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Ethogram for blacktip reef sharks (*Carcharhinus melanopterus*)

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Abstract

The *chondrichthyan* lineage diverged from the *osteichthyan* line around 440 million years ago, resulting in a vast evolutionary gulf between modern elasmobranchs and other vertebrates. Though this has supported the assumption that as an ancient line, elasmobranchs are dangerously stupid, intelligent actions including social interactions have been noted in the field, while laboratory studies have confirmed a variety of cognitive capacities. Yet, due to fear of sharks and the difficulties of observing them in their aquatic environments, few ethological studies have been done, so their natural behaviour remains little known. On noting that the blacktip reef shark, *Carcharhinus melanopterus*, displayed complex actions during incidental meetings, a long-term ethological study of the species was carried out on the north shore of Mo'orea Island, French Polynesia. During the 6.5 years of the study, new behaviours continued to present. The 35 context-specific actions identified as comprising the behavioural repertoire of *C. melanopterus* are described.

Keywords

blacktip reef shark, *Carcharhinus melanopterus*, shark behaviour, shark ethology, shark ethogram.

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 a lineage that is very different from other vertebrates. Along with their cartilaginous skeletons, for example, the fossil record shows that sharks were already using internal fertilization 390 million years ago (Brazeau & Friedman, 2014). Their behaviour in the wild also presents great differences. While aggression is common in the *osteichthyan* line, for example, fighting among sharks has not been documented (e.g. Allee & Dickinson, 1954; Hobson, 1963; Myrberg & Gruber, 1974; Johnson, 1978; Klimley, 1982, 1987; Gruber et al., 1988). Studies have identified what appears to be warning displays in social contexts (Johnson & Nelson, 1973; Sperone et al., 2010; Klimley, 2023a–c, this issue; Klimley et al., this issue) which take different forms in different species, and which are unique to elasmobranchs. Some fall under the definition of agonistic displays; for a review see Martin (2007). Others are more difficult to categorize (Porcher, 2022). These suggest that elasmobranch behaviour may be more complex than was formerly thought, for shark science has been strongly influenced by fisheries and by the idea that sharks, as an ancient line, are unintelligent and lacking in behavioural complexity (Castro, 2016). However, very few submarine ethological studies have been done, not only due to fear of sharks (Johnson & Nelson, 1973; Randall & Helfman, 1973; Gruber & Myrberg, 1977; Klimley, 2023a), but also because they are fast moving and aquatic (Gruber & Myrberg, 1977; Castro, 2016).

Northcutt (1977, 1978) found that the development and comparative size of the elasmobranch brain are comparable with those of birds and mammals and large relative brain size is positively correlated with complexity of ecological behaviour and cognitive capacities in other vertebrates. Guttridge et al. (2009) reviewed learning reported in earlier studies of elasmobranchs, and since then there has been more interest in intelligent elasmobranch behaviour. They have been found to use cognitive maps (Papastamatiou et al., 2011; Mourier et al., 2011), recognize conspecifics as individuals (Myrberg & Gruber, 1974; Guttridge et al., 2011; Jacoby et al., 2014), use the Earth's magnetic field to navigate (Keller et al., 2021) and to be 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). Laboratory studies have found elasmobranchs to be 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; Brown & Schluessel, 2022).

Remote technologies of increasing sophistication have been used to monitor shark movements in nature and to infer social networks (Mourier et al., 2019).

Ethology is concerned with the natural behaviour of a species in the environment in which it evolved. It involves close, long-term observation of the behaviour of many individuals to gain knowledge of the species' behaviour in different contexts. It emphasizes observing animals under natural conditions in order to understand the evolution, adaptation (function), causation, and development of the species' behavioural repertoire (Tinbergen, 1963). Since mental states are closely tied to behaviour (Jamieson & Beckoff, 1992), direct knowledge of the actions presented by a species in its natural environment can also provide clues to its use of cognition and other subjective states and how they evolved (Jamieson & Beckoff, 1992). To gain such knowledge of a species of elasmobranch, a method for observing their behaviour in detail, long-term, was needed (Gruber & Myrberg, 1977).

Carcharhinus melanopterus (Quoy & Gaimard, 1824) is one of the most abundant reef sharks on tropical coral reefs throughout the Indian and Pacific Oceans (Randall & Hoover, 1995). Their 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). Individual blacktips were easy to observe in the lagoons of French Polynesia, where females, juveniles, and the occasional male of the species ranged (Mourier et al., 2011). When casual observation revealed a variety of behaviours not seen in terrestrial wildlife, it was decided to study the community in the local lagoon as individuals. Johnson (1974, 1978), had observed blacktips extensively in Polynesia and had identified *Nose-to-Tail* following (3.5.1), plus an agonistic display in the closely related grey reef shark (*Carcharhinus amblyrhynchos*). Yet otherwise, little had been published on the species at the time, with the exception of a collection of anecdotes by Randall & Helfman (1973) in an effort to prove that they are dangerous to humans. More recently, Johann Mourier has studied the same blacktip community, using different methods and focusing on their sociality (e.g. Mourier et al., 2012). However, an ethogram, which is the essential first step in the study of the behaviour of a species (Lorenz, 1973) has not been done. The 35 behaviours presented by *C. melanopterus* individuals, in a variety of contexts over a span of nearly seven years, are described here.

2. Methods

The study area was the lagoon between Opunohu and Cook's Bay on the north shore of Mo'orea Island (Galzin & Pointer, 1985). It is between 3 to 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. It was divided into 5 regions for study purposes (Figure 1).

Being watched had a marked effect on the wild sharks, so it was necessary to habituate them to the author's presence. Staged encounters, which involve deliberately attracting the species, provide a method for studying wildlife behaviour (Jamieson & Bekoff, 1992). Accordingly, between 11 April 1999 and 29 September 2005 fish scraps were brought once weekly to specific sites in the nearby lagoon. This tactic was effective in habituating the blacktips to the observer, so that in encounters without food between the feeding sessions they appeared to behave naturally. Using provisioning to form a gathering of sharks for observation has since been used by other researchers in Polynesia (e.g., Mourier et al., 2011; Brena et al., 2018) and elsewhere (e.g. Bouveroux et al., 2021).

Feeding sessions were held during the hour before sunset due to the black-tips' heightened level of alertness at that time. The fish scraps consisted of

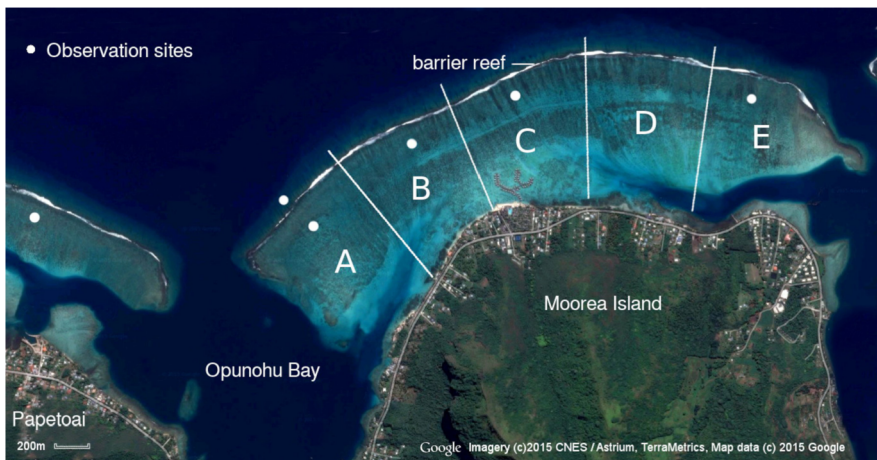


Figure 1. The lagoon divided for reference, showing the location of observation sites. Latitude and longitude: Site A, 17.485568°S, 149.855474°W; Site B, 17.482010°S, 149.849751°W; Site C, 17.479502°S, 149.844196°W; Site E, 17.479668°S, 149.830348°W; Papetoai lagoon site, 17.485447°S, 149.870780°W; Outer reef site, 17.483705°S, 149.857041°W.

the remains of oceanic fish after the meat had been removed for sale by a fish shop or hotel, and the amount varied considerably depending on the supply. As the fishing boats came in on Friday, the scraps were available on Saturday, so the weekly session was held on Saturday at sunset. Occasionally, fish scraps were available during the week, permitting an extra feeding session.

Between feeding sessions, visits were made at random times during the day. The author accessed the lagoon by kayak, went underwater (snorkelling) on the western border, and finned slowly in a zig-zag course eastward for one or two hours, frequently pausing to watch, and moving with any blacktips encountered. Observations were made 1 to 5 times weekly. If the ocean swell exceeded 1.5 m, or the winds exceeded 60 km/h, the session was postponed until the conditions were calm enough. Extra observation sessions were made when some uncommon event occurred, such as a group of rare visitors, a spawning event, a sick or injured shark, or a disappearance (the sharks were sometimes absent from the area). The lagoon borders, the fore-reef opposite site A, and the nurseries at both ends of the barrier reef were monitored to acquire supplementary information about the actions of the species.

The sites were chosen in the deeper channel just within the barrier reef, because both older juvenile blacktips and adults were present there, and the patch reefs tended to be large and well-spaced, allowing a fairly unobstructed view through the coral. Each site required an open area of sand to place the food, big enough to allow at least a dozen adult blacktips to circle with ease. There had to be enough space between the patch reefs for them to access the site easily if they followed the scent-trail up-current, and plenty of space for them to exit on the opposite side. A dead coral structure was required, to use for stabilization while watching, up-current from the food. Once located, the same site was always used in each section. Each feeding session followed the same procedure. The anchor was dropped to allow the kayak to line up between wind and current behind the dead coral used for stabilization. Underwater, equipped with mask, snorkel and fins, the author trailed the kayak to the centre of the site, placed the fish scraps on the sand, finned to the dead coral structure, and watched the sharks while taking notes on a slate. The region near the reef was seldom visited by other people so observations could be obtained without disturbance.

Each blacktip individual encountered was identified using photo-identification techniques (Porcher, 2005) and accurate drawings of both sides of the dorsal fin (see the Identification catalogue at [10.6084/m9.figshare](https://doi.org/10.6084/m9.figshare)).

Table 1.

Summary of the study effort in each section (Figure 1).

Location	Time period	Sessions	Hours	Sightings
Section A				
Site One weekly sessions	4 November 1999–18 March 2005	304	307.75	8734
Day time visits	3 April 2000–6 March 2005	38	37.50	215
Lagoon border	Infrequent	5	8.00	27
Mid section	15 May 2001–30 December 2001	15	12.00	58
Eastern side	21 May 2001–29 September 2005	67	67.25	1140
Section B	3 June 2001–2 August 2003	48	43.70	1070
Section C	8 June 2001–13 April 2002	11	14.50	107
Section E	30 May 2004–4 August 2004	4	2.50	39
Outer Slope	19 May 2002–18 May 2003	5	6.50	60
Papetoai Lagoon	25 May 2000–15 July 2002	7	7.25	64
Totals		504	506.95	11 514

22268605). The length, colour, sex, scars, marks, behaviour, and any other distinguishing features were included in the description of each shark. Over the years, 474 individuals were identified and noted on subsequent sightings (see the Identification catalogue at 10.6084/m9.figshare.22268605), along with the time, marine conditions, and incidental details. The notes made underwater were entered in a computer spreadsheet on landing and used to write a full description of the session. The region near the reef was seldom visited by other people so observations could be obtained without disturbance.

Table 1 summarizes the study effort.

3. Results

The blacktips attending the first feeding sessions held in Section A were mature females whose core areas included the feeding site. Here they are termed ‘residents’ of that area. At first they would not eat when the author was present, circling out of visual range, most of the time, with only brief approaches into view. (The visual range referred to is the distance at which the water becomes opaque due to the accumulation of suspended particles). Occasionally a blacktip snatched a scrap and accelerated away with it, but

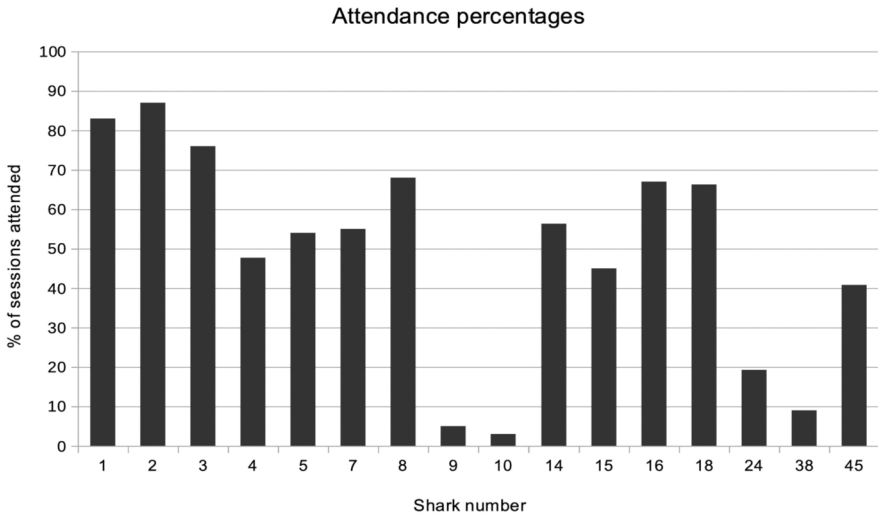


Figure 2. Percentage of sessions attended between Session 10 (8 June 1999) and Session 110 (29 June 2000) by each of the adult sharks identified in Section A during the first three months. Approximately 39% of those identified were juveniles. They are not counted here because they had not yet established a definitive core area and rarely appeared at the sessions long-term.

it was not until the fifth session that the three mature female residents of that region first approached in Triangular-Formation (see Section 3.5.6), circled the author, then the kayak, approached the food, and eventually chose a scrap. On subsequent sessions, these females, Shark Nos 1, 2 and 3, who were soon joined by 8 (see the Identification catalogue at 10.6084/m9.figshare.22268605), were usually to be found within visual range on arrival underwater. By the time three months had passed, all the blacktips arriving within the first half hour at nearly every session had been identified. Most of these were residents with core areas in the vicinity (Figure 2).

Blacktips were considered to be residents when they attended more than 50% of the sessions on average, despite being absent, sometimes for extended periods of time, mostly during the reproductive season (Porcher, 2005). Residents were also seen regularly in the area on transects without food between feeding sessions. Nos 9 and 10 were seen a few times over a period of a few weeks and never again. Nos 4, 5 and 7 were among the few males who resided in the lagoon instead of on the outer slope of the barrier reef. They attended regularly if less frequently.

That first aggregation of sharks would disperse within half an hour, after which as yet unidentified sharks would often arrive. Sometimes they were solitary, other times they came in groups of up to six blacktips of the same sex and approximate size. Each individual was then identified and subsequent sightings were noted. With time and further investigation, it was possible in some cases to learn the locations of these individuals' core areas. For example Sharks No. 24 and 45 (Figure 2) were later found to be residents of Section B. In other cases, it was not possible to learn the origin of the visitors, some of which are now known to have come from other islands (Mourier & Planes, 2013). Some of the identified individuals only returned annually, often with the same companion(s), apparently in correlation with the reproductive season.

Once habituated to the routine of the sessions, the blacktips circled the region while the scraps were placed, then approached individually to glide above the food. Eventually, one would seize a scrap. If it was a vertebral column, the shark would accelerate away with it, shaking it to remove a piece, with several others in pursuit. When it fell, it was swept up by another blacktip, and energetically shaken again. Thus, it was passed from one shark to another until it was gone or dropped in the coral. The smaller scraps were unhurriedly taken and eaten.

In spite of the presence of food, individuals did not avoid each other, and often touched as they came close to each other while investigating the fish scraps. Video 1 at [10.6084/m9.figshare.22268605](https://doi.org/10.6084/m9.figshare.22268605) shows 15 min of feeding session No. A304, starting at $t = 9$ min. The smooth locomotion, velocity, and directional changes typical of the species are seen in site A and vicinity.

During the six and a half years of this study, *C. melanopterus* individuals, especially the residents of Section A, were observed in many different circumstances and the following 35 actions were seen as contextual responses to specific situations.

3.1. Locomotion

3.1.1. Normal Locomotion

Normal Locomotion is the species' way of moving forward. The caudal fin beats back and forth horizontally, driving the shark ahead, which results in an undulation moving through the body (Figure 3a). The shark turns its head in its intended direction, while its fins stabilize it. Video 1 at [10.6084/m9.figshare.22268605](https://doi.org/10.6084/m9.figshare.22268605) illustrates Normal Locomotion by blacktips, which

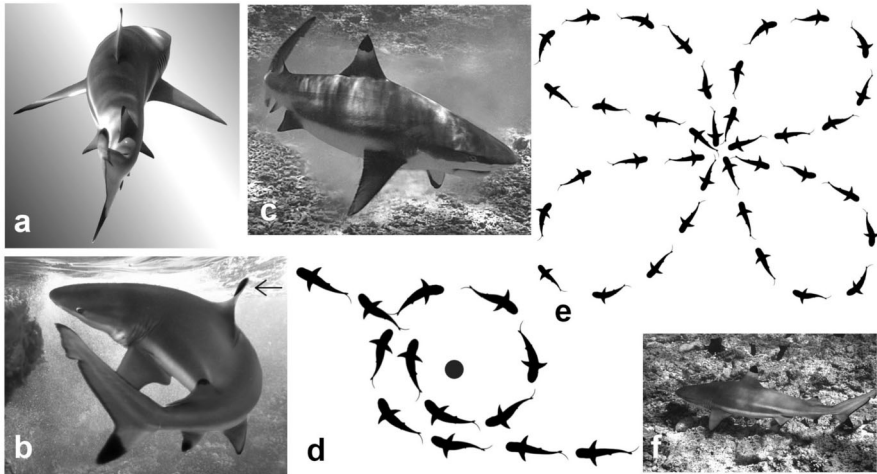


Figure 3. (a) Normal Locomotion. (b) Braking. The arrow indicates the dorsal fin turned perpendicular to the animal's forward motion. (c) Explosive Glide. Note the lowered pectoral fins. (d) Graphic depiction of an advancing blacktip seeing an object of interest and turning towards it, resulting in Circling. (e) Ranging. Graphic depiction of the looping pathways used by *C. melanopterus*, oriented each time in a different direction. (f) A female blacktip Resting.

motion is obligatory due to ram ventilation (Jacoby et al., 2015). Normal Locomotion can be done so slowly that only the tip of the caudal fin moves slightly, or at high velocity, involving strong undulatory motion of the whole animal, while the head remains most stable.

In the shallow lagoon, the blacktip travels in mid-water, from which position it ascends or descends on detecting something interesting enough to investigate.

3.1.2. Braking

The blacktip decelerates by changing its trajectory. Its dorsal fin is seen to be perpendicular to its former direction of travel (Figure 3b).

3.1.3. Gliding

Gliding intersperses Normal Locomotion. The blacktip's horizontal undulations almost cease as it moves forward under its own momentum, its pectoral fins in the normal, essentially horizontal position. Gliding results in deceleration, and often occurs when something has apparently caught the animal's attention and it pauses before possibly altering its trajectory.

3.1.4. *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 are usually lowered during this action (Figure 3c).

3.1.5. *Circling*

The blacktip circles something of interest. Since it cannot cease Normal Locomotion to look at something due to obligate ram ventilation, Circling is the way it stays in one location (Figure 3d). It begins by fixing its closest eye upon the object, and in looking, it turns in that direction and thus pursues a circular path, usually at a distance of 2 to 3 m. However, at times, certain sharks would circle steadily around the feeding site at a distance of about 15 m, so the radius of the circle appears to depend on the shark, the situation, and the shark's reaction to the situation.

3.1.6. *Ranging*

When travelling to a specific place or region, the blacktip shark takes a direct route. However, the species was observed to spend a large proportion of its active time following a sinuous path through its preferred range in roughly oval pathways (using Normal Locomotion). Each new loop is oriented in a different or opposite direction from the last one so that the pathway forms rough figures-of-eights and cloverleaves as viewed from above (Figure 3e).

3.1.7. *Resting*

As the sun rose above about 45°, the resident blacktips went to a place where the lagoon was relatively open and free of obstacles to cruise slowly, Resting, a few centimetres above the sea floor, mostly with one or more companions (Figure 3f). They were much less alert at such times, to the degree that they could be surprised. A wide barren region of coral rubble between Sections A and B was deeper than average and used for Resting by individuals from both Sections. At times, some of the females went to deeper water off the fore-reef to cruise, Resting, in mid-water, not far past the turbulence of the waves breaking on the barrier reef. They reportedly did not attend the shark feedings held for divers farther out (Philippe Molle, Boumediene Boucif pers. commun., 2002), which took place at a depth of about 30 m. This suggests that when the females went onto the fore-reef, they remained in relatively shallow water. The blacktips became active and alert again in the late afternoon, after the sun descended past approximately 45° above the horizon.

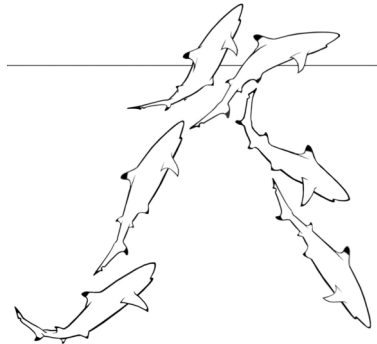


Figure 4. Breaching. The horizontal line represents the water surface.

3.1.8. Breaching

Blacktip sharks Breach by speeding near-vertically through the surface from below. In the study lagoon, the water averaged about 2 m deep and they began their upward acceleration by turning just above the sand (Figure 4).

3.2. Eating-related behaviour

3.2.1. Search Mode

The shark moves just above the sea floor, often changing direction using smooth circles, figures-of-eights and ovals (see Video 1 at 10.6084/m9.figshare.22268605). Sometimes it lowers the pectoral fins to the sand; they are also lowered when making tight turns. This circling can be done over a small region and involve continuous turning, with the shark's body taking the shape of its pathway, the nose near the caudal fin. In this study, the blacktips were seen to adopt Search Mode as they looked around for scraps that had been dropped by other blacktips, or swept into the surrounding coral by the current, after the original pile was gone.

3.2.2. Sniffing

The shark pauses in mid-water, raising its snout, apparently to sniff the current. This was regularly observed when blacktips passed through a known scent trail (Video 2 at 10.6084/m9.figshare.22268605), as when they sniffed down-current from the kayak (drain holes permitted scent to escape into the water from the well where the fish scraps were kept).

3.2.3. Suction feeding

Often when a blacktip chose a scrap, even though it was still 20 cm away, it opened its mouth and the scrap was sucked in, apparently through suction

feeding. The scraps were more usually picked up with the jaws however, so suction feeding was used only intermittently, usually at times when a smaller scrap lay separated from others on the sand.

3.2.4. *Palatoquadrate adjustment*

Blacktips will protract the *palatoquadrate* (the upper jaw), while eating. After eating, individuals were sometimes observed alone in the coral, opening and closing their jaws in an apparent effort to readjust them.

3.2.5. *Head-shake*

On taking a scrap too big to swallow (such as the vertebral column of a large oceanic fish), the blacktip shakes its head several times in the horizontal plane while accelerating and rising into the clearer area above the coral (Video 1 at 10.6084/m9.figshare.22268605). As a result, the saw-like teeth cut out a mouthful of food. The only other time shaking of the head was observed was in just one case, when a shark shook its head several times at intervals in an apparent attempt to rid itself of a remora attached to its chin.

3.2.6. *Predation*

The blacktip makes a sudden, targeted acceleration, often near-vertically, to snap up a fish. Conspecifics were seen to be attracted and go into high-velocity Search Mode throughout the vicinity.

3.3. *Grooming behaviours*

3.3.1. *Chafe*

A blacktip will flip onto its back to wriggle with its dorsal surface against the sand, or whip its side against a sand bank, presumably to free itself of ectopic parasites. It will also position itself to Chafe its ventral surface on worn, dead coral (Figure 5).

3.4. *Investigative behaviour*

A state of vigilance characterized the actions of the blacktips, yet they showed a strong tendency to investigate things in their environment. This combination generated a variety of tactics that they used to remain hidden while investigating novel phenomena.

3.4.1. *Approach*

At the limit of the observer's visual range, the shark passes into view and out again. A few minutes later it makes a closer pass. It repeats this pattern,

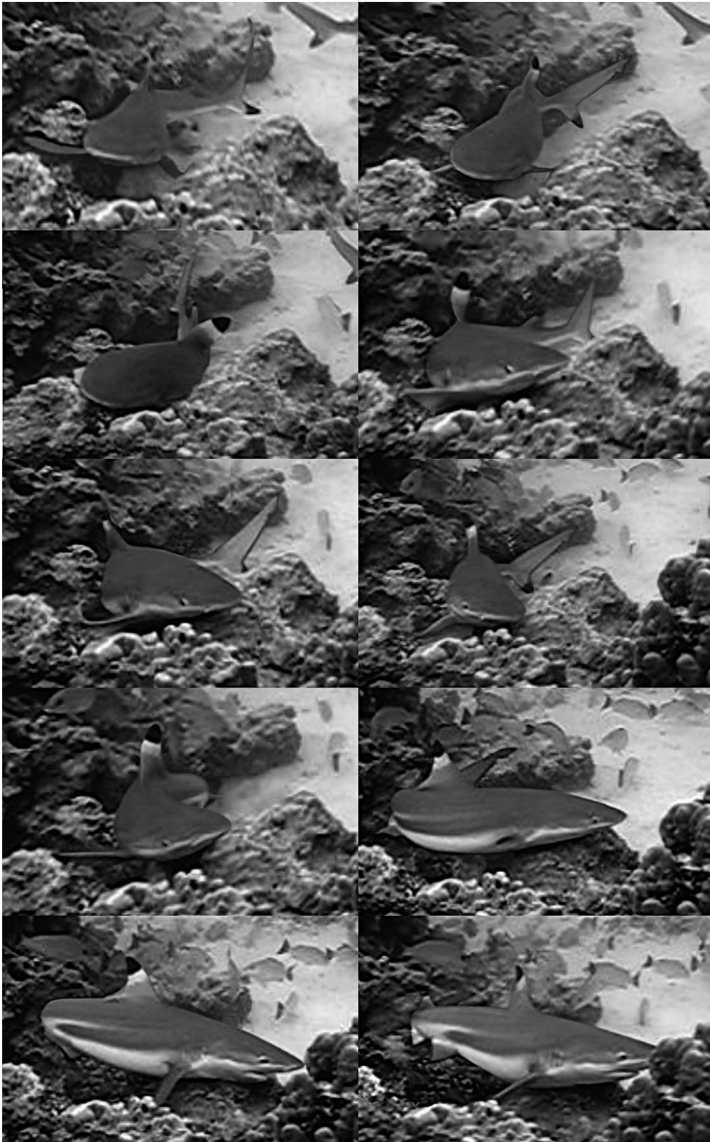


Figure 5. A young female blacktip chafes the ventral surface on worn coral. The images are in a series of intervals of less than a second.

approaching more directly each time, until it might make a direct, close Approach (Figure 6). This general pattern varied depending on the context and individual.

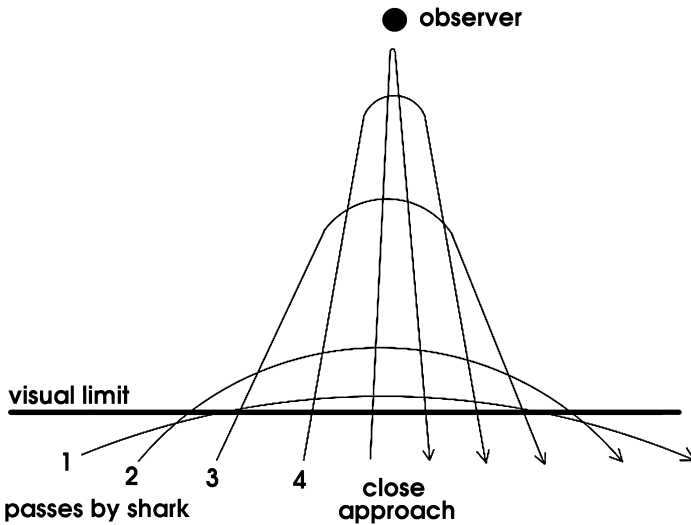


Figure 6. The progressive approach pattern of *C. melanopterus*.

3.4.2. Following

The shark follows another animal (in this case the observer) beyond visual range. This was exemplified on observation excursions through the lagoon. Certain residents would follow the author, sometimes for hours, apparently 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 blacktips were Following by waiting, unmoving, until they came into view, usually together.

3.5. Social behaviours

Social behaviour was commonly seen among the blacktips. Visiting blacktips regularly appeared, singly or in groups of up to six of the same sex and approximate size. The resident females would merge with the visiting females, accelerate, and soar through the vicinity in a ragged linear formation. There were occasions when the fish scraps were ignored, suggesting that socializing took precedence over eating at these times. Certain annual visitors arrived year after year with the same companions, though other visitors always appeared alone. Certain groups, including some of those that visited rarely, and certain visitors, aroused more interest and triggered longer periods of higher velocity interaction, than others. 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, presumably to seek an opportunity to mate. On occasions when they paused at the feeding site, some of the resident females reappeared and moved with them.

3.5.1. *Nose-to-Tail following*

One shark follows another with its snout within 30 cm of the leader's tail. Resident female blacktips interacting with female visitors were observed to catch up with another female until her nose was at the other's caudal fin (Figure 7a). She would usually advance to swim at the other's side at a distance of <math><0.5\text{ m}</math> for several seconds before resuming her arcing pathway, then catching up with a different female, and briefly accompanying her before circling on.

3.5.2. *Circling Head-to-Tail*

Two blacktips follow each other Nose-to-Tail, their bodies arced to form a circle. This was often seen in the smaller juveniles, and especially in the nurseries among the pups, but not in adults.

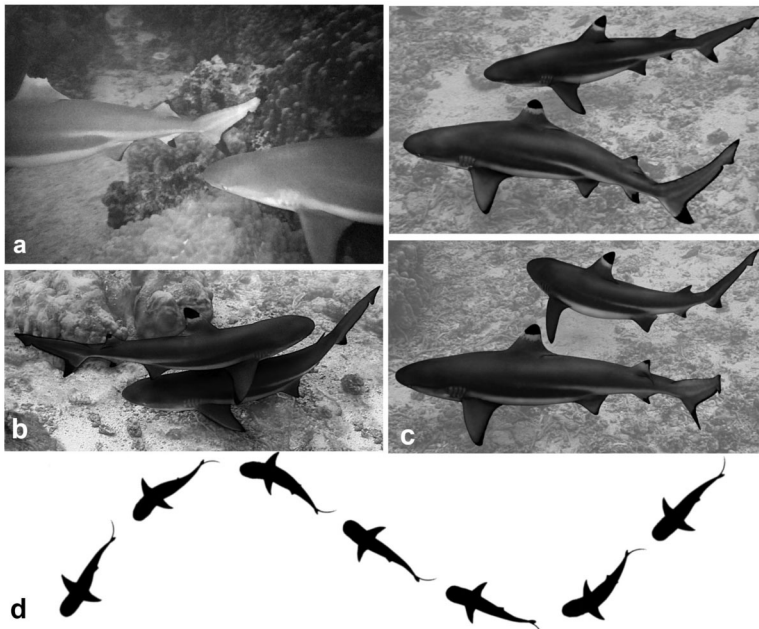


Figure 7. (a) Nose-to-Tail following. (b) Two juveniles perform a Swim-By. (c) Two female sharks with overlapping core areas turn towards each other and Parallel briefly on meeting. (d) Graphic depiction of Follow-Formation.

3.5.3. *Swim-Bys*

When meeting in the lagoon, companion sharks and acquaintances, mostly individuals of the same sex and approximate size, often perform a Swim-By, as named by Sperone et al. (2010). The blacktips would arc towards each other until they were approaching head on, then pass each other with an inter-animal distance of <10 cm (Figure 7b; Video 3 at 10.6084/m9.figshare.22268605).

3.5.4. *Parallel*

When two blacktip acquaintances meet, they will often approach each other and move parallel to each other (Parallel) with an inter-animal distance of <0.5 m for a few seconds (Figure 7c; Video 3 at 10.6084/m9.figshare.22268605). They also move in Parallel as described above (Section 3.5.1), after one individual has caught up to another from behind.

3.5.5. *Follow-Formation*

Follow-Formation presented as Nose-to-Tail following by more than one blacktip simultaneously, usually, but not always, by sharks of the same sex (Figure 7d). When visitors were present, many instances of Follow-Formation, most not involving more than three or four sharks, formed and dissolved as the gathering of blacktips moved swiftly and flexibly together.

3.5.6. *Triangular-Formation*

When confronted by a novel or challenging situation, blacktips will occasionally approach in Triangular-Formation to investigate — one in front and two, one on either side, about a body length apart and equidistant, directly behind the leading shark.

3.5.7. *Cutting Across*

A blacktip travelling with another decelerates and turns at right angles to Cut Across the other's path.

3.5.8. *Travelling with companions*

The blacktip travels with one or more companions. The wide circles they pursue while Ranging take them out of visual range of each other, then back into each others' vicinity at regular intervals.

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, pursuing a sinuous pathway of loops and figures-of-eight which repeatedly

brought them back together. Shark pups were especially easy to observe from above the surface in the shallows and nurseries. Repeatedly they circled together, then arced away to move through the surroundings, always coming together again through their orbits and figures-of-eights. Often they Circling Head-to-Tail. These continuously circling patterns resembled the ranging patterns of movement presented by the adults on a larger scale.

3.5.9. *Circling Together*

Sometimes the gathering of resident blacktips Circling Together around something of interest. Most circled in the same direction, though some moved counter to that; individuals usually showed a directional preference. The preferred direction when Circling Together was counter-clockwise among the blacktip residents of Site A.

3.6. *Interactive behaviour*

These behaviours involve other species (including the observer).

3.6.1. *Close Approach*

The blacktip approaches the face directly, then passes close by, or turns away at an acute angle (Figure 6). When the resident blacktips had become familiar with the sessions at Site A, on arrival underwater, up to six of the female residents (depending which ones were present) would turn towards the author and one by one perform a Close Approach very slowly.

The Close Approach was done at different speeds, depending on the circumstances. At the feeding sessions, a blacktip would occasionally make a Close Approach to a Javanese moray eel (*Gymnothorax javanicus*), when one emerged from its hole and approached the fish scraps. The shark appeared to pause at a distance that depended on the eel's reaction to the gesture.

Another variation was used on Tahitian spear-fishermen, who reported (various pers. comm.) that blacktips would harass them in an effort to get their catch of fish (they said) by dashing up to their faces and away again.

3.6.2. *Charging*

Under certain circumstances, the blacktips would Charge, advancing at medium to high speed and passing just to one side (Figure 8a). Charging differed from the Close Approach in that it was directed towards the mid-body and was usually repeated at intervals. Conspecifics might join in, often in Follow-Formation.

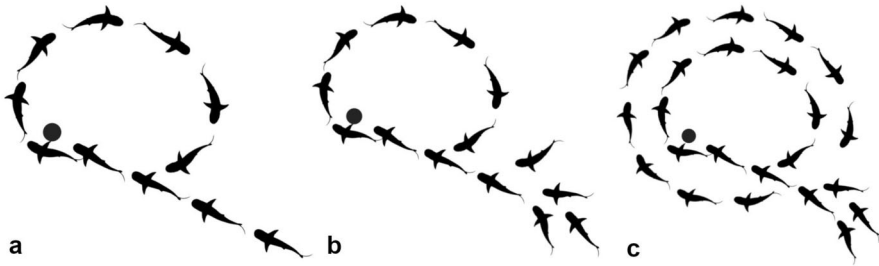


Figure 8. (a) Charging. (b) Conspecifics join in, in Follow Formation. (c) Circling Charging.

3.6.3. Circling Charging

On rarer occasions, Charging, circling away and Charging again results in Circling Charging as other sharks join in and their level of arousal increases (Figure 8b). Other blacktips join in Follow-Formation initially, following the leading shark directly up to the target before turning away. Then these individuals will often begin Charging independently (Figure 8c). A period of an hour is the longest that the author witnessed Circling Charging to continue, and the entire gathering of 36 blacktips, including two rare visitors, took part. This behaviour pattern can break out into Slamming.

3.6.4. Slamming

The blacktip accelerates towards a target and Slams into it with the force of its momentum. 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 (Figure 9). Slamming can be done with great force.

These actions were seen in a variety of circumstances. Once a leading shark had begun, the others present joined in. Intimidating, high-speed Close Approaches became Charging, Circling Charging, then Slamming, and involved the entire company of blacktips present (Porcher, 2022).

3.6.5. Undulating Against Another

The shark Undulates Against Another body. During this study, but after several years, certain residents began Undulating Against the author's kayak on its arrival in the lagoon. Initially, they Undulated Against the boat while remaining at the surface (Figure 10a).

After two episodes, the individuals involved began ascending directly upwards from the sand beneath (Figure 10b), Undulating Against the craft

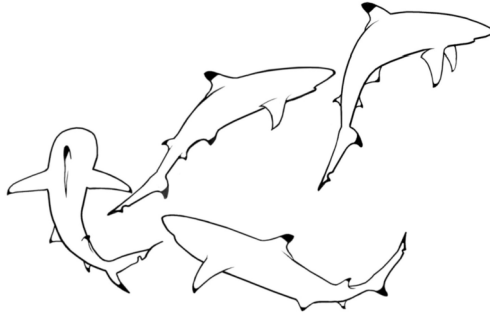


Figure 9. Slamming involves the shark turning beneath the target and gaining altitude while lowering the tail and hunching the back. With the powerfully beating tail pointing straight downwards, it accelerates upwards with great force.

(Figure 10c), then turning to go straight downwards, so that their tails emerged through the surface (Figure 10d). 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 action than simply performing a brief Undulation Against Another at the surface. These individuals performed this action each time the author arrived at Site A thereafter.

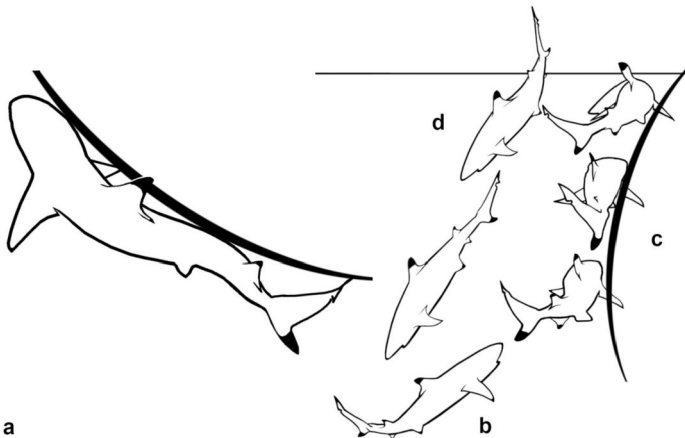


Figure 10. (a) Undulation Against Another at the surface. (b) Undulation Against Another starting below and descending again. The line at the top represents the surface. The blacktip turns at the sand. (c) On arrival at the surface it Undulates Against the other. (d) The blacktip descends.

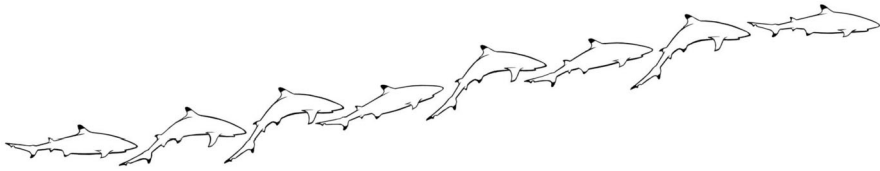


Figure 11. Graphic depiction of the Startle Response. With several sharp vertical hunches, the blacktip rises into the clear area above the coral and accelerates out of visual range.

3.7. Fear reactions

3.7.1. Bolting

The shark accelerates out of visual range. This is the usual fear reaction (Video 4 at 10.6084/m9.figshare.22268605).

3.7.2. Startle response

The blacktip accelerates away from a source of fear while arching its back vertically and depressing its pectoral fins in a series of rapid jerks. 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 (Figure 11) out of visual range.

The Startle Response was commonly seen in juveniles as a reaction to a near-collision with a much larger shark, usually a nurse shark (*Ginglymostoma cirratum*). Adult blacktips too, would sometimes accelerate away with a few sharp vertical undulations when Startled by a near-collision with another shark.

3.7.3. Shiver Mode

After fleeing as a result of the Startle Response, the blacktip is likely to circle back in Shiver Mode. Shivers run through its body, and it suddenly twists and changes direction erratically. Though Shiver Mode was usually seen in juveniles, shivering and unpredictable turns were also occasionally observed in adults who appeared in an aroused state for unknown reasons. Moving swiftly, while shivering and twitching at times, the animal would make sudden rushes, then whip back around in a tight circle. The restless Shivering, flicking, and twisting usually continued for less than one or two minutes, but on one occasion an individual remained in Shiver Mode for about, 20 min, suggesting that it can also indicate a longer-term negative subjective state (Porcher, 2023).

4. Discussion

Watching the individuals in this community of wild blacktips in semi-controlled conditions over a period of several years provided the opportunity to gather much information on their natural behaviour. Many of their actions have been noted by other researchers, including in other species, which suggests that they are likely part of the behavioural repertoire of closely related species, and possibly evolved in ancestral forms.

The ways sharks use to advance through the water column, for example, has been intensely studied in many species and is described in detail in Klimley et al. (this issue). The Explosive Glide was first identified by Myrberg & Gruber (1974), in bonnethead sharks (*Sphyrna tiburo*) while ranging has also been seen by other researchers. The pattern here observed closely resembles the descriptions of Stevens (1984) at Aldebra Atoll (Seychelles). He wrote that the blacktips 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”.

Papastamatiou et al. (2009b) described blacktips at Palmyra Atoll (Line Islands) using patches that were 3 to 17% of the scale of their home range for periods of days. They repeated straight movements along ledge habitats, which was theorized to be the most efficient search strategy when foraging is unpredictable. They moved using a ‘direct walk’ while in preferred foraging patches, and appeared to move randomly between them.

The observed Ranging pattern provides good coverage of a given region, and appears to be well suited for locating prey visually, as well as intercepting scent flows, including the chemical signatures of conspecifics from beyond visual range (Johnson & Nelson, 1978). Blacktips would presumably also be aware of the underwater sounds made by other sharks within range (Myrberg et al., 1976) through hearing and the lateral line sense (Gardiner & Atema, 2007, 2014; Bleckmann & Zelick, 2009).

Papastamatiou et al. (2015) found that the need to regulate the body temperature had a strong influence on the species’ daily routines in Palmyra Atoll. At different times blacktips chose warmer or cooler water to serve their needs. They presented a peak of activity in the low-light period at and just after sunset, for at that time, blacktips not only have a sensory advantage over their prey, but also a thermal one (Papastamatiou et al., 2015).

They found that the blacktips of Palmyra Atoll also tended to Rest in deeper water (Papastamatiou et al., 2015), which correlates with the patterns of Mo'orea blacktips observed. In the barren area or in the ocean where the blacktips in this study went to Rest, their forward motion was relatively unimpeded by coral structures. Further, in the deeper water, they were out of the brilliantly lit shallows of the white-sand lagoon. Papastamatiou et al. (2009a) also noted that multiple sharks Rested in the same area, as was observed here. A possible reason might be the sharks' lowered level of awareness at these times. With many sharks Resting in the same region, if there was a disturbance, the reaction of the sharks directly affected would be perceived by others through the lateral line, even though the disturbance was beyond visual range.

A series of actions similar to Search Mode was documented in bonnet-head sharks and termed Manoeuvring by Myrberg & Gruber (1974), who noted that it had been reported in other species and was thought to be the sharks' way of orienting to a spot on the substrate. They also described the Head-shake, which they saw not only when feeding, but in association with the Explosive Glide (Myrberg & Gruber, 1974) and what they termed 'competitive situations.' The Head-shake has also been documented in grey nurse sharks (Smith et al., 2015). Klimley (1985, 2023b (this issue)) noted that scalloped hammerhead sharks (*Sphyrna lewini*) perform a Head-shake as a social reaction while retreating after a competitive encounter. However, the blacktips did so only to extract a bite of food from a large piece, with the one exception of an attempt to be rid of a remora (Section 3.2.5).

Palatoquadrate adjustment was regularly seen in the blacktips during and after feeding, and has also been noted in the grey nurse shark (*Carcharias taurus*) (Smith et al., 2015). The palatoquadrate is not fused to the brain case (Moss, 1972) and the jaws are supported instead by the cartilaginous 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 (Moss, 1972).

Chafing has also been widely documented in sharks. Chafing against the sand is widely described (e.g. Myrberg & Gruber, 1974; Ritter, 2011; Smith et al., 2015; Williams et al., 2021). Here, the blacktips were observed to turn on their backs to Chafe against the sand, and to rub their ventral surfaces against smoothly-worn dead coral structures. Their consistent choices of an appropriate feature on which to scratch, whip against, or Chafe upon, suggest

active structure selection, providing an example of decision making (Wang et al., 2004).

Nose-to-Tail following in *C. melanopterus* was first documented by Johnson & Nelson (1978); a male blacktip approached a female from behind and followed Nose-to-Tail prior to copulation. Mourier et al. (2011) also observed blacktips following Nose-to-Tail. The behaviour has been reported in bonnethead sharks (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 observed that Nose-to-Tail following occurred most often with the arrival of a newcomer. That is consistent with these present observations of socializing blacktips approaching each other from behind and following briefly Nose-to-Tail when visitors were present. Circling Head-to-Tail, in which both sharks follow Nose-to-Tail simultaneously, was reported in bonnethead sharks by Myrberg & Gruber (1974).

Moving in Parallel was noted in this same community of blacktips by Mourier et al. (2011), and in white sharks by Sperone et al. (2010). They also documented Swim-Bys being performed by white sharks and specified that this social action, along with moving in Parallel, was most often performed by individuals of the same sex and approximate size, as was seen here.

Other behaviour patterns were evident in the context of this study.

4.1. Eating behaviours

The blacktips' behavioural pattern of eating together is curious because in this situation, it was not the best nutritional strategy. While they were chasing through the surroundings, repeatedly snatching up a scrap that had been bitten by a conspecific and dropped, the fish and nurse sharks often took the rest of the fish scraps. Thus, the blacktips would have benefited more had each one taken their own piece of food. Since in general blacktips are solitary predators (Frisch et al., 2016), an explanation for their actions is not evident, for this pattern of behaviour suggests that blacktips do have a tendency to eat together. Possibly they frequently acquire pieces of food that are large enough to eat this way — for example, when feeding off a large carcass. Further observations might provide insight into the reasons for their actions.

Although *C. melanopterus* usually took the fish scraps in their jaws, they were observed at times to suck in a scrap from a distance of up to about

20 cm, after which there was a burst of cloudy water from the gills. This resembled the suction feeding described for nurse sharks (Motta et al., 2002) in which 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.

It was repeatedly noted that after an act of predation by a blacktip, conspecifics in the vicinity suddenly went into high-velocity Search Mode. This might be due to the fish releasing what has been termed a ‘fright’ substance that warns conspecifics of danger (von Frisch, 1941), or possibly fish vocalize when caught. Otherwise, the cause of this reaction is unknown.

4.2. *Attending beyond the visual limit*

The apparently systematic use of the visual limit for concealment by *C. melanopterus* suggests that individuals of this species are comfortable perceiving events from beyond visual range, apparently by integrating information from other senses. Moving through a vibrating realm in which light travels less easily than sound, blacktips’ use hearing (Myrberg, 2001) and the lateral line sense (Gardiner & Atema, 2007, 2014; Bleckmann & Zelick, 2009), which directly perceives underwater vibrations. Sharks in general hear well (Myrberg, 2001) and are particularly sensitive to low frequency sounds of 40 Hz to approximately 800 Hz, which includes sounds made by other animals moving in the vicinity. The lateral line sense does not respond to acoustic stimuli (Myrberg, 2001), but to pressure changes, such as those generated by other animals as they move, and to waves made by their own actions, bouncing off obstacles (Gardiner & Atema, 2007, 2014; Bleckmann & Zelick, 2009). It even contributes to the location of scent flows (Gardiner & Atema, 2007). While the ampullae of Lorenzini are extremely sensitive to electric stimuli, heat, mechanical influences, and salinity (Kalmijn, 1966; Sisneros & Tricas, 2002; Josberger et al., 2016; Anderson et al., 2017), they work at close range only.

Shark vision has been found to be acute (Gruber & Cohen, 1978), and the blacktips’ repeated passage into visual range suggests that visual input was also important to them. Myrberg (1991) hypothesized that contrasting fin markings may play a role in species recognition in *C. melanopterus* and 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.

The blacktips' habit of Following another animal while remaining beyond visual range is another example of their routine integration of input from several senses to analyse ongoing events. They doubtless also Follow other species, remaining beyond visual range.

During the blacktip sessions it was noted that the whitetip reef sharks (*Triaenodon obesus*) and sicklefin lemon sharks (*Negaprion acutidens*) who attended intermittently, also used the visual limit for concealment. Tiger sharks (*Galeocerdo cuvier*) and Atlantic lemon sharks (*Negaprion brevirostris*), observed for shorter periods of time in the Bahamas, performed in a similar way. When approaching a gathering of scuba divers and other sharks, they passed just within visual range for a look, came closer <5 min later, then nearer again after another delay, though it was observed that tigers tended to pass overhead for a close look. For oceanic species especially, the visual limit is the only thing available to use for concealment, which might explain why it is used by so many species.

4.3. Social behaviours

Myrberg & Gruber (1974) noted that Follow-Formation, involving 3 to 6 sharks following a conspecific in single file, was occasionally adopted by their captive bonnethead sharks, particularly after the biggest female was introduced. However, in that case the Followers consisted of males, while here, Follow-Formation was most often presented by socializing female blacktips (within the lagoon). The natural sex segregation in the wild blacktips as opposed to the bonnethead sharks' being in a state of confinement in an aquarium, could explain this difference. Follow-Formation was also adopted most often with the appearance of certain individuals. For example, when Shark No. 24, an aged female from Site B (who was also one of the biggest blacktips attending), visited Site A, she always attracted attention from those present. Follow-formations formed and dissolved behind her almost continuously as she moved. On one occasion, she performed a U-turn in a narrow coral canyon, and all six of her followers did too.

Follow-Formation was not only adopted by the blacktips when following a conspecific, but also when confronted with a novel scene. An example is the blacktips' reaction to perceiving a scuba diver (who once accompanied the author to a session) for the first time. After disappearing beyond visual range for a full 10 min, they suddenly came forward in Follow-Formation: 35 blacktips in two lines, single-file, following two sharks who had shown

leadership tendencies in the past (Guttridge et al., 2011). Possibly the bonnethead sharks were not stimulated to take Follow-Formation by the type of unexpected events that regularly confronted the wild blacktips. As Myrberg & Gruber (1974) noted, these formations are context-specific.

Triangular-Formation was adopted more rarely, also when individuals confronted challenging situations. The best example of it here observed, was the initial approach to a feeding session by Shark Nos 1, 2 and 3 — Session 5 on 7 May 1999. They came in Triangular-Formation. Though No. 3 was the individual who usually took the lead among those residents, in this case, it was No. 2, who otherwise did not distinguish herself, who was in the leading position. Three years later — in Session 247 on 11 May 2002 — those same three sharks, in the same positions in Triangular-Formation, left the centre of the gathering where the food was and accelerated forward to Slam the author. After being fought off, they immediately regained the same positions in Triangular-Formation to return to the food area.

The adoption of Follow formation and Triangular-Formation in challenging situations is a possible indication of social buffering in the species (Kikusui et al., 2006), wherein individuals prefer to approach novel situations or objects together rather than alone. Further observation of this type of behaviour in blacktips and other species might provide greater understanding of such group-actions, especially in terms of their social natures and accompanying cognition. Such instantaneous, seemingly coordinated behaviour among several individuals presented the appearance of planning and structure, yet the blacktips' movements were always flexible and liquid — the formations suddenly formed and dissolved with no visible sign of any communication taking place.

The circling, Ranging pattern that blacktips use is evidently suited to crossing and recrossing scent trails as well as visible prey. Given that we know that this species picks up the scent trail of conspecifics (Johnson & Nelson, 1978), we can hypothesize that blacktip companions remain in loose contact through repeated crossing of each others' scent trails. While it is also likely that they are aware of conspecifics in the vicinity using hearing and the lateral line, the way they would systematically follow companions and other conspecifics to catch up with them from behind, suggests that chemoreception is likely the primary focus in this context.

Cutting Across was used flexibly in a variety of circumstances and differently by different individuals. For example, Shark No. 1 always Cut Across

if the author tried to accompany her, prior to accelerating away. On several occasions a blacktip who had been travelling in the vicinity of the author for a period Cut Across before turning 180° and departing, always in the region that bordered her core range. An unknown female blacktip Cut Across 5 times while being followed 1.5 km along a different lagoon for 35 min.

The blacktips frequently Breached in this study to access the fish scraps held in the back of the kayak when it arrived at the site. After they broke through the surface, they saw them, leaned towards them, and snapped at them — they had found a new foraging technique. Breaching to access the scraps was done independently by two different gatherings of sharks. In one case it was initiated by one shark, in the other by three or four, then the others present did the same, apparently by copying them. Thus, their actions appear to be a case of social learning (Guttridge et al., 2013).

When the Section A blacktips Circled Together, the direction was counter-clockwise, although two or three would circle clockwise, counter to all the others. Most of the blacktips appeared to have a preferred direction, though it was not evident whether they had a preferred eye or a preferred circling direction, or both. Lateralization has been widely found across the animal kingdom (Brown, 2014) and closely analysed in fish (Bisazza & Brown, 2011; Brown, 2014). However, the pattern varies between species, populations, and individuals, so the presence of lateralisation in the blacktips is impossible to interpret with relevance here.

4.4. Interactive behaviour and agonistic displays

Agonistic displays have been seen in a variety of shark species. The first was documented in the grey reef shark by Johnson & Nelson (1973). Since then, more agonistic displays have been identified. Klimley et al. (1996) found evidence of a ritualization of conflict in the great white shark. 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; Klimley, 2023a (this issue)). The exchange appears to be a communication involving a show of power, which allows the great sharks to decide and agree on which of them will get the seal. Thus a physical battle that would badly damage both sharks is avoided.

Martin's comprehensive review (2007) describes agonistic displays in 23 species of sharks from 6 families including the great white, the tiger (*Gale-*

ocerdo 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. 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 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 review (2007) indicates that agonistic displays are likely widespread in elasmobranchs, but what evidence exists is mostly anecdotal and incomplete. Though the grey reef shark's posturing is exceptional in its form and presentation, in other species such displays seem less clearly defined or predictable (Martin, 2007). As in the blacktips, 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.

Though the blacktips most familiar with the author performed the Close Approach slowly as an apparent greeting gesture, when it is done fast, it appears to carry the intention of intimidation. The blacktip habit of accelerating up to spear fishermen with the intention of harassing them into giving up their catch is an illustration. In such cases, the action falls under the definition of an agonistic display, though lacking the components of vertical hunching and muscular flexing. However, these are present in Slamming behaviour, into which the Close Approach can escalate. But Slamming is not a display. It is an instantaneous attack without pre-signalling (Porcher, 2016).

The incident in which the entire gathering of blacktips accelerated from beyond visual range up to the face of the visiting scuba diver in two lines of Follow-Formation (Section 4.5) appeared to be a mass Close Approach

done fast; that is, with the intention of intimidating. The diver was enveloped in a swirl of swiftly moving sharks and he fell over backwards. Though an experienced dive club owner and shark diver, he was intimidated.

Other researchers have concluded that such actions are intentional efforts to communicate a negative subjective state (Johnson & Nelson, 1973; Klimley et al., 1996; Martin, 2007), and several of the blacktips' actions, especially Charging, Circling Charging, and Slamming, also presented as such (Porcher, 2022).

In the case of blacktips approaching Javanese moray eels, the Close Approach resembled predator inspection, with the inspector 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, apparently for a closer look. Here, the Close Approach by a blacktip to an eel involved another meso-predator 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 blacktips might have learned something about them from experience. Johnson (1978) includes an incident wherein he witnessed a moray eel wrap itself around a shark's gills after a dispute over food, whereupon the shark tried to bash the eel off by writhing and whacking itself on the surrounding coral structures (Johnson, 1978).

Martin's review (2007) names *C. melanopterus* among the species that will display, yet includes no details, mentioning only that blacktips will lower their pectoral fins while turning past a diver. However, this observation seems inconclusive when they lower their fins in tight turns (Section 3.2.1). In spite of attending recreational dives with dive clubs on several islands as well as Mo'orea, in which blacktip sharks were among those present, the author did not identify any such agonistic gesture towards divers.

Martin does not identify the commonly-presented Close Approach of the species as an agonistic display, nor the Startle Response. 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 various species of sharks through 'sustained, oriented pursuit' and stated that they had been unable to illicit an agonistic display in *C. melanopterus*.

The blacktips' Startle Response presents as being homologous to the grey reef's agonistic display, but it is neither a display, nor agonistic. It appears to be a reflexive reaction 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 blacktip rapidly departs, and this upward trajectory is also achieved by the arching of the back, resulting in the powerful tail pointing downwards. The vertical jerking during acceleration as the blacktip takes flight likely enhances predator avoidance by making the shark more difficult to grasp.

Myrberg & Gruber (1974) identified a startle reaction in bonnethead sharks, however in their case, no vertical jerking was noted. They also defined a Hunch posture which caused the tail to lower. However, this was not connected with fleeing, but was described as an agonistic display towards a newcomer in the pool, a smaller shark, or a diver present.

Carcharhinus melanopterus arched the back and accelerated upwards while Slamming, but never in warning. By the time the back hunched, the shark was already launching itself, and it 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 blacktips 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. During this study, including two occasions on which blacktips suddenly Slammed the author personally, it was used only as a method of attack (Porcher, 2016, 2022).

Although Martin (2007) mentioned a brief ‘shivering’ in the silvertip shark during an agonistic display, his description does not resemble the shuddering and randomly darting behaviour, here termed Shiver Mode, that often followed the Startle Response in the blacktips, and which left no doubt that the behaviour 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 blacktips appearing in Shiver Mode, which also involved repeated twitching, had been negatively disturbed (Porcher, 2023 (this issue)).

It is possible that gestures and displays in the various species of sharks differ between geographical regions. The blacktips of the volcanic islands in the central Pacific are descended from those individuals who crossed thousands of kilometres of ocean from the continents to the west to find them

(Maisano Delser et al., 2019). 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.

A curious aspect of the blacktips' behaviour is the way certain individuals would begin an action, and, at times instantaneously, be followed by the rest of the blacktips present. This was especially notable in Charging and Slamming. When aroused, they moved so fast and decisively that they appeared to act in unison, though in many cases the author had seen the leaders and knew the context (Porcher, 2022). The behaviours were initiated by one or a few blacktips and picked up by the entire gathering. This tendency suggests the possibility of emotional contagion (Hatfield et al., 1993), in which subjective states are communicated among other conspecifics present. Further investigation would be necessary to confirm this as a facet of shark social behaviour.

The lack of intra-specific aggression documented among the blacktips in this study, even in the presence of food, has been noted in a wide variety of elasmobranchs, e.g., smooth dogfish (*Mustelus canis*) (Allee & Dickinson, 1954), bonnethead sharks (Myrberg & Gruber, 1974), lemon sharks (Gruber et al., 1988), scalloped hammerhead sharks (*Sphyrna lewini*) (Klimley, 1982, 1987) and white sharks (Fallows et al., 2013). Fallows, who studies the great white shark in South Africa, wrote in a personal communication (2022) that in more than thirty years he had never seen them fight, nor had he seen them bite each other while feeding together on a whale carcass. Nor yet 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.

Although mating wounds are inflicted on female blacktips (Porcher, 2005) and females of other species while mating, males very rarely showed shallow teeth marks. No fighting, and no evidence of fighting, was seen.

Especially given their reputation (Randall & Helfman, 1973), it is worth noting that *C. melanopterus* is the only species among many (including a wide variety of birds, mammals, reptiles, and fish), with which this author has been in long-term intimate contact, that did not bite, either by accident or due to a negative subjective state (they Slammed instead). I hypothesize,

therefore, that *chondrichthyans* might not share the strong tendency to use the mouth to bite under a variety of circumstances that is common in the *ostechthyan* phylogenetic line, including *Homo sapiens*. The lack of a documented incident of any species of sharks fighting supports this conjecture.

4.5. Conclusions

The actions of the blacktips were far more complex than expected, especially in terms of their social and agonistic behaviours. Given that mental states are closely tied to behaviour, their swift and decisive actions, particularly when a gathering of them moved in concert to confront novel objects and scenes, provide intriguing clues to the complexity of their cognitive functions (Jamieson & Beckoff, 1992). Further, their actions suggest that they are peaceful compared with terrestrial predators, even while feeding, in spite of their largely media-generated reputation as ‘mindless killers’ in modern society (Muter, 2013; Neff, 2015; Le Busque & Litchfield, 2021).

These observations are offered to add to the information available about *C. melanopterus*. Further study of blacktips and other species in their natural environments, will doubtless be richly rewarded with more detail, and deeper insight, into their behaviour.

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