The Shark Research Institute
Operation Whale Shark

Proposal for Study of Whale Shark Behavior in Tanzanian Waters

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In Collaboration with
The Kairos Company, LTD.

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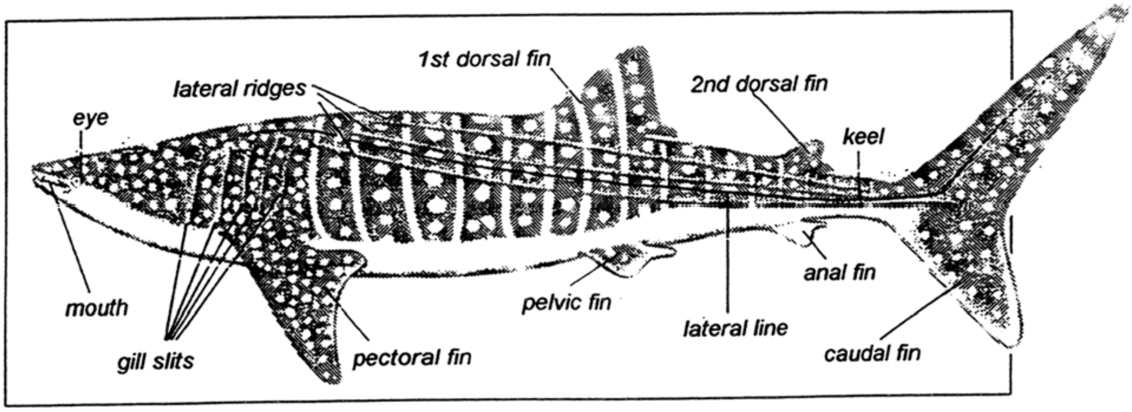
Abstract

The Shark Research Institute (SRI), a non-profit organization based in the United States of America, is engaged in a worldwide study to locate, tag, and document the behavior of whale sharks. The Kairos Company, LTD. is a Tanzanian business dedicated to running oceanographic expeditions on a diving live-aboard vessel out of Dar-Es-Salaam. On previous expeditions the M/V Kairos has encountered whale sharks in Tanzanian waters. SRI and the Kairos Company have formed a partnership with the goal of running a series of oceanographic expeditions to study the behavior of whale sharks in the area. Methodology includes visual and satellite tagging of whale sharks in accordance with SRI's global project "Operation Whale Shark". SRI has employed similar methodology in many countries with much success, and aims to add information on whale sharks found in Tanzanian waters to its comprehensive data bank. The Kairos Company, LTD. will immerse customers in the whale shark research and promote shark education and conservation through direct study of the whale sharks.

Introduction

The Shark Research Institute (SRI) is a non-profit organization dedicated to promoting shark research and conservation worldwide. In an effort to achieve these goals, SRI has initiated several research projects whose aim is to gather information on sharks to better manage and conserve them as a living resource. The cornerstone of SRI's work has been their ongoing program "Operation Whale Shark", which is a comprehensive and multinational study to locate, tag, track, and document the behavior of the whale shark, *Rhincodon typus*. Whale sharks are still targeted in many artesian fisheries in many parts of the world, mainly to support consumption in Eastern markets. In recent years there has been a boon in the legal protection of whale sharks in the territorial waters of several countries SRI works in. A goal of the organization is the global ban on trade in whale shark products, and worldwide protection of the species. This is especially difficult because there was never a true commercial fishery, and therefore we do not have much baseline data for whale shark populations. The research efforts of SRI may help in the efforts to determine global whale shark population estimates, migration patterns, and reproductive patterns. Many parameters of their basic biology are still unknown or highly debatable, even simple things like life span and growth rates are only able to be guessed at. The use of DNA technology may finally allow us to determine if there is a single global population of whale sharks, or if they have several discrete populations. (I have included an except from Compagno's FAO Sharks of the World, as a complete and accurate summary of the bank of knowledge on the whale sharks to date.)

Figure 1. Basic Anatomy of Study Subject, the Whale Shark (*Rhincodon typus*)



SRI researchers have studied whale shark distribution and abundance patterns in the Indian Ocean since 1993. They have placed visual ID tags on over 400 whale sharks from areas off South Africa, Mozambique, and the Seychelles. Direct research expeditions allow for the deployment of new tags and collection of DNA samples. Whale shark information is also collected year round via large numbers of whale shark sighting reported to SRI via their webpage (www.sharks.org). SRI has expanded its whale shark research to establish programs in Honduras, Costa Rica, Mexico, Ecuador (Galapagos), and Australia. With their recent partnership with the Kairos Company, SRI has looked to devote renewed research efforts into the Indian Ocean and interesting trends may be able to be seen by comparing the new data gained with the tagging and migration data from over 10 years ago.

Major support for SRI's whale shark research will be given by the Kairos Company, LTD. The Kairos Company is dedicated to giving a live-aboard dive experience well beyond a basic vacation. The centerpiece of the company is the M/V Kairos – a fully provisioned oceanographic research vessel with the versatility and capabilities to accommodate a range of projects and support diving activities. The M/V Kairos works out of Dar-Es-Salaam and frequents the surrounding waters, including areas but Pemba, Mafia Island and Zanzibar. The Kairos Company develops expedition concepts, involving exploration, scientific research, or documentary film-making. They bring in trained experts to lead the specific expeditions. Those individuals create a specific program to accomplish the goals of the expedition. The trip leader brings specialized or relevant equipment to add to the resources of the M/V Kairos. The trip leader provides training and education for trip participants and oversees all expedition activities. The trip participants get a unique experience through specialized training and actual participation in the expedition program.

Research Problem

Whale sharks, despite being the largest fish in the sea, still inhabit a cryptic environment and are difficult to study. Observations in the past have shown that whale sharks may follow migrational cycles and tend to frequent certain areas during specific months of the year. The large number of whale shark sightings off the Tanzania coast in the months of roughly Oct-March presents us with an opportunity. With the support of a live-aboard dive vessel, a team headed by an SRI researcher can make valuable in situ observations and collect data about these aggregations of sharks. To make statements about the population of whale sharks, individuals must be identified and direct observation of their behaviors need to be made. Estimates of population size and demographic structure can then be ascertained. Telemetry via satellite tags may help in looking at questions of where the sharks go after they leave Tanzanian waters. Finally, DNA samples can answer many questions about population structure that direct observations can not.

Research Objectives

The research objectives for this expedition are simple and straight-forward. The collaboration between SRI and the Kairos Company has mainly come about to address the unique opportunity to study the numerous whale sharks that appear in Tanzanian waters. We hope to identify individuals via tagging and photo/video analysis of spot patterns. We can get estimates of the population size and demography from our tagging and in situ observations. Deployment of archival satellite tags will allow us to get a glimpse of where the whale sharks go after they pass through Tanzanian waters and will distinguish other geographical areas that research and conservation efforts could be applied. Finally, we will get tissue samples for DNA extraction. DNA analysis will allow us to compare the whale sharks of Tanzania to other populations in the world and see if those populations are localized or global in their mating habits. The involvement of dive customers into a research expedition atmosphere will promote their comprehension of the levels of science and conservation required to address our research goals. Background education on sharks and promotion of the importance of maintaining the sustainability of marine resources will be recurring themes emphasized to all SRI/Kairos expedition participants. Basic scientific training, with stress on the scientific method, experimental design, and implementation of in situ observations will be covered. The atmosphere of academic professionalism and direct experiences gathering the data will ensure all expedition participants fully comprehend the research program and their contributions will foster the enthusiasm to spread the education and conservation messages we will instill in them.

Significance of Research

Sharks breed very slowly; some species take more than 20 years to reach breeding size, and then have only 2 pups every other year. At present we are killing 100 million sharks a year; we are killing sharks much faster than they can reproduce. Some scientists estimate that the rate of depletion may be as high as 2% per year for certain species. A few years ago it was thought that if the carnage continued, species that have lasted some 400 million years could vanish within 50 to 100 years. That appears to be overly optimistic; a recent study conducted by Dalhousie University indicated that from 1986 to 2000, nearly all shark species declined at least 50%, with populations of some approaching collapse. Tiger shark populations plummeted 65%, numbers of white sharks fell 79%, and hammerhead sharks declined 89%. Aerial studies along the coast of South Africa from 1993 to 2001 documented an 83% decline in whale sharks. The reproductive biology of the whale shark creates great concern with its ability to absorb large population decreases. Tagging and observing the behaviour of whale sharks in situ give insights as to the status of the whale shark populations in a particular area. Observations and data can help in the long term monitoring of whale shark populations in an area. The deployment of satellite telemetry tags can help to disseminate the migration routes of whale sharks and identify other areas that the population may be utilizing. The large range and pelagic tendencies of this species requires a comprehensive and international plan of conservation for any chance at success. The more areas we can establish the study and identification of shark populations the more prepared we will be to effectively protect them.

Methodology

1. Visual Tag Deployment

Deployment and recording information. The project uses yellow placard tags with large black numbers and SRI contact information. The tag is attached to the shark below its first dorsal fin. The tag is implanted by a diver using a modified spear gun that limits penetration of the tag's anchor in the shark's epidermis.

2. Satellite Tag Deployment

Activating, deploying and recording information. See above for details on the satellite tagging phase of the research. Attachment of the satellite tag to the shark is similar to that of the visual tag.

Figure 2. Visual ID Tag & Archival Satellite Tag Attached to Whale Shark

Figure 3. Deployment of Archival Satellite Tag via Spear gun

3. Tissue Sampling

Extracting, handling and preserving. Tissue samples are used for mtDNA analysis to determine whale shark relationships in regions around the world. A tiny tissue sample is extracted from the shark using a biopsy tag head on the tip of a modified spear. Once obtained, the tissue sample is carefully handled using surgical gloves and sterile instruments to avoid contamination. The tissue sample is placed inside a vial containing a preservative, and then the vial is sealed and labeled.

4. Photography

Still photos are also taken as part of the on-going photo ID program. Visual tags may detach from the host animal making them unreliable for identification purposes. The dot and stripe pattern of the whale shark are unique to each animal and may be used for identifying individual sharks. Digital cameras will be used so that they can easily be transferred to the computer database.

5. Videography

Video footage will be taken from both the surface and below the water. The footage is used to document the research as well as for behavioral analysis.

6. Surface Data

Daily weather and ocean surface conditions will be recorded on data sheets.
Parameters to be recorded and methods include:

a. Temperature - using an accurate glass/mercury laboratory thermometer
b. Wind speed and direction - compass and ships instruments
c. Cloud coverage - with reference to standard meteorological guidelines and observations
d. Wave height and direction - using compass and estimates
e. Atmospheric pressure - using standard meteorological barometer
f. Rainfall and humidity - using 24-hour rain gauge and humidity instrument
g. Record moon phase - from astronomical reference and observations

7. Sub-Surface Data

This oceanographic data set will be valuable as we study correlations between whale shark sightings and ocean conditions. Additionally, information gathered about the underwater environment will be invaluable as we try to determine global and long-term environmental changes. Repeated underwater measurements not only provide short-term correlation to environmental perturbations such as flooding or high temperature events, but they also create unique data sets that can be used as baselines for changes which occur over time frames extending to years, and even decades. A CTD probe will be used whenever possible. The probe will be attached to the individual doing the tagging, and will yield measurements of salinity, temperature, and depth that the whale shark was encountered at. Current speed and direction, and water visibility will be estimated from direct observation.

8. Whale Shark Encounter Guidelines

To ensure that you have a safe, enjoyable experience and to prevent the animals from being harmed or disturbed, the following code of conduct applies when interacting with whale sharks:

Swimmers and Divers must not:

• Attempt to touch or ride on a whale shark
• Restrict the normal movement or behaviour of the shark
• Approach closer than 3 metres from the head or body and 4 metres from the tail
• Use motorized propulsion

WHALE SHARK STUDY
DATA COLLECTION FORM

Support Vessel: ___________

Captain: ________________

SURFACE DATA

Air temperature: ___________

Cloud conditions: __________

Wind direction & strength: ____

Barometric Pressure: ________

SUBSURFACE DATA

Visibility: ____________ ft.
(measured or estimated)

Water Temperature
Bottom: _____ Surface: _____

Chemistry: ______________

Current
Direction: _______ to _______
Strength: _______________

Waves
Height: _____ Strength: ____

Water depth: _____________

Depth shark encountered: ___

Swimming direction: ________

Environmental conditions: (reef, plankton, schooling fish)

PHOTO/VIDEO

U/W Photos by: ____________

U/W Video by: ____________

REPORT COMPLETED BREPORT COMPLETED BY::

Name: ________________

Contact Info: ____________

Country/Island: ______________________________

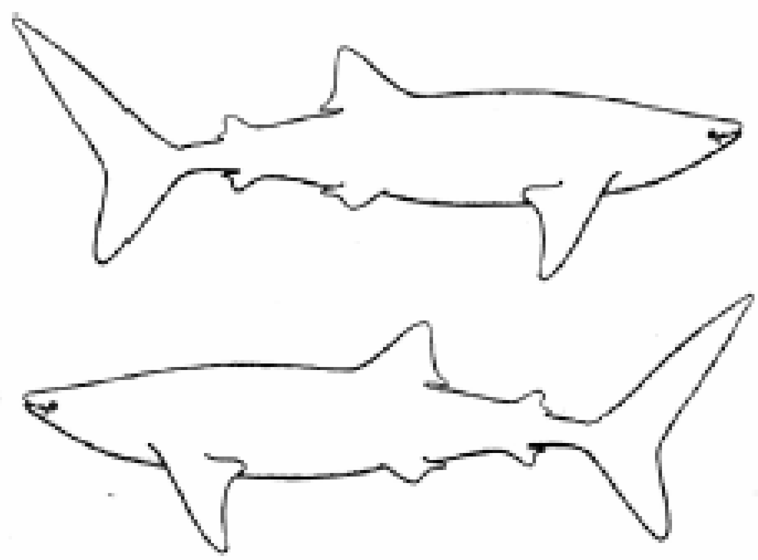
Date: _____________________ Time: ___________

GPS: ____________________________________

Location (Describe surroundings - on surface, on bottom, etc.)

Size of shark: ________________ Sex of shark: ________

Notes: (Describe scars & markings. Mark any unusual pattern or scars on the drawing below. Attach photo if available.)



TABBING INFORMATION

Visual ID Tag # __________ Tagger: _____ Date: ______

Satellite Tag # ___________ Tagger: _____ Date: ______

Tissue Sample# __________ Vial # ______ Date: ______

Name of shark: ______________________________

BEHAVIOR OF THE SHARK

Reference

The Whale Shark (Rhincodon typus), from FAO Sharks of the World
by Leonard J. V. Compagno, Ph.D., Director of the Shark Research Institute

Family RHINCODONTIDAE
Diagnostic Features: Head very broad and greatly flattened, without lateral flaps of skin. Snout truncated. Eyes laterally situated on head and without subocular ridges below them. Eyes without movable upper eyelids or subocular pockets and ridges. Spiracles moderate-sized but much smaller than eyes, without raised external rims; spiracles behind but not below eyes. Gill slits very large, fifth gill is well-separated from fourth and not overlapping it; internal gill slits with unique filter screens, consisting of transverse lamellae that cross each gill slit, with ramose processes on their inner surfaces that interconnect to form the filters. Nostrils with rudimentary barbels and no circumnarial folds and grooves. Nasoral grooves very short and shallow. Mouth very large, transverse and terminal on head. Lower lip not trilobate and without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, without a longitudinal symphysial groove on chin. Lower labial furrows ending far lateral to symphysis, not connected medially by a mental groove or groove and flap. Teeth not strongly differentiated in upper and lower jaws, with symphysial teeth not enlarged and fang-like. Tooth row count extremely high, in over 300 rows in either jaw of adults and subadults. Teeth with a strong medial cusp, no cusplets and no labial root lobes. Teeth osteodont with crown partially filled with a plug of osteodentine. Body cylindrical or moderately depressed, with prominent ridges on sides. Precaudal tail shorter than body. Caudal peduncle with strong lateral keels and an upper precaudal pit. Pectoral fins very large, relatively narrow and falcate. Pectoral fins plesodic and with fin adials strongly expanded into fin web. Pectoral propterygium small and fused to mesopterygium; pectoral-fin radial segments 3 to 10, and with longest distal segments about 0.8 times the length of longest proximal segments. Pelvic fins much smaller than first dorsal fin but subequal to second dorsal and anal fins, much smaller than pectoral fins and with anterior margins about 0.3 times the pectoral-fin anterior margins. Claspers without mesospurs, claws or dactyls. First dorsal fin much larger than second. First dorsal-fin origin well anterior to pelvic-fin origins and over abdomen behind pectoral-fin free rear tips, first dorsal-fin insertion over the pelvic-fin bases. Anal fin about as large as second dorsal, with broad base, angular apex, about opposite first third of second dorsal fin base, and insertion separated by a space somewhat greater than base length from lower caudal-fin origin. Caudal fin elongated and semicrescentic, strongly heterocercal with its upper lobe at a high angle above the body axis (lower in young than adults and subadults); dorsal caudal-fin margin less than a third as long as the entire shark. Caudal fin with a vestigial terminal lobe and subterminal notch but with a strong ventral lobe (longer in adults than young), preventral and postventral margins strongly differentiated and deeply notched. Vertebral centra with well-developed radii and prominent annuli connecting them. Total vertebral count 174, monospondylous precaudal count 42, diplospondylous precaudal count 40, diplospondylous caudal count 92, and precaudal count 82. Cranium very broad and greatly expanded laterally. Medial rostral cartilage rudimentary, reduced to a low nubbin. Nasal capsules greatly depressed, slightly fenestrated anteriorly, internarial septum low, broad and depressed. Orbits with enlarged fenestrae for preorbital canals, medial walls not fenestrated around the optic nerve foramina although foramen itself is very large. Supraorbital crests present on cranium and laterally expanded and pedicellate. Suborbital shelves very broad and not greatly reduced. Cranial roof with a continuous fenestra from the anterior fontanelle to the parietal fossa. Basal plate of cranium with pairs of separate carotid and stapedial foramina.

Adductor mandibulae muscles of jaws with three divisions. Preorbitalis muscles extending onto posterodorsal surface of cranium. No anterodorsal palpebral depressor, rostromandibular, rostronuchal or ethmonuchal muscles. Valvular intestine of ring type with 69 to 74 turns. Development ovoviviparous. Size gigantic with adults 700 cm or longer, while young are born at about 55 to 64 cm. Colour pattern unique, consisting of small to large white or yellowish spots and vertical and horizontal stripes in the form of a checkerboard on a dark background.

Local Names: Whale sharks, Ching sha k'o, Jimbeizame-ka (Japan); Kitovye akuly (Russia).

Remarks: As recognized here the family Rhincodontidae includes only a single genus and species, the
whale shark, Rhincodon typus.

Field Marks: An unmistakable huge shark, one of three large filter-feeding species (apart from devil rays), with a broad, flat head and truncated snout, immense transverse and virtually terminal mouth in front of eyes, minute, extremely numerous teeth, and unique filter screens on its internal gill slits; prominent ridges on sides of body with the lowermost one expanding into a prominent keel on each side of the caudal peduncle, a large first dorsal and small second dorsal and anal fin, lunate or semilunate caudal fin without a prominent subterminal notch. Colour: a unique checkerboard pattern of white or yellow spots, horizontal and vertical stripes on a grey, bluish, reddish or greenish brown dorsal surface, abruptly white or yellowish on the underside of the body.

Distribution: Circumglobal in all tropical and warm temperate seas, oceanic and coastal. Western Atlantic: Canada (south of Nova Scotia), United States (Gulf of Maine and New York south to North Carolina and Florida, and Gulf of Mexico coast from Florida to Texas), Mexico (Gulf of Mexico coast to Quintana Roo), Belize, Honduras, Panama, Colombia, Venezuela, and central Brazil, also Bermuda, Bahamas, Caribbean including Cuba and Haiti. Eastern Atlantic: Azores, Senegal, Mauritania, Cape Verde Islands, Côte d'Ivoire, Gulf of Guinea, Gabon, Angola, South Africa (Western Cape Province). Indo-West and Central Pacific: East coast of South Africa (Western Cape, Eastern Cape, KwaZulu- Natal), Mozambique, Madagascar, Seychelles, Kenya, Tanzania, Somalia, the Red Sea and Straits of Bab-al-Mandab (Eritrea, Sudan, Saudi Arabia), Yemen, Oman, Persian Gulf, the Maldives, Pakistan, India (both coasts), Sri Lanka, possibly Bangladesh, Malaysia (including Sabah, Borneo), Singapore, Thailand (including Gulf of Thailand), Viet Nam, China, Taiwan (Province of China), FAO Species Catalogue for Fishery Purposes No. 1 204 Japan (Southeastern Honshu, Okinawa, and Bonin Islands), Philippines, Indonesia (Kalimantan, Borneo; Java), New Guinea (Papua-New Guinea and Irian Jaya, Indonesia), Australia (Western Australia, Queensland, Northern Territory, with isolated records from New South Wales and Victoria), New Caledonia, Hawaiian Islands, Tuomotu Archipelago, Phoenix Islands. Eastern Pacific: United States (southern California), Mexico (Baja California and Gulf of California south to Acapulco, Oaxaca, and Chiapas), El Salvador, Nicaragua, Costa Rica, Panama, Ecuador, Galapagos Islands, and between Panama and the Hawaiian Islands).

Habitat: An epipelagic and neritic, oceanic and coastal, tropical and warm-temperate pelagic shark, often seen far offshore but regularly coming close inshore off beaches and coral reefs and sometimes entering lagoons of coral atolls. In the western Pacific it apparently prefers areas where the surface temperature is 21 to 25°C with cold water of 17°C or less upwelling into it, and salinity of 34.0 to 34.5 ppt. Recent satellite tagging (Eckert and Stewart, 1996) in the Gulf of California suggested that the sharks prefer water over 26°C and up to 34°C, although they were recorded in water masses at temperatures down to 10°C; the sharks tended to move out of parts of the Gulf of California where surface water cooled below 26°C with upwelling. These conditions may be optimal for production of plankton and small to moderate-sized nektonic organisms, all of which are prey of the whale shark. The whale shark is generally seen or otherwise encountered close to or at the surface in warm waters, although recent satellite tagging in the Caribbean Sea off Belize shows that the whale shark may dive to depths of 700 m and may transit in cold deep water down to 7.8°C (R. Graham, pers.comm.). Off Ningaloo Reef in Western Australia a sonic-tagged shark frequently dived during two 18 hr tracks and ranged from the surface to near the bottom at depths of 40 to 70 m (Stevens et al., 1997), with salinity at 34.9 to 35.2 ppt and temperatures of 26.8 to 27.5°C at the surface to 26.4 to 25.4°C at the bottom. Strandings of whale sharks are common in some areas, including both coasts of South Africa, and it is suspected that off the west coast of South Africa whale sharks ride the warm Agulhas current during the summer into areas where upwelling occurs and plumes of cold bottom water hit the surface. It was thought that sharks may be stunned or even killed by sudden chilling and then wash up on the shore with no signs of disease or physical damage (Beckley et al., 1997). Tracking of whale sharks in water down to 10°C in the Gulf of California and their presence near patches of upwelling water down to 6°C (Eckert and Stewart, 1996) makes this simple explanation suspect however, and an explanation for the phenomenon of stranding off the Western Cape requires further research. Rough seas and sudden storms along the narrow continental shelves of KwaZulu-Natal, South Africa (which is subtropical and optimal for whale sharks) may contribute to strandings on the beaches there.

Biology: The whale shark is a facultatively social shark, and has been recorded as single individuals or in schools or aggregations of up to hundreds of sharks. In the Indian Ocean it is common around the Seychelles, Mauritius, Zanzibar, Kenya, Madagascar, Mozambique and northernmost KwaZulu-Natal. In the western Pacific it is common in the Kuroshio current in the fishing grounds for skipjack (Scombridae). It is reportedly abundant in the Gulf of California and from Cabo San Lucas to Acapulco in the eastern Pacific, and in the Gulf of Mexico and the Caribbean in the western Atlantic. Aerial spotting of whale sharks has been successfully attempted off Kenya, South Africa, and Western Australia, as well as whale shark surveys by boat in these same localities (Gifford, 1994; Wamukoya, Mirangi and Ottichilo, 1995; Beckley et al., 1997; Stevens et al. 1997; Colman, 1997), while whale shark observation records are collected routinely from dive operators in Western Australia (as with the various basking shark sighting programs in the United Kingdom). The Shark Research Institute (http://www.sharks.org) runs an Internet-based program encouraging people who sight whale sharks to send in reports by Email to their central database, which so far has received several hundred responses. Whale sharks are highly migratory, with their movements probably timed with localized blooms of planktonic organisms and changes in temperatures of water masses. Several whale sharks have been tagged with radio satellite tags using the ARGOS system in the Gulf of California (Eckert and Stewart, 1996) over times of up to a year, with maximum speed recorded about 2.3 km/hr. Satellite tracking has revealed extensive movements, and tagged whale sharks have moved out of the Gulf of California along rugged bottom topography of the Clipperton Fracture Zone to the Revilligigedo and Clipperton Islands, with one shark travelling 1 723 km in about three months and another 3 708 km in five months. Satellite tagging suggested that whale sharks in the Gulf of California showed some segregation by size, with smaller sharks frequenting the northern Gulf and possibly absent from the southern part. Observation of whale sharks off Ningaloo Reef, Western Australia suggests that mostly adolescent males between 6 and 7.5 m length are seen there, with one (possibly mature) male measured live with a rope at 9.1 m; between 80 and 91% of the sharks seen in 1996 and 1997 were male (Stevens et al., 1997; Gunn et al. 1999). Some 53 individuals were ‘body-printed’ with scarring and colour patterns recorded, and 29 resighted from one to 14 times (Stevens et al. 1997) over at least two years. In South Africa, SCUBA divers working under the auspices of the Shark Research Institute tag whale sharks underwater using modified spearguns with detachable spearheads attached to giant spaghetti tags, and have resighted the tagged sharks later by approaching them closely and reading the tag numbers (Gifford, 1994); at least one of these sharks had been resighted off the Seychelles (ca 3 700 km). Satellite tagging has also been attempted on whale sharks off KwaZulu-Natal, South Africa, and off Ningaloo Marine Park, with tracks of limited range so far. Whale sharks are often associated with schools of pelagic fish, especially scombrids. They apparently show curiosity in the presence of people and will approach divers and boats, possibly to examine them. The behaviour and sociobiology of the whale shark is sketchily known at present, but as with the basking and white sharks their detailed behaviour should be amenable to elucidation by divers and observers in boats using cinematography as well as telemetry. The most extensive close-in behavioural research to date has been at the famous whale shark viewing site at Ningaloo Reef (Ningaloo Marine Park), Australia (Stevens et al., 1997; Gunn et al., 1999), where sonic tracking and archival tagging showed that whale sharks made numerous dives during a 24 hour period, ranging from the surface to near the bottom and varying in speed from 0.1 to 1.8 m/sec. The sharks' dives appeared to be independent of hydrographic features and seemed to be associated with food search. Whale sharks showed an ability to accurately sense the bottom and swim very close to it without colliding. Some behaviour patterns observed in association with and in part in reaction to ecotouristic snorkel-divers at Ningaloo include diving, where sharks descended out of view of the divers; porpoising, a movement away from the surface, but not out of sight; changes in speed, where sharks go slow (snorkelers easily keep up with the sharks at 0 to 1 knots), medium (where divers strain to keep up at a speed of 1 to 2 knots), and fast (where sharks pull away from the divers at over 2 knots); degree of mouth distension (mouth closed to fully open on a six-point scale, possibly related to feeding); banking, in which the shark rolls and presents its dorsal surface towards the recorder; and eye-rolling, which was observed by divers next to the whale shark's head.

Reproduction: The mode of reproduction of the whale shark is apparently ovoviviparous, but it was long disputed and assumed to be oviparous by some authors. In 1953 a large eggcase, 30 cm long, 14 cm wide and 9 cm high containing a nearly full-term, 36 cm embryo whale shark was collected from the Gulf of Mexico, and the assumption was made that the species is oviparous (Baughman, 1955; Reid, 1957; Garrick, 1964; Bass, D'Aubrey and Kistnasamy, 1975c). However, the rarity of 'free-living' whale-shark eggs, the extreme thinness of its walls and lack of tendrils on the only known deposited eggcase, the considerable yolk and partially developed gill sieve in the embryo within it, and the presence of umbilical scars on larger freeliving specimens 55 cm long suggested an alternative explanation (Wolfson, 1983), that the Gulf of Mexico egg was aborted before term, and that the whale shark is normally ovoviviparous. This was recently confirmed by an adult female whale shark caught in Taiwan (Province of China) which had some 300 young (sex ratio of 237 young with about 1.0:1.1 male:female ratio) in her uteri (Joung et al., 1996). These young whale sharks were three size classes: embryos with yolk sacs in egg cases that were 42 to 52 cm long, embryos with yolk sacs in egg cases 52 to 58 cm long, and apparent term foetuses without egg cases and with reabsorbed yolk sacs between 58 and 64 cm long. The type of ovoviviparity practised by the whale shark is possibly a relatively simple sort very similar to that of the related nurse sharks Ginglymostomatidae: *Ginglymostoma*), with retention of the egg case *in utero* until the embryo hatches from it, and then is born. The three classes of young reported in the Taiwan (Province of China) female suggest that successive batches of eggs are retained in utero, with the oldest hatching and then being born. One additional adult female whale shark from Taiwan (Province of China) was recorded as having 16 egg cases in her uteri while another was reported as having 200 eggs in her ovary. Although many whale sharks have been caught in the Taiwan (Province of China) fishery, very few have been reported as obviously mature females over the last half of the twentieth century (Joung et al., 1996). The gestation period is not known, but Castro, Woodley and Brudek (1999) suggest that the whale shark may reproduce every other year as with the nurse shark (*Ginglymostoma cirratum*). The smallest free-living whale sharks are 55 to 59 cm long, have an umbilical scar. Such small whale sharks have been found off tropical West Africa in the East-Central Atlantic and near Central America in the eastern Pacific, near continental waters and in the open ocean far from land (Wolfson, 1983; Kukuyev, 1996), suggesting that young may be born in the ocean and that pupping grounds and possibly nursery areas exist there.

The whale shark is a versatile suction filter-feeder, and feeds on a wide variety of planktonic and nektonic organisms. Whale sharks are known to appear off coral reefs when these are producing blooms of planktonic organisms and the corals are spawning (Colman, 1997). Masses of small crustaceans (including copepods) are regularly reported as food, along with small and not so small fish such as sardines, anchovies, mackerel, and even small tunas and albacore as well as squid. Whale sharks may aggregate along with tuna in association with spawning of lanternfish (*Diaphus*, Myctophidae) in the Coral Sea off Queensland; and off Christmas Island in the eastern Indian Ocean between Java and Western Australia in association with mass spawning of red crabs (*Geocarcoidea natalis*; Colman, 1997). Recent research (Heyman et. al, in press) indicates that large (ca. 25
individuals) and predictable groups of whale sharks gather around snapper (*Lutjanus cyanopterus* and L. jocu) spawning aggregations at Gladden Spit, in the barrier reef off Belize. Whale sharks feed at dusk and dawn on the released gametes of the snappers, during the full moon periods between April and June and show good site fidelity between one spawning period and the next. The whale shark feeds at or close to the surface, and often assumes a vertical position with its mouth up above its body. Phytoplankton often occurs in the stomachs of whale sharks, but whether this is a major component of the diet of this shark is rather doubtful. Small whale sharks 3.2 to 5.2 m long have been observed feeding on copepods at the surface in the Gulf of California (Clark and Nelson, 1997); they aimed at patchy areas of dense concentrations of copepods (at least 13 species, mostly *Acartia clausi*) and turned from side to side, lifted the dorsal surfaces of their heads partially out of the water with the upper jaw exposed, and opened and closed their mouths and gill openings at rates of 7 to 28 times per minute, apparently gulping in plankters. Turning movements increased with gulping rate, and, when sharks passed through copepod concentrations into clear water, they sharply turned and circled back to the concentrations to renew feeding. When not feeding the sharks dropped their heads below the surface with mouth slightly open, and stopped moving their mouths and gill openings and swam faster while apparently ram-ventilating their gills. Larger whale sharks 6 to 10 m were observed by Clark and Nelson to feed underwater with their heads not exposed, but with a similar gulping action of 16 to 20 times per minute. Clark and Nelson also noted that similar feeding behaviour is shown by whale sharks kept at the Okinawa Expo Aquarium, fed by ladle at the surface. Some air may be swallowed during feeding, but it is unknown if it is expelled or can function for assisting buoyancy as in the sand tiger sharks (*Carcharias taurus*).

The suction-filter mechanism of the whale shark is more versatile than the dynamic filter mechanism of the basking shark in the range of prey species that can be taken. The basking shark, with its huge scoop-like mouth, hydrodynamically ‘clean’ gill rakers, and huge gill slits, has little if any suction capacity and must depend for the most part on its relatively slow forward motion to carry animals into its mouth; this limits it to eating small planktonic crustaceans and other invertebrates trapped on mucus on its gill rakers. The whale shark is not dependent on forward motion to operate its filters, and can probably achieve relatively high intake velocities of water into its mouth, that enable it to readily ingest larger, active nektonic prey in addition to masses of planktonic crustaceans. A disadvantage of the suction plankton feeding of the whale shark over the dynamic method used by the basking shark is that the structures involved can filter a far smaller volume of water per unit time and hence are far less efficient in concentrating diffuse plankters. Hence the whale shark may be more dependent on higher concentrations of plankters than the basking shark to optimally utilize such food (such as reef blooms or copepod aggregations), but has the option of utilizing much larger nektonic organisms for prey that cannot be caught by the basking shark or are marginal for that species. Observations by Clark and Nelson (1996) suggest that the whale shark is capable of homing in on such concentrations and adjusts its activities to target them.

The predators of whale sharks are little-known apart from humans. A newborn specimen was found inside the stomach of a blue shark (*Prionace glauca*; Kukuyev, 1996), and other large pelagic and coastal carcharhinoid and lamnoid sharks may take young whale sharks also. Adult whale sharks, with their thick hides and great size, may have few natural predators, killer whales, (*Orcinus*) and large white sharks being two possibilities; the giant extinct megatooth shark *Carcharodon megalodo*n is another likely candidate. The chief predator of whale sharks is humanity. Pauly (in press) used a von Bertalanffy growth curve partially based on data for the basking shark (*Cetorhinus maximus*) to give a tentative estimate of age and growth for this species. Using a conservative maximum length of 14m he suggested that the whale shark may be especially long-lived, with a tentative longevity of about 100 years, "which strikes one as rather high, but may not be impossible" (Pauly, in press). His growth curve suggests that adult males at about 7 m would be about 20 years old. In contrast, Castro, Woodley and Brudek (1999) suggested that, based on captive growthof a term foetus in Taiwan (Province of China) from the adult female reported by Joung et al. (1996), as well as the few records of small whale sharks in the 1 to 3m range, the whale shark may prove to be the fastest-growing shark. Long-term tagging and bodyprinting of free-ranging individuals with periodic remeasuring of registered individuals that return to viewing sites over several years (as per the methodology of Stevens et al., 1997), may clarify this seeming disparity, and the writer suspects that very fast initial growth (if also shown by free-living neonates) would slow down markedly as the sharks approach maturity. A preliminary DNA analysis of cytochrome b genes from several whale shark skin samples from the Gulf of California, and a few from Philippines and South Africa, showed no variation (Eckhart and Stewart, 1996). Further studies are underway with other genes to determine if there are any genetic indications of differences within whale sharks from a given area or from distant areas.

Size: This is by far the world's largest fish-like vertebrate, with an uncertain maximum size. Old sight records as well as recent tagging studies and whale shark fishers' reports suggest a maximum length of 17 to 18 m or even 21.4 m. Specimens are uncommon above 12 m, and 30 specimens reported from South Africa by Beckley et al. (1997) were 4 to 11 m long. A length of 13.7 m is often given as the maximum size measured, 12.1 m the most recently accurately measured, while most reported in the literature are between 3 and 12 m long. The late Margaret M. Smith showed the writer a letter describing a beach-stranded specimen from Angola, with measurements suggesting it was about 15.9 m long.

Size at birth of the whale shark is between 55 and 64 cm, with freeliving individuals as small as 55 and term foetuses known at 58 to 64 cm. Males are immature at 299 cm or less and adolescent at 390 to 540 cm while adult males of 705 to 1 026 cm have been recorded. Females from 340 cm or less, to 760 cm, were immature, while a pregnant female was about 10.6 m long (Joung et al. 1996) and weighed 16 t; and another adult female may have been about 12 m long. Pauly (in press) assumed a maximum length of 14 m and a weight of approximately 20 t for the whale shark using an isometric length-weight equation also used with the basking shark: $W(t) = 0.0075TL(m)3$.

Recent records suggest a higher maximum length, however. Eckert and Stewart (1996) tracked 12 whale sharks by satellite tags for which size estimates were given to a tenth of a metre; 10 of their tagged sharks were 3.0 to 7.1 m long, but two big females tagged in 1996 and tracked for four months were 15.0 and 18.0 m long. Taiwanese fishers reported several whale sharks between 15 and 36 t weights (Joung et al., 1996), suggesting lengths of about 12 to 17 m using Pauly's equation.

Interest to Fisheries and Human Impact: Apparently of limited value for conventional fisheries despite expanding markets and increasing values for whale shark products. Small harpoon fisheries traditionally existed in Pakistan and India for local utilization; it is also taken by harpoon in the Maldives, China, Taiwan (Province of China), and Philippines, and has been captured and utilized in Senegal; it is also caught as a bycatch in fish traps in Philippines but was generally released until it increased in value and was killed for export, and hopefully is now being released again following nation-wide protection. More importantly, an increase in demand for whale shark meat in Taiwan (Province of China) stimulated the development of a targeted fishery for whale sharks developed by ex-whalers operating in the Bohol Sea. Whaling harpoons or gaffs were used to subdue them and knives (bolos) to kill them (WWF-Philippine Program, 1996). It is also caught with longlines and in gill nets in Taiwan (Province of China). Whale shark meat is eaten by people fresh, fresh-frozen, dried or dried-salted, the skin is eaten in Taiwan (Province of China), the fins enter the oriental fin trade at a high value because of their size, the dried gill rakers have been utilized in the Philippines, and the flesh has been used to treat boat hulls in Pakistan. The whale shark is generally considered harmless despite its size, and moderate-sized to very large individuals have been repeatedly approached closely by divers and have been touched, ridden and otherwise contacted by them without the sharks reacting aggressively. They may suddenly dive or flee the vicinity of divers when disturbed but without showing much excitement. Their docility and ready access in shallow water in many localities has popularized them as the subject of ecotouristic diving charters. The best known site is off Ningaloo Reef (Ningaloo Marine Park) in Western Australia, but sites also exist off the KwaZulu-Natal coast of South Africa, off Mozambique, Kenya, Seychelles, Thailand, Philippines, the Hawaiian Islands, the Gulf of California (Mexico), the Pacific coast of Costa Rica and Colombia, Chile, the Gulf of Mexico coast of the United States (Texas, Florida), and Belize. These sites allow divers to examine whale sharks underwater, and in some instances (Ningaloo Marine Park) access to whale sharks is restricted by a strict code of conduct limiting interference with these sharks by divers and boats (Colman, 1997). The effect of ecotourism on the behaviour and local abundance of whale sharks off Western Australia is currently under detailed study (Stevens et al., 1997). The whale shark dive industry is highly regulated by the Western Australian government, with limited numbers of operators and vessels (16 in 1993 decreasing to 14 in 1996 according to Colman, 1997). Operators require commercial tourist licences with yearly or two-year renewal, and pay a fee per tourist per day. A benefit of ecotouristic activity with whale sharks, particularly in Western Australia but also in the Gulf of California, South Africa and elsewhere, is a rise in scientific activity focusing on the whale shark, often in cooperation with ecotouristic dive operators. There have been a few cases of whale sharks butting sportsfishing boats (Smith, 1967), possibly after becoming excited by hooked fishes being played from the boats or by bait, but ordinarily they do not contact boats although they may investigate them very closely. Far more commonly human beings inadvertently ram whale sharks with ships and boats as the sharks bask or swim on the surface (documented in numerous papers by Eugene W. Gudger, cited in Wolfson and de Sciara, 1981).

During 1998, a whale shark swam into and became caught in a cooling water intake of a coastal nuclear power station at Koeberg, Western Cape, South Africa. The affected reactor had to be shut down and boats and divers were called in to extract the shark. The shark was still alive after about a day and divers 'walked' it until it increased its vigour and swam away! The shark may have been attracted to the warm plume of water released by the power plant, and whale sharks have been sighted in the immediate vicinity of the powerplant before. The whale shark has been kept in captivity in Japan and Taiwan (Province of China) and is relatively hardy if properly fed and handled. At least 14 largish (3.9 to 6.3 m) individuals have been kept in Japan, primarily in a large oceanarium tank at the Okinawa Expo Aquarium (Clark and Nelson, 1997) for extended periods of over a year. These have learned to feed at the surface of the tank when presented with a long-handled ladle filled with food such as euphausiid shrimp, squid, and fish, and so fed do not require planktonic food in their tank. More recently term foetuses from a pregnant female whale shark were successfully kept in captivity in Taiwan (Province of China) and Japan. The conservation status of the whale shark is of major concern to scientists and to the public, with expanding fisheries and increasing value of whale shark products such as flesh and fins in Philippines, India, Taiwan (Province of China) and elsewhere in the late 1990s. This runs counter to the increasing international popularity of live whale sharks as subjects of ecotouristic dives, as well as increasing public sympathy for these animals worldwide as harmless "gentle giants" or "gentle monsters of the deep" (Clark, 1992) that (as with cetaceans) should be conserved because of their intrinsic worth and emotional appeal. Although whale sharks have been caught off Taiwan (Province of China) for many decades of the twentieth century, whale shark flesh became very popular fresh for human consumption in Taiwan (Province of China) over the past two decades, which caused a major increase in the value of whale shark products there, encouraged Taiwanese fishers to catch more whale sharks, apparently caused a decline in catches of whale sharks off Taiwan (Province of China), but also stimulated the fishing of whale sharks in Philippines until the fishery declined and it was banned in 1998. The Taiwanese market has also stimulated expanded and substantial export fisheries for whale sharks off India, which developed from traditional artisanal fisheries there and which are apparently declining at present due to overfishing. Whale shark meat was valued at about 400 New Taiwanese Dollars per kilo in 1996 (Joung et al., 1996; equivalent to US$13 in 2000 and nearly US$200 000.00 for the meat alone from a 36 t shark if two-fifths of its weight is muscle). Fin prices are uncertain but are probably very high at present as with fins of other large sharks. It is uncertain what effects the now banned drift net fisheries had on whale sharks (and for that matter mantas and devil rays) as discarded bycatch during the peak period of their use during the late 1980s and early 1990s. No countries that report shark catch statistics to FAO currently report whale shark catches.

The whale shark has been listed on the IUCN Red List for the past few years, is protected by the United States east coast shark management plan, and in the Maldives. More recently (1998), it was protected by the Philippine government with bans on killing and selling them following steep declines in numbers in Philippine waters; similar protection was given to this species off Gladen Spit, Belize (2000). Ecotouristic viewing of whale sharks is being actively promoted by the World Wide Fund for Nature as an economic alternative to whale shark fisheries in Philippines (M.N.R. Alava and A.A.S.P. Yaptinchay, pers. comm.). After lobbying by the Shark Research Institute the Honduran government declared total protection for the whale shark off Honduras in 1999 (M. Levine, pers. comm.). The species is under consideration for total protection in South Africa also (1999 to 2000). International protection for the whale shark is probably necessary, perhaps in the form of a CITES listing with a worldwide ban on fishing them for international trade as well as regional agreements and national regulations for protecting them or limiting exploitation. Whale shark fins and meat fall into international trade and regulation, but the highly migratory whale shark ranges close inshore and is also subject to local fisheries supplying local markets as well as pelagic fisheries and international exporters. There is considerable concern that whale sharks are extremely vulnerable to overexploitation due to their relatively low abundance, large size, ease of access at the surface, and possibly very slow growth and exceptional longevity (see above). They are a ready target of coastal and pelagic fishing operations, and are easily harvested by small boats in shallow coastal waters. It is a natural extension, as in Philippines, for former whale-hunters to transfer their activities to whale sharks. This parallels whale fisheries that also took basking sharks. With the current high values of whale shark flesh and fins, whale sharks could be targeted in international waters by long-range fishing vessels run like miniature whale factory ships (for example, a few converted ocean-going stern trawlers of modest displacement set up for processing carcasses and blast-freezing the meat and fins) and using small 'killer' boats, harpoonguns, light helicopters or microlight aeroplanes as spotters, and even remote sensing from satellites to fish these sharks pelagically. Small specialist killer boats with harpoon-guns already exist in the declining basking shark fishery, and could be applied to the whale shark fishery for shore-based operations or serving small factory ships. Fortunately this has not happened to date, and hopefully will never happen, as the effect of even a few such vessels or a small fleet could be devastating in short order. It may be possible that decreases of whale sharks from shore-based small operations may preclude high-technology pelagic whale shark fishing on economic impracticality.

Pauly (in press) suggested that because of the whale shark's slow growth and other life-history parameters any plan for targeted exploitation of whale sharks as fisheries resources would lead to a quick collapse of numbers, and that even ecotouristic viewing of whale sharks on feeding and mating grounds should be carefully monitored to prevent even indirect mortality which these sharks probablycould not accommodate. His prediction apparently was verified while his paper was in press (1997 to 2000), with the steep decline of the Taiwanese and Philippine whale shark fisheries and possible declines of whale sharks in the western Indian Ocean following the developing Indian fishery.

It is quite possible, however, that whale sharks are far more valuable in terms of long-term and longrange revenue generated from ecotourism than current fisheries, which have the potential to decimate them and remove the source of revenue. For Ningaloo Marine Park, Western Australia, revenue from whale shark ecotourism has been growing at 15% per year and is estimated at being worth A$12.8 million in the year 2000 despite being highly seasonal and of short duration, between March and May of each year (Colman, 1997). If the same sharks visit different viewing sites, as is suggested by longrange tagging and tracking, and are long-lived, they each may generate far more revenue as a live animal viewed repeatedly by diving ecotourists over several decades and at several sites rather than that received as a one-off fee from killing them (and with low value often received by fishers in Developing countries compared to fin and meat dealers in the developed world). This may be particularly important in places such as the Philippine Islands, where ex-whale shark fishers are becoming involved in whale shark ecotourism (M.N.R. Alava and A.A.S.P. Yaptinchay, pers. comm.) and even a whale shark museum. Extraordinarily high profits from flesh and fins drive the current fisheries, but their existence is probably ephemeral as whale sharks may be unable to sustain them for very long because of their biological limits.