ECOTOURISM EFFECTS ON THE INTERACTIONS BETWEEN WHITE SHARKS AND CAPE FUR SEALS AROUND A SMALL ISLAND SEAL COLONY

by

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B.Sc., McGill University, 1999

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

In the
Department
of
Biological Sciences

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SIMON FRASER UNIVERSITY

Summer 2006

APPROVAL

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Degree: Master of Science

Title of Thesis:

Ecotourism effects on the interactions between white sharks and Cape fur seals around a small island seal colony

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Abstract

This thesis examines the effects of a provisioning ecotourism operation on the behaviour of white sharks *Carcharodon carcharias* and their prey, Cape fur seals *Arctocephalus pusillus pusillus*, around a small island seal colony in South Africa. In the absence of human activity, adult seal tactics appear evolved to minimize predatory risk from the sharks, whereas shark tactics do not seem to consider adult seal availability. Pup seals, however, often behave in a manner which leaves them at substantial risk, and shark tactics appear influenced by this behaviour. The system is probably not affected by ecotourism, which seems to have a relatively minor effect on the movement patterns of most sharks. The result is that shark predatory pressure on the seals likely remains at near constant levels during ecotourism activity, and thus that white shark ecotourism probably has little effect on seal behaviour, or on the remainder of the ecosystem.

Key Words: white shark, Cape fur seal, provisioning ecotourism, predator-prey behavioural tactics, behavioural game, indirect interactions

Dedication

To my parents. For everything.

Acknowledgements

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Chapter 1

General Introduction

Indirect interactions on an ecological scale require at least three species. They occur when changing a property of one species, termed the 'initiator', causes some change in a second species, called the 'transmitter'. This in turn affects a third species within the community, dubbed the 'receiver' (after Abrams 1995). Thus, two distinct direct interactions (initiator-transmitter, transmitter-receiver) are mediated through some change in the transmitter to produce an indirect interaction between the initiator and receiver (Wootton 1993, Abrams 1995). This would be labelled a behaviourally mediated indirect interaction (BMII) if it arose from a change in the transmitter's behaviour (Dill et al. 2003). It would further qualify as a facilitating BMII if the end result improved the receiver's condition, or ability to engage in some beneficial activity.

This definition does not exclude human activity. In fact, humans most likely generate, or form a link in, a substantial number of such interactions: we can easily adopt the role of initiator, transmitter, or even receiver, depending on the context (Carney and Sydeman 1999, Pinnegar et al. 2000, Frid and Dill 2002, Alonzo et al. 2003a, Dill et al. 2003). One context within which humans may be creating a BMII is the white shark *Carcharodon carcharias* ecotourism industry in South Africa. Every winter, tour boats

transport eager tourists out to Cape fur seal *Arctocephalus pusillus pusillus* colonies located along the south coast of South Africa to attract and observe the white sharks which congregate in those areas, during those times of the year, to prey on the seals (Ferreira and Ferreira 1996, personal observation). In this particular environment, a BMII would be occurring if human presence, as an initiator, changes shark behaviour (transmitter) from hunting seals to scavenging on tourist offerings, and the seals, as receivers, are able to detect this alteration in shark behaviour and change their own as a consequence.

The key to describing this speculative BMII lies in developing a solid understanding of the direct predator-prey interaction between sharks and seals. There are two generally accepted routes by which predators can exert an influence on prey populations. The first of these is through actual predation, or directly reducing prey numbers through imposed mortality. Alternatively, predators can affect their prey indirectly, in a sub-lethal manner, by causing a shift in behaviour or life history strategies away from those observed in the absence of the predator (Lima and Dill 1990, Hugie and Dill 1994, Yodzis 2000, Altendorf et al. 2001). Indeed, prey species will often avoid engaging in some beneficial activity to reduce predation risk, and a sizeable body of literature exists demonstrating a foraging gain/predation risk trade-off in many animal species (see Lima and Dill 1990 for an overview, Brown 1999, 2002). Should the Cape fur seals be engaging in a trade-off while the sharks are present, then the indirect interaction alluded to above could be considered facilitating if ecotourism activity altered shark behaviour such that the predation risk they imposed upon the seals was reduced,

thus improving the seals' ability to engage in some beneficial activity such as feeding (Dill et al. 2003).

The sharks too are players in the direct predator-prey interaction, however, and are free to change or adapt their behaviour in response to any change on the seals' part, just as they could for any stimulus presented by the ecotourism operators. In fact, because the preferred outcome of this direct interaction will necessarily differ for both hunter and hunted, but will ultimately only be under the partial control of either, the optimal course of action for one will most likely depend on the other's behaviour (Hugie and Dill 1994). Thus, cultivating a clear understanding of the predator-prey interaction dynamics will require adopting a game-theoretical approach (Maynard Smith 1982, van Baalen and Sabelis 1993, Brown et al. 1999, 2001, Alonzo 2002, Alonzo et al. 2003b) and this can then be used to assess the effect of ecotourism.

The goal of this thesis was therefore to examine the behaviour of Cape fur seals and white sharks around a South African island colony which supports ecotourism activity. More specifically, the objectives were: (i) to investigate the natural behaviour of sharks and seals in isolation and in relation to each other, and to use these data to develop a model of the predator-prey interaction around the colony every winter; and (ii) to quantify ecotourism activity at this colony and determine whether this had an impact on the relationship described above.

1.1 Study site

The research for this thesis was conducted at Seal Island in False Bay, South Africa (Fig. 1.1). This island supports a year round colony of Cape fur seals which at any

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time numbers between 30 000 and 60 000 individuals (Warneke and Shaughnessy 1985,). Every winter (in the southern hemisphere), large numbers of white sharks congregate around the island, resulting in a high rate of predatory interactions (Stewardson 1999, personal observation). As a result, the island also sustains a small white shark ecotourism industry, with two boats making the daily trip to the island. Seal Island is an ideal location to study this speculated BMII for two reasons: (i) the overt predatory activity (that which can be observed at the surface) is seemingly greater at Seal Island than at any other location in the world (predations occur at a ten-fold greater frequency here than at any other South African colony, and are several times more frequent than at colonies in California where predatory events have been recorded; Klimley et al. 1992, Martin et al. 2005), ensuring that the potential exists for an important game between the sharks and seals; (ii) the ecotourism activity at Seal Island is minor compared to other locations in South Africa (personal observation), which not only allows an examination of natural conditions, but also makes it possible to exert some experimental control over the amount and types of organic material used to attract the sharks to the boat.

1.2   Study species

My research examined the movements of South African (or Cape) fur seals *Arctocephalus pusillus pusillus* and white sharks *Carcharodon carcharias* around Seal Island. Cape fur seals are pinnipeds of the family Otariidae, and thus possess the strong foreflippers characteristic of this family, which allow for increased mobility on land as compared to pinnipeds of the family Phocidae (true seals; David 1987). Male seals are about 230-235 cm long and weigh about 360 kg., while females are about 180 cm long

and weigh 120 kg. Pups are 60-80 cm long and weigh 6 kg at birth. The research in this thesis focused primarily on the movements of nursing mothers and pups.

Cape fur seals can be found along the coasts of South Africa and Namibia, and are the only pinniped species indigenous to the area (David 1987). They are generalist predators, and have been noted to consume numerous species of bony and cartilaginous fishes, along with cephalopods, crustaceans, and even birds. Female seals mature at the age of 3, while the age at maturity for males is unknown. Adult males arrive at breeding sites in mid-October and fight for territory before females come ashore. These arrive at the end of November, and give birth within a two week span in December. They will mate with males approximately a week after giving birth, but delay implantation for approximately 4 months. Lactation can last up to 12 months, but is typically 6-9 months, with pups first being weaned at the beginning of the winter, typically in May or June (David 1987).

White sharks are the largest predatory fish in the world (Compagno 1984). They can reach nearly 7 m in length and weigh more than 2 tons. Juveniles are primarily piscivorous, eating bony fish, rays and other sharks. Adults are also piscivorous, but also hunt larger prey, including pinnipeds, small toothed whales, sea otters and sea turtles. They also eat carrion, including the carcasses of large whales. White sharks are highly migratory animals, capable of trans-oceanic migrations and deep dives (up to 1000 m), but are often found in association with isolated islets and archipelagos inhabited by pinnipeds (Compagno 1984).

1.3   Chapter summaries

During the South African winter of 2004 I conducted experiments around Seal Island which mimicked ecotourism, while using acoustic telemetry equipment to track the movements of both seals and sharks. In Chapter 2, I present the tracking results collected during periods with no ecotourism activity, along with a game model of shark and seal tactics. In Chapter 3, I address whether ecotourism activity has an effect on the natural movements described in Chapter 2.

1.4   Literature cited

Abrams PA (1995) Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. American Naturalist 146:112-134

Alonzo SH (2002) State-dependent habitat selection games between predators and prey: the importance of behavioural interactions and expected lifetime reproductive success. Evolutionary Ecology Research 4:759-778

Alonzo SH, Switzer PV, Mangel M (2003) An ecosystem-based approach to management: using individual behaviour to predict the indirect effects of Antarctic krill fisheries on penguin foraging. Journal of Applied Ecology 40:692-702

Altendorf KB, Laundré JW, Lopez Gonzalez CA, Brown JS (2001) Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy 82:430-443

Brown JS (2002) Indirect effects of trophic interactions: Prey behavioral responses to the risk of predation. Ecological Society of America Annual Meeting Abstracts 87:11-12

Brown JS, Kotler BP, Bouskila A (2001) Ecology of fear: foraging games between predators and prey with pulsed resources. Annales Zoologici Fennici 38:71-78

Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385-399

Carney KM, Sydeman WJ (1999) A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22:68-79

Compagno LJV (1984) An Annotated and Illustrated Catalog of Shark Species Known to Date 1. Hexanchiformes to Lamniformes. FAO (Food and Agriculture Organization of the United Nations) Fisheries Synopsis:1-249

David JHM (1987) South African Fur Seal *Arctocephalus pusillus pusillus*. NOAA Technical Report NMFS:65-72

Dill LM, Heithaus MR, Walters C (2003) Behaviorally-mediated indirect interactions in marine communities and their conservation implications. Ecology 84:1151-1157

Ferreira C, Ferreira T (1996) Observations on white sharks along the South African coast. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, p 375-384

Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:Unpaginated [URL:http://www.consecol.org/Journal/vol6/iss1/art11/manuscript.html]

Hugie DM, Dill LM (1994) Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45:151-169

Klimley AP, Anderson SD, Pyle P, Henderson RP (1992) Spatiotemporal patterns of white shark *Carcharodon carcharias* predation at the South Farallon Islands California. Copeia:680-690

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640

Martin AR, Hammerschlag N, Collier RS, Fallows C (2005) Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. Journal of the Marine Biological Association of the UK 85:1125-1135

Maynard Smith J (1982) Evolution and the Theory of Games, Vol. Cambridge University Press, Cambridge

Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien ML, Hereu B, Milazzo M, Zabala M, D'Anna G, Pipitone C (2000) Trophic cascades in benthic marine ecosystems: Lessons for fisheries and protected-area management. Environmental Conservation 27:179-200

Stewardson CL (1999) Preliminary investigations of shark predation on Cape fur seals *Arctocephalus pusillus pusillus* from the Eastern Cape coast of South Africa. Transactions of the Royal Society of South Africa 54:191-203

Van Baalen M, Sabelis MW (1993) Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. American Naturalist 142:646-670

Warneke RM, Shaughnessy PD (1985) *Arctocephalus pusillus*, the South African and Australian fur seal: Taxonomy, evolution, biogeography, and life history. In: Ling JK, Bryden MM (eds) Studies of sea mammals in South latitudes, Vol 1. South Australian Museum, Adelaide, p 53-77

Wootton JT (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. American Naturalist 141:71-89

Yodzis P (2000) Diffuse effects in food webs. Ecology 81:261-226

1.5   Figures legends

Fig. 1.1:   Seal Island, in False Bay, South Africa. Waters to the South and West of the island drop off quickly to depths greater than 20 m, while depths to the North and East increase more gradually.

1.6   Figures

Fig. 1.1:
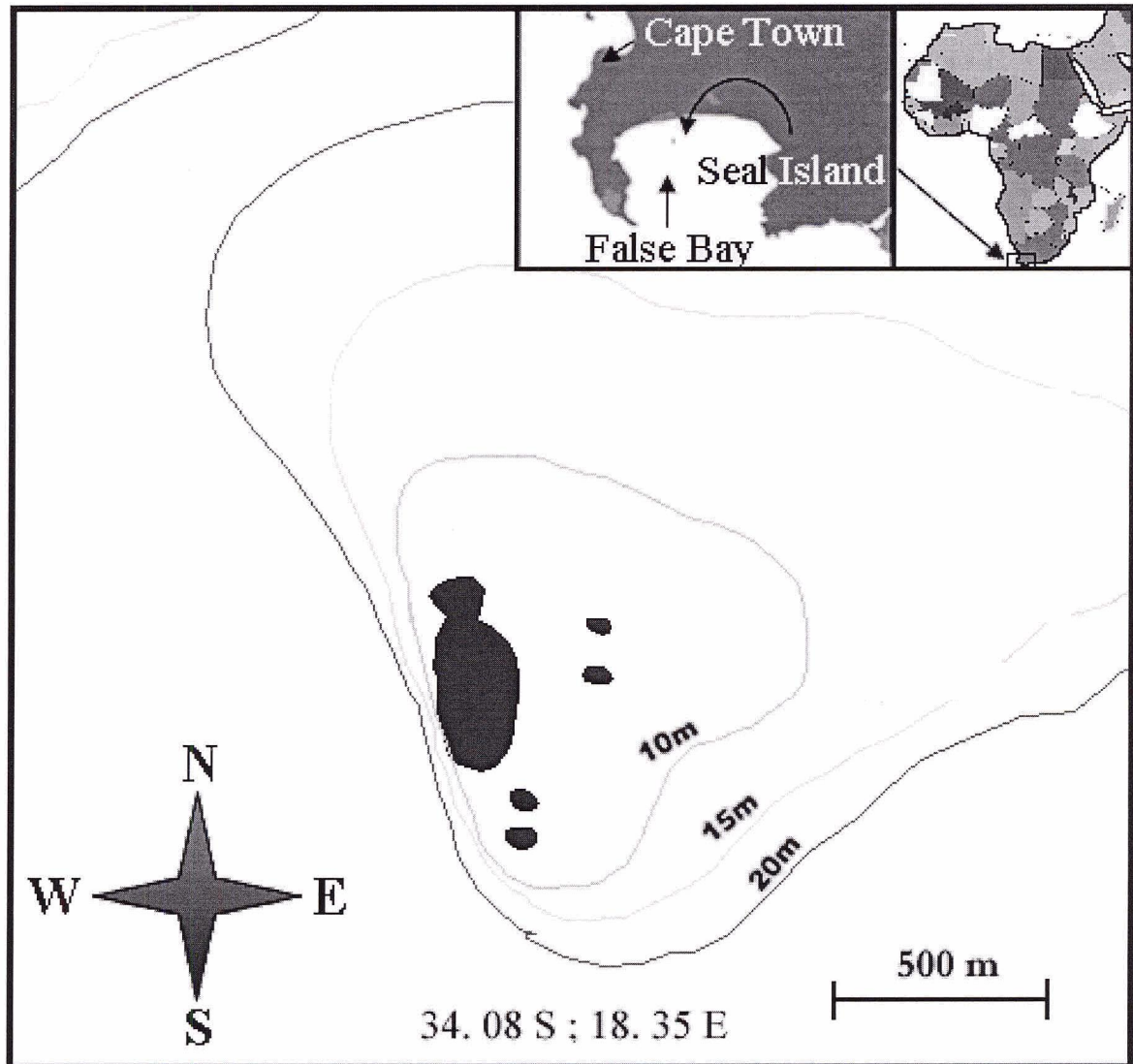
Chapter 2

Interactions between sharks and seals around a small island colony: a predator-prey behavioural game?

2.1 Abstract

Behaviour of both species in predator-prey systems often evolve within the context of behavioural games, the result of which should be equilibrium strategies for each species which maximize payoffs based on the other's tactics. Here we present results from research exploring a potential predator-prey game between white sharks *Carcharodon carcharias* and Cape fur seals *Arctocephalus pusillus pusillus* around a small island colony in South Africa. Behavioural tactics recorded for adult seals appeared to account for the hypothesized variance in risk from the sharks, but, although shark tactics corresponded well with the generally accepted hypothesis for how sharks hunt pinnipeds, they did not seem to consider availability of adult seals. Instead, recorded shark tactics seemed more influenced by the behaviour of pup seals, likely because these acted in a manner which left them at substantial risk. This suggests that seal pups are players in a game with the sharks which has not evolved to an equilibrium where the strategy of each player is the best response to that of their opponent, possibly because of a constraint on their behaviour, because they trade-off predation risk against some other important factor, or because Seal Island represents an open system. Instead, it seems likely that seal pups act as initiators in a behaviourally mediated indirect interaction with adults, mediated by the behaviour of the sharks. The results of this study demonstrate that separate 'subunits' within a population may behave differently, and that this variation needs to be accounted for when modeling the behaviour of a species.

2.2 Introduction

Prey species will often trade-off a degree of benefit to reduce predation risk imposed on them by predators (see Lima & Dill 1990 for an overview, Bouskila et al. 1998, Brown et al. 1999, Lima 2002). However, predators can also alter their behaviour in response to prey. Thus, the optimal course of action for either species will most likely depend heavily on the other's behaviour (Hugie & Dill 1994, Sih 1998, Welton et al. 2003), and interactions between a predator and prey can often be viewed as a behavioural game.

The importance of considering behavioural games when modeling predator-prey interactions has been demonstrated repeatedly (Brown 1992, Van Baalen & Sabelis 1993, Hugie & Dill 1994, Bouskila et al. 1998, Sih 1998, Altendorf et al. 2001, Brown 2002). Further, these models have recently been expanded to include consideration of an individual's state (Houston & McNamara 1999, Clark & Mangel 2000, Alonzo 2002, Alonzo et al. 2003). However, to this point, all models have considered prey behaviour in response to both predation risk and resource distribution. In this paper, we employ the principles of a behavioural game to explore a system where prey behavioural choices appear centered around predation risk – that of white shark *Carcharodon carcharias* predation on Cape fur seals *Arctocephalus pusillus pusillus* in South Africa.

White sharks are important pinniped predators, whose primary hunting strategy appears to involve patrolling the waters near a seal colony and attacking seals as they move to or from their haul-out sites (Bruce 1992, Klimley et al. 1992, Klimley 1994, Klimley et al. 2001, Kock 2002). The result is that seals are relatively safe from white shark predation once they've made it about 1000 m from land, or when in the shallow

waters immediately adjacent to their haul-out, where they are observed rafting (large groups of seals 'playing' in the water, possibly for thermoregulatory reasons; David 1987). However, they will experience a substantial level of risk when traveling to or from the colony, because the sharks concentrate within several hundred meters of shore.

This predatory pressure could have led to the evolution of a predator-prey behavioural game between sharks and seals. For this to have occurred, however, both species must have a range of behavioural options available to them. A game could then produce a pair of evolutionarily stable strategies (ESS; Maynard Smith 1979) able to persist within populations of the two species, and an equilibrium between the two where-by each one's strategy is the best response to that of the other.

The key to determining whether this has occurred in our system is to understand the costs and benefits associated with every behavioural tactic. In this paper, we will therefore explore the various tactical options available to both species, in terms of risk to the seals and opportunity for the sharks, to determine whether their interaction has led to the equilibrium state of a predator-prey behavioural game.

2.3 Materials and methods

2.3.1 Study site

The research was conducted around Seal Island, a small island located in False Bay, in the Western Cape region of South Africa. Water depths are not uniform around Seal Island (Fig. 2.1): the ocean floor drops down very quickly to depths greater than 20m off the southern and western sides of the island, while the slope is much more gradual on the northern and eastern sides. Seal Island is populated year-round by

anywhere between 36 000 and 77 000 Cape fur seals (unpublished data from South African Marine and Coastal Management), and is the only Cape fur seal breeding colony within the bay (Shaughnessy 1987). White sharks are present in large numbers around the island during the Southern Hemisphere's winter months (May-September), but are scarce during other times of the year (Kock 2002).

2.3.2 Acoustic equipment

Fifteen adult female Cape fur seals, who had been observed actively nursing pups, were tagged with Vemco Rcode acoustic transmitters, of which 5 were model V16, and the remainder model V16P (added pressure sensitivity for swimming depth measurement). In all cases, seals were captured on Seal Island with large nets, restrained with straps and braces, and transmitters glued to their dorsal fur using quick setting epoxy which the seals would shed during the summer molt.

Seventeen white sharks were tagged with V16 transmitters, of which 7 were model V16, and the remainder V16P. In all cases, sharks were enticed to our boat by means of various forms of attractant (fish oil, sardine, shark liver, whale blubber), and coaxed to stay with large chunks of fish bait. Sharks were lured very close to the boat, at which point a tag was attached subcutaneously by means of a small plastic barb and a metal spear.

Data were collected from the acoustic transmitters using 6 Vemco model VR2 data logging receivers. These were deployed along the ocean floor at various locations around Seal Island (Fig. 2.1), anchored to the bottom by means of a truck tire filled with concrete.

2.3.3   Visual records

Information on seal movement was also collected by means of systematic visual observation from an 8 m vessel during June-October 2004. Attempts were made to be present at Seal Island whenever possible, and we averaged 15 days per month. Waters surrounding Seal Island were divided into 6 sectors (later re-grouped into 2 zones, see Fig. 2.1), and time of day divided into 4 2.5-hour blocks between 07:30 and 17:30 (hours were occasionally extended on either side). Our activity at the island was then randomly assigned to a specific sector for each time block, using Microsoft Excel's random number function. In total, we were present for, and collected data during, 169 time blocks.

Two methods were used to collect visual records. The first involved recording all seal movements observed while in a specific sector, noting the direction a group was moving (to or from the island), the group size, the average seal size within the group, and the location of the movement around the island. Movement type was also recorded, classified either as 'long distance porpoising' (LDP; directional surface swimming for longer than 45 sec), or not; seals which disappeared from view for longer than 30 sec were recorded as not using LDP. This categorization was used to distinguish visual records of diving seals from those moving at the surface, and could be applied to most seal groups that were observed for the requisite amount of time.

Seal movement was also recorded visually by means of focal follows (n=44), whereby a group of seals moving to or from the island was followed for approx 750 m, at a distance of approx 50 m. The follows themselves did not appear to affect seal behaviour, as similar movement patterns were observed while our vessel was anchored. All behaviours witnessed within each 50 m segment of their path were recorded, as well

as the time between segments. If the seals dove at any point, the boat was stopped until they were re-sighted; we would then catch up to them and resume the follow.

2.3.4 Analysis – Individual species

2.3.4.1 Seals

Four of the VR2 receivers were placed in locations such that their receptive radii extended to the island itself (Fig. 2.1), making it impossible to directly differentiate those data which corresponded to seal movement from those which consisted of rafting behaviour. Consequently, it was necessary to make the following assumptions to isolate discrete instances of seal movement to or from the island:

1. Seals only raft within a small annulus around Seal Island, and presence outside of this area indicates movement.

2. Seals moving to or from the island do so with a general intent, i.e., to get from the island to open water or vice versa as soon as possible, with as few detours as possible.

3. Seal mothers follow the typical behaviour pattern of leaving the island to feed for a few days then returning to suckle (Gentry & Kooyman 1986, Bradshaw et al. 1999, Goldsworthy 1999, Gamel et al. 2005), and the period between suckling bouts increases throughout the year as the pup is weaned.

4. Depth records below 20 m on the south and west, and 15 m in other areas, indicate movement, because seals could not attain these depths within the rafting zone.

5. Records from the SE and NE VR2s indicate movement, as the receptive ranges of these receivers didn't extend into the rafting zone.

6. Seals swim almost exclusively by porpoising at the surface, or by swimming very near to the ocean floor. While moving, they are only found in the middle of the water column on their way between the surface and the bottom.

The first five assumptions are based on personal observation at Seal Island, references from the literature, and common sense, while the last was conceived theoretically as optimal risk management behaviour based on patterns of shark swimming depth (see

Results). Nonetheless, they remain assumptions, and must be considered when weighing the validity of seal data presented here.

Assumption 4 created a reliance on depth records for identifying many instances of movement, which effectively rendered unusable the data obtained from seals tagged with V16 transmitters (not depth-sensitive), reducing the overall seal sample size from 15 to 10. It also had the effect of removing the E receiver from consideration, because the average depths in this area were too shallow to allow distinction between movement and rafting records. However, this loss was compensated for by the receptive range of the SE receiver, which covered most of the area through which the seals would swim before or after swimming through the E receiver receptive field (see Fig. 2.1). Assumption 5 would also seem to create a bias towards increased identification of instances of movement for the SE and NE receivers. However, daytime patterns of movement obtained from all receivers were quite similar to those expected based on the visual observations, so this does not seem to be a problem.

Once discrete instances of seal movement were identified, assumption 3 was applied to the broad-scale temporal patterns within the data recorded from individual animals, to designate movement as either 'departing' or 'returning'. Data were then weighted to reflect the variation in receptive ranges for each VR2 (Fig. 2.1), by measuring the greatest angle subtended by each receiver (radians) against a hypothetical circle centered at the island's center. Records were also adjusted to reflect time relative to sunrise and sunset, rather than clock time, and grouped into one of four time periods: midnight to sunrise (1), sunrise to noon (2), noon to sunset (3), and sunset to midnight (4).

Seal receiver records were first analyzed as one-way randomized complete block ANOVAs to determine whether movement varied as a function of receiver location, time category, and swimming depth, using individual seal identification as blocking variables. Having examined these three parameters separately, 3-way ANCOVA was employed to determine whether interactions existed between them.

Seal visual records provided information on seal group size and movement direction, as well as on behavioural differences between seal size classes (a surrogate variable for seal age). One-way ANOVA was used to determine whether any behavioural differences observed were statistically significant. Unfortunately, it was only possible to collect seal visual records during the day, as well as in the hours immediately preceding sunrise and following sunset. Consequently, it was necessary to make a further assumption:

7. Seal group sizes observed moving at the surface between 06:00 and 20:00 are similar to those throughout the remainder of the night.

This assumption appears reasonable, in that group sizes are likely determined by the departing and returning circumstances, rather than by time of day or light levels. Nonetheless, like the other assumptions, it must be taken into account when considering the results.

2.3.4.2 Sharks

Shark data obtained from individual receivers were first weighted by the receptive area of each receiver, and then adjusted for sunrise/sunset and grouped into one of four categories, in a similar manner to the seal data. The depth data (meters below the surface) obtained from sharks with V16P sensors were analyzed according to depth in meters, and

subsequently aggregated to reflect the sharks' presence in each of three levels of the water column: upper, mid, and lower. These three levels did not correspond to fixed depths around the island, but rather were conceived to reflect the estimated ability of each species to detect the other (described in Appendix).

Shark receiver data were analyzed in a similar manner to the seal data. One-way randomized complete block ANOVAs were first used to determine whether records varied as a function of location, time, and depth, using individual sharks as the blocking variables. Interactions between the terms were then explored using a 3-way ANCOVA.

2.3.5   Analysis – Species interaction

Examining the interaction between sharks and seals meant defining the circumstances leading to the event which characterizes this interaction: the attack. For both species, these circumstances were taken to represent the approximate payoff for any tactic, i.e., for seals the payoff was avoiding an attack (and thus staying alive), while for sharks the payoff was the opportunity to launch an attack (and obtain a meal). For the purposes of this model, the interaction was deemed to end once an attack was initiated, implying that all shark attacks resulted in successful kills. Although this certainly wasn't the case, it seems reasonable to assume that a seal's best option would be to avoid being attacked in the first place, while conversely it seems likely that sharks wouldn't launch attacks without some reasonable expectation of success. The result is that the behavioural tactics adopted by both species likely reflect the chances of an attack occurring, regardless of its outcome.

For an individual seal, the risk of shark attack for any specific movement tactic, characterized by a time of day t, a swimming depth D, a location around Seal Island l, a group size g, and a seal size state s, is defined as:

$$R_{tDlgs} = \sum_{d=upper}^{lower} P \cdot \delta_d \qquad (1)$$

where P is a context-specific relative weight estimated to reflect the effect of environmental, group size, and seal size conditions on the chance of a predatory strike occurring if a seal adopted tactic R_{tDlgs} and a shark was in either of the three possible shark depth strata d (a matrix of P values was estimated for every possible combination of seal and shark tactics, see Appendix), and δ_d is the density of sharks at shark depth level d for each specific P. Thus, the risk to an individual seal employing any given tactic is the sum of the shark densities in the three depth strata at the corresponding time and location, each weighted by the chance that a shark could launch an attack within that specific context.

Similarly, for a shark, the availability of seals to attack for any specific patrolling tactic, consisting of a time of day t, a swimming depth D, and a location around Seal Island l, is defined as:

$$A_{tdl} = \sum_{D=Deep}^{Surface} P \cdot \sigma_D \qquad (2)$$

where P is the same context-specific relative weight as for the seals, although now corresponding to the effect of environmental, group size, and seal size conditions on the chance of a predatory strike occurring if a shark adopted tactic A_{tdl} and a seal was in

either of the two possible seal depth strata D, and δ_D is the density of seals at seal depth level D for each specific P. Thus, the availability of seals for an individual shark employing any given tactic is the sum of the seal densities in the two depth strata at the corresponding time and location, each weighted by the chance that a shark could launch an attack within that specific context (which includes seal group size and seal size). Shark intraspecific interactions were not considered when formulating R or A, because no evidence exists to suggest any form of territoriality or pre-feeding competition within this species.

2.4 Results

2.4.1 Seals

Seal data obtained from VR2 receivers were analyzed separately according to whether the seals were departing from, or returning to, Seal Island. This distinction was made because of the marked difference in average group sizes of seals engaged in the two activities (Fig. 2.2): departing groups were generally much larger than returning ones. This discrepancy could theoretically have led to a substantial difference in the risk incurred by an individual seal in the two contexts, which would have been masked if the two were grouped together.

2.4.1.1 Returning seals

Seal movement did not differ with receiver location around Seal Island, i.e., the seals returned in similar numbers from all sides of the island (one-way RCB ANOVA, p=.203, Fig. 2.3). However, there was a clear difference in the times and depths at which they chose to move (Fig. 2.4). Seals returned to the island substantially more under the

cover of darkness, returning throughout the night; they also chose to return primarily at depth. There was a significant interaction between these two variables (2-way ANCOVA, p=0.0154), but this likely resulted from a lack of 'Surface' data, rather than from any meaningful biological phenomenon.

2.4.1.2 Departing seals

Departing seals demonstrated a clear preference for the South side of the island (the S and SE receivers; Fig. 2.3), as well as for swimming at the surface (71% of departing records). They also chose to depart the island almost exclusively in the dark (78% at night), although their movement was concentrated within a period of approximately two hours following sunset, rather than spread out over the entire night. There was a highly significant interaction between the three variables (3-way ANCOVA, p<0.0001; Table 2.1), indicating that the preferred seal choice for departing from Seal Island is to porpoise at the surface, in a southerly direction, immediately after sunset.

2.4.1.3 Seal visual records

Visual records were used to determine seal group sizes for the two movement directions (Fig. 2.2) and to provide resolution of daytime movement on an hourly scale (Fig. 2.5). They were also used to explore differences in seal behaviour based on age class. Only results pertaining to returning seals will be presented here; most departing seals, regardless of age, appeared to use the tactics discussed above.

Seals of different age spent different amounts of time swimming at the surface (Fig. 2.6). From the focal follows, it was possible to count the total number of 50 m segments in which seals were observed at the surface, as well as how far they swam when

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they dove. Smaller seals didn't travel as far underwater as the larger ones, with a difference in mean diving distance of almost 400 m between pups and adults. Consequently, younger seals spent a significantly greater proportion of their time swimming at the surface.

The visual records also provided a means to compare choice of returning location between adult seals and pups. Whereas adults returned in relatively similar numbers from all directions, pups returned significantly more over the deeper waters from the southerly and westerly directions ($\overline{x}$ = 4.2 counts/hour ± 3.3 sd) than over the more shallow waters to the north and east ($\overline{x}$ = .8 counts/hour ± 1.1 sd; t= 12.426; p<0.0001).

2.4.2   Sharks

The same three variables used to investigate seal VR2 records (location, time, swimming depth) were also used to examine shark movement. The sharks clearly displayed an inclination for swimming on the South side of the island, and were present in the greatest numbers in the morning (Fig. 2.7). Mean shark swimming depth was also approximately the same, between 12 and 14m, regardless of prevailing water depth (Fig. 2.8). These depths corresponded to the 'Mid' range of the water column, resulting in a very clear preference for swimming at this level (LSM Transmissions/m^2, $\overline{x}$ upper level = 3.5 ± .14 E-05 se; $\overline{x}$ mid level = 11.2 ± .22 E-05 se; $\overline{x}$ lower level = 4.4 ± .25 E-05 se; one-way ANOVA p<0.0001). Depth also explained 65% of the variance observed in a 3-way co-variance model (Depth Level F Ratio=251.2368; 3-way interaction term p<0.0001), and was therefore removed from the model in order to further explore the relationship between location and time. The result was a clear interaction between South and morning (2-way ANCOVA, p<0.0001; Fig. 2.7).

2.4.3   Shark-seal interaction

The first P matrix was created solely for adult seals, because this was the size class for which telemetry data existed. Shark receiver records were used as the measure of shark density to calculate R_{tDlg} for every seal movement tactic, and these were then plotted against actual seal receiver data (Fig. 2.9). The result suggests that seals moved more frequently when the risk index was lower, i.e. that adult seals were maximizing their payoff (chance of avoiding an attack) from the predator-prey interaction by moving when risk of predation was lowest. The converse side of the interaction was then explored, using adult seal receiver records to calculate A_{tdl} for each shark tactic. These hypothetical values were then plotted against real shark data, but no clear pattern emerged (Fig. 2.10), suggesting that the sharks didn't consider adult seal availability when choosing when and where to patrol. This would imply that sharks were not maximizing their payoff (opportunity to attack) from the interaction, at least with regard to adult seal tactics.

However, adult seals comprised only 22% of the visual records, meaning that the A_{tdl} values in Fig. 2.10 fail to account for 78% of the animals available to the sharks. Since transmitters were only attached to nursing mothers, telemetry data were only available for adult female seals. It was therefore necessary to employ visual records, obtained for all seal size classes as the indicators of seal density required to calculate A_{tdl}. These were adapted to correspond with the criteria for each relative context weight by employing the seal data assumptions, by using the Long Distance Porpoising (LDP) distinction to differentiate between 'deep' and 'surface' seals, and by roughly equating

the locations of visual records with the VR2 receptive radii (Fig. 2.1; see Materials and methods section).

Expanding P to include all size classes and adjusting for differences in mass (unpublished data from seal captures) indicated that younger seals were substantially more available to the sharks than the older ones (Fig. 2.11). One explanation for this is that seal pups, unlike adults, didn't predominantly choose tactics which would limit their overall risk (Fig. 2.12). Consequently, it seems reasonable to assume that the sharks would behave in a manner that takes the availability of smaller seals into consideration; indeed, a plot of A_{tdl} for all seals against the shark presence data obtained from the receivers produced a very strong relationship (Fig. 2.13).

These results are very speculative, given that most values in the P matrix are essentially educated guesses. Consequently, a sensitivity analysis was conducted to assess the relative importance of the estimated P weights. This analysis indicated that the basic trends presented in the results above were inherent in the data themselves. Thus, it seems likely that the context dependent weights only strengthened the relationships observed, rather than actually creating them (see Appendix).

2.5 Discussion

The evolution of a behavioural game requires the presence of at least two 'players' with conflicting interests, each of whose actions directly impact on the other's evolutionary fitness; it also necessitates that each player have available to them a 'strategy set' of various behavioural tactics (Maynard Smith 1979). The shark–seal system at Seal Island would appear to meet these criteria, suggesting that a predator-prey

game may exist. However, to determine whether the tactics recorded reflect the equilibrium state of such a game, it is necessary to comprehend why the animals might have chosen to exhibit the behavioural patterns we observed.

2.5.1   Behavioural patterns

Much of our data can be explained using the widely accepted hypothesis for how white sharks hunt for seals: swimming at depth to exploit the visual advantage that light provides them against seals at the surface (see Appendix for discussion of the importance of light levels), and using this advantage to launch ambush attacks (Klimley 1994, Ferreira & Ferreira 1996, Strong 1996, Kock 2002; unpublished data from Seal Island).

2.5.1.1 Temporal patterns

This hunting strategy can account for the temporal distribution pattern of both species. For one, low light levels at night would reduce any visual advantage, making it difficult to launch successful attacks. Thus, independent of any potential behavioural game, shark density should be higher during the day and lower at night, which is what we observed. However, increased light levels would also provide for greater visibility underwater, allowing seals to detect sharks at greater depths. Consequently, sharks would have to swim lower in the water column during the day to maintain their visual advantage, which was also observed (unpublished data). This could have a negative impact on the sharks' hunting success, however, in that the time provided for the seals to detect an attacking shark and avoid it would increase.

It thus follows that crepuscular periods might provide the best conditions for hunting seals. The light levels necessary for backlighting are probably achieved long before sunrise, while underwater visibility will still be relatively low, as light penetration

into the water is minimal until mid-morning. This would provide the sharks with the optimal combination of seal spotting ability and crypsis, allowing them to swim relatively high in the water column while remaining undetected.

However, a preference for crepuscular periods doesn't explain why the sharks would be present in high numbers at dawn but minimal levels at dusk, as we observed (Fig. 2.7). Instead, an explanation for this result could come from the temporal pattern of seal behaviour. Seals moved predominantly at night (Fig. 2.4; Table 2.1), most likely due to the decreased risk of predation afforded by low light levels. However, the need to separate seal receiver records into four time periods obscured an important facet of the data: a large number of seals moved at sunrise, mostly in the return direction, but movement of any kind was negligible in the hours preceding sunset (Fig. 2.5). It instead began as soon as the last vestiges of light had disappeared, with extremely large seal groups departing from the island in unison for approximately an hour, after which movement decreased to moderate levels. This meant that there were seals for the sharks to hunt during the optimal conditions at sunrise, but that sunset offered very few opportunities. Shark temporal presence reflected this pattern perfectly.

One might wonder, then, why seals would avoid moving at dusk, but not at dawn. The answer to this question could lie in their foraging habits. Cape fur seals can travel long distances (David 1987), and have been observed feeding several hundred kilometres offshore (Shaughnessy et al. 1981, Trillmich 1987, Arnould & Hindell 2001). Consequently, the inbound trip to Seal Island could take many hours or even days, undoubtedly making the total travel time difficult for the seals to gauge. Thus, seal movement at sunrise may simply represent a miscalculation of total traveling time.

However, this explanation only holds if predation risk is low enough to keep late seals from waiting outside the danger zone for safer conditions. This may be the case, as we recorded a mean of 15 predatory events per day (Kock et al. in prep) but typically close to 100 seal groups in the morning alone.

Departing seals wouldn't face this timing problem, as they could synchronize their departure in order to leave when risk is lowest, i.e. once the sun has completely set. Such coordination of movement would serve to explain the large group sizes observed when the seals departed the island. Conversely, fur seals are typically solitary foragers (Arnould & Hindell 2001, Staniland et al. 2004), and return to Seal Island from any number of different directions. Thus, the coordinated timing of departure would be impossible to achieve upon return, forcing the seals to make their way back alone or in small groups, with arrival times spaced out over the course of the night and the morning. These basic results (more returning than departing seals in the morning) differ from visual records of seal movement presented in Martin et al. (2005). However, their data were not collected in a systematic fashion, and are thus highly suspect.

2.5.1.2 Depth

Shark hunting strategy may also help to explain the depth patterns evident in our data. While searching for seals, shark swimming depth is likely influenced by several factors. The first of these is the ability to remain undetected by seals at the surface, a selective pressure which would favour sharks remaining deeper in the water column. Conversely, the visibility of Snell's window decreases with depth (Muntz 1974), reducing the contrast of surface seals; this would act as a selective pressure towards swimming higher in the water column. These two factors, acting in opposition, would

define an optimal hunting depth independent of bottom depth – a pattern evident in our data (Fig. 2.8).

Seal swimming depth around Seal Island may also be an evolved response to shark hunting strategy, although the form of the response is probably related to group size. Large seal groups are extremely obvious, regardless of movement tactic. However, the benefits accrued from large group size (see Bertram 1978) probably outweigh these costs, making big groups advantageous for the individual seal. With no possibility of remaining covert, the seals would then likely adopt the easiest and fastest means of moving away from the island. Surface porpoising is a more energetically efficient means of aquatic movement (Au & Weihs 1980, Weihs 2002), and also appears to be faster (unpublished data from seal focal follows), so large seal groups would be expected to adopt this tactic.

This likely would not apply to returning seals, however, because small groups don not offer the same benefits are large ones. Stealth should therefore become the seals' best tactic. Seals that swim along the ocean floor in small inconspicuous groups could potentially avoid detection by a majority of the sharks, and wouldn't be splashing at the surface and providing obvious silhouettes. This deep diving tactic has been observed in other pinniped species (Le Boeuf et al. 1996), and was evident from our data, with returning seals moving almost exclusively at depth. In contrast, most departing seals we recorded did so at the surface.

2.5.1.3 Location

Location of seal movement was probably influenced by the physical geography of the surrounding area. Seal Island is located on the north side of False Bay, which opens to

the south (Fig. 2.1). Therefore, although seals can be observed in all parts of the bay, a majority likely head south to forage. Still, a higher proportion of departing records than expected indicated movement to the south. The most likely explanation for this is that the benefits of large groups outweigh the costs of a protracted detour. Thus, seals that intended to move in another direction may have departed towards the south with the majority of their conspecifics, only to double back in the direction they preferred to go once outside the danger zone. Returning seals don't benefit from large groups, but this also means that their direction of movement would not be determined by majority rule. Consequently, seals might return directly to the island from any location, and we did observe a higher proportion of non-southerly returns in the data.

Finally, shark choice of location initially appears easy to comprehend: more seals were recorded on the south side of the island, and so it is logical for shark presence to mimic this pattern.

2.5.2   Interaction

Both shark and seal behavioural patterns can thus be explained, to a degree, by the behaviour of the other species. In particular, adult seal tactics seem chosen to minimize risk from the sharks (Fig. 2.9), while shark location appears to be influenced by seal presence. Shark temporal behaviour, however, doesn't appear to take adult seal activity into account (Fig. 2.10). If sharks were seeking to maximize their payoffs from the predator-prey interaction with adult seals, the expectation would be that sharks would adjust their behaviour based on A_{tdl} of adults, which was at its highest overnight owing to the number of seals in the water. Thus, even with limited visual hunting capacities, sharks would theoretically have profited from increased opportunities at night, which should

have led to a greater shark presence in the dark. Instead, low night-time shark presence suggests that the shark strategy did not evolve in response to the strategy of adult seals.

Young seals, however, appear to be much more available to the sharks than adults. A portion of this availability stems from temporal movement tactics, since pups comprised the bulk of seals recorded moving at dawn. However, pups also spent more time at the surface of the water than any other age class. Even the largest bull seals observed appeared to require a small amount of surface time before the final dive to the island, but they were able to initiate this approximately 800 m from land, allowing them to traverse the most dangerous stretch underwater. Slightly smaller seals didn't seem able to swim quite as far, and were thus forced to surface in the heart of the high risk zone. This need for air creates a trade-off within the returning deep dive tactic: seals are likely at little risk when swimming inconspicuously at the bottom, but are at high risk during the brief periods when they surface to breath.

Many pups didn't bother diving at all, and those that did were not able to swim very far underwater (Fig. 2.6). This pattern could reflect a degree of naïveté among the pups, but may also result from a physiological inability to hold their breath for extended periods of time (Le Boeuf et al. 1996, McCafferty et al. 1998, Hastings et al. 2001, Arnould et al. 2003). Regardless, it meant that there were many more pups than adults at the surface of the water in the high risk zone, resulting in substantial availability for the sharks.

When all seal age classes were considered, A_{tdl} values suggested that sharks were responding almost exclusively to the behaviour of pups (Fig. 2.13), and that these did not appear to behave in a manner that accounts for risk (Fig. 2.12). Such behaviour could

arise if pups are constrained from responding to predation risk, or if they trade-off risk against some other important factor. Unfortunately, identifying any such pup constraints or trade-offs was beyond the scope of this study, leaving it as a question for further research.

Thus, although the behavioural tactics recorded around Seal Island display the presence of obvious game elements (adult seal and shark tactics seemingly influenced by R and A, respectively), our current understanding of pup seal behaviour prevents analysis of the system within a complete game framework. For one, shark and adult seal tactics most likely don't constitute a complete game, because pup behaviour probably prevents adult tactics from affecting shark fitness. Conversely, seal pups and sharks appear to have an impact on each other's fitness, and clearly each has a set of behavioural tactics available to them; thus, by definition their interaction represents a game, and yet pup behaviour does not appear to be influenced by predation risk. Pup strategy may still represent an ESS, if any potential trade-offs or constraints on seal behaviour make a risk-ignoring pup strategy the best response to a population of pups who have adopted this same strategy. If this is true, and shark strategy also represents an ESS, then the game interaction between the two would be at an equilibrium point, because the strategies of both players would be resistant to invasion by other strategies. However, a complete analysis would require a more substantial understanding of pup behaviour.

This interpretation assumes that the Seal Island represents a closed system, where resident sharks and seals evolve strictly in relation to each other and to local environmental variables. In reality, both sharks and seals are free to move to other colonies, where local conditions could dictate optimal tactics different to those postulated

here. In particular, male seals often move between colonies in an attempt to establish successful breeding territories (Oosthuizen 1991). The possibility therefore exists that breeding males at Seal Island were subjected to different selective pressures when they were weaned, which would remove the genetic component required for a shark-pup game at Seal Island to evolve towards equilibrium, and would explain why observed pup tactics don't appear to account for risk levels.

Regardless of whether risky pup behaviour reflects some physiological constraint, a developmental trade-off against predation risk, or the gene flow between seals from varying colonies, it appears to be at the root of an interesting intra-specific behaviourally mediated indirect interaction: seal pup behaviour influences the behavioural tactics adopted by the sharks, which in turn dictate the tactics employed by adult seals. Thus, seal pup behaviour may indirectly influence adult seal behaviour, through the behavioural response of their common predator.

Despite the apparent logic of this conclusion, it must still be considered with caution, in that it was arrived at based on a foundation of speculation: R and A were essentially derived on the basis of estimation and assumptions (but see sensitivity analysis in Appendix), as were seal movement data. However, despite these conjectures, the final result is supported by empirical data. For one, the sharks' distribution pattern around Seal Island corresponded more closely to movements of the pups than to those of the adults, whose pattern of return direction (even those obtained from visual records; unpublished data) was not as skewed to the south as that of the pups. Further, sharks are only present in large numbers at Seal Island during the Southern Hemisphere's winter months (May-September), the exact time when pups are weaned (Warneke &

Shaughnessy 1985, Gentry & Kooyman 1986). Finally, predatory data clearly demonstrate that many more young seals are consumed than adults, even after adjustment for the total number of seals in the water (Kock et al. in prep).

The ultimate goal of this study was to examine a unique system which seemed likely to be at the evolutionary equilibrium point of a predator-prey behavioural game. However, the discovery that there probably wasn't a simple game occurring leads to an important conclusion. Most predator-prey game models created to this point consider prey as a uniform group, although some extend this to include a distribution of prey energy states (Alonzo 2002, Alonzo et al. 2003). However, as this study clearly demonstrates, a prey population as a whole, particularly those of larger vertebrates, may be composed of subunits that differ markedly in behavioural patterns. In this study these subunits were based on age, but other possible factors could include size, sex, or social rank. It thus becomes imperative to consider these behaviourally distinct subunits when modeling the choices and actions of a species, because otherwise the end result could differ substantially from that expected, and may obscure important inter- and intra-specific relationships.

2.6 Literature cited

Alonzo SH (2002) State-dependent habitat selection games between predators and prey: the importance of behavioural interactions and expected lifetime reproductive success. Evolutionary Ecology Research 4: 759-778

Alonzo SH, Switzer PV, Mangel M (2003) Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. Ecology 84: 1598-1607

Altendorf KB, Laundré JW, Lopez Gonzalez CA, Brown JS (2001) Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy 82: 430-443

Anderson SD, Henderson RP, Pyle P, Ainley DG (1996) White shark reactions to unbaited decoys. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 223-228

Arnould JPY, Hindell MA (2001) Dive behaviour, foraging locations, and maternal-attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). Canadian Journal of Zoology 79: 35-48

Arnould JPY, Luque SP, Guinet C, Costa DP, Kingston J, Shaffer SA (2003) The comparative energetics and growth strategies of sympatric Antarctic and subantarctic fur seal pups at Iles Crozet. Journal of Experimental Biology 206: 4497-4506

Au D, Weihs D (1980) At high speeds dolphins save energy by leaping. Nature 284: 548-550

Bertram BCR (1978) Living in groups: predators & prey. In: Krebs JR, Davies NB (eds) Behavioural ecology an evolutionary approach. Blackwell Scientific Publications, Oxford, pp 64-96

Bleckmann H (1994) Reception of hydrodynamic stimuli in aquatic and semiaquatic animals. Progress in Zoology 41: 1-115

Bouskila A, Robinson ME, Roitberg BD, Tenhumberg B (1998) Life-history decisions under predation risk: Importance of a game perspective. Evolutionary Ecology 12: 701-715

Bradshaw CJA, Lalas C, Perriman L, Harcourt RG, Best H, Davis LS (1999) Seasonal oscillation in shore attendance and transience of New Zealand fur seals. Canadian Journal of Zoology 77: 814-823

Brown JS (1992) Patch use under predation risk: I. Models and predictions. Annales Zoologici Fennici 29: 301-309

Brown JS (2002) Indirect effects of trophic interactions: Prey behavioral responses to the risk of predation. Ecological Society of America Annual Meeting Abstracts 87: 11-12

Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80: 385-399

Bruce BD (1992) Preliminary observations on the biology of the white shark *Carcharodon carcharias* in South Australian Waters. Australian Journal of Marine and Freshwater Research 43: 1-11

Clark CW, Mangel M (2000) Dynamic state variable models in ecology. Oxford University Press, New York

Collier RS, Marks M, Warner RW (1996) White shark attacks on inanimate objects along the Pacific coast of North America. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 217-222

David JHM (1987) South African Fur Seal *Arctocephalus pusillus pusillus*. NOAA Technical Report NMFS: 65-72

Dehnhardt G (2002) Sensory systems. In: Hoelzel AR (ed) Marine mammal biology: an evolutionary approach. Blackwell Science, Oxford, pp 116-141

Dehnhardt G, Mauck B, Bleckmann H (1998) Seal whiskers detect water movements. Nature 394: 235-236

Demski LS, Northcutt RG (1996) The brain and cranial nerves of the white shark: an evolutionary perspective. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 121-130

Enger PS, Kalmijn AJ, Sand O (1989) Behavioral investigations on the functions of the lateral line and inner ear in predation. In: Coombs S, Gorner P, Munz H (eds) The mechanosensory lateral line: Neurobiology and evolution. Springer, New York, pp 575-588

Ferreira C, Ferreira T (1996) Observations on white sharks along the South African coast. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 375-384

Gamel CM, Davis RW, David JHM, Meyer MA, Brandon E (2005) Reproductive energetics and female attendance patterns of cape fur seals (*Arctocephalus pusillus pusillus*) during early lactation. American Midland Naturalist 153: 152-170

Gentry RL, Kooyman GL (1986) Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton

Goldsworthy SD (1999) Maternal attendance behaviour of sympatrically breeding Antarctic and subantarctic fur seals, *Arctocephalus* spp., at Macquarie Island. Polar Biology 21: 316-325

Hamilton WD (1971) Geometry for the selfish herd. Journal of Theoretical Biology 31: 295-311

Hastings KK, Small RJ, Simpkins MA, Swain UG (2001) Dive behavior of adult and subadult harbor seals from Kodiak Island and Southeast Alaska. Alaska Department of Fish and Game Annual Report

Houston A, McNamara J (1999) Models of adaptive behaviour. Cambridge University Press, Cambridge

Hueter RE, Mann DA, Maruska KP, Sisneros JA, Demski LS (2004) Sensory biology of Elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, pp 273-310

Hugie DM, Dill LM (1994) Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45: 151-169

Klimley AP, Anderson SD, Pyle P, Henderson RP (1992) Spatiotemporal patterns of white shark *Carcharodon carcharias* predation at the South Farallon Islands California. Copeia: 680-690

Klimley AP, Le Boeuf BJ, Cantara KM, Richert JE, Davis SF, Van Sommeran S, Kelly JT (2001) The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. Marine Biology (Berlin) 138: 617-636

Kock AA (2002) Predatory activity of great white sharks (*Carcharodon carcharias*) around a Cape fur seal colony. Honour's Thesis, University of Cape Town

Kock AA, Johnson R, Laroche RK, Griffiths C, Compagno LVJ Predation by white sharks on Cape fur seals at Seal Island, False Bay (in prep)

Le Boeuf BJ, Crocker DE, Klimley AP, Ainley DG (1996) Diving behavior of elephant seals: implications for predator avoidance. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 193-205

Lima SL (2002) Putting predators back into behavioral predator-prey interactions. Trends in Ecology and Evolution 17: 70-75

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640

Lythgoe JN (1979) The ecology of vision. Clarendon Press, Oxford

Lythgoe JN (1984) Visual pigments and environmental light. Vision Research 24: 1539-1550

Martin AR, Hammerschlag N, Collier RS, Fallows C (2005) Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. Journal of the Marine Biological Association of the U.K. 85: 1125-1135

Maynard Smith J (1979) Game theory and the evolution of behaviour. Proceedings of the Royal Society of London Series B Biological Sciences 205: 475-488

McCafferty DJ, Boyd IL, Taylor RI (1998) Diving behaviour of antarctic fur seal (*Arctocephalus gazella*) pups. Canadian Journal of Zoology 76: 513-520

Muntz WRA (1974) Visual resolution underwater. Aerospace Medicine 45: 61-66

Nelson DR (1967) Hearing thresholds, frequency discrimination and acoustic orientation in lemon shark *Negaprion brevirostris*(Poey). Bulletin of Marine Science 17: 741-754

Oosthuizen WH (1991) General movements of the South African (Cape) fur seals *Arctocephalus pusillus pusillus* from analysis of recoveries of tagged animals. South African Journal of Marine Science 11: 21-29

Pitcher TJ (1986) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) The behaviour of teleost fishes. Croom Helm, London, pp 294-337

Shaughnessy PD (1987) Population size of the Cape fur seal *Arctocephalus pusillus pusillus*. Department of Environmental Affairs, Sea Fisheries Research Institute, South Africa. Report 130: 18-23

Shaughnessy PD, Semmelink A, Cooper J, Frost PGH (1981) Attempts to develop acoustic methods of keeping Cape fur seals *Arctocephalus pusillus* from fishing nets. Biological Conservation 21: 141-158

Sih A (1998) Game theory and predator-prey response races. In: Dugatkin LA, Reeve HK (eds) Game theory and animal behavior. Oxford University Press, New York, pp 221-238

Staniland IJ, Reid K, Boyd IL (2004) Comparing individual and spatial influences on foraging behaviour in Antarctic fur seals *Arctocephalus gazella*. Marine Ecology Progress Series 275: 263-274

Strong WR, Jr. (1996) Shape discrimination and visual predatory tactics in white sharks. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 229-238

Taylor RJ (1979) The value of clumping to prey when detectability increases with group size. American Naturalist 113: 299-301

Taylor RJ (1984) Predation. Chapman and Hall, New York

Trillmich F (1987) Behavior of Fur Seals. NOAA Technical Report NMFS 51: 195-204

Van Baalen M, Sabelis MW (1993) Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. American Naturalist 142: 646-670

Warneke RM, Shaughnessy PD (1985) *Arctocephalus pusillus*, the South African and Australian fur seal: Taxonomy, evolution, biogeography, and life history. In: Ling JK, Bryden MM (eds) Studies of sea mammals in South latitudes. South Australian Museum, Adelaide, pp 53-77

Weihs D (2002) Dynamics of dolphin porpoising revisited. Integrative and Comparative Biology 42: 1071-1078

Welton NJ, McNamara JM, Houston AI (2003) Assessing predation risk: Optimal behaviour and rules of thumb. Theoretical Population Biology 64: 417-430

2.7 Tables

Table 2.1. Interaction of location, time and depth parameters for departing seals, produced by 3-way ANCOVA analysis. Numbers represent least square mean values of seal transits $(radian)^{-1}$. The interaction term of the three parameters was highly significant ($p<0.0001$), and was driven by the combinations highlighted in bold, which were not statistically discernable from each other. The results suggest that adult seals highly favour departing at the surface, on the south side of Seal Island, some time between sunset and midnight.

Location	Depth	Time Period			
		Midnight-Sunrise	Sunrise-Noon	Noon-Sunset	Sunset-Midnight
N	Deep	0.064	0	0.065	0
	Surface	0	0	0	0
NE	Deep	0	0	0	0.091
	Surface	0	0	0	0
W	Deep	0	0.162	0	0
	Surface	0	0	0	0
SE	Deep	0	0	0.081	0
	Surface	0.081	0.081	0.161	**0.745**
S	Deep	0.211	0	0	0
	Surface	0.249	0	0	**0.806**

2.8 Figure legends

Fig. 2.1: Seal Island, False Bay, South Africa. Indicated on the map are the locations of the six VR2 receivers, as well as the approximate receptive area of each. Waters around the island were divided into six sectors; these were subsequently grouped into two zones, corresponding to the major water depth trends of deeper waters to the south and west, and more shallow waters to the north and east.

Fig. 2.2: Frequency distribution of seal group sizes for each movement direction. X axis shows group size categories, as well as number of seals per group size category. Departing group sizes were substantially larger than returning ones.

Fig. 2.3: Total movement events of tagged seals per VR2 receiver, weighted by the radians of island circumference covered by each. Whereas seals departed almost exclusively to the south and southeast, return trips were more evenly spaced out around the island.

Fig. 2.4: Interaction of time period and seal swimming depth for seals returning to Seal Island. The Y axis shows the least square mean values of seal transits to the island, weighted by the radians of island covered by the respective receivers; the X axis displays the 4 time periods (1: midnight - sunrise; 2: sunrise - noon; 3: noon - sunset; 4: sunset - midnight). Error bars represent 95% confidence intervals. Seals returned to the island substantially more often at depth and in the dark.

Fig. 2.5: Visual records of seal movement for both movement directions, displayed as the mean number of seal groups observed per hour, for each hour that visual observations were conducted. Returning seal movement was greatest in the morning, while departures occurred most often immediately after sunset. Movement of any kind was negligible in the hours preceding sunset.

Fig. 2.6: Seal travel swimming patterns. Left Y axis (light line, squares) represents the mean distances travelled underwater by seals of the different age classes. Right Y axis (black line, circles) shows the percent time spent at the surface while moving. Dive distance for young seals was substantially less than for adults, resulting in them spending significantly more time at the surface of the water. Error bars represent 95% confidence intervals.

Fig. 2.7:   Shark density in relation to location around Seal Island and time period. Y axis shows the least square means of shark transmissions weighted by the receptive area of each receiver; X axis displays 4 time periods as in Fig. 2.4. Error bars represent 95% confidence intervals. Sharks spend more time to the south of the island, and are present in greater numbers in the morning (time period 2). Consequently, there is a strong significant interaction between the south and period 2 variables, isolating this as the preferred choice in time and space for shark presence.

Fig. 2.8:   Mean shark swimming depth for each receiver as a function of the average bottom depth within the receptive area of each receiver. Error bars represent one standard deviation, hatched line indicates 1:1 line of maximum shark swimming depth. Mean shark depth appears similar for all areas of the island, despite increasing bottom depth, except for the east (E) receiver, where the sharks are swimming at the bottom which is shallower than their usual swimming depth.

Fig. 2.9:   Seal movement data obtained from VR2 receivers plotted against estimated shark risk. Risk values for all group sizes were summed to account for lack of telemetry data. The negative trend line suggests that adult seals take shark risk into account when choosing movement tactics.

Fig. 2.10: Shark density obtained from VR2 receivers plotted against estimated adult seal availability. The flat trend line suggests that sharks don't take the behaviour of adult seals into account when choosing hunting tactics.

Fig. 2.11: Estimated seal availability for each seal age class, weighted by the average biomass of each class. Seal pups are substantially more available to the sharks than are adults.

Fig. 2.12: Seal pup movement obtained from visual records plotted against estimated shark risk. Visual records were obtained for daylight hours, and 6 visual sectors were grouped into two receptive zones (Fig. 2.1). The flat trend line suggests that seal pups don't consider risk when moving to or from Seal Island.

Fig. 2.13: Shark density obtained from VR2 receiver records plotted against estimated seal availability for all seal age classes combined. Shark receiver records were pooled together to roughly correspond with the two zones used to categorize visual records, and only receiver records collected during time periods with corresponding visual records were used. When all age classes are considered, shark presence closely matches expected values of food availability.

2.9 Figures

Fig. 2.1:
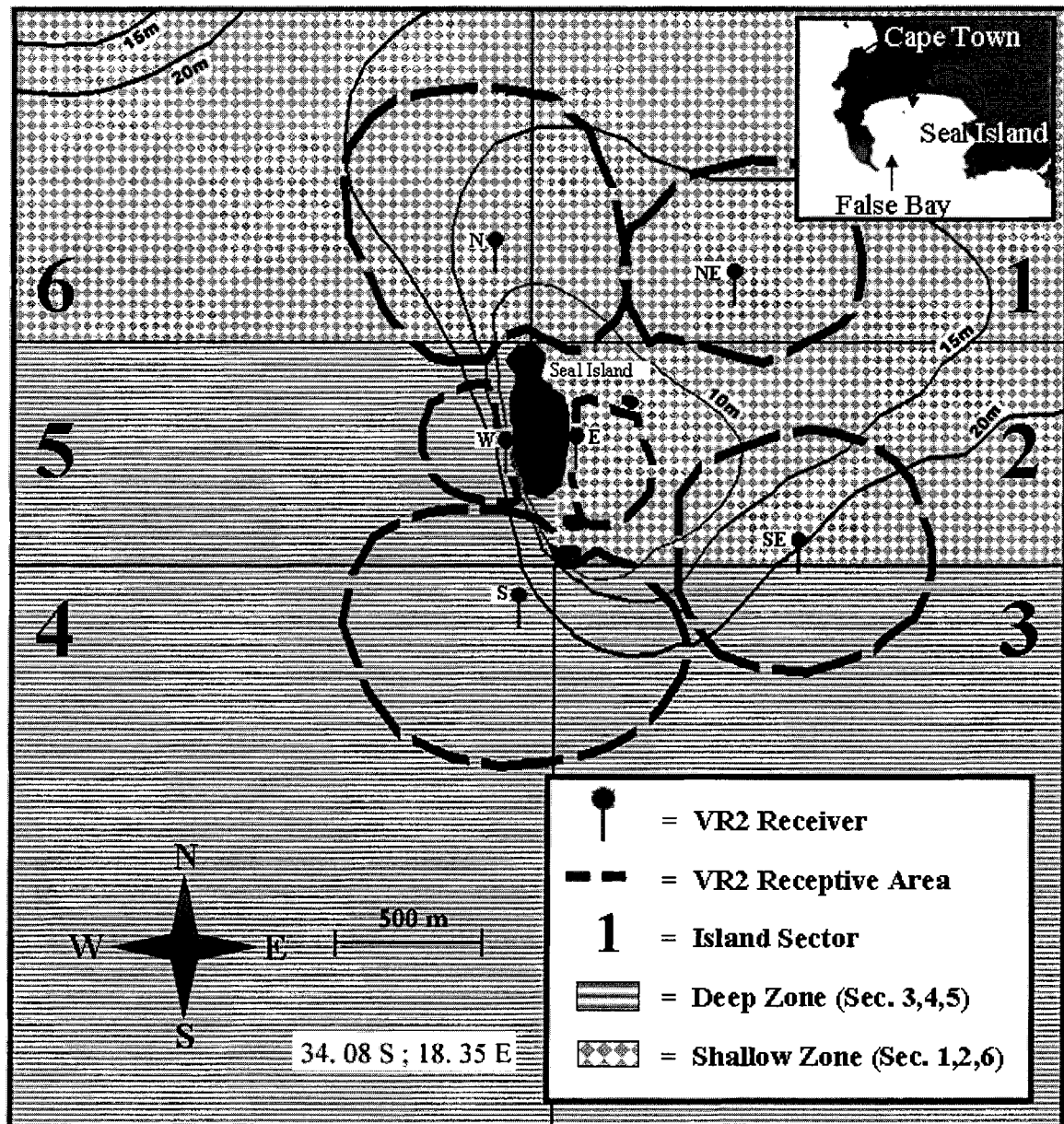
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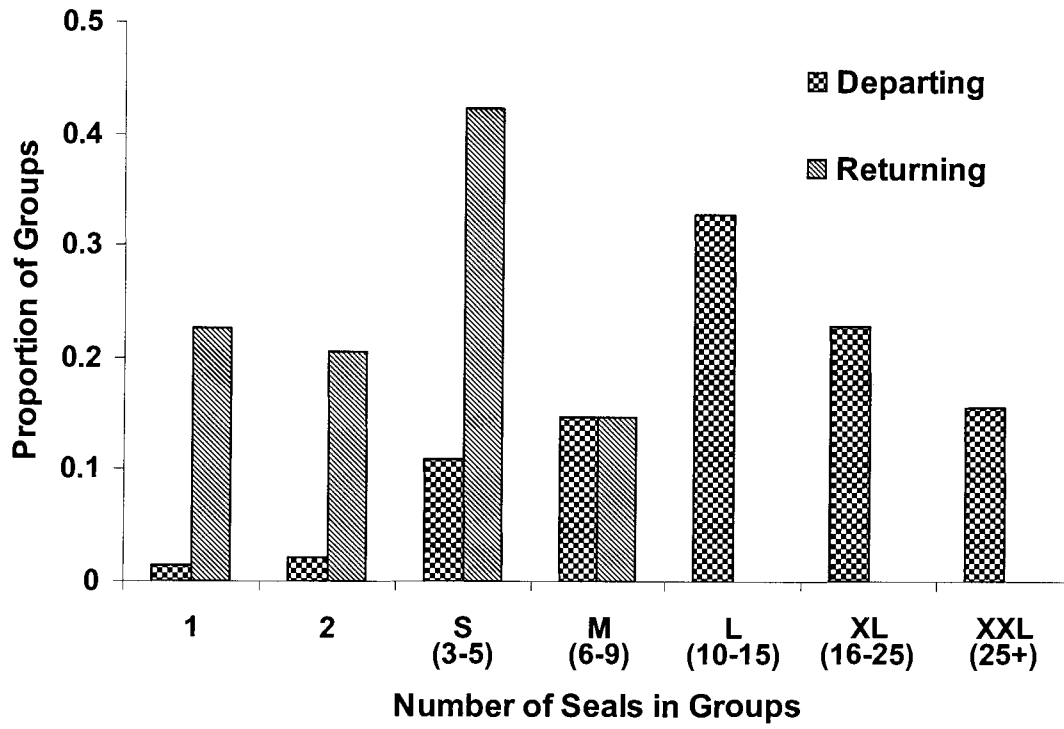
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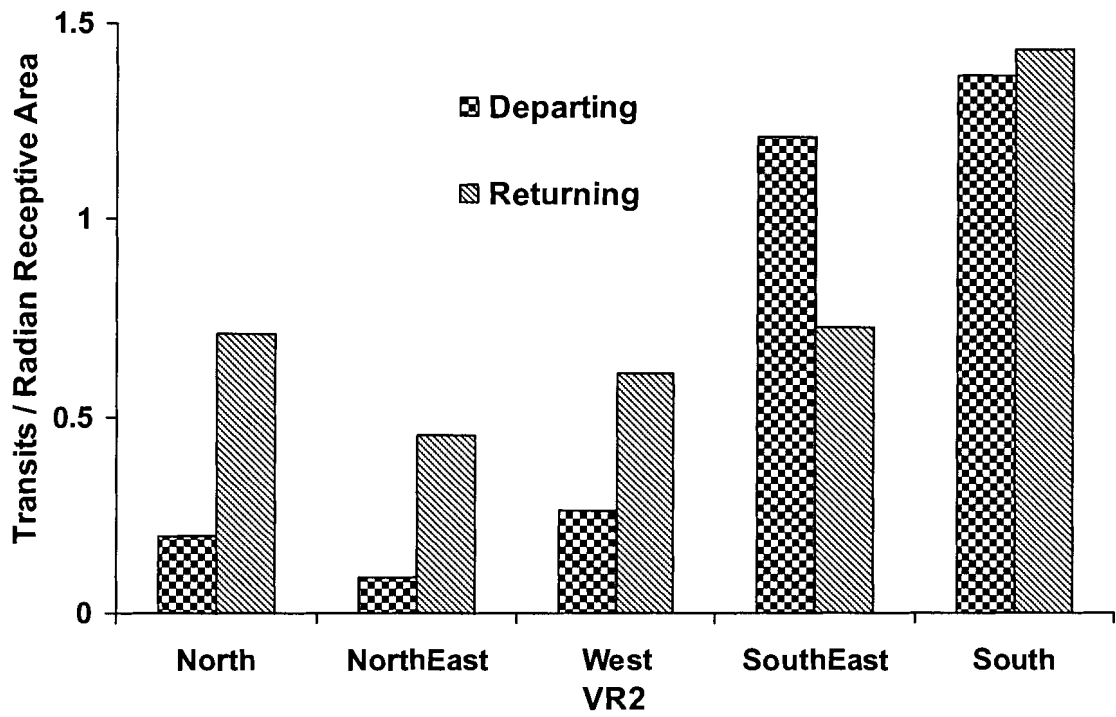
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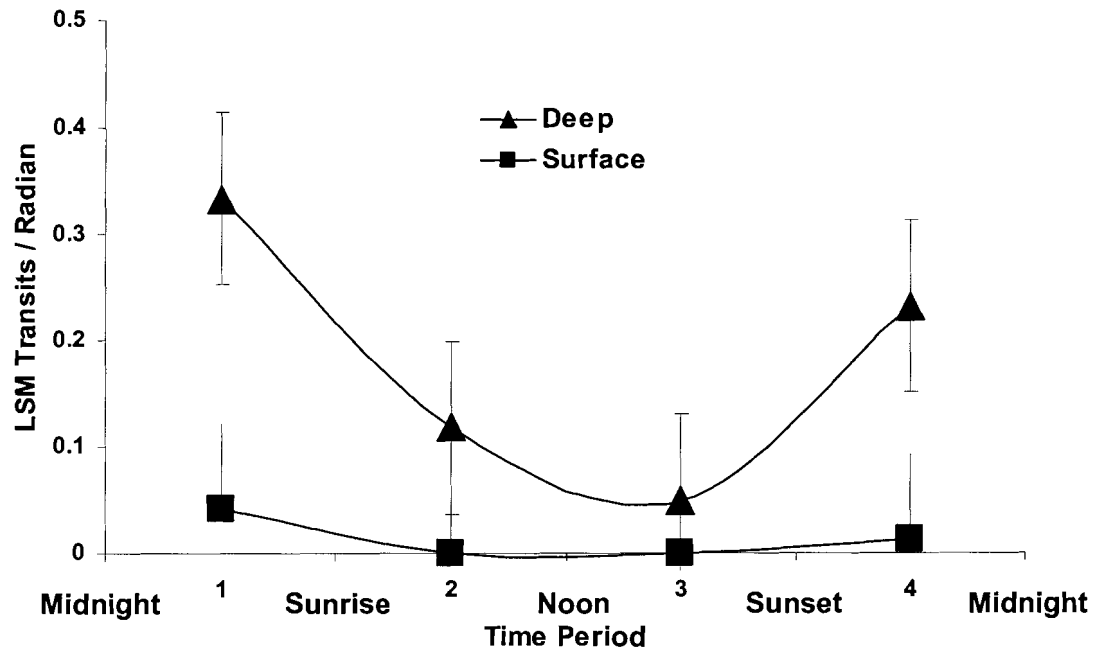
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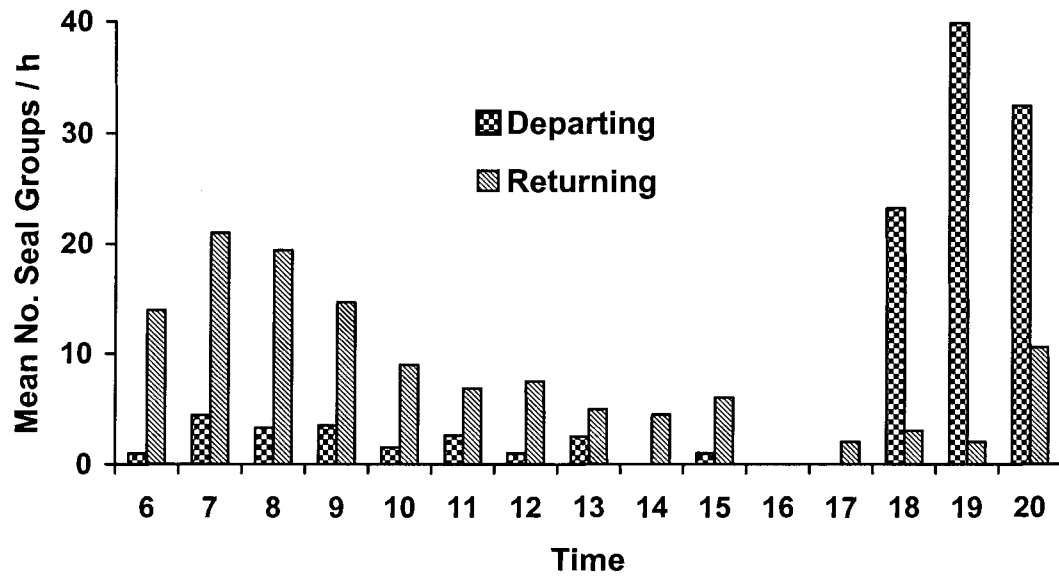
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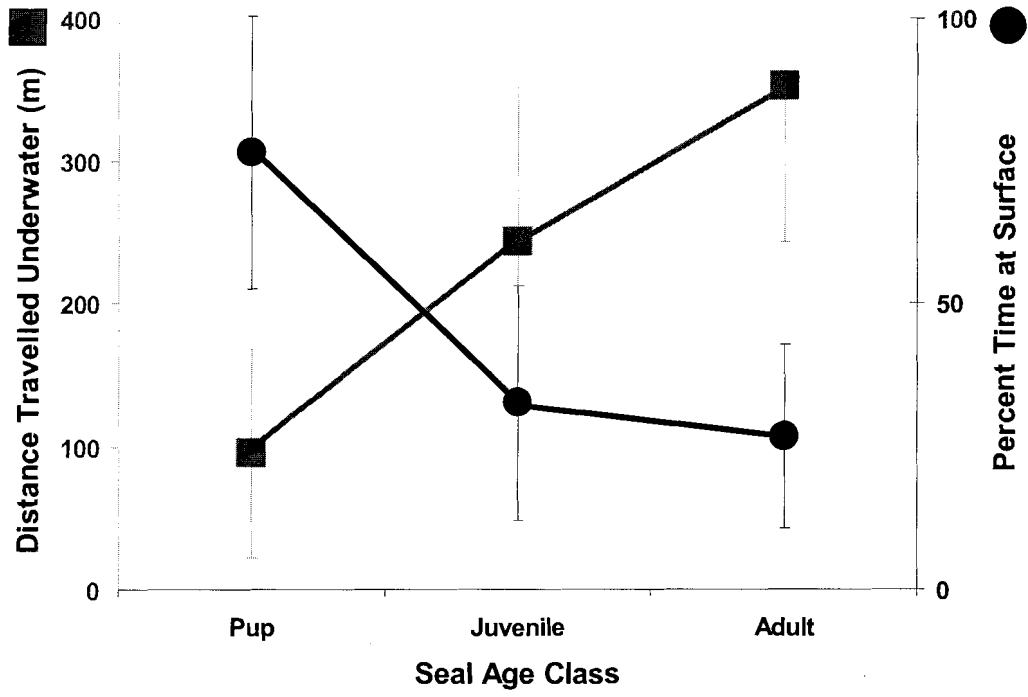
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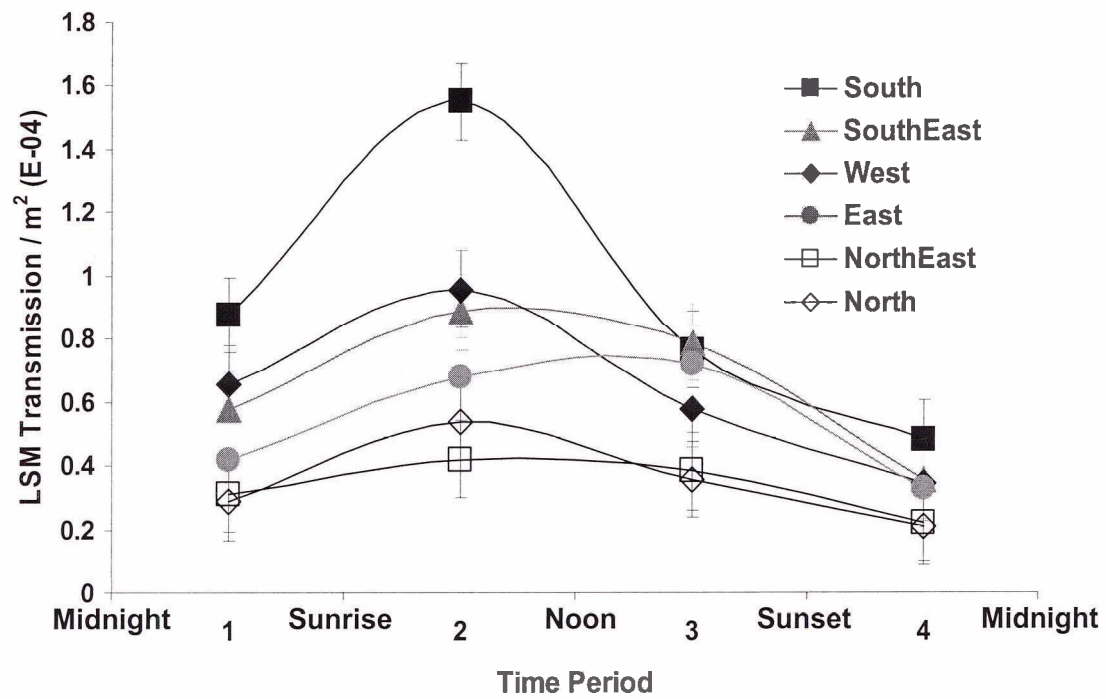
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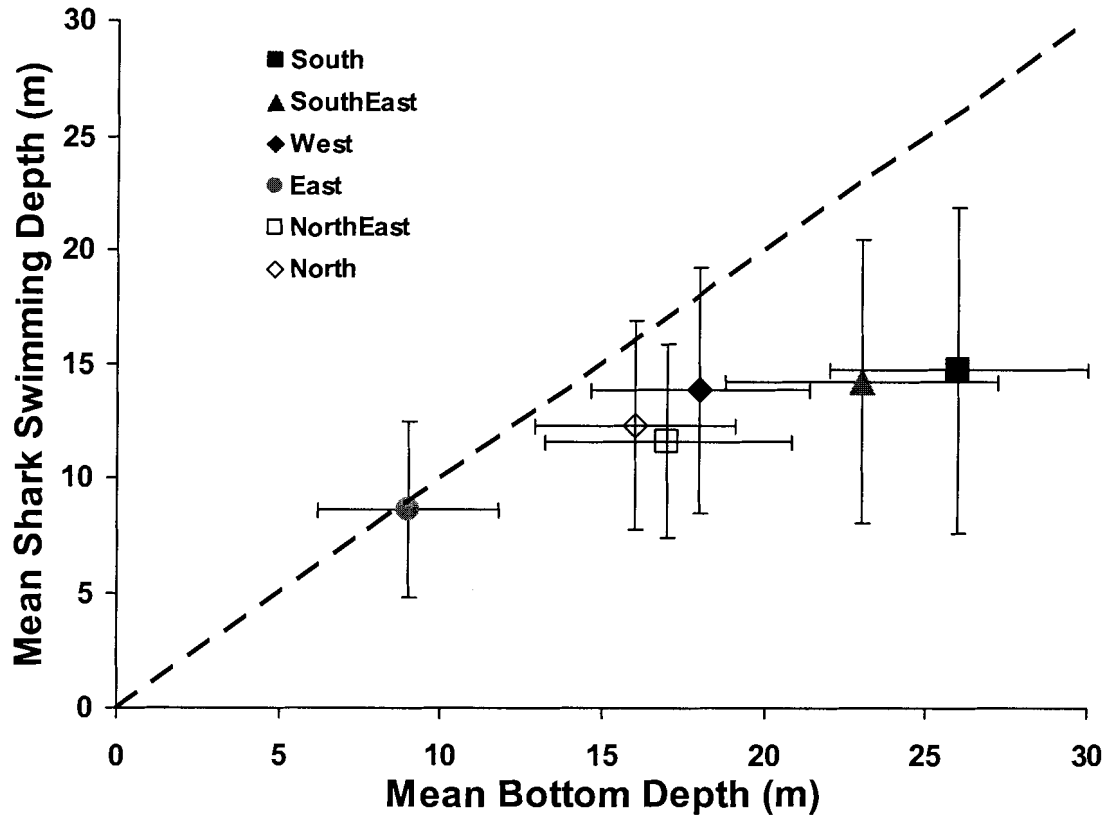
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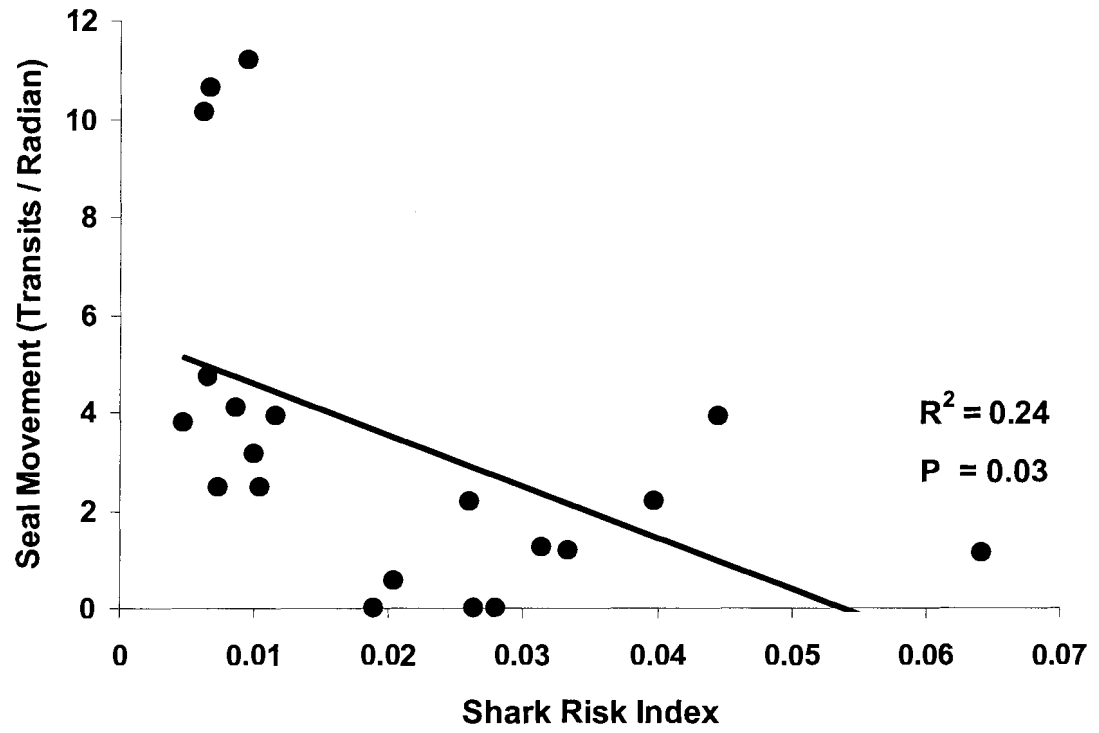
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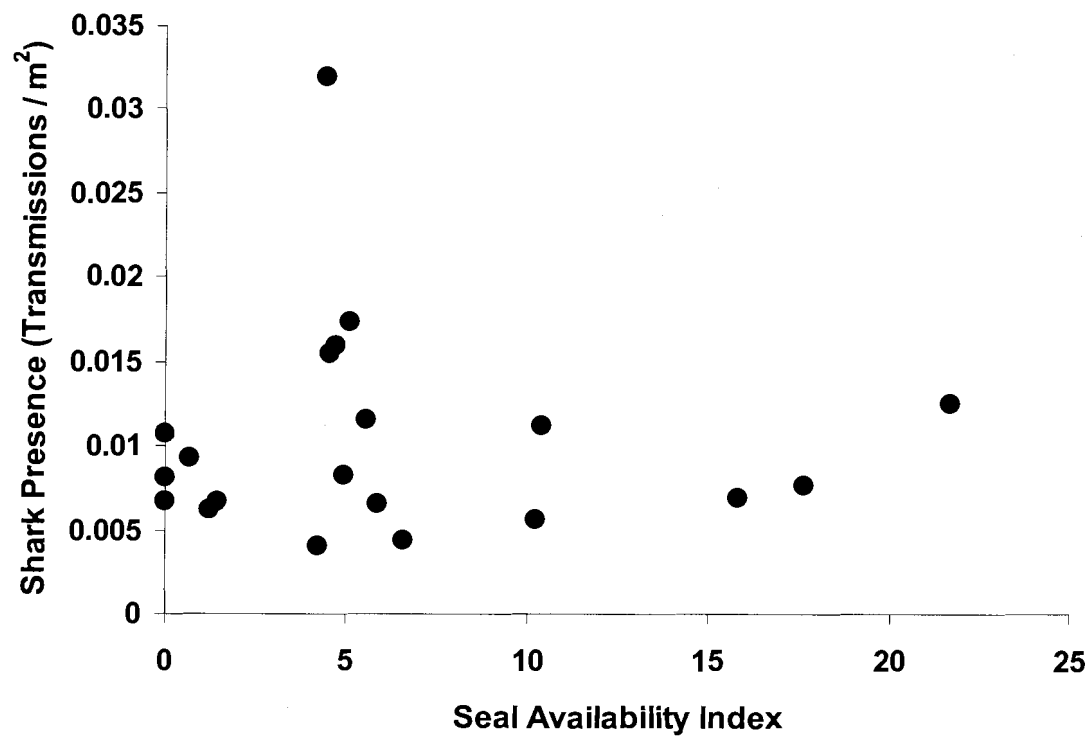
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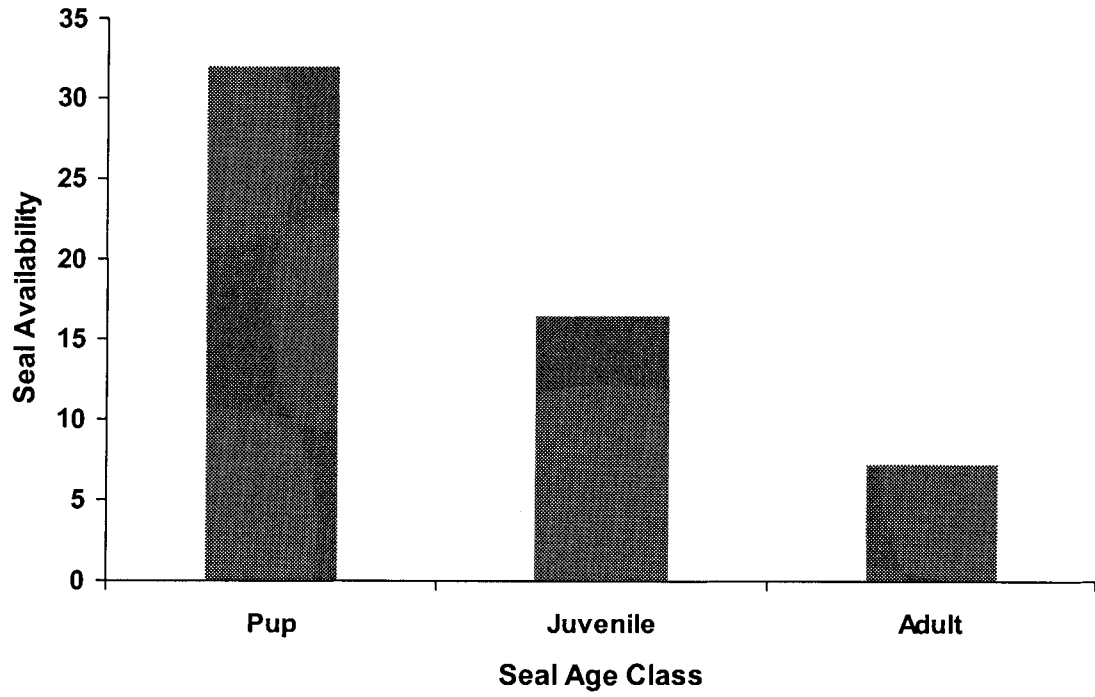
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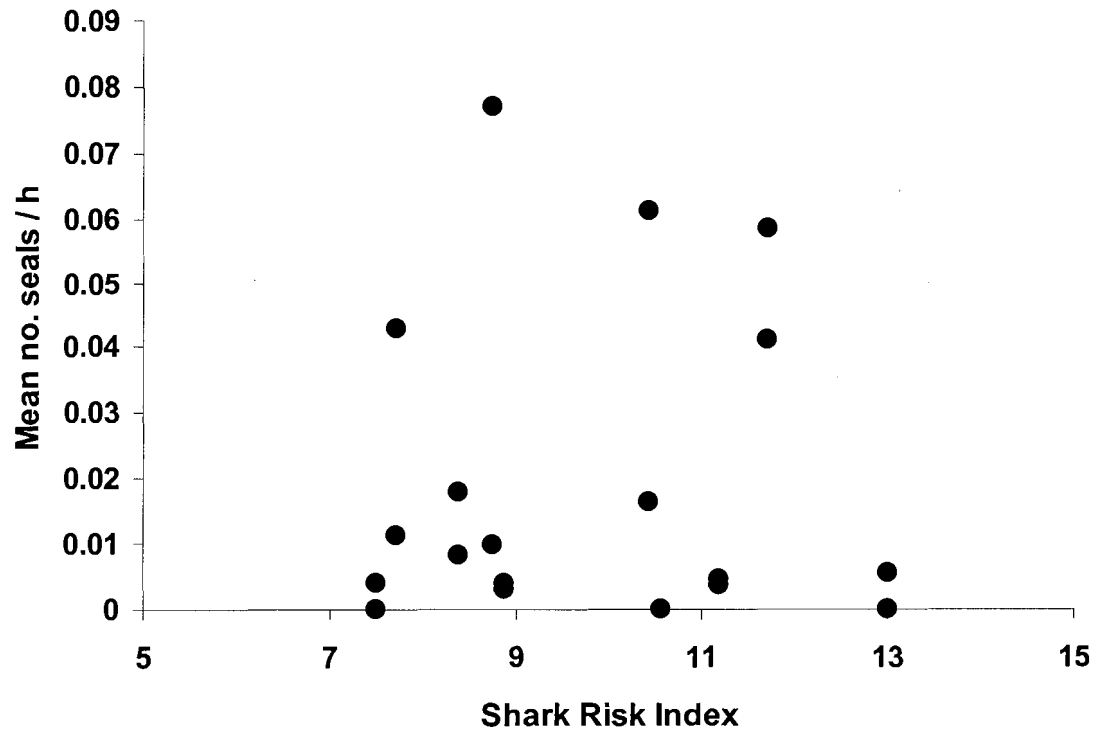
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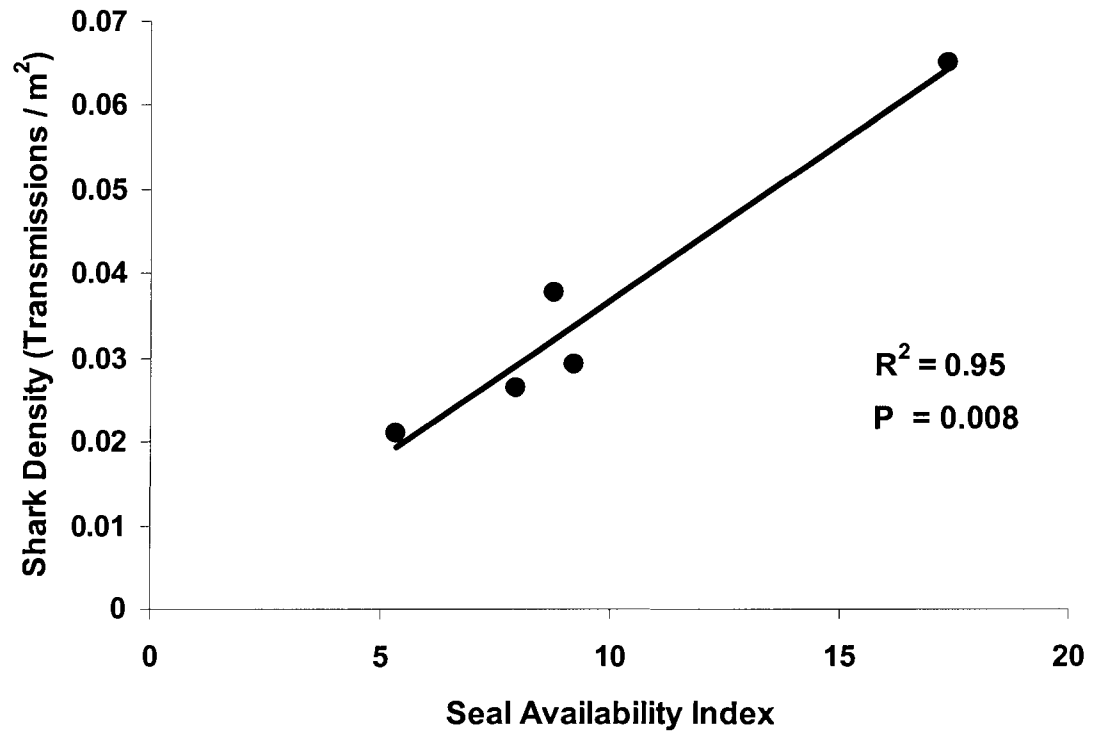
2.10 Appendix

2.10.1 The importance of light

The probability of an attack occurring is presumably influenced by how well each species is able to detect the other. Consequently, light levels and vision are probably the key elements which shape the patterns of predatory behaviour observed at Seal Island. Of course, on top of excellent vision, both species also possess acute auditory and olfactory senses, as well as the ability to detect minute water vibrations (through whiskers in seals and the lateral line in sharks; Dehnhardt 2002, Hueter et al. 2004). However, it is unlikely that any of these senses play as large a part as vision in the initiation of predatory interactions.

For instance, the large number of seals and sharks in the vicinity of Seal Island ensures that the surrounding waters already contain copious amounts of seal and shark olfactory traces, making it highly improbable that any individual animal could be singled out by means of olfaction. Further, the mechanosenses of sharks and seals are predominantly near-field in nature, in that they respond to a stimulus (flow amplitude) which decreases rapidly with distance from the source (dissipated within one or two body lengths of the source; Bleckmann 1994). Consequently, they're probably only useful during relatively close encounters (Enger et al. 1989, Dehnhardt et al. 1998).

Finally, although sound could play a minor role, because seals create a lot of noise while porpoising at the surface, it's doubtful that these cues rival the importance of visual stimuli. For one, low frequency ambient noise levels around Seal Island are extremely high (unpublished data obtained using alternative acoustic tracking methods), as swells

are constantly breaking over the South facing reefs. These sounds are likely in the same frequency range as those produced by porpoising seals, and could thus potentially mask the noise produced by groups of seals. Further, localization of a sound source can be difficult, certainly when compared to a light source. Laboratory studies on other species of elasmobranch demonstrated that they can localize a sound source to within approximately 10˚ (Nelson 1967). Assuming this resolution also applies to white sharks (comparative studies of elasmobranch brain sizes indicate that the auditory center of white sharks is proportionately of similar size to that of many other species; Demski & Northcutt 1996), such auditory capabilities would serve well for initially identifying the presence of prey, but would likely be insufficient for launching the precise, high-speed attacks required to kill seals.

Vision is different, however. The exponential absorption of light with increasing depth (Lythgoe 1984), the scattering of light by water and suspended particles (Muntz 1974), and the phenomenon of Snell's window (Lythgoe 1979) all create a range of visual conditions around the island which the animals can exploit. For one, these properties mean that an individual of either species would gain visual obscurity with depth. Furthermore, an animal that wasn't too deep would be afforded excellent contrast between the silhouettes of any animals above it and the backlighting provided by Snell's window (Strong 1996). Finally, both of these properties fluctuate dramatically with light levels, meaning that visual conditions vary over the course of the day, as the oblique solar angles during crepuscular periods result in less light penetrating into the water (Lythgoe 1979). The end result is that the visual environment provides opportunities for both species to gain the upper hand, depending upon the tactic they choose. Consequently,

although both species have impressive senses at their disposal, predation at Seal Island is likely mediated by light levels, and relative visual advantage almost certainly determines whether or not an attack will occur.

This assertion is supported by empirical data, as well as by observations collected during our field season. Of primary importance is the fact that the vast majority of predatory events occur in the morning (Kock et al. in prep, Martin et al. 2005). Light conditions during these hours provide the optimal combination of back-lighting contrast and low light penetrance into the water, allowing the sharks to swim relatively near to the surface while remaining undetected by seals above them. No other physical properties can account for this daily pattern of predatory activity.

Incidental observations also support the importance of vision. White sharks have been observed inspecting a variety of floating objects in many areas around the world (Anderson et al. 1996, Collier et al. 1996, Strong 1996), and were recorded doing the same at Seal Island. In fact, we could reliably attract sharks to the surface by simply floating a small seal shaped piece of carpet approximately 5m from our boat. This seal decoy was a purely visual stimulus, presenting no auditory, olfactory, mechanosensory, or electrosensory signals whatsoever, yet sharks would routinely approach it vertically, from below, to visually inspect, mouth (mechanically inspect), or attack it.

Seal observations also illustrated the importance of vision in identifying and avoiding predators. A notable seal behaviour recorded around Seal Island was 'looking down', where seals would invert themselves at the surface, such that their hind flippers were protruding from the water and their heads were pointing towards the ocean floor. They would then clearly move their heads from side to side, presumably visually

scanning the water below them for any signs of a shark (although they may have been employing other senses as well). This behaviour was most commonly observed after a failed predation attempt, presumably as the seal tried to re-localize its attacker, but was also often noted before seals prepared to dive.

Ultimately, then, it seems probable that the physical properties of light in the ocean determine how well sharks and seals are able to detect each other, and thus play an important role in the choice of swimming depth for both species, as well as in the probability that an attack will occur.

2.10.2   Depth levels

Seal swimming depth was classified as either 'surface' or 'deep' (see Materials and methods), while shark depth was aggregated to reflect the sharks' presence in each of three levels of the water column: upper, mid, and lower. However, these levels were not defined based on fixed depths. Instead, they were a function of mean shark swimming depth, the attenuation of light with increasing depth, and on estimates of how the interaction of these would impact on each species' ability to detect the other.

The 'upper' level was thus defined as the depths at which we assumed a seal could spot a shark swimming below it, impeding the shark's ability to launch a surprise attack. The assumed 'mid' level upper boundary was defined as the depth below which it was estimated that the attenuation of light would allow a shark to remain unseen by a seal at the surface. The 'mid' level lower boundary was then an estimate of the deepest depth still providing optimal opportunities for attacking seals at the surface. Below this depth, the decreasing resolution of Snell's window as a result of light scattering by suspended particles (Muntz 1974) would lead to a reduction in contrast between a seal and the

surface, likely making surface seals more difficult to spot. The 'attack time', or time between initiation of the attack and the actual strike, would also increase with depth. The result would be increased opportunities for the seal to detect the shark and avoid it, or even an increased chance that the seal would alter its course at random, thus inadvertently defeating the shark's predation attempt. Both of these factors combined would likely render successful attacks increasingly difficult from greater depths, and the lower 'mid' level boundary was defined as the depth at which these costs became prohibitive. Finally, the 'lower' level was estimated as the depths where a seal, swimming along the ocean floor, could remain unseen by a shark present at the mean shark swimming depth. Because the 'lower' level's upper limit wasn't always identical to the lower boundary of the 'mid' level, the actual demarcation between the two levels was set as the average of the two borders.

2.10.3   *P* matrix

The probability of an attack occurring was defined as being contingent on the following variables: time of day (t), swimming depth of both species (D for seals, d for sharks), location of the animals around Seal Island (l), seal group size (g), and average seal size in a group (s). Each possible combination of these therefore characterized a unique probability context $\{P = (t, D, d, l, g, s)\}$ (Table 2.A.I). Unfortunately, insufficient data exist to explicitly quantify each possible P. Instead, the relative effects of the specific environmental, group size, and seal size conditions on the probability of attack were estimated as weighting values scaled against an arbitrary baseline value of 1, which was allocated to the context of an adult seal (s), swimming alone (g) at the surface (D) above the South receiver (l) during daylight hours (t), versus a shark who was also

swimming at the surface, or 'upper' level (*d*), during the aforementioned conditions. The value of 1 was assigned because it was assumed that this context offered the most equal footing between the species, a situation where the probability of the shark spotting the seal first and launching an ambush attack was equal to the probability of the seal detecting the shark first and initiating evasive manoeuvres, thus preventing an attack. All other values, for every other *P*, were defined relative to this baseline value of 1, based on the product of relative weights which were estimated for discrete categories of each variable. The specific numbers comprising each of these individual weights remain educated guesses, and are therefore open to debate. However, the patterns which formed the basis for these approximations are each rooted in scientific theory and common sense, and thus likely represent the general trends occurring at Seal Island.

2.10.3.1 Visual conditions

The visual conditions for a particular context were defined by the interaction of *t*, *D* and *d*. As a result, we did not attempt to tease apart the effects of each of these variables, but instead assigned a relative weighting value to each possible combination of their discrete categories.

The overall probability of attack was estimated to be lower at night, as extremely low light levels would all but eliminate any visual tactical advantages. The sharks and seals would therefore have to rely predominantly on their other senses, and, since these are well developed in both species, their ability to detect each other should be approximately on par for most night-time contexts. Consequently, the night-time relative context weights did not differ greatly from 1. For example, 'deep' seals are likely at the most risk from sharks in the 'lower' segment of the water column (Fig. 2.A.I, panel A),

where they should be on approximately equal footing (similar to the base value of 1 assigned to surface seals and upper sharks). However, seals swimming along the bottom would eventually have to come up for air, where they would be at increased levels of risk from sharks at all depths. Consequently, the relative 'night' weight for 'deep' seals and 'lower' sharks was estimated to be higher than 1, while for 'mid' sharks it was set at 1, and for 'upper' sharks at 0.1. 'Deep' seals would most likely face no risk at all from 'upper' sharks were it not for these brief intervals of surface breathing, for it would seem highly unlikely that a shark could identify a seal 20m below it in the dark.

Departures from the baseline value of 1 were similarly small in the relative weights estimated for seals swimming at the surface during the night (Fig. 2.A.I, panel B). A weight of 1 was assigned to the combination of 'surface' and 'upper', as this was assumed to be equivalent to the base value set for daylight conditions. However, instead of the weighting factors decreasing as differences in swimming depth increased (as they did for deep seals), they were assigned a marginal increase. This was based on the potential effect of moonlight: during our study, there were numerous occasions where moonlight would have provided ample light for visual hunting. This would have put surface seals at substantial risk from sharks at the 'mid' and 'lower' levels, although less so from the latter because, even in the brightest moonlight, it would probably have been difficult to spot seals at the surface from a 20m depth. Still, despite this potential for increased risk, the relative rarity of these extremely bright nights limited the increase in relative weight which we estimated for these contexts.

The general trends estimated for night conditions were carried over into the day, as the interactions were assumed to be governed by the same general principles.

However, given the likely importance of vision to the sharks' hunting strategy, the increase in light levels with daylight were estimated to increase the relative weights beyond those for night, meaning an increased probability of an attack occurring in the daytime (Fig. 2.A.I, panels C and D). This was particularly the case for surface seals, which would find themselves at the greatest of all visual disadvantages against sharks below them. This context is likely the one which leads to the majority of observed predatory events, indicating that the risk (and corresponding relative P weighting value) for 'surface' seals from 'mid' sharks is probably substantially higher than for any other context. 'Surface' seals would also face a considerable risk from 'lower' sharks, although probably less than from sharks in the middle of the water column, due to the decrease in contrast of surface seals and the increased attack time which both accompany greater depths (see section on Depth levels).

2.10.3.2 Location around Seal Island

The relative context weights assigned for each combination of t, D, and d formed the basis for the P matrix. However, other variables (l,g,s) also played a part in defining individual attack contexts. Specific functions were therefore derived for each of these, based on relative weights estimated for each of their discrete categories, and these were multiplied by the weights which defined the visual environment, to obtain final values for P in each context. Relative weights for each of these secondary variables were estimated in the same manner as previously described, i.e. scaling the relative effect for each category of a specific variable against the category of that variable used in the baseline context (defined above), which was assigned a value of 1.

The first of the secondary variables considered was the location around Seal Island, as defined by the receptive areas of each VR2 receiver. Location was actually a surrogate variable for water depth, and was therefore only pertinent for certain contexts. All contexts where the shark was at the surface, as well as when seals were at the surface and sharks were 'mid', were thus deemed to be equivalent to the baseline context, and were assigned weighting values of 1 (Fig. 2.A.II).

Location, and hence water depth, was estimated to have an inverse effect on the probability of an attack occurring. The basis for this assertion is the absorption and scattering of light in water; being further away from something underwater decreases its visual contrast and thus detectability (Muntz 1974). This phenomenon is compounded by environmental conditions (wind, swells, and currents, all of which are prevalent at Seal Island), which lead to increases in suspended particulate matter, and an increase in the scattering of light. The result is that waters around Seal Island typically have poor visibility, in the range of 3-10m (unpublished data collected using a secchi disk).

Visibility was assumed to have little effect on the North and East sides of the island, where average bottom depths rarely exceeded the 'mid' shark level. However, on the Southern and Western sides, the bottom drops off very quickly to greater depths. Thus, sharks swimming near the bottom, in the 'lower' level, probably had a reduced view of the surface; similarly, sharks swimming mid-water probably would not have been able to detect seals swimming along the bottom, as they could have been over 10 meters away. The end result was that the increased depths on the Southern and Western sides of Seal Island were assumed to decrease the probability of attack for certain contexts.

To reflect this assumption, relative weights for affected contexts were assigned decimal values. The greatest drop was estimated to occur at night for 'deep' seals vs. 'mid' sharks (Fig. 2.A.III, panel A), where the low light conditions would probably have made it extremely difficult for a shark to spot a seal only a few meters below it. Thus, a precipitous drop in weights was assigned between the 'mid' range average depths of the Northern VR2s, and the 'Lower' average depths of the Southern and Western ones. This reasoning was also applied to the combination of 'deep' seals and 'mid' sharks during the day (Fig. 2.A.III, panel B). However, this decline was estimated as being more linear, because the greater visibility provided in daylight would likely have made it easier for 'mid' sharks to spot 'deep' seals, even in Southern waters.

Relative weights were also estimated to decrease slightly with average bottom depth for the combination of 'deep' seals and 'lower' sharks at night (Fig. 2.A.IV), while during the day it was estimated that there would be no effect (Fig. 2.A.II). This differential effect was once again based on light levels. Greater depths towards the south mean a greater separation distance between the ocean floor and the upper boundary of the 'lower' level. Thus, seals might manage to escape totally undetected at night, when sharks would be obliged to rely on short range senses, and would therefore be less likely to have full cognizance of seal movement in the entire level at once. However, this opportunity wouldn't exist during the day, as light levels would likely allow sharks to monitor the entire 'lower' level at once.

Finally, the combination of 'surface' seals and 'lower' sharks was also estimated to produce a declining probability of attack with depth, once again due to a decrease in underwater contrast with distance and an increase in attack time (Fig.2.A.V, panels A and

B). However, these effects were presumed to be greater at night, given the further constraints imposed by low light levels.

2.10.3.3 Group size

It is well-documented in the literature that an individual within a large group will gain a measure of anti-predatory benefit in the event of an attack (Hamilton 1971, Bertram 1978, Taylor 1984). However, what is also well-documented is that these benefits must be traded-off against detectability; large groups are often easy for predators to detect and hunt, yet remain advantageous to individuals within the group because of an overall decrease in the chance of predation (Taylor 1979, Pitcher 1986). These principles likely apply just as well to seals moving to or from Seal Island. Consequently, relative P weights for group size were derived from the interaction between a weighting function estimating the risk to an individual seal within a group, and a second weighting function estimating the relative effect of group size on detection. These functions were derived such that their products would represent the context weight for an individual seal in a given seal group size relative to the baseline context value of 1, which was assigned to a group size of 1.

Separate weighting functions were created for 'deep' and 'surface' seals, given the dramatically different visual conditions associated with each tactic. 'Surface' seals are undoubtedly easy to detect visually, regardless of group size. Consequently, the detection curve was estimated based predominantly on sound, such that it increased quickly with more than 1 seal (more seals meant more noise) but levelled off as seal numbers reached a point where any extra surface noise made little difference. Conversely, risk to an individual seal was estimated to decrease with group size, although marginal benefits

would diminish as group size increased. The product of the two curves estimated that the relative P context weight would decrease with group size, although the additional benefits accrued would become minimal as groups became extremely large (Fig. 2.A.VI).

'Deep' seals would face an entirely different set of circumstances. They move in an environment where visual conditions are in their favour, allowing them to detect sharks above them, while remaining undetected below. Thus, in 'deep' contexts, the expectation would be of a premium on stealth, at the expense of group benefits. Consequently, the effect of group size on detection was modeled to increase exponentially, reflecting the non-cryptic nature of extremely large groups, while the decrease in individual risk was modeled in the same manner as for surface seals. The relative product weights reflected our estimate that smaller group sizes would be more beneficial for 'deep' movement (Fig. 2.A.VII).

2.10.3.4 Seal size

The final factor which defined P was seal size, used as a surrogate for age class. It is a nearly ubiquitous fact in nature that juvenile animals are more susceptible to predation than adults, and the relative P context weights for s were modeled to reflect this trend (Fig. 2.A.VIII). Seal size 1 represented neonates, 2 were young of the year pups, 3 were juveniles/adult females, and 4 were mature bulls. Neonates were not observed, as pupping occurred 4 months before our field season began. However, over the course of the study, several seals were observed which, for whatever reason, were smaller than size 2 pups. These were classified as size 1.5, and were invariably attacked (although not always consumed). Consequently, the relative weight was set extremely high for this size class (Fig. 2.A.VIII). It was also estimated to be high for pups because of their nature as

physiologically limited, naïve explorers of a new environment. The base context was defined as a size 3 seal, meaning that this size class was assigned a 1. Finally, size 4 seals were assigned a weight below 1, as it was estimated that their imposing size would intimidate many of the smaller sharks around Seal Island, ultimately decreasing the overall chance of an attack occurring. Calculated relative P values for all possible contexts are presented in Table 2.A.I.

2.10.3.5 Final product

Final values of P were calculated as the product of the individual weights which comprised a specific contexts. Thus, for example, in a context where a size 3 seal (weight: 1) was swimming at the surface in a small group (weight: 0.82) on the South side of the island at night vs. a shark at the 'lower' depth (visual condition weight for Lower in Surface Seals – Night: 1.3; location weight for S in Surface-Lower-Night: 0.05), the estimated relative weight was 0.05. This number represented the prediction that, in our estimation, an attack was only 5% as likely to occur in this context as in the baseline context of an adult seal, swimming alone at the surface during the day, vs. a shark that was also swimming at the surface.

2.10.4   Sensitivity analysis

Given the speculative nature of the P matrix, a sensitivity analysis was conducted in order to assess the robustness of the conclusions under a variety of relative context weights. Each of the 4 variables (location l, group size g, seal size s, and 'visual conditions' (time t, seal depth d, and shark depth D)) was examined separately to isolate its impact on the final results (Table 2.A.II). For each variable, every individual weight was first doubled, then halved, and finally set to 1 to assess a 'no effect' situation.

Finally, the entire P matrix was removed from consideration by setting every weight to 1, in order to test the worst case scenario that none of the variables actually influence the shark seal interaction.

The conclusions proved relatively robust, such that only the 'no effect' case produced significant changes. The result illustrating a clear shark response to seal availability (Fig. 2.13) was primarily affected by elimination (no effect) of seal size (Fig. 2.A.IX) and group size (Fig. 2.A.X) weights, owing to the high weights attributed to solitary pups (which comprised the majority of predation events). However, the basic pattern remained consistent (albeit not significant), even when all context weights were ignored (Fig. 2.A.XI), indicating that the data themselves, rather than the chosen P values, drove the observed relationship.

The result indicating an adult seal response to shark behaviour (Fig. 2.9) remained similarly unaffected. Adjusting and eliminating the relative weights for seal size and group size had very little effect (the former because only adults were considered, the latter because adult group sizes were fairly consistent), while the effect of manipulating location weights was discernable but not significant. Only the elimination of the visual condition weights had an important effect (Fig. 2.A.XII), most likely as a result of removing the relative safety attributed to moving in the darkness. Nonetheless, as before, even the worst case scenario displayed the same basic pattern (Fig. 2.A.XIII), once again indicating that the results presented were primarily driven by the data themselves, and were merely reinforced by the relative context weights we assigned.

2.10.5 Appendix Tables

Table 2.A.I: *P* matrix, comprising the products of context weights for visual conditions, average receiver bottom depth (i.e., receiver location), and group size. Numbers represent estimates for size 3 seals. *P* for other size classes is obtained by multiplying the entire table by the appropriate age weight (Fig. 2.A.VIII).

		Group Size	1	1	1	2	2	2
		Shark Depth	Upper	Mid	Lower	Upper	Mid	Lower
Seal Depth	Time Period	Receiver						
Deep	1	North	0.10	1.00	1.10	0.10	0.95	1.05
Deep	1	NorthEast	0.10	0.90	1.08	0.10	0.86	1.03
Deep	1	West	0.10	0.20	1.06	0.10	0.19	1.01
Deep	1	SouthEast	0.10	0.13	1.03	0.10	0.12	0.99
Deep	1	South	0.10	0.10	1.01	0.10	0.10	0.96
Surface	1	North	1.00	2.00	1.30	1.03	2.06	1.34
Surface	1	NorthEast	1.00	2.00	1.21	1.03	2.06	1.25
Surface	1	West	1.00	2.00	0.81	1.03	2.06	0.83
Surface	1	SouthEast	1.00	2.00	0.42	1.03	2.06	0.43
Surface	1	South	1.00	2.00	0.07	1.03	2.06	0.07
Deep	2	North	0.10	1.40	1.65	0.10	1.33	1.57
Deep	2	NorthEast	0.10	1.33	1.62	0.10	1.27	1.54
Deep	2	West	0.10	0.95	1.58	0.10	0.91	1.51
Deep	2	SouthEast	0.10	0.66	1.55	0.10	0.63	1.48
Deep	2	South	0.10	0.36	1.52	0.10	0.35	1.45
Surface	2	North	1.00	10.00	8.00	1.03	10.30	8.24
Surface	2	NorthEast	1.00	10.00	7.76	1.03	10.30	7.99
Surface	2	West	1.00	10.00	6.80	1.03	10.30	7.00
Surface	2	SouthEast	1.00	10.00	5.52	1.03	10.30	5.69
Surface	2	South	1.00	10.00	4.16	1.03	10.30	4.28
Deep	3	North	0.10	1.40	1.65	0.10	1.33	1.57
Deep	3	NorthEast	0.10	1.33	1.62	0.10	1.27	1.54
Deep	3	West	0.10	0.95	1.58	0.10	0.91	1.51
Deep	3	SouthEast	0.10	0.66	1.55	0.10	0.63	1.48
Deep	3	South	0.10	0.36	1.52	0.10	0.35	1.45
Surface	3	North	1.00	10.00	8.00	1.03	10.30	8.24
Surface	3	NorthEast	1.00	10.00	7.76	1.03	10.30	7.99
Surface	3	West	1.00	10.00	6.80	1.03	10.30	7.00
Surface	3	SouthEast	1.00	10.00	5.52	1.03	10.30	5.69
Surface	3	South	1.00	10.00	4.16	1.03	10.30	4.28
Deep	4	North	0.10	1.00	1.10	0.10	0.95	1.05
Deep	4	NorthEast	0.10	0.90	1.08	0.10	0.86	1.03
Deep	4	West	0.10	0.20	1.06	0.10	0.19	1.01
Deep	4	SouthEast	0.10	0.13	1.03	0.10	0.12	0.99
Deep	4	South	0.10	0.10	1.01	0.10	0.10	0.96
Surface	4	North	1.00	2.00	1.30	1.03	2.06	1.34
Surface	4	NorthEast	1.00	2.00	1.21	1.03	2.06	1.25
Surface	4	West	1.00	2.00	0.81	1.03	2.06	0.83
Surface	4	SouthEast	1.00	2.00	0.42	1.03	2.06	0.43
Surface	4	South	1.00	2.00	0.07	1.03	2.06	0.07

| Seal Depth | Time Period | Group Size | S | S | S | M | M | M |
| | | Shark Depth | Upper | Mid | Lower | Upper | Mid | Lower |
		Receiver						
Deep	1	North	0.10	0.99	1.09	0.13	1.33	1.46
Deep	1	NorthEast	0.10	0.89	1.07	0.13	1.20	1.43
Deep	1	West	0.10	0.20	1.05	0.13	0.27	1.40
Deep	1	SouthEast	0.10	0.13	1.03	0.13	0.17	1.37
Deep	1	South	0.10	0.10	1.01	0.13	0.13	1.35
Surface	1	North	0.82	1.65	1.07	0.62	1.24	0.81
Surface	1	NorthEast	0.82	1.65	1.00	0.62	1.24	0.75
Surface	1	West	0.82	1.65	0.66	0.62	1.24	0.50
Surface	1	SouthEast	0.82	1.65	0.34	0.62	1.24	0.26
Surface	1	South	0.82	1.65	0.05	0.62	1.24	0.04
Deep	2	North	0.10	1.39	1.64	0.13	1.86	2.19
Deep	2	NorthEast	0.10	1.32	1.61	0.13	1.77	2.15
Deep	2	West	0.10	0.95	1.57	0.13	1.27	2.11
Deep	2	SouthEast	0.10	0.65	1.54	0.13	0.87	2.06
Deep	2	South	0.10	0.36	1.51	0.13	0.48	2.02
Surface	2	North	0.82	8.24	6.59	0.62	6.22	4.98
Surface	2	NorthEast	0.82	8.24	6.40	0.62	6.22	4.83
Surface	2	West	0.82	8.24	5.61	0.62	6.22	4.23
Surface	2	SouthEast	0.82	8.24	4.55	0.62	6.22	3.43
Surface	2	South	0.82	8.24	3.43	0.62	6.22	2.59
Deep	3	North	0.10	1.39	1.64	0.13	1.86	2.19
Deep	3	NorthEast	0.10	1.32	1.61	0.13	1.77	2.15
Deep	3	West	0.10	0.95	1.57	0.13	1.27	2.11
Deep	3	SouthEast	0.10	0.65	1.54	0.13	0.87	2.06
Deep	3	South	0.10	0.36	1.51	0.13	0.48	2.02
Surface	3	North	0.82	8.24	6.59	0.62	6.22	4.98
Surface	3	NorthEast	0.82	8.24	6.40	0.62	6.22	4.83
Surface	3	West	0.82	8.24	5.61	0.62	6.22	4.23
Surface	3	SouthEast	0.82	8.24	4.55	0.62	6.22	3.43
Surface	3	South	0.82	8.24	3.43	0.62	6.22	2.59
Deep	4	North	0.10	0.99	1.09	0.13	1.33	1.46
Deep	4	NorthEast	0.10	0.89	1.07	0.13	1.20	1.43
Deep	4	West	0.10	0.20	1.05	0.13	0.27	1.40
Deep	4	SouthEast	0.10	0.13	1.03	0.13	0.17	1.37
Deep	4	South	0.10	0.10	1.01	0.13	0.13	1.35
Surface	4	North	0.82	1.65	1.07	0.62	1.24	0.81
Surface	4	NorthEast	0.82	1.65	1.00	0.62	1.24	0.75
Surface	4	West	0.82	1.65	0.66	0.62	1.24	0.50
Surface	4	SouthEast	0.82	1.65	0.34	0.62	1.24	0.26
Surface	4	South	0.82	1.65	0.05	0.62	1.24	0.04

| Seal Depth | Time Period | Group Size | L | L | L | XL | XL | XL |
| | | Shark Depth | Upper | Mid | Lower | Upper | Mid | Lower |
		Receiver						
Deep	1	North	0.20	2.04	2.24	0.30	6.00	6.30
Deep	1	NorthEast	0.20	1.83	2.20	0.30	6.00	6.30
Deep	1	West	0.20	0.41	2.15	0.30	1.80	6.15
Deep	1	SouthEast	0.20	0.26	2.11	0.30	1.80	6.00
Deep	1	South	0.20	0.20	2.06	0.30	0.60	6.00
Surface	1	North	0.50	1.01	0.66	0.40	0.81	0.52
Surface	1	NorthEast	0.50	1.01	0.61	0.40	0.81	0.52
Surface	1	West	0.50	1.01	0.41	0.40	0.81	0.28
Surface	1	SouthEast	0.50	1.01	0.21	0.40	0.81	0.28
Surface	1	South	0.50	1.01	0.03	0.40	0.81	0.16
Deep	2	North	0.20	2.85	3.36	0.23	6.30	6.75
Deep	2	NorthEast	0.20	2.71	3.29	0.23	6.30	6.75
Deep	2	West	0.20	1.94	3.23	0.23	3.60	6.30
Deep	2	SouthEast	0.20	1.34	3.16	0.23	3.60	5.85
Deep	2	South	0.20	0.74	3.09	0.23	2.25	4.50
Surface	2	North	0.50	5.04	4.03	0.40	0.81	0.52
Surface	2	NorthEast	0.50	5.04	3.91	0.40	0.81	0.52
Surface	2	West	0.50	5.04	3.43	0.40	0.81	0.28
Surface	2	SouthEast	0.50	5.04	2.78	0.40	0.81	0.28
Surface	2	South	0.50	5.04	2.10	0.40	0.81	0.16
Deep	3	North	0.20	2.85	3.36	0.23	6.30	6.75
Deep	3	NorthEast	0.20	2.71	3.29	0.23	6.30	6.75
Deep	3	West	0.20	1.94	3.23	0.23	3.60	6.30
Deep	3	SouthEast	0.20	1.34	3.16	0.23	3.60	5.85
Deep	3	South	0.20	0.74	3.09	0.23	2.25	4.50
Surface	3	North	0.50	5.04	4.03	0.40	0.81	0.52
Surface	3	NorthEast	0.50	5.04	3.91	0.40	0.81	0.52
Surface	3	West	0.50	5.04	3.43	0.40	0.81	0.28
Surface	3	SouthEast	0.50	5.04	2.78	0.40	0.81	0.28
Surface	3	South	0.50	5.04	2.10	0.40	0.81	0.16
Deep	4	North	0.20	2.04	2.24	0.30	6.00	6.30
Deep	4	NorthEast	0.20	1.83	2.20	0.30	6.00	6.30
Deep	4	West	0.20	0.41	2.15	0.30	0.60	6.00
Deep	4	SouthEast	0.20	0.26	2.11	0.30	0.60	6.00
Deep	4	South	0.20	0.20	2.06	0.30	0.60	6.00
Surface	4	North	0.50	1.01	0.66	0.40	0.81	0.52
Surface	4	NorthEast	0.50	1.01	0.61	0.40	0.81	0.52
Surface	4	West	0.50	1.01	0.41	0.40	0.81	0.28
Surface	4	SouthEast	0.50	1.01	0.21	0.40	0.81	0.28
Surface	4	South	0.50	1.01	0.03	0.40	0.81	0.16

		Group Size	XXL	XXL	XXL
		Shark Depth	Upper	Mid	Lower
Seal Depth	Time Period	Receiver			
Deep	1	North	0.33	6.50	6.83
Deep	1	NorthEast	0.33	6.50	6.83
Deep	1	West	0.33	1.95	6.66
Deep	1	SouthEast	0.33	1.95	6.50
Deep	1	South	0.33	0.65	6.50
Surface	1	North	0.32	0.65	0.42
Surface	1	NorthEast	0.32	0.65	0.42
Surface	1	West	0.32	0.65	0.23
Surface	1	SouthEast	0.32	0.65	0.23
Surface	1	South	0.32	0.65	0.13
Deep	2	North	0.25	7.00	7.50
Deep	2	NorthEast	0.25	7.00	7.50
Deep	2	West	0.25	4.00	7.00
Deep	2	SouthEast	0.25	4.00	6.50
Deep	2	South	0.25	2.50	5.00
Surface	2	North	0.32	0.65	0.42
Surface	2	NorthEast	0.32	0.65	0.42
Surface	2	West	0.32	0.65	0.23
Surface	2	SouthEast	0.32	0.65	0.23
Surface	2	South	0.32	0.65	0.13
Deep	3	North	0.25	7.00	7.50
Deep	3	NorthEast	0.25	7.00	7.50
Deep	3	West	0.25	4.00	7.00
Deep	3	SouthEast	0.25	4.00	6.50
Deep	3	South	0.25	2.50	5.00
Surface	3	North	0.32	0.65	0.42
Surface	3	NorthEast	0.32	0.65	0.42
Surface	3	West	0.32	0.65	0.23
Surface	3	SouthEast	0.32	0.65	0.23
Surface	3	South	0.32	0.65	0.13
Deep	4	North	0.33	6.50	6.83
Deep	4	NorthEast	0.33	6.50	6.83
Deep	4	West	0.33	0.65	6.50
Deep	4	SouthEast	0.33	0.65	6.50
Deep	4	South	0.33	0.65	6.50
Surface	4	North	0.32	0.65	0.42
Surface	4	NorthEast	0.32	0.65	0.42
Surface	4	West	0.32	0.65	0.23
Surface	4	SouthEast	0.32	0.65	0.23
Surface	4	South	0.32	0.65	0.13

Table 2.A.II: Table of values used in the sensitivity analysis. Each of the four P variables was tested separately, and for each all relevant categories (those with values other than 1) were doubled, halved, or set to 1. Values were doubled and halved relative to 1, i.e. a value of 6.5 has an effect of 5.5 more than 1, so a doubled effect is 11 + 1, or 12.

P Matrix Variable	Category		P Weight	Double	Half	No Effect
Size (Age) Class	Pup		6.5	12	3.75	1
s	Adult		0.5	0.05	0.75	1
Group Size g	Deep	2	0.95	0.9	0.975	1
		S	0.99	0.98	0.995	1
		M	1.33	1.66	1.165	1
		L	2.04	3.08	1.52	1
		XL	4.27	7.54	2.635	1
	Surface	2	1.03	1.06	1.015	1
		S	0.82	0.64	0.91	1
		M	0.62	0.24	0.81	1
		L	0.5	0.05	0.75	1
		XL	0.4	0.04	0.7	1
		XXL	0.33	0.033	0.665	1
Location (Bottom Depth) l	Deep - Mid - Night	N	1	1	1	1
		NE	0.9	0.8	0.95	1
		W	0.2	0.02	0.6	1
		SE	0.13	0.013	0.565	1
		S	0.1	0.01	0.55	1
	Deep - Mid - Day	N	1	1	1	1
		NE	0.95	0.9	0.975	1
		W	0.68	0.36	0.84	1
		SE	0.47	0.047	0.735	1
		S	0.26	0.026	0.63	1
	Surface - Lower - Night	N	1	1	1	1
		NE	0.93	0.86	0.965	1
		W	0.62	0.24	0.81	1
		SE	0.32	0.032	0.66	1
		S	0.05	0.005	0.525	1
	Surface - Lower - Day	N	1	1	1	1
		NE	0.97	0.94	0.985	1
		W	0.85	0.7	0.925	1
		SE	0.69	0.38	0.845	1
		S	0.52	0.04	0.76	1
Visual Conditions (t,d,D)	Deep - Upper - Night		0.1	0.01	0.55	1
	Deep - Upper - Day		0.1	0.01	0.55	1
	Deep - Lower - Day		1.65	2.3	1.325	1
	Deep - Mid - Day		1.4	1.8	1.2	1
	Surface - Lower - Night		1.3	1.6	1.15	1
	Surface - Mid - Night		2	3	1.5	1
	Surface - Mid - Day		10	19	5.5	1
	Surface - Lower - Day		8	15	4.5	1

2.10.6   Appendix Figure Legends

Fig. 2.A.I: Relative context weights for visual conditions, as defined by light levels (day or night), and by the swimming depths of both species.

Fig. 2.A.II: Relative context weights based on varying bottom depth. N, NE, W, SE, and S refer to receiver location. Water depth was not estimated to have an effect on any contexts where sharks were in the 'upper' level of the water column, as well as any contexts defined by seals at the 'surface' and sharks at 'mid' level, and the contexts comprising 'deep' seals and 'lower' sharks during the day.

Fig. 2.A.III: Relative context weights based on average receiver bottom depth for 'deep' seals and 'mid' sharks during both light level conditions. N, NE, W, SE, and S refer to receiver location.

Fig. 2.A.IV: Relative context weights based on average receiver bottom depth for 'deep' seals and 'lower' sharks at night. N, NE, W, SE, and S refer to receiver location. During the day, location was assumed to have no effect on the deep seal – lower shark relative weight (Fig. 2.A.II).

Fig.2.A.V: Relative context weights based on average receiver bottom depth for 'surface' seals and 'lower' sharks during both light level conditions. N, NE, W, SE, and S refer to receiver location.

Fig. 2.A.VI: Relative context weights assigned as a function of surface seal group size. These weights were modeled to have a 'effect on detection' component, and a 'risk to an individual seal' component, which were multiplied together to give the final group size weight.

Fig. 2.A.VII: Relative context weights assigned as a function of deep seal group size. Weights were modeled using the same method as for Fig. 2.A.VI. However, the effect on detection curve was modeled to increase sharply with group size, rather than level off (as for 'surface' seals), in order to express the importance of stealth in the 'deep' swimming tactic.

Fig. 2.A.VIII: Relative context weights assigned as a function of seal size, used as a surrogate for seal age. Size 1.5 seals were pups that were not large enough to be size 2, and yet were observed moving in the water. These were invariably attacked, and thus necessitated a high relative context weight. Size 4 seals were mature bulls, too large for many of the sharks around Seal Island to attack.

Fig. 2.A.IX: Sensitivity analysis of Fig. 2.13, conducted with no effect (relative weights set to 1) of seal size s.

Fig. 2.A.X: Sensitivity analysis of Fig. 2.13 conducted with no effect (relative weights set to 1) of seal group size g.

2.10.7 Appendix Figures

Fig. 2.A.I:

Fig. 2.A.II:

All Upper Level Sharks
All Surface Swimming Seals– Mid Level Sharks
Deep Swimming Seals– Lower Level Sharks – Day

Fig. 2.A.III:

Deep Swimming Seals

Mid Level Sharks

Night — A

N NE W SE S

1, 0.9, 0.2, 0.13, 0.1

Day — B

N NE W SE S

1, 0.95, 0.68, 0.47, 0.26

Relative Context Weight (y-axis): 0, 0.5, 1, 1.5

Average Receiver Bottom Depth (x-axis): 10, 20, 30

Fig. 2.A.IV:

**Deep Swimming Seals
Night**

Fig.2.A.V:

Surface Swimming Seals

Average Receiver Bottom Depth

Fig. 2.A.VI:

Surface Swimming Seals

Fig. 2.A.VII:

Deep Swimming Seals

Fig. 2.A.VIII:
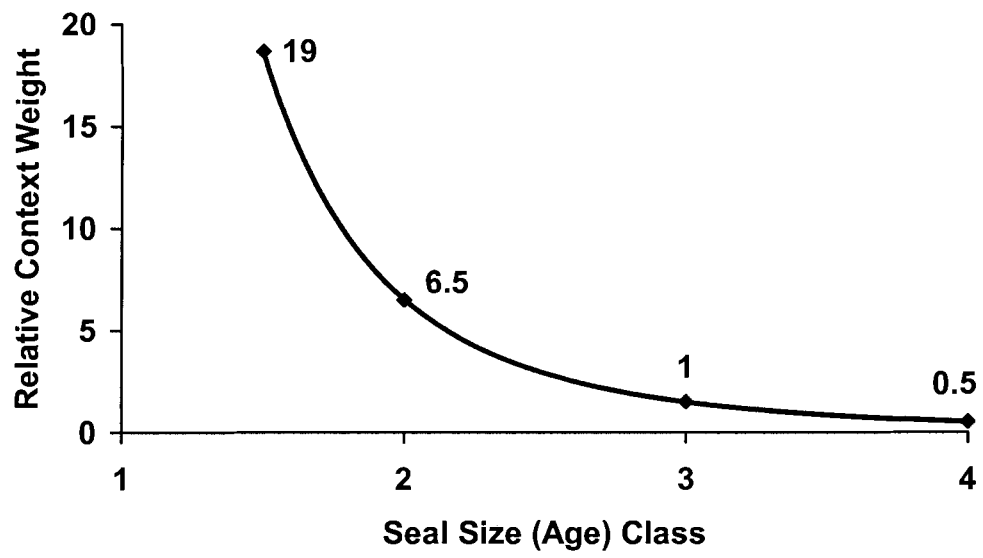
Fig. 2.A.IX:
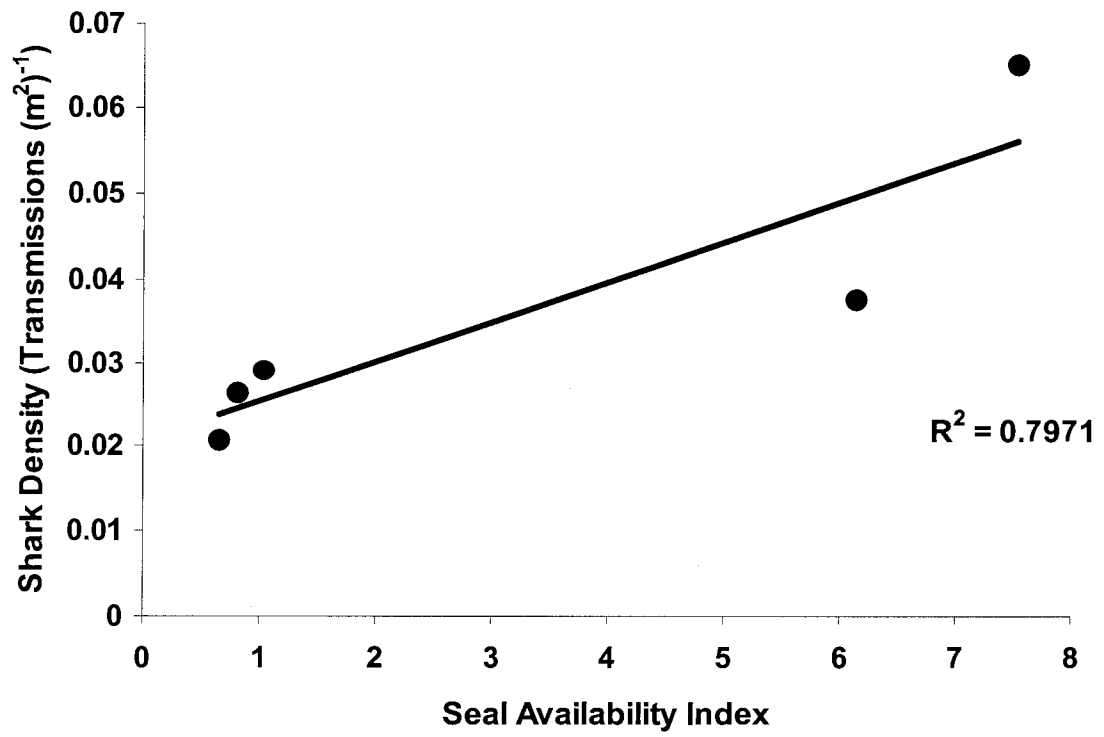
Fig. 2.A.X:
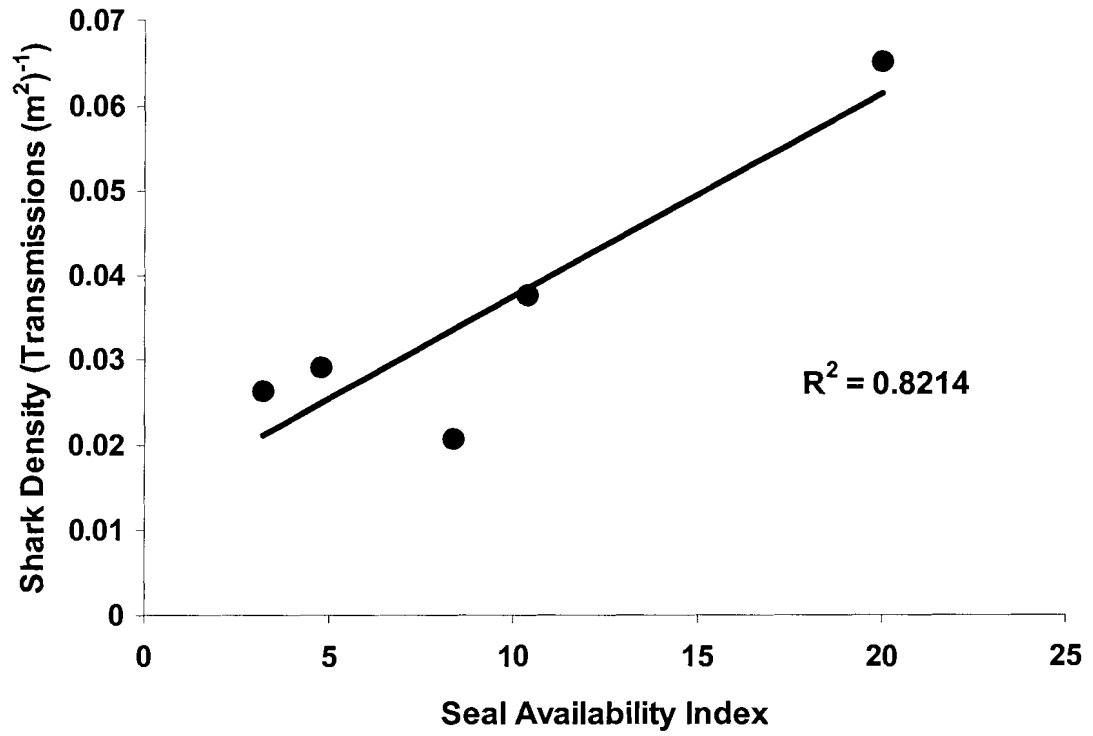
Fig. 2.A.XI:

Fig. 2.A.XII:

Fig. 2.A.XIII:

Scatter plot with x-axis labeled "Shark Risk Index" ranging from 0 to 0.25, and y-axis labeled "Seal Movement (Transits Radian^{-1})" ranging from 0 to 12. Annotation reads $R^2 = 0.0272$.
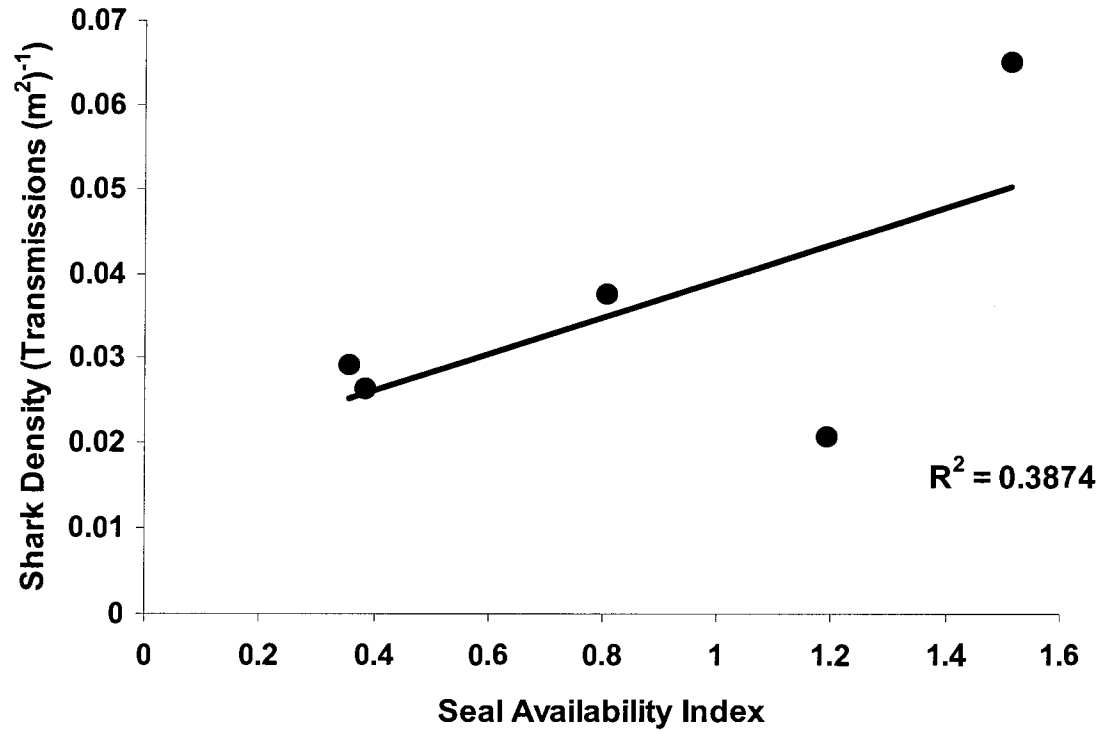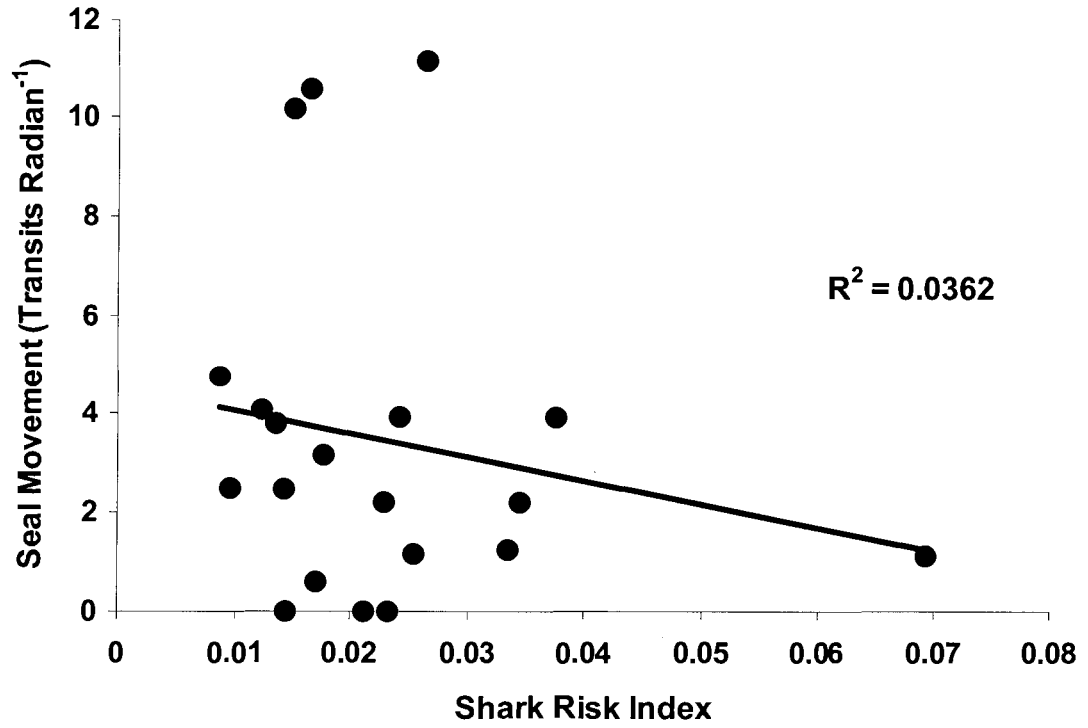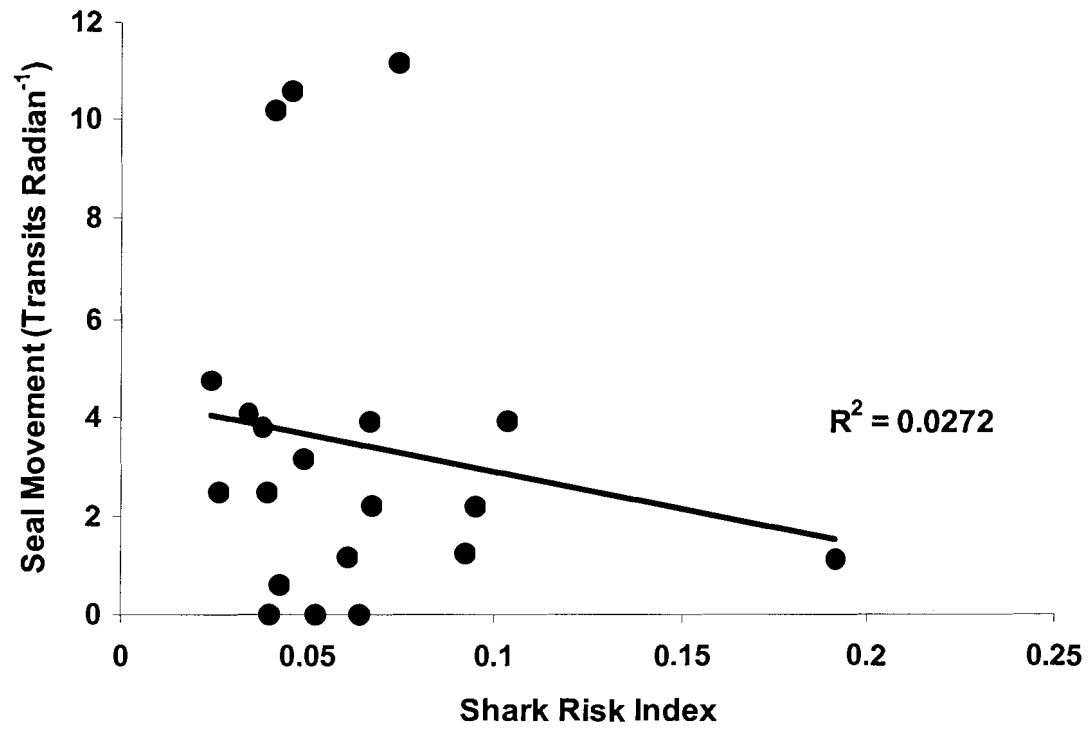
Chapter 3

Effects of provisioning ecotourism on the movement patterns of white sharks, *Carcharodon carcharias*

3.1   Abstract

Ecotourism operations which provide food to large predators have the potential to negatively affect their target species, by conditioning them to associate humans with food, or by generally altering their behavioural patterns. This latter effect could potentially have detrimental consequences for the predator's ecosystem, because any behavioural changes could affect the species with which they interact. Here we present the results of an experimental study examining the effects of provisioning ecotourism on the behaviour of white sharks around a seal colony on a small island in South Africa. Although ecotourism activity had an effect on the behaviour of some sharks, this was relatively minor, and the majority of sharks showed little interest in the food rewards being presented. It's unlikely that conditioning would occur from the amount of ecotourism activity tested, because even those identified sharks which supplied most of the data presented here (and which may possess a stronger predisposition towards conditioning, because their persistence around the boat is what allowed them to be identified) showed a nearly ubiquitous trend of decreasing response with time. Further, even those sharks which succeeded in frequently acquiring food rewards typically stopped responding after several interactions. Consequently, moderate levels of ecotourism probably have only a minor impact on the behaviour of white sharks, and are therefore unlikely to create behavioural effects at the ecosystem level.

3.2 Introduction

Nature-based tourism, or ecotourism, is a rapidly growing industry on a worldwide scale (Wearing & Neill 1999). It allows humans to interact with a multitude of species in different environments, and can offer benefits ranging from local economic development, to the fostering of conservation-friendly attitudes in the general populace (Miller 1993, Orams 1995, Mangel et al. 1996, Barkin 2003, Kiss 2004, Jones 2005, Krueger 2005). However, ecotourism activity also has the potential to adversely affect a target species, by creating a disturbance which significantly alters an animal's behaviour. One way this could happen is if the animals being observed perceive benign human presence as a predation risk (Burger & Gochfeld 1998, Williams et al. 2002, McClung et al. 2004, Nevin & Gilbert 2005). In this context, any risk averse behaviour adopted by the animals would likely result in the reduction of other fitness accruing activities (i.e., foraging, resting, etc.; Gill & Sutherland 2000, Frid & Dill 2002).

However, other forms of ecotourism seek to deliberately alter the behaviour of their target species, by using food incentives to bring animals to the tourists (Orams 2002). These operations often showcase elusive predators that would usually ignore or avoid tourists altogether (Orams et al. 1996, Burgess 1998). Still, despite such invasive practices, it's unlikely that this type of provisioning ecotourism would affect an animal's fitness in the manner described above: tourist food can be obtained at little or no energy cost, and the animals can depart if conditions become unfavourable. Thus, tourist presence would not be perceived as a negative threat, but rather as a positive feeding opportunity. Nonetheless, provisioning ecotourism could negatively affect a target

species, for example by creating a dependency on tourist food, fostering aggression towards humans, or through incidental disease or injury (Orams 2002).

Further, and perhaps most importantly, the predators sought out by these operations are a component of an ecosystem, and surely interact with numerous species, including their prey. Consequently, changing the predator's behaviour brings with it the possibility of altering the dynamics of these interactions (Orams 2002). The end result could be a series of behaviourally mediated indirect interactions between the tourists, the predators, and any other species; the positive and negative effects of which could theoretically cascade throughout the ecosystem (Wootton 1993, Abrams et al. 1996, Yodzis 2000, Dill et al. 2003).

Given its apparent potential for inducing behavioural changes, the need to determine the direct impact of provisioning ecotourism on the behaviour of a target species should be evident. To address these questions, we explored the potential effects of a provisioning ecotourism operation on a large predator: South Africa's white shark, Carcharodon carcharias, ecotourism industry.

Shark ecotours operate at several locations along the South African coastline, all based on specific Cape fur seal, *Arctocephalus pusillus pusillus*, colonies (Ferreira & Ferreira 1996), a preferred prey item of the white shark. The waters surrounding these colonies have large numbers of sharks during the Southern Hemisphere's winter (May-September), a time at which sharks are in full hunting mode (Martin et al. 2005). Evidence from numerous sites around the world suggest that this involves swimming at depth and inspecting the water above for seal-shaped silhouettes (Klimley 1994, Anderson et al. 1996, Strong 1996, Kock 2002; unpublished data from Seal Island). This

strategy would allow the sharks to easily spot any seals above them, while remaining cryptic themselves. The end result is an ambush attack, limiting the shark's energy expenditure and risk of injury, while maximizing success rate (Martin et al. 2005).

Unfortunately, the basic goals of the ecotourism industry are in complete conflict with this strategy. These goals are simple: to attract as many sharks as possible to the surface, and to keep them around the tour boat for as long as possible. If successful, the sharks could spend far less time hunting, and at the very least would forfeit the tactical advantage they gain by remaining low in the water column and not remaining in one clearly defined area. Thus, the potential exists for the white shark tourism industry to not only alter the sharks' behaviour, but for this result to reduce the predatory pressure they exert on the seals: a possible step towards tourism effect cascading throughout the entire ecosystem. The key to determining whether this is occurring is to first establish if white shark ecotourism boats are altering the behaviour of their target species.

3.3   Materials and methods

3.3.1   Study site

The research was conducted around Seal Island, a small island located in False Bay, in the Western Cape region of South Africa (Fig. 3.1). The island is populated year-round by anywhere between 36 000 and 77 000 Cape fur seals (unpublished data from South African Marine and Coastal Management), and is the only seal breeding colony within the bay (Butterworth et al. 1987, Shaughnessy 1987). The waters surrounding the island also support large numbers of white sharks from May through September. The South African government issues permits to three white shark ecotourism operators every

year for the 'high season', allowing these individuals to approach close to natural predatory events, as well as to attract sharks to their boats for tourists to view.

The typical ecotour excursion to Seal Island involves arriving at the island shortly before sunrise and drifting for 2-3 hours to freely move to predation events. A seal-shaped decoy is then usually towed around the island (an activity designed to elicit shark predatory breaches) for approximately 30 minutes, and finally the boats anchor and disperse organic attractant (chum: typically mashed sardine and fish oil, although occasionally including minced tuna or shark liver; bait: fish chunks or shark heads) in the water with the hopes of luring nearby sharks to the boat. Chumming will often continue into the early afternoon, after which operators return to port. This standard of ecotourism activity is adhered to on the majority of excursions, and was developed to exploit the fact that most shark predatory behaviour at the island is observed during the hours around sunrise (Martin et al. 2005). Still, operators did occasionally deviate from the model, for example by chumming or towing the entire day.

3.3.2 Acoustic equipment

At various times during the field season (May-October, 2004), 17 white sharks were tagged with Vemco Rcode acoustic transmitters, of which 7 were model V16, and the remainder V16P (added pressure sensitivity for swimming depth measurement). In all cases, sharks were enticed to our boat by means of various forms of attractant (fish oil, sardine, shark liver, whale blubber; also a seal-shaped decoy cut from carpet), and coaxed to stay with large chunks of fish bait. Sharks were lured close to the boat, at which point a tag was attached subcutaneously by means of a small plastic barb and a metal spear.

Data were collected from the acoustic transmitters using 6 Vemco model VR2 data logging receivers. These were deployed along the ocean floor at various locations around Seal Island (Fig. 3.1), anchored to the bottom by means of a truck tire filled with concrete.

3.3.3 Experimental activity

Chumming experiments were conducted from June-October 2004, during which time we traveled to Seal Island whenever possible, for an average of 15 days per month. When present at the island, our time was split between two distinct activities: (1) dedicated watching for predatory activity and seal movement (Watching), which meant that the boat was adrift and no attractant was placed in the water; and (2) chumming for sharks (Chumming), where the boat was anchored and attractant was deployed.

Waters surrounding Seal Island were divided into 6 sectors (Fig. 3.1), and time of day broken up into four 2.5 hour blocks between 0730 and 1730 (hours were occasionally extended on either side). Our choice of either activity at the island was then randomly assigned to a specific sector for each time block, using Microsoft Excel's random number function. In total, we were present for, and collected data during, 169 time blocks.

3.3.4 Visual records

Visual records were kept of observed shark activity around our boat. Individual sharks were described using unique scarring or pigmentation patterns, to facilitate identification. Unfortunately, markings on most sharks were not distinct enough to allow for clear recognition over multiple days. However, some sharks were easily distinguishable, and were thus recorded as 'identified sharks' if re-sighted on any subsequent days. All tagged sharks were individually identified.

Shark presence at the boat was recorded on a minute by minute basis. The total number of minutes during which a shark was recorded at our boat on a single day was defined as its 'contact time'. This measure was weighted by the total potential contact time during a day (i.e., the total number of minutes during which attractant was in the water), providing a 'proportional contact time' with which to measure shark response to chum.

3.3.5 Analysis

The general hypothesis underpinning this study was that sharks would respond favourably to the presence of chum. As a result, the expectation was that sharks would spend more time within the vicinity of the boat (and the nearest VR2 receiver) when chum was in the water, and correspondingly less time around other areas of the island (i.e. the other 5 receivers). This expectation was tested by contrasting the differences in receiver records between chumming and non-chumming conditions for the receivers closest to the chum source (anchoring location around the island was randomly assigned), as well as those that were successively further away.

However, despite implementation of the experimental protocols described above, the realized 'chumming' environment around Seal Island often departed from ideal experimental conditions. The presence of ecotourism boats sometimes meant that there were several sources of attractant at once, occasionally on opposite sides of the island. Further, the basic pattern of ecotourist activity was very predictable, which meant that the application of experimental treatments (chumming bouts) was not randomized.

Consequently, data recorded during ecotourist chumming could not be reconciled with the requirements of rigorous statistical analysis, making it necessary to exclude them

from the final results. This dramatically decreased the overall data set, and imposed several constraints on the analysis. Most importantly, we were forced to make the assumption that sharks would only respond to chum, and not to the presence of the boats themselves. This was mandated because the reduced data set was not large enough to provide for two separate control states differing only in the presence or absence of boats. Instead, those data recorded with and without boats were combined into one unified 'no chum' control, making the assumption of no boat effect necessary.

The non-regimented nature of ecotourist presence also forced us to analyze the data within a different time frame than the one established through experimental protocols. Although our activity at Seal Island was based around four 2.5 hour blocks, these delineations proved unworkable during the analysis because too many data were lost to ecotourist activity (e.g., ecotourist chumming from 1200-1300 would have invalidated all the data from 1000-1500). Thus, data were broken up into 1 hour collection periods, usually making it possible to salvage data recorded before, and occasionally even after ecotourism activity.

Two facets of shark behaviour were explored separately within the VR2 receiver data: shark presence, and shark swimming depth. Both were examined by delineating within the data a set of paired 'chumming' and 'control' (or non-chumming) one hour periods. A pair of these periods thus consisted of the data collected by each receiver during an hour of chumming, and the data collected by each receiver during the same hour on a separate day when no chumming was taking place. Periods were selected to be as similar as possible with regard to individual shark presence and acoustic conditions. The following criteria were used to identify the periods:

1. Paired periods could be no more than two days apart
2. Wind strength could differ by no more than 10 Kph
3. Swell height could differ by no more than one meter

The first hour-long experimental chumming period for a particular day (and its corresponding control) was only defined one hour after chumming actually began, providing for chum dispersal time. Successive hour-long periods were then identified up until the point where chumming ceased, or until a disruptive event occurred, such as the initiation of ecotourist chumming. In total, 54 separate one hour-long pairs of experimental and control periods (108 total hours) were isolated over 20 different paired days (40 total days). The hour preceding experimental chumming, along with the one situated one hour after the cessation of chumming (to allow for any chum effects to abate), were also considered whenever possible, and were defined as 'pre-chumming' and 'post-chumming' periods, respectively.

Before conducting any analyses, all records of shark presence were first weighted by their respective receiver's average receptive area, as well as by the shortest distance from their receiver to the chum source (to control for varying anchoring locations; the mean distance from the source to the closest receiver was 153 m, to the furthest 964 m). Data were then summed for each receiver during each hour-long period, and these values divided by the total records collected from all 6 receivers within the time period. This transformed the data for each receiver into a proportion of total records for that period, correcting for any differences in overall shark abundance between pairs of periods. These proportional values were used to calculate the mean proportional presence per hour-long period per day for each receiver. In so doing, the unit of measurement was shifted from a

period to a day, a step which was required to address the obvious non-independence of successive hours measured over one day.

Paired experimental and control days were contrasted as the difference between the mean proportional presence/period/day for each receiver during both conditions (exp. – con.). These results were then grouped to reflect receiver distance from the chum source on each experimental day, i.e., the receiver nearest to our chumming position on any given day was considered together with the closest receivers from other days, regardless of where around Seal Island we set anchor, and similarly for successively further receivers. Mean differences were found for each receiver distance group, and t-tests used to ascertain whether mean differences between chumming and control conditions varied with distance from a chum source, as well as to determine whether any of the means were statistically distinguishable from zero. Analysis of shark depth was conducted using the same methodology, but by substituting a measure of mean swimming depth/period/day for each receiver in the place of proportional shark presence.

The same analysis was also conducted by first calculating the difference in proportional shark presence data during experimental and control hour-long periods for each separate shark at each receiver. However, for this analysis, periods were defined on an individual basis for each animal, to prevent artificial constructs from influencing the results. For each shark, the first hour-long period started at the point when the shark was first recorded after chumming commenced (or the corresponding time on control days), and the last period was defined as the last full hour before the end of experimental conditions. Data were transformed into proportions by weighting the records for each shark at a particular receiver during a time period by the total records for that shark

collected from all receivers within the same period. These measures were used to examine the records with regard to each individual shark's reactions to chumming conditions over time. However, this further limited the data set, because only sharks which were recorded during both experimental and control conditions within each paired data set could be utilized.

The first analysis undertaken was an examination of effect differences over the course of successive hours in one day. To this end, all hour periods during which sharks were recorded were considered separately. Means were calculated for each receiver using the first hour exp. – con. differences of each individual shark on a given day (mean first hour difference in proportional presence/receiver/day), and t-tests employed to test the same statistical hypotheses as above. The subsequent hour-long period was also analyzed in the same fashion to provide a comparison between successive hours, but there were insufficient data to test the hypotheses beyond the second hour.

Individual shark differences were also used to test chum effects over repeated days of exposure. For this, only records taken from the receivers nearest to the chum source were considered, and periods were again defined on an individual basis. A measure of mean difference in proportional presence/period/day was calculated for each shark, on each successive day it was recorded. A 2-way ANCOVA was then employed to test for independence of individual data points, by determining whether a statistically significant interaction existed between sighting number and the measure of shark presence for each individual shark. A simple linear regression was used on a scatter-plot of the data to describe any prevailing patterns.

Visual records were also used to analyze shark contact times. A two-sample Kolmogorov-Smirnov test was employed to test the hypothesis of no difference between the distribution of proportional contact times of tagged and untagged animals. Visual records over repeated encounters were also analyzed in the same manner as the receiver records, presenting the regression of a scatter-plot of proportional contact times as a function of the number of times a shark had been sighted. A 2-way ANCOVA was also employed to test for statistical independence of these data.

3.4   Results

3.4.1   Shark presence

No statistical differences between paired segments were observed in the receiver records collected during the hour immediately preceding chumming (Fig. 3.2a; n=19), nor during post-chumming (Fig. 3.2c; n=9). However, a significant difference between receiver distances was apparent when contrasting experimental and control conditions, driven by a mean positive difference for the receiver nearest to the chum source (greater shark presence while chumming; Fig. 3.2b; n=20, p=0.039). This would be the expected result if chum were influencing shark spatial behaviour, but the associated error bars suggest that any possible effects of chum may not be great.

This result is supported by visual records. The distribution of contact times for all sharks observed at our boat indicates that the vast majority of sharks only passed by briefly (Fig. 3.3a), and demonstrated very little response to the food incentive we were offering. Tagged individuals (which supplied the data for Fig. 3.2), did demonstrate a greater inclination towards remaining within sight of the boat than untagged sharks

(Fig. 3.3b,c; Kolmogorov-Smirnov test, Z=3.884, p<0.001), but even these sharks most frequently responded with a quick pass.

These results were obtained by summing the data (either receiver or visual records) for all sharks. However, when the same analyses were conducted by first measuring differences in proportional presence for individual animals, a more distinct result emerged. During the first experimental hour that a shark was recorded, chum appeared to have a significant effect on its behaviour (Fig. 3.4a; n=20, p=0.0016). However, this effect was greatly diminished during the second hour (Fig. 3.4b; n=13), although a small sample size and large variances render this result suspect.

The data were further explored to gauge the response of individual animals to chum over repeated days of exposure. Unfortunately, this placed further constraints on the data set, because only 9 sharks appeared in the period records on more than one day, and of these only 5 appeared on more than two. Nonetheless, a scatter-plot of the mean paired differences per day for each shark (only for the receivers closest to the chum source) suggests a declining trend in shark response with repeated exposure (Fig. 3.5). This trend was not statistically significant (p=0.1720), but is supported by the establishment of a clear empty domain in the upper right portion of the graph. A test of independence did not demonstrate a significant interaction between the number of days recorded and the weighted signal measure of each individual shark (2-way ANCOVA interaction term p=0.4864), providing confidence in the observed result.

Once again visual records support the receiver data. A regression run through a similar scatter plot of proportional contact times for all successive sightings of identified sharks demonstrates the same decreasing trend in response, this time with statistical

significance (Fig. 3.6a; 16 re-sighted sharks, p=0.0029). Unfortunately, very few sharks were sighted more than 5 times, raising the possibility that this pattern was driven by the behaviour of only one or two animals. However, a plot of the data gathered from the 7 sharks that were sighted at least 5 times reveals the same significant trend (Fig. 3.6b, p=0.0023), lending credence to the previous outcome. Unfortunately, a test of independence revealed a significant interaction between the number of days a shark was sighted and proportional contact time for all 16 sharks, suggesting non-independence of the data (2-way ANCOVA interaction term p=0.0171). However, a closer inspection of these data reveals that this interaction is primarily driven by the behaviour of one shark, who displayed the proposed pattern substantially more than the other sharks (Shark 31; see Appendix). When this shark is removed from consideration, the interaction is no longer significant (2-way ANCOVA interaction term p=0.1649). Proportional contact time plots for all sharks are presented in the Appendix.

Although the receiver and visual records display similar results, a contrast of the two provides further support that shark response to chum is limited and decreases with time. Overall, sharks were only observed at our boat while we were chumming on 36% of the occasions that they were concurrently recorded around Seal Island, and the majority of these appearances occurred early in the season. This pattern is illustrated by three of the most frequently observed sharks (Fig. 3.7), who obtained more reward than any others (no other shark obtained more than 1 bait). Despite this, all three responded to the attractant only occasionally, and sharks 32 and 39 clearly stopped responding completely with time.

3.4.2   Shark swimming depth

Chumming appeared to have a slightly more obvious impact on shark swimming depth. A significant difference in change of swimming depth was observed between the receiver nearest to the chum source and the remaining 5 (Fig. 3.8; $n=20$, $p=0.023$), stemming from a negative difference in swimming depth (more shallow) nearest to the chum source and the boat, while none of the other mean differences were statistically distinguishable from zero. This result likely reflects that sharks venture up to the surface to investigate the chum source, while they maintain their normal swimming depth patterns around the remainder of the island.

3.5   Discussion

Despite offering numerous positive benefits, nature-based tourism also has several potential pitfalls, the most important of which is the possibility of altering the behaviour of the target species. This problem is of particular importance when considering ecotourism operations which provide food to the animals, because their success guarantees at least some deviation away from natural behaviour in the absence of human activity. This study sought to examine the effect of such provisioning practices by the South African white shark ecotourism industry on the behaviour of their target species.

3.5.1   Direct impact on sharks

Sharks are probably present at Seal Island for the sole purpose of hunting seals. Consequently, if chumming had a direct impact on the sharks, this would likely be most evident through a change in some element of their feeding behaviour. Data collected over the field season suggest that no decrease in predation rate occurred during chumming periods, although the non-systematic methodology used to collect these data renders the

result highly suspect, and prevented its inclusion in this paper. Nonetheless, an unaffected predation rate does not necessarily preclude the possibility of direct impacts on the sharks' feeding activities.

For one, ecotourists could be conditioning sharks to associate tour boats with food rewards. Such effects could theoretically occur without a drop in predation rate, assuming the sharks never substituted ecotourism fare for live kills, but rather only supplemented their intake. Alternatively, the effects of conditioning in this system might only be manifested over a period longer than the course of this study. However, even in this event, the expectation would be that the overall behavioural patterns prevalent in the data would point towards the potential for conditioning to occur.

This clearly did not appear to be the case. The expected result from a conditioning effect would be an escalation in response or contact time with increased exposure, one which would be especially prevalent in those animals that consistently received more reward. Instead, we observed a nearly ubiquitous trend of decreasing response with time, and those animals that obtained more reward showed no greater inclination for remaining near the boat (Fig. 3.7). It should be noted that the contrasts of visual and receiver records don't necessarily rule out the possibility that sharks were present at other tour boats on days when not observed at ours. However, several identified sharks (including those depicted in Fig. 3.7) were easy enough to recognize that it was possible to confirm their presence/absence with observers on the tour boats (N. Hammerschlag, pers. comm.).

These results emerged despite the fact that our data may represent a sample of sharks that actually have a greater predisposition towards conditioning. Over the course of the field season, it became clear that certain sharks consistently have different

temperaments than others, for example by displaying decreased wariness around boats or increased aggression towards the bait. These sharks were generally ones that displayed a greater affinity for ecotourism offerings, and were more likely to obtain reward. They also were the ones that placed themselves in situations which allowed them to be identified or tagged. Consequently, our results likely overestimate the potential for chumming to lead to conditioning in white sharks.

Unfortunately, conditioning is not the only way that chumming can directly affect the sharks. Extra provisioning could potentially alter residency times at the island, in either a positive or negative direction. It could also theoretically affect shark population structure around the island, if dominant and subordinate individuals react to the chum in different ways. However, despite the fact that it would seem reasonable to surmise that the patterns observed in our data would not translate into changes in shark residency times at the island, nor could the impacts of sparse provisioning have substantial effects on population structure, the short-term nature of the study makes it impossible to draw any inferences regarding these topics.

3.5.2   Indirect effects on other species

The species most closely associated with white sharks at Seal Island are their specific prey in this area, the Cape fur seals. Consequently, any changes in shark behaviour elicited by ecotourism would likely have the greatest impact on the seals. However, behavioural data recorded for these animals during this study suggested no change in seal activity as a result of ecotourism presence (Laroche et al. submitted), despite the significant change in shark swimming depth during chumming (Fig. 3.8), which could theoretically have led to a reduction in shark predatory pressure (Strong

1996, Chapter 2). The most likely explanation for this, and our estimation that predation rates were unaffected by chumming, is the general disinterest in the chum source which most sharks displayed (Fig. 3.3). During most daylight hours over the 'high season', there are between 10 and 20 white sharks circling the waters around Seal Island (unpublished data), and although several of them may have a greater inclination towards remaining near the surface of the water and within proximity of the boat, the majority pay very little attention, thus maintaining predatory pressure at near constant levels. The result is that the mild effect of ecotourism, displayed in only a small subset of the shark population, likely has little effect on the remainder of the ecosystem.

3.5.3 No boat effect assumption

Many of the results presented in this paper rest on the assumption that white sharks respond only to the attractant which is dispensed, and not to the presence of the boats themselves. Were the latter effect to have occurred, the receiver results would be obscured by the fact that a portion of the control data actually reflected experimental conditions. However, several lines of evidence are consistent with the assumption, and the interpretation of the receiver data based on it.

The first of these comes from the visual records. If sharks were responding in a similar manner to boat presence itself, they would have been sighted during non-chumming conditions. Instead, although sharks did occasionally approach the boat unsolicited, these occurrences were rare, and were always extremely brief (unless some form of bait or decoy was deployed to catch their interest).

Further evidence in favour of the assumption comes from the manner in which sharks typically approached the boat. Over 85% of the initial sightings were of sharks

approaching from directly below, and, of these initial approaches, the majority were made towards the seal-shaped decoy (unpublished data). This suggests that sharks were initially responding to the visual cues provided by the floating objects, in accord with their hypothesized hunting strategy (Klimley 1994), rather than responding to the olfactory cues offered by the chum. This result is significant because it provides additional evidence against conditioning, which would have needed to occur for sharks to respond to boats without chum, because this response would not have developed on its own. The visual records of contact time also contradict the notion of conditioning, and these would not have been impacted by the assumption. Thus, our assumption of no boat effect is probably sound, and the receiver results interpreted appropriately.

3.5.4   Experimental power

Seal Island is only one of three locations along the South African coast which support ecotourism operations. However, it is unique in the amount of overt predatory activity which occurs in its waters, because visible interactions occur roughly two orders of magnitude more frequently at Seal Island than anywhere else in South Africa (unpublished data). Consequently, the possibility does exist that white sharks behave differently at Seal Island than anywhere else, and are less prone to respond to ecotourism offerings.

Another potential pitfall with our results is that they are limited to the impact of a sole ecotourism operation, given that the data presented here were collected when we were the only boat chumming. However, three operators are granted permits to attract sharks at Seal Island, while another location on the South African coast supports eight operations (Dyer Island, Gansbaai; Johnson et al. in prep.). This raises the possibility that

the amount of chum used in our study simply was not strong enough to elicit the changes in shark behaviour that can occur through current ecotourism activities.

Consequently, the results of this study must be viewed cautiously, and apply predominantly in the context of low ecotourism activity at Seal Island. However, emerging data from the other ecotourism locations resemble the results presented here (Johnson et al. in prep), suggesting that moderate levels of ecotourism activity may not have a significant impact on white shark behaviour. Regardless, this study has provided evidence that, although white sharks do respond to attractant (if they did not, ecotourism operations would not be viable), they are equally able to ignore the stimulus, and are thus not mindless eating machines as they have so often been portrayed. This result also brings into question whether other ecotourism operations, invasive or otherwise, have significant impacts on their target species. Our expectation was that tour boats would substantially affect shark behaviour, because this was their ultimate goal, and yet this did not appear to be the result. Further research is required, with this species and with others, to determine whether ours was an isolated result, or whether moderate levels of ecotourism are ubiquitously benign.

3.6   Literature cited

Abrams PA, Menge BA, Mittelbach GG, Spiller DA, Yodzis P (1996) The role of indirect effects in food webs. In: Polis GA, Winemiller KO (eds) Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, pp 371-395

Anderson SD, Henderson RP, Pyle P, Ainley DG (1996) White shark reactions to unbaited decoys. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 223-228

Barkin D (2003) Alleviating poverty through ecotourism: Promises and reality in the Monarch butterfly reserve of Mexico. Environment Development and Sustainability 5: 371-382

Burger J, Gochfeld M (1998) Effects of ecotourists on bird behaviour at Loxahatchee National Wildlife Refuge, Florida. Environmental Conservation 25: 13-21

Burgess GH (1998) Diving with Elasmobranchs: a Call for Restraint. Shark News, pp 1-3

Butterworth DS, David JHM, McQuaid LH, Xulu SS (1987) Modeling the Population Dynamics of the South African Fur Seal *Arctocephalus pusillus pusillus*. NOAA Technical Report NMFS: 141-164

Dill LM, Heithaus MR, Walters C (2003) Behaviorally-mediated indirect interactions in marine communities and their conservation implications. Ecology 84: 1151-1157

Ferreira C, Ferreira T (1996) Observations on white sharks along the South African coast. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 375-384

Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6: Unpaginated [URL:http://www.consecol.org/Journal/vol6/iss1/art11/manuscript.html]

Gill JA, Sutherland WJ (2000) Predicting the consequences of human disturbance from behavioural decisions. In: Gosling LM, Sutherland WJ (eds) Conservation Biology Series (Cambridge); Behaviour and Conservation. Cambridge University Press, Cambridge, pp 51-64

Jones S (2005) Community-based ecotourism - The significance of social capital. Annals of Tourism Research 32: 303-324

Kiss A (2004) Is community-based ecotourism a good use of biodiversity conservation funds? Trends in Ecology & Evolution 19: 232-237

Klimley AP (1994) The predatory behavior of the white shark. American Scientist 82: 122-113

Kock AA (2002) Predatory activity of great white sharks (*Carcharodon carcharias*) around a Cape fur seal colony. Honour's Thesis, University of Cape Town, South Africa

Krueger O (2005) The role of ecotourism in conservation: panacea or Pandora's box? Biodiversity and Conservation 14: 579-600

Mangel M, Talbot LM, Meffe GK, Agardy MT, Alverson DL, Barlow J, Botkin DB, Budowski G, Clark T, Cooke J, Crozier RH, Dayton PK, Elder DL, Fowler CW, Funtowicz S, Giske J, Hofman RJ, Holt SJ, Kellert SR, Kimball LA, Ludwig D, Magnusson K, Malayang BSIII, Mann C, Norse EA, Northridge SP, Perrin WF, Perrings C, Peterman RM, Rabb GB, Regier HA, Reynolds JEIII, Sherman K, Sissenwine MP, Smith TD, Starfield A, Taylor RJ, Tillman MF, Toft C, Twiss JR, Jr., Wilen J, Young TP (1996) Principles for the conservation of wild living resources. Ecological Applications 6: 338-362

Martin AR, Hammerschlag N, Collier RS, Fallows C (2005) Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. Journal of the Marine Biological Association of the U.K. 85: 1125-1135

McClung MR, Seddon PJ, Massaro M, Setiawan AN (2004) Nature-based tourism impacts on yellow-eyed penguins *Megadyptes antipodes*: does unregulated visitor access affect fledging weight and juvenile survival? Biological Conservation 119: 279-285

Miller ML (1993) The rise of coastal and marine tourism. Ocean & Coastal Management 20: 181-199

Nevin OT, Gilbert BK (2005) Perceived risk, displacement and refuging in brown bears: positive impacts of ecotourism? Biological Conservation 121: 611-622

Orams MB (1995) Towards a more desirable form of ecotourism. Tourism Management 16: 3-8

Orams MB (2002) Feeding wildlife as a tourism attraction: a review of issues and impacts. Tourism Management 23: 281-293

Orams MB, Hill GJE, Baglioni AJ (1996) "Pushy" behavior in a wild dolphin feeding program at Tangalooma, Australia. Marine Mammal Science 12: 107-117

Shaughnessy PD (1987) Population size of the Cape fur seal *Arctocephalus pusillus pusillus*. Department of Environmental Affairs, Sea Fisheries Research Institute, Report 130, South Africa

Strong WR, Jr. (1996) Shape discrimination and visual predatory tactics in white sharks. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 229-238

Wearing S, Neill J (1999) Ecotourism: Impacts, Potentials and Possibilities. Butterworth Heinemann, Oxford, UK

Williams R, Trites AW, Bain DE (2002) Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: Opportunistic observations and experimental approaches. Journal of Zoology 256: 255-270

Wootton JT (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. American Naturalist 141: 71-89

Yodzis P (2000) Diffuse effects in food webs. Ecology 81: 261-226

3.7   Figure legends

Fig. 3.1:   Seal Island, False Bay, South Africa. Indicated on the map are the locations of the six VR2 receivers, as well as the average receptive area of each. Waters around the island were divided into six sectors, from which the location of a given activity was randomly selected.

Fig. 3.2:   Means of the differences between proportional shark presence during paired experimental and control days for the pre- (panel a) and post-chumming (panel c) hours, as well as during experimental chumming conditions (panel b). Records from each paired hour-long period for each receiver were transformed into proportions of the total records for that period by dividing by the sum of all weighted records collected by the 6 receivers during that period. For the pre- and post-chumming periods, these proportions were immediately contrasted as experimental – control for each receiver. For chumming conditions, however, the means of the proportions from all periods were calculated for each day, providing a measurement of mean proportional presence per hour-long period per day for every receiver. These were then categorized for each set of paired conditions based on proximity of the receiver to the source of attractant, and grouped together using these categories (represented on the X axes; closest at the origin). Y axes in panels a and c represent the mean difference in proportional shark presence for the hour-long pre- or post-chumming periods, respectively; Y axis in panel b displays the mean difference in the mean proportional presence per hour on any day. Error bars are 95% confidence intervals. Attractant was not dispensed during either pre- or post- periods, and thus the expectation would be of no difference between experimental and control conditions, which is what was observed. However, an effect of chum on shark movement was detected, indicated by a positive mean difference closer to the chum source. However, the error bars suggest that this effect is likely not substantial.

Fig. 3.3:   Distribution of visual shark contact times at the boat, weighted by the total amount of time spent chumming on a given day, to give a measure of proportional contact time. Distinction was made between all sharks sighted (panel a), untagged animals (panel b), and only those sharks tagged with acoustic transmitters (panel c). The vast majority of sightings were very brief, although identified sharks, particularly tagged ones, did spend a higher proportion of time within visual range of the boat.

Fig. 3.4:   Mean effect differences over single chumming bouts. Results were calculated by first contrasting paired experimental and control hour-long periods for each shark, rather than by combining data for all sharks as in Fig. 3.2. These individual differences were then categorized and grouped as in Fig. 3.2. Error bars are 95% confidence intervals. The first (panel a) and second (panel b) hours during which a shark was recorded were considered separately from any subsequent hours, from which there were insufficient data to test the hypotheses (see text). The effect of chum on shark movement was more

clearly defined and statistically significant during the first hour. This effect was greatly diminished during the second hour, although a small sample size and large variances created substantial errors for these data, preventing the inclusion of confidence intervals in panel b.

Fig. 3.5:   Mean effect differences for individual sharks measured over each successive day the shark was recorded. Y axis represents the difference in proportional shark presence per hour-long period recorded for each individual at the receiver nearest to the chum source; X axis represents the days a particular individual was recorded. A non-statistically-significant decreasing trend was observed in shark response with repeated exposure (supported by the empty domain in the upper right portion of the graph), although few sharks appeared in paired records more than 3 times.

Fig. 3.6:   Proportional contact times (as per Fig. 3.3) as a function of the number of times a shark was re-sighted for all 16 re-sighted individuals (panel a), and for the 7 sharks which were sighted at least 5 times (panel b). Both plots reflect a decreasing trend in shark presence at the boat with repeated sightings, but a test of independence revealed non-independence for the data plotted in panel a. However, this likely resulted from the exceptionally dramatic decrease in response of a single shark, and is not considered to be biologically significant. The plots of response over time for each individual shark are included in the Appendix.

Fig. 3.7:   The number of days that the 3 most observed and most well provisioned sharks were recorded visually during chumming conditions, along with the number of days that they were recorded by the VR2 receivers while we were chumming. These data include periods where ecotourism boats were chumming as well, but information from observers on the boats suggests that ecotourism response would be similar to that presented here. The last visual observation of shark 32 was extremely brief and uncertain, as the shark only swam past the boat at approximately 8m depth. Identification thus needed to be confirmed with receiver records.

Fig. 3.8:   Means of the differences between paired experimental and control days for shark swimming depth. Results were calculated in the same way as for Fig. 3.2, except to substitute recorded values of shark swimming depth in the place of measures of proportional shark presence. X axis therefore displays the same categories as Fig. 3.2, and the Y axis represents the difference in depth (m). Error bars are 95% confidence intervals. Sharks nearest to the chum source demonstrated a significant negative change in swimming depth (their average swimming depth was more shallow), while sharks recorded around the remainder of the island showed no change.

3.8   Figures

Fig. 3.1:

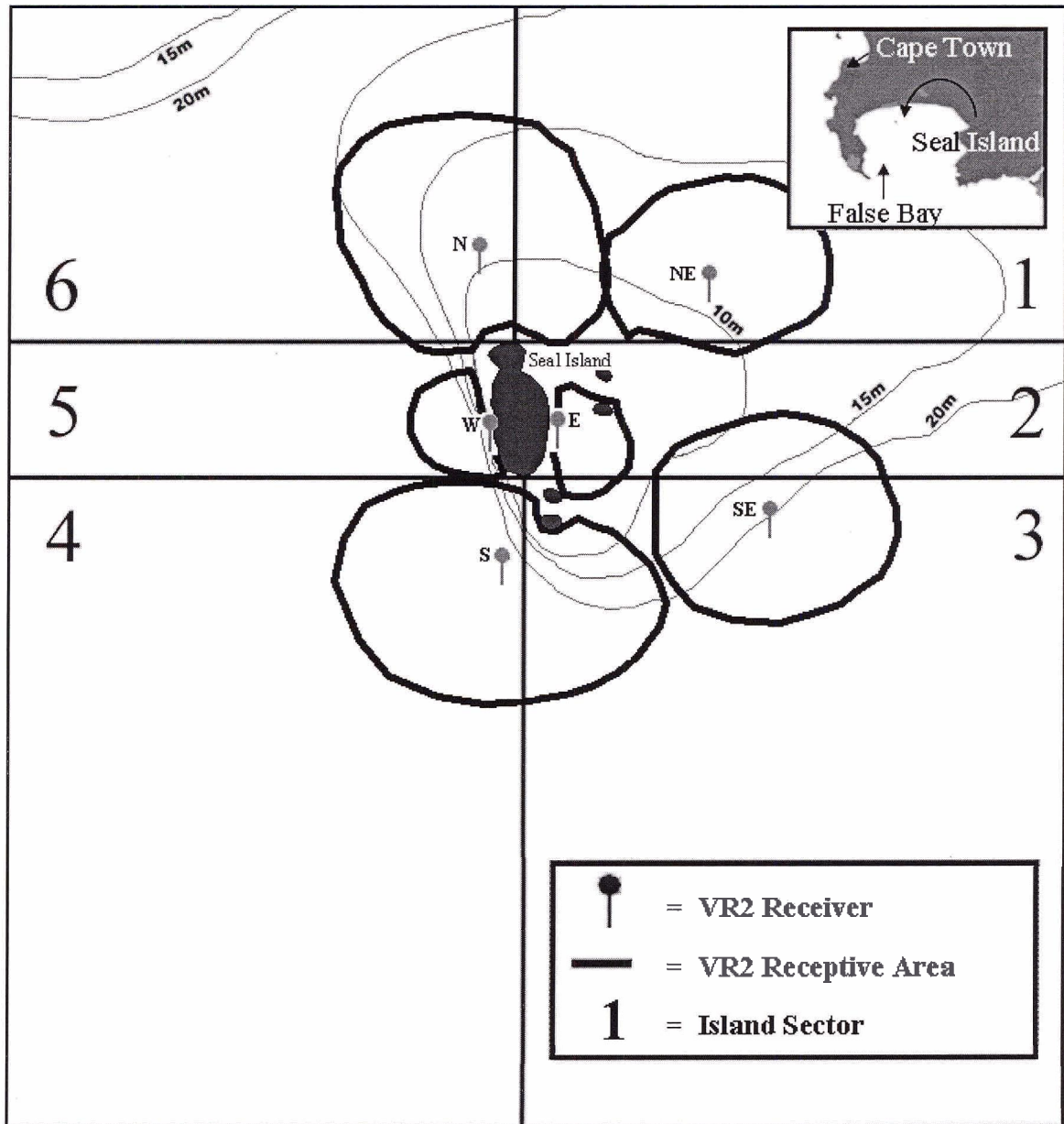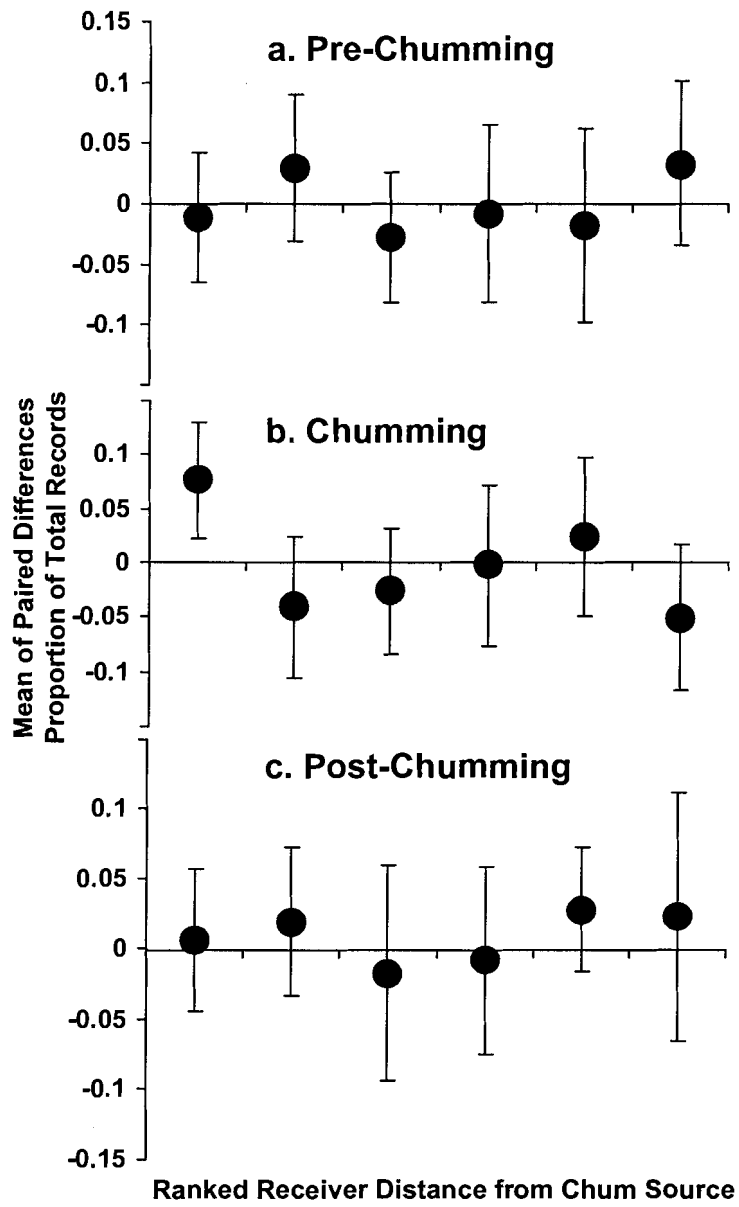Fig. 3.2:

Ranked Receiver Distance from Chum Source

Fig. 3.3:

Fig. 3.4:

Fig. 3.5:

Fig. 3.6:

a. All Re-Sighted Sharks

$R^2 = 0.12$

b. 7 Sharks Sighted 5 Times

$R^2 = 0.248$

Proportional Contact Time

Number of Days Sighted

Fig. 3.7:

▲ = Visual ID   ◆ = Receiver Record During Chumming

a. Shark ID 32   Baits Consumed: 8

09/06/2004   23/06/2004   07/07/2004   21/07/2004   04/08/2004   18/08/2004

b. Shark ID 521   Baits Consumed: 9

21/04/2004   14/05/2004   06/06/2004   29/06/2004   22/07/2004   14/08/2004

c. Shark ID 39   Baits Consumed: 3

15/06/2004   02/07/2004   19/07/2004   05/08/2004   22/08/2004   08/09/2004

Dates

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Fig. 3.8:

Figure showing Mean of Paired Differences (m of water depth) versus Ranked Receiver Distance from Chum Source.

3.9   Appendix

Fig. 3.A.I: Plots of proportional contact times against number of days sighted for all 16 re-sighted identified sharks. Only sharks 38 and D demonstrated a positive response to chum, while the increase in slope for shark 521 is mitigated by a single point. A 2-way ANCOVA test of independence resulted i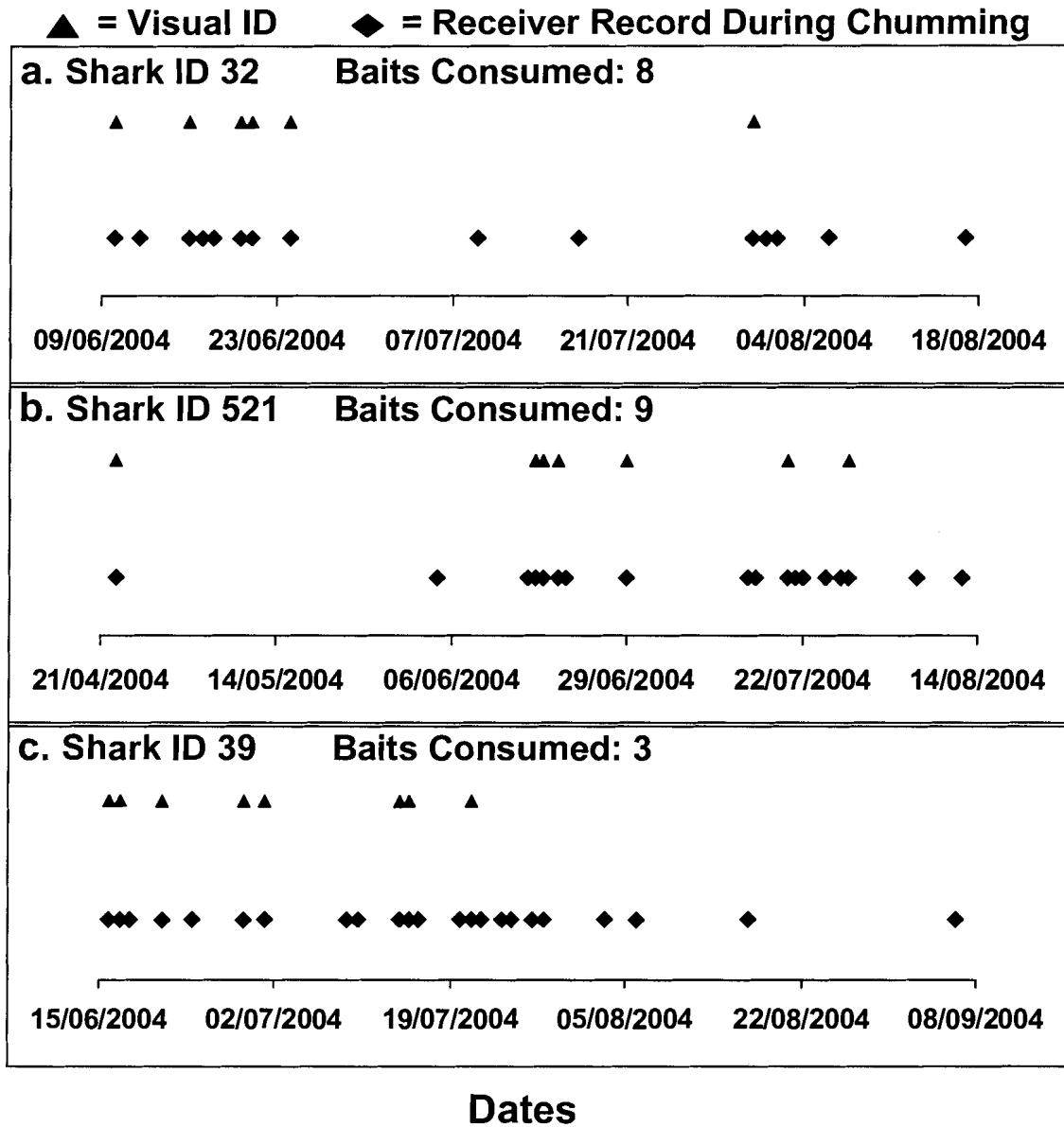n a statistically significant interaction term between contact time and sighting number for all 16 sharks (p=0.0171). However, shark 31 demonstrated an extremely sharp decrease in response. When this animal was removed from the analysis, a test of independence suggested no statistically significant interaction between the terms (p=0.1649).

Proportional Contact Time

Number of Days Sighted
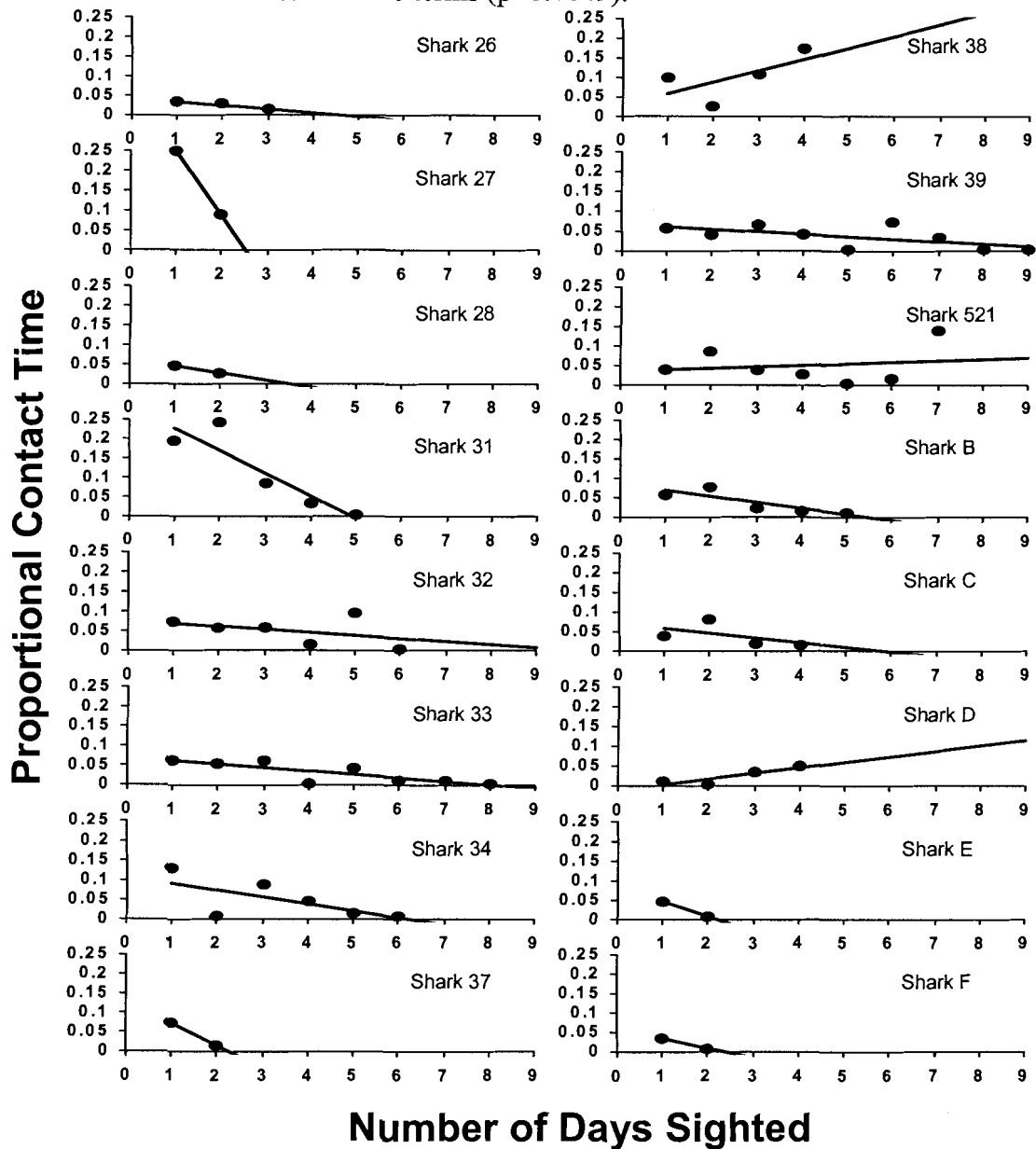
Chapter 4

General Discussion

There are many ways that humans can affect natural systems, both by having direct impacts upon certain species, and also through indirect interactions with other species not directly affected by human activity. This thesis sought to examine whether a reportedly conservation-friendly ecotourism industry, South Africa's white shark viewing industry, could be creating such direct and indirect effects, with potential repercussions for the local ecosystem. The first step towards answering this question, however, was to develop a clear understanding of the natural interactions between sharks and their primary prey in the areas where ecotourism is prevalent, the Cape fur seals.

Data collected for Chapter 2 suggested that both the sharks and adult seals have evolved strategies for moving around Seal Island (the small island seal colony where the research was conducted) whose tactics have the best chance of maximizing payoffs, i.e., for seals staying alive, and for sharks obtaining a meal. For adult seals, this meant moving predominantly at night and during periods of low shark abundance, as well as departing in large, obvious groups at the surface of the water, but returning in small, inconspicuous groups and swimming along the ocean floor. For sharks, the best opportunities for killing seals presented themselves in the early morning if they were

swimming in the middle of the water column, which allowed them to exploit the visual advantage gained from low light levels at sunrise (providing sufficient backlighting for viewing surface silhouettes from below, but insufficient light penetrance into the water to allow surface seals to spot sharks below them).

Seal pups, however, did not appear to employ tactics to minimize the risk associated with a movement decision; they were often recorded moving by themselves at the surface of the water in the hours around sunrise, which would almost certainly be the riskiest possible context. As a result, most predatory events were recorded around sunrise, and the vast majority of these were on seal pups. This seemingly sub-optimal behaviour could be explained if seals were trading-off predation risk against some other developmentally important factor which yielded benefits which outweighed the cost of potential predation.

Regardless of why they do it, pup behaviour appears key to the dynamics of shark-seal interactions around Seal Island. By placing themselves in high risk situations, pups prevent adults from having to do the same, and shark tactics do not need to evolve to compensate for the adult's risk-averse (night swimming) strategy because the sharks can easily feed on pups. The result appears to be an intra-specific behaviourally mediated indirect interaction (BMII), whereby adult tactics are indirectly influenced by those of the pups, mediated by shark response to pup availability. This result is important, because it suggests that adult seals might not necessarily exploit any daytime reduction in predation risk associated with ecotourism activity, unless moving during the day conferred some extra benefit that wasn't available to those seals that moved at night. It also implies that

pup seals probably wouldn't take advantage of any potential reduction in risk either, because their current behaviour doesn't appear to account for risk levels.

Nonetheless, Chapter 3 explored the potential effects of ecotourism activity on the movement patterns of sharks around Seal Island, as a first step towards uncovering any potential BMII between tourists and seals. The results indicated, however, that effects on shark movement were relatively minimal, and that most sharks failed to respond to ecotourist offerings to any significant degree. Consequently, it seems unlikely that ecotourism activity, to the extent practiced at Seal Island, could have indirect effects on seal fitness, because the predation risk imposed on them by sharks did not fluctuate to a significant extent with ecotourist presence.

The effects of provisioning ecotourism can't solely be gauged based on population means, however. For organisms like white sharks, that are potentially dangerous to humans, effects must also be examined on an individual basis, for conditioning even one shark to expect food from boats could have extremely serious consequences. Fortunately, my results suggested that conditioning did not occur in any of the sharks observed; even those sharks which demonstrated the greatest inclination for responding to attractant and bait, and which correspondingly obtained more reward than others, showed a decreasing trend in response with time, the exact opposite of the expected result if conditioning were occurring.

4.1   Future studies

The most intriguing question to arise from this study revolves around pup behaviour. The results presented in Chapter 2 would suggest that pups behave sub-

optimally, by employing movement tactics which place them at high levels of risk. Although simplistic explanations for this behaviour could contend that pups are naïve or physiologically incapable of adopting more risk averse tactics (like diving for extended periods while returning), these don't explain why pups haven't evolved to be more capable or to swim exclusively at night. One hypothesis for this behaviour could be that pups trade-off predation risk against some other developmentally important factor. However, further research will be required to ascertain whether this is true, and if so to determine exactly what it is that's worth more than the high cost of predation risk.

The most important avenue for future research, however, remains the exploration of the effects of ecotourism, primarily on shark movements. Although this study demonstrated relatively conclusively that conditioning wasn't occurring, only instances of low ecotourism activity (i.e., one source of attractant) were considered. However, three locations in South Africa currently support ecotourism operations, and entrepreneurs in other areas of the world appear to be following the South African model for success. In some of these areas, ecotourism levels are similar to those tested at Seal Island; in others, the amount of activity is much higher (Dyer Island, off a town called Gansbaai approx. 200 Km from False Bay, supports 8 operations; Johnson et al. in prep.). Thus, it is possible that the quantity of attractant used in this study wasn't sufficient to create a conditioning response in sharks, but that this could still be a concern in locations with more tour boats.

Furthermore, white shark behaviour around Seal Island appears to be unique. Overt predatory interactions between sharks and seals, including shark vertical breaches out of the water, are recorded substantially more often at Seal Island than anywhere else

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in the world (Martin et al. 2005, Kock et al. in prep.). Reasons for this behavioural difference remain unclear. Regardless, although most white shark ecotourism operations in the world are based on pinniped colonies, or at the very least situated near them (Burgess 1998), it is possible that sharks present at Seal Island may be more focused on hunting seals than are sharks in other parts of the world, and could thus be less prone to the conditioning effects of ecotourism activity. Given the potentially dangerous consequences of conditioning white sharks to expect food from boats, it behooves government regulatory agencies to ensure that the activities of any white shark ecotourism operations are not having an effect on these animals first and foremost, but also to explore whether effects on the target species are having an indirect impact on the remainder of the biological system of which they are a part.

4.2   Literature cited

Burgess GH (1998) Diving with Elasmobranchs: a Call for Restraint. Shark News, pp 1-3
Johnson RL, Keswick T, Bester MN, Oosthuizen WH. White shark cage diving: does the practice of chumming and baiting cause white sharks to associate boats with food? In preparation.
Martin AR, Hammerschlag N, Collier RS, Fallows C (2005) Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. Journal of the Marine Biological Association of the U.K. 85: 1125-1135