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The behaviour of sharks

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Introduction to the problem of studying shark behaviour

The word 'shark' can clear a beach or fill a movie theatre. Viewed by man with both fear and intrigue, sharks are uniquely adapted to their home in the sea. While they appear invincible in pursuit of their prey, significant declines have been noted in the populations of several commercially fished species. Recovery from heavy fishing activities has been slow, with populations sometimes requiring decades to reach former levels (Pratt and Casey, 1990). A classic example is the collapse of the porbeagle fishery in the western North Atlantic Ocean (Fig. 1) (for scientific and family names of shark species mentioned in this review, see Table 1).

Similar declines have been noted in catches of common thresher sharks, which declined from 1200000 t to 200000 t over a 5 year period (Bedford, 1987; Stick and Hreha, 1988). The fishable biomass of spiny dogfish was reduced by 75% over a 12 year fishing effort (Ketchen, 1969). The spiny dogfish is typical among sharks in that reproductive and growth rates are slow. Sexual maturity comes late (approximately 12 years in the

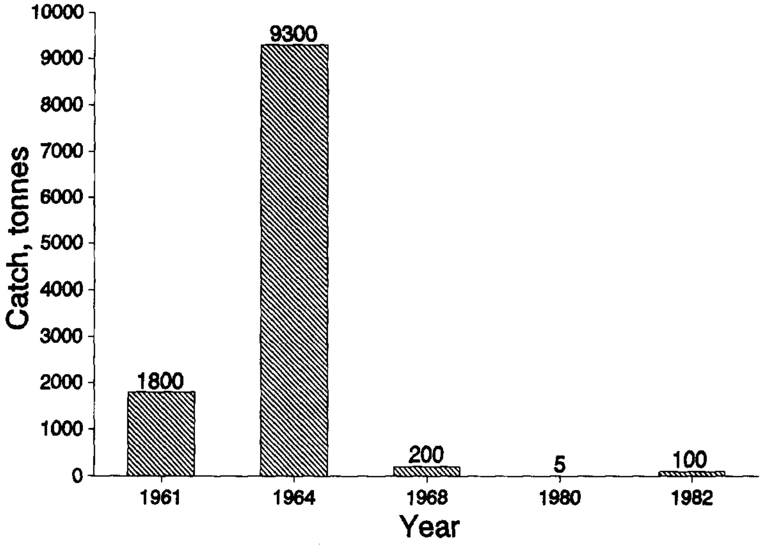

Fig. 1. The porbeagle fishery underwent a dramatic decline in productivity between 1961 and 1964 (Casey *et al.*, 1978). Attempts to revive the fishery in the 1980s revealed a profound effect of that brief exploitation. By 1982, the population had apparently not recovered to prefishery levels.

spiny dogfish) and although litter size may increase as population density decreases, replacement cannot keep pace with increasing fishing pressure (Nammack *et al.*, 1985).

In an effort to address conservation concerns while assuring sustainable commercial and recreational fisheries, The National Marine Fisheries Service of the United States has prepared a Draft Secretarial Shark Fishery Management Plan for the Atlantic Ocean. The plan is scheduled for implementation in 1993, but may not provide the restrictions required to prevent further inroads into declining populations. More research on almost every aspect of physiology, ecology, and behaviour is needed to determine how to manage and protect these species, but gathering data on sharks can be challenging.

Most sharks tend to avoid divers, especially divers using open-circuit scuba (Nelson, 1974), and so it is difficult to maintain a regular observation schedule. Even those species with circumscribed home ranges tend to traverse the boundaries of their activity space during their diel cycle. Many species of shark also undergo vertical migrations and spend extended periods of time below scuba depth. Most sharks are either crepuscular or nocturnal, and therefore many behavioural responses occur under cover of darkness (Nelson, 1974). In addition, generalized behavioural patterns cannot be inferred from the actions of a few individuals, or even be extrapolated confidently from one species to another (Gilbert, 1963).

In order to understand and interpret shark behaviour, investigators must understand their capabilities and how they function in the aquatic environment. The acuity of several shark senses far exceeds ours, and their electromagnetic sense has no parallel in humans. For most species, however, complete information about physiology, life history, and ecology is notably lacking. This article is a brief review of what is known about the sensory capabilities and behaviour of sharks.

Table 1. Common and scientific names of sharks.

Common name	Scientific name	Family
Basking shark	*Cetorhinus maximus*	Cetorhinidae
Blacknose shark	*Carcharhinus acronotus*	Carcharhinidae
Blacktip reef shark	*Carcharhinus melanopterus*	Carcharhinidae
Blue shark	*Prionace glauca*	Carcharhinidae
Bonnethead shark	*Sphyrna tiburo*	Sphyrnidae
Bull shark	*Carcharhinus leucas*	Carcharhinidae
Catshark	*Scyliorhinus canicula*	Scyliorhinidae
Chain dogfish	*Scyliorhinus retifer*	Scyliorhinidae
Cookie-cutter shark	*Isistius brasiliensis*	Squalidae
Crocodile shark	*Pseudocarcharias kamoharai*	Pseudocarchariidae
Dusky shark	*Carcharhinus obscurus*	Carcharhinidae
Epaulette shark	*Hemiscyllium ocellatum*	Hemiscyllidae
Galapagos shark	*Carcharhinus galapagensis*	Carcharhinidae
Goblin shark	*Mitsukurina owstoni*	Mitsukurinidae
Grey reef shark	*Carcharhinus amblyrhynchos*	Carcharhinidae
Great hammerhead	*Sphyrna mokarran*	Sphyrnidae
Greenland shark	*Somniosus microcephalus*	Squalidae
Gulper shark	*Centrophorus* spp.	Squalidae
Horn shark	*Heterodontus francisci*	Heterodontidae
Kitefin	*Dalatias licha*	Squalidae
Lantern shark	*Etmopterus* spp.	Squalidae
Lemon shark	*Negaprion brevirostris*	Carcharhinidae
Leopard shark	*Triakis semifasciata*	Triakidae
Lesser spotted dogfish	*Scyliorhinus canicula*	Scyliorhinidae
Mako shark	*Isurus* spp.	Lamnidae
Marbled catshark	*Galeus arae*	Scyliorhinidae
Nurse shark	*Ginglymostoma cirratum*	Rhincodontidae
Oceanic whitetip shark	*Carcharhinus longimanus*	Carcharhinidae
Pacific angel shark	*Squatina californica*	Squatinidae
Porbeagle	*Lamna nasus*	Lamnidae
Port Jackson shark	*Heterodontus portusjacksoni*	Heterodontidae
Sand tiger shark	*Eugomphodus taurus*	Odontaspididae
Sandbar shark	*Carcharhinus plumbeus*	Carcharhinidae
Scalloped hammerhead	*Sphyrna lewini*	Sphyrnidae
School shark	*Galeorhinus galeus*	Triakidae
Silky shark	*Carcharhinus falciformis*	Carcharhinidae
Silvertip shark	*Carcharhinus albimarginatus*	Carcharhinidae
Sixgill shark	*Hexanchus griseus*	Hexanchidae
Smooth dogfish	*Mustelus canis*	Triakidae
Spinner shark	*Carcharhinus brevipinna*	Carcharhinidae
Spiny dogfish	*Squalus acanthias*	Squalidae
Swell shark	*Cephaloscyllium ventriosum*	Scyliorhinidae
Thresher shark	*Alopias vulpinus*	Alopiidae
Tiger shark	*Galeocerdo cuvier*	Carcharhinidae
Whale shark	*Rhincodon typus*	Rhincodontidae
White shark	*Carcharodon carcharias*	Carcharhinidae
Whitetip reef shark	*Triaenodon obesus*	Carcharhinidae

Shark sensory capabilities

Vision

Contrary to early hypotheses, anatomical data now suggest that sharks have great visual acuity, with both day and night vision capabilities. It has been established by Gruber and Cohen (1978, 1985), Gruber (1967), and Gruber *et al.* (1975) that most sharks have a duplex retina, containing both rods and cones. Cone photoreceptors are of the type usually associated with photopic vision. Photopic vision implies colour vision and enhanced acuity. Gruber (1967) demonstrated increased visual sensitivity with dark adaptation in lemon sharks, within a range comparable to that of human vision.

Hueter (1991) noted that density of cones (number per unit area) predicts the morphological acuity of a retina, and density of ganglion cells may indicate regional retinal specializations for spatial information. Hueter discovered a horizontal band of highly concentrated cone and ganglion cells in the retina of juvenile lemon sharks. The positioning of the band, combined with behavioural observations in field and laboratory situations, suggests that this 'visual streak' may be an adaptation for a benthic lifestyle, facilitating orientation and movement in a horizontal plane. Gruber and Cohen (1985) also found evidence of regional retinal specialization in sharks. Examination of the white shark retina showed that the ratio of rods to cones and of receptors to ganglion cells varied around the retina. Cones and ganglion cells reached their maximal density in the central retina; no cones were present at the periphery. They concluded that, as with humans and other vertebrates, the central retina was specialized for day vision, whereas the periphery functioned best at night or in dim light.

Behavioural studies have confirmed that sharks can discriminate among objects by using visual cues. The ability to select a target based on differential brightness was demonstrated in lemon sharks by Gruber and Cohen (1978), Wright and Jackson (1964) and Clark (1959), and in nurse sharks by Wright and Jackson (1964). Graeber and Ebbesson (1972) trained juvenile nurse sharks to discriminate black from white targets and between horizontal and vertical stripes. The sharks retained this discriminatory ability, even with removal of the optic tectum. Ablations of the visual portion of the central telencephalic nucleus, however, inhibited acquisition of visual behaviours.

Gruber (1975) reported that one lemon shark was able to discriminate among different-coloured targets of equal brightness. The shark responded to changing chromatic-adapting fields with no auditory cues. Other researchers have noted that sharks may be attracted to or may avoid brightly coloured objects. Wallace (1972) confirmed the ability of bull sharks and sand tiger sharks to discriminate between different colours of underwater mesh netting. Bull sharks tended to avoid the brighter yellow nets. Hess (1962) reported the attraction of oceanic sharks to fluorescent orange objects, and McFadden and Johnson (1971) noted that sharks were attracted to bright yellow survival gear (sometimes referred to as 'yum yum' yellow), but ignored the same gear when it was painted black.

Visual cues may play a role in intra- and interspecific social interactions. Field studies by Johnson and Nelson (1973) with grey reef sharks have shown that visual cues (such as the presence of a diver) are important in triggering highly stereotyped pre-attack behaviours. Display was elicited by aggressive diver approach. There appeared to be a direct correlation between proximity and the intensity of the agonistic display. Myrberg (1991) suggested that distinctive fin markings may play a role in species recognition and size judging of sympatric species (such as the whitetip, blacktip, and grey reef sharks).

Gruber *et al.* (1988) found that lemon sharks use the sun as a visual cue for diel movements. Clark and Kristof (1990) observed a 'pineal window' in three groups of deep sea sharks. These species (including sixgill, gulper, and lantern sharks) make vertical migrations between the euphotic and aphotic zones. Clark and Kristof speculate that the pineal gland functions as a light-receiving organ which may play a role in diel vertical migration and prey location.

Mechanical and acoustical senses

Although sharks have no external ears, they have a well-developed sense of hearing. Several studies have noted the ability of sharks to hear and respond to sounds transmitted through the water. The rapid approach of sharks to the sounds of struggling fish has often been noted (Hobson, 1963; Nelson and Gruber, 1963; Myrberg, 1978). Data from Nelson and Johnson (1970, 1972) and Myrberg *et al.* (1969, 1972, 1975a, b, 1976) show that over 20 species of both shallow- and deep-water carnivorous sharks are attracted to natural and artificially created sounds under field conditions. The authors noted that the qualities of 'attractive' sound include elements from the low-frequency range (below 1000 Hz with the optimum at 60 Hz or below) and repetitive, irregular pulsing. Duration of individual pulses (Nelson and Johnson, 1972) and signal strength (Myrberg *et al.*, 1972) do not appear to be critical components for attraction.

Response to sound usually drops off when the signal strength is 15–25 dB above the ambient noise level. In order to attract sufficient numbers of sharks, field studies used loud sounds (37–55 dB) that carried long distances before dropping below ambient noise levels. Under natural conditions, owing to attenuation and the low level of the initial signal, sharks probably detect biological sounds less than 100 m from the source (Myrberg, 1978).

An interesting spectrum of behaviours has been noted in response to an acoustic attractant. Aggressive behaviours such as agonistic displays, attack and even consumption of the sound apparatus have been observed by Myrberg and Gruber (1974), Nelson and Johnson (1972), and Myrberg *et al.* (1969). On the opposite side of the spectrum, Banner (1972) observed that certain sounds caused immediate departure in young lemon sharks. Myrberg (1978) invoked a similar retreat behaviour in adult silky sharks. Called a 'startle response', rapid flight behaviour is elicited by a single loud tone (well above established threshold levels) or a pulsed tone with long intervals (several seconds). A sudden increase in volume (15–20 dB) as the subject closed on the source also triggered the startle response. The same sound stimuli, however, produced mixed results in oceanic whitetip sharks, suggesting species variability in this regard.

Tactile receptors are sparsely distributed on the body, but there are areas of heightened sensitivity around the head, jaws and fins. Several authors have reported that sharks will bump possible prey with their snouts prior to feeding (Springer, 1960; Randall and Helfman, 1973; Moss, 1981). This behaviour may enable sharks to assess prey texture by means of sensory nerve endings (Roberts, 1978).

The receptors of the lateral line system are sensitive to water displacements. Hair cell sensitivity is acute (Roberts, 1978). Using this input, sharks can orientate to a disturbance in three dimensions and follow the vibrations to their source. As sharks swim, this 'mechanical sense' provides information about the location of moving and stationary objects around them (Hueter, 1991). Roberts (1978) predicted that the lateral line system should play a major role in locating prey, predator avoidance and social encounters, but the complete role of the lateral line in determining behavioural responses is, as yet, unclear.

Electroreception

The shark has a unique and highly specialized bioelectrical sensory system called the ampullae of Lorenzini. Pores to the receptors form dispersed patterns on the head and snout. Kalmijn (1966) showed that this sensory system is capable of detecting the presence and location of weak electric fields. It allows the shark to locate prey even though the prey may seem to be invisible. Thus, sharks can overcome the camouflage and burying techniques that certain animals employ for defence, by sensing the electric fields that they produce.

At close range, the movements of the muscles and gills of an aquatic animal produce d.c. and low-frequency voltage gradients in water. Sharks are most responsive to d.c. frequencies below 8 Hz. They can detect frequencies as low as 0.1 Hz (Murray, 1962) and only a few microvolts in amplitude. Blue and dogfish sharks can detect fields as weak as 0.005 $\mu V\ cm^{-1}$, twice the sensitivity required to locate prey fishes (Kalmijn, 1982).

Kalmijn (1978, 1971) demonstrated the ability of the smooth dogfish, leopard, lemon, and catsharks to locate buried prey in the absence of visual, mechanical, and chemical cues. Buried flounder or plaice were confined in an agar chamber, which concealed them, yet allowed electrical current to flow through. On all occasions, the sharks were able to home directly in on these concealed prey items. When prey were enclosed in an electrically insulating polyethylene film, the sharks were unable to detect them. When the experiments were repeated using electrodes to simulate the flounder's bioelectric field, sharks repeatedly attacked the buried electrodes. The sharks displayed the same feeding behaviour in response to the electrodes as they did to actual prey. In fact, the sharks often ignored a piece of bait fish on the substrate to dig at the buried electrodes. Kalmijn concluded from these observations that the electric fields provided a much stronger feeding stimulus than the sight or odour of the bait.

In experiments with dogfish and blue sharks (Kalmijn, 1982), both attacked electrodes with current running through them in preference to control electrodes or an odour source. Blue sharks directed 31 of 40 bites (78%) toward the prey-simulating electrodes. Tricas and McCosker (1984) reported that white sharks chose bait emitting a pulsed electric field three times as often as bait with control electrodes attached. Static fields were not similarly attractive (only 44% of strikes). Although the sample size was small ($n = 17$), it indicates a possible role of electroreception in the predatory behaviour of this species.

Scharold (1989) noted that in lemon, blue and leopard sharks, no electrical signals could be detected from heart activity unless electrodes were placed directly in the pericardium. She suggested that the pericardium electrically insulates the heart, and prevents receipt of distracting signals by the shark's electroreceptors, thereby facilitating detection of bioelectric signals from prey. Scharold also hypothesized that the steep gliding descents employed by blue sharks when hunting were a behavioural adaptation for reducing muscle activity, again minimizing interference with electrosensory receptors.

Seasonal migrations play an important role in the life histories of many species. McLaughlin and O'Gower (1971) observed that the Port Jackson shark can return with pinpoint accuracy to specific reef locations after absences of several years and travelling distances of hundreds of kilometres. The ampullae of Lorenzini may be the cornerstone of a 'compass sense' that enables sharks to navigate relative to ocean currents and the Earth's magnetic field (Kalmijn, 1977). Although results are as yet inconclusive, tests with the leopard shark suggest that geomagnetic orientation may play a role in long-distance migration and homing (Kalmijn, 1978).

Kalmijn (1978) suggested that attacks on underwater equipment may be elicited by electric fields resembling those of regular prey. Although amusing to contemplate, these 'malfunctions' may be expensive and inconvenient to correct. Damage to sonar arrays has been attributed (by bite patterns) to the cookie-cutter shark (Johnson, 1978). Several attacks on submerged fibre-optic telecommunication cables in the Canary Islands in 1985 have been traced (by embedded teeth) not only to deep-water species such as the goblin shark and crocodile shark but also to shallow-water carcharhinids (Wallerstein *et al.*, 1988). In the latter case, the problem was corrected by designing a 'biteproof' cable. Tests showed that resisting the bite pressure of a shark required sheathing the cable in a double layer of helical steel tape coated with a polyethylene shell.

Olfaction

Sharks have a keen sense of smell. Johnson and Teeter (1985) examined the ability of bonnethead sharks to orientate towards food by means of chemical cues. Using a direct stimulus system (blue crab homogenate was delivered through head-mounted tubes inserted into the nostrils), they showed that bonnetheads were capable of tropotaxis (comparison of concentration at paired receptors) and klinotaxis (comparisons over time). Sharks were able to maintain their orientation course even after the odour trail was disrupted. Observed behaviour was highly stereotyped, in that once triggered, the behaviour was the same whether the initiating stimulus was small and brief or large and persistent.

Interacting with other factors, such as water quality, rate and direction of flow, and light intensity, olfaction plays an important role in predatory behaviour (Kleerekoper, 1978). Following the odour of a bait up current, sharks swim in an S-shaped pattern, homing in on the area of strongest concentration of odour (Hodgson and Mathewson, 1971). Hobson (1963) and Tester (1963) carried out experiments with several species of sharks, including blacktip reef sharks, grey reef sharks, scalloped hammerheads, tiger sharks, and whitetip reef sharks. Hobson spent hours 'hiding' wounded prey fishes in holes and caverns and watching whitetip sharks unerringly track them down. Both Hobson and Tester observed behavioural responses to tissue extracts, and to water in which "agitated" but undamaged fishes had been held. Both Hobson and Tester concluded that sharks can detect prey based only on olfactory cues as a normal component of predatory behaviour, and that these cues may be the most important factor in detection of prey at a distance. The importance of olfactory cues in prey location has also been established in the Port Jackson shark (McLaughlin and O'Gower, 1971).

Neural integration

The variation in brain size in sharks (ratio of brain volume to body weight) is comparable to that found in other groups of vertebrates. In general, sharks possess large brains, comparable in relative size to those of birds and mammals (Northcutt, 1978). Recent research suggests that there is considerable overlap and integration of sensory information in various brain centres. The tectum of the mesencephalon (an important visual centre in sharks) also appears to function in mediation of electrosensory orientation and motor functions, and may be involved in behavioural responses to novel or threatening visual stimuli (Bodznick, 1991).

Field and laboratory observations of sharks suggest that detection of prey and performance of various social behaviours depend on the simultaneous integration of several types of sensory information. Northcutt (1977) has shown that the development of the major divisions of the elasmobranch brain is similar to that in birds and mammals. If this indicates comparable neural capacities, one would expect sharks to exhibit complex behaviours analogous to those already identified in other large-brained vertebrates. Many examples of complex behaviours (such as dominance hierarchies and adaptive learning) have been observed in various shark species.

Behavioural advantages of endothermy

Several species of lamniform sharks maintain a body temperature which may be up to 6.5–10°C above that of the surrounding water. These include the mako, porbeagle, and white shark (Carey *et al.*, 1982; McCosker, 1987). A well-developed system of retia mirabilia, which act as countercurrent heat exchangers, is the cornerstone of an effective system for heat conservation. It is believed that this elevated body temperature results in more efficient muscle contraction and digestion, which results in increased energy for swimming. McCosker (1987) has noted that white sharks feed on swift, endothermic prey which require accelerated pursuit through rapidly changing water temperatures. He suggested that the evolutionary development of endothermy in the lamnid sharks may be an adaptive response to these requirements.

Distribution and migration patterns

Most shark species studied to date have been found to migrate seasonally. Travel distances for several shark species have been obtained from the Cooperative Shark Tagging Program of the United States. Currently this programme has tagged and recaptured more than 3200 sharks, representing 32 species (Casey and Kohler, 1991). Additional information has been obtained from radio telemetry, fishery records and direct observation. The distances travelled by pelagic and even coastal pelagic species are impressive (Fig. 2). Even relatively small coastal species may undertake long journeys. Although less than 1 m in length, Port Jackson sharks may travel over 850 km in their seasonal migrations (O'Gower and Nash, 1978). Schools of hammerheads have been noted moving south in the Gulf Stream off the coast of Florida (Jennings, 1985). The function of these schools is unknown. They may represent localized population movements. Ainley *et al.*, (1985) found that seasonal abundance of the white shark off the California coast was directly correlated with availability of seals, a preferred prey. Basking sharks disappear from their usual range during certain seasons of the year (winter in the Atlantic Ocean and summer in the Pacific). No information is available on their activities and location during these periods.

Many species make extensive vertical migrations occasionally or on a diel basis. Clark and Kristof (1990) reported a new depth record for tiger sharks. A female was filmed by their deep submersible at a depth of over 300 m. The horn shark, often thought of as a shallow-water species, has been caught at depths of over 150 m; it appears that this

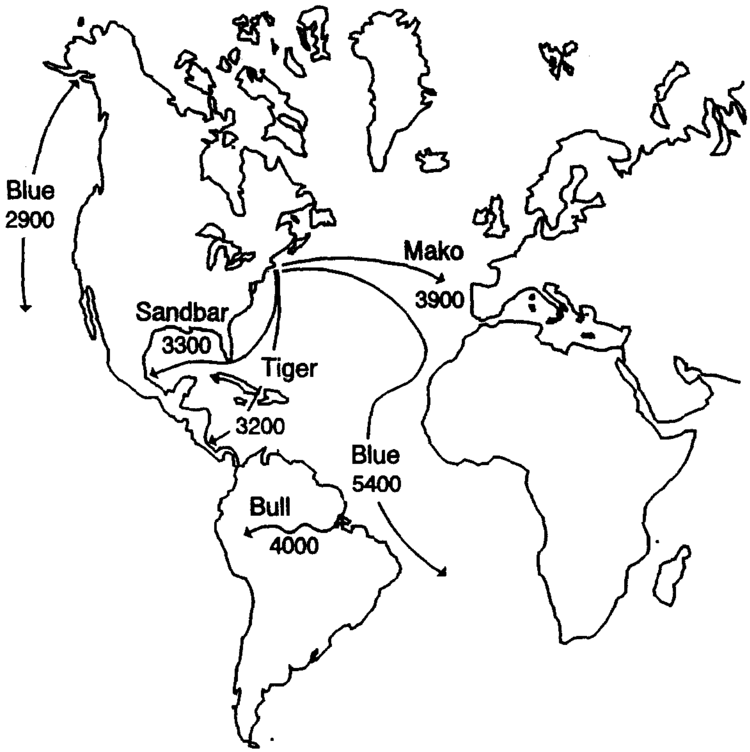

Fig.2. Tag returns in the Atlantic Ocean show movements for various species ranging from over 3000 to 5400 km. Migration distances not attributed to specific authors represent rounded averages of tag-and-recapture data (NMFS Cooperative Shark Tagging Program, 1962–1982). Blue sharks in the Pacific undergo seasonal migrations from 20°N to 57°N (Strasburg, 1958; Neave and Hanavan, 1960), more than 2800 km. Bull sharks, the only shark known to habitually frequent salt, brackish, and fresh water, have been captured in the Amazon River over 4000 km from the Atlantic Ocean (Thorson, 1972).

species may change depths seasonally (Dempster and Herald, 1961). Cookie-cutter sharks may perform vertical migrations of 2000–3000 m in each direction, on a daily basis (LeBoeuf *et al.*, 1987).

Patterns of activity and space utilization

Information about the daily movements and activity patterns of some sharks has only been obtained in the last few years. Field observations are complicated by the logistical and visual difficulties of working in an aquatic environment. Fishery statistics and tag recoveries provide information, but only on long-term movements. As an additional complication, Springer (1963) suggested that vertical movements (possibly following temperature gradients) are common. In many species, movements will probably have to be described in three-dimensional space. However, with advances in acoustic telemetry, even small transmitters can carry sophisticated sensors enabling researchers to gather information on movement patterns and locate the shark for direct observations.

Morrissey (1991) reported on the movements of young (< 75 cm in length) lemon sharks in the Bahamas. Specimens were induced to swallow ultrasonic transmitters, allowing Morrissey to track them for up to 39 days in order to develop an outline of their daily activity patterns. He discovered that the sharks inhabited restricted home ranges (about 0.7 km^2) in protected nursery areas. Gruber *et al.* (1988) found that Bimini Lagoon was divided into habitat zones utilized by different lemon shark age groups. The young remained in shallow coastal waters for up to 4 years. The home range enlarged proportionally as age increased and shifted progressively farther off shore. No evidence of aggressive territoriality was found, but the sharks remained in their home region. Tagged sharks were recaptured in the same area even after 3 years had elapsed. Similar behaviour has been reported for young nurse sharks by Carrier (1991). In tag-and-recapture studies in the Florida Keys, Carrier noted that most were recaptured in the same area as originally tagged, even after as long as 3 years. Ultrasonic tracking revealed that daily movements were minimal. Carrier cites a case in which one animal, tracked for 96 consecutive hours, moved less than 0.6 km. As with lemon sharks, however, home range increased with age, and may be related to the onset of sexual maturity.

An unusual migratory pattern between fresh and salt water is seen in bull sharks. Bull sharks have been identified in bodies of fresh water around the world, including Lake Nicaragua in South America, the Mississippi River and Chesapeake Bay in North America, the Ganges River in India, and the Gambia River in West Africa. The large number of tagged specimens recovered (Thorson, 1971, 1972; Montoya and Thorson, 1982) clearly demonstrates that movement into rivers and lakes is a normal component of their life history. Many female bull sharks ascend rivers to give birth. The young sharks may remain in the rivers, relatively free from predation, for several years.

Information concerning shark movements and diel patterns is obtained by electronic tracking of individuals. Carey *et al.* (1982) observed no obvious diel activity patterns in a white shark which was tracked for 3.5 days by acoustic telemetry. Most other species studied so far, however, have shown some diel periodicity. Tricas *et al* (1981) observed a diel activity pattern in a single tiger shark tracked for 48 h in the Hawaiian Islands. Both diurnal and nocturnal activity was noted with some suggestion of an established home range. Specific home ranges (about 1.3 km^2) have also been identified for the Pacific angel shark by Standora and Nelson (1977). They found that angel sharks were primarily nocturnal, moving offshore to feed at night. Nelson and Johnson (1970) demonstrated in the laboratory that both the horn shark and the swell shark were noctural. This has also been confirmed for blue sharks by Sciarotta and Nelson (1977). Blue sharks make diurnal seasonal migrations into shallow water, possibly following the distribution and abundance of squid populations (Sciarotta and Nelson, 1977). Scharold (1989) found that their daily pattern of vertical migrations spanned depths up to 450 m. The deepest dives occurred during the day, and shallower dives at night. The pattern of diving (active downward swimming accompanied by steep gliding descents) led Scharold to conclude that these dives were for the purpose of feeding.

Gruber *et al.* (1988) concluded that lemon sharks are crepuscular, with activity peaks in the morning and evening. However, no diel periodicity has been observed in feeding behaviour (Cortes and Gruber, 1990). At odds with this conclusion is the finding by Nixon and Gruber (1988) that both activity level and metabolic rate (as measured under laboratory conditions) increase significantly at night, with indications that this cyclicity is controlled by an endogenous circadian rhythm.

McKibben and Nelson (1986) examined the diel activity patterns of grey reef sharks over a 4 year period at Enewetak in the Marshall Islands. They discovered that some sharks returned to a home range area on a daily basis while others were 'nomadic' and roamed the reef margins. The nomadic individuals showed a repetitive pattern of movement along the reef (up to several kilometres per move) alternated with several stationary days in a new location. In both home-ranging and nomadic individuals, peak activity periods occurred at night, and McKibben and Nelson speculated that feeding took place at that time. Grey reef sharks at Rangiroa in French Polynesia were also found by Nelson and Johnson (1980) and Johnson (1978) to have similar, predictable daily movement patterns. Klimley *et al.* (1988) found a well-defined diel periodicity to activity levels of scalloped hammerhead sharks, which gathered around a seamount in the Gulf of California: the days were spent in a relatively inactive state in a restricted area along the seamount ridge; in the evening, the animals dispersed over an extensive area to feed.

Population structure and social interactions

Most species of sharks form groups that are segregated by size and sex, as noted by Galvan-Magana and Nienhuis, 1989), Gruber *et al.* (1988), Klimley (1985) and Stevens (1984). Even juvenile sharks tend to segregate by sex. Such segregation has been cited by Snelson *et al.* (1984) in bull sharks, by Bass (1978) in dusky sharks, by McLaughlin and O'Gower (1971) in Port Jackson sharks, by Bullis (1967) in marbled catsharks, and by Ripley (1946) in school sharks. Separation by depth distribution is most common in small species, whereas larger species may be geographically isolated (Bass, 1978). Klimley (1987) suggested that sexual segregation in the scalloped hammerhead shark is an adaptive behaviour resulting in females attaining a larger body size at maturity (frequenting areas of more abundant prey), thus maximizing reproductive capacity. This pattern is echoed in several other species that form segregated schools.

Schooling behaviour has been observed in several species. Springer (1967) reported large 'social groups' of sandbar sharks, silky sharks, great hammerheads, tiger sharks, spinner sharks, and blacktip reef sharks. Gruber *et al.* (1988) observed several examples of schooling and social interactions in lemon sharks, similar to patterns reported by Myrberg and Gruber (1974). No interspecific aggression was observed. In addition to species-specific groupings, lemon sharks also formed what may be mutualistic associations with large teleost fishes such as jacks (*Caranx* spp., Carangidae).

Large polarized schools of scalloped hammerheads can be found congregating around seamounts in the Gulf of California. Individual sharks are extremely site specific. Tagged sharks returned only to that seamount at which they were tagged, distinguished (perhaps by environmental cues) from similar sites only a short distance away (Klimley, 1988). Klimley and Nelson (1981) defined the parameters of one such group after tracking individual movements with ultrasonic telemetry. There was a well-defined diel periodicity to activity levels, with days spent in a relatively inactive state in a restricted area along the seamount ridge. In the evening, the animals dispersed over an extensive area, returning to the seamount the next morning. No feeding was observed during the day at the seamount, even when large schools of prey fish were present. It was later demonstrated that these nightly excursions were for the purpose of foraging (Klimley, 1988). The sharks did not take bait or respond to attractant sounds during the day (Klimley and Nelson, 1984). Klimley and Nelson noted that this observed behaviour was similar to that described by Hamilton and Watt (1970) as a refuging system. The refuging system is defined as a large social grouping centred on a geographically restricted core area during the inactive phase of the diel cycle. Individuals disperse to forage during their main activity period. Klimley and Nelson concluded that this refuging behaviour serves an adaptive function in the scalloped hammerhead, either to optimize energy output or to facilitate social interactions.

Refuging behaviour has also been observed in the grey reef shark by McKibben and Nelson (1986) and Nelson and Johnson (1980). Diurnal behaviour was characterized by low activity groupings (both polarized schools and loose aggregations were present) in a restricted area of their home range. The sharks dispersed at dusk, presumably to forage. Whitetip reef sharks frequently form small, inactive groups during the day in caves and disperse in the evening to feed. Nelson and Johnson (1980) observed that the same individuals returned to the same caves several days in succession. Similar behaviour was observed by McLaughlin and O'Gower (1971) in their study on the Port Jackson shark. Small groups refuged during the day in caves and dispersed at night, again presumably to feed on benthic invertebrates.

The first direct evidence of social organization in sharks was reported by Allee and Dickinson (1954) for members of a captive colony of smooth dogfish. They noted that smaller individuals within the colony definitely avoided larger ones if the difference in body length exceeded 7.4%. Sex did not appear to play a role in formation of dominance hierarchies, which were formed only on the basis of size. Allee and Dickinson found no evidence of territoriality, interspecific competition, or aggression during their study, even during group feeding in a restricted space. Springer (1967), based on his observations that "small sharks actively avoid larger sharks", concluded that the basis of segregation by size in migrating schools was probably individual choice. Since that time, evidence of a dominance hierarchy based on size and/or sex has been discovered in several species, including bull sharks and sandbar sharks (Weihs *et al.*, 1981), bonnethead sharks (Myrberg and Gruber, 1974), lemon sharks (Clark, 1963), and Galapagos sharks (Limbaugh, 1963). Myrberg (1991) suggested that distinctive body markings on various shark species are visual signals which play a role in the maintenance of size-dependent dominance hierarchies. The markings could enable a shark to rapidly estimate the size of an approaching conspecific, and also to recognize members of other sympatric species as not subject to species-specific dominance constraints.

Myrberg and Gruber (1974) observed 17 distinctive movement patterns in a study of captive bonnethead sharks enclosed in a large mixed-species pool. They were able to document several of these behaviours which were important in determining the social organization and a size-based dominance hierarchy. Sex was also important in determining dominance, with males being subordinate to females. A primary component was the 'give way' behaviour in which a smaller shark would alter its course out of the path of the larger. They also remarked on the relative lack of interspecific aggression over a six-month period. Although infrequent agonistic encounters occurred, most instances involved responses to individuals newly introduced to the group.

Seligson and Weber (1990) observed captive sharks in a very large mixed species enclosure (21.5×10^6 l). The sharks had definite patterns of space utilization, frequenting only limited sections of the enclosure. Although the introduction of new individuals crowded some tank residents (a large bull and tiger shark) out of their preferred activity space, no aggressive behaviours were seen toward newly added group members.

Agonistic encounters, while unusual, do occur. Johnson and Nelson (1973) described a 'hunching' posture that was part of a series of stereotyped movements that consistently preceded an aggressive attack. Myrberg and Gruber (1974) noted the same hunched posture in captive bonnetheads and blacknose sharks, not only in response to divers, but also in response to newly introduced conspecifics. They postulated that these behaviours were homologous in the various species, considering the similarities in motor patterns and the similar types of situations which evoke this response.

Foraging behaviour and diet selection

Dill (1983), in a review of fish foraging behaviour, concluded that fishes, living in a generally variable environment, showed foraging behaviour characterized by 'adaptive flexibility'. Citing examples from the literature, he showed that fish possess the behavioural repertoire to adjust their diet choices in response to alterations in prey abundance, increased time budget constraints (such as the need for territorial defence), risk of predation, or increased predation efficiency (as a learned response to increased exposure to a prey). He considered learning to be the underlying mechanism for adaptive behavioural responses. The level of development of the shark brain implies that sharks ought to be capable of the types of foraging decisions predicted by Dill.

Griffiths (1975) first proposed a model of optimal foraging based upon net energy of a food, weighted according to its abundance. He recognized two different categories of foragers: number maximizers, which feed indiscriminately on all prey encountered, and energy maximizers, which rank prey according to the ratio of energy content to handling time. Energy maximization is a potential goal since selection of larger or more energetic prey could give an increased potential for growth. An animal would maximize its chance of survival by keeping its energy reserves as far as possible above the maintenance level. Larger fish have an increased foraging efficiency (Gerritsen, 1984). In addition, age at maturity is often size dependent. Faster growth leads to maturity at an earlier age. This model predicts that animals would select prey items that provide the highest energy return per unit effort.

Number maximization is also a potential goal. Bres (1986, 1989), Anderson (1984) and Stein *et al.* (1984) all found that models of optimal foraging frequently underestimate a fish's potential energy gain as a generalist (number-maximizing) feeder. Therefore, the energy penalties of utilizing a number maximization strategy may not be sufficient to force development of the capabilities required to make more complex foraging decisions. The number maximization model predicts that as a prey item increases in its relative abundance, it should increase in the diet. Tests of optimal foraging in lemon sharks did not support the use of an energy maximization strategy for this species (Wetherbee *et al.*, 1990). Diet choices did, however, match the predictions for a number maximization strategy. Observations demonstrating the importance of prey relative abundance in shark diets have been made for several other species (Table 2).

Glasser (1984) suggested that consumers might become facultative strategists. Facultative strategists would excel in unpredictable environments, in which the cost of this behavioural flexibility is offset by the energy rewards of successful foraging. Optimal foraging theory predicts switches in prey preference when predation efficiency increases significantly. One type of learned behaviour that would decrease recognition time is search image formation. Decreased recognition time can be an evolutionary adaptation which will enable a predator to specialize on certain types of prey, thus maximizing energy intake (Krebs, 1981).

Table 2. Number maximization in shark diets. In these studies, shark diet composition reflected the relative abundance of prey species. Shifts in prey selection may be due to seasonal changes in prey abundance or availability.

Species	Reference
Blue	LeBrasseur (1964), Tricas (1979) and Harvey (1979, 1989)
Leopard	Talent (1976)
Mako	Stillwell and Kohler (1982)
Kitefin	Matallanas (1982)
Lesser spotted dogfish	Lyle (1983)
Scalloped hammerhead	Clark (1971)

There are several reports of prey specialization in sharks, especially in captivity (Van de Elst *et al.*, 1983; Crow and Hewitt, 1988). Additional research demonstrates that some free-ranging sharks are selective feeders and have preferences for specific prey. Some sharks may even employ energy maximization strategies, such as optimal foraging. Stillwell and Kohler (1982) reported that large increases in relative abundance of squid (*Illex illecebrosus* and *Loligo pealei*) were not reflected in mako shark diets. Bluefish constituted 85% of the total stomach volume and occurred in 65% of the stomachs sampled. Stillwell and Kohler suggested that mako sharks may selectively feed on the larger prey (bluefish) as an energy maximization strategy, because they assumed the energy expended in capture to be the same for squid and bluefish. Tricas and McCosker (1984) proposed an energy maximization strategy for white sharks as a possible adaptation for feeding at infrequent intervals (correlated with regional or long-distance movements). Small white sharks feed primarily on fishes, whereas larger sharks shift their diets and feed primarily on cetaceans and pinnipeds. Marine mammals have a higher fat content than fish and thus are a higher-energy prey. The shift in diet may also be related to morphological differences in tooth shape: young sharks have narrow, grasping teeth suitable for impaling fish; older sharks have triangular, slicing teeth ideal for biting chunks out of large prey.

Scharold (1989) suggested two divergent optimality strategies for mako and blue sharks, both continuously swimming, pelagic species. The mako shark swims at higher speeds, with a relatively large energy expenditure, and covers a wide geographic area in which it is more likely to encounter potential prey, thus maximizing energy intake. The blue shark utilizes low-speed cruising and vertical diving to locate prey, a strategy of energy minimization. Both blue and mako sharks are reported to make frequent steep descents (up to several hundred metres) in search of prey (Carey and Scharold, 1990).

Most species feed primarily on other fishes (up to 90% of their diets) and secondarily on various invertebrates, such as squid (Moss, 1981; Wetherbee *et al.*, 1990). Benthic sharks feed mainly on fishes, molluscs, and crustaceans, and a few species, such as the whale shark and the basking shark, filter feed on planktonic organisms. Feeding may vary seasonally or annually, such as that of the school shark, which is tied to a seasonal migration and reproductive cycle (Peres and Vooren, 1991).

Some species are nocturnal feeders, others crepuscular. Some, like the lemon shark (Gruber *et al.*, 1988), appear to have no preferred feeding time. For many species, even this elementary information is lacking. Myrberg (1991) suggested that conspicuous fin markings on the oceanic whitetip shark may be adaptations for prey capture. The markings may function as 'bait' because, when observed from a distance, they resemble a school of small prey fish. This would attract larger predatory fishes (the prey of the whitetip shark) to its immediate vicinity, where they can be captured by the whitetip with a brief burst of high-speed acceleration. Use of fishing lures has also been suggested by Castro (1983) for the Greenland shark, as an explanation of how such a slow-moving animal can capture its agile prey. The potential lures are luminescent copepods that attach themselves to the shark's cornea.

There have been few accounts of natural feeding behaviour in the field. Evidence of cooperative feeding has been noted in several studies, among them Morrissey (1991) with young lemon sharks, and Eibl-Eibesfeldt and Hass (1959) with blacktip reef sharks. Several individuals would herd a school of small fishes toward the shore, providing food for all. Feeding patterns may also be inferred from analysis of stomach contents. For example, the white shark feeds on both surface and benthic prey found in shallow, inshore waters (Klimley, 1984). This is more likely to bring the shark into contact with scuba divers and bathers.

Strong *et al.* (1990) described an attack sequence of a great hammerhead shark on a southern stingray (*Dasyatis americana*, Dasyatidae). The shark pursued the ray and subdued it by several heavy blows with its head on the dorsal surface of the ray (Fig. 3). The shark took several bites while continuing to hold the ray down with its head. Because

Fig.3. An attack by a great hammerhead shark on a southern stingray. The shark pursued the ray and subdued it by several heavy blows with its head on the ray's dorsal surface. (After Strong *et al.*, 1990.)

skates and rays appear to be preferred prey items for hammerhead sharks (Compagno, 1984), Strong *et al.* concluded that this use of a uniquely shaped head is an excellent example of feeding specialization optimized by adaptive biomechanical design.

In some cases, predatory behaviours have a clearly definable, stereotyped sequence. Tricas (1985) observed that, in the white shark, prey attack at the water's surface took place in a predictable series of actions which never varied in sequence, and only slightly in timing of component actions. McCosker (1985) reported that filming of attack behaviour revealed that the white shark's eyes close before a strike. The shark may rely on its electromagnetic sensing capability for final prey location (Tricas and McCosker, 1984). McCosker (1985) also noted an attack and retreat pattern which he described as "bite and spit" behaviour, in which the shark takes an initial bite, then retreats a short distance until the victim stops struggling. Engana and McCosker (1984) suggest that the higher mortality rate from white shark attack in Chile (where two of three attacks result in fatalities) compared to California (where death occurs in only five of 40 cases) is directly related to the 'bite and spit' behaviour. In contrast to solitary Chilean divers, California divers usually have companions, who rescue them during the five to ten minute 'wait period' before the attack resumes.

Courtship and mating behaviour

Courtship and mating activities have been observed for few species of sharks, and most of these observations have occurred in captivity. For example, in the chain dogfish, mating has been observed only once in 10 years of study (Castro *et al.*, 1988). In most species in which mating behaviour has been observed, the male bites and often holds the female. This has been reported in the epaulette shark by West and Carter (1990), the reef whitetip by Uchida *et al.* (1990), the chain dogfish by Castro *et al.* (1988), horn sharks by Dempster and Herald (1961), and nurse sharks by Klimley (1980). The behaviour has been inferred in more species by scarring patterns commonly found on the female's body. These bites most commonly occur on the fins, tail, or in the gill region. Wourms (1977) suggested that biting may act as a releaser that triggers mating acceptance in the female.

Johnson and Nelson (1978) reported pre-copulatory behaviour in the blacktip reef shark and the reef whitetip shark. The behaviour was distinguished by males following very closely behind females, with snouts less than 30 cm from the lead shark's tail. The females held their tails up in a curiously erect posture. Johnson and Nelson hypothesized olfaction-mediated recognition and pairing, since in some cases the males were able to intercept females when visual, sound, and vibrational cues were absent. Following behaviour as an expression of sexual interest has also been observed in the nurse shark (Klimley, 1980) and the bonnethead shark (Myrberg and Gruber, 1974). Female pheromones may be produced which trigger sexual behaviour in males (Demski, 1990a). This close following behaviour, however, has also been observed in the bonnethead and grey reef sharks in non-copulatory situations, and may have additional social implications in other contexts.

In those groups that form schools, population density may play an important role in reproduction (Demski, 1990b). It has been observed in birds and mammals that the sight and sound of a 'critical mass' of individuals is necessary to trigger mating behaviour. Klimley (1987) suggested that, in scalloped hammerhead sharks, the position of females within the school may have implications for mating success. Visual and chemical cues may also be important for mate selection within a group. Results of studies to date emphasize the complexity and variety of shark reproductive behaviours (Demski, 1990a). Several zoos and aquaria are initiating captive breeding programmes and more information on this subject may soon be forthcoming.

Captive behaviour and operant conditioning

Laboratory studies on operant conditioning, combined with information on behaviour observed in the field, gives us an outline of the potential of shark intelligence. Northcutt (1978) outlined several criteria by which we can assess whether learning plays an important role in elasmobranch life history. He suggested that sharks would relate learning to their environment in a significant way if they learn to recognize one another in a social context, learn to identify and respond to potential predators, learn to maximize their use of environmental resources, and learn migratory routes.

Evidence is accumulating that sharks have the ability to relate learning situations to their environment. Substantial evidence exists that sharks can modify their behaviour in response to specific environmental stimuli (Graeber, 1978; Beulig, 1982). They acquire and retain a variety of learned tasks as well as most mammals. The observation that juvenile members of most species are more 'curious', less cautious, and more unpredictable than adults implies learning by experience (Myrberg 1978, 1991).

Establishment of dominance hierarchies indicates that individuals do learn to recognize one another in social contexts. Aggressive displays toward divers and submersibles and, alternatively, habituation to divers (Nelson, 1977) and to attractant acoustic signals, indicate that sharks learn to recognize potential predators and ignore negligible threats. Diel and seasonal movement patterns for feeding and reproduction establish that they are able to identify and locate seasonally limited resources. Information is too sketchy to determine what portion of orientation and navigational behaviour is learned and what is innate; however, most sharks increase their home range and travel distances as they age, so there is some evidence for the role of learning in this behaviour.

Several studies of simple learned behaviours have been carried out with sharks. Classical conditioning experiments were used by Gruber and Schneiderman (1975) to determine whether lemon sharks could detect various types of visual stimuli. The sharks were trained to produce a nictitating membrane response (eye blinking) in response to a light flash. This study and others demonstrate that the shark's learning ability is comparable to that of birds, mammals, and teleosts.

Clark (1963) observed that sharks in captivity are easily trained to go to a specific feeding location, even in the absence of olfactory cues. She designed a series of experiments with a group of lemon and nurse sharks to determine their ability to acquire conditioned behaviours using visual and audible cues. She demonstrated that lemon sharks were easily conditioned to associate target-pushing (which rang a bell) with the delivery of food. Once acquired, there was a long retention period for this behaviour. Even after a lapse of 10 weeks, sharks quickly pressed the target (Clark, 1959). There was some evidence that they learned to associate the ringing of a bell with food delivery as well. Sharks that were not being tested would quickly dart to the food source when the bell rang, sometimes succeeding in stealing the food from the test subject.

Several other interesting observations were made in the course of this study. Once they had learned it, the sharks seemed to incorporate the target pushing behaviour as a fixed component of their feeding routine. Even when food was already in the water, sharks touched the target before feeding. Second was an indication of a play element in the learned behaviour. Sharks, when well fed, would touch the target but make no effort to retrieve the food.

In Clark's experiments, nurse sharks did not learn to make the association between the target and food delivery. Aronson *et al.* (1967) carried out some similar experiments with nurse sharks, but in this case, the sharks were tested individually. Aronson *et al.* demonstrated that nurse sharks are capable of using both visual and tactile cues to locate a target, and the individuals were easily trained to strike the target to obtain food. Learning was rapid, comparable to the time required for mammals and teleost fish to learn the same behaviours. The sharks were also able to discriminate between light and dark to select the appropriate target for a food reward.

McManus *et al.* (1984) conditioned two juvenile nurse sharks to search for and touch a target (Fig. 4) and to retrieve a ring to obtain a food reward. They noted that subsequent training proceeded more quickly, since the sharks had already mastered the 'art' of learning. The response behaviour was retained after a 6 month hiatus. Bronstad and coworkers (unpublished data) at the Pacific Rim Center for Elasmobranch Studies trained an immature sand tiger shark to touch a target with and without a simultaneous sound. Although conditioning was successful with only the visual stimulus, they found that the success rate was significantly greater with the addition of sound reinforcement. As with Clark (1959)

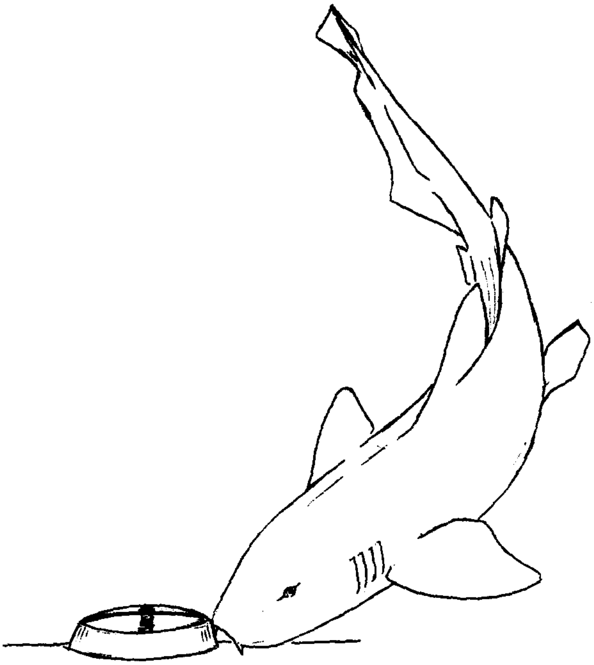

Fig.4. Operant conditioning of a young nurse shark. The shark presses the target to receive a food reward. (After McManus *et al.*, 1984.)

and McManus *et al.* (1984), the response to the target remained strong after a 5 week period.

Aggressive behaviours and interactions with man

Springer (1963) considered that populations of large migratory sharks are divided into the 'principal population', defined as the main breeding population, and the 'accessory population', which consists of a smaller number of solitary individuals that have become separated from the main group and are thus out of synchrony with the reproductive cycle. He speculated that although there are relatively few individuals in accessory populations, such sharks are frequently to be found in shallow, coastal waters, and are thus more likely to be involved in attacks on humans. In addition, Springer noted that the feeding habits of solitary individuals differ greatly from those of the main population, and that this may also be a contributory factor in shark attack on man. Baldridge (1988) suggested that size-specific segregation of local shark populations might also be a contributing factor in the risk of shark attack. Coastal areas may support populations of individuals that present a greater risk.

Although shark attacks have been reported from several families of large carnivorous sharks (such as Carcharhinidae, Sphyrnidae and Amnidae), only a few species comprise the majority of all attacks. These include the white shark, tiger shark, bull shark, and the great hammerhead (Gruber *et al.*, 1984). Most attacks on man may not be motivated by hunger, but instead are either defensive or offensive aggressive encounters. Even inoffensive species such as the nurse shark are known to attack when approached too closely, especially in a confined space (Limbaugh, 1963). Baldridge (1988) suggests that any species, given the proper attack motivation, is potentially dangerous to humans. These motivations include interference with reproductive behaviour, the appearance of the victim as a perceived threat, and trespass on a shark's territory or personal sphere. This suggestion is supported by the observations of Nelson *et al.* (1986), who found that aggressive advances by divers, especially when the shark's retreat was prevented by the reef structure, dramatically increased the probability of attack. Nelson *et al.* identified both foraging and non-foraging motivations for shark attack. The grey reef shark has been responsible for many attacks on divers and small submersibles. Nelson *et al.* (1986), Nelson (1981), and Johnson and Nelson (1973) noted that these attacks are always prefaced by a stereotyped threat posturing behaviour. Evidence suggests that the intensity of this behaviour is related to the degree of perceived threat on the part of the shark. Other observations reveal that display intensity is, in some cases, site related. Whether this is an expression of territoriality has yet to be demonstrated (Nelson, 1981). The other three species present in the reef area (whitetip, blacktip, and silvertip) responded to diver proximity and pursuit by flight. Only the grey reef sharks responded by attack. Clearly there is still much to learn about motivation for aggression in these large predators. Gruber (1988) suggests that the role of various environmental and motivational factors underlying attack is likely to be highly complex. However, determination of the trigger that initiates attack is necessary to develop effective anti-shark measures.

Records of shark encounters with bathers world-wide reveal several factors that appear to be associated with attack. Davies (1965) found a strong correlation between the incidence of shark attack and water temperatures in excess of 21°C off the coast of Natal, South Africa. In addition, he cited turbidity, proximity of deep channels, and number of swimmers as factors promoting attack. The white shark frequently attacks surface prey in a high-speed rush from behind or below (Ainley *et al.*, 1985). This may possibly lead to mistaken attacks on humans: a person floating on a surf board looks very similar to a seal or sea lion from beneath. The white shark is also known to attack boats and cause sufficient damage for the boats to sink. It is possible that, in these instances, corroded hull or motor parts produced electric fields which were misinterpreted as prey (Tricas and McCosker, 1984). The human body produces d.c. bioelectric fields that can be detected by sharks (Kalmijn, 1971). The Johnson shark screen, a large, heavy plastic bag with an attached flotation ring which is currently the most effective form of protection for victims of marine disasters, may provide concealment from three shark senses: vision, olfaction and electroreception.

Research on chemical repellents continues, not only to protect humans but also to prevent damage to towed hydrophone arrays, telecommunication cables, and other sensitive oceanographic equipment. Because of difficulties with captive maintenance of large sharks, species tested in the laboratory are seldom those that figure most prominently in attack incidents. Smith (1991) tested the effectiveness of chemical repellents in the laboratory with swell, horn, and leopard sharks. Gruber *et al.* (1984) and Gruber and Zlotkin (1982) tested the effectiveness of several repellents, including inexpensive synthetic surfactants. The chemicals were tested on young lemon sharks in the laboratory and blue sharks in the field.

Positive indications of repellent qualities (Gruber and Zlotkin, 1982; Gruber *et al.*, 1984) included cessation of feeding behaviour (in both laboratory and field situations), termination of tonic immobility induced in the laboratory (a condition in which inverted sharks remain in a trance-like state), and retreat from the general area where the chemical was released. Some chemicals were delivered directly to the oral cavity by means of an ingenious mechanism in which a plastic tube was inserted into the centre of a large bait fish. When the shark took the bait, a valve opened and the chemical flowed into the shark's mouth. In other trials, the chemicals were squirted directly at various locations around the head and gills. The third method of application was simple release of the chemical into the odour corridor of the bait. Effective chemicals include a variety of surfactants (such as sodium lauryl sulphate, a common ingredient of shampoos and detergents). Shark Chaser (cupric acetate) and rotenone were ineffective. Randall and Helfman (1973) report several incidents of attack by blacktip reef sharks (not usually considered aggressive or dangerous) on humans who were collecting fishes with rotenone. The chemical presented no deterrent to the sharks.

To date, direct application of repellent chemicals to sensitive head areas seems most effective in both field and laboratory situations. This method, of course, has limited applicability for victims of marine disasters or even for the average scuba diver.

Summary

Despite the recent upsurge of interest in shark research, the current status of knowledge of the behavioural repertoire of most species is alarmingly incomplete. Clearly, from the steadily decreasing numbers of sharks caught by commercial and sport fishermen, sharks are highly vulnerable to human exploitation. Although education is making inroads, there is still steady opposition to the enforcement of catch limits and management strategies for most species. Accurate life history and behavioural information is required to enforce management policies. Wetherbee *et al.* (1990) cited a case in which commercial fishermen accused the spiny dogfish of stripping the commercial and recreational fisheries of their herring and salmon catch. A detailed study of the spiny dogfish diet disproved their claims.

Sharks are clearly not mindless eating machines, as they have been labelled in the past. They are intelligent and have complex patterns of movement, space utilization, and social organization. Using a combination of remote and direct observational techniques, the scientific community is beginning to have a more complete understanding of these important apex predators in coral reef and oceanic ecosystems. More importantly, researchers who are interested in pursuing the fascinating field of shark behaviour still have a wide choice of direction.

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