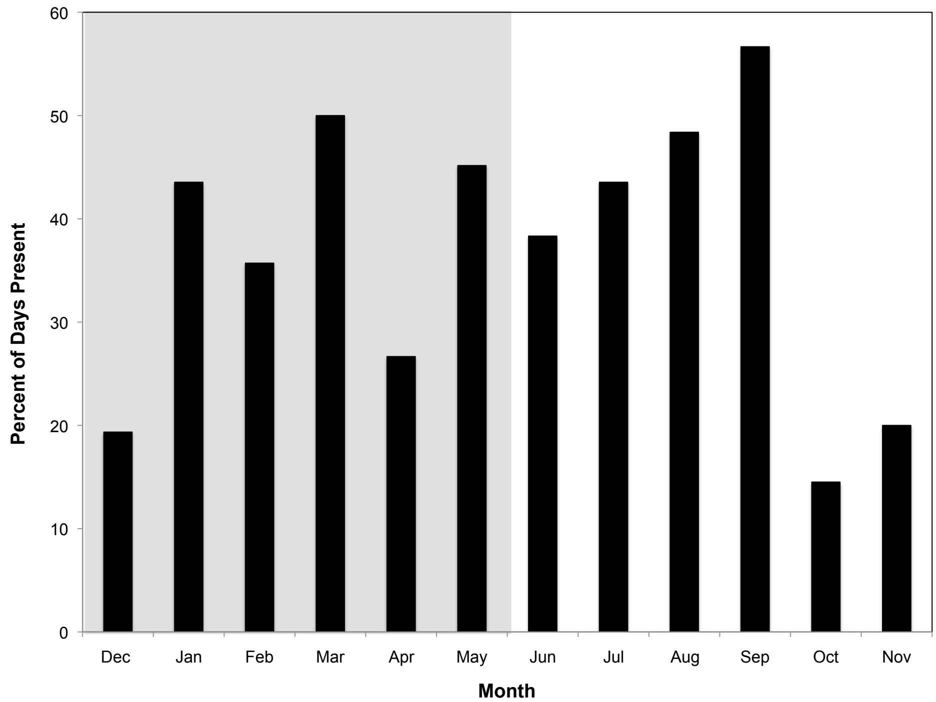
Appendix 5i. Tiger shark 1487 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



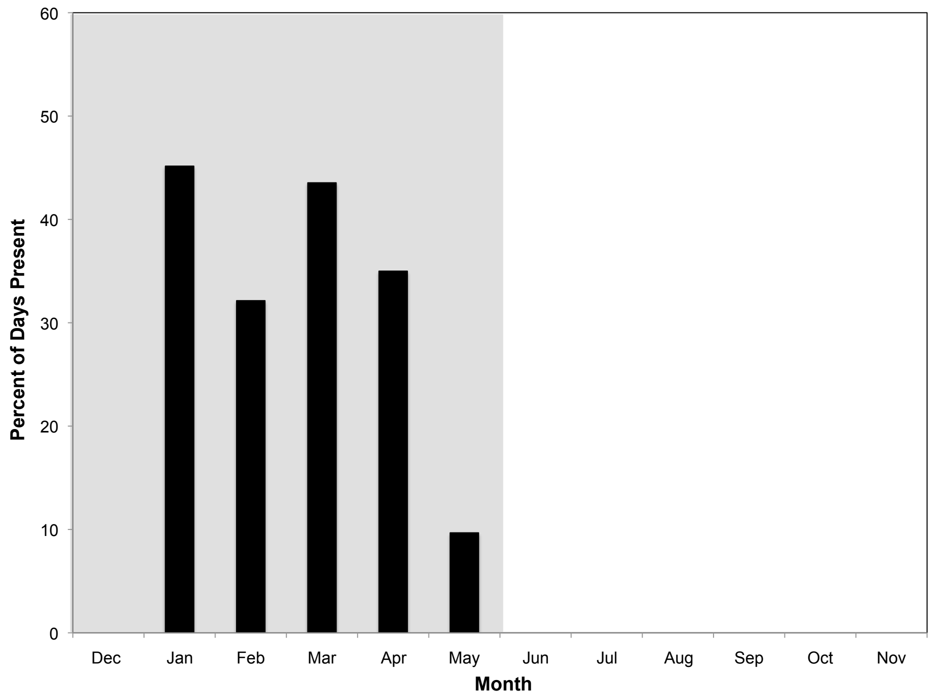
Appendix 5j. Tiger shark 3738 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



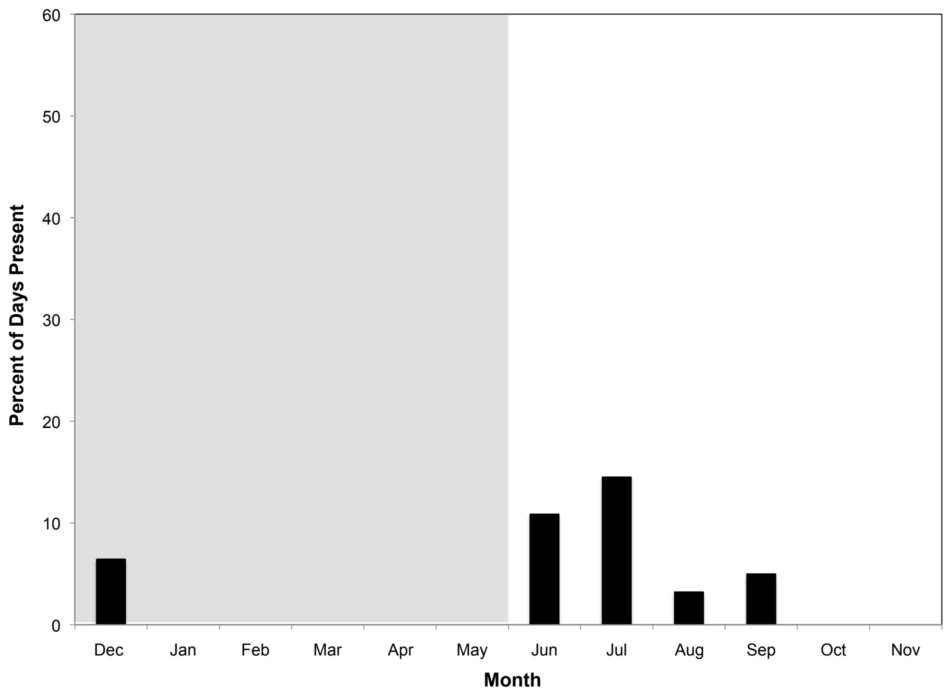
Appendix 5k. Tiger shark 3738 percent of days present at the FSA site each month during 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



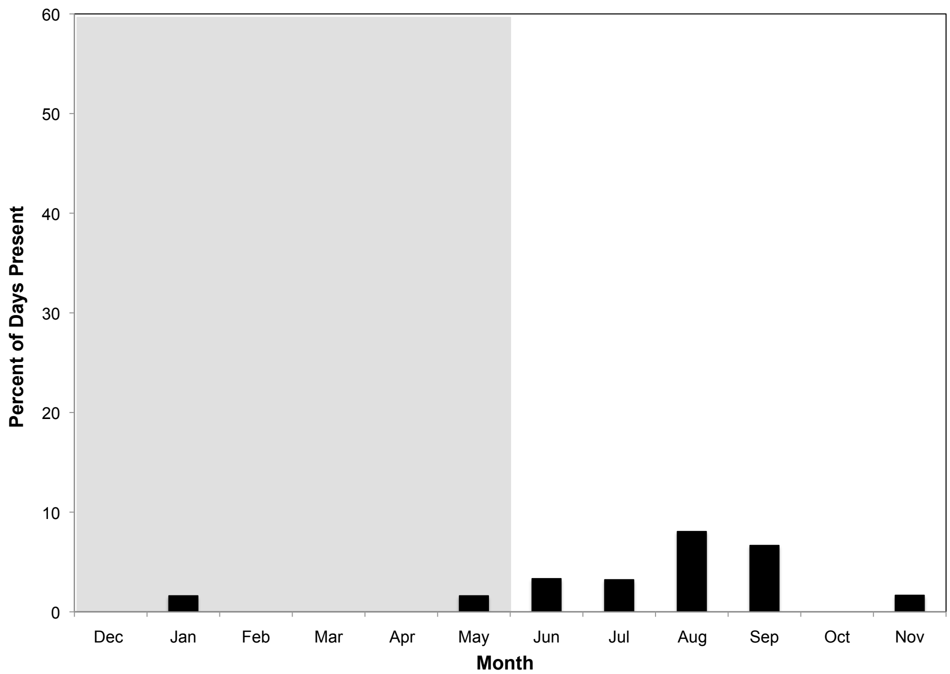
Appendix 5l. Tiger shark 3738 percent of days present at the FSA site each month during 2010. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



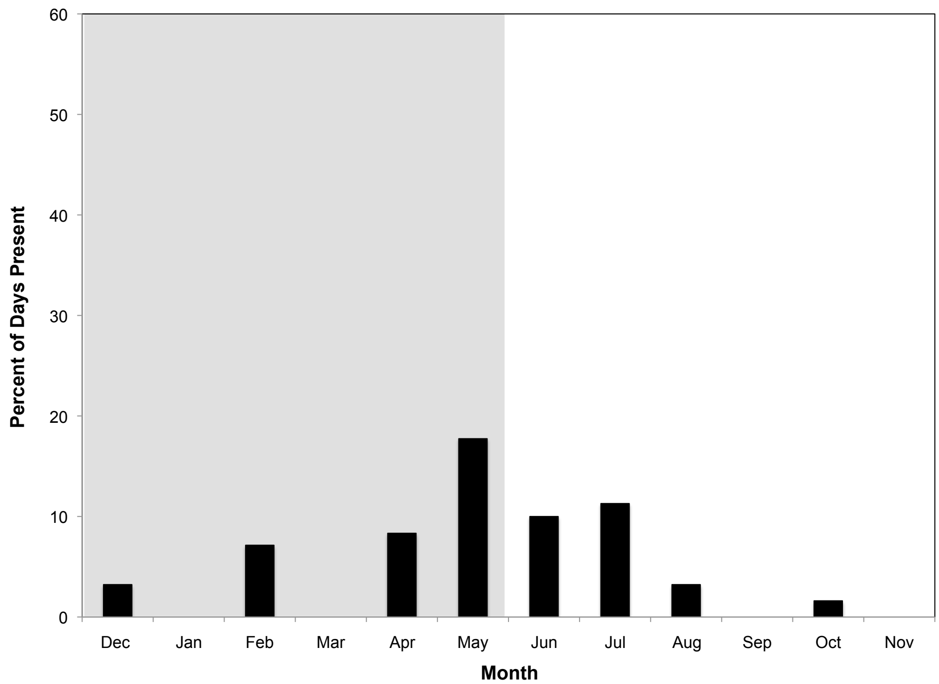
Appendix 5m. Tiger shark 3738 percent of days present at the FSA site each month during 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



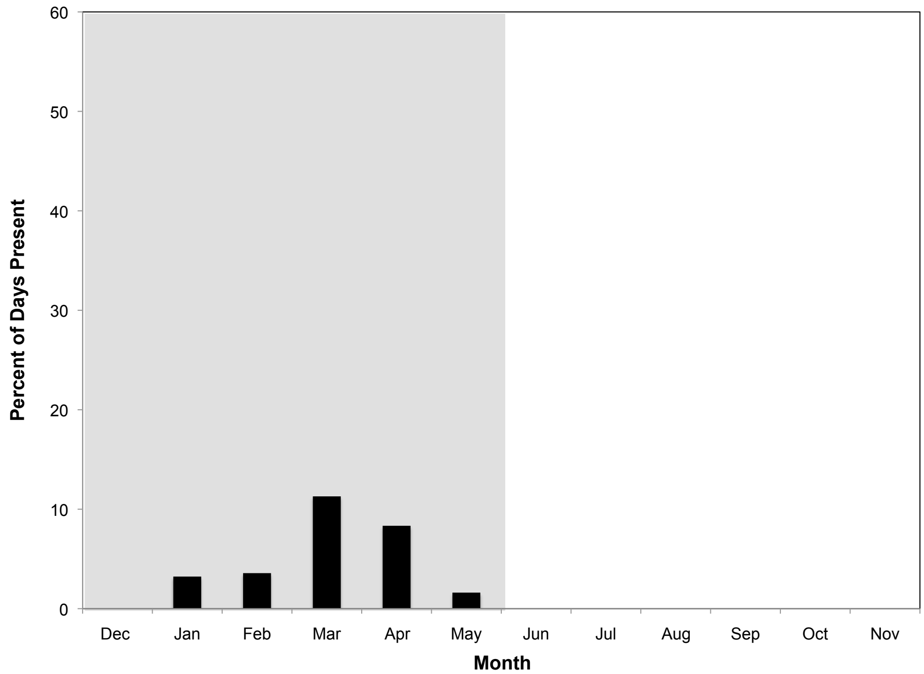
Appendix 5n. Tiger shark 3739 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



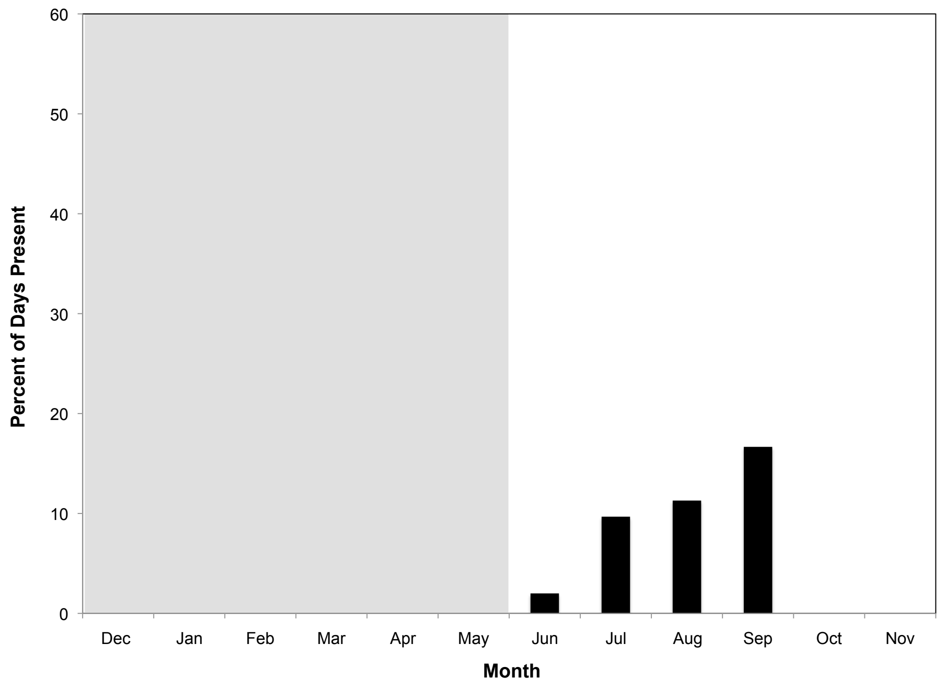
Appendix 5o. Tiger shark 3739 percent of days present at the FSA site each month during 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



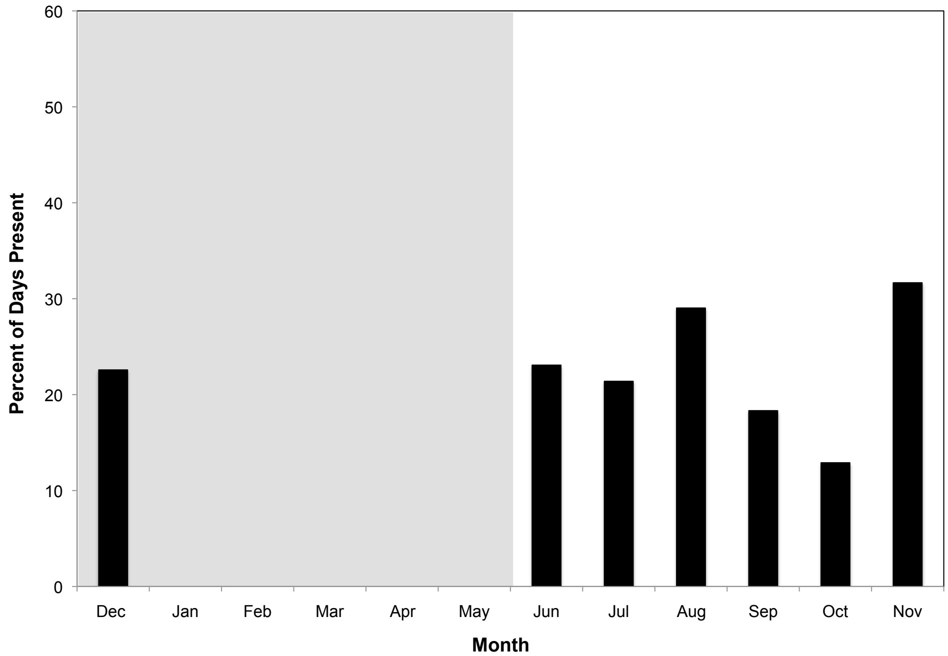
Appendix 5p. Tiger shark 3739 percent of days present at the FSA site each month during 2010. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



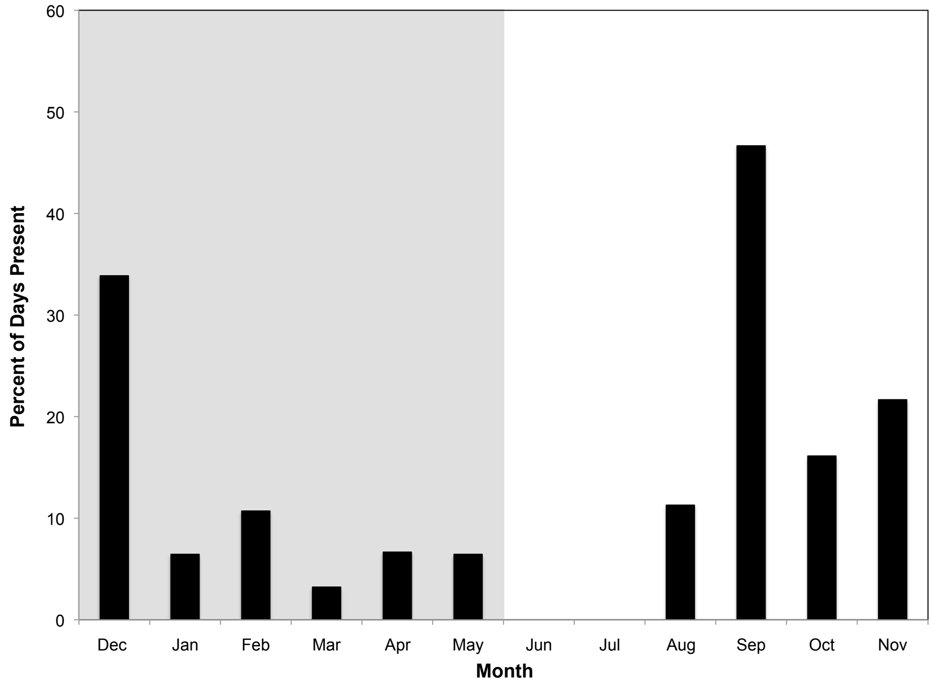
Appendix 5q. Tiger shark 3739 percent of days present at the FSA site each month during 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



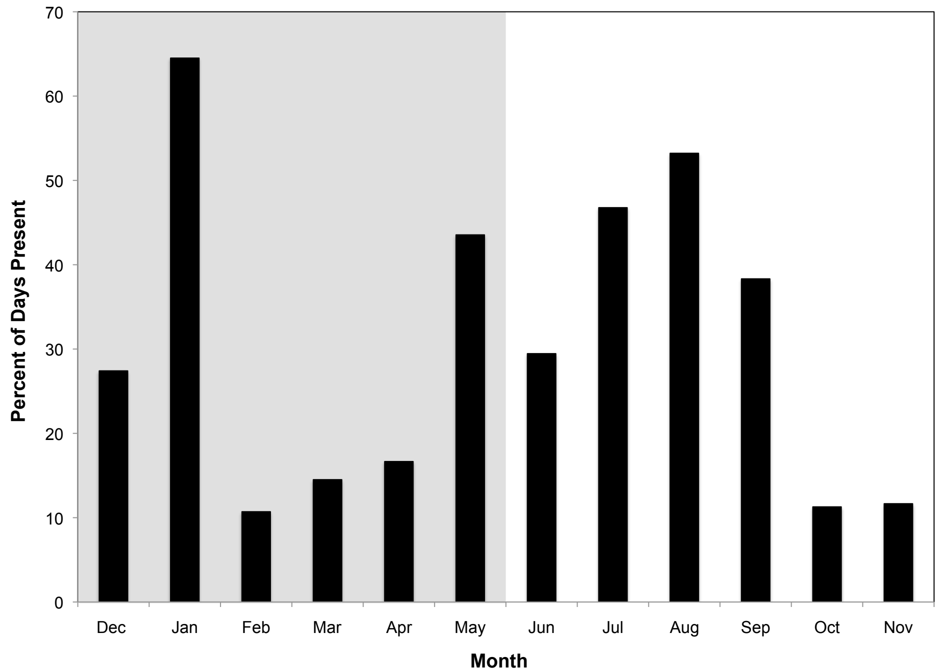
Appendix 5r. Tiger shark 3740 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



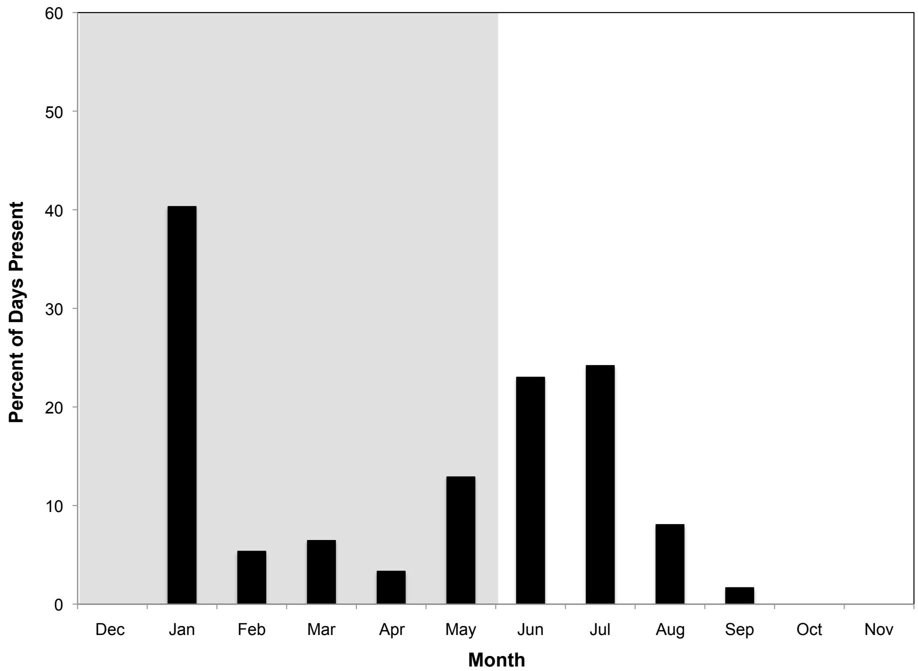
Appendix 5s. Tiger shark 3741 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



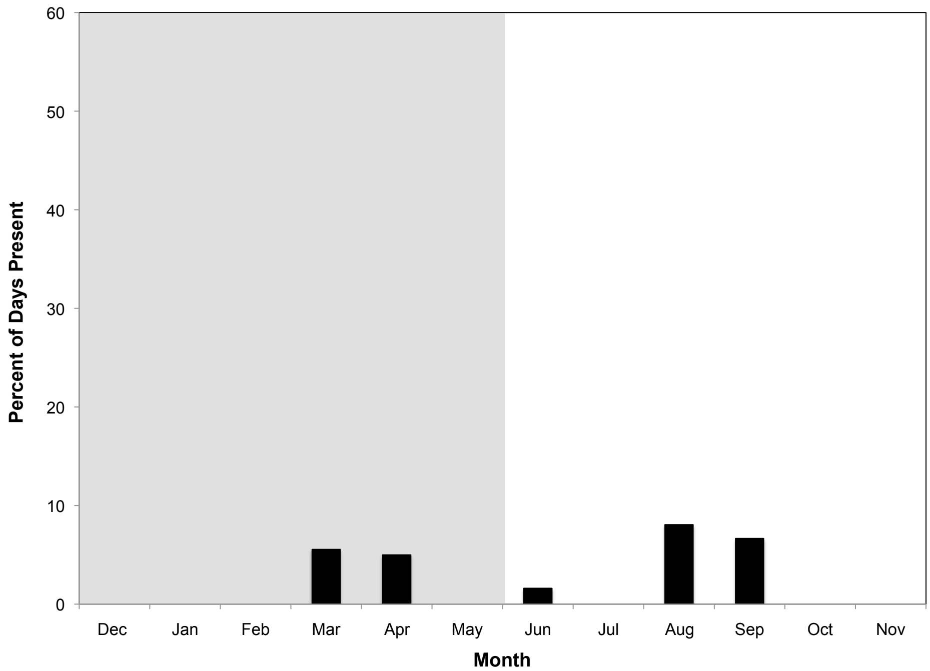
Appendix 5t. Tiger shark 3741 percent of days present at the FSA site each month during 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



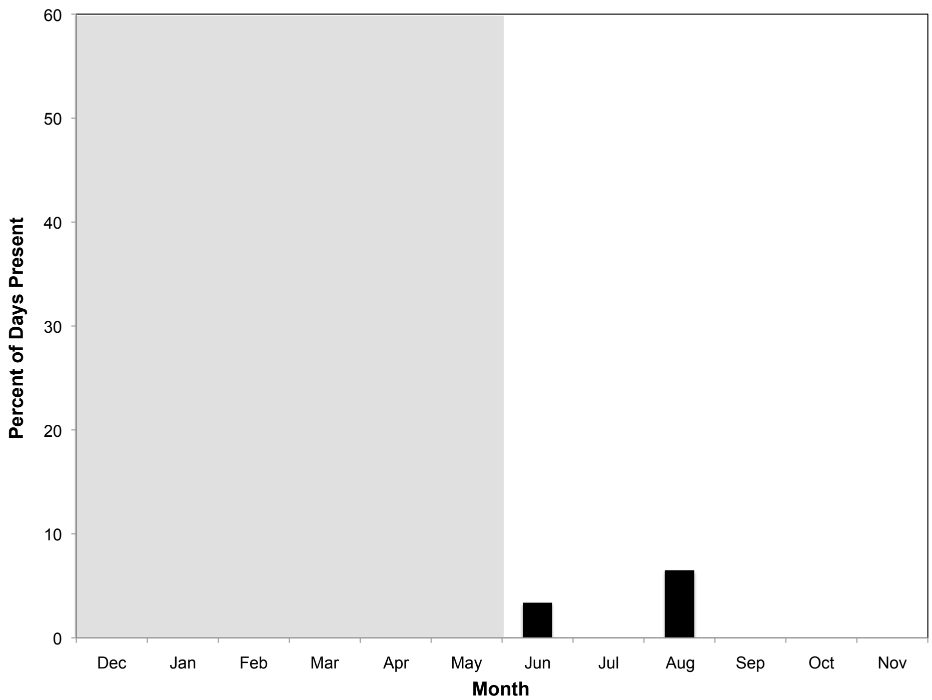
Appendix 5u. Tiger shark 3741 percent of days present at the FSA site each month during 2010. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



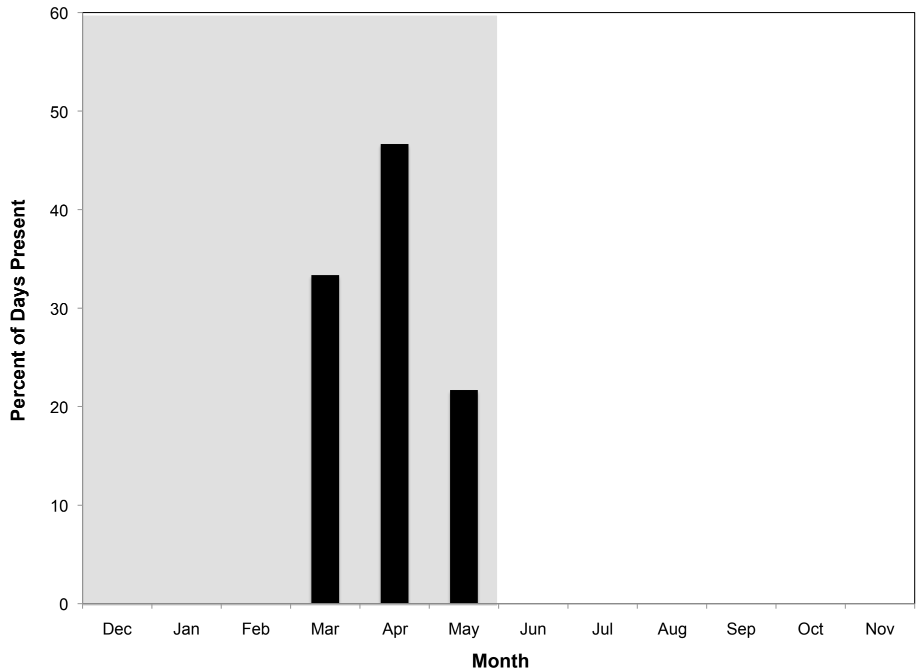
Appendix 5v. Tiger shark 3741 percent of days present at the FSA site each month during 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



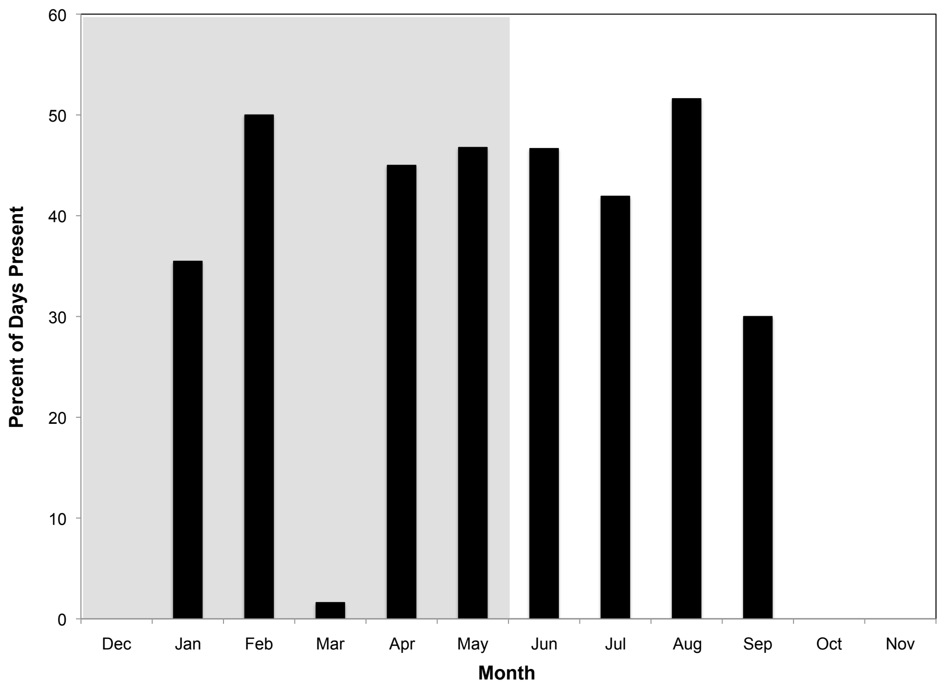
Appendix 5w. Tiger shark 12385 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



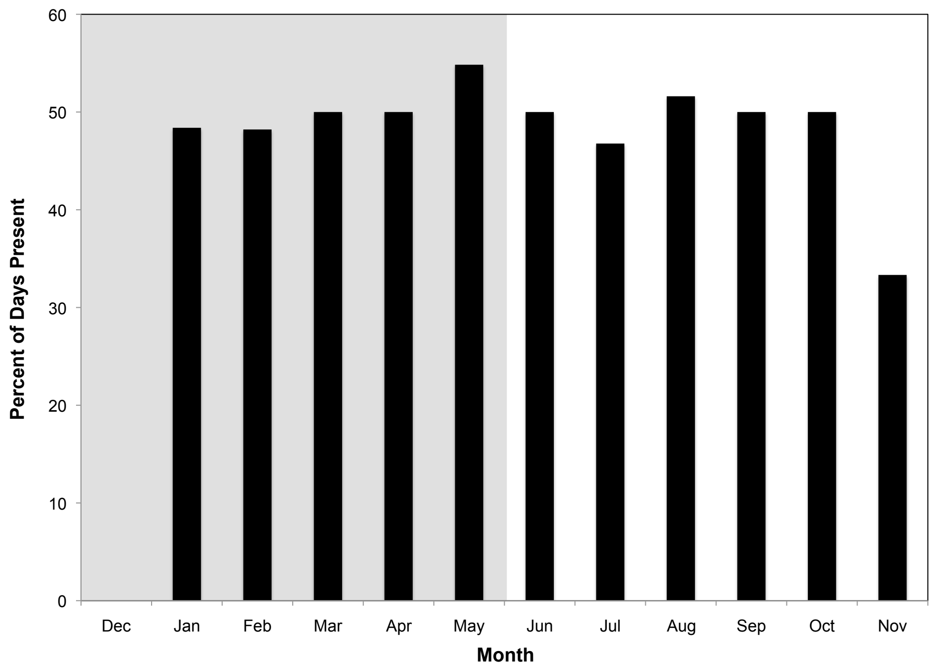
Appendix 5x. Tiger shark 49874 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



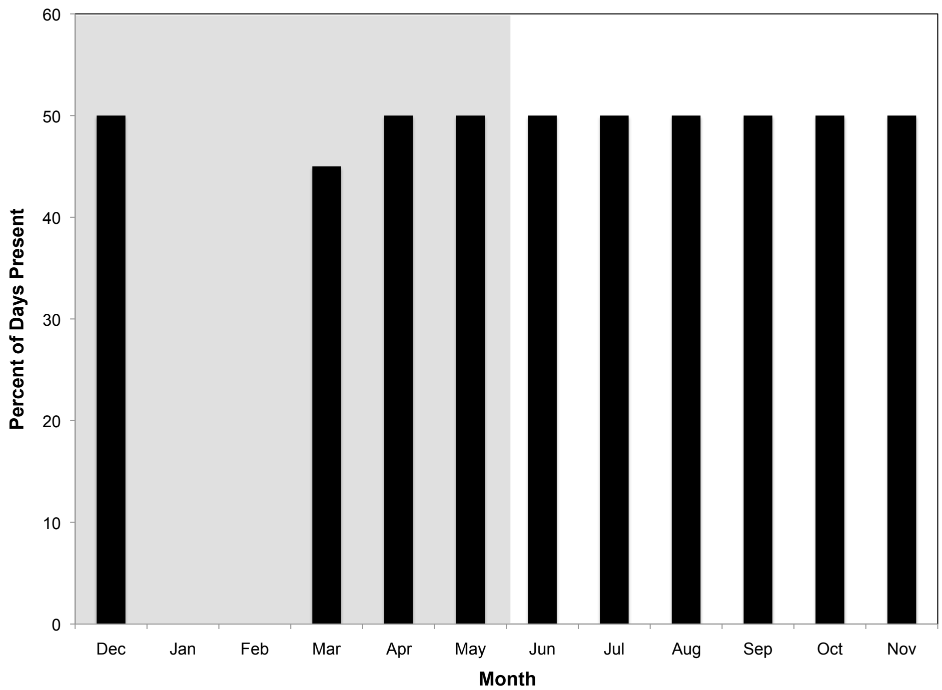
Appendix 6a. Caribbean reef shark 1478 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



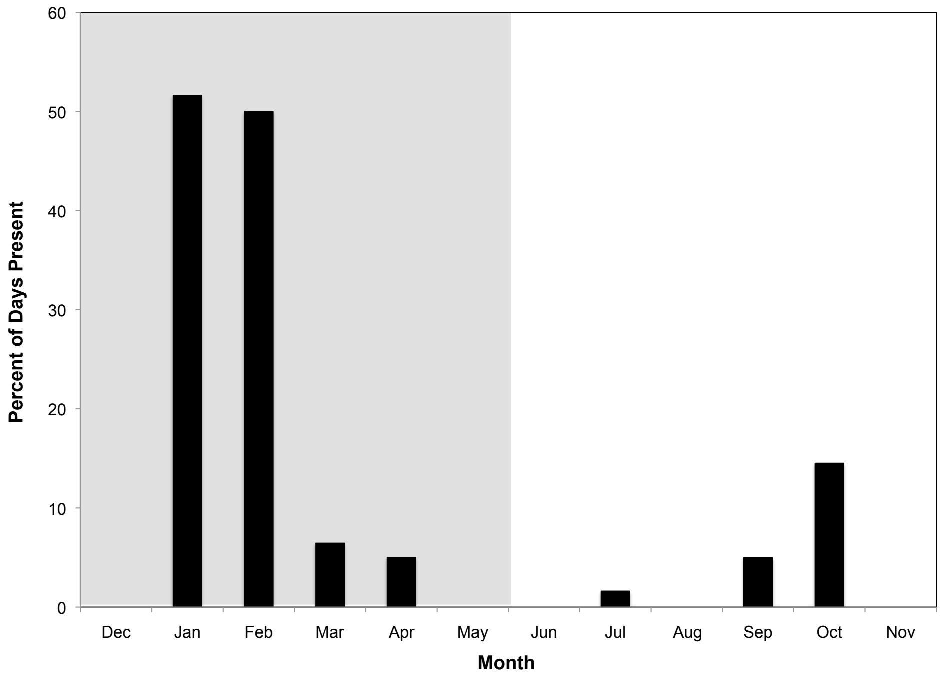
Appendix 6b. Caribbean reef shark 1478 percent of days present at the FSA site each month during 2010. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



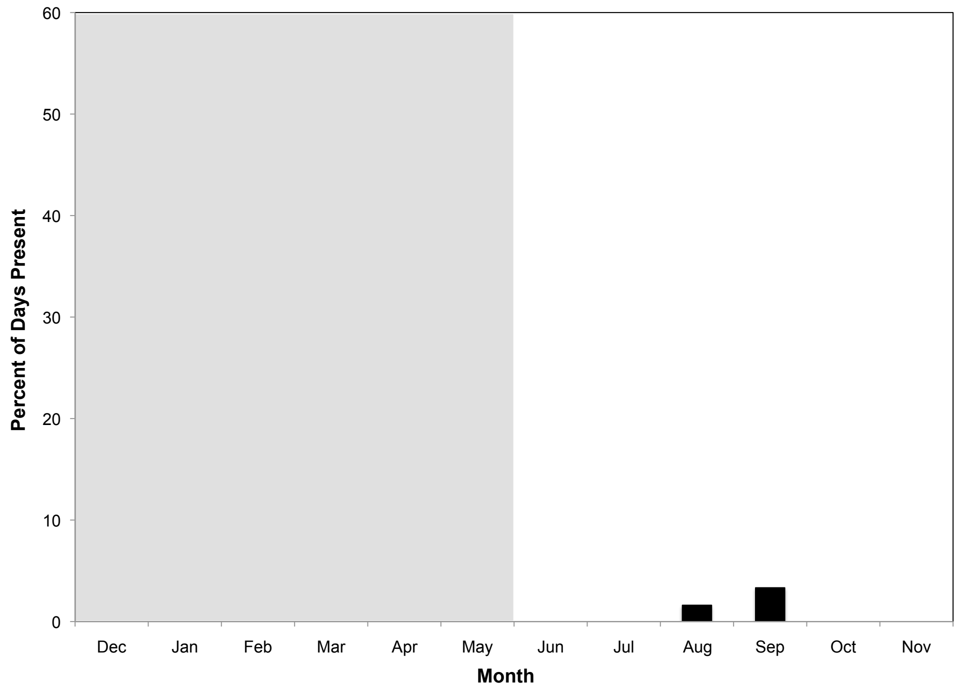
Appendix 6c. Caribbean reef shark 1478 percent of days present at the FSA site each month during 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



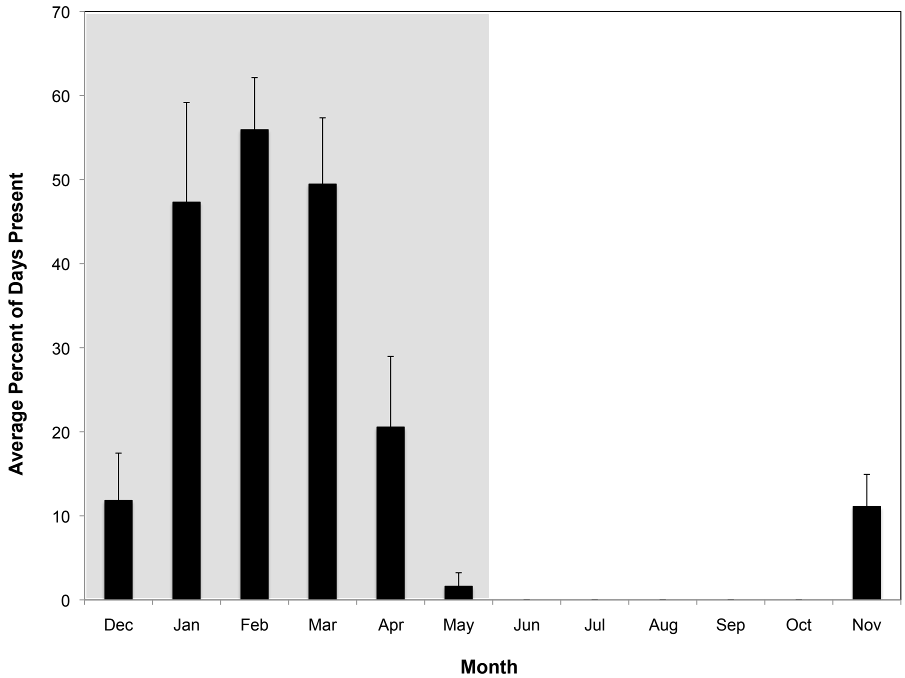
Appendix 6d. Caribbean reef shark 1486 percent of days present at the FSA site each month during 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



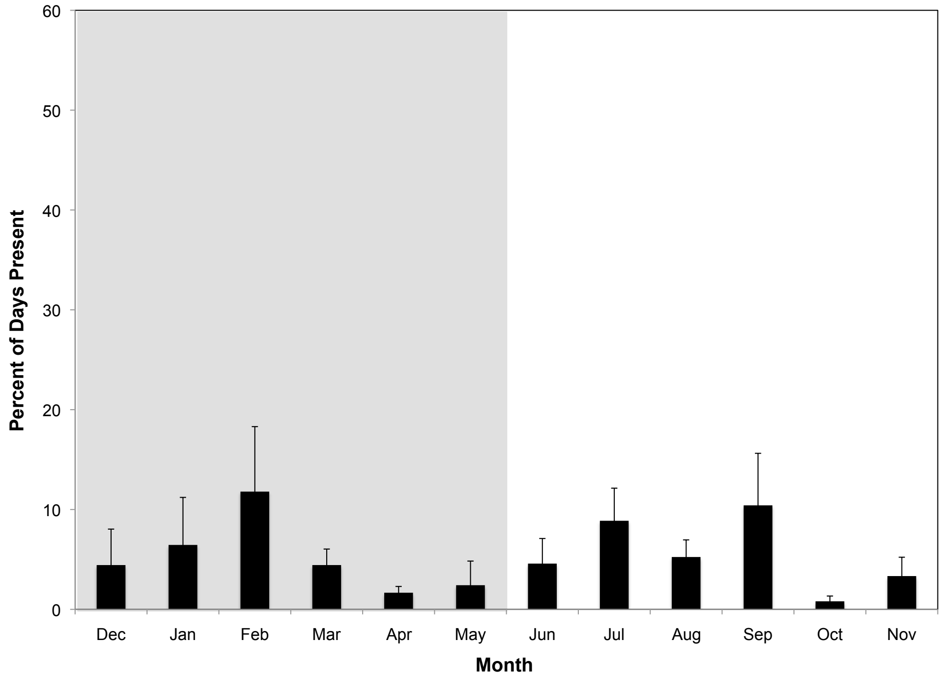
Appendix 6e. Caribbean reef shark 1486 percent of days present at the FSA site each month during 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



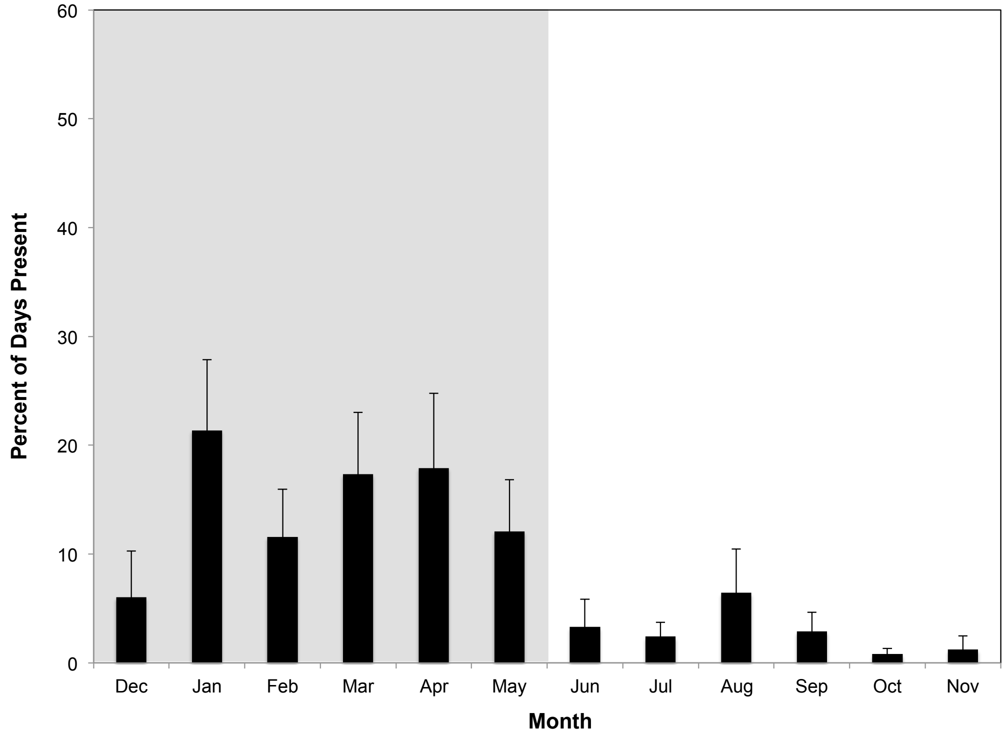
Appendix 6f. Caribbean reef shark 1486 percent of days present at the FSA site each month during 2010. The gray area represents the grouper spawning season months and the white area represents the non-spawning months.



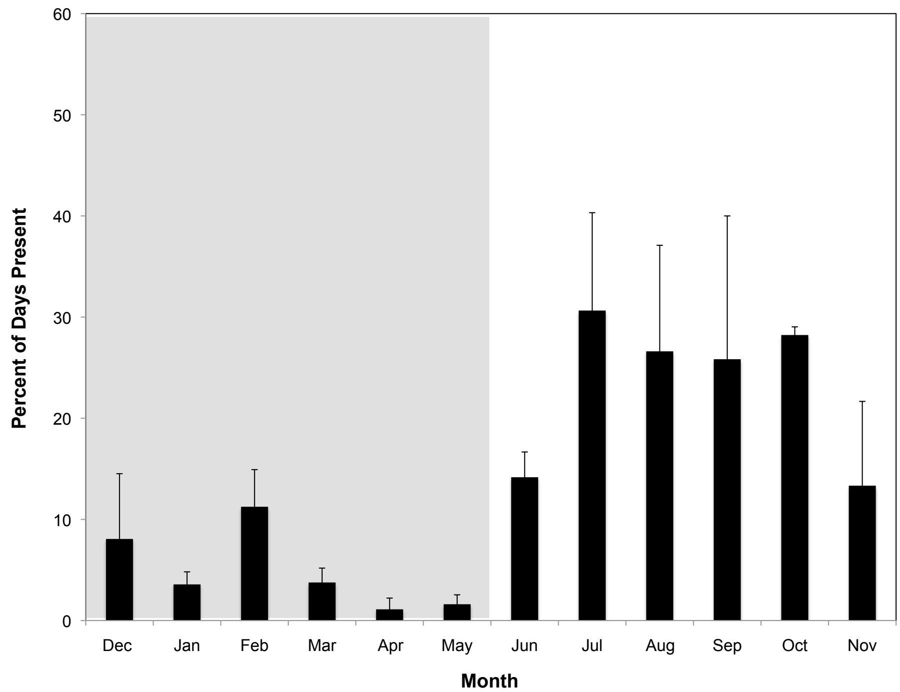
Appendix 7a. Lemon shark 1475 average percent of days at the FSA site each month from 2007 – 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



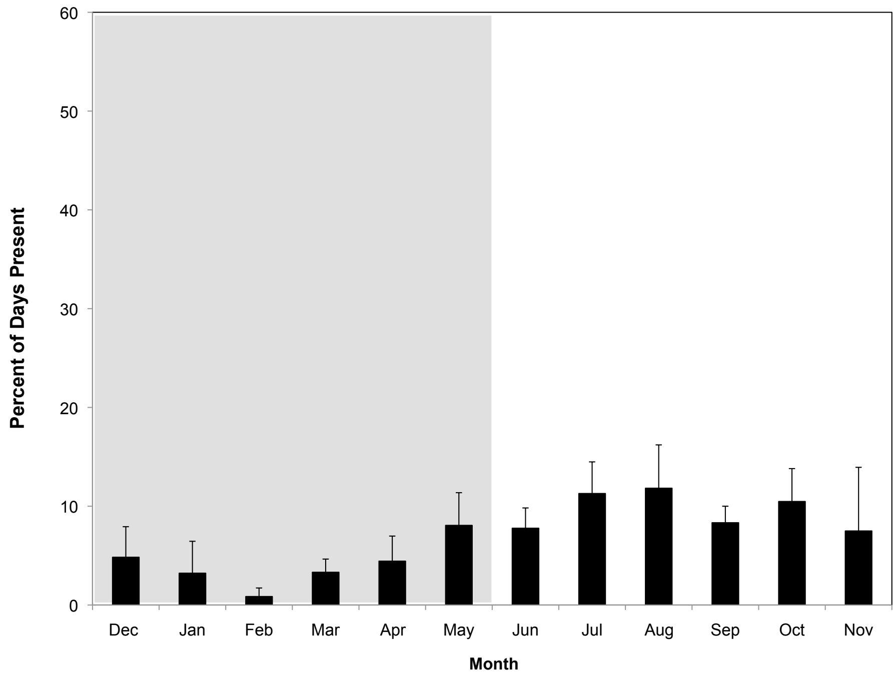
Appendix 7b. Lemon shark 1479 average percent of days at the FSA site each month from 2007 – 2010. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



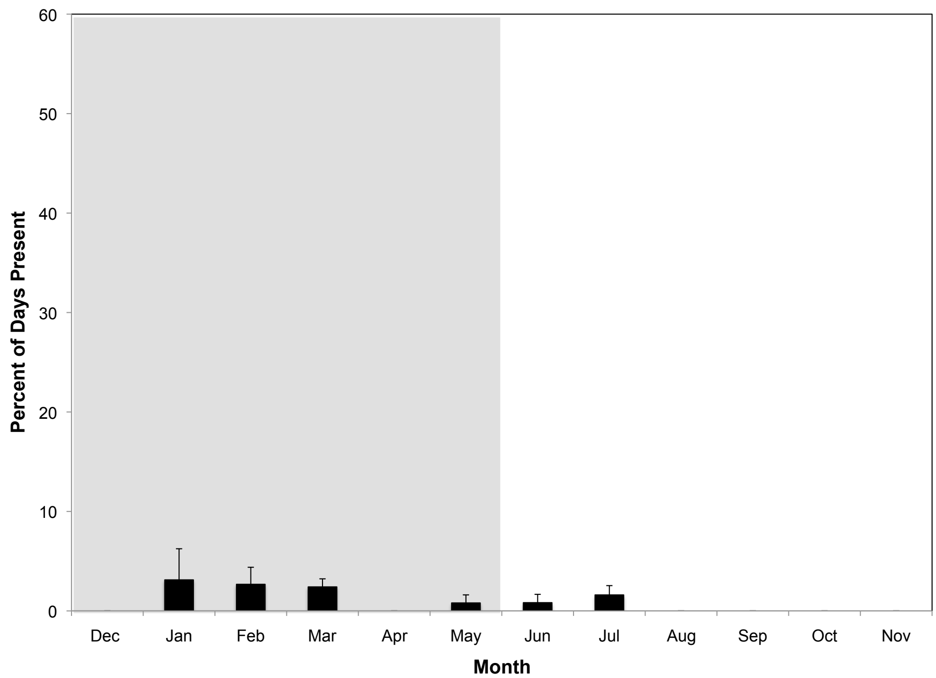
Appendix 7c. Lemon shark 3747 average percent of days at the FSA site each month from 2008 – 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



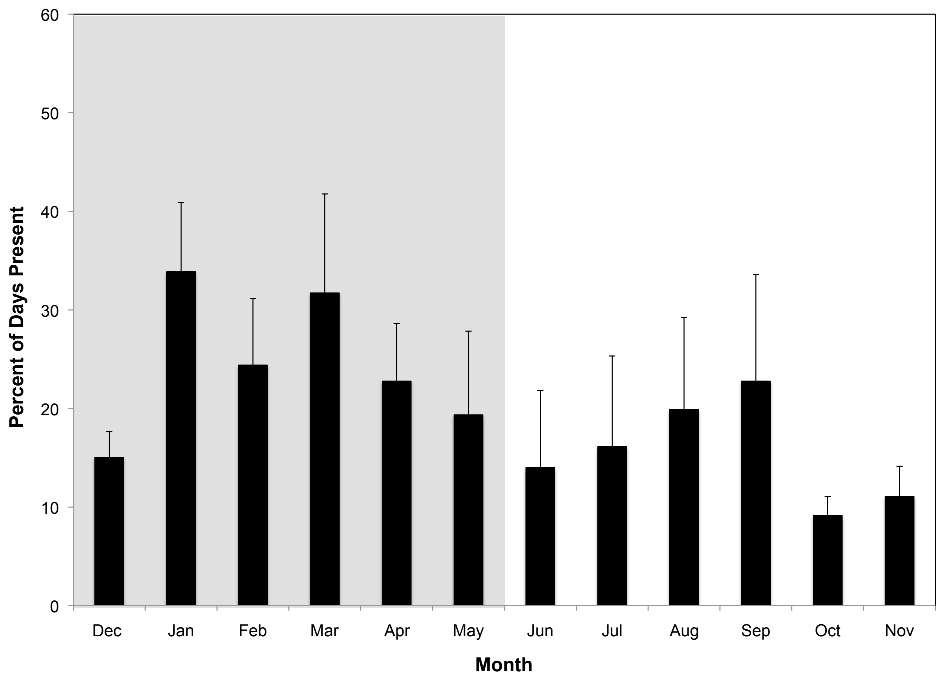
Appendix 7d. Tiger shark 1476 average percent of days at the FSA site each month from 2007 – 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



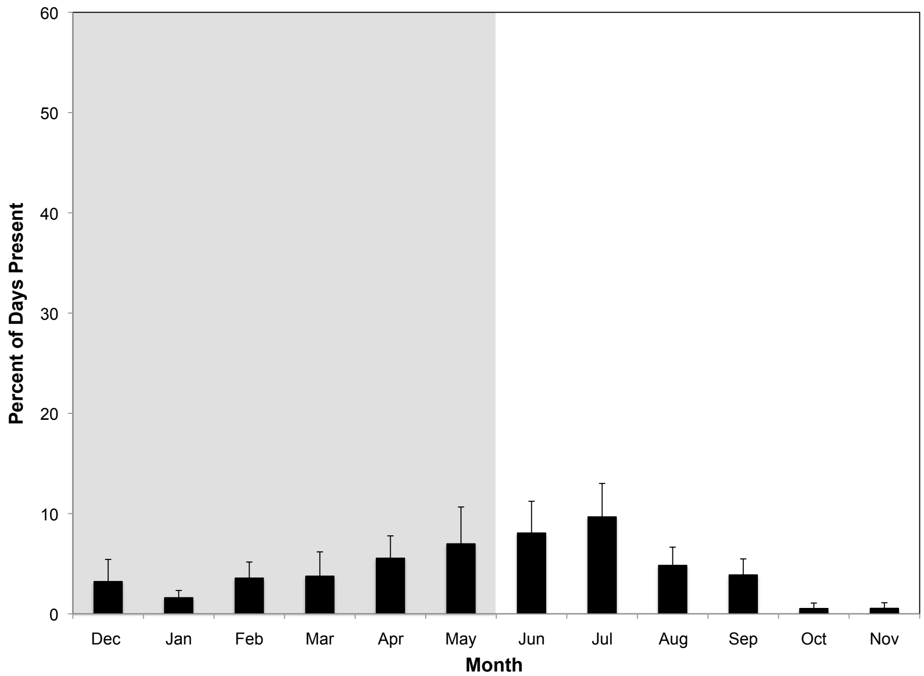
Appendix 7e. Tiger shark 1484 average percent of days at the FSA site each month from 2007 – 2009. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



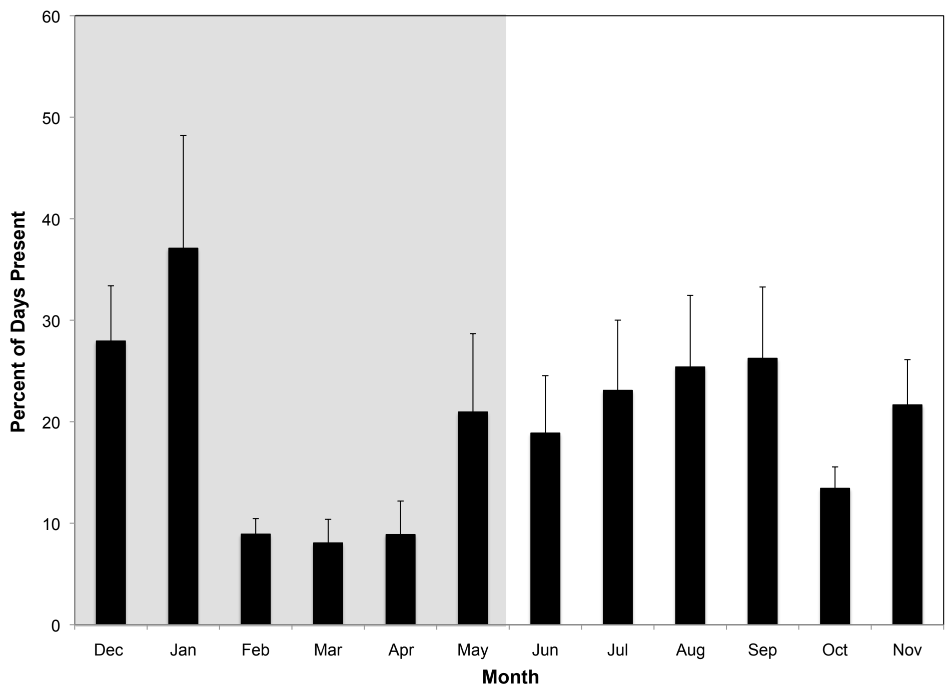
Appendix 7f. Tiger shark 1487 average percent of days at the FSA site each month from 2007 – 2008. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



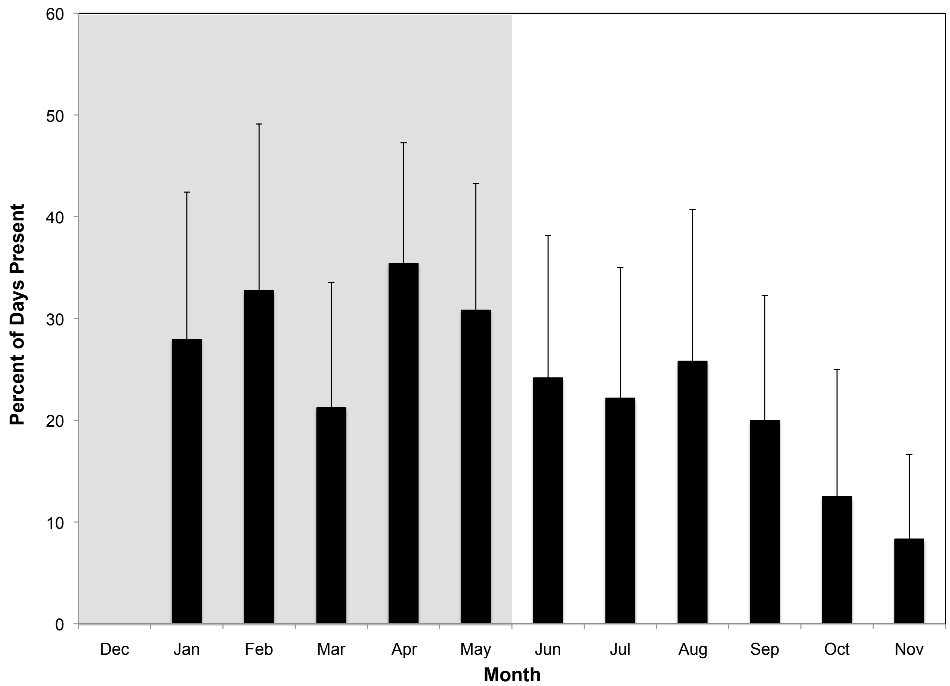
Appendix 7g. Tiger shark 3738 average percent of days at the FSA site each month from 2008 – 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



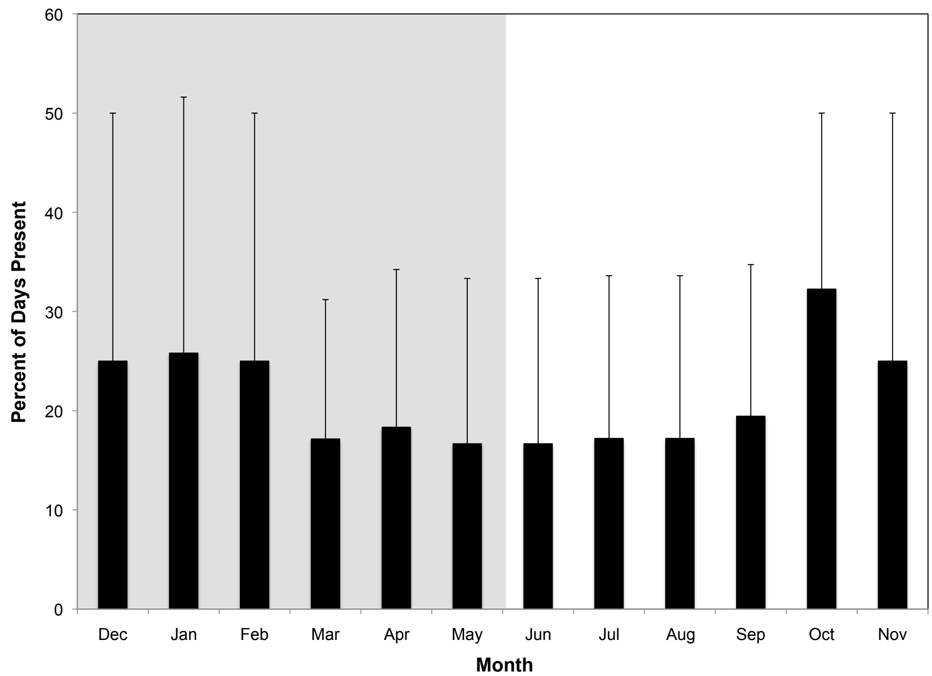
Appendix 7h. Tiger shark 3739 average percent of days at the FSA site each month from 2008 – 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



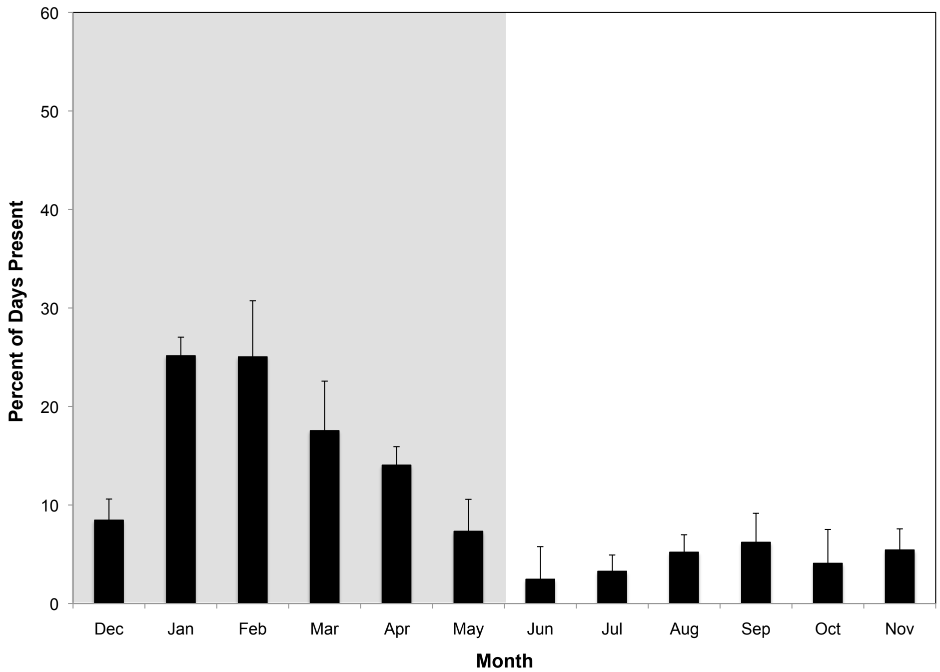
Appendix 7i. Tiger shark 3741 average percent of days at the FSA site each month from 2008 – 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



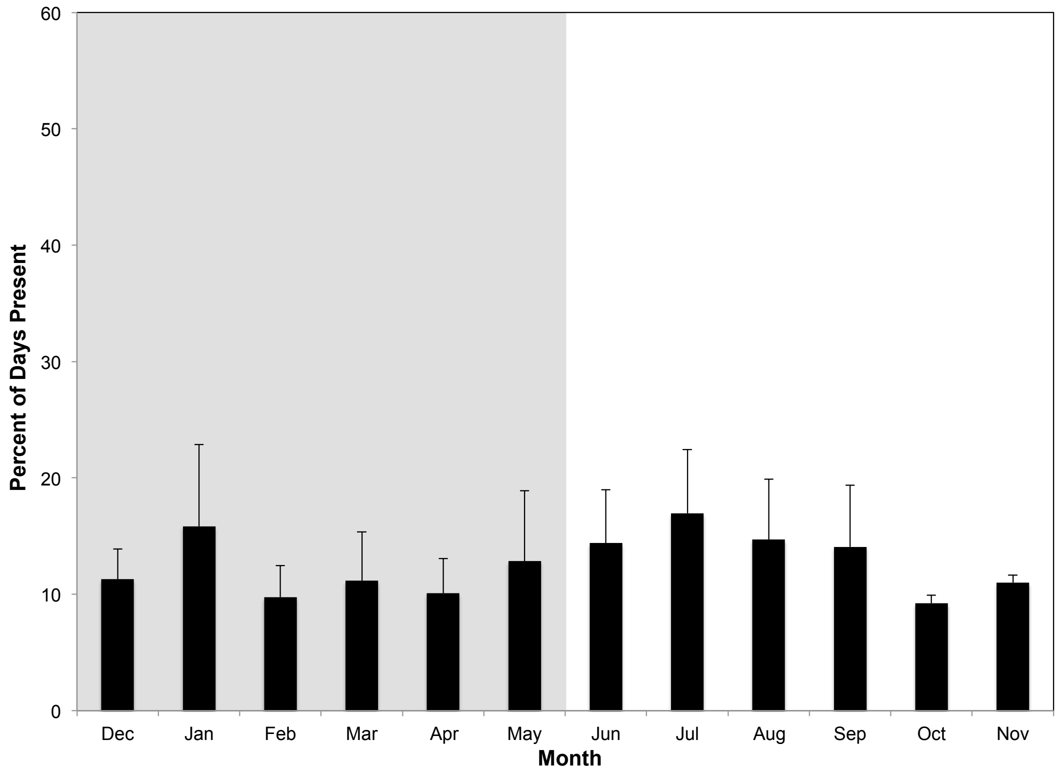
Appendix 7j. Caribbean reef shark 1478 average percent of days at the FSA site each month from 2008 – 2011. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



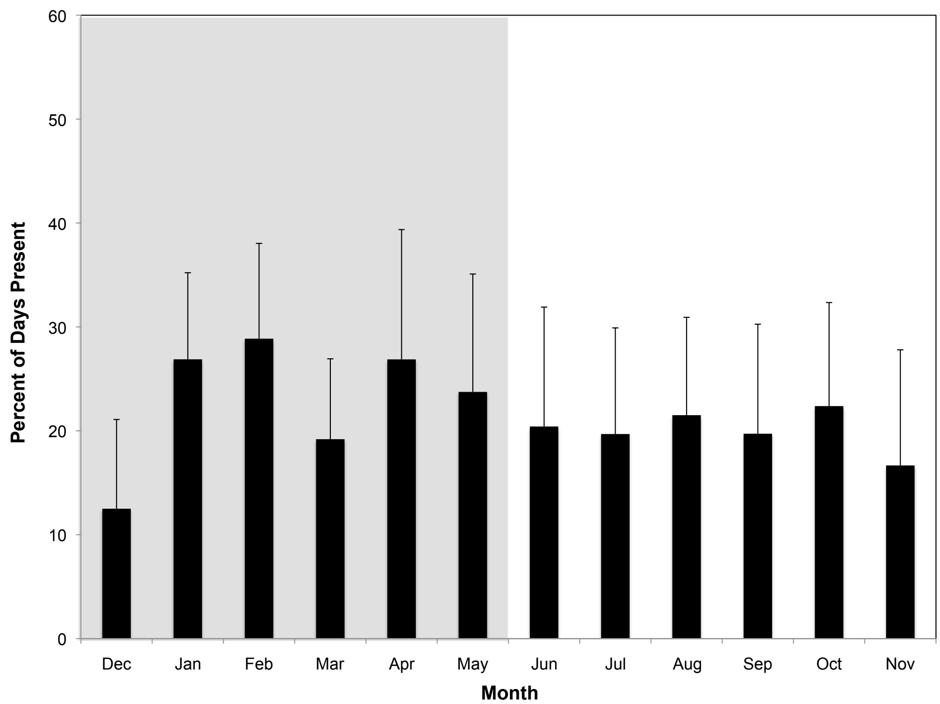
Appendix 7k. Caribbean reef shark 1486 average percent of days at the FSA site each month from 2008 – 2010. The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



Appendix 8a. Lemon shark average percent of days present at the FSA site each month from 2007 – 2011 (n=6). The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Lemon sharks were present at the FSA site a larger percentage of days during the spawning month (*p*=0.008). Bars represent mean and standard error.



Appendix 8b. Tiger shark average percent of days present at the FSA site each month from 2007 – 2011 (n=10). The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.



Appendix 8c. Caribbean reef shark average percent of days present at the FSA site each month from 2007 – 2011 (n=2). The gray area represents the grouper spawning season months and the white area represents the non-spawning months. Bars represent mean and standard error.

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