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## Population structure, spatial distribution and life-history traits of blacktip reef sharks *Carcharhinus melanopterus*

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During a survey of the population of blacktip reef shark *Carcharhinus melanopterus* in Moorea (French Polynesia) between 2007 and 2011, population structural characteristics were estimated from 268 individuals. Total length ( $L_T$ ) ranged from 48 to 139 cm and 48 to 157 cm for males and females, respectively, demonstrating that the average  $L_T$  of females was larger than that of males. The *C. melanopterus* population at Moorea showed an apparent spatial sexual segregation with females preferentially frequenting lagoons and males the fore-reefs. Mean growth rate was *c.* 6 cm year<sup>-1</sup>. Males reached sexual maturity at 111 cm  $L_T$ . This study reports on the population characteristics of this widespread carcharhinid shark species and makes comparisons with other locations, confirming high geographic variability in the population structure of the species.

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Key words: capture–recapture; geographic variability; growth; life history; sexual segregation; shark.

### INTRODUCTION

Habitat choice is one of the processes influencing population distribution, abundance and hence the potential availability of a marine species to fisheries exploitation (Freon & Misund, 1999). Sex-based differences in behavioural strategies of wild populations are critical components of ecosystem-based management plans (Wearmouth & Sims, 2008). In a conservation context, sexual segregation has important implications for the management of marine populations, as it will provide information on the spatial-dynamics of male and female distribution, their abundance and thus the differential anthropogenic exploitation of the sexes through spatially focused fishing pressure (Sims, 2005; Mucientes *et al.*, 2009).

Sharks are one marine group known to show sexual segregation. Sharks also display particular life-history traits such as slow growth, late maturity, low fecundity and a long life span compared to teleosts (Stevens *et al.*, 2000), which may further exacerbate their vulnerability to overexploitation (Jennings *et al.*, 1998; Stevens

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*et al.*, 2000). Indeed, the harvest and by-catch of sharks has risen in recent decades, resulting in the decline of numerous species (Fowler *et al.*, 2005). While anthropogenic disturbance is increasing, knowledge of their life-history variables and their intraspecific variability is lacking and this study aims to determine the presence of sexual segregation and life-history characteristics of a shark species from a currently unfished area, Moorea in French Polynesia.

The blacktip reef shark *Carcharhinus melanopterus* (Quoy & Gaimard, 1824) is a common species of Indo-West Pacific coral reefs (Compagno *et al.*, 2005) inhabiting shallow reefs and sand-flats of both atolls and high islands (Hobson, 1963; Nelson & Johnson, 1980; Stevens, 1984; Papastamatiou *et al.*, 2009a, 2010; Speed *et al.*, 2011; Mourier *et al.*, 2012) and occasionally non-reef environments (Chin *et al.*, 2012), where it is one of the most abundant apex predators, although their numbers have been reduced by overfishing at many locations (Heupel *et al.*, 2009).

*Carcharhinus melanopterus* is often observed in small aggregations, especially when feeding, but is considered neither a solitary nor a schooling shark (Nelson & Johnson, 1980; Papastamatiou *et al.*, 2009b), and has only recently been found to demonstrate complex social interactions (Mourier *et al.*, 2012). It also shows a high degree of site attachment and individual spatial overlap (Stevens, 1984; Papastamatiou *et al.*, 2009b; Mourier *et al.*, 2012). While some life-history parameters and population characteristics have been previously estimated from multiple locations (Bass *et al.*, 1973; Randall, 1977; Stevens, 1984; Lyle, 1987; Papastamatiou *et al.*, 2009a; Chin *et al.*, 2012; Mourier *et al.*, 2012), they show considerable variability (Table I). In this study, the population characteristics and estimated additional life-history variables were investigated and the data compared with those from other locations in the Indo-Pacific Ocean.

## MATERIALS AND METHODS

### STUDY SITE AND SAMPLING

Sharks were caught at Moorea Island [ $17^{\circ} 30' S$ ;  $149^{\circ} 50' W$ ; Fig. 1(a)] from 2007 to 2011 and identified to the species level. *Carcharhinus melanopterus* usually spend most of their time close to the sea floor (Mourier *et al.*, 2012); therefore, to avoid by-catch of other fishes they were attracted to the surface with bait and fishing rod with barbless hooks at multiple locations within and outside the lagoon [Fig. 1(b)]. The depths at all sampled sites were from 1 to 20 m and all *C. melanopterus*, once they had been lured from deeper waters, were captured at a depth of  $<2$  m. They were brought alongside the boat where they were inverted and placed in tonic immobility (Watsky & Gruber, 1990). Pups were caught from the shore with gillnets positioned perpendicular to the shoreline in their potential nursery area (Mourier & Planes, 2013). Each individual was sexed and total length ( $L_T$ ) was measured from the snout tip to the end of the upper caudal lobe. All sites on the fore-reef (*i.e.* locations on the ocean side of the reef) were characterized by continuous coral structures at depths of 15 to 25 m. Habitat characteristics were more variable within the lagoon and can be divided into three main categories: (1) shallow coral reefs with patches of sand at depths from 5 to 15 m (Mareto, PK23 and Varari), (2) sandy bottoms with depths from 5 to 20 m (Maatea, Tiahura and Nuurua) and (3) muddy and sandy substrata at depths  $<2$  m (Haapiti and Pihaena).

### SEX RATIO AND SIZE-FREQUENCY DISTRIBUTIONS

The sex ratio (male:female) was analysed at the island scale, as well as by area and size. The  $\chi^2$  goodness-of-fit test [ $\alpha=0.05$ ; Zar (1999)] was used to examine significant

TABLE I. Summary of geographical variability in *Carcharhinus melanopterus* population characteristics. For all localities the following characteristics are indicated when available: recapture rate (R), sex ratio (M:F), mean growth rate, total length ( $L_T$ ) at maturity for males and females, maximum  $L_T$  reported for males and females, mating and parturition periods, gestation duration, estimated  $L_T$  at birth, litter size, reproductive cycle and the sources of the data.

Location	R (%) (M:F)	Growth rate (cm year <sup>-1</sup> )	Male $L_T$ at maturity (cm)	Female $L_T$ at maturity (cm)	Male maximum $L_T$ (cm)	Female maximum $L_T$ (cm)	Mating	Parturition	Gestation (months)	$L_T$ at birth (cm)	Litter size	Reproductive cycle	Reference
Indian Ocean													
Aldabra	23.2	3.50	105	110	130	140	October to November	October to January	10–11	50	2–5	Biennial	Stevens (1984)
Europa and Madagascar			<110	<119			June to July and December to January			46–52	2–4		Fourmanoir (1961)
Southern Africa			<109		180					57			Bass <i>et al.</i> (1973)
Ningaloo, Australia					134	151				<60			Speed <i>et al.</i> (2011)
Oman			<108			156		February and September			5–6		Henderson <i>et al.</i> (2007)
Red Sea													
							May	August	16	50	2–4		Melouk (1957)
							June to July and December to January			61	4		Gohar & Mazhar (1964)
Indo-Pacific Ocean													
Northern Australia			95	125			November to March		8–9	45–50		Annual	Lyle (1987)

TABLE I. *Continued*

Location	R (%)	Sex ratio (M:F)	Growth rate (cm year <sup>-1</sup> )	Male $L_T$ at maturity (cm)	Female $L_T$ at maturity (cm)	Male maximum $L_T$ (cm)	Female maximum $L_T$ (cm)	Mating	Parturition	Gestation (months)	$L_T$ at birth (cm)	Litter size	Reproductive cycle	Reference
Indonesia		1:27:1		108	~120	130	142		August to September		50–54	3		White (2007)
Pacific Ocean Palmyra	3.1	1:1:03	4.40	95		119	137				34			Papastamatiou <i>et al.</i> (2009b)
Marshall Islands Great Barrier Reef, Australia				95–99		115–119	160–164				33			Bonham (1960) Chin <i>et al.</i> (2012)
	21.0	1:7:00	6.29	100		135	154	December to April	November to March		57			A. Chin, pers. comm.
Moorea, French Polynesia								November to March	September to January	9–10			Annual	Porcher (2005)
	23.5	1:19:10*	6.08	111		139	157			9		1–2	Annual	Mourier & Planes (2013)
Captivity			22.90†					November to March			48			This study Randall (1977)

\*Sex ratio was male-biased on the fore-reef and female biased in the lagoon.

†Only in the two first years after birth.

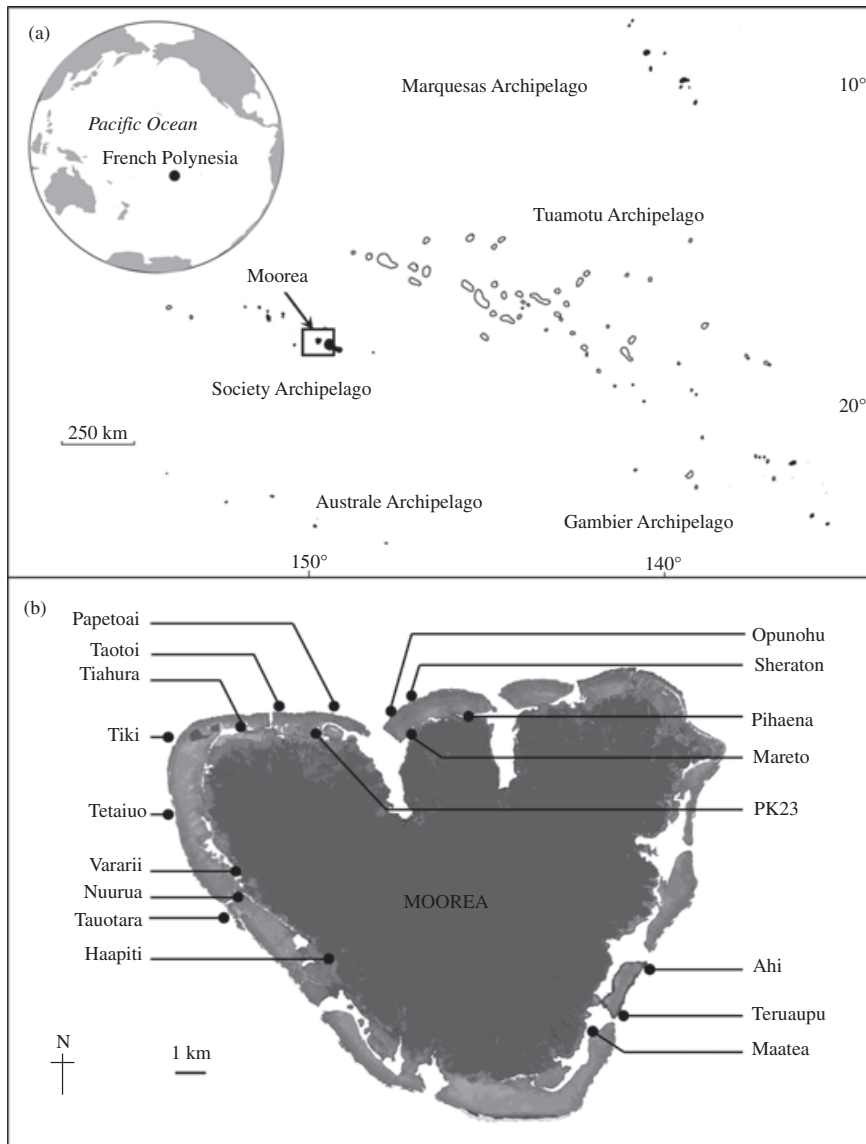


FIG. 1. Study location: (a) map of French Polynesia and (b) locations in Moorea sampled for *Carcharhinus melanopterus*.

deviations from the expected 1:1 sex ratio. Size-frequency distributions of males and females were compared using a two-sample Kolmogorov–Smirnov test (Zar, 1999). Size-frequency distributions for males and females combined were also compared between sampled locations as well as between the lagoon and fore-reef.

## GROWTH RATE

Growth rate was estimated using  $L_T$  measurements from *C. melanopterus* that were captured and later recaptured. *Carcharhinus melanopterus* were identified by photo-identification,

which is a suitable technique for this species (Mourier *et al.*, 2012). When the time interval between capture and recapture (time at liberty) was short, measurement errors may confound growth estimates (Casey *et al.*, 1985), therefore individuals at liberty for <200 days were excluded from the growth analysis (Simpfendorfer, 2000). The recapture samples were all within a narrow  $L_T$  range, and thus a narrow age range, therefore an annual mean growth rate was estimated rather than constructing a growth curve (Fabens, 1965).

## SIZE AT MATURITY FOR MALES

Male *C. melanopterus*  $L_T$  at maturity was estimated using non-invasive methods. Maturity was directly determined by visually examining clasper length  $L_C$  (cm) and degree of calcification (Bass *et al.*, 1973). The percentage of mature individuals per 5 cm  $L_T$  class was estimated. Length at 50% maturity (calcified claspers) was determined by fitting a logistic curve to the data and the  $L_T$  at which 50% of individuals were sexually mature was calculated (King, 1995) using the equation:  $p_i = [1 + e^{(a+bL_T)}]^{-1}$ , where  $p_i$  is the proportion of mature individuals in the  $L_T$  class  $i$ , and  $a$  and  $b$  are fitted parameters that can change during the life cycle. The mean  $L_T$  at sexual maturity was calculated as  $L_{T50} = -ab^{-1}$ .

## RESULTS

### SEX RATIO

A total of 122 females and 146 males were caught at Moorea. The total number of adults of each sex did not differ significantly from unity ( $\chi^2$  test,  $P > 0.05$ ; Table II). Significant differences in sex ratios were found, however, when the fore-reef and the lagoon were analysed separately (Table II). Although, sex ratios for adult *C. melanopterus* did not differ from unity for over half of the individual locations at Moorea (seven out of 12), the locations at Tetaiuo, Ahi and Sheraton on the fore-reef were significantly male-biased (Table II), and Mareto and Nuurua within the lagoon were significantly female-biased (Table II). Overall, sex ratios for adult *C. melanopterus* were significantly male-biased on the fore-reef ( $\chi^2$  test,  $P < 0.001$ ; Table II) and significantly female-biased inside the lagoon ( $\chi^2$  test,  $P = 0.001$ ; Table II). Within the two main nurseries at Varari and Haapiti (Mourier & Planes, 2013), the sex ratio did not differ from unity (Table II).

### SIZE DISTRIBUTION

A total of 268 *C. melanopterus* between 2007 and 2011 were sampled. Individuals ranged from 48 to 157 cm  $L_T$  (48–139 and 48–157 cm  $L_T$  for males and females,). Average female  $L_T$  (mean  $\pm$  s.e. = 121.24  $\pm$  2.95 cm, median = 135 cm) was higher than that of males (mean  $\pm$  s.e. = 108.46  $\pm$  2.17 cm, median = 119 cm; independent samples  $t$ -test:  $t = 3.67$ , d.f. = 268,  $P < 0.01$ ). There was a significant difference in  $L_T$  frequency distribution of males and females (Kolmogorov–Smirnov test,  $P < 0.001$ ).

Inside the lagoon, Varari and Haapiti on the west coast had different  $L_T$  frequency distributions compared to all other lagoonal locations (Fig. 2; Kolmogorov–Smirnov tests,  $P < 0.001$  for all comparisons). Individuals from these locations ranged mainly between 48 and 69 cm  $L_T$  suggesting the presence of pups (newborns) and that Varari and Haapiti are nursery areas (Fig. 2; Mourier & Planes, 2013). On the fore-reef, the Sheraton location on the north coast had a smaller  $L_T$  frequency distribution than all

TABLE II. Sex ratios for *Carcharhinus melanopterus* caught inside the lagoon and on the fore-reef of Moorea. Only sites where at least five individuals were caught are shown and only the sex ratio of adults are shown, except for potential nursery areas where pup sex ratios are presented (\*). *P* values for  $\chi^2$  tests are given.

Location	Males (M)	Females (F)	Ratio M:F	$\chi^2$ test Statistic	<i>P</i>
Total Moorea	105	97	1.08:1	0.316	>0.05
<b>Total fore-reef</b>	<b>79</b>	<b>42</b>	<b>1.8:1</b>	<b>11.314</b>	<b>&lt;0.001</b>
<b>Total lagoon</b>	<b>26</b>	<b>55</b>	<b>1.2:1</b>	<b>10.383</b>	<b>&lt;0.001</b>
Potential nursery areas*	25	19	1.31:1	0.818	>0.05
<i>Fore-reef</i>					
<b>Tetaiuo</b>	<b>7</b>	<b>0</b>	–	<b>7.000</b>	<b>&lt;0.01</b>
Tiki	13	6	2.1:1	2.578	>0.05
<b>Ahi</b>	<b>5</b>	<b>0</b>	–	<b>5.000</b>	<b>&lt;0.05</b>
Opunohu	24	16	1.5:1	1.600	>0.05
<b>Sheraton</b>	<b>9</b>	<b>2</b>	<b>4.5:1</b>	<b>4.454</b>	<b>&lt;0.05</b>
Taotoi	12	12	1:1	0.000	>0.05
Papetoai	6	5	1.2:1	0.091	>0.05
<i>Lagoon</i>					
Haapiti*	14	12	1.2:1	0.153	>0.05
Varari*	11	7	1.57:1	0.889	>0.05
Maatea	4	6	1:1.5	0.400	>0.05
<b>Mareto</b>	<b>2</b>	<b>9</b>	<b>1.4:5</b>	<b>4.454</b>	<b>&lt;0.05</b>
PK23	2	4	1:2	0.666	>0.05
Tiahura	4	7	1:1.7	0.818	>0.05
<b>Nuurua</b>	<b>14</b>	<b>29</b>	<b>1.2:0.7</b>	<b>5.236</b>	<b>&lt;0.05</b>

other oceanic locations (Kolmogorov–Smirnov tests,  $P < 0.05$  for all comparisons) (Fig. 2). Overall,  $L_T$  frequency distributions were different between the fore-reef and the lagoon (Kolmogorov–Smirnov test,  $P < 0.001$ ), even when the nursery areas, Varari and Haapiti, were removed from the analyses (Kolmogorov–Smirnov test,  $P < 0.05$ ). Excluding nurseries (Varari and Haapiti), *C. melanopterus* were larger within the lagoon (mean  $\pm$  s.e. =  $129.47 \pm 1.83$  cm) than on the fore-reef (mean  $\pm$  s.e. =  $123.71 \pm 1.19$  cm; independent samples *t*-test:  $t = 2.62$ , d.f. = 217,  $P < 0.01$ ) which is probably due to the higher proportion of females, the larger sex, inside the lagoon and a larger proportion of males, the smaller sex, on the fore-reef (Table II).

## GROWTH

Of the 63 recaptures, 34 occurred with a time at liberty of <200 days, while an additional nine did not have measurable differences in  $L_T$  between capture and recapture and therefore were also excluded from growth rate calculations. The time at liberty for the 20 recaptured *C. melanopterus* included in the analysis ranged from 201 to 714 days. Mean  $\pm$  s.e. annual growth rate for recaptured *C. melanopterus* was  $6.08 \pm 0.76$  cm year<sup>-1</sup>.

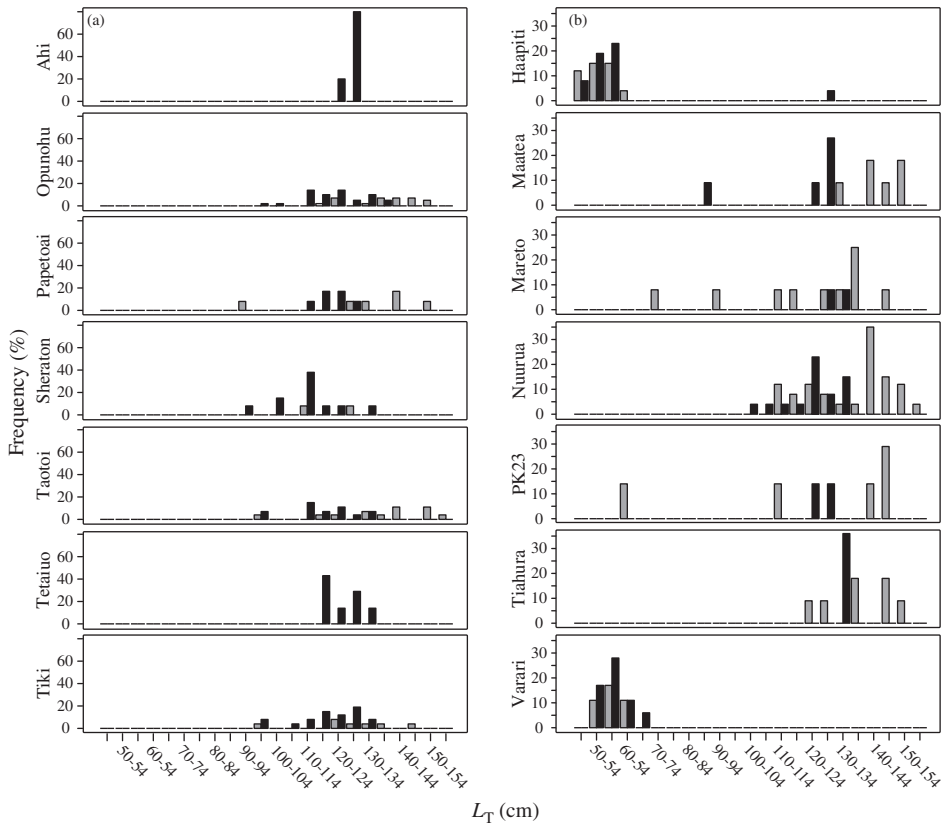


FIG. 2. Total length ( $L_T$ ) frequency histogram for 268 *Carcharhinus melanopterus* (■, males; ▒, females) caught in different locations around Moorea: (a) fore-reef (sampling locations on the ocean side) and (b) lagoon (sampling locations inside the lagoon).

## SIZE AT MATURITY FOR MALES

The  $L_T$  and  $L_C$  were measured for 94 male *C. melanopterus* between 2009 and 2011 of which 31 had non-calcified claspers and 63 had calcified claspers. On the basis of the logistic curve, 50% of male *C. melanopterus* had calcified claspers at 111.01 cm  $L_T$  (Fig. 3). Clasper elongation and calcification generally occurs between 111 and 114 cm  $L_T$ ; the smallest male with calcified claspers measured 111 cm  $L_T$  and the largest immature male was 114 cm  $L_T$  (Fig. 3).

## DISCUSSION

### HABITAT USE AND HABITAT PARTITIONING

Contrary to Palmyra Atoll where *C. melanopterus* were mainly found inside the lagoon (Papastamatiou *et al.*, 2009b), they were abundant both inside and outside the lagoon at Moorea (French Polynesia), sharing their habitat with the pink whipray



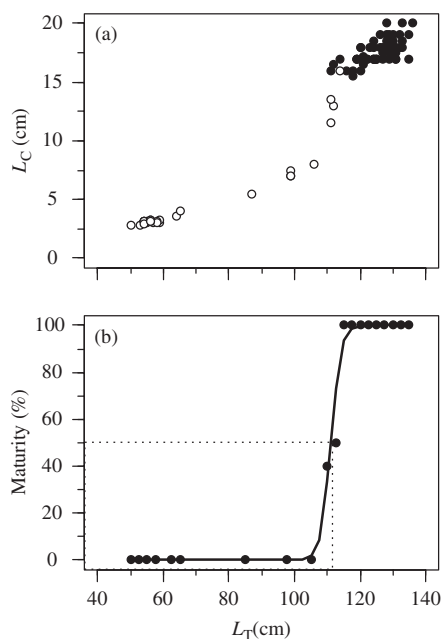


FIG. 3. (a) Relationship between total length ( $L_T$ ) and clasper length ( $L_C$ ) for male *Carcharhinus melanopterus* at Moorea (●, calcified claspers; ○, non-calcified claspers). (b) Maturity of males from calcified claspers. A logistic curve was fitted to the data:  $y = [1 + e^{(a+bx)}]^{-1}$  where  $a = -75.1441$  and  $b = 0.6769$ ,  $P < 0.05$ . -----,  $L_T$  at which 50% have calcified claspers (111.01 cm).

*Himantura fai* Jordan & Seale 1906 within the lagoon (Gaspar *et al.*, 2009), and with sicklefin lemon sharks *Negaprion acutidens* (Rüppell 1837) (Buray *et al.*, 2009) and grey reef sharks *Carcharhinus amblyrhynchos* (Bleeker 1856) on the fore-reef. Juvenile *C. melanopterus* also shared their potential nursery habitat with juvenile *N. acutidens* as the latter were also caught in the nursery areas, Haapiti and Varari, during this study.

## SEXUAL SEGREGATION

These data show patterns of spatial sexual segregation: the overall proportion of females was higher inside the lagoon, while the proportion of males was higher on fore-reef habitats, although some site variability was evident (Table II). Spatial segregation of the sexes is a widespread phenomenon in sharks (Wearmouth & Sims, 2008; Jacoby *et al.*, 2012) and can be categorized into two types: habitat segregation and social segregation. Habitat segregation occurs when the sexes differ in their use of the habitat, and social segregation is the tendency for a species to form single-sex groups.

It was previously found that within a small area *C. melanopterus* formed mixed-sex social groups in which associations were assorted by size and sex (Mourier *et al.*, 2012). Therefore a pattern of social segregation has been observed, although it is not possible to fully understand the evolutionary advantage of preferentially associating with individuals of similar sex.

Such social segregation may be purely the result of conspecific segregation after habitat segregation has occurred. Habitat segregation may be influenced by different factors including sexual dimorphism, differential activity budgets between the sexes (Jacoby *et al.*, 2012) or sex-specific temperature preferences. Evidence was found for sexual dimorphism at Moorea (females are larger than males) which is likely to confer significant differences in predation risk, nutritional requirements and activity budgets between the sexes that subsequently influence the spatial and temporal habitat use by each sex (Sims, 2005; Wearmouth & Sims, 2008). In addition, the selection of shallower habitats by female *C. melanopterus* may be related to sex-specific temperature preferences (Wearmouth & Sims, 2008). Other female shark species occupy warmer, inshore refuges for thermoregulation purposes (Hight & Lowe, 2007), which may enhance gestation and embryonic development. Although all females caught within the lagoon were mature ( $>120$  cm  $L_T$ ; Fig. 2 and Table I), and the lagoon is significantly warmer than the fore-reef (mean temperature  $\pm$  S.E.; lagoon =  $27.798 \pm 0.011^\circ$  C; fore-reef at 25 m =  $27.756 \pm 0.006^\circ$  C; paired  $t$ -test:  $t = 5.0063$ ,  $P < 0.001$ ; between 2008 and 2010; J. Mourier, unpubl. data), this small difference in temperature would probably not confer any physiological advantage. Rather, pregnant females may choose habitats that are safe from predators and display behaviours that reduce the risk of predation in order to increase offspring survival and their reproductive success, whereas males seek habitats with high food availability (Galzin, 1987; Sims, 2005). Otherwise, females may also seek refuge in the shallow waters of the lagoon to avoid male harassment for mating (Economakis & Lobel, 1998; Wearmouth *et al.*, 2012).

Alternatively, if there are sex-specific dietary preferences with different foraging strategies and energy requirements between the sexes (McCord & Campana, 2003) then differences in habitat or prey distribution at the island scale could also contribute to the observed sexual segregation. Galzin (1987) found that fish communities were spatially variable around the island of Moorea depending on habitat configuration; fish community composition was found to be different between the lagoon and fore-reef in Moorea with additional variability in lagoonal communities between the three coasts (Galzin, 1987). This hypothesis could be verified in the future by testing differences in isotopic signatures between the sexes and linking them back to differences in their diet (Hussey *et al.*, 2012). The observed sexual segregation of *C. melanopterus* at Moorea may therefore arise through a combination of sexual habitat segregation and social preferences.

## SIZE DISTRIBUTION

The size-frequency distributions are typical of an unfished population with a high proportion of large individuals. The smallest *C. melanopterus* caught in Moorea were six 48 cm  $L_T$  neonates with apparent open umbilical scars signifying that they were born very recently. This birth size is larger than that reported for *C. melanopterus* at both the Marshall Islands and at Palmyra Atoll in the Pacific Ocean (Table I), but was similar to that described for *C. melanopterus* in northern Australia, at Aldabra in the Indian Ocean, in the Red Sea and at other locations (Table I). Papastamatiou *et al.* (2009a) argued that the small size at birth that they found may be more characteristic of atolls in the Pacific Ocean because free-ranging *C. melanopterus* as small as 33 cm  $L_T$  were found in Marshall Islands (Bonham, 1960). Despite being a

Pacific Island, however, Moorea had larger neonates than both Palmyra and Marshall Islands.

In agreement with other studies on this species (Table I), females were larger than males in Moorea. Furthermore, the maximum  $L_T$  of females caught in Moorea (157 cm) was larger than that in Aldabra, in Palmyra and in northern Australia (Table I). Males reached a maximum  $L_T$  of 139 cm at Moorea which was also longer than that reported in Palmyra, in Aldabra and all other locations (Table I), but Bass *et al.* (1973) reported an exceptional maximum  $L_T$  of 160–180 cm on the east coast of southern Africa. Variation in maximum sizes is generally attributed to varying levels of intra and interspecific competition limiting the food resources (Stevens, 1984; Papastamatiou *et al.*, 2009a). Except for the east coast of southern Africa, maximum sizes for both males and females in Moorea are larger than in previous studies, implying that *C. melanopterus* densities, or that of other competing species, at Moorea are low or are not limited by food resources. Regarding other competing shark species, the *N. acutidens* population at Moorea is small (Buray *et al.*, 2009) and *C. amblyrhynchos* seem to be relatively abundant only at one location in Moorea [Tiki, Fig. 1(b)]. Moreover, these two co-occurring species are not often found in the lagoon (Buray *et al.*, 2009; Gaspar *et al.*, 2009; Clua *et al.*, 2010; Mourier *et al.*, 2012) although *C. melanopterus* are abundant both within and outside the lagoon. Therefore, the low level of interspecific competition is likely to be one factor determining the longer  $L_T$  of *C. melanopterus* at Moorea. Anthropogenic pressures (*e.g.* tourism activities, habitat degradation, eutrophication and exploitation) may also influence demographic and biological variables (Clua *et al.*, 2010) compared to pristine atolls (Stevens, 1984; Papastamatiou *et al.*, 2009a). Finally, differences in maximum sizes may also result from local adaptation of *C. melanopterus* and different evolutionary strategies (DiBattista *et al.*, 2007; DiBattista, 2008). For instance, larger individuals may have a decreased susceptibility to predation risk, access to a greater range of food types, greater competitive ability, increased resistance to extreme conditions or disease, earlier maturation and greater reproductive output (DiBattista *et al.*, 2007). Future studies in other locations in French Polynesia will determine the contribution of local factors to the demographic and biological characteristics of *C. melanopterus* populations.

Although there appears to be an absence of *C. melanopterus* of an intermediate size (75–85 cm  $L_T$ ) between juveniles and adults, this may be related to ontogenetic changes in habitat selection by immature or old juveniles, such as deeper parts of the lagoon that were not sampled. This pattern has also been reported in other locations (Papastamatiou *et al.*, 2009a; Chin *et al.*, 2012). Alternatively, this intermediate size may also represent a period of fast growth.

## GROWTH

The mean annual growth rate in Moorea is very similar to the rate observed in *C. melanopterus* on the Great Barrier Reef and at Palmyra (estimate based on only one specimen), but was almost twice the rate of that of *C. melanopterus* from Aldabra (Table I) determined by length increment data obtained from tagging.

Future additional capture–recapture data, including more individuals at the juvenile stage, will allow for von Bertalanffy growth curve and length-at-age estimates. Furthermore, additional capture–recapture data will also allow for a comparison of

sex differences in growth rate that may explain why females reach a larger  $L_T$  than males. Estimates should also be verified through the use of other techniques such as vertebral analyses. Nevertheless, this study is one of the largest sampling efforts ever carried out to date for this species.

## MATURITY

On the basis of the  $L_C$  and degree of calcification (Bass *et al.*, 1973),  $L_T$  at maturity for male *C. melanopterus* in Moorea was estimated at 111 cm, larger than that for the species in northern Australia, in Palmyra, in Aldabra and all other locations previously sampled (Table I). These differences may be related to variation in productivity between small atolls and coastal locations or high islands such as Moorea, as well as anthropogenic and density-dependent demographic factors. Palmyra and Aldabra are two small atolls; northern Australia, however, is a wide and continuous coastal region and is believed to have high productivity (Chin *et al.*, 2012). The larger observed size at maturity found at Moorea may also be related to natural selection and may be correlated with the larger maximum size of *C. melanopterus* in Moorea compared to other studied locations. Size at maturity for male *C. melanopterus* at Moorea is the largest ever reported for this species (Table I). These results should be further confirmed from steroid analyses using plasma testosterone level as an indicator of male maturity (Mills *et al.*, 2010).

This study contributes to the general knowledge of a poorly known, but widespread reef-associated shark species: *C. melanopterus*. Overall, the results confirm that *C. melanopterus* is a long lived, slow growing (mean growth rate of 6 cm year<sup>-1</sup>) and late maturing species (male size at maturity being 111 cm  $L_T$ ) and thus recovery times from periods of overexploitation would be considerable. The *C. melanopterus* population of Moorea showed an apparent spatial sexual segregation with females being more numerous inside the lagoons and males on the fore-reef. The combination of these *K*-selected characteristics and patterns of sexual segregation highlights the degree of vulnerability of reef-associated shark species to rapid anthropogenic disturbances. Moreover, this study confirms the geographic variability of life-history traits found in this species and highlights the importance of local conditions in shark population life-history traits and degrees of vulnerability.

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