Fisheries Research 197 (2018) 34–44

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Research paper

Local indicators of abundance and demographics for the coastal shark assemblage of Bimini, Bahamas

Alexander C. Hansell[a,b,*], Steven T. Kessel[b,c], Lauran R. Brewster[b,d,e], Steven X. Cadrin[a], Samuel H. Gruber[b,f], Gregory B. Skomal[g], Tristan L. Guttridge[b]

[a] Department of Fisheries Oceanography, School for Marine Science and Technology, University of Massachusetts Dartmouth, 836 South Rodney French Blvd., New Bedford, MA 02719, USA
[b] Bimini Biological Field Station Foundation, South Bimini, Bahamas
[c] Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA
[d] Institute of Estuarine and Coastal Studies, University of Hull, HU6 7RX, UK
[e] International Fisheries Institute, University of Hull, Hull HU6 7RX, UK
[f] Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149, USA
[g] Massachusetts Division of Marine Fisheries, New Bedford, MA 02744, USA

ARTICLE INFO

Handled by Dr. B Arara

Keywords:
Fisheries-independent survey
Tiger shark
Nurse shark
Blacktip shark
Lemon shark

ABSTRACT

Understanding population dynamics is essential for implementing effective conservation and management of coastal sharks. Fisheries-independent surveys can offer valuable information for such data-limited situations. A 12-year (2004–2015) standardized, shallow water longline survey was conducted monthly in the coastal waters of Bimini, Bahamas. Each monthly survey comprised five longline sets, totaling 75 hooks, with a soak time of 24 h. A total of 770 sharks from nine species were caught over the course of the study, with tiger (*Galeocerdo cuvier*), nurse (*Ginglymostoma cirratum*), blacktip (*Carcharhinus limbatus*) and lemon (*Negaprion brevirostris*) sharks comprising 95% of the catch. The majority of tiger (87%), nurse (62%), blacktip (67%), and lemon (82%) sharks were of immature lengths. A greater number of captured tiger (77%) and blacktip (66%) sharks were female, while nurse (55%) and lemon sharks (73%) were predominantly male. Poisson generalized additive models were used to analyze local abundance trends and examine how catch rates were influenced by year, month, location, tide, hour of capture, and lunar cycle. Seasonal trends indicate greater catches of the nurse, blacktip and lemon sharks during the summer months. Annual trends indicated relatively stable catch rates for the tiger, blacktip and lemon shark. Nurse shark catch rates were highly variable during the survey. Results from this study improve our understanding of the coastal shark assemblage in Bimini, Bahamas, and provide important local abundance trend information that could be beneficial for conservation and regional assessments.

1. Introduction

Coastal waters are economically important and environmentally variable habitats that support a diversity of fauna (Beck et al., 2001; Harley et al., 2006). Sharks are important components of these dynamic ecosystems. As predators, sharks can influence the equilibrium of an ecosystem, often occupying high trophic levels and maintaining ecological balance through direct (Heithaus et al., 2008) and indirect (Simpfendorfer et al., 2001) effects. A scarcity of sharks to perform these roles can have broad ecological consequences and possibly increase mesopredator populations or create a trophic cascade (Shepherd and Myers, 2005; Ferretti et al., 2010). Therefore, understanding which species and life stages inhabit coastal areas is an important initial step in conservation.

Many sharks are especially susceptible to anthropogenic pressures, due to their late sexual maturity, long gestation periods and low fecundity (Dulvy and Forrest, 2010). The close proximity of coastal ecosystems to land increases risks associated with human accessibility and activity. Coastal development can physically alter habitats (Vitousek et al., 1997), prey availability (Knip et al., 2010), and reduce shark survival rates (Jennings et al., 2008). Fishing can impact nearshore ecosystems (Jackson et al., 2001) and shark populations (Stevens et al., 2000). Sharks comprise a high proportion (as much as 94%) of bycatch in pelagic fisheries (Mandelman et al., 2008), and can also contribute significantly to landings by coastal fisheries (Ansell et al., 1996; Castillo-Géniz et al., 1998). In the northwest Atlantic, the United

* Corresponding author at: Department of Fisheries Oceanography, School for Marine Science and Technology, University of Massachusetts Dartmouth, 836 South Rodney French Blvd., New Bedford, MA, 02719, USA.
E-mail address: ahansell@umassd.edu (A.C. Hansell).

http://dx.doi.org/10.1016/j.fishres.2017.09.016
Received 15 April 2017; Received in revised form 14 September 2017; Accepted 18 September 2017
Available online 03 October 2017

States (U.S.) has an active commercial longline fishery that targets large coastal sharks from Virginia to Florida, and throughout the Gulf of Mexico (Hale et al., 2013). These shark species are currently managed through a combination of quotas, catch limits, and fishing seasons in U.S. waters (Atlantic States Marine Fisheries Commission, 2008).

With growing conservation concerns and a prevalent human fascination with sharks, interest in shark protection and conservation has increased. Some U.S. states prohibit the catch of particular species (Atlantic States Marine Fisheries Commission, 2008). In June 2011, The Bahamas created a shark sanctuary covering 630,000 km^2 of the northwest Atlantic, protecting all shark species from fishing (Chapman et al., 2013) and banned the import and export of all shark products. However, even as conservation measures continue to increase, the impacts of these management decisions are relatively unknown. As the human population living in coastal areas is expected to increase (Vitousek et al., 1997; DeMaster et al., 2001), it is important to understand the status of shark populations and the extent to which these species use coastal waters. This understanding will be critical for effective conservation and management.

Inferences on the relative abundance of sharks in the northwest Atlantic Ocean are available from a combination of fisheries-dependent data sources (Campana et al., 2006; Baum and Blanchard, 2010) and fisheries-independent surveys (Simpfendorfer et al., 2002; Kessel et al., 2016). Stock assessments of sandbar (*Carcharhinus plumbeus*; southeast data assessment review (SEDAR, 2006), dusky (*Carcharhinus obscurus*; Cortés et al., 2006), great hammerhead (*Sphyrna mokarran*), scalloped hammerhead (*Sphyrna lewini*), smooth hammerhead (*Sphyrna zygaena*; Hayes et al., 2009; Jiao et al., 2009), bonnethead (*Sphyrna tiburo*) and Atlantic sharpnose (*Rhizoprionodon terraenovae*; SEDAR, 2013) sharks indicated suspected declines of 36–80% with respect to unexploited population levels. In contrast, relative abundance trends from the same region were stable with annual variability for sand tiger (*Carcharias taurus*), bull (*Carcharhinus leucas*), tiger (*Galeocerdo cuvier*), spinner (*Carcharhinus brevipinna*) and lemon sharks (*Negaprion brevirostris*; Carlson et al., 2009, 2012; Kessel et al., 2016). Fisheries-dependent data has resulted in disagreement regarding the status of many coastal shark species in the northwest Atlantic (Baum et al., 2003; Burgess et al., 2005). Stock assessments that include multiple sources of information (e.g., catch, life history, and abundance trends) are best for determining species status (Maunder and Punt, 2013). However, when data are limited, relative abundance trends alone can provide information to assess the effectiveness of management and conservation decisions (Carruthers et al., 2014).

Although shark conservation measures have been implemented in The Bahamas, population assessments for these species are lacking in this part of the northwest Atlantic and, therefore, the efficacy of these measures cannot be evaluated. The present study used a fisheries-independent longline survey to target coastal sharks in the near-shore waters of the Bimini Islands, Bahamas, from 2004 to 2015. The mangrove-fringed islands of North and South Bimini are biologically diverse (Jennings et al., 2012) and a lemon shark nursery (Chapman et al., 2009; Guttridge et al., 2012). Bimini is also part of the Bahamian shark sanctuary. The objectives of this study were to: 1) determine the coastal shark assemblage of Bimini, Bahamas; 2) quantify local relative abundance trends; 3) evaluate the influence of abiotic factors on catch rates; and 4) generate baseline data for future understanding of shark sanctuary impacts.

2. Materials and methods

2.1. Study site

This study was conducted from January 2004 through December 2015 in the waters of Bimini, Bahamas (Fig. 1). The Bimini islands are situated approximately 85 km east of Miami, Florida on the western edge of the relatively shallow Great Bahama Banks (approximately

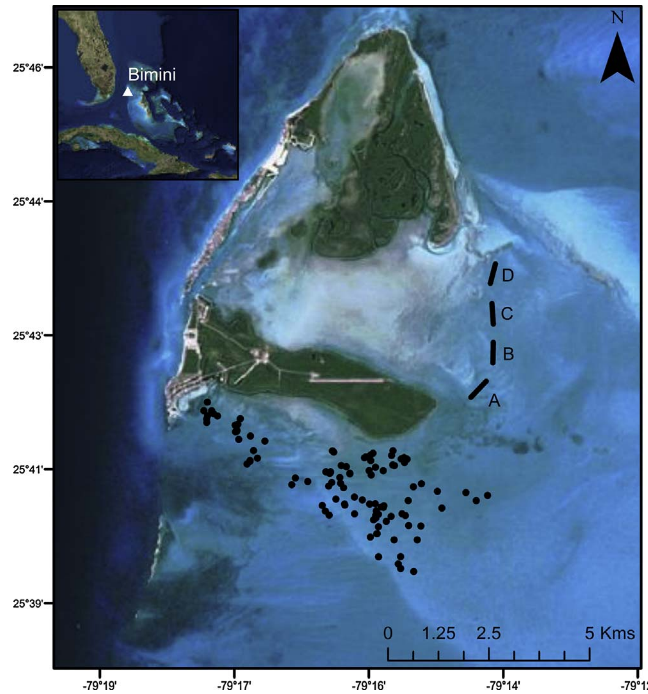

Fig. 1. Satellite image of the study site, Bimini Bahamas; monthly placements of lines A-D are marked accordingly, along with set locations (black dots) of the non-standardized wild card (WC) line.

25 m maximum depth), east of the deep Straits of Florida (roughly 1200 m maximum depth). The two islands, North and South Bimini, are separated by a shallow tidal lagoon (about 3 m maximum depth), approximately 21 km^2 in area.

2.2. Sampling

Longlines modified for Bimini's shallow water environment were deployed monthly. For each survey, four longlines (A–D) were set at fixed locations and one longline (WC) was set at a non-standardized location, haphazardly chosen by the scientific staff, off of South Bimini (Fig. 1). The bathymetry of the sample locations ranged from 1 to 4 m in depth and the sea bed was relatively uniform consisting primarily of sand, sea grass and rock substrate. All five longlines were set on the same day, however day of deployment within each month varied throughout the study. During the study longlines were set in sequential order (i.e., A, B, C, D, WC), with the first line being set at 14:30 and the last line being deployed around 16:30. All five longlines remained deployed over a 24-h period and were hauled in the same order they were set. Each longline was 500 m in length with 15 baited 16/0 circle hooks distributed at 30 m intervals. Bait varied, but was composed primarily (> 80%) of ½ kg pieces of barracuda (*Sphyraena barracuda*). Circle hooks were selected to minimize the possibility of a shark being foul-hooked in the throat or stomach and to increase catch retention (Kerstetter and Graves, 2006). The gangion was designed specifically to target shallow water (< 5 m depth) coastal sharks, with hooks positioned mid-water column below a small buoy that lifted the gangion wire off the sea floor. In order to reduce mortality, longlines were visually checked every four hours and captured sharks were processed and released. Clear water conditions allowed sharks to be identified and captured without hauling the longlines.

On capture, sharks were identified and restrained. The gangion was secured to the bow cleat of the vessel (5 m, center console skiff), and separated from the mainline, allowing the vessel to drift away. The shark was then brought under control with the use of a tail-rope and secured to the stern cleat of the vessel. Capture location was recorded (decimal degrees) with a Garmin GPSmap 62 s (± 3 m). A tape measure was used to measure the total length (TL) of all sharks to the nearest centimeter (cm). Recapture was determined if individuals had a pre-existing National Marine Fisheries Service (NMFS) conventional tag (Kohler et al., 1998) or a passive integrated transponder (PIT) tag (Gruber et al., 2001). If the shark was not a recapture, a small incision was made adjacent to the first dorsal fin and a PIT tag was injected into the sub-dermal layer (Gruber et al., 2001; Destron Fearing Inc). Newly captured sharks > 140 cm TL were also marked with a NMFS tag by fixing a metal anchor into the musculature at the base of the dorsal fin (Kohler et al., 1998). Physical characteristics were recorded (mating scars, hook location, etc.) along with sex of each individual. Following data collection the shark was released and the corresponding hook and gangion were removed from the longline.

2.3. Abiotic factors

We examined the effects of abiotic factors, including tide, lunar cycle, hour of capture and location on species-specific catch rates over the course of the 12-year study. Capture times were compiled into four categories based on tide: low, flood, high, and ebb. Captures were determined to occur at low or high tide if they happened within one hour either side of event. Historical lunar records were obtained from the U.S. Naval Observatory (U.S. Naval Observatory, 2016). Lunar cycle was determined as day of capture from last new moon. Hour of capture was determined by the check of longlines sharks were captured on. Location was determined by whether sharks were caught in the lagoon opening (i.e., lines A–D) or off South Bimini (i.e., WC).

2.4. Demographics

All statistical analyses were conducted in R (version 3.3.2) and significance was determined at the 0.05 level. The following analyses were performed on only the most abundant species (> 75 individuals) caught during the 12-year survey. Total length size structure was compared among species. Literature was reviewed to estimate whether individuals were mature (Brown and Gruber, 1988; Randall, 1992; Castro, 1996; Castro, 2000). Significant differences in size distribution between males and females were tested with a two-sample Kolmogorov-Smirnov test. Sex ratio was examined using a chi-square goodness-of-fit test to determine if ratios deviated from 1:1. Size and sex ratios were compared across month and year using a Kruskal-Wallis rank sum test. If differences were found to be significant, a post-hoc procedure was performed to investigate which months or years were significant. All post-hoc calculations used the 'pgirmess' package (Giraudoux, 2011).

2.5. Modeling shark catch rates

Capture rates were modeled by longline check (i.e., every 4 h) to avoid combining capture records and loss of information (Maunder and Punt, 2004). Effort was standardized, because the amount of hooks (75) and length of soak time (24 h) were the same for each monthly survey. This allowed count data to be used to estimate local abundance indices. Count data of shark captures can have a high amount of zero observations, because sharks are infrequently captured (Minami et al., 2007). When the proportion of zeros is large, captures do not readily fit standard distributions (i.e., Poisson or negative binomial). To deal with this problem, multiple techniques have been developed, including zero inflated distributions (Zuur and Ieno, 2012). However, a high proportion of zeros does not always equate to zero inflation, and therefore it is important to compare the fit of normal and zero-inflated distributions (Warton, 2005).

Several approaches are available to model catch-rate series (Maunder and Punt, 2004), with recent applications for sharks including generalized additive models (GAMs) (Afonso et al., 2014; Kessel et al., 2016). To determine the appropriate distribution of shark captures in Bimini, Bahamas, three GAMs were compared for each species: Poisson, negative binomial, and zero inflated Poisson (ZIP). Poisson and negative binomial models were constructed in the 'mgcv' package (Wood, 2006), while ZIP models were built in the 'gamlss' package (Rigby and Stasinopoulos, 2005). Poisson and negative binomial models used a log-link function, while the ZIP model used a logit-link function. Six covariates (year, month, tide, lunar cycle, hour of capture and location) of longline catch were tested for each model. Co-linearity of covariates was investigated using generalized variance-inflation factor (GVIF) scores. Any covariate with a score greater than three was removed and the GVIFs were recalculated (Zuur and Ieno, 2012). Regardless of level of significance, year was kept in all models, because the primary objective was to detect local relative abundance trends over time (Maunder and Punt, 2004). A smoothing spline was used to analyze the covariate year, while a cyclic smoothing spline ("cc") was used to examine month, and lunar cycle. Tide, hour and location were all treated as factors.

The appropriate distribution was determined by model validation and by comparing a dispersion parameter, which was calculated as the sum of Pearson residuals divided by the sample size minus the number of parameters (Zuur and Ieno, 2012). Once the appropriate distribution was selected, second order Akaike information criterion (AICc) scores chose the final covariates for each model. All AICc scores were calculated using the 'MuMIn' package (Barton, 2016). If AICc scores were within two, the most parsimonious model was selected (Burnham and Anderson, 2003). After AICc scores chose the optimal model P-values of explanatory variables were examined to approximate level of significance for each covariate (Zuur et al., 2009). The degree of smoothing for each term was determined using cross validation (Wood, 2006; Zuur and Ieno, 2012). Model validation was conducted by analyzing diagnostic plots (i.e., QQ-plot, histogram of residuals, residuals vs. linear predictors and observed vs. predicted values).

3. Results

From January 2004 through December 2015, a total of 144 longline sets, with 10,800 circle hooks, caught 770 sharks representing nine species. No teleost species were caught and it was rare if more than four sharks were captured on a single longline. Tiger (32%), nurse (*Ginglymostoma cirratum*) (29%), blacktip (23%) and lemon (11%) sharks comprised the majority of the catch. Bull (2%) and Atlantic sharpnose (2%) sharks were caught less frequently, while blacknose (*Carcharhinus acronotus*, < 1%), great hammerhead (< 1%), and Caribbean reef (*Carcharhinus perezii*, < 1%) sharks were rarely captured.

3.1. Demographics

Males comprised 23% of tiger shark captures and the sex ratio deviated significantly from a 1:1 ratio ($p \le 0.05$, $X^2 = 55.31$, df = 1). Tiger shark sex ratios did not significantly vary between months or years of the survey. Mean size was not significantly different between male and female tiger sharks. Among captured individuals, tiger sharks had the largest average size ($\overline{X}$=204 ± standard deviation 67 cm) and size range (85–385 cm). Based on size, 23% of males and 10% of females were assumed to be mature (Fig. 2). Size of tiger sharks significantly varied between months ($X^2 = 22.44$, df = 11, $p \le 0.05$). A post-hoc comparison indicated significant ($Diff._{Obs} = 71.59$; $Diff._{Cri} = 69.19$) differences in size between March ($\overline{X}$=247 ± 65 cm) and September ($\overline{X}$=193 ± 55 cm; Fig. 3). Size of tiger sharks did not significantly vary between years.

Males comprised 55% of nurse shark captures and the sex ratio did not deviate significantly from a 1:1 ratio. Nurse shark sex ratios did not significantly vary between months or years of the survey. Mean size was not significantly different between male and female nurse sharks. Nurse sharks had the second largest average size ($\overline{X}$=190 ± 44 cm) third largest average size range (70–251 cm). Based on size, 46% of males

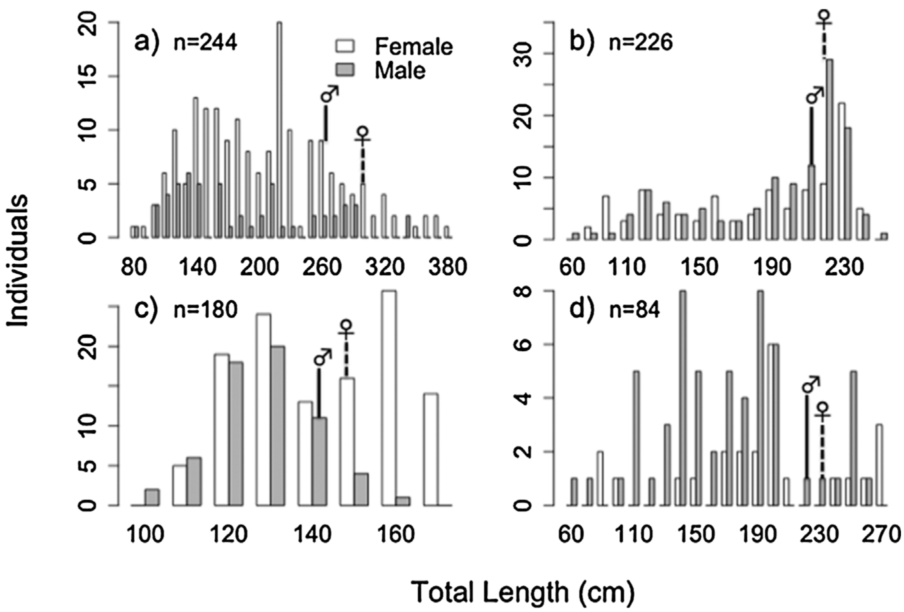

Fig. 2. Size distribution and frequency of sharks captured on longlines in Bimini, Bahamas: (a) tiger shark, (b) nurse shark, (c) blacktip shark and (d) lemon shark. The y-axis represents the number of individuals and n is the total number of captures for each species. Symbols (♂ male/♀ female) and corresponding lines represent predicted size at maturity for each sex. N is the sample.

and 28% of females were assumed to be mature (Fig. 2). Size of nurse sharks did not significantly vary between months. Annual variation in size was significant ($Diff._{Obs}$ = 76.21; $Diff._{Cri}$ 71.37). A post-hoc comparison indicated a significant difference in mean size between 2006 ($\bar{X}$=207 ± 39 cm) and 2012 ($\bar{X}$=170 ± 42 cm; Fig. 4).

Males comprised 34% of blacktip shark captures and the sex ratio deviated significantly from a 1:1 ratio (X^2 = 17.42, p ≤ 0.05, df = 1). Blacktip shark sex ratios did not significantly vary between months or years of the survey. Mean size was significantly different between male and female blacktip sharks (D = 0.47, p ≤ 0.05), with more large (> 150 cm TL) females (n = 57) than males (n = 5; Fig. 2). The blacktip shark had the smallest average size (142 ± 18 cm) and size range (108–179 cm). Based on size, 16% of males and 42% of females were assumed to be mature (Fig. 2). Size of blacktip sharks did not significantly vary between months or years of the survey.

Males comprised 73% of the lemon shark catch and the sex ratio deviated significantly from a 1:1 ratio (X^2 = 13.349, p ≤ 0.001 df = 1). Lemon shark sex ratios did not significantly vary between months or years of the survey. Mean size was not significantly different between male and female lemon sharks. The lemon shark had the third largest average size ($\bar{X}$=180 ± 18 cm) and second largest size range (69–274). Based on size, 15% of males and 25% of females were assumed to be mature (Fig. 2). Size of lemon sharks did not significantly vary between months or years of the survey.

3.2. Catch rates

For all species, the dispersion parameter of Poisson GAMs was approximately one, revealing that Poisson was the appropriate distribution to model shark catch rates in Bimini. Final covariates and model results (Tables 1–4; Table A1) varied for each species.

The catch rates for each dominant shark species appeared to change over the time series, but these changes were only significant for the nurse shark (Tables 1–4; Fig. 5). Tiger shark catch rates were lower than average from 2008 to 2011 and subsequently higher than average from 2012 to 2015 (Fig. 5). Nurse shark catch rates varied annually, with

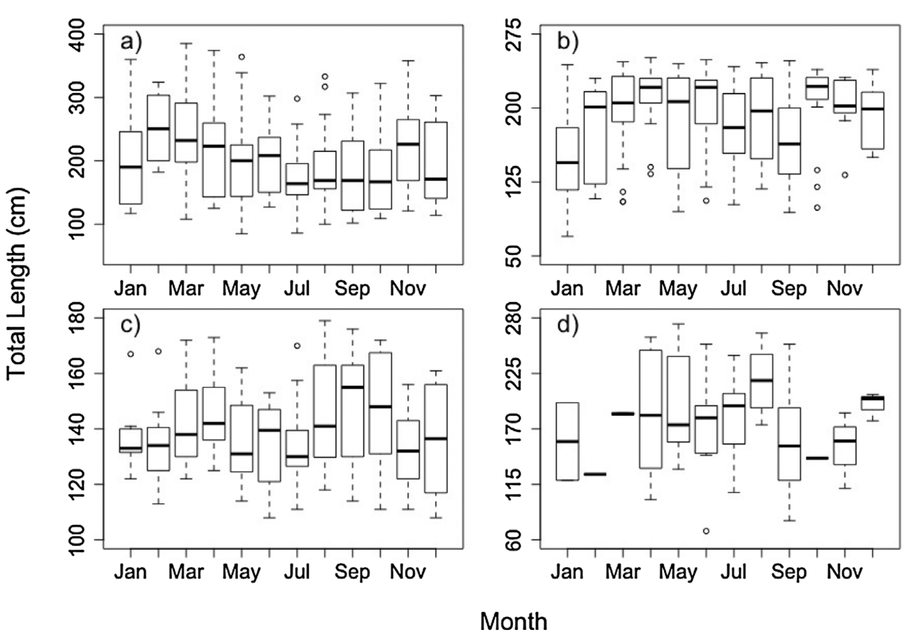

Fig. 3. Aggregated monthly size distribution of sharks captured on longlines in Bimini, Bahamas: (a) tiger shark, (b) nurse shark, (c) blacktip shark and (d) lemon shark. The boxes represent the first and third quartile, the black line represents the median and the whiskers represent 1.5 times the interquartile range. The circles represent outliers.

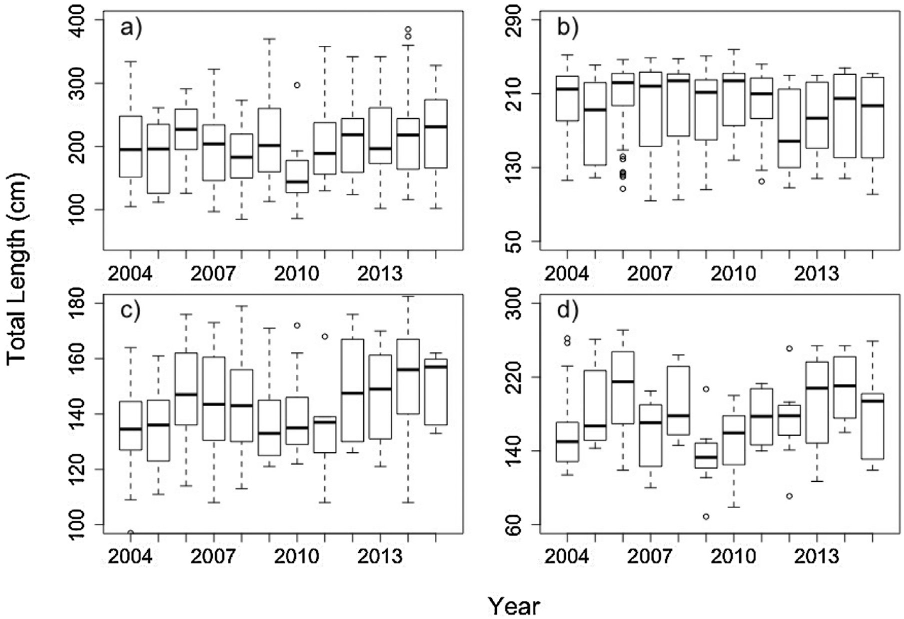

Fig. 4. Annual size distribution of sharks captured on longlines in Bimini, Bahamas: (a) tiger shark, (b) nurse shark, (c) blacktip shark and (d) lemon shark. The boxes represent the first and third quartile, the black line represents the median and the whiskers represent 1.5 times the interquartile range. The circles represent outliers.

greater catch rates occurring in 2009 (Fig. 5). Blacktip shark captures remained relatively stable, however the lowest catch rates were observed in 2015 (Fig. 5). Lemon shark catch rates remained relatively stable, however captures were higher than average in 2004 and 2012 (Fig. 5).

Other variables were found to significantly influence catch rates of shark species in Bimini, Bahamas. The capture rates of nurse, blacktip, and lemon sharks varied significantly with month (Tables 2–4; Fig. 6), while hour of capture was significant for only nurse and blacktip sharks with both species captured most frequently four hours into the longline set (Tables 2 and 3; Fig. A1). The catch rate of tiger sharks was significantly higher during a flood tide (Table 1; Fig. A1) and the location of capture significantly influenced the catch rate of this species as well as the blacktip and lemon shark (Table 1; 3–4). More tiger sharks were caught off of South Bimini, while the majority of blacktip and lemon sharks were captured in the lagoon opening (Table 1; 3–4).

4. Discussion

The status of shark populations remains largely unknown in The Bahamas due to the lack of fisheries-independent data sources. In this study, we used a 12-year longline survey to characterize the demography and relative abundance of sharks in the near-shore waters of Bimini, Bahamas. In these coastal waters, the tiger, nurse, blacktip and lemon sharks comprised 95% of the catch. Although all life stages were represented in the catch, most (> 50%) of the sharks were not mature (Fig. 2). Catch rates varied for all four species, however increases and decreases in catch rates may be attributed to other factors (e.g., the environment and dynamics of the population) than local density (Maunder et al., 2006). Given the broad distribution of these species in The Bahamas and beyond, these catch rates do not likely reflect trends in total population abundance, but they can be used to monitor local relative abundance.

Our fisheries-independent survey in Bimini, Bahamas avoids issues that have historically complicated fisheries dependent surveys such as accounting for abiotic factors and the standardization of gear, vessel, and fishing location. However, our survey naturally still has constraints. Species that rarely inhabit the locations of our sets might be under-represented. For example, using different fishing methods (polyball or float fishing) outside the survey area, we captured and tagged more than 30 great hammerhead sharks (Guttridge et al., 2017) and more than 35 bull sharks since 2012. Further, Bimini has a well-established site where great hammerhead, Caribbean reef and blacknose sharks are frequently fed for ecotourism and, on any given dive, more than ten individuals can be observed (Gruber pers. comm.). All four of these species comprised less than 5% of the catch in this survey. The longline gear used in Bimini, specifically hook size, may cause size-selectivity and preclude the capture of many juvenile sharks. Bimini is a well documented lemon shark nursery (Chapman et al., 2009; Guttridge et al., 2012) and supports a substantial resident juvenile (defined as < 90 cm TL) nurse shark population of at least 50 individuals (Brewster, unpublished data). These smaller sharks were not well represented in this particular survey. It is also possible larger, presumably mature sharks were able to escape capture on occasion, as straightened

Table 1
Results of final Poisson generalized additive model investigating the catch rates of tiger sharks in Bimini, Bahamas. Outcomes of smoothers include: covariate, effective degrees of freedom (edf), reference degrees of freedom (ref.df), chi-squared value (X^2), and *p*-value. Outcomes of factors include: covariate, level, coefficient, standard error (SE), z-value and *p*-value. Overall adjusted R^2 value, and total percent deviance explained are displayed as well.

Covariate		edf	ref.df	X^2	p-value	R^2 (adj.)	% Deviance Exp.
Year		4.8	5.85	8.66	0.18	0.1	9.1
Month		1.3	8	2.29	0.11		
Lunar Cycle		2.688	4	5.099	0.11		
–	Level	Coefficient	SE	z-value	–		
Tide	Intercept	−1.44	0.17	−8.36	≤0.05		
	Flood	0.44	0.2	2.2	≤0.05		
	High	0.16	0.24	0.66	0.51		
	Ebb	0.11	0.21	0.54	0.59		
Location	South Bimini	1.08	0.46	2.34	≤0.05		

Table 2
Results of final Poisson generalized additive model investigating the catch rates of nurse sharks in Bimini, Bahamas. Outcomes of smoothers include: covariate, effective degrees of freedom (edf), reference degrees of freedom (ref.df), chi-squared value (X^2), and *p*-value. Outcomes of factors include: covariate, level, coefficient, standard error (SE), z-value and *p*-value. Overall adjusted R^2 value, and total percent deviance explained are displayed as well.

Covariate		edf	ref.df	X^2	p-value	R^2 (adj.)	% Deviance Exp.
Year		8.37	8.89	34.44	≤0.05	0.17	21.3
Month		7.41	8	35.97	≤0.05		
–	Level	Coefficient	SE	z-value	–		
Hour	Intercept	−0.57	0.11	−5.02	≤0.05		
	8	−1.2	0.22	−5.40	≤0.05		
	12	−1.09	0.21	−5.12	≤0.05		
	16	−2.16	0.33	−6.47	≤0.05		
	20	−0.93	0.20	−4.64	≤0.05		
	24	−0.75	0.18	−3.97	≤0.05		

hooks were observed during the haul of longlines. Bait type, retention and size can influence the capture rate of sharks (Driggers et al., 2016). Bait was not included in the abundance models in this study. However, a previous longline study in Bimini found bait type does not affect the catch rates of tiger, nurse, blacktip or lemon sharks (Kessel, 2010). Even with these few limitations, our fisheries-independent survey in Bimini addresses variation that complicates interpretation of fisheries-dependent data, and provides an insight into tiger, nurse, blacktip and lemon shark trends in this region of the northwest Atlantic.

4.1. Tiger shark

The tiger is classified by the International Union for the Conservation of Nature (IUCN) as near threatened (Simpfendorfer, 2009) and in this study we observed higher than average capture rates for this species during the latter years of the time series (Fig. 5). Similar catch trends have been reported elsewhere for the tiger shark. For example, in the northwest Atlantic catch rates have been reported as stable (Baum and Blanchard, 2010) or even increasing (Carlson et al., 2012). Off Australia, annual catch rates for tiger sharks have been reported to fluctuate (Green et al., 2009; Holmes et al., 2012), with certain years having increased capture rates (Reid et al., 2011).

The high catches of tiger sharks (87%) smaller than the published size at maturity suggest that Bimini could act as a nursery for this species. Pregnant tiger sharks have been observed in The Bahamas (Sulikowski et al., 2016), with size at birth in the northwest Atlantic occurring at roughly 61 cm fork length (Natanson et al., 1999). Juveniles have been defined as shorter than 180 cm fork length (Driggers et al., 2008). In our study, we found that 33% of the tiger sharks caught in Bimini were less than 236 cm TL (=180 cm FL). Natanson et al. (1999) reported a tiger shark nursery off the coast of Florida in the northwest Atlantic, out to a depth of 100 m. The shallow sand flats of the Great Bahama Bank, adjacent to Bimini, are a potentially similar shallow water habitat. However, more information is needed on the spatial distribution of these species to determine whether or not this area is indeed a nursery.

More tiger sharks were caught off South Bimini throughout the research period than in the lagoon opening, which could be associated with close proximity to the deep Gulf Stream (Table 1). Tiger shark abundance has been positively correlated with depth (Carlson et al., 2012), with individuals moving inshore to forage (Randall, 1992). Further, edge habitats (such as the coastal waters of South Bimini) are typically productive with a high abundance of prey and are commonly used as foraging sites for top-level marine predators (Heithaus et al., 2006; Papastamatiou et al., 2009). Thus, tiger sharks may be moving from the deep Gulf Stream to the adjacent shallow flats off South Bimini to feed.

We found that more tiger sharks were captured during a flood tide in Bimini (Table 1; Fig. A1). However, the absence of hook timers prevented fine scale evaluation. It should also be noted that tidal phases were not of equal length in the abundance models, as high/low tide were each two hours long and flood/ebb were each four hours long. Tidally influenced movements in sharks are thought to relate to energy conservation (Ackerman et al., 2000), foraging range (Carlisle and Starr, 2010), and predator avoidance (Guttridge et al., 2012). Previous catch rates of tiger sharks have been linked to tidal amplitude (Afonso et al., 2014). Similarly, the movement of tiger shark prey (i.e., bar-bellied sea snake (*Hydrophis elegans*)) has been suggested to be tidally driven in order to reduce chances of predation (Kerford et al., 2008). The intertidal lagoon and the near-shore waters off South Bimini are not deep enough for tiger sharks during all tidal phases. Hence, tiger sharks might be moving into these areas during rising tides to increase their foraging range, especially since these locations have a high diversity of prey (Jennings et al., 2012).

Table 3
Results of final Poisson generalized additive model investigating the catch rates of blacktip sharks in Bimini, Bahamas. Outcomes of smoothers include: covariate, effective degrees of freedom (edf), reference degrees of freedom (ref.df), chi-squared value (X^2), and *p*-value. Outcomes of factors include: covariate, level, coefficient, standard error (SE), z-value and *p*-value. Overall adjusted R^2 value, and total percent deviance explained are displayed as well.

Covariate		edf	ref.df	X^2	p-value	R^2 (adj.)	% Deviance Exp.
Year		5.74	6.49	11.45	0.1	0.24	26.9
Month		2.7	6	22.49	≤ 0.05		
Lunar Cycle		0.55331	8	0.62	0.3		
–	Level	Coefficient	SE	z-value	–		
Hour	Intercept	−0.63	0.17	−5.35	≤0.05		
	8	−0.6	0.19	−3,23	≤0.05		
	12	−1.46	0.25	−5.74	≤0.05		
	16	−1.92	0.31	−6.22	≤0.05		
	20	−1.92	0.31	−6.22	≤0.05		
	24	−2.01	0.32	−6.26	≤0.05		
Location	Intercept	1.08	0.46	2.34	≤0.05		
	South Bimini	−1.53	0.12	−13.18	≤0.05		

Table 4
Results of final Poisson generalized additive model investigating the catch rates of lemon sharks in Bimini, Bahamas. Outcomes of smoothers include: covariate, effective degrees of freedom (edf), reference degrees of freedom (ref.df), chi-squared value (X^2), and *p*-value. Outcomes of factors include: covariate, level, coefficient, standard error (SE), z-value and *p*-value. Overall adjusted R^2 value, and total percent deviance explained are displayed as well.

Covariate		edf	ref.df	X^2	p-value	R^2 (adj.)	% Deviance Exp.
Year		3.45	4.27	7.71	0.11	0.06	13.8
Month		2.39	8	26.73	≤0.05		
–	Level	Coefficient	SE	z-value	–		
Location	Intercept	−2.45	0.14	−17.36	≤0.05		
	South Bimini	−1.37	0.58	−2.35	≤0.05		

4.2. Nurse shark

Catch rates from Bimini indicate the nurse shark is the second most abundant species, with variable capture rates over the 12-year period (Fig. 5). According to the IUCN the nurse shark is data deficient (Rosa et al., 2006) and information on its distribution and habitat use is limited (Ferreira et al., 2013). In the northwest Atlantic, nurse sharks are considered a single population (Karl et al., 2012) and thought to be the most abundant shark species in shallow tropical waters (Castro, 2000; Castro and Rosa, 2005). Although precise nurse shark population estimates are lacking, a recent study from Atol das Rocas Marine Reserve, Brazil, found at least 400 individuals living in a 6 km^2 area (Castro and Rosa, 2005).

Previous abundance trends from the South Atlantic displayed no seasonal trends in nurse shark presence (Santander-Neto et al., 2011; Ferreira et al., 2013). However, strong seasonal shifts in sex ratios were observed (Santander-Neto et al., 2011). In contrast, we found no sex differences between seasons and catch rates increased over the summer months (Fig. 6). The increase in seasonal catch rates in Bimini might be a result of water temperature, as nurse shark captures have been positively correlated with water temperature (Heithaus et al., 2007). Moreover, escalating water temperatures will increase metabolic demand thereby requiring nurse sharks to forage more frequently (Di Santo and Bennett, 2011), possibly increasing capture rates. It also feasible that nurse sharks could be moving into the shallow waters around Bimini during this time to reproduce (Castro, 2000; Pratt and Carrier, 2001), as copulation events were directly observed by the authors in the months of July and August.

Increased nurse shark captures were observed during the first four hours of the study (Table 2; Fig. A1). Longline sets were temporally standardized, therefore these increased catch rates could be influenced by light levels. Shark foraging ecology has been linked to time of day, with different species preferring to feed at different times (Randall,

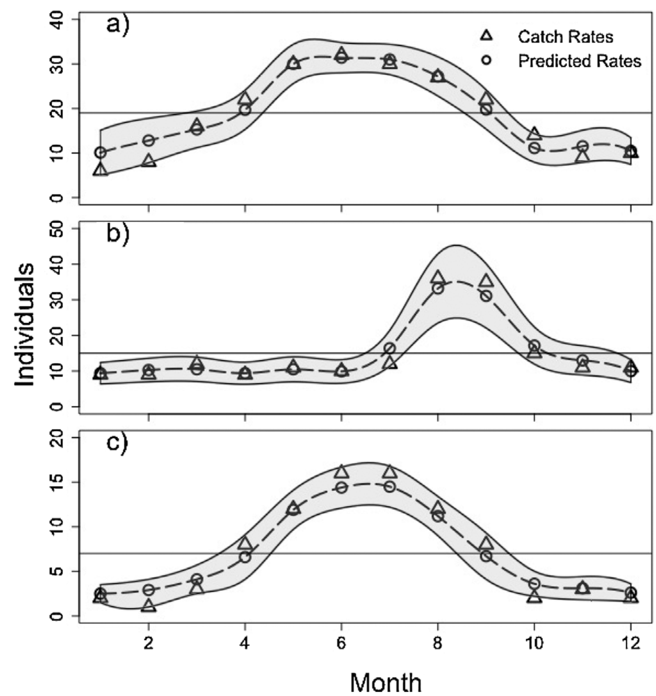

Fig. 6. Aggregated monthly standardized relative abundance indices for the: (a) nurse shark, (b) blacktip shark and (c) lemon shark. All sharks were caught in Bimini, Bahamas, and all abundance estimates are based on final Poisson generalized additive models. Y-axis is number of individuals captured. Shaded grey areas represent ± two standard error. Horizontal black line represents the average capture rate.

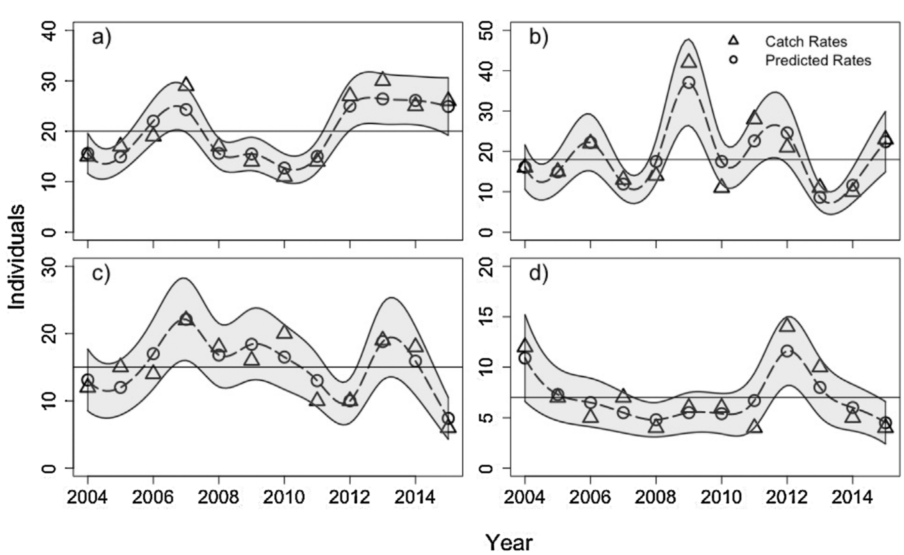

Fig. 5. Annual standardized relative abundance indices for the: (a) tiger shark, (b) nurse shark, (c) blacktip shark and (d) lemon shark. All sharks were caught in Bimini, Bahamas, and all abundance estimates are based on final Poisson generalized additive models. Y-axis is number of individuals captured. Shaded grey areas represent ± two standard error. Horizontal black line represents the average capture rate.

1992; Heithaus, 2001; Castro, 2011). The nurse shark is a nocturnal predator, which becomes active at dusk and moves into shallower water (Castro, 2011). Thus, nurse sharks may prefer to feed in the shallow coastal waters of Bimini during the early evening. It is also possible that bait lost odor and ability to attract nurse sharks as time increase.

4.3. Blacktip shark

Catch trends from our survey found fairly consistent blacktip capture rates throughout the entire study period (Fig. 5). The blacktip shark is classified, by the IUCN, as near threatened (Burgess and Branstetter, 2009) and has genetically distinct sub-populations in the Atlantic (Keeney and Heist, 2006). Despite Bimini's close proximity (85 km) to the U.S., blacktip sharks caught in Bimini are genetically distinct from the U.S. population, and most closely related to nursery sites in the Yucatan and Belize (Gledhill et al., 2015). This species is currently managed in the U.S. as the Gulf of Mexico stock and the northwest Atlantic stock (SEDAR, 2006). The former is not overfished and overfishing is not occurring (SEDAR, 2006), but the status of blacktip sharks in the northwest Atlantic remains unknown (Kiszka and Heithaus, 2014).

Significantly more blacktip sharks were caught in the lagoon opening than off of South Bimini (Table 3). This difference is potentially the result of fishing effort, which was four times higher in the lagoon opening. It is also possible that there are less blacktip sharks off South Bimini due to the high presence of tiger sharks, a known predator (Castro, 2011).

Seasonal captures indicate that more blacktip sharks were caught during August and September (Fig. 6). We suggest that blacktips might be using Bimini during this time for reproductive purposes as fresh mating scars have been observed (Gledhill et al., 2015). It is also possible that blacktip sharks may be using near-shore waters for prey availability (Kajiura and Tellman, 2016) or thermoregulation (Hight and Lowe, 2007) during this time. September has the warmest water temperatures of the year around Bimini, and blacktip shark movement is strongly correlated with water temperature (Kajiura and Tellman, 2016). Further, the warm near-shore waters could augment metabolic processes, digestion and somatic growth (Hight and Lowe, 2007; Papastamatiou et al., 2015). Therefore, an increase in catch rates might be due to reproduction, prey, physiological functions or a combination.

Hour of capture influenced the catch rate of blacktip sharks in Bimini, with captures decreasing as deployment time increased (Table 3; Fig. A1). In other regions of the northwest Atlantic blacktip catch rates did not increase until 5–9 h into longline deployment (Morgan and Carlson, 2010). In our study, it is unclear what factors are causing blacktips to be captured more frequently at the beginning of longline sets. However, these results are similar to those observed for nurse sharks, and as previously mentioned this trend could be due to either time of day or bait.

4.4. Lemon shark

Bimini, Bahamas is a well-documented lemon shark pupping ground and nursery (Chapman et al., 2009; Guttridge et al., 2012) that contributes to the near threatened (as classified by the IUCN; Sundström, 2015) western Atlantic population (Feldheim et al., 2001). In this study, more lemon sharks were caught in the lagoon opening than off of South Bimini, which is in accordance with previous tracking studies (Gruber et al., 1988; Guttridge et al., 2012). From the results obtained by Chapman et al. (2009)—investigating the probability, based on TL, of sharks caught in Bimini being locally born—it can be estimated that approximately 33% of lemon sharks captured on this survey were born in Bimini. Female lemon sharks move into Bimini's lagoon to give birth during April-May (DiBattista et al., 2011). During these months our survey found no significant differences in size or sex composition. However, over the course of the summer months, lemon shark captures did increase (Fig. 6). These findings are in accordance with an increased presence of lemon sharks in the lagoon during the summer (Kessel et al., 2013).

Lemon shark catch rates have been reported as both stable (Carlson et al., 2012) and variable (Kessel et al., 2016) in the northwest Atlantic. Stable catch rates were observed in this study (Fig. 5). It is important to note that dredging and mangrove deforestation, due to resort development, has occurred on Bimini's North Island since 2001 (Jennings et al., 2008). In Bimini's North Sound, this anthropogenic disturbance has resulted in habitat destruction, degradation, reduced community complexity and reduced prey abundance of the juvenile lemon shark's preferred prey species yellowfin mojarra (*Gerres cinereus*, Jennings et al., 2008). This has slowed growth for juveniles and negatively impacted survival (Gruber and Parks 2002; Jennings et al., 2008).

4.5. Conclusion

With the current lack of relative abundance data and species-specific demography for sharks in The Bahamas, the current study used a 12-year fisheries-independent survey in Bimini, Bahamas to determine the local demographics, local abundance trends and local abiotic factors that influence the catch rates of tiger, nurse, blacktip and lemon sharks. These abundance trends provide valuable baseline data for the evaluation of shark sanctuary impacts on local populations. The historic abundance of tiger, nurse, blacktip and lemon sharks is relatively unknown. However, in our study relative local abundance trends point to variable nurse and stable tiger, blacktip and lemon shark catch rates. It is important to not base the status of these species solely off this survey, because more comprehensive and integrated stock assessment models are the most robust analysis for understanding populations. However, in the absence of these methods, local abundance trends can provide an improved understanding of these data-limited species.

Acknowledgments

This work was supported by: U.S. National Science Foundation; Save Our Seas Foundation; Bimini Biological Field Station Foundation; National Geographic Research Grants; Guy Harvey Research Grants; University of Massachusetts Dartmouth School for Marine Science and Technology; the Food and Agricultural Organization of the United Nations; and the Swiss Shark Foundation. The authors would like to acknowledge all past/present Bimini Biological Field Station Foundation staff and volunteers. We would also like to thank the Cadrin Lab and Gavin Fay at the University of Massachusetts Dartmouth School for Marine Science and Technology for all of their help and support. Thank you to the two anonymous reviewers for their comments and suggestions. This research was carried out under a permit from the Department of Fisheries of the Commonwealth of the Bahamas.

Appendix A

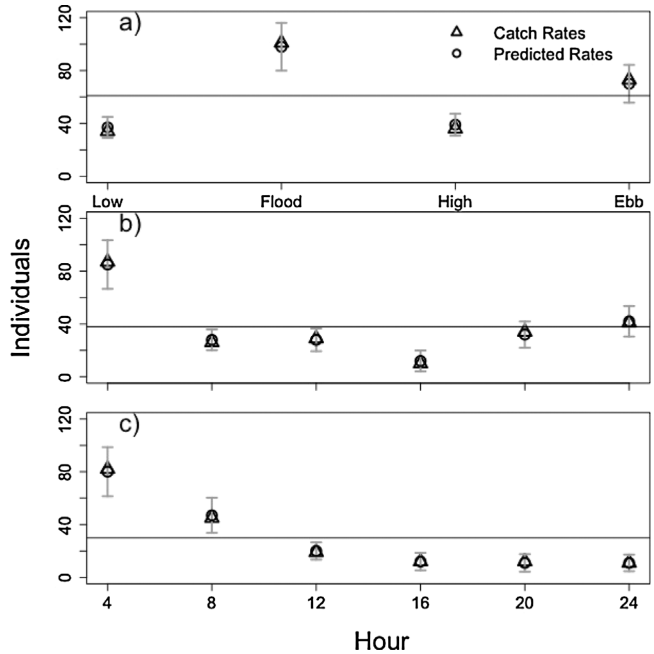

Fig. A1. Tidal phase abundance estimates for the (a) tiger shark. Hour of capture abundance estimates for the (b) nurse shark, and (c) blacktip shark. All sharks were caught in Bimini, Bahamas, and all abundance estimates are based on final Poisson generalized additive models. Y-axis is number of individuals captured. Shaded grey areas represent standard error estimates. Horizontal black line represents the average capture rate.

Table A1
Optimal Poisson generalized additive models for investigating shark catch rates in Bimini, Bahamas. Lowest second order Akaike information criterion (AICc) score determines optimal model.

Species	Covariates	AICc	ΔAICc
Tiger	Year + Month +Lunar Cycle + Tide + Location	1140	–
	Year + Month + Lunar Cycle	1144	4
	Year+ Month + Tide	1144.8	4.8
	Year	1145.3	5.3
	Year + Month	1146	6
Nurse	Year + Month + Hour	994.3	–
	Year + Month + Lunar Cycle + Hour	994.3	–
	Year + Month + Lunar Cycle + Tide + Hour	999.1	4.8
	Year + Lunar Cycle + Hour	1021.9	27.6
	Year + Hour	1023.7	29.4
Blacktip	Year + Month + Lunar Cycle + Hour + Location	829.2	–
	Year + Month + Hour + Location	836.6	7.4
	Year + Hour + Location	840.2	11
	Year + Month	865.7	36.5
	Year + Lunar Cycle	866	36.8
Lemon	Year + Month + Location	515.6	–
	Year + Month + Hour + Location	516.9	1.3
	Year + Month	518.1	3.5
	Year + Hour	519.6	4
	Year + Lunar Cycle + Tide	523.7	8.1

References

Ackerman, J.T., Kondratieff, M.C., Matern, S.A., Cech, J.J., 2000. Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. Environ. Biol. Fishes 58 (1), 33–43.

Afonso, A.S., Andrade, H.A., Hazin, F.H., 2014. Structure and dynamics of the shark assemblage off Recife, northeastern Brazil. PLoS One 9, e102369.

Ansell, A., Gibson, R., Barnes, M., Press, U., 1996. Coastal fisheries in the Pacific Islands. Oceanogr. Mar. Biol.: Annu. Rev. 34, 531.

Atlantic States Marine Fisheries Commission, 2008. Interstate Fishery Management Plan for Atlantic Coastal Sharks. Fishery Management Report. . Available at: http://www.asmfc.org/uploads/file/interstateFMPforAtlanticCoastalSharks.pdf (Accessed on 29 December 2016).

Barton, K., 2016. MuMIn; Multi-Model Inference. R Package Version 1.15.6.

Baum, J.K., Blanchard, W., 2010. Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. Fish. Res. 102, 229–239.

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science (New York, N. Y.) 299, 389–392.

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates A better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. Bioscience 51, 633–641.

Brown, Craig A., Gruber, Samuel H., 1988. Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. Copeia 747–753.

Burgess, H.G., Branstetter, S., 2009. Carcharhinus Limbatus. The IUCN Red List of Threatened Species. http://dx.doi.org/10.2305/IUCN.UK.20092. (RLTS. T3851A10124862. en. Accessed on 25 July 2017).

Burgess, G.H., Beerkircher, L.R., Cailliet, G.M., Carlson, J.K., Cortés, E., Goldman, K.J., Grubbs, R.D., Musick, J.A., Musyl, M.K., Simpfendorfer, C.A., 2005. Is the collapse of

shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? Fisheries 30, 19–26.
Burnham, K.P., Anderson, D.R., 2003. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer Science & Business Media (pp. 169–176).
Campana, S.E., Marks, L., Joyce, W., Kohler, N.E., 2006. Effects of recreational and commercial fishing on blue sharks (*Prionace glauca*) in Atlantic Canada, with inferences on the North Atlantic population. Can. J. Fish. Aquat.Sci. 63, 670–682.
Carlisle, A.B., Starr, R.M., 2010. Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. Environ. Biol. Fishes 89, 31–45.
Carlson, J.K., McCandless, C.T., Cortés, E., Grubbs, R., Andrews, K., MacNeil, M.A., Musick, J.A., 2009. Update on the Status of the Sand Tiger Shark, Carcharias Taurus in the Northwest Atlantic Ocean. National Oceanic Atmospheric Administration Technical Memorandum NMFS-SEFSC-585.
Carlson, J., Hale, L., Morgan, A., Burgess, G., 2012. Relative abundance and size of coastal sharks derived from commercial shark longline catch and effort data. J. Fish Biol. 80, 1749–1764.
Carruthers, T.R., Punt, A.E., Walters, C.J., MacCall, A., McAllister, M.K., Dick, E.J., Cope, J., 2014. Evaluating methods for setting catch-limits in data-limited fisheries. Fish. Res. 153, 48–68.
Castillo-Géniz, J., Márquez-Farias, J., Rodríguez De La Cruz, M.C., Cortés, E., Del Prado, A.C., 1998. The Mexican artisanal shark fishery in the Gulf of Mexico: towards a regulated fishery. Mar. Freshw. Res. 49, 611–620.
Castro, A.L., Rosa, R.S., 2005. Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol das Rocas Biological Reserve, Brazil. Environ. Biol. Fishes 72, 213–221.
Castro, J.I., 1996. Biology of the blacktip shark, Carcharhinus limbatus, off the southeastern United States. Bull. Mar. Sci. 59 (3), 508–522.
Castro, J.I., 2000. The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahama Islands. Environ. Biol. Fishes 58, 1–22.
Castro, J.I., 2011. The Sharks of North America. Oxford University Press, pp. 5–275.
Chapman, D.D., Babcock, E.A., Gruber, S.H., DiBattista, J.D., Franks, B.R., Kessel, S.A., Guttridge, T., Pikitch, E.K., Feldheim, K.A., 2009. Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. Mol. Ecol. 18, 3500–3507.
Chapman, D.D., Frisk, M.G., Abercrombie, D.L., Safina, C., Gruber, S.H., Babcock, E.A., Feldheim, K.A., Pikitch, E.K., Ward-Paige, C., Davis, B., Kessel, S., Heithaus, M., Worm, B., 2013. Give shark sanctuaries a chance. Science (New York N. Y.) 339 757–757.
Cortés, E., Brooks, E., Apostolaki, P., Brown, C., 2006. Stock Assessment of Dusky Shark in the US Atlantic and Gulf of Mexico. Panama City Laboratory Contribution, pp. 6.
DeMaster, D.P., Fowler, C.W., Perry, S.L., Richlen, M.F., 2001. Predation and competition: the impact of fisheries on marine-mammal populations over the next one hundred years. J. Mammal. 82, 641–651.
Di Santo, V., Bennett, W.A., 2011. Effect of rapid temperature change on resting routine metabolic rates of two benthic elasmobranchs. Fish. Physiol. Biochem. 37, 929–934.
DiBattista, J.D., Feldheim, K.A., Garant, D., Gruber, S.H., Hendry, A.P., 2011. Anthropogenic disturbance and evolutionary parameters: a lemon shark population experiencing habitat loss. Evol. Appl. 4 (1), 1–17.
Driggers III, W.B., Ingram Jr., G.W., Grace, M.A., Gledhill, C.T., Henwood, T.A., Horton, C.N., Jones, C.M., 2008. Pupping areas and mortality rates of young tiger sharks Galeocerdo cuvier in the western North Atlantic Ocean. Aquat. Biol. 2, 161–170.
Driggers III, W.B., Campbell, M.D., Hannan, K.M., Hoffmayer, E.R., Jones, C.M., Jones, L.M., Pollack, A.G., 2016. Influence of bait type on catch rates of predatory fish species on bottom longline gear in the northern Gulf of Mexico. Fish. Bull. 115 (1).
Dulvy, N.K., Forrest, R.E., 2010. Life Histories, Population Dynamics and Extinction Risks in Chondrichthyans. Biology of Sharks and Their Relatives, vol. 2. CRC Press, Boca Raton, pp. 639–679.
Feldheim, K., Gruber, S., Ashley, M., 2001. Population genetic structure of the lemon shark (*Negaprion brevirostris*) in the western Atlantic: DNA microsatellite variation. Mol. Ecol. 10, 295–303.
Ferreira, L.C., Afonso, A.S., Castilho, P.C., Hazin, F.H., 2013. Habitat use of the nurse shark, Ginglymostoma cirratum, off Recife, Northeast Brazil: a combined survey with longline and acoustic telemetry. Environ. Biol. Fishes 96, 735–745.
Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K., 2010. Patterns and ecosystem consequences of shark declines in the ocean. Ecol. Lett. 13, 1055–1071.
Giraudoux, P., 2011. Pgirmess: Data Analysis in Ecology. R Package Version 1.5.1.
Gledhill, K., Kessel, S., Guttridge, T., Hansell, A., Bester-van der Merwe, A., Feldheim, K., Gruber, S., Chapman, D., 2015. Genetic structure, population demography and seasonal occurrence of blacktip shark Carcharhinus limbatus in Bimini, the Bahamas. J. Fish Biol. 87, 1371–1388.
Green, M., Ganassin, C., Reid, D., 2009. Report into the New South Wales (NSW) Shark Meshing (Bather Protection) Program. NSW DPI Fisheries Conservation and Aquaculture Branch Orange, NSW.
Gruber, S., Parks, W., 2002. Mega-resort development on Bimini: sound economics or environmental disaster? Bahamas J. Sci. 9, 2–18.
Gruber, S.H., Nelson, D.R., Morrissey, J.F., 1988. Patterns of activity and space utilization of lemon sharks, Negaprion brevirostris, in a shallow Bahamian lagoon. Bull. Mar. Sci. 43, 61–76.
Gruber, S.H., De Marignac, J.R., Hoenig, J.M., 2001. Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. Trans. Am. Fish. Soc. 130 (3), 376–384.
Guttridge, T.L., Gruber, S.H., Franks, B.R., Kessel, S.T., Gledhill, K.S., Uphill, J., Krause, J., Sims, D.W., 2012. Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. Mar. Ecol. Prog. Ser. 445, 279–291.
Guttridge, T.L., Van Zinnicq Bergmann, M.P.M., Bolte, C., Howey, L.A., Finger, J.S., Kessel, S.T., et al., 2017. Philopatry and regional connectivity of the great hammerhead shark, Sphyrna mokarran in the US and Bahamas. Front. Mar. Sci. 4 (3).
Hale, L.F., Gulak, S.J., Mathers, A.N., Carlson, J.K., 2013. Characterization of the Shark and Reeffish Bottom Longline Fishery 2011. National Oceanic Atmospheric Administration Technical Memorandum NMFS-SEFSC-634.
Harley, C.D., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9, 228–241.
Hayes, C.G., Jiao, Y., Cortés, E., 2009. Stock assessment of scalloped hammerheads in the western North Atlantic Ocean and Gulf of Mexico. N. Am. J. Fish. Manage. 29, 1406–1417.
Heithaus, M.R., Hamilton, I.M., Wirsing, A.J., Dill, L.M., 2006. Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. J. Anim. Ecol. 75, 666–676.
Heithaus, M.R., Burkholder, D., Hueter, R.E., Heithaus, L.I., Pratt, J., Harold, L., Carrier, J.C., 2007. Spatial and temporal variation in shark communities of the lower Florida Keys and evidence for historical population declines. Can. J. Fish. Aquat.Sci. 64, 1302–1313.
Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol. Evol. 23, 202–210.
Heithaus, M.R., 2001. The biology of tiger sharks, Galeocerdo cuvier, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environ. Biol. Fishes 61, 25–36.
Hight, B.V., Lowe, C.G., 2007. Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? J. Exp. Mar. Biol. Ecol. 352, 114–128.
Holmes, B.J., Sumpton, W.D., Mayer, D.G., Tibbetts, I.R., Neil, D.T., Bennett, M.B., 2012. Declining trends in annual catch rates of the tiger shark (*Galeocerdo cuvier*) in Queensland, Australia. Fish. Res. 129, 38–45.
Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science (New York, N. Y.) 293, 629–637.
Jennings, D.E., Gruber, S.H., Franks, B.R., Kessel, S.T., Robertson, A.L., 2008. Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas. Environ. Biol. Fishes 83, 369–377.
Jennings, D.E., DiBattista, J.D., Stump, K.L., Hussey, N.E., Franks, B.R., Grubbs, R.D., Gruber, S.H., 2012. Assessment of the aquatic biodiversity of a threatened coastal lagoon at Bimini, Bahamas. J. Coast. Conserv. 16, 405–428.
Jiao, Y., Hayes, C., Cortés, E., 2009. Bayesian hierarchical models for fish-complex stock assessment without species-specific data. ICES J. Mar. Sci. 66, 367–377.
Karl, S.A., Castro, A.L., Garla, R.C., 2012. Population genetics of the nurse shark (*Ginglymostoma cirratum*) in the western Atlantic. Mar. Biol. 159, 489–498.
Keeney, D., Heist, E., 2006. Worldwide phylogeography of the blacktip shark (*Carcharhinus limbatus*) inferred from mitochondrial DNA reveals isolation of western Atlantic populations coupled with recent Pacific dispersal. Mol. Ecol. 15, 3669–3679.
Kerford, M.R., Wirsing, A.J., Heithaus, M.R., Dill, L.M., 2008. Danger on the rise: diurnal tidal state mediates an exchange of food for safety by the bar-bellied sea snake *Hydrophis elegans*. Mar. Ecol. Prog. Ser. 358, 289–294.
Kerstetter, D.W., Graves, J.E., 2006. Effects of circle versus J-style hooks on target and non-target species in a pelagic longline fishery. Fish. Res. 80, 239–250.
Kessel, S., Gruber, S., Gledhill, K., Bond, M., Perkins, R., 2013. Aerial survey as a tool to estimate abundance and describe distribution of a carcharhinid species, the lemon shark, *Negaprion brevirostris*. J. Mar. Biol. 597383, 1–10. http://dx.doi.org/10.1155/2013/597383.
Kessel, S., Hansell, A., Gruber, S., Guttridge, T., Hussey, N., Perkins, R., 2016. Three decades of longlining in Bimini, Bahamas, reveals long-term trends in lemon shark Negaprion brevirostris (*Carcharhinidae*) catch per unit effort. J. Fish Biol. 88, 2144–2156.
Kessel, S., 2010. An Investigation into the Behavior and Population Dynamics of the Lemon Shark (Negaprion Brevirostris). PhD Thesis. Cardiff University, UK.
Kiszka, J.J., Heithaus, M.R., 2014. The state of knowledge on sharks for conservation and management. Sharks: Conservation, Governance and Management. pp. 69.
Knip, D.M., Heupel, M.R., Simpfendorfer, C.A., 2010. Sharks in nearshore environments: models, importance, and consequences. Mar. Ecol. Prog. Ser. 402, 1–11.
Kohler, N.E., Casey, J.G., Turner, P.A., 1998. NMFS cooperative shark tagging program, 1962–93: an atlas of shark tag and recapture data. Mar. Fish. Rev. 60, 1–87.
Mandelman, J.W., Cooper, P.W., Werner, T.B., Lagueux, K.M., 2008. Shark bycatch and depredation in the US Atlantic pelagic longline fishery. Rev. Fish Biol. Fish. 18, 427–442.
Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of recent approaches. Fish. Res. 70, 141–159.
Maunder, M.N., Punt, A.E., 2013. A review of integrated analysis in fisheries stock assessment. Fish. Res. 142, 61–74.
Maunder, M.N., Sibert, J.R., Fonteneau, A., Hampton, J., Kleiber, P., Harley, S.J., 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. ICES J. Mar. Sci.: J. Cons. 63, 1373–1385.
Minami, M., Lennert-Cody, C.E., Gao, W., Roman-Verdesoto, M., 2007. Modeling shark bycatch: the zero-inflated negative binomial regression model with smoothing. Fish. Res. 84, 210–221.
Morgan, A., Carlson, J.K., 2010. Capture time, size and hooking mortality of bottom longline-caught sharks. Fish. Res. 101, 32–37.
Natanson, L., Casey, J., Kohler, N., Colket, T., 1999. Growth of the tiger shark, *Galeocerdo cuvier,* in the western North Atlantic based on tag returns and length frequencies; and

a note on the effects of tagging. Fish. Bull. 97, 944–953.
Papastamatiou, Y.P., Lowe, C.G., Caselle, J.E., Friedlander, A.M., 2009. Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90, 996–1008.
Papastamatiou, Y.P., Watanabe, Y.Y., Bradley, D., Dee, L.E., Weng, K., Lowe, C.G., Caselle, J.E., 2015. Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? PLoS One 10, e0127807.
Pratt Jr., H.L., Carrier, J.C., 2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. Environ. Biol. Fishes 60, 157–188.
Randall, J.E., 1992. Review of the biology of the tiger shark (*Galeocerdo cuvier*). Mar. Freshw. Res. 43, 21–31.
Reid, D., Robbins, W., Peddemors, V., 2011. Decadal trends in shark catches and effort from the New South Wales, Australia, shark meshing program 1950–2010. Mar. Freshw. Res. 62, 676–693.
Rigby, R.A., Stasinopoulos, D.M., 2005. Generalized additive models for location, scale and shape. J. R. Stat. Soc.: Ser. C (Appl. Stat.) 54, 507–554.
Rosa, R.S., Castro, A.L., Furtado, W., Monzini, J., Grubbs, R.D., 2006. Ginglymostoma Cirratum. The IUCN Red List of Threatened Species. http://dx.doi.org/10.2305/IUCN.UK.2006. (RLTS.T60223A12325895. en. Accessed on 25 July 2017).
SEDAR, 2006. Southeast Data Assessment and Review (SEDAR) 11 Stock Assessment Report: Large Coastal Shark Complex, Blacktip and Sandbar Shark. . Available at: http://www.nmfs.noaa.gov/sfa/hms/hmsdocument_files/FMPs.htm/ (Accessed on 1 November 2016).
SEDAR, 2013. SEDAR 34 – Atlantic Sharpnose Shark Stock Assessment Report. SEDAR, North Charleston, SC Available online at: http://sedarweb.org/docs/sar/S34_ATSH_SAR.pdf.
Santander-Neto, J., Shinozaki-Mendes, R.A., Silveira, L.M., Jucá-Queiroz, B., Furtado-Neto, M.A., Faria, V.V., 2011. Population structure of nurse sharks, Ginglymostoma cirratum (*Orectolobiformes*), caught off Ceará state, Brazil, south-western equatorial atlantic. J. Mar. Biol. Assoc. U.K. 91, 1193–1196.
Shepherd, T.D., Myers, R.A., 2005. Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. Ecol. Lett. 8, 1095–1104.
Simpfendorfer, C.A., Goodreid, A.B., McAuley, R.B., 2001. Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier,* from Western Australian waters. Environ. Biol. Fishes 61, 37–46.
Simpfendorfer, C.A., Hueter, R.E., Bergman, U., Connett, S.M., 2002. Results of a fishery-independent survey for pelagic sharks in the western North Atlantic, 1977–1994. Fish. Res. 55, 175–192.
Simpfendorfer, C.A., 2009. Galeocerdo Cuvier. The IUCN Red List of Threatened Species. http://dx.doi.org/10.2305/IUCN.UK.20092. (RLTS.T39378A10220026. en. Accessed on 25 July 2017).
Stevens, J., Bonfil, R., Dulvy, N., Walker, P., 2000. The effects of fishing on sharks, rays, and chimaeras (*chondrichthyans*), and the implications for marine ecosystems. ICES J. Mar. Sci.: J. Cons. 57, 476–494.
Sulikowski, J.A., Wheeler, C.R., Gallagher, A.J., Prohaska, B.K., Langan, J.A., Hammerschlag, N., 2016. Seasonal and life-stage variation in the reproductive ecology of a marine apex predator, the tiger shark *Galeocerdo cuvier*, at a protected female-dominated site. Aquat. Biol. 24, 175–184.
Sundström, L.F., 2015. Negaprion Brevirostris. The IUCN Red List of Threatened Species. http://dx.doi.org/10.2305/IUCN.UK.2015. (RLTS.T39380A81769233. en. Accessed on 25 July 2017).
U.S. Naval Observator, 2016. U.S. Naval Observatory Lunar Data. Available at: http://aa.usno.navy.mil/data/docs/MoonFraction.php (Accessed on 1 November 2016).
Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.
Warton, D.I., 2005. Many zeros does not mean zero inflation: comparing the goodness-of-fit of parametric models to multivariate abundance data. Environmetrics 16, 275–289.
Wood, S., 2006. Generalized Additive Models: An Introduction with R. CRC press, pp. 131–238.
Zuur, A.F.S., Ieno, A.A., 2012. Zero Inflated Models and Generalized Linear Mixed Models with R. Highland Statistics Limited, Newburgh pp. 231–257.
Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Spring Science and Business Media, New York, NY pp. 32–66.