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Insights into the Ecology and Movements of the Blacktip Reef Shark (*Carcharhinus melanopterus*)

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Abstract

A challenge in studying the natural behaviour of wild animals is the need for detailed observations spanning extended periods of time, which are particularly difficult to obtain in the case of sharks. As a result, tagging and remote sensing technologies are usually employed. In this study, 475 blacktip reef sharks (*Carcharhinus melanopterus*) were identified using direct underwater observation. Subsequent sightings of individual sharks were recorded at various locations along the north shore of Mo'orea Island over a period of 6.5 years. The key factors influencing their movements were the reproductive season and the lunar phase. In addition, tendencies to avoid turbulent regions and to leave the area after fishing mortality were observed. Significant variation existed between individuals. While some sharks left their ranges for only two weeks twice a year for mating and parturition, others were absent for months. Juveniles displayed high mobility prior to settling into a home range during the year before maturity, at the age of about 4 years. The understanding of such movements is important for the effective protection of sharks through the establishment of Marine Protected Areas and other conservation strategies.

Keywords: blacktip reef sharks; *Carcharhinus melanopterus*; shark movements; shark ecology; shark ethology

1. Introduction

The behaviour and movement patterns of elasmobranchs remain poorly understood due to the challenges of studying highly mobile marine species (Castro, 2017). Yet movement is a fundamental aspect of their biology, influencing ecological roles and population dynamics (Papastamatiou *et al.*, 2010; Gallagher *et al.*, 2021). Reef sharks adjust their home range size and residency based on habitat quality and intraspecific competition (Chin *et al.*, 2016). Their movements reflect a complex interplay of biotic and abiotic factors governing access to food, mates, and refuge (Papastamatiou *et al.*, 2010). As mesopredators, reef sharks exert consistent predatory pressure, regulating smaller fish and invertebrate populations, fostering biodiversity and resilience in reef ecosystems (Okey *et al.*, 2004; Bascompte *et al.*, 2005; Freire *et al.*, 2008; Papastamatiou *et al.*, 2010; Frisch *et al.*, 2016; Chin *et al.*, 2020). Understanding their spatial ecology thus provides critical insights into the intricate relationships sustaining coral reefs (Chin *et al.*, 2016; Papastamatiou *et al.*, 2019).

The blacktip reef shark (*Carcharhinus melanopterus*), with its preference for shallow coastal habitats, is an ideal species for studying movement patterns as these areas facilitate direct observation (Papastamatiou *et al.*, 2009; Mourier *et al.*, 2012, 2013; Chin *et al.* 2013, 2016). Quantifying movements not only deepens understanding of the species but is vital for conservation, particularly amid global shark population declines driven by the shark fin trade and illegal, unreported, and unregulated fishing (Gallagher *et al.*, 2021; Porcher and Darvell, 2022; Worm *et al.*, 2024). Marine Protected Areas (MPAs) are a cornerstone of shark conservation, yet their efficacy hinges on movement data as many reef sharks range beyond protected boundaries, with patterns varying seasonally and across habitats (Papastamatiou *et al.*, 2009, 2010; White *et al.*, 2017; Pike *et al.*, 2024). The species' slow growth, low

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reproductive rate, and reliance on coastal habitats for mating, pupping, and juvenile development, heighten its vulnerability to pollution and habitat degradation, underscoring the need to protect adult females (Porcher, 2005; Chin *et al.*, 2013; Porcher and Darvell, 2022).

This study investigated blacktip reef shark movements over six and a half years in a fringing lagoon along the north shore of Mo'orea Island, French Polynesia, primarily during daylight and sunset hours. Building on a prior ethogram, which catalogued 35 behaviours to provide a behavioural baseline (Porcher, 2023a), we tracked movements of identified individuals to document patterns of habitat use and behavioural flexibility. By elucidating the spatial ecology of this reef-associated predator we add to the evidence informing conservation strategies for coral reef ecosystems.

2. Materials and Methods

2.1. The Lagoon

The study was conducted in the back reef between Opunohu and Cook's Bay (Galzin and Pointer, 1985) by one observer (IFP). This region spans a distance of 3 to 4 km in length and extends from 0.8 to 1.2 km from the shoreline to the barrier reef. At the time of the study it was a thriving coral habitat, with an average depth of about 2 m. For the purpose of the study it was subdivided into five regions (Figure 1).

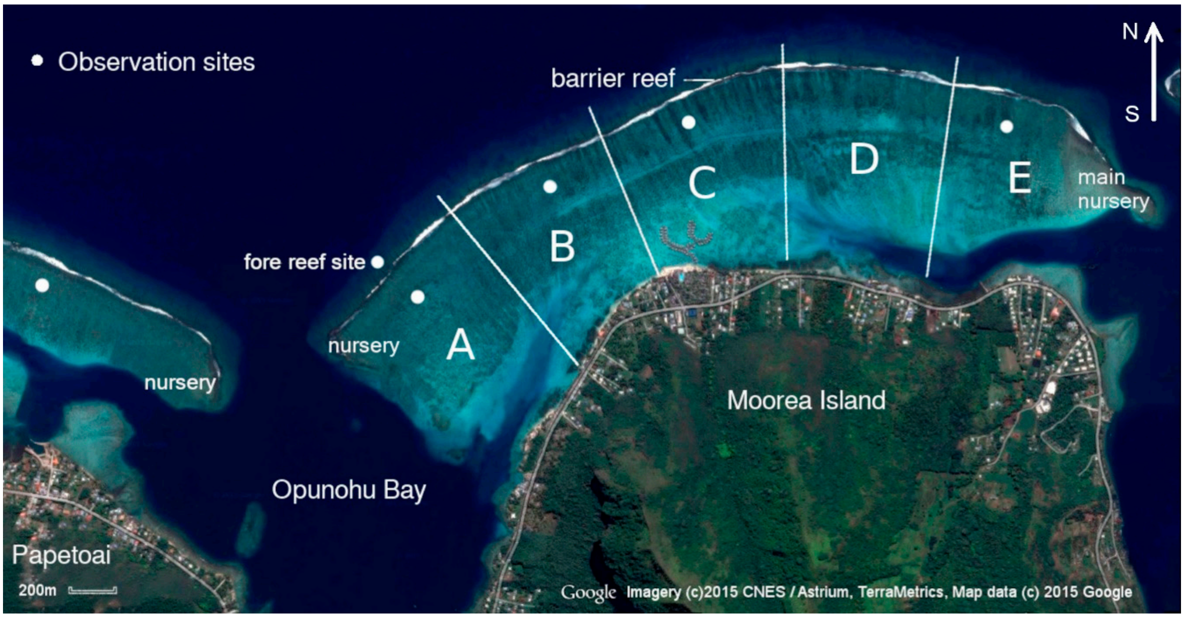

Figure 1. The study lagoon divided for reference, showing the location of the observation sites. South latitude and west longitude: A: –17.485568, –149.855474. B: –17.482010, –149.849751. C: –17.479502, –149.844196. E: –17.479668, –149.830348. Papetoai lagoon site: –17.485447, –149.870780. Fore reef site: –17.483705, –149.857041. (Area D was not used).

Due to logistical constraints, Section A served as the primary study area, with additional observation sites (Sections B–C, E) supplementing the dataset. Monitoring extended to the lagoon boundaries, the fore reef opposite Section A, and nursery areas at the ends of the barrier reef to gather complementary data on blacktip reef shark movements.

Located on the north shore of Mo'orea Island, French Polynesia, the study lagoon is sheltered from the prevailing oceanic swell which strikes the southwestern coast. It features diverse microhabitats shaped by varying environmental conditions (Galzin and Pointer, 1985). From white sand shores, the lagoon floor—composed of coral rubble and sand—slopes to the barrier reef, where it reaches a maximum depth of approximately 3 m. This deeper region functions as a corridor for larger species, including barracuda (*Sphyraena spp*.), jackfish (*Carangidae*), and reef sharks. The area adjacent to this channel is dominated by large, widely-spaced patch reefs, while the barrier reef itself supports short, robust coral growth. Its crest is composed of worn, dead coral and forms a broad band that breaches the surface under calm conditions. It is colonized by *Turbinaria spp*. algae.

Hydrodynamic patterns in the lagoon are shaped by breaks in the barrier reef at river outflows. Oceanic waves spill over the reef, traverse the lagoon, and exit through these passes. The flow accelerates in correlation with the height of the oceanic swell due to channel constriction. Water depth in the lagoon and passes is thus governed by oceanic conditions, with solar-driven tidal fluctuations exerting minimal influence (Hench *et al.* 2008).

Over the 6.5-year study period, coral health declined. By September 2005, much of the coral was dead, algae-covered, or diseased, even near the reef where the effect of shore runoff pollution was minimal. In April 1999, however, Section A featured a white sand substrate with patch reefs (1–3 m diameter, spaced several meters apart) dominated by *Porites spp*. colonies. These supported branching *Acropora, Pocillopora*, and *Millepora* spp., alongside *Turbinaria* and *Sargassum* algae on degraded sections. The area teemed with reef fish, eels, and invertebrates.

Moving east through Section A, patch reefs grew more dense and shallow zones near the barrier reef hosted intricate coral thickets that sheltered blacktip pups slightly larger than neonates. Further east, patch reefs increased in size and spacing, transitioning into a barren, rubble-floored expanse (>200 m wide) extending from the barrier reef more than halfway to shore. This feature, nearly devoid of coral, delineated core ranges of blacktip reef sharks and served as a midday resting area for individuals from both Sections A and B (Porcher, 2023a).

Section B, east of the barren zone, hosted tall, slender *Porites* colonies growing closely together in a fish-rich habitat. This dense coral matrix provided refuge for juvenile blacktips of all ages, leading to juvenile-dominated observations at the Section B site. In Section C, the water grew deeper and the patch reefs were larger, and more dispersed, with algae-covered coral and reduced fish abundance relative to other sites. Section D mirrored Section A's habitat characteristics, a pattern persisting into Section E. The eastern boundary of Section E gradually sloped into reef flats, then a broad blacktip reef shark nursery area where the barrier reef curved into Cook's Bay and was thus more protected from ocean waves.

2.2. The Observation Sessions

To mitigate the influence of observation on the natural behaviour of wild blacktip reef sharks, habituation to the observer's presence was essential. Staged encounters, involving deliberate attraction of the target species, represent an established methodology in ethological studies (Jamieson and Bekoff 1992; Mourier *et al.* 2011; Brena *et al.* 2018) and were employed in this investigation. Fish scraps were systematically deployed at predetermined locations on a weekly schedule to facilitate habituation.

Study sites were situated in the deepest region, near the inner margin of the barrier reef. This region was characterized by expansive, widely-spaced patch reefs that afforded relatively unobstructed visibility through the coral matrix. Each site necessitated an open area for provisioning, sufficient to accommodate at least twelve adult blacktip reef sharks manoeuvring in a circular pattern. Clear ingress and egress pathways were critical to enable sharks to follow olfactory cues into the site and depart from the opposing side. Once selected, sites and procedures remained consistent across sessions. Arriving by kayak, the observer anchored it to align with prevailing wind and current behind a dead coral formation used for stabilization. Underwater, equipped with mask, snorkel and fins, the observer trailed the kayak to the site's centre, deposited the fish scraps on the substrate, returned to the coral structure, and recorded observations on a slate. The isolated nature of the reef minimized external disturbances during data collection.

Observation sessions were conducted during the hour of sunset to coincide with periods of heightened activity in blacktip reef sharks, as supported by studies indicating crepuscular movement and foraging patterns (*e.g.*, Papastamatiou *et al.*, 2009; Mourier *et al.*, 2016).

Fish scraps, comprising remnants of oceanic species (*e.g.*, tuna, bonito, and mahi-mahi) discarded after marketable portions were excised at local fish shops or hotels, varied in quantity depending on availability. Typically, fishing vessels delivered catches on Fridays, the scraps were available on Saturday, and the session was held on Saturday at sunset. Sporadic midweek availability occasionally permitted supplementary sessions.

Shark feeding activities were conducted once weekly on Mo'orea, French Polynesia between 1999 and 2005. During this period, no institutional, local, or national regulations governed such activities; regulations were only enacted later. All procedures followed contemporary best field practice.

2.3. Observing Without Food

Between provisioning sessions, visits to the study area were conducted at varying times of day to capture a broader spectrum of behavioural data. The observer accessed the western perimeter of the lagoon by kayak and proceeded eastward underwater, adopting a zigzag trajectory. Pauses were made to observe and shadow any encountered blacktip reef sharks. As resident individuals grew accustomed to the observer's presence, their natural behaviours became observable, which was a marked shift from the pre-habituation phase prior to the initiation of feeding sessions.

Individual blacktip reef sharks were identified using photo-identification techniques, supplemented by detailed sketches of both sides of the dorsal fin, executed while the shark remained in view to ensure accuracy (Porcher 2005). Morphological and behavioural characteristics, including sex, body length, colouration, scars, markings, and other distinguishing traits, were systematically recorded. Males were differentiated from females by their slimmer, more muscular build and the presence of claspers, while pups and juveniles were readily identifiable by their distinct appearances (see the Identification Catalogue, Supplementary Information).

Sessions were deferred when ocean swells exceeded 1.5 m or wind speeds surpassed 60 km/h until conditions were favourable. Supplementary observations were undertaken in response to notable events, including the appearance of rare transient individuals, fish spawning taking place in the study area, encounters with diseased or injured sharks, or absences of the blacktip community from the study area (Porcher 2023b).

Movements of blacktip reef sharks were recorded at the coral reef sites 1 km from shore over six and a half years, from April 11, 1999 to September 29, 2005, with observations conducted one to five times weekly. The primary focus for data collection was Section A (Figure 1), where regular sessions were held during the initial three years. Following *a period in which the blacktips exhibited increasing aggression, culminating in three individuals attempting to slam the observer (Porcher 2022) i*n May 2002, the weekly sessions were relocated to Section B. Sessions were resumed sporadically in Section A at the time of the blacktip shark disappearance in July, 2002 (Porcher 2023b), and were continued intermittently thereafter to monitor the residents of Section A, especially when intensive finning of the reef sharks began in August, 2003.

2.4. Data Analysis

During each observation session, detailed notes were taken including time, marine conditions, the presence of individual sharks, and incidental events. Upon returning to shore, these data were transcribed into a computer spreadsheet and used to write a comprehensive description of the session.

Analysis of re-sighting data revealed distinct categories of individuals based on their visitation patterns: residents, periodic transients, rare transients, and individuals observed either once or for one brief duration. The frequency of sightings for each individual depended on the total number of sessions possible. To standardize this variability, a Residency Index (Bond *et al.* 2012) was calculated as the ratio of sessions at which an individual was observed, to the total number of sessions occurring between its first and last sightings. Periodic transients were defined as those observed regularly but infrequently, while rare transients were documented in the study area annually or less.

At each site, identified sharks were grouped according to their attendance frequency. Subsequently, the proportions of males, females, and juveniles within each category were compared. Re-sighting data were further evaluated based on the number of sites at which each individual was recorded. The monthly proportion of transients among sharks attending sessions during the first three years at Site A was quantified, and their appearances were analysed for correlation with lunar phase.

3. Results

Blacktip reef sharks were the predominant elasmobranch observed in the study area, though other species, including whitetip reef sharks (*Triaenodon obesus*), nurse sharks (*Nebrius concolor*), pink whiprays (*Himantura fai*), and eagle rays (*Aetobatus narinari*), were also present on the back reef. Sporadic sightings of lemon sharks (*Negaprion acutidens*) and grey reef sharks (*Carcharhinus amblyrhynchos*) were also recorded.

The initial feeding sessions in Section A primarily attracted the mature female blacktip reef sharks whose core ranges included the observation site. Over time, additional blacktips became aware of the weekly provisioning events. Many of them gathered in advance, *presumably cued by the sound of the kayak traversing the back reef towards Site A. A few* mature males occasionally joined the females, as did juveniles exceeding an estimated 70 cm in standard length.

After approximately three months, all resident individuals had been identified and were recognizable. These sharks tended to arrive at the beginning of the feeding sessions and dispersed roughly 30 minutes later. Following their departure, and often after an interval devoid of shark activity, new individuals appeared. These were found to be transients, prompting consideration of their origins. Individual identification of these transients showed that movement is a key component of *C. melanopterus'* behavioural ecology.

The provisioning sessions resulted in an aggregation of reef blacktips that facilitated social interactions. Many of these occurred down-current from the food source, beyond visual range. By drifting unobtrusively down-current, the observer could approach sufficiently to observe these interactions. Socializing occasionally superseded feeding, as evidenced by instances where food remained untouched on the substrate.

Figure 2 shows blacktip attendance at the sessions held at Sites A and B from 99-04-11 to 05-09-29.

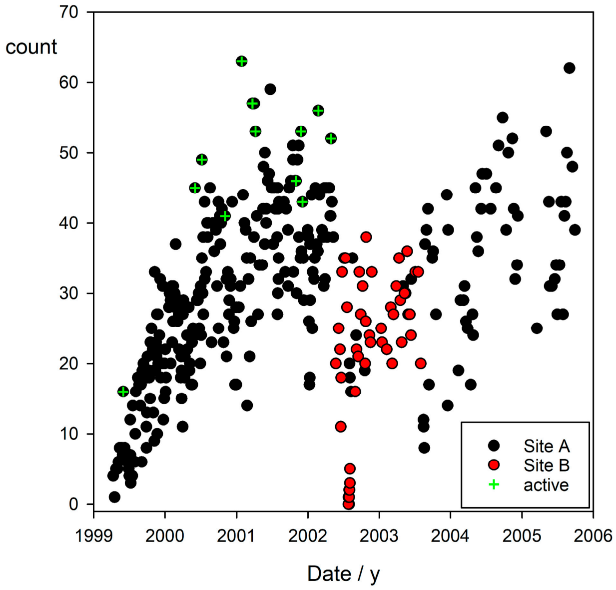

Figure 2. The numbers of sharks attending the sessions at Sites A and B between 99-04-11 and 05-09-29. The absences between 02-07-23 and 02-08-05 when the sharks evacuated (Porcher 2023b) are evident. There is a break

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in attendance when intensive shark finning began in August, 2003 and the subsequent disruption of the community is also reflected. Other breaks in attendance are due to bad conditions during the stormy months between November and February when not all sharks present could be identified, or the sites were inaccessible. Some peaks (green +) mark unusually animated sessions (3.3.3).

Observations totalled 506 hours across 501 sessions, with 67 % of observation time (338 hours) during low-light sunset conditions, a key period for activity (Papastamatiou et al. 2009). The sessions recorded 11,514 behavioural events, including ranging, habitat shifts, agonistic displays, and social interactions, resulting in an ethogram (Porcher 2023a). A total of 475 reliably-distinguishable individual sharks were identified, culled from 581 initial records for consistent re-identification.

3.1. The Community

Female *C. melanopterus* exhibited pronounced site fidelity to core home ranges of an estimated 0.5 km². The lagoon's natural features significantly influenced their spatial dynamics, with a marked preference for the outer third of the lagoon along the barrier reef, where the coral habitat was healthiest.

Table 1 presents the counts of adult blacktip reef sharks identified at each study site, detailing the numbers of residents, the average Residency Index, periodic transients, rare transients, and individuals observed either once or during a single brief period.

Table 1. The number of adults in each category identified at each site: residents, periodic transients, rare transients and those that passed only once or for one span of time. The average Residency Index of the adults recorded at Site B is lower due to the disruption caused by the shark disappearance in July—August, 2002.

	No. of Sessions	Males						Females					
		N	# Res-idents	Residency index average	Periodic transient	Rare transient	One stay	N	# Res-idents	Residency index average	Periodic transient	Rare transient	One stay
Site A	372	104	6	0.55	3	9	86	124	15	0.67	8	24	77
Site B	48	13	1	0.39	1	4	7	12	2	0.39	2	3	8
Site C	11	16	0	-	7	1	8	24	0	N/A	7	-	17
Site E	4	0	0	-	-	-	-	6	4	0.562	-	-	-
Papetoai	7	0	0	-		-	-	14	6	0.66	-	-	-
Fore reef	5	9	-	-	-	-	-	3	-	-	-	-	-

Certain individuals, both adults and juveniles, scored a Residency Index exceeding 0.5 for a continuous period spanning multiple months. Upon their disappearance, it was not possible to determine whether they had died or departed; neither were the reasons behind their consistent temporary presence evident. In one instance, the carcass of the individual was found, whereas in all other cases, the reason—death or departure—remained unknown.

A notable individual, designated #109, attended sessions exclusively between December and April for over three consecutive years, then disappeared in 2004 amid intensive shark finning activities. During her seasonal presence, she maintained a Residency Index above 0.6, yet she was not a year-round resident. Her case highlights the behavioural variability in the species (Porcher 2022).

Sharks with home ranges west of the study site were not only aware of the auditory cues of the approaching kayak but were also positioned to detect and follow the westward-flowing scent trail to the feeding sessions. Conversely, individuals with core ranges up-current (east) of the site were less likely to encounter these cues and scored lower Residency Indexes.

Some individuals—predominantly males—appeared at intervals of some months, suggesting a cyclical movement pattern, though their core ranges remained unidentified.

During the years of the study, all adult blacktip reef sharks residing within the lagoon were eventually identified. However, the limited number of sessions conducted at Site E and Papetoai precluded accurate determination of temporary visitors in those areas. As the majority of observation sessions occurred in Section A, most adult blacktips ranging across the western half of the lagoon were first observed and catalogued there, and are listed in Table 1 under 'Site A.'

Juvenile blacktip reef sharks identified during the study are detailed in Table 2, categorized as residents, periodic transients, or individuals observed either once or for a single period. No rare transients were identified among juveniles. Sharks initially recorded as young-of-the-year matured over the course of the study, with each assigned to a category based on its status at first identification.

Table 2. The number of juveniles (males, females, and pups (50 ~ 70 cm, estimated) in each category identified at each site: residents, periodic transients, and those seen once or during one span of time. The Residency Index average (defined in the text) is specified in the third column. Site E was adjacent to a major nursery so no realistic estimate of the many juveniles attending the few sessions held there could be made.

Males	No. of Sessions	N	# Residents	Residency Index average	Periodic transient	One stay
Site A	372	17	6	0.52	4	7
Site B	48	6	3	0.7	0	3
Site C	11	0	-	-	-	-
Site E	4	N/A	-	-	-	-
Papetoai	7	4	4	0.58	-	-
Fore reef	5	0	-	-	-	-
Females						
Site A	372	48	18	0.55	8	22
Site B	48	7	1	0.78	0	6
Site C	11	1	0	-	-	-
Site E	4	N/A	3	0.69	-	-
Papetoai	7	8	3	0.5	-	-
Fore reef	5	0	0	-	-	-
Pups						
Site A	372	43	8	0.47	9	26
Site B	48	10	3	0.57	4	3
Site C	11	0	-	-	-	-
Site E	4	N/A	-	-	-	-
Papetoai	7	1	-	-	-	-
Fore reef	5	0	-	-	-	-

If the sightings were essentially random, and the sharks showed no site preference, then we would expect the calculated residency to be a binomial random variable centred on 0.5. With a large enough sample, the distribution would approach normal. Accordingly, the data can be plotted as cumulative proportion on a normal probability scale *vs*. Residency Index (R). For this, the n Residency Index values are sorted in ascending order, *i.e*. given a rank value, k, and the adjusted proportion, p, found from (Mandel 1964):

$$p = \frac{k - \frac{3}{8}}{n + \frac{1}{4}}$$

which gives a good approximation to linearity for truly normal data. These plots are shown in Figure 3.

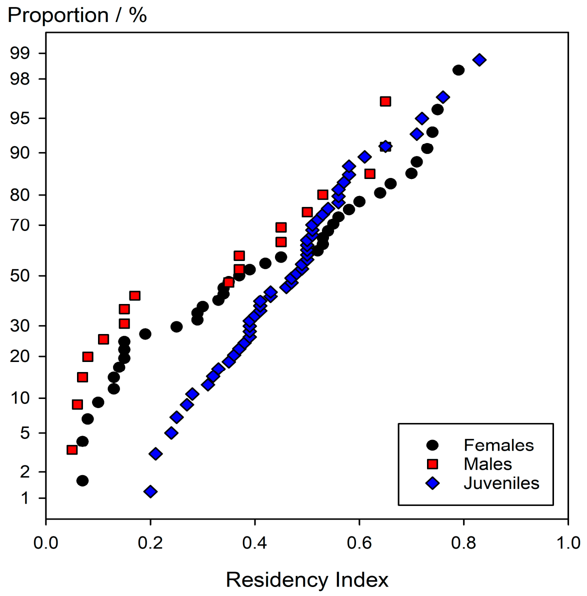

Figure 3. Residency data plotted as cumulative proportion on a normal probability scale *vs*. Residency Index value.

It is apparent from these plots that, firstly, none shows a reasonable approach to linearity, secondly that they are not centred on 0.5, and thirdly that samples are clearly not from the same distribution: males, females and juveniles differ. Were the data simply from a distribution other than normal then simple curvature would be apparent, which is not the case. Given that and the first point means that they are each a mixed distribution. It is then appropriate to 'censor' or section the data according to the apparent more or less abrupt changes of slope and replot each portion accordingly (*i.e.* recalculating the proportion, p, for each subset). These sectioned data are shown in Figure 4. In all except the 'middle' group of females the plots show a reasonable approach to a straight line, suggesting that these individual data subsets are near-normal in distribution.

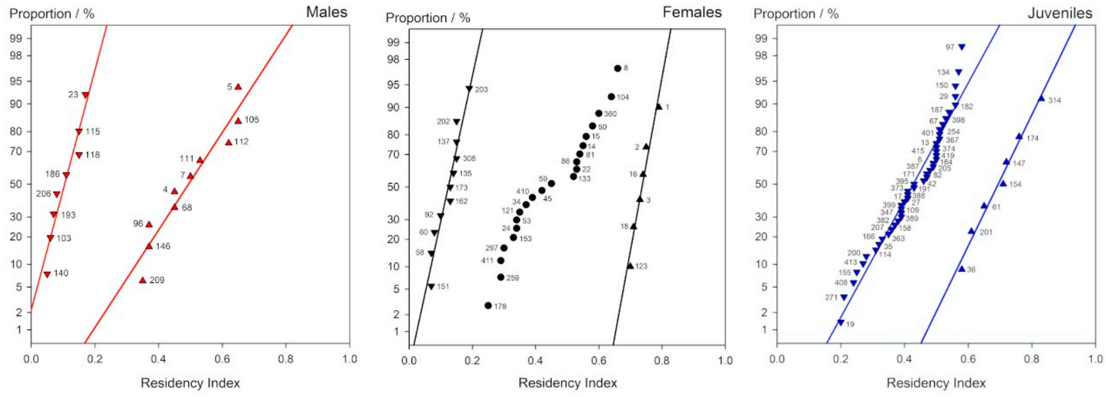

Figure 4. Residency Index probability plots having sectioned the data lists according to the apparent discontinuities in Figure 3. Shark numbers shown. Regression lines added for eye guidance only.

Thus, for the males, there is a strong change of slope at R ~0.2. The weighted mean residencies are 0.13 and 0.52. These values would suggest that the 8 sharks of the first group were periodic transients while the other 10 show significant site fidelity to Section A.

The female plot in Figure 4 initially suggests discontinuities at R ~0.17 and ~ 0.68. Replotting accordingly it is seen that again a group (some 11 sharks) shows a low weighted mean R_w ~0.13 and thus a low tendency to visit, while 6 have a strong bias towards the Section A region (R_w ~0.74). The remainder however, albeit with a mean close to 0.51, in fact do not yield an acceptable approach to a straight line plot, again strongly implying a mixed distribution. The break here appears to be at R ~0.5. Making the further section at this point yields Figure 5. Here now all four plots show an acceptable approach to linearity, with similar slopes (equivalent to standard deviation). The two middle groups have R_w ~0.37 and ~0.58.

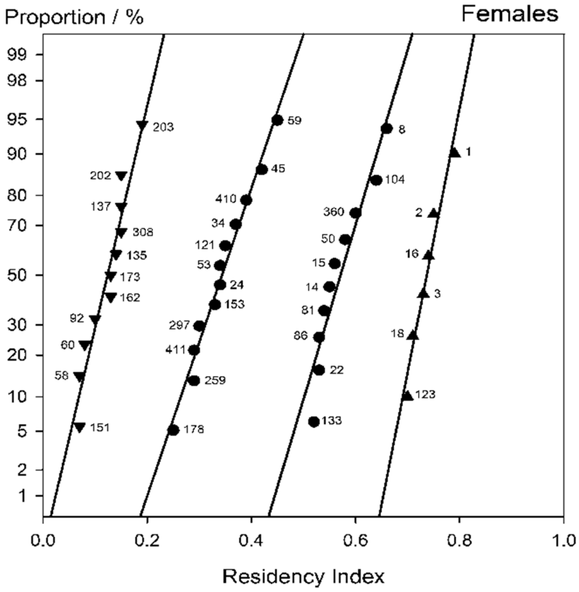

Figure 5. Further sectioning of the 'middle' Female data of Figure 4 implies four distinct residency groups.

Treating the juveniles similarly, the slope change appears at about R ~ 0.6 as seen in Figure 4. The weighted mean residencies are ~0.47 and ~0.67. This suggests that a small group (7 sharks) strongly preferred the study areas, while the rest visited less often (this also looks like a mixed distribution, but any break point is not clear). Given that juveniles were observed to prefer the thick coral labyrinths of western Section B, up current from Site A, this is not surprising.

It must be borne in mind that censoring is an absolute cut, while it can be expected that for mixed distributions the tails overlap. That is, say in Figure 4 for males, and more clearly so for juveniles, the lower subset could include members of the lower tail of the upper set, and *vice versa.* Full identification of the members of each set is not possible. The same applies in similar fashion to the four sets of Figure 5, and indicates the danger involved in sectioning in this fashion. In these circumstances, statistics for the various sets are necessarily biased by that censorship, and care is required to avoid strong implications. A further caution is necessary: absence of observation does not mean absence from the larger area – sampling is necessarily biased, and the R values biased downwards as a result: even a fully-resident shark would not be expected to be observed on every occasion.

Overall, then, avoiding over-interpretation, there would simply appear to be evidence that there are behavioural differences between groups within and between males, females and juveniles, the sources of which variations are yet to be identified. Even so, one possibility that could be explored is the effect of core ranges with (as might be expected) diffuse boundaries (Figure 6).

Suppose the observation site study area was in the overlap between two such ranges, closer to the centre of one than the other. The frequency of observation would be greater for the one, yet both sharks would in fact be fully resident in their core range. If now each such range had several occupants, the effect would be as observed in Figures 4 and 5, where the Residency Index is now in part a measure of relative location of the observation study site to the barycentre of each. Of course, ranges vary in size and shape depending on the habitat, while sharks roam widely in as yet unknown ways. Individual variation in terms of distances travelled and roaming tendencies result in transient observations at different frequencies. The subsets of those sectioned residency plots therefore may represent distinct roaming patterns used by sharks coming from distant ranges, possibly some on the same island, others on different islands. Distinguishing and mapping their ranges would require multiple study sites with data density similar to that for Site A.

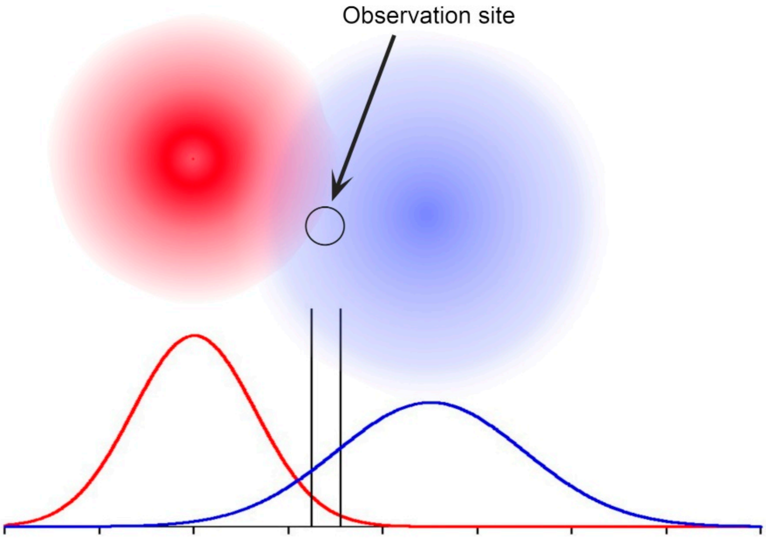

Figure 6. The effect of relative location of Site A with respect to two well-defined but overlapping shark ranges on the frequency of observation and thus the imputed residency. (Distribution within a core range is shown as normal for illustrative purposes only.).

3.1.1. The Nurseries and Juveniles

A prominent blacktip reef shark nursery was identified along the curvature of the barrier reef adjacent to Cook’s Bay (Section E), where an annual influx of 100–200 neonates was consistently documented. In contrast, smaller nurseries at the western extremity of the reef and the eastern end of the Papetoai lagoon hosted the offspring of only one or two females.

Approximately 6 weeks to 2 months post-parturition, neonates (measuring an estimated 50 cm) began dispersing along the reef in small groups. They exhibited heightened vigilance, repeatedly circling outward before regrouping, always poised to retreat to their shallow refuges.

Young-of-the-year occupied shallow zones characterized by dense coral formations which were scattered throughout the lagoon (Galvin and Pointer, 1985). Between the ages of one and two years they reached an estimated length of about 70 cm, and began to roam freely in the lagoon, mingling with adult conspecifics without displaying avoidant behaviour. However, they were not seen in the deeper regions of the lagoon, including the area around Site C, and parts of the barren area separating Sections A and B.

Juvenile male sharks exhibited reduced growth rates compared with their female counterparts, with some individuals only marginally larger than neonates upon initial observation at feeding sessions. Clasper development commenced approximately two years later, during the third to fourth year of life, with claspers initially appearing as small buds. Fully-proportional clasper development was typically achieved within one year, corresponding to an age of approximately four to five years.

The onset of clasper development displayed inter-individual variability in timing, possibly attributable to differences in birth dates—the earliest in September, and the latest in February. In some males, clasper maturation occurred sufficiently early to enable mating the same year. However, in others, clasper development initiated later in the year, resulting in immature claspers at the onset of the mating season. Consequently, while some males were capable of mating in their fourth to fifth year, others did not reach reproductive maturity until their fifth to sixth year, likely due to the misalignment of the timing of clasper development with the reproductive season.

By the year preceding maturity, males measured approximately 80 cm to 1 m (estimated) and initiated a transition to the fore reef, a shift corroborated by visual assessment of clasper length (Mourier *et al.*, 2013). Juveniles were never seen on the fore reef.

One male individual, #19, was first identified on August 4, 1999 presumably in his second year. He was periodically observed at Site A during his maturation. Subsequent sightings when he was in his fourth year occurred at the fore reef site during a two year period in which he was not seen in the lagoon—from May 11, 2002, to April 26, 2004. In 2008, he was identified and re-sighted multiple times by Mourier *et al.* (2012) at their Opunohu observation site on the fore reef opposite Section A, as shown in Figure 7.

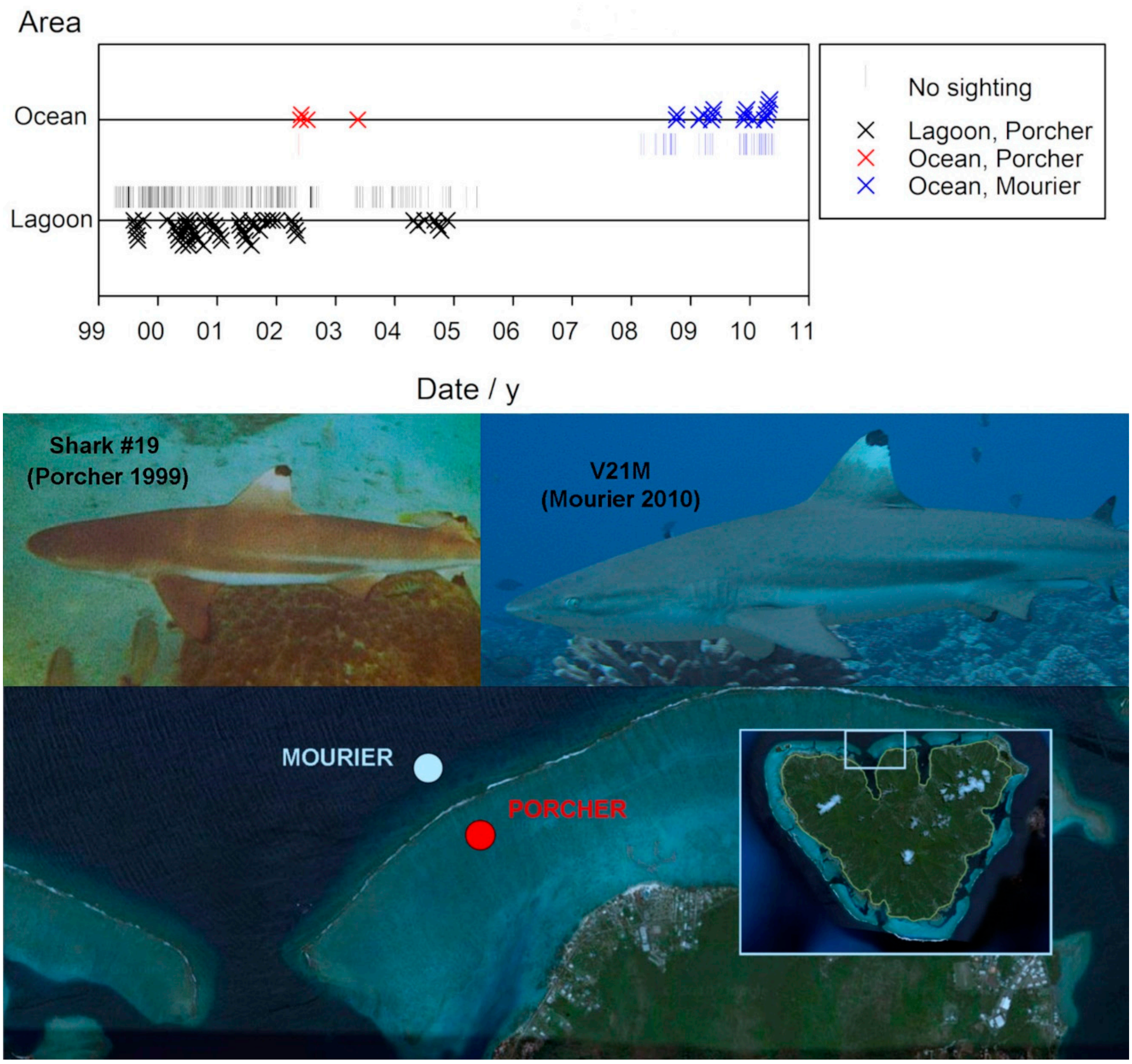

Figure 7. Sightings of Shark 19 both within the lagoon while a juvenile and during his transition to the ocean where he was sighted by Johann Mourier years later, still roaming the reef's outer slope. (Occurrence symbols staggered for clarity.) Data, image of 19 and study site location provided by Johann Mourier.

It was also during the subadult phase, between approximately 4 and 5 years of age, that female sharks established their home ranges. They were notably larger than the males, approaching full size at an estimated 1.5 m. Although mating was evident in subadult females, as indicated by the presence of extensive mating wounds, pregnancy was not observed, with the exception of one individual (Shark #29). In contrast, mature females consistently achieved pregnancy annually following mating, with no exceptions recorded. Only two instances were documented where mature females failed to carry pregnancies to term. In one such case, the pregnancy terminated within three days of a spear or knife wound into the lateral body surface.

Unlike mature females, subadults retained a slender physique and displayed frequent rapid acceleration and enhanced velocity. Their behavioural profile included a pronounced inclination for exploration and a tendency towards bolder actions. By the subsequent year, these individuals had developed a more robust build, accompanied by a relative reduction in agility as pregnancy progressed, and often the loss of their earlier boldness (see Porcher, 2022, for an anecdotal account of this transformation).

3.2. Movements

Figure 8 compares the percentage of identified adults and juveniles in each of the categories specified in Tables 1 and 2.

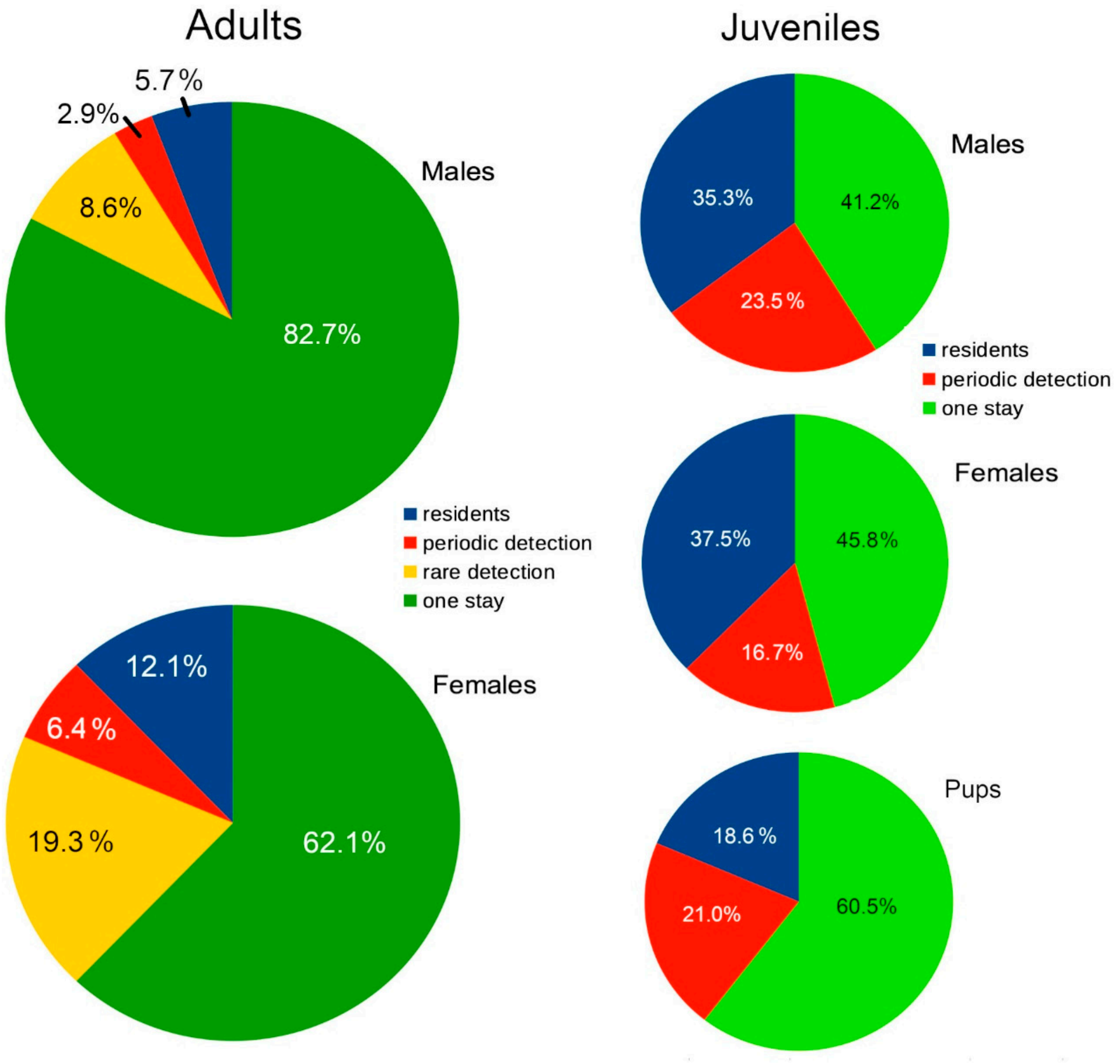

Figure 8. The percentages of identified blacktips in each category found to be residents, periodic transients, rare transients, or those who passed through once, or for one period of time, during the 6.5 years in which sessions were held in Section A. Rare transients are those recorded as passing through the area once annually or less, while periodic transients passed through regularly if infrequently.

3.2.1. Inter-Site Movements

Figure 9 shows blacktip reef shark movements observed between sites during the 6.5 years of the study.

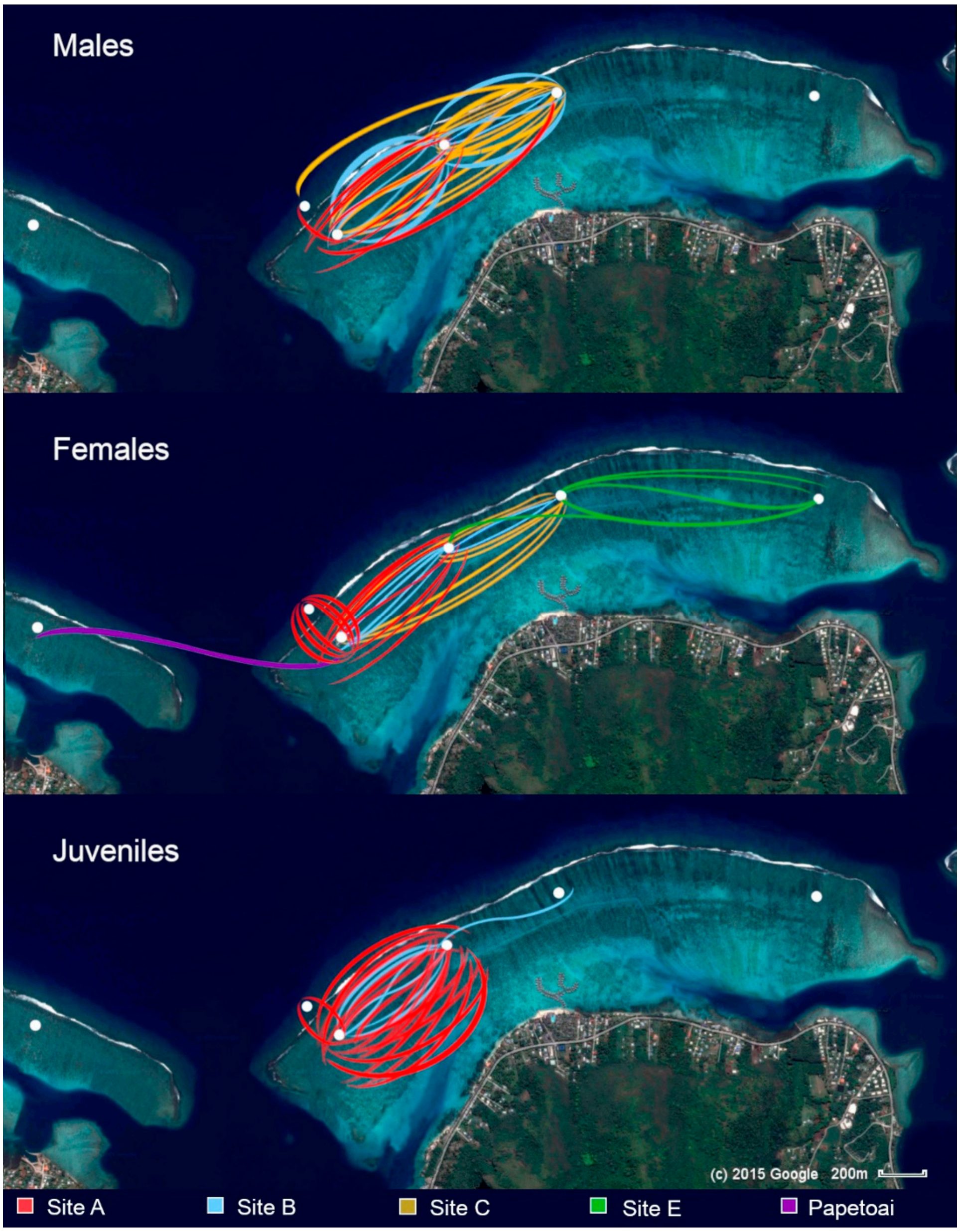

Figure 9. Individual blacktip reef shark movement between sites. Each line shows the movement of one resident shark to another section. The colours represent the site where the individual was a resident or had been sighted most often.

Despite approximately 300 m of deep water (Opunohu Bay) separating the study area from the Papetoai lagoon, distinct communities of blacktip reef sharks were observed in each region. These communities consisted of females, juveniles, and occasional males, with minimal evidence of inter-bay movement. Only one female, #179, consistently identified and re-sighted in the Papetoai lagoon, was recorded at Site A, appearing there twice in two different years. No individuals from the study lagoon were observed in the Papetoai lagoon.

Although resident females from Section A exhibited reluctance to cross the bay, they were sighted during daylight hours on the fore reef opposite their core ranges, occasionally displaying behaviours suggestive of hunting as they moved parallel to the reef beneath breaking waves. Blacktip reef sharks were frequently observed entering the back reef from the fore reef with incoming waves, indicating that hunting fish beneath the waves breaking along the fore reef might constitute a component of their predatory repertoire.

During observational sessions in Section E, only two unidentified female blacktips were recorded; the remainder had been previously identified at Site C, with 67 % of individuals identified at Site E also frequenting Site C. However, no females identified at Site A were observed at Site C. Of the 37 females documented at Site C, only 7 (19 %) were ever sighted in Section A, typically on a single occasion. Adult individuals observed at Site C appeared to be transients, with different individuals present at each session and no residents identified. Juveniles largely avoided this location, with only one recorded sighting of two older juveniles travelling together. Logistical constraints precluded additional sessions at Site C and in Sections D and E, which might have further elucidated these patterns.

A notable female, designated #351, was initially identified at Site C and subsequently re-sighted there on five separate occasions. She was also observed at Site A sessions on 22 occasions and at Site B sessions on 13 occasions. Despite this extensive sighting record across the western side of the lagoon, her exact core range could not be determined. Due to long periods of absence, it is likely that her home range was not in the study lagoon.

3.2.2. Males

The male blacktip reef sharks that roamed the back reef displayed reduced site fidelity to specific core ranges compared with females, attending feeding sessions irregularly throughout the year, with some appearing infrequently. Their Residency Indexes were generally lower than those of the females.

In 1999, three adult males and one maturing juvenile were regularly observed; subsequently, one succumbed to a wasting disease and was later succeeded by a maturing male juvenile. Between three and six additional males, presumed to inhabit the back reef rather than the fore reef, were sporadically sighted at Sites B and C. In contrast, males ranging the fore reef typically appeared on the back reef solely during the mating season (November to March; Porcher, 2005), arriving in pairs or small groups (<6) and not associating with lagoon-ranging males.

Males ranging Section A were occasionally observed traversing both Sections A and B within a single morning, though, with one exception, they were not observed at Site C. Long term observation suggests that males used larger core ranges and exhibited greater daily mobility than females. During the reproductive season, they were frequently absent, sometimes for periods as long as five months.

Only one male identified at the fore reef site was recorded at Site A (on a single occasion), and another had originally been identified—seen only once—at Site C. At the fore reef site, water depth was approximately 7 m, and since male blacktips moved near the seafloor, their identification required diving to the bottom to sketch dorsal fin markings on both sides while maintaining continuous visual contact, without resurfacing for air. Consequently, most males encountered on the fore reef remained unidentified, limiting their representation in the dataset. Nonetheless, it was determined that these unidentified individuals were distinct from those previously identified on the back reef.

A distinction in coloration was seen in blacktips ranging the fore reef, as opposed to the back reef, which reflected their respective habitats. Those residing on the fore reef, and remaining near the seafloor where they were shielded from solar radiation, exhibited light brown or yellow-ochre hues. In contrast the sharks residing in the lagoon were subjected to prolonged sunlight exposure in shallow waters, and displayed dark brown or grey pigmentation. This difference is shown in Figure 10.

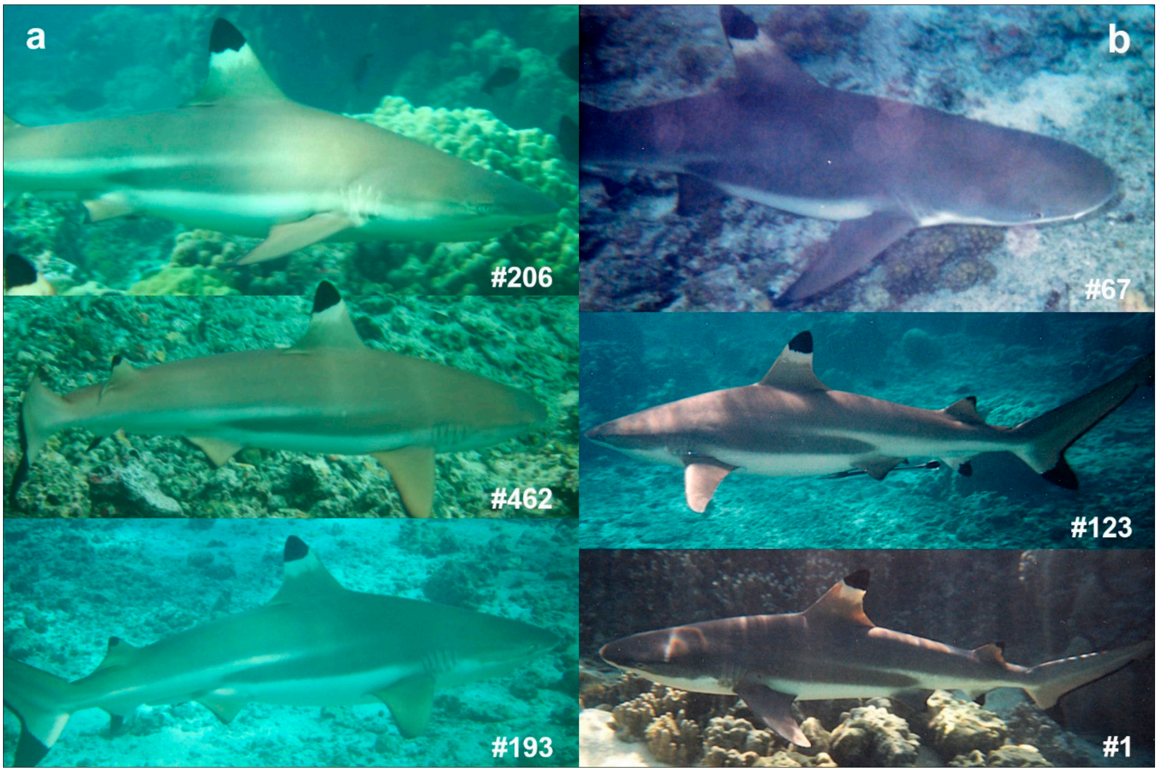

Figure 10. a: Typical light pigmentation of fore reef dwellers. b: Darker pigmentation of back reef dwellers.

Such chromatic variation provided a reliable indicator of an individual's primary habitat. Similar sun-induced colour changes in shallow-water environments have been documented in other shark species, including nurse sharks (Johnson, 1978) and hammerheads (Lowe and Goodman-Lowe, 1996). However, colour also has a genetic basis, for neonates varied from pale yellow-ochre, to bronze, brown, and grey; most were variations thereof. In addition, mating and birthing were observed at times to result in a sudden, and at times extreme, colour change.

3.2.3. Females

Female blacktip reef sharks identified as residents exhibited pronounced fidelity to their core ranges, to the extent that it was frequently possible to find a particular individual by going to her range and submerging. Each individual pursued her own roaming pattern. Some, exemplified by #3, were absent for approximately two weeks during mating and another two weeks for parturition, while another, exemplified by #15, displayed absences of up to three months during the period of reproduction between September and April (Porcher 2005). Other females exhibited absences along a continuum within this range, with most departures aligning with the reproductive season. Nonetheless, additional absences occurred outside this period, as well as sightings of rarely seen female blacktips, alone, in dyads, or groups of up to six individuals, traversing the study area. No consistent behavioural 'type' (Jacoby *et al.*, 2014) emerged since each female followed her own movement pattern.

Their daily behavioural routines also displayed substantial variability. Some individuals, for example, repeatedly navigated the same coral formations at nearly identical times on successive evenings for multiple nights, before remaining absent from the area for an extended period, as much as a year. There were days when all resident females were absent from their ranges, contrasted with occasions when they assembled to interact with groups of infrequent transients. On most days at midday the resident females were resting in the barren region between Sections A and B (Porcher 2023a) while, occasionally, no reef blacktips were found there at midday.

3.2.4. Juveniles

Small juvenile blacktips were frequently observed at both Sites A and B, a pattern not observed among adults. Juveniles that encountered the feeding sessions in Section A and attended regularly, soon became attuned to the sessions when they were held at Site B, presumably due to the scent plume from Site B dispersing through the dense coral region of Section B, where they predominantly resided.

Across all categories, the greatest proportion of individuals consisted of those sighted only once. Unexpectedly, among juveniles, it was the smallest, the pups, who exhibited the highest percentage of individuals sighted once, or for a short period only. Throughout the study, a consistent stream of the smallest juveniles was observed traversing the area, with no subsequent re-sightings. Whether these individuals died or settled elsewhere—and the extent of their dispersal—remained unknown. Only two (#29 and #36), initially identified as juveniles passing through, were later re-sighted as subadults, at which time they established residency in the region.

Given the research emphasis on identifying adults, coupled with the pups' tendency to remain beyond visual range due to their elevated vigilance, the definitively-identified pups represent merely a small subset of their true numbers. Initially, 581 blacktip reef sharks were identified; however, individuals insufficiently documented for reliable future recognition and never re-sighted were excluded from the dataset, reducing the confirmed number of uniquely identifiable sharks to 475. A large fraction of the excluded individuals consisted of pups observed only once within the study area, indicating that their actual abundance significantly exceeded the recorded figures.

3.2.5. Periodic and Rare Transients

While many transients were solitary, they also arrived in dyads or small groups of up to six individuals. As a rule, there was much high-velocity interaction on their arrival. Residents and transients would accelerate through the coral habitat surrounding the feeding site, following each other and moving nose-to-tail or in parallel (Porcher, 2023a).

The arrival of these transient groups frequently aligned with the light and dark phases of the lunar cycle, with groups typically lingering in the area until the next lunar phase transition—approximately two weeks—before leaving. On several occasions, certain female residents temporarily departed their core ranges to accompany these departing groups of conspecifics along the back reef. Their behaviour underscored the species' inclination toward socialization (Mourier *et al.* 2012) and affinity for interactions with many of the female transients.

Some of the transient groups of females were consistently accompanied by a single male, the same one each time, who invariably entered the observation site one to two minutes ahead of the females.

Rare female transients moving through for parturition often displayed a pattern of annual return within a few days of the previous year's date.

Since resident females were not systematically observed together because of their circling movement patterns (Porcher, 2023a) the movements of consistent travelling companions were most discernible among rare transients who maintained the same associates across multiple years.

Figure 11 shows four such pairs.

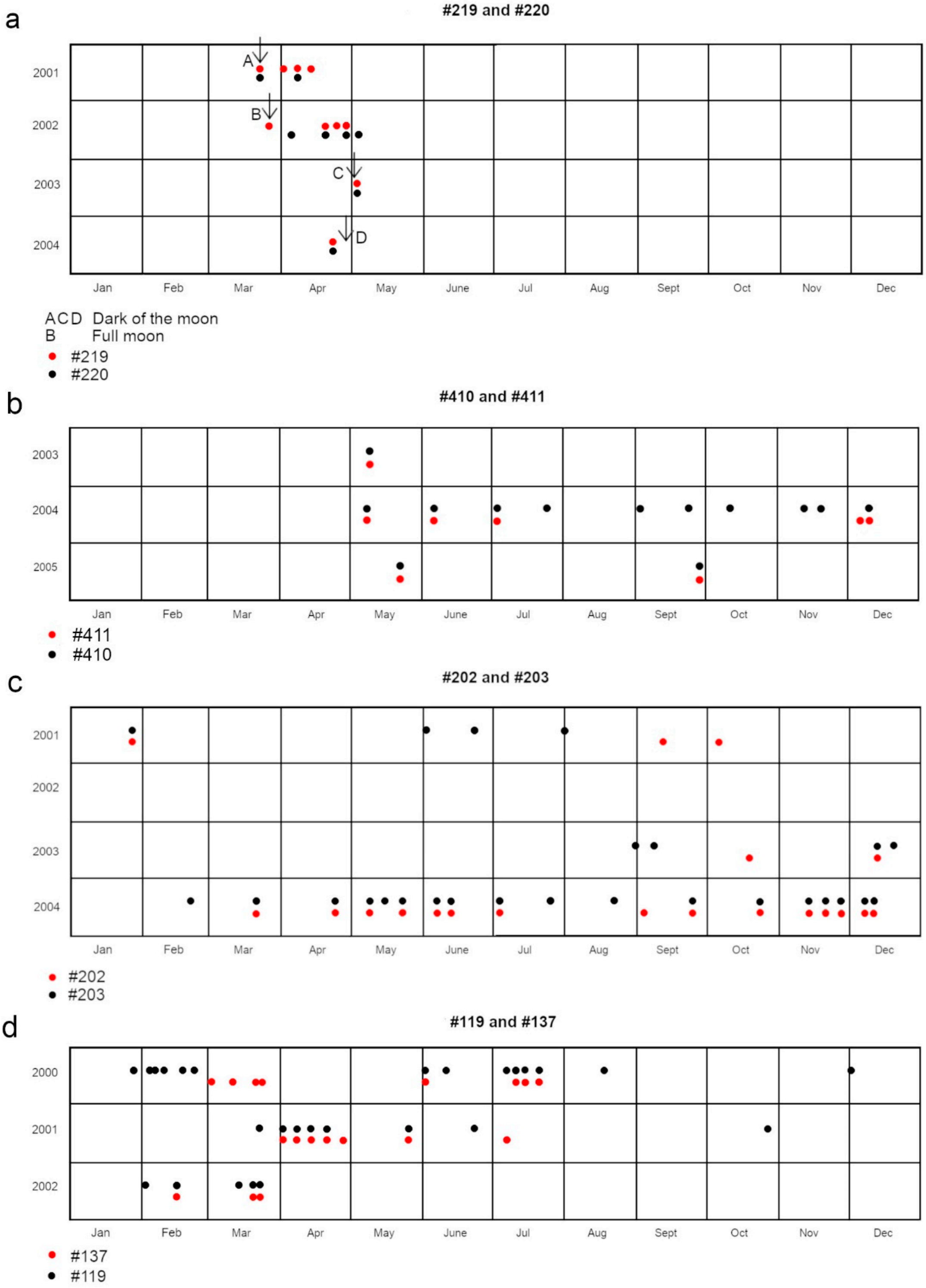

Figure 11. Each dot represents one sighting of the indicated individual. a. Blacktips #219 and #220 showed strong correspondence with the lunar phase, as indicated by the arrows in the legend. b. Blacktips #410 and #411 tended to arrive as the full moon phase was passing. In 2004, their first three visits took place a moon apart. c. Blacktips #202 and #203 travelled together at times but at other times they roamed separately. d. Blacktip #119 exhibited a distinctive appearance, characterized by unusually dark pigmentation, scattered white speckles, and a prominent white patch positioned symmetrically on each side of her head. In 2001, she was documented consistently at dusk across five consecutive sessions. However, at the sixth session, a similar individual, #137, appeared. This lookalike bore identical white patches on her head, though her overall coloration was marginally lighter. Initially, their striking resemblance suggested a potential association based solely on morphology.

Confirmation of their association emerged three months later when #119 and #137 arrived together, moving in a nose-to-tail formation.

3.3. Influences on Blacktip Reef Shark Movements

The primary influences on the blacktip reef sharks' movements were the reproductive season and the lunar cycle.

3.3.1. The Reproductive SEASON

The reproductive period commenced in September, marked by previously unidentified and infrequently observed gravid female blacktip reef sharks traversing the study area. New unidentified females passing through at this time were documented throughout the study. Concurrently, resident females approached parturition, subsequently returning after an absence in an emaciated state.

After a resting period of 1.5 to 2 months, each resident female began to appear with mating wounds, while groups of males were observed arriving in the lagoon after sunset. These males, observed exclusively during the mating season, were presumed to inhabit the fore reef, consistent with the majority of male conspecifics. Consequently, the reproductive season emerged as a period of heightened mobility for the species. An analysis of the percentage of adult blacktip transients present at the observation sessions during the period of regular sessions between 1999-04-11 and 2002-05-11 in Section A (247 sessions) is shown in Figure 12. This used unweighted non-linear regression, treating the frequencies as binomial (SigmaPlot v16; Grafiti, Palo Alto, CA, USA). The calculation is shown in Table 3.

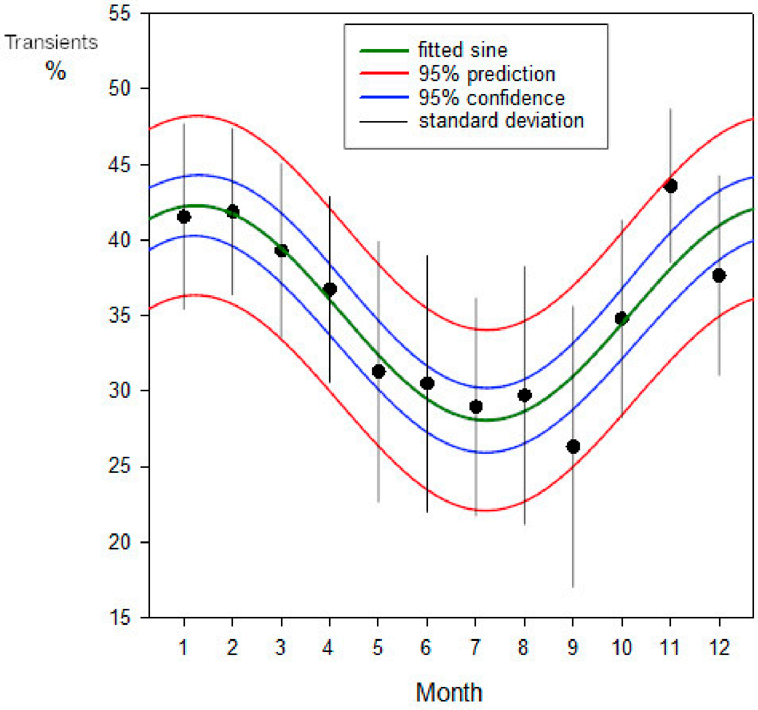

Figure 12. Percentage of transients among the individuals attending feeding sessions during each month between 1999-04-11 and 2002-05-11 in Section A (247 sessions). The occasional missed sessions due to hurricanes and storms during December and January, central to the reproductive season, resulted in lower figures than would otherwise have been recorded for those months. Binomial standard deviation given by √(np(1-p)), where n = number of transient sightings, and p = n/total sessions. Continuity assumed across year ends.

Table 3. Regression analysis of monthly data for transient appearances in Section A for the fitted function: $f = y_0 + a.\sin(2\pi x/b + c)$. a: amplitude, b: cycle frequency, c: offset, y_0: overall mean.

R	R^2	Adj. R^2	Std. Error of estimate
0.8998	0.8097	0.7796	2.6680

Coefficient		Std. Error	t	P
a	7.1184	0.7940	8.9654	<0.0001
c	11.9272	0.4004	29.7846	<0.0001
c	0.9135	0.1652	5.5309	<0.0001
y_0	35.1807	0.5921	59.4159	<0.0001

Analysis of Variance					
	DF	**SS**	**MS**	**F**	**P**
Regression	3	575.3235	191.7745	26.9407	<0.0001
Residual	19	575.3235	7.1184		
Total	22	710.5731	32.2988		

Mating begins in November and continues until the end of March as each female follows her own temporal cycle (Porcher 2005). Parturition begins in September and continues until January. Each female again mates 1.5 to 2.5 months after parturition, thus completing an annual reproductive cycle. All resident sharks under observation followed this pattern. Evidence of reproductive events presented by transient females conformed with the pattern of the residents. Figure 13 shows mating and parturition recorded in each month (Porcher, 2005).

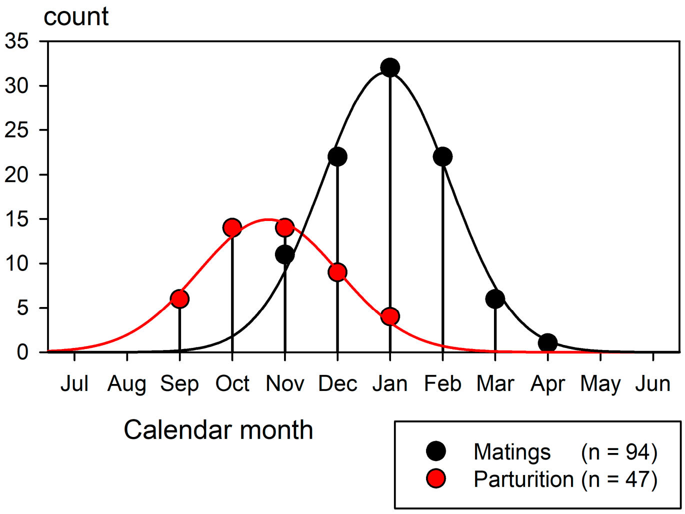

Figure 13. Monthly distribution of mating and parturition events, using records of females observed immediately following mating or parturition. Fitted Gaussian distributions for illustrative purposes only.

A comparison with Figure 12 illustrates the impact of the reproductive season on the blacktips' movement patterns. A substantial portion of their travels were driven by this powerful instinctual imperative.

3.3.2. The Lunar Phase

The movement patterns of blacktip reef sharks with respect to the lunar day were analysed in similar fashion to the monthly data above. A notable correlation with lunar phase (Table 4, Figure 14) was exhibited, as evidenced by the numbers of transients recorded at feeding sessions across each lunar day. Peaks occurred at both new and full moon.

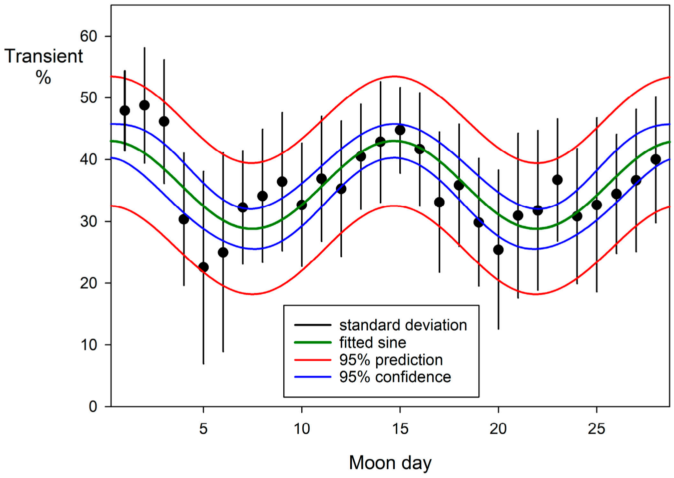

Figure 14. Percentage of transients among the adult blacktips attending sessions held on each day of the lunar phase. The fifteenth day represents the day of the full moon, taking the lunar cycle as 28 days long. The period of regular sessions between 99-04-11 and 02-05-11 in Section A are used for the calculation. Analysis conditions as for Figure 12.

Table 4. Regression analysis of lunar day data for transient appearances in Section A for the fitted function f = y_0+a.sin(2πx/b + c). a: amplitude, b: cycle frequency, c: offset, y_0: overall mean.

R	R^2	Adj. R^2	Std. Error of estimate
0.7304	0.5335	0.4752	4.8305

Coefficient		Std. Error	t	P
b	14.3491	0.8304	17.2806	<0.0001
c	1.5634	0.4086	3.8261	0.0008
y_0	35.7627	1.0012	35.7192	<0.0001

Analysis of Variance					
	DF	**SS**	**MS**	**F**	**P**
Regression	3	640.3576	213.4525	9.1479	0.0003
Residual	24	560.0070	23.3336		
Total	27	1200.3646	44.4579		

3.3.3. Unusual Sessions

A distinct pattern emerged from sessions that deviated from the usual. These occurred sporadically with intervals of many months. Only 12 such sessions were documented during the 6.5-year study (Figure 2), with nearly all correlating with the full moon and the dark lunar phase. These sessions attracted up to twice the usual number of blacktip reef sharks, and were distinguished by a high proportion of infrequent transients. They were characterized by social interactions featuring high-velocity, synchronized movements throughout the area (Porcher, 2023a). Conversely, during certain full moon phases, an opposing trend occasionally emerged, marked by the absence of the resident females. Only juveniles and one or two lagoon-dwelling males attended.

Of these unusual sessions, six (50 % of the total 12) coincided with the full moon. One such session saw the arrival of two groups of rare transients, including individuals #219 and #220, as well as #119 and #137 (Figure 11). Four sessions (33 %) occurred during the dark lunar phase, while the remaining two (17 %) took place when the moon was 42 % illuminated (lunar day 7), on 00/07/07/ and 00/11/03. The latter session was notable for the appearance of the Papetoai resident female (#179), marking one of her two recorded visits to Section A. A rare periodic male transient (#103), present in the area solely during November and December, was also observed at this session and during #179’s second documented appearance in Section A.

An intriguing associated observation involved the presence of a lemon shark (*Negaprion acutidens*) at six sessions over the 6.5-year study period. Four of these occurrences aligned with the full moon, while the remaining two coincided with the dark lunar phase (new moon). This species infrequently entered the back reef; juvenile blacktips use those shallow waters as a refuge from such large predators.

3.3.4. Other Influences

During storm events, increased oceanic swell transformed the lagoon into a dynamic, riverine environment. Gravid female blacktips, particularly larger individuals, exhibited reduced manoeuvrability in strong currents, necessitating substantial energy expenditure to navigate the complex coral reef environment under turbulent conditions. Consequently, a significant proportion of these females vacated the lagoon during such events, possibly seeking refuge in the deeper waters adjacent to the fore reef. In contrast, the smallest juvenile sharks, characterized by a streamlined morphology and the highest surface-to-volume ratio, demonstrated greater ease in navigating turbulent conditions. Despite their much smaller body size, their caudal fins were comparable in size to those of the heavy-set females, facilitating efficient propulsion through the environment during periods of high turbulence. These juveniles also possessed a stronger tendency to remain within the protective shallows.

Under calm conditions, the average attendance of adult sharks across 149 sessions was ~24. In contrast, during 41 sessions marked by adverse conditions, the average adult attendance dropped to ~18. Notably, in more extreme conditions, adult female attendance was nearly absent, with only a few juveniles present.

In August 2003, when a Singapore-based company began finning the reef sharks, those not immediately killed fled the area. Though some returned within ten days, most took more than two weeks to return, and some did not reappear in their core ranges until the same period of the following lunar cycle. As a result of this tendency and the ongoing slaughter that removed all the elderly females, and nearly every mature blacktip under observation, the shark communities originally observed never returned to their former state. By the time international pressure won their protection in 2006, the population of the back reef consisted of juveniles. (The adults were believed to leave the back reef and roam the ocean at night [Richard Johnson, pers. comm.] where they were vulnerable to fishing vessels but evidently the juveniles did not, for they alone survived). The reef sharks inhabiting the waters on some of the islands in Polynesia were completely fished out, while observers in the wilder parts of the island nation reported countless vessels laden with drying shark fins.

A further unidentified influence resulted in the evacuation of all the blacktips under human observation on Mo'orea Island between July 23 and August 5, 2002 (Porcher, 2023b), including the smallest pups from their shallow coral refuges. In spite of extensive investigation, no reason for their disappearance was found.

4. Discussion

4.1. Limitations of Observations

While it could be argued that the provisioning sessions affected the behaviour of the reef sharks familiar with them, the extended duration of the study—combined with observations conducted outside of feeding times—enabled the observer to develop a comprehensive understanding of blacktip reef sharks. This helped offset potential biases introduced by provisioning.

Feeding sessions were held exclusively during the hour of sunset, and it was repeatedly observed that shark gatherings were constrained to that period. Visits to the area at random times confirmed that the blacktips congregated only before sunset. Many individuals met the observer at the lagoon's border and followed the kayak to the feeding site. On multiple occasions, the observer swam to the site at different times and from other directions to check for shark presence. At no time, in all the years of observation, were sharks found congregating outside the provisioning window; it was rare to come into visual range of a blacktip shark in that region at any other time. Given the limited size of the back reef and the sharks' relatively small home ranges, their behaviour appeared deliberate, with individuals responding only to familiar cues.

Further, the data clearly shows that no shark attended all feeding sessions. The Residency Index for the three immediate residents of the vicinity of the feeding site was 0.73 to 0.79. Individuals often missed sessions, they did not stop their wide-ranging movements to stay in the area because of them, and in spite of them, the greatest number of individuals in all categories were those who passed only one time, or for one short period of time. As found by other researchers, a few fish scraps offered weekly had minimal effect on their movements (Maljković and Côté, 2011).

The advantage of the provisioning sessions compensated for any short term disruption caused, because prior to initiating them, it was impossible to observe the natural behaviour of the blacktip reef sharks using the study area. But after they became familiar with the observer, they pursued their lives as if no one were watching.

Although blacktip reef sharks are known to exhibit peaks in activity at night (Papastamatiou *et al.*, 2009; Mourier *et al.*, 2013), nighttime observations were not feasible due to the lack of visibility and safety concerns given the study sites' 1 km distance from shore.

However, the 6.5-year dataset—comprising 506 hours across 501 observation sessions—helped to mitigate this limitation. The observed blacktips presented a peak of activity in the low-light period at, and just after, sunset, as seen by other researchers (Papastamatiou *et al.*, 2009). Papastamatiou *et al.* (2015) found that at that time blacktips not only have a sensory advantage over their prey, but also a thermal one.

It was for this reason that 67 % (337.8 hours) of the observations were conducted during the low-light conditions around sunset. Alongside frequent unprovisioned observations, the study documented natural patterns of movement and habitat use across 475 identified individuals, which exceeds, by many times, that of any telemetry study done so far on the species. By increasing representation of the observed patterns, it enhances confidence in the detection of behavioural trends, including inter-individual variability and differences between the movements of males, females, and juveniles. Such a large dataset also offers insights into population-level patterns that may be obscured in smaller-scale studies.

Building on an existing ethogram of 35 context-specific behaviours observed in this species (Porcher, 2023a), the present study provides a robust foundation for expanding current understanding of the spatial ecology of *C. melanopterus.*

4.2. The Community

The marked site fidelity observed in this species aligns with the findings of other researches in French Polynesia (Mourier *et al.*, 2013) and is corroborated across diverse locales, including Australia (Speed *et al.*, 2011; Chin *et al.*, 2013; Schlaff *et al.*, 2020), Palmyra Atoll (Papastamatiou *et al.*, 2009, 2010), and Aldabra Atoll (Stevens *et al.*, 1984). The back reef predominantly hosted adult females and juveniles, with scant male presence, while the fore reef was primarily occupied by males (Mourier *et al.*, 2013). Lagoon-resident females visited the fore reef more frequently than fore reef males entered the back reef. Habitat-specific ecological attributes significantly influenced the distribution of reef blacktips, with physical landmarks and environmental features delineating their ranges (Papastamatiou *et al.*, 2010; Eustache *et al.*, 2023).

Sexual segregation, a prevalent phenomenon in shark populations (Wearmouth and Sims, 2008; Jacoby *et al.*, 2012), is frequently linked to reducing female harassment and injury risks. Yet, throughout this 6.5-year study, no instances of harassment by lagoon males sharing overlapping ranges with females were recorded. Mating-associated biting was restricted to instances of female receptivity, and neither sex excluded the other from potentially resource-rich habitats. During incursions of male groups from the fore reef—presumably for mating—resident females engaged without avoidance (Mourier *et al.*, 2013; Klimley *et al.*, 2023). Consequently, sexual segregation in *C. melanopterus* appears unrelated to male aggression or female apprehension.

C. melanopterus displays sexual dimorphism (Carrier *et al.*, 2012), accompanied by divergent male and female instincts. Evolutionary pressures possibly favoured females inhabiting shallower, nearshore waters—for safety as well as enhanced food availability for their larger bodies—while testosterone-driven males exhibited greater roaming tendencies. This behavioural differentiation likely improved reproductive success in the ancestral lines and shaped contemporary instincts.

Chin *et al.* (2013) documented exclusive presence of juveniles and adult females in shallow refuges at Magnetic Island, Queensland, with subadults and males largely absent. In contrast, Papastamatiou *et al.* (2009, 2010) reported a more equitable male distribution across Palmyra Atoll lagoons, with minimal sexual segregation. In the present study, the lagoon accommodated juveniles of all ages alongside a few males. This variation suggests flexibility in segregation behaviour and habitat utilization within the species.

The transient nature of blacktip reef sharks at Site C might be attributable to its widely spaced, predominantly dead, patch reefs with reduced fish abundance, compounded by the noise of persistent boat traffic from a shoreline hotel featuring overwater bungalows (Bleckmann and Zelick, 2009). It is to be noted that daily shark provisioning for tourists by the hotel, for a year prior to these observations, had not induced residency in this suboptimal environment.

The utilization of small and shallow nursery areas by neonates aligns with findings in other studies (*e.g.* George et. al., 2019; Papastamatiou *et al.*, 2009; Trujillo Moyano, 2023; Eustache *et al.*, 2023; Bouyoucos *et al.*, 2020). These shallow regions were typically inhabited by a variety of juvenile fish, providing suitable prey for the neonate sharks. However, the co-occurrence of adults with pups of approximately one year of age challenges current theory, which considers that size segregation reduces predation on neonates and juveniles. Observations by Chin *et al.* (2013), as in the present study, consistently reveal that adult females interacted with small juveniles in a manner analogous to larger conspecifics (Porcher, 2023a). The gradual exploration away from nursery areas by pups over time was also noted by Bouyoucos *et al.* (2020).

Comparable ontogenetic habitat shifts are evident in lemon sharks (*Negaprion brevirostris*) at Bimini lagoon, where juveniles transition to deeper waters with maturity (Gruber *et al.*, 1988). This suggests that it is a successful strategy used by other species as well as by blacktip shark pups for predator avoidance (Bouyoucos *et al.*, 2020; Trujillo Moyano, 2023; Eustache *et al.*, 2023).

4.3. Movements

Categorizing the movement patterns of blacktip reef sharks in this study proved challenging due to substantial inter-individual variability. Although previous studies have reported sedentary tendencies and site fidelity in this species (Stevens, 1984; Papastamatiou *et al.*, 2009; Chin *et al.*, 2013, 2016), our data emphasize movement as a central feature of blacktip reef shark behaviour. Across all sighting categories, most identified individuals were transients observed either once or for a brief span of time; 82.7 % of males and 62.1 % of females. This predominance is particularly striking given that these individuals were unfamiliar with both the observer and the observation setting, making them less likely to enter the feeding site and remain within visual range long enough for identification and inclusion in the dataset. Furthermore, unidentified sharks were present during every session (but excluded from analysis), suggesting that the actual number of transients was significantly higher than reported here.

The unidentified sharks were predominantly juveniles and males because the observer focused first on identifying the mature females at the sessions as they were the primary occupants of the back reef. Further, their slower movements and greater willingness to approach and circle the fish scraps alongside resident females facilitated identification (Porcher, 2023a). Consequently, many more males and juveniles remained unidentified and were excluded from the dataset. Nonetheless, it was these groups that exhibited the highest rates of transience, underscoring their significant contribution to the observed movement dynamics.

4.3.1. Males

The elevated proportion of blacktip reef sharks observed either once or for a single period suggests that roaming is a critical behavioural trait in the species. Male-biased dispersal was found to be a life-history trait in French Polynesia by Vignaud *et al.* (2013), who considered that otherwise philopatry (Mourier and Planes, 2013) each year (Porcher, 2005) would prevent the species from colonizing new areas. The males inhabiting the back reef displayed dark grey-brown colouration, except upon returning from post-reproductive season excursions, when they frequently re-appeared significantly paler. This change in pigmentation (Johnson, 1978; Lowe and Goodman-Lowe, 1996) suggests extended oceanic sojourns (Mourier and Planes, 2013). Since the females occupy the lagoons, the males could have circumnavigated Mo'orea while remaining in those shallow waters. However, their colour change indicates that instead they travelled in the ocean, possibly to visit other islands in the archipelago (Mourier and Planes, 2013; Vignaud *et al.*, 2013; Schlaff *et al.*, 2020). Their absences were frequently two to five months in length.

4.3.2. Females

While male-biased dispersal would help to consolidate blacktip communities in new areas, females would be required to establish them. To populate the island chains that formed across the Pacific Ocean in recent geological times—Mo'orea formed between 1.5 and 2 million years ago (Neall and Trewick, 2008)—females as well as males necessarily traversed vast oceanic distances. Blacktip reef sharks are distributed across the Indo-Pacific, from the Red Sea and East Africa to the Hawaiian Islands and French Polynesia, from their origin in the coastal regions near Asia (Maisano Delser *et al.*, 2019).

Female philopatry does pose a challenge to range expansion because it ties females to specific sites, reducing their likelihood of colonizing distant areas. However, it is not absolute. Rare instances of female dispersal—potentially driven by environmental pressures, resource competition, or stochastic events such as storms and currents—could have facilitated females reaching new reefs or islands, especially during glacial periods with lower sea levels exposing more reefs.

Subadult females possibly played a critical role. Their behavioural repertoire is characterized by a pronounced tendency to exploration, risk-taking, and boldness (Porcher, 2022), traits that may have facilitated long-range dispersal events across reef networks, particularly during favourable environmental conditions such as Pleistocene sea level fluctuations. Once established in new areas, these females could have transitioned to philopatric behaviour, anchoring new populations, while males, with their greater dispersal tendency, supported the persistence and diversity of newly established communities by mating across fragmented populations and reinforcing the gene flow.

Though Vignaud et al., (2013) found that *C. melanopterus* rarely travels more than 50 km to other island groups, in Australia, where habitats are less fragmented, Speed *et al.*, (2016) reported significantly longer parturition-related movements in female *C. melanopterus*—as long as 275 km—while mean activity space estimates were 12.8 ± 3.1 km² for adults and 7.2 ± 1.3 km² for juveniles. This illustrates the species' adaptability across varying habitat configurations, and underlines the reef blacktips' potential for long-distance movements.

The Pacific's archipelagoes form a network of reefs and islands that could have acted as stepping stones for blacktip reef shark expansion. They likely colonized these areas incrementally, with both males and females occasionally moving to nearby islands over generations. Given the pronounced individual variation observed, certain *C. melanopterus* individuals likely undertake occasional journeys exceeding the distances inferred from limited datasets.

Sharks navigate using infrasound (Myrberg, 1978) and the Earth's magnetic field (Klimley and Ainley, 1996; Keller *et al.*, 2021), with chemoreception likely enabling recognition of distinct island chemical signatures. Undoubtedly a unique scent trail, long and slow, drifts through the ocean from each island, carried from its lagoons and rivers. Sharks traversing ocean stretches could use such island scent trails for navigation. If beneficial, sporadic long-range travel could constitute an innate behavioural trait in reef blacktips, which would help explain the observed roaming tendencies of the small juveniles as well as certain adult individuals.

These strong roaming tendencies, including long-range travel, warrants consideration in MPA design. For instance, a study at Ningaloo Reef, Australia, revealed that *C. melanopterus* ranges extended well beyond MPA boundaries (Speed *et al.*, 2016). Given the naturally limited population sizes of reef sharks, particularly in fragmented habitats (Vignaud et al., 2013), effective conservation strategies must account for their dispersal patterns.

In the present case, the lack of sightings of Papetoai's resident sharks in the study lagoon could stem from a preference for westward movement, driven by geographical constraints. Papetoai's lagoon is narrow, with nursery habitats and other features predominantly located to the west and along Mo'orea's west coast (Mourier et al., 2013). Observations in Papetoai excluded the reproductive season, when some female residents from the study lagoon might have traversed Papetoai en route to west coast nurseries. Papastamatiou et al. (2010) similarly noted limited inter-lagoon movement and variable residency durations across regions, though the underlying drivers—potentially trophic ecology—remain unresolved (Papastamatiou et al., 2010).

Most gravid transients observed in Sections A and B were likely migrating toward west coast nurseries for parturition (Mourier *et al.*, 2012, 2013). However, some north shore Mo'orea females have been documented travelling to other islands for this purpose (Mourier and Planes, 2013). Resident females absent for extended periods, as well as annual transients, and some of those sighted just once, might also have been undertaking inter-island journeys.

4.3.3. Juveniles

Blacktip reef shark pups with an estimated length of approximately 70 cm exhibited the highest proportion (60.5 %) of juveniles observed within the study region once or for a single period. This finding is unexpected, particularly given that the dataset is biased against such an outcome due to the reduced likelihood of positively identifying them. Nevertheless, a consistent stream of the smallest juveniles traversed the study area throughout the investigation, with most not reappearing. This pattern suggests that these very young blacktips disperse from their natal region without returning.

The philopatric behaviour of the species (Mourier and Planes, 2013) offers insight into this phenomenon. If adults undertake extensive journeys, including inter-island movements to return to their natal nurseries, then juveniles must initiate dispersal from their birth areas during early life stages and travel far, prior to establishing their home ranges. Observations in this present study indicate that such dispersal may commence as early as 1.5 to 2.5 years of age. Similarly, Chin *et al.* (2013, 2016) reported that juveniles tend to exhibit short-term residency, supporting the notion of early dispersal in this species.

A unique observation of rare coordinated group movement occurred during the return of the community to the study lagoon following their unprecedented ten-day evacuation in July–August, 2002 (Porcher, 2023b). T**he community of sharks appeared from the lagoon perimeter in a widespread formation with several small male juveniles** travelling at high velocity some metres ahead of the others; some were tens of metres ahead. **While the underlying mechanisms remain uncertain, this observation, though anecdotal, highlights the unknown and potentially important behavioural dynamics within blacktip shark communities. The prominence of these young male individuals during the re-entry event suggests that they may play a previously underappreciated role.** (Porcher, 2023b).

4.4. Influences on Blacktip Reef Shark Movements

4.4.1. Transients from Different Origins

Research on *C. melanopterus* (Mourier *et al.*, 2012) and other shark species indicates that some form companion relationships. Strong interpersonal bonds have been documented in bull sharks (Bouveroux *et al.*, 2021) and grey reef sharks (Papastamatiou *et al.*, 2020). Consistent with these findings, the present study has documented companion sharks integrating with other groups before separating to continue their journeys together—a dynamic termed 'fission and fusion' (Mourier *et al.*, 2012).

In this investigation, most blacktip reef sharks had preferred companions, although some, including infrequent transients, were consistently solitary. The overlapping core ranges of resident sharks, frequent path crossings, regular mutual sightings, and coordinated departures from the study area suggest that these interactions foster the formation of robust bonds among select individuals (Papastamatiou *et al.*, 2018). Multi-year associations and the evident excitement during social encounters highlight the importance of sociality in *C. melanopterus* (Mourier and Planes, 2012; Porcher, 2023a,b), a trait shared with numerous shark species (Papastamatiou *et al.*, 2023; Klimley *et al.* 2023).

Long-term bonding is likely to be beneficial through enhanced safety in numbers. Resident sharks were also consistently observed to approach challenging situations in groups, while solitary individuals were seen to linger beyond visual range until they could join conspecifics, and approach with them. Such behaviour is indicative of "social buffering" (Kikusui *et al.*, 2006), where collective presence mitigates stress in novel or demanding contexts. This is considered to imply emotional capacity and social complexity in the species (Kikusui *et al.*, 2006). Such emotional underpinnings could also drive reef blacktips to bond with familiar companions sharing their ranges when traversing unfamiliar environments. Additional advantages include cooperative foraging and the leveraging of dual sensory inputs to locate prey (Papastamatiou *et al.*, 2010).

Over 6.5 years of observing Section A residents, it became apparent that companions frequently circled out of visual range, only to reconnect as their paths converged (Porcher, 2023a). This pattern is likely to enhance foraging efficiency, with pairs potentially locating more food than solitary individuals (Papastamatiou *et al.*, 2010).

The companion behaviour observed in blacktip reef sharks challenges the premise that spatial proximity inherently reflects social affiliation. Numerous studies on shark sociality employing remote technologies (Mourier *et al.*, 2019) rely on the 'gambit of the group' concept, which assumes that individuals present at provisioning sessions constitute a cohesive 'group', though the precise nature of the 'group' is not defined. In contrast, this study determined that a substantial fraction of sharks attending feeding sessions were transients from varied origins, meaning that those attending did not form a ‘group’ (Figure 12). Being non-territorial, resident blacktips exhibited an attraction to transients (Porcher, 2023a,c), and so were frequently observed in close proximity to individuals from different regions, while the species’ characteristic circling movement patterns meant that close companions were not in close proximity most of the time.

Transients eliciting the most excited social interactions (Porcher, 2023a) were often the rarest, suggesting that resident sharks maintain acquaintances encountered annually or less, implying a capacity for long-term individual recognition. Given the complex travel patterns already documented for these sharks (Mourier and Planes, 2013; Maisano Delser, 2019) it is plausible that they maintain knowledge of other blacktip reef sharks with distant home ranges that they infrequently encounter, which provides further evidence of social and cognitive sophistication.

4.4.2. The Lunar Phase

Unlike regions where lunar phase correlations align with tidal patterns, in Polynesia, the tide is solar. This distinction results in only minor fluctuations in water levels, with a mere few centimetres’ difference between low and high tides in lagoons, along their perimeters, and at the passes (Hench *et al.*, 2008). Water depth in these zones is predominantly governed by oceanic conditions which determine the volume of water spilling over the reef (Hench *et al.*, 2008). Consequently, the observed correlation between blacktip reef shark movements and lunar phases cannot be attributed to the opening and closing of waterways. Lunar cycle associations have been documented in great white sharks (*Carcharodon carcharias*) (Klimley and Ainley, 1996) and aggregations of sharpnose sharks (*Rhizoprionodon longurio*) (Pérez-Jiménez *et al.*, 2002), with both bright and dark phases proving significant. Conversely, Gallagher *et al.* (2021) found no lunar influence on the movements of Caribbean reef sharks (*Carcharhinus perezii*) or tiger sharks (*Galeocerdo cuvier*).

The use of moonlight for navigation within complex coral habitats is plausible, offering visual cues to avoid obstacles. However, the utility of the dark lunar phase is less apparent. It is possible that blacktips exploit this period’s darkness to hunt fish, leveraging their Ampullae of Lorenzini. Certain rare transients consistently arrived in the study area during or immediately following the dark lunar phase (Figure 11a). As these individuals are most likely to originate from other islands, their timing suggests an awareness of reduced detectability (Porcher, 2023a), potentially advantageous for mesopredators vulnerable to oceanic shark predation (Frisch *et al.*, 2016).

4.4.3. Other Influences

The tendency for sharks to vacate the area after some of their number are fished was regularly mentioned by the native Tahitians, who had wanted their sharks neither fished nor disturbed (Johnson, 1978). A similar response was observed in tiger sharks in the Bahamas, where they remained absent for approximately two months post-disturbance (Abernethy J, pers. comm., 2016).

The abrupt evacuation of blacktip reef sharks from Mo’orea’s north shore between July 23 and August 5, 2002, remains unexplained (Porcher, 2023b). Despite extensive investigation, no cause was identified that could explain the disruption of the population followed by the mass departure of all individuals across both back and fore reefs, including pups from their dense coral refuges. Subsequently, not all the residents, and few of the pups, returned.

5. Conclusions

This investigation into the movement ecology of blacktip reef sharks in Mo’orea’s waters has elucidated key aspects of their behaviour. Despite certain sedentary traits, substantial movement was evident, mostly driven by the reproductive cycle.. The correlation between the sharks’ movements and the lunar phases emerged as a distinctive influence.

This study enhances the understanding of the complex lives of blacktip reef sharks and emphasizes the need to account for individual variation, behavioural flexibility, and sophisticated social structures in ecological studies and conservation frameworks. It found enduring bonds among individuals, underscoring the critical role of sociality in the species. The interactions among individuals, characterized by multi-year companionships and dynamic fission-fusion patterns, suggest capacities for individual recognition and social learning, aligning with observations in other shark species (*e.g.*, Papastamatiou *et al.*, 2020; Bouveroux *et al.*, 2021; Guttridge *et al.*, 2013).

The importance of movement to all categories of blacktips, as found in this study, which likely involved long-distance inter-island movements, as established by Mourier and Planes (2013) and Vignaud *et al.* (2013), necessitate broader protective measures. MPAs must be redesigned to encompass the full extent of the movement ranges of this species, as demonstrated by instances where ranges exceeded protected boundaries (Speed *et al.*, 2016).

The near total depletion of the adult population of blacktips during the study underlines the need for the effective protection of sharks in the face of the shark fin trade; the takes of shark liver oil, with at-sea processing, is of the same character (Sea Shepherd, 2017a,b). These ongoing threats, heightened by the success of illegal, unreported, and unregulated (IUU) fishing, demand urgent international action (Pike *et al*. 2024). Given the lucrative shark fin trade's illegal nature, driven by high prices and rich customers with little interest in sustainability, a CITES Appendix I listing is recommended to effect a ban on international trade in all sharks, manta rays, devil rays, rhino rays, chimaeras, and their derivatives (Porcher and Darvell, 2022). Sharks should be reclassified globally as protected wildlife rather than commercial fishery resources.

A binding international treaty to protect sharks, as well as threatened biodiversity in general, should be the immediate goal (Dasgupta, 2021).

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org.

References

Bascomte, J., Melián, C.J., Sala, E. (2005) Interaction strength combinations and the overfishing of a marine food web. Proc. Nat. Acad. Sc. USA 102, 5443–5447. DOI: *10.1073/pnas.0501562102.*

Bleckmann, H. and Zelick, R. (2009). Lateral line system of fish. Integr. Zool. 4(1), 13– 25.

Bond, M.E., Babcock, E.A., Pikitch, E.K., Abercrombie, D.L., Lamb, N. F., Chapman, D. D. (2012). Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the mesoamerican barrier reef. PLoS ONE, 7(3): e32983. DOI: 10.1371/journal.pone.0032983

Bouveroux, T., Loiseau, N., Barnett, A., Marosi, N.D., Brunnschweiler, J.M. (2021). Companions and casual acquaintances: The nature of associations among bull sharks at a shark feeding site in Fiji. Front. Mar. Sci. www.frontiersin.org/articles/10.3389/fmars.2021.678074 DOI: 10.3389/fmars.2021.678074

Bouyoucos, I.A., Romain, M., Azoulai, L., Eustache, K., Mourier, J., Rummer, J.L. *et al.* (2020). Home range of newborn blacktip reef sharks (Carcharhinus melanopterus), as estimated using mark-recapture and acoustic telemetry. Coral Reefs 39, 1209–1214. DOI: 10.1007/s00338-020-01965-z

Brena, P.F., Mourier, J., Planes, S., Clua, E.E. (2018). Concede or clash? Solitary sharks competing for food assess rivals to decide. Proc. Roy. Soc. Lond. B: Biol. Sci. 285: 20180006. DOI: 10.1098/rspb.2018.0006.

Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.). (2012). Biology of sharks and their relatives (2nd ed.). CRC Press, Boca Raton.

Castro, J.I. (2017). The origins and rise of shark biology in the 20th century. Mar. Fish. Rev. 78, 14–33.

Chin, A., Tobin, A.J., Heupel, M.R., Simpfendorfer, C.A. (2013). Population structure and residency patterns of the blacktip reef shark Carcharhinus melanopterus in turbid coastal environments. J. Fish. Biol. 82, 1192–1210. DOI: 10.1111/jfb.12057

Chin, A., Heupel, M.R., Simpfendorfer, C.A., Tobin, A.J. (2016). Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. Mar. Ecol. Prog. Ser. 544: 197–211. DOI: 10.3354/meps11545

Dasgupta P. (2021) The *Economics of Biodiversity: The Dasgupta Review*. Abridged Version. (London: HM Treasury).

doi:10.20944/preprints202310.0585.v2

Eustache, K. B., van Loon, E., Rummer, J. L., Planes, S., Smallegange, I. (2024). Spatial and temporal analysis of juvenile blacktip reef shark (*Carcharhinus melanopterus*) demographies identifies critical habitats. J. Fish. Biol. 104(1), 92–103. DOI: 10.1111/jfb.15569.

Freire, K.D., Christensen, V., and Pauly, D. (2008). Description of the East Brazil Large Marine Ecosystem using a trophic model. Scientia Marina 72, 477–491. *DOI: 10.3989/scimar.2008.72n3477.*

Frisch, A.J., Ireland, M., Rizzari, J.R., Lönnstedt, O.M., Magnenat, K.A., Mirbach, C.E. et al. (2016). Reassessing the trophic role of reef sharks as apex predators on coral reefs. Coral Reefs. 35, 459–472. DOI: *10.1007/s00338-016-1415-2*

Gallagher, A.J., Shipley, O.N., van Zinnicq Bergmann Maurits P.M., Brownscombe, J.W., Dahlgren, C.P., Frisk, M.G. *et al*. (2021). Spatial connectivity and drivers of shark habitat use within a large marine protected area in the Caribbean, the Bahamas Shark Sanctuary. Front. Mar. Sci. 7:608848 . DOI:10.3389/fmars.2020.608848

Galzin, R., and Pointer, J.P. (1985). Moorea Island, Society Archipelago. In: B Delesalle, R Galzin and B. Salvat (Eds). 5th International Coral Reef Congress, Tahiti, 27 May to 1 June 1985. Volume I: French Polynesian Coral Reefs: 73-02

George, L.W., Martins, A.P.B., Heupel, M.R., Simpfendorfer, C.A. (2019). Fine-scale movements of juvenile blacktip reef sharks Carcharhinus melanopterus in a shallow nearshore nursery. Mar. Ecol. Prog. Ser. 623, 85–97. www.jstor.org/stable/26789875

Gruber, S.H., Nelson, D.L.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(1), 61-76.

Guttridge, T.L., Dijk, S., Stamhuis, E.J., Krause, J., Gruber, S.H., Brown, C. (2013). Social learning in juvenile lemon sharks, Negaprion brevirostris. Anim. Cogn. 16, 55 – 64. DOI: 10.1007/s10071-012-0550-6

Hench, J.L., Leichter, J.J., Monismith, S.G. (2008). Episodic circulation and exchange in a wave-driven coral reef and lagoon system. Limnology and Oceanography. 53(6), 2681–2694.

Jacoby, D.M.P., Croft, D.P., Sims, D.W. (2012). Social behaviour in sharks and rays: analysis, patterns and implications for conservation. Fish. Fish. 13: 399–417. DOI: 10.1111/j.1467-2979.2011.00436.x

Jacoby, D.M.P., Fear, L.N., Sims, D.W., Croft D.P. (2014). Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. Behav. Ecol. Sociobiol. 68, 1995–2003. DOI: 10.1007/s00265-014-1805-9

Jamieson, D. and Bekoff, M. (1992). On Aims and Methods of Cognitive Ethology. PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association, Vol. Two: Symposia and Invited Papers, pp. 110–124.

Johnson, R.H. (1978). Sharks of Polynesia, Papeete: Les Editions du Pacifique Papeete, Tahiti, French Polynesia

Keller, B.A., Putman, N.F., Grubbs, R.D., Portnoy, D.S., Murphy, T.P. (2021) Map-like use of Earth's magnetic field in sharks. Curr. Biol. 31(13), 2881–2886.e3. DOI: 10.1016/j.cub.2021.03.103.

Kikusui, T., Winslow, J.T., Mori, Y. (2006). Social buffering: Relief from stress and anxiety. Philos. Trans. R. Soc. B, Biol. Sci. 361(1476), 2215–2228.

Klimley, A. P., and Ainley, D. G., (1996). *Great white sharks: the biology of Carcharodon carcharias*. Academic Press. San Diego, USA.

Klimley, A.P., Porcher, I.F., Clua, E.E., Pratt, H.L., Jr. (2023). A review of the behaviours of the Chondrichthyes: a multi-species ethogram for the chimaeras, sharks, and rays. *Behaviour 160*(11–14), 967–1080. DOI: 10.1163/1568539X-bja10214

Lowe, C. *and* Goodman-Lowe, G. (1996). Suntanning in hammerhead sharks. Nature 383, 677 DOI: 10.1038/383677a0

Maljković, A., and Côté, I.M. (2011). Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark, Biological Conservation 144(2), 859–865, DOI: 10.1016/j.biocon.2010.11.019.

Mandel, J. (1964). The statistical analysis of experimental data. New York: Dover.

Mourier J., Vercelloni J., Planes, S. (2012). Evidence of social communities in a spatially structured network of a free-ranging shark species. Anim. Behav. 83: 389–401.

Mourier, J., and Planes, S. (2012). Inferring social behaviour and mating patterns in a reef shark from social network and molecular analyses. Abstract In: Book of Abstracts. 12th International Coral Reef Symposium, 9–13 July 2012, Cairns, Queensland, Australia: 306–307

Mourier, J., and Planes, S. (2013). Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. Mol. Ecol. 22(1), 201–214.

Mourier, J., Mills, S.C., Planes, S. (2013). Population structure, spatial distribution and life-history traits of blacktip reef sharks Carcharhinus melanopterus. J. Fish. Biol. 82(3), 979–993.

Mourier, J., Maynard, J., Parravicini, V., Ballesta, L., Clua, E., Domeier, M.L. *et al.* (2016). Extreme inverted trophic pyramid in the coral reef ecosystem of Fakarava, French Polynesia: the dominance of low-energy fish and shark populations. PLoS ONE. 11(9), e0162235.

Myrberg, A.A., jr., Gordon, C.R., Klimley, A.P. (1976). Attraction of free ranging sharks to low frequency sound, with comments on its biological significance. In Schuijf, A. and Hawkins, A.D., eds. Sound Reception in Fishes. New York: Elsevier, pp. 205–28.

Neall, V.E. and Trewick, S.A. (2008). The age and origin of the Pacific islands: a geological overview. Philos. Trans. R. Soc. B: Biol. Sci. 363(1508), 3293–3308.

Okey, T.A., Banks, S., Born, A.F., Bustamante, R.H., Calvopiña, M., Edgar, G.J. *et al.* (2004). A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecol. Model. 172, 383–401.

Papastamatiou, Y.P., Bodey, T.W., Caselle, J.E., Bradley, D., Freeman, R., Friedlander, A.M. *et al.* (2020). Multiyear social stability and social information use in reef sharks with diel fission–fusion dynamics. Proc. R. Soc. B 287: 20201063. DOI: 10.1098/rspb.2020.1063

Papastamatiou, Y.P., Caselle, J.E., Friedlander, A.M., Lowe, C.G. (2009). Distribution, size frequency, and sex ratios of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra Atoll: a predator-dominated ecosystem. J. Fish. Biol. 75(3), 647–54. DOI: 10.1111/j.1095-8649.2009.02329.x.

Papastamatiou, Y.P., Friedlander, A.M., Caselle, J.E., Lowe C.G. (2010). Long-term movement patterns and trophic ecology of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra Atoll. J. Exp. Mar. Bio. Ecol., 386(1–2): 94–102. DOI: 10.1016/j.jembe.2010.02.009.

Pike, E.P., MacCarthy, J.M.C., Hameed, S.O., Harasta, N., Grorud-Colvert, K., Sullivan-Stack, J. *et al.* (2024). Ocean protection quality is lagging behind quantity: Applying a scientific framework to assess real marine protected area progress against the 30 by 30 target. *Conservation Letters*, 17, e13020. DOI: 10.1111/conl.13020

Porcher, I.F. (2005). On the gestation period of the blackfin reef shark, *Carcharhinus melanopterus* in waters off Mo'orea, French Polynesia. Mar. Biol. 146, 1207–1211.

Porcher, I.F. (2022). Commentary on emotion in sharks. Behaviour. 159(8–9), 849–866. DOI: 10.1163/1568539X-bja10145

Porcher, I. F. (2023a). Ethogram for blacktip reef sharks (*Carcharhinus melanopterus*). *Behaviour, 160*(11-14), 1167–1204. DOI: 10.1163/1568539X-bja10213

Porcher, I.F. (2023b). Shark evacuation from Mo'orea island in 2002. *Behaviour. 160*(11–14), 1319–1328. DOI: 10.1163/1568539X-bja10198

Porcher, I.F., and Darvell, B.W. (2022). Shark Fishing vs. Conservation: Analysis and Synthesis. *Sustainability 14*, 9548. DOI: 10.3390/su14159548

Schlaff, A.M., Heupel, M.R., Udyawer, V., Simpfendorfer, C.A. (2020). Sex-based differences in movement and space use of the blacktip reef shark, Carcharhinus melanopterus. PLoS ONE 15(4): e0231142. DOI: 10.1371/journal.pone.0231142

Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Harcourt, R.G., Stevens, J.D. *et al.* (2016). Reef shark movements relative to a coastal marine protected area, Reg. Stud. Mar. Sci. 3, 58–66. DOI: 10.1016/j.rsma.2015.05.002.

Stevens, J.D. (1984). Life history and ecology of sharks at Aldabra Atoll, Indian Ocean. Proc. Roy. Soc. Lond. B. 222(1226), 79–106. DOI: 10.1098/rspb.1984.0050.

Trujillo Moyano, J.E. (2023). Investigating escape tactics in newborn tropical reef sharks to understand essential habitat use: a behavioural, kinematic, and physiological approach (Thesis, Doctor of Philosophy). University of Otago. Retrieved from http://hdl.handle.net/10523/15471

Vignaud, T., Clua, E., Mourier, J., Maynard, J., Planes, S. (2013). Microsatellite Analyses of Blacktip Reef Sharks (Carcharhinus melanopterus) in a Fragmented Environment Show Structured Clusters. PLoS ONE 8(4), e61067. DOI: 10.1371/journal.pone.0061067

Wearmouth, V.J. and Sims, D.W. (2008). Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. Adv. Mar. Bio. 54, 107–170.

White, T. D., Carlisle, A.B., Kroodsma, D.A., Block, B.A., Casagrandi, R., De Leo, G. A. *et al.* (2017). Assessing the effectiveness of a large marine protected area for reef shark conservation. Bio. Cons. 207, 64–71.

Worm, B.S., Orofino, S., Burns, E.S., D'Costa, N.G., Manir Feitosa L., Palomares, M.L.D., *et al.* (2024). Global shark fishing mortality still rising despite widespread regulatory change. *Science* 383, 225–230