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Review

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A review of the behaviours of the Chondrichthyes: a multi-species ethogram for the chimaeras, sharks, and rays

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Abstract

In this review of the behavioural patterns of chondrichthyan fishes, we have strived to produce a comprehensive catalogue of events and states and develop standardized terminology. Hence, actions that are slightly different, will be pooled under inclusive titles. Those used by different investigators are included in quotations within the textual descriptions of the motor patterns. This standardized ethogram will ideally lead to an increase in inter-observer reliability, giving researchers more confidence when reading colleagues' papers that report behaviours that appear

similar to theirs despite being described for different species. The descriptions are presented under the following categories: (1) maintenance (2) courtship (3) filter feeding (4) scavenging (5) predation (6) sociality (7) aggression and (8) defence. The many actions are illustrated by line drawings and photographs in composite figures with an attempt to provide an example of each action for a chimaera, shark, and ray. The diversity of patterns is evident from this ethogram, consistent with observation that the brain-to-body mass ratios of cartilaginous fishes are greater than a third of the bird species and greater than those for some mammalian species. The major impetus for assembling this ethogram is to demonstrate the diversity of behaviours exhibited by members of the Chondrichthyes and to dispel the apocryphal belief that members of this taxon are 'simple feeding machines'.

Keywords
behaviour, chimaeras, Chondrichthyes, cognition, ethogram, rays, sharks.

1. Introduction

An ethogram is a catalogue of behavioural patterns, and its construction is of fundamental importance to the design of any study of the behaviour of animals in their natural environment. Typically, an ethogram comprises a list of behavioural events and states observed with a single species or group of species with corresponding definitions of each (Martin & Bateson, 2007). One of the first ethograms was a comprehensive description of the behavioural patterns of the cichlid fishes in the order Cichliformes (Baerends & Baerends-Van Roon, 1950). This was followed by an in-depth description of the behavioural repertoire of gulls in the order Charadrilformes (Tinbergen, 1979). Konrad Lorenz, the co-founder of ethology and Nobel Prize awardee in Physiology and Medicine along with Nikolas Tinbergen and Karl von Frisch in 1973, was adamant about the importance of this first-step in field studies of the behaviour of animals in the wild (Lorenz, 1973).

The chondrichthyans have a long ancestral lineage, stretching back to the Ordovician, over 400 million years ago. The movements of the earth's crust during the Permian and Triassic Periods, 200 million years ago, coincided with a second major diversification of the cartilaginous fishes. The single continent of Pangea that was present during the Permian split into Gondwana, a southern continent, and Laurasia, a northern continent, separated by a narrow body of water at the mid latitudes in the northern hemisphere. During the Permian, a large body of water straddled the equator within the single continent. The continental plate within the northern hemisphere moved counterclockwise away from the equator. This rotation created the

triangular-shaped Tethys Sea in the southern hemisphere, which was tropical in climate. Not only was there an increase in the extent of the continental shelf, a favoured habitat of cartilaginous fishes, but also the range of temperatures in the waters surrounding the continent. This opened new niches for exploitation by the cartilaginous fishes. The oceans were cool at the poles, warm at the middle latitudes, and hot near the equator. The sharks radiated a second time likely in response to this increase in the variety of habitats, occupying the estuaries and bays, the continental shelf, and the open ocean. However, the chimaeras did not radiate at this time. None of the earliest sharks, which flourished during the Carboniferous, survived the harsh conditions at the end of the Permian (Benton, 2005). This is apparent in the constriction in the main trunk of an evolutionary tree of the chondrichthyans (Figure 1) (Klimley, 2013). It is most likely that the ctenacanths gave rise to the modern sharks, or Euselachi. During the Mesozoic and Cenozoic, the chondrichthyans radiated into 13 orders of chimaeras, sharks, and rays.

The first ethogram for the members of the order Chondrichthyes, or cartilaginous fishes, was developed by two postdoctoral students of Konrad Lorenz for the bonnethead shark, *Sphyrna tiburo*, in the order Carchari-

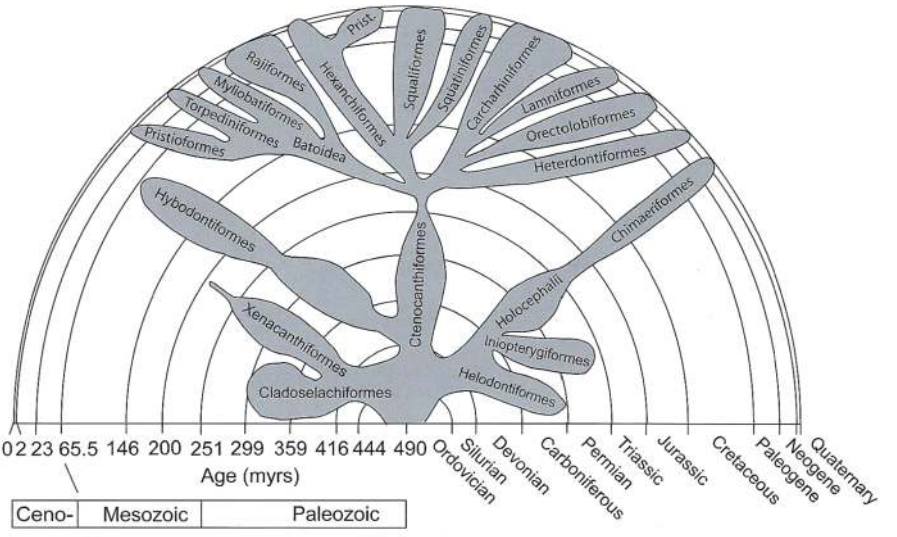

Figure 1. Phylogenetic history of the cartilaginous fishes. The diversity of cartilaginous fishes over geological time with each branch denoting the orders of ancestral and modern Chondrichthyes. The width of each branch is proportional to the diversity and abundance of a particular taxon during that time in geological history.

formes (Myrberg & Gruber, 1974). Subsequently, partial ethograms have been built for other species in the same and other orders such as the nurse shark, *Ginglymostoma cirratum* (Klimley, 1980; Pratt & Carrier, 2001), scalloped hammerhead shark, *Sphyrna lewini* (Klimley, 1985), white shark, *Carcharodon carcharias* (Klimley et al., 1996a; Martin et al., 2005) and tiger shark, *Galeocerdo cuvieri* (Clua et al., 2013), but these have been restricted to a narrow range of behaviours of species with motivations such as courtship, intra-specific aggression, predation, and scavenging. More recently, an ethogram was developed with a broader range of behaviours for the grey nurse shark, *Carcharias taurus* (Smith et al., 2015) and in 2002 a community of blacktip reef sharks, *Carcharhinus melanopterus*, was studied resulting in an ethogram for that species (Porcher, 2023). However, there has yet to be constructed an ethogram for the broad taxon of Chondrichthyes, which includes the sharks, rays, and chimaeras. The senior author of this manuscript, a M.Sc. student of Drs. Myrberg and Gruber, carries their legacy forward by creating an ethogram for the entire group of chondrichthyan fishes.

Prior to some of the above-mentioned studies, few scientists were willing to observe sharks in their natural environment due to their fear of entering the water without protection and being attacked. The documentary 'Blue Water — White Death' in 1974 and movie 'Jaws' in 1975 further instilled fear of these species, in particular the white shark, in both the public and scientists. The notion that the white and other shark species are mindless feeding machine was created in the former film by luring white sharks to the vicinity of a cage for humans within the cage to view and film them. The sharks were attracted to the cage with an olfactory attractant, either ground fish or mammalian blood, and presented baits, either fish or cattle meat, to elicit feeding responses — the opening of their jaws wide to seize the baits.

One indicator of intelligence, the brain to body mass ratio of the chondrichthyan fishes is comparable to that of many species in the other vertebrate classes (Northcutt, 1978). Vertebrates living in air such as the birds and terrestrial mammals have a large optic tectum because they rely mainly on vision. The cartilaginous fishes have a smaller optic tectum because vision is less important to them underwater in the limited visibility. However, their cerebellum is large because the efferent nerve impulses from their electroreceptors, the Ampulla of Lorenzini, are processed within this region of the brain. This sensory system depends upon the conductivity of ocean salts

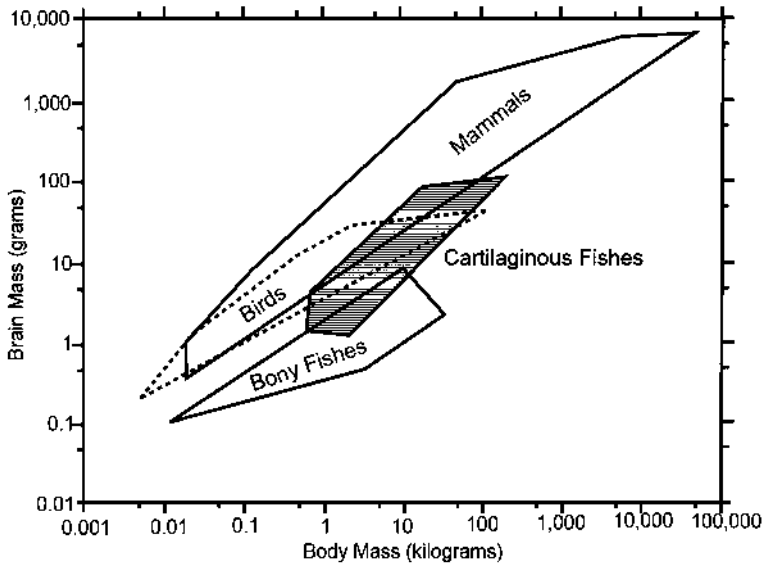

Figure 2. Brain capacity. Brain versus body mass indicated by a minimum convex polygons drawn between values for members of four vertebrate taxa, bony fishes, cartilaginous fishes, birds and mammals (Northcutt, 1978).

for its effectiveness. Another reason for the large size of the cerebellum in the cartilaginous fishes is the efferent output from the mechanoreceptors, the neuromasts on the skin, the lateral line, and inner ear, is processed there. Aquatic species are capable of detecting vibrating objects in water at a greater distance than terrestrial species in air. The sum of the sizes of the different regions of the brain can be used as an indicator of mental development (Northcutt, 1978). The brain mass of the cartilaginous fishes exceeds that of most bony fishes of similar body size (Northcutt, 1978). This is apparent from the higher elevation of the polygon for the former (see stippling) than that of the latter in a graph of brain mass versus body mass (Figure 2). The brain-to-body mass ratios of cartilaginous fishes are greater than a third of the bird species and greater than those for some mammalian species. We hope in this review to convince readers that the behavioural repertoire of the chondrichthyan fishes rivals that of some members of the other vertebrate classes such as the birds and mammals, and not consist of simple feeding behaviours.

The majority of researchers have developed partial ethograms with regard to the specific focus of a particular study. The challenge with creating

more comprehensive ethograms is their extended length may exclude them from journals where space is limited. However, as evident in the publications of Baerends & Baerends-Van Roon (1950) and Tinbergen (1959), *Behaviour* has been willing to devote enough space to publish comprehensive ethograms. With respect to many of the partial ethograms limited by space, they often lack consistent definitions for particular behaviours. In this review of the behavioural patterns of chondrichthyan fishes, we have strived to produce a comprehensive catalogue of behavioural events and states, and attempted to develop a standardized terminology. Hence, behaviours that are slightly different, will be pooled under inclusive titles, yet the diversity of them will be included in tables under the titles in quotations for members of the different orders. This will ideally lead to an increase in inter-observer reliability, giving researchers more confidence when reading colleagues' papers that report behaviours that appear similar to theirs despite being described for different species.

2. Methods

Published papers with descriptions of behaviours exhibited by the chondrichthyan fishes were found using search engines such as Google Scholar, JSTOR, Science Direct and Wiley On-Line Library. The searches were conducted by pairing taxonomic groupings with phylogenetic terms such as 'Holocephali' and 'Elasmobranchii' or common names such as 'chimaeras', 'sharks', and 'rays' with subject terms such as 'behaviour', 'ethogram', 'courtship', 'predation', and 'scavenging'. The article author names, dates, titles, journals, volume, and page numbers were entered into End Note. The articles, once retrieved, were placed in a file on a PC.

An attempt was made to identify common behaviours from species in as many of the 13 orders of cartilaginous fishes as possible and to enter them into a series of tables. The behavioural patterns are referred to either an 'event' of a brief duration or a 'state' with an extended duration. The former is identified in the Results section using a noun such as a 'breach', whereas the latter is identified with a participle phrase such as 'remaining stationary on bottom'. In each table there is a column for the following: (1) general behaviour, (2) descriptive notes, (3) order, (4) genus and species, (5) citation and (6) figures. The description in the column for general behaviour is succinct and consistent in length throughout the manuscript. Following

the tables are more comprehensive descriptions of the behaviours and the social and environmental contexts in which they occur. These may vary in length relative the complexity of the behaviour and the relationship with other species as well as the environment. Our list of citations in the tables and references in the bibliography is not exhaustive, but includes the papers with the most detailed descriptions of each behaviour. If the reader is interested in learning what other chondrichthyan species perform them, the reader should consult the biographies of the papers included in the review for the panoply of species displaying the described behaviours. Only in this way could we provide an ethogram of all types of behaviours for members of such a large taxon.

We have attempted to place the ethogram in the context of the evolutionary history of the taxon and relate behavioural complexity and diversity in part to the evolution of increasing brain to mass ratios in the more derived species in Figures 1 and 24. The evolutionary history of the orders is given in Figure 1 and representative pictures of the members within each order as well as the numbers of species in Figure 3. The examples chosen in this review best provide the behavioural and ecological context of each behaviour.

There are eight tables summarizing this information, and they are the following categories: (1) maintenance behaviours, (2) courtship, (3) filter feeding, (4) scavenging, (5) predation, (6) sociality, (7) aggression and (8) defensive behaviour. The behavioural actions are illustrated by line drawings and photographs within the main body of the manuscript and with videos made available as supplemental information.

3. Results

3.1. Maintenance behaviours (Table 1)

Table 1, which includes maintenance behaviours, summarizes the various modes of locomotion under the heading, 'General'. Parasitic and self-body cleaning behaviours are summarized under the heading 'Cleaning'. Each behaviour is numbered beside the table number. The various modes of swimming are illustrated in Figure 4 (Klimley, 2013).

3.1.1. Remaining stationary on bottom

Solitary whitetip sharks have been observed lying motionless on the bottom at Cocos Island off Costa Rica (Klimley, pers. commun.) or close together in

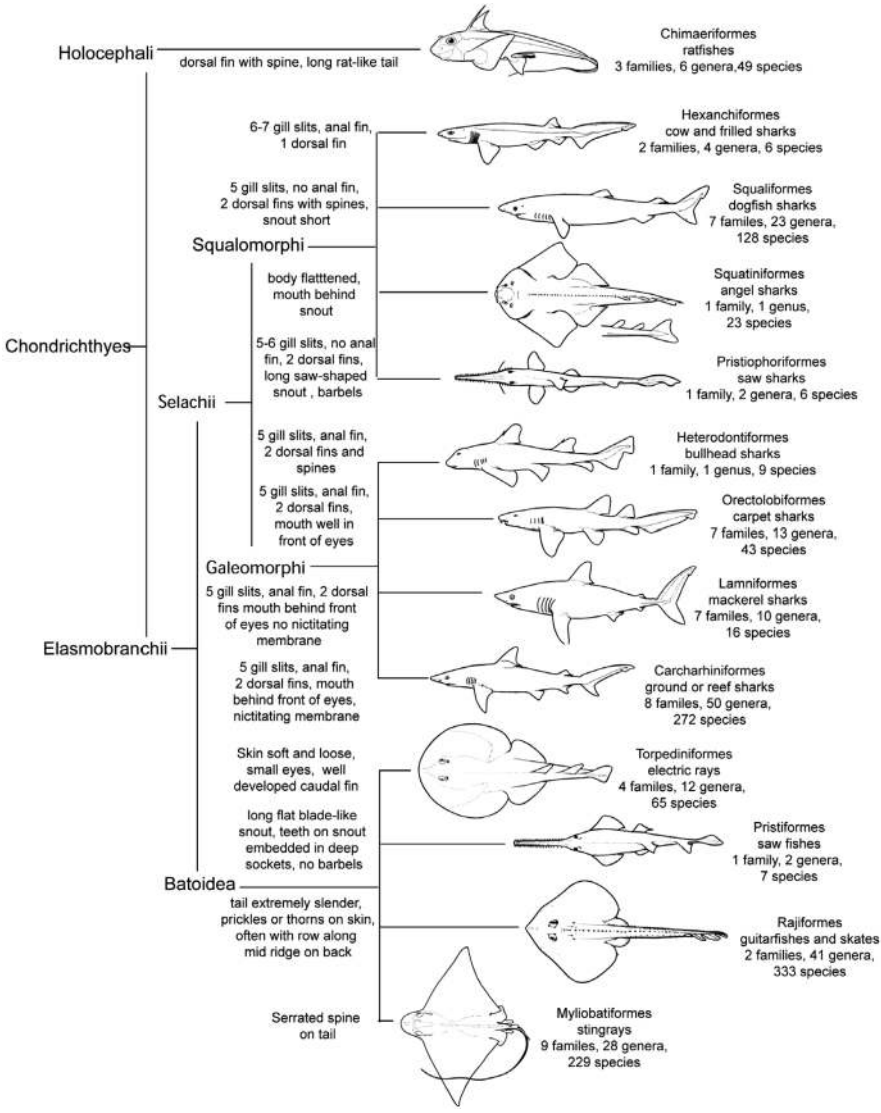

Figure 3. The modern cartilaginous fishes. Representatives of the thirteen orders of sharks, rays, and chimaeras together with their distinguishing features as well as the numbers of families, genera, and species in each order (Klimley, 2013).

groups on ledges of Roca Partida, a small island within the Revillagigedo Archipelago off the tip of the Baja Peninsula of Mexico (Klimley, pers. commun.). Klimley et al. (2022b) conducted a pilot study, using acoustic

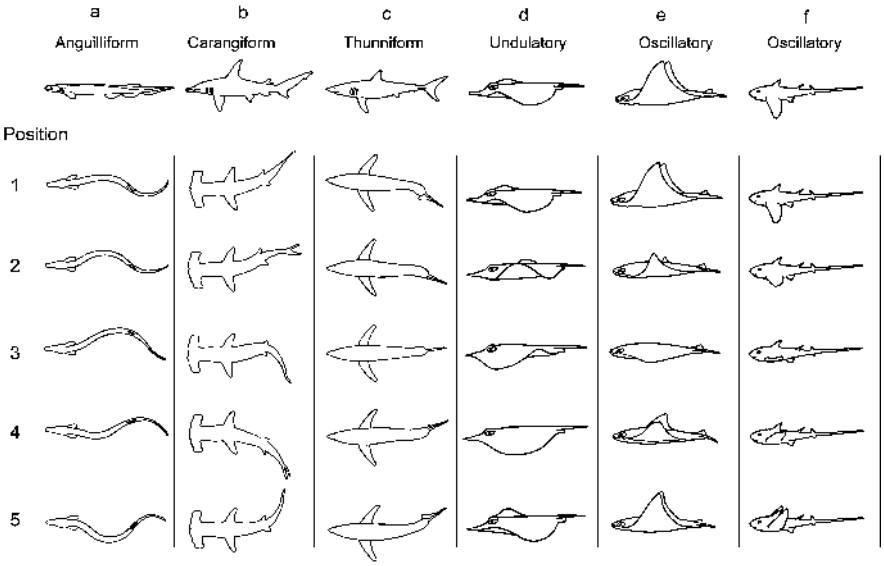

Figure 4. The modes of propulsion of cartilaginous fishes. The fusiform sharks move themselves forward by undulating their body along its longitudinal axis, and their modes of swimming are (a) anguilliform (b) carangiform and (c) thunniform motion (Klimley, 2013). The dorsally and ventrally flattened rays propel themselves forward by passing a wave along their body or moving their appendages, modes of locomotion termed (d) undulatory and (e) oscillatory. (f) The chimaeras propel themselves forward by oscillating their fins. The successive bending of the torso over one swimming cycle is shown below on the horizontal axis.

telemetry, to examine the vertical habitat use of four species of sharks at this very small (length 100 m) but highly productive pinnacle in the open ocean. It may represent an 'oasis' for large marine predators. Individuals of four predatory species, the dusky, *Carcharhinus obscurus*, Galapagos, *Carcharhinus galapagensis*, silvertip, *Carcharhinus albimarginatus*, and whitetip reef shark, *Traenodon obesus*, were detected at Roca Partida for varying periods over two and a half years, exhibiting high levels of residency. Members of each species carried an acoustic transmitter outfitted with a depth sensor that communicated continuously with two stationary receivers, one on either side of the pinnacle, if the sharks were within the detection ranges of at least one of the receivers. There was evidence of vertical habitat separation between species which may be due to resource partitioning.

The whitetip reef sharks were active during both the day and night, swimming at depths greater than the other three species — being detected at depths as great as 175 m. As an example, one whitetip exhibited relatively rapid

changes in depth during nighttime at 11 pm and 2 am on the western side and at 3 am on the eastern side of the rock on the 10th of June as well as 2: 30 and 4 am on the eastern side during the 11th of June. The whitetip reef sharks appeared more active than individuals of the other species, chasing and feeding upon prey mainly during nighttime. However, that same whitetip appeared to rest on the bottom at a depth of 85 m on the eastern side of the rock for a period of ten-and-one half hours from 7: 30 am to 6 pm on the 11th of June 2011. This was consistent with the authors observing whitetip reef sharks lying on ledges during free or SCUBA dives at the pinnacle. This behaviour is likely an attempt to minimize energy output during the daytime when their prey, reef fishes, were less vulnerable, swimming in the water column, than during nighttime when they are wedged into hiding spaces between rocks where the sharks can detect them from their bioelectric fields, dislodge, and then consume them

3.1.2. Slow, straight-line swimming

Rarely is the speed of slow, sustained swimming been measured in the field. However, Nakamura et al. (2011) put an acceleration data logger that recorded swimming speed, depth, temperature, and tri-axial acceleration on four adult tiger sharks, *Galeocerdo cuvier*, and tracked them for periods of seven hours or less along the coast of the island of Hawaii. These sharks swam with continuous tail beats with repeated vertical 'yo-yo' diving excursions at mean rates of 0.5 to 0.9 m/s. These sharks made burst accelerations that exceeded 1.6 m/s. The tailbeat frequencies ranged from 0.4 Hz for speeds of 0.25 m/s to 0.7 Hz for speeds 1.25 m/s.

There are different ways the chimaeras, sharks and rays accomplish straight-line swimming. Each of the three lineages has one or more separate styles of locomotion. The sharks mainly exhibit three types of locomotion: anguilliform, carangiform, and thunniform swimming. The prefixes in front of the suffix, 'form', refer to the families of bony fishes that exhibit these modes of swimming, the eels of the family Anguillidae, the jacks of the family Carangidae, and the tunas of the family Thunnidae.

The shark's torso and tail in anguilliform swimming conforms to a sinusoidal wave with a positive and negative peak (see position 5 in Figure 4a). The muscles on one side of the anterior torso contract so that the forward body bends to that side — directed upward in the illustration. This loop transmits down the length of the shark's body with the posterior surface of the loop pushing water backward while resulting in forward movement. When

the mid body is bent most (see position 3), muscles on the other side of the anterior torso begin to contract while bending the body to the other side with the posterior surface of this new loop pushing more water backwards and producing further forward movement. Nurse, cat, and frilled sharks use this form of locomotion. The shark shown in Figure 4a is the frilled shark, *Chlamydoselachus anguineous* of the order Hexanchiformes. It is elongated and eel-like with a flattened snake-like head and has a terminal mouth full of widely separated, needle sharp, three cusped teeth. Frill sharks live in the deep sea, where they likely do not have to move very quickly to feed on deep water squid and fishes (Compagno et al., 2005). A few members of the species have been observed swimming at the surface but most of them have been collected from the bycatch of fisherman deploying deep bottom trawls and gill nets.

The majority of sharks propel themselves forward with fewer undulations of the body using the carangiform mode of swimming. The grey nurse shark, *Carcharias taurus*, of the order Lamniformes and the bonnethead shark of the order Carcharhiniformes swim in this manner. Smith et al. (2015) termed this behaviour 'cruising' in their ethogram, defining it as the sandtiger shark swimming at low speeds with few directional changes. Myrberg & Gruber (1974) called it 'patrolling' in their ethogram noting the bonnethead sharks swam just above the substrate, although this might be attributed to the shallow nature of the tidal pool at the Miami Seaquarium, where they conducted their observations. They found this to be the most common mode of swimming by the bonnethead sharks. The head of the shark was observed to move through a horizontal arc of 30–40° during each stroke cycle, with the posterior torso swinging laterally in a compensatory fashion. The sharks using this mode of swimming bend the posterior half of the torso from side to side. Blackfin reef sharks, *Carcharhinus melanopterus*, are shown swimming over a coral reef while bending their posterior torsos to one side and to the other to propel themselves forward (Figure 4b; Video 1 at 10.6084/m9.figshare.22310587). The same type of behaviour is exhibited in the movement of scalloped hammerhead sharks 20 km away from a seamount and back to the seamount by orienting to a magnetic ridge created by magnetic particles embedded in basalt that likely flowed away from the seamount during an ancient eruption (Klimley, 1993). These swimmers still move in a relatively sinuous manner, although they bend their body less than anguilliform swimmers.

The shortfin mako, *Isurus oxyrinchus*, white, and salmon sharks, *Lamna nasus*, are thunniform swimmers. Thunniform-swimming sharks are somewhat less flexible in body than carangiform swimming sharks in that in the latter sharks each of the lateral muscles are attached to different vertebrae while in the former sharks all of the lateral muscles are attached to the base of the tail (Shadwick, 2005). Lamniform-swimming sharks bend only the posterior quarter of their body. A shortfin mako shark is shown moving its tail back and forth from one side to the other (Figure 4c). Notice that only its caudal fin moves back and forth while the rest of its body is held rigid. This makes the body appear stiffer for lamniform than anguilliform and carangiform modes of locomotion.

Dorso-ventrally flattened rays propel themselves forward in either of two ways. Most rays pass a propulsive wave down the length of their flat and enlarged pectoral disk to force water backward and propel themselves forward — a form of locomotion described as undulatory (Figure 4d). Electric rays, skates, and most stingrays of the orders Torpediformes, Rajiformes, and Myliobatiformes use this mode of locomotion. Notice the southern stingray, *Dasyatis americana*, initially lifts its pectoral fin in a small upward loop that first increases and then decreases in size as the loop passes toward the rear pushing water backward (see positions 1–3) (Rosenberger, 2001).

However, other stingrays of the order Myliobatiformes exhibit oscillatory swimming. They flap their pectoral fins up and down with the posterior edge of the fin lagging behind the anterior part of the fin, thus pushing the water backwards. Shown here is the up and down flapping of the cownose ray, *Rhinoptera bonasus*, that migrates each year in massive schools up and down the eastern coast of North America (Figure 4e, Rosenberger, 2001). This same mechanism is used by the chimaeras such as the spotted ratfish, *Hydrolagus collei*, which also oscillate their pectoral fins upwards and downwards, to propel themselves slowly forward or upward and downward (Figure 4f).

3.1.3. Tilted swimming

Great hammerhead sharks, *Sphyrna mokarran*, generate lift with their very high dorsal fin, which is higher than their pectoral fins are long, by swimming on their side. By swimming with this body posture, they travel in a more efficient way than in swimming in an upright position (Payne et al., 2016). A shark, carrying an onboard video camera, at the Great Barrier Reef, Australia, spent 90% of a 18-h period from early evening till late morning

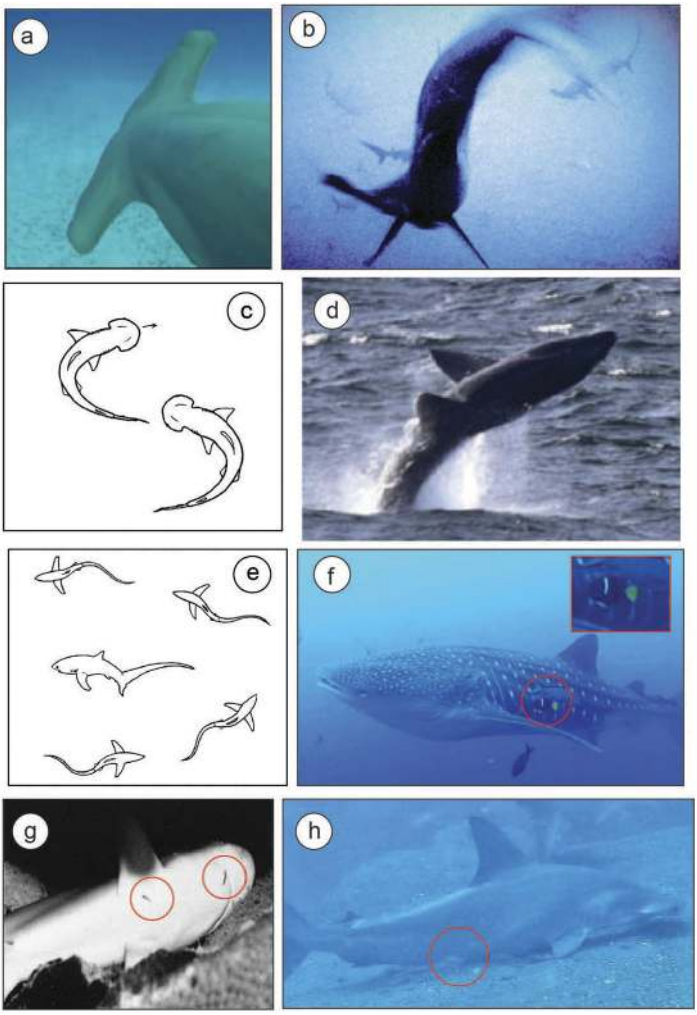

Figure 5. Maintenance behaviours of cartilaginous fishes. (a) Tilted swimming: a great hammerhead swims at a tilted angle (Payne et al., 2016); (b) accelerated swimming: a scalloped hammerhead quickly propels itself forward (Klimley, 2013); (c) maneuvering: a bonnethead shark makes a series of rapid turns (Myrberg & Gruber, 1974); (d) breach: a basking shark leaps out of the water (Johnston et al., 2018); (e) circular-stance swimming: a thresher shark assumes a hunch and swims in a circular trajectory to attract parasite cleaners (Oliver et al., 2018); (f) parasitic body cleaning: a king angelfish removes parasites from a whale shark's body (Quimbayo et al., 2017); (g) parasitic body cleaning: two gobies clean parasites from a Caribbean reef shark at a cleaning station (Sazima & Moura, 2000); (h) self-body cleaning: a scalloped hammerhead dragging his claspers through the sand (Moyo-Serrano & Salinas-de-Leon, pers. commun.). Red circles draw attention to the cleaners.

swimming on its side at absolute roll angles between 50 and 75° (Figure 5a). The shark exhibited this rolling behaviour whether it was ascending, descending, or swimming at a constant depth, alternating between rolling to the left and right sides roughly every 5 to 10 min. Members of polarized schools of scalloped hammerhead sharks have been recorded on video taken by a free diver synchronously swimming on their sides, based on the reflection of light from their upwardly rotated torsos, at a seamount in Gulf of California, Mexico (Klimley, pers. commun.).

3.1.4. Accelerated swimming

Smith et al. (2015) define 'active/accelerated swimming' as a grey reef shark, *Carcharhinus amblyrhynchos*, moving persistently in one direction at a greater speed than slow milling, defined in the Cambridge Dictionary as "moving around in a large group, with no particular purpose, or in no particular direction". 'Acceleration' was defined by Klimley (1985) as a rapid burst of swimming by a scalloped hammerhead shark with rapid tail beats along with compensatory shaking of the head with successive swings of the head quickly decreasing in arc as the individual continued to move through the water (Figure 5b). It differs from Head-shake, a behaviour to be described later in Table 7 (7.20), which summarizes the aggressive behaviours, as in this behaviour the swings of the head do not immediately decrease in arc.

3.1.5. Accelerated swimming and glide

An 'explosive-glide' was the name Myrberg & Gruber (1974) gave to a rapid swimming movement of bonnethead sharks. It started with several rapid and strong tailbeats followed by a long glide covering a distance of 5 m or more, roughly five body lengths. They observed a subtle colour change often accompanied explosive-glides — the normal colour of the body, which is light grey, fading to dull white in the belly region during acceleration, becoming darker during the glide, and remaining dark for the next few moments.

3.1.6. Maneuvering

This movement consisted of a series of rapid turns, often to such an extent that the shark was bent almost double with its head nearly touching the caudal peduncle (Figure 5c). Myrberg & Gruber (1974) found that this mode of swimming was common to small and medium-sized bonnethead sharks, occurring most often in very shallow water in the tidal pool exhibit. The swimming pattern appeared to be associated with attempts to orient to a spot on the substrate or to catch a small fish.

3.1.7. Hovering

Smith et al. (2015) observed grey nurse sharks appeared motionless while swimming in the water column. They termed this swimming mode 'hovering', noting that sharks faced into a current and did not gain net forward motion as their tail beats maintained a stationary position within the water column.

3.1.8. Breach

The fast swimming and associated breaches exhibited by the endothermic white shark are well suited to the capture of agile prey such as pinnipeds. The multiple forms of this behavioural pattern will be described in Table 5, the summary of predatory behaviours. In contrast, the breach has been observed by Johnston et al. (2018) in the basking shark, *Cetorhinus maximus*, which often swims slowly near the surface with its mouth agape while filter-feeding upon zooplankton. The energy expended by a basking shark making such a breach is half that of a white shark and amounts to around 1/17th of its daily standard metabolic cost. The function of this behaviour by the basking shark is not yet known to the scientific community, but in the opinions of the above-mentioned authors it might (1) involve the establishment of dominance among local sharks (2) serve to attract females to males (3) result in the concentration of zooplankton in response to the particle water displacements caused by the impact of body contacting the sea surface, or (4) self-clean the body by dislodging parasites attached to the shark's torso. It is due to the uncertainty of the function of this form of breaching that it is described and illustrated here in Table 1 on maintenance behaviours (Figure 5d). The similarity of the breaching speeds of basking sharks to that of white sharks, an active endothermic lamnid, challenges the public and scientific perceptions that these large filter feeding sharks are always inactive and cannot perform the acrobatic behaviours exhibited by endothermic sharks. Porcher (2023) observed breaching of blackfin reef sharks, a member of the Carcharhinformes, in water as shallow as 2 m deep on the north shore of Mo'orea Island, French Polynesia.

3.1.9. Parasitic body cleaning

There are examples in the scientific literature of members of three orders of sharks, the Lamniformes, Orectolobiformes, and Carcharhiniformes, and one order of rays, the Myliobatiformes, being cleaned by small fishes. Interactions between pelagic thresher sharks, *Alopias pelagicus*, a lamniform, and

cleaner wrasses were observed by Oliver et al. (2011) at Monad Shoal, a seamount, rising 250 m from the sea floor in the Visayan Sea in the Philippines. SCUBA divers video recorded sharks being cleaned by wrasses at five cleaning stations separated by 100 m, each consisting of coral rubble, the product of dynamite fishing. Thresher sharks performed this 'circular-stance-swimming,' to solicit cleaner inspections. While straight-line swimming did not solicit cleaning, swimming of multiple sharks in a circle with a large diameter did attract cleaners when the sharks lowered their caudal fins as shown in the center of Figure 5e. Cleaners showed preferences for foraging on specific areas of a thresher shark's body. The order of preference was as follows: (1) the pelvis of the shark, (2) its pectoral fins, (3) its caudal fin, (4) its torso, (5) its head, dorsal fin, and gills, respectively. The king angelfish, *Holacanthus passer*, was photographed picking parasites from the body of a whale shark, an orectolobiform, while swimming up in the water column at Cocos Island in the tropical Eastern Pacific Ocean (Figure 5f) (Quimbayo et al., 2017). The same species was observed picking parasites off silky sharks, *Carcharhinus falciformis*, Galapagos sharks, *Carcharhinus galapagensis*, and scalloped hammerhead sharks, all three carcharhiniforms, as they hovered over cleaning stations on the rocky bottom in the waters along the shoreline. The blacknose butterfly fish, *Johnrandallia nigrirostris*, was seen cleaning a spotted eagle ray, *Aetobatus narinario*, a myliobatiform, as it swam over the rocky reefs. Sazima & Moura (2000) found that juvenile Caribbean reef sharks, *Carcharhinus perezi* sought out cleaning stations on the bottom tended by yellownose gobies, *Elacatinus randalli*, at Fernando de Noronha Archipelago in the Western South Atlantic. The sharks remained stationary on the bottom at these stations while being cleaned (see wrasses within red circles in Figure 5g). The species' remaining stationary on a substrate possibly facilitates cleaning interactions with the bottom-dwelling cleaner gobies. Sharksuckers, *Echeneis naucates*, initiate bouts, in which they remove parasites from the mouths of lemon sharks, *Negaprion brevirostris*, by moving along their snouts while maintaining torso contact or swimming in a 'dance-like' manner in front of the sharks' eyes to announce their intention (Ritter & Amin, 2016). Sharksuckers perform this behaviour until the sharks opens their mouths to let the suckers enter. Lemon sharks always assume one of two positions, either lying on the sea floor or propped up on their two pectoral fins. The sharksuckers appear to remove parasites from the teeth in the upper jaw of the sharks. The sharks terminate the cleaning bout by spitting the cleaners out of their mouths.

3.1.10. Self-body cleaning

Myrberg & Gruber (1974) observed bonnetheads perform 'chafing' or a rolling of the body with the abdomen coming into contact with the bottom. The same behaviour has been observed in grey nurse sharks, presumably to remove parasites from their ventrum (Smith et al., 2015). Caribbean reef sharks and blacktip sharks, *Carcharhinus limbatus*, swim along the bottom with their abdomens coming into contact with ripples in the sand to enhance 'chafing', apparently to dislodge parasites. Blackfin reef sharks rub the bellies against rocks in French Polynesia (Video 2 at 10.6084/m9.figshare.22310587) (Porcher, 2023). Multiple scalloped hammerhead sharks were recorded on a small volcanic patch of sand at Wolf Island in the Galapagos archipelago swimming over the sandy bottom to scratch parts of their torsos (Moyo-Serrano & Salinas-de-Leon, pers. commun.). The parts of the body making contact with the substrate included the underside of the snout, the ends of the pectoral fins, the ventral surface of the body, and the claspers. The sharks began clasper cleaning by curving their ventral regions close to the anal fins so that both claspers were fully inserted into the sand while continuing to swim forward a few seconds (see claspers within solid red circle in Figure 5h). The sharks then extracted their claspers and rose upward slightly and shook their claspers back and forth for few seconds. The 'gill-puff', another apparent cleaning behaviour, consisted of a momentary expansion of the branchial region. Myrberg & Gruber (1974) observed bonnethead sharks performing it and Smith et al. (2010) observed grey reef sharks displaying it. This behavioural pattern was exhibited usually after an object had been taken into the mouth or after the substrate had been disturbed during tight maneuvering behaviour. Its function was apparently to clear the gills of either particles acquired while manuevering near the bottom or from parasites.

3.2. Reproductive behaviours (Table 2)

A summary of behavioural patterns involved in courtship and copulation are summarized in Table 2. Note that the general titles of the motor patterns are inclusive allowing some variation in the behaviours due to the diversity of chimaeras, sharks, and rays exhibiting them.

3.2.1. Group circular swimming

Chondrichthyan courtship that leads to copulation begins with a diversity of motor patterns. One such pattern is group circular swimming, first described in basking sharks by Harvey-Clark et al. (1999). They provided video and

photographic documentation showing 13 6–8-m-long sharks, swimming clockwise in a compact circle, oriented nose to tail, in the northeastern Atlantic Ocean off Nova Scotia, Canada. Some of the sharks had white patches on the dorsum and appendages, evidence of possible body biting, an action that stimulates acquiescence by females to engage in courtship (see later description of body biting in Section 3.2.8, Table 2.8 or Figure 9b). This behaviour, called a 'torus', was later described in greater detail by Sims et al. (2022), who made underwater and aerial video recordings of these groups during late summer, August and September, in the eastern north Atlantic Ocean (Figure 6a). The individuals swam not only to the side of each other, but also on top of each other in layers from the surface to a depth of 16 m. Both sexes were involved in the circling groups with females identified by their lighter colouration than males as observed for the nurse shark during courtship by Klimley (1980). The males possessed swollen claspers with abrasions, and the females had abrasions on their pectoral fins like the basking sharks observed by Harvey-Clark et al. (1999). The sharks were observed to interact through fin to fin and fin to body touching, rolling on their sides to expose their light ventral surfaces to adjacent sharks, and often breached. Klimley (2019) observed multiple leopard sharks, *Triakis semifasciata*, swimming in a line, oriented snout to tail, that eventually became a circle. In the same aggregation, individuals swam, snout to tail, in two lines with individuals turning their heads to the side near their neighbour's midsection, as if sampling for a pheromone emanating from the vent (see *investigation of individuals* (Section 3.6.5, Table 6 or Figure 20e,g). Hence, the author inferred that this might be an element of the courtship ritual.

3.2.2. Paired close following

This behaviour was observed exhibited by species in five orders, the Chimaeriformes, Lamniformes, Orectolobiformes, Carcharhiniformes and Myliobatiformes. Van Dykhuizen (2011) observed male spotted ratfish, *Hydrolagus colliei*, swimming with synchronous tail beats in a position just to the side of females' pectoral fins, at times touching the female (Figure 6b). This was followed by body clasping, in which the chimaera's cephalic tentacula grasped the female's pectoral fin. Male sand tiger sharks come from behind and underneath a female and place their snouts just behind their cloaca, possibly attracted by a chemical pheromone (Gordon, 1993). A male nurse shark, *Ginglyostoma cirratum*, is shown exhibiting close following next to a female in Figure 6c. Male grey reef sharks and lemon sharks,

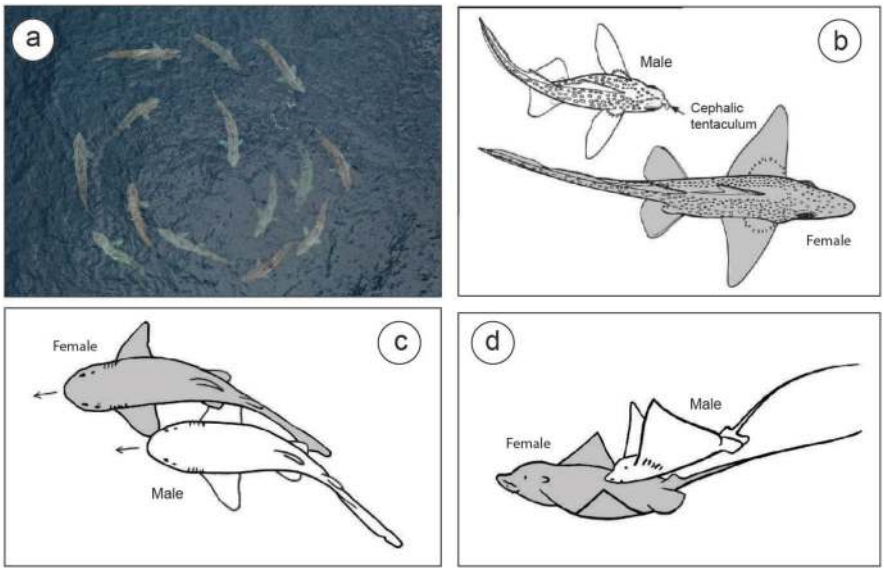

Figure 6. Modes of swimming in reproductively active cartilaginous fishes. (a) Group circular swimming: a group of basking sharks swimming in a circular formation (Sims et al., 2022; taken by Simon Berrow); (b) paired close following: a male and female spotted ratfish swimming parallel to each other (Van Dykhuizen, 2011); (c) two nurse sharks swim next to each other in a parallel alignment (Klimley, 1980); (d) male and female eagle rays swimming in a parallel manner (Uchida et al., 1990).

Negaprion brevirostris, swim with synchronous tail beats, side by side, and the first two often bend their heads close to the female vent just posterior of her pectoral fins (Johnson & Nelson, 1978; Clark, 1963). With regard to the batoids, males spotted eagle rays follow females just to the side of the pectoral fins as do the sharks (Figure 6d, Uchida, 1990). Male manta rays, *Manta birostris*, chase females, maintaining a position just behind the tail (Yano et al., 1999) as do bat rays, *Myliobatis californica* (Feder et al., 1974) while at times bobbing and swaying with their bodies (Tricas, 1980).

3.2.3. Grouped close following

Often more than a single male will follow a female closely and for a prolonged period. As many as five nurse sharks have been observed to follow a single, reproductively active female (Pratt & Carrier, 2003). Multiple male reef whitetip sharks, *Triaenodon obesus*, have also been seen to rapidly pursue a reproductively active female (Whitney et al., 1994). This collective behaviour is common for batoids, particularly members of the Myliobati-

formes. such as reef manta ray, *Manta alfredi* (Stevens, 2016). One to 26 males of the reef manta ray increase their swimming speed and follow in single file behind the tail of a female in a courtship train with their cephalic palps often unfurled but mouths closed (Stevens et al., 2018). The female's cephalic palps often remain furled during this chase. These courtship trains can last for many hours at a time. Multiple individuals of other species in the same order pursue females closely behind in what might be termed a courtship train to initiate courtship (Feder et al., 1974; Tricas, 1980; Uchida et al., 1990).

3.2.4. Clasper flexing

Gordon (1991) and Claus et al. (2021) both described a variety of behavioural patterns exhibited by sand tiger sharks housed in the spacious aquaria at Oceanworld Manly, Sydney, Australia and in the National Aquarium, (Washington DC, USA), respectively. Male sharks in these two aquaria were observed to rotate both claspers outward and away from their torsos or inward and across their bodies, while crossing their paired clasper (Figure 7a). At times, the males spread the rhipidion, hook, and spur of the distil end of their claspers. The clasper tip is opened like an umbrella after insertion into the female's cloaca during copulation (Klimley, 2013). Male whitetip sharks, *Triaenodon obesus*, have been observed not just rotating the clasper to the side but forward with the simultaneous spreading of their distal ends in their natural habitat at Roca Partida in the Revillagigedos archipelago (Ritter & Compagno, 2013). To distinguish this external form of spreading from the internal mechanism used to anchor the clasper within the cloaca, the authors referred to this behaviour as 'flaring'.

3.2.5. Torso thrust with clasper flexion

Bonnethead sharks suddenly accelerate with the lower section of their torso arching outward, while rolling on the side, and then pivoting a clasper outward in what Myrberg & Gruber (1974) termed 'clasper flexion with thrust'. Although appearing reproductive in function, it was rarely performed and occurred in the absence of a nearby shark, precluding any interpretation directly associating it with incipient sexual behaviour. Torso-thrust of a scalloped hammerhead began as a male explosively accelerated from its normal swimming speed at the edge into the center of a school of hammerhead sharks (Figure 8, Klimley, 1985). Tail beats were emphatically directed to one side, propelling the shark's anterior torso laterally. The shark tilted at

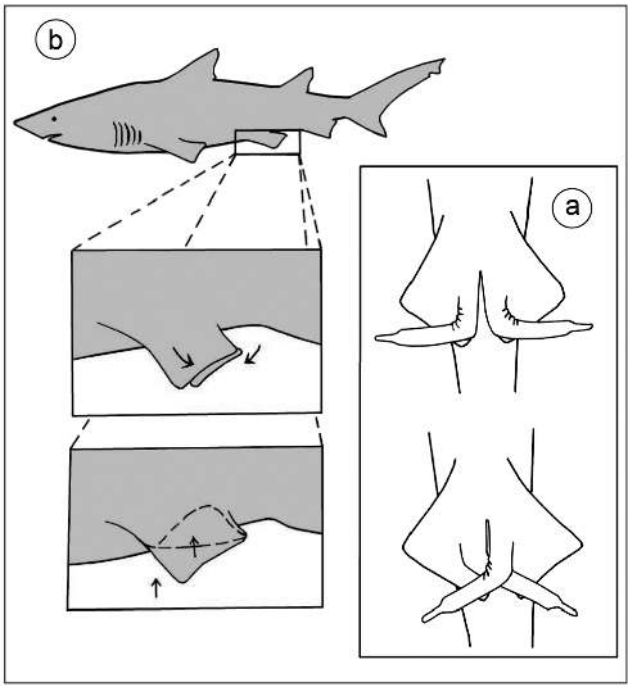

Figure 7. Attraction. (a) Clasper flexion; male sharks rotate both claspers outward and away from their torsos or inward and across their bodies, while crossing their paired clasper (Gordon, 1993); (b) pelvic fin cupping and flaring: female sandtiger sharks move their pelvic fins inward into a cup shape, an action termed 'cupping' and then spread her pelvic fins outward to expose her cloaca, a behaviour called 'flaring' (Gordon, 1993).

this time, and light often reflected off its upwardly rotated ventral surface. Mainly due to the fact that this reflection usually alerted the senior author to the performance of the action, he suspected that the reflected light was visible

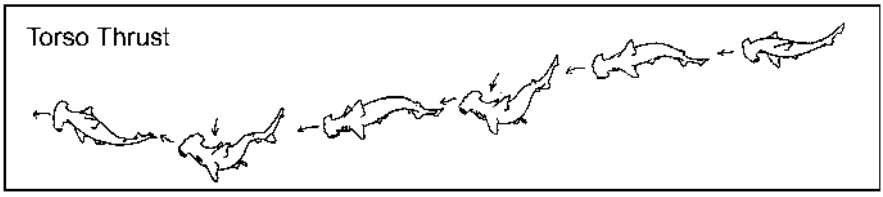

Figure 8. Male solicitation of pairing with female. Torso thrust: a male scalloped hammerhead dashes into school repeatedly bending the mid-section of his torso to one side while flexing his clasper (Klimley, 1985).

to neighbouring sharks and would be an integral sensory component if this action pattern were a display. This action differed from the clasper-flexion-with-thrust described by Myrberg & Gruber (1974) for the bonnethead in the pronounced bending of the scalloped hammerhead's torso into an 'S' shape and the swimming path downward or upward from the shark's original plane. The frequency with which clasper flexion was associated with thrusting of the body to one side indicated that it might have different functions. One could be communicative such as to attract a female's attention for pairing and copulation and another could be to fill the male's siphon sac with water for later expulsion of spermatozoa during copulation such as occurs in the spiny dogfish, *Squalus acanthias*, and dusky smooth-hound, *Mustelus canis* (Gilbert & Heath, 1972).

3.2.6. Pelvic fin cupping and flaring

Female sandbar sharks also exhibited behaviours that led to copulation with a male. A female was observed to swim very slowly with her head lower than the plane of tail by about 15° and expose her pelvic region just prior to copulation. At this time, she moved her pelvic fins inward into a cup shape, an action termed 'cupping' (Figure 7b), and then spread her pelvic fins outward to expose her cloaca, a behaviour termed 'flaring' (Figure 7b) (Gordon, 1993). This behaviour was often proceeded by the male flexing his claspers (Gordon, 1993). Female nurse sharks arch their bodies toward males and 'cup' their pelvic fins (Carrier et al., 1994). With regard to the batoids, female clearnose skates, *Raja eglanteria*, arch their backs and undulate their pectoral fins to attract males in courtship (Luer & Gilbert, 1985).

3.2.7. Body clasping

Males of the spotted ratfish, a chimaeriform, have a cephalic tentaculum, a stalked appendage with a bulbous end covered with small hooks. This is usually withdrawn into a depression on the forehead but can be protruded to direct its hooks outward and moved to either side. The male spotted ratfish follows the female while remaining just behind her pectoral fin. He then accelerates momentarily so that he is next to her, swimming in a synchronous manner, with their bodies touching while his cephalic tentaculum extends outward and grasps on either to the pectoral fin or body of the female (Figure 9a). The male ratfish then coils his body around the female, secures himself to her flank by extending his posterior, or pre-pelvic, clasper and affixing it to the side of her body, and only then inserts the calcified internal radius with its hook at the end of the bifurcate clasper into her cloaca

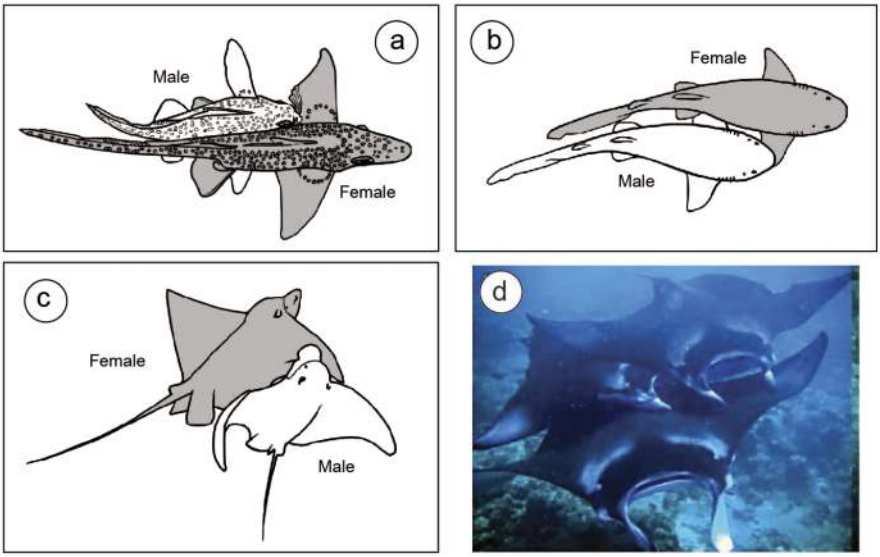

Figure 9. Modes of grasping the female. (a) Body clasping: a male spotted ratfish seizing a female's pectoral fin with his cephalic tentaculum (Van Dykhuizen, 2011); (b) Body biting: a male scalloped hammerhead seizing the pectoral of a female (Klimley, 1980); (c) male eagle ray grasping pectoral fin of female with his jaws (Uchida et al., 1990); (d) two male manta rays swimming close to a female and attempting to grasp her pectoral fins (Stevens, 2016).

(Van Dykhuizen, 2011). There is evidence that the tentaculum is affixed at times to the surface of the dorsum near the base of the dorsal fin. Scars have been observed on the backs of female spotted ratfish consisting of 5–15 lacerations (Dean, 1906). The anterior scars are punctures while posterior ones are scratches. The number of penetrations corresponds to the number cusps along the frontal edge of the hook-bearing club. This relationship was demonstrated by placing a tentaculum next to the region of the body of the female bearing the lacerations. The presence of more than one scar on a female indicates that a male or several males likely attempt to copulate with a particular female multiple times.

3.2.8. Body biting

Male chimaeras, sharks, and rays commonly seize the female with their jaws during courtship. This behaviour serves two functions that ensure a successful copulation. Firstly, it serves as a behavioural releaser. This stimulus induces the female to remain motionless while the male inserts his clasper into her cloaca and fertilizes her egg with his sperm. Secondly, it provides

the support needed for him to twist his body around and insert his forward oriented intromittant organ into her vent. This precopulatory behaviour has been observed in members of six orders of the Chondrichthyes, the Chimaeriformes, Heterodontiformes, Orectolobiformes, Lamniformes, Carcharhiniformes and Myliobatiformes. Stevens (1974) and Pratt (1979) described scars on female blue sharks, *Prionace glauca*, from bites inflicted by males. Pratt (1979) through dissection found sperm in the oviducal glands of the females from mating in the summer with males in the offshore waters of the western North Atlantic Ocean. Male spotted ratfish have flat teeth for crushing bivalves with hard shells or crustaceans with hard external skeletons. These teeth would be ineffective at seizing and holding a female during copulation. Yet males of the spotted ratfish have been observed to bite the pectoral fin of the female during courtship. The horn shark, *Heterodontus francisci*, a heterodontiform, has small pointed teeth with a central cusp flanked by a pair of lateral cusplets at the front of the jaws but much larger, elongated lengthwise, molar-like in the rear of their jaws. Scars from male biting have been found on the gills, pectoral fins, dorsum and tail of reproductively mature female horn sharks (Dempster & Herald, 1961). Male nurse sharks, an orectolobiform, have been observed to bite the pectoral fins of females (Figure 9b; Video 3 at 10.6084/m9.figshare.22310587) (Klimley, 1980; Carrier et al., 1994; Pratt & Carrier, 2001). Scarring from precopulatory biting are found on the pectoral fin and head of the sand tiger, a lamnid shark (Smith et al., 2015). Body biting has been observed in many carcharhiniform sharks. Male blue sharks, *Prionace glauca*, mainly seize the main torso of the female, inflicting semicircular jaw impressions, tooth slashes, and individual tooth nicks (Stevens, 1974; Pratt & Carrier, 2001). Similarly, male blackfin reef sharks inflict tooth slashes and individual tooth nicks on the pectoral fins and dorsal surfaceof females (Porcher, 2005). Bites to the pectoral fin are inflicted by male scalloped hammerhead (Salinas-de-Leon et al., 2017) and reef whitetip sharks, *Traiaenodon obesus* (Uchida et al., 1990; Tricas & Lefeuvre, 1985). Other species bite other parts of the body such as the gills, body, and tail as well as the pectoral fins such as the chain catshark, *Scyliorhinus retifer* (Castro et al., 1988) and cloudy catshark, *Scyliorhinus torazame* (Uchida et al., 1990).

Similarly, body biting is common among the Myliobatiformes. Male spotted eagle rays seize either the pectoral fin or body of the female (Figure 9c)

(Uchida et al., 1990), whereas male cownose, *Rhinoptera bonasus*, and flapnose rays, *Rhinoptera javanica*, inflict 'gouging' and 'nibbling' bites to the female's dorsum (Tricas, 1980; Uchida et al., 1990). A female reef manta ray was observed to remain motionless while two males attempted to grasp her pectoral fins (Figure 7d) (Stevens, 2016). This behaviour will be described in greater detail under 'positioning and alignment'.

3.2.9. Accepting

Female nurse sharks complete mating with males 5% of the time in solo encounters (Carrier et al., 1994). A female indicates acceptance by ceasing to avoid, relax, or arch her body away from the male but cupping her pelvic fins to permit clasper insertion by the male using his tail to gain purchase. To aid clasper alignment the female's tail is caught, tucked, in a fork between the males tail and the active clasper to permit copulation (Video 3 at 10.6084/m9.figshare.22310587) (Carrier et al., 1994).

3.2.10. Carrying

After a female nurse shark is grasped in shallow water <0.5 m deep while 'refuging' according to Pratt & Carrier (2001), she most often avoids the male (Carrier et al., 1994). In 5% of the time, the female accepts the male's overtures. The male carries the female into water deep enough (>1.0 m) to permit copulation using powerful tail beats and his grasp of her pectoral fin (Video 3 at 10.6084/m9.figshare.22310587) (Pratt & Carrier 2001). Carrying may cover a distance as long as 100 m in the Dry Tortugas.

3.2.11. Positioning and alignment

This was first described for nurse sharks in the Miami Seaquarium (Miami, FL, USA) (Klimley, 1980). Male nurse sharks were observed to follow receptive female nurse sharks in the shark channel in the Miami Seaquarium. One male was observed to seize the margin of the pectoral fin of a female in his mouth, bite down on her fin, and in response she pivoted her anterior torso over an arc of approx. 90° in front of the male (Figure 10a). He then released her fin from his jaws and pushed her anterior torso around with his snout until she was lying parallel beside him on her back. The female remained motionless and rigid with her pectoral fins outstretched all of this time. The male then swam on top of the female and inserted his clasper. The male rolled on to his back revealing his clasper inserted into the female's cloaca. A detailed description of precopulatory and copulatory behaviour of nurse sharks in the field is given below.

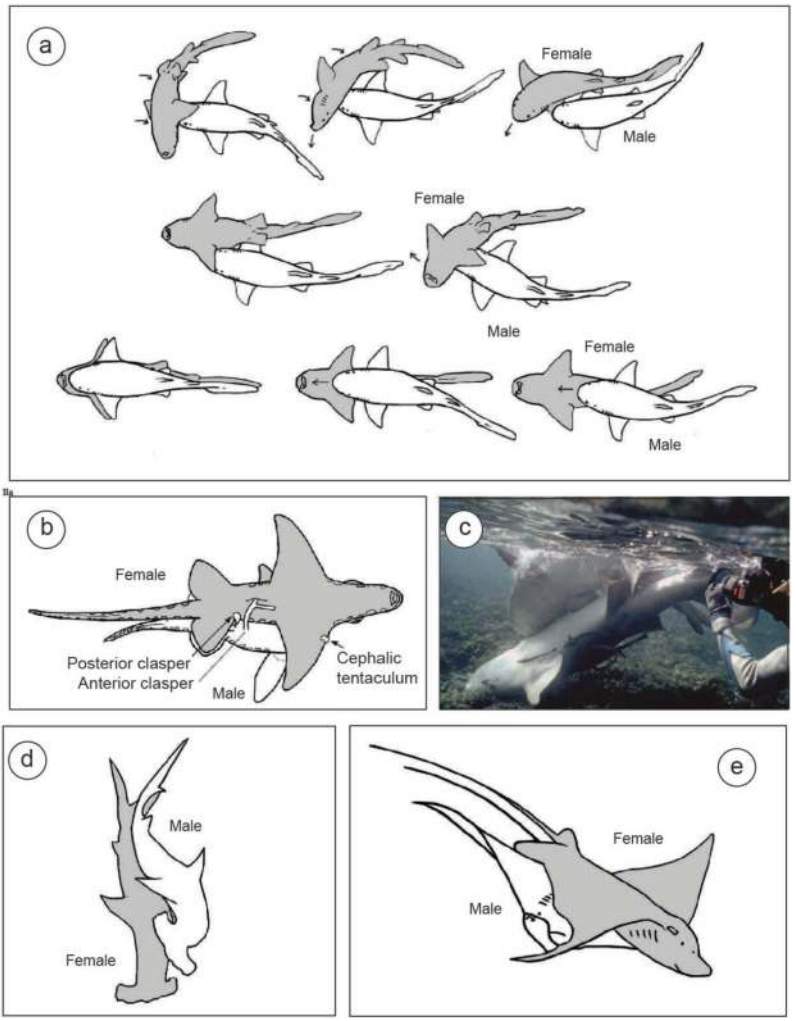

Figure 10. Positioning, alignment of female, and copulation. (a) Positioning and alignment: a female nurse shark turns over in response to a male bite, with the male then nudging her parallel to him, before swimming on top (Klimley, 1980); (b) paired copulation while on bottom: a female spotted ratfish rolls over on back next to male with male's clasper inserted and his tentaculum seizing pectoral fin (Van Dykhuizen, 2011); (c) male nurse shark arching his body over female while copulating with the female's head nudged into bottom to facilitate male thrusting (Pratt, pers. commun.); (d) paired copulation while swimming or sinking in water column: Male has clasper inserted in female scalloped hammerhead as they sink in water column together (Salinas-de-Leon et al., 2017); (e) male and female eagle rays swimming abdomen to abdomen with male's clasper inserted in female's cloaca (Uchida et al., 1990).

The most detailed description of this behaviour in batoids exists for the reef manta ray (Stevens et al., 2018). Females reduce their swimming speed while rising in the water column close to the surface. The male then positions himself on top of the female's back, at which time he uses his unfurled cephalic palms to guide his mouth down the leading edge of the female's pectoral fin until his open mouth seizes the tip of the female's pectoral fin and grasps it firmly. Once the male has a firm grip he rotates his body underneath the female until the pair are positioned abdomen to abdomen.

3.2.12. Paired copulation while on the bottom

There is not that much variation in this behaviour among members of the chondrichthyan orders. The male spotted ratfish, a chimaerid, coils his body around the female, secures himself to her flank by extending his posterior, or pre-pelvic, clasper and affixing it to the side of her body, and only then inserts the calcified internal radius with its hook at the end of the bifurcate clasper into her cloaca (Figure 10b) (Van Dykhuizen, 2011). This behaviour, in which the tentaculum is attached to the pectoral fin and clasper inserted within the cloaca, can only be accomplished because the mature male is much smaller than the mature female. The two then lie on the bottom and then swim together with the clasper inserted in the female for up to two hours. The male horn shark wraps his body around the female, lying on her back on the bottom, and inserts a single clasper in her cloaca (Dempster & Herald, 1961). Carrier et al. (1994) and Pratt & Carrier (2001) observed many instances of courtship and copulation in the Dry Tortugas, Florida, USA (Video 3 at 10.6084/m9.figshare.22310587). In the field, the males never relinquish their grip on the female's pectoral fin once they have initiated courtship. The males often curl their caudal fin around her torso and use her body for leverage while inserting their clasper into her vent. The females remain quiescent and immobile during clasper insertion and copulation as observed in the Miami Seaquarium. The males can catch the female's body between their forward-pointing clasper and their curving tail arching forward for clasper insertion. The male's torso undulates as he compresses his peritoneal cavity and perhaps the subdermal sperm sac. Stored seawater is forced out of his sperm sac to propel sperm through the claspers' central groove and into the cloaca of the female. A male nurse shark is shown arching his body over a female while copulating with the female's head nudged into the bottom to facilitate male thrusting (Figure 10c) (Pratt & Carrier, 2005). A pair of white sharks, a lamnid, were seen courting and copulating in the waters

near a shore-based colony of New Zealand fur seals, *Arctocephalus forsteri*, from a clifftop vantage point in southern New Zealand (Francis, 1996). The observer "… thought at the beginning they were fighting as one animal appeared to be attempting to grasp the other with its great mouth, making great gouges in its side…". However, they had eventually become motionless, one under the other, turning over from time-to-time belly to belly. This mating ritual lasted some forty minutes before the animals finally parted and glided off in opposite directions.' The male carcharhiniform sharks such as the grey reef shark (McCauley et al., 2010), reef whitetip (Tricas & Lefeuvre, 1985; Whitney et al., 1994), and chain catshark (Castro et al., 1988) hold on to the pectoral fin of the female while pinning her to the bottom while inserting their claspers into her cloaca. The male clearnose skate holds on to the trailing edge of the female's pectoral fin, swings his tail beneath her, and inserts one clasper (Luer & Gilbert, 1985). They copulate for 1–4 hours while lying at rest on the bottom.

3.2.13. Paired copulation while swimming or sinking in water column

Clark (1963) observed two lemon sharks swimming in an apparently synchronized manner in the process of copulation. Scalloped hammerhead shark courtship and copulation was recorded on video at Manuelita Island, located off the northeastern coast of Cocos Island, in the tropical eastern Pacific Ocean off the coast of Costa Rica (Salinas-de-Leon et al., 2017). The mating event started at 5 m depth and ended on the nearby seabed located at 45 m depth. It is likely that the pairing of the male and female occurred within a school, which commonly is observed at this site. A male and one female of a similar size of approx. 2.5 m total length were observed swimming slowly parallel to each other near the surface. The male grasped her pectoral fin while arching his body so that his pelvis was close to the female's cloaca with his clasper rotated anteriorly. The male then inserted his clasper into the female's cloaca and his siphon sac was seen to expand as it filled with water. The two sharks then stopped swimming and descended in the water column in a spiraling trajectory (Figure 10d). This was followed by the repeated rapid thrusting of his pelvic region toward the female's pelvic region.

Members of five species in the order Myliobatiformes have been observed abdomen to abdomen with the male's clasper inserted into the female's cloaca. Male reef manta rays continue to beat their pectoral fins while the females usually remain motionless in the water column near the surface. The males make rapid pelvic thrusts and the intertwined pair often spirals around

in a clockwise motion while slowly sinking. Copulation lasts for approx. 30–40 s. (Stevens et al., 2018). Oceanic manta rays also swim in copula near the surface (Yano et al., 1999; Stevens et al., 2018). Spotted eagle rays swim in copula at mid-depths in an aquarium (Figure 10e) (Uchida et al., 1990) and cownose and flapnose rays start swimming in this manner at the surface and descend to the bottom (Uchida et al., 1990).

3.2.14. Grouped attempts at copulation

Multiple sharks and rays compete among themselves to copulate with females at the same time. For example, five male nurse sharks, orectolobiforms, attempted to move a female from the bottom in shallow water into deeper water to copulate with her in the Dry Tortugas (Figure 11a) (Carrier et al., 1994; Pratt & Carrier, 2005). Four male reef mantas have been observed to attempt to position themselves on top of the dorsal surface of a female (Figure 11b) (Stevens et al., 2018) Many male reef whitetip sharks, carcharhiniforms, surrounded a female and attempted to copulate with her while swimming in the water column in Southeastern Australia (Whitney et al., 1994). This eventually resulted in copulation on the bottom.

3.2.15. Altruism

In group encounters one male nurse shark may exhibit cooperative behaviour by positioning his body at a perpendicular angle in front of a copulating pair of sharks to provide support for the female and male (Pratt & Carrier, 2005). This blocking enabled the second male to thrust repeatedly once his clasper was in her cloaca (Figure 11c; Video 3 at 10.6084/m9.figshare.22310587) (Carrier et al., 1994).

3.2.16. Post-copulatory ejaculation

A male whitetip shark was observed to eject sperm from his clasper after an unsuccessful attempt at copulation (Whitney et al., 1994).

3.2.17. Post-release gaping

A male nurse shark was seen to swim away after releasing his grip on the fin of a female with his mouth his mouth agape presumably to maximize water flow into mouth and over gills in the Dry Tortugas (Figure 11d) (Pratt, pers. commun.). The same behaviour was observed to be displayed by a male reef whitetip sharks (Whitney et al., 1994).

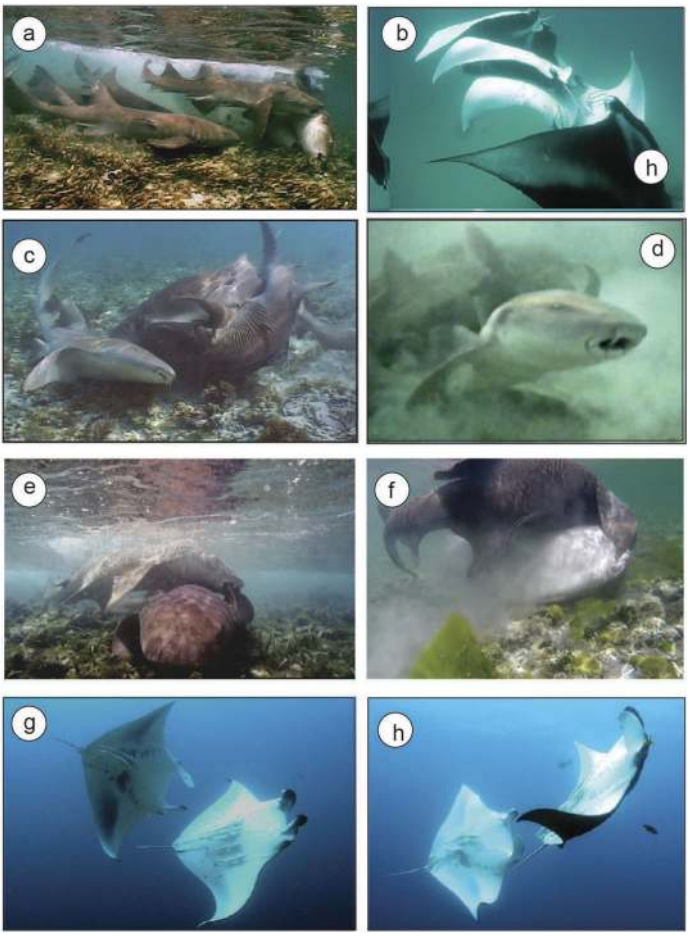

Figure 11. Copulation related behaviours. (a) Group attempts at copulation: Six male nurse sharks attempt to move a female into deeper water to copulate with her (Carrier et al., 1994); (b) four male reef mantas attempt to position themselves directly on top of dorsal surface of female (Stevens et al., 2018); (c) altruism: a male nurse shark exhibits cooperative behaviour by positioning his body at perpendicular angle to provide support for the female and male (Carrier et al., 1994); (d) post-release gaping: a male nurse shark swims away after releasing grip on female fin with mouth agape to maximize water flow into mouth and over gills (Pratt, pers. commun.); (e) avoidance: a female nurse shark holds herself stationary on the bottom despite her pectoral fin being seized in order to prevent the male from turning her over and inserting his clasper into her cloaca (Pratt, pers. commun.); (f) the female rolls over in an attempt to force the male to release his bite (Pratt, pers. commun.); (g) a male reef manta ray approaches female to mate with her (Stevens et al., 2018); (h) the female exhibits evasive action by flipping her body over in the first of multiple forward somersaults (Stevens et al., 2018).

3.2.18. Avoidance

Female sharks and rays discourage males from copulating with them with a diversity of behavioural patterns. Female sand tiger sharks 'shield' or press their pelvic fins close to the bottom to prevent males access to their cloacas (Gordon, 1993). When approached by patrolling males, females go to the shallowest parts of the lagoon, often less than 40 cm in depth. Possibly, they were reluctant to mate with less fit males. There they ceased swimming and rested on the bottom. If a male bit the pectoral fin of a nonreceptive female, she often attempted to escape by twisting her body so that her cloaca was either against the bottom or less commonly out of the water. If the male did not lose interest within a few moments, she often twisted out of his grasp and rapidly swam away. In the Dry Tortugas off the tip of Florida, USA, females visit the shallow waters biennially to court and copulate (Pratt & Carrier, 2001). Shark mating is a rough and energetic action. By retreating into shallow water (<1 m deep) a female can easily avoid and select males with which to mate. A female is shown arching her body over the head and back of a male the instant the tip of her pectoral fin is grasped in an apparent attempt to release his hold on her fin (Figure 11e–f; Video 3 at 10.6084/m9.figshare.22310587). A total of 95% of the solo male nurse shark's attempts at mating ended with the female avoiding copulating with the male (Pratt & Carrier, 2001). The manner by which sharks avoid copulation was described in detail for the whitetip reef shark (Whitney et al., 1994). A male whitetip shark was observed seizing the pectoral fin of a female for over a minute but was unable to achieve clasper insertion due to three female evasive actions. First, the female kept her ventral surface in contact with the substrate, making it difficult for him to insert his clasper into her cloaca. Second, she rolled the distal half of her left pectoral fin under her body, keeping it away from other males, while using it to provide leverage to keep her in an upright position. Third, as a male attempted to thrust his clasper into her cloaca, she kept her tail tightly arched below his abdomen and curved against his clasper, thus preventing access to her cloaca and maintaining upright stability so she could not be overturned.

In the batoids, female spotted eagle rays lift their dorsum out of the water and slap the surface with their pectoral fins to discourage males from mating with them (Uchida et al., 1990). Male stingrays can be impaled by the caudal spine of a female unwilling to copulate with a male (Michaels, 1993). Female

reef manta rays make erratic twists and turns while accelerating their swimming speed to avoid males that are chasing them. They maneuver around fixed obstacles and other reef manta rays in the water column to avoid males that approach them closely from behind (Stevens et al., 2018). They may undertake backward somersaults, forward flips, and may also leap clear of the water (Stevens et al., 2018). The males attempt to mirror the female's movements.

3.3. Filter feeding behaviours (Table 3)

3.3.1. Ram feeding on plankton or small fishes

Whale sharks often swim in a straight line with their mouths open and their heads slightly above the water surface so that either part or all of the dorsum between the rostrum and first dorsal fin are exposed (Figure 3a) (Motta et al., 2010). A basking shark is filmed underwater as it feeds on plankton off the coast of North Ireland (Video 4a at 10.6084/m9.figshare.22310587) (Johnston, pers. commun.). They swim at an average rate of 1.1 m/s, equivalent to the speed of a moderately fast walk. Their mouth opening is elliptical with the width greater than the height. The flow around the lateral margins of the mouth creates a bow wave, and this forces more water to enter the mouth. Sometimes the sharks cough while feeding on the surface, expelling material forcefully out of their mouths. Whale sharks feeding off Cabo Catoche in the Yucatan, Mexico, fed at the surface mostly early and late during the day, rarely at night. In this region they feed mainly on sergestid shrimps, calanoid copepods, chaetognaths, and fish larvae. Basking sharks have also been observed ram feeding at the surface on euphausiid shrimps off the coast of Central California, USA (Figure 3b) (Klimley, 2013). However, whale sharks do not feed exclusively on plankton but also feed on 'baitballs' of tightly schooling small fishes, as observed at Ningaloo Reef, Western Australia (Lester et al., 2022). Multiple individuals herd the fishes into more dense schools to maximize their feeding success.

3.3.2. Funnel orientation of cephalic palps

Much has been learned about the filter feeding of manta rays by observing them in the clear waters of the Maldive Islands in the Western Pacific Ocean (Stevens, 2016). Individuals of both ray species, the giant manta, *Manta birostris*, and the reef manta, *Manta afredi*, feed most commonly in an independent manner by swimming forward in a straight line with their

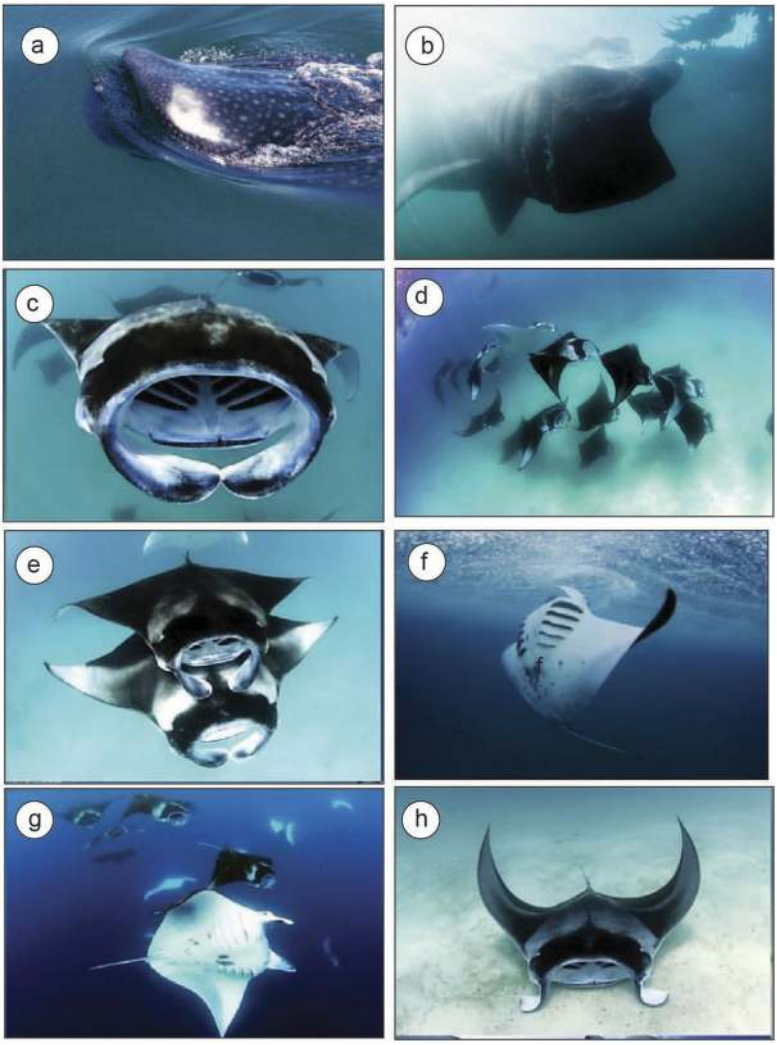

Figure 12. Feeding on plankton. (a) Ram feeding on plankton or small fishes: whale shark moves along surface with mouth open to feed on plankton (Motta et al., 2010); (b) basking shark swimming at surface with mouth open to feed on plankton (Klimley, 2013); (c) reef manta unfurles it's cephalic palps to create biological funnel to trap plankton (Stevens, 2014); (d) chain feeding: multiple mantas lined up in head-to-tail formation to feed on plankton (Stevens, 2016); (e) piggy-back feeding: smaller manta positions itself on top of another when straight-line feeding (Stevens, 2016); (f) somersault feeding: manta performs tight backward loops to capture plankton (Stevens, 2016); (g) sideways feeding: manta swims rotated 90° from horizontal when feeding (Stevens, 2016); (h) bottom feeding: manta swims along bottom with unfurled cephalic palps to trap prey (Stevens, 2016).

cephalic palps held open in front of the mouth (Figure 12c). These paddle-like appendages almost touch in the center forming a wide oval shape which funnels zooplankton, most often copepods, into the manta's buccal cavity. These are referred to here as 'palps', defined by the Oxford Dictionary as "a pair of elongated segmented appendages near the mouth of an arthropod, usually concerned with the senses of touch and taste". The definition is expanded here to describe a pair of vertebrate appendages. The reef manta feeds on the horizontal plane through the water with its head titled upward so that its top jaw is positioned at, or above, the water surface. Its close proximity to the water's surface requires that the manta has to reduce the up-stroke of the pectoral fin to prevent its pectoral fins from lifting above the water's surface.

3.3.3. Chain feeding

Reef mantas line up head-to-tail to form a tight feeding chain with individuals oriented closely head to tail, often with up to several dozen individuals (Figure 12d). During major feeding events the chain may expand to consist of multiple loosely interlinked chains several animals' wide, stretching back to form a tail of over 40 individuals.

3.3.4. Piggy back feeding

Reef mantas at times follow others closely and position themselves directly on the back of others that are feeding while swimming in a straight line, matching their pectoral fin strokes to the other manta. Multiple individuals piggyback on top of each another, resulting in stacks of as many as five rays feeding together. Two individuals performing piggy back feeding are shown here (Figure 12e).

3.3.5. Somersault feeding

Reef manta rays display tight backward loops with their mouths held wide open and their unfurled cephalic palps positioned just in front of the lower jaw in order to increase the ability to funnel plankton into the buccal cavity (Figure 12f).

3.3.6. Cyclone feeding

Reef mantas feed upon zooplankton while swimming in an anticlockwise spiral, creating an underwater cyclone approx. 15 m in diameter (Video 4b at 10.6084/m9.figshare.22310587) (Corbett, pers. commun.). If the zooplankton is denser close to the seafloor, the cyclonic pattern in which the mantas swim becomes compressed in height, forming more of a spiraling circle of mantas close to the seabed.

3.3.7. Sideways feeding

Giant manta rays at times swim with bodies rotated 90° from the horizontal plane. Sideways-feeding mantas do not unfurl their cephalic palps (Figure 12g). Two or more sideways-feeding individuals can form a chain.

3.3.8. Bottom feeding

Reef manta rays also swim along the seabed with their open mouth positioned very close to the seafloor (Figure 12h). The cephalic palps are unfurled to funnel zooplankton into their buccal cavities. Red abrasions are caused by the regular contact of the manta ray's cephalic palps and gill slits with the seabed during bottom feeding and the contact with the substrate can rub away the tips of their cephalic palps.

3.4. Scavenging behaviours (Table 4)

3.4.1. Parading

At Guadalupe Island, Baja California Norte, Mexico, white sharks were observed to swim slowly around baits, which were often decoys (Figure 13a) attached to tethers leading from the ecotourism boats without orienting to the item (Becerril-Garcia et al., 2019). They moved at a distance of one to ten meters from the item. This was a common behaviour, representing 19% of all behavioural patterns recorded during the monitoring of white shark tourism at the island (Becerril-Garcia et al., 2019).

3.4.2. Close inspection

White sharks moved close to the bait at a distance of less than a meter without opening their mouths to try to consume the item, a behavioural pattern recorded in 24% of the time (Figure 13b) (Becerril-Garcia et al., 2019).

3.4.3. Horizontal bite

White sharks swam directly toward the bait and opened their mouths to seize it. This behaviour was termed 'horizontal attack' and was observed 30.1% of all behavioural patterns observed from sharks attracted to the ecotourism boats (Becerril-Garcia et al., 2019). White sharks were photographed scavenging on the carcass of a humpback whale, *Megaptera novaeangliae*, near Point Reyes, central California, U.S.A. (Curtis et al., 2006). Although solitary white sharks fed most often on the carcass of the whale, simultaneous feeding by two white sharks was observed at times. The sharks swam up to the whale at the surface on the horizontal plane and removed bites of the

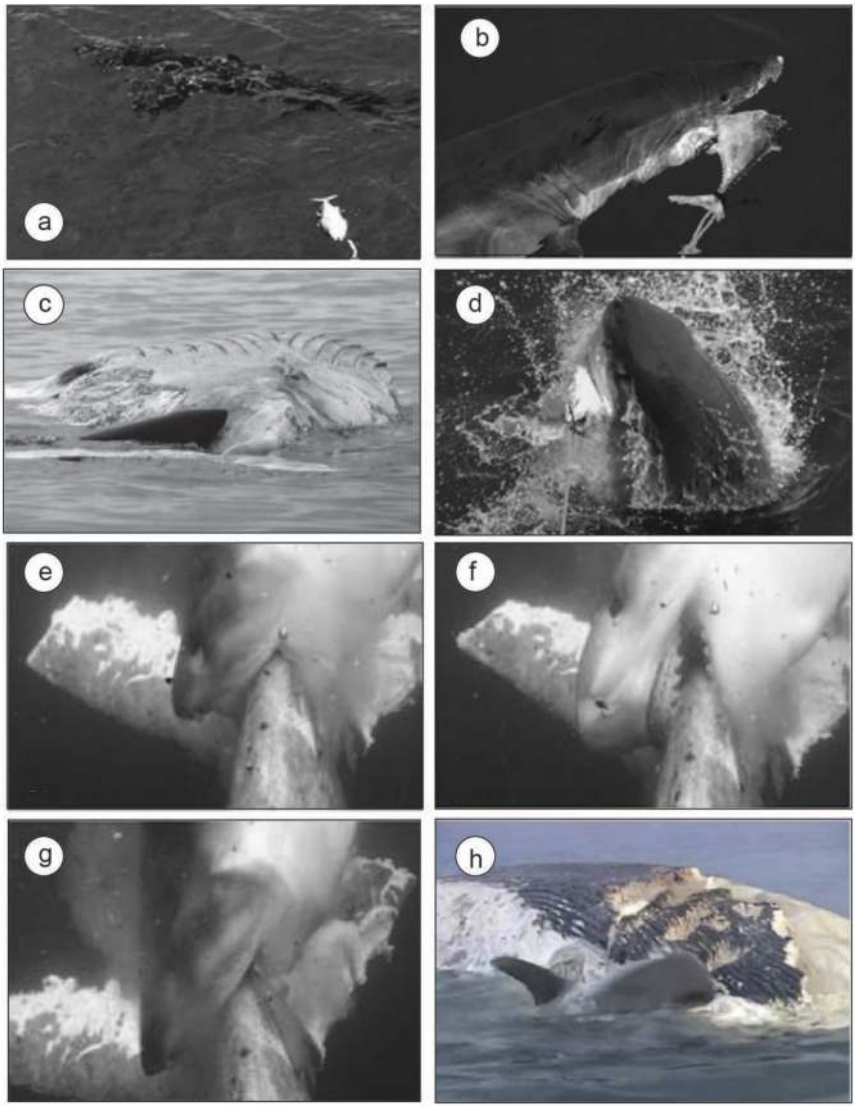

Figure 13. Feeding on carrion or scavenging. (a) Parading: white shark swims slowly around bait without seizing it (Becerril-Garcia et al., 2019); (b) close-inspection: the white shark swims near the bait without seizing it (Becerril-Garcia et al., 2019); (c) horizontal bite: the shark moves toward the shark on a horizontal plane while driving his body upward as he bites a whale (Curtis et al., 2006); (d) vertical bite: shark swims upward from deep to seize a bite or remove a bite from a whale (Becerril-Garcia et al., 2019 (e–g) saw bite: tiger shark removes pieces of flesh with a side to side movement of the jaws (Clua et al., 2013); (h) rotary bite: shark moves forward and backward or spins to remove a bite (Clua et al., 2013).

outer blubber layer of the carcass, avoiding previously exposed muscle tissue (Figure 13c). It has been argued that white sharks prefer to feed upon fatty prey such as seals and sea lions due to their high fat content (Klimley et al., 1996a). Fallows et al. (2013) observed white sharks feeding on carcasses of two Bryde's whales, *Balaenoptera edeni*, and two southern right whales, *Eubalaena australis*, in False Bay, South Africa. The sharks exhibited an initial preference for feeding on the whale caudal peduncle and fluke, before continuing to feed along the rest of the body. The sharks also clearly showed preference for areas of high blubber content, a finding which is consistent with previous observations and interpretation of the energetic value of such preferential feeding. Typically, the white sharks would approach the whale slowly, then they would swim around and mouth different parts of the carcass before settling on a specific blubber-rich spot, and usually they would repeatedly bite down from a horizontal position to remove flesh. Bouts of scavenging would typically last 15–20 s.

3.4.4. Vertical bite

At times white sharks moved directly upward from below in the direction of the bait with their mouths open for capture. They swam in a trajectory of 44–90° in relation to the surface. This behaviour comprised 7.2% of all of the behavioural events observed near the ecotourism boats (Becerril-Garcia et al., 2019). Similarly, whale carcasses in Central California and South Africa were approached by sharks rising from the bottom and biting from a vertical position (Figure 13d) (Curtis et al., 2006; Fallows et al., 2013).

3.4.5. Saw bite

White sharks removed large bites by side-to-side shaking of the head, termed 'saw biting' by Randall (2006) and 'lateral headshakes' by Fallows et al. (2013). Tiger sharks, *Galeocerdo cuvier*, exhibited this behavioural pattern when scavenging on the carcass of a blue whale, *Balaenoptera musculus*, in Prony Bay, southern New Caldonia (Clua et al., 2013). A time series of photographs is presented showing saw biting, based on lateral side-to-side movement of the head around the pectoral girdle axis, which resulted in swift cutting of pieces of flesh including cartilage (Figure 13e–g; Video 5 at 10.6084/m9.figshare.22310587). A tiger shark often needed to perform up to 10 rotations to extract a mouthful of the tough tissues and cartilage of the carcass such as those present at the caudal peduncle.

3.4.6. Rotary bite

This biting technique involved rolling and spinning the body. Near the end of the feeding event, some tiger sharks lodged their jaws deep into the carcass before using their body mass as a leverage either by moving forward and backward or by spinning their body on its longitudinal axis, which enabled them to retrieve large pieces of flesh with less effort (Figure 13h) (Clua et al., 2013).

3.5. Predatory behaviours (Table 5)

3.5.1. Ambushing active prey

One form of this behaviour is 'stalking'. This is an elaboration of the ambushing strategy because the predator utilizes camouflage to approach the prey undetected and then rushes forward to make a sudden assault (Klimley, 2013). White sharks, a lamniform, congregate close to shore at Southeastern Farallon Island during October and November where they capture juvenile northern seals, one and two years old, as they converge upon a few beaches, which they colonize in great numbers. White sharks stalk seals and sea lions as they pass to and from their shore-based colonies (Klimley et al., 1992). The common name, 'white shark', which refers to the colour of its underside, is misleading with regard to its mode of prey capture. The colour of the shark's dorsum varies from solid to mottled grey and this colouration matches the hues of the rocky bottom or the murky water below its prey. This camouflage enables white sharks to approach their prey close enough from below to see its silhouette against the surface. The seal is particularly vulnerable when making a dive after breathing at the surface. The shark, positioned beneath the seal, accelerates upward to seize it by the head as the seal begins its descent on its return to the island. Over 40% of seal carcasses observed after initial seizure by a white shark at the Southern Farallon Islands had bites on the head and anterior trunk of the body (Klimley et al., 1996a). The sharks appear to carry seals downward and hold them in their jaws before biting down and removing parts of the seals when they are no longer bleeding. This ensures that seals are immobile and can't escape once released from their grip (Figure 14a). This mode of immobilization is termed 'exsanguination' or blood deprivation. The shark lets go of the seal after taking a bite. It is at this time that other sharks converge upon the carcass. They compete with the primary attacker for the prey by participating in a ritualized combat that involves splashing water on each other with their tails,

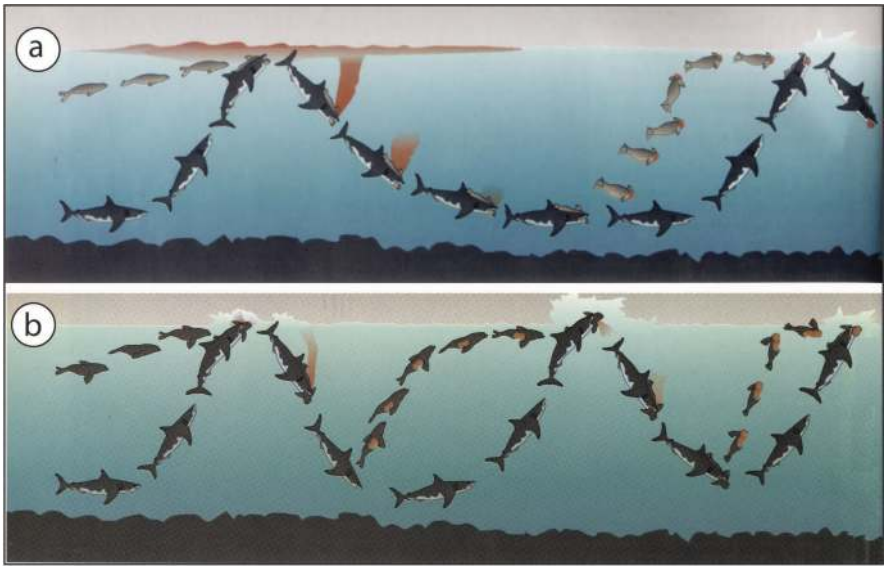

Figure 14. Ambushing active prey at surface. *Ambushing active prey*: white shark accelerates upward from bottom, where it matches the dark rock bottom, to seize seals (a) and sea lions (Klimley, 1994) (b).

which will be described later with other aggressive behaviours. The sharks rarely immobilize California sea lions on the first strike because they manage to wrest themselves free from the shark's grip by biting and scratching (Figure 14b). White sharks almost always need to seize them a second time to immobilize them.

An ambush predator can conceal its presence while remaining stationary, lying in wait for the prey to swim close. This mode of predation is common among the dorsal-ventrally compressed angel sharks of the order Squatiniformes, guitarfish in the order Rhinopristiformes, and skates in the order Rajiformes. Members of these orders remain motionless on the bottom with a colour pattern matching the surrounding background. Pacific angel sharks, *Squatina californica*, lie partially buried in mud or sand with their terminal mouth oriented upward ready to draw in an above-swimming fish or squid (Fouts & Nelson, 1999). They do this by rapidly opening their mouths while expanding their branchial, or gill chamber, to create a vacuum and draw their prey into their mouths (Figure 15a). These sharks prefer to lie on the bottom near reefs populated by small fish, where they can easily ambush unsuspecting prey. Individuals migrate between different hunting grounds at nighttime.

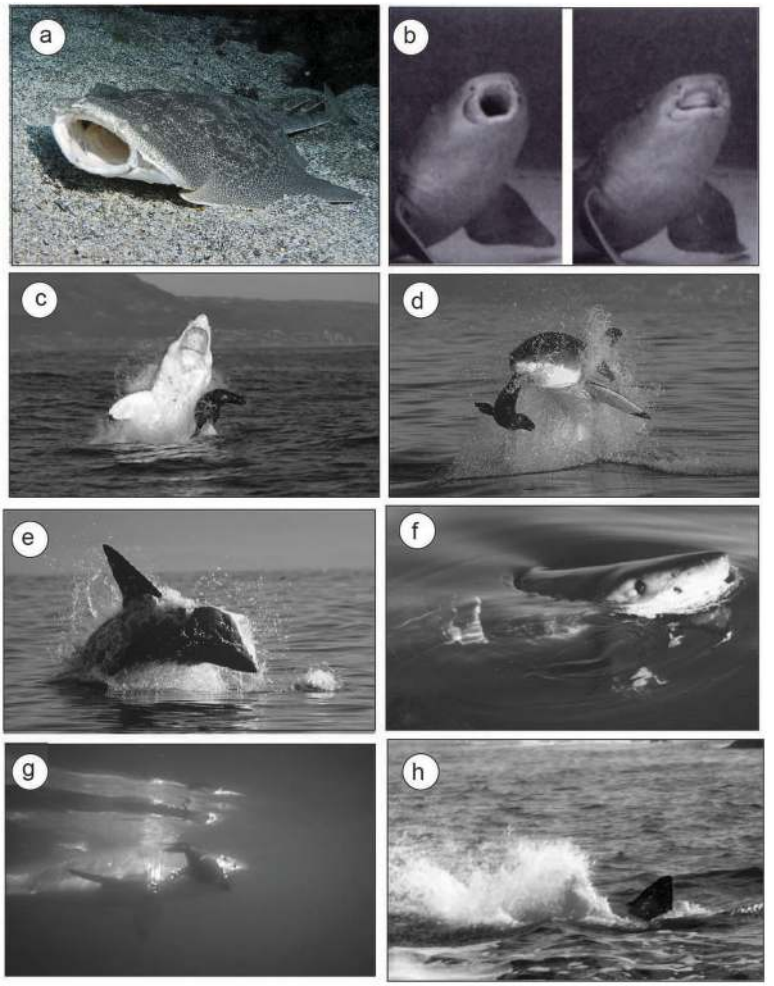

Figure 15. Feeding on active prey. (a) Ambushing active prey: a cryptic angel shark lying on bottom draws prey into mouth when it opens its mouth creating a suction inward (Fouts & Nelson, 1999); (b) suction feeding: free-swimming nurse shark opens mouth to create suction to draw prey into mouth (Motta, 2004); (c) vertical breach with prey seizure: white shark leaps out of water while seizing seal (Martin et al., 2005); (d) horizontal breach with ventrum downward: white shark leaps out of water with belly down at an angle seizing seal (Martin et al., 2005); (e) horizontal breach with ventrum upward: white shark leaps out of water down side upward at an angle seizing seal (Martin et al., 2005); (f) horizontal bite at surface: white shark approaches prey swimming at surface and seizes it (Martin et al., 2005); (g) carry prey underwater: white shark carries prey under the surface with exaggerated tail beats to propel the additional load (Martin et al., 2005); (h) lateral head shake: head moved back and forth with jaws on prey to dislodge bite of flesh (Martin et al., 2005).

3.5.2. Suction feeding

Suction feeding is a less common mode than active seizure but is often used to ingest prey. It is utilized mainly by the carpet sharks of the order Orectolobiformes and the skates and stingrays of the Rajiformes and Myliobatiformes, respectively. Motta (2004) described the biomechanics of this behaviour. The process is illustrated with two photographs of prey seizure by the nurse shark (Figure 15b). A negative pressure or suction is generated in the branchial cavity to draw prey inside the mouth. These sharks lower their jaws and lift their heads at the beginning of an expansive phase to draw prey inside their mouth with a strong suction. The upper jaw is then protruded and moved downward toward the lower jaw during a compression phase. Suction feeders have a small mouth, little teeth, and large labial cartilages. They also have highly developed muscles for opening their mouths rapidly and expanding their buccal and branchial cavities.

3.5.3. Vertical breach with prey seizure

White shark predation was first studied in the natural environment where the sharks fed mainly on northern elephant seals, *Mirounga angustirostris*, and California sea lions, *Zalophus californianus*, in the nearshore waters surrounding the South Farallon Islands in Central California, USA (Klimley et al., 1993, 1996a). These predators propelled two thirds of the entire body out of the water at a 30–60° angle with the sea surface, seizing pinnipeds and holding them in their jaws. Illustrated with a video is a white shark seizing a California sea lion, *Zalophus californianus*, while breaching (Video 6 at 10.6084/m9.figshare.22310587). While the sharks were airborne, they bent their anterior torsos downward and lifted their tails so that they reentered the water head first. They termed the behaviour 'leap'. Martin et al. (2005) studied natural predations by white sharks on Cape fur seals, *Arctocephalus pusillus pusillus*, at Seal Island, South Africa. They defined as a 'polaris breach' a shark leaping partially or completely out of the water in a vertical or nearly vertical head-up orientation either with or without a seal grasped in its jaws. They found that the sharks jumped as much as three meters above the surface of the water while rotating their tails over their heads before reentering the sea head-first near to the original exit point (Figure 15c). If the prey was not grasped by the shark and continued evasive maneuvering, the shark often turned its head mid-flight as though visually following the seal's movement and path (Martin et al., 2005). They distinguished a 'surface intercept' from a 'polaris breach'. The former occurred when the shark that

had been chasing an injured or uninjured seal along the surface in a straight line, leapt partially or completely out of the water to the side, to intercept the seal, which suddenly had changed course, and grasped it with the jaws.

3.5.4. Horizonal breach with ventrum downward

Martin et al. (2005) termed 'surface breach' and 'lateral breach' when sharks leapt partially or completely out of the water in an upright orientation with their body axis at an angle with the sea surface less than 45° with or without a seal in their jaws, cleared the water less than or equal to a meter above the sea surface, and reentered the water in the direction of travel and reentered one half to one and a half body lengths away from the original exit point (Figure 15d).

3.5.5. Horizontal breach with ventrum upward

The shark leapt partially or completely out of the water with either part or all of its belly exposed in an inverted orientation with its body axis forming an angle with the horizon of less than 45° with or without a seal in its jaws (Figure 15e). The sharks' bodies completely cleared the water by less than a meter and reentered the water in the direction of travel half to one and a half body lengths from the original exit point. Martin et al. (2005) called this an 'inverted breach.'

3.5.6. Horizontal bite at surface

White sharks took a 'horizontal bite' out of the prey after seizing it while swimming horizontally on the sea surface (Klimley et al., 1996a) at the South Farallon Islands. A white shark is shown in a video tearing bites from an elephant seal, *Mirounga angustirostris* (Video 7 at 10.6084/m9.figshare.22310587). Martin et al. (2005) termed a 'direct surface approach' when the sharks approached the seal very slowly but directly along the surface to seize either a dead or weakly swimming seal. If a shark accelerated quickly toward an injured or uninjured seal at the surface with its back partially out of the water, holding its jaws open, with or without its jaws protruded, while exposing its teeth — Martin et al. (2005) called this a 'surface lunge' (Figure 15f). These behaviours when followed by biting the seal were termed 'surface grasp, horizontal approach' (Martin et al., 2005).

3.5.7. Vertical bite at surface

Klimley et al. (1996a) defined 'vertical bite' as when the shark swam upward from beneath the prey and grasped the prey in its jaws at the surface. The angle of the sharks' bodies to the sea surface ranged from 60 to 90°.

3.5.8. Carrying prey underwater

White sharks at the South Farallon Islands were observed to swim with an immobile or struggling pinniped held in their jaws, a behavioural state termed 'carrying'. The tail was moved back and forth over a wider arc than when the shark did not hold the prey in its mouth to generate sufficient force to propel the body forward with its extra load (Video 7 at 10.6084/m9.figshare.22310587) (Klimley et al., 1996a). Martin et al. (2005) entitled the behaviour, 'subsurface carry', when the sharks slowly carried a dead or otherwise incapacitated seal underwater for half a minute while transporting it roughly 50 m before feeding on it (Figure 15g). Similarly, the sharks' swimming speed was reduced and the tail beats were increased nearly 50% over that exhibited during normal swimming.

3.5.9. Lateral head shake

This differed in degree from the saw bite, described earlier, in which the bites were taken from a large whale floating stationary in the water. The mass of the prey was great relative to the shark, enabling the shark to use it to enable it to cut a bite from the whale. Klimley et al. (1996a) observed that the forward movement of white sharks were slowed as they shook their anterior bodies from side to side in the horizontal plane, using the resistance of the water to dislodge the bite (see Video 7 at 10.6084/m9.figshare.22310587). This movement often dislodged a piece of flesh from a pinniped held in the mouth. The remainder of the carcass floated to the surface. Similarly, Martin et al. (2005) saw sharks grasp a dead seal in their mouths and shake their heads violently from side-to-side describing an arc of 90°, while removing a piece from the carcass with the remains typically floating to the surface (Figure 15h).

3.5.10. Ram feeding

This mode of feeding is the most common mode of feeding by the mackerel sharks in the order Lamniformes and reef and hammerhead sharks in the order Carcharhiniformes. This differs from the Ram feeding on plankton or small fishes, described earlier (Section 3.3.1), in that shark or ray's mouth is not held open for long periods of time while swimming forward so that zooplankton enter the mouth with the flow of water and are trapped in the gill mesh without active suction. The sequence typically occurs in less than a second and can be separated into four phases although they are continuous actions. This process is illustrated with a time series of photographs of

prey seizure by the Caribbean reef shark (Motta, 2004). Firstly, the mouth is opened slightly in a preparatory phase to move water through the gills to extract oxygen (Figure 16a). Secondly, the lower jaw is lowered while the head is lifted in an expansive phase (Figure 16b). The mouth is opened at this time as the labial cartilages attached to the lower and upper jaws move apart and the branchial chamber is expanded to produce an inward suction. Thirdly, a compressive phase starts when the mouth is opened its widest (Figure 16c). The lower jaw is now elevated and the upper jaw protruded forward and downward toward the lower jaw. At this time, the head is lowered. The prey is either seized between the teeth or drawn within the buccal, or mouth cavity, by the end of the compressive phase. Fourthly, the upper jaw is retracted while the other elements in the jaw return to the initial resting positions during the recovery phase (Figure 16d).

3.5.11. Electrical debilitation

In a sense, the Pacific electric ray, *Torpedo californica*, uses an ambushing strategy to stun and capture its prey (Lowe et al., 1994). Members of this species lie motionless on the bottom during the day, indistinguishable from sandy or rocky background. From this position, they propel themselves upward and over a crustacean or small fish by a few rapid beats of the tail. They then bend their pectoral fins around it and discharge their electric organs. An electric ray is shown being presented with a reef fish at the end of a spear (Figure 16e). The rays then swim over to an incapacitated prey item and rotate it using their pectoral fins so that it can be swallowed head-first. An electric ray is pictured with a fish partially in its mouth (Figure 16f). At night, the rays slowly drift above the bottom and lunge downward toward small fish swimming below. They then orient the underside of their electrical organ-bearing pectoral fins downward toward the fish and discharge their organs to stun it with a debilitating electrical field.

3.5.12. Head and jaws excavation

Stingrays of the order Myliobatiformes such as the spotted eagle ray dig bivalves out of the substrate with protruding jaws (Motta, 2004). The stingrays then crush the prey with their pavement-like teeth. The lower tooth plate extends outward farther than the upper tooth plate, the extension being termed the ‘spade’. It is used to remove sand from the bottom to uncover the buried bivalves.

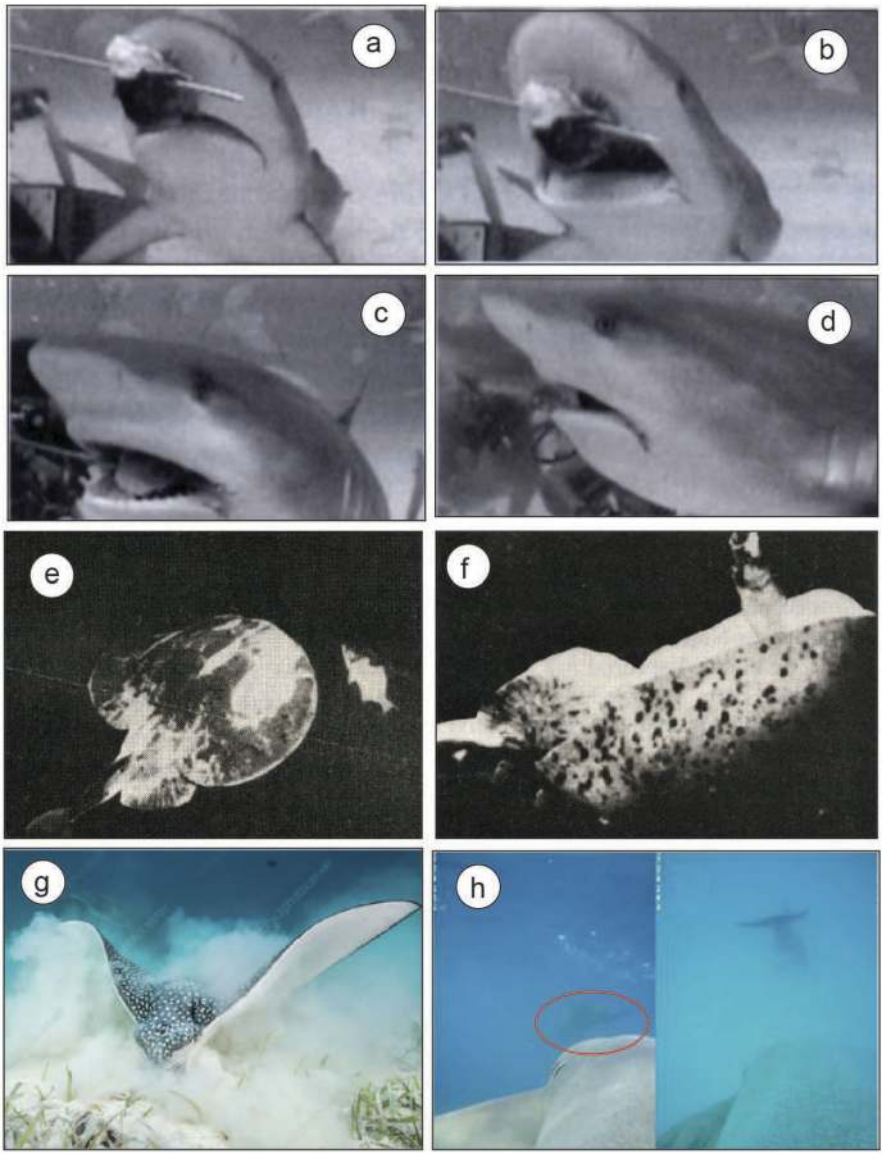

Figure 16. Feeding on living prey. Ram feeding: This consists of (a) preparatory (b) expansive (c) compressive and (d) recovery phases (Motta, 2004); (e, f) electrical debilitation: Pacific electric ray is offered prey at the end of a spear and it surrounds the item with its body, discharges a voltage to disable the potential prey, and ingests it (Lowe et al., 1994); (g) pectoral stirring of substrate: eagle ray excavates prey by moving its pectoral fins; (h) commensal feeding: nurse shark follows dolphin and feeds upon dislodged prey items (White et al., 2022).

3.5.13. Pectoral stirring of substrate

Cownose rays excavate their prey, mostly bivalves, with a stirring movement of the pectoral fins (Figure 16g). They then open their jaws wide to use suction to seize and ingest the bivalves (Smith & Merriner, 1985).

3.5.14. Release from jaws

The shark releases an intact object from its mouth (see Video 8 at 10.6084/m9.figshare.22310587). Martin et al. (2005) defined 'food release' as when sharks released a whole or partial seal carcass, which then floated to the surface, and did not reclaim it for roughly ten minutes. Often, at least one other shark was visible in the immediate vicinity. The seal carcass was usually consumed by either its original possessor or another white shark. Occasionally, the carcass simply drifted away from the kill site and out of visual range. This phenomenon of 'release' is likely explained by a lack of palatability of the prey (Curtis et al., 2012).

Tricas & McCosker (1984) argued that white sharks strike humans at the surface because they resemble pinnipeds. However, to the contrary, Collier et al. (1996) found that white sharks strike a diversity of objects, some not resembling pinnipeds such as crab pot buoys, otter boards, even an inflatable raft. Tricas & McCosker (1984) argued that white shark bite humans, spit them out, and then wait until they stopped struggling from their wound before consuming them. This was based in part on divers surviving shark attacks with only teeth marks indicating they were held by the shark. Klimley et al. (1996a) were able to evaluate this hypothesis based on witnessing predations on seals and sea lions, the most common prey of white sharks, in Central California. Verification of this 'bite, spit, and wait' hypothesis would require sharks being observed seizing pinnipeds, releasing them struggling in an intact yet wounded condition, waiting nearby until the prey became immobile, and soon after feeding upon them. This behavioural sequence was never observed in 131 video records of predations at the pinniped colonies on the South Farallon Islands in Central California. Did white sharks release seals in a wounded but intact condition? Sharks removed flesh in 94.4% of the feeding bouts on phocids immediately after the shark's initial strike. Similarly, sharks removed flesh in 90.9% of the feeding bouts on otariids Did white sharks always wait until pinnipeds became immobile before returning to complete feeding? Phocids and otariids were first seen as they lay motionless on the surface in 72.2 and 38.5% of the predations on each, respectively. The absence of movement appeared to be a reliable indicator of death. Only

in one instance did a phocid or otariid begin swimming after floating motionless. When pinnipeds survived the initial strike and remained at the sea surface, sharks usually did not wait until these prey items were motionless before feeding. Pinnipeds were seen after the initial strike at the surface moving limbs, bobbing, rolling, intermittent swimming, or slow swimming in 27.8 and 61.5% of the attacks on phocids and otariids, respectively. Sharks attacked 64.4% of the phocids and 75% of the otariids performing such actions (Klimley et al., 1992).

Could white shark refrain from feeding upon items due to their low energy value? Certain prey could be deemed less palatable after initial sampling. A brown pelican and human were observed to be seized close to the island and released by a white shark, which then left the area of the initial strike. Other species also are seized and released by white sharks. Randall et al. (1988) recovered jackass penguins, *Spheniscus demersus*, having shark bite scars. Ames & Morejohn (1980) found sea otters having wounds in which white shark tooth fragments were embedded but from which no flesh was removed. The birds, sea otter, and human are composed mainly of muscle tissue, whereas pinnipeds and cetaceans possess a great deal of superficial fat tissue. Sharks may prefer energy-rich marine mammals in favour of energy poor prey. Supporting this are observations of sharks selectively feeding on the blubber but not the muscle layers of mysticete whales (Pratt et al., 1982; Long, pers. commun.). Klimley (1987) also observed that white sharks readily consumed seal carcasses but would only seize and release sheep carcasses, which are devoid of a fatty layer. The polar bear, *Ursus maritimus*, and the leopard seal, *Hydrurga leptonyx*, often remove only the fatty tissue from phocids when feeding (D. Siniff, pers. commun.). The most likely explanation for 'bite, spit, and wait' without consumption hypothesis is that the white shark performs an exploratory strike at something moving at the surface and then determines its palatability upon seizure of the prey and not mistaken identity as Clua & Meyer (2023) cogently argue in this issue. In support of this, a badly decomposed and gas-filled sea lion carcass was observed floating away from Southeast Farallon Island (Klimley et al., 1996a). A white shark swam slowly near the carcass. The shark then momentarily grasped the rotting carcass in its jaws and quickly released it without removing any flesh six times before removing only a single bite. The shark swam away and appeared to reject the carcass due to its advanced state of decomposition (Video 8 at 10.6084/m9.figshare.22310587).

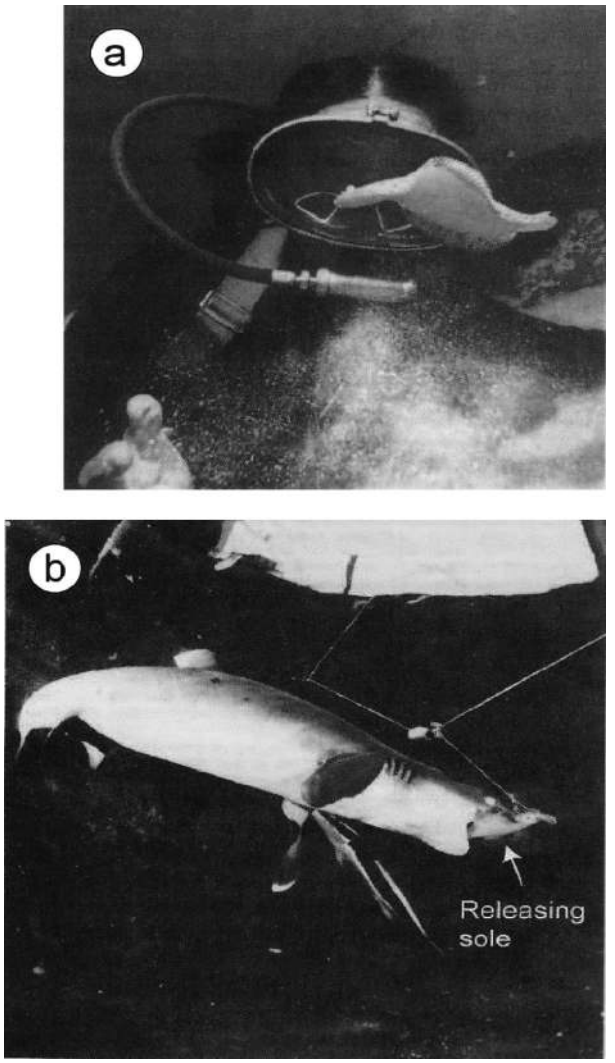

Figure 17. Release of prey due to release of toxic chemical. (a) Release from jaws: secretion of milky fluid from the base of dorsal and anal fins of Moses sole (Klimley, 2013); (b) whitetip reef shark exhibits stress response to the toxin secreted by sole when seized by shark (Klimley, 2013).

A milky secretion from pores at the base of the dorsal and anal fins of the Moses sole, *Pardachirus marmoratus*, is highly repellent to sharks (Clark, 1974, 1983). Pardaxin is a milky substance (Figure 17a) that exudes from the pores of the base of the dorsal and anal fins and inhibits a predator from

biting down on it (Figure 17b). Live and dead specimens of the species tied to a set line interspersed with other non-toxic reef fish were found to be uneaten by four different species of shark, the silvertip, blacktail reef, blacktip, and whitetip shark*s*, after periods of ten hours. This was in contrast to the other prey fish, which were consumed by the sharks within an hour. Captive whitetip sharks exhibited distressful responses after seizing and attempting to swallow the flatfish in their mouth. They immediately expelled the sole from their mouth and violently shook their head. They then accelerated around the tank, swimming with jerky movements while holding their mouth open for up to a minute as if trying to rid their mouth of the noxious liquid. A chemical analysis of the secretion of Moses sole indicated that the toxic component is an acidic protein composed of 162 amino acids (Primor et al., 1974). A dose of 25 μg ml^{-1} of this protein introduced into the water near the head of a restrained piked dogfish, *Squalus acanthias*, resulted in the shark immediately displaying an averse response. It struggled spasmodically while keeping its mouth wide and slowing its opercular rate to minimize the swallowing of water. The chemical is lethal to dogfish after a period of one hour, if dispensed into water at a dosage of 5.1 μg/ml per•g body mass. The chemical likely irritates to some extent either the chemoreceptors in the olfactory capsule, free nerve endings in the oral cavity, or the taste buds. However, the likely site of its toxic and lethal action is the gill membrane, where osmoregulation is disrupted resulting in a lethal imbalance in ionic composition of the body fluids.

3.5.15. Commensal feeding

Commensalism is defined by the Oxford Dictionary as 'an association between two organisms in which one benefits and the other derives neither benefit nor harm.' One such example is a nurse shark that followed a pod of bottlenose dolphins, *Tursiops truncatus*, in order to feed on benthic prey disturbed by dolphin foraging. Records from a shark-borne camera and datalogger that measured swimming acceleration and depth as well as temperature revealed that a nurse shark followed a dolphin pod for a period of quarter of an hour while exhibiting multiple, rapid vertical ascents from a depth of 24 m to near the surface following the dolphins. The shark also performed gliding descents behind the dolphin's back to the bottom and repeatedly swam through clouds of sand that were produced by dolphin crater feeding behaviour. See the vague image of dolphins performing this behaviour encircled with a red oval in Figure 16h. The shark appeared to

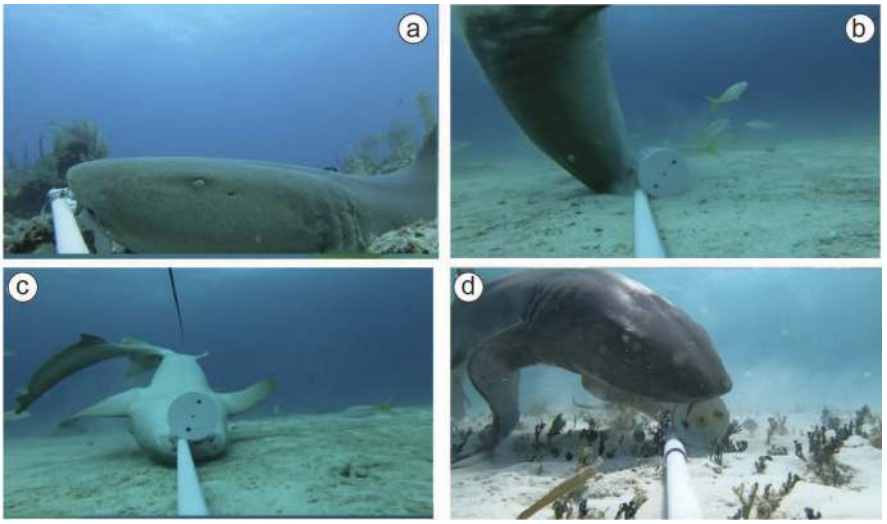

Figure 18. Commensal feeding. (a) Stationary horizontal feeding: the nurse shark is in horizontal position with head exhibiting suction feeding close to a bait cannister (Parton et al., 2022); (b) 'vertical feeding': exhibits suction feeding near the bait cannister with a head-down posture (Parton et al., 2022); (c) 'ventral feeding': rotates 180° on to dorsum and positions head below the bait cannister (Parton et al., 2022); (d) 'pectoral positioning': bends one or two pectoral fins downwards and gains purchase, permitting it to maneuver itself into a better position to feed (Parton et al., 2022; Gallagher & Shipley, pers. commun).

find a benthic prey item as it changed direction abruptly, stopped swimming, and likely exhibited a bout of suction feeding close to the bottom, as was evident from the clouds of sand expelled suddenly from its gills.

Parton et al. (2022) recorded another example of commensal feeding by nurse sharks. They fed on food at baiting stations associated with camera deployments used to make a census of the shark population in the Turks and Caicos Islands in the Bahamas. Nurse sharks exhibited four modes of feeding: (1) Stationary horizontal feeding — a shark assumed a horizontal position with head exhibiting suction feeding close to the bait cannister (Figure 18a); (2) 'vertical feeding' — the shark exhibited suction feeding near a bait cannister with a head-down posture (Figure 18b); (3) 'ventral feeding' — the shark rotated its body 180° onto its dorsum and positioned its head below the bait cannister (Figure 18c); and (4) 'pectoral positioning' — the shark bent one or both pectoral fins downwards to gain purchase, permitting it to maneuver itself into a better position to feed (Figure 18d).

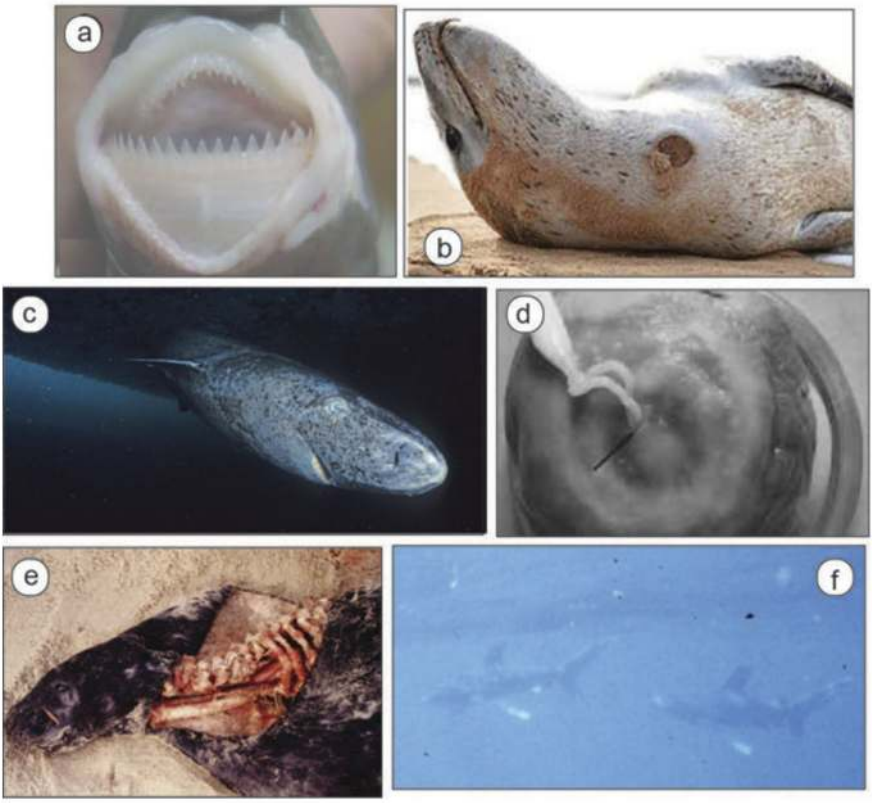

Figure 19. Luring to proximity for seizure. (a) Smalltooth cookiecutter sharks may attract potential predator with their bioluminescent eyes; (b) they then lunge into contact with their torso and rotate its circular jaws to one side and then another to remove a plug of flesh from prey such as a seal leaving a crater wound (courtesy of Mark McGrouther); (c) harbour seals eaten by Greenland sharks have been recovered at Sable Island; (d) the sharks may attract prey with bioluminescent copepod on eyes; (e) they open their mouth wide and draw prey into mouth using a vacuum, then flense prey moving its jaws back and forth (photograph provided to senior author by Z. Lucas); (f) oceanic whitetip sharks swim close together so that their conspicuous white markings on their pectoral fins attract epipelagic fishes close enough to dash forward and seize them (taken by senior author).

3.5.16. Luring prey into proximity for seizure

Smalltooth cookiecutter sharks, *Isistius brasiliensis*, may attract potential predators with their bioluminescent eyes, then lunge into contact with their torso and rotate their jaws to one side and then the other to remove a plug of flesh from the prey. The teeth are arranged in a circular formation (Figure 19a) and they remove a circular plug of tissue from their prey (Fig-

ure 19b). The species is highly specialized as a facultative ectoparasite in its dentition, suctorial lips, and modified pharynx that allow it to attach to the side of large prey, drive its saw-like lower jaw teeth into the skin and flesh of its victim, cut a conical plug of flesh, and then pull itself free with the plug cradled by its scoop-like lower jaw and held by the hooklike upper jaw teeth. The hollowed-out craters, smooth edged at the margin, are about the size of a tennis ball. These wounds have been observed on oceanic fish and members of deep-diving species such as the northern elephant seal (Le Boeuf & McCosker, 1987), beaked, sperm, and baleen whales and several species of porpoises (Mackintosh & Wheeler, 1929; Van Utrecht, 1959), fishes (Jones, 1971), and even a nuclear submarine (Johnson, 1978). The smalltooth cookiecutter shark is epipelagic to bathypelagic and is known from all tropical oceans, extending northward to off Japan and Baja California and southward to Lord Howe Island. It is typically caught by midwater trawl at depths between 85 and 3500 m; however, it is occasionally found at the surface at night. The shark is thought to be a diurnal vertical migrator.

The flensed carcasses of harbour seals, *Phoca vitulina*, often wash up on the shores of Sable Island in the northwestern Atlantic Island, where Greenland sharks, *Somniosus microcephalus* (Figure 19c) occupy the nearshore waters (Lucas & Strobo, 2000). Adam Ravetch, an underwater cinematographer, who worked often in the frigid cold arctic waters, took a seal carcass underwater and tethered it to the bottom near a Greenland shark. That shark slowly moved toward the seal, opened its mouth wide, sucking the seal into its jaws, and then slowly rotated one way and another to remove the fatty layer from the seal, leaving only the vertebral column and head unconsumed (Figure 19e, Adam Ravetch, pers. commun.). One wonders how this sluggish species gets close enough to its prey to seize it the way a slurp gun operates. The sharks do not have keen eyesight as a 30 mm long pinkish-white parasitic copepod, *Ommatokoita elongata*, attaches to their corneas (Figure 19e). The parasite surely causes severe visual impairment, yet it may serve a mutualistic function, gaining nutrition from the shark while facilitating its ability to capture prey. Berland (1961) argued that the copepods are bioluminescent and attract seals to them to feed, then are drawn into their cavernous mouth as it opens quickly to create a suction.

Myrberg et al. (1974) observed pelagic whitetip sharks swimming near an offshore buoy when conducting sound playback experiments in the Tongue

of the Ocean in the Bahamas. They swam very slowly in a lethargic manner generally in pairs and were difficult to see due to the counter-shaded nature of their body with a gradient of dark to light colour from dorsal to ventrum, which camouflaged their bodies against the blue-grey background. However, the attention of Myrberg & Klimley (1974) was drawn to the large paddle-shaped dorsal and pectoral fins coloured a conspicuous, bright white colour that transmitted at great distance to the observers (Figure 19f). This led them to wonder how they could catch the rapidly moving pelagic fishes that schooled around the buoy. Any proximate feature that stands out in visually rather homogenous oceanic waters would probably be noticed by the rapidly moving epipelagic fishes. It is likely that oceanic fishes would move toward these slowly moving, small white objects, to investigate them. If the predators were unable to discriminate the outline of the shark at a distance from the background, they might be drawn into close proximity to the whitetip sharks before noticing that the white spots were not actually prey. At that moment, the shark might accelerate quickly over a short distance and could overcome the sudden changes in direction that the fish might take to evade capture. Myrberg & Klimley (1974) observed the tremendous speed, rapidly attained by these sharks over a distance of a few meters. It is possible that the large paddle-shaped fins of the pelagic whitetips have evolved to a much larger size with brighter white colouration at their tips than those of other reef sharks to serve as lures.

3.6. General social behaviours (Table 6)

3.6.1. Following

One bonnethead shark closely follows another shark and repeating the leader's movements. Myrberg & Gruber (1974) considered a 'follow' only when an individual followed another for a distance of at least a meter with the former obviously copying changes in direction over that distance (Figure 20a). The behaviour was frequently observed in the tidal pool exhibit of the Miami Seaquarium, particularly after the introduction of a new-comer. This was unlike paired close following in that it occurred not just by a male behind a female but between two males and or two females and did not appear to lead to copulation.

3.6.2. Turn back

This is an abrupt turning maneuver that positioned one bonnethead shark directly behind another after the latter had just passed by, moving in the

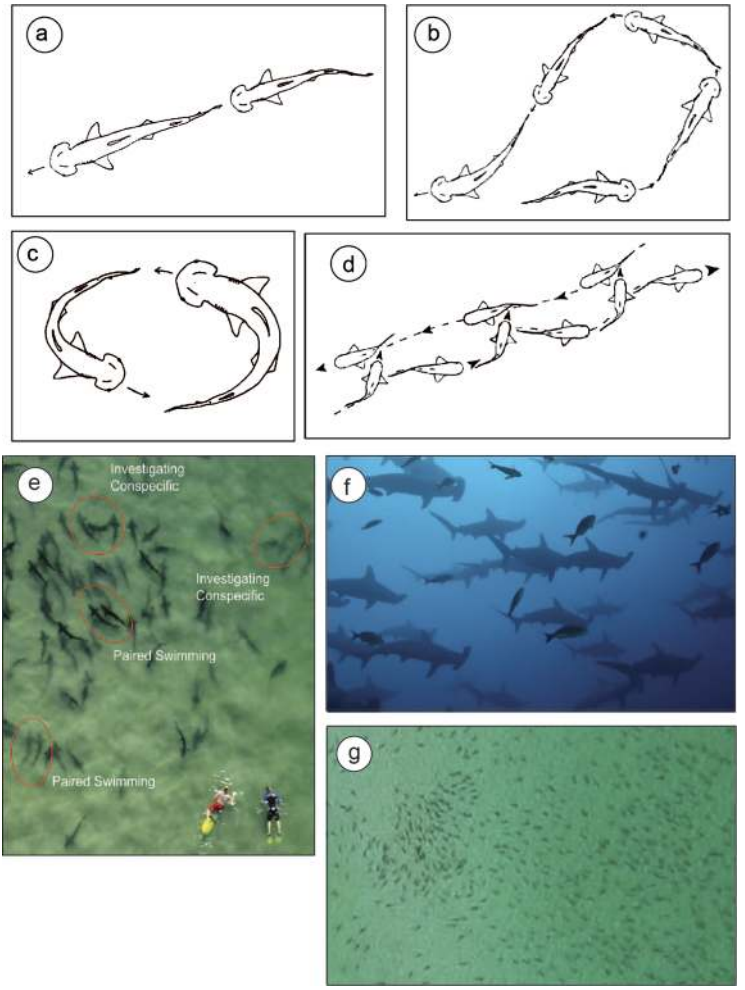

Figure 20. General social behaviours. (a) Following: One bonnethead shark follows another, simultaneously changing direction (Myrberg & Gruber, 1974); (b) follow formation: multiple bonnethead sharks follow each other, changing direction with the shark in front of it (Myrberg & Gruber, 1974); (c) circling head-to-tail: two bonnethead sharks circle together with the head of one immediately behind the tail of the other (Myrberg & Gruber, 1974); (d) grouped investigation of individuals: lines of leopard sharks moving in different directions with individuals moving their snouts toward vents of others (Klimley, 2019); (e) Individual investigation: at times, pairs of leopard sharks swam side by side, a behaviour called 'paired swimming' and moved their snouts toward another (see red circles); (f) schooling: scalloped hammerhead sharks swim together in polarized school (Klimley & Nelson, 1981; Klimley, 1985); (g) aggregating: large numbers of blacktip sharks swim in close proximity to each other, however moving in multiple directions (Kajiura & Tellman, 2016).

opposite direction. This behaviour occurred in the following social contexts: (1) large males turned back toward large females (2) a large female turned back more often toward males than females, and (3) a small male turned back more often toward larger males than any of the females. Myrberg & Gruber (1974) were unable to explain the function of this behaviour.

3.6.3. Follow formation

Male sand tiger sharks followed each other in the National Aquarium (Washington, DC, USA) (Claus et al., 2021). This differed from the chain following of reef mantas in that they were not positioned so as to funnel zooplankton into their mouths. Three to six bonnethead sharks formed a procession behind a leader, each following accurately all directional changes by the individual in front of it (Figure 20b). Myrberg & Gruber (1974) called these processions 'follow formations'. They were comprised primarily of males, with both small and large bonnetheads taking part. Klimley (2019) observed leopard sharks forming a line, each a body length apart, swimming in a straight line. It was referred to as 'tandem swimming'. At times, they swam oriented nose to tail in a circle, a behaviour called 'circle swimming.' The sex of the sharks could not be determined as they were observed from a distance from a building situated above the water on a cliff in La Jolla, California. Follow-formation was displayed by wild blacktip reef sharks during periods of socializing with passing groups of conspecifics, and when approaching novel situations (Porcher, 2023).

3.6.4. Circling head-to-tail

Two bonnethead sharks often moved in a tight circle, oriented head-to-tail (Figure 20c). Myrberg & Gruber (1974) found this behaviour not only connected with maintaining a specific distance from an object on the substrate, as was noted for the 'maneuvering' behavioural pattern but possibly an instance of a 'follow formation.'

3.6.5. Investigating individual

At times, pairs of leopard sharks have been observed to swim side by side, called 'paired swimming' (Klimley, 2019) (Figure 20e). At times, one individual would tilt its body toward the midsection of the other as if orienting to a pheromone emanating from the cloaca of a female (see red circles in Figure 20e), although the sex of individuals could not be determined from the observer stationed above a steep cliff at the Fisheries Center, La Jolla, California. Often, two lines of leopard sharks swam past each other in reverse

directions, less than a body length apart, aptly described as 'parallel tandem swimming.' On some occasions, each of the sharks from one line tilted toward the midsection of their neighbours in the line swimming in the opposite direction as if again perceiving a pheromone (Figure 20d).

3.6.6. Heading

This behaviour consisted of two sharks swimming slowly parallel to each other and touching their heads in the area just posterior to the eye (Claus et al., 2021). The behaviour was displayed by sand tiger sharks in the National Aquarium (Washington, DC, USA) and occurred between males and between a male and a female.

3.6.7. Schooling

Scalloped hammerhead sharks form polarized schools at seamounts and offshore islands (Figure 20f; Video 9 at 10.6084/m9.figshare.22310587) (Klimley & Nelson, 1981; Klimley, 1984). These schools are present at seamounts in the Gulf of California, the Revillagigedo archipelago off the tip of the Baja Peninsula, Cocos Island off the coast of Costa Rica, Malpelo Island off the coast of Colombia, and the two northernmost islands of the Galapagos Archipelago, Wolf and Darwin Islands (Klimley et al., 2022a). Hammerheads within these schools swim in very similar directions with a directional commonality as high as obligate schooling teleosts (Klimley, 1985). This was evident from the distributions of individuals' elevation and bearing deviations from the mean school direction. The mean elevation deviation was only 5.8° and the mean bearing deviation was only 9°. The mean deviations from school direction of the hammerhead were smaller than those of four obligate schooling teleostean species. They also swam with inter-individual distances of 1.1 to 1.5 body lengths from above another school member and 1.1 to 1.6 body lengths below another member of the school, similar to the inter-individual distances of the obligate schooling teleostean fishes.

3.6.8. Aggregating

Massive aggregations of migrating blacktip sharks overwinter in nearshore waters of southeast Florida. Aerial surveys using a video camera and still camera mounted out of an airplane window provided a continuous record of a belt transect, occupied by these sharks, which extended 200 m seaward from the shoreline between Boca Raton Inlet and Jupiter Inlet, FL, USA (Figure 20g) (Kajiura & Tellman, 2016). These sharks were found singly, in small groups, or large aggregations of up to thousands of individuals.

When occurring in small groups the sharks were typically swimming in a polarized manner such as for the scalloped hammerhead sharks engage in at seamounts and offshore islands. However, in large aggregations the sharks did not necessarily swim in a polarized school with individuals often oriented in different directions (Figure 20g). Although the sharks were not observed feeding, they were sometimes seen to associate with large schools of baitfish. Some of the blacktip sharks were observed jumping out of the water, but it was impossible to determine whether they exhibited any other social behaviours.

3.6.9. Parallel swimming

Two individuals approach from different directions and and move parallel to each other with an inter-animal distance of <0.5 m for <5 s before turning away. Parallel swimming was first observed between white sharks of the same sex and size by Sperone et al. (2010) and later by blacktip reef sharks (Mourier et al., 2011; Porcher, 2023).

3.6.10. Swimming by

When two sharks are close to each other, both will turn toward each other and meet head on and pass each other with an inter-animal distance of <20 cm (Video 10 at 10.6084/m9.figshare.22310587). This behaviour was documented by Sperone et al. (2010) for white sharks and (Porcher, 2023) for blacktip reef sharks.

3.7. Aggressive behaviours (Table 7)

These displays, or conspicuous and stereotyped behaviours, provide information about the likely intent and degree of commitment of the signaller and may yield information on relative fighting ability. For example, agonistic displays emphasize body size, weaponry, or status badges, and may also include a tactical element, placing the signaler in a better position to attack or flee (Bradbury & Vehrencamp, 1998).

3.7.1. Hunching

This consisted of elevating, or the 'hunching up' of the dorsum with the tail slightly lowered and the head slightly raised. The pectoral fins are simultaneously dropped lower than usual (Myrberg & Gruber, 1974). In all but one instance, 'hunching' occurred when a bonnethead shark slowly passed within 2 m of, and lateral to, a human observer seated on the bottom of the tidal pool at the Miami Seaquarium. In the remaining instance, it occurred when a large

male slowly passed, laterally, in front of a small newcomer, swimming in a straight line in the center of the pool. The actor rapidly intercepted the newcomer and performed the display 1 m from its head, whereas the newcomer turned rapidly to one side and moved on. The pattern was also performed twice by blacknose sharks, *Carcharhinus acronotus*, as a resident intercepted a conspecific newcomer. In each instance, the actor was less than one meter from the approaching shark. Both newcomers moved to one side, but in only one case did it move away rapidly. Although the posture was uncommon, it was associated with the following factors: (1) a resident shark confronted by a new arrival, (2) a bonnethead shark was oriented toward another individual and (3) the shark performing the 'hunch' was slightly larger than the target of the behaviour. Martin reported 'back arching' in two lamniform species, the white and shortfin mako, and in five carcharhinform species (see Table II in Martin, 2007).

3.7.2. Jaw gaping

In white sharks, 'jaw gaping' consisted of a slow and exaggerated opening of the mouth, conspicuously wider than during ram ventilation, in the presence of conspecifics (Martin, 2007; Klimley & Hoyos-Padilla, 2023). In his review of aggressive behaviours, Martin reported 'jaw gaping' in members of the Lamniformes, such as the white, sand tiger and shortfin mako shark, and in members of the Carcharhiniformes such as 11 species in the family, Carcharhinidae, and one species, the scalloped hammerhead shark, in the family, Sphyrnidae (see Table II in Martin, 2007). A white shark approaching a shark cage with divers emitting bubbles at Guadalupe Island, Mexico, exhibited jaw gaping (Figure 21a; Video 11 at 10.6084/m9.figshare.22310587) (Klimley & Hoyos-Padilla, 2023). The same behavioural pattern was exhibited by sand tiger sharks in the presence of competitors (Smith et al., 2010). Tiger sharks also directed this display at conspecifics when feeding on a blue whale carcass in Prony Bay, New Caledonia (Clua et al., 2013). At times, this behaviour was directed at the main research vessel or the motor of a small skiff.

3.7.3. Gill pouch billowing

Martin believed the spinnaker-like expansion of the branchial region, observed in white sharks, was an element of an agonistic display, not simply to rid the gills of substrate materials or parasites like the 'gill puff' described by Myrberg & Gruber (1974) for bonnethead sharks. Martin reported that it

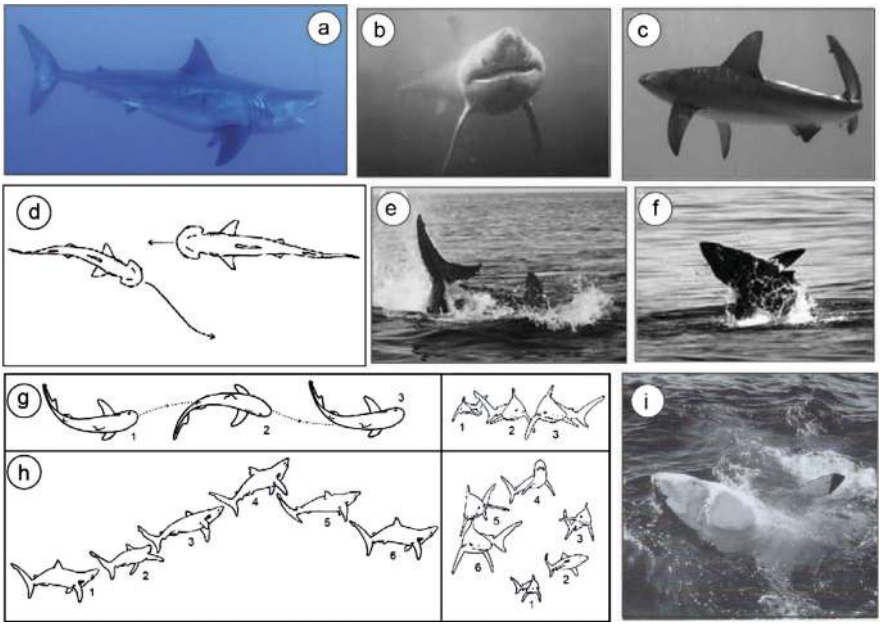

Figure 21. Intra- and interspecific aggression. (a) Jaw gaping, flank displaying, pectoral fin depression and body shuttering: all four elements comprise the agonistic display of the white shark at Guadalupe Island off Mexico (Klimley & Padilla-Hoyos, 2022); (b) pectoral fin depression: a basking shark with lowered pectorals (Martin, 2007); (c) pectoral fin depression: juvenile Galapagos shark with lowered pectoral fins (Martin, 2007); (d) give-way: smaller shark often gives way to an approaching bonnethead shark (Myrberg & Gruber, 1974); (e) tail slap: white shark splashes water toward other shark (Martin et al., 2005); (f) breach: white shark leaping out of the water (Martin et al., 2005); (g) exaggerated tail beats: grey reef shark swings tail back and forth in wide tail beats (Johnson & Nelson, 1973); (h) looping: grey reef shark swims in a looping trajectory (Johnson & Nelson, 1973); (i) repetitive aerial gaping: white shark shakes head back and forth in putative frustration venting behaviour (Strong, 1996).

was exhibited by bull sharks, *Carcharhinus leucas*, and bonnethead sharks (see Table II in Martin, 2007).

3.7.4. Jaw opening and closing

A lemon shark opened and closed its jaws repeatedly while moving back and forth in tight loops in front of a diver swimming toward it wearing a wet suit with the colour pattern of a killer whale with a wooden cut-out painted black resembling its dorsal fin (Klimley, 2019). Martin termed this behaviour 'ritualistic jaw snapping' and reported it was exhibited by the white, lemon and bonnethead sharks (see Table II in Martin, 2007).

3.7.5. Stiff and jerky movements

Martin reported this behaviour in four lamnid species, 14 carcharhiniform species in the family Carcharhinidae and four species in the family Sphyrnidae (Table II in Martin, 2007). Smith et al. (2010, 2015) observed this behaviour exhibited by sand tiger sharks in the waters off eastern Australia.

3.7.6. Spasmodic body shaking

Convulsive body shuddering of a white shark was recorded on video as it approached two large metallic shark cages, each with multiple divers standing within them (Klimley & Hoyos-Padilla, 2023). Having arrived at the source of an olfactory corridor, this white shark was confronted with highly visible cages made with aluminum bars, likely a frightening stimulus. The divers use hookah air hoses to breathe and were therefore releasing bubbles, which reflect light and generate sounds as they oscillate toward the surface. The photographers may also have been taking pictures of the shark with their flash-bulb equipped cameras, which produce a sudden disruptive flash of irradiance. The body of the shark shudders convulsively and he opens his mouth, keeping it open for a prolonged period of 2.8 s as he passed close to the cage, while (1) depressing his pectoral fins, (2) hunching his back and (3) keeping his caudal fin held at right angle to the axis of view, all likely in an attempt to increase his apparent size (Figure 21a; Video 11 at 10.6084/m9.figshare.22310587). Martin described 'body shivering', consisting of a quivering or rapid shaking of the entire body by a silvertip shark, *Carcharhinus albimarginatus*, that was associated with elements of a lateral display (Martin, 2007).

3.7.7. Flank displaying

This common agonistic behaviour consists of sustained perpendicular body orientation toward a receiver, displaying the shark's entire lateral surface. Martin reported this had been observed in three species of lamnids, the white, sand tiger, and shortfin mako sharks, seven species in the family Carcharhinidae, and one in the family Sphyrnidae, the scalloped hammerhead shark (see Table II in Martin, 2007). This behavioural pattern was displayed by a white shark approaching two shark cages at Guadalupe Island (Figure 21a; Video 11 at 10.6084/m9.figshare.22310587) (Klimley & Hoyos-Padilla, 2023). Sand tiger sharks expose the underside of their bodies toward a perceived threat (Smith et al., 2015). Tiger sharks directed flank displays

toward conspecifics by holding their bodies perpendicular, also maximizing their apparent size toward conspecifics, while competing to feed on the carcass of a blue whale (Clua et al., 2013). At times, this behaviour was directed at the main research vessel or the motor of a small skiff.

3.7.8. Pectoral fin depression

Martin reported the sustained lowering of both pectoral fins in the presence of conspecifics in members of the lamniformes such as the white (Figure 21a; Video 11 at 10.6084/m9.figshare.22310587), sand tiger, and basking sharks (Figure 21b) and members of the Carcharhiniformes in the families Triakidae such as the dusky smoothhound, *Mustelus canis*, and the family Carcharhinidae such as the Galapagos shark (Figure 21c) and 12 other species, as well as four species in the Sphyrnidae (see Table II in Martin, 2007). This bilateral lowering of the two fins should not be confused with the unilateral lowering of one pectoral fin whose purpose is to facilitate a change of trajectory of the shark.

3.7.9. Give way

Sand tiger sharks were observed to change their course of direction to avoid an approaching conspectific in aggregations off eastern Australia (Smith et al., 2015). Two bonnethead sharks approached each other from opposite directions with one veering out of the path of the approaching shark (Figure 21d). Myrberg & Gruber (1974) described this behaviour as two sharks approached on a head-on 'collision' course with one 'yielding the right of way'. Their preliminary observations indicated that some social organization existed among bonnethead sharks in the tidal pool exhibit at the Miami Seaquarium. A dominance hierarchy was described by recording those sharks taking part in interactions involving give ways. In the course of such interactions, one shark actively avoided another by abruptly changing course. The second shark maintained both its prior direction and velocity. The latter shark was scored as dominant and the former as subordinate. By this means they were able to demonstrate a social hierarchy. The number of give ways shown by smaller sharks to larger sharks was significantly larger than the converse. Thus, larger sharks usually dominated any interaction. This established that a dominance hierarchy existed within the colony and that this hierarchy was reasonably straight-line and size-dependent. This action was rarely recorded from the videotape samples of scalloped hammerheads within schools in the Gulf of California, Mexico (Klimley, 1985).

Because the schooling sharks swam in a common direction and remained separated by a constant distance, there was little chance for one shark to encounter another shark from a different direction. The scarcity of give-ways in schools of the scalloped hammerhead was in marked contrast to the high frequency reported by Myrberg & Gruber (1974) in the colony of bonnetheads in the tidal pool exhibit in the Miami Seaquarium. If two tiger sharks of a different size approached each other on a 'collision' course near a whale carcass off eastern Australia, the smaller individual would perform a give way, veering away from the larger shark (Clua et al., 2013).

3.7.10. Tail slap

Multiple white sharks compete to feed on a partially consumed seal carcass when it floats to the surface. The sharks perform the tail slap, consisting of lifting the caudal fin and splashing water toward the accompanying shark (Figure 21e, Video 12 at 10.6084/m9.figshare.22310587). Klimley et al. (1996b) found that a combatant was permitted to feed further on a seal only if the vigor and frequency of its tail slaps were greater than those of its opponent. Thus, this is an agonistic display, functioning to ward off potential competitors. Recently, more researchers have described tail slapping by white sharks among conspecifics at Seal Island, South Africa (Martin et al., 2005; Martin, 2007) and at Guadalupe Island off the Baja Peninsula of Mexico (Becerril-Garcia et al., 2019). This behaviour was also directed at boats and shark cages at Guadalupe Island (Becerril-Garcia et al., 2019) and at Dyer Island, South Australia (Sperone et al., 2012). Clua et al. (2013) described tail slapping within an aggregation of tiger sharks around a whale carcass, and it was obvious that this behaviour was based on competition and intimidation between individual sharks. If two or more tiger sharks were present at the same time at the carcass of a blue whale in Prony Bay, New Caledonia, they were observed to stop eating for a period of five seconds and swim toward each other in order to observe each other better. At times, they directed a tail slap at their competitors and frequently left the area with violent tail slapping.

In the use of surface-generated signals, the white and tiger sharks are behaviourally convergent with unrelated species that either visit or spend time at the sea surface. The pirarucu, *Arapaima gigas*, an obligate air-breathing fish that inhabit the rivers in South America, have been photographed slapping water at the surface toward the head of conspecifics as they rise to the surface to breath (Jordan, R., pers. commun.). In form, the

tail slap resembles lobtailing by whales, in which the tail flukes are raised out of the water and slammed against sea surface (Leatherwood et al., 1982). Lobtailing is performed by male humpback whales, *Megaptera novaeangliae*, competing for social dominance in order to obtain access to females (Silber, 1986). American alligators, *Alligator mississippiensis*, perform a head-slapping display, in which jaws are suddenly closed as the undersurface of their heads are slapped against the surface of the water (Vliet, 1989). This display, performed primarily by males, is a declaration of their presence, eliciting tail slapping by other alligators.

3.7.11. Breach

White sharks have been observed to propel two thirds of their body out of the water at a 30–60° angle to the sea surface and land flat, causing a large splash (Figure 21f) (Klimley et al., 1994b; Martin et al., 2005). A breach was performed by a white shark during the first of two predation events at the South Farallon Islands separated by less than an hour. Less than a minute after the breach, a carcass floated to the surface and was quickly consumed by a shark. Possibly the sound (pressure oscillation or particle displacement) created by the tail slap could frighten a conspecific, carrying the carcass in its mouth, and causing it to release the prey item. Multiple white sharks were in the area as the two sharks competed with bouts of tail slapping during the second event. Breaching of white sharks was also observed when feeding on seals at seal island, South Africa (Martin et al., 2005; Martin, 2007). This behaviour, in form, does not differ from the breach described earlier in the section on maintenance behaviours. However, here the function is known, serving in inter-specific competition for prey. Hence, it is mentioned in connection with agonistic behaviours.

3.7.12. Exaggerated tail beating

Johnson & Nelson (1973) described the exaggerated back and forth movements of the caudal fin of the grey reef shark when confronted with a diver moving directly toward it (Figure 21g, Video 13 at 10.6084/m9.figshare.22310587). The best way to distinguish this form of locomotion is to study a time series of the postures of a displaying shark. A normally swimming shark moves its tail back and forth over an arc of roughly 60° while keeping the forward part of its torso pointed directly ahead. In exaggerated swimming, the shark moves its tail from one side to the other over a larger arc, 90°, while its forward torso swings slightly to one side and then to the other in a

compensatory manner (left and right panels in Figure 21g). The trajectory of the displaying shark is best viewed from the side (left panel in Figure 21h). The shark moves slightly upward and rolls on to its side while moving its tail to one side (see postures 1 and 2) and then accelerates upward and rolls to the other side while moving its tail in an exaggerated manner to the other side. Its ultimate culmination of inflicting a slashing wound to the intruder was demonstrated by approaching the shark with a submersible (Nelson et al., 1986). Martin termed this 'laterally exaggerated swimming' and reported that it had been witnessed additionally in Galapagos sharks (see Table II in Martin, 2007).

3.7.13. Looping

The shark swims back and forth in a looping trajectory. Johnson & Nelson (1973) noted that grey reef sharks may alternatively continue upward and then downward repeatedly in a spiraling path, termed 'spiral looping' (see postures 3–6 in left and right panel in Figure 21h; Video 13 at 10.6084/m9.figshare.22310587). Martin reported this behaviour was also observed performed by the blacktip shark, *Carcharhinus limbatus* (Table II in Martin, 2007).

3.7.14. Charging

This behavioural pattern consisted a rapid approach toward a perceived threat, usually ending with a quick turn away. Martin reported this behaviour was observed in the white shark, the dusky smoothhound, and five reef sharks of the family Carcharhinidae (see Table II in Martin, 2007). Smith et al. (2015) observed this behaviour in aggregations of sand tiger sharks off the eastern coast of Australia. Porcher (2023) observed blacktip reef sharks to exhibit this behaviour, advancing at medium to high speed toward the mid-body of a conspecific and at the last moment turning away.

3.7.15. Slamming

Porcher (2023) witnessed reef blacktip sharks accelerating towards a conspecific and hitting it with the full force of its momentum. The actor usually swam upwards with an arched back contacting another shark behind the head in front of the dorsal fin. The approaching shark lowered its pectoral fins just before contacting its neighbour with great force.

3.7.16. Repetitive aerial gaping

This behaviour was observed in six bait-attracted white sharks that were impeded from feeding on baits at the surface that were withdrawn each time

a shark advanced to feed upon them. It thus occurred only following a series feeding attempts. It took the following form — the shark held its head above water, rolled on to its flank, and opened and closed its mouth in a series of slow, rhythmical, mouth gapes, while swimming slowly and awkwardly at the surface (Figure 21i). These stereotyped movements of the mouth were not directed at any object as during feeding. Strong (1996) argued that this was a manifestation of 'frustration' from thwarted feeding events and might function to lessen intraspecific aggression.

3.7.17. Chasing

This consisted of the pursuit over a short distance of one scalloped hammerhead by another. This behaviour was recorded only once at a seamount in the Gulf of California (Klimley, 1985).

3.7.18. Hit

This consisted of lunging the head downward to contact the back of a shark swimming below between the first and second dorsal fins. As a bonnethead shark approached over the body of another, it directed a 'hit' to the body of the shark swimming underneath (Myrberg & Gruber, 1974). The shark positioned underneath immediately accelerated, leaving the upper individual behind. Often, contact was severe enough to produce a mild contusion, evidenced by a light mark on the dorsum. Myrberg & Gruber (1974) observed this behaviour during the first hour after a new individual had been introduced to the tidal pool at the Miami Seaquarium. This behaviour was observed in schools of scalloped hammerhead sharks (Klimley, 1985). It consisted of the hammerhead bringing the underside of its jaw in contact with a conspecific's torso, lateral or anterior to the first dorsal fin (Figure 22a). This contact often resulted in a light contusion where dermal denticles were removed. Although occasionally a conspecific, swimming above another scalloped hammerhead, moved its head downward to strike that hammerhead, a more common occurrence was that a shark, completing the 'cork screw', a behaviour to be described next, continued downward to make contact with a neighbour. Contusions gradually became pigmented as they healed. In contrast, Myrberg & Gruber (1974) observed this behaviour in a bonnethead when a shark approached over a conspecific and lunged its head downward to deliver a strike. The hit was also directed at a different part of the bonnethead's body, the dorsum between its first and second dorsal fins.

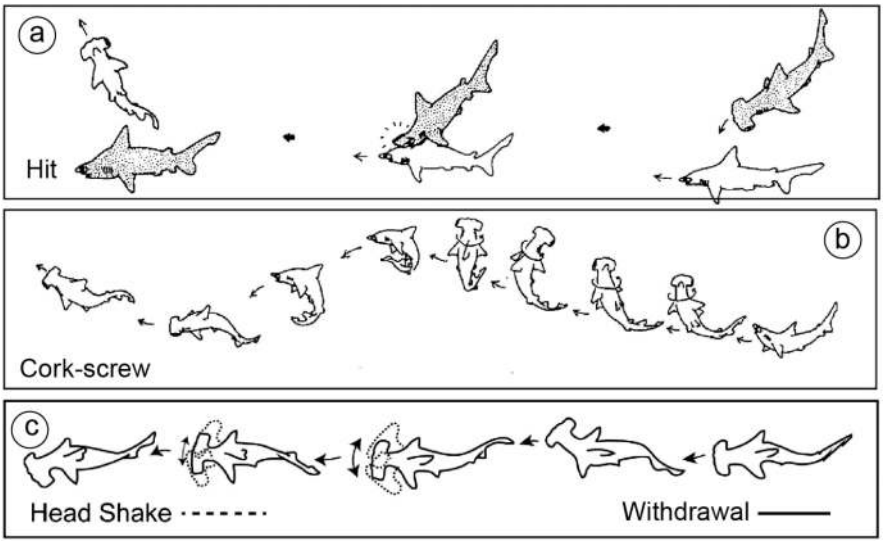

Figure 22. Intra-group aggression and withdrawal. (a) Hit: A scalloped hammerhead shark strikes a shark swimming below it with the underside of its snout, leaving a white contusion (Klimley, 1985); (b) corkscrew: Scalloped hammerhead makes burst acceleration into a tight looping trajectory with the shark rotating its torso 360° on longitudinal axis before entering the circular trajectory (Klimley, 1985); (c) head shake: head swung back and forth over wide arc several times in quick succession with rapid tail beats to propel itself out of a school of sharks and then gliding for an extensive distance (Klimley, 1985).

3.7.19. Cork screw

This action pattern involved a rapid burst of swimming into a tight looping trajectory with the shark rotating its torso almost 360°on its longitudinal axis before entering the circular trajectory (Figure 22b). Most of the rotation occurred as the shark‘s body was only partially bent. Light was reflected from the ventrum of the shark, leading Klimley (1985) to believe that there was a visual component to this display.

3.7.20. Head shake

During this behaviour the hammerhead swung its head back and forth over a wide arc several times in quick succession while suddenly propelling itself forward with rapid tail beats (Figure 22c). Although often the head was moved laterally, at times it was moved upward at the end of the arc. The behaviour was largely performed by female scalloped hammerhead sharks as they moved to the periphery of a school in response to aggressive behaviour directed at them by larger female within the interior of the school. In form

and context, it was not identical to the *saw bite* performed by sharks while removing bites from a whale carcass or the *lateral head shake* displayed when tearing a bite from a seal carcass while swimming with it in their jaws.

The examination of the size, sex, and positional relationships of sharks performing the hit, corkscrew, headshake, and acceleration action patterns lead Klimley (1985) to the conclusion that members competed for favoured positions within the schools. Sharks which performed corkscrew and hit, approach-type actions, mostly remained at the center of the schools. On the other hand, sharks performing headshake and acceleration, withdrawal type actions, generally moved to the school's edge. A significantly greater number of sharks performing cork screw were larger in relation to their nearest neighbour than for headshake. The sizes of sharks, measured using a stereo-camera, increased significantly with distance into the schools using a regression analysis. Smaller sharks left the center of the groups, performing headshake and acceleration, to remain at the group's periphery. Klimley (1985) argued that males, entering the schools composed primarily of females performing torso thrust, were seeking to pair with large, reproductively mature females.

3.7.21. Head snap

This behaviour consists the slight rolling of the body, followed by the anterior portion moving slightly upward and then rapidly downward along a diagonal plane. The pattern, noted during straight-line swimming, did not appear to Myrberg & Gruber (1974) to be correlated with any particular element in the environment. Head snap appeared to Klimley (1985) to be agonistic in nature, however it was not performed within the school at a conspecific, but rather outside the school at an approaching diver.

3.7.22. Dominance biting

This was observed in the National Aquarium (Washington, DC, USA) (Claus et al., 2021). Male sand tiger sharks were observed to bite females, a behaviour which may have been reproductive in nature, but also to bite males, which appeared to function to establish dominance. A dominant male quickly approached a subordinate male from a ventral position and took a directed bite on the ventral surface of the subordinate male between the pectoral fins and pelvic fins, remaining locked together for up to a few minutes. The subordinate male occasionally bit back, like retaliatory biting by a female during attempted copulation. The dominance hierarchy in males

changed during the study, but the changes occurred at the subordinate position.

3.7.23. Territoriality biting

This type of biting was studied intensively in the 1970s and 1980s and has been attributed either to either dominance or territoriality. In the latter case, the shark seeks to evict an intruder from a space where it is in close contact with that shark. It was most of the time described for the grey reef shark, but it is exhibited by other species of Carcharhinidae (Martin, 2007) and Sphyrnidae (Myrberg & Gruber, 1974). This behaviour is often preceded by an agonistic behaviour such as 'hunching' (see 7.1), stiff and jerky movements (7.5) as well as the depression of pectoral fins (see 7.8) (see Video 8 at 10.6084/m9.figshare.22310587). McNair (1975) promoted 'territoriality' as a motivation for this behaviour as follows: 'The same shark might be aggressive on one piece of a reef while half a mile away the same individual may be docile or shy... territoriality seems the only logical conclusion.'

3.7.24. Reflex biting

This type of bite can be expected when a shark is feeding in the company of other sharks (Nelson et al., 1986). A shark may involuntarily bite another shark, most of the time on the snout (Video 14 at 10.6084/m9.figshare.22310587). These bites can also be the result of reflexes or clumsiness when a confused shark bites a diver, who is holding bait in an attempt to attract sharks to the vicinity of recreational divers for viewing (Clua, 2018). In this case, the feeder's hands are most likely to be bitten.

3.7.25. Competition biting

This type of bite occurs when a shark is competing to access a food resource either with one or multiple other sharks or a human (Nelson et al., 1986). As stated by Balbridge (1988), the diver can be considered 'as competition in the form of an unfamiliar presence, ... to which the shark responds with a preemptive strike...'. Specific contexts occur such as feeding frenzies during which sharks bite without discrimination, including people or even inert material (Nelson et al., 1986). Specifically, competition bites are frequently encountered in French Polynesia when a spearfisherman tries to remove a speared and wounded fish in the presence of a hungry grey reef shark (Clua et al., 2023). In this specific case, there is no warning signs from the shark as for the territoriality biting (see 7.23).

3.7.26. Open-jawed tooth raking

A shark makes a forceful tooth-raking contact with a perceived threat. Martin reported this occurred in the white shark, shortfin mako, and sand tiger sharks, all lamniformes, and three species of carcharhiniform sharks (see Table II in Martin, 2007). This was also observed by Smith et al. (2015) in aggregations off eastern Australia where sand tiger sharks inflicted 'forceful and injurious contact' with conspecifics.

3.8. Defensive behaviours (Table 8)

3.8.1. Rapid withdrawal

This is a rapid withdrawal of a shark from a perceived threat. Martin recorded this common behaviour in the white and shortfin mako shark, both lamniformes, and numerous carchariforms such as the dusky smoothhound of the Triakidae, 13 species of reef sharks in the Carcharhinidae, and the bonnethead and scalloped hammerhead shark in the Sphyrnidae (see Table II in Martin, 2007). Smith et al. (2015) observed the behaviour in aggregations of sand tiger sharks off the eastern coast of Australia. Clua et al., 2013 observed it in tiger sharks scavenging on a whale in Prony Bay, New Caledonia. Porcher (2023) defined 'startled' as an acceleration of a shark 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 sea floor as it flees. Porcher (2023) saw this performed by juvenile blackfin reef sharks as a reaction to near-collision with a much larger individual, usually a nurse shark. However, adult blackfins reef sharks would sometimes accelerate away with a few sharp vertical undulations in response to a near-collision with another adult shark.

3.8.2. Withdrawal from high amplitude sounds

The first sound found in nature to frighten sharks was the intense shriek-like sound emitted by killer whales, *Orcinus orca*, while hunting in groups. This sound begins with a continuous tone of 500 Hz, rises over quarter of a second to 2000 Hz, and ends with the higher continuous tone. You can make this loud sound yourself by shrieking the following: 'wheee... oooh... wheeee'. This 'scream' was played back to grey whales, *Eschrichtius robustus*, as they passed within 150–450 m of their boat near Point Loma off San Diego (Cummings & Thompson, 1971). The reactions to the killer whale sounds were notable. Whales that were at the surface suddenly changed direction

and headed directly away from the sound projected from the boat. Many of the whales were swimming just outside the kelp. These whales fled into the heavy growth of the kelp forest and stayed there until the sounds stopped.

The senior author played the killer scream to lemon sharks swimming around a circular channel together with two other control sounds. The first control was composed of 'pink noise', whose sound energy was equally distributed over the bandwidth of the scream but had none of the unique tonal modulation. The second control was a pulsed low-frequency sound, 150–300 Hz, similar to the sounds of a struggling fish that had attracted sharks in previous studies. Surprisingly, the pink noise frightened the sharks more often than the scream. Even the pulsed low frequency sound frightened the sharks when played at high amplitudes despite being attractive at lower ones. Additional tests, in which the pink noise was increased to the same level at different rates, indicated that sounds with an abrupt, impulsive onset were most frightening to the sharks. It appears the lemon sharks were not frightened per se by the sound of the killer whale but exhibited a startle response to a sudden sound. This result might be anticipated because they rarely come in contact with each other — the lemon shark mainly inhabits tropical waters while the killer whale stays mainly in cold temperate and boreal waters. This reflexive withdrawal response from the sharks is similar to the reflexive forward movement of your body upon hearing a sudden, loud slam of a door behind you.

There is some evidence that white sharks avoid killer whales. Using long-term electronic tagging and survey data, Jorgensen et al. (2019) found that brief visits of killer whales led white sharks to leave the South Farallon Islands in Central California, where they were feeding upon the pinnipeds that occupy the shore and coastal water. Firstly, white sharks, carrying individually coded acoustic beacons, were no longer detected by autonomous receivers at the South Farallon Islands after these brief visits but were detected by autonomous receivers at another nearby aggregation site, Año Nuevo Island, in Central California. Secondly, the number of observed predations on pinnipeds by white sharks at these islands were negatively correlated with close encounters with killer whales, including one observed feeding of a killer whale on a white shark (Pyle et al., 1999). The shark feeding behaviour was disrupted for extended periods at this aggregation site. It is possible that the white sharks detected the presence of the killer by their unique 'screams', and fled from sites from fear of predation, although this has never been experimentally demonstrated.

3.8.3. Spine thrust

Stingrays of the order Myliobatiformes live in the tropical and temperate oceans worldwide as well as in estuaries and freshwater rivers (Klimley, 2013). There are nine families of stingrays. The barbs of the whip stingrays of the family Dasyatidae have the longest barbs reaching up to 37 cm in length, the butterfly rays of the Gymnuridae the next longest with a maximum length of 12 cm, while the eagle rays of the Myliobatidae and round rays of the Urolophidae have the smallest barbs with maximum lengths of 4 and 2.5 centimeters, respectively (Germain et al., 2000). They are named for the poisonous barb on their caudal fin. If a predator approaches too closely, either alerting the ray by water motion or contact, the stingray will lift its tail in a whip-like manner with its spine to be thrust into the predator to release venom stored within the notches of the spine. Stingrays are common in shallow waters, where they remain buried just under the sand or mud with their eyes exposed waiting to seize crustaceans and fishes as they swim by them near the bottom. If a predator approaches too closely, the stingray will raise its tail in a whip-like manner and its spine will be thrust into the predator releasing the venom stored within the spine. Stingrays also can move quickly and agilely in a circle while thrusting their barb sideways or backwards over their bodies to hit the predator (Diaz, 2008). The position of the barb on the tail, the number of serrations on either side of the barb, and the number of barbs varies greatly with the species of stingray, its sex, and its habitat (Schwartz, 2008). The location of the venom secretory cells differs among species. In some species, they are either concentrated around or inside the serrations, and this difference in location results in more or less severe envenomation. Their location in the epithelial layer also differs between species. Multiple rows of secretory vesicles are either interspersed with epithelial cells or exist in separate layers below the integumentary sheath (Dehghani et al., 2010). The freshwater stingrays of the family Pomatotrygonidae have secretory cells situated along the entire length of the barb in contrast to the marine species that have them located only within and around the ventral, or lower, grooves on the side of the barb. The larger number of secretory cells, distributed along the length of the barbs of freshwater stingrays, explains why these species inflict more severe envenomations than the marine stingrays (Pedroso et al., 2007).

3.8.4. Tonic immobility

This state of immobility with the body remaining limp has been interpreted to function as: (1) an innate defensive passive response against a predatory attack, (2) a component of courtship and copulation and (3) a protective mechanism limiting the effect of overwhelming sensory stimulation (Miranda-Páez et al., pers. commun.). This behaviour has been reported in four orders of sharks, the Squaliformes, Orectolobiformes, Lamniformes and Carcharhiniformes, as well as two orders of rays, the Rajiformes and Myliobatiformes (see Table I in Miranda-Páez et al., unpubl. manuscript). It has been elicited most often by manipulating many species of sharks and rays into a horizontally inverted position with their ventral surfaces facing upward (Henningsen, 1994; Table I in Miranda-Páez et al., unpubl. manuscript). It can also be induced with the zebra shark, *Stegostoma fasciatum*, and other sharks by grasping the caudal fin tightly with the hands (Williamson et al., 2018). Researchers have used this technique to immobilize sharks to facilitate electronic tag implantation (Kessel & Hussey, 2015). A white shark exhibited this behaviour while being carried upside down in the jaws of a killer whale at the South Farallon Islands (Pyle et al., 1999). Female nurse sharks have been observed to exhibit this behaviour during copulation, presumably permitting the male to keep his clasper within the female's cloaca (Klimley, 1980).

3.8.5. Anti-predatory biting (8.5)

First described by Fellows & Murchinson (1967) as a 'defensive behaviour provoked by pursuit in a confined area, possibly signifying intention of attack'. The bite is motivated by the perception of a potential threat by the shark and the distance between the shark and the human is a determining factor in the shark attack, especially if the human swims quickly towards the shark or reduces its range of escape (Johnson & Nelson, 1973). For example, a SCUBA diver approaching a shark quickly with an underwater scooter may evoke a strike and bite by a shark such as seen in Video 15 at 10.6084/m9.figshare.22310587 (Copyright@UnderThePole-France).

3.8.6. Defensive or retaliatory biting

This type of bites directed at divers in response to a threat from a human being based on the fact that '… fear motivates… defensive bites.' (Gruber, 1988). In French Polynesia, local spearfishermen receive these bites because they often shoot grey reef sharks with spear guns in order to scare them

Table 1.
Summary of maintenance behaviours for the Chondrichthyes, the Holocephalii and Elasmobranchii.

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
General						
3.1.1.	Remaining stationary on bottom	Remaining on bottom for prolonged periods	Carcharhiniformes	*Traenodon obesus*	Klimley et al. (2022b)	
3.1.2.	Slow, straight-line swimming	Anguilliform swimming	Hexanchiformes	*Chlamydoselachus anguineus*	Compagno et al. (2005)	Fig. 4a
		Carangiform swimming or 'cruising'	Lamniformes	*Carcharias taurus*	Smith et al. (2015)	
			Carcharhiniformes	*Carcharhinus melanopterus*	Porcher, pers. commun.	Video 1
		Carangiform swimming	Carcharhiniformes	*Sphyrna lewini*	Klimley (2013)	Fig. 4b
		Carangiform swimming or 'patrolling'	Carcharhiniformes	*Sphyrna tiburo*	Myrberg & Gruber (1974)	
		Thunniform swimming	Lamniformes	*Isurus oxyrinchus*	Klimley (2013)	Fig. 4c
		Undulatory swimming	Rajiformes	*Dasyatis americana*	Rosenberger (2001)	Fig. 4d
		Oscillatory swimming	Myliobatiformes	*Rhinoptera bonasus*	Rosenberger (2001)	Fig. 4e
			Chimaeriformes	*Hydrolagus colliei*	Klimley (2013)	Fig. 4f
3.1.3.	Tilted swimming	Larger dorsal fin than pectorals produces more efficient lift	Carcharhiniformes	*Sphyrna mokarran* *Sphyrna lewini*	Payne et al. (2016) Klimley (pers. commun.)	Fig. 5a
3.1.4.	Accelerated swimming	'Active/accelerated swimming'	Lamniformes	*Carcharias taurus*	Smith et al. (2015)	
		'Acceleration' or rapid burst of swimming	Carcharhiniformes	*Sphyrna lewini*	Klimley (1985)	Fig. 5b
3.1.5.	Accelerated swimming and glide	An 'explosive glide' with several strong tail beats followed by glide in which tail is kept stationary	Carcharhiniformes	*Sphyrna tiburo*	Myrberg & Gruber (1974)	

Table 1.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.1.6.	Maneuvering	A rapid series of turns with its head near the caudal peduncle		*Sphyrna tiburo*	Myrberg & Gruber (1974)	Fig. 5c
3.1.7.	Hovering	Appearing motionless in the water column	Lamniformes	*Carcharias taurus*	Smith et al. (2015)	
3.1.8.	Breach	Shark propels body out of water, function unknown		*Cetorhinus maximus*	Johnston et al. (2018)	Fig. 5d
				Carcharhinus melanopterus	Porcher (2023)	
Cleaning						
3.1.9.	Parasitic body cleaning	'Circular-stance swimming', lowering caudal fin and swimming in circle to attract cleaners to multiple regions of body	Lamniformes	*Alopias pelagicus*	Oliver et al. (2011)	Fig. 5e
		King angelfish picks parasites off body while swimming slowly in water column	Orectolobiformes	*Rhincodon typus*	Quimbayo et al. (2017)	Fig. 5f
		Five species of cleaner reef fishes pick parasites off the bodies of hovering sharks on rocky reef at station on rocky reef	Carcharhiniformes	*Carcharhinus falciformis*, *C. galapagensis*, *Sphyrna lewini*	Quimbayo et al. (2017)	
		Cleaner fish removes ectoparasites from body of shark while close to the bottom at cleaner station		*Carcharhinus perezi*	Sazima & Moura (2000)	Fig. 5g
		Sharksuckers enter mouths of shark to remove parasites from their teeth		*Negaprion brevirostris*	Ritter & Amin (2016)	

Table 1.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
		Reef cleaner fish picks parasites off body of ray at feeding station on reef	Myliobatiformes	*Aetobatus narinari*	Quimbayo et al. (2017)	
3.1.10.	Self-body cleaning	'Chafing' or rolling body along substrate to remove parasites from ventrum	Lamniformes	*Carcharias taurus*	Smith et al. (2015)	
		Use sand ripples to enhance chafing of ventrum	Carcharhiniformes	*Carcharhinus limbatus*, *C. perezi*	Ritter (2011)	
		Wiggle with dorsal surface against sand or rub its ventral surface on dead coral		*Carcharhinus melanopterus*	Porcher (2023)	Video 2
		Dragging of claspers under sand to 'maintain healthy condition'		*Sphyrna lewini*	Moyo-Serrano & Salinas-de-Leon (pers. commun.)	Fig. 5h
		'Chafe' or sudden rolling of body with abdomen coming into contact with substrate.		*Sphyrna tiburo*	Myrberg & Gruber (1974)	
		A 'Gill puff' or expansion of gills to remove objects		*Carcharias taurus*	Smith et al. (2010, 2015)	
				Sphyrna tiburo	Myrberg & Gruber (1974)	

The videos referred to in this table can be accessed at 10.6084/m9.figshare.22310587.

Table 2.
Summary of reproductive behaviours of the Chondrichthyes, the Holocephali and Elasmobranchii.

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.2.1.	Group circular swimming	Multiple sharks swimming slowly snout to tail in circle with mating contusions, bite scars on sharks	Lamniformes	*Cetorhinus maximus*	Harvey-Clark et al. (1999)	
		Multiple sharks swimming slowly snout to tail in circle			Sims et al. (2022)	Fig. 6a
		Multiple sharks swimming in line form circle with snouts to tails	Carcharhiniformes	*Triakis semifasciata*	Klimley (2019)	
3.2.2.	Paired close following	♂ next to ♀ swimming synchronously just behind pectoral with bodies touching	Chimaeriformes	*Hydrolagus colliei*	Van Dykhuizen (2011)	Fig. 6b
		♂ comes up from behind and places nose next to cloaca	Lamniformes	*Carcharias taurus*	Gordon (1993); Smith et al. (2015)	
		♂ & ♀ swimming side by side synchronously	Orectolobiformes	*Ginglymostoma cirratum*	Klimley (1980)	Fig. 6c
		♂ following ♀ close to female's vent, possibly olfactory-mediated	Carcharhiniformes	*Carcharhinus melanopterus*	Johnson & Nelson (1973)	
		♂ and ♀ swim with body axes parallel		*Negaprion brevirostris*	Clark (1963)	
		♂ rapidly chases ♀ near tail	Myliobatiformes	*Aetobatus narinari*	Uchida et al. (1990)	Fig. 6d
		♂ bobs and sway while following females			Tricas (1980)	
		♂ rapidly chases ♀ close to her tail		*Manta birostris*	Yano et al. (1999)	
		♂ ventral to ♀ with pectoral beats synchronized		*Myliobatus californica*	Tricas (1980)	
		♂ follows ♀			Feder et al. (1974)	

Table 2.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.2.3.	Grouped close following	Up to five ♂♂ observed following reproductively active ♀	Orectolobiformes	*Ginglymostoma cirratum*	Carrier et al. (1994)	Fig. 11a
		Multiple ♂♂ rapidly follow reproductively active ♀	Carcharhiniformes	*Triaenodon obsesus*		
		Common for multiple ♂♂ to follow single ♀ in 'courtship train'	Myliobatiformes	*Manta alfredi*	Stevens (2016)	
				Dasyatidae and Myliobatidae	Feder et al. (1974); Tricas (1980); Uchida et al. (1990)	
3.2.4.	Clasper flexing	♂ crosses claspers across body or spreads claspers away from body	Lamniformes	*Carcharias taurus*	Claus et al. (1993); Gordon (1993); Smith et al. (2015)	Fig. 7a
		♂ rotates clasper and spread distil ends	Carcharhiniformes	*Triaenodon obsesus*	Ritter & Compagno (2013)	
3.2.5.	Torso thrust	Rolls body as the clasper pivoted on the side moving upward		*Sphyrna tiburo*	Myrberg & Gruber (1974)	
		Clasper rotated while thrusting torso to side when entering school, possibly filling siphon sac			Klimley (1985)	Fig. 8
3.2.6.	Pelvic fin cupping or flaring	♀ moves pelvic fin inward, 'cupping' and outward, 'flaring'	Lamniformes	*Carcharias taurus*	Claus et al. (1993); Gordon (1993); Smith et al. (2015)	Fig. 7b
		♀ arches body at ♂ and creates 'cup' with pelvic fins	Orectolobiformes	*Ginglymostoma cirratum*	Pratt & Carrier (2001)	

Table 2.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
		♀ arches dorsum and undulates pectoral fins	Rajiformes	*Raja eglantera*	Luer & Gilbert (1985)	
3.2.7.	Body clasping	♂ extends cephalic tentaculum outward and grasps ♀'s pectoral fin	Chimaeriformes	*Hydrolagus colliei*	Van Dykhuizen (2011)	Fig. 9a
3.2.8.	Body biting	♂ bites ♀'s pectoral fin	Chimaeriformes	*Hydrolagus colliei*	Van Dykhuizen (2011)	
		♂ bites ♀'s gills, pectoral, body, tail	Heterodontiformes	*Heterodontus francisci*	Dempster & Herald (1961)	
		♂ bites and holds ♀'s pectoral fin	Orectolobiformes	*Ginglymostoma cirratum*	Klimley (1980); Carrier et al. (1994)	Fig. 9b, Video 3
		♂ bites ♀	Laminformes	*Carcharias taurus*	Smith et al. (2017)	
		♂ bites main torso of the female	Carcharhiniformes	*Prionace glauca*	Stevens (1974); Pratt (1979)	
		♂ bites ♀'s gills, pectoral, body, tail	Carcharhiniformes	*Scyliorhinus retifer*	Castro et al. (1988)	
		♂ bites ♀'s gills, pectoral, body, tail		*Scylorhinus torazame*	Uchida et al. (1990)	
		♂ bites ♀'s pectoral fin while arching his body so pelvis is close to ♀ cloaca with clasper rotated anteriorly		*Sphyrna lewini*	Salinas-de-Leon et al. (2017)	
		♂ seizes the main torso of ♀, inflicting semicircular jaw impressions, tooth slashes, and individual tooth nicks		*Prionace glauca*, *Carcharhinus melanopterus*	Stevens (1974); Pratt & Carrier (2001); Porcher (2005)	

Table 2.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
		♂ bites and holds ♀'s pectoral fin		*Traiaenodon obesus*	Tricas & Lefeuvre (1985); Uchida et al. (1990)	Fig. 9c
		♂ uses unfurled cephalic palps to guide his mouth to seize the ♀'s pectoral fin	Myliobatiformes	*Manta alfredi*	Stevens (2018)	
		♂ delivers 'gouging' and 'nibbling' bites to the ♀'s pectoral fin and dorsum	Myliobatiformes	*Aetobatus narinari*	Uchida et al. (1990)	
		♂ delivers 'gouging' and 'nibbling' bites to the ♀'s dorsum		*Rhinoptera bonasus*	Tricas (1980)	
		♂ delivers 'gouging' and 'nibbling' bites to the ♀'s dorsum		*Rhinoptera javanica*	Uchida et al. (1990)	
		♀ motionless while 2 ♂♂ try to grasp pectoral fin		*Manta birostris*	Stevens (2016)	Fig. 9d
3.2.9.	Accepting	♀ permits approach and grasp of ♂	Orectolobiformes	*Ginglymostoma cirratum*	Carrier et al. (1994)	Video 3
3.2.10.	Carrying	After a successful pectoral grasp in 0.5 m of water, ♂ carries ♀ to deeper water to copulate	Orectolobiformes	*Ginglymostoma cirratum*	Pratt & Carrier (2001)	Fig. 11a, Video 3
3.2.11.	Positioning and alignment	After pectoral bite, ♀ rolls on to side at right angle to ♂, male nudges parallel to himself	Orectolobiformes	*Ginglymostoma cirratum*	Klimley (1980)	Fig. 10a
		After pectoral bite, male rolls ♀, then aligns for insertion of clasper			Carrier et al. (1994)	Video 3

Table 2.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
		♂ tucks post-pelvic tail surface behind ♀'s first dorsal to guide clasper	Orectolobiformes	*Ginglymostoma cirratum*	Carrier et al. (1994)	
		♀ reduces swimming speed, ♂ positions himself on top of the ♀'s back whereupon uses his unfurled cephalic palps to guide his mouth down the ♀'s pectoral fin ♂ grasps it firmly and rotate his body underneath the female until positioned abdomen to abdomen	Myliobatiformes	*Manta alfredi*	Stevens et al. (2018)	
3.2.12.	Paired copulation while on bottom	♂ and ♀ roll and lie on backs	Chimaeriformes	*Hydrolagus colliei*	Van Dykhuizen (2011)	Fig. 10b
		♂ bites ♀ and wraps around her body	Heterodontiformes	*Heterodontus francisci*	Dempster & Herald (1961)	
		♂ on top of ♀, inserts clasper	Orectolobiformes	*Ginglymostoma cirratum*	Klimley (1980)	
		♂ and ♀ roll over and lie on back with clasper in F				
		♂ and ♀ heads to substrate, tails elevated or lying parallel			Carrier et al. (1994)	
		♂ arches his body over female while copulating with ♀'s head nudged into bottom to facilitate clasper insertion			Pratt & Carrier (2005)	Fig. 10c, Video 3

Table 2.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
		♂ and ♀ appear motionless, one under the other, turning over from time to time belly to belly	Lamniformes	*Carcharodon carcharias*	Francis (1996)	
		♂ bites ♀ pectoral fin, pins rostrum to ground while clasper inserted	Carcharhiniformes	*Carcharhinus melanopterus*	McCauley et al. (2010)	
		♂ bites ♀, heads to substrate, sharks undulate to keep tails elevated		*Triaenodon obesus*	Tricas & Lefeuvre (1985)	
		♂ parallel to ♀ on bottom with clasper inserted, expelling sperm from siphon sac		*Triaenodon obesus*	Whitney et al. (1994)	
		♂ bites ♀, wraps around her body		*Scyliorhinus retifer*	Castro et al. (1988)	
		♂ bites ♀ pectoral fin; inserts clasper	Rajiformes	*Raja eglanteria*	Luer & Gilbert (1985)	
3.2.13.	Paired copulation while swimming or sinking	Coordinated pair swimming while copulating	Carcharhiniformes	*Negaprion brevirostris*	Clark (1963)	
		♂ and ♀ sinking in water column		*Sphyrna lewini*	Salinas-de-Leon et al. (2017)	Fig. 10d
		Abdomen to abdomen in mid-depths of tank	Myliobatiformes	*Aetobatus narinari*	Uchida et al. (1990)	
		Abdomen to abdomen near surface		*Manta birostris*	Yano et al. (1999)	
		Abdomen to abdomen starting near surface, continuing on bottom		*Rhinoptera bonasus*	Uchida et al. (1990)	
		Abdomen to abdomen starting near surface, continuing on bottom		*Rhinoptera javanica*		

Table 2.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.2.14.	Grouped attempts at copulation	Multiple ♂♂ compete attempt to insert clasper into female uterus	Orectolobiformes	*Ginglymostoma cirratum*	Carrier et al. (1994); Pratt & Carrier (2005)	Fig. 11a
		Four ♂♂ attempt to position themselves directly on top of ♀	Myliobatiformes	*Manta alfredi*	Stevens et al. (2018)	Fig. 11b
		Multiple ♂♂ attempt to grasp pectoral	Carcharhiniformes	*Triaenodon obesus*	Whitney et al. (1994)	
		Many captive ♂♂ overwhelm a ♀ for multiple copulations	Myliobatiformes	*Rhinoptera javanica*	Uchida et al. (1990)	
3.2.15.	Altruism	One cooperating ♂ propped against ♀, block*s* both sharks and enables mating ♂ to perform torso thrust	Orectolobiformes	*Ginglymostoma cirratum*	Pratt & Carrier (2005)	Fig. 11c, Video 3
3.2.16.	Post copulatory ejaculation	♂ expels sperm into water column 5 s after releasing grasp on ♀	Carcharhiniformes	*Triaenodon obesus*	Whitney et al. (1994)	
3.2.17.	Post-release gaping	♂ releases pectoral grasp, swims away with mouths agape to maximize water flow into mouth and over gills	Orectolobiformes	*Ginglymostoma cirratum*	Pratt (pers. commun.)	Fig. 11d
			Carcharhiniformes	*Triaenodon obesus*	Whitney et al. (1994)	
3.2.18.	Avoidance	♀ keeps pelvic fins close to bottom to prevent males access to cloaca	Lamniformes	*Carcharias taurus*	Gordon (1993); Smith et al. (2015)	Video 3
		♀ retreats to shallow water (<1 m) to 'refuge'	Orectolobiformes	*Ginglymostoma cirratum*	Pratt & Carrier (2001)	
		♀ rolls and arches over in an attempt to force the male to release his bite	Orectolobiformes	*Ginglymostoma cirratum*	Carrier et al. (1994)	Fig. 11e

Table 2.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
		♀ keeps ventrum on substrate, rolls pectoral under body, and arches tail to side to prevent ♂ access to cloaca	Carcharhiniformes	*Triaenodon obesus*	Whitney et al. (1994)	Fig. 11g
		♂ approaches ♀ to mate with her ♀ exhibits evasive action by flipping her body over in the first of multiple forward somersaults	Myliobatiformes	*Manta alfredi*	Stevens et al. (2018)	Fig. 10h
		♀ raises dorsum out of water and slaps her pectoral 'wings' on surface	Myliobatiformes	*Aetobatus narinari*	Uchida et al. (1990)	
		♀ bury in sand to avoid males		*Urolophus halleri*	Tricas et al. (1995)	
		♀ impale ♂ with caudal fin spine			Michaels (1993)	

♂ = male; ♀ = female. Based in part on Table 1 in Pratt & Carrier (2001) and Table 11.2 in Klimley (2013). The videos referred to in this table can be accessed at 10.6084/m9.figshare.22310587.

Table 3.
Summary of filter feeding behaviours of the Chondrichthyes, the Holocephali and Elasmobranchii.

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
Filter feeding						
3.3.1.	Ram feeding on plankton or small fishes	Slow straight-line swimming at surface with mouth open	Orectolobiformes	*Rhincodon typus*	Motta et al. (2010); Boldroccchi et al. (2020)	Fig.12a
				Cetorhinus maximus	Klimley (2013); Johnston (pers. commun.)	Fig.12b, Video 4a
			Myliobatiformes	*Manta alfredi*, *Manta birostrsis*	Stevens (2016)	
		Active movement to capture fish in wide open mouth	Lamniformes	*Rhincodon typus*	Lester et al. (2022)	
3.3.2.	Funnel orientation of cephalic palps	Unfurling of cephalic palps to create funnel to direct plankton into mouth	Myliobatiformes	*Manta alfredi*	Stevens (2016)	Fig. 12c
3.3.3.	Chain feeding	Line up head-to-tail in linear formation to feed			Stevens (2016)	Fig. 12d
3.3.4.	Piggyback feeding	Second manta positions itself on back of straight-feeding manta			Stevens (2016)	Fig. 12e
3.3.5.	Somersault feeding	Performs tight backward loops			Stevens (2016)	Fig. 12f
3.3.6.	Cyclone feeding	Mantas form spiral formation to trap plankton and feed upon it			Stevens (2016)	Video 4b
3.3.7.	Sideways feeding	Manta swims rotated 90° from horizontal when feeding			Stevens (2016)	Fig. 12g
3.3.8.	Bottom feeding	Manta swims along bottom with unfurled cephalic palps			Stevens (2016)	Fig. 12h

The videos referred to in this table can be accessed at 10.6084/m9.figshare.22310587.

Table 4.
Summary of scavenging behaviours of the Chondrichthyes, the Holocephali and Elasmobranchii.

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figures
3.4.1.	Parading	Swimming slowly around bait	Lamniformes	*Carcharodon carcharias*	Becerril-Garcia et al. (2019)	Fig. 13a
3.4.2.	Close inspection	Swimming close to the bait without opening its mouth for consumption			Becerril-Garcia et al. (2019)	Fig. 13b
3.4.3.	Horizontal bite	Biting whale carcass or bait from a horizontal position			Curtis et al. (2006); Fallows et al. (2013); Becerril-Garcia et al. (2019)	Fig. 13c
3.4.4.	Vertical bite	Biting whale carcass or bait from a vertical position			Curtis et al. (2006); Fallows et al. (2013); Becerril-Garcia et al. (2019)	Fig. 13d
3.4.5.	Saw-bite	Side-to side twisting of the head, resulting in fast cutting of whale carcass	Carcharhiniformes	*Galeocerdo cuvier*	Curtis et al. (2006) Randall (1992); Clua et al. (2013)	Fig. 13e–g Video 4
3.4.6.	Rotary bite	Rolling and spinning the body around to remove a bite from the whale carcass			Clua et al. (2013)	Fig. 13h

The videos referred to in this table can be accessed at 10.6084/m9.figshare.22310587.

Table 5.
Summary of predatory behaviours of the Chondrichthyes, the Holocephali and Elasmobranchii.

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.5.1.	Ambushing active prey	Dashes to surface to seize prey from position near bottom, camouflaged against dark rocky background	Lamniformes	*Carcharodon carcharias*	Klimley (1994)	Fig. 14a,b
		Lying partially buried with mouth upward, draw in above swimming prey	Squatiniformes	*Squatina californica*	Fouts & Nelson (1999)	Fig. 15a
3.5.2.	Suction feeding	Lower jaws, lift head, create suction in branchial cavity to draw prey into mouth	Orectolobiformes	*Ginglymostoma cirratum*	Motta (2004)	Fig. 15b
3.5.3.	Vertical breach with prey seizure	'Leap' with pinniped in jaws; 'polaris breach', 'surface intercept above water' with seal in jaws	Lamniformes	*Carcharodon carcharias*	Klimley et al. (1996a); Martin et al. (2005)	Fig. 15c, Video 6
3.5.4.	Horizontal breach with ventrum downward	'Surface broach', 'lateral broach', 'surface intercept above water'			Martin et al. (2005)	Fig. 15d
3.5.5.	Horizontal breach with ventrum upward	'Inverted broach'			Martin et al. (2005)	Fig. 15e
3.5.6.	Horizontal bite at surface	'Direct surface approach', 'surface grasp horizontal approach', 'surface lunge', 'horizontal bite			Klimley et al. (1996a); Martin et al. (2005)	Fig. 15f, Video 7
3.5.7.	Vertical bite at surface	'Vertical bite', 'surface feed'			Klimley et al. (1996a); Martin et al. (2005)	

Table 5.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.5.8.	Carrying prey underwater	'Exaggerated swimming', 'subsurface carry'			Klimley et al. (1996a); Martin et al. (2005)	Fig. 15g, Video 7
3.5.9.	Lateral head shake	'Lateral head shake' with carcass in jaws to remove bite			Klimley et al. (1996a); Martin et al. (2005)	Fig. 15h; Video 7
3.5.10.	Ram feeding	Preparatory, expansive, compressive, recovery phase of prey seizure and ingestion	Carcharhiniformes	*Carcharhinus perezi*	Motta (2004)	Fig. 16a–d
3.5.11.	Electrical debilitation	Bend body around prey, discharge electrical stunning prey, swallow prey headfirst	Torpediniformes	*Torpedo californica*	Lowe et al. (1994)	Fig. 16e–f
3.5.12.	Head and jaws excavation	Dig prey out from substrate with protruding jaws with pavement-like fused teeth	Myliobatiformes	*Aetobatus narinari*	Motta (2004)	
3.5.13.	Pectoral stirring of substrate	Stirring motions of pectoral fins combined with suction excavate deeply buried bivalves		*Rhinopterus bonasus*	Smith & Merriner (1965)	Fig. 16g
3.5.14.	Release from jaws	'Release' of item, 'food release', 'no feeding'	Lamniformes		Klimley et al. (1996a); Martin et al. (2005); Becerril et al. (2019)	Video 8

Table 5.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
		Release of Moses sole in response to release of surfactant	Carcharhiniformes	*Carcharhinus amblyrhynchos*, *C. albimarginatus*, *C. limbatus*, *Triaenodon obesus*	Clark (1974, 1984)	Fig. 17a,b
3.5.15.	Commensal feeding	Following a bottlenose dolphin, feeding on prey that the dolphin excavates	Orectolobiformes	*Ginglymostoma cirratum*	White et al. (2022)	Fig. 16h
		'Stationary horizontal feeding': shark is in horizontal position with head exhibiting suction feeding close to bait cannister			Parton et al. (2022)	Fig. 18a
		'Vertical feeding': shark exhibits suction feeding near bait cannister with a head-down posture			Parton et al. (2022)	Fig. 18b
		'Ventral feeding': shark rotates 180° on to dorsum and positions head below bait cannister			Parton et al. (2022)	Fig. 18c
		'Pectoral positioning': bends one or two pectoral fins downwards and gains purchase, permitting it to maneuver itself into a better position to feed			Parton et al. (2022)	Fig. 18d

Table 5.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.5.16.	Luring prey into predator's proximity for seizure	May attract prey with bioluminescent eyes, rotate jaws to one side and then another to remove a plug of flesh from the prey	Squaliformes	*Isistius brasiliensis*	Le Boeuf & McCosker (1987)	Fig. 19a,b
		May attract prey with bioluminescent copepod on eyes, opens mouth wide and draws prey in mouth using vacuum, then flenses prey moving its jaws back and forth		*Somniosus microcephalus*	Berland (1961); Borucinska et al. (1998)	Fig. 19c–e
		Paired sharks attract prey to bright white fins in homogenous blue oceanic environment, then dash toward and capture of prey	Carcharhiniformes	*Carcharhinus longimanus*	Myrberg et al. (1974)	Fig. 19f

The videos referred to in this table can be accessed at 10.6084/m9.figshare.22310587.

Table 6.
Summary of general social behaviours of the Chondrichthyes, the Holocephali and Elasmobranchii.

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.6.1.	Following	One shark follows another, changing direction with that shark	Lamniformes	*Carcharias taurus*	Smith et al. (2015)	
			Carcharhiniformes	*Sphyrna tiburo*	Myrberg & Gruber (1974)	Fig. 20a
				Carcharhinus melanopterus	Porcher (2023)	
3.6.2.	Turn back	An abrupt turning maneuver that positioned one shark directly behind another			Myrberg & Gruber (1974)	
3.6.3.	Follow formation	'Chain following' of multiple males or males following females	Lamniformes	*Carcharodon carcharias*	Claus et al. (2021)	Fig. 20b
		Multiple sharks follow each other following leader when changes direction	Carcharhiniformes	*Sphyrna tiburo*,	Myrberg & Gruber (1974)	
				Triakis semifaciata	Klimley (2019)	
				Carcharhinus melanopterus	Porcher (2023)	
		'Chain following' of multiple males or males following females	Lamniformes	*Carcharias taurus*	Claus et al. (2021)	
3.6.4.	Circling head-to-tail	Two sharks circle with each other head-to-tail	Carcharhiniformes	*Sphyrna tiburo*	Myrberg & Gruber (1974)	Fig. 20c
3.6.5.	Investigating individual	One shark moves snout to vent area of female when swimming in opposite direction in line	Carcharhiniformes	*Triakis semifaciata*	Klimley (2019)	Fig. 20d–e

Table 6.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.6.6.	Heading	sharks swim parallel and slowly and touch regions of the head in the area just posterior to the eye	Lamniformes	*Carcharias taurus*	Claus et al. (2021)	
3.6.7.	Schooling	Swim with directional commonality	Carcharhiniformes	*Sphyrna lewini*	Klimley & Nelson (1981); Klimley (1985)	Fig. 20f, Video 9
3.6.8.	Aggregating	Massive aggregation of sharks, swimming in non-polarized manner	Carcharhiniformes	*Carcharhinus limbatus*	Kajiura & Tellman (2016)	Fig. 20g
3.6.9.	Parallel swimming	Upon arriving from different directions sharks swim parallel side by side	Lamniformes	*Carcharodon carcharias*	Sperone et al. (2010)	
			Carcharhiniformes	*Carcharinus melanopterus*	Mourier et al. (2011); Porcher (2023)	
3.6.10.	Swimming by	Two sharks turn towards each head upon head as they approach closely	Lamniformes	*Carcharodon carcharias*	Sperone et al. (2010)	
			Carcharhiniformes	*Carcharinus melanopterus*	Porcher (2023)	Video 10

The videos referred to in this table can be accessed at 10.6084/m9.figshare.22310587.

Table 7.
Summary of aggressive behaviours of the Chondrichthyes, the Holocephali and Elasmobranchii.

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.7.1	Hunching	Hunching up of the back with the tail slightly lowered and the head slightly raised	Carcharhiniformes	*Sphyrna tiburo*	Myrberg & Gruber (1974); see table II in Martin (2007)	
3.7.2	Jaw gaping	Slow exaggerated opening of the jaws	Lamniformes	*Carcharodon carcharias*, *Carcharias taurus*	See table II in Martin (2007); Klimley & Hoyos-Padilla (2023; Smith et al. (2010, 2015)	Fig. 21a, Video 11
			Carcharhiniformes	*Galeocerdo cuvier*	Clua et al. (2013)	
3.7.3	Gill pouch billowing	Spinnaker-like expansion of the branchial region of the shark's torso	Lamniformes	*Carcharodon carcharias*	See table II in Martin (2007)	
			Carcharhiniformes	*Sphyrna tiburo*	Myrberg & Gruber (1974)	
3.7.4	Jaw opening and closing	Jaws opened and closed, moves back and forth in tight loops in front of intruder	Carcharhiniformes	*Negaprion brevirostris*	Klimley (2019); see table II in Martin (2007)	Fig. 21a, Video 11
3.7.5	Stiff and jerky movements	Awkward body movements during swimming	Lamniformes	*Carcharias taurus*	Smith et al. (2015); see table II in Martin (2007)	
3.7.6	Spasmodic body shaking	Mouth opened for prolonged period, pectoral fins depressed, caudal fin kept at right angle to viewer in shark cage, and body shaken with spasmodic oscillations	Lamniformes	*Carcharodon carcharias*	Martin (2007); Klimley & Hoyos-Padilla (2023)	Video 11

Table 7.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
			Carcharhiniformes	*Carcharhinus albimarginatus*	Martin (2007)	
3.7.7	Flank displaying	Sustained perpendicular body orientation toward a receiver, showing its lateral surface	Lamniformes	*Carcharodon carcharias*, *Carcharias taurus*	Martin (2007); Smith et al. (2015); Klimley & Hoyos-Padilla (2023)	Fig. 21a; Video 11
			Carcharhiniformes	*Galeocerdo cuvieri*	Clua et al. (2013)	
3.7.8	Pectoral fin depression	Sustained depression of both pectoral fins	Lamniformes	*Carcharodon carcharias*	See table II in Martin (2007); Smith et al. (2015); Klimley & Hoyos-Padilla (2023)	Fig. 21a; Video 11
				Cetorhinus maximus	Martin (2007)	Fig. 21b
			Carcharhiniformes	*Carcharhinus galapagensis*	Martin (2007)	Fig. 21c
3.7.9	Give way	One shark moves out of the swimming path of another as approached from another direction	Carcharhiniformes	*Sphyrna tiburo*, *Sphyrna lewini*	Myrberg & Gruber (1974); Klimley (1985); Smith et al. (2015)	Fig. 21d

Table 7.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.7.10	Tail slap	Tail lifted out of water, brought down, directing water at conspecific	Lamniformes,	*Carcharodon carcharias*,	Klimley et al. (1996b); Martin et al. (2005, 2007); Sperone et al. (2012); Becerril-Garcia et al. (2019)	Fig. 21e, Video 12
				Carcharias taurus	Smith et al. (2015))	
			Carcharhiniformes	*Galeocerdo cuvier*	Clua et al. (2013)	
3.7.11	Breach	Body propelled out of the water, splashing water toward conspecific			Klimley et al. (1996b); Martin (2007)	Fig. 21f
3.7.12	Exaggerated tail beats		Carcharhiniformes	*Carcharhinus amblyrhynchos*	Johnson & Nelson (1973)	Fig. 21g, Video 13
3.7.13	Looping	Shark swims with a looping trajectory	Carcharhiniformes	*Carcharhinus amblyrhynchos*, *Negaprion brevirostris* *Carcharhinus limbatus*	Johnson & Nelson (1973); Klimley (2019); see Table II in Martin (2007)	Fig. 21h, Video 13
3.7.14	Charging	Rapid approach toward perceived threat, usually ending in a quick turn away	Lamniformes	*Carcharodon carcharias*, *Carcharias taurus*	See Table II in Martin (2007); Smith et al. (2015)	

Table 7.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
			Orectolobiformes	*Ginglymostoma cirratum*	Pratt (pers. commun.)	
			Carcharhiniformes	*Mustelus canis*, *Carcharhinus melanopterus*	See Table II in Martin (2007); Porcher (2023)	
3.7.15	Slamming	Accelerating towards a conspecific and hitting it with the full force of its momentum	Carcharhiniformes	*Carcharhinus melanopterus*	Porcher (2023)	
3.7.16	Repetitive aerial gaping	Head shaking while on back after being deprived of bait	Lamniformes	*Carcharodon carcharias*	Strong (1996)	Fig. 21i
3.7.17	Chase	One shark pursues another over short distance	Carcharhiniformes	*Sphyrna lewini*	Klimley (1985)	
3.7.18	Hit	Shark brings down underside of jaw in contact with body of conspecific swimming below	Carcharhiniformes	*Sphyrna tiburo*, *Sphyrna lewini*	Myrberg & Gruber (1974); Klimley (1985)	Fig. 22a
3.7.19	Corkscrew	Rapid burst into a tight looping trajectory with the shark rotating its torso *360°* on longitudinal axis before entering the circular trajectory	Carcharhiniformes	*Sphyrna lewini*	Klimley (1985)	Fig. 22b
3.7.20	Headshake	Head swung back and forth over wide arc several times in quick succession while suddenly propelling itself forward with rapid tail beats	Carcharhiniformes	*Sphyrna lewini*	Klimley (1985)	Fig. 22c

Table 7.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.7.21	Head snap	The head moving slightly upward and then rapidly downward along a diagonal plane	Carcharhiniformes	*Sphyrna tiburo*, *Sphyrna lewini*	Klimley (1985)	
3.7.22	Dominance biting	Larger male bites the ventrum of subordinate male	Lamniformes	*Carcharias taurus*	Claus et al. (2021)	
3.7.23	Territoriality biting	A shark that bites another shark or a human that has its home range	Carcharhiniformes	*Carcharhinus melanopterus*, *C. amblyrhynchos*, *Negaprion acutidens*	Limbaugh (1963); Baldridge & Williams (1969); Johnson &Nelson (1973); Nelson (1981); Nelson et al. (1986); Balbridge (1988); Gruber (1988), Jublier & Clua (2018); Clua & Haguenauer (2019)	
3.7.24	Reflex biting	A shark competing for food inadvertently bites another shark or a human	Carcharhiniformes	*Carcharhinus melanopterus*, *C. amblyrynchos*, *C. leucas*, *Negaprion acutidens*	Nelson et al. (1986); Clua (2018)	Video 14

Table 7.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figure
3.7.25	Competition biting	A shark competing with a human for food purposely bites the human	Carcharhiniformes	*C. amblyrynchos*	Nelson (1981); Nelson et al. (1986); Balbridge (1988); Collier (2003); Clua et al. (2023)	
3.7.26	Open jawed tooth raking	Upper teeth of shark make forceful tooth raking contact with a perceived threat	Lamniformes	*Carcharodon carcharias*; *Carcharias taurus*	Martin (2007); Smith et al. (2015)	

The videos referred to in this table can be accessed at 10.6084/m9.figshare.22310587.

Table 8.
Summary of defensive behaviours of the Chondrichthyes, the Holocephali and Elasmobranchii.

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figures
3.8.1.	Rapid withdrawal	Fast movement away from a perceived threat	Lamniformes	*Carcharodon carcharias*, *Carcharias taurus*	Martin (2007); Smith et al. (2015);	
			Carcharhiniformes	*Galeocerdo cuvier*, *Carcharhinus melanopterus*	Clua et al. (2013); Porcher (2023)	
3.8.2.	Withdrawal from high amplitude sounds	Change in direction and flight away from sound source	Carcharhiniformes	*Sphyrna tiburo*	Myrberg et al. (1978); Klimley & Myrberg (1979)	
3.8.3.	Spine thrust	Thrust spine into predator swimming above	Myliobatiformes	Nine families, including the Dasyatidae, Gymnuridae, Myliobatidae, Urolophidae	Germain et al. (2000); Pedroso et al. (2007); Diaz (2008); Dehghani et al. (2010); Klimley (2013)	
3.8.4.	Tonic immobility	A general immobility of the shark or ray after being turned upside down or grasped by the caudal fin	Squaliformes	*Mustelus canis*	Whitman et al. (1986)	
			Orectolobiformes	*Stegostoma fasciatum*	Whitman et al. (1986)	
			Lamniformes	*Carcharodon carcharias*	Pyle et al. (1999)	
			Carcharhiniformes	Seven species	See Table I in Miranda Páez et al. (unpubl. manuscript)	

Table 8.
(Continued.)

Section	General behaviour	Descriptive notes	Order	Genus species	References	Figures
			Rajiformes	*Raja clavata*, *Raja eglanteria*, *Rhinobatus productos*	See Table I in Miranda Páez et al. (submitted)	
			Myliobatiformes	*Urolophus jamaicensis*, *Rhinoptera bonasus*	Henningsen (1994)	
3.8.5.	Anti-predatory biting	Bite on a human who voluntarily or involuntarily appears as a potential threat to the shark	Carcharhiniformes	*Carcharhinus melanopterus*, *C. amblyrynchos*; *Sphyrna tiburo*	Fellows & Murchinson (1967); Myrberg & Gruber (1974); Nelson et al. (1986); Balbridge (1988); Gruber (1988); Martin (2007), Clua (pers. commun., Copyright@UnderThePole-France)	Video 15
3.8.6.	Self-defense or retaliatory biting	Bite on a human that voluntarily or involuntarily has threatened the shark	Carcharhiniformes	*Carcharhinus amblyrynchos*, *Negaprion acutidens*	Gruber (1988); Clua & Haguenauer (2019)	

The videos referred to in this table can be accessed at 10.6084/m9.figshare.22310587.

away to prevent them from taking their speared fish. Clua & Haguenauer (2019) reported the case of a Polynesian fisherman who died in 1977 after several defensive bites by a sicklefin lemon shark, *Negaprion acutidens*, that he accidentally speared after misidentifying it with a nurse shark, *Nebrius ferrugineus*.

4. Discussion

There is a diversity of behaviour described in the chondrichthyan ethogram we have presented here. They have been described in eight categories: (1) 10 behavioural patterns under maintenance, (2) 18 under reproduction, (3) 8 under filter feeding, (4) 6 under scavenging, (5) 16 under predation, (6) 10 under social, (7) 26 under aggressive and (8) 6 under defensive behaviours. The behaviours and the contexts in which they occur, are described in the body of the manuscript. We have attempted to make the titled behavioural types inclusive because many authors use different names for the same behavioural acts.

Is a greater diversity and complexity of behaviours exhibited by the most recently evolved chondrichthyan species? To find this out, one must be aware of the evolutionary history of the chimaeras, sharks, and rays. This has been described based upon the molecular, anatomical, and fossil history of the species. Presented is an evolutionary tree indicating the phylogenetic relationships among the modern sharks and rays based on molecular (left) and anatomical (right) similarity (Figure 23). The bold lines indicate the presence of species preserved in the fossil record and the thin lines the relationships inferred only on the basis of the two types of similarity (Klimley, 2013).

This diagram can be likened to a tree, but one that is not upright but lying on its side. It consists of a trunk with a series of diverging limbs and branches. The species on each bifurcation or trifurcation are related by the possession of at least one characteristic shared with a common ancestor on the branch serving as its origin. The cartilaginous fishes can be related to each other based on the similarity of their sequences of genes (see left tree in Figure 23) (Maisey et al., 2004) and common derived anatomical features (see right tree in Figure 23) (Shirai, 1996). All comparisons of evolutionarily related taxa must be placed in the context of an unrelated ‘outgroup’ to demonstrate that they are more related to each other than to an evolutionary divergent group. It is not possible to identify just when each order appeared using this method

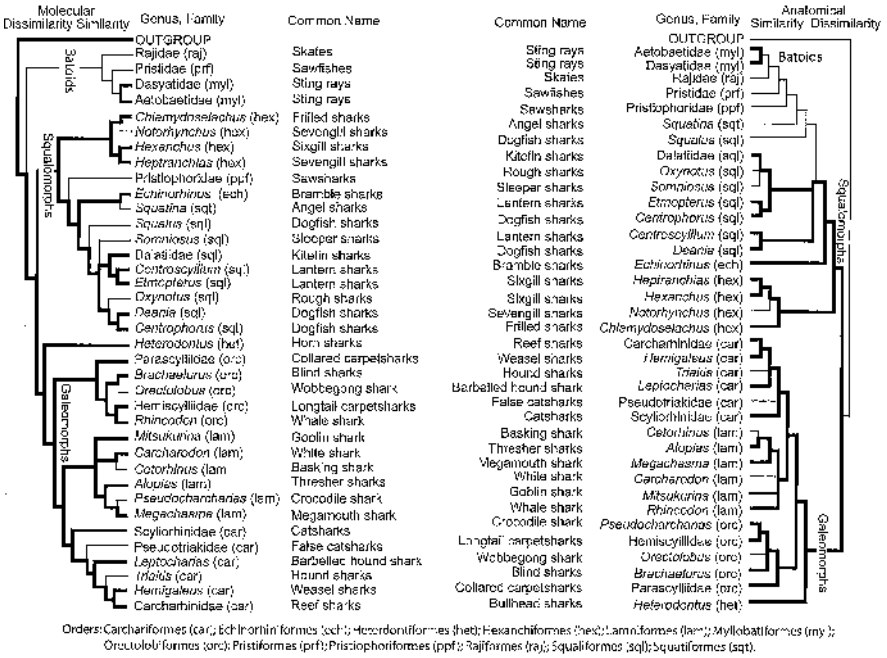

Figure 23. Phylogenetic relationships of Chondrichthyes. Evolutionary trees indicating the phylogenetic relationships among the modern sharks and rays based on molecular (left) and anatomical (right) similarity. The bold lines indicate the presence of species preserved in the fossil record and the thin lines the relationships inferred only on the basis of the two types of similarity (Klimley, 2013).

of analysis and that must be based on the discovery of fossils in sedimentary deposits dated to a particular age.

One of the ctenacanths that survived the inclement conditions of the Permian, was likely the common ancestor of the modern sharks. It constitutes the base of this phylogenetic tree of chondrichthyan fishes. Notice the second limb from the trunk of the tree, based on similarity in genetic code, leads to the Batoidea, the subclass of the rays and their relatives. This tree limb bifurcates with the first branch leading to the Rajiformes, the skates, and the second to the Pristiformes, the sawfishes, and the Myliobatiformes, the stingrays. The limb structure of this phylogenetic tree indicates that the rays are only distantly related to the modern sharks. Yet this conclusion is inconsistent with the branching of the evolutionary tree based on shared skeletal and muscular characters (Shirai, 1996). The first limb off the trunk of this tree leads to the galeomorphs and squalomorphs, with a limb from the latter

leading to a series of bifurcations with the first leading to the Hexanchiformes. The second branch leads to three groups: the Echinorhiniformes, the majority of the Squaliformes, and a third group. This group consists of the dogfish sharks of the genus *Squalus*, the angel sharks of the genus *Squatina*, and the skates and stingrays. It is more likely that the molecular tree indicates the correct evolutionary relationship between the sharks and rays. Two genetic studies, one based on the similarity of sequences of mitochondrial genes (Douady et al., 2003) and the other based on the similarity of sequences of nuclear genes (Winchell et al., 2004), indicate that the rays diverged early from the sharks before the evolution of the squalomorphs. Fossils in sedimentary deposits in Europe indicate that the rays were present in the oceans in the early Jurassic when the earliest modern sharks began to flourish (Maisey, 1996).

Both cladistic and genetic analyses indicate that the modern sharks are divided into two lineages, the squalomorphs and galeomorphs. Notice the separation of the trunk of the two trees near the base to form two main limbs, each leading to the different families and genera. The Squalomorphi are considered to be more primitive in their anatomy, possessing smaller brains, and having evolved in deep water environments, where they are currently more abundant (Grogan & Lund, 2004). The Galeomorphi are judged to be more advanced in their anatomy, have larger brains, and likely to have evolved in shallow water tropical environments, where they are currently most abundant (Klimley, 2013).

The similarities between the evolutionary trees based on shared molecular and morphological similarities can be combined with fossil evidence to provide insights into the evolutionary history of the modern sharks. The first squalomorph sharks to appear were the six and sevengill sharks of the order Hexanchiformes (Campetta et al., 1993). The Squatiniformes appeared later in the seas at the beginning of the Cretaceous and became widespread by the middle Cretaceous. The Squaliformes appeared after the Hexanchiformes and Squatiniformes (Capetta, 1987). The sawsharks of the Pristiophorifomes were the last of the squalomorphs to diversify. The first galeomorphs to inhabit the seas were the Heterodontiformes (Douady et al., 2003). The earliest fossils are from Germany dated from the late Triassic and early Jurassic. The Orectolobiformes were the second order of galeomorphs to appear in the fossil record. The Lamniformes appeared next at the end of the Jurassic. The members of *Carcharhinus*, characterized by a large brain size, complex

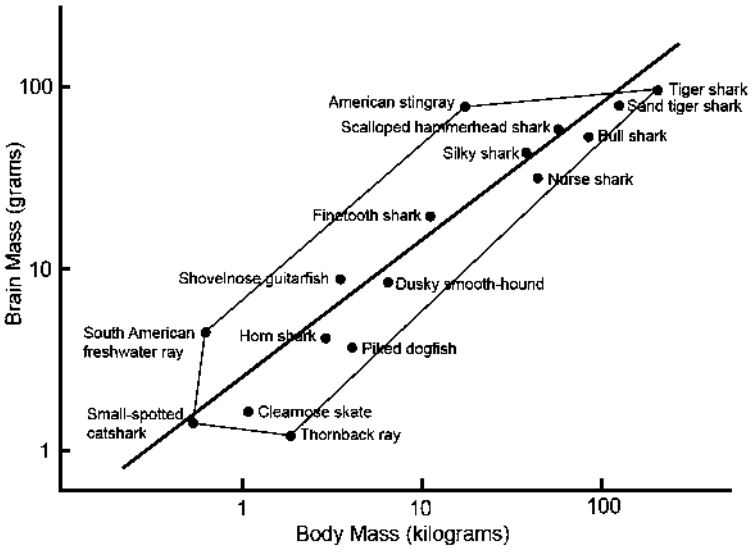

Figure 24. Brain capacity. Minimum convex polygon drawn around brain masses plotted as a function of body mass (Northcutt, 1978). This gives you an idea of the relative sensory and intellectual capacity of the cartilaginous fishes. The coefficient of allometry of 0.8 (indicated by the solid line and its slope) denotes a rough proportional relationship of brain with body size versus growth (1.0 equals a perfect correlation).

social behaviour, and the ability to migrate over long distances, appeared next, 53 mya in the Paleogene.

How do the members of the different orders differ in complexity? One way of looking at this is by comparing their brain sizes of the different species as well as the taxon of cartilaginous fishes to other vertebrate taxa. The overall brain sizes of members of different species of sharks can be plotted as a function of the body mass (Northcutt, 1978). A brain to body mass comparison is most valid when the species have a comparable body size. For example, the brain weight of a squaloform species such as the piked dogfish, *Squalus acanthias*, can be compared on the graph with brain weight of a galeoform species of similar size such as the dusky smooth-hound, *Mustelus canis* (see small separation between them on ordinate in Figure 24). The dogfish has a brain mass of roughly 4 g and the smooth-hound a brain mass of 9 g, whereas the former's body weight is 7 kg and the latter's weight is 9 kg. Comparisons such as this one reveal that the primitive squalomorph sharks generally possess low brain-to-body ratios and the more advanced geoleomorph sharks of the order Carcharhiniformes possess high ratios. The evolution of the modern

sharks has resulted in a twofold to sixfold increase in brain size (Northcutt, 1978). The points for the rays are scattered throughout the minimum convex polygon on the plot of brain-to-body mass (Figure 24). Members of the order Rajiformes such as the clearnose skate, *Raja eglanteria*, have a low brain-to-body ratio, but members of the order Myliobatiformes such as the American stingray, *Dasyatis sabina*, have among the highest of the ratios for the cartilaginous fishes. The ground sharks of the order Carcharhiniformes, such as the silky and scalloped hammerhead sharks, have very high brain-to-body ratios.

Among the highest brain to body ratios, apparent in Figure 24, are three members of the Carcharhiniformes such as the tiger, scalloped hammerhead and bull sharks, the Lamniformes such as the sand tiger, the Myliobatiformes, such as the American stingray, and the Orectolobiformes, such as the nurse shark. Consistent with these neurological differerences is that members of these four orders comprise 18 of 20 (90.0%) of the species exhibiting maintenance behaviours in Table 1, 19 of 22 (86.4%) of the species displaying reproductive motor patterns in Table 2, 4 of 4 (100.0%) of the species performing filter feeding in Table 3, 2 of 2 (100.0%) of the species exhibiting scavenging behaviours in Table 4, 11 of 14 (78.6%) of the species performing predatory acts in Table 5, 7 of 7 (100.0%) of the species performing general social behaviours in Table 6, 22 of 25 (88.4%) of the species exhibiting aggressive motor patterns in Table 7, 18 of 21 (85.7%) of the species performing defensive acts in Table 8. Hence, the ethogram indicates that the more derived sharks and rays in the chondrichthyan lineage, have evolved the most diversity and complexity in their behavioural patterns.

However, a caveat to the above conclusion is that most of the chimaeriforms such as the spotted ratfish exist in cold temperate and sub-polar waters such as Northern California and British Columbia, where divers are unlikely to spend a considerable amount of time in the water observing them or in the deep-sea where it is only accessible by submersible. Furthermore, most of the squalomorph species of sharks exist at the edge of the continental shelves of continents or in the deep sea. Ideally, more studies in the natural environment and aquarium environments will be carried out on these species to augment this ethogram. Finally, some of the behaviours are described for sharks and rays that were observed in captivity, and it is possible that the behaviours that they exhibited are not displayed in the natural environment. Yet for sake of inclusion, we have described these behaviours in this paper.

4.1. Conclusions

The notion that chondrichthyan fishes, particularly the sharks, are mindless feeding machines was created by luring them to the vicinity of a cage for humans within the cage to view and film them. The sharks were attracted to the cage using an olfactory attractant such ground fish, cattle meat, or mammalian blood to elicit feeding responses — the opening of their jaws wide to seize the baits. For this reason, during much of the senior author's career the general consensus among the public as well as most scientists was that sharks were dumb feeding machines, which exhibited little complexity in behaviour. The major impetus for assembling this ethogram of chondrichthyan behavioural patterns by the authors was to demonstrate the diversity of behaviours exhibited by members of this taxon and to dispel the apocryphal belief that sharks are simple feeding machines. By compiling and synthesizing this literature, we hope to provide a standardized reference for future study of the behaviour of this diverse group of marine vertebrates.

Acknowledgements

We would like to thank the many scientists, who let us reproduce figures from their scientific papers in this ethogram of the chondrichthyan fishes. There are so many that it would be difficult to mention all of them by name here. They are credited with citations in the figure captions and a supplementary file providing their names, email addresses, and permissions. The manuscript was improved vastly through guidance provided by Dr. Brian D. Wisenden, Editor-in-Chief of *Behaviour*. He recommended that we place the ethogram in a phylogenetic context with a discussion of the evolutionary histories of the species and orders. We followed his advice. He also read the manuscript in detail and provided welcome fine-scale editing.

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List of supplementary videos

These videos can be accessed at 10.6084/m9.figshare.22310587.

Video 1. Slow straight-line swimming (Table 1, Section 3.1.2).

Video 2. Self-body cleaning (Table 1, Section 3.1.10).

Video 3. Courtship and Copulation (Table 2, Sections 3.2.8–3.2.12, 3.2.15, 3.2.18).

Video 4a. Basking shark ram feeding on plankton (Table 3, Section 3.3.1).

Video 4b. Reef manta rays ram feeding on plankton (Table 3, Section 3.3.6).

Video 5. Saw Bite (Table 4, Section 3.4.5).

Video 6. Vertical breach with prey seizure (Table 5, Section 3.5.4).

Video 7. Horizontal bite and lateral head shake (Table 5, Sections 3.5.6, 3.5.8–3.5.9).

Video 8. Scavenging on sea lion (Table 5, Section 3.5.14).

Video 9. Schooling (Table 6, Section 3.6.7).

Video 10. Swim by (Table 6, Section 3.6.10).

Video 11. Aggressive behaviours (Table 7, Sections 3.7.2, 3.7.4–3.7.5, 3.7.7–3.7.8)

Video 12. Tail slap (Table 7, Section 3.7.10).

Video 13. Exaggerated tail beats and looping (Table 7, Section 3.7.12).

Video 14. Reflex biting (Table 7, Section 3.7.24).

Video 15. Anti-predatory biting (Table 8, Section 3.8.5).