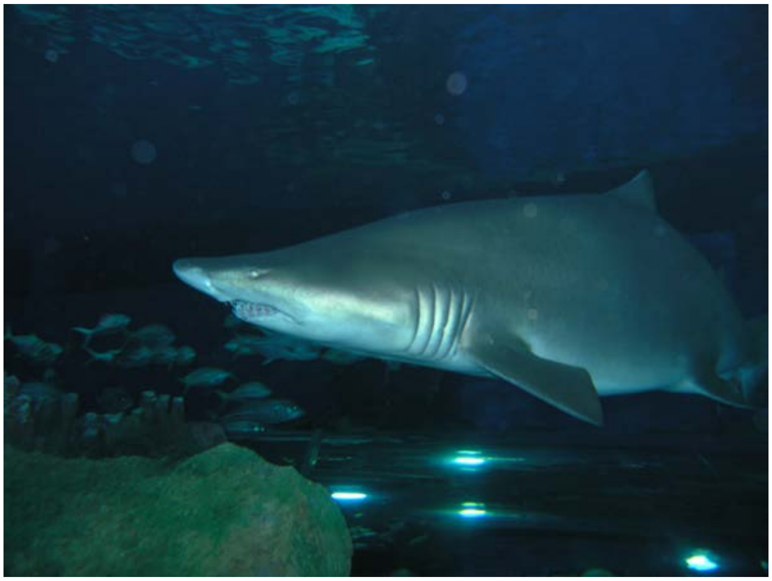
The University of Hull

M.Sc. Biological Sciences

The Behaviours and Spatial Distributions of Captive Sand Tiger Sharks (*Carcharias taurus*) in a Marine Aquarium.



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Abstract

This study was conducted between January 2003 and November 2004 to determine the effects of season (mating and non-mating), feeding regime and time period on voluntary swimming speeds, spatial distribution and behaviours of sand tiger sharks (*Carcharias taurus*) at the Blue Planet Aquarium, England. Each shark was observed for periods of 15 minutes and every 15 seconds the position of a focal shark and its behaviour were recorded. In total over 200 hours of observations were made.

In previous years, mating behaviours had been observed in this aquarium from January through to May (hereafter "the mating season"). Males increased swimming speed significantly and the females decreasing speed during the mating season. Spatial distribution in the tank was significantly different between mating - and non-mating seasons, with males spending more time in the areas commonly frequented by females during the mating season. The nearest neighbour and give-way occurrences, measures which may reflect the dominance hierarchy between sharks, were not influenced by mating season. *C. taurus* individuals who frequently gave-way at encounters were significantly more likely to avoid encounters at distance. During the mating season, pre-copulatory behaviours were also recorded. Numbers of displayed mating behaviours differed significantly between individuals. Furthermore, there was a significant positive correlation between swimming speeds and mating behaviours, male sharks with the fastest swimming speed displayed the most mating behaviours.

To determine feeding regime effects, data were recorded on both feeding and non-feeding days. Swimming speed was not found to significantly change between feeding and non-feeding days. Likewise, there was no effect on give-way occurrences between feeding and non-feeding days. Spatial distribution was however effected, and on feeding days the sharks spent more time in and around the sections where they were fed.

Time of day was divided in to six periods with varying lighting conditions and different diver and visitor presence/absence. Time period affected all variables recorded, and swimming speeds were significantly faster during the night time periods. Spatial distribution differed between the day and night time periods, and the sharks are particularly active at night (i.e. they spent a higher proportion of time patrolling and less time resting at night). Throughout the day time periods there were no detectable changes in shark swimming speed, spatial distribution and behaviours between, and the analysis suggests that presence of divers and visitors has no detectable effects on these sharks.

1. Introduction

1.1 Biodiversity and Extinction

Human activity is resulting in the continued alteration and destruction of ecological habitats worldwide, requiring scientists and conservationists alike to augment preservation of flora and fauna, thus minimising species extinction and maximising biodiversity. The Convention on Biological Diversity (C.B.D.) defines biodiversity as the variability among living organisms from all sources including, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; including inter- and intraspecific diversity as well as that of ecosystems (Gaston & Spicer, 2004).

There are numerous estimates of future extinction rates, the variation in estimates arise from the different assumptions made. There is however a general consensus that between 15 - 20% of the planet's vertebrate taxa will be lost in the next 100 years (Magurran, 2005). Scientists and conservation societies endeavour to understand the extinction process to enable valued judgements to be made about how to respond to biodiversity loss.

The International Union for the Conservation of Nature and Natural Resources (IUCN), the world's largest conservation network, aims to increase scientific understanding of natural ecosystems and their benefits to mankind. Such knowledge is then used practically to bring together policy makers, scientists, business leaders and Non-Governmental Organisations to impact the way the world values and interacts with nature. To assess species conservation status the Red List was introduced. This document uses an objective and scientific system to determine the threat status of individual species. In 1994, extremely precise Red List Categories and Criteria were adopted by the IUCN. There are nine categories; extinct, extinct in the wild, critically endangered, endangered, vulnerable, near threatened, least concern, data deficient and not evaluated. Currently there are approximately 45,000 species covered on the IUCN Red Lists and this figure is predicted to rise to around 60,000 by 2010 [1]. Marine species are at present lacking representation on the Red List, but 591 species chondrichthyes are currently listed on the Red List, with 205 deemed data deficient [2].

1.2 Threats Facing Marine Life

The Jakarta Mandate stated the main threats to marine life and causes of extinction of coastal and marine organisms are: physical alteration and destruction of habitats, pollution, introduction of exotic species and overexploitation (United Nations Environmental Program, 1995). Of these causes the two most important factors appear to be habitat alteration and overexploitation (Wolff, 2000), both of which have resulted in species extinctions on a global scale, (Carlton, 1993; Vermeij 1993; Del Hoyo *et al.* 1992, 1996).

Marine habitat alteration and destruction is on the increase. Many coral reefs in Asia have been destroyed or severely damaged by cyanide and dynamite fishing (Mak *et al.* 2005). Regional surveys published in 2000 state that only 4.3% of the Philippine reefs and 6.7% of those in Indonesia are still in excellent condition (Simpson, 2001). Furthermore recent estimates suggest that it could take several hundred years for coral reefs to recover from cyanide damage (Raymundo *et al.* 2007, Riegl and Luke, 1998). In

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[1] http://www.iucnredlist.org/static/programme

[2] http://www.iucnredlist.org/documents/2008RL_stats_table_3a_v1223294385.pdf)

addition to the threat of extinction to many fish species, cyanide is a non-selective poison that also destroys coral polyps, symbiotic algae and other small reef organisms essential for sustaining a healthy reef (Jones and Steven 1997). Marine habitat alteration and destruction are global problems affecting areas including the Wadden sea, the North sea, Wallacea and many coastal regions of the United States of America and Australia (Wolff, 2000; Kearney *et al*. 1996, Yamada *et al*. 1987, Kemp *et al*. 2005).

Marine overexploitation is such that an estimated one third of all marine produce is removed from the seas by humans as combination of harvest and by-catch (Frid and Dobson, 2002). Of that, it is believed that one quarter of fish catches globally are discarded, dead or dying, back into the sea (Alverson *et al.* 1994). The over-harvesting and exploitation of fish species have resulted in many becoming endangered (Primack, 2006). Theoretically, harvesting living organisms should be a sustainable process as reproduction allows stocks to replenish their own numbers. Sustainable harvesting is therefore beneficial in both economic and conservation terms. However, for a given level of fishing mortality to be sustainable there must be a balance between mortality (both natural and harvesting) and reproduction (Russell, 1931). In addition mortality and reproduction are not entirely independent of each other, but fluctuate between limits set by abiotic factors such as the weather and biotic factors such as predation (Begon *et al.* 1996). Maximum sustainable yield models have been formulated with the aim of harvesting populations at sustainable levels (Frid and Dobson, 2002). However, such models do not always produce accurate estimates that may result in an increased risk of extinction and a possible collapse of the fishery (Atarhouch *et al*. 2006). In addition as the majority of fish recruitment is extremely variable, there will always be elements of uncertainty in recruitment estimates due to climatic and biological phenomena (Dippner 1997, Neill *et al*. 1994). This unpredictability of fishery industries can be illustrated by the collapse of the *Engraulis ringens* (Peruvian anchovy) due to overfishing exacerbating an El Nino-induced population crash (Krebs, 1994) and the repeated overfishing and recruitment failures in New Foundland in the early 1990s (Chantraine, 1993; Schrank, 2005). In both cases, population collapse resulted from inaccurate population models coupled with overfishing superimposed on climatic and biological impacts.

In addition to the direct effects on the species that is being overexploited, indirect effects of fishing can include habitat destruction and result in biodiversity loss, particularly with gears such as bottom trawls and dredges (Engel and Kvitek, 1998; Coleman and Williams, 2002; Watson *et al*. 2006). Furthermore overfishing may result in trophic cascades that can cause further declines in species richness (Steneck, 1998).

1.3 Threats Facing Sharks

Present day sharks, whose ancestors survived both the Permian and Jurassic mass extinctions, are now under serious threat; not because of global changes but as a direct consequence of human activity (Burgess *et al.* 2005).

By virtue of a relatively *K*-selected life history strategy, conducive to longer life spans and stable, less productive populations, elasmobranchs are more vulnerable to exploitation (Walker, 1998). Extinction in the near future is a possibility for some species of sharks as this slow reproductive rate and high mortality rate, caused primarily by shark fining, combine to paint a bleak future for some species.

Most nations have relatively low landings of sharks (Compagno, 1990), yet shark stocks are extremely sensitive to over-fishing by virtue of their life history parameters. Numerous shark stocks have been severely depleted following brief periods of overexploitation (Anderson, 1990). The Food and Agriculture Organisation (FAO) determined that there had been severe population declines for almost all 26 shark species for which catch or landing data had been available for more than ten years, (Castro *et al.* 1999). Over the past two decades coastal shark populations in the Atlantic have declined by as much as 85% (Camhi, 1999; Baum *et al*. 2003). In 2003, the country carrying out the most shark fishing was Indonesia, followed by Taiwan and India. Spain ranked and the U.S.A. (Lack and Sant, 2006).

Scientists estimate that 100,000,000 sharks are killed globally each year for the shark fin trade[3]. It is believed that shark fins have been harvested since the second century BC throughout Asia (Cunningham-Day, 2000). In the marine environment of Wallacea, shark fining is a major problem; in the areas of Nusa Tenggara and Maluku sharks are generally only taken for their fins and tails, the carcass is thrown back into the sea (Monk *et al*. 1997). Fining is not exclusive to developing countries, European and U.S. fishermen provide a high percentage supply of shark fins to the Asian market, and that market demand is on the increase (Prestowitz, 1996).

Regulations to protect sharks from fining have been established throughout the world, however many conservation groups believe these are not effective. The European Union’s fining regulation (Council Regulation EC 1185/2003) prohibits the removal of shark fins at sea, yet permits can be issued on request to allow sharks to be processed on board vessels[4]. A maximum fin weight to carcass ratio was introduced in an attempt to prevent fining under these permits. However, this ratio is 60% above the science based IUCN standard and results in the potential fining of 2 out of 3 sharks caught by European vessels. EU registered boats may also legally land fins and carcasses in separate ports thereby rendering enforcement of the regulations near impossible. Spain now leads all other fin exporters in the world by a wide margin (Clarke and Mosqueira, 2002). Additionally, European participation in the Hong Kong fin market has increased from negligible levels in the early 1990s to almost one third of declared imports by 2006, evidencing a global market and phenomenon. Accordingly, the U.S.A. has recently introduced the Shark Conservation Act of 2008, a bill which attempts to improve the conservation of sharks by amending and strengthening the High Seas Moratorium and the Magnuson-Stevens Fishery Conservation and Management Acts.

In addition to an increased demand for shark fins, the shark cartilage medicine industry is also on the rise. In 1996 an estimated 100,000 people were taking shark cartilage for its reputed cancer-curing properties, and that figure is probably greater still today (Dold, 1996). Despite such claims Miller *et al.* (1998) carried out a three month study which provided terminally ill cancer patients with shark cartilage; the disease did not slow with the addition of cartilage. Yet the demand for shark cartilage continues to rise and as twenty seven pounds of shark cartilage produces only one pound of extract the numbers of sharks being processed to satisfy demand also increases.

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[3] http://www.sharktrust.org/content.asp?did=26881#what

[4] http://europa.eu.int/eur-lex/lex/lexuriserv/lexuriserv.do?uri=CELEX:32003R1185:EN:HTML

1.4 *In situ* and *ex situ* conservation

The best strategy for long-term protection of biodiversity is the preservation of natural populations in their natural environment (*in situ*); this however is not always viable, primarily due to human disturbance (Gaston and Spicer, 2004). Wild populations may decline, or even become extinct, in their natural environment for a variety of reasons such as overexploitation, habitat loss, competition from exotic species, disease, inbreeding or genetic drift (Frankham *et al*. 2003). If the remaining population is composed of a small number of individuals or if remaining individuals occur outside protected areas, *in situ* conservation is unlikely to be effective. Therefore, to prevent species extinction, individuals can be kept in an artificial environment under human supervision, (*ex situ*), (Conway 1980; Dresser 1988; Seal 1988; Cohn 1991; Xia *et al.* 2005). At present there are 25 species of animal which survive only in captive colonies, these include *Equus caballus przewalski* (Przewalski's horse) and *Elaphurus davidianus* (Pere David's deer) (Frankham *et al*. 2003). Over the next 200 years it is estimated that between 2000 and 3000 species of terrestrial vertebrates will require captive breeding to prevent them from becoming extinct (Soulé *et al*. 1986; Tudge, 1995).

Ex situ and *in situ* conservation strategies are complimentary approaches (Robinson 1992; Farnsworth *et al.* 2006). *Ex situ* methods can also help preserve wild species by periodically releasing individuals from *ex situ* populations into natural populations. This helps to maintain numbers and genetic variability in the wild (Powell and Cuthbert 1993; Cade and Jones 1993). In addition research on captive populations can provide insight into the basic behaviour and biology of species which may in turn result in the development of new conservation strategies (Primack, 2006). *In situ* conservation is also important to *ex situ* strategies, in particular for the survival of species which have proven difficult to maintain in captivity, such as *Dicerorhinus sumatrensis* (Sumatran rhinoceros) (Zahari *et al.* 2005).

Despite limitations, *ex situ* conservation strategies are believed to be a viable alternative when *in situ* preservation of a species is difficult or impossible (Soulé 1987). One of the primary limitations is genetic adaptation to artificial conditions which may occur if a species is kept in captivity for many generations. This may pose a problem if reintroducing individuals to the wild. Individuals in *ex situ* populations may also lose their knowledge of their natural environment, (i.e. become behaviourally adapted), again resulting in problems of reintroduction (Primack, 2006). For example, captive bred animals may not be able to locate water sources or recognise edible foods if released back into the wild. There is also the problem of *ex situ* efforts being concentrated in a relatively small area which results in the entire population being at risk from catastrophes such as fire or epidemic (Rout *et al*. 2006). Furthermore *ex situ* conservation requires a continuous supply of funds and a permanent institutional policy which is not always the case. Van Oosterhout *et al.* (2007) also found that captive-bred individuals were more prone to infections disease on reintroduction into their natural environment; reduced levels of immunogenic variation due to inbreeding and lack of exposure to natural parasites were found to be the cause.

Captive environments may select for different behaviours than wild rearing conditions in cultured fish species. Aquaria and hatcheries are high density environments, thus captive reared fish often show increased competition, increased aggression, reduced defence of territories and refugia and reduced predator avoidance in comparison to their wild counterparts (Brännäs and Brännäs, 2004, Orpwood *et al*. 2004 Sundström *et al.* 2003, Weber and Fausch, 2003). However, it remains unknown whether similar effects operate on captive elasmobranchs, which are often held at lower densities than the aforementioned fish.

1.4.1 *Ex Situ* Conservation in Aquaria

Public aquaria have historically oriented toward the display of colourful and unusual fish species, but have recently tended to increase involvement in conservation in response to threats to marine life. For example, the Deep Submarium, Hull England, supports both scientific research of their captive species and holds public education of conservation in the utmost importance. This attitude change of the majority of aquaria comes as concern for species extinction has increased (Primack, 2006). Recently programs, developed to increase knowledge of endangered species with the aim of preventing further species extinction, feature increasing synergy between aquaria, marine research institutes and government fisheries departments.

The ease with which a species can be studied in the wild varies greatly. Some taxa which have large home ranges are difficult to study; this is made increasingly difficult in aquatic species as tracking and following an individual poses many additional problems. Sharks are an example of a group of animals which can travel large distances making it problematic to studying these predators in the wild. Transoceanic migration of *Carcharodon carcharias,* (great white sharks) has been observed through satellite tagging; individuals travelled from the Australian to the South African coasts (Bonfil *et al.* 2005). Aquaria provide an ideal opportunity to study these apex predators at a level of detail not possible in the natural environment (Newman 1999). Aquaria and zoos are useful for conducting observational research, which can be used to establish how to maintain a species in captivity, or even how to re-establish the species in the wild (Burghardt, 1975). With aquaria and zoos it is now possible to observe interactions between species which might not occur in nature, or which might occur in reduced frequency and duration in the wild (Seligson and Weber, 1990). Although the behaviour of captive sharks almost certainly differs from that in the wild it is still important to investigate their behaviour to ensure the continued success of these largely misunderstood animals in captive situations.

Most sharks are not only difficult to collect and transport, but once in captivity, often refuse to feed and therefore die (Myrberg, 1989). Therefore, early shark research was related to capture, transportation and transition of sharks into captivity. Once the problems of transporting sharks are overcome, understanding their behaviour is valuable for ensuring their successful maintenance in captivity (Gruber and Keyes, 1981). Accurate life history and behavioural information is also required to enforce management policies in fisheries and is useful for the conservation of the species in the wild. Now that the techniques of capturing and holding sharks employed by aquariums have improved, these institutions are proving more successful in maintaining some of the larger species of shark in captivity (Newman, 1999). While captive studies may not be useful for forecasting typical behaviour in the wild, they can be useful for comparative studies and can contribute to the understanding of a species in captivity.

1.5. Shark Reproduction

There is relatively little known about shark mating behaviour either in the wild or in captive situations. For many species of shark, the mating period appears to be the only time when they come into contact with members of their own species. There are often distributional and behavioural barriers which result in gender segregation, however during the mating period such barriers breakdown (Lucifora *et al.* 2002). During a ten year study by Castro *et al.* (1988) on *Scyliorhinus retifer* (chain dogfish); copulation was only observed once, illustrating the difficulties of observing mating behaviour. Mating and courtship has, however, been observed in a small number of shark species, most of which have been observed in captivity (Gordon, 1993). The mating behaviour most commonly observed involves the male biting the female on the fins, tail or in the gill region. Species of shark where this biting mating behaviour has been observed include *Heterodontus francisci*, (horn sharks), *Ginglymostoma cirratum* (nurse sharks), *Hemiscyllium ocellatum* (epaulette sharks) and *Triaenodon obesus* (whitetip reef sharks), (Dempster and Herald, 1961, Klimley, 1980, West and Carter, 1990, Uchida *et al.* 1990). Other captive shark species have not been observed carrying out this mating behaviour but corresponding scarring patterns on the females' body indicate this behaviour may have occurred. It has been suggested that the biting may act as a releaser that triggers mating acceptance in the females (Wourms, 1977).

Figs.1.5.a Bite marks resulting from mating attempts of a captive sand tiger shark at The Blue Planet Aquarium, Ellesmere Port, U.K.

Another mating behaviour observed in sharks is the close following of the female by the male (Myberg and Gruber, 1974). Johnson and Nelson (1978) studied the pre-copulatory behaviour in *Triaenodon obesus* (whitetip reef sharks) and *Carcharhinus melanopterus* (blacktip reef sharks). They found that the male's snout was within 30cm of the tip of the female's caudal fin while the females held their tails in an erect posture. They hypothesised that olfaction-mediated recognition and pairing was occurring as in some instances the males were able to intercept females when sound, visual and vibrational cues were not present. Klimley (1980) also observed this following behaviour as an expression of sexual interest in *G. cirratum*. However, such behaviour has also been observed in some shark species in non-copulatory situations. Results of previous studies emphasize the variety and complexity of shark reproductive behaviours (Demski, 1990), suggesting the need for direct observation whenever possible.

There are three broad reproductive strategies seen in sharks with varying fecundity. Oviparous sharks, such as the order *Heterodontidae*, deposit eggs on the ocean floor (Castro, 1996a). Water temperature is believed to influence the time taken for the eggs to hatch, and dependent on species it can take anything from a year to just a few weeks (Compagno, 2005). Ovoviviparous sharks, such as dogfish, give birth to multiple live young with the eggs developing within the mother's body (Cunningham- Day, 2001). Within a brood the embryonic development is in different stages and is likely to be a result of sequential ovulation (Castro, 2000). Viviparous sharks, such as *Carcharinidae*, give birth to live young which obtain food from the mother during gestation. In both instances, once born the offspring receives no parental care. In some species, such as *Carcharias taurus* (sand tiger shark), only one dominant pup survives in each of the paired uteri as these species show intrauterine cannibalism (Gilmore *et al.* 1983).

Fig.1.5.b Dissected C. taurus uteri containing a dominant pup in each uterus with smaller pups killed by their siblings. Provided by Dr. J.I. Castro Mote Marine Lab.

In some species of viviparous sharks a complex pregnancy occurs whereby nutrients from the mothers blood passes through the placenta to the embryo via the umbilical cord, as in humans. Examples of such sharks include *Negaprion brevirostris* (lemon sharks), *Carcharhinus leucas* (bull sharks) and *Sphyrna zygaena* (hammerhead sharks) (Castro, 1984).

Scientific studies have led to the discovery that reproductive cycles exist in sharks, although the full details of how they reproduce is unknown. Defined by Koob and Callard (1999) shark reproductive cycles are – continuous for those species that reproduce throughout the year, seasonal for those species that are reproductively active for only part of the year and punctuated for those species that are pregnant for approximately one year and the next pregnancy is at least a year later. The occurrence of reproductive cycles is species specific. Lucifora *et al.* (2002) studied the reproductive ecology of *C. taurus* from the south-western Atlantic ocean. They found significant differences in the reproductive condition through time of male individuals. Through January and February the males' seminal vesicles were full of spermatophores, but by April the vesicles were empty. It is therefore extremely likely that mating takes place during January and February. A sex ratio 2:1 in favour of males was found indicating a possible strong competition in males for mates. Castro (1996 b) concluded, based on the presence of ovulatory females with fresh bites on their flanks or spermozeugmata in their uteri, that mating and ovulation occur in *Carcharhinus limbatus* (blacktip sharks) in Bulls Bay from May to June. Wetherbee (1996) studied *Etmopterus granulosus* (southern lantern shark) in New Zealand and saw no evidence of a seasonal reproductive cycle. Likewise Richardson *et al.* (2000) found *Holohalaelurus regani* (Izak catshark) to be reproductively active throughout the year. Despite the lack of evidence to support the occurrence of reproductive cycles there is a possibility they may still occur. The mating period appears to mainly be associated with variations in ambient temperature that elicit a hormonal response designed for reproduction. This has often been found to coincide with the beginning of the migratory period (Jutagate *et al.* 2006).

1.6 The Sand Tiger Shark – *Carcharias taurus* (Rafinesque, 1810)

Carcharias taurus has a variety of regional common names including the spotted ragged-tooth, the grey nurse and the sand tiger shark.

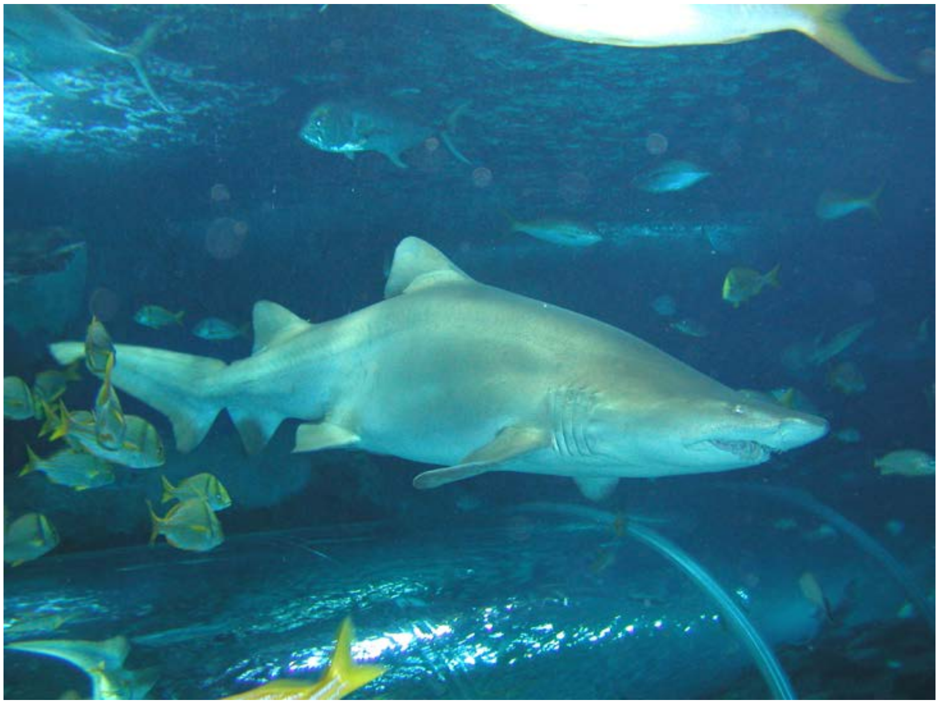

Fig. 1.6 Photograph of a captive C. taurus

C. taurus are approximately one meter in length at birth and can reach sizes of three meters (Bass 1975, Smale 2005). The species has an undeserved reputation as a man-eater in Australia, but this may be due to confusion with other sharks as it is inoffensive unless provoked (Compagno *et al*. 2005).

The bodies of *C. taurus* are stout with two similar sized dorsal fins (Compagno, 1984). The first dorsal fin is located nearer to the pelvic fins than to the pectoral fins. *C. taurus* have brown/red spots scattered over the tail and rear of the body which fade with age and have disappeared when individuals reach 180 – 200cm TL (Castro, in preparation). Their diet consists primarily of teleosts, elasmobranchs and cephalopods (Castro, 1996a). Smale (2005) found that both reef associated and benthic fish typical of sandy substrate were part of the diet of *C. taurus* in the Eastern Cape of South Africa. From this it was inferred that although they preferred to swim around high relief reefs with gullies and caves by day, they must also hunt over soft substrate, possibly at night.

C. taurus are common littoral sharks in temperate and tropical waters (Compagno, 2001). They are found in shallow bays, coastal waters and rocky or tropical reefs from shallow waters down to a depth of about 200m. *C. taurus* has been reported in numerous localities worldwide: Australia (Whitley, 1940), western and eastern Indian Ocean (Bass *et al*. 1975; Smale, 2002; Dicken *et al.* 2006), eastern Atlantic and the Mediterranean (Cadenat and Blache, 1981), Bermuda (Smith Vaniz *et al*. 1999), western Atlantic (Bigelow and Schroeder, 1948) and South Atlantic (Menni, 1986). *C. taurus* is a strong but slow midwater swimmer, and is highly migratory (Compagno, 1984), presumably for reproductive purposes (Taylor, 1997). Despite the migratory nature of this species, it readily adapts to captivity and is a popular aquarium fish due to its fierce looks. The first captive *C. taurus* was held at New York Aquarium in 1896 and was maintained successfully for many years (Koob 2004).

Essapian (1962) described *C. taurus* in captivity as swimming continuously at mid-depth. Crow and Hewitt (1987) made a distinction between adult and juvenile *C. taurus*, with the larger individuals nearer the surface, and the juveniles near the bottom.

C. taurus is well known for hovering motionless in the water column. Although most sharks rely on their oily livers for buoyancy, C. taurus swallow air and hold it in the stomach to attain near neutral buoyancy (Compagno, 2001). Hussain (1989) calculated that the weight of a *C. taurus* in water increased by 3kg after the air in the stomach had been removed.

C. taurus are an aplacental viviparous species. Embryos are initially nourished by stored yolk. *C. taurus* eggs are 7 – 10mm in diameter and have only enough stored yolk to nourish the embryo through the first weeks of development. Hatching from their egg cases when 40 – 50mm long the yolk from their yolk sac is consumed by the time they have grown to 100mm. Thereafter oophagy and intrauterine cannibalism occur (Gilmore, 1983). At early stages there are as many as seven embryos in each uterus, however only one embryo in each uterus survives to full term. Embryos develop precocious dentition by 50mm and when the largest embryo reaches 80 – 100mm it seeks and kills the smaller embryos (Bass *et al*, 1975). *C. taurus* have one of the lowest reproductive rates known among elasmobranchs giving birth to only 1 or 2 pups every 2 years (Pollard, 2000; Dicken *et al.* 2006). Branstetter and Musick (1994) determined that *C. taurus* mature at around six years old. The low reproductive output and age of maturation makes this species vulnerable to over exploitation, (Smale, 2002).

The numbers of *C. taurus* in the wild have decreased rapidly over recent years. Individuals are taken through fishing, both sport and commercial, as by-catch, for the aquarium trade and by bather protection nets in areas such as KwaZulu-Natal, South Africa (Dudley and Cliff 1993). Due to this decline *C. taurus* is now listed as vulnerable on the IUCN Red List of Threatened Species. The two categories which currently qualify this species as vulnerable are first, there has been a population reduction of at least 20% over the last 10 years or 3 generations, whichever is longer, by direct observation and an index of abundance appropriate for the taxon. Second, there has been a population reduction of at least 20% projected or suspected in the next 10 years or 3 generations whichever is longer, based on actual or potential levels of exploitation.

As different populations of *C. taurus* have varying risk of extinction the IUCN Shark Specialist Group (SSG) are now assessing the risk of extinction of individual populations and sub-populations on a local level. For example the Eastern Australian sub-population (New South Wales), has declined primarily due to sports and commercial fisheries (Compagno *et al.* 2005). Now estimated to consist of less than 500 individuals and possibly as few as 300, this sub-population has been classified as critically endangered (Otway *et al.* 2003; Pollard *et al.* 2003a). Although steps have been taken to protect *C. taurus* in this area since 1984 they have become locally extinct at many previously known recruitment sites. In contrast the Western Australian coast sub-population is relatively stable, therefore requiring less urgent protection. Despite never having been specifically targeted, it is recognized that the by-catch of *C. taurus* may lead to sub-population declines in this species due to low intrinsic rate of increase for this species. This sub-population is thus classified as near threatened (Pollard, 2003b).

As populations of *C. taurus* continue to decline, steps are being taken to help save this species from extinction. In 1984 this species received a fully protected status in

Australian waters. In April 1997 the National Marines Fishery Service (NMFS) of the United States prohibited all direct commercial and recreational fishing of sand tiger sharks on the Atlantic coast (Castro, in preparation). However, such measures are yet to counteract the decline in numbers.

With the difficulties associated with observing *C. taurus* in the wild, this study aims to identify baseline captive behaviours of this species and how factors such as stocking density, sex ratios, lighting and feeding regimes affect such behaviours. Occurrence and frequency of mating behaviours and factors which may optimize successful captive breeding will also be recorded; of the 100+ aquaria that keep *C. taurus* only three have had captive births. As numbers are decreasing in the wild, captive breeding may be a way for aquaria to reduce their impact on wild populations and if successful potentially reintroduce captive born individuals back into wild populations.

2. Aims and Hypotheses

2.1 Aims

The aim of this study was to further scientific understanding of intra specific variation in behavioural patterns, providing quantitative results on captive *Carcharias taurus*. To achieve this, the objectives were firstly to record baseline data of each individual to include a variety of morphological and behavioural parameters. In addition the effects of day (feeding or non-feeding), season (mating or non-mating) and time period on these behaviours were examined. The results were interpreted to draw any inferences with regard to mating behaviour, dominance hierarchies, behavioural differences, spatial distribution and swimming speeds within the study group.

As discussed in 1.6, due to the distribution of wild *C. taurus* it is difficult to study their spatial distributions and interactions with others of their species in the wild. The high densities of *C. taurus* in captivity allows us to observe such behaviours, but it is questionable whether they represent behaviours displayed by their wild counterparts. Nevertheless, given that ex-situ conservation of this species is of increasing importance, the current study enables us to learn more about this species in captivity, particularly in terms of spatial distributions, nearest neighbour preferences and dominance hierarchies. This information will help improve the holding conditions of these sharks, which is ultimately of importance for both their conservation and welfare.

2.2 Questions and Hypotheses

In this section seven sets of questions and there corresponding null hypotheses are formulated to examine the factors that influence the spatial and temporal distribution of captive sharks, as well as the behaviours and interactions between sharks.

2.2.1 Spatial Distribution

1A. Do individual sharks differ in their use of space of the tank?

Sections of the tank do not differ in the frequency by which they are occupied by sharks (i.e. the spatial distribution of sharks).

1B. **Do male and female sharks differ in their use of space in the tank?**

There is no difference between male and female sharks in spatial distribution within the aquarium.

1C. **Do sharks differ in their use of space in the tank with season?**

There is no difference between sharks in spatial distribution in the tank when observed in mating and non mating seasons.

1D. **Do sharks differ in their use of space in the tank with feeding regime?**

There is no difference between sharks in spatial distribution in the tank when observed in feeding and non feeding days.

1E. **Do sharks differ in their use of space in the tank with time of day?**

There is no difference between sharks in spatial distribution in the tank when observed in different time periods.

2.2.2 Water Column Depth

2A. Do sharks prefer a certain depth in the tank?

There is no preferred swimming depth in the tank by sharks.

2.2.3 Nearest Neighbour

3A. Do individual sharks show nearest neighbour preferences?

There is no nearest neighbour preference.

3B. Do nearest neighbour preferences change between mating and non mating season?

There is no variation in nearest neighbour preferences between mating and non mating seasons.

3C. Do nearest neighbour preferences change with feeding regime?

There is no variation in nearest neighbour preferences between feeding and non feeding days.

3D. Do nearest neighbour preferences change with time of day?

There is no variation in nearest neighbour preferences between different time periods.

2.2.4 Dominance Hierarchy

4A. Does a dominance hierarchy exist between *C. taurus* at the Blue Planet Aquarium?

There are no dominance relationships between sharks.

4B. Is one gender more dominant than the other?

There are no dominance relationships between males and females.

4C. Do dominance relationships change between mating and non mating season?

There is no variation in dominance relationships between mating and non mating seasons.

4D. Do dominance relationships change between feeding and non feeding days?

There is no variation in dominance relationships between feeding and non feeding days.

4E. Do dominance relationships change between time periods?

There is no variation in dominance relationships between different time periods.

2.2.5 Swimming Behaviour

5A. Do individual sharks differ in their swimming behaviours (patrolling or resting)?

There is no difference in swimming behaviour between individual sharks.

5B. Do sharks differ in their swimming behaviours (patrolling or resting) with time of day?

There is no difference in swimming behaviour between time periods.

2.2.6 Swimming Speeds

6A. Do individual sharks have different average swimming speeds?

There is no variation between swimming speed in individual sharks.

6B. Does gender influence the average swimming speed?

There is no variation in swimming speed between male and female sharks.

6C. Do average swimming speeds of the sharks alter between mating and non mating season?

There is no variation in swimming speed between mating and non mating seasons

6D. Do average swimming speeds of the sharks alter between feeding and non feeding days?

There is no variation in swimming speed between feeding and non feeding days

6E. Do average swimming speeds of the sharks alter with time of day?

There is no variation in swimming speed between time periods.

2.2.7 Frequency of mating behaviours

7A. Does season affect the occurrence of pre-copulatory behaviours in sharks?

There is no difference in pre-copulatory mating behaviour frequency between mating and non mating season

7B. Does feeding regime affect the occurrence or pre-copulatory behaviours in sharks?

There is no difference in pre-copulatory mating behaviour frequency between feeding and non feeding days

7C. Does time of day affect the occurrence or pre-copulatory behaviours in sharks?

There is no difference in pre-copulatory mating behaviour frequency between time periods.

7D. Do some female sharks display more pre-copulatory behaviours than others?

There is no difference in pre-copulatory mating behaviour frequency between female sharks.

7E. Do some male sharks display more pre-copulatory behaviours than others?

There is no difference in pre-copulatory mating behaviour frequency between male sharks.

3. Materials and Methods

3.1 Sand Tiger Shark Behavioural Study

3.1.1 Study Area

The Blue Planet Aquarium, Ellesmere Port, was selected as the study site as it is home to the largest population of captive *C. taurus* in the United Kingdom.

The tank which housed *C. taurus* was an irregular polygon approximately 25 meters wide, 36 meters long, and predominantly three meters deep but reaching the depth of six meters in front of the aqua-theatre. Sculptured rockwork provided artificial reef areas (created by spraying concrete onto a framework) in contrast to a generally sandy bottom, with areas of rock debris, artificial corals and a shipwreck. The main structure in the tank was a large central column of rock extending to the surface from a reef-like structure.

The whole system contained 3.8 million litres of water, of which 2.8 million litres was in the tank at any one time. Fresh tap water piped into the building was passed through a number of ion exchange resins to remove chemicals and soften the water. This then entered a salt mix chamber where the appropriate quantity of salt was added. The new salt water was then transferred to a salt water holding reservoir from where it could be pumped to the main tank for water changes.

Once in the system 78% of the re-circulated tank volume passed through gravity sand filters containing 16/30 grade silica sand. There were six such filters measuring six meters cubed. The water entered the filters by gravity from a common weir running the length of the tank. A central submerged pump in each filter then drew the water down through the sand before pumping it across the tank to be disgorged into a common supply trough on the opposite side of the tank. These gravity sand filters carried out both physical and biological filtration to ensure that the water was of the highest quality for the animals. A side loop of roughly 12% of the re-circulated tank volume passed over a separate weir at the aqua-theatre end of the tank into a large chamber of approximately in volume. Here two further submersible pumps supplied the two protein skimmers which had ozone dosing on them. A third pump supplied ozone to a contact chamber which then pumped the treated water back to the degassing chamber and then to each filter where it is returned to the main tank.

The salt was added to the fresh tap water to maintain the salinity at approximately 32 and the pH is maintained at ~8.0. Other abiotic factors also regulated included dissolved oxygen which was maintained at 8.0 mg/l. The water was heated to mimic natural conditions with a minimum water temperature of and a maximum of 27.. A current was maintained by a laminar flow system which ran across the tank right to left. There is a 90-minute system turnover, therefore the flow rate can be calculated as 3.8 million litres/ 90 minutes; equivalent to 4.2 x litres per minute.

The photoperiod was maintained at 12L:12D, with the lights on at 10.00am and off at 10.00pm daily. Lighting was provided by four metal halide lights, with low level lighting at night to simulate moonlight.

3.1.2a The Animals

Three species of shark were held at the Blue Planet Aquarium in their large, tropical shark tank. These were sand tiger sharks (*Carcharias taurus)*, nurse sharks (*Ginglymostoma cirratum)* and lemon sharks (*Negaprion brevirostris*).

When the study began there were, three *G. cirratum*, two *N. brevirostris* and seven *C. taurus*, the latter comprising of three males and four females. However two of the female *C. taurus* developed spinal deformities and were euthanized on the February 2004.

The tank also contained many species of fish. These included lookdown jacks (*Selene vomer*), porkfish (*Anisotremus virginicus*), black triggerfish (*Melichthys niger*) and a green moray eel (*Gymnothorax funebris*). Keeping *A. virginicus* in the tank was beneficial as they acted as cleaner fish for the sharks.

3.1.2b Animal Identification

All of the sharks at the Blue Planet Aquarium were assigned by the staff or chosen by children who had visited the aquarium. However, in this study, for ease of understanding, a code using the first letters of the shark genus, species and sex was used (eg. CtF = *Carcharias taurus female)*, followed by an assigned number. Sharks were identified by species, sex and identifiable markings, details provided in appendix 1.

3.1.3 Animal Husbandry

C. taurus were hand fed by the divers four times a week (Tuesdays, Thursdays, Saturdays and Sundays) at 14:00. To ensure diver safety when feeding *C. taurus* there were always three divers present. The first diver was a lookout and would bang two bolts together to warn the other divers if any of the sharks got too close. The remaining two divers would both wear protective gloves and hold buckets, at least one of which would contain fish. The second bucket may also contain fish or simply be a decoy to ensure the sharks did not swamp a sole feeding diver. Only if the sharks approached the diver from a straight horizontal trajectory at the chest height of the diver would the shark be given a fish. They were most commonly fed chub mackerel (*Scomber japonicus*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and white trevally (*Pseudocaranx dentex*). The food was never fresh due to the risk of parasites; instead it was frozen and then defrosted before feeding.

3.1.4 Methodology

Before the data were collected a 20-hour period was spent observing the sharks gaining, accurate knowledge of individual shark identification, observing different behaviours and practicing the data collection methods. An ethogram was used to identify the behaviours (Newman, 1999) (appendix 2). The sharks were also filmed during this period allowing their marking to be analysed in detail.

For the purpose of data collection, the tank was divided into eight sections - A1, A2, A3, B1, B2, B3 ,C1 and C2 (Fig. 3.1.4).

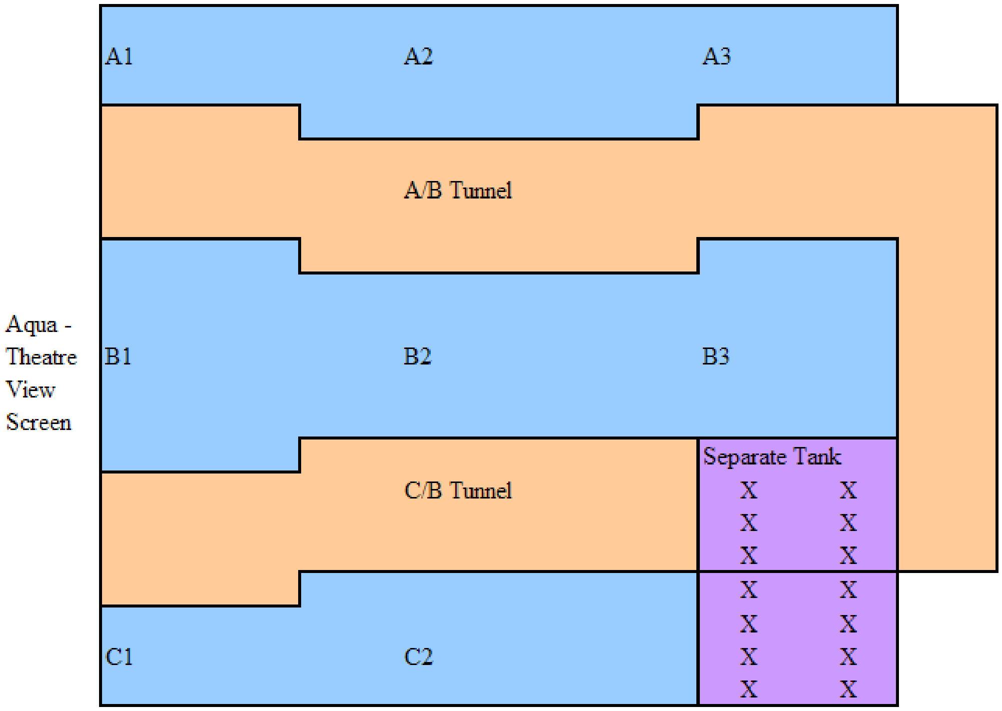

Fig. 3.1.4 Diagrammatic representation of the top view of the main tank at The Blue Planet Aquarium.

The A sections were to the left of the first tunnel as entered from the aqua-theatre. B sections were the central area of the tank, between both tunnels, while section C was on the left of the second tunnel. Once rockwork and additional structures in the tank were taken into account all 8 sections were approximately equal in size.

C. taurus mating attempts and behaviours had been observed in previous years from January to May. Therefore for this study these months were designated “mating season”, with July to November termed “non-mating season”. Data were not collected in June or December as these were transitionary months.

Throughout the observation periods, data were recorded at a range of times from 08:00 through to 04:00. For purposes of statistical testing, observations were split into six time periods during which the spectator and diver presence/absence remained constant as did the lighting (Table 3.1.4a).

Time Period	Actual Time Range	Description
1	08:00 – 10:00	"Dawn" - Early Morning - no visitors, no divers, lights just beginning to come on.
2	10:00 – 14:00	Morning - Spectators and divers present. Full lighting. Pre-feeding (on feeding days).
3	14:00 – 16:00	Afternoon - Spectators and divers present. Full lighting. Post-feeding (on feeding days).
4	18:00 – 22:00	Evening - No spectators or divers. Full lighting.
5	22:00 – 00:00	"Dusk" – No divers or spectators. Main lights just out, moonlighting only.
6	00:00 – 04:00	Night - No divers or spectators. Moonlighting only.

Table 3.1.4a: Time period definitions.

3.1.4.a Study Period 1 – Mating season 2003

The sharks were observed during the months of February through to April 2003. During each time period each shark was observed for 15 minutes. The order that they were observed was randomised using a randomised number generator in excel, and each shark was observed 15 minutes later than the previous observation period for the equivalent day, i.e. the next feeding or non feeding for the *C. taurus*. Sunday constituted a second consecutive feeding day and consequently data were not collected on this day. It could not be assumed that the behaviours would be the same as on a non- consecutive feeding day and so could not be grouped together.

During the observation periods, focal animal sampling was used (Altmann, 1974) with the sharks' position and depth plotted every 15 seconds, using the location code determined previously. Simultaneously, the nearest neighbour and any interactions of the focal shark with other sharks were recorded, such as give-ways (when a shark changes direction to avoid a collision course with another shark). The frequencies of occurrence of any essentially instantaneous behaviours were also recorded such as jaw flexes or burst swimming (defined in appendix 2). Swimming behaviours were divided into patrolling and resting and again recorded every 15 seconds. The occurrence of any mating behaviours were also monitored. Mating behaviour terminology was used as defined by Gordon (1993) (Table 3.1.4b).

Term	**Terminology**
Flaring	The curving and spreading of the pelvic fins in females.
Cupping	Female retracting her pelvic fins into a cup shape and exposing the cloaca when males approaching, done immediately after flaring.
Clasper Flexion	Movement of individual claspers backwards and forwards by patrolling male shark.
Clasper Splaying	Male contorting and opening his claspers up to 90 degrees to body axis.
Shielding	Female swimming very close to the bottom in order to prevent males approaching cloaca.
Nosing	Male coming from behind and underneath the female and placing his snout just below the cloaca.
Tailing	One male following another male closely, restricting normal fluent tail movement of the forward shark.

Table 3.1.4b, I, Gordon Mating Behaviour Terminology (1993)

In order to determine if there was any variation in swimming speed of individual sharks or between time periods, the sharks were timed between sections of the tunnel. Both tunnels were divided into 1.79m wide sections, which was the distance between the joints of the acrylic of which the tunnel was made of. This provided many identical reference points throughout the tank. A stopwatch was started as the tip of the nose passed the first point and stopped as the tip of the sharks' nose reached the second reference point.

A total of 43 hours and 45 minutes of observations were carried out during this first study period, consisting of six hours and 15 minutes of observations for each shark.

3.1.4.b Study Period 2 Mating season 2003, Simultaneous Observations

On March 2003, all *C. taurus* were observed simultaneously over three, two hour periods. 14 observers were present in total, two to track each shark. Observers were given an hour lecture, in-depth handouts to study and two hours on-site training in identification and observation methods. They were also tested to ensure that they were able to correctly identify the sharks and their behaviours. Use of volunteers has proven successful in other biological studies and without loss of quality data so long as adequate training and testing is provided (Wahaj & Holekamp, 2006). Marsh & Hanlon, (2004), have also shown that accurate behavioural data can be collected despite variations in observers' initial expectations. The observation periods were as follows –

19.00 – 21.00 (evening, daylight),

22.00 – 00.00 (dusk, moonlighting)

01.30 – 03.30 (night, moonlighting).

The recordings were less detailed than in study period 1 due to time limitations for training observers. Every 15 seconds the location and nearest neighbour of each shark was recorded, along with swimming speeds and any mating behaviour observations.

3.1.4.c Study Period 3 Non-mating season 2003

During July 2003 *C. taurus* were observed following procedures described for study period 1. There were no modifications to procedures. The total observation time was seven hours.

3.1.4.d Study Period 4 Mating season 2004

The *C. taurus* were studied between February and April 2004 with observations recorded following the procedures described for study period 1. Initially a total of seven hours of data were collected for all seven sharks. Following the removal and subsequent euthanasia of two individuals, (CtF3 Sky and CtF4 Wanda), on the February 2004 all further recordings were for the remaining five sharks. A further 70 hours of observations were performed.

3.1.4.e Study Period 5 Mating Season 2004, Simultaneous Observations

On April 2004 *C. taurus* were simultaneously observed and data collected following the procedures and times described for study period 2. As the observers were a different set to those from the previous simultaneous observations, they all received the training described in study period 2 and were tested to ensure accurate data collection. As for the simultaneous observations in 2003, six hours of data were recorded.

3.1.4.f Study Period 6 Non Mating Season 2004

C. taurus were observed following the procedures described in study period 1, between the and July 2004. A total of 40 hours of observations were recorded, therefore 8 hours of data were collected for each shark.

3.2 Statistics

Before the statistical analyses could be conducted the data needed to be non-independent to avoid pseudo-replication. This was done by determining the time interval when it was no longer possible to predict the position of a shark based on the previous observation.

Statistical evaluation of the data was then conducted on the computer package Minitab version 12.1. To analyse the spatial distribution data a test was used; the expected value in the was calculated by multiplying the sum of the rows and columns in the contingency table, and dividing this by the sum across all cells. A Kruskal-Wallis statistical test was used to analyse depth data. The general linear model test (GLM) was used to analyse swimming speed data and social interactions between sharks based on the nearest neighbour data. Binomial distribution test and was used to analyse the give-way data. Fisher exact tests were used when the data was not suited for a analysis, e.g. when the expected value was below 5 counts (Sokal & Rohlf, 1998). Regression analysis was then carried out to determine if the individuals giving way were more likely to avoid encounters in the first instance. The Friedman test was used to analyse swimming behaviour data.

4. Results

4.1 Spatial Distribution

Pseudoreplication is a source of error in statistical inferences which results from treating observational data as independent when in fact they are interdependent, (Hurlbert 1984). This occurred in the spatial distribution observations as the spatial position of each *C. taurus* in the tank was recorded at 15 second intervals which resulted in an autocorrelation of the data (Fig. 4.1.1).

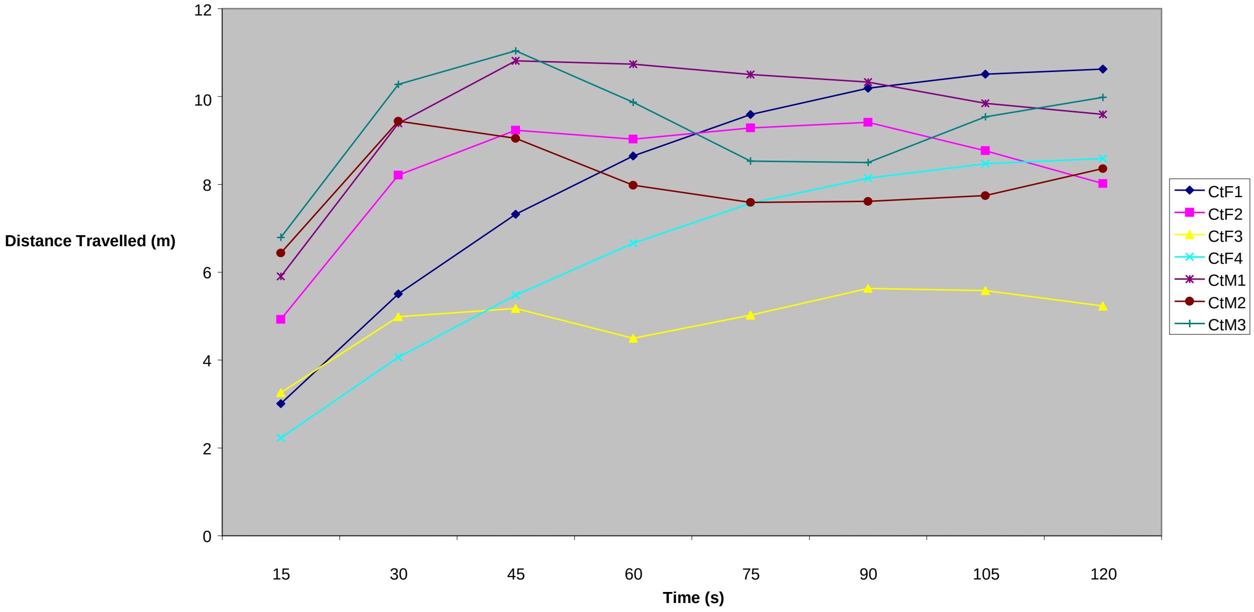

Fig. 4.1.1 Exploration Curve of Captive Sand Tiger Shark Spatial Distribution Data to determine time required (Tx) for distance travelled to be independent of (T0)

This figure shows that the distance between a shark's initial and current position increases when recordings are taken with an increased time-interval (i.e. 15, 30….120

second time intervals). The exploration curve in this figure shows however, that the distance between a shark's initial and current position no longer increases after 120 seconds. At this point, data has become independent, which means that the position of the shark can no longer be predicted from its initial position. Therefore only data collected every 120 seconds were used in spatial distribution analyses, which overcame the problem of non-independence and avoided pseudoreplication.

There was a highly significant difference in shark occupancy between the sections of the tank (χ^2 = 1477.42, d.f. = 7, P = 0.0001) (see Fig. 4.1.2). Sections B1 and B2 which are situated in the centre of the tank are the most frequented areas.

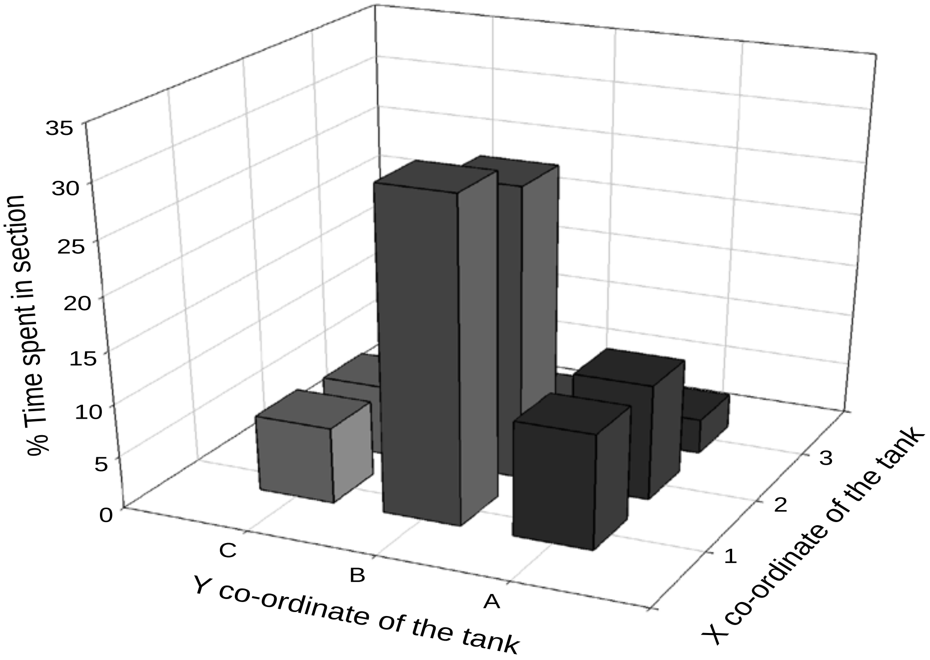

Fig. 4.1.2 Percentage of time spent in each section of the tank for all sand tiger sharks at the Blue Planet Aquarium

In addition, there was a highly significant difference in spatial distribution among individual sharks ($\chi^2 = 944.249$, d.f. = 42, P = 0.0001), (see Fig. 4.1.3). Some sharks, e.g. CtF3, showed a strong preference for the less densely populated areas in the tank such as A1 and A2. CtF3 also spent more time on the surface than other sharks (see below), which is possibly due to a spinal deformity (see Discussion).

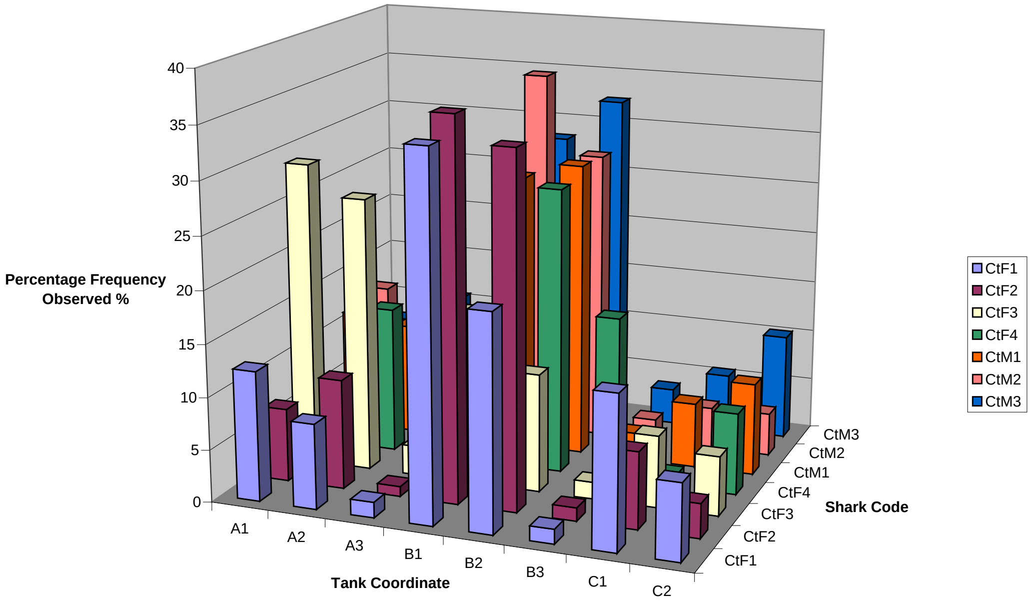

Fig. 4.1.3 Use of Tank Space between Sand Tiger Sharks at the Blue Planet Aquarium

The sex of the shark affected the spatial distribution as indicated by the significant difference between males and females in location in the tank ($\chi^2 = 52.71$, d.f. = 7, P = 0.0001). Males were relatively more observed in B2 (centre of the tank), whereas females preferred the more secluded edge (A1, A2 and C1).

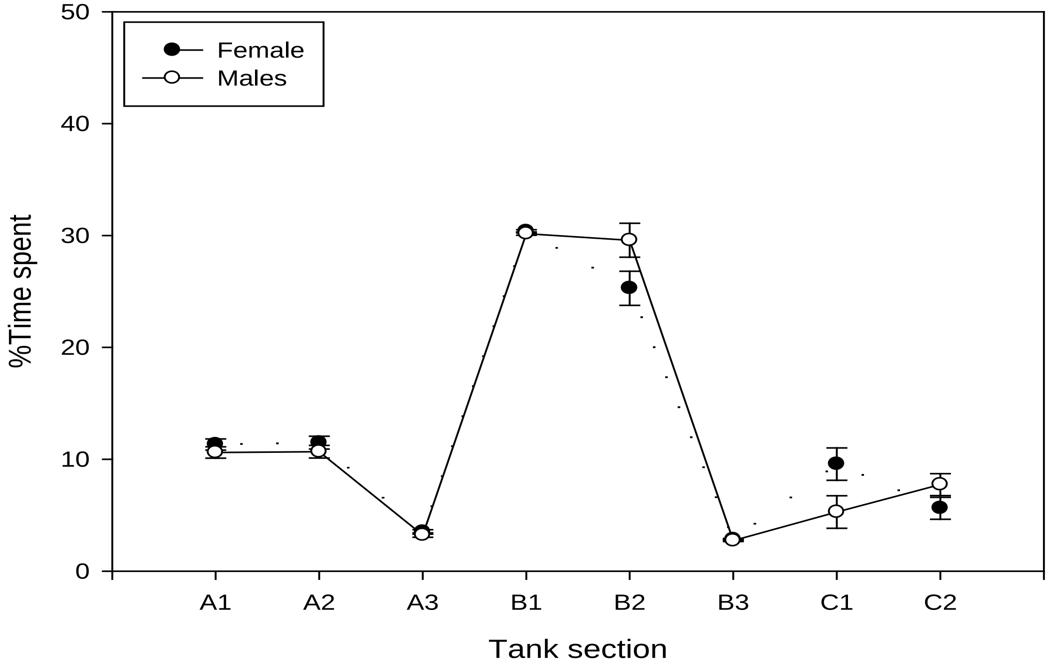

Fig. 4.1.4.Mean (±SEM) percentage time male and female sharks spent in different sections of the tank.

There was a highly significant difference in the relative percentage time spent in each section between mating and non-mating seasons ($\chi^2 = 96.606$, d.f. = 7, $P = 0.0001$). During the non-mating season section B1, the front centre section and deepest area of the tank, was frequented on more occasions than during the mating season. Furthermore, the secluded edge (C1 and A2) that is preferred relatively more by females than by males (see Fig. 4.1.5) is more frequently occupied during the mating season than in the non-mating season, possibly because males are in search of (or courting) female sharks at those locations.

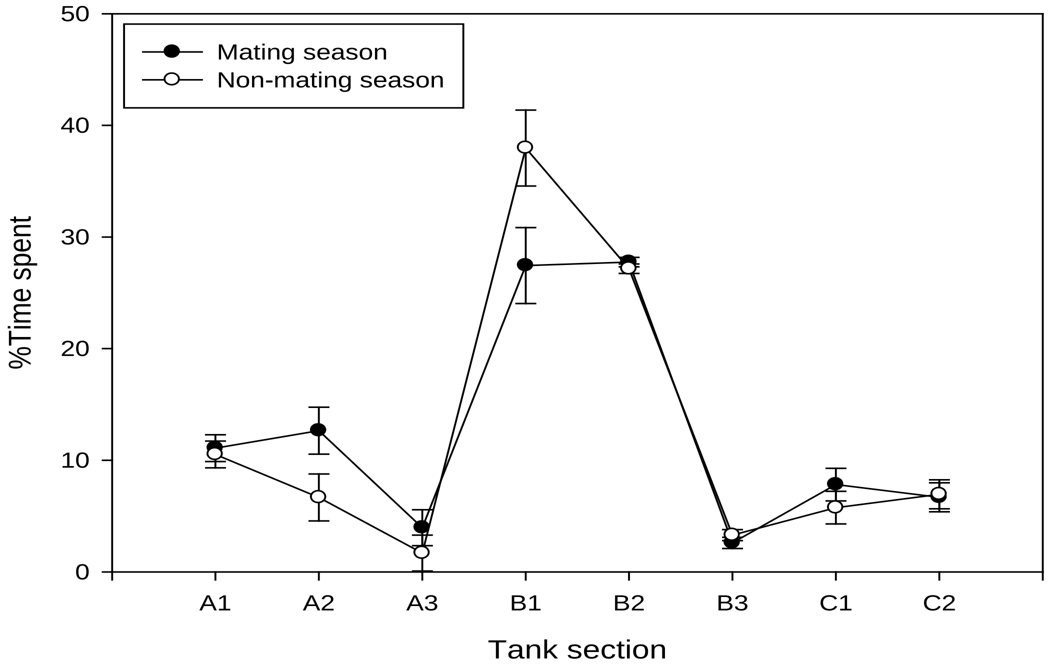

Fig. 4.1.5. Mean (±SEM) percentage time sharks spent in different sections of the tank in mating and non-mating seasons.

There are small differences between the feeding and non-feeding days in the relative percentage time spent in each section ($\chi^2 = 15.165$, d.f. = 7, $P = 0.034$). However, given the number (N=3) of tests conducted on the spatial distribution of sharks, the critical value alpha was Bonferroni corrected ($\alpha' = \alpha/3 = 0.015$), which means that this result is no longer statistically significant. On feeding days sharks spent relatively more time in sections A2, A3, B2 and B3 of the tank compared to non- feeding days. This is expected as they are fed in sections A2 and A3. Nevertheless, also on feeding days, sharks spend most time in the central sections B1 and B2.

The difference in spatial distribution among the six time periods was highly significant ($\chi^2 = 487.96$, d.f. = 35, P = 0.0001). During all time periods, sharks spent relatively more time in sections B1 and B2, representing the centre and deepest area of the tank. The one exception to this was time period 1 where A1 had a high percentage. This may be linked to a number of sharks regularly resting in this area during this time period and the low number of overall hours of observations in time period 1 (fig 4.1.6).

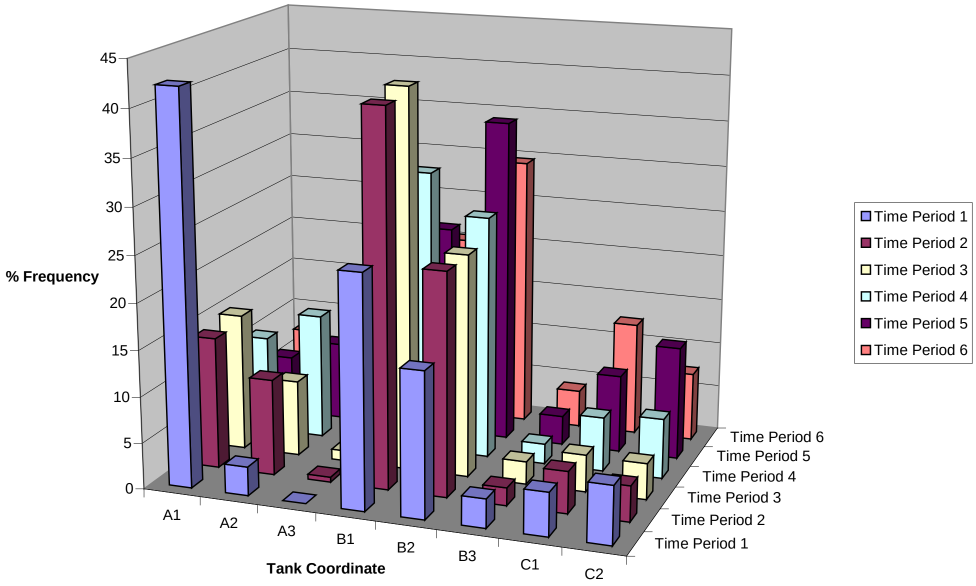

Fig. 4.1.6 Observed Spatial Distribution of Sand Tiger Sharks at the Blue Planet Aquarium during Different Times of Day

There was no significant difference in spatial distribution of a shark during the first and second half of the week ($\chi^2 = 5.830$, d.f. = 5, P = 0.323). This confirms that the spatial distribution data were not influenced by day in the week the observations were recorded.

4.2 Water Column Depth

C. taurus have been well documented as mid – water swimmers (Essapian, 1962, Crow and Hewitt, 1988). The individuals in this study conform to this pattern and as a group spend 98.4% of their time swimming at mid depth.

There is a significant difference between sharks in the time spent at the surface (Kruskal-Wallis H = 52.66, d.f.= 6, P<0.001). In particular CtF3, and to a lesser extent CtM1, spent more time on the surface than other sharks, this is possibly due to a spinal deformity in the case of CtF3 (see Discussion).

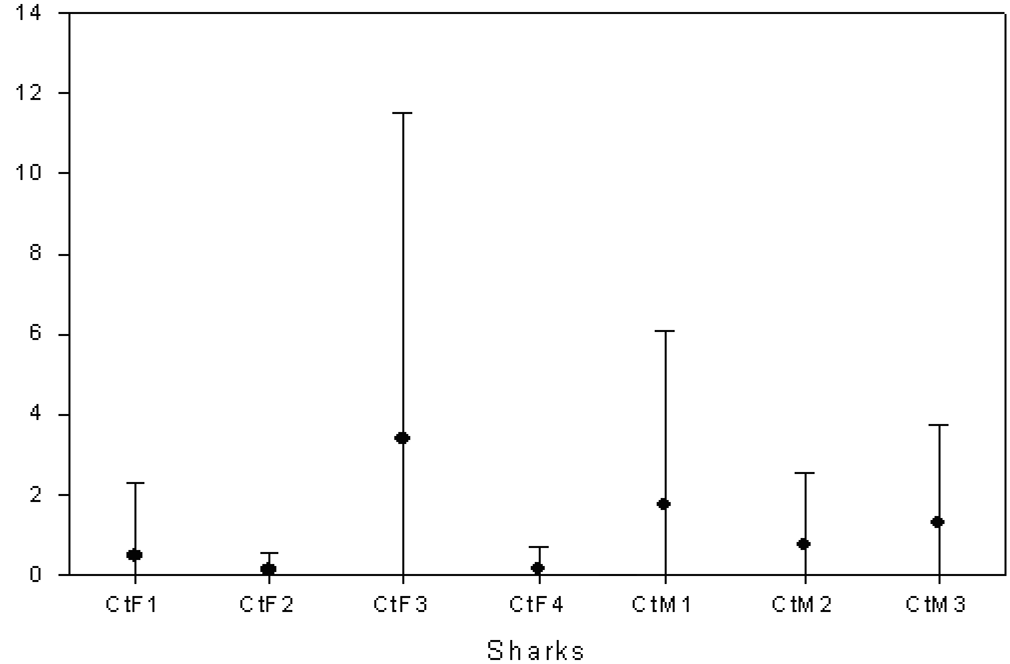

Fig 4.2.1 Percentage time spent by each shark at the surface of the tank.

A significant difference was observed between the sharks in the time spent at the bottom of the tank (Kruskal-Wallis H = 13.44 d.f. = 6 P = 0.037), which may be associated to the amount of time they spent resting (see Discussion).

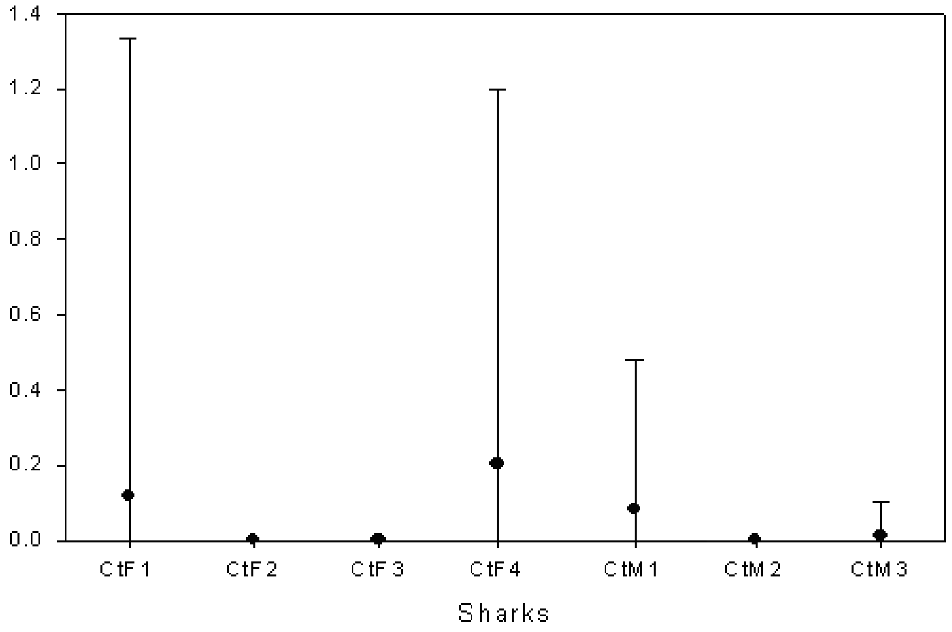

Fig 4.2.2 Percentage time spent by each shark at the bottom of the tank.

4.3 Behavioural Interactions

4.3.1 Nearest Neighbour

A General Linear Model (GLM) test was used to analyse the social interactions between sharks based on the nearest neighbour data. There is no difference in the percentage time spend as nearest neighbour between the sharks ($_{,34}$=2.10, P=0.102) or between the seasons ($_{,34}$=2.02, P=0.164). Apparently, individual sharks do not alter their swimming behaviours to have certain individuals as their nearest neighbour or close by (see appendix 3).

4.3.2 Give-Way Data

A binomial distribution test was used to analyse the incidence that a shark changes direction when on a collision course with another shark (for brevity, "gives-way"). The probability a shark gives-way was set at p=0.5 (and similarly, the prior probability of not changing direction and "taking-way" was equal to 1-p=0.5). The results showed that no shark was "giving-way" or "taking-way" significantly more often than expected (all test results: $P \geq 0.089$). Flare, CtM3, is the only shark that "gave-way" slightly less often, although this was not significant at the $\alpha=0.05$ critical level (Binomial probability; P = 0.089), These findings suggests that there is not an apparent "dominance structure" between sharks in the tank (see Discussion), and that all sharks have an equal probability of avoiding a head-on collision with a conspecific.

A Chi-square test showed there is no statistically significant difference between males and female sharks in the relative number of times they gave-way (= 0.006; df = 1, P = 0.938).

For subsequent analysis on give-way data Fisher exact tests were used as there were zero values which ruled out Chi-square analysis. A Fisher exact test was conducted to determine whether there were differences between give-way data during mating and non-mating seasons. The sharks did not differ significantly in the relative frequency of taking-way or giving-way between the seasons (Fisher exact test, P = 0.062). Notice, however, that CtF2 only gives-way, and CtM3 generally takes-way during the mating season, and that this apparent bias does not exist in the non-mating season, as in this season all sharks give and take way at approximately similar rate

A Fisher exact test was then carried out to determine whether there were differences between give-way data on feeding and non-feeding days. There was no significant difference in the relative frequency they take-way or give-way between feeding and non-feeding days (Fisher exact test P = 0.936). In addition, sharks did not differ significantly in the relative frequency they take-way or give-way between time periods, (Fisher exact test P = 0.686).

Finally, a regression analysis showed that sharks that frequently were "giving-way" were more likely to avoid encounters (Figure 4.3.2; Regression analysis: = 85.9%; t= -5.0302, p=0.0151). This suggests that either sharks have a hierarchical dominance in behaviour, which causes the subordinate sharks to avoid encounters, or that there is a difference among the sharks in ability to sense and/or avoid an approaching conspecific from a distance (see Discussion).

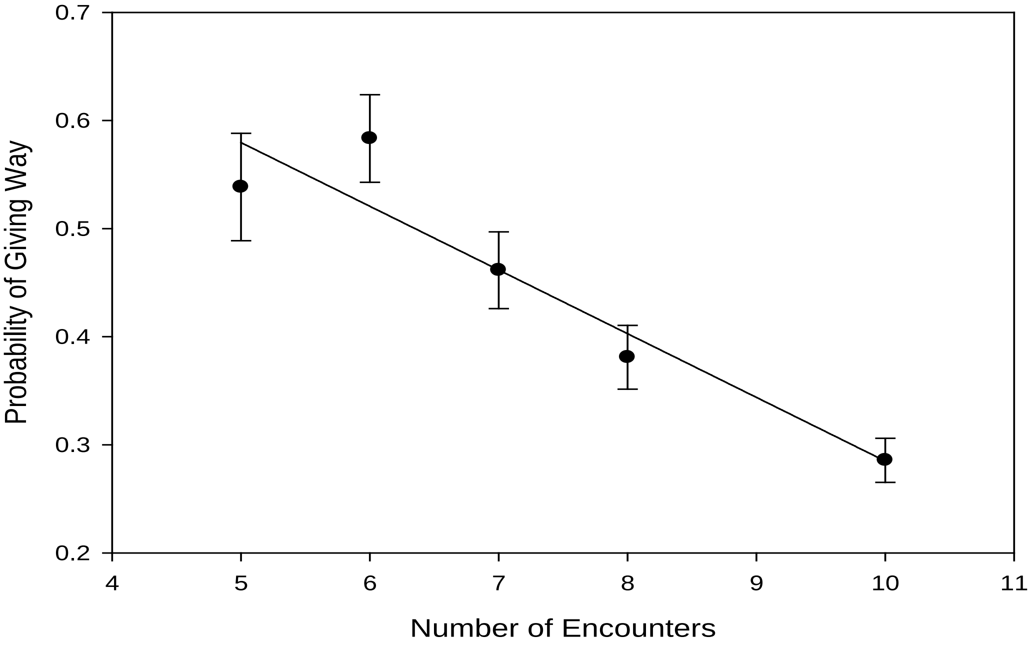

Fig. 4.3.2. The mean (and SE) probability of giving way (Y-axis) versus the number of encounters (X-axis) of individual Sand Tiger sharks in the Blue Planet Aquarium.

4.4 Jaw Flex Data

Sharks perform occasional jaw flexes; in order to test whether this behaviour was more often performed by certain individuals, the distribution of the jaw flex data was compared to a Poisson distribution. Given a mean of 5.4 jaw flexes per shark, the observed standard deviation (=2.3) did not fall outside the simulated range of a Poisson distribution with similar mean. Hence, the distribution of the number of jaw flexes per shark did not differ significantly from a Poisson distribution and no shark displayed this behaviour more or less often than expected by chance (Randomisation test P = 0.55).

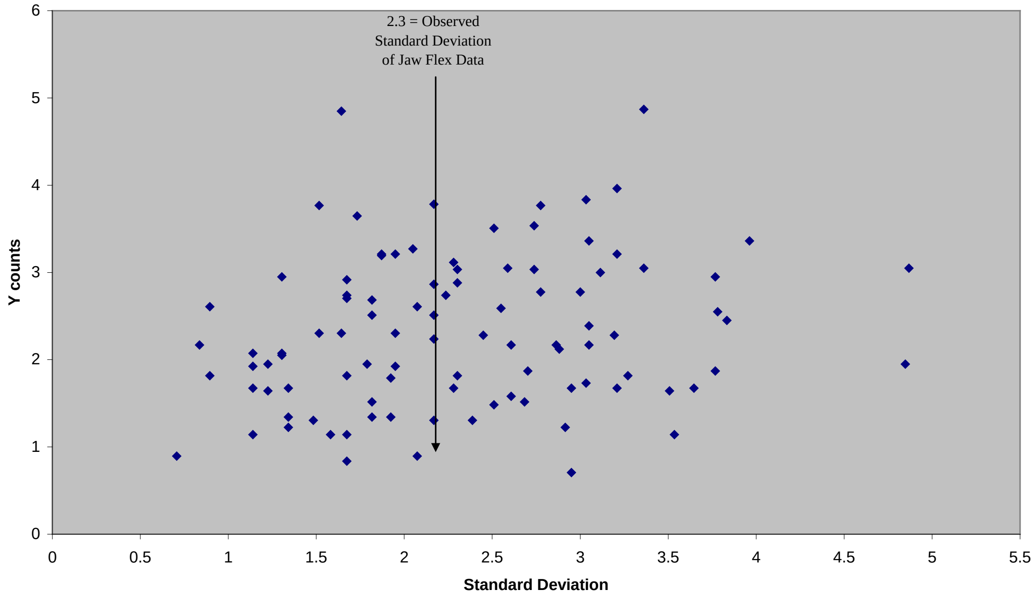

Fig. 4.4 Observed (arrow) and simulated distribution of standard deviation (σ2) of a Poisson distribution with the mean μ= 5.4

4.5 Swimming Behaviour

A Friedman test, blocked by time period, was carried out to compare swimming behaviour between individual sharks. There was found to be a significant difference for both patrolling (S = 23.03, d.f = 6, P = 0.001) and resting behaviours (S = 22.32, d.f = 6, P = 0.001).

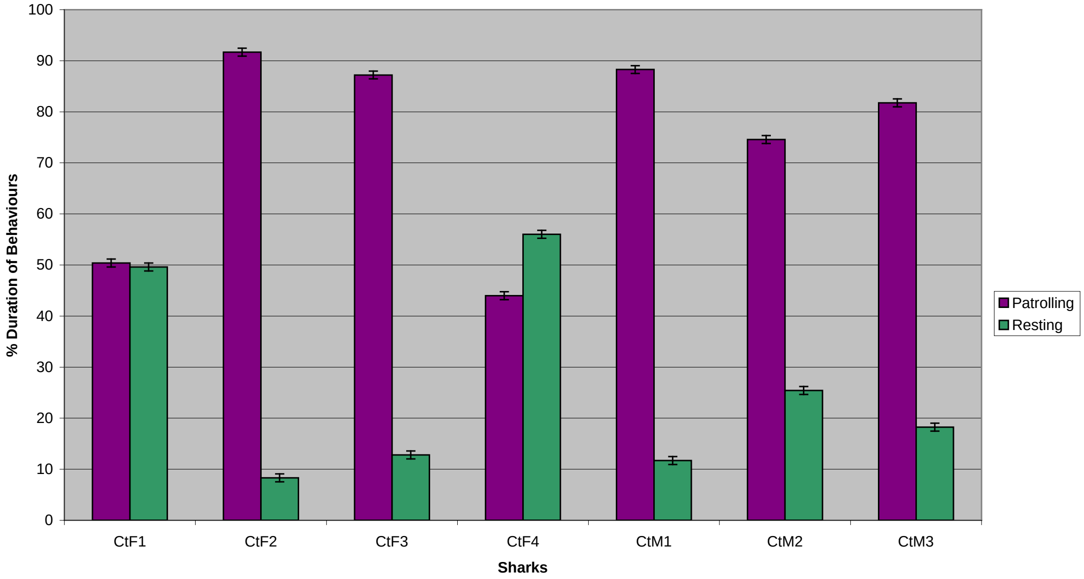

Fig. 4.5.1. Percentage of time spent on each swimming behaviour of individual C. taurus

However from fig. 4.5.1 it becomes apparent that these differences are due to an abnormally high proportion of resting behaviour shown by CtF1 and CtF4. When the tests were repeated without the inclusion of these two individuals there was shown to be no significant difference between the remaining sharks in resting (S = 1.7, d.f = 4, P = 0.788) and patrolling behaviour (S = 2.26, d.f = 4, P = 0.687)

A Friedman test was then carried out to compare swimming behaviour between time periods, now blocked by individual sharks. Both swimming behaviours were found to be significantly different between time periods (patrolling: S = 13.68, d.f = 5, $P < 0.05$ and resting: S = 13.01, d.f = 5, $P < 0.05$).

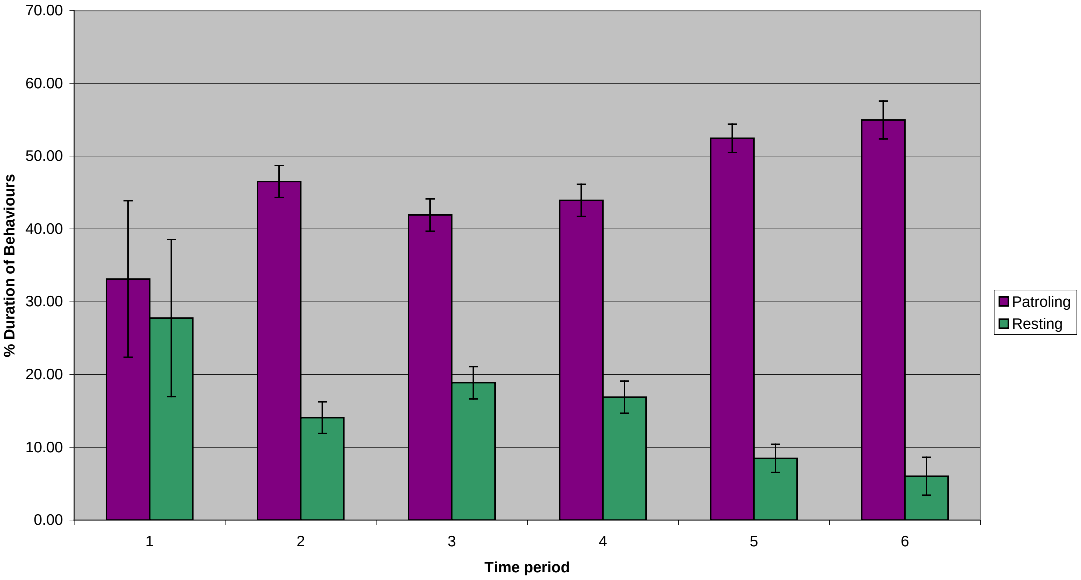

Fig. 4.5.2. Percentage of time spent on each swimming behaviour of C. taurus by Time Period

4.6 Swimming Speeds

The swimming speeds of *C. taurus* varied considerably between individual sharks (Fig 4.6.1). The fastest shark was CtM3 with a mean swimming speed of 0.63 m/s. The slowest shark was CtF4 with a mean swimming speed of 0.16 m/s. Complete swimming speed data of each individual shark were represented graphically (appendix 4).

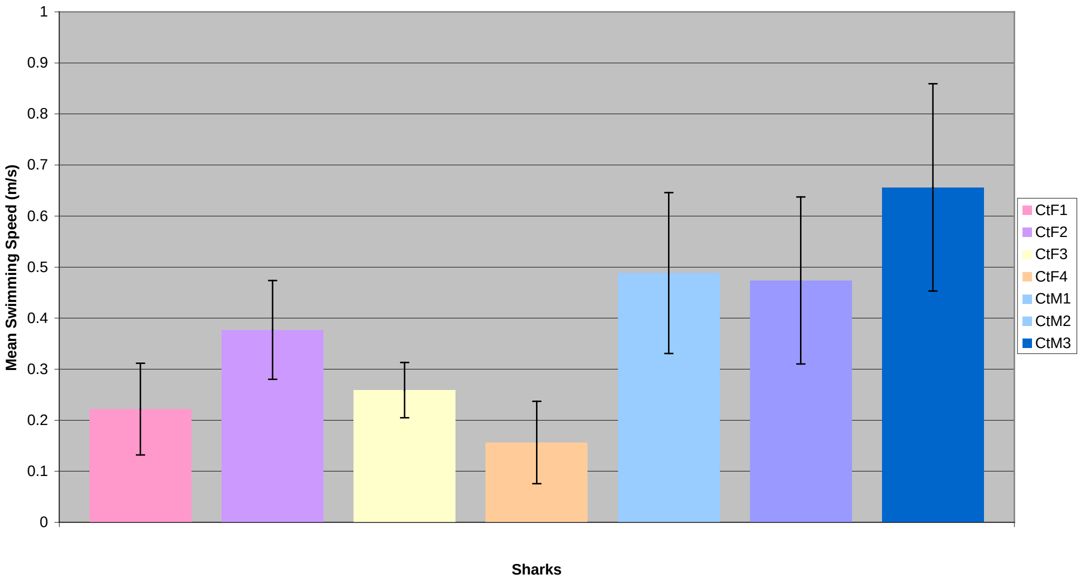

Fig. 4.6.1 Mean (±SE) Swimming Speed of Individual Sharks Combined over all Observation Periods

Using a General Linear Model (GLM), I then analysed whether the differences in swimming speeds between individual sharks could be explained by the differences in sex, time period, feeding regime and season (Table 4.6). The fixed factors in the model were season, feeding regime and sex, (fixed factors were used when we a prediction could be made explicit to the experimental design, e.g. speed is likely to increase during the mating season). Random factors were used where no prior knowledge was available; in this analysis time of day was a random factor.

Factor	d.f.	M.S.	F	P
Seasons	1	0.7352	36.66	<0.001
Feeding/Non Feeding Day	1	0.0029	0.14	0.704
Time Period	5	0.1901	9.48	0.002
Sex	1	2.8533	142.28	<0.001
Season * Sex	1	4.1139	205.14	<0.001
Error	696	0.0201		
Total	701			

Table 4.6.1 GLM with swimming speed as response variable and Seasons, Feeding/Non-feeding periods and Sex as fixed factors, and Time of day as random factor.

Highly significant differences in swimming speed were detected for the factors sex ($_{,696}$ = 142.28; P<0.01) and season ($_{,696}$ = 36.66; P<0.01), (Table 4.6). Males were faster swimmers than females (Fig. 4.6.2) and the swimming speed was faster in the mating season (February - May) than non mating season (Fig. 4.6.3).

Feeding or non-feeding days were shown not to have a significant effect on swimming speed of *C. taurus,* ($_{,696}$ = 0.14; P=0.704). There was a small but significant difference in *C. taurus* swimming speeds in relation to time period ($_{,696}$ = 9.48; P=0.002), with time period 6, (00:00 –04:00h) containing the highest average swimming speed (Fig 4.6.4).

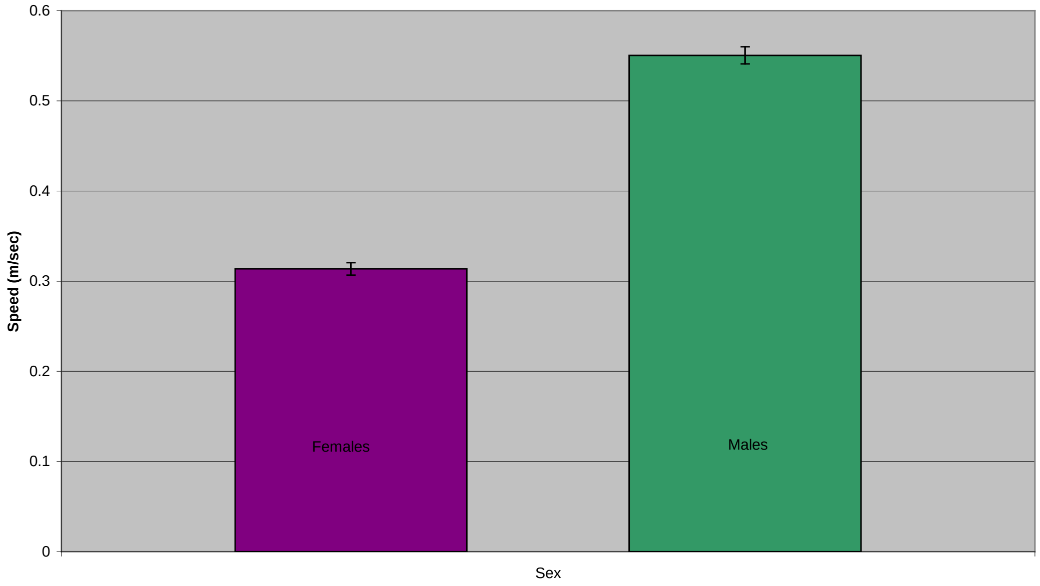

Fig. 4.6.2 Mean Swimming Speeds and Standard Error of Sand Tiger Sharks by Sex

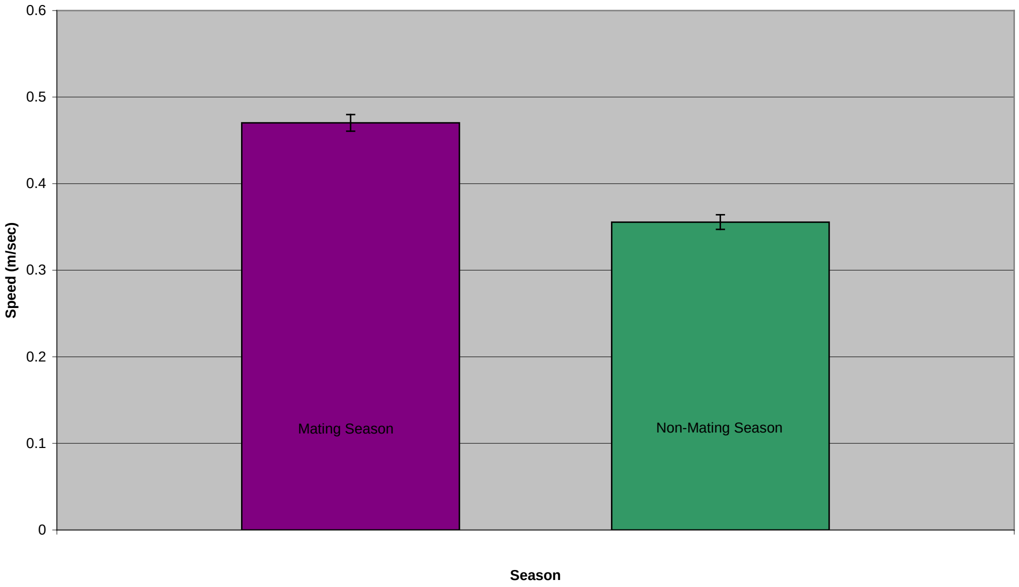

Fig. 4.6.3 Mean Swimming Speeds and Standard Error of Sand Tiger Sharks by Season

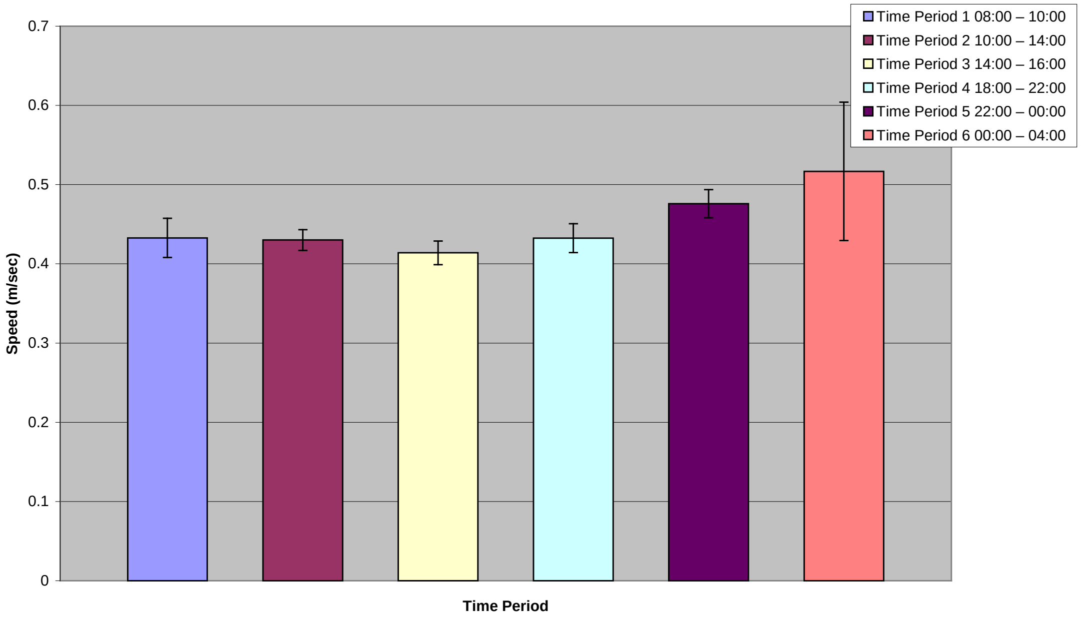

Fig. 4.6.4 Mean Swimming Speeds and Standard Error of Sand Tiger Sharks by Time Period

Interestingly, there was a highly significant interaction between sex and season ($_{,696}$ = 205.14; P= <0.001), which reveals that males increase their average swimming speed during mating season where as females swimming speed remained the same or decreased slightly Fig. 4.6.5.

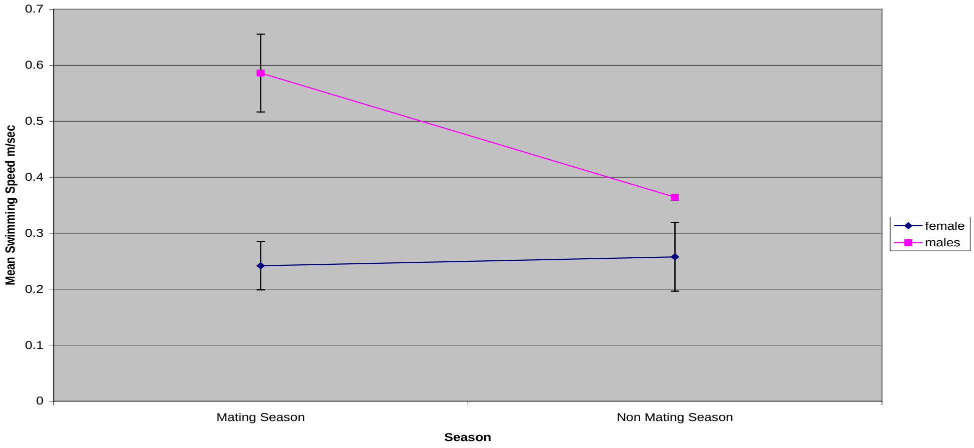

Fig 4.6.5 Mean Swimming Speeds (+-S.E.) of Male and Female C. taurus by Season

None of the other interactions were statistically significant and hence those crossed factors are omitted from the analysis presented in Table 4.6.

Next I analysed the biological significance and implications of differences in swimming speed between individual sharks focusing on the mating season only. A regression analysis was therefore carried out on swimming speed between (explanatory variable and the frequency of pre-copulatory mating behaviours). This analysis shows that fast swimming males displayed more pre-copulatory mating behaviours than slower swimming males ($_{,16}$=13.58, P = 0.002 =42.5%). However, for females the trend is opposite, with the females with the faster swimming speeds tending to exhibit less mating behaviours. This trend is however not significant at alpha 0.05 (=8.1%, $_{,10}$=1.97, P = 0.191).

Factor	d.f.	MS	F	P
Sex	1	0.11771	14.06	0.006
Mating Behaviours	1	0.026536	3.17	0.113
Sex crossed with Mating Behaviours	1	0.048961	5.85	0.042
Error	8	0.008373		
Total	11			

Table 4.6.2 GLM with swimming speed as response variable and Seasons and Sex as fixed factors.

The effect of sex and mating behaviours on swimming speed were then analysed using a GLM, which showed that there was a significant difference in swimming speeds between sexes ($_{,8}$ =14.06, P = 0.006) and a significant interaction between sex and mating ($_{,8}$ = 5.85, P = 0.042). These analyses show a positive relation between the occurrence of pre-copulatory mating behaviours and swimming speed of males, and in contrast, a negative relation between female mating behaviour and swimming speed. This could explain the significant interaction term sex * season in table 4.6.1. It appears that faster swimming females more effectively avoid copulation with males, while faster swimming males are more likely to copulate with (slower swimming) females.

4.7 Descriptive Analysis of Captive Mating

In most taxa, observations of matings have allowed scientists to learn a vast amount about mating systems. Sexual selection, for example, has been shown to shape the evolution of male advertisements in reproductive behaviour of most vertebrates, including many fish species such as guppies and sticklebacks. However, much less is known about reproductive behaviour in sharks, and with the exception of a few species, mating behaviour in sharks is rarely observed. Our knowledge of the behaviour of sharks is expected to benefit from the development of large modern aquaria which allow for behavioural observations on these previously illusive creatures. A potentially important drawback of studies in aquaria is that the behaviour of captive animals may differ from that of their wild counterparts.

Recordings in the Blue Planet Aquarium (UK)

On the May 2004, a mating between a pair of *C. taurus* was filmed at the Blue Planet Aquarium in Cheshire. This aquarium has a programme whereby members of the public can dive in the tank. Approximately 15 minutes before the footage was recorded a group of divers were due to enter the tank. However an attempted mating began at the diver entry point so the public dive was cancelled. This attempted mating was between the female CtF2 and a male CtM2. It was unsuccessful and only progressed to the initial spiral stage, where the female bit back and the male disengaged his mating attempt. Two of the Blue Planet dive team then entered the tank and filmed the subsequent events. The following analysis is based on the footage obtained.

The female (CtF2), is approached by male CtM3. Despite having a prolapsed jaw his mating ability does not appear to be impeded. He closely follows her for 26 seconds, then gradually moves closer until his snout is next to her cloaca (nosing).

Fig. 4.7.1 CtM3 nosing female CtF2

The male then powerfully bites the right pelvic fin of the female and the initial spiral stage of mating begins. The pair spiral in a clockwise direction for 14 seconds and the female appears to be trying to bite the male back, but is unsuccessful on this occasion. This retaliating biting attempt suggests that the female is unreceptive to the mating advances. However after the spiral and failing to bite the male she appears to submit. This may be partially due to exhaustion as she had previously been involved in a mating spiral with CtM2 20 minutes prior to this attempt.

Fig. 4.7.2 Initial bite

Fig. 4.7.3 Mating Spiral

From the right pelvic fin of the female, the male works his grip up to her right pectoral fin as he slowly swims them both around the tank for 55 seconds. His focus is completely on the female as he even collides with an artificial coral while he is manoeuvring around the tank.

Fig.4.7.4 CtM3 manoeuvres CtF2 around the tank, while moving his grip from her right pelvic fin to her right pectoral.

The male then turns the female on to her back and inserts his right clasper into her cloaca. The male is also upside down during copulation, which lasts for 32 seconds.

Fig.4.7.5. Copulation

After withdrawal the male swims off with his claspers crossed and he initially circles the central rockwork where the female is still lying. After this it is uncertain from the footage if he continues to circle or if he blocks any other males from approaching her in this vulnerable position. After speaking with the aquarists present during the mating they were not aware if any guarding of the female occurred. This is not to say it is a certainty that there was no guarding as both divers primarily concentrate on the female shark post – copulation. After 24 minutes the female turns herself into an upright position and swims off.

Subsequently the female did not pup indicating copulation was unsuccessful. A possible explanation is that the female may not have been in season hence the mating spiral where she appeared to resist and as the copulation was forced by the male the female was unreceptive. Support for this interpretation is that CtF2 only gives-way during the mating season (and CtM3 always take-way during this season), and that copulation rate appears to be positively correlated to swimming speed in males and negatively to that of females. Note however that CtF2 appeared to be a healthy female without spinal deformities, and that she had a more than average swimming speed overall, and showed little resting behaviour compared to other sharks. Another possibility is that the aquaria conditions were not suitable for gestation of *C. taurus*

Recordings in Underwater World (Australia)

Mating in *C. taurus* has never been observed in the wild. This is only the second occasion where a captive *C. taurus* mating has been seen. In the Australia aquarium Underwater World a mating was seen and filmed. The male swam in, nosed the female, bit her left pectoral fin, continued swimming and mated while doing so. The whole process lasted approximately 20 seconds. There was no mating spiral and the female did not resist in any other way.

5. Discussion

This study focussed on the spatial distribution, behavioural interactions, jaw flex behaviour, swimming behaviours and mating behaviour of seven captive Sand tiger sharks (*Carcharias taurus*) kept at the Blue Planet Aquarium, Ellesmere Port, England, in May 2004.

The aim of this study, to further understanding of intra specific variation in behavioural patterns, providing quantitative results on captive *Carcharias taurus,* was effectively completed. I successfully recorded baseline data of each individual shark to include a variety of morphological and behavioural parameters, following which the effects of day (feeding or non-feeding), season (mating or non-mating) and time period on these behaviours were examined. The results were analysed and in this section are discussed to draw any inferences regarding to mating behaviour, dominance hierarchies, behavioural differences, spatial distribution and swimming speeds within the study group.

Although the captive behaviours of *C. taurus* are unlikely to represent behaviours displayed by their wild counterparts, this study enables us to learn more about this species in captivity, in particularly in terms of spatial distributions, nearest neighbour preferences and dominance hierarchies. This information will help improve the holding conditions of *C. taurus*, which is ultimately of importance for both the conservation and welfare of these sharks.

5.1 Spatial Distribution

The sharks were not distributed equally across the tank. Furthermore, the preference for certain areas of the tank varied between individual sharks, the season (mating versus non-mating), feeding days and sex.

Sections B1 and B2 were frequented more regularly which was expected as these are the central and deepest areas of the tank. The primary swimming pattern observed in this captive population of *C. taurus* was circular around the main central coral, resulting in more time spent in B1 and B2 crossing to the other sections. On occasions where individuals were circling the coral tightly they would not enter any other section at all (pers. obs.).

Individual sharks also differed in their spatial distribution suggesting either natural variation among individuals (Heithaus *et al*. 2006), or that antagonistic (behavioural) interaction between sharks polarises their spatial distribution (Johnson and Nelson, 1973). For example CtF1 was found to spend less time in B2 and more time in C1 than expected. CtF3 spent a higher than expected proportion of time in sections A1 and A2. Some of these differences in preference might be explained by the sex and health status of an individual (see below), but some variation cannot be accounted for and this may simply reflect behavioural stereotypes (Lyons *et al*. 1997) or behavioural syndromes (Sih et al. 2004) characteristic of individual sharks.

There was a highly significant difference between spatial distribution of the sexes; males were found to spend more time in B2 (centre of the tank) while females spent more time than expected in C1, A1 and A2. These areas are the outer sections of the tank and are both more secluded and less manoeuvrable.

Spatial distribution was found to differ significantly between mating season (January – May) and the non-mating season (July – November). During the mating season more time than expected was spent in A2, A3 and C1 and during the non-mating season more time than expected was spent in B1. This is most likely due to a change in behaviour by the male *C. taurus* as during the mating season they spend more time following females who spend a higher proportion of their time in the outer sections.

Spatial distribution of *C. taurus* was found to differ between feeding and non-feeding days. They spent more time in sections A2, A3, B2 and B3 on feeding days which was expected as they are fed in the A2/A3 sections, B2 is adjacent to A2 and is often the section from which *C. taurus* begin their approach. Section B3 is the diver entry point.

Time period was found to have a highly significant effect on spatial distribution. The *C. taurus* spend more time than expected in the outer areas of the tank, (A3, B3 and C1) in time periods 5 and 6 and much less time in B1. At both of these time periods the main lighting in the tank is switched off which infers a preference switch in location between day and night. *C. taurus* are more active at night (Castro, 1996). However it has only been inferred through stomach content analysis that their choice of location may vary between day and night (Smale, 2005).

These findings may not be representative of other captive populations; a previous study on captive *C. taurus* at a different aquarium concluded that they have a constant even distribution around the tank throughout the day (Newman, 1999). However that study did not monitor behaviour in the evening or at night which is when the main differences were observed in this population. Furthermore, the present study has been conducted over a longer duration (24 months) and is more detailed with increased hours of observation.

5.2 Water Column Depth

C. taurus swim continuously at mid-depth, (Essapian, 1962, Crow and Hewitt, 1988). Observations from this study corroborate previous findings as over 98% of the time *C. taurus* swam at mid-depth.

When time at the surface was examined between individual sharks, CtF3 spent a significantly higher proportion of her time at the surface than other individuals. Here I would like to suggest that a spinal deformity of CtF3 affected her swimming lift and drag thus causing her to spend significantly more time at the surface compared to other sharks. The scoliosis in her spine caused a 'C' shape bend and was progressively getting more severe. Both staff and I noted that as the spinal condition worsened she spent more time at the surface, often gulping for air. A complication of this particular case may be that she needed to gulp more air than normal to maintain neutral buoyancy. This hypothesis can not be applied to all *C. taurus* spinal deformities however as CtF4 also had multiple scoliosis of the spine which presented as a 'S' shape bend and did not increase the time she spent at the surface. Both CtF4 and CtF1 did however spend a significantly higher amount of time at the bottom of the tank compared to other *C. taurus*. While CtF1 increased time at the bottom of the tank can be attributed to a high amount of shielding from mating attempts the same cannot be said for CtF4 as she attracted no male interest at all. It is therefore a possibility that this deformity decreased her swimming lift, thus rendering it preferable to spend more time at the bottom of the tank. Such sinking of *C. taurus* with spinal deformities has been observed in other aquariums (Preziosi *et al*. 2006).

Spinal deformities are not uncommon in many species of fish; different factors have been suggested and implicated as the causes. These include nutritional imbalance, primarily related to vitamins (Treasurer 1992; Mbuthia 1994), genetic causes (Treasurer 1992; Longshaw *et al.* 2003), parasite infection (Lom *et al.* 1991) and traumatic injury during capture and transportation and captive management issues (Silverstone and Hammell, 2002; Berzins *et al.* 2002). Furthermore in *C. taurus* there is an additional possibility that their behaviour of gulping air for extra buoyancy may link to curvature of the spine due to an over inflated stomach, (I.K. Berzins, pers. com.). It is highly likely that the causes of spinal deformities in *C. taurus* are multifactoral (Berzins *et al.* 2002; Preziosi *et al.*, 2006) and at present there are no definitive conclusions. This however continues to be a problem with captive *C. taurus* worldwide and further study into causes and preventative measures need to be addressed.

The implications of the spatial distribution and water column depth findings are that the tanks built to house *C. taurus* need to be designed such that the most preferred areas are maximised. Ideal holding areas have large central and deep areas. Given that the sharks prefer the outer areas and deep water, a donut shaped holding area might be the preferred design. The tank would also need to be large so there is sufficient room for the animals to manoeuvre with ease which may minimize the risk of spinal deformities.

5.3. Behavioural Interactions

5.3.1 Nearest Neighbour

There was no nearest neighbour preference between sharks or between seasons. Males did spend more time in the mating season following females, (pers. obs.) however this was not a significant change from that in the non-mating season. This was likely counteracted by the amount of time the males spent tailing each other to block female encounters during the mating season. In the non mating season, nearest neighbours were often simply in the same area of the tank and not displaying active following or tailing behaviours displayed during the mating season.

5.3.2 Dominance Hierarchies – Give-Way Analyses

A problem associated with studying shark dominance is the lack of aggression exhibited by sharks. This lack of intraspecific aggression seems characteristic of many shark species, having been observed by Allee and Dickenson (1954) in Smooth Dogfish (*M. canis),* by Eible-Eibesfeldt (1959) in Grey Reef sharks (*C. menisorrah),* by Hobson (1963) in White Tip Reef sharks (*Triaenodon obesus)* and Black Tip Reef sharks (*C. melanopterus)* and by Myrberg and Gruber (1974) in Bonnethead sharks (*Sphyrna tiburo*).

Due to this lack of aggression, dominance in sharks was defined as the avoidance of another shark. The dominance was determined when two sharks are swimming head-on, with the shark giving way deemed to have lost the encounter, therefore being the subordinate shark.

CtM3 was found to be the shark that "gave-way" slightly less often than expected, however this was not at the significant level therefore a dominance hierarchy could not be established. This partially correlates with the observations of the staff of the Blue Planet Aquarium; they believe that CtF1 and CtM3 are the most dominant sharks in the tank.

There was also no significant difference between individuals sharks give-way occurrences, between mating and non-mating season, feeding and non-feeding days or time period.

There were relatively few give-way encounters between any of the sharks during observation periods. In total 32 give-way encounters were observed over more than 200 hours of observations. This may partially be due to the size and layout of the tank but it was also possible that individuals who frequently "gave-way" were more likely to avoid encounters. A regression analysis confirmed this was in fact the case. This suggests one of two possibilities; either (1) sharks have a hierarchical dominance behaviour causing the subordinate sharks to actively avoid encounters or (2) there is a difference among sharks in ability to sense an approaching conspecific from a distance. From this study it could not be determined conclusively which of these possibilities is in fact the case.

5.4 Jaw Flex

Occurrences of jaw flexes were found to be both infrequent (only 30 observed in total) and statistically randomly distributed among sharks. From this can be concluded that this behaviour is probably involuntary and of little or no diagnostic value with regards to the health or well-being of *C. taurus* in captivity.

5.5 Swimming Behaviour

Swimming behaviours, both patrolling and resting, were significantly different between sharks. These differences however can be attributed to two sharks, CtF1 and CtF4 who patrol significantly less and rest significantly more than the other five sharks. CtF1 is the oldest shark in the tank, however this may not be the reason for her high level of resting as age has not been studied in relation to swimming behavioural changes. As previously mentioned CtF4 is from South Africa, a different geographic location to the other *C. taurus*, which may be an additional factor, as may her severe spinal deformity.

Time period also had a significant effect on swimming behaviours. This was primarily due to an increase in time spent patrolling and reduced time resting during time period 5 (22:00 – 00:00) and 6 (00:00 – 04:00). These time periods are when the main aquarium lights are out and there are no divers or members of the public. Wild *C. taurus* have been reported to be most active at night (Castro, 1996), linking with the findings in this captive population.

As discussed the results showed differences between day and night rather than differences between time periods 2 (time), 3 (time) and 4 (time). As there are no significant differences between swimming behaviours at these times it demonstrates that visitors to the aquarium and diver presence in the tank had no effect on *C. taurus* behaviour (as conditions in time periods 2, 3 and 4 were identical except for the absence of visitors and divers in time period 4). Nelson (1977) found that habituation of captive sharks to divers occurs and the sharks simply ignore the divers, as they pose no threat, which appears to also be the case here.

5.6 Swimming Speeds

The fastest individual shark was CtM3, (Flare) and the slowest shark was CtF4 (Wanda). Although natural variation within populations is likely there are two other possible explanations for CtF4 slow swimming speed. CtF4 was from a South African population while the rest of this captive population was from the east coast of the U.S.A. Differences could thus be due to natural variation between populations, although this is not supported by observations in the wild. Another explanation is that CtF4 was suffering from a severe spinal deformity hence her slow speeds. Loss of forward speed has been observed in other *C. taurus* with spinal deformities (Preziosi *et al*, 2006), hence this is the more likely explanation.

Females were noted to have significantly slower swimming speeds than males. The overall average swimming speed in *C. taurus* increases during the mating season, this however is due to a large swimming speed increase in males, this is examined further is section 5.8.

As there was found to be no difference in swimming speed in *C. taurus* sharks on feeding and non-feeding days this suggests that there is no alteration of speed in anticipation of food. This may be a natural phenomenon as a result of confined captive conditions. However a study carried out by Newman (1999) at the National Marine Aquarium, Plymouth showed an increase in the average swimming speed during feeding days for *C. taurus*. This may indicate that habituation had not yet occurred in these sharks. Alternatively it may be a result of fewer feeding days and more sharks than at the Blue Planet Aquarium, therefore increasing competition for food and speed may be a factor in successful feeding.

Time period was shown to have a small but significant difference in swimming speeds. Time period 5 (22:00 – 00:00) and 6 (00:00 – 04:00) had the two highest average swimming speeds. These are both periods when the main aquarium lights are out and there are no divers or members of the public. Although this behaviour has not been previously documented in *C. taurus*, Lowe (2002) found that wild juvenile scalloped hammerhead sharks (*Sphyrna lewini*) swam significantly faster during crepuscular periods and at night than during daylight.

In a similar study carried out by Myrberg and Gruber (1974) on Bonnethead sharks (*Sphyrna tiburo)* the sharks were shown to increase patrolling speed in the afternoon, suggesting diurnal rhythmicity in that species. However this sort of rhythmicity has never been reported in *C. taurus* before this present study. If similar changes in patrolling speed are indeed found also in wild *C. taurus*, it might be beneficial for aquaria to mimic natural lighting conditions to encourage more natural swimming and patrolling behaviours of the species.

5.7 Captive Mating Behaviours

5.7.1 Mating behaviours and interactions with speed and sex during the mating season

Swimming speeds of male *C. taurus* are on average faster during the mating season. Yano *et al.* (1999) noted a similar speed increase in male manta rays (*Manta birostris*) during the mating season. In wild male *C. taurus* a benefit of increased speed during the mating season would be more encounters with females, hence increased chance of mating.

Conversely, the average swimming speed of female *C. taurus* decreases slightly in the mating season. There are two possibilities for this decrease in speed. Firstly the decrease in speed may be linked to the acceptance of a male and may be a sign she is ready to mate. Slower swimming speeds were observed in female captive *C. taurus* in Oceanworld Manly just prior to mating. The males showed no interest in the female until the female slowed her swimming rate (Gordon, 1993). Alternatively in the wild a slower swimming speed by females may result in fewer encounters with males, (assuming that males can track females by chemical cues released in the female's wake; Gardiner and Atema, 2007). This avoidance would limit their damage by minimising matings, hence reducing mating bite injuries. Such mating conflict relates to the asymmetries between the sexes in the benefits of mating versus its costs (Parker 2006). Female blue sharks (*Prionace glauca*) have been observed to receive such a high level of precopulatory biting that they often appear severely wounded during the mating season (Stevens, 1974; Pratt 1979). It has been demonstrated that *P. glauca* females have a significantly thicker skin than males. Such sexual dimorphism in skin thickness is also believed to be present in many other shark species. However, despite thicker skin deep cuts still occur and have a high potential to damage females due to blood loss or infection (Pratt and Carrier 2001). Therefore to minimise such sexual conflict, I suggest that females may have a reduced swimming speed in the mating season. Although this will not apply to captive individual as they are in a confined space this reduction of speed during the mating season may occur due to inherent behaviours from the wild.

5.7.2 Descriptive Analysis of Captive Mating

Mating in wild *C. taurus* has not been observed to date, therefore although it can not be ascertained that it will be the same as captivity, the likelihood is that there will be at least some similarities. Although the mating observed during this study did not result in pregnancy on this occasion, it is not possible to conclude definitive reasons for this.

5.8 Problems and Alterations

A problem of this study was the limited number of individuals available to observe, which is typical of studies on large captive vertebrate species. The small sample size resulted in reduced power and reliability of the statistical tests, although confounding issues such as pseudoreplication have been prevented by the applied statistical analyses.

The collection of the data could be improved in several ways. The use of tracking equipment could help reduce spatial distribution error by recording which areas the shark visited, rather than the areas that the shark was in every fifteen seconds. This way, the time spent in each section could be recorded, rather than using a frequency of observations in each area.

A problem associated with studying the swimming speeds of captive sharks was the recording methods. The swimming speed was only measured over a short distance (1.79m); a longer distance would have given more precise results. The reason the distance was not extended to two divisions of the tunnel (3.58m) was that the sharks rarely swam parallel to the tunnel for this distance and the number of swimming speeds recorded would be drastically reduced.

Human error in the data collection was reduced by practicing data collection techniques prior to the collection of the final data set.

6. Final Comments and Conclusions

- The mating season saw an increase in swimming speed by male *Carcharias taurus* and decrease in females. There was a correlation between swimming speed and mating behaviours; males with the fastest swimming speeds displayed more mating behaviours.

- During the mating season spatial distribution differed with male sharks spending more time in areas commonly frequented by females.

- Spatial distribution differed significantly between feeding and non-feeding days.

- *C. taurus* are more active at night, spending more time patrolling and less time resting than during the day.

- Spatial distribution varies with time period, particularly between day and night.

- *C. taurus* swimming speeds were faster at night.

- There is no nearest neighbour preference in this captive population of *C. taurus*.

- A dominance hierarchy could not be established due to low occurrence of give-way encounters. However, *C taurus* who frequently gave-way at encounters were more likely to avoid encounters to begin with.

- *C. taurus* are predominantly mid-water swimmers.

From this study it can be concluded that aquarium visitors and divers had no detectable effect on the behaviour of any of the captive sharks. This is positive because although there are behavioural changes resulting from being held in captivity, as these factors remain constant it indicates that aquarium activities have no adverse effects on the sharks. Minimising shark stress and maximising wellbeing of such captive animals is of the utmost importance. Captive sharks can be seen as ‘giving up’ their natural lives in the oceans to benefit their species. Their presence in aquaria allows scientific study to take place which may improve our understanding of their species and possibly aid wild populations. Their presence in captivity also increases interest in sharks and can increase awareness of the many problems that wild sharks are facing.

Although no definitive conclusions can be made from this study as to comparisons with wild counterparts, it has enabled us to further our understanding and increase our baseline data of this species in captivity.

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Appendix 1 – Shark Identification

Initially the sharks could be identified by any recent injuries (such as slipped vertebrae, or bite marks/grazes). Although some markings heal quite rapidly, they were useful for quick identification during this study. There were also more permanent detailed identification markings, such as scars, tears and body shape which further aided identification. White spots can be seen on captive *C. taurus* but were not observed for the duration of this study. The cause of these markings is thought to be a fungal infection, (Leibovitz and Leibovitz 1985). These white markings can be used for identification; however the marks are transient (with seemingly no adverse effect to the shark) and so are not reliable for long-term identification. The main identification markings of each shark are summarized in table Ap1.1.

Species	Sex	Name (Code)	Main Identification Marking
Carcharias taurus	F	Wilma CtF1	Dark spot on right pelvic fin.
Carcharias taurus	F	Storm CtF2	Largest shark. Arched back. V shaped cut in left pectoral fin
Carcharias taurus	F	Sky CtF3	Smallest female. Black spot on left pectoral fin.
Carcharias taurus	F	Wanda CtF4	South African - very distinct markings from the other *C.taurus*. Dark speckled colouration with a white underside. Scar on right side.
Carcharias taurus	M	Cloud CtM1	Upturned nose. 2 distinct scars on underside of jaw and 3 large scars on caudal fin.
Carcharias taurus	M	Blaze CtM2	2 large pale spots on pectoral fins. Many dark spots on claspers. Rectangular scars on left side.
Carcharias taurus	M	Flare CtM3	Displaced jaw. Dark edges and a light spot in the centre of both of pelvic fins.

Table Ap1.1: Shark species, sex, name and code, with their main identification markings.

Appendix 2 – Ethogram

Ethograms are essential for recording the behaviours of the sharks, as it is important to know what exactly to record. Below is a section of the ethogram from Newman (1999) which was relevant to the behaviours observed during this study. The behaviours are listed with an empirical description, a description in terms of body parts, movements and postures, and for the ease of recording, the names of some the behaviours are more functional.

Burst Swim (Flight) – Rapid change of direction followed by a couple of strong tail beats and a rapid temporary increase in speed. This is accompanied by a lowering of the pectoral fins, the whole process is very rapid, and for a detailed physiological description, the behaviour should be filmed and watched at a slower speed. The flight is halted once the shark is out of danger or reaches the other side of the tank.

Following – When one shark closely follows another, repeating the leader's movements. Described as a common pattern by Myrberg and Gruber (1974) when they studied bonnethead sharks, a follow can be hard to identify in a small tank.

Glide – Movement through the water on a level plane or slight downward gradient, with neither movement of fins or body.

Jaw Flex – Opening of mouth wide with distension of upper jaw. Only observed during very slow swimming or a slow glide. This looks similar to a yawn in human, however as this implies a function, when one is not definitely known, it is referred to as a jaw flex.

Manoeuvring – Movement characterized by a series of rapid turns or turnbacks. Manoeuvring may be to such an extent that the head is near the tail, and the body is nearly bent double.

Such manoeuvring probably results from the inability of some sharks to maintain a position in the water column without moving (Myrberg and Gruber, 1974). In a similar way to the turnback, manoeuvring could be utilized by the shark to raise its position in the water column.

Patrolling – Variable speed swimming in any direction around the tank, at variable depths. This is used as the default behaviour, and is quite general. There are definite differences in technique of patrolling by different species of shark:

Sand tiger shark – Head movements very limited. Head is held lower than lower edge of caudal fin, with the caudal fin movements varying greatly with speed. During slow cruising just the upper caudal fin tip is moved, with little body or head movement. Occasional movement of anal fins for balance.

Turnback – Physiologically identified as the lifting of the head and flexing of the body in one tail beat. Combined with the lowering of the pectoral fins aids in the turning of the fish. A dropping of the head and a levelling of the body follow this.

Surface look – Only observed in the sand tiger sharks only.

Almost vertical positioning of the body in the water column. This is followed by a raising of the head and eyes above the waters surface.

Appendix 3 – Behavioural Interaction Graphs

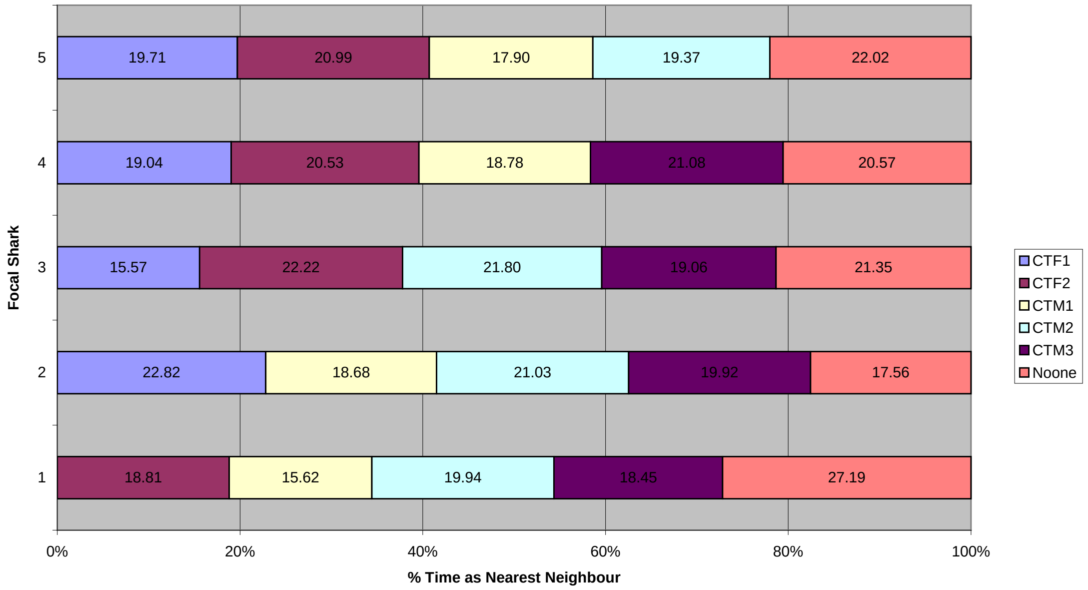

Fig A.3.1 Nearest Neighbour % for Captive C. taurus

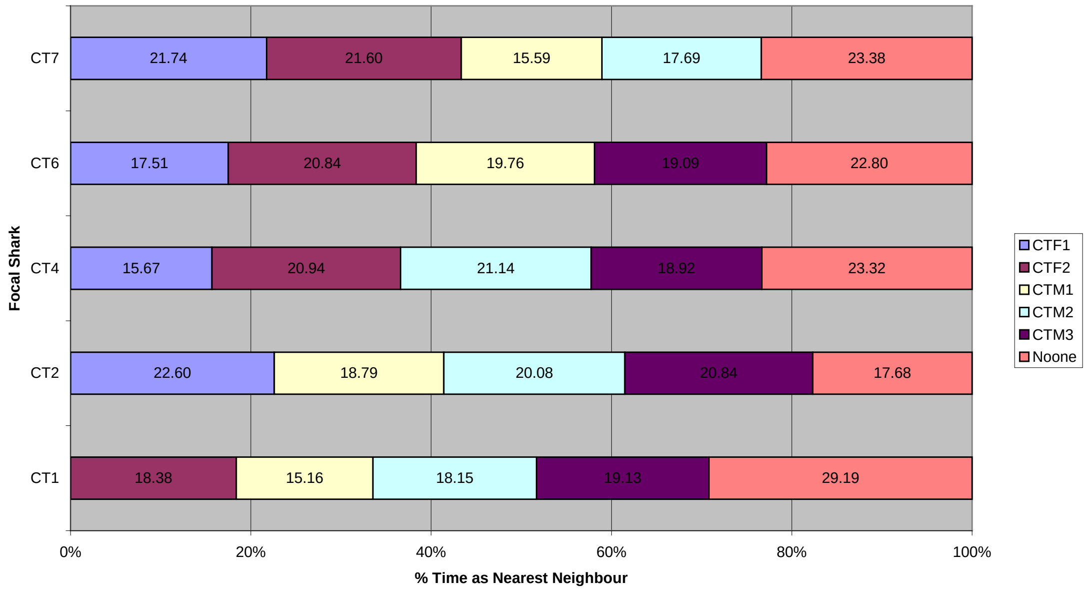

Fig A.3.2 Nearest Neighbour % of Captive C. taurus During Mating Season

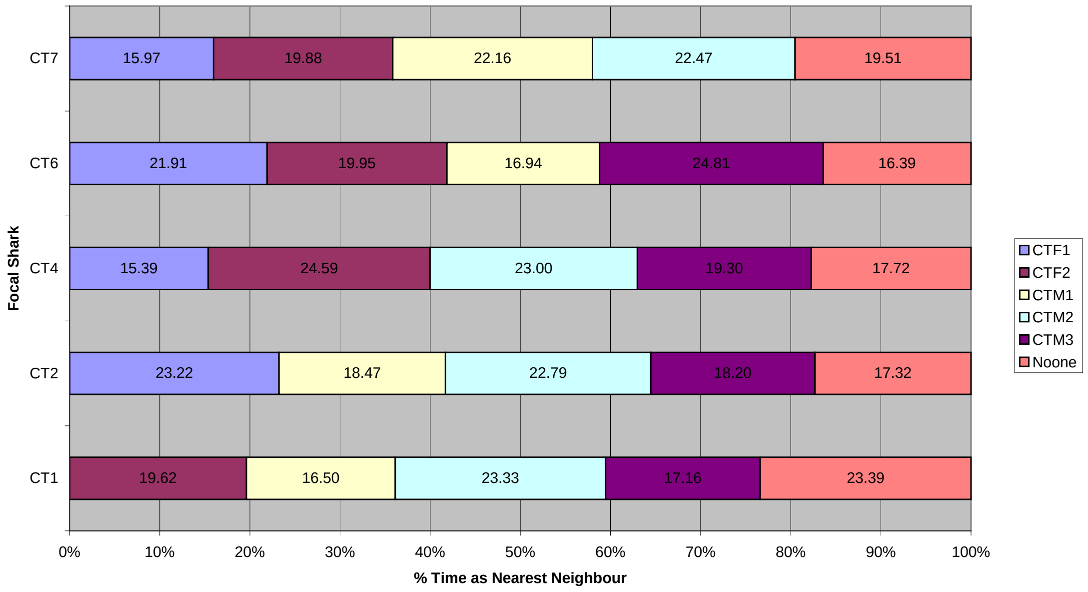

Fig. A.3.3 Nearest Neighbour % of Captive C. taurus During Non-Mating Season

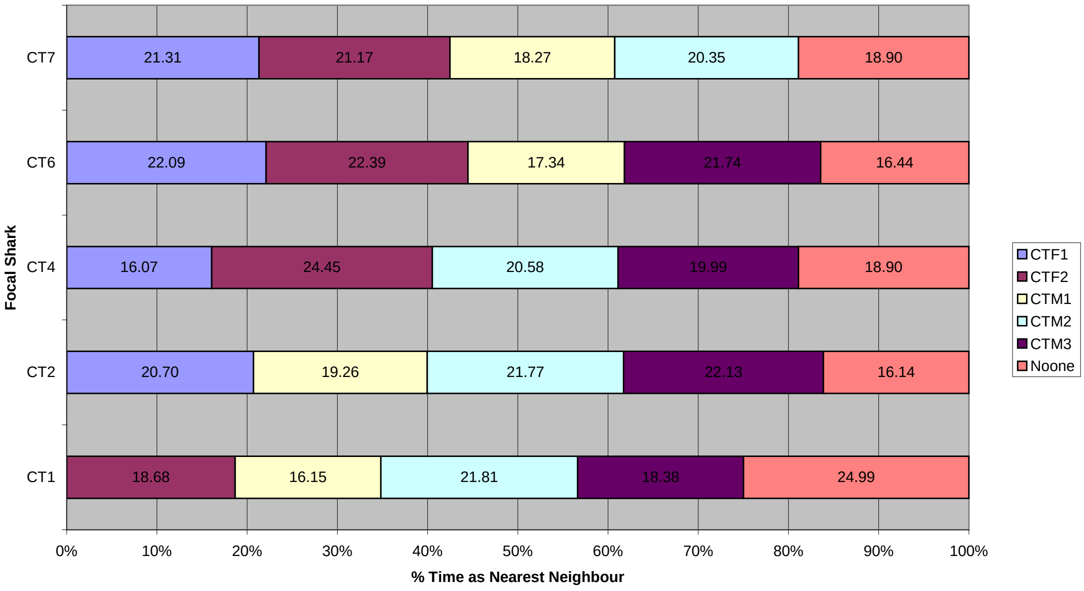

Fig. A.3.4 Nearest Neighbour % of Captive C. taurus During Feeding Days

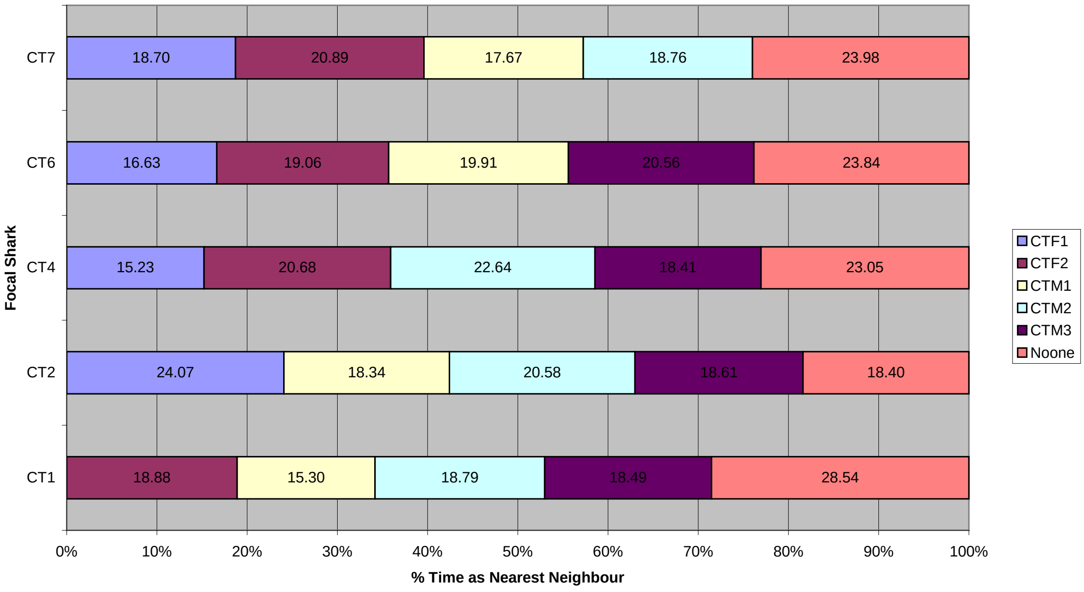

Fig. A.3.5 Nearest Neighbour % of Captive C. taurus During Non Feeding Days

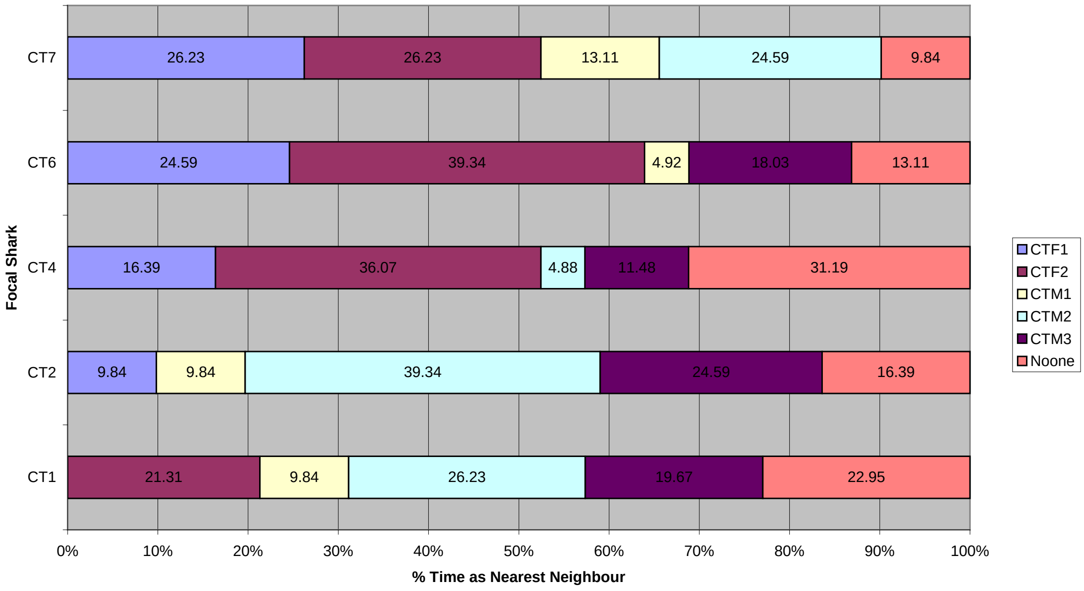

Fig. A.3.6 Nearest Neighbour % of Captive C. taurus During Time Period 1

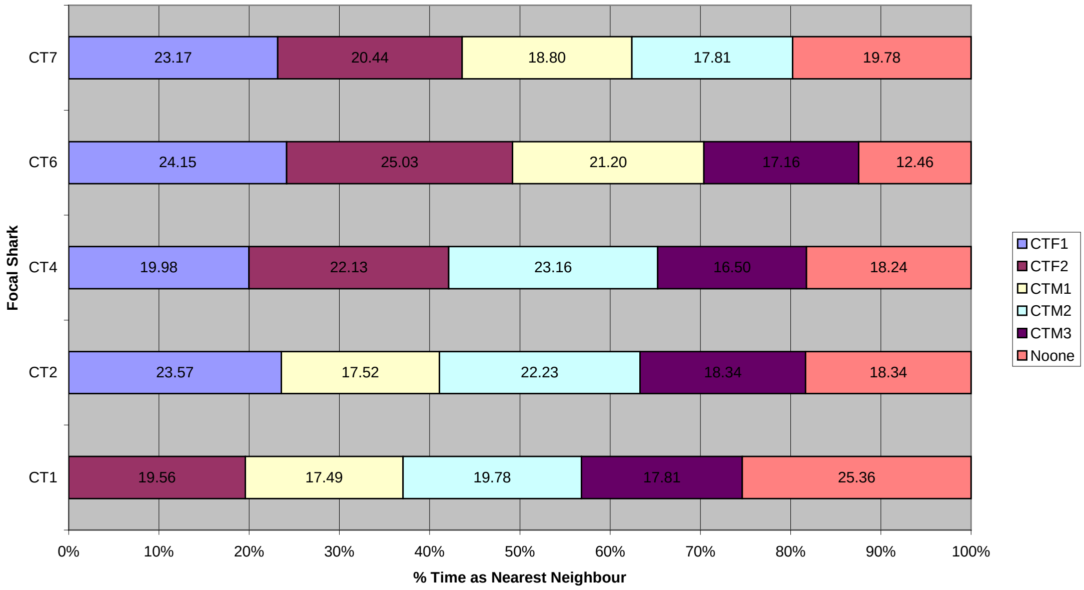

Fig. A.3.7 Nearest Neighbour % of Captive C. taurus During Time Period 2

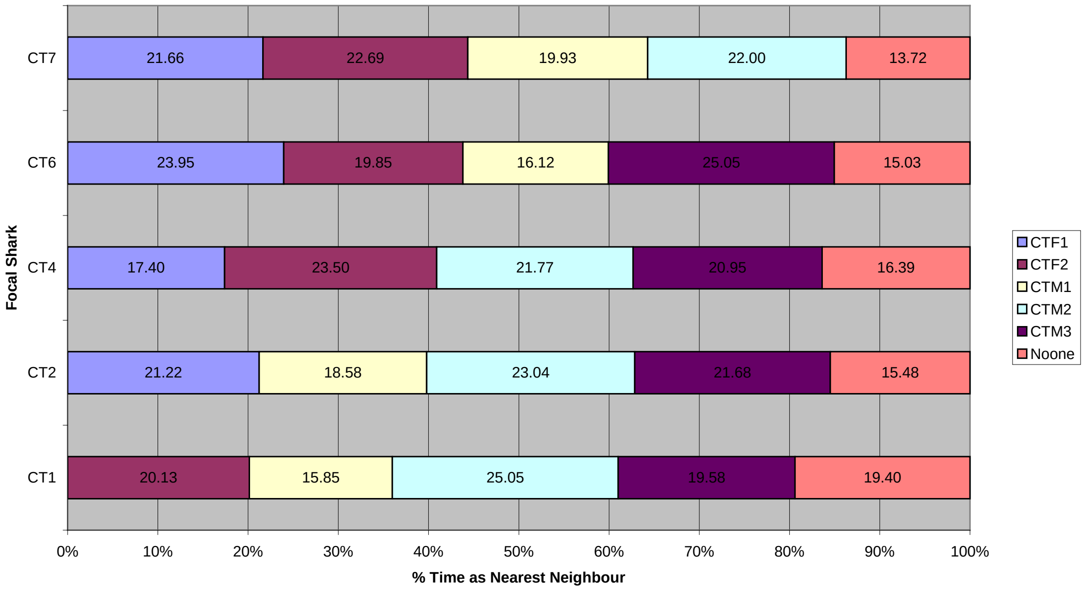

Fig. A.3.8 Nearest Neighbour % of Captive C. taurus During Time Period 3

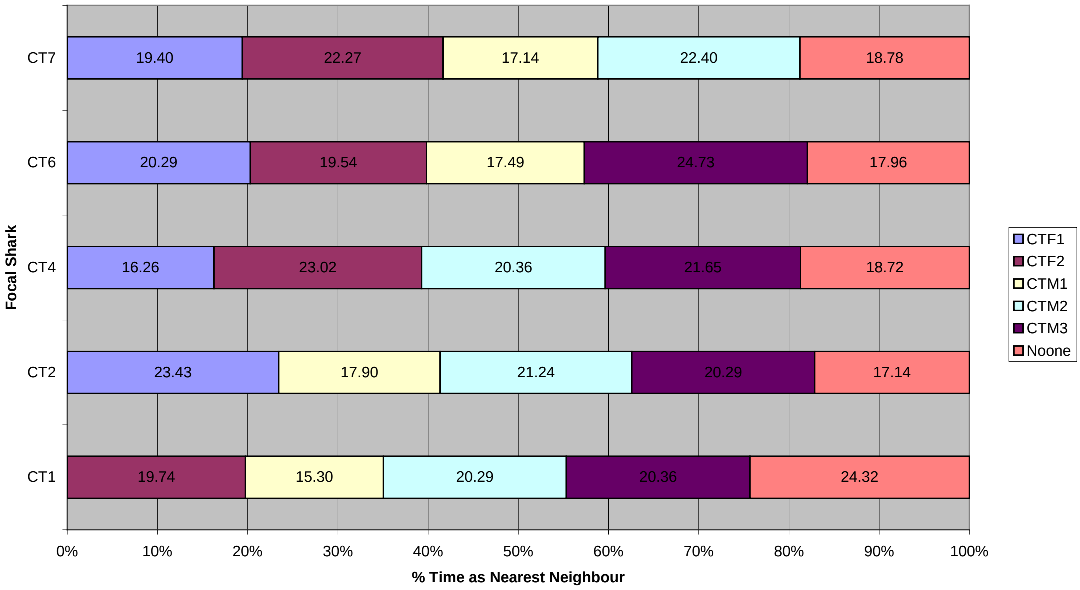

Fig. A.3.9 Nearest Neighbour % of Captive C. taurus During Time Period 4

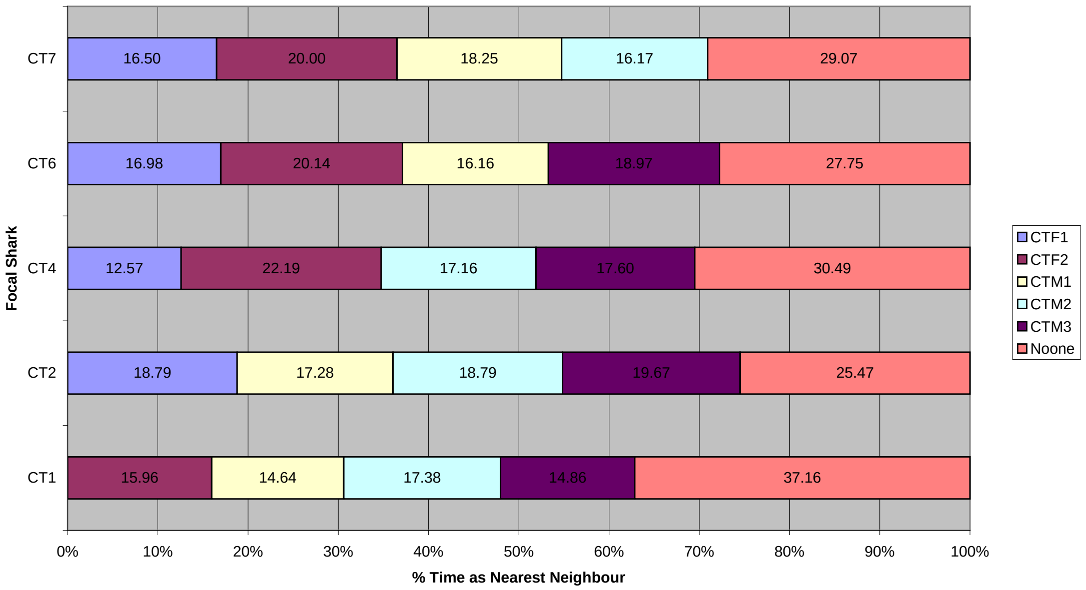

Fig. A.3.10 Nearest Neighbour % of Captive C. taurus During Time Period 5

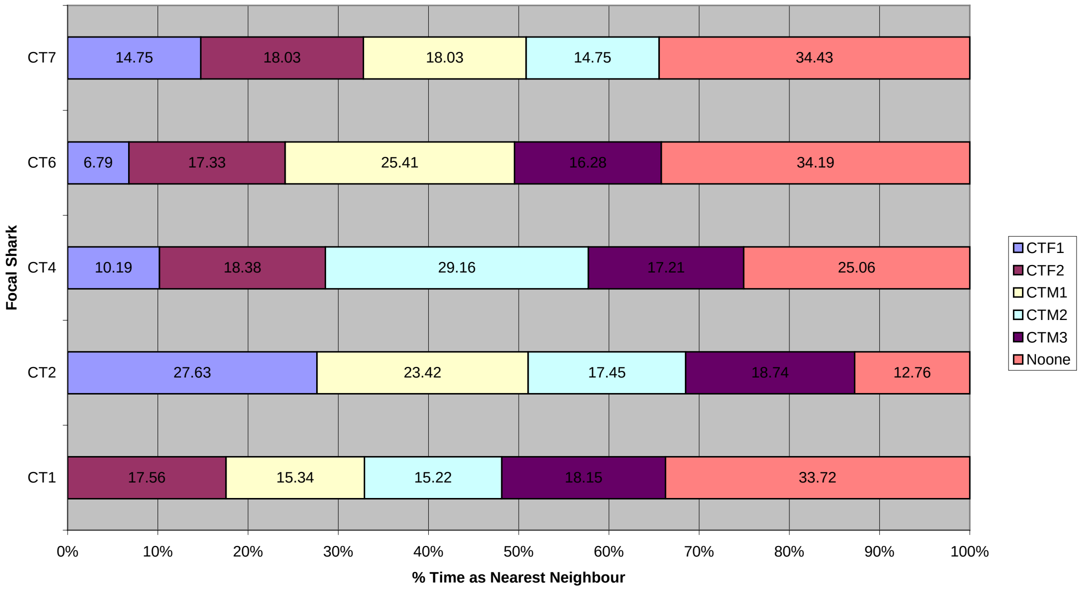

Fig. A.3.11 Nearest Neighbour % of Captive C. taurus During Time Period 6

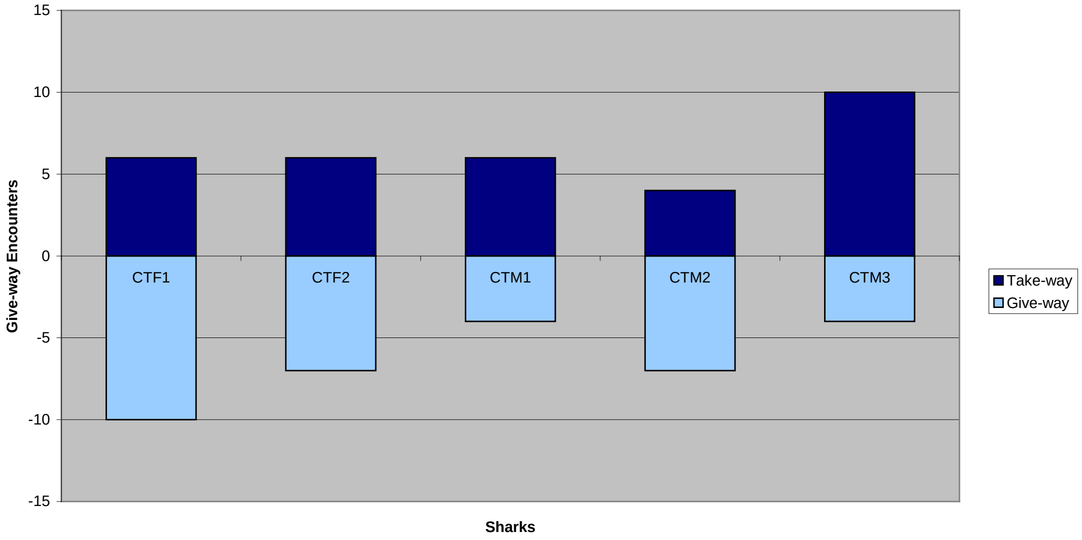

Fig. A.3.12 Frequency of Give-way Encounters of Sand Tiger Sharks at the Blue Planet Aquarium

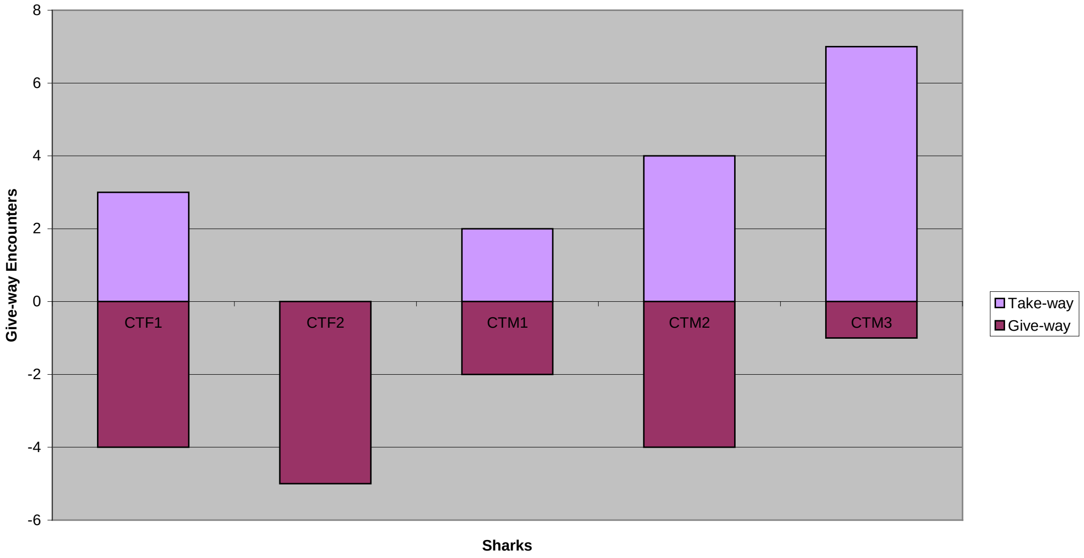

Fig. A.3.13 Frequency of Give-way Encounters of Sand Tiger Sharks during the Mating Season at the Blue Planet Aquarium

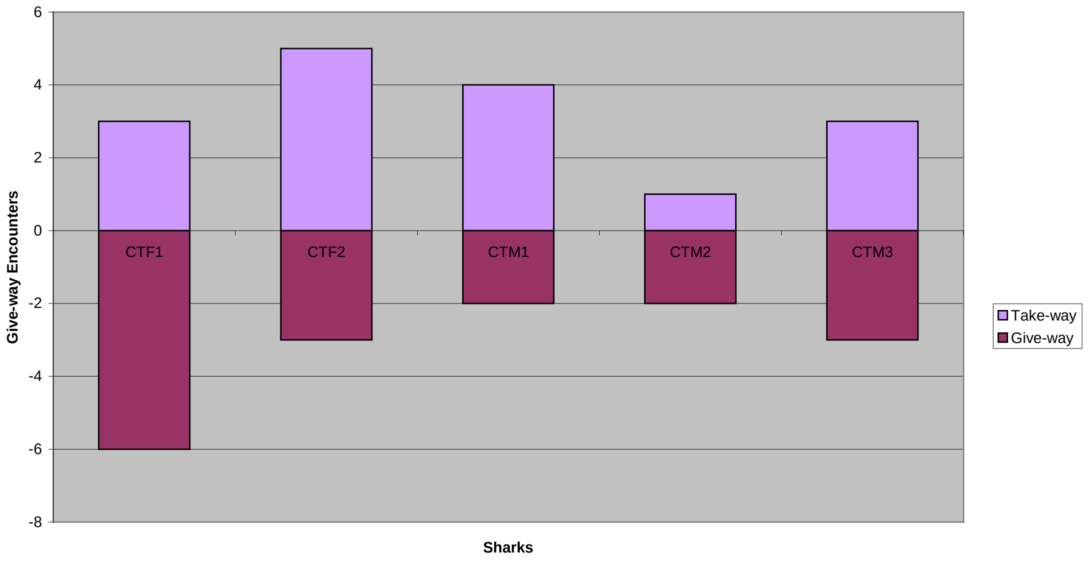

Fig. A.3.14 Frequency of Give-way Encounters of Sand Tiger Sharks during the Non-Mating Season at the Blue Planet Aquarium

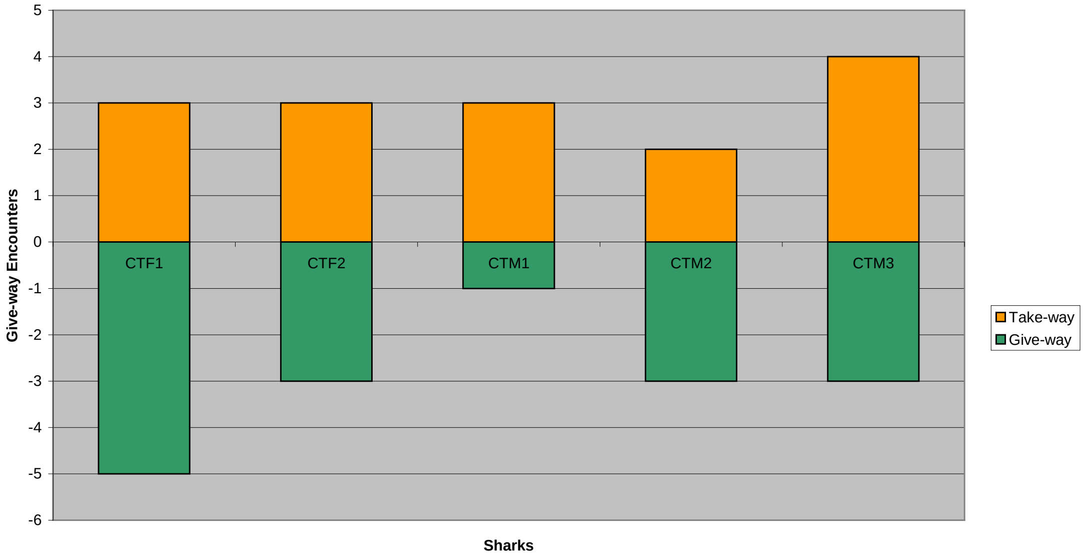

Fig. A.3.15 Frequency of Give-way Encounters of Sand Tiger Sharks on Feeding Days at the Blue Planet Aquarium

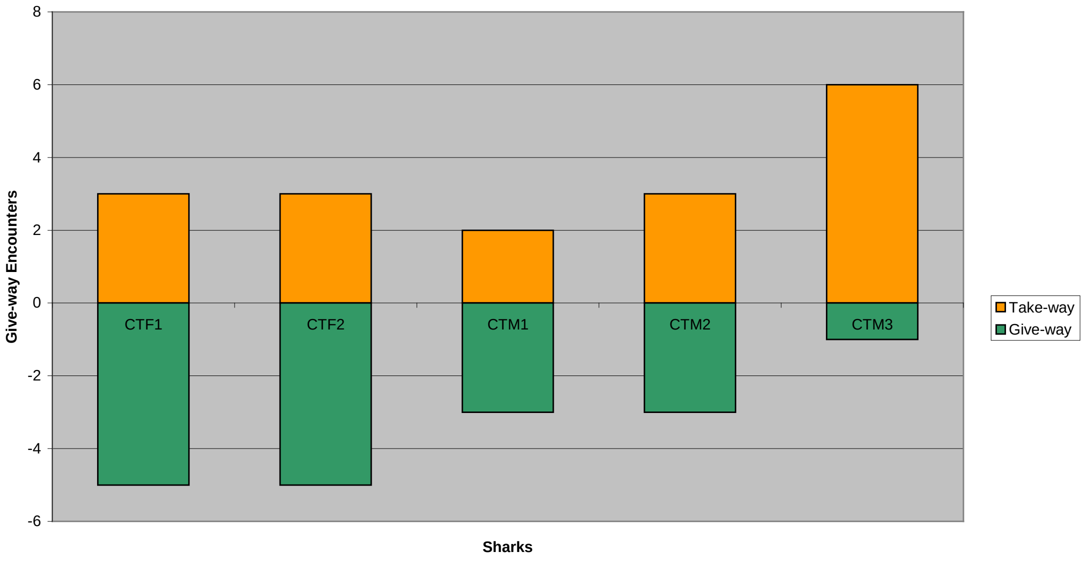

Fig. A.3.16 Frequency of Give-way Encounters of Sand Tiger Sharks on Non-Feeding Days at the Blue Planet Aquarium

Appendix 4 – Swimming Speed Graphs

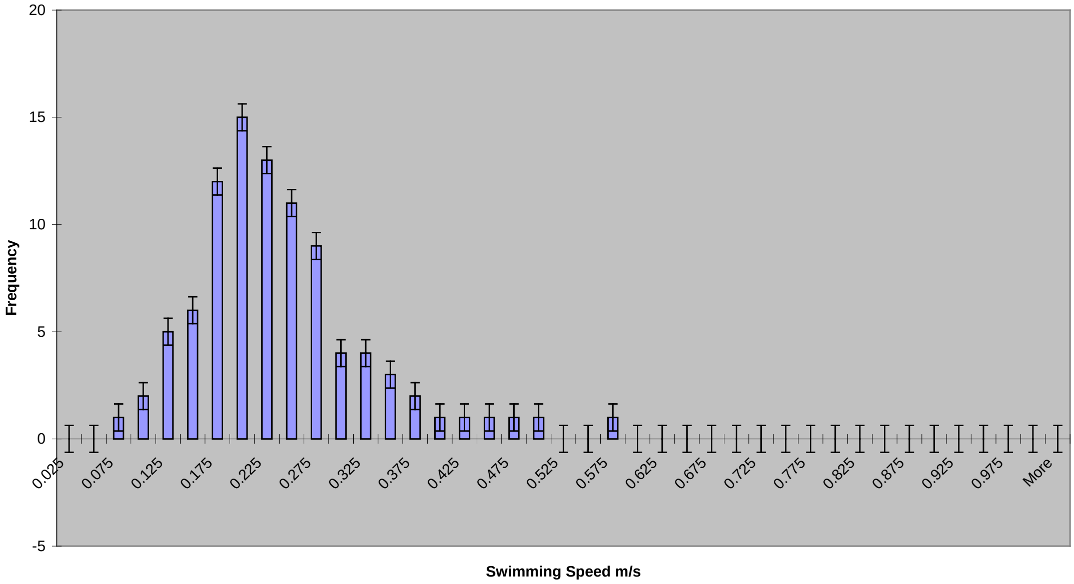

Fig. A.4.1 Swimming Speed Frequency (+-S.E) of CTF1

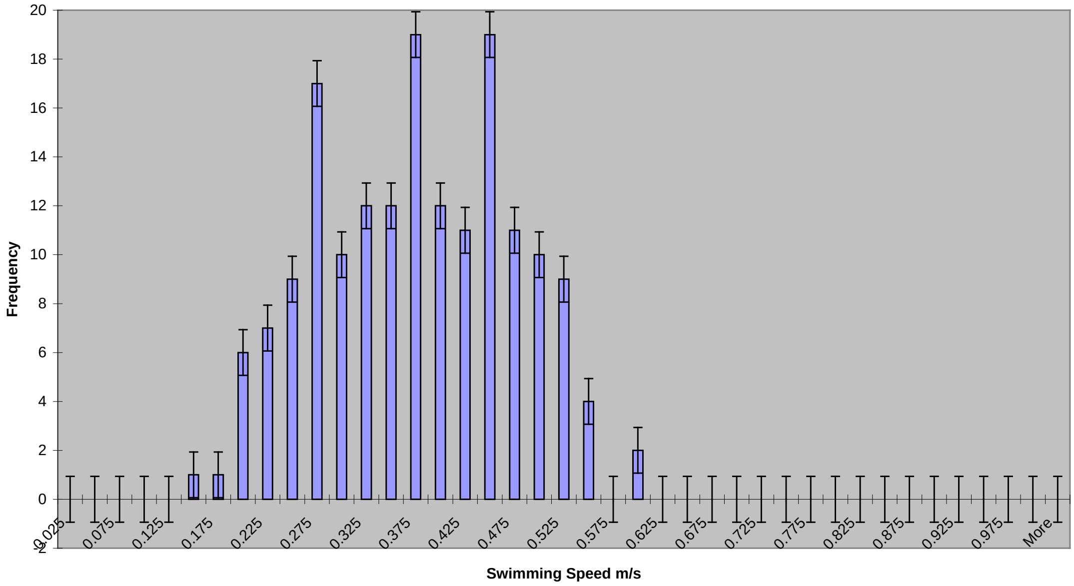

Fig. A.4.2 Swimming Speed Frequency (+-S.E.) of CTF2

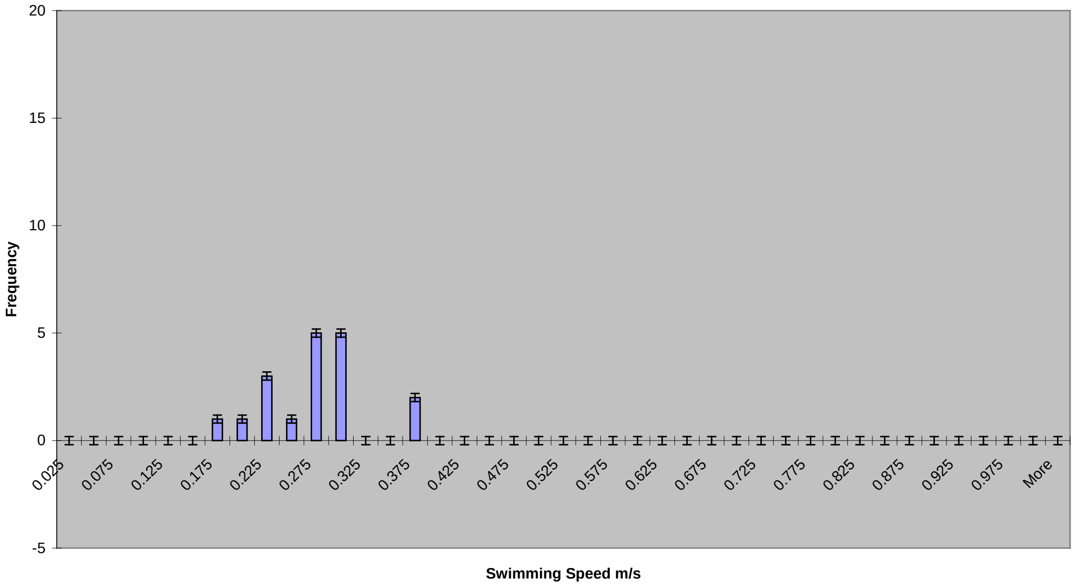

Fig. A.4.3 Swimming Speed Frequency (+-S.E.) of CTF3

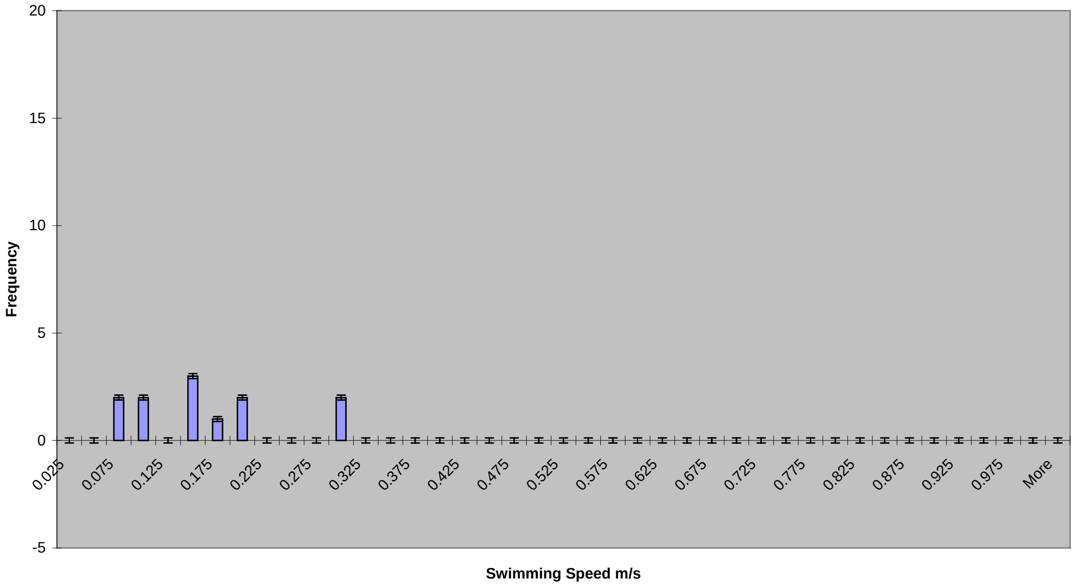

Fig.A.4.4 Swimming Speed Frequency (+-S.E.) of CTF4

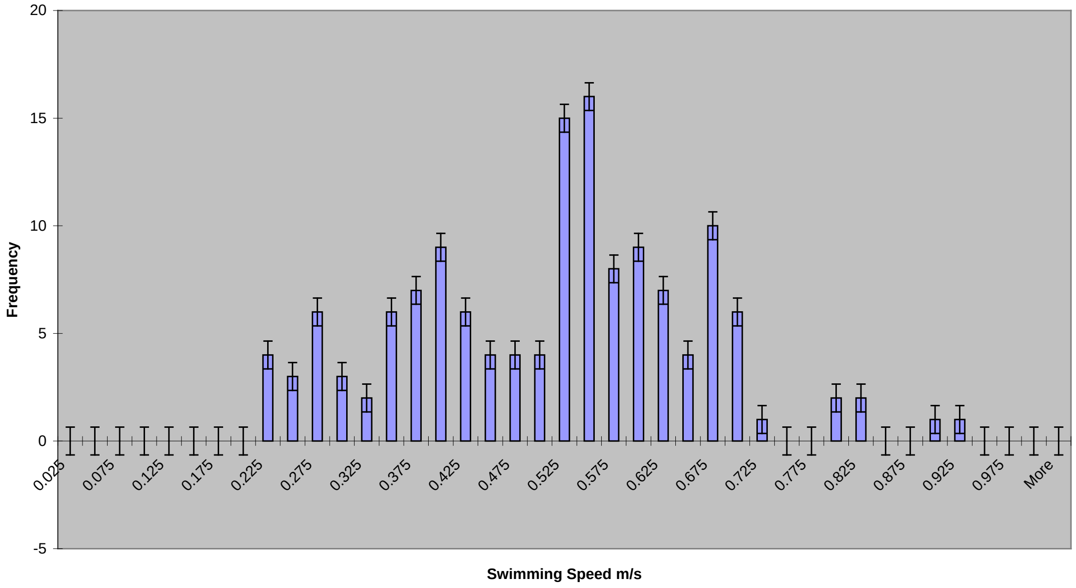

Fig. A.4.5 Swimming Speed Frequency (+-S.E.) of CTM1

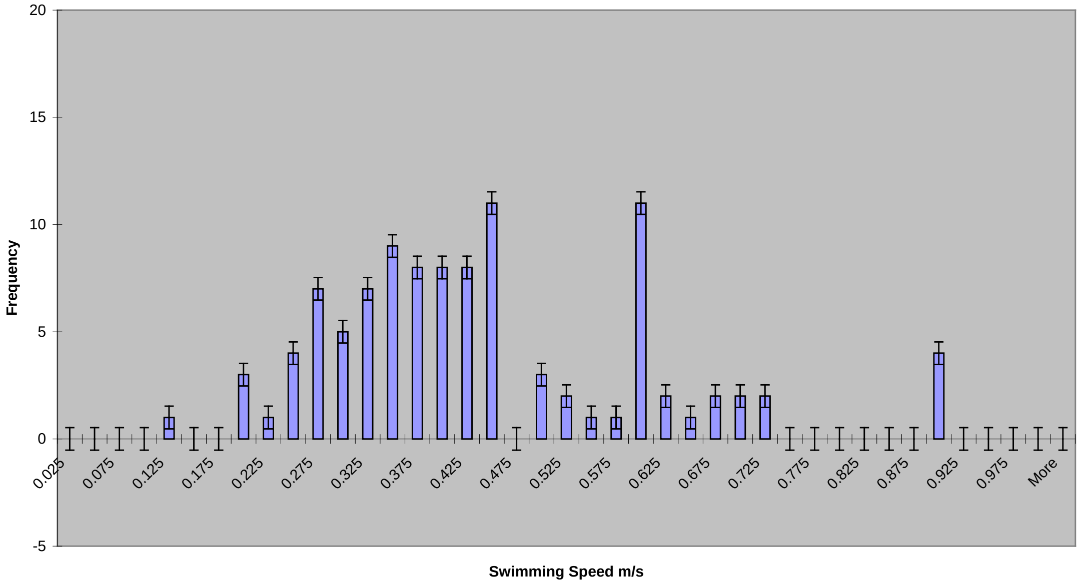

Fig. A.4.6 Swimming Speed Frequency (+-S.E) of CTM2

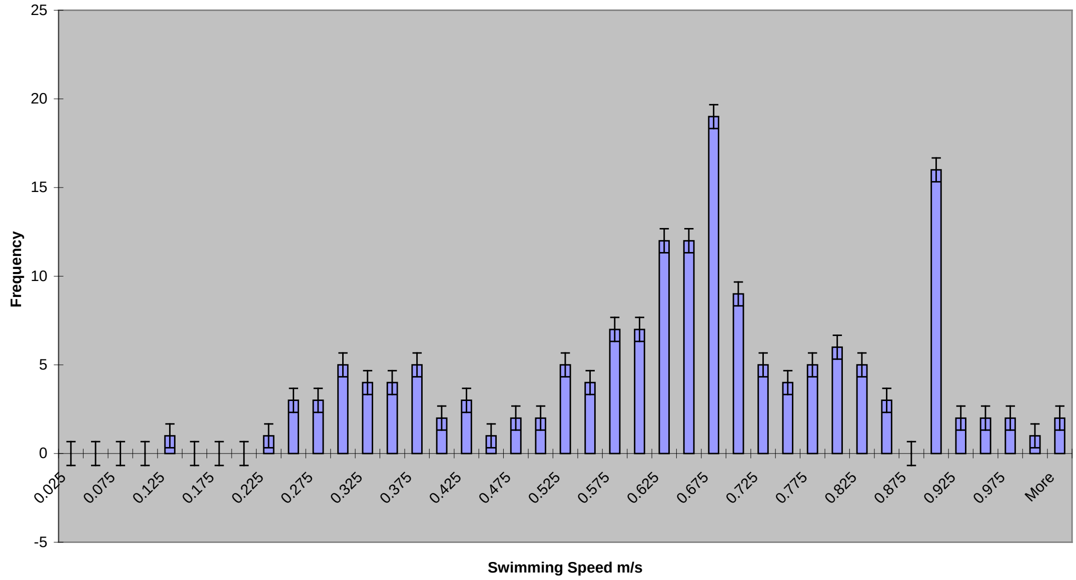

Fig. A.4.7 Swimming Speed Frequency (+-S.E) of CTM3

Appendix 5 - Questionnaire

Sand Tiger Questionnaire

Name:
Position:
Institution:

Are you responsible for the maintenance of sharks at your institution Yes/No

If no, please give the name/ e-mail of this contact ________________________

Section A

1. Do you keep Sand Tiger sharks? ☐
2. If yes can you please complete the table below for each Sand Tiger shark you have

	Name of Sand Tiger Shark	Sex *Please tick*		Age (Years) *Please tick an age group for each shark*						Size (cm) *Please tick a size class for each shark*				
		Male	Female	0 - 4	4. – 8	8.-12	12.-16	16+	Unknown	90 – 140	140 - 190	190-240	240-290	290+
1														
2														
3														
4														
5														
6														
7														
8														
9														
10														
11														
12														

3. Where is the source of your Sand Tiger sharks (please tick)

   South Africa ☐
   Australia ☐
   East Coast of America ☐
   Other *please state where* ☐
   Another aquarium *please state which* ☐

Section B

1. What are the dimensions of your tank?
2. What is the shape of your tank?
3. What is the water turnover rate?
4. What is the water temperature?
5. What pH is the water maintained at?
6. What are the levels of nitrate?
7. What are the levels of ammonia?

Section C

1. Have any of the Sand Tiger sharks you have kept had any history of spinal deformities? Yes/No
2. Were these treatable? Yes/No
3. Were these treated? Yes/No
4. Have your Sand Tiger sharks experienced any other health problems e.g. Prolapsed jaw etc? If so please state what
5. What is the feeding regime?

(Please state food type and amount and how many times per week the sharks are fed. If known please state the ratio of food items to % body weight/week)

6. Do you supplement the diet of you Sand Tiger sharks with vitamins? Yes/No
   If yes what is the dose rate and make of the vitamins?

7. Do you take blood samples or tissue samples from your Sand Tiger sharks? Yes/No
   If yes please give details in the box provided

Section D

1. Have your Sand Tiger sharks had any attempted matings? Yes/No
2. Have your Sand Tiger sharks had any successful matings? Yes/No
3. Have your Sand Tiger sharks displayed any mating behaviour? Yes/No

4. If you have answered yes to any question in Section D, please give details below.

Section E

1. Would you willing to contribute data and/or material to this study at a future time? Yes/No
2. Are there any addition questions you think we should have asked, if so what are they and how would you have answered them?

Many thanks for completing this questionnaire and supporting this study

Appendix 6 – Additional Questionnaire Data

A questionnaire was designed with a combination of open and closed questions for aquariums (appendix 5), with the aim of gathering information on tanks, feeding regimes and *C. taurus*.

In total 45 aquariums responded to the questionnaire worldwide, 22 of which kept *C. taurus*. The data from these institutes were collated and analysed. A binary logistic regression was carried out on mating behaviour occurrence, number of sharks, sex ratio and country of origin. The variance was not explained by any of these variables, (G = 0.249, d.f. = 1, P = 0.618).

Aquarium	**Country**	**Source of *C. taurus***	**Total *C. taurus***	**Total Females**	**Total Males**	**Mating Behaviours Occurring**	**Mating Attempts**
Aquarium La Rochelle	France		2	1	1	No	No
Aquarium of the Pacific	U.S.A.		4	1	3	No	No
Barcelona Aquarium	Spain	S. Africa & East coast of U.S.A.	6	2	4	No	No
Henry Doorly Zoo	U.S.A.		4	1	3	No	No
Houston Downtown Aquarium	U.S.A.		11	5	6	No	No
London Aquarium	U.K.	East coast of U.S.A	3	1	2	Yes	Yes
Mandalay Bay	U.S.A.	East coast of U.S.A	9	1	8	Yes	Yes
Manly Aquarium	Australia	Australia	9	5	4	Yes	Yes
Minnesota Aquarium	U.S.A.	East coast of U.S.A	3	1	2	Yes	Yes
Moody Gardens Aquarium	U.S.A.		4	2	2	Yes	Yes
Mystic Aquarium	U.S.A.		3	2	1	Yes	Yes
National Marine Aquarium	U.K.	East coast of U.S.A	4	2	2	Yes	Yes

Aquarium	**Country**	**Source of *C. taurus***	**Total *C. taurus***	**Total Females**	**Total Males**	**Mating Behaviours Occurring**	**Mating Attempts**
New England Aquarium	U.S.A.	East coast of U.S.A	1	1	0	No	No
New Jersey State Aquarium	U.S.A.	East coast of U.S.A	4	4	0	Yes	Yes
Newport Aquarium	U.S.A.		5	2	3	No	No
Oceanario de Lisboa	Portugal		2	0	2	Yes	Yes
Oceanopolis	France	S. Africa	2	0	2	Yes	No
SAAMBR	South Africa	S. Africa	6	4	2	Yes	Yes
San Diego Sea World	U.S.A.		8	2	6	Yes	No
South Carolina Aquarium	U.S.A.	Another Aquarium	1	1	0	Yes	Yes
The Blue Planet Aquarium	U.K.	S. Africa & East coast of U.S.A.	7	4	3	Yes	Yes
The Deep	U.K.	S. Africa	2	1	1	Yes	No
Underwater World	Australia	Australia	7	4	3	Yes	Yes

Table A.6.1 Aquarium Questionnaire Response Table 1

Insufficient data was provided for other factors such as nitrate levels and pH to determine the effect of such variables, (appendix 5). Water temperature ranges within aquaria were also too large to enable an accurate analysis with effects on mating behaviours.

Aquarium	**Water Temp.()**	**pH**	**Nitrate**	**Ammonia**	**Tank Dimensions**	**Shape**
Aquarium La Rochelle	23 - 25	8	80mg/l NO3	0	13m * 15m * 9.5m deep	
Aquarium of the Pacific	24.40	8.1 - 8.2	<30ppm	<0.01ppm	35' * 55' * 6 feet deep	Oval
Barcelona Aquarium	19.00	7.9	<10ppm	0.02ppm	4000 m^3	

Aquarium	**Water Temp.()**	**pH**	**Nitrate**	**Ammonia**	**Tank Dimensions**	**Shape**
Henry Doorly Zoo	23.3 - 24.4					
Houston Downtown Aquarium	25.00					
London Aquarium	22.00	8 - 8.2	48.8ppm	0	longest length 20m, 5.5m deep	
Mandalay Bay	23 - 25					
Manly Aquarium						Donut
Minnesota Aquarium	24.40					
Moody Gardens Aquarium	25.00					
Mystic Aquarium	22.00	8.1				
National Marine Aquarium	18.00	8.1		0	25m long *16m wide*10.7m deep	Oval
New England Aquarium	25.00	7.9 - 8.1	25 - 55ppm	<70ppb	23' deep * 40' diameter	Cylindrical
New Jersey State Aquarium	20 - 20.5					
Newport Aquarium	22.2 - 23.9					
Oceanario de Lisboa	22.5 C	8.1	90ppm	0	5000 m^3	Octagonal
Oceanopolis	22 - 23	8 - 8.4	0 - 3mg/l	0	1000m^3	Circular
SAAMBR	18 - 27	8 - 8.1			14m *9m*3.2m deep	Rectangle, rounded corners
San Diego Sea World	23.8 - 24.4					
South Carolina Aquarium	23.8 - 28.3	8 - 8.4		0	48' across * 42' deep	D shaped
The Blue Planet Aquarium	20 - 27	7.5 - 8.4		0	36m *25m *3 to 6m deep	Rectangle
The Deep	24 - 25	7.95	80 - 140ppm	0 - 0.04ppm	Width 12m max 4m min. Length 22m. Depth 10m	Wedge shaped shelf@5m
Underwater World	17 - 29					

Table A.6.2 Aquarium Questionnaire Response Table 2