THE BEHAVIOURAL ECOLOGY OF THE WHITE SHARK (*CARCHARODON CARCHARIAS*) AT DYER ISLAND.

by

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Abstract. The aim of this study was to investigate various aspects of the life history of white sharks *Carcharodon carcharias* at Dyer Island, South Africa, between August 1999 and January 2001. Inter-specific predatory interactions between the white shark and various potential prey species such as the Cape fur seal *(Arctocephalus pusillus pusillus)*, African penguin *(Spheniscus demersus)*, Cape cormorant *(Phalacrocorax capensis)*, bank cormorant *(P. neglectus)*, crown cormorant *(P. coronatus)* and white-breasted cormorant. *(P. carbo)* were observed.

White sharks were attracted daily to a research vessel positioned at various anchorages in the vicinity of Dyer Island. Spatial and temporal abundance, and population composition of white sharks were recorded throughout the year and revealed seasonal trends in habitat utilisation. White sharks occupied inshore waters, away from the Geyser Rock seal colony in the summer. Sharks became abundant in the near vicinity of Geyser Rock in the winter period. The summer inshore population was characterised by the increased total length of sharks and the exclusive presence of female sharks.

Prey resembling decoys were used to investigate trends in the 'predatory motivation' of white sharks in relation to various independent variables. White sharks displayed greatest predatory motivation in close proximity to a seal colony, in overcast conditions, and when water clarity was low. White sharks evidently elevate their motivation to hunt large prey, which are difficult to catch, in situations where the likelihood of encountering valued prey and completing a successful attack is greatest. Ontogenetic difference in predatory motivation towards the decoys existed, with sharks above 325 cm TL displaying greater predatory motivation than smaller sharks.

Various choice tests were conducted to determine the visual discriminatory ability and prey preference of white sharks at Dyer Island. The results suggested that white sharks preferred a biologically familiar shape (pinniped) over an inanimate shape (rectangle), smaller (75 mm TL pinniped) over larger (1800 mm TL pinniped) prey, and a pinniped decoy over a penguin decoy of similar size. Selectivity in larger white sharks (>375 cm TL) was most noticeable in the prey shape (pinniped vs. rectangle) experiment, which suggests they may readily utilise a speculative hunting strategy based on rough similarities between detected potential prey and recognised prey. In this situation mistaken identification of prey is more possible. Smaller white sharks (a majority of the sample) displayed most selectivity in the prey size experiment, with strong preference for the smaller seal decoy over the large one. This pattern indicates that prey size may be a partial limiting factor in the feeding of smaller white sharks.

Negative impacts (such as conditioning or distraction) of cage-diving on white sharks were assessed by the measurement of white shark contact time and visit time in relation to the chumming vessel. These results revealed that smaller sharks had longest visit times, and that sharks in the vicinity of Geyser Rock displayed visitation patterns indicative of hunting sharks. Particular vigilance should be kept by operators not to allow small sharks to take bait (reward). The channel area appears to be an important hunting ground and white shark cage-diving should perhaps be restricted in this area. White sharks also showed greater activity around the chumming vessel on cloudy days and operators must be particularly vigilant to deny sharks any rewards (bait) under these conditions.

Both the white sharks and Cape fur seals predate and/or attack seabirds and predatory interactions were quantified and qualified by the routine collection and inspection of seabird carcasses and injured birds, as well as opportunistic observations of live attacks throughout this study. White sharks are infrequent predators of seabirds in this ecosystem, perhaps due to an abundance of Cape fur seals (a preferred prey), anti-predator behaviour by penguins, and seabirds not being a sought after prey type. Cape fur seals were a more conspicuous seabird predator, annually attacking a significant percentage of the adult penguin (1.99-2.52%), white-breasted cormorant (5.21-5.72%), and crowned cormorant (3.13%) populations. A minimum estimate of 1.09% of the fledgling Cape cormorant population also succumbed to Cape fur seal predation.

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CHAPTER 1

General introduction

The white shark C*archarodon carcharias,* (order Lamniformes, class Chondricthyes, superclass Pisces) is a widely recognized macro predator, with an infamous reputation as a 'man eater' due to rare, but graphical, encounters with humans (Bruce 1995; Burgess & Callahan 1996). This reputation was enhanced by the misconceptive, but stereotypical, representation of white sharks in the 1970's movie *JAWS.* The unjustified reputation of the white shark has 'railroaded' many studies into its life history, and subsequently, much scientific and popular information on this species is written in the context of 'shark attacks on humans'. The realities of the white shark's life history have effectively been hidden by this inaccurate image (Klimley & Ainley 1996b; Compagno *et al.* 1997). Due to the limited scientific information available, efforts to responsibly manage the consumptive and non-consumptive exploitation of the white shark has often had to rely on unsatisfactory data and insufficient knowledge.

1.1 Status, management and conservation of the white shark

1.1.1 Protection

After three decades of consumptive exploitation for sport fishing and the selling of shark products within South Africa, the vulnerabilities associated with targeted fishing for white sharks were acknowledged and appreciated (Compagno 1991). On 11th of April 1991 the white shark was afforded protection status by fisheries legislation in South Africa (Compagno 1991). This legislation was based on the precautionary principle, due to the species being a poorly known apex predator that has great notoriety, a high commercial value and is the subject of much negative human interest (Compagno 1991). This legislation made it illegal to catch, kill or disturb a white shark, or trade any white shark products except if authorized by the Department of Environmental Affairs and Tourism.

Other countries have followed South Africa's initiative, and Australia, Namibia, Maldives, Malta, and parts of the USA issued protective legislation for the white shark between 1994 and 2000. At present, the white shark is listed by the World Conservation Union (IUCN) as 'vulnerable' to extinction (ratings A1b,c,d, A2 c,d), due to past and foreseen population declines (Compagno 1997; Camhi *et al.* 1998).

1.1.2 Consumptive exploitation and threats

The white shark reproduces via aplacental viviparity (Frances 1996) and utilises a reproductive strategy which is based on late maturity, few offspring and a high offspring survival rate (or a K-selected life history) (Calliet *et al.* 1985; Bruce 1992; Uchida *et al.* 1996; Pratt 1996). This K-selected reproductive strategy, and subsequent low productivity, is the reason why white sharks are highlighted as a species particularly susceptible to consumptive exploitation (Walker 1998; Watts 2001). Additionally, because of its long-standing reputation as a 'man eater', the white shark continues to receive very little public sympathy when irrationally targeted by fishermen.

The IUCN Species Survival Commission, and other researchers, have identified incidental catches of the white shark by commercial fisheries, such as purse seine, trawling and long-lining, as the major cause of human induced mortality to this species (Camhi *et al.* 1998; Bruce 1995). During the first year of an Australian white shark tagging program, 3 of the 18 white sharks initially tagged were returned dead after only 78 days at liberty following human capture (Murphy 1996). The white shark depicted in Figure 1.1 was incidentally caught in a purse seine net in South Africa only hours after studied by South African scientists (June 2001). Although quantifiable information is scarce, incidental catches of white sharks are thought to be one of the most immediate dangers to the sustainability of the species both in South Africa and globally (Camhi *et al.* 1998; Bruce 1995).

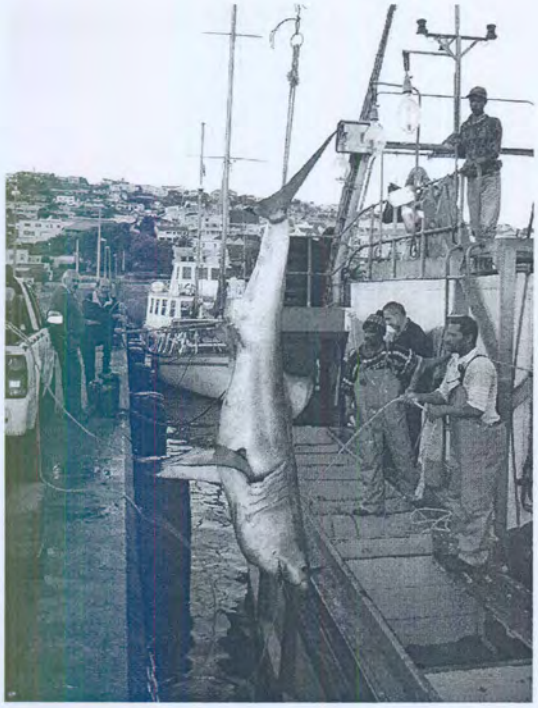

Figure 1.1 A *circa* 350cm white shark incidentally caught in a purse seine net at Mossel Bay, South Africa, June 2001. Mossel Bay has a high abundance of white sharks, yet incidental catches are rarely reported.

Prior to their protection in 1991, targeted capture of white sharks in South Africa was on the increase due to its high commercial value compared to other shark species (Compagno 1991; Camhi *et al.* 1998). Even following protection, the monetary value of white shark products and the lack of international trade restrictions motivates some poaching of white sharks in South Africa (Fig. 1.2). The value of white shark jaws and teeth has risen sharply over the past decade, and at present a large jaw can be worth R14,000 locally (Compagno 1991), or up to 10,000 USD on the international market (Camhi *et al.* 1998). Additionally, due to increasing affluence in Asian countries, such as China, demand for shark fin soup has reached unprecedented levels (Dayton 1991; Watts 2001). A bowl of shark fin soup can reach up to 100 USD, meaning the demand for shark fins has greatly increased, thus placing additional pressures on the world's shark populations (Dayton 1991; Watts 2001). Quantifying the extent of this black market trade is difficult, therefore only rough estimates can be made as to its impacts on the white shark population.

Figure 1.2 A white shark recovered from Gansbaai, South Africa, August 2001. Fins and jaws have been illegally removed for trading. © M.C. Scholl.

In addition to white sharks being caught unintentionally (as bycatch) or by poaching, sharks continue to be intentionally fished on the east coast of South Africa by the Natal Sharks Board (NSB), which operate a shark control program designed to protect swimmers from shark attacks (Cliff *et al.* 1988). Over 40 beaches in KwaZulu Natal are netted, in which between 20 and 50 (mean = 39) white sharks are captured annually (Cliff *et al.* 1989; 1996a). Of 616 white sharks captured between 1978 and 1993, only 97 (15.7 percent) were released alive (Cliff *et al.* 1996b).

1.1.3 Non-consumptive exploitation

The development of the South African cage-diving sector paralleled the 1991 decision to protect the white shark. The first operations started around 1991-1992 at Seal Island, False Bay. Subsequently, the sector has extended to other areas of South Africa, with operations beginning in Gansbaai (1992) and Mosselbaai (1993). The industry has grown significantly and currently permits to attract white sharks have been allocated to twelve operators in South Africa (Mossel Bay (1), Dyer Island (8) and False Bay (3)).

Cage-diving is classified as a non-consumptive eco-tourism activity, enabling participants to actively attract and interact with white sharks (Fig. 1.3). Granting of this permit holds with it the responsibility to ensure that such practices are sustainable and cause minimal injury, disturbance and stress to the white sharks and its marine ecosystem. The cage-diving sector does, however, have a controversial reliance upon chumming and baiting to lure white sharks to the observation boats (Bruce 1995; York 1998). This potentially could have adverse effects on the white sharks and their interactions with co-existing fauna. Concerns have been expressed regarding possible changes in the distribution and localized concentrations of white sharks, changes in the feeding and behavioural ecology of white sharks, conditioning of white sharks to boats and divers (i.e. sharks forming an association between boats and food), loss of fear by white sharks to divers and boats (habituation), and injuries sustained by white sharks resulting from cage-diving operations.

Cage-diving is, however, a powerful conservation and educational tool for this much maligned species. Furthermore, cage-diving creates a non-consumptive economic value for white sharks, that further aids the protection status of white sharks in South Africa and elsewhere. At present most concerns are based on speculation and emotive arguments. However, the aforementioned potential threats that cage-diving holds for white sharks and the ecosystem do still require scientific evaluation.

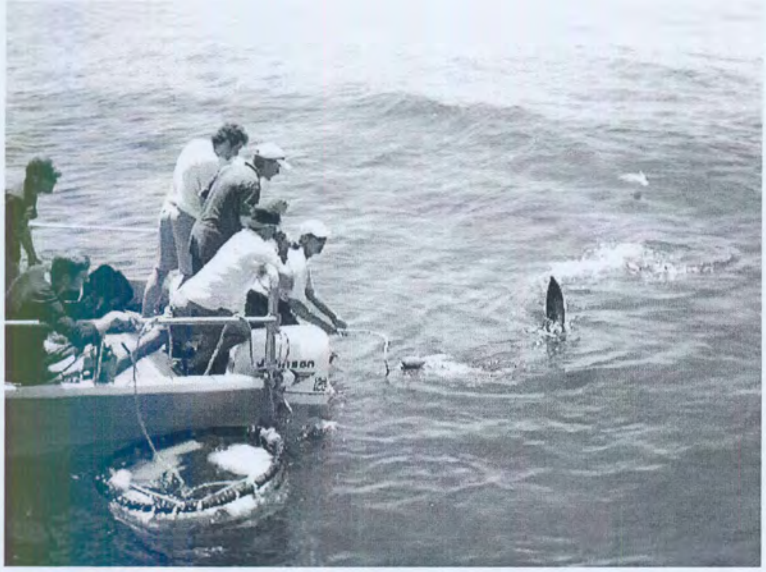

Figure 1.3 Example of white shark cage-diving. Shark handler (M. Rutzen) interacting with a white shark during a cage-diving tourism operation at Dyer Island, Gansbaai.

1.2 Ecological and biological knowledge of the white shark

Fortunately, in the last decade a rise in appreciation of white sharks has resulted in an increase in research into many aspects of its life history, such as its distribution and abundance, reproduction, feeding behaviour and sensory systems (Klimley & Ainley 1996a). Some aspects of the white shark's life history are summarized below.

1.2.1 Range and distribution globally and within South Africa

Like other laminid species, white sharks elevate their body temperature (including muscle, viscera, brain, eyes and stomach) above that of the ambient environment (Carey 1982; Tricas & McCosker 1984; Carey *et al.* 1985; Goldman *et al.* 1996). This adaptation enables them to inhabit and utilise the cooler waters of the temperate and sub-tropical zones of both the northern and southern hemispheres. They are most frequently observed and caught in inshore temperate continental waters of the Western North

Atlantic, Mediterranean Sea, Southern Africa, Southern Australia, New Zealand and the Eastern North Pacific (Compagno *et al.* 1997) (Fig. 1.4).

Southern Africa is identified as one of the centers of abundance for white sharks in the world, where their range extends from southern Angola to southern Mozambique (Compagno 1991), and are frequently encountered and observed within the south-western Cape region of South Africa (*pers. obs.*). White sharks congregate for certain periods of time within this broad geographical range; these areas are typically associated with the presence of seal rookeries, seabird islands and reefs or banks with abundant teleost and cartilaginous fish (Compagno *unpub. report*). Such examples within South Africa include; Dyer Island-Geyser Rock; Seal Island, False Bay, St Croix and Bird Island, Port Elizabeth; Seal Island, Mosselbaai; and Struisbaai (Compagno *unpub. report*).

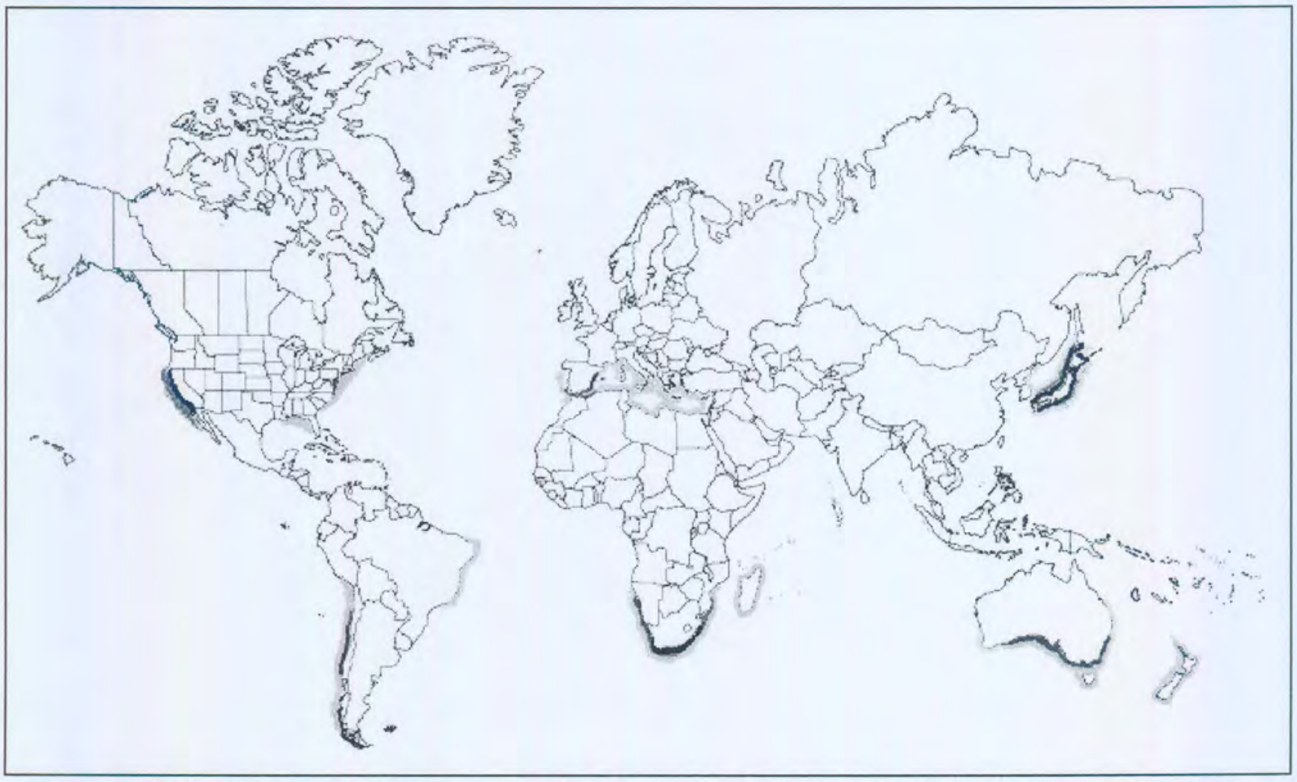

Figure 1.4 Worldwide distribution of the white shark (dark shading – centres of abundance, light shading – presence recorded). Information derived from reviews and accounts of white shark occurrence (Nakaya 1994; Bruce 1995; Fergusson 1996; Gadig & Rosa 1996; Compagno *et al.* 1997).

1.2.2 Movement patterns

Recent genetic analysis has indicated that continental populations of white sharks in the southern hemisphere are not genetically independent populations (Pardini *et al.* 2001). Sex specific movement patterns exist, with evidence that males migrate between Australia and South Africa, while females stay near their respective continental home ranges (Pardini *et al.* 2001). Recent evidence of long distance movements by white sharks (Block *et al.* 2002) between California and Hawaii further suggests that the white shark is a wide-ranging species. Within South Africa, tagged white sharks have been recorded moving large distances in short periods of time. For example, one shark tagged at Struis Bay, South Africa traveled 1409km before capture 527 days later in the NSB shark nets (Cliff *et al.* 1996b) and another tagged at Dyer Island traveled approximately 1475km before capture in the NSB shark nets only 84 days later (*unpub. data*).

1.2.3 Population status

During the 1996 workshop on the white shark, eight methods were presented to estimate white shark population sizes (Klimley & Ainley 1996; Cailliet 1996). The documentation of white sharks occurrence through records of incidental bycatch and targeted commercial fishing, was the simplest method (Klimley 1985; Casey & Pratt 1985; Fergusson 1996). However, this approach did not account for fishing effort, but only documented the spatial and temporal occurrence of white sharks. A more advanced, but lethal, method used in South Africa is based on catch per unit effort (CPUE) trends (Cliff *et al.* 1996a; 1996b). It used white shark catch trends in the bather protection shark netting program in Kwazulu-Natal to estimate the relative population size. Additionally, since 1989 tagging and releasing of white sharks found alive in the nets has allowed preliminary population estimates to be made based on mark-recapture technique (Cliff *et al.* 1996b). An alternative non-lethal mark-recapture techniques used was the tagging of free swimming white sharks with colour coded tags (Strong *et al.* 1996). Attempts in South Africa have highlighted a number of practical problems with this latter method, such as marine growth on tags, tag removal by humans and natural tag loss (Scholl 2002). A further mark-recapture method utilises the unique markings and shape of a white shark's dorsal and caudal fin to identify individuals (Scholl 2002). This method is proving to be successful, owing to its non-invasive nature, reliable identification accuracy and ability to generate large sample sizes (Scholl 2002).

Despite the many attempts, little information on long term trends of white shark numbers exists. The catch per unit effort (CPUE) of white sharks produced by the NSB bather protection program is the only long-term population status data set of white sharks within South Africa. Between 1973 and 1993 a significant decline in shark capture rate was recorded, the biological significance of which is uncertain (Cliff *et al.* 1996a). Within Australia a decline in catch rate has also been observed (Bruce 1995) prompting concern over the status of white sharks in Australian waters. This information generates cause for concern as these studies are the only indications of long-term population trends in the world.

1.2.4 Reproduction

White sharks are characterized by maturing late, having few and infrequent offspring, and relying on a high offspring survival rate to ensure sufficient recruitment into the population (Calliet *et al.* 1985; Bruce 1992; Uchida *et al.* 1996; Pratt 1996). The white sharks' uterine development is aplacental viviparous, with embryos being nourished by oophagy (i.e. developing embryos feed on the oocytes) (Uchida *et al.* 1996; Francis 1996). The female white shark only becomes reproductively mature at between 450cm and 500cm in length (Francis 1996) and the male at approximately 380cm (Pratt 1985; Pratt 1996), or as small as 350cm (Cliff *et al.* 1996a). Based on body length growth curves for Pacific white sharks whose age's had been estimated, age at maturity is estimated to be 12-15 years for females and 8-9 years for males (Cailliet *et al.* 1985). Females gives birth to only a few well-developed pups at a time (litter sizes between 4 - 8) (Uchida *et al.* 1996), and it is suspected that the gestation period of the white shark is upwards of a year, with a suggested reproductive periodicity of between two and three years (Camhi *et al.* 1998).

1.2.5 Sensory abilities

White sharks utilise a number of senses including hearing, water movement detection, touch, taste, sight, smell, and electrosense (the detection of electrical fields). Demski & Northcutt (1996) studied the brain and cranial nerves of the white shark and concluded that all major sensory systems involved with shark prey detection are well represented. However, from a comparative standpoint between senses, only their olfaction and vision seemed to be exceptional (Demski & Northcutt 1996).

The olfactory sensitivity of sharks to chemicals is attested through many examples: injured survivors of boating accidents being circled or attacked by sharks; the loss of freshly shot fish of a spear fisherman to a shark and the use of chum by fishermen or cage-diving operators to lure sharks close to boats. The white shark has the largest relative olfactory bulb size among cartilaginous fishes studied (Demski & Northcutt 1996), suggesting that chemical stimuli may be important in guiding feeding, sexual, social and perhaps other types of behaviour.

Vision in the white shark appears to be geared towards daylight feeding. The ratio of cone receptors to rod receptors is high indicating well-developed daytime vision (Gruber & Cohen 1985). The large size of the eyes and extraocular muscles further suggests well-developed vision, while the presence of an orbital vascular rete used to increase the temperature of the eyes and brain may allow for faster, more efficient processing of visual information (Demski & Northcutt 1996).

1.2.6 Prey preference

Stomach contents analysis, observation of wounds on surviving prey animals and live white shark attacks have been used to determine the primary prey and the prey diversity of the white shark. Primary prey includes pinnipeds and cetaceans, teleost fish, elasmobranchs and cephalopods (Le Boeuf *et al.* 1982; Bruce 1992; Cliff *et al.* 1989,1996a; Long *et al.* 1996).

Predation by white sharks has been spectacularly observed on a number of pinniped species, including the Monk seal *Monachus schauinslandi* (Alcorn & Kam 1986), the Northern elephant seal *Mirounga angustirostris,* Californian sea lion *Zalophus californianus*, Steller sea lion *Eumetopias jubatus* (Ainley 1981; 1985; Le Boeuf *et al.* 1982; Klimley *et al.* 1992), the harbour seal *Phoca vitulina* (Long *et al.* 1996), and the Cape fur seal *Arctocephalus pusillus pusillus* (Stewardson 1999).

Occasional species reported to have been bitten or consumed include the African penguin *Spheniscus demersus* (Bass *et al.* 1975; Randell *et al.* 1988), sea otters *Enhydra lutris* (Ames & Morejohn 1980; Ames *et al.* 1996), logger head *Caretta caretta* and leatherback *Dermochelys coriacea* sea turtles (Long 1996) and humans (Burgess & Callahan 1996). Furthermore, a number of inanimate objects have displayed bite marks inflicted by white sharks including crab traps, inflatable boats, small boats, float bags and many more (Collier *et al.* 1996; Anderson *et al.* 1996a). Such studies suggest that white sharks are fairly opportunistic and consume or investigate a wide variety of prey types and objects.

1.2.7 Hunting behaviour

Spatial and temporal patterns of live shark attacks have been extensively studied at the Farallon Islands, California, since 1969 (Ainley 1981; Klimely *et al.* 1992; Klimely *et al.* 1996; Anderson *et al.* 1996b; Pyle 1996). These studies have provided unprecedented information on the nature of white shark attacks on pinnipeds in this area. In particular, seasonal trends were apparent with a clear peak in attack rate between September and November (Ainley *et al.* 1981 1985; Klimely *et al.* 1992). Spatial hotspots were also described, with 81 percent of attacks (N = 146) occurring between 25m and 449m from the island shore (Klimley *et al.* 1992). A significant correlation existed between elevated up-welling on the previous day (affecting water visibility) and high occurrence of predatory encounters (Pyle *et al.* 1996). This suggests that optimum environmental conditions (i.e. murky, eutrophic water), which enhance the ability of white sharks to camouflage themselves, could be linked with a successful attack on a pinniped. Tidal characteristics (Anderson *et al.* 1996b) were also important, with a high number of attacks observed during the periods of high tide. Tidal height was thought to influence spatial competition between pinnipeds inhabiting the island, and resulted in a higher proportion of the pinnipeds entering the water to become potential victims. Following these studies a number of hypotheses on the nature of white shark attacks and feeding behaviour were proposed and are discussed below.

(a) Bite, Spit and Wait hypothesis. The tendency of white sharks to release humans following the initial attack, and the frequent occurrence of pinnipeds sporting a single shark bite wound, lead to the '*bite, spit, and wait*' attack hypothesis (McCosker 1985). Following the initial strike white sharks were presumed to release their intended prey and wait for them to bleed to death. This minimised the possibility of sustaining injuries from the resisting prey. However, live predation events at the Farallon Islands showed that in 94% and 91% of attacks on phocids (true seals) and otariids (sea lions and fur seals) respectively, tissue was removed from the victim during the initial strike (Klimely *et al.*1996).

(b) Mistaken identity: Stemming from human-shark confrontations, the '*mistaken identity*' hypothesis attempts to explain why white sharks sometimes attack swimmers and surfers. From below the water a surfer or swimmer may resemble the shape of a pinniped (McCosker 1985). Thus an attack from a white shark may have resulted from it mistaking the silhouette of a human with that of a seal. This hypothesis helped explain why white sharks do not often return to feed on a surfer or swimmer following the initial

strike (Klimley 1994). In a case of mistaken identity one might expect the shark to discontinue the attack on the basis that it was not the sharks intended prey, and possibly unpalatable.

(c) Below and behind: Much speculation exists as to how white sharks orientate themselves towards their prey in order to maximize successful attacks. The '*below and behind*' hypothesis was based upon the speculative advantages of attacking from below and behind rather than rushing along the surface (Strong 1996). These advantages included:

- Increased camouflage from lack of light at greater depth, thus reducing the distance at which the shark will be detected,
- Cut off a number of escape routes for the prey,
- Making use of the natural dark dorsal colouration to further minimize the detection distance.

This behaviour is strongly suspected, but difficult to prove due to the difficulty of observing attacks prior to the initial strike. Strong (1996) attempted to test this hypothesis using seal cut-outs, but failed to show a preference of vertical attacks on stationary decoys. Recent documentation of white sharks breaching on towed lures does give some credence to this hypothesis, as white sharks appear to stay low in the water column before rushing the decoy at a vertical, or near vertical, orientation.

(d) Investigatory vs. attacking: Tactile identification of objects by white sharks is achieved by mouthing, and a number of supposedly predatory encounters could be driven by non-feeding related curiosity or determining the suitability of unknown potential prey types as food (Collier *et al.* 1996). This hypothesis could help explain the multitude of items bitten that hold no resemblance to recognised prey items.

(e) Rejection and acceptance of prey: This hypothesis offers a further explanation to the unusual diversity of objects being bitten by white sharks. It suggests that prey identification and suitability is

determined following the initial strike, wherein the shark determines the 'worthiness' of the potential food item. Experimentation using fat free sheep versus blubber rich seals revealed that consumption of a sheep would not occur following an initial bite (Klimley 1994). This suggests that white sharks may initially investigate objects to ascertain their calorific value (i.e. fat content) and suitability as a prey item. Only following an initial bite would the decision to continue to feed be made.

(f) Play hypothesis: The African penguin is commonly attacked by white sharks in South Africa (Randall *et al.* 1988). In 1985 and 1986 white sharks were possibly responsible for a number (N = 70) of predatory related injuries accrued by the penguins at Bird Island (N = 55) and Saint Croix Island (N = 15), Agola Bay. However, to date only a single African penguin has been discovered within a white sharks stomach (Bass *et al.* 1975). The conflicting results could imply that white sharks are intentionally hunting these penguins as a form of play, rather than for feeding purposes.

1.3 Required research areas

South Africa's waters are one of the centers of abundance of white sharks in the world (Compagno *et al.* 1997). Despite local protection, the white sharks still face a number of threats (Compagno *et al.* 1997). It is speculated that incidental and targeted catch of this species could at most be unsustainable, and at least, retard the recovery of this population following past fishing. White shark cage diving represents an economically viable non-consumptive alternative for the utilisation of this species. For this reason, and the educational potential it holds, cage diving represents a potentially powerful conservation tool. Despite the positive aspects of this ecotourism initiative, interacting with a vulnerable and protected species, that is potentially dangerous to humans, holds with it the responsibility to ensure minimal impact on the white shark and surrounding ecosystem (Compagno *et al.* 1997; Bruce 1995).

Minimising the impacts of both the consumptive and non-consumptive exploitation of white sharks is essential to manage this species sustainably in South Africa. It was highlighted during the 1996 workshop on white sharks (see Klimley & Ainley 1996a) that almost all investigations on white sharks at that stage were qualitative and based on inductive science or anecdotal accounts, with only a few limited attempts to manipulatively test hypotheses (Klimley & Ainley 1996b). Furthermore, the lack of knowledge regarding the white shark's population structure, its relative abundance and its spatial and temporal distribution throughout its range was highlighted as being some of the major factors limiting the further advance in the study of this species (Cailliet 1996).

The first step of successfully managing and conserving a species is to have a good idea of its basic biology and ecology, including aspects such as its habitat utilisation, population status, life history, and its feeding strategies. It is thus vital that a more comprehensive understanding of the white shark's life history must be established.

1.4 Research objectives

This study aims to address a number of gaps in our knowledge of the white shark and its interspecific relationships with prey species within South Africa. The chapters of this thesis were prepared as separate papers, and this has led to a certain amount of repetition between them. Each chapter has individual objectives and key questions, however, the overall objectives of this work are to:

- Describe the spatial and temporal patterns of occurrence and activity of the white shark at Dyer Island and surrounding locations.
- Investigate the complexities in the population structure of the white sharks frequenting the Dyer Island area.
- Investigate the predatory behaviour of the white shark using manipulative experiments.

- Investigate the magnitude and nature of behavioural and predatory interactions between the white shark and its Cape fur seal, African penguin and other seabird prey at Dyer Island, and
- Determine what, if any, impacts cage diving has on the aforementioned behavioural characteristics of the white shark at Dyer Island.

CHAPTER 2

Trends in habitat utilisation of the white shark (*Carcharodon carcharias*) within the Dyer Island area.

2.1 Introduction

The white shark is a wide-ranging, yet rare, macro predator. They are most frequently observed and caught in inshore temperate continental waters of the Western North Atlantic, Mediterranean Sea, Southern Africa, Southern Australia, New Zealand and the Eastern North Pacific (Compagno *et al.* 1997). Southern Africa waters is identified as one of the centers of abundance for white sharks in the world, where they range from southern Angola to southern Mozambique and occur along the entire coast of South Africa (Compagno 1997, *unpub. report*). Infrequent records have also placed white sharks north of Mozambique in areas such as Mauritius, Zanzibar, Madagascar, and Kenya (Cliff *et al.* 2000). Despite the importance of South Africa's waters to the white sharks' global population, little is known about their spatial and temporal patterns of habitat utilisation, distribution and movements within South Africa's waters (Compagno 1991). Furthermore, limited information is available on their basic population structure and how each sex and different size classes utilise their environment. This lack of basic knowledge impedes the effectiveness of management efforts aiming to sustainably utilise South Africa's white shark population.

2.1.1 Threats

Like many shark species, the white shark displays a K-selected life history, which is characterised by slow growth, late maturity, few offspring and long intervals between parturition (Pratt & Casey 1990; Uchida *et al.* 1996; Francis 1996). This reproductive strategy results in the white shark's inherent low resistance and resilience to targeted or accidental consumptive fishing (Walker 1998). Despite regional protection within South African waters (Compagno 1991), the white shark still faces a number of fishing threats, such as incidental bycatch (Compagno 1997; Camhi *et al.* 1998; Bruce

1995), illegal poaching (*pers. obs.*), and permitted targeted fishing in the bather protection nets set along the KwaZulu Natal coastline (Cliff *et al.* 1989; 1996a; 1996b). (See chapter 1 for more detail). The extent of incidental fishing and targeted poaching of white sharks in South Africa is largely unknown (Compagno 1991), however, incidental catches of white sharks worldwide are believed to be their most significant threat (Bruce 1995; Camhi *et al.* 1998). Some long-term data also suggests decline in local white shark populations within South Africa (Cliff *et al.* 1996a) and in other countries (Bruce 1995).

2.1.2 Habitat utilisation

Within the white sharks' broad geographical range there appears to be areas where they congregate for certain periods of time. These are typically associated with the presence of seal rookeries, seabird islands and reefs or banks with abundant teleost and cartilaginous fish (Compagno *unpub report*). Such examples within South Africa include; Dyer Island-Geyser Rock group; Seal Island, False Bay; St Croix and Bird Island, Port Elizabeth; Seal Island, Mosselbaai; and Struisbaai. Knowledge of how white sharks space themselves throughout South Africa's waters is often anecdotal, yet information on the general life history of the white shark allows for some discussion.

2.1.3 Effects of pinnipeds on distribution

Directed observations of South Africa's white shark population via active chumming have generally been restricted to areas adjacent, or close, to offshore pinniped colonies, such as Dyer Island, Seal Island (False Bay) and Seal Island (Mossel Bay). This is primarily due to frequent observations of white shark attacks on pinnipeds at such islands worldwide (Ainley *et al.* 1981; Klimley *et al.* 1992). Within such areas, site specific trends in distribution and occurrence have been reported, such as seasonal trends in occurrence (J. Smit; R. Portway; C. Fallows *pers. comm.*), dial variation in observation rate (A. Hartman *pers. comm.*), and changes in the white shark population structure (M.C. Scholl; B. Macfarlane *pers. comm.*). Cage diving operators working in South Africa are the basis of all these observational reports. This suggests that factors, in addition to prey availability in the form of pinnipeds, influence their spatial distribution.

Observations of sharks fitted with colour coded streamer tags and acoustic transmitters in South Africa suggest some orientated movement between pinniped rookeries (DEAT & University of Pretoria *unpub. data*), however, white sharks do not exclusively concentrate within such areas. Pinnipeds are not the primary prey for many white sharks, particularly smaller sharks that most frequently feed on teleosts and other elasmobranchs (Cliff *et al.* 1989; Bruce 1992). Spear fishermen and divers frequently observe white sharks in areas devoid of seal islands such as Struisbaai and Cape Aguluas (A. Hartman *pers. comm.*), while bather protection nets in KwaZulu Natal catch on average 39 white sharks per annum (Cliff *et al.* 1996a). The most southern of these nets (Mzamba) is set more than 500km northwards from the nearest Cape fur seal colony at Black rock Island, Algoa bay.

2.1.4 Reproductive influences on distribution

Many teleost and chondricthyan fish display spatial and temporal patterns of distribution that are related to life history strategies such as breeding (Camhi *et al.* 1998). A number of elasmobranch species are known to utilise inshore sheltered waters and estuaries for birthing where protection from predators exists and neonate and embryonic survival is higher (Castro 1993; Simpfendorfer & Milward 1993). Some evidence suggests that globally white sharks also mate and birth in coastal waters during the spring-summer (Uchida *et al.* 1996; Pratt 1996). Observations of near parturition pregnant females are generally restricted to the summer period in both the Northern (Pratt 1996; Uchida *et al.* 1996) and Southern hemispheres (Francis 1996). Furthermore, the capture of most neonate white sharks is in the summer period (Klimely 1985; Francis 1996), while the single account of mating that has been reported occurred close to shore in New Zealand, and was probably observed during November (early summer) 1991 (Francis 1996). Based on this evidence, congregating for reproductive purposes may therefore have a strong influence on the spatial distribution of white sharks in the spring and summer periods in South Africa.

2.1.5 Social aggregations

Anecdotal reports of con-specific bite marks on non-mature white sharks suggest that social interactions do occur at a level other than reproduction (Bruce 1992). Furthermore, sex segregation has been observed on a small spatial scale in South Australia (Strong *et al.* 1992) and may be related to social reasons apart from reproduction, as the phenomenon was observed in sharks as small as 220cm total length (TL) (Strong *et al.* 1992). Further evidence of social grouping was discovered during routine aerial surveys in South Africa, during which observations of small aggregations of white sharks circling each other, but not displaying any kinds of behaviour that would resemble mating or feeding, were observed (G. Todd *pers. comm.*). White sharks may at times form loose social aggregations in South Africa independent from either feeding or reproduction.

2.1.6 Effect of the local environmental on distribution

A majority of the neonate and juvenile white sharks that are observed or captured throughout the world, are located in the warmer waters of this species' range (Casey & Pratt 1985; Klimley 1985; Fergusson 1996). Alternatively, larger individuals are generally observed in the cooler geographic areas were pinnipeds are sometimes more abundant (Klimley 1994). Along the coast of California, the white sharks display large-scale segregation with respect to size. Neonates are born along the southern coast and migrate northwards as they grow and begin to seek out the northerly pinnipeds colonies (Klimley 1994). Sexually mature sharks may temporally migrate south for parturition (Klimley 1994). This differential utilisation of the coastline may be indicative of size specific physiological tolerances within the white sharks' range. Like other laminid species, white sharks elevate their body temperature (including muscle, viscera, brain, eyes and stomach) above that of ambient (Carey 1982; Tricas & McCosker 1984; Carey *et al.* 1985; Goldman 1997). This appears to be an adaptation to exploit the cooler waters of the temperate zones while maintaining their place as an effective and aggressive hunter of swift moving teleost, elasmobranch and pinniped prey (Goldman 1997). Smaller white sharks have a higher surface area to volume ratio, suggesting that they will have more difficulty maintaining this optimal body temperature in colder waters due to comparatively greater heat loss through convection and conduction (Goldman *et al.* 1996). No such trend has as yet been documented in South Africa with regard to large-scale spatial separation of size classes.

2.1.7 Aims

The aims of this chapter are to accrue information on the habitat utilisation and population composition of the white shark in the greater Dyer Island area.

The specific objectives are to determine if:

- Occurrence of white sharks within the study area is independent of season,
- Habitat utilisation is random throughout the study area,
- Distribution of the white shark is independent of sex and size,

2.2 Methods

2.2.1 Study site

The Dyer Island group (34°41'S 19°25'E) lies off the South Western Cape, South Africa. The Dyer Island group consists of two islands. Dyer Island is the largest with a surface area of 20ha, and is home to over 15 species of breeding seabirds (Appendix 1). Geyser Rock is the smaller island, and lies 230m southwest of Dyer Island, and is a host to an estimated 55,000 Cape fur seal *Arctocephalus pusillus pusillus* (J.M. David *pers. comm.*). The study area (Dyer Island region) included the Dyer Island group and extended to the inshore areas (Jobert se Dam, Holbaai and Geelbek Gat) adjacent to the mainland, which lies between 3km and 9km to the northeast (Fig. 2.1). The closest access point for boats from the land is at Kleinbaai, 9 km from the island. Danger Point Lighthouse is in a north-westerly direction from the island, approximately 13 km distant (Fig. 2.1).

The waters of the Dyer Island region are characterised by a high abundance of white sharks (Chapter 2). Other fauna includes numerous pelagic fish such as geelbek (*Atractoscion aequidens)*, yellow tail

(*Seriola lalandi*) as well as reef fish such as hottentot (*Pachymetopon* spp.) and galjoen (*Coracinus capensis*). Dense kelp beds extend out from Dyer Island to the numerous reefs around the island. The water is typically between 8 – 15 m in depth and the abundance of reefs results in a number of breakers, swells and areas of highly aerated water.

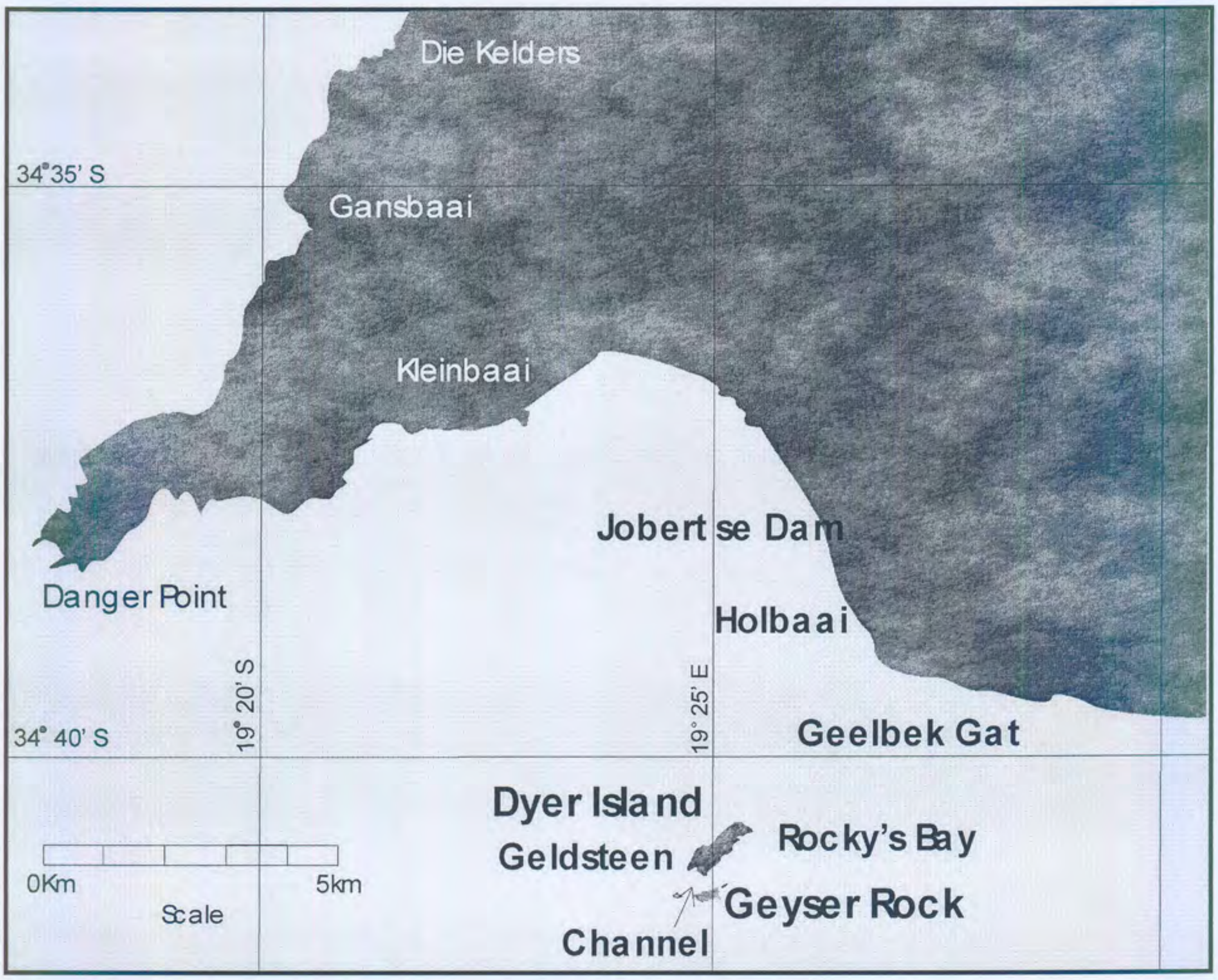

Figure 2.1 Map of greater Dyer Island region, showing the three specific locations defined in study, the inshore area (incl. Jobert se Dam, Holbaai and Geelbak Gat) and the Islands peripheries (incl. Rocky's Bay, and Geldsteen) and the channel area (incl. Channel).

2.2.2 Experimental procedure

The study extended from August 1999 to January 2001. During this time two research vessels worked simultaneously within the Dyer Island region. White sharks were attracted independently to each vessel anchored at strategic locations within the study area. To investigate possible trends in white shark's spatial habitat utilisation three areas were identified within the study area. These included anchor locations around within the channel area (Channel), anchor locations at the island's peripheries (Rocky's Bay, Geldsteen, and West of Channel) and inshore locations (Holbaai, Jobert se Dam and Geelbek Gat) (Fig. 2.1). Throughout the study we attempted to get equal coverage of all areas. The inshore location was identified early spring 2000 allowing only limited information to be obtained from this area. Sharks were attracted for four to six hour periods from between 08h00 and 17h00. Operation times did, however, vary due to the unpredictable nature of the local weather. Furthermore, one vessel was operating as a commercial cage-diving vessel and at times it had to accommodate the welfare and wishes of tourists.

Sharks were attracted to the research vessels by creating an odour corridor (chum slick), that consisted of oil released from shark liver, sardines, fish guts or a combination thereof. The chum was submerged from the stern of a research vessel and the oil contained within seeped out creating the slick. To ensure that the slick was maintained at a constant level, the chum bag(s) were occasionally squeezed to increase the release of oil. On occasions when shark liver was not available alternative chum including sardines, fish oil and fish guts were used. The latter were generally ladled into the water.

2.2.3 Shark observations

On arrival at a vessel, sharks were enticed to stay by the presence of bait, foam rubber decoys or a combination thereof. The size (to the nearest half metre) and sex of the shark were recorded, based on the presence or absence of claspers in the cloaca region. A combination of photographs, video recordings and sketches were taken of white sharks to identify individuals. Size, sex, colouration patterns, body scars/marks and the dorsal fin shapes were used as identifying characters.

2.2.4 Data analysis

The frequency of shark sightings at the chumming vessels was calculated to determine the localised abundance (sighting rate per hour) of white sharks. Due to frequently observing no sharks during a chumming period the data set was not normally distributed (left skew), the Kruskal-Wallis test was therefore used to analyses patterns in sighting rate. The statistical test was preformed using the software packages Statistica and Sigma Stat. The means and standard error calculated and graphically displayed. Due to small sample size, data gathered from the 'channel area' and 'island peripheries' was combined (Dyer Island group) for the size and sex analysis. Sex and size specific data was analysed using goodness of fit techniques based upon relevant contingency tables and the chi-squared test. When only two dependant categories were present the Yates correction for continuity was applied.

2.3 Results

Between November 1999 and January 2001, 476 chumming periods were completed in the Dyer Island region. These trips constituted 1875 hours of observation effort and a total of 1144 white shark sightings were recorded.

2.3.1 Spatiotemporal patterns in abundance

White sharks were observed throughout the entire year, but significant seasonal differences existed in the rate of sharks observed within the Dyer Island region ($H_{(11,N=474)} = 104.52$, $P < 0.01$) with white sharks observed less frequently from November to February (Fig. 2.2a). White sharks utilised the waters of the Dyer Island group on a seasonal basis both at the island periphery ($H_{(119,N=286)} = 87.77$, $P < 0.001$) (Fig. 2.2b), and within the channel directly adjacent to the seal colony ($H_{(11,N=113)} = 33.840$, $P < 0.001$) (Fig. 2.2c). At the island periphery white sharks occurred most frequently during winter and autumn and became less abundant during the spring and summer months from October to February (Fig. 2.2b). This seasonal pattern was, however, not so clear cut within the channel and probably results from a small sample size during some months (Fig. 2.2c). At the inshore locations white sharks were comparatively abundant during the spring and summer periods from October to January (Fig. 2.2d). On the very few occasions of inshore chumming during the autumn (April and May) no sharks were observed, which contributed to the significant seasonal trend in observation rate ($H_{(7,\ N=75)} = 23.56$, $P < 0.01$) (Fig. 2.2d). Preliminary analysis of data collected in successive years (2001-2003 data not presented) suggests a continued high abundance of white sharks inshore from October to January.

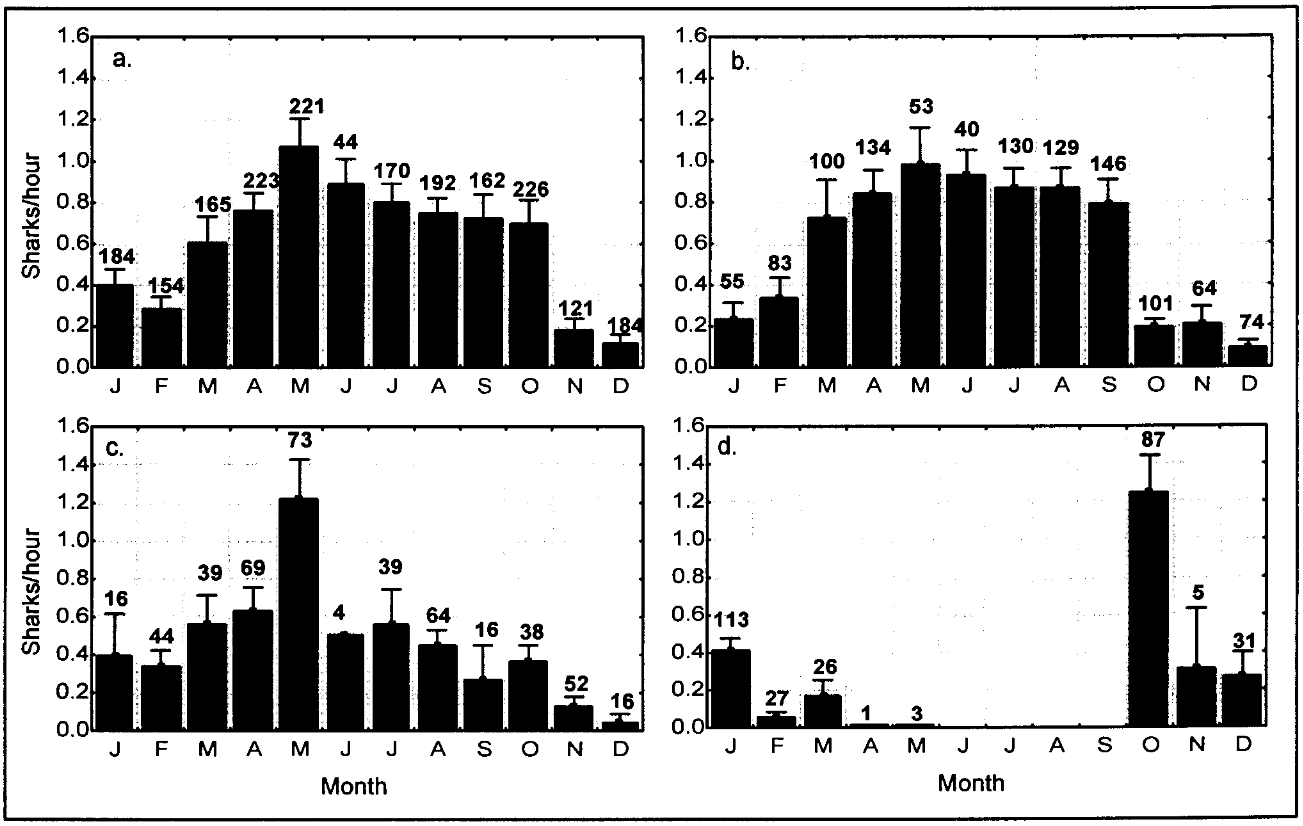

Figure 2.2. Seasonal occurrence of sharks at Dyer Island region from the period November 1999 to January 2001. Figures: 2.2a – Dyer Island region, 2.2b – Dyer Island periphery (Rocky's Bay, Geldsteen), 2.2c – Channel area (adjacent to Geyser Rock), 2.2d – Inshore areas (Holbaai, Jobert se Dam and Geelbak Gat). Data labels represent effort (hours chumming).

2.3.2 Spatiotemporal trends in sex ratios

Some 45.7 percent (N = 519) of the white sharks observed were successfully sexed. Most (70.3 percent, N = 365) of the 519 sharks sexed in the Dyer Island region were female, introducing a statistically significant bias (Yates correction for continuity applied, $\chi^2_{(1,519)} = 84.97$, $P < 0.01$) (Fig. 2.3a).

A total of 185 sharks were successfully sexed in the Dyer Island region (79.5%, N = 147, female and 20.5%, N = 38, male) between October and May (period when sharks were observed in all areas of Dyer Island region). Only two male sharks were observed inshore during this period (Fig. 2.3b), although a number of males (N = 36) were observed at the Dyer Island group during this spring/summer period (Fig. 2.3c). Females appeared equally distributed inshore (N = 86) and at the Dyer Island group (N = 61). The absence of males inshore caused a significant non-random distribution of the sexes within the Dyer Island region (Yates correction for continuity applied, $\chi^2_{(1,185)} = 33.98$, $P < 0.01$) (Fig. 2.3b,c).

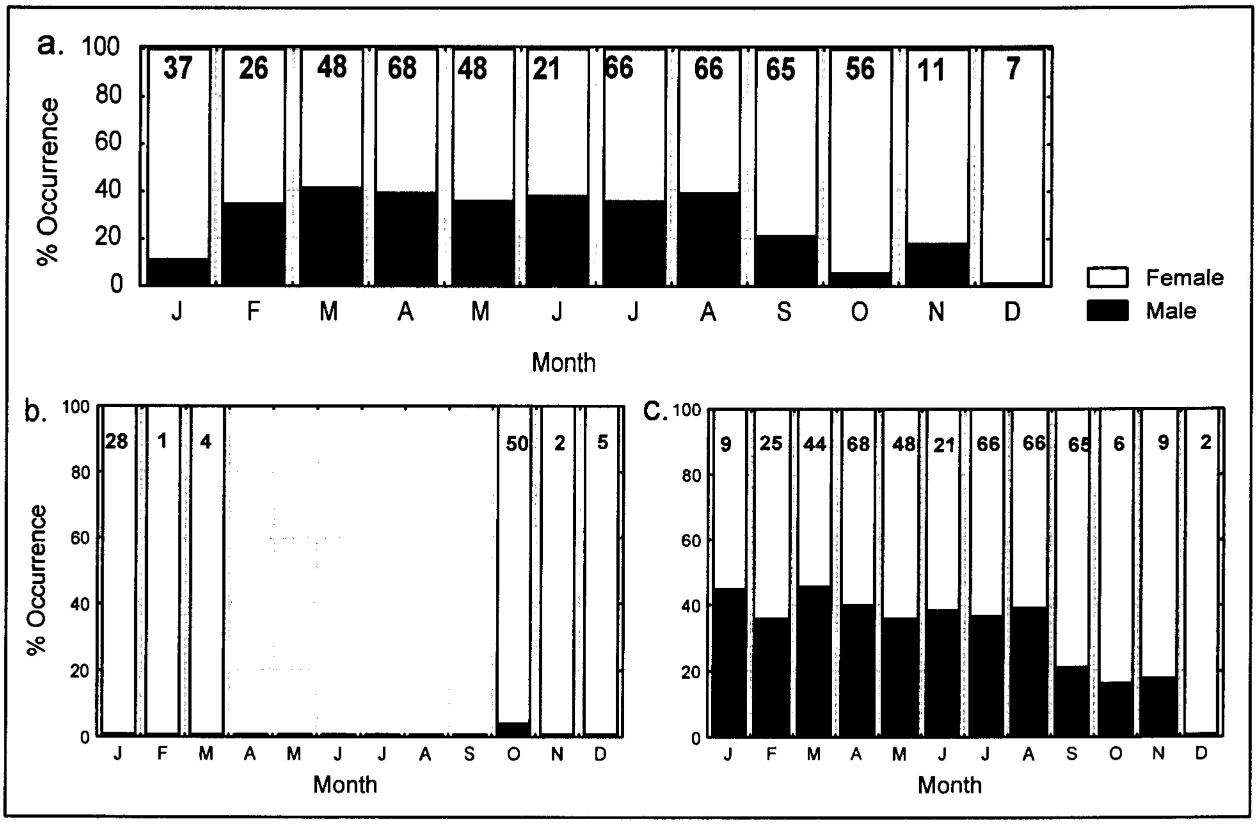

Figure 2.3 Seasonal sex ratio composition of sharks observed within the Dyer Island region. Figures: 2.3a – Locations combined, 2.3b – Inshore locations only, 2.3c – Dyer Island locations only. Data labels represent number of sharks observed.

2.3.3 Sex specific size composition

A linear relationship existed between shark length (N = 510, both shark TL and sex recorded) and sexing success, with fewer smaller sharks being successfully sexed than larger sharks ($\chi^2_{(1,510)}$ = 15.09, $P < 0.05$) (Fig. 2.4). The mean TL for males (338.0 cm) was smaller than for females (353.6 cm), which reflected in a significantly different TL distribution ($\chi^2_{(7,510)}$ = 19.06, $P < 0.001$). This appeared due to comparably few male sharks estimated at over 375 cm TL (16.7% of males and 32.5% of females) (Fig. 2.5).

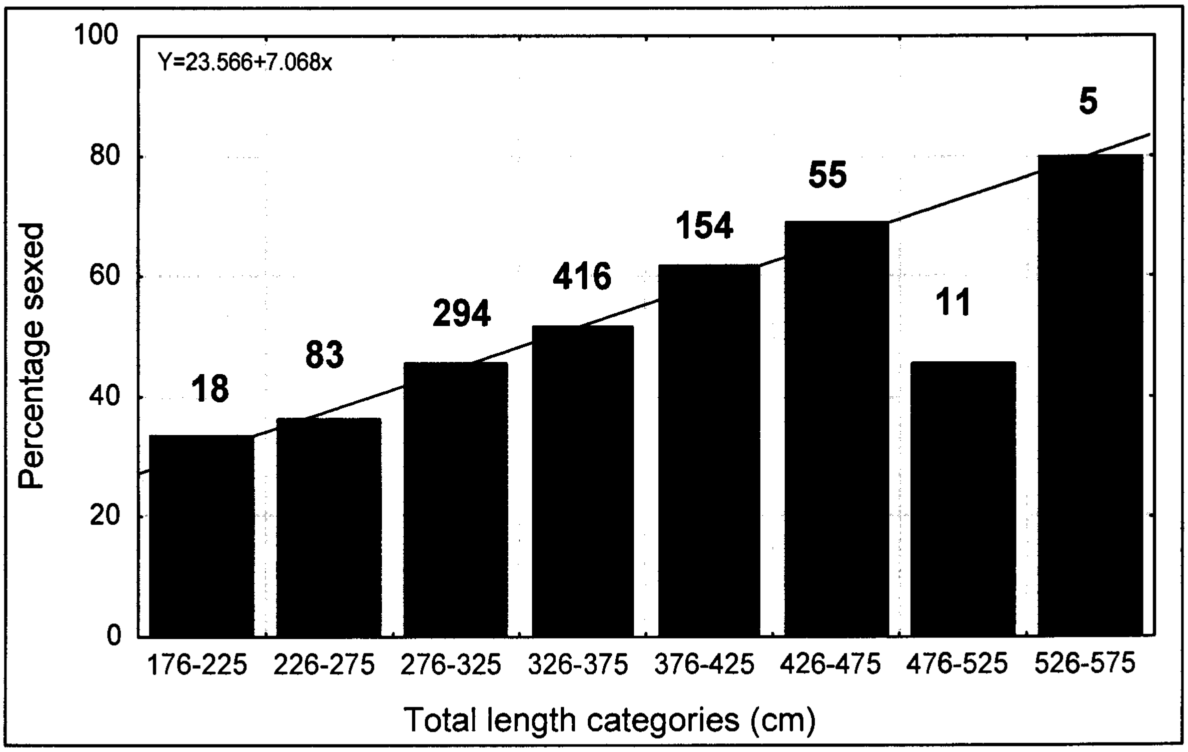

Figure 2.4 Success rate of sexing white sharks of various size groupings observed throughout the study. Data labels represent sample size of each size category. Data labels represent number of sharks.

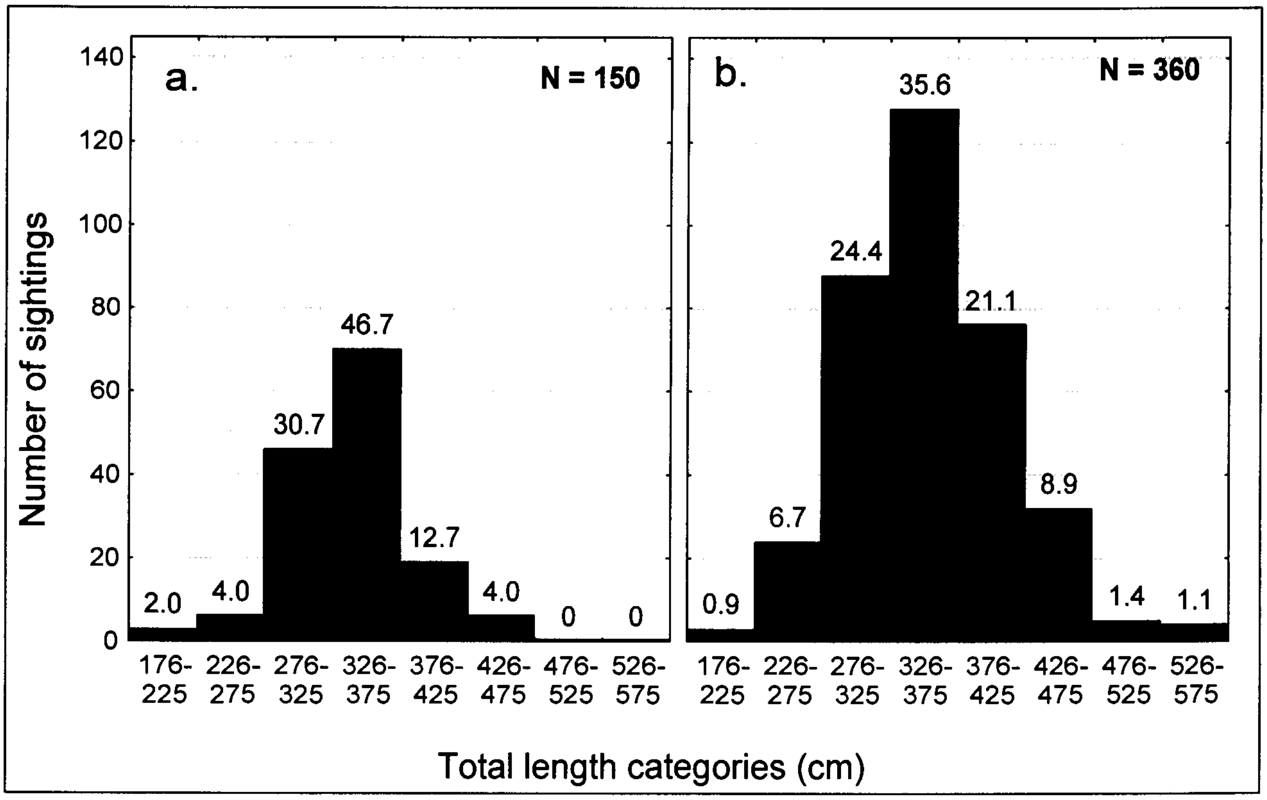

Figure 2.5. Sex specific size composition of white sharks observed. Figures 2.5a - Male white sharks, 2.5b - Female white sharks. Data labels represent percentage of sample.

2.3.4 Spatial trends in size composition

A total of 1036 of the 1144 (90.5%) sharks recorded were successfully sized (TL) during this experiment. The modal size class of these sharks was 326-375cm (40.2%), while the mean TL was 336 cm (N = 1036). Some 16 sharks were estimated to have a TL over 475 cm (assumed sexual maturity for females, Fig. 2.6), nine were female and the remaining seven unidentified. These nine sharks constituted 2.5 percent of the female sharks with TL estimates (N = 360). Discrete concentrations of assumed mature female sharks occurred inshore during October and January, while at Dyer Island sporadic sightings were recorded during the winter period (Fig. 2.7). A number (N = 225, 21.7%) of sharks were estimated at a > 376 cm TL (assumed sexual maturity for males, Fig 2.6), of which 25 were identified as male, the remainders were either non-sexed (N = 83) or female (N = 117). These 25 sharks constituted 16.7 percent of the male sharks with TL estimates (N = 150). Mature males were observed exclusively at Dyer Island throughout the study, while the most frequent time of sighting was in winter from April to September (92%, N = 24) (Fig. 2.7).

The mean TL of white sharks in the inshore area (364 cm) was greater than the mean TL observed at the Dyer Island group (336 cm), with some 33.4% (N = 161) sharks observed inshore > 375cm TL, versus only 19.5% (N = 875) observed at Dyer Island (Fig. 2.8). Throughout the study, sharks observed inshore were significantly larger than those occurring at the Dyer Island group (Channel and Island periphery locations) ($\chi^2_{(7,1036)} = 38.63$, $P < 0.001$) (Fig. 2.8).

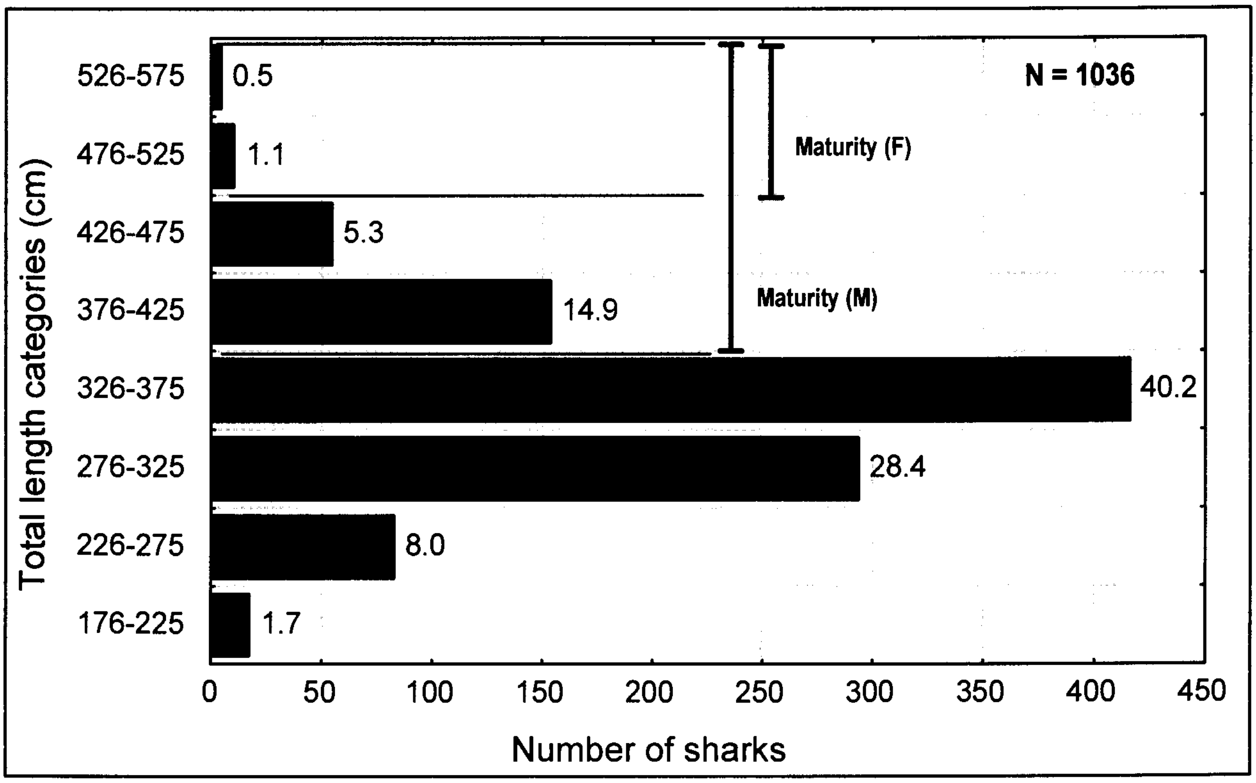

Figure 2.6. Size composition of the white shark population. Data labels represent percentage of sample. Total length groupings for assumed sexual maturity are shown.

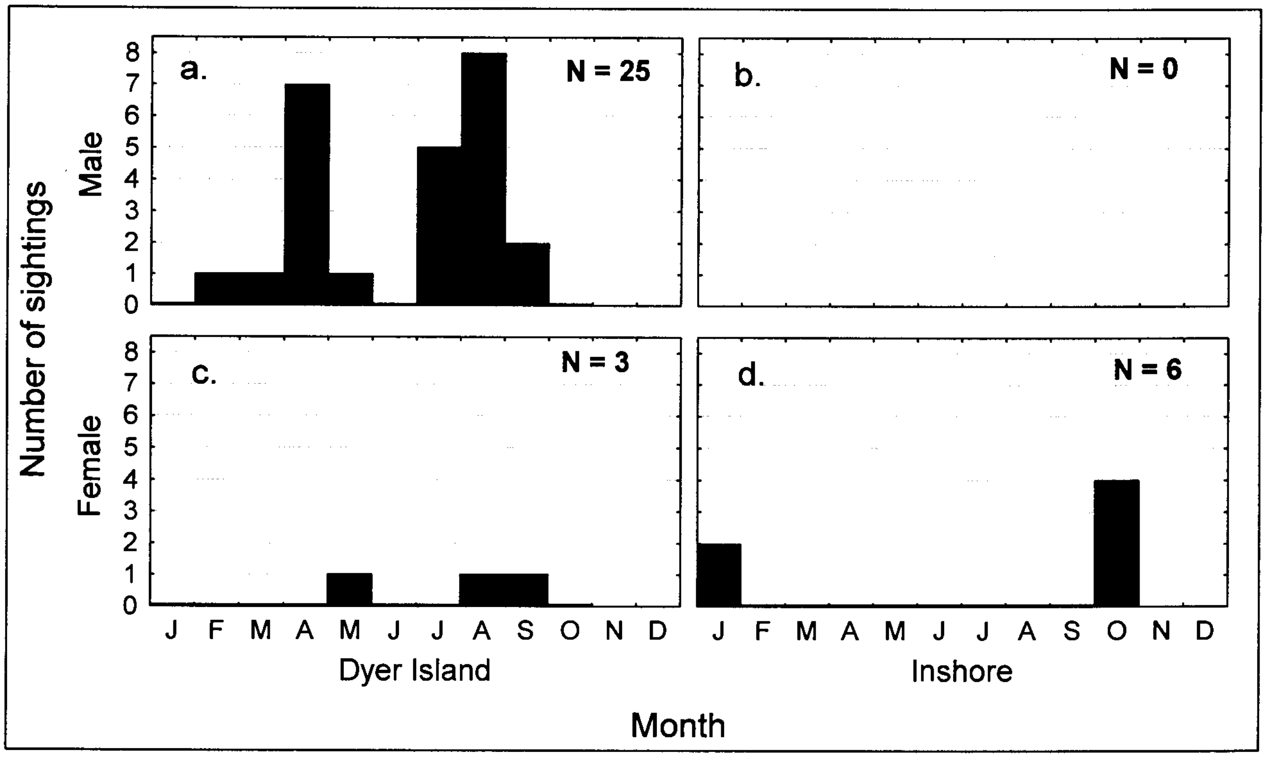

Figure 2.7 The spatiotemporal patterns of occurrence of sexually mature male and female white sharks. Figures: 2.7a – Males at Dyer Island group, 2.7b – Males inshore, 2.7c – Females at Dyer Island group, 2.7d – Females inshore.

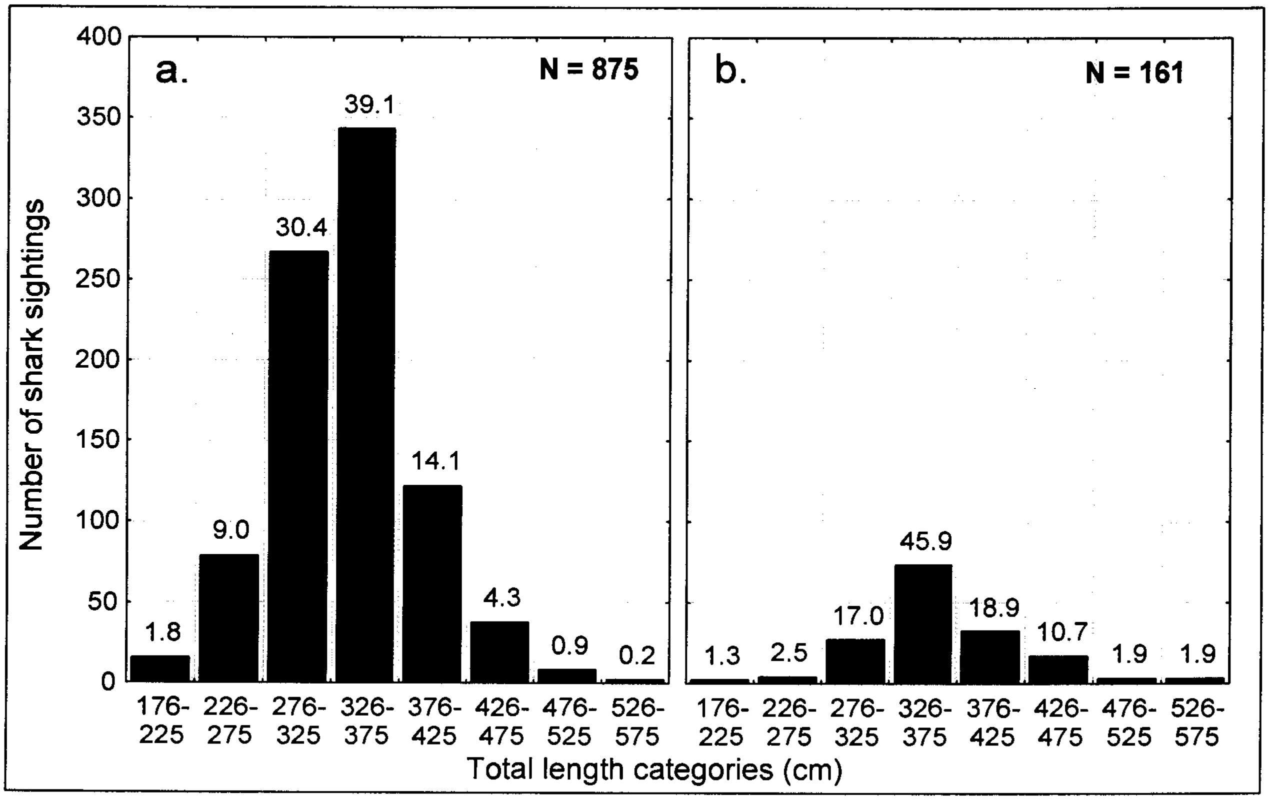

Figure 2.8. Site-specific total length ranges of white sharks observed within Dyer Island region. 2.8a – Dyer Island group, 2.8b – Inshore area. Data labels represent percentage of sample.

2.3.5 Seasonal trends in size composition

The TL of white sharks differed slightly throughout the year (Fig. 2.9a) as a result of the influx of large sharks during October and January and the large number of smaller (226 - 325cm TL) sharks in February (12 x 8 contingency table, $\chi^2_{(77,1036)} = 118.9$, $P < 0.01$). Over the six months that sharks were observed inshore there was no significant change in their TL (6 x 8 contingency table, $\chi^2_{(40,161)} = 36.06$, $P > 0.05$) (Fig. 2.9b), the higher means calculated for March and November primarily resulted from small sample sizes. Around the Dyer Island group a larger percentage of smaller sharks were observed during the summer period, particularly during November, December and January (12 x 8 contingency table, $\chi^2_{(77,884)} = 157.82$, $P < 0.01$) (Fig. 2.9c).

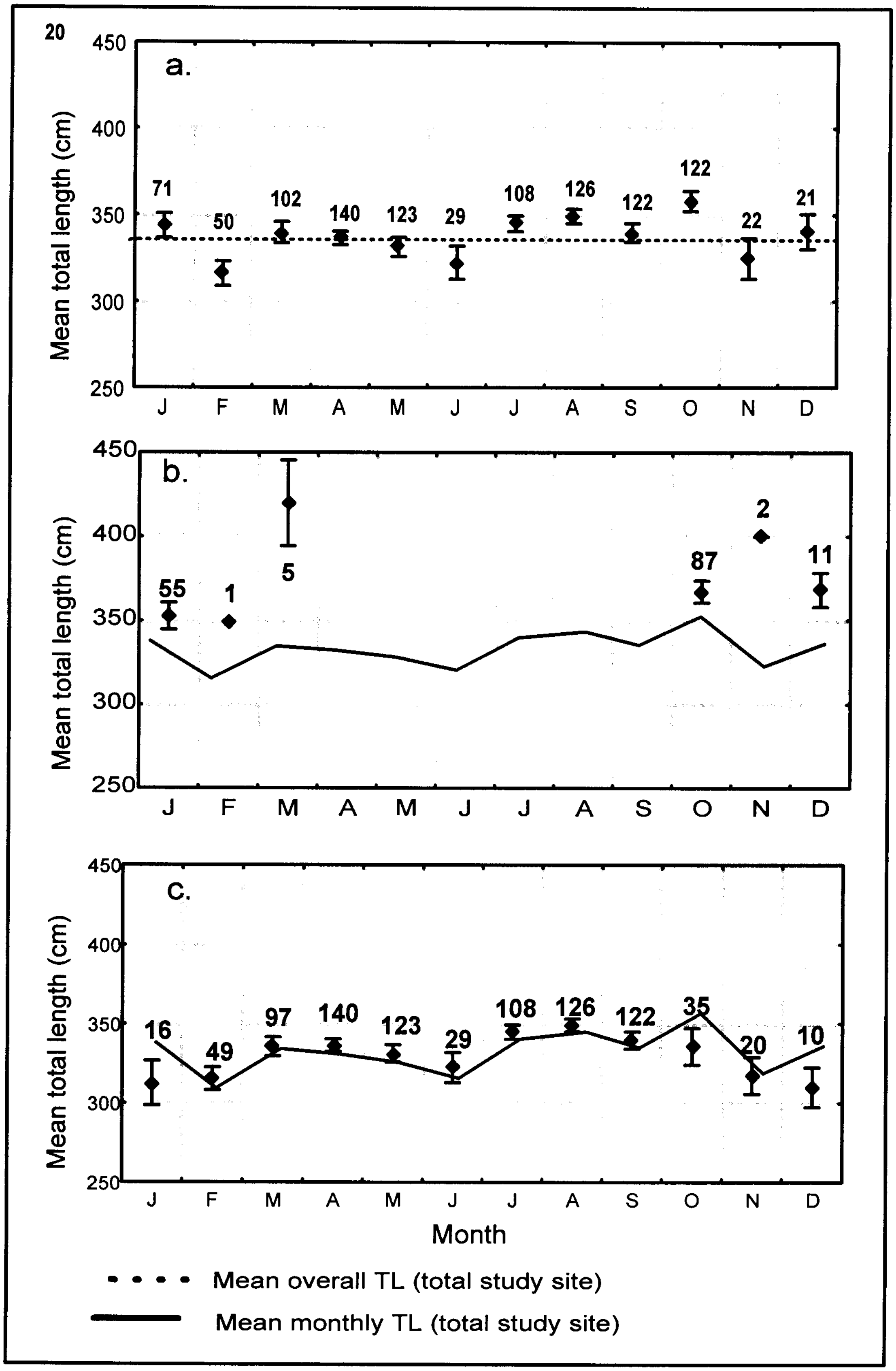

Figure 2.9 Monthly trends in total lengths of white sharks observed within study area. Figures: 2.9a – Dyer Island region, 2.9b – Inshore area, 2.9c – Dyer Island group. Data labels represent monthly sample size.

2.4 Discussion

White sharks occurred within the Dyer Island region throughout the year. The seasonal change in sighting frequency (lower from November to February) probably resulted from our tentative knowledge of their use of the inshore area during summer, and our spending time searching for sharks around Dyer Island. The most drastic change in spatial utilisation was the low numbers of white sharks sighted in the Dyer Island area during spring and summer, when they sought the inshore areas. Past restrictions of cage-diving to the near vicinity of Dyer Island obscured this phenomenon until midway through the study and led to the incorrect assumption that white sharks were seasonal visitors to the Dyer Island region. This reported seasonal occurrence is apparently still evident in the white sharks population in later years (2001 and 2002), suggesting that the observed seasonal change in distribution may have persisted (*unpub. data*). In addition, this seasonal and spatial patterns in the population composition of white sharks is the first scientifically reported occurrence of size and sex segregation of white sharks in South Africa. Below I discuss a number of possible explanations as to the cause of these changes in spatial distribution and population composition and the implications it has for our understanding of the life history of the white shark in South Africa.

2.4.1 Effect of prey type and availability

The evolutionary history of the *Carcharodon* genus is characterised by an increase in diversification and abundance at a similar time to the evolution of marine mammals (Purdy 1996; Applegate & Espinosa-Arrubarrena 1996). It is thought that marine mammals are prey species important to the success of this genus. Thus, the absence of white sharks from the channel and Dyer Island, areas during the Cape fur seal pupping season (November and December) (David 1987) is an enigma. Neonate fur seals begin to swim at six weeks of age, the period preceding this time is characterised by a large number being washed from Geyser Rock and drowning (*pers. obs.*). The rejection, by absence, of this readily available food resource is contradictory to the feeding strategy of most predators, which frequently target young, old, or sick individuals. Newborn pups may, however, not be an attractive prey item to the white shark due to low body fat levels as suggested by Klimley

(1994). Yet, this is unlikely to cause an absence of white sharks from the area as juveniles, sub-adults and adult female seals continue to be available.

Cape fur seals have been seen harassing (mobbing) white sharks in the vicinity of a seal colonies on a few occasions (*present study*, Stewardson & Brett 2000). Within the present study, this behaviour comprised of groups of seals harassing sharks from behind as they patrolled the relatively shallow (circa 3-5m) coast of Geyser Rock. In addition to the newborn pups, an influx of mature bulls occurs during the spring and summer for mating purposes. During this period, large bull seals have elevated levels of aggression related to territory maintenance and competition for mates (Rand 1967) and is probably caused by functional gonads and their androgens products (Stewardson *et al.* 1998). The presence of large aggressive bull seals may result in increased levels of harassment experienced by white sharks entering the channel area, and result in their subsequent avoidance of this area while aggressive bulls are present. It is, however, doubtful as to whether harassment and mobbing by large bull seals could explain the absence of white sharks from the peripheral areas of Dyer Island from November to February where seal concentrations are low and mobbing was not observed.

Although pinnipeds are a primary prey source for white sharks (Compagno *et al.* 1997), they also feed extensively on teleost fish and other elasmobranchs (Bruce 1992; Compagno *et al.* 1997; Cliff *et al.* 1989; 1996a). Stomach content analysis shows that pinnipeds are not as numerically important a prey type as frequently suggested (Bruce 1992), particularly for white sharks below 350cm TL (Tricas & McCosker 1984; Cliff 1989). The size composition of the white sharks observed at Dyer Island suggested primarily immature white sharks, of which 78.3 percent were estimated at a total length of less than 375cm (nearest TL category). Although many sharks capable of attacking large pinnipeds were observed, a majority of the sharks were of a TL that predominantly feeds on teleosts, elasmobranches and other smaller prey (Cliff *et al.* 1989; Bruce 1992). Thus the presence of the seals as a food resource may not be a major factor affecting the localised distribution of white sharks when within the greater Dyer Island area.

Local fisherman initially brought to our attention the near shore occurrence of white sharks during spring and summer. These fishermen also concentrate their fishing activity inshore during this period when geelbek (*Atractoscion aequidens*), snoek (*Thysites atun*) are abundant (M. Rutzen, F. Rutzen, *pers. comm.*). Alternatively at Dyer Island, game fish, such as yellow tail (*Seriola lalandi*), which are abundant in the winter, disappear during the summer period. This change in teleost distribution could be partly responsible for the change in white shark distribution, as white sharks may follow prey closer to shore.

2.4.2 Changes in the physical environment.

White sharks are endothermic, however the surrounding water temperature affects the ease at which their optimal body temperature is maintained, as heat is lost via conduction and convection (Carey *et al.* 1982; Tricas & McCosker 1984; Goldman 1997). This possibly affects the distribution of juvenile white sharks, which in California are more frequently observed in the warmer waters of the sub-tropical latitudes where thermal stress is less (Klimley 1994; Goldman 1997). Dyer Island is situated at the junction of two major ocean currents. From the west, the Benguela current brings cold water from the Antarctic region, while warmer water from the Agulhas current flows down the north-east coast of Africa. This results in water temperatures ranging from 9°C to 21°C, the variation of which is directly related to season. Although water temperature drops throughout the Dyer Island region in spring and summer (due to the dominance of the Benguela current), it is less noticeable inshore due to greater solar radiation and pockets of warmer water being trapped within the protected bay. Utilising the inshore area during the summer months may enable white sharks, especially small white sharks, to more easily gain and maintain their optimal physiological operating temperature.

2.4.3 Reproductive behaviour

Little is known about the reproductive behaviour of white sharks, due to few mature and/or gravid specimens being examined, and only a single account of mating reported (see above). It is possible that the spring-summer utilisation of the inshore habitat is partly for mating and/or parturition purposes. The presence of a number of sexually mature females in this area during the summer possibly indicates a concentration of this segment of the white shark population for breeding purposes. Mating of free swimming sharks have rarely been observed for any species (Francis 1996), however, a number of physical signs have been used to infer the occurrence of recent mating. These include semen or spermatophores flowing from claspers, swollen siphon sacs, chafed claspers, and con-specific bite marks on females (Pratt 1979; Gilmore *et al.* 1983; Bruce 1992). During the spring and summer periods the inshore population of white sharks is almost exclusively female so it has not been possible to inspect the condition of male claspers, yet the regular occurrence of fresh con-specific bite marks is possibly indicative of mating (*unpub. data*).

2.4.4 Implications for management and conservation.

This study offer new insights into understanding the spatial and temporal distribution, and population composition of white sharks along South Africa's coast. This knowledge has a number of implications on how white sharks in South Africa are managed and conserved. At present incidental bycatch of white sharks is probably the major cause of human induced mortality in South Africa. Identifying areas where white sharks congregate for certain periods of the year potentially enables the impacts of dangerous fisheries to be minimised, while benefiting fishermen and industries that use nets (aquaculture and fish farming). These fishermen can actively avoid areas where considerable damage may be inflicted on their fishing gear by white sharks, which by law are commercially worthless. Apart from hotspots being recognised at pinniped islands, white sharks may also congregate within inshore bays during the spring and summer for reproductive, social and feeding purposes. This phenomenon is not unique to the white shark, and many teleost and elasmobranch species follow similar reproductive strategies (Castro 1993; Simpfendorfer & Milward 1993). This information highlights the importance of minimising fishing induced disturbance in these areas, particular in the spring and summer when many species are known to give birth.

Very few of the white sharks observed during this study were either sexually mature (females: 1.6%, males 16.6%) or newborn. The rarity of these sharks implies that recruitment into the breeding population is still very low, and the low percentage of white sharks (particularly female) reaching maturity is of concern. The abundance of white sharks within South Africa's waters may place impact current protective legislation, however, the rarity of mature and neonate sharks indicate that the population is still under pressure and not suitable for consumptive exploitation in any form.

2.4.5 Synthesis.

The major anomaly found in this study was the absence of white sharks from Dyer Island during the Cape fur seals pupping season when ample readily available food was present. Without disputing the importance marine mammal evolution had on the success of the *Carcharodon* genus (Applegate & Espinosa-Arrubarrena 1996), evidence does suggest that pinnipeds may not be as an important a food source as once considered. This implies that factors divorced from pinniped availability may be influential in determining the spatial and temporal patterns of white shark occurrence.

Here I tentatively propose that social functions, possibly involving mating and parturition, have an influence on the seasonal patterns of habitat utilisation. Mature sharks, and those approaching maturity, could be utilising inshore waters in spring and summer to fulfill social and reproductive function. Evidence of white shark reproduction stems from catch reports on mature, pregnant and new born white sharks, extrapolation from reproductive strategies of other sharks (con-specific bite marks), anatomical studies on the reproductive physiology of white sharks, and a single observed account of mating white sharks. Our assessment is consistent with the information that other studies have produced.

This reproductive based hypothesis to explain the seasonal distribution change, however, fails to account for the distribution of immature sharks, which make up a vast majority of the sharks observed. I suggest that the presence of these sharks is ascribed to, in part, by both physical factors (related to the local environment), and biological factors, (the availability and distribution of teleost and elasmobranch prey). The feeding ecology of the white shark is characterised by heavy utilisation of teleost fish and elasmobranches (Cliff 1989; Bruce 1992), such as, geelbek, snoek, and soup fin shark, could result in a localised high abundance of white sharks that have followed the prey closer to shore. In addition, the warmer, more constant water temperature in the protected inshore area may reduce thermal stress on white sharks during the summer when the south easterly trade winds cause the water temperature around Dyer Island to drop and fluctuate.

CHAPTER 3

Predatory motivation of the white shark (*Carcharodon carcharias*)

3.1 Introduction

The white shark, *Carcharodon carcharias* (Linnaeus 1758), family Lamnidae, is a widely recognised macro predator. Despite the unprecedented attention this shark species has received in the last three decades, still relatively little is known about its life history, behaviour, or how it interacts with other species (Klimley & Ainly 1996b). For many years the notoriety of the white shark as the 'man-eater' of *Jaws* fame, has focused research efforts towards that of a one-dimensional ultimate predator (Compagno *et al.* 1997). Only recently has the essential and complex role that sharks, including the white shark, play in the marine ecosystem been recognised (Dayton 1991; Klimley & Ainley 1996b; Camhi *et al.* 1998). The hunting and feeding behaviour of the white shark is one such discipline that despite gaining much popular attention is only rudimentarily understood.

3.1.1 Prey types

Stomach content analysis has been used to determine the primary prey types of the white shark, which includes pinnipeds, cetaceans, cephalopods, teleost fish and elasmobranchs (Le Boeuf *et al.* 1982; Bruce 1992; Cliff *et al.* 1989, 1996a). Additionally, irregular prey species, such as the African penguin *Spheniscus demersus* (Bass *et al.* 1975; Randall *et al.* 1988), the sea otter *Enhydra lutris* (Ames *et al.* 1996), the leatherback sea turtle *Dermochelys coriacea,* the loggerhead turtle *Caretta caretta* (Long 1996), and a pygmy sperm whale *Kogia breviceps* (Long 1991) have also been identified as either consumed or bitten by white sharks. Furthermore, a number of inanimate objects display bite marks inflicted by white sharks, such as crab traps, inflatable boats, ski boats, float bags and many more (Collier *et al.* 1996). The findings of these studies suggest that white sharks are consuming a wide variety of prey items and actively investigating an even wider array of inanimate objects. The diversity of objects and prey types targeted by white sharks is the basis of a number of hypotheses regarding the hunting behaviour of the white shark.

3.1.2 Hypothesis on predatory behaviour

Observations of white sharks attacking prey (generally pinnipeds) have been carried out since 1968 at the South Farallon Islands, California (Ainly *et al.* 1981, Klimley *et al.* 1992; Klimley *et al.* 1996). The frequency of predatory encounters has been correlated with a number of biological and environmental variables to determine their importance in defining predatory relationships. The vast majority of attacks were observed in autumn from late August to early December, and were thought to be due to a local influx of white sharks (Ainly *et al.* 1985; Klimley *et al.* 1992). An overall increase in predation rate observed since 1968 is, however, ascribed to a gradual increase in the local pinniped populations (particularly the northern elephant seal) (Ainley *et al.* 1981; Pyle *et al.* 1996). Additionally, a significant correlation existed between elevated up-welling on the previous day (affecting water visibility) and a high occurrence of attacks (Pyle *et al.* 1996). This suggested that environmental conditions like murky, eutrophic water, which enhance the ability of the white shark to camouflage itself, could be positively linked with the completion of a successful attack. Tidal characteristics were also important to the success of an attack, with a high number of attacks observed during periods of high tide (Anderson *et al.* 1996b). The incoming tide was thought to increase spatial competition between pinnipeds inhabiting the seal island, forcing a higher proportion of the pinnipeds to enter the water and become potential victims.

3.1.3 Limitations of previous research

Research at the Farallon Islands (3.1.2) has generated unprecedented knowledge on predatory interactions between white sharks and pinnipeds. Yet, it has also highlighted the limitations and difficulties of formulating an all-encompassing hypothesis on the predatory strategies based on *post hoc* observations and accounts. The local predator abundance, prey abundance, the behaviour of the prey species, and importantly, the behaviour of the predator in terms of predatory and hunting motivation, all potentially shape the observed trends (Ainley *et al.* 1981; Ainly *et al.* 1985; Klimley *et al.* 1992; Pyle *et al.* 1996). To date, all methods used to study predatory interactions involving the white shark do not allow conclusive discernment between these defining variables.

3.1.4.Aims

The aim of this research is to experimentally investigate the variation in the hunting and predatory motivation of white sharks, and to determine what role predatory motivation plays in defining the spatial and temporal occurrence of natural predatory encounters.

The specific objectives are to determine if:

- Predatory motivation in white sharks is independent of proximity to a seal colony,
- Predatory motivation in white sharks is independent of shark size class and shark gender,
- Predatory motivation in white sharks is independent of the season and time of day,
- Predatory motivation in white sharks is independent of local environmental variables such as cloud cover, water visibility, wind speed, and swell height.

3.2 Methods

3.2.1 Experimental set-up and procedure

The study was carried out within the waters of the Dyer Island region (see 2.2.1 for detail) and continued from August 1999 until January 2001. Sharks were attracted to the research vessel by creating an odour corridor (chum slick). (see 2.2.2 for detail on chumming and shark attraction procedures).

Two foam rubber decoys resembling potential prey (namely seal decoy's, a penguin decoy and a rectangular decoy) were deployed simultaneously from the stern of the vessel. The decoys were deployed from either gunnel of the research vessel (separation of 2-3 m was maintained by the current) and suspended 8-10 m down current (Fig 3.1). The decoys were attached to the boat by a 90 kg breaking strain monofilament line. Observations were taken from above water to avoid any impact a caged diver may have on the behaviour of the visiting white shark. On arrival of a shark the decoys were left stationary with minimal interference and movements by the observer. Only when the shark had initiated an attack, and a decoy was in danger of being lost due to the actions of a shark, was the decoy actively pulled away to prevent it from breaking free.

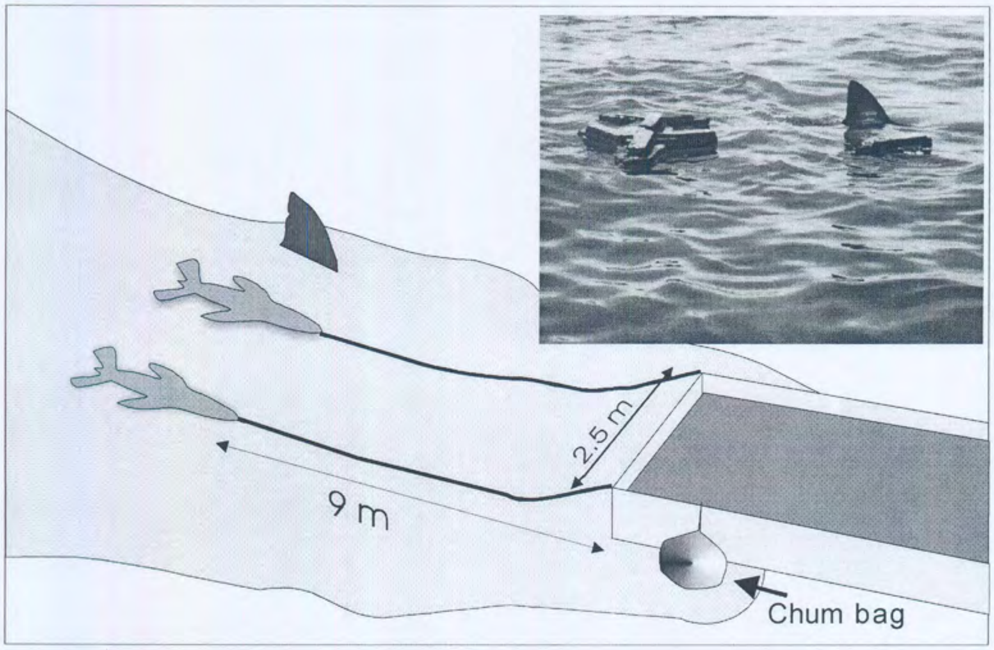

Figure 3.1 Experimental set-up consisting of two decoys simultaneously deployed from the stern of the vessel. Photo insert: A ~300cm white shark passing behind decoys.

3.2.2 Dependent variables

In order to describe variation in the behaviour of white sharks to acquire or investigate a potential prey item the term 'predatory motivation' was coined, and used to reference the psychological state of an investigating shark.

An ethogram of the five most common behaviours that white sharks displayed towards the prey resembling decoys was constructed. These behaviours represented five successive levels of predatory motivation, and included: circling, passing, bumping, low-speed attacks and high-speed attacks (Table 3.1). Following entry into the experimental area a shark's movement was tracked in relation to the two decoys, the port and starboard corners of the vessel's stern, and the marked midpoints between the decoys and where they were tethered to the research vessel. In order to remove observer biases associated with various weather conditions behaviours that occurred at a depth of greater than approximately three metres were noted, but excluded from all analyses, as well as all data collected when water visibility measured below two metres. Further observer bias potentially existed on overcast days when some visibility was lost because of glare, this was minimised by the observer wearing polarized glasses and the data was treated as normal.

3.2.3 Independent variables

Independent variables that were recorded throughout this study included shark size, shark sex, time of day and date, and the locality of encounter relative to the seal colony on Geyser Rock. A number of potentially important environmental variables, such as swell height, wind speed, water visibility, and cloud cover were also recorded.

Table 3.1. Ethogram of feeding type behaviours directed at decoys.

Behaviour	Description
Circling	Swimming in a complete or partial arc around the decoy array, at a distance of between 2 – 6 m.
Pass	Shark passing within 2 m of the decoy array.
Bumping	Shark making contact with the decoy with a part of the body other than its mouth.
Low-speed Attack	Shark biting/mouthing either of the decoys, approaches at normal swimming speed.
High-speed Attack	Shark using mouth to attack decoy, accelerates above normal swimming speed when attacking decoy.

On arrival of a shark, the shark's TL was estimated (to the nearest 0.5m) and sex recorded where possible. The presence (male) or absence (female) of claspers determined the sex, but if the cloacal region was not visible then the sex was recorded as unknown. A combination of photographs, video footage and sketches were taken of white sharks to allow individual identification of each shark. The size, sex, colouration patterns, body scars/marks were used as identifying characters.

The study area was divided into three location, or habitat types, dependant on the proximity to the seal colony on Geyser Rock. The 'channel' location consisted of the area directly adjacent to Geyser Rock where a high number of rafting seals was continuously present (Fig. 2.1, Channel). The 'Island periphery' location included all anchor sites within approximately 1km of the Dyer Island group, but outside of the channel (Fig. 2.1, Rocky's Bay, Geldsteen). The third defined location 'inshore' included anchor sites > 3km from the Dyer Island group. These areas included Holbaai and Jobert se Dam (Fig. 2.1). Due to logistical constraints operations were limited to daylight hours and only three temporal categories were defined. The morning period stretched from 06h00 to 10h00, the midday period lasted from 10h00 to 14h00 and the afternoon period from 14h00 to 18h00.

Environmental variables were measured by a combination of visual estimators and specific recording equipment. Water visibility was measured to the nearest 1m using a secci disk. Wind speed was recorded with an aeronometer, and swell height was visually estimated to the nearest 0.5 m. Cloud cover was estimated to the nearest 10% coverage. All independent variables were grouped into 2 to 7 categories (Table 3.2) for the purpose of analysis. Environmental variables were recorded at least three times throughout an observation period and the most recent recordings were assigned to a shark's visit.

Table 3.2. Categorical grouping of biological and physical independent variables.

Variable	**Group 1**	**Group 2**	**Group 3**	**Group 4**	**Group 5**	**Group 6**	**Group 7**
Shark size (cm)	175-225	226-275	276-325	326-375	376-425	426-475	476-525
Shark sex	Male	Female					
Time of year	D, J, F (Summer)	M, A, M (Autumn)	J, J, A (Winter)	S, N, D (Spring)			
Time of day	06 –10:00 (Morning)	10:01 –14:00 (Midday)	14:01 –18:00 (Afternoon)				
Location	Channel	Island Periphery	Away from Island				
Water vis. (m)	2 – 3.9	4 – 5.9	6 >				
Swell height (m)	0 – 0.4	0.5 – 0.9	1.0 – 1.4	1.5 – >			
Wind speed (Km h^{-1})	0 - 09	10 - 19	20 - 29	30 - >			
Cloud cover (% coverage)	0 – 19 (Clear)	20 – 79 (Part cloud)	80 – 100 (Overcast)				

3.2.4 Data analysis

The five behaviours were each accorded a 'predatory motivation value' that was subjectively based upon each behaviours level of predatory motivation in relation to the other four behaviours (predatory motivation values were determined during a preliminary study). Circling and passing were almost similar investigatory type behaviours and were accorded the lowest values of predatory motivation (0.04 and 0.06 respectively). Bumping the decoy with a body part other than the mouth represented a markedly higher level of predatory motivation and was accorded a predatory motivation value of 0.25. Low speed and high speed attacks represented actual attacks on assumed prey and were allocated the highest values in terms of predatory motivation at 0.30 and 0.35 respectively. The relative frequency of the five behaviours was used to derive a index value for a white shark's predatory motivation during its visit to the vessel. These 'index values' represented scores on a continuous scale. The following formula was used to calculate the index values:

$$\text{In.Val.} = \frac{(X_1 * N_1) + (X_2 * N_2) + (X_3 * N_3) + (X_4 * N_4) + (X_5 * N_5)}{(N_1 + N_2 + N_3 + N_4 + N_5)}$$

In.Val: Index value, Xi: predatory motivation value, Ni: Behaviour frequency

The resultant range of index values was termed 'Index A', and was non-normally distributed. The non-parametric Kruskal-Wallis test were used to test the index A data set. The software package Statistica was used to compare the results.

A second method used to measure predatory motivation derived from the percentage of white sharks that initiated an attack on the decoys (including both low and high-speed attack categories) (Index B). This differed from the 'predatory motivation index' by not considering the amount of investigatory (circling, passing and bumping) type behaviours prior to, or following attacks. The dependent variable (bite or not bite) was categorical, thus analysis of frequency techniques were used (Chi-squared). When appropriate the Yates' correction for continuity was applied. The software package Statistica was used to compare the results.

3.3 Results

3.3.1 Effect of shark size

There was a highly significant positive correlation between the level of predatory motivation directed towards the decoys and TL ($H_{(6,N=309)} = 14.222$, $P < 0.05$) (Fig. 3.2a). Sharks from the larger size categories displayed higher predatory motivation than those from the smaller size categories. The steepest rise in predatory motivation was observed between sharks of the 276-325 cm category and those in the 326-375 cm category. The apparent drop in predatory motivation within the 526–575 cm class is due to the small sample size ($N = 7$). No difference existed between size classes when comparing the percentage occurrence of sharks that attacked the decoys ($\chi^2_{(0.05,6)} = 4.08$, $P > 0.20$) (Fig. 3.2b). These conflicting findings result from the smaller sharks performing a comparatively greater number of investigatory behaviours, such as circling and passing, prior to, and/or following an attack on the decoys.

3.3.2 Effect of gender

Some (39.8%) sharks were conclusively sexed during this experiment. Within this group, sharks of opposing sexes did not differ in terms of the predatory motivation index ($H_{(2,N=145)} = 0.306$, $P > 0.20$) (Fig. 3.3a). The percentage occurrence of attacks on decoys was also independent of shark sex (Yates' correction for continuity applied, $\chi^2_{(0.05,1)} = 0.008$, $P > 0.05$) (Fig. 3.3b).

3.3.3 Effect of location

Sharks within the channel area displayed significantly higher levels of predatory motivation than sharks in the other two areas ($H_{(2,N=287)} = 13.368$, $P < 0.01$) (Fig. 3.4a). The percentage of sharks that attacked the decoys did not differ with respect to location ($\chi^2_{(0.05,2)} = 3.31$, $P > 0.05$). The highest percentage of sharks that attacked the decoys occurred within the channel (Fig. 3.4b).

3.3.4 Diurnal trends

No significant difference in the level of predatory motivation of white sharks with respect to the time of day existed ($H_{(3,N=309)} = 0.194$, $P = 0.932$) (Fig. 3.5a). The percentage of sharks that attacked the decoys also did not differ with respect to the time of day ($\chi^2_{(0.05,2)} = 0.60$, $P > 0.05$) (Fig 3.5b).

3.3.5 Seasonal trends

A clear, but non-significant, seasonal trend in predatory motivation levels existed in the white sharks at Dyer Island group ($H_{(3,N=309)} = 6.283$, $P > 0.05$) (Fig. 3.6a). Despite the non-significance, sharks appeared to display a higher level of predatory motivation from March through to August than during the other months (Fig. 3.6a). A similar, but non-significant, trend was also observed in the percentage of sharks that attacked the decoys throughout the year ($\chi^2_{(0.05,3)} = 4.47$, $P >0.05$) (Fig. 3.6b).

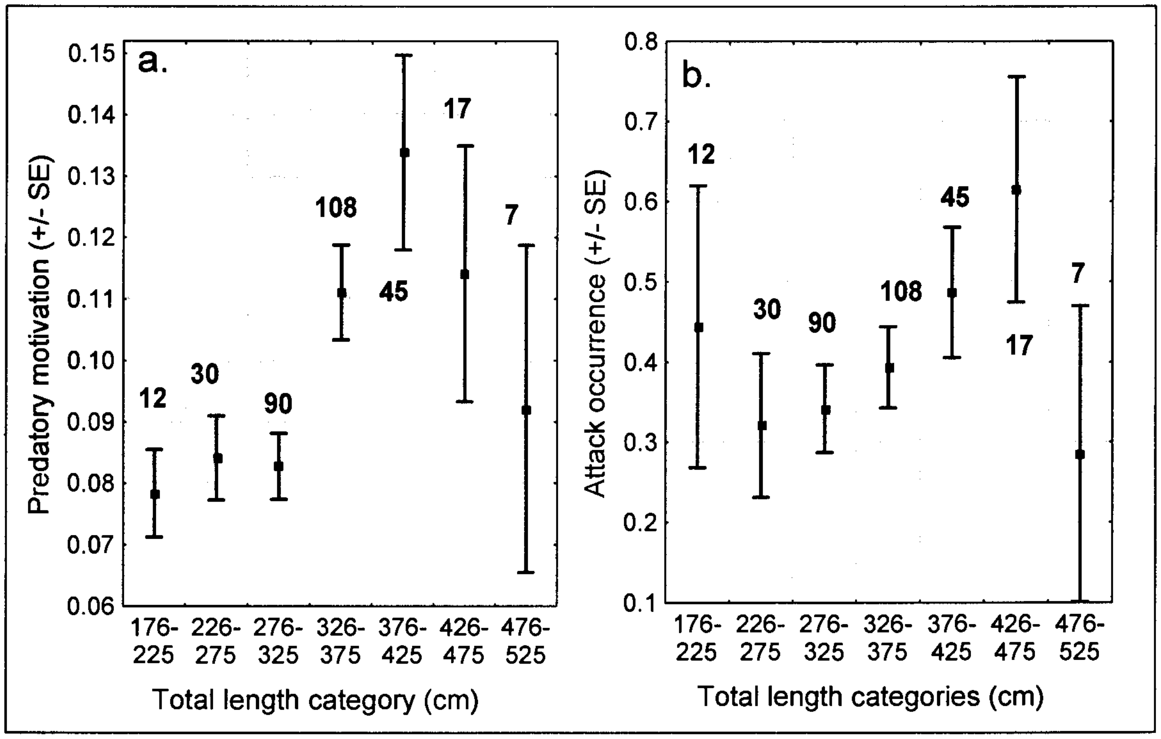

Figure 3.2 Effect of shark size on the predatory motivation of white sharks. Figures: 3.2a – Index A, 3.2b – Index B.

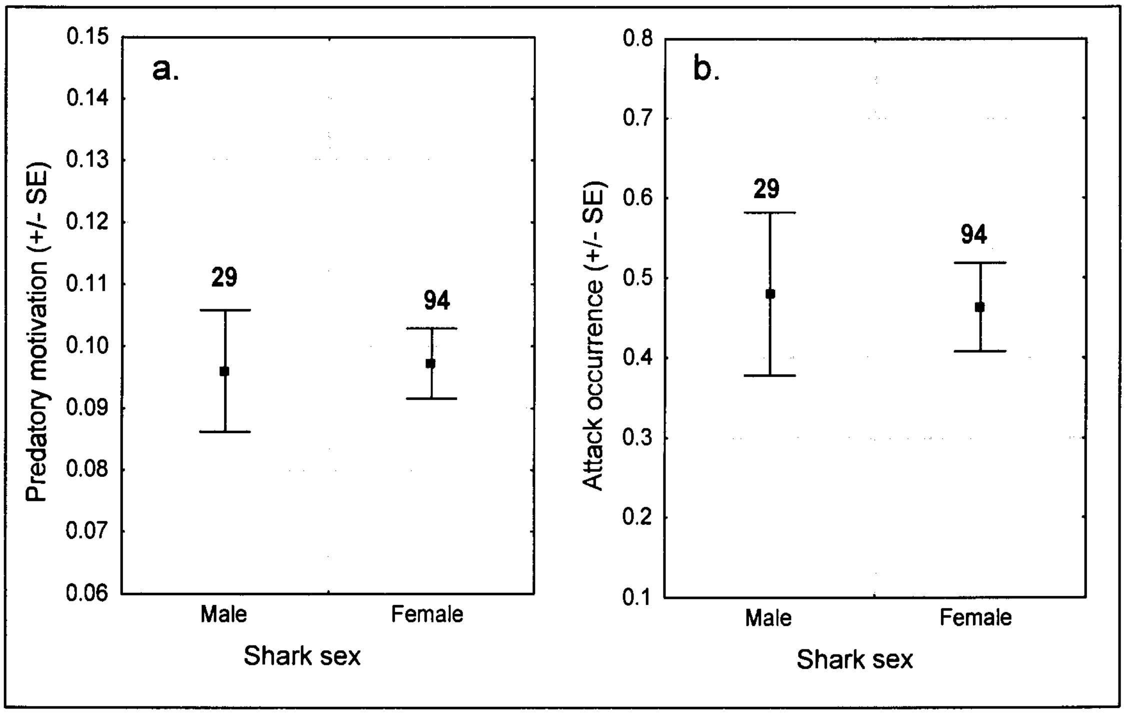

Figure 3.3 Effect of shark sex on predatory motivation of white sharks. Figures: 3.3a – Index A, 3.3b – Index B.

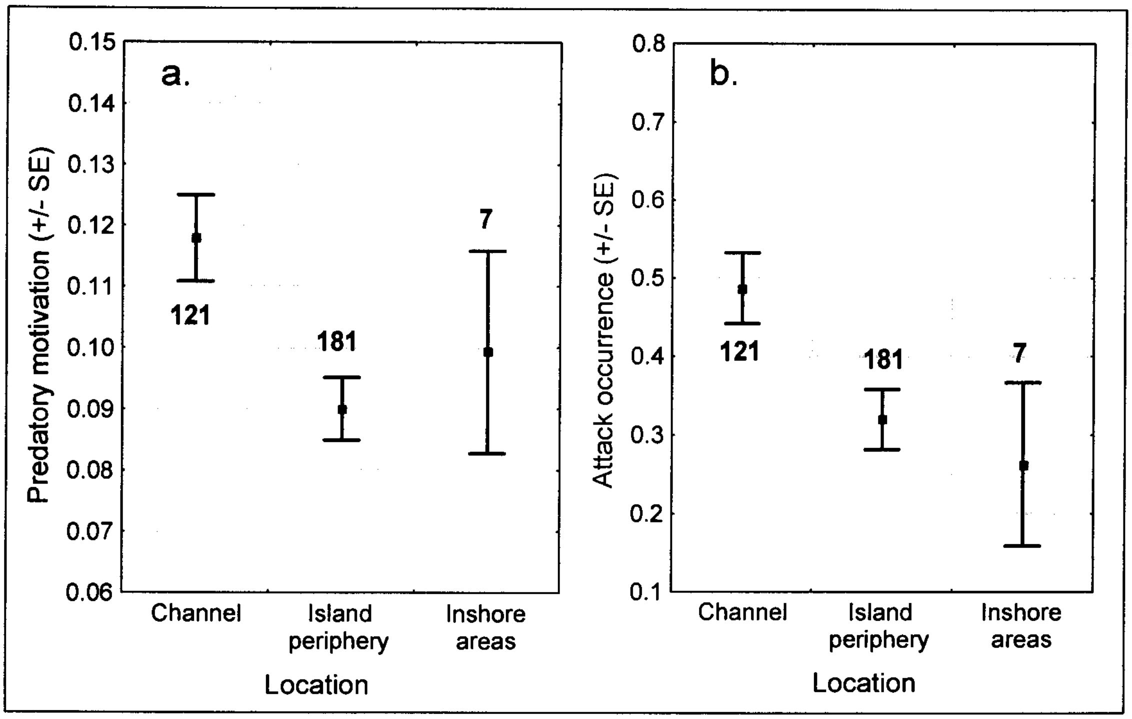

Figure 3.4 Effect of location on predatory motivation of white sharks. Figures: 3.4a – Index A, 3.4b – Index B.

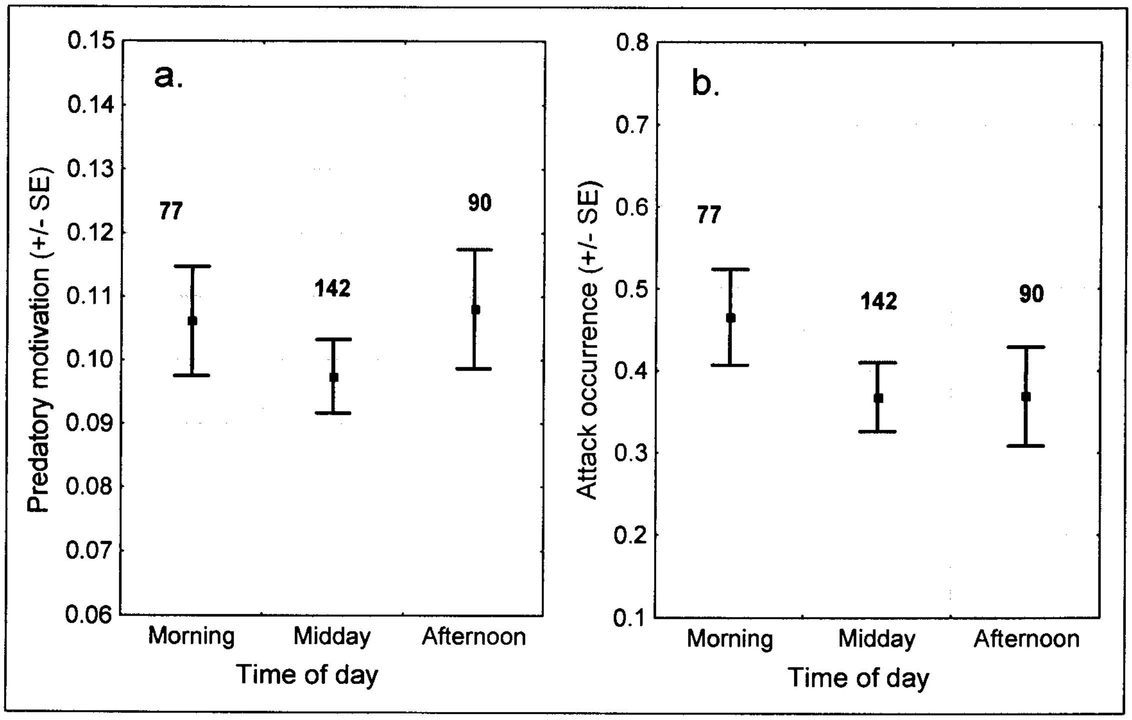

Figure 3.5 Diurnal effect on predatory motivation of white sharks. Figures: 3.5a – Index A, 3.5b – Index B.

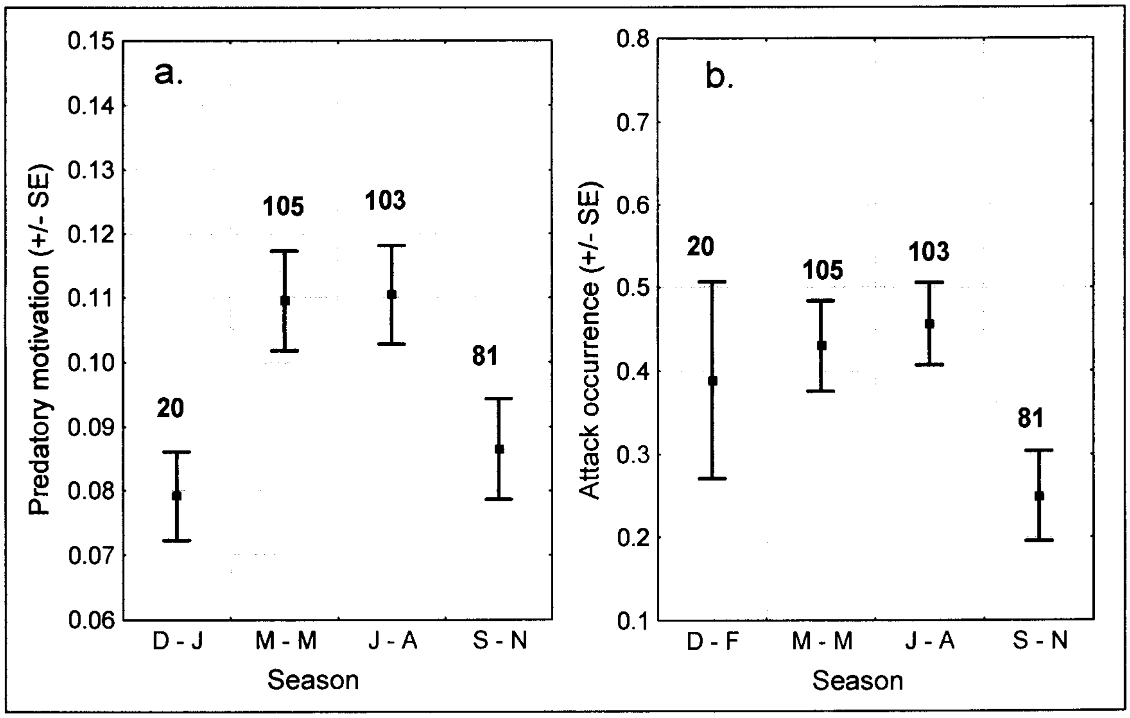

Figure 3.6 Effect of season on predatory motivation of white sharks. Figures: 3.6a – Index A, 3.6b – Index B.

3.3.6 Effect of swell height

The protection offered by Geyser Rock and Dyer Island resulted in a lower than expected swell height compared to other areas throughout the study (2 x 4 contingency table, $\chi^2_{(0.005,3)} = 21.49$, $P < 0.01$). For this reason, analysis of the effects of swell height on the predatory motivation was preformed using data collected outside of the channel where less protection existed. In these areas swell height did not affect the predatory motivation index ($H_{(2,N=178)} = 4.456$, $P > 0.20$) (Fig 3.7c), or the percentage of sharks that attacked the decoys ($\chi^2_{(0.05,3)} = 1.77$, $P > 0.05$) (Fig 3.7d).

3.3.7 Effect of cloud cover

Predatory motivation was dependent on the local atmospheric conditions. The calculated predatory motivation index suggested that high cloud cover increased the predatory motivation of white sharks ($H_{(2,N=299)} = 8.904$, $P < 0.05$) (Fig. 3.8a). The percentage of sharks that attacked the decoys was not significantly affected by the extent of cloud cover ($\chi^2_{(0.05,2)} = 5.46$, $P > 0.05$) although a similar trend was evident (Fig. 3.8b).

3.3.8 Effect of wind strength

Wind strength had a significant effect on the predatory motivation of white sharks ($H_{(2,N=304)} = 8.733$, $P < 0.05$) (Fig. 3.9a). In calmer conditions sharks displayed a lower level of predatory motivation towards the decoys. The likelihood of sharks attacking the decoy was not affected by wind strength ($\chi^2_{(0.05,3)} = 1.41$, $P > 0.05$) (Fig. 3.9b).

3.3.9 Effect of water visibility

A significant trend existed between predatory motivation and water clarity, with white sharks displaying higher predatory motivation in poor water clarity ($H_{(2,N=296)} = 9.613$, $P < 0.01$) (Fig. 3.10a). The percentage of white sharks that attacked the decoys did not change with respect to water visibility ($\chi^2_{(0.05,2)} = 1.39$, $P > 0.05$) (Fig. 3.10b).

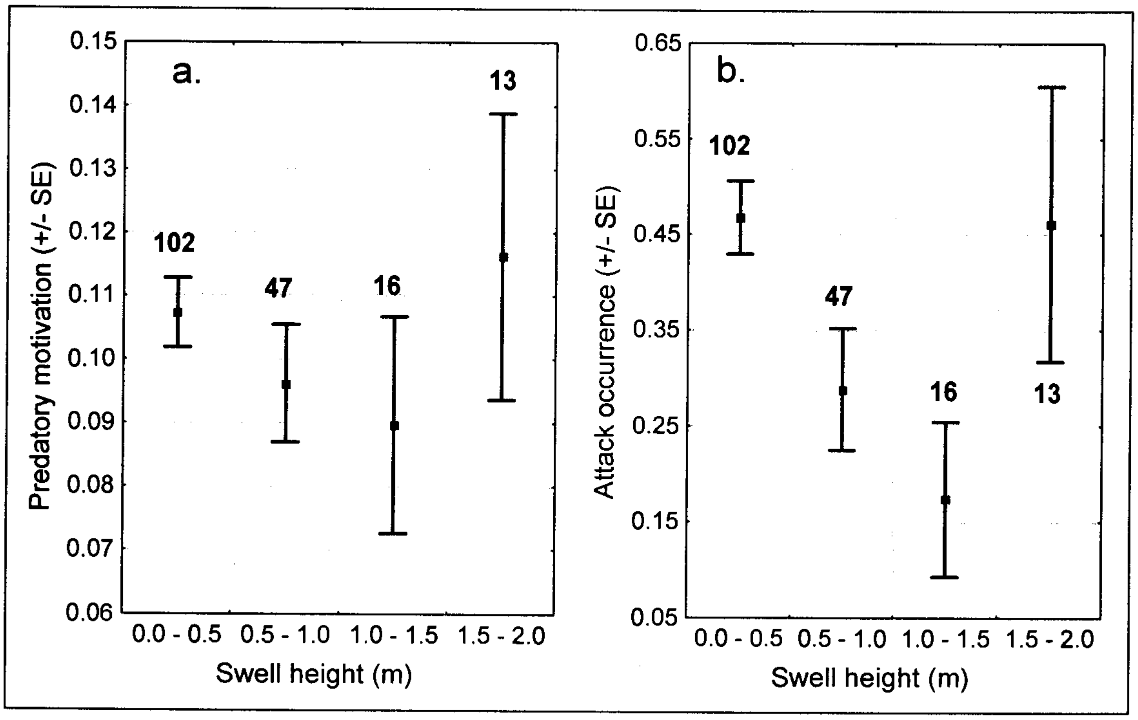

Figure 3.7 Effect of swell height on the predatory motivation of white sharks. Figures: 3.7a – Index A, 3.7b – Index B.

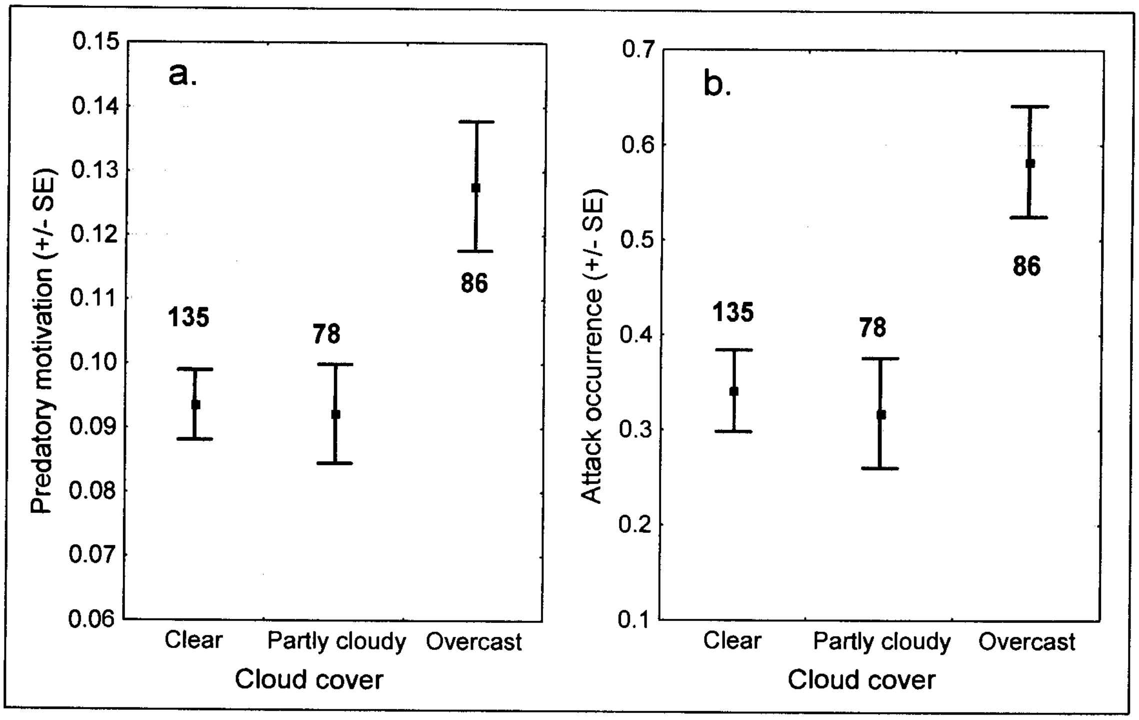

Figure 3.8 Effect of cloud cover on the predatory motivation of white sharks. Figures: 3.8a – Index A, 3.8b – Index B.

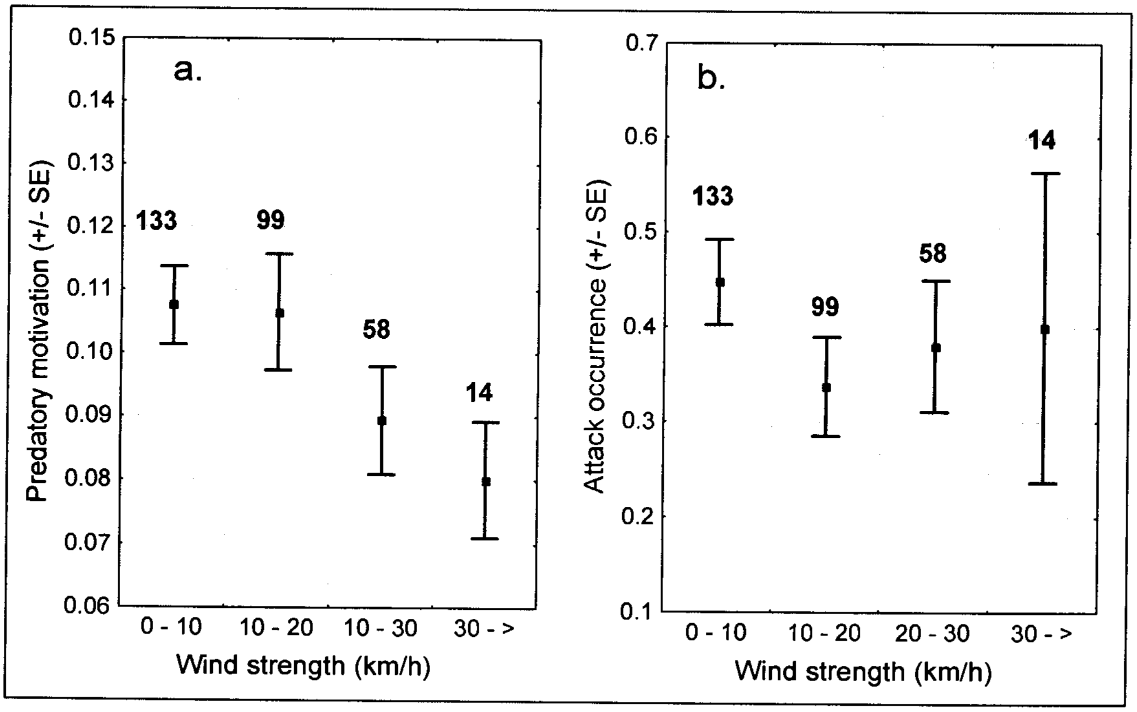

Figure 3.9 Effect of wind strength on predatory motivation of white sharks. Figures: 3.9a – Index A, 3.9b – Index B.

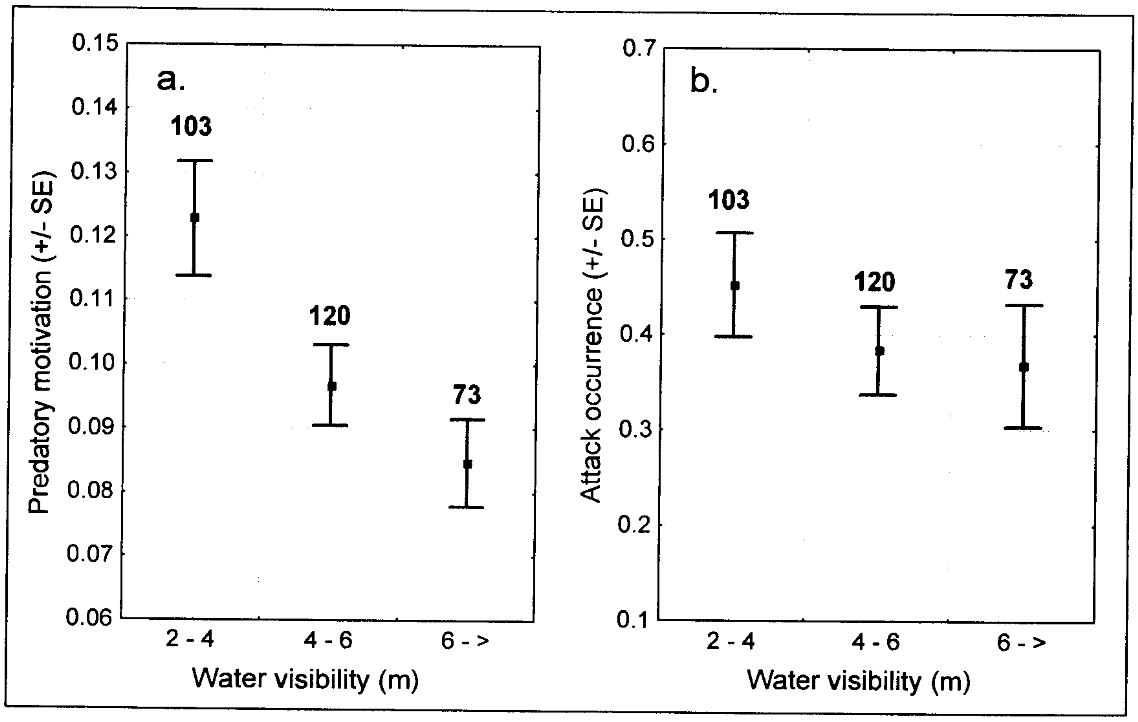

Figure 3.10 Effect of water visibility on predatory motivation of white sharks. Figures: 3.10a – Index A, 3.10b – Index B.

3.4 Discussion

White sharks displayed varied levels of predatory motivation towards the decoys, this response correlated with a number of biological and physical variables. It became evident that white sharks are not purely opportunistic, and do not follow a uniformed response following initial detection of potential prey. This has implications on how we understand their hunting and feeding behaviour. It is suggested here that both biological and environmental variables play a role in determining the predatory motivation of a specific white shark, and thus helps us to understand the dynamics governing the natural hunting behaviour of the white shark.

3.4.1 Effect of shark characteristics on predatory behaviour

Sharks estimated at 326 cm and above displayed greater predatory motivation towards the decoys than smaller sharks. However, throughout the size groups a similar percentage of sharks attacked the decoys. Smaller sharks displayed comparatively more investigative type behaviours (circling and passing) in addition to biting the decoys, thus causing the difference between the two predatory motivation estimates. The behaviour pattern (many investigative type behaviours) displayed by smaller sharks seems more indicative of scavenging or investigative feeding strategies rather than active hunting, as little effort to camouflage themselves and surprise the potential prey was shown. Scavenging off dead pinnipeds or attacking sick and drowning pup seals, may be important learning encounters for smaller white sharks prior to gaining the experience and competence necessary for attacking larger prey. In addition to limited experience, smaller white sharks are also limited by morphological constraints, such as long and slender teeth that are more suited to grabbing and swallowing smaller prey items (Tricas & McCosker 1984). Only as white sharks mature does their dentition develop into the classical triangular shape ideally suited to removing flesh from larger prey. The lack of difference in the predatory response of male and female white sharks to the experimental array suggests similar feeding strategies between sexes.

3.4.2 Effect of location on predatory behaviour

Sharks in close proximity to the Geyser Rock (channel) displayed higher levels of predatory motivation (via predatory motivation index), and greater likelihood of attacking a decoy, than sharks at other locations. The existence of 'attack prone' microsites first suggested by Collier (1992), was based on the occurrence of rare, but repeated, attacks on human in the same location. The elevated predatory motivation of sharks within the channel area is consistent with this idea of spatial 'microsites' in which white sharks more readily attack or investigate potential prey. These findings also suggest that the high frequency of live attacks observed in similar areas (Klimley *et al.* 1992; C. Fallows *pers. comm.*) is not solely caused by an increased likelihood of shark-seal encounters in areas where both predator and prey are abundant. White sharks appear to adopt a behavioural strategy that sees them more willing to investigate and/or attack potential prey located at, or near, the surface. The Cape fur seal is highly maneuverable, thus the probability of escaping an attack is maximised if a predator is detected early. This fact may result in white sharks adopting a more speculative hunting strategy in areas of high pinniped abundance, to ensure that they maximise the level of surprise.

A further explanation for high predatory motivation in the channel is related to the feeding and hunting behaviour of individual sharks. It is reasonable to assume that the energetic requirements needed to satisfy the white sharks metabolism is high in comparison to other sharks due to its level of endothermy (Carey 1982; Tricas & McCosker 1984; Carey *et al.* 1985; Goldman *et al.* 1996). It is unknown what effect hunger has on the swimming patterns of white sharks, other than pinniped islands frequently being identified as hotspots (Compagno *et al.* 1997). Goldman & Anderson (1999) suggested that the distinct swim patterns of white sharks near to pinniped haul-out areas were related to hunting behaviour and search patterns. White sharks that are more motivated to hunt or feed may patrol in the near vicinity of Geyser Rock to increase the likelihood of completing a successful attack on a pinniped. Thus the increased predatory motivation observed amongst these sharks may result from observing a subset of actively hunting white sharks.

3.4.3 Effect of environmental factors on predatory behaviour

Water visibility and cloud cover are two environmental factors that affected the level of predatory motivation in white sharks. Sharks displayed higher predatory motivation during overcast days, and in low water visibility. Strong (1996) surmised that the success of a white shark attack is dependent on minimising the distance between itself and the prey prior to detection. The combination of low light levels (overcast conditions) and poor water visibility would increase the ability of white sharks to camouflage themselves during the approach phase of an attack, thus allowing them to minimise the detection distance. Increasing hunting and feeding motivation under favourable environmental conditions could be paramount to the predation success of the white shark on highly manoeuvrable pinniped species.

A further reason for the increase in predatory motivation during overcast days and conditions of low water visibility may be related to the reduced reliance on vision for prey identification. White sharks readily attack a wide diversity of animate and inanimate objects (Collier *et al.* 1996), and some of this is motivated by investigation and determination of prey suitability. In environmental conditions where vision is limited, white sharks would increasingly rely on alternative senses including olfaction, electro-reception and tactile (biting/mouthing) investigation. An increased frequency of predations when water clarity was poor, and an increased number of surface sightings on overcast days, were observed at the Farallon Islands (Pyle *et al.* 1996). Pyle *et al.* (1996) emphasised the reduced ability of a pinniped to detect a shark as the cause of the increased attack and observation rates. However, this work suggests that the increased interactions between white sharks and prey may, in part, have been caused by increased motivation to attack and/or for tactile investigation of potential prey in this environment.

3.4.4 Temporal trends in predatory behaviour

Anderson *et al.* (1996b) linked the frequency of seal attacks at the Farallon Islands with tidal height. The increased spatial competition between seals at high tide led to more seals entering the water, and an increase in prey availability. The study failed to show any conclusive temporal change in hunting motivation throughout daylight hours. The findings are consistent with a link between diurnal trends in attacks and prey behaviour and abundance (Anderson *et al.* 1996b), rather than with changes in the predatory motivation of white sharks. Within South Africa, however, diurnal trends in shark/seal attacks have been observed at Seal Island, False Bay, with peaks in predatory incidents in the early morning and late afternoon (C. Fallows *pers. comm.*). Futhermore, cage-diving operators assert that white sharks react with increased 'aggression' towards their baits during the morning and late afternoon, but become more docile and easier to work with during the midday period (A. Hartman pers. *comm.*). Work throughout the entire 24-hour period is required to conclusively determine if diurnal parameters influence the predatory motivation of white sharks.

A non-significant trend existed with respect to seasonal changes in predatory motivation of white sharks in the Dyer Island region, and may be related to seasonal trends in feeding and habitat utilisation by white sharks. The absence of white sharks from the Dyer Island group during the summer period (see Chapter 2) is possibly indicative of an acute seasonal change in feeding behaviour and prey preference. During the spring-summer period pinnipeds may become less important and sought after, as indicated by the infrequent occurrence of white sharks at the Dyer Island group, or other similar pinniped islands (Klimley 1992; C. Fallows *pers. comm.*). If this was the case it may reflect in a reduction in predatory motivation towards the seal and other types of decoys in the summer.

3.4.5 Synthesis

The predatory behaviour of white sharks is a very topical discussion point for scientists and enthusiasts alike. This work has produced evidence of a number of suspected behavioural strategies as well as some unexpected ones. Since it has proved impossible to work with white sharks in captivity, this kind of experimental set-up represents the most controlled circumstances that white sharks have been subjected to for behavioural studies. Morphological constraints in tooth structure (Tricas & McCosker 1984), size similarity with prey, and limited experience are suggested as reasons that smaller white sharks (<325cm) do not feed on pinniped prey as often as larger sharks. This study's findings are consistent with the idea that the white shark's confidence, and ability, as a predator of large prey is a function of shark size, with sharks becoming more prominent predators of pinnipeds at around 350cm TL.

The motivation of white sharks to attack/investigate potential prey is related to areas of high prey abundance. While in the vicinity to Geyser Rock, white sharks displayed a greater willingness to investigate and attack the decoys. This appears to be a behavioural strategy adopted when in an environment where the likelihood of encountering energy rich prey is greatest. These findings suggest that the high number of attacks seen in the near vicinity of seal islands is, at least in part, caused by increased motivation of white sharks to attack and/or investigate potential prey, and is consistent with Collier's (1992) suggestion of attack prone 'micro-sites'. The increased frequency of attacks observed on days of poor water clarity, and increased number of surface sightings on overcast days, as at the Farallon Islands (Pyle *et al.* 1996), may result from a combination of focused investigative and hunting for potential prey, in addition to, the reduced ability of prey to detect and escape from white sharks as they approach. Diurnal and seasonal changes in predatory motivation were not conclusive (this study). Experimentation throughout 24 hour-periods is required to fully investigate dial trends in predatory motivation as the composition of the white sharks eye suggests they are diurnal hunters (Gruber and Cohen 1985). While not significant, levels of predatory motivation in the winter and autumn appeared to be higher than in spring and summer, and are consistent with observed trends in habitat utilisation by white sharks (Chapter 2). Sharks occurring in dense numbers at seal islands during the winter and autumn months (Klimley 1992; C. Fallows *pers. comm; this study.*) suggest that this is the main period for feeding on pinnipeds. Absence during the summer and spring imply that white sharks may be preferentially feeding on other prey, such as teleosts and smaller elasmobranchs.

CHAPTER 4

Activity patterns of white sharks (*Carcharodon carcharias*) at chumming vessels

4.1 Introduction

4.1.1 Shark management

The management and sustainable utilisation of the world's chondrichthyan fish populations are coming under closer scrutiny as increased consumptive exploitation results in many species being depleted and some considered threatened with extinction (Dayton 1991; Camhi *et al.* 1998). Shark cage diving for tourism can assist in the conservation of shark species through education and creating a non-consumptive economic value for shark species (Oosthuizen & Johnson 2001). Despite this, the perceived danger that sharks pose to humans, and other reasons, has resulted in much discussion regarding the pros and cons of these activities (Bruce 1995; Compagno *et al.* 1997; York 1998)

4.1.2 White shark cage diving

In April 1991, following two decades of consumptive exploitation, the threats posed by fishing of white sharks in South Africa were recognised. In an unprecedented move the South African government declared the white shark a protected species based on the precautionary principle (Compagno 1991). The development of the white shark cage-diving tourism sector shortly followed the 1991 legislative decision (Sadie 1998). Cage-diving is a non-consumptive tourism activity, enabling permit holders to actively attract and interact with white sharks. This sector is likely to be a powerful conservation tool, with far-reaching educational potential and a positive influence on the public's perception of this much-maligned species. Furthermore, the sector creates significant economic value through the non-consumptive utilisation of white sharks, that is in line with the Department of Environmental Affairs and Tourism's (DEAT) policy of sustainable utilisation of

South Africa's marine resources. The first commercial cage-diving operations began in 1992 in False Bay, and now the industry has extended to other areas of South Africa including Mosselbaai (one operator), the Dyer Island region (eight operators) and False Bay (three operators). At present permits have been issued by DEAT to allow these 12 operators to actively attract white sharks for tourism purposes (Fig. 4.1).

White shark cage diving typically involves taking tourists in boats to offshore islands occupied by pinniped populations. Upon arrival a fish based chum slick (shark liver, fish guts, sardines, tuna, snoek etc.) is set. The oils and dissolvable products slowly release into the current creating a slick that may reach upwards of 5 km (Sadie 1998). White sharks are attracted up this olfactory trail to the tourism vessel, where they are lured closer to the vessel by a roped piece of bait. The general objective is to rely on the skill of the 'shark handler' to elicit gapes and displays from the sharks, while preventing them from actually taking and feeding off the offered baits (Fig. 4.2). On occasions sharks do get the bait and feed on it, this generally results from unintentional miscalculation by the handler, or 'occasionally' intentionally, so that guests can observe a spectacular struggle between man and shark.

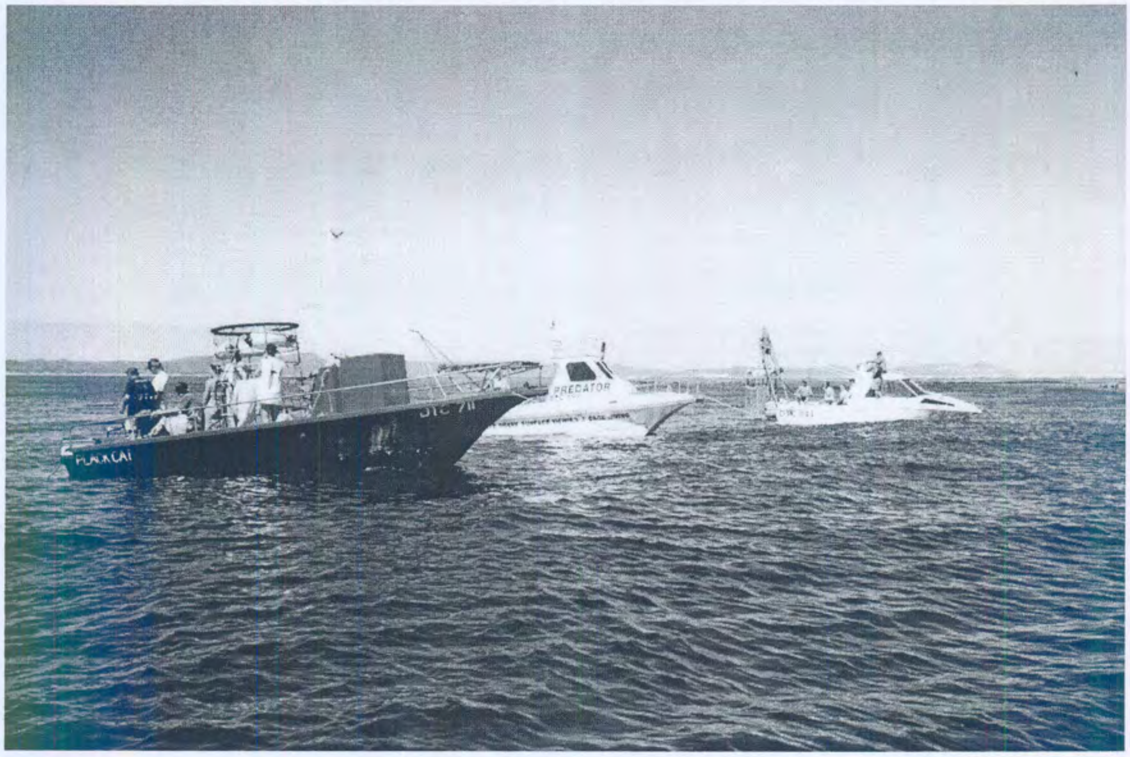

Figure 4.1 Three white shark cage-diving tourism vessels anchored off the Dyer Island group. At present eight operators have been issued permits to attract white sharks in the waters of the Dyer Island region.

Figure 4.2 On arrival to a chumming vessel white sharks are lured close using a roped piece of bait. The intention is to induce the shark to 'perform' without accessing the bait.

4.1.3 Potential negative impacts of white shark cage-diving

The granting of the right to actively attract and interact with a protected, and potentially dangerous, species holds with it a number of responsibilities for permitted operators and managers. They must ensure that the resource is sustainably utilised, that the sector operates in a manner to ensure stability, and that the conservation status of the white shark and its ecosystem is not jeopardized. Despite the positive aspects of white shark cage-diving, the standard chumming and baiting procedures have led to highly motivated concerns regarding the potential hazards to white sharks, the environment and humans (Bruce 1995; Compagno *et al.* 1997; York 1998) and a call for research in this area. Key concerns include:

- The conditioning of white sharks to associate divers and boats with food,
- The distraction of sharks from normal behavioural activities including feeding, resting and social interactions,
- Injury and stress sustained by the sharks from the cage diving activities,
- Modification of the natural predator-prey dynamics in areas where cage diving operates.

4.1.4 Aims

At present, anecdotal reports and non-scientific observation of commercial cage-diving operators are the main sources of knowledge on the behavioural response of white sharks to chumming vessels. Although much insight can be gained from these reports, validating expressed concerns can only be resolved through scientific research and not emotive arguments.

The objectives of this study are to:

- Develop a protocol to accurately measure the activity patterns and exposure of white sharks to chumming vessels,

- Determine whether total visit time, total contact time, and proportion of time in contact with a chumming boat are independent of shark size and sex, proximity to the seal colony, season, time of day, and environmental conditions,
- Evaluate the validity of concerns regarding impacts by the white shark cage-diving sector.

4.2 Methods

4.2.1 Study site

The study was carried out in the Dyer Island region (see 2.2.1 for detail on Dyer Island region) and continued from September 1999 until January 2001. The waters of the Dyer Island region have been demarcated as one of the three areas in South Africa where white shark cage-diving can take place. During this study five operators attracted white sharks to vessels for tourism purposes.

4.2.2 Experimental set-up and procedure

White sharks were attracted to the research vessels by an odour corridor (chum slick) similar to that used by commercial cage-diving operations (See 2.2.2 for detail of shark attraction). The experimental set-up was not entirely comparable with cage-diving operations, as it did not replicate the exact set-up or operational procedure, i.e. use of stationary foam rubber decoys in place of manoeuvrable baits (See 3.2.1). This was, however, necessary due to other experimental requirements (see Chapters 3 and 5).

4.2.3 Independent variables

During the daily chumming activities, a number of independent biological and physical variables were recorded. Relevant biological variables included total length (TL) (nearest half metre) and the sex of sharks arriving at the chumming vessels. Physical variables included the spatial and temporal characteristics of an interaction episode, which included the time of day (first sighting of shark), the date, and the locality relative to the seal colony. Finally, localised environmental conditions were recorded during each day's activities. This included the swell height, wind speed, water visibility and cloud cover (see 3.2.4 for detail on recording environmental data)

4.2.4 Dependant variables

Three methods were used to determine the exposure and behavioural response of white sharks to chumming vessels. These included total visit time (TVT), time in contact (TIC) and proportion in contact (PIC) (Table 4.1). Timing of events was calculated to the closest minute. For a shark to be recorded present during a given minute it had to be observed at least once within the experimental array. On occasions commercial cage-diving operators anchored in close vicinity to the research vessel (< 100 m). On these occasions it was possible that a white shark was moving between two or more boats thus compromising recordings of activity patterns. Unless clear evidence existed that no sharing occurred during a shark's visit (no sharks observed at other vessel during visit time) this data was excluded from the analysis.

Table 4.1 Description of various measures used to determine the behavioural response of white sharks to chumming vessels

Abbr.	**Visit parameter**	**Description**
TVT	Total visit time	The number of minutes between first and last sighting of a shark during a day's operation at the vessel (< ~10m).
TIC	Time in contact	Sum total of minutes between first and last sighting of a shark at the vessel.
PIC	Proportion in contact	Equals contact time / total visit time.

4.2.5 Data analysis

The independent physical and biological variables recorded during this study were categorised from two to seven categorical groups. The visitation patterns of white sharks to the chumming vessel (See Table 3.2) were represented as continuous dependant variables. Due to a non-normal distribution of the dependant variables (a large number of sharks observed only once for a single minute) a non-parametric equivalent (Kruskal-Wallis statistical test) to an Analysis of Variance test was used. The statistical software package Statistica was used to test the data.

4.3 Results

4.3.1 Effect of shark size

The 'total visit time' (TVT) of sharks to the chumming vessel was significantly affected by shark size ($H_{(6,237)} = 14.275$, $P < 0.05$) (Fig. 4.3). Smaller sharks (TL < 326cm) generally stayed in the vicinity of the chumming vessel for a longer time throughout the day than their larger counterparts. The number of minutes that sharks were observed at the boat (TIC) was independent of shark size ($H_{(6,237)} = 10.06$, $P > 0.10$). The percentage duration (PIC) of a visit by sharks to the chumming vessel was also affected by shark size ($H_{(6,237)} = 23.72$, $P < 0.01$) (Fig. 4.3b), with smaller sharks being observed at the vessel for a smaller proportion of their overall visit (Fig. 4.3c).

4.3.2 Effect of shark sex

The TVT was independent of shark sex ($H_{(1,100)} = 1.838$, $P > 0.1$) (Fig 4.4a). The mean number of minutes spent by females in contact (TIC) with the chumming vessel was higher than for males (Fig. 4.4b), but it was not a statistically significant result ($H_{(1,100)} = 0.333$, $P > 0.50$). Likewise, the PIC was independent of sex ($H_{(1,100)} = 2.263$, $P > 0.10$), although females spent a lower proportion of a visit in contact with the chumming vessel (Fig. 4.4c).

4.3.3 Effect of season

Season did not appear to influence the TVT of sharks to the chumming vessel ($H_{(3,239)} = 7.532$, $P > 0.05$) (Fig. 4.5a). The TIC of sharks was significantly influenced by season ($H_{(2,238)} = 8.434$, $P < 0.05$) (Fig. 4.5b), with sharks observed at the boat for longer periods between December and February compared to the rest of the year. The PIC also appeared to be constant throughout the year with no difference observed ($H_{(2,238)} = 4.268$, $P > 0.20$) (Fig. 4.5b).

4.3.4 Diurnal effect

The TVT of white sharks observed during midday and in the morning was similar, while the drop in TVT during the afternoon was not statistically significant ($H_{(2,239)} = 4.542$, $P > 0.10$) (Fig. 4.6a). Similarly, the TIC was independent of time of day ($H_{(2,238)} = 3.263$, $P > 0.20$) (Fig. 4.6b). The PIC of a visit appeared higher in the afternoon than at other times of the day, but was not significant ($H_{(2,238)} = 3.263$, $P > 0.20$) (Fig 4.6c). This was probably construct of the experimental design, with sharks arriving late at the boat having fewer opportunities to depart and return prior to the ceasing of the experiment.

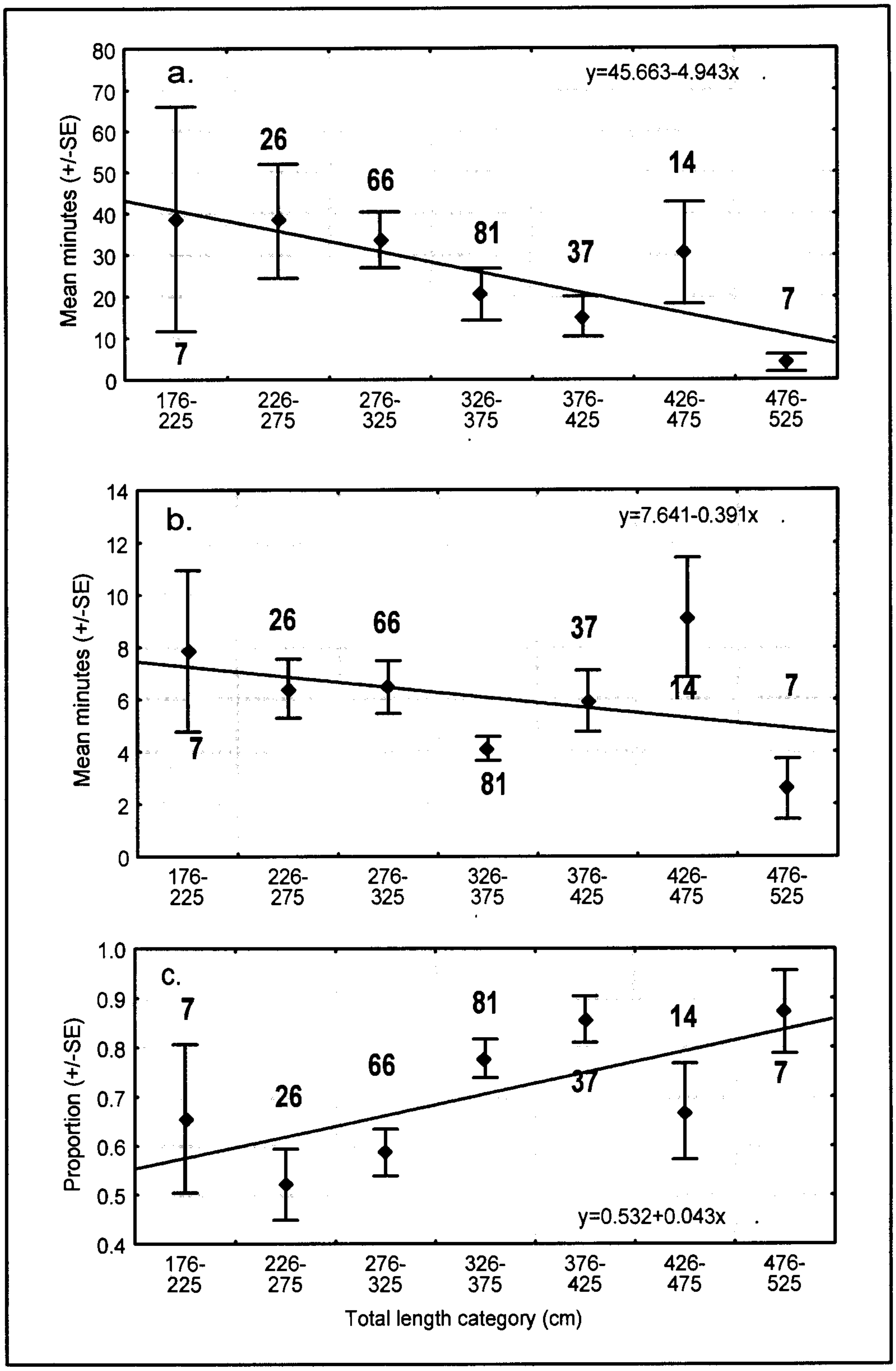

Figure 4.3 Effect of shark size on the visitation patterns of white sharks to a chumming vessel. Figures: 4.3a – Total visit time, 4.3b – Time in contact, 4.3c – Proportion in contact. Data labels represent N.

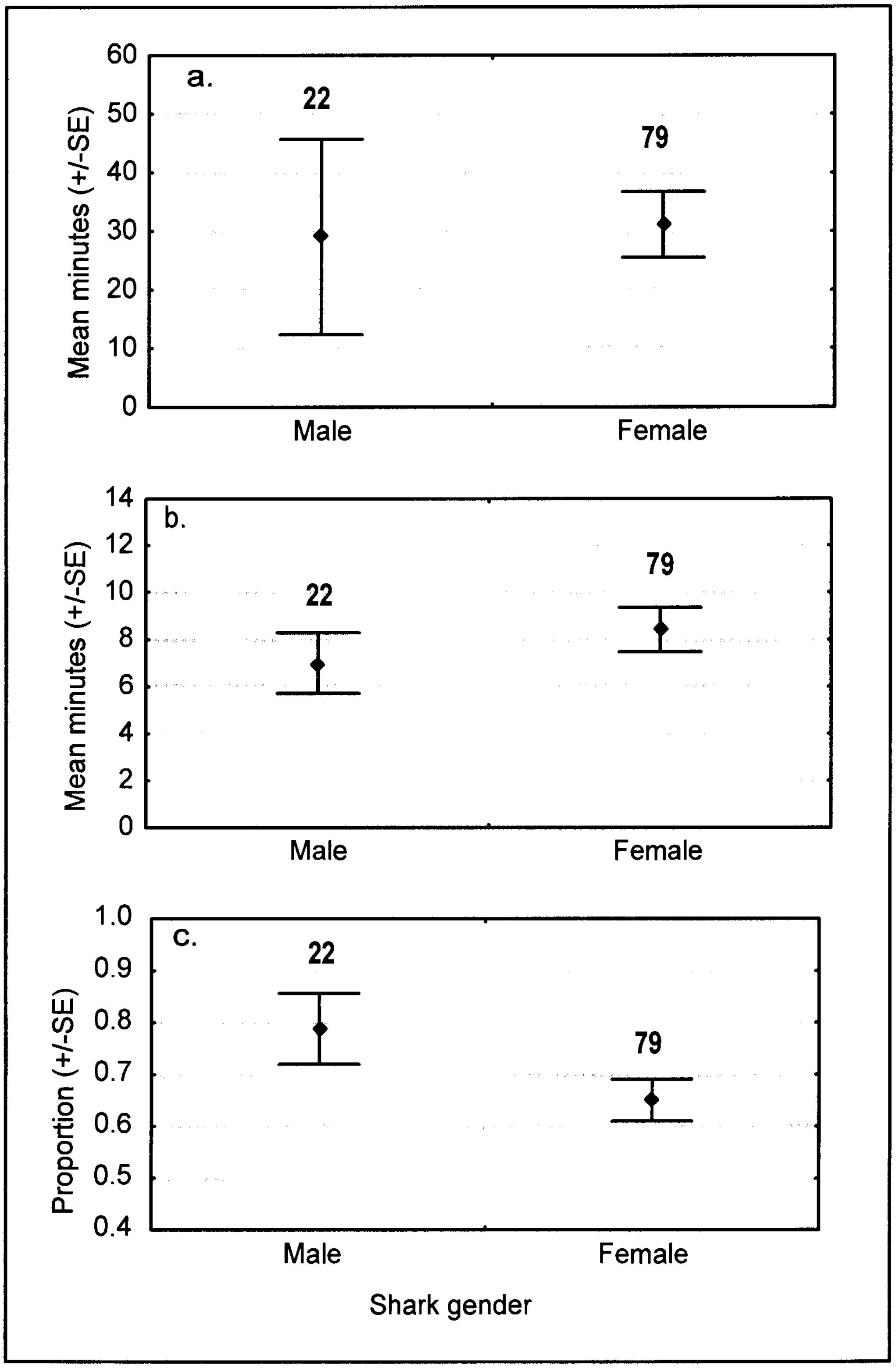

Figure 4.4 Effect of shark gender on the visitation patterns of white sharks to a chumming vessel. Figures: 4.4a – Total visit time, 4.4b – Time in contact, 4.4c – Proportion in contact. Data labels represent N.

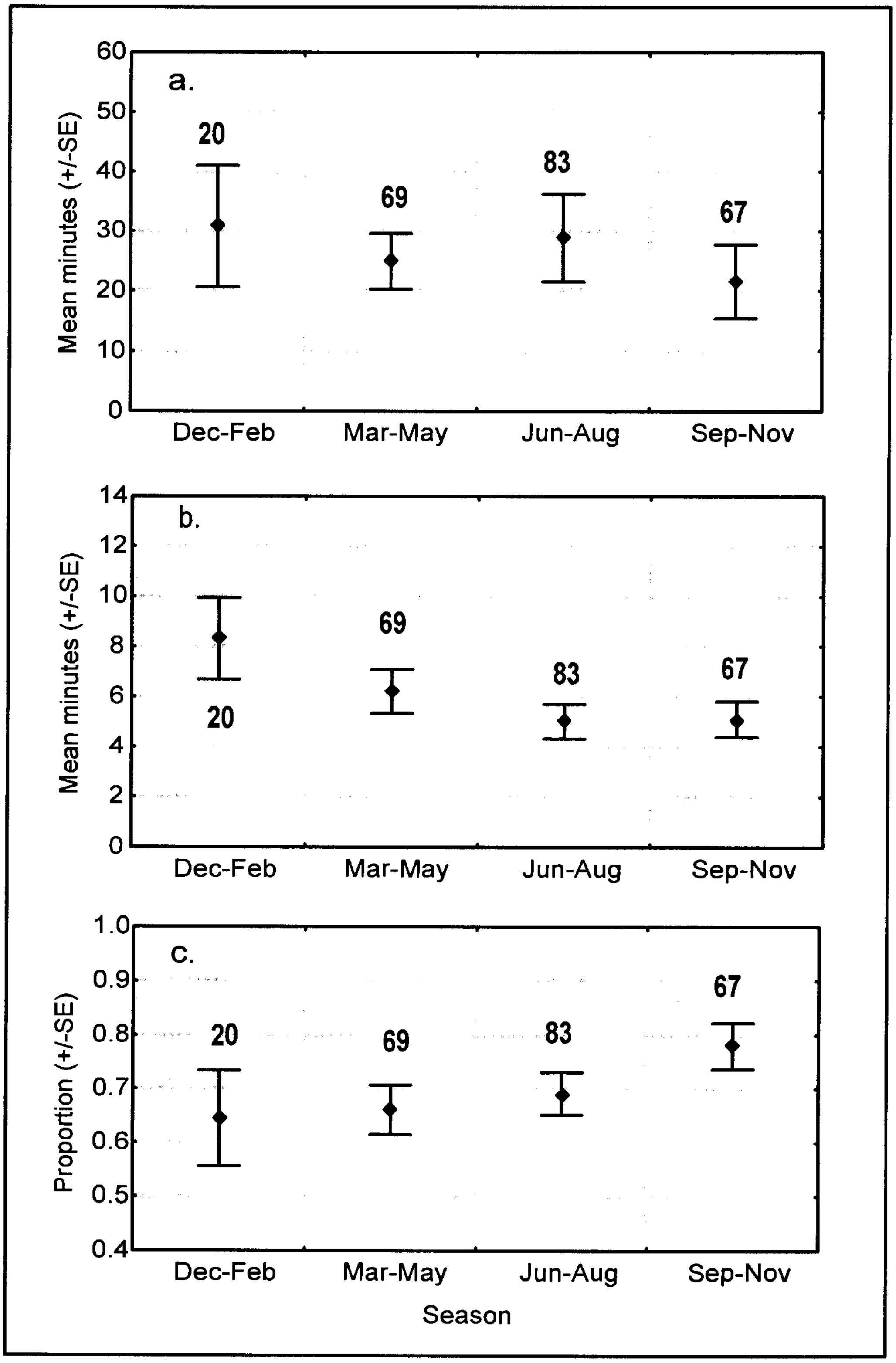

Figure 4.5 Effect of season on the visitation patterns of white sharks to a chumming vessel. Figures: 4.5a – Total visit time, 4.5b – Time in contact, 4.5c – Proportion in contact. Data labels represent N.

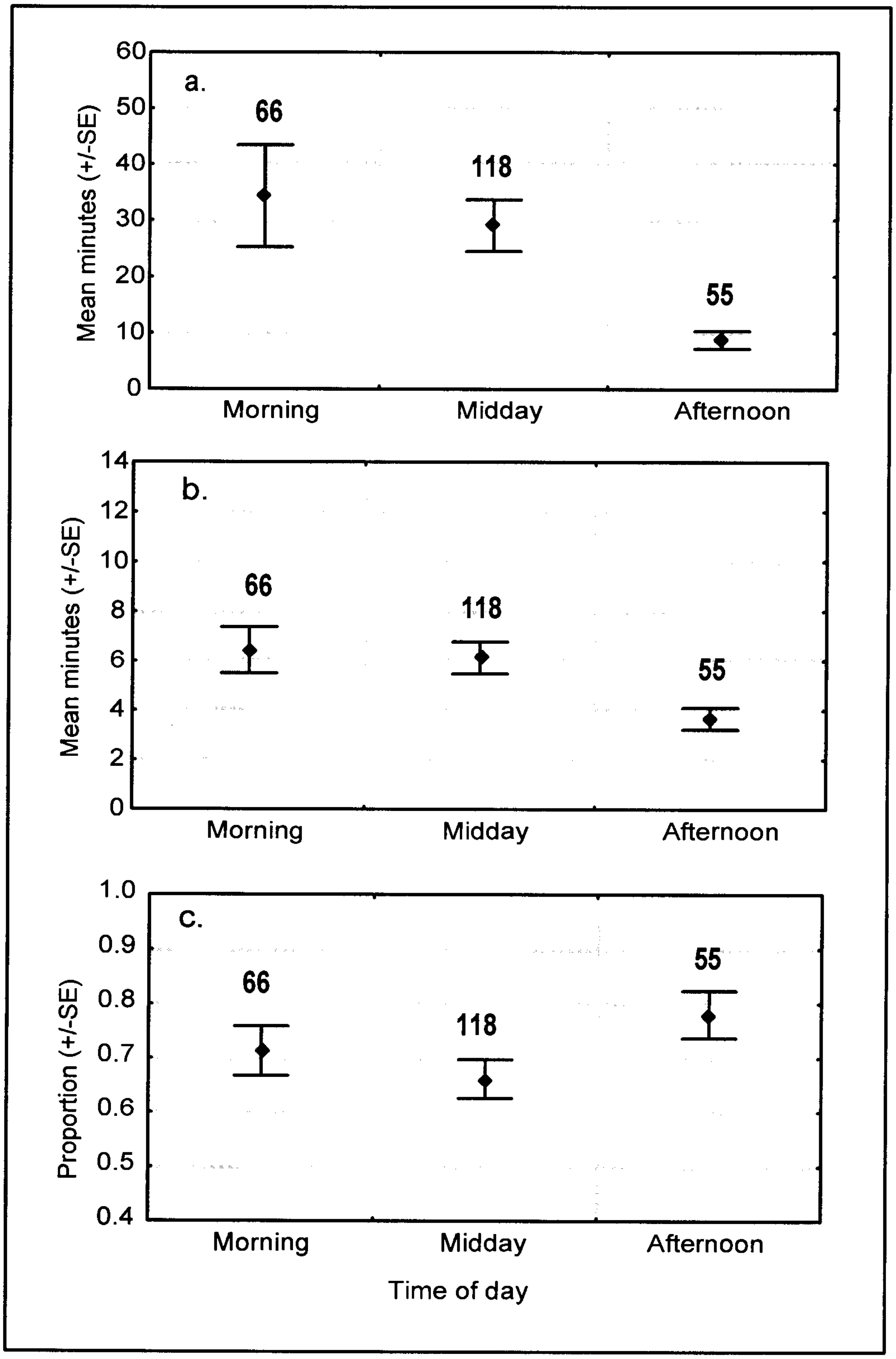

Figure 4.6 Diurnal effects on the visitation patterns of white sharks to a chumming vessel. Figures: 4.6a – Total visit time, 4.6b – Time in contact, 4.6c – Proportion in contact. Data labels represent N.

4.4.5 Effect of location

The TVT of sharks to a boat was dependent on location ($H_{(2,239)} = 7.878$, $P < 0.05$) (Fig. 4.7a). White sharks within the channel were observed for a longer time daily (TVT) than in other locations. The number of minutes that sharks spent at the vessel (TIC) was independent of location ($H_{(2,238)} = 1.176$, $P > 0.50$) (Fig. 4.7b). The PIC of the sharks did differ significantly with respect to location ($H_{(2,237)} = 17.12$, $P < 0.01$), as the sharks in the channel spent a smaller percentage of a daily visit at the boat compared to sharks observed elsewhere (Fig. 4.7c).

4.4.6 Effect of swell height

TVT was independent of swell height ($H_{(6,227)} = 3.495$, $P > 0.20$), although there was a non-significant trend that suggested that the total visit time of sharks was greatest in smaller swells (Fig. 4.8a). Swell height had no influence on the TIC of visiting sharks ($H_{(3,227)} = 1.767$, $P > 0.50$) (Fig. 4.8b). The PIC of shark visits was independent of swell height ($H_{(3,227)} = 4.182$, $P > 0.24$), although a non-significant trend suggested that sharks spent a lower percentage of a visit at the vessel during calmer days (Fig. 4.8c).

4.4.7 Effect of wind strength

The TVT of white sharks was independent of wind strength ($H_{(3,235)} = 3.459$, $P > 0.20$) (Fig. 4.9a). The number of minutes that sharks was observed at the chumming vessel (TIC) ($H_{(3,234)} = 5.642$, $P > 0.10$) (Fig. 4.9b) and the PIC was independent of wind strength ($H_{(3,234)} = 1.76$, $P > 0.64$) (Fig. 4.9c).

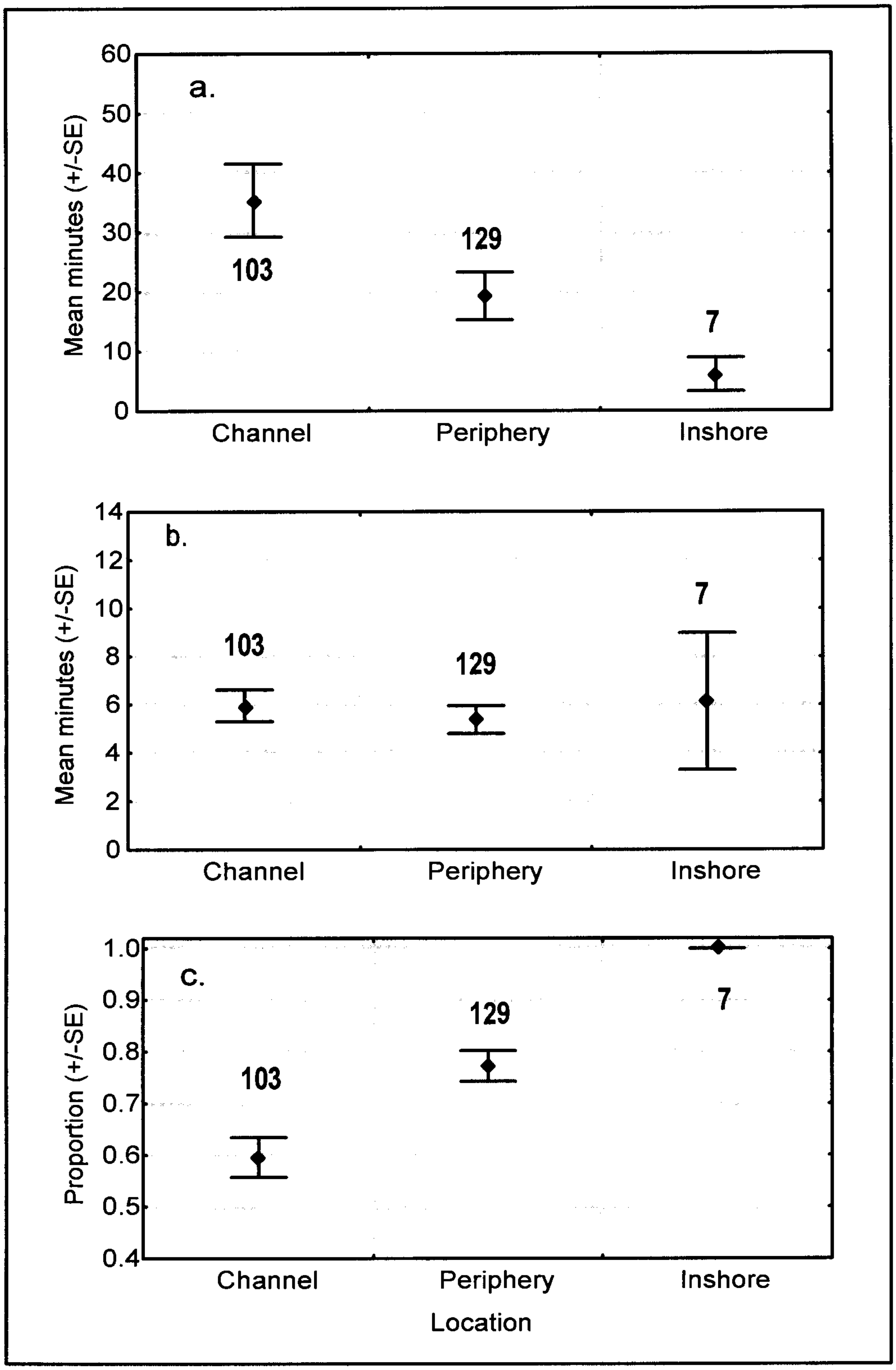

Figure 4.7 Effect of location on the visitation patterns of white sharks to a chumming vessel. Figures: 4.7a – Total visit time, 4.7b – Time in contact, 4.7c – Proportion in contact. Data labels represent N.

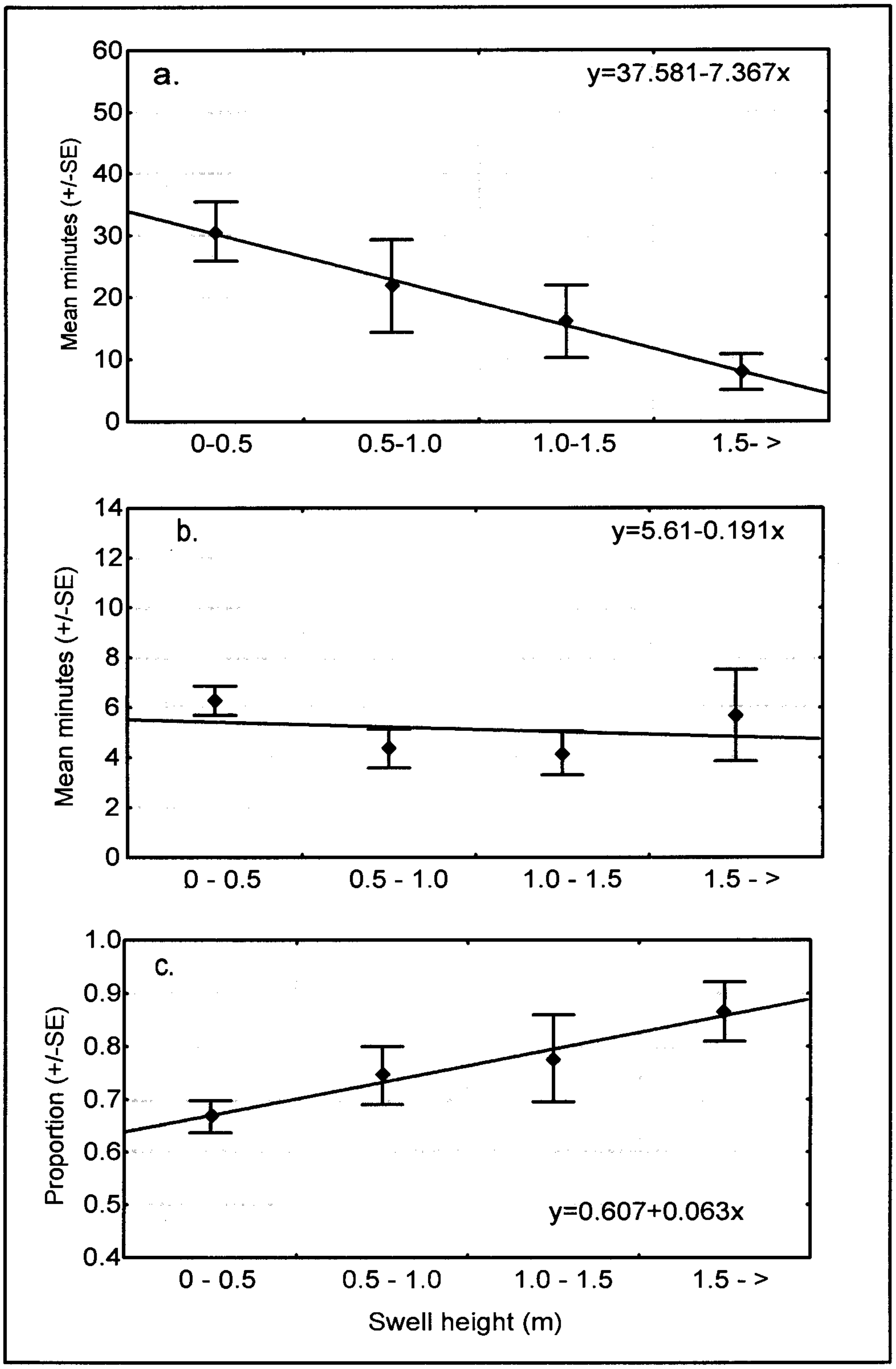

Figure 4.8 Effect of swell height on the visitation patterns of white sharks to a chumming vessel. Figures: 4.8a – Total visit time, 4.8b – Time in contact, 4.8c – Proportion in contact. Data labels represent N.

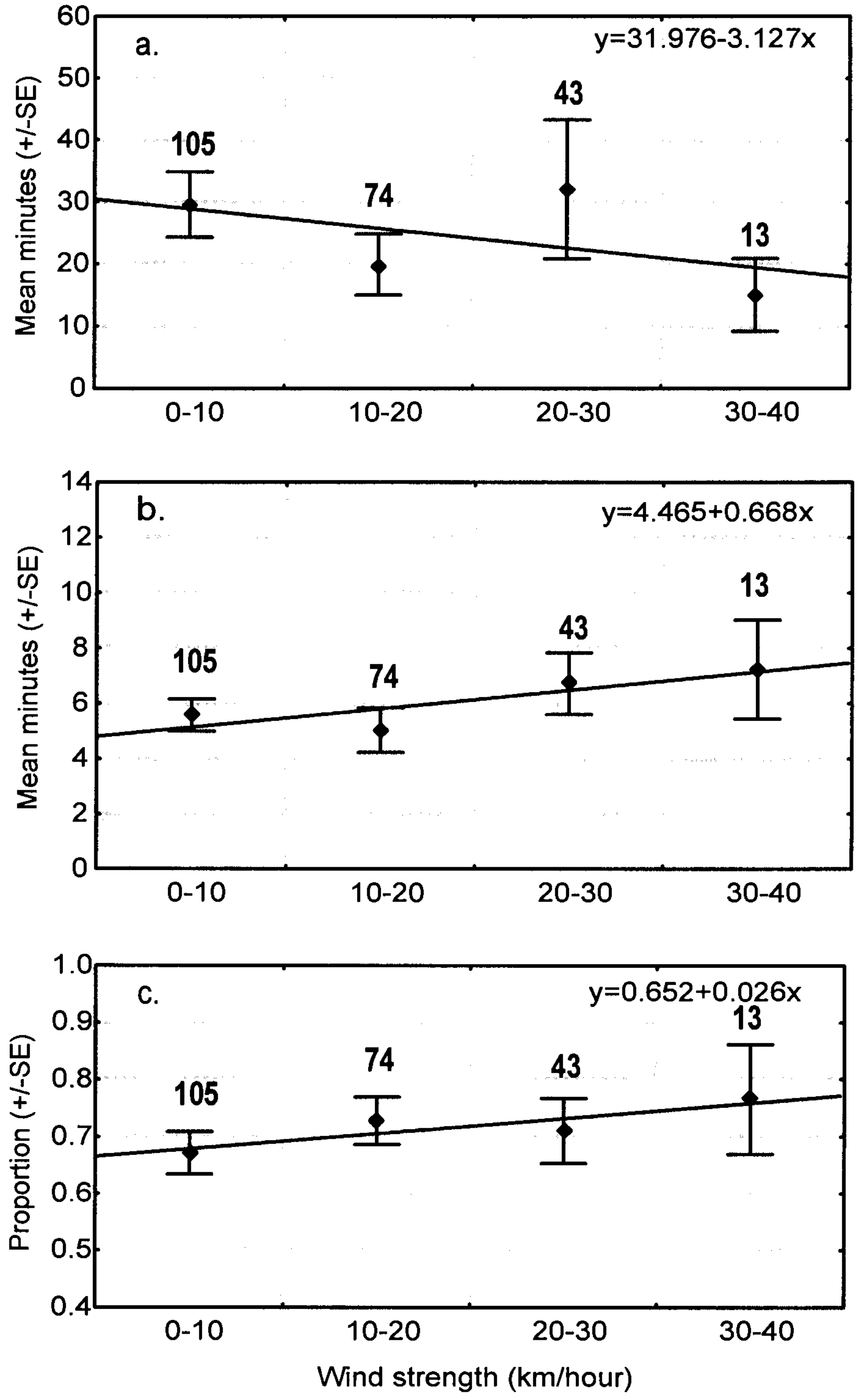

Figure 4.9 Effect of wind strength on the visitation patterns of white sharks to a chumming vessel. Figures: 4.9a – Total visit time, 4.9b – Time in contact, 4.9c – Proportion in contact. Data labels represent N.

4.3.8 Effect of water visibility

Water visibility significantly affected the daily TVT of white sharks to the chumming vessel ($H_{(2,229)} = 8.414$, $P < 0.05$), in good visibility the daily TVT was greatest (Fig. 4.10a). Although sharks appeared to spend more minutes in contact with the boat in days of better water clarity (Fig. 4.10b), this was not statistically significant ($H_{(2,229)} = 4.518$, $P > 0.10$). The PIC at the chumming vessel was also independent of water visibility ($H_{(2,229)} = 5.856$, $P > 0.05$) (Fig 4.10c).

4.3.9 Effect of cloud cover

The TVT of white sharks to the vessel was significantly affected by the atmospheric conditions (level of cloud cover) ($H_{(2,228)} = 8.414$, $P < 0.05$). Sharks had the greatest TVT on overcast days compared to clear and partly cloudy days (Fig. 4.11a). Sharks observed during overcast and partly cloudy conditions spent significantly longer time in the vicinity of the boat (TIC) than sharks observed on clear days ($H_{(2,228)} = 8.010$, $P < 0.05$) (Fig. 4.11b). The PIC was independent of cloud cover ($H_{(2,228)} = 4.668$, $P > 0.05$), despite the lower percentage of a shark's visit being spent in the vicinity of the boat on overcast days (Fig. 4.11c).

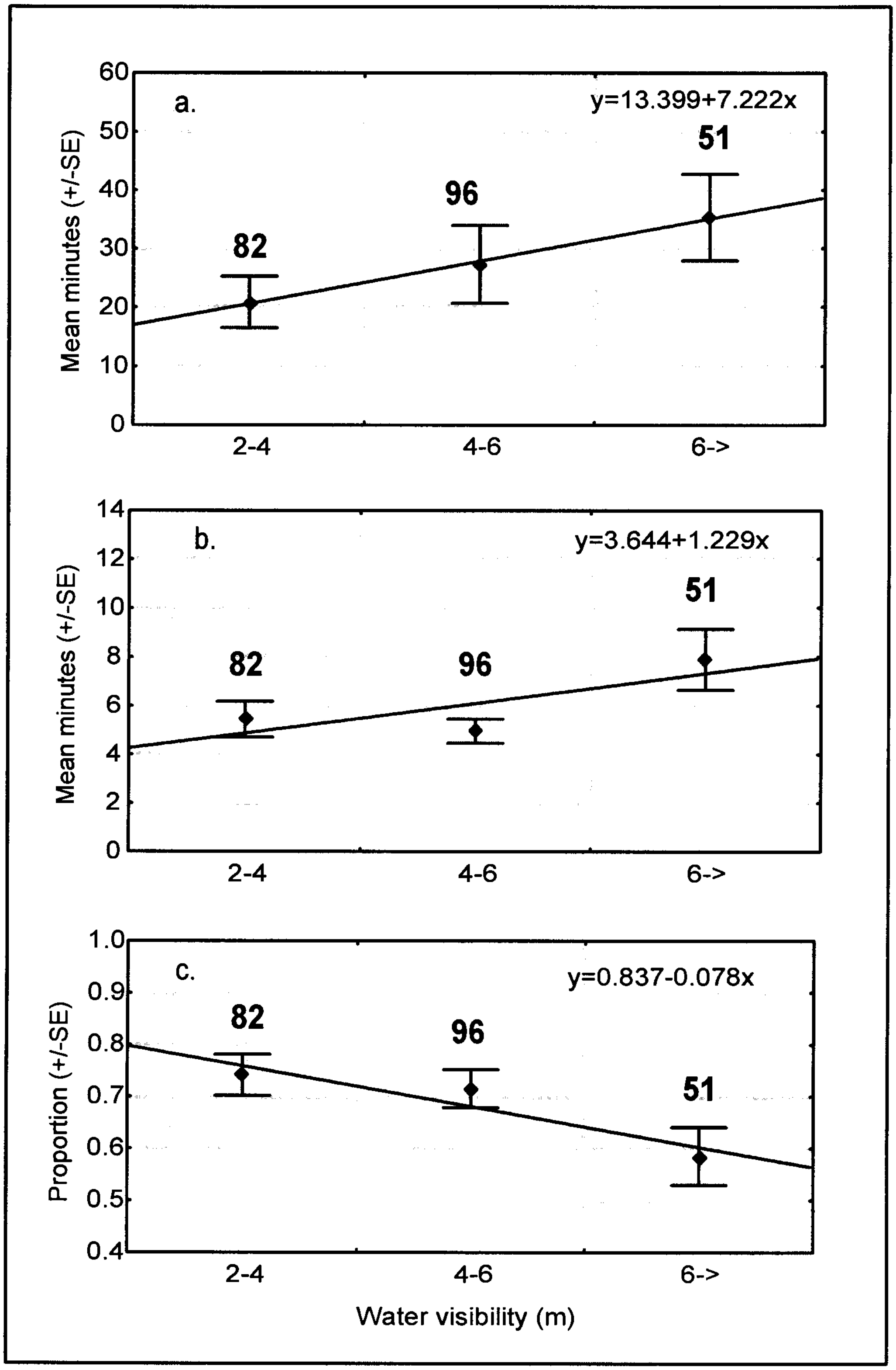

Figure 4.10 Effect of vertical water visibility on the visitation patterns of white sharks to a chumming vessel. Figures: 4.10a – Total visit time, 4.10b – Time in contact, 4.10c – Proportion in contact. Data labels represent N.

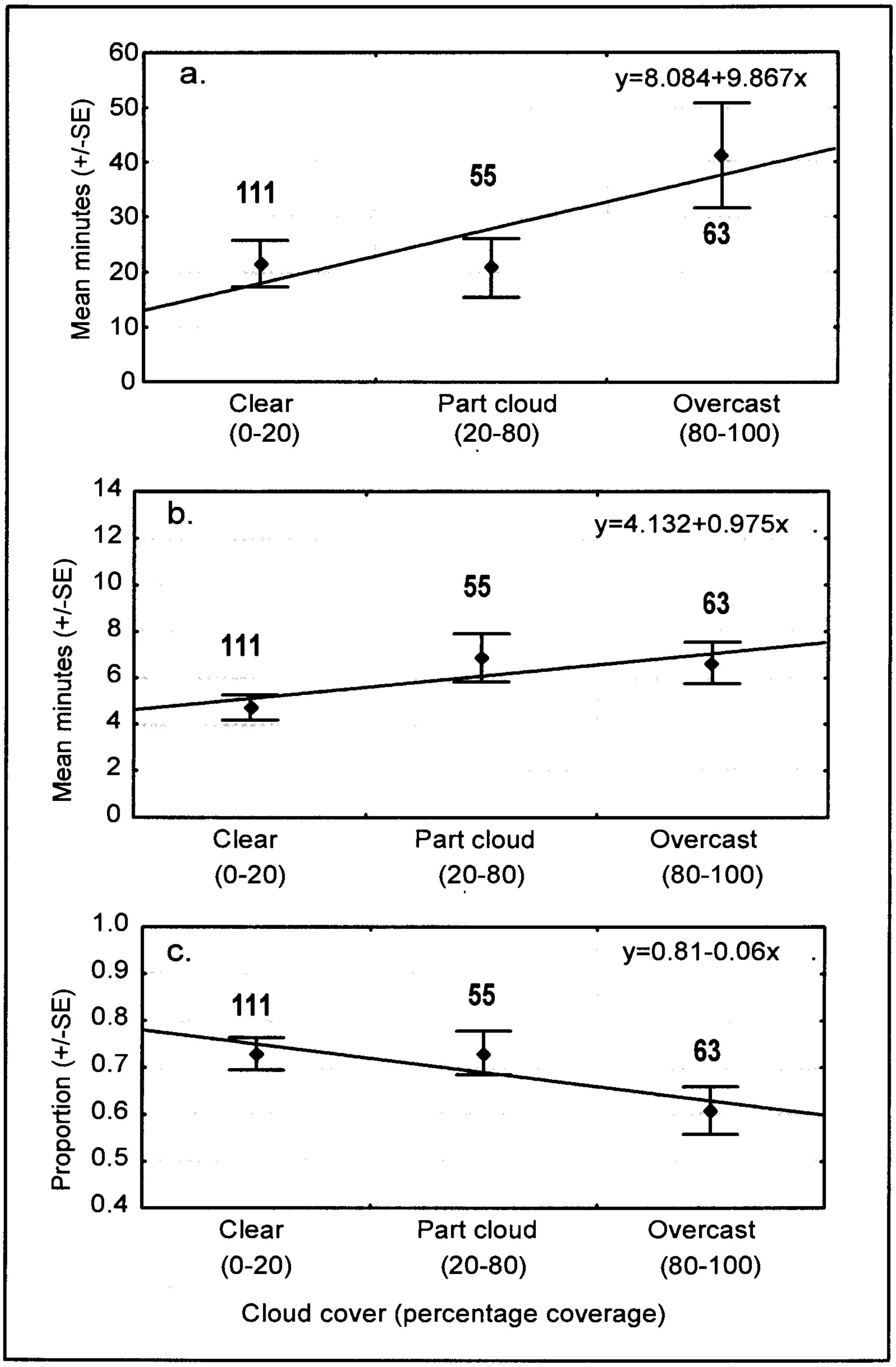

Figure 4.11 Effect of percentage cloud cover on the visitation patterns of white sharks to a chumming vessel. Figures: 4.11a – Total visit time, 4.11b – Time in contact, 4.11c – Proportion in contact. Data labels represent N.

4.4 Discussion

4.4.1 Limitations of study

This work gives some initial indications on the behavioural response of white sharks to chumming vessels, and although similar to the operational procedure of white shark cage-diving distinct differences did exist. Despite these differences, the presence of chum, focal points (decoys as opposed to bait) and a boat mimics a chumming vessel situation and the resultant behavioural response of white sharks to an extent. Within the scope of this work we can begin to assess issues surrounding the potential for conditioning of white sharks and the level of distraction chumming vessels cause to white sharks.

4.4.2 Conditioning of white sharks

The most strongly voiced concern directed towards cage-diving is the potential for white sharks to be conditioned to associate boats and divers with food, and thus directly increase the threat that white sharks pose to humans. Associative learning could occur if white sharks were predictably fed (unconditioned response) on the bait (unconditioned stimulus) while in the vicinity of the chumming boat and/or divers (conditioned stimulus) over a fairly long period of time (Sadie 1998). The likelihood of white sharks being conditioned is thus dependant on the behavioural response of white sharks to cage-diving vessels (experience, exposure level and behavioural patterns), and the predictability at which they gain rewards (bait) during the cage-diving operations.

White sharks that have attacked humans are generally large, with the most common length estimate being between 4.4 and 5.0m (26%) (Burgess & Callahan 1996). Within the present study it appears that the very large white sharks generally react little to the presence of a chumming vessel as illustrated by their significantly lower TVT and TIC. The fact that smaller white sharks displayed greater TVT and TIC than their larger counterparts indicates greater short-term fidelity and/or responsiveness to the chumming stimulus. Furthermore, during associative conditioning experiments, juvenile lemon and bull sharks were conditioned more readily than their adult counterparts (Wright & Jackson 1964), suggesting that juvenile white sharks may also be the most vulnerable to a situation where associative conditioning may occur. This increased short-term exposure of small white sharks to a chumming vessel in conjunction with a suspected greater ability to learn, suggests that they are the most vulnerable size category to any possible conditioning influences arising from cage-diving operations.

Another variable that could influence the likelihood of white sharks being conditioned is cloud cover. White sharks interacting at chumming boats is partly motivated by feeding, and low light levels associated with overcast conditions are conducive to successful hunting due to increased camouflage (Strong 1996). This kind of environment seems to elicit more motivated feeding responses from white sharks, which was reflected in increased exposure (TVT, TIC) to the chumming vessel. The increased activity and short-term exposure of white sharks during overcast conditions suggest greater vulnerability to associated negative impacts, such as conditioning. This, coupled with increased camouflage (due to glare) to the shark handler may result in greater likelihood of white sharks regularly gaining bait (rewards).

The second environmental variable that appears to influence the visitation pattern of white sharks to cage-diving vessels is water visibility. Surprisingly, sharks appear more active and willing to stay around the chum source on days of good water visibility. Many indications suggest that white sharks are more active hunters during times of poor water visibility (Chapter 3, Pyle *et al.* 1996), presumably due to the positive influences of this environment on successful hunting. It would thus be expected that when water visibility is low white sharks would be more active at boats. This result is difficult to explain, but may be related to factors, such as the ease at which the chumming vessel could be located, or sharks being more comfortable around the 'typically foreign' boat when water clarity is high.

Despite similar visitation patterns of each sex, difference in long-term exposure might exist with respect to shark sex. The skewed sex ratio (in favour of females) observed at the Dyer Island region (Chapter 2) and in other cage diving areas in South Africa (*unpub. data*) suggests that some sexual segregation does occur, with females possibly concentrating in areas where pinniped colonies exist and where cage diving occurs. If this is the case, then female white sharks may be exposed to chumming vessels on a more regular basis than their males counterparts.

At present it is very unlikely for any conditioning influence to result from cage-diving, due to the overall limited exposure and the non-consistent gaining of rewards by white sharks when at cage-diving vessels. No resident white sharks were observed during the study, which suggests that long term exposure to cage-diving is unlikely. However, as trends in behavioural response to chumming vessels do exist, it is important to identify situations when the greatest possibility of this negative impact being realised exists. One of the key precursors for conditioning to occur is 'experience' of the unconditioned stimulus, in this case the chumming vessel. Particular care must be taken by operators when working with sharks, or in situations when the behavioural response to chumming vessels is going to result in much contact and the possibility of conditioning exists. During these operational situations extra precautions must be made by sharks handlers to minimise the amount of bait lost to these sharks.

4.4.3 Distraction of white sharks from typical activities

Potential negative impacts, such as distraction of white sharks from typical activities, may have the greatest impact in areas, or during times, of important life history events, such as breeding or hunting.

Keeping a white shark at the boat for upwards of an hour is impacting on the movement patterns of the white shark. Time that could have been well spent searching for live prey has been wasted tracking down and locating an unrewarding source of chum, resulting in energy expenditure without any gain.

Goldman & Anderson (1999) found differential swim and behavioural patterns in white sharks with respect to location. Within areas where pinnipeds were abundant, and attacks on them were frequent, large white sharks patrolled in a routine pattern for extended periods of time (Goldman & Anderson 1999). Similarly, the intermittent visitation patterns of white sharks in the Dyer Island channel appears closely linked with directed patrolling and searching for prey. Within the channel area at Dyer Island, the tendency for white sharks to have a high TVT, that is characterised by short bouts of activity at the boat, interspersed with periods of absence, (low PIC) is consistent with observed hunting strategies at the Farallon Islands. The channel area appears to be an important hunting ground for this species. Distraction from patrolling and other predatory related behaviours implies a comparatively greater distractive impact by cage-diving within the channel.

Season did not seem to play an important role in defining the behavioural response of white sharks to a chumming vessel (present study). Amongst cage-diving operators there is, however, a distinct perception that sharks in the winter (June – August) are far more active than those observed during the summer period. These sharks are commonly termed ‘players’ and frequently stay around a vessel for upwards of an hour (M.C. Scholl, M. Rutzen, A. Hartman *pers. comm.*). The absence of baits at the research vessel compared to their use at cage diving vessels presumably caused these differences. If a white shark’s responsiveness to chumming vessels proves to be seasonal, and activity peaks during the winter, this could possibly be an indication of season-specific feeding strategies. The increased concentration of sharks at the Dyer Island group (as opposed to inshore locations) during the winter possibly indicates a feeding strategy that focuses on large energy rich prey, such as fur seals during this time (Chapter 2; Klimley 1992). Spending large amounts of time at chumming vessels during the winter months may distract greatly from the amount of time available to hunt such prey.

The high abundance of cone receptors in the white shark retina suggests that the white shark can see well during the day and is probably a diurnal hunter (Gruber & Cohen 1985). Live attacks on pinnipeds at the Farallon Islands also indicated peaks in hunting pinnipeds during daylight hours (Klimley *et. al.* 1992). The behavioural response of white sharks was consistent throughout the daylight hours in the present study. Work throughout entire 24-hour periods is required to determine trends in the occurrence of natural attacks within cage diving areas. Diurnal trends in shark/seal attacks have been observed at Seal Island, False Bay with peaks in predatory incidents occurring in the early morning and late afternoon (C. Fallows *pers. comm.*). Futhermore, cage-diving operators in South Africa suggest that the behaviour of white sharks varies throughout the day (A. Hartman *pers. comm.*), with increased 'aggression' towards the baits during the morning, with them becoming more docile and easier to work with throughout the midday period. If hunting behaviour proves to be crepuscular then the impacts of distracting white sharks away from hunting would be greatest during the early morning and late afternoon periods.

4.4.7 Synthesis and future work

Of the various categories of sharks observed, we suggest that small sharks (<275cm TL) are probably the most vulnerable to being conditioned due to longer visitation patterns (TVT) at a chumming vessel, and possibly through their greater sensitivity to associative learning situations. White sharks also displayed longer visitation patterns (TVT) on overcast days, which, in conjunction with glare-induced camouflage (possibly causing greater rewarding rate of hunting sharks) could result in greater likelihood of conditioning.

Based on available information the possibility of cage diving causing associative conditioning in white sharks, and subsequently increasing the threat of white sharks to humans, is insignificant. However, due to the white sharks being a highly publicised species that is potentially dangerous to humans, it is essential that every precaution be taken to ensure that conditioning does not occur, and that effects of other impacts (injury, distraction, stress) are minimised through active management by the legislative bodies controlling this sector. This will go a long way towards stabilising the cage diving sector and allowing the educational and conservation value of cage diving to be realised.

Some evidence exists to suggest that areas directly adjacent to pinnped islands are important hunting grounds, particularly in the early morning and late afternoon. During such times white sharks regularly patrol these areas in the hope of ambushing pinnipeds. The distractive impact of chumming and attracting a white shark to a chumming vessel would be greatest in this kind of situation. Additionally, indications that white sharks most frequently attack pinnipeds during the early morning and late afternoon suggest that these times are also important for white sharks to be involved in natural predatory behaviour. In these situations cage-diving should be curtailed to ensure minimal interference. The channel area adjacent to the local seal colony at Geyser Rock is one such area that appears to be an important hunting ground for white sharks. Mitigating the impact of cage-diving, which inherently distracts white sharks from patrolling/hunting activities, could be achieved by greatly restricting operations within this, and other similar areas.

Further research is urgently required to assess which trends are valid with respect to the cage-diving. Research (preferably from the tourism boats themselves) into the behavioural response of white sharks to cage-diving vessels is the only way to conclusively determine the short-term behavioural response of white shark to this situation. Extrapolation of the results of the present study is limited, and a few trends observed by cage dive operators (particularly seasonal trends) were not observed. Further research is also required to establish the residency and long-term exposure patterns of white sharks to chumming vessels while within cage-diving sites, as well as the extent of feeding that occurs when sharks are at cage-diving vessels.

CHAPTER 5

Prey preference and visual discriminatory ability in the white shark (*Carcharodon carcharias*) determined by multiple choice tests.

5.1 Introduction

5.1.1 Studies on predatory behaviour

The primary prey of white sharks are taxa, such as teleosts, elasmobranchs, cephalopods and marine mammals (Le Boeuf *et al.* 1982; Cliff *et al.* 1989, 1996a; Klimley *et al.* 1992). Surprisingly, however, white sharks bite a wide diversity of objects that are often unpalatable or not recognised as a prey species (Collier *et al.* 1996; Anderson *et al.* 1996a; Strong 1996; Compagno *et al.* 1997). This behaviour has led to much conjecture on the cognitive and selective process of white sharks following detection of potential prey (Klimley 1994; Strong 1996; Collier *et al.* 1996).

Understandably, investigating the selective process governing white shark attacks has proved a difficult proposition for scientists due to the rarity and nature of the predatory encounters. Previously, methods have been restricted to *post hoc* inference of attack evidence, such as analysis of shark stomach contents (Le Boeuf *et al.* 1982; Cliff *et al.* 1989, 1996a; Bruce 1992) and observation of fresh bite wounds and scarring on surviving victims or retrieved carcasses (Ainley 1981, 1985; Le Boeuf *et al.* 1982; Tricas & McCosker 1984). Furthermore, observations of live attacks have been used with success in the Farallon Islands to describe patterns of white shark attacks on the northern elephant seal (*Mirounga angustirostris*), California sea lion (*Zalophus californianus*) and steller seal lion (*Eumetopias jubatus)*, as well as describing these attacks following the initial strike (Klimley *et al.* 1992, 1996; Anderson *et al.* 1996b; Pyle *et al.* 1996).

5.1.2 Limitation of current methods to investigate prey preference

The limitation of these studies is that only following a successful initial strike can information be garnered. The process prior to the initial strike (detection, identification, approach and decision to attack) cannot be investigated. The difficulties to observe attack behaviour prior to the initial strike have restricted the ability to conclusively determine what cues are required for an attack/investigation to be initiated. Observation of a large array of objects and prey types displaying evidence of white shark biting them (Collier *et al.* 1996) implies that white sharks are opportunistic predators that require only a few basic cues before initiating an attack. This, however, may also be misleading, in that no quantifiable information exists as to the comparative frequency of attacks on various inanimate objects and unusual prey types. These possible 'rare events' may be infrequent exceptions, the motivation of which is not related to feeding. Furthermore, the presence of confounding sensory cues may lead to attacks being initiated in error. Many fishing boats release chum to attract fish, while spear fishermen often have fish attached to themselves or to their spear gun while fishing.

It is thus likely that these speculative hypotheses derived from incidental observations simplify complexities in prey preference and choice of the white shark. The infrequency of attacks/incidences involving humans and white sharks in South Africa (Cliff 1991) is evidence enough that the hunting behaviour of the white sharks is more complex than these aforementioned hypotheses would permit. This is particularly true when appreciating the near shore distribution pattern of white sharks during spring and summer at areas like the Dyer Island region (see 2.3.1).

5.1.3 Use of inanimate prey resembling decoys

The use of inanimate decoys resembling various prey species and shapes have been introduced to solicit predatory responses from white sharks. These methods aim to increase information regarding prey preference, as well as to determine the ability of the white shark to visually discriminate between various shapes (Strong 1996; Anderson *et al.* 1996a). This method allows the detection, identification, and approach phases of a white shark attack to be directly observed rather than inferred from post attack analysis.

5.1.4 Aims

The objectives of this chapter are to investigate the selectivity and preferences of white sharks in the presence of a number of combinations of inanimate decoys resembling prey. Furthermore, I intended to establish whether variation in selectivity patterns is a function of shark size or proximity to a seal colony.

The specific objectives of this chapter is to determine:

- If white sharks discriminate and/or prefer certain prey resembling shapes over others,
- If the selective tendencies of the white shark are independent of shark size,
- If the selective tendencies of the white shark are independent of proximity to a seal colony.

5.2 Methods

5.2.1 Experimental set-up and procedure

The choice test experiments were carried out in the Dyer Island region (see 2.2.1 for detail) (Fig 5.1). The study continued from September 1999 until January 2001, during which time observations were made on 136 days, for a total of 617 hours of boat based observations. During experimentation 292 white sharks visited the boat (individuals were identified on a daily basis only), some of which accounted for a total of 398 contacts with the experimental decoys.

Five types of high-density foam rubber decoys of specific shapes and sizes were used throughout the prey preference trials (Fig. 5.2). Two decoys (relevant to the particular choice test) were deployed simultaneously from the stern of the vessel in the standard experimental set-up (see 3.2.1 for detail). The particular decoys used in a trial were randomly assigned (by blind selection) to either the starboard or port side. Sharks were attracted to the experimental set-up utilising the standard chumming procedure (see 2.2.1 for shark attraction details), and on arrival a standard operational protocol was followed (see 3.2.1 for detail).

In choice tests carried out by Strong (1996) a 'selection' of a decoy was defined as an 'orientated approach' towards one decoy by a white shark. However, in the preliminary study into the movement and interactions between sharks and decoys this criterion for a selection was considered weak, as to much observer subjectivity existed. Subsequently, physical contact (namely: bumping, low speed attacks or high speed attack – see 3.2.2) was the defining character that fulfilled the requirements of a 'selection'.

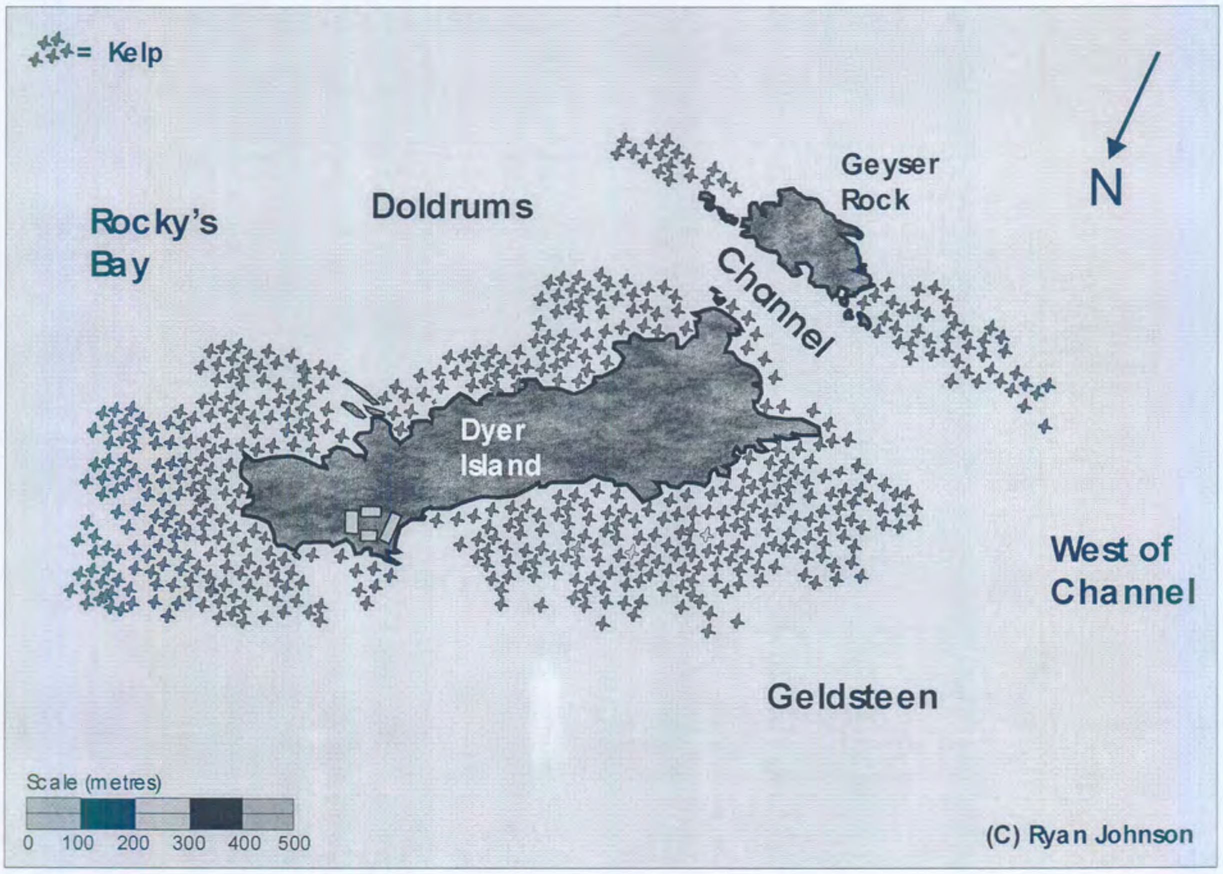

Figure 5.1 Common anchor locations in the waters surrounding Dyer Island. These include: Channel (Channel area) and Rocky's Bay, Geldsteen, Doldrums and West of Channel (Island periphery areas).

5.2.2 Choice tests conducted

Four choice tests were carried out during this study, which included:

- A control experiment (expt. 1 – Fig. 5.2) consisting of two similar sized juvenile seal decoys (1100 mm), differing only by individual marking on the top surface (out of the view of an approaching shark).
- The juvenile sized seal (TL 1100 mm) and rectangular decoys (1000 mm x 700 mm) were deployed from the vessel to test the shape preference by white sharks (expt. 2 – Fig. 5.2). The surface areas of the two decoys were approximately similar and both were coloured dark grey.
- Two seal decoys representing an adult (1800 mm TL) and a pup (750 mm TL) seal were deployed (expt. 3 – Fig. 5.2) to test prey size preference.
- The forth experiment determined preference between the Cape fur seal (recognised prey) and African penguin (irregular prey) (expt. 4 – Fig. 5.2). These decoys differed in shape and colouration, but little difference in size, with the seal decoy being only slightly longer (750 mm TL vs. 600 mm TL).

5.2.3 Data Analysis

Rarely did individual sharks make more than three contacts with the decoys during a day's visit. Thus, when sufficient sample sizes existed, only the first three contacts were subjected to analysis. The first, second and third contacts were analysed independently to avoid pseudo-replication. Data was analysed using analysis of frequency statistical tests (chi-squared). Data was corrected using Yate's correction for continuity due to there being only two dependent variables.

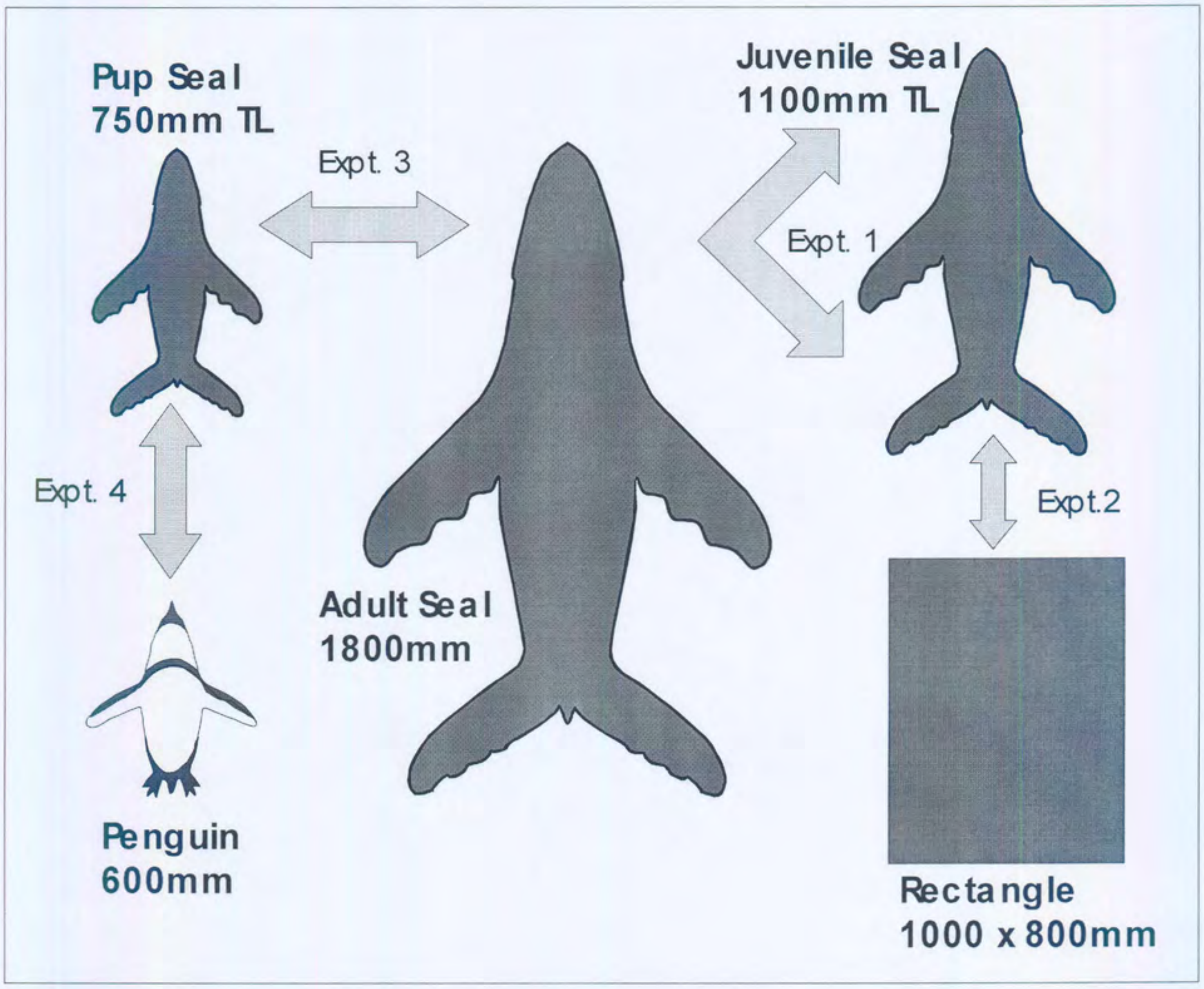

Figure 5.2 Decoys of potential prey constructed and summary of choice tests conducted.

5.3 Results

5.3.1 Control experiment (juvenile seal vs. juvenile seal)

White sharks showed no preference for either of the two identical decoys (decoy one vs. decoy two) ($\chi^2_{(0.05,1)} = 0.052$, $P > 0.95$) (Fig 5.3b, Table 5.1), or for either side (left decoy vs. right decoy) of the experimental set-up during their initial selections ($\chi^2_{(0.05,1)} = 0.473$, $P > 0.95$) (Fig. 5.3a, Table 5.1). In subsequent contacts (2nd and 3rd contacts) by the same individuals, they again hit the decoys randomly with no preference for either decoy or side (Fig. 5.3a,b, Table 5.1).

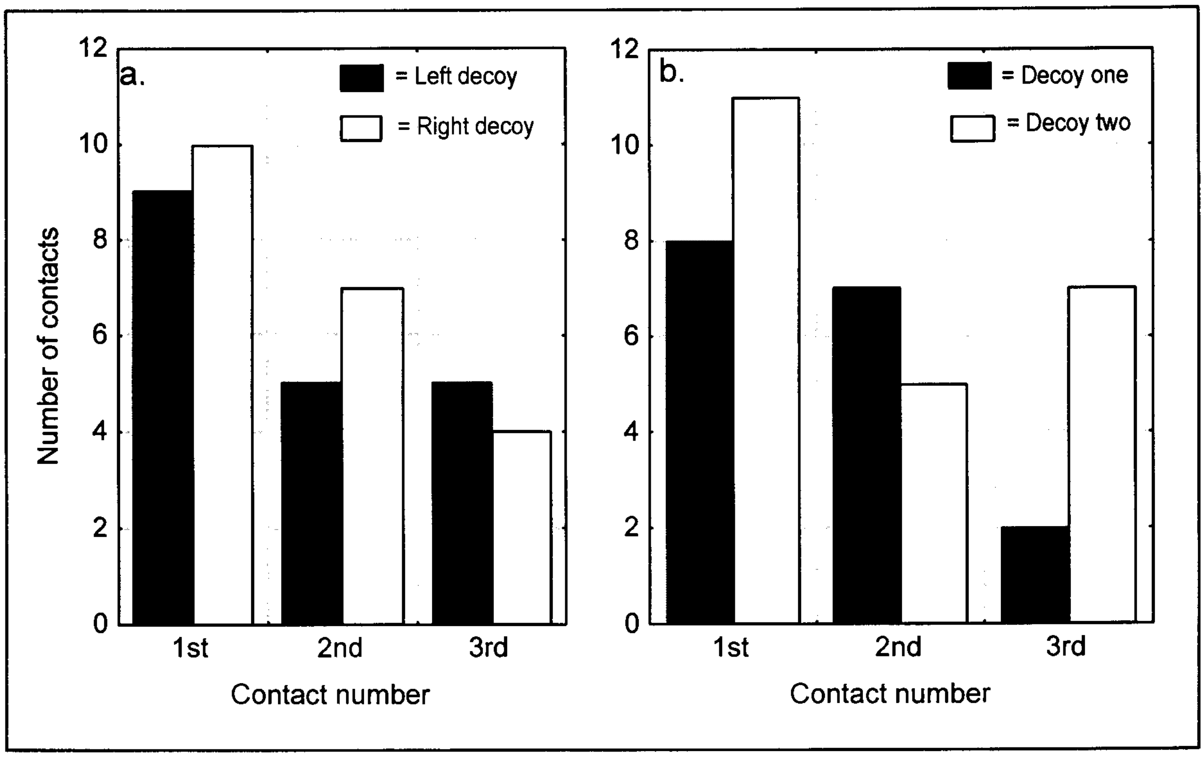

Figure 5.3 Results from control experiment consisting of two identical Cape fur seal decoys. Figures: 5.3a – Test for preference of side of experimental set-up, 5.3b – Test for preference of each decoy.

Table 5.1 Results from control experiments to determine neutrality of experimental set-up. Decoys used in experiment were two identical juvenile seals (χ^2 values calculated after applying Yates' correction for continuity).

		Decoy 1		**Decoy 2**			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
1	19	47	9	53	10	0.000	>0.05
2	12	42	5	58	7	0.083	>0.05
3	9	56	5	44	4	0.000	>0.05
		Left Side		**Right Side**			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
1	19	42	8	58	11	0.473	>0.05
2	12	58	7	42	5	0.333	>0.05
3	9	22	2	78	7	2.777	>0.05

5.3.2 Shape preference experiment (juvenile seal vs. rectangle)

White sharks showed a significant preference for the seal decoy over the square decoy during the initial contact in this experiment ($\chi^2_{(0.05,1)} = 7.2$, $P < 0.01$, $N = 20$) (Fig. 5.4a, Table 5.2). Following the initial contact the observed white sharks showed no preference between decoys in successive (2nd and 3rd) contacts (Table 5.2a, Fig. 5.4a).

Outside of the channel white sharks significantly preferred the seal decoy ahead of the square decoy during the 1st contact ($\chi^2_{(0.05,1)} = 5.8$, $P < 0.025$, $N = 16$) (Fig. 5.4c, Table 5.2), to few data was collected to test preference in the 2nd and 3rd contacts. Too few data was collected from sharks within the channel to allow statistical testing. Sharks below 375 cm did not show a preference for either of the decoys in their initial contact ($\chi^2_{(0.05,1)} = 0.818$, $P > 0.20$, $N = 11$), to few data was collected to test preference in subsequent (2nd and 3rd) contacts.

Larger sharks (>375 cm) initially showed a significant preference for the seal decoy over the square decoy ($\chi^2_{(0.05,1)} = 9$, $P < 0.005$, $N = 9$) (Fig. 5.4b, Table 5.2), but to few data was collected to determine if this trend persisted in subsequent (2nd and 3rd) contacts.

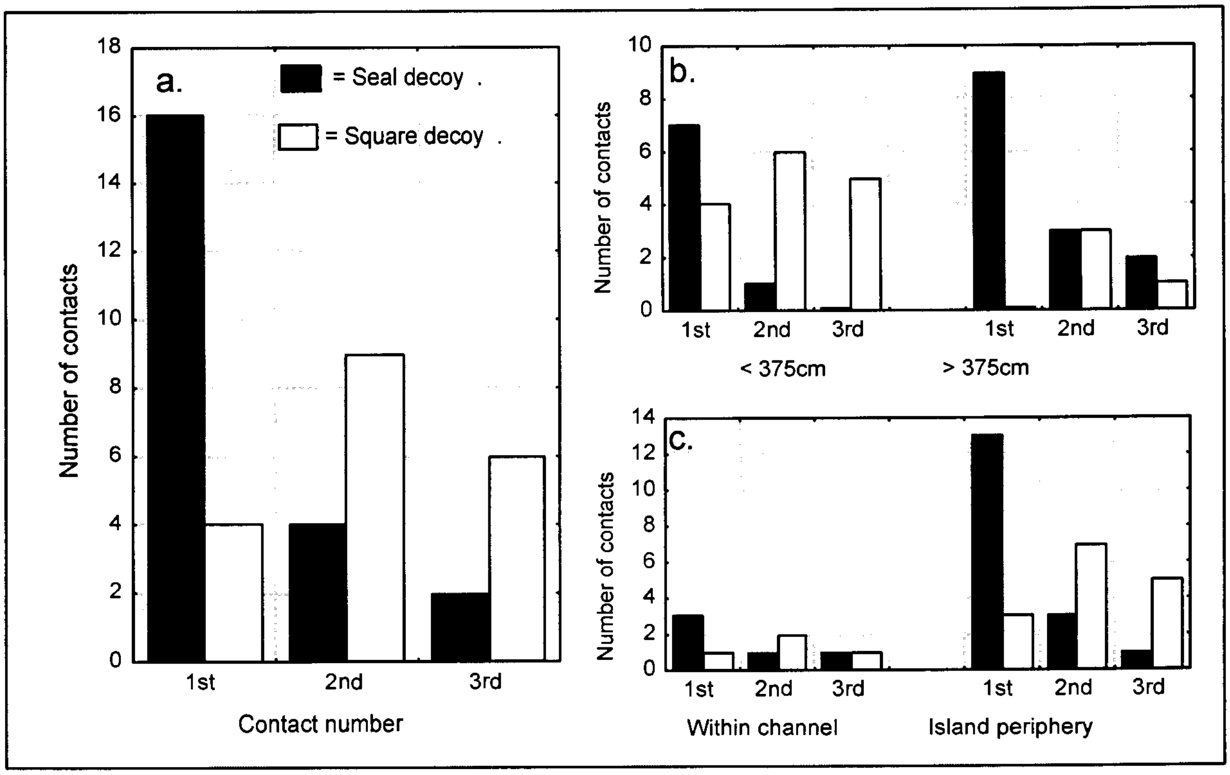

Figure 5.4 Results from shape experiment consisting of a seal decoy and a rectangle decoy. Figures 5.4a – Combined results, 5.4b – Divided for shark size, 5.4c divided for location.

Table 5.2a Overall selection of each decoy type by white sharks in shape experiment.

		Seal		**Square**			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
1	20	80	16	20	4	6.05	**<0.05**
2	13	31	4	69	9	1.23	>0.05
3	8	25	2	75	6	1.13	>0.05

Table 5.2b Selection of each decoy by white sharks with respect to proximity to the seal colony.

		Seal		**Square**			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
Within channel							
1	4	75	3	25	1	NA	NA
2	3	33	1	67	2	NA	NA
3	2	50	1	50	1	NA	NA
Outside channel							
1	16	81	13	19	3	5.06	**<0.05**
2	10	30	3	70	7	0.90	>0.05
3	5	17	1	83	5	NA	NA

Table 5.2c Selection of each decoy by white sharks with respect to shark size.

		Seal		**Square**			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
Small grouping (<375cm)							
1	11	64	7	36	4	0.36	>0.05
2	7	14	1	86	6	NA	NA
3	5	0	0	100	5	NA	NA
Large grouping (>375cm)							
1	9	100	9	0	0	7.11	**<0.01**
2	6	50	3	50	3	NA	NA
3	3	67	2	33	1	NA	NA

5.3.3 Size preference (pup seal vs. adult seal)

There was a clear, yet non-significant, trend to select the pup seal decoy over the adult seal decoy during the sharks first contacts ($\chi^2_{(0.05,1)} = 2.57$, $P > 0.10$, $N = 14$) (Fig. 5.5a, Table 5.3). Insufficient sharks made successive contacts (2nd contact: N = 7, 3rd contact: N = 6) with the decoys to allow any statistical testing. White sharks initially (1st contact) preferred the pup seal decoy over adult seal decoy when observed within the channel ($\chi^2_{(0.05,1)} = 6.4$, $P < 0.025$, $N = 10$) (Fig. 5.5b, Table 5.3). The sample size outside the channel was insufficient to determine any statistical trends ($N = 4$). Small white sharks (<375 cm) showed a initial (1st contact) preference for the pup seal decoy over the adult seal decoy ($\chi^2_{(0.05,1)} = 4.45$, $P < 0.05$, $N = 11$) (Fig. 4.5c, Table 5.3). An insufficient number of large white sharks made contact with the decoys (1st contact: N = 3) to statistically test whether the trend was also prevalent within this group. Of the three large (>375 cm) white sharks that made a selection, two initially targeted the adult seal decoy.

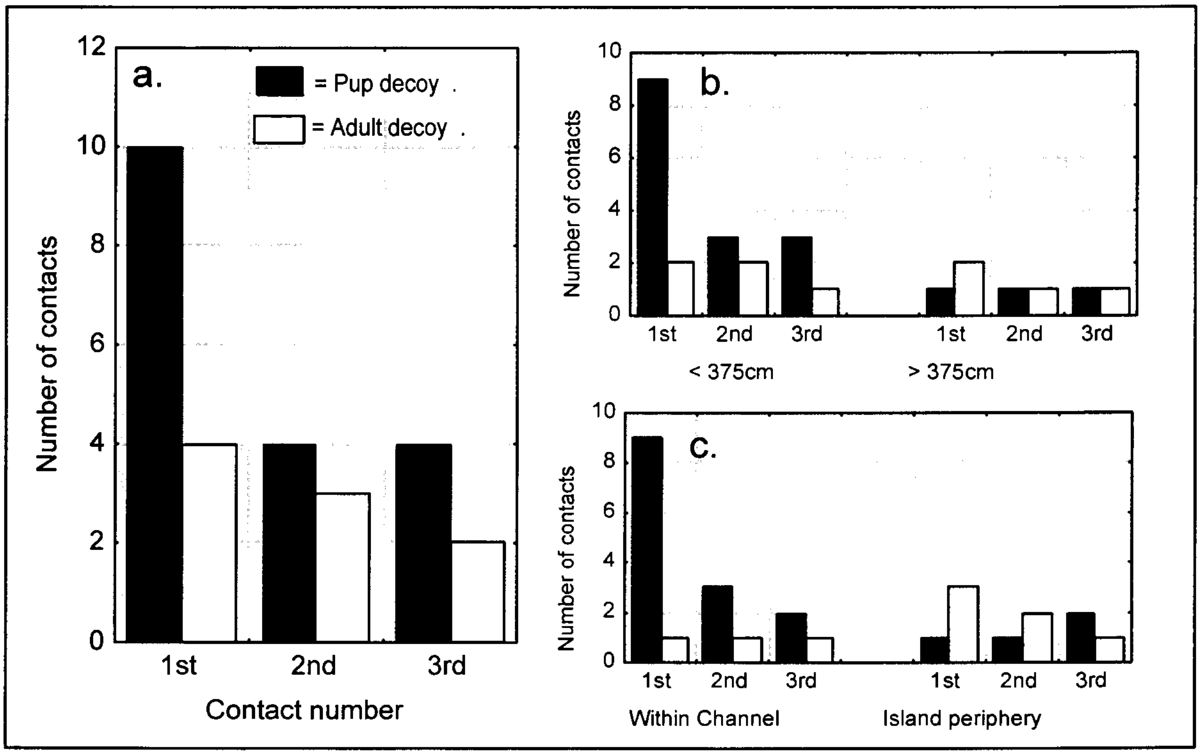

Figure 5.5 Results from size experiment consisting of a pup seal decoy and an adult seal decoy. Figures: 5.5a – Combined results, 5.5b – Divided for shark size, 5.5c – Divided for location.

Table 5.3a Overall selection of each decoy by white sharks in size experiment.

		Pup Seal		Adult Seal			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
1	14	71	10	29	4	1.78	>0.05
2	7	57	4	43	3	NA	NA
3	6	67	4	33	2	NA	NA

Table 5.3b Selection of each decoy by sharks, with respect to proximity to the seal colony.

		Pup Seal		Adult Seal			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
Within channel							
1	10	90	9	10	1	4.90	**<0.05**
2	4	75	3	25	1	NA	NA
3	3	67	2	33	1	NA	NA
Outside channel							
1	4	25	1	75	3	NA	NA
2	3	33	1	67	2	NA	NA
3	3	67	2	33	1	NA	NA

Table 5.3c Selection of each decoy by white sharks, with respect to shark size.

		Pup Seal		Adult Seal			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
Small grouping (<375cm)							
1	11	82	9	18	2	3.27	**< 0.05**
2	5	60	3	40	2	NA	NA
3	4	75	3	25	1	NA	NA
Large grouping (>375cm)							
1	3	33	1	67	2	NA	NA
2	2	50	1	50	1	NA	NA
3	2	50	1	50	1	NA	NA

5.3.4 Species preference experiment (pup seal vs. African penguin)

White sharks initially (1st contact) preferred the seal decoy to the penguin decoy during this experiment ($\chi^2_{(0.05,1)} = 5.85$, $P < 0.025$, $N = 58$) (Fig. 5.6a, Table 5.4). No preference for either decoy was observed in the 2nd and 3rd contacts (Fig. 5.6a, Table 5.4b,c). Within the channel the seal decoy was preferred during the 1st ($\chi^2_{(0.05,1)} = 4.17$, $P < 0.05$, $N = 29$) and 3rd contacts ($\chi^2_{(0.05,1)} = 5.81$, $P < 0.05$, $N = 10$), but not the 2nd (Fig 5.6c, Table 5.4b). No significant preference was observed outside of the channel during the initial (1st contact) ($\chi^2_{(0.05,1)} = 1.69$, $P > 0.15$, $N = 29$) or subsequent (2nd and 3rd) selections (Fig. 5.6c, Table 5.4b). Smaller (<375 cm) white sharks preferred the seal decoy over the penguin decoy during their 1st ($\chi^2_{(0.05,1)} = 7.90$, $P<0.005$, $N = 41$) (Fig. 5.6b), and 3rd contacts ($\chi^2_{(0.05,1)} = 3.30$, $P<0.05$, $N = 14$), but not the 2nd (Fig 5.6b, Table 5.4c). Large white sharks showed no initial (1st contact) preference for either decoy ($\chi^2_{(0.05,1)} = 0.067$, $P>0.20$, $N = 15$) (Fig. 5.6b, Table 5.4). Too few data was collected to determine if any preference existed in subsequent (2nd and 3rd) contacts (Fig. 5.6b, Table 5.4).

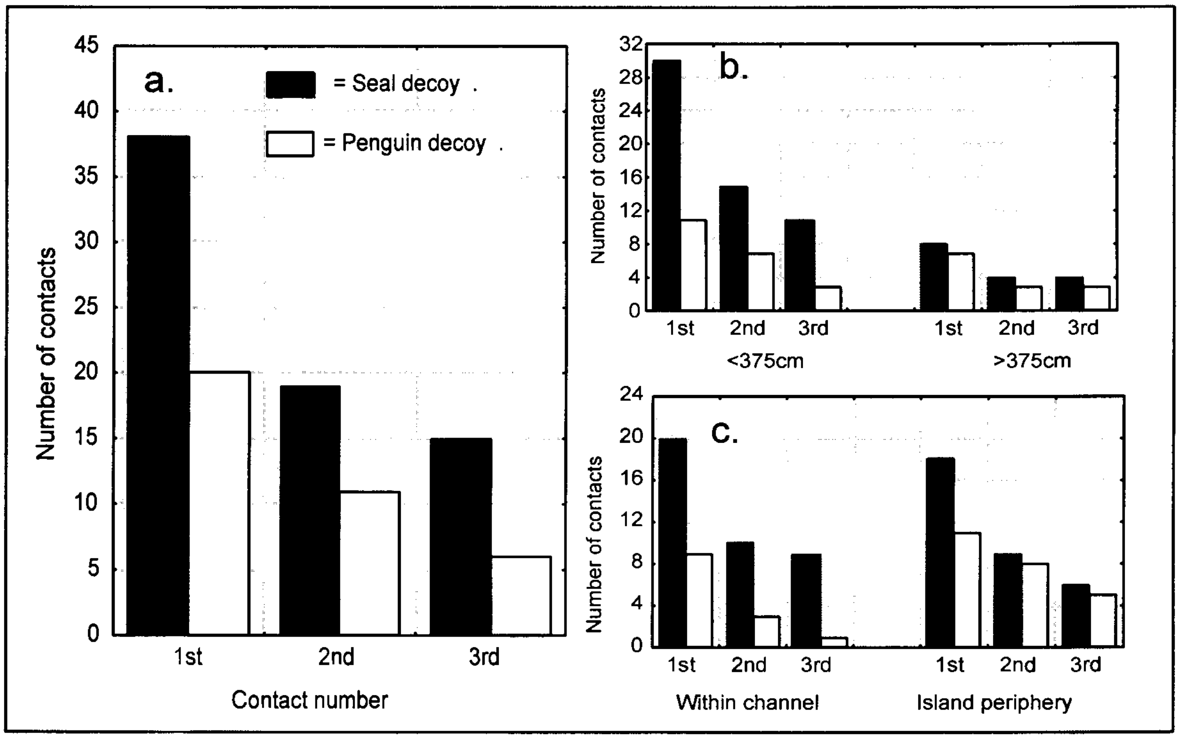

Figure 5.6 Results from species experiment consisting of a seal decoy and a penguin decoy of similar size. Figures 5.6a – Combined results, 5.6b – Divided for shark size, 5.6c – Divided for location.

Table 5.4a Overall selection of each decoy by white sharks in species experiment.

		Seal		Penguin			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
1	58	66	38	34	20	4.98	**<0.05**
2	30	63	19	37	11	1.63	>0.05
3	21	71	15	29	6	1.89	>0.05

Table 5.4b Selection of each decoy by sharks, with respect to proximity to the seal colony.

		Seal		Penguin			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
Within channel							
1	29	69	20	31	9	3.44	**<0.05**
2	13	77	10	23	3	2.76	>0.05
3	10	90	9	10	1	5.81	**<0.05**
Outside channel							
1	29	62	18	38	11	1.44	>0.05
2	17	53	9	47	8	0.00	>0.05
3	11	55	6	45	5	0.00	>0.05

Table 5.4c Selection of each decoy by white sharks with respect to shark size.

		Seal		Penguin			
Contact No.	**Total (N)**	**%**	**N**	**%**	**N**	χ^2	**P value**
Small grouping (<375cm)							
1	41	73	30	27	11	7.90	**<0.01**
2	22	68	15	32	7	2.23	>0.05
3	14	79	11	21	3	3.30	**<0.05**
Large grouping (>375cm)							
1	15	53	8	47	7	0.00	>0.05
2	7	57	4	43	3	NA	NA
3	7	57	4	43	3	NA	NA

5.4 Discussion

5.4.1 Hypotheses on prey identification and selection

White sharks have large eyes, large extraocular muscles and the presence of an orbital vascular retina, thus suggesting they have well-developed vision (Demski & Northcutt 1996). The presence of a high number of cone receptors, which are used for daytime vision, indicates that they are probably diurnal rather than nocturnal hunters (Gruber & Cohen 1985), and subsequently rely heavily on vision in the detection and identification of prey.

Despite the difficulty in observing white sharks selecting prey, a number of hypotheses concerning prey selection have been proposed. The 'mistaken identity' hypothesis was proposed to explain the occasional tendency of white sharks to attack humans (McKosker 1985). It was suggested that the similarity in shape between humans swimming or surfing and pinnipeds caused white sharks to be confused and mistakenly attack a human. Collier *et al.* (1996), however, highlighted the extensive diversity of objects that do not resemble pinnipeds and which white sharks have bitten. This includes crayfish pots, boats, buoys and others. This diversity of objects bitten led to the proposal that white sharks utilise an investigative hunting strategy. In this hypothesis white sharks purportedly investigate objects out of curiosity or to determine their potential as a food source. This hypothesis is closely linked to the speculative/opportunistic hunting strategy. Due to limited ability to discern and identify prey it is suggested that the presence of a few basic sensory cues is sufficient for a white shark to initiate an attack on a potential victim. Only following the initial strike is the food value and prey suitability to a white shark assessed and the decision to continue to feed is made (Klimley 1994). The results pertaining from the current experiments offer a number of insights into the use of vision by white sharks during the detection, approach and identification phases of a predatory type encounter.

5.4.2 Discrimination ability

Visually the two most similar decoys simultaneously deployed were the pup seal and penguin decoys, and much of the colouration differences would have been hidden from a distance. Both decoys could conceivably appear as similarly shaped black silhouettes to an approaching white shark. The significant preference of sharks <375 cm TL for the seal decoy illustrated that discrimination between the decoys was possible. It further implies that discrimination was also possible during experiments involving more dissimilar decoys. Therefore, it was assumed that all incidences of non-selection resulted from a non-preference for either decoy, rather than an inability to discern between the decoys.

5.4.3 Preference for a biologically familiar shapes

The evolutionary history of the genus *Carcharodon* is characterised by a diversification and increase in abundance during the rise of marine mammals in the Oligocene (Purdy 1996; Applegate & Espinosa-Arrubarrena 1996). In addition, specific evolutionary adaptations of the largest present day species from the *Carcharodon* genus, the white shark, suggest that pinnipeds and marine mammals are important prey for this species. Adaptations include broad and robust tooth dentition (Tricas & McCosker 1984, Applegate & Espinosa-Arrubarrena 1996), large size, and a degree of endothermy allowing them to utilise cooler waters where pinnipeds are abundant (Goldman & Anderson 1999). Given this information, it was not surprising that white sharks significantly selected the seal decoy as opposed to the rectangular decoy. Furthermore, shark size influenced the level of selection, with larger sharks (>375 cm) showing a greater preference for selecting the seal decoy than smaller sharks (<375 cm). This trend may have resulted from the differences in importance of pinnipeds as primary prey to the two groups of sharks. This finding is consistent with the results of stomach content analysis of white sharks, which indicate that smaller white sharks feed predominantly on teleosts and elasmobranchs, while larger sharks often carry remains of pinnipeds within them (Le Boeuf *et al.* 1982; Cliff 1989).

5.5.4 Role of prey size in prey preference

Much speculation and *post hoc* studies suggest that white sharks would prefer larger pinnipeds prey due to the high levels of energy contained within the blubber (Le Boeuf *et al.* 1982; Klimley 1994). Observation of wounded seals on Año Nuevo Island and Año Nuevo Mainland, California, appeared to confirm this, with a majority of the wounded elephant seals *M. angustirostris* observed being adult (Le Boeuf *et al.* 1982). Furthermore, at the Farallon Islands, California, the fatter Northern elephant seals are attacked more frequently than the leaner California sea lion *Z. californianus* and Steller sea lion *E. jubatus* (Klimley 1994). This attraction to blubber is linked to the white shark's high metabolic requirements for maintaining an elevated body temperature to enable efficient hunting in cooler waters (Klimley 1994; Goldman *et al.* 1996; Goldman 1997). Within the context of this experiment, a preference for the adult seal decoy over the pup seal decoy would be expected.

On the contrary, however, no preference for either decoy was observed over the entire experiment, while amongst smaller sharks (TL < 375cm) the pup seal decoy was preferentially selected. This finding could be related to the limited ability of smaller sharks to attack and kill large pinnipeds. Despite their fearsome reputation, white sharks are vulnerable to injury during predatory encounters. The extensive wounds inflicted to the face and body of white sharks by pinnipeds testify to the defensive capabilities of seals against this predator (*pers. obs.*). This vulnerability would be particularly relevant to smaller white sharks (*circa* 200-350cm) that could be inexperienced hunters of pinnipeds, as well as similar in size, or only slightly larger than a bull fur seal or large cow. Furthermore, additional morphological limitations exist for smaller white sharks. The classical triangular shaped tooth, that is ideally suited to removing flesh from larger prey items (Tricas & McCosker 1984) only forms once a white shark approaches approximately 350 - 400 cm TL. Until that size is reached, dentition is characterised by long slender teeth more suited to grabbing small prey. These constraints may restrict small white sharks from successfully killing and then feeding off the carcasses of large prey. This notion appears vindicated, as most reported attacks on noticeably large prey, such as elephant seals (Le

Boeuf *et al.* 1982), humans (Burgess & Callahan 1996), and a pygmy sperm whale *Kogia breviceps* (Long 1991) were generally carried out by large white sharks. Subsequently, smaller sharks (<375cm, which constituted a majority of the shark's seen) may be less willing to investigate the adult seal decoy that was presented in the present study.

5.4.4 Preference for seal or seabird shaped decoys.

During the species experiment an overall preference for the seal decoy was detected. To date only a single African penguin has been discovered within the stomach of a white shark (Bass *et al.* 1975), while throughout this study very little evidence of white sharks attacking African penguins was evident (Chapter 6). This implies that penguins are not a primary prey type of white sharks and thus the preference for the seal decoy was expected.

Despite indications that pinnipeds are not a major prey type for small white sharks (this study; Cliff *et al.* 1989; Bruce 1992), a clear preference for the seal decoy over the penguin decoy was observed in white sharks below 375 cm TL. This apparent anomaly may be caused by a combination of two factors. Firstly, during this study, two successful attacks involving pup seals and white sharks *circa* 250cm TL were observed within the channel area, suggesting that small white sharks may prey upon pinniped pups. The use of a pup seal decoy in the experimental set-up may have removed prey size limitations that smaller white sharks are typically faced with, thus enabling them to more confidently approach and investigate a seal decoy. Secondly, the behaviour of the pup seal decoy (stationary, not attempting to escape) may have more readily elicited investigatory type behaviours from smaller sharks, as an apparently dead, injured or a sleeping seal, would be unlikely to offer much resistance to an attack.

The channel area is characterised by high pinniped presence and high numbers of shark-seal attacks (*unpub. data*). The greater preference for the seal decoy over the penguin decoy in this area probably results from a combination of factors. White sharks demonstrated orientated swim/search patterns in areas of high shark-pinniped interaction (Goldman *et al.* 1996; Goldman & Anderson 1999) presumably related to patrolling for potential pinniped prey. The presence of multitudes of additional sensory stimuli (olfactory, visual, chemical) indicating seal activity may lead to the immediate association of this area with the presence of seals. It is realistic to expect that sharks observed within the channel area are more likely to be hunting for pinnipeds than sharks observed elsewhere. If so, these patrolling sharks will be actively searching for pinnipeds and this will be reflected in comparatively greater attention being directed towards the seal resembling decoy.

5.4.5 Influence of shark size on selective tendencies

The selection process that governs the prey choice of large white sharks differ from that of smaller sharks. The different results with regard to shark size stems from discrete differences in the behavioural process following the initial visual detection of potential prey and differential values in what is deemed as attractive. The overriding characteristic that defines visual attractiveness of prey to large white sharks appears to be general shape resemblance to a known prey type such as pinnipeds, rather than prey size or other slight changes in appearance from pinnipeds (as illustrated by the penguin decoy). The lack of selection by large white sharks in the 'species; and 'size' experiments suggests that a roughly similar shape to familiar biological prey is sufficient for these sharks to view a potential prey as 'visually attractive' and worthy of either investigatory or predatory attention. Only the rectangular decoy held no resemblance to biological familiar prey types, and as a result was clearly selected against by large white sharks. The approach behaviour of larger white sharks may also affect the role of vision in prey identification. Approaches on the decoys were often indicative of actively hunting sharks which required maximum surprise to complete a successful attack (rushing the decoys upon first detection). This approach strategy, by default, reduces the amount of visual information available and limits the use of alternative sensory cues in assisting to identify prey. This speculative type hunting strategy may mean that vision is only used to locate prey and broadly categorise it based on general shape similarity to known prey.

During this species experiment, large white sharks often initiated their attacks from the edge of the visual field upon first visual detection of the seal and penguin decoys. The difference in decoy shape and the differential colouration patterns may not have been visually determined due to backlighting and the small variation in shape. Thus attacks on the penguin decoy could have resulted from erroneously identifying it as a seal. This approach behaviour may lead to more non-prey items being bitten due to mistaken identity, and may help explain the occurrence of bites on biologically similar shaped objects, such as sea otters, humans, seabirds, turtles and penguins that are reported (Ames *et al.* 1996; Long 1996; Randell *et al.* 1988; Burgess & Callahan 1996).

Alternatively, smaller white sharks seem to place the greatest importance on prey size when determining the visual attractiveness of the decoys. The differences in what they deemed as visually attractive appear to arise from a combination of morphological constraints, and less experience and competence as a predator (discussed above). Smaller white sharks more often circled and passed the experimental array prior to initiating an attack (Chapter 3). This behaviour is not consistent with the high-speed, ambush style attacks frequently observed when white sharks attack pinnipeds, and if performed in a natural setting, would certainly lead to a healthy pinniped escaping. Motivation to select a decoy may have often been based on curiosity, investigation or possibly scavenging, rather than active hunting. The attraction to the pup seal decoy (species and size experiment) could have been based on a rare opportunity to attack a prone and vulnerable pinniped that would offer little resistance in terms of catching, killing and consuming it. This would provide a young white shark with practise, as well as gaining a valuable resource without much energy expenditure (i.e. chasing prey, removing large chunks of flesh, and quickly being able to consume the pup seal minimising the possibility of losing the prey to a larger white shark).

CHAPTER 6

Predation by the white shark *Carcharodon carcharias* and the Cape fur seal *Arctocephalus pusillus pusillus* on seabirds at Dyer Island

6.1 Introduction

In Southern Africa, seabirds such as the African penguin *Spheniscus demersus* and cormorants *Phalacrocorax sp.* are vulnerable to an variety of biotic and abiotic threats (Barnes 2000). A number of human induced (oil pollution, egg harvesting, human disturbance) (Shelton 1984; Hockey & Hallinan 1981; Crawford *et al.* 2000) and natural (predation, interspecific competition for nesting sites, modification to fish stocks) (Crawford *et al.* 1989; Crawford *et al.* 1990; Crawford & Dyer 1995; Marks *et al.* 1997) factors have been implicated as possible contributors to these declines. The Dyer Island complex in South Africa is proclaimed a nature reserve in terms of the Nature Conservation Ordinance (number 19 of 1974). The overriding guiding policy for the management of this reserve is to ensure the continuous protection and survival of the reserve's indigenous biota, especially rare, endemic and/or endangered seabird taxa. Dyer Island is at present off limits to the general public.

6.1.1 Seabirds of Dyer Island

Birds dominate the vertebrate fauna of Dyer Island, both in terms of diversity and numbers (Appendix 1 provides a checklist of birds recorded on the island). There are at least 15 species of breeding seabirds on Dyer Island. The African penguin, Leach's storm petrel *Oceanodroma leucorhoa*, bank cormorant *P. neglectus*, crowned cormorant *P. coronatus*, African black oystercatcher *Haematopus maquini*, roseate tern *Sterna dougallii,* kelp gull *Larus dominicanus vetula,* hartlaub's gull *L. hartlaubii,* white-breasted cormorant *P. carbo* and the Cape cormorant *P.*

capensis all have high conservation priority or importance for management purposes due to their conservation status and presence on the island (Johnson *unpub. report*).

6.1.2 Predators of seabirds

Predators, such as the white shark *C. carcharias* and Cape fur seal *A. p. pusillus* have been implicated to attack and/or feed on significant numbers of seabirds (Boersma 1976; Randell *et al.* 1988, Marks *et al.* 1997). Randall *et al.* (1988) determined that white sharks were responsible for a majority (no exact percentage given) of the injured and dead penguins found on the shoreline of St Croix Island and Bird Island, South Africa (55 at St Croix, 15 at Bird Island from 1985 - 1986). These findings suggest that white sharks are an important attacker of penguins in this area. Interestingly, to date only a single African penguin has been found in the stomach of a white shark (Bass *et al.* 1975). The presence of a large Cape fur seal colony (estimated at about 55,000 individuals) residing on Geyser Rock may contribute to attracting large numbers of white sharks to the Dyer Island area, necessitating the need to evaluate the white sharks predatory impact on the local bird populations.

A more prolific predator of Southern Africa's seabirds is the Cape fur seal (Marks 1997; Du Toit 2002). Seals have been recorded hunting and feeding on seabirds as diverse as the Cape Gannet (*Morus capensis*), petrels, cormorants and penguins (Shaughnessy 1978; Cooper 1974; Du Toit 2002). Quantifiable accounts of the extent of predation on bird populations are rare, although Marks *et al.* (1997) calculated that up to 7.1% of the fledgling population of Cape cormorants at Dyer Island may fall victim to seal predation. The behaviour of seals feeding on seabirds has been possibly attributed to a few possibly regular penguin predators (rogue seals) (Cobley & Bell 1998; Du Toit 2002).

6.1.3 Seabirds vulnerable to predation at Dyer Island

Two resident seabirds at Dyer Island (African penguin and Cape cormorant) have been identified in the literature as vulnerable to predation by either the white shark or Cape fur seal (Randall *et al.* 1988; Du Toit 2002, Marks 1997). Unpublished accounts of Cape fur seals attacking three additional species of resident seabirds exist, namely the white-breasted cormorant (Crawford *in press A*), crowned cormorant (Crawford *in press B*) and bank cormorant (Crawford *in press C*) have been given. The African penguin is the sole endemic penguin in Southern Africa and the only species that breeds in Africa. Its breeding range extends from Hollams Bird Island, Namibia to Bird Island, Algoa Bay, Port Elizabeth (Crawford *et al.* 1995). The African penguin population is now listed as 'Vulnerable' (Crawford *in press D*) because of a continued population decrease of 13%/generation since 1976 (Ellis *et al.* 1998; Barnes 2000). It has been included in Appendix II for both CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) and CMS (Convention for the Conservation of Migratory Species of Wild Animals). Factors implicated in the decline include habitat alteration and disturbance associated with commercial exploitation of guano and penguin eggs (Frost *et al.* 1976; Crawford *in press D*). Recently, reduced availability of pelagic fish due to competition with commercial fisheries has been postulated to be responsible for persistent declines (Crawford *et al.* 1990, 2001). Other factors include mortality due to oil spills (Crawford *et al.* 2000), predation by seals (Marks *et al.* 1997; Stewardson 1999; Du Toit 2002) and entanglement in fishing gear and other marine debris. Recently, fears have been expressed that the establishment of the white shark cage diving sector may lead to an increase in white shark attacks on penguins and other seabirds (Oosthuizen *pers. com.*). Especially at locations of significant cage-diving effort, such as Dyer Island, where white sharks may be concentrated.

Four species of cormorants are resident at Dyer Island namely the crowned cormorant, bank cormorant, white-breasted cormorant and Cape cormorant. The crowned cormorant is endemic to the Benguela system and the western Agulhas Bank, and is regarded as *Near-threatened* because of its small population size (Barnes 2000). The bank cormorant is an endemic to the west coast of Southern Africa. It is currently classed as *Vulnerable* (Barnes 2000), but it is expected to be reclassified as *Endangered* due to ongoing population declines (Crawford *in press C*). The Cape cormorant is the most numerous cormorant species on Dyer Island. It is classed as *Near-threatened* due to a population decrease from 277000 pairs to *circa* 72000 pairs between 1977 and 1996 (Barnes 2000). The white breasted cormorant is not threatened in South Africa (Barnes 2000).

6.1.4 Aims

Dyer Island is primarily a nature reserve for seabirds, and it is essential that a full and complete understanding of the scope and magnitude of predatory pressures on the resident seabirds is established. The objective of this chapter is to qualify and quantify the spatiotemporal trends in seabird predations occurring at Dyer Island. It's intended to describe the magnitude and scope of each predatory interaction type and to identify specific predatory interactions involving the aforementioned taxa that could adversely affect the sustainability of local seabird populations.

The specific objectives are to:

- Qualify the nature and scope of predatory interactions between white sharks, Cape fur seals and the multitude of seabirds species residing on Dyer Island,
- Determine the relative importance of each predatory interaction type,
- Determine spatial and temporal trends in the observed interactions.

6.2 Methods

6.2.1 Study site

The study area consisted of the Dyer Island region (34°41'S 19°25'E) (see 2.2.1 for detail), in which observations and surveys were carried out directly from Dyer Island and from the waters directly surrounding the Dyer Island group (Fig. 6.1). The Dyer Island group mainland was split into eight zones (6 on Dyer Island, 2 on Geyser Rock) for the purpose of this and other studies (Fig. 6.1).

6.2.2 Quantifying attacks on seabirds

Predatory encounters were quantified using a multifaceted approach consisting of live observation of attacks, collection of bird carcasses and observation and/or collection of injured seabirds. Daily searches for injured birds and seabird carcasses were carried out in the coastal area of Dyer Island. The survey comprised a circumnavigating patrol of Dyer Island's intertidal zone. During these patrols, all washed up seabird carcasses discovered were removed, examined and buried. During the post-mortem examination records of each birds taxon (species level), date, location (zone), age class, sex (for sexually dimorphic species only) and stage of decomposition were taken. Where applicable the injury type was described and categorised, and where possible the predator was identified from the specific wound pattern. Injured sea birds were either collected for examination and treatment or examined in the field depending on the injury's severity and the amount of disturbance the collection of data would cause. During examination the wound characteristics were described and categorised, and when possible the predator species identified from wound pattern. Other pertinent information included the zone, age-class, sex and state of health of the victim.

Observations of live attacks were made on an opportunistic basis from a number of vantage points, and during various activities, on and around Dyer Island, including a tower (4m) constructed within the island's living compound, observations during daily research patrols, and from a research vessel anchored at various locations in the near vicinity of the island (Fig. 5.1). Predation cues used included: water splashing; hovering kelp gulls; a splashing seal and occasionally an emanating oil slick. Pertinent information on the predation encounters included the species involved, the time and location, local environmental conditions, and a description of the encounter. Live attacks were recorded on an incidental and opportunistic basis, for this reason both spatial (most effort from living compound) and temporal (lowest effort in early morning and late afternoon) effort biases exist.

6.2.3 Describing breeding and moulting trends of resident seabirds

Population estimates of the resident cormorant *spp.* and African penguins were needed to calculate the predatory impact by Cape fur seals and white sharks on these taxa. Moulting and breeding trends in the African penguin colony were established using recognised methodology (Crawford & Boonstra 1993; Crawford & Dyer 1995) which consisted of fortnightly moult counts of penguins in their feather shedding stage, and a monthly nest count. A total of 34 moult counts of the African penguin were completed between August 1999 and December 2000. The penguin moult was subdivided into juvenile and adult stages, with only penguins displaying adult plumage being included in the analysis to determine the total potential breeding population. Counts done between November 1999 and October 2000, December 2000 and November 2000 and January 2000 to December 2000 were summed independently. These three totals were then averaged to gain an estimate of the number of potentially breeding African penguins occurring at Dyer Island during the study. Monthly nest counts included all occupied nests, defined as sites defended by adult birds or sites with eggs or chicks. Peak nests counts of the Cape, bank, crowned and white-breasted cormorant species were used to estimate the numbers of these birds at Dyer Island. Multiplying this peak nest count by two (breeding pairs) allowed a conservative estimate of the cormorant populations. Furthermore, the spatial distribution of each taxon's nests, during their peak nest count, was used as the baseline to determine the expected distribution of washed up carcasses.

4.2.6 Data analysis

The minimal predatory impact of Cape fur seals on the African penguin population was established by calculating the percentage of adult population (established by moult counts) that was killed between January 2000 and January 2001 and washed up on Dyer Islands shore. The fledgling population of Cape cormorants was calculated by multiplying the peak nest count by 2.36 (average eggs/nest) (Crawford 1992). The survival coefficients between eggs and chicks (0.87) and chicks to fledglings (0.91) were then used to establish the fledgling population (Crawford *in press E.*). The annual minimal predatory impact on the Cape cormorant fledgling population represented the percentage of fledglings killed by Cape fur seal predation that washed up on Dyer Island's shores. Multiplying by two the peak nest count of the crowned, bank and white-breasted cormorants established their breeding populations. The minimal annual predatory impact of Cape fur seals was the percentage of the population killed by seals during the corresponding 12 months. For each analysis, the lower minimum estimate includes only carcasses conclusively killed by seals, while the upper minimal also includes skeletal remains of birds.

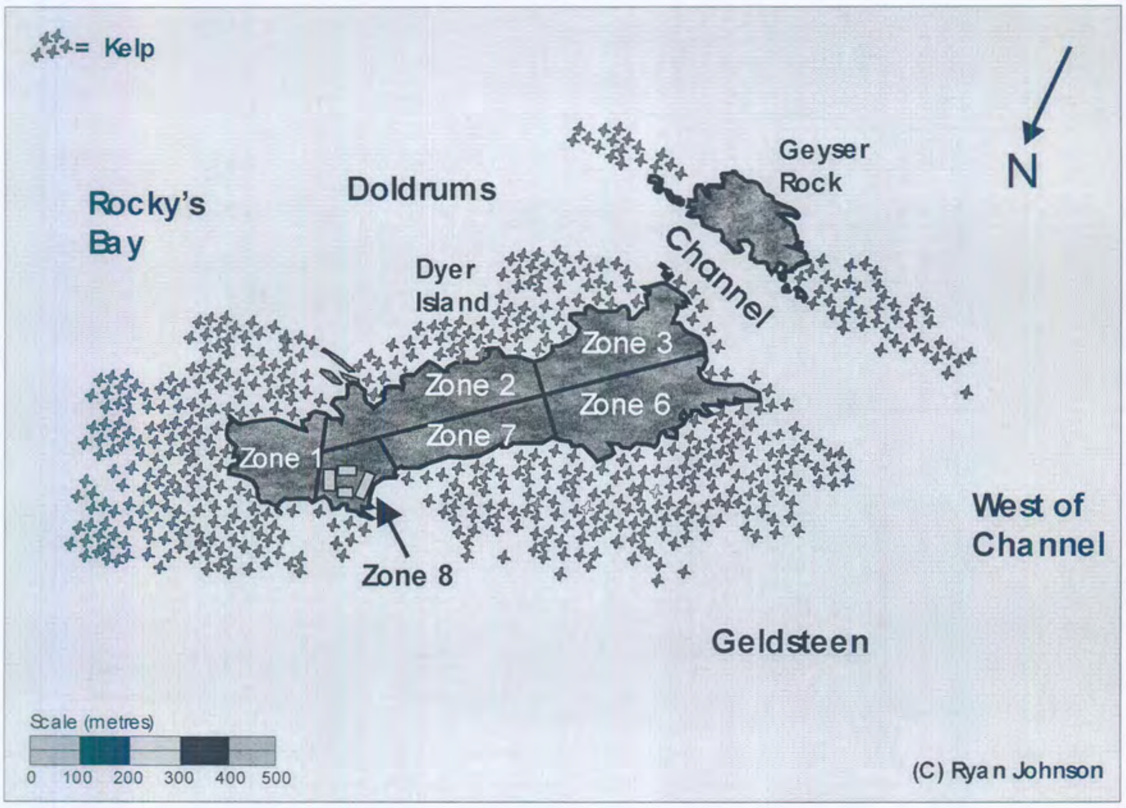

Figure 6.1 Map of the Dyer Island study site with the zonation shown.

6.3 Results

6.3.1 Attack types

The predator of each attack was identified by the characteristic wound pattern on the carcass. Cape fur seals typically attack seabirds from below, upon capture they vigorously snap the bird to and fro above the surface, which typically leads to skin separating from the body and inverting over the head to expose the birds flesh, effectively 'degloving' it (Marks *et al.* 1997). Other types of wounds observed resulting from seal attacks were bites to the abdomen and the neck regions (Table 6.1). Bites of this nature have been well documented and are conclusively the result of pinnipeds, such as the Cape fur seal (Marks *et al.* 1997, Du Toit 2002). Randall's *et al.* (1988) work on the occurrence of white shark attacks on African penguins identified five general types of injury that can be assigned to white shark bites (Table 6.1). Other types of carcasses collected from Dyer Island included birds in which the level of decomposition disguised the cause of death (skeletal remains) and carcasses with no apparent injuries (Table 6.1).

6.3.2 Collection of seabird carcasses

Between September 1999 and January 2001 a total of 812 bird carcasses were collected and examined (Table 6.2). Of these carcasses, six seabird species displayed evidence of predation, and included the African penguin, Cape cormorant, bank cormorant, crowned cormorant, white-breasted cormorant and Cape gannet. The African penguin (26.5%, N = 154) and Cape cormorant (68.1%, N = 396) were predominantly predated on, accounting for 94.6% (N = 581) of the total number of predated carcasses collected. Predation by Cape fur seals was identified as the cause of death for 71.5% (N = 581) of the carcasses, while no carcasses displayed evidence of white shark bites (Table 6.2). No evidence of predation was seen in only 7.8% (N = 61) of the carcasses. Advanced decomposition prevented the cause of death to be established in the remaining 21.6% (N = 170) of carcasses.

Table 6.1 Classification of wound types and causes of death in seabird carcasses and injured seabirds found on Dyer Island, South Africa.

Source of wound	Wound Type	Wound Description
Cape fur seal	Degloving	The pelt of the seabird is stripped and inverted from the body of the victim.
Cape fur seal	Neck bite	A single bite where tissue is removed from the neck region.
Cape fur seal	Abdominal bite	A single or multiple bite(s) where tissue is removed from the abdomen.
White shark	Type 1	An arc of large radius, with longitudinal cuts (>5cm spacing between cuts).
White shark	Type 2	An almost straight cut(s) transverse to the body scars.
White shark	Type 3	An arc of small radius with closely spaced cuts, usually transverse to the long axis of the penguin.
White shark	Type 4	Miscellaneous injuries including isolated ragged cuts and puncture marks.
White shark	Type 5	Two jaw bites, where an additional series of (ir)regular cuts/punctures is present.
Unknown	Skeletal remains	Where carcass decomposition is such that the cause of death cannot be identified.
Unknown	No apparent injury	A carcass without visible injuries or wounds.

6.3.3 Comparative frequency of wound types

Some 87.9% (N = 511) of the corpses that displayed Cape fur seal inflicted predatory wounds were classed as degloving (Table 6.3). Abdomen and the neck bites accounted for the remaining 5.2% (N = 29) and 7.1% (N = 41) of carcasses respectively (Table 6.3). The occurrence of deglovings in relation to partial wounds (neck and abdominal bites) was significantly different between the penguin and cormorant taxa (5 x 2 contingency table, $\chi^2_{(4,0.005)} = 50.4$, $P < 0.01$). This was primarily caused by the greater than expected number of wounds without evidence of feeding (neck and abdominal bites) observed within the penguins (28.0%) in comparison to cormorants (6.4%).

Table 6.2. Cause of death in the various species of seabird carcasses collected from the intertidal region of Dyer Island between September 1999 and January 2001.

Species	Cause unknown		No injuries apparent		C.F.S. wounds present		W.S. wounds present		Total no. of carcasses
Afr. penguin	45	(21.0%)	15	(07.0%)	154	(72.0%)	0	(00.0%)	214
Cape corm.	115	(17.4%)	42	(11.3%)	396	(71.6%)	0	(00.0%)	553
Bank corm.	0	(00.0%)	0	(00.0%)	1	(100%)	0	(00.0%)	1
Crown. corm.	1	(07.7%)	3	(23.1%)	9	(69.2%)	0	(00.0%)	13
WB. corm.	3	(12.5%)	1	(04.2%)	20	(83.3%)	0	(00.0%)	24
Gannet	0	(00.0%)	0	(00.0%)	1	(100%)	0	(00.0%)	1
Corm. *sp.*	6	(100%)	0	(00.0%)	0	(00.0%)	0	(00.0%)	6

Table 6.3 Relative occurrence of wound types inflicted by Cape fur seals on seabirds.

Species	**Degloving**		**Neck bite**		**Abdominal bite**	
Afr. penguin	111	(72.0%)	38	(24.7%)	5	(03.3%)
Cape corm.	371	(93.7%)	2	(00.5%)	23	(05.8%)
Crown. corm.	8	(88.9%)	0	(00.0%)	1	(11.1%)
WB. corm.	19	(95.0%)	1	(05.0%)	0	(00.0%)
Bank corm.	1	(100%)	0	(00.0%)	0	(00.0%)
Gannet	1	(100%)	0	(00.0%)	0	(00.0%)

6.3.4 Occurrence of injured seabirds

Injured seabirds that were observed and/or collected included the African penguin and Cape cormorant. Excluding birds injured due to oil pollution, a total of 31 injured birds were recorded throughout the study. Of these, the African penguin was the majority species, accounting for 26 of the injured birds, while the remaining five birds were Cape cormorants. Identifying the cause of the injury was problematic, and predation was adjudged as the certain cause of an injury in only 10 of the birds (Table 6.4). Other suspected causes of injury included con-specific inflicted injuries, entanglement with fishing line and netting, and other naturally sustained injuries.

6.3.5 Live observations of attacks

Observation of live attacks allowed prey identification to the species level for the African penguin and to the genus level for cormorants. A total of 204 attacks by Cape fur seals on African penguins and cormorant *spp.* were observed throughout the study. Of these 46.6% involved the African penguin, and 38.7% a cormorant *spp.* In 14.7% of the cases the victims was not identified to genus level (Table 6.5). Additionally, three encounters between white sharks and kelp gulls were observed (Table 6.5).

Table 6.4 Injured seabirds collected and/or observed on Dyer Island (excluding oiled seabirds).

	White shark	Cape fur seal	Unknown	Total
Afr. Penguin	2	5	19	26
Cormorant *spp.*	0	3	2	5

Two of the penguins collected showed evidence of white shark bites (Table 6.4). The injuries sustained by these penguins were the sole evidence of white sharks attacking the African penguin in this study. The first penguin showing evidence of white shark inflicted wounds was collected in August 1999. The wound was characterised by a single deep elongated puncture to the dorsal surface of the penguin (Fig. 6.2). Randell *et al.* (1988) observed wounds of this nature in 13% (at Bird Island) and 7% (at St. Croix Island) of the penguins attacked by white sharks. This wound was classified as a 'Type 2' injury and described as an almost straight cut transverse to the body of the penguin. This deep puncture wound resulted in massive internal injury and the penguin was subsequently put down. The second penguin showing evidence of a shark-inflicted injury was collected from Dyer Island in October 1999 (Fig. 6.3). The wound consisted of a row of deep elongated punctures on the left-hand side of the penguin. On inspection, individual tooth punctures could clearly be observed. No wounds were apparent on the opposite side of the bird's body.

Figure 6.2 A single elongated puncture is visible on the dorsal surface of this African penguin collected from Dyer Island.

Figure 6.3 This African penguin collected at Dyer Island displays multiple punctures to the body cavity. The jaws of a white shark inflicted these wounds.

Table 6.5 Live attacks by various predators on seabirds occurring at Dyer Island. 'Unsuccessful attempt' represents all occasions when predator(s) made an unambiguous attempt to attack the potential prey but failed.

	White shark	**Cape fur seal**
Successful Attacks		
African Penguin	0	92
Cormorant *spp.*	0	79
Kelp Gull	1	0
Unknown	0	32
Unsuccessful Attacks		
African Penguin	0	0
Cormorant *spp.*	0	1
Kelp Gull	2	0
Unknown	0	0

Two attempted attacks and one successful attack on kelp gulls by white sharks were observed. The following accounts were recorded:

- On the 24 October 1999, a 375-425cm female white shark attempted to attack two adult kelp gulls hovering approximately five metres above the sea surface. At 1525 the white shark was observed circling the research vessel. The shark had been attracted to the boat by an odour corridor of shark liver. At 1623 the white shark breached, i.e. vertically exited the water at high speed, directly under the two hovering kelp gulls. The shark reached within *circa* 1m of the kelp gulls before slapping back down into the water (Fig. 6.4, Attack A).

- On 16 March 2000 a flock of approximately 20 kelp gulls were floating on the sea. They simultaneously flew into the air and moments later a white shark erupted from the water in a semi-breach. The shark failed to make contact with any of the gulls and was not observed again (Fig. 6.4, Attack B).

- On 15 April 2000 a white shark was observed hitting the gull at high speed from below. The white shark immediately disappeared and the gull surfaced dead. The shark did not return to eat or inspect the victim. Inspection of the carcass revealed two small wounds to the head of the gull, and no other injury (Fig. 6.4, Attack C).

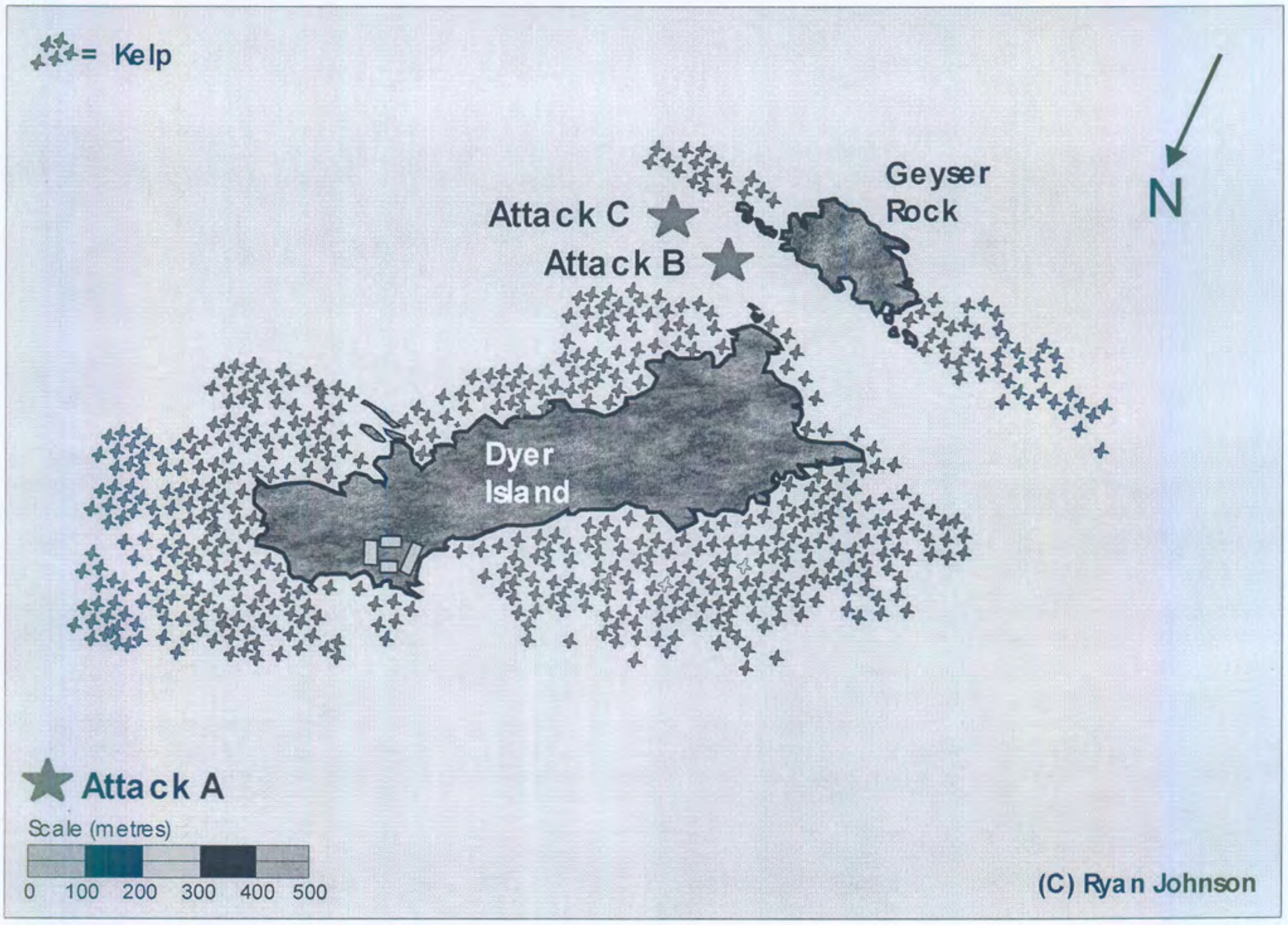

Figure 6.4 Location of successful and unsuccessful attacks by white sharks on kelp gulls within the study area.

6.3.6 Seasonal occurrence of seabird carcasses

Attacks on African penguins by Cape fur seals occurred throughout most of the year. Very few penguin carcasses were collected between November and January, and a clear seasonal trend was evident ($\chi^2_{(0.05,17)} = 168.1$, $P < 0.01$) (Fig. 6.5a). This reduction in carcasses found correlated strongly with both the moulting peak of the penguins (Fig. 6.6a) and the vulnerable fledgling period of the Cape cormorant (Fig. 6.5a).

Predation on Cape cormorants by Cape fur seals showed a significant seasonal pattern ($\chi^2_{(0.05,17)} = 904.8$, $P < 0.01$) with large numbers of carcasses collected between November and January in both 1999 and 2000 (Fig. 6.5a). Nest counts of Cape cormorants reflected the seasonal breeding pattern of this species at Dyer Island. In 1999 nesting began in earnest during September, while in 2000 it began slightly earlier in August (Fig. 6.7b). At the start of the estimated fledging period (6-8 weeks later) attacks by Cape fur seals on this species rose dramatically (Fig 6.5a). Attacks on cormorants began earlier in 2000 than in 1999, as did the onset of Cape cormorants carcasses washing to shore (2 x 4 contingency table, $\chi^2_{(0.05,3)} = 69.28$, $P < 0.01$), caused by the comparatively early onset of nesting and fledging in 2000 (Fig. 6.7b). White breasted cormorant carcasses were collected throughout the year ($\chi^2_{(0.05,17)} = 21.4$, $P > 0.25$) (Fig 6.6a) without a seasonal trend. The recovery of crowned cormorant carcasses was not seasonal ($\chi^2_{(0.05,17)} = 21.0$, $P > 0.10$), although 92% of the carcasses collected in the winter period extended from April to September (Fig. 6.6b). Only a single carcass of a bank cormorant (Fig. 6.6c) was recovered.

The seasonal trends in live attacks on both penguin and cormorant taxa mimicked those seen for the washed up carcasses (Fig 6.5b). African penguins were attacked throughout the year, excluding November to January ($\chi^2_{(0.05,15)} = 92$, $P < 0.001$), while the majority of the attacks involving cormorant *spp.* occurred during November and December, the fledging period of the Cape cormorant ($\chi^2_{(0.05,15)} = 139.5$, $P < 0.001$).

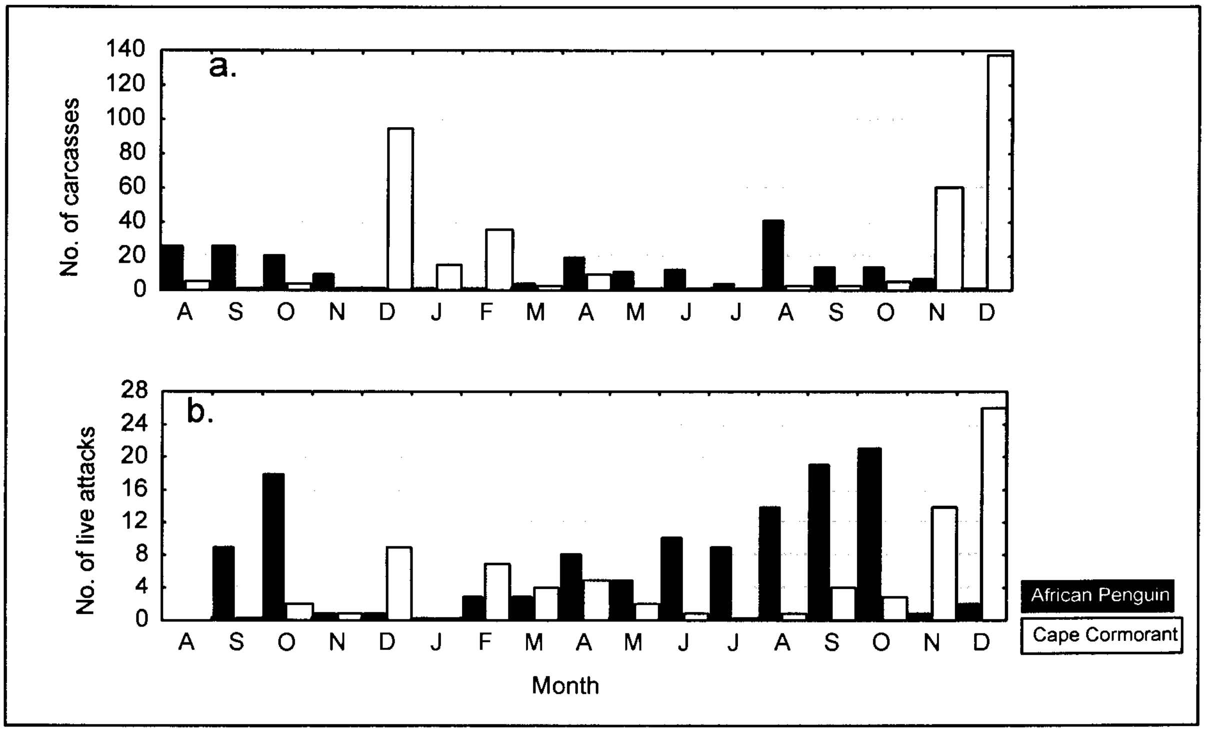

Figure 6.5 Seasonal trends in seabird predation at Dyer Island. Figures: 6.5a – Collected seabird carcasses, 6.5b – Observed attacks by Cape fur seals.

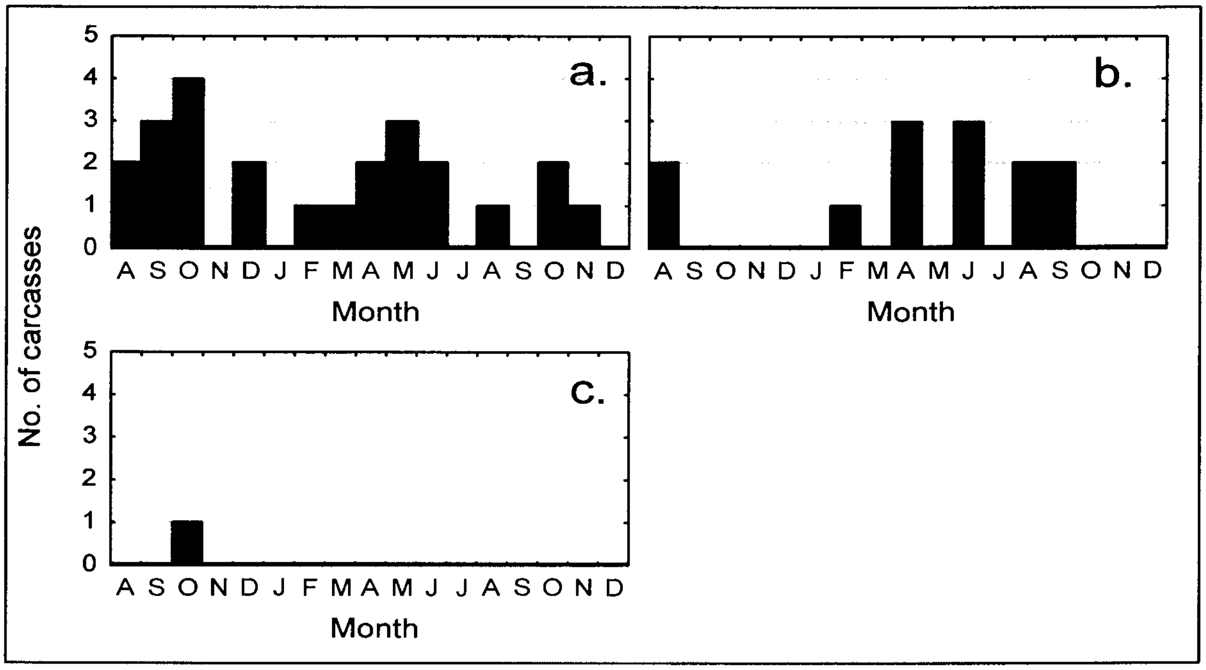

Figure 6.6 Seasonal patterns of carcass collection for three species of cormorants resident on Dyer Island. Figures: 6.6a – White-breasted cormorant, 6.6b – Crowned cormorant, 6.6c – Bank cormorant.

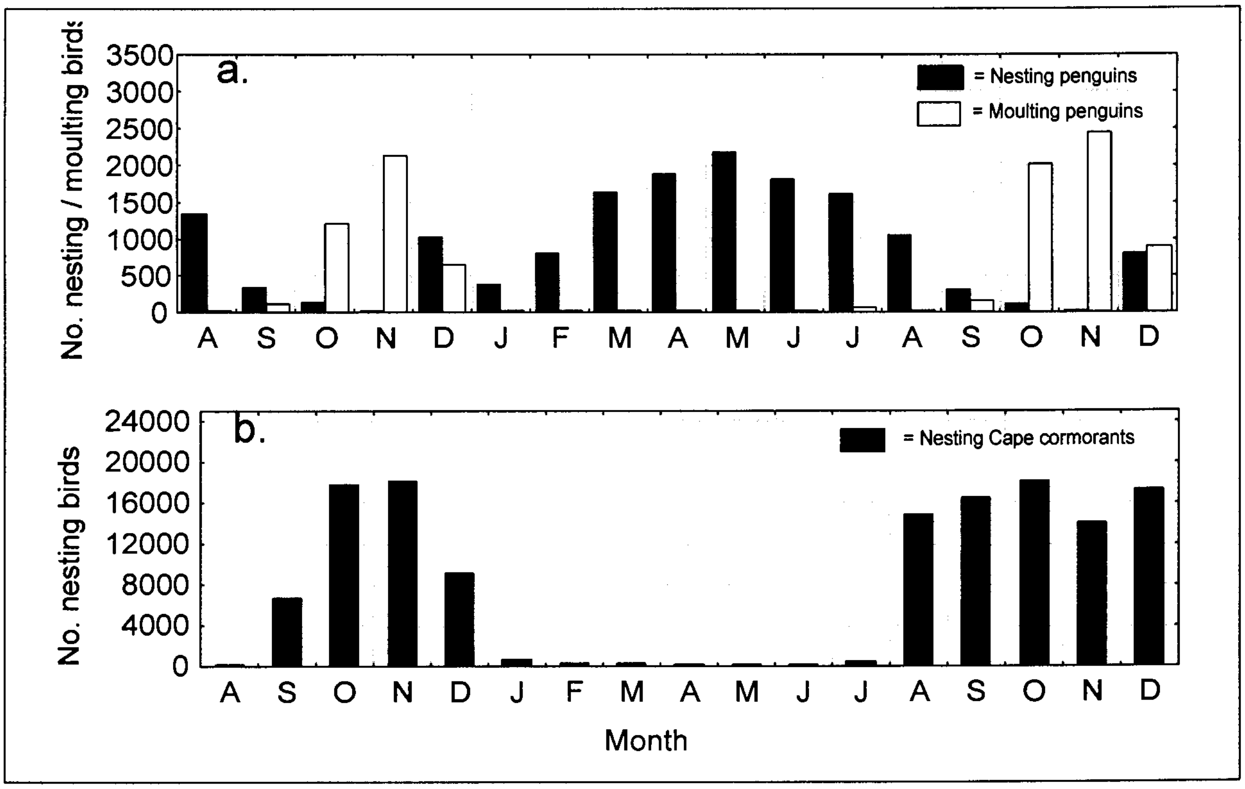

Figure 6.7 Seasonal nesting and moulting trends of seabirds at Dyer Island. Figures: 6.7a – African penguins, 6.7b – Cape cormorants.

6.3.7 Diurnal trends in live attacks

Significant diurnal trends in the number of attacks existed within both the penguin ($\chi^2_{(0.005,13)} = 71.13$, $P < 0.01$) and cormorant taxa ($\chi^2_{(0.005,13)} = 24.21$, $P < 0.05$) (Fig. 6.8b). Interspecific comparison of diurnal patterns of attacks between the penguin and cormorant taxa also showed unique diurnal predation trends for each (2 x 14 contingency table, $\chi^2_{(0.005,13)} = 45.25$, $P < 0.01$). A crepuscular trend in penguin attacks, with peaks in the morning and late afternoon was observed. Attacks on cormorants increased throughout the morning period, reached a peak at 13h00, and trailed off in the afternoon (Fig. 6.8b).

6.3.8 Spatial occurrence of attacks

Some 93% of live attacks were observed in Zones 8 and 1, a manifestation of increased observation effort in these areas (Fig. 6.8a), due to the good view from the living quarters and the constructed observational tower.

The distribution of carcasses (all taxa combined) collected from Dyer Island was not random ($\chi^2_{(0.005,5)} = 91.63$, $P < 0.01$), with zones six, seven, and eight under-represented. Significant differences in the spatial patterns of collected carcasses existed between the three cormorant species (excluding the bank cormorant) and African penguin (4 x 6 contingency table, $\chi^2_{(0.005,15)} = 131.56$, $P < 0.01$). Cape cormorants were collected from all zones, but mostly from the Southwestern end of the island in zones 3 (32.0%) and 6 (14.8%) (Fig. 6.8c). Only 7.6% of African penguin carcasses were collected in zones 3 and 4, most occurring on the eastern side of the island in zones 8 (17.8%), 1 (35.6%) and 2 (27.4%) (Fig. 6.8a).

A significant difference existed between the presence of African penguin carcasses and their nest sites ($\chi^2_{(0.005,5)} = 145.5$, $P < 0.001$) (Fig. 6.8a). The spatial distribution of Cape cormorant nest sites and abundance of carcasses washed up roughly matched each other throughout the study site, apart from the greater than expected number of carcasses recovered in zone eight, ($\chi^2_{(0.005,5)} = 107.0$, $P < 0.001$) (Fig. 6.8a). The low numbers of bank, crowned and white-breasted cormorant carcasses collected prevented statistical interpretation, although carcasses of the crowned cormorant, which nests exclusively within the Island living compound (zone 8), were collected only from zones eight, and the adjacent zones (1 and 2) (Fig. 6.8d). White-breasted cormorants concentrate their breeding in the islands interior at zones 3 and 6, but the majority of carcasses were collected from zone 1 and 2 (Fig. 6.8b). The single bank cormorant carcass was collected in zone 2, adjacent to the nesting area of the species.

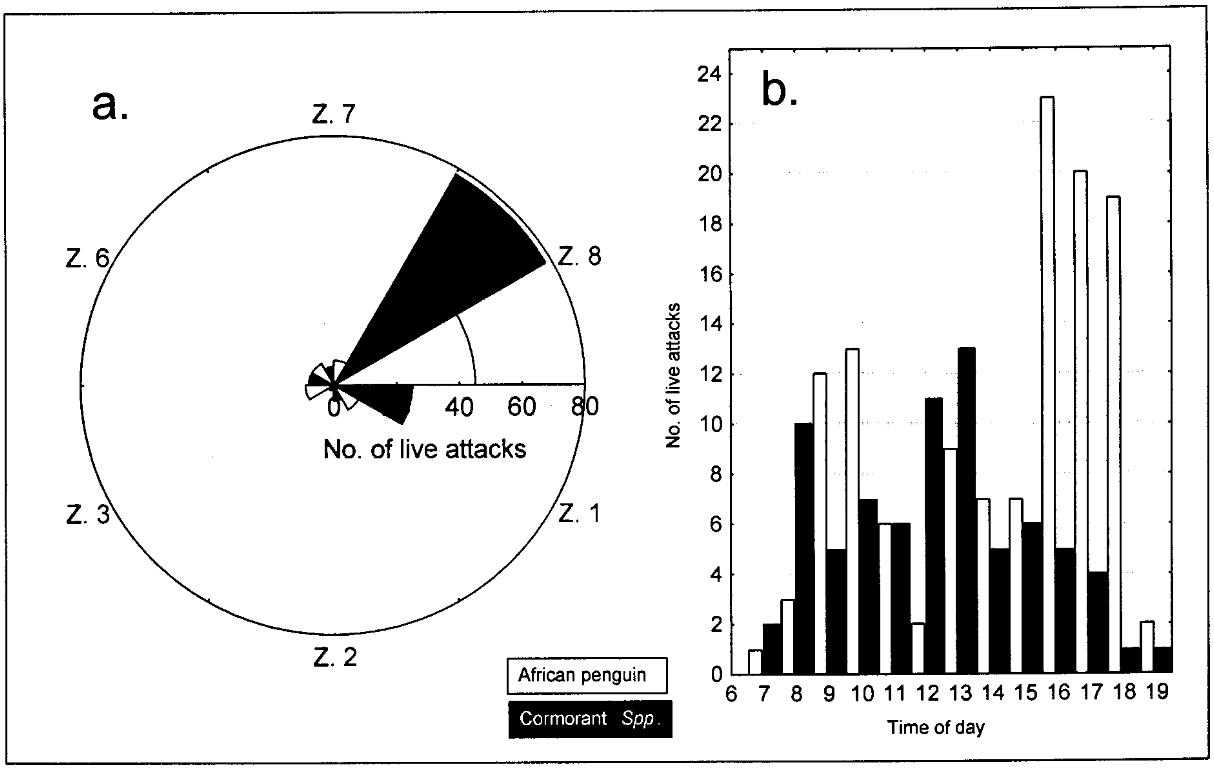

Figure 6.8 Spatiotemporal patterns in attacks on seabirds at Dyer Island. Figure 6.7a – Spatial distribution of live attack, 6.7b – Diurnal trends of live attacks.

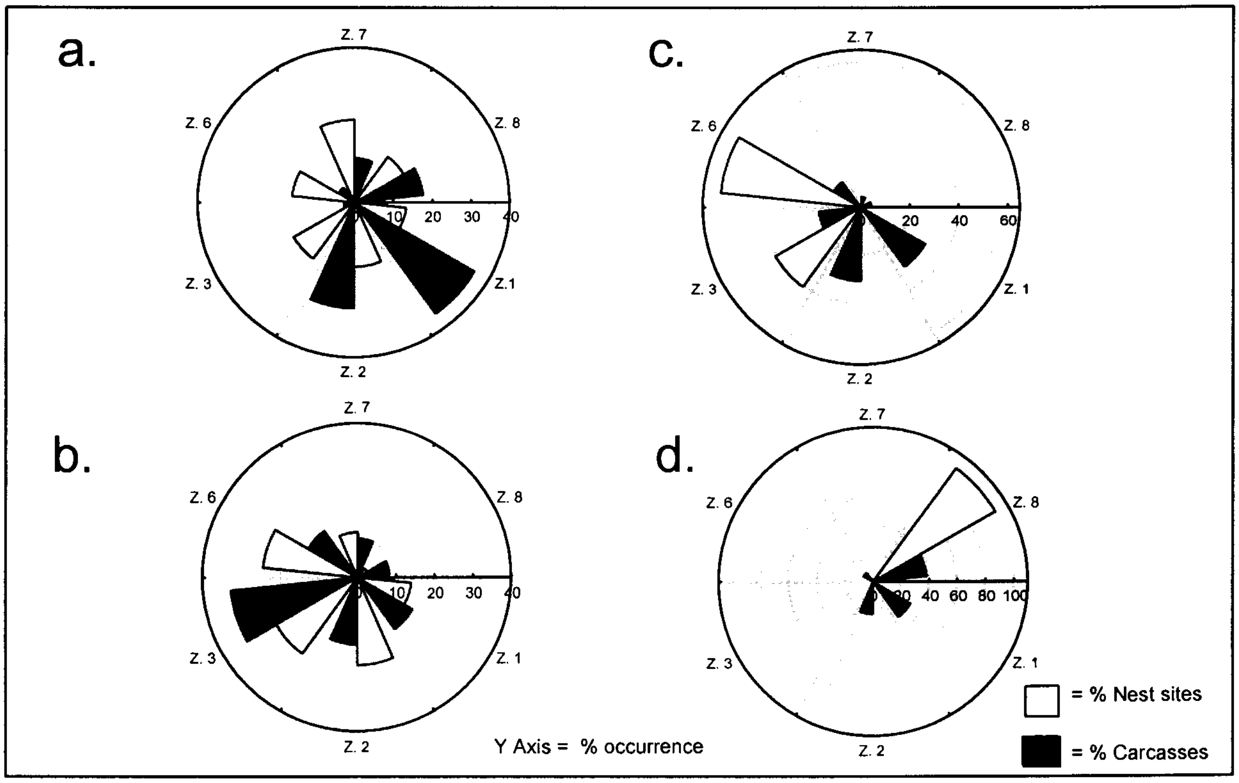

Figure 6.9 Spatial comparison of seabird nesting sites and the location of seabird carcasses washed up. Figures: 6.8a – African penguin, 6.8b – Cape cormorants, 6.8c – White-breasted cormorants 6.8d – Crowned cormorants.

6.3.9 Importance of predation on penguin mortality

An African penguin breeding population of 5081 birds was estimated (Table 6.6). During the corresponding 12 months (Dec 1999 – Nov 2000) a total of 134 penguin carcasses were collected of which 101 showed evidence of predation by Cape fur seals. The remaining 33 birds were either too decomposed to establish the cause of death (27 birds), or no injuries were apparent (6 birds). Therefore a lower minimum of 1.99 percent (and upper minimum of 2.52 percent) of the breeding population died as a result of Cape fur seal predation during this time.

Table 6.6 Population estimate of adult African penguins occurring on Dyer Island in 1999/2000.

Estimate Technique	Total
Σ moults from Nov 1999 – Oct 2000	4839
Σ moults from Dec 1999 – Nov 2000	5100
Σ moults from Jan 2000 – Dec 2000	5303
Adult population	**5081**

6.3.10 Importance of predation on cormorant mortality

White-breasted cormorants were the most vulnerable cormorant species to seal predation, with potentially 5.7 percent of the population incurring this fate. The crown cormorant (3.13%) and bank cormorant (0.00%) appear less affected. The peak nest count of Cape cormorants (18,105) equated with a population of 33,827 fledglings during the 2000-20001 breeding period. A lower minimum of 280, and upper minimum of 370 fledgling Cape cormorants were collected from the island in the corresponding period. This equates with an annual minimum predation rate of between 0.83% and 1.09% of the fledgling population.

Table 6.7 Predatory impact of Cape fur seals on cormorant *spp.* at Dyer Island between January and December 2000.

Species	Peak nest count	Population estimate	Seal predation		Annual predation impact
Bank cormorant	42	84	Low min:	0	0.00%
			Upp. min:	0	0.00%
Crowned cormorant	128	256	Low min:	8	3.13%
			Upp. min:	8	3.13%
White-breasted cormorant	96	192	Low min:	10	5.21%
			Upp. min:	11	5.72%

6.4 Discussion

6.4.1 Predation by white sharks on seabirds

White sharks do not appear to be a major threat to seabirds at Dyer Island. The rare incidences of white sharks attacking seabirds suggest that this kind of interaction is the exception, rather than the rule. There are, however, a number of alternative explanations why this interaction type was so infrequent at Dyer Island. It is feasible that white sharks would attack seabirds comparatively further from Dyer Island than Cape fur seals, which regularly attack seabirds in the kelp beds surrounding the island that are inaccessible to white sharks. Consequently, the likelihood of seabird carcasses resulting from white shark attacks reaching Dyer Island may be comparatively less. However, at Bird Island and St Croix Island penguin carcasses washed up in abundance and injured penguins were frequently observed (Randall *et al.* 1988). This suggests that the methods used are usable for this kind of study.

Vision, tactile investigation, olfaction and electro-reception are all senses used by white sharks to locate, identify and assess the quality of prey. The presence of a large (*circa* 55,000) and conspicuous seal colony may increase the selectivity of white sharks towards pinnipeds. Consequently, they would be less willing to spend energy attacking prey that is not as energetically rewarding, and not part of their typical diet (Bass *et al.* 1975; Cliff *et al.* 1989; 1996a). Anti-predator behaviour of African penguins in the vicinity of pinnipeds has been well documented (Randall *et al.* 1988), and was frequently observed at Dyer Island (this study). This predator (pinniped) avoidance behaviour could also make them less vulnerable to investigatory bites from white sharks.

Surviving penguins offered the only evidence of white sharks attacking them. The gentle nature of these bites suggests curiosity or inspection as the motivation, rather than predatory intent. That only a single bite was administered in both occasions suggests that the white sharks did not return following the initial incidence. Observation of a white shark successfully attacking a kelp gull further suggests that these rare attacks on seabirds are motivated by curiosity and/or inspection as the white shark failed to return to feed on the dead gull.

6.4.2 Predation by Cape fur seals on seabirds

Cape fur seals are conspicuous predators of African penguins and cormorant species resident on Dyer Island. The most common form of attack was degloving, which allows the seal access to the flesh while avoiding the skin and feathers of the bird (Marks *et al.* 1997). A significantly larger percentage of cormorant carcasses displayed this kind of injury compared to penguins that often displayed neck and abdominal bites. Neck and abdominal bites generally represent successful kills, but only partial feeding. The increased likelihood of penguins showing wounds indicting partial feeding (neck and abdominal bites) suggests that Cape fur seals were less motivated, willing or found it harder to feed on this taxa following a successful attack.

6.4.3 Seasonality of attack rates

Penguin carcasses displaying evidence of predation were collected throughout the year. However, during the moulting peak the number of carcasses dropped dramatically. This trend was also observed in the occurrence of live attacks of this nature. Penguins do not enter the sea during the moult, except for preening and drinking (Cooper 1978). Some 90 to 95% of penguins on Dyer Island moulted between October and December, which strongly corresponds with the drastic drop in attacks. The seasonal nature of attacks on penguins implies that penguins are most vulnerable to attacks by seals during their regular movements to and from Dyer Island, rather than from disturbance arising from human activity on the island. The abundance of fledging Cape cormorants during the summer period further reduces the predation pressure on penguins. Fledgling Cape cormorants appear very vulnerable to predation by seals due to them often landing in the inshore waters of Dyer Island following failed attempts of flying and/or as a result of disturbance.

6.4.4 Cause of observed diurnal trends in attack rates

The crepuscular trend of live attacks on penguins seems to be linked to daily movement of this species to and from the island to their foraging grounds. Wilson *et al.* (1988) determined that the mean departure and arrival time of foraging breeding penguins was 08h00 and 17h30 hours respectively at Marcus Island, Western Cape. At Dyer Island penguins typically show a similar movement trend (*pers. obs.*), which coincides with the crepuscular patterns of attacks. On the other hand, Cape cormorants tend to be attacked throughout the day, with a peak at around midday. Disturbance from the island and failed flight attempts often left large number of fledgling cormorants swimming in the waters just off Dyer Island. This is particularly likely to occur when approach from humans causes a chain reaction of panic, and masses of fledglings flee to the water.

6.4.5 Spatial distribution of carcasses

The distribution of African penguin carcasses around Dyer Island appears to be related to natural swimming paths and haulout areas of this species. The concentration of penguin carcasses in zones 8, 1 and 2 appears consistent with the apparent high number of penguins moving through this part of the island to/from foraging grounds (*pers. obs.*). However, the spatial occurrence of cormorant carcasses appears to be more strongly correlated with nesting location, particularly the crowned cormorant (Zones 1 and 8) and Cape cormorant. This implies that disturbance at nesting sites plays a relatively greater role in facilitating attacks on cormorants. The most likely contributing factor to the elevated number of Cape cormorant carcasses collected from zone eight was the large numbers of birds entering the water due to the high level of human disturbance at the jetty which was heavily used by fledgling Cape cormorants.

6.4.6 Impact of predations on seabird populations

Predation by Cape fur seals on penguins accounts for at least 1.99% of the adult breeding population, an underestimation as only a fraction of carcasses end up on Dyer Island's shore. In addition to the loss of adult penguins, the loss of both eggs and chicks would further compound the predation impact. The continual decrease in penguin numbers within South Africa suggests that management should attempt to minimise all factors contributing to the decline. Active removal of seals habitually attacking seabirds would assist to lower the mortality of penguins.

An estimated 1.09% of the Cape cormorant fledgling population succumb to seal predation, this is noticeably lower than the 7.1% calculated by Marks *et al.* (1997). The level of human disturbance may have contributed to the large difference in predation rate. Necessary observations from the South-Western point of Dyer Island occurred during Mark's *et al.* (1997) study, and may have contributed to more fledglings entering the water due to human disturbance. Comparatively, little disturbance occurred during the present study with only a single patrol conducted daily. Human disturbance should be minimised during the Cape cormorants breeding and fledgling period to reduce the number of seal attacks.

CHAPTER 7

Summary

Trends in habitat utilisation of the white shark (*Carcharodon carcharias*) within the Dyer Island area.

- White sharks occurred in the study area throughout the year. They frequent waters adjacent to the Dyer Island group during winter, and move inshore (Joubert se Dam and Holbaai) during the summer.

- This change in habitat utilisation may be partially related to breeding behaviour. An influx of female white sharks of assumed breeding size (TL > 450 cm) supports this theory. However, a study over a number of years would be required to establish such a trend. Additionally, con-specific bite marks (a sign of breeding in sharks) were more often observed during the summer, but again, this would require a consecutive annual investigation.

- The occurrence of smaller sharks inshore, away form the seal island may be related to physical and biological factors. A white shark's diet is extensively comprised of fish, and the occurrence of species such as geelbek, snoek and other fish inshore during the summer may motivate white sharks to follow these species.

- Water temperature drops and fluctuates at Dyer Island during the summer period, which is related to intense summer upwelling in the region. Inshore waters are more sheltered, thus here this abiotic effect is not so acute (water temperature is generally warmer). White sharks are endothermic, but their body temperature is still affected by the ambient environment. Utilising inshore areas may reduce thermal stress on white sharks in the area.

Predatory motivation of the white shark

- White sharks displayed varied levels of predatory motivation towards the decoys. The response correlated with a number of biological and physical variables suggesting that white sharks tend to investigate potential prey items and that their feeding motivation fluctuates.

- The size (total length) of sharks affected their predatory motivation. Larger sharks (>375 cm TL) displayed greater predatory motivation than smaller sharks (< 375 cm TL) towards the decoys. Experience and thus related competence as a predator may therefore affect an individual shark's tendency to hunt as opposed to mere investigation. Morphological constraints (small size, slender teeth) may also be a factor determining different responses towards the decoys.

- In close proximity to the seal colony (Geyser Rock) white sharks displayed elevated predatory motivation. White sharks actively hunting seals may be drawn to this area and their hunting motivation could be reflected in their attention towards the decoys. Alternatively, when white sharks enter this area the increase of sensory cues which denotes the presence of seals, may induce a more speculative hunting strategy where potential prey is more aggressively investigated.

- Low water visibility and abundant cloud cover also resulted in white sharks responding with higher predatory motivation towards the offered decoys. This environment is conducive to the successful hunting of a species such as the Cape fur seal where the element of surprise is critical. By early initiation of an attack on potential prey under such circumstance white sharks are maximising the possibility of successful attack. Furthermore, in such environments white sharks may use additional senses to identify prey (specifically touch) and the increased biting of the decoys could reflect this.

- No seasonal or diel trends in predatory motivation were recorded. Further research throughout entire 24 h periods is required to conclusively determine any diel aspect of the white shark predatory motivation.

Activity patterns of white sharks at chumming vessels

- Conditioning is most likely to occur when exposure of white sharks to chumming vessels is high. Smaller white sharks had a longer overall visit time at the chumming vessel. These, in conjunction with research that shows juvenile sharks more readily respond to associative conditioning experiments, suggest that smaller white sharks are more vulnerable to any potential conditioning influence by a chumming boat.

- Cloud cover (80-100% coverage) resulted in longer visitation patterns by white sharks to the chumming vessel. These conditions may also affect operators' ability to detect white sharks (due to increased glare), and result in more rewards been gained by sharks, thus facilitating conditioning. Operators in these conditions should be particularly vigilant.

- At present associative conditioning is unlikely to occur, as exposure of individual sharks to cage-diving appears to be minimal. However, further research into residency time, and long term exposure to cage-diving boats is required to address the conditioning issue fully. Furthermore, direct observations from cage-diving boats is required to quantify the extent of rewards gained from these activities as this is crucial to establish 'conditioning' of a shark.

- Distraction from normal activities (e.g breeding, hunting, moving and resting) is a further impact of cage diving. Distraction has the greatest impact in areas, or at times, when sharks are performing important life history activities (e.g. breeding, hunting). The activity patterns of white sharks within the channel suggests that it is a hunting area, thus the distraction impact is greatest there.

- This research only approximated a white shark cage-diving set-up. Observations directly from a cage-diving vessel is required to conclusively determine potential vulnerability of white sharks to conditioning (the association of boats with food).

Prey preference and visual discriminatory ability in the white shark determined by multiple choice tests.

- The eye structure of the white shark suggests they are diurnal hunters and use vision for detection and identification of potential prey. Pinnipeds are thought to be a major prey item of the white shark. The choice tests illustrated that white sharks could discriminate between a seal silhouette and a rectangle, and found the seal visually more attractive. A higher percentage of sharks within the larger (>375 cm TL) size category selected the seal decoy over the rectangle decoy compared with sharks within the smaller (<375 cm TL) size category. This may reflect pinnipeds becoming an increasingly important prey item as white sharks grow in size.

- The attraction of pinnipeds as prey is possibly related to the high energy content of blubber. Surprisingly, white sharks favoured a smaller seal decoy in preference to a larger seal decoy, despite the fact that smaller seals generally carry less blubber than larger seals. It appears that smaller sharks (a majority of the sample) are not confident hunters of large seals (high risk of injury, less chance of success) and thus select the smaller pinniped for this reason.

- The seal decoy was favoured over a penguin decoy. Although seabirds have been attacked by white sharks, it appears that they are rarely consumed after the initial attack. This experiment showed that a seal shape was more visually attractive than a penguin shape although little differences in size and shape between the decoys existed. This result is consistent with the assertion that attacks on seabirds arise from investigation or mistaken identity.

- The most important feature in selection of decoys by larger white sharks is resemblance to a biologically familiar shape (seal vs rectangle). No selection preferences were observed in any other experiment. This may arise from larger sharks adopting more aggressive and speculative hunting strategies, initiating attacks upon first detection and with little visual information. This could result in more attacks on non-prey items as a result of mistaken identity.

- The most important feature in selection of decoys by smaller white sharks was prey size. Morphology (size, tooth structure) and little experience may restrict the ability of smaller sharks to attack large pinniped prey. Strong preference in the species experiment (seal vs penguin) does suggest that it was important for these sharks to acquire visual information prior to interacting with a decoy (i.e. circling and passing). This behaviour is more indicative of scavenging and investigating than of hunting.

Predation by the white shark and the Cape fur seal (*Arctocephalus pusillus pusillus*) on seabirds at Dyer Island

- White sharks do not appear a major predator of seabirds at Dyer Island. This is despite evidence that they attack a significant number of African penguins at other seabird islands in South Africa. The presence of circa 55,000 Cape fur seals may increase the selectivity of white sharks towards a favoured prey species. Additionally, the seals may induce penguins to use anti-predator (fleeing to and from the island) behaviour, inadvertently making them less vulnerable to white sharks.

- Cape fur seals attack penguins seasonally, with a reduction in attack frequency during the summer, coincident with the penguin moult (at which time they do not venture into sea). Concurrent to the penguin moulting period is the fledgling period of the Cape cormorant. During this period fledglings are vulnerable to Cape fur seal attacks and may further reduce the predation pressure on penguins.

- Peaks in attacks on penguins occur during the early morning and late afternoon. This time of day is when penguins leave and return to the island from their foraging trips. It suggests that attacks on this species are related to these natural, daily movements. Cape cormorants are attacked throughout the day, particularly during the midday period. Attacks arise from cormorants entering the inshore water because of disturbance, failed flight attempts or for bathing. Human disturbance from the nest and roosting sites may significantly impact the frequency of Cape fur seal attacks.

- The predation impact on seabirds is significant, with minimum estimates of about 1.99% of African penguins, 3.13% of Crown cormorants, 5.21% of white-breasted cormorants and 1.09% of the fledgling Cape cormorant populations succumbing to Cape fur seal attacks. A single degloved bank cormorant carcass was also collected

- The frequency of seal attacks on seabirds at Dyer Island is significant enough for active management measures to be introduced as part of an island management plan. Further modeling research is required to assess whether the attack rate will affect the sustainability of the seabird populations. Small seabird populations in particular are vulnerable to stochastic events that could cause local extinction.

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Appendix 1. Bird list for Dyer Island

Roberts' Number	Common name	Status	Breed
3	African penguin	Resident	Yes
17	Southern giant petrel	Vagrant	No
32	White-chinned petrel	Vagrant	No
37	Sooty shearwater	Vagrant	No
43	Leach's storm petrel	Resident	Yes
53	Cape gannet	Visitor	No
55	White-breasted cormorant	Resident	Yes
56	Cape cormorant	Resident	Yes
57	Bank cormorant	Resident	Yes
59	Crowned cormorant	Resident	Yes
59	Eastern white pelican	Visitor	No
62	Grey heron	Visitor	No
63	Blackheaded heron	Visitor	No
67	Little egret	Resident	Yes
76	Blackcrowned night heron	Visitor	No
91	Sacred ibis	Visitor	No
102	Egyptian goose	Resident	Yes
244	African black oystercatcher	Resident	Yes
246	Whitefronted plover	Resident	Yes
248	Kittlitz's plover	Resident	Yes
249	Threebanded plover	Visitor	No
254	Grey plover	Resident	No
258	Blacksmith plover	Visitor	No
262	Turnstone	Resident	No
272	Curlew sandpiper	Visitor	No
281	Sanderling	Resident	No
290	Whimbrel	Resident	No
307	Arctic skua	Vagrant	No
312	Kelp gull	Resident	Yes
315	Caspian tern	Visitor	No
316	Greyheaded gull	Visitor	Yes
322	Hartlaub's gull	Resident	Yes
324	Swift tern	Resident	Yes
326	Sandwich tern	Visitor	No
327	Common tern	Resident	No
328	Arctic tern	Resident	No
329	Antarctic tern	Resident	No
330	Roseate tern	Visitor	Yes
332	Sooty tern	Vagrant	No
348	Feral pigeon	Vagrant	No
349	Rock pigeon	Resident	Yes
428	Pied kingfisher	Vagrant	No

664	Fantailed cisticola	Vagrant	No
698	Fiscal flycatcher	Vagrant	No
713	Cape wagtail	Resident	Yes
757	European starling	Resident	Yes
801	House sparrow	Resident	Yes
803	Cape sparrow	Resident	Yes