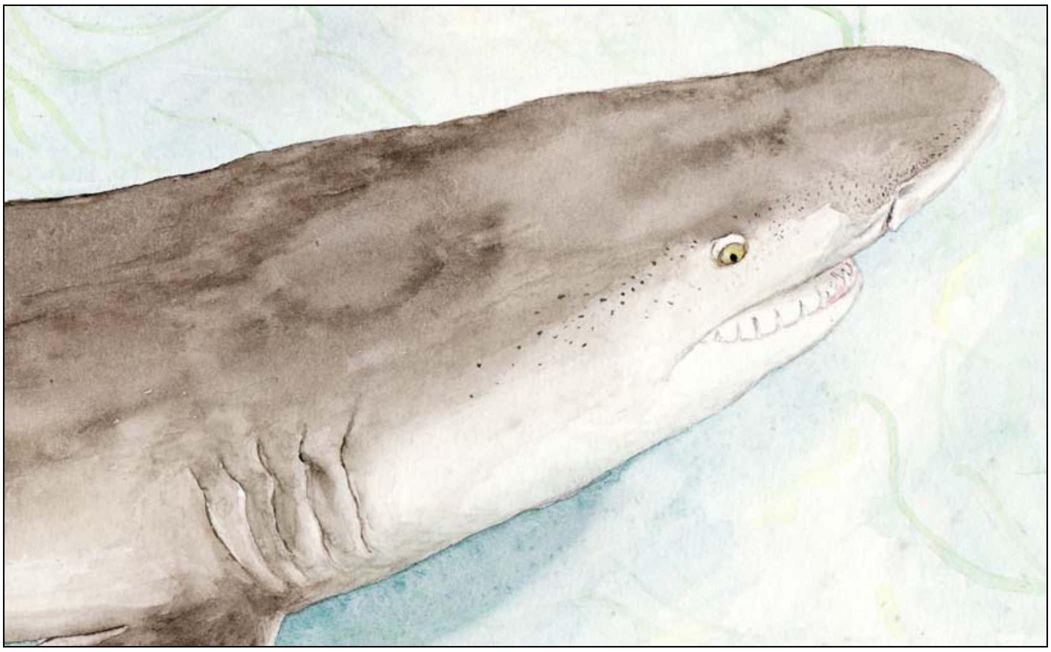
Movement pattern and space utilisation of sub-adult Lemon Sharks, *Negaprion brevirostris*, of Bimini, Bahamas



Master's Thesis in Marine Biology
by
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Simon Caviezel
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Abstract

Tracking projects of subadult Lemon Sharks (*Negaprion brevirostris*) have been made regularly in the Main Lagoon of Bimini Islands, Bahamas, over the last 25 years. This study tried to combine and show changes over time of four previous studies and current data. The focus was laid on 1) home range sizes, 2) movement patterns and 3) space utilisation described with the factors daytime, tidal phases and water depth.

The four actively tracked sharks in this study showed a much smaller home range size (1.09 – 3.74 km^2) than previous studies showed (mean approx. 21 km^2). The passive tracking data showed a similar size of home ranges as in previous studies. The movement patterns found in the study of DeMarignac (1997) could not be confirmed. This study showed movement patterns of subadult Lemon Sharks in direct contrast to DeMaringacs findings: long distance West-East migrations between day and night.

This study showed the influence of tidal phases throughout the years to the movement pattern of the sharks. The sharks used the Main Lagoon in strong relation to the tidal phases. The extreme cases, low and high tide, showed separation of the location of the sharks. All sharks used most frequently an area that runs dry at spring low tides. At high tides they were very rarely in a deeper area.

The analysis of the water depth showed that the subadult Lemon Sharks preferred a certain depth of the water column. In more than 50% of the records they swam in a depth range of between 60 – 90 cm with a positive correlation to their body size. The depth of the water column did not differ between tidal phases.

However, this study points out that the day-night movement pattern changes over time. The influence of the tidal phases was shown for the previous and current studies and the factor of the water depth is described for the range of approximately 25 years. More intensive tracking projects are needed to describe clearly the movement patterns and space utilisation of the subadult Lemon Sharks in the Main Lagoon of Bimini and provide comparison with more factors of previous studies. Too little is known to allow final conclusions.

1. Introduction

There are over 500 (and rising) known species of sharks in the world’s oceans (Compagno et al., 2005). They have inhabited the oceans since before the time of the dinosaurs, for roughly 400 million years (Westheide et al., 2004). Sharks are highly adapted fish that fulfil crucially important roles in the various ocean ecosystems in which they live. They are apex predators and therefore at the top of the food chain (Senn David G., personal communication).

If this important position and its function become upset by humans, the ecosystem could become highly destabilised from its natural balance. Already Volterra (1928) has shown the importance of predators in the functioning of ecosystems, especially with reference to population dynamics and exchanges of energy between trophic levels. Smith (1974), Steele (1974), Hassel (1976) and others showed with computer models that predators can exert both stabilising and oscillating influences on ecosystem dynamics (teleost predators). Sharks have been entirely overlooked. So the assumption is close that sharks as apex predators have a similar effect on the ecosystem, or even a stronger effect.

In order to better understand the ecosystem it is necessary to increase our knowledge of the life history of these top predators. A number of shark populations of various species are being threatened by anthropogenic influences, which has already resulted in a number being included on the IUCN Red List.

In the past, biologists often studied sharks to learn how to protect humans from sharks, but now research more commonly centres on how to best protect sharks from humans. There has been such a rapid expansion in recreational and commercial shark fishing, that we may be catching sharks faster than they can reproduce to sustain their population sizes (Branstetter Steve, 1990).

The Bimini Biological Field Station (BBFS) is the ideal facility in which to conduct this nature of research on elasmobranches. For over 20 years from the nineties onwards professor Dr. Samuel Gruber has conducted research on sharks from Bimini through research cruises with great success (Gruber, 1982; Morrissey, 1993; Sundström, 2001). The main aim of the BBFS’s research is to elucidate the role of these amazing animals and their place in the ocean and to spread the message of conservation.

The BBFS has captured and recorded over 12 species of sharks in the shallow waters around Bimini. One taxon proved out for a model species: *Negaprion brevirostris*, Lemon Shark.

Juvenile Lemon Sharks (<120 cm) spend the first 3-4 years of their lives in the mangrove nurseries of Bimini. Subadult Lemon Sharks (120-234 cm; ~ 4-12 years) then increase their home ranges to encompass the Main Lagoon between North and South Bimini. Mature Lemon Sharks frequent Bimini every spring to mate and give birth to live pups in the nursery areas, which make up much of Bimini's shallow coastline. Because of the fact that Bimini Island is relatively well isolated from other islands, reefs and other possible habitats for the Lemon Sharks, the continuous tracking of all individuals (94% recapture rate, Gruber S. H.) allows exceptionally good study of the life history of the model species Lemon Shark.

Gruber found in his first expeditions to the Bimini Lagoon in the 1980’s (Gruber et al., 1988) a movement pattern in a west – east direction of subadult Lemon Sharks of the size of 150 cm, 168 cm and 230 cm (total length; TL). Mostly these sharks were found in the night in a position west of the lagoon and during the day in a position east of the lagoon.

This pattern was confirmed by Correia J. and DeMarignac J. (1995). They tracked four subadult Lemon Sharks with a total length (TL) of between 150 and 186 cm for 3 months. DeMarignac (2000) identified 5 diel patterns based of mid-eastern positions, but they were all day-night controlled. Harry A. (2005) could confirm some small patterns (South-North, Mini-East-West) but not the large (7-8 km) east-west migration. This is not surprising, because Sundström (2001) showed that only the large subadult Lemon Sharks caught on long lines set on the eastern side of the Main Lagoon exhibited this large migration.

Today there are a lot more movements of boats and other vehicles observable close to Alice and Bailey Town in contrast to the 1990s. At the very west end of the Main Lagoon is the natural channel, which is used as a shipping channel. This channel has been extended and a lot more shipping traffic has been established. More people are living in these two towns and on the northern edge a big holiday resort has been built. All these man made impacts must have an influence on the marine environment around the town, especially in the channel and the west part of the main lagoon.

This thesis gives attention to the matter of fact, that the aforementioned west-eastern/night-day movement pattern is no longer seen today. It is not known how the subadult sharks are moving today and which factors are influencing these movements.

2. Background

2.1. Evolution of Fish

2.1.1. Chordata

In the formation of higher animals the development of the „chorda dorsalis“ was very important. It has a supporting function and from this starting point the development of poles, anterior and posterior, moved on. Orientated movements now became possible. The foundation stone for “front” and “back” was laid.

Through the division into three characteristic parts – head, trunk and tail – the building structure of **Craniota** was constructed. It is common in science that initially **Chordata** did not have a head (**Acrania**). The most famous representative of those taxa is *Branchiostoma lanceolatum* (or *Amphioxus*). One possible explanation is that an orientated movement for the way of life was not yet necessary.

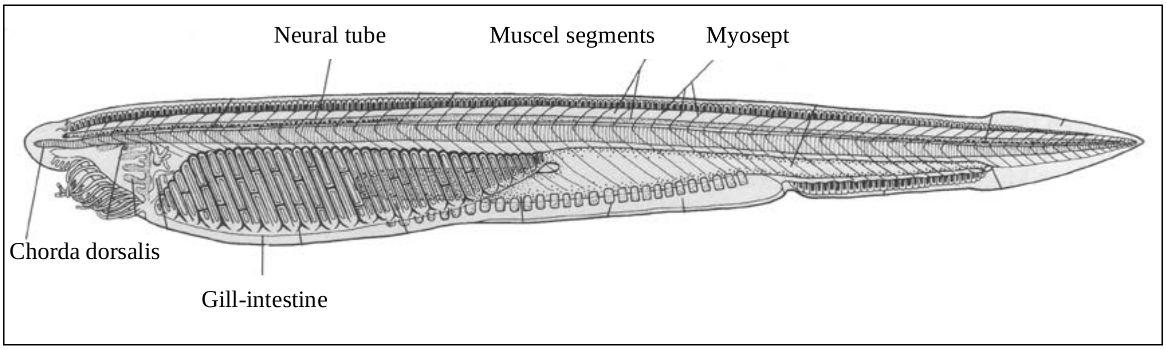


Fig. 1: *Branchiostoma lanceolatum*, Schema to demonstrate the muscle segments (Myomere) (from several authors)

A. S. Romer defined the oldest existing pattern as a head with a gill-intestine and sensory organs. Movement of this construct was developed as an outgrowth or lengthening of trunk/tail. That lengthening is supported by the chorda dorsalis. An initial form could have had an anatomical appearance like that of a larva of Ascidia.

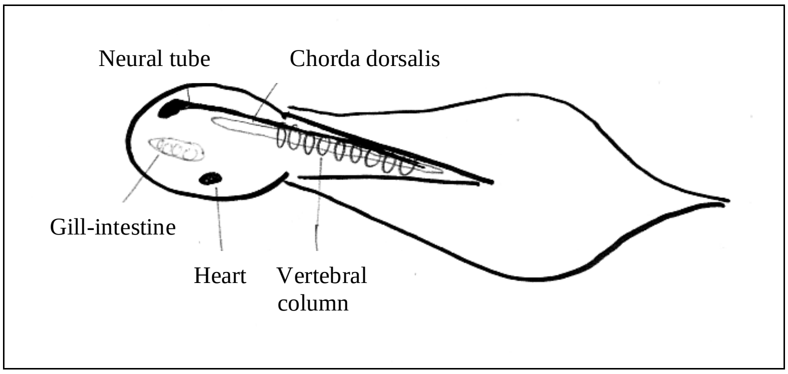


Fig. 2: Larva of Ascidia, schematic (personal communication with Senn, modified Caviezel)

The thesis that the initial structure plan was a head with trunk and tail persisted through the science of biology for a long time, hence the most famous explanation being that the head develops out of vertebrae (also J. W. von Goethe). Today we know that such a development is embryonically not possible. **Dietrich Starck** (1908-2001) has developed an embryo based thesis: namely that during formation of the head the neural strip has a important role - it does not only deliver the nerve cells but also much of the cell material of the head mesenchym that develops into skull, teeth and head musculature.

First discussed group of fish is

2.1.2. **Agnatha**, Jawless

They are known certainly since Ordovician (495-443 Ga) but occurred very likely already in higher Cambrian (545-495 Ga). They had their great flower in the beginning of Silur (443-417 Ga) and have been very manifold since Devonian (417-358 Ga).
Nowadays we know only two groups: **Myxinoidea** (hag fish) and **Petromyzonta** (lamprey).
Their first development took place most likely in flat, marine regions. Only in the Silurian the settlement of fresh water took place. The lack of jaws and the organisation of the mouths let us conclude that the Agnatha probably possessed gill intestines and a filtering nutrition still.
The most remarkable structural component of both extant types is the so-called tongue apparatus in the mouth. In the mouth area horn denticles are trained. In both Taxa extremities in pairs and belt formations are missing completely. The vertebral column item is those of time life persisting Chorda dorsalis. Vertebrae are missing in fossil Agnatha and Myxinoidea; Petromyzonta had simple, small cartilage bits laterally the Chorda dorsalis. The endoskeleton is cartilaginous; the ability for bone formation is missing in the extant types completely (but can be induced in experiments in Petromyzonta). In both taxa in somatic musculature of the trunk a Septum Horizontale is missing, as are epaxonic and hypaxonic musculature groups. The gill pockets are located within the gill arcs and not outside as in Gnathostomata. Chest fins are in most taxa fossils available but in extant unavailable. Pelvic fins are missing in most taxa.
The fossils Agnatha are diversified in form. They are mostly small and are primary marine animals. They have armour which is made out of different skin scales/plates, hence the older name “Ostracodermata” fits better. Their skull was partially grown together with skin bones and sometimes they had a head shield. Extant forms have reduced the scales completely and produce a film of slime.
Due to the reason no Agnatha had effective mouth tools, they had to feed on small organisms. In those days these were systematically above all Polychaeta. All taxa fed on detritus.

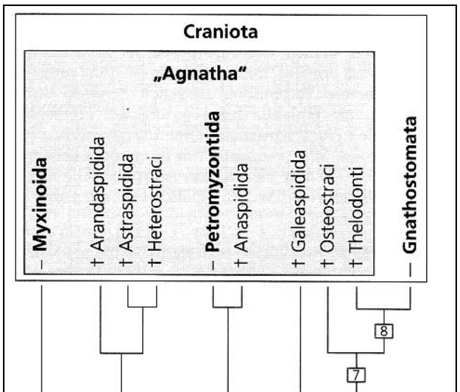


Fig. 3: Phylogenetic-systematic classification of Agnatha
(from Westheide and Rieger, 2004)

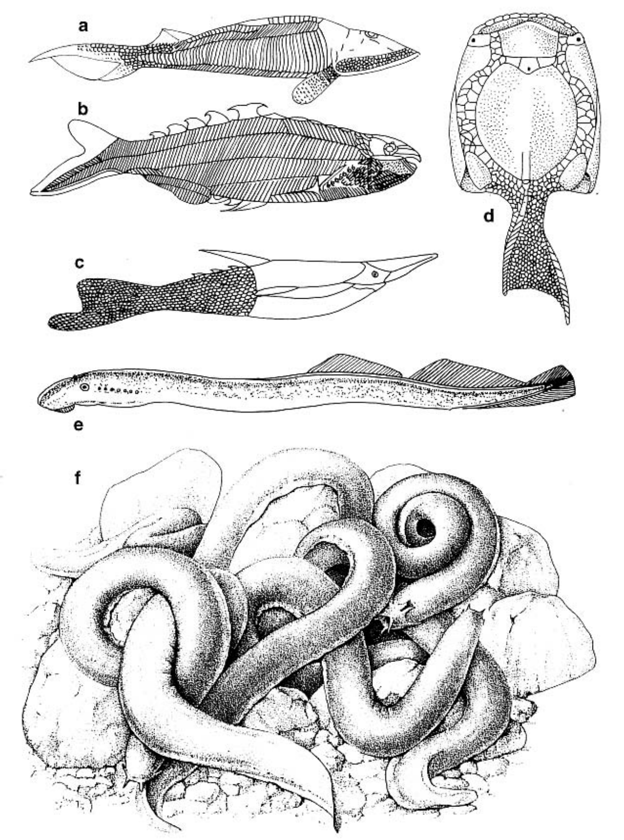


Fig. 4: Agnatha: a-d. Fossil formes. a. *Hemicyclapsis* (Osteostraci), b. *Birkenia* (Anapsida), c. *Pteraspis*, d. *Drepanaspis* (both Heterostraci), e. *Petromycon*, f. *Eptatretus*, group of animals on the seabed (Myxinoidea) (from Storch and Welsch, 2004)

2.1.3 Gnathostomata, (jawed vertebrates)

This group includes all vertebrates from Placoderma to Mammalia. Their most important achievement by evolution are the jaws, as the name says. They have a mouth with one jaw arc: Upper jaw (also Palatoquadratum) and lower jaw (Mandibular). They have at most 7 gill slits.

The development of jaws brought with it the possibility to now grab and hold something. This means that these predators had much success. With the possibility to grab, hold and chew up their prey, the intake of energy into the body can increase in new dimensions. For that reason bigger and faster organisms could develop.

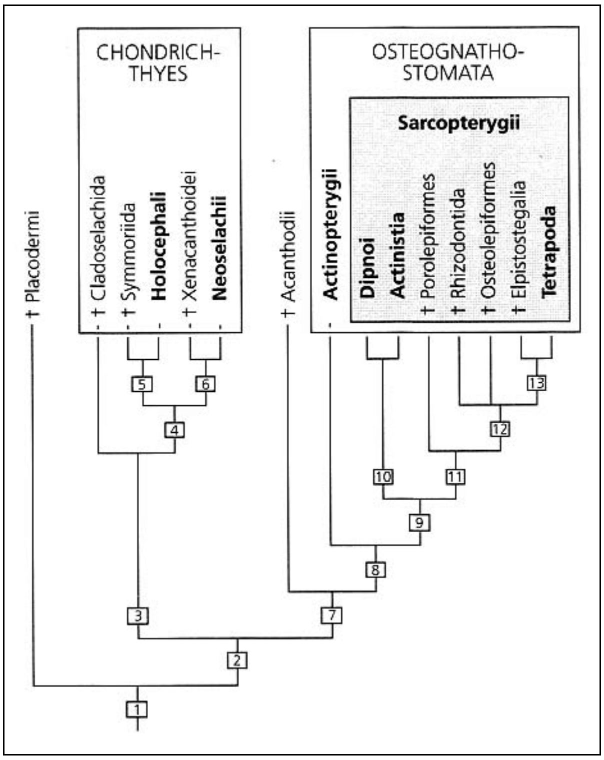


Fig. 5: Phylogenetic-systematic classification Gnathostomata, (from Westheide and Rieger, 2004)

2.1.4. Placodermi †

Placodermi are an isolated animal group, which occurred only in the Palaeozoic. They developed in the Silurian and had their bloom in the Devonian, when they were the most prevalent vertebrates, vanishing in the Lower Carboniferous. Most forms were marine, some few freshwater forms are known. Most genera are benthic, some few pelagic.

The head and trunk are in many species enclosed in bone armour. Head and trunk are externally separated. Gill lids exist which do well covering the delicate gills. Derivatively is the lacking of teeth, which are replaced by bone peaks. The upper jaw is immovable fixed to the skull (autostylie). Two pairs of extremity are developed. The Chorda is persistent, vertebrae are lacking. In such a well-armoured body vertebrae are needless. The longitudinal axis has not to be supported.

Members of this class are: *Coccosteus,* 20-45 cm length, Europe; *Dunkleosteus,* up to 10 m length.

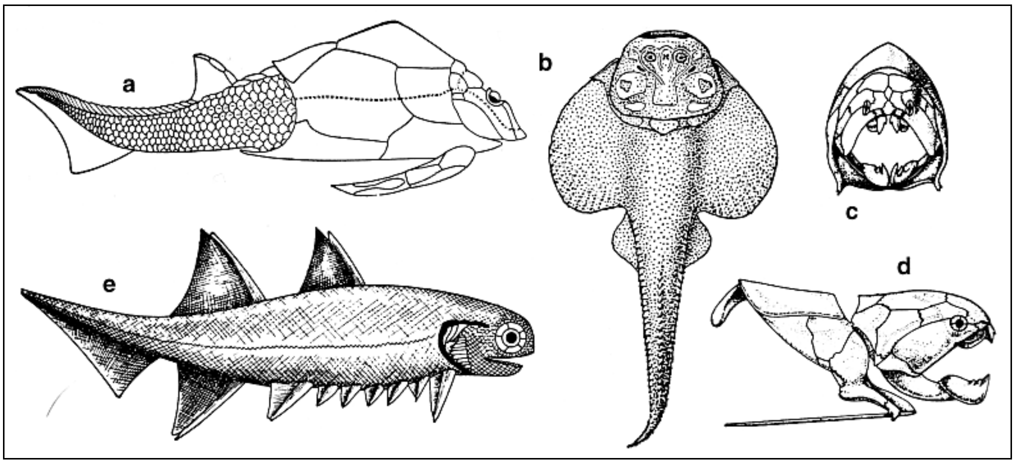


Fig. 6: Placodermii and Acanthodii: a. *Pterichthyodes* (Antiarchi), b. *Gemuendina* (Rhenanida), c, d. *Dunkleosteus* (Arthrodira), e. *Climatius* (Acanthodii) (from Storch and Welsch, 2004)

2.1.5. Acanthodii † (spiny sharks)

Acanthodii had as a characteristic a spine in front of each fin. The spines and scales can be found in Silurian, possibly also in Ordovician. Until the Carboniferous they were very common, proven up to the lower Permian.

The Acanthodii were globally distributed, mostly marine. Only the youngest forms could advance into fresh water. They are small creatures; just one form (Ischnacanthida †) being able to grow up to 2 m. They had also a head and trunk with bone plates and scales. Highly developed forms show a trend to a lightweight construction: The skin armour is strongly atrophied, a premise for the settlement of the three-dimensional water column. Teeth are mostly non-existent, and if existent they are without enamel. Gill lids existed. Original forms have 2 dorsal fins, 1 anal fin, 1 pectoral fin pair and 1 pelvic fin pair, between which more spine pairs exist. The spine was missing only in front of the heterocercal caudal fin. Also the number of fins was reduced and showed a trend of lightweight construction into the younger forms.

Member of this class is: *Climatius reticulatus*, lower Devonian.

2.1.6. Chondrichthyes (Elasmobranchs)

Chondrichthyes appear first in Devonian, survived the big extinction on the border of Devonian/Carboniferous and could never grow to a big variety of forms. Chondrichthyes are today present and this shows how successful their concept of body building design was.

Skull, vertebral column and fin skeleton are cartilaginous, but often very hard because of calcification. This state was likely built by reduction of bone tissue and results in a lighter body construction. The apical end of the skull is often elongated to a rostrum, which is propped up with a consistent appendix or with several cartilaginous pieces. Primitive Selachii have amphystile (relatively stiff jaws) skull, higher forms have hyostile (more agile jaws) skull. The oldest Selachii had a strong, continuous Chorda dorsalis with simply attached arch elements. Neoselachii (modern sharks) have calcified vertebral bodies in which between the Chorda dorsalis is reduced. This brings the benefit of stability over the whole body without losing flexibility. These results let us conclude that a locomotion that is induced with the whole body is therefore very strong and quick. The pectoral fins are aligned horizontally. They are outspread during swimming and are used as elevator or as wings (rays). The caudal fin is asymmetrical (heterocercal) but can externally look symmetrical (homocercal, propeller drive). Additionally, the heavy skin plates have been reduced to small, protective scales. The gill caps have also been reduced. These scales are named placoid scales and consist of bony like, subepidermal basal plate and a tooth on each of these plates that pierces the skin. The surface of the tooth builds enamel, the core dentin. The placoid scales cover the whole body of Selachii. On Batoidea (rays) and Holocephali (chimaeras) the scales are reduced, but can be formed in stings. This tooth dress does not only reduce the body weight, it also reduces the friction force on the skin. The contact surface for the water and the number and size of eddies are dramatically reduced. These preconditions allow the Selachii faster and more arduous swimming and allow them to be the apex predators in the oceans. This position in the food chain they have also because of their dentition: the borders of the jaws are continuously forming strong teeth. They are continuously produced from inside and old teeth are replaced (revolver dentition). But nevertheless the biggest forms of Selachii are plankton feeders.

Representatives of these classes are:

Carcharodon carcharias (white shark), Selachii

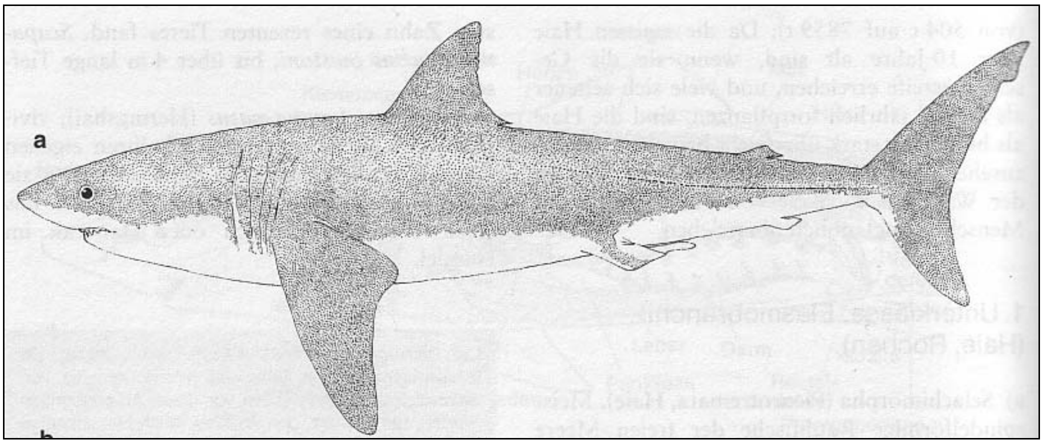


Fig. 7: White Shark, *Carcharodon carcharias* (from Storch and Welsch, 2004)

Manta birostris (manta ray), Batoidea

Fig. 8: Manta ray, *Manta birostris* (by Caviezel)

Chimaera cubana, Holocephali

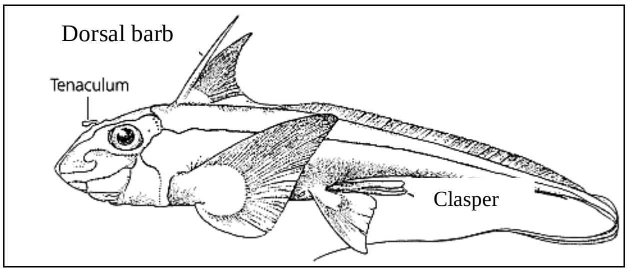


Fig. 9: Holocephali, *Chimera cubana* (from Westheide and Rieger, 2004)

2.1.7. Osteichthyes (bony fish)

Osteichthyes are known from the higher Silurian through fossil bones and scales. They can, based on their histology, form, chemical composition and surface structure, possibly already count to the Actinopterygii (ray-finned fish) or Sarcopterygii (lobe-finned fish). The oldest, completely conserved fossils are known from the Lower Devonian.

The formation of bones in the skeleton isolates this class only from the living cartilaginous fish and the Agnatha, not from their fossil ancestors. The skull is more complicatedly developed. Its numerous pieces cannot be named homologous on a skull of a Tetrapod partially. The caudal fin can be heterocercal (sturgeon, paddlefish), but is mostly homocercal. The most successful development is the lung/swim bladder organ: it is a protuberance of the foregut, primarily paired with respiration function (lungs). It has very thin walls and is strongly supplied with blood. First it was a protuberance in which atmospheric air could be pressed, but over the course of time these protuberances lined out from the foregut, so that a fully detached swim bladder developed. The swim bladder had now the function of a hydrostatic organ. This was an important step for energy reduced, pelagic life. With the agile gill caps water flow through the mouth and gills is induced. This means that the fish had no more need to move to breathe. This class became through this development one of the most species-rich classes (min. 22'000 species).

Actinopterygii (ray-finned fish) have established the alleviation of the body through the development of the swim bladder. The supporting and moving functions of the paired fins are reduced and while swimming tied up. The part of the flesh with muscles and skeleton is shortened: from the skeleton remain just few radalia and basalia at the fin base. The main parts of the fins are skinlike, supported through fin rays. Light ganoin scales are present, imbricatively arranged (agile). Ganoin becomes further reduced in Teleosts. They have in their epidermis an especially high number of mucilage cells. Secondary it could be incorporated bone plates in the skin (trunkfish, armoured catfishes, sea horses).

The oldest forms, Chondrostei, still have a heterocercal caudal fin and rhomboidal scales (sturgeon, paddlefish).

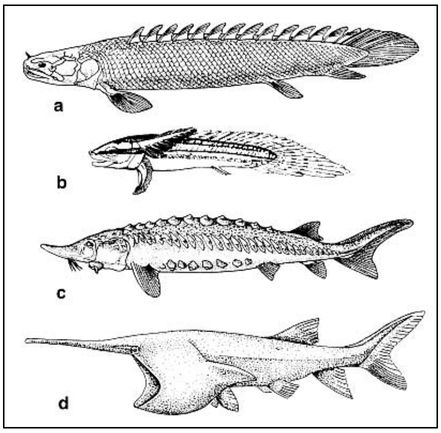


Fig. 10: Chondrostei: a. *Polypterus* adult, b. *Polypterus* larva, c. *Acipenser sturio* (Sturgeon), d. *Polyodon spathula* (Paddlefish) (from Storch and Welsch, 2004)

The younger forms, Holostei, still have a heterocercal caudal fin, the swim bladder still has respiratory function and they have totally reduced their Chorda dorsalis (Lepisosteidae, garfish).

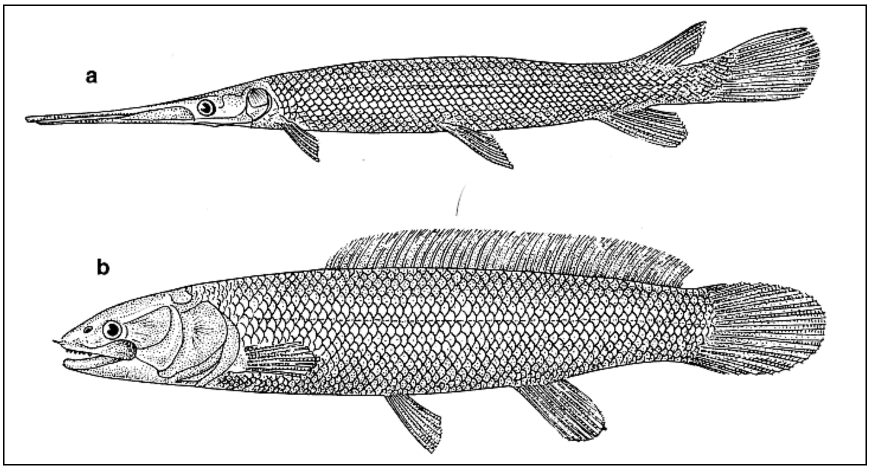


Fig. 11: Holostei: a. *Lepisosteus osseus* (garfish), b. *Amia calva* (bowfin) (from Storch and Welsch, 2004

The youngest forms, Teleosts, made an enormous expansion of species. They settled most available niches. The Ganoin coating of the scales is fully reduced. The inner skeleton is strongly ossified, the swim bladder fully developed and has no respiration function any more.

Fig. 12: Trout blue, Good Friday menu (from www.kaisers.de)

Sarcopterygii (lobe-finned fish) have, as the name implies, not reduced the skeleton in their extremities. Nor have they made the reduction of the appendages of the gut. They are divided into Dipnoi (lung fish) and Crossopterygii (crossopterygians).

The oldest representatives of Dipnoi conform in their design of the skeleton with the most Crossopterygii. The modern Dipnoi have physiological and anatomical similarities with the tetrapod vertebrates: lung respiration (in O_2-poor water, otherwise gill respiration), recirculation of the O_2-rich blood through the lung vein (no mixture with O_2-poor blood). This is a fundamental precondition for land vertebrates. Only because of this can they provide enough oxygen for the energy rich metabolism. They are a discrete group since the Devonian.

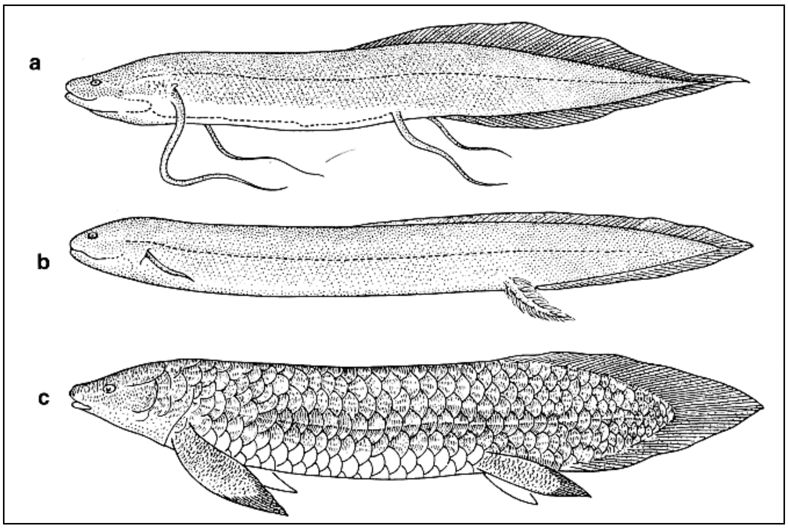


Fig. 13: Dipnoi. a. *Protopterus aethiopicus,* b. *Lepidosiren paradoxa,* c. *Neoceratodus forsteri* (from Storch and Welsch, 2004)

To the Crossopterygii we count two divergent rows: the extinct Rhipidistia and the Actinistia, which are known through one single genus (*Latimeira)*. In their front fins one can exactly identify humerus, radius, ulna, radial, ulnare and intermedium – in the same order as they are found in tetrapod vertebra, but not in the same number. The teeth have a folded wall structure, like amphibians. They have strong Cosmoid scales, muscle rich fins and tusks in the mouth. They make a cross-coat, as it is only seen by tetrapod vertebrates.

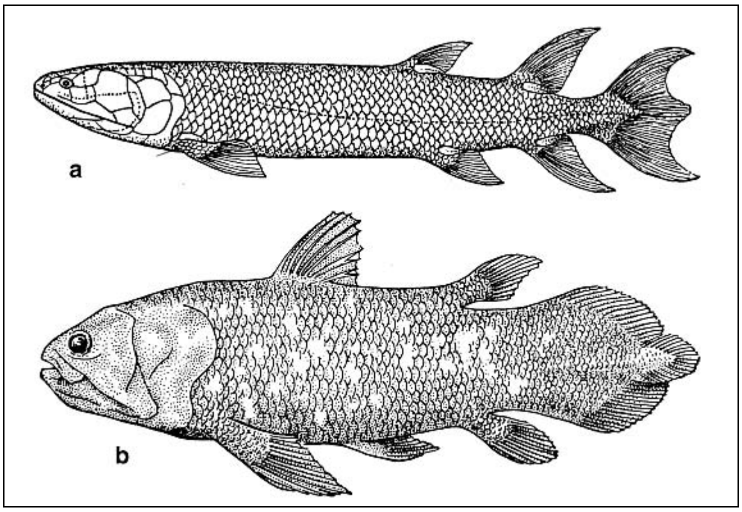


Fig. 14: Crossopterygii: a. *Eusthenopteron,* b. *Latimeria* (from Storch and Welsch, 2004)

Sarcopterygii were apparently not very successful in their ancestral milieu of the water. But they made some important developments, which allowed their progeny to conquer the land and settle it.

Fig. 15: Phylogenetic tree of the animals, (Senn D. G, 1980)

2.2. Systematic of Sharks

Sharks belong to the taxonomic class Chondrichthyes. There are two main groups of chondrichthyan fish. The largest of these is the subclass Elasmobranchii (“elasmo” = plate, “branchii” = gills), which includes the sharks, skates and rays. The Elasmobranches are easily recognised by the multiple (five to seven) paired gill openings on the sides of their heads. The subclass Holocephali (“holo” = whole, “cephalic” = head) contains the chimaeras, which are a much smaller group of living animals. A soft gill cover with just a single opening on each side of the head protects the four pairs of gill openings in holocephalans.

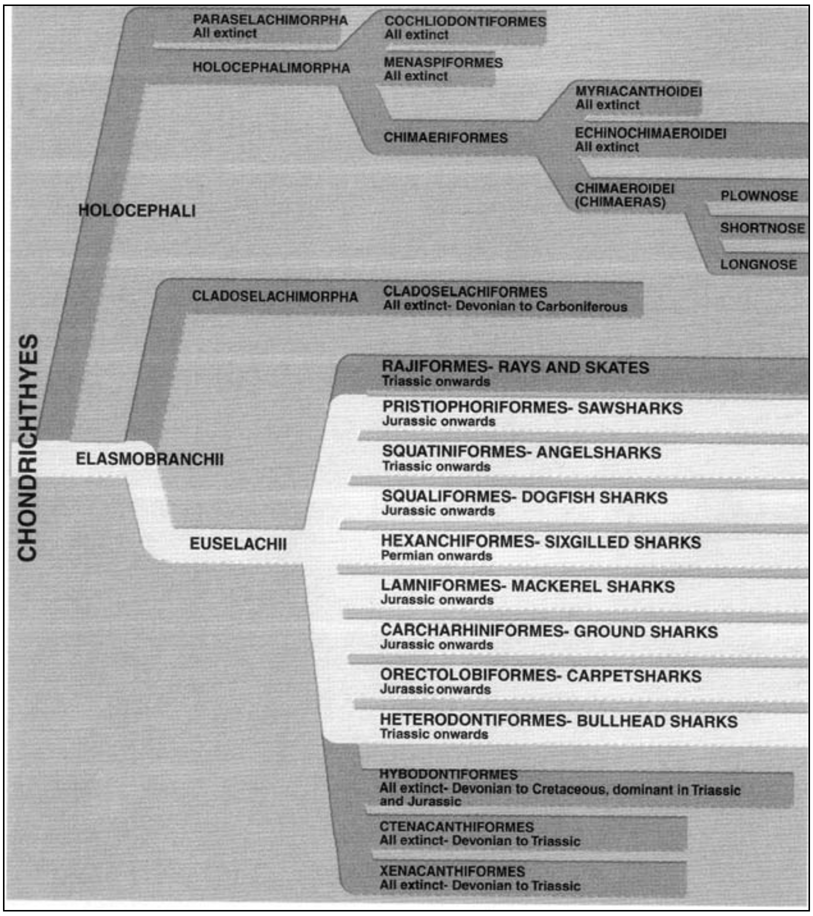


Fig. 16: Family tree of chondrichthyes
(from Compagno et al., 2005)

There are ten extant orders of Chondrichthyes; eight of them are sharks. To give an overview of these orders, I confine myself to list all orders with the number of families and genera (Fig. 17). Today we know approximately 500 species of elasmobranches.

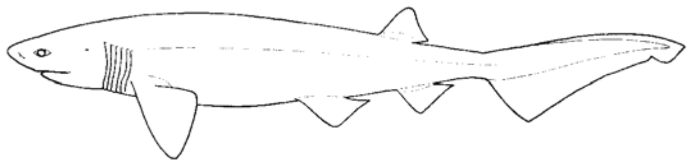
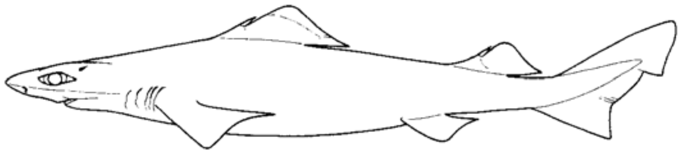
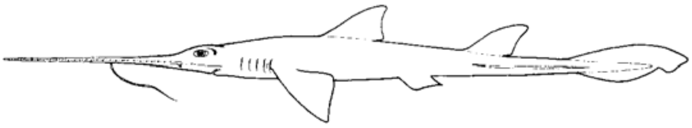
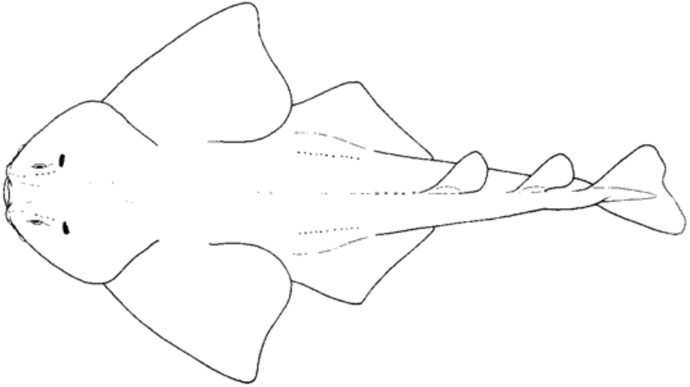
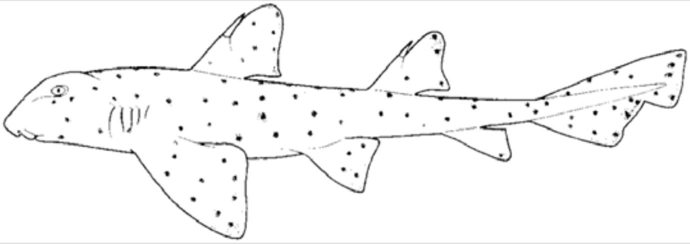
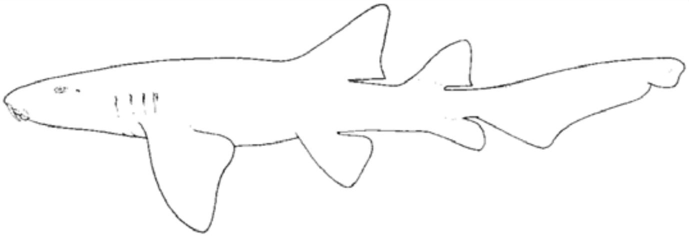
Hexanchiformes (Cow and Frilled Sharks) 6 or 7 gills slits, anal fin, 1 dorsal fin	
Two families	
Four genera e.g. *Hexanchus griseus*	
Squaliformes (Dogfish Sharks) 5 gills slits, no anal fin, 2 dorsal fins, dorsal fin spines, snout short	
Seven families	
Twenty-five genera e.g. *Centrophorus granulosus*	
Pristiophoriformes (Sawsharks) 5 or 6 gills slits, no anal fin, 2 dorsal fins, snout long and saw shaped with long barbels	
One family	
Two genera e.g. *Pristiophorus schroederi*	
Squatiniformes (Angel Sharks) 5 gills slits, no anal fin, 2 dorsal fins, body flattened, mouth terminal	
One family	
One genus e.g. *Squatina squatina*	
Heterodontiformes (Bullhead Sharks) 5 gills slits, anal fin, 2 dorsal fins, dorsal fin spines	
One family	
One genus e.g. *Heterodontus francisci*	
Orectolobiformes (Carpet Sharks) 5 gills slits, anal fin, 2 dorsal fins, mouth well in front of eyes	
Seven families	
Fourteen genera e.g. *Ginglymostoma cirratum*	

Fig. 17: Extant orders of sharks (after Compagno et al., 2005, modified)

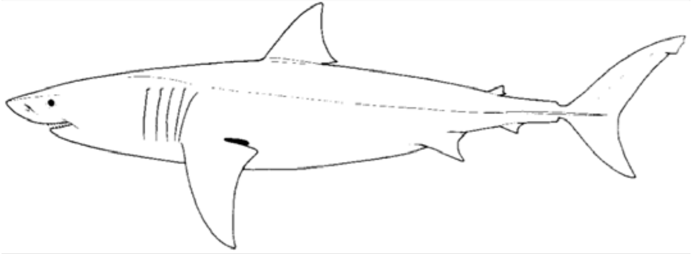
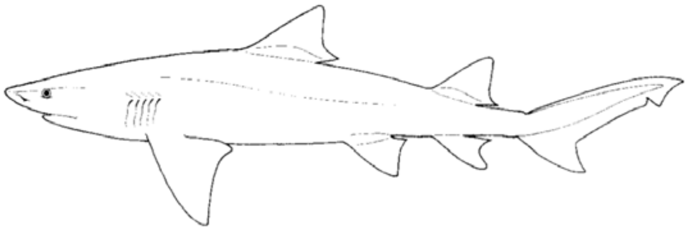
Lamniformes (Mackerel Sharks) 5 gills slits, anal fin, 2 dorsal fins, mouth behind front of eyes, no nictitating eyelids	
Seven families	
Ten genera e.g. *Carcharodon carcharias*	
Carcharhiniformes (Ground Sharks) 5 gills slits, anal fin, 2 dorsal fins, mouth behind front of eyes, nictitating eyelids present	
Eight families	
Fifty genera e.g. *Negaprion brevirostris*	

Fig. 17: Continued - Extant orders of sharks (after Compagno et al., 2005, modified)

2.3. Species around Bimini Island, Bahamas

- Carcharhiniformes
  - Carcharhinidae
    - *Carcharhinus acronotus* (Blacknose Shark)
    - *Carcharhinus brevipinna* (Spinner Shark)
    - *Carcharhinus leucas* (Bull Shark)
    - *Carcharhinus limbatus* (Blacktip Shark)
    - *Carcharhinus perezi* (Caribbean Reef Shark)
    - *Galeocerdo cuvier* (Tiger Shark)
    - *Negaprion brevirostris* (Lemon Shark)
    - *Rhizoprionodon porosus* (Caribbean Sharpnose Shark)
    - *Rhizoprionodon terraenovae* (Atlantic Sharpnose Shark)
  - Sphyrnidae
    - *Sphyrna lewini* (Scalloped Hammerhead)
    - *Sphyrna mokarran* (Great Hammerhead)
    - *Sphyrna tiburo* (Bonnethead Shark)

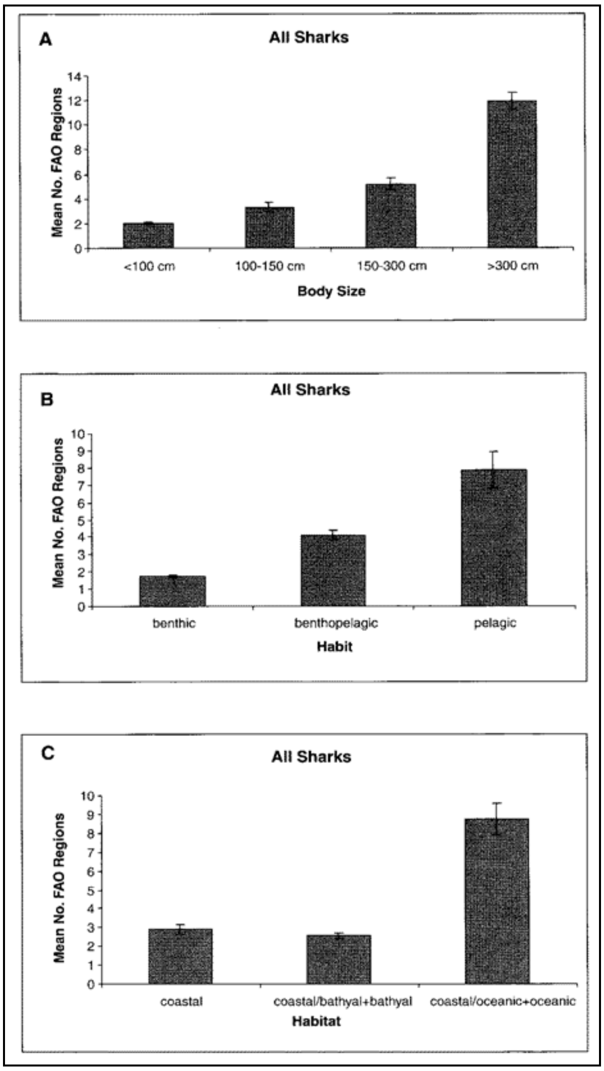
- Orectolobiformes
  - Ginglymostomatidae
    - *Ginglymostoma cirratum* (Nurse Shark)
  - Rhincodontidae
    - *Rhincodon typus* (Whale Shark)

- Hexanchiformes
  - Hexanchidae
    - *Hexanchus nakamurai* (Bigeye Sixgill Shark)

2.4. Adaptations and Anatomy

2.4.1. Ocean Distribution

Sharks live in all marine waters around the earth. Some shark species may be euryhaline and capable of residence in freshwater, but they are members of marine families.
Only few species are found circumglobal and use a huge range. Most of the species are small, needing also a small part of the ocean in which to live. This we can see in the two analyses of Compagno (1984) and Cortés (1999): They showed nicely that the body size of sharks correlates with the Fishing Areas Occupied FAO. The bigger the sharks are, the more FAO they are using in most cases (Fig. 18 A). But in the bigger areas more species are not found. The smaller the shark species are, the more the number of species are found (Fig. 19 A). This can be explained with the habits and habitats of these smaller sharks: Mostly they live benthic or benthopelagic in coastal and bathyal areas and in these living spaces the possibility of empty niches is much higher than in pelagic and oceanic areas. Opposite to the pelagic areas the benthic areas are enormous and more differentiated, and over the time of the evolution many niches could be occupied.



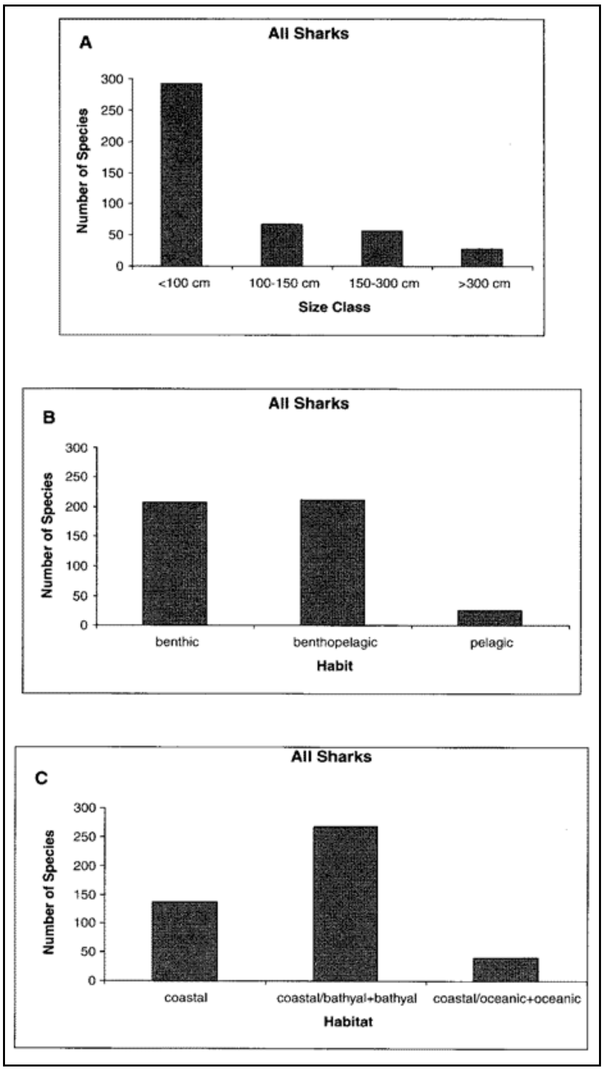


Fig. 18: Ocean distribution of sharks:
FAO Fishing Areas occupied
(from Carrier et al., 2004)

Fig. 19: Ocean distribution of sharks:
Number of Species
(from Carrier et al., 2004)

2.4.2. Body Structure

The basic body structure of sharks has virtually not changed for hundreds of millions of years. It consists of a head (from snout to gills), trunk (from pectoral girdle to anus) and tail. The head is comprised of the snout (rostrum) in front of the eyes and mouth, the orbital region (including the eyes and mouth), and the branchial region, with gills and spiracles (the latter have been lost in many species). The body is defined from the paired pectoral fins to the paired pelvic fins and vent. The tail is subdivided into the precaudal tail (which may have an anal fin) and the caudal fin. The first dorsal fin is usually located on the trunk, the second, if present, on the precaudal tail. While these characteristics are constant, there is huge variation in size and shape. The largest sharks are up to 20 m (Whale Sharks), the smallest reach a mature size of 30 cm and less (e.g. Smalleye Pygmy Shark).

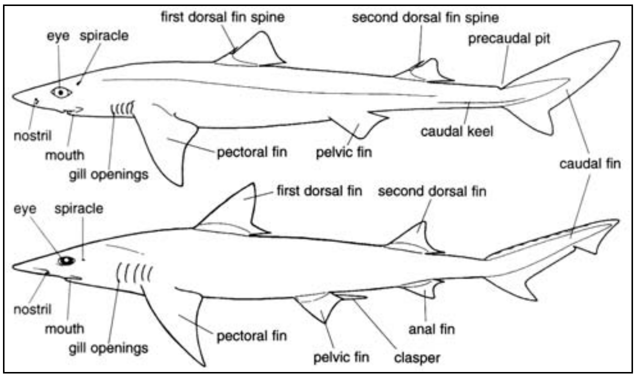


Fig. 20: Lateral views: (top) female squalid shark; (bottom) male hemigaleid shark, (from Compagno et al., 2005)

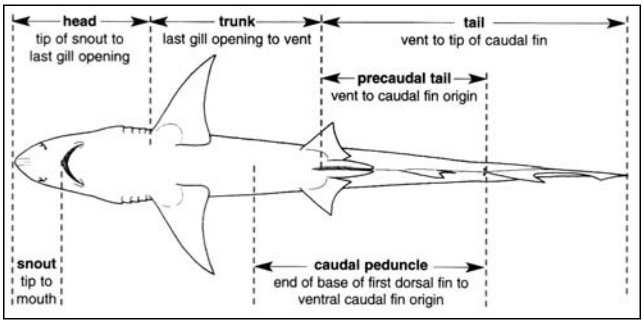


Fig. 21: Ventral view showing body regions, (from Compagno et al., 2005)

2.4.3. Skin and Scales

A very tough skin, usually covered with small sharp tooth-like placoid scales (dermal denticles), typically protects sharks. Some species have none on their ventral surface. These denticles are very similar in structure to shark teeth, with crowns covered in hard enamel anchored into the skin by dentine bases. Their shapes are incredibly varied, between species and on different parts of the body. One of the most important functions of the dermal denticles, apart from physical protection, is to provide a surface that minimises surface drag and maximises swimming efficiency by producing a laminar flow along the tiny gullies and ridges on the surface of the skin. Industry has been trying for a couple of years to mimic this function of shark's skin to produce energy efficient surfaces for several utilisations: Airplane wings, swimming suits, underwater vehicles etc.

Dermal denticles fall out continuously during the life of a shark, with replacements growing out through the skin. Because male sharks may hold the female with their teeth during mating, the skin of females is often much thicker than males.

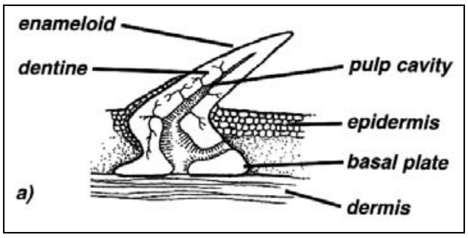


Fig. 22: Cutaway of placoid scale (from Compagno et al., 2005)

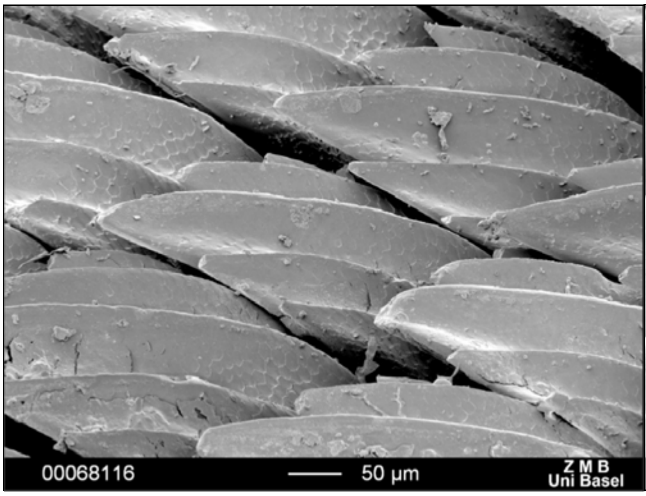


Fig. 23: Placoid scales of a mature Great Hammerhead female, TL = 279 cm (by Caviezel)

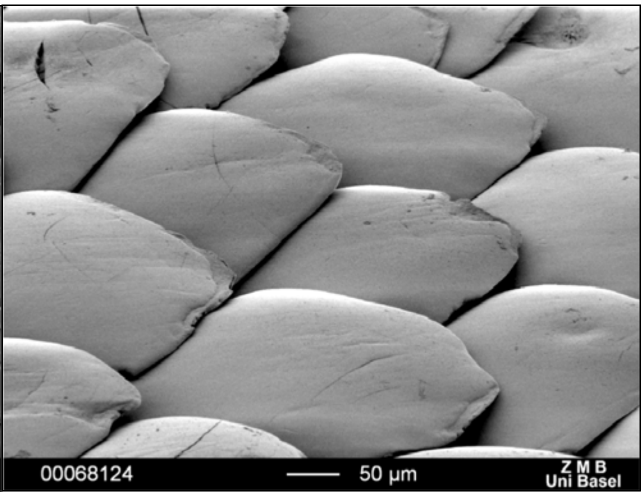


Fig. 24: Placoid scales of a juvenile Lemon Shark female, TL = 97.8 cm, (by Caviezel)

2.4.4. Teeth and Jaws

All sharks have multiple rows of teeth along the edges of their upper and lower jaws. New teeth develop in a deep groove inside the mouth. These replacement teeth move forward from inside the mouth in a sort of conveyor belt. The oldest front teeth become worn and fall out. The teeth fall out in an interval of 8-10 day up to several months. This adds up to a lot of teeth in the lifetime of a shark.

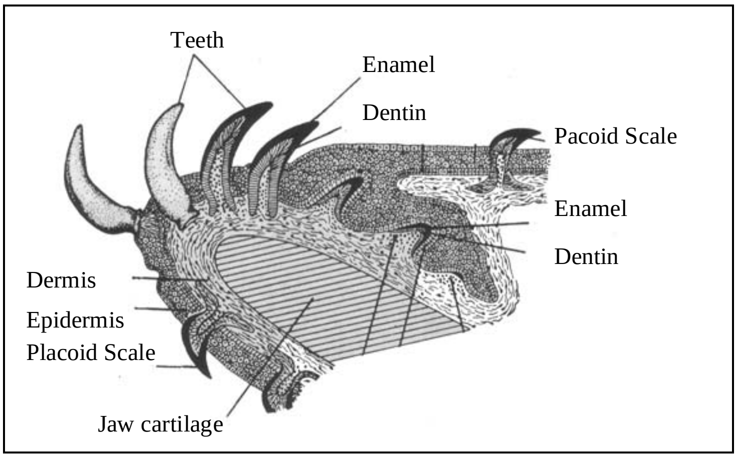


Fig. 25: Cutaway of jaw with teeth and placoid scales (after Storch and Welsch, 2004, modified)

The jaws of sharks are most unusual compared with those of mammals and bony fishes, as the upper jaw is not part of the skull. The upper jaw can move independently. Both the upper and lower jaws may be protruded away from the skull during feeding. This enables the teeth to be rotated outwards so that a larger piece of prey can be bitten off, or providing for more effective suction feeding.

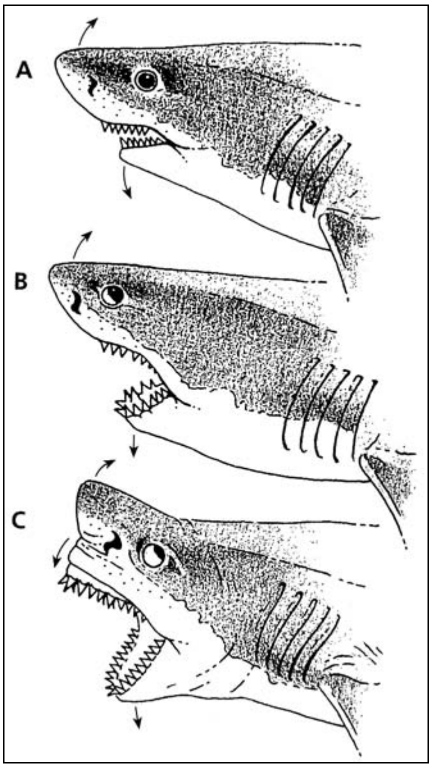


Fig. 26: Carcharodon carcharias, feeding movements. The arrows show the movements of skull and jaws (from Westheide and Rieger, 2004)

2.4.5. Movement

For efficient swimming several preconditions must be met. First the sharks need a hydrodynamic body shape. Only with a shape that reduces big eddies and allows an approximately laminar water flow on the surface (skin) is energy efficient swimming possible. Therefore the most efficient shark needs to be shaped in a shaft form (Fig. 27). In this body shape the whole body must be the drive for a strong and fast movement: The musculature has to be packed tightly along the body. Sharks solved this with zigzag segmented muscle fibres that run from head to tail. Forward movement is produced when these muscle fibres contract - first on one side of the body, then on the other side, pulling against the central vertebral column. So a series of undulations along the body and a sinuous swimming movement powered by the caudal fin is induced (Fig. 28). While forward thrust and acceleration is produced by these muscle contractions, the more that a shark’s body bends, the less efficient is its use of energy. The fastest sharks (mackerel shark family) tend to be teardrop in shape, with crescent-shaped tails very similar to those of tunas and a very stiff body, while the slow swimming frilled and cow sharks are longer and thinner with a very long upper tail lobe. A very symmetric, crescent-shaped tail acts like a propeller. The large paired pectoral fins act like wings to counter the downward movement. Fast oceanic swimmers also have broad keels in front of the tail that provide them with extra stability.

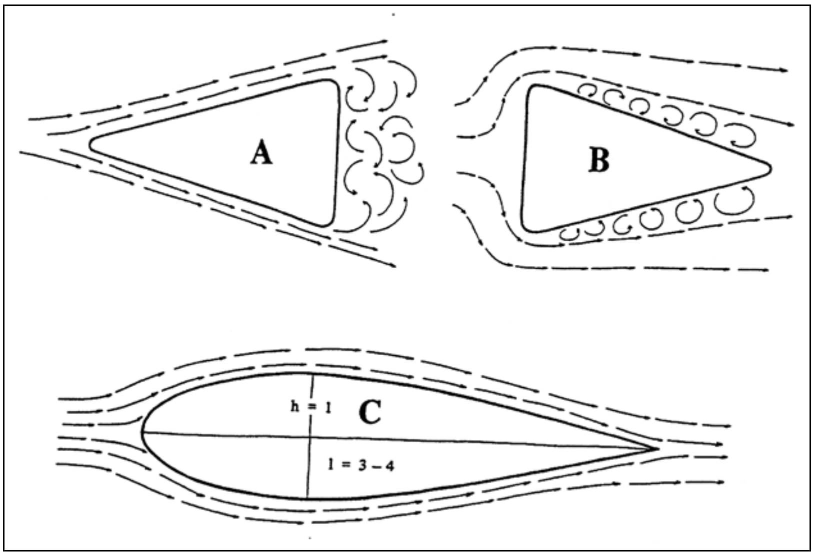


Fig. 27: The shape of around circulated bodies: A. Big resistance develops at the flat end because of big eddies. B. The slow down resistance is smaller, smaller eddies develop at the conical end. C. Shaft-shaped form with rounded front. Ideal proportion of thickest diameter (h) and length (l) is 1:4 to 1:3 (from Senn, 1998)

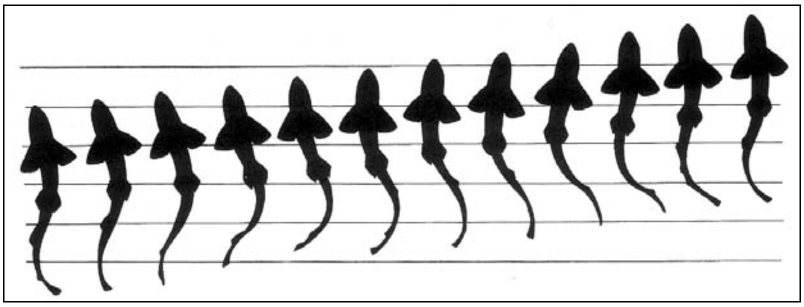


Fig. 28: Ventral view showing swimming sequence in a catshark, the sinusoidal movement begins at the head and flows down the body becoming more pronounced at the caudal fin (from Geoffrey Waller, 2000)

2.4.6. Warm Blooded Sharks

Actively swimming sharks need a lot of oxygen; therefore they have large hearts (posterior to the gills and protected by the pectoral girdle) to pump a lot of blood around the body and through their large gills. They also produce large amounts of heat in their muscles. Most species of sharks lose this heat immediately when the heated blood from their muscles passes through the narrow-walled blood vessels in the gills in order to pick up oxygen. However, for example the White Shark can retain this warmth in their bodies, so that they keep a constant body heat even when swimming in polar regions with several tens of degrees colder than their own temperature. This makes them more efficient swimmers and faster growing. They achieve this with the development of a heat exchange system: A network of tiny blood vessels (capillaries) packed tightly together. This is known as “rete mirabile”. Within this structure, in one direction thin walled blood vessels coming from the gills carry cold oxygenated blood. In the opposite direction thin capillaries carry warm deoxygenated blood from the muscles on its way back to the gills. These two sets of vessels exchange heat so effectively as they run alongside each other that the warmth from the body ends up returning to the muscles with the oxygenated blood. In warmer water sharks are able to direct the blood through another pathway around the rete mirabile directly into the gills.

2.4.7. Osmoregulation

All marine fish have to cope with the challenge of being immersed in a salty aquatic environment that draws body water out across skin and gill membranes into the seawater. Different from bony fish sharks do not drink large amounts of seawater and excret the excess of salt through their gills. They have a completely different strategy: They retain high concentrations of “waste” chemicals (salts) in their body, so they can control the direction in which water tends to travel, if needed into or out of their body. One of the most important chemicals is urea. Urea is excreted rapidly in urine of mammals and most other animals, but sharks accumulate it in their blood. Sharks also excrete excess salt across their gills, like bony fish, and they have a special gland, the rectal gland, that extracts salt out of the blood for excretion through the gut. All these adaptations work so well, that for example Bull Sharks are able to manage the enormous osmotic pressure changes while swimming freely into estuaries, freshwater rivers and lakes. They do so by completely changing kidney function to excrete large quantities of urea in watery urine and by reversing the direction of movement of salts across the gills, from excretion to absorption from the environment.

2.4.8. Senses

Sharks are highly evolved complex predatory animals and therefore need relatively large brains. The largest and most complex of all brains are found in the hammerhead sharks. Different sections of the brain have been identified of their functions, but scientists still do not understand the functions of many parts of these large brains.

Smell and taste are of huge importance to sharks. Not only are they used to detect potential prey or other food items at long distance, but they are likely also important when it comes to detecting shark pheromones in order to find mates, and possibly even for location during their long transoceanic migrations between feeding, mating and pupping grounds. In studies with the underwater electro-olfactogram (EOG) and electroencephalographic (EEG) in nurse and lemon sharks it could be shown that the sharks can recognise a squid extract with thresholds between 10^{-6} and 10^{-8} M (Silver 1979, Zeiske et al., 1986, Hodgson and Mathewson, 1978). These levels are similar to those reported for teleosts.

Vision in sharks is probably equally important. Shark eyes are very sophisticated and extremely similar to those of mammals. The iris surrounds a pupil that can be opened wide to let in a lot of light or contracted to a pinhole. Behind this is a crystalline lens used to focus images onto the retina, which contains structures known as “cones” for good vision and rods for high sensitivity to low levels of lights. Sharks cannot close their eyelids to protect their eyes, but some groups have developed a third eyelid called the nictitating eyelid to do this.

Another shark sense that is not just similar to that in mammals, but rather more advanced and mostly overlooked, is that of detection of changes in pressure. Sound is simply changes in pressure causing vibrations in air or water that are picked up by the inner ear. Sharks inner ears are highly sensitive to low frequency signals. Many species can even identify the precise direction of such sound (e.g. from the movements of an injured fish). Sharks do not have an outer ear. The entrance is just a small pore that is filled with a gelatinous compound.

Touch is simply the detection of changes in pressure applied to the skin. But sharks evolved an additional sense. This is the mechanosensory system, which operates using the lateral line: In a seawater-filled canal underneath the skin connected through small pores to the seawater are located special cells, the neuromasts, with tiny sensory hairs. The neuromasts are covered in a gelatinous dome. Only the hairs (cilia) protrude into the canal and can detect very small pressure changes. Therefore the sharks can interpret such pressure changes as nearby prey, predators or other sharks, even if other senses cannot be used.

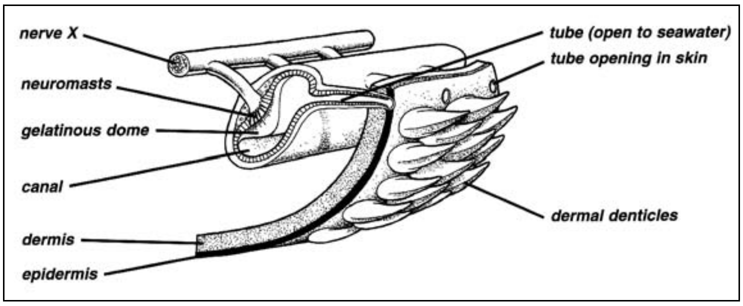


Fig. 29: Cutaway of the lateral line system in a shark (from Geoffrey Waller, 2000)

The most extraordinary sense detects the electric field given off by living animals and inanimate objects. It is also shown, that sharks can recognise the electric field emerging by salt water moving through the earth’s magnetic field. The detectors needed for this sense are the so-called ampullae of Lorenzini (Fig. 30). These receptors consist of circular arranged cells around a canal that is filled with special gelatine. The canals lead into a pore in the skin. They are scattered around the head and mouth of the sharks. The sharks can use these organs to detect prey at close quarters, even when completely buried in the seabed (up to 50 cm). Hammerheads have their ampullae of Lorenzini spread out over their wing-like heads and are therefore particularly skilled at this and can precisely triangulate the location of the prey; they do not have more receptors as other sharks, but with the spreading out of them they can increase the sensitivity of this sense (personal communication with R. Dean Grubbs, Virginia Institute of Marine Science). Deepwater sharks have been known to bite on transatlantic cables because of the electric fields that they produce. The electro-reception is also used to orient sharks in the earth’s magnetic field when undertaking long cross-ocean migrations.

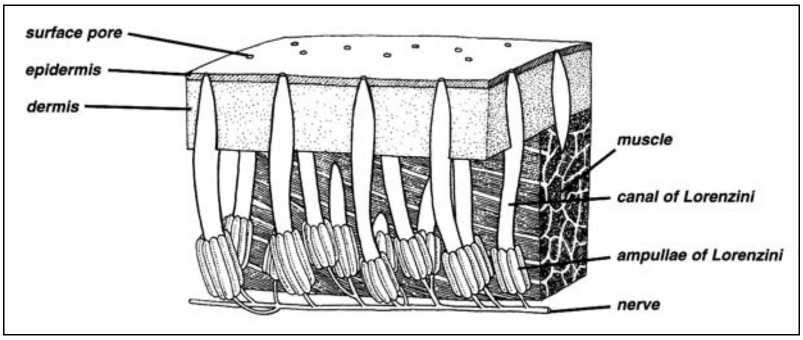


Fig. 30: Cutaway of the ampullae of Lorenzini (from Compagno et al., 2005)

2.4.9. Feeding and Digestion

Sharks have the reputation of eating just about anything that come across and fits in their mouths. This may indeed be true for a few species such as Tiger Sharks, which have been found with a large amount of diverse object in their stomachs. However, most sharks are very selective with what they eat. Most species are specialised to feed on a relatively small range of prey items.

The huge plankton feeders as Whale Sharks, Basking and Megamouth Sharks are the best examples of such specialisation. They all feed on the same prey, plankton and small fish, but interestingly they developed different strategies. Whale Sharks are random-feeders, swimming steadily through plankton blooms with wide open mouths. Megamouth Shark made their suction feeding extra efficient through the use of luminescent tissue inside of their mouths to attract prey in the deep ocean. Plankton feeding becomes only possible with the development of an efficient sieve, which is formed with gill rakes (long slender filaments).

It is interestingly remarkable that in all marine animals, plankton feeders are some of the biggest species. It has something to do with the energy flow through the food chain. From one step to the next step in the food chain energy is lost as waste products, heat energy etc. If a final consumer of

the food chain like a Whale Shark or a Blue Whale feasts on the smallest items, the plankton, they jump several steps of the chain and can use the energy without loss thereby growing big.
Once the sharks have eaten, it can be a long process of digestion, especially in cold-blooded sharks. The food moves from the mouth into the stomach, which is "J" shaped and used for storing and some initial digestion. Unwanted items never get any further than the stomach and are backed up through inverting the stomach inside out. The next part of the gut is the intestine. This is extremely short in contrast to mammals. This is achieved by the use of a "spiral valve" with multiple turns within a short section of gut instead of a very long tube-like intestine (Fig. 31). It provides a very long surface area for the digestion of the food, requiring it to pass around and around inside the apparently short gut until fully digested. Then remaining waste products pass into the cloaca and vent. The length of the valve and the number of turns depends on the type of food typically eaten.

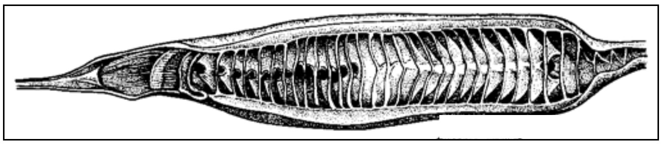


Fig. 31: Spiral valves of the Frilled Sharks (from Compagno et al., 2005)

The most obvious internal organ in sharks is the huge liver. It fills most of the body cavity. The liver makes up about 25% of a shark's body weight. This was a major product from traditional Basking Shark fisheries because it contained up to 80% in weight of very high quality light squalene oil, important for industrial, cosmetic and pharmaceutical use. The liver has two main purposes beside the normal liver functions: buoyancy and energy storage. Sharks have not evolved a swim bladder. They outweigh water and sink to the bottom if they do not swim. During the long pregnancy of the female shark the storage of energy is particularly important. The size of the liver shrinks several times during the time of pregnancy and therefore it is no wonder that in many species female sharks need at least one year "off" before the next pregnancy.

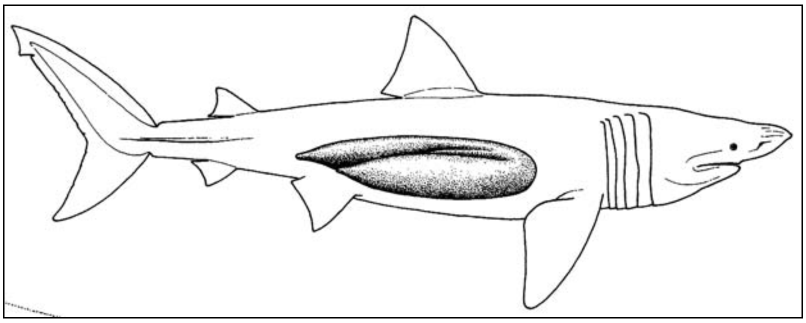


Fig. 32: The relative size of the Basking Shark's, *Cetorhinus maximus*, liver to its body (from Compagno et al., 2005)

2.5. Life History

Reproduction takes many forms in sharks. But all perform internal fertilisation. Mating has only been observed in a few species. In larger sharks, males bite the females to hold her alongside while using one of the paired claspers to transfer the sperm package. Smaller and more flexible species twine around each other.
The eggs may be laid (oviparity, in about 40% of shark species) almost immediately after fertilisation. They are carefully anchored onto the seabed, algae or corals. The size and form of the eggs vary a lot, from screw-shaped to single sacks (Fig. 33).

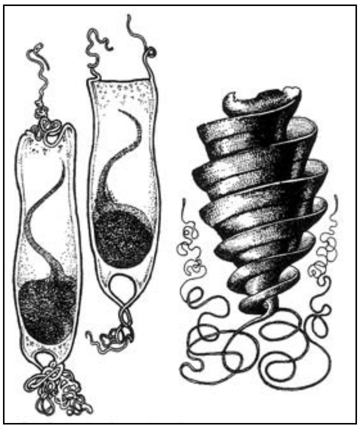


Fig. 33: Eggcases of a catsharks (left) and a hornshark (right) (from Compagno et al., 2005)

The simplest further development of oviparity is the ovoviviparity (or aplacental yolk sac viviparity, in about 25% of shark species). The female retains the eggs until they have absorbed all egg yolk, completed their development and hatched safely inside the female. Then she gives birth to fully developed pups.

Other species have developed ways to increase the amount of food available to the young inside the female, so that they are larger and better developed at birth. Some of the lamnoid sharks produce many infertile eggs that are steadily released to feed the growing young inside the uterus (oophagy). Some species produce only one fertile egg from each ovary: all the others being infertile and destined to feed the pups. Others produce several fertilised eggs and can give birth to pretty large litters. The Sandtiger Shark is notorious for “intra-uterine cannibalism”. Its pups not only eat infertile eggs inside the mother, they also eat brothers and sisters until just one survives.

The most advanced form of reproduction (in about 10% of shark species) is placental viviparity. In these species (e.g. Blue Shark, Hammerheads) the yolk sac develops into a placenta, becoming attached to the wall of the uterus. Large litters can be nourished in this way. This strategy is very similar to mammalian reproduction, but developed in sharks long before mammals evolved. But the big difference is the absence of parental care of young after birth (Fig. 34).

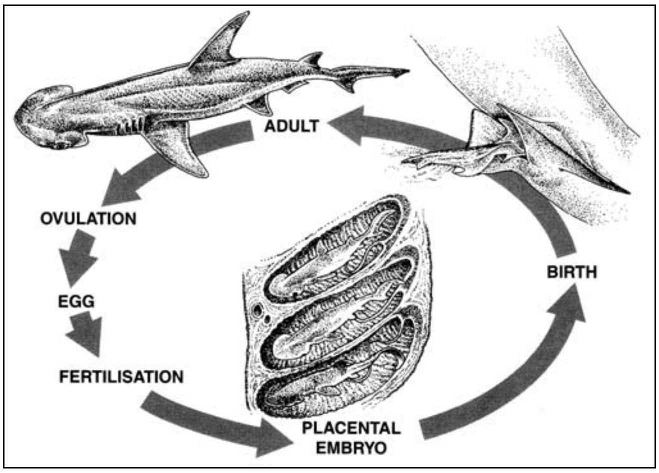


Fig. 34: Viviparity in a hammerhead shark
(from Compagno et al., 2005)

In general the life pattern of sharks may be characterized by slow growth, delayed maturity, low fecundity combined with production of a few advanced offspring, longevity, multiple breeding and large size. This pattern can be found in a number of terrestrial and marine creatures and represents one end of a scale of life history patterns. Certain bony fish might illustrate the other end. For example a salmon’s life history pattern includes rapid growth, early maturity, high fecundity combined with the production of thousands of tiny, poorly developed, delicate offspring, single breeding followed by death: a short, fast life cycle. These two ends of the scale of the life history pattern were defined by the famous ecologist Robert Mc-Arthur in 1958. He was able to explain the significance of these two ongoing patterns. He named the two strategies after the constants in Alfred J. Lotka’s formula for population growth (1926) “r-Selected” and “K-Selected”. The former species have a high adult mortality compared to that of juveniles; single breeding is favoured, so as with the salmon. In “K-Selected” species low fecundity combined with high juvenile mortality would tend to favour repeated breeding. Expanding populations will have a lower age at maturity; stable or declining populations will have delayed maturity especially when increased size, age or social status favours reproductive success. This is the case for sharks.

It can be predicted that increased predation will favour large offspring while increased resources favour smaller ones. For the Lemon Shark the most critical time is the first year when competition and predation is high. Only about half of the Lemon Shark pups survive the first year due to this competition and predation. However as they grow, their chances for survival increase to a point where there would be very few predators, other than man, that could kill a six-foot Lemon Shark.

This K-Selected life history strategy was successful for sharks the last four hundred million years. But the requirements of stable conditions, sufficient resources and low predations in many cases are no longer existent: Humans, the super-predators, have seriously impacted the environment with oil spills, chemical pollution and physical degradation. Also the fishing efforts of humans have increased in the last hundred years with huge ships and thousands of kilometres nets in the water every single day. Today this places the K-Selected species like sharks, turtles and whales in jeopardy.

(after Gruber S. H., 1990)

3. Materials and Methods

3.1. Environment

Bimini is located approximately 86 km east of Miami and lies on the north-western edge of the Andros platform of the Great Bahama Bank (25°42’N/79°17’W). The study area lies between the two Bimini Islands (northern and southern island, approximately 10 km^2 and 8 km^2 respectively) and represents the main lagoon (approximately 21 km^2). It includes the areas North Sound, Alice Town Channel, Shark Land, Bone Fish Hole and other areas (Fig. 35). It is a mangrove fringed lagoon, which presents two of the three nursery grounds for the Lemon Sharks at Bimini. This Lagoon has two openings to the sea: One small and deep Channel between South Bimini and North Bimini at the west side and a large and shallow opening at the east side. The tidal range is between 73.2 cm (National Oceanic & Atmospheric Administration, NOAA, Washington, USA). Water temperatures are throughout the year in a range between 24-28.5°C (Newell et al., 1959), in this study recorded temperatures were between 20-31°C.

Along the shoreline the red mangrove (*Rhizophora mangle*) dominates, but black mangroves (*Avicennia germanians*) are also found, if less abundantly (Newman, 2003). In the water we find the following seagrass habitats in different occurrances: turtle grass (*Thalassia testudinum*), shoal grass (*Halodule beaudetti*), manatee grass (*Cymodocia manatorum*), sargassum weed (*Sargassum spp.*) and laurencia (*Laurencia spp.*).

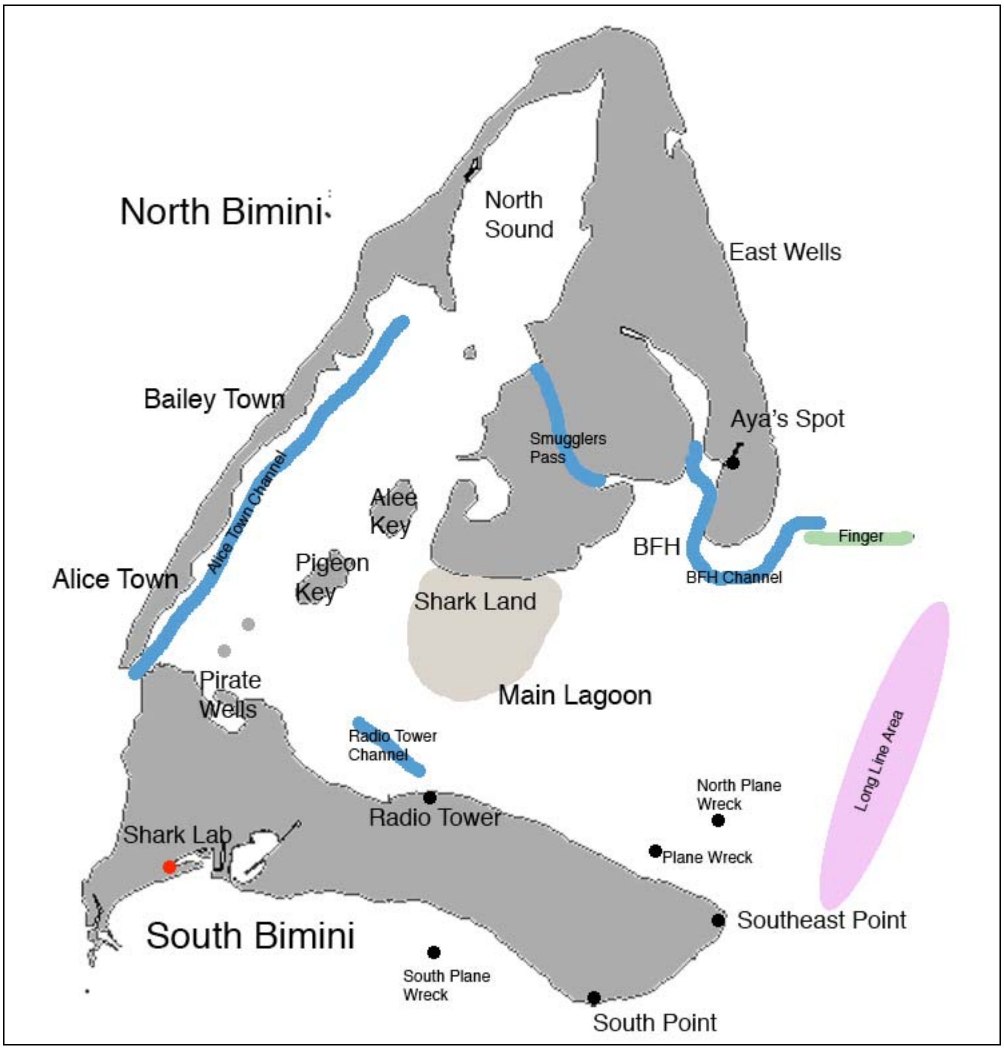


Fig. 35: Overview Bimini Islands, Bahamas.

3.2. Objectives

1) Determine home range extent of subadult Lemon Sharks around Bimini Islands through computer analysis of the collected manual and passive tracking data;

2) Determine movement pattern of subadult Lemon Sharks in the Main Lagoon of Bimini Island through manual and passive tracking techniques;

3) Compare findings to those of previous studies (Gruber S. H. 1988; DeMarignac J., 2000; Sundström F., 2001; Harry, A. 2005) to describe change of home range utilisation and movement pattern over time.

4) To identify the causes behind any spatial differences in the utilisation of the waters surrounding the Bimini Islands.

3.3. Data Collection

Subadult lemon sharks are caught from a 5.4 m powerboat (Proline, Ft. Lauderdale, Florida, USA) with rod and reel fishing in the Main Lagoon of Bimini Island, Bahamas (specifically Bone Fish Hole, Shark Land, Airplane Wreck. See Fig. 35). Therefore we used a short rod with a 50 lbs monofilament and a circle hook on a 200 cm leader wire attached with a swivel. Circle hooks were used to minimise the risk of shark being hooked in the stomach. A balloon was used as a float to guarantee that the bait floats in the water column. This was done to minimise the risk of catching stingrays. As bait were used freshly obtained grunts (*Haemulidae spp.*), snappers (*Lutjanidae spp.*), mojaras (*gerreidae spp.*) and jacks (*Carangidae spp*). The bait was caught by spear fishing. To attract the sharks frozen chum blocks, Menhaden Oil and when available, freshly caught fish (bled, diced) were used.

Once a shark was hooked, it was reeled in and the leader wire was attached to a cleat on the bow of the boat. The shark was then held in position on the first dorsal fin until a rope was attached with a hangman’s noose to the caudal fin. The other end of this rope was attached to another cleat in the stern of the boat. The shark was now secured and ready to process safely. First the length was measured in three positions: pre-caudal length (PCL), fork length (FL) and total length (TL). Then sex was specified and fitness defined.

The sharks with the predetermined criteria (species Lemon Shark, healthy, 125-200 cm) received an active, continuous acoustic transmitter array (CT-05-36, Sonotronics, Tucson, Arizona, USA, detectable from both a manual hydrophone and Sonotronics Underwater Receiver) attached at the base of the shark's first dorsal fin (Fig. 36). The transmitter was attached with stainless steel darts and 150 lbs test monofilament through the shark’s skin located at the base of the first dorsal fin on the right or left side. Then the shark was immediately released and tracked for several minutes to ensure it was swimming healthily. Handling of a shark took no longer than 10 minutes to minimise the stress to the animal. No sharks were killed as a result of the handling procedure.

We used transmitters with a typical battery life of 36 months and which emitted ultrasonic pulses between 76-81 kHz. Each transmitter was pre-programmed with a unique three or four-digit code.

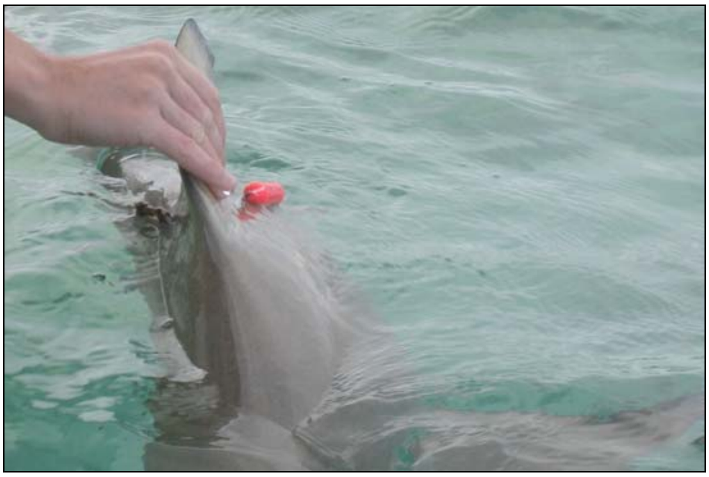


Fig. 36: Attached transmitter to the shark Katris (by Tristan Guttridge 2007)

Lemon sharks with a transmitter were tracked using a hydrophone and receiver from small flat-bottomed Carolina Skiffs (Carolina Skiff, Waycross, Georgia, USA) with 25 hp or 50 hp outboard motors (Mercury, Inc.). The hydrophone, model DH-2 (Sonotronics, USA), was used to detect the signal output from the ultrasonic transmitters. The sensitivity was -84 dBV, the beam width +/-6° at half power points. The hydrophone was assembled on PVC piping with 125 cm length. The receiver model USR-D (Sonotronics, USA) with a bandwidth in the range between 67-82 kHz was used. A 12 V motorcycle battery powered it. To listen to the output a pair of headphones was attached to the receiver. The whole tracking equipment was packed in a small cooler during tracking to prevent it from becoming wet and for simple and secure transportation.

Sharks were tracked using teams of 2 to 4 people. Tracks for 8, 16, 24, 48, or 72-hours were planned: teams tracked for 6 or 8 hour shifts and then were relieved by another crew. These tracks were continuous: we tracked throughout day and night and across all tides. Tracking crews remained between 30-100 meters from the shark depending on water depth and ocean conditions. One person sat at the bow of the skiff with the hydrophone in the water listening for the shark. This person told the driver of the boat the bearing and distance of the signal. Every 5th minute of tracking we recorded the location of the boat (GPS, Garmin, Olathe, Kansas, USA), the compass bearing to the shark and an estimated distance to the shark based upon the strength of the acoustic signal. From this the position of the shark relative to the GPS location of the boat was calculated. Every 6th location or every 30 minutes additional environmental data was recorded, including water temperature, water depth, surface conditions, tidal state, wind speed, cloud coverage, bottom formation and lunar cycle. Temperature was recorded with ibuttons (MAXIM integrated products, Sunnyvale, CA, USA) every 5 minutes, hanging outside of the boat in PVC tube attached with a cord. Depth was recorded with a depth stick (PVC tube, 150 cm in length, 0-150 cm labelled in 1 cm intervals) that was stuck three times into the water, recording the average of the three readings. This information allowed determining whether certain environmental factors were influencing the shark's movements.

Three types of search pattern were done. The starting point of the first pattern was South-East-Point from where we searched around the east corner of South Bimini in direction north, zigzagged the large entrance of the Main Lagoon up north till Finger/Bone Fish Hole and back into the entrance of the Main Lagoon. The second pattern started just around the east corner of South Bimini, headed first towards Alice Town and then crossed the Main Lagoon towards Bone Fish Hole. The third pattern started at Radio Tower, crossed Radio Tower and zigzagged from Pirate Wells up north towards Pigeon Keys (Fig. 37).

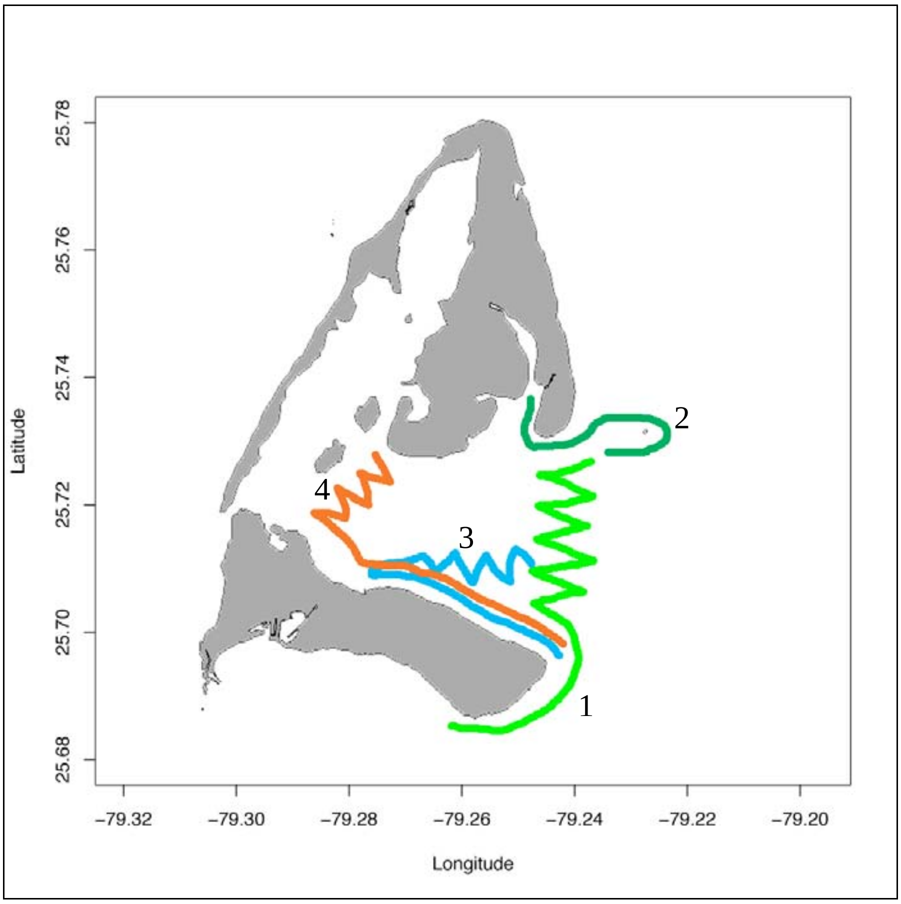


Fig. 37: Used search patterns. 1) Starting at South Point approximately 100 m away from shore, when reached lagoon zigzagging towards Bone Fish Hole and eventually zigzagging back. 2) If zigzagging a third time of pattern 1 was not successful: searching around finger into the Bone Fish Hole Channel and back. 3) Starting at South-East Point, following along the channel, passing the wreck till Radio Tower is reached, turning and zigzagging back further away from shore. Then falling into pattern 1. 4) Starting at South-East Point, following the channel, passing plane wreck, passing Radio Tower, following Radio Tower Channel, zigzagging from Pirate Well towards Shark Land and back.

Passive tracking was established with 9 submersible ultrasonic receivers from Sonotronics, model SUR-1 with a battery lifetime of 5-6 months. Due to other studies the receivers were set in the area of Bone Fish Hole, North Sound and Shark Land/Pirate Wells (Fig. 41). The depth of the receivers was chosen aground the water depth at low tide so that no receiver ran dry, as the hydrophones of the receiver have to be in the water to recognise the signal. The receivers logged for 5 months.

3.4. Data Analysis

Data was stored with Microsoft Excel. All shark locations were then plotted on a map of the waters surrounding Bimini using R (v. 2.5.1, open source statistical program, GNU, language and environment). This allowed visualising of the areas that the sharks were using during different times of the day and to define home ranges of subadult Lemon Sharks. The movement patterns were analysed for following factors: daytimes, tide phases and water depth. To evaluate differences in space usage and movements in different day periods, the data was divided into four periods: dawn (05:00-06:59h), day (07:00-17:59), dusk (18:00-19:59h) and night (20:00-4:59). The tide phases were divided into 4 categories: high tide (dead high ±1.5h), low tide (dead low ±1.5h), falling and rising tides (between high and low tides). Dead high and dead low tide were taken from tide tables from National Oceanic & Atmosphere Administration, Washington, USA (NOAA) and corrected with a factor of 30 minutes delay, which was defined through experiments at the landing stage of the Shark Lab and in Bone Fish Hole. Data was then converted into text file (.txt) format to allow importation into R.

The data was analysed in the following order: A) home range with 95% minimum convex polygon (MCP95) approach of each shark, B) home range core with 50% MCP, C) daytime movement pattern, D) tidal phase movement pattern and E) depth of water column in which sharks are swimming.

4. Results

Four sharks (145-196 cm TL, females) were telemetered and actively tracked between November 2006 and January 2007. A total of 613 position fixes were taken, representing approximately 51 hours of tracking. We had contact with each shark between 2-5 times and took position fixes between 14-85 per track (Fig. 38). Eleven sharks (including the four actively tracked sharks) were tracked passively with the submersible receivers. A total of 1004 usable records were taken in the time between 26th January and 15th June 07.

This information was compared with previous studies:

-Harry A. & Franks B. (2005): 6 sharks, 2228 position fixes and 186 hours tracking
-Sundström F. (2001): 10 sharks, 4709 position fixes and 417 hours tracking
-De DeMarignac J. (1997): 28 sharks, 11785 position fixes and ~2200 hours tracking
-Morrissey & Gruber (1988): 6 sharks, 228 contact hours
(Summary in Appendix Tab. 5).

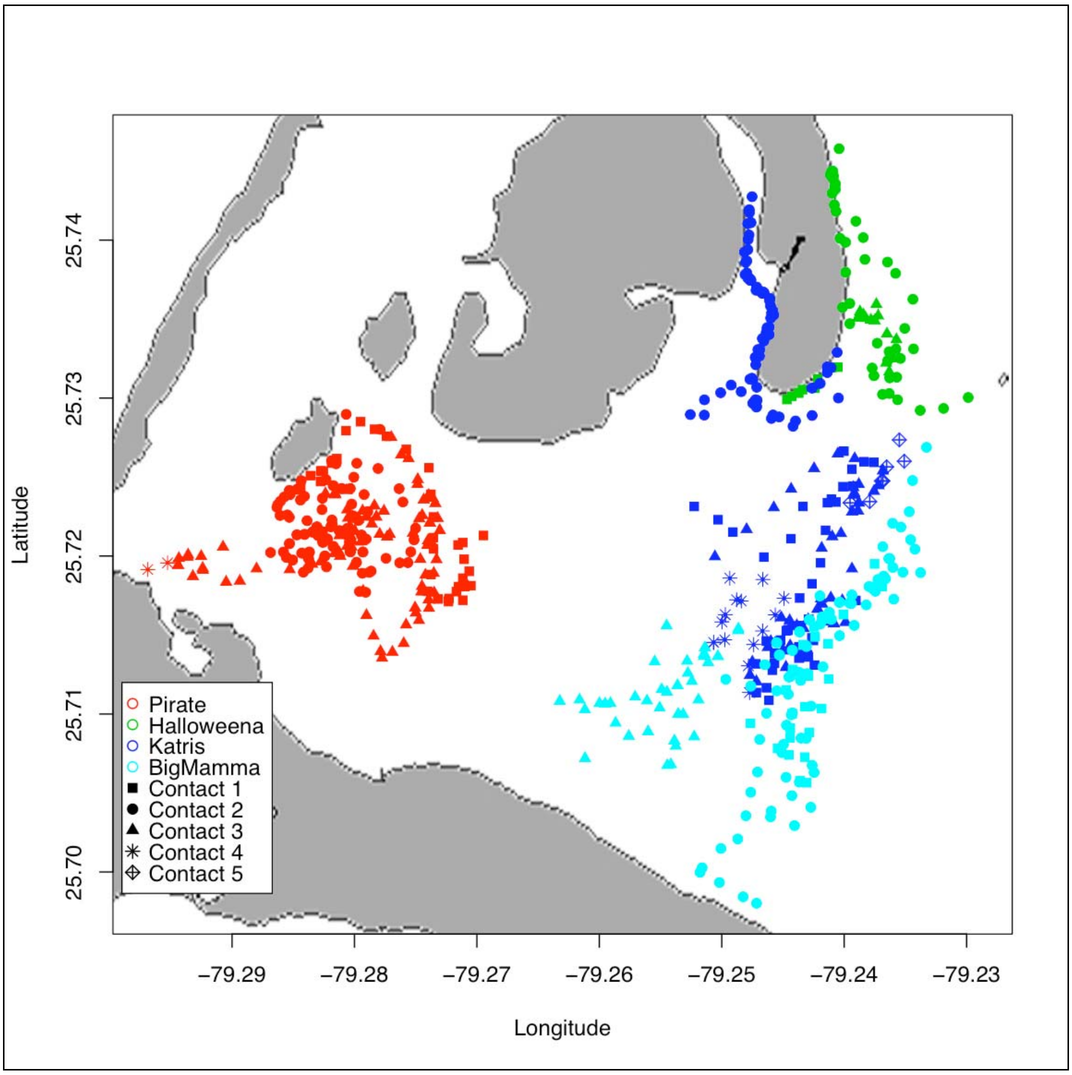


Fig. 38: 5-minutes-GPS positions of all four sharks, coloured in shark individual and signed in contact numbers.

4.1. Home Range

The Minimum Convex Polygon (MCP) analysis for each shark showed home ranges between 1.09-3.74 km^2 (Tab. 1). To preclude outlying points only 95% of the MCP were calculated:

% of MCP	Pirate [km^2]	Halloweena [km^2]	Katris [km^2]	Big Mamma [km^2]
95	2.24	1.09	3.74	3.62
100	2.73	1.40	4.13	5.19
Ratio	0.82	0.78	0.91	0.70

Tab. 1: Minimum Convex Polygon (MCP) analysis for each shark.

The Ratio between 95% MCP and 100% MCP shows an estimate of how far the excluded points are distributed. Excursive ascents in the higher percent calculations show outlying points or “excursions” out of the usually used home range (Fig. 39). The 95% MCP home range of Pirate was 2.24 km^2, Big Mamma 3.62 km^2, Halloweena 1.09 km^2 and Katris 3.74 km^2.

The positions of the submersible receivers included into the 95% MCP increased the home range size multiple times.

In previous studies home range sizes of between approximately 5-27 km^2 were found, with a mean of approximately 21 km^2. DeMarignac found in his study that more than half of the home ranges were in between 17-22 km^2 (Harry A. 2005).

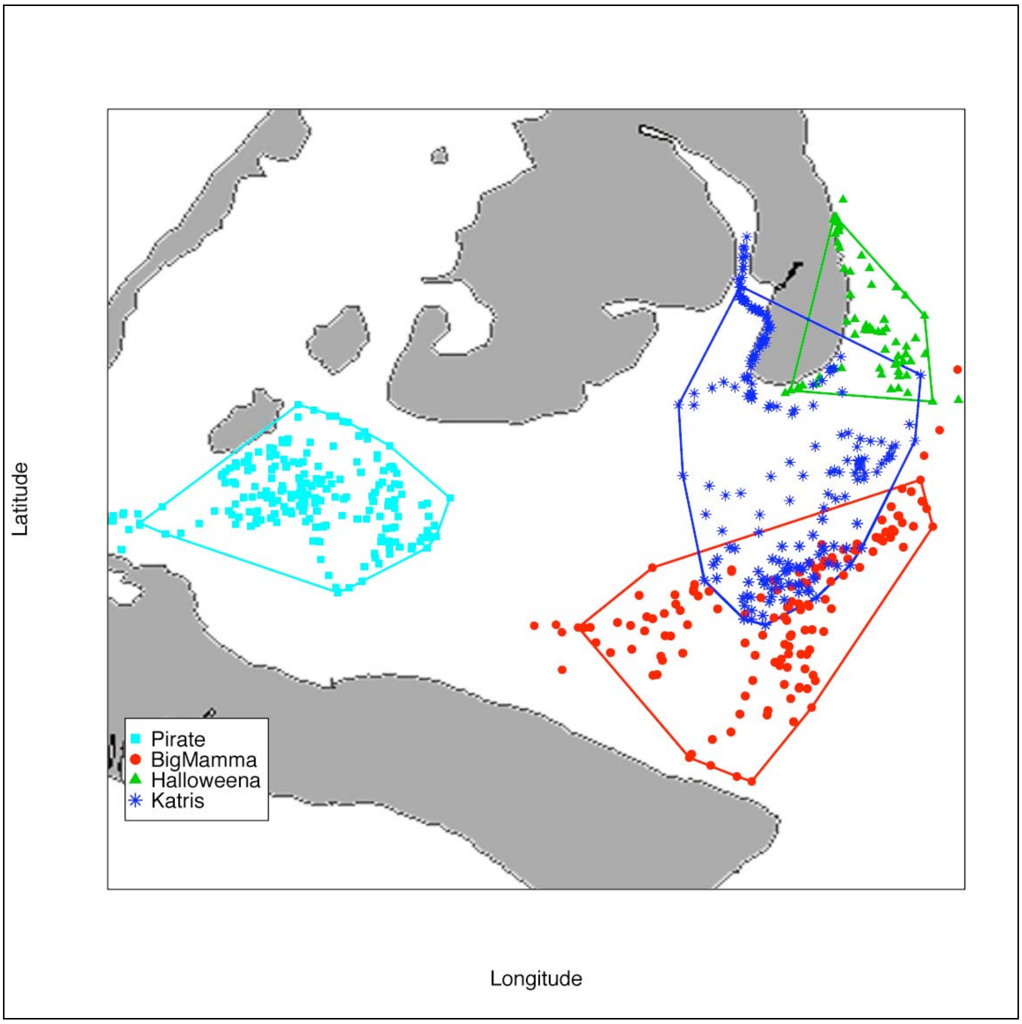


Fig. 39: Home range visualisations of all four sharks: 95% Minimum Convex Polygon utilisation distribution estimate.

4.2. Movement Patterns

4.2.1. Different Daytimes

In the longest track of “Pirate” the pattern which DeMarignac (2000) called “Mini E-W” (Fig. 47, appendix) can be seen. This pattern is defined as following: The positions at daylight are in a location approximately between Pigeon Key - Radio Tower Channel - Pirate Wells and during dusk Pirate was heading towards Alice Town Channel. This shark showed a similar pattern also in other tracks, but in this study the sharks were usually lost before or during dusk. Therefore are no data available from Pirate in nightly active tracking. It is not known if Pirate was close to Alice Town or not. The passive tracking method showed a similar behaviour: this shark was very few times in the night in the area of Pirate Wells and Shark Land (each 1 record) and Pirate was never recorded during night in another area. But during daytime it was seen very often in passive tracking around Pirate Wells and Shark Land (223 records). Only 3 records were made in the entrance to the North Sound. This could be a indication to the Mini E-W pattern as described from DeMarignac, but without more data from this shark it is not possible to define an exact pattern.

The shark “Big Mamma” was the only shark which it was possible to track over a longer time during the night. In the longest track of her the positions show a N-S pattern over the whole track. The shark swam up and down all over during the day until night, whereby she headed towards South Bimini. When she reached the island, she swam in the Channel outwards in the direction of East Point and was lost. The passive tracking showed a very different trend of pattern: Big Mamma was found 101 times in Shark Land, 9 times in Pirate Wells and 5 times in Nurse Channel during the daytime. Big Mamma was never recorded passively at night. This could show a long distance East-West distribution but without data from nights no pattern can be defined definitely.

“Halloweena” did not show any known pattern. This shark was found every time around Bone Fish Hole Channel entrance and East Wells and was only actively tracked during daytime. The passive tracking points show a few logs in Bone Fish Hole during the day and 19 logs inside this area in the entrance of Smugglers Pass. Interestingly this shark was recorded 2 times in the entrance of North Sound.

In the longest track of shark “Katris” an opposite pattern to “Big Mamma” can be seen: a S-N pattern. It seems as if this shark was swimming from a daily location in the middle of the Main Lagoon entrance to a more northern location towards Bone Fish Hole. A few points in another track of “Katris” were recorded at night in the Bone Fish Hole Channel (BFH Channel). This could be an additional indication for such a S-N pattern. The passive tracking data showed that this shark is intensively using the area of Nurse Channel and Bone Fish Hole during day. This supports the thesis of a S-N pattern. But the shark was also recorded during day in the inner area of BFH and even in the area on the other side of the Smuggler Pass in the North Sound. During the night this shark was recorded in a similar frequency as during the day in Aya’s Spot and Smugglers Pass. But Katris was not recorded in Nurse Channel during the night as many times as during the day (night 10, day 123).

Six of the other seven sharks in the passive tracking program showed a strong use of the areas around Bone Fish Hole and North Sound. Some showed a trend towards a day-night pattern between these areas in one and the other direction. But one shark showed, similar to Pirate and Big Mamma, a W-E pattern with daily stays in Pirate Wells and Shark Land (30 records). At night this shark was found 40 times at Aya’s Spot.

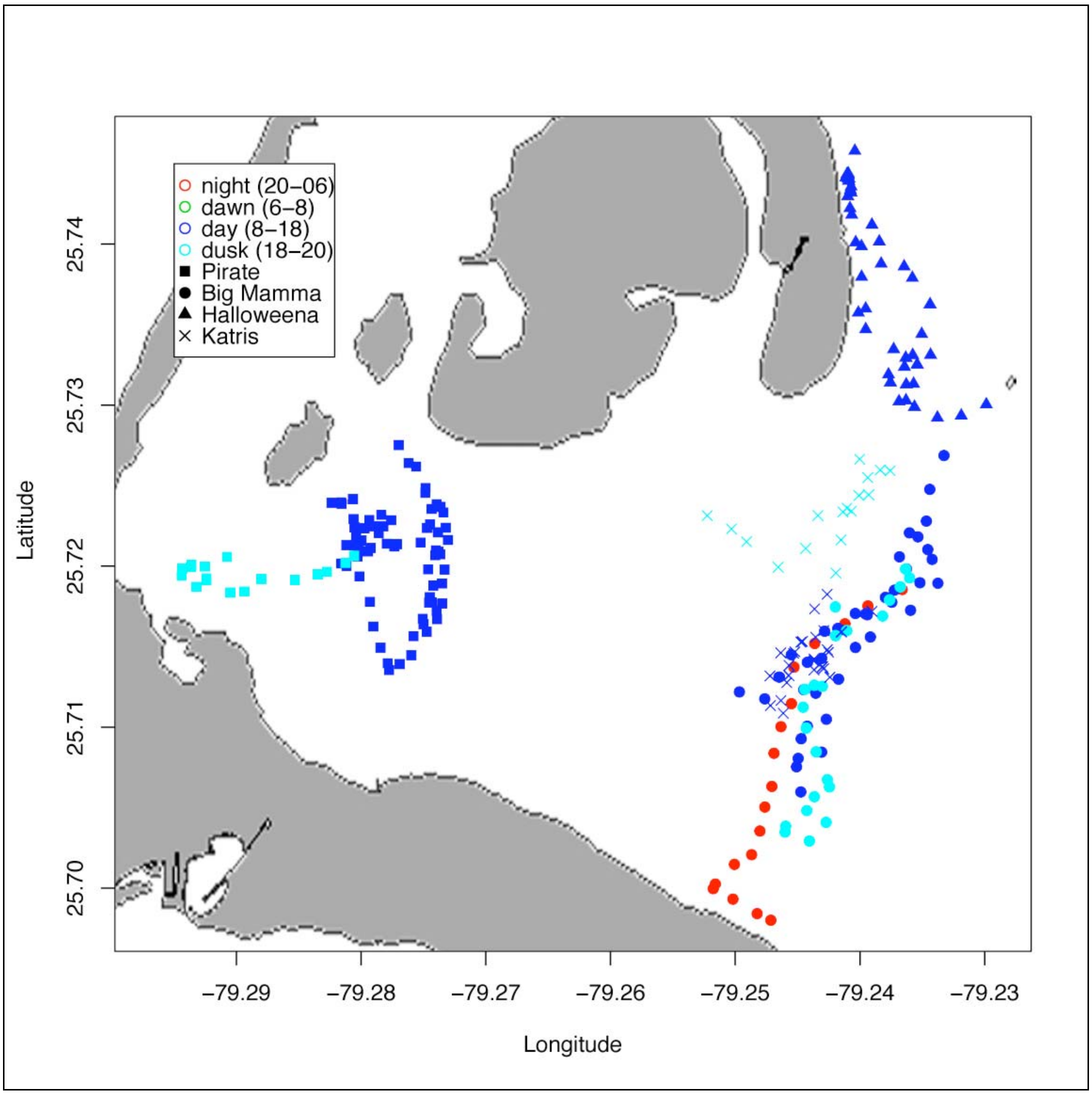


Fig. 40: Longest track of each of the four sharks. Individuals are marked with different signs, times of day with different colours.

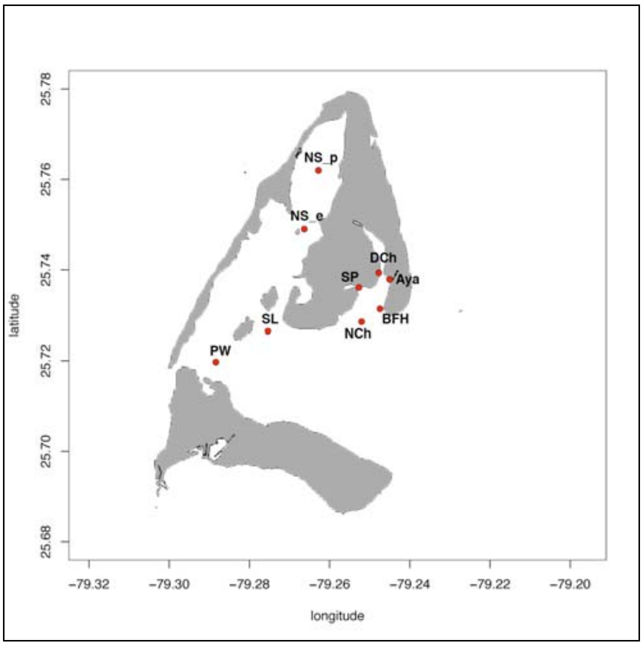


Fig. 41: Overview submersible receiver locations: NS_p = North Sound pole, NS_e = North Sound east, SL = Shark Land, PW = Pirate Wells, NCh = Nurse Channel, BFH = Bone Fish Hole, SP = Smugglers Pass, Aya = Aya's Spot, DCh = Drug Channel

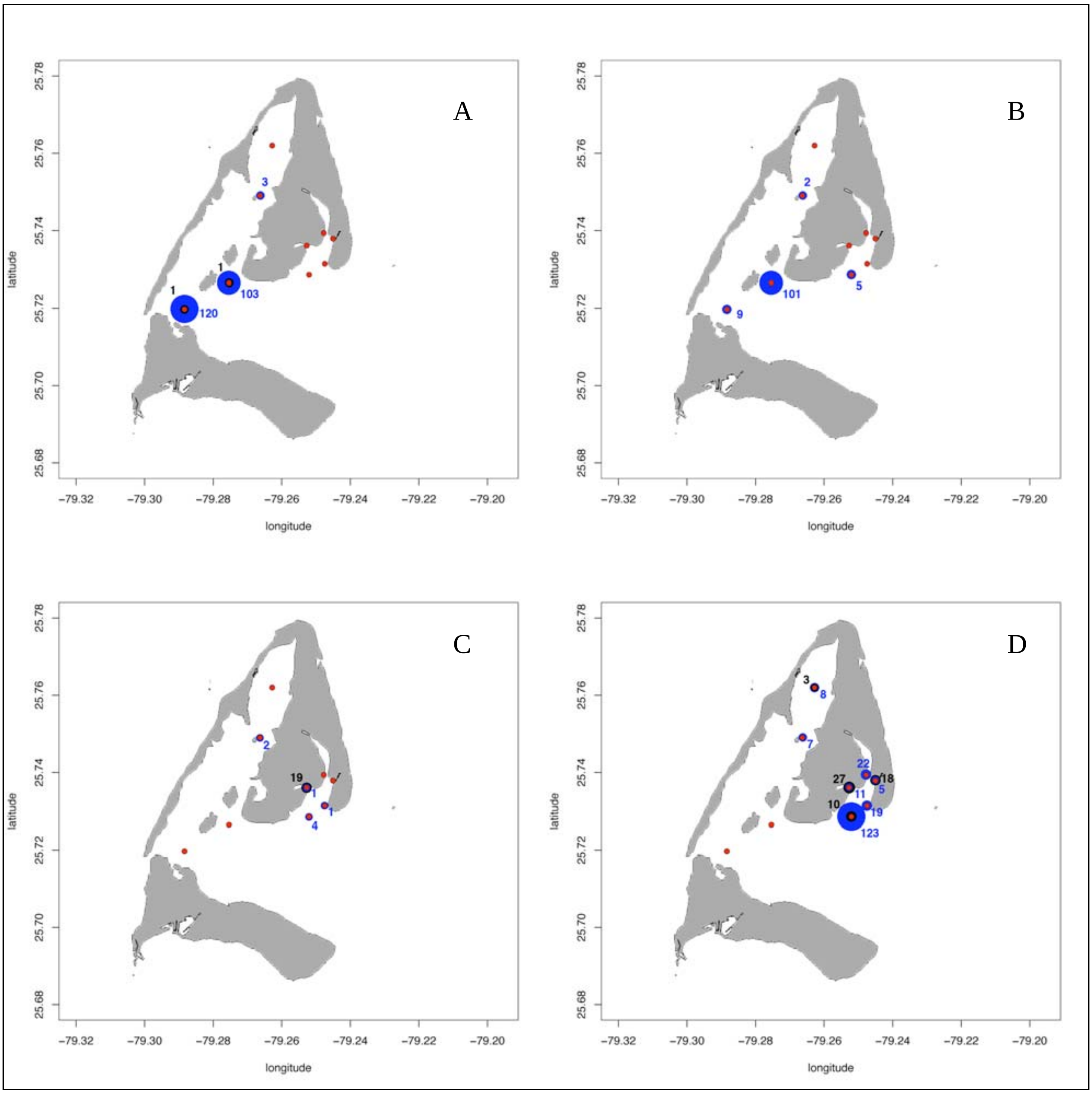


Fig. 42: Submersible receiver records of four sharks. A) Pirate. B) Big Mamma. C) Halloweena. D) Katris. In blue are marked the records during day and in black the records during night.

4.2.2. Different Tidal Phases

All 5-minutes-GPS positions were analysed according to which tidal phase they were recorded in (Fig. 41A). The high tide (red) and low tide (green) are separate from each other and the other colours are in between. The high tide points are all located in a position in the middle of the lagoon, where the seabed dries out at spring low tides. The low tide points are all located in an area in which water is always deeper. Especially are the dots in the north around BFH and BFH Channel: One track was in the channel over falling-low-rising and therefore the shark could not swim in another area as inside the channel. When the shark swam outside in deeper waters, it was close to high tide and night and the signal was lost.

The round dots represent the shark “Halloweena”. This shark was very close to the shore (shallow water) at high tide and swam eastwards into deeper waters the closer the low tide came during falling tide (dark blue). During high tide she was never found eastwards in the deeper area.

“Big Mamma” (stars) and “Katris” (triangles) were located in a very similar area. Both used similar location at different tides: at high tides they were found more close to Shark Land where the lagoon sometimes dries out, but never more eastwards in deeper water. Only at low tide were these two sharks found in easterly positions in deeper water.

“Pirate” (squares) showed a comparable pattern to “Big Mamma” and “Katris”: she was also located close to Shark Land at high tides and only at low tides she was found in deeper areas. But she was swimming in deeper areas located in a westerly position in the lagoon.

If we look at previous studies, we see a similar pattern. In Figure 41 B all GPS positions of A. Harry’s study (2005) are shown coloured in different tide phases. The red dots, symbolising the high tide, are found at the location of shallow areas and mid-tide in the middle of the Main Lagoon or very close to the shore. Just a few points are outlying this pattern. The points at falling and rising tides are in between the high and low tide dots.

In figure 41 C and D the GPS location of the studies of Sundström and DeMarignac are shown. To better visualise, only high and low tides are shown. In these figures the distribution of the locations is especially well visible. Red dots are found in the middle of the Main Lagoon and very close to the shore. Green dots are located at the periphery of the Main Lagoon and bit further away from shore.

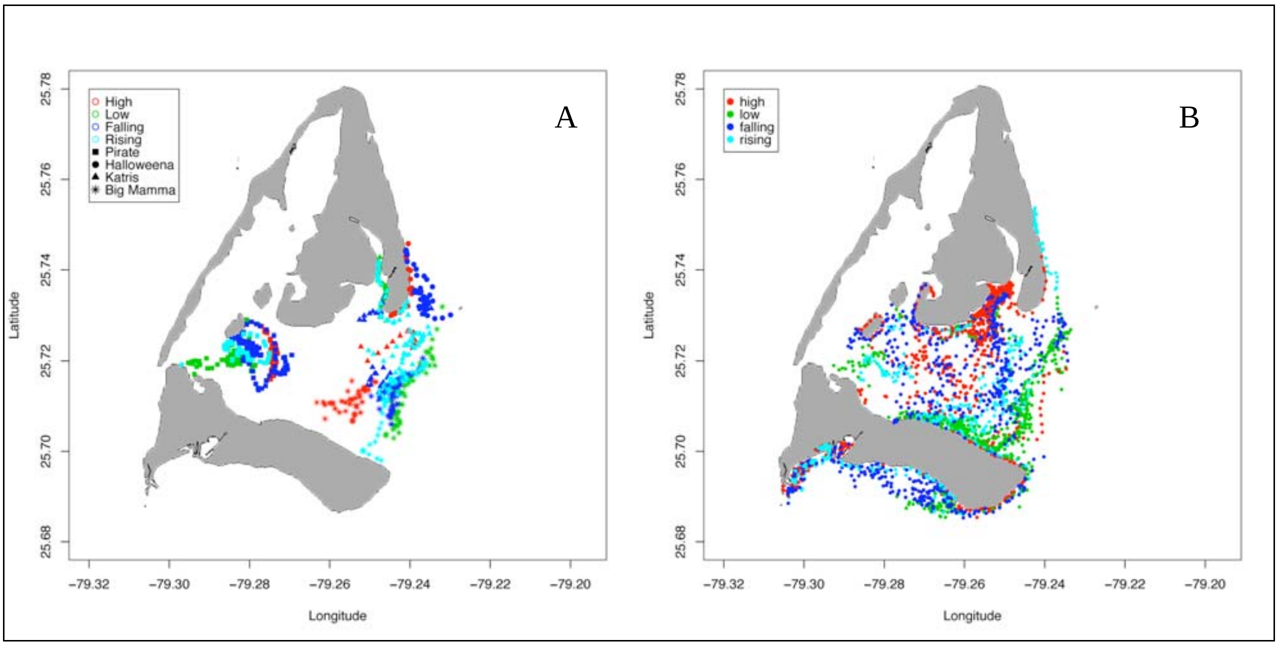


Fig. 43: GPS locations of the tracked sharks coloured in different tide phases. A) Study of Caviezel S., 2006-2007. All points of the four sharks are shown. B) Study of Harry A./Franks B., 2003-2005. All points of the six sharks are shown. To be continued.

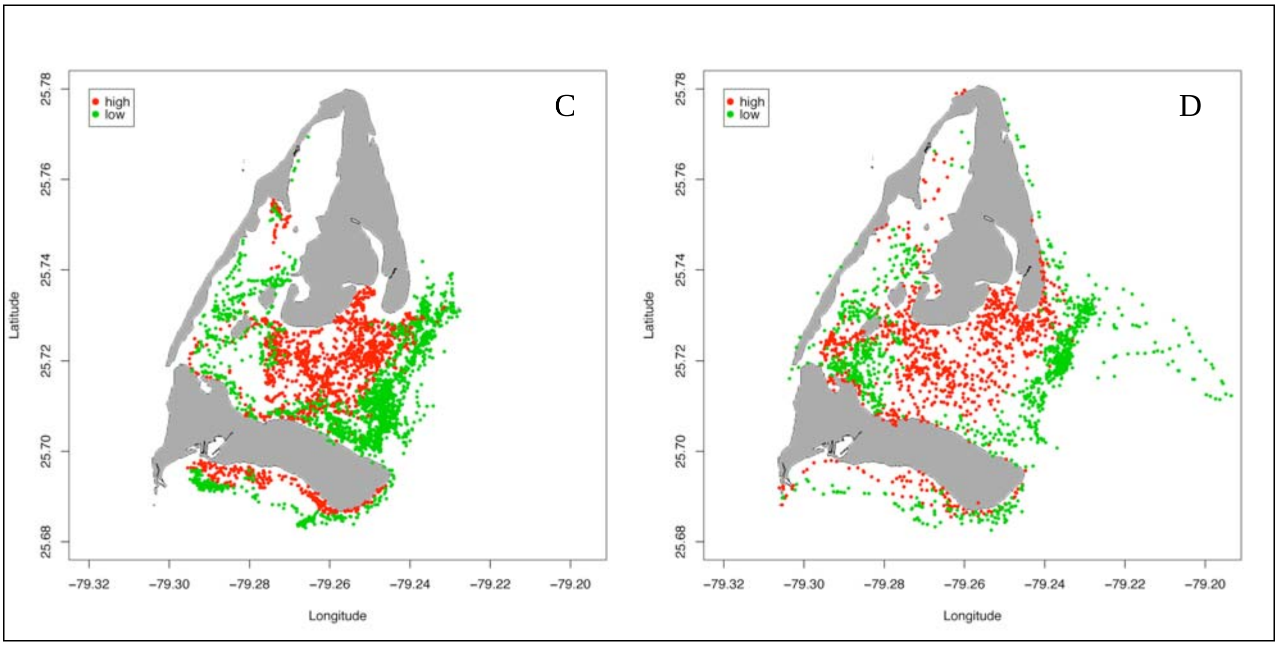


Fig. 43: continued. C) Study of Sundström F., 1996-1997. All points of the ten sharks at high and low tides are shown. D) Study of DeMarignac J., 1992-1995. All points of 24-hours tracks from the 28 sharks at high and low tides are shown.

4.2.3. Water Depth

The distribution of the water depth for all four sharks is normal (Fig 42A). 579 data points were used, mean = 84.58 cm, 1st Quartile = 60 cm, 3rd Quartile = 85 cm. The shark's specific water depths compared to the different tides at that time was proven with the analysis of variance (ANOVA). This gives the result that the depths are not significantly different: P= 0.0859, but as the Adjusted R-squared of 0.0062 shows, the explanatory power is very low. The box plot in Figure 42B shows that the sharks are using a depth range of between 65-80 cm at all tides approximately 50% of the time.

The same analysis was done with all four studies (DeMarignac 1997, Sundström 2001, Harry 2005 and this study)(Fig. 42C+D). 11'854 data points were used, mean = 78.62 cm, 1st Quartile = 60 cm, 3rd Quartile = 90 cm. The results of the box plot are listed in table 4. Anova test gives P = $1.6564e^{-8}$, Adjusted R-squared = 0.003878 (also very low). This box plot shows an almost identical depth range that the sharks are using at all tides approximately 50% of the time, namely a range of between 60-85 cm.

Single sharks of this study were analysed and the results of Anova showed that the depths are significantly different: Katris P = 0.00377, Halloweena P = 0.002823, Big Mamma P = $1.016e^{-5}$. Only Pirate showed no significant differences: P = 0.1869. The Adjusted R-squared values are: Katris = 0.05786, Halloweena = 0.1248, Big Mamma = 0.1544, Pirate = 0.0093.

The water depth within which the sharks are swimming does correlate with the shark size (TL). But in contrast to the expected result, depth negatively correlates with the body size (Fig. 43 A). The combined result taking into account all 48 sharks from all studies (current study included) shows a positive correlation as expected (Fig. 43 B).

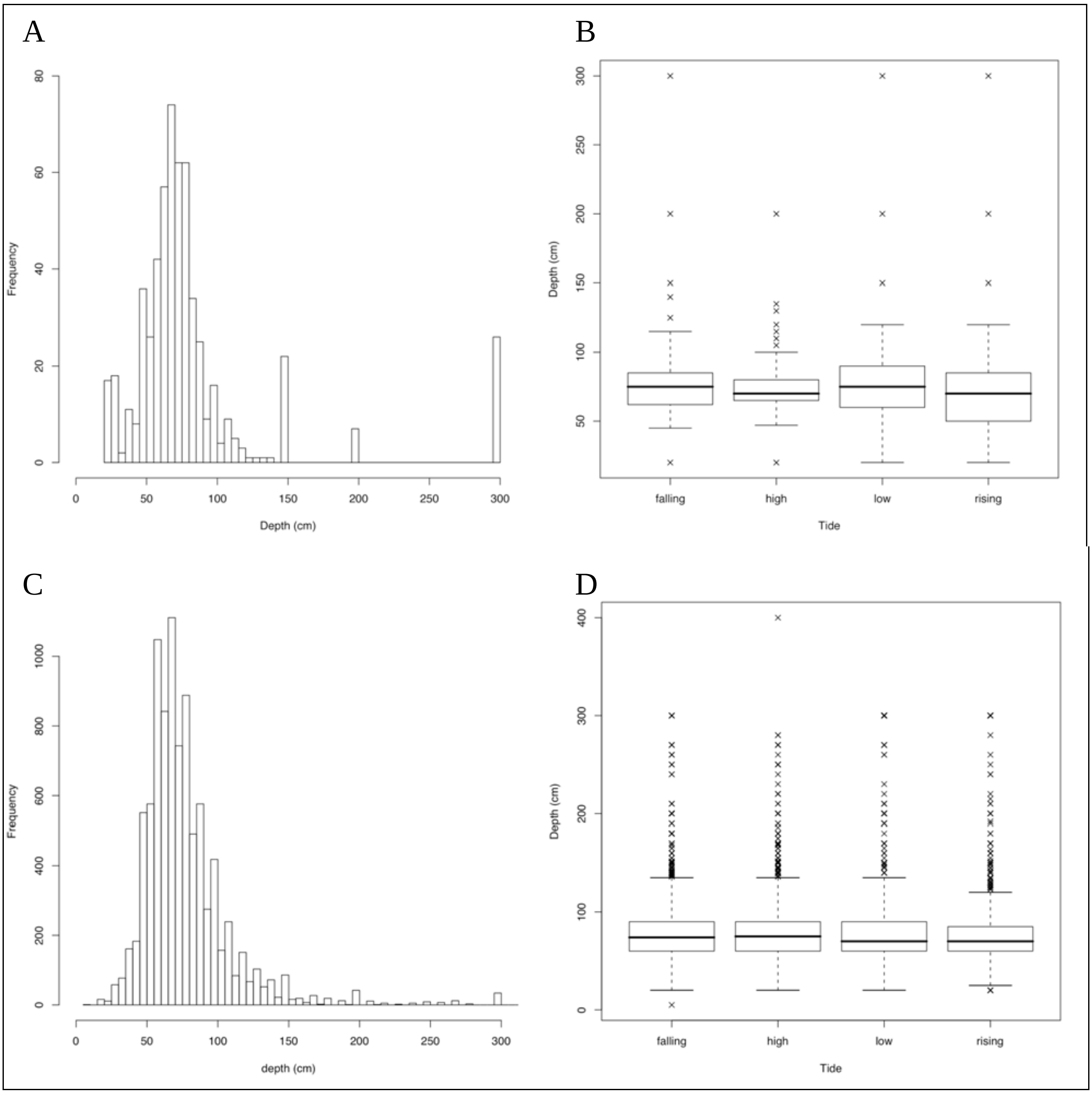


Fig 44: A) Histogram of the depth distribution in this study. B) Box plot of water depth at different tide phases in this study. C) Histogram of the depth distribution in all four studies combined. D) Box plot of water depth at different tide phases in all four studies combined.

This study				
[cm]	high	falling	low	rising
Minimum	20.00	20.00	20.00	20.00
1st Quartile	65.00	62.00	60.00	50.00
Median	70.00	75.00	75.00	70.00
Mean	76.26	81.90	93.63	84.70
3rd Quartile	80.00	85.00	90.00	85.00
Maximum	200.00	300.00	300.00	300.00

Tab. 2: Results of the box plot comparing water depth at different tide phases of this study.

All four studies combined				
[cm]	high	falling	low	rising
Minimum	20.00	5.00	20.00	20.00
1st Quartile	60.00	60.00	60.00	60.00
Median	75.00	74.00	70.00	70.00
Mean	80.79	80.10	77.95	75.38
3rd Quartile	90.00	90.00	90.00	85.00
Maximum	400.00	300.00	300.00	300.00

Tab. 3: Results of the box plot comparing water depth at different tide phases of all four studies.

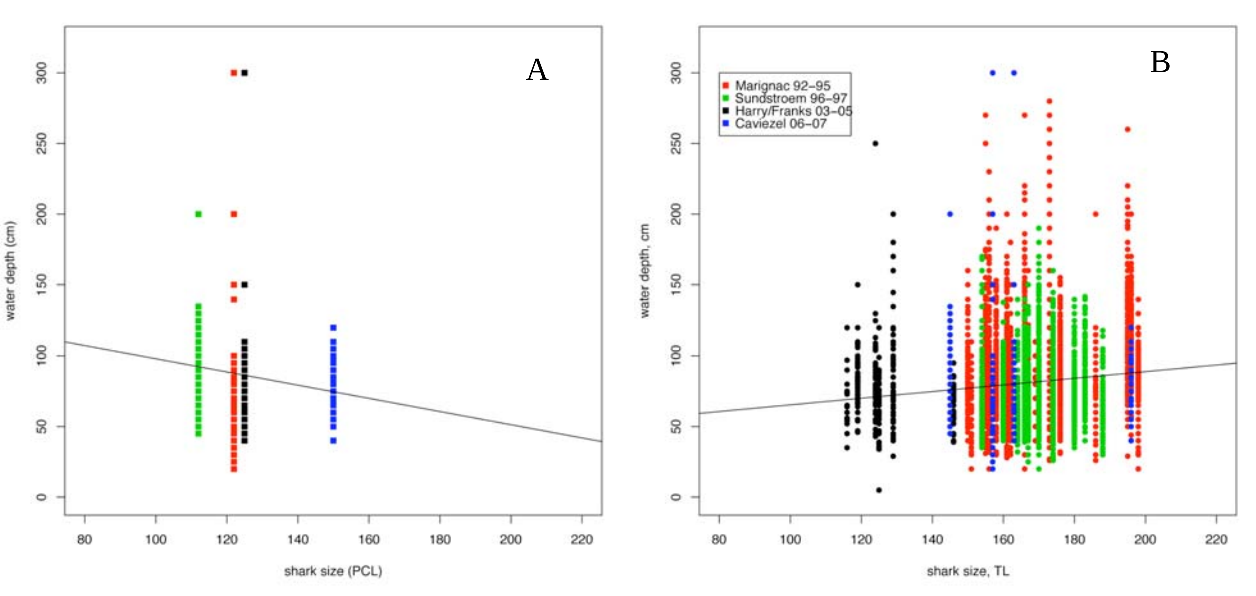


Fig. 45: A) Shark Size (TL) compared with water depth of all four sharks of this study. P-value: 0.00952, Adjusted R-squared: 0.00988. B) Shark Size (TL) compared with water depth of all 48 sharks of the three previous studies and this study. P-value: < 2.2e-16, Adjusted R-squared: 0.01103, Minimum = 5, 1st Quartile = 61, Median = 75, Mean = 81.35, 3rd Quartile = 93, Maximum = 400, TL 116-198.

5. Discussion

5.1. Home Range

The small Minimum Convex Polygon of 95% of home range sizes (MCP95) of active tracking in this study showed that the sharks prefer to stay over a long time in a relatively fixed area (1.09-3.74 km^2). In the four weeks of the biggest effort in active tracking some sharks were rarely found there in passive tracking. After this time these sharks were recorded in very different places to the active tracking locations. This is an indication that the sharks were using a small habitat for a couple of weeks and changed the location.

In all three previous studies this behaviour of having relatively small and fixed home ranges from active tracking was never recognised. If we include passive tracking data, the home ranges are similar in size. A big influence on the shark's behaviour could have been the newly built shipping channel as an elongation of the Alice Town Channel. This was done to guarantee secure access for big boats to the new holiday resort north of Bailey Town. All these building activities had an influence on the environment (mangrove areas got cleared, landmass got dislocated, houses of an amount of 1/3 of the town were built etc.). Another more likely explanation is that we are just too low on data and did not get records of the sharks when they were making an excursion. The MCP95 areas from active tracking compared with the core home ranges (MCP50) of the previous studies showed that these results are of an equal size. This means that in this study sharks were observed only in the core area of their home range and we did not have the luck to follow them into a bigger area. The sharks were observed most often during daytimes and only very few times at night. Most likely it would be possible to get bigger home ranges with more data throughout the day and, essentially, at night. The calculated home ranges complied with the daylight home range the best. The total of 51 hours of tracks and 2-5 contacts to a shark are very little data. This small amount of data came from the long time we needed to catch the sharks. The aim was to catch approximately 10 sharks, starting in October after the first month of preparing, setting and learning the tracking techniques. In September, the beginning of this study, the sharks were taking the hooks and we had at least on shark almost every fishing trip. At the end of October/beginning of November the weather got colder fast. The air temperature fell from about 36°C down to 18°C in two days and stayed around 18-20°C until February. The water temperature suffered a similar collapse: it fell from about 28-30°C down to 20°C. From this time on we sat for long days on the boat with the fishing rod. At the time assigned to track the Lemon Sharks, unfortunately the sharks were not attracted by the large amount of fish chum, fish oil, freshly caught and bled fish we threw into the water. We also altered our position from day to day. The sharks did not bite. This was never observed before (personal communication Gruber S.) and simply cannot be explained. It seemed that the sharks were not hungry anymore after the temperature drop. The sharks were regularly sighted in the fishing areas, but we could not attract them. The fact that the sharks did not spent time hunting is most likely an indication that for the sharks there is no positive benefit in the ratio between getting energy from food and losing energy from hunting the food.

First shark we caught was at the end of October, the second in the beginning of November and then we did not catch a further shark for a long time, although a lot of effort was put into fishing. On 3rd of January the third shark was caught and almost a month later, at the end of January, the fourth shark was caught. The first tracking was tried on the two first telemetered sharks in November, but with little success. Although the sample size of 4 sharks was very small, we started the tracking program with much effort in January. For four weeks almost every single day a crew was out for tracking. Unfortunately it was not possible for me to stay longer at the research station for carrying on the tracking project and due to the other projects no time could be invested to continue the tracking on these four sharks after my departure.

5.2. Movement Patterns

5.2.1. Different Daytimes

Gruber et al. (1988) showed for the first time a day-night movement pattern. They found a general tendency for sharks during the day to be located eastward of their night time activity space.

On the base of these findings DeMarignac (2000) made an extensive tracking project in the same study site from 1992-1995. With the tracking of 28 Lemon Sharks and approximately 12’000 data points he described 5 movement patterns that are made by the sharks between day and night (Fig. 47 in appendix). All these movement patterns were confirmed by Sundström (2001) in his study from 1996-1997. But Sundström found that only subadult Lemon Sharks caught on long lines eastwards of the Main Lagoon showed the long east-west migration. In the study of Harry from 2003-2005 and this study this long distance migration was not found. This is not surprising because in both studies no sharks were caught in the long lining area eastwards of the Main Lagoon. In this study only one shark, Big Mamma, was caught on long line, but in an area more north of the mentioned area, namely in the entrance of Bone Fish Hole Channel. In the same spot the lemon shark Katris was caught, which was smaller in size. Both sharks showed a very similar use of the same area. But the submersible receiver records showed for these two sharks a different pattern. Katris was many times found in Bone Fish Hole area during the day and night, but Big Mamma used this area very little and was the majority of the time around Shark Land during the day. If we assume that Big Mamma was possibly often in the entrance of the Main Lagoon at night, it would result a W-E pattern. This is especially interesting because this long distance W-E pattern is the exact opposite of the pattern DeMarignac described. Due to the lack of passive tracking data around the entrance of the Main Lagoon it cannot be said that this forms a W-E pattern. It is only a trend recognisable.

The fact that only sharks from long lines showed the long distance pattern in previous studies could be an indication to the existence of at least two different groups within the population with different behaviour. Different arrangements of nursery areas that sharks from the same species are using, most likely result in different behaviour. One group is possibly located in the long line area outside of the entrance of the Main Lagoon and have long east-west migration. Another group is possibly a bit further inside of the Main Lagoon, but also in the entrance and does not show this long distance pattern. A third group could be found inside the Main Lagoon between Shark Land, Pigeon Key and Pirate Wells.

In this study it was simply not possible to prove the pattern described by DeMarignac due to the small sample size and almost complete lack of night data. Only two sharks showed an approximation of the described pattern with one track each. But these two patterns are only trends, because we do not have enough nightly points to show that sharks stayed during the night in these locations. These findings could be a part of such a pattern, but it could also be possible these were simply accidentally made tracks and perhaps a few minutes later after losing the signal the sharks would have been back in their daily locations or in any possible direction.

5.2.2. Tidal phases

Due to the fact that some areas run dry due to the topography at spring low tides, it is obviously not possible to find sharks in these locations at low tide. In the opposite situation with high tide, the sharks were swimming in the vast majority of cases from areas with enough water during low tide into these flooded areas. They obviously had the possibility to stay in the “low-tide” areas, but they did not. The reason for this behaviour was not proven by this study. There are many different factors that are assumed to be potentially involved: predation risk, food availability, water temperature, energy saving, anthropogenic factors and more. Most of these factors are difficult to measure. It is also most likely that the influence of many factors together affect the shark’s movements. Even if we do not know why, this study showed that the sharks do move with the tidal phases. The distribution of the points of high and low tide showed a very strong separation. The positions of the sharks are very infrequently overlapping, although it would be possible to swim into the opposite areas. The locations of the sharks also showed nicely the topography of the seabed. In locations where it seems that the locations were overlapping, the seabed is a deeper water area very close to shallow areas (like a channel or a pool). This is seen around Pirate Wells or Radio Tower. Therefore the tidal phases movements are likely linked to the water depth.

5.2.3. Water Depth

The shark in a specific water depth did not statistically differ between tide phases (Anova: P = 0.0859) and this difference cannot be explained with the tide phases (adjusted R-squared values = 0.0062). The reason for the different variances is not to be found in different tide phases. More likely is the assumption that the depth is a result of being in deep enough water to manoeuvre well, being in enough shallow water to be protected from enemies and using a big enough area to find and catch the needed food. The box plot (Fig. 42B) showed at first view that 50% of the measurement data (indicated with the box) had a value that is very similar to all tide phases. The data lacks on the information to prove statistically what factor was responsible for this behaviour.

The results of the depth differences between high and low tide do differ just a few centimetres. Compared to the tidal mean range of approximately 73 cm (from NOAA, Washington, USA) this is a very small difference and cannot be explained with differences in tide ranges. The sharks are using at all times a similar water depth of between 65-80 cm and do therefore follow the tidal phases.

It seems that each shark has its own individual environment preferences and therefore acts freely. The result of the negative correlation between depth and size in this study is most likely accidentally generated because of the small sample size and the lack of data. Because all four studies are consolidated and the sample size increased to a number of 48 the result is clear and fits therefore to the expectations.

6. Conclusions

The four subadult Lemon Sharks which were tracked in this study did not show long distance movements. This cannot be qualified as an effect of any factor. The data is too low on records especially at night to get a good quality on results. The tracking effort that was afforded in January and February 2007 should be carried on over at least 3 months to get a coarse home range analysis, which could be well compared with previous studies. The passive tracking method with bottom monitors could detect movement patterns over a long time without much effort. However, more than 10 bottom monitors in well selected locations would be, for this effort, indispensable.

Lemon Sharks are swimming at high tide into areas which could not be accessed at low level tides. They do it to swim at the preferred height of the water column and most likely also to expand their feeding areas. To evaluate the reasons behind this tide linked pattern more tracking projects with data analyses of the environment are necessary. Factors as prey abundance and availability, bottom natural cover composition and water flow should be included.

The results of the water column pose the question of where in the water column the sharks are swimming. Is it close to the bottom, close to the surface, in between bottom and surface or an oscillation in the water column? With this information conclusions to behaviours like feeding, travelling etc. may be found. It would be interesting to compare the swimming depth with the tidal phases, daytimes, locations and seabed composition. Perhaps these findings would give more explanations for the reasons of the found movement patterns. The vertical use of the water column cannot be examined with the collected data, but would give another interesting view into the behaviour of these Lemon Sharks.

7. Indexes

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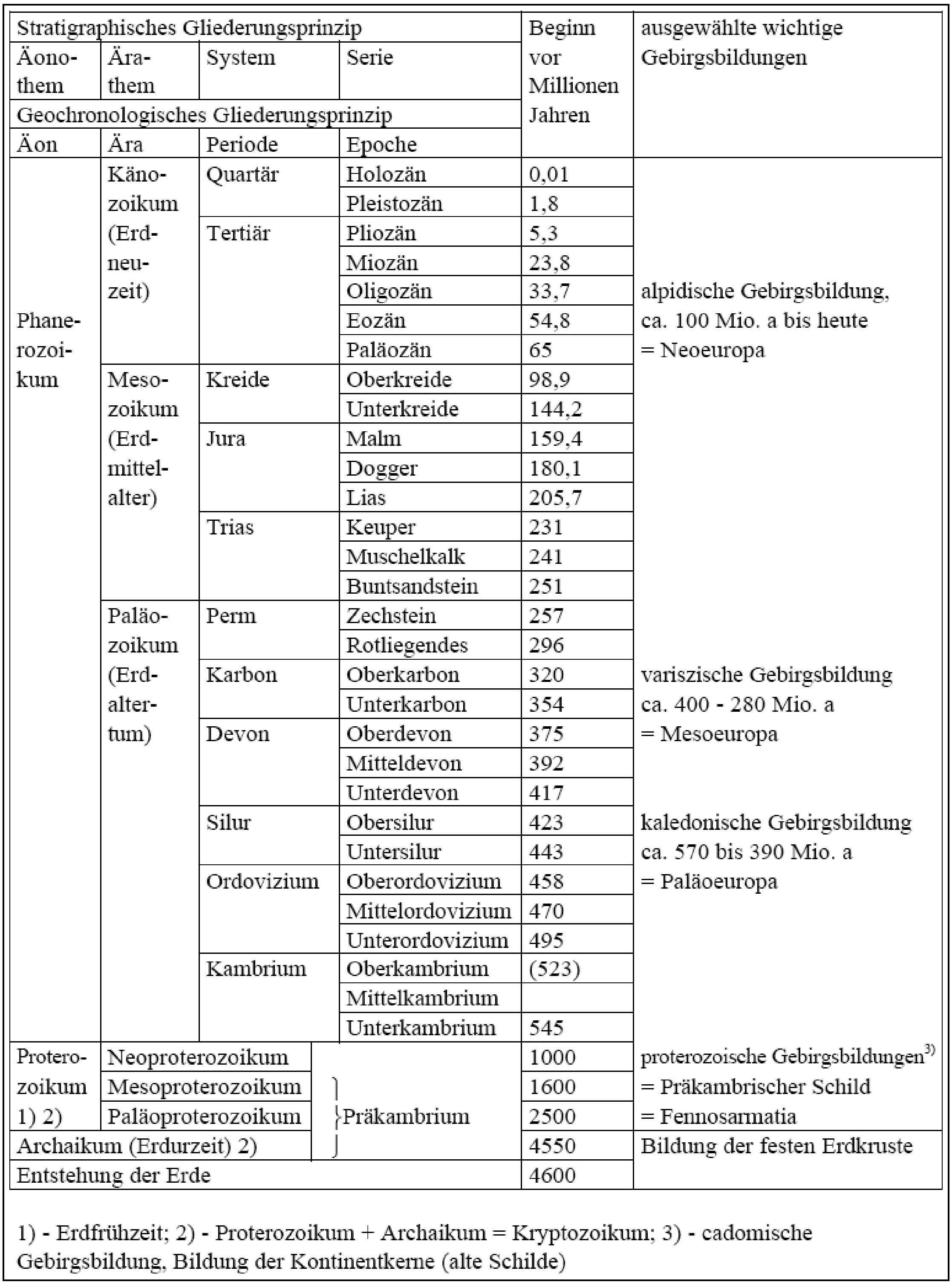
8. Appendix



Stratigraphisches Gliederungsprinzip				Beginn vor Millionen Jahren	ausgewählte wichtige Gebirgsbildungen
Äonothem	Ärathem	System	Serie		
Geochronologisches Gliederungsprinzip					
Äon	Ära	Periode	Epoche		
Phanerozoikum	Känozoikum (Erdneuzeit)	Quartär	Holozän	0,01	
			Pleistozän	1,8	
		Tertiär	Pliozän	5,3	
			Miozän	23,8	
			Oligozän	33,7	alpidische Gebirgsbildung, ca. 100 Mio. a bis heute = Neoeuropa
			Eozän	54,8	
			Paläozän	65	
	Mesozoikum (Erdmittelalter)	Kreide	Oberkreide	98,9	
			Unterkreide	144,2	
		Jura	Malm	159,4	
			Dogger	180,1	
			Lias	205,7	
		Trias	Keuper	231	
			Muschelkalk	241	
			Buntsandstein	251	
	Paläozoikum (Erdaltertum)	Perm	Zechstein	257	
			Rotliegendes	296	
		Karbon	Oberkarbon	320	variszische Gebirgsbildung ca. 400 - 280 Mio. a = Mesoeuropa
			Unterkarbon	354	
		Devon	Oberdevon	375	
			Mitteldevon	392	
			Unterdevon	417	
		Silur	Obersilur	423	kaledonische Gebirgsbildung ca. 570 bis 390 Mio. a = Paläoeuropa
			Untersilur	443	
		Ordovizium	Oberordovizium	458	
			Mittelordovizium	470	
			Unterordovizium	495	
		Kambrium	Oberkambrium	(523)	
			Mittelkambrium		
			Unterkambrium	545	
Proterozoikum 1) 2)	Neoproterozoikum	Präkambrium		1000	proterozoische Gebirgsbildungen[3)] = Präkambrischer Schild = Fennosarmatia
	Mesoproterozoikum			1600	
	Paläoproterozoikum			2500	
Archaikum (Erdurzeit) 2)				4550	Bildung der festen Erdkruste
Entstehung der Erde				4600	

1) - Erdfrühzeit; 2) - Proterozoikum + Archaikum = Kryptozoikum; 3) - cadomische Gebirgsbildung, Bildung der Kontinentkerne (alte Schilde)

Tab. 4: Strongly simplified timetable of geology, Deutsche Stratigraphische Kommission (from Menning, 2002)

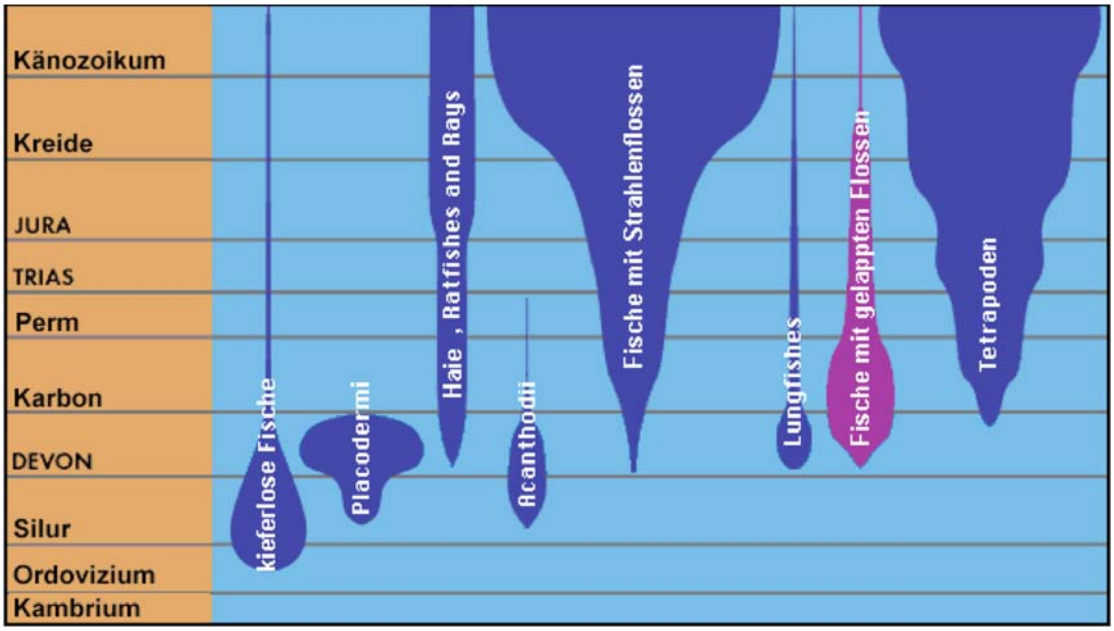


Fig. 46: Timetable of the evolution of fishes (from Heintges Lehr- und Lernsystem, 1998)

Researcher	Shark ID	Tagged	TL (cm)	Sex	Total Fixes	Time (h)
DeMarignac	AND	3-Nov-92	182	F	226	56.5
DeMarignac	MAT	3-Nov-92	190	M	83	20.8
DeMarignac	PIC	12-Nov-92	144	M	89	22.3
DeMarignac	ENI	13-Nov-92	183	M	50	12.5
DeMarignac	LIS	13-Nov-92	156	F	180	45.0
DeMarignac	YOL	13-Nov-92	153	F	43	10.8
DeMarignac	CAP	20-Feb-93	160	F	481	120.3
DeMarignac	NAN	21-Feb-93	156	M	265	66.3
DeMarignac	ZEL	21-Feb-93	166	F	47	11.8
DeMarignac	GON	22-Feb-93	150	M	50	12.5
DeMarignac	SEB	22-Feb-93	164	M	33	8.3
DeMarignac	BAC	19-Jan-94	151	M	658	164.5
DeMarignac	URS	21-Jan-94	173	F	396	99.0
DeMarignac	JUN	24-Jan-94	169	M	80	20.0
DeMarignac	TOO	25-Jan-94	186	F	529	132.3
DeMarignac	QUE	16-Jun-94	176	F	736	184.0
DeMarignac	DAM	17-Jun-94	162	M	492	123.0
DeMarignac	ROX	18-Jun-94	155	F	600	150.0
DeMarignac	WAG	19-Jun-94	161	F	1172	293.0
DeMarignac	IAG	21-Jun-94	158	M	397	99.3
DeMarignac	OJ	21-Jun-94	198	M	286	71.5
DeMarignac	FOX	3-Aug-94	150	F	132	33.0
DeMarignac	KRU	25-Aug-94	196	M	379	94.8
DeMarignac	HOM	28-Aug-94	167	M	19	4.8
DeMarignac	XLA	29-Aug-94	161	F	409	102.3
DeMarignac	DRG	22-Jan-95	156	M	1465	366.3
DeMarignac	VER	22-Jan-95	166	F	1160	290.0
DeMarignac	PRI	10-Apr-95	195	M	1328	332.0
Sundström	12-4	29-Jan-96	154	F	680	56.7
Sundström	11-5	26-Feb-96	188	M	246	20.5
Sundström	9-7	15-Mar-96	170	F	876	73.0
Sundström	339A	9-Mar-97	166	M	633	52.8
Sundström	339B	8-May-97	167	M	692	57.7
Sundström	348B	27-Jun-97	164	F	894	74.5
Sundström	348A	7-Jul-97	160	F	531	44.3
Sundström	348C	27-Jul-97	174	F	1008	84.0
Sundström	267B	8-Aug-97	180	M	945	78.8
Sundström	267A	22-Aug-97	183	M	545	45.4
Harry & Franks	354	26-Nov-03	129	M	537	44.8
Harry & Franks	374	27-Jan-04	119	F	492	41.0
Harry & Franks	365	8-Jul-04	116	F	148	12.3
Harry & Franks	446	5-May-05	124	M	501	41.8
Harry & Franks	234	6-Jul-05	125	M	338	28.2
Harry & Franks	222	31-Jul-05	146	M	211	17.6
Caviezel	Halloweena	31-Oct-06	145	F	67	5.6
Caviezel	Pirate	12-Nov-06	163	F	201	16.8
Caviezel	Katris	3-Jan-07	157	F	179	14.9
Caviezel	Big Mamma	31-Jan-07	196	F	140	11.7

Tab. 5: Summary of all subadult lemon shark tracking data used in this thesis. From different researchers collected between 1992-2007.

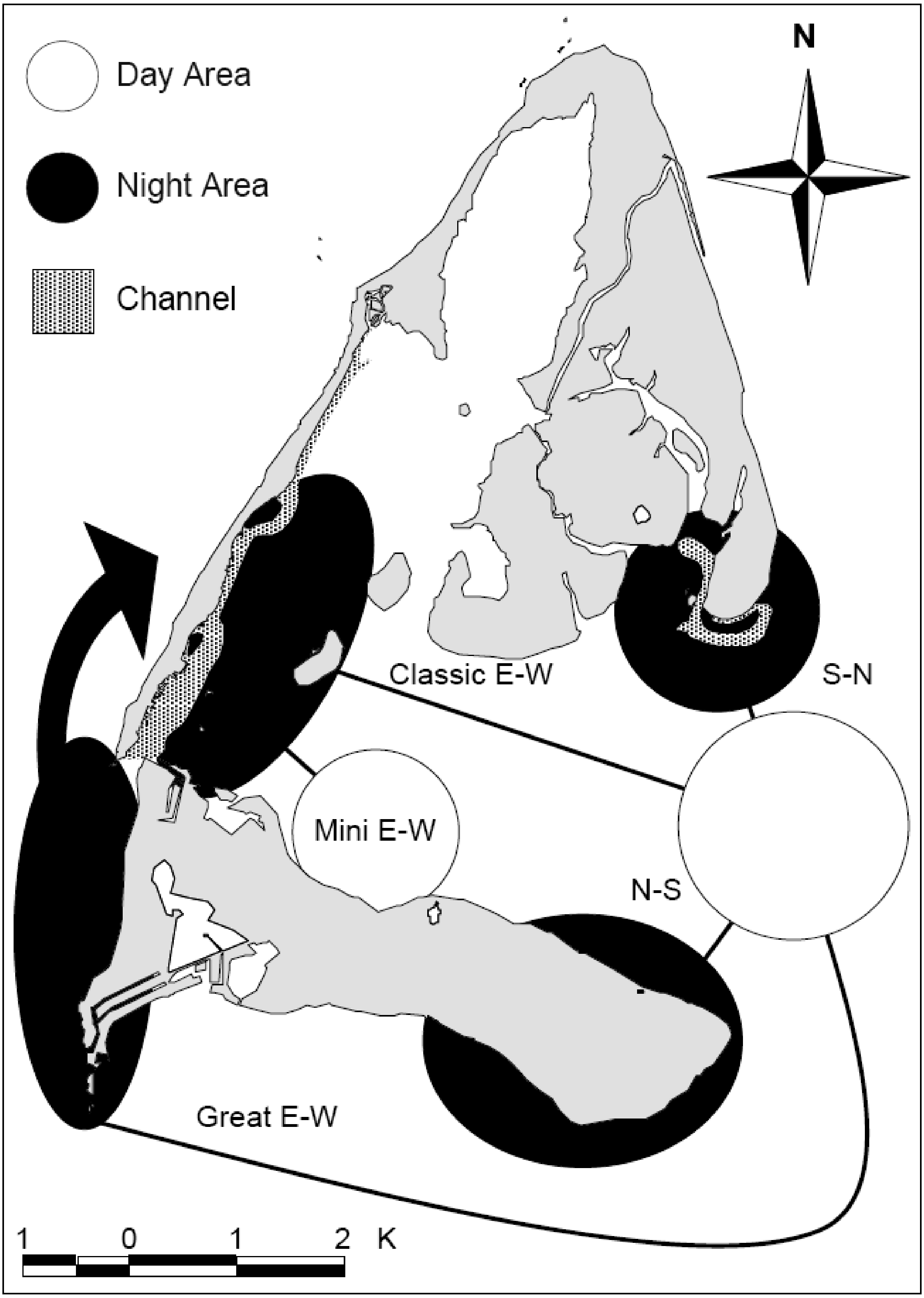


Fig. 47: Five different diel patterns found in large, subadult lemon sharks tracked during 1992-1995, from DeMarignac (2000)

The food chain backwards. Sherman’s Lagoon Copyright 2005, Andrews & McMeel Puplishing.