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Seasonal abundance, philopatry and demographic structure of Caribbean reef shark (*Carcharhinus perezi*) assemblages in the north-east Exuma Sound, The Bahamas

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Abstract The Caribbean reef shark (*Carcharhinus perezi*), an abundant coral-reef-associated apex predator, is one of the most economically and ecologically important, yet least studied species of large shark in the greater Caribbean region. The relative abundance and population structure of *C. perezi* off Cape Eleuthera, The Bahamas, was surveyed by standardised longline surveys from May 2008 to October 2011, which resulted in the capture of 331 sharks. Abundance peaked in the summer and was lowest during the winter. Females were 1.6 times more abundant than males and the assemblage was dominated by immature female sharks (45.5 %). The abundance of mature male and female sharks peaked a month apart in June and August, respectively. All 331 sharks were tagged and released with 15.4 % being recaptured after periods at liberty between 5 and 1,159 days (Mean = 333.4 ± 42.7 SE). The mean distance between tagging and recapture was 1.77 km for recaptures in excess of 6 months, indicating seasonally stratified philopatry in this species. *C. perezi* inhabiting Bahamian waters have developed complex habitat use patterns that are both spatiotemporally and demographically segregated, most probably in response to the large and diverse habitat mosaic available on the Bahamas Banks compared to contemporary study sites. This study represents an important step in understanding the spatiotemporal population structure of *C. perezi* and illustrates the potential for studies examining behavioural plasticity in response to environmental variation and anthropogenic disturbance.

Introduction

The Caribbean reef shark (*Carcharhinus perezi*) is an abundant, large-bodied, reef-associated predator (Compagno 1984), distributed throughout the tropical and subtropical western Atlantic, Gulf of Mexico and greater Caribbean (Castro 2011; Driggers et al. 2011). As the

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mainstay of the shark-diving industry in a number of countries, it is one of the most economically important species in the region (Cline 2008; Gallagher and Hammerschlag 2011; Maljkovic and Côté 2011); in addition, it is thought to play a vital ecological role as an apex predator in Caribbean coral reef ecosystems (Opitz 1996; Bascompte et al. 2005; Heithaus et al. 2008; Ferretti et al. 2010).

Despite its economic and ecological importance, very few scientific papers have been published to date dealing specifically with the biology and ecology of *C. perezi* (see Bond et al. 2012; Chapman et al. 2005, 2007; Pikitch et al. 2005; Garla et al. 2006a, b; Tavares 2009; Maljkovic and Côté 2011), and it remains one of the least studied species of large sharks in the region. The maximum reported size of *C. perezi* is 2.43 m of total length (L_T), but size-at-maturity data are scarce (Castro 2011). The synthesis of size at maturity estimates from contemporary publications is challenging given the lack of standardised reporting; however, based on previous estimates, a size of maturity of male sharks of 1.50–1.70 m and of females 1.80–1.90 m is reasonable (Pikitch et al. 2005; Tavares 2009; Castro 2011). Mating in The Bahamas is thought to take place in June and July as ascertained by the presence of mature females with fresh mating scars at local shark feeding sites (C. Zenato, pers. com., Maljkovic and Côté 2011).

The available research suggests that there are ontogenetic shifts in habitat use with smaller juveniles (<1.10 cm L_T) being more common inshore than larger conspecifics that tend to frequent the fore-reef area adjacent to deep water (>400 m) (Pikitch et al. 2005). Acoustic telemetry and stomach content analysis suggest that larger reef sharks (>1.10 cm L_T) regularly visit shallow reef areas to feed at night (Chapman et al. 2005; Garla et al. 2006a). Furthermore, large reef sharks are known to make deep dives (>356 m) into cold water ($\sim$12.4 °C) on a regular basis and increase the proportion of time spent in the upper 40 m of the water column at night (Chapman et al. 2007). There is evidence to suggest that juvenile and adult sharks exhibit a high degree of site fidelity (Bond et al. 2012; Garla et al. 2006b; Maljkovic and Côté 2011), and there is further evidence of increased activity space with ontogeny (Garla et al. 2006b).

Sharks in the Caribbean, as with some populations all over the globe, are in decline (Stallings 2009; Ward-Paige et al. 2010) due to wide-scale fisheries exploitation and habitat degradation (Field et al. 2009; Ward-Paige et al. 2012). Fisheries data specifically pertaining to *C. perezi* are sparse or absent for much of its range, although there are indications that it is fished extensively (Amorim et al. 1998; Arocha et al. 2002; Rosa et al. 2006). The IUCN currently lists *C. perezi* as 'near threatened', with the caveat that it is likely to meet the criteria of 'vulnerable' when additional fisheries data become available (Rosa et al. 2006). In some regions (e.g. USA, The Bahamas), *C. perezi* is protected by fisheries legislation (Morgan et al. 2009), but despite this, there is a paucity of fundamental ecological information that is likely to have hindered the implementation of conservation and management plans. Given this lack of information, the purpose of this study was to characterise the seasonal abundance, habitat use, site fidelity and population structure of *C. perezi* in the waters off Cape Eleuthera in the north-east Exuma Sound, The Bahamas.

Methods

This study was conducted between 8 May 2008 and 11 October 2011 in the waters adjacent to Cape Eleuthera, Eleuthera, The Bahamas (24.54N, 76.12W). All research was carried out under the Cape Eleuthera Institute research permit (MAF/FIS/17 and MAF/FIS/34) issued by the Bahamian Department of Marine Resources in accordance with CEI animal care protocols developed within the guidelines of the Association for the Study of Animal Behaviour and the Animal Behaviour Society (Rollin and Kessel 1998).

The island of Eleuthera is situated on the eastern edge of the Great Bahamas Bank, the largest of the three carbonate platforms which comprise the Bahamian archipelago (Buchan 2000). The Great Bahamas Bank is divided by two deep-water inlets of the Atlantic Ocean. The north-east corner of one of these inlets, the Exuma Sound, is located immediately adjacent to Cape Eleuthera, on the south-eastern tip of Eleuthera (Fig. 1). The Exuma Sound ranges in depth from 1,500 to 1,800 m and is characterised by steep walls dropping from 20 to 30 m to over 1,000 m along their margins (Buchan 2000).

Longline surveys

Stationary midwater longlines, approximately 500 m in length with $\sim$35 ($\pm$10) baited gangions, were set for 90-min durations. Gangions were 2.5 m in length and spaced $\sim$6 m apart along the mainline with a support buoy attached to 2 m snoods, every six hooks. In the wall zone ($\sim$20 m deep) where the majority of sampling took place, the effective fishing depth of these hooks was from $\sim$5 m below the surface for gangions closest to the support floats, to $\sim$15 m for those at the centre point between floats. In the shallower banks and mid-banks areas ($\sim$5–10 m deep), the mainline was tightened using the boat to minimise sagging and to keep baits off the bottom. Each gangion ended in a 16/0, non-offset circle hook baited with a 100-g chunk of bonito tuna (*Sarda sarda*). Sea surface temperature (°C), water depth (m) and location (UTM) were

recorded using a boat-mounted chart plotter (Garmin GPS Map 450 s, Kansas City, USA) at the centre point of each longline. All surveys were conducted in daylight hours.

All sharks captured were identified to species, sexed, and the pre-caudal (L_{PC}), fork (L_F) and total length (L_T) measured to the nearest cm prior to release. The maturity of male sharks was assessed through observations of clasper length relative to total body length, and the degree of calcification claspers (Chapman et al. 2007; Pikitch et al. 2005), and that of females was estimated by size. Females with a total length in excess of 1.85 m, half way between the most recent estimates of 1.80 m (Tavares 2009) and 1.90 m (Castro 2011), were considered sexually mature. Animals with a visible umbilical scar were considered young-of-the-year. Evidence of mating in the form of bite marks and scars on females and inflamed claspers on males was also noted. Two external tags were affixed to all captured sharks: a 'rototag'-style livestock tag attached to the upper third of the first dorsal fin (DuFlex, Destron Fearing, South St. Paul, Minnesota) and a dart tag inserted in basolateral dorsal musculature (Hallprint, Victoria Harbour, Australia). For sharks hooked in the jaw, the hook was removed by cutting the barb and rotating the hook free. For sharks hooked in the throat or gut, attempts were made to remove as much of the hook and steel leader as possible prior to release.

Sampling structure

An initial sampling period ran from June 2008 to June 2009 and was spatially stratified by three zones differentiated by coarse habitat type, water depth and distance from the deep water of the Exuma Sound (Fig. 1; Table 1). Each zone consisted of four 500 × 500 m (0.25 km²) sample sites 2 km apart and orientated approximately north–south along the long axis of the Exuma Sound (Fig. 1). Sampling in this period was also temporally stratified by season (summer: June–August; autumn: September–November; winter: December–February; spring: March–May). Part of the data derived from surveys conducted in this period was used in Brooks et al. (2011) for the purpose of baited underwater video survey method validation. The data presented in this study were derived over a much wider time span (3 years) and have been subjected to a more detailed statistical analysis, and the conclusions drawn take an ecological focus as opposed to a methodological validation. Based on results from June 2008 to June 2009, sampling from June

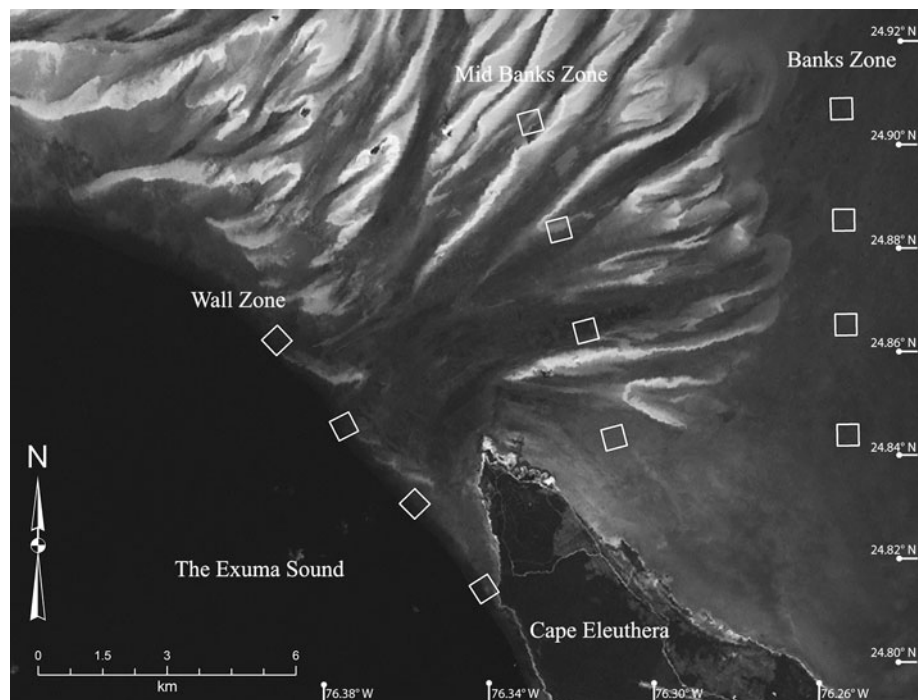**Fig. 1** Distribution of sampling zones in the north-east Exuma Sound, The Bahamas

Table 1 Key environmental characteristics of the three sampling zones

Zone	Mean depth (m)	Habitat description	Dist. Exuma Sound (km)
Wall zone (WZ)	15.3	Coral reef, sand flats and seagrass.	0
Mid-banks zone (MBZ)	4.1	Shallow sand banks and deep channels.	5
Banks zone (BZ)	4.3	Seagrass, sand flats and patch reef.	12

2009 to November 2011 was restricted to the wall zone and only three of the four seasons (spring, summer and autumn). In 2010, the sampling resolution was higher than in previous years, aimed at identifying finer trends in the abundance of specific demographics.

Relative abundance estimates

Relative abundance indices are a common method of describing the comparative spatial and temporal abundance of terrestrial and aquatic flora and fauna (Southwood and Henderson 2000). The most common expression of relative abundance for longline surveys is catch-per-unit-effort (CPUE), usually expressed in sharks per hook hour (sharks hook^{-1} h^{-1}) or multiples thereof (Pikitch et al. 2005; Simpfendorfer et al. 2002; Brooks et al. 2011). The traditional expression of longline CPUE is as follows (Eq. 1):

$$CPUE = \frac{Catch}{Number\ of\ hooks \times soak\ time} \tag{1}$$

The standard calculation for CPUE relies on the assumption that baits remain on the hook and actively fish for the entire duration of the set, an assumption that has previously been shown to be incorrect (Heithaus 2001). To account for these disparate rates of bait loss, the protocols established by Wirsing et al. (2006) for drum line surveys were incorporated into the longline CPUE formula. It was assumed that every hook retrieved without bait, or on which a shark had been captured, had ceased fishing half way through the survey, and fishing effort was adjusted accordingly. The adapted formula used to calculate CPUE in the present study is as follows (Eq. 2):

$$CPUE = \frac{Catch}{(Number\ of\ hooks \times soak\ time) - \left((number\ of\ baits\ lost + catch) \times \left(\frac{soak\ time}{2}\right)\right)} \tag{2}$$

Data analysis

Catch-per-unit-effort data, like most abundance data, are characterised by large numbers of zeroes leading to a heavily skewed distribution (Fletcher et al. 2005; Martin et al. 2005) and, as a result, fail the assumptions of the majority of traditional statistical techniques (Zar 1984). Ignoring the characteristics of these zero-inflated CPUE data sets compromises the detection of trends and alternatively can lead to the identification of trends that do not exist (Martin et al. 2005).

In the present study, a two-stage hurdle model was used to identify the relationship of reef shark abundance to season and habitat type (Fletcher et al. 2005; Fletcher and Faddy 2007; Bejarano et al. 2010). This technique splits the analysis into two parts using two data sets derived from a single abundance (CPUE) data set: one binary, indicating the presence or absence of *C. perezi*, and a second continuous data set of CPUE data, which is truncated to exclude sets where reef sharks were not encountered.

The first stage of modelled presence/absence data using contingency analysis, following which chi-squared tests were used to test the null hypothesis that the distribution of presence and absence was equal across categories. Where significant differences were indicated, post hoc, serial chi-squared tests were performed to identify category-specific differences. If a specific analysis was conducted over multiple years, a Cochran–Mantel–Haenszel test was used instead of Pearson's chi-squared test, as it tests the consistency of trends over a third blocking variable, in this case year. The threshold of significance (α) for post hoc tests was not adjusted as the use of Bonferroni corrections when performing multiple comparisons has been strongly contested, given that it reduces the probability of Type I error at the cost of inflating the probability of the equally deleterious Type II error (Rothman 1990; Perneger 1998; Nakagawa 2004).

Where the presence/absence data identified significant trends, the second stage of the analysis was implemented whereby relative abundance (CPUE) data were analysed using analysis of variance (ANOVA) with post hoc Tukey's analysis (see Fletcher et al. 2005; Bejarano et al. 2010 for details). Prior to analysis, the distribution of CPUE data were analysed using Shapiro–Wilk W test and, where necessary, transformed using the Box–Cox procedure (Box and Cox 1964). All analyses were performed using JMP 7.0.1 (SAS Institute, Cary, NC, USA), and the level of significance (α) for all tests was 0.05.

Results

During the study, 377 standardised longline surveys were conducted resulting in the capture of 331 *C. perezi*. It was found that the rate of bait loss was significantly higher in the wall zone compared to the other habitat zones (Kruskal–Wallis: $\chi^2 = 99.4$, $p < 0.001$), presumably due to the higher density of scavenging fishes compared to other habitats, thus validating the use of the adjusted CPUE estimates outlined previously. At-vessel mortality rates were low at 2.72 % ($n = 9$), of which approximately half ($n = 4$) could be attributed to hooking in the gut or throat. Subsections of the data set were selected for specific analyses based on the homogeneity of sampling effort within that period, a key assumption for all relative abundance analyses (Southwood and Henderson 2000).

Demographic population structure and size-at-maturity

Of the 331 sharks captured during this study, sex was identified in 314 individuals (Table 2). Females were more abundant than males with an observed ratio of 1.6 females for every male captured. Immature sharks were approximately 1.8 times more abundant than mature sharks. The catch was dominated by immature females representing 45.5 % of the animals caught. Length frequency distribution suggested a wide range of life stages are present off Cape Eleuthera, with the exception of smaller, young-of-the-year sharks (Fig. 2; Table 2). Indeed, only four individuals, all of

which were male, were identified as young-of-the-year, ranging in size from 0.75 to 0.89 m L_T. The smallest mature and the largest immature male animals were 1.37 cm and 1.59 m, respectively, and the mean size of all mature males was 1.66 m L_T ± 0.15 S.E. Logistic regression indicated a significant relationship between maturity and total length for male sharks ($r^2 = 0.69$, $p < 0.001$; Fig. 3). Based on this logistic function, 50 % of the male population are predicted to be mature at 1.48 m L_T (Fig. 3). Fresh mating wounds were identified on only three females in the month of June, and well-healed mating scars were identified in a further three females in the month of September.

Table 2 Population structure of Caribbean reef sharks captured 2008–2011 in the north-east Exuma Sound, The Bahamas

Demographic	Count	% Catch	Total length range (cm)	Total length mean (cm)
All	314	100	75–222	153.33
Male	122	38.9	75–189	145.84
Female	192	61.1	91–222	158.22
Mature	112	35.7	n/a	n/a
Immature	202	64.3	n/a	n/a
Immature females	143	45.5	91–184	144.24
Immature males	60	19.1	75–169	129.92
Mature females	49	15.6	185–222	199.88
Mature males	62	19.7	137–189	165.69

Fig. 2 Length frequency of female (**a**) and male (**b**) Caribbean reef sharks (*Carcharhinus perezi*) captured 2008–2011 in the north-east Exuma Sound, The Bahamas. *Vertical black lines* represent the approximate size-at-maturity based on published articles to date (Pikitch et al. 2005; Tavares 2009; Castro 2011)
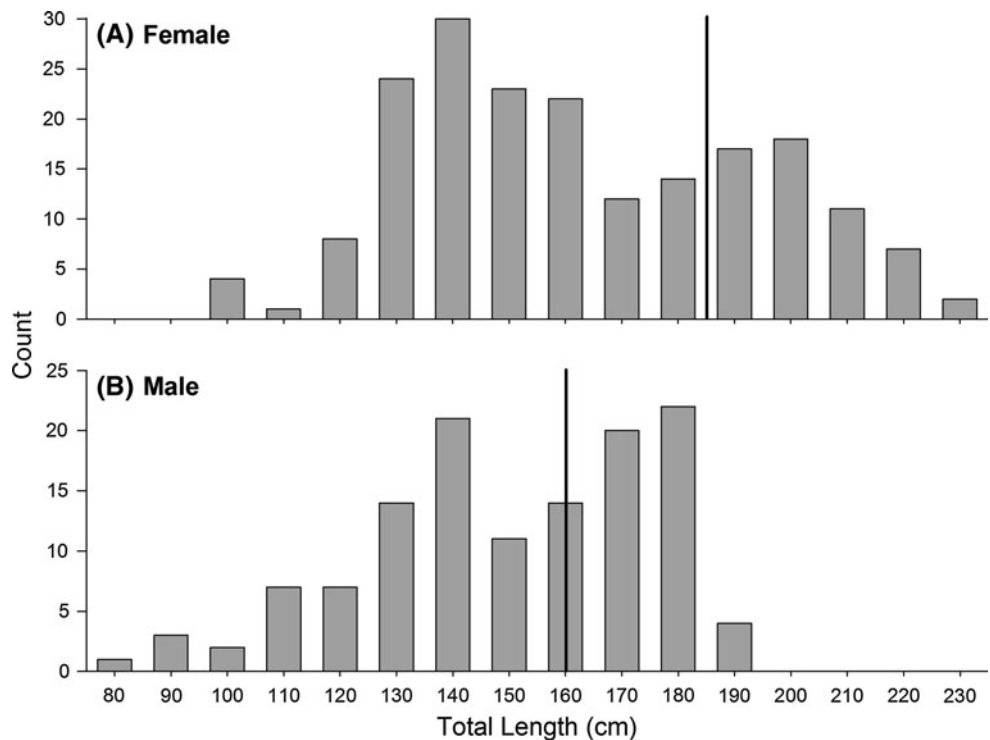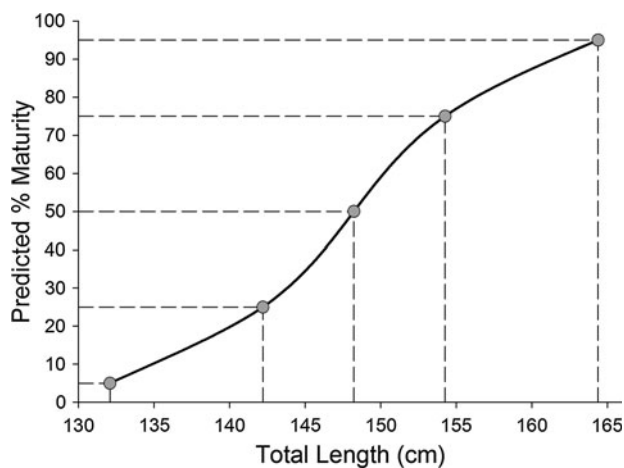
Fig. 3 Logistic relationship between maturity and total length of male Caribbean reef sharks (*Carcharhinus perezi*). *Data points* represent the predicted size at which 5, 25, 50, 75 and 95 % of the male population is mature

Variation in abundance

Seasonal and spatial variation in abundance

This analysis incorporated 161 longline surveys conducted from June 2008 to June 2009 evenly distributed between the four seasons ($\bar{x} = 40.25 \pm 2.53$ S.E. per season) and three habitat zones ($\bar{x} = 53.7 \pm 5.67$ S.E. per zone). There was a significantly higher probability of catching *C. perezi* in the summer compared to all other months and significantly higher capture probability in the autumn compared to winter (Contingency Analysis—$\chi^2 = 40.55$, $p = <0.001$; Fig. 4a, b). Sharks were more commonly encountered in the wall zone compared to the mid-banks and banks zones and more commonly encountered in the mid-banks than the banks zone (Contingency Analysis—$\chi^2 = 42.16$, $p = <0.001$; Fig. 4c, d). Analysis of the zero-truncated CPUE data indicated that sharks were significantly more abundant in the wall zone compared to both the mid-banks and banks zones (ANOVA—$F_{2,56} = 14.75$, $p = <0.001$).

These seasonal and spatial trends remained consistent across demographics. Significant increases in relative abundance during the summer were evident for both mature (Contingency Analysis—$\chi^2 = 26.50$, $p = <0.001$; Fig. 4a) and immature animals (Contingency Analysis—$\chi^2 = 24.81$, $p = <0.001$; Fig. 4b). Furthermore, relative abundance was significantly higher in the wall zone for both mature (Contingency Analysis—$\chi^2 = 10.48$, $p = <0.001$; Fig. 4c) and immature animals (Contingency Analysis—$\chi^2 = 39.92$, $p = <0.001$; Fig. 4d). Analysis of zero-truncated CPUE data showed no significant differences in any of the above analyses (Multiple ANOVAs—$p = >0.05$).

Temporal variation in abundance

This analysis incorporated 166 longline surveys conducted from May to October 2010 and 2011 ($\bar{x} = 23.7 \pm 3.36$ S.E. surveys per month). Mature *C. perezi* were significantly more likely to be encountered in June, July and August compared to April, May, September and October (Cochran–Mantel–Haenszel test—$\chi^2 = 26.313$, $p = <0.001$; Fig. 5a). Furthermore, stage two hurdle analysis indicated that mature *C. perezi* were significantly more abundant in June compared to July (ANOVA—$F_{4,21} = 3.652$, $p = 0.016$). There was no significant variation in the abundance of immature animals over the same period (Cochran–Mantel–Haenszel test—$\chi^2 = 8.025$, $p = 0.236$, Fig. 5b).

Significant variation in the presence and absence of both mature male (Cochran–Mantel–Haenszel test—$\chi^2 = 25.5987$, $p = <0.001$; Fig. 6a) and mature female sharks were identified (Cochran–Mantel–Haenszel test—$\chi^2 = 15.699$, $p = 0.016$; Fig. 6b); however, peaks in maximal abundance were a month apart, with maximal mature male abundance in June compared to maximal mature female abundance in August. Stage two analysis of the zero-truncated data set indicated that mature male *C. perezi* were significantly more abundant in June compared to July (ANOVA—$F_{3,19} = 5.879$, $p = 0.005$); however, no significant trends were identified in mature females ANOVA—$F_{3,8} = 1.909$, $p = 0.206$).

Influence of temperature on abundance

C. perezi were captured in sea surface temperatures ranging from 22.4 to 30.0 °C (Mean = 27.40°C $\pm$ 0.30 S.E.). Temperature had a significant effect on the presence or absence of *C. perezi* (Logistic Regression—$\chi^2 = 26.43$, $p = < 0.001$), and inverse prediction based on this logistic function suggests that there is a >50 % probability of *C. perezi* being present on a survey at water temperatures >27.93 °C. The effect of temperature was consistent and statistically significant for all demographic groups including mature males (Logistic Regression—$\chi^2 = 8.80$, $p = 0.030$), mature females (Logistic Regression—$\chi^2 = 12.19$, $p = <0.001$), immature males (Logistic Regression—$\chi^2 = 4.95$, $p = 0.026$) and immature females (Logistic Regression—$\chi^2 = 8.07$, $p = 0.005$).

Mark recapture

Of the 331 sharks captured and tagged, a total of 52 (15.4 %) were recaptured after periods at liberty between 5 and 1,159 days ($\bar{x} = 333.4 \pm 42.7$ S.E.). There was no significant difference in the sex ratios between

Fig. 4 Seasonal and spatial variation in relative abundance in mature (**a** & **c**) and immature (**b** & **d**) Caribbean reef sharks (*Carcharhinus perezi*) in the north-east Exuma Sound, The Bahamas. Significant differences are illustrated by *dissimilar letters*, and sample size is indicated at the *column base*
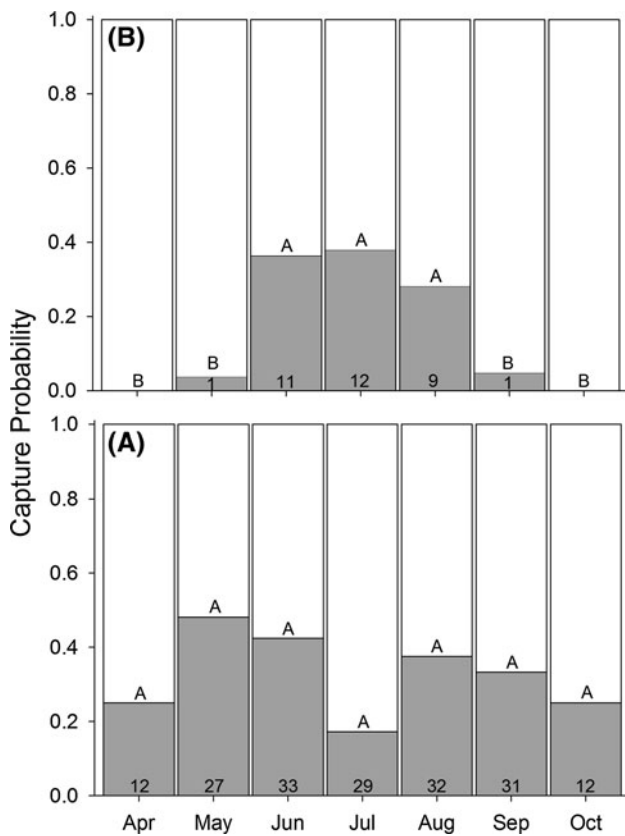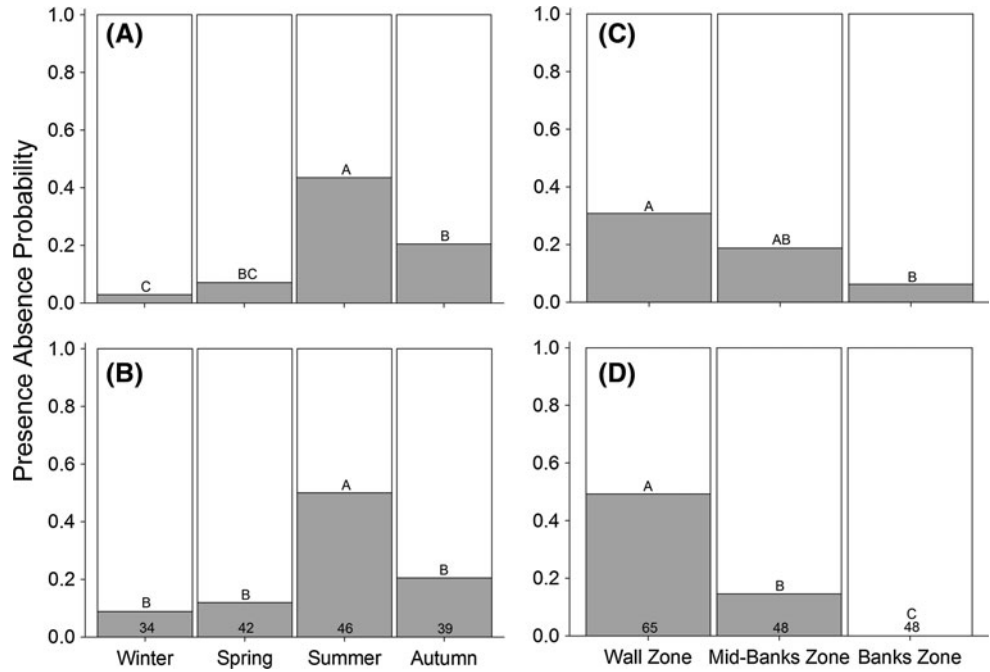

Fig. 5 Monthly capture probability of mature (**a**) and immature (**b**) Caribbean reef sharks (*Carcharhinus perezi*) in the north-east Exuma Sound, The Bahamas. Significant differences are illustrated by *dissimilar letters*, and sample size is indicated at the *column base*
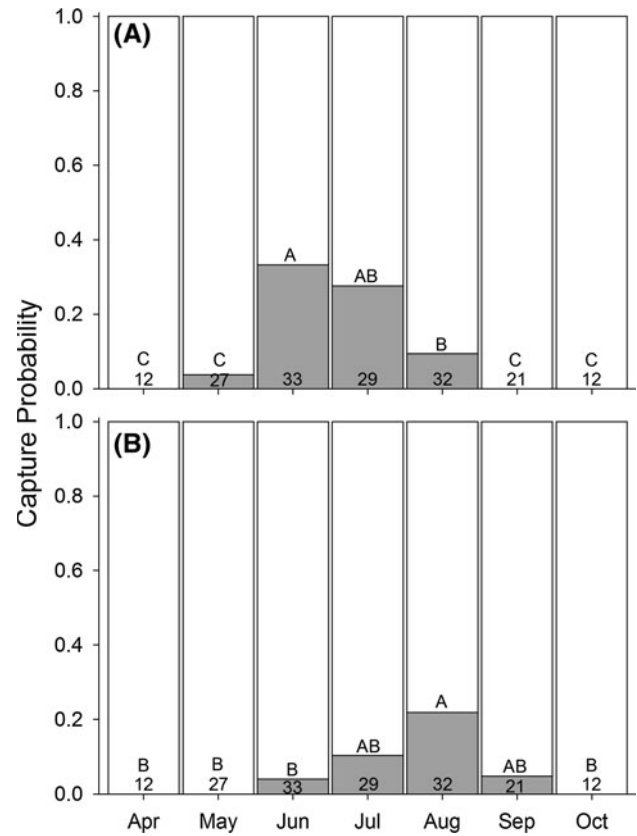
Fig. 6 Monthly capture probability of mature male (**a**) and mature female (**b**) Caribbean reef sharks (*Carcharhinus perezi*) in the north-east Exuma Sound, The Bahamas. Significant differences are illustrated by *dissimilar letters*, and sample size is indicated at the *column base*
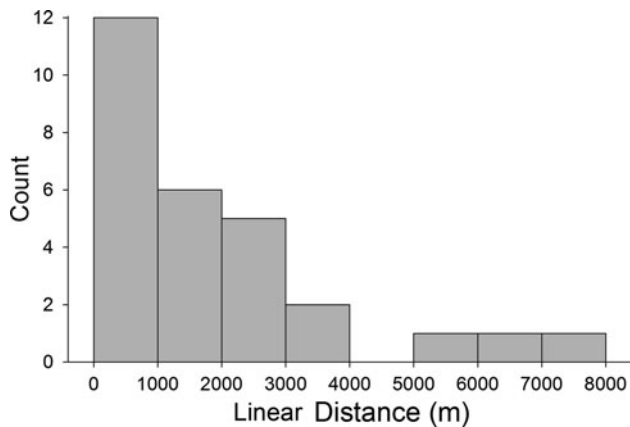
Fig. 7 Linear distance frequency of recaptured Caribbean reef sharks (*Carcharhinus perezi*) in the north-east Exuma Sound, The Bahamas

captured and recaptured animals (Chi-Squared—$\chi^2 = 0.811$, $p = 0.368$).

In order to quantify long-term philopatry, the recapture data set was truncated to include only recaptures in excess of 180 days (6 months) at liberty. For these recapture events ($n = 28$), the straight-line distance between the point of capture and the point of recapture was calculated using Pythagorean Theorem. The mean linear distance between capture and recapture after a minimum of 6 months at liberty was $1{,}767$ m ± 365.23 S.E. (Fig. 7). There was no significant relationship between days at liberty and mean linear distance between capture and recapture (Linear Regression—$r^2 = 0.018$, $p = 0.494$).

Discussion

Identifying spatiotemporal patterns of movement and habitat association, in particular those that incorporate sexual or size-based segregation, is critical when developing effective management and conservation strategies for sharks (Dingle 1996; Speed et al. 2012). While the movement patterns of *C. perezi* have been studied in several locations (see Chapman et al. 2005; Garla et al. 2006a, b; Bond et al. 2012), this is the first time spatiotemporal and demographic population structuring has been described. This study identified clear increases in abundance during the summer, in addition to precise, year-to-year philopatry, indicated by a high rate of recapture and short distances between capture and recapture points. In some cases, recaptures occurred after multiple years at liberty, suggesting that annual migrations are precise and cyclical. Philopatry, which is often spatiotemporally stratified by sex and ontogeny, is a common behaviour in a large number of marine species, including sharks (Hueter et al. 2005), and has been previously identified in populations of *C. perezi* in

other regions. Recapture rates of juvenile *C. perezi* (<110 cm) in the Fernando de Noronha Archipelago (15.3 %) were almost identical to the present study (15.4 %); furthermore, the linear distances between capture and recapture were also comparable (Garla et al. 2006a). Telemetry studies in both the Fernando de Noronha Archipelago and Belize identified distinct philopatry in both juvenile (Garla et al. 2006a) and adult (Chapman et al. 2005; Bond et al. 2012) *C. perezi*; however, no seasonal variation in movements was identified in any of these studies, in direct contrast to the findings of the present study.

Philopatry in species closely related to *C. perezi* found in the greater Caribbean region is common. Natal philopatry, whereby mature females return to their natal region to give birth, is thought to occur in lemon sharks (*Negaprion brevirostris*; Feldheim et al. 2002), blacktip sharks (*Carcharhinus limbatus*, Keeney et al. 2005) and bull sharks (*Carcharhinus leucas*; Tillett et al. 2012); however, natal philopatry has yet to be directly demonstrated in any species of shark. Sexually stratified philopatry was identified in nurse sharks (*Ginglymostoma cirratum*) whereby males returned to a mating site annually in contrast to females which followed a biennial cycle (Pratt and Carrier 2001). Philopatry, which is seasonally, but not sexually or ontogenetically stratified, is exhibited by blacknose sharks (*Carcharhinus acronotus*) which occupy large embayments on the gulf coast of Florida in the summer for mating and feeding (Hueter et al. 2005). The grey reef shark (*Carcharhinus amblyrhynchos*), an Indo-Pacific species thought to inhabit a similar ecological niche as *C. perezi*, also exhibits philopatric behaviour, but is known to undertake large-scale movements (>250 km) on occasions (Heupel et al. 2010; Barnett et al. 2012). Given the presence of spatiotemporal, sexual and ontogenetic structure to philopatric behaviour in these closely related species, the structured philopatry identified in the present study is unsurprising; however, the driving forces behind this structure remain unknown.

The movement patterns contributing to the summer increase in abundance are compounded by apparent demographic stratification within the *C. perezi* population in this region. Sexual and size-based segregation is considered widespread in shark populations (Springer 1967; Sims 2005; Mucientes et al. 2009; Speed et al. 2012); however, this is the first reported instance of *C. perezi* sex ratios diverging from the 1:1 male to female ratio identified in Belize (Pikitch et al. 2005) and Venezuela (Tavares 2009). Previous studies captured small young-of-the-year sharks (<100 cm L_T) in habitats similar to those sampled in the current study (Garla et al. 2006b), suggesting that habitat use by this life stage is likely different in The Bahamas compared to contemporary study areas.

Size-based variation in habitat use has been described in this species before, whereby small sharks (<1.10 m L_T) are more commonly found inshore in lagoons and larger sharks (>1.10 m L_T) are more common on deeper fore reefs adjacent to deep water (Pikitch et al. 2005). The abundances of these two size classes have been found to mirror each other on a diurnal basis, suggesting that smaller sharks avoid larger conspecifics (Chapman et al. 2007). It is clear that *C. perezi* populations in The Bahamas are also ontogenetically segregated, but over a larger geographic scale than previously described.

Recent studies have focused on the relatively small and isolated oceanic islands of Fernando de Noronha in Brazil and Glovers Reef in Belize, which are approximately 26 and 400 km^2 in area, respectively (Garla et al. 2006a, b; Chapman et al. 2007). In contrast, the present study was conducted on the Great Bahamas Bank, which encompasses an area of ∼113,000 km^2, the majority of which is a diverse mosaic of marine habitats interspaced with multiple islands, banks and channels. *C. perezi* in the Great Bahamas Bank region have access to a larger and potentially more diverse range of habitats which different population components can use and re-visit on a seasonal basis. We hypothesise that this greater habitat complexity drives the spatiotemporal and demographic population structuring observed in this study. Animal movements are driven by activities and environmental conditions that promote growth, survivorship and reproductive success (Dingle 1996). As different habitat types impart advantages and disadvantages to different demographics at different times of the year, it is probable that different life stages have developed more complex habitat use patterns based on their biological requirements in comparison with populations studied to date.

It should also be noted that The Bahamas is found at higher latitudes than the aforementioned studies, and as a result, has a wider seasonal range of water temperatures. Satellite-derived sea surface temperature (SST) data generated in 2003 indicate seasonal ranges of 26.4–29.2 °C around Fernando de Noronha and 26.2–29.7 °C around Glovers Reef (Hayes and Goreau 2008), yielding seasonal differences of 2.8 and 3.5 °C, respectively. Similarly derived data for Nassau, which is approximately 95 km north-west of the study site, yield seasonal SST ranges of 24–29.1 °C (Hayes and Goreau 2008) and a 5.1 °C difference from summer to winter. In the present study, a wider range of SST (18.6–31.8 °C) was recorded compared to the satellite-derived values, yielding a 13.2 °C seasonal difference. This larger variation is potentially due to the northward flow of cool water from the Atlantic into the Exuma Sound (Colin 1995) and the strong, highly directional currents that transport hot water on and off the banks each turn of the tide (Rankey and Reeder 2011), creating a

very dynamic thermal environment within the study area. This much wider thermal variation within the study area suggests that thermoregulation might account for some of the observed seasonal movements. However, *C. perezi* is known to tolerate temperatures as low as 12.4 °C during short duration deep dives (Chapman et al. 2007), so the cooler winter temperatures of ∼19 °C in Bahamian waters are likely to be well within its physiological tolerance, although this has yet to be empirically tested. Furthermore, the effect of temperature was consistent across all demographics, and thus cannot account for the demographically stratified nature of the trends.

The specific stimuli that have driven the development of these demographically segregated abundance patterns and the precise year-on-year philopatry are not yet clear; however, based on the available data, some tentative hypotheses can be proposed. The dominance of immature female sharks, combined with peaks in mature male and female abundance occurring over a month apart, suggests that mating is not the primary activity within the study area. This is further supported by the presence of fresh mating wounds on only three (6 %) mature female sharks, all of which were in June which coincides with mating activity observed in other parts of the Bahamas (C. Zenato, pers. com.; Maljkovic and Côté 2011). If mating was the primary activity within the aggregation, a much higher proportion of females bearing mating scars would be expected. Seasonally abundant food sources are known to cause concomitant increases in shark abundance (Dudley and Cliff 2010), although it is suggested that this stimulus would act over an entire population equally, not selecting specific demographics at different times as in the present study. A more likely hypothesis is based on the idea that smaller sharks utilise different habitats to avoid larger conspecifics (Guttridge et al. 2012), either to reduce predation risk or to decrease foraging competition (Heithaus et al. 2008). The avoidance of larger conspecifics has been identified on a smaller scale in populations of *C. perezi* in Belize (Chapman et al. 2007), and it is possible that the trends observed at Cape Eleuthera are a spatiotemporal expansion of this behaviour in response to the larger and more diverse habitat mosaic of the Great Bahamas Bank. At present, there are no data with which to test this hypothesis, and it is unclear whether this size-based segregation is due to the avoidance of larger conspecifics or the avoidance of larger predators in general.

The present study suggests that *C. perezi* may mature at a smaller size than recent estimates indicate; however, making meaningful comparisons is challenging given the lack of standardised reporting of size-at-maturity parameters in previous studies. Pikitch et al. (2005) state a size-at-maturity of male sharks at Glovers Reef, Belize, of 1.50–1.70 m L_T, which coincides with data from Venezuela

(Tavares 2009), but is wider in range than the more recent 1.68–1.70 m L_T estimate of Castro (2011). The most recent female size-at-maturity estimate is 1.90 m L_T (Castro 2011), whereas the mean length of mature female sharks in Venezuela was 1.83 m L_T, and the smallest mature female was 1.54 m L_T (Tavares 2009). In general, this study has yielded the smallest size-at-maturity estimates for male *C. perezi* to date. The mean lengths of mature males (1.66 m L_T) and the smallest mature male (1.37 m L_T) in the present study were 0.15 and 0.12 m smaller, respectively, compared to populations studied in Venezuela (Tavares 2009). Furthermore, the size at which 50 % of the male population are predicted to reach maturity (1.48 m L_T) was on the lower bounds of the range given by Pikitch et al. (2005). With respect to females, reports of small ($\sim$1.55 m L_T) mature female sharks in Venezuela (Tavares 2009) and the presence of several females <1.80 m L_T with healed mating scars in the present study suggest that previous estimates for females might be too large, and there is greater individual variation than previously thought. One caveat is that the aforementioned size-based segregation of local populations could be considered a source of error; however, a theoretical 0.15 m L_T drop in the size-at-maturity for females to 1.70 m L_T still yields a skewed mature to immature ratio of 1:1.7, and immature females would still represent 39.5 % of the catch, suggesting that even if the proportions change, the population is still clearly segregated.

In order to facilitate meaningful size-at-maturity comparisons, standardised reporting of size-at-maturity data is necessary. This should include the smallest mature and largest immature lengths, mean length of mature animals and logistic length predictions at which 50 % of the population reach maturity, the latter of which is commonplace in the literature pertaining to many species of sharks (e.g. Carlson and Baremore 2003; Norman and Stevens 2007; Papastamatiou et al. 2009). Furthermore, additional research into female size-at-maturity is needed prior to drawing firm conclusions about sexual segregation and demographically stratified movement patterns. Given the recent development of hormonal assays to establish reproductive status (see Sulikowski et al. 2007; Awruch et al. 2008; Heupel and Simpfendorfer 2010), this work can now be conducted via a time series of non-lethal blood samples.

The results of this study suggest that *C. perezi* conforms more closely to the classic life history model of a coastal carcharhinid shark than previous research suggests (Springer 1967). Indeed, demographically segregated populations and seasonally stratified movements are widespread among chondrichthyan species (Speed et al. 2012; Mucientes et al. 2009), and the identification of these characteristics within *C. perezi* populations within The Bahamas is unsurprising. This study suggests that *C. perezi*

have developed seasonal, demographically stratified movement patterns that create concomitant variation in demographic population structure in some areas. At present, the driving forces behind these movements and habitat use patterns are unclear, but we hypothesise that it is due to the highly diverse habitat mosaic available to this sub-population, which is distributed over a wider scale compared to previously studied areas. Further research is needed to elucidate the complex habitat use model that *C. perezi* has developed within Bahamian waters, information which has important management and conservation implications for this species throughout its range. Furthermore, the apparent development of geographically discrete behavioural patterns within this species suggests potential for studies investigating behavioural plasticity in response to environmental variation and anthropogenic disturbance.

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