 doi:10.20944/preprints202208.0139.v1

Article

Field Observations of the Behaviour of Blackfin Reef Sharks (*Carcharhinus melanopterus*)

Ila France Porcher

Independent Researcher, 44000 Essaouira, Morocco
ilafranceporcher@protonmail.com

Abstract: The chondrichthyan lineage diverged from the *osteichthyan* line 440 million years ago, resulting in a vast evolutionary gulf between modern elasmobranchs and other vertebrates. Though this has supported the assumption that sharks are ancient, dangerous, and binary-minded, the few ethological studies done have noted intelligent actions including social exchanges. Yet their behaviour remains little known. On seeing that *Carcharhinus melanopterus* displayed complex actions during incidental meetings, a long-term ethological study of the species was carried out using artificial aggregations, at several sites in the fringe lagoon of Mo'orea Island, French Polynesia. Short and long-term behaviour was recorded in 473 individuals, including an ethogram, roaming patterns, social interactions, and cognition. *C. melanopterus* is considered sedentary, yet the home range could also be viewed as a place to pause between travels, for most individuals left for long periods. The study community and its visitors travelled in correlation with the lunar phase, in groups of up to six individuals, socializing with conspecifics encountered along the way, and displaying fluid social dynamics. *C. melanopterus* was highly alert to danger yet prone to investigate novel objects, a combination that generated a variety of tactics to remain hidden while investigating the environment. Basic to this was the use of the visual limit for escape or to screen their presence, indicating an awareness of being present and observable. Using their other senses, they could focus their attention on events beyond visual range and made swift decisions to act as circumstances unfolded. In their non-territorial, non-hierarchical society, any shark could lead, but it was usually the same ones that did so. Therefore, unusual individuals had a significant effect on events through social learning, suggesting the potential for culture. Actions in a variety of situations suggested complex cognition, and individuals displayed both positive and negative subjective states including playfulness.

Keywords: blackfin reef shark; *Carcharhinus melanopterus*; shark behaviour; shark ethology; shark cognition

1. Introduction

The *chondrichthyan* lineage separated from the *osteichthyan* line at least 440 million years ago (Coates *et al.* 2018; Andreev *et al*. 2020) and has been evolving separately ever since, into very different forms of life. Along with their cartilaginous skeletons, the fossil record shows that sharks already had claspers, the penis-like male organs that evolved through a modification of the pelvic fins, 390 million years ago (Brazeau & Friedman 2014), so they were already using internal fertilization then, though mammals were yet to appear. A further major difference is that they are the only class of social vertebrates that do not vocalize. While convergent evolution is likely responsible for certain similarities between modern sharks and the vertebrates of the osteichthyan line, assumptions about their capabilities based on comparisons with other animals are unlikely to be correct.

Elasmobranchs have been assumed to be incapable of any higher mental abilities due to the prevailing idea they are at the bottom of a phylogenetic hierarchy which places *homo sapiens* at the top. They were considered to be too dangerous to study through direct observation (Johnson & Nelson 1973; Gruber & Myrberg 1977; Randall & Helfman 1978; Klimley 2022 submitted) so there have been few underwater ethological shark studies.

 doi:10.20944/preprints202208.0139.v1

Finally, Klimley (1982, 1985, 1988) broke through this psychological barrier, but his findings that sharks display complex social gestures through body language (Klimley 1982, 1985, 1988) to the degree of ritualizing conflict (Klimley 1996a), were received with considerable skepticism by his colleagues, due to the deep, anthropocentric bias against sharks. Shark science has been strongly influenced by fisheries and sharks have been studied mostly through dissection or tagging (Castro 2016).

More recently, remote technologies have been used to monitor shark movements and infer social networks (Mourier *et al.* 2019). While these are increasingly sophisticated, in the absence of ethological understanding of the animal's behaviour, much must be assumed (*Villegas-Ríos* et al. *2022).*

Northcutt (1977, 1978) found that the development and comparative size of the elasmobranch brain is comparable to birds and mammals. Large relative brain size correlates with complexity of ecological behaviour and cognitive capacities in other vertebrates, and has also been found to do so in elasmobranchs (Montgomery *et al.* 2012). Learning in elasmobranchs was noted in earlier studies as reviewed by Guttridge *et al.* (2009). Sharks use cognitive maps (Papastam*atiou et al.* 2011; Mourier & Planes 2012), recognize conspecifics as individuals (Myrberg & Gruber 1974, Guttridge *et al.* 2011; Jacoby *et al.* 2016), use the Earth's magnetic field to navigate (Keller *et al.* 2021) and are capable of social learning (Guttridge *et al.* 2013). Stingrays (*Potamotrygon castexi*) learned to use water as a tool to extract food (Kuba et al. 2010), and have been observed to play (Burghardt 2015). They are capable of a variety of other cognitive tasks including distinguishing between visual objects and electrical fields, categorizing objects, and perceiving illusory contours and bilateral symmetry (Fuss *et al.* 2014; Schluessel 2015).

Ethology is concerned with phylogeny (evolution), function (adaptation), causation, and development (ontogeny). Finding answers to these questions begins with careful observation and description of the repertoire of behaviours of the species performed in various contexts. To know a species according to ethological principals, it is therefore necessary to watch the activities of many different individuals long-term (Jamieson & Bekoff 1992), in the animals' environment where natural selection is occurring (Jamieson & Beckoff 1992). This includes not only spontaneous behaviour in response to a given circumstance, but long-term, temporal modulation including daily, lunar, and annual cycles (Myrberg & Gruber 1974), as well as ontological changes as pups mature. Even anecdotal accounts are valuable as revealed by the long history of anecdotal reports in the field of natural history *comparative animal behaviour (Sándor & Miklósi).*

Blackfin reef sharks (*Carcharhinus melanopterus*) (Quoy & Gaimard, 1824) inhabit the lagoons of Mo'orea Island and is one of the most abundant reef sharks on tropical coral reefs throughout the Indian and Pacific Oceans (Randall & Hoover 1995), although their numbers have been reduced by overfishing at many locations (Heupel *et al.* 2009). The species has also colonized the eastern Mediterranean Sea by way of the Suez Canal (Fowler *et al.* 2005). It inhabits shallow reefs and sand-flats of both atolls and high islands (Hobson, 1963; Stevens 1984; Papastamatiou *et al.* 2009; Mourier *et al.* 2012) and occasionally non-reef environments (Chin *et al.* 2012). The name derives from the Greek word '*melas'* meaning 'black' and '*pteron'* meaning 'fin' or 'wing.' Though they are also called 'blacktips,' this leads to confusion with the blacktip shark (*Carcharhinus limbatus*) (Johnson 1978).

Casual observation of blackfin reef sharks over a period of several years, showed that wild individuals systematically approached for a close look (within 30 cm) when a person had their head above the surface, or was looking the other way. One might also pass closely behind a person and was usually not seen when doing so. Since such behaviour suggested complex cognition by inferring that the shark was aware of the human placement of attention, and was using this awareness to its advantage, an ethological study of the species was undertaken.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

2. Method

C. melanopterus individuals inhabiting the lagoon on the north shore of Mo'orea island (*Galzin & Pointer 1985)* were easy to observe underwater, but the presence of the observer had a marked effect on their actions. Staged encounters provide a method for studying wildlife behaviour (Jamieson & Bekoff 1992), so beginning in April 1999, fish scraps were placed once weekly at specific observation sites. This tactic was effective in habituating the blackfins to the observer and has been used by other researchers in Polynesia since (*e.g.* Mourier *et al.* 2011; Brena *et al.* 2018).

The deeper channel just within the barrier reef was used for the observation sites. Both older juvenile blackfins and adults were present there, and the patch reefs were well spaced, allowing a fairly unobstructed view through the coral. Feeding sessions were held during the hour before sunset due to the blackfins' heightened level of alertness at that time.

Resident blackfins circling through the region would cross the scent flow and follow it to the observation session, while visitors were attracted by the submarine sounds made by the residents, and on approaching the feeding area would circle close enough to be identified. Photo-identification techniques were complimented with accurate drawings of both sides of the dorsal fin to identify each individual (Porcher 2005). The length, colour, gender, scars, marks, behaviour, and any other distinguishing features were included in the description of each shark. Figure 1 provides an example of a dorsal fin drawing as copied into the record book.

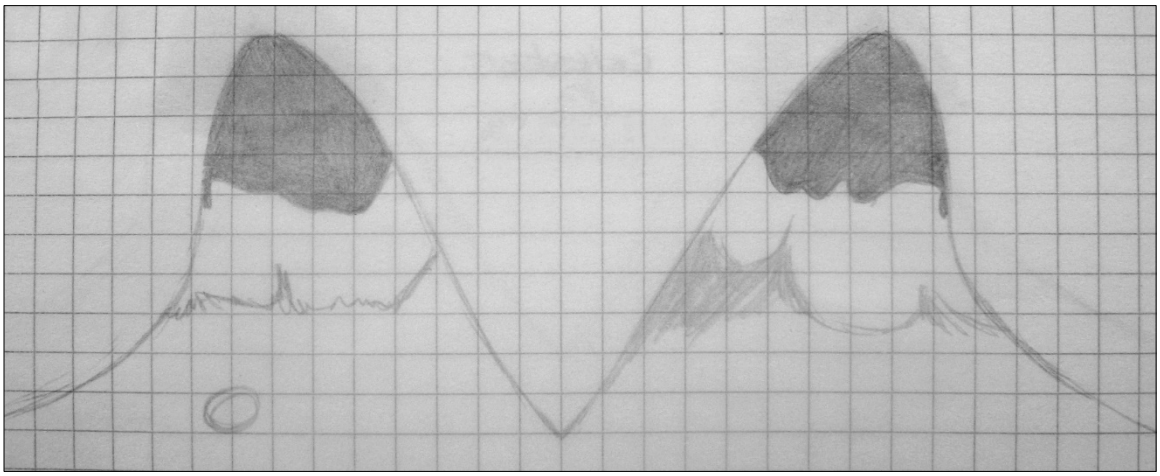


Figure 1. Example of a dorsal fin drawing used for identification.

Sicklefin lemon sharks (*Negaprion acutidens*), grey reef sharks (*Carcharhinus amblyrhynchos*), whitetip lagoon sharks (*Triaenodon obesus*), and nurse sharks (*Ginglymostoma cirratum*) also attended feeding sessions at times.

The lagoon between Opunohu Bay on the west and Cook's Bay to the east is from 3 - 4 km long, and from 0.8 to 1.2 km from shore to barrier reef. At that time it was a rich coral habitat, about two metres deep on average.

Figure 2 shows how it was divided it for reference.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

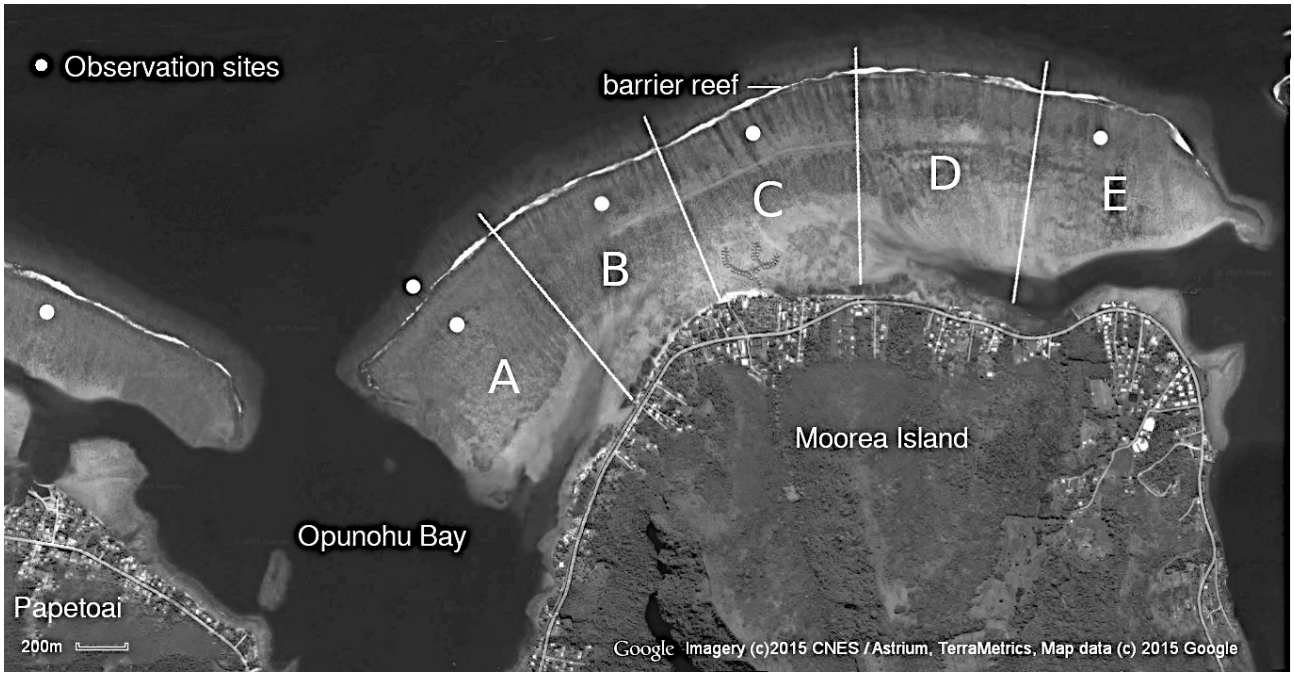


Figure 2. The study lagoon was divided into 5 sections for reference.

The blackfins were observed at random times during the day between feeding sessions. Observations were carried out 2 to 3 times weekly, conditions permitting, and more often when some event, such as a group of rare visitors, a sick or injured shark, a disappearance, a spawning event, or other unexpected circumstance demanded it. The lagoon borders, the fore-reef opposite Section A, and the nurseries at both ends of the barrier reef were monitored to acquire supplementary information about the activities of *C. melanopterus*. The region was seldom visited by other people so observations could be obtained without disturbance and the animals rarely if ever encountered other humans.

Thus, 473 individuals were definitively identified and noted on each subsequent sighting along with the time, marine conditions, and incidental details. The notes made underwater were entered in the computer on landing and used to write a full description of the session.

Table 1. summarizes the study effort.

Location	Time Period	Sessions	Hours	Sightings
Section A				
Site One	11/04/99 - 18/03/05	304	307.75	8734
Day sessions	03/04/00 - 06/03/05	38	37.50	215
Border	infrequent	5	8.00	27
Mid section	15/05/01 - 30/12/01	15	12.00	58
Eastern side	21/05/01 - 29/09/05	67	67.25	1140
Section B	03/06/01 - 02/08/03	48	43.70	1070
Section C	08/06/01 - 13/04/02	11	14.50	107
Section E	30/05/04 - 28/08/04	4	2.50	39
Outer Slope	19/05/02 - 18/05/03	5	6.50	60
Papetoai Lagoon	25/05/02 - 15/07/02	7	7.25	64
Totals		**501**	**506.20**	**11,514**

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

3. Results

The blackfins attending the first feeding sessions held in Section A were mature females whose home ranges encompassed the site. At first they would not eat when the observer was present, circling out of visual range most of the time with only brief forays forward to circle and sniff the kayak, circle the observer, and glide over the food. They were extremely sensitive to whether or not the observer was looking at them and would come for a close look when her head was above the surface, but accelerate beyond visual range when she looked at them again. Occasionally a shark snatched a scrap and accelerated away with it, but it was not until the fifth session that the three residents with ranges there first approached in Triangular formation, to openly investigate the observer and kayak and then to take the food.

Once habituated, when the fish scraps were placed on the sand, the blackfins circled slowly through the area and approached individually to glide above the food. Then, one would seize a piece and accelerate away with it, shaking it to remove a bite, with several individuals following. When the scrap fell, it was swept up by another blackfin, and energetically shaken again. Thus, it was passed from one shark to another until it was gone or dropped in the coral. But this was not the best strategy because while the blackfins were thus occupied, often the fish and nurse sharks took the rest of the scraps. The blackfins would have benefited more had each one taken its own piece of food.

With the passing of time, more blackfins learned of the weekly sessions, including those that ranged up-current, and gathered at the site when they heard the kayak approaching across the lagoon. A pair of male sharks joined the females at times as did juveniles > about 70 cm. Individuals did not avoid each other, nor display a need to preserve an inter-animal distance or 'personal space' (Evans & Howard 1973). They often touched, no shark 'Gave way' (Myrberg & Gruber 1974), and they presented neither aggression nor competition. Video 1 shows 15 minutes of feeding session No. A304, starting at T=9 minutes. The smooth locomotion, velocity, and directional changes typical of the species are shown in the site environment. Details are named in subtitles (Porcher 2022).

The smallest juveniles would usually wait until the adults had dispersed before coming to eat, but they did at times take food when the biggest females were present. Those adults treated the small juveniles the same as other conspecifics.

The residents did not attend all the sessions, and sometimes came too late to eat. On occasion, the gathering of blackfins socialized and ignored the food. Juveniles did not pause in their wide-ranging travels because of the food; residents left for months at a time; and visiting blackfins did not stay in the area because of the sessions. Their long-term roaming appeared unaffected by the weekly feeding. When hungry, predation seemed easy for them.

3.1. The blackfin community

The numbers of residents are summarized in Table 2.

Table 2. The numbers of female, male, and juvenile blackfin residents in each section. The more detailed record of Section A terminates in August 2003, when intensive finning of the reef sharks began, unnaturally skewing the numbers. The sections give only an approximate idea of the home ranges, which were margined by landmarks, not lines. The numbers of juveniles in the eastern end, close to a major nursery where 100-200 pups entered the world each year, were too numerous to identify all of them with certainty.

	Section A					Section B	Section C	Section D	Section E	Papetoai
Year	**1999**	**2000**	**2001**	**2002**	**2003**	**00-03**	**01-02**	**01-04**	**2004**	**2002**
females	11	12	18	18	21	17		27		13
males	3	3	3	2	4	5		4		0
juveniles	25	30	24	24	20	21	0	-	-	15

 doi:10.20944/preprints202208.0139.v1

The current parted to flow either east or west at a point just east of the observation site in Section C, and this partition apparently divided the residents. Some of the female blackfins seen in Section C also ranged throughout the eastern half of the lagoon, while others were only seen in the western half. The area around the observation site in Section C was 4 – 5m in depth, instead of the usual 2m on average elsewhere, and consisted of large, widely spaced patch reefs. No juveniles, even older ones, were ever seen there, and neither was a resident female identified. Those attending the sessions there appeared to be just roaming by. This was especially curious because by the time the sharks in Section C were identified, commercial shark feeding tours had been held there almost daily (opposite a new hotel) for more than a year. For this reason, the cells under Section C in Table 2 are split, accordingly.

The sharks identified in the Papetoai lagoon were a different community. Only one female identified there, the one ranging in the extreme east, was seen in Section A, two times in different years, suggesting that the blackfins rarely if ever crossed the bay.

The lagoon residents were maintained by maturing juveniles; some that survived to adulthood established a home range there during the year before they matured (at about 4 years old). In spite of the feeding sessions, adults did not move in from other regions.

The females were larger than males. Mourier *et al.* (2013) found that the males measured 48 – 139 cm and the females 48 – 157 cm in total length on this island. Stevens (1984) and Papastamatiou *et al.* (2009) found that they were smaller on Palmyra Atoll and Aldebra Atoll, yet Mourier's study was done after the oldest and largest sharks in the study lagoon had been finned. Therefore in that study young adults were measured, who had been in the protection of the lagoon during the shark finning between 2003 and 2006, after the larger, older females under observation had been removed with almost all of the other adults. It is possible therefore, that on Mo'orea, blackfins that attained old age were larger than those that Mourier *et al.* (2013) measured.

With the notable exception of a few males inhabiting the lagoon, the male blackfins roamed the outer slope of the barrier reef, while the females and juveniles occupied the lagoons. Each female spent most of her time in a preferred area called a *home range* approximately 0.5 km across. Individual differences in roaming patterns blurred any clear definition of this range, however landmarks, such as barren regions, the quality of the coral patch reefs, and the lagoon's borders, were factors in defining them. Females ranged almost exclusively along the outer third of the lagoon, possibly because the water there was cleanest. Closer to shore, a high fraction of the coral was dead and the water was polluted by agriculture, run-off, and septic tanks. Old-timers reported that long ago, however, blackfins came to the shore to benefit when they cleaned their fish catch.

The males were less attached to a home range than the females. Those ranging the outer slope visited the lagoon only during the reproductive season, between November and March (Porcher 2005), while the lagoon males regularly, if infrequently, attended the sessions throughout the year. Some appeared every few months as if on a circuit. It was unusual to see a male lagoon resident in the company of the males from the outer slope when they visited. The lagoon males were seen together at times; there were companionships among them.

Though site fidelity remained strong as the years passed, no evidence of aggressive territoriality was observed.

The ocean dwellers were paler in colour—gold, bronze, or ochre—while the lagoon males were dark brown or grey from suntanning in the shallow water. This colour difference was an important indicator of whether a blackfin spent most of its time on the fore-reef or back-reef.

Pups appeared between September and February (Porcher 2005) in nurseries at both ends of the barrier reef. After about 6 weeks, they began to explore the vicinity in cautious groupings. For their first 3 years they took refuge in the shallow regions of thick coral scattered throughout the lagoon (*Galzin & Pointer 1985)*. As they grew, they ventured into deeper areas but were always ready to flee back to shelter. When they attained approximately 70 cm, they began to mingle with the other blackfins in the lagoon, but even then,

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

they remained with juveniles of their own age and avoided its deeper and more barren areas.

Figure 3 shows the changing silhouette of a growing female blackfin.

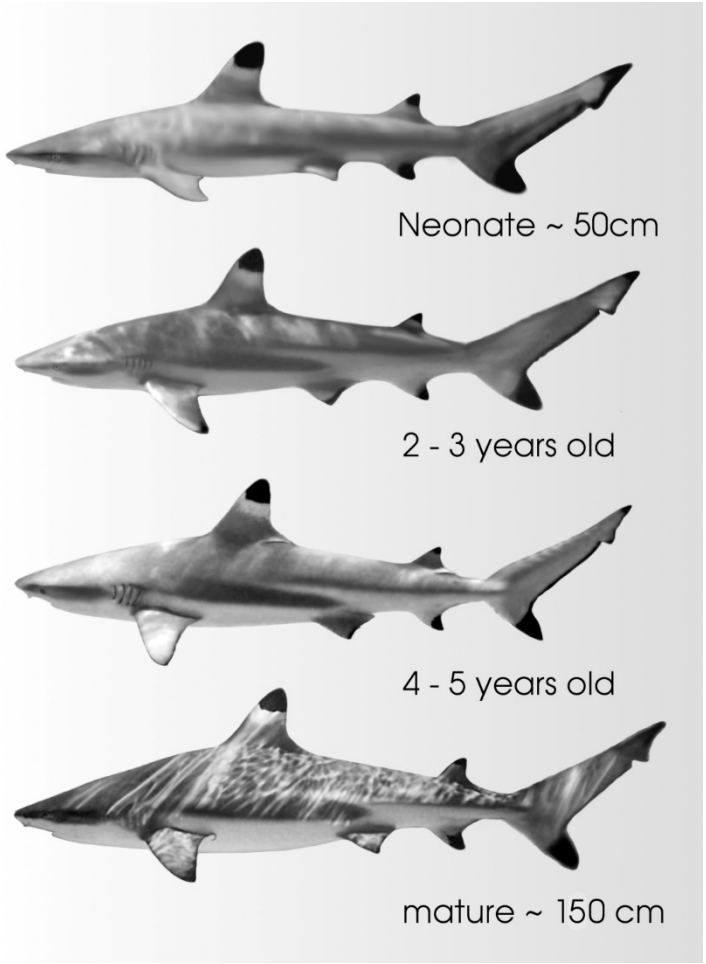


Figure 3. Growth of female *C. melanopterus.*

Attendance at the feeding sessions by the growing juveniles suggested that they did not stay in one region long-term as the adults did. Sometimes they were seen again and often they were not. Only rarely did an identified juvenile return after an absence of about two years and establish its home range in the area. That the juveniles could be travelling to other islands (Mourier & Planes 2013) has emerged as an explanation for these observations.

3.2. Ethogram of short-term behaviours

The following 35 actions were displayed by *C. melanopterus.*

3.2.1 Locomotion

3.2.1.1 Normal Locomotion

Normal locomotion is the usual way of advancing. A rhythmic undulation passes from head to tail like a heart-beat, resulting in forward motion which is guided by the fins and the attention of the shark as it turns in its intended direction. The angle of arc of the head varies with velocity. Figure 4 shows this undulation which is also displayed in Video 1 (Porcher 2022).

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

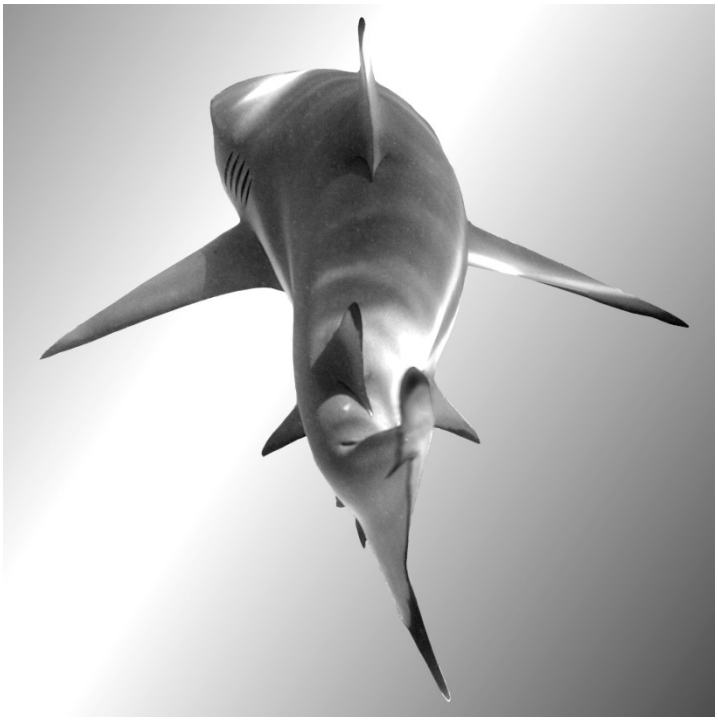


Figure 4. Normal Locomotion.

In the shallow lagoon the blackfin travels in mid-water, from which it ascends or descends at will. In the ocean, *C. melanopterus* tends to stay within view of the ocean floor.

3.2.1.2 Circling

The blackfin circles something of interest. Since it cannot cease Normal locomotion to look at something, circling is its way of staying in one location.

3.2.1.3 Ranging

Using Normal locomotion, the shark follows a sinuous path through its home range (and at times the surrounding region), following roughly oval pathways. It was repeatedly observed that each new loop is oriented in a different or opposite direction from the last one, so that the route forms rough figure-of-eights and cloverleafs when viewed from above. In that lagoon, each loop took about ten minutes to complete, which may be due to the width of the band of cleaner water along the back-reef. When travelling to a specific place or region, the blackfin might take a more direct route.

3.2.1.4 Bolting

The shark accelerates out of visual range. This is the usual fear reaction as shown in Video 2 (Porcher 2022b).

3.2.1.5 Gliding

Gliding often follows an acceleration, and intersperses Normal locomotion. The blackfin's horizontal undulations almost cease as it moves forward under its own momentum, its fins in the normal position. Gliding is connected with deceleration, and often occurs when something has caught the animal's attention so it pauses before possibly altering its trajectory.

3.2.1.6 Explosive glide

In an aroused state, the shark accelerates suddenly, then glides for several metres, often arcing around an object of interest. The pectoral fins might be lowered during this action as seen in Figure 5. The Explosive glide was first described in bonnethead sharks by Myrberg and Gruber (1974).

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

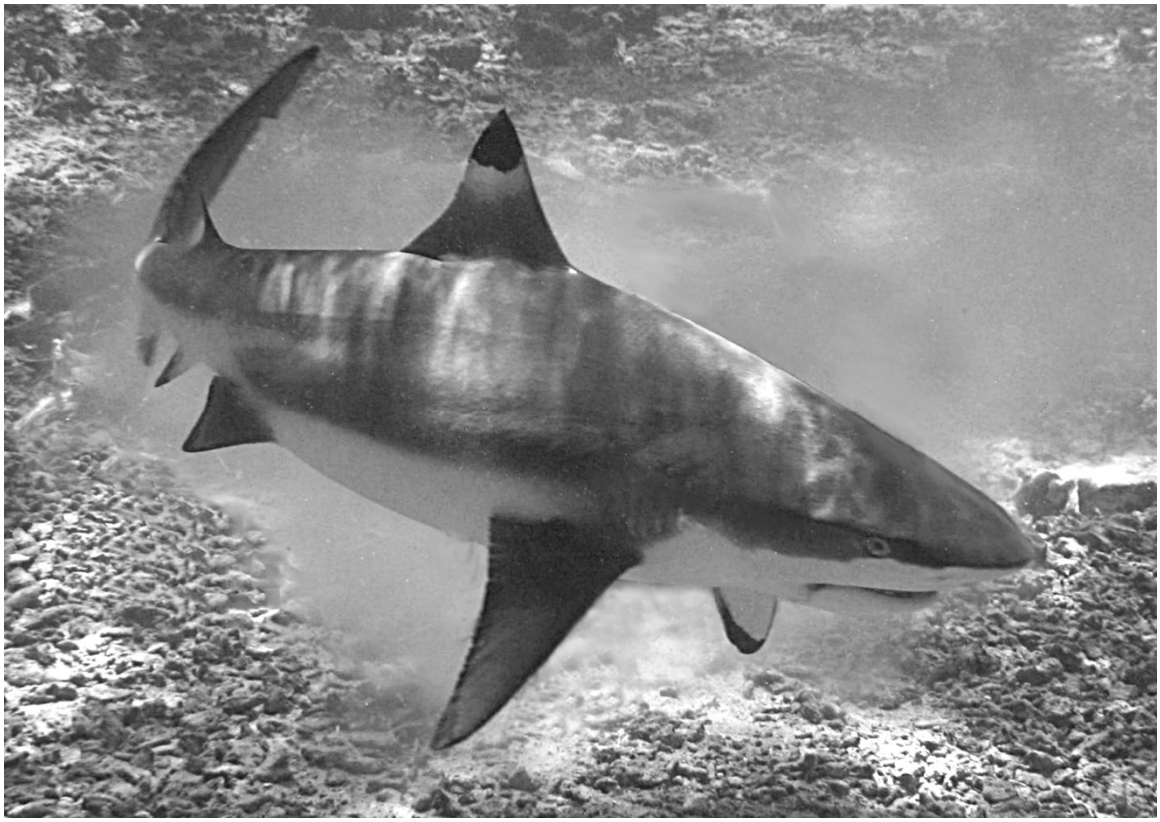


Figure 5. A female blackfin in an Explosive glide.

3.2.1.7 Braking

The shark turns its dorsal fin perpendicular to its motion as it slows, as shown in Figure 6.

Figure 6. A shark Brakes, turning its dorsal fin at right angles.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

When in Search mode in the observation site, the blackfins moved around each other, subtly adjusting the position of their fins to guide their trajectory as seen in Video 1.

3.2.1.8 Breaching

Blackfin sharks breach by speeding vertically through the surface from below. In the lagoon the water was about 2 m deep and they began their upward acceleration by turning just above the sand.

The first time the sharks Slammed the observer's kayak, they Breached through the surface after striking and saw that their scraps were inside it. The next time they Slammed and Breached, they leaned towards the fish scraps and snapped at them, managing to grab some. Then, and on subsequent occasions when they were in an aroused state, they Breached to access the scraps and the others present followed their example. Then they would nose around the stern with their heads above the surface, to see if there was a piece visible over the gunwale that they could take without leaping. Once this behaviour was initiated by one shark, it was copied by the others present, and was practised afterwards by the sharks in that gathering. This happened with two different sets of sharks on different occasions, showing their ability to learn from observing each other, which is called *social learning*.

3.2.1.9 Resting

The diurnal rhythm of the blackfins was at its peak of activity during the period of low light around sunrise and sunset, when the sun was at an angle of less than 45°. As the sun rose higher they went to a place where the landscape was relatively open and free of obstacles to cruise slowly, a few centimetres above the sea floor, most with one or more companions. They were much less alert at such times, to the degree that they could be surprised. Their level of activity during the night could not be observed.

A wide region of coral rubble between Sections A and B was deeper than average and used for Resting by blackfins with home ranges on both sides. At times, some of the females went to deep water off the fore-reef to cruise, Resting, in mid-water, often not far past the turbulence of breaking waves. There, locomotion was also unimpeded, and they were out of the brilliant shallows of the white sand lagoon. They became active again in the late afternoon, after the sun descended past approximately 45° above the horizon.

3.2.2. Eating-related behaviour

3.2.2.1 Search mode

The shark moves just above the sea floor, often changing direction using smooth circles, figure-of-eights, and ovals, while searching for chemical (Klimley 2013) or visual clues. Sometimes it lowers the pectoral fins to the sand for stability; the pectoral fins are also lowered when making tight turns. This circling can be done over a small region and involve nearly continuous turning, with the shark's body taking the shape of its pathway.

3.2.2.2 Sniffing

The shark pauses and remains almost motionless in mid-water, raising its snout to Sniff the current. This was regularly observed when blackfins passed through a known scent trail as shown in Video 3 (Porcher 2022c) For example, the blackfins regularly Sniffed the current flowing past the kayak, presumably to learn if fish scraps remained in it. (Drain holes permitted scent to escape into the lagoon.)

3.2.2.3 Suction feeding

When a blackfin chose a scrap, even though it was still 20 cm away, at times it opened its mouth and the scrap was sucked in, as described in nurse sharks (Motta *et al.* 2002). The shark expands its buccal cavity and protrudes its jaws, creating a suction that pulls the food in. Then, as the parts return to their normal position, the decreasing volume inside the mouth forces the water out through the gill openings as shown in Figure 7.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

Figure 7. A blackfin using suction feeding, forcing water out through the gill openings.

3.2.2.4 Palatoquadrate adjustment

Blackfins often protract the *palatoquadrate,* the upper jaw, while eating, as shown in Figure 8. The palatoquadrate is not fused to the brain case (Moss 1972) and the jaws are supported instead by cartilaginous elements, the *hyoid elements*, which brace them against the cranium when the shark bites down. This arrangement permits the jaws to move independently from the rest of the shark's head.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

Figure 8. A juvenile male blackfin, with his palatoquadrate protracted, holding a fish scrap.

After eating, blackfins were sometimes observed paused, alone in the coral, opening and closing their jaws in an apparent effort to readjust them.

3.2.2.5 Head shake

On taking a scrap too big to swallow, the blackfin shakes its head several times along the horizontal plane while accelerating and rising into the clearer area above the coral. As a result the teeth saw out a mouthful of food. The only other time shaking of the head was observed was incidentally in an effort to shake loose a remora.

3.2.2.6 Predation

The blackfin makes a sudden, targeted acceleration, often vertically, to snap up a fish. Conspecifics are attracted and go into high velocity Search mode. Predated fish release what has been termed a "fright" substance that warns conspecifics of danger (*von Frisch 1941)*. This might help explain the extreme reaction by blackfins in the vicinity, to a conspecific's act of predation.

3.2.3. Grooming behaviours

3.2.3.1 Chafe

A blackfin will flip onto its back to wriggle against the sand, or whip its side against a sand bank to free itself of a remora or ectopic-parasites. It will also position itself to Chafe its ventral surface on worn, dead coral as shown in Figure 9.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

Figure 9. A young female blackfin Chafes the ventral surface on worn coral. The images are in a series less than a second apart.

3.2.4 Investigative behaviour

A state of vigilance characterized the actions of the blackfins, yet they were naturally curious. This combination generated a variety of tactics which they used to remain hidden while investigating things they were curious about.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

3.2.4.1 The Approach

At the limit of the visual range, the shark passes into view and out again. A few minutes later it makes a closer pass. It repeats this pattern, approaching more directly each time, until, if interested enough, it might make a direct, close approach. The pattern, which varies with circumstances and the individual, is illustrated in Figure 10.

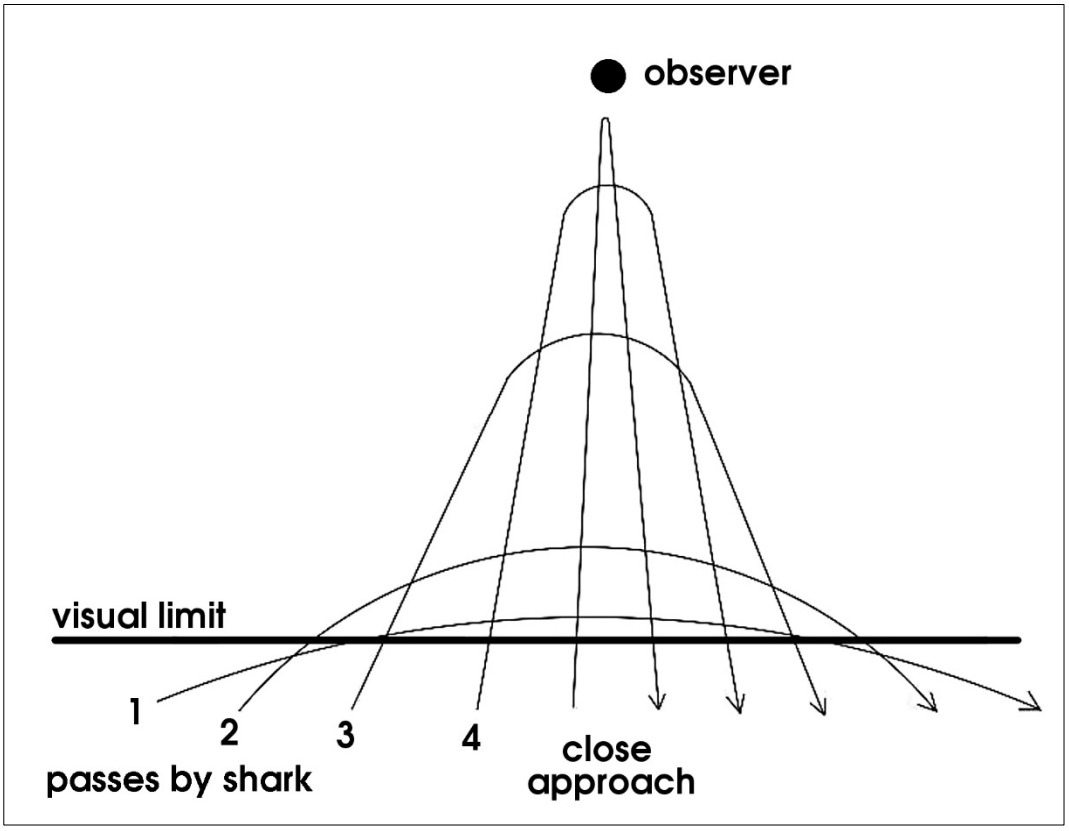


Figure 10. The approach pattern of C. *melanopterus*.

3.2.4.2 Looking

The shark looks closely at an object of interest as shown in Figure 11, and in turning towards it, begins to Circle.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

Figure 11. The blackfin looks and fixes the closest eye upon the object. As it turns in that direction, it begins Circling.

Visiting blackfins would often fix the observer with the eye with which they had first seen it, resulting in Circling. Sometimes it would Circle for some time, always showing the same side. This was a serious problem on shark encounters without food to distract the animal's attention. If the dorsal fin could not be drawn on both sides, the identification would remain incomplete, and rare visitors were unlikely to reappear again for many months.

Efforts to manoeuvre to see the other side of the shark were countered by the animal, for it appeared reluctant to take that eye off the observer for even a moment. After circling enough, it would turn and accelerate directly away, the other side of its dorsal fin never showing.

3.2.4.3 Following

The shark Follows something of interest, perceiving what is taking place from beyond visual range. This was exemplified on observation excursions through the lagoon. Certain residents would Follow, sometimes for hours, remaining hidden beyond visual range except for the occasional pass into view, usually about once or twice per hour, depending on the individual. It was possible to see which blackfins were Following by waiting, unmoving, until they came into view, usually Following in a group. Blackfins doubtless Follow other species beyond visual range.

3.2.5 Social behaviours

Visiting blackfins regularly appeared, singly or in groups of up to six. Occasionally, one of the lagoon males accompanied a travelling group of females, typically appearing 1 – 2 minutes ahead of them. The resident females would merge with the visitors, accelerate, and in a ragged formation they would soar through the vicinity. At times, the feeding sessions seemed more important as an opportunity to socialize than to eat. Many travelled year after year with companions of the same gender, though others always appeared alone.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

During the reproductive season, males frequently arrived at the lagoon sites from the fore-reef as night fell, also in groups of up to six individuals, to seek an opportunity to mate.

3.2.5.1 Nose-to-tail following

One shark follows another with its snout within 30 cm of the leader's tail. Resident female blackfins socializing with female visitors were observed to follow their scent trails. Gradually, the blackfin under observation would catch up with another female until her nose was at the other's caudal fin. Often the two moved on in Parallel for several seconds, then the first individual would resume her arcing pathway, catch up with a different female, and briefly accompany her.

The blackfins were locating other individuals by intercepting and following their scent trails. While it is also likely that they were aware of others in the vicinity using the lateral line sense, the way they caught up with others from behind suggests that chemoreception was the primary focus in this context. Figure 12 shows a female catching up to another as described.

Figure 12. A female blackfin catches up to another after following her scent trail.

3.2.5.2 Circling-head-to-tail

Two blackfins follow each other Nose-to-tail with the result that together they pursue a circular pathway. This was often seen in the smaller juveniles, but rarely in adults.

3.2.5.3 Follow-formation

Follow-formation presented as Nose-to-tail following by several blackfins simultaneously, usually by sharks of the same gender. It was especially notable in the case of certain visitors. For example, when Shark #24, an elderly female from Section B, visited Section A, she always attracted attention from those present and they Followed her. On one occasion, she performed a U-turn in a narrow coral canyon, and all six of her followers did too. When visitors were present, many instances of Follow-formation, most not involving more than two or three sharks, formed and dissolved as the gathering of blackfins moved swiftly and flexibly together.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

The blackfins also assumed Follow-formation when confronted with a novel scene. The best example to illustrate this behaviour occurred when a visitor wearing scuba gear accompanied the observer. The blackfins accelerated beyond visual range and for ten minutes no shark appeared. Then Sharks #3 and #109, both of whom had shown leadership tendencies in many other situations (Guttridge *et al.* 2011; Porcher 2021), came in Parallel through the coral canyons with the rest of the three dozen blackfins in Follow-formation behind them in two single-file lines. The leaders did a fast Close approach to the scuba diver and he was enveloped in a swirl of swiftly moving sharks—he fell over backwards. The sharks' action appeared to be an attempt to intimidate, and indeed, the diver, though an experienced dive club owner and shark diver, *was* intimidated.

3.2.5.4 Triangular formation

When confronted by a novel situation, blackfins will also approach in Triangular formation to investigate—one in front and two, one on either side, behind.

3.2.5.5 Swim-bys

When meeting in the lagoon, companion sharks and acquaintances, mostly individuals of the same gender and approximate size, often perform a Swim-by, as named by Sperone *et al.* (2010). Examples are shown in Figure 17 and Video 4 (Porcher 2022d).

Figure 17. Two juvenile companions 'Swim-by' each other.

3.2.5.6 Parallel

When two blackfin acquaintances meet, they will approach each other and swim in Parallel for a few seconds before going on. This is illustrated in Figure 18 and Video 4.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

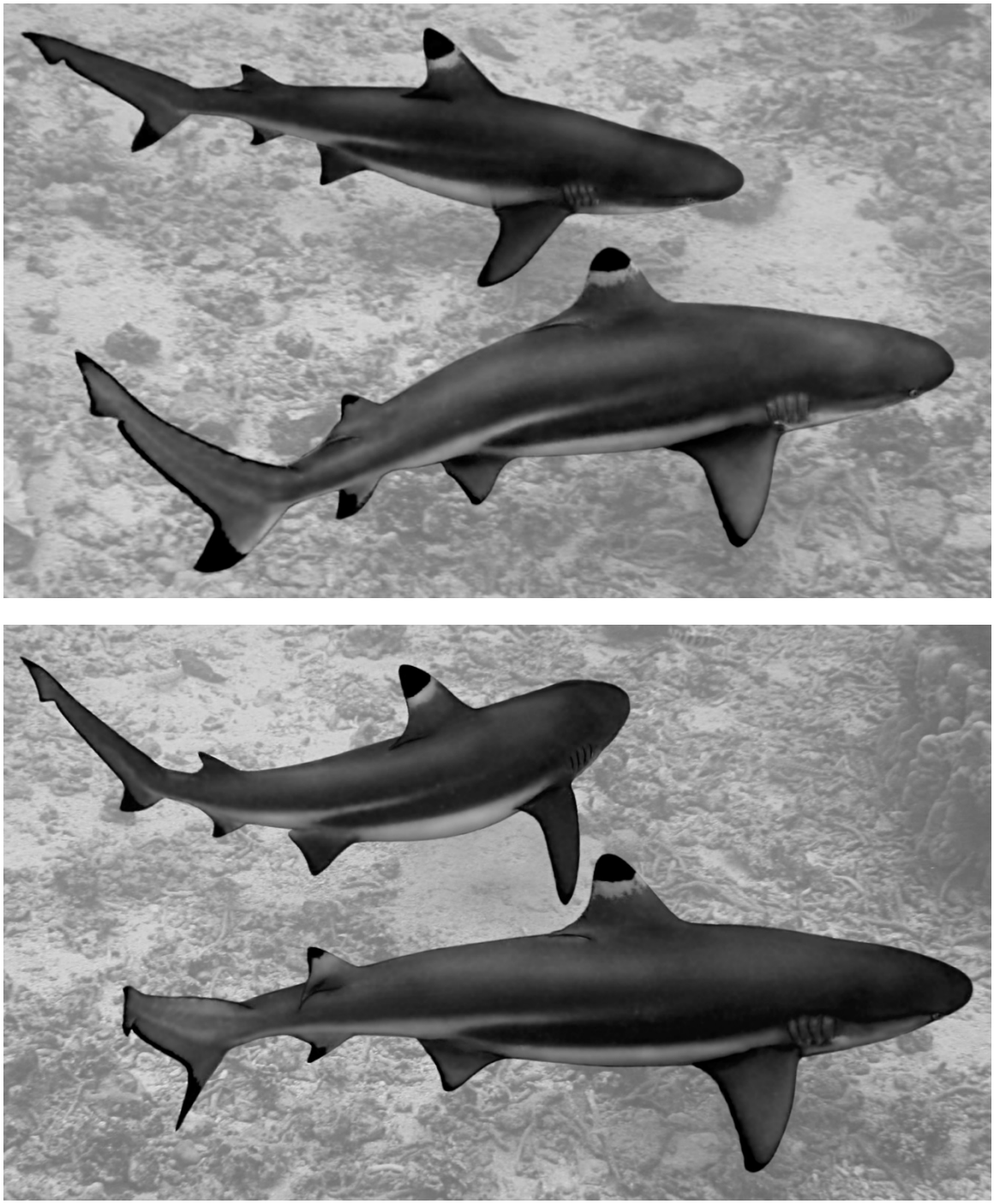


Figure 18. Two female residents turn towards each other and briefly swim in Parallel on meeting.

3.2.5.7 Travelling with companions

The blackfin travels with one or more companions, usually out of visual range. Blackfins appeared to remain in loose contact with each other using chemoreception, hearing, and the lateral line sense. Their wide circling patterns while ranging, also described by Stevens (1984) bring them repeatedly across the scent trails of other blackfins in the vicinity—not only companions, but others with over-lapping home ranges, and any travellers passing through.

There were places in the lagoon where deeper water and a more open terrain permitted the observation of companions moving through a wide area. They alternately travelled in Parallel, Nose-to-tail, or independently. They followed a pathway of loops and figure-of-eights, and their circling patterns brought them back together time after time.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

At times, shark pups were easy to watch from above the surface, in the shallows they preferred. They would circle together then arc away to move through the surroundings, always coming together again through their repeating orbits and figure-of-eights. Often they circled Head-to-tail. This seemed to be the general pattern of movement among the adults too, but on a larger scale.

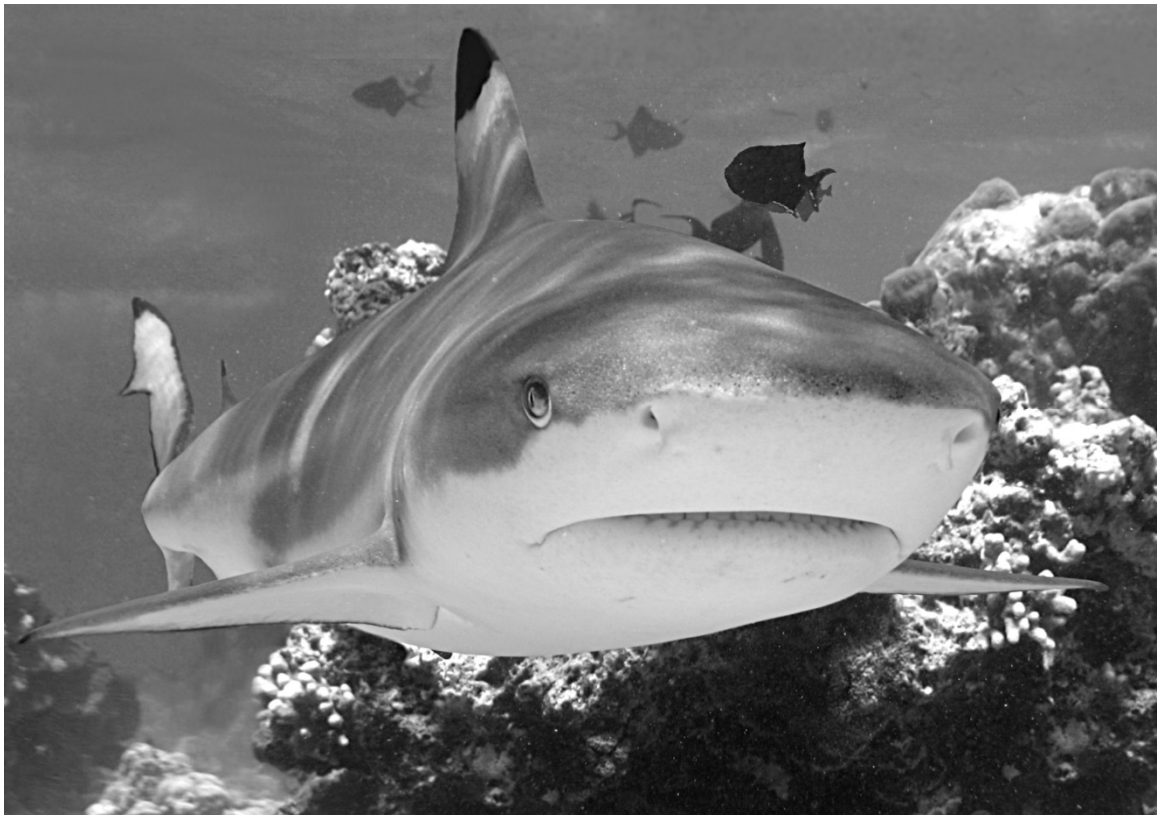
3.2.5.8 Circling together

Sometimes the gathering of resident blackfins circled together around something of interest. Most circled in the same direction, though some individuals circled counter to that—individuals usually presented a directional preference. The preferred direction when circling together was counter-clockwise among the blackfin sharks of the study area.

3.2.6 Interactive behaviour

3.2.6.1 The Close approach

The blackfin approaches the face of another, passing close by, or turning away at an acute angle as shown in the image sequence in Figure 19. It was always done slowly, by several resident females in turn, to the observer on arrival underwater at the observation sites. But it could be done at different speeds, depending on the circumstances and the intentions of the shark.



Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

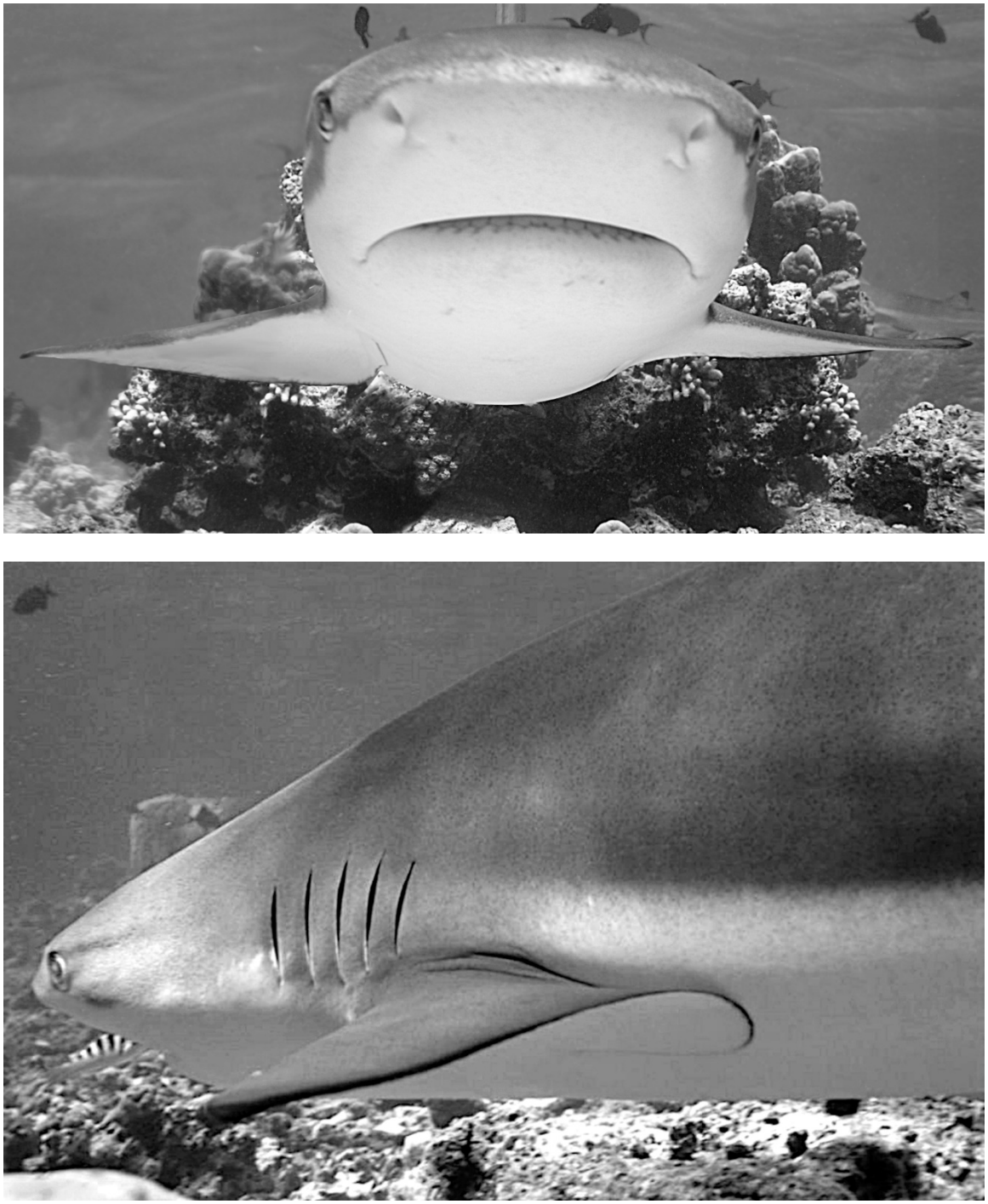


Figure 19. The Close approach.

For example, at the feeding sessions, a blackfin would occasionally make a Close approach to a Javanese moray eel (*Gymnothorax javanicus*), when one came from its hole and approached the fish scraps. The shark appeared to pause at an appropriate distance from the eel, depending on its reaction to the offensive gesture. In this context, the Close approach appeared to be a test of the mettle of the other animal: Would it flee or not?

Another variation was used on Tahitian spear-fishermen, who reported blackfins dashing up to their faces and away again as part of an effort to persuade them to relinquish their fish catch.

3.2.6.2 Cutting across

A companion blackfin decelerates, turns at right angles, and swims across the other's path. This is an indication that the actor wants to stop the ongoing forward motion.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

Cutting across is used flexibly in a variety of circumstances and differently by different individuals. For example, it was done when an accompanying blackfin had reached the limit of its range and was reluctant to go further. Once it was done to the observer when the blackfin wanted the fish scraps she was carrying.

3.2.6.3 Charging

At times, the blackfins charged. One or more advanced at medium to high speed and passed just to one side. A charging shark will often repeat the charge at intervals of a few minutes, and can be followed or accompanied by several conspecifics, often in Follow-formation.

3.2.6.4 Circling charging

In exceptional circumstances, Charging, circling away, and charging again, results in Circling charging as other sharks join in Circling and Charging the offending character and their level of arousal increases. Follow-formation is adopted by many blackfins in the gathering as the pattern develops. After following a few times, some begin Charging alone. A period of an hour is the longest the observer witnessed Circling charging to continue, and the entire gathering of blackfins took part in the action. This behaviour pattern can break out into Slamming.

3.2.6.5 Slamming

The blackfin accelerates towards another and Slams into it. The shark might Slam initially with the shoulder (Porcher 2016), and as its level of arousal grows, it approaches from below and spirals upwards with arched back to slam with the region behind the head in front of the dorsal fin, lowering the pectoral fins just at the moment before impact as shown in Figure 20. Slamming can be done with great force (For details see Porcher 2021).

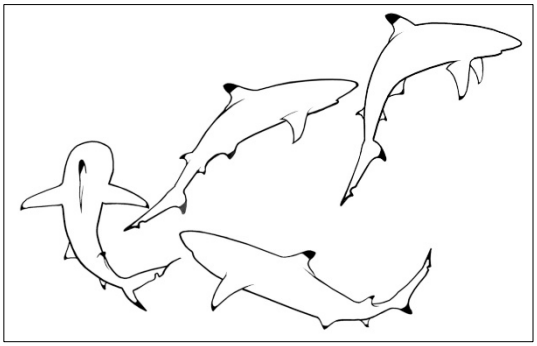


Figure 20. Slamming involves the shark turning beneath the target and gaining altitude while lowering the tail and hunching the back. With the powerfully beating tail pointing straight downwards, it accelerates upwards with speed and force.

These actions were seen in a variety of circumstances. Once a leading shark has begun, the others present will join in, suggesting *emotional contagion* (*Hatfield* et al. *1993). T*he Close approach escalated at times from intimidation to Charging, then Slamming, and involved the entire company of sharks present. On another occasion, three individuals left the other blackfins and adopted Triangular formation to Slam the observer, suggesting *social buffering* (*Kikusui et al. 2006*).

3.2.6.6 Startle response

The blackfin accelerates away from a source of fear while arching its back vertically in a series of rapid jerks. This was commonly seen in juveniles as a reaction to a near-collision with a much larger shark, usually a nurse shark (*Ginglymostoma cirratum),* but sometimes a large female blackfin. The arching of the back results in the tail pointing downwards, which causes the shark to rise into the open area above the coral as it flees. Adult sharks too, would sometimes accelerate away with a few sharp vertical undulations when startled.

3.2.6.7 Shiver mode

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

After fleeing as a result of the Startle reflex, the blackfin is likely to circle back in Shiver mode. Shivers run through its body, and it suddenly twists and changes direction erratically. The restless flicking and twisting can continue for many minutes. This state was presented most often by juveniles after being Startled. Shivering and unpredictable turns were also occasionally seen in adults who appeared in an aroused state. Moving swiftly, while shivering and twitching at times, the animal would make sudden rushes, then whip back around in a tight circle. Shiver mode was a short-term reaction most of the time, but on one occasion an individual remained in Shiver mode for at least 20 minutes, suggesting that it can also indicate a longer-term subjective state of tension, agitation, or fear (Porcher 2022 submitted).

3.2.6.8 Undulating against another

The shark undulates against another body. In this study, after several years, the resident females began undulating against the observer's kayak on arrival in the lagoon as described in Porcher (2021). Initially, the blackfins just undulated against the boat at the surface as shown in Figure 21.

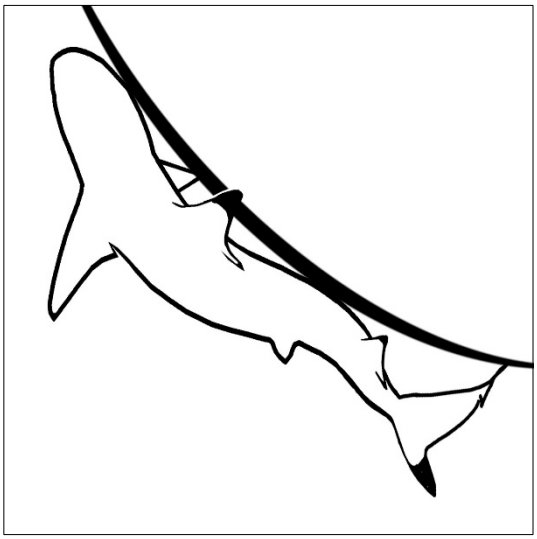


Figure 21. Undulation against another at the surface.

After two episodes, the individuals involved began coming straight upwards from the sand beneath, undulating against the craft, then turning close to 180° to go straight downwards, so that their tails came through the surface as they turned. Several performed this action at once, so that their tails flicked through the surface at the same moment, several on each side of the kayak. This was therefore a different gesture (body language) than simply performing a brief undulation against another at the surface.

Why they would perform in unison, and the circumstances in which blackfins might Undulate against another in their daily lives, are unknown.

The action is shown in Figure 22.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

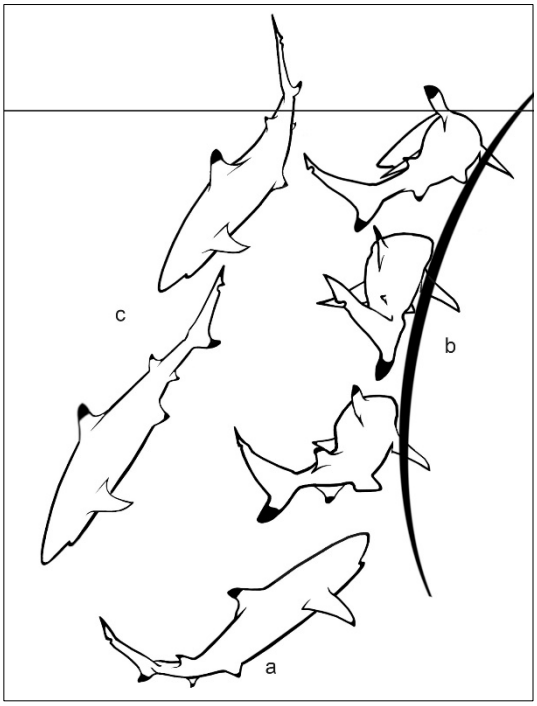


Figure 22. Undulation against another starting below. The line at the top represents the surface.

a) The blackfin turns at the sand.
b) On arrival at the surface it undulates against the other.
c) The blackfin descends.

3.3. Long-term behaviour

3.3.1 Roaming

Adult blackfins circled through their home ranges much of the time but sometimes they left, and in their tendency to travel they displayed great individual differences. Some left their home ranges only for about two weeks for mating and two weeks for parturition, while others were absent for months at a time. The rest presented gradients in between. A blackfin could often be found in the same place day after day, but the next day, it could be in the ocean at that time. Sometimes a lone blackfin would pass the same location at the same time several nights in a row, then disappear for a year. There were some days when the resident females were absent from the study area, and others when they were socializing with visiting neighbours. Sometimes at high noon they were all Resting in a nearby barren region, and on other days, the vast expanse was empty.

The main influences on their wanderings were the reproductive season and the lunar cycle.

3.3.1.1 The reproductive season

Figure 23 shows the ratio of adult visitors and residents at the sessions for each month. Only the count of the first three years in Section A is used, prior to the start of shark finning in August 2003. 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.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

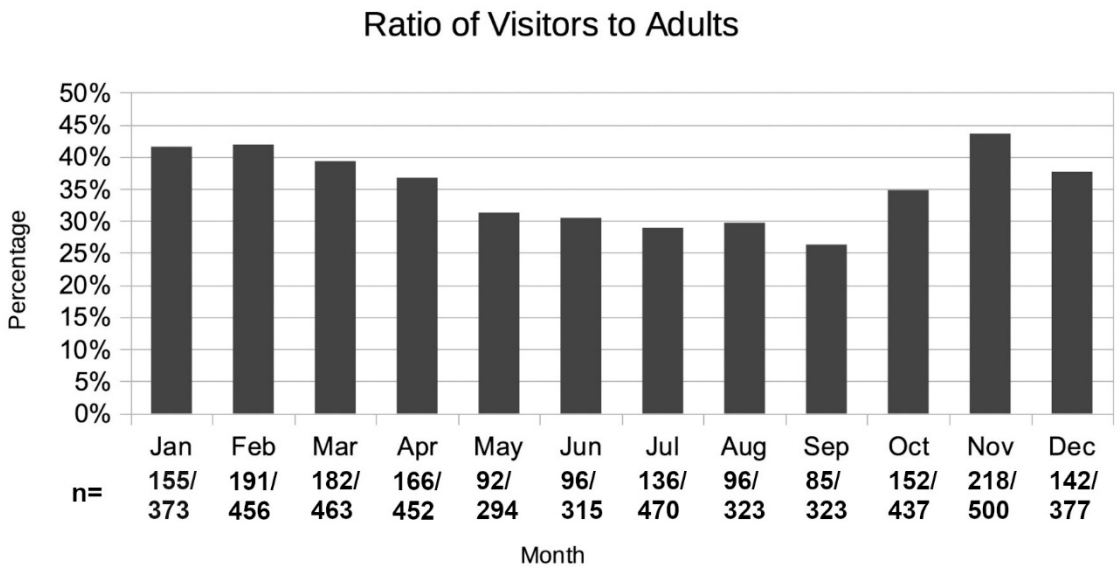


Figure 23. Percentage of visitors each month.

Figure 24 shows mating and parturition recorded in each month. A comparison with Figure 23 illustrates the influence of the reproductive season on the travels of the blackfins.

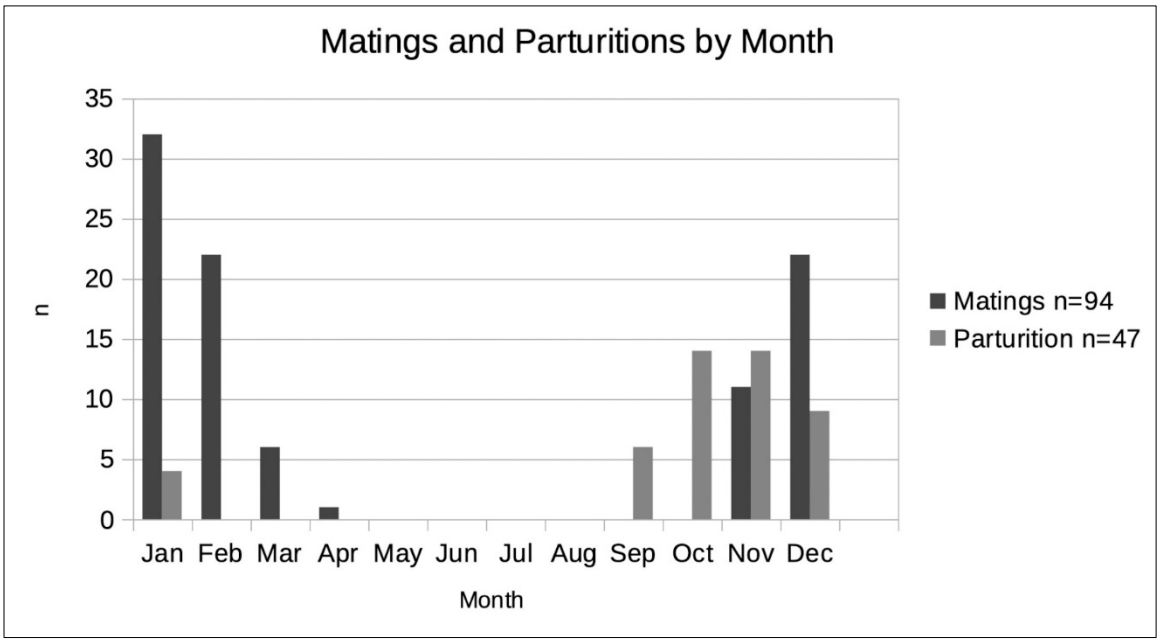


Figure 24. Mating and parturition for each month.

3.3.1.2 The lunar phase

The tendency of C. melanopterus to travel in correlation with the lunar phase is illustrated in Figure 25. Only the first three years of sessions in Section A are counted before the shark finning began. The higher proportion of visitors during the dark of the moon, as well as the full moon, is evident.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

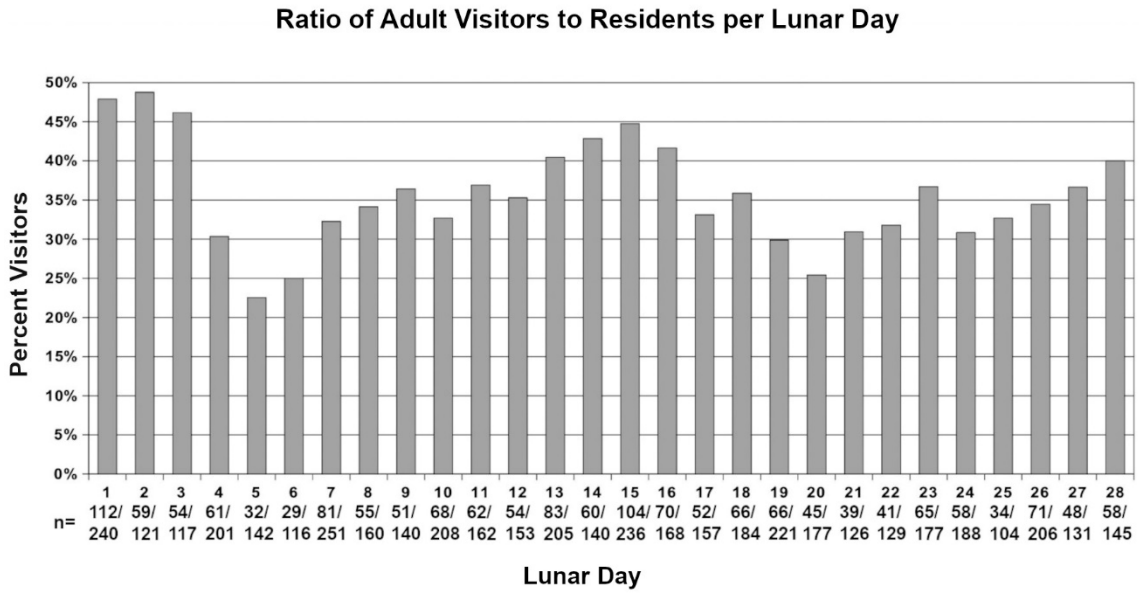


Figure 25. The percentage of visitors on each lunar day graphed. Fifteen represents the full moon.

Once every several months there was an unusual session attended by as many as twice the usual number of blackfins and numerous visitors. These unusual sessions were marked by high velocity socializing in which large numbers of sharks participated, and nearly always coincided with the light or dark lunar phase. On other occasions, during the full moon period there were fewer sharks present because the resident females had left, leaving only the juveniles and one or two of the lagoon males.

The males inhabiting the lagoons were normally dark grey in colour, but on returning from their travels after the reproductive season, they were considerably paler, indicating that they had spent significant lengths of time in the ocean during their absences. Since the female sharks are in the lagoons, and these males could have circumnavigated the island while remaining in the lagoons had they wished, such long travels through the ocean suggest that they left the island, likely to visit others in the surrounding archipelago (Mourier & Planes 2013; Vignaud *et al.* 2013; Schlaff *et al.* 2020).

3.3.1.3 Other influences

On the rare occasions when two feeding sessions were held on consecutive nights, in general, most of the sharks attending the second were those that had not come to the first. There was a tendency to leave the area after a feeding session, suggesting that roaming was not necessarily associated with foraging.

During storms, oceanic waves transformed the lagoon into a river. The big females, particularly when they were pregnant, were relatively ungainly in heavy current and left. Probably they took refuge in the deep water off the fore-reef because of the extra energy required for navigating the complex coral environment in such strong turbulence. The slender juveniles were the least willing to leave the protection of shallow water and being small, they managed the current more easily. When the oceanic swell topped 2.5m, they were usually the only blackfins to be found in the lagoon.

When a company from Singapore 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 home ranges until the same period of the following lunar cycle. This tendency was also mentioned by the native Tahitians, who had wanted their sharks neither fished nor disturbed (Johnson 1978). The tendency to leave the area after some of their number were fished was also observed in tiger sharks in the Bahamas (Abernethy J pers. comm. 2016).

During the period of July 23 to August 5, 2002, all the blackfins under human observation on Mo'orea Island disappeared (Porcher 2022 submitted) including the smallest

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

pups from their shallow refuges among the coral. In spite of an intensive investigation in search of the reason for the evacuation, no explanation was found. Something not monitored by the local authorities—possibly a magnetic field anomaly—might have disturbed the sharks, causing the entire population to vacate the shallow waters around the island. Not all the adult residents, and very few of the pups, returned.

3.3.2 Socializing

Socializing was important to the blackfins. Though they appeared to be alone much of the time, they were actually in loose contact with others of their species via the lateral line and olfactory cues which they intercepted as they circled through their ranges. They were frequently found in dyads, triads, or larger gatherings, especially while Resting in the middle of the day.

There was much high velocity interaction when visitors arrived. Residents and visitors would soar through the surroundings in pairs and small groups. An old shark who normally never accelerated would suddenly shoot vertically, shake off her remora, and streak out of sight so fast that the eye could scarcely follow her, Followed by many others. Then she and her entourage would rocket back through the scene and disappear in the opposite direction. At times, one to two dozen sharks—females, males, and older juveniles—would accelerate away and return from another direction, moving in a ragged, elongated group with an inter-animal distance of 0.5 to 1m as shown in Figure 26.

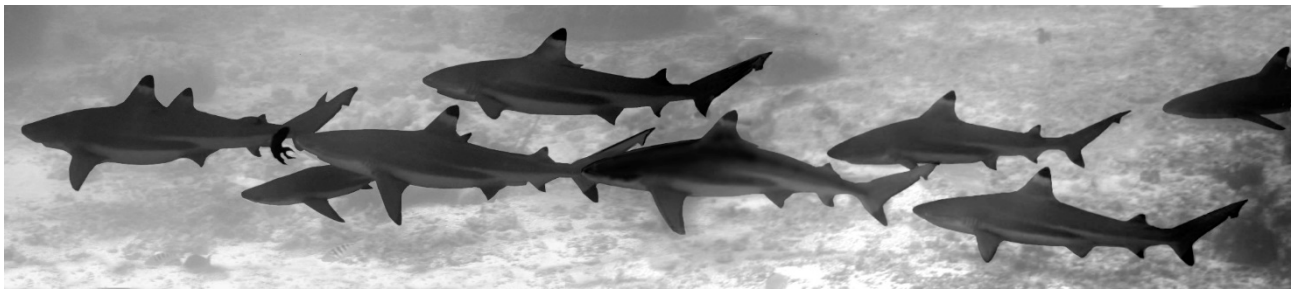


Figure 26. Socializing blackfins.

Shark #24 usually arrived after nightfall, long after the fish scraps were gone. She was often observed down-current, socializing, without having appeared in the feeding site. Apparently she had passed by for social reasons only.

Groups of visitors usually arrived in correlation with the light or dark lunar phase and stayed in the region for about two weeks—until the next lunar phase peaked—then travelled on. It was observed on several occasions that some of the resident female blackfins left their ranges for a few days to accompany these groups along the lagoon when they left.

Many of the blackfins travelled with the same companion long-term—another individual of the same gender and about the same size. Companionships appeared to be between sharks with overlapping home ranges. Due to the way companions travel out of visual range much of the time, companionships were most evident to a visual observer in rare visitors. Figure 27 shows the visits of four pairs of companions.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

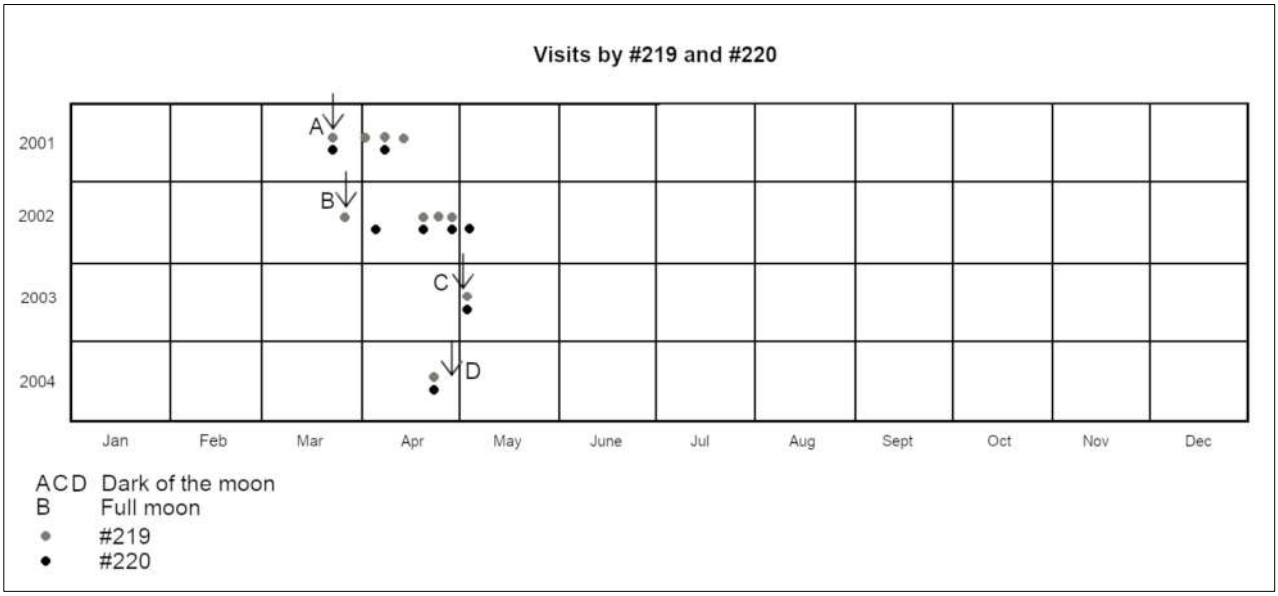


Figure 27a. Sharks #219 and #220 both showed signs of ageing. Their visits corresponded strongly to the lunar phase. Each dot represents an appearance at a session and the arrows point to the precise time of the lunar phase noted in the legend.

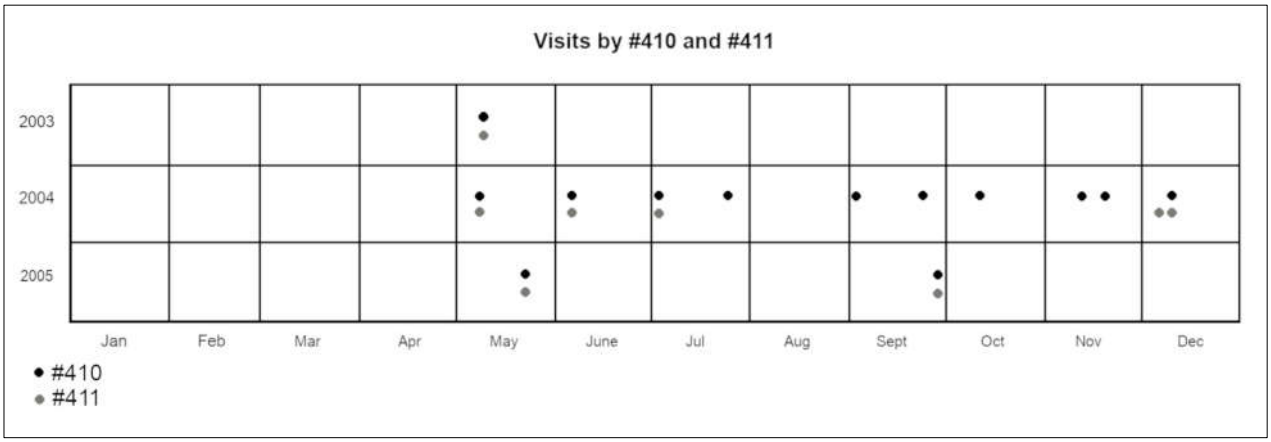


Figure 27b. Sharks #410 and #411 tended to arrive as the full moon phase was passing. In 2004 their first three visits took place a moon apart. Each time they arrived after sunset and each time No. 410 appeared first and circled the observer clockwise. Two minutes later, #411 came into view and circled the observer counter-clockwise.

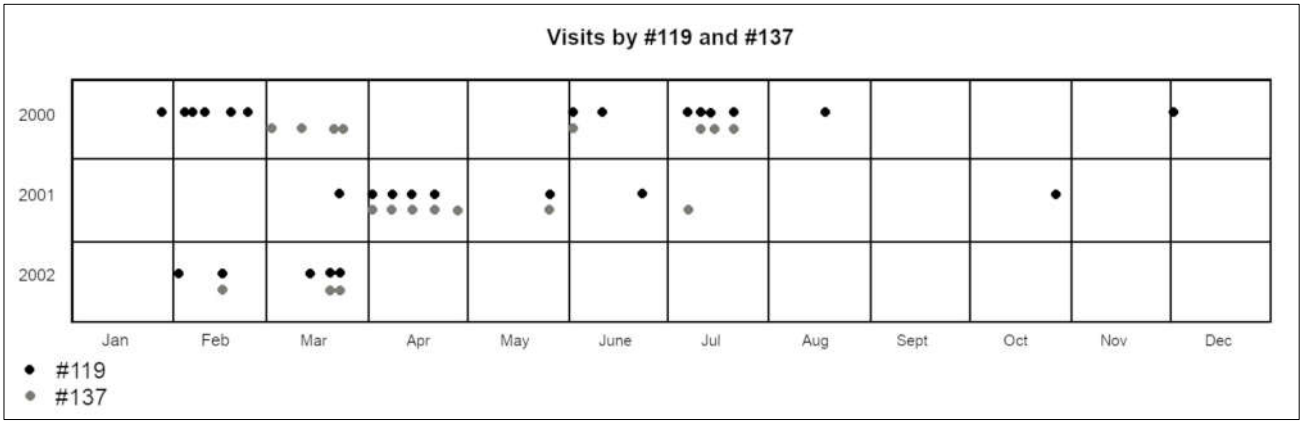


Figure 27c. Sharks #119 and #137.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

Shark #119 was very large, old, and nearly black. She had rashes of white speckles and a large white fleck on each side of her head. Her skin was rough, her dorsal fin unique. She glided in as night fell on six consecutive sessions. But as it grew dark on the seventh session, a #119 lookalike, including the white flecks on her head, appeared. It seemed certain that there was an association between them based on appearance alone, but three months passed before they suddenly arrived two minutes apart, #137 following, apparently in #119's scent trail. When shark #119 disappeared, #137 began travelling with a different companion.

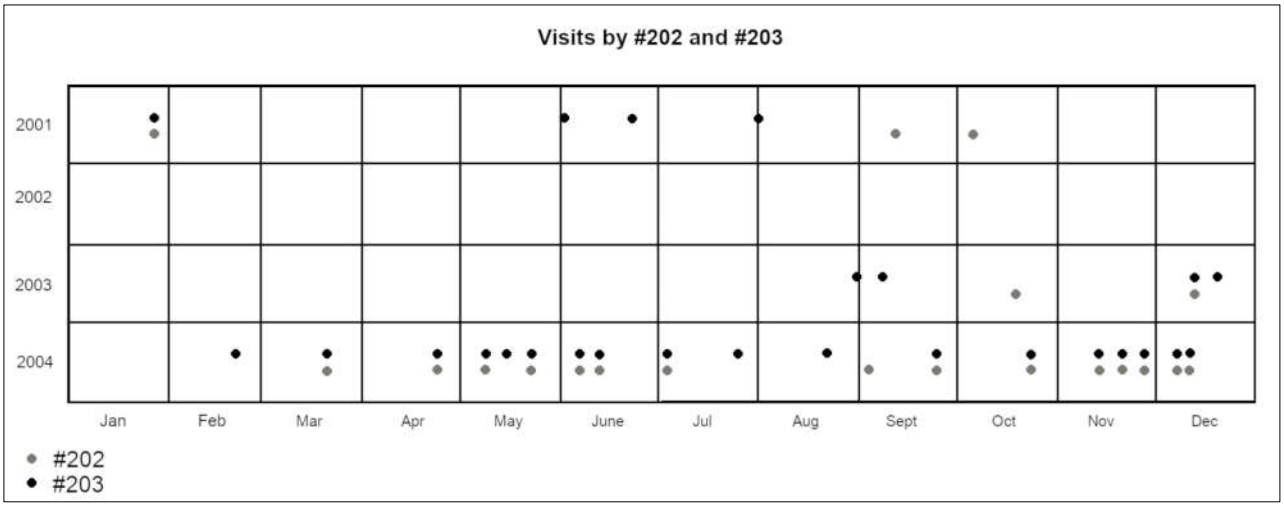


Figure 27d: Sharks #202 and #203 often travelled together, but at times they roamed separately.

On discovering a feeding session for the first time, visiting blackfins would tend to remain beyond visual range unless there was a group present that they could join. After a long period of passing intermittently into visual range, these newcomers would usually approach in the company of one of the residents, often in Triangular formation, again suggesting social buffering (*Kikusui et al. 2006*).

The resident who brought the visitors to the session had often come at the beginning and left, yet returned up to an hour later with the newcomer(s), apparently with the intention of showing them the novel event. This was often done by Shark #3, a middle-sized female with a tendency to leadership in a variety of situations.

3.4. Signs of Cognition

The investigative behaviours of C. melanopterus result from the assimilation of sensory information from acoustic, vibrational, visual, chemical, and electromagnetic field sources with the neural system, and result in the shark making swift decisions to act appropriately in accordance with the circumstances. *Decisions, which involve attention, learning, memory, and the integration of experience* (Overmier & Hollis 1990) *are an indicator of cognition* (Wang et al. 2004). C. melanopterus' ability to focus on events from beyond visual range provides basic evidence of the species' capacity for long-term attentional focus, as does their practice of Following another individual for long periods. Learning in a variety of species of sharks is already well documented (Guttridge et al. 2009).

3.4.1 Memory

The ability to make appropriate decisions is dependent on being able to remember events in the past on which to base those decisions, as well as the capacity to learn (Guttridge *et al.* 2009). Many actions by different individuals suggest that the blackfins remembered events for long periods and were aware of the passage of time. During the first two years of the study, if it was at a different place or time than usual, the residents became

 doi:10.20944/preprints202208.0139.v1

cautious and remained beyond visual range, intermittently passing into view but not approaching, just as they had when the sessions were new to them.

Familiar individuals recognized the observer underwater though the interim duration was months-long, even when far outside their home ranges. For example, on a visit two years after the study ended, Shark #182 met the kayak as soon as it entered the lagoon, followed it, performed a Close approach underwater, and accompanied the observer during the two-hour visit though no food was present. Since no unknown shark would behave in such a way, it was clear that #182 remembered the observer from two years before.

Shark #115 was a male blackfin that visited every few months. His first four visits were precisely at sunset—actually at the moment that the sun rested like a ball upon the line of the horizon—and four days before the darkest night of the lunar cycle. His precise timing was an initial clue that *C. melanopterus* roams in correlation with both the sun and moon.

Often individuals arrived at a session at the time, to the minute, as they had on the previous night or the previous occasion. Some adult visitors reappeared a year, plus-or-minus one or two days, after their former visit. Few people demonstrate such fine-tuned scheduling.

One of the maturing female residents of Section A, Shark #18, always met the kayak, accompanied the observer to place the fish scraps, and ate well at the beginning of each session. When she suddenly began arriving at the end, the time of her arrival relative to sunset was recorded as shown in Table 3.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

Table 3. The time of Shark #18's arrival at Section A sessions from 20/11/99 to 09/04/02 relative to sunset.

Session No	Date	Shark #18 came	Time of sun-set	Minutes before sunset
52	20/11/99	At sunset	18:14:00	0
		Absent, or there on arrival		
106	11/06/00	At sunset	17:31:00	0
		Absent, or there on arrival		
113	07/07/00	17:31:00	17:37:00	6
114	07/08/00	17:35:00	17:37:00	1
115		Absent		
116	14/07/00	17:33:00	17:39:00	6
117	15/07/00	17:25:00	17:43:00	18
118	21/07/00	17:35:00	17:45:00	10
119	22/07/00	Absent		
120	29/07/00	17:36:00	17:44:00	8
121	03/08/00	There on arrival		
122	06/08/00	17:17:00	17:46:00	29
123	08/08/00	17:27:00	17:47:00	20
124	19/08/00	17:23:00	17:49:00	26
125	26/08/00	Absent		
126	02/09/00	17:45:00	17:53:00	8
		Absent, or there on arrival		
132	07/10/00	17:37:00	17:57:00	20
134	14/10/00	17:35:00	17:58:00	23
135	18/10/00	17:36:00	18:00:00	24
		Absent, or there on arrival		
145	02/12/00	18:20	18:21	1
		Absent, or there on arrival		
158	22/02/01	18:25	18:37	12
		Absent, or there on arrival		
187	20/07/01	17:25	17:41	16
		Absent, or there on arrival		
192	01/08/01	17:41:00	17:45:00	4
193	03/08/01	17:41:00	17:46:00	5
		Absent, or there on arrival		
197	07/09/01	17:37:00	17:52:00	15
		Absent, or there on arrival		
202	06/10/01	17:27:00	17:57:00	30
		Absent, or there on arrival		
208	04/11/01	18:15:00	18:06:00	9 mins after; just passed by
		Absent, or there on arrival		
211	16/11/01	18:00:00	18:13:00	13
		Absent, or there on arrival		
234		18:05:00	18:23:00	18
		Absent, or there on arrival		
241	09/04/02	17:31:00	17:53:00	22

Shark #18 was unusual in that she was only seen in the lagoon once during the day during this period, though that was the usual realm of the females, but she was found apparently hunting along the outer slope of the barrier reef beneath the breaking waves. Her case is an example of how much individuals can differ, for she was not observed to travel with a companion and she did not distinguish herself as a leader. She changed her behaviour on her own.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

Shark #18 showed awareness of how much time had passed on an occasion when the session ended after only ten minutes. When the anchor was put in the kayak, she, along with several other residents including #134 and #182, accelerated to the observer and began to circle, followed by the lagoon fish, who, along with the gathering of sharks, formed formed an opaque, swirling cloud around the observer. But she left anyway and the entire company of sharks followed the kayak out of the lagoon and partway down the bay, which had never happened before, when the usual schedule was followed.

3.4.3 Decisions

Blackfins made swift decisions to come forward or remain hidden depending on expected or unexpected circumstances, which structure or surface to use when Chafing, and in countless other actions while socializing, investigating food sources and novel objects, Following, and pursuing other intentional activities.

It is not easy to find examples of specific decisions made by wild sharks, but one clear, counter-intuitive decision was observed. It occurred when the observer stopped at the lagoon's border to watch striated surgeon fishes (*Ctenochaetus striatus*) spawning. Sharks #123 and #254, whose ranges were nearby, were roaming through the clustering fish and for the duration of the stay, they intermittently approached. When the observer arrived at the objective 1 km farther east, #123 and #254 were found waiting underwater, having followed the kayak there. It was nine months since those individuals had attended a feeding session due to a site change, and there could be no association with the time of day, because feeding sessions were held at sunset and this incident happened at noon.

The two blackfins had made their choice based on a nine month-old memory, even though that meant leaving the place where the water was full of the scent of spawn and fish, and they could see and hear prey moving in a stimulating way.

3.4.4 Play

Certain female blackfins made a close approach to the observer each time they met, and occasionally, when few other sharks were present, the observer made a close approach back to that individual when she circled back. In response, the shark repeated the Close approach whereon the observer did too. Sometimes the gesture was repeated back and forth several times, particularly with Shark #182, until it seemed playful. Another instance of play-type behaviour was presented by #134, a juvenile male. When the observer dove down and flipped over on the sand to try to photograph him from beneath, he would speed above, accelerate around the site, and zoom over again, while several other juvenile male sharks joined in. At times they kept it up for long periods, showing every sign of playing.

3.4.5 Subjective states

There were occasions in which *C. melanopterus* displayed evidence of positive and negative subjective states (Porcher 2021). Their high-velocity socializing, instances of apparent playfulness, and practice of accompanying groups of visitors away from their ranges when they left, suggest positive subjective states (Broom 2010). Outbreaks of Slamming, Charging, and Circling charging, on the other hand, presented as being highly energetic expressions of negative subjective states. Other researchers have concluded that agonistic displays are indicative of a particular attitude by the actor towards the target of the display (Johnson & Nelson 1973; Nelson *et al.* 1986; Martin 2007; Brena *et al.* 2018). Sequences of events recorded in this study, including a violent attack on the observer following a build-up from Charging, Circling charging, then Slamming, suggest that blackfins experience subjective states based on mental representations that matter to them a lot (Porcher 2021). But what motivated the blackfin gathering to act so energetically together at such times, and how they coordinated their movements, remains unknown.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

3.4.6 Novel objects

The blackfins showed their most complex behaviour in response to novel things and situations. Their act of forming two lines behind leading sharks and performing a swift Close approach when confronted for the first time by a diver, is an example.

Another example of a complex reaction to a novel object was their behaviour in front of a mirror (60 x 80 cms) which was placed in the site with some pieces of fish meat in front of it. Shark #3 was the first to arrive, and on seeing her reflection as she approached the food, she shied away, then circled tightly in front of it, moving with sudden, strong thrusts of her tail. She arced away and returned to repeat the tight circling three times, her body curved into a circle right in front of the mirror. Then she approached the side, positioned herself with one fin against the coral, the other on the sand, and pushed her nose against the mirror's edge. One of her eyes was in front of it, the other behind, as though she was examining it from the back and side. After more circling right in front of it, she made a second approach from the other side to touch the other edge. Finally, she took the food.

This reaction was typical of many of the resident blackfins but #3 was the only one who approached the side to touch the mirror edge-on.

After a brief period of investigation, each blackfin lost interest in the mirror and turned its attention to the food. Each seemed to understand that the moving image in the mirror was not another shark, and their heightened interest in it and investigation suggested a problem-solving approach. This was emphasized by the way #3 intentionally examined the novel object from different angles. The sharks seemed to understand that nothing was really there in spite of the illusion, because after their investigation they ignored their reflections suddenly appearing beside them as they moved past it.

3.4.7 Individual differences

C. melanopterus displayed pronounced individual differences. Each presented a unique pattern of attendance at the sessions, and reacted differently in different situations. Some entered the site, circled the food, and chose a morsel on their first visit. Others lingered out of view, session after session. Some reacted very fast, and others remained on the periphery without acting decisively. Some had close companions, while others always travelled alone. One rare visitor, who always came alone, would accelerate in from the left, grab a scrap, and speed out again. She never circled slowly through the scene with the others. Another would pass slowly through the site from left to right, always in the same way, at the same depth, always at about the same time, and always when the observer was looking the other way. Occasionally she passed close behind. She did this for 8 months before beginning to circle in the site and approach the fish scraps with the others.

Sharks #3 and #109 tended to take leading roles. Both were more alert, energetic, and decisive than the others. It was they who first noticed something and went to investigate. However, on one occasion, it was Shark #2 who was observed to lead Sharks #1 and #3 in Triangular formation. So their actions were flexible, depending on the situation. Any individual could initiate a leading act, but usually it was the same ones who did so.

Shark #109 was the most unusual individual out of the hundreds known. While most of the female residents stayed in their home ranges except for the odd excursion, #109 attended sessions only from mid-December to April, and when she was in the region, she came to nearly every one. She was an audacious and energetic animal—she was the most enthusiastic shark to perform a Close approach to the observer underwater. Originally a juvenile, she was small and moved very fast. She would swerve up to my face, zoom over my shoulder from behind when I was watching the other sharks, then turn like lightning and orbit my head. No effort to dissuade her, such as pushing her, slapping the surface, or using the kayak as a barrier and banging on it, had any effect on her relentless advances. She had no trouble remembering the sessions and the observer from year to year but mercifully as she matured, she did not move so fast.

 doi:10.20944/preprints202208.0139.v1

Her behaviour in the year she matured exerted a strong influence on other maturing females during a period in which the gathering of sharks began displaying a variety of agonistic behaviours towards the observer including Charging, Circling charging and Slamming. Blackfins at that age (about 4 years old) are nearly full-sized, yet, unlike mature females, they are slender, their usual speed is faster, and they easily accelerate. They are more curious, and have a tendency to be more daring than they are after they mature. By the following year, the shooting torpedo has become a hefty and much slower pregnant shark. The actions of #109 had a profound effect on the community of sharks, as the other maturing females, and then the rest of the residents, began following her lead.

While emotional contagion was part of this situation, social learning seemed to be a facet of it too. Regardless, the way the convictions of #109 spread among the rest of the blackfins presented a dramatic example of how much an unusual individual could influence its community.

The spread of the influence of unusual individuals is a requirement for the development of *culture*.

3.4.8 Pain

Since the question of whether or not fish feel pain is considered important (Sneddon *et al.* 2018), a brief mention of the subject is made here. Though nociceptors, the sensory receptors that are responsible for the sensation of pain in other animals, have not been studied in sharks, there is preliminary evidence that they are encoded in the shark genome. Further, they are present in all animals including invertebrates, so it would be extremely unusual for sharks to be the only known animal taxa that lack them (C. Brown pers. comm. 2022).

Behavioural evidence is also revealing. For example, when watching a fish eat a sea urchin, it is evident that the possibility of receiving tissue damage is of concern to the animal, suggesting not only the experience of a negative sensation like pain, but also dread of suffering, and therefore sentience. Indeed, the evolution of a host of oceanic stingers has depended precisely upon the sensitivity of fish to pain.

Similarly, there was no doubt during this study that the blackfins sensed tissue damage as a negative sensation (pain) and associated it with a negative subjective state (suffering). Sharks that had escaped being landed for finning, many of whom had large hooks stuck into their jaws, as well as female sharks with extensive fresh mating wounds (Porcher 2005), showed the same signs of experiencing pain as the other classes of animals observed. They were less alert, less reactive, and their movements were markedly slower, which is considered to indicate suffering (Grandin & Deesing 2002). At feeding sessions, they remained down-current until there was a calm moment, then picked up a scrap and left.

Notable too, was the reaction of sharks who accidentally collided with a coral structure, slamming their noses straight into the ungiving, rock-like barrier with the full force of their momentum. Without exception, there was a moment in which the shark stopped moving as if stunned, whereon it left the area. They were always careful to avoid collisions with each other.

4. Discussion

4.1. The Community

The observations of gender segregation and fidelity to a home range is consistent with research elsewhere (Stevens 1984; Mourier *et al.* 2013; Papastamatiou *et al.* 2009; Schlaff *et al.* 2020, Chin *et al.* 2013). Segregation by gender has also been reported in other shark species (Klimley *et al.* 1988; Smith *et al.* 2009), as has fidelity to a home range (Gruber *et al.* 1988). Lemon sharks of different ages were found to occupy different regions of the Bimini lagoon; juveniles move into deeper water as they grow older (Gruber *et al.* 1988). This suggests that it is a successful strategy used not only by blackfin shark pups for predator avoidance.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

The lack of aggressive territoriality seen in *C. melanopterus* has also been documented in other species of sharks (*e.g.* Allee & Dickinson 1954; Hobson 1963; Myrberg & Gruber 1974; Johnson 1978; Gruber *et al.* 1988; Klimley 1982, 1988).

Suntanning has been reported in other species, too, including nurse sharks (Johnson 1974) and hammerheads (*Sphyrnidae*) (Lowe & Goodman-Lowe 1996).

4.2. The Ethogram

4.2.1 Actions known in other species

Many of the actions seen in blackfin reef sharks have been documented in other species, starting with Normal locomotion. Myrberg & Gruber (1974) termed Normal locomotion "Patrolling" in the captive bonnethead sharks in their study. But the word 'patrol' suggests being in a watchful and intentional state, and seems inapplicable to wild blackfins who advance due to obligate ram ventilation. Their level of alertness during Normal locomotion can be too low to justify the idea that their are Patrolling in an intentional state. The word "swim" is also avoided because of its anthropocentric implications.

Myrberg & Gruber (1974) specified that captive bonnethead sharks (*Sphyrna t. tiburo)* moved their heads through an arc of about 30 to 40° during Norman locomotion, but in the wild blackfins, a far more sleek undulation was the rule and, except in aroused states, it scarcely involved the head.

The ranging pattern seen in *C. melanopterus* is very similar to the observations made by Stevens (1984) at Aldebra Atoll. He wrote that they appeared

"*to be continually searching, crossing and recrossing their path, often remaining in a small area for an hour or two before moving off and repeating this pattern in another area. They rarely moved in a straight line for more than a few minutes*."

A series of actions similar to Search mode was documented in bonnethead sharks which was thought to be the sharks' way of orienting to a spot on the substrate and termed Manoeuvring by Myrberg & Gruber (1974). It was also seen in other species by Eibl-Eibesfeldt & Haas (1959) Hobson *et al.* (1963), and Banner (1967).

The Head shake has been reported in lemon sharks (Myrberg & Gruber 1974) and grey nurse sharks (Smith *et al.* 2015). Myrberg & Gruber (1974) reported that it was performed in response to restriction of the shark's movements in the laboratory, so termed it agonistic. Klimley (1985) noted that scalloped hammerhead sharks (*Sphyrna lewini*), perform a Head shake as a social reaction while retreating after a competitive encounter. However, the blackfins did so only to extract a bite of food from a large piece, and very occasionally, one shook the head in a similar fashion in an apparent effort to dislodge a remora.

Palatoquadrate adjustment has been noted in the grey nurse shark (*Carcharias taurus*) (Smith *et al.* 2015).

Papastamatiou *et al.* (2009) found that *C. melanopterus* in Palmyra Atoll presented a diel pattern similar to the blackfins of Mo'orea, slowing their velocity during the day. They were more active at night. They also noted that multiple sharks refuged in the same area. This may be because of their lowered level of awareness at these times. With many sharks Resting in the same region, if there was a disturbance and one shark reacted, the others would sense it through the lateral line and be warned, even though the disturbed shark was far beyond visual range. Myrberg & Gruber (1974) also documented their bonnethead sharks moving with increasing velocity as the afternoon passed, while Gruber *et al.* (1988) found that lemon sharks use the sun as a visual cue for their diel movements.

Nose-to-tail following in *C. melanopterus* was seen by Johnson (1974), who observed a male blackfin approach a female from behind and follow Nose-to-tail prior to copulation. The behaviour has also been reported in bonnetheads (Myrberg & Gruber (1974), basking sharks, (*Cetorhinus maximus*) (Sims *et al.* 2000), white sharks (*Carcharodon carcharias*) (Martin 2003), and oceanic whitetip sharks (*Carcharhinus longimanus*) (Gallagher *et al.* 2014). In both white sharks (Martin 2003) and bonnetheads (Myrberg & Gruber 1974) it was noted that Nose-to-tail following occurred most often with the arrival of a newcomer

 doi:10.20944/preprints202208.0139.v1

to the group. That is consistent with these observations of socializing blackfins approaching each other from behind and following Nose-to-tail when visitors arrived.

Circling head to tail, in which both sharks follow Nose-to-tail, was also reported in bonnethead sharks by Myrberg & Gruber (1974).

Swim-bys and Paralleling have been documented in white sharks (Sperone *et al.* 2010), also by individuals of the same gender and approximate size. This suggests that such social gestures (body language) in different forms might be found widely across shark species.

Though other studies have reported sharks 'Chafing' against the sand (e.g. Myrberg & Gruber 1974; Ritter 2011; Smith *et al.* 2015; Williams *et al.* 2021), the blackfins were observed to turn on their backs on the sand and rub their ventral surfaces against smoothly worn coral. Their consistent choices of an appropriate feature on which to scratch, whip against, or Chafe, indicate that they look over the structures in their environment and decide which one to use. Thus they are holding a mental image of what is needed and referring to it while searching. Though this is not tool use, it does involve the basic step of searching out and making a decision about which object among those available will best serve their needs. It is another behaviour pattern that demonstrates their use of cognition.

4.2.2 Follow-formation

Follow-formation was described in bonnethead sharks by Myrberg & Gruber (1974) when three to six sharks followed one another in single file. It was noted rarely, but happened 12 times after the biggest female was introduced. However, in their case the Followers consisted of males, while among the blackfins, Follow-formation was most often seen in socializing female blackfins. The natural gender segregation in the wild blackfins as opposed to the bonnethead sharks' being in a state of confinement in an aquarium, could explain this difference. It could also be that the bonnethead sharks were not stimulated to take Follow-formation by the type of unexpected events that regularly confronted the blackfins.

Follow-formation was not only adopted in the pursuit one another's scent trails. It was a behaviour pattern that was adopted when confronted with a novel scene, as exemplified by the blackfins' reaction to perceiving a diver for the first time. The blackfins spontaneously organized themselves to come forward together, following two natural leaders, in Follow-formation. Along with adopting Triangular formation in challenging situations, it presents as an example of social buffering (*Kikusui et al. 2006*), wherein individuals prefer to approach challenging or novel scenes together rather than alone. Social buffering is considered to be an indication of social complexity (*Kikusui et al. 2006*).

4.2.3 Concealment behind the visual limit

The use of the visual limit for concealment was systematic in *C. melanopterus* and was facilitated by the ability to focus for long periods on events beyond visual range. Moving through a vibrating realm in which light travels less easily than sound, they clearly depended on hearing and the lateral line sense (Bleckmann & Zelick 2009; Klimley 2010), which directly perceives underwater vibrations. These senses are especially suited to underwater perception. Sound spreads in a uniform spherical pattern and sharks hear well (Myrberg 1978). They are particularly sensitive to particle displacement, such as those caused by the actions of other animals and crashing waves (Myrberg *et al.* 1976; Nelson & Gruber 1963). However, their need to pass into visual range at intervals shows that having a look was also important to them and the vision of requiem sharks is also acute (Gruber & Cohen 1978). Myrberg (1991) hypothesized that contrasting fin markings may play a role in species recognition in *C. melanopterus* and similar sympatric reef sharks, which emphasizes the importance of vision in these animals that spend much of their lives in clear and shallow waters studded with coral obstacles.

Yet their behaviour demonstrates that vision may not be of prime importance to them. Their reaction to a mirror supports the hypothesis that *C. melanopterus* individuals

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

require more than just a visual image to analyse what is there and what is not. Their simultaneous integration of sensory input from different senses to analyse ongoing events, provides a clue to the corresponding complexity of their subjective states.

Whitetip reef sharks and sicklefin lemon sharks have also been observed to use the visual limit to screen themselves from view. Tiger sharks (*Galeocerdo cuvier*) and Atlantic lemon sharks, observed for shorter periods of time, performed in a similar way. They passed just within visual range for a look, came closer a few minutes later, then nearer again, though tigers tended to pass overhead when they came near. For oceanic species especially, the visual limit is the only thing available to hide behind, so the use of it for concealment might have evolved in ancestral species.

An animal that is aware of the eye-gaze of others and takes action to avoid being seen, is showing that it is aware of being present and observable and hence self-aware to that degree (Griffin 1982; Olsen 1990). It must also understand that it is distinct from others. Given evolutionary continuity, and that to survive, every life form must, first and foremost, be a self-serving entity, awareness of the self would provide a distinct selective advantage. Levels of self awareness are therefore likely widespread throughout the animal kingdom in different forms (Morin 2006; de Waal 2019; Lage et al. 2021).

4.2.4 Circling together

Most of the blackfins appeared to have a preferred direction. They had preferred circling directions and possibly a preferred eye. Lateralization has been widely found across the animal kingdom (Brown 2014) and closely analysed in fish (Brown 2014; Bisazza and Brown 2011). However, the pattern varies between species, populations and even individuals, so the presence of lateralisation in the blackfins is impossible to interpret with relevance here. Nevertheless, it was clearly present.

4.2.5 Agonistic displays

Agonistic displays have been found in a variety of shark species, the first in the grey reef shark by Johnson & Nelson (1973). When grey reef sharks were chased and cornered, they would arch the back, raise the snout, lower the pectoral fins, and swim towards the offending diver with exaggerated horizontal undulations, sometimes rolling or looping in a spiral. Then they would either flee, or, with a lightning gesture, deliver an open-mouthed slashing attack. The display increased in intensity in correlation with the speed and directness of the diver's approach, and the degree to which the escape route was blocked.

Since then, more agonistic displays have been identified including the Tail slap in great white sharks. Klimley *et al.* (1996) found that conflict can be ritualized in this species. When a seal that one of them has killed comes under dispute, each slaps the water at an angle with its tail, and the shark that raises the most water and blasts it farthest, wins the prey (Klimley *et al.* 1996). It is notable that both sharks 'agree' on which of them is the winner, which suggests not only self awareness, but a self image, not to mention the ability to distinguish the self from the other. Further, for the ritual to be effective, each shark must understand it, and the loser must acknowledge the winner to avoid a physical battle for the seal, which would badly damage both individuals.

Martin's (2007) review describes agonistic displays in 23 species of sharks from 6 families including the great white, the tiger (*Galeocerdo cuvier*), the sand tiger (*Carcharias taurus*), the scalloped hammerhead (*Sphyrna lewini)*, the silky shark, (*Carcharhinus falciformis*), the blue (*Prionace glauca*), several reef sharks, and the basking shark (*Cetorhinus maximus*). Jerky, exaggerated movements or sudden turns, accompanied by the sustained depression of the pectoral fins, are most typical. The shark might also arch its back, hold its mouth open, billow its gills, or gape repeatedly. Charging was reported, and Smith *et al.* (2015) observed Charging in grey nurse sharks (*Carcharias taurus*).

On the Great Barrier Reef, silvertip sharks *(Carcharhinus albimarginatus)* performed a stiff-bodied display towards divers. After an initial acceleration away, several returned to

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

a distance of about two body lengths, turned broadside, and moved slowly past the divers. Each displaying shark lowered its pectoral fins and tail, gaped its jaws rhythmically, and vibrated its entire body as if shivering, while passing. Then it accelerated away (Martin 2007). The sandbar shark *(Carcharhinus plumbeus)* has also turned broadside to divers with depressed pectoral fins. Female sandbar sharks were reported to have rammed divers with their snouts, while the males veered off without coming closer than a body length away (Martin 2007).

Martin's comprehensive review indicates that agonistic displays are likely widespread among the different species of sharks and that what evidence exists is anecdotal and incomplete. Though the grey reef shark's posturing is exceptional in its form and presentation, in other species such displays are less clearly defined or predictable. As in the blackfins, they are likely used flexibly according to the circumstances, which makes them challenging to describe in structured terms, particularly when they have only been observed incidentally and not in a variety of circumstances.

When used to intimidate, the Close approach of the blackfin falls under the definition of an agonistic display, though it lacks the components of a hunched back and muscular flexing. However, these are present in Slamming behaviour, into which the Close approach can escalate under the right circumstances. But Slamming is not a display. It is a direct attack without pre-signalling (Porcher 2016).

In the case of blackfins approaching Javanese moray eels, the Close approach resembled *predator inspection*, with the inspector highly attuned to the reaction of the inspectee. Predator inspection is a behaviour pattern that has been described in certain fish and other taxa (Fishman *et al*. 1999). It involves members of a prey species approaching a predator for a closer look. Here, the Close approach by a blackfin to an eel involved another mesopredator, in a situation involving competition over food rather than fear of being eaten. Only juvenile males were observed to approach the big eels in this way, suggesting that the older blackfins might have learned something about them from experience.

In other cases, the Close approach was done very swiftly, apparently with the intention to intimidate. The incident in which the blackfins present accelerated from beyond visual range up to the face of the diver in Follow-formation (as described above) appeared to be a mass Close approach done fast. The way blackfin sharks accelerate up to Tahitian spear fishermen to persuade them to relinquish their catch, provides further support for the hypothesis that the actor intends to intimidate, in which case the action is an agonistic display.

Martin's review names *C. melanopterus* among the species that will display, yet includes no details, mentioning only that blackfins will lower their pectoral fins while turning past a diver. However, this observation seems inconclusive when they lower their fins in tight turns. In spite of attending recreational feeding dives with dive clubs on several islands as well as Mo'orea, this observer did not identify any such agonistic gesture by blackfins towards divers.

Martin does not identify the commonly presented Close approach of the species as an agonistic display, nor the Startle response, in which the blackfin accelerates away with arched back, depressed pectoral fins, and a series of jerky vertical undulations. This could be due to his method of pursuing the sharks, but not startling them. Nelson *et al.* (1986) used a diver propulsion vehicle to trigger agonistic displays in different species of sharks through "sustained, oriented pursuit" and stated that they had been unable to illicit an agonistic display in *C. melanopterus*.

The blackfins' Startle response presents as being homologous to the grey reef's agonistic display, but it is neither a display, nor agonistic. The reaction appears to be a reflex response that evolved to protect the shark by making it harder to grab by a predator. The swift lowering of the pectoral fins at the moment the shark is startled could be associated with its rise in the water column as it flees the area. An ascent from the more crowded region on the reef into the open space above the coral structures is typical of responses in which a shark rapidly departs, and this upward trajectory is also achieved by the arching

 doi:10.20944/preprints202208.0139.v1

of the back, resulting in the powerful tail pointing downwards. The vertical jerking during acceleration as the blackfin takes flight likely enhances predator avoidance.

Myrberg and Gruber (1974) identified a startle response in bonnethead sharks, however in their case, the vertical jerking was not noted. They defined a "Hunch" posture which caused the tail to lower, but this was not connected with fleeing. It was described as an agonistic display towards a newcomer in the pool, a smaller shark, or a diver present.

C. melanopterus arched the back and accelerated upwards while Slamming, but never as a warning gesture. By the time the back hunched, the shark was already launching itself, and lowered its pectoral fins only momentarily, less than a second prior to impact (Porcher 2016).

Slamming behaviour has not been reported elsewhere, and how it normally expresses is unknown. Possibly blackfins Slam large floating carcasses together, in order to break them up and help free pieces of food. However, on no occasion did any of the sharks slam into their pile of fish scraps to break them up and make them easier to access. In the study, including two occasions on which different blackfins suddenly Slammed the observer personally, it was used only as a method of attack (Porcher 2016).

Though Martin mentioned a brief "shivering" in the silvertip shark during an agonistic display, his description does not resemble the shuddering and randomly darting behaviour that often followed the Startle response in the blackfins. In them, there was no doubt that the Shivering was part of a fear reaction. Tester & Kato (1966) noted in their experiment on visual discrimination in *C. melanopterus* that when one was given an electric shock, its body "twitched noticeably," which helps to confirm that blackfins appearing in Shiver mode, which also involved repeated twitching, had been negatively disturbed (Porcher 2022 submitted).

It is possible that gestures and displays in the various species of sharks differ in different geographical regions. The blackfins of the volcanic islands in the central Pacific are descended from the sharks who crossed thousands of kilometres of ocean from the continents to the west to find them (Maisano Delser *et al.* 2019). Therefore, their repertoire of behaviour patterns could have changed as they crossed the Pacific Ocean, and were subject to different conditions and experiences while remaining isolated. For example, Martin (2007) found that, unlike the grey reef sharks of French Polynesia, those in the waters off Queensland would not display; when chased, they simply departed.

4.2.6 Biting

Given the dentition and reputation of sharks in general and *C. melanopterus* in particular (Randall & Helfman 1978) it is notable that they are the only species of animal, wild or domestic, with which the observer has been in intimate contact long-term that did not bite, either through accident or a negative subjective state. Given the lack of aggression noted in so many shark species too, it may be that sharks lack the automatic tendency to open the mouth and bite in defence and aggression, that is instinctive in the osteichthyan phylogenetic line of vertebrates. When expressing a strong negative subjective state, for example, they Slammed instead of biting.

4.3 Roaming

In spite of their sedentary behaviour in some respects (Stevens 1984), roaming is a prominent facet in the lives of these blackfins. The finding that females are philopatric and that some travel to nurseries off other islands for parturition (Mourier & Planes 2013) suggests that juvenile blackfins roam very far prior to establishing a home range at about 4 years of age. The picture of their community that emerges is far larger than that of individuals living sedentary lives in over-lapping home ranges (Stevens 1984). Instead of the home range being the focus of their lives, for many of them it appears to be a place to pause in a life of complex travel which can include one or more of the surrounding islands (Mourier & Planes 2013). Though Vignaud *et al.* (2013) found that they rarely if ever travel

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

more than about 50 km to other island groups, their presence in the waters of Pacific Island chains that originated in the recent geological past—Mo'orea formed between 1.5 and 2 million years ago (Neall & Trewick 2008)—means that the ancestors of the sharks living there now did travel across vast expanses of ocean from their origin near Asia (Maisano Delser *et al.* 2019). Some *C. melanopterus* individuals may still at times do so. Those residents that were regularly absent for months at a time, as well as the rare visitors, were likely travelling among the nearby islands.

While in other parts of the world, correlations with the lunar phase are often associated with the tides, in Polynesia, the tide is solar. There are only a few centimetres of difference in water level between the low and high tides in the lagoons, along the borders, and in the passes, where oceanic conditions and the volume of water pouring over the reef determine water depth. So the correlation with the lunar phase cannot be explained by the opening and closing of waterways. Klimley & Ainley (1996) noted a correlation with the lunar cycle in great white sharks as did Pérez-Jiménez *et al.* (2002) in aggregations of sharpnose sharks (*Rhizoprionodon longurio*). In both cases the bright and dark lunar phases were significant.

The importance of using moonlight for travelling when navigating the coral habitat is understandable for avoiding obstacles, but the preference for the dark of the moon is less evident. The use of the dark lunar phase for travelling might be another case of the blackfins' awareness of concealment. Certain rare visitors nearly always arrived in the study area during or just after the period of the dark of the moon, one example of which is shown in Figure 27a. Since the rare visitors are most likely to be those that came from other islands, they might have chosen that time for traversing an expanse of ocean. As meso-predators, they are the prey of oceanic sharks (Frisch et al. 2016).

Sharks make navigational decisions using infrasounds (Myrberg 1978) and the Earth's magnetic field (Klimley & Ainley 1996; Keller *et al*. 2021). Chemoreception likely permits them to recognize the scents of the many islands, each through its chemical signature. Undoubtedly a unique scent trail, long and slow, drifts through the ocean from each island, carried from the lagoons and by its rivers' waters. Sharks traversing ocean stretches could use such island scent trails for navigation.

4.4 Social behaviour

The blackfins' preference for particular companions shows that they, and other shark species that form companionships *e.g.* bull sharks (Thibault *et al.* 2021), grey reef sharks (Papastamatiou *et al.* 2020), and white sharks (Findlay *et al.* 2016) know each other as individuals, which is basic to a complex social life (Chung *et al.* 2020). Myrberg & Gruber (1974) noted that bonnethead sharks respond to conspecifics as individuals. This capacity has also been found in many species of fish (Bshary *et al.* 2002; Brown 2014), visually and acoustically (Myrberg & Riggio 1985).

C. melanopterus pups begin leaving their nurseries as a cautious assembly of tiny sharks, frequently circling away and regrouping again. Already they know each other as individuals and treat each other as companions. The way certain companionships were between blackfins that closely resembled each other in detail—including gender, size, age, colour, and the nature of the patterns on the colour line and fin tips, suggests that they could be siblings. This hypothesis is reinforced by the philopatric nature of the females, and their preference for travelling together. Companion visitors passing through for parturition, on their way to the nursery of their birth, were both born there. Though Mourier & Planes (2021) found that in general shark kinship does not "predict the structure of a shark social network" this does not negate the possibility that some companionships between blackfins are between siblings.

The blackfins' tendency to approach with conspecifics in unfamiliar situations, often in Follow- or Triangular-formation indicates that they practice social buffering (*Kikusui et al. 2006*). The cases in which a resident who had already attended a session returned sometime later with newcomers, provides another example. These actions emphasize the

 doi:10.20944/preprints202208.0139.v1

virtual lack of competition in the species, as well as the attraction to visitors shown by the female blackfins. It also suggests a form of cooperation. Cooperation is little studied in animals other than mammals (Cheney 2011) and it is not possible to analyse this unexpected social behaviour with any hope of accuracy in terms of what was really going on between the individuals involved, but it does provide further insight to the blackfins' social natures.

C. melanopterus displayed no inter-specific aggression in spite of the presence of food (see Video 1), which is consistent with other research (Allee & Dickinson 1954; Springer 1967; Myrberg & Gruber 1974). Intra-specific aggression is common among vertebrates and has long been correlated with territorial behaviour (*Schjelderup-Ebbe1922; Lorenz 1963*). The territory provides a safe place to rest and raise young, but brings with it the need to defend the border against the encroachment of neighbours and raiders. Since sharks show no signs of being territorial, do not give their young post-natal care, and do not sleep to rest, it is not surprising in consequence that intra-specific aggression among them is almost unknown.

Chris Fallows, who studies the great white shark in South Africa, wrote in a personal communication (2022) that in more than thirty years he has never seen them fight. Neither has he seen them bite each other while feeding together on a whale carcass. Nor have they reacted by biting when they have been lured to baits at cage diving boats and have mistakenly collided when swimming from one side of the boat to the other when they could not see each other. Over the years, he has seen many with conspecific bite marks, but does not know under what circumstances they were inflicted. He feels that they let their size and personality dictate the outcome of events rather than physical engagement. Evidently, even among great white sharks, according to human mythology a veritable demon of the sea (Muter 2013; Neff 2015; Le Busque & Litchfield 2021), conflictual biting and fighting, so common among vertebrates of the osteichthyan line, is not seen.

Among the blackfins, no social hierarchy was found. Each individual shark had its preferred range and knew the other sharks roaming through the vicinity, of which one or more were usually, but not always, travelling companions. Fission and fusion seemed very fluid as travelling dyads, triads, and gatherings paused to socialize with the residents they encountered along the way. These bonds were sometimes very strong, in that the sharks always travelled together, but could lie along a scale to slight acquaintance. When familiar blackfins met they would usually either Swim-by each other or briefly Parallel. Dyads, with a variety of acquaintances, were found in bull sharks identified during ecotourism in Fiji (Thibault *et al.* 2021), in juvenile lemon sharks (Gruber *et al.* 2011), and around feeding aggregations in white sharks off South Africa (Findlay *et al.* 2016).

C. melanopterus showed a positive reaction to visitors, which is the opposite of what is seen in territorial animals (Lorenz 1963). Since some of the visitors that were received with most high-velocity socializing were among the rarest (annual visitors), they appeared to have acquaintances they saw very infrequently suggesting that they have the capacity to remember other individuals long-term. Given their complicated travels (Mourier & Planes 2013; Maisano Delser 2019) it is possible that they know other blackfins with distant ranges that they rarely see.

The gathering of blackfins often acted in concert, as in the example of their mass Close approach to the scuba diver in two lines in single file. When faced with a novel situation, they could act together, residents and visitors coordinating their actions. This suggests *emotional contagion* (*Hatfield* et al. *1993)*. However, they do not vocalize and how they coordinated their movements for these actions was not perceived. In spite of much effort to discern them, their spontaneous actions in unison, particularly when Slamming and Undulating against, remain unfathomable. More underwater observation may result in a better understanding of their fluid and complicated social dynamics.

Allee & Dickinson (1954) and Myrberg & Gruber (1974) based their assumption that dogfish and bonnethead sharks form a dominance-subordinate hierarchical social structure on collision avoidance. However, such hierarchies are formed through repeated agonistic interactions between individuals, characterized by a consistent outcome (Chase

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

1982; Drews 1993) and this was not seen. No mechanism was identified by which the presumed dominance was enforced, though Allee & Dickinson (1954) crowded and starved the dogfish. Further, the collision avoidance by smaller sharks was not consistent. Shark juveniles are extremely vigilant and alert in novel situations, have a faster reaction time (Myrberg & Gruber 1974), and likely have a self-protective instinct to stay out of the way of larger predators, including larger sharks.

This is to be expected in such living torpedoes. As the length of a blackfin (and dogfish) increases, its mass increases as a function of its linear measurements *cubed*. Thus a blackfin shark 50 cm long will weigh 1.79 kg (wiki-fish calculator), while one a metre long will weigh 14.86 kg. A large female 1.6 m long will weight 51.16 kg. Though just three times its length, she weighs 28.58 times the weight of the pup. Thus, in any collision, a small shark runs a far greater risk of bodily harm than a larger shark, given the speed, mass, and momentum involved, as well as the fragility of their bodies, which lack the protective support of a bony skeleton. Indeed, near collisions were the only observed trigger for the Startle response in this study. Blackfins were careful to avoid collisions, especially with the coral formations, which was always evident when watching them, particularly in heavy current. Collision avoidance alone is no evidence of a dominance-subordinate hierarchical social structure.

Figure 28 shows a tiger shark avoiding a collision with a much smaller lemon shark.

Figure 28. It is not always the smaller shark that avoids a collision.

There have been few ethological long-term observational studies of wild shark behaviour done, mostly because the animals were believed to be too dangerous (Myrberg & Gruber 1978; Randall & Helfman 1978; Klimley 2022 submitted). So the details of their social lives remain virtually unknown (Mourier *et al.* 2019).

Remote sensing technology including drones (Rieucau *et al.* 2018) and telemetry systems (Mourier *et al.* 2019) are increasingly used to study shark behaviour. In the past ten years, social network software has been used to generate images representing "social structure" (Mourier *et al.* 2012; Jacoby *et al.* 2016; Papastamatiou *et al.* 2020; *Thibaut et al.* 2021). These correlate space with social connectedness, and involve assuming that sharks

 doi:10.20944/preprints202208.0139.v1

observed in the same area during the same period of time are part of the same "group," though the "group" is not defined. Here, Figures 23 and 25 show that in this study, a significant fraction of *C. melanopterus* individuals present were visitors, and no such "group" was apparent. Blackfin companions travel much of the time out of visual range of each other, and are often significantly separated, which, along with the complexity of their roaming, has not been mentioned as being taken into account by the 'social structure' software outputs.

The blackfin individuals attending the feeding sessions were more comparable to patrons at a bar on a Saturday night: each one had a different history resulting in his or her presence there at that time. Though some people may be local and know each other, all those visiting a bar during the same period of time cannot be assumed to be part of the same social group or network. Further, 'social networks' generated with different techniques are not comparable (Castles *et al.* 2014), calling into question how much any given software-generated network might conform to the actual way of life of the species under examination (Castles *et al.* 2014). This is particularly relevant when the software analysis is called on to stand in for underwater observation, so that unknown but possibly relevant facets of the species' behaviour and life-style are not taken into account.

Many researchers and divers have reported that when food is scarce, competition among the sharks present intensifies (Springer 1967; Myrberg & Gruber 1974; Brena *et al.* 2018). Their velocity increases (Myrberg & Gruber 1974) and agonistic gestures are displayed more often in some species (Brena *et al.* 2018). However, close-range, incidental competition does not indicate a rigid social network (Drews 1993) in the absence of any other evidence. When inter-specific, such competition is likely more reflective of the species' natural relationship in the ecosystem (Huepel *et al*. 2018).

4.5 Cognition

There is increasing recognition that animals, including at least some invertebrates, are using cognition to make the decisions and perform the actions needed to successfully pursue their lives (*e.g.* Griffin 1992; Bshary 2002; Broom 2010; Brown 2014; Allen & Trestman 2016). The capacity to experience subjective states relating to circumstance as perceived by the senses is considered to be closely linked (Paul *et al.* 2005). Fish have been found to be cognitively complex (Bshary et al. 2002; Brown 2014) and fulfil the criteria for conscious awareness and sentience (Broom 2010). Sharks have also been found to be capable of cognition in a variety of ways (Schluessel 2015). The actions of the blackfins showed that they were using cognition, and complex cognition at times.

Just their ability to recognize each other as individuals and navigate indicate their use of mental representations (Broom 2010). Sharks make long-distance migrations during which they use the Earth's magnetic field for guidance (Keller et al. 2021). Edrin & Gruber (2005) displaced juvenile lemon sharks up to 16 km from their home ranges and they returned home at twice their usual velocity, in spite of there being good habitat nearby. They appeared to have a preferred direction of motion initially—east—but quickly adjusted their trajectory in the direction of their home ranges. Their actions indicate an ability to home using an unknown mechanism—a capacity lacking in humans—but which likely involves the integration of cues from several senses, from geomagnetic to olfactory.

4.5.1 Memory

Many of the actions of C. melanopterus, as well as their lifestyle, suggest that they have excellent long-term memories. The sharks in the study had no trouble remembering the observer after many months, and one for two years. Their complex travels and scheduling provide further evidence of fine-grained memories of times and events.

The example in which they reacted when the session was cut short after ten minutes, suggests that they are aware of expected versus unexpected outcomes. In order to judge whether an outcome is expected or unexpected they must be holding their expectations in mind in order to compare them to the ongoing situation. In this case, their reaction was

 doi:10.20944/preprints202208.0139.v1

instantaneous and decisive, as if they were very sure of their perceptions and conclusions about them. The incident is a sign, not only of complex cognition, but of consciousness.

Experimental evidence has found that one lemon shark could remember how to obtain food for up to ten weeks (Clark 1959). More recently, two Port Jackson sharks (Heterodontus portusjacksoni) were seen to remember two events and learned associations, one for 24 hours and one for 40 days (Guttridge & Brown 2014).

However, C. melanopterus travels between islands and is philopatric (Mourier & Planes 2013), and no mechanism has been identified that would allow them to return to the island of their birth years later, without remembering the way. Sharks are long lived animals; the lifespan of the Greenland shark is more than two centuries (Nielsen et al. 2016). It seems likely, therefore, that they have correspondingly long memories, especially for significant events.

4.5.2 Decisions

A variety of actions by the blackfins involved making decisions while calling upon memories to do so. When mental representations are held in readiness for use in controlling choices as events unfold, the animal is using access consciousness (Cohen et al. 1997; Squire et al. 2015; Allen & Trestman 2016). Access consciousness involves the use of declarative memories—those that are available to the mental processes to guide actions.

The incident in which two sharks made a decision to leave a spawning dome, where there was scent and prey moving in a stimulating way, to follow a nine month-old memory, is an example. In doing so, the sharks granted mental representations greater significance than the perception of their visible prey, suggesting that there was an overseer doing the thinking, or conscious awareness.

Declarative memories and access consciousness are considered necessary for some of the actions performed by fish, also (Overmier & Hollis, 1990; Maren 2001; Lovibond & Shanks 2002; Chandroo et al. 2004).

Beckoff & Sherman (2004) describe levels of awareness in animals, specifying that when they think about their behaviour in relation to the actions of others, they are demonstrating self conscious subjectivity. This seemed to be the case in many of the blackfins' actions when they made an effort to learn something, while remaining out of view, by 'listening' to events beyond visual range. They did this when 'listening' while out of view at the sessions, when watching a person while waiting for a chance to approach unseen, and when following the observer through the lagoon beyond visual range. The shark maintains awareness of past events, while watching to see events unfold into a future that it might influence, again indicating access consciousness, for the expectation must be compared with the outcome to make the decision. These actions again suggest that blackfin sharks are not only using complex cognition, but are conscious.

The practice seen in shier blackfins—of coming to look from behind, when the person's head is above the surface, or when they are looking the other way—also suggests awareness of the other's placement of attention. Since they could not understand attention placement if they did not have it themselves, their actions suggest that they, too, voluntarily control their attention.

The sharks were clearly aware of the moments in which they were visible, and those in which they could act while remaining unseen and they were always prepared to accelerate away. Their systematic use of this insight to their advantage, suggests the ability to attribute mental states to others, which is called a Theory of Mind (ToM) (Lage et al. 2021). Such an awareness would bestow great selective advantage for both predators and prey and is also considered to be widespread across the animal kingdom (Lage et al. 2021).

The blackfins' behavioural flexibility, which was always on display any time they were observed, is another strong indication of consciousness (Baars 1997).

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 8 August 2022 doi:10.20944/preprints202208.0139.v1

4.5.3 Play

Playfulness is difficult to identify in animals, so Burghardt (2015) developed a set of five criteria to help pinpoint instances of play which he sums up as being "*repeated, seemingly non-functional behavior differing from more adaptive versions structurally, contextually, or developmentally, and initiated when the animal is in a relaxed, unstimulating, or low stress setting*." According to these guidelines, reptiles, fish, and even invertebrates have been found to play, and Burghardt specifically found play in elasmobranchs. Stingrays were described as "*batting around balls and competing for the opportunity to do so*."

Therefore, it is possible that the blackfins were being playful, which is another clue that they experience positive subjective states.

4.5.4 Subjective states

Body language expressed through gestures, or by instinctive actions that displayed the subjective state of the animal, appeared to be an important form of communication among the multitude of species in the lagoon community. Through a variety of actions including Charging, Slamming, Shiver mode and Undulating against another, blackfins powerfully expressed both negative and positive subjective states (Porcher 2021). Many times some of the most extreme subjective outbursts were instigated by certain individuals, and almost instantaneously adopted by the entire company. Though how this was coordinated among the sharks is unknown, it does suggest emotional contagion (Hatfield et al. 1993), in which the subjective state of one or a few animals are adopted by others present. Emotional contagion is considered to be an indication of complex social behaviour as well as cognition, since it involves perception and adoption of the subjective states of others present.

The way female residents would often accompany some of their visitors away from the home range as they left, is another indication that socializing is not only important to the blackfins, but that they experience positive subjective states when socializing.

4.5.5 *Novel objects*

Through their combination of strategies involving vigilance and curiosity, the blackfins displayed their most complex behaviour when confronted with novel objects, the example of their approach to the diver as described above being an example.

Their reactions to a mirror were energetic and appropriate. The mark test (Gallup 1970), which purports to establish self-awareness, has biased mirror reactions in an anthropocentric way, thus distracting attention from what other reactions might indicate (Broom 2010; de Waal 2019). Many animals appear to see a conspecific in the mirror (Kusayama et al. 2000), including fish, who tend to react aggressively (Josi & Frommen 2021) and others perform self directed actions in front of it (Broom 2014; Ari & D'Agostino 2016).

The blackfins devoted considerable energy to investigating the mirror as a novel object, working to gain information that would allow them to understand it and make an appropriate decision about it. Yet after their brief, if intense investigation, they did not react in any way to the sudden appearance of a reflected shark beside them when they passed it, suggesting that they realized that in spite of appearances, nothing was really there. The mirror provides a visual image, but no corresponding information for their other senses. Being animals used to integrating sensory input from four or five senses at once, this point may have helped them to come to the right conclusion.

Their problem-solving efforts, including, in the case of Shark #3, two approaches to the side to touch the edge, provide further evidence of their use of cognition.

4.5.6 Individual differences

Individual difference among Mo'orea blackfins was also noted by Mourier et al. (2011) and have been documented in other species (Myrberg & Gruber 1974; Guttridge et al. 2011; Byrnes & Brown 2016). Individual behavioural consistency, a component of

 doi:10.20944/preprints202208.0139.v1

personality, has already been established in sharks (Jacoby et al. 2014; Byrnes & Brown 2016; Towner et al. 2016). Guttridge et al. (2011) found that certain juvenile lemon sharks would lead others in aggregations.

Given genetic individuality and the theory of evolution, it follows that each individual will be different, and not always in terms of leadership, as presented by the case of Shark #18. Each blackfin in the study was different from the others.

Among the unusual individuals were some that tended to lead. When they discovered a new foraging technique on Breaching through the surface and grabbing some of the fish scraps in the kayak, those following their example were demonstrating social learning—they were learning from a conspecific through observation (Brown 2014) which signals cognitive complexity (Brown 2014). Under normal circumstances, the space above the surface is not something that sharks would have reason to consider, but the blackfins in the study were in a situation in which the food in which they were interested came to them from above it. They would have stored memories about the surface from the occasions, particularly when they were small, when they swam through it, up against it while chasing a fish, or when they were startled, but it seems unlikely that they could have gained more than a vague impression that there was a separated volume above the surface. Yet their behaviour suggested that they were aware of a volume above in which things could exist, come and go. They were, for example, aware that their food was in the kayak before it was in the water, and that there could be food in the kayak at other times. Their considerations about their decisions included thoughts about what was in the kayak and out of their view. They had no trouble with the concept of object permanence.

Social learning can lead to the development of culture, since it results in the accumulation of information, and allows the discoveries of unusual individuals to benefit the others (Van Schaik 2016). Over time, the ability to learn new tactics would cause a separated population to evolve a new repertoire of behaviours through experimentation with strategies relevant to the novel situation. It is therefore associated with intelligent species (Van Schaik 2016).

Indeed, the way a population of a given species, depending upon the ingenuity and resilience of its leading individuals, finds ways to adapt to changes, is an essential part of the evolutionary process. Many natural phenomena indicate that it is behaviour that drives evolution's response. Among the blackfins, the importance of the unusual individual as an influence was repeatedly observed (Porcher 2021).

5. Conclusion

This study was carried out because of the observation that wild blackfins approached the observer while trying to remain unseen, whether this involved the use of the visual limit, or by coming when her head was above the surface or she was looking the other way. The many observations of blackfin individuals in a variety of circumstances during this study confirms that the species does have a fast thinking, fast acting intelligence suggesting complex cognition and a variety of subjective states including something akin to rage, pleasure while socializing, and play. Their intentional, decisive actions in a variety of situations suggest that they have their own perspective that very much matters to them (Nagel 1974). Though it is impossible to really comprehend their subjective realities due to the vast evolutionary gulf that separates them from our own species, their finely tuned abilities to perceive the actions of others, roam according to a schedule correlating with the sun and moon, investigate unusual circumstances and objects, navigate long distances through the ocean, and express both positive and negative subjective states, suggest that they have a high level of intelligent awareness and a conscious experience of their lives. Other life forms evolving in the marine environment including fish, dolphins, and octopi have also evolved high intelligence so the finding of intelligence, cognition, and likely conscious awareness in sharks is not a surprise.

 doi:10.20944/preprints202208.0139.v1

These observations are offered to add to the information available about *C. melanopterus*. More underwater observation of them and other species will doubtless be rewarded by many new and interesting findings.

References

Allee, W. & Dickinson Jr. (1954) Dominance and subordination in the smooth dogfish, Mustelus canis (Mitchill). Physiol. Zool. 27:356-364.

Allen, C. & Trestman, M. (2016) "Animal Consciousness" The Stanford Encyclopedia of Philosophy (Winter 2016 Edition), Edward N. Zalta (ed.), <https://plato.stanford.edu/archives/win2016/entries/consciousness-animal/>. *(accessed on 20 June 2022)*

Andreev, P.S., Zhao, W., Wang, N.-Z., Smith, M.M., Li, Q., Cui, X., Zhu, M. & Sansom, I.J. (2020) Early Silurian chondrichthyans from the Tarim Basin (Xinjiang, China). PLoS ONE 15(2): e0228589. https://doi. org/10.1371/journal.pone.0228589

Ari, C. & D'Agostino, D.P. (2016) Contingency checking and self-directed behaviors in giant manta rays: Do elasmobranchs have self-awareness?. J. Ethol. 34, 167–174 . https://doi.org/10.1007/s10164-016-0462-z

Baars, B.J. Some essential differences between consciousness and attention, perception, and working memory. Conscious Cogn. 1997 Jun-Sep;6(2-3):363-71. doi: 10.1006/ccog.1997.0307. PMID: 9262417.

Banner, A. (1968) Attraction of young lemon sharks, Negaprion brevirostris*, by sound. Copeia 1968:871-872.*

Bekoff, M. & Sherman, P. (2004) Reflections on animal selves. Trends Ecol. Evol. , 19, 176-180.

Bisazza, A. *&* Brown, C. (2011) Lateralization of cognitive functions in fish. In: Brown C, Krause J, Laland KN (eds) *Fish cognition and behavior.* Wiley, Oxford, pp 298–324

Bleckmann, H. *&* Zelick, R. (2009) Lateral line system of fish. Integrative zoology, 4(1), 13- 25.

Brazeau, M.D. & Friedman, M. The characters of Palaeozoic jawed vertebrates. Zool J Linn Soc. 2014 Apr;170(4):779-821. doi: 10.1111/zoj.12111. Epub 2014 Mar 7. PMID: 25750460; PMCID: PMC4347021.

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. Lomd. B: Biol. Sci. 285: 20180006. DOI:10.1098/rspb.2018.0006.

Broom, D. (2010) Cognitive ability and awareness in domestic animals and decisions about obligations to animals. Applied Animal Behavior Science, 126(1/2), 1-11.

Brown, C. (2014) Fish intelligence, sentience and ethics. Anim. Cogn. 18, 1–17. https://doi.org/10.1007/s10071-014-0761-0

Bshary, R., Wickler, W. *&* Fricke, H. (2002) Fish cognition: a primate's eye view. Animal Cognition 5: 1-13

Burghardt, G.M. (2015) Play in fishes, frogs and reptiles. Curr Biol. Jan 5;25(1):R9-10. doi: 10.1016/j.cub.2014.10.027. PMID: 25562306.

Byrnes, E.E. *&* Brown, C. (2016) Individual personality differences in Port Jackson sharks Heterodontus portusjacksoni. J. Fish Biol. 89, 1142 – 1157. doi:10. 1111/jfb.12993

Castles, M., Heinsohn, R., Marshall H.H., Lee, A.E.G., Cowlishaw, G., Alecia, J. *&* Carter, A.J. (2014) Social networks created with different techniques are not comparable, Anim. Beh. 96: 59-67, ISSN 0003-3472. doi.org/10.1016/j.anbehav.2014.07.023.

Castro, J.I. (2017) The origins and rise of shark biology in the 20th century. Mar. Fish. Rev. 78: 1433.

Chandroo, K.P., Yue, S. *&* Mocci, R.D. (2004) An evaluation of current perspectives on consciousness and pain in fishes. Fish Fish. 5. 281-295

Chase, I.D. (1982) Dynamics of hierarchy formation: The sequential development of dominance relationships. Behaviour. 80: 218-240 Department of Sociology, State University of New York at Stony Brook, Stony Brook, N.Y. 11794, U.S.A.

Cheney, D.L. (2011) Extent and limits of cooperation in animals. Proc Natl Acad Sci U S A. 2011 Jun 28; 108 Suppl 2(Suppl 2):10902-9. doi: 10.1073/pnas.1100291108. Epub 2011 Jun 20. PMID: 21690405; PMCID: PMC3131815.

Chin, A., Simpfendorfer, C., Tobin, A. *&* Heupel, M. (2013) Validated age, growth and reproductive biology of *Carcharhinus melanopterus*, a widely distributed and exploited reef shark. Mar. Freshw. Res. **64**, 965-975. doi.org/10.1071/MF13017

Chung, M., Wang, M.-Y., Huang, Z. *&* Okuyama, T. (2020) Diverse sensory cues for individual recognition. Develop Growth Differ. 62: 507– 515. doi.org/10.1111/dgd.12697

Clark, E. (1959) Instrumental conditioning of lemon sharks. Science 130, 217-18.

Coates, M.I., Finarelli, J.A., Sansom, I.J., Andreev, P.S., Criswell, K.E., Tietjen, K., Rivers, M.L. *&* La Riviere, P.J. (2018) An early chondrichthyan and the evolutionary assembly of a shark body plan. Proc. R. Soc. B 285: 20172418. http://dx.doi.org/10.1098/rspb.2017.2418

Cohen, N. J., Poldrack, R. A. *&* Eichenbaum, H. (1997). Memory for items and memory for relations in the procedural/declarative memory framework. Memory, 5, 131–178.

de Waal, F.B.M. (2019) Fish, mirrors, and a gradualist perspective on self-awareness. PLoS Biology 17 (2), 3000021. doi.org/10.1371/journal.pbio.3000112.

Drews, C. (1993) The Concept and Definition of Dominance in Animal Behaviour. Beh. 125.3/4: 283–313.

Edrin, S.M.C. *&* Gruber. S.H. (2005) Homing ability of young lemon sharks, *Negaprion brevirostris*. Environ. Biol. Fishes 72: 267-281

Eibl-Eibesfeldt, I. (1964) Im Reich der tausend Atolle. Piper, Munich. And Haas H. 1959 Erfahrungen mit Haien. Z.F. Tierpsychologie 16:733-746

Evans, G. W. & Howard, R. B. (1973) Personal space. Psych. Bull. 80(4), 334–344. doi.org/10.1037/h0034946

Findlay, R., Gennari, E., Cantor, M. *et al.* How solitary are white sharks: social interactions or just spatial proximity?. Behav. Ecol. Sociobiol. 70, 1735–1744 (2016). doi.org/10.1007/s00265-016-2179-y

Fishman, M. A. (1999) Predator Inspection: Closer Approach as a Way to Improve Assessment of Potential Threats. J. Theor. Biol. Jan 21;196(2):225-235.

Fowler, S.L., Cavanagh, R.D., Camhi, M., Burgess, G.H., Cailliet, G.M., Fordham, S.V., Simpfendorfer, C.A. & Musick, J.A. (2005) Sharks, Rays and Chimaeras: The Status of the Chondrichthyan Fishes. International Union for Conservation of Nature and Natural Resources. pp. 296–297. ISBN 2-8317-0700-5.

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

*Fuss, T., Belackmann H. & Schleussel, V. (2014) The brain creates illusions not just for us: sharks (*Chiloscyllium griseum*) can ''see the magic'' as well. Front. Neural. Circuits 8:24*

Gallagher, A.J., Romeiro, J., Canabal, D., Canabal V. & Hammerschlag, N. (2014) Novel social behaviors in a threatened apex marine predator, the oceanic whitetip shark Carcharhinus longimanus, *Ethol. Ecol. Evol. Doi: 10.1080/03949370.2014.896831*

Gallup, G.G. Jr. (1970). "Chimpanzees: Self recognition". Science. 167 (3914): 86–87. doi:10.1126/science.167.3914.86.

Galzin, R. & Pointer, J.P. (1985) Moorea Island, Society Archipelago. In: B Delesalle, R Galzin & B. Salvat (Eds). 5th International Coral Reef Congress, Tahiti, 27 May to 1 June 1985. Volume I: French Polynesian Coral Reefs: 73102

Goldman, A.I. (2012) Theory of mind. In: Margolis, E., Samuels, R., Stich, S. (Eds.), Oxford Handbook of Philosophy and Cognitive Science. Oxford University Press, pp. 402–424.

Griffin D. (1992) Animal Minds. *Chicago: The University of Chicago Press.*

Gruber, S.H. & Myrberg. A.A. Jr. (1977) Approaches to the Study of the Behavior of Sharks, Am. Zool. 17: 471–486 doi.org/10.1093/icb/17.2.471

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. & Brown, C. (2014) Learning and memory in the Port Jackson shark, Heterodontus portusjacksoni. *Anim. Cog. 17(2):415-425. DOI: 10.1007/s10071-013-0673-4. PMID: 23955028.*

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)

Guttridge, T.L., Gruber, S.H., DiBattista, J.D., Feldheim, K.A., Croft, D.P., Krause, S. & Krause, J. (2011) Assortative interactions and leadership in a free-ranging population of juvenile lemon shark Negaprion brevirostris. *Mar. Ecol. Prog. Ser. 423, 235 – 245. (doi:10.3354/meps08929)*

Guttridge, T.L., Gruber, S.H., Krause, J. & Sims, D.W. (2010) Novel Acoustic Technology for Studying Free-Ranging Shark Social Behaviour by Recording Individuals' Interactions. PLoS ONE 5(2): e9324. doi.org/10.1371/journal.pone.0009324

Guttridge, T.L., Myrberg, A.M., Porcher I.F., Sims, D.M. & Krause, J. (2009) The role of learning in shark behavior. Fish. Fish. 10: 450–469

Hatfield, E., Cacioppo, J. & Rapson, R. L. (1993) Emotional contagion. Current Directions in Psychological Science. 2, 96–99.

Heupel, M.R., Lédée, E.J.I. & Simpfendorfer, C.A. (2018) Telemetry reveals spatial separation of co- occurring reef sharks. Mar. Ecol. Prog. Ser. 589:179–192

Hobson, E. S. (1963) Feeding behavior in three species of sharks. Pac. Sci. 17:171-194.

Jacoby D.M.P., Papastamatiou, Y.P., & Freeman, R. 2016 Inferring animal social networks and leadership: applications for passive monitoring arrays. J. R. Soc. Interface 13: 20160676. dx.doi.org/10.1098/rsif.2016.0676

Jacoby, D.M.P., Fear, L.N., Sims, D.W., David, M.P. & Croft, D.P. (2014). Shark personali- ties? 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. & Bekoff M. (1992) On Aims and Methods of Cognitive Ethology. PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association, Vol. 1992, Volume Two: Symposia and Invited Papers, pp. 110-124

Johnson, R. H. & Nelson, D. R. (1973) Agonistic display in the gray reef shark, Carcharhinus menisorrah, and its relationship to attacks on man. Copeia, 1973: 76–84.

Johnson, R. H. & Nelson, D. R. (1978). Copulation and Possible Olfaction-Mediated Pair Formation in Two Species of Carcharhinid Sharks. Copeia, 1978(3), 539–542. doi.org/10.2307/1443626

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

Josi, D. & Frommen, J.G. (2021). Through a glass darkly? Divergent reactions of eight Lake Tanganyika cichlid species towards their mirror image in their natural environment. Ethology, 127, 925– 933. doi.org/10.1111/eth.13207

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. 2021 Jul 12;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. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 361(1476), 2215-2228.

Klimley A. P. & Ainley D.G. (1996) *Great White Sharks: The Biology of Carcharodon carcharias.* Nature 517 pages.

Klimley, A. P., Butler, S. B., Nelson, D. R. & Stull, A. T. (1988) Diel movements of scalloped hammerhead sharks, Sphyrna lewini *Griffith and Smith, to and from a seamount in the Gulf of California. Jour. Fish. Bio. 33:751-761.*

Klimley, A.P. (1982) Social organization of schools of scalloped hammerhead shark, Sphyrna lewini (Griffith and Smith), in the Gulf of California. Dissertation. - University of California, San Diego.

Klimley, A.P. (1985) Schooling in the large predator, *Sphyrna lewini*, a species with low risk of predation: a non-egalitarian state. Ethology. 70: 297-319.
Klimley, A.P. (1993) Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biology*, 117:1-22.
Klimley, A.P. (2013) "Chapter 6. Sense of Smell: Chemoreception" *The Biology of Sharks and Rays*, Chicago: University of Chicago Press. 125-152. doi.org/10.7208/9780226923086-006
Klimley, A.P., Pyle, P., & Anderson S.D. (1996) Tail slap and breach: Agonistic displays among white sharks? In: Klimley AP, Ainley DG, editors. Great White Shark: The Biology of Carcharodon carcharias. San Diego, CA: Academic Press, p 241-55.
Kret, M., and Roth, T. (2020). Call for Papers for Behaviour on Special: Anecdotes in Animal Behaviour. Available online at: https://brill.com/fileasset/downloads_ products/BEH_Call_for_Papers_Anecdotes.pdf
Kuba, M.J., Byrne, R.A. & Burghardt, G.M. (2010) A new method for studying problem solving and tool use in stingrays (*Potamotrygon castexi*). Anim. Cogn. (3):507-13. doi: 10.1007/s10071-009-0301-5. Epub 2009 Dec 18. PMID: 20020169.
Kusayama, T., Bischof, H.-J. & Watanabe, S. (2000) Responses to mirror-image stimulation in jungle crows (Corvus macrorhynchos) Anim. Cogn. 3: 61-64
Lage, C.A., Wolmarans, W. & Mograbi, D.C. (2022) An evolutionary view of self-awareness. Behav. Processes. 194:104543. doi: 10.1016/j.beproc.2021.104543. Epub 2021 Nov 17. PMID: 34800608.
Le Busque, B. & Litchfield, C. Sharks on film: an analysis of how shark-human interactions are portrayed in films. Human Dimensions of Wildlife. 2021, 27(2), 1-7.
Lorenz, K. (1963) *Das Sogenannte Böse, Zur Naturgeschichte der Aggression* by Verlag Dr Borotha-Schoeler, Vienna, Austria
Lovibond, P.F. & Shanks, D.R. (2002) The role of awareness in Pavlovian conditioning: empirical evidence and theoretical implication. Journal of Experimental Psychology 28 3-26
Lowe, C. & Goodman-Lowe, G. (1996) Suntanning in hammerhead sharks. Nature 383, 677 . doi.org/10.1038/383677a0
Maisano Delser, P., Corrigan, S., Duckett, D. *et al.* (2019) Demographic inferences after a range expansion can be biased: the test case of the blacktip reef shark (*Carcharhinus melanopterus*). Heredity 122, 759–769. doi.org/10.1038/s41437-018-0164-0
Martin R.A. (2003) Field guide to the great white shark. Vancouver, Canada: ReefQuest Centre for Shark Research.
Martin, R.A. (2007) A review of shark agonistic displays: comparison of display features and implications for shark–human interactions. Mar. Freshw. Behav. Physiol. 40.1 : 3-34.
Montgomery, J.C., Bodznick, D. & Yopak, K.E. (2012) The cerebellum and cerebellum-like structures of cartilaginous fishes. Brain Behav. Evol. 2012;80(2):152-65. doi: 10.1159/000339868. Epub 2012 Sep 13. PMID: 22986830.
Morin, A. (2006) Levels of consciousness and self-awareness: A comparison and integration of various neurocognitive views. Consciousness and Cognition, 15(2) 358-371, ISSN 1053-8100, doi.org/10.1016/j.concog.2005.09.006.
Moss, S.A. (1972) The feeding mechanism of sharks of the family Carcharhinidae. Journal of Zoology, 167: 423-436. doi.org/10.1111/j.1469-7998.1972.tb01734.x
Motta, P.J., Hueter, R.E., Tricas, T.C. & Summers, A.P. (2002) Kinematic Analysis of Suction Feeding in the Nurse Shark, *Ginglymostoma cirratum* (*Orectolobiformes, Ginglymostomatidae*) Copeia, (1), pp. 24–38
Mourier, J. & 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. & Planes, S. (2021) Kinship does not predict the structure of a shark social network, *Behav. Ecol.* 32(2): 211–222 doi.org/10.1093/beheco/araa119
Mourier, J., & Planes, S. (2013) Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. Molecular ecology, 22(1), 201-214.
Mourier, J., Lédée, E., Guttridge, T. & Jacoby, D.M.P. (2019) "Network analysis and theory in shark ecology–methods and applications," in *Shark Research: Emerging Technologies and Applications for the Field and Laboratory*, eds J. C. Carrier, M. R. Heithaus, and C. A. Simpfendorfer (Boca Raton: CRC Press), 337–356.
Mourier, J., Mills, S.C., & Planes, S. (2013) Population structure, spatial distribution and life-history traits of blacktip reef sharks *Carcharhinus melanopterus.* Jour. Fish. Bio. 82(3) 979-993.
Mourier, J., Vercelloni, J. & Planes, S. (2011) Evidence of social communities in a spatially structured network of a free-ranging shark species, Anim. Beh. doi:10.1016/j.anbehav.2011.11.008
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(2) 389-401. ISSN 0003-3472, doi.org/10.1016/j.anbehav.2011.11.008.
Muter, B.A., Gore, M.L., Gledhill, K.S., Lamont, C. & Huveneers, C. (2013) Australian and US news media portrayal of sharks and their conservation. Cons. Biol. 27(1): 187-196.
Myrberg A. A. & Riggio R. J. (1985) Acoustically mediated individual recognition by a coral reef fish *(Pomacentrus portitus)* Anim. Behav. 33: 411-416.
Myrberg Jr., A.A. & Gruber, S.H. (1974) The behavior of the bonnethead shark, *Sphyrna tiburo.* Copeia. 1974: 358-374.
Myrberg, A. A. (1991) Distinctive markings of sharks: Ethological considerations of visual function. J. Exp. Zool. 256: 156–166. doi:10.1002/jez.1402560520
Myrberg, A.A. (1978) Underwatcr sound - its effect on thc behavior of sharks. In Hodgson,
E.S. and Mathewson, R.F., cds. Sensory Biology of Sharks, Skates, and Rays. Arlington, VA:
Office of Naval Research, pp. 391-418.

Myrberg, A.A., jun., Gordon, C.R. and Klimlcy, 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.
Nagel, T. (1974) What Is It Like to Be a Bat? The Philosophical Review, 83(4):435–450. doi.org/10.2307/2183914
Neall, V.E. & 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.
Neff, C. (2015) The Jaws effect: How movie narratives are used to influence policy responses to shark bites in Western Australia. Austral. J Pol. Sci. 50(1): 114-127.
Nelson, D.R. & Gruber S.H. (1963) "Sharks: Attraction by Low-Frequency Sounds." Science 142(3594):975–77 www.jstor.org/stable/1711607
Nelson, D.R., Johnson, R.R., McKibben, J.N. & Pittenger, G.G. (1986). Agonistic attacks on divers and submersibles by gray reef sharks, *Carcharhinus amblyrhynchos:* antipredator or competitive? Bull. Mar Sci.: 38: 68-88.
*Nielsen, J., Hedeholm, R.B., Heinemeier, J., Bushnell, P.G., Christiansen, J.S., Olsen, J., Ramsey, C.B., Brill, R.W., Simon, M., Steffensen, K.F. & Steffensen, J.F. (2016) Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus). *Science. 353 (6300): 702–4. doi:10.1126/science.aaf1703.*
Northcutt, R.G. (1977) Elasmobranch central ncrvous systcm organization and its possible evolutionary significancc. Am. Zool. 17, 411-29.
Northcutt, R.G. (1978) Brain organization in the cartilaginous fishes. In: Hodgson ES, Mathewson RF (eds) Sensory biology of sharks, skates and rays. Office of Naval Research, Arlington, pp 117–193
Olsen, L.A. (1990) The Cognitive Complexity of the Grizzly Bear Trumpeter. ISSN: 0832-6193 https://trumpeter.athabascau.ca/index.php/trumpet/article/view/473/789 (Accessed 3 May 2022)
Overmier, J.B. & Hollis, K.L. (1990) Fish in the think tank: learning, memory, and integrated behaviour. Neurobiology of Comparative Cognition (eds Kesner RP, Olson DS), Lawrence Erlbaum, Hillsday, NJ. pp. 205-236
Papastamatiou, Y.P., Bodey, T.W., Caselle, J.E., Bradley, D., Freeman, R., Friedlander, A.M. & Jacoby, D.M.P. (2020) Multiyear social stability and social information use in reef sharks with diel fission–fusion dynamics. Proc. R. Soc. B 287: 20201063. dx.doi.org/10.1098/rspb.2020.1063
Papastamatiou, Y.P., Cartamil, D.P., Lowe, C.G., Meyer, C.G., Wetherbee, B.M. & Holland, K.N. (2011) Scales of orientation, directed walks, and movement path structure in sharks. J. Anim. Ecol. 80, 864–874.
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. PMID: 20738562.
Papastamatiou, Y.P., Watanabe, Y.Y., Demšar, U., Leos-Barajas, V. Bradley, D., Langrock, R., Weng, K., Lowe C.G., Friedlander, A.M., & Caselle, J.E. (2018) Activity seascapes highlight central place foraging strategies in marine predators that never stop swimming. Mov. Ecol. 6(9) doi.org/10.1186/s40462-018-0127-3
Paul, E.S., Harding, E.J. & Mendl, M. (2005) Measuring emotional processes in animals: the utility of a cognitive approach. Neurosci. Biobehav. Rev. 29 (3) 469-491, ISSN 0149-7634, doi.org/10.1016/j.neubiorev.2005.01.002.
Pérez-Jiménez, J.C., Sosa-Nishizaki, O., Furlong-Estrada, E., Corro-Espinosa, D., Venegas-Herrera, A. & Barragan-Cuencas, O. V. (2005) Artisanal Shark Fishery at "Tres Marias" Islands and Isabel Island in the Central Mexican Pacific. J. Northw. Atl. Fish. Sci., 35: 333-343. doi:10.2960/J.v35.m489
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. (2016) Sharks: Agonistic Behaviour in the Blackfin Reef Shark. https://www.youtube.com/watch?v=tj3RX-3DT0k (Accessed on 28 May 2022)
Porcher, I.F. (2021). Commentary on emotion in sharks, *Behaviour*. doi.org/10.1163/1568539X-bja10145
Porcher, I.F. (2022) Video 1 *C. melanopterus* behaviour at Session 304. www.youtube.com/watch?v=_Wi7Q0rlYk8
Porcher, I.F. (2022) Video 2 *C. melanopterus* behaviour: Bolting https://www.youtube.com/watch?v=gK5G0jYpWkQ
Porcher, I.F. (2022) Video 3 *C. melanopterus* behaviour: Sniffing www.youtube.com/watch?v=noCXAi8QYS4
Porcher, I.F. (2022) Video 4 *C. melanopterus* behaviour: Swim-by and Paralleling. www.youtube.com/watch?v=WRiy6V4yg7o
Ramsay, M.S. and Teichroeb, J.A. (2019), Anecdotes in Primatology: Temporal Trends, Anthropocentrism, and Hierarchies of Knowledge. American Anthropologist, 121: 680-693. https://doi.org/10.1111/aman.13295
Randall, J.E. & Helfman, G.S. (1973) Attacks on humans by the blacktip reef shark (*Carcharhinus melanopterus*). Pac. Sci. 27(3): 226-238. hdl.handle.net/10125/799
Randall, J.E. & Hoover J.P. (1995). Coastal Fishes of Oman. University of Hawaii Press. p.33. ISBN 0-8248-1808-3
Rieucau, G., Kiszka, J.J., Castillo, J.C., Mourier, J., Boswell, K.M. & Heithaus, M.R. (2018) Using unmanned aerial vehicle (UAV) surveys and image analysis in the study of large surface-associated marine species: a case study on reef sharks *Carcharhinus melanopterus* shoaling behaviour. J. Fish. Biol. 93(1): 119-127. doi: 10.1111/jfb.13645. PMID: 29855056.
Ritter, E.K. (2011) Use of Sand Ripples to Enhance Chafing in Caribbean Reef Sharks (*Carcharhinus Perezi*) and Blacktip Sharks (*Carcharhinus Limbatus*). Bull. Mar. Sci. 87(3): 413-419(7) doi.org/10.5343/bms.2010.1082
Sándor K, Miklósi Á. (2020) How to Report Anecdotal Observations? A New Approach Based on a Lesson From "Puffin Tool Use". Front. Psychol. 11:555487. doi: 10.3389/fpsyg.2020.555487. PMID: 33192808; PMCID: PMC7606989.
Schjelderup-Ebbe, T. (*1922*) Beitrage zur Sozialpsychologie des Haaushuhns. Zeitsch F. *Psychol 88*: *226-252*.

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.org/10.1371/journal.pone.0231142

Schluessel, V. (2015) Who would have thought that 'Jaws' also has brains? Cognitive functions in elasmobranchs. Anim. Cogn. 18: 19–37 doi.org/10.1007/s10071-014-0762-z

Schluessel, V. (2015) Who would have thought that 'Jaws' also has brains? Cognitive functions in elasmobranchs. Anim. Cogn. 18: 19–37. doi.org/10.1007/s10071-014-0762-z

Sims, D.W., Southall, E.J., Quayle, W.A., Fox, A.M. (2000) Annual social behaviour of basking sharks associated with coastal front areas. Proc. R. Soc. Lond. series B 267: 1897-904.

Smith, K.R., Scarpaci, C., Louden, B.M. & Otway, N.M. (2015) Behaviour of aggregated grey nurse sharks *Carcharias taurus* off eastern Australia: similarities and differences among life-history stages and sites. Endang. Species Res. 27:69-85. doi.org/10.3354/esr00652

Sneddon, L. U., Lopez-Luna, J., Wolfenden, D. C. C., Leach, M. C., Valentim, A. M., Steenbergen, P. J., Bardine, N., Currie, A. D., Broom, D. M., Brown, C. (2018) Fish sentience denial: Muddying the waters. Animal Sentience 21(1)

Sperone, E., Micarelli, P., Andreotti, S., Brandmayr, P., Bernabò, I., Brunelli, E. & Tripepi, S. (2012) Surface behaviour of bait-attracted white sharks at Dyer Island (South Africa), Mar. Biol. Res. 8(10): 982-991. Doi: 10.1080/17451000.2012.708043

Sperone, E., Micarelli, P., Andreotti, S., Spinetti, S., Andreani, A., Serena, F., Brunelli, E. & Tripepi, S. (2010) Social interactions among bait-attracted white sharks at Dyer Island (South Africa), Mar. Biol. Res. 6(4) 408-414. Doi: 10.1080/17451000903078648

Springer, S. (1967) Social organization of shark populations. In Gilbert, P.W., Mathewson, R.F. and Rail, D.P., eds. Sharks, Skates, and Rays. *Baltimore, MD: Johns Hopkins Pr. pp. 149-74.*

Squire, L.R. & Dede, A.J.O. (2015). Conscious and unconscious memory systems. Cold Spring Harbor Perspectives in Biology. 7: a021667.

Stevens, J.D. (1984). "Life history and ecology of sharks at Aldabra Atoll, Indian Ocean". Proc. R. Soc. Lond. 222 (1226): 79–106. Bibcode:1984RSPSB.222...79S. doi:10.1098/rspb.1984.0050. S2CID 85954905.

Tester, A.L. & Kato, S. (1966) Visual Target Discrimination in Blacktip Sharks (*Carcharhinus melanopterus*) and Grey Sharks (*C. menisorrah*) Pac. Sci. 20:4 461--471

Thibaut, B., Nicolas, L., Adam, B., 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 8: Doi: 10.3389/fmars.2021.678074

Towner, A.V., Leos-Barajas, V., Langrock, R., Schick, R.S., Smale, M.J., Kaschke, T., Jewell, O.J.D. & Papastamatiou, Y.P. (2016) Sex-specific and individual preferences for hunting strategies in white sharks. Funct. Ecol. 30, 1397 – 1407. (doi:10.1111/1365-2435. 12613)

Van Schaik, C., Graber, S., Schuppli, C., & Burkart, J. (2016). The Ecology of Social Learning in Animals and its Link with Intelligence. Span. J. Psychol. 19, E99. doi:10.1017/sjp.2016.100

Vignaud, T.M., Mourier, J., Maynard, J.A., Leblois, R., Spaet, J.L., Clua, E. & Planes, S. (2014). Blacktip reef sharks, Carcharhinus melanopterus*, have high genetic structure and varying demographic histories in their Indo-Pacific range. Mol. Ecol. 23(21) 5193–5207.* doi.org/10.1111/mec.12936

Villegas-Ríos, D., Jacoby, D.M.P. & Mourier, J. (2022) Social networks and the conservation of fish. Commun Biol 5, 178 https://doi.org/10.1038/s42003-022-03138-w

von Frisch, K. (1941) Uber einen Schreckstoff der Fischhaut und seine biologische Bedeutung. Z vergl Physiol 29:46–145

Wang, Y., Liu, D. & Ruhe, G. (2004) "Formal description of the cognitive process of decision making," Proceedings of the Third IEEE International Conference on Cognitive Informatics, 2004., 2004, pp. 124-130, doi: 10.1109/COGINF.2004.1327467.

Wiki Fish calculator https://www.wikifish.co.za/home *(Accessed 14 May 2022)*

Williams, L. H., Anstett, A., Bach Muñoz, V., Chisholm, J., Fallows, C., Green, J. R., Higuera Rivas, J. E., Skomal, G., Winton, M. & Hammerschlag, N. (2022). Sharks as exfoliators: widespread chafing between marine organisms suggests an unexplored ecological role. Ecology 103(1):e03570. 10.1002/ecy.3570