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Distribution, size frequency, and sex ratios of blacktip reef sharks *Carcharhinus melanopterus* at Palmyra Atoll: a predator-dominated ecosystem

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Blacktip reef sharks *Carcharhinus melanopterus* were the most abundant predator in the lagoons at Palmyra Atoll. They were evenly distributed throughout the lagoons, although there was some evidence of sexual segregation. Males reach sexual maturity between 940–1020 mm L_T. Bird remains were found in some *C. melanopterus* stomachs. *C. melanopterus* at Palmyra appear to be smaller than those at other locations.

Key words: CPUE; diet; sexual segregation; size of maturity.

INTRODUCTION

Blacktip reef sharks *Carcharhinus melanopterus* (Quoy & Gaimard) are found on shallow sand-flats and coral reefs throughout the Pacific and Indian Oceans (Hobson, 1963; Compagno *et al.,* 2005). At many islands and atolls, they are one of the most abundant apex predators, although their numbers have been reduced at many locations from over fishing (Hobson, 1963; Stevens, 1984; Sandin *et al.,* 2008). Dietary analysis at multiple locations indicate that *C. melanopterus* primarily consume teleosts, but also crustaceans, cephalopods and in some locations reptiles (Stevens, 1984; Lyle, 1987; Lyle & Timms, 1987; Salini *et al.,* 1992). Their high abundance and occupation of tertiary trophic positions suggests that these fish may exert top-down control of some coral ecosystems and their removal could partially explain the atoll-wide shifts in assemblage structure observed at some atolls exposed to fishing activity (Cortes, 1999; DeMartini *et al.,* 2008; Sandin *et al.,* 2008). With

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the exception of one study, however, the ecology and life-history characteristics of *C. melanopterus* populations at coral reef atolls have not been studied (Stevens, 1984). In particular, little is known for unfished ecosystems, where high population densities are found (Sandin *et al.,* 2008). In order to obtain an understanding of the distribution, and population structure of *C. melanopterus* at a predator-dominated ecosystem, a 4 year fishing study was conducted at Palmyra Atoll.

Palmyra (5°53′ N; 162°05′ W) is an uninhabited atoll located in the central Pacific Ocean and has been a U.S. National Wildlife Refuge since 2001. Due to Palmyra's protected status and remote location, it supports a large population of sharks which make up to 60% of the fish biomass (DeMartini *et al.,* 2008; Sandin *et al.,* 2008). The atoll is *c*. 12·5 km in length, has an area of 27·6 km^2 and consists of two large lagoons (west and east) that are connected by a small channel. A large channel (2 km

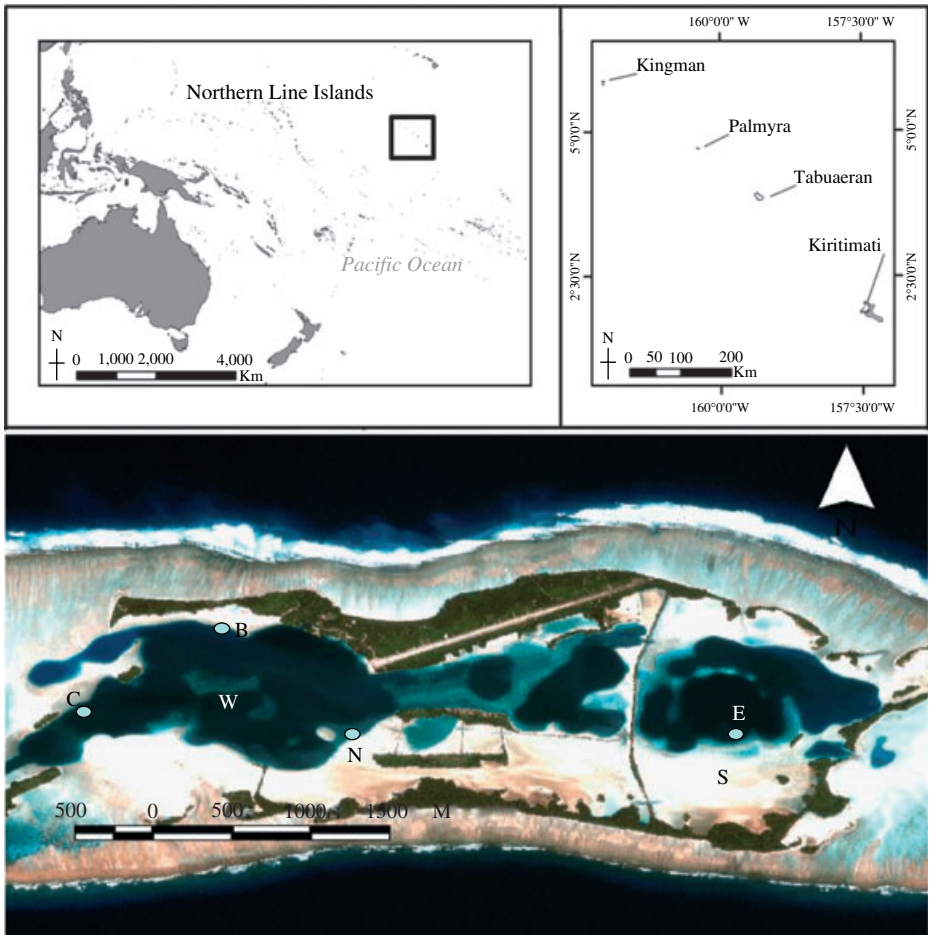

FIG. 1. Location of the Line Islands in the Pacific Ocean (box), and Palmyra's location within the Line Island chain. Aerial image shows the location of the West (W) and East (E) Lagoons, as well as sand-flat fishing locations (○): Banjos (B), Channel (C), Nursery (N) and Sixes (S).

length, 5 m deep) connects the west lagoon to the outer reefs (Fig. 1). The lagoons are also connected to extensive sand-flats that are exposed during extreme low tides.

MATERIALS AND METHODS

Carcharhinus melanopterus were caught at selected locations in both the west and east lagoons at Palmyra. They were caught on hand-lines with barbless hooks and brought alongside the boat, where they were restrained, inverted and placed in tonic immobility (a trance-like state). They were measured, sexed and a numbered dart tag was applied just below the dorsal fin through the epaxial muscle. Sexual maturity in males was estimated by measuring clasper length and by assessing whether claspers were calcified. Generally, calcified claspers are considered a sign of sexual maturity in male sharks, although it should be noted that in some cases there can be a lag between calcification of claspers and testicular development. The total length (L_T) at which 50% of males had calcified claspers was determined by fitting a logistic regression to the clasper length and state data where $y = 100\,[1 + e^{(a-bL_T)}]^{-1}$ where $y =$ percentage of fish with calcified claspers at x mm L_T and $L_{50} = (-a\,b^{-1})$.

Carcharhinus melanopterus neonates and young-of-the-year (YOY) utilize very shallow sand-flat habitats (Papastamatiou *et al.,* 2009). A 20 m seine was used to sample pups at these locations, by herding fish into the net which was positioned perpendicular to the shoreline, where they were measured and weighed. Based on the two age and L_T classes apparent in the size frequency distribution, fish were separated into two classes: <650 mm L_T and those >650 mm L_T. The L_T was $\log_{10}$ transformed to conform to the assumptions of normality and homogeneity of variance, and compared between males and females separately for the two age classes using a t-test.

Fishing was conducted at three sites in the West Lagoon (ledges of Banjos, Nursery and Channel Sand-flats) and one site in the East Lagoon (ledge of Sixes Sand-flat; Fig. 1). Catch per unit effort (CPUE), defined as the number of fish caught per hook per hour, was determined for each fishing location. Due to logistical difficulties associated with getting to Palmyra, fishing could not be conducted year round so CPUE data from different times of the year were combined for each location. CPUE data were square-root transformed and a one-way ANOVA followed by a Tukey's honestly significant differences (HSD) *post hoc* test was used to examine pair-wise differences in CPUE between locations. Sex ratios for *C. melanopterus* were calculated for the whole atoll and then by fishing location. In each case, sex ratios were compared against an expected 1:1 ratio using a χ^2 test for goodness of fit.

Stomach samples were obtained from a small number of fish using a non-lethal gastric evacuation method. While in tonic immobility, a lubricated PVC pipe (60 mm in diameter) was gently inserted into the stomach *via* the buccal cavity. Approximately 500 cm^3 of sea water was poured down the pipe into the stomach and the fish was quickly brought into the boat and tipped head down so that stomach contents exited through the PVC pipe and were collected in a bucket.

RESULTS

In total, 254 *C. melanopterus* were caught and measured between March 2004 and November 2007. Fishing occurred at all times of the day at every location, although no fishing was done at night. In addition, while fishing, eight whitetip reef sharks *Triaenodon obesus* (Rüppell), four grey reef sharks *Carcharhinus amblyrhynchos* (Bleeker) and four giant trevally *Caranx ignobilis* (Forsskål) were caught. Male *C. melanopterus* ranged in L_T from 340 to 1190 mm (mean ± S.D. 930 ± 200 mm) and females from 370 to 1370 mm (960 ± 260 mm; Fig. 2). There were two apparent size classes at Palmyra, one for juveniles with a mode of 500 mm and

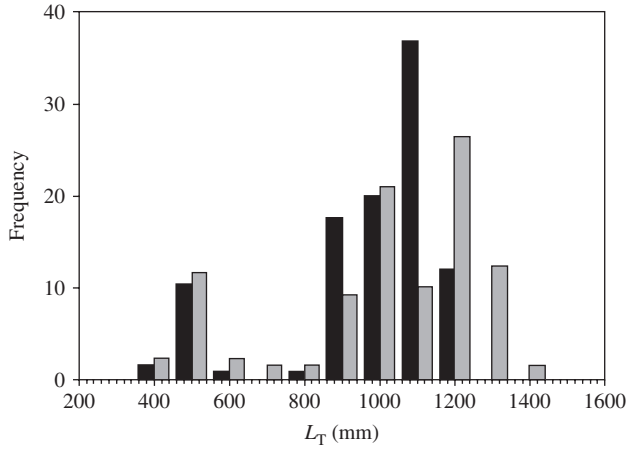

FIG. 2. Total length (L_T)-frequency histogram for 254 *Carcharhinus melanopterus* (▒, females; ■, males) caught at Palmyra Atoll. Data are for both mature and immature individuals.

another for sub-adults and adults with a mode at 1100 mm (Fig. 2). For the sub-adults and adults, females (1070 ± 140 mm) were caught at larger sizes than males (1000 ± 100 mm; *t*-test, d.f. = 107, $P < 0{\cdot}001$). Juvenile males (450 ± 50 mm) did not differ in size from females (470 ± 60 mm; *t*-test, d.f. = 21, $P > 0{\cdot}05$). Similarly, female *C. melanopterus* reached larger L_T than males at both Aldabra Atoll, Indian Ocean (Stevens, 1984) and in Northern Australia (Lyle, 1987). Although there appeared to be an absence of fish in the intermediate L_T range between juveniles and adults, this may be related to gear selectivity as adults were caught using hook and line, while pups were caught in seines. A L_T and mass (M, g) regression was constructed for juveniles which was best described with a linear regression where $M = 2{\cdot}84L_T - 845{\cdot}6$ (d.f. = 20, $r^2 = 0{\cdot}92$, $P < 0{\cdot}001$). Regressions between pre-caudal length (L_{PC}), fork length (L_F) and L_T were also determined for this species (Table I).

CPUE varied among fishing locations in the West and East Lagoon (ANOVA, d.f. = 3, 34, $P < 0{\cdot}001$; Table II). The CPUE at Banjos ($0{\cdot}512 \pm 0{\cdot}307$, individuals per hook per h) was significantly lower ($P < 0{\cdot}05$) than the CPUE at all other locations, but there were no differences in CPUE between the ledges at the Channel,

TABLE I. Linear regression relationships for *Carcharhinus melanopterus* at Palmyra Atoll. Coefficients are for the model $y_i = b_0 + b_1 x_i$. S.E. of the means are in parenthesis

x	y	b_0	b_1	r^2
L_{PC}	L_T	4·25 (0·72)	1·25 (0·01)	0·98
L_T	L_{PC}	−2·18 (0·60)	0·79 (0·01)	0·98
L_F	L_T	2·96 (0·80)	1·15 (0·01)	0·98
L_T	L_F	−1·00 (0·71)	0·85 (0·01)	0·98
L_{PC}	L_F	1·48 (0·39)	1·08 (0·01)	0·99
L_F	L_{PC}	−0·91 (0·37)	0·92 (0·00)	0·99

L_{PC}, pre-caudal length (mm); L_F, fork length (mm); L_T, total length (mm).

TABLE II. Mean ± S.D. catch per unit effort (CPUE; fish per hook per hour) and sex ratios for *Carcharhinus melanopterus* caught on sand-flat ledges within the West (Channel, Banjos, Nursery) and East (Sixes) Lagoons at Palmyra Atoll. *P* values for χ^2 tests are given. All values in bold are statistically significant

Location	CPUE	Males (M)	Females (F)	Ratio M:F	*P*
Channel	1·59 ± 0·37	15	42	**1:3·2**	<0·01
Banjos	**0·51 ± 0·31**	9	8	1·1:1	>0·05
Nursery	1·30 ± 0·72	61	47	1·3:1	>0·05
Sixes	1·69 ± 0·51	29	20	1·5:1	>0·05

Nursery or Sixes Sand-flats (Table II). Based on a concurrent telemetry study, *C. melanopterus* show stronger site fidelity to the Banjos and Channel ledges than they do to the Nursery ledge, which may suggest that the Banjos ledge supports a small number of site-attached fish (Papastamatiou *et al.,* 2009). When quantifying CPUE using fishery-dependent methods, however, it is important to recognize that CPUE is not always equivalent to abundance. For example, differences in water current strength and direction while fishing can lead to differences in CPUE but not necessarily abundance.

A total of 125 males and 129 females were caught at Palmyra (both mature and immature individuals), which did not differ significantly from unity (χ^2 test, d.f. = 128, $P > 0{\cdot}05$). Sex ratios at individual locations within the West and East Lagoons also did not differ from unity, with the exception of the Channel Sand-flats, where 42 females and 13 males (3·2:1) were caught, which differed significantly from unity (χ^2 test, d.f. = 41, $P < 0{\cdot}01$; Table II). It should be noted that juveniles were only found high up on the sand-flats and were not caught at the lagoon fishing stations (Papastamatiou *et al.,* 2009). Several explanations for sexual segregation in elasmobranchs exist, including females moving to more productive areas where they can attain faster growth rates, and females seeking refuge from males and subsequent energy demanding mating activities outside the mating season (Sims, 2003). The reproductive cycle of *C. melanopterus* at Palmyra is unknown, but at Aldabra Atoll, female *C. melanopterus* breed every other year with a 10 to 11 month gestation period (Stevens, 1984), while fish in Moorea reproduce annually with a similar gestation period (Porcher, 2005). It was hypothesized that high levels of intra and interspecific competition could be causing the alternate-year breeding cycle at Aldabra Atoll (Stevens, 1984).

Based on the logistic curve ($r^2 = 0{\cdot}99$, adjusted $r^2 = 0{\cdot}99$, $P < 0{\cdot}001$), 50% of male *C. melanopterus* had calcified claspers at *c*. 970 mm L_T (Fig. 3). The smallest male with calcified claspers was 940 mm L_T, while the largest with non-calcified claspers was 1020 mm L_T [Fig. 3(a)]. Assuming that males are sexually mature at 970 mm L_T, 56·8% of males caught were mature. This size of maturity is larger than the size of maturity for fish in Northern Australia, where all individuals were mature by 950 mm L_T (Lyle, 1987), but smaller than those at Aldabra, where maturity is reached at *c*. 1050 mm L_T (Stevens, 1984). These differences may be related to differences in productivity between small atolls and coastal waters.

Gastric evacuations were performed on 14 fish of which seven (50%) had empty stomachs. Of the remaining fish, remains of teleosts (scales and eye lenses) occurred in three individuals. One fish had unidentified algae in its stomach and one had

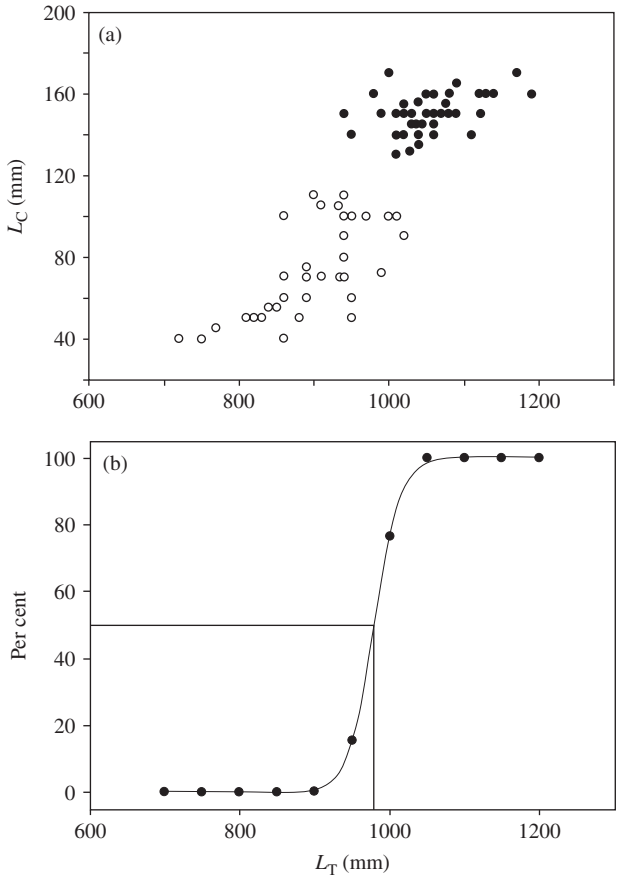

FIG. 3. a) Relationship between total length (L_T) and inside clasper length (L_C) for male *Carcharhinus melanopterus* at Palmyra Atoll (●, calcified claspers; ○, non-calcified claspers). (b) Percentage of male *C. melanopterus* with calcified claspers. A logistic curve has been fitted to the data: $y = 100\,[1 + e^{(a-bx)}]^{-1}$ where $a = 100{\cdot}46$ (0·35) and $b = -56{\cdot}75$ (1·23) (S.E. in parenthesis). The horizontal line represents the size at which 50% of males have calcified claspers.

rat *Rattus rattus* (L.) fur. Four fish (29%) had seabird remains in the stomach, one of which included the wing of a sub-adult or adult red footed boobie *Sula sula* (L.). The smallest fish containing bird remains was 1030 mm L_T. This is the first documentation of predation on seabirds by *C. melanopterus*, and while this could be simply documenting scavenging, active predation on seabird chicks that have fallen out of their nests overhanging the water edges has also been observed (Y. P. Papastamatiou, pers. obs.). It is unclear how important birds are to the diet of *C. melanopterus*, or if induced mortality on seabirds by *C. melanopterus* is compensatory or additive (*i.e.* will chicks that fall into the water die regardless of predation?).

A total of six out of the 193 (3·1%) *C. melanopterus* externally tagged (144 West Lagoon, 49 East Lagoon) were recaptured. Distance travelled from the original tagging location varied from 0 to 1·6 km with a median of 0 km. All fish were

recaptured in the same lagoon they were originally tagged in after 5–166 days (median 65 days) at liberty. The fish at liberty for 166 days had grown 20 mm. The low recapture rate suggests a large population of *C. melanopterus* at Palmyra. High fish mortality from tagging is an unlikely explanation for the low recapture rate based on a concurrent telemetry study of fish movements within the lagoons (Papastamatiou *et al.,* 2009). All recaptures occurred in the same lagoon as original tagging, which agrees with the telemetry study suggesting strong site fidelity to lagoons with limited movements between lagoons (Papastamatiou *et al.,* 2009; unpubl. data).

DISCUSSION

As measured by fishing success, *C. melanopterus* are the most abundant top-level predator in the lagoons and over the sand-flats of Palmyra Atoll. Although they are also present on the outer fore-reefs, there they are replaced in abundance by *C. amblyrhynchos* and the twin spot snapper *Lutjanus bohar* (Forsskål) (DeMartini *et al.,* 2008; Y. P. Papastamatiou, pers. obs.). *Carcharhinus melanopterus* at Palmyra are smaller than those in other locations, where fish can be found as large as 1600–1800 mm L_T (Bass *et al.,* 1973; Compagno *et al.,* 2005). Furthermore, pups as small as 340 mm L_T were caught at Palmyra, which is considerably smaller than the size at parturition in Aldabra and Northern Australia, where *C. melanopterus* pups are born between 480 and 500 mm L_T (Stevens, 1984; Lyle, 1987). This may be more a characteristic of atolls in the Pacific Ocean because free-swimming *C. melanopterus* as small as 330 mm L_T have been found in the Marshall Islands (Bonham, 1960). It is hypothesized, however, that *C. melanopterus* are food limited at Palmyra due to high levels of intra-specific competition resulting from high population densities. The small sizes of fish at Aldabra were also attributed to high levels of intra and interspecific competition (Stevens, 1984). The growth rate calculated for one fish at Palmyra (50 mm year^{-1}) was very similar to the rates observed in *C. melanopterus* at Aldabra Atoll (Stevens, 1984).

The apparently high numbers of *C. melanopterus* in the Palmyra lagoons suggests that they may regulate the trophic food web by some form of top-down control. The importance of understanding the social system and age structure of apex predators in healthy unfished ecosystems is also highlighted by the small spatial scale over which CPUE and sex ratios can vary. How are mating and parturition activities regulated in an atoll that only measures 12 km in length? Future studies should aim to determine whether fish at the atoll are indeed food limited and whether this is a common feature of apex predators in environments with minimal anthropogenic impacts.

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